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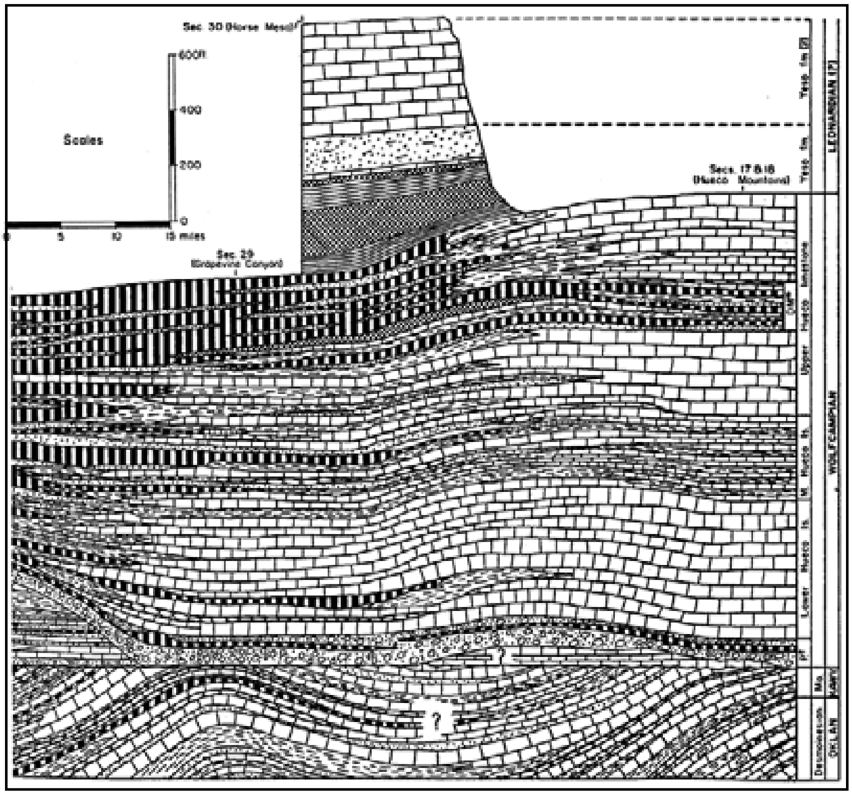
New Mexico Museum of Natural History & Science

A Division of the
DEPARTMENT OF CULTURAL AFFAIRS

The Carboniferous-Permian Transition



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Cover illustration: Diagrammatic cross section of Carboniferous-Permian transition from the Hueco Mountains of West Texas to the Sacramento Mountains near Alamogordo, New Mexico. From Thompson, M. L. (1954) American Wolfcampian fusulinids: University of Kansas Paleontological Contributions, Protozoa Article 5.

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THE CARBONIFEROUS-PERMIAN TRANSITION

MAY 20-22, 2013

An international meeting devoted to all aspects of Carboniferous-Permian geology with special emphasis on the Carboniferous-Permian transition.

Hosted by the New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA

Organizing Committee: Spencer G. Lucas (Albuquerque), James E. Barrick (Lubbock), Vladimir Davydov (Boise), William DiMichele (Washington, D. C.), Karl Krainer (Innsbruck), John Nelson (Champaign), Joerg W. Schneider (Freiberg) and Sebastian Voigt (Thallichtenberg)

Schedule:

19 May

Pre-meeting fieldtrip to the Carboniferous-Permian transition section at Carrizo Arroyo, central New Mexico (limited to 25 participants).

20-22 May

Talks and posters.

21 May

Afternoon fieldtrip to Late Pennsylvanian Kinney Brick Quarry.

23-25 May

Post-meeting fieldtrip to Pennsylvanian-Permian rocks exposed in Joyita Hills-Cerros de Amado east of Socorro, New Mexico

Fieldtrips:

Trip 1: Carrizo Arroyo is one of the most paleontologically diverse localities across the Carboniferous-Permian boundary. It exposes mixed marine and nonmarine strata of the Bursum Formation that yield everything from plants and insects to fusulinids and brachiopods. This section plays a key role in global marine/nonmarine correlations because of the co-occurrence of conodonts and insect-zone species. Access is difficult, by 4-wheel-drive vehicle over difficult roads, so the number of participants is limited to 25 persons.

Trip 2: The Kinney Brick quarry is a world class Late Pennsylvanian Lagerstätte, located just east of Albuquerque. It is also important for marine/non-marine correlations due to the occurrence of conodonts, fusulinid, branchiosaur and insect zone species. All participants will take an afternoon excursion to the quarry as a break in the meeting technical program

Trip 3: East of Socorro, marine and nonmarine sedimentary rocks of Middle Pennsylvanian-Early Permian age are exposed along the eastern margin of the Rio Grande rift. This is one of the best exposed and most studied Pennsylvanian-Permian sections in New Mexico, and recent work has brought forth diverse paleofloras, detailed conodont biostratigraphy, extensive ichnofossil assemblages, and much more. The three-day trip, headquartered in Socorro, will work through this entire section, focusing on issues of stratigraphy, sedimentation and paleontology.

Symposium proceedings:

Proceedings of the symposium and a field guide will be published by the New Mexico Museum of Natural History and Science. Contributions on all aspects of Carboniferous and Permian geology are appropriate for the proceedings. Contributions to the proceedings can range from abstracts to full length articles.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

THE CONODONT *NEOGNATHODUS BOTHROPS* MERRILL, 1972 AS THE MARKER FOR THE LOWER BOUNDARY OF THE MOSCOVIAN STAGE (MIDDLE PENNSYLVANIAN)

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Abstract—The Moscovian Stage constitutes the Middle Pennsylvanian Series of the Carboniferous System, but a biostratigraphic marker and GSSP for it have not yet been designated. The exact position of the Moscovian boundary cannot be defined properly because in the type area the basal Vereian unconformably overlies the Mississippian limestone or the alluvial and lagoonal Aza Formation of the uppermost Bashkirian. The Task Group to establish a GSSP close to the existing Bashkirian-Moscovian boundary suggested several potential markers among foraminifers and conodonts, but the search for a marker near traditional base of the global Moscovian Stage has stalled. It may be more productive to search for FADs in the lower Moscovian, above the traditional base, to designate the lower boundary of the stage. Relatively rich Vereian and Kashirian conodont assemblages have been recovered from the southwest Moscow Basin, as well as from the Oka-Tsna Swell. The most complete information on the distribution of conodonts in the Vereian- Kashirian boundary interval was obtained from the Yambirno section (Oka-Tsna Swell). The greatest change in conodont assemblages does not occur near the level of the traditional base of the Moscovian, but stratigraphically higher. There is a sharp change at both the species- and genus-levels in conodont assemblages at the boundary between the Vereian Ordynka Formation and the overlying the Kashirian Tsna Formation. The FAD of *Neognathodus bothrops* Merrill, 1972 has the greatest potential for correlation of a new position of the lower boundary of the Moscovian near the base of the Kashirian.

INTRODUCTION

The Moscovian Stage constitutes the Middle Pennsylvanian Series of the Carboniferous System (Gradstein et al., 2004). However, a biostratigraphic marker and GSSP for it have not yet been designated. The Task Group to establish GSSP close to the existing Bashkirian-Moscovian boundary has suggested several potential markers among foraminifers (first occurrences of *Aljutovella aljutovica*, *Depratina prisca*, or the genus *Eofusulina*). However, foraminifers are restricted geographically and have less potential than conodonts for international correlation. Among conodonts three potential events were originally proposed to designate the base of the Moscovian (Groves and Task Group, 2006): (1) The first appearance datum (FAD) of *Declinognathodus donetzianus* in the evolutionary lineage *D. marginodosus* (Grayson, 1984) – *D. donetzianus* Nemirovskaya, 1990. (2) The FAD of *Idiognathoides postsulcatus* in the lineage *I. sulcatus* Higgins and Bouckaert, 1968 – *I. postsulcatus* Nemyrovska, 1999. (3) The FAD of *Neognathodus nataliae* Alekseev and Gerelzezeg, 2001.

Of these three, the most promising marker for the establishment of the boundary appears to be the FAD of *Declinognathodus donetzianus*, which occurs at the base of the Moscovian Stage (Aljutovo Formation of the Vereian Substage, Makhlina et al., 2001). The evolutionary lineage *D. marginodosus* – *D. donetzianus* is well documented in the Donets Basin (Nemirovskaya, 1990; Nemyrovska et al., 1999). However, this species has a limited geographic distribution. To date, it has only been found near the Donets Basin in the Moscow Basin (Makhlina et al., 2001), in the Aegiranum Marine Band of the basal Bolsovian in Great Britain (Boogard and Bless, 1985), and in the Southern Urals (Basu section, Pazukhin et al., 2006). Recently it was identified in the lower Atokan of the Appalachian Basin (Work et al., 2012), but the illustrated specimen possesses only one incurved node on the platform. This North American occurrence supports the possibility of using *D. donetzianus* as the marker species, but a better specimen has to be illustrated.

Based on the study of the Naqing (Nashui) section in South China, it was proposed to use the FAD of *Diplognathodus ellesmerensis* in the lineage *D. coloradoensis* (Murray and Chronic, 1965) – *D. ellesmerensis* Bender, 1980 (Qi et al., 2007). *Diplognathodus ellesmerensis* is an easily identifiable species and occurs near the base of the Moscovian Stage in the Aljutovo Fm. of the Vereian Substage (Makhlina et al., 2001) and in limestone K3 in the Donets Basin (Nemyrovska, 1999). However, the species has a very long stratigraphic range, for it been found significantly higher in the upper Moscovian Podolskian Substage in the Moscow Basin and in the Arkhangelsk Region and in the southern Urals (Dalniy Tyulkas section). In addition, it occurs only sporadically and its ancestor is not well defined. All these factors reduce its correlation potential.

Subsequently, the FAD of advanced forms of *Streptognathodus expansus* Igo and Koike, 1964 or *S. suberectus* Dunn, 1966 was presented as a potential marker for the Bashkirian-Moscovian boundary (Qi et al., 2010). The primitive forms of *S. expansus* were re-named as “*S. praexpansus*,” and were considered as an ancestor of *S. expansus* (Qi et al., 2010, 2011). However, typical examples of S. expansus occur in the undoubtedly older upper Bashkirian limestones G1 to H6 in the Donets Basin (Nemyrovska, 1999). Use of this maker is unacceptable because it would lower the base of the Moscovian almost to a level within the middle of the Bashkirian.

Thus, the search for the base of the global Moscovian Stage marker near its traditional position has stalled and the most recent proposals have attempted to shift this boundary to a level within the middle or upper Bashkirian. In contrast, we suggest that it may be more productive to search for FADs of conodont species within the lower part of the traditional Moscovian that may have greater potential for boundary designation and international correlation.

LOWER MOSCOVIAN CONODONTS OF THE MOSCOW BASIN, RUSSIA

The base of the Moscovian Stage in the Moscow Basin coincides with the lower boundary of the Vereian Substage (Fig.1), which corresponds to the base of the ammonoid *Diaboloceras-Winslowoceras* Zone and fusulinid *Aljutovella aljutovica-Schubertella pauciseptata* Zone. Most of the Vereian is a siliciclastic succession, and carbonate marine units occur only at its base and top (Alekseev et al., 2004). The younger

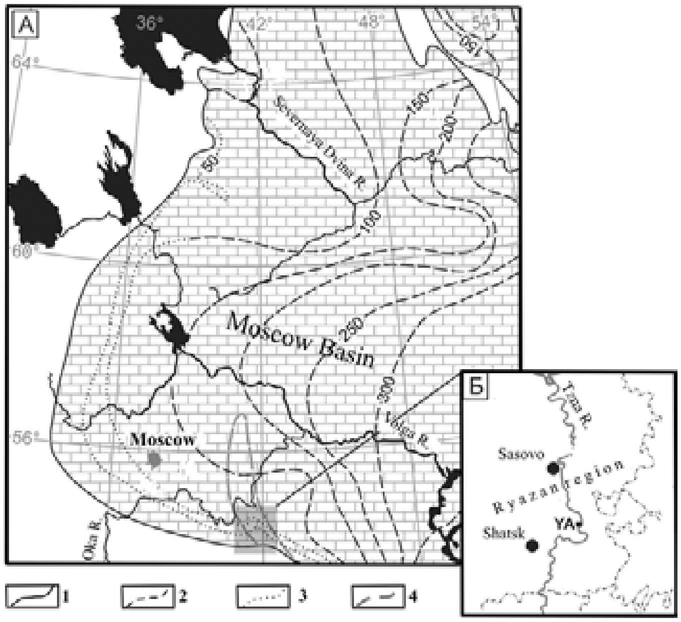


FIGURE 1. Moscovian Stage of the Central East European Platform (modified from Atlas litologo-paleogeographicheskikh kart SSSR, 1966). **1**, Speculative Moscovian time shoreline. **2**, Moscovian isopachs in the subsurface. **3**, Moscovian isopachs in the outcrop belt. **4**, Approx. limit of Oka-Tsna Swell. **B**, Location of the Yambirno (YA) section (from Kabanov and Alekseev, 2011).

Kashirian Substage is represented mainly by shallow water marine carbonates with an abundant and diverse marine fauna. Several subordinate siliciclastic units occur as well. Relatively rich Vereian conodont assemblages have been reported from the southwestern Moscow Basin, from the Oka-Tsna Swell (Goreva, 1984; Makhlina et al., 2001) and in the northern Moscow Basin (Alekseev et al., 1994). Two zones and beds have been identified. The *Declinognathodus donetzianus* Zone includes the Aljutovo and Skniga formations. Beds with *Idiognathoides ouachitensis* encompass the lower part of the Ordynka Formatiom. The following species have been recognized in the Aljutovo Formation: *Declinognathodus donetzianus* Nemirovskaya, *D. marginodosus* (Grayson), *Idiognathoides tuberculatus* Nemirovskaya, *Id. ouachitensis* (Harlton), *Id. sinuatus* (Harris and Hollingsworth), *Id. alujtovensis* Alekseev et al., *Idiognathodus volgensis* Alekseev et al., and *Streptognathodus parvus* Dunn. The conodont assemblage of the upper part of the Aljutovo Formation is less abundant, but contains *Neognathodus atokaensis* Grayson. The Ordynka Fm., in addition to all the species listed above, contains *Neognathodus nataliae* Alekseev and Gerelzezeg, *N.* aff. *N. uralicus* (Nemirovskaya and Alekseev), and occasional "*Streptognathodus*" *transitivus* Kossenko.

The platform conodonts of the overlying Kashirian Substage differ significantly in their morphology and taxonomy from Vereian conodonts. Conodonts occur in a number of outcrops and boreholes in the southern part of the Moscow Basin and in the Oka-Tsna Swell. The conodont assemblage in the lower part of the Kashirian Substage (Tsna Formation) is taxonomically different and is characterized by the dominance of *Neognathodus* species: *N. bothrops* Merrill, *N. tsnensis* Alekseev and Gerelzezeg, *N. medadultimus* Merrill, and *N. colombiensis* (Stibane). Ranging up from the Ordynka Fm., *N. atokaensis* and *N. nataliae* Alekseev and Gerelzezeg also occur in the lower part of the Kashirian. *Idiognathodus praeobliquus* Nemyrovska et al., *I. obliquus* Kossenko, and *I. delicatus* Gunnell are common in the Tsna Formation. No *Declinognathodus* and only a few small specimens of *Idiognathoides* have been found in the Kashirian limestones.

The most complete information on the distribution of conodonts in the Vereian-Kashirian boundary interval was obtained from the Yambirno section (Fig. 2), in a quarry located in the Oka-Tsna Swell along the left bank of Tsna River (Ryazan Region). The original quarry section was studied in detail, and reliable data on lithology and biostratigraphy were obtained. The correlation between conodont and fusulinid zones was established. Detailed cyclostratigraphic research was conducted recently (Kabanov and Alekseev, 2011). Unfortunately, the exploitation of this quarry ceased during recent decades, which made some of the previously well-represented outcrops in the quarry bottom unavailable for additional study. A total of 4796 conodont specimens were extracted from more than 80 samples weighing more than 100 kg. Based on newly obtained data, the distribution of conodont species has been significantly updated (Fig. 3).

In the Ordynka Formation (Vereian) two assemblages were established – one for beds with *Idiognathoides ouachitensis* (beds 1–5) and the second for the *Streptognathodus transitivus* Zone (beds 6–9). For this interval, in addition to the index species, *Idiognathoides ouachitensis*, *Neognathodus atokaensis*, *N. nataliae*, *Idiognathodus aljutovensis* Alekseev et al., *Diplognathodus ellesmerensis* Bender, *D. ohioensis* (Merrill) are represented. Significantly, first occurrences of *Idiognathodus praeobliquus*, *Neognathodus bothrops* and *N. tsnensis* are at the base of the Tsna Formation, bed 10. *Neognathodus nataliae* and *N. atokaensis* also occur in bed 10 and range higher (Fig. 3). In the middle part of the formation (beds 25–30), the assemblage is enriched by the appearance of *N. colombiensis* (Stibane) and *Idiognathodus izvaricus* Nemyrovska. At the top of the Tsna Formation, together with the species listed above, the first *Idiognathodus obliquus* is present (bed 30). Characteristic species for the Ordynka and Tsna formations are shown on Figure 4.

Declinognathodus marginodosus and *Neognathodus atokaensis* are the most characteristic conodont taxa of the Vereian, and both these species have their FADs in the Bashkirian. Representatives of the genus *Idiognathoides* are common in the Vereian assemblage, but they first appear in the low in the Bashkirian. Only two species of this genus (*Id. ouachitensis* and *Id. tuberculatus*) appear later, but they still predate the Vereian. However, a few *Idiognathoides* species range into the Moscovian, as high as the top of the Podolskian in the Northern Timan (Goreva et al., 1997) and the Southern Urals (Nemirovskaya and Alekseev, 1995; Kulagina et al., 2001). Thus, a substantial change in species and generic composition of conodont assemblages is documented at the boundary between Vereian Substage (Ordynka Formation) and Kashirian Substage (Tsna Formation).

CONODONT PHYLOGENY

To define a conodont species that could be a potential boundary marker, the phylogeny of *Neognathodus* during late Vereian and Kashirian time was studied based on the data from the Moscow Basin, and the evolution of species of this genus reconstructed. The first study of morphological changes in *Neognathodus* during the Early and Middle Pennsylvanian was conducted by Merrill (1972) based on material from the Appalachian Basin. The morphology of the carina and its relationship to parapets permit us to identify a number of evolving species. In the Moscow Basin representatives of *Neognathodus* from the Verian include two species – *N. atokaensis* and *N. nataliae*. Both species continue into the lowest Kashirian Substage.

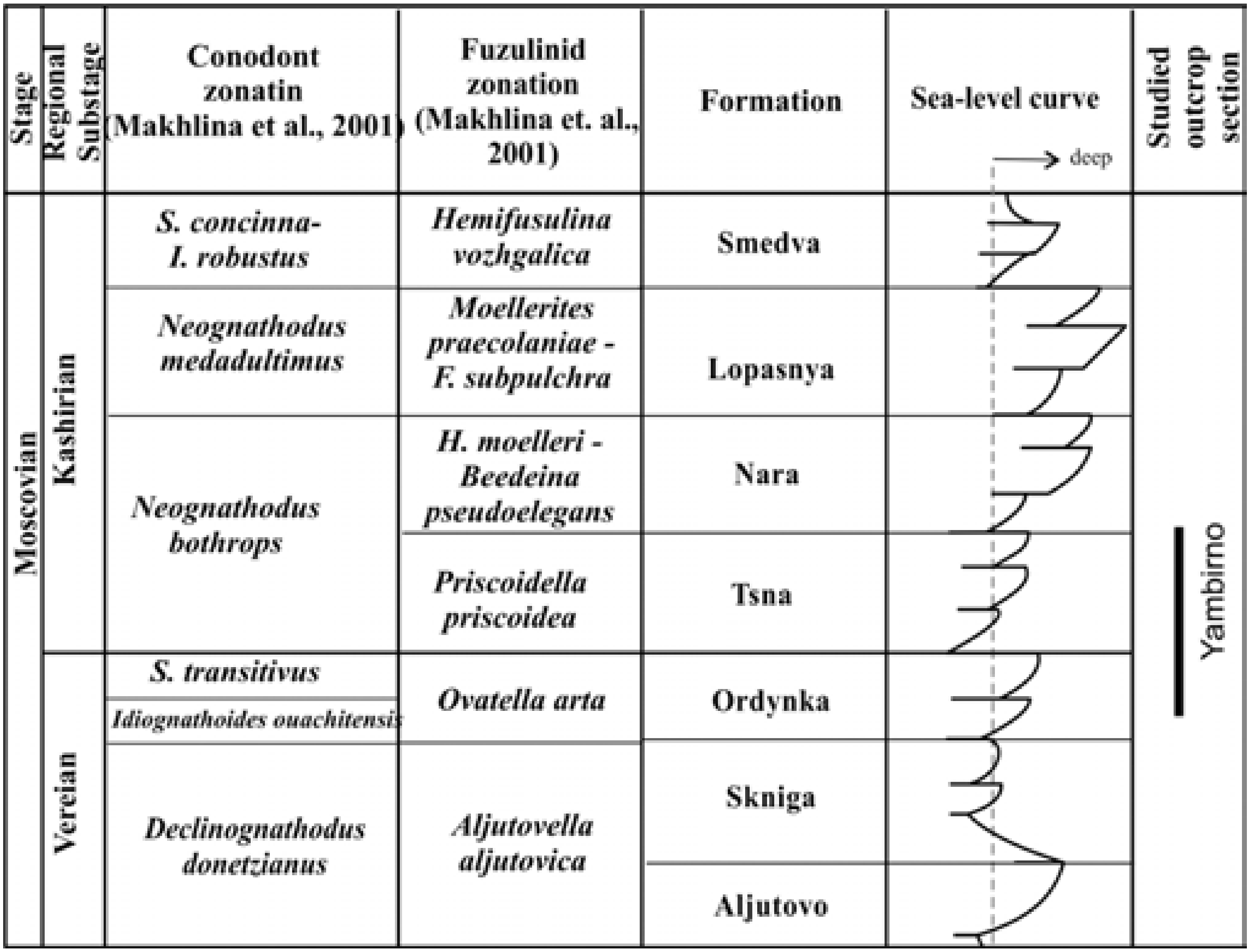
Neognathodus atokaensis is an important link in the evolution of the genus *Neognathodus*. This species has an asymmetrical and wide, more or less triangular platform. The carina extends to the end of the platform. The inner parapet is slightly reduced and typically merges with the carina at the posterior end as two nodes (Figure 4.2). On his plate caption, Grayson (1984) designated two different specimens as the holotype when erecting *N. atokaensis*. We take for the species concept features inherent to the morphotype with a wider platform, illustrated in his plate 3, fig. 1. The very narrow morphotype, including the paratype (Grayson, 1984, plate 3, fig. 16) with both parapets fused to posterior nodes of carina should be separated as a new species, although many conodont workers (e.g., Barrick et al., 2004) prefer consider it as cf. *N. bothrops*.

The development of the two parallel phylogenetic lines began with *N. atokaensis* in the Kashirian. The first lineage comprises *N. atokaensis-N. bothrops-N. medadultimus*, a group of species with an elliptical outline of the platform, tapering to the anterior end, and with both parapets extending to the posterior end of the carina. The morphological transformation from *N. atokaensis* to *N. bothrops* is expressed in the platform outline, which became narrower and more lanceolate. Both parapets extended to the posterior end of the platform, converged continuously, and fused at the point with last node of the carina (Figure 4.5, 4.7). Also, in *N. atokaensis*, according to our concept, the anterior end of the outer parapet in is shorter than that of the inner one, but in *N. bothrops* they are equal in length. The transition from *N. bothrops* to *N. medadultimus* during the Kashirian is an evolutionary trend expressed morphologically by the bending of the carina and its fusion with the outer parapet, as is typical for Kashirian and Podolskian neognatodids. During the Kashirian, the gradual transformation of *N. bothrops* into *N. medadultimus* can be traced; the carina and outer parapet in *N. medadultimus* are joined at one-third of the length of the platform.

Another descendant of *N. atokaensis* that originated simultaneously with *N. bothrops* is *N. colombiensis* (Stibane), which created a second lineage in the Kashirian. The latter species has a wide, triangular and symmetrical platform with deep adcarinal troughs. Representatives of this lineage are rare in the Moscow Basin, but were found in large numbers in the Donets Basin, the Southern Urals and the Caspian Basin. Both lineages continue their development in the Podolskian and Myachkovian, suggesting different environmental conditions for their representatives. Other types of platform conodonts diversify within the Kashirian neognathodid assemblage. Neognathodus tsnensis is found in the lower part of the lower Kashirian Tsna Formation. It is characterized by a narrow, lanceolate, strongly acute platform with a sinusoidal curve of the carina that merges to almost half of the outer parapet. Its descendant, N. kashiriensis Goreva, 1984 is common in the upper part of the Kashirian, imitating the morhology of the lower Bashkirian species Declinognathodus lateralis.

A NEW PROPOSED LEVEL FOR THE BASE OF THE MOSCOVIAN STAGE

The Verian/Kashirian boundary is characterized by a substantial change in the conodont assemblages. The FAD of *Neognathodus bothrops* has the greatest potential for global correlation of a new, higher, position of the boundary for the base of the Moscovian Stage. *Neognathodus bothrops* occurs in the Moscow Basin, Northern Timan, the North American Midcontinent region (Iowa, upper part Atokan, lower Cherokee Series: Grayson, 1984; Lambert and Heckel, 1990 (as *Neognathodus* sp. B); Lambert, 1992), in the Appalachian and Illinois basins of North America (Merrill, 1972), and in South China (Qi et al., 2010, Luokun and Dianzishang sections). The proposed significant reduction (about 25%) in the scope of the Moscovian Stage and transfer of the Vereian Substage



Stage	Regional Substage	Conodont zonatin (Makhlina et al., 2001)	Fuzulinid zonation (Makhlina et. al., 2001)	Formation	Sea-level curve → deep	Studied outcrop section
Moscovian	Kashirian	*S. concinna-I. robustus*	*Hemifusulina vozhgalica*	Smedva		
		Neognathodus medadultimus	*Moellerites praecolaniae - F. subpulchra*	Lopasnya		
		Neognathodus bothrops	*H. moelleri - Beedeina pseudoelegans*	Nara		
			Priscoidella priscoidea	Tsna		Yambirno
	Vereian	*S. transitivus* *Idiognathoides ouachitensis*	*Ovatella arta*	Ordynka		
		Declinognathodus donetzianus	*Aljutovella aljutovica*	Skniga		
				Aljutovo		

FIGURE 2. Local stratigraphic scheme of the Verian and Kashirian regional substages of the Moscow Basin.

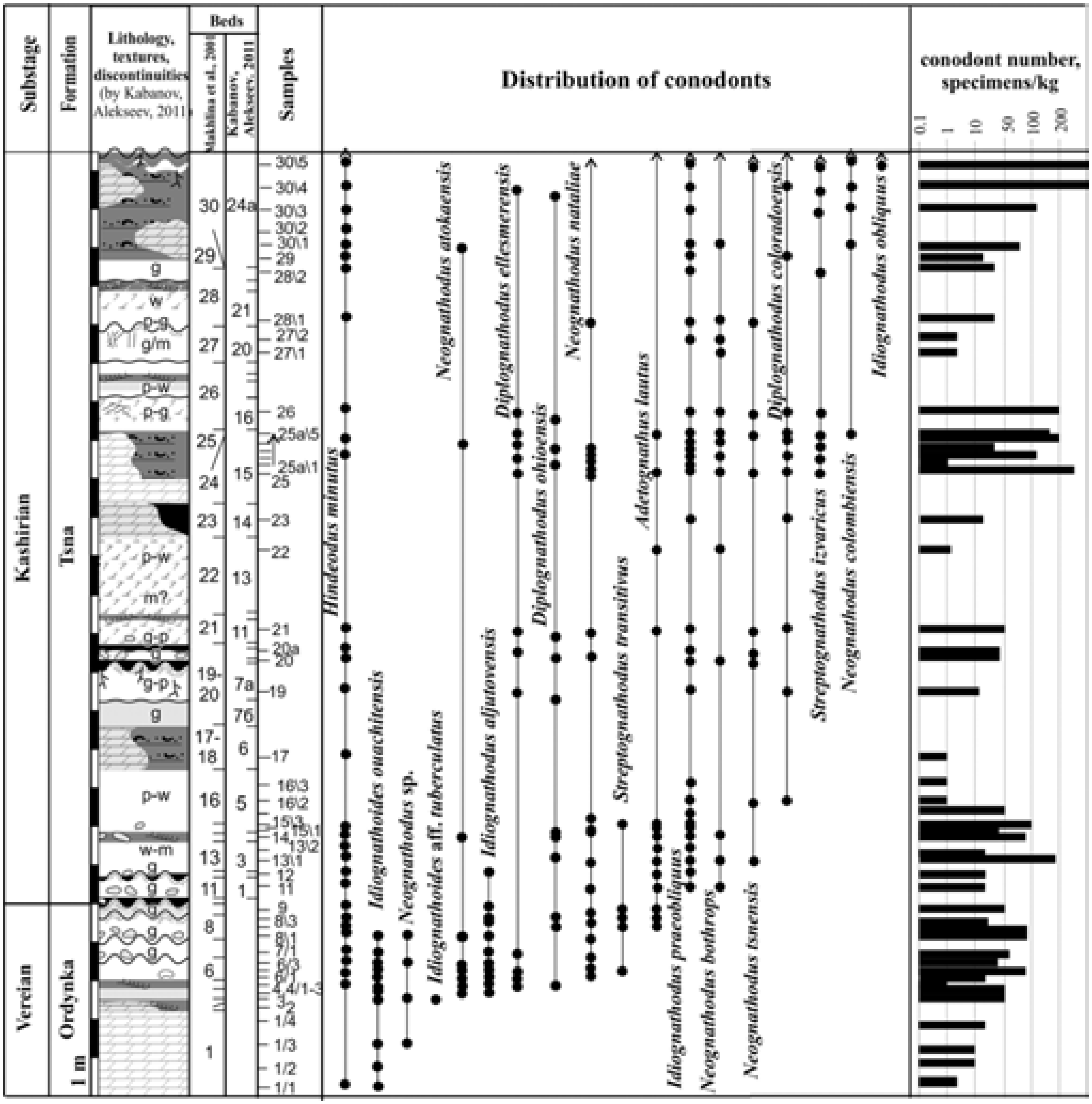


FIGURE 3. Distribution of the conodonts in the lower Moscovian at the Yambirno section.

to the Bashkirian is supported by the great similarity of the conodont assemblages of the Melekessian-terminal Bashkirian and Vereian (Alekseev et al., 1994), which cannot be properly, separated biostratigraphically. The data on conodonts are in good agreement with the evolution of ammonoids, where the most dramatic changes occur at the boundary of the *Diaboloceras-Winslowoceras* and *Paralegoceras-Wellerites* zones at the base of the Kashirian. It is interesting to mention that Ruzhencev (1978) preferred to include the Vereian in the Kayalian Stage (= upper Bashkirian). Also, fusulinids of the lower part of the Kashirian differ greatly from those of the Vereian. The FADs of *Taitzehoella* and *Hemifusulina* coincide with the lower boundary of the Kashirian. The case for a rather abrupt change in brachiopod assemblages at the Vereian/Kashirian boundary was argued by Lazarev (Makhlina et al., 2001).

The base of Kashirian Substage, coinciding with the FAD of *Neognathodus bothrops*, would be an easier level for global correlation than the base of the Vereian Substage, the current level of the base of the Moscovian in the Moscow Basin. We recommend that the Task Group include the level of the FAD of *N. bothrops* in their discussions of potential biostratigraphic markers and their correlation potential for the base of the Moscovian Stage.

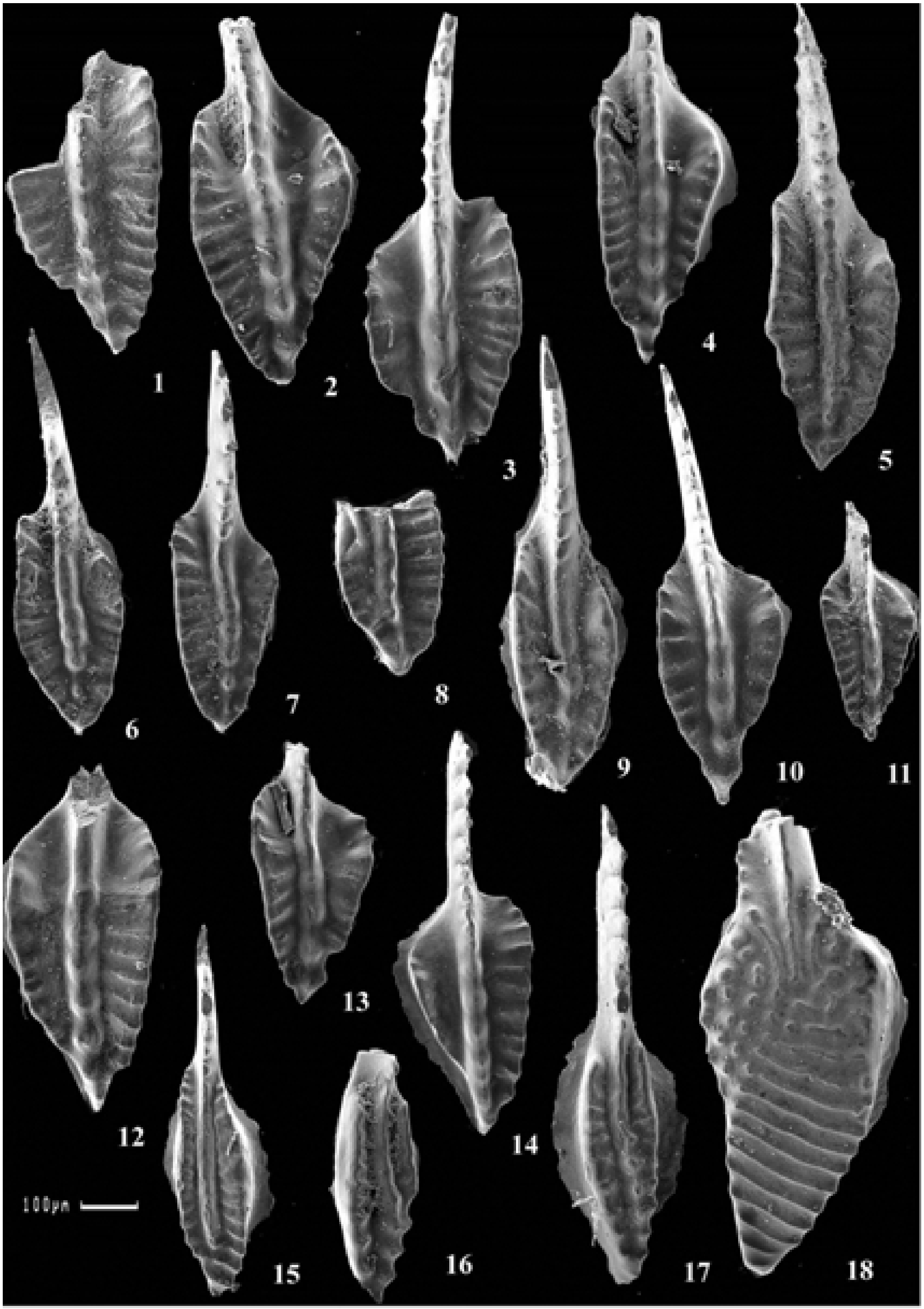


FIGURE 4. SEM micrographs (100X) of Pa elements of conodonts of stratigraphic importance (scale bar represents 100 μm) in the lower Moscovian at the Yambirno section. **1-4**, *Neognathodus atokaensis* Grayson: **1**, Sample 22; **2**, Sample 8/14; **3**, Sample 4; **4**, Sample 30a/4. **5-9**, *Neognathodus bothrops* Merrill: **5**, Sample 30/1; **6**, Sample 14; **7**, Sample 34; **8**, Sample 11; **9**, Sample 25/5. **10-14**, *Neognathodus nataliae* Alekseev and Gerelzezeg: **10**, Sample 4; **11**, Sample 8/1; **12-13**, Sample 30/1; **14**, Sample 4/3. **15**, *Streptognathodus transitivus* Kossenko, Sample 8.2. **16-17**, *Neognathodus tsnensis* Alekseev and Gerelzezeg: **16**, Sample 14; **17**, Sample 25a/5. **18**, *Idiognathodus praeobliquus* Nemirovska, Perret-Mirouse and Alekseev, Sample 26.

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A NEW SPECIES OF *GLAPHYROPHLEBIA* HANDLIRSCH, 1906 (INSECTA: NEOPTERA: BLATTINOPSIDAE) FROM THE LOWER PERMIAN WELLINGTON FORMATION OF NOBLE COUNTY, OKLAHOMA, USA

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Abstract—Two species of the fossil insect genus *Glaphyrophlebia* are known from the Wellington Formation of Kansas (USA). In 1909, E. H. Sellards described *G. ovata* (Sellards, 1909) in the genus *Pursa* and *G. speciosa* (Sellards, 1909) in the genus *Sindon*. In 1966, Carpenter assigned both species to *Glaphyrophlebia* Handlirsch (1906a). *Glaphyrophlebia anderhalterorum* n. sp. is described from a specimen collected from the Wellington Formation in Noble County, Oklahoma. Most species of *Glaphyrophlebia* are known from fossil remains of forewings (often fragmentary), and occasionally hind wings. The holotype of *G. amderhalterorum* is a compression fossil comprising a nearly intact insect in dorsal aspect with articulated wings, and with portions of the hind, mid and fore-legs, thorax, and a portion of the head and abdomen preserved. This appears to be only the second glaphyrophlebiid fossil for which significant portions of body parts are preserved; a specimen of *G. uralensis* (Martynov, 1940) comprised a complete insect in lateral aspect, with body, head, legs, wings, and genitalia intact. *G. anderhalterorum* is the first species of *Glaphyrophlebia* to be described from the Oklahoma Permian.

INTRODUCTION

Handlirsch (1906a) described his new fossil insect genus *Glaphyrophlebia* in a new order, Protoblattoidea, new family Oryctoblattinidae. He characterized *Glaphyrophlebia* as having "much more reduced" venation (Handlirsch, 1906a, p. 707) than other genera he placed in the family (e.g., *Blattinopsis* Giebel, 1867). The type species was *G. pusilla* Handlirsch, 1906a, from the Pennsylvanian of Mazon Creek, Illinois.

In 1909, E. H. Sellards described two species from the Elmo, Kansas insect fossil beds that he placed in Oryctoblattinidae: *Pursa ovata* Sellards, 1909 and *Sindon speciosa* Sellards, 1909. In 1925, Bolton described the new family Blattinopsidae, to which he assigned "…a part of the Oryctoblattinidae of Handlirsch" (Bolton, 1925, p. 23). He included genus *Blattinopsis* in the family Blattinopsidae, but made no mention of *Glaphyrophlebia*, *Pursa* or *Sindon*. In her review of the family Blattinopsidae, Kukalová (1959) placed a number of genera, including *Glaphyrophlebia*, *Pursa*, *Sindon*, in the family, which she argued for placement in the order Protorthoptera. In 1966, Carpenter redescribed Sellards' species, assigning them both to *Glaphyrophlebia*.

The most recent review of family Blattinopsidae (Hörnschemeyer and Stapf, 2001) lists 13 species of *Glaphyrophlebia* from the Upper Carboniferous through the Late Permian, from North America, England, Asian and European Russia, France, Germany, and Czech Republic (species list is repeated in Appendix herein for completeness, along with references to figures of species to facilitate comparisons and diagnoses). The new species described here is the third species of the genus from the Wellington Formation, the fourth from North America, and the fourteenth overall.

METHODS

Photomicrographs of the part and counterpart were made using two systems: a Nikon 990 digital camera with an American Optical dissecting microscope and an external strobe flash (Nikon SB-26) or a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscope lens and custom fiber-optic strobe illuminators. Flash orientation was optimized to show details of interest. The photographed images were processed using Adobe Photoshop 6.0 and imported into a vector-graphics software program (XARA Extreme 4.0, XARA Group, Ltd., London), where they were assembled into composite images. The venation reconstruction drawing was made as an overlay (Fig. 1), using photographs of both part and counterpart.

Interpretation and nomenclature for the wing venation follows Kukalová-Peck (1991), as amended by Kukalová-Peck & Brauckmann (1992). To facilitate comparison with species discussed in the review of the Blattinopsidae of Hörnschemeyer and Stapf (2001), we note the following correspondence:

Vein	Notation used here	Notation of Hörnschemeyer and Stapf
posterior subcosta	ScP	Sc
anterior radius	RA	R
posterior radius	RP	RS
posterior media	M P	M P
anterior cubitus	CuA	CuA
posterior cubitus	CuP	CuP
anterior analis	AA	A
vein bow	vb	vb

SYSTEMATIC PALEONTOLOGY

INSECTA

NEOPTERA

Blattinopsidae Bolton, 1925

Glaphyrophlebia Handlirsch, 1906a

Glaphyrophlebia anderhalterorum n. sp.

Figures 1-3

Diagnosis: The new species is assigned to family Blattinopsidae based on broad area between ScP and RA (see Fig. 1 for venational nomenclature), presence of vein bow, nearly parallel CuA and posterior branch of MP with distinct diagonal brace ("strut" of Béthoux and Nel, 2002; "arculus" of Kukalová-Peck and Brauckmann, 1992); assigned to genus *Glaphyrophlebia* on the basis of the following characters (as elucidated by Hörnschemeyer and Stapf, 2001): no reticulation in distal half of wing; only a few cross veins connecting branches of RA and MP; longitudinal furrows between branches of RA and MP running from the

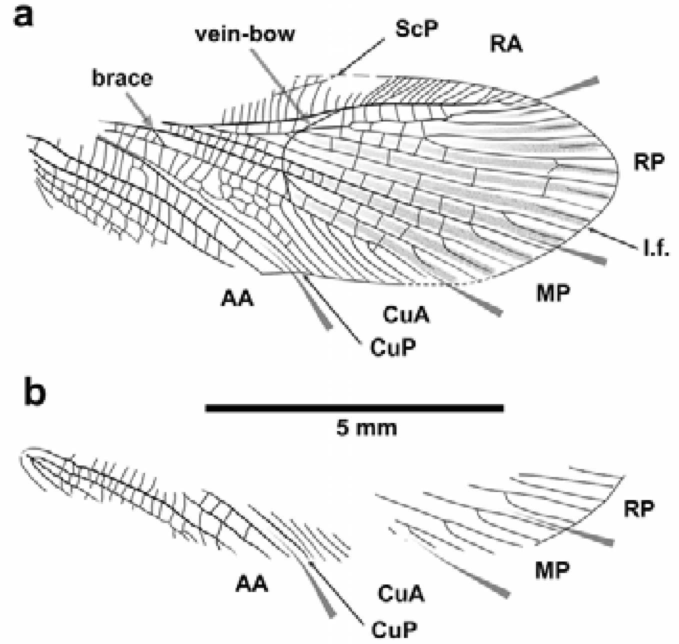

FIGURE 1. Reconstruction of forewings of *Glaphyrophlebia anderhalterorum* n. sp. **a**, Right forewing. **b**, Left forewing. Scale bar 5 mm long. ScP = posterior subcostalis; RA = anterior radius; RP = posterior radius; l.f. = longitudinal furrow (indicated by gray shading; depicted only on RFW); MP = posterior media; CuA = anterior cubitas; CuP = posterior cubitus; AA = anterior analis. Notation and interpretation of venation follows Kukalová-Peck, 1991.

posterior wing margin to or slightly basal of vein-bow; basal cubital field with large cells formed by a network of cross veins.

Species-level Differential Diagnosis: *Glaphyrophlebia anderhalterorum* differs from *G. arnulfi* Hörnschemeyer and Stapf, 2001 in size (FW length 10.5 mm vs. 21 mm); fewer and more widely spaced cross veins in RP field; MP with two vs. one main branch.

Differs from *G. clava* Kukalová, 1965 by closely-spaced vs. widely-spaced slanted cross veins between R and the costal margin distal of ScP termination; lack of network of cells formed by cross veins between RA and most anterior branch of RP at wing apex; simple cross veins in radial-medial field basal of vein-bow; CuP and AA1 with space between them widening towards posterior margin of wing rather than closely spaced and parallel.

Differs from *G. delicatula* Handlirsch, 1906 in fewer simple cross veins in distal Rs field; lack of cross veins between branches of RP and intercalary veins (type of *G. delicatula* comprises only the distal half of ScP and RA and the RP field, with remainder of wing missing).

Differs from *G. jeckenbachi* Hörnschemeyer and Stapf, 2001 by two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than single branch forking distal to vein-bow; CuA with distal branches pectinate vs. CuA forking once or twice and pectinate branches arising from most posterior branch of fork; simple cross veins in medial field basal of vein-bow vs. unevenly spaced and slanted cross veins; simple and more evenly spaced cross veins in anal field vs. slanted veins and networks of veins.

Perhaps most similar to *G. ovata* (Sellards, 1909), *G. anderhalterorum* differs from that species by simple cross veins between RA and ScP basal of vein bow rather than double row of cells; width of field between RA and ScP about ½ width of field between ScP and costal margin rather than subequal at level of vein bow; two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than single branch; CuA with distal branches pectinate vs. CuA forking at vein bow and pectinate branches arising from most posterior branch of fork; simple cross veins in cubital field near brace rather than network of cells; fewer cross veins in RP and MP fields distal to vein-bow.

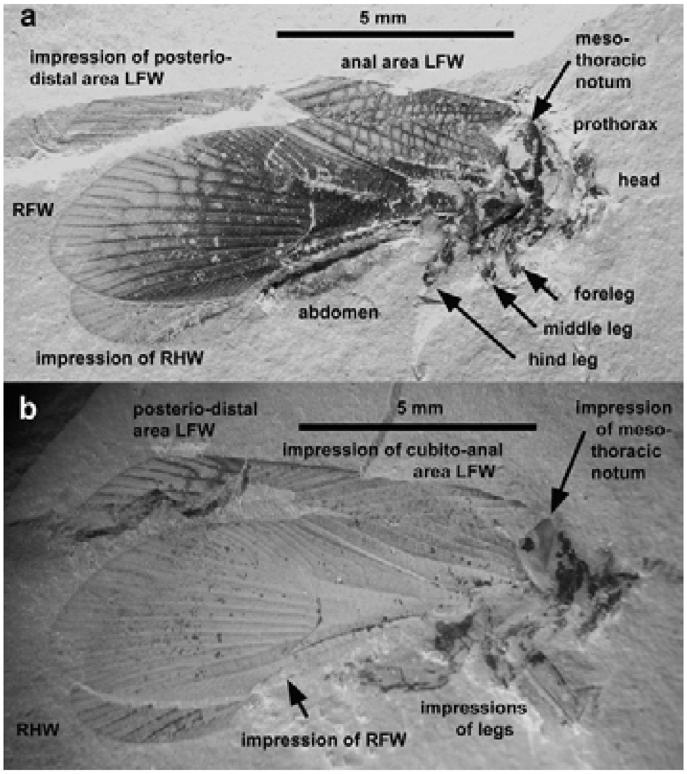

FIGURE 2. *Glaphyrophlebia anderhalterorum* n. sp. Photographs of Holotype. **a**, Part: Specimen KU-R5-4-26-04-001a. Dorso-lateral view of nearly complete insect with articulated wings and legs, showing color pattern with darkening of wing veins and of the membrane of the basal radio-medial fields, the membrane lightening in color distally. **b**, Counterpart (image digitally flipped): Specimen KU-R5-4-26-04-001b. Impression of insect. Both scale bars 5 mm. RFW = right forewing; LFW = left forewing; RHW = right hind wing.

Differs from *G. parvavena* Hörnschemeyer and Stapf, 2001 in vein-bow terminating on RA at level of ScP terminating on costal margin vs. vein-bow terminating on RA well distal of ScP termination; more and more uniformly-spaced cross veins in RP and MP fields; simple cross veins rather than network of cross veins between first two anal veins; general shape of longitudinal veins straight rather than sinuate or curved.

Differs from *G. pusilla* Handlirsch, 1906 by two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than a single forked branch; simple cross veins between ScP and RA and RP and most anterior branch of RP rather than forked cross veins; CuA straight rather than sinuate.

Differs from *G. pygmaea* (Meunier, 1907) by two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than free MP with 4 anteriorly pectinate branches.

Differs from *G. rohwedderi* Hörnschemeyer and Stapf, 2001in total forewing length 10.5 mm vs. 15.8-16.5 mm, width 3.7 mm vs. 6.4-6.7 mm; CuA with distal branches pectinate vs. CuA forking once or twice and pectinate branches arising from most posterior branch of fork; large cells vs. irregular mesh of cells between CuA and CuP; simple cross veins vs. network of cells between anal veins basally, few widely-spaced cross veins vs. dense system of cross veins in RP and MP fields.

Differs from *G. speciosa* (Sellards, 1909) by more closely spaced

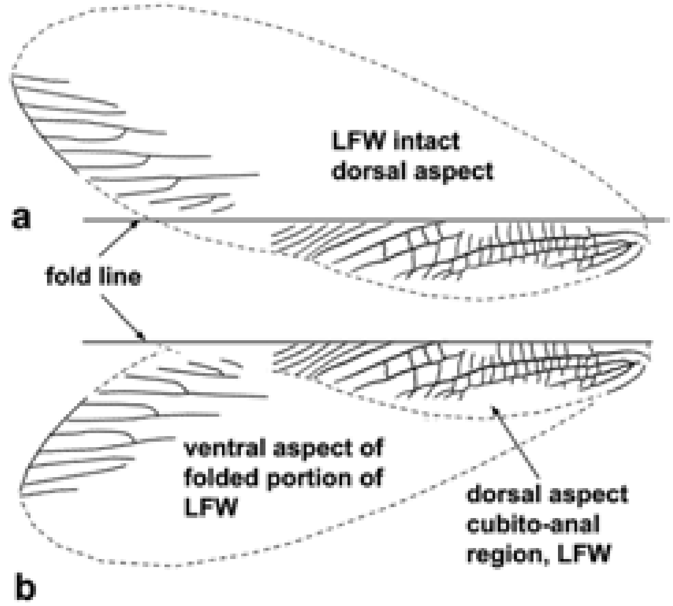

FIGURE 3. Drawing depicting likely geometry of the folding under of the left forewing (LFW) of the insect during preservation. The wing may have simply folded, or may have broken off; the arrangement of preserved portions suggests that the wing folded ventrally along a line running through the cubital field. **a**, The preserved portions of the left forewing presented as they would have appeared on the intact wing, with the supposed fold line indicated. **b**, The wing as preserved, reflecting result of the ventral folding.

slanted cross veins between RA and costal margin distal of ScP termination; vein-bow terminating on RA at level of vs. distal to ScP termination; two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than MP free and unforked; pectinate branches of CuA closely spaced and parallel vs. widely spaced and curved, branches of CuA more nearly parallel to anterior branch; simple cross veins rather than network of cells between anal veins basally.

Differs from *G. subcostalis* (Martynov, 1928) by two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than MP free and unforked; CuA with distal branches pectinate vs. CuA forking and pectinate branches arising from posterior branch of fork; simple cross veins vs. network of cells between anal veins basally.

Differs from *G. uralensis* (Martynov, 1940) by posterior branch of MP straight and forked at level of vein-bow vs. curved and simple; CuA straight vs. curved; pectinate branches of CuA parallel and simple vs. unevenly spaced and sometimes separated from main branch by irregular cells.

Differs from *G. wettinensis* (K. v. Fritsch, 1899) by more closely spaced slanted cross veins between RA and costal margin distal of ScP termination; posterior branch of MP straight and forked at level of vein-bow vs. posterior branch forking twice, fork basal to vein-bow, second fork on posterior branch of first fork; pectinate branches of CuA straight, parallel and simple vs. curved or branched, unevenly spaced and separated from main branch by irregular cells.

Differs from possible *Glaphyrophlebia* (gen. et sp. indet. Prokop et al., 2012: p. 279, figs. 7, 8) by short versus long stem of RP; simple cross veins vs network of cells between MP and CuA basal to brace vein; fewer and more widely spaced cross veins in radial and medial fields.

Etymology: The specific epithet *anderhalterorum* honors my maternal grandmother, the late Katherine Vollet Anderhalter, and her son, the late Prof. Dr. Oliver Anderhalter. My grandmother encouraged me from my earliest school days to excel academically so that I might follow in my uncle's footsteps and earn a PhD. Her expectations and his example nurtured in me an early interest in science and learning that has lasted a lifetime.

Type Locality: Raasch 5 locality (Raasch, 1946), Noble County, Oklahoma, USA; Wellington Formation, Artinskian, Lower Permian.

Type Material: Holotype specimen KU-R5-4-26-04-001a,b. Collected in April, 2004 by Joseph Hall of Tulsa, Oklahoma, and provided to the author for contribution to the Fossil Insect Collection, Entomology Division (Paleoentomology) of the University of Kansas Natural History Museum.

Part (001a, Figure 2a): Well-preserved insect exposed in dorsal aspect, with some rotation about the lengthwise body axis to expose portion of right side; wings articulated to pterothorax; significant three-dimensionality of body and wing venation intact; dorsal surface of entire right forewing (RFW) nearly complete, but with subcostal region and extreme anterio-basal portion missing; impression of anterio-distal portion of right hind wing (RHW) visible because of rotation of body; anal area of LFW preserved, but LFW apparently folded ventrally along a line through the cubital area (see Fig. 3), leaving an impression of the posterio-distal portion of the ventral LFW; right legs articulated, each with portion of leg distal to approximately mid-femur obscured; meso-thoracic notum with triangular shaped and rounded bulge above level of wings; prothoracic tergum and fragments of head visible; antennae missing or obscured; ventral portion of abdomen visible, terminalia missing or obscured.

Counterpart (001b, Figure 2b): Clear and detailed impression of dorsal aspect of insect revealing some portions of wing venation of both LFW and RFW not visible in part; portion of ventral surface of posterio-distal portion of folded LFW preserved; impressions of legs with more distal portion of femur preserved, especially in foreleg, for which nearly the entire femur appears to be impressed; three-dimensionality of mesothoracic notum particularly noticeable in impression.

Description: Forewing (Fig. 1a, b): Preserved length 10.3 mm, estimated total length 10.5 mm, width 3.5 mm, ratio length to width: 3.0; except for sinuate RA, longitudinal veins and branches straight and evenly spaced, often parallel to a marked degree; ScP terminates at 5.5 mm from wing base (at mid-wing), closely-spaced, slanted simple or y-shaped cross veins between RA and costal margin distal to ScP termination, cross veins between RA and ScP more widely spaced and simple; at level of vein bow, field between RA and ScP ½ the width of field between ScP and costal margin; RA sinuate and terminating 8.7 mm from base, RP separating from RA at 3.4 mm from wing base, forking 5 times, with few cross veins between longitudinal branches of RP; MP with two straight branches, anterior branch separating from RA 3.1 mm from wing base, posterior branch forking at level of vein-bow; longitudinal furrows between branches of RP and MP, extending from margin of wing to vein-bow; CuA separates from MP+CuA 2.4 mm from wing base; CuA straight, with 9 branches terminating on wing margin, closely spaced and pectinate, some large cells in CuA field basal to vein bow, simple cross veins between CuA and CuP basal to these cells; CuA and anterior branch of A not parallel, distance wider at wing margin than basally, sharp fold line between CuP and A; at least six parallel anal vein branches with simple cross veins, lacking network of cells; cross veins in RP/MP field distal of vein-bow few and widely separated; vein bow definitely and distinctly vein-like, extending from RA at the level of ScP termination, curving basally, terminating on CuA 4.8 mm from wing base; wing veins and membrane in basal 2/3 of wing distal to anal region darkened; width of thorax between forewing attach points 1.8 mm.

Thorax: Mesothorax with triangular-shaped, dorsally-rounded tergum, 1.8 mm wide, 1 mm long; prothoracic tergum 1 mm wide by 0.8 mm long.

Abdomen: Short, apparently three terminal segments and possibly extreme basal portion of terminalia (latter indistinct) preserved; approximately 4 mm preserved length; forewing extends 4 mm beyond abdomen.

Discussion: The type specimen of *Glaphyrophlebia anderhalterorum* n. sp. has extremely well-preserved venation, and the vein-bow, viewed by some authors as possibly an impressed mark (e.g., Bolton, 1925; Kukalova, 1959), is definitely present here as a strong vein, as strong as the longitudinal veins it crosses, supporting the assertion of Hörnschemeyer and Stapf (2001) that it likely plays a role in stiffening the wing basal to the vein-bow while allowing flexing of the distal surface.

In the differential diagnosis (vide supra) I have chosen to take note of differences in the branching of MP, even though that vein system is known to be highly variable in the Blattinopsidae; in each case, there are other significant differences supporting the specific identity of *G. anderhalterorum*.

Specimens of Blattinopsidae from the Wellington Formation are not abundant, although the Elmo species, *G. ovata* and *G. speciosa*, are represented by at least several specimens each from Kansas, and the author has also seen small numbers of specimens of *G. speciosa* from the Noble County, Oklahoma beds. Thus far only one specimen of *G. anderhalterorum* has been found. As noted by Beckemeyer and Hall (2007), from data based on a set of 120 species of insects known from the Elmo, Kansas fossil beds, the mean number of specimens per species was 21, the median 2 and the mode 1, verifying that most of the Elmo species are known from a single specimen.

According to Hörnschemeyer (1998), only 56 fossils of Blattinopsidae had been mentioned in the literature prior to the discovery of about 100 specimens from the Lower Permian Niedermoschel fossil site. The unusual numerical abundance of blattinopsiid fossils at Niedermoschel resulted in the addition of four species from that locality to the genus *Glaphyrophlebia*. It is interesting that although *Glaphyrophlebia* specimens are much less abundant in the Wellington Formation, there are now three species known.

As noted by Hall (2004) and Beckemeyer (2011) the Oklahoma Wellington Formation insect deposit facies are derived from marginal marine lagoon sediments, with insect remains likely comprised of allochthonous material washed in by streams. This undoubtedly accounts for the preponderance of fossils from the deposits being comprised of wings and wing fragments. The preservation of this fine example of a nearly complete glaphyrophlebiid is thus unusual; hopefully, continued collection from the Wellington Formation beds will provide additional such surprises.

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Mr. Joseph Hall, of Tulsa, Oklahoma has been my field companion and fellow collector for a number of years. He has always generously parted with even the most exceptional specimens in the interest of the advancement of science. Prof. Dr. Michael Engel supports my work through affiliation with his Paleoentomology Laboratory at the University of Kansas Natural History Museum, Division of Entomology (Lawrence, Kansas). Ms. Betty Sherwood of the Wichita State University Inter-Library Loan department (Wichita, Kansas) provided timely access to many difficult-to-find references. Dr. Danil Aristov of the Paleontological Institute of the Russian Academy of Sciences (Moscow) provided a critical reference not otherwise available. Drs. Michael Engel and Jakup Prokop (Faculty of Science, Department of Zoology, Charles University, Prague) provided comments on an earlier version of this manuscript. The work reported here is a contribution of the University of Kansas Natural History Museum, Division of Entomology.

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APPENDIX

Species of *Glaphyrophlebia* with References to Reconstruction Figures or Photographs (Species list after Hörnschemeyer & Stapf, 2001)

Glaphyrophlebia Handlirsch, 1906a
- *G. anderhalterorum* n. sp.
  [Figs. 1 (reconstruction drawing), 2 (photograph) and 3 (reconstruction drawing) herein]
- *G. arulfi* Hörnschemeyer & Stapf, 2001
  [p. 99-100, fig. 12: reconstruction]
- *G. clava* Kukalová, 1965
  [p. 85, fig. 14: reconstruction, pl. 7: fig. 2: photograph of FW]
- *G. delicatula* Bolton, 1934
  [p. 284, fig. 5: reconstruction, pl. 9: fig. 5: photograph of FW]
- *G. jeckenbachi* Hörnschemeyer & Stapf, 2001
  [p. 95-97, figs. 8: reconstruction, fig. 9: photograph]
- *G. ovata* (Sellards, 1909) (Pursa)
  [p. 155, fig. 4: reconstruction; Carpenter, 1966, p. 71, fig. 9: reconstruction of neotype]
- *G. paravena* Hörnschemeyer & Stapf, 2001
  [p. 100-101, fig. 13: reconstruction]
- *G. pusilla* Handlirsch, 1906a
  [p. 707: fig. 35: reconstruction of type species for genus; Handlirsch, 1906b, pl. 16, fig. 10: reconstruction]
- *G. pygmaea* (Meunier, 1907) (Blattinopsiella)
  [p. 524: fig. 2: reconstruction; Hörnschemeyer and Stapf, 2001, p. 89, fig. 2: photograph of wings]
- *G. rohwedderi* Hörnschemeyer & Stapf, 2001
  [p. 98, fig. 10, p. 99, fig. 11: reconstructions]
- *G. speciosa* (Sellards, 1909) (Sindon)
  [p. 155, fig. 1: reconstruction; Carpenter, 1966, p. 70, fig. 8: reconstruction of neotype; Carpenter, 1992, p. 104, fig. 59.9: reconstruction of neotype]
- *G. subcostalis* (Martynov, 1928) (Sindonopsis)
  [pl. 12, fig. 3, FW; pl. 7, fig. 7, HW (as *Sindonopsis reducta*); Martynov, 1931 (as Sindon rossicum), p. 154, fig. 4; Sharov, 1962, p. 116, fig. 277: reconstruction of HW; Rasnitsyn, 1980, p. 32, fig. 29a: reconstruction of FW, fig. 29b: reconstruction of HW; Novokshonov, 1998, p. 30, fig. 6: reconstruction of complete insect in lateral view; Rasnitsyn and Quicke, 2002 (p. 108, fig. 110: photograph of FW and HW)]
- *G. uralensis* (Martynov, 1940) (Sindon)
  [(p. 14, text fig. 9, plate II, fig. 4); Sharov, 1962, p. 116, fig. 276: reconstruction of FW; Rasnitsyn, 1980, p. 32, fig. 28a: reconstruction of complete insect in lateral view, p. 32, fig. 28b: artist's conception of living insect; Rasnitsyn and Quicke, 2002 (p. 108, fig. 110: photograph of complete insect in lateral view)]
- *G. wettinenesis* (K. v. Fritsch, 1899) (Prisca)
  [v. Fritsch does not figure P. wettinensis; Handlirsch, 1906b, pl. 6, fig. 12: reconstruction; Hörnschemeyer & Stapf, 2001, p. 91, fig. 3: reconstruction after Handlirsch, 1906b]

gen. et sp. indet. (likely glaphyrophlebiid) (Prokop et al., 2012)
  [p. 289, figs. 7,8]

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

REDISCOVERED PHOTOGRAPHS OF A 1927 VISIT BY FRANK MORTON CARPENTER TO THE ELMO, KANSAS, FOSSIL INSECT BEDS

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Abstract—Five photographs related to a visit of the famous paleoentomologist, Frank Morton Carpenter, to the Elmo, Kansas, fossil insect beds in 1927 are presented. That visit was his second to the locality, the first having been an exploratory trip in 1925. Photographed by Dr. Reginald H. Painter of Kansas State University, the pictures show Carpenter and co-workers at the locality, and illustrate the physiographic setting of the beds and the manner of working them. Given the importance of these Lower Permian fossil insect deposits and of Frank M. Carpenter's role in studying them, the photos were considered to be of sufficient historical significance to document for posterity.

INTRODUCTION

Frank M. Carpenter (1902-1994) and Robin J. Tillyard (1881-1937) were the two most influential workers who contributed to our knowledge of the entomofauna of the famous Elmo, Kansas fossil insect beds. Together, they published some two-dozen papers describing the fossil insects of the Kansas Permian (a list of their publications may be found in Beckemeyer, 2000). However, little information has been published related to their trips and expeditions to this historic and renowned site.

Recently, the author was contacted by Dr. Kirby C. Stafford III, Vice Director, Chief Entomologist, and State Entomologist of the Department of Entomology of The Connecticut Agricultural Experiment Station (Stafford, personal commun., 2012). Dr. Stafford informed me that, as an M.S. graduate student at Kansas State University, he had rescued a discarded folder that contained photographs and notes regarding visits to the Elmo fossil beds. He had kept the folder for many years, and, having recently come across my short history of the Elmo fossils (Beckemeyer, 2000), contacted me to determine my interest. Eventually, Dr. Stafford sent me the entire folder, which I digitally scanned and returned to him. He will be offering the original photos to the Yale Peabody Museum for archiving (Stafford, personal commun., 2012). The folder contained photographs and notes pertaining to a visit to Elmo in 1927 by Carpenter, along with photographs and documentation regarding Tillyard's visits to Elmo in 1928 and 1933 (the latter material has appeared elsewhere, see Beckemeyer, 2012). Given Carpenter's status as one of the world's greatest paleoentomologists, and the fact that his very first scientific publication was on the Elmo, Kansas fossil insects (Carpenter, 1926; Furth, 1994), it seems worth documenting the 1927 visit by presenting the material here.

NOTES ON THE ELMO, KANSAS FOSSIL INSECT LOCALITY

Location

The Elmo fossil insect locality is located in southern Dickinson County, Kansas (Fig. 1). Dickinson County lies almost entirely in the Flint Hills physiographic unit, the only extensive area of native tallgrass prairie remaining in the United States. The hills were formed by erosion of Permian limestones and shales. The limestones here contain bands of chert, and the shallow cherty soil has kept the land from being broken by plow; the Flint Hills are used almost exclusively for cattle ranching. Wellington Formation insect-bearing layers were tracked from Dickinson County south through Marion, Harvey, Sedgwick and Sumner counties, Kansas into Kay, Noble, and northern Payne counties in Oklahoma by Paul Tasch (1962) (Fig. 1). The insect-fossil bearing layers are only readily accessible at Elmo and at the Midco beds in Noble and Kay counties in Oklahoma (the latter discovered by Gilbert Raasch (1946) and the insect fossils studied by Carpenter and Tasch - see references to their work in Beckemeyer, 2000). The Wellington Formation beds from Marion County south through Sumner County are largely covered over by thick alluvial deposits of the Wellington-McPherson and Arkansas River Lowland physiographic regions.

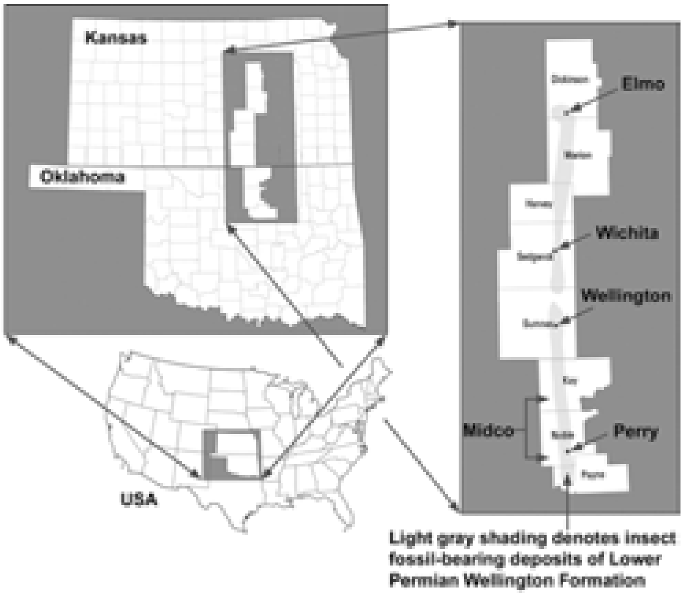

FIGURE 1. Location of Elmo, Kansas fossil insect beds and relationship to the extent of the Lower Permian Wellington Formation fossil insect deposits in Kansas and Oklahoma. The formation runs some 270 km through eight counties. After Tasch, 1962, Hall, 2004 and Beckemeyer and Hall, 2007.

The Discovery and Study of the Elmo Fossil Insect Beds

In 1898, Dr. Charles Sterling of the University of Kansas, who grew up on a family farm in southwest Dickinson County, Kansas, discovered on that property "…some well-preserved fossil plants," which he showed to Elias Sellards (Sellards, 1899-1900, p. 208). Sellards, also affiliated with the University of Kansas, made subsequent visits to that site and others in the vicinity, collecting many specimens. He wrote about the plants he and Sterling had collected in a 1901 paper. In that paper he noted, in commenting on some scars on the midribs of

Taeniopteris ferns: "The comparison to insect stings was suggested to me originally to be the close resemblance of the scars to the stings on the common *Amorpha fructicosa* (false indigo), said to be made by some of the orthopteroid insects, a supposition which the more recently discovered presence, among the plants, of two well preserved orthopterous insects may be taken to strengthen" (Sellards, 1901: p. 11). The two insects he found were sufficient incentive for him to return to the site during the summer of 1902, where he "discovered a rich insect locality…in the southern portion of Dickinson county [sic], Kansas. The preservation of the insects is exceptionally good. A very large proportion of the wings are complete and their details of structure clear, even the minute hairs often being present…some six hundred specimens [were] collected" (Sellards, 1903, p. 323). Although he was not an entomologist, Sellards went on to survey the insect fossils he had collected in a series of three publications (Sellards, 1906, 1907, 1909).

With the exception of visits by members of The University of Kansas (KU) and Kansas State University (KSU, then known as Kansas State College) faculty and students that might have been made in the interim, the fossil beds were apparently neglected after Sellards' visits to the site. However, in 1920, the famous entomologist/palaeoentomologist Robin J. Tillyard (employed at that time at the Cawthron Institute, Nelson, New Zealand) made a fateful visit to the Yale Peabody Museum. Tillyard's enthusiastic response on seeing some of the fossils that Sellards had collected and deposited in the Yale collection inspired Charles Schuchert and Carl O. Dunbar to make an expedition to Elmo in 1921. They collected some 2000 specimens that provided material that was studied by Tillyard for the remainder of his career; he published 21 papers on the Elmo fossil insects between 1923 and his death in 1937 (see Beckemeyer, 2000 for a list of Tillyard's publications on Elmo fossil insects).

Frank M. Carpenter made his first visit to Elmo in 1925 with Professor P. E. Raymond, who was in charge of the Harvard Summer School of Field Geology during the 1925 session (Carpenter, 1926; Henshaw, 1926; Brosius, 1994). Carpenter was, at the time, working on his M.S. and Ph. D. at the Bussey Institution at Harvard.

Elizabeth Brosius, who was an Assistant Editor at the University of Kansas, Paleontological Institute, worked with Prof. Frank Carpenter to complete his *Treatise on Invertebrate Paleontology* volumes on fossil insects (Carpenter, 1992). She wrote a warm biographical sketch about Carpenter (Brosius, 1994) as a memorial on the occasion of his death. In it she reported that the 1925 trip was Carpenter's first visit to any fossil insect locality:

> "'This was my first trip outside New England,' Carpenter said. 'The train stopped right in Elmo, a town of perhaps 15 houses, and Professor Raymond met me as I got off.' Carpenter and Raymond scouted around the fossil site, a pasture three miles south of town, and unearthed enough fossil insects to be convinced that another extensive collection could be made." (Brosius, 1994, p. 122). Elmo, Kansas was a stop for the Missouri-Pacific Railroad Line (Beckemeyer, 2007). A photo of Elmo as it appeared in the early 1900's was published previously (Beckemeyer and Hall, 2007)

Carpenter returned to Elmo many times over the years, building up a huge collection at the Museum of Comparative Zoology. He worked on the fossils collected there for most of his life; his final contributions on the Elmo entomofauna were made in the two volumes of the *Treatise on Invertebrate Paleontology* (see Beckemeyer, 2000, for a list of Carpenter's 13 papers specifically addressing Elmo fossil insects).

THE 1927 VISIT

Encouraged by the 1925 collection, Carpenter spent much of 1927 collecting fossils. Brosius (1994) wrote an account of his time at Elmo:

> "Carpenter returned to Elmo in 1927 and spent six months prospecting … For two months he was assisted by two other graduate students from Harvard." (Brosius, 1994, p. 122.)

The two graduate students were mentioned by name by William M. Wheeler, Dean of the Bussey Institution, in his report to Harvard College for 1926-1927:

> "Appointment to a Sheldon scholarship has enabled Mr. F. M. Carpenter to do important work on fossil insects. He devoted the summer and the past few months to visiting various fossiliferous strata in Colorado and to collecting more than 2000 insects in the Permian formations of Kansas. These specimens will be later deposited in the Museum of Comparative Zoology. In the work of excavation at Abilene, Kansas, he was assisted by two of our students, Messrs. W. S. Creighton [1902-1973] and J. W. Wilson, who spent the earlier part of the summer observing and collecting Hymenoptera in Colorado and the adjacent states." (Wheeler, 1928, p. 174.)

Figures 2 and 3 show Carpenter (standing in Fig 2; standing in cap, knickers and jacket in Fig. 3) and were taken by Dr. Reginald H. Painter of the Kansas State University Entomology Department. Painter was newly arrived at KSU, having come in 1926 after receiving his Ph.D. from Ohio State University. He apparently took on the task of being the informal photographer for the Department for field trips and events. I have been unable to determine if either of the two Harvard students who worked with Carpenter at Elmo in 1927 are among those in the photo. I would expect that Painter's presence would indicate that most of the other people are entomology or other biology or geology majors from Kansas State University.

Carpenter apparently maintained relationships with both the KSU and the University of Kansas (KU) entomology departments. An article in the Lawrence Journal World newspaper in 1927 reported that Carpenter gave a talk to the KU entomology club:

> "Dr. Frederic [sic] Carpenter, of Harvard University, returned yesterday after a stay of a few days in Lawrence. He spoke Monday at a meeting of the K. U. entomology club. Dr. Carpenter was in Kansas on a Harvard expedition in Dickinson County to collect insect fossils. He reported that the expedition was unusually successful. Among his finds were fossils of a group of insects with three pairs of

FIGURE 2. Photograph of Frank Carpenter (standing) and a small group (probably students from Kansas State University) at the Elmo fossil insect locality. Members of the group are seated and appear to be using hand lenses to check the rocks for insect fossils. Photographer Dr. Reginald H. Painter of KSU. Note written in Painter's handwriting on back of photo: "Right Frank Carpenter & group at fossil beds Spring 1927."

FIGURE 3. Another photograph of Frank Carpenter and the group of students at the Elmo fossil beds in Spring 1927. No label on the back, but the individuals and their clothing indicates this was taken by Reginald Painter the same day as Figure 2. This photo shows quite well the landscape of the Flint Hills region, with rolling hills cut by drainage features. Note the cattle grazing in the background.

> wings. The University of Kansas has a small collection from the Dickinson County region, which is becoming one of the most famous in the world for fossil insects, according to Dr. H. B. Hungerford, professor of entomology. A study of about 5,000 insects which have been taken from the beds in Dickinson county have already thrown much light on the relationship of present day insects, Dr. Hungerford said." (Anonymous, 1927, p. 1)

Figures 4, 5, and 6 illustrate a typical exposure of the insect bed, the placement of dynamite for removing overburden, and a blast, respectively. These vividly document Brosius' (1994) record of Carpenter describing his work at Elmo in 1927:

> "Instead of scouring the picked-over rock outcrops, Carpenter's team opened new quarries, using dynamite to blast through the 5- to 8-foot-thick overburden. 'We'd put the sticks about 5 inches above the insect bed in a line about 15 feet long.' … With the bulk of the soil and rock out of the way, the men easily removed the remaining debris and exposed the insect bed, a layer of limestone 4 or 5 inches thick. They broke the rock into manageable chunks and split them open with a rock hammer." (Brosius, 1994, p. 122)

A photograph of Frank M. Carpenter actually splitting rocks with a hammer at the Elmo site in 1927 was reproduced previously (Beckemeyer, 2000, p. 13, fig. 19). This photograph was given to Elizabeth Brosius by Frank Carpenter. The photographer is unknown. Brosius (1994, p. 122) wrote of this picture:

> "A photograph taken that summer shows Carpenter perched on a campstool in the middle of the treeless prairie, rock in one hand, hammer in the other. On a good day, they found as many as 50 specimens…"

Four additional photographs of the 1927 Harvard Elmo quarry sites may be found in Plate 1 of Carpenter's 1930 paper. The photographer was not credited.

Carpenter's very successful trip to Elmo in 1927 gave his career a kick-start. In his 1929 report to Harvard, William Wheeler noted:

> "Dr. F. M. Carpenter … was given a national research scholarship and will during the coming year take up the

FIGURE 4. A typical exposure at Elmo. The hammer and block of rock rest on the top of the insect-fossil-bearing layer. Note the shovel and the rocks taken from the insect layer littering the ground at the top of the picture. Also visible are the extensive root systems of the prairie grasses. Photographer: Dr. Reginald H. Painter.

FIGURE 5. A photograph of the placement of dynamite charges for removal of overburden. Three detonation wires can be seen running from holes along the bottom edge of the photo. Photographer: Dr. Reginald H. Painter. Note written in Painter's handwriting on back of photo: "dynamite charge in place Spring 1927."

FIGURE 6. A blast removing overburden from the insect bed. Photographer: Dr. Reginald H. Painter. Note on back of photo written in Painter's handwriting: "use of dynamite to clear & break up overburden Spring 1927."

> study of the large amount of Permian insect material which he collected in Kansas during the summer of 1927." (Wheeler, 1929, p. 183)

Three years later, Carpenter would publish the first of his many papers on the Elmo, Kansas Permian insect fauna (Carpenter, 1930; Furth, 1994). His 1927 trip to the Elmo fossil beds provided a strong foundation for an outstanding career in palaeoentomology.

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DO LEAF MARGIN-CLIMATIC PROXIES EXIST FOR THE PALEOZOIC?

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Leaf margin analysis (LMA), while useful in paleoclimatic interpretations, is constrained in application to angiosperm-dominated assemblages of the late Mesozoic and Cenozoic. To date, no studies have attempted to determine whether climatic parameters that induce changes in leaf margin state in angiosperms do the same for living members of Paleozoic-diverging seedless vascular plant lineages. Using two 5-month growth chamber treatments of 15°C and 25°C, temperature-influences were tested on leaf margin shape in three extant lycopsids (Lycopodiaceae) and one evergreen fern species (Polypodiaceae) with serrated leaf margins. Using Digital Leaf Physiognomy Approach we assess whether significant differences in four leaf margin parameters occur intraspecifically across these two early-diverging vascular plant lineages.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

PALYNODIVERSITY PATTERNS FROM CISURALIAN DEPOSITS OF THE SOUTHMOST PARANÁ BASIN, WESTERN GONDWANA

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Abstract—This work analyzes palynological changes in terms of diversity trends and processes of generic extinction and appearance throughout the Early Permian in samples from three boreholes from northeast Uruguay and southernmost Brazil. The number of genera (generic richness) present in 96 samples was considered for analysis. Three phases were recorded from the base to the top of the lithostratigraphic columns. An increase in diversity is observed during the first phase (hereafter, DI phase), a diversity stability period (DS phase), and a last period where diversity decreases (DD phase). Richness trends, generic extinction and origination throughout the time interval analyzed correlates with the different sedimentary facies, which are related to climatic changes that occurred in this region of Gondwana. The first stage (DI phase) was associated with climatic amelioration. Later, a gradual turnover is registered during DS phase, in which the first evidence of vegetation more adapted to dry conditions appeared (bisaccate and striate pollen grains). Finally, the extinction of hydrophilic genera represented by spores and monosaccate pollen grains is associated with a decrease of diversity and the establishment of more arid conditions (DD phase).

INTRODUCTION

In the Early Permian strata of the southern Paraná Basin, Brazil and Uruguay, rich palynofloras have been identified and used for biostratigraphic zonation (Souza and Marques-Toigo, 2003; Beri et al., 2011; Mori and Souza, 2012). In some cases, clear changes are observed and the biohorizons delimited can be identified in other Gondwanan basins (Russo et al., 1980; Césari and Gutiérrez 2000; Gutiérrez et al., 2003; Césari, 2007). Despite this, few studies have analyzed palynofloral diversity at this time and place (Goldberg, 2004; Beri et al., 2013).

The Paleozoic spore and pollen record has much potential to study patterns of evolution, biodiversity, biogeography, morphological disparity, patterns of origination, extinction and taxonomic longevity, as well as rates of evolution (Servais and Wellman, 2004). Species richness patterns through time are ultimately the result of the interaction between processes of speciation, extinction and dispersal (Ricklefs, 1987). With an aim to understand some of these issues, the present work is a first approach towards the analysis of diversity changes through time, including the processes influencing plant extinction and origination, as recorded by palynomorphs, throughout the Early Permian of the Paraná Basin. To achieve this, published data from three boreholes from northeastern Uruguay and southern Brazil were used (Beri et al., 2011; Mori and Souza, 2012). These boreholes are very close together, and samples are drawn from the same lithostratigraphic units (although given different formal names in Brazil and Uruguay), which also have similar palynological content.

MATERIAL AND METHODS

Published data of 96 samples from borehole 254 (Paso de las Toscas) drilled in Uruguay, and boreholes HN05 and HN25, drilled in Brazil, were used for analysis (Fig. 1). General information and detailed geological data from boreholes are available in Beri et al. (2010, 2011, 2013) and Mori and Souza (2012).

In borehole 254, samples come from levels corresponding, in stratigraphic ascending order, to the San Gregorio/Cerro Pelado, Tres Islas, Frayle Muerto, Mangrullo and Paso Aguiar formations. In boreholes HN25 and HN05, samples are from levels belonging to the Itararé Group, Rio Bonito, Palermo, Irati, Serra Alta and Teresina formations. The Brazilian and Uruguayan lithostratigraphic units are correlated as follows: Itararé Fm. with San Gregorio/Cerro Pelado Fms.; Rio Bonito Fm. with Tres Islas Fm.; Palermo Fm. with Frayle Muerto Fm.; Irati Fm. with Mangrullo Fm.; Serra Alta and Teresina Fms. with Paso Aguiar Fm. (see Milani et al., 2007 for the Brazilian portion of the Paraná Basin and Santa Ana et al., 2006 for the Uruguayan portion). Geochronological assignments are based on dates obtained by Santos et al. (2006) for the Irati Formation (278.4 ± 2.2 Ma) and Mori et al. (2012) for the uppermost Rio Bonito Formation (281.4 ± 3.4 Ma), in the Brazilian portion of the Paraná Basin; whereas dates available for the Uruguayan side are derived from Rocha Campos et al. (2006) for the Mangrullo Fm. (275.9 ± 4.8 Ma and 269.8 ± 4.7 Ma).

Since samples from different countries were analyzed by different authors, and, consequently, some biases related to taxonomic identification, total individual palynomorph counts, and species splitting arise when the data are combined. The number of samples per lithostratigraphic unit and borehole as well as the number of specimens counted per sample were uneven, hence only samples with more than 10 specimens were used for analysis. In the present study, the original term for biodiversity, referred to as taxonomic richness, was employed (Whittaker et al., 2001), with lists of genera preferred over species in order to avoid biases potentially associated with the use of species (see below). The range-through approach (Cleal, 2005) was applied to analyze taxonomic diversity, origination and extinction.

All analyses were performed with PAST 2.16 (Hammer et al., 2001) and Tilia 1.7.16 (Grimm, 2004).

RESULTS

Generic richness patterns from the three boreholes are similar. A variably steep increase in diversity can be observed in the lowermost stratigraphic levels of each borehole, followed by a period of relatively constant diversity, and ending with a decrease towards the end of each stratigraphic column (Fig. 2). In borehole 254, a total of 77 genera were found. Diversity started with 19 genera, reaching a maximum of 61 at 241 m and decreasing to 21 genera in the highest sample (Fig. 2). The same trend is observed in borehole HN25, in which a total of 36 genera is recorded. Diversity starts with 11 genera, reaches a maximum of 24 and decreases to only three (Fig. 2). In borehole HN05, a total of 44 genera

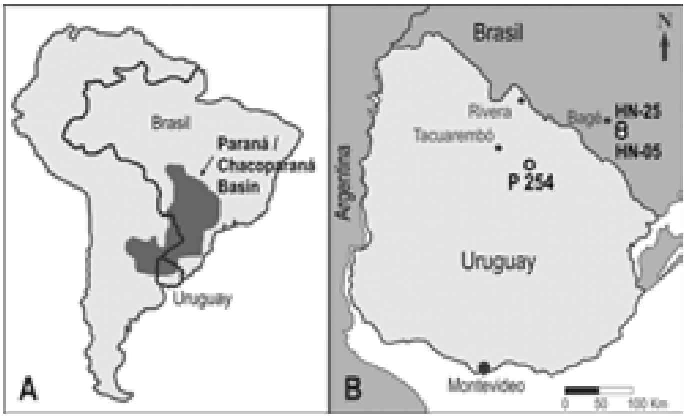

FIGURE 1. **A**, Distribution of the Paraná/Chacoparaná Basin. **B**, Locations of boreholes.

was identified; seven genera are recorded in the first sample; a maximum of 31 genera is reached at 126 m and richness decreases to 5 genera in the last sample (Fig. 2).

As can be seen in the evolution of diversity, extinction and appearance curves shown in Figure 2, similar trends are observed in all boreholes, where three stages can be identified: 1) an increase in diversity (hereafter, DI phase), 2) a diversity stability period (DS phase), and 3) a decrease in diversity (DD phase). In fact, in borehole 254, richness rises in the lower stratigraphic levels (DI phase) due to the appearance of genera that then remain present throughout the two succeeding intervals, up to the end of the column; in these levels hardly any extinction is recorded. The sampled facies correspond to glacial and deltaic environments. In these, sea level rose during the deposition of glacial sediments and dropped during deposition of deltaic systems. A similar pattern is observed in borehole HN05; however, glacial facies are not represented in the sediments. In borehole HN25 an initial increase in diversity is observed but a decrease occurs towards the upper third of the deltaic facies.

In the middle stratigraphic levels, richness is stable (DS phase) but generic appearances and extinctions are present through this phase, particularly at 241 m (borehole 254) and 126.35 m (borehole HN05), corresponding to shallow marine facies in a context of high sea level. In borehole HN25 a more pronounced loss of diversity occurs in the initial levels of this phase. Then, the number of genera stabilizes but some generic turnover is observed.

In the third stage (DD phase) towards the end of each column, a steady diversity decrease is observed in all boreholes due to an increase in extinction rates. This process begins in restricted marine environments and continues in epineritic marine environments, as indicated by the sedimentary facies. In these levels, sea level remains high but with some fluctuations. In borehole HN25 diversity trends show some differences; for example, towards the end of the restricted marine facies in which an increase in origination occurs (Fig. 2).

In general terms, events of generic appearance tend to be higher in the lower and middle levels of each core and relatively rare in the upper stratigraphic levels. Extinction has an opposite trend, showing higher rates in the upper stratigraphic levels. Both processes, generic extinction and appearance, occur in the middle levels.

The processes of extinction and origination did not occur in all sporomorph groups in the same way. Disregarding those genera that are present throughout the entire stratigraphic column, in borehole 254 a steady decrease in diversity of monosaccate pollen grains, apiculate and cingulizonate spores can be observed. During the DS phase, few apiculate and cingulizonate spores genera originate, while during the DD phase monosaccate pollen genera also contribute to the diversity loss.

On the other hand, bisaccate and striate pollen grains characterize palynofloras from the upper strata. Both groups contribute to the DI phase, have a minimum of extinction and account for most of the appearances during the DS phase. They also have a minimal loss during the last DD phase. Despite differences in the total number of genera among the cores, similarities can be noticed. For instance, laevigate, apiculate and cingulizonate spores and, to a lesser extent, monosacate pollen grains suffer the highest extinction in all three cores. The patterns of distribution of bisaccate and striate pollen are also congruent among the cores, since they appear in the DS and do not undergo major extinction afterward.

DISCUSSION

The use of pollen and spores to analyze vegetation dynamics has a number of limitations related to differences in pollen production by, degree of dispersion from, and preservational potential of palynomorphs from different parent plants. The palynological record is not a full replicate of the vegetation of an area due to the reasons mentioned above. An additional problem arises when it comes to inferring paleoecological conditions from Paleozoic palynomorphs. For example, there is a limited record of pollen and spores found in biological connection with macrofossils, which makes it difficult to assign botanical affinities to many palynomorphs. In addition, many distinct morphotypes can be produced by the same plant (Lindström et al., 1997). Even so, palynomorphs can be assigned to plant groups considering the available evidence of organic connection between macrofossils and microfossils (Balme, 1995), and taking into account general ecological requirements of potential parental plants. In fact, several authors consider Paleozoic gymnosperms, producers of bisaccate and striate pollen, as plants with more mesophilic and xerophilic requirements, whereas monilophytes and lycophytes, producers of spores, are regarded as plants with hydrophilic requirements (e.g., Marques-Toigo et al. 1982; Vergel, 1986; Gutiérrez and Limarino, 2001; Gutiérrez et al., 2006).

Moreover, pollen and spore richness, or palynological richness, as coined by Birks and Line (1992), cannot be interpreted directly as floristic richness due to a number of further biases, including differences in pollen representation and preservation, vegetation structure, basin size, and taxonomic accuracy in the identification of pollen and spores. This is true regardless of the absolute number of taxa recognized from each locality.

Even making due allowance to the effects of these biases, it can be observed that some shared general trends in generic richness are present in all the boreholes analyzed in this study. Thus, despite the described noise and such differences as those due to taxonomic identification and counting, the results are encouraging about the validity of this approach.

Several authors have studied the change in palynofloras of the Lower Permian in the Paraná Basin. Iannuzzi and Souza (2005), Iannuzzi et al. (2007) and Beri et al. (2013) pointed out an apparent stasis observed throughout the glacial, fluvio-deltaic, and part of the shallow marine facies, which could correspond to the DI and DS phases. The analysis conducted here, taking into account the changes in diversity, is consistent with the findings of these authors, since the spatial change in the strata under study is relatively gradual. This gradual change has hampered the establishment of biohorizons as a basis for biostratigraphic subdivisions.

However, plant communities represented in the oldest palynofloras are different and more diverse than those represented in the younger strata. In the shallow marine or restricted marine facies related to the DD phase, Beri et al. (2013) described an important change in the composition of palynological assemblages, considering the lithostratigraphic units as the units of analysis. Moreover, Iannuzzi et al. (2007) recognized this same change, but interpreted it as having occurred in a lower lithostratigraphic unit in Brazil (Palermo Formation). This turnover pattern shows that new genera gradually appear, coexisting with the older ones. Then, most genera of the oldest group become extinct and few appearances occur, resulting in a generically-depleted palynoflora.

The evolution of the palynofloras discussed here can be explained

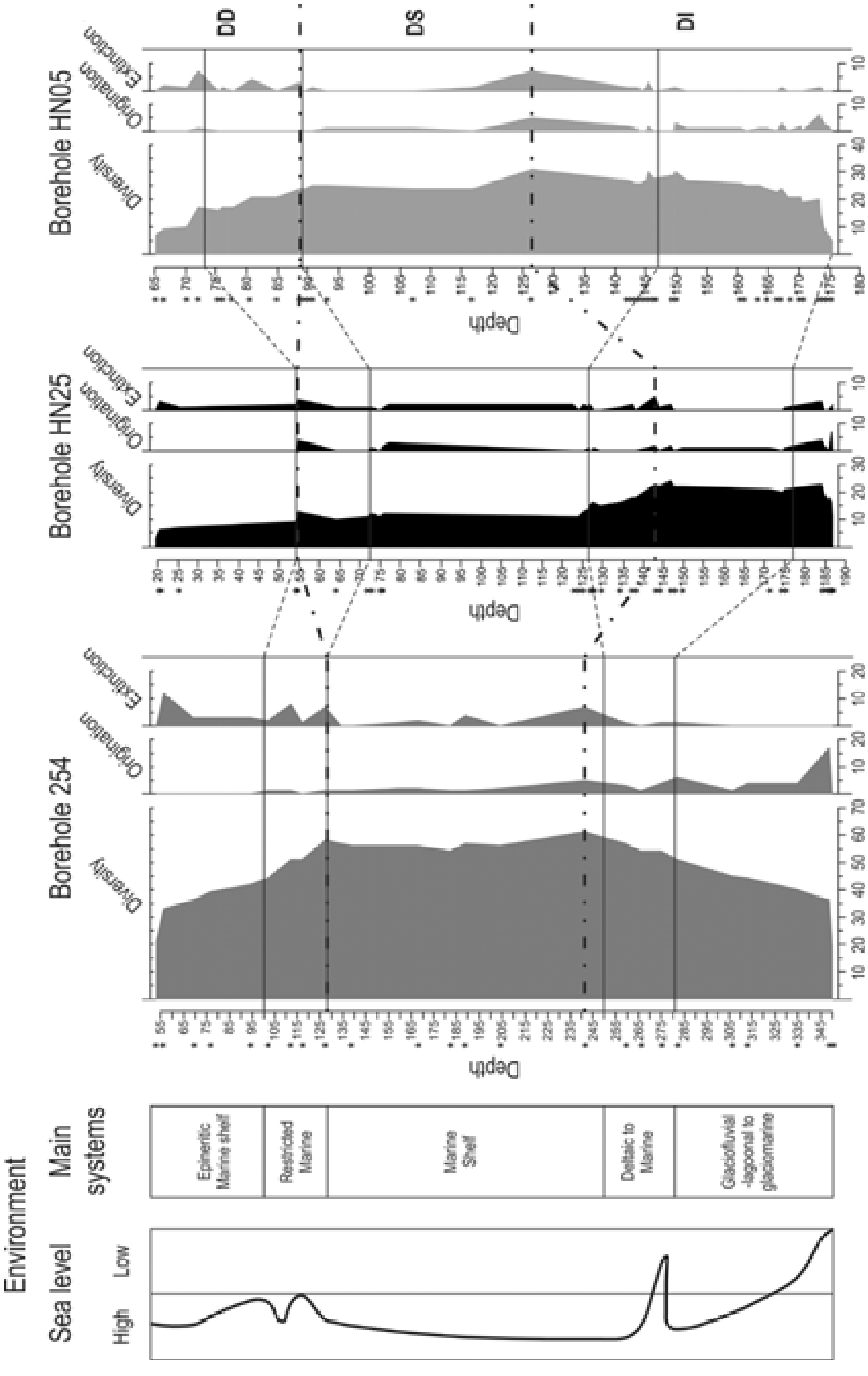

FIGURE 2. Generic diversity, origination and extinction curves for boreholes 254, HN25 and HN05. **Abbreviations: DI**, diversity increase phase; **DS**, diversity stability phase; **DD**, diversity decrease phase.

in light of climatic changes that took place during this period. Among other factors, those changes were due to the location of the continents in southern Pangea (Limarino et al., 1996, Limarino and Spalletti, 2006). Indeed, it is possible to observe a fairly close relationship between diversity and the facies represented in the study interval. In turn, those facies reflect sedimentary conditions heavily influenced by climatic contexts that ranged from glacial to arid conditions, going through a wetter stage (Limarino et al., 1996).

In such a climatic background, the evolution of diversity, its relationship with sedimentary facies and the behavior of different sporomorph groups, can be interpreted in the terms proposed by Guerra-Sommer et al. (2001), based on plant remains. According to those authors, there is a first stage of diversity rise due to climatic amelioration (our DI phase). Later, they identify a gradual turnover where it is possible to observe the first evidence of vegetation more adapted to dry conditions (bisaccate and striate pollen grains). “Exotic” elements may represent the vegetation growing on drier substrates immediately adjacent to the basin, therefore, palynomorph input could come from different types of vegetation (our DS phase). Finally, the extinction of hydrophilic genera represented by spores and monosaccate pollen grains must have taken place.

Most of these genera are not recorded in younger Permian strata of the region; however, it is difficult to assess if this is a global extinction, a local extinction, or a process that removed the taxa from the sample area due to environmental changes. To formulate a more robust hypothesis more data covering a broader geographical area and, especially, more adjusted correlations in and between other Gondwanic basins are needed. As aridization deepened, and taking into account the botanical affinities of the palynological assemblages, it seems that palynomorph input came mainly from the low-diversity vegetation adapted to dry conditions. This made the appearance of new genera rare (our DD phase). Such impoverishment also could be due to a preservation bias, since there is a shift in rock color, suggesting increased oxidization. However, even if palynological content is scarce in these strata, in borehole 254 it was possible to obtain 200 specimens classified to the species level. Moreover, low diversity is to be expected in arid environments (Huenneke and Noble, 1996), or could be due to an input from a low diversity gymnosperm community, similar to that suggested for Early Permian sediments in the Northern Hemisphere (DiMichele et al., 2007).

These features have been observed in other parts of Gondwana based on palynological data (e.g., Stephenson, 2008). In Permian sections in India, Venkatachala et al. (1995) reported patterns that corroborate the main trends recorded in the Paraná Basin, including patterns of appearance, diversification and dissipation (extinction) of the main palynological groups and distinctive morphological characters. In general, these variations reflect climate changes that affect, directly or indirectly, the palynofloral communities.

CONCLUSIONS

Despite the limitations of analysis of Paleozoic palynological diversity, including precautions concerning vegetational interpretations, the preliminary results reported here indicate a shared pattern of palynofloral diversity evolution throughout the Cisuralian in the three boreholes from the southern Paraná Basin; diversity rises in the lower stratigraphic levels, and decreases in the upper strata.

Generic diversity, extinction and appearance trends through time are correlated with different facies, associated with climatic changes occurring in this Gondwana region. It is possible to observe a gradual replacement of different groups of sporomorphs consistent with a possible post-glacial climatic amelioration and the beginning of an arid phase.

Further studies are needed to understand the processes related to palynological diversity and their relationship with vegetation and climate. For this purpose, a better understanding of sporomorph botanical affinities and a greater number of samples and boreholes seems to be essential.

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DIADECTOMORPHS, AMNIOTES OR NOT?

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Abstract—The controversy of whether Diadectomorpha should be considered the sister clade to Amniota (Synapsida + Reptilia) or to Synapsida within the crown-clade Amniota is revisited. In essence, these two hypotheses attempt to answer the question of whether diadectomorphs should be considered amniotes or not. A cladistic analysis is presented to determine not only the intrarelationships of the Diadectomorpha, but also the interrelationships of Diadectomorpha, Synapsida, and Reptilia, collectively Cotylosauria. The analysis incorporates a combination of previously used characters, whose character states in many instances have been reinterpreted or modified, and new characters based on published anatomical data. With the exception of the exclusion of the Lower Permian *Ambedus pusillus* Kissel and Reisz, 2004, judged a member of Diadectidae by its authors, the analysis of Diadectomorpha yields a monophyletic clade unchanged in content and intrarelationships from those purposed previously, with *Diadectes* and *Diasparactus* forming a terminal dichotomy and *Desmatodon*, *Orobates*, *Tseajaia*, and *Limnoscelis* being related as progressively more distant sister taxa. It is argued that a diadectid assignment of *A. pusillus*, consisting solely of isolated maxillaries and dentaries possessing molar-like cheek teeth resembling in morphology and wear patterns those in diadectids, relies on too insufficient data to support such a relationship. Most importantly, the analysis presented here resolves Diadectomorpha as the sister taxon to Synapsida, which dictates it should be considered a member of the crown-clade Amniota. This is also suggested by a high number of synapomorphies uniting Cotylosauria.

INTRODUCTION

Studies attempting to resolve the phylogenetic relationship of Diadectomorpha to Amniota have produced two opposing hypotheses that bear directly on the question of whether or not diadectomorphs should be considered amniotes. The majority of these studies (Gauthier et al., 1988; Laurin and Reisz, 1995, 1997, 1999; Lee and Spencer, 1997; Reisz, 2007) have indicated that Diadectomorpha is the sister taxon to Amniota, consisting of the sister taxa Synapsida and Reptilia (Sauropsida of some), with the three clades constituting Cotylosauria. In these studies a node-based, crown-clade definition of Amniota is applied, which restricts Amniota to the most recent common ancestor of the sister clades Synapsida and Reptilia and their descendants. Lee and Spencer (1997) have argued, however, that even if Diadectomorpha lies outside the crown-clade definition of Amniota, it may have possessed the amniote egg. Although their cladistic analysis of amniotes and their nearest amphibian-grade relatives, including diadectomorphs, produced the same pattern of relationships, it recognized an inordinately large number of synapomorphies uniting diadectomorphs and amniotes. This was interpreted by Lee and Spencer (1997) as suggesting that “some radical ecological and/or developmental breakthrough occurred at the base of the node” uniting the cotylosaurs that may have included the acquisition of the amniote egg. Thus, using an apomorphy-based definition of Amniota, diadectomorphs would be included. A less widely accepted phylogeny of the cotylosaurs argues that Diadectomorpha and Synapsida are sister clades, which in turn form the sister clade to Reptilia (Sumida et al., 1992; Berman et al., 1992; Berman, 2000). This topology would dictate the inclusion of Diadectomorpha in Amniota.

As in previous analyses of Cotylosauria, three ingroup families of Diadectomorpha are recognized: Limnoscelidae, Tseajaiidae, and Diadectidae. Although several limnoscelids have been described and named, a recent taxonomic review of the family (Wideman, 2002; Wideman et al., 2005) demonstrates persuasively that only two Late Pennsylvanian taxa are valid, the type species of *Limnoscelis* Williston, 1911, *L. paludis*, from New Mexico and *L. dynatis* Berman and Sumida, 1990, from Colorado. Since the original description by Williston (1911a, b, 1912) of the holotype of *L. paludis* (consisting of a complete, articulated skeleton), there have been several detailed restudies of the skull (Romer, 1946, Fracasso, 1983, 1987; Berman et al., 1992, 2010; Berman, 2000; Reisz, 2007), as well as the description of disarticulated elements of *L. dynatis* (Berman and Sumida, 1990). Numerous, important errors in the description of the cranial anatomy of *L. paludis* by Romer (1946), but most notably by Fracasso (1983, 1987), were corrected by Berman (2000), Berman et al. (2010), and Reisz (2007).

The Lower Permian *Tseajaia campi* Vaughn, 1964, the sole member of Tseajaiidae, was described by Vaughn (1964) and Moss (1972) on the basis of a single, complete, articulated skeleton from Utah, but some aspects of the skull anatomy were updated subsequently on the basis of a second skeleton discovered in Lower Permian of New Mexico (Berman et al., 1992). Seven diadectid genera are currently recognized, but three of these, the Lower Permian genera, *Phanerosaurus* Meyer, 1860, and *Stephanospondylus* Geinitz and Deichmuller, 1882, from Germany and *Ambedus* Kissel and Reisz, 2004, from Ohio, are too incompletely known to be included in a cladistic study of Cotylosauria. Of the remaining four genera, *Diadectes* Cope, 1878, is represented by numerous, well-preserved specimens distributed widely across North America from localities considered either Permo-Pennsylvanian (Berman, 1993; Eberth and Berman, 1993) or Lower Permian (Case, 1911; Olson, 1947; Berman, 1971; Berman et al., 1992; Reisz and Sutherland, 2001), and the Lower Permian of Germany (Berman et al., 1998). The most recently described diadectid, *Orobates pabsti* Berman et al., 2004, is based on well-preserved, partial to complete skeletons from a single locality in the Lower Permian of Germany (Berman et al., 2004). In contrast, specimens of *Desmatodon* Case, 1908, and *Diasparactus* Case, 1911, are represented by rare specimens of fragmentary skulls and disarticulated postcranial elements and are restricted to a very few Upper Pennsylvanian localities that include one each in Pennsylvania, Colorado, New Mexico, and Oklahoma (Case, 1908, 1910; Case and Williston, 1913; Vaughn, 1969, 1972; Fracasso, 1980; Berman and Sumida, 1995; Kissel and Lehman, 2002).

Recent, more detailed anatomical studies and the continued search for additional shared-derived characters among members of the cotylosaurs now allows a revised cladistic exploration of the controversy of whether or not diadectomorphs should be considered amniotes.

ABBREVIATIONS

The following abbreviations are used to refer to institutional repositories of specimens: **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **MNG**, Museum der Natur, Gotha, Germany; **UCMP**, University of California Museum of Paleontology, Berkeley; **YPM**, Yale Peabody Museum, New Haven.

Key to abbreviations used in figures for anatomical structures: **bo**, basioccipital; **ec**, ectopterygoid; **eo**, exoccipital; **f**, frontal; **m**, maxilla; **op**, opisthotic; **p**, parietal; **pal**, palatine; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pp**, postparietal; **prf**, prefrontal; **pt**, pterygoid; **ptf**, posttemporal fenestra; **q**, quadrate; **qj**, quadratojugal; **so**, supraoccipital; **sq**, squamosal; **st**, supratemporal; **t**, tabular; **v**, vomer.

INTRARELATIONSHIPS OF COTYLOSAURIA

Most Recent Analysis

In the most recent cladistic analysis having a direct bearing on the intrarelationships of Cotylosauria by Kissel and Reisz (2004), the primary goal was a phylogenetic analysis of Diadectomorpha. However, the question of the relationship of Diadectomorpha to Amniota (Synapsida+Reptilia) was unavoidable, and their analysis resolved them as sister taxa. The analysis was prompted by the description of a new genus and species of what they believed to be a small diadectid, *Ambedus pusillus*, from the Lower Permian Dunkard Group of Ohio (Kissel and Reisz, 2004). Yet, for several reasons, *A. pusillus* is eliminated from the present analysis. Its assignment to Diadectidae was based solely on several isolated maxillae and dentaries possessing a heterodont dentition with cheek teeth that exhibit a resemblance in their molar-like morphology and wear pattern of the crowns to those in diadectids: crowns transversely expanded; a central cusp flanked by labial and lingual shoulders; and development of wear facets on the lingual and labial shoulders of the crowns. Although Kissel and Reisz (2004) reasonably concluded that these features suggest that *A. pusillus* was probably herbivorous, as are all the diadectids, its assignment as the basalmost member of Diadectidae becomes highly suspect when considering the five plesiomorphic characters listed in their diagnosis as distinguishing it from all other diadectids: 1) shallow rather than deep dentary; 2) relatively high maxillary and mandibular tooth counts; 3) lack of a labial parapet of the dentary; 4) anterior teeth of maxilla and dentary conical, rather than incisiform; and 5) shallow alveolar shelf, indicating a relatively shallow tooth implantation. It is not surprising that these characters would indicate a basalmost position of *A. pusillus* within Diadectidae, but they fail also to differentiate it from the great majority of late Paleozoic taxa quite divergent from the diadectid clade. Therefore, their diadectid assignment of *A. pusillus* relies solely on a resemblance of its cheek teeth with those in diadectids. This becomes evident also with a reassessment of those characters and their states applicable to *A. pusillus* in the cladistic analysis by Kissel and Reisz (2004) of the interrelationships of the diadectomorphs (below). The late occurrence of *A. pusillus* near the end of the diadectid fossil record in an upper level of the Lower Permian also casts doubt also on the assertion that it represents the basalmost member of the diadectid clade. In contrast, the earliest known diadectids, which occur in the Upper Pennsylvanian (*Desmatodon* and *Diasparactus*), not only exhibit the entire suite of unique diadectid maxillary and dentary dental characters, but they are also far more developed than in *A. pusillus*. This demands the acceptance of an extremely long ghost lineage for *A. pusillus*, perhaps extending back to the Middle Pennsylvanian.

Also calling into question the diadectid assignment of *Ambedus pusillus* by Kissel and Reisz (2004), is that it could be coded for only seven of the 37 characters in their cladistic analysis of Diadectomorpha. With one exception, by their analysis, only *A. pusillus* among the diadectomorphs was coded for the primitive state in three of the seven characters, 20, 22, and 28, and therefore are uninformative: 1) lower jaw shallow rather than deep; 2) labial parapet absent; and 3) anterior teeth of maxilla and dentary conical rather than incisiform, respectively. The one exception was the coding of *Orobates* as exhibiting the primitive state of character 20, possession of a shallow lower jaw. Yet, in the description of *Orobates* by Berman et al. (2004) illustrations of excellently preserved skulls show clearly that it has a deep mandible, although certainly not quite as deep as in the more derived diadectids. Therefore, among the diadectids only *A. pusillus* exhibits the primitive state for this character. Because the derived states of these three characters are otherwise synapomorphies of all diadectids, they are retained here, although modified, as characters 17, 18, and 19 in the character list presented below for analysis of Cotylosauria.

As for the other four characters that Kissel and Reisz (2004) coded *Ambedus pusillus* for, 26, 27, 30, and 31, they assigned derived states. However, on closer scrutiny the states of these characters are considered, in great part, as being poorly or insufficiently defined, incorrectly coded, or not recognizing the use of closely related states of different characters as a form of redundancy. Thus, the characters can be redefined on the basis of being more inclusive in their assigned states and, therefore, presented more accurately and concisely. Regarding the states of character 26 (character 20 here), which compares root length to crown height, Kissel and Reisz (2004) scored *A. pusillus*, as well as *Limnoscelis* and *Tseajaia*, as exhibiting the derived state 1 of deep marginal roots, but with a root length less than the crown height. This was contrasted to a derived state 2 exhibited by diadectids in which root length exceeds crown height. However, the derived state 1 coded for *A. pusillus* cannot be distinguished from the primitive state 0 of the outgroups Lepospondyli and Amniota, which describes implantation as simply "not deep." This is made obvious by their illustrations of a maxilla and dentary of *A. pusillus* in medial views (their figs. 1 and 4, respectively), which clearly show the alveolar shelves as being extremely shallow and indicative of maximum root lengths that are obviously less, often far less, than 50% of the crown height. Therefore, the depth of the implantation of the marginal teeth in *A. pusillus* exhibits clearly the primitive state 0 compared to the more derived state of the diadectomorphs and, therefore, should have been coded as such. It can be noted also that in none of the illustrated specimens of *A. pusillus* is a root exposed and can be measured directly.

Characters 27, 30, and 31 of Kissel and Reisz (2004) describe closely related, derived states of the molarization of the midseries cheek teeth shared by all diadectids and, therefore, are judged in great part as redundant: character 27, heterodont dentition, was coded as either absent, state 0, or present, state 1, to indicate the possession of transversely expanded crowns; character 30, degree of molarization, was coded as either absent, state 0, low, state 1, or high, state 2, to indicate a ratio of anteroposterior length to mediolateral width and dorsoventral height to mediolateral width as both being less than 0.50; and character 31, presence of labial and lingual cusps or shoulders of the crowns, was coded as absent, state 0, weakly developed, state 1, or well developed, state 2. Character 27, heterodont dentition, is retained here but is incorporated into character 19 presented here, so that the derived state definition includes also the presence of anterior incisiform teeth of the maxilla and dentary, rather than just the presence of transversely expanded cheek teeth. Therefore, in the present analysis *A. pusillis* is scored as exhibiting the primitive state 0 for character 19. Characters 30 and 31 and their states are combined in character 22 presented here, as degree of molarization, with *A. pusillus* exhibiting the derived state 1, a low degree of molarization.

With these revisions the seven of thirty-seven characters used in the analysis by Kissel and Reisz (2004) to resolve the phylogenetic position of *A. pusillus* within Diadectomorpha is reduced to five. Therefore, if *A. pusillus* was included in the analysis presented here, it would be coded for the primitive state 0 in characters 17, 18, 19, and 20, and the derived state1 for only character 22. The identification of only one synapomorphy uniting *A. pusillus* with diadectids is judged too insufficient data to realistically consider it a diadectid and include in an analysis of the intrarelationships of Diadectomorpha. One additional change is made to the characters of Kissel and Reisz (2004), the codings of states 0 and 1 of their characters 25, 34, and 37, characters 19, 30, and 31 presented here, are reversed. This follows the analyses of Berman (2000) and Lee and Spencer (1997), who reject lepospondyls among the nearest amphibian-grade amphibians as the sister group of Cotylosauria.

Finally, in the cladistic analysis by Kissel and Reisz (2004), character states are not determined separately for Synapsida and Reptilia, but rather for their combined taxon Amniota. This presumes that the relationship of Diadectomorpha as the sister taxon of Amniota (Synapsida+Reptilia) is unchallengeable. Unfortunately, this ignores the potential of recognizing shared-derived characters linking Diadectomorpha with either Synapsida or Reptilia. Thus, a cladistic test of whether Diadectomorpha is the sister taxon to either Synapsida or Reptilia was avoided.

Present Analysis

In the cladistic analysis of Diadectomorpha by Kissel and Reisz (2004), Amniota (Synapsida+Reptilia) and Lepospondyli were selected as outgroups, and Lepospondyli was resolved as the sister clade to Cotylosauria. In the present analysis lepospondyls are rejected as a nearest sister clade to Cotylosauria. This follows the cladistic analysis by Berman (2000), which focused on the origin and early evolution of the occiput and adjoining dermal elements of the skull roof of several amphibian-grade taxa and cotylosaurs. It was argued that the occipital region is well known for nearly all major groups of Paleozoic tetrapods, including lepospondyls, but most importantly is highly stable to evolutionary change, and the few distinctive patterns of variation were therefore considered highly reliable in resolving phylogenetic relationships within higher level taxa. This analysis included Lepospondyli, Temnospondyli, Seymouriamorpha, Baphetidae, and Anthracosauria (including *Eoherpeton* Panchen, 1975, and Embolomeri), and cotylosaurs, which resolved Anthracosauria, Baphetidae, and the unresolved trichotomy of Lepospondyli, Temnospondyli, and Seymouriamorpha as progressively more distant clades to Cotylosauria. This agrees also with the analysis by Lee and Spencer (1997), who also excluded Lepospondyli from the nearest amphibian-grade outgroups of Cotylosauria.

The sources of the characters and the descriptions of their states used in the present analysis of the interrelationships of the Cotylosauria can be credited in great part to a relatively few analyses using either formal cladistic programs or cladistic methodology, but in some instances with modifications. In addition, new characters and their states have been incorporated into the present analysis. Anthracosauria is selected as the primitive outgroup for determining character polarity, which follows Lee and Spencer (1997), in part, and Berman (2000). When possible the eothyridid caseasaurs *Eothyris* and *Oedaleops*, known almost solely by their skulls, are used to score the character states in Synapsida. This is in accordance with the recent cladistic analysis of Reisz et al. (2009), which recognized the eothyridids as the most primitive genera among the basal synapsids and as the best available representatives of the primitive skull morphotype of synapsids. In all, 40 skull and postcranial characters were identified to resolve the relationship of Diadectomorpha to the amniote clades Synapsida and Reptilia, as well as to test the monophyly and generic intrarelationships of Diadectomorpha of previous publications.

Characters and Their States Used in the Present Analysis

The characters discussed below are assigned consecutive Arabic numbers, whereas their states are indicated by parenthetically enclosed Arabic numbers. This allows direct reference to Table 1, where their taxon distribution is designated in a character-taxon matrix.

Character 1. Sutural relationship of postorbital, supratemporal, intertemporal, parietal, and squamosal (Fig. 1).—The intertemporal is present and the parietal is widely separated from contact with the squamosal by an intertemporal-supratemporal contact (0); intertemporal is incorporated into the parietal as a lateral lappet, and the postorbital is of normal size or in some cases elongated posteriorly and does not contact the supratemporal, allowing a substantial parietal-squamosal contact (1); postorbital elongated and contacts the supratemporal to exclude parietal lappet of parietal from contacting the squamosal (2).

This character and its states were originally described with minor differences in the cladistic analysis by Berman et al. (1992, character 3). Subsequently, a shortened version of this character was incorporated into the cladistic analysis by Kissel and Reisz (2004, character 2), and the character states were defined simply as the presence or absence of a lateral parietal lappet.

Character 2. Lateral, orbital process of frontal (Fig. 1).—Contribution of a lateral, orbital process of the frontal to the dorsal orbital margin is absent or extremely narrow (0); broad and forms most of the dorsal margin of the orbit (1).

This character and its states are incorporated from the cladistic analyses by Lee and Spencer (1997, character 4), Kissel and Reisz (2004, character 1), and Laurin and Reisz (1997, character 8). However, in contrast to these analyses, in the present analysis Synapsida is coded as exhibiting the primitive rather than the derived state, which follows the cladistic analysis of the relationships of eothyridids by Reisz et al. (2009, character 29).

Character 3. Postparietal (Figs. 1, 3).—Paired (0); single (1).

This character and its states are incorporated from the cladistic analyses by Laurin and Reisz (1997, character 22) and Kissel and Reisz (2004, character 4). The primitive state (1) coding for synapsids is based on the cladistic analysis of the eothyridids by Reisz et al. (2009).

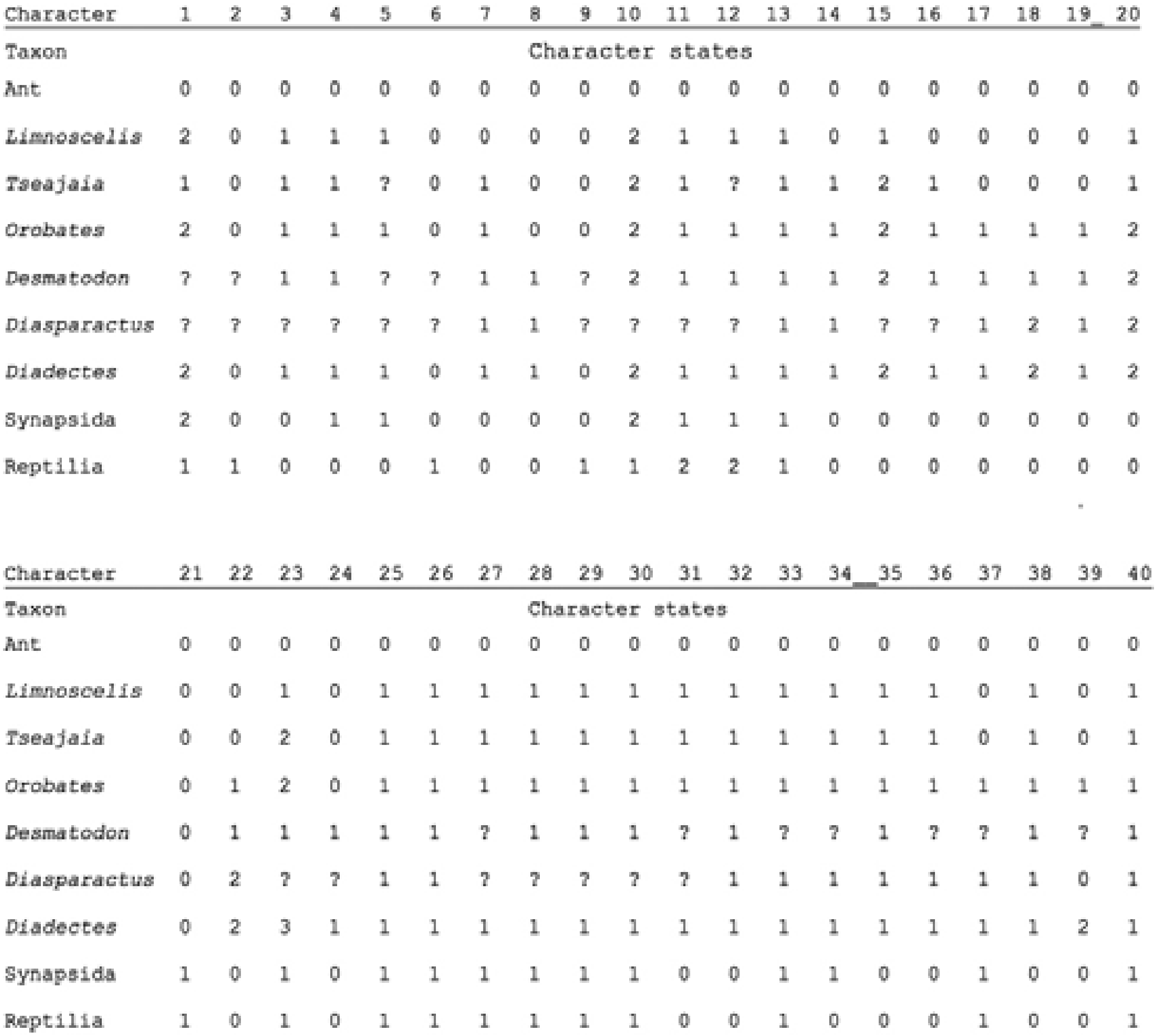
Character. 4 Parietal foramen diameter (Fig. 1).—Less than 22% of the anteroposterior length of the parietal midline suture (0); greater than 22% (1).

This character and its states are incorporated from the cladistic analysis by Kissel and Reisz (2004, character 3). However, the percentages have been modified to emphasize the actual, wider separation between the two states.

Character 5. Structure and position of septomaxillae.—Septomaxilla narrow, crescent-shaped element bordering the posterior margin of the external naris with the external surface being confluent with that of the skull roof (0); lies deep within the external naris and has in general an hourglass outline with large, flared ventral and dorsal ends that are separated by a short, narrow, thickened, pillar-like strut. Ventrally the septomaxilla contacts mainly the premaxilla and very narrowly the maxilla and lacrimal along the ventral and posterior margins of the naris, respectively, whereas dorsally it is narrowly separated from contacting the nasal bordering the dorsal margin of the naris. The pillar-like strut is pierced anteroposteriorly by a septomaxillary canal and a septomaxillary foramen is bordered anteriorly and posteriorly by the septomaxilla and lacrimal, respectively (1).

Romer and Price (1940) and Wible et al. (1990) have described in detail the septomaxilla in synapsids, which is the basis of the derived state. The common possession of the derived state by diadectomorphs, although the septomaxillae is unknown in *Tseajaia*, and Synapsida, was first noted by Berman et al. (1998, 2010). In the cladistic analysis by Reisz et al. (2009) two separate characters and states were described based on the shape and position of the septomaxilla that presents a confusing combinations of the states noted here: in one of the characters (10) the primitive state describes the septomaxilla as being “curled in external naris,” with two derived states described as a “pillar in external naris” and as “on surface.” The second character (11), incorporated from the analysis by Reisz and Dilkes (2003, character 42), describes the primitive state as a “lateral, sheet-like exposure absent” and the derived state as it being “present.” Lee and Spencer (1997, character 3) simply described the primitive state of the septomaxillae as exposed on the skull roof immediately behind the external naris and the derived state as lying entirely within the external naris.

TABLE 1. Characters-taxon matrix used for phylogenetic analysis. Description of characters and their states among the taxa discussed in text. **Ant**, outgroup Anthracosauria.



Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Taxon								Character states												
Ant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnoscelis	2	0	1	1	1	0	0	0	0	2	1	1	1	0	1	0	0	0	0	1
Tseajaia	1	0	1	1	?	0	1	0	0	2	1	?	1	1	2	1	0	0	0	1
Orobates	2	0	1	1	1	0	1	0	0	2	1	1	1	1	2	1	1	1	1	2
Desmatodon	?	?	1	1	?	?	1	1	?	2	1	1	1	1	2	1	1	1	1	2
Diasparactus	?	?	?	?	?	?	1	1	?	?	?	?	1	1	?	?	1	2	1	2
Diadectes	2	0	1	1	1	0	1	1	0	2	1	1	1	1	2	1	1	2	1	2
Synapsida	2	0	0	1	1	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0
Reptilia	1	1	0	0	0	1	0	0	1	1	2	2	1	0	0	0	0	0	0	0

Character	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Taxon								Character states												
Ant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnoscelis	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1
Tseajaia	0	0	2	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1
Orobates	0	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Desmatodon	0	1	1	1	1	1	?	1	1	1	?	1	?	?	1	?	?	1	?	1
Diasparactus	0	2	?	?	1	1	?	?	?	?	?	1	1	1	1	1	1	1	0	1
Diadectes	0	2	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1
Synapsida	1	0	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	0	0	1
Reptilia	1	0	1	0	1	1	1	1	1	1	0	0	1	0	0	0	1	0	0	1

Character 6. Temporal notch.—Small and located at the dorsal, posterior margin of the cheek, where it is bordered dorsally by posterior processes of tabular and supratemporal, although the former element may be greatly reduced, and anteriorly by a posteroventrally sloping squamosal (0); absent (1).

In the cladistic analyses of the Cotylosauria by Berman et al. (1992, character 6) and in a discussion by Berman et al. (2004) the structural features of a temporal notch and otic or temporal embayment (character 7 below) of the cheek were combined as a single character, rather than two separate characters as considered here. The descriptions of *Eothyris* and *Oedaleops* by Reisz et al. (2009) are the basis here of the primitive-state coding of this character in synapsids.

Character 7. Temporal embayment.—Absent (0); shallow and occupies entire posterior margin of cheek (1).

This character and its states with one change in the coding of *Limnoscelis* are incorporated from the cladistic analysis by Kissel and Reisz (2004, character 8). The detailed description of the cranial anatomy of *Limnoscelis* by Berman et al. (2010) indicates strongly its possession of the derived rather than the primitive state.

Character 8. Secondary palatal shelf formed by palatine and ectopterygoid.—Absent (0); present (1).

The derived state of this character was first described in *Diadectes* by Olson (1947) and subsequently noted in *Diadectes* (Berman and Sumida, 1995; Berman et al., 1998) and *Desmatodon* (Berman and Sumida, 1995), whereas its absence in *Orobates* was noted by Berman et al. (2004). This character and its states were incorporated into the cladistic analysis by Kissel and Reisz (2004, character 12).

Character 9. Sutural relationship between vomer and pterygoid (Fig. 2).—Narrow, ventrally thickened, ridge-like, palatal processes of the vomers are united along the midline to form essentially the entire length of the medial borders of the internal nares. The joined anterior ends of the palatal rami of the pterygoids may extend between the pos-

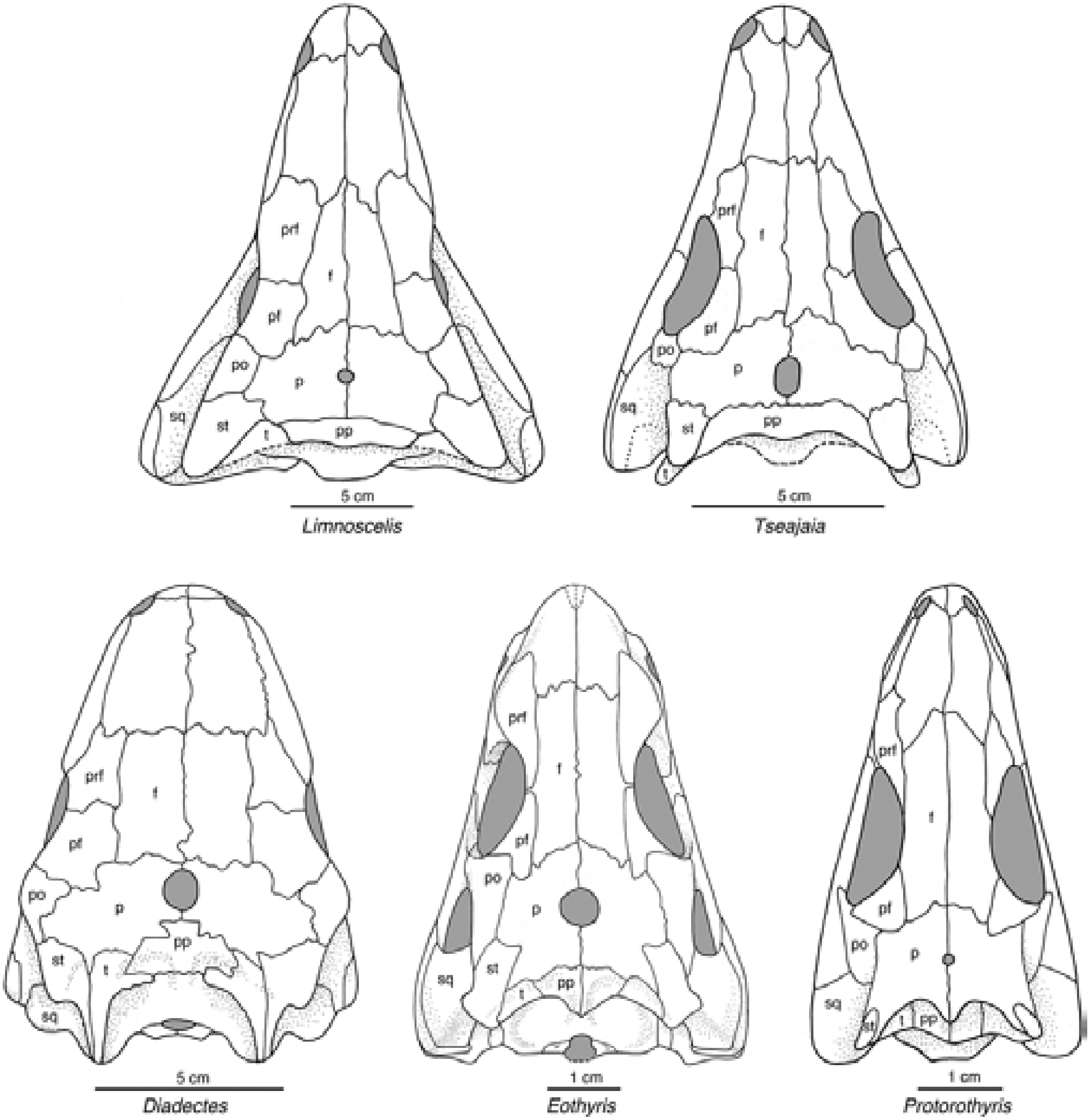


FIGURE 1. Skulls in dorsal view of selected cotylosaurs. *Limnoscelis* (Diadectomorpha) based on holotype of *L. paludis* YPM 811 (after Berman et al., 2010); *Tseajaia* (Diadectomorpha) based on holotype of *T. campi* UCMP 59012 and CM 38033 (after Berman et al., 1992); *Diadectes* (Diadectomorpha) based on *Diadectes* sp. CM 25741 (Berman et al.,1992) and holotype MNG 8853 and paratype MNG 8747 of *D. absitus* (Berman et al., 1998); *Eothyris* (Synapsida) based on holotype of *E. parkeyi* MCZ 1161 (after Reisz et al., 2009); and *Protorothyris* (Reptilia) based on holotype of *P. archeri* MCZ 1532 (after Clark and Carroll, 1973).

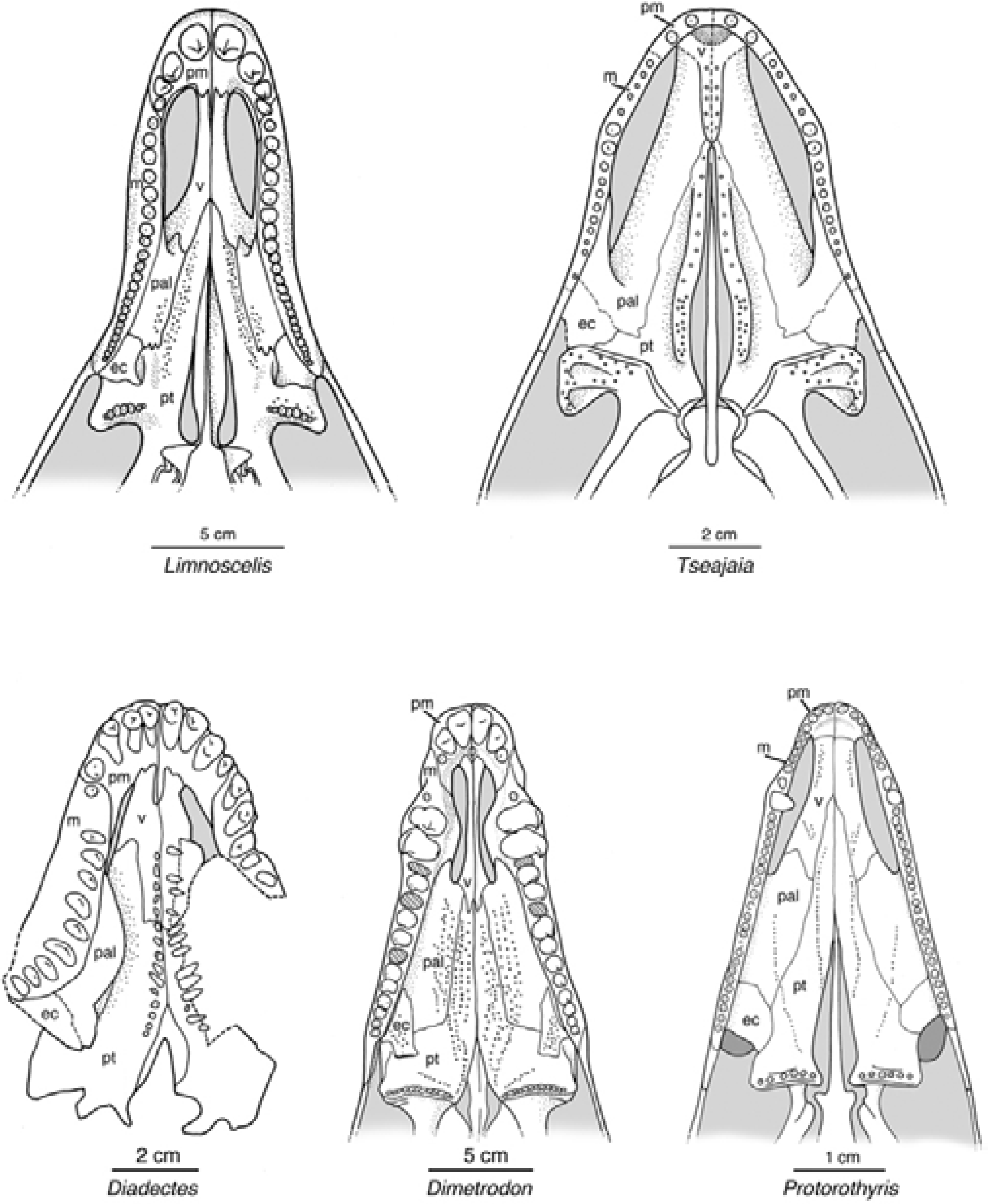


FIGURE 2. Anterior palatal region of selected cotylosaurs. *Limnoscelis* (Diadectomorpha) (source as in Fig. 1); *Tseajaia* (Diadectomorpha) based on holotype of *T. campi* UCMP 59012 (after Moss, 1972); *Diadectes* (Diadectomorpha) based on paratype of *D. absitus* MNG 8747 (after Berman et al., 1998); *Dimetrodon limbatus* (Synapsida) (after Romer and Price, 1940); and *Protorothyris* (Reptilia) (source as in Fig. 1).

terior ends of the palatal processes of the vomers for a very short distance (0); horizontally oriented, strap-like palatal processes of the vomers border the entire length of the medial margin of the internal nares, but are united anteriorly along the midline for only approximately the anterior third or less of their length, whereas posteriorly they are separated by the united, anterior ends of the pterygoids and angled laterally from the midline (1).

In Moss' (1972) description of the palate in the holotype of *Tseajaia campi* he was unable to locate the palatine-vomer contact, as indicated by the dashed sutures shown in his reconstruction (Fig. 2). As a result, his reconstruction (fig. 16, p. 51) portrays falsely the palatine as extending from its contact with the ectopterygoid a short distance posterior to the internal naris and forming the entire length of the medial border of the internal naris. A more likely interpretation is that the palatine-vomer contact lies just anterior to the level of the posterior margin of the naris. Thus, the vomers would have formed nearly the entire, if not the entire, length of the medial border of the naris. In addition, Moss' reconstruction almost certainly misinterprets the pterygoids as extending far anteriorly between the vomers to a level a short distance beyond the midlength of the internal nares. This is contradicted, however, by his photograph of the skull in ventral view (pl. 4, p. 69). The photograph reveals a small sutural separation between the united anterior ends of the pterygoids a short distance anterior to their closure of the interpterygoid vacuity and the united, posterior ends of the vomers at about the level of, or slightly anterior to, the anterior margins of the ectopterygoids. On this basis then, the midline contact between the pterygoids and vomers occurs at about the level of the posterior margin of the internal nares. Assuming these corrections are correct, then the sutural relationship between the vomer and pterygoid in *Tseajaia* should be coded for the primitive state of this character.

In *Diadectes* (Berman et al., 1998) the palatal rami of the pterygoids are unique in extending far anteriorly, but laterally adjacent to the greater posterior length of the midline union of the palatal processes of the vomer. Anteriorly the pterygoids end, contacting the posterior margin of a small, laterally projecting, wing-like process of the vomer. Here they also form a portion of the medial border of the internal nares, preventing a vomer-palatine contact. The midline sutural relationship of vomer and pterygoid, however, can still be coded as expressing the primitive state of this character. It is not known whether a similar structural pattern occurs also in other diadectids.

Protorothyris, *Romeria*, and *Brouffia* are rare examples among the basal captorhinomorphs in which the palates are well enough preserved to be confidently reconstructed (Carroll and Baird, 1972; Clark and Carroll, 1973) and are the basis of the definition of the derived state here. It should be noted, however, that the reconstructions of the palates of the basal captorhinids *Cephalerpeton* and *Paleothyris* by Carroll and Baird (1972) and Carroll (1969), respectively, were based on disarticulated, poorly preserved vomers and pterygoids and were reconstructed as depicting the primitive state. The reconstruction of their palates, however, could have been just as easily interpreted to depict the derived state. This character is described here for the first time.

Character 10. Occiput of skull (Fig. 3).—Opisthotic and supraoccipital not co-ossified into a single, massive, broad, vertical occipital plate, and the exoccipitals unite the occiput directly with the skull roof (0); opisthotic weakly ossified and not co-ossified with supraoccipital as a single element, and the supraoccipital unites the occiput directly with the skull roof (1); opisthotic and supraoccipital strongly co-ossified into a single, massive, broad, vertical occipital plate with the supraoccipital united directly with the skull roof (2).

The states of this character among late Paleozoic tetrapods were described in a cladistic analysis by Berman (2000, character 1).

Character 11. Occipital flanges of the tabular and supratemporal (Fig. 3).—A non-sculptured, ventromedially directed occipital flange of the tabular encloses the lateral half of the posttemporal fenestra, and the supratemporal lacks an occipital flange and is restricted to the skull table and well separated from the occipital margin of the skull roof (0). Two derived states are recognized: tabular and supratemporal are positioned along the occipital margin of the skull table and possess occipital flanges that are greatly elongated ventrally as narrow processes in contact with one another marginally and with the tabular contacting the lateral margin of the occiput to a level below the posttemporal fenestra. Thus, the tabular flange encloses laterally a small posttemporal fenestra, which is bordered ventrally by the paroccipital process of the opisthotic (1); tabular and supratemporal restricted essentially to the occipital margin of the skull table and lack prominent, non-sculptured occipital flanges. As a result, the tabular contact with the supraoccipital is either greatly restricted to its dorsolateral corner or absent, and the posttemporal fenestra is open widely laterally (2).

The states of this character among the cotylosaurs were described and included in a cladistic analysis by Berman (2000). However, his coding of the derived state 2 of character 5 (state 1 here), describing in the holotype of *Limnoscelis paludis* a contact between the distal end of the occipital flange of the tabular and the distal end of the paroccipital process, was strongly questioned by Kissel and Reisz (2004) and Reisz (2007), who insisted that there is no direct evidence of such a contact. They failed to take into consideration, however, several obvious features of attrition of these structures, which would easily account for their very narrow separation, as noted by Berman et al. (2010). The occipital flanges of the tabular and supratemporal, which are well represented only on the left side of the occiput in the holotype, differ from those in diadectids and synapsids in being shorter, wider, and having the form of flat, blade-like structures. However, their ventral extensions are similar in being joined marginally and distally curving medially to within only about 3 mm of the distal end of the paroccipital process. Berman et al. (2010), however, presented three lines of reliable evidence to suggest that one or both of the occipital flanges of the tabular and supratemporal contacted the distal end of the paroccipital process, as indicated in Romer's (1946) and Berman's (2000) description and reconstruction of the *Limnoscelis* occiput (their fig. 8, p. 154, fig. 1, p. 940, respectively): 1) the distal ends of the occipital flanges are obviously incomplete distally. Weathering and/or aggressive preparation by previous researchers (i.e. Fracasso, 1983, 1987) likely account, at least in part, for the gap separating one or both flanges from the distal end of the paroccipital process; 2) the left paroccipital process of the opisthotic, as seen in the photographs and illustrations of the skull in occipital view by Berman (2000) and Berman et al. (2010), is obviously also incomplete distally, as it is noticeably shorter than the right process; and 3) the very narrow separation between the occipital flanges and the distal end of the paroccipital process could be accounted for easily by the dorsoventral crushing of the skull, which has resulted in the cheeks being splayed ventrolaterally from their original, more vertical orientation. The alterations of these structures were either overlooked or ignored in the discussions by Kissel and Reisz (2004) and Reisz (2007).

Only in the holotype of *Tseajaia* is the occiput preserved well enough to adequately describe its major features (Moss, 1972, figs. 3-4). Whereas most indicate a state (1) coding, there are some minor differences. The supraoccipital and opisthotic form a single, large, thick, vertically oriented, complex that is sutured directly with the occipital margins of the postparietals and tabulars of skull roof. In addition, the tabular and supratemporal possess marginally joined, ventral, process-like occipital extensions with the tabular contacting the lateral margin of the occiput. However, they extend only to within a short distance of the dorsal margin of the posttemporal fenestra, which is represented by a shallow, concave notch on the ventral, lateral margin of the occiput. As a result, the posttemporal fenestra is open widely laterally, but is bordered ventrally by the paroccipital process of the opisthotic.

Character 12. Location of the posttemporal fenestra and its bordering elements (Fig. 3).—Posttemporal fenestra located near the dorsolateral corner of the occiput. Its lateral half is enclosed by a ventromedially directed occipital flange of the tabular, the medial half of its

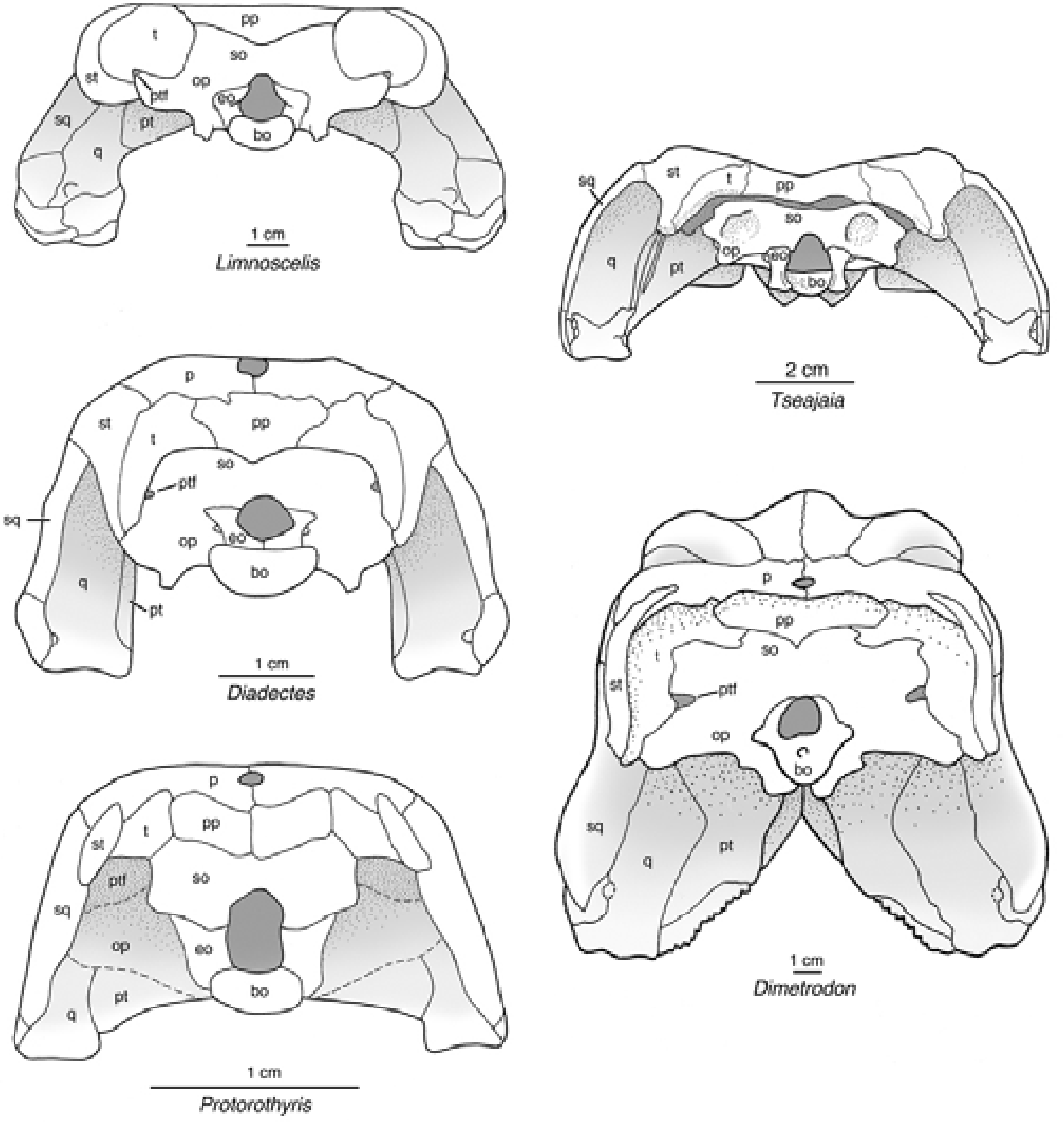


FIGURE 3. Skulls in occipital view of selected cotylosaurs. *Limnoscelis* (Diadectomorpha) based on holotype of *L. paludis* YPM 811 (after Berman, 2000); *Tseajaia* (Diadectomorpha) (source as in Fig. 2); *Diadectes* (Diadectomorpha) based on holotype of *D. absitus* MNG 8853 (after Berman, 2000); *Dimetrodon limbatus* (Synapsida) (source as in Fig. 2), and *Protorothyris* (Reptilia) (source as in Fig. 1).

dorsal border by a short, ventrally directed occipital flange of the postparietal, and its ventral border by a dorsolaterally directed paroccipital process of the opisthotic (0). Two derived states are recognized: the posttemporal fenestra is located at the ventrolateral corner of the occiput and is bordered dorsally by a prominent lateral extension or process of the supraoccipital, laterally by marginally united, ventrally elongated processes of the occipital flanges of a lateral supratemporal and medial tabular, and ventrally by the laterally directed paroccipital process of the opisthotic (1); absence of the occipital flanges of the supratemporal and tabular resulting in a posttemporal fenestra that is greatly enlarged laterally and both elements separated widely from distal end of the ventrally displaced, laterally directed paroccipital process of the opisthotic that borders the fenestra ventrally (2).

This character and its states among the colylosaurs were described in the cladistic analysis by Berman (2000, character 3).

Character 13. Lateral line grooves on skull roof.—Present (0); absent (1).

This character and its states are incorporated from the cladistic analysis by Lee and Spencer (1997).

Character 14. Position of the jaw articulation.—At approximately the same level as the dental occlusal plane (0); below level of dental occlusal plane (1).

This character and its states are incorporated from the cladistic analysis by Kissel and Reisz (2004, character 19).

Character 15. Medial or infra-Meckelian fenestra of mandible.—Absent (0); narrow and elongate (1); tall and elongate, with the ratio of the greatest dorsoventral height to the anteroposterior length is 25% or greater (2).

This character and its states are incorporated from the cladistic analysis by Kissel and Reisz (2004, character 21).

Character 16. Palatal dentition along medial margins of vomer and pterygoid (Fig. 2).—Absent (0); present (1).

Although the vomer is unknown in *Desmatodon,* it is assumed to have also possessed a single, medial row of large teeth, since the pterygoid possesses this feature (Berman and Sumida, 1995). On this basis, *Desmatodon* is scored as exhibiting the derived state. This character and its states were first described in the cladistic analysis by Kissel and Reisz (2004, character 14). However, Moss (1972, fig. 16) was the first to recognize the common possession of the derived state in *Tseajaia* and *Diadectes.*

Character 17. Deep lower jaw.—Absent (0); present, where the ratio of the dorsoventral height of the mandible at the level of the coronoid eminence to the anteroposterior length of the jaw is 30% or greater (1).

This character and its states are incorporated from the cladistic analysis by Kissel and Reisz (2004, character 20). However, they described *Orobates* as having a shallow lower jaw among diadectids and therefore exhibiting the primitive state (0). This ignores the fact that the mandible of *Orobates* is deep (Berman et al., 2004), although not quite as deep as those in the more derived diadectids. Berman et al. (2004) clearly demonstrated the depth of the mandible in *Orobates* increases relative to its length with growth, reaching a maximum of 31% in the specimens they had at hand. By reducing the threshold value applied originally by Kissel and Reisz (2004) from of 33 to 31% to separate the two states, *Orobates* now falls within the range of the derived state they attributed to all diadectids and, thus, is recoded here accordingly. Berman et al. (2004) also demonstrated a similar ontogenetic proportional change in mandibles of North American species of *Diadectes*, with values ranging from about 35 to 51%.

Character 18. Labial parapet.—Absent (0); low, where the parapet never projects higher than the bases of the cheek teeth (1); tall, where the parapet is as tall or taller than the occlusal surface of the teeth near the posterior end of the tooth row (2).

This character and its states are incorporated from the cladistic analysis by Kissel and Reisz (2004, character 22), as well as recognized subsequently by Reisz (2007).

Character 19. Heterodont dentition characterized by the presence of incisiform anterior teeth and transversely expanded molar-like cheek teeth.—Absent (0); present (1).

This character and its states are incorporated from the cladistic analysis by Kissel and Reisz (2004), but here combines their characters 27 and 28.

Character 20. Implantation of the tooth roots of the marginal teeth.—Not deep (0); deep with the root length less than crown height (1); and root length greater than crown height (2).

This character and its states are incorporated from the cladistic analysis by Kissel and Reisz (2004, character 26), which was recognized subsequently also by Reisz (2007).

Character 21. Infolding of dentine.—Present (0); absent (1)

This character and its states are incorporated from the cladistic analysis by Kissel and Reisz (2004, character 25), which was recognized subsequently also by Reisz (2007), but the coding has been reversed based on the outgroup used here.

Character 22. Degree of molarization of the largest preserved midseries cheek teeth.—Absence of molarization (0); low degree of molarization in the development of labial and lingual cusps or shoulders and transverse expansion of crowns (1); high degree of molarization in which labial and lingual cusps or shoulders are well developed and the ratio of the anteroposterior length to mediolateral width and dorsoventral height to mediolateral width of the midseries cheek teeth are both less than 0.50 (2).

The states of this character among diadectids were described by Berman and Sumida (1995) and Berman et al. (1998, 2004) and subsequently incorporated into the cladistic analysis of Kissel and Reisz (2004, character 30).

Character 23. Presence of teeth on transverse flange of pterygoid (Fig. 2).—Transverse flange absent and pterygoid covered by shagreen of teeth; (0); transverse flange with large teeth aligned along the posterior margin (1); presence of small teeth not aligned along posterior margin of flange (2); flange lacks teeth (3).

The states of this character are an expanded version of those given in the cladistic analysis by Kissel and Reisz (2004, character 16), which merely noted the absence (0) or presence of well-developed teeth on the posterior margin of the transverse flange of the pterygoid (1).

Character 24. Extent of ossification of Meckelian cartilage of the lower jaw.—Short (0); extraordinarily elongated anteriorly (1).

As described by Berman and Sumida (1995) and Berman et al. (2004), the articulars of the mandibles in *Desmatodon* and *Diadectes* are unique among all Paleozoic tetrapods in possessing an unusually long anterior process of the articular extending from the anterolateral edge of its medial facet and were interpreted as an ossification of the Meckelian cartilage. The processes in both genera are identical in having the form of a mediolaterally flattened, blade-like structure that contacts the lateral surface of the prearticular with only a narrow margin being exposed along the posterodorsal border of the medial or infra-Meckelian fenestra. Wells (1941) described this structure in *Diadectes*, but could only trace it anteriorly as nearly reaching the level of the posterior end of the alveolar shelf of the dentary. Berman and Sumida (1995) described the identical process in a very large left lower jaw (UCMP 59023, length 25.5 cm) of *Diadectes* extending to the level of the anterior end of the dorsal border of the medial or infra-Meckelian fenestra. Kissel and Reisz (2004) recognized this synapomorphy uniting *Desmatodon* and *Diadectes* in their cladistic analysis (character 23), but without citing the original source of its description.

Character 25. Presplenial or anterior splenial of lower jaw.—Present (0); fused or absent (1).

This character and its states are incorporated from the cladistic analyses by Laurin and Reisz (1997, character 86) and Lee and Spencer (1997, character 23).

Character 26. Number of presacral vertebrae.—Twenty-eight or more (0); 26 or fewer (1).

This character and its states are incorporated from the cladistic analysis by Lee and Spencer (1997, character 32).

Character 27. Processes of the atlantal neural spines.—Atlantal neural spines possess large, posterodorsally directed processes (0); the atlantal neural spines possess small epipophyses (1).

This character and its states are incorporated from the cladistic analysis by Sumida and Lombard (1991) and were subsequently in included in the cladistic analysis by Sumida et al. (1992, character 5).

Character 28. Atlantal pleurocentrum.—Atlantal pleurocentrum is composed of paired elements (0); a single, ossified element in mature individuals (1).

This character and its states are incorporated from the cladistic analysis by Sumida and Lombard (1991) and were subsequently included in the cladistic analysis by Sumida et al. (1992, character 6).

Character 29. Fusion of the axial neural arch and pleurocentrum.—Axial neural arch and pleurocentrum are not fused (0); fused (1).

This character and its states are incorporated from the cladistic analysis by Sumida et al. (1992, character 7).

Character 30. Relationship of atlantal pleurocentrum to axial intercentrum.—Atlantal pleurocentrum contacts or is narrowly separated from anterior surface of axial intercentrum (0); atlantal pleurocentrum articulates with or is fused to the dorsal surface of the axial intercentrum (1).

This character and its states were discussed by Reisz (1980) and were subsequently included in the cladistic analysis by Sumida et al. (1992, character 8).

Character 31. Anteriorly directed, midventral process of axial intercentrum.—Midventral process of axial intercentrum absent (0); present (1).

This character and its states were described by Sumida and Lombard (1991) and were subsequently included in the cladistic analysis by Sumida et al. (1992, character 9).

Character 32. Neural arches.—Neural arches flat or concave (0); neural arches swollen (1).

This character and its states are incorporated from the cladistic analyses by Laurin and Reisz (1997, character 107) and Kissel and Reisz (2004, character 33). The latter analysis erroneously coded amniotes as having the derived state based on Lepospondyli as the sister taxon of Cotylosauria. The present coding follows Sumida and Modesto (2001) in recognizing the derived state only in diadectomorphs.

Character 33. Sacrum.—Sacrum consists of one vertebra (0); consists of at least two vertebrae (1).

This character and its states are incorporated from the cladistic analyses by Laurin and Reisz (1997, character 119) and Kissel and Reisz (2004, character 35).

Character 34. Processes and external shelf of ilium (Fig. 4).—Ilium is dominated by a long, narrow, posteriorly or posterodorsally directed, mediolaterally flattened blade-like process with a weakly developed or absent dorsal blade or process and lacks an external shelf (0); a pronounced external iliac ridge or shelf extends anteroposteriorly across the dorsal blade or process and the narrow, mediolaterally flattened, blade-like posterior process (1).

The ilium of basal captorhinomorphs retains the primitive state seen in anthracosaurs and primitive temnospondyls. The derived state is seen in the diadectomorphs *Limnoscelis*, *Orobates*, *Diadectes*, and *Tseajaia*, in which the dorsal iliac blade is tall and broadly expanded with a narrow, mediolaterally flattened, blade-like posterior process. A pronounced external iliac ridge or shelf traverses anteroposteriorly across both structures and forms a dorsally facing trough that was occupied presumably by epaxial musculature (Romer and Price, 1940; Romer, 1956). Near identical ilia are possessed by the eothyridids Oedaleops (Langston 1965), ophiacodontids, and varanopids. Noting the striking similarity between the ilia in *Oedaleops* and *Limnoscelis*, Langston (1965) commented that if it were not for the association of the ilium with postcranial material of "pelycosaurian" nature it certainly would have been identified as belonging to a cotylosaur (diadectomorphs as defined here).

In ophiacodontids and varanopids the dorsal blade above the external iliac ridge is greatly reduced, but possesses a prominent iliac shelf that is continued posteriorly across a prominent, blade-like process, that suggested to Romer and Price (1940) and Romer (1956) a posterior shift, at least in part, in the origin of the dorsal limb musculature. They theorized that this structure represented an intermediate stage in the development of a secondary dorsal blade. In more advanced basal synapsids they suggested that there was a dorsalward expansion of the iliac ridge and a concomitant ventralward reduction of the primitive dorsal blade above the ridge. This, they reasoned, produced a shift in the position of the epaxial musculature to the medial surface of the ilium, which allowed a greater development of the dorsal limb musculature, whose origin was the expanded lateral or external surface of the ilium.

This is an expanded version of a character originally described by Heaton (1980) and incorporated into the cladistic analyses by Laurin and Reisz (1995, character 107) and Kissel and Riesz (2004, character 36).

Character 35. Shape of humerus.—Humerus is short and robust and without a distinct shaft (0), humerus with a distinct shaft (1).

This character and its states are incorporated from the cladistic analysis by Laurin and Reisz (1995, character 104), and a modified version was subsequently included in the cladistic analysis by Kissel and Reisz (2004, character 37). In the present analysis, however, the coding of the states is reversed based on the outgroup used here.

Character 36. Ossification of the tarsus.—Elements of the tarsus are fully ossified (0); many of the elements are unossified or not fully ossified and presumably were represented in life partially or completely by cartilage.

This character and its states among the cotylosaurs were originally described by Berman and Henrici (2003) and Berman et al. (2004) and are included in a cladistic analysis for the first time here.

Character 37. Astragalus.—Tibiale, intermedium, and proximal centrale not fused to form an astragalus (0); fused in adults to form an astragalus (1).

The states of this character among cotylosaurs were originally described by Berman and Henrici (2003) and Berman et al. (2004) and included in a cladistic analysis for the first time here. Kissel et al. (2001, 2002) demonstrated the same homology of the astragalus in the captorhinid *Captorhinus*.

Character 38. Shape of unguals of manus and pes.—Long, narrow, recurved, and pointed (0); hooflike in being short, flattened, bluntly pointed to rounded with the dorsal and ventral surfaces meet along the lateral and distal margins in a narrow edge (1).

Berman et al. (2004) described the unguals of the manus and pes in all the diadectomorphs except *Tseajaia* as exhibiting the derived state. On further study and in agreement with Moss (1972), however, those of *Tseajaia* are reconsidered as being identical to those in other diadectomorphs and therefore recoded as exhibiting the derived state. This character is included in a cladistic analysis for the first time here.

Character 39. Size relationships of phalangeal elements of manus and pes.—All but terminal phalanx of digits 2-4 of manus and pes exhibit a gradual serial decrease in size distally (0); nonterminal phalanges exhibit very little or no serial decrease in size distally and most of those of the pes are subequal in size (1); extreme proximodistal shortening of penultimate phalanges of digits 1-4 in manus and 2-4 in pes (2).

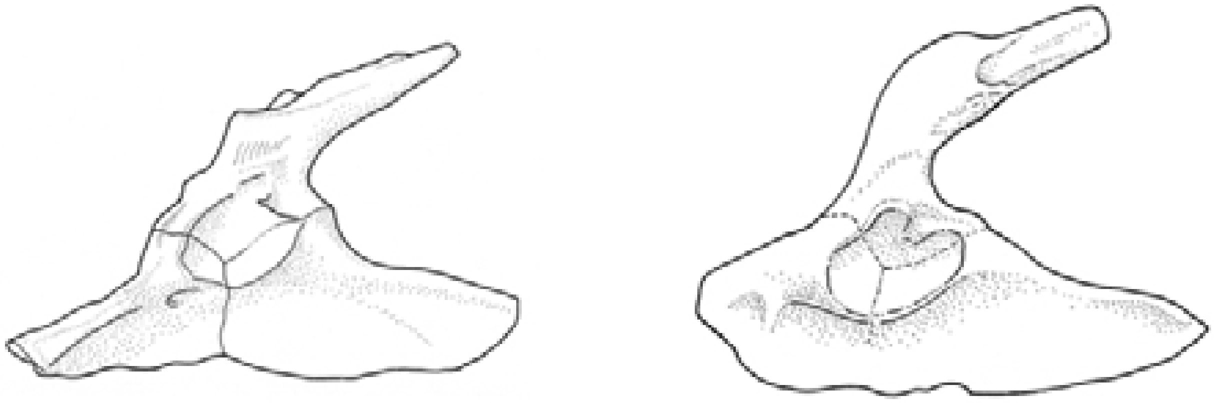
Among the ingroup taxa all exhibit the primitive state 0 except *Orobates* and *Diadectes*. In *Orobates* many of the nonterminal phalanges exhibit very little or no serial decrease in size distally, state 1, with 1 and 2 of the second digit, 2 and 3 of the third, and 2-4 of the fourth in the manus, and 2 and 3 of the third digit and 3 and 4 of the fourth in the pes being subequal in size. *Diadectes* is the only diadectomorph to exhibit derived state (2). Considering the close relationship of *Orobates* and *Diadectes*, the two derived states could reasonably be considered related

4 cm
Limnoscelis

2 cm
Tseajaia

1 cm
Diadectes

3 cm
Oedaleops



4 cm
Ophiacodon

1 cm
Protorothyris

FIGURE 4. Left pelves in lateral view of selected cotylosaurs. Limnoscelis paludis (Diadectomorpha) (after Romer 1946); Tseajaia (Diadectomorpha) (source as in Fig. 1); Diadectes (Diadectomorpha) (after Romer, 1922, 1956; Sumida, 1997); probably Oedaleops campi UMPC 67246 (Synapsida) (after Langston, 1965); Ophiacodon retroversus (Synapsida) (after Romer and Price, 1940); and Hylonomus lyelli (Reptilia) (after Carroll, 1969).

as an ordered transformational series, as reasoned by Berman et al. (2004). This character is included in a cladistic analysis for the first time here.

Character 40. Keratinous sheath or claw of manus and pes unguals.—Absent (0); present (1).

Based on morphological features of the terminal phalanges Maddin and Reisz (2007) were able to infer the presence of a keratinous sheath or claw not only in several basal synapsids, but most interestingly also in *Diadectes* as well. In addition, they noted also that except for a few minor proportional differences, the unguals of *Orobates* are identical to those of *Diadectes*, and, therefore, probably also supported a claw. As they pointed out, among extant tetrapods the possession of keratinous claws or their modifications is otherwise an exclusively amniote feature. Therefore, they reasoned that because *Diadectes* apparently possessed claws, this structure must have originated outside of the crown group Amniota. However, in the perspective of this study the possession of claws by *Diadectes* and *Orobates* could be interpreted alternatively as an indication that both genera attained amniote status. As noted in Character 38, unguals are known in all the diadectomorphs except *Desmatodon*, and exhibit the same unique structure and probably, as in amniotes, possessed keratinous claws. This character is included in a cladistic analysis for the first time here.

ANALYSIS AND RESULTS

Cladistic analysis of Cotylosauria was performed using the Willi Hennig Society edition of TNT (Tree Analysis Using New Technology) by Goloboff et al. (2008), and Mesquite, version 2.74, by Maddison and Maddison (2010), to produce the character-taxon matrix of Table 1. No characters were ordered. The analysis produced only one most parsimonious tree (Fig. 5) with a length of 56 steps, Consistency and Retention indices of 0.911, and of 0.894, respectively.

Except for the exclusion of the supposed diadectid *Ambedus*, the analysis presented here agrees with that of Kissel and Reisz (2004) in recognizing Diadectomorpha as a monphyletic clade with *Diadectes* and *Diasparactus* forming a terminal dichotomy and *Desmatodon*, *Orobates*, *Tseajaia*, and *Limnoscelis* as progressively more distant sister taxa (Fig. 5). Undoubtedly, the most important and controversial relationship revealed by the present analysis is the resolution of Synapsida and Diadectomorpha as sister clades, indicating that the latter is a member of the crown-clade Amniota. This is in sharp contrast to previous analyses (Gauthier et al., 1988; Laurin and Reisz, 1995, 1997, 1999; and Kissel and Reisz, 2004) that resolve Diadectomorpha as the sister clade to Amniota (Synapsida + Reptilia), but in agreement with those of other studies (Sumida et al., 1992; Berman et al., 1992; and Berman, 2000). As indicated in the characters-taxon matrix of Table 1, only one synapomorphy (character 21) was found uniting Synapsida and Reptilia as sister taxa. The inclusion of Diadectomorpha in the crown-clade Amniota also endorses the argument of Lee and Spencer (1997) that the relatively high number of synapomorphies they recognized as defining the Cotylosauria clade could be interpreted, using an apomorphy-based definition of Amniota, that diadectomorphs and amniotes may have also shared the acquisition of the amniote egg. In the present analysis a relatively high number (9) of synapomorphies (characters 13, 25-30, 33, 40 of Table 1) is also recognized as defining Cotylosauria. Hopefully, the present assessment of diadectomorphs as amniotes will be considered a plausible hypothesis worthy of serious investigation in future studies.

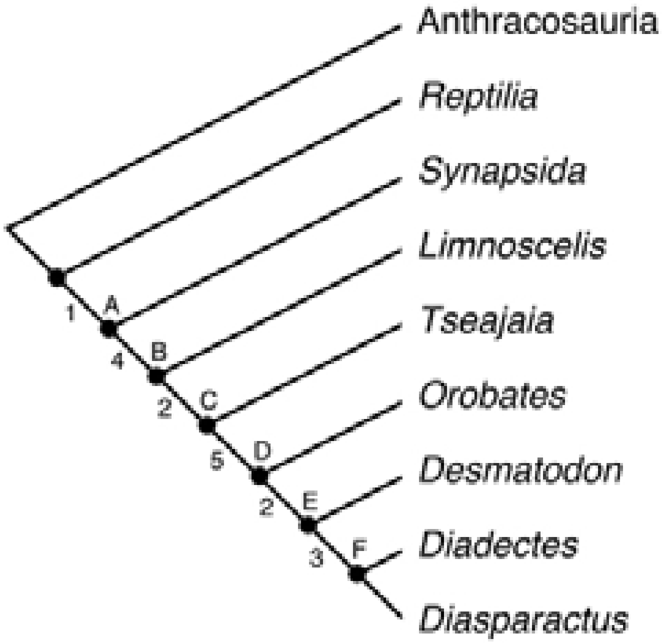


FIGURE 5. Cladogram illustrating hypothesis of intrarelationships of Cotylosauria based on one most parsimonious tree (tree length = 56 steps) and the character-taxon matrix of Table 1. Nodes are labeled by upper-case letters and are supported by the following character states: Node A, Synapsida + Diadectomorpha, 4, 5, 34; Node B, Diadectomorpha, 3, 20, 31, 32, 35, 36, 38; Node C, 7, 14, 16; Node D, Diadectidae, 17, 18, 19, 20(2), 22; Node E, 8, 24; Node F, 18, 22(2). A derived state other than "1" is indicated in brackets (2). Bremer decay values are given next to nodes.

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OPHIACODON (SYNAPSIDA, OPHIACODONTIDAE) FROM THE LOWER PERMIAN SANGRE DE CRISTO FORMATION OF NEW MEXICO

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Abstract—A partial skeleton of a large *Ophiacodon* is described from the Lower Permian Sangre de Cristo Formation of San Miguel County, northern New Mexico. It is the largest reported for the state and is most comparable to the Texas species *Ophiacodon retroversus* on the basis of a few morphological features and size. The Sangre de Cristo form also shares a few characters of the pes with the smaller New Mexico species *O. mirus*, as well as exhibiting a uniquely shaped astragalus. Although this specimen of *O. retroversus* may represent a new species, the prudent course is taken to defer definite specific assignment until more complete material becomes available. Based on the close similarity between the Sangre de Cristo *Ophiacodon* and *O. retroversus*, the lower portion of the Sangre de Cristo Formation is judged correlative with the Lower Permian Archer City and Petrolia formations in north-central Texas and the Organ Rock Shale in southeastern Utah and adjacent area of Arizona. Thus, the Sangre de Cristo *Ophiacodon* indicates either an upper Coyotean or a Seymouran age close to the Wolfcampian-Leonardian age boundary.

INTRODUCTION

Ophiacodon is a member of the basalmost, amniote synapsids, often simply referred to as “pelycosaurs,” which are restricted to, but widely distributed and commonly encountered throughout, the Permo-Pennsylvanian in North America, mainly Texas, New Mexico, and Utah. Six species of *Ophiacodon* are currently recognized as valid (Romer and Price, 1940; Reisz, 1986): *Ophiacodon uniformis*, *O. retroversus*, and *O. major* from Texas, *O. navajovicus* and *O. mirus* from New Mexico, and *O. hilli* from Kansas. All are from the Lower Permian, except for the Upper Pennsylvanian *O. navajovicus*, and are represented by remains ranging from fragmentary to complete, or nearly complete, skeletons. They are slender in build and ranged in maximum weight and length from about 32 kg and 130 cm to about 230 kg and 300 cm (Romer and Price, 1940) and are generally interpreted as amphibious animals that fed primarily on large fish, which were abundant during their occurrence. As an extremely conservative group, specific distinctions rely on a few structural features, size, and disproportionate growth of structures (Romer and Price, 1940). Interestingly, some of these distinctions can be arranged in a developmental series within the genus as the stratigraphic column is ascended, which may indicate species lineages.

Lower Permian vertebrate localities and their assemblages from the Sangre de Cristo Formation of north-central New Mexico were last reviewed by Berman (1993), and only a brief summary is needed here. The scattered collecting sites occur along the upper reaches of the Pecos River drainage from Glorieta Pass at Glorieta on the eastern border of Santa Fe County southeastward to about 8 km south of Ribera, San Miguel County. In this area the Sangre de Cristo Formation is as much as 200 m thick and can be divided into two lithostratigraphic units (Fig. 1). The lower unit is dominated by thick, channelform sandstone and conglomerate bodies, whereas laterally persistent sheet sandstones characterize the upper unit (Soegaard and Caldwell, 1990). All of the fossil-borne localities in the Sangre de Cristo Formation are from the lower unit, whereas extensive fossil footprint assemblages (e.g., Hunt et al., 1990) are found in the upper unit (Fig. 1). We are currently working on a more detailed stratigraphic organization of the vertebrate fossil localities in the Sangre de Cristo Formation that will be presented elsewhere.

The vertebrate fossils discovered in the Sangre de Cristo Formation in the southern Taos trough consist almost entirely of fragmentary remains predominately from coarse-grained, arkosic stream-channel deposits, and their few descriptions have been limited almost exclusively to taxonomic lists of specimens collected by field parties from the University of California, Berkeley (Langston, 1953) and Harvard University (Romer, 1960) in the 1930s, and the University of California, Los Angeles, and the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, in the early 1960s (Vaughn, 1964b) and 1970s (Berman, 1993), respectively. As reported by Berman (1993), the vertebrate assemblage from the Sangre de Cristo Formation of the Pecos River valley includes: a xenacanth shark, the lungfish *Gnathorhiza*, the temnospondyl amphibians *Eryops* sp., *Platyhystrix* cf. *P. rugosus*, and indeterminate form(s), the lepospondylus amphibians *Phlegethontia* sp, *Diplocaulus* sp., and *Lysorophus* sp., the diadectomorph *Diadectes* sp., a captorhinomorph, and the basal synapsids *Sphenacodon* sp. and *Ophiacodon*. Skeletal elements of only three of these vertebrates have been reported: tooth plates of *Gnathorhiza* and vertebrae of *Diplocaulus* (Berman and Reisz, 1980); and a complete skull of *Diadectes* (Berman et al., 1992). In addition, cylinders resembling the natural casts of aestivation burrows of the lungfish *Gnathorhiza* were reported by Vaughn (1964b) from near the top of the Sangre de Cristo Formation, but, unfortunately, no bones were associated with them. In the same paper Vaughn reported also finding remains of amphibians and reptiles, but without more specific identifications, from lower in the Sangre Cristo Formation in the same region about 2 km south of Ribera. This collection, also from coarse, arkosic stream-channel deposits, consisted mainly of isolated elements and only a few partially articulated specimens. With the exception of the burrow casts (Vaughn, 1964b), Berman (1993) reported that all the vertebrate fossils from the Sangre de Cristo Formation are from approximately the lower third of the section and almost certainly of Wolfcampian age.

Here, we describe a partial skeleton of a large *Ophiacodon*, the largest reported for the state of New Mexico, from the lower third of the Sangre de Cristo Formation exposed along the Pecos River Valley. It is part of the collection of vertebrates made by Vaughn in the mid-1960s, which was permanently transferred to and incorporated into the collections of the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, in 1988. The *Ophiacodon* described here was recovered in a single block of matrix from a coarse, arkosic stream-channel sandstone marginal to its interruption by the Pecos River, about 2 km south of Ribera on the eastern side of State Highway 3 south of its intersection with I-25, San Miguel County, New Mexico.

With the exception of *O. hilli*, fragmentary remains of *Ophiacodon* species have been utilized repeatedly in lithostratigraphic and biochronological correlations with the Virgilian Pennsylvanian-Early

Wolfcampian-Leonardian red-bed sections of Texas and New Mexico. The Sangre de Cristo *Ophiacodon* is similarly useful.

ABBREVIATIONS

CM, acronym referring to the institutional repository of the Carnegie Museum of Natural History, Section of Vertebrate Paleontology. Key to the abbreviations used in figures for anatomical structures: **as**, astragalus; **ca**, calcaneum; **fe**, femur; **fi**, fibula; **ppi**, posterior process of ilium; **pu**, pubis; **ppc**, posteriormost presacral centrum; **ri**, rib of probable anterior caudal vertebra; **sv1-2**, first and second sacral vertebrae; **ti**, tibia; **1-5**, distal tarsals; **I-V**, metatarsals.

DESCRIPTION AND COMPARISONS

The Sangre de Cristo *Ophiacodon* specimen, CM 47771, consists of a partial, articulated skeleton that includes the portions of two sacral vertebrae with firmly fused ribs and the centrum of the last presacral vertebra, partial pelves, and left hind limb and most of the pes, and scattered, probable anterior caudal ribs. Figure 2 shows most of the specimen in dorsal view except for the femur, which is rotated nearly 180° on its long axis, exposing its ventral surface, and the first and second digits that are folded laterally so that their ventral surfaces contact the ventral surface of the rest of the pes. The limb and pes have been reoriented relative to the pelves, so as to be directed posteriorly and medially. The Sangre de Cristo *Ophiacodon* exhibits no features that would contradict its generic assignment, and the following description emphasizes features that provide a basis for comparison with the well-known species of Texas and New Mexico, which are based on the descriptions of Romer and Price (1940).

The vertebral column is represented by the centrum of the presumably posteriormost presacral vertebra and portions of the first and second sacral vertebrae with firmly fused ribs (Fig. 2). All are slightly disarticulated and closely associated with the dorsal blade of the ilia, and none appears to deviate from those in *Ophiacodon* and therefore do not add anything substantial to this discussion. At least two presumably anterior caudal ribs and parts of others are preserved scattered in an area a short distance from the anterior margin of the pubes. They are com-

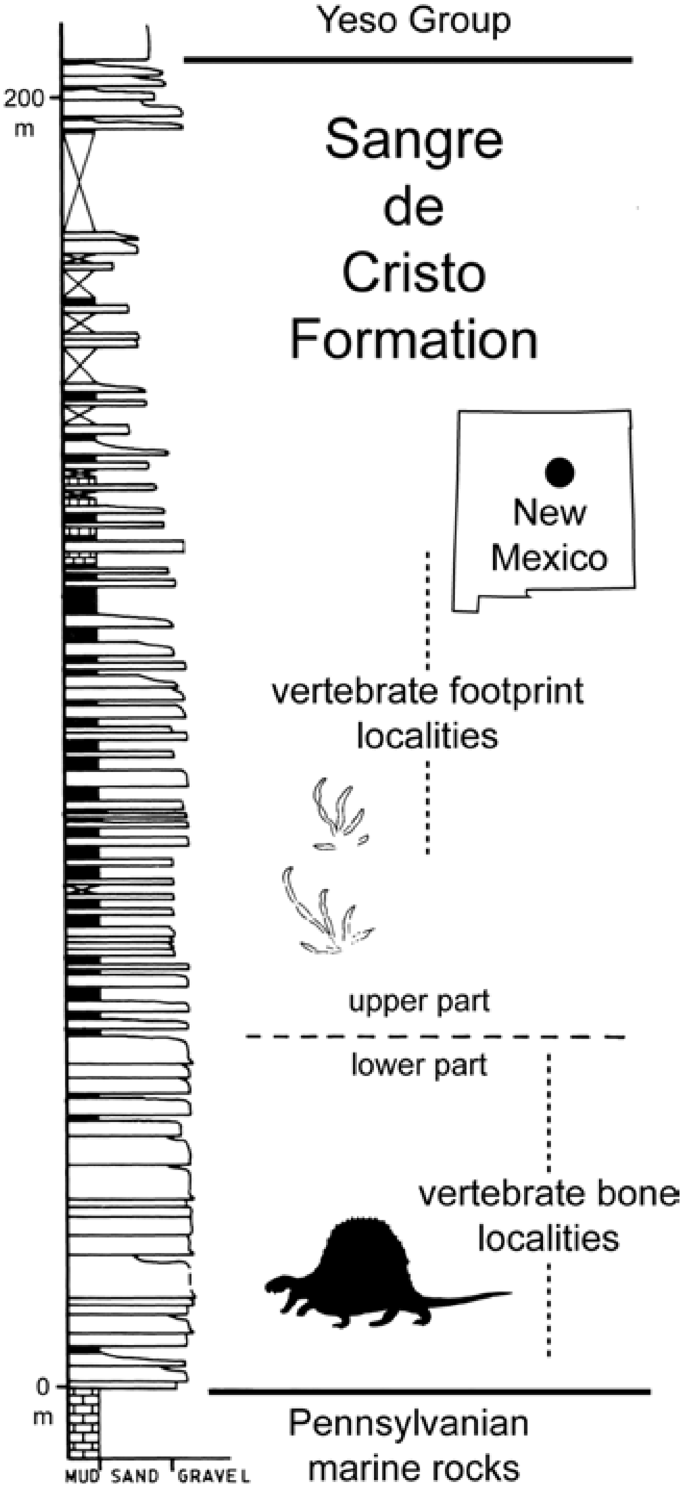


FIGURE 1. Generalized stratigraphic section of the Sangre de Cristo Formation in the southern Taos trough (after Soegaard and Caldwell, 1990), showing generalized stratigraphic distribution of fossil vertebrate localities.

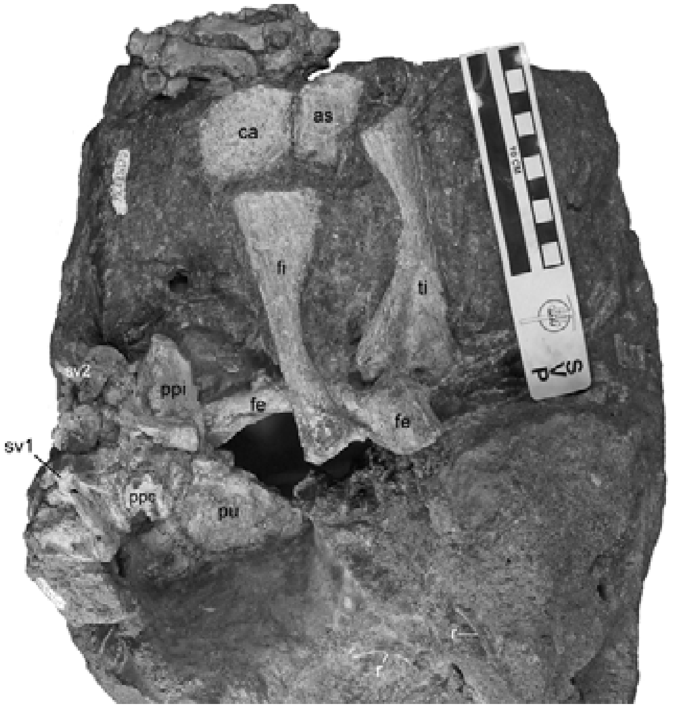


FIGURE 2. Block containing *Ophiacodon*, CM 47771, with all elements except the femur exposed in dorsal view.

plete and fully exposed, curved slightly, measure 33 mm in length, and taper gradually distally from a proximal width of about 4 mm to a blunt point.

The greater portions of the elements of the pelves (Fig. 2) are preserved but not entirely exposed. Both ilia are present but lack the distal portion of the posterior process of the dorsal blade. The ilium is typical of ophiacodonts in consisting of a greatly reduced dorsal blade from which a long, mediolaterally flattened, blade-like process extends posteriorly. Furthermore, as in ophiacodonts, a pronounced external iliac shelf traverses anteroposteriorly across the dorsal blade and posterior process to form a prominent, dorsally facing, trough-like structure. The pubes are complete, but the anterior portion of the right has not been completely exposed. The ischia (not visible in Fig. 2) are incomplete posteriorly at the edge of the block, and at least the posterior third of the left, the more intact of the two, is absent. There is no diamond-shaped opening along the midline union of the pelves at the intersection of the pubes and ischia as seen in many individuals of *Ophiacodon*, an indication of incomplete ossification. It can be assumed that, because endochrondral bones in *Ophiacodon* are characteristically slow to ossify, this indicates an advanced age of the Sangre de Cristo specimen.

The pubic tubercle (not visible in Fig. 2) in the Sangre de Cristo *Ophiacodon* is represented by a rugosity close to the acetabular region. In *Ophiacodon* there is an interesting series of specific changes toward the loss of the pubic tubercle. As noted by Romer and Price (1940, p. 230): "In *O. navajovicus* the material is imperfect but suggests that this structure was present in a rather reduced form. In *O. mirus* and *O. uniformis* a nubbin of this structure remains, whereas in *O. retroversus* it has disappeared and is represented by a rugosity near the acetabular region, as in sphenacodonts."

The femur (Fig. 2) is perhaps the most diagnostic element of the Sangre de Cristo *Ophiacodon* and along with other features leaves little doubt as to its generic identity. It is a stout element with little development of the narrow shaft seen in other basal synapsids. The intertrochanteric fossa is very broad and shallow and extends 40% of the femur length. It possesses the specialized fourth trochanter of *Ophiacodon*, which appears as a small tuber on the distal end of the posterior bounding margin of the intertrochanteric fossa. Perhaps the most uniquely *Ophiacodon* feature of the femur is the presence of a secondary or posterior adductor ridge or crest. This structure exhibits a considerable range of development within the genus, and according to Romer and Price (1940, p. 230), "In *O. navajovicus* the adductor crest is represented by only rugosities, as in the ophiacodontids *Clepsydrops* and *Varanosaurus*. In *O. mirus* there is a slight development of a ridge along the posterior margin. *O. uniformis* shows this ridge in a somewhat more advanced stage, and in *O. retroversus* and *O. major* this secondary adductor crest is very highly developed." Although the entire length of the adductor ridge is not exposed in the Sangre de Cristo *Ophiacodon*, it is quite evident that it had reached an advanced stage of development comparable to that in *O. retroversus* (Romer and Price, 1940, p. 236, fig. 50). The tibia and fibula of the Sangre de Cristo *Ophiacodon* conform very closely to those of this genus; this is especially true of the greatly flared distal end of the fibula. The ends of the limb bones are well ossified, indicating an advanced adult age.

The greater portion of the left pes is preserved (Fig. 3), missing only the medial and lateral centralia, and several distal phalanges of the third through fifth digits that include the fourth, second through fifth, and first through fourth, respectively. A reconstruction of the pes is given in Figure 4. The pes conforms very closely in structure and proportions to those in *Ophiacodon mirus* and *O. retroversus*, the only members of the genus in which this structure is well known, but more so in the former. The astragalus is as expected, L-shaped, but the distal, horizontal limb is unexpectedly very short, giving the entire element a relatively very narrow outline that is more comparable to those in sphenacodontids than in ophiacodontids, especially *Ophiacodon*. In *Ophiacodon mirus* and *O. retroversus* the length and width are subequal, whereas in the Sangre de Cristo specimen the length exceeds the width by 30%. The calcaneum is subcircular in outline except for the straight margin that apposes the astragalus. Its greatly expanded lateral margin more closely compares with that in *O. mirus* than in *O. retroversus*. As in ophiacodontids, the passage of the perforating artery is close to the distal end of the opposing margins of the astragalus and calcaneum.

All of the distal tarsals are well represented and comparable to those in *O. mirus* and *O. retroversus* (Romer and Price, 1940, fig. 41, p. 164), but with a few distinct differences. The first distal tarsal is more like that in *O. retroversus* in being mediolaterally elongated, rather than being square in outline, and having a broader contact with the metatarsal. The second and fifth distal tarsals are similar in their small size and outline to both genera, whereas the third and fourth are distinctly more like those in *O. mirus*. The similarities include a larger and more proximodistally elongation of the third, and the fourth, largest of the series, as is typical of basal synapsids, having a greatly expanded, convex proximal margin that fits into a relatively deep, concave emargination at the distal end of the astragalus-calcaneum articulation. The lengths of the digits are significantly shorter and slightly broader relative to those of basal, carnivorous synapsids, and the ungual phalanges are uniquely *Ophiacodon* in being broad, flat, and bluntly pointed.

TAXONOMIC ASSIGNMENT

Although there is no doubt about the taxonomic assignment of the Sangre de Cristo specimen CM 47771 to *Ophiacodon*, what is questionable is whether it represents a new or previously recognized species. According to Romer and Price (1940), five species of *Ophiacodon* from Permo-Pensylvanian beds of Texas and New Mexico are well known and can be regarded as valid. They include, from earliest to latest occurrences, *Ophiacodon uniformis*, *O. retroversus*, and *O. major* from Texas and *O. navajovicus* and *O. mirus* from New Mexico. The genus is an extremely conservative group in which species can be distinguished only on the basis of a few morphological features, mostly size (weight and length), and disproportionate growth of structures (Romer and Price, 1940). In both groups there appears to be a steady increase in size, based on averages of presumably young adults, as the stratigraphic columns are ascended. The increasing weight/lengths calculated for the three species from Texas are 47 kg/150 cm, 121 kg/228 cm, and 230 kg/303 cm and those for the two species from New Mexico are 32 kg/131 cm and 52 kg/167 cm. By reference to the measurements provided by Romer and Price (1940, tables 4 and 5), the Sangre de Cristo specimen, the largest known from New Mexico, falls within the lower end of the range of the largest specimens of *O. retroversus* from Texas. Assuming that the Sangre de Cristo specimen represents an adult of advanced age, its size would be comparable to those of young adults of *O. retroversus* (Table 1).

On consideration of morphological comparisons, the Sangre de Cristo specimen most closely approaches *Ophiacodon retroversus* among the five genera of *Ophiacodon* from Texas and New Mexico. Thus, the pubic tubercle is reduced to a rugosity and the secondary adductor crest of the femur is strongly developed, as in *O. retroversus*. Of the two species in which the pes is known, *O. mirus* and *O. retroversus*, the Sangre de Cristo form compares more closely to the latter in the first distal tarsal being more mediolaterally elongated and having a broader contact with the metatarsal. On the other hand, the Sangre de Cristo form compares more closely to *O. mirus* in the greater expansion of the lateral margin of the calcaneum and the shapes and contacts of the third and fourth distal tarsals. The only apparent, unique feature of the pes distinguishing the Sangre de Cristo specimen from both genera is the distal, horizontal limb of the L-shaped astragalus being very short. Whereas these comparisons support the suggestion that the Sangre de Cristo specimen may represent a new species, it seems best to defer that decision until additional anatomical material becomes available, and for the present recognize that it is most closely related to *Ophiacodon retroversus*.

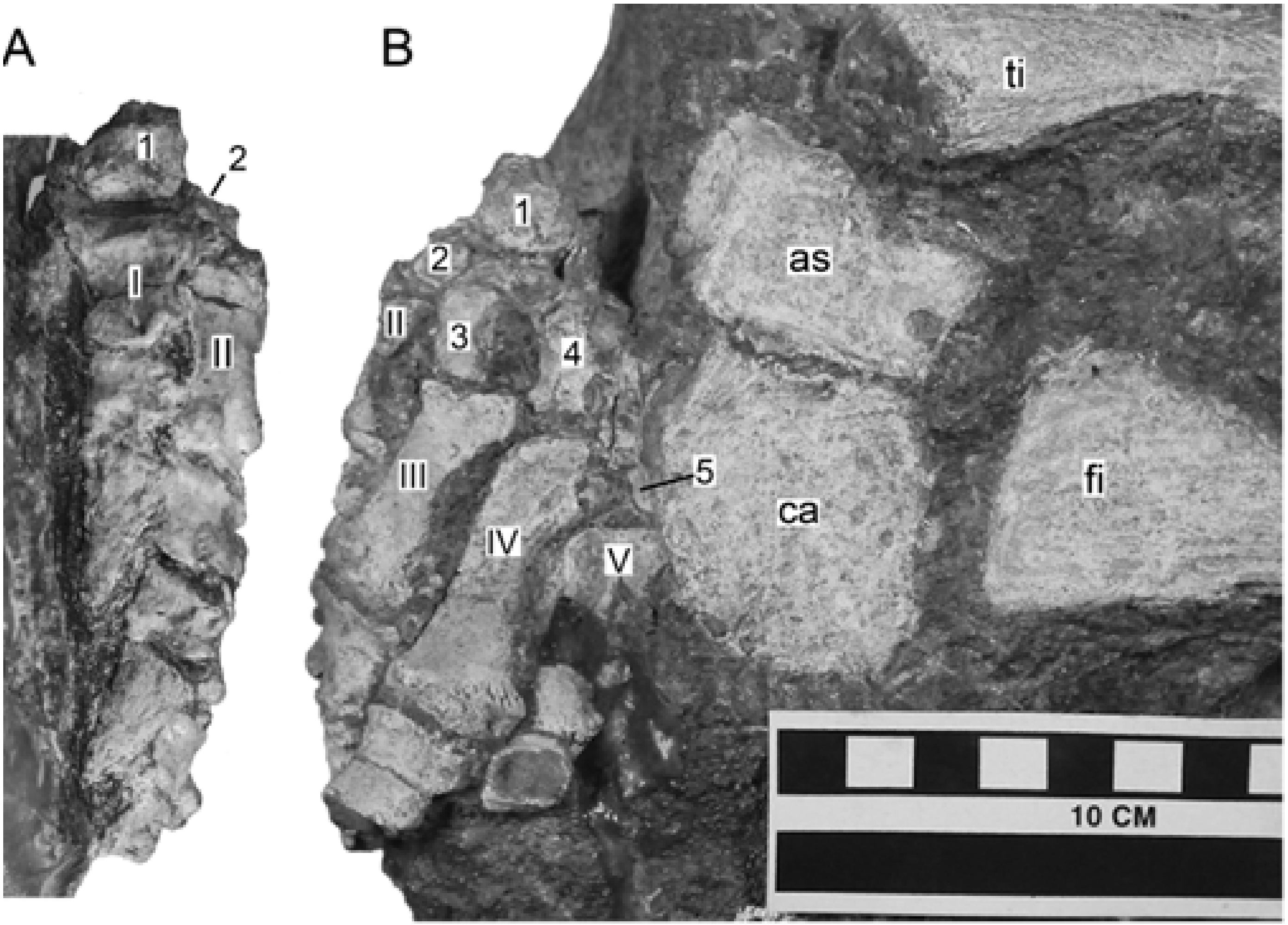


FIGURE 3. Partial left pes of *Ophiacodon*, CM 47771. **A**, Dorsal view of distal tarsals and digits 1 and 2 folded against ventral surface of lateral portion of the pes of **B**. **B**, Dorsal view of astragalus, calcaneum, and distal tarsals and proximal portions of digits 3-5 as seen in Figure 2.

AGE

Before a biostratigraphic age of the Sangre de Cristo *Ophiacodon* can be assessed, it is advisable to comment briefly on the latest revisions of the lithostratigraphic and biochronological correlations of the latest Virgilian - Wolfcampian-Leonardian red-bed sections of Texas and New Mexico. Until recently, the universally accepted lithostratigraphic subdivisions and nomenclature of the classic Lower Permian, vertebrate collecting localities in Texas had been that of Plummer and Moore (1921). In 1988, Hentz presented a completely revised scheme, which has become widely accepted, but with some modifications by Lucas (2006). In addition, Lucas (2005, 2006) has similarly revised the stratigraphy and biostratigraphy of the richly fossiliferous, latest Pennsylvanian-Lower Permian localities of north-central New Mexico. Most importantly, however, using terrestrial, tetrapod index fossils, he has recognized 10 time intervals that span the latest Pennsylvanian Virgilian and Permian, which are referred to by him as land-vertebrate faunachrons and abbreviated by the acronym LVF. This biochronology has provided a tetrapod-based timescale for determining age correlations of widely separated tetrapod assemblages in the USA. Both his lithostratigraphic and LVF chronofaunal subdivisions and correlations for the Permo-Pennsylvania sections of Texas and New Mexico are followed here (Fig. 5).

Based on the data of Romer and Price (1940) *Ophiacodon retroversus* is most abundant in the Admiral and Belle Plains formations of the Wichita Group of Texas and roughly equivalent to the upper portion of the Archer City and the entire Petrolia formations of this paper (Fig. 5). Applying the chronofaunal subdivisions constructed by Lucas (2005, 2006), the lower portion of the Sangre de Cristo Formation, based on the *Ophiacodon* specimen CM 47771, is correlative with the late Coyotean and much of the Seymouran LVFs, which straddle the Wolfcampian-Leonardian age boundary.

Ophiacodon specimens have also been used in part by Vaughn (1962, 1964a) in assigning litho-biostratigraphic correlations to the Halgaito and Organ Rock shales, Cutler Group, of the Permo-Pennsylvanian formational succession in the Four Corners region of southeastern Utah and adjacent Arizona. Based on similarities in size and morphological features recorded by Romer and Price (1940), those from the Halgaito Shale were judged by Vaughn (1962) as closely related to, if not conspecific with, *Ophiacodon navajovicus* from the El Cobre Canyon of New Mexico. Although noting additional biostratigraphic matches, he could offer only the imprecise correlation of the Halgaito Shale with the Wolfcampian Wichita Group of Texas. A more precise stratigraphic correlation of the Halgaito can now be provided (Fig. 5), based on its *Ophiacodon* form, to most of the Virgilian-Wolfcampian El Cobre Canyon Formation, the lower of two units of Lucas' (2006) revised lithostratigraphy of the Cutler Group of the Chama basin in northern New Mexico, and an assignation of a Coyotean age (Fig. 5). This also indicates a lithostratigraphic correlation of the Halgaito Shale to the upper part of the Markley Formation, the basalmost unit of the revised Wichita Group, Texas, and also the lower part of the Archer City Formation.

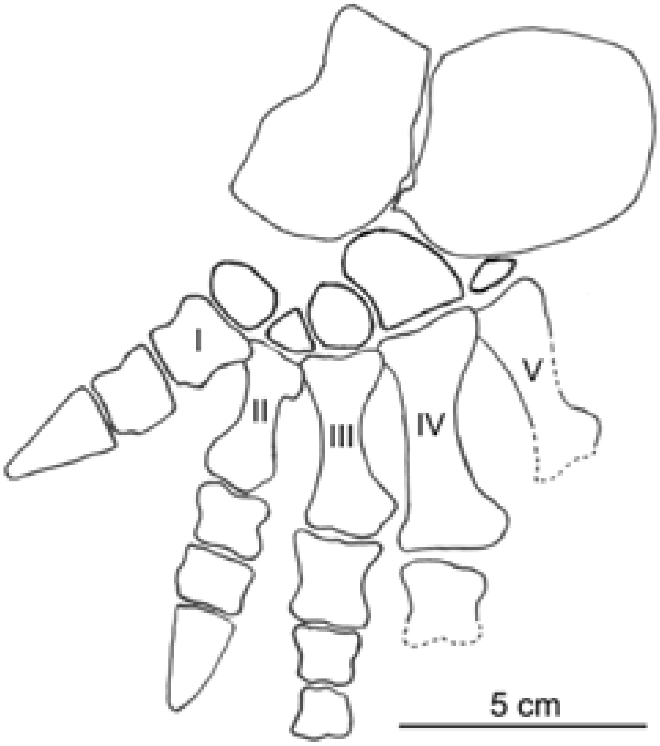


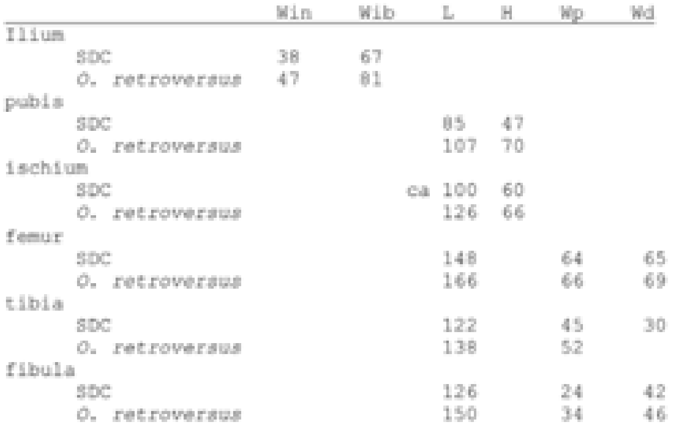
FIGURE 4. Outline reconstruction of partial left pes of *Ophiacodon*, CM 47771.

More germane to this discussion, however, Vaughn (1964a) also reported large *Ophiacodon* remains, the largest for Utah, from the Organ Rock Shale, the uppermost unit of the Cutler Group in the Four Corners. Again, based on data provided by Romer and Price (1940), he described them as falling well within the size range of *O. retroversus*, and, although believing they probably represent a new species of *Ophiacodon*, refrained from doing so. The Organ Rock Shale vertebrate fauna was assessed by Vaughn as indicating an equivalence to a horizon in the upper part of the Wichita Group and an earliest Leonardian age. This essentially agrees with our lithostratigraphic correlation of the Sangre de Cristo Formation based on its *Ophiacodon* form to the Arroyo del Agua Formation, the upper unit of the here revised Cutler Group of New Mexico, which spans the later Coyotean and most of the Seymouran LVFs. This assessment also agrees with the correlation of the Organ Rock Shale with parts of the Archer City and Petrolia formations, Wichita Group, of the revised Texas sequence, and the LVFs assigned to them, which are very close in age to (and in part straddle) the Wolfcampian-Leonardian boundary (Fig. 5). Note, also, that our correlation of the Sangre de Cristo Formation is consistent with recognition of a substantial hiatus (unconformity) at the base across much of the Taos trough (Baltz and Myers, 1999).

ACKNOWLEDGMENTS

Jason Anderson and Stuart Sumida provided helpful reviews of the manuscript.

TABLE 1. Linear measurements (in mm) of elements of pelves and hind limb of Sangre de Cristo Formation Ophiacodon, abbreviated as SDC, and for comparison with averages of young adults of Ophiacodon retroversus from Romer and Price (1940, table 5). **Abbreviations: H**, height; **L**, length; **Wib**, width of ilium base; **Wd**, maximum width of distal end; **Win**, minimum width of ilium neck; **Wp**, maximum width of proximal end.



	Win	Wib	L	H	Wp	Wd
Ilium						
SDC	38	67				
O. retroversus	47	81				
pubis						
SDC			85	47		
O. retroversus			107	70		
ischium						
SDC			ca 100	60		
O. retroversus			126	66		
femur						
SDC			148		64	65
O. retroversus			166		66	69
tibia						
SDC			122		45	30
O. retroversus			138		52	
fibula						
SDC			126		24	42
O. retroversus			150		34	46

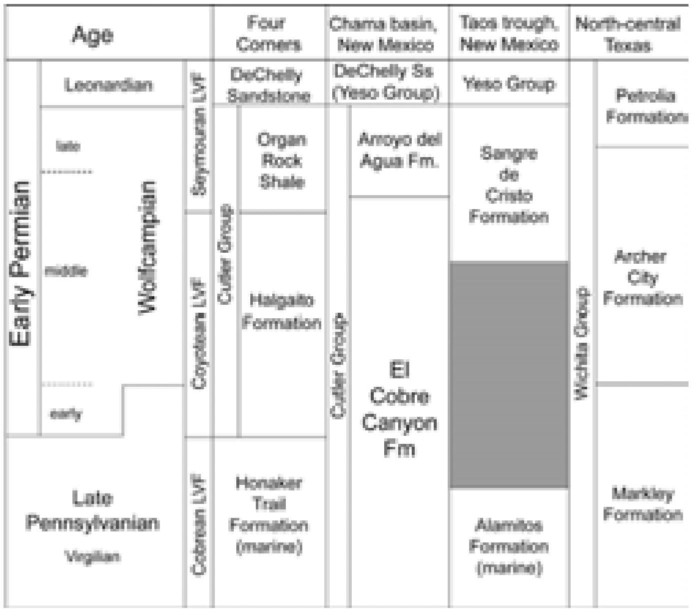


FIGURE 5. Land-vertebrate-faunachron (LVFs) subdivisions of the Wolfcampian+Leonardian time span and vertebrate-biostratigraphic-based correlation of the Lower Permian, red-bed sections of the Four Corners, northern New Mexico, and north-central Texas (see text for discussion).

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ICHNOLOGY AND STRATIGRAPHY OF THE CRESCENT VALLEY MINE: EVIDENCE FOR A CARBONIFEROUS MEGATRACKSITE IN WALKER COUNTY, ALABAMA

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Abstract—Early Pennsylvanian trace fossil-bearing deposits from the Crescent Valley Mine of Walker County in Alabama are correlated with those from the nearby Minkin Paleozoic Footprint Site. These represent end-members of a megatracksite that spans an environmental gradient from the inland, freshwater part of a deltaic system at the Minkin site to more near shore environments at Crescent Valley, where variable salinity conditions and tidal processes prevailed. This is reflected by preservation of a depauperate ichnofauna at the Crescent Valley mine. Recorded trace fossils are identified and interpreted as amniote trackways (*Attenosaurus subulensis* and *Cincosaurus cobbi*), apterygote insect trackways (*Stiaria*) and jumping traces (*Tonganoxichnus*), myriapod trackways (*Diplichnites-Diplopodichnus*), invertebrate burrows (*Arenicolites* and *Treptichnus*), and bivalve resting traces (*Lockeia*). A continuum of trail morphologies from chevronate, to feather-stitch and leveéd forms is also observed. These are interpreted as recording the activities of juvenile xiphosurans and possibly bivalves in a shallow-water tidal environment. *Arborichnus*, present in deeper-water facies, is interpreted as recording the combined resting and swimming activities of adult xiphosurans. In contrast to the Minkin site, *Kouphichnium* is absent. The spatial and environmental separation of these different trace fossils attributed to xiphosurans reflects that of different phases in their life cycles. The environmental distinction from the Minkin site may explain the apparent absence of temnospondyl amphibians. The fish-fin trace *Undichna* is common at the Minkin site but absent from the Crescent Valley mine, which may be due to interrelated environmental and preservational conditions.

INTRODUCTION

The discovery of the Minkin Paleozoic Footprint Site by amateur collectors in 1999 (Buta et al., 2005) rejuvenated interest in the vertebrate trackways found in the Pennsylvanian-age rocks of Alabama. The Minkin site originated as a strip mining operation that exposed Carboniferous trackways and other trace fossils in the interval between two coal beds. The traces are preserved in a dark gray shale that was originally a tidal mud flat. The deposit is Westphalian A (313 Ma), about the same age as the oldest known amniote body fossils (Clack, 2012). By this time, the colonization of land was well underway. Permo-Carboniferous trace fossil-bearing strata representing coastal settings from other locations in the southern USA include the Tonganoxie Sandstone of Kansas (Buatois et al., 1997, 1998a), and the Robledo Mountains of New Mexico (Lucas and Heckert, 1995; Lucas et al., 1998; Minter and Braddy, 2009; Voigt et al., 2013). In this paper, we describe a new tracksite in Alabama that sheds further light on the nature of Carboniferous tetrapod communities. Further, it seems that the best-known Carboniferous track sites in Alabama are age equivalent, suggesting the existence of a megatracksite in Walker County.

Aldrich and Jones (1930) first described trace fossils from the Early Pennsylvanian strata of the Black Warrior basin in north-central Alabama. Workers at the Galloway Coal Company No. 11 mine, an underground slope mine located less than a mile south of Carbon Hill, had noticed tetrapod tracks in collapsed roof shale and exposed ceilings above the Jagger coal seam and brought them to the attention of knowledgeable authorities. Aldrich and Jones (1930) named nine ichnospecies of small vertebrate tracks, two ichnospecies of large vertebrate tracks, and two other uncertain forms. Haubold et al. (2005) concluded that seven of the ichnospecies these authors assigned to small vertebrate tracks were made by the same animal or animals and that there was only one distinct type, *Cincosaurus cobbi*, thought to have been made by an early amniote. No definite temnospondyl amphibian traces were recognized by Aldrich and Jones (1930), nor were invertebrate traces a significant part of their study. The largest and best-defined tracks found were assigned to the ichnospecies *Attenosaurus subulensis*. It is unfortunate that much of the original material figured by Aldrich and Jones (1930), including the holotypes of *C. cobbi* and *A. subulensis*, appears to be lost (Haubold et al., 2005).

The Crescent Valley Mine (CVM) is an active (at the time of this writing) surface coal mine in Walker County that was opened by National Coal Company in 2008 into the northern edge of the old Galloway No. 11 mine. The CVM was discovered in April 2011 to be a rich new track site, and its proximity to the original discovery site provides an opportunity not only to find more specimens like those seen by Aldrich and Jones (1930), but also to gain a more complete inventory of the trace fossil assemblage in the area. Over a period of 18 months, more than a thousand slabs of tracks and traces were collected from mine spoil piles, photographed, and posted on a website (http://bama.ua.edu/~rbuta/cvm/cvm.pl). Our goals with this paper are to describe the ichnofauna found at the CVM, present a modern examination of the rock layers exposed by the mining operation there, explain how the trace and plant fossils relate to the stratigraphy of the site, and compare the results with what was found at the Minkin site.

LOCALE

The location of the CVM relative to the boundaries of the old No. 11 mine is shown in Figure 1, which is based on an early 1930s map made around the time the mine was formally closed. This schematic also indicates the main trackway locales of Aldrich and Jones (1930). The trackways described by these authors were mostly found in an area called the Southwest Slope, 4th left entry, approximately 2 km southwest of the mine entrance. The old mine was of the room and pillar type,

FIGURE 1. A schematic map of the No. 11 Mine of the Galloway Coal Company and its location relative to the Crescent Valley Mine. The No. 11 map is based on a 1930 original map. The first trackways in Alabama were mostly found along the "Southwest Slope," approximately 2 km from the mine entrance. The mine boundary is the dotted outline. Several special underground tunnels (such as the "4th left entry," cited as a primary locale for many of the main tracks illustrated by Aldrich and Jones) are indicated. The solid dots show points where figured Aldrich and Jones (1930) specimens were found. The CVM is highlighted by the dashed curve.

and was in operation long enough (ca. 1912 to 1933) that it left behind hundreds of coal-excavated chambers over an area of nearly 8 km^2. Several of these chambers were exposed when the CVM was opened in 2008. What originally attracted professional geologists to the No. 11 mine was reports of long trackways in the ceilings of some of the mine tunnels. In a repeat of history, when the CVM operation began, miners once again reported seeing tracks in the ceilings of exposed cavities from the old mining operation (D. Williams, foreman of Kansas Mine No. 2, 2011, private communication). To our knowledge, no professional geologists were contacted to view or photograph these finds, and all were destroyed by the subsequent mining operation. Figure 2 shows a photograph of one of the cavities exposed in 2011.

SITE SIGNIFICANCE

The Crescent Valley Mine provides exceptional insight into the geologic setting and habitat of the makers of *Cincosaurus cobbi* and other tetrapod trace fossils in Walker County. The traces occur in the Mary Lee coal zone of the Pottsville Formation, which is of Early Pennsylvanian (Langsettian) age and was deposited in the Black Warrior basin, an ancient foreland basin that flanks the Appalachian and Ouachita orogenic belts in Alabama and Mississippi (Mellen, 1947; Thomas, 1988; Pashin, 2004). The Pottsville Formation is locally more than 2,600 m thick and contains virtually all of the economic coal resources in northern Alabama (McCalley, 1886, 1900; Butts, 1926; Culbertson, 1964; Pashin and Gastaldo, 2009). The vast majority of the coal mined in the state comes from the Mary Lee coal zone, one of 13 major Pottsville coal zones. Numerous geological studies have been conducted of the Mary Lee, which was deposited in fluvial-deltaic environments on an ancient coastal plain flanking the ancestral Appalachian Mountains (e.g., Gastaldo et al., 1990, 1993; Pashin, 1994, 2005).

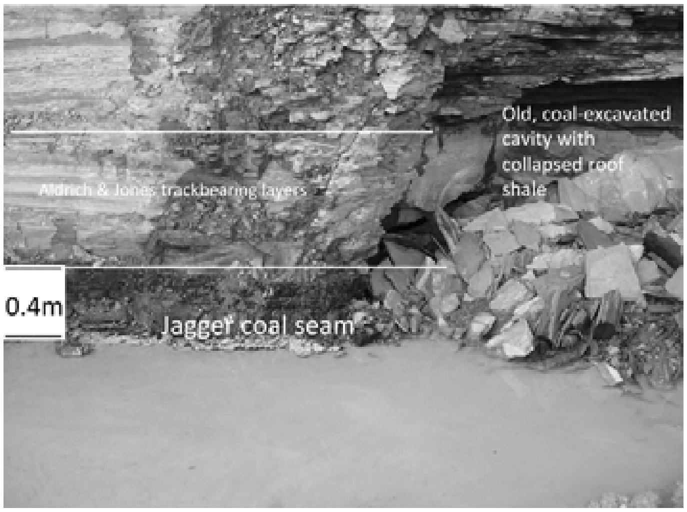


FIGURE 2. Photographs of part of the highwall in a (now reclaimed) pit at the Crescent Valley Mine. The dark band above the muddy water is the Jagger coal seam, 43 cm thick. The track-bearing layers should be within about 1 meter of the top of the seam. To the right is part of a cavity left in the rock when Jagger coal was extracted during the underground mining operation in the 1920s/30s. Most or all of the rocks seen in the cavity collapsed from the roof and some should include the track-bearing layers. This was confirmed when one large slab in the cavity was found to have 35 *C. cobbi* tracks in a 1 m long trackway (CVM 201).

We have noted that the initial discovery of *Cincosaurus cobbi* and *Attenosaurus subulensis* came from the roof strata of the No. 11 Mine. Abandoned underground mine workings exposed in the CVM highwall, as in Figure 2, arguably are part of the same complex in which the tetrapod traces were discovered. The CVM thus offers an unparalleled opportunity to recover and examine these fossils from a vertical mine face that reveals the character of the strata in which the tracks were preserved. Here we use the rock types, the sedimentary structures, and the fossil content of the sedimentary rock to interpret the ancient environments of deposition in the area and the types of processes that operated in those environments. The CVM further provides a basis for comparison with the prolific Minkin Paleozoic Footprint Site to the east, which is another well-characterized *Cincosaurus cobbi* locality in the Mary Lee coal zone (Buta et al., 2005).

STRATIGRAPHIC ANALYSIS

Jagger Bedrock Through Jagger Coal

At CVM, four coal seams are being mined from the lower 20 m of a nearly vertical highwall (Fig. 3). Above the coal seams is a thick interval dominated by shale, and the total height of the highwall locally exceeds 40 m. At the base of the highwall is a thin, unnamed coal seam. This coal overlies a quartz-rich sandstone that miners in the Carbon Hill area refer to as the Jagger bedrock (Table 1). This sandstone is thought to have been deposited as part of a beach system in an area of high tide range (Gastaldo et al., 1993; Pashin, 1994). Above the unnamed coal is about 3 m of gray shale and mudstone containing abundant plant fossils, including the arborescent lycopod bark impression, *Lepidodendron*, and the horsetail fossil, *Calamites*. The coal and mudstone are thought to be the products of ancient swamps. The coal represents fossil peat, which is a wetland soil made primarily of organic matter, whereas the mudstone is a muddy wetland soil that accumulated during major flood events as sediment-laden streams overflowed their banks into the swamps (e.g., Demko and Gastaldo, 1992).

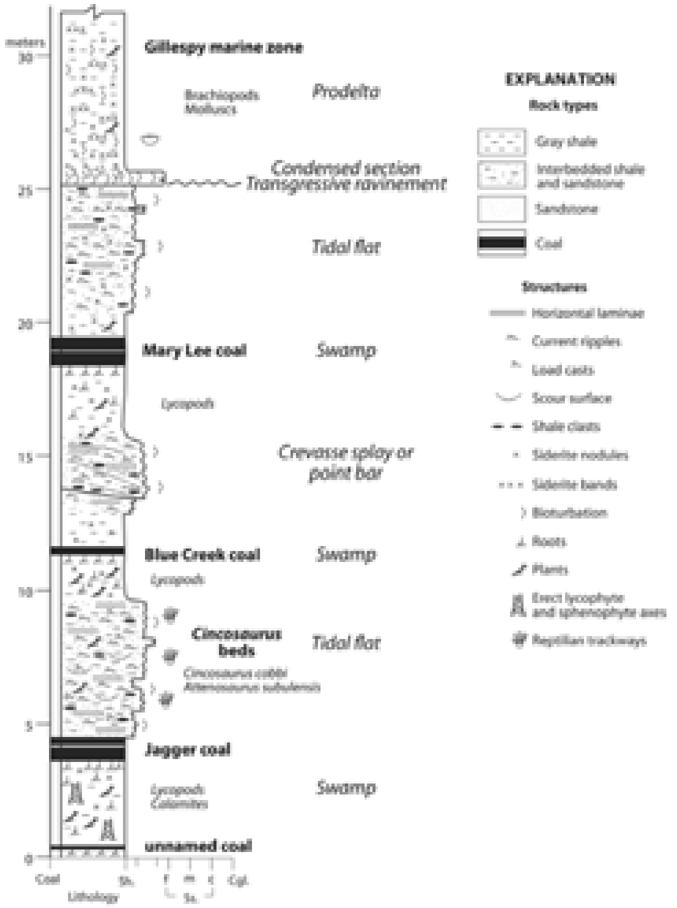


FIGURE 3. Schematic stratigraphic section showing the four coal seams being mined at the CVM. Standard terminology is used for different rock types and sub-units.

The Jagger coal overlies the plant-bearing mudstone (Fig. 3). With a thickness of about 1 m, the Jagger seam provides one of the principal mining targets in the Carbon Hill area. The coal is blocky and contains a very dark gray mudstone bed. Where measured, the mudstone bed is 0.15 m thick and is 0.30 m below the top of the coal seam. This coal represents renewed establishment of widespread peat-forming swamp environments in western Walker County. The mudstone layer within the coal can be correlated among outcrops and in the subsurface, and thus represents a significant interruption of peat deposition, which will be discussed later in the section on stratigraphic correlation. Pillars of the coal left over from older underground mining operations are exposed in the CVM highwall, and the strata forming the roof of the Jagger seam have collapsed into the voids among the old mine pillars (Fig. 2).

The *Cincosaurus* Beds

The roof strata above the Jagger coal are highly fractured and unstable. Examination of these strata in the highwall and in fresh mine spoils proved rewarding because they contain well-preserved specimens of *Cincosaurus cobbi* and reveal a distinctive depositional style. Because most if not all tetrapod trackways from the CVM were recovered from the interval between the Jagger and Blue Creek seams, these strata are called the *Cincosaurus* beds. This name also was applied to the trackway-bearing part of the Mary Lee coal zone at the Union Chapel Mine by Pashin (2005) (Table 1).

The *Cincosaurus* beds at CVM are dominated by thinly interbedded dark-gray shale and medium- to light-gray siltstone and sandstone (Fig. 4). Pinstripe, lenticular, wavy, and flaser bedding are present throughout the interval, and current-ripple cross-laminae are abundant. Most beds within the *Cincosaurus* beds form graded sandstone-shale couplets thinner than 3 cm. Other primary sedimentary structures in the *Cincosaurus* beds include load casts, flute casts, and a variety of other sole markings. Structures on the tops of the beds include sinuous ripple marks, wrinkle marks, and crater-like circular impressions. Prostrate plant fossils occur sporadically in the *Cincosaurus* beds and include lycopod axes and fern-like foliage. Progressive thickening and thinning of successive graded sandstone-shale couplets is a distinctive attribute of the *Cincosaurus* beds. Analysis of correlative strata at a nearby coal mine by Demko et al. (1991) and Sonett et al. (1996) indicates that this progression is cyclic, with an average periodicity of 18 couplets per cycle. A 1.8 m interval of sandy underclay gradationally overlies the trackway-bearing interval and is, in turn, overlain sharply by the Blue Creek coal (Fig. 3). The underclay contains abundant specimens of *Stigmaria*, which is a name applied to the root systems of lycopods rather than a unique taxon.

TABLE 1. Correlation of coal seams and the *Cincosaurus* beds in the Mary Lee coal zone.

Carbon Hill area, Crescent Valley Mine	Cordova area, Union Chapel Mine	Subsurface of Walker, Jefferson, and Tuscaloosa Counties	Blue Creek syncline, Jefferson and Tuscaloosa Counties
New Castle coal	absent	New Castle rider	absent
Mary Lee coal	New Castle coal	New Castle coal	New Castle coal
Blue Creek coal	absent	unnamed coal	absent
Cincosaurus beds	*Cincosaurus* beds	unnamed shale and sandstone	unnamed shale and sandstone
Jagger coal	Mary Lee coal	Mary Lee coal, Blue Creek coal	Mary Lee coal, Blue Creek coal
unnamed coal	absent	Jagger coal	Jagger coal
Jagger bedrock	Lick Creek Sandstone	Lick Creek Sandstone	Lick Creek Sandstone

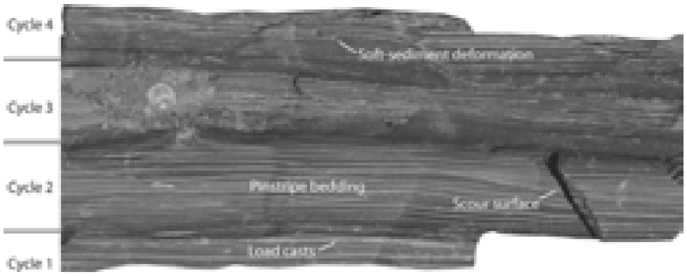


FIGURE 4. The *Cincosaurus* beds at the CVM included inter-bedded dark gray shale and medium to light gray siltstone and sandstone.

The graded sandstone-shale couplets indicate that sedimentation was episodic and dominated by suspension settling of sand and mud in response to decelerating flows. Load casts and other soft-sediment deformation structures indicate that the sediment was highly fluid at the time of sedimentation. Flute casts and other sole markings indicate that the base of many sandstone layers is erosional and that the tidal currents were at times capable of transporting larger objects than is indicated by the fine grain size of the sediment alone. Indeed, no plant fossils were observed in life position in the *Cincosaurus* beds; they were instead transported by currents to the site of deposition. This is a major contrast with the *Cincosaurus* beds at the Minkin site where erect axes of seed ferns and *Calamites* were observed (Pashin, 2005). Current-ripple cross-laminae in the *Cincosaurus* beds indicate that turbulent flows were common, whereas pinstripe bedding indicates frequent laminar flows as well. Circular impressions are abundant at the Minkin site and are thought to be principally gas-escape structures (Rindsberg, 2005), and some may be raindrop imprints (Pashin, 2005).

Demko and Gastaldo (1992) interpreted strata equivalent to the *Cincosaurus* beds as a freshwater to brackish tidal flat deposit, and observations at the CVM are consistent with a variable salinity, tidally-influenced, coastal plain system. The cyclicity of the sandstone-shale couplets is indicative of spring-neap tidal cycles. The 18-event periodicity of the cycles recognized by Demko et al. (1991) is suggestive of a strongly asymmetrical, mixed system of diurnal (daily) and semidiurnal (twice daily tides). A true diurnal system would have periodicity of 14 tides, and the occurrence of additional events may reflect occasional preservation of sediment deposited by the subordinate semidiurnal tide. Alternatively, this periodicity may be influenced by preservational bias related to erosional surfaces and discontinuous layering (Sonnett et al., 1996). The underclay below the Blue Creek coal signifies the encroachment of a muddy wetland into the area of the tidal flat, and the Blue Creek coal marks a return to peat deposition.

Blue Creek Coal Through Gillespy Marine Zone

The Blue Creek coal is about 0.37 m thick at the CVM. The coal is blocky and, in contrast to the other seams at the mine, lacks muddy partings. Above the Blue Creek coal is more than 6.1 m of shale, sandstone, and underclay. The shale and sandstone are similar to those lower in the section, although no confirmed tetrapod tracks have been recovered. The roof of the coal seam is dominated by shale with siderite nodules, and it is difficult to discern internal structures in this part of the section. In the overlying sandstone, grain size and bedding tend to fine and thin upward, respectively. The vertical trend is from flaser and wavy bedding to lenticular and pinstripe bedding. The sandstone-bearing part of this section exhibits the most lateral variation of any stratigraphic unit in the mine. Internal bedding surfaces are inclined, defining accretionary beds with a gentle, northward apparent dip. The sandstone-bearing interval fines upward into about 3 m of mudstone and underclay resembling that below the Blue Creek coal.

The Blue Creek coal signifies renewed establishment of peat-forming environments. The lack of mudstone partings indicates that this part of the swamp was not prone to influxes of muddy sediment. Sedimentary structures in the interbedded mudstone and sandstone section resemble the tidal flat deposits of the *Cincosaurus* beds. However, the accretionary bedding in this interval suggests sedimentation in a tidally-influenced point bar or crevasse-splay system. Similar deposits have been documented in other mines in the Carbon Hill area (Gastaldo et al., 1990). The underclay that caps the mudstone-sandstone interval marks establishment of yet another muddy wetland.

Above the underclay is the Mary Lee coal which, with a total seam thickness of 1.1 m, is the thickest coal exposed at the CVM. A dark gray mudstone parting with a thickness of 0.1 m is developed 0.5 m from the top of the seam and can be traced throughout the highwall. The roof strata above the Mary Lee resemble those above the Blue Creek seam. Gray shale immediately overlies the coal and grades upward into more than 4.5 m of thinly interbedded shale and sandstone that is dominated by lenticular and pinstripe bedding. The upper contact of this unit is sharp and marks the top of the Mary Lee coal zone at the CVM.

The Mary Lee coal was deposited as part of a widespread peat swamp, and the thin parting in the upper half of the seam marks an episode when muddy sediment flowed into the mire, thus interrupting peat accumulation. The thinly interbedded shale and sandstone above the coal is interpreted as another tidal flat deposit similar to the *Cincosaurus* beds. The sharp contact at the top of the Mary Lee coal zone is a widespread erosional surface that extends throughout most, if not all, of the Black Warrior basin (Liu and Gastaldo, 1992; Pashin, 2004). Indeed, the New Castle coal, which is a thin (< 7 cm) coal in the Carbon Hill area, is absent at the CVM. Stratigraphic cross sections indicate that the New Castle bed has been eroded at many locations near Carbon Hill (Gastaldo et al., 1990; Liu and Gastaldo, 1992). This surface has erosional relief less than 4.5 m and is thought to have formed as a ravinement generated by marine flooding and shoreface erosion during a major rise of sea level (Liu and Gastaldo, 1992).

Above the Mary Lee coal zone is a calcareous sandstone unit that is 0.52 m thick and contains a thin shaly parting 0.18 m from the base. The sandstone is mottled with burrows, and many of the burrows are filled with siderite. At the upper contact the sandstone grades into a thick interval of gray shale with pebble- to cobble-size siderite concretions. This shale is part of the Gillespy marine zone, which overlies the Mary Lee coal zone throughout the Black Warrior basin. The shale is bioturbated, and some of the concretions contain shells of brachiopods and molluscs, pyrite nodules, and plant fragments. Forming the upper 15 m of the mine highwall, the shale is largely inaccessible.

The calcareous sandstone above the Mary Lee coal zone is interpreted as a condensed deposit that formed during the most rapid part of the sea level rise. The calcareous sandstone is widespread in the Black Warrior basin, and the characteristics of the deposit vary among outcrops. Whereas only siderite-filled burrows were observed at CVM, other outcrops contain an array of marine body fossils, including brachiopods, molluscs, crinoid ossicles, and solitary rugose corals (Gastaldo et al., 1990; Liu and Gastaldo, 1992). The fossiliferous shale above the sandstone forms a thick, regionally extensive marine zone. The shale was deposited in prodelta and delta front environments during a major highstand of relative sea level that followed inundation of the entire Black Warrior basin (Pashin, 1994; Pashin and Raymond, 2004). Although this shale records the youngest Pottsville sedimentation at the CVM, several younger marine zones and coal zones are preserved farther south in the interior of the Black Warrior basin and provide many opportunities for paleontologic and sedimentologic discovery.

Crescent Valley Trace Fossil Beds

Most of the trace fossils from the Crescent Valley Mine have been recovered from mine tailings. Part of the challenge is therefore in assigning trace fossils to particular beds and facies. It is unclear if *Cincosaurus* and *Attenosaurus* are restricted only to the *Cincosaurus* beds, considering that similar strata occur at multiple stratigraphic levels. However, our surveys of the mine face and the mine tailings indicate that tetrapod tracks are rare outside of the *Cincosaurus* beds. Tracks were only found in spoil piles that the mine manager said were made of Jagger shale; piles made of shale from above the Blue Creek and Mary Lee coal beds did not yield tracks. Also, a limited amount of *in situ* collecting verified the location of the *Cincosaurus* beds. The cavity shown in Figure 2 yielded a large slab (CVM 201) with 35 footprints of *C. cobbi* along a trackway nearly a meter long. This was found in collapsed roof shale and would have come from the original Aldrich and Jones layers within a meter of the top of the Jagger coal bed. Higher layers than these also were found to contain tracks: several small slabs with *C. cobbi* tracks were pulled directly out of the highwall 2.5-3 m (8-10 ft) above the top of the Jagger coal bed at two different locations. This is still several meters below the Blue Creek coal bed.

The invertebrate trace fossils discovered from CVM are frequently found on small slabs and are rarely preserved together with vertebrate trackways. The principal exceptions are *Arenicolites* and *Treptichnus* burrows associated with *Cincosaurus*. Many of the other invertebrate ichnofossils occur in similar strata, but it is not possible to rule out that they may come from other parts of the Mary Lee coal zone. Indeed, considerable work remains to increase our understanding of the composition and interrelationships among the trace fossil assemblages at the CVM.

The occurrences of *Cincosaurus* and *Attenosaurus* differ markedly from those at the Minkin site, where the trace fossil assemblage is much more diverse and includes *Kouphichnium* and several additional vertebrate ichnotaxa, including those made by amniotes and anamniotes (Haubold et al., 2005). The *Cincosaurus* beds at the Minkin site were interpreted primarily as a fresh-water deposit in which tidal cyclicity is extremely weak. In contrast, the strong spring-neap cyclicity at CVM combined with the more restricted ichnofossil assemblage suggests stronger tidal influence and perhaps variable salinity, freshwater to brackish conditions. The makers of *Cincosaurus cobbi* and *Attenosaurus subulensis* were amniotes (Haubold et al, 2005), and thus better adapted to cope with saline water than temnospondyl amphibians, which are conspicuously absent from CVM. However, much remains to be learned about the environmental tolerances of early tetrapods, which may differ from those of modern taxa (Laurin and Soler-Gijon, 2010).

Staub and Esterle (1994) suggested that the Rajang Delta of Indonesia is a useful modern analog for Pennsylvanian coal-bearing deposits. Pashin (2005) noted that the combination of beach and deltaic deposits on the Rajang is similar to the deposits preserved in the Mary Lee coal zone (Fig. 5). The quartzose sandstone of the Jagger bedrock has been interpreted to include ancient beach sand, and the mud-rich coal-bearing strata of the Mary Lee coal zone represent a tidally influenced deltaic complex. Within this context, the Minkin site probably represents the inland part of the deltaic system, where fresh water conditions prevailed and riverine processes dominated over tidal processes. By contrast, the CVM appears to represent environments closer to the strandline, where brackish conditions and tidal processes prevailed.

Correlation of Coal Seams and the *Cincosaurus* Beds

Aldrich and Jones (1930) discovered *Cincosaurus cobbi* and *Attenosaurus subulensis* in the roof strata of the Jagger coal seam near the CVM. At the Minkin site, however, the *Cincosaurus* beds occur in the roof strata of the Mary Lee coal seam. Thus, at first glance, it would appear that the *Cincosaurus* beds occur at different stratigraphic intervals of the Mary Lee coal zone in different parts of the Black Warrior basin. However, one must be very careful when applying the names of coal seams in disparate areas, because coal seams commonly split and merge and are discontinuous (e.g., Ferm and Weisenfluh, 1989). In the case of the Mary Lee coal zone, nomenclature is complicated by the fact that mining began independently in different parts of the basin. Although four names (Jagger, Blue Creek, Mary Lee, New Castle) are applied to coal seams of the Mary Lee zone throughout the basin, it is not clear that those names were always applied consistently. Subsurface drilling for natural gas in the Pottsville Formation, however, provides a wealth of stratigraphic information that enables refinement of the correlations among coal seams (e.g., Pashin and Raymond, 1994) (Table 1).

During the late 1850s, coal mining began along the southeastern margin of the Black Warrior basin in an area called the Blue Creek syncline in Jefferson and Tuscaloosa Counties. Many of the seam names, such as Jagger and Blue Creek, originated in that area (McCalley, 1886; Semmes, 1929). Mining began shortly thereafter across the basin in Walker County, and miners immediately began applying the seam names that were already in use, and named additional seams, such as the New Castle coal. Table 1 shows the results of correlating coal seams from the Blue Creek syncline through the gas fields of Tuscaloosa and Walker Counties to the Union Chapel and Crescent Valley mines. This exercise demonstrates the complex nomenclature that has been applied in the Mary Lee coal zone, as well as distinct inconsistency in the application of the classic seam names. The end result is that the Mary Lee coal of the Minkin site correlates with the Jagger coal at the CVM and that the *Cincosaurus* beds constitute the same stratum at each locality. Accordingly, occurrences of *Cincosaurus cobbi* appear to be restricted to a narrow stratigraphic interval but cover much of Walker County (Fig. 6). Considering that the trackway beds cover an area of at least 400 km^2, Walker County can be classified as a megatracksite, following the terminology of Lockley and Meyer (2000).

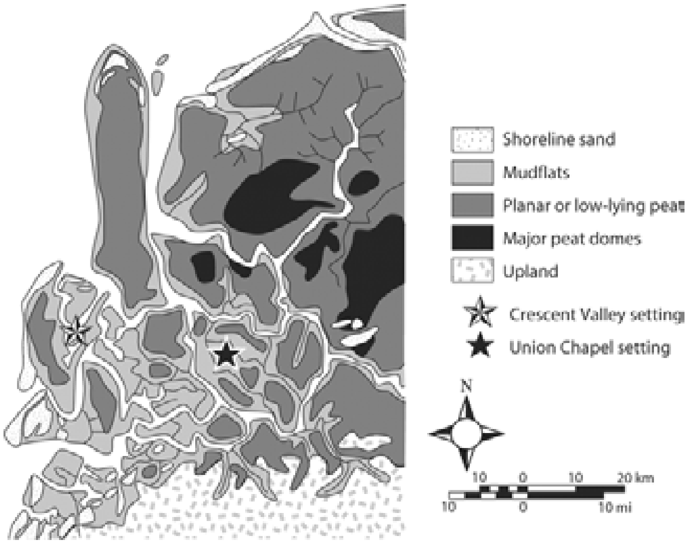


FIGURE 5. Schematic of the Rajang delta in Indonesia, a modern analog of Pennsylvanian coal-bearing deposits.

DESCRIPTION OF CVM TRACE FOSSILS

Methods

Standard trackway parameters have been used to characterize the vertebrate trace fossils found at the CVM. These include the pace, stride, trackway width, width of individual tracks, and pace angulation. Pace is the distance from the base of manus digit imprint III to the base of the same digit imprint on the next manus track. Stride is the distance from the base of manus digit imprint III to the base of the same digit imprint on the next manus track on the same side of the body. Track width was measured normal to the midline. Trackway width was measured between the outermost parts of tracks on each side of the mid-line, also normal to the

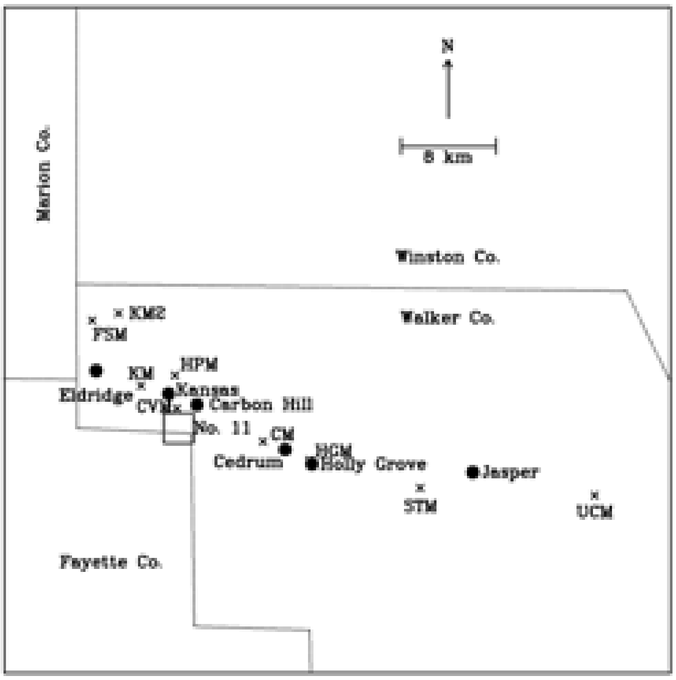


FIGURE 6. A map of all known track sites in Walker County, Alabama, relative to the cities of Eldridge, Kansas, Carbon Hill, Holly Grove, and Jasper. The mines shown are: CM-Cedrum Mine; CVM-Crescent Valley Mine; FSM-Fern Springs Road Mine; HGM-Holly Grove Mine; HPM-Hope Pit Mine; KM-Kansas Mine; KM2: Kansas Mine No. 2; No. 11 Mine-Galloway Coal Company mine where first tracks were documented; square indicates rough actual size; STM-Sugar Town Mine; UCM-Union Chapel Mine (=*Steven C. Minkin Paleozoic Footprint Site*).

mid-line. Pace angulation is the angle defined by connecting the bases of manus digit imprint III on three successive manus prints. Because most specimens are undertracks, measurements are not strictly comparable to those that would have been made on surface tracks. However, the only measurement likely to be greatly distorted is track length. This is because the tips of the grooves made by toes tend to disappear rapidly in undertracks as one moves down from the sediment surface.

All trackway measurements were made on digital photographs posted on the website http://bama.ua.edu/~rbuta/cvm/cvm.pl. All of these photographs were taken in full sunlight at medium to very low sun angle, usually in both full slab view and multiple close-ups. A mm ruler scale was included in all photographs, and every specimen was assigned a running CVM number and catalogued.

Vertebrate Trackways

Two vertebrate trackway ichnospecies have been recognized at the CVM: *Cincosaurus cobbi* and *Attenosaurus subulensis*. The former is attributed to an amniote and the latter to an anthracosaur (Haubold et al. 2005). *C. cobbi* is the most abundant tetrapod trackway found at the CVM. The ichnotaxonomy of *Cincosaurus* and similar trackways is in need of revision. Pending a full revision, and for simplicity, we follow the assignments of Haubold et al. (2005).

Attenosaurus subulensis Aldrich, 1930

Figs. 7-8

The holotype of this ichnospecies has been lost, but numerous specimens from the Minkin site allowed Haubold et al. (2005) to document its characteristics. The only reservation they had about referring Minkin site specimens to *Attenosaurus* is the possibility that *A. subulensis* (rare large tracks) and *Cincosaurus cobbi* (common small tracks) were made by different-sized members of a single tetrapod species. Haubold et al. (2005) did not attempt to test this hypothesis. Minkin site specimens referred to *A. subulensis* by Haubold et al. (2005) have: manus and pes tracks with five digit imprints; are larger than specimens referred to *C. cobbi* (up to 25 cm in pes track length); exhibit a wider trackway pattern; and have different digit imprint proportions (pes digit imprint IV is shorter than III). With one exception, CVM specimens of *A. subulensis* are too few and too fragmentary to add much to our knowledge of ichnospecific morphology, and they do not provide enough information to answer the question of whether the two ichnospecies are characterized by distinct size distributions. The CVM specimens extend the known paleogeographic range of the ichnospecies, but only slightly, because the CVM is very close to the Galloway No. 11 mine, where the original type specimens of *A. subulensis* were collected by Aldrich and Jones (1930).

The specimens shown in Figures 7A and B are single footprints on relatively large slabs with no other tracks included. Both are deeply impressed and may be *A. subulensis* surface tracks. The main track seen in Figure 7C is one of the largest footprints found at the CVM. The tracks in Figure 7D appear to be deep undertracks made when the animal was likely moving slowly.

The longest *A. subulensis* trackway found at the CVM was on a 1-2 ton slab, and comprises nine footprints, including seven pes tracks and two manus tracks, in a trackway 1.17 m long (CVM 1100, Fig. 8A-B). The three front tracks are impressed in a slightly higher layer than the rest of the tracks and are doubled. The other tracks are deeper single undertracks. From three of the large pes tracks we estimate a stride of 33.8 cm, a pace of 21.8 cm, and a pace angle of 157°. The ratio of pace to stride is 0.6. Pes tracks are 15.7 cm long x 6.9 cm wide; manus are 5 cm long x 4.8 cm wide, on average. Manus track width is 0.7 times pes track width. The three front tracks are all pes tracks averaging 18.8 cm x 7.6 cm. The reason for the doubling of these tracks is unknown, but they may be pes-over-manus prints.

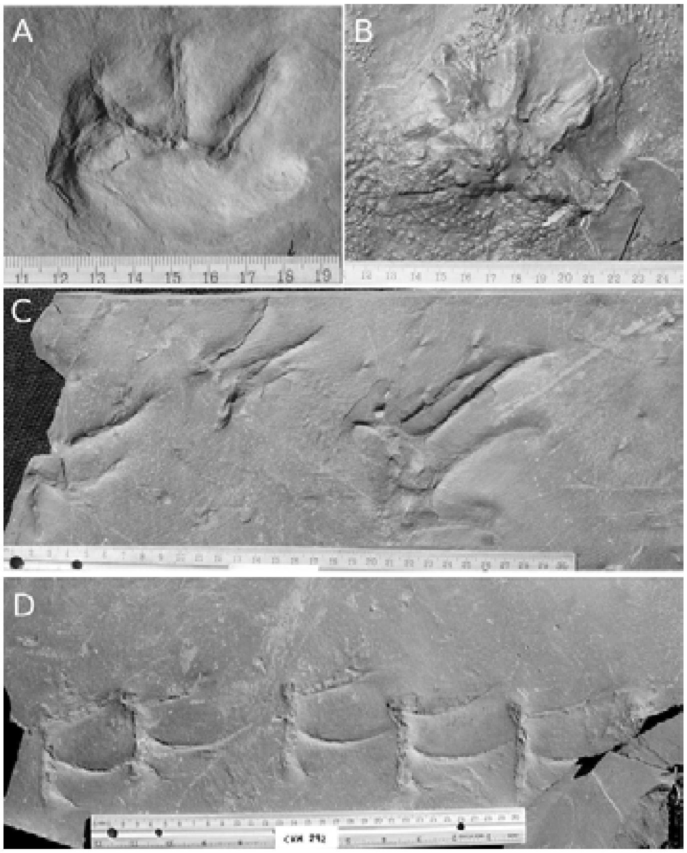


FIGURE 7. *Attenosaurus subulensis*, Crescent Valley Mine, scales in cm. **A**, Single track, negative epirelief, CVM 1036; **B**, single track, positive hyporelief, made on previously dimpled sediment surface, CVM 637; **C**, parts of three tracks, negative epirelief, CVM 641; **D**, five tracks, negative epirelief, CVM 292.

Cincosaurus cobbi Aldrich, 1930

Figs. 9-12

This taxon was revised by Haubold et al. (2005), which can be referenced for emended diagnosis and synonymy. Specimens from the CVM, like those from the Minkin site, are primarily undertracks. They have characteristics consistent with those of *C. cobbi* as described by Haubold et al. (2005) and by Aldrich and Jones (1930). These include: manus tracks with digit imprints splayed; track turned towards the mid-line, with the middle digit imprint at an angle of about 40° to 55° to the direction of travel; digit imprints I to IV successively longer; digit imprint V slightly shorter than III (CVM 1079, Fig. 9C); digit imprints straight or gently curved medio-posteriorly; and digit imprint I short and shallowly impressed. In the undertrack in Figure 9C, digit imprint I is visible only in some manus tracks, and four of the eight manus tracks in this trackway exhibit deeply impressed heel marks. Another shallow undertrack (CVM 786, Fig. 10C) has the best definition of manus digit imprints. This track shows clearly that digit imprint I is by far the smallest, and that digit imprint II is at least 3/4 length of the remaining three. This undertrack is probably slightly deeper than that illustrated in Figure 9C, as indicated by the faint and featureless heel impressions in the former.

Pes tracks in Figure 9C are limited to the imprints made by digits II to IV. There is no heel impression. The two medial digit imprints are long and sinuous, and parallel to the direction of travel. They were made by toes II and III. These are the most deeply impressed, and III is longer than II. Lateral to these, digit imprint IV angles outward at 15° to 35°. Digit imprint V is visible in two pes tracks; its angle of inclination is the

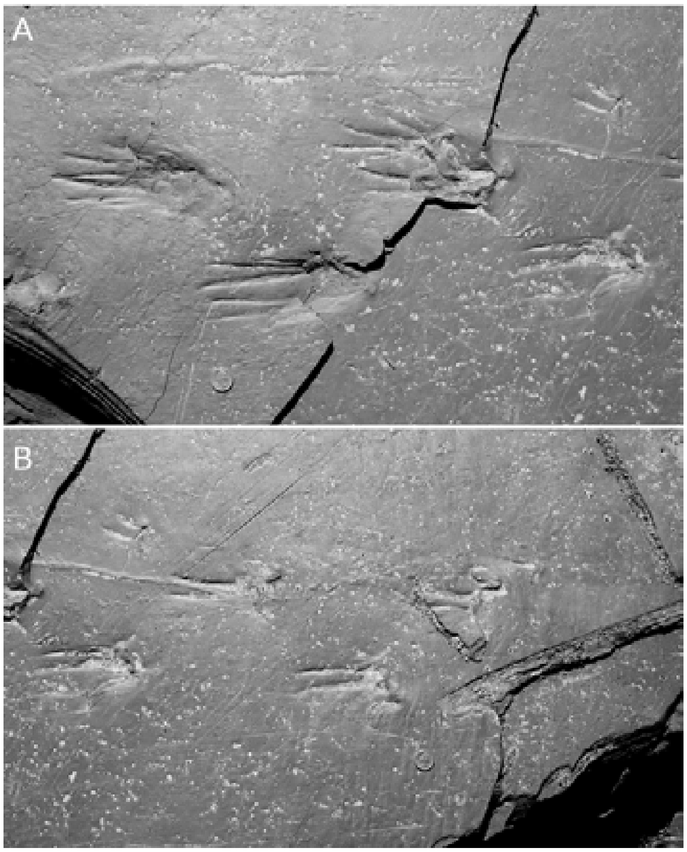


FIGURE 8. *Attenosaurus subulensis*. CVM 1100, the longest trackway of this type found at the CVM. The trackway is 1.17 m long and is shown in two parts. The pictures were taken on-site at low Sun angle. The quarter has a diameter of 0.955 in (2.426 cm). The three main tracks in **A** are doubled and are on a slightly higher layer than the other six. The tracks were in negative epirelief on part of a 1-2 ton slab and were not successfully retrieved from that slab.

same as that of IV. Some undertracks (CVM 348-9, Fig. 9A; CVM 325, Fig. 11A) indicate a short digit imprint I closer to the center line than the rest, and less deeply impressed. The specimen illustrated in Figure 9A, and other specimens, include up to four dimples at the bases of the digit imprints. At least one of the specimens collected at the CVM shows a complete pes imprint (Fig, 9D, white arrow). Pes dimensions are not determinable from the partial undertracks (the same is true for samples from the Minkin site; Haubold et al., 2005 did not quote any pes dimensions).

Figure 12 shows several possible surface trackways recognized as such because they have deeply impressed tail drag marks and sloppy indistinct footprints. The rows of footprints are relatively close together, indicating a narrow gait. The numbers of toes cannot be counted, and parameters such as pace and stride are not determinable.

Trackway parameters have been measured on eight figured specimens, which were chosen nonrandomly because they illustrated various characteristics of the tracks. An additional random sample of 38 specimens was measured in the same way. Every fifth specimen (by accession number, which corresponds to sequence of collection) was examined, but only 38 of these could be measured, because most of the more than 900 specimens contain too few well-preserved tracks to be analyzed (Table 2). The average trackway is 4.9 cm wide, pace averages 3.7 cm, and stride averages 5.9 cm. Manus tracks average 1.6 cm wide and 1.8 cm long; pace angulation averages 107º. Manus track length is a minimum, because digits commonly are truncated in undertracks. All specimens form a coherent array of values for every size measure (Fig. 13A).

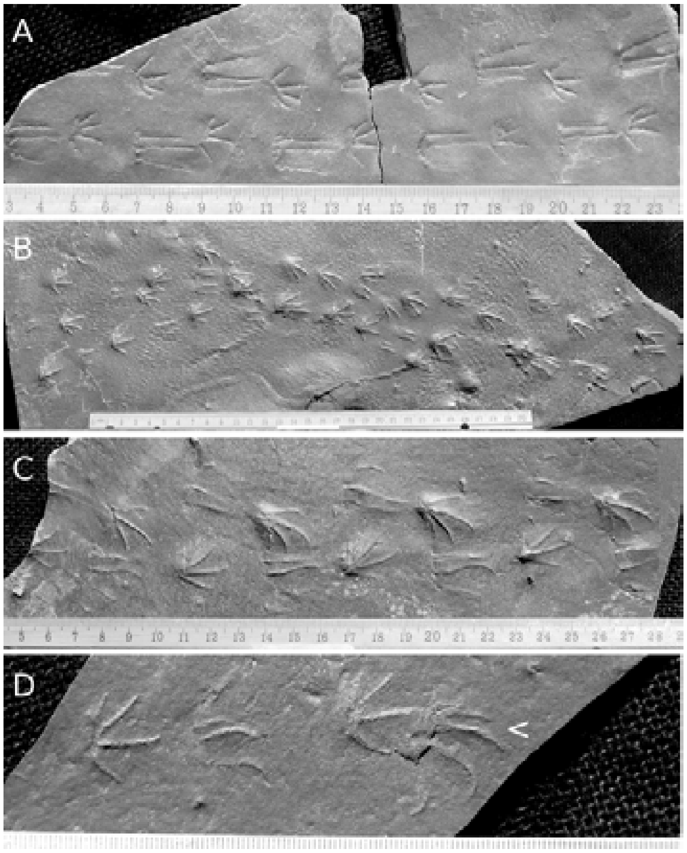


FIGURE 9. *Cincosaurus cobbi*, Crescent Valley Mine, scales in cm. **A**, Well-preserved undertrack made by an animal moving from left to right, manus in front of pes, negative epirelief, CVM 348-349; **B**, Two undertracks that cross, one made center left to lower right (equal spacing) and the other lower left to center right (manus in front), positive hyporelief, meandering horizontal burrow in lower left, foam marks, CVM 634; **C**, Well-preserved undertrack made by an animal moving from left to right, equal spacing, positive hyporelief, CVM 1079. **D**, Complete pes print (short arrow) in *Cincosaurus cobbi*, CVM 15.

Invertebrate Trace Fossils

The Crescent Valley Mine invertebrate ichnofauna consists of *Arborichnus*, *Tonganoxichnus*, *Lockeia*, *Arenicolites*, *Treptichnus*, *Stiaria*, and transitional *Diplichnites*-*Diplopodichnus* traces. Also present are chevronate, feather-stitch and leveéd trails that are similar to *Dendroidichnites*, *Protovirgularia* and *Nereites*, respectively. However, these three morphologies of trails are also observed to intergrade with one another and also extend to string-of-pits, crescent-shaped, and looping *Gordia*-like forms. *Kouphichnium* is notably absent.

Stiaria
Fig. 14A

Stiaria is comparatively rare from CVM in contrast to the material recovered from the Minkin site. Despite extensive collecting efforts, the only known specimen consists of several trackways preserved on a single surface (Fig. 14A). The trackways consist of series of two to three tracks with slightly staggered symmetry. Push-back mounds are present behind the tracks. A continuous medial impression is also present. The slightly staggered to almost alternate symmetry of the trackways and presence of a medial impression distinguishes them from *Paleohelcura*

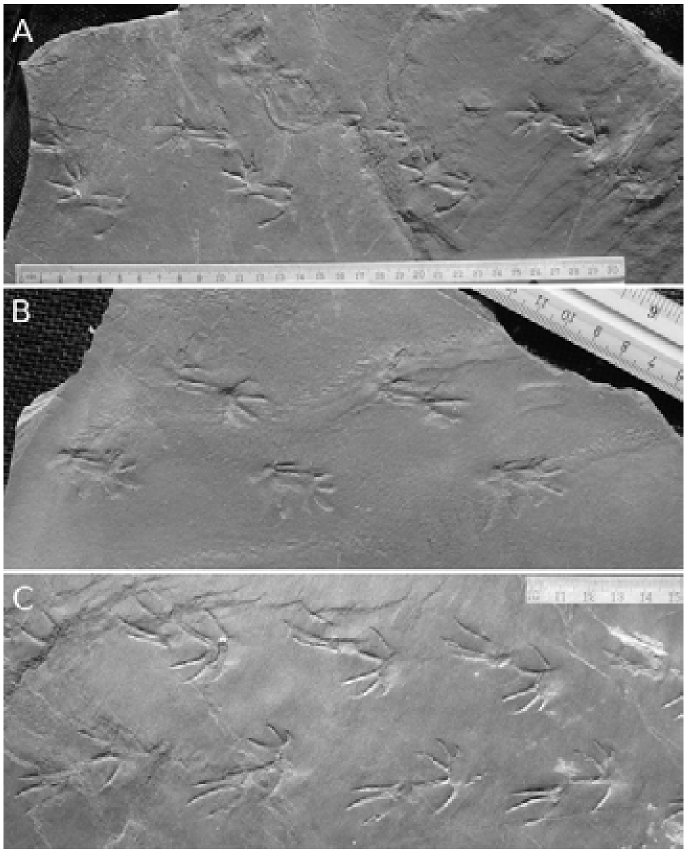


FIGURE 10. *Cincosaurus cobbi*, Crescent Valley mine, scales in cm. **A**, CVM 1081, interesting pattern of nearly overlapping tracks, possible loping gait; **B**, CVM 309, close track pairs with manus in front; **C**, CVM 786, close track pairs with manus behind.

(Gilmore, 1926; Brady, 1947, 1961) and identifies them as *Stiaria* (Smith, 1909; Walker, 1985; Buatois et al., 1998a; Minter and Braddy, 2009).

Tonganoxichnus
Fig. 14B

Tonganoxichnus is also comparatively rare from the CVM. Examples are partial, consisting of a pair of anterior medial linear imprints, one pair of lateral linear imprints and an elongate posterior medial imprint (Fig. 14B). Such a preservational style is similar to many examples from intertidal flat deposits from the type locality of *Tonganoxichnus* in the Carboniferous Tonganoxie Sandstone at Buildex Quarry in Kansas (Mángano et al., 1997) and the Permian Robledo Mountains Formation of New Mexico (Minter et al., 2007; Minter and Braddy, 2009).

Diplichnites-Diplopodichnus
Figs. 14C-D

In addition to *Stiaria* trackways, traces transitional between *Diplichnites* trackways and *Diplopodichnus* trails are also present (Figs. 14C, D). These consist of parallel grooves or ridges with superimposed tracks and are similar to material from tidal flat deposits of the Carboniferous Tonganoxie Sandstone of Kansas (Buatois et al., 1997, 1998a, b).

Chevronate, Feather-stitch and Leveéd Trails
Figs. 15-19A

Chevronate, feather-stitch and leveéd trails make up the majority of invertebrate trace fossils from CVM. The chevronate trails consist of a succession of nested chevrons (Fig. 15A, B) and are similar to examples of *Dendroidichnites* (Demathieu et al., 1992; Buatois et al., 1998a; Minter and Braddy, 2009). The feather-stitch trails are similar but there is a greater degree of separation between the chevrons (Fig. 15B, C). The interior angle between the limbs of the chevrons is also more open and, in some examples, almost forms a single line perpendicular to the mid-line of the trail (Fig. 15D). These trails are similar to some examples of *Protovirgularia* (e.g. Mángano et al., 1998) and some may indeed represent true *Protovirgularia*. The leveéd trails typically comprise a central furrow and then raised ridges of sediment on either side (Fig. 16A), and on occasion these ridges are formed of pads or beads of sediment (Fig. 16B). These traces are similar to some modern trails described as being *Nereites*-like (Martin and Rindsberg, 2007). However, true *Nereites* is an endichnial burrow with an axial tunnel and lateral lobes (Mángano et al., 2000). The chevronate, feather-stitch and leveéd trail forms are observed to intergrade in one "Rosetta stone" specimen (Fig. 17), which indicates that they may all form part of a continuum. However, it cannot be ruled out that particular examples represent truly distinct forms and this awaits further comprehensive study. Circular to ovate impressions are also observed along the lengths or at the terminations of some of the trails (Figs. 16B, 17). The different morphologies of the trails may reflect variations in substrate consistency and the position of the animal relative to the observed plane; whether it be crawling on or just above the surface, plowing through the substrate or shallowly burrowing. These trails also extend to string-of-pits (Fig. 18A), crescent-shaped (Fig. 18B, C) and looping *Gordia*-like forms (Figs. 18D, 19A). A further trace is similar to the chevronate trails but has alternate rather than opposite symmetry

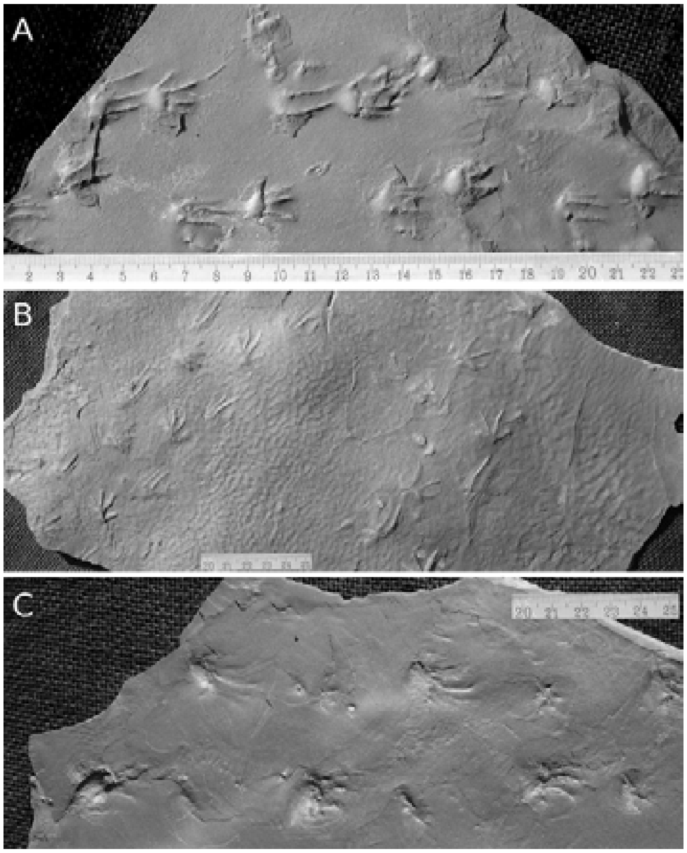


FIGURE 11. *Cincosaurus cobbi*, Crescent Valley mine, scales in cm. **A**, Well-preserved undertrack made by an animal moving from left to right, manus in front of pes, positive hyporelief, CVM 325; **B**, two well-preserved undertracks made by animals moving from bottom to top, pes in front on left, manus in front on right, positive hyporelief, foam marks, CVM 908; **C**, Interesting case of poorly defined shallow undertracks where pes print is large compared to manus; made by tetrapod moving from left to right, evenly spaced, negative epirelief, CVM 182.

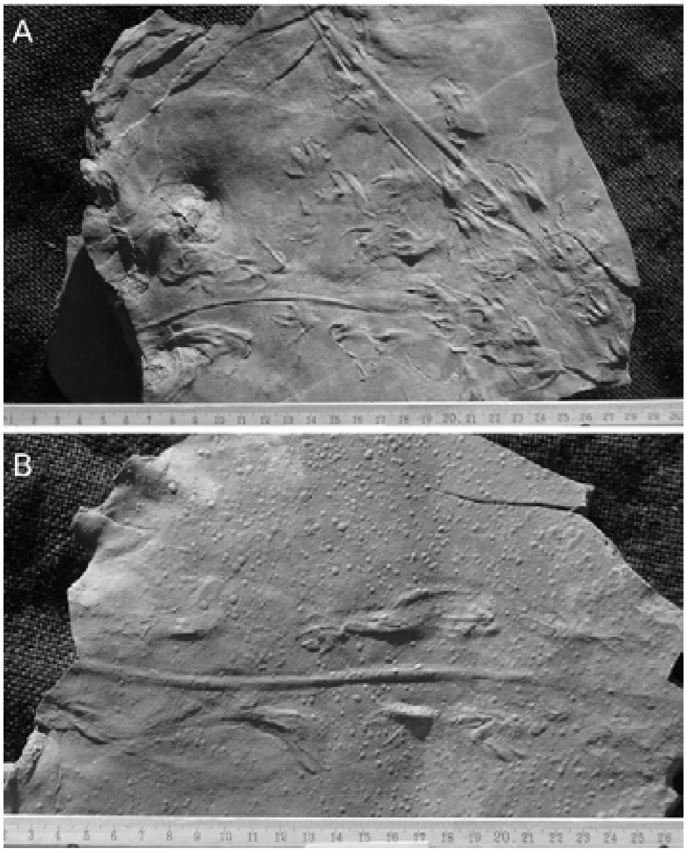


FIGURE 12. *Cincosaurus cobbi*, Crescent Valley mine, surface tracks, scales in cm. **A**, Two tracks with indistinct footprints and tail drag, negative epirelief, CVM 468; **B**, Track with indistinct footprints and tail drag, made on surface subsequently spattered with raindrop impressions, positive hyporelief, CVM 469.

(Fig. 18E). Such a pattern is suggestive of *Lithographus* (e.g. Minter and Braddy, 2009), but the form of the trace is not such that it may be assigned to this ichnogenus with confidence. It is tentatively included within the continuum of chevronate, feather-stitch and leveéd trails herein.

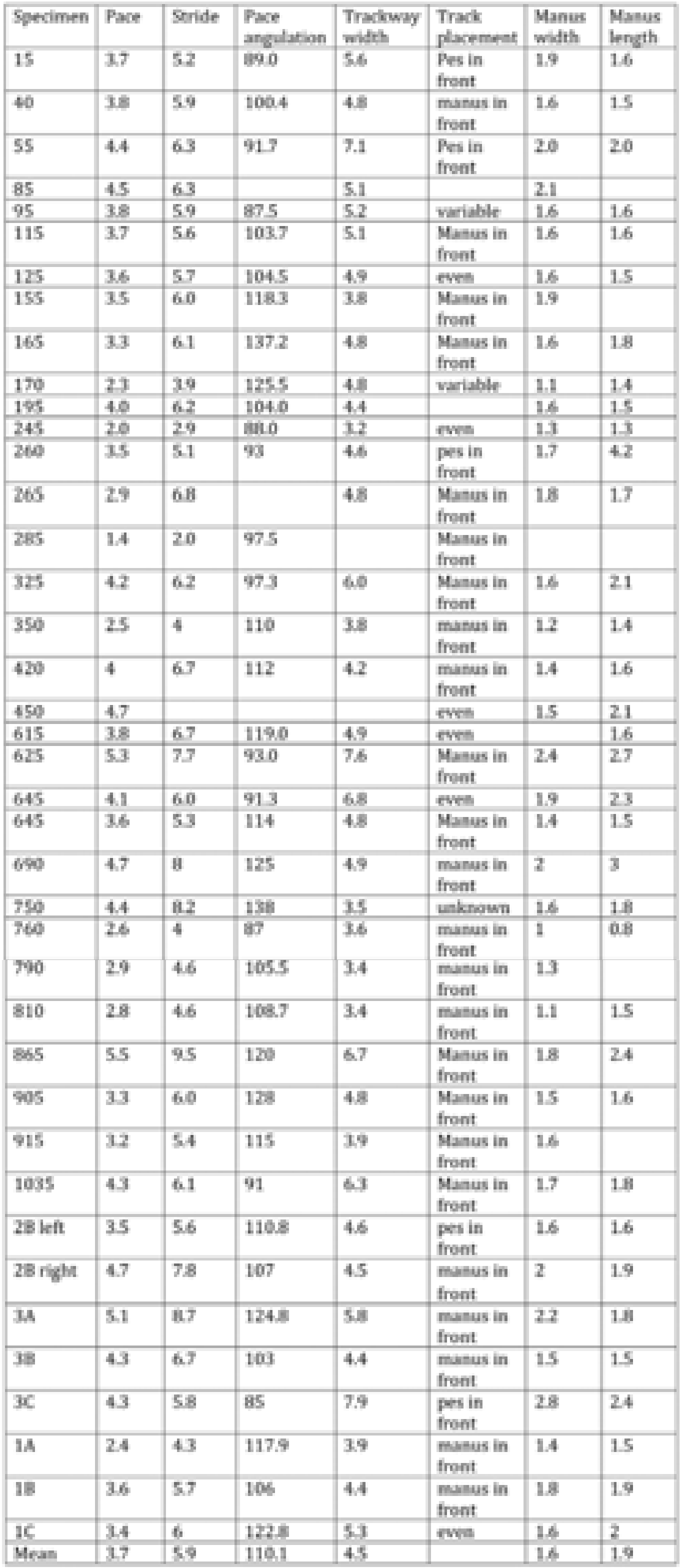
Invertebrate Burrows
Figs. 19B-D, 20A

The infaunal burrows, *Treptichnus* and *Arenicolites*, are also present and in some instances are preserved in association with examples of *Cincosaurus cobbi* (Fig. 19B, D). This scenario is common from the Minkin site (Rindsberg and Kopaska-Merkel, 2005). Examples of *Treptichnus* record the characteristic zig-zag course (Fig. 19B-D) whereas *Arenicolites* is observed as paired burrow tops (Fig. 19D) and the bases of vertical U-shaped burrows (Fig. 20A).

Arborichnus
Fig. 19E, 20A

The CVM section has also yielded examples of *Arborichnus*. In common with the Minkin site, these traces are recorded in a different lithology from those preserving tetrapod trackways and the majority of invertebrate trace fossils (Pashin, 2005). The specimens consist of bilaterally symmetrical scratch traces with five scratch marks on each side oriented perpendicularly to the mid-line of the trace. These traces conform to the diagnosis of *Arborichnus* (Romano and Melendez, 1985). In one specimen, the traces occur in a repeated linear succession (Fig. 19E) as for *A. repetita* (Romano and Meléndez, 1985); whereas they are more random in their distribution and the surface is cross-cut by later shallow U-shaped burrows (*Arenicolites*) in another (Fig. 20A).

TABLE 2. Measurements (in cm and degrees) of CVM trackways.



Specimen	Pace	Stride	Pace angulation	Trackway width	Track placement	Manus width	Manus length
15	3.7	5.2	89.0	5.6	Pes in front	1.9	1.6
40	3.8	5.9	100.4	4.8	manus in front	1.6	1.5
55	4.4	6.3	91.7	7.1	Pes in front	2.0	2.0
85	4.5	6.3		5.1		2.1	
95	3.8	5.9	87.5	5.2	variable	1.6	1.6
115	3.7	5.6	103.7	5.1	Manus in front	1.6	1.6
125	3.6	5.7	104.5	4.9	even	1.6	1.5
155	3.5	6.0	118.3	3.8	Manus in front	1.9	
165	3.3	6.1	137.2	4.8	Manus in front	1.6	1.8
170	2.3	3.9	125.5	4.8	variable	1.1	1.4
195	4.0	6.2	104.0	4.4		1.6	1.5
245	2.0	2.9	88.0	3.2	even	1.3	1.3
260	3.5	5.1	93	4.6	pes in front	1.7	4.2
265	2.9	6.8		4.8	Manus in front	1.8	1.7
285	1.4	2.0	97.5		Manus in front		
325	4.2	6.2	97.3	6.0	Manus in front	1.6	2.1
350	2.5	4	110	3.8	manus in front	1.2	1.4
420	4	6.7	112	4.2	manus in front	1.4	1.6
450	4.7				even	1.5	2.1
615	3.8	6.7	119.0	4.9	even		1.6
625	5.3	7.7	93.0	7.6	Manus in front	2.4	2.7
645	4.1	6.0	91.3	6.8	even	1.9	2.3
645	3.6	5.3	114	4.8	Manus in front	1.4	1.5
690	4.7	8	125	4.9	manus in front	2	3
750	4.4	8.2	138	3.5	unknown	1.6	1.8
760	2.6	4	87	3.6	manus in front	1	0.8
790	2.9	4.6	105.5	3.4	manus in front	1.3	
810	2.8	4.6	108.7	3.4	manus in front	1.1	1.5
865	5.5	9.5	120	6.7	Manus in front	1.8	2.4
905	3.3	6.0	128	4.8	Manus in front	1.5	1.6
915	3.2	5.4	115	3.9	Manus in front	1.6	
1035	4.3	6.1	91	6.3	Manus in front	1.7	1.8
2B left	3.5	5.6	110.8	4.6	pes in front	1.6	1.6
2B right	4.7	7.8	107	4.5	manus in front	2	1.9
3A	5.1	8.7	124.8	5.8	manus in front	2.2	1.8
3B	4.3	6.7	103	4.4	manus in front	1.5	1.5
3C	4.3	5.8	85	7.9	pes in front	2.8	2.4
1A	2.4	4.3	117.9	3.9	manus in front	1.4	1.5
1B	3.6	5.7	106	4.4	manus in front	1.8	1.9
1C	3.4	6	122.8	5.3	even	1.6	2
Mean	3.7	5.9	110.1	4.5		1.6	1.9

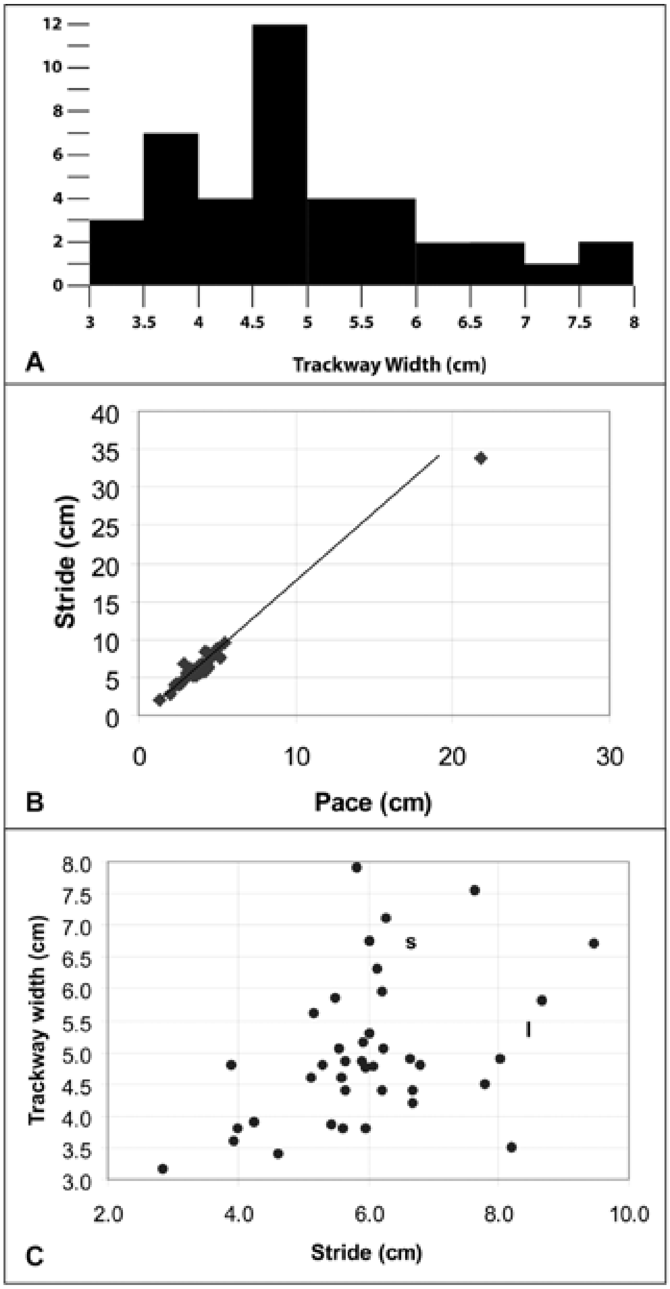


FIGURE 13. **A**, Size distribution of measurements of trackway width in *Cincosaurus cobbi* from the CVM. Unimodal distribution with coarse tail. **B**, Linear relationship between stride and pace in *Cincosaurus cobbi* from the CVM. Large specimen of *Attenosaurus subulensis* fits the trend. Trend line fitted by eye. **C**, Relationship between stride and trackway width for *C. cobbi* from the CVM.

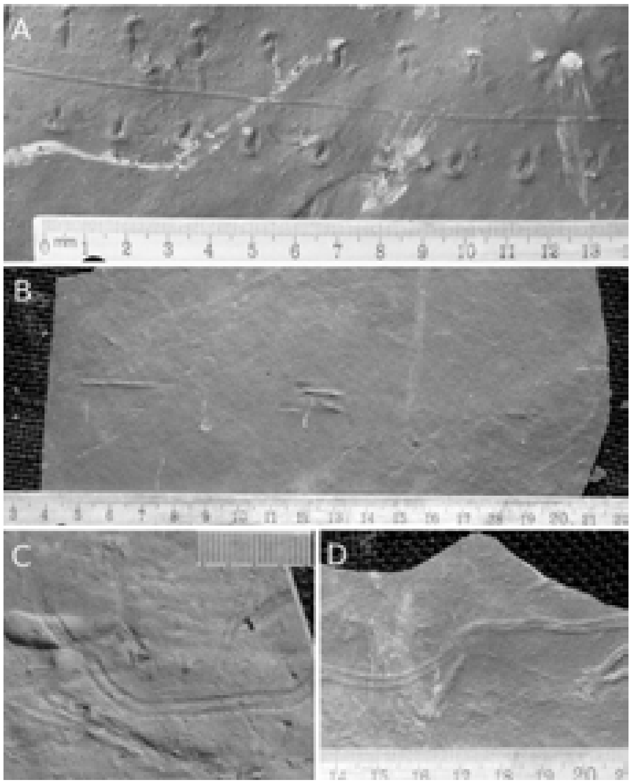


FIGURE 14. Invertebrate traces. **A**, *Stiaria*, CVM 655; **B**, *Tonganoxichnus*, CVM 960; **C**, *Diplichnites-Diplopodichnus*, CVM 221; **D**, *Diplichnites-Diplopodichnus*, CVM 728.

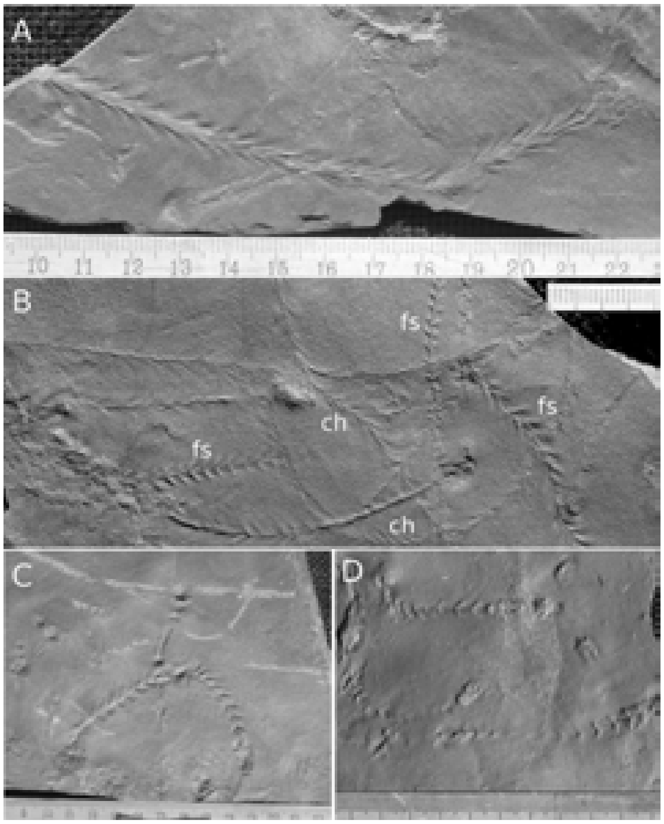


FIGURE 15. Chevronate (**A-B**) and feather-stitch trails (**B-D**). **A**, CVM 27; **B**, CVM 1120, chevronate (ch) and feather-stitch (fs) trails; **C**, CVM 523; **D**, CVM 224.

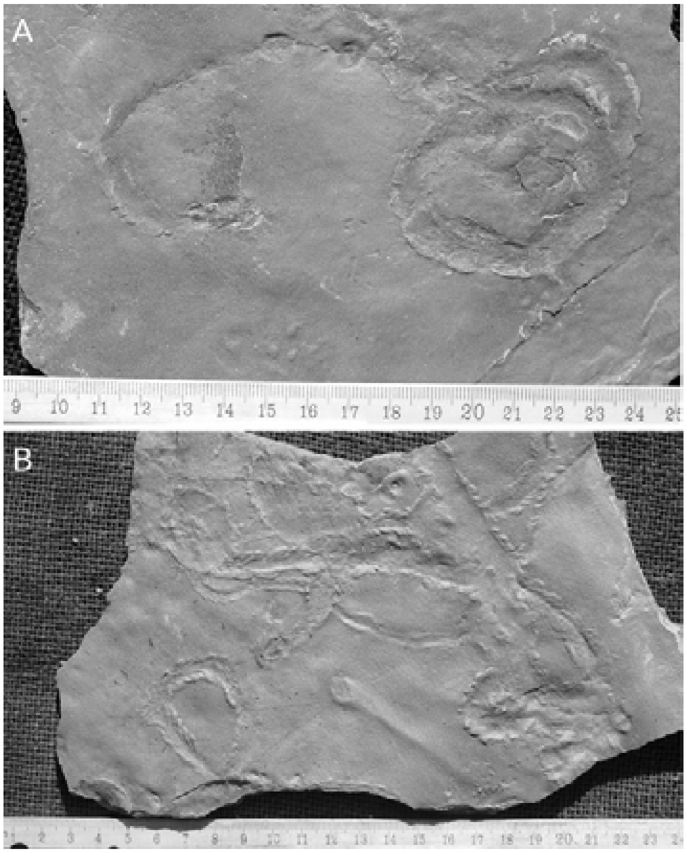


FIGURE 16. Leveéd trails. **A**, CVM 1024; **B**, CVM 955.

Lockeia
Fig. 20B

Material identifiable as *Lockeia* has also been recognized at the CVM. It consists of small, isolated, thin, almond-shaped traces (Fig. 20B) and conforms to the emended diagnosis of *Lockeia* (Schlirf et al., 2001). The figured example also includes a semi-circular region at one end.

Problematica
Fig. 20C

Aldrich and Jones (1930) also described and named a structure as *Ctenerpeton primum*, considering it to be the impression of the abdomen of a lizard-like animal. However, it most likely represents an abiogenic chevron groove produced by a tool moving over the substrate in a flow (e.g. Dzulynski and Sanders, 1962). Similar structures have also been observed in the course of this study (Fig. 20C).

DISCUSSION

Our qualitative observations of CVM trace fossils indicate that vertebrate trackways are strongly dominated by specimens of *Cincosaurus cobbi*, and that the remaining specimens could all be assigned to *Attenosaurus subulensis*. A thorough examination of all vertebrate trackways found at the site did not turn up a single convincing example of a four-digit manus track, considered diagnostic of temnospondyl amphibian trackways. The 46 trackways of *C. cobbi* for which quantitative data were obtained (Table 2, omitting the large *Attenosaurus*) form a coherent array of values for every size measure, and the size distribution is roughly normal, plus the expected coarse tail corresponding to rare large (old) individuals (Fig. 13A). These measurements provide no evidence for the co-occurrence of two or more populations within *C. cobbi*, whether identified as differing species, genders, or age cohorts. Nearly every vertebrate trackway preserved at the CVM was made by a single kind of small amniote.

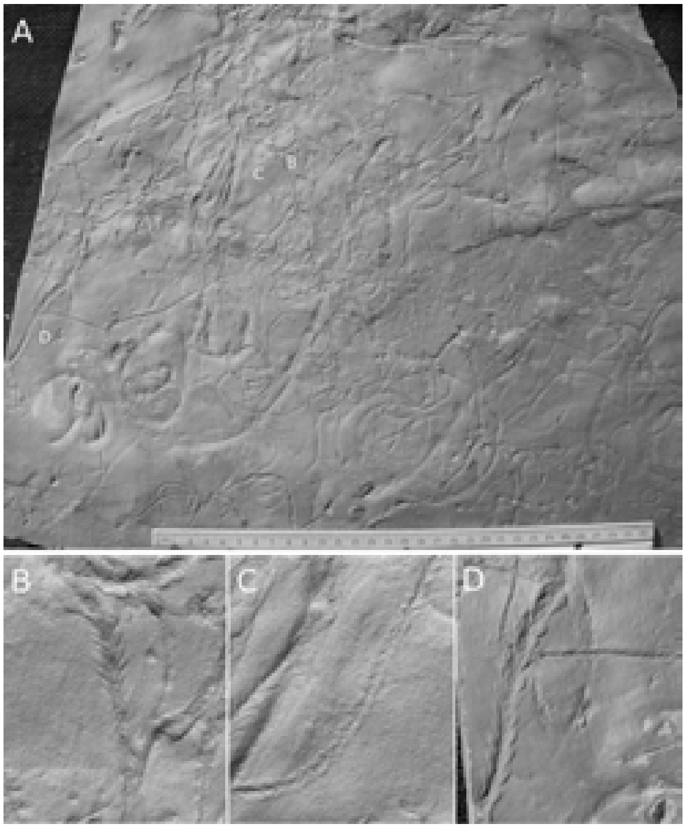


FIGURE 17. Inter-grading of chevronate, feather-stitch and leveéd trails in a single “Rosetta stone” specimen. The points labeled **B**, chevronate, **C**, feather stitch, and **D**, leveéd, are shown enlarged below.

The measured CVM specimens of *C. cobbi* in Table 2 encompass a substantial (5-cm) size range in trackway width. To our knowledge, no comprehensive morphometric study of *C. cobbi* has been made that might explain this, and the CVM data are inadequate for that purpose. Still, a few observations are possible. The smallest *C. cobbi* manus tracks are greater than 1 cm wide. Perhaps fear of predation caused very small *C. cobbi* track makers to avoid the soupy mudflats on which tracks were preserved. Alternatively, the smallest known *C. cobbi* may have been made by hatchlings. It is possible that smaller animals were present, but that their tracks were eroded, rather than preserved. Smaller organisms made lasting impressions on the mud at the Minkin site; the trackways of temnospondyl amphibians and invertebrates much lighter than the makers of *C. cobbi* are common there. By contrast, only a few small arthropod trackways have been found at the CVM. Shallowly impressed tracks that are common at the Minkin site (for example, *Undichna*, *Diplichnites*, *Stiaria*) are rare or absent at the CVM. If water energy was slightly higher at the CVM, faint traces could have been destroyed. At least slightly higher water energy levels at the CVM are suggested by flute casts and ripple-cross strata, which are much more common than at the Minkin site.

The largest *C. cobbi* prints measured are less than 3 cm wide, which may correspond to the largest size commonly attained by the track makers, unless *Attenosaurus subulensis* and *Cincosaurus cobbi* were made by mature and immature specimens of a single tetrapod species. Haubold et al. (2005) deemed this unlikely because of the different relative lengths of digit imprints III and IV in the pes track. Specimens from the CVM shed no light on this matter of pes digit proportions. However, other proportions of the long *Attenosaurus* trackway from

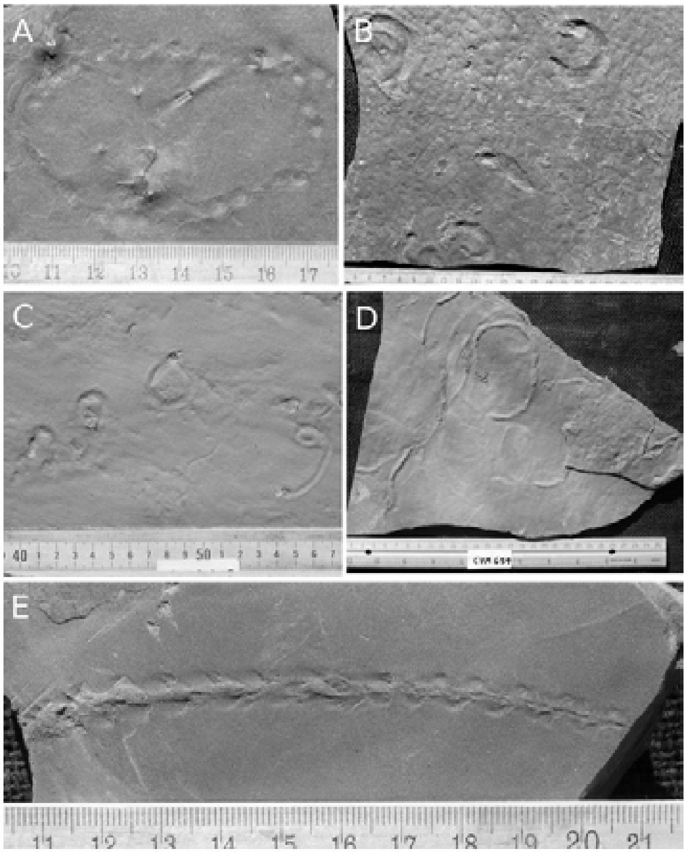


FIGURE 18. Other trail forms. **A**, String-of-pits, CVM 886; **B**, crescent-shaped, CVM 910; **C**, crescent-shaped, CVM 56; **D**, looping form, CVM 654; **E**, form with alternate symmetry, CVM 498.

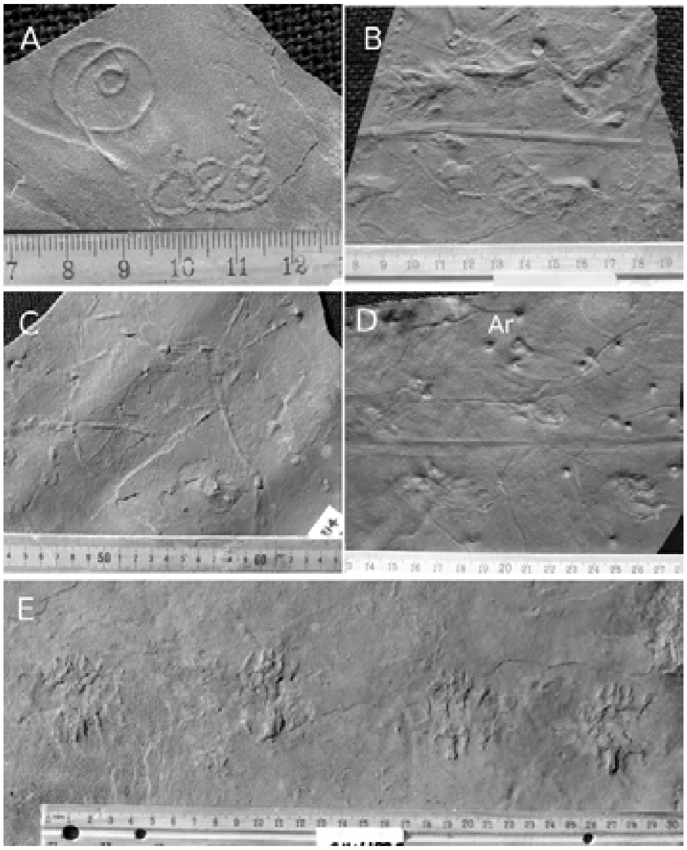


FIGURE 19. Other trace fossils. **A**, Looping form, CVM 872; **B**, *Treptichnus* and *Cincosaurus cobbi*, CVM 365; **C**, *Treptichnus*, CVM 214; **D**, *Treptichnus*, *Arenicolites* (Ar) and *C. cobbi*, CVM 1039; **E**, *Arborichnus*, CVM 1075.

CVM (Fig. 8) are consistent with those of *C. cobbi* from the CVM (Fig. 13B). Although a trendline drawn through the stride and pace data for *C. cobbi* passes very close to the single data point from the large *Attenosaurus* trackway, the size gap (Fig. 13B) is very large. We regard *C. cobbi* and *A. subulensis* as different ichnospecies made by different tetrapod species for two reasons: (1) the great size difference and, (2) the distinct toe morphology reported by Haubold et al. (2005).

Although *C. cobbi* is common at both sites, there were important ecological differences. Temnospondyl amphibians were common at the Minkin site, but conclusive examples have not been found at the CVM. As we noted previously, this suggests that the water at the CVM was perhaps brackish or of more variable salinity than at the Minkin site. In addition, a diverse suite of invertebrate trace fossils that is abundant at the Minkin site is poorly represented at the CVM (*Diplichnites gouldi* on 19 out of 2201 slabs in the Minkin site online database (http://bama.ua.edu/~rbuta/monograph/index.html), 59/2201 *Tonganoxichnus robledoensis*, 542/2201 *Kouphichnium* isp plus *Stiaria* isp, and many hundreds of *Treptichnus apsorum* and *Arenicolites* isp; Kopaska-Merkel, unpublished data). This also might be related to salinity. The presence of *Lockeia* and possible *Protovirgularia* also supports brackish water conditions, at least on occasion; although other trace fossils considered typical of brackish water conditions at this time such as *Teichichnus*, *Psammichnites* and *Asteriacites* (Buatois et al., 2005) are absent.

Spacing of tracks varies from one trackway to another (Table 2; Fig. 10). Some specimens of *C. cobbi* have manus tracks directly in front of pes tracks on either side of the trackway (Fig. 10B), and in some the relationship is reversed (Fig. 10C). The relative positions of manus and pes tracks are related to gait. Specimens with the pes track in front have a shorter stride relative to trackway width (1.0 vs. 1.3) and a smaller pace angulation (93º) than do manus-in-front trackways (110º). Stride is a function of animal size and gait. Trackway width and manus track width are measures of track maker size, so stride is proportional to either for a given gait (c.f., Martin, 2001). By contrast, pace angulation is roughly constant for a given gait. The relationship between stride and trackway width in specimens of *C. cobbi* from the CVM is complex (Fig. 13C). For smaller specimens (trackway width smaller than about 5 cm) most specimens form a single elongate cluster on a graph of stride versus trackway width. Larger specimens form two distinct groups, which are completely separate on the graph. Some individuals took relatively short strides (group "s"), whereas others took longer strides (group "l"). This latter group is characterized by longer manus prints (1.8 to 3.0 cm vs 1.6 to 2.7 cm) and less deeply impressed foot-pad impressions. No evidence of mud spraying behind rapidly moving feet was observed. Group "l" specimens may or may not record faster movement, but Figure 13C does appear to show a differentiation into two different gaits exhibited by larger individuals.

Slabs bearing multiple *C. cobbi* trackways may provide information about interactions between individuals. CVM 908 (Fig. 11B) has two trackways made by animals of about the same size and traveling in the same direction (trackways diverge at an angle of 20º). Both trackways are undertracks, and appear to have been made at a common depth. It is possible that two individuals were moving together. A large slab collected from the Minkin site bears multiple parallel trackways assigned to *Cincosaurus cobbi*, which have been inferred to record group behavior (Martin and Pyenson, 2005). A few other CVM slabs (e.g., CVM 634, Fig. 9B) show multiple trackways that may not be contemporaneous.

Most rock specimens collected at the CVM are relatively small, which limits the opportunity to observe trace fossils in close proximity. Co-occurrence of ichnotaxa on CVM slabs is rare (Figs. 9B, 19B, D, F). Fewer than 2% of samples contain multiple ichnospecies. By contrast, the *Cincosaurus* beds at the Minkin site preserve an ichnofauna that was both more diverse and more densely populated (Buta et al., 2005). For

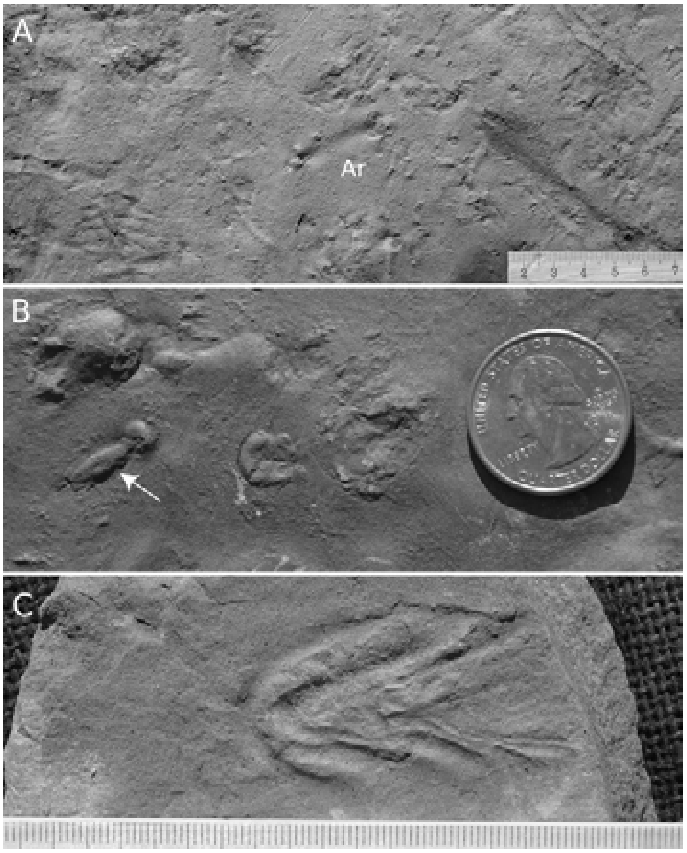


FIGURE 20. Other trace fossils. **A**, *Arborichnus* and *Arenicolites* (Ar), CVM 1077; **B**, *Lockeia* (arrow), field photograph; **C**, *Ctenerpeton primum*, CVM 430.

example, of the 94 specimens of *Undichna* sp. in the Online Trackway Database of Minkin site specimens, about 4% of the entire online database of 2201 specimens, 27 (nearly a third of *Undichna* specimens) co-occur with other ichnospecies (Kopaska-Merkel, unpublished observations). In contrast to the Minkin site, *Undichna* is absent from the CVM. This may be related to the environment and taphonomic conditions, with fish-fin trails and their preservation being most common in inland, freshwater-dominated, low energy parts of tidal flats compared to more seaward environments (Archer, 2004; Voigt et al., 2013).

Of the invertebrate trace fossils, *Tonganoxichnus* and *Stiaria* are both well attributed to apterygote insects including monurans (Mángano et al., 1997, 2001; Minter and Braddy, 2006, 2009). The example of *Tonganoxichnus* resulted as either a resting trace or combined landing and jumping trace; in contrast, the slightly staggered arrangement of the track series in the *Stiaria* indicates they were produced by the legs moving almost in phase as the animal hopped forward a short distance each time. The presence of angular sections in *Treptichnus* indicates that it was made by a short-bodied arthropod and not a vermiform animal. These types of traces are observed to be made by modern insect larvae (Uchman, 2005). *Arenicolites* is attributed to animals including worms and arthropods, and those from the Minkin site have been attributed to the same insect larvae or other arthropod that made *Treptichnus* (Rindsberg and Kopaska-Merkel, 2005). Those *Arenicolites* associated with *Arborichnus* and occurring in a different facies were likely made by different animals from those found with tetrapod trackways and the majority of trace fossils from the CVM.

The chevronate, feather-stitch and leveéd trails are observed to intergrade, which attests to them all being made by the same type of animal. *Dendroidichnites* is generally attributed to a multipodous arthropod such as a myriapod (Buatois et al., 1998a), *Protovirgularia* to a cleft-foot protobranch bivalve (Seilacher and Seilacher, 1994) and *Nereites* to a worm (Seilacher, 1986). The solution as to the producer likely lies in modern *Nereites*-like trails observed being made by juvenile limulids in intertidal sandflats on Sapelo Island, Georgia (Martin and Rindsberg, 2007). Indeed, circular to ovate impressions along the lengths or at the terminations of some of the trails from CVM (Figs. 16B, 17) may represent juvenile xiphosuran resting traces. Alternatively, the possibility that some of these traces were also produced by protobranch bivalves cannot be excluded. This is consistent with the presence of *Lockeia*, which is generally attributed to bivalves (Mángano et al., 1998).

The different morphologies of the trails may reflect variations in substrate consistency and the position of the animal relative to the observed plane, whether it be crawling on or just above the surface, ploughing through the substrate or shallowly burrowing. The trace with alternate symmetry that is tentatively included as part of this continuum (Fig. 18E) is indicative of an animal using an out-of-phase gait. This is characteristic of a hexapod, although the trace lacks other diagnostic features that would allow us to attribute it confidently to such an animal. It may be more parsimonious to include it within the variants of juvenile xiphosuran traces.

The attribution of at least some of the chevronate, feather-stitch and leveéd trails to xiphosurans raises a question. Why is there no *Kouphichnium* at CVM? This ichnogenus is present at the Minkin site but is less common than originally identified (Buta et al., 2005) because the majority of those specimens can be assigned to *Stiaria*. Resolution to this conundrum may be found in the life cycle of xiphosurans. Adults of the extant limulid, *Limulus polyphemus*, migrate onshore en masse to breed. Juveniles then remain in shallow waters for the first couple of moult stages before moving to deeper water (Rudloe, 1979; Shuster, 1979; Braddy, 2001; Martin and Rindsberg, 2007). The trace-fossil recording deposits at CVM may therefore represent such a nursery for juvenile xiphosurans in a shallow water tidal flat setting, where more brackish or variable salinity conditions and tidal processes prevailed. In contrast, *Kouphichnium* at the Minkin site represents the locomotion activities of adult xiphosurans, most likely associated with onshore migration and breeding, in the inland part of the deltaic system, where fresh water conditions prevailed and riverine processes dominated. The rarity of other invertebrate trace fossils such as *Stiaria* and *Tonganoxichnus* at CVM, which are common at the Minkin site, and contrastingly the presence of *Lockeia* and possible *Protovirgularia* at CVM supports this environmental delineation. *Arborichnus*, present at both the CVM and the Minkin site, represents combined swimming and grazing traces of larger adult xiphosurans in more distal facies after they have moved to deeper waters.

CONCLUSIONS

The Crescent Valley Mine near Carbon Hill is now among the best documented tracksites in Alabama. Crescent Valley strata record a different environment than at the Minkin site, which is located 37 km (23 mi) east. Indeed, paleoenvironmental conditions at CVM favored amniotes over temnospondyl amphibians as a dominant vertebrate group, excluded fish-fin traces, and acted as a nursery for juvenile xiphosurans. Although the CVM clearly merits long-term study, the site by law will be fully reclaimed in the near future.

The CVM database provides new and much needed insight into the original No. 11 mine discoveries, by on one hand providing many more specimens from the same area preserved under a wider variety of substrate conditions, and on another by filling the gap on invertebrate traces from the area, which were not described or named by Aldrich and Jones (1930).

We have also shown that the Minkin site and CVM trace fossils are from the same stratigraphic interval, which indicates that Walker County is a megatracksite. Significantly, the megatracksite incorporates an environmental transect from the inland part of a deltaic system, where riverine and fresh water conditions prevailed, to near shore environments, where brackish or variable salinity conditions and tidal processes prevailed. Any new site that opens up in the county and is documented as comprehensively as these mines can add considerably to our knowledge of coastal and coastal-plain environmental conditions and the paleoecology of a wide swath of coal age Alabama.

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GEOLOGICAL REMARKS ON THE CARBONIFEROUS–PERMIAN CONTINENTAL SUCCESSIONS OF SOUTHWESTERN EUROPE

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Abstract—This paper is focused on selected Upper Carboniferous and Permian continental successions of southwestern peri-Mediterranean Europe, in order to discuss key stratigraphic problems and recent field results. Following our previous work, the stratigraphic framework of this region is correlated with geodynamic and geomagnetic events on a large scale.

INTRODUCTION

Upper Carboniferous to Triassic nonmarine deposits of southwestern Europe, around the north Mediterranean domain, are representative of many geological events that can be compared and correlated. In this paper we review and update the most significant stratigraphic sections of this area region by region.

STRATIGRAPHIC FRAMEWORK

Southern Alps

The Late Paleozoic continental successions of the central Southern Alps are mainly characterized by two primary and well differentiated tectono-sedimentary cycles (lower/upper, one/two), or tectono-stratigraphic units (TS1/TS2). These units are separated by a Mid–Permian regional unconformity that, in places, represents up to 20 million years. The Lower Cycle, more than 2 km thick, consists of alluvial-to-lacustrine sediments and calc-alkaline, acidic-to-intermediate volcanic products, both infilling fault-bounded intracontinental basins. These have been interpreted as strike-slip or pull-apart basins affected by a transcurrent regime (Cassinis and Perotti, 1994). Paleontological evidence (macro-microfloral assemblages and tetrapod footprints) and isotopic data establish that this Lower Cycle ranges generally from the Middle Carboniferous (Moscovian/Westphalian) to the Early Permian (Kungurian). In particular, the well-studied South-Alpine sections in the Collio Basin, Brescia province, include (base to top) the following stratigraphic units: basal conglomerate, “lower quartz porphyries” *Auctt.*, Collio Formation, Dosso dei Galli Conglomerate and Auccia Volcanics (Cassinis, 1966). Radio-isotopic zircon ages from the bounding rhyolitic volcanic rocks indicate that this lower volcano-sedimentary cycle is Artinskian in age and was deposited over 3.5 million years (Schaltegger and Brack, 2007). In addition, these radio-isotopic ages helped to resolve the age of the Collio macro-microfloras (De Sitter and De Sitter Koomans, 1949; Cassinis, 1966; Wopfner, 1984; Pittau, 1999).

Carboniferous strata are not present in the Collio Basin, but in western Lombardy, in the Logone continental deposits (west of Lake Como), Venzo and Maglia (1947) collected a large number of plant fossils ascribed to a Westphalian C age. Jongmans (1951, 1960) described a macroflora of probable Westphalian B-C age in the Manno molasse (Lugano, Switzerland). Pittau et al. (2008a) also recognized in the same basal clastics that the palynoflora of Brezzo di Bédero (near Luino, Lake Maggiore) contains abundant miospores characteristic of the late Westphalian and early Stephanian assemblages of Western Europe. The Italian Pennsylvanian floras have recently been summarized by Ronchi et al. (2012).

In western Lombardy and the nearby Canton Ticino (Switzerland), alluvial polymict conglomerates and breccias interbedded with sandstones and fine-grained clastics (Ponte Gardena Conglomerate) occur beneath the Permian deposits from the high Adige Valley to the east. Despite a lack of biostratigraphic data, these strata have been interpreted as Early Permian, not Carboniferous, in age (Dal Cin, 1972; Wopfner, 1984; Krainer, 1989).

The Lower Cycle was interrupted, due to erosion and/or nondeposition, by a widespread geological event (the so-called “Mid-Permian Episode” of Deroin and Bonin, 2003), which indicates a plate reorganization and the opening of the Neotethys ocean.

The South-Alpine Upper Cycle, devoid of volcanic rocks, is more widespread, but less thick than the previous cycle, and was dominated by an extensional regime linked to crustal thinning. It consists primarily of the Verrucano Lombardo/Val Gardena (Gröden) Sandstone fluvial red clastics (from 0 up to 800 m thick), which are in part laterally and upwardly replaced, east of Val d’Adige, by the evaporitic-marine Bellerophon Fm. From continental (macro-microfloras and tetrapod footprints) and marine (foraminifers, algae, brachiopods, and so on) fossils, this cycle is generally related to the Late Permian and heralds the onset of the long Alpine evolution.

Tuscany

In northwestern Tuscany, in the Pisani Mountains, continental deposits rest above the metamorphic basement, which consists of the Buti Banded Quartzites and Phyllites (?Late Ordovician). The continental succession consists of the alluvial-to-lacustrine San Lorenzo Schists, rich in plant fossils, which are unconformably overlain by the Asciano Breccia; both units were probably deposited from Westphalian D (?) to Early Permian time (Remy, in Rau and Tongiorgi, 1974). R. Wagner (pers. comm. to G.C.) recently suggested a “Stephanian C (= lower Autunian)” age for the classic flora described by De Stefani (1901; Landi Degl’Innocenti et al., 2008) from the San Lorenzo Scists of Valle del Guappero. Wagner and Álvarez-Vázquez (2010, p. 247) assign the whole Autunian to the latest Carboniferous, specifically to the Gzhelian stage, and not to the Permian (Asselian + Sakmarian), in contrast to many European workers.

In the lower part of the San Lorenzo Schists, new marines faunas (?brachiopods, bivalves, bryozoans, crinoids; Pandeli et al., 2008) have been recently collected in the Montuolo area (SW of San Lorenzo a Vaccoli and at the foot of Monte Moriglion di Penna). These discoveries change the current reconstructions of the Late Carboniferous paleogeography and paleoenvironment in this Northern Apennines province.

The discovery of rhyolitic phenoclasts at the base of the Triassic Verrucano suggests the possible presence of older volcanics (related to a presumed Early–Middle Permian age on account of extensive correlations) in the Pisani area. The Verrucano Formation together with the overlying Mt. Serra Quarzites form a fluvio-deltaic shelf complex, dated ?late Ladinian to Carnian, which is followed upward by Norian carbonate sediments (Rau et al., 1988).

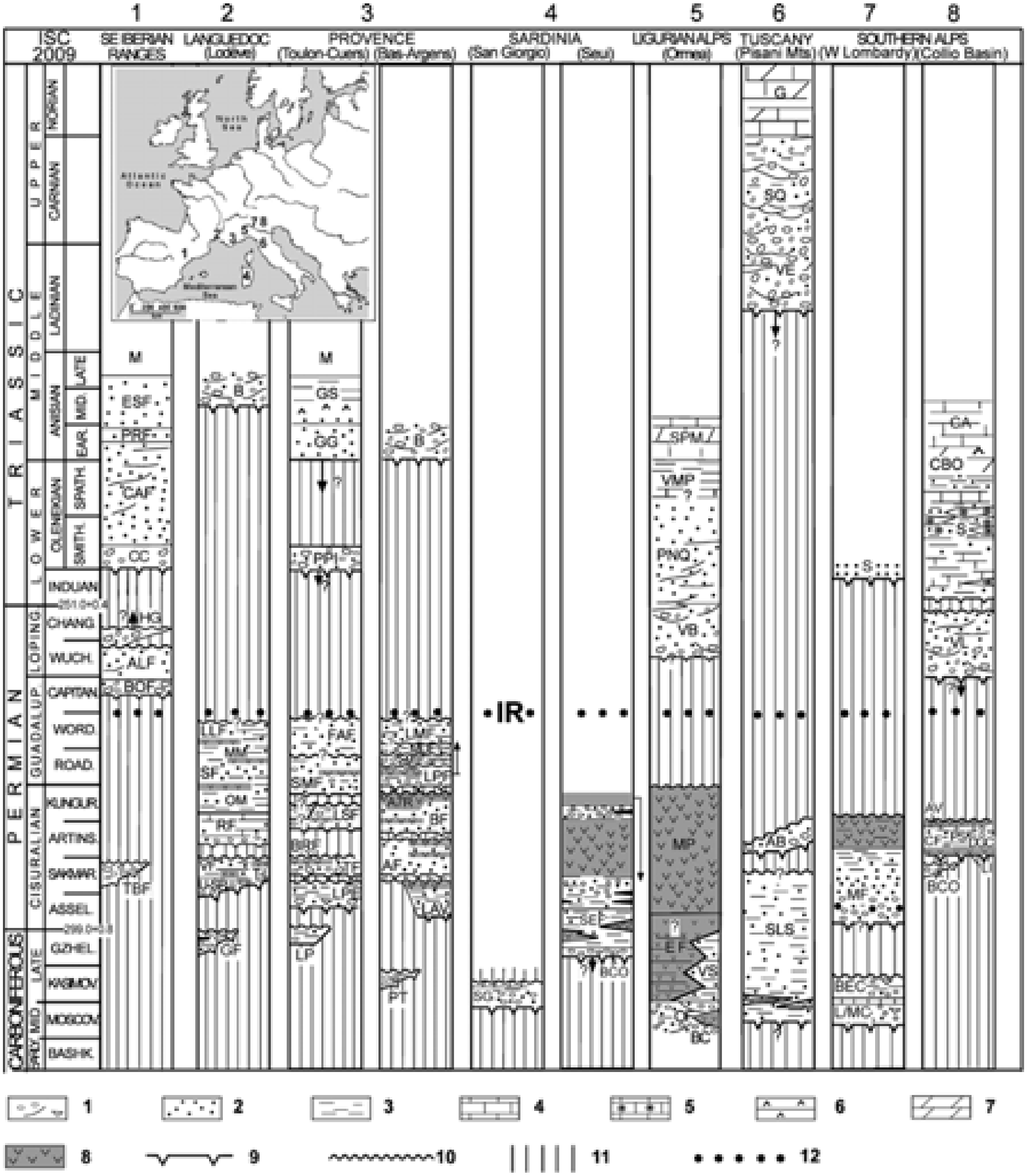

FIGURE. 1. Chronostratigraphic correlation and comparison of Upper Carboniferous, Permian and Triassic continental sections of Southern Europe. **Lithostratigraphic units (in alphabetical order): AB**, Asciano Breccia; **AF**, Ambon Fm.; **ALF**, Alcotas Fm.; **AV**, Auccia Volcanics; **A7R**, Rhyolite; **B**, Buntsandstein; **BC**, Bric Crose Tuffs; **BCO**, Basal Conglomerate; **BEC**, Bédero Conglomerate; **BF**, Bayonne Fm.; **BOF**, Boniches Fm.; **BRF**, Bron Fm.; **CA**, Angolo Limestone; **CAF**, Cañizar (= Rillo de Gallo) Fm.; **CBO**, Bovegno Carnieule; **CC**, Chequilla Conglomerate; **CF**, Collio Fm.; **DGC**, Dosso dei Galli Conglomerate; **EF**, Eze Fm.; **ESF**, Eslida Fm.; **FAF**, Fabregas Fm.; **G**, Grezzoni; **GF**, Graissessac Fm.; **GG**, Gonfaron Sandstones; **GS**, Solliès Sandstones; **HG**, Hoz del Gallo Conglomerate; **LAV**, L'Avellan Fm.; **LI**, Lower Ignimbrites; **LLF**, La Lieude Fm.; **L/MC**, Logone and Manno Conglomerates; **LMF**, La Motte Fm.; **LP**, Les Playes Fm.; **LPE**, Les Pellegrins Fm.; **LPF**, Les Pradinaux Fm.; **LSF**, Les Salettes Fm.; **M**, Muschelkalk; **MF**, Mesenzana Fm.; **MIF**, Le Mitan Fm.; **MM**, Merifons Mbr. (Salagou Fm.); **MP**, Melogno Porphyroids; **MUF**, Le Muy Fm.; **OF**, Ollano Fm.; **OM**, Octon Mbr. (Salagou Fm.); **PNQ**, Ponte di Nava Quartzites; **PPI**, Port-Issol Conglomerate; **PRF**, Prados Fm.; **PS**, Pietra Simona Mbr. (Conglomerato del Dosso dei Galli Fm.); **PT**, Plan-de-la-Tour Fm.; **RF**, Rabejac Fm.; **S**, Servino Fm.; **SEF**, Seui Fm.; **SF**, Salagou Fm.; **SG**, San Giorgio Fm.; **SLS**, San Lorenzo Schists; **SMF**, St-Mandrier Fm.; **SPM**, San Pietro dei Monti Fm.; **SQ**, Mt. Serra Quartzites; **T-L**, Tuilières-Loiras Fms.; **TBF**, Tabarreña Fm.; **TF**, Transy Fm.; **U-SP**, Usclas-St Privat Fms.; **VB**, Verrucano Brianzonese; **VE**, Verrucano Fm.; **VF**, Viala Fm.; **VL**, Verrucano Lombardo; **VMP**, Val Marenca Pelites; **VS**, Viola Schists. **Lithology: 1**, conglomerates and breccias; **2**, sandstones and siltstones; **3**, pelites, siltstones and marlstones; **4**, limestones; **5**, oolitic limestones; **6**, evaporites; **7**, dolostones; **8**, volcanic rocks. **Other symbols: 9**, unconformity; **10**, erosional surface; **11**, stratigraphic gap; **12**, IR - Illawarra Reversal geomagnetic event (ca. 265 Ma; Menning, 2001). Geologic time scale by Gradstein et al. (2004).

Ligurian Alps

Recently, the Permo-Carboniferous volcanic and sedimentary deposits of the Ligurian Briançonnais in the Maritime Alps have been isotopically dated as Permian (Sakmarian–Wuchiapingian, according to the International Chronostratigraphic Chart of ICS, August 2012), in contrast with previous interpretations (Dallagiovanna et al., 2009). However, in our opinion, these new stratigraphic results should be subjected to further rigorous controls, as macrofloral investigations assigned these sediments to the late Westphalian–Stephanian (e.g., Portis, 1887; Block, 1966). This age assignment is in agreement with similar stratigraphic successions south of Briançon (Brousmiche-Delcambre et al., 1996). Consequently, the previous Late Paleozoic stratigraphic schemes proposed by Vanossi et al. (1986) and Cortesogno et al. (1988, 1993) should be re-evaluated.

It should be noted that the mid-Permian gap in the uppermost Melogno Porphyroids would represent a unique example of volcanic activity during the Late Permian within the investigated regions. Based on recent research (Dallagiovanna et al., 2009), we note that the Melogno Porphyroids display two distinct ages, 273 Ma (C lithozone, Kungurian) and 258 Ma (D lithozone, Wuchiapingian), both separated by a break of about 14 Ma, effectively the entire Middle Permian.

These volcanics, through a Late Permian unconformity, are followed upwards by the Verrucano Brianzonese conglomerates and the Early Triassic whitish quartzites capped by fine-grained clastic and carbonate deposits.

Sardinia

In Sardinia the trans-tensional tectonics that deeply affected the dismantling of the Variscan orogen led to the opening of intramontane basins, which were subsequently filled with lacustrine to alluvial sediments (Ronchi et al., 2008 and references therein). These small basins yield megafossils and/or palynomorphs of Westphalian-Stephanian (San Giorgio, Tuppa Niedda), Stephano-Autunian (Lake Mulargia, Seui-Seulo and Montarbu) or Autunian age (Guardia Pisano, Escalaplano, Perdasdefogu and Lu Caparoni), suggesting a differentiated opening of basins in Late Paleozoic times related to post-Hercynian tectonic events (Cassinis et al., 1999; Pittau et al., 2008b).

The reduced San Giorgio Basin sequence, which crops out in the Iglesiente region, is the only unambiguous evidence of post-orogenic clastic deposition on the island and has been studied in detail by Cocozza (1967) and Barca and Costamagna (2003). The finer sediments of this basin, yielding a rich microflora, which have been assigned a late Westphalian and early Stephanian (A and B) age (Pittau and Del Rio, 2002). At Tuppa Niedda (Arburese), a short sequence of conglomerates with sandy to muddy intercalations contains sporomorphs, which are late Westphalian-early Stephanian in age based on comparisons to similar palynomorphs within the San Giorgio sequence (Pittau et al., 2008b).

In central-eastern Sardinia, there are two basins with transitional "Stephano-Autunian" macrofloras: the Lake Mulargia (Sarcidano region), and the Seui-Seulo/Montarbu (Barbagia di Seulo region; Pittau et al., 2008b; Ronchi et al., 2008; Cassinis et al., 2003a).

Provence

In southern France, the Toulon-Cuers Basin of SW Provence includes the small Upper Carboniferous continental trough of Les Playes (east of Sanary), which yields a macro-microflora of middle to late Stephanian age. The Toulon- Cuers Basin has a succession similar to the Nurra of Sardinia, probably due to the proximity of these regions during the Permian (Cassinis et al., 2003b). The most distinct difference is the Bau Rouge Member, the uppermost member of the Les Salettes Fm., which is characterized by fluvio-lacustrine, macro-microfloral-bearing sediments of disputed age (Cassinis et al., 2012, p. 145).

To the east, in the Bas-Argens and Estérel Basins, several outcrops interpreted as Upper Carboniferous nonmarine deposits are confined within two narrow sub-meridian troughs (Durand, 2008). In the Maures Massif, the Plan-de-la-Tour Basin consists of a 400 m thick sequence of conglomerates, rhyolites or microgranites, and conglomeratic arkoses with coal beds containing lower Stephanian floras (Basso, 1985). The isotopic dating of the rhyolites revealed a K-Ar age of 290 ± 10 Ma (Roubault et al., 1970) and an ^{39}Ar-^{40}Ar age of 295.4 ± 2.4 Ma (Morillon, 1997). These Early Permian ages (Gradstein et al., 2004) encourage a re-examination of the relationships between the volcanic strata and sedimentary deposits.

In the northeastern part of the Tanneron Massif the Reyran Basin consists of a thick succession (more than 1000 m) with coal seams containing a microflora succession from late Westphalian through early Stephanian, without any apparent breaks (Basso, 1985, 1987). Both basins are generally accepted to be transtensional in origin, and due to general north-south compression (Toutin-Morin and Bonijoly, 1992; Toutin-Morin et al., 1992), but this has been recently disputed (Bellot, 2005 in Durand, 2008). During late Stephanian time, both basins underwent similar east-west tightening.

After an important unconformity, a period of intense acidic-mafic alkaline volcanism took place. This volcanism allows radio-isotopic and geochemical analysis to aid in correlation (such as the attribution of the A7 Rhyolite to 272.5 Ma., e.g., to Kungurian time). Also, abundant fossiliferous beds provide some age control (e.g., the Les Pradinaux Formation as Middle Permian). The eo-Alpine Buntsandstein unconformably overlies this succession, and yields early Anisian palynomorphs.

Languedoc

In Languedoc, the Lodève Basin succession rests unconformably on both Cambrian metamorphic basement and the Carboniferous Graissessac Formation. The Graissessac Formation consists of lacustrine coal beds sandwiched between coarse-grained fluvial to deltaic deposits (Becq-Giraudon, 1973; Saint-Martin, 1993 in Lopez et al., 2008). This formation was dated by Bruguier et al. (2003) to 295.5 ± 5.1 Ma (U-Pb) (i.e. Asselian/Sakmarian), and the macroflora was interpreted as late Stephanian by Doubinger et al. (1995). According to Gand (pers. comm.), the local stratigraphy of the Lodève Basin needs revision for an accurate chronostratigraphic classification of the Carboniferous/Permain boundary in this area.

The Lodève succession includes a lower cycle, ~700 m thick, with fluvio-deltaic and variegated formations (Usclas-St Privat, Tuillières–Loiras, Viala), known as the Autunian Group *sensu* Gand et al. (1997), which has assigned to the early Cisuralian (Asselian + Sakmarian) based on the macro-microfloras and ichnofaunas. The upper cycle is ~2,000 m thick, separated from the lower cycle by a regional unconformity and is late Cisuralian (Artinskian–Kungurian) to middle Guadalupian (beneath the Illawarra Reversal geomagnetic event) in age. The lower fluvial Rabejac Formation evolves to the silty red mudstones and thin playa-lake dolomites of the Salagou Formation, which is topped by the La Lieude Formation. In the La Lieude Formation, immediately below the Illawarra Reversal the ichnoassociation IV was dated to Middle Permian (Wordian) by Gand and Durand (2006, p. 170). However, recently workers' study (Körner et al., 2003; Körner and Schneider in Legler et al., 2004; Lopez et al., 2005) have assigned the La Lieude Formation a Lopingian age, ranging from Wuchiapingian to Changhsingian. However, this recent interpretation is not clearly supported by the magneto-stratigraphic results (Bachtadse, University of München), which indicate a Capitanian (lower Tatarian) age for the basal facies of the La Lieude Formation (Lopez et al., 2005, p. 34; Roscher and Schneider, 2006, p. 99).

In the Lodève Basin, the ?Mid–Late Permian to Middle Triassic part of the section is represented by the Middle Anisian Buntsandstein. The Anisian age assignment of this unit is based on palynological data and its deposition is linked to the Alpine cycle.

Southeastern Iberian Ranges

Many authors, e.g., Arche and López-Gómez (2006), identified Early Permian (Autunian) fluvio-lacustrine basins, bearing volcanic rocks, within the Iberian Ranges. Only the Minas of Henarejos includes coal horizons with a rich macroflora of Stephanian C (?)-early Autunian (?) age (Wagner et al., 1983; Meléndez et al., 1983). The Early Permian (Autunian) sedimentary sequence always rests unconformably on the Variscan basement and is unconformably overlain by Late Permian (Thuringian *sensu* Visscher, 1971) to Early Triassic cycles. Calc-alkaline volcanism took place in both the Castilian and Aragonian branches of the Iberian Ranges (Muñoz et al., 1985; Lago et al., 2002, 2004). This volcanism is represented by amphibolic andesites and daci-andesites (first phase) and gabbros, pyroxenic andesites, basalt and rhyolites (second phase). Radio-isotopic ages range from 293 ± 2.5 Ma to 283 ± 2.5 Ma (Hernando et al., 1980; Conte et al., 1987; Lago et al., 1991), which, according to the Gradstein et al. (2004) scale, are within the Sakmarian and Artinskian stages of the Cisuralian (Lower Permian). After a major hiatus between the Lower (Autunian) and the Upper Permian deposits, the second cycle, which is late Capitanian to Wuchiapingian in age, consists of basal quartzite conglomerates of limited extent (Boniches Fm.) and overlying red mudstones and fine-grained clastics (Alcotas Fm.), which include well-dated pollen and spore assemblages.

The third cycle consists of the Hoz del Gallo Formation, which contains abundant Changhsingian palynomorphs, and the fluvial Cañizar (= Rillo de Gallo) Formation. The Hoz del Gallo Formation rests unconformably on the Variscan basement or on the Alcotas Formation. This third cycle can be compared with the Buntsandstein facies s.s. of central Europe. The Cañizar Formation is Induan (?)/Olenekian-early Ansian in age. The lowermost part of the formation is known as Chequilla Conglomerate (Bourquin et al., 2007). This third sequence marks, like the “Poudingue de Port-Issol” of Provence and the “Conglomerato del Porticciolo” of Sardinia, the beginning of the Alpine Cycle.

GENERAL REMARKS AND CONCLUSIONS

Historically the continental Carboniferous-Permian boundary in the studied region lacks evidence due to the numerous stratigraphic and tectonic discontinuities that affect the stratigraphic succession. Through our examination and reading of the literature, we conclude that the wider transitional characteristics of the two systems deserve more detailed studies.

The greatest problem facing Upper Carboniferous-Lower Permian continental stratigraphy is the interpretation and age of the Autunian successions. Wagner (2010) equates Stephanian C with the lower Autunian. Following this interpretation the Autunian in south-central France correlates with the higher and the Lower Rotliegend of central and eastern Europe, which suggests that the middle and upper Autunian (i.e. the Autunian s.s., viz. the Muse, Surmoulin, and Millery formations of the French stratotype) should be assigned to the Carboniferous. This constitutes the highest substage of the Stephanian (also upper Gzhelian). Alternatively the French workers suggest that the Autunian is latest Carboniferous to early Cisuralian (Gzhelian–early Sakmarian)..

In our view, the southern European continental domains contain two very different tectonic and sedimentary settings. The lower megacycle was affected by a transcurrent regime, during which volcanic to fluvio-lacustrine deposits infilled fault-bounded intracontinental basins, mainly interpreted as strike-slip or pull-apart basins. This tectonic framework was widespread across paleo-Europe and was induced by the north-directed subduction of the Paleotethys active oceanic ridge. This resulted in dextral strike-slip orogen and a diffuse transform margin across the western Eurasia Variscan chain. During this period the basins developed under wet and dry climatic phases and spanned from mid-Late Carboniferous to Early Permian time.

The upper megacycle was first characterized by widespread deposition of coarse-to-fine semi-arid to arid red beds, which mirrors the final erosion and dismantling of the Variscan orogen. This was followed by the opening of a new sea and its advance on a progressively flattened landscape. This period was devoid of volcanic activity, which ended with a dramatic change in the geodynamic setting. This younger depositional cycle was probably linked to a vigorous reorganization of tectonic plates, which led to the birth of Neotethys and to widespread extensional tectonism.

The major regional angular unconformity between the two Permian megacycles was probably caused by a wide and deep tectonic impulse, which induced faulting, gentle folding, uplift and erosion or non-deposition. This event, which emphasized the change from a transcurrent to an extensional regime, can be related to the above-mentioned “Mid-Permian Episode,” which was locally characterized by (trans)compressional activity (e.g. Prost and Becq-Giraudon, 1989; Cadel et al., 1996).

The boundary between the two major tectono-sedimentary cycles (or the tectono-stratigraphic units TS1/TS2) was approximately synchronous with the geomagnetic “Illawarra Reversal” event, which took place during the Middle Permian (Guadalupian) (Menning, 1995, 2001; Steiner, 2006; etc.). This event has been linked to the above-cited Permian geodynamic change. Some authors (e.g., Isozaki, 2009) have argued that the trigger agent for this remarkable change in geomagnetism related to the Illawarra Reversal, as well as for the breakup of Pangaea, is a major change in the Earth’s geodynamo, the result of superplume activity.

Regardless of mechanism, within the peri-Mediterranean area these two major successions, respectively ascribed to the closure of the Variscan movements and the onset of the Alpine cycle, are separated by a variable, but long-lasting period, of erosion and/or non-deposition. This period began in the “Middle Permian” and extended through the Early Triassic.

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NEW OCCURRENCE OF AN ARTHROPLEURID TRACKWAY FROM THE LOWER PERMIAN OF UTAH

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The giant arthropod *Arthropleura* was a common member of the late Paleozoic continental biota of paleo-equatorial biomes for more than 35 million years, from the Early Carboniferous (late Viséan) through the Early Permian (Asselian). Schneider et al. (2010) presented a comprehensive review of arthropleurid tracksites and body fossils in order to better interpret the paleoenvironmental preferences and the paleobiology of *Arthropleura*. They concluded that *Arthropleura* was well adapted to alluvial environments of ever wet/humid to seasonally dry and semihumid climates, and that the preferred habitats of these large arthropods were open, vegetated, riverine landscapes. Here, we add further data to support this conclusion by documenting a well-preserved trackway of a large arthropleurid, assignable to *Diplichnites cuithensis* Briggs, Rolfe and Brannan, from the lower part of the Halgaito Formation on the Lime Creek Anticline of southeastern Utah, strata that were fluvially deposited under a seasonally dry climate.

The trackway was collected between Comb Ridge and the Valley of the Gods in southeastern Utah. The collecting site (USNM 43579) is situated on the eastern limb of Lime Ridge Anticline (Fig. 1). Exact locality information is on file at the National Museum of Natural History, Department of Paleontology and with the U. S. Bureau of Land Management. The USNM 43579 locality, named East Flank of Lime Ridge, has produced a large collection of plant remains, predominantly walchian conifers and the calamitalean foliage *Annularia*. It was during an exploration of these beds that the large *Diplichnites* trackway was identified. The large trackway was associated with numerous smaller trackways, most of which were either faint, obscured by other biologic or sedimentologic bedding features, or incomplete. The large illustrated specimen (Fig. 2) suggests that many, if not all, of the other similar features were made by arthropleurids. Given the large number and size variation among the trackways at the site, it is clear that a substantial population of track-making arthropods inhabited the local area.

In the Valley of the Gods area in southeastern Utah, the Honaker Trail Formation is overlain by the Halgaito Formation, which forms the slopes around the base of buttes, which are topped by remnants of the Cedar Mesa Sandstone. Where the Halgaito Formation has been removed by erosion, much of the landscape is held up by one of the upper limestone beds at the top of the Honaker Trail Formation. At the locality where the *Diplichnites* trackway was collected, the upper limestone is identified as the "Lime Creek." Located on the eastern limb of Lime Ridge, the locality is in the lower Halgaito Formation, approximately 25 m above the base of the formation (Fig. 1). The Halgaito is composed of repeating cyclic packages of mixed eolian (dune and interdune), fluvial (channel and floodplain), and shallow marine rocks, interpreted to be the result of glacio-eustatic and coupled climatic change. Relative sea-level lowstand was coincident with aridity and generation of eolian deposits. Sea level rise was coincident with a change to more seasonal conditions, reduction in eolian sedimentation and dune deflation, and expansion of fluvial systems across former dune fields (Jordan and Mountney, 2012).

The specimen was found towards the top of a 2.5 m thick fluvial/channel facies composed of stacked, 0.3-0.5 m thick, sandstone beds arranged in shallow, overlapping, 6 m wide scours, often with 1-4 cm thick mudstone or claystone drapes capping each scour. Plant debris and identifiable fossils of *Walchia*, *Annularia* and *Cordaites* were found in the mudstone drapes, likely as strand deposits. Below was approximately 10 m of thinly bedded, calcareous siltstone (loess) with rooting and possible caliche horizons. This succession of strata is consistent with a climatic and depositional transition from arid aeolianites, to more seasonal fluvial deposits, as described by Jordan and Mountney (2012). Therefore, we interpret the trackway as having been created during a seasonally (arid) climate regime. The Pennsylvanian-Permian boundary is placed at the top of the Honaker Trail Formation, thus the southeastern Utah specimen is of Early Permian age.

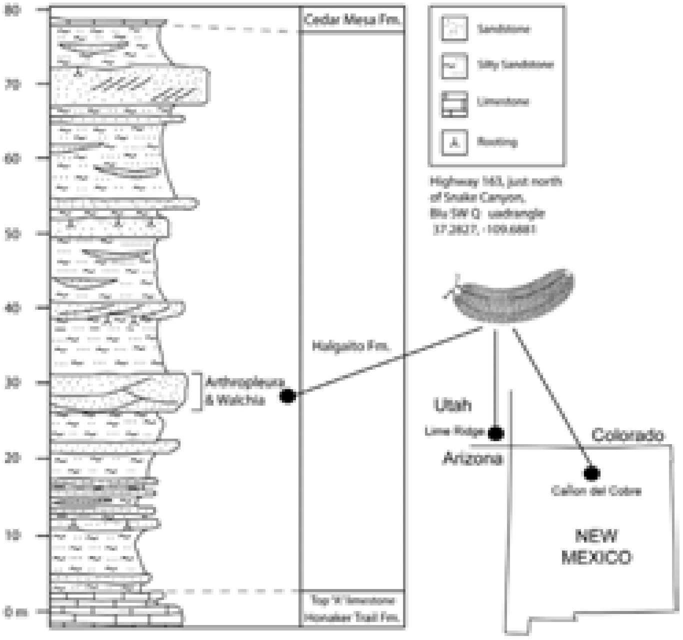

FIGURE 1. Location and stratigraphic position of arthropleurid trackway in southeastern Utah, USA.

The trackway, USNM 547011 (Fig. 2), is preserved in concave epirelief and consists of two track rows of slightly crescentic imprints that are oriented perpendicular to the midline and extend over a distance of about 104 cm. External trackway width is ~ 25 cm, and internal trackway width is ~ 21 cm. Imprints are 3-4 cm wide and up to 1 cm deep. Spacing between imprints is < 1 cm, and each imprint is ~ 1 cm long. There are 42 imprints on the right side of the trackway, and 54 on the left side. Most of the individual imprints are slightly crescent shaped, but include transversely ovoid and meniscate impressions as well. We regard most of these shape differences as being due to erosion, the fact that the trackway clearly is an undertrack and the variability of imprints made by repetitive, overlapping footprints of more than one appendage.

We assign the trackway to *Diplichnites cuithensis* Briggs, Rolfe and Brannan. Briggs et al. (1979) diagnosed that taxon as a very large *Diplichnites* with rare trifid tracks shallowing toward the trail axis. Their emended diagnosis of *Diplichnites* reads: "morphologically simple trail, up to 36 cm wide, consisting of two parallel series of tracks (each up to 9 cm wide); individual tracks elongate roughly normal to trail axis, spaced closely and regularly, at up to about one per cm" (Briggs et al., 1979, p. 289). The large trackway from Lime Ridge fits this diagnosis except that

FIGURE 2. *Diplichnites cuithensis*, USNM 547011, trackway in concave epirelief, from the Halgaito Formation in southeastern Utah.

the trifid tracks toward the trail axis are not preserved. Indeed, the Lime Ridge trackway well resembles illustrated specimens of *Diplichnites cuithensis* (e.g., Briggs et al., 1979, 1984; Briggs and Rolfe, 1983; Almond, 1985; Wright et al., 1995; Martin and Greb, 2009; Schneider et al., 2010).

The largest known trackway of *Diplichnites cuithensis* has a width of about 38 cm (Lucas et al., 2005; Schneider et al., 2010), and it is slightly larger than the famous Arran, Scotland trackway, which is 36 cm wide (Briggs et al., 1979), and those found at Gardner Creek, New Brunswick, Canada, which are also about 36 cm wide (Briggs et al., 1984). Smaller trackways, the size of the Lime Creek trackway, 21-24 cm wide, are known from various localities, including Scotland (Pearson, 1992). *Diplichnites cuithensis* is generally considered to be the trackway of the giant myriapod-like *Arthropleura*. Arthropleurids are the largest terrestrial invertebrates known (Schneider and Werneburg, 1998).

The Lime Ridge record of *Diplichnites cuithensis* is its first published record from Utah and its second documentation in the American Southwest. *Arthropleura* trackways, usually assigned to the ichnospecies *D. cuithensis* or *D. aenigma* Dawson, are well known from the Carboniferous of eastern Canada (New Brunswick and Nova Scotia: Ferguson, 1966, 1975; Rolfe, 1979; Briggs et al., 1984), and, in the USA, *D. cuithensis* has been reported from Kansas, New Mexico and Kentucky (Mángano et al., 2000; Lucas et al., 2005; Martino and Greb, 2009; Schneider et al., 2010). A large (15 cm wide by 3 m long) trackway from the Casselman Formation (Conemaugh; Stephanian equivalent), in Cambria County, Pennsylvania, described by Marks et al. (1998), may also have been made by *Arthropleura*. Trackways made by *Arthropleura* are Viséan to Asselian in age (Schneider et al., 2010). The age of the Lime Ridge occurrence of *Diplichnites cuithensis* thus makes it among the youngest occurrences of such trackways. The sedimentological context of the Utah trackway also is consistent with the conclusion of Schneider et al. (2010) that the arthropleurids that made these trackways were not inhabitants of coal swamps and dense forests but instead were more likely denizens of more open, riverine floodplain settings.

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SWAMP FLORA CHANGES THROUGH THE PENNSYLVANIAN – EARLY PERMIAN INTERVAL IN THE GONDWANA FLORISTIC PROVINCE OF THE BRAZILIAN PORTION OF THE PARANÁ BASIN

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INTRODUCTION

During the Pennsylvanian-Early Permian interval, the global climate gradually underwent transformational change. The Late Paleozoic Ice Age (LPIA), which began in the late Devonian/Early Mississippian periods, left marks of the last great era of glaciation prior to the Cenozoic Ice Age. Records of this glaciation are found in the southernmost portion of Gondwana as far as 30°S (Parrish et al., 1986; Fielding et al., 2008). Therefore, during this interval there where various glacial pulses, which Heckel (2008) related to cyclothems (alternation of paleosols with marine units as result of periodic and repetitive regression and transgression events). Apparently these derive from the Earth's orbital parameters (Milankovitch cycles). Natural causes of carbon capture and fluctuations are still uncertain (Montañes et al., 2007). However, it is certain that, due to such fluctuations, climatic changes and, thereafter, alternation between glacial and inter-glacial periods occur. This also causes glacio-eustatic fluctuation. Proof of this linkage is in the geological record, because, for the LPIA on Laurasia, there are findings of carbon sinks, which occurred during coal bed formation beginning in the Mississippian (Rowley et al., 1985; DiMichele and Hook, 1992; Anderson et al., 1999). These glacial cycles continued until the Artinskian/Kungurian Stage, and the final deglaciation occurred relatively quickly (Gibbs et al., 2002). Poulsen et al. (2007) remark that, in all of Pangaea at the end of the glaciation, drier conditions and warmer temperatures on the continents were present in the equatorial region, as well as a shift of tropical biomes, with deserts expanding and forests undergoing reduction.

High latitude regions have a different behavior from those observed in lower latitudes. Formerly covered by ice, they went on to have a rich flora in the Early Permian. Paleofloras (macro and micro floras) from the Pennsylvanian-Early Permian interval in the Paraná Basin reflect the paleoclimatic changes that occurred in late Paleozoic Gondwana. The Paraná Basin was located in the southwestern portion of Gondwana, with a sedimentary area covering more than 1,500,000 km^2 in the southeastern portion of South America, and extended to South Africa (Karoo Basin) and Namibia. Layers produced by the alternation of glacial and interglacial periods are found in the sedimentary rocks from the Itararé Group (Middle Bashkirian-Early Asselian) of the Paraná Basin (Fig. 1A), deriving from the youngest episodes of the Pennsylvanian/Early Permian glacial period (Santos et al., 1996; Mori et al., 2012). The oldest floristic record is of Kasimovian age. On the other hand, the Guatá Group from the Early Asselian-Early Artinskian (as well as its basal formation, the Rio Bonito Formation, in the Basin's southern portion, and the Tatuí Formation of the northern portion) represents deposition in milder, post-glacial climates, as well as during a worldwide rise in sea level (Haq and Schutter, 2008). It is necessary to stress that the Tatuí Formation was deposited after the Itararé,but the Rio Bonito Formation, at it's top portion, is syndepositional with the Itararé Group in parts of the basin, though it does not present the same glacialorigin sediments. The Tatuí Formation presents records of stems and trunks only, and non-abundantly. Plus, taphonomic studies indicate these fossils to have been transported (Chahud, 2011), thus making them unsuited for the present study. In that manner, comparison is restricted to the Rio Bonito Formation, which has evidence of sea levels and tempestites thorough it's whole columnar section. Locally, restricted lagoonal conditions occurred along the coastal fringe, where turf developed.

The biggest difficulty in working with the formally described formations from the Itararé Group (Lagoa Azul, Campo Mourão and Taciba formations, other than the Aquidauana Formation) derives from the fact that the group has a great number of intertwined facies that expose the advance and retreat of glacial fronts during various glacial cycles, causing erosion and redeposition of sediments through a very large time period (approximately 75 million years). Geologically, França and Potter (1988) characterized it by the presence of sedimentation cycles, with grains thinning towards the top, corresponding to cyclical climatic changes in a glacial regime and sea level fluctuations. The geologic record shows, yet, that there are carbon layers associated with the clastic glacial deposits. Parts of the floristic record of the Itararé Group are found in those layers; however, it is not possible to affirm that such levels would be related to periods of higher temperature (interglacials).

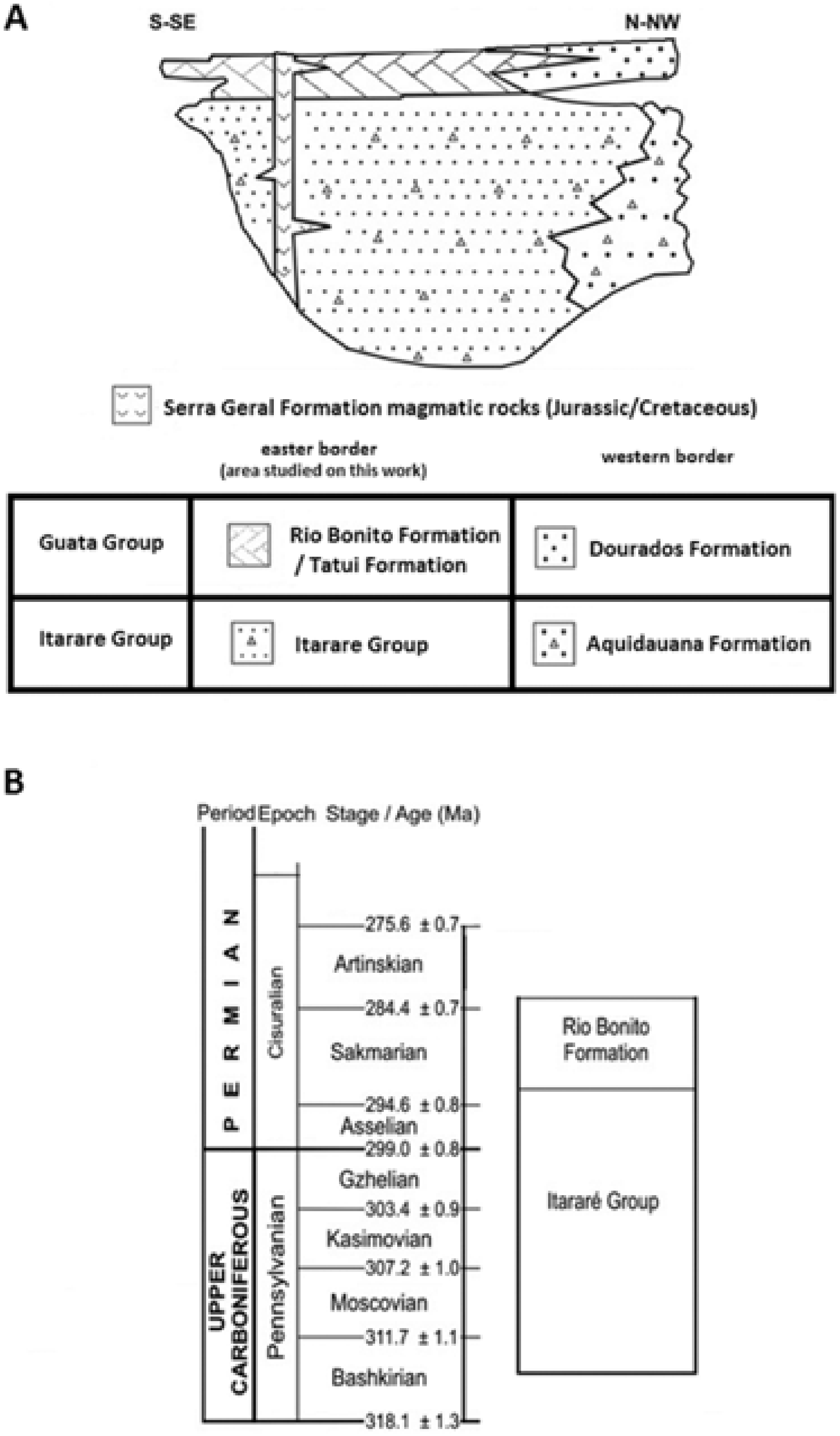
In the present research, we chose to consider the Itararé Group undivided, because more than one glacial/interglacial cycle occurred in it in during the course of the Pennsylvanian and it has a relatively restricted fossil record. This makes it possible to compare this flora, developed under such cold climate intervals, with that of the superjacent Rio Bonito Formation, which represents milder climates, already into the Permian.

Thus, paleofloras described for the Itararé Group correspond to periglacial and coastal swamp vegetation, even though the record cannot be considered continuous. A record of pteridosperms and gymnosperms also occurs in the Itararé Group. On the other hand, the Rio Bonito Formation paleofloras were deposited in coastal and swampy environments that came into existence (despite the rise of sea level during the Permian, the Paraná Basin already was an inland sea) at the end of the glaciation, and include coal beds where the Gondwana Floristic Province is preserved in the basin.

The present study is based on a composite database containing all paleophytogeographic information for the later Paleozoic in the Paraná Basin, developed by Christiano-de-Souza (2011). Data corresponding to 142 plant fossil occurrences were linked to the Pennsylvanian-Early Permian in the eastern portion of the Paraná Basin in Brazil (states of São Paulo, Paraná, Sta. Catarina, and Rio Grande do Sul). These data were then georeferenced and transferred to ArcGIS software, where occurrence distribution maps were generated, to understand the patterns of floristic distribution within the basin. Furthermore, through the maps it was possible to understand changes in distribution patterns for the Pennsylvanian-Early Permian interval.

MATERIALS AND METHODS

To understand the environments of fossilization for the interval under study, only taxa representing specimens that inhabited swamps were selected, because they offer more precise information about paleoenvironments. They also represent glacial intervals in the Itararé Group (at locales where there was no permafrost nor ice caps, which would make it impossible for plants and peat to develop), and post-glacial intervals in the Rio Bonito Formation (Guatá Group), the latter associated with coal beds. Megaspores were also used to represent swamp



	easter border (area studied on this work)	western border
Guata Group	Rio Bonito Formation / Tatui Formation	Dourados Formation
Itarare Group	Itarare Group	Aquidauana Formation

FIGURE 1. **A**, Stratigraphic setting of the Itararé Group / Guatá Group transition (modified from Mori et al., 2012). **B**, Stratigraphic column of Itararé Group / Rio Bonito Formation, on Paraná Basin (modified from Milani, 1997, and Mori et al., 2012).

communities, as signs of the reproduction of lycopsids, which possess less dispersal capability than microspores (Tyson, 1995), and so may better reflect local vegetational patterns. Regarding fossil plants, the chosen taxa were mainly those pertaining to the genera in the Bryopsida, Lycopsida, and Equisetopsida. Taxa from the Polypodiopsida/ Spermatophytina lineages were also taken into account, however, they are labeled as *incertae sedis* as they do not have a well-established classification due to the lack of diagnostic characters that would permit their inclusion in these lineages.

From these data, a composite database was prepared, assembling all occurrences cited in the specialized literature (formed by abstracts presented at conferences, reports, articles, which, as they were published mostly in Portuguese, would make them difficult for an international audience to find). Besides basic information on each fossil plant, geographic location, geology, and paleobotanical systematic data were included. Once georeferenced, the database was transferred to the GIS platform through the ArcGIS program. The later was plotted over the geological map provided by the CPRM (The Geological Map of Brazil, scale of 1:1000000, pages SF21, SF22, SF23, SF24, SG21, SG22, SG23, SH21, SH22 e SI22; covering all the outcropping area of the Itararé and Passa Dois Groups).

RESULTS AND DISCUSSION

The selection of plant fossils included those that had affinities with swamp communities. As noted above, these mostly come from genera of the Bryopsida, Lycopsida and Equisetopsida, but include genera of the Polypodiopsida/Spermatophytina, specifically *Adiantites*, *Eusphenopteris*, *Paleovittaria*, and *Triphyllopteris*. Megaspore species included pertained to the genera *Banksisporites*, *Calamospora*, *Cystoporites*, *Duosporites*, *Lagenoisporites*, *Setosisporites*, *Sublagenicula*, and *Trileites*, because they have affinities with the Lycopsida and are indicative of the same type of community. Even if transport had occurred, it would not affect the results, given the study-area dimensions (an area larger than 1,500,000 km^2 in Brazil).

Regarding the megaspores, two new occurrences were included (Porto Feliz and Aterro Delta outcrops) related to interglacial intervals of the Itararé Group in the northern portion of the basin (state of São Paulo) where the presence of megaspores and bryophytes was identified. Distribution maps in the present study were generated jointly and separately for megaspores and macrofossils, in order to understand the distribution of such fossils.

As for the spatial distribution of macrofossils present in the Itararé Group, they are concentrated only in the southern and northern portions of the exposed section of the basin (corresponding to the states of Rio Grande do Sul and São Paulo), probably where the shallower and less affected (by glacial fronts) environments were. Thus, despite the short interglacial intervals, the development of a flora and its fossilization, as well as the formation of coal beds, were fostered. The absence of fossil plants in the central portion of the basin (the states of Santa Catarina and Paraná) may be due to erosion or to the fact that the depositional environments there were more distal to the sites of plant growth, so the flora is represented only by occurrences of palynomorphs.

The Rio Bonito Formation represents a time of milder climates in the Gondwana paleocontinent, attested by the greater abundance and spatial dispersion of fossil occurrences, which extend from the central area to the southern parts of the study area. Thus, portions that in the older interval offered no plant-fossil occurrences (in the states of Santa Catarina and Paraná) have a great number of coal beds, with associated plant fossils in the younger units. Among all formations pertaining to the Gondwana Floristic Province in the Paraná Basin, the Rio Bonito Formation is the one that has the largest diversity of species. The tendency in the basin, as the end of the Paleozoic approached, was a decrease in the number of species (the Rio do Rasto Formation, which represents the end of the floristic province in the Permian, for example, has only 21 species, in an environment already regarded as semiarid) and a high concentration towards the central portion of the basin. For the passage from the Itararé Group to the Rio Bonito Formation, it is possible that the first dispersion of species occurred from the edges to the center of the basin.

There is a great change in the distribution of genera and species during the passage from the Pennsylvanian to the Permian in the swamps of the Gondwana Floristic Province. Firstly, the Itararé Group has 29 different species distributed among 18 outcrops; the Rio Bonito Formation has 33 species distributed among 22 outcrops. Out of the 54 species that occur in the study interval, only 5 are common to both units: *Brasilodendron pedroanum*, *Cyclodendron brasiliensis*, *Lepidophloios laricinum*, *Phyllotheca australis*, and *Paracalamites australis*. Added to that list are 3 genera without defined species that occur repeatedly: *Paracalamites* sp., *Phyllotheca* sp., and *Sphenophyllum* sp.. It must be noted, however, that the genera *Paracalamites*, *Phyllotheca* and *Sphenophyllum* occur differently in each lithostratigraphic unit. In the Itararé Group, *Paracalamites levis* and *P. montemorensis* were found; while in the Rio Bonito Formation, only *P. cambuyensis* was found. In the case of *Phyllotheca*, *P. brevifolia* was found in the Itararé Group, whereas *P. griesbachii*, *P. indica*, and *P. muelleriana* were found in the Rio Bonito Formation. For identified species of *Sphenophyllum*, *S. churulianum*, and *S. rhodesii* were found in the Itararé Group; *S. brasiliensis* and *S. oblongifolium* were found on the Rio Bonito Formation.

Megaspore assemblages occur principally in the northern region of the basin (state of São Paulo) for the Itararé Group. Regarding the Rio Bonito Formation, megaspores occur only in the central and southern portions (the states of Santa Catarina, Paraná and Rio Grande do Sul). Megaspore and Lycopsida occurrences are remarkably coincident in every part of the basin, i.e., where there are megaspores, there are also Lycopsida. This low dispersion of megaspores can be visually confirmed on the maps.

Of the megaspores encountered among the 6 outcrops from the Itararé Group, there were 9 described species. For the Rio Bonito Formation, 15 different species were identified on 7 outcrops. From a total of 17 species, 7 occurred through the entire interval: *Bankisisporites endosporiferus*, *Bankisisporites labiosus*, *Bankisisporites tenius*, *Lagenoisporites scutiformis*, *Sublagenicula brasiliensis*, *Triletes nites*, and *Triletes vulgatus*.

Thus, it can be concluded that the Rio Bonito Formation also has a greater diversity of megaspores than the Itararé Group. Megaspores follow the same spatial patterns as the macrofossils. It is interesting to note that megaspore and lycopsid occurrences match when superposed – which shows that megaspores have minor allochthony, which is markedly different from spores and pollen.

In that manner, spatial study of phytofossil occurrences demonstrates their localization in two places: the present northern portion (state of São Paulo) and its southern portion (state of Rio Grande do Sul), which are geographically distant. On studies of their temporal distribution (Mune and Bernardes-de-Oliveira, 2007; Mori et al., 2012) (Fig. 1B), it is observable that their development was distinct through the Carboniferous/Permian interval, even though all registers indicate glacial conditions. Registers of the northern portion are older, dating from the Middle Bashkirian, and there is a continuous presence of fossil occurrences, extending to the late Gzhelian. The flora then stops in the Asselian, to return in the early Sakmarian, until the end of Itararé Group deposition (middle Sakmarian). This is directly superposed by the Tatuí Formation (which presents a few occurrences of *Tietea* and trunks attributed to gymnosperms or pteridosperms) (Chaud, 2011). Such disposition is in agreement with the theory that, during the Early Permian, a great glacial advance occurred, which would have not allowed floral development (Montañes et al., 2007; Fielding et al., 2008).

In the southern portion of the basin, geological and phytofossil records of the Itararé Group are restricted to the Asselian, where a great abundance of fossil occurrences is found, indicating that, at least for that region of the basin, there was not such intense activity from the glacial fronts. In the early Sakmarian, the Itararé Group meets the Rio Bonito Formation, in which fossil plants occur in association with organic-rich beds throughout its vertical structure. Geology shows clearly that the thaw began in the present southern portion of the basin, and progressively extended to the north, where the most recent glacial deposits are found.

Through the present study, it is noticeable that, with the end of glaciation in the Paraná Basin, a substitution of species occurred, accompanied by an increase in diversity. In places that during the Pennsylvanian there was less occurrences of swamp plants, such deposits became abundant in the Early Permian (with such a number that they are commercially exploited). This represented a widespread migration towards the more central portions of the basin, culminating in drastic landscape changes. The interval also represented the appearance and diversification of a plant not related to this kind of environment, but which is the signature plant of the Gondwana Floristic Province: the genus *Glossopteris*.

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SWAMP FLORA CHANGES THROUGH THE PENNSYLVANIAN – EARLY PERMIAN INTERVAL IN THE GONDWANA FLORISTIC PROVINCE OF THE BRAZILIAN PORTION OF THE PARANÁ BASIN

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INTRODUCTION

During the Pennsylvanian-Early Permian interval, the global climate gradually underwent transformational change. The Late Paleozoic Ice Age (LPIA), which began in the late Devonian/Early Mississippian periods, left marks of the last great era of glaciation prior to the Cenozoic Ice Age. Records of this glaciation are found in the southernmost portion of Gondwana as far as 30°S (Parrish et al., 1986; Fielding et al., 2008). Therefore, during this interval there where various glacial pulses, which Heckel (2008) related to cyclothems (alternation of paleosols with marine units as result of periodic and repetitive regression and transgression events). Apparently these derive from the Earth's orbital parameters (Milankovitch cycles). Natural causes of carbon capture and fluctuations are still uncertain (Montañes et al., 2007). However, it is certain that, due to such fluctuations, climatic changes and, thereafter, alternation between glacial and inter-glacial periods occur. This also causes glacio-eustatic fluctuation. Proof of this linkage is in the geological record, because, for the LPIA on Laurasia, there are findings of carbon sinks, which occurred during coal bed formation beginning in the Mississippian (Rowley et al., 1985; DiMichele and Hook, 1992; Anderson et al., 1999). These glacial cycles continued until the Artinskian/Kungurian Stage, and the final deglaciation occurred relatively quickly (Gibbs et al., 2002). Poulsen et al. (2007) remark that, in all of Pangaea at the end of the glaciation, drier conditions and warmer temperatures on the continents were present in the equatorial region, as well as a shift of tropical biomes, with deserts expanding and forests undergoing reduction.

High latitude regions have a different behavior from those observed in lower latitudes. Formerly covered by ice, they went on to have a rich flora in the Early Permian. Paleofloras (macro and micro floras) from the Pennsylvanian-Early Permian interval in the Paraná Basin reflect the paleoclimatic changes that occurred in late Paleozoic Gondwana. The Paraná Basin was located in the southwestern portion of Gondwana, with a sedimentary area covering more than 1,500,000 km^2 in the southeastern portion of South America, and extended to South Africa (Karoo Basin) and Namibia. Layers produced by the alternation of glacial and interglacial periods are found in the sedimentary rocks from the Itararé Group (Middle Bashkirian-Early Asselian) of the Paraná Basin (Fig. 1A), deriving from the youngest episodes of the Pennsylvanian/Early Permian glacial period (Santos et al., 1996; Mori et al., 2012). The oldest floristic record is of Kasimovian age. On the other hand, the Guatá Group from the Early Asselian-Early Artinskian (as well as its basal formation, the Rio Bonito Formation, in the Basin's southern portion, and the Tatuí Formation of the northern portion) represents deposition in milder, post-glacial climates, as well as during a worldwide rise in sea level (Haq and Schutter, 2008). It is necessary to stress that the Tatuí Formation was deposited after the Itararé,but the Rio Bonito Formation, at it's top portion, is syndepositional with the Itararé Group in parts of the basin, though it does not present the same glacialorigin sediments. The Tatuí Formation presents records of stems and trunks only, and non-abundantly. Plus, taphonomic studies indicate these fossils to have been transported (Chahud, 2011), thus making them unsuited for the present study. In that manner, comparison is restricted to the Rio Bonito Formation, which has evidence of sea levels and tempestites thorough it's whole columnar section. Locally, restricted lagoonal conditions occurred along the coastal fringe, where turf developed.

The biggest difficulty in working with the formally described formations from the Itararé Group (Lagoa Azul, Campo Mourão and Taciba formations, other than the Aquidauana Formation) derives from the fact that the group has a great number of intertwined facies that expose the advance and retreat of glacial fronts during various glacial cycles, causing erosion and redeposition of sediments through a very large time period (approximately 75 million years). Geologically, França and Potter (1988) characterized it by the presence of sedimentation cycles, with grains thinning towards the top, corresponding to cyclical climatic changes in a glacial regime and sea level fluctuations. The geologic record shows, yet, that there are carbon layers associated with the clastic glacial deposits. Parts of the floristic record of the Itararé Group are found in those layers; however, it is not possible to affirm that such levels would be related to periods of higher temperature (interglacials).

In the present research, we chose to consider the Itararé Group undivided, because more than one glacial/interglacial cycle occurred in it in during the course of the Pennsylvanian and it has a relatively restricted fossil record. This makes it possible to compare this flora, developed under such cold climate intervals, with that of the superjacent Rio Bonito Formation, which represents milder climates, already into the Permian.

Thus, paleofloras described for the Itararé Group correspond to periglacial and coastal swamp vegetation, even though the record cannot be considered continuous. A record of pteridosperms and gymnosperms also occurs in the Itararé Group. On the other hand, the Rio Bonito Formation paleofloras were deposited in coastal and swampy environments that came into existence (despite the rise of sea level during the Permian, the Paraná Basin already was an inland sea) at the end of the glaciation, and include coal beds where the Gondwana Floristic Province is preserved in the basin.

The present study is based on a composite database containing all paleophytogeographic information for the later Paleozoic in the Paraná Basin, developed by Christiano-de-Souza (2011). Data corresponding to 142 plant fossil occurrences were linked to the Pennsylvanian-Early Permian in the eastern portion of the Paraná Basin in Brazil (states of São Paulo, Paraná, Sta. Catarina, and Rio Grande do Sul). These data were then georeferenced and transferred to ArcGIS software, where occurrence distribution maps were generated, to understand the patterns of floristic distribution within the basin. Furthermore, through the maps it was possible to understand changes in distribution patterns for the Pennsylvanian-Early Permian interval.

MATERIALS AND METHODS

To understand the environments of fossilization for the interval under study, only taxa representing specimens that inhabited swamps were selected, because they offer more precise information about paleoenvironments. They also represent glacial intervals in the Itararé Group (at locales where there was no permafrost nor ice caps, which would make it impossible for plants and peat to develop), and post-glacial intervals in the Rio Bonito Formation (Guatá Group), the latter associated with coal beds. Megaspores were also used to represent swamp

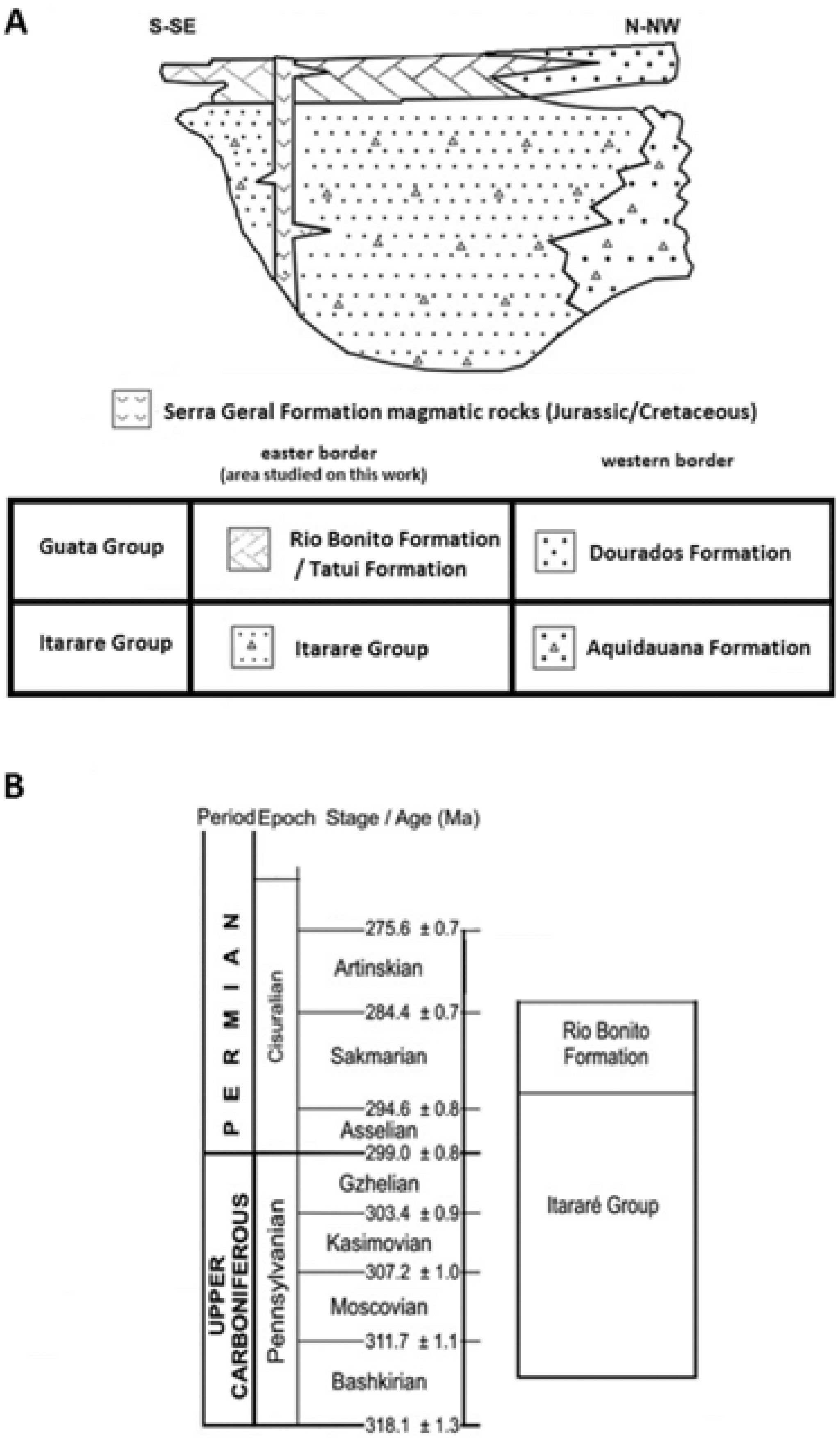

FIGURE 1. **A**, Stratigraphic setting of the Itararé Group / Guatá Group transition (modified from Mori et al., 2012). **B**, Stratigraphic column of Itararé Group / Rio Bonito Formation, on Paraná Basin (modified from Milani, 1997, and Mori et al., 2012).

communities, as signs of the reproduction of lycopsids, which possess less dispersal capability than microspores (Tyson, 1995), and so may better reflect local vegetational patterns. Regarding fossil plants, the chosen taxa were mainly those pertaining to the genera in the Bryopsida, Lycopsida, and Equisetopsida. Taxa from the Polypodiopsida/Spermatophytina lineages were also taken into account, however, they are labeled as *incertae sedis* as they do not have a well-established classification due to the lack of diagnostic characters that would permit their inclusion in these lineages.

From these data, a composite database was prepared, assembling all occurrences cited in the specialized literature (formed by abstracts presented at conferences, reports, articles, which, as they were published mostly in Portuguese, would make them difficult for an international audience to find). Besides basic information on each fossil plant, geographic location, geology, and paleobotanical systematic data were included. Once georeferenced, the database was transferred to the GIS platform through the ArcGIS program. The later was plotted over the geological map provided by the CPRM (The Geological Map of Brazil, scale of 1:1000000, pages SF21, SF22, SF23, SF24, SG21, SG22, SG23, SH21, SH22 e SI22; covering all the outcropping area of the Itararé and Passa Dois Groups).

RESULTS AND DISCUSSION

The selection of plant fossils included those that had affinities with swamp communities. As noted above, these mostly come from genera of the Bryopsida, Lycopsida and Equisetopsida, but include genera of the Polypodiopsida/Spermatophytina, specifically *Adiantites*, *Eusphenopteris*, *Paleovittaria*, and *Triphyllopteris*. Megaspore species included pertained to the genera *Banksisporites*, *Calamospora*, *Cystoporites*, *Duosporites*, *Lagenoisporites*, *Setosisporites*, *Sublagenicula*, and *Trileites*, because they have affinities with the Lycopsida and are indicative of the same type of community. Even if transport had occurred, it would not affect the results, given the study-area dimensions (an area larger than 1,500,000 km^2 in Brazil).

Regarding the megaspores, two new occurrences were included (Porto Feliz and Aterro Delta outcrops) related to interglacial intervals of the Itararé Group in the northern portion of the basin (state of São Paulo) where the presence of megaspores and bryophytes was identified. Distribution maps in the present study were generated jointly and separately for megaspores and macrofossils, in order to understand the distribution of such fossils.

As for the spatial distribution of macrofossils present in the Itararé Group, they are concentrated only in the southern and northern portions of the exposed section of the basin (corresponding to the states of Rio Grande do Sul and São Paulo), probably where the shallower and less affected (by glacial fronts) environments were. Thus, despite the short interglacial intervals, the development of a flora and its fossilization, as well as the formation of coal beds, were fostered. The absence of fossil plants in the central portion of the basin (the states of Santa Catarina and Paraná) may be due to erosion or to the fact that the depositional environments there were more distal to the sites of plant growth, so the flora is represented only by occurrences of palynomorphs.

The Rio Bonito Formation represents a time of milder climates in the Gondwana paleocontinent, attested by the greater abundance and spatial dispersion of fossil occurrences, which extend from the central area to the southern parts of the study area. Thus, portions that in the older interval offered no plant-fossil occurrences (in the states of Santa Catarina and Paraná) have a great number of coal beds, with associated plant fossils in the younger units. Among all formations pertaining to the Gondwana Floristic Province in the Paraná Basin, the Rio Bonito Formation is the one that has the largest diversity of species. The tendency in the basin, as the end of the Paleozoic approached, was a decrease in the number of species (the Rio do Rasto Formation, which represents the end of the floristic province in the Permian, for example, has only 21 species, in an environment already regarded as semiarid) and a high concentration towards the central portion of the basin. For the passage from the Itararé Group to the Rio Bonito Formation, it is possible that the first dispersion of species occurred from the edges to the center of the basin.

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A RARE EXAMPLE OF *ICHNIOTHERIUM* (POHLIG, 1892) WITH BODY/TAIL IMPRESSION FROM THE EARLY PERMIAN BROMACKER LOCALITY OF GERMANY

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In 1898, the Amherst College Museum of Natural History (now the Beneski Museum of Natural History, here abbreviated ACM), Massachusetts, USA, purchased a large sandstone slab containing trace fossils from the Early Permian Tambach Formation of the Thuringian Forest in central Germany (Fig. 1). The most prominent feature of this slab is a single tetrapod trackway identified as *Ichniotherium sphaerodactylum* (Pabst, 1895). Documentation of this specimen is important, because it is only one of two *Ichniotherium* trackways from the Tambach Formation with a body/tail impression.

For more than 100 years, numerous excellently preserved Early Permian tetrapod tracks from central Germany have been identified as *Ichniotherium cottae* (Pohlig, 1892) and *Ichniotherium sphaerodactylum* (Pabst, 1895). The track-bearing sandstone slab in the ACM collection comes from the Bromacker locality approximately 1.5 km north of Tambach-Dietharz village at the northern margin of the Thuringian Forest (Voigt, 2001). Like most other *Ichniotherium* tracks from the Tambach Formation, the ACM trackway is preserved as natural casts in convex hyporelief (Voigt, 2001; Voigt et al., 2007).

Ichniotherium is the trackway of a quadruped with pentadactyl manus and pes impressions that are 5.5-13 cm long (Voigt, 2005; Voigt et al., 2007). In both manus and pes, digits increase in length from I through IV, and digit V is shorter than or the same length as digit III. Digits are typically somewhat curved or bent toward the trackway axis, and often have (in the pes) expanded distal tips that give them a “drumstick-like” appearance. The ichnospecies *I. sphaerodactylum* is characterized by a relatively long digit V, measuring about 66% and 80% the length of digit IV in the manus and pes, respectively, and in having a mediolaterally expanded oval sole impression of the pes (Voigt et al., 2005).

ACM 62/1 (Fig. 1) is a continuous trackway 149 cm long and 46 cm wide consisting of manus and pes impressions. The continuous trackways of *Ichniotherium sphaerodactylum* such as ACM 62/1 exhibit only minor or no overlapping of manus-pes imprints. In continuous trackways the manus impression is also slightly smaller than the pes impression (Voigt et al., 2007), which is evident in the ACM 62/1 trackway. The manus impressions are close to the pes impressions and slightly rotated toward the trackway midline. There are approximately eight manus impressions that are slightly smaller than the pes impressions. The distal portion of the manus impression has a characteristic triangular shape, which can be best seen in the most anterior portion of the trackway. The pes impressions (eight in total) have a characteristically expanded, mediolateral oval outline that is approximately twice as wide as the proximodistal length and lies opposite to digits II-IV (Voigt et al., 2007). As in other examples of *I. sphaerodactylum* (Voigt et al., 2007), the pace angulation in ACM 62/1 is between 70° and 110°. The ratio of the stride length to the pes length is 2.5-4.4:1, whereas the ratio of the stride length to the apparent body length is 0.8-1.4:1. A body/tail impression is present in ACM 62/1 as a relatively deep, nearly linear imprint that is situated along the middle two-thirds of the trackway. This is a phenomenon most likely caused by the substrate consistency, which affected the gait and mode of locomotion of the track maker, and also caused the animal to lower its body that left its impression on the substrate. Tracks and trackways referred to *I. sphaerodactylum* normally do not preserve body/tail impressions, suggesting that the track maker held its body/tail above the ground during walking.

The track maker of the ichnogenus *Ichniotherium* was diadectids (Fichter, 1998; Voigt and Haubold, 2000). Indeed, a correlation has been established between *Ichniotherium* and articulated skeletal fossils of the diadectids

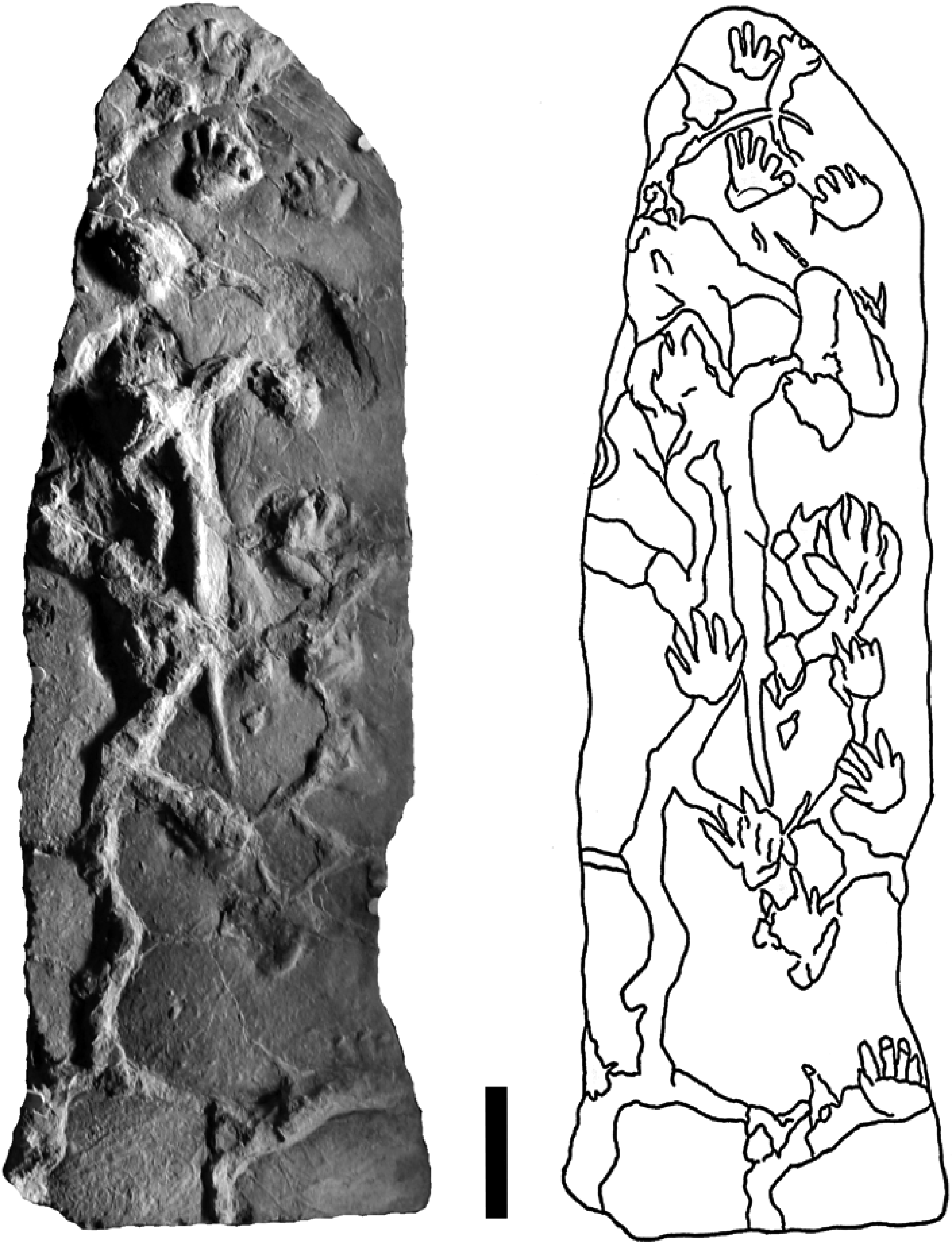

FIGURE 1. *Ichniotherium sphaerodactylum* (Pabst, 1895) ACM 62/1 from the Bromacker (central Germany) locality of Tambach-Dietharz village at the northern margin of the Thuringian Forest. Left, natural cast of the trackway preserving body/tail impression. Right, interpretive drawing of the trackway. Scale bar equals 10 cm.

Diadectes absitus and *Orobates pabsti* (Voigt et al., 2007). *Orobates* is restricted to the Bromacker locality (Berman et al., 2004), where *Ichniotherium sphaerodactylum* are the most common tracks (Voigt et al., 2007). Therefore, the track maker of *I. sphaerodactylum* was very likely *O. pabsti*.

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CLIMATE FLUCTUATIONS WITHIN THE WESTERN PANGEAN TROPICAL SHELVES – THE PENNSYLVANIAN/ PERMIAN RECORD FROM BENTHIC FORAMINIFERA

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Abstract—Benthic foraminiferans including fusulinids (symbiont-bearing benthic foraminiferans) are among the best indicators of paleoclimate and paleogeography in the Carboniferous and Permian. The dynamics of distribution of benthic foraminiferans in space and time constrain important tectonic and climatic events at a global scale. The North American shelves during Pennsylvanian and Permian time were geographically within the tropical belt characterized by permanent temperate environments with significantly lower foraminiferal diversification and rare occurrences of warm water Tethyan forms. The temperate water environments allow documentation of warming episodes that are associated with abrupt immigration of warm-water and exotics in the area--taxa that earlier evolved elsewhere. Several warming and cooling episodes are described and discussed. The differences of taxonomic changes in each event could potentially be used for provisional estimation of the degree of change. The occurrences of the exotic to North American forms during warming episodes are always delayed depending on the scale and the intensity of the warming episodes. The cooling events associated with decreasing taxonomic diversity and appearances of endemic forms are characteristic for temperate water provinces only. The occurrence of these forms in the Boreal and North American provinces appears to be isochronous, as their environments are uniform and this stimulated their uniform and isochronous distribution.

INTRODUCTION

The late Paleozoic is commonly regarded as a time of a global greenhouse-icehouse climate transition. The most recent data suggest multiple phases of glaciation-deglaciation processes, although the number of these phases and their age constraints are debated (Isbell et al., 2003; Montanez et al., 2007; Fielding et al., 2008b). Marine biotas are sensitive to local, regional or global environmental changes, and the exceptionally well-studied benthic foraminiferans are among the best indices of paleoenvironments (Murray, 2006 and references herewith). The Cenozoic record of benthic foraminiferal diversity (Hallock et al., 1991) shows a strong correlation with well-studied climatic changes for that time (Zachos et al., 2001), and this model of the interaction between tropical benthic Foraminifera and climate is applied in this paper to understanding the Late Paleozoic climatic fluctuations through the proxy changes of climatically sensitive biotas (Davydov and Arefifard, 2013).

PALEOBIOLOGY AND PALEOECOLOGY OF FUSULINACEANS

Late Paleozoic foraminifers were some of the most advanced protistans, and they had leading role in benthic assemblages during the Late Paleozoic: they dominated numerically within the micro-benthic communities, they were globally wide-spread within the tropics and subtropics and they were evolved rapidly, reaching high taxonomic diversity. The fusulinids were generally distributed in the tropical-subtropical belt (up to 35-40° S/N paleolatitude) within carbonate to mixed carbonate-siliciclastic shallow-water settings (Ross, 1995). Based on similarities in size, test morphology and with the biofacies associations of modern larger benthic foraminifers (Beavington-Penney and Racey, 2004; Hohenegger, 2004; Murray, 2006), the fusulinids are assumed to have hosted photosynthetic symbionts (Ross, 1982; Vachard et al., 2004). Benthic foraminifers are poikilothermic, i.e., their body temperature is very close to that of the surrounding water, and responds very quickly to even small changes in the ambient water temperature (Beavington-Penney and Racey, 2004). Temperature is generally considered to be the single most important physical factor influencing the distribution of symbiont-bearing protistans in seas of normal salinity (Fuhrman et al., 2008).

Shallow-water assemblages of present-day larger foraminifers in optimal water temperatures (20-30°C) generally are much more diverse than those in temperatures greater than 30°C or less than 20°C (Beavington-Penney and Racey, 2004; Hohenegger, 2004; Murray, 2006). Similar changes in diversity are apparent in the latitudinal distribution of the late Paleozoic fusulinids and these are assumed to correspond to tropical-subtropical temperature changes (Ross, 1995). During global warm episodes, larger symbiont-bearing foraminifers could migrate to higher latitudes. By contrast, cooling led to emigration of parts of the foraminiferal fauna from higher to lower latitudes, stepwise extinction of some of the larger taxa, increasing provincialism and the preferential survival of eurytopic faunas adapted for a broader range of facies and environments (Stanley, 1984; Kalvoda, 2002; Mayhew et al., 2012).

Mid-latitudes are the areas where climatic fluctuations and the velocity of climate change are most significant, as has been shown in the modern world (Burrows et al., 2011) and in Permian models (Winguth et al., 2002). Fusulinid faunas provide a particularly sensitive index of climate change in these mid-latitude regions. Permian climate simulation models (Winguth et al., 2002) suggest a significant 5-7 C° latitudinal shift in average sea-surface temperature and associated climatic belts under glacial versus non-glacial (warm) climate states. This model for the mid-latitudinal regions has been successfully applied in the understanding of climate dynamics during the late Gzhelian (latest Pennsylvanian of Timor and Australia) (Davydov et al., in press) and Guadalupian (Oman-Zagros areas) time (Davydov and Arefifard, 2013).

The other model of global foraminiferal diversity variation as a proxy of the climate fluctuations has been proposed recently (Davydov, 2008; Davydov et al., 2012). Here the data of global diversity variations will be combined with the pattern of immigration of fusulinids from Tethys into North American shelves.

TEMPERATE ENVIRONMENTS IN NORTH AMERICAN SHELVES DURING THE LATE PALEOZOIC

It was noted in several studies that there is a significantly lower diversity of foraminifers in North America in comparison with corresponding assemblages in Tethys and even in Boreal faunas (Fig. 1). (Davydov, 2008; Groves and Wang, 2009). The here proposed interpre-

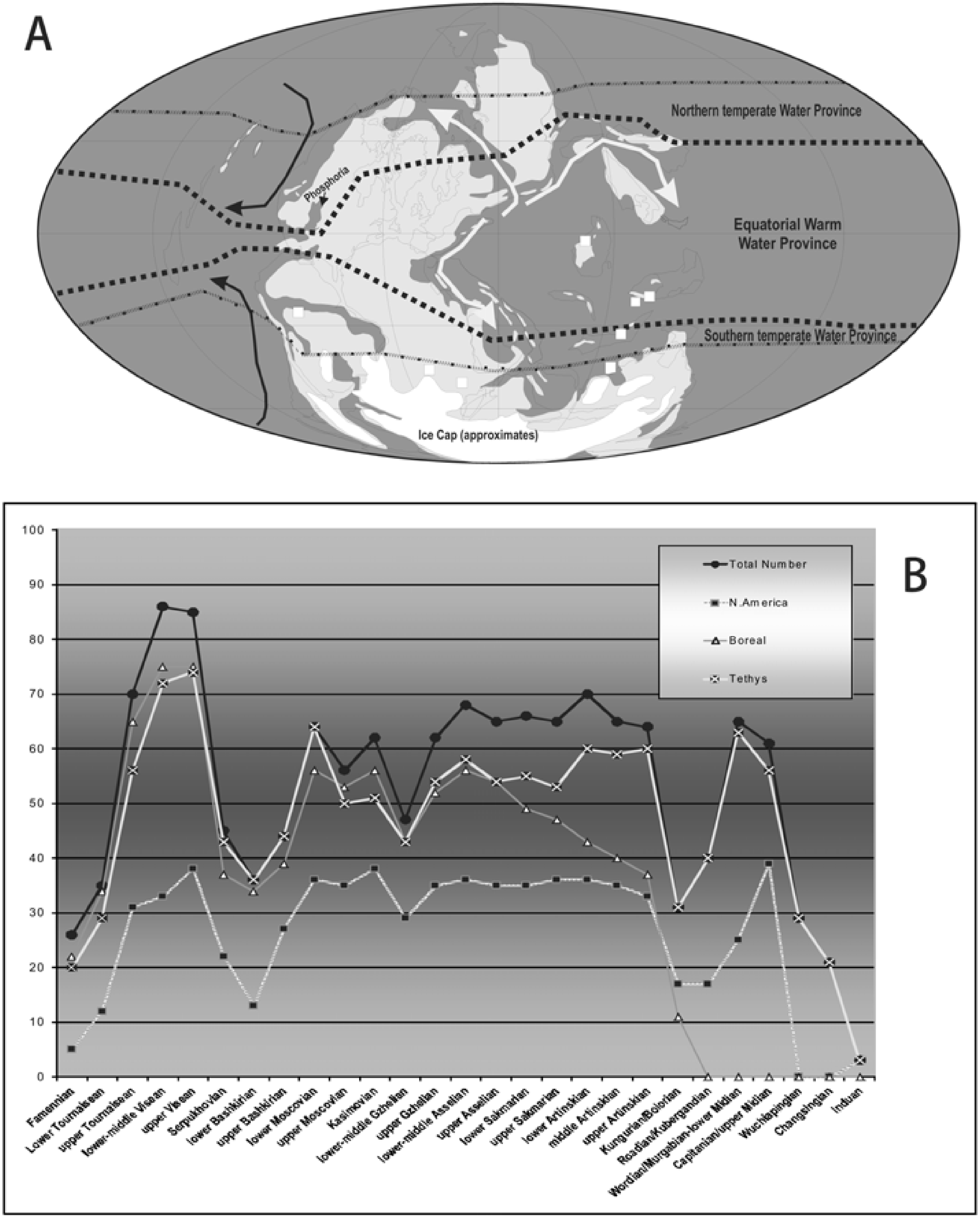

FIGURE 1. **A**, Distribution of warm- and temperate water environments during the Pennslvanian-Cisuralian. The reconstruction is simplified after Ziegler et al. (1997). B, Fusulinids--generic global and provincial diversity patterns.

tation suggests predominantly temperate environments within the geographically tropical shelves of North America as the major factor that produced such a phenomenon (Davydov, 2008). The permanent regional climate cooling in the Permian of western Laurentia has been documented from several benthic fossils (Clapham, 2010). Similarly, several temperate-index fossils, such as conulariids and other cold-water pelecypods were documented within the North America shelves in Idaho, Nevada, and West Texas, (Kauffman and Runnegar, 1975; Meldon and Shi, 2003). Potential glendonites in the Bashkirian and middle Moscovian of Nevada were reported from the western margin of the North American craton (Bishop et al., 2007). The evidence of alpine glaciation in this topical zone was documented in the Devonian (Brezinski et al., 2010) and Pennsylvanian (Soreghan et al., 2008). Because of the shift of the cool-water thermocline southwards along Laurentia the environments in the shelves here were as sensitive as in the mid-latitudes elsewhere in the Boreal and Tethyan provinces (Davydov and Arefifard, 2013; Davydov et al., 2013).

In terms of fusulinacean taxonomy, west Laurentia assemblages often includes taxa (genera) that commonly occur in higher temperate mid-latitudes in the Boreal and Tethyan provinces (i.e., *Pseudofusulinella*, *Wedekindellina*, *Eoparafusulina*, etc.).

Nevertheless, the elements of typical warm-water taxa occasionally and abruptly occur throughout the Late Paleozoic in North America fusulinid successions and potentially provide valuable information on the dynamics of Late Paleozoic climate within a well-documented and precisely constrained benthic foraminiferal record (Ross, 1995; Davydov, 2008; Davydov et al., 2012). Particularly, the record of warming episodes could be well documented within the successions as it is highlighted by the occurrence of warmer-water tropical taxa that are exotic for this regional fauna. These exotic elements appear in the local communities suddenly due to migration at the warming episodes and do not have any evolutionary roots with local faunas.

At the same time, there are several genera that are abruptly occurring in both the Boreal and the North American provinces isochronously. These events might be interpreted as cooling events because these faunal elements are a low diversity; they occur only within certain horizons most probably characteristic to temperate environments and not known in the warm water assemblages. There is no time lag in their occurrences throughout and thus the environments were uniform and appropriate for the fast distribution of these temperate forms. Only four fusulinid-determined cooling events were recognized at the moment (Fig. 2).

At the beginning of Bashkirian time after the closure of the Rheic pathway the connection of western and eastern shelves of Pangaea was cutoff (Saltzman, 2003). The genus *Millerella* evolved at this time and was widely distributed globally approximately isochronously. The fusulinid diversity in North American shelves during the Morrowan, i.e., the major part of the Bashkirian, is the lowest within the entire Late Paleozoic. Only single *Millerella* species and several long-ranging and rare *Eostaffella* occur in North American shelves at this time (Groves, 1986) . The Bashkirian assemblages in Tethys at this time include several genera and many species (Groves et al., 1999). The Morrowan low foraminiferal diversity can be linked with the Bashkirian glacial event recently constrained in Gondwana (C2 glaciation) (Fielding et al., 2008a; Gulbranson et al., 2010).

The first warming episode in North American shelves at the beginning of Atokan time is associated with the immigration of *Pseudostaffella* and slightly later *Schubertella*/*Schubertina* (Groves, 1986; Davydov, 2011). The genus FAD in western Pangea and elsewhere in Tethys is in the lower Bashkirian (Reitlinger, 1971), and the delay of the genus occurrence in North America is about 2.3-3.0 Ma (Groves et al., 1999; Davydov et al., 2012) .

The second important immigration event and perhaps the warming episode associated with the occurrence of *Profusulinella* in upper Atokan time (Groves et al., 1999) is right at the beginning of the global early Moscovian transgression. The event is well documented within the shelves from Bolivia to the Great Basin and western Canada (McGugan and Rapson, 1979; Groves and Sanderson, 1990; Sakagami and Mizuno, 1994). The delay of occurrence of *Profusulinella* in North America to the FAD in Tethys was approximately 4-4.5 Ma (Davydov et al., 2012).

Two cooling events can be recognized within the Moscovian-Kasimovian transition. The first one is marked by the sudden and isochronous occurrence of *Wedekindellina* in both North American and Boreal shelves. *Wedekindellina* is restricted only to these two areas and never documented elsewhere. The evolutionary roots of the genus are not clear, but the stratigraphic range and first occurrence datum in both areas are well constrained.

The second event corresponds with the major extinction event in the fusulinid evolution at the Moscovian-Kasimovian boundary. This extinction is well expressed in Tethys. In Boreal and North America it is associated with the occurrence of *Eowaeringella*, which in both areas marked the Moscovian-Kasimovian boundary (Stewart, 1968; Davydov, 1997a; Remizova, 2004).

The next warming event in the North American shelves is associated with the immigration of *Triticites*. The genus evolved in Tethys during the early to middle Kasimovian and occurs in North America only in the upper Kasimovian (Thompson et al., 1956; Davydov, 1997b). The time lag in the occurrence of the genus in North America is 1.0-1.5 Ma (Fig. 2).

The warming event of the late Gzhelian in the Tethys and Boreal provinces is associated with the highest peak in foraminiferal diversity and a worldwide distribution of the common species (Davydov et al., 2012; Davydov et al., in press). In North American shelves it corresponds with the occurrence of *Schellwienia*, which is commonly named as *Schwagerina* and/or *Pseudofusulina* (Wilde, 2006). *Schellwienia* in Tethys appears in the late Gzhelian *Daixina sokensis* zone (Davydov, 1986), whereas in North America in the latest Gzhelian (Schmitz and Davydov, 2012). The difference of around 1 Ma or less suggests a very rapid onset of the global warming at this time.

The occurrence of *Pseudoschwagerina*, the origination of which is hidden, is well documented in the Tethys at the middle Asselian (Scherbovich, 1949). In the Boreal province and North America it seems to occur during late Asselian time (Thompson, 1954; Konovalova, 1991; Schmitz and Davydov, 2012). There are several other lines of evidence of warming event during the late Asselian in the North American and Boreal shelves. For example, *Biwaella*, which appears in Tethys in the early Gzhelian, migrated in the late Asselain into the Boreal province (Nilsson and Davydov, 1997). The species *Pseudofusulina attenuata* Skinner and Wilde from the Klamath microcontinent migrated into North American shelves as reported in Nevada (Davydov et al., 1997) and western Canada (Zubin-Stathopoulos et al., 2012). The difference in the occurrence of *Pseudoschwagerina* in Tethys and North America is minimal and does not exceed 1-1.5 Ma, and thus this warming event was short. However, it was not as extensive as the late Gzhelian event because of the overall lower foraminiferal diversity in the late Asselian (Fig. 2).

The widespread and isochronous occurrence of *Eoparafusulina* in Boreal and North American shelves at the beginning of the Sakmarian perhaps indicates cooling events. The range of *Eoparafusulina* in the Boreal province is very short, within the lower Sakmarian only (Davydov, 1997a; Remizova, 2004), whereas the genus extended up to the Kungurian in North America (Dunbar and Skinner, 1937).

The late Artinskian warming event in temperate zones is associated with the occurrence of several genera. The most prominent genus is *Chalaroschwagerina*, which appears in Tethys sometime in the middle Artinskian (Davydov et al., 2013) and is widespread in Tethys and the Klamath microcontinent through the Kungurian. It occurs in North American shelves in the late Artinskian (*Ch. hawkinsi*, *Ch. nelsoni*, *Ch. solita*) (Dunbar and Skinner, 1937; Davydov et al., 1997). The delay in occurrence of the genus in N. America is about 2-2.5 Ma. In addition to *Chalaroschwagerina*, typical Tethyan *Robustoschwagerina*, although known from a single occurrence, has been documented from the upper Artinskian in Texas (Dunbar, 1953). Also, *Biwaella* and *Rugosochusenella*

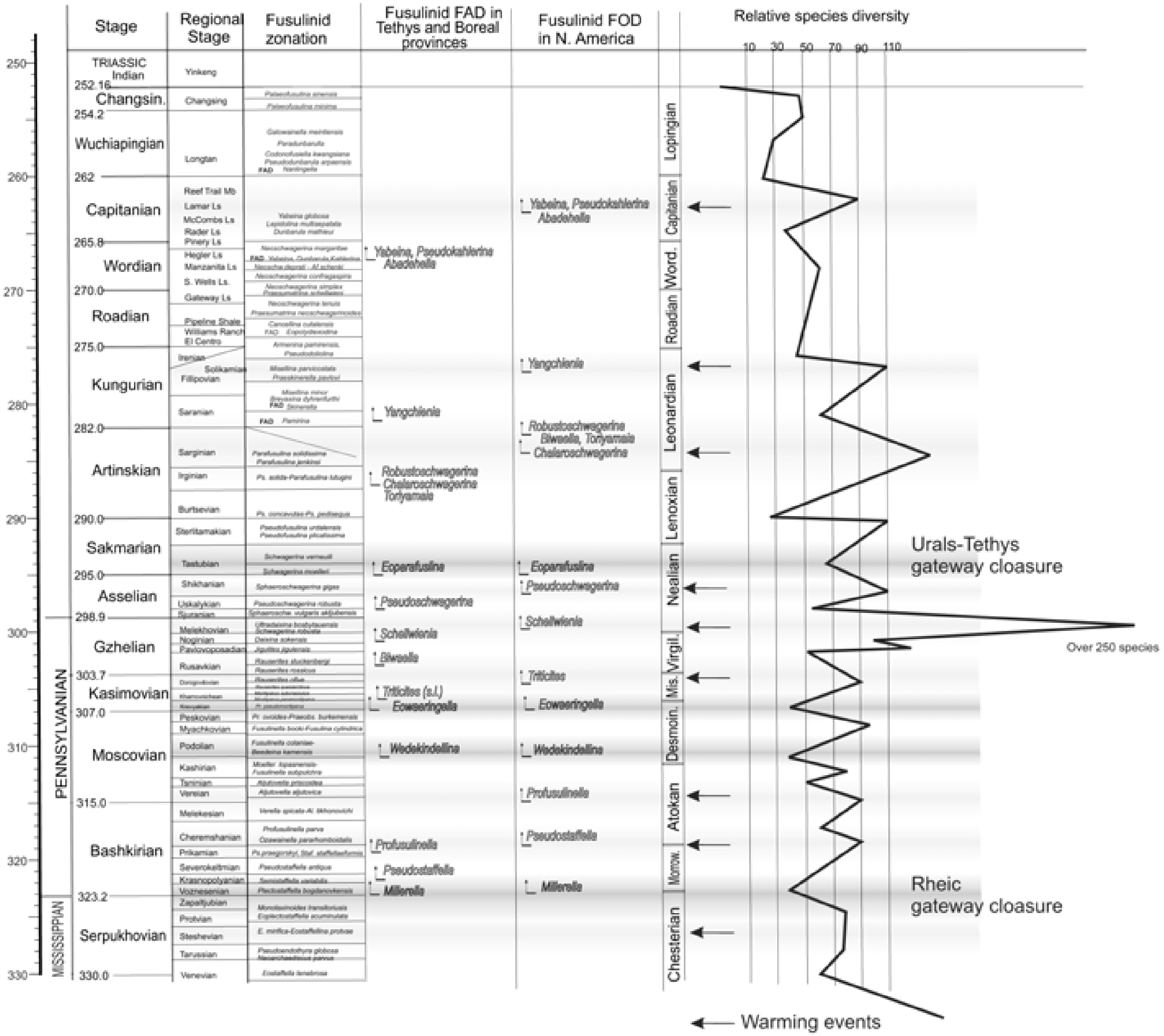

FIGURE 2. Warming and cooling events along the North American shelves during the Pennsylvanian and Permian. At cooling episodes, the distribution between the North American and Boreal provinces was isochronous, whereas during warming episodes the exotic taxa occur in North America with noticeable delay.

is known from New Mexico (Skinner and Wilde, 1965). The latter two genera appear in Tethys in Gzhelian time (Davydov, 1986, 2011) .

Because of strong provincialism of the fusulinid assemblages in Kungurian-Wordian time, no Tethyan elements are found, except the occurrence of rare *Yangchienia iniqua* in the lower, Kungurian part of the Road Canyon Formation (Yang and Yancey, 2000). The late Kungurian is associated with a high fusulinid diversity peak in Tethys (Fig. 2) and most probably with a warming episode. The genus had appeared in the Tethys in the early Kungurian (Leven et al., 1992). The difference in the time of the occurrences in Tethys and North America is about 4-4.5 Ma.

The last and very prominent warming event associated with immigration is in the upper Capitanian in Texas with a vast number of Tethyan fusulinids, such as *Yabeina*, *Pseudokahlerina*, *Paradoxiella*, *Reichelina*, *Codonofusiella*, *Rauserella* and *Lanchichites*. Also, a very characteristic Tethyan smaller foraminifera *Abadehella* has been found above *Yabeina* in Texas (Dunbar and Skinner, 1937; Skinner and Wilde, 1955; Nestell et al., 2006). Among them, *Yabeina* is the most important taxon. Verbeekinids, to which *Yabeina* belongs, are a very sensitive foraminiferan that survived only in very warm environments where surface water exceed a yearly temperature of about 20-22° C (Davydov and Arefifard, 2013) . It seems the climatic shallow water condition in Texas at that time was marginal for verbeekinds because *Yabeina* there is represented by a small and primitive form. The rest of the fusulinids, most of which belong to schubertellids and ozawainellids, were more resistant to the cooler temperature (Davydov, 2011) and thus they are more diverse and abundant in the upper Capitanian. *Yabeina* appeared in Tethys some time during the late Wordian (early Midian in Tethys) together with the other diverse verbeekinds and schubertellids and ozawainellids mentioned above. In North America, *Yabeina* occurs during the late Capitanian. The time lag is about 4-4.5 Ma.

CONCLUSIONS

The North American shelves during Pennsylvanian and Permian time being geographically within the tropical belt were characterized by permanent temperate environments with significantly lower foraminiferan diversification and rare occurrences of warm water Tethyan forms. The temperate water environments allow documentation of warming episodes that were associated with the abrupt immigration to the region of warm-water and exotic taxa that earlier evolved elsewhere. Several warming and cooling episodes are described and discussed. The differences of taxonomic changes in each event could potentially be used for provisional estimation of the degree of change in temperature. The occurrences of the exotic to North America forms during warming episodes are always delayed depending on the scale and the intensity of the warming episodes.

The cooling events are associated with a decrease in taxonomic diversity and the appearance of endemic forms characteristic of temperate water provinces only. The occurrence of these forms in Boreal and North American provinces appears to be isochronous as their environments are uniform and this stimulated their uniform and isochronous distribution.

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A NEW TRACE FOSSIL FROM THE PERMIAN COCONINO SANDSTONE OF NORTHERN ARIZONA

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Abstract—Trace fossils consisting of small conical pits are reported from the Middle Permian Coconino Sandstone of northern Arizona. These occur singly or in groups at the foot of dune faces and on eroded bounding surfaces. Their architecture most closely resembles that of the traps constructed by modern antlion larvae (Myrmeleodontidae) but as these organisms are only known in the fossil record to the Early Cretaceous it may be that the pits represent predatory behavior on the part of another insect taxon.

INTRODUCTION

The Coconino Sandstone is a widespread formation that crops out over much of the southern Colorado Plateau south of the Utah-Arizona border. It represents an enormous sand-sea or erg that covered much of what is now the southwestern United States during the early Middle Permian (Middleton et al., 2003). Body fossils have not been reported from the Coconino Sandstone and so the only evidence of the organisms that lived in the Coconino desert is trace fossils. Most work has been carried out on the vertebrate traces, starting in 1918 when Lull described tracks from the Grand Canyon. This was followed by a series of papers by Gilmore through the 1920's (see refs. in Hunt et al., 2005) that resulted in the naming of 17 vertebrate ichnotaxa. Although these descriptions were not reviewed for many decades afterwards more recent work (Haubold, 1996; McKeever and Haubold, 1996) has shown that all the vertebrate tracks can be accommodated within three species of one ichnogenus, *Chelichnus*, described by Jardine in 1850. The first invertebrate trace fossils from the Coconino Sandstone were also described by Lull in his 1918 publication. More were described through the 1920's in the publications by Gilmore, resulting in five new genera and species, all of which consisted of surface trails. Further descriptions of invertebrate traces were published by L.F. Brady between 1939 and 1961 (see refs. in Middleton et al., 2005) resulting in a total of ten invertebrate ichnotaxa. Unlike the vertebrates no recent review of these taxa has been carried out. In this paper we briefly describe a new invertebrate trace fossil that consists of conical pits similar in size and configuration to those made by modern antlions (Myrmeleodontidae).

Trace Fossil Preservation

The difficulty of forming and preserving traces in dry sand was recognized by Brady (1939), who noted that several of the described traces were similar to those formed by the modern scorpion *Centruroides* in dry sand when the temperature was about 60° F (15° C). McKee (1947) showed that preservation was likely only in dry cohesionless sand deposited on gentle slopes or horizontally, and that small invertebrates could not make tracks in sand that was wet or had dried out to form a crust. He further showed that for the traces to be preserved the surface needs to be moistened after the tracks are formed. Desert sands generally have low moisture content, but modern deserts such as the Namib Desert in western Africa have varying moisture contents depending on their proximity to onshore coastal winds, to basin margin and basin-central fluvial systems, and also to the magnitude of the water table rise during wetter seasons (Middleton et al., 2005). Trace fossils thus provide information not only on the trace makers and direction of movement but also provide information concerning substrate moisture conditions.

Localities

All the specimens come from a series of disused quarries near Ash Fork, west of Flagstaff, Arizona. The principal specimens were found at a quarry located about 10 km northeast of Ash Fork (Locality 3 of Millhouse, 2009), where they occur with vertebrate trackways identified as *Chelichnus bucklandi*.

TRACE FOSSIL DESCRIPTION

The new traces consist of small conical pits found on bedding plane and erosional surfaces at a number of localities within the Coconino Sandstone (Fig. 1A-B). They vary in size but are usually about 15 mm in diameter and 6 mm deep (averages from 16 measured examples on two collected slabs) but vary between 25.5 and 7.5 mm wide and 11.5 to 3.3 mm deep. Each pit consists of a cone that may have a circular, or more rarely oval, margin in plan view. The pits have a central axis that is usually vertical but may be angled, and it is noticeable that an angled axis is usually associated with pits that have an oval surface outline and that are situated on sloping surfaces. The rim of the pit is often slightly raised and in some cases sand that appears to have been thrown out of the pit can be seen forming a surrounding pad (Fig. 1B). The walls of the pit are usually smooth, and narrow to a sharp basal point. However, in a number of cases one or more concentric ridges can be seen within the pit, with slight changes of slope angle apparent at each ridge (Fig. 1A). Broken specimens show that the pits are not connected to tubes or burrows below the surface.

The pits occur on a variety of surfaces. They occur on sloping dune faces (Fig. 1A), and where seen in situ they are placed at the foot of the dune. Pits in these situations show the greatest variability in size and may occur in linear sets, at right angles to the slope of the dune surface. They are also known to occur on bounding surfaces, in which erosion has beveled a horizontal or near-horizontal surface. In these cases they form clusters of between three and 18 burrows that closely approximate each other in size (Fig. 1B).

TRACE FORMER

We have not found any sedimentary structures similar to these pits reported in the literature and there are several features that suggest they were caused by animal activity. These include their regular shape and size, and the fact that pads of sand surround some of them suggesting material thrown out as the pit was formed. Several known trace fossils present as more or less conical surface pits but in each case these are the surface expression of burrows within the sediment (e.g. *Diplocraterion*, *Histioderma*, or *Laevicyclus*) and in any case are known only from aquatic sediments not sand dunes (Häntzschel, 1975; Sargeant, 1983). Modern organisms that form pits similar to these can be narrowed down to the antlions (Myrmeleodontidae), which are concentrated in arid, sandy re-

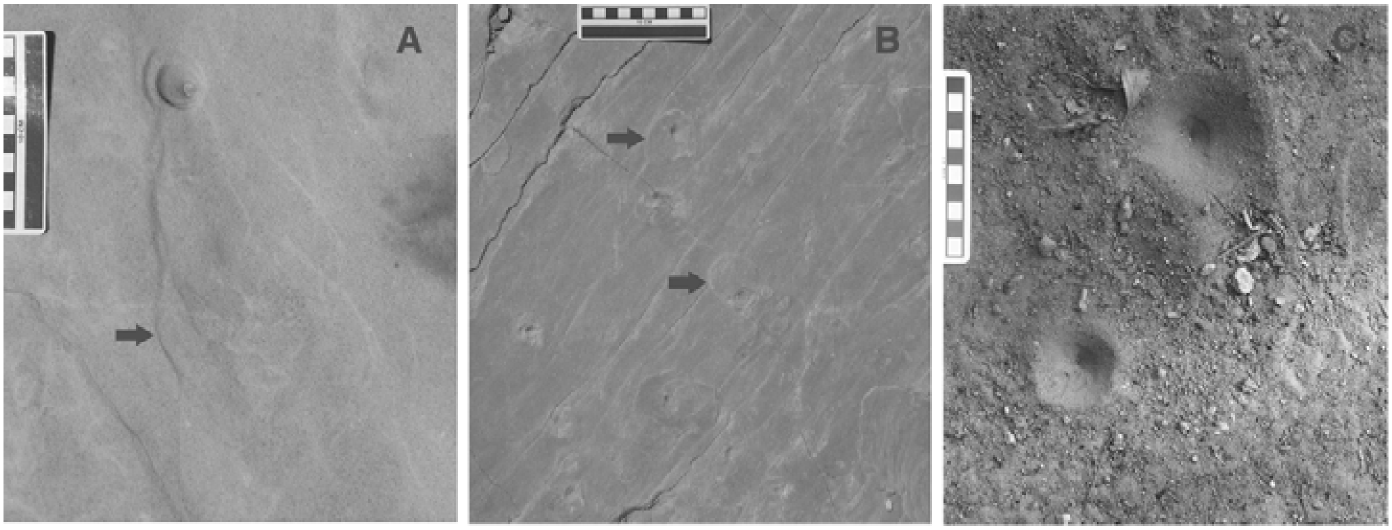

FIGURE 1. **A**, Single pit on a dune face in the Coconino Sandstone showing a slump (arrowed) below the pit, and concentric ridges within the pit. **B**, A group of pits on a bounding surface in the Coconino Sandstone showing pads of sand around the pits (arrowed). **C**, Modern antlion pits showing built-up rims and concentric ridges within the pits. **A**-**B**, Coconino Sandstone, Ash Fork, Locality 3 of Millhouse (2009); **C**, Popa Falls, Namibia. Scale=100 mm.

gions and some of which have larvae that dig conical pit traps (Fig. 1C). These are constructed by the larvae scuttling backward in a tightening spiral while displacing sand to the side, forming a conical depression (Grimaldi and Engel, 2005). They stop when the critical angle of slope is reached and then lie in wait at the bottom of the pit, covered in sand. Any small prey that stumbles into the pit will slide down and be captured. Dry, fine-grained sediments are preferred by antlions as these allow prey to be dislodged more easily from the sides of the pit. The morphology of the structures from the Coconino Sandstone is similar to that of modern pits (Fig. 1C), including the size and shape, and details such as the concentric ridges that are occasionally present within the pits. Because of this we suggest that the fossil examples may be evidence of predatory behavior similar to that of antlions today. The Myrmeleodontidae are documented back to the Early Cretaceous (perhaps latest Jurassic) of China, Brazil, and Israel, but no fossil example of their pits have been reported and the predators in this case might have been another insect taxon using the same predation strategy.

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ICHNOLOGICAL DIVERSITY OF THE CONTINENTAL MISSISSIPPIAN MAUCH CHUNK FORMATION, EASTERN PENNSYLVANIA

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Abstract—In eastern Pennsylvania, the Mississippian (Visean/Chesterian) Mauch Chunk Formation is a more than 1-km-thick succession of siliciclastic red beds that yields continental trace fossils, especially tetrapod footprints. In 1843, Isaac Lea first reported tetrapod footprints from the Mauch Chunk Formation at Mount Carbon, PA, naming the tracks *Sauropus primaevus* (later emended to *Palaeosauropus primaevus*). Trace fossils have been recovered from the type locality and at nine other localities in eastern Pennsylvania. Most of these localities are within the Indian Run Member of the Mauch Chunk Formation. Deposition of the Indian Run Member was from low-sinuosity braided fluvial systems in a semi-arid to arid setting. Invertebrate ichnofossils recovered from the Mauch Chunk Formation are assigned to the ichnotaxa *Diplichnites gouldi*, *Diplopodichnus biformis*, *Gordia* isp., *Kouphichnium* isp., *Planolites beverleyensis*, *Rusophycus carbonarius*, *Stialla pilosa*, *Stiaria intermedia* and *Taenidium barretti*. Of these, only *Planolites* and *Taenidium* are abundant, thus the Mauch Chunk Formation invertebrate ichnoassemblage well represents the *Scoyenia* ichnofacies. Both the *Diplichnites* and *Scoyenia* ichnoguilds are present, confirming that the terrestrial invertebrate fauna had fully colonized fluvial environments by the Mississippian Period. Vertebrate ichnofossils from the Mauch Chunk Formation include an unusually large tetrapod burrow, probably made by an amphibian, diverse fish swimming traces assigned to *Undichna brittanica*, *U. unisulca*, *U. quina* and *U.* isp., as well as unique temnospondyl body impressions (*Temnocorpichnus isaacleai*) that support speculation about social (courtship) behavior among some Mississippian amphibians. Tetrapod footprints are abundant in the Indian Run Member of the Mauch Chunk Formation, and are assigned to *Batrachichnus salamandroides*, *Characichnos* isp., *Hylopus hardingi*, *Matthewichnus* isp., *Palaeosauropus primaevus* and *Pseudobradypus* isp. The limited tetrapod body fossil record of the Mauch Chunk Formation (one species of temnospondyl, and two species of anthracosaurs and some fragmentary remains of other taxa) does not provide an adequate roster of trackmakers for all of the Mauch Chunk Formation tetrapod footprint assemblage. The tetrapod footprint assemblage of the Mauch Chunk Formation is interpreted as being dominated by temnospondyls with rare anthracosaurs. This footprint assemblage is assigned to the *Batrachichnus* ichnofacies. The global record of Carboniferous tetrapod footprints can be divided into three time intervals: (1) *Palaeosauropus* biochron of Mississippian age, which encompasses temnospondyl-dominated footprint assemblages that lack reptile footprints; (2) *Notalacerta* biochron of Early-Middle Pennsylvanian age, which remains temnospondyl dominated but includes the oldest reptile footprints; and (3) *Dromopus* biochron of Late Pennsylvanian (and Early Permian) age, which includes diverse reptile footprints and the first record of characteristic Early Permian footprints of the ichnogenus *Dromopus*. Footprints of *Pseudobradypus* occur in Mississippian strata and are not necessarily those of reptiles. Instead, the ichnogenus encompasses the tracks of reptiliomorphs (especially anthracosaurs); this homeomorphy makes it impossible to use *Pseudobradypus* to identify the oldest record of reptiles. The Mauch Chunk Formation tetrapod footprint record is consistent with the body fossil record of tetrapods in being dominated by the footprints of amphibians of diverse sizes and also containing rare reptiliomorph footprints but no assignable reptile footprints.

INTRODUCTION

The Mississippian-age Mauch Chunk Formation in eastern Pennsylvania produced some of the first discovered, and oldest known, tetrapod tracks and trackways (Lea, 1849, 1853, 1855), and thereby played an important role in early debate about the ascent of the land-dwelling amphibians (Lucas et al., 2007; Fillmore et al., 2009a, b). Initial work by Isaac Lea was followed by nearly 150 years during which Mauch Chunk Formation ichnofossils were collected in eastern Pennsylvania. However, essentially no information about these tetrapod footprints appeared in the scientific literature. Our collecting since 2003 has greatly expanded the number of invertebrate and vertebrate ichnofossils known from the Mauch Chunk Formation, and thus has allowed a detailed characterization of the ichnology (Fillmore et al., 2004, 2006, 2007, 2009a, b, 2010, 2011, 2012; Lucas et al., 2006; 2007, 2010a, b; Simpson et al., 2006; =Smith et al., 2009, 2012; Storm et al., 2010). Our research presents a detailed ichnology of the Mauch Chunk Formation, encompassing work on the historical study of traces and all aspects of the invertebrate and vertebrate ichnology. Fillmore et al. (2012) provides a comprehensive review of all Mauch Chunk Formation ichnofossils available to us for study, establishing the Mauch Chunk Formation ichnoassemblages as among the best-documented continental ichnoassemblages of Mississippian age. This paper provides a short synopsis of these findings.

EARLY STUDIES

Some of the best outcrops of the Mauch Chunk Formation in eastern Pennsylvania are located near the town of Pottsville (Fig. 1).

Although relatively unknown, the region near Pottsville has been visited often by scientists, both amateur and professional, famous and not, in order to research the geology and paleontology of the Mauch Chunk Formation. Some of the more notable scientists include: (1) Isaac Lea (1792-1886), a self-educated, amateur scientist, who, in his lifetime, gained national and international recognition for his contributions to natural science. Lea frequently visited the Mount Carbon area (locality #1, Fig. 1, Table 1) and, in 1849, discovered fossil footprints he named *Sauropus primaevus* (Lea, 1849), later emended to *Palaeosauropus primaevus* (Hay, 1902) that then received international publicity. (2) Joseph Leidy (1823-1891), the renowned anatomist and vertebrate paleontologist, often referred to as the father of American vertebrate paleontology, visited the Tumbling Run area around 1854 (locality #2) (Lea, 1855), and (3) Henry Darwin Rogers (1808-1866), the accomplished American geologist and director of the first state geology and natural history surveys of New Jersey and Pennsylvania, visited the Pottsville Gap (near Mt. Carbon, locality #1) and West Branch (near Indian Run, locality #3) areas around 1855 (Rogers, 1855, 1858).

Of these early scientists, Isaac Lea's contributions to the ichnology of the Mauch Chunk Formation in eastern Pennsylvania are the most notable, as they became the basis of all subsequent studies.

COLLECTIONS

Over the past several years, the authors have collected several hundred ichnofossil specimens from the Mauch Chunk Formation in eastern Pennsylvania. Although originally stored by the Kutztown University of Pennsylvania (KU), in Kutztown, Pennsylvania, most KU specimens, and all the KU specimens described in this report, have been donated to the Pennsylvania State Museum in Harrisburg, PA (SMP), and to the New Mexico Museum of Natural History and Science (NMMNH) in Albuquerque, New Mexico.

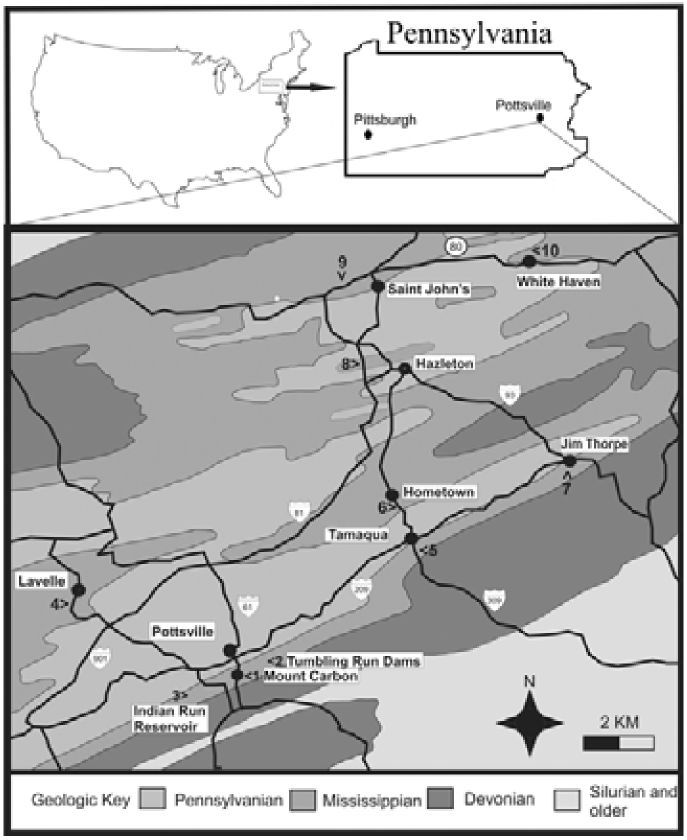


FIGURE 1. Location of the study area in eastern Pennsylvania, USA and geologic map showing collection sites with trace fossils (modified from Berg, 1980a and Edmunds, 1980). Trace fossil localities (see also Table 1) are numbered and identified by an arrow and number (e.g., 1>). Towns and points of interest near a locality are identified by name.

TABLE 1. Mauch Chunk Formation trace fossil localities (see Figure 1).

KU Number	NMMNH Number	Locality	UTM Zone 18, NAD83 / WGS84	Description
1	7009	Mount Carbon	399683E, 4503142N	Rocky outcrop on the western side of Center Street, just south of the intersection with Main Street in Mount Carbon.
2	7004	Tumbling Run Dams	400442E, 4503691N	Earthen breasts and spillways – the dams are on the south side of Tumbling Run Road just south of Pottsville.
3	7014	Indian Run Reservoir	395880E, 4501471N	Hiking trail along an abandoned railway a few hundred meters northeast of the Indian Run Reservoir.
4	8594	Lavelle	383252E, 4512379N	East East side of Rte. 901, approx. 1.5 km. north of Rte. 8.
5	7013	Tamaqua	418786E, 4515392N	Abandoned railway line, now a hiking trail, along Rte. 309, approx. 2 km south of Tamaqua.
6	7011	Hometown	417465E, 4519059N	East side of Rte. 309, approx. 1.5 km south of Hometown.
7	8595	Jim Thorpe	437945E, 4524340N	East side of Rte. 209, just outside of the town of Jim Thorpe.
8	8596	Hazleton	415140E, 4539136N	East side of northbound Rte. 81, near the Hazleton exit, mileage marker 147.5.
9	8597	Saint John's	435422E, 4545229N	South side of eastbound Rte. 80, near the Rte. 93 exit, mileage marker 272.5.
10	8598	White Haven	435217E, 4549466N	West side of southbound Rte. 537, 0.2 km south of the Rte. 80 White Haven exit.
11	8671	Jennings Site	399908E, 4503291N	Green – gray rocky outcrop on the south east corner of Route 61 and Tumbling Run Road, Pottsville.

The Academy of Natural Sciences, in Philadelphia, PA (ANSP), has several vertebrate ichnofossil specimens from the Mauch Chunk Formation, including the holotype of *Palaeosauropus*, collected by Isaac Lea. The National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), has an important plaster cast of *Palaeosauropus* footprints collected by Isaac Lea. The North Museum, in Lancaster, Pennsylvania, has a collection of a few dozen ichnofossil specimens, preserved on rocks of sandstones and shales of a reddish brown color, from the Mauch Chunk Formation, that were donated by Richard P. Busch. Kinsey (1986) described the North Museum fossils. Busch, as Curator of Paleontology, discussed and illustrated one of his more detailed Mauch Chunk Formation specimens (DC3), and mentioned that he collected the specimen in 1985 (Kinsey, 1986).

The Reading Public Museum in Reading, PA (RPM) has a collection of a few hundred specimens of rocks, plant fossils, and trace fossils from the Mauch Chunk Formation. The specimens are part of the "Herbein Collection" and were found near Pottsville, Pennsylvania. Most of the specimens come from outcrops of the Mauch Chunk Formation in the vicinity of Mount Carbon and the Tumbling Run Reservoir, both south of Pottsville (Fig.1).

GEOLOGICAL CONTEXT

In eastern Pennsylvania, during the Mississippian and Pennsylvanian periods, a northwestward prograding clastic wedge infilled the subsiding foreland basin. The basin continued to develop after the cessation of the Acadian orogeny and into the onset of the Alleghenian orogeny (Hoque, 1968; Levine and Slingerland, 1987; Robinson and Prave, 1995; Faill, 1997). This clastic wedge consists of the braided-alluvial systems of the Pocono Formation (Fig. 2; Epstein et al., 1974; Cotter, 1978; Robinson and Slingerland, 1998), and fluvial systems of the Mauch Chunk, Pottsville, and Lewellyn formations (Barrell, 1907; Stancel, 1982; Wood et al., 1986; Levine and Slingerland, 1987).

The Mauch Chunk Formation has produced a limited number of age-diagnostic paleofloras (Jennings, 1985) and is considered to be Chesterian or Visean based on the lateral interfingering facies relationships with biostratigraphically dateable carbonates in western and southwestern Pennsylvania and northwestern West Virginia (Fig 2; Wood et al., 1969; Busanus, 1974). Tetrapod body fossils from the Mauch Chunk Formation (Hotton, 1970; Godfrey, 1989) are suggestive of a Mississippian-age, but are not precise age indicators (Lucas, 2003). Paleopole reconstructions and magnetostratigraphic correlations are consistent with a Late Mississippian-age assignment (Tan and Kodama, 2002). Opdyke and DiVenere (2004) subdivide the Mauch Chunk Formation into 5 magnetozones that can potentially correlate this red bed sequence at a finer-scale of resolution than is currently possible from biostratigraphy alone.

Lithostratigraphy

In eastern Pennsylvania (Fig. 1), the Mississippian Mauch Chunk Formation is overlain by the Lower Pennsylvanian Pottsville Formation and underlain by the Mississippian Pocono Formation (Fig. 2; Wood et al., 1969). The Mauch Chunk Formation is subdivided into three members from oldest to youngest, Lavelle, Indian Run, and Hometown members (member names formally defined in Fillmore et al., 2012).

The type section of the Lavelle Member is the section at West Branch Gap of Second Mountain in Schuylkill County of Wood et al. (1969, fig. 35). Here, the Lavelle Member is ~ 154 m thick and consists of red lithic sandstones and shales interbedded with gray shales and lithic sandstones and conglomerates. Gray shales, sandstones, and conglomerates are also typical lithologies assigned to the underlying Mississippian Pocono Formation and attest to the interbedded nature of the lower Mauch Chunk Formation contact (Wood et al., 1969). Wood et al. (1969, p. 65-66) provide additional information on the lithology and distribution of the Lavelle Member.

The type section of the Indian Run Member is our measured section at Mount Carbon (Fig. 3), but reflects the facies that are characteristic of the member. A complete but very generalized section of the Indian Run Member in the Schuylkill Gap (Wood et al., 1969, fig. 35) shows the unit to be ~ 790 m thick and to have a gradational (though largely covered) lower contact with the Lavelle Member. The Indian Run Member often is the locus of fault movement. As a result, the true thickness at Schuylkill Gap is problematic.

Red beds with minor gray lithic sandstones characterize the Indian Run Member (Wood et al., 1969; Wood, 1973) (Fig. 4). Also present are mud-draped ripple bedforms (Fig. 4B), rain drop impressions (Fig. 4C), rill features and pedogenic carbonate horizons (Fig. 4A). This member also contains all of the tracks and traces reviewed here. The Indian Run Member is present at the intersection of Route 61 and Tumbling Run Road in the Pottsville quadrangle. At that Tumbling Run Road and Route 61 locality, the characteristic features of the Indian Run Member are well developed. To the west the Indian Run Member interfingers with the carbonate-rich Loyalhanna Member. Age constraints from marine strata interbedded with the Mauch Chunk Formation in southwestern and central Pennsylvania indicate that the Indian Run Member is of Late Mississippian-age, early Chesterian (late Visean) (e.g., Brezinski, 1999), which is approximately 330 Ma (Davydov et al., 2004, 2010).

The type section of the Hometown Member is the Schuylkill Gap section of Wood et al. (1969, fig. 35), where the Hometown Member is ~ 197 m thick (Fig. 3) and is described in detail by Levine and Slingerland (1987). Red beds, typically shales, interfingering with olive-colored lithic sandstones and polymictic conglomerates characteristic of the Tumbling Run Member of the Pottsville Formation, are grouped into the Hometown Member and demonstrate the interbedded relationship of the Mauch Chunk Formation and overlying strata in the southern anthracite field of Pennsylvania (Wood et al., 1969; Wood, 1973).

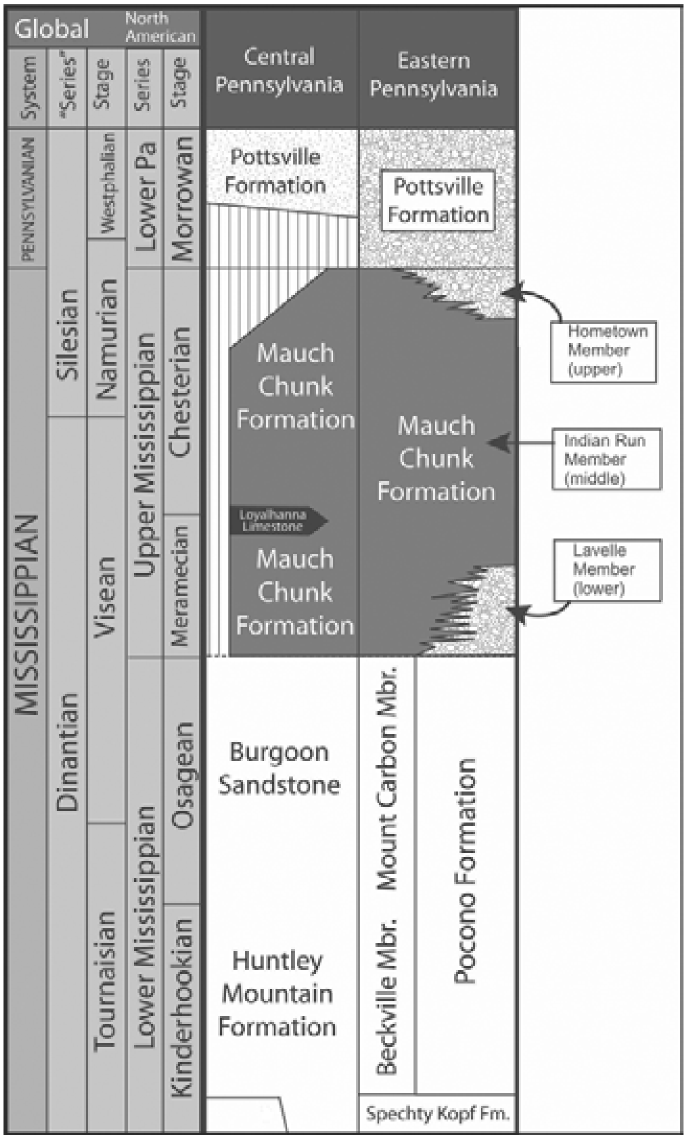


FIGURE 2. Correlation of Mississippian to Lower Pennsylvanian strata (modified from Brezinski, 1999, fig. 9-3, p. 141).

Facies Descriptions

Incomplete sections of the Indian Run Member of the Mauch Chunk Formation were measured at a cm-by-cm scale at two localities, Mount Carbon (Fig. 1, locality #1) and Tumbling Run Dams (Fig. 1, locality #2). Lithofacies, invertebrate and vertebrate traces were identified at the Mount Carbon section (#1; Fig. 3), but are typically found throughout the Indian Run Member. The following facies were identified, all of a reddish-brown coloration: (1) mudstone/siltstone/sandstone laminations/beds, (2) paleosol, (3) carbonate-clast conglomerate/sandstone, (4) sandstone, and (5) sandstone with mudstone drapes. Table 2 summarizes the several facies and some of their more significant features. These facies are grouped into overall upward-fining sequences (Fig. 3).

Depositional Environment

Barrell (1907), in a classic study, conducted a detailed investigation of the strata of the Mauch Chunk Formation in eastern Pennsylvania and argued that a braided stream setting was the best environmental interpretation for Mauch Chunk Formation strata. The Mauch Chunk Formation was deposited in a semi-arid to arid setting typified by low-sinuosity, braided fluvial systems (Levine and Slingerland, 1987; Fillmore et al., 2012). High discharge flood events inundated flood plains, with

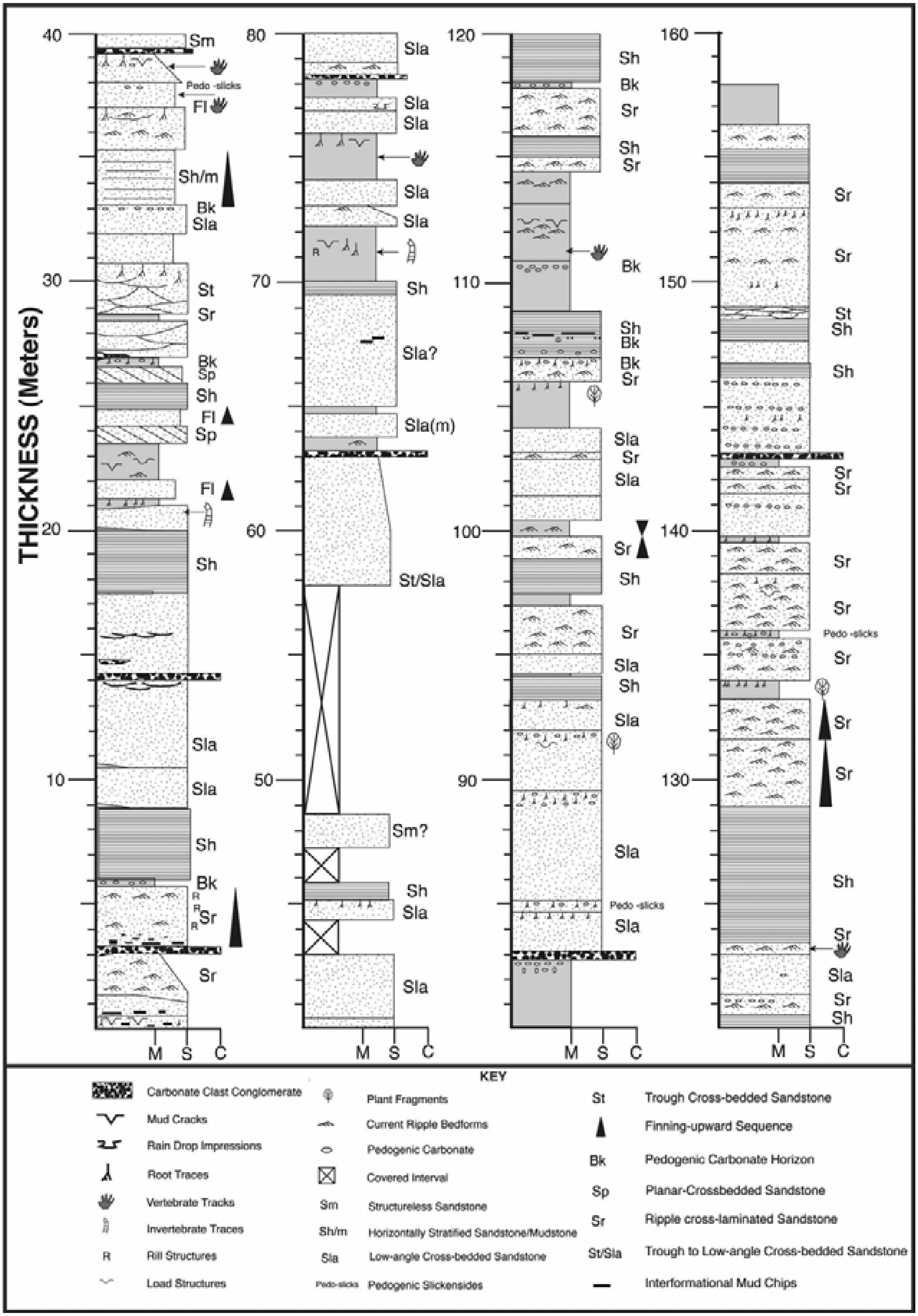


FIGURE 3. Stratigraphic section of the Indian Run (middle) Member of the Mauch Chunk Formation at Mount Carbon, Pennsylvania. This is Lea's (1849) type locality of *Palaeosauropus primaevus* (Fillmore et al., 2009c).

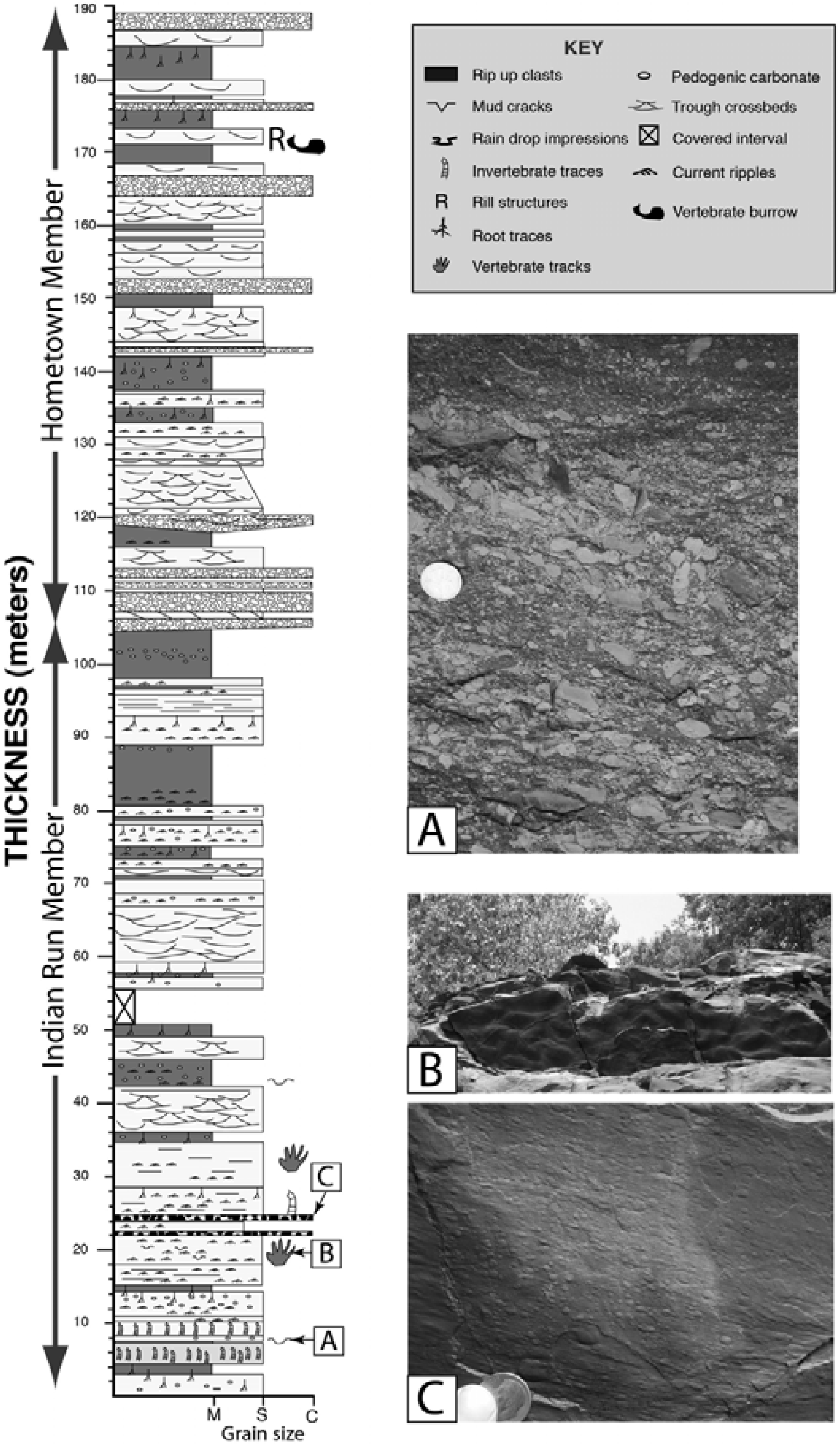
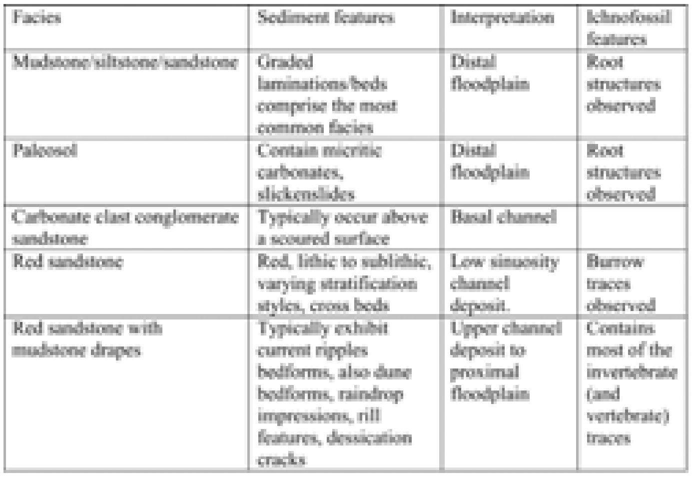


FIGURE 4. Stratigraphic section of the Indian Run and Hometown members of the Mauch Chunk Formation. **A**, Carbonate-clast (interformational Bk horizons) conglomerate at the base of channel. **B**, Preserved rippled bedforms with mudstone drapes. Note that the rippled bedforms have *Palaeosauropus* trackways. **C**, Cast of raindrop impressions in mudstone.

TABLE 2. Lithofacies and features of the Indian Run Member of the Mauch Chunk Formation.



Facies	Sediment features	Interpretation	Ichnofossil features
Mudstone/siltstone/sandstone	Graded laminations/beds comprise the most common facies	Distal floodplain	Root structures observed
Paleosol	Contain micritic carbonates, slickenslides	Distal floodplain	Root structures observed
Carbonate clast conglomerate sandstone	Typically occur above a scoured surface	Basal channel	
Red sandstone	Red, lithic to sublithic, varying stratification styles, cross beds	Low sinuosity channel deposit.	Burrow traces observed
Red sandstone with mudstone drapes	Typically exhibit current ripples bedforms, also dune bedforms, raindrop impressions, rill features, dessication cracks	Upper channel deposit to proximal floodplain	Contains most of the invertebrate (and vertebrate) traces

lesser magnitude events topping bars and covering the upper reaches of channels. Flood events deposited mud and, during the short-term, raised the groundwater table, enhancing the probability of preservation of the invertebrate and vertebrate trace fossils near the channel systems (Fillmore et al., 2012).

Our facies descriptions and the recognition of fining-upward sequences are in agreement with the braided-ephemeral river interpretation of the depositional environmental reconstructions. The difference between a braided stream versus an meandering stream interpretation is resolved by the recent recognition that significant volumes of mudstone may be present in braided stream systems with high rates of tectonic subsidence (Singh, 1984; Miall, 1996).

The interpretation of the depositional environment of the interfingering Loyalhanna Limestone has been problematic, shifting from eolian to marine (Fig. 2; Butts, 1926; Hickok and Moyer, 1940; Flowers, 1956; Adams, 1970; Berg, 1980b; Smosna and Koehler, 1993). The application of rigorous criteria to determine wind-ripple strata has indicated an eolian origin for some of the Loyalhanna Limestone (Ahlbrandt, 1996; Krezoski et al., 2005). The recognition of an interbedded articulated brachiopod fauna indicates that a complex interplay of environments may be present (Brezinski and Kollar, 2006). Golonka et al.'s (1994) palaeoclimatic models put the Mauch Chunk Formation depositional setting in the lee of the rising Appalachians.

Nevertheless, the deposition of the Mauch Chunk Formation is best described as fluvial, not eolian: The ephemeral river systems and associated palaeosols of the Mauch Chunk Formation of eastern Pennsylvania are congruent with the hypothesized paucity of precipitation. Episodic discharge and small scale topographic and substrate diversity within the Mauch Chunk Formation fluvial system provided optimal local settings for the preservation of continental invertebrate and vertebrate traces. Retallack (2011) has recently advanced the idea that early tetrapod evolution took place in subhumid woodlands, and he supported this conclusion with data from the Mauch Chunk Formation. We do agree with the assertion of Retallack (2011) that semiarid deposition dominated the Mauch Chunk Formation. We also concur with Retallack that the Indian Run Member of the Mauch Chunk Formation does preserve at least one "wetter" interval, well represented by the fossil plant site described by Jennings (1985), our locality #11 (Table 1). However, we do not agree with many of the other assertions in Retallack (2011), as discussed at length in a separate report (Fillmore et al., 2012) and in particular do not agree with his assertion that the Mauch Chunk tetrapods are associated with wetter intervals (Fillmore et al., 2012). We continue to maintain that the preponderance of evidence indicates that early tetrapods from the Mississipian-aged Mauch Chunk Formation are associated with semiarid deposits.

INVERTEBRATE ICHNOLOGY

Invertebrate trace fossils from the known Mauch Chunk Formation trace fossil localities are relatively rare; approximately three-fourths of the more than 600 specimen slabs collected by the authors over the past several years contain vertebrate ichnofossils, and about one fourth of the total contain sedimentary features. Only about two dozen of the more than 600 specimen slabs contain examples of invertebrate traces and approximately a dozen contain both vertebrate and invertebrate ichnotraces. The invertebrate traces from the Indian Run Member of the Mauch Chunk Formation (Fillmore et al., 2010) are identified as *Cruziana problematica*, *Diplichnites gouldi*, *Diplopodichnus*, *Gordia*, *Helminthoidichnites tenuis*, *Kouphichnium* isp., *Planolites*, *Rusophyscus*, *Stialla pilosa*, *Stiaria intermedia*, and *Taenidium*.

- ***Cruziana problematica* (Schindewolf, 1928), Fig. 5A:** Trails are bilaterally symmetrical, bilobate and curved, and all trails have a medial furrow. Additional scratch-mark structures are consistently mm-wide, raised convex serial ridges arranged perpendicular to or slightly oblique to the medial furrow and arranged in a herringbone pattern. In a marine setting, *Cruziana* has been interpreted to be the product of trilobites (Häntzschel, 1975). In continental settings, the trail maker is more problematic and may be notostracan branchiopod crustaceans (Bromley and Asgaard, 1972; Pollard, 1985; Minter et al., 2007), aglaspids (Fischer, 1978), vertebrates (Shone, 1978), or insect or non-insect arthropods (Pollard, 1985; Garvey and Hasiotis, 2008).
- ***Diplichnites gouldi* (Gevers et al., 1971):** Straight to slightly curved trackways consisting of two approximately parallel rows of tracks. It has been attributed to various types of invertebrates, most notably myriapods (Smith et al., 2003).
- ***Diplopodichnus biformis* (Brady, 1947):** Traces are two unbranched, straight to winding, horizontal parallel concave grooves or convex ridges that occasionally contain slightly impressed and closely spaced round to ellipsoidal tracks that are perpendicular to the trace axis. The morphologic overlap with *Diplichnites* in the Mauch Chunk Formation specimens indicates that the same trackmaker made both *D. biformis* and *D. gouldi* (Buatois et al., 1998a).
- ***Gordia* (Emmons, 1844):** Trace consists of overlapping loops and meandering trails. Various organisms have been called upon to generate *Gordia*, including polychaetes (Ksiazkiewicz, 1977), worms or gastropods (Yang, 1984; Geyer and Uchman, 1995) and (more speculatively) the erratic behavior of a flying insect trapped in a thin film of water above the sediment-water interface (Hasiotis, 2002).
- ***Kouphichnium* (Nopsca, 1923), Fig. 5B:** Trackways are composed of a series of very small (0.8 to 1.3 mm in length) bifid or trifid tracks. *Kouphichnium* has been interpreted to be the product of xiphosurid arthropod walking (Romano and Whyte, 2003) or crawling traces (Bandel, 1967).
- ***Planolites beverleyensis* (Billings, 1862), Fig 5C:** *Planolites* is the most abundant ichnofossil in the Indian Run Member of the Mauch Chunk Formation. The specimens are simple, smooth, cylindrical tubes with a circular to ellipsoidal cross-section, with tube diameters ranging from 1 to more than 10 mm with lengths highly variable. The tracemaker may have been suspension feeders or predators (Pemberton and Frey; 1982) or, in freshwater settings, crustaceans or insects (D'Alessandro et al., 1987; Miller, 1993).
- ***Rusophycus carbonarius* (Dawson, 1864), Fig. 5A:** Traces consist of isolated, symmetrical, bilobate, ovoid, round to rectangular forms in concave epirelief displaying a medial furrow with transverse striations, and are associated with the *Cruziana* described previously; a few are the terminus of a *Cruziana* trace. *Rusophycus* is the resting trace of an arthropod (Lessertisseur, 1955; Seilacher, 1955; Osgood, 1970).
- ***Stialla pilosa* (Smith, 1909):** A single specimen is preserved in convex hyporelief and has axial grooves that terminate in a series of radiating scratches, and no axial row of tracks. The arcuate axial grooves occur as either a single groove or as a series of three grooves. The origin of *Stiallia pilosa* is problematic (Buatois et al., 1998b), with various

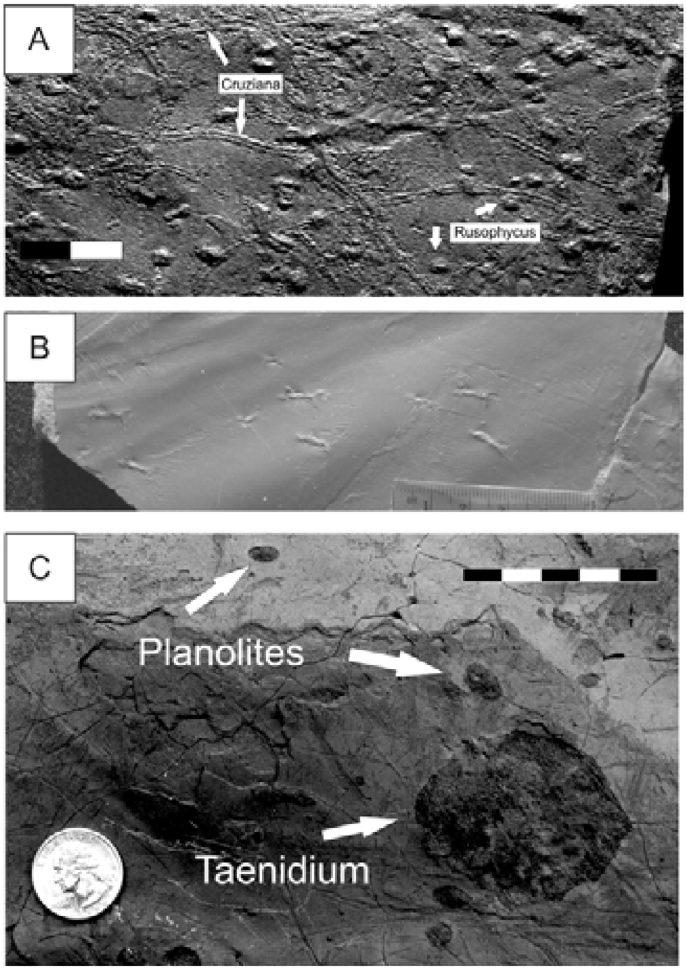


FIGURE 5. Invertebrate traces. **A**, *Cruziana-Rusophycus* traces. Note the linkage of some *Cruziana* and *Rusophycus* traces. Convex hyporelief, SMP IP-8788. **B**, *Kouphichnium aspodon*. Trackway with bifid tracks. Convex hyporelief, SMP IP-8797. **C**, Field photograph of rip-rap block containing *Taenidium barretti* (large burrow) and *Planolites beverlyensis* (smaller burrows), SMP IP-8804. All scale bars in cm.

workers interpreting it as resting traces of isopods (Bandel, 1967), locomotion of a myriapod (Buatois et al., 1998b), locomotion of an arthropod skimming the substrate (Walker, 1985), locomotion followed by resting behavior (Buatois et al., 1998b).

- ***Stiaria intermedia* (Smith, 1909):** The *Stiaria* trackways have either a continuous or a discontinuous medial groove. Apterygote insects are the likely trace makers (Manton, 1972; Walker, 1985; Minter and Braddy, 2006), or by archaeognathans (Getty et al., 2012).
- ***Taenidium barretti* (Bradshaw, 1981), Fig 5C:** In the Indian Run Member of the Mauch Chunk Formation, *Taenidium barretti* and *Planolites beverlyensis* are usually found in association. All *Taenidium* specimens have been recognized from thick beds of sandstone with preserved mudstone drapes. The burrows are sinuous, with the burrow diameter changing along its length, varying in diameter from 50 to 100 mm. Burrow walls are approximately parallel, sharp with respect to the infill, and have smooth to slightly undulating to crenulated wall edges. No lining of the burrow wall is apparent. Various animals have been proposed as the originators of *Taenidium*, including polychaetes (Gevers et al., 1971), amphibians or reptiles (Ridgeway, 1974), and arthropods (Bradshaw, 1981; Keighley and Pickerill, 1997; Morrissey and Braddy, 2004). The presence of menisci and lack of a burrow lining in *T. barretti* indicate that it was actively backfilled, with each meniscus representing a period of activity. In the Mauch Chunk Formation setting, *Taenidium* found in thick-bedded sandstone with mudstone-draped ripple bedforms supports an environmental interpretation of a near-channel setting with periodic flows that transported the fauna

Invertebrate Ichnofacies

The Mauch Chunk Formation invertebrate ichnoassemblage consists of backfilled burrows of deposit feeders, both meniscate (*Taenidium*) and non-meniscate (*Planolites*) that typically crosscut bedding; arthropod trackways (*Diplichnites*, *Diplopodichnus*, *Kouphichnium*, *Stialla* and *Stiaria*); striated trails (*Cruziana*) and resting traces (*Rusophycus*); and surface or shallow subsurface grazing trails or burrows (*Gordia*). The Mauch Chunk Formation invertebrate ichnoassemblage thus corresponds well to the *Scoyenia* ichnofacies as used by Buatois et al. (1998a) and Buatois and Mángano (2002) in consisting of simple burrows, trackways, striate and bilobate trails and pits and simple meniscate burrows. Furthermore, both the *Diplichnites* and the *Scoyenia* ichnoguilds (*sensu* Buatois et al., 1998a) are well represented by the Mauch Chunk invertebrate trace fossils. This indicates a terrestrial invertebrate fauna dominated by both a mobile epifauna and a shallow, deposit-feeding fauna.

The Mauch Chunk Formation invertebrate ichnofossil assemblage resembles other Devonian through Permian ichnoassemblages from ephemeral fluvial red beds in terms of ichnotaxa present. This confirms that the terrestrial invertebrate fauna had already colonized fluvial environments by Mississippian time, as was suggested by Buatois et al. (1998a). Nevertheless, the Mauch Chunk Formation invertebrate ichnofauna is more diverse than any single Devonian ichnoassemblage from a fluvial setting (cf. Buatois et al.,1998a; Buatois and Mángano, 2007). Most of this higher ichnodiversity is due to a greater diversity of ichnotaxa of arthropod trackways in the Mauch Chunk Formation, so this suggests a greater diversity of terrestrial arthropod tracemakers (or tracemaker behavior) in the Mississippian than in the Devonian. Furthermore, the development of the *Scoyenia* ichnoguild in the Mauch Chunk Formation, in the form of abundant traces of deposit feeders of a shallow to intermediate depth infauna (esp. *Taenidium*), is unusually early, when compared to the Paleozoic record as summarized by Buatois et al. (1998a) and Buatois and Mángano (2007; also see Miller, 1984). Intense bioturbation recognized within the Mauch Chunk indicates that the onset of intense bioturbation in nonmarine settings developed earlier than previously thought (Smith et al., 2012).

The Mauch Chunk Formation record now establishes that prolific ichnoassemblages of the *Scoyenia* ichnoguild were present by Mississippian time (Smith et al., 2012). Typically, trace fossils of the *Scoyenia* ichnofacies indicate opportunistic behaviors in subaerial environments that are temporarily or periodically inundated. Indeed, the sedimentological context of the Mauch Chunk Formation invertebrate ichnocoensis suggests that most of the trace fossils were made in the sediments of inactive or intermittently active channels.

VERTEBRATE ICHNOLOGY

Four kinds of vertebrate ichnofossils are known from the Mauch Chunk Formation: a large structure interpreted as a tetrapod burrow, fish swimming traces assigned to *Undichna*, amphibian body resting traces and tetrapod footprints, which are the most common trace fossils (other than *Planolites*) in the formation. Here, we describe each kind of vertebrate trace fossil separately.

Tetrapod Burrow

The fossilized remains of a relatively large burrow were discovered in the Mauch Chunk Formation at the Lavelle locality (Table 1 and Fig. 1, locality #4) (Storm et al., 2010). The burrow is housed in and cross cuts red mudstone (Fig. 6). Two, normally graded, conglomerate to sandstone beds fill the structure, with the oldest fill being the thickest.

The burrow structure is characterized by: (1) a flared opening leading into a narrower linear tunnel, (2) a tunnel that bends 40° and ends in an inflated ovate chamber, and (3) a flared opening that is higher in

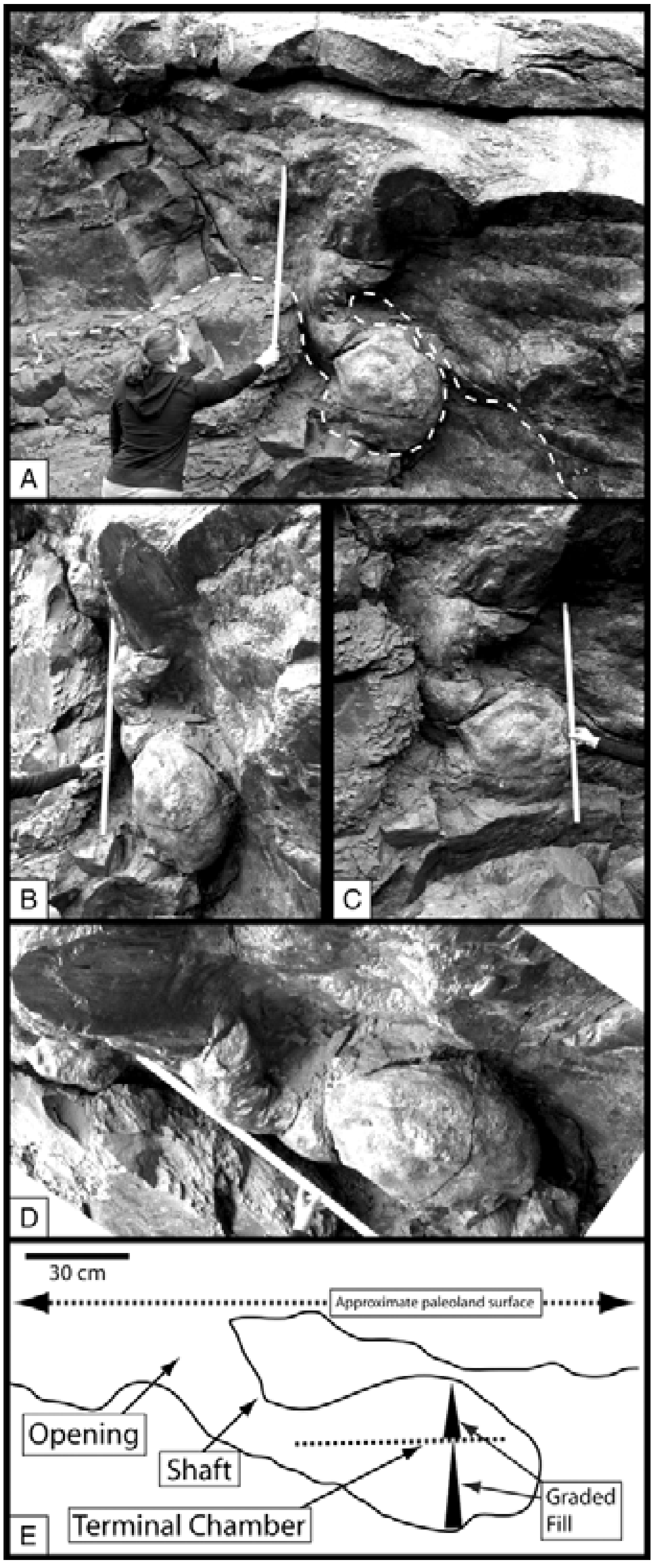


FIGURE 6. Vertebrate burrow field photographs. **A**, Outcrop photograph of dipping mudstone-conglomerate contact. Burrow is located near the center. Figure holds a meter stick. **B**, Lateral view. **C**, Ventral view. **D**, Lateral view with bedding dip rotated to approximate horizontal in Photoshop for the foreground of the photograph. Note the dip of the bed is present in the background of the photo. Note the downward slope of the tunnel terminating in the chamber. **E**, Line drawing with various parts of the burrow labeled and orientation of paleoland surface indicated. Note the graded bed filling is indicated on the diagram. Meter stick for scale.

elevation than the base of the chamber (Storm et al., 2010). The tunnel has a semicircular cross section. The geometries, angle changes, large termination, width-to-height ratios of the terminal chamber, and graded fill indicate the structure was an open burrow during sedimentation.

This structure is best interpreted as a burrow made by a tetrapod vertebrate, most likely an amphibian (Storm et al., 2010; Fillmore et al., 2012). The geometry and size of the Mauch Chunk Formation structure is incompatible with known invertebrate burrows and erosional features. Associated trackways indicate the burrow was most likely made by an amphibian the size of the trackmaker of *Palaeosauropus primaevus*. The burrowing behavior was most likely due to the environmental stress related to seasonal droughts as local water sources disappeared.

Amphibian Body Impressions

An exceptional case of preservation of body impressions of Mauch Chunk Formation tetrapods shows the outline of most, or all, of the animal (Fig. 7; Lucas et al., 2010b) and provides direct evidence of body shape, texture of the integument, and possible social behavior. Named *Temnocorpichnus isaacleai* (Lucas et al., 2010b), the specimen (Fig. 7) is the resting trace (cubichnion) of a temnospondyl amphibian with a smooth integument, triangular head impression, four robust limbs with *Batrachichnus* tracks, relatively short trunk and long and tapering tail. The presence of three body impressions on a single bedding plane could be fortuitous, representing three individuals who happened to rest (or die) in one place at one time. However, we think it likely that the three body impression preserved together are suggestive of some sort of gregarious behavior, and this encourages us to speculate about the possibility that the body impressions may indicate a kind of social behavior known in some extant salamanders (Lucas et al., 2010b).

Undichna

Specimens of *Undichna* (Fillmore et al., 2011) were collected from outcrops of the Indian Run Member of the Mauch Chunk Formation (Fig. 1, locality #8). The slabs bearing the ichnofossils were all collected from a single talus pile. As an example, we illustrate specimens that exhibit sets of two intertwined sinusoidal waves assigned to *Undichna britannica* (Fig. 8A, B; Higgs, 1988).

We are not aware of any substantiated reports of fish body fossils from the Mauch Chunk Formation, so the identity of the specific *Undichna* trailmaker is unknown. Thus, we cannot safely identify the specific *Undichna* trailmaker – at most, we can say that the trailmaker was a relatively small fish with an anal and caudal fin that each reached to the same approximate depth.

TETRAPOD FOOTPRINTS

The most common trace fossils collected from the Mauch Chunk Formation are tetrapod footprints. They belong to five ichnogenera (*Batrachichnus*, *Hylopus*, *Palaeosauropus*, *Matthewichnus*, and *Pseudobradypus*) and comprise one of two extensive tetrapod footprint assemblages of Mississippian-age (the other is from the Lower Mississippian Horton Bluff Formation in Nova Scotia, Canada):

- ***Batrachichnus salamandroides* (Geinitz, 1861), Fig. 8C, D:** *Batrachichnus* is the second most abundant tetrapod ichnotaxon in the Mauch Chunk Formation collections. Pes lengths and widths are mostly 10-20 mm, and a wide range of extramorphological variation is present. Thus, tridactyl manus and pes underprints are present, as are tetradactyl pes impressions. Digits are normally short, straight and blunt tipped, but slightly curved digits and pointed digit tips are present as well. Bifurcated digit tips can be seen on some specimens. Some specimens have body/tail drags, but most do not. *Batrachichnus* has a stratigraphic range of Mississippian-Triassic (see Klein and Lucas, 2010, fig. 56 for a Triassic record from the Moenkopi Group in Utah), that is almost coextensive with the bone record of temnospondyls. However, trackways of some Cenozoic and extant salamanders (e.g., Peabody, 1959) are also assignable to *Batrachichnus*, indicating convergence in foot structure and

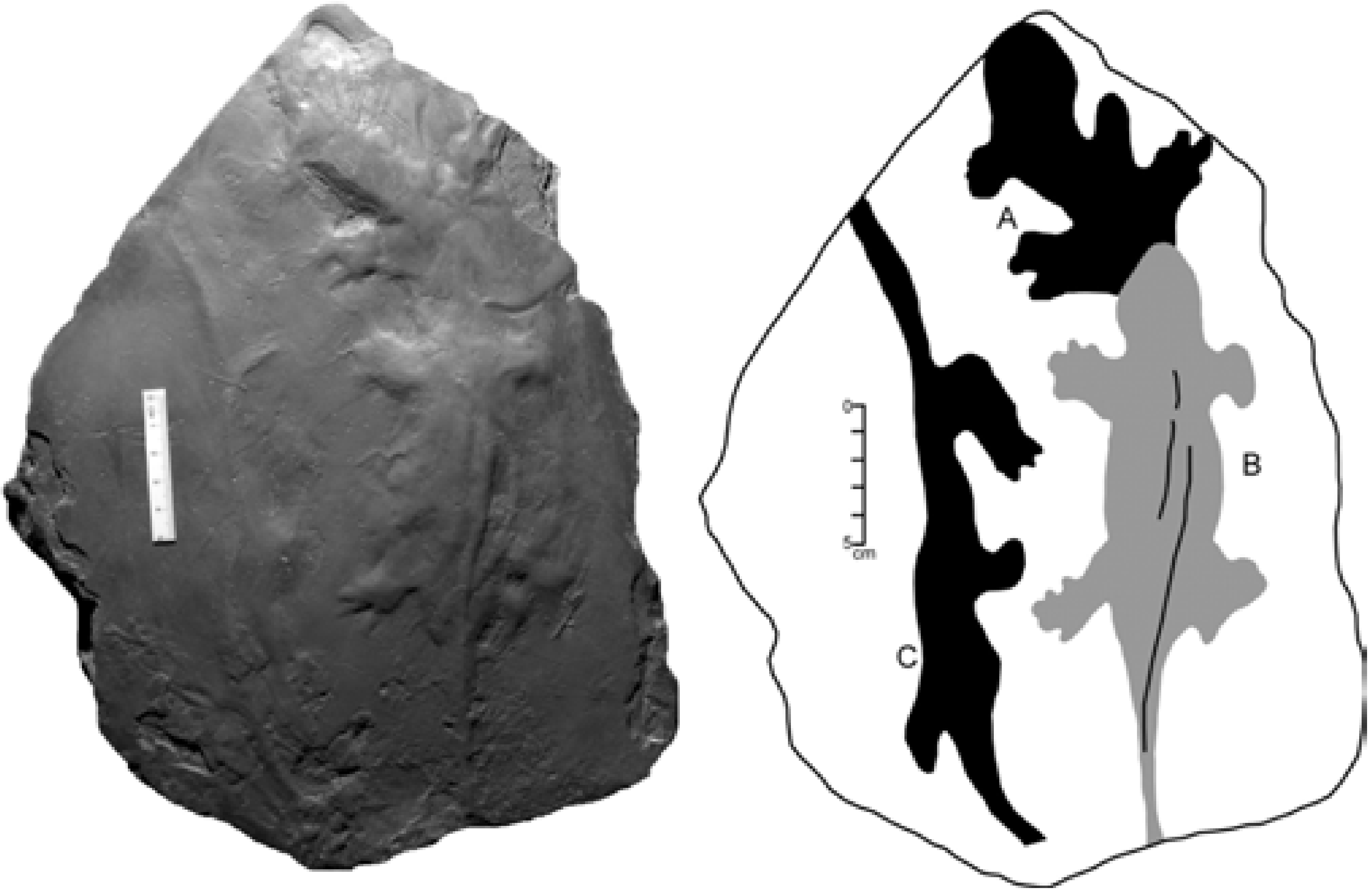


FIGURE 7. *Temnocorpichnus isaacleai*. **Left**, Photograph of specimen RPM 77-32-1. **Right**, Line drawing outlining the resting traces. Three resting traces are labeled A through C. Note the overlap of the posterior region of A with the head of B.

locomotory pattern between Paleozoic-Mesozoic temnospondyls and some Cenozoic lissamphibians.

- ***Characichnos* (Whyte and Romano, 2001); *Characichnos* isp., Fig. 8E, F:** The Mauch Chunk specimens assigned to *Characichnos* are long, relatively thin, slightly arcuate or sinuous scratch marks, two to four (usually three) in parallel series (e.g., Fig. 8E). Size is often relatively large, with total lengths and widths up to 100 and 60 mm, respectively. Most of the scratch marks are on surfaces with *Palaeosauropus* footprints, and were likely produced by the same trackmaker (a temnospondyl) (see Fig. 8F).

- ***Hylopus hardingi* (Dawson, 1882), Fig. 9A, B:** Footprints of a quadrupedal tetrapod in which the manus is tetradactyl and the pes is pentadactyl. The manus and pes are of approximately equal size (especially their widths), generally plantigrade, and may be overstepped, as illustrated in Fig 9A. The manus digits are often relatively thin and curved medially, and digit IV is much longer than the rest. (There is ichnological discussion about fossil tetrapod tracks which may otherwise meet the criteria for *Hylopus* but occasionally display what could be interpreted as a fifth digit on the manus. This is a perplexing issue that merits future research).

- ***Matthewichnus* (Haubold, 1970):** *Matthewichnus* is the footprints of a quadruped in which the pes is much larger than the manus. Both manus and pes are plantigrade, the manus is tetradactyl and approximately as wide as long. The pes is pentadactyl and has digits II-IV longer than digit V. The manus imprint is medial to and sometimes overstepped by the pes imprint. Tail/body imprints are sometimes present. Very few Mauch Chunk Formation footprint specimens can be assigned with confidence to *Matthewichnus* because relatively few show clearly associated manus and pes imprints in which a small, tetradactyl manus is substantially smaller than the pentadactyl pes. The trackmaker of *Matthewichnus* is perceived of as a temnospondyl (note the tetradactyl manus), but unlike the temnospondyl trackmakers of *Batrachichnus*, *Hylopus*, and *Palaeosauropus*, this temnospondyl must have had a much more specialized limb structure and gait.

- ***Palaeosauropus primaevus* (Lea, 1849), Fig. 9C, D:** The tracks preserve, to varying degrees, key features of *Palaeosauropus*, including tetradactyl manus, pentadactyl pes, wide and blunt tipped digits, manus digit III longest, pes digit IV longest and near overstepping of the manus by the pes. Their size also compares well with that of the type material of *Palaeosauropus primaevus*. The trackmaker of *Palaeosauropus* has long been considered a temnospondyl amphibian, either an edopoid or an eryopoid (e.g., Haubold, 1971, 1984). This is primarily because of the relatively large size and the digital formula of the track—four digits in the manus and five in the pes--that is matched in temnospondyl skeletons.

- ***Pseudobradypus* (Matthew, 1903), *Pseudobradypus* ichnosp., Fig. 9E:** Specimen RPM B-13 is the clearest example, preserving parts of five manus-pes pairs and a body/tail drag. The pes imprints are plantigrade, antero-posteriorly long and have anteriorly-directed digits. The manus imprints are about half as long as the pes imprints but of approximately the same width. They have forward-directed digits, are immediately anterior to the pes imprints, and both manus and pes imprints are symmetrical around a median tail/body drag imprint. The preservation is not good enough to allow accurate digit counts, but the manus and pes imprints have at least four digits each. *Pseudobradypus* is not common in the Mauch Chunk Formation, with only a few specimens recognized. We attribute them to a reptiliomorph (non-amniote) trackmaker and we regard them as extremely important in establishing the oldest record of reptiles (amniotes) as discussed below.

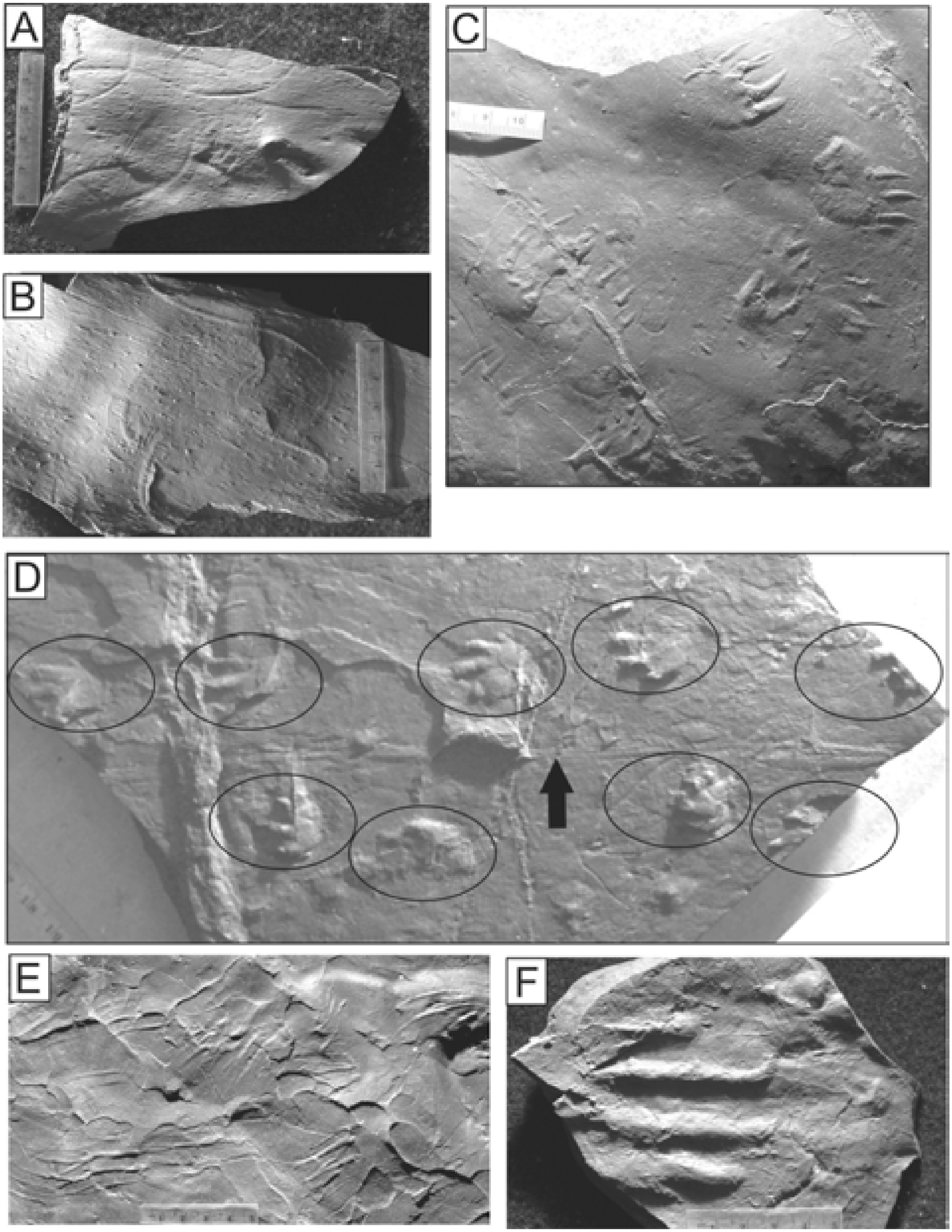


FIGURE 8. *Undichna* and vertebrate footprints. **A-B**, *Undichna britannica*. **A**, Specimen SMP VP-3395, concave epirelief. **B**, Specimen SMP VP-3394, concave epirelief. **C-D**, *Batrachichnus salamandroides*. **C**, Specimen RPM H61, convex hyporelief. **D**, Specimen RPM B33, convex hyporelief. Ovals identify footprints, arrows identify tail drags. **E-F**, *Characichnos* isp. **E**, Specimen NMMNH P-64274. **F**, Specimen NMMNH P-64264, convex hyporelief. Ruler in photos (cm/mm) for scale.

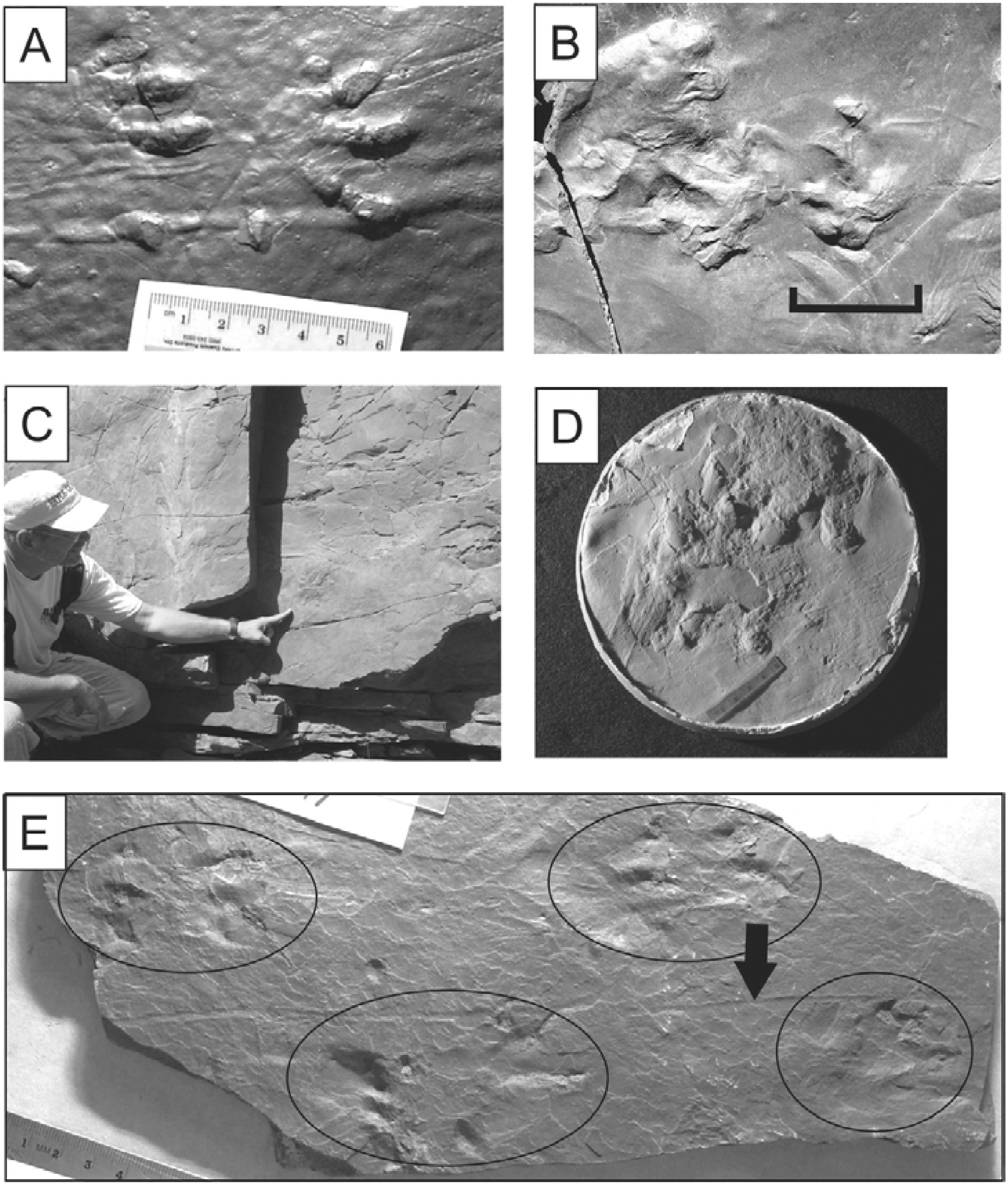


FIGURE 9. Vertebrate footprints. **A**-**B**, *Hylopus hardingi*. **A**, Specimen RPM 1011, convex hyporelief. **B**, Specimen NMMNH P-64275, convex hyporelief. **C**-**D**, *Palaeosauropus primaevus*.Field photograph of specimen SMP VP-3423 (convex hyporelief). **D**, Cast from mold of footprint in **C**. **E**, *Pseudobradypus* isp., Ovals identify footprints, arrows identifies tail drags. Pes nearly oversteps manus. Specimen RPM B13, concave epirelief. Rulers are cm/ mm.

Tetrapod Ichnofacies

The tetrapod footprint assemblage of the Mauch Chunk Formation comprises a moderate ichnodiversity of footprints of quadrupedal carnivores (mostly temnospondyl amphibians). It thus fits well into the concept of the *Batrachichnus* ichnofacies of Hunt and Lucas (2007), which they identified as occurring in Devonian-Middle Triassic tidal flat and alluvial plain paleoenvironments. Because the Mauch Chunk Formation lacks reptile footprints, the alternate ichnocoenoses to the *Batrachichnus* ichnofacies that Hunt and Lucas (2007) distinguished by different reptile trackmakers, cannot be discriminated. The Mauch Chunk Formation tetrapod footprints come from an alluvial plan depositional setting, so they are consistent with the range of paleoenvironments envisioned for the *Batrachichnus* ichnofacies.

MAUCH CHUNK FORMATION TETRAPOD FOOTPRINTS AND CARBONIFEROUS TETRAPOD FOOTPRINT BIOSTRATIGRAPHY AND BIOCHRONOLOGY

Carboniferous tetrapod footprints have a strictly Euramerican distribution, as does the Carboniferous tetrapod body fossil record (with the exception of one discovery in Australia: Thulborn et al., 1996). The single largest hindrance to interpreting Carboniferous tetrapod footprints has been the confused and confusing state of the ichnotaxonomy of Mississippian and Pennsylvanian tetrapod footprints. The necessity for vast ichnotaxonomic revision is very obvious, and an attempt to bring clarity to some morphologies has been presented in our monographic study of Mauch Chunk ichnology (Fillmore et al., 2012).

Lucas (2003, 2007) concluded that three intervals of Carboniferous time (Fig. 10) can be discriminated using footprints: Mississippian, Early-Middle Pennsylvanian (approximately Westphalian) and Late Pennsylvanian (approximately Stephanian). The Early-Middle Pennsylvanian time interval was given the term "*Pseudobradypus* biochron," but Lucas (2003, 2007) did not assign names for the other two. We suggest new terms below for these three time intervals, but do not significantly modify the Carboniferous footprint biochronology of Lucas (2003, 2007).

The three intervals of Carboniferous time that can be discriminated using tetrapod footprints are:

1. The Mississippian track record (mostly known from North America) is temnospondyl dominated with no reptile tracks. Characteristic ichnogenera include *Batrachichnus*, *Palaeosauropus*, and *Hylopus*, and we term this the *Hylopus* biochron (Fig. 10). The Mauch Chunk Formation footprint assemblage belongs to this biochron and is one of only two (the other is Horton Bluff, Nova Scotia) extensive tetrapod footprint assemblages of Mississippian age.

2. The Early-Middle Pennsylvanian (Westphalian) record shows a mixture of temnospondyl tracks and reptile tracks. The presence of reptile tracks distinguishes the Westphalian sites from the Mississippian sites. Lucas (2007) termed this interval the *Pseudobradypus* biochron, but given that Mississippian footprint assemblages contain *Pseudobradypus*, we rename this biochron the *Notalacerta* biochron for this characteristic, reptile-generated track (Fig. 10).

3. The Late Pennsylvanian track record includes diverse reptile tracks and the lowest occurrence of *Dromopus*, an ichnotaxon characteristic of the younger, Early Permian ichnofauna. This is the beginning of the *Dromopus* biochron of Lucas (2007; also see Lucas and Hunt, 2006), which continues through the Early Permian.

The tetrapod body-fossil record can be used to divide Carboniferous time into only four intervals (Lucas, 2003), largely because of the limited geographic distribution, low taxonomic diversity and rarity of Carboniferous tetrapod fossils (Carroll, 1979). In essence, these four tetrapod-based time intervals are global chronofaunas. They provide poor biochronological resolution and a limited basis for tetrapod-based correlation, but accurately map current understanding of the major phases in Carboniferous tetrapod evolution. The footprint record thus resolves Carboniferous time almost as well as the body fossil record, though both provide very poor temporal subdivision of the Carboniferous, which in marine rocks is divided into as many as seven epochs that encompass 25 stages, though a globally applicable timescale may discriminate only about eight stages (e.g., Davydov et al., 2004, 2010; Heckel and Clayton, 2006; Menning et al., 2006).

MAUCH CHUNK FORMATION TETRAPOD FOOTPRINTS AND CARBONIFEROUS TETRAPOD EVOLUTION

The Mauch Chunk Formation tetrapod footprints are of Visean age, which was a time when the body fossil record indicates that characteristic tetrapods were temnospondyl amphibians, anthracosaurs and some other non-amniote reptiliomorphs (*sensu* Ruta et al., 2003) (also see Lucas, 2003; Carroll, 2009). The dominance of the Mauch Chunk Formation tetrapod footprint assemblage by temnospondyl footprints is consistent with the body fossil record. Only footprints identified as *Pseudobradypus* are not those of a temnospondyl, and we attribute them to an anthracosaur trackmaker. Indeed, it is significant that the Mauch Chunk Formation tetrapod footprint record is very similar to that of the Lower Mississippian Horton Bluff Formation in Nova Scotia—both share the ichnogenera *Batrachichnus*, *Hylopus*, *Palaeosauropus* and *Pseudobradypus*. Thus, even though the Horton Bluff and Mauch Chunk Formation footprint assemblages are separated by what has been called "Romer's Gap" (Coates and Clack, 1995), there is no obvious comparable change in the tetrapod footprint assemblages. From the standpoint of footprint assemblages, Romer's Gap looks like an artifact of sampling, not a critical juncture in Mississippian tetrapod evolution.

The oldest known reptile body fossil is *Hylonomus lyelli* from the Lower Pennsylvanian (middle Langsettian) at Joggins, Nova Scotia (Dawson, 1895; Carroll, 1964, 1970, 1988, 2009; Reisz, 1977; Clack, 2002). However, Falcon-Lang et al. (2007) recently claimed to have found older evidence of reptiles in the form of footprints they identify as *Pseudobradypus* from the Grande Anse Formation in New Brunswick, Canada.

We agree with Falcon-Lang et al. (2007) that the footprints they documented should be identified as *Pseudobradypus*, but we do not think they necessarily indicate a reptile trackmaker. This is such, despite the fact that *Pseudobradypus* has generally been associated with a reptilian trackmaker (largely because of its pentadactyl manus), either a captorhinoromph or a pelycosaur (Haubold, 1971; Milner, 1996). Certainly, the pentadactyl manus of *Pseudobradypus* excludes an amphibian trackmaker, but there are a variety of reptiliomorphs sensu Ruta et al. (2003)—anthracosaurs, seymouriamorphs and diadectomorphs—that have a pentadactyl manus.

Recognizing this, Falcon-Lang et al. (2007) compiled metric data on 14 selected genera of reptiliomorphs and early reptiles to establish criteria that they claimed distinguish the feet (and footprints) of reptiles from those of more primitive reptiliomorphs. They thus argued that true reptiles have a longer and more slender manus and pes with less splayed digits than do reptiliomorphs. According to Falcon-Lang et al. (2007), the footprint ichnogenus *Pseudobradypus*, notable among Carboniferous footprints for the relatively long and slender manus and pes imprints, is the footprint of a reptile. Furthermore, Falcon-Lang et al. (2007) argued that the forward-oriented footprints with a sole imprint behind digits III-IV, the straight tail drag and the pace angulation of up to 121° seen in *Pseudobradypus* trackways are also indicative of a reptile. Falcon-Lang et al. (2007) also claimed the presence of "putative" or "debatable" reptile-like scale impressions on some of the New Brunswick *Pseudobradypus* manus imprints.

Nevertheless, Keighley et al. (2008) critiqued the conclusions of Falcon-Lang et al. (2007), pointing out first that the Grande Anse Formation footprints are not definitely older than the Joggins Formation footprint and bone record, which includes definite reptile body fossils. Keighley et al. (2008) thus argued that there is no evidence that the

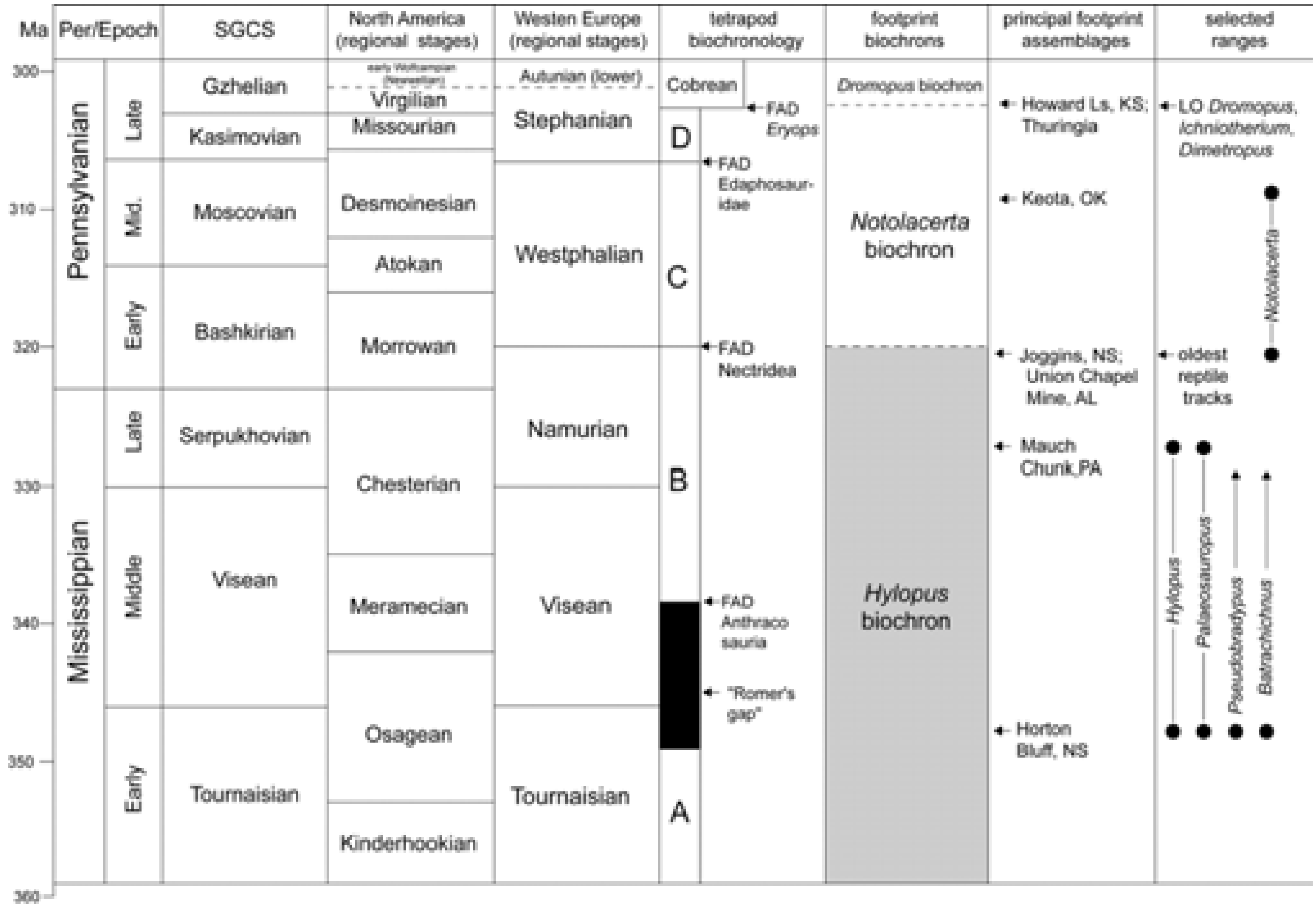


FIGURE 10. Carboniferous tetrapod footprint biochronology. Timescales (radioisotopic ages, subdivisions of Mississippian and Pennsylvanian, SGCS, North American and western European regional stages) and their correlation to each other based on Davydov et al. (2004, 2010), Heckel and Clayton (2006) and Menning et al. (2006). Tetrapod biochronology modified from Lucas (2003). **Abbreviations are: FAD**, first appearance datum; **SGCS**, standard global chronostratigraphic scale.

Grande Anse Formation track record is older than middle Langsettian, the age of the Joggins Formation.

Keighley et al. (2008) also noted that there is a fair degree of overlap in the degree of digital splay between reptiliomorphs and reptiles and there is not a clear separation of the two groups based on the ratio of foot length and width. They thus rejected the metric criteria advanced by Falcon-Lang et al. (2007) to distinguish the feet and footprints of reptiles from those of reptiliomorphs. Finally, Keighley et al. (2008) pointed out that the so-called scale imprints on the New Brunswick *Pseudobradypus* are well matched by non-scale textures on amphibian footprints from the Mississippian of West Virginia documented by Sundberg et al. (1990).

We concur with the conclusion of Keighley et al. (2008). Indeed, in reply to Keighley et al. (2008), Falcon-Lang and Benton (2008) apparently conceded their major points. Nevertheless, the entire discussion of *Pseudopbradypus* as a reptile track, including the table of metrics found in Falcon-Lang et al. (2007), was repeated subsequently by Falcon-Lang et al. (2010).

Pseudobradypus has definite Mississippian records, both in the Mauch Chunk Formation and in the older, Lower Mississippian Horton Bluff Formation footprint assemblage from Nova Scotia (Lucas et al., 2010c). If Falcon-Lang et al. (2007, 2010) are correct that *Pseudobradypus* is a reptile footprint, then this means the footprint record indicates reptiles as old as the Early Mississippian. We think this unlikely and conclude that there is a clear problem of homeomorphy with the footprints of early reptiles and of some reptiliomorphs. Thus, we hold that the footprint ichnogenus *Pseudobradypus* was made by both reptiliomorphs (especially anthracosaurs) and by early reptiles, and given the similarity in overall foot structure, there is no obvious way to distinguish the trackmaker.

Perhaps a more detailed study of a large sample of *Pseudobradypus* footprints may identify features that distinguish two groups, one made by reptiliomorphs and one made by reptiles. However, we doubt this to be the case, as we are unable to distinguish *Pseudobradypus* footprints of Mississippian age (presumably not made by reptiles) from those of Pennsylvanian age. Therefore, we conclude that the Carboniferous footprint record does not indicate reptiles older than *Hylonomus* from Joggins. Mississippian footprint assemblages lack reptile footprints.

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A PRELIMINARY REPORT ON A WOLFCAMPIAN AGE FLORAL ASSEMBLAGE FROM THE TYPE SECTION FOR THE NEAL RANCH FORMATION IN THE GLASS MOUNTAINS, TEXAS

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Abstract—The Nealian regional sub-stage of the Wolfcampian North American regional stage is typified by the Neal Ranch Formation in the Wolf Camp Hills in southwest Texas. This marine sedimentary succession has long been known to contain plant remains, but to date these have not been described systematically. This paper provides a preliminary synopsis of the taxonomic diversity of this adpression flora and reports fossils assigned to 27 genera, including species such as *Sigillaria brardii*, *Annularia spicata*, *Oligocarpia gutbieri*, *Pecopteris oreopteridia*, *Autunia naumannii*, *Callipteridium gigas*, *Dicksonites plukenetii*, *Sphenopteridium manzanitanum*, *Ernestiodendron filiciforme*, *Gomphostrobus bifidus* and cf. *Gigantonoclea lagrelii*, and places them in a stratigraphic and geographic context.

INTRODUCTION

Changes in the floral composition across the Pennsylvanian-Permian boundary and during the Permian have been termed the "Paleophytic-Mesophytic" transition, but over simplistically have been equated to a shift from a predominantly wetland to a seasonally dry vegetation (DiMichele et al., 2011). A transition towards generally drier tropical conditions does appear to occur, at least in western and central equatorial Pangea, and can be considered an "oscillatory trend" in which the number and length of intervals of wet tropical climate decline (DiMichele et al., 2008, 2011). This transition may relate to the final assembly of Pangea or to uplift resulting from the Hercynian/Variscan orogeny (Kerp, 1996; Cecil et al., 2011). However, overprinted on this long-term trend are shorter-term changes, most notably those reflecting shifts between cool and wet to warm and dry tropical climatic conditions that were governed by global glacial (cool/wet tropics) and interglacial (warm/dry tropics) cyclicity (Cecil and Dulong, 2003; DiMichele et al., 2011). Occurring within cyclothemic sequences, this climate cyclicity is reflected in the composition of floral assemblages (DiMichele et al., 2011). Paleobotanical data indicate that dry-adapted vegetation began to appear by the Middle Pennsylvanian in Europe and North America (e.g., Galtier et al., 1992; Falcon-Lang et al., 2009; Plotnick et al., 2009; Scott et al., 2010; Dolby et al., 2011) at roughly the time when coals in western North America effectively disappeared in the middle Moscovian (Lucas et al., 2009). However, in central and east-central Pangea, floral assemblages adapted to drier environments increased in frequency, but coals and wetland plants persisted into the Early Permian (DiMichele et al., 2011).

In North America, the Cisuralian Epoch of the Permian includes the basal Wolfcampian regional stage that spans the Asselian-Artinskian global stages and is succeeded by the Leonardian regional stage, the base of which coincides with the Kungurian global stage. In the Glass Mountains of westernmost Texas, the Wolfcampian is divided into the Nealian and Lenoxian regional substages (Ross, 1963). The lower of the two substages, the Nealian, is typified by the Neal Ranch Formation in the Wolf Camp Hills, while the Lenoxian is typified by the Lenox Hills Formation that crops out along the base of the Glass Mountains escarpment (Ross, 1963; Ross and Ross, 2003; Fig. 1). These marine beds yield stratigraphically significant conodonts and fusilinids (Wardlaw and Davydov, 2000; Ross and Ross, 2003) and are important stratigraphic and paleontologic reference sections for other areas of western North America (e.g., Ross and Ross, 2003).

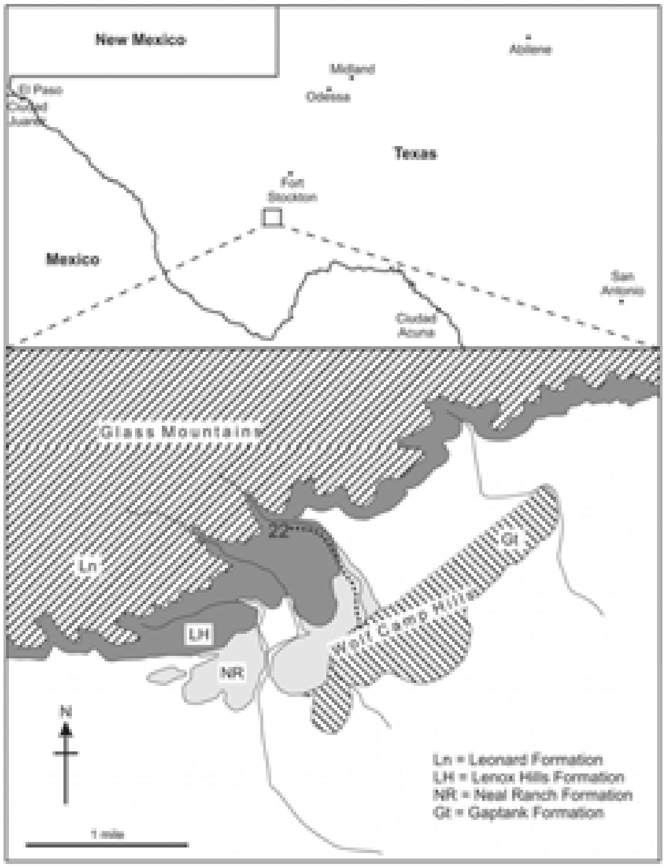

FIGURE 1. Geological map re-drafted from Ross (1963) illustrating the locality of Section 22 (Ross, 1963 pg. 20-21), the type section of the Neal Ranch Formation, and the section in Texas along which the flora was collected.

The Neal Ranch Formation represents a pro-delta sequence comprising siltstones with common plant debris and limestone and limestone-conglomerate interbeds (Ross, 1963; Wardlaw and Davydov, 2000) that was deposited in a shallow embayment that opened toward the northwest into deeper-water environments (Ross, 1963; Wardlaw and Davydov, 2000; Ross and Ross, 2003). The formation rests uncomformably on the Gray Limestone Member of the Gaptank Formation that is exposed in three discrete areas, namely the Wolf Camp Hills, the Gap Tank, and within the Dugout structural fold belt (Ross and Ross, 2003). In the Wolf Camp Hills, the Neal Ranch Formation was deposited as a series of sedimentary wedges onto the Gray Limestone Member, onlapping from west to east over a distance of about a 1.5 km (see fig. 2 of Ross and Ross, 2003); hence, the base of the formation becomes younger and its thickness decreases in an eastward direction. The formation has been divided into 16 fourth-order cyclothemic depositional sequences (Ross, 1963; Ross and Ross, 2003), though only some of these are present in section 22, the type section of the Nealian (Ross and Ross, 2003), and the section from which the fossils of this study were collected. These fourth order sequences can be subdivided into three settings. The early part of the formation (NR1-7) reflects high amplitude, short frequency regressive and transgressive events, where sea-level change was large and rapid. The middle part of the Nealian (NR-8) experienced lower-magnitude sea-level change and is typified by bioherm development. The upper part of the formation (NR9-16) lacks deep-water black shales and exhibits erosional bases to the cycles. It is therefore interpreted as a predominantly shallow-water facies, where sea level reached its relatively highest point and accommodation space had been nearly filled (Ross and Ross, 2003).

Wardlaw and Davydov (2000) placed the Carboniferous-Permian boundary within the Gray Limestone Member of the Gaptank Formation, and the base of the Sakmarian at 52 m above the base of the Neal Ranch Formation (in Bed 12; Fig. 2) based upon the first occurrence of the conodont *Streptognathodus barskovi*. However, following recent research in the Urals, subsequent formal proposals for the definition of the base of the Sakmarian have been made and this is now defined by the first appearance datum of the conodont *Sweetognathus merrilli* (Chuvashov et al., 2002), a taxon also recognized by Wardlaw and Davydov (2000) as co-occurring with *Streptognathodus barskovi* and *Streptognathodus isolatus* at this horizon in the base of the *Streptognathodus barskovi* Zone.

Examination of fusulinids in NR-9 reveals a fauna comprising *Paraschwagerina gigantea*, *Pseudoschwagerina texana*, *Paraschwagerina* aff. *P. gigantea*, *Schwagerina* cf. *S. longissimoidea*, *Rugosofusulina*? spp. and *Pseudoschwagerina uddeni* (data from table 1 in Ross and Ross, 2003). These fusulinids are reported to be comparable in their general morphology to those from the middle of the Council Grove Group (Beattie Limestone) in Kansas (Ross and Ross, 2003) that has been correlated with the middle to late Asselian based upon the occurrence of the conodont *Streptognathodus fusus* (Schmitz and Davydov 2012), and Ross and Ross (2003, fig. 22) have indicated the Nealian sequence NR-9 was deposited within this interval.

RESULTS

The plant fossils reported here were collected from yellow-brown weathering, calcareous siltstone/shale in Bed 12 (NR-9) close to Section 22 (field number Q83-7 in Fig. 2). The flora itself was clearly deposited in a marine setting, and a range of cephalopod, bivalve and brachiopod fossil casts are present alongside the plants (Fig. 3A-B). The plant fossils themselves (Fig. 3C-J) are small and fragmentary adpressions, the matrix not being conducive to the extraction of large blocks. This stratigraphically important assemblage requires further in depth taxonomic analysis, however, preliminary identifications suggest the presence of lycopsids (*Sigillaria brardii*), sphenopsids (*Annularia spicata*, *Calamites* sp., *Palaeostachya* sp., *Sphenophyllum angustifolium*, *Sphenophyllum* cf. *verticillatum*), gleichenaceous (*Oligocarpia gutbieri*, *Oligocarpia leptophylla*) and marattialean (*Pecopteris ameromii*, *Pecopteris cyathea*, *Pecopteris hemitelioides*, *Pecopteris oreopteridia*, *Pecopteris polymorpha*) ferns, peltasperms (*Autunia naumannii*, *Dichophyllum flabellifera*, *Peltaspermum* sp., *Supaia* sp.), other pteridosperms (*Callipteridium gigas*, *Dicksonites plukenetii*, *Neurocallipteris neuropteroides*, *Neurocallipteris planchardii*, *Neurodontopteris auriculata*, *Neuropteris* sp., *Odontopteris lingulata*, *Odontopteris schlotheimii*, *Sphenopteridium manzanitanum*), conifers (*Culmitzschia laxifolia*, *Culmitzschia speciosa*, *Ernestiodendron filiciforme*, *Gomphostrobus bifidus* and *Otovicia hypnoides*) as well as plants of more enigmatic affinities, including gigantopterids (cf. *Gigantonoclea lagrelii*), noeggerathialeans (*Tingia* sp.) putative cycads (*Phasmatocycas* sp., *Taeniopteris abnormis*), roots assigned to *Radicites* sp. and cardiocarpalean and trigonocarpalean gymnosperm ovules.

DISCUSSION

The taxa identified clearly have morphological similarities with other Late Pennsylvanian to Early Permian assemblages reported from the USA, in particular Texas, (e.g. Mamay, 1986; DiMichele and Aronson, 1992; DiMichele and Chaney, 2005; DiMichele et al., 2001, 2006, 2010, 2011) and Europe (Kerp and Fichter, 1985). The preliminary findings indicate a compositionally unusual assemblage, probably reflective of its allochthonous accumulation that combines floral elements usually considered typical of both seasonally dry and wetland substrates. This flora suggests comparison with the Missourian age, Kinney Quarry assemblage, with which it shares compositional and taphonomic similarities (e.g. Mamay, 1990, 1992; Mamay and Mapes, 1992). However, further extensive taxonomic characterization and paleoecological interpretation is still required and will be presented elsewhere.

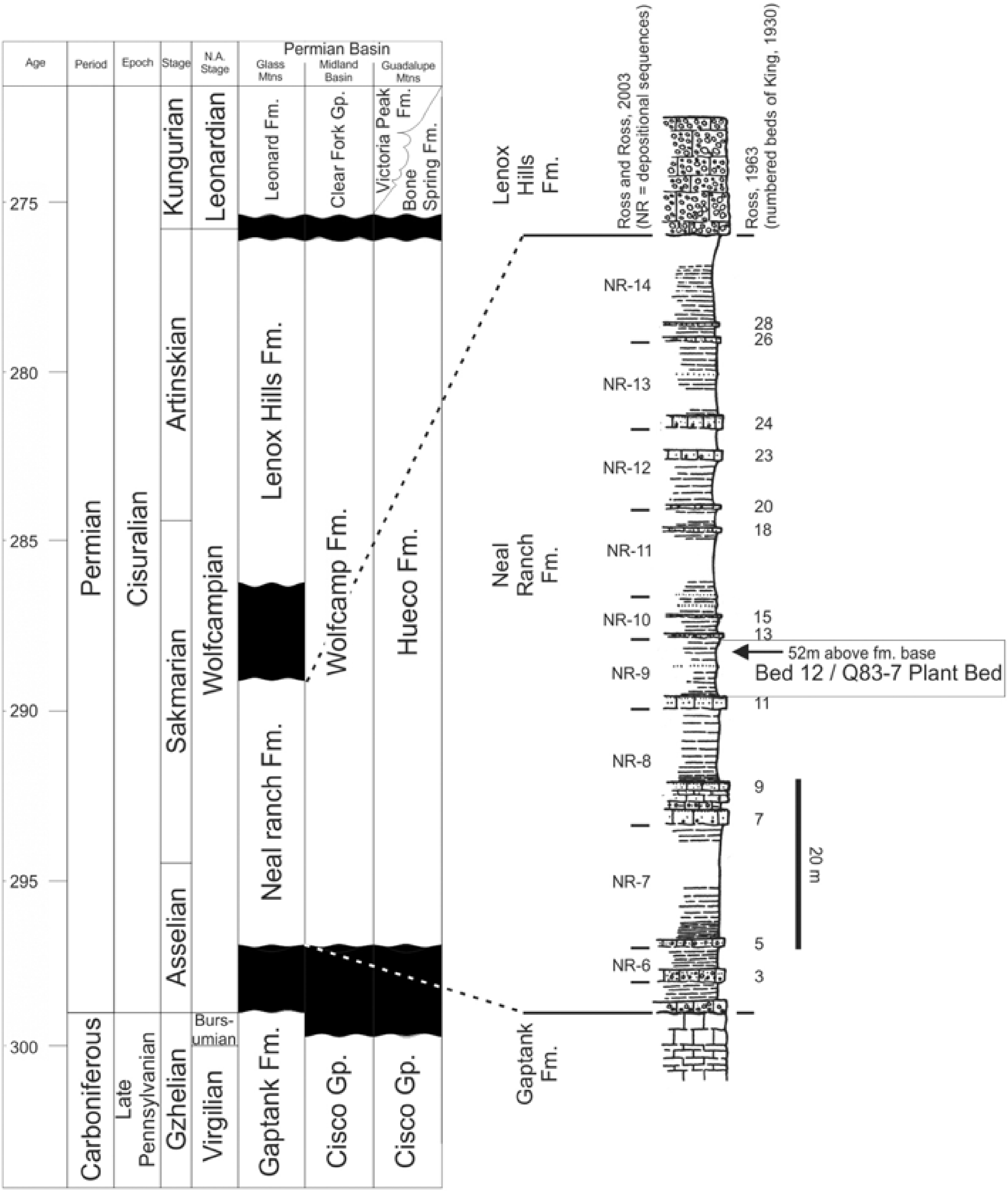

FIGURE 2. Reproduction of Ross’s (1963) stratigraphic column for the type section of the Neal Ranch Formation (Section 22) in context with chronostratigraphic data from Koch and Frank (2011) and sequence stratigraphic data from Ross and Ross (2003).

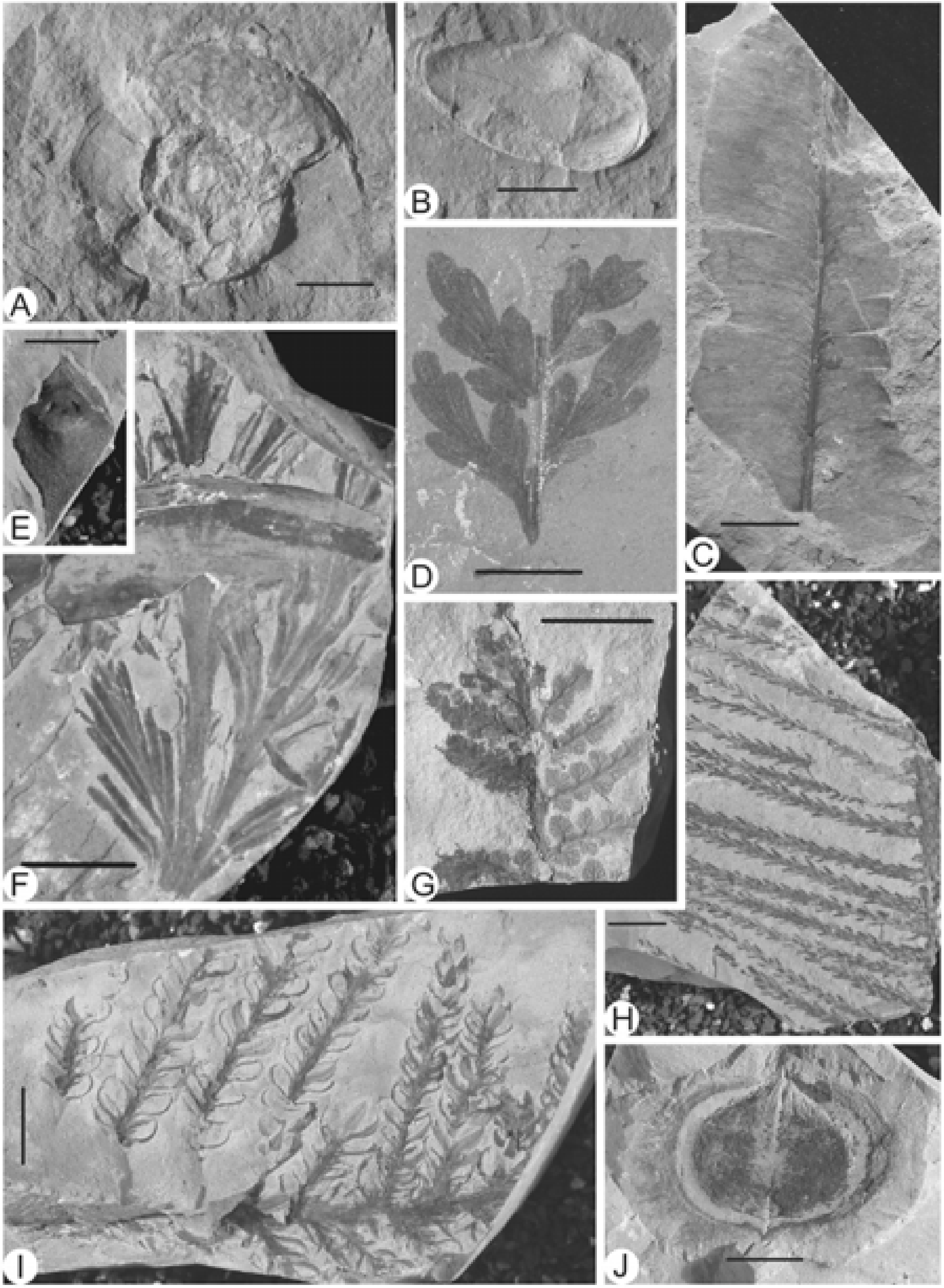

FIGURE 3. Examples of preserved faunal and floral components of the Neal Ranch Formation plant bed; all scale bars = 10 mm. **A**, Unidentified ammonoid found in association with the plant fossils. **B**, Cast of an unidentified bivalve from the plant bed. **C**, *Taeniopteris abnormis*. **D**, *Sigillaria brardii*. **E**, *Sphenopteridium manzanitanus*. **F**, *Dichophyllum flabellifera*. **G**, *Oligocarpia gutbieri*. **H-I**, Walchian conifer foliage: **H**, *Otovicia hypnoides*; **I**, *Culmitzschia speciosa*; **J**, Cardiocarpalean ovule.

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A NEW BASAL HYBODONT (CHONDRICHTHYES, HYBODONTIFORMES) FROM THE MIDDLE PERMIAN (ROADIAN) KAIBAB FORMATION, OF NORTHERN ARIZONA

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Abstract—The teeth of a new basal hybodont shark are described from the Middle Permian (Roadian) Kaibab Formation of northern Arizona. *Diablodontus michaeledmundi* gen. et sp. nov. represents the only known non-durophagous (crushing toothed) hybodont from the marine Middle Permian. Dental morphology suggests a close relationship between *D. michaeledmundi* gen. et sp. nov. and the Pennsylvanian and early Permian "*Maiseyodus*," both of which belong to an indeterminate family of hybodontid hybodonts that was ancestral to the *Hybodus* clade. D. *michaeledmundi* gen. et sp. nov. could have inhabited a littoral habitat and had an ecomorphotype similar to extant hound sharks (Triakidae).

INTRODUCTION

The Kaibab Formation in Arizona has long produced a rich marine invertebrate fossil record (McKee, 1938; Miller and Unklesbay, 1942; Nicol, 1944; Brezinski, 1991). However, until recently, the vertebrate record for the Kaibab Formation was sparse, comprising a few short descriptions of fish remains collected between the north rim of the Grand Canyon to just north of Sedona (McKee, 1938; Hussakof, 1943; David, 1944; Gass, 1963; Ossian, 1976; Johnson and Zidek, 1981). Most notable is the large and enigmatic pristodont petalodont chondrichthyian *Megactenopetalus kaibabanus,* the holotype of which was collected from Point Sublime on the North Rim of the Grand Canyon (David, 1944) and additional remains from south of Flagstaff (Ossian, 1976). Additional chondrichthyan fossils collected over the years are housed at the Museum of Northern Arizona, Flagstaff (Hussakof, 1943; Gass, 1963).

Recent collecting efforts by the authors from localities in the vicinity of Flagstaff (Fig. 1) are starting to show that the Kaibab Formation may have one of the most diverse marine Permian chondrichthyan faunas globally (Hodnett, et. al., 2011a, 2011b, 2012; Elliott and Hodnett, in press). The analysis of micro-vertebrate localities from the Flagstaff area has shown that approximately 40 chondrichthyan taxa are present, representing 8 orders and 18 families. Additional non-chondrichthyan remains hint at a rich but unknown depth of diversity of osteichthyans as well.

Hybodont Sharks

The group of euselachian chondrichthyans commonly referred to as the "hybodonts" is a monophyletic clade (Hybodontiformes) characterized by: a complex system of many large labial cartilages; scales with several neck canals and lacking a pronounced neck; two deeply inserted dorsal fin spines with longitudinal ribbed costae and posterior marginal denticles; paired cephalic spines with "*Sphenonchus*" morphology; and teeth lacking specialized nutritive foramina (Maisey, 1978, 1982). Hybodont teeth are extremely varied in the number and shape of cusps (Ginte, et al., 2010; Cappetta, 2012; Cuny, 2012), but all taxa share in having enameloid consisting of single apatite crystallites (Reif, 1973), and root vascularization conforming to an anaulacorhize (sponge-like) pattern (Maisey, 1987; Cappetta, 2012). Hybodonts were highly successful, having an early fossil record starting in the mid-Paleozoic and extending until the K/T extinction event (Maisey, 1982; Rees, 2008; Ginter et al., 2010).

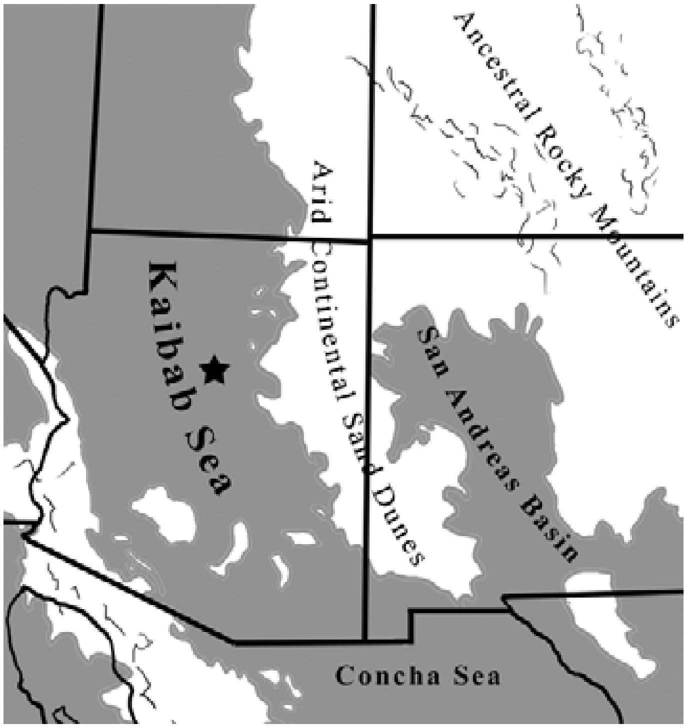

FIGURE 1. Paleogeography of the western United States during the Middle Permian. The star shows the location of the fossil site (from Hodnett et al., 2012).

Pre-Permian Hybodonts

The earliest appearance of hybodonts in the fossil record is from the Famennian (Late Devonian) of central Iran with the durophagous *Roongodus phijani* (Hairapetian and Ginter, 2009), and *Lissodus brousclaudiae* and *L. tursuae* in Belgium (Derycke-Khatir, 2005). Durophagous hybodonts occur throughout much of the Carboniferous with Mississippian records of *Lissodus khamari*, *L. pectinatus*, and *L. wirksworthensis*, and *Onychoselache traquairi* (Ginter et. al., 2010), followed by the Pennsylvanian *Lissodus lacustris* and *L. lopesae*, the first appearance of *Polyacrodus* with *P. lapalomensis*, *Acrodus* with? *A. olsoni*, *Dabasacanthus inskasi*, and *Hamiltonichthyes mapesi* (Ginter et.

al., 2010). Non-durophagous hybodonts first appeared in the Tournaisian (Early Mississippian) with *Mesodmodus exsculptus*, a taxon with heavily ornamented teeth with a tall central cusp and small lateral cusplets and an occlusal crest running the length of the tooth (Ginter et. al., 2010). Additional species of *Mesodmodus* also are known from the Tournaisian (*M. explanatus* and *M. khabenji*) to the Visean (Late Mississipian; *M. ornatus*) (Ginter et al., 2010). *Tristychius arculatus* from the Visean-Serpukhovian (Late Mississippian) of Scotland had unicuspid or multicuspid crowns with a tall central crown and were bluntly pointed, with some posterolateral teeth with a blade-like distal portion to the crown (Dick, 1978; Ginter et al., 2010). The Pennsylvanian record of multicuspid hybodont tooth types comprises a single taxon from Nebraska and the Ohio Valley region that, at present, lacks a formal description (Ossian, 1974; Hanson, 1986; Ginter et. al., 2010). First described as "*Hybodus nebraskensis*" (Ossian, 1974) from the Peru fauna (Kasimovian and Gzhelian; Late Pennsylvanian) of southeastern Nebraska, it has a tall central cusp and three lateral cusps with a rectangular tooth base. Similar teeth from the older (Moskovian-Gzhelian) Pennsylvanian marine sediments of eastern Ohio and adjacent areas were named "*Maiseyodus johnsoni*" (Hanson, 1986). Ginter et al. (2010) concluded that these specimens belong to an indeterminate basal hybodontiform. We here refer to these teeth as "*Maiseyodus*."

Permian Hybodonts

Durophagous taxa dominate the Permian Hybodontiformes. Several taxa are known from the Wichita-Albany Group (Leonardian) of Texas, including *Lissodus zideki*, *Polyacrodus lapalomensis*, *P. richiei*, *P. wichitaensis*, ?*Acrodus olsoni*, and ?*A. sweetlacruzensis*, all of which have either a blunt single cusp or single broad crushing apex to the crown (Johnson, 1981). A durophagous hybodont, *Gansuselache tungseni*, closely related to *Lissodus*, was described from the Fangshankou Formation of the Gansu Province of China (Wang et. al., 2009), and *Lissodus xiushiensis* and *Polyacrodus jiangxiensis* from the Late Permian of Zhejiang and Jiangxi provinces of China (Wang et. al., 2007). Additional specimens of ?*Polyacrodus* sp. and ?*Acrodus* sp. were reported from the Late Permian Hambast Formation of central Iran (Hampe et al., 2013). A species of *Lissodus* is listed from the Early Permian (Asselian to Artinskian) of the Middle and South Urals (Ivanov, 2005), and polyacrodont hybodonts and *Lissodus* are reported from the Middle Permian of Russia and the Guadalupe Mountains of Texas (Ivanov, 2012) and the Khuff Formation of Oman (Angiolini et al., 2003; Fischer, 2008). A single *Hybodus*-like taxon has been recorded from a nearshore fauna from the Wreford megacyclothem (Wolfcampian) deposits of Kansas (Schultze, 1985).

The Kaibab Formation has a rich record of hybodont teeth, fin spines, and dermal denticles that were collected at the turn of the century. A preliminary account of the tooth-based taxa (Hodnett et al., 2011a) indicates a large number of durophagous hybodonts, including small and large species of *Acrodus*, *Polyacrodus* sp., and indeterminate durophagous hybodonts. A *Lissodus*-like taxon has been recently recognized. Also reported was a *Hybodus*-like taxon, which is the subject of this paper.

GEOLOGICAL SETTING

The Kaibab Formation is found over much of northern Arizona, southern Utah, and southeastern Nevada (McKee, 1938; Cheevers, 1980; Hopkins and Thompson, 2003). It was deposited during the eastward transgression of a shallow sea (Fig. 1), and thins towards the east as the paleo-coastline is approached (McKee, 1938; Norton, 1990; Hopkins and Thompson, 2003). The Kaibab Formation was initially divided into three members; the alpha, beta, and gamma (McKee, 1938). These were later reorganized into the Harrisburg Member (alpha) and the Fossil Mountain Member (beta and gamma) (Sorauf, 1962).

The Kaibab Formation is composed of yellow to gray calcareous limestones, yellow to orange sandy limestones, calcareous sandstones, and red chert beds (McKee, 1938). Sand in the limestone units is derived from coastal deserts along the western shore of the continent to the east (McKee, 1938; Hopkins, 1986; Norton, 1990; Hopkins and Thompson, 2003). The Fossil Mountain Member is divided into eastern and western regions (Cheevers, 1980; Hopkins and Thompson, 2003), with resistant fossiliferous limestones with scattered sandstone and dolomite units and abundant chert nodules to the west and a predominantly dolomitic unit with the percentage of sand increasing to the east (Hopkins and Thompson, 2003). The Harrisburg Member includes a basal gypsum unit followed by red siltstone ledges and resistant limestones with chert nodules, interspersed with beds of gypsum. Both members thicken to the west (Cheevers, 1980; Hopkins and Thompson, 2003).

The Fossil Mountain Member represents a shallow, open-marine environment to the west, while to the east there was a shift to restricted, near-shore, and increasingly saline environments (Hopkins and Thompson, 2003). In the Harrisburg Member the restricted environments became common as the sea retreated to the west and the faunas changed from brachiopods and other open-marine species to bivalves and gastropods (Cheevers, 1980; Hopkins and Thompson, 2003).

The age of the Kaibab Formation had been established as Leonardian based on comparison of brachiopod faunas and distribution of the siliceous sponge *Actinocoelia maeandrina* (McKee, 1938; Hopkins and Thompson, 2003). This has been further supported by conodont studies that confirm a late Leonardian age and help to establish correlation with other Permian sequences (Thompson, 1995; Hopkins and Thompson, 2003). However, conodont and brachiopod data support a Roadian age for the upper part of the Fossil Mountain Member (Hopkins and Thompson, 2003), and a correlation between the San Andres Formation of New Mexico, which ranges from the Leonardian to Capitanian in age, and the Kaibab Formation has been proposed (Brezinski, 1991; Sonnenfeld, 1993). It therefore seems probable that the upper part of the Fossil Mountain Member and all of the Harrisburg Member is early Guadalupian in age.

The specimens discussed in this paper come from a single locality, the Kachina Microsite (KMS), which has also produced the teeth, dermal denticles, and spines of ctenacanth sharks, including the holotypes of *Kaibabvenator swiftae*, *Nanoskalme natans*, and *Neosaivodus flagstaffensis* (Hodnett et. al., 2012), a new species of the basal xenacanth *Bransonella* (Elliott and Hodnett, in press), other Hybodontiformes (Hodnett et al. 2011a), basal euselachians, Eugenodontiformes, Petalodontiformes (Hodnett et al. 2011b), and Holocephali. Non-chondrichthyan vertebrates include cranial and postcranial elements, isolated teeth, and scales of paleoniscoid and possible coelacanthiforms, and conodonts and highly silicified invertebrates also occur. This locality, Museum of Northern Arizona (MNA) locality 1645, is located in Kachina Village, approximately 11.5 km south of Flagstaff. The fossils from KMS were collected from a 1 m-thick section within an approximately 3 m-thick tan-orange sandstone of the Fossil Mountain Member. This sandstone lies above a 6 m-thick, resistant, light gray, sandy limestone. Chert nodules with sponge spicules are common throughout the section, with the largest concentration found 1.5 m above the collecting horizon. Burrow casts of various sizes, highly silicified crinoid stems and plates, and urchin plates and spines are common.

METHODS AND MATERIALS

Specimens described here were collected from bulk samples screen washed through graded screens. Residues were dried and then picked under a stereomicroscope. Picked specimens were imaged using the Scanning Electron Microscope at Northern Arizona University. Additional illustrations were made using a Motic digital microscope at 20x to 40x magnification and rendered with a stylus and tablet with Adobe Illustrator. All specimens are housed at the Museum of Northern Arizona.

Institutional Abbreviations— KUVP, University of Kansas Museum of Natural History, Lawrence Kansas; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona; **OSU**, Ohio State University, Columbus, Ohio.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES
Cohort EUSELACHII Hay, 1902
Order HYBODONTIFORMES Maisey, 1975
Superfamily HYBONDONTOIDEA Owen, 1846
Family INDETERMINATE
Diablodontus gen. nov.

Type Species: *Diablodontus michaeledmundi* gen. et sp. nov.

Etymology: From *diablo*, Spanish for devil, and Greek *dontus*, for teeth, in reference to a horned entity and the paired cephalic spines present in hybodont sharks.

Diagnosis: As for species.

Diablodontus michaeledmundi gen. et sp. nov.
Fig. 2

Holotype: MNA V10474, a tooth.

Referred Specimens: Teeth, MNA V10446, 10450, 10475, 10484.

Type Locality: MNA LOC 1645, Kachina Microsite, Coconino County Arizona, lower Fossil Mountain Member, Kaibab Formation, Roadian.

Etymology: In honor of Michael Edmund Hodnett for his support of the Kaibab shark project and for introducing the lead author to the joys of collecting shark teeth.

Diagnosis: Multicusped teeth 3-10 mm mediolaterally long, 3-6 mm tall, and 2-3 mm labiolingually wide. Tooth base shallow, rectangular, mediolaterally elongated, lingually offset from crown, ventrally concave, and anaulacorhize. Tooth crown with prominent median cusp taller than two lateral cusps. Cusps flattened labially and convex lingually; re-curved lingually. Coarse cristae on crown. Small intermediate and lateral accessory cusplets present.

Description: The tooth base is rectangular, concave ventrally, plate-like, and offset to the crown lingually. Multiple small nutrient foramina are present on the ventral side of the tooth base, forming long thin channels, with the highest and larger foramen concentrated on the labial edge of the base. An anaulacorhize (sponge-like) structure is present labially between the edge of the base and the beginning of the crown, forming a shallow depression. Three prominent cusps are present, with single lateral cusps flanking a taller median cusp and a significant gap between the median cusp and the first lateral cusp. Cusps are flattened labially, convex lingually, and re-curved lingually. Accessory cusplets are present intermediate to the main cusps and/or on the outer edge of the tooth base. Coarse prominent cristae ornament the labial and lingual sides of the cusps. The cristae on the labial side of the crown extend down to the top of the shallow anaulacorhize depression. Cristae vary in number between eight and nine on the median cusp and seven to nine on the lateral cusps, with the posterior dentition typically having a slightly larger number.

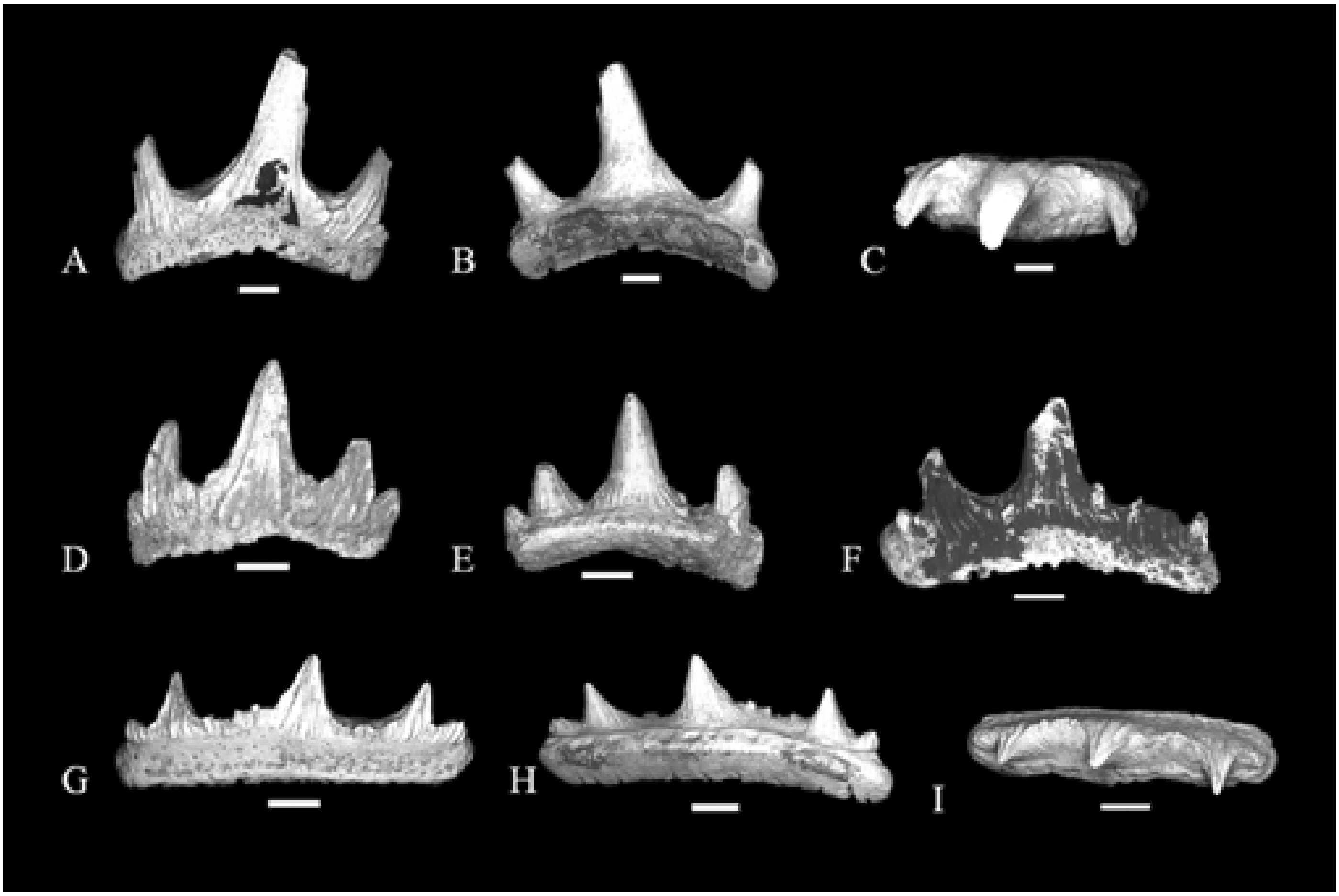

FIGURE 2. *Diablodontus michaeledmundi* gen. et sp. nov. **A-C**, Holotype, anterior/symphisial tooth MNA V10474, **A**, labial, **B**, lingual, **C**, occlusal; **D-E**, mediolateral tooth MNA V10475, **D**, labial, **E**, lingual; **F**, lateral tooth MNA V10450, labial; **G-I**, posterolateral tooth MNA V10446, **G**, labial, **H**, lingual, **I**, occlusal. Scale= 1 mm.

Morphological variation observed in these teeth suggests that *Diablodontus michaeledmundi* gen. et sp. nov. had a monognathic heterodont dentition. The mesiodistal width, curvature of the tooth base, and cusp height and shape varies according to the position of the teeth in the jaw. Anterior teeth are shorter mesiodistally and more concave ventrally (Fig. 2A-C), teeth positioned more posteriorly are proportionately more elongated mesiodistally and the ventral curvature is reduced (Fig. 2 D-F), while the most posterior teeth are nearly flat (Fig. 2G-I). Cusps in the anterior dentition are tall and slender and are connected by a thin labial cutting ridge (Fig 2A-C). The posterior dentition has cusps that are short and broad (Fig 2G-I), with more accessory cusplets and lacking the thin cutting ridge. The teeth of *D. michaeledmundi* gen. et sp. nov. represent a small hybodont shark with tearing and cutting dentition (see discussion below).

Comparison: The crown morphology in hybodont sharks is highly variable in size and structure, but all are characterized by the anaulacorhize (sponge-like) structure in the tooth base, which is a synapomorphy of the Hybodontiformes (Maisey, 1987; Ginter et al., 2010). The teeth of *Diablodontus michaeledmundi* gen. et sp. nov. have a primitive, plate-like base with labial ventral foramina as in basal euselachians (Ginter et al. 2010). However, basal non-hybodont euselachians have straight rows of foramina (Ginter et al., 2010), and in *D. michaeledmundi* gen. et sp. nov. the structure between the base and the crown is anaulacorhize with fine sporadic foramina, most extensive on the labial side. This character indicates that *D. michaeledmundi* gen. et sp. nov. is a hybodont. *Tristychius* and the Pennsylvanian "*Maiseyodus*" have a tooth base structure similar to *D. michaeledmundi* gen. et sp. nov. in that they have plate-like bases with sporadic foramina present on the labial side. The anterior teeth of *Tristychius* differ from both "*Maiseyodus*," *D. michaeledmundi* gen. et sp. nov., and from other hybodonts in that the lingual torus is primitively well developed in *Tristychius* and reduced in the other taxa (Dick, 1978; Ginter et al. 2010).

The crown of *Diablodontus michaeledmundi* gen. et sp. nov. differs from other Permian hybodonts in its multiple slender cusps, as most other contemporaneous taxa had a single blunt crown (*Acrodus* and *Lissodus*), or simple robust cusps (*Polyacrodus*) (Ginter et al., 2010). *Tristychius* has anterior teeth with a single conical cusp and mediolateral teeth with two to three triangular, blunt, grasping cusps (Dick, 1978). *D. michaeledmundi* gen. et sp. nov. is most similar to "*Maiseyodus*" (Hanson, 1986). The most anterior teeth of both taxa have three prominent cusps; the median and posterior teeth are multicuspid, and the height of the cusps progressively reduces posteriorly with each tooth position. *Diablodontus* differs from "*Maiseyodus*" in having a prominent gap between the median cusp and the next lateral cusp. There are also a reduced number of lateral cusps in *Diablodontus*, especially seen in the median teeth, as "*Maiseyodus*" has three lateral cusps and *Diablodontus* has two. The cristae in *Dibalodontus* are greater in number, thinner, and form additional jagged cutting edges compared to the cristae in "*Maiseyodus*," which are reduced in number, coarse, and lack the jagged cutting edges.

We propose that the dental organization of *Diablodontus michaeledmunti* gen. et sp. nov. was similar to the model proposed by Hanson (1986) for "*Maiseyodus*," in which there was a morphological gradation in the tooth series with at least five specific variations. We presently can only recognize four distinct variations (anterior/symphysial, mediolateral, lateral, and posterolateral) for *Diablodontus* due to the rarity of this taxon from the KMS locality, but the overall similarities between the two taxa would suggest that *D. michaeledmundi* could have had at least five variations as well (Fig. 3). Hanson (1986) modeled "*Maiseyodus*" after the dental and jaw structures of *Hybodus* (Patterson, 1966) and *Egertonodus* (Maisey, 1983), which have nine and 11-12 tooth rows, respectively. Furthermore, in "*Maiseyodus*," like *Hybodus* and *Egertonodus*, a distinction between upper and lower dentitions can be made, in which the upper dentition had distinctly longer cusps than the lower dentition (Hanson, 1986). This trait can also be seen as well with *D. michaeledmundi* gen. et sp. nov. We propose that *D. michaeledmundi* gen. et sp. nov. had at least 9-10 tooth rows in the upper and lower jaws, with the upper dentition distinguished by longer cusps than the lower dentition.

DISCUSSION AND CONCLUSIONS

Diablodontus michaeledmundi gen. et sp. nov. is a Permian hybodont shark with grasping and gouging teeth, representing a rare feeding morphology for Hybodontiformes as they were almost entirely durophagous at this time. The only other Permian hybodont with similar dentition is "*Hybodus* sp." (KUVP 82668) from the Three Mile Limestone locality of the Kansas Wreford megacyclothem deposits (Schultze, 1985, fig 3.6). This specimen is considered to be a "*Maiseyodus*" record extending into the Early Permian. Presently, *D. michaeledmundi* gen. et sp. nov. is the only known non-durophagous hybodont from the marine Middle Permian.

Relationships

The dental morphology of *Diablodontus michaeledmundi* gen. et sp. nov. suggests a close relationship to the Pennsylvanian and Early Permian "*Maiseyodus*." Both taxa share a plate-like base, anterior teeth with three prominent cusps, and multicuspid lateral tooth families, which gradually reduce posteriorly in cusp height. *D. michaeledmundi* is considered here more derived than "*Maiseyodus*" as it has a pronounced anaulacorhize structure between the ventral plate-like tooth base, a reduced cusp number, prominent gracile cusps, and well developed cutting cristae.

The relationship of these two taxa to the Hybodontiformes is unclear. Hanson (1986) noted that his "*Maiseyodus*" specimens shared a few characters with *Tristychius*, such as a plate-like base, but the lack of an enlarged lingual torus and multiple cusps in the anterior dentition separate "*Maiseyodus*" and *D. michaeledmundi* from the Tristychiidae. Maisey (1989) proposed a phylogeny for Paleozoic and Mesozoic members of the Hybodontoidea. An important dental character used was elongation of the lateral teeth, a trait *Diablodontus* shares with *Hamiltonichthys*, *Lissodus*, *Polyacrodus*, *Palaeobates*, *Asteracanthus*, *Acrodus*, *Egertonodus*, and *Hybodus*. *Tristychius* and *Onychoselache* lack elongated lateral teeth, placing them basal within the Hybodontoidea (Maisey, 1989; Coates and Gess, 2007). Both "*Maiseyodus*" and *Diablodontus* have elongated lateral teeth, similar to the proportions seen in *Egertonodus* and *Hybodus*, though not to the extreme seen in *Hamiltonichthys*, *Lissodus*, *Polyacrodus*, *Acrodus*, *Palaeobates*, and *Asteracanthus*. In addition, "*Maiseyodus*" and *Diablodontus* have high-crowned multicuspid teeth, a synapomorphy shared by members of Maisey's (1989) Hybodontinae. Based on the dental traits we propose that "*Maiseyodus*" and *Diablodontus* belong to an indeterminate family that was basal to either the *Acrodus*/*Asteracanthus* and *Hybodus*/*Egertonodus* clades, or was a sister group to the *Hybodus*/*Egertonodus* clade itself. A phylogenetic analysis of this hypothesis will be presented elsewhere.

Ecological Considerations

The teeth of *Diablodontus michaeledmundi* gen. et sp. nov. represent the only non-durophagous hybodont occurring in the Kaibab Formation and the only other shark outside the Ctenacanthiformes that has a grasping/cutting dentition (Hodnett et al, 2012). Hanson (1986) proposed that "*Maiseyodus*," with its grasping medial teeth and "crushing" posterior teeth, fed on a variety of prey that ranged from fish to invertebrates. We propose that the fine and jagged cristae of *D. michaeledmundi* enhanced the cutting surfaces of the dentition, therefore, *Diablodontus* may have evolved to be an active predator with teeth less suitable for the regular consumption of hard-shelled invertebrates. This kind of tooth morphology is similar to *Egertonodus basanus* from the Early Cretaceous of England (Maisey, 1983). Hanson (1986) speculated that the teeth of "*Maiseyodus*" represented a "diminutive fish," with tooth di-

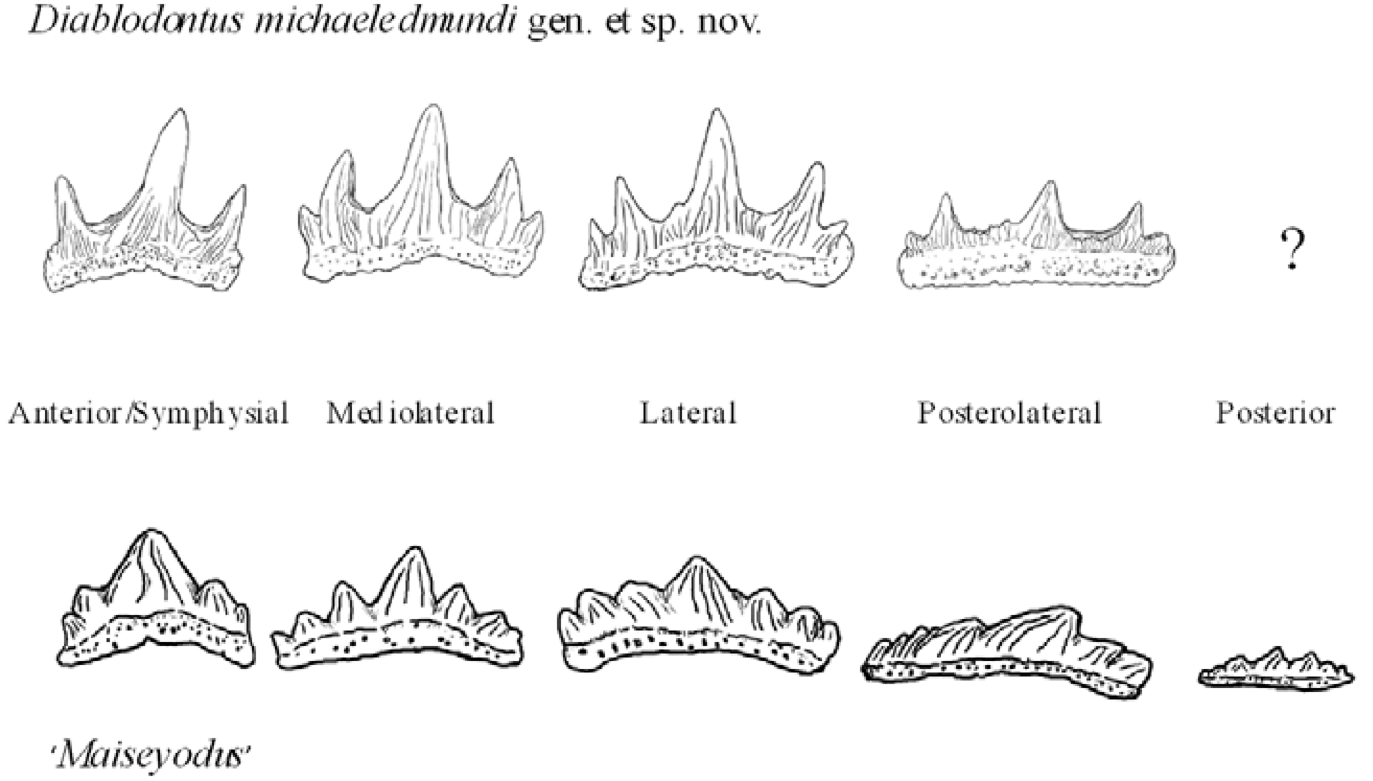

FIGURE 3. Labial comparison of the tooth series for *Diablodontus michaeledmundi* gen. et sp. nov. and "*Maiseyodus*" from OSU. "**?**" represents presently unknown posterior tooth for *Diablodontus michaeledmundi* gen. et sp. nov. ("*Maiseyodus*" re-drawn and modified from Hanson, 1986). Teeth are not to scale.

mensions from < 2 mm to 10 mm. The smaller dimensions for "*Maiseyodus*" are similar to those seen in *Tristychius arcuatus*, a shark approximately 50 cm in length (Dick, 1978; Hanson, 1986). From Hanson's (1986) estimations for "*Maiseyodus*," *D. michaeledmundi* may have ranged from a half meter to a meter in length.

Compagno (1990) proposed feeding ecologies for living and extinct chondrichthyans based on the morphology of sharks that occur within certain environments. Compagno (1990) proposed that hybodonts like *Hybodus*/*Egertonodus* inhabited a littoral ecomorphotype, which is characterized as a generalized and unspecialized active shark that lives near continental and insular shelves. This ecomorphotype is the most common feeding ecology in chondrichthyans (Compagno, 1990) including the Kaibab Ctenacanthiformes (Hodnett et al., 2012). Other hybodonts, like *Tristychius*, may have been bottom-dwelling squatinobenthic sharks (Compagno, 1990), flat-bodied specialists for bottom-lurking ambush predation. Based on the morphological data and dental similarities with *Egertonodus*, *D. michaeledmundi* gen. et sp. nov. could have behaved like extant hound sharks (Triakidae), which habit coastal waters between the bottom and mid-water, feeding on fish, marine arthropods, and soft bodied invertebrates.

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ARTINSKIAN (EARLY PERMIAN) CONODONTS FROM THE ELM CREEK LIMESTONE, A HETEROZOAN CARBONATE SEQUENCE ON THE EASTERN SHELF OF THE MIDLAND BASIN, WEST TEXAS, U.S.A.

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Abstract—The Elm Creek Limestone Member of the Belle Plains Formation (Albany Group) on the Eastern Shelf of the Midland Basin, West Texas, comprises a stratigraphic sequence of just over 20 meters of heterozoan (foramol and bryomol/bryoderm) carbonates, strikingly different from the normal marine photozoan carbonates of the underlying upper part of the Cisco Group. The appearance of heterozoan carbonates in the Early Permian on the Eastern Shelf is attributed to widespread high mesotrophic–eutrophic to low mesotrophic, variable salinity conditions that arose in response to the terrigenous input to the shelf interacting with the subtle sea-level flucuations of a greenhouse world. Conodonts were largely excluded from the foramol carbonate facies, but a short stratigraphic interval within the bryoderm carbonates in the upper part of the Elm Creek Limestone yielded numerous examples of *Sweetognathus whitei* and *Rabeignathus bucaramangus*, in addition to other shallow-water, nearshore taxa. The occurrence of *S. whitei* with *R. bucaramangus* indicates that the Elm Creek Limestone is most likely middle to late Artinskian (late Wolfcampian) in age. The Elm Creek Limestone appears to have formed near the time, late Artinskian, of the transition from the P2 icehouse to the onset of true ice-free conditions on Gondwana and a greenhouse style of sequence architecture on the Eastern Shelf.

INTRODUCTION

The Eastern Shelf of the Midland Basin of West Texas (Fig. 1) preserves a relatively continuous record of Late Paleozoic (Pennsylvanian and Permian) tropical climate evolution and sea-level dynamics (Holterhoff, 2010). Recent work on the Gondwanan subcontinents shows that the Early Permian marks the transition from the acme of the late Paleozoic global icehouse in the earliest Permian to an essentially ice–free middle Early Permian world (Fielding et al., 2008a). This transition had a significant impact on terrestrial (Tabor and Montanez, 2004; DiMichele et al., 2006) and marine depositional systems and sequence stratigraphic architecture of the strata filling the Midland Basin along the Eastern Shelf (Holterhoff, 2006, 2009b, 2010).

The upper part of the Cisco Group succession (Fig. 2) conforms well to the icehouse model of sequence architecture (Boardman, 1993; Boardman et al., 1998; Holterhoff, 2010). The thin, high-frequency sequences display rapid, significant drowning of the Eastern Shelf in accord with models of rapid onset of interglacial conditions and melting of glacial ice during the Pleistocene (Stanley and Warne, 1994; Fleming et al., 1998). The glacial-eustatic transgression provided accommodation space on the shelf for interglacial siliciclastic highstand depositional systems, such as deltas and shorefaces, to aggrade and prograde out onto the Eastern Shelf (Brown et al., 1990). However, highstand progradation was comparatively short lived, and the ensuing glacial-eustatic fall in sea level forced depositional systems across the shelf, initiating incised valley formation and paleosol development across the subaerially exposed Eastern Shelf.

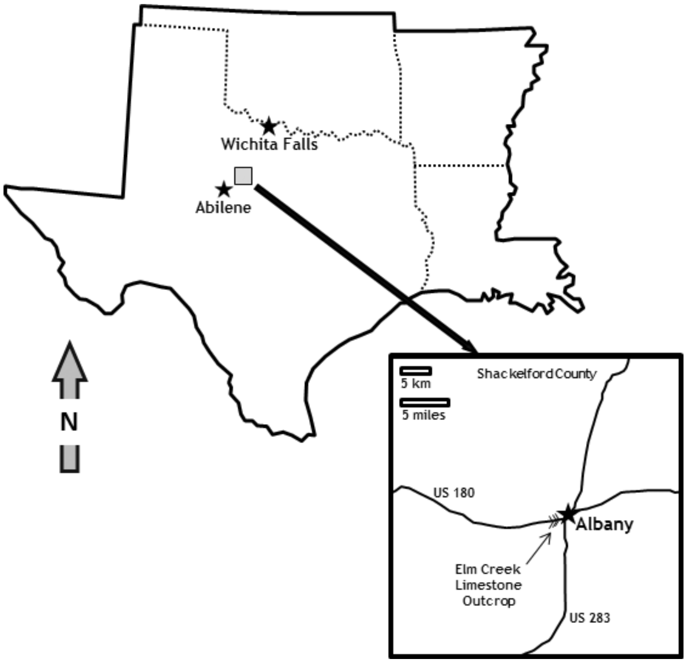
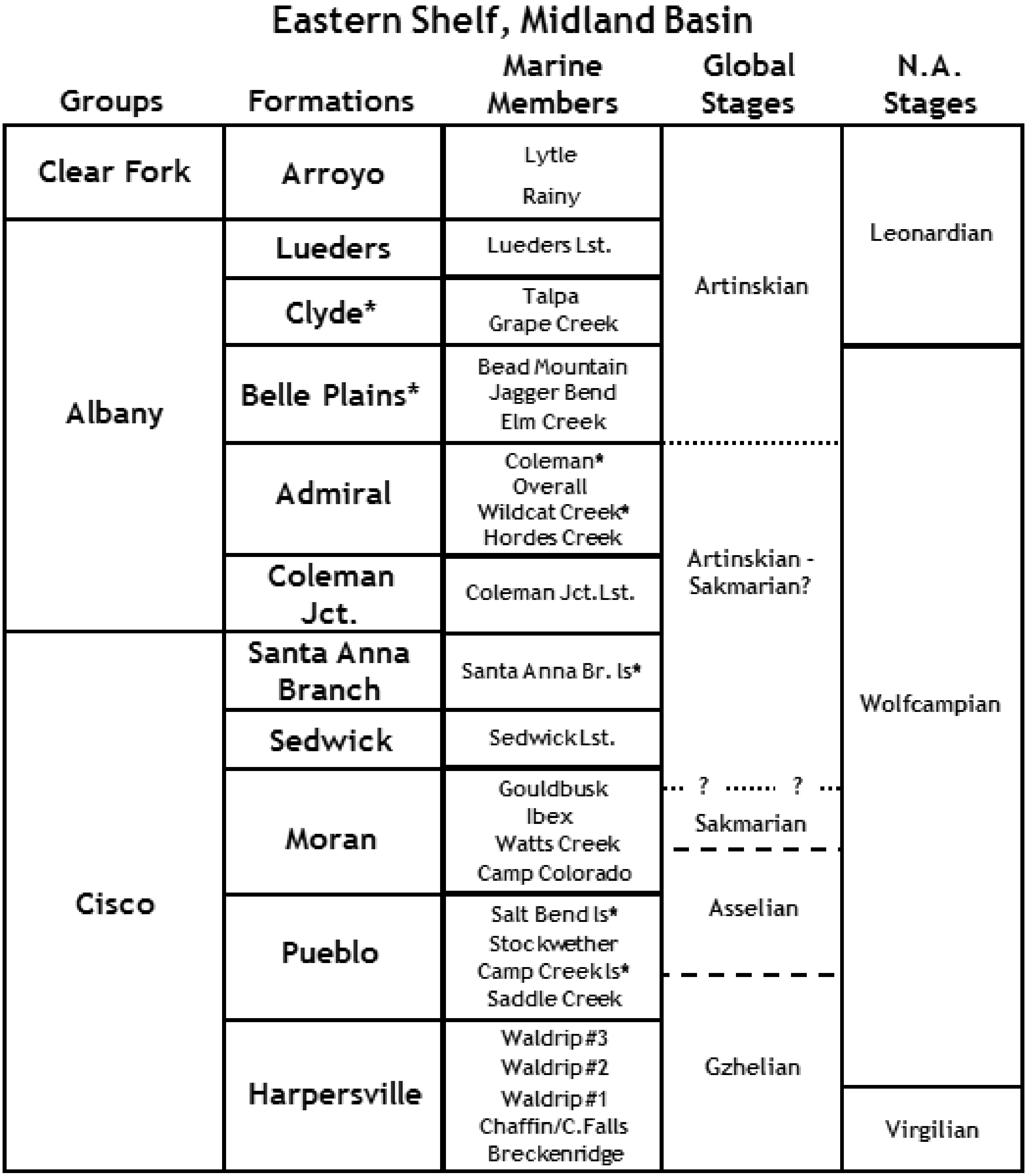


FIGURE 1. The Elm Creek Limestone creates an escarpment immediately west of Albany, Texas. The studied section is an extensive exposure in a roadcut along US 180 (32.7177° N., 99.3177° W).

The Albany Group above the Admiral Formation (Fig. 2) possesses a sequence architecture more characteristic of greenhouse climate regimes, and records a major long-term rise in relative sea level (Holterhoff, 2009a, 2010). Bedset stacking patterns observed within the upper part of the Albany Group sequences display a more complex nested hierarchy of organization, indicating subtle changes in base level compared to the pronounced base-level changes of the upper part of the Cisco Group. Slower, stepped rises and falls in sea level account for the observed facies transitions and thicker sequences of the upper part of the Albany Group. Transgression would have been protracted across the Eastern Shelf, allowing for the thick carbonate–dominated sequences to develop. However, the transgression was slow enough for nearshore molluscan-foraminiferal carbonates to keep up with accommodation space on the shelf rather than being replaced by offshore, fossiliferous carbonates as in the upper part of the Cisco Group. The subsequent fall in base level was equally subtle, because significant truncation and shelf–wide exposure surfaces have not been identified in the upper part of the Albany Group.



Eastern Shelf, Midland Basin

Groups	Formations	Marine Members	Global Stages	N.A. Stages
Clear Fork	Arroyo	Lytle Rainy	Artinskian	Leonardian
Albany	Lueders	Lueders Lst.		
	Clyde*	Talpa Grape Creek		
	Belle Plains*	Bead Mountain Jagger Bend Elm Creek		Wolfcampian
	Admiral	Coleman* Overall Wildcat Creek* Hordes Creek	Artinskian - Sakmarian?	
	Coleman Jct.	Coleman Jct. Lst.		
Cisco	Santa Anna Branch	Santa Anna Br. ls*		
	Sedwick	Sedwick Lst.		
	Moran	Gouldbusk Ibex Watts Creek Camp Colorado	? ? Sakmarian	
	Pueblo	Salt Bend ls* Stockwether Camp Creek ls* Saddle Creek	Asselian	
	Harpersville	Waldrip #3 Waldrip #2 Waldrip #1 Chaffin/C. Falls Breckenridge	Gzhelian	Virgilian

FIGURE 2. Lithostratigraphy and stage correlations of the Eastern Shelf Upper Pennsylvanian and Lower Permian succession. Lithostratigraphy after Brown et al. (1972) and Kier et al. (1976). Names followed by an asterisk are either informal terms or resurrected from Plummer and Moore (1921) and Moore (1949). Uncertain stage boundaries indicated by dashes and question marks. From Holterhoff (2010).

The upper part of the Cisco Group straddles the Pennsylvanian–Permian boundary and includes Virgilian (Gzhelian) and Wolfcampian (Asselian-Sakmarian) strata. The Cisco Group high–frequency, icehouse–style sequences are coeval with the widespread P1to P2 glacial interval of Fielding et al. (2008a) (Holterhoff, 2010). The absence of fusulinids and rarity of other open marine organisms in strata of the Albany Group has made it difficult to determine the position of the base of the Artinskian on the Eastern Shelf, as well as to correlate the stratigraphic level of the de-glaciation event and ocean volume increase associated with the transition from the P2 icehouse to the subsequent post-P2 greenhouse climatic regime. In this paper we describe a low diversity conodont fauna from the upper part of the Elm Creek Limestone, in the lower part of the Belle Plains Formation of the middle part of the Albany Group (Fig. 2), and discuss how this fauna provides sufficient information to constrain the age of at least part of the Albany Group.

ELM CREEK LIMESTONE

The Elm Creek Limestone is the lowest thick (> 20 m) extensive carbonate unit above the Coleman Junction Limestone in the Albany Group. Walsh (2002) discussed the regional surface and subsurface stratigraphy of the Elm Creek Limestone on the Eastern Shelf and described several sections across the outcrop belt. The Elm Creek Limestone is best exposed along US Highway 180, west of Albany, and this is the section from which age-diagnostic conodonts were recovered (Fig. 1). Walsh (2002) originally described this section, subdivided the Elm Creek into three major packages, and reported the presence of conodonts near the top of the section. Holterhoff and Blair (2010) provided more extensive lithological descriptions and facies interpretations and placed the Elm Creek units into a sequence stratigraphic framework (Fig. 3). The Elm Creek Limestone at the Highway 180 section represents a comparatively large–scale depositional sequence with well-developed systems tracts defined by eight parasequences and four parasequence sets (Holterhoft and Blair, 2010).

The base of the Highway 180 outcrop exposes approximately 2 meters of the top of the Jim Ned Shale Member of the Admiral Formation. The Jim Ned Shale is a medium gray, blocky mudstone with a thin laminated gray mudstone zone at the top. The lowest 6 meters of the Elm Creek, which is characterized by interbedded limestone and mudstone, is Unit A of Walsh (2002). The overlying carbonate-dominated succession is the thicker Unit B (14 m), and the thin (2 m) interbedded limestone and mudstone interval at the top of the exposure is Unit C.

Unit A comprises carbonate mudstone, molluscan–foraminiferal wackestone, packstone and lesser grainstone, interbedded with brown to black mudstone. Walsh (2002) recognized lower subunit A and upper subunit A packages based upon carbonate and mudstone thickness trends, both of which are capped by dark gray to black mudstone, the upper one of which contains zones of ostracodes, concostrachans, vertebrate debris and plants. Holterhoff and Blair (2010) interpreted Unit A as a shallowing–upward set of two parasequences recording successive flooding events followed by progradation of the coastal plain across the shelf.

The B1 to B3 parasequences form a distinct parasequence set in which the three parasequences thicken upward, mudstone separating the parasequences become progressively thinner upward, and grainstone beds capping each parasequence become thinner upward (Holterhoff and Blair, 2010). Nodular molluscan-foraminiferal packstone occurs in the lower part of each parasequence and shale partings contain ostracodes, fenestrate bryozoans, and spirorbiform microconchids, and small, spiral encrusting worm tubes. Bedded molluscan-foraminiferal grainstone occurs in the upper part, which is capped by gray mudstone. The molluscan fauna appears to be dominated by bellerophontid gastropods and pinnid bivalves, which are commonly found in life position. Physical sedimentary structures are not preserved in these facies, which are dominated by pervasive bioturbation. A well developed *Glossifungites* firmground occurs at the top of the B1 grainstone at the contact with the overlying gray mudstone.

The B1, B2, and B3 parasequences display a distinctive spectral gamma ray (SGR) signature of very low CGR values and elevated U (Holterhoff and Blair, 2010). The low CGR values indicate that siliciclastic material (especially clay) is of very low concentrations, implying that siliciclastics were essentially sequestered along the coastal plain, ostensibly during flooding episodes, and suggesting that coastal plain aggradation and marine onlap were significant. Each parasequence represents a separate flooding event, followed by minor progradation of the coastal plain across the shelf. This pattern implies a more significant flooding of the Eastern Shelf than for the underlying A parasequence set. Together, the A and B1-B3 parasequence sets define a long term relative rise in sea level and expansion of the shallow marine carbonate realm well onto the coastal plains to the east and north and comprise the Transgressive Systems Tract of the Elm Creek Sequence (Fig. 3).

Parasequences B4 and B5 show increased proportions of echinoid and bryozoan material relative to the molluscan–foraminiferal fauna of parasequences B1–B3. Parasequence B4 is approximately 3.5 meters of dominantly nodular packstone. Ostracodes, mollusks and small foraminifers make up a significant skeletal component with small contributions from bryozoans and rare echinoids. A thin layer of ostracode packstone caps the limestone interval and is overlain by a thin, medium gray mudstone at the top of the parasequence. The SGR signature of B4 displays a subtle but distinctive increase in the CGR log, indicating the input of fine siliciclastics into the carbonate realm, even during the B4 flooding event (Holterhoff and Blair, 2010). Parasequence B4 does not display an obvious shoaling–upward trend in limestone fabric or skeletal preservation, and bryozoan and echinoid remains are relatively more common. B4 appears to represent a thick succession of bioturbated, deeper platform facies analogous to the B1–B3 nodular packstone. The B4 parasequence is dominated by deeper platform facies with an abrupt, but conformable transition into shallow, marginal marine and coastal plain facies.

Parasquence B5 caps the main outcrop of the Elm Creek Limestone. Even bedding is much better developed in B5 than in the underlying units, although bioturbation is pervasive. Echinoid and bryozoan debris makes up a significant proportion of the rock volume, but mollusks and foraminifers remain the most important contributors to the rock volume. Many of these units are grain-dominated packstone, and the uppermost beds are grainstone. The B5 limestone parasequence is overlain by a mudstone–dominated interval over a meter thick. Unlike the B4 parasequence, the B5 parasequence displays a distinctive shoaling upward trend in rock fabric, proceeding from nodular and bedded packstone below, to medium- to thick-bedded grain–dominated packstone to grainstone in the upper B5 limestone. B5 appears to represent a less extensive flooding of the shelf where deeper water packstone grades into shallower, higher energy facies. The capping mudstone interval represents the encroachment of the siliciclastics into the carbonate shelf environment and eventual progradation of the coastal plain across the shelf.

The base of parasequence C is a highly bioturbated molluscan–foraminiferal packstone ledge approximately 0.7 meters thick that grades upward into thinly laminated ostracode–bryozoan packstone with fossiliferous mudstone interbeds. The remainder of the C parasequence is composed of decimeter-scale cycles of highly bioturbated ostracode–bryozoan–echinoid packstone and gray mudstone with only minor molluscan material. Although the bases of the limestone beds are often in sharp contact with the underlying mudstone, the contact between limestone and mudstone is usually gradational, with a significant amount of bioturbation piping mudstone into the packstone. The fauna of the C interval above the basal ledge is composed of ostracodes, bryozoans and echinoids. Spirorbiform microconchids are also common in Unit C.

Parasequences B4, B5 and C display a progressive trend from a deeper water platform parasequence (B4) to a shallower, more shoal-dominated platform parasequence (B5) into a parasequence (C) with significant siliciclastic input and a more restricted, nearshore fauna. This interval is interpreted to be the Highstand Systems Tract of the Elm

Creek Limestone (Fig. 3). B4 and B5 comprise a parasequence set representing the early, aggradational phase of the Elm Creek highstand and C and overlying unexamined section are the later, progradational phase of the Elm Creek highstand, reflecting the long–term offlap of carbonate facies down the platform and expansion of the coastal plain across the shelf.

Elm Creek Heterozoan Carbonates

Walsh (2002) noted that the fauna composing the Elm Creek Limestone is not typical for tropical platform carbonate depositional systems. Indeed, early geologists to the region recognized that the molluscan-dominated, "Mesozoic" aspect of the carbonate units above the lower part of the Albany Group was quite different than the typical "Carboniferous" faunas (White, 1891).

Mollusks such as *Aviculopinna*, myalinids and other bivalves along with *Straparollus* (*Euomphalus*), bellerophontids, and other gastropods are the most common macrofaunal elements in the Elm Creek fauna. Encrusting and other small foraminifers are a significant component of the microfauna. Walsh (2002) referred to the Elm Creek limestones as foramol carbonates, one of several types of heterozoan carbonate (James, 1997). In the upper Elm Creek (B4, B5, and C parasequences), fenestrate and ramose bryozoans and echinoid echinoderms are important components. These are also heterozoan carbonates, often referred to as bryomol or bryoderm carbonates (James, 1997). Ostracodes can dominate thin packstone beds associated with mudstone units, often at the transition between foramol or bryomol carbonate and overlying mudstone. Vermiform and spirorbiform microconchids (Taylor and Vinn, 2006; Vinn, 2010), formerly called serpulid or spirorbid worms in this succession, are encrusting organisms that are locally significant contributors to the skeletal fraction as well.

Autotrophs such as skeletal green algae (i.e., codiacean phylloids and dasycladaceans) and mixotrophs such as the large benthic foraminifers (fusulinids) are apparently absent from the Elm Creek Limestone. Other normal marine platform faunal elements such as corals, crinoids and brachiopods, as well as typically tropical non–skeletal carbonate elements, such as ooids and peloids, are also rare to absent in the Elm Creek Limestone. In contrast, these faunal elements and carbonate grain types are common in open marine carbonate facies of the underlying strata of the upper part of the Cisco Group.

Although foramol and bryomol heterozoan carbonates are sometimes referred to as "cool–water carbonates," they only indicate that the conditions necessary for tropical, "photozoan" carbonate facies to form were not present (James, 1997). The position of the Eastern Shelf of the Midland Basin at equatorial latitudes (e. g., Tabor and Poulsen, 2008) eliminates temperature stress as a potential factor on the Eastern Shelf. However, salinity and nutrient input were potential controls on carbonate production during deposition of the Elm Creek Limestone (Holterhoff, 2010). Coastal upwelling was not a viable source for nutrient–rich waters onto the Eastern Shelf because the coeval shelf margin for the Elm Creek Limestone lay hundreds of kilometers west of the outcrop belt. Terrestrial inputs are the more likely source of nutrient flux to the platform. If fresh-water flux into the marine realm was the dominant salinity variable in the Elm Creek carbonate system, then both salinity and nutrient fluxes might have been linked and both suppressed the development of photozoan carbonate (Hallock and Schlager, 1986)

Holterhoff (2010) proposed that the dark gray to black mudstone and associated thin carbonate beds represent proximal, low-energy, coastal environments with significant nutrient input and preservation of organic matter. The molluscan-foraminiferal heterozoan carbonate represents distal, open platform environments during times of significant nutrient loading to the platform (high mesotrophic–eutrophic) and possibly lower salinity. The bryozoan–echinoderm heterozoan carbonate facies represents distal, open platform conditions during intervals of reduced nutrient input to the platform (low mesotrophic) and more normal marine salinity. The ostracode-bryozoan-echinoid packstone facies associated with interbedded gray mudstone represent proximal coastal environments during low nutrient intervals (low mesotrophic). At no time during Elm Creek Limestone deposition did truly tropical, oligotrophic conditions prevail across the outcrop belt.

CONODONTS AND THE AGE OF THE ELM CREEK LIMESTONE

Most samples of the Elm Creek Limestone that were processed for conodonts were barren (Walsh, 2002). Because of its excellent exposure, the Highway 180 section west of Albany was heavily sampled, but Units A and C were barren. Samples from the B1–B4 parasequences produced low diversity faunas comprising just a few elements of *Ellisonia*, *Sweetognathus whitei* and *S. inornatus*. The highest abundance and variety of conodonts came from the upper beds of the B5 parasequence in the upper Elm Creek Limestone (Table 1), the part of the section that is characterized by the greatest abundance of bryozoans and echinoids. All of the specimens of *Rabeignathus bucaramangus* and *Sweetognathus* species A, as well as numerous *S. whitei* elements, were obtained from a one-meter interval of carbonate within B5 (Walsh, 2002). Only a small number of elements of *Sweetognathus* and *Ellisonia* were recovered from other sections (Walsh, 2002).

The *Sweetognathus* conodont biofacies is generally interpreted to represent a tropical, shallow water, normal marine carbonate environment (e. g., Kozur, 1995; Mei et al., 2002; Boardman et al., 2009). The high mesotrophic–eutrophic and possibly lower salinity environments of the majority of the Elm Creek parasequences appear to have excluded conodonts, as well as most typical normal marine late Paleozoic organisms. When low mesotrophic and more normal marine salinity conditions prevailed during Elm Creek Limestone highstand deposition (parasequence B5), the *Sweetognathus* biofacies was able to develop. The good to excellent preservation of the conodont elements, including delicate ramiforms, suggests that relatively little postmortem transport occurred, and that these conodonts were able to survive at the more marine margin of the Elm Creek Limestone heterozoan carbonate setting.

Only two species of conodonts with potential biostratigraphic significance were obtained from the Elm Creek Limestone, *Sweetognathus whitei* (Rhodes 1963) and *Rabeignathus bucaramangus* (Rabe 1977). *Sweetognathus whitei* is a widely distributed species that may encompass a number of morphotypes. The point of derivation of *S. whitei* from its ancestor, *S. binodosus*, is the faunal marker for the base of the Artinskian (Chuvashov et al., 2002; Wardlaw et al., 2004). However, some workers have indicated that the North American *S. whitei* may be a slightly different form and appear at a slightly different time than the *S.* "*whitei*" that occurs in the proposed Artinskian stratotype, the Dal'ny-Tulkus section in the Urals (Henderson and Kotlyar, 2009; Henderson et al., 2012).

On the Eastern Shelf of the Midland Basin, *Sweetognathus whitei* occurs well below the Elm Creek Limestone, as low as the Goldbusk Limestone of the Moran Formation (Boardman and Nestell, 1993, fig. 5). *Sweetognathus whitei* is considered to be an index for the Artinskian, where it reaches its greatest abundance and distribution. Mei et al. (2002, p. 88) indicate that *S. whitei* is restricted to the Artinskian, but Ueno et al. (2002, p. 748) report that it ranges into the early Kungurian. The base of the Kungurian is to be placed at a level that coincides with the first appearance datum (FAD) of *Neostrepognathodus pnevi* within the chronomorphocline from advanced *N. pequopensis* (Chuvashov et al., 2002; Henderson et al., 2012). This level is somewhat higher than that often used to mark the base of the Kungurian and may make the LAD of *S. whitei* lie within the Artinskian.

Rabeignathus bucaramangus, as well as many other taxa incorrectly assigned to *Rabeignathus*, occurs in association with *S. whitei*. In Utah, *R. bucaramangus* occurs with both *Mesogondoella bisselli* and *S. whitei*, but below the range of *N. pequopensis* (Ritter, 1986). Mei et al. (2002, fig. 1) show that "*Sweetognathus*" *bucaramangus* ranges from the Winfield Limestone into the Nolans Limestone of the Chase Group in Kansas, and indicate that these units are Artinskian in age, without

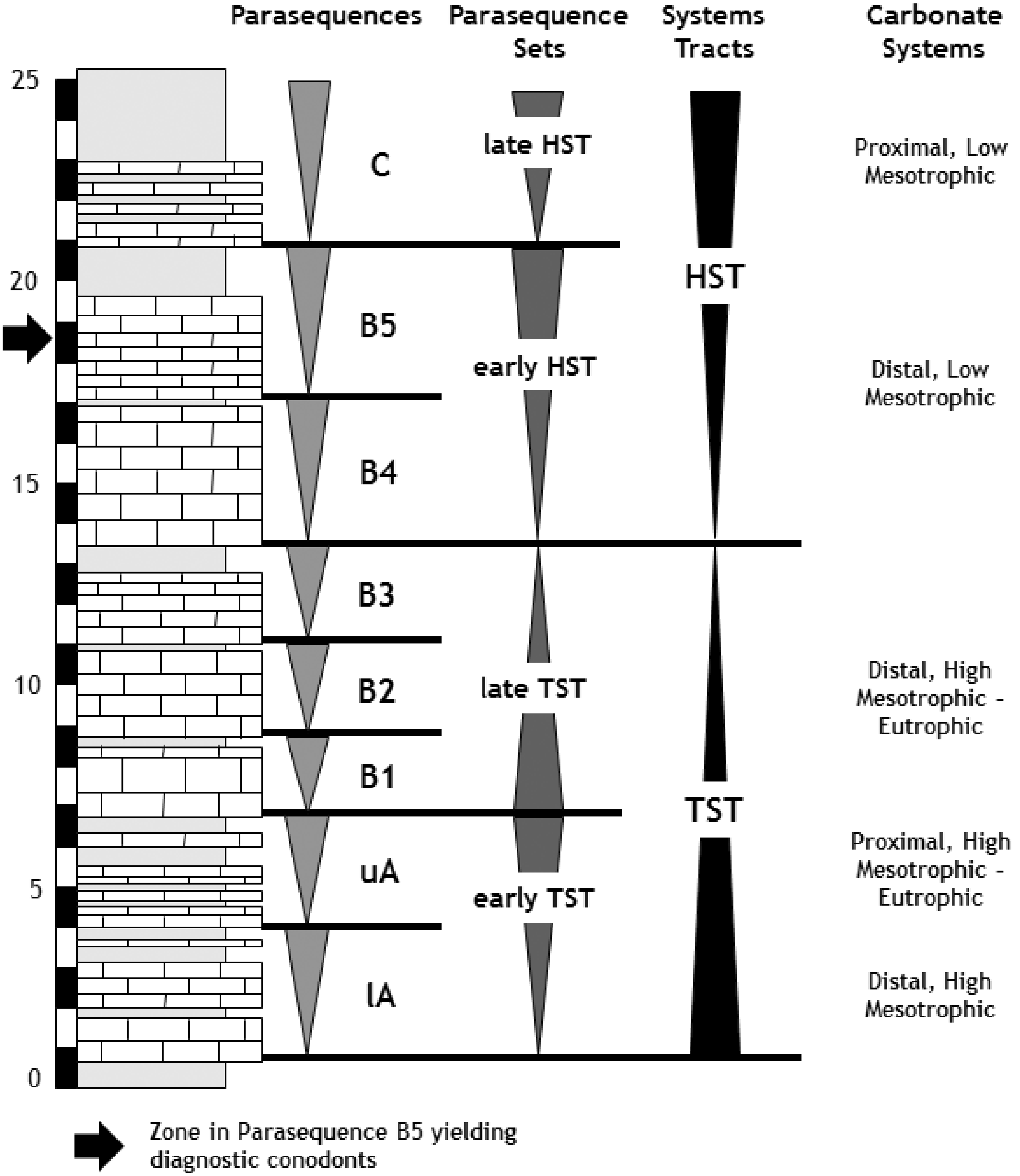
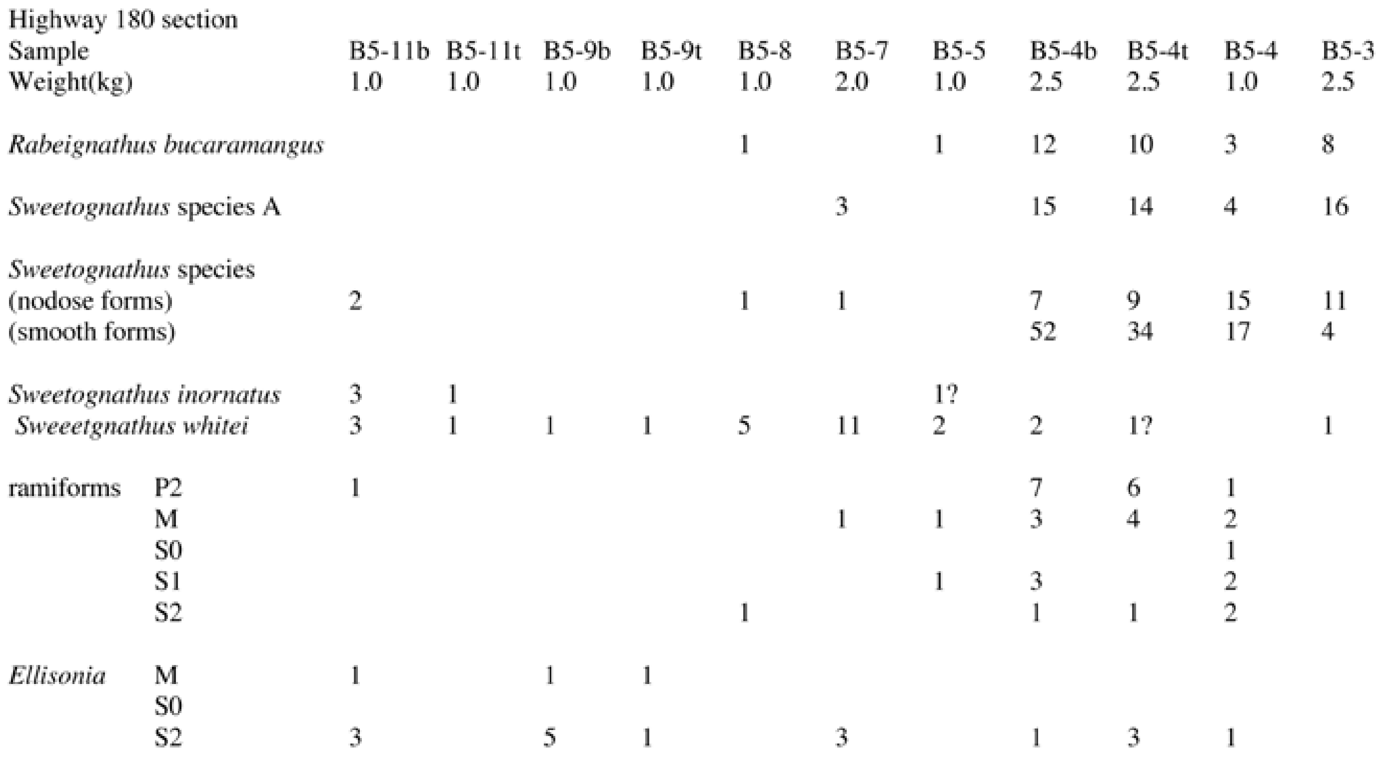


FIGURE 3. Schematic sequence stratigraphic interpretations and inferred carbonate trophic systems for the Elm Creek Limestone at the U.S. Highway 180 section. Scale on left in meters. From Holterhoff and Blair (2010).

TABLE 1. Distribution of conodonts in the B5 parasequence of the Elm Creek Limestone at the US Highway 180 section. The limestone section of the lower part of the B5 parasequence is 2.6 m thick; details of sampling are given in Walsh (2002). Stratigraphically lowest samples are on the left of the table.



Highway 180 section

Sample		B5-11b	B5-11t	B5-9b	B5-9t	B5-8	B5-7	B5-5	B5-4b	B5-4t	B5-4	B5-3
Weight(kg)		1.0	1.0	1.0	1.0	1.0	2.0	1.0	2.5	2.5	1.0	2.5
Rabeignathus bucaramangus						1		1	12	10	3	8
Sweetognathus species A							3		15	14	4	16
Sweetognathus species												
(nodose forms)		2				1	1		7	9	15	11
(smooth forms)									52	34	17	4
Sweetognathus inornatus		3	1					1?				
Sweeetgnathus whitei		3	1	1	1	5	11	2	2	1?		1
ramiforms	P2	1							7	6	1	
	M						1	1	3	4	2	
	S0										1	
	S1							1	3		2	
	S2					1			1	1	2	
Ellisonia	M	1		1	1							
	S0											
	S2	3		5	1		3		1	3	1	

discussion or documentation. In Kansas, *S. whitei* appears in the Florence Limestone Member of the underlying Barneston Limestone (Boardman et al., 2009) and may range higher into the Winfield Limestone with *R. bucaramangus* (Mei et al., 2002, fig. 1). Mei and Henderson (2002, p. 601-602), however, recognized *N. pequopensis* in the fauna of Rabe (1977; *Gnathodus* aff. *G. whitei*, pl. 4, fig. 14, 15) from which *R. bucaramangus* was originally described. *Rabeignathus bucaramangus* clearly appears during the Artinskian after the first occurrence of *S. whitei*, but the highest occurrence in time of *R. bucaramangus* is still uncertain.

Based on the presence of *Sweetognathus whitei* with *Rabeignathus bucaramangus* in the Elm Creek Limestone, Walsh (2002) and Walsh and Barrick (2002) suggested that the Elm Creek Limestone is Artinskian in age. Wardlaw (2005) presented a correlation chart for the Late Pennsylvanian-Early Permian succession of North Central Texas, in which he showed the Elm Creek as being Artinskian in age, and the base of the Kungurian lying much higher, at the base of the Talpa Formation (Fig. 2). He reported *Rabeignathus* sp. from the Elm Creek Limestone as well as the stratigraphically lower Hords Creek Limestone, but did not discuss the basis for these identifications nor illustrate the forms. Our consideration of the Elm Creek conodont fauna leads us to interpret the unit to be approximately middle to late Artinskian in age.

Glacial deposits were widespread across Gondwana and Siberia during the earliest Permian (Asselian and Sakmarian), including the P1 and P2 glacial phases of Fielding et al. (2008a, b). However, the paucity of glacial deposits of upper Artinskian and lower Kungurian age indicates an extended interval of ice-free conditions during this time, the P2/P3 non-glacial phase. The middle to late Artinskian age interpreted here for the Elm Creek Limestone conodonts indicates that the end of the P2 glacial interval and the onset of true ice-free conditions on Gondwana is correlative with strata of the lower to middle part of the Albany Group and the establishment of greenhouse style of sequence architecture on the Eastern Shelf of the Midland Basin.

Walsh (2002) indicated that the Elm Creek was most likely late Wolfcampian in age based on what was known about the range of *Rabeignathus* at that time. Traditionally, the base of the Leonardian on the Eastern Shelf has been placed at what was considered to be a regional unconformity in the upper shale member (Jim Ned Shale) of the Admiral Formation (Cheney, 1940; Moore, 1949; Hentz, 1988). Thus, the overlying part of the Albany Group, including the Elm Creek Limestone, was considered to be Leonardian in age. However, A. K. Miller (in King, 1942) noted that ammonoids from the Belle Plains Formation at the Bead Mountain level (above the Elm Creek) were “most definitely Wolfcamp in aspect,” whereas the ammonoid fauna from the overlying Clyde Formation appeared to be Leonardian. This report caused King (1942) to only tentatively accept Cheney’s (1940) position of the Leonardian boundary within the Admiral Formation, noting that the base of the Leonardian should lie within the Clyde Formation. Definitive basal Leonardian fusulinids (*Schwagerina crassitectoria*) were recovered from outcrops of the Talpa Limestone of the Clyde Formation near Novice, Texas (Myers, 1968). This occurrence showed the Talpa Limestone and the upper portion of the Albany Group are Leonardian in age, but it did not establish the position of the base of the Leonardian.

Wardlaw (2004) concluded that the boundary between the North America Wolfcampian and Leonardian stages correlates essentially to the Artinskian-Kungurian boundary, which is how the boundaries were shown in Wardlaw et al. (2004). Wardlaw (2004) reported that the base of the Skinner Ranch Formation (base of type Leonardian) contains *Neostreptognathodus pequopensis*, a conodont species that is latest Artinskian. A fauna with “*N. exsculptus*” appears 17 m higher. Because *N. exsculptus* and *N. pnevi* co-occur in sections in Nevada, Wardlaw (2004) correlated this higher West Texas fauna to the base of the Kungurian. On the basis of conodonts alone, the Artinskian Elm Creek Limestone, is probably late Wolfcampian in age, and the base of the Leonardian lies higher, probably near the base of the Clyde Formation.

SYSTEMATICS

Illustrated specimens are reposited in the collections of the Department of Geoscience, the University of Iowa, SUI.

Genus *Rabeignathus* Kozur 1978

Type species: *Gnathodus bucaramangus* Rabe, 1977.

Diagnosis: Carminiscaphate P1 element with dorsal end of carina expanded broadly, often with pustulose nodes on each side of the central axis of the carina. Asymmetrically flared basal cavity with nodose ornamentation on the oral surface arranged into discontinuous rows that run parallel to the carina on one or both sides. Dorsal carina extends beyond expanded basal cavity.

Remarks: Rabe (1977) erected the species *Gnathodus bucaramangus* to include cariminiscaphate P_1 elements that possess two primary features, the distinctive expanded carina that bears pustulose nodes adjacent to the carina, as well as large irregular nodes on both side of the upper surface of the basal cavity that are arranged in short rows. When Kozur (1978, p. 144) erected the genus *Rabeignathus*, with *G. bucaramangus* as the type species, he emphasized that the presence of thickened nodes on the oral surface of the basal cavity was the primary means by which it could be distinguished from *Sweetognathus* Clark and *Iranognathus* Kozur. Ritter (1986) amended the diagnosis of *Rabeignathus* and reported that the Type III carina (laterally expanded) and the presence of one or two knot-like parapets flanking the carina were the diagnostic features of the genus.

Subsequent workers have largely followed the less restrictive generic concept of Kozur, where *Rabeignathus* has been used to designate P_1 elements like those of *Sweetognathus* that possesses nodes on the upper surface of the basal cavity. The species from the Southeast Pamir assigned to *Rabeignathus* by Riemers (1991; *R. pamiricus*) and Riemers (1999; *R. mononodosus* and *R. binodosus*) possess a variable number of simple nodes on the oral surface of a biconvex basal cavity, but lack a clearly expanded dorsal carina. Specimens assigned to *R. bucaramangus* by Riemers (1999) have a weakly expanded dorsal carina, but the multiple nodes on the upper surface of the basal cavity are not arranged into rows.

Mei et al. (1999; 2002) recommended that *Rabeignathus* be considered as a junior synonym of *Sweetognathus* because they believed that the presence of accessory nodes was a variable character and was not sufficient to justify a separate genus. Their diagnosis of *S. bucaramangus* (Mei et al., 2002, p. 83) includes only the presence of accessory pustulose nodes as the diagnostic feature of the species. The specimen they illustrated from China has a slightly expanded dorsal carina and a few nodes (5) on the upper surface of a biconvex basal cavity. Ueno et al. (2002) followed this recommendation and noted further that specimens from the Baoshan Block, West Yunnan, China, that they assigned to *S. bucaramangus*, were characterized by a narrower dorsal carina and possess relatively few nodes on the upper surface of the basal cavity. Wang et al. (2004) named two new species assigned to *Rabeignathus*, *R. ritterianus* and *R. yunnanensi*, also from the Baoshan Block. The former species possesses irregular nodes across the surface of the basal cavity and the latter species possesses nodes in a linear pattern parallel to the carina like *R. bucaramangus*. However, both species appear to lack the well-expanded dorsal carina characteristic of typical *R. bucaramangus*.

Ji et al. (2004) illustrated additional forms assigned to *Rabiegnathus* from the Baoshan Block, West Yunnan. These authors reported a discussion with H. Kozur, who indicated that *Rabeignathus* should comprise forms with nodes on both the cup and on the carina, as opposed to *Sweetognathus*, which should comprise forms without nodes on the cup but with nodes on the carina. The authors endorsed this distinction, but the specimens illustrated as *R. bucaramangus* possess only a slightly expanded dorsal carina and the nodes on the oral surface of the basal cavity tend to fuse into a row on each side that flare strongly away from the carina toward the dorsal end. Ji et al. (2004) also assigned *S. fengshanensis* Mei and Wardlaw 1998 (in Mei et al., 1998) to *Rabeignathus* because this species has accessory nodes on the oral surface of the basal cavity. Other workers appear to have based their assignment of specimens to *Rabeignathus* primarily on the presence of accessory nodes on the upper surface of the basal cavity (e.g., Ji et al., 2006; Leven et al., 2007).

We choose to restrict the definition of *Rabeignathus* to essentially the original characters proposed by Rabe (1977) and discussed by Ritter (1986). The two most important criteria are the broadly expanded dorsal carina, which typically appears as two distinct pustulose nodes on either side of the thin medial line of the carina, and the clear arrangement of most pustulose nodes on the oral surface of the basal cavity into rows that parallel, or diverge slightly from, the carina in the dorsal direction. The overall shape of the basal cavity is expanded further laterally than in most species of *Sweetognathus*, with the expansion widest near the dorsal end on the rostral side and widest near the vental end on the caudal side. The entire area of the basal cavity that bears the rows of nodes is elevated well above the level of margins of the basal cavity, and sometimes a clearly defined rim is present. The relatively high dorsal margin of the carina extends beyond the dorsal end of the expanded basal cavity. These features can be seen clearly in the illustrations of Rabe (1977, pl. 4, figs. 1-6) and of Ritter (1986, pl. 1, figs. 14-17, 20 (only); pl. 2, figs. 15, 17).

We include only two species in *Rabeignathus, R. bucaramangus* (Rabe 1977) and *R. asymmetricus* Ritter 1986, which appear to be restricted in geography to North and South America. Other forms from Asia that have been assigned to *R. bucaramangus* and other species that have been placed in *Rabeignathus* we interpret to represent different taxa. Mei et al. (2002, p. 82) indicated that many characters associated with sweetognathid P1 elements, especially the presence of accessory lobes, may vary with stratigraphic cycles. We suggest that paleogeography may have also played a part, and that simple accessory nodes may have appeared in different arrangements at different times in different regions.

Only a few P_2, M, and S elements were recovered from samples that contain P_1 elements of *Rabeignathus*. Because P_1 elements of *Sweetognathus* sp. A also occur in the same samples, we cannot determine with certainly to which species they belong.

Rabeignathus bucaramangus (Rabe, 1977)
Fig. 4.15-4.18

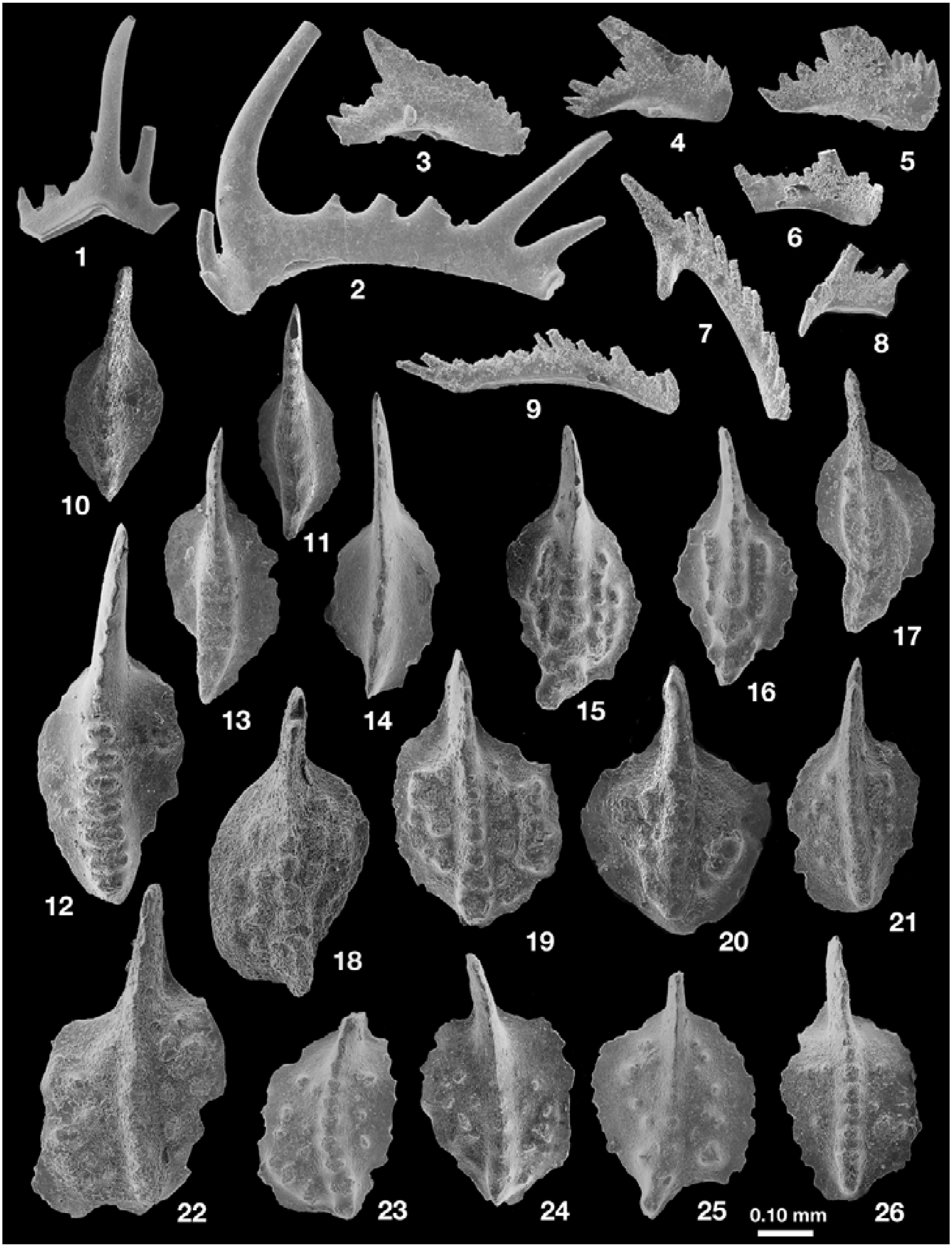
1977 *Gnathodus bucaramangus* n. sp. - Rabe, p. 219, pl. 4, fig. 1-6.
1979 New genus A - Clark et al., pl. 1, figs. 24-25.
1986 *Rabeignathus bucaramangus* (Rabe 1977) - Ritter, p. 148-149, pl. 1, figs. 14-17, 20 (only), pl. 2, fig. 15, 17.

Diagnosis: A species of *Rabeignathus* in which rows of pustulose nodes run parallel with the carina on both sides of the carina.

Remarks: Much of the description of Ritter (1986) fits the specimens that were obtained from the Elm Creek Limestone. Our specimens have a somewhat shorter blade relative to the length of the expanded basal cavity than the Utah specimens. Even relatively small specimens can be recognized because of the regular way in which the growth of the nodose rows occurs, with the nodes on the caudal side appearing before those on the rostral side. Because we have restricted the concept of *Rabeignathus* as discussed above, two specimens that Ritter considered as examples of *R. bucaramangus* (pl. 1, figs. 18, 19) are tentatively excluded from the species. These two specimens appear to lack the distinctive shape of the dorsal carina, the nodes are more randomly scattered over the oral surface of the basal cavity, and the basal cavity lacks the rostral-caudal asymmetry characteristic of *R. bucaramangus*. We include these specimens in our *Sweetognathus* sp. A.

Genus *Sweetognathus* Clark, 1972

Type species: *Spathognathodus whtiei* Rhodes, 1963.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0.10 mm
26

Remarks: Ritter (1986) and Mei et al. (2002) discussed the various aspects of *Sweetognathus*, but were not in agreement on which forms to include in the genus and how to distinguish species of the genus. Here we remove *Rabeignathus* from *Sweetognathus* as discussed under *Rabeignathus*. The problem of distinction of species of *Sweetognathus* is well presented in Mei et al. (2002), but we suspect that their use of broadly defined variable species will obscure the evolutionary history as well as ecological and paleogeographical information that may be included in the various morphotypes. Because at least some species of *Sweetognathus*, *S. whitei*, *S. windi* Ritter 1968, and *Sweetognathus* species A, possess different P_2 elements, features of the P_2 element may assist in species discrimination.

Sweetognathus whitei (Rhodes, 1963)
Fig. 4.3, 4.7, 4.12, 4.13

1963 *Spathognathodus whitei* n. sp. - Rhodes, p. 409, pl. 47, figs. 4, 9, 10, 25, 26.
1975 *Sweetognathus whitei* (Rhodes, 1963) - Behnken, 1975, p. 312, p. 1, fig. 26.
2002 *Sweetognathus whitei* (Rhodes, 1963) - Ueno et al., 2002, p. 747-748, figs. 4.14-4.16, 4.18.
2009 *Sweetognathus whitei* (Rhodes, 1963) - Boardman et al., 2009, p. 140, pl. 24, fig. 2; pl. 27, figs. 1-8, 10-12; pl. 28, fig. 10; pl. 30, fig. 6-9 (see for further synonymy).

Remarks: Ritter (1986) and other authors have attempted to distinguish several species of *Sweetognathus* based on characteristics of the carina, whereas Mei et al. (2002) and Ueno et al. (2002) combined many of these forms into one species. In our collections occur P_1 elements with a narrow biconvex basal cavity in which the denticles of the dorsal carina are expanded laterally into pustulose nodes. These specimens we assign to *S. whitei*. Associated with the *S. whitei* P_1 elements is a P_2 element that is identical to that illustrated in a reconstruction of *S. whitei* by Ritter (1986, pl. 3, fig. 8).

Sweetognathus inornatus Ritter, 1986
Fig. 4.10, 4.11, 4.14

1986 *Sweetognathus inornatus* n. sp. - Ritter, p. 150, pl. 3, figs. 1, 6, 7, 12-15; pl. 4, figs. 2, 9, 13, 14.

Remarks: Ritter (1986) erected the new species *S. inornatus* to comprise P_1 elements that possess well-defined pustulose carinal nodes that are not expanded laterally as in *S. whitei*. Both Mei at al. (2002) and Ueno et al. (2002) considered *S. inornatus* to be the “narrow morphotype” of *S. whitei*. In our collections occur several P_1 elements that possess the characteristics of *S. inornatus* and we use this name to designate them.

Sweetognathus species A
Fig. 4.4-4.6, 4.8, 4.9, 4.19, 4.20, 4.22-4.25

1986 *Rabeignathus bucaramangus* (Rabe 1977) - Ritter, pl. 1 figs. 18, 19 (only).

Diagnosis: A species of *Sweetognathus* in which the P_1 element has a flattened basal cavity, the upper surface of which is ornamented by randomly arranged pustulose nodes. The dorsal carina is expanded laterally as thickenings of the denticles, and may form a knot of nodes at its dorsal margin.

Description: The P_1 element has a broad, subcircular, flat basal cavity and a short free blade. The entire basal cavity region is flattened. The dorsal carina rises slightly above the upper surface of the basal cavity, the upper surface of which slopes smoothly to the outer margin. Nodes on the upper surface of the basal cavity appear in random order during ontogeny and typically lack any clear ordering into rows. The dorsal end of the carina terminates before the dorsal margin of the basal cavity and comprises thickened pustulose denticles. In the largest specimens, the dorsal end of the carina may expand into an irregular knot of pustulose nodes.

P_2 elements associated with the P_1 elements are similar to the P_2 elements of *Sweetognathus whitei*, but possess a much shorter and higher ventral process. The anterior process bears 4-5 partially fused compressed denticles, all of equal height. The short posterior process slopes downward aborally and bears 4-6 closely spaced biconvex denticles. M and S elements appear identical with those illustrated for other species of *Sweetognathus*.

Remarks: The nature of the dorsal carina, linear arrangement of the pustulose nodes on the upper surface of the basal cavity, and overall higher profile of the oral surface distinguish the P_1 elements of *Rabeignathus bucaramangus* that occur with those *Sweetognathus* species A in our samples. The distinction between the two different P_1 elements is apparent in moderately sized elements and larger forms. A few larger specimens that posses some indication of nodes forming rows are assigned to *S.* species A because they lack the characteristic dorsal carina of *Rabeignathus*. The P_2 and S elements attributed to *Sweetognathus* species A might comprise also part of the apparatus of *Rabeignathus*, but this cannot be determined from our limited collections.

Several names have been proposed for species of *Sweetognathus* that bear nodes on the oral surface of the basal cavity, most of which were originally assigned to *Rabeignathus*, as discussed under that genus. Because at least one of these names is likely to be appropriate for the species we describe here, we leave our form in open nomenclature.

Sweetognathus spp.
Fig. 4. 21, 4.26

Remarks: Many of our specimens of *Sweetognathus*-like P_1 elements are relatively small and difficult to assign to species with confidence. Among the larger of these small specimens two groups can be recognized. P_1 elements of the first group (nodose forms; Table 1; Fig. 4.21, 4.26) bear a few isolated nodes on the oral surface of a broad flattened basal cavity, but lack features that allow confident assignment to *Sweetognathus* species A. The second group comprises P_1 elements that have a flattened basal cavity but lack nodes (smooth forms; Table 1).

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FIGURE 4. Conodonts from the Elm Creek Limestone. Scale bar = 0.10 mm (X100). **SUI:** University of Iowa. **1-2**, *Ellisonia* sp.: **1**, S element, SUI 134513, EM; **2**, SUI 134514, B5-9t. **3**, **7**, **12**, **13**, *Sweetognathus whitei* (Rhodes, 1963): **3**, P_2 element SUI 134515, B5-11b; **7**, M element SUI 134516, B5-4t; **12**, P_1 element SUI 134517, B5-7; **13**, P_1 element SUI 134518, B5-8. **4-6**, **8**, **9**, **19**, **20**, **22-25**, *Sweetognathus* species A: **4**, P_2 element SUI 134519, B5-4b; **5**, P_2 element SUI 134520, B5-4t; **6**, S_2 element, SUI 134538, B5-4b; **8**, S_2 element SUI 134521, B5-4; **9**, S_1 element SUI 134522, B5-11b; **19**, P_1 element SUI 134523, B5-7; **20**, P_1 element SUI 134524, B5-4b; **22**, P_1 element SUI 134525, B5-4t; **23**, P_1 element SUI 134526, B5-3; **24**, P_1 element SUI 134527, B5-2; **25**, P_1 element SUI 134528, B5-3. **10**, **11**, **14**, *Sweetognathus inornatus* Ritter, 1986: **10**, P_1 element SUI 134529, B-4t; **11**, P_1 element SUI 134530, B5-11t; **14**, P_1 element SUI 134531, B5-4t. **15-18**, *Rabeignathus bucaramangus* (Rabe, 1977): **15**, P_1 element SUI 134532, B5-2; **16**, P_1 element SUI 134533, B5-3; **17**, P_1 element SUI 134534, B5-4; **18**, P_1 element SUI 134535, B5-7. **21**, **26**, *Sweetognathus* spp.: **21**, P_1 element SUI 134536, B5-7; **26**, P_1 element SUI 134537, B5-3.

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COPROLITE-RICH HORIZONS IN UPPER PENNSYLAVIAN MARINE STRATA IN LAURUSSIA

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Vertebrate coprolites are facies fossils and therefore are nonrandomly distributed in the rock record. In nonmarine environments, coprolites are often concentrated in laterally discontinuous rock bodies such as channels or pond deposits that sometimes have a restricted stratigraphic distribution (e.g., “ponds” in the Lower Permian El Cobre Canyon Formation of northern New Mexico: Hunt et al., 2005). Rarely, there are laterally extensive beds with vertebrate coprolites in nonmarine environments (e.g., uppermost Upper Triassic Chinle Group of northeastern Utah: Hunt et al., 1993).

Clearly, marine environments exhibit more laterally extensive facies. Marine bonebeds of nearshore origin are often of great lateral extent and an important source of coprolites (e.g., uppermost Triassic Rhaetic bonebed of England: Duffin, 1979). In the Pennsylvanian there are several records of narrow stratigraphic intervals in marine shales that occur over many square kilometers and yield hundreds or thousands of spiral coprolites and disseminated fish debris.

The Weber Formation of Colorado, USA, contains a 20-m-thick zone that yields abundant spiral coprolites over a wide area in Park and Chaffee Counties (Johnson, 1934). Johnson (1934) collected several thousand specimens. The lower Belden Formation in Bassam Park, Colorado, also contains a horizon with many spiral coprolites (Houck et al., 2004).

Price (1927) described a large sample of more than a thousand specimens of coprolites from the Morgantown area of West Virginia, USA. These coprolites occur in a narrow stratigraphic interval in the Conemaugh Group over an area of several square kilometers.

Coprolites are common in the upper Göttelborner Beds (Lower Ottweiler Group) of Saarbrücken, Saarland, Germany in a widespread horizon (Kneuper and Schönenberg, 1962).

Currently, these thin stratigraphic intervals characterized by an abundance of spiral coprolites over a large lateral extent appear to be particularly prevalent in, if not unique to, the Late Pennsylvanian of Laurussia.

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THE FOSSIL RECORD OF CARBONIFEROUS AND PERMIAN VERTEBRATE COPROLITES

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Abstract—The fossil record of vertebrate coprolites from the Carboniferous-Permian is potentially one of the largest and most important. These abundant traces pertain to an important period in vertebrate evolution (“Romer’s gap,” rise of the “reptiles,” origins of tetrapod herbivory) and provide information in a wide range of areas, from biogeography to biochronology to the paleobiology of the evolution of digestive systems. This paper provides an overview of the vertebrate coprolites record in the Carboniferous and Permian. The record of Mississippian vertebrate coprolites comes from Canada, the USA, the United Kingdom and China. Pennsylvanian coprolites are known from Canada, the USA, Belgium, the Czech Republic, Germany and the United Kingdom. A more global vertebrate coprolite record from the Permian includes records from the Gondwana continents. A similar pattern is seen in the bone record and this is due, at least in part, to the glaciations in Gondwana during parts of the Carboniferous, which restricted the distribution of vertebrates in the southern continents. Permian records of coprolites come from the USA, Czech Republic, France, Germany, Russia, the United Kingdom, South Africa, Namibia, Brazil and Antarctica. The Carboniferous record includes the first abundant samples of vertebrate coprolites.

INTRODUCTION

Coprolites are the least collected and least studied of all vertebrate fossils. The fossil record of coprolites from the Carboniferous-Permian is potentially one of the largest and most important. Buckland (1836, p. 199) visited a locality in the Pennsylvanian of Scotland where coprolite-bearing concretions were “strewed so thickly upon the shore, that a few minutes sufficed to collect more specimens than I could carry.” More recently, Price (1927) described an ichnofauna of over 1000 coprolites from the Pennsylvanian of West Virginia, Lohman and Sachs (2001) noted a sample of 800 coprolites from the Early Permian of Germany and Dentzien-Dias et al. (2012) a collection of 500 from the Middle-Upper Permian of Brazil. These abundant traces pertain to an important period in vertebrate evolution (“Romer’s gap,” rise of the “reptiles,” origins of tetrapod herbivory) and could provide important information in a wide range of areas from biogeography to biochronology to the paleobiology of the evolution of digestive systems. The purpose of this paper is to provide an overview of the vertebrate coprolites record in the Carboniferous and Permian (Figs. 1-2). Many references only mention coprolites in passing. Although the first publication of coprolites from this time period was 1709 (Mylius, 1709; Duffin, 2012) it is only in the past ten years that there have been many papers focused on detailed studies of Carboniferous-Permian coprolites. USNM refers to the National Museum of Natural History, Smithsonian Institution in Washington, DC.

MISSISSIPPIAN COPROLITES

North America

Canada

Nova Scotia: Mansky et al. (2012) described coprolites and cololites from the Early Mississippian (Tournaisian) Blue Beach and Hurd Creek members of the Horton Bluff Formation.

United States

Arkansas: Coprolites are common in the Fayetteville Shale of northern Arkansas and some form the cores of concretions (Zangerl et al., 1969).

Kentucky: The Hancock County tetrapod locality yields spiral coprolites (Garcia et al., 2006).

Michigan: Abandoned underground gypsum mines yield coprolites from the Michigan Formation in the western part of the state (Van Regenmorter, 2004; Noll et al., 2008).

Montana: The Bear Gulch Lagerstätte has yielded a small sample of coprolites (Zidek, 1980; Hunt et al., 2012c). These specimens derive from the Bear Gulch Limestone Member of the Tyler Formation, which is Chesterian in age, and include *Ostracobromus snowyensis* (coprolite or regurgitalite) and five morphotypes.

Oklahoma: Coprolites occur in the Fayetteville Shale in northeastern Oklahoma (Murthy et al., 2004).

Europe

United Kingdom

Scotland: Coprolites are known from a number of localities in Scotland (Sumner, 1993) and include ichnofaunas from the Early (Dinantian) and Middle (Viséan) Mississippian of the southeastern part of the country (Buckland, 1836; Pollard, 1985; Sumner, 1994).

England: Buckland (1835, p. 231, pl. 30, figs. 31-41) described and illustrated coprolites from Carboniferous Limestone Series (“Mountain Limestone”) from Clifton near Bristol.

Asia

China

The Benxi Formation in northern China yields small coprolites that could have been produced by fish (Gong et al., 2010).

PENNSYLVANIAN COPROLITES

North America

Canada

Coprolites are common in the fossil-bearing tree stumps of the Joggins Formation in Nova Scotia (e.g., Dawson, 1854, 1862).

United States

Colorado: The Weber Formation contains a 65-ft (20-m) thick zone that yields abundant spiral coprolites over a wide area in Park and Chaffee Counties (Johnson, 1934). The lower Belden Formation in Bassam Park also contains a horizon with many spiral coprolites, (Houck et al., 2004).

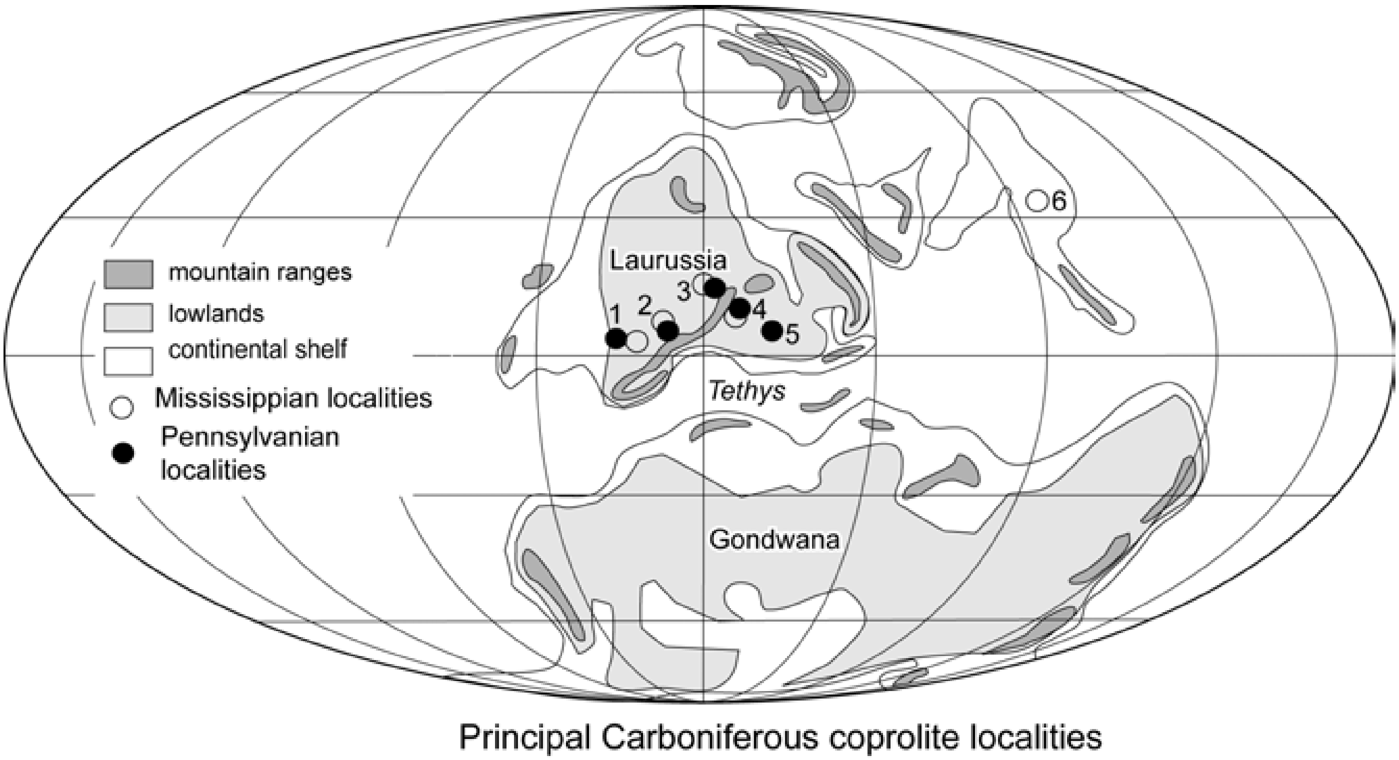

FIGURE 1. Distribution of significant Carboniferous localities of vertebrate coprolites. Localities are: **1**, Western USA; **2**, Central and eastern USA; **3**, Canada; **4**, Scotland and England; **5**, Western and central Europe; **6**, China. Base map from DiMichele et al. (1992).

Illinois: The Francis Creek Shale Member of the Carbondale Formation (Desmoinesian) yields the classic nodular Mazon Creek Lagerstätte. Vertebrate coprolites are present, but not extensively studied (Zangerl and Richardson, 1963; Richardson and Johnson, 1971; Baird et al., 1986; Shabica and Godfrey, 1997; LoBue, 2010).

Indiana: Zangerl and Richardson (1963) published a classic study of the paleoecology of the Middle Pennsylvanian (Desmoinesian) Mecca Quarry Shale Member and Logan Quarry Member of the Carbondale Formation in western Indiana, and described multiple coprolites and other bromalites.

Kansas: McAllister (1988) described Late Pennsylvanian coprolites and regurgitalites from Hamilton Quarry. Spiral coprolites are uncommon in this Lagerstätte. The USNM collection includes three uncatalogued coprolites on matrix from Upper Pennsylvanian strata on Little Mission Creek (Hunt et al., 2012a).

New Mexico: Konservat Lagerstatten of Late Pennsylvanian age in the central part of the state yield extensive coprofaunas from lagoonal and estuarine shales. The Tinajas Lagerstätte of late Missourian age includes *Conchobromus kinneyensis* (possibly a regurgitalite), *Crassocoprus mcallesteri*, *Spierocoprus socorroensis*, *Elongatocoprus amadoensis*, *Elacacoprus williamsi* and *Crustacoprus tinajaensis* (Lerner et al., 2009; Hunt et al., 2012f). The Kinney Brick Quarry Lagerstätte is of middle Missourian age and has produced more than 50 specimens of bromalites including *Conchobromus kinneyensis* (Hunt, 1992; Hunt et al., 2012e). Farther south in New Mexico, a Late Pennsylvanian coprofauna consisting of diverse spiral coprolites is present in marine offshore shale of the Beeman Formation of late Missourian age (Hunt et al., 2012d). The Beeman coprofauna includes *Liassocoprus hawkinsi*, *Heteropolacoprus texaniensis*, *Hyronocoprus amphipola*, *Kalocoprus oteroensis* and *Bibliocoprus beemanensis* (Hunt et al., 2012d).

Ohio: Burdsall and Zaleha (2011) reported spiral coprolites from an outcrop of the Pennsylvanian-Permian Dunkard Group, in the southeastern part of the state.

Texas: The Finis Shale is a unit of the Graham Formation of the Cisco Group of Upper Pennsylvanian (Virgilian) age. Hunt et al. (2013b) described vertebrae coprolites from a locality with diverse invertebrate fossils.

West Virginia: Price (1927) described a large sample of more than a thousand specimens of coprolites from the Morgantown area. These coprolites occur in a narrow stratigraphic interval in the Conemaugh Group (Formation) over an area of several square miles. These specimens include many coprolites assignable to *Hyronocoprus* (e.g., Price, 1927, pl. 11, fig. 18) and *Heteropolacoprus* (e.g., Price, 1927, pl. 12, fig. 12).

Europe

Belgium

The USNM collection includes four morphotypes from Maffle, Hainaut (Hunt et al., 2012a).

Czech Republic

Bayer (1934) described Pennsylvanian coprolites from the western part of the country.

Germany

Coprolites are common in the Göttelborner Beds at Saarbrücken in a widely dispersed horizon (Goldenberg, 1873, 1877; Guthörl, 1959; Kneuper and Schönenberg, 1962; Hunt et al., 2012b).

United Kingdom

England: Buckland (1836) first noted coprolites from the Pennsylvanian of England, from the Coal Measures of Newcastle-under-Lyme. The USNM collection includes three specimens from the “Soapstone bed” in the Lower Coal Measures at Burnley (Hunt et al., 2012a).

Scotland: Coprolites are locally common in the Pennsylvanian of Scotland (e. g., Buckland, 1836). The collections of the Natural History

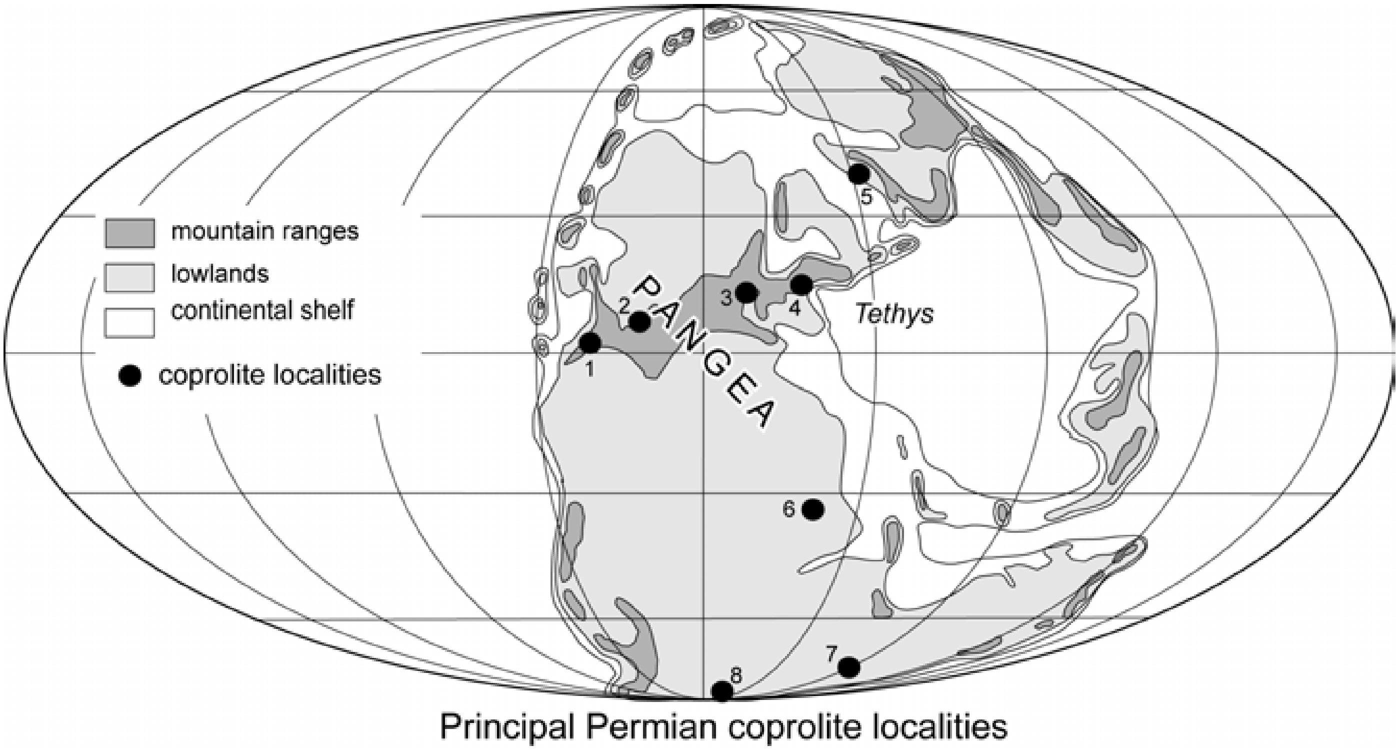

FIGURE 2. Distribution of significant Permian localities of vertebrate coprolites. Localities are: **1**, Western USA; **2**, Eastern USA; **3**, England; **4**, Western and central Europe; **5**, Russia; **6**, Brazil; **7**, South Africa and Namibia; **8**, Antarctica. Base map from DiMichele et al. (1992).

Museum in London include two coprolites from the "Coal Measures" and "Ironstone Formation" near Edinburgh and Glasgow (Hunt et al., 2012b).

PERMIAN COPROLITES

North America

United States

Kansas: Williams (1972) and McAllister (1985) described spiral coprolites from the Lower Permian Wymore Shale near Manhattan that we assign to *Heteropolacoprus*.

New Mexico: Vertebrate coprolites are locally common in the Permian portion of the Cutler Group in north-central New Mexico (Langston, 1953; Eberth and Miall, 1991). Hunt et al. (2005b, 2013a) described *Heteropolacopros texaniensis, Hyronocopros amphipola*, "*Megaheteropolacopros sidmcadamsi*" and unnamed morphotypes from the El Cobre Canyon Formation.

Cantrell et al. (2012) described a coprofauna from the Scholle Member of the Abo Formation in Socorro County, southern New Mexico. The assemblage includes *Dakyronocopros arroyoensis, Alococopros triassicus, Heteropolacopros texaniensis* and amorphous coprolites.

Oklahoma: The Early Permian redbeds of Oklahoma yield vertebrate coprolites from many localities (e.g., Olson, 1971, 1977). The USNM collection includes specimens of *Heteropolacoprus* sp., *Liassocoprus* sp., ?*Strophocoprus* sp. and aff. *Malericoprus* sp., and the NHMUK collection includes cf. *Saurocoprus* sp. (Hunt et al., 2012a, b).

Ohio: Spiral coprolites occur in a thin black shale in the middle Conemaugh Group in the southeastern part of the state (Krishnaswamy et al., 1994).

Texas: The Early Permian (Wolfcampian-Leonardian) sequence of nonmarine redbeds in northern Texas has yielded large samples of vertebrate coprolites (Neumayer, 1904; Olson, 1966; Olson and Mead, 1982; Sander, 1989; Hunt and Lucas, 2005a-b, Hunt et al., 2005a, 2012a). *Dakyronocoprus arroyoensis* occurs in the Nocona Formation (early Wolfcampian; Hunt and Lucas, 2005a), Arroyo Formation (Middle Leonardian: Hunt and Lucas, 2005a), and Archer City Formation (late Wolfcampian: Hunt and Lucas, 2005a). *Strophocoprus valensis* and "*Megaheteropolacopros sidmcadamsi*" are restricted to the Vale Formation (Middle Leonardian: Hunt and Lucas, 2005b; Hunt et al., 2005a; Hunt et al., 2013a).

Europe

Czech Republic

Coprolites occur in the Early Permian Rotliegend redbeds and Brandschiefer (e.g., Girard, 1843; Reuss, 1856; Geinitz, 1861; Hoffman, 1863; Makowsky, 1876; Fritsch, 1895, 1907; Augusta, 1936; Lemke and Weiler, 1942).

France

Coprolites occur in the Rotliegend including *Liassocoprus* (Gaudy, 1887, fig. 8). Hunt et al. (2012b) described *Malericoprus* sp. and *Heteropolacoprus* sp. from the Upper Permian "Magnesian Limestone" of Saône-et-Loire.

Germany

Coprolites are locally common in the Lower Permian Rotliegend (e.g., Troschel,1851; Geinitz, 1861; Ammon, 1889; Credner, 1890; Lohmann and Sachs, 2001; Eichler and Werneburg, 2010) and Upper Permian Kupferschiefer (e.g., Mylius, 1709; Germar, 1840; Geinitz, 1842; Hundt, 1910-1911; Wagenbreth, O., 1944; Schaumberg, 1977; Malzahn, 1984; Diedrich, 2009; Duffin, 2012).

Russia

Vertebrate coprolites are common in the Middle and Upper Permian of European Russia (Olson, 1966; Ochev, 1974; Orlov, 1992;

Silantiev, 1999; Silantiev et al., 2000a, 2000b; Fröbisch and Reisz, 2009; Owocki et al., 2012; Sennikov and Golubev, 2012). Specimens from the Upper Permian strata (Vyatkian Regional Stage) have been described in the most detail (Owocki et al., 2012; Sennikov and Golubev, 2012).

United Kingdom

Coprolites are common in the Upper Permian Marl Slate of northern England (Bell et al., 1979).

Africa

South Africa

Vertebrate coprolites occur rarely throughout the Upper Permian portion of the Beaufort Group rocks in the main Karoo Basin but they are relatively more common in mudrocks of the Middle Upper Permian *Tropidostoma* Assemblage Zone (Smith and Botha-Brink, 2011). Smith (1993; Smith and Botha-Brink, 2011) described coprolites, many bone-bearing, from a number of localities in the Hoedemaker Member of the Teekloof Formation that are from the therapsid-dominated *Tropidostoma* Assemblage Zone fauna.

Namibia

Abundant vertebrate coprolites occur in the lower Permian Gai-As Formation of the Huab basin. Coprolites are up 30 mm long and have inclusions of scales and teeth of paleoniscids (Warren et al., 2001). Coprolites also occur in the slightly older Tsarabis Formation in the Huab basin (Horsthemke et al., 1990).

South America

Brazil

Ruedemann (1929) described coprolites from the Early Permian portion of the Itataré Group. Spiral coprolites have been reported from the Guadalupian Corumbataí Formation in São Paulo state (Ragonha, 1987) and in the Kungurian Pedra de Fogo Formation of Piauí and Tocantins states (Schwanke and Souto, 2007; Alves, 2010). The largest sample (> 500) is from the Rio do Rasto Formation (Middle-Upper Permian) in southern Brazil and includes a specimen containing tape worm eggs (Dentzien-Dias et al., 2012, 2013).

Antarctica

Retallack and Krull (1999) described unusual putative coprolites from the Middle Permian Buckley Formation. These specimens have a variety of morphologies, including spiral, and are composed of sandstone. The only other described vertebrate coprolites composed of sandstone are from the Silurian of the British Isles (Gilmore, 1992).

BIOSTRATIGRAPHY AND BIOCHRONOLOGY

Coprolite ichnotaxa have utility in biostratigraphy and biochronology (e.g., Hunt et al., 1994, 2005a, 2007; Laojumpon et al., 2012). Currently, several Late Paleozoic coprolites appear to have potential in this regard:

1. *Dakyronocopros arroyoensis* has a broad distribution in the Early Permian of Texas and New Mexico, occurring from the Wolfcampian to the middle Leonardian (Hunt et al., 2005a; Cantrell et al., 2012).
2. "*Megaheteropolacopros sidmcadamsi*" occurs in the early Wolfcampian to the middle Leonardian of Texas and New Mexico (Hunt et al., 2013a).
3. *Hyronocopros amphipola* ranges from the Late Pennsylvanian to the Early Permian (Wolfcampian) in New Mexico and West Virginia (Hunt et al., 2005b, 2012d).
4. Several long-ranging ichnotaxa have their FAD (first appearance datum) in the Carboniferous and Permian: *Liassocoprus hawkinsi* and *Heteropolacoprus texaniensis* in the Late Pennsylvanian (Missourian), *Alococopros triassicus* in the Early Permian (Wolfcampian) and *Malericoprus* sp. in the ?Early Permian.

It is clear that vertebrate coprolites will demonstrate greater utility in biostratigraphy and biochronology as more Late Paleozoic coprofaunas are described in detail.

ICHNOFACIES

Recurrent patterns of coprolite associations allow for the recognition of ichnocoenoses (e.g., Hunt et al., 1994, 1998). The best sampled record of Late Paleozoic coprolites is in North America and three principal ichnocoenoses appear to be recognizable:

1. Shallow marine shale with localities/stratigraphic horizons that contain abundant (almost exclusively spiral) coprolites, with three dimensional preservation, that weather free from the matrix (e.g., Beeman Formation of New Mexico, Conemaugh Series of West Virginia, Weber Formation of Colorado).
2. Lagoonal/deltaic shale (often Lagerstätte) with often flattened coprolites that are principally collected by splitting shale and contain a minority of spiral coprolites (e.g., Tinajas, Kinney, Hamilton and Bear Gulch Lagerstätte).
3. Nonmarine redbeds that yield localized concentrations of coprolites, often in association with bones and from pond deposits or intraformational conglomerates, that include both spiral and non-spiral coprolites (e.g., Early Permian of New Mexico, Texas and Oklahoma).

DISCUSSION

Vertebrate coprolites of the Carboniferous and Permian are clearly both abundant and understudied. They have proven potential in a wide range of areas from biochronology (e. g., Hunt et al., 2005a) to interpreting prey ingestion (Smith and Botha-Brink, 2011). There is a need for more systematic descriptions of Late Paleozoic coprolites, and the good news is that the pace of study seems to have been increasing during the last five years (e.g., Smith and Botha-Brink, 2011; Dentzien-Dias et al., 2012; Cantrell et al., 2012; Hunt et al., 2012c-f; Owocki et al. 2012).

The Carboniferous record represents the first abundant samples of vertebrate coprolites (Turner, 1999). It is a strictly Laurussian record that later globalizes to include Gondwana in the Permian (Figs. 1-2). A similar pattern is seen in the bone record and this is due, at least in part, to the glaciations in Gondwana during parts of the Carboniferous, which restricted the distribution of vertebrates in the southern continents (Lucas, 2006, fig. 2).

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THE SIGNIFICANCE OF VERTEBRATE COPROLITES IN LATE PALEOZOIC (AND YOUNGER) LAGERSTÄTTEN

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Trace fossils in general, and coprolites in particular, have been understudied in Lagerstätten. Their presence, abundance and preservation can provide significant information of on the paleoecology of the ancient ecosystem and its taphonomy. Vertebrate coprolites are distinct from the majority of ichnofossils in that they are virtually always formed in a different location from where they are preserved.

Vertebrate coprolites first become common in the Mississippian, and they are important components of Carboniferous body-fossil Lagerstätten (McAllister, 1988; Hunt et al., 2012a-c). Exceptional trace fossil assemblages of Late Paleozoic age can be considered as Konzentrat Lagerstätten, such as the Lower Pennsylvanian Union Chapel site in Alabama (Hunt et al., 2005) and Early Permian Robledo Mountains tracksites in southern New Mexico (Lucas et al., 1998).

The majority of Paleozoic vertebrate coprolites pertain to fish. Carboniferous Lagerstätten display a range of preservation of coprolites versus fish specimens: (1) multiple articulated fish and abundant coprolites (e.g., Kinney Brick Quarry Lagerstätte: Lucas et al., 2011); (2) multiple articulated fish and few coprolites (e.g., Bear Gulch Lagerstätte: Hunt et al., 2012a); and (3) abundant coprolites, but only fragmentary fish specimens (e.g., Tinajas Lagerstätte: Lerner at et al., 2009).

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LATE PENNSYLVANIAN COPROFAUNA FROM THE FINIS SHALE OF NORTH-CENTRAL TEXAS

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INTRODUCTION

During the past 20 years several Pennyslvanian coprofaunas have been described from New Mexico (e.g., Hunt, 1992; Lerner et al., 2009; Hunt et al., 2012a-c) and Kansas (e.g., McAllister, 1978; Hunt et al., 2012d). However, no coprolites of this age have previously been described from Texas. The purpose of this paper is to give a preliminary description of a small sample of vertebrate coprolites from the Finis Shale of north-central Texas. These coprolites are not only the first Pennsylvanian coprolites to be described from Texas, but also represent the first occurrence of vertebrate coprolites of this age in association with a diverse marine invertebrate fauna.

PROVENANCE

The Finis Shale is a unit within the Graham Formation of the Cisco Group, is of Upper Pennsylvanian (Virgilian) age and crops out in north-central Texas near the Oklahoma border (Barnes, 1987). The Finis Shale is principally marine in origin with a basal nonmarine unit and has yielded a diverse marine invertebrate fauna particularly notable for its ammonoids (e.g., Miller and Downs, 1950; Lobza et al., 1994). NMMNH locality 8588 in the Finis Shale has yielded a diverse marine invertebrate fauna including horn corals, gastropods, fenestrate bryozoans, conulariids, crinoids and brachiopods. The coprolites from this locality were collected by one of us (KD) in close association with numerous marine invertebrate fossils

COPROLITES

The coprolites are generally sub-cylindrical in shape and range in length from about 20 mm to 40 mm. The surface texture is not finely preserved and all the specimens appear to be slightly abraded or weathered and several preserve small grooves on their surface. They represent six morphotypes and one already named ichnotaxon.

Morphotype A

Morphology: Elongate ovoid.

Referred specimens: NMMNH P-66982 (Fig. 1A-D); NMMNH P-66983; NMMNH P-66984 (Fig. 1I-L); NMMNH P-66990 (Fig. 1AA-BB).

Description: These coprolites are longer than wide, with rounded ends and they are not spiral. They are laterally flattened with ovoid to sub-circular cross sections. All the specimens display small grooves on their surfaces, which are principally located on one side of the coprolite, and also exhibit some type of patterning (e.g., parallel grooves) perpendicular to their long axis. No obvious inclusions are present.

NMMNH P-66982 (Fig. 1A-D) is the most elongate of the specimens, with a maximum length of 28.2 mm and a maximum width of 13.2 mm. It is asymmetrical in lateral view and is slightly anisopolar (*sensu* Thulborn, 1991). NMMNH P-66983 (Fig. 1E-H) is relatively broader in lateral view, with a length of 28.9 mm and a maximum width of 17.7 mm. NMMNH P-66984 (Fig. 1I-L) and NMMNH P-66990 (Fig. 1AA-BB) are more parallel-sided in lateral view, with broadly rounded ends. NMMNH P-66984 (Fig. 1I-L) has a length of 26.3 mm and a maximum width of 14.8 mm, whereas NMMNH P-66990 (Fig. 1AA-BB) has a length of 26.4 mm and maximum width of 13.0 mm.

Discussion: This is the most common coprolite morphotype in the sample.

Morphotype B

Morphology: Flattened cylinders.

Referred specimens: NMMNH P-66985; NMMNH P-66986 (Fig. 1M-P); NMMNH P-66987 (Fig. 1Q-T).

Description: Three specimens represent elongate, un-spiraled cylinders that are laterally flattened (ovoid) in cross section. All exhibit a maximum length that is at least three times the maximum width, and rounded (most common) to sub-pointed ends. They display the same patterning of small grooves as in morphotype A.

NMMNH P-66985 is a broken specimen with a maximum preserved length of 17.6 mm and a maximum width of 10.2 mm. NMMNH P-66986 (Fig. 1M-P) is the only complete specimen, and it is 36.8 mm long with a maximum width of 13.4 mm. It is slightly curved in lateral view. NMMNH P-66987 (Fig. 1Q-T) is broken at one end and has a maximum preserved length of 27.4 mm and a maximum width of 11.5 mm.

Discussion: This is the second most common coprolite in the collection after morphotype A. Thus, the majority of the Finis coprolite specimens are not spiral.

Morphotype C

Morphology: Spindle shaped.

Referred specimen: NMMNH P-66996 (Fig. 1U-X).

Description: A single isopolar coprolite is sub-ellipsoidal in lateral view, with acute tips. The exterior surface is featureless and does not exhibit the grooves seen in morphotypes A and B. NMMNH P-66996 (Fig. 1U-X) is one of the smaller coprolites in the collection, with a length of 19.3 mm and a maximum width of 6.4 mm.

Discussion: This is a very distinctive morphology that has not been identified in other Pennsylvanian coprolite ichnofaunas.

Morphotype D

Morphology: Tapering cylinder.

Referred specimen: NMMNH P-66989 (Fig. 1Y-Z).

Description: NMMNH P-66989 (Fig. 1Y-Z) is an anisopolar coprolite with an anterior end that is acute and a posterior end that is broadly rounded. The coprolite is 39.4 mm long, with a maximum width of 13.7 mm. This specimen exhibits the groove ornamentation seen in morphotypes A and B. No primary spiraling is present.

Discussion: Several of the morphotypes have very similar surface grooves, which suggests that they are taphonomic features. This specimen superficially resembles *Elacacoprus williamsi* from the Late Pennsylvanian Tinajas Lagerstatte in New Mexico (Hunt et al., 2012d, fig. 6A-B)

Morphotype E

Morphology: Weakly heteropolar.

Referred specimen: NMMNH P-66991 (Fig. 1CC-DD).

Description: NMMNH P-66991 (Fig. 1CC-DD) is ovoid in lateral view, with a slight indication of a spiral at the acute posterior end.

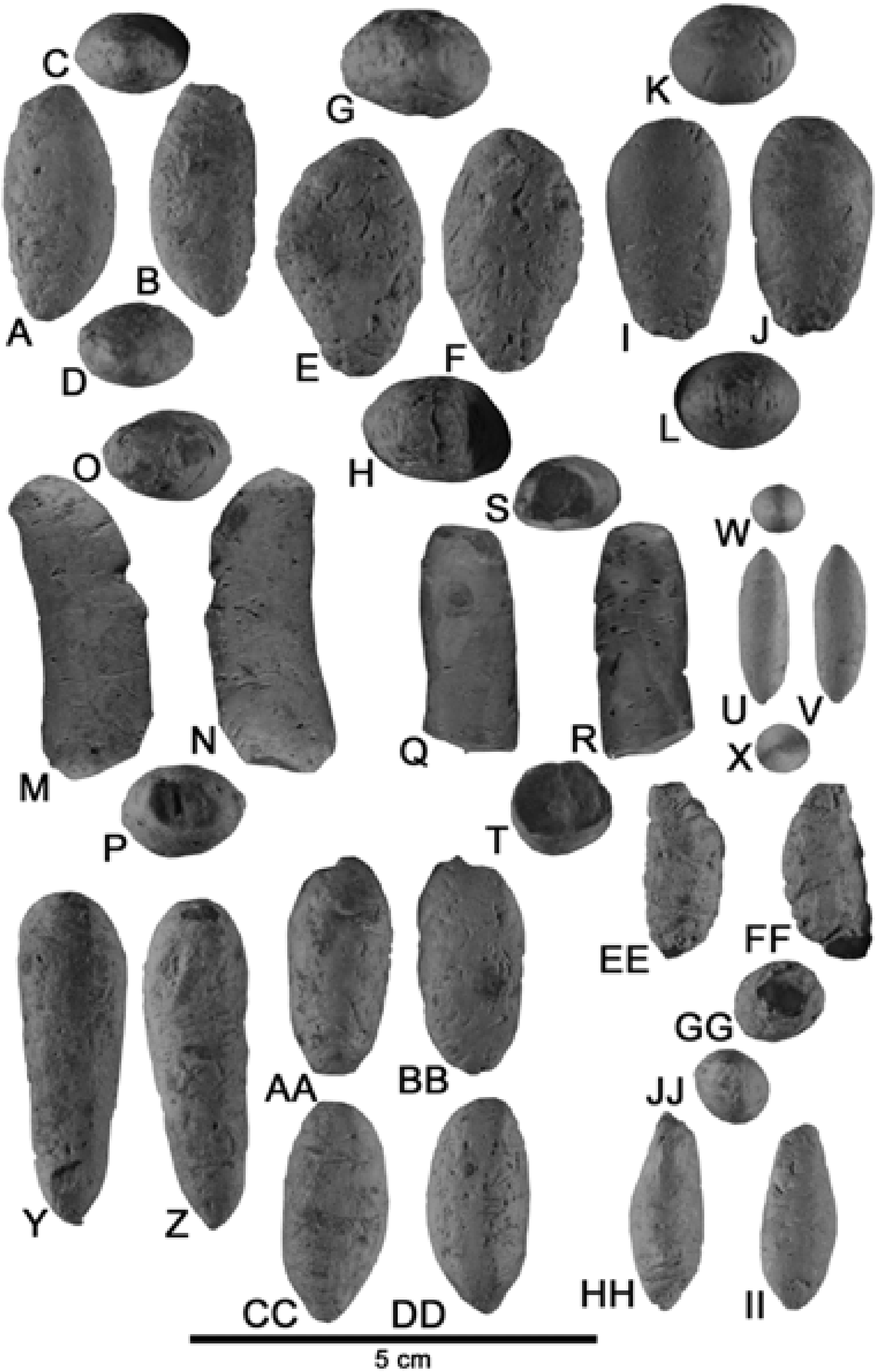

FIGURE 1. Finis Shale coprolites. **A-L**, **AA-BB**, Morphotype A - elongate ovoid coprolites in **A-B**, **E-F**, **I-J**, **AA-BB**, lateral and **C-D**, **G-H**, **K-L**, polar views. **A-D**, NMMNH P-66982. **E-H**, NMMNH P-66983. **I-L**, NMMNH P-66984. **AA-BB**, NMMNH P-66990. **M-T**, Morphotype B - flattened cylinders in **M-N**, **Q-R**, lateral, **O-P**, **S**, polar and **T**, cross-sectional views. **M-P**, NMMNH P-66986. **Q-T**, NMMNH P-66987. **U-X**, NMMNH P-66996, Morphotype C – spindle shaped in **U-V**, lateral and **W-X**, polar views. **Y-Z**, NMMNH P-66989, Morphotype D – tapering cylinder in lateral views. **CC-DD**, Morphotype E – weakly heteropolar coprolite. **CC-DD**, NMMNH P-66991 in lateral view. **EE-GG**, NMMNH P-66993, Morphotype F - coiled coprolite in **EE-FF**, lateral and **GG**, polar views. **HH-JJ**, NMMNH P-66994, *Heteropolacoprus texaniensis* in **HH-II**, lateral and **JJ**, polar views.

The coprolite is 26.2 mm long with a maximum width of 12.5 mm.

Discussion: If the specimen is indeed spiral, it represents an unusual morphotype of heteropolar coprolite in that the posterior spire is very short with a consequently elongate coil 1 (*sensu* Hunt and Lucas, 2012).

Morphotype F

Morphology: Coiled.

Referred specimen: NMMNH P-66993 (Fig. 1EE-GG).

Description: NMMNH P-66993 (Fig. 1EE-GG) is an enigmatic coprolite that is 21.7 mm long and 9.9 mm in maximum width. The coprolite exhibits coiled, and possibly spiral structure. This coprolite possesses the small grooves seen in morphotypes A, B and D, most prominently on one side. The pattern of grooves somewhat overprints the coiling/spiral structure.

Discussion: The preservation of the surface detail of this coprolite hinders its interpretation.

Heteropolacoprus texaniensis Hunt et al., 1998

Referred specimen: NMMNH P-66994 (Fig. 1HH-JJ).

Description: NMMNH P-66994 (Fig. 1HH-JJ) is a microspiral heteropolar coprolite with a sub-rounded cross section. The coprolite has a length of 23 mm and a maximum width of 9.6 mm. Some small grooves are on the coprolite and overlie the spirals.

Discussion: This microspiral heteropolar coprolite is very similar in morphology to specimens of *Heteropolacoprus texaniensis* (e.g., Hunt et al., 1998, fig. 2C-L) and is clearly assignable to that ichnospecies.

PENNSYLVANIAN COPROFAUNAS

There appear to be two broad ichnocoenoses of vertebrate coprolites in the marine/marginal marine Pennsylvanian of North America:

1. Lagoonal/deltaic shales (often Lagerstätte) that contain dominantly non-spiral coprolites that are often flattened and are generally collected by splitting matrix (e. g., Kinney, Tinajas and Hamilton Lagerstätten: McAllister, 1988; Hunt et al., 2012c-d).
2. Shallow marine shales with three dimensional coprolites (often in the absence of any other fossils), which are dominantly spiral and usually weather out of the outcrop (e.g., Beeman, Conemaugh: Price, 1927; Hunt et al., 2012b).

The Finis Shale coprofauna is similar to the second ichnocoenose in that the coprolites are three dimensional and that they weather free from matrix, but it differs in the small proportion of spiral forms. However, this coprofauna is similar to the first ichnocoenose in the high percentage of non-spiral forms. The Finis coprolites differ from both ichnoenoses in being associated with a diverse invertebrate fauna.

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THE CARBONIFEROUS-PERMIAN FLORAL TRANSITION IN THE PARANÁ BASIN

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Abstract—This contribution provides an overview of the Carboniferous-Permian megafloral transition in the Paraná Basin. Based on analysis of previous data from floral and palynofloral successions, associated with climate and paleoenvironmental changes, seven floral events are recognized and named, in ascending order, F1 through F7. These events represent the appearances and disappearances and/or the diversification and dominance of different plant groups through the Pennsylvanian-Permian interval. The results indicate a direct correlation between floral changes and the transgression/regression events and associated climatic conditions. Apparently, the transition from Carboniferous to Permian in the Paraná Basin, from the point of view of paleobotany, was a long-term and complex process, which remains poorly understood, and involved a significant climate driver of the observed floral changes. Additionally, comparisons with global patterns are also tentatively established and reveal a coincident correspondence between basinal events and inferred periods of marked warming and sea-level rise during the Carboniferous-Permian interval.

INTRODUCTION

The transition from Carboniferous to Permian in Gondwanan terrestrial sequences is historically marked by the appearance of the first glossopterids (Iannuzzi and Souza, 2005). Even the recent dating obtained in western Gondwanan deposits (Gulbranson et al., 2010; Césari et al., 2011) does not contradict this paradigm. In terms of palynofloras, this transition is characterized by the appearance of *Vittatina* and alien bissacate grains (Stephenson, 2008). Traditionally, these were the same fossil guides used to define the Carboniferous-Permian boundary in deposits of the Paraná Basin, southern Brazil (Rösler, 1978; Souza, 2006). However, it has been long appreciated that floral markers in terrestrial associations, capable of precisely constraining temporal intervals, especially Period boundaries, do not exist. In fact, these boundaries exist as undefined horizons within transitional intervals in which some existing forms become extinct while new ones arise successively. This pattern has been relatively well demonstrated through the late Paleozoic terrestrial sequences of Europe and North America. In Gondwanan terrains the transitional intervals still need to be established firmly. Over time, various researchers have proposed that glossopterids must have evolved within the Carboniferous. However, the occurrence of glossopterids in deposits of Late Carboniferous age has not been confirmed (Césari et al., 2011). If such a discover were to be made, it could provide for biostratigraphers the Holy Grail for Gondwanan continents.

In this context, this contribution does not propose to solve this longstanding biostratigraphic problem by establishing the precision of stratigraphic ranges of one or more fossil-guides across the Permo-Carboniferous boundary in Gondwanan basins. Rather, the main goal of this paper is to illustrate that the Permo-Carboniferous transition in the Paraná Basin, from the point of view of paleobotany, was a long-term and complex process, which remains poorly understood, and involved significant climatic change as the driver of the observed floral changes. Moreover, comparison with global patterns is tentatively established.

GEOLOGICAL SETTING

The Paraná Basin is a huge intracratonic basin that developed on the South American platform, and that spans an area of 1,700,000 km^2 in Brazil, Uruguay, Argentina and Paraguay. The basin is filled by tectonically and eustatically driven sedimentary packages that reach a thicknesses of ca. 5000 meters. Milani et al. (1994, 1998) proposed six second-order depositional sequences within the basin fill, ranging in age from Late Ordovician to Late Cretaceous. This paper focuses on the third sequence of Milani et al. (1994), e.g., the Gondwana I Supersequence, ranging from the Late Carboniferous to the Late Permian.

The Gondwana I Supersequence can be divided lithostratigraphycally into two main units, the Tubarão Supergroup and the Passa Dois Group (Fig. 1). The Tubarão Supergroup comprises the Itararé Group (Lago Azul, Campo Mourão and Taciba formations), overlain by the Rio Bonito and Palermo formations (Guatá Subgroup). These last units are correlated with the Tatuí Formation in the northeastern region of the basin. The Passa Dois Group comprises the Irati, Serra Alta, Teresina and Rio do Rasto formations, in ascending order.

The Itararé Group contains continental and glacio-marine deposits interbedded with marine, fluvio-deltaic and lacustrine/lagoonal deposits, representing glacial sedimentation as well as sediments that accumulated during the subsequent deglaciation phases. The Rio Bonito Formation consists of fluvio-deltaic, floodplain and barrier-lagoonal facies containing carbonaceous shales and shoreline and supratidal facies. The Palermo Formation is composed of inter- and supratidal facies, perhaps related to development of a restricted epicontinental sea. The depositional system of the Irati Formation included internal, intermediate, and distal ramps, consisting of facies related to a gulf and/or an epicontinental sea with restricted marine conditions. The overlying Serra Alta Formation is interpreted to have formed in a relatively deep marine environment. The Teresina Formation is characterized by platformal, tidal, lagoonal and intertidal deposits. The youngest unit, the Rio do Rasto Formation, includes lacustrine, fluvial and eolian deposits. A summary of this lithostratigraphic subdivision and its geological significance is given by Milani and Zalán (1999) and Holz et al. (2010).

Transgressive-Regressive Cycles

The Gondwana I Supersequence corresponds to a major transgressive-regressive cycle (Fig. 1). The Itararé Group comprises at least three transgressive-regressive cycles, interpreted to record three long-term intervals of glaciation and deglaciation. The lower-middle Rio Bonito Formation corresponds to a minor transgressive system. The upper Rio Bonito-Palermo, Irati and Serra Alta formations record the maximum extent of marine flooding in the basin, defining three transgressive/regressive cycles. The Teresina and Rio do Rasto units record a major regressive system (Holz et al., 2010). Based on these cycles, six transgressive events can be recognized throughout the Late Carboniferous-Permian interval in the Gondwana I Supersequence, which are successively named here, from the oldest “T1” to the youngest “T6” (Fig. 1). Each transgressive event corresponds to a major flooding episode that extended across

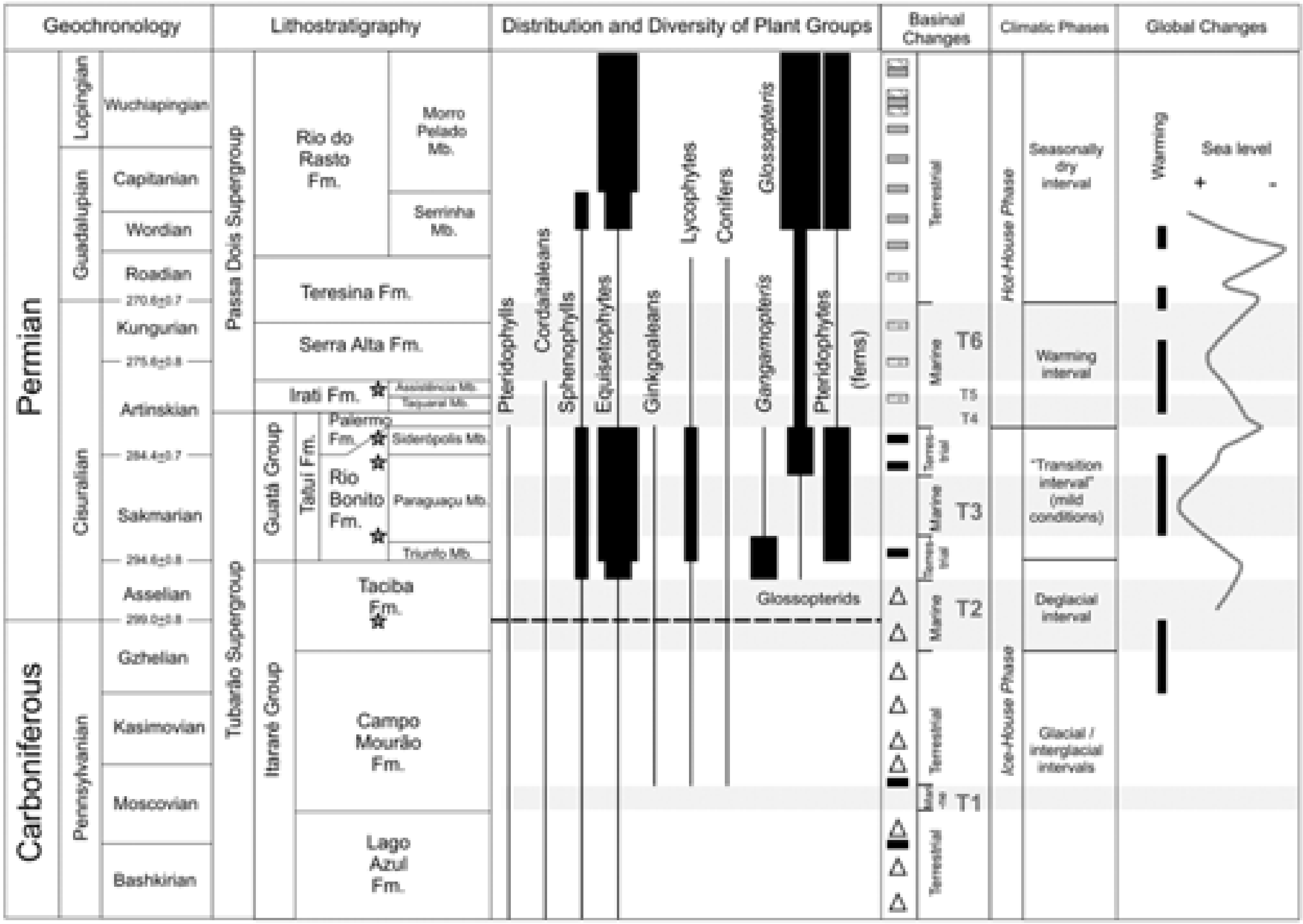

FIGURE 1. Stratigraphy and geochronology of Paraná Basin for Carboniferous–Permian interval showing: i, distribution and diversity variation of main plant groups; ii, basinal changes; iii, climatic phases; and iv, global changes in terms of warming and eustatic events, conforming to Montañez et al. (2007). **Legend:** stars, radiometric dating (see text); thick dashed line, Carboniferous-Permian boundary; triangles, glacial deposits; black rectangles, coal-beds; rectangles with bricks, carbonates; grey rectangles, red beds; rectangles with diagonal lines, eolian deposits; T1 to T6, transgressions (see text).

the basin. Because of this, they have traditionally been interpreted by most researchers as being tectonically controlled (Milani et al., 1994, 1998; Milani and Zalán, 1999). However, in this paper we will try to relate them to the global eustatic curve, attributing the cause of sea-level change to major glacial-deglaciation episodes (Fig. 1). In order to establish a correlation between the six transgressive events and the lithostratigraphy of the basin, each flooding event will receive a denomination according to the unit to which it corresponds along the depositional sequence of the basin (see Holz et al., 2010), namely: T1 – Roncador Transgression; T2 – Lontras Transgression; T3 – Paraguaçú Transgression; T4 – Palermo Transgression; T5 – Irati Transgression; T6 – Serra Alta Transgression.

Paleoclimatic Indicators

A general overview of the distribution of climatically sensitive rock types throughout the latest Carboniferous-Permian interval of the Paraná Basin is useful to understand the tremendous climatic changes that occurred in this area of the continent. Tillites, striated pavements and dropstones are restricted to the Itararé Group strata. Coals are distributed in the Itararé Group through Rio Bonito Formation. Carbonates and evaporites become abundant in the Irati and the Teresina formations. Red beds and eolian deposits are known only from the Rio do Rasto Formation. This latest Carboniferous through Permian succession records a climatic evolution from cool to warm conditions, especially during the Permian (Fig. 1). In a broad sense, one could say that the climate evolved from an Ice-House Phase to a Hot-House Phase, following the global tendency assigned to this interval (Montañez et al., 2007). However, a Transitional Interval could be admitted during the depositional time of the upper Itararé Group (= Taciba Formation) and Rio Bonito Formation, when mild (= temperate) climatic conditions prevailed (Fig. 1). Significant flooding events recording the deglaciation phases occur in the middle-to-upper Taciba Formation (Lontras Shale, Rio do Sul Formation and Budó Facies), registering the last direct evidence of glacial sedimentation (see Holz et al., 2010). Indirect evidence of glacial influence is the presence of marine faunas indicative of cold waters within the Paraguaçú Member (=T3 Paraguaçú Transgression), lower-middle Rio Bonito Formation (R.G. Netto, pers. comm.).

Geochronology

Few horizons have been dated through the radiometric analysis using the volcanic zircons obtained from tonsteins found in the Itararé Group and Rio Bonito and Irati formations. The preliminary results presented by Rocha-Campos et al. (2006) were controversial. Initially, they furnished a Late Carboniferous age of 323.6±15 Ma (using the timescale of Gradstein et al., 2004) for the "Passinho Shale," situated in the uppermost Itararé Group (equivalent to the upper Taciba Formation and Budó Facies). Nonetheless, in a recent publication (Rocha-Campos et al., 2007), these same authors re-interpreted this age, suggesting that this horizon should be considered as earliest Permian in age, Asselian-earliest Sakmarian. The later age is accepted here bearing in mind the biostratigraphic framework previously established for this interval (Fig. 1).

Absolute ages have been obtained from several tonsteins within the coal seams of the middle to upper Rio Bonito Formation in the Rio Grande do Sul State. Matos et al. (2000, 2001) obtained the first date of 267.1±3.4 Ma (U/Pb) from a tonstein in the lower coal seam in the Candiota Coalfield, situated approximately in the middle Rio Bonito (Iannuzzi, 2010). However, this coal seam and the upper coal seam in the Candiota Coalfield were subsequently re-dated by Guerra-Sommer et al. (2008a), yielding ages for the four analyzed tonsteins (Lower Candiota 1 and 2, Upper Candiota 1 and 2) of between 288.4±2.6 to 293±3.5 Ma. These latter ages (Guerra-Sommer et al., 2008a) are considered the only valid ones, suggesting an age for this interval between earliest to latest Sakmarian (Gradstein et al.'s time-scale, 2004).

Guerra-Sommer et al. (2008a, b) also furnished new U-Pb zircon ages of 285.4±8.6 Ma and 288.76±1.4 Ma from a tonstein interbedded with coal seams at the Faxinal Coalfield, middle to upper Rio Bonito Formation in Rio Grande do Sul. These dates correspond to the earliest mid to late Sakmarian interval. As a conclusion, Guerra-Sommer et al. (2008a) established a mean average age of 290.6±1.5 Ma for tonsteins of both the Candiota and Faxinal Coalfields, indicating a middle Sakmarian age for these coals.

Tuff beds in the upper Irati Formation analyzed by SHRIMP zircon dating yield ages of 278.4±2.2 Ma (Santos et al., 2006) and 278±2.2 Ma (Rocha-Campos et al., 2007). These dates are indicative of a late Artinskian age for this unit (Gradstein et al., 2004).

FLORAL SETTING

The stratigraphic distribution of plant groups from the Late Carboniferous-Permian interval in the Paraná Basin was first focused on by Adami-Rodrigues and Iannuzzi (2001). An updated overview of this distribution is shown in Figure 1.

Pteridophylls, cordaitaleans, sphenophylls and equisetophytes are the oldest groups represented in the Late Carboniferous strata (Fig. 1). Their first appearance is in the lowermost Itararé Group. All of them span from the Late Carboniferous Itararé Group (Rösler, 1978; Iannuzzi and Souza, 2005; Mune and Bernardes-de-Oliveira, 2007) through the Permian units (Fig. 1), vanishing in different horizons through the Permian Period. Pteridophylls, mostly represented by the genus *Botrychiopsis*, is the first group to disappear, going extinct in the Early Permian, upper Rio Bonito Formation, late Sakmarian/early Artinskian interval (Fig. 1). Cordaitaleans disappear in the overlying upper Irati Formation (Assistencia Member), considered to be late Artinskian in age (Fig. 1). Sphenophylls and equisetophytes survived into the Late Permian, disappearing respectively at the top of the Serrinha (Wordian/early Capitanian) and Morro Pelado (late Capitanian/Wuchiapingian) members of the Rio do Rasto Formation (from Guadalupian to Lopingian – Fig. 1).

The ginkgoaleans, lycophytes and conifers are the next groups to arise in the Carboniferous (Fig. 1). They have been recovered from the middle Itararé Group. Similar to the aforementioned groups, they occur in the Late Carboniferous Itararé Group (Rösler, 1978; Iannuzzi and Souza, 2005; Iannuzzi, 2010) through Permian deposits (Fig. 1). Ginkgoaleans disappeared along with the pteridophylls in the Early Permian upper Rio Bonito Formation (Fig. 1). Lycophytes and conifers went extinct in the top of the Teresina Formation, during the beginning the late Permian, late Rodian (Fig. 1).

Lastly, glossopterids and ferns correspond to the only groups that arose exclusively within the Permian. Glossopterids appeared a little earlier in the uppermost portion of the Itararé Group, upper Taciba Formation, probably deposited during the late Asselian (Fig. 1). The first appearance of ferns occurs in the Triunfo Member of the lowermost Rio Bonito Formation, considered earliest Sakmarian in age (Fig. 1). Both groups diversified through the Permian, becoming extinct in the Rio do Rasto Formation at the close of this period (late Capitanian/Wuchiapingian interval) (Rösler, 1978; Rohn and Rösler, 2000; Iannuzzi, 2010).

During the Permian, sphenophylls, equisetophytes, glossopterids and ferns increased in diversity, exhibiting peaks in their species richness in two stratigraphic intervals: (1) uppermost Itararé-uppermost Rio Bonito (late Asselian/early Artinskian interval) and (2) middle Serrinha-uppermost Morro Pelado (Wordian/Wuchiapingian interval), within the Rio do Rasto Formation (Fig. 1).

Palynostratigraphy

Four zones characterize the palynological succession of the Late Carboniferous-Permian interval of the Paraná Basin, in ascending order: *Ahrensisporites cristatus*, *Crucisaccites monoletus*, *Vittatina costabilis* and *Lueckisporites virkkiae* Interval Zones (Souza and Marques-Toigo, 2003, 2005; Souza, 2006). The two former zones are assigned to the Carboniferous, while the two latter are considered as Permian in age (Fig. 2). Both Carboniferous zones, *Ahrensisporites cristatus* and *Crucisaccites monoletus*, are characterized by the dominance of spores and monosaccate pollen grains, differing only by the range of some spores that are restricted either to the underlying *Ahrensisporites cristatus* unit or by the appearance of a few new species of pollen grains, e.g., *Scheuringipollenites maximus* and *Crucisaccites monoletus* (Souza, 2006). The *Vittatina costabilis* Zone is marked by the first appearance of the genus *Vittatina* and some species of *Protohaploxypinus*, and *Illinites unicus*. Pollen grains, in general, are more abundant than spores, and the frequency of taeniate and polyplicate grains increases upward toward the top of the unit (Souza, 2006). The last zone, *Lueckisporites virkkiae*, is characterized mainly by the appearance of the genus *Lueckisporites* and species of *Staurosaccites*, and *Weylandites lucifer*. The taeniate and polyplicate pollen grains dominate this zone, making up to 80% of the associations, while the spores and monosaccates become rare (Souza and Marques-Toigo, 2001, 2003).

Plant Stratigraphy

The Late Carboniferous-Early Permian interval of the Paraná Basin was divided into four successive informal floras by Iannuzzi and Souza (2005), in ascending order: Pre-*Glossopteris* (Pre-Gl), *Phyllotheca-Gangamopteris* (Phy-Ga), *Glossopteris-Brasilodendron* (Glo-Br) and *Polysolenoxylon-Glossopteris* (Po-Glo) floras (Fig. 2). Also, in 2005, Bernardes-de-Oliveira et al. proposed a subdivision of the Late Carboniferous interval into four floral associations, from the oldest to the youngest: *Dwykea-Sublagenicula-Calamospora, Eusphenopteris-Nothorhacopteris-Botrychiopsis, Paranocladus-Ginkgophyllum-Brasilodendron* and *Dwykea* associations (Fig. 2). For the Late Permian (Gaudalupian-Lopingian), Rohn and Rösler (2000) defined three formal zones, in rising order: *Lycopodiopsis derbi*, *Sphenophyllum paranaensis* and *Schizoneura gondwanensis* Range Zones (Fig. 2).

The Late Carboniferous Pre-*Glossopteris* Flora is in general characterized by the total absence of glossopterid elements. In turn, the *Eusphenopteris-Nothorhacopteris-Botrychiopsis* Association is distingtuished by the presence of typical taxa found in the "*Nothorhacopteris-Botrychiopsis-Ginkgophyllum* (NBG) Zone" from the Carboniferous of Argentina (Bernardes-de-Oliveira et al., 2005). The overlying *Paranocladus-Ginkgophyllum-Brasilodendron* Association is marked by the first appearance of conifers, ginkgoaleans and lycophytes (Bernardes-de-Oliveira et al., 2005). The oldest and youngest associations of this interval, e.g., *Dwykea-Sublagenicula-Calamospora* and *Dwykea*, are similar floras that are facies-controlled and occur repeatedly through the Itarare Group (Bernardes-de-Oliveira et al., 2005). Consequently, the latter associations could be regarded as an ecofacies within the *Eusphenopteris-Nothorhacopteris-Botrychiopsis* and *Paranocladus-Ginkgophyllum-Brasilodendron* Associations. Because of this they will be discarded from the present analysis, as they cannot contribute to understanding the evolutionary steps of floral succession.

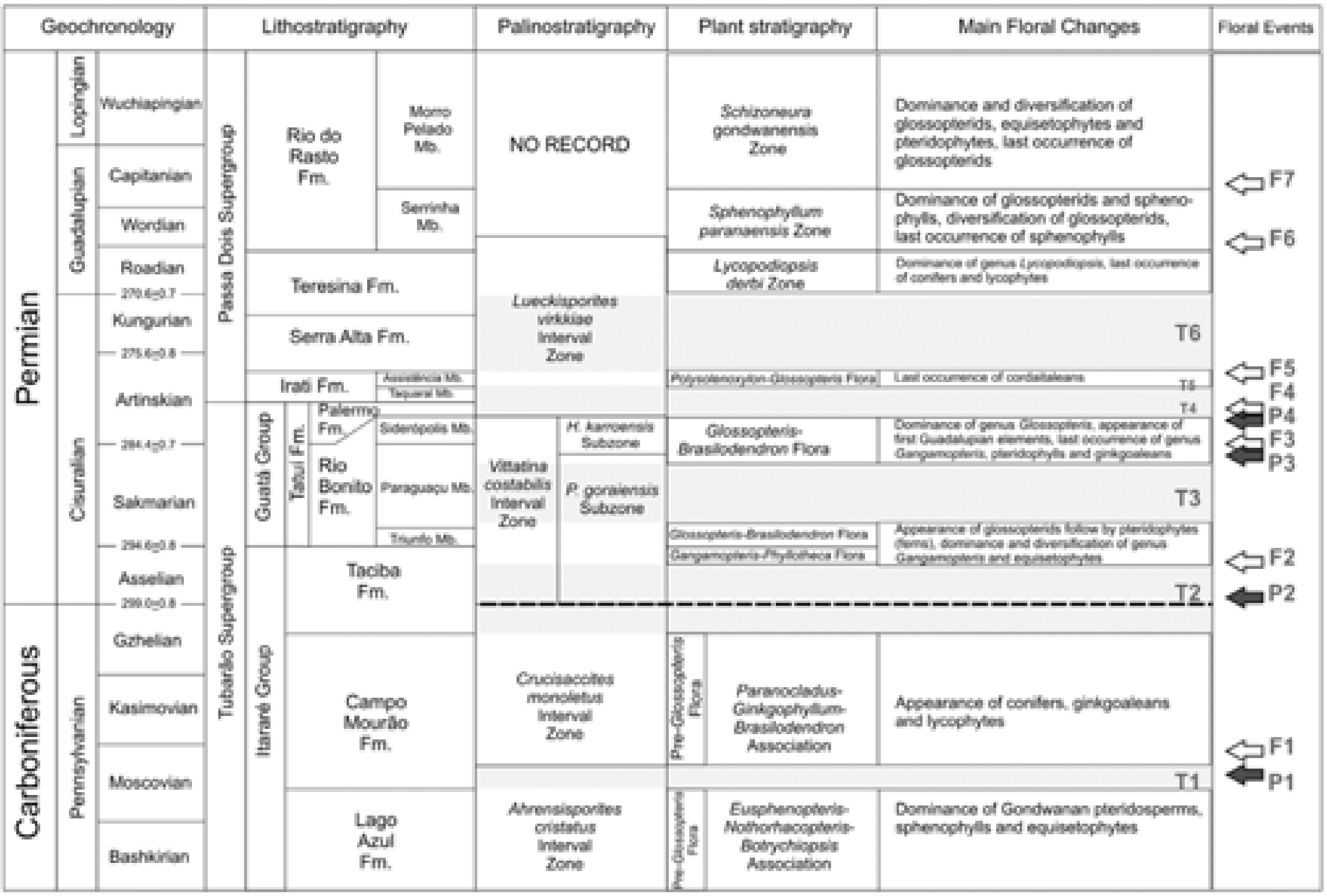

FIGURE 2. Stratigraphy and geochronology of Paraná Basin for Carboniferous–Permian interval showing: i, palynozones; ii, plant zones; and iii, main floral changes, which delineate seven floral (F1 to F7) and four microfloral (P1 to P4) events (see text). **Legend:** thick dashed line, Carboniferous-Permian boundary; T1 to T6, transgressions (see text).

The oldest Permian floral stage, the *Phyllotheca-Gangamopteris* Flora, is characterized by the first appearance of glossopterid elements and by the abundance of *Phyllotheca*-like equisetophytes (Iannuzzi and Souza, 2005). The genus *Gangamopteris* is dominant and diversified while the genus *Glossopteris* is generally rare and represented by few species in the leafy associations. The overlying *Glossopteris-Brasilodendron* Flora is identified by the first appearance of ferns and the reappearance of lycophytes that become locally abundant (Iannuzzi and Souza, 2005). *Glossopteris* is in general more abundant than *Gangamopteris*, and the frequency and diversity of this genus increases upwards to the top of the floral unit. Distinct from the underlying floras, the *Polysolenoxylon-Glossopteris* Flora is mainly composed of petrified wood rather than compressed-impressed material. Considering the difficulty in assigning a systematic affinity to this type of material, the taxa studied include elements with probable glossopterid, cordaitalean, and conifer alliances. This flora represents the last record of cordaitalean plants. The three Late Permian zones, *Lycopodiopsis derbi*, *Sphenophyllum paranaensis* and *Schizoneura gondwanensis*, are characterized by the range and abundance of their eponymous species, respectively (Rohn and Rösler, 2000). Furthermore, the *Lycopodiopsis derbi* Zone is marked by the last occurrence of lycophytes and conifers, while the two overlying zones, *Sphenophyllum paranaensis* and *Schizoneura gondwanensis*, are defined by the dominance and diversification of glossopterids and ferns. Finally, the sphenophylls disappear in the upper limit of the *Sphenophyllum paranaensis* Zone and equisetophytes diversify in the next zone, *Schizoneura gondwanensis* (Rohn and Rösler, 2000).

DISCUSSION AND CONCLUDING REMARKS

Analyzing the data presented here, the main conclusion is that there is a very strong correlation between transgressive events and floral and microfloral changes, as follows:

T1: Roncador Transgression (lower-middle Itararé): marked by appearance of conifers, ginkgoaleans and lycophytes (F1), and a few new pollen grains (P1);

T2: Lontras Transgression (upper Itararé): marked by appearance of glossopterids follow by ferns (F2), and several new pollen grains, including the genus *Vittatina* (P2);

T3: Paraguaçú Transgression (within the Rio Bonito unit): marked by appearance of first Guadalupian elements and dominance of the genus *Glossopteris* (F3), and a few new pollen grains, including elements of overlying *L. virkkiae* Zone (P3);

T4: Palermo Transgression (the ‘‘Rio Bonito-Palermo transition”), marked by last occurrence of the genus *Gangamopteris* and the pteridophyll and ginkgoalean groups (F4), as well as spores and monosaccates typically found in underlying zones (P4);

T5: Irati Transgression (within the Irati unit), marked by last occurrence of cordaitaleans (F5);

T6: Serra Alta Transgression (the ‘‘Teresina-Rio do Rasto transition”), marked by the last occurrence of conifers and lycophytes (F6);

For obvious reasons, given the continental nature of the Rio do Rasto deposits, the last floral change (F7 - marked by the last occurrence of sphenophylls, in Figure 2), which occurred prior to the Permian-Triassic boundary, cannot be related to a transgressive event (Fig. 1). If these basinal transgressive events really correspond to eustatic sea-level rises driven by major glacial-deglaciation events recorded in other regions of Gondwana (e.g., Antarctica and Australia: Montañez et al., 2007), and consequently driven by periods of marked global warming, the floral changes registered here can be inferred to have been trigged by significant climatic shifts. In view of this context and floral succession, the Carboniferous-Permian transition in the Paraná Basin could be considered as a long-term and complex process that started in the latest Carboniferous, marked by the appearance of conifers and ginkgoaleans, and finished within the Early Permian (early-late Artinskian), characterized by the disappearance of pteridophylls, ginkgoaleans and cordaitaleans, the last relict elements from Carboniferous times. However, the termination of this process of floral replacement extends up to the horizons containing the last occurrence of conifers, in the upper Teresina Formation. In this case, the entire transition could have spanned from the latest Carboniferous (approx. Moscovian) through the early Late Permian (late Rodian), corresponding to a time span of around 40 Ma.

In this paper, we delineate a relationship between the floral changes and the eustatic changes, attributing the cause of sea-level changes to major glacial-deglaciation intervals recorded from the Gondwana deposits (Fig. 2). In the future, higher precision radiometric dating integrated with bio- and chemo-stratigraphic tools (e.g., C isotopes, stomatal analysis, and paleoclimate proxies) is needed to further test the hypothesized temporal relationship between floral changes and sea-level and climatic events.

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CARBONIFEROUS AND PERMIAN STRATA OF THE TEPUEL-GENOA BASIN, PATAGONIA, ARGENTINA: A NEAR-CONTINUOUS, DEEP-WATER RECORD OF POLAR GONDWANA DURING THE LATE PALEOZOIC ICE AGE

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The Pampa de Tepuel and Mojón de Hierro formations in the Tepuel-Genoa Basin exposed in the Sierra Tepuel between Tecka and Gobernador Costa, Argentina, constitute an ~5000 m thick, near-continuous Mississippian (late Viséan) to Permian (Sakmarian-early Artinskian) succession that contains at least 6 glacimarine and glacially-influenced marine horizons separated by non-glacial intervals (Taboada et al., 2009; Pagani and Taboada, 2010; Taboada, 2010; Taboada and Pagani, 2010). During much of the Carboniferous and Permian, Patagonia was located near or within the South Polar circle. Thus, these strata represent the thickest and most complete record of polar conditions for the late Paleozoic ice age.

The Tepuel-Genoa Basin was interpreted by López-Gamundí and Breitkreuz (1997) as a foreland basin, and by Forsythe (1982) and Ramos (2008) as either a forearc or a peripheral foreland basin. Regardless of tectonic scenario, rapid basin subsidence was required to produce such a thick Carboniferous to Permian succession.

Dropstone- and fossil-bearing strata of the Pampa de Tepuel and lower portion of the Mojón de Hierro formations were previously interpreted by González-Bonorino (1992) and González and Díaz Saravia (2010) as intercalated glacial and marine strata deposited in subglacial to littoral/near-shore marine environments. The occurrence of striated and grooved surfaces was used as evidence for either terrestrial subglacial conditions or as evidence of grounded ice advance into a shallow glacimarine setting. Conversely, López-Gamundí and Limarino (1984) interpreted strata in the Pampa de Tepuel Formation as submarine debris flow, sandy turbidity current, and hemipelagic deposits.

In our ongoing investigation, we identify numerous facies, which include:

1) wave rippled and hummocky cross-stratified sandstone; 2) thick fossil-bearing mudrock; 3) lonestone-bearing mudrock; 4) discontinuous blocks of sandstone overlying shear planes; 5) folded and brecciated sandstone overlying shear planes; 6) thin-bedded sandstone; 7) massive sheet and channel-form sandstone; 8) microbially-mediated sandstone, 9) massive, stratified, and thin-bedded diamictite; 10) graded, reverse-graded, and massive clast-supported sheet and channel-form conglomerate; and 11) deformed conglomerate resting on shear planes. We interpret these units as wave-influenced shelf, neritic, hemipelagic, iceberg-rafted, glaciomarine meltwater plume, mass movement (slide blocks and slumps), turbidite/bottom current, sandy debris flow, muddy debris flow, and submarine channel deposits. Analysis of grooved and striated surfaces within the succession suggests that these features formed as glide planes beneath slide and slump blocks and as iceberg keel marks.

Clinoforms occur at the Tepuel Hill Section, suggesting that strata at this site were deposited within the basin near the shelf-slope break. At the same locality, wave rippled and hummocky cross-stratified sandstone and associated mudrock within topset beds and at the top of clinoforms indicate deposition on the outer shelf and upper slope. Thick successions of hemipelagic mudrock, horizons of slump/slide blocks, dropstones, diamictites, and channelized and sheet turbidites within clinoforms suggest deep-water sedimentation on the slope and possibly on the basin floor. The arrangement of the deposits suggests that during relative sea-level lowstands, clastic systems, including glaciers, transited the shelf and shed clastics into the deep basin. Fossil-bearing horizons occur above lowstand deposits and may represent condensed zones that developed during transgression/highstand and/or the retreat of glaciers and clastics across the shelf. The ages of the youngest known glacial deposits in the Tepuel-Genoa Basin are poorly constrained. Fossil floral data suggest deposition during the Late Carboniferous (Cúneo, 1990); whereas, fossil invertebrates suggest an age no younger than middle Artinskian (Taboada et al., 2009; Pagani and Taboada, 2010; Taboada, 2010; Taboada and Pagani, 2010). Plant fossils and deltaic deposits located in the upper Mojón de Hierro and in the Río Genoa formations indicate a shallowing of the basin by the late Early Permian (Andreis and Cúneo, 1989; Cúneo, 1990).

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ABNORMAL SERRATION ROWS ON A TOOTH OF THE PENNSYLVANIAN CHONDRICHTHYAN *EDESTUS*

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Abstract—Teeth of many extant and extinct chondrichthyans have serrated edges (carinae). The extensive literature on dental abnormalities in Recent and fossil sharks does not appear to include any descriptions of split or supernumerary serration rows. A tooth of the Carboniferous chondrichthyan *Edestus minor* has two anomalies: a serrated carina that splits into two serrated carinae and a supernumerary row of serrations on one of the lateral faces. A tooth of the Neogene neoselachian *Carcharocles megalodon* with a split serrate carina is figured and described. The extra carina on the *C. megalodon* tooth is abnormal in that it is not serrated. In both cases, the split carinae are shaped like inverted Ys if teeth are oriented with the apices upward. This indicates that development of these teeth proceeded from apex to base, as in Recent sharks, and not the reverse, which may have been the case for some xenacanthimorph chondrichthyans.

INTRODUCTION

In the course of a search of museum collections of teeth of the Carboniferous chondrichthyan *Edestus* Leidy, 1856, a tooth of *Edestus minor* Newberry, 1866 [Newberry, in Newberry and Worthen (1866)] was discovered in which a serrated carina splits, with the two carinae continuing toward the base. An additional row of serrations appears also on one of the lateral faces. This discovery prompted a search for other examples of such anomalies in chondrichthyan teeth. No other examples of abnormal serration rows were found in *Edestus* teeth. However, inquiries made to collectors and dealers of fossil shark teeth revealed that split serrated carinae are known to occur, rarely, in teeth of *Carcharocles megalodon* (Agassiz, 1843).

Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY, USA; UCM, University of Colorado Natural History Museum, Boulder, CO, USA.

SERRATIONS IN CHONDRICHTHYAN TEETH

Teeth with serrated carinae are found in several neoselachian lineages. Some extant examples are *Carcharodon carcharias* and *Galeocerdo cuvier*. Extinct examples include *Carcharocles megalodon* and *Squalicorax pristodontus*. Serrated teeth are less common in non-neoselachian chondrichthyans. Only three hybodontiform species, *Priohybodus arambourgi*, *Pororhiza molimbaensis*, and *Thaiodus ruchae*, have serrated teeth (Duffin and Cuny, 2008). A few Paleozoic chondrichthyans, including the genera *Edestus*, *Helicoprion*, *Carcharopsis*, *Orthacanthus*, *Lebachacanthus*, and *Dicentrodus*, have serrated teeth (Duffin and Cuny, 2008; Ginter et al., 2010). The recently-described ctenacanthiform *Kaibabvenator swiftae* from the Lower Permian of Arizona has serrated teeth (Hodnett et al., 2012, fig. 4c).

Frazzetta (1994) concluded that serrated shark teeth have a greater cutting effect than smooth-edged shark teeth for the same force, but are more prone to binding in the prey tissue and are less efficient at piercing prey. Abler (1992), based on experiments with simulated teeth, concluded that teeth of *Carcharocles megalodon* cut in a similar fashion to serrated hacksaw blades, while teeth of tyrannosaurid dinosaurs cut like a dull smooth blade.

ABNORMALITIES IN CHONDRICHTHYAN TEETH

There have been numerous studies of developmental abnormalities of fossil shark teeth (Botella, 2006; Hampe, 1997; Johnson, 1987, 2005; Lebedev and Esin, 2007; Tulu and Godfrey, 2008) and Recent shark teeth (Cadenat, 1962; Delpiani et al., 2012; Gudger, 1937). Some studies deal with abnormalities of teeth of both fossil and Recent sharks (Balbino and Antunes, 2007; Becker et al., 2000). Some of the types of abnormalities, such as rows of smaller than normal teeth, partial rows of teeth inserted between normal rows, missing rows, or polarity reversals (reversals of the mesial-distal crown asymmetry) (Becker et al., 2000; Gudger, 1937) are only discernible in articulated dentitions and so would rarely be observed in the fossil record, since articulated fossil dentitions are rarely found. Other forms of abnormalities, like twisted, bent, notched, split, fused, or perforated crowns (Balbino and Antunes, 2007; Becker et al., 2000) or missing or extra cusps, as on some xenacanthimorph teeth (Hampe, 1997), can be discerned in the fossil record.

Studies of abnormalities in shark teeth have provided insights into development and pattern formation of chondrichthyan dentitions (Reif, 1978, 1984; Smith et al., in press). The observation of supernumerary tooth rows in the jaws of Recent sharks (e.g., Gudger, 1937) and the fact that such abnormalities appear to be induced by damage to the dental lamina, for example by a sting-ray spine (e.g., Becker et al., 2000), has led to a model of tooth formation from tooth "germs" or "protogerms" (Reif, 1978, 1984). Tooth germs are now interpreted as collections of stem cells (Smith et al., in press). Splitting of a tooth germ by damage to the dental lamina can lead to the formation of a supernumerary tooth row in this model. The observation of rows of teeth with reversed polarity can be explained by the splitting of a tooth germ, accompanied by a spatial gradient in the concentration of a morphogen controlling the crown shape (Reif, 1978, 1984; Smith et al., in press).

SPLIT AND SUPERNUMERARY SERRATION ROWS ON A TOOTH OF *EDESTUS*

Edestus Leidy, 1856 is a genus of Pennsylvanian chondrichthyans distinguished by having serrated symphyseal teeth, joined at the bases to form tooth whorls in both the upper and lower jaws. Although often assumed to have a close relationship with the Permian genus *Helicoprion* Karpinsky, 1899, *Edestus* differs from *Helicoprion* in that the outermost teeth were shed rather than being retained in a spiral and in having tooth whorls in both the upper and lower jaws (Hay, 1912; Zangerl and Jeremiah, 2004). Well-preserved specimens of *Helicoprion* from Idaho, USA, including some cranial material, show that a tooth whorl was present only in the lower jaw (Bendix-Almgreen, 1966; Lebedev, 2009).

Figure 1 shows a partial tooth whorl of *Edestus* minor (AMNH FF438) having one tooth with a supernumerary row of serrations. Figures 2 and 3 show that this tooth, in addition to having a supernumerary serration row, has an initially normal serration row that splits into two rows, one of which continues nearly to the base, the other of which stops

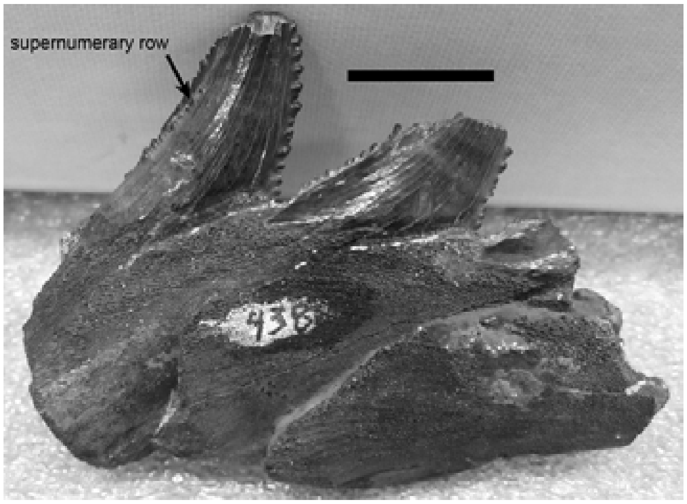

FIGURE 1. Partial tooth whorl of *Edestus minor* (AMNH FF438). Anterior end of whorl is to the right. Arrow points to a supernumerary serration row on the lateral face of the most posterior tooth crown. Scale bar = 2 cm.

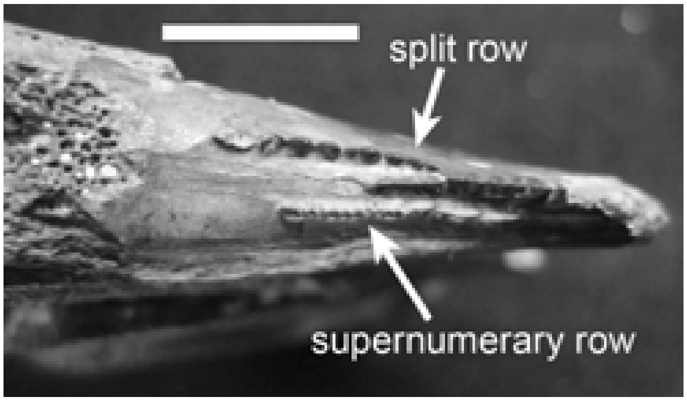

FIGURE 2. Posterior view of crown of most posterior tooth of AMNH FF438. The serration row on the posterior edge (carina) splits into two serration rows. A supernumerary serration row is developed along a posterolateral face. Scale bar = 1 cm.

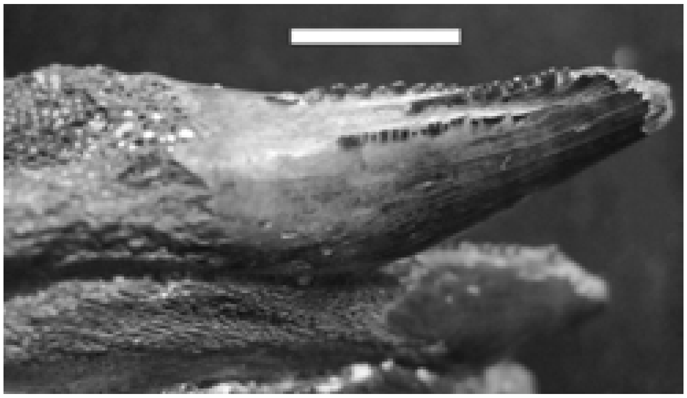

FIGURE 3. Posterolateral view of crown of most posterior tooth of AMNH FF438. Scale bar = 1 cm.

after a short distance. The nodes of the supernumerary row are smaller and more closely spaced that those on the normal serrated carinae.

Given the low catalog number, AMNH FF438 is probably part of the Newberry collection, which was transferred to the AMNH from Columbia University in 1903 after Newberry's death in 1892 (Hussakof, 1908). For example, AMNH FF225, the type specimen of *Edestus giganteus*, and AMNH FF485, a cast of a specimen referred to *Edestus minor*, are both listed as belonging to the Newberry Collection by Hussakof (1908, p. 46-47). The dark coloration of AMNH FF438 is consistent with it being found in a carbonaceous shale, like other specimens of *Edestus* from the Carbondale Formation of Illinois or Indiana (Desmoinesian, Middle Pennsylvanian), such as AMNH FF225. Occurrences of *Edestus minor* have been reviewed by Koenig (1965) and Itano et al. (2012).

SPLIT CARINA ON A TOOTH OF *CARCHAROCLES MEGALODON*

Carcharocles megalodon (Agassiz, 1843) is the well-known Miocene-Pliocene giant "megatooth shark." Split, serrated carinae are a rare abnormality on teeth of *C. megalodon* (G. Hubbell and S. Alter, personal communications). This particular abnormality occurs most commonly on the most distal teeth (S. Alter, personal communication), possibly because of crowding of teeth in adjacent rows in the more distal part of the jaws inducing trauma to the developing crowns.

Figures 4 and 5 show a distal tooth of *C. megalodon* having a split carina near the base. The original serrate carina continues to develop more or less normally after the second carina forms on the labial face of the crown. The second carina is abnormal in that it has no serrations.

Various examples of abnormal shark teeth, mostly of *C. megalodon*, are shown by Renz (2006, p. 119-127). The *C. megalodon* tooth in the unnumbered figure on the upper left of p. 123 appears to have a split carina, similar to that on UCM 105853. Other photographs on the same page show *C. megalodon* teeth with deformed serrate carinae or with randomly-placed nodes on the crown faces, but none with a supernumerary serration row on one of the faces, as is seen on AMNH FF438.

DISCUSSION

Split or supernumerary serration rows in chondrichthyan teeth may be induced by injury to the developing tooth crown, although there might be other causes. In the case of the *Edestus* tooth (AMNH FF438) a genetic cause (mutation) seems unlikely, since the abnormality is seen on only one of the teeth of a single whorl. The partial independence of carina formation and serration formation is seen in the fact that on the

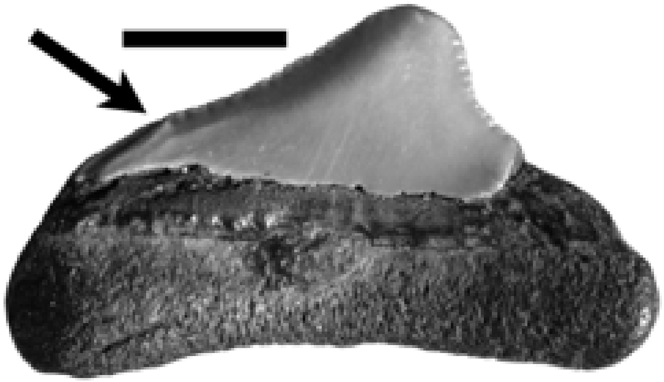

FIGURE 4. Labial view of distal tooth of *Carcharocles megalodon* (UCM 105853) from the Miocene Hawthorn Formation, Fernandina Beach, Nassau County, Florida, USA. Mesial end of tooth is to the left. Point at which a second carina splits from the main one is indicated by arrow. Scale bar = 1 cm.

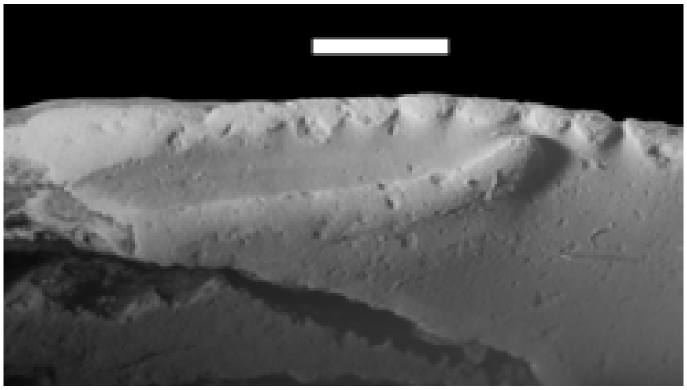

FIGURE 5. Abnormal carinae of tooth of *Carcharocles megalodon* (UCM 105853). Scale bar = 2 mm. Tooth is coated with ammonium chloride.

Edestus tooth, there is a serration row on a crown face, not associated with a carina, while on the *Carcharocles* tooth (UCM 105853), the additional carina formed after the splitting has no serrations. The fact that the abnormal serration rows or carinae have different forms in the two species is not surprising, given that serrations must have evolved separately in these two species.

On both the *Edestus* tooth and the *Carcharocles* tooth, the split carinae have the form of an inverted Y, if the apex is pointed upward. This implies that the crown formed from the apex toward the base, since it is much more probable that a normal carina would split than that two carinae would join and create a single, normal carina. Recent shark teeth are known to form from the apex of the crown, with the base forming last (e.g., Smith et al., in press, fig. 7). Hence, the observation that *Edestus* and *Carcharocles* teeth form from the apex toward the base would be a trivial observation if not for the fact that some Paleozoic xenacanthimorph teeth have been described in which the apices are less developed than the bases (Johnson, 2005). The cause of the anomalous development of these teeth has not been determined, but it should be noted that none of the hybodont teeth in the same sample have this abnormal form of development. Xenacanthimorph teeth in which the apices are less developed than the bases have also been observed by Hampe (1997) and by Johnson and Thayer (2008).

Given that the crowns of both the *Edestus* and *Carcharocles* teeth developed from the apex toward the base, it can be inferred that the splitting occurred early in the development of the *Edestus* tooth (since the split occurs closer to the apex than to the base), but late in the development of the *Carcharocles* tooth (since the split occurs very near the base). This is consistent with the hypothesis that the splitting was induced by trauma caused by another object. The developing *Edestus* tooth would have been exposed to other objects, possibly including prey or teeth of the opposing whorl (see Zangerl and Jeremiah, 2004, fig. 4). However, the developing *Carcharocles* tooth would have been deep inside the oral cavity until nearly in a functional position, as in Recent sharks. In this case, trauma might have been induced at a late stage of development, for example by an overlapping tooth row.

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CHONDRICHTHYANS FROM THE EARLY/LATE CARBONIFEROUS BOUNDARY BEDS OF THE GISSAR MOUNTAINS, UZBEKISTAN

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Abstract—Chondrichthyan microremains are described from the Late Serpukhovian-Early Bashkirian of the Aksu sections, Surkhantau Range, southwestern Gissar Mountains, Uzbekistan. The fauna contains an assemblage including diverse symmoriiforms, *Denaea* cf. *D. williamsi* Ginter and Hansen, *Denaea* sp., *Stethacanthulus decorus* (Ivanov), *S. meccaensis* (Williams), a euselachian, *Gissarodus flabellatus* gen. et sp. nov, and various chondrichthyan denticles and scales.

INTRODUCTION

Chondrichthyan microremains described below have been found in the marine Early/Late Carboniferous boundary beds of the Aksu sections (Fig. 1). These sections (four outcrops) are located in the watershed between the Aksu (Ak-Su) and Vakhshivardara (Vakhshivar-Dar'ya) rivers in the Surkhantau Range, Surkhan-Dar'ya Region of southeastern Uzbekistan (Nikolaeva, 1995). The Surkhantau Range forms a part of the Southwest Gissar Mountains, South Tien-Shan Mountain System. The sections expose the deep-water deposits of the Khodzhir-Bulak Formation according to Nikolaeva (1995) or the Badava and Suffa formations of Nemirovskaya and Nigmadganov (1993). The deposits contain limestones interbedded with cherts, shales and mudstones. Detailed descriptions of these sections and their fossils are given by Nemirovskaya, Nigmadganov and Nikolaeva (Nigmadganov and Nemirovskaya, 1992a, b; Nikolaeva and Nigmadganov, 1992; Nemirovskaya and Nigmadganov, 1993, 1994; Nikolaeva, 1994a, b, 1995). The Aksu section was proposed as a potential candidate for the Mid-Carboniferous boundary stratotype (Nikolaeva, 1994b). The deposits also yield ammonoid and conodont remains. The interval represented in the sections corresponds to the Late Serpukhovian *Gnathodus bilineatus bollandensis* and Early Bashkirian *Declinognathodus noduliferus* conodont Zones or two Late Serpukhovian conodont Zones (*Gnathodus bilineatus bollandensis* and *G. postbilineatus*), and two Early Bashkirian conodont Zones (*Declinognathodus praenoduliferus* and *D. noduliferus*) of Nemirovskaya and Nigmadganov (1994). The interval belongs also to the Late Serpukhovian *Fayettevillea-Delepinoceras* ammonoid Genozone and Early Bashkirian *Homoceras-Hudsonoceras* ammonoid Genozone, and *Isohomoceras subglobosum* and *I. ventrosum* ammonoid Zones (Nikolaeva, 1995).

The chondrichthyan remains were recovered from 12 samples taken from nine stratigraphic levels in the Late Serpukhovian- Early Bashkirian: in Aksu sections 1 and 2 of Nikolaeva (1995) or Aksu I of Nemirovskaya and Nigmadganov (1994), Aksu II-IV of Nigmadganov and Nemirovskaya (1992b) and Nemirovskaya and Nigmadganov (1994). Samples NN-7 – NN-18 (Aksu I), 3/20 (section 2) are the Late Serpukhovian; whilst samples NN-19 – NN-23 (Aksu I), 3/21, 3/22 (section 2), 3/69, 3/70, 3/75, (section 1), NN-32 (Aksu II), and NN-35 (Aksu III) belong to the Early Bashkirian (Nigmadganov and Nemirovskaya, 1992b; Nemirovskaya and Nigmadganov, 1994; Nikolaeva, 1995).

The chondrichthyans are represented by numerous and diverse teeth of symmoriiform sharks, the teeth of a new euselachian, various denticles and scales of chondrichthyans, and a few actinopterygian teeth. The studied specimens were obtained from acid-treated samples collected for conodonts. The specimens are housed in the Paleontological Museum of St. Petersburg State University, St. Petersburg, Russia (PM SPU 66).

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Superorder CLADODONTOMORPHI Ginter, Hampe and Duffin, 2010
Order SYMMORIIFORMES Zangerl, 1981
Family SYMMORIIDAE Dean, 1909
Denaea Pruvost 1922
Denaea cf. *D. williamsi* Ginter and Hansen, 2010

Figs. 2A-E

Referred specimens: Nine isolated teeth from samples NN-7, NN-8, NN-10, NN-23, 3/20, 3/22, Khodzhir-Bulak Formation, Late Serpukhovian-Early Bashkirian, Aksu sections.

Description: The small teeth range in size from 0.4 to 0.7 mm along the base. The teeth have a cladodont crown with four to five cusps. The crown is slightly inclined lingually, and symmetrical to slightly asymmetrical. The cusps are recurved lingually, sharply-pointed, oval in cross section, slightly compressed labio-lingually, and have clearly separated bases. The central cusp is considerably higher than the lateral ones. The intermediate cusps are the smallest on the crown and may be absent. The intermediate and lateral cusps are strongly divergent from the central cusp. The labial and lingual faces of the cusps are covered by distinct cristae. One or two pairs of long cristae merge before reaching the cusp top and form a lanceolate, inverted "V"-nested structure on the labial face of the crown. Further straight or slightly curved, shorter ridges are located in the middle part of the cusp below the lanceolate ridges. The lingual ornamentation consists of straight, parallel cristae diverging basally from the cusp top and one central crista which bifurcates toward the base. The tooth base is lingually extended and subtriangular in shape, and with slightly curved latero-lingual edges. The central part of the lingual rim is pointed. The quite thick, rounded apical button is placed on the pointed part of the base and subdivided into two portions by the median depression which housed the foramen of the main vascular canal. The base has a slender labio-basal tubercle without distinct margins, and a slightly concave or flat basal side with the foramen of the main vascular canal located on the base center.

Remarks: The teeth described here are distinguished from those of *Denaea williamsi* Ginter and Hansen (Savitskiy et al., 2000; Ginter et al., 2010; Ginter and Hansen, 2010) by the higher and more divergent lateral and shorter intermediate cusps, in the lesser number of cristae in the cusp ornamentation, their more simplified lingual ornamentation, and by the wider and subdivided apical button. The teeth from the Aksu sections are very similar to the teeth described as *Stethacanthus* cf. *S. altonensis* (St. John and Worthen) by Wang et al. (2004) from the Serpukhovian of China in the structure of the crown and the shape of apical button. Thus, the teeth from Uzbekistan and China should belong to the same species of *Denaea*.

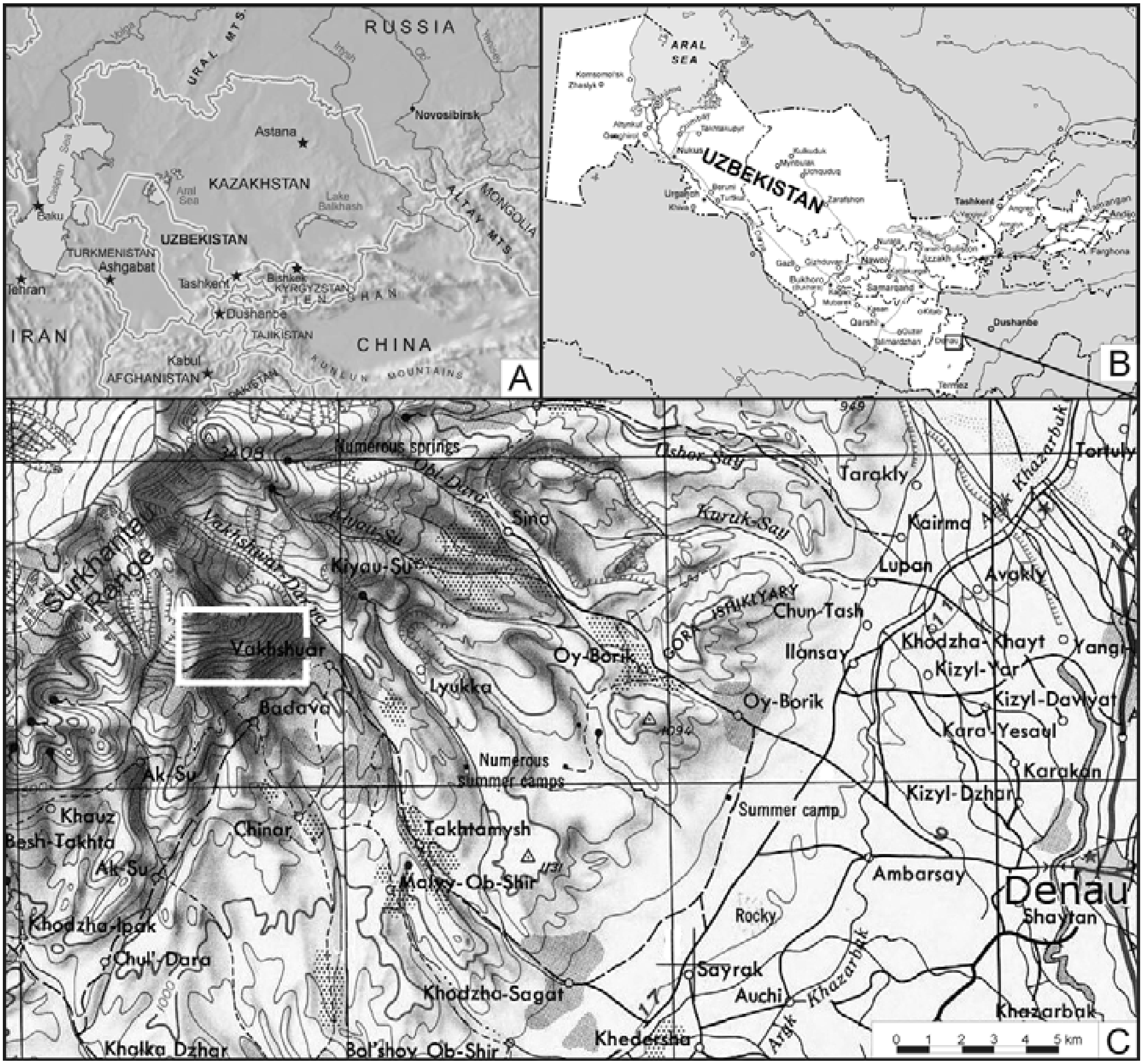

FIGURE 1. Maps showing location of the Aksu sections (white box in C) in the Surkhantau Range of southeastern Uzbekistan.

Denaea sp.
Fig. 2F

Referred specimens: Two isolated incomplete teeth from sample NN-10, Khodzhir-Bulak Formation, Late Serpukhovian, section Aksu I.

Description: The teeth are 0.6 mm in size along the base. These cladodont teeth possess seven cusps in a slightly asymmetrical crown and a lingually extended base. The cusps are smooth, rounded in cross section, and slightly inclined lingually. The large central cusp and a pair of moderate outer intermediate cusps lie on one line, but the inner intermediate and lateral cusplets are displaced labially. The base is lingually extended and subtriangular, with slightly curved latero-lingual edges, possessing a shallow labial depression and a weak labio-basal projection.

Remarks: These teeth resemble those of *Denaea saltsmani* Ginter and Hansen from the Pennsylvanian of the USA (Ginter and Hansen, 2010) and *D. wangi* Wang, Jin and Wang from the Visean to Serpukhovian of Belgium, Germany, Poland and China (Wang et al., 2004; Ivanov and Derycke, 2005; Ginter et al., 2010). But, the preservation of the specimens from the Aksu section does not permit determination to species level.

Stethacanthulus Zangerl, 1990
Stethacanthulus decorus (Ivanov, 1999)
Fig. 3

Referred specimens: 54 isolated teeth from samples NN-7, NN-10, NN-16, NN-18, NN-19, NN-32, NN-35, 3/20, 3/21, 3/22, 3/69, 3/70, 3/75, Khodzhir-Bulak Formation, Late Serpukhovian - Early Bashkirian, Aksu sections.

Description: The teeth range in size from 0.5 to 1.1 mm along the base. The teeth have a cladodont crown with five to seven cusps. The cusps are thin, slightly sigmoidally incurved, considerably inclined lin-

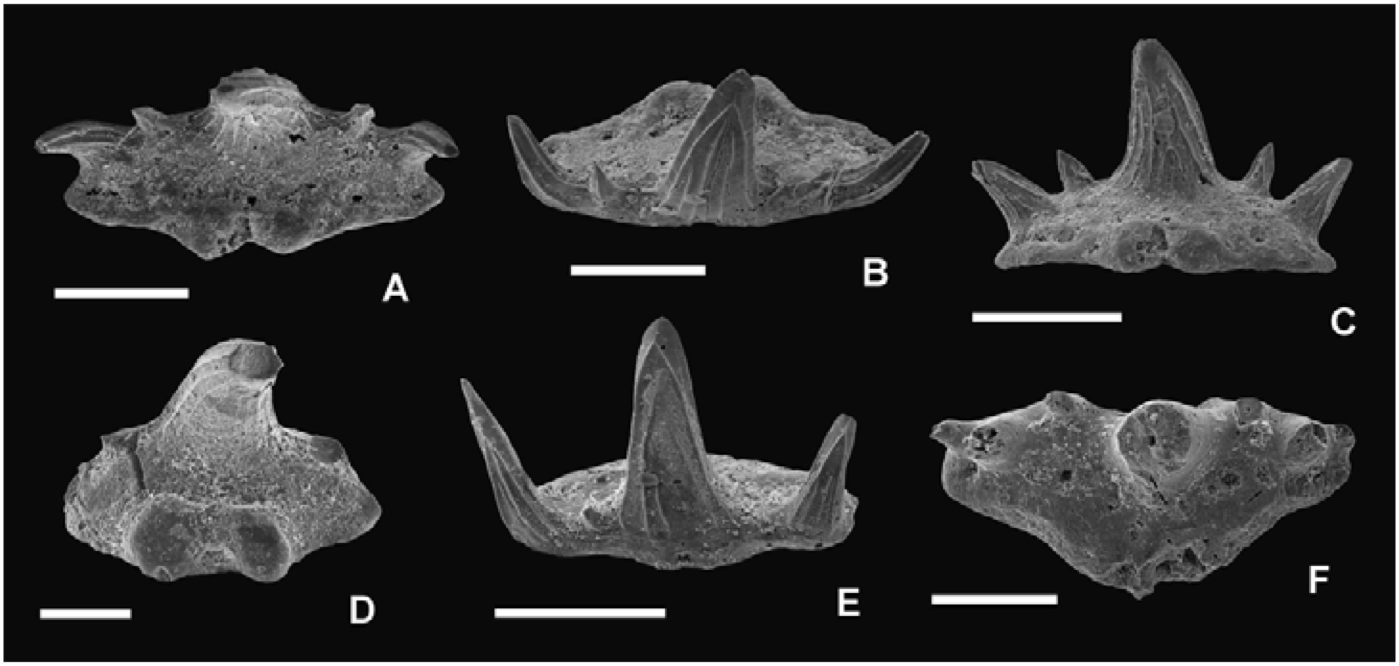

FIGURE 2. Teeth of symmoriiform *Denaea*. **A**-**E**, *Denaea* cf. *D. williamsi* Ginter and Hansen, 2010, **A**-**C**, PM SPU 66-1, sample 3/20, **A**, occlusal, **B**, oblique labial, and **C**, lingual views; **D**, PM SPU 66-2, sample NN-7, lingual view; **E**, PM SPU 66-3, sample 3/22, labial view. **F**, *Denaea* sp., PM SPU 66-4, sample NN-10, occlusal view. All scale bars = 200 µm.

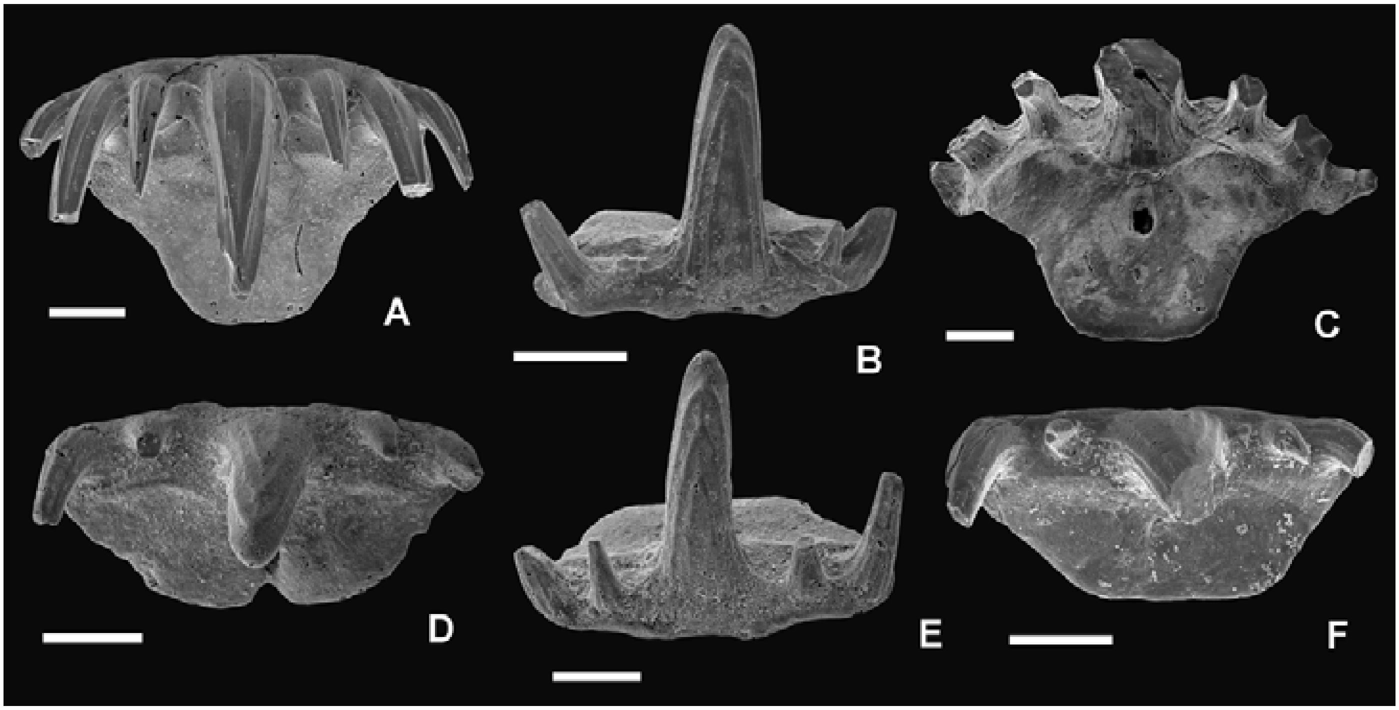

FIGURE 3. Teeth of symmoriiform *Stethacanthulus decorus* (Ivanov, 1999). **A**, PM SPU 66-5, sample 3/69, occlusal view. **B**, PM SPU 66-6, sample NN-32, labial view. **C**, PM SPU 66-7, sample 3/20, lingual view. **D**-**E**, PM SPU 66-8, sample 3/22, **D**, occlusal and **E**, labial views. **F**, PM SPU 66-9, sample NN-35, occlusal view. All scale bars = 200 µm.

gually, are clearly separated from each other and have rounded cross sections. The crown is composed of three high main, and two to four short accessory cusps. The main cusps are the central and lateral in the five-cuspid teeth or outer intermediate in the seven-cuspid teeth. The shorter accessory cusps are the inner intermediate in all teeth, plus the lateral in the seven-cuspid teeth. The central cusp is rather higher and wider than the outer intermediate ones. The lateral and outer intermediate cusps are inclined distally from the central cusp. The labial and lingual sides of the cusps bear distinct ornamentation. The labial ornamentation consists of long, curved, two to three cristae that form a lanceolate structure in the upper part of the cusp. Shorter cristae are located in the middle part of the cusp below the lanceolate cristae. The straight cristae on the lingual side are thinner than on the labial side, and do not reach the top of the cusp. The tooth base has a central, lingually extended part, giving rise to a trapezoidal shape in occlusal view. The occlusal surface of the base is sloped, with the triangular median depression extending to the lingual edges. The foramen of the main vascular canal opens on the top of this depression. The sloped part is limited by the distinct lingual ledges located on each side of the foramen, some distance from the crown/base boundary. The lingual extension of the base varies from short in the five-cusped teeth to long in the seven-cusped teeth with curved, latero-lingual edges. A small median notch may be present on the lingual rim of the five-cusped teeth. The basal surface of the base has an arched transverse prominence centrally, with two lateral depressions on each side. The center of the basal prominence is perforated by the foramen of the main canal.

Stethacanthulus meccaensis (Williams, 1985)

Fig. 4

Referred specimens: 203 isolated teeth from samples NN-7, NN-10, NN-16, NN-18, NN-19, NN-20, NN-22, NN-32, NN-35, 3/20, 3/21, 3/22, 3/69, 3/70, 2/75, Khodzhir-Bulak Formation, Late Serpukhovian-Early Bashkirian, Aksu sections.

Description: The teeth range in size from 0.3 to 1.0 mm along the base. These teeth possess a cladodont crown with three to seven cusps and a lingually extended base. The cusps are thin, incurved and inclined lingually, ornamented or smooth, and rounded in cross section. The central cusp is slightly higher than the outer cusps. The lateral and intermediate cusps are closely adjacent to each other. The labial surfaces of the cusps are covered by two to four distinct, straight cristae reaching the top of the cusp, while the lingual surface is either smooth or bears sparse tiny striations. The occlusal surface of the base slopes baso-lingually at a very shallow angle, with the shallow triangular median depression smoothly integrated into its surface. The lingual ledges are poorly developed on the occlusal side. The slender basal transverse prominence is gradually extended into very shallow lateral depressions. The foramina of the main vascular canal open on the top of the triangular depression on the occlusal side and on the basal prominence close to the labial edge.

There are several tooth morphotypes represented in the described collection. The first morphotype is characterized by a narrow crown with three to five cusps which are smooth or poorly ornamented; and by a spoon-like, strongly lingually extended base (Fig. 4 A-D). The central cusp in such teeth is considerably higher than others. The teeth of the second morphotype have a wide, five-cusped crown with high lateral cusps and a trapezoidal, short base (Fig. 4 L). The teeth of the third morphotype have a wide crown containing five to seven cusps and a trapezoidal base with an elongated lingual part (Fig. 4 E-K).

Remarks: This species was originally described by Williams (1985) as belonging to *Denaea*. A second species, "*D.*" *decora* Ivanov, was established later and placed in a group with *D. meccaensis* based on the same type of tooth morphology (Ivanov, 1999) but was noted as being considerably different from the *Denaea* species such as *D. fournieri* Pruvost, *D. wangi* Wang, Jin and Wang, *D. saltsmani* Ginter and Hansen, and *D. williamsi* Ginter and Hansen. Zangerl (1990) mentioned that the teeth of *D. meccaensis* Williams are indistinguishable from those of *Stethacanthulus longipeniculus* Zangerl. Maisey (2007, 2008) assigned "*D.*" *meccaensis* and "*D.*" *decora* to the genus *Stethacanthulus*, and noted that *S. longipeniculus* is a junior synonym of *S. meccaensis*. These two species are attributed here to the genus *Stethacanthulus* until all *Denaea*-like elasmobranchs have been compared and revised.

Cohort EUSELACHII Hay, 1902

Order and family incertae sedis

Gissarodus, n. gen.

Type species: *Gissarodus flabellatus*, sp. nov.

Distribution: Late Serpukhovian - Early Bashkirian, Carboniferous of Uzbekistan.

Etymology: Derived from the Gissar Mountains, and the Greek ὀδούς – tooth.

Diagnosis: As for species.

Gissarodus flabellatus, n. sp.

Fig. 5

Holotype: PM SPU 66, isolated tooth from sample NN-18 (Fig. 5 A-C).

Type locality: Aksu section 1, watershed between Aksu and Vakhshivardara rivers, Surkhantau Range, South-West Gissar Mountains, Surkhan-Dar'ya Region, south-eastern Uzbekistan.

Formation/Age: Khodzhir-Bulak Formation, *Declinognathodus praenoduliferus* conodont Zone, *Isohomoceras subglobosum* ammonoid Zone, Early Bashkirian, Late Carboniferous.

Etymology: From the Latin *flabellatus* – fan-like.

Referred specimens: 48 isolated teeth and two tooth files, samples NN-7, NN-10, NN-18, NN-32, NN-35, 3/20, 3/21, 3/22, 3/69, Khodzhir-Bulak Formation, Late Serpukhovian - Early Bashkirian, Aksu sections.

Diagnosis: Multicuspid teeth, elongated mesio-distally; crown strongly inclined lingually, flattened labio-lingually, includes seven to eleven cusps, with wide, triangular central, moderate outer intermediate, short inner intermediate and lateral cusps; cusps separated from each other, slightly fused basally, divergent and form a fan-like structure, with distinct lateral carina; lateral cusps strongly inclined distally; labial ornamentation comprises two long cristae forming a lanceolate patten, and intervening short cristae; base arched and lingually shortly extended, with occlusal thickening, longitudinal groove, shallow labial depression and delicate labio-basal projection; one or two larger foramina in the middle of lingual rim, two to four foramina in the center of basal surface.

Description: The elongate teeth range in size from 0.6 to 1.4 mm mesio-distally along the base. The teeth have a multicuspid crown possessing from seven to eleven cusps in the isolated teeth but not in the tooth files. The crown is strongly inclined lingually, flattened labio-lingually, and symmetrical to slightly asymmetrical. The crown of most teeth is composed of the central, inner and outer intermediate and lateral cusps. The cusps are separated from each other or only slightly fused basally. They diverge from the crown center forming a fan-like structure. The lingual inclination of the cusps increases medially and distally away from the central cusp. The central cusp is wide and triangular, mainly only slightly higher than the outer intermediate cusps. The inner intermediate and lateral cusps in the seven-cusped teeth are smaller, equal in height, or the lateral ones are shorter. The lateral cusps are commonly recurved and strongly inclined distally. A distinct lateral carina separates the labial and lingual cusp faces, forming a cutting edge. The labial face of the crown bears a distinctive ornamentation composed of straight or curved cristae. Two long cristae form a lanceolate, inverted "V"-nested structure that is sub-parallel to the cusp edges. The space between such long cristae is sometimes filled with short, closely spaced cristae. The lingual face of the higher cusps is covered by delicate cristae not reaching the cusp top.

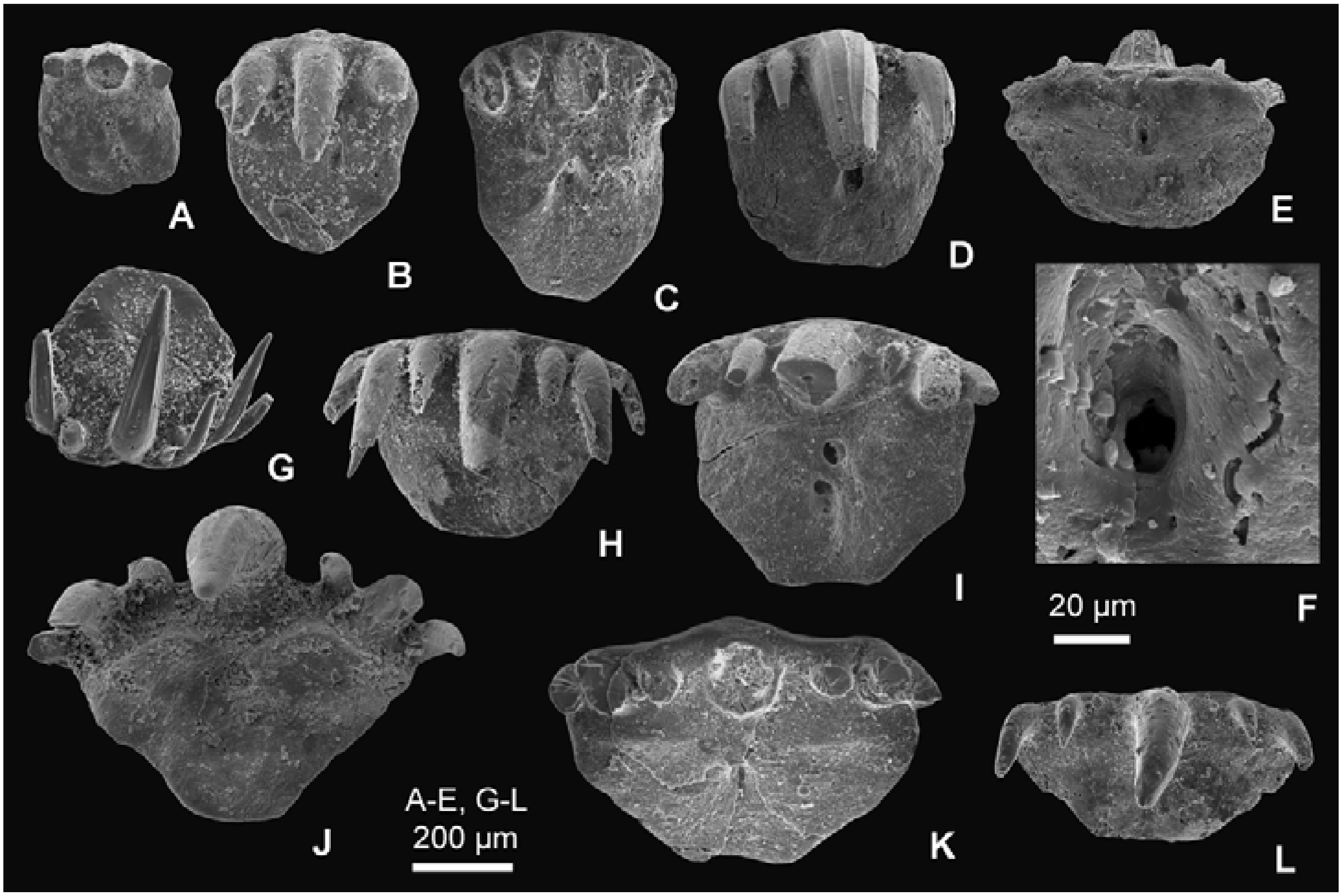

FIGURE 4. Teeth of symmoriiform *Stethacanthulus meccaensis* (Williams, 1985). **A**, PM SPU 66-10, sample NN-19. **B**, PM SPU 66-11, sample NN-19. **C**, PM SPU 66-12, sample NN-19. **D**, PM SPU 66-13, sample 3/69. **E-F**, PM SPU 66-14, sample NN-10, **F**, detail with parasite microborings. **G**, PM SPU 66-15, sample 3/69. **H**, PM SPU 66-16, sample NN-18. **I**, PM SPU 66-17, sample NN-19. **J**, PM SPU 66-18, sample NN-18. **K**, PM SPU 66-19, sample NN-19. **L**, PM SPU 66-20, sample 3/20. **A-D**, **H**, **I**, **K**, **L**, occlusal views; **E**, basal view; **G**, oblique labial view; **J**, lingual view. Scale bars - in the figure.

The tooth base is lingually shortly extended, arched, elongated oval to rectangular in shape, convex on the occlusal side and concave on the basal side, with occlusal thickening. The latter is separated by a longitudinal groove marking the crown/base boundary. The shallow labial depression is developed beneath the central cusp. The base bears a delicate but distinct labio-basal projection extending along much of the labial margin but not reaching the lateral edges. One or two larger foramina of the main vascular canal open in the middle of the lingual rim. The basal surface of the base is perforated by two to four such foramina centrally.

The most common teeth in the studied collection possess a seven-cusped crown, the central cusp being quite wide (Fig. 5 A-M). Several teeth have a multicuspid crown with nine to ten cusps (Fig. 5 N, P). The central cusp of such teeth is slightly wider than the others but equal in height or slightly shorter than the two pairs of high, outer, intermediate cusps. The inner intermediate cusps are shorter than the central and outer intermediate cusps but higher than the lateral ones. Small accessory cusplets can be present irregularly between the intermediate cusps.

Five teeth possess a crown with 11 cusps (Fig. 5 Q, R). These teeth lack a central cusp and are divided into two parts, separated by a wide depression on the labial side and a triangular notch in the lingual rim. Each part of the tooth possesses a high and wide cusp placed almost in the center. These high cusps are surrounded distally and mesially by intermediate cusps of different height. Probably, such a tooth is two teeth fused along their lateral edges.

The tooth files (Fig. 5 O) are composed of three teeth with partly fused bases. The crowns are tricuspid. The central cusp is considerably higher than the lateral ones. The labial faces of the teeth are concave. The base has a flat basal side.

The described teeth demonstrate the morphological variation in number of the cusps, height of the intermediate cusps, curvature and inclination of the cusps, width and shape of the base, and length of the labio-basal projection.

Remarks: The jaws of *Gissarodus* probably had a heterodont dentition. The tricuspid teeth with partly fused bases (tooth files) were possibly located in the symphyseal part of the jaw. The teeth with a seven-cusped crown could have occupied in the mesial, anterolateral and lateral position; the multicuspid teeth with nine to eleven cusps could be posterior teeth. There is other possible reconstruction of hetrodonty in the *Gissarodus* jaw when the seven-cusped teeth were the anterolaterals and posterolaterals but the multicuspid with nine to eleven cusps – the laterals.

The teeth of *Lesnilomia sandbergi* Ginter from the Frasnian, Late Devonian of Utah, USA (Ginter, 2008) resemble the teeth of the new taxon but differ by the less flattened and inclined crown, the higher central cusp and shorter intermediate cusps, the less divergent lateral cusps, the more coarse, straight numerous cristae on the labial side, the flatter base, and by the presence of two longitudinal rows of foramina on the occusal side of the base. Ginter (2008; Ginter et al., 2010) assigned *Lesnilomia* to primitive Elasmobranchii *incertae sedis* and noted that this genus should be situated between ctenacanthiforms and basal euselachians.

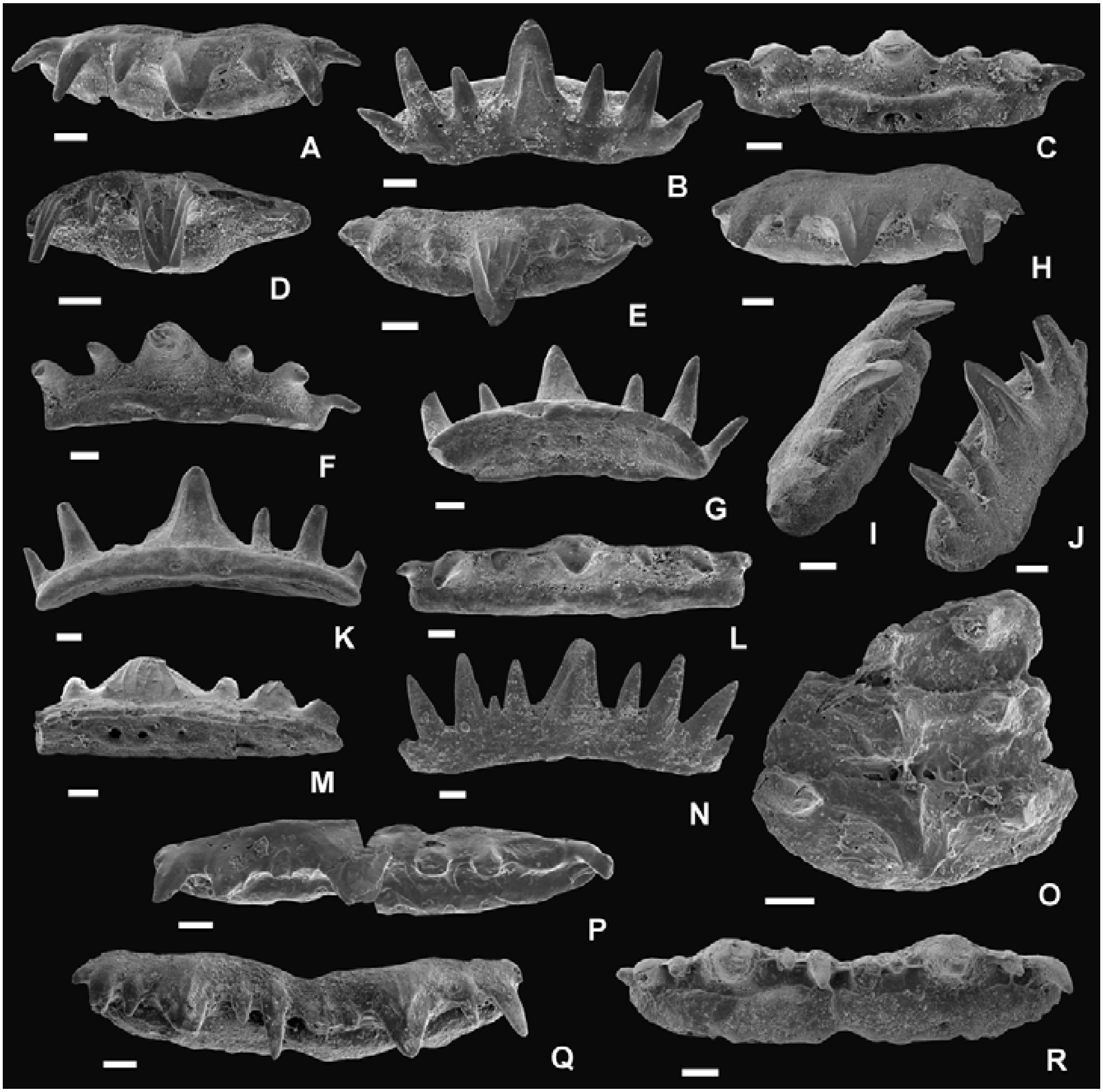

FIGURE 5. Teeth of euselachian *Gissarodus flabellatus*, n. sp. **A-C**, holotype PM SPU 66-21, sample NN-18, **A**, occlusal, **B**, labial, and **C**, lingual views. **D**, PM SPU 66-22, sample 3/69, occlusal view. **E**, PM SPU 66-23, sample 3/21, occlusal view. **F-G**, PM SPU 66-24, sample 3/21, **F**, lingual and **G**, oblique basal views. **H-J**, PM SPU 66-25, sample 3/22, **H**, occlusal, and **I-J**, two oblique lateral views. **K-L**, PM SPU 66-26, sample 3/21, **K**, lingual and **L**, occlusal views. **M**, PM SPU 66-27, sample NN-7, oblique basal view. **N**, PM SPU 66-28, sample 3/21, labial view. **O**, tooth file with fused bases, PM SPU 66-29, sample NN-7, occlusal view. **P**, PM SPU 66-30, sample NN-18, occlusal view. **Q-R**, PM SPU 66-31, sample NN-32, **Q**, occlusal and **R**, lingual views. All scale bars = 100 µm.

The teeth described here are also similar to those of the hybodontoid *Mesodmodus khabenji* Derycke-Khatir from the Tournaisian, Early Carboniferous of Belgium (Derycke-Khatir, 2005). However, the teeth of *M. khabenji* are distinguished from those of *Gissarodus* in the pyramidal crown, the considerably higher, wider central cusp and shorter intermediate cusps, the flat base, and the presence of a foramina row on the basal side of the base.

The teeth of *Gissarodus* are similar to those of the Paleozoic synechodontiform neoselachians, such as *Synechodus antiquus* Ivanov from the Sakmarian- Artinskian, Early Permian (Cisuralian) of the South Urals (Ivanov, 2005) in that the crown is strongly inclined lingually and flattened labio-lingually, the lateral carina is well developed, the base is arched, and two foramina are present in the middle of the lingual rim. The teeth of *S. antiquus* are distinguished from those of *Gissarodus* in their more strongly asymmetrical crown, their higher and more distally inclined central cusp, their thinner base, and the presence of a row of foramina along the labial edge.

Thus, *Gissarodus flabellatus*, based on tooth morphology can be attributed to the euselachian sharks and possesses some features of both hybodontoids and early synechodontiforms.

Chondrichychthyan denticles and scales
Fig. 6

Referred material: 25 denticles and 35 scales from samples NN-7, NN-10, NN-18, NN-19, NN-20, NN-23, NN-32, NN-35, 3/20, 3/21, 3/22, 3/69, Khodzhir-Bulak Formation, Late Serpukhovian - Early Bashkirian, Aksu sections.

Description and remarks: The denticles are represented by three types. The denticles of type 1 have a narrow crown with three to five cusps (Fig. 6 A-F). The cusps are conical, sharp, recurved, inclined posteriorly, rounded in cross section, divergent from the crown center, and separated from each other by narrow depressions. The crown includes a large central and two small lateral cusps. The tiny accessory lateral cusplets present in the five-cusped crown are strongly inclined laterally. The central cusp may have a lateral carina. The lateral cusps and accessory lateral cusplets are located anteriorly in comparison to the central one. The median depression is located on the anterior side of the denticle. The base is larger than the crown and extended posteriorly, with conical external and flat or slightly concave basal surfaces. Such denticles possibly belong to the gill-arch or pharyngeal regions. The similar den-

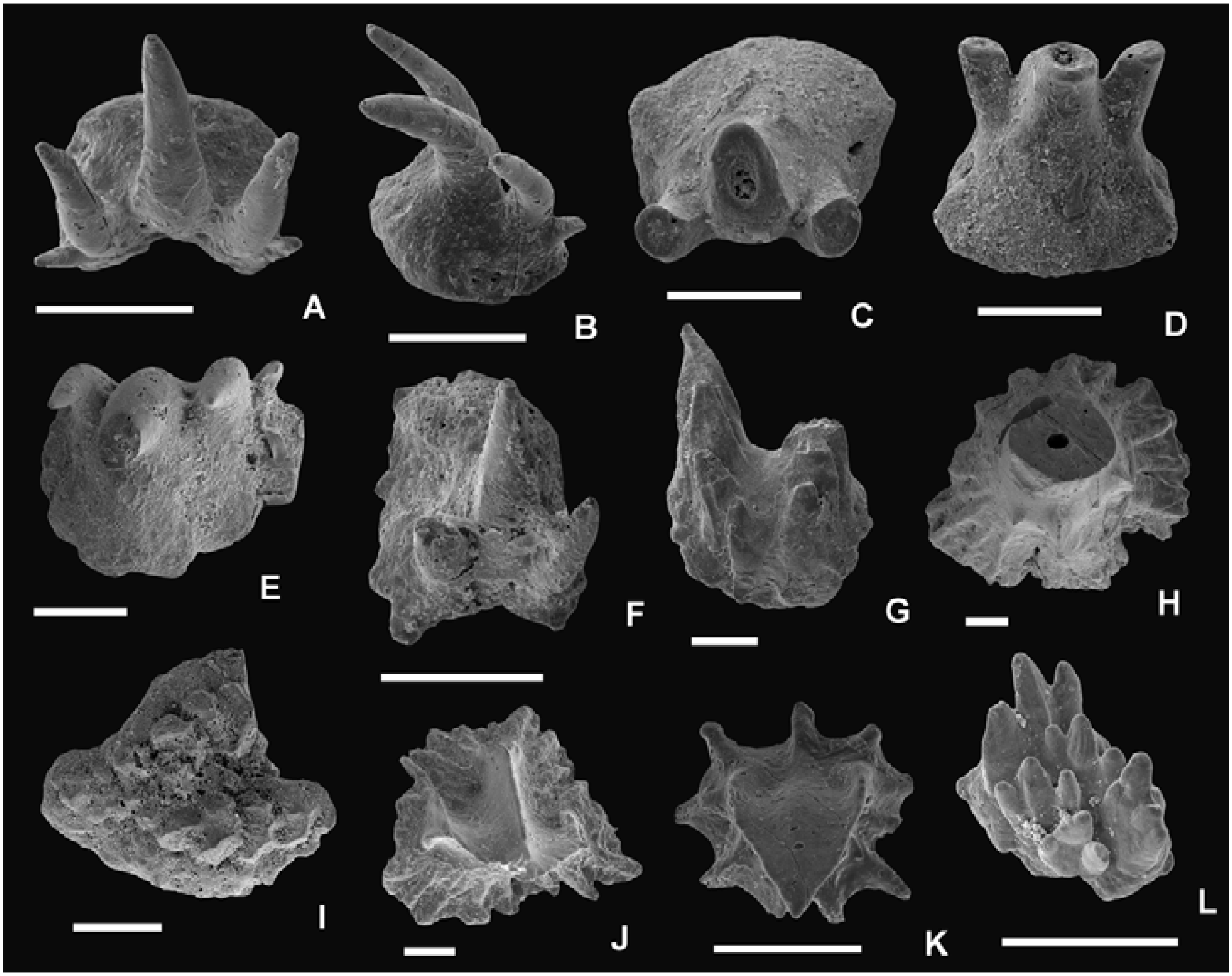

FIGURE 6. Chondrichthyan denticles and scales. **A-F**, Denticles of type 1, **A-B**, PM SPU 66-32, sample 3/21, **A**, crown and **B**, oblique lateral views; **C-D**, PM SPU 66-33, sample 3/20, **C**, crown and **D**, ? posterior views; **E**, PM SPU 66-34, sample 3/20, oblique crown view; **F**, PM SPU 66-35, sample 3/20, crown view. **G**, Buccopharyngeal denticle ("*Stemmatias*"-type), PM SPU 66-36, sample NN-32, anterior view. **H**, Monocuspid denticle, PM SPU 66-37, sample NN-32, crown view. **I**, Scale of type 1, PM SPU 66-38, sample NN-19, crown view. **J-K**, Scales of type 2, crown views, **J**, PM SPU 66-39, sample NN-23, **K**, PM SPU 66-40, sample NN-18. **L**, Scale of type 3, PM SPU 66-41, sample NN-18, crown view. All scale bars = 200 µm.

ticles of *Stethacanthulus meccaensis* (Williams) were illustrated by Williams (1985) and considered as probably gill-arch denticles.

The presumably buccopharyngeal denticles possess a multicuspid, double-rowed crown and a slightly convex base (Fig. 6 G). The crown includes the flattened, sharp, recurved cusps which consecutively overlap each other and increase in length posteriorly. The cusp rows diverge posteriorly from the center of the anterior edge. Such denticles have been attributed to the formal taxon "*Stemmatias* (*Stemmatodus*) *bicristus*" (St. John and Worthen, 1875). These buccopharyngeal denticles have been described in several symmoriiforms: *Stethacanthus* (Williams, 1985; Zidek, 1993; Coates and Sequeira, 2001), *Denaea* and *Symmorium* (Williams, 1985).

The monocuspid denticle has a single cusp in the crown and a wide base (Fig. 6H). The cusp is located centrally and is oval in cross section. The denticle base is rounded, with an undulating margin, convex external and flat basal surfaces, with numerous ridges enclosing triangular grooves diverging from the cusp base. The canal foramina open in the top of the triangular grooves. Such denticles have been described from the spine-brush complex or cranial cap of several symmoriiforms, including *Damocles* (Lund, 1986), *Falcatus* (Lund, 1985), *Orestiacanthus* (Lund, 1984), and *Stethacanthus* (Lund, 1974; Zidek, 1993; Coates and Sequeira, 2001). Monocuspid denticles described as the monocuspid teeth of the *Cobelodus* dentition (Zangerl and Case, 1976) actually appear to be denticles derived from the cranial cap on the surface of the shark's head as in *Stethacanthus* (Coates and Sequeira, 2001).

The scales of type 1 possess convex external and basal surfaces (Fig. 6I). The crown includes tubercles of different sizes and shapes occupying the greater part of the base. They are commonly densely packed but may occasionally be separated by grooves. The tubercles bear undulated and branched ridges.

The most common scales of type 2 are characterized by the posteriorly inclined, conical crown bearing two lateral ridges, and sometimes also a median ridge (Fig. 6 J, K). These ridges reach to the sharp top of the crown and may branch basally. They may be separated by either shallow or deep depressions. The base is larger than the crown, has a convex external surface with numerous strong ridges radiating from the cusp base and is separated by triangular grooves. The ridges terminate in marginal processes, forming the strongly undulated edge of the base. The basal surface of the base is concave and wavy.

The crown of the type 3 scales is a complex polyodontode crown that consists of conical, inclined, slightly striated cusp-odontodes (Fig. 6 L), which increase in height from the anterior to posterior edges. The base is polygonal in outline, and slightly wider than the crown, with convex basal surface.

DISCUSSION

The assemblage of chondrichthyans from the Early/Late Carboniferous boundary beds of the Gissar Mountains is quite diverse and contains four taxa of symmoriiforms and a new euselachian. Teeth of *Gissarodus flabellatus* and *Stethacanthulus meccaensis* are dominant in the assemblage. Some of the chondrichthyan teeth, denticles and scales bear traces of parasitism (Fig. 4F). These traces are narrow and very long, sinuous microborings, rounded in cross section, with microgrooves on the boring surface. Such microborings have been reported in teeth of Mesozoic and Cenozoic sharks (Underwood et al., 1999; Delsate et al. 2002; Underwood and Mitchell, 2004) as well as in Carboniferous chondrichthyans (Ivanov, 2007).

The denaeid symmoriiforms are widely distributed Late Paleozoic elasmobranchs. They are common in the Carboniferous and Early Permian. *Denaea williamsi* Ginter and Hansen was found in the Visean-Serpukhovian, Early Carboniferous (Mississippian) of Illinois, USA, England, Scotland, Poland and Moscow Region, Russia (Ginter et al., 2010). *D. fournieri* Pruvost occurs in the Visean of Belgium, *D. saltsmani* Ginter and Hansen - in the Pennsylvanian (Bashkirian-Gzhelian) of the USA (Ginter et al., 2010), and *D. wangi* Wang, Jin and Wang in the Visean-Serpukhovian of Belgium, Germany, Poland and China (Wang et al., 2004; Ivanov and Derycke, 2005; Ginter et al., 2010).

Stethacanthulus meccaensis (Williams), apart from the Carboniferous of Uzbekistan, is known from the Middle Pennsylvanian (Moscovian) of Indiana, Iowa and Oklahoma, USA (Ginter et al., 2010; Pope et al., 2011), and the Wordian-Capitanian, Middle Permian (Guadalupian) of West Texas (Ivanov et al., 2011, 2012b). *Stethacanthulus decorus* (Ivanov) occurs in the Serpukhovian, Early Carboniferous (Mississippian) and Asselian- Artinskian, Early Permian (Cisuralian) of the Urals, Russia (Ivanov, 1999), and in the Roadian, Middle Permian (Guadalupian) of West Texas (Ivanov et al., 2012a). The new joint occurrence of *Stethacanthulus decorus* and *S. meccaensis* in the Late Serpukhovian-Early Bashkirian of the Gissar Mountains, Uzbekistan is a first and was unknown before.

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FISH ASSEMBLAGE FROM THE CAPITANIAN (MIDDLE PERMIAN) OF THE APACHE MOUNTAINS, WEST TEXAS, USA

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Abstract—Fish microremains have been described from the strata equivalent in age to the Lamar Limestone and Reef Trail members of the Bell Canyon Formation, latest Capitanian from the EF and M sections in the Apache Mountains, West Texas, USA. The assemblage includes the symmoriiform *Stethacanthulus meccaensis* (Williams), undetermined symmoriiforms, the jalodontid *Texasodus* sp., euselachian *Sphenacanthus* sp., undetermined euselachians, a probable hybodontoid, and other chondrichthyans, an elonichthyiform *Varialepis* sp., and undetermined actinopterygians.

INTRODUCTION

Fish remains from the Middle Permian (Guadalupian) of West Texas have been previously known mostly from the Guadalupe Mountains and only in one section from the Apache Mountains of the Delaware basin. In the Guadalupe Mountains, they have been recorded in the upper part of the Roadian Cutoff and Brushy Canyon formations, the Roadian-Wordian Cherry Canyon Formation, and the Wordian-Capitanian Bell Canyon Formation (Fig. 1).

Fish microremains were first reported and illustrated by Babcock (1977) from several sections of the Capitan forereef and Lamar Limestone Member of the Bell Canyon Formation outcropping along the Lamar Cuesta, which runs from the Guadalupe Mountains on the north to the northwestern part of the Apache Mountains on the south. Chondrichthyan and actinopterygian microremains were found in 86 samples but not determined by the author (Babcock, 1977). They are represented by isolated cladodont teeth of a symmoriiform (Babcock, 1977, fig. 14-18); a monocuspid denticle probably belonging to a symmoriiform (ibid., fig. 14-7); the teeth of probably a jalodontid *Texasodus* (ibid., figs. 14-12, 13); various chondrichthyan scales (ibid., figs. 12-6, 7; 14-8 – 11, and actinopterygian teeth (ibid., figs. 14-1, 2, 4). An incomplete jaw with dentition belonging to holocephalians was recorded also from the Lamar Limestone Member in Guadalupe National Park (Bell and Polcyn, 2011). Shark teeth and other fish remains have also been noted from the Brushy Canyon (Roadian) and Cherry Canyon (Roadian-Wordian) formations of Guadalupe National Park (Hunt et al., 2006).

Two new genera and species of jalodontid sharks, *Isacrodus marthae* Ivanov, Nestell and Nestell and *Texasodus varidentatus* Ivanov, Nestell and Nestell (Ivanov et al., 2012a) were described recently from two sections in the Guadalupe Mountains: the Quarry section (Williams Ranch Member, Cutoff Formation, Roadian) and the PI section (Hegler and Pinery Limestone Members, Bell Canyon Formation, upper Wordian-lower Capitanian).

An assemblage of diverse fishes has been found in the Williams Ranch Member of the Cutoff Formation in the Guadalupe Mountains (Ivanov et al., 2012b). Fish remains are represented by teeth of the symmoriiform *Stethacanthulus decorus* (Ivanov); stethacanthid teeth; buccopharyngeal denticles of symmoriiforms; jalodontid teeth of *Isacrodus marthae* and of *Adamantina foliacea* Ivanov; teeth of a new species of hybodontoid *Polyacrodus*; anachronistid teeth of *Cooleyella amazonensis* Duffin, Richter and Neis and C. sp. nov.; various chondrichthyan scales; actinopterygian skull bones, teeth, tooth plates, pharyngeal denticles, vertebrae and scales belonging to a haplolepid and some elonichthyids such as *Alilepis* sp. nov.

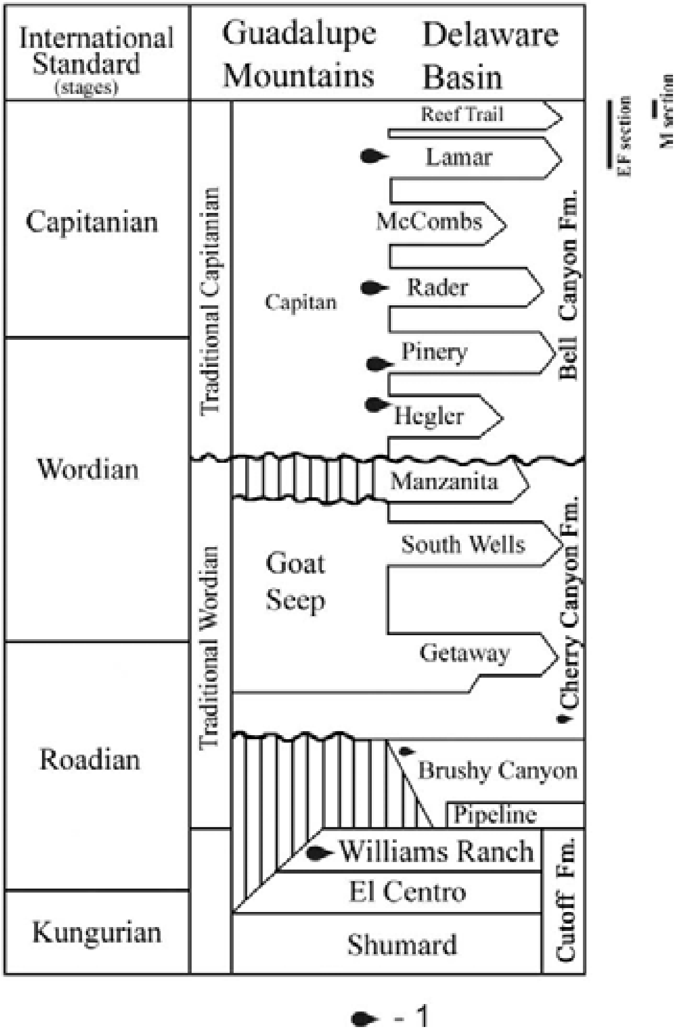

FIGURE 1. Stratigraphic position of the EF and M sections and the known occurrences of fish assemblages in the Guadalupian Stratigraphic Scale of the Delaware basin in West Texas. **1**, Position of the previously known occurrences of the fish assemblages (see "Introduction").

The PI section of the Hegler and Pinery Limestone members of the Bell Canyon Formation yields teeth of the symmoriiform *Stethacanthulus meccaensis*, symmoriiform buccopharyngeal denticles, teeth of the jalodontid *Texasodus varidentatus*, a tooth of the anachronistid *Cooleyella* sp., cartilage fragments and chondrichthyan scales, actinopterygian teeth, denticles and tooth plates, scales of elonichthyids and *Alilepis* sp. nov. (Ivanov et al., 2012a; Nestell et al., 2012).

A fish assemblage has been reported in the Rader Limestone Member of the Bell Canyon Formation in the "Rader slide" section of the Guadalupe Mountains (Ivanov et al., 2011). The assemblage includes chondrichthyan and actinopterygian microremains: a tooth of the jalodontid *Texasodus varidentatus*; teeth of the symmoriiform *Stethacanthulus meccaensis*, several symmoriiform buccopharyngeal denticles; teeth of a family of hybodontoid sharks similar to *Polyacrodus*; euselachian scales; teeth of a new species of *Cooleyella*; elonichthyd scales and actinopterygian gill-raker denticles.

In the northwestern part of the Apache Mountains, fish microremains were known previously only from section H' of Babcock (1977), which is located in a road cut about 15 km north of the EF section on TX FM 2185. The fish microremains are represented by an isolated tooth of the symmoriiform *Stethacanthulus meccaensis* (Williams) (Babcock, 1977, fig. 14-17); tricuspid denticles probably belonging to symmoriiforms (Ibid., Fig. 14-16); various chondrichthyan scales (ibid., figs. 12-1, 2, 5, 6, 8, 9, 14-5, 6, 14, 15, 19); scales similar to those of elonichthyiform actinopterygians (ibid., figs. 12-3, 4), and actinopterygian teeth (ibid., fig. 14-3).

Fish microremains presented here occur in strata equivalent in age to the Lamar Limestone and Reef Trail members of the Bell Canyon Formation in the EF and M sections in the Apache Mountains. The fish assemblage contains isolated chondrichthyan teeth, scales and denticles, actinopterygian teeth, tooth plates, denticles and scales. The fish microremains were extracted from conodont residues recovered by detailed bed-by-bed sampling of the limestone strata and their standard processing by formic acid and heavy liquid separation.

GEOLOGICAL SETTING

The EF and M sections are outcrops in road cuts located along the Texas Farm to Market road (FM) 2185 about 50 km northeast of Van Horn, Culberson County, Apache Mountains (Fig. 2). In the EF section the uppermost beds of the Bell Canyon Formation of late Guadalupian age and a few meters of the overlying laminated strata of the Castile Formation (early Lopingian) crops out on the west side of the road cut (Lambert et al., 2002; Nestell et al., 2006; Nestell and Nestell, 2010; Wardlaw and Nestell, 2010). The strata of the EF section are divided onto five units: A, B, C, D and E (Nestell and Nestell, 2010). Unit A is a fining upward carbonate debris flow with coarse fossiliferous clasts in the lower part and laminated fine-grained limestone in the upper part. This unit contains two small blocks of thin-bedded limestone, one in the lower part and another one in the upper part (Fig. 3). The lower block with a thickness of approximately 2 m contains the fusulinids *Paradoxiella pratti* Skinner and Wilde, radiolarians *Follicucullus scholasticus* Ormiston and Babcock, and conodonts *Jinogondolella shannoni* Wardlaw and *J. postserrata* (Behnken). The conodonts designate the age of this block as equivalent to the Lamar Limestone Member (Wardlaw and Nestell, 2010). The second block, with a thickness of less than 1 m, contains poorly preserved radiolarians and conodonts *Jinogondolella altudaensis* (Kozur) referred to the *J. altudaensis* Zone, which is recognized in the Reef Trail Member of the Guadalupe Mountains area (Nestell et al., 2007a). This zone also includes units B, C and D of the EF section (Lambert et al., 2002; Nestell et al., 2007b; Wardlaw and Nestell, 2010). The detailed lithological description of these units can be found in Nestell and Nestell (2010). Unit E contains the fusulinids *Paraboultonia splendens* Skinner and Wilde, radiolarians and the conodonts *Clarkina hongshuiensis* Henderson, Mei and Wardlaw, *J. altudaensis* and *J. granti* (Mei and Wardlaw) referred to the *Clarkina hongshuiensis* Zone of the uppermost Guadalupian (Lambert et al., 2002; Wardlaw and Nestell, 2010). Thus, the EF section includes the strata equivalent in age to the Lamar Limestone and Reef Trail members of the Bell Canyon Formation of the Guadalupe Mountains.

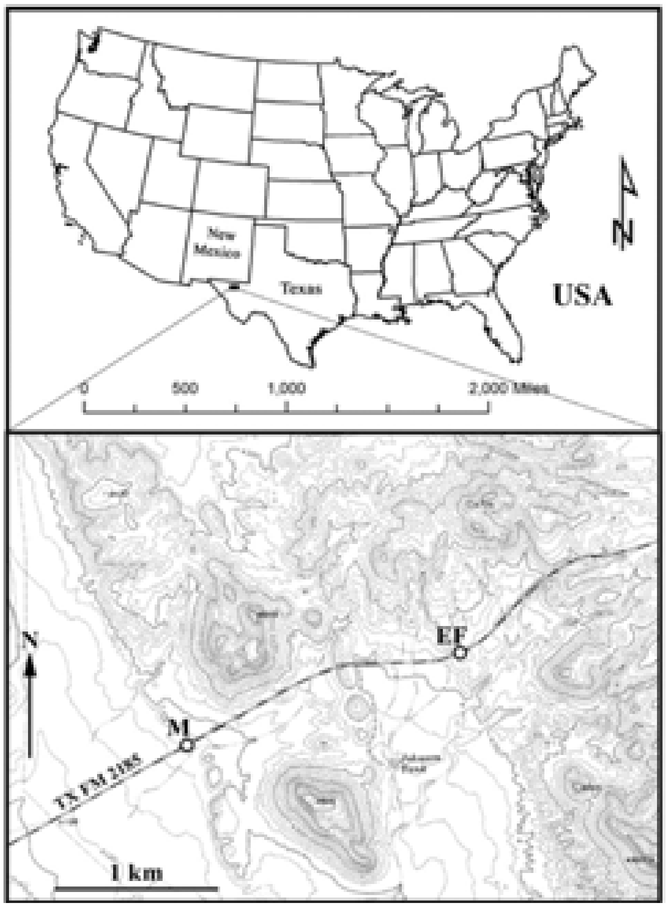

FIGURE 2. Location of the EF (31.3083N, 104.5422W) and M (31.3031N, 104.5596W) sections along the Texas FM road 2185 in the Apache Mountains, West Texas.

The M section is located along the Texas FM road 2185 about 1.8 km west-southwest of the EF section and in shallow road cuts on both sides of the road (Nestell et al., 2006). The most complete section is exposed on the west side of the road and is subdivided onto six lithological units which can be correlated with the upper part of the unit C, units D, and E of the EF section according to fossil content (Nestell et al., 2006). The section is very similar lithologically to that of the EF section with the exception of the presence of a debris flow of several thin beds in unit 2 (equivalent to the upper part of unit C in the EF section) containing abundant *Paraboultonia splendens*. Evidence of this debris flow is not present in the EF section. Another distinctive difference of the stratigraphic succession of the M section is the presence of siltstone beds in units 5 and 6 (in strata equivalent to the upper part of unit E of the EF section). The conodont succession is very similar to that occurring in units C, D, and E in the EF section.

Fish remains were found in 14 stratigraphic levels of the EF section (Fig. 3) and in three levels of the M section (samples M-2, M-15, M-19).

SYSTEMATIC PALEONTOLOGY

The specimens described here are deposited in the collections of the U.S. National Museum in Washington D. C. as specimens USNM 557852-557882.

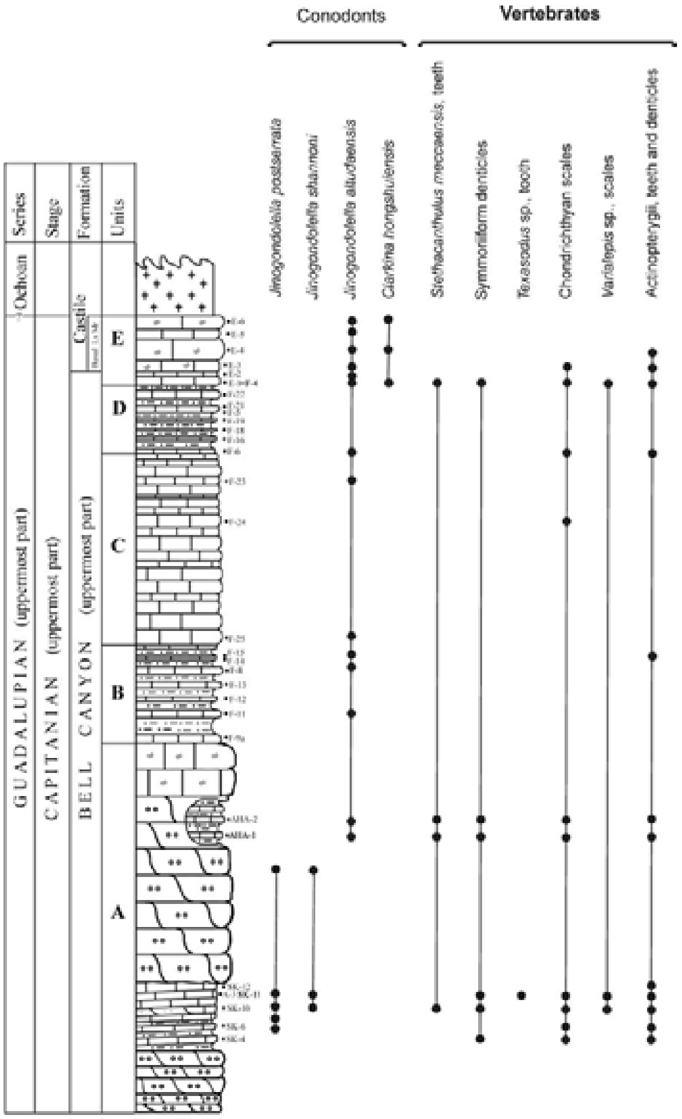

FIGURE 3. Distribution of some conodont and fish taxa in the EF section (stratigraphic column after Nestell and Nestell, 2010).

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Superorder CLADODONTOMORPHI Ginter, Hampe and Duffin, 2010
Order SYMMORIIFORMES Zangerl, 1981
Family SYMMORIIDAE Dean, 1909
Stethacanthulus Zangerl, 1990
Stethacanthulus meccaensis (Williams, 1985)
Figure 4A-B

Referred specimens: Six isolated teeth and tooth fragments from the EF section, samples SK-10 (equivalent of the Lamar Limestone Member), F-4, AHA-1 and AHA-2 (equivalent of the Reef Trail Member).

Description: The teeth have a cladodont, five-cusped, narrow crown and considerably lingually extended base. The cusps are thin, slightly sigmoidal incurved and rounded in cross section. The central cusp is slightly higher than the lateral cusps. The small intermediate cusplets are rather separated from the central cusp. The lateral cusps are quite inclined from the central one. The labial surface of all cusps bears two-three distinct, straight ridges, but the lingual surface is covered by rare tiny striations. A gentle lateral carina marks the boundary between the labial and lingual cusp faces. The crown is formed at an angle with the base of about 40°.

The tooth base has a spoon-like shape with narrow labial and extended lingual parts. The outlines of the base vary from oval, elongated lingually to rounded, extended mesio-distally. The base lacks any articulation elements, but possesses a lingual depression on the occlusal surface, and a transverse medial prominence on the basal surface. The lingual depression is shallow and triangular in shape: the apex of that triangle is placed just lingually from the central cusp. The arched prominence is limited by two lateral depressions on each side. Two foramina of the main vascular canal open on the occlusal side of the base, in the apex of triangular lingual depression, and on the labio-basal edge below the central cusp.

Remarks: There is a series between two distinct morphotypes among the teeth of *Stethacanthulus meccaensis* (Williams, 1985; Ivanov, 1999). The first morphotype is characterized by a narrow crown including three to five cusps; oval or rounded, elongated lingually, and a spoon-like base wider then the crown. The teeth of the second morphotype possess a wide crown containing five to seven high cusps; numerous ridges in the labial ornamentation; and a trapezoidal base without the elongated lingual part. The teeth described here belong to the first morphotype.

Order incertae sedis
Family JALODONTIDAE Ginter, Hairapetian and Klug, 2002

Type genus: *Jalodus* Ginter, 1999

Referred genera: *Jalodus* Ginter, 1999; *Adamantina* Bendix-Almgreen, 1993; *Isacrodus* Ivanov, Nestell and Nestell, 2012a; *Texasodus* Ivanov, Nestell and Nestell, 2012a.

Texasodus Ivanov, Nestell and Nestell, 2012a
Texasodus sp.
Figure 4H-J

Referred material: One isolated tooth from the EF section, sample SK-11 (equivalent of the Lamar Limestone Member).

Description: The tooth has a tricuspid, diplodont crown with small central and high lateral cusps. The lateral cusps are oval in cross section, diverge from the central one and are slightly incurved laterally. The central cusp is straight, rounded in cross section. The cusps are curved lingually, bear a distinct lanceolate ornamentation on the labial surface and a few straight cristae on the lingual side. The labial ornamentation consists of three inverted “V”-nested cristae.

The tooth base is rectangular in shape, considerably extended lingually, convex on the occlusal side and concave on the basal side, has a thickened lingual part that is separated by a shallow depression. The base bears two slightly prominent, oval labio-basal tubercles separated by a very narrow depression. Their axes lie on one line.

Remarks: The described tooth differs from the tricuspid teeth of *Texasodus varidentatus* Ivanov, Nestell and Nestell (Ivanov et al., 2012a) in having a considerably smaller central cusp and a rectangular shape of the tooth base that is most extended lingually. The lateral cusps in such teeth are equal in height or slightly higher than the central one. Some teeth of the noted species with four cusps in the crown have a pair or one inner cusps that are smaller than the lateral ones. The foramina of the vascular canals are located in the center of the lingual rim and of the basal surface.

Cohort EUSELACHII Hay, 1902
Order incertae sedis
Family SPHENACANTHIDAE Maisey, 1982
Sphenacanthus sp.
Figure 4K

Referred material: One isolated tooth from the M section, sample M-19 (equivalent of the Reef Trail Member).

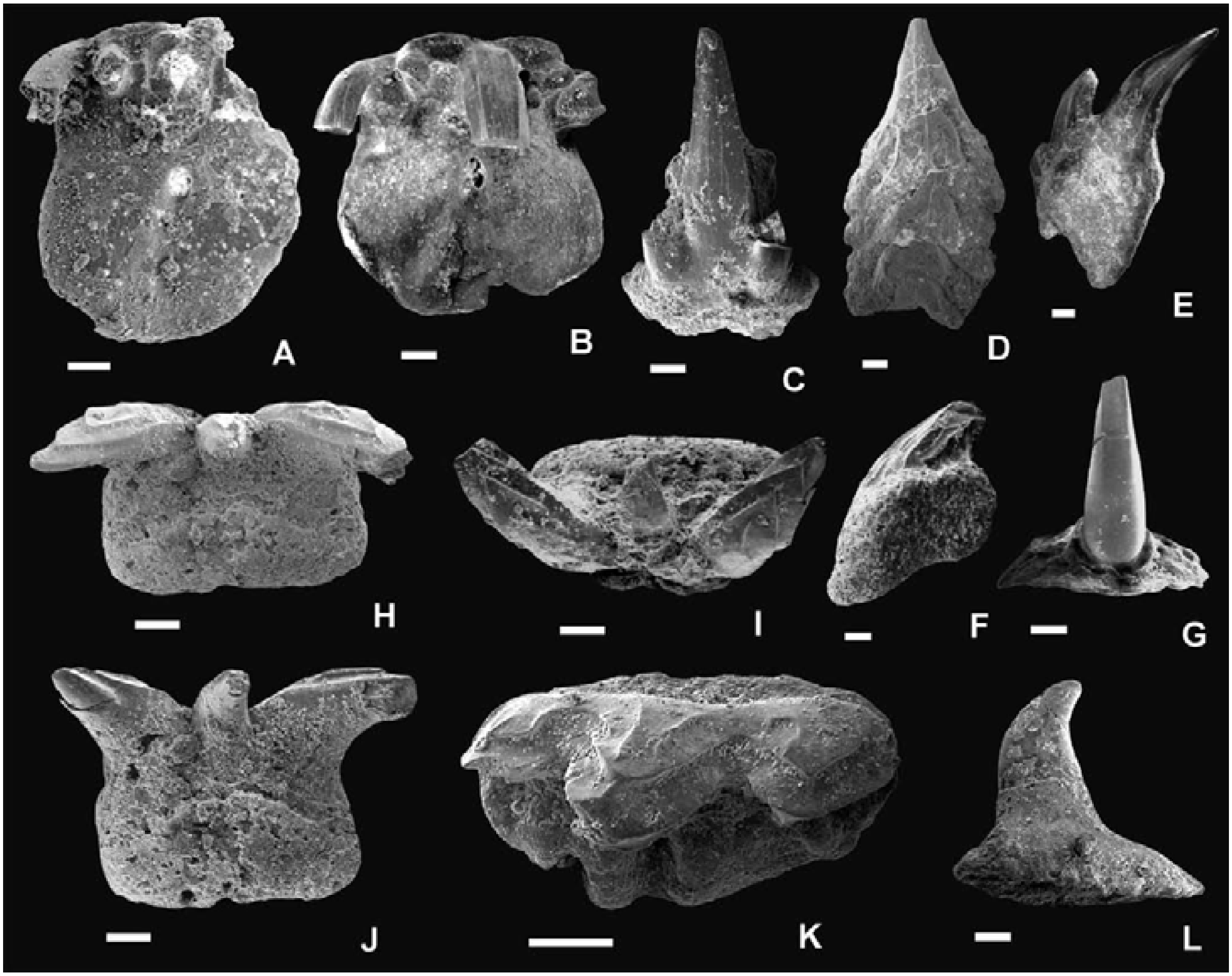

FIGURE 4. Chondrichthyan microremains from the EF (**A-J**, **L**) and M (**K**) sections of the Apache Mountains. **A-B**, *Stethacanthulus meccaensis* (Williams, 1985), teeth in occlusal views, **A**, USNM 557851, sample SK-10, **B**, USNM 557852, sample AHA-1. **C**, Symmoriiform tricuspid denticle in crown view, USNM 557853, sample SK-11. **D-E**, Symmoriiform buccopharyngeal denticles ("*Stemmatias*"-type) in crown (**D**) and lateral (**E**) views, **D**, USNM 557854, sample SK-10, **E**, USNM 557855, sample SK-10. **F**, Symmoriiform monocuspid denticle in lateral view, USNM 557856, sample F-4. **G**, Symmoriiform brush complex denticle in anterior view, USNM 557857, sample F-4. **H-J**, *Texasodus* sp., tooth in occlusal (**H**), labial (**I**) and lingual (**J**) views, USNM 557858, sample SK-11. **K**, *Sphenacanthus* sp., tooth in occlusal view, USNM 557859, sample M-19. **L**, Possible hybodontoid cephalic spine in lateral view, USNM 557860, sample SK-11. Scale bar = 100 µm.

Description: The teeth possess a pyramidal, slightly asymmetrical crown. Three cusps are rounded in cross section, separate but basally fused, inclined lingually and laterally. The central cusp is higher and thicker than the lateral ones. One lateral cusp inclined to the tooth center is slightly larger than the other lateral one. The cusps are covered by coarse ridges on all of the cusp surfaces. The ridges on the lingual side form a lanceolate structure of inverted "V"-nested crista traced along the crown, from one lateral cusp to other. The middle part of the cusps under the lanceolate crista bears one or two subparallel, straight ridges, some not reaching the crista.

The tooth base is of euselachian-type, arched and thick, quite lingually and slightly labially extended, with convex occlusal and concave basal surfaces. The lingual part is perforated with large foramina of vascular canals.

Remarks: Various authors after the establishment of the family Sphenacanthidae by Maisey (1982) assigned this family to the superfamily Ctenacanthoidea (Zangerl, 1981), or to Euselachii incertae sedis (Ginter et al., 2010). Probably after a completed revision of all representatives of such elasmobranchs, the Sphenacanthidae could belong to the superfamily Hybodontoidea based on the similarities in the structures of teeth and fin spines.

Chondrichychthyan denticles and scales

Buccopharyngeal denticles of symmoriiforms ("*Stemmatias*"-type)

Figure 4D-E

Referred material: Five denticles from the EF section, samples SK-10, SK-11 (equivalent of the Lamar Limestone Member), AHA-1, AHA-2 (equivalent of the Reef Trail Member), and from the M section, sample M-19 (equivalent of the Reef Trail Member).

Description and remarks: These denticles have a multicuspid, single-rowed crown consisting of conical, sharp, recurved cusps. The cusps consecutively overlap each other increasing in height (Fig. 4D) or form a whorl with a space between the cusps (Fig. 4E). The cusps bear straight, distinct cristae and lateral carinae. The denticle base in the first type is flat or concave, wider than the crown. The whorl-like denticle has a considerably convex base, equally as wide as in the crown.

Such "*Stemmatias*"-type denticles are known as buccopharyngeal denticles in several symmoriiform sharks: *Cobelodus* (Zangerl and Case, 1976), *Stethacanthus* (Williams, 1985; Coates and Sequeira, 2001), and *Symmorium* (Williams, 1985).

Tricuspid denticles
Figure 4C

Referred material: Two denticles from the EF section, samples SK-10 and SK-11 (equivalent of the Lamar Limestone Member).

Description and remarks: The denticle has one large central and two small lateral cusps. They are conical, sharp, striated, inclined posteriorly, oval in cross section. The central cusp bears lateral carina. The lateral cusps are located anteriorly in comparison with the central one. The base is wider than the crown, with convex external and basal surfaces.

Williams (1985) illustrated similar denticles of *Stethacanthulus* (*Denaea*) *meccaensis* (Williams) and considered that they are probably gill-arch denticles.

Monocuspid denticles
Figure 4F, G, L

Referred material: Seven symmoriiform denticles from the EF section, samples SK-5, SK-8, SK-10 (equivalent of the Lamar Limestone Member), F-4, and from the M section, sample M-19 (equivalent of the Reef Trail Member); one possible hybodontoid cephalic spine from the EF section, sample SK-11 (equivalent of the Lamar Limestone Member).

Description and remarks: The denticles with a single cusp in the crown are represented by three morphotypes. Denticles of the first type possess a thick cusp, are curved posteriorly, flattened laterally, and are covered by coarse cristae (Fig. 4F). The base of such denticles is thick and considerably extended basally. They can belong to the denticles of the spine-brush complex or to the monocuspid buccopharyngeal denticles of symmoriiform sharks.

The denticles of the second morphotype have a long, thin, smooth cusp, circular in cross section, slightly incurved posteriorly, and with an oval, laterally extended base with convex upper and flat basal surfaces (Fig. 4G). Such denticles have been described in the spine-brush complex or cranial cap of several symmoriiforms, such as *Stethacanthus* (Lund, 1974; Zidek, 1993; Coates and Sequeira, 2001), *Orestiacanthus* (Lund, 1984), *Falcatus* (Lund, 1985) and *Damocles* (Lund, 1986), but only some denticles from the spine-brush complex or the cranial cap of *Stethacanthus* have a curved crown (Zidek, 1993; Coates and Sequeira, 2001).

The third denticle type possesses a single hook-like cusp and an oval, longitudinally elongated base (Fig. 4L). The cusp is smooth, oval in cross section, incurved slightly in the basal part and strongly in the top part, displaced anteriorly. The base has a convex external and considerably concave basal surface. The denticle resembles the cephalic spine of some hybodontoids. Such cephalic spines were reported in the Mesozoic hybodontoids (e.g. Rees, 1999; Rees and Underwood, 2008).

Scales of type 1
Figure 5A-B

Referred material: 14 scales from the EF section, samples SK-7, SK-8, SK-10, SK-11 (equivalent of the Lamar Limestone Member), AHA-2, AHA-3, F-4, F-6, F-24, and from the M section, sample M-2 (equivalent of the Reef Trail Member).

Description and remarks: These typical placoid scales have a drop-like, elongate crown, well developed neck and small base. The crown is inclined, the pointed posterior edge overtops under the round anterior part. The flat external surface of the crown bears distinct lateral and medial ridges. The medial ridge varies from short, placed anteriorly (Fig. 5A) to wide and long, reaching the posterior edge (Fig. 5B). The lateral ridges can project behind the lateral margins in crowns with a long medial ridge. The scale neck is narrow, low in the anterior part and high posteriorly. The base is pyramidal, with a concave basal surface. Two to four foramina of vascular canals open in the shallow depression of the neck, as well as one foramen – in the center of the basal surface. Such scales were described as the formal taxon *Moreyella* by Gunnell (1933) or *Fragilicorona* and *Labrilancea* by Johns et al. (1997), and are usually assigned to euselachian sharks.

Scales of type 2
Figure 5C

Referred material: Six scales from the EF section, samples SK-4, SK-11 (equivalent of the Lamar Limestone Member), AHA-2, E-3, and from the M section, sample M-19 (equivalent of the Reef Trail Member).

Description and remarks: The crown of such scales is slightly inclined anteriorly, oval with a convex external surface, has a short acuminate posterior and slightly undulating anterior edges. Four to five distinct, low and parallel ridges cover the external surface of the crown and mostly do not reach the posterior edge. The neck is moderate and high, bears two foramina of vascular canals on the posterior surface. The base is pyramidal, with slightly undulating external and flat basal surfaces, rather wider than the crown. They resemble some scales described as *Proprigalea* by Johns et al. (1997) and probably belong to euselachians.

Scales of type 3
Figure 5D

Referred material: Five scales from the EF section, samples SK-11 (equivalent of the Lamar Limestone Member), AHA-1, AHA-2, E-3, F-4 (equivalent of the Reef Trail Member).

Description and remarks: The scales of type 3 possess a high crown elongated upward and inclined anteriorly. The crown has three strong ridges terminated in three acuminate, long apices and separated by deep depressions. The slopes of a depression bear serrated ridges and striations oriented normally to the ridge axis. The scale neck is not distinct. The base has undulated edges, convex external and concave basal surfaces, and numerous grooves with canal foramina at the scale neck. These scales are mostly referred to hybodontoid elasmobranches (e.g., Reif, 1978).

Scales of type 4
Figure 5E-F

Referred material: Four scales from the EF section, samples SK-10, SK-11 (equivalent of the Lamar Limestone Member), and AHA-2 (equivalent of the Reef Trail Member).

Description and remarks: The crown of the type 4 scales is shallowly inclined anteriorly, elongated, from almost rounded with a short, slightly acuminated posterior part (Fig. 5F) to long and narrow with a thin posterior part and sharp apex (Fig. 5E). The external surface of the crowns bears four to six narrow, high ridges separated by deep depressions. They do not reach the posterior edge in narrow scales with a long and smooth posterior part. The neck is very low in the anterior part and slightly higher posteriorly. The base is low, smaller than the crown, with convex external and flat basal surfaces. The scales of type 4 were reported as the formal taxon *Cooperella* by Gunnell (1933). They possibly belong to euselachians. Similar scales were described and illustrated for some euselachians (e.g., Böttcher and Duffin, 2000; Wang et al., 2009).

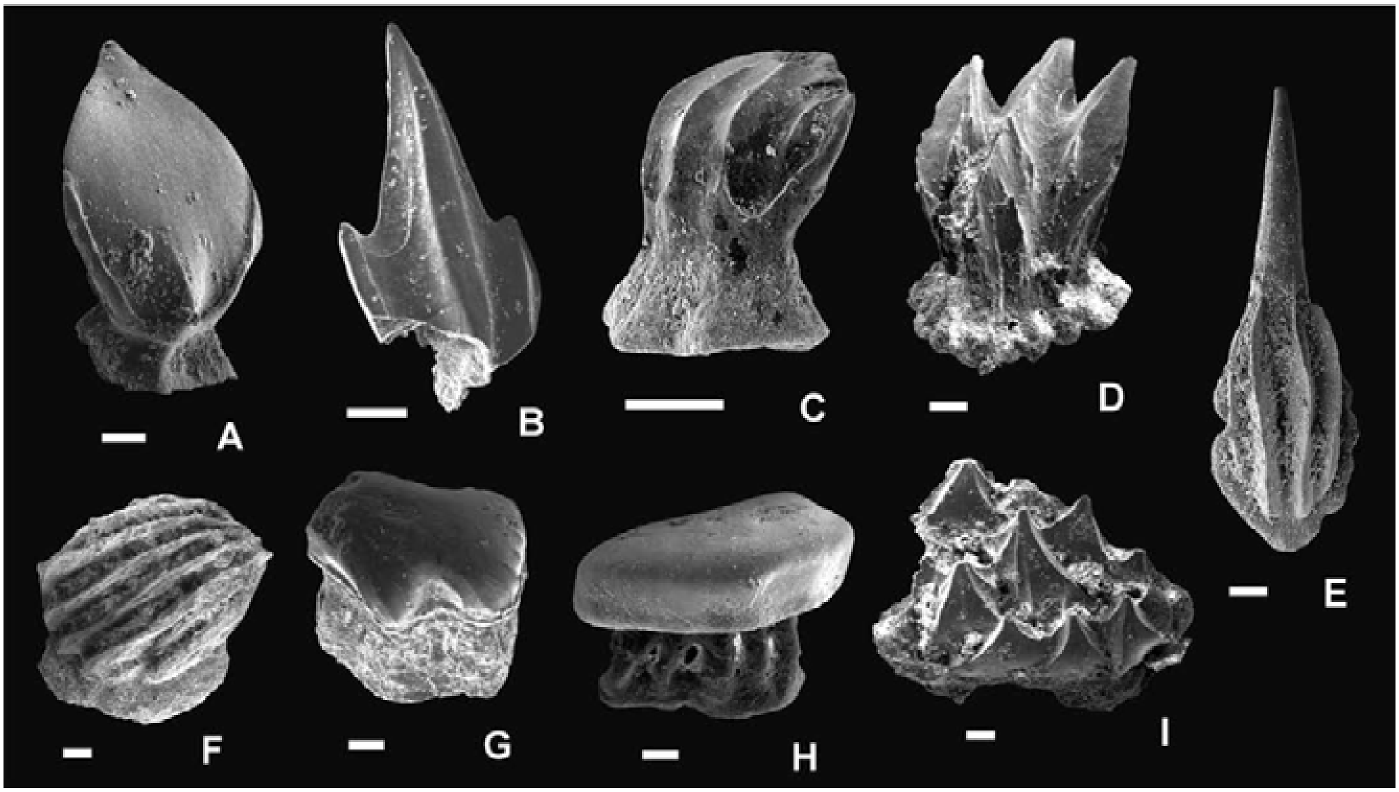

FIGURE 5. Chondrichthyan scales from the EF (**A-B**, **D-L**) and M (**C**) sections of the Apache Mountains. **A-H**, Euselachian scales, **A-B**, Scales of type 1 in anterior views, **A**, USNM 557861, sample F-4, **B**, *Moreyella* type, USNM 557862, sample SK-11, **C**, Scale of type 2 in oblique lateral view, USNM 557863, sample M-19, **D**, Scale of type 3 in anterior view, USNM 557864, sample F-4, **E-F**, Scales of type 4 (*Cooperella* type) in crown (**E**) and oblique crown (**F**) views, **E**, USNM 557865 sample SK-11, **F**, USNM 557866, sample SK-10, **G-H**, Scales of type 5 (*Kirkella* type) in oblique crown (**G**) and lateral (**H**) views, **G**, USNM 557867, sample SK-10, **H**, USNM 557868, sample SK-10. **I**, Scales of type 6 (ctenacanthid type) in crown view, USNM 557869, sample SK-11. Scale bar = 100 µm.

Scales of type 5
Figure 5G-H

Referred material: Eight scales from the EF section, samples SK-10, SK-11 (equivalent of the Lamar Limestone Member), AHA-2, F-4, and from the M section, sample M-2 (equivalent of the Reef Trail Member).

Description and remarks: The scales of type 5 possess a flat, thick, polygonal crown and a high base. The crown has a horizontal or slightly inclined external surface, and vertical lateral sides. The edges of the crown are rounded and sometimes undulated with tiny, short ridges. The crown/base boundary is distinct but with a well developed neck. The base is rather rounded or polygonal in cross section, higher but narrower than the crown, has almost vertical lateral and flat basal surfaces. It is perforated with numerous foramina of vascular canals opening in the top of the vertical grooves. Gunnell (1933) named such scales *Kirkella*.

Scales of type 6
Figure 5I

Referred material: Three scales from the EF section, samples SK-7, SK-11 (equivalent of the Lamar Limestone Member).

Description and remarks: The scales have a complex polyodontode crown and polygonal base. The crown consists of seven to eight odontodes fused at the base. They are conical, inclined, with acuminate apices directed posteriorly, covered by ridges reaching the apex. The neck is not developed. The base has a slightly convex basal surface, and is slightly larger than the crown. Such type of scales is often considered to be ctenacanthid scales.

Class OSTEICHTHYS Huxley, 1880
Subclass ACTINOPTERYGII Cope, 1887
Order ELONICHTHYIFORMES Kazantseva, 1977
Family VARIALEPIDIDAE A. Minikh, 1990
Varialepis A. Minikh, 1990

Remarks: The year of genus establishment was usually indicated as 1986, but this manuscript was not published and the first description of the genus should be specified as 1990 (Minikh, 1990).

Varialepis sp.
Figure 6A-C

Referred material: Four scales from the EF section, samples SK-10, SK-11 (equivalent of the Lamar Limestone Member), and F-4 (equivalent of the Reef Trail Member).

Description: These flank scales are rhomboidal, with a ganoine-covered field, and a narrow overlapping area along the dorsal edge. The anterior and ventral edges of the scale are straight, the dorsal one is sinuously curved, the posterior (caudal) edge is straight or serrated. The ganoine-covered field includes two to four long ridges in the anterior part and a rhomboid, unornamented ganoine posterior part. The ganoine ridges are separated by grooves of the same width or narrower. The first ridge is straight, closely spaced and parallel to the anterior edge; other ridges gradually become more curved and shorter in the direction to the scale center. The dorsal articular peg is not developed. One scale has a rather extended rostro-dorsal process (Fig. 6A). The unornamented ganoine posterior part bears rare elongated pore holes.

Remarks: The described scales of *Varialepis* sp. are quite similar to some scales of *V. vitalii* A. Minikh and *V. oris* Yankevich (Minikh and

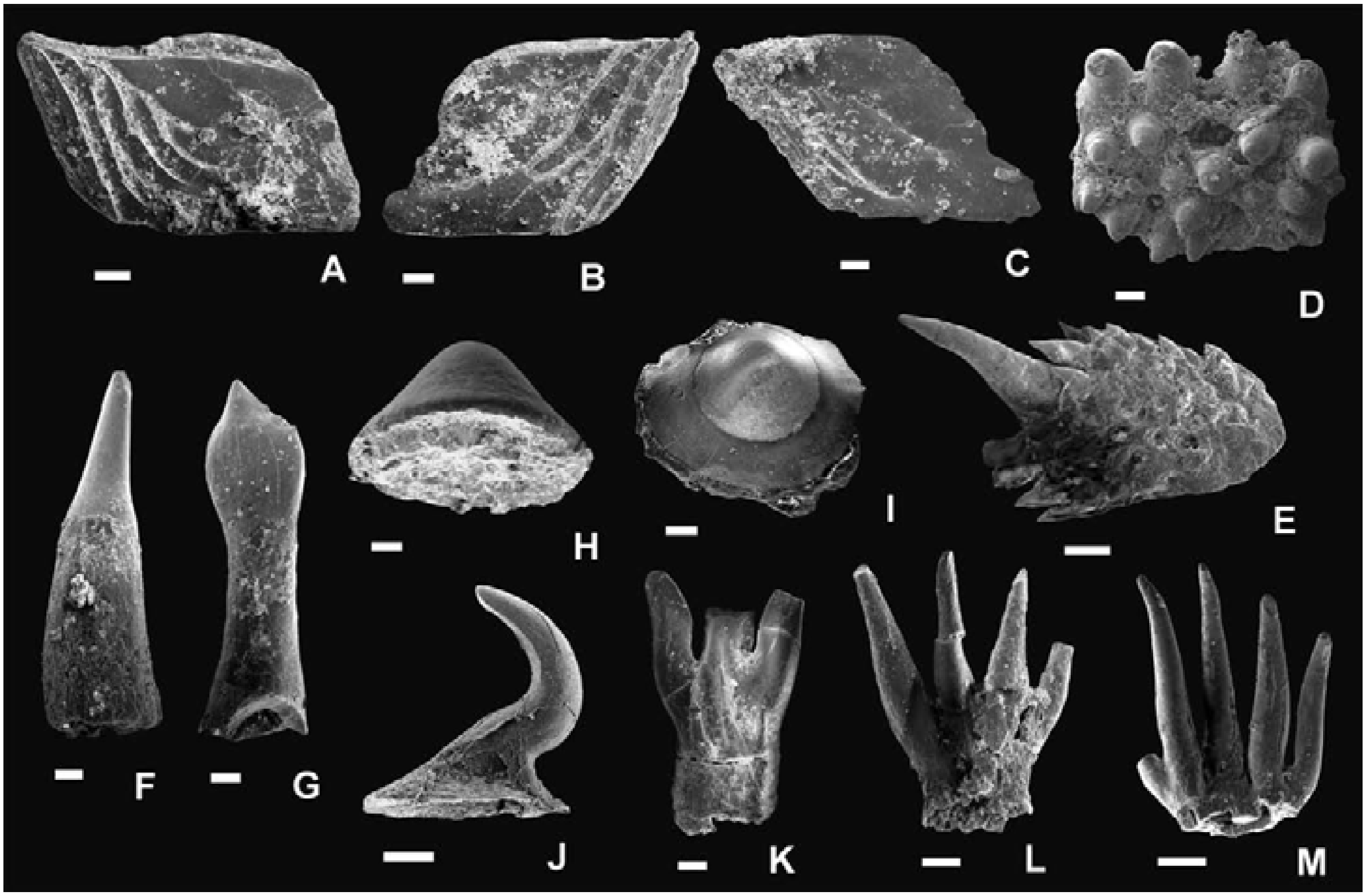

FIGURE 6. Actinopterygian microremains from the EF section of the Apache Mountains. **A-C**, *Varialepis* sp., scales in external view, **A**, USNM 557870, sample SK-11, **B**, USNM 557871, sample SK-10, **C**, USNM 557872, sample SK-11. **D-E**, Actinopterygian tooth plates, **D**, USNM 557873, sample SK-11, **E**, USNM 557874, sample E-3. **F-I**, Actinopterygian teeth in lateral (**F-H**) and oblique occlusal (**I**) views, **F**, USNM 557875, sample SK-10, **G**, USNM 557876, sample SK-11, **H**, USNM 557877, sample SK-10, **I**, USNM 557878, sample E-1. **J-M**, Actinopterygian possible gill-raker denticles in lateral (**J**) and ?anterior (**K-M**) views, **J**, USNM 557879, sample E-3, **K**, USNM 557880, sample SK-11, **L**, USNM 557881, sample F-6, **M**, USNM 557882, sample E-3. Scale bar = 100 µm.

Minikh, 2009) but differ from them by the larger unornamented ganoine posterior part and wider grooves between the ganoine ridges.

Actinopterygian tooth plates, teeth and denticles
Figure 6D-M

Referred material: Two tooth plates from the EF section, samples SK-11 (equivalent of the Lamar Limestone Member), E-3 (equivalent of the Reef Trail Member). 23 isolated teeth from the EF section, samples SK-4, SK-7, SK-8, SK-10, SK-11, SK-12 (equivalent of the Lamar Limestone Member), AHA-1, AHA-2, AHA-3, E-3, E-4, F-4, F-6, F-7, F-15 (equivalent of the Reef Trail Member), and from the M section, samples M-2, M-15, M-19 (equivalent of the Reef Trail Member). Seven isolated denticles from the EF section, samples SK-10, SK-11 (equivalent of the Lamar Limestone Member), E-3, F-4, F-6 (equivalent of the Reef Trail Member).

Description and remarks: One tooth plate is a small dentigerous platelet with 21 conical and smooth teeth or places of tooth attachment and with a concave basal surface (Fig. 6D). The teeth are located in parallel rows, and are higher in one marginal row and grow down at the opposite side. A second tooth plate has an oval, slightly convex bone base bearing numerous conical, smooth small teeth on all external surface and one large curved tooth at the plate edge (Fig. 6E).

The isolated teeth are smooth with acrodin caps typical of palaeoniscoid actinopterygians. They are represented by three morphotypes. The first morphotype has straight or slightly curved, high-conical teeth with a distinct boundary of acrodin (Fig. 6F). The teeth of morphotype 2 are cylindrical with flattened but sharpened apices (Fig. 6G). The teeth of morphotype 3 are characterized by a low-conical, broad based form (Fig. 6H-I).

There are two types of denticles in the collection from the EF and M sections. The first type of denticles possesses a hook-like shape with an incurved toward, sharpened crown and an oval and low-conical base with a concave basal surface (Fig. 6J). The denticles of the second type have a cylindrical low part and a wide multicuspid crown (Fig. 6K-M). The cusps are from three to five, thin, long, straight or slightly curved, rounded in cross section. These denticles possibly are gill-raker denticles or pharyngeal teeth of actinopterygian fishes.

DISCUSSION

The strata exposed in the Apache Mountains as equivalents of the Lamar Limestone and Reef Trail members (EF section) and equivalent of the Reef Trail Member (M section) contain the remains of symmoriiform *Stethacanthulus meccaensis* (Williams), undetermined symmoriiforms, jalodontid *Texasodus* sp., euselachian *Sphenacanthus* sp., undetermined euselachians, probably a hybodontoid, and other chondrichthyans, elonichthyiform *Varialepis* sp. and undetermined actinopterygians. The actinopterygian microremains are dominant in the fish assemblage from the EF section. Their isolated teeth occur almost in each of the samples containing fish remains. Actinopterygian scales and tooth plates, chondrichthyan teeth are rarely found, but chondrichthyan scales denticles are quite common.

Symmoriiform sharks are common in the Late Paleozoic. Their radiation began in the Serpukhovian, Early Carboniferous (Mississippian) and continued until the Artinskian, Early Permian (Cisuralian). They were not diverse in the Middle Permian and are represented generally by the two genera *Stethacanthulus* and *Stethacanthus*. The latter survived to the end of the Late Permian. Besides, in the Capitanian of the Apache Mountains, *Stethacanthulus meccaensis* occurs in the Middle Pennsylvanian (Moscovian) of Indiana, Iowa and Oklahoma, USA (Ginter et al., 2010; Pope et al., 2011), in the Lower/Upper Carboniferous boundary beds of the Gissar Ridge, Uzbekistan (Ivanov, 2005), in the Bell Canyon Formation, the Hegler and Pinery Limestone members (Wordian-Lower Capitanian), and the Rader Limestone and Lamar Limestone members (Capitanian) of the Guadalupe Mountains, West Texas, USA (Babcock, 1977; Ivanov et al., 2011, 2012a).

The teeth of the jalodontid shark *Texasodus varidentatus* Ivanov, Nestell and Nestell have been found in the Hegler, Pinery and Rader Limestone members of the Wordian–Capitanian Bell Canyon Formation in the Guadalupe Mountains, West Texas, USA (Ivanov et al., 2011, 2012a). Representatives of genus *Sphenacanthus* are widely distributed in the Carboniferous, from the Serpukhovian to the Gzhelian (Ginter et al., 2010), also occur in the Artinskian, Early Permian of Brazil (Chahud et al., 2010) and in the Kazanian, Middle Permian of the East European Platform, Russia (Ivanov, 2012).

Species of the elonichthyiforms genus *Varialepis* A. Minikh occur in the Permian basins on the territory of East European Platform and the Cis-Urals (Minikh and Minikh, 2009). *Varialepis* appeared beginning from the Ufimian and is widely distributed in the Urzhumian and Tatarian. The oldest species *Varialepis oris* Yankevich is known from the Ufimian of the North Cis-Urals (Minikh and Minikh, 2009). Occurrences of *V. bergi* A. Minikh and *V. orientalis* (Eichwald) were reported from the Urzhumian of the East European Platform and Cis-Urals; *V. stanislavi* A. Minikh was reported from the Severodvinian and *V. vitalii* A. Minikh – from the Vyatkian of the Cis-Urals (Minikh and Minikh, 2009). Thus, the occurrence of *Varialepis* in the Guadalupian in the Apache Mountains is the first reported outside the territory of European Russia.

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XENACANTH SHARKS AND OTHER VERTEBRATES FROM THE GERALDINE BONEBED, LOWER PERMIAN OF TEXAS

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Abstract—The Geraldine Bonebed occurs in the Nocona Formation (Wichita Group, Sakmarian age) in Texas. It has historically yielded a large number of mostly complete skeletons of four tetrapod taxa, for which it is famous, and also a diverse flora as well as other vertebrates. Bulk samples of matrix were recently screen-washed and sorted to produce a variety of vertebrate microfossils, including sharks, especially xenacanths. The non-xenacanth sharks are rare and include a petalodont tooth (*Janassa*?), *Helodus* sp. (4 teeth) and one partial hybodont tooth. These are all considerably more common higher in the Wichita Group. Only the petalodont and possibly the hybodont and *Helodus* represent a marine component in the fauna, but the marine faunas are more extensive higher in the Wichita. Also new to the fauna are acanthodians, actinopterygians, *Cardiocephalus* and *Ophiacodon*. Among the xenacanths are two typically small *Xenacanthus* sp. occipital spine fragments, two *Orthacanthus* sp. occipital spine fragments (one small, one very small) and hundreds of *Orthacanthus* teeth. *Orthacanthus texensis* teeth are much more common than *O. platypternus* teeth. Teeth of *O. texensis* and *O. platypternus* are comparable in size distributions, as determined by statistical analyses of the tooth-base measurements, to those higher in the Wichita Group. With one possible exception (the exact locality cannot be confirmed), *O. texensis* and *O. platypternus* are not known to occur below the Nocona Formation in Texas, nor are they anywhere older than Sakmarian age.

INTRODUCTION

The purpose of this study is to add additional taxa to the previously known fauna of the Geraldine Bonebed with emphasis on the xenacanth sharks, obtained by bulk processing of matrix to yield a vertebrate microfossil component (Johnson et al., 1994). This bonebed, discovered by A. S. Romer in 1932 in central Archer County, probably represents the most prolific source of articulated tetrapod skeletons in the Lower Permian of North America (Sander, 1987). These include 11 mostly articulated skeletons of *Archeria crassidisca*, an embolomerous amphibian; 15 or more associated or articulated skeletons of the labyrinthodont amphibian *Eryops megacephalus*; 14 or more partial to complete skeletons of the herbivorous synapsid *Edaphosaurus boanerges*; and three associated skeletons of a carnivorous synapsid, *Dimetrodon natalis*. Sander (1987) provided a history of collecting these specimens together with pertinent associated details. He also provided a detailed study of the sedimentology, flora (some two dozen taxa) and taphonomy of the bonebed. It is of Sakmarian (Wolfcampian) age and occurs in the Nocona Formation, Wichita Group (Figs. 1-2). Sander (1987) noted the low diversity of the vertebrate fauna with only three amphibian taxa (including *Diadectes* sp.) and three amniote taxa (including *Bolosaurus striatus*) from the bonebed proper, plus two more amphibians (*Trimerorachis insignis* and *Zatrachys* sp.) and one additional synapsid (*Ophiacodon uniformis*) from the same vicinity. Among the fishes, only one shark (*Orthacanthus texensis*) and one crossopterygian (*Ectosteorachis nitidus*) were recorded from the bonebed, plus one lungfish (*Sagenodus* sp.) from nearby.

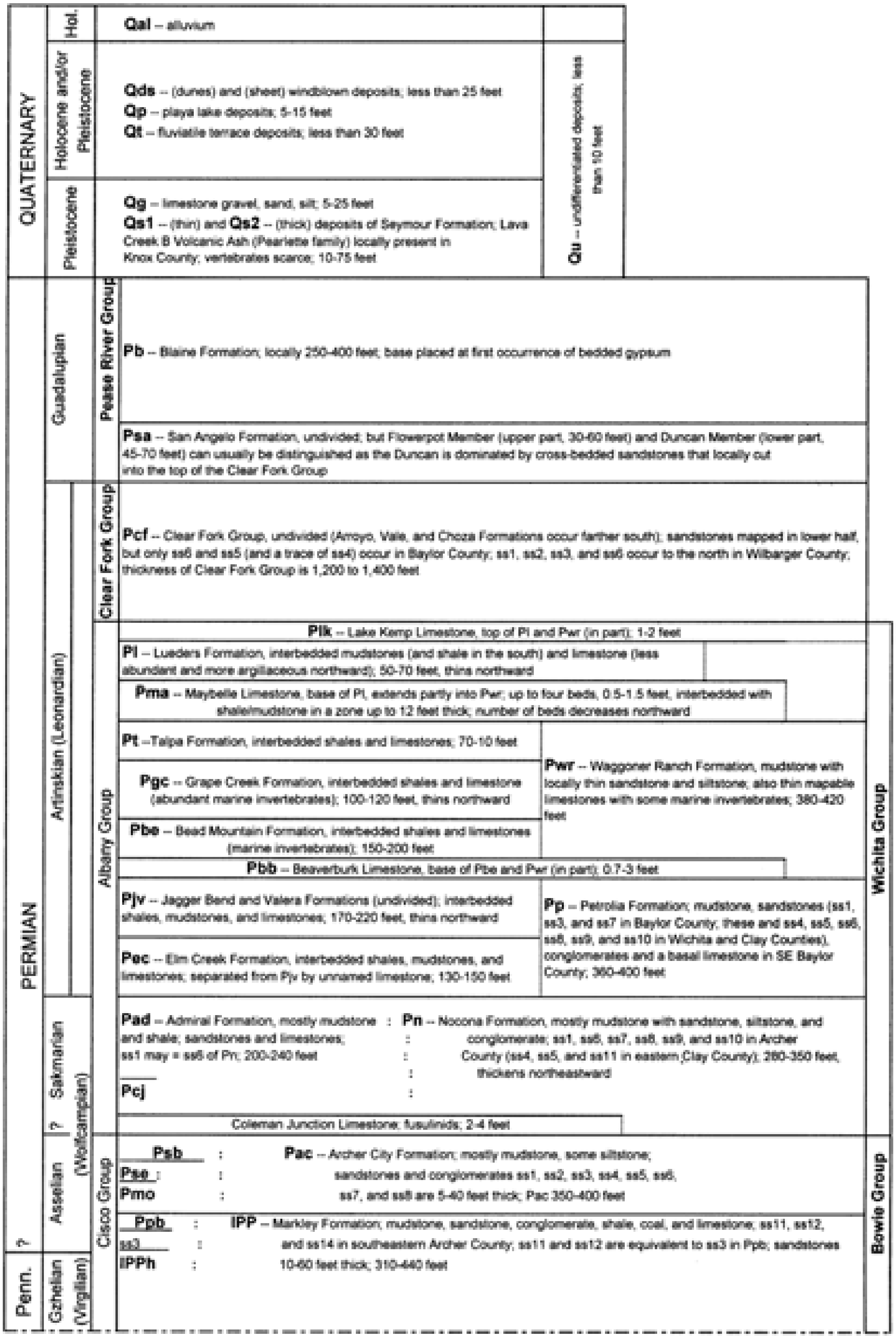
Sander (1987) concluded that the Geraldine Bonebed and related sediments and flora constituted a floodbasin of a small meandering river system. The vertebrate-bearing facies contain only a minor fine-grained sandstone with ripple bedding in what otherwise is mudstone (Sander, 1987, fig. 3), which he interpreted to represent a freshwater pond in an overall swamp environment. Although he presumed the presence of oxbow lakes in the region, he did not specify such an occurrence for the bonebed, presumably because of the geometry of the facies distribution. Sander (1989) provided an analysis of the sedimentology of a portion of the Nocona Formation and subjacent Archer City Formation (Bowie Group) in central Archer County (Fig. 2) and recognized four types of associated deposits. One of these, a catastrophic event bonebed, is represented by the Geraldine Bonebed, but Sander's (1989) primary intent was to describe four occurrences of floodplain pond bonebeds. All four of these probably contain a more diversified vertebrate fauna than does the Geraldine Bonebed (three of the faunal lists were updated by Johnson, 2007, 2012). The other two types of deposits recognized by Sander (1989) are isolated skeletons and lag bonebeds.

In his description of the pond bonebeds, Sander (1989) did not recognize any evidence of marine incursions. Hentz (1988, figs. 11-12) presented a broad overview of the paleogeography of north-central Texas during the time of deposition of the Archer City Formation (Asselian age). Based on this, Sander's (1989) pond bonebeds occurred in the upper part of a lower coastal plain. This could reasonably explain the presence of marine taxa in these bonebeds under varying circumstances, although their occurrence in the Geraldine Bonebed is more problematic.

GERALDINE BONEBED VERTEBRATE FAUNA

Taxa in addition to those listed by Sander (1987, table II), including indeterminate partial bones and teeth plus tooth and bone fragments that were obtained by bulk processing of matrix from the bonebed, are cataloged as SMU 76693-76753 (Shuler Museum of Paleontology, Southern Methodist University Locality 161). Additional surface-collected fossils (SMU 69461-69472, 69499) did not add any taxa to those listed by Sander (1987). The screen-washed bulk samples (two sites several meters apart within the bonebed) produced the following taxa (catalog numbers in parentheses; the xenacanths are treated separately below; * taxa not listed in the bonebed proper by Sander, 1987):

- Class Chondrichthyes
  - Subclass Elasmobranchii
    - *hybodontid indet. (partial tooth, 76713)
    - *Orthacanthus texensis*
    - **O. platypternus*
    - **Xenacanthus* sp.
  - Subclass Holocephali
    - **Helodus* sp. (4 teeth, 76714)



Qal – alluvium

Qds -- (dunes) and (sheet) windblown deposits; less than 25 feet

Qp -- playa lake deposits; 5-15 feet

Qt -- fluviatile terrace deposits; less than 30 feet

Qg -- limestone gravel, sand, silt; 5-25 feet

Qs1 -- (thin) and **Qs2** -- (thick) deposits of Seymour Formation; Lava Creek B Volcanic Ash (Pearlette family) locally present in Knox County; vertebrates scarce; 10-75 feet

Qu -- undifferentiated deposits; less than 10 feet

Pb -- Blaine Formation; locally 250-400 feet; base placed at first occurrence of bedded gypsum

Psa -- San Angelo Formation, undivided; but Flowerpot Member (upper part, 30-60 feet) and Duncan Member (lower part, 45-70 feet) can usually be distinguished as the Duncan is dominated by cross-bedded sandstones that locally cut into the top of the Clear Fork Group

Pcf -- Clear Fork Group, undivided (Arroyo, Vale, and Choza Formations occur farther south); sandstones mapped in lower half, but only ss6 and ss5 (and a trace of ss4) occur in Baylor County; ss1, ss2, ss3, and ss6 occur to the north in Wilbarger County; thickness of Clear Fork Group is 1,200 to 1,400 feet

Plk -- Lake Kemp Limestone, top of Pl and Pwr (in part); 1-2 feet

Pl -- Lueders Formation, interbedded mudstones (and shale in the south) and limestone (less abundant and more argillaceous northward); 50-70 feet, thins northward

Pma -- Maybelle Limestone, base of Pl, extends partly into Pwr; up to four beds, 0.5-1.5 feet, interbedded with shale/mudstone in a zone up to 12 feet thick; number of beds decreases northward

Pt --Talpa Formation, interbedded shales and limestones; 70-10 feet

Pgc -- Grape Creek Formation, interbedded shales and limestone (abundant marine invertebrates); 100-120 feet, thins northward

Pbe -- Bead Mountain Formation, interbedded shales and limestones (marine invertebrates); 150-200 feet

Pwr -- Waggoner Ranch Formation, mudstone with locally thin sandstone and siltstone; also thin mapable limestones with some marine invertebrates; 380-420 feet

Pbb -- Beaverburk Limestone, base of Pbe and Pwr (in part); 0.7-3 feet

Pjv -- Jagger Bend and Valera Formations (undivided); interbedded shales, mudstones, and limestones; 170-220 feet, thins northward

Pec -- Elm Creek Formation, interbedded shales, mudstones, and limestones; separated from Pjv by unnamed limestone; 130-150 feet

Pp -- Petrolia Formation; mudstone, sandstones (ss1, ss3, and ss7 in Baylor County; these and ss4, ss5, ss6, ss8, ss9, and ss10 in Wichita and Clay Counties), conglomerates and a basal limestone in SE Baylor County; 360-400 feet

Pad -- Admiral Formation, mostly mudstone and shale; sandstones and limestones; ss1 may = ss6 of Pn; 200-240 feet

Pn -- Nocona Formation, mostly mudstone with sandstone, siltstone, and conglomerate; ss1, ss6, ss7, ss8, ss9, and ss10 in Archer County (ss4, ss5, and ss11 in eastern Clay County); 260-350 feet, thickens northeastward

Coleman Junction Limestone; fusulinids; 2-4 feet

Pac -- Archer City Formation; mostly mudstone, some siltstone; sandstones and conglomerates ss1, ss2, ss3, ss4, ss5, ss6, ss7, and ss8 are 5-40 feet thick; Pac 350-400 feet

lPP -- Markley Formation; mudstone, sandstone, conglomerate, shale, coal, and limestone; ss11, ss12, and ss14 in southeastern Archer County; ss11 and ss12 are equivalent to ss3 in Ppb; sandstones 10-60 feet thick; 310-440 feet

FIGURE 1. Stratigraphic section of western North-Central Texas; from Johnson (2011), based on Hentz and Brown (1987). **Abbreviations: Pcj**, Coleman Junction Formation; **Psb**, Santa Ana Branch Shale; **Pse**, Sedwick Formation; **Pmo**, Moran Formation; **Ppb**, Pueblo Formation; **lPP**, Pennsylvanian-Permian; **lPPh**, Harpersville Formation.

- Subclass Incertae Sedis
    - **Janassa*? (single incomplete petalodont tooth, 76717)
- Class Incertae Sedis Acanthodii
    - **Acanthodes* sp. (partial fin spines and scales, not common, 76715, 76716)
- Class Osteichthyes
    - Subclass Actinopterygii
        - *palaeoniscids indet. (scales and teeth common, 76718, 76719)
        - **Platysomus*? (single "button tooth," 76720; see Johnson and Zidek, 1981)
    - Subclass Sarcopterygii
        - crossopterygian indet. (skull fragments, scales common, 76722)
        - *Sagenodus* sp. (5 partial tooth plates, 76725)
- Class Amphibia
    - Order Temnospondyli
        - *Trimerorhachis* sp. (teeth and partial jaws uncommon, 76729)
        - *Eryops* sp. (skull and jaw fragments common, 76728)
    - Order Anthracosauria
        - *Archeria* sp. (6 vertebrae, 76726)
    - Order Microsauria
        - **Cardiocephalus* sp. (3 teeth, 76731)
- Class Reptilia
    - Order Parareptilia
        - *Bolosaurus* sp. (14 teeth, partial jaw, 76730)
- Class Synapsida
    - **Ophiacodon* sp. (teeth common, 76735)
    - *Dimetrodon* sp. (neural spine fragments and teeth common, 76733, 76734)
    - *Edaphosaurus* sp. (neural spine fragments common?, 76736)

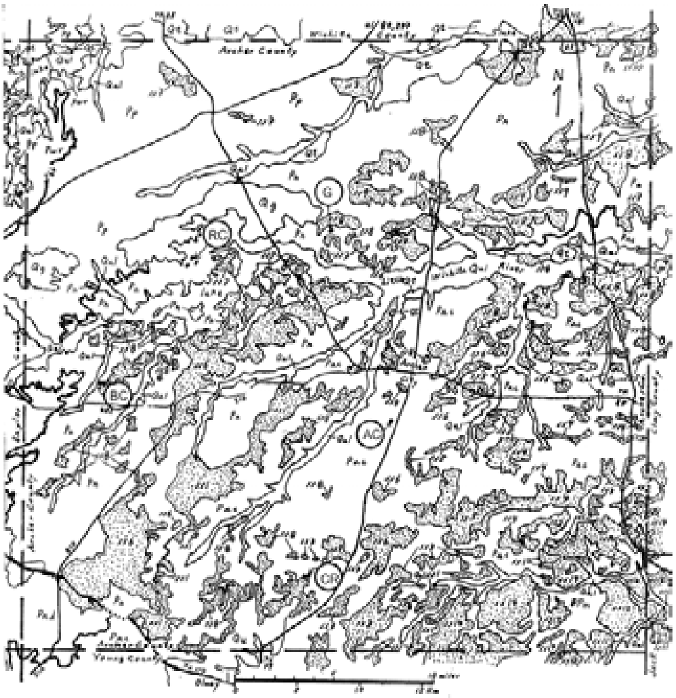


FIGURE 2. Sketch of Archer County, Texas, geology from Hentz and Brown, 1987. **Abreviations: AC**, Archer City Bonebed 3; **BC**, Briar Creek Bonebed; **CR**, Conner Ranch Bonebed; **G**, Geraldine Bonebed; **RC**, Rattlesnake Canyon Bonebed (all indicated by letters in circles with arrows); **Pac**, Archer City Formation; **Pn**, Nocona Formation; **Pp**, Petrolia Formation; see Fig. 1.

In addition, there are a variety of fish teeth including actinopterygians (SMU 76621, 76723, 76724), amphibian teeth (76732) and a reptile caudal? vertebra (76737) and claw (76738). Three small coprolites (76739) are present; the smallest (6 mm) has a spiral structure and the other two contain palaeoniscoid scales. A variety of partial bones, isolated teeth and fragments are present (76740-76745), some of which are probably identifiable.

XENACANTH SHARKS IN THE GERALDINE BONEBED

Three species of xenacanths (Xenacanthiformes Berg, 1937, 1940; Xenacanthodii Olson, 1946?; Xenacanthida Glikman, 1964) occur in the bonebed. *Orthacanthus texensis* is represented by teeth (SMU 76693-76702) as is *O. platypternus* (SMU 76703-76707). Two *Orthacanthus* sp. small to very small occipital spine fragments (SMU 76709) were recovered. Also, two small spine fragments of *Xenacanthus* sp. (SMU 76710) occur in the fauna, but *Xenacanthus* teeth were not recovered, similar to the faunas in the Archer City Bonebed 3 and Conner Ranch Bonebed (Fig. 2; Johnson, 2012). Xenacanths are also represented by denticles and prismatic cartilage (SMU 76711, 76712).

Orthacanthus texensis teeth are very common (total of 1808) in the Geraldine fauna. Besides normal teeth, 13 teeth are germinal (underdeveloped; Johnson, 2005) and three are deformed (Johnson, 1987) (SMU 76697, 76698). Of the remaining teeth, 141 were measured (Fig. 3A). A statistical analysis is summarized in Table 1. The anteromedial-posterolateral (length of tooth base) dimension is taken as the independent variable because it is usually easier to measure in *Orthacanthus* teeth. The measured population may be skewed toward the lower range (Fig. 3A) because nearly all of the larger teeth were probably removed by earlier surface collecting. Forty-nine teeth were surface-collected (SMU 69461), but they are incomplete with some badly worn or weathered. Sander (1987, p. 228) noted that the teeth are smaller than those from other localities in the vicinity of Geraldine. However, the comparison shown in Table 1 with the next stratigraphically highest measured sample (Rattlesnake Canyon, Fig. 2) shows little difference. Teeth from the Briar Creek Bonebed (Fig. 2) have been collected (SMU 69473, 69571, 69572, 76628-76635, 76637-76641, including other xenacanth species) but not analyzed.

Orthacanthus texensis teeth typically have a base wider (labiolingual) than long (anteromedial-posterolateral), a thick base as seen in labial view and serrated principal cusps (Johnson, 1999). In some larger teeth higher in the Wichita Group, both carinae on each principal cusp may be serrated, but none of the Geraldine teeth, where a determination can be made, have serrations on the medial carinae (Fig. 4; what appears to be medial serrations are an artifact of preservation combined with preparation of the photographs; only the lateral carinae are serrated). However, about 2.5% of nearly 1000 isolated cusps (SMU 76699, 76700) have serrations on both carinae. The problem is that very few of the teeth have intact cusps. This also prevents a determination of the extent of heterogeneity of the teeth (compare with Johnson, 1999, p. 233-234). An exception is the occurrence of 14 probable posterior teeth (SMU 76696) that are very small and lack an intermediate cusp; however, the principal cusps bear serrations on their lateral carinae. Typically, *O. texensis* posterior teeth lack serrations (Johnson, 1999, p. 233), and such is the case for a 15th tooth, which has an intermediate (broken) cusp, shown in Fig. 5.

Orthacanthus platypternus teeth are much less common (total of 88) at Geraldine, similar to the rest of the Wichita Group (out of 54 faunas, there is but one exception; Johnson, 1999, table 1). One of these teeth is a germinal tooth (SMU 76705; Johnson, 2005), otherwise the rest are normal. *O. platypternus* teeth are typically longer than wide (Table 1, Fig. 3B), have a thin base as seen from the labial side (compare Figs. 6B, E, H with 4B, E, G), nonserrated principal cusps and the base sometimes has a distinct anterior extension or flange (Fig. 6B, H; Johnson, 1999, p. 236-237).

Some of the Geraldine *Orthacanthus* teeth are unusual. Three *O.*

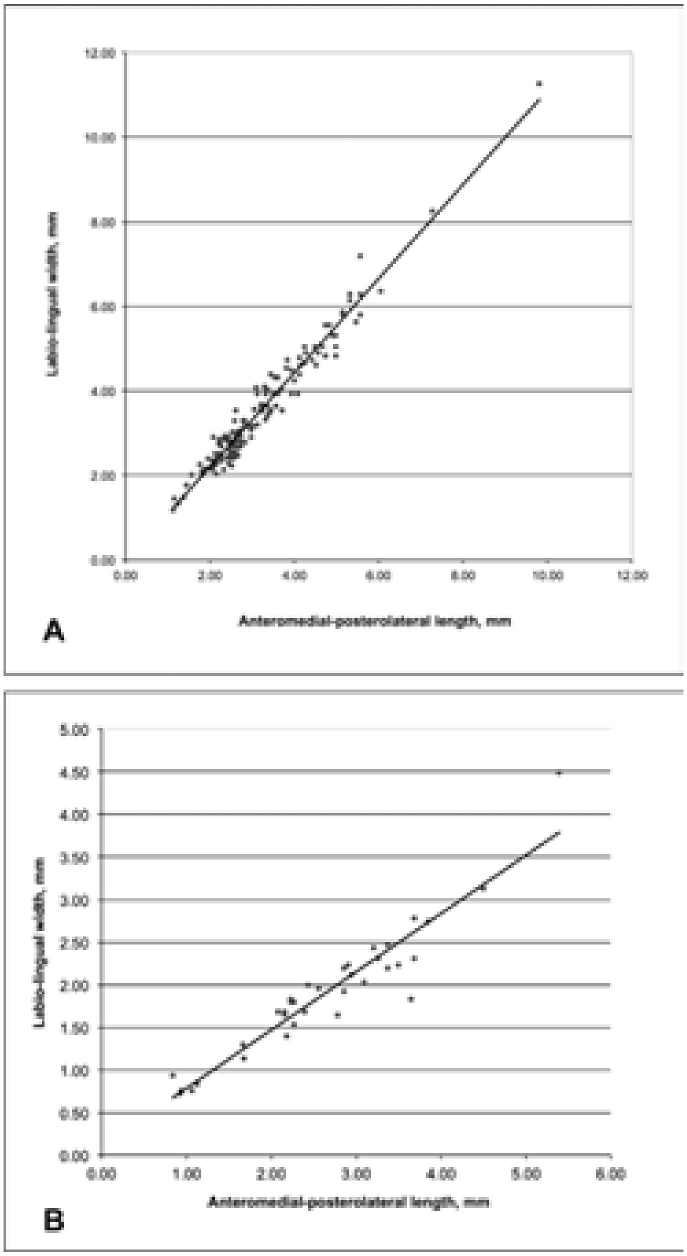
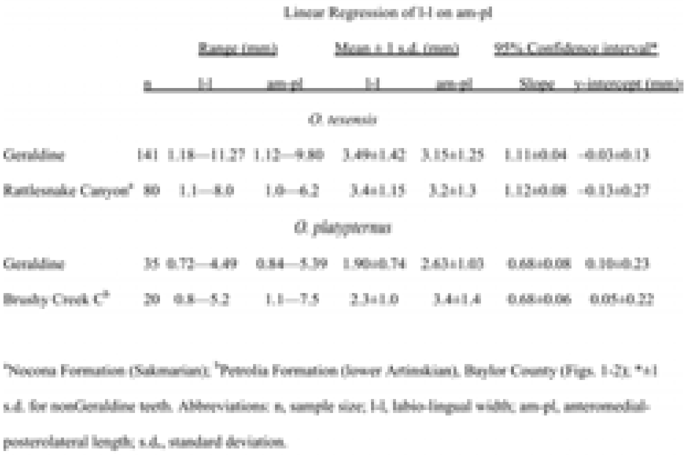


FIGURE 3. Linear regression plots of measured *Orthacanthus texensis* teeth (**A**) and *O. platypternus* teeth (**B**) from the Lower Permian Geraldine Bonebed, Archer County, Texas. See Table 1.

?*texensis* teeth (SMU 76702) have relatively thin bases suggestive of *O. platypternus*, but otherwise bear little resemblance to the latter species. Another *O.* ?*texensis* tooth (SMU 76701) is worn, but resembles the possibly symphyseal teeth assigned to *O.* ?*compressus* (Johnson, 2012, p. 373-375) from the Archer City Bonebed 3 (Fig. 2). One *O.* ?*platypternus* tooth (SMU 76707) has a typically thin base, but otherwise is suggestive of *O. texensis*, although the cusps are broken.

TABLE 1. Measurements of *Orthacanthus* teeth from the Geraldine Bonebed; *O. texensis* (SMU 76746, n = 1-137; SMU 76747-76750, n = 138-141) and *O. platypternus* (SMU 76603, n = 1-32; SMU 76751-76753, n = 33-35). For comparison, the previously available stratigraphically lowest measurements (Johnson, 1999, table 2) are included.



		Range (mm)		Mean ± 1 s.d. (mm)		Linear Regression of l-l on am-pl 95% Confidence interval*	
	n	l-l	am-pl	l-l	am-pl	Slope	y-intercept (mm)
				O. texensis			
Geraldine	141	1.18—11.27	1.12—9.80	3.49±1.42	3.15±1.25	1.11±0.04	-0.03±0.13
Rattlesnake Canyon[a]	80	1.1—8.0	1.0—6.2	3.4±1.15	3.2±1.3	1.12±0.08	-0.13±0.27
				O. platypternus			
Geraldine	35	0.72—4.49	0.84—5.39	1.90±0.74	2.63±1.03	0.68±0.08	0.10±0.23
Brushy Creek C[b]	20	0.8—5.2	1.1—7.5	2.3±1.0	3.4±1.4	0.68±0.06	0.05±0.22

[a]Nocona Formation (Sakmarian); [b]Petrolia Formation (lower Artinskian), Baylor County (Figs. 1-2); *±1 s.d. for nonGeraldine teeth. Abbreviations: n, sample size; l-l, labio-lingual width; am-pl, anteromedial-posterolateral length; s.d., standard deviation.

DISCUSSION

The Geraldine fauna includes the earliest known occurrence of *Orthacanthus texensis* and *O. platypternus* teeth. Their supposed precursor, *O.* ?*compressus*, occurs in the next older known faunas in Archer City Bonebed 3 and Conner Ranch Bonebed (Fig. 2; Johnson, 2012). However, the first two species also occur at the Benson's pasture locality, which may occur in the upper Archer City Formation (discussed in Johnson, 2012). Efforts to establish the geographic position, and therefore the stratigraphic position, of this locality have not been successful, but it probably occurs in extreme southwestern Archer County (Fig. 2).

Although the evidence is meager (one petalodont tooth fragment), the Geraldine Bonebed may have been closer to the marine paleoshore than Sander (1987) realized. Carroll (1988, p. 80) suggested that *Helodus* was freshwater, but Johnson (1990) considered it (referring to helodonts) as marine; Carpenter et al. (2011) listed it as marine (p. 651) or brackish-water (p. 653). The single hybodont tooth fragment listed above is different from all of the teeth described by Johnson (1981); it may represent a new species, but could be part of an unrecognized morphotype in the heterodont dentition of an established species. Species of hybodonts found higher in the Wichita Group (Johnson, 1981) were at least in part marine, given the widespread occurrence of *Lissodus* (*Polyacrodus*) *zideki* (discussed in Johnson, 2011, p. 31), the occurrence of three species of Wichita hybodonts in the Kaibab Formation in Arizona (Hodnett et al., 2011) and a species similar to one of yet another Wichita species in the Upper Permian of Iran (Hampe et al., 2011, 2013). The presence of *Xenacanthus* spines, but not teeth, suggests that it may have been restricted to a nearshore marine habitat as discussed in Johnson (2012, p. 370-371). Also, cladodont teeth (*Glikmanius occidentalis*) occur in much of the Wichita Group (Johnson, 2008, table 1). And finally, the strange but common occurrence of iniopterygians at Rattlesnake Canyon (Fig. 2; Johnson, 2006), together with the petalodonts, cladodonts and hybodonts, suggest many of the Wichita faunas were in close proximity to the marine paleoshore.

Parrish (1978, p. 212) thought that the Thrift Bonebed probably occurred at a stratigraphic level roughly coincident with the Bead Mountain Formation (marine facies) to the south. Based on Hentz and Brown (1987) and the discussion by Hentz (1988, p. 22), he was essentially correct, as that bonebed lies very close to the contact between the Petrolia Formation and overlying Waggoner Ranch Formation with the Beaverburk Limestone at its base (Fig. 1). Parrish (1978, p. 235) concluded that this lag bonebed (Sander, 1989, p. 2) was produced by a catastrophic tropical storm surge, as the animals (six taxa, strongly dominated by *Trimerorhachis insignis*) and one shark taxon (listed as *Xenacanthus*, but is very likely *Orthacanthus texensis*) inhabited mudflat ponds that were only one kilometer from the paleoshoreline (Parrish, 1978, p. 233-234). Although no marine vertebrates were recovered by Parrish (1978), it seems likely that they would occur in the fauna as it is one of the best-documented near-marine faunas in the Wichita Group, perhaps second only to that described by Berman (1970). Although the Geraldine Bonebed is much lower in the Wichita, it is not unreasonable to conclude that it

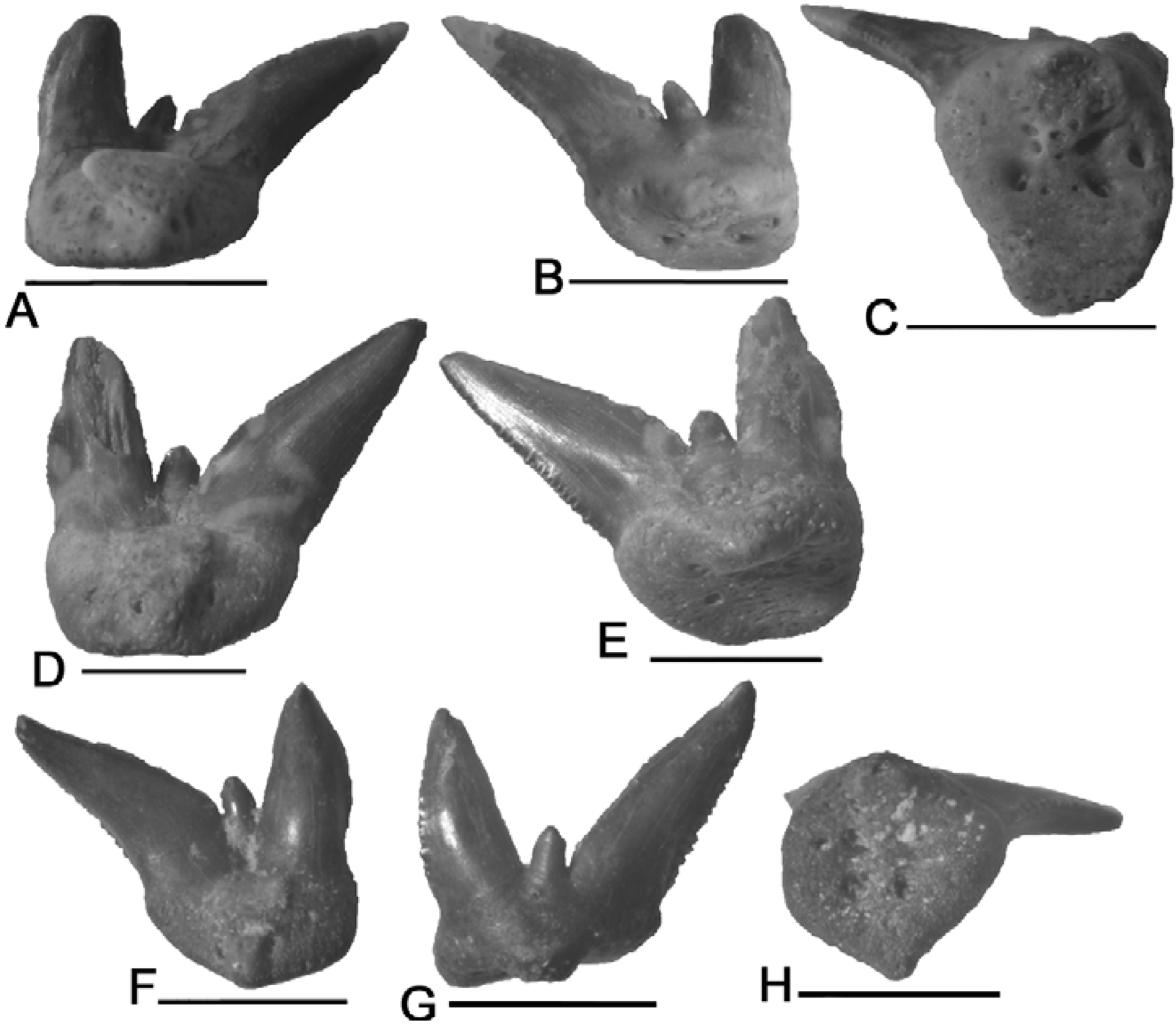


FIGURE 4. *Orthacanthus texensis* teeth from the Lower Permian Geraldine Bonebed, Archer County, Texas. **A**, Lingual, **B**, labial, and **C**, aboral views of SMU 76747; **D**, lingual-occlusal, and **E**, labial views of SMU 76748; and **F**, lingual-occlusal, **G**, labial, and **H**, aboral views of SMU 76749. Scale bars equal 3 mm (**A**-**E**) and 2 mm (**F**-**H**).

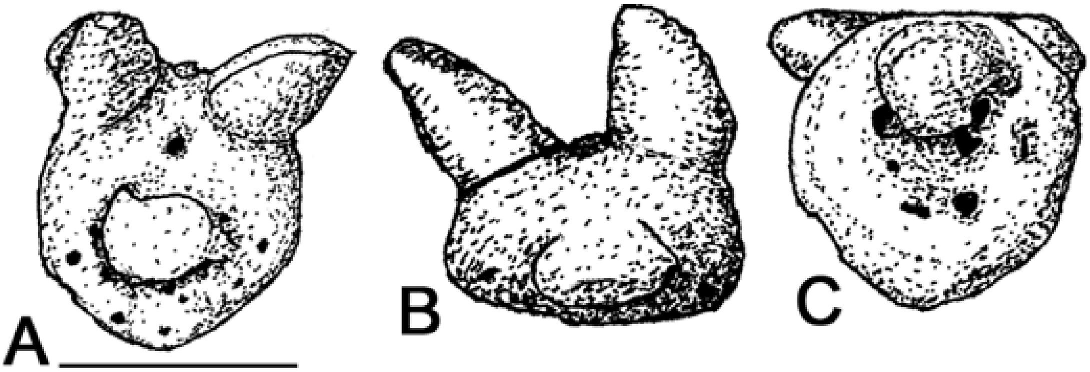


FIGURE 5. Probable posterior tooth of *Orthacanthus texensis* from the Lower Permian Geraldine Bonebed, Archer County, Texas. **A**, Lingual-occlusal, **B**, labial, and **C**, aboral views of SMU 76750. Scale bar equals 1 mm.

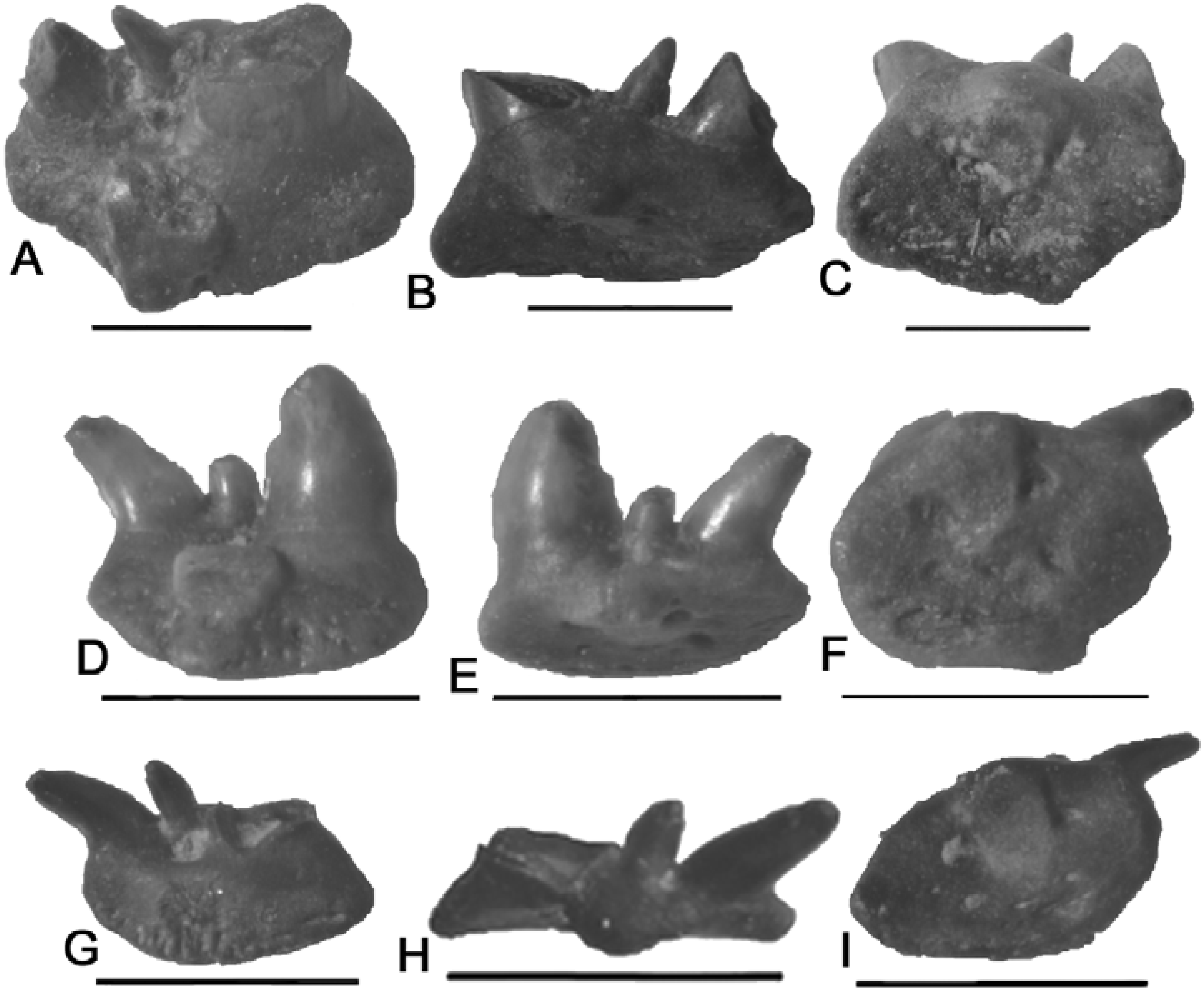


FIGURE 6. *Orthacanthus platypternus* teeth from the Lower Permian Geraldine Bonebed, Archer County, Texas. **A**, Lingual-occlusal, **B**, labial, and **C**, aboral views of SMU 76751; **D**, lingual-occlusal, **E**, labial, and **F**, aboral views of SMU 76752; and **G**, lingual-occlusal, **H**, labial, and **I**, aboral views of SMU 76753. Scale bars equal 3 mm (**A**-**C**) and 2 mm (**D**-**I**).

was close to the marine paleoshore, given the constantly changing sea-level changes that continued into the Sakmarian (Stanley and Powell, 2003).

The assumption that all of the tetrapods in the Geraldine Bonebed were freshwater-terrestrial is assumed, given the presence of the associated synapsids and flora. But some late Paleozoic amphibians may have tolerated a marginal marine habitat, as reviewed in Laurin and Soler-Gijón (2010). Furthermore, this bonebed fauna is somewhat comparable to that described by Carpenter et al. (2011) in which a fish-dominated assemblage occupied brackish water in an estuarine environment (R. Soler-Gijón, personal commun. 2012).

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THE OCCURRENCES OF *GNATHORHIZA* (OSTEICHTHYES: DIPNOI) IN THE TEXAS LOWER PERMIAN WICHITA GROUP AND EQUIVALENT FORMATIONS IN OKLAHOMA

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Abstract—Of the lungfish that occur in North America during the Early Permian, *Gnathorhiza* often receives the most attention because its presence is used as one example to suggest climatic seasonality. The presumed absence of this burrower (suggesting aestivation) in certain strata suggested to some authors that a more persistent humid climate existed during this interval. It has also been suggested that this dichotomy is moot because *Gnathorhiza* was in fact marine. In North America, Texas probably has the most complete record of nonmarine vertebrates in the Lower Permian. *Gnathorhiza* has long been known to be present in the Clear Fork Group. Its absence in the underlying Wichita Group was presumed by those that used it as a climatic indicator, even though its presence in some equivalent strata in Oklahoma had long been established. In fact, it is persistently common in all but the lowest part of the Wichita Group in Texas. These Texas and Oklahoma new occurrences are documented herein with some 35 and five, respectively. New occurrences in the Wichita Group of the lungfish, *Sagenodus*, are also included.

INTRODUCTION

In the past, various authors were unaware that the lungfish, *Gnathorhiza* Cope, 1883, is present throughout at least most of the Wichita Group in north-central Texas, possibly because there were few published accounts of its occurrence. However, occurrences in equivalent strata in Oklahoma had been well documented. The purpose of this note is to document the Texas occurrences and also additional occurrences of *Gnathorhiza* burrows and skeletal remains in Oklahoma. Among the Paleozoic genera of lungfish, *Gnathorhiza* has been of considerable interest since Romer and Olson (1954) reported the occurrence of aestivation burrows in the Arroyo Formation (lower Clear Fork Group, Leonardian/Artinskian age; see below) of Texas. They suggested an ecological succession from a more humid climate in the underlying Wichita Group (Wolfcampian-Leonardian/Sakmarian-Artinskian) where another lungfish, *Sagenodus* Owen, 1867, presumably a nonaestivator, occurs, to a less humid climate represented by the Clear Fork Group and *Gnathorhiza*.

All Texas specimens are deposited in the Waggoner Ranch Collection, Shuler Museum of Paleontology, Southern Methodist University (SMU), Dallas, Texas. Oklahoma specimens are deposited in the Sam Noble Oklahoma Museum of Natural History (OMNH), University of Oklahoma, Norman.

PUBLISHED RECORDS OF *GNATHORHIZA* BELOW THE CLEAR FORK GROUP

Gnathorhiza first appears in the Pennsylvanian (reviewed by Romer and Smith, 1934; Schultze, 1995). It occurs near the base of the Permian in southeastern Nebraska, along with *Monongahela* (see comment below), both preserved in burrows (Huttenlocker et al., 2005; Small et al., 2006). Rare occurrences were reported in the Wichita Group (Fig. 1) by Romer and Olson (1954), but specific examples were not provided. Their locality in the Arroyo Formation (SMU locality 460, specimens SMU 68651, 68804, 68805) occurs just above the contact with the Lueders Formation, based on Hentz and Brown (1987). Dalquest (1968) reported the presence of *Gnathorhiza* in the Lueders Formation (adjacent to SMU locality 345, Table 1), then considered as the uppermost formation in the Wichita Group. The nonmarine facies of the Lueders is now considered part of the upper Waggoner Ranch Formation (Wichita Group) and its marine facies part of the Albany Group between the Wichita and Clear Fork Groups in north-central Texas (Hentz and Brown, 1987; Johnson, 1996; not shown in Fig. 1). However, the Lueders Formation of Hentz and Brown (1987) in this area (Baylor and Wilbarger Counties) contains nonmarine facies. Berman (1968, 1970) also reported occurrences of *Gnathorhiza* in the Lueders Formation; two of his three sites are the same as SMU 344 and 345 (Table 1). Dalquest and Carpenter (1975) reported the occurrence of lungfish burrows, inferred to belong to *Gnathorhiza*, which was confirmed by Berman (1976a). They presumed the locality to be in the Lueders Formation. Based on Hentz and Brown (1987), and SMU locality 461 (SMU 68806, burrows with bone), it is close to the Lueders-Waggoner Ranch boundary. Dalquest et al. (1989) reported a new occurrence of burrows and stated that *Gnathorhiza* had never been found in Texas below the Lueders Formation. They stated this locality is in the Arroyo Formation, but based on their locality description (4.0 km east of the Dalquest-Carpenter locality), it definitely occurs in the upper Waggoner Ranch Formation, based on Hentz and Brown (1987).

Burrows were reported from the Wellington Formation in Oklahoma (Fig. 1) at Perry sites 1, 2 and 5 by Olson (1967) and at Olson's Perry sites 1, 2 and 3 by Carlson (1968). Olson (1967) also indicated the presence of *Gnathorhiza* at his Perry site 4 and Orlando site, but did not mention burrows. Olson (1970, p. 392, 398) presented an expanded faunal list for his Perry site 6, including a tooth plate, but did not report any burrows. *Gnathorhiza* is present in the overlying Garber Sandstone in Olson's (1967) Pond Creek site; no burrows were mentioned. Olson (1970) discussed the stratigraphic distribution of the genus. The Perry and Orlando sites are in Noble County, and the Pond Creek site is in Grant County (Olson, 1967, fig. 7).

Several investigators have tended to rely on the supposed Wichita (*Sagenodus*)–Clear Fork (*Gnathorhiza*) dichotomy to support the idea of increasing aridity, and apparently were not aware of the Oklahoma occurrences of *Gnathorhiza* in formations equivalent to part of the Wichita Group (see earlier literature cited by Olson, 1967). Also, co-occurrences of these genera appear in two Pennsylvanian age Kansas localities listed by Schultze et al. (1994, p. 447). Dalquest (1968) and Berman (1968) mentioned this dichotomy, taking note of the Lueders occurrences. In her paleoecology discussion, Sequeira (1998, p. 256) noted the absence of *Gnathorhiza* from the Wichita Group. The presence of lungfish burrows

FIGURE 1. Simplified comparison of the suggested Wellington Formation-Garber Sandstone boundary in Oklahoma with Texas Lower Permian (part) stratigraphy. Some of the correlations, such as Dunbar et al. (1960) and the COSUNA attempts (Hills and Kotlowski, 1983; Mankin, 1987) were probably based in part on marine strata.

in the earliest Permian assist in supporting the concept of a seasonal wet/dry climate (Huttenlocker et al., 2005). The aforementioned dichotomy based only on *Gnathorhiza* may therefore be problematic, although an increase in aridity during the Early Permian is quite likely (Tabor and Montañez, 2004; Huttenlocker et al., 2008). However, Schultze (2009, p. 128) suggested *Gnathorhiza* may have been marine. This may be valid for the Wichita Group occurrences, but it would be difficult to accept this interpretation for its occurrences in the Clear Fork Group in northwestern North-Central Texas where only terrestrial facies occur; they become increasingly marine farther to the south (Hentz and Brown, 1987; Olson, 1989).

Finally, at least some of the occurrences in the Wichita Group may be of *Monongahela* rather than *Gnathorhiza*. The tooth plates illustrated here that are assigned to the latter genus actually belong to *Monongahela* (A. Kemp, personal commun., 2012). A taxonomic discussion is beyond the scope of this paper, so following the literature to the present, the generic name *Gnathorhiza* is used.

DISTRIBUTION OF *GNATHORHIZA* IN THE WICHITA GROUP AND IN OTHER STRATA

Occurrences of isolated *Gnathorhiza* tooth plates in the Wichita and Albany Groups in Texas are summarized in Table 1, based on Johnson (1979, p. 580-632; 1996). The stratigraphic distribution is somewhat uneven because several of the local faunas occur at the same, or nearly the same, horizon in some instances; a more representative distribution of these faunas is in Johnson (1981, fig. 3; 1999, table 1). *Gnathorhiza* has not been documented in the lower Nocona Formation (Fig. 1, Table 1; Johnson, in press), although it is questionably present in the underlying Archer City Formation (Bowie Group; Johnson, 2012, p. 370). Continuation of the distribution into the Clear Fork Group was given in Murry and Johnson (1987). The fossils were obtained by bulk-sampling methods (Johnson et al., 1994; the 'ac' suffix in the locality names in Table 1 refer to faunas obtained from rock treated with acetic acid).

Gnathorhiza occurs in Olson's (1967) Perry Site 4 (OMNH 07995, burrow with skull, Table 2) and just north of Olson's (1967) Orlando Site, also in the Wellington Formation (SMU Locality No. 385C); one of us (WM) later discovered *Gnathorhiza* remains in one of the burrows (OMNH 72799). Although burrows are not present at the Orlando Site, *Gnathorhiza* is the dominant osteichthyan present (Johnson, 1994). And a burrow with skull fragments (OMNH 55723) was discovered in Olson's (1967) Pond Creek Site (Table 2). They have been reported from the older (Wolfcampian) Abo Formation in New Mexico (Berman, 1976b), and Schultze (1985) reviewed occurrences in the Wolfcampian (Gearyan) Speiser Shale and Blue Springs Shale Member of the Matfield Shale in Kansas. Schultze (1985) suggested that *Gnathorhiza* was tolerant of salt water, based on the occurrence of burrows in nearshore marine sediments in the Speiser Shale. However, Wardlaw et al. (2004, fig. 1) indicated the presence of paleosols in the Speiser Shale (middle Sakmarian) and also in the Blue Springs Shale Member, and further indicated largely terrestrial deposition for both units. But it can be successfully argued that the facies interpreted by them as paleosols are not paleosols (for example, see the discussion on intertidal/coastal marine environments in Reineck and Singh, 1980; H.-P. Schultze, personal commun., 2012).

Definitive correlation of Lower Permian stratigraphic units between Oklahoma and north-central Texas remains problematic. The Wellington Formation is equivalent to part of the Wichita Group, but specific suggestions vary (Fig. 1). Dunbar et al. (1960) correlated the Wellington with the Belle Plains and overlying Clyde Formations in the Wichita Group (see Hentz and Brown, 1987, for updated stratigraphic terminology in Texas; Johnson, 1996, 1999, table 1). Olson (1967, fig. 12) provisionally correlated the Wellington with the Admiral and Belle Plains Formations in the Wichita Group. Simpson (1979, figs. 2, 3) showed the Wellington equivalent to only the Belle Plains. Schultze and Chorn (1997, fig. 52) correlated the Wellington with the Clyde Formation which in part agrees with Hills and Kotlowski (1983). Sullivan and Reisz (1999, fig. 6) correlated the Wellington with the Waggoner Ranch Formation (Table 1 and Fig. 1), which appears to largely agree with Mankin (1987). The Garber Sandstone (Formation) was correlated with the Clyde, Lueders, and Arroyo Formations, thereby spanning the Wichita-Clear Fork Group boundary, by Simpson (1979, figs. 2, 3), similar to the provisional correlation by Olson (1967, fig. 12; he included the Clyde and Lueders in the Clear Fork Group). Earlier, Dunbar et al. (1960) correlated the Garber with the Lueders and lower Arroyo Formations. Schultze and Chorn (1997, fig. 52) correlated the Garber with the Lueders Formation (Limestone) and Arroyo Formation, thereby also spanning the Wichita-Clear Fork boundary. Sullivan and Reisz (1999, fig. 6) and Lucas and Suneson (2002, fig. 4) correlated the Garber with the Arroyo Formation (Fig. 1), but were uncertain of its upper boundary; both appear to more or less agree with Mankin (1987). But current

TABLE 1. Distribution of *Gnathorhiza* tooth plates in the Wichita Group, north-central Texas (from Johnson, 1979, 1996).

Local Fauna	SMU Catalog numbers	SMU Locality Number	prearticulars	pterygoids	vomerines	indeterminants
Lueders Formation (Albany Group)						
Little Moonshine Creek	64852-64853	268	5	0	1	14
lower upper Waggoner Ranch Fm.						
Southwest Butte/ac	68990-68992	343	1	2	0	0
Tit Butte/ac	68982-68989	344	12	18	1	7
Lake Kemp B	68975-68981	345	16	6	2	13
Lake Kemp B/ac	68967-68974	345	10	7 + 1?	1	9
Lake Kemp A	68957-68966	340	13	7	3	11
upper middle Waggoner Ranch Fm.						
Mitchell Creek H	68956	347	0	1	0	1
Mitchell Creek G	68955	348	0	1	0	0
middle Waggoner Ranch Fm.						
Mitchell Creek E	68954	350	1	0	0	0
Mitchell Creek E/ac	68948-68953	350	5	2	0	0
Mitchell Creek C	68927-68947	352	88	37	16	212
Mitchell Creek A	68913-68926	353	392	14	47	152
Mitchell Creek B	68912	160	8	0	0	2
Mitchell Creek B/ac	68905-68911	160	85	5 + 1?	4	85
Bluff Creek C	68902-68904	354	5	1	0	5
Spring Creek B/ac	68895-68900	357	30	10	2	7
La Paloma/ac	68901	358	2	1?	0	1
Spring Creek A/ac	68891-68894	359	4	1	1?	1
Spring Creek/ac	68890	360	1	0	0	0
Old Military Crossing	68885-68889	361	11	10	4	123
lower middle Waggoner Ranch Fm.						
West Franklin Bend C	68884	286	0	2?	0	1
West Franklin Bend C/ac	68879-68883	286	24	1?	0	12
Hackberry Creek C	68877	339	0	0	0	1?
West Franklin Bend B/ac	68878	362	2	0	0	0
Hackberry Creek B	68876	364	1	0	0	0
Hackberry Creek A/ac	68873-68875	365	9	9	0	18
Franklin Bend A/ac	68869-68872	366	7	4	1	16
Franklin Bend A	68865-68868	366	0	2	3	7
upper Petrolia Fm.						
Wolf Creek B/ac	68864	285	0	1?	0	0
Wolf Creek B	68862-68863	285	3	3?	0	0
Wolf Creek A	68859-68861	285	2	5	0	0
Wolf Creek/ac	68855-68858	285	5	8	1	0
Brushy Creek M/ac	68854	370	0	0	0	1
Brushy Creek L/ac	68843-68853	371	141	108	12	64 + 3?
Brushy Creek K/ac	68840-68842	372	4	1	1	0
Brushy Creek J/ac	68835-68839	373	9	7 + 1?	1	6
Brushy Creek I	68834	338	0	0	1	5
Brushy Creek G	68833	374	1	0	0	3
Brushy Creek F	68828-68832	276	4	5	1	22
Brushy Creek E	68823-68827	375	3	5 + 1?	3 + 1?	6
Brushy Creek D	68819-68822	376	5	4	2	12
Brushy Creek C/ac	68816-68818	377	5	5	1	2
upper Nocona Fm.						
Rattlesnake Canyon	68814-68815	284	1	0	0	2

TABLE 2. Distribution of *Gnathorhiza* remains in Oklahoma.

Locality	OMNH Catalog numbers*	Comments
middle Garber Sandstone		
Pond Creek		Olson, 1967
Pond Creek		Simpson, 1979 (table 4; based on Olson, 1967?)
Pond Creek	55723	burrow with skull fragments
Pond Creek	55724-55726	skull elements
Pond Creek	55731	scales in matrix
Wellington Formation		
Perry Site 1		burrows, Olson, 1967; Carlson, 1968
Perry Site 2		burrows, Olson, 1967; Carlson, 1968
Perry Site 3		burrows, Carlson, 1968
Perry Site 4	7995	burrow with skull; Olson, 1967
Perry Site 5		burrows, Olson, 1967
Perry Site 6		tooth plate, Olson, 1970
Orlando Site		Olson, 1967; Johnson, 1994
north of Orlando Site	72799	burrow with bones

*previously unpublished

TABLE 3. Distribution of *Sagenodus* tooth plates in the Wichita Group, north-central Texas (from Johnson, 1979).

Local Fauna	SMU Catalog numbers	SMU Locality Number	prearticulars	pterygoids	vomerines	indeterminants
lower upper Waggoner Ranch Fm.						
Lake Kemp B	69235	345	0	1	0	0
Lake Kemp B/ac	69236	345	0	1?	0	0
middle Waggoner Ranch Fm.						
Mitchell Creek C	69233-69234	352	0	1 + 1?	0	0
Mitchell Creek A	69230-69232	353	0	5 + 11?	0	0
Mitchell Creek B	69229	160	0	1	0	0
Mitchell Creek B/ac	69228	160	0	3?	0	0
Bluff Creek A	69227	356	0	1	0	0
Spring Creek B/ac	69224-69225	357	0	2	0	0
La Paloma B	69226	384	0	1	0	0
Spring Creek A/ac	69223	359	0	0	1?	0
lower middle Waggoner Ranch Fm.						
West Franklin Bend C	69222	286	0	0	1?	0
West Franklin Bend C/ac	69221	286	0	5	0	0
Franklin Bend A	69220	366	1	0	0	0
upper Petrolia Fm.						
Wolf Creek B	69000, 69218, 69219	285	1?	1 + 2?	0	0
Wolf Creek A	68999	285	3?	0	0	0
Wolf Creek/ac	68998	285	0	0	1?	0
Brushy Creek K/ac	68997	372	0	1	0	0
Brushy Creek F	68996	276	0	1	0	0
Brushy Creek E	68995	375	1?	0	0	0
Brushy Creek C	68994	377	0	0	0	1?
Brushy Creek C/ac	68993	377	0	3?	0	0

evidence strongly suggests that much of the Garber correlates with the upper Wichita Group (Zidek et al., 2003; see also May et al., 2011, fig. 3).

For the sake of completeness, the distribution of *Sagenodus* Owen, 1867, in the Wichita Group is shown in Table 3, based on Johnson (1979, p. 580-632). All specimens were obtained by bulk-sampling except an incomplete pterygoid tooth plate (SMU 69226, Table 3). Reasonably complete tooth plates of *Sagenodus* (Fig. 2) are uncommon. Fragmentary prearticular and pterygoid tooth plates of this genus are difficult to distinguish (compare figs. 43 and 44 in Schultze and Chorn, 1997); those with some semblance of a base are considered to be pterygoid tooth plates. However, the lack of listed prearticulars in Table 3 may be explained by the questioned occurrences of pterygoid tooth plates, as in the Mitchell Creek A local fauna, and failure to recognize possible wear patterns (see below). The only undoubted prearticular (SMU 69220, Table 3) is 50 mm long and possesses six transverse ridges. Some fragments are assigned to *Sagenodus* only on the basis of size. However, large prearticular fragments of *Gnathorhiza*, approaching 20 mm if complete, appear in the Lake Kemp A and B local faunas (Table 1), which are comparable in size to the Clear Fork specimens (Murry and Johnson, 1987). Although no larger identified *Gnathorhiza* elements are present, large size does not preclude the possibility that some of the specimens in Table 3 do not belong to *Sagenodus* (A. Kemp, personal commun.,

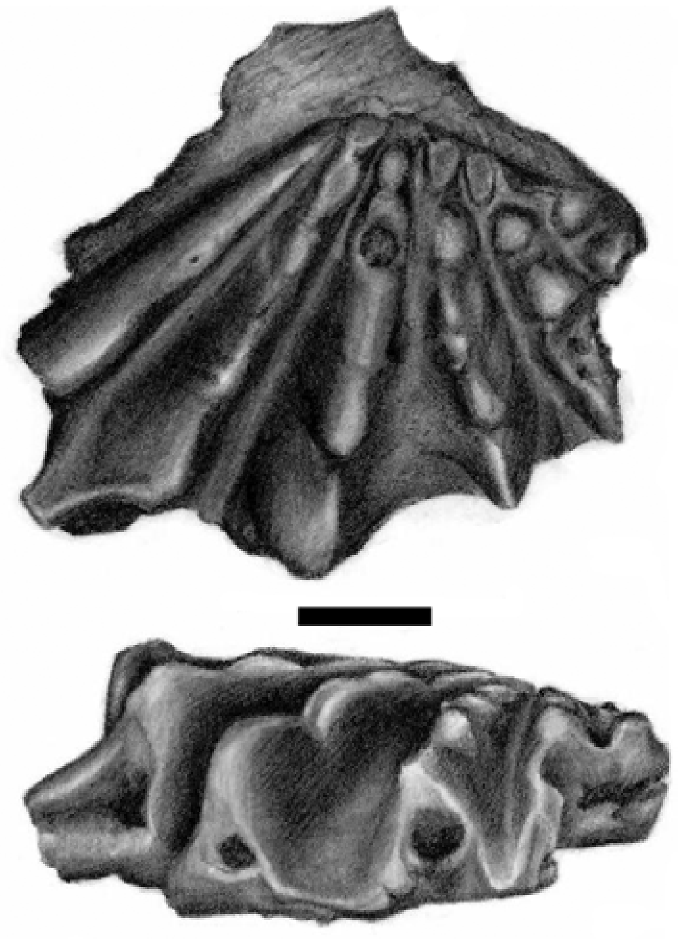

FIGURE 2. *Sagenodus* Owen, 1867, mostly complete pterygoid tooth plate (SMU 69224) from the Spring Creek B/ac local fauna, middle Waggoner Ranch Formation; occlusal (upper) and labial views. Scale bar equals 2 mm.

2004). However, the ridges in *Sagenodus* tooth plates do not radiate from a common point as is the tendency in *Gnathorhiza* tooth plates, so they are not likely to be confused. Although Schultze and Chorn (1997) did not mention the presence of juveniles in their studied material, the minimum number of ridges in their Table II is considerably greater than in *Gnathorhiza*. It therefore seems unlikely that any of the tooth plates listed in Table 1 could be *Sagenodus* juveniles.

TERMINOLOGY

The bladelike tooth- or cusp-bearing moieties that comprise the *Gnathorhiza* tooth plates are here termed ridges, following the commonly accepted practice (A. Kemp, personal commun., 2004; e.g. Carlson, 1968; Lund, 1970). However, “blade” often more appropriately describes these moieties in *Gnathorhiza*, and was used by Berman (1976a). The upper tooth plate is supported by the pterygoid, which more correctly should be termed the ptergopalatine (A. Kemp, personal commun., 2004; e.g. Kemp, 1992). But, because earlier descriptions of *Gnathorhiza* (e.g., Carlson, 1968; Lund, 1970; Berman, 1976a) invoke “pterygoid,” it seems appropriate to continue its use for the present. However, in deference to Kemp (1992), “ptergopalatine” should probably be used in formal descriptions.

DISCUSSION

No attempt has been made to distinguish or identify species of *Gnathorhiza* in the Wichita Group (Table 1). More than one is likely present, based on a combination of size and stages of development of the tooth plates. The species *G. serrata* Cope, 1883, *G. dikeloda* Olson, 1951, and *G. noblensis* Olson and Daly, 1972, all from the Clear Fork Group, and *G. bothrotreta* Berman, 1976b, from the Abo Formation in New Mexico, were reviewed by Berman (1976a, b), who considered them to be the only valid Lower Permian species. Although most of the specimens are highly fragmentary, an adequate number of tooth plates are probably present to allow determination of growth series in individual taxa based on cusp development on the individual ridges. Perhaps the best example for doing so is in the Brushy Creek L/ac local fauna from the upper Petrolia Formation (Table 1). Several of the pterygoids possess an intact prominent ascending process (ptergopalatine process of Kemp, 1992, fig. 1; see also Berman, 1976a, p. 1026 and fig. 4G) above one of the tooth-plate labial ridges, but otherwise it is broken away where its presence can be determined. Most of the specimens in the Wichita Group are <5 mm long, and they would not exceed this length even if they were complete (Fig. 3; this may actually be *Monongahela*, as discussed above).

One of the most curious variants among the prearticulars is the possession of but a single ridge with no evidence of a labial ridge (Fig. 4; actually *Monongahela*?). This is somewhat comparable to the short-ridge anomaly of Kemp (2003, p. 530). They occur throughout much of the sampled section: SMU localities 372, 371, 362, 286, 357, 160, 353, 345, 344, and 343, in stratigraphic succession (Table 1). Although most of these local faunas have only a few single-ridge prearticulars, nearly all of the prearticulars in the West Franklin Bend C/ac (286), Mitchell Creek B/ac (160), and Mitchell Creek A (353) local faunas are single-ridged. The variation they display may not be accounted for only by ontogenetic development and suggests that more than one species of *Gnathorhiza* is present. However, normal variability within a single species would first have to be established (H.-P. Schultze, personal commun., 2012), which is not a likely possibility. Berman (1968) noted the presence of single-ridged prearticulars, up to 6 mm long, which is two or three times the length observed here. Lund (1970) also noted the single-ridged condition in a significant number of *Monongahela stenodonta*, Lund, 1970, prearticulars from the Upper Pennsylvanian; but none occur in *M. dunkardensis*, Lund, 1973 (Pennsylvanian to mostly Lower Permian, Wolfcampian; Lund, 1973). (Schultze, 1994, placed *Monongahela* Lund, 1970, in synonomy with *Palaeophichthys* Eastman, 1908, but see Kemp, 1998.) There are no observed pterygoids that would seem to match these prearticulars. Berman (1968) and Lund (1970) also did not find comparable pterygoids, which led Berman (1968) to conclude that the pterygoid had no functional role during this ontogenetic stage in *Gnathorhiza*. It seems unlikely that these prearticulars represent a developmental abnormality (Lund, 1970, p. 257), given their abundance in some of the

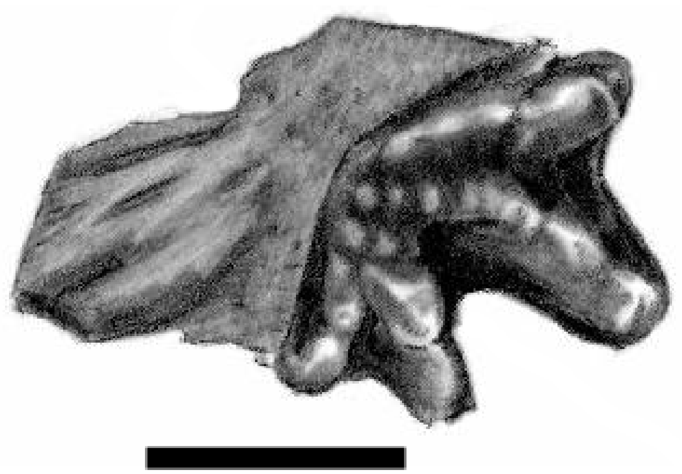

FIGURE 3. *Gnathorhiza* Cope, 1883, nearly complete pterygoid tooth plate (SMU 68913) from the Mitchell Creek A local fauna, middle Waggoner Ranch Formation. Scale bar equals 1 mm.

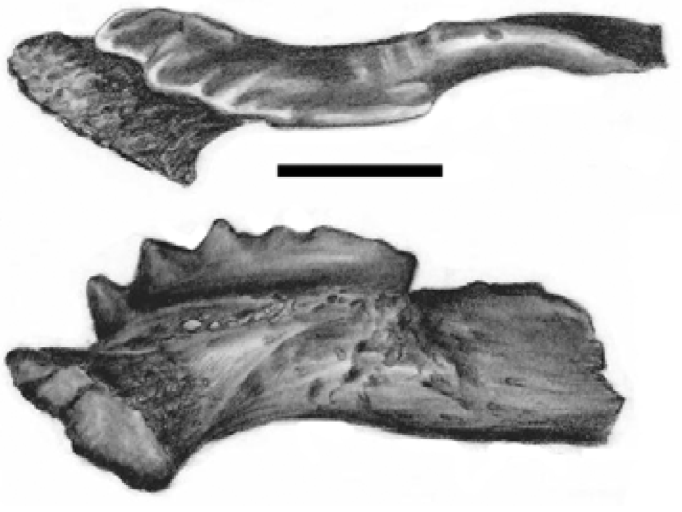

FIGURE 4. *Gnathorhiza*, nearly complete single-ridge prearticular tooth plate (SMU 68879) from the West Franklin Bend C/ac local fauna, lower middle Waggoner Ranch Formation; occlusal (upper) and lingual views. Scale bar equals 1 mm.

Wichita local faunas, widespread stratigraphic distribution, and possible occurrence in more than one taxon. The Wichita specimens may represent a separate, unnamed, taxon (A. Kemp, personal commun., 2004; but would include *Monogahela*, personal commun., 2012) or even more than one taxon, but this interpretation might be difficult to effectively establish (H.-P. Schultze, personal commun., 2012). Failure to recognize comparable pterygoids may result from the inability to distinguish upper from lower tooth plates. However, differences in wear patterns is a useful criterion for distinguishing isolated tooth plates (A. Kemp, personal commun., 2004); but that may not be possible in some of the very small elements present in the Wichita Group.

The variation displayed by the pterygoid tooth plates (and also the vomerine tooth plates), as well as in the prearticular tooth plates, suggests that more than one species of *Gnathorhiza* is present, although this would be difficult to demonstrate without additional evidence. Some of the variation is accounted for by presumed developmental anomalies (Kemp, 2003). For example, a pterygoid tooth plate (SMU 68986) from Berman's (1970) Tit Butte locality (SMU 344, Table 1) possesses only one labial ridge, but one end of the main ridge is thicker than normal with essentially no cusps at this thickened end except cusps occuring on a ridge that is fused with the main ridge at this end. Of additional interest is the interior of the crown of SMU 68986, which shows a remarkable structure (most of the base is absent), which practically defies description. A similar complexity of structure, consisting of a manifold of radiating tubes, is visible in some weathered prearticulars (SMU 68940) in the Mitchell Creek C local fauna, for example.

CONCLUSIONS

The presence of *Gnathorhiza* in the Wichita Group is firmly established. More than one taxon may be present, including the possibility that *Monongahela* is also or exclusively present. Despite the lack of evidence of aestivation(?) burrows in the Texas Wichita (except possibly the Dalquest et al., 1989, locality), but given their occurrence in equivalent strata in Oklahoma, climatic inferences for the Early Permian of North America based on lungfish should be approached with caution. Taxonomic studies utilizing the Wichita specimens (Table 1) along with those from Oklahoma should be undertaken.

The variance in suggested correlations of Lower Permian formations between Oklahoma and Texas was often based on terrestrial and freshwater faunas (Simpson, 1979, fig. 3, for example). Inadequate data and differing interpretations are likely responsible for the confusion. Clearly, an exhaustive effort (additional faunas, possibly correlating depositional sequences) will be required to resolve the problems that surprisingly occur over such a short (< 100 km) distance.

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PALEOZOIC PHYTOLITHS: OLD MICROFOSSILS, NEW TOOLS

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The end-Permian biotic crisis had a major impact on the Earth's marine and terrestrial ecosystems as evidenced by sedimentary records from many parts of the world. Unfortunately, however, in the vast area of western and central Pangea, evidence for terrestrial ecosystem dynamics during these times of biosphere reorganization has been severely limited due to the absence of plant macro- and microfossils.

Whereas traditional end-Permian paleobotanical research has focused on macrofossil and palynological records, these fossil types were not preserved in the oxidized rocks that almost entirely make up the sedimentary record in Permotriassic low-latitude Pangea. In contrast, phytoliths – microfossils that consist of robust concretions of hydrated silica – are resistant to decay under oxic conditions. Their inorganic nature makes them excellent candidates for the reconstruction of plant communities that grew outside the anoxic depositional environments.

Sedimentary strata from the Panthalassan continental margin of tropical Pangea – in what now is southwestern North America – largely consist of heavily oxidized sedimentary rocks, such as those found in our study sites in Caprock Canyon State Park (Texas). Here fluvial sandstones and overbank mudstones of the Quartermaster Formation preserve the end-Permian biotic crisis, as indicated by U-Pb dating of single crystal zircons and Ar-dating of biotite from volcanic ashes. Caprock Canyon’s sedimentary rocks, which are typical oxidized red bed formations, have yet to yield fossil pollen and are considered to be barren of plant macrofossils. Yet, when samples were processed according to standard phytolith extraction techniques, numerous fossil vascular plant forms were discovered.

Analysis of the samples revealed that almost all contain phytoliths, most notably those with imprints of circular boarded pits that are characteristic features of coniferous wood. This suggests that, in contrast to earlier assumptions, conifer-rich vegetation was present along the coastal Panthalassa margin of Pangea during the end Permian. Extraction methods have been improved and a reference database is being populated, which will allow us to establish the botanical affinity of the encountered phytolith morphotypes while increasing our sample set.

This growing phytolith data set is likely to reveal major vegetation turnover across the Permo-Triassic boundary, and will be developed into a biostratigraphic tool for the part of the sedimentary record that has been considered void of fossils.

A BROAD-LEAVED PLANT FROM THE ABO FORMATION OF NORTHERN NEW MEXICO: LAZARUS TAXON, PALEOBIOGEOGRAPHIC ANOMALY OR CONVERGENT EVOLUTION?

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The world of the Permian Period was vastly different from that of the world of today, not only in terms of its biological composition, but in species diversity and possibly in the geographic area covered by various biomes (greater than today). These differences may have underlain unique evolutionary and ecologic dynamics or at least permitted certain kinds and spatio-temporal scales of dynamics to be seen more easily than in a more diverse and spatially complex world. Conditions such as these are ideal for the investigation of questions concerning matters such as niche construction and the relationships between diversity and stability of species assemblages. Additionally, ice-age dynamics of warming and cooling during the late Paleozoic, including significant changes in global CO_2 levels, allow for an enhanced interpretation of vegetative community reaction to changes in climate and atmospheric composition. Theoretical interpretations of this nature aid in the prediction of biotic compositional changes in response to environmental shifts during modern climate changes.

This study examines the systematic and biogeographic implications of Early Permian age paleobotantical specimens from the western Pangean equatorial region. These plants are from Abo Formation red beds in the Zuni Mountains of northwestern New Mexico. They represent a singular occurrence of large, obovate leaves. The specimens are preserved in a siltstone that appears to have buried the plants rapidly, as some are found still in attachment to stems. No such plants have been reported from or found anywhere else in the Abo Formation throughout its area of exposure, largely in central New Mexico. The Abo Formation red beds were deposited in an extensive, flat-lying, seasonally dry coastal plain (Lucas et al., 2013). At most of the nearly 200 sites from which fossil plants have been collected, the dominant elements are walchian conifers and the peltasperm *Supaia thinnfeldioides*, with a minor component of callipterid peltasperms, mainly *Autunia conferta* (DiMichele et al., 2013). Thus, the Zuni Mountains collection stands out as peculiar and unconnected to any other Abo assemblage, including other collections in the immediate area, which also are conifer dominated.

The specimens in question are large, obovate, apetiolate leaves with rounded apices and open, dichotomous venation. They are morphologically similar to the Early and Middle Pennsylvanian plant *Lesleya*, a rare element of floras that appear to have grown on limestone soils in areas of moisture limitation, or to the Early Permian Gondwanan plant *Glossopteris*, a widespread dominant in seasonally cold, paleo-southern hemisphere climates. However, variations in venation and subtle aspects of leaf shape encourage the interpretation that these specimens may represent an instance of morphological convergence.

Of three possible interpretations that can be drawn from these comparisons, the most likely explanation is convergence in form. In this case, the Abo specimens would represent a new taxon of uncertain affinities, and reaffirm the presence on the equatorial landscape of plants, and perhaps entire biomes, nearly unknown to us. If related to *Lesleya*, a rarely occurring plant, even within its known stratigraphic range, these specimens record a remarkable instance of the "Lazarus" effect – the reappearance of a taxon well beyond its previously known stratigraphic terminus (Jablonski, 1986). If relatives of *Glossopteris*, a means of linkage between northern and southern populations of the lineage is called for (Leary, 1990, 1993).

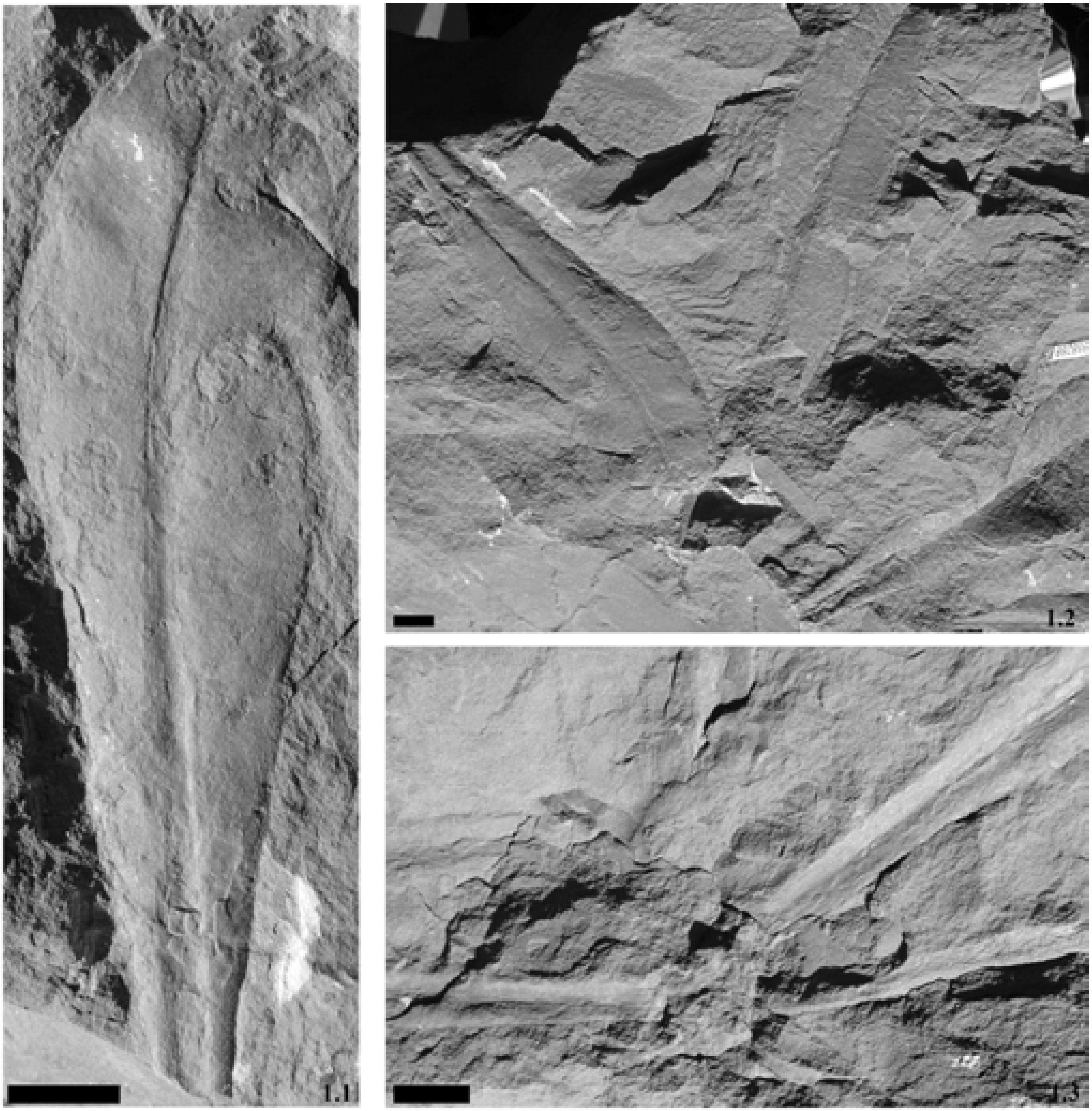

FIGURE 1. **1.1-1.3**, Unknown obovate, apetiolate leaves with rounded apices and open, dichotomous venation collected from Abo Formation red beds in the Zuni Mountains of northwestern New Mexico, USNM locality 43680. **1.1**, USNM specimen 588289. **1.2**, USNM specimen 558288. **1.3**, USNM 559287. All scale bars = 1 cm.

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FIELD TRIP GUIDEBOOK TO THE STEVEN C. MINKIN PALEOZOIC FOOTPRINT SITE, WALKER COUNTY, ALABAMA

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Abstract—This paper provides a guide to the trace and plant fossils found at the Minkin Paleozoic Footprint site, a state-protected former strip mine located in Walker County, Alabama. Amateur collectors in the Birmingham Paleontological Society (and its later offshoot, the Alabama Paleontological Society) discovered Paleozoic tetrapod footprints and also invertebrate trace fossils at this site in late 1999 and early 2000, and brought them to the attention of professionals. The paper provides some of the background behind the discovery and preservation of the site, assessments of its global paleontological significance, and illustrations and descriptions of the trace fossils found there. This is a re-formatted version of a guidebook written for visitors to the site.

How was Alabama's most important trace-fossil site preserved? Two critical decisions were made. The first was to hold a meeting to bring trackways to a central location for photographic documentation. The second was to invite local professional ichnologists to inspect the trackways and assess the significance of the site. The first studies of the trackways led Pyenson and Martin (2001) to conclude early on that the Union Chapel Mine is "one of the most important Carboniferous tracksites in the world" (Buta and Minkin, 2005).

INTRODUCTION

A former coal mine in Walker County may be the most important fossil locality in the state of Alabama. Yet most of the fossils there are simply patterns in the rock; not shells or bones. How would you behave if you knew that more than 300 million years from now somebody would be looking at your footprints and wondering what you had been doing?

This guidebook is intended to introduce you to the Steven C. Minkin Paleozoic Footprint site, which is in Walker County, Alabama (Fig. 1). We want to give you an idea of the importance of the site, what can be found there, and how to identify some of the common fossils. A great deal of information about the site is available online; see the section entitled "Further Information" for how to find it. Contact the Alabama Paleontological Society (http://alabamapaleo.org) if you want to visit the site.

The Minkin site is the most important vertebrate trackway site of its age in the world. So said Prof. Hartmut Haubold, a German expert on vertebrate tracks, after he examined hundreds of specimens that had been collected from the site. Fossil vertebrate tracks have been known from the Black Warrior basin of Alabama at least since the 1920s (Aldrich and Jones, 1930). Between 1930 and 1999, even though tracks were discovered in several Alabama coal mines (Gastaldo et al., 1990; Jim Lacefield, 2010, personal commun.), they received little attention. Then everything changed.

Ashley Allen is a high school science teacher from Oneonta, Alabama. When he told his students that he would like to take them to visit a coal mine to look for fossils, Jessie Burton said his grandmother owned a mining company.

"It was November of '99, and I went out there on a scouting expedition.... I find a slab that had a definite trackway going through it.... It looked like tire tracks of a small truck or little radio-operated vehicle.... I look around a bit longer, and I find another [trackway] that, in the Aldrich and Jones publication, is *Bipedes aspodon*, which I think they had listed as some sort of amphibian, but which we now recognize as an arthropod track.... I split [a] slab open, and there were three …. beautiful tetrapod trackways, ... little footprints running three different directions on the slab.... I yelled "Yahoo!" (Ashley Allen, 2010, personal commun.).

Since Ashley's discovery, thousands of specimens have been collected from the former Union Chapel mine, now the Minkin site. A substantial volume has been published about the site (Buta et al., 2005a), and another is in preparation, to be published by the University of Alabama Press. Scientific papers have been published; specimens are housed in museums, including the Smithsonian Institution in Washington D. C., the McWane Science Center in Birmingham, and the Alabama Museum of Natural History in Tuscaloosa; and the site continues to yield remarkable fossils with every visit.

GEOLOGIC SETTING

The geologic history of Alabama has been explained in a way that is accessible to the general public by Jim Lacefield (2000). The geologic setting of the Minkin site was described by Buta et al. (2005a). We briefly summarize it here.

The Minkin site is located in the Black Warrior basin (Fig. 2A), a depositional basin in west-central Alabama that is filled with Mississippian and Pennsylvanian rocks. The Pennsylvanian rocks in the basin are referred to as the Pottsville Formation. The Pottsville is a thick unit dominated by sand and mud eroded from the great Appalachian-Ouachita mountain chain of the eastern United States and Canada. Most of the coal deposits in the eastern United States, including Alabama, are in the Pottsville.

Why did so much coal form during the Pennsylvanian? This was a major episode of ancient mountain building in what is now eastern North America and northwestern Europe. At the time, there was no Atlantic Ocean. You could walk from New England to old England. Tectonic plates collided, mountains pushed up, and long valleys formed between them. The climate was warm and humid, and large rivers ran along the valleys. Where the land was low and flat, swamps formed. Pennsylvanian swamp forests covered a lot of territory. They may have been comparable in scope to the modern taiga, or boreal forests, which today cover much of Earth's high northern latitudes. These ancient swamps were perfect places for the lush plant growth that eventually created some of the world's largest coal deposits.

Where does the Minkin site fit in? South of the ancient plateaus and west of the mountains of north and northeast Alabama lies the Black Warrior basin. This area sank while the mountains were rising. The basin filled with a wide variety of sedimentary rocks. Sedimentary rock in the

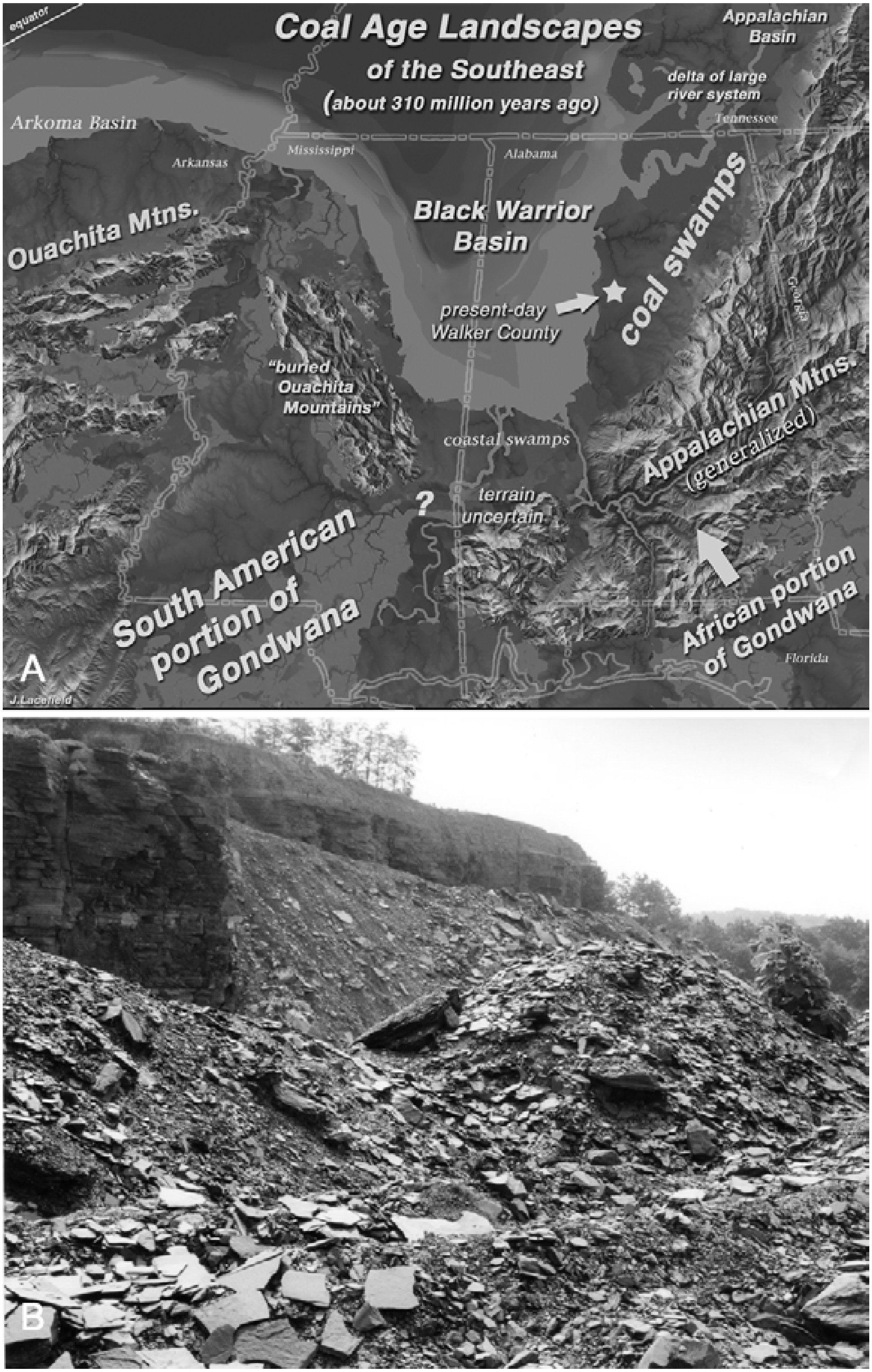

FIGURE 1. Steven C. Minkin Paleozoic Footprint site. **A**, Location and paleogeographic setting of Walker County and the Minkin site (Jim Lacefield). **B**, Field photograph, January 23, 2000, date of first BPS trip to the site.

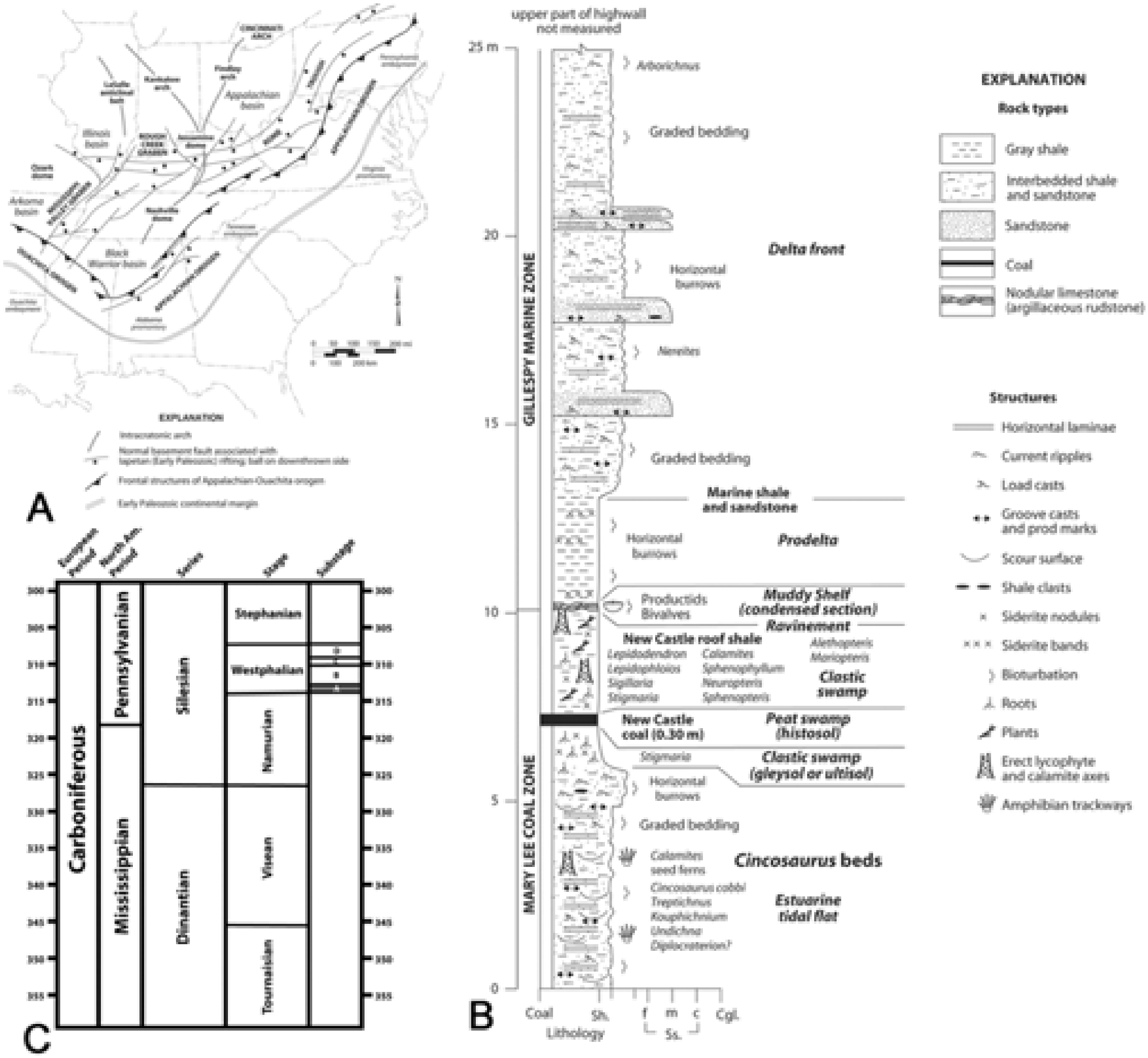

FIGURE 2. Geologic setting of the Steven C. Minkin Paleozoic Footprint site. **A**, Map showing tectonic setting of Black Warrior basin, after Thomas (1988). **B**, Measured stratigraphic section (Pashin, 2005). **C**, Age of the track-bearing *Cincosaurus* beds (shaded band), Minkin site, Walker County.

basin approaches 2 kilometers in thickness, attesting to the vast volumes of sand, mud, and other material eroded from the Appalachian Mountains. Sediment that filled the Black Warrior basin included the coal that, more than 300 million years later, was mined at Union Chapel.

Most of the trace fossils collected at the Minkin site come from the *Cincosaurus* beds (Pashin, 2005), a thin layer of shale between the Mary Lee and New Castle coal seams of the Pottsville Formation (Fig. 2B) (but see Buta et al., this volume, for an updated interpretation). The *Cincosaurus* beds are about 313 million years old (Fig. 2C). Both of these coal seams were exposed at the Union Chapel mine when it was in operation, although the Mary Lee, the older unit, is now buried (and is therefore not shown on Fig. 2B). Pottsville coal seams are typically a meter or so (1-6 feet) thick. Each seam is all that remains of a succession of swamps that repeatedly occupied the area about 300 million years ago. The coal is the remains of plants: trees, shrubs, everything down to pond scum. These plants died and formed layers of peat that were buried by mud. Peat is organic rich soil that is thought to be the precursor of nearly all coal. The plants didn't decay because they were quickly buried and because the stagnant swamp water was depleted in oxygen. Bacteria that normally degrade plant material need oxygen. Heat, pressure, time, and chemicals dissolved in groundwater transformed the dead plant material. The process of coal formation strips away much of what composed the dead plants, leaving behind mostly carbon and hydrogen (with minor oxygen, nitrogen, and sulfur). The process is complex, and the result (coal) doesn't really look like it's made out of plants unless you examine it with a microscope. However, mud layers laid down before the coal swamp reached its peak, or that buried the swamp when environmental conditions changed, are a different story. Isolated fossil leaves, pieces of bark, seeds, roots, or other plant parts are commonly preserved in shale layers associated with coals. These fossils indicate what kinds of plants lived in the ancient swamps, which in turn provides more information about the environmental conditions under which the plants grew.

These shale layers may contain other kinds of fossils, too. In general, a 0.3 m (1 foot) thick Pottsville coal seam represents 3 m (10 ft) of original peat before compression (Pashin 2005).

A familiar principle in geology is that of superposition: older sedimentary layers are underneath younger layers. The *Cincosaurus* beds at the Minkin site were deposited in association with coal swamps, which are terrestrial. But some layers higher up on the cliff include marine fossils, such as brachiopods. So the higher, younger layers were deposited at the bottom of an ancient sea. The *Cincosaurus* beds themselves were formed either in fresh water, or in brackish water that was just slightly salty. We know this because amphibians were abundant and amphibians cannot live in salt water. There are common traces made by insects, and no insects live in salt water. Finally, the kinds of plants preserved in the *Cincosaurus* beds are typical of fresh-water swamps.

Most of the trace fossils at the Minkin site appear to be restricted to the *Cincosaurus* beds, but similar trace fossil suites have been found at other coal mines in the Black Warrior basin in slightly younger or older rocks, associated with slightly older or younger coal seams (Gastaldo et al., 1990; Jim Lacefield and Ron Buta, unpublished field notes, but see Buta et al., this volume). So, just as swamp floras have been preserved in association with multiple coal deposits, traces of the animals that lived in those swamps have been preserved as well. Not all of the trace fossils from the Minkin site come from the *Cincosaurus* beds. For instance, *Arborichnus* and *Rusophycus*, two very different invertebrate resting traces, are found on deltaic sand beds that are quite a bit younger than the *Cincosaurus* beds.

This repetition of coal seams and associated fossiliferous shales is a result of cyclic sedimentation. Two of the biggest factors controlling sediment deposition during the early Pennsylvanian in the Black Warrior basin were mountain building and southern glaciation (Gastaldo et al., 1990; Pashin 1994, 2004; Pashin and Raymond, 2004). The Appalachian mountains were rising to the east and they shed great quantities of mud and sand into the basin. When the rate of sedimentation increased it was difficult for coal seams to form, because mud flooded the swamps and diluted the dead plant material. When the rate of sedimentation from the mountains decreased, and especially during early stages of sea level rise when water tables were high , thick layers of plant material accumulated and later became coal. In the same way that the recent glaciation caused environmental cycles in North America over the past few million years, Pennsylvanian glaciation on the southern continents caused sea level to oscillate, and brought other climate changes as well. As glaciers waxed and waned, conditions became more or less conducive to coal formation. The repeated rock sequences thus produced are called cyclothems.

TRACE FOSSILS

Animals can leave three kinds of evidence about their former existence: descendents, body fossils, and trace fossils. A small amphibian living in an Alabama estuary 313 million years ago might have left descendants. We could analyze and compare the genomes of living amphibians and learn quite a lot about the genetic makeup of their ancestors. We wouldn't learn anything about a particular time and place. Amphibians have hard internal skeletons, which provide a lot of information about their former appearance and physical capabilities. However, amphibian body fossils are rare. None have been found in Pennsylvanian rocks of Alabama, although they are known from similar age strata in other parts of the world. Also, because bones can be moved by scavengers, water, and other agents after death, they may not be found where their former owners lived. Trace fossils (footprints, burrows, and any other marks made by once-living organisms) don't tell you exactly what an organism looked like. But they do tell you where it lived and how it behaved. Trace fossils are all about behavior. And it so happens that we have thousands of trace fossils from the Minkin site. Just for instance, we have tens of thousands of tetrapod footprints. We know how big the creatures were, how they moved, the kind of sediment they walked through, how they interacted when they met (who avoided or ate whom), whether they formed packs or herds, and how many toes they had, among other things. And because footprints in mud and other traces are too fragile to move, we know where all of the makers lived.

Some definitions are needed here. Most trace fossils at the Minkin site are either on the tops or the bottoms of beds. When an animal steps in mud it leaves an impression. When that mud is covered by other sediment, that hardened sediment becomes a counterimpression. A rock bearing fossil footprints may have impressions on its top surface and/or counterimpressions on the bottom surface. The impressions on the top will be indentations, just like fresh footprints. The counterimpressions on the bottom are raised. An impression is in negative epirelief, which simply means it is an indentation on the top of a bed. A counterimpression is in positive hyporelief, which means it is a protrusion from the bottom of a bed. It is not always obvious which is the top of the bed and which is the bottom, but we look for unequivocal evidence. For instance, a tetrapod footprint on the top of a bed will be depressed and a similar footprint on the bottom of a bed will be raised. We also refer to undertracks. When an animal steps on a sediment surface its foot makes a depression in the surface. At the same time, underlying layers of sediment are compressed and deformed. Later, when sediment has become rock, it may split on one of those underlying surfaces. What you see there is an undertrack, and it won't look quite the same as a surface track. This depends on sediment consistency, animal weight, and depth below the surface.

FAUNA AND FLORA OF THE *CINCOSAURUS* BEDS

The Minkin site, and specifically the *Cincosaurus* beds, is a lagerstatte, a remarkable fossil occurrence. How remarkable? Well over 2500 pieces of rock with trace fossils on them have been collected. Fifteen different species of trace fossils have been recognized at the site (Table 1), as well as at least six different unnamed traces, and four arthropod body fossils (Atkinson, 2005; Beckemeyer et al., 2011). Thirty-one species of plant fossils were identified by Dilcher et al. (2005) in specimens collected from the site. However, most of these come from shale layers in the roof of the New Castle Coal seam, and not the *Cincosaurus* beds. Only *Calamites* and some seed ferns are known to have been preserved in the *Cincosaurus* beds. All together, at least 50 species have been found at the site, of which about 25 were recovered from the *Cincosaurus* beds. An additional source of complexity in the study of ancient fossil communities comes from the fact that species of body fossils of animals, trace fossils, and body fossils of plants are not strictly comparable. This is discussed in the next section. Following that, we describe many of the kinds of fossils found at the site, and reproduce photographs of some specimens. We also cite other photographs, listed by UCM number, that can be viewed in the online database.

The Definition of Species

The following is widely accepted as the definition of a biological species: a population or group of populations freely interbreeding in nature. Of course we don't know whether fossil organisms could or did interbreed. We fall back on proximity and morphology. In the case of body fossils, such as shells, we have a great deal of information about how these fossils look. When we find similar fossils that occur together and vary around an average form we call those a species. When we find similar fossils that vary around two different average forms (large or small, wide or narrow, having some special feature or lacking it, or some such) we may identify these as belonging to two species (we have to be careful not to confuse gender and age differences with species differences). One source of complexity arises for body fossils that consist of multiple parts, like vertebrate skeletons. One first has to satisfy oneself that bones are fit together correctly, or are at least assigned to the correct species, before proceeding with further study. The approach described above works just fine for animals. Not so for plants. A leaf and a piece of bark do not necessarily make clear whether they came from the same plant. Paleobotanists identify species of leaves, bark, roots, flowers, and

TABLE 1. Fossil species found at the Minkin Site.

Kind of Organism	Taxon (general)	Taxon (specific)	Comments	UCM no.	Strat. Position*
Invertebrate traces	**Inferred maker**				
	Chelicerate				
		Kouphichnium			Cinc.
	Myriapod				
		Diplichnites gouldi			Cinc.
	Insect				
		Arenicolites longistriatus	same maker as *T. apsorum*		Cinc.
		Treptichnus apsorum	same maker as *A. longistriatus*		Cinc.
		Stiaria	same maker as *T robledoensis*		Cinc.
		Tonganoxichnus robledoensis	same maker as *Stiaria*		Cinc.
	Trilobite				
		Rusophycus			higher than Cinc.
	Unknown				
		Arborichnus repetitus			higher than Cinc.
		Nereites			higher than Cinc.
Vertebrate traces	**Inferred maker**				
	Amphibian				
		Matthewichnus caudifer			Cinc.
		Nanopus reidiae			Cinc.
	Reptile				
		Attenosaurus subulensis			Cinc.
		Cincosaurus cobbi			Cinc.
		Notalacerta missouriensis			Cinc.
	Fish				
		Undichna			Cinc.
Unnamed traces			**Some examples are listed**		
		arthropods with alternate foot placement	numerous and diverse	485j, k; 669	Cinc.
		minute trackways	double row, single row	1264, 1338	Cinc.
		possible *Octopodichnus*		73, 1384	Cinc.
		arthropod jumping traces		919, 4021	Cinc.
		ovoid resting trace		425	Cinc.
		coiled backfilled burrow		425	Cinc.
Arthropod body fossils					
	Insect				
		Megasecoptera (*Agaeoleptoptera uniotempla*)	wing	2368, 2369	Cinc.
		Syntonopterodea (*Anniedarwinia alabamensis*)	pair of wings	1076a, b	Cinc.
		Diaphanopterodea (*Camptodiapha atkinsoni*)	wing	3045	Cinc.
	Arachnid				
		Trigonotarbid		2281	Cinc.
	Unknown				
		abdomen		1881	Cinc.
		possible body fossil		1272	Cinc.
Plant fossils					
	Lycopod				
		Lepidodendron aculeatum			higher than Cinc.
		Lepidodendron obovatum			higher than Cinc.
		Lepidophloios larisinus			higher than Cinc.
		Lepidostrobus			higher than Cinc.
		Lepidostrobophyllum cf. majus			higher than Cinc.
		Lepidophylloides intermedium			higher than Cinc.
		Aspidiopsis			higher than Cinc.
		Syringodendron			higher than Cinc.
	Seed fern				
		Trigonocarpus ampulliforme			Cinc. or higher
		Trigonocarpus sp.			Cinc. or higher
		Whittleseya elegans			Cinc. or higher
		Sphenopteris elegans			Cinc. or higher
		Sphenopteris pottsvillea			Cinc. or higher
		Neuralethopteris biformis			Cinc. or higher
		Neuralethopteris pocahontas			Cinc. or higher
		Lyginopteris hoeninghausi			Cinc. or higher
		Alethopteris valida			Cinc. or higher
		Cyclopteris sp.			Cinc. or higher
		Neuralethopteris pocahontas			Cinc. or higher
		Neuralethopteris biformis			Cinc. or higher
		Myeloxylon sp.			Cinc. or higher
		Holcospermum sp.			Cinc. or higher
		Carpolithes sp.			Cinc. or higher
	Horsetail				
		Calamites goepperti			Cinc. or higher
		Calamites undolatus			Cinc. or higher
		Calamites suckowii			Cinc. or higher
		Calamostachys			Cinc. or higher
		Asterophyllites charaeformis			Cinc. or higher
	Cordaitales				
		Artisia sp.			higher than Cinc.
		Cordaicarpon sp.			higher than Cinc.
		Cordaites sp.			higher than Cinc.

***Cinc.=Cincosaurus beds**

so on, knowing full well that many of these "go together." In other words, one species of living plant might correspond to four or five or more species of an existing fossil plant named for different plant parts. If you want to compare animal and plant species diversity, it might be best to look at whatever plant part is most diverse or most recognizable in the rock unit and use this as an estimate for the number of plant species (in the sense that we would use the term for living plants) that have been preserved. Trace fossils present a different problem. A footprint doesn't preserve a lot of morphological information about the foot that made it. Some toes may not leave an impression in some footprints, for instance. Two different creatures of about the same size may make footprints that are essentially indistinguishable. Also, a creature that can run, walk, crawl, hop, and burrow, can make multiple trace fossils that are assigned not just to different species but to different genera. Trace fossil species are named based on the physical appearance of the traces, without explicit reference to the organisms that made them. So a particular species of tetrapod might make trackways consisting of footprints and tail drag marks, which would get one trace fossil name. Another tetrapod of about the same size and shape, obviously different if we saw the skeleton, might make a trackway that we cannot distinguish from the trackway made by the first tetrapod. One of the tetrapods may dig burrows during droughts and perhaps the other species does not. We have no way of knowing that some of the trackways and all of the burrows were made by one kind of tetrapod and that the rest of the trackways were made by a different one. The number of trace fossil species, like the number of plant species, can be inflated relative to the number of biological species that left traces of their former existence.

Trace Fossils Ascribed to Invertebrates

Arborichnus repetitus Romano and Meléndez (1985)

Fig. 3

Minkin site trace fossils assigned to this taxon (briefly described by Lucas and Lerner (2005) and photographed by Buta et al. (2005b)) consist of paired grooves (in epirelief and, less commonly, ridges in hyporelief) flanking an oval central disturbed area (Fig. 3). Well-preserved specimens display four complete pairs of grooves. The grooves are straight to strongly curved and splay outward, almost like fireworks. Curved specimens are assumed by convention to be concave posteriorly. Successively more posterior pairs of grooves are slightly longer in some specimens. The central area is raised (in epirelief), but in some specimens is excavated at its anterior end [UCM 719, 2230]. A few specimens appear to bear traces of a pair of short grooves located anterior or posterior to four longer pairs (Plates 105b, 105a, 104b, in Buta et al. (2005b); UCM numbers 415, 743, 1155, 2233, 2449). The grooves on one side of one specimen appear to bifurcate (split in two) at the proximal ends (close to the middle of the trace) with short posteriorly directed grooves just behind the longer ones (UCM 888).

Specimens of *Arborichnus* from the Minkin site strongly resemble the original description of *A. repetitus*. The central disturbed area in some Minkin-site specimens may result from a difference in preservation. Both type specimens and the Minkin site specimens appear to be undertracks. If the type specimens were deeper undertracks, that could explain the disappearance of a central disturbed area.

Arborichnus is interpreted as an invertebrate resting or feeding trace. The makers appear to have had four pairs of legs. The central disturbed area suggests that the body was pressed into the sediment, likely during takeoff. Another possible explanation for the central disturbed area is feeding at the sediment surface, but it's difficult to see how the appendages around the mouth could have reached as far back as the last pair of legs. The trace was made by an arthropod with at least 8 legs. The maker is not known, but was probably not a horseshoe crab, as has been suggested. Horseshoe crabs usually leave drag marks made by their "tails," their appendages are forked and commonly leave Y-shaped grooves, and their footprints are relatively short and differently arranged.

Minkin site *Arborichnus* are found on thick solid sandstone slabs. They come from higher in the stratigraphic section than the *Cincosaurus* beds, which means that they are younger. Specimens of *Arborichnus* occur with few other trace fossils. On the shifting sands where they lived, no other creatures were able to make a lasting impression. Most slabs bearing *Arborichnus* specimens have multiple traces (22 of 26 slabs figured in the online database), suggesting that the organisms commonly clustered together. However, collecting bias against heavy rocks with single traces may have caused slabs with multiple traces to be over-represented in collections.

Arenicolites longistriatus

Treptichnus apsorum

Rindsberg and Kopaska-Merkel 2005

Fig. 4A-B

A. longistriatus and *T. apsorum* are virtually ubiquitous in the *Cincosaurus* beds (a few examples: UCM 147, 417, 1030, 2026; Buta et al., 2005b). They are interpreted as two different expressions of burrowing by insect larvae. *A. longistriatus* consists of shallow U-shaped vertical burrows and *T. apsorum* brings together several varieties of zigzag horizontal burrows. These trace fossils are the two most common at the site, commonly occur together, and are shown by the characteristics of transitional forms to have been made by the same critters. Trace fossil species are named by reference to their morphology, not according to who made them. This way, if interpretations change, names don't have to.

Species of *Arenicolites* and *Treptichnus* from other parts of the world are similar to the two described here, but are not necessarily made by the same organisms. The Minkin site specimens of *Arenicolites* and *Treptichnus* share certain diagnostic characteristics that strongly indicate in this particular case that both were made by one actor. For example, *Arenicolites* from the Minkin site have longitudinal grooves scored into the floors of the burrows (Fig. 4A). These grooves strongly resemble those in burrows made by modern fly larvae (Uchman, 2005). Specimens of *T. apsorum* from the Minkin site show the same kind of longitudinal grooves. Burrows made by modern fly larvae also resemble the Carboniferous *T. apsorum* in another way. Many specimens of *T. apsorum* consist of line segments in which successive segments are oriented at distinctly different angles, each segment jutting a short distance past the origin of the next one, just like in burrows made by modern fly larvae (Fig. 4B).

Body fossils of flies and their relatives are only known as far back as the late Triassic. A few arthropod body fossils have been found from the Minkin site, and none of these are flies. The Minkin site burrows in question might have been made by unknown early dipterans, or by other arthropods of similar body plan and behavior.

Diplichnites gouldi Gevers 1971

Fig. 5

Diplichnites is commonly interpreted as a myriapod (centipede or millipede) trackway. This name is assigned to meandering double rows of imprints that are closely spaced and very small (Fig. 5). Imprints are ellipsoidal or transverse or posteromesially directed scratches. These distinctive trackways are uncommon at the Minkin site (examples include UCM 154, 155, 270, 370, 373, 393, 394, 953, 954, 1113-15, 1228, 1370, 1371, 1724, 1820, 1854, 2443). A few examples of *D. gouldi* occur with other trace fossils; notably, *T. apsorum*. *Diplichnites* was reproduced quite well in an experimental study using a living giant millipede (Davis et al., 2007).

Some authors have ascribed *Diplichnites* to other kinds of arthropods, such as trilobites. In opposition to this view, myriapods have many pairs of legs and don't taper much from head to tail. Most Carboniferous trilobites had 8 to 10 pairs of legs, and they tapered pretty sharply (Harrington, 1959). Their rear legs would have been set

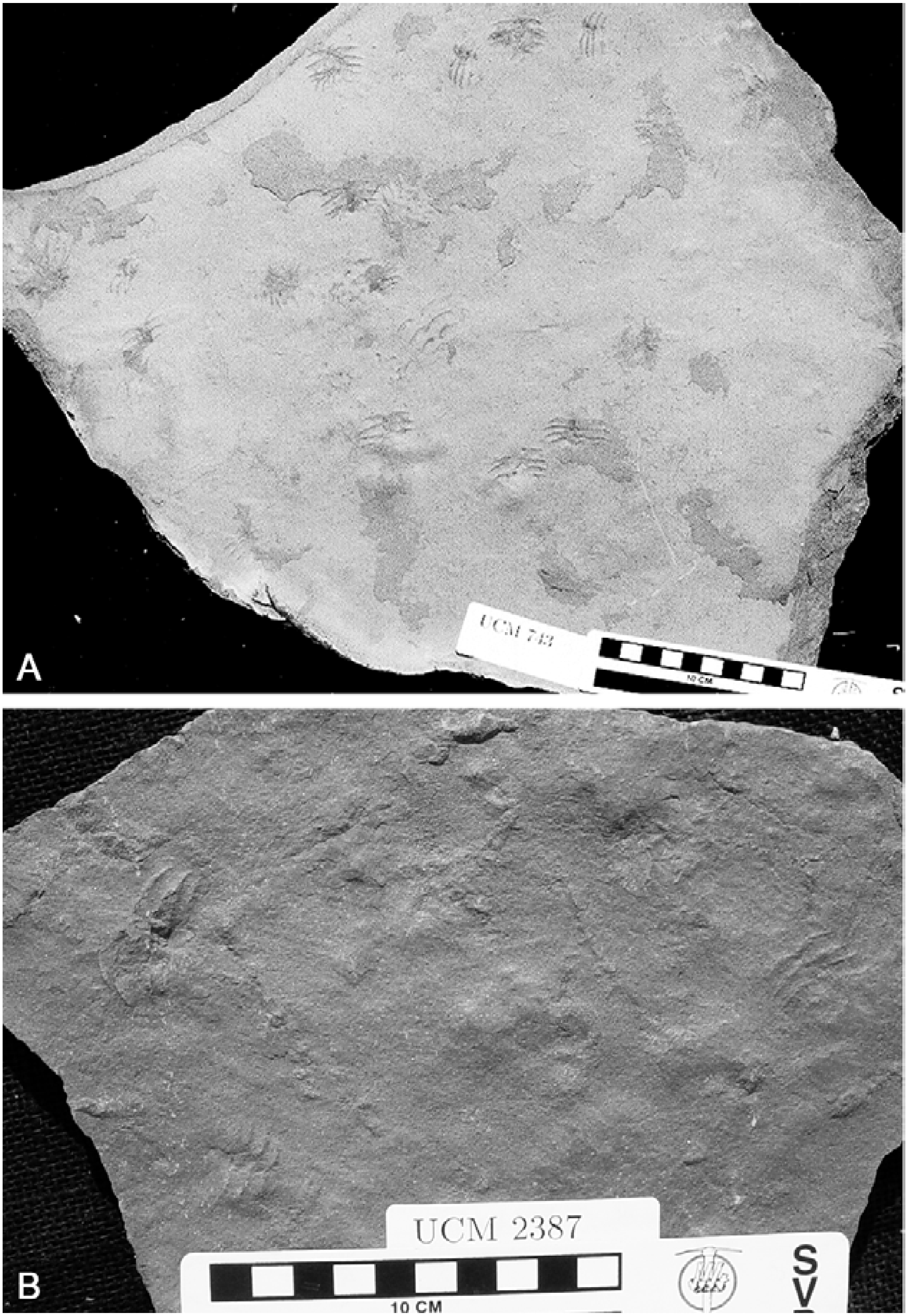

FIGURE 3. *Arborichnus repetitus*. **A**, UCM 743, Multiple arthropod resting traces on bottom side of slab. Note disturbed central area in some specimens. **B**, UCM 2233, Another example. Note scarcity of co-occurring trace fossils.

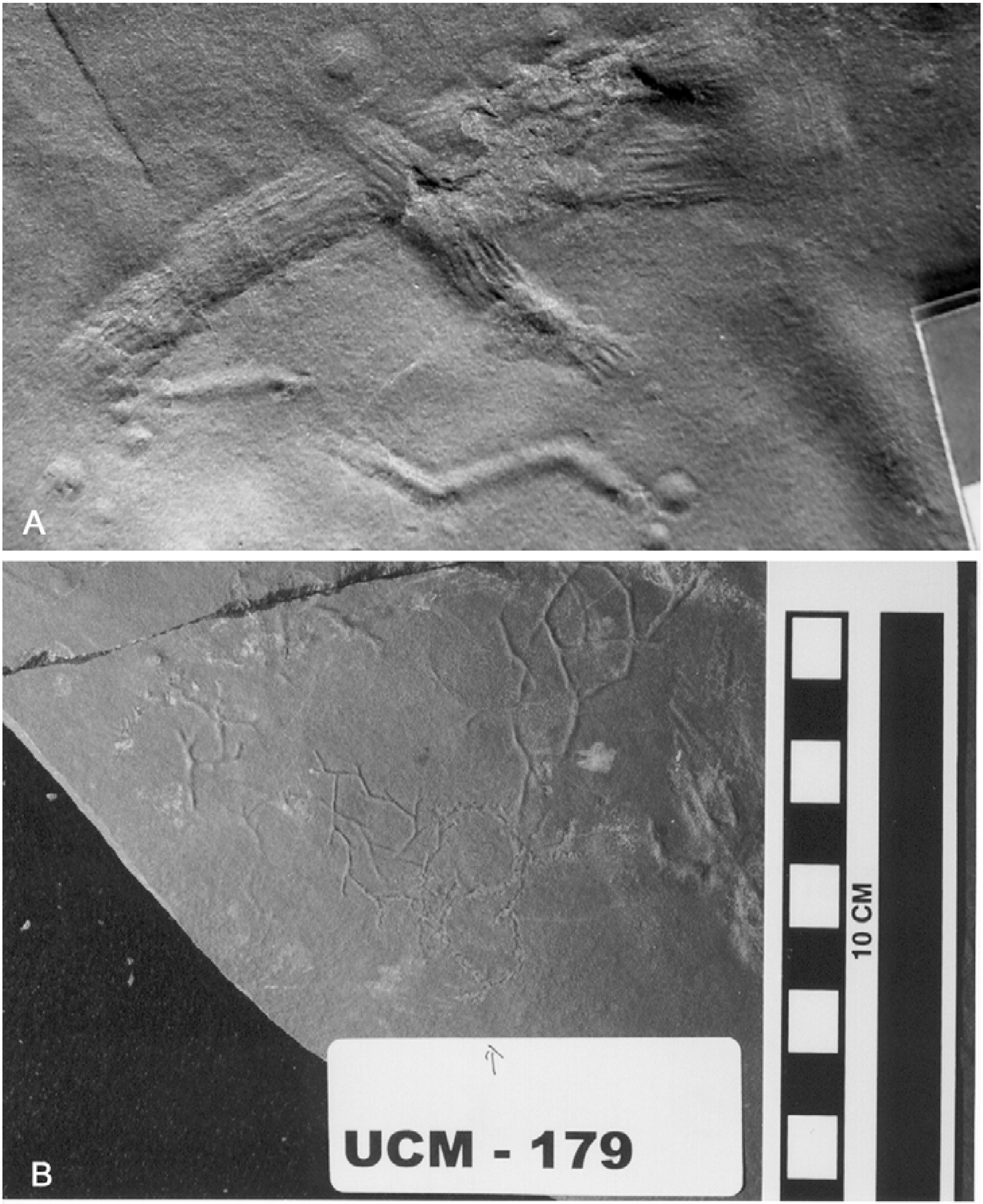

FIGURE 4. *Arenicolites longistriatus* and *Treptichnus apsorum*. Bottom sides of slabs. **A**, UCM 2038, Large and clearly striated specimens of *A. longistriatus* associated with smaller *T. apsorum* and gas-bubble impressions. **B**, UCM 179, Several specimens of *T. apsorum* showing distinct blind burrow projections past places where burrow-direction changes.

FIGURE 5. *Diplichnites gouldi*. UCM 666, Typical specimen. Bottom side of slab.

down in the sediment pretty close together compared to their front legs, which would have yielded traces resembling nested V's or multiple overlapping rows of foot impressions. Most kinds of trilobites would have been hard-pressed to make the simple double rows of imprints that comprise *Diplichnites*. Trilobite walking traces are more commonly assigned to *Petalichnus* (Rindsberg, 1990) than to *Diplichnites*. One piece of negative evidence suggests that Minkin site *Diplichnites* might not have been made by millipedes. Living millipedes have a characteristic behavior in which they travel some distance, stop, appear to search from side to side with their heads, and then continue moving forward. Modern millipede trackways show this behavior clearly; no examples are known from the Minkin site.

Kouphichnium **sp. Nopsca 1923**
Fig. 6

This name has been applied to invertebrate trackways characterized by Y-shaped footprints that have been found at the Minkin site (for example, Lucas and Lerner (2005), their figure 2, E; as well as UCM 67, 117, 437, 474, 901, 1207, 1337, 1376-78). *Kouphichnium* (Fig. 6) is made by crawling horseshoe crabs, as is well documented from study of living horseshoe crabs. Hundreds of specimens from the Minkin site have been called *Kouphichnium*. However, Dr. Nic Minter has concluded that some don't fit the description. At this point, there is no telling how many different kinds of multi-legged creatures were crawling around on the mud flats 300 million years ago. Minter notes: "*Kouphichnium* is a trackway that has groups of five tracks on either side of the trackway and a linear medial impression. The tracks on either side have opposite symmetry (i.e., the equivalent tracks on either side line up with one another and are 'in phase') and the inner four tracks on either side are simple and linear in form with occasional bifurcating terminations. The outer tracks on either side have a different morphology with a central region and then several imprints around this that make them superficially look like a tetrapod footprint." (Minter, 2010, personal commun.) Caster (1938) provided a detailed description and analysis of trackways that are now called *Kouphichnium* and compared them to trackways made by living horseshoe crabs. Horseshoe crabs can make a wide variety of trackways. When you add in the distortions found in undertracks, the possibilities multiply. The four illustrations included here are meant to show some of the possible variation.

Many arthropods, such as trilobites and millipedes, have feet that all look about the same on a given animal. Horseshoe crabs have four or five pairs of walking feet that end with small pincers known as chelae. These are biramous appendages, which simply means that they have two tips, and they are pretty much like Y's. However, the back pair of legs on a horseshoe crab are tipped with spiny paddles. This is why they leave different kinds of footprints and it's why well-preserved horseshoe crab trackways are easy to recognize. Sea scorpions (eurypterids) were related to horseshoe crabs and also had more than one kind of foot. Horseshoe crabs and eurypterids are grouped together in the class Merostomata. It takes detailed detective work, and body-fossil information we don't have, to tell what kind of merostome made a given example of *Kouphichnium*. The *Cincosaurus* beds were deposited in fresh water or water that was almost fresh. Unfortunately, both horseshoe crabs and eurypterids could live in freshwater, so this doesn't help us discriminate between the two groups.

Rusophycus **Hall 1852**
Fig. 7

Ovate, bilobate burrows characterized by paired, transverse scratches (Fig. 7). Scratches range from a few to more than a dozen pairs. Generally found in positive relief on the bottoms of beds. *Rusophycus* is an arthropod resting trace, almost exclusively Paleozoic in age, and mostly made by trilobites. Pennsylvanian trilobites had between 8 and 17 pairs of legs; most had 8-10 pairs (Harrington et al., 1959). Minkin site *Rusophycus* have 17 pairs of transverse scratches, which is certainly consistent with a trilobite origin. However, there are good reasons to think that some *Rusophycus* were not made by trilobites. First, trilobites died out at the end of the Paleozoic era in the greatest mass extinction the world has ever known. Yet some *Rusophycus* occur in younger rocks, even though trilobites don't. Second, some *Rusophycus* are found in rocks thought on other grounds to have formed in fresh water. Trilobites, responsible for most occurrences of *Rusophycus*, were entirely marine. Other arthropods, such as spiders and scorpions, invaded freshwater and the land long before trilobites went extinct. Some of these adventurers may have been able to make *Rusophycus*. Any compact arthropod with many pairs of similar legs can make *Rusophycus*. This body plan is a primitive arthropod type, which is why it is not common today. Modern arthropods have specialized limbs that have evolved to serve the creatures well in a variety of different ways.

Rusophycus at the Minkin site are found on the undersides of

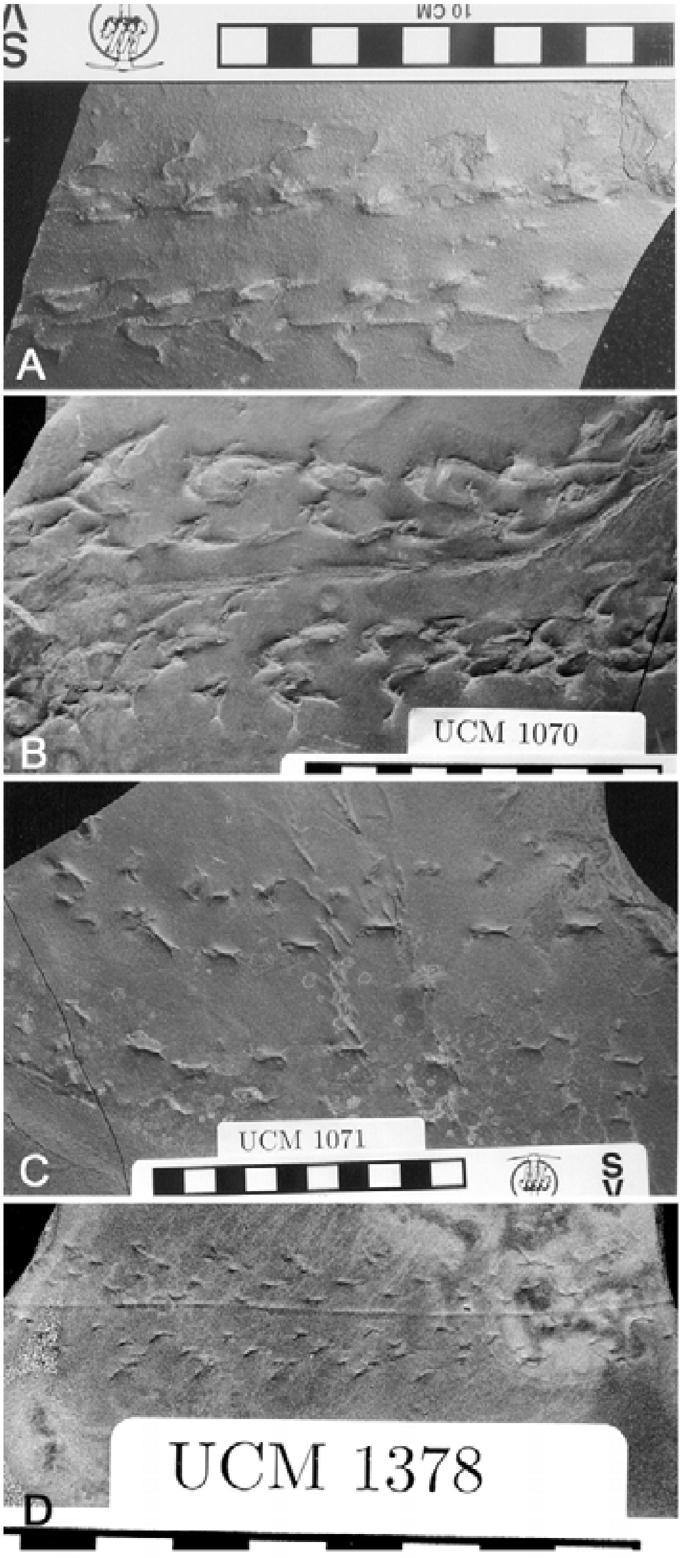

FIGURE 6. *Kouphichnium* sp. Illustrating the wide variety of trackways assigned to this species. **A**, UCM 117, Note Y-shaped marks made by biramous appendages. Bottom side of slab. **B**, UCM 1070, Top side of slab. **C**, UCM 1071, A very different expression of the tracks. Bottom side of slab. **D**, UCM 1378, Yet another variation. Bottom side of slab.

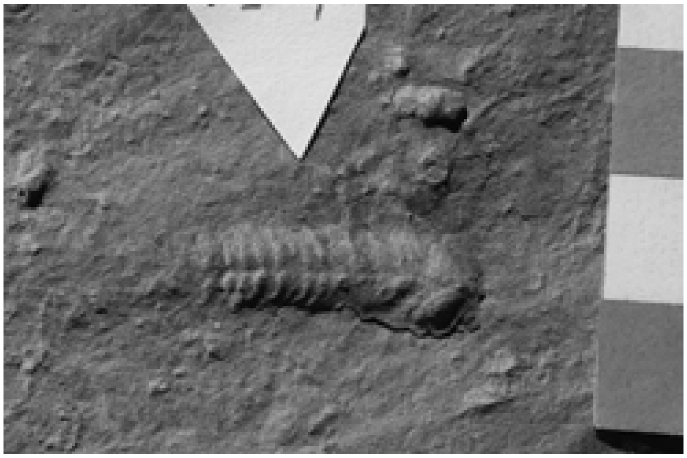

FIGURE 7. *Rusophycus* sp. UCM 3781, Bottom side of slab.

hard, thick sandstone beds higher in the section than the *Cincosaurus* beds. They are not associated with estuarine trace fossils such as horseshoe crab traces and amphibian trackways, which are so abundant in the *Cincosaurus* beds. Minkin site *Rusophycus* are well within the size range of known Carboniferous trilobites. These *Rusophycus* probably were made by trilobites, and, along with brachiopod shells, indicate times when marine water flooded the Minkin site long after deposition of the *Cincosaurus* beds.

Stiaria Smith 1909
Fig. 8

Stiaria is a trackway with a central drag mark and repeated sets of paired linear or curvilinear depressions, three on each side (Fig. 8). The groups of three prints on either side are opposite one another, as if the animal progressed by making short hops. Examples include UCM 723, 1119, 1402, 1742, and 1748. Minkin site specimens are undertracks, and some retain only two pairs of depressions per set. And therein lies *Stiaria*'s problem.

Undertracks of *Kouphichnium*, of which there are many, commonly don't show the pusher marks made by the posterior pair of walking/swimming appendages. The tracks look like *Stiaria* when the bifid nature of the appendages is not apparent (it commonly isn't). For a recent discussion of *Stiaria* in the strict sense, see Buatois et al. (1998).

The makers of *Stiaria* were gregarious (Fig. 8). They thronged together like diehard fans at a music festival. However, most *Stiaria* occur apart from other kinds of traces, even where they are found in criss-crossing abundance. Their makers were abundant, and indulged in a common behavior en masse, but away from other animals. Were they feeding? We don't know. It is odd that such common and stunning trackways are so poorly understood.

Tonganoxichnus Mángano et al. 1997
Tonganoxichnus robledoensis Braddy and Briggs 2002
Fig. 9

The species is named for the Robledo mountains of New Mexico, famed for vertebrate trackways, but home to beautiful and diverse invertebrate traces as well. The diagnosis of the species is as follows: "regularly repeated, bilaterally symmetrical, epichnial trace consisting of three medial imprints; a deep anterior elongate imprint (sometimes absent), a tapering (sometimes segmented) or hourglass-shaped posterior imprint, and a long thin, terminal imprint. Three pairs of short, anteriorly directed, curvilinear (sometimes straight) imprints occur laterally." *T. robledoensis* (Fig. 9) is a jumping trace. For further discussion see Minter and Braddy (2006). Well-preserved examples illustrated in the online database include UCM 990, 1053, 1056 (possibly 8 walking legs), 1057,

FIGURE 8. *Stiaria* sp. UCM 1749, Multiple trackways on bottom side of slab. Note the small *T. apsorum*.

1060, 1066 (shows directionality), and 1441. *Tonganoxichnus* is about the same width as *Stiaria* and they commonly occur together (Fig. 9B). Both trace fossils seem to have been made by hexapodal arthropods of the same size. These observations suggest that one critter made both, but here's what really clinches it. Several examples have been found of *Stiaria* turning into *Tonganoxichnus* and of *Tonganoxichnus* turning into *Stiaria* (Fig. 9B). Six of these examples are online (UCM 1287, 1349, 1410, 1411, 1514, 1928). These traces were attributed to monuran insects by Braddy and Briggs (2002).

Treptichnus apsorum

See *Arenicolites longistriatus*.

Trace Fossils Ascribed to Vertebrates

Attenosaurus subulensis Aldrich in Aldrich and Jones 1930

Figs. 10-11

Interpreted to have been made by an anthracosaur (a proto-reptile). Anthracosaurs shared many characteristics with early reptiles, but their eggs, like those of modern amphibians, could only develop in water. Amniote eggs (one of the defining characteristics of reptiles and their descendents) are enclosed by specialized membranes and, if they're laid outside the body, protective shells. The amniote egg, more than anything else, allowed true reptiles to conquer the land. One of the most interesting things about the Minkin site is that amphibians, reptile-like amphibians, and early reptiles all left their trackways in the same place.

The original specimen from which this species was named has been lost, but numerous specimens from the Minkin site provide sufficient documentation (UCM 24, 124, 213, 1074, 1621 (largest known print), 1754, 2250, 2251; Fig. 10). The only reservation that Haubold et al. (2005) had about referring these specimens to *Attenosaurus* is the possibility that *A. subulensis* (rare large tracks) and *Cincosaurus cobbi* (common small tracks) were made by different-sized members of a single species.

Minkin site specimens referred to as *A. subulensis* by Haubold et al. (2005) are larger (up to 25 cm in pes length), exhibit a wider trackway pattern, and have different digit proportions (pentadactyl manus, and pes imprints 4 are shorter than 3) than *Cincosaurus*. Because the specimens from the Minkin site are undertracks they don't look quite like the feet that made them, and it is difficult to compare them to specimens collected elsewhere. Problems with classifying and recognizing the makers of large Carboniferous tetrapod trackways were discussed by Haubold et al. (2005).

A different analysis of the large tracks from the Minkin site divided them among three ichnogenera, and identified most specimens as traces of pelycosaurs, early amniote reptiles (Hunt et al., 2004). Amniotes lay eggs, like those of birds and modern reptiles, in which the embryo is protected by a tough membrane. This contrasts with amphib-

FIGURE 9. *Tonganoxichnus robledoensis*. Bottom sides of slabs. **A**, UCM 1060, Insect was hopping from left to right. Note two fern leaflets. **B**, UCM 1410, Insect was moving from right to left. *Stiaria* changed to *Tonganoxichnus*.

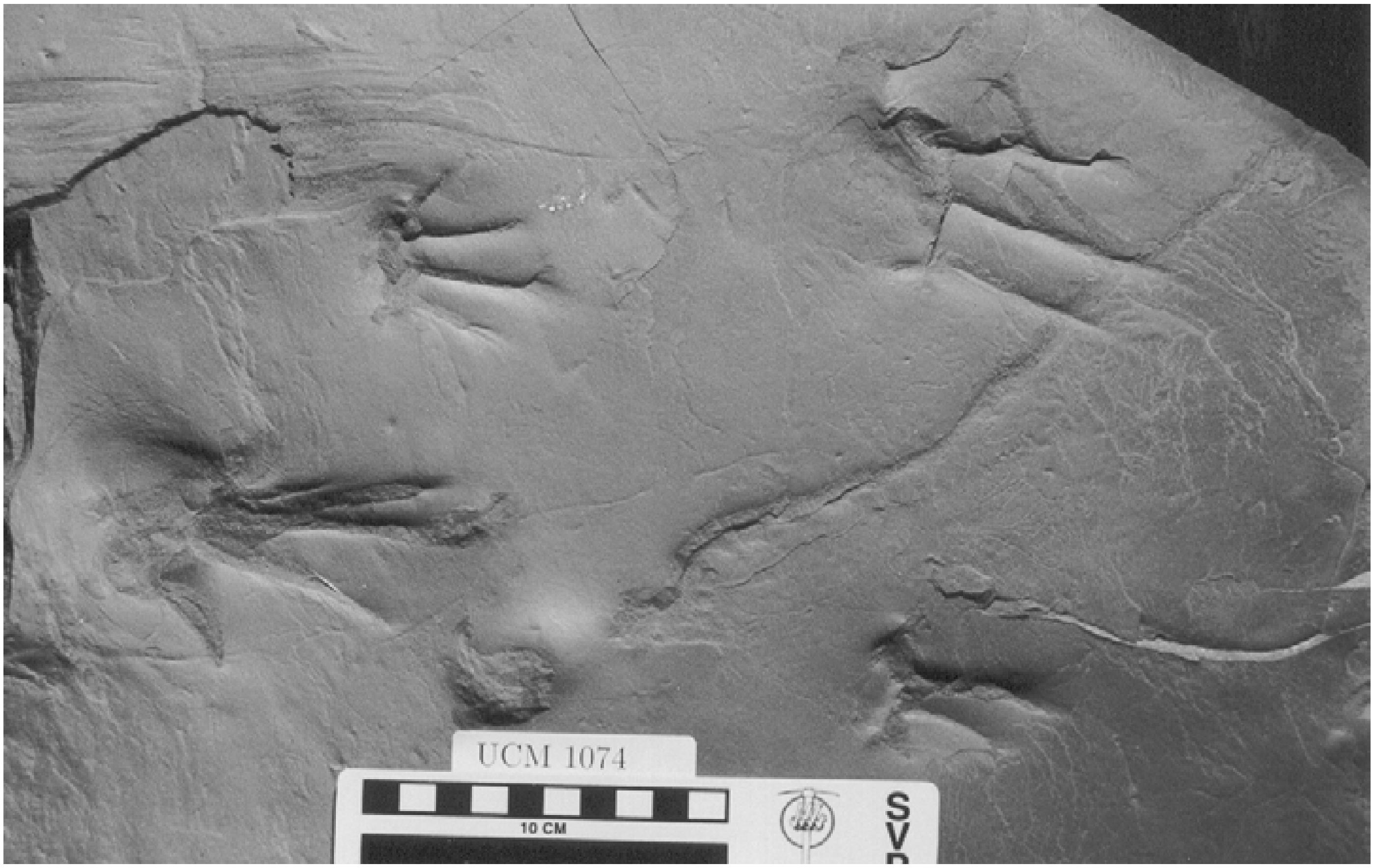

FIGURE 10. *Attenosaurus subulensis*. UCM 1074, Top side of slab.

ian eggs, which have little protection from drying out. The conclusion that most large tracks at the Minkin site were made by reptiles, which could lay their eggs on land, contradicts the interpretation given first that the trace maker had to lay its eggs in water. This is an ongoing scientific discussion, which will probably be settled by further careful research. In the meantime we know two things. First, the oldest known pelycosaur body fossils are late Pennsylvanian. If large Minkin site tetrapod tracks were made by pelycosaurs, they represent the oldest known pelycosaurs. And second, the *Cincosaurus* beds at the Minkin site were deposited at the interface between land and water. Whether the large tetrapods living there were tied to the water by fragile jelly-clad eggs or could roam inland more freely, their role as top carnivores on the mud flats was assured. Figure 11 is a painting showing how *A. subulensis* may have looked in life.

Cincosaurus cobbi **Aldrich, *in* Aldrich and Jones (1930)**
Figs. 12-13

Small tetrapod footprints (Fig. 12) interpreted to have been made by an amniote (reptile; Fig. 13). One of the most significant things done by Haubold et al. (2005) was the synonymy of eight different fossil species proposed by Aldrich in 1930. In other words, Aldrich looked at trackways of small reptiles and saw differences. Haubold et al. looked at the same specimens (along with numerous specimens discovered since 1930) and saw similarities (for example, UCM 206, 209, 250, 252, 821, 1842). This is a common theme in paleontology. When you only have a few specimens they all look different. Later, when additional specimens have been discovered, it becomes clear that there are intermediate forms among all or some of those that were found first. Some are larger and some are smaller. Some are fatter and some are thinner. They are all small reptiles of a particular early Pennsylvanian species. Intermediate forms between *Attenosaurus* and *Cincosaurus* have not been recognized, suggesting that the large and small tracks represent two valid species.

Diagnosis (list of distinguishing characteristics; emended from Haubold et al., 2005): Tetrapod trackways with pentadactyl (five-toed) imprints of manus (forefoot) and pes (hind foot), both in reptilian-like arrangements. The length of digits increases gradually from 1 to 4, and 5 is shorter and, on the pes, angled backwards and outward. Known size range for the manus is 15 to 35 or 40 mm. The pes is slightly larger. Most trackways show the manus directed inward and the pes parallel to the midline, each related to the orientation of digit 3. The trackways are narrow.

In many undertracks the pes is reduced to 3 or 4 parallel digit imprints, which terminate posteriorly at a nearly straight, transverse line.

Nearly all specimens of *C. cobbi* from the Minkin site are undertracks. This means that the morphology of the species is poorly known. This is unfortunate, because *C. cobbi* is abundant, widespread (where we find Pennsylvanian tetrapod trackways in Alabama, especially in western Walker County, *C. cobbi* is one of the most common forms), and the name has been seriously misused (applied to almost any trackway of roughly the same size). A golden opportunity for a young researcher looking for a project!

Haubold et al. (2005) noted that the huge variety of tetrapod trackways from the Minkin site makes it very important for understanding Carboniferous tetrapod footprints. In particular, the abundance and diversity of styles of preservation, and specifically of undertracks, at the Minkin site will enhance understanding of why they look the way they do and how to interpret characteristics of the trace-making organism and its behavior from undertracks.

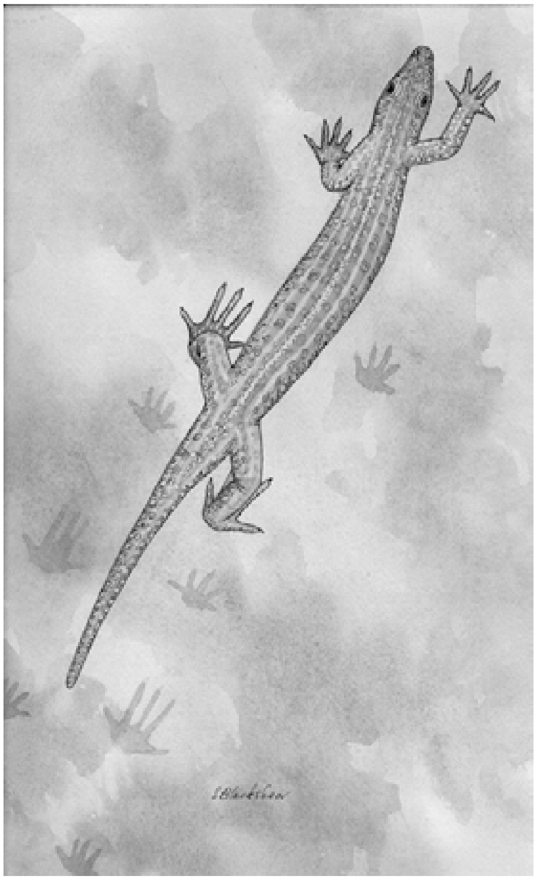

FIGURE 11. Artist's depiction of maker of *Attenosaurus subulensis*, based on UCM 1074. Painting by Sue Blackshear.

Matthewichnus caudifer Kohl and Bryan 1994
Figs. 14-15

Interpreted to have been made by a temnospondyl amphibian (Fig. 14). The name of the group refers to the characteristic appearance of the vertebrae in which some elements are separate. Early Pennsylvanian temnospondyls were abundant, and the group contained many small species that resembled salamanders (Fig. 15). Temnospondyls differed from modern amphibians in several ways; many temnospondyls had bony armor and claws. Individual tracks range from a few mm to slightly more than 1 cm across. The span from left to right feet ranged up to about 2 cm. Manus tetradactyl (four toed), roughly as wide as long. Digits 2 and 3 of roughly equal length, slightly more than half the length of the entire print. Digits 1 and 4 also subequal, approximately 1/3 the length of the entire print. Pes pentadactyl, larger than manus, with digits of increasing length from 1 to 4, digits 3 and 5 subequal (Haubold et al., 2005). Other examples include UCM 469, 652, and 969.

Nanopus reidiae Haubold et al. 2005
Figs. 16-17

Interpreted to have been made by a temnospondyl amphibian (see discussion of *M. caudifer*). Individual tracks less than 1 cm across; trackways roughly 1-3 cm wide (Fig. 16). The makers of *N. reidiae* were, on average, slightly smaller than those of the related *M. caudifer*. Specimens assigned to this species include UCM 2, 4, 11, 140, 167, 177, 191, 281, 302, 312, 313, 318, 364, 448, and 1856.

The diagnosis (Haubold et al. 2005) reads as follows: Footprints of tetrapods with tetradactyl (four-toed) manus and pentadactyl (five-toed) pes imprints. The length of pes digits 1 to 5 are nearly equal, pes digit 3 parallels the midline (direction of trackway), and digits 1 to 5 are outspread at an angle of 90°. The manus imprints are smaller, only 60% of the size of the pes imprints. Along the trackway, manus and pes imprints appear close together in sets with a changing pattern. In addi-

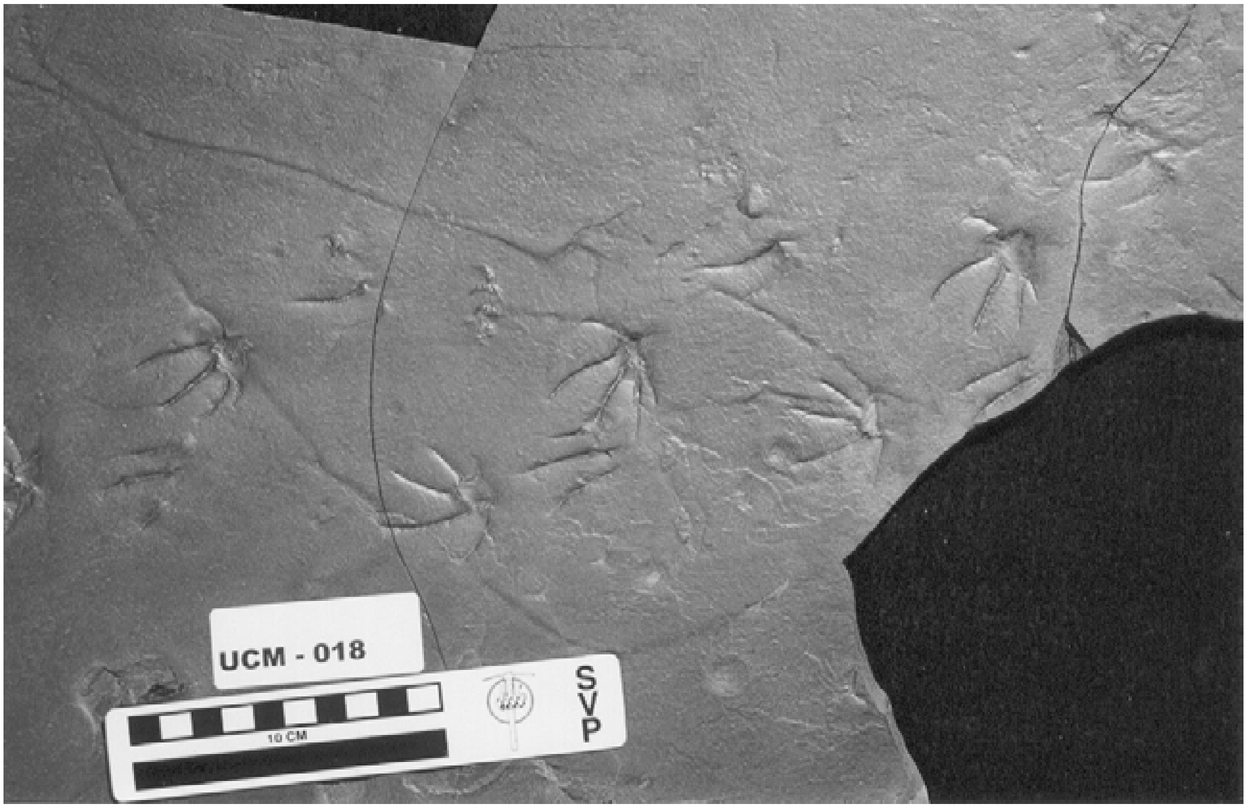

FIGURE 12. *Cincosaurus cobbi*. UCM 18, Top side of slab.

FIGURE 13. Artist’s depiction of maker of *Cincosaurus cobbi*, based on UCM 263. Painting by Sue Blackshear.

tion to the size difference, the relative lengths of pes digit impressions distinguish *N. reidiae* from *M. caudifer* (Fig. 17).

Notalacerta missouriensis Butts 1891

Notalacerta is thought to have been made by an amniote because the gait is less sprawling than that typical of amphibians and because the manus had five toes. Four toes on the "hand" is typical of amphibians. Fossil bones have not yet been found at the Minkin site, but fossil reptiles are known from rocks of the same and slightly greater age in other places.

Specimens of *N. missouriensis* collected from Alabama indicate a pentadactyl manus about 18 mm long and pes about 22 mm long (Haubold et al., 2005). In trackways, the manus is directed inward and the pes directed outward, with a stride of 50 to 65 mm and a proportionally wider trackway than that of *C. cobbi*. The digits of the manus increase substantially from 1 to 4, with the latter distinctly longer than the former. Trackway width and manus-digit proportions distinguish the species from *C. cobbi*. Important information about the characteristics of the species was published by Chesnut et al. (1994). Only a few specimens have been recognized in the Minkin site material.

Undichna sp. Anderson 1976
Fig. 18

All fish trails found at the Minkin site (more than 100 of them) belong to this ichnogenus (Fig. 18). Sinusoidal grooves, sometimes paired, are interpreted as a record of fins grazing the sediment surface as fish swam close to the bottom, perhaps in very shallow water. Living fish do the same thing. Martin and Pyenson (2005) illustrated examples and discussed what they showed about Pennsylvanian fish physical characteristics, behavior, and environment. They reported the earliest known example of schooling in fish. Many modern fish swim in schools. This is a sophisticated behavior that fish use to confuse predators. When did they learn to do this? The answer to this question has implications for

FIGURE 14. *Matthewichnus caudifer*. UCM 285, Bottom side of slab. Note deeply impressed tail-drag mark.

FIGURE 15. Artist's depiction of maker of *Matthewichnus caudifer*, based on UCM 469. Painting by Sue Blackshear.

predator-prey interactions in the ocean and fish behavioral evolution. Of the 2201 fossil slabs in the online Photographic Trackway Database, 94 contain *Undichna*. Nine (10%) exhibit parallel and/or overlapping *Undichna* made by fish moving at similar velocities (determined by the frequency of side to side movement of the caudal, or tail, fin), suggesting schooling behavior. Examples include UCM 64, 1728, 2237, 2382.

Most trace fossils from the Minkin site were collected from a thin interval called the *Cincosaurus* beds. But the thin sheets of shale where the trace fossils are found are not all the same. For instance, on the subaerial part of the tidal flat, amphibians and reptiles lived together. The tetrapods shared space with horseshoe crabs, springtails, dipteran larvae, and millipedes. Winged insects hunted each other and probably landed on the mud. We haven't yet recognized their footprints, but several wings have been found (Atkinson, 2005). Fern leaves and other plant parts fell or were blown onto the muddy surface. Gas bubbles popped and rain fell, making similar but distinguishable impressions.

In shallow water just meters away small fish were abundant. The fish could not have been the only denizens of the estuary, yet other trace fossils are conspicuously absent from slabs bearing fish-fin traces. Of the 94 slabs bearing specimens of *Undichna* in the online database, 23 also include either *A. longistriatus* or *T. apsorum*, both made by fly larvae. This may seem like a lot, but dipteran larvae burrowed nearly half of all slabs bearing trace fossils. They are found on fewer than 25% of fish-trace slabs, indicating that the two kinds of organisms tended not to occur together. Only four other specimens include any trace fossil with *Undichna* (1 *C. cobbi*, 3 small meandering trails). Sixty-seven *Undichna* occur on slabs bearing no other trace fossils whatsoever. Small fish were abundant in intertidal waters during deposition of the *Cincosaurus* beds, but we know virtually nothing about other organisms from that environment.

Incidentally, *Undichna* is limited to environments that 1) are hospitable to fish, and 2) don't experience much churning of the sediment by burrowing organisms. Among these environments are lake deposits and the relatively fresh parts of estuaries and bays (de Gibert et al., 1999).

FIGURE 16. *Nanopus reidiae*. UCM 357, Bottom side of slab. Note faintly impressed invertebrate trackway on the right.

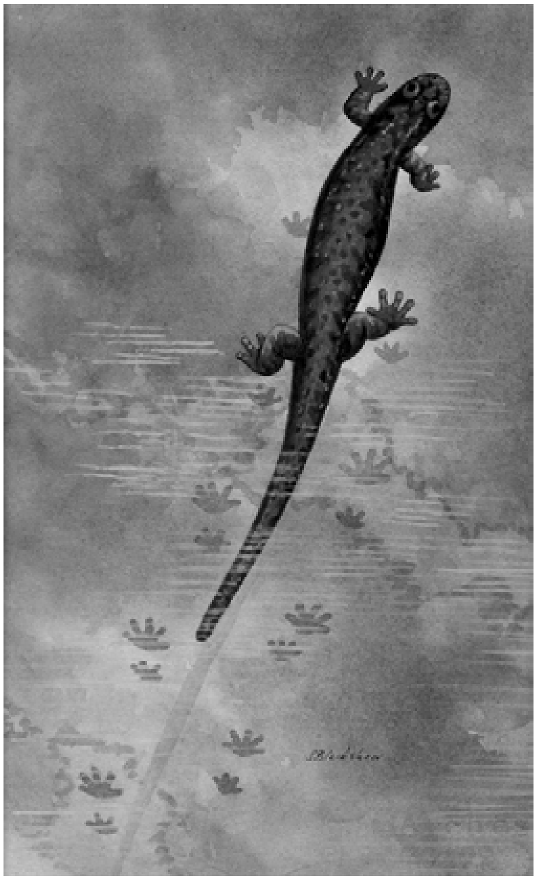

FIGURE 17. Artist’s depiction of maker of *Nanopus reidiae*, based on UCM 677. Painting by Sue Blackshear.

The *Cincosaurus* beds are interpreted as relatively fresh-water deposits on other grounds, but the conclusion is corroborated by the presence of *Undichna*.

Body Fossils

In this section we consider arthropod body fossils, which are rare, but not brachiopod and mollusk shells. These are common, but not in the *Cincosaurus* beds. Marine shells come from higher (younger) strata. Marine shells at the Minkin site have not been studied in detail.

A few arthropod body fossils have been found at the site, in the *Cincosaurus* beds (Fig. 19). All body fossils found at the site are invertebrates, and include three insect wings, one spider-like trigonotarbid, and two others of unknown nature. Arthropod exoskeletons are made of chitin, an organic material that is chemically more stable than bone in the acidic environments in and near coal swamps. This is why fragile insect wings have lasted while bone has not. All the specimens are preserved in laminated shale that seems to be from the *Cincosaurus* beds. All are different, and each of the wing specimens is a previously unknown species. Preliminary descriptions of some of these and another insect wing fossil from Alabama have been published (Atkinson, 2005; Beckemeyer and Engel, 2011). Any fossil arthropod is a rare and scientifically important discovery. Please show any possible body fossil to your trip leaders.

Plant Fossils

Plants are common and diverse at the Minkin site, although only seed ferns and *Calamites* (giant horsetails) are known from the *Cincosaurus* beds. However, plant fossils are common at almost every coal mine. After all, what's coal made out of? So even though well-preserved ferns, lycopods, and other components of the Westphalian (a Stage, a unit of geological time ranging from 304-313 Ma) swamp forest are common in the spoil piles, they haven't received much attention. That's a shame, because a well-preserved, abundant, and diverse flora has

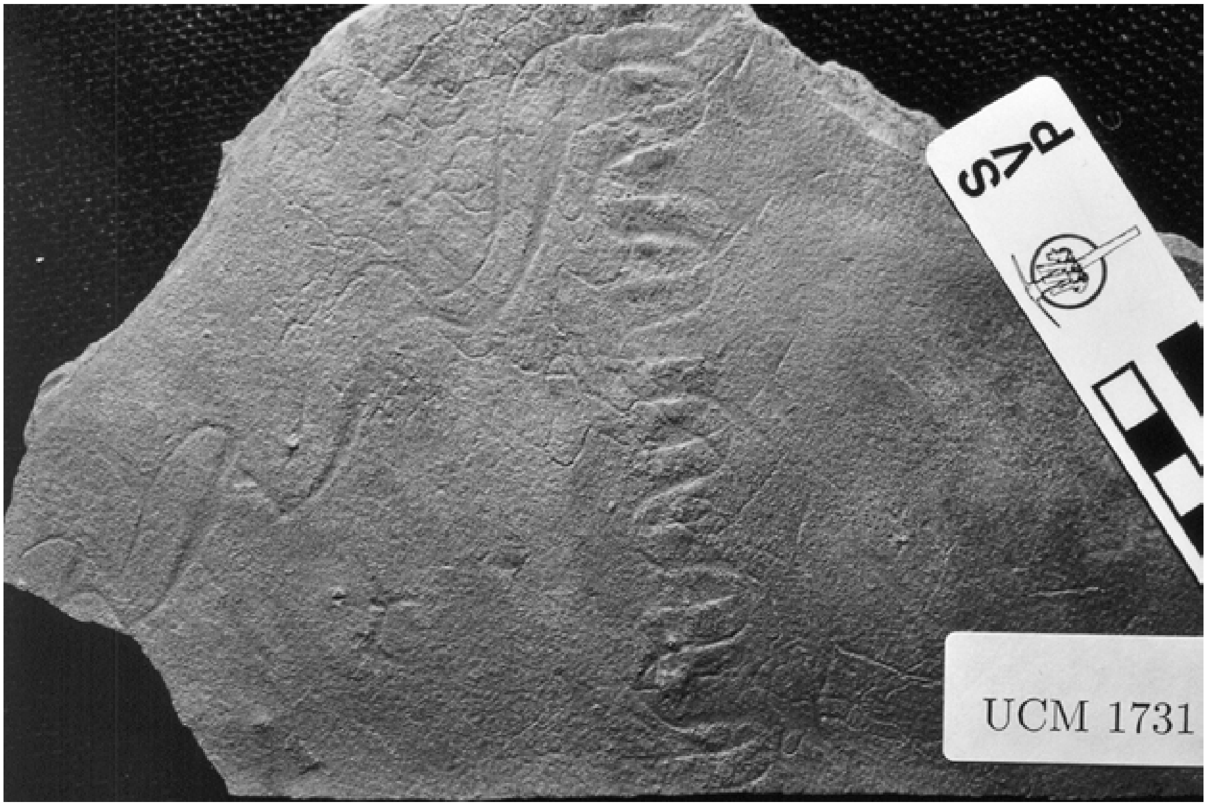

FIGURE 18. *Undichna* sp. UCM 1731, Rare slab with two *Undichna* specimens, both showing the marks of two fins. Top side of slab.

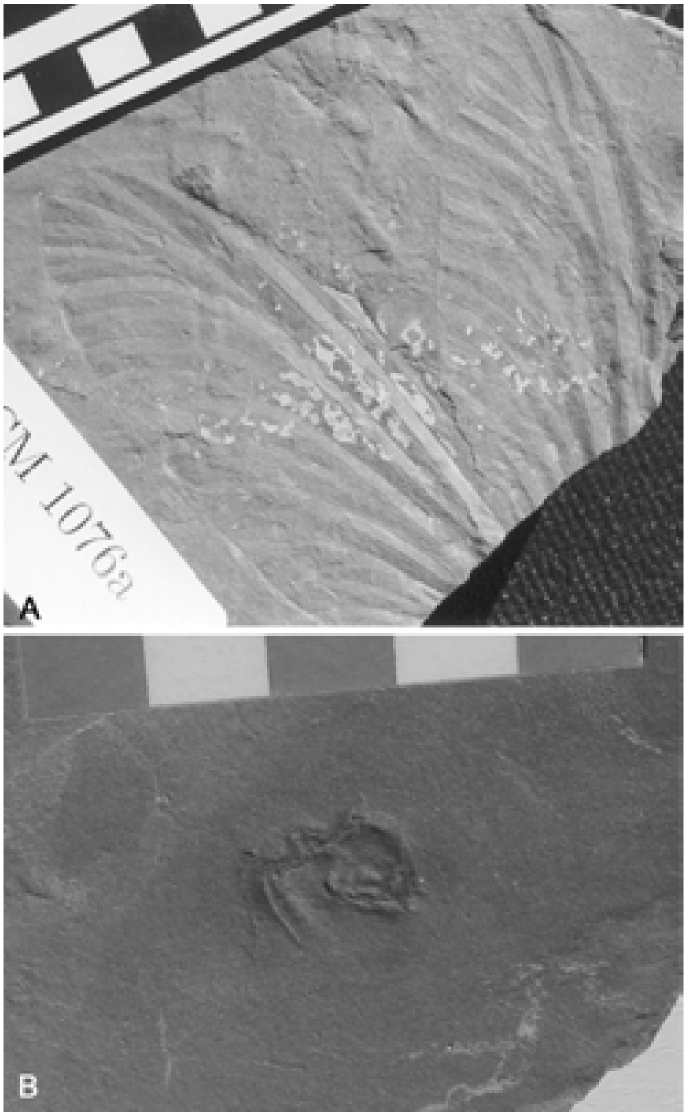

FIGURE 19. Arthropod body fossils. **A**, Wings of *Anniedarwinia alabamensis* Beckemeyer and Engel 2011, UCM 1076a. **B**, Trigonotarbid, an arachnid, UCM 2281.

been recovered from the site (Dilcher et al., 2005; Dilcher and Lott, 2005). Common plants found at the site include arborescent lycopods (bark and upper branch impressions), sphenopsids, ferns, seed ferns and cordaites. Examples of these major groups are still living today except for the seed ferns and the cordaites (a group distantly related to conifers). Lycopods, *Calamites*, and seed ferns dominate. The condition of the material indicates that it has not been transported far; the plants grew where we find them. The Minkin site was a peat swamp.

Plant fossils are common and widespread in the Pennsylvanian coal measures of the eastern United States. Plant fossils from the Pennsylvanian of Alabama have been illustrated by Lacefield (2000), Dilcher et al. (2005), and Dilcher and Lott (2005) in readily accessible publications. Accordingly, only a few common forms are illustrated here (Fig. 20).

Trees evolved about 364 my (Scheckler, 2001), and forests with well-developed canopies by 345 my (Dilcher et al., 2004). By the Westphalian, forests had been around for about 35 my. The swamp forests of the Minkin site represented a well-established ecosystem. By this time, multi-story forest canopies had developed, though ecosystem complexity continued to increase after the Westphalian. Carboniferous forests contained lycopod "pole (or scale) trees" up to about 40 m (132 ft.) tall, and understory plants that subsisted on sunlight that made it through the open lycopod canopy (Scheckler, 2001). Large lycopods found at the Minkin site include *Lepidodendron* and *Lepidophloios*. Understory plants included *Cordaites* and relatives up to about 30 m (99 ft.) tall, the giant horsetail *Calamites* (up to about 20 m; 66 ft.), and tree ferns (up to about 10 m; 33 ft.). The roots of many of these plants show physical adaptations for swamp life (Dilcher et al., 2005), such as tissue containing open channels that make it easier for oxygen to reach submerged portions of roots.

Carboniferous forests were not like the forests of today. Most "trees" were open and did not branch and branch again to form dense canopies. Lycopods, the tallest trees, branched once, a few times, or not at all. They weren't furred with broad leaves in dense clusters on myriads of twigs. They had long narrow leaves that didn't stick around for long. *Calamites* looked like giant bamboo without the leafy side branches. Tree ferns, seed ferns, and *Cordaites* and its relatives were thick with leaves, but they were understory trees.

Note of comparison: The traces we have described are those found at the Minkin site. While tracks can be found at other coal mines in Walker County, the biota can differ from mine to mine. For example, at the Crescent Valley Mine in western Walker County, invertebrate trackways like *Stiaria*, *Kouphichnium*, *Tonganoxichnus*, or *Diplichnites* are much rarer, and no definitive amphibian trackways have yet been identified. Instead, the vast majority of trackways at that site are *Cincosaurus cobbi* (Buta et al., 2013). The few invertebrate trace fossils found there include several forms that are unknown or very rare from the Minkin site. *Undichna* also has not been found, and ferns and *Calamites* are much rarer than at the Minkin site. The Crescent Valley Mine is 23 mi (37 km) west of the Minkin site and the bulk of the traces found there are older than those from the Minkin site (but see Buta et al., this volume). Different mines can preserve fossils from different environments as well as times, all recorded in Pottsville rocks.

FURTHER INFORMATION

Alabama Paleontological Society: Contact the Society if you want to visit the site.

http://alabamapaleo.org/Alabama_Paleontological_Society.html

Pennsylvanian Footprints in the Black Warrior Basin of Alabama (Downloadable book): Also available as a printed book.

http://bama.ua.edu/~rbuta/monograph/monofiles/monofiles.html

Encyclopedia of Alabama (Online article about the site):

http://eoa.duc.auburn.edu/face/Article.jsp?id=h-1371

The Photographic Trackway Database (Online database of photographs of fossils from the site): This database was made before the fossils had received very much study. The fossil identifications are not necessarily accurate or complete.

http://bama.ua.edu/~rbuta/monograph/database/database.html

Interactive Trackway Databases (An update of the earlier Minkin site Photographic Trackway Database, and a new database from a different mine, for those who might want to try classifying trace fossils):

Minkin Paleozoic Footprint Site:
  http://bama.ua.edu/~rbuta/scm/
Crescent Valley Mine:
  http://bama.ua.edu/~rbuta/cvm/cvm.pl

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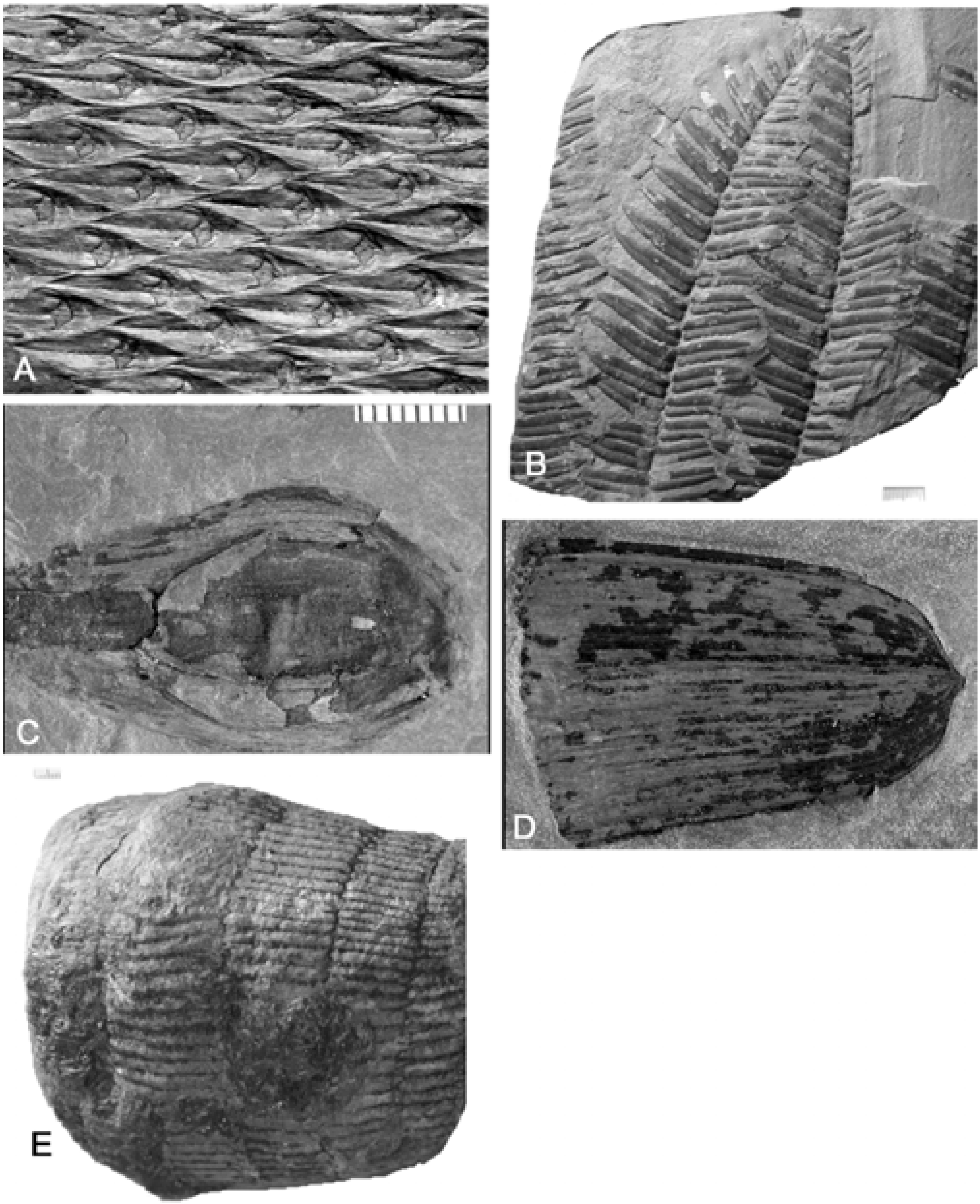

FIGURE 20. Common plant fossils. **A**, *Lepidodendron aculeatum* (lycopod "tree" bark). **B**, *Neuralethopteris biformis* (seed fern). Scale in mm. **C**, *Trigonocarpus ampulliforme* (seed case). Scale in mm. **D**, *Whittleseya elegans* (pollen organ). Scale in mm. **E**, *Calamites undulatus* (pith cast of trunk of horsetail). Scale in mm. (Dilcher et al., 2005)

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Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

A DIVERSE ASSEMBLAGE OF EARLY PERMIAN CONIFEROPSID TREE-TRUNKS FROM LAS CRUCES, NEW MEXICO

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We describe the anatomy of silicified trees found in the middle part of the Early Permian Community Pit Formation (Hueco Group) near Las Cruces, south-central New Mexico, U.S.A. Several hundred tree-trunks, up to 0.6 m diameter with preserved lengths of up to 3 m, were observed; however, we could only locate 17 specimens that showed preservation of the pith region (based on hand lens examination), which is crucial for identification. Following thin-sectioning, 10 specimens showed sufficient preservation for a reasonably thorough description. Four distinct morphotypes have been identified. Morphotype 1 shows a broad (~20 mm diameter), non-septate, homocellular pith and a mesarch, non-sympodial vasculature. Morphotype 2 is very similar to morphotype 1, differing only its heterocellular pith characterized by secretory cells with dark contents. These fossils (30% of the assemblage) share similarities with certain cordaitaleans, conifers and some pteridosperm specimens of *Eristophyton*-type. Morphotype 3 has a broad (~20 mm diameter), non-septate pith that contains prominent sclerotic nests, and a vasculature with endarch maturation. These fossils (60% of the assemblage) are somewhat similar to material known widely from Gondwana (Argentina, Australia, Brazil, India, Namibia and South Africa) under the name *Kaokoxylon*, and are probably coniferous. Morphotype 4 shows a septate, homocellular pith, but cannot be fully described due to incomplete preservation; it may be a cordaitalean or a conifer. All four morphotypes show very similar araucarioid secondary xylem of generic *Agathoxylon*/*Dadoxylon*-type, although subtle differences exist between taxa. SEM studies of charred wood from the lower part of the Community Pit Formation reveal a structure most similar to that found in *Kaokoxylon*-type silicified specimens. Several specimens of charred and silicified wood show prominent tree-rings indicative of growth in a seasonal, most likely seasonally-dry, setting.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

HIGH-FREQUENCY CYCLICITY PRESERVED IN NONMARINE AND MARINE DEPOSITS (PERMIAN, GERMANY AND NORTH SEA)

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Abstract—Permian nonmarine and marine deposits in the Southern Permian Basin in Europe provide the opportunity to test the preservation potential of high-frequency cyclicity in different depositional environments. Deposition in the landlocked basin was influenced by arid to semi-arid climate and fluctuations of precipitation and evaporation rates are recorded. Several orders of high-frequency cyclicity are imprinted in non-marine and marine deposits. Variations in earth orbital parameters (eccentricity and precession) influenced the strongly monsoonal climate during the Permian. Although c. 400 ka, c. 100 ka and c. 20 ka cycles can be interpreted in non-marine and marine deposits, only log motifs of interpreted c. 400 ka cycles are correlatable in non-marine deposits. The marine record allows correlation of all orders of cyclicity. Hiatus, erosion and cycle superposition markedly influenced non-marine deposits.

INTRODUCTION

Cyclicity in the sedimentary record is a well-known phenomenon and the study of high-frequency cycles is not new. Orbital forcing is expressed by variations in eccentricity, obliquity and precession influencing climate and ultimately the sedimentary record (e.g. de Boer and Smith, 1994). These Milankovitch cycles are imprinted in the rock record throughout earth history. Berger et al. (1989) calculated periodicities of Milankovitch cycles for the Permian with (1) eccentricity: 400 ka, 100 ka; (2) obliquity: 44.3 ka, 35.1 ka; (3) precession: 21 ka and 17.6 ka.

However, depositional environments react differently to both external controls and the timescales over which they operate, resulting in varying preservation potential of certain frequencies. In this paper we summarize external control mechanisms that likely influenced deposition during the Upper Permian (Wordian to Changhsingian) in the Southern Permian Basin (SPB) in Northern Germany and the Southern North Sea. Further, we review previous accounts and interpretations of higher-order cyclicity recorded in these non-marine and marine strata deposited during the Upper Permian (Wordian to Changhsingian). Non-marine Rotliegend and marine Zechstein deposits were formed under semi-arid to arid conditions. The structural style of the SPB remained unchanged during this time and tectonic influence on deposition was limited. We compare preserved cyclicity in both non-marine and marine settings and discuss implications of the depositional environment on preservation potential of cyclical deposits.

GEOLOGICAL SETTING

The SPB was a large sedimentary basin located in central and northwest Europe (Fig. 1). Initiated as a rift basin during the early Permian the SPB extended, after a phase of thermal subsidence and wrench tectonics, from Poland to England during the mid- to late Permian (e.g. Bachmann and Hoffmann, 1995, 1997; Van Wees et al., 2000; Geluk, 2005; Gast and Gundlach, 2006). The Permian basin-fill is lithostratigraphically subdivided into the non-marine Rotliegend and the marine Zechstein groups. Up to 2500 m of Rotliegend siliciclastics and evaporites and about 2000 m of Zechstein siliciclastics, carbonates and evaporites (Ziegler, 1990; Gast et al., 2010; Peryt et al., 2010) were deposited in Northern Germany. The paleogeographical setting of the intracontinental basin at about 10–25° north of the paleoequator resulted in the influence of an arid to semi-arid climate, leading to deposition in a range of desert environments (Glennie et al., 2003). Rotliegend deposition was characterized by alluvial fans and aeolian dunes at the basin margins, with evaporitic sandflats in the transition to a salt lake, which covered large areas of the basin center. Rotliegend deposition was terminated by a rapid marine flooding of the entire basin, establishing the Zechstein inland sea (e.g. Smith, 1979; Peryt et al., 2010). This rapid flooding initially resulted in anoxic bottom-water conditions in the deeper parts of the basin, leading to deposition of a basin-wide black shale, the Kupferschiefer. Subsequent Zechstein deposition was characterized by fully marine to hypersaline conditions. Carbonates and evaporites dominate the Zechstein succession with well-developed cyclicity (Fig. 2).

Few chronostratigraphical markers exist to correlate Rotliegend and Zechstein deposits with the global time scale, but estimation of cycle periodicity requires abundant and robust age data. Various and at least partially contradicting age data and possible correlations to the global time scale are discussed in Menning et al. (2005), and Slowakiewicz et al. (2009) among others. The Illawarra reversal, which was detected by Menning et al. (1988) in the Parchim Formation, indicates an early Capitanian (265–266 Ma; Menning et al., 2006) or Mid- to Late Wordian age (267 Ma; Steiner, 2006). Alternatively, the age of the base of the Parchim Formation is given by Slowakiewicz et al. (2009) as 275.4 Ma. Base Zechstein is biostratigraphically dated with the occurrence of the conodont *Mesogondolella* (*Jinogondolella*) *britannica* as early Wuchiapingian (Kozur, 1998; Kozur and Wardlaw, 2002; Legler et al., 2005). Ogg et al. (2008) gave an age of 260.4 Ma for the base Wuchiapingian. The Kupferschiefer at the base of the Zechstein was dated by Brauns et al. (2003) as 257.3±2.6 Ma using Re-Os isotopy. Based on magnetostratigraphy, the Zechstein-Buntsandstein boundary is defined at 252.6 Ma (Menning et al., 2005). The duration of Zechstein deposition is therefore still a matter of debate (Menning et al., 2005; Slowakiewicz et al., 2009; Paul, 2010), and Menning et al. (2005) discussed durations of both 2.8 Ma and 5 Ma.

EXTERNAL MECHANISMS LIKELY TO HAVE INFLUENCED DEPOSITION

Tectonic Activity

The Upper Rotliegend II was deposited during a phase of overall thermal subsidence in the SPB (Bachmann and Hoffmann, 1997) and strike-slip/transtensional tectonics influenced deposition to a certain degree by dictating the overall accommodation regime (Gast and Gundlach, 2006). Fault reactivation during the Altmark I-IV movements, recognized in the German Rotliegend successions, resulted in differential subsidence and locally in basaltic extrusions (Gast, 1988; Hoffmann et al.,

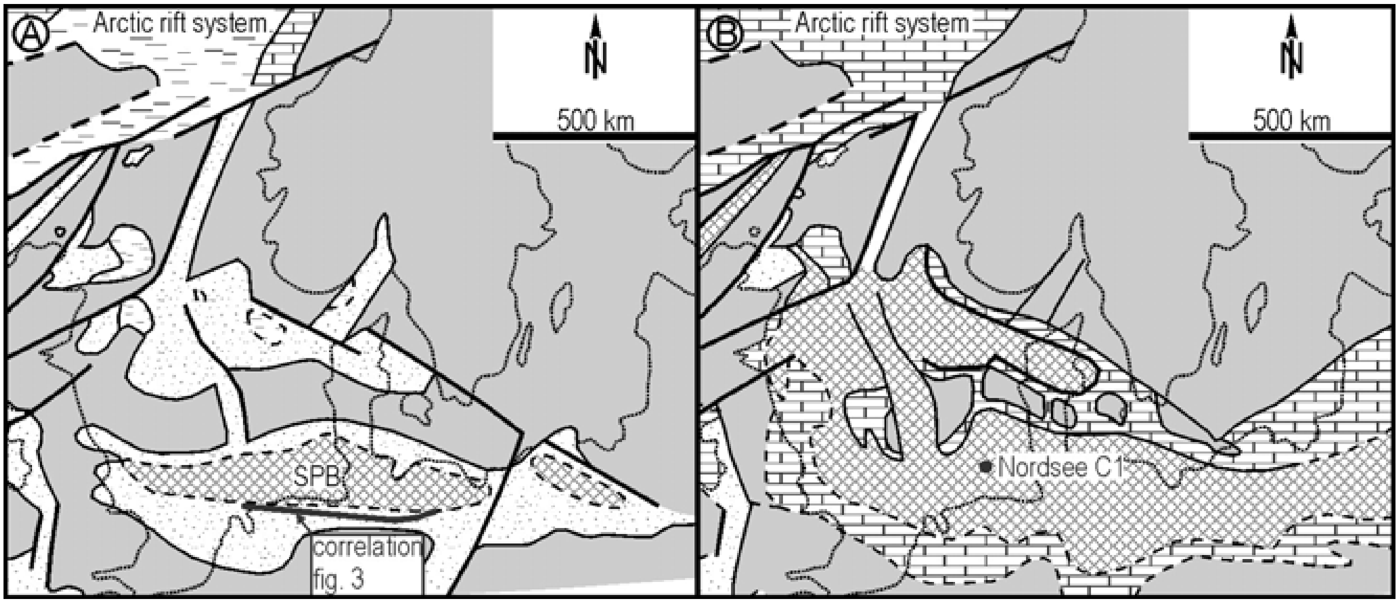


FIGURE 1. Generalized palaeogeography of NW Europe during **A**, Rotliegend and **B**, Zechstein deposition (after Glennie et al., 2003; see fig. 2 for legend).

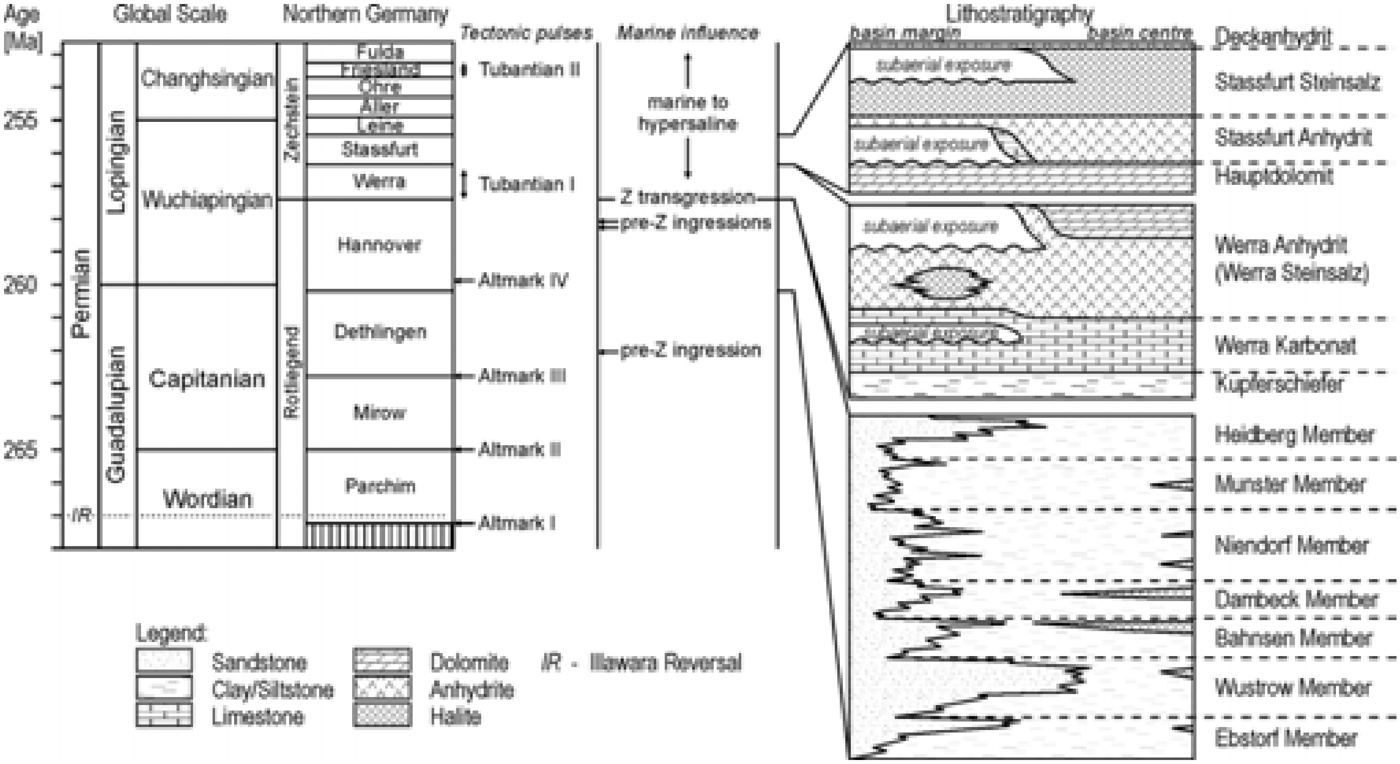


FIGURE 2. Lithostratigraphy of Rotliegend and Zechstein deposits in Northern Germany and correlation to the global stratigraphic scale with detailed lithostratigraphy for the Hannover Formation and Werra and Stassfurt folgen (lithostratigraphic charts not to scale; based on Plein, 1995; Kaiser, 2003; Gast et al., 2010; Peryt et al., 2010). Note that the base of the Hannover Formation was placed somewhat below the maximum progradation of coarse clastics (Wustrow Member) for historical reasons, and the top is defined by the Kupferschiefer (Schroeder et al., 1995; Plein, 1995). Due to these conventions, the Hannover Formation shows strictly speaking an upward coarsening-fining-coarsening trend.

1989; Hoffmann, 1990; Gebhardt et al., 1991). Altmark movements resulted in basinward progradation of coarse-clastic deposits due to uplift at the basin margins and accommodation space creation in the basin centre. During periods of tectonic quiescence the input of coarse clastic deposition waned (e.g. Hoffmann et al., 1989; Gebhardt et al., 1991). These fluctuations resulted in the development of four stacked fining-upward cycles in the Upper Rotliegend II deposits in the German part of the SPB. These basin-wide correlatable, tectonically controlled fining-upward cycles were used to establish the lithostratigraphical formations Parchim, Mirow, Dethlingen, and Hannover (Schroeder et al., 1995; Plein, 1995) in the German Rotliegend succession (Fig. 2). Faulting at the Texel-Ijsselmeer-High in the Netherlands probably occurred contemporaneously and can also be linked to the Altmark II and III movements (Geluk et al., 1996; Geluk, 1999). Tectonic activity also controlled the paleogeomorphology and deposition in the Polish part of the SPB in the Upper Rotliegend and the Lower Zechstein (Kiersnowski et al., 2010).

Rifting in the Arctic Rift System/Viking Graben created routes for rapid flooding of the SPB and formation of the Zechstein Sea (Smith and Taylor, 1989). Extensional tectonics also affected marginal parts of the SPB and resulted in the formation of sub-basins (Ziegler, 1990), fault reactivation and differential subsidence during the Tubantian I movements (Geluk, 1999; Gast et al., 2010). The Altmark I-IV and Tubantian I tectonic phases occurred with a periodicity of c. 2 Ma. The Tubantian II tectonic interval resulted in faulting and half-graben formation during the Upper Zechstein (Geluk, 1999).

Climate

Late Permian deposition in the SPB was influenced by arid to semi-arid climate as is recorded by aeolian and evaporitic Rotliegend deposits and thick evaporitic Zechstein successions. The paleogeographical position of the SPB and the strong continentality within Northern Pangea resulted in dry climatic conditions. This dry climate, characteristic for large parts of Europe and Northern Africa during the Late Permian, was only interrupted by a wet phase in the Wuchiapingian (Roscher and Schneider, 2008). Time equivalent Zechstein (Boreal) and Bellerophon (Tethyan) transgressions influenced regional climate and resulted in decreased continentality (Schneider et al., 2008). However, on the smaller scale of the SPB during Upper Rotliegend II and Lower Zechstein deposition, high frequency climatic fluctuations are interpreted from the sedimentary record (e.g. Gast, 1991; Wagner and Peryt, 1997 in Slowakiewicz et al., 2009). The higher frequency fluctuations were previously interpreted to occur within the Milankovitch frequency band, linked to waxing/waning cycles of ice shields (e.g. Glennie, 1986) or variability of monsoon circulations (Legler et al., 2011).

Sea Level Fluctuations

Rotliegend deposition was indirectly influenced by sea-level fluctuations. Marine ingressions into the SPB are paleontologically and geochemically proven (Gebhardt, 1994; Legler et al., 2005; Legler and Schneider, 2008). These short-termed ingressions from the north occurred during high sea level in the Arctic rift system, but were also likely to have been linked to rift tectonics prior to the Zechstein transgression. They resulted in an increased size of the saline lake and interfered with climatically driven lake-level changes. Additionally, distinct increases in the size of the Rotliegend saline lake occurred with an estimated periodicity of c. 1 Ma (Legler and Schneider, 2008). They can possibly be correlated to sea-level highstands in the Arctic rift system (Legler and Schneider, 2008), as sea-level highstands probably had a feedback effect on regional climate. Maritime influence on extended shelf areas might have triggered higher precipitation rates in Central Europe.

The Zechstein transgression finally flooded the SPB and established marine conditions. From this time onwards global sea-level fluctuations directly affected deposition in the Zechstein Sea and six evaporation cycles formed in response to 3rd-order sea-level fluctuations (e.g. Tucker, 1991; Strohmenger et al., 1996). Fully marine conditions existed in the SPB only during high global sea-level, the connections to the sea were more tortuous during lowstands when restricted marine to hypersaline conditions were established. These eustatic connections to the open marine realm potentially occurred with a periodicity of c. 1 Ma. Higher frequency sea-level fluctuations within the Milankovitch frequency band are commonly interpreted from Zechstein deposits (e.g. Gerlach and Knitschke, 1978; Pöhlig, 1986; Mawson and Tucker, 2009).

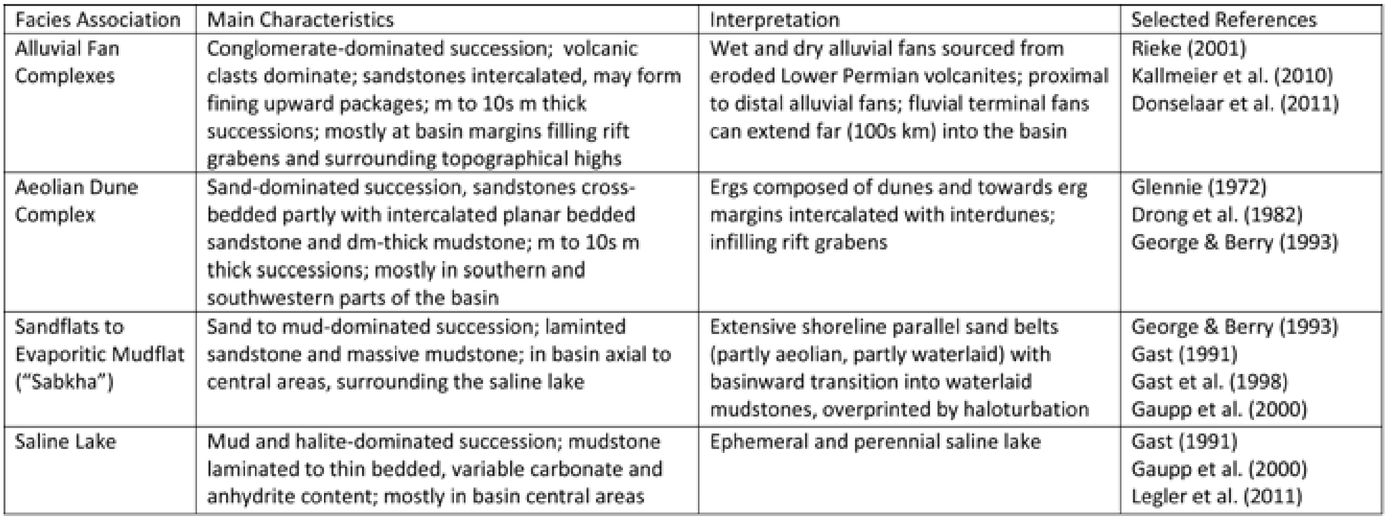
LOW-FREQUENCY CYCLICITY (1–2 MA)

Cyclicity of lower order than within the Milankovitch frequency band is recorded in Rotliegend and Zechstein deposits and was triggered by various factors as already discussed. Fining-upward cycles of c. 2 Ma-periodicity in Rotliegend deposits were triggered tectonically (e.g. Hoffmann et al., 1989). Circa 1 Ma-cyclicity in Rotliegend deposits was driven by climate variability and short-term marine ingressions into the SPB affecting size of the basin central saline lake and base level in the basin (Legler and Schneider, 2008). Cyclicity of 1–2 Ma is recorded in carbonate-evaporite cycles in Zechstein deposits (e.g. Menning et al. 2005) and was probably linked to global sea-level fluctuations and resulting marine ingressions into the SPB.

HIGHER-FREQUENCY CYCLICITY IN NONMARINE UPPER ROTLIEGEND II DEPOSITS (<1 MA)

Rotliegend deposition was dominated by aeolian sandstones and lacustrine mudstones, with fan conglomerates at the basin margins (Table 1). High-frequency cyclicity in Rotliegend deposits is expressed in various ways, depending on the location within the basin. In the basin centre, lake-level fluctuations are expressed in claystone – anhydritic claystone – halite successions and vice versa. They reflect increases and decreases in brine concentration. At the saline lake margin, lake contraction is recorded by a shift of facies belts and lake deposits are overlain by saline mudflat, aeolian sandflat and dune deposits. The reverse trend is often expressed by thinner successions of lake extension. But phases of lake extension are partially completely missing with lacustrine deposits directly overlying aeolian dunes. Beyond the extent of the saline lake extensive dune fields developed and deposition was controlled by fluctuating groundwater level. Successions of increasing aridity, hence falling

TABLE 1. Overview of Rotliegend facies associations in the SPB.



Facies Association	Main Characteristics	Interpretation	Selected References
Alluvial Fan Complexes	Conglomerate-dominated succession; volcanic clasts dominate; sandstones intercalated, may form fining upward packages; m to 10s m thick successions; mostly at basin margins filling rift grabens and surrounding topographical highs	Wet and dry alluvial fans sourced from eroded Lower Permian volcanites; proximal to distal alluvial fans; fluvial terminal fans can extend far (100s km) into the basin	Rieke (2001) Kallmeier et al. (2010) Donselaar et al. (2011)
Aeolian Dune Complex	Sand-dominated succession, sandstones cross-bedded partly with intercalated planar bedded sandstone and dm-thick mudstone; m to 10s m thick successions; mostly in southern and southwestern parts of the basin	Ergs composed of dunes and towards erg margins intercalated with interdunes; infilling rift grabens	Glennie (1972) Drong et al. (1982) George & Berry (1993)
Sandflats to Evaporitic Mudflat ("Sabkha")	Sand to mud-dominated succession; laminted sandstone and massive mudstone; in basin axial to central areas, surrounding the saline lake	Extensive shoreline parallel sand belts (partly aeolian, partly waterlaid) with basinward transition into waterlaid mudstones, overprinted by haloturbation	George & Berry (1993) Gast (1991) Gast et al. (1998) Gaupp et al. (2000)
Saline Lake	Mud and halite-dominated succession; mudstone laminated to thin bedded, variable carbonate and anhydrite content; mostly in basin central areas	Ephemeral and perennial saline lake	Gast (1991) Gaupp et al. (2000) Legler et al. (2011)

groundwater level, are recorded by sandflat/erg margin deposits passing upwards into large scale aeolian dunes (erg deposits; Howell and Mountney, 1997). Periods of increased groundwater level resulted in extensive sandflat formation. Howell and Mountney (1997) point out that sandflat formation is associated with longer periods of sediment bypass and/or erosion. Alluvial fan deposits at the basin margin record phases of fan progradation and backstepping in response to tectonics and catchment runoff.

Depositional cycles occur at different scales within Upper Rotliegend II deposits in the SPB. Large-scale cycles are some 10s of meters thick and can be correlated through large parts of the basin (Fig. 3). In the absence of core material, correlation is based on gamma-ray log expression. In basin axial parts this approach is straight forward, as the maximum extent of the saline lake formed time-equivalent horizons marked by claystones (Gast, 1991). However, beyond the distribution of lacustrine deposits correlation without core material is more difficult and less reliable (Gast, 1991; Maynard and Gibson, 2001). Based on this approach, Gast (1991) recognized 23 depositional cycles in Upper Rotliegend II successions in the basin center. These 10s of meter thick cycles can further be subdivided into cycles of higher frequency. Cycles of m-, dm-, and cm-scale can be identified (Fig. 4), in particular in basin axial parts. Recognition of cm-scale cycles is limited to lacustrine horizons, which in parts also show mm-rhythmicity of siliciclastic and evaporitic laminae.

Cyclicity in Upper Rotliegend II deposits is interpreted to have been triggered by climate fluctuations (e.g. Gast, 1991; Yang and Nio, 1994; Howell and Mountney, 1997). Climatically triggered deposition in hydrologically closed basins is controlled by fluctuations in precipitation and its influence on base level (lake level, groundwater table) and the amount of surface run off. Described cyclicity in Upper Rotliegend II deposits reflects drying-wetting upward cycles (Fig. 5). Depending on the position within the basin, base level and surface runoff influenced Rotliegend deposition to a varying degree. Basin axial deposition was directly controlled by fluctuations in lake-level and towards the basin margin groundwater level was the main controlling factor. Alluvial fans responded directly to variability in surface runoff, although tectonic control on fan development cannot be excluded (Kallmeier et al., 2010).

Climatically driven drying-wetting upwards cycles of different scale are interpreted to reflect Milankovitch and higher order cycles of different order. Gast (1991) estimated periodicity of several 10s of meter thick cycles with c. 400 ka, based on the duration of Upper Rotliegend II deposition and number of preserved cycles. 400 ka cycles are interpreted to reflect long-term eccentricity cycles. Meter-scale cycles are interpreted as c. 100 ka eccentricity cycles and c. 20 ka precession cycles (Gast, 1991). Decimeter to cm thick cycles might be caused by climate variability at millennial scale and mm rhythmicity potentially reflects seasonal variation in precipitation.

Spectral analysis of wireline logs was used to recognize cyclicity of different scales from gamma ray logs in the Netherlands (Yang and Baumfalk, 1994; Yang and Krouwe, 1995) and in the UK North Sea (Maynard and Gibson, 2001). Sliding window spectral analysis allows delineation of cyclicity and recognition of breaks in the rock record, and was used to correlate between different wells in the SPB (e.g. Yang and Baumfalk, 1994; Maynard and Gibson, 2001). To enable correlation between different facies belts, log sections need to be corrected for compactional differences of sand and shale. Although breaks in deposition will be detected by this kind of cycle analysis, duration of breaks representing events of non-deposition or erosion remain unknown. The second attempt in cycle analysis is to estimate the order and duration of cyclicity imprinted in the rock record. Interval spectral analysis computes a spectrogram of cyclicity in a chosen interval and ratios of wavelength for spectrum peaks can be calculated (e.g. Yang and Krouwe, 1995 for details). To test the assumption that Milankovitch cyclicity controlled Rotliegend deposition, Yang and Krouwe (1995) compared re-

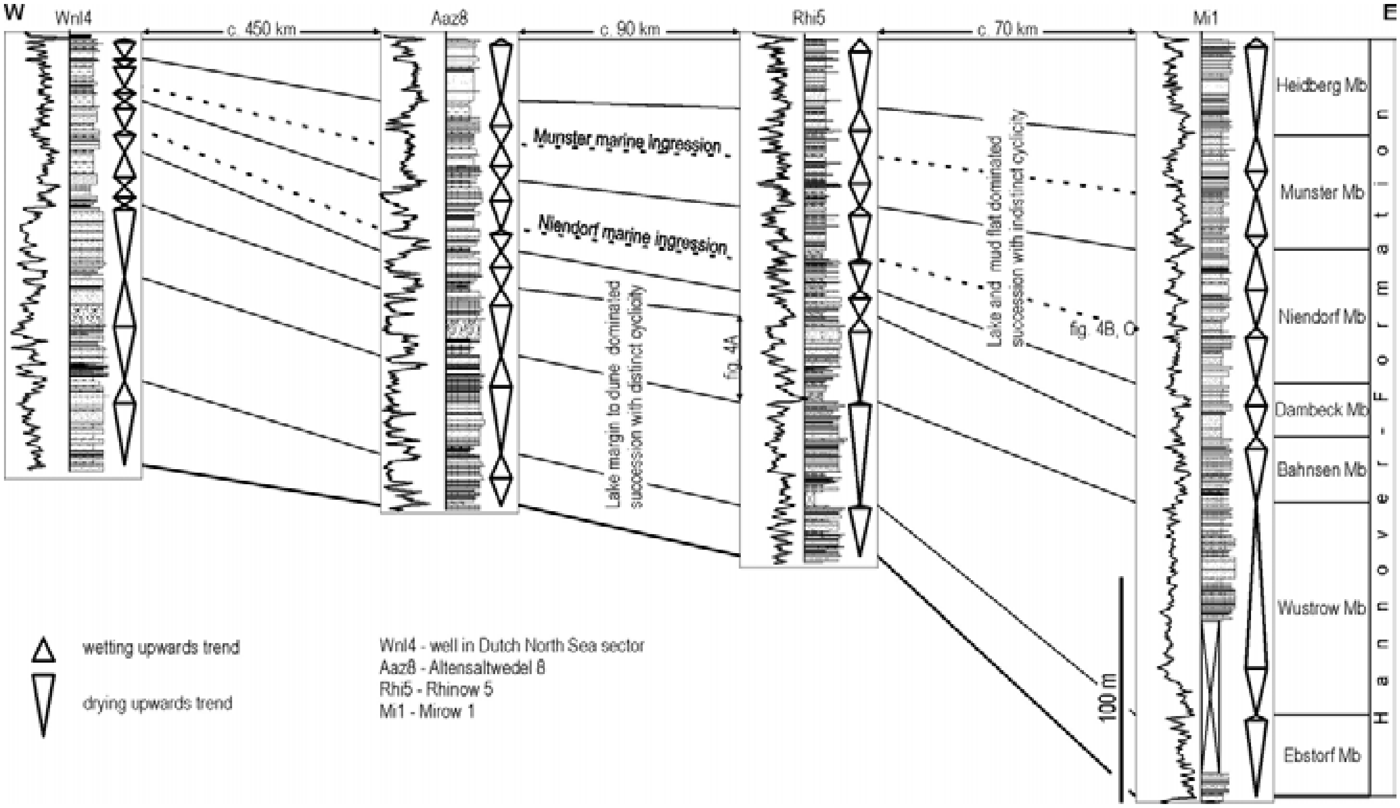


FIGURE 3. Correlation of the Hannover Formation and equivalents from the Netherlands to Northeast Germany. 10s of m thick cycles controlled by lake level fluctuations are very well expressed and correlatable over 100s of kilometers. Marine ingressions are superimposed on cycles of the Niendorf and Munster members (location see Fig. 1).

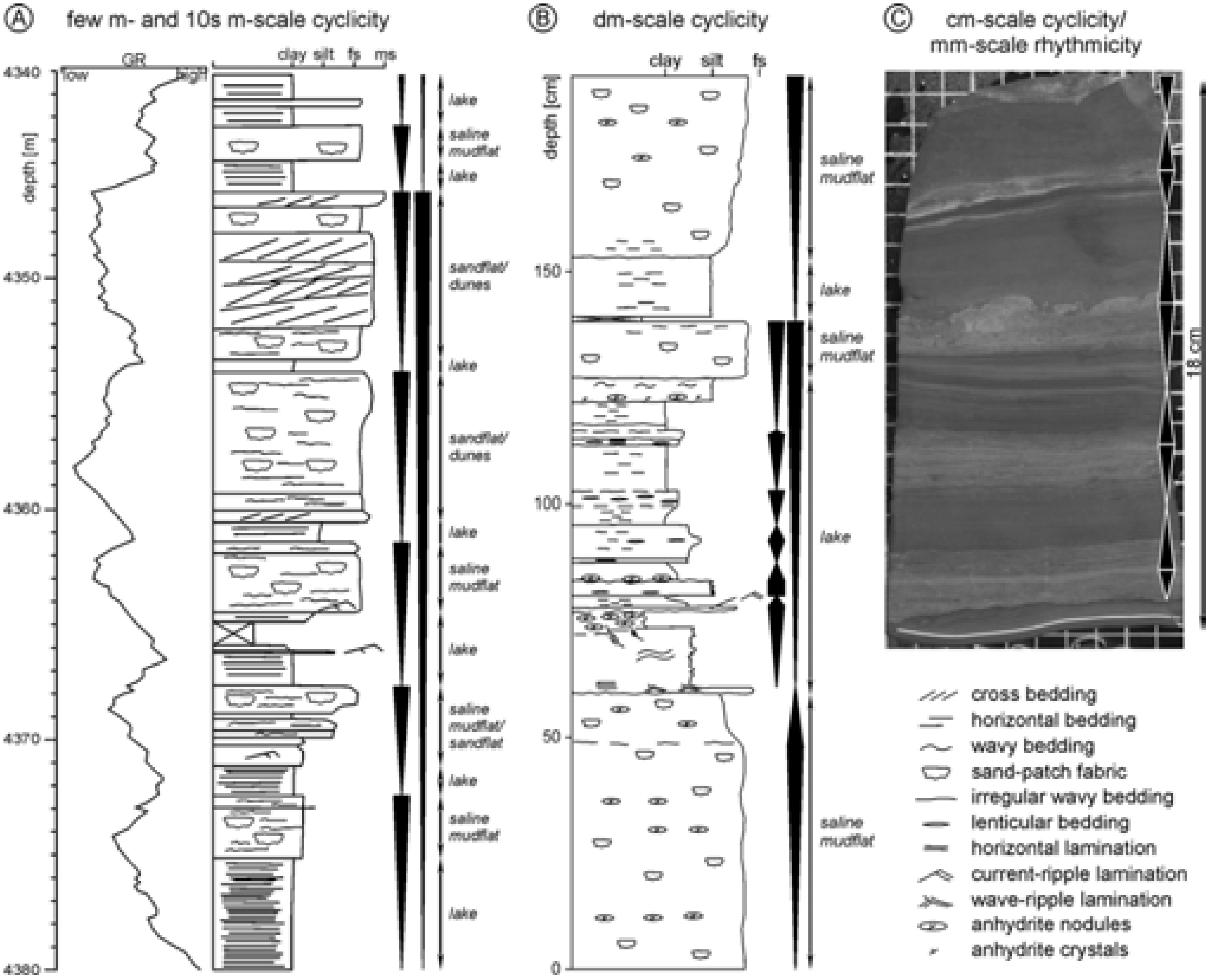


FIGURE 4. Cycles of different scales imprinted in Rotliegend deposits. **A**, 10s of meters thick drying-wetting upward cycle, interpreted to represent c. 400 ka, composed of several c. 100 ka and c. 20 ka cycles (Gast, 1993, 1995; Bahnsen Member, well Rhinow 5). **B**, dm-scale cyclicity drying-wetting upward cycles, resulting in fluctuations of lake level and brine saturation (Legler et al. 2011; Niendorf Member, well Mirow 1). **C**, cm-scale cyclicity and mm-scale rhythmicity within single saline lake horizons, red laminae claystone, grey laminae gypsum arenite (Niendorf Member, well Mirow 1).

corded ratios of wavelengths with ratios of Milankovitch periodicity. Some intervals show great conformance with both ratios, leading to the conclusion that eccentricity, obliquity and precession cycles are all imprinted in the Rotliegend succession (Yang and Krouwe, 1995). However, some periodicities are frequently missing in the Rotliegend data set and additional periodicities may occur. Based on the recognition of Milankovitch cyclicity in Rotliegend deposits, Yang and Baumfalk (1994) and Yang and Nio (1994) estimated a duration of Rotliegend deposition offshore of the Netherlands of 10.7 Ma. However, the Rotliegend succession in the Netherlands correlates only to the upper part of the Upper Rotliegend II succession in Germany (e.g. Gast et al., 2010) and in light of the stratigraphic framework of the Upper Rotliegend II the duration given by Yang and Baumfalk (1994) and Yang and Nio (1994) is largely overestimated (George and Berry, 1997; Bailey, 2001). Further criticisms of interval spectral analysis results are focussed on the ignorance of periods of non-deposition or erosion, which are likely to record more time than deposition periods in areas outside the saline lake (Bailey, 2001).

HIGH-FREQUENCY CYCLICITY IN MARINE BASAL ZECHSTEIN DEPOSITS (<1 MA)

High-frequency cycles within the Milankovitch frequency band were interpreted previously, and different frequencies are imprinted in Zechstein deposits (e.g. Richter-Bernburg, 1985; Strohmenger et al., 1996; Mawson and Tucker, 2009). We focus here entirely on initial Zechstein deposition, i.e. the Kupferschiefer and its equivalents at the basin margin and on basin central highs.

Kupferschiefer in Basin-axial Parts

The Kupferschiefer is an organic-carbon rich black shale that occurs throughout the SPB. The shale is laminated and consists of variable content of organic, carbonate and terrigeneous matter. In the basin center, the Kupferschiefer is few decimeters thick and thickness commonly increases towards basin margins (Fig. 6). The Kupferschiefer was deposited as a result of rapid marine flooding of the SPB, leading to interruption of clastic sediment supply into the basin and the establishment of

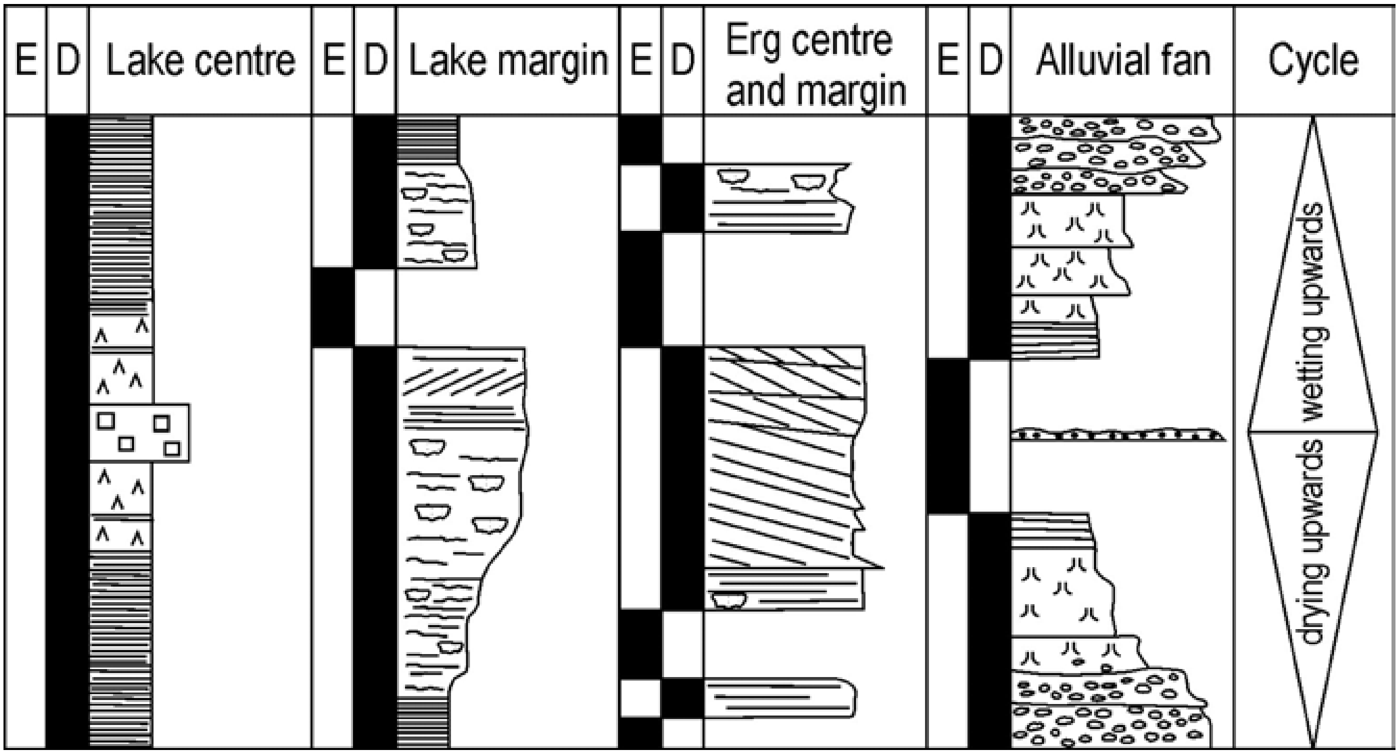


FIGURE 5. Summary of idealized expressions of drying and wetting upward trends in climatically driven Rotliegend cycles (modified after Howell and Mountney, 1997). **Abbreviations: D**, deposition; **E**, erosion.

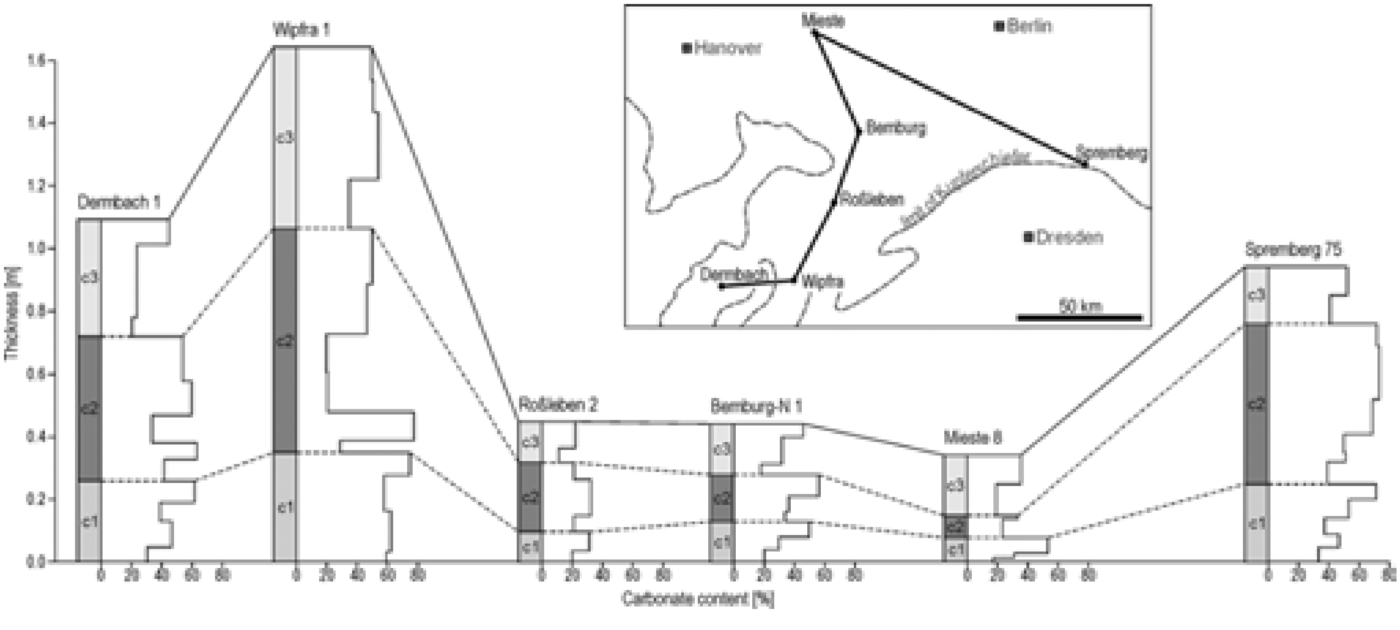


FIGURE 6. Correlation of Kupferschiefer cycles, note the increasing carbonate content toward each cycle top. The thickness of the Kupferschiefer increases toward the basin margin coinciding with an occurrence of additional (sub-) cycles (based on Rentzsch, 1965); inset. location of correlation pan (limit of Kupferschiefer distribution from Wedepohl, 1964).

dysoxic to anoxic bottom-water conditions. Three depositional cycles occur in the Kupferschiefer (Rentzsch, 1965; Gerlach and Knitzschke, 1978; Paul, 2006) and within each cycle the proportion of carbonate, terrigenous clastics and organic carbon varies (Fig. 6). In general, carbonate content increases towards the top of each cycle, but detailed analyses show further internal complexity. These three cycles are correlatable over 100s of km. As the thickness of the Kupferschiefer decreases basinward, cycle thickness decreases accordingly. Cyclicity in Kupferschiefer deposits was previously interpreted to reflect either climatic variability or sea-level fluctuations (Paul, 2006). Carbonate production was driven by water temperature, and in shallow, warm-water areas close to the basin margins high carbonate production is expected. A general decrease in carbonate content towards the basin center (Fig. 6) supports this hypothesis. But temperature of the upper water column in the entire Zechstein Sea might have responded to climate variability. Additionally, water temperature of the entire water column is expected to increase in shallow seas, hence sea-level fluctuations will also have affected sea-water temperature. Observations from the basin center alone do not allow conclusive differentiation between climate or sea-level control on cyclicity. The Kupferschiefer cyclicity was probably orbitally forced, but the cycle duration is debatable. Kupferschiefer deposition is, based on modern deposition rates of black shales and laminae counting respectively, estimated to record a time span of 20–60 ka (Füchtbauer, 1968; Ölsner, 1959). Based on 60 ka duration, intra-Kupferschiefer cycles could readily be interpreted to span c. 20 ka each and are therefore interpreted to reflect precession cycles. However, higher-frequency cyclicity cannot be excluded.

Kupferschiefer-equivalent Deposits at the Basin Margin

Cyclicity in basal Zechstein deposits also occurs along the basin margins and at intra-basin highs, where Kupferschiefer-equivalent sediments were deposited. In the Gera Bight, an embayment at the southern margin of the Zechstein Sea, a succession of Kupferschiefer and Kupferschiefer equivalent rocks crop out (Fig. 7). Rotliegend alluvial fan deposits are storm-wave reworked at the top, and the basal Zechstein conglomerate contains marine bivalves. Organic carbon-rich, sandy limestone (Mutterflöz) overlies the conglomerate. In the Gera Bight, the Mutterflöz is characterized by an upwards increase in carbonate content. Along the southern margin of the SPB the Mutterflöz shows varying thicknesses. It passes upwards into Kupferschiefer black shale. The Kupferschiefer is overlain by a bioclastic limestone, the Productusbank. Laterally, the thickness of these coquina beds varies greatly over short distances (few 100s m). The Zechstein carbonate (Ca1) overlies the Productusbank and can be correlated throughout the basin.

The Zechstein conglomerate, Mutterflöz and Kupferschiefer are interpreted to have been deposited during the transgressive phase of the Zechstein Sea. They record flooding and successive rise in sea level within the SPB. The Zechstein conglomerate formed above storm-wave base and represents a transgressive lag deposit. Due to rapid initial flooding of the SPB, transgressive lags were not developed in deeper parts of the basin. Deposits in the Gera Bight, close to the basin margin, indicate a slower transgression leading to wave-reworking of Rotliegend deposits. The transition between storm-wave reworked Zechstein conglomerate and Mutterflöz reflects increasing water depth and deposition below storm-wave base. The organic carbon content of the Mutterflöz indicates dysoxic conditions at the sediment surface. Further rise in sea-level resulted in stagnant anoxic bottom-water conditions and formation of the Kupferschiefer. The Productusbank is interpreted to be deposited as tempestite above storm-wave base; laterally varying thickness reflects preserved topography of storm-wave deposits. Deposition of the Productusbank reflects destratification and mixing of the water column. Change in sea level within the SPB seemed to be the dominant factor controlling basal Zechstein deposition in the basin marginal position of the Gera Bight. The three horizons: (1) Zechstein conglomerate, (2) Mutterflöz and (3) Kupferschiefer/Productusbank can potentially be interpreted as lateral equivalents of the three Kupferschiefer cycles in the basin center. However, a hiatus associated with the Zechstein conglomerate at the basin margin cannot be excluded. Laterally variable thickness of the Mutterflöz could indicate local preservation of more than one cycle of Kupferschiefer equivalent. Laterally equivalent deposition of cycles at the basin margin and in the basin center would imply control by the same parameter. Hence Kupferschiefer cycles in the basin center were equally controlled by sea-level fluctuations and are not purely driven by climatic variability.

Kupferschiefer Equivalent at Intra-basin High

Basal Zechstein deposits, formed at an intra-basinal high in the central parts of the SPB, were described by Legler et al. (2005). The Kupferschiefer equivalent in the well Nordsee C1 is composed of laminated, calcareous siltstone with intercalated halite (Fig. 8, phase 1). This light grey Kupferschiefer equivalent contains marine fauna, indicating Wuchiapingian age, and is overlain by red siltstone. The red siltstone is arranged into five vertically stacked packages of laminated siltstone passing upward into siltstone with sand-patch fabric (Fig. 8, phase 2; Smoot and Olsen, 1988). The top of the cored interval is composed of a 4 m-thick succession of intercalated laminated and oolitic limestone (Fig. 8, phase 3). Faunal diversity is highest at the base of each package.

These basal Zechstein deposits are interpreted to have been deposited in an embayment, which was formed when the Zechstein Sea flooded the flanks of the intra-basin high (Legler et al., 2005). Shallow water within the embayment was, in contrast to the deeper Zechstein basin, well oxygenated. The succession shows pronounced cyclicity, interpreted as shallowing/drying upward cycles (Fig. 8). The Kupferschiefer equivalent shows two shallowing-upward successions (Fig. 8, phase 1). Falling sea level resulted in isolation of the embayment and halite precipitated in the upper part of the first shallowing-upward package. Subsequently, the embayment was flooded and an upper laminated package of Kupferschiefer equivalent deposited, before the embayment desiccated again. Overlying packages of laminated siltstone and siltstone with sand-patch fabric resulted from cyclically recurring sabkha flooding and desiccation. Intercalation of laminated and oolithic limestone is interpreted to document shallowing upward successions, whereas laminated limestone was deposited in deeper water than oolithic limestone.

Cyclicity of two different frequencies is imprinted in basal Zechstein deposits in well Nordsee C1. Lower and frequent cyclicity controls the depositional environment and is, as the fauna indicates, triggered by relative sea-level fluctuations. Higher frequency cyclicity reflects water level within the embayment and was also controlled by sea-level fluctuations of the Zechstein Sea (Legler et al., 2005). Similar high frequency cyclicity is also known for younger Zechstein deposits (e.g. Pöhlig, 1986; Peryt and Dyjaczynski, 1991; Strohmenger et al., 1996; Mawson and Tucker, 2009) and is attributed to sea-level fluctuations within the Milankovitch frequency band.

DISCUSSION

Cycle Duration and Correlatability in Nonmarine and Marine Deposits

Reliable calculation of depositional cycle duration is possible under two ideal circumstances: (1) preservation of varves of known origin (e.g. representing seasonal variations), which can be counted; or (2) existence of a very tight framework of chronostratigraphic markers. Both cases are very rare.

Most commonly a coarse stratigraphic framework is used to calculate cycle duration by dividing the overall duration by the number of depositional cycles. This approach can work if cycles are of equal duration and in the absence of erosional gaps, but is often a rather imprecise estimate. This can be seen in both settings presented here. In Rotliegend deposits the available chronostratigraphic data are sufficient to estimate cycle duration without too much contradiction. Uncertainties are far bigger in Zechstein deposits. Estimating frequency of cycles might also prove difficult when cycles are not recorded due to non-deposition or erosion, which is common in non-marine settings (apart from perennial lakes). Sub-aerial exposure during relative low sea level leads to the same effect in marine environments. The opposite effect of too many cycles may be caused by superposition of different cycle frequencies. The interplay between various triggers, e.g., climate and tectonics, further complicates the recorded pattern.

The approach of spectrogram analysis can be helpful in detecting cyclicity, but the results of calculating cycle duration are rarely reliable (Bailey, 2001). The main reason is the assumption of continuous deposition with constant depositional rates. This is unlikely to be the case, particularly in non-marine settings and in evaporite systems.

Despite all these known limitations, cycles in Rotliegend and Zechstein deposits have been interpreted as orbitally forced cycles, and are without doubt very useful correlation tools. Due to the palaeogeographical position of the SPB in low latitudes during the Per-

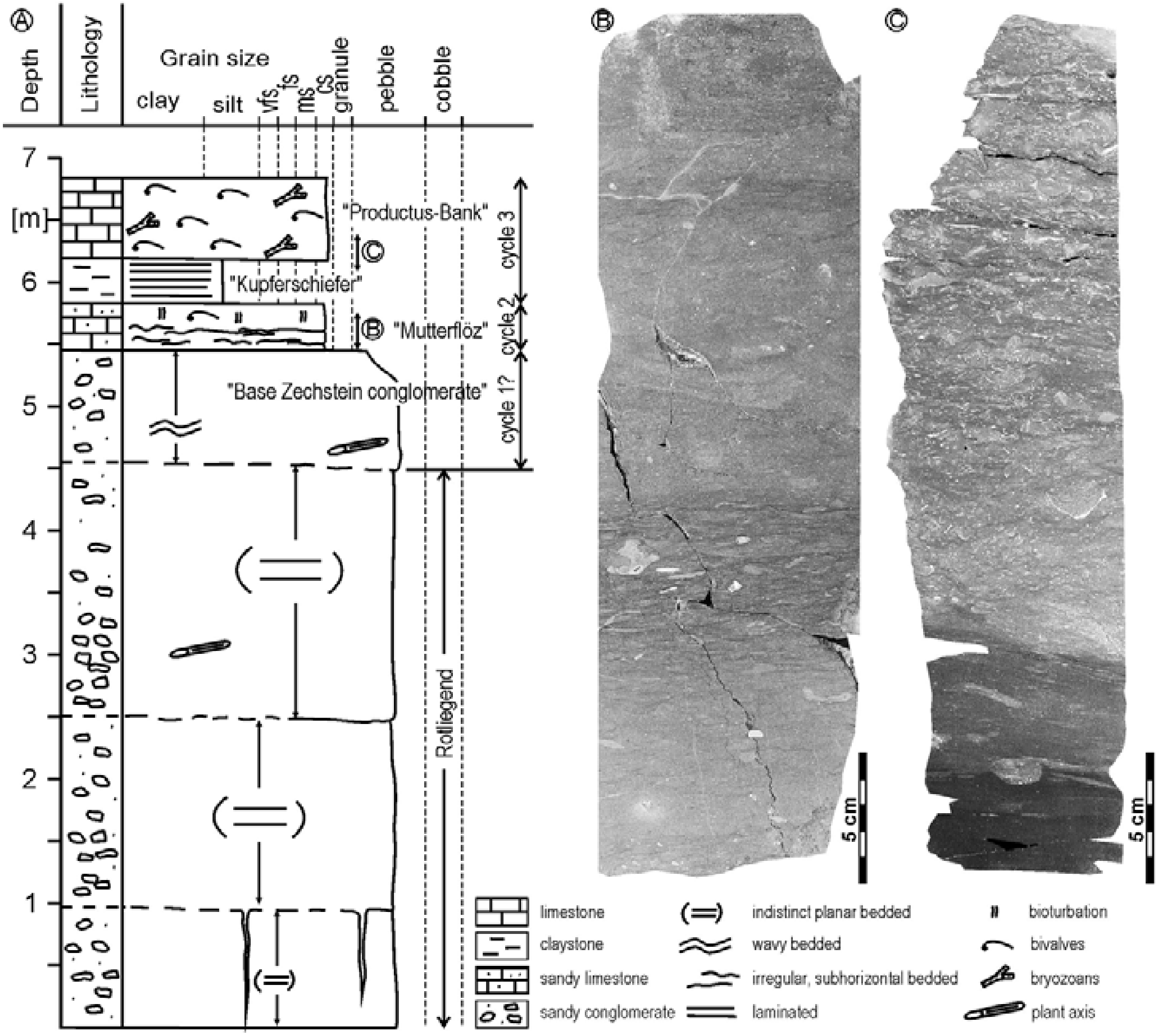


FIGURE 7. Kupferschiefer and Kupferschiefer equivalents in the Gera Bight (Gera Märzenberg/Schiefergasse). **A**, Log through Rotliegend-Zechstein transitional profile, interpreted correlative cycles to Kupferschiefer in basin centre annotated. **B**, Sample of the Mutterflöz. **C**, Sample of top Kupferschiefer (lower 7 cm) and base Productus-Bank.

mian, eccentricity and precession cycles are expected to have most influence on deposition (de Boer and Smith, 1994). Hence, durations of 400 ka, 100 ka, and 20 ka were allocated to Rotliegend and Zechstein cycles. Comparison of non-marine Rotliegend and marine Zechstein deposits shows different correlatability of cycles. Higher frequency cycles (100 ka, 20 ka) are not correlatable in non-marine deposits across the entire SPB, although they can be interpreted at every point in the basin. This reflects facies changes over short distances in Rotliegend deposits. Basal Zechstein deposits show correlatable small-scale cycles (probably 20 ka) over 100s of kilometers because of the lateral extent of the Zechstein Sea, with very little facies change in the basin during Kupferschiefer deposition.

Effects of Milankovitch Cyclicity

Variations of earth orbital parameters and resulting changes in insolation have a direct effect on global temperature. During ice ages, these changes trigger glaciation and deglaciation, resulting in high-frequency sea-level fluctuation. Accordingly, Milankovitch cycles were first reported from the Pleistocene (de Boer and Smith, 1994). Similarly, Milankovitch cyclicity in Rotliegend and Zechstein deposits was previously attributed to high-frequency waxing and waning of ice sheets during the Late Paleozoic glaciation (e.g. Glennie, 1986). But the main phase of glaciation terminated in the Sakmarian (e.g. Roscher and Schneider, 2006; Fielding et al., 2008), and Rotliegend and Zechstein deposition post-dates the Late Palaeozoic ice age.

Milankovitch cycles also influence monsoonal climate. Climate models by Kutzbach and Gallimore (1989) suggest a strong monsoonal climate for Permian times and later climate models showed that both eccentricity and precession cycles strongly influenced the Pangean megamonsoon (Crowley et al., 1992; Reinhardt and Ricken, 2000; Vollmer et al., 2008). Hence, precipitation rates during Rotliegend and Zechstein deposition were very likely influenced by orbital forcing, leading to fluctuating lake-levels of the Rotliegend saline lake.

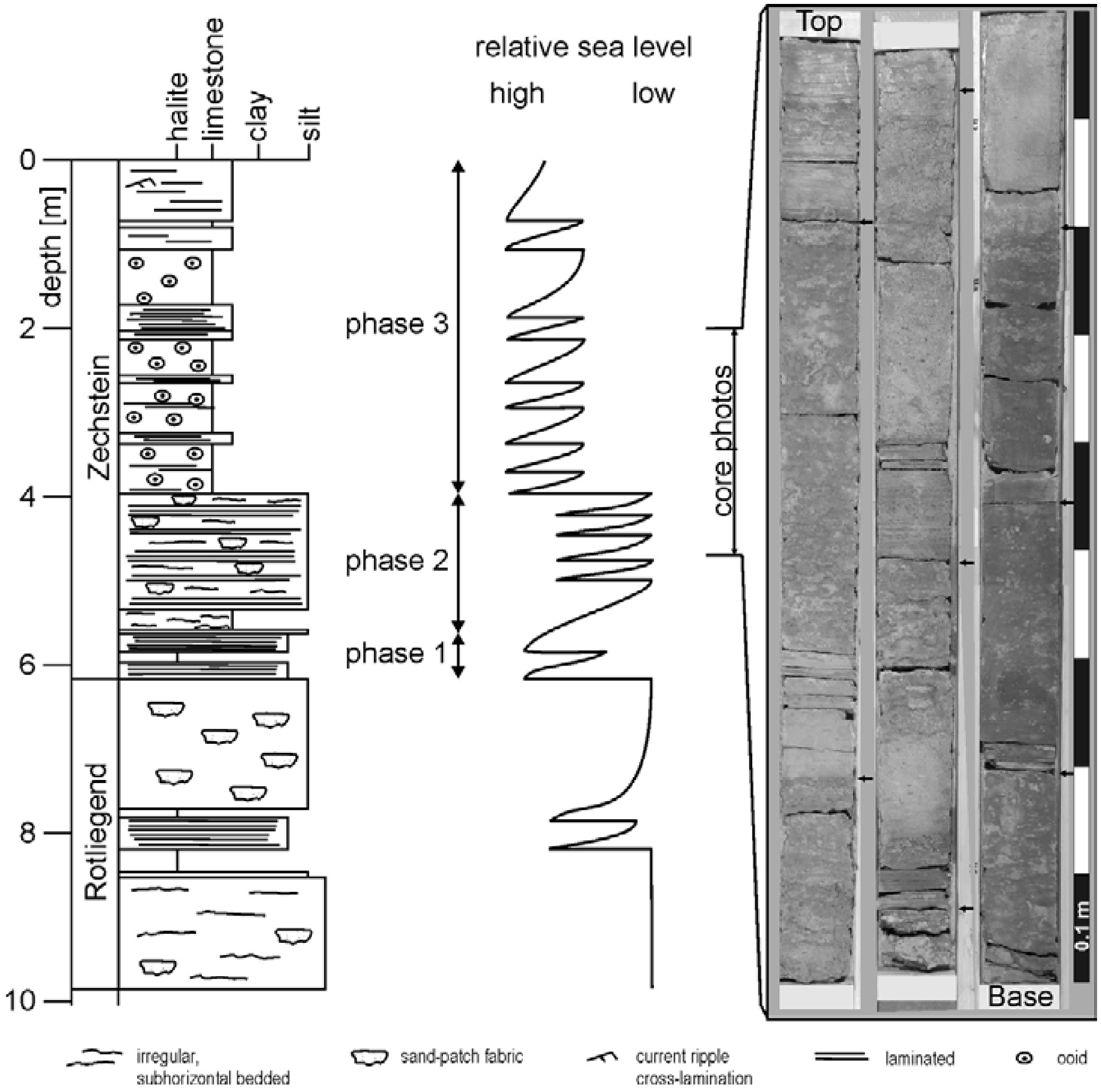


FIGURE 8. Log section and core photographs through Rotliegend-Zechstein transitional succession in well Nordsee C1 (after Legler et al., 2005); flooding surfaces (base of laminated horizon or base or limestone) in core photos are marked by arrows.

The influence of Milankovitch cycles on eustatic sea-level fluctuations in greenhouse climates is highly speculative (de Boer and Smith, 1994). Due to the relatively isolated nature of the Zechstein Sea, shallowing-upward cycles in the Kupferschiefer might reflect phases of decreased precipitation. In that case the Zechstein Sea would not reflect eustatic sea-level changes but merely evaporation cycles within an epicontinental sea. Associated with that trigger mechanism, phases of maximum insolation will have resulted in increasing water temperature in the Zechstein Sea, favouring carbonate precipitation.

CONCLUSIONS

Cycles of different orders are preserved in non-marine and marine Rotliegend and Zechstein deposits in the SPB. They are interpreted to reflect Milankovitch cycles and were mainly triggered by climate variability. Changes in earth orbital parameters triggered enhanced or attenuated monsoon intensity leading to fluctuations in precipitation and evaporation rates. Due to deposition in low latitudes, eccentricity and precession cycles are best developed (de Boer and Smith, 1994). Frequencies of 400ka, 100 ka and 20 ka are all preserved in the studied non-marine and marine deposits. Although higher-frequency cyclicity is interpreted in non-marine deposits, only 400 ka cycles are correlatable basin-wide. The marine environment favors preservation of correlatable cycles of both eccentricity and precession cycles. Hence, depositional environment does not necessarily limit overall preservation potential of depositional cycles but restricts preservation potential of correlatable cycles. In non-marine deposits local influence of hiatus, erosion and cycle interference is far greater than in apparently stable marine environments.

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A POSSIBLE DIPLOPOD FROM THE LOWER MISSISSIPPIAN (TOURNAISIAN) HORTON BLUFF FORMATION, BLUE BEACH, NOVA SCOTIA, CANADA

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The Horton Bluff Formation at Blue Beach, Nova Scotia, eastern Canada contains one of the most important Mississippian continental fossil records, and this occurs in a poorly-sampled Tournaisian interval known as Romer's Gap. The paleontology of the Horton Bluff Formation at Blue Beach was recently reviewed by Mansky et al. (2012) and Mansky and Lucas (2013, this volume) and encompasses a significant record of plants, vertebrate body and trace fossils, and invertebrate body and trace fossils. The non-marine invertebrate body fossil record contains microconchids ("*Spirorbis*"), ostracodes, conchostracans, the xiphosuran ***Euproops***, and agglutinated foraminifers. This assemblage is considered to be marginal marine in origin and comes from strata deposited in a large lagoon, or isolated marine embayment, which was at least intermittently connected to the sea (Tibert and Scott, 1999; Mansky et al., 2012).

The Horton Bluff Formation also contains an unusual diversity of ichnofossils, considering the low diversity of Devonian continental ichnofossil assemblages (Mansky et al., 2012). The invertebrate ichnoassemblage includes burrows, resting traces, and trackways from numerous productive nearshore beds, with the majority of the invertebrate traces occurring as two separate facies-controlled associations; a *Palaeophycus* association and a *Rusophycus* association (Lucas et al., 2010; Mansky et al., 2012). The paleoenvironment in which the majority of the Blue Beach ichnofauna occurs has been interpreted to represent storm-dominated intervals, where the attendant ichnodensity and ichnodiversity are enriched (Mansky and Lucas, 2013, this volume)

We add here to the Blue Beach record an invertebrate body fossil (Fig. 1) and discuss its identification. The specimen, CM 10089 (Fig. 1A), is in the Blue Beach Museum collection, Nova Scotia, Canada. The specimen is preserved as an external mold on a small slab of fine-grained argillaceous sandstone that is typical of the Blue Beach Member of the Horton Bluff Formation. A latex peel of the specimen, cataloged in the NMMNH collection as C-5034 (Fig. 1B), was used in this description as noted.

The specimen is elongate in overall appearance and straight in alignment with a gentle bend seen towards one end. The exposed length of the specimen along the latitudinal axis approaches 60 mm and is rounded in cross-section as seen on the peel. There are at least 14 variably preserved segments, and these are about 2 mm long and about 12 mm wide. The segment surfaces as seen on the peel are featureless and separated by thin (~1 mm) raised margins. These margins are typically straight across their midlength, but have pointed lateral terminations that are somewhat curved and variably directed. The raised margins between the segments are 20 mm wide at their greatest extent. One end of the specimen is marked by a short and curved raised margin as seen on the peel. The matrix contacting this area is depressed as seen on the slab. The other end of the specimen is poorly preserved and marked by an area of disrupted matrix. There are three curved and relatively large lateral projections seen along one of the margins at this end. There is a conspicuous lateral projection located midlength of the specimen on this same margin. This projection is relatively large and 4 mm wide at its base. It tapers to a blunt point at its termination, although there is a faint impression of a pointed continuation of this structure seen on the peel. There are a few small invertebrate burrows preserved on the slab in close proximity to the specimen.

We identify the specimen as the external mold of a dorsally preserved invertebrate that consists of probable mid-body tergites showing raised pleura with pointed lateral extensions. The animal may have possessed spines, as indicated by the relatively large lateral projection seen on the midlength section, but it is too poorly preserved to state this with certainty. The overall length, size, and organization of the specimen suggest that it may be a diplopod (millipede), but the fossil lacks the requisite diagnostic characters to make more than a questionable assignment.

The report of a possible diplopod from Blue Beach has some importance because millipedes are extremely rare in the fossil record due to their terrestrial habits and lightly mineralized cuticle (Wilson, 2005). Although paleontological investigation at Blue Beach began as early as 1841, when it was first discovered by Canadian geologist W. E. Logan (Mansky et al., 2012), this is the first report of a possible fossil millipede from Blue Beach. This report has additional importance because it comes from Romer's Gap, an Early Mississippian time interval from which few terrestrial vertebrate and arthropods are known (Ward et al., 2006; Smithson et al., 2012). Indeed, until recently the oldest known Carboniferous millipedes following the Devonian were those from the Viséan of East Kirkton, Scotland (Shear, 1994). However, recent discoveries of Tournaisian-age localities in Scotland have produced new records of terrestrial tetrapods and arthropods, including as yet undescribed myriapods (Smithson et al., 2012).

The *Rusophycus*-dominated trace fossil assemblage (Assemblage 2) from Blue Beach that was documented by Lucas et al. (2010) contains diverse arthropod locomotion traces, including *Diplichnites* and *Diplopodichnus*. The most commonly cited producer of these ichnogenera are myriapods (Minter et al., 2007), and neoichnological experiments have shown that millipedes are capable of producing these forms (Davis et al., 2007). The possible diplopod body fossil reported here suggests that millipedes were a component of the Blue Beach terrestrial fauna as well as the producers of some of the *Diplichnites* and *Diplopodichnus* within Assemblage 2. The forested wetlands represented by the fossil record in the Blue Beach Member includes abundant plant debris of *Lepidodendropsis*, pterophytes, and *Archaeocalamites* (Melrose and Gibling, 2003; Mansky and Lucas, 2013, this volume). These forests could have provided suitable habitats for millipedes, which have been important detritivores of plant litter in terrestrial ecosystems for over 420 million years (Wilson, 2005).

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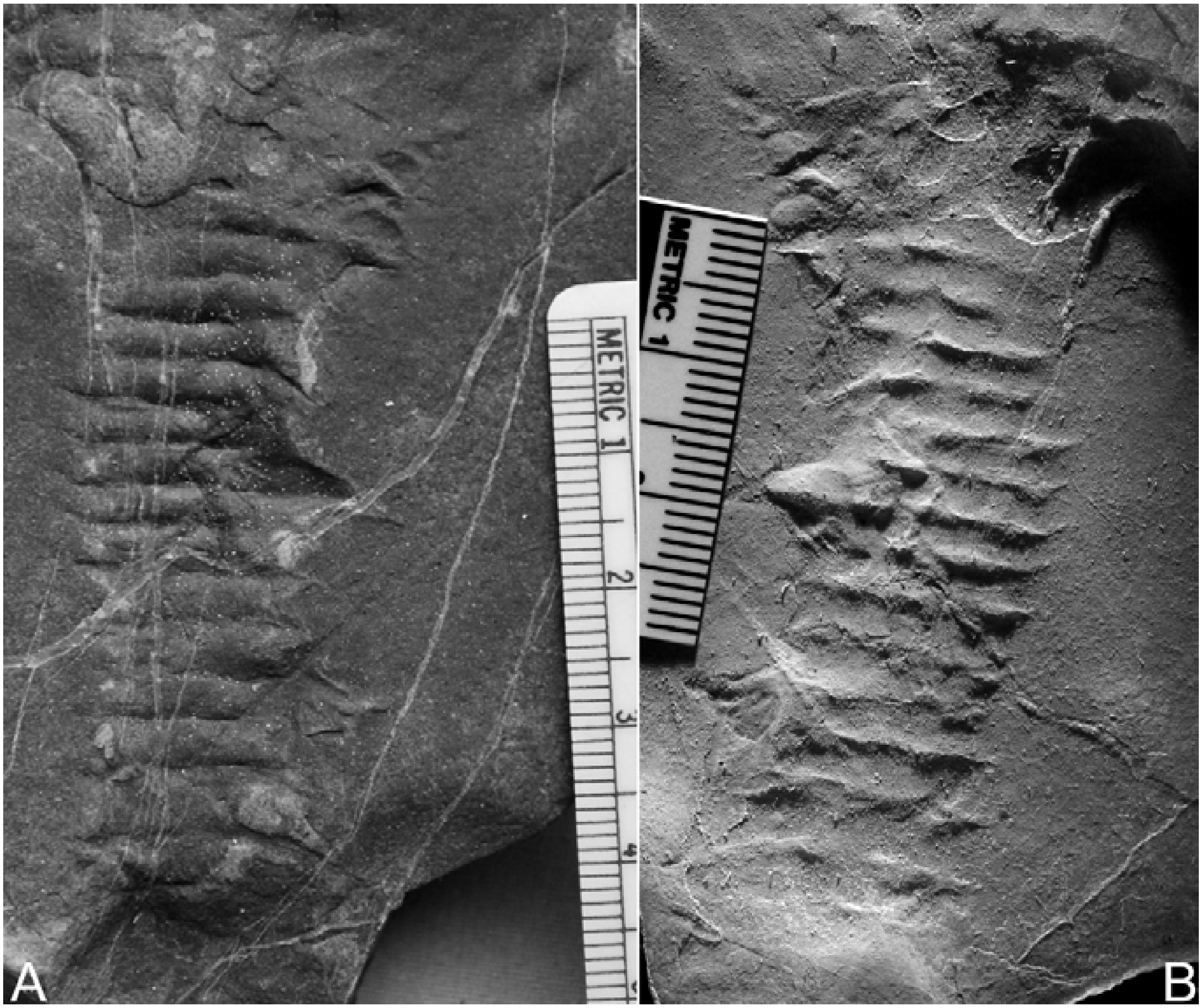

FIGURE 1. Possible diplopod from the Blue Beach Member of the Horton Bluff Formation at Blue Beach, Nova Scotia, Canada. **A**, CM 10089 as preserved on the slab. **B**, NMMNH C-5034, latex peel of CM 10089 (whitened).

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NATURAL HISTORY OF A PLANT TRAIT: BRANCH-SYSTEM ABSCISSION IN PALEOZOIC CONIFERS

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Within conifers, active abscission of complete penultimate branch systems is not common and has been described mainly from juveniles. Evidence is presented for the abscission of penultimate branch systems within early so-called walchian conifers—trees with a plagiotropic branching pattern. The specimens studied originate from a middle Early Permian gymnosperm-dominated flora within the middle Clear Fork Group of north-central Texas. Complete branch systems of three walchian conifer morphotypes are preserved; all have pronounced swellings and smooth separation faces at their bases. The source plants grew in a streamside habitat under seasonally dry climatic conditions. The evolution of active branch abscission appears to correspond to an increase in the size of conifers, and this combination potentially contributed to the restructuring of conifer-rich late Paleozoic landscapes. Moreover, shedding of branch systems led to the production of abundant litter with the potential to affect the fire regime. This is a factor of evolutionary importance because wildfires must have been a source of frequent biotic disturbance throughout the hyperoxic Early Permian.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

CHARACTERIZING MORPHOLOGIC VARIABILITY IN FOLIATED PALEOZOIC CONIFER BRANCHES – A FIRST STEP IN TESTING ITS POTENTIAL AS PROXY FOR TAXONOMIC POSITION

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Abstract—As a first step to test the taxonomic potential of a leaf-based classification, methods were developed to identify different leaf morphotypes of Paleozoic conifer branches. The specimens in this study originate from the Colwell Creek Pond Flora, an exceptionally well-preserved middle Early Permian flora from the middle Clear Fork Group of north-central Texas. This gymnosperm-dominated flora is characterized by three-dimensionally preserved penultimate branch systems of walchian conifers, an extinct paraphyletic group of small trees with a plagiotropic branching pattern. The branch systems within this flora were shed as single units with ultimate branchlets and their leaves still attached. The distribution of variability of gross morphological features among ultimate leaves of these walchian conifers is analyzed in order to define discrete branch system morphotypes. Included in the analysis are frequency distributions of leaf dimensions and angle, which formed the basis for four walchian conifer morphotypes. Two of the morphotypes were further split into two types, each at a lower level of dissimilarity.

INTRODUCTION

Plants shed organs, such as leaves and reproductive structures, throughout their lifetime (Addicott, 1991). The various plant organs can be separated before or after death. Since different organs have different dispersal dynamics and may require different preservation regimes, they are rarely found in connection, or even in geographical proximity to one another (e.g., Gastaldo, 1992; Martin, 2009). In the fossil record, this creates a major challenge for paleobotanists because it is difficult to tell which parts belonged together. Fossil conifer branches commonly occur as compression fossils - revealing little more than gross leaf-architectural features (e.g., shape and angle; e.g., Broutin and Kerp, 1994; Harris, 1979). They commonly lack more taxonomically diagnostic characteristics, such as reproductive structures or epidermal features. Therefore, it is often challenging to arrive at a meaningful taxonomic description for conifer branches (i.e., reflecting the underlying phylogeny) based on leaf morphology alone. However, the lack of good taxonomically diagnostic characters for most fossil conifer leaves does not absolve us from an obligation to somehow categorize them. Even preliminary classifications that merely hypothesize phylogenetic relations are important for our field, or as Visscher et al. (1986, p 89) stated: "...overall leaf morphology alone rarely provides accurate criteria for recognizing natural coniferous genera and families. Yet external morphological characters should never be neglected since we are faced with the fact that leafy shoots are among the most frequent occurring conifer remains to be classified."

If we do classify these taxonomically uncertain morphological groups, it is important to be explicit about the inherently hypothetical nature and potentially low phylogenetic validity of hypotheses derived from this type of data. Moreover, we must find ways to maximize relevance and information content in our quantitative morphological description of such fossils. In the light of the new "Melbourne Code" for naming plant fossil taxa (the International Code of Nomenclature for algae, fungi and plants), with its "one fossil, one name" policy (see: McNeill and Nicolas, 2011), a comprehensive account of morphological variability within a taxon has become even more essential.

This paper serves as the first stage in a test of the taxonomic potential of leaf-based morphotype classification of plagiotropic conifer branches. We used walchian conifer branch systems that dominate the para-autochthonous Colwell Creek Pond flora, preserved in the late Early Permian (Kungurian) of North-Central Texas (Chaney and DiMichele, 2007). These abscised penultimate branches still bear their foliated ultimate branchlets (Looy, 2013), and have been preserved as petrifactions. The preservation is exceptional and shows cellular details of epidermal and sub-epidermal tissues of the penultimate and ultimate leaves, and wood structure. Some of the branches bear ovuliferous and polleniferous cones (Chaney and DiMichele, 2007). In this preliminary study, however, we will treat these remains as if they only revealed general leaf characteristics of the branches' ultimate leaves. Subsequently, we will test how our leaf-based morphotype model holds up when the leaf data are included in a comprehensive morphologic and taxonomic analysis of the branch systems. This study will include the more diagnostic cellular information and reproductive structures and will be published elsewhere.

Here, we will characterize the distribution of variability of gross morphological features among ultimate leaves of walchian conifers in order to define discrete branch system morphotypes. We developed a classification system that aims at maximizing relevant information recorded in variability of general leaf morphology. This method utilizes between-branch differences in the shape of the within-branch frequency distributions of simple leaf characters. It entailed a stepwise reduction of the dimensions in the data set (using multivariate data reduction techniques), resulting in simple metrics for differences in the shape of morphological variability. The latter were used to define our morphogroups rather than more commonly used metrics, such as average values and encountered minima and maxima.

In summary, the purpose of this paper is threefold: (1) to provide a detailed quantitative description of within- and between-branch-system variability in general morphology of ultimate leaves of Colwell Creek Pond conifers, (2) to devise and discuss a method of classification based on overall leaf morphology, and (3) to take a first step in exploring to what degree variability in general leaf morphology of Paleozoic walchian conifer branches can serve as a proxy for their taxonomic position within the group.

MATERIALS AND METHODS

Colwell Creek Pond Conifers

The walchian conifer branches described in this paper originate from the Colwell Creek Pond locality, Knox County, Texas. The locality is in the middle part of the undivided Clear Fork Group (Nelson et al., 2001), which is Leonardian (Kungurian) in age (Wardlaw, 2005). The plant fossils were found in laminated red claystones of oxbow lakes or abandoned channel segments within a coastal plain setting on the Eastern Shelf of the Midland Basin. The fossils are preserved as three-dimensional goethite petrifactions (Fig. 1), and in many specimens the anatomical structure is preserved at the cellular level (see Chaney et al. 2009). The specimens used for this paper are listed under USNM collecting locality numbers 42292, 42305, and 42306. The collection with locality number 42292 accurately represents the proportional taxonomic composition of the deposit. The objective of collections 42305 and 42306 was to collect well-preserved complete specimens and additional rare specimens. The exact locality information of the Colwell Creek Pond locality is not recorded at the request of property owners, but is on file at the National Museum of Natural History (NMNH), Smithsonian Institution, Washington D.C. For additional information on the geological setting and biostratigraphy see Chaney and DiMichele (2007).

Collected specimens were prepared using dissection needles and an air scribe, and photographed using a Kodak DCS Pro14n digital camera. Images were stored as TIFF files. The specimens are housed in the NMNH's Paleobotanical Collections. Illustrated or traced specimens are stored in the Paleobotanical Type and Illustrated Collections under the USNM catalogue numbers 530912, 530937, 530965, 530966, 530990, 530991, 530992, 530993, 530994, 531002, 531003, 531004, 531005, 531006, 531007, 531011, 536440, 536456, 539423, 539425, 539433, 539440, 539450, 539451, 539452, 539453, 543989, 543990, 543991, and 543992.

Morphotyping

In 30 well-preserved branch systems, three different leaf parameters were measured (Fig. 2). These parameters include (1) the distance between the base and the tip of leaves (length or L; as proxy for leaf length), and (2) the angle between the ultimate branch, and the leaves in their point of inflexion (angle or A), and the width of leaves (width or W) for the few leaves that were in face view. In the case of large branch systems, with many ultimate shoots covered in anatomically preserved leaves, a region of interest was chosen in which leaf characteristics were measured. This resulted in 3885 measurements with on average 49 leaf length, 18 width and 54 angle measurements per branch system.

Since the three parameters (L, W and A) were never measured for the same individual leaf, the morphometric data do not constitute coupled observations, thus ruling out the possibility of straightforward multivariate analysis of the data. Instead, as a metric for differences in the shape of the morphological variability among the leaves on the same branch system, we used a stepwise nested reduction of the dimensions in the data set (see Figs. 3A-C for a fictitious example). Summarizing, data on leaf lengths, widths and angles were converted to standardized frequency distributions reflecting within-branch-system variability (Fig. 3D). Scores on the first-fourth axes obtained in Detrended Correspondence Analyses (DCA) of the respective length, width and angle distributions provided us with a measure for between-branch variability of within-branch variabilities (Fig. 3E). Finally, clustering of these DCA branch scores gave us quantitative tools for the classification of groups of branches in discrete morphotypes (Fig. 3F). Below, we will give a more detailed account of the steps taken in the quantitative classification method of the branch systems we employed:

(1) Length and width data were log-transformed. The reasoning behind this is that a variation of 1 mm in the L distribution for a branch with leaves that are 2 mm long on average should have a similar weight as a deviation of 10 mm in a distribution of leaf lengths that are on average 20 mm (Fig. 3A).

(2) Log-length, log-width and angle values were then standardized to percentages of the full gradient length within each measurement (Fig. 3B), e.g., for length a value of 0 was assigned to the shortest leaf in the data set, and 100 to the longest.

(3) For each branch system, the numbers of standardized values were counted in 22 consecutive equally-sized intervals (~4.5%) of the full gradient length in all measurements. The number and size of these bins was optimized (Fig. 3C) by using the histogram option in PAST (Hammer et al., 2001) which chooses the optimal number of bins according by following the zero-stage rule of Wand (1997). Note, in the fictitious example in Fig. 3, only ten bins were used.

(4) For inter-branch comparison, the resulting discrete frequency distributions were then further standardized, so that the total of frequency values in all intervals was set at 100% (Fig. 3D).

(5) In order to summarize and quantify (dis)similarities in the shape of the frequency distributions, Detrended Correspondence Analyses (DCAs) were performed separately for each of the three types of leaf character frequency distributions (Fig. 3E). For these multivariate analyses we used the software package CANOCO (Ter Braak and Šmilauer, 1998). DCA is especially well-suited for the separation of unimodally distributed "species" in samples taken along a gradient. In our case the gradient being size- or angle-bin frequencies in large branch systems. The scores of each branch system on the first four DCA axes therefore provided a characterization of the shape of branch systems, based on the leaf character frequency distributions. The differences between DCA scores

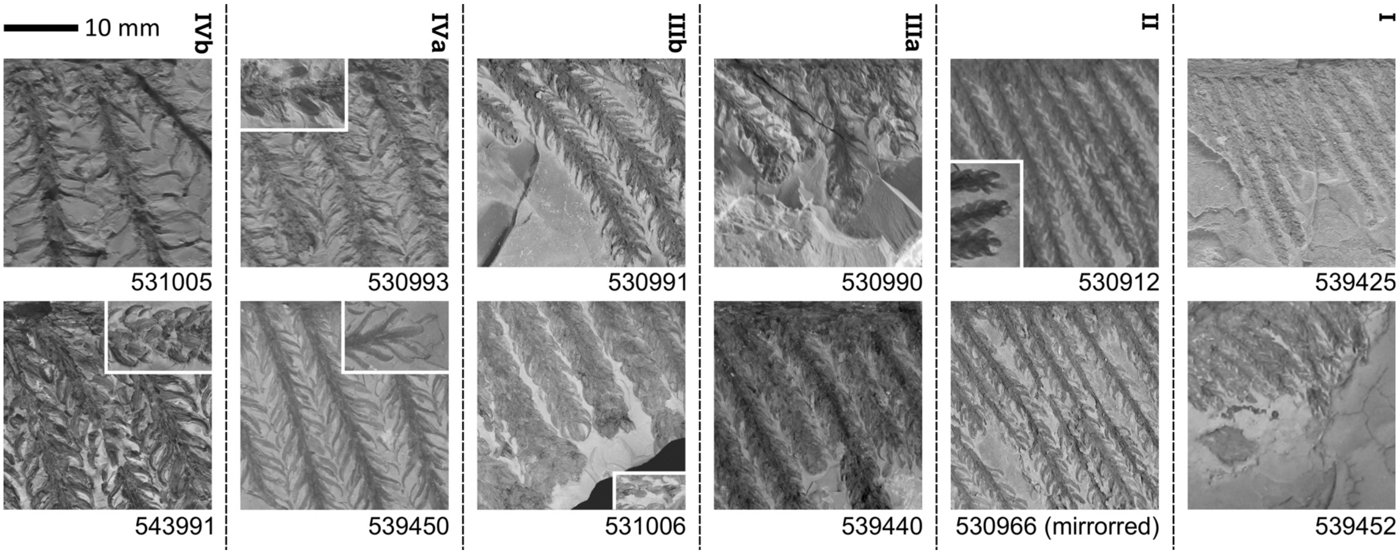


FIGURE 1. Colwell Creek Pond conifers. Details of foliated ultimate branches, all shown at the same scale. Each pair of the photographs represent one of the morphotypes defined in this study; indicated by the Roman numerals. Next to each photograph the USNM specimen numbers are shown.

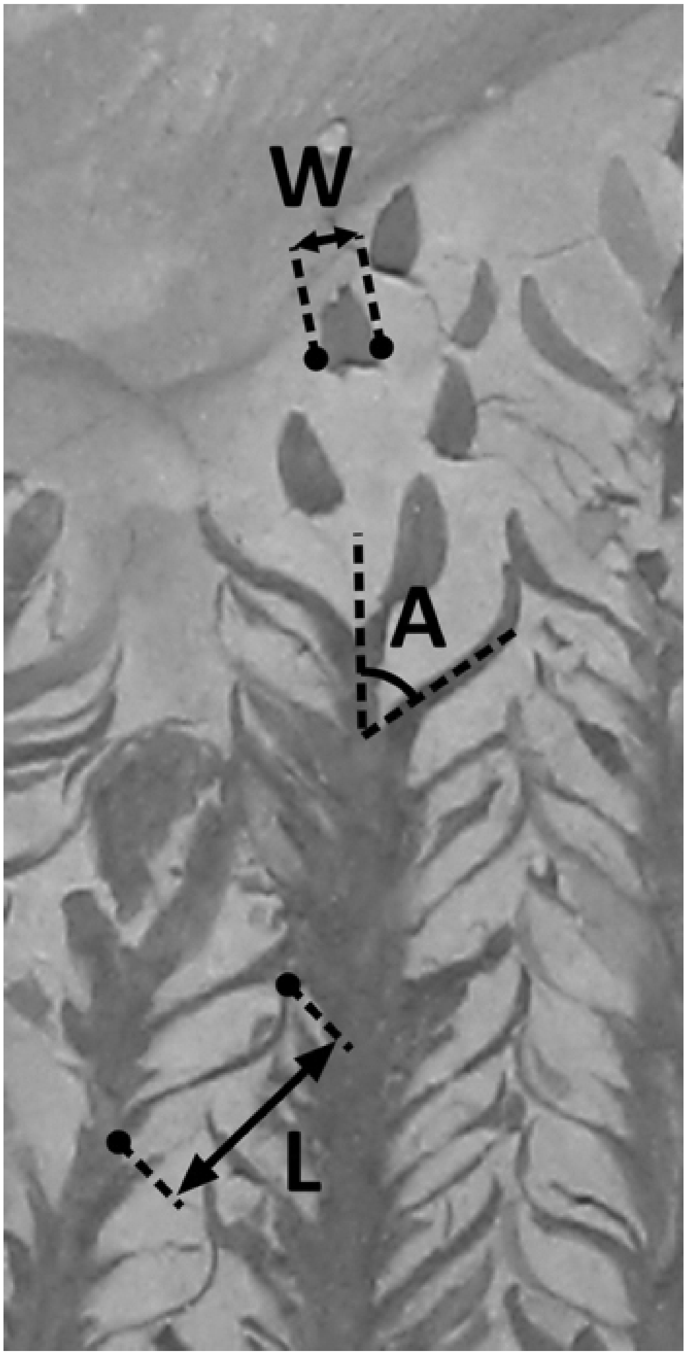


FIGURE 2. The measured leaf (USNM CC668) characteristics: length, width, and angle.

of different branch systems are given in standard deviations (SD). These provided a crude estimate of the degree of overlap between their size or angle frequency distributions (a distance of ca. 4 SD means virtually no overlap in the case of normal distributions).

(6) The DCA scores on the first four axes of each branch system for the log-length, log-width and angle data sets formed a 30×12 matrix that was used in a cluster analysis (using online Free Statistics Software; Wessa, 2013), which helped define the different leaf-based morphotypes. Euclidean distance was used as a dissimilarity index and a complete linkage, or farthest neighbor algorithm for agglomerative clustering (Fig. 3F). The latter is perhaps not a very common method in clustering of data sets, but was here chosen a priori, since it prevents the so-called chaining phenomenon, i.e., the grouping of elongated clusters (e.g., as in single linkage clustering). This would have been a problem with this data set, because the cloud of data points in our 12-dimensional hyperspace is very elongated due to strongly co-varying length and width distributions.

(7) Two cut-off levels were chosen in the hierarchical cluster tree for the grouping of morphotypes. The first cut-off was at a Euclidean distance of 6 SD and defined the primary groups I-IV. The second one at 5 SD revealed the secondary within-cluster groups, identified by “a” or “b.”

RESULTS

Although within most branch systems the measured values were quite variable, the shape of their distribution strongly suggests that most of this variation originated from unimodal distributions of the underlying morphological variability (Fig. 4). Distributions deviating most from unimodality are mostly those based on a rather limited number of observations. The distributions of the values within bins formed the input for three DCAs – one for each leaf character (Fig. 4). The results of these DCAs can therefore be interpreted as a measure of between-branch-system distance, based on within-branch-system variability. The lengths of the gradients on the first axes of the DCAs (Table 1) were all greater than 4 standard deviations, respectively 11.5, 8.1 and 5.0 SD for log-length, log-width and angle. These results suggest there is no overlap in the morphometric distributions of branch systems on opposite ends of the axes.

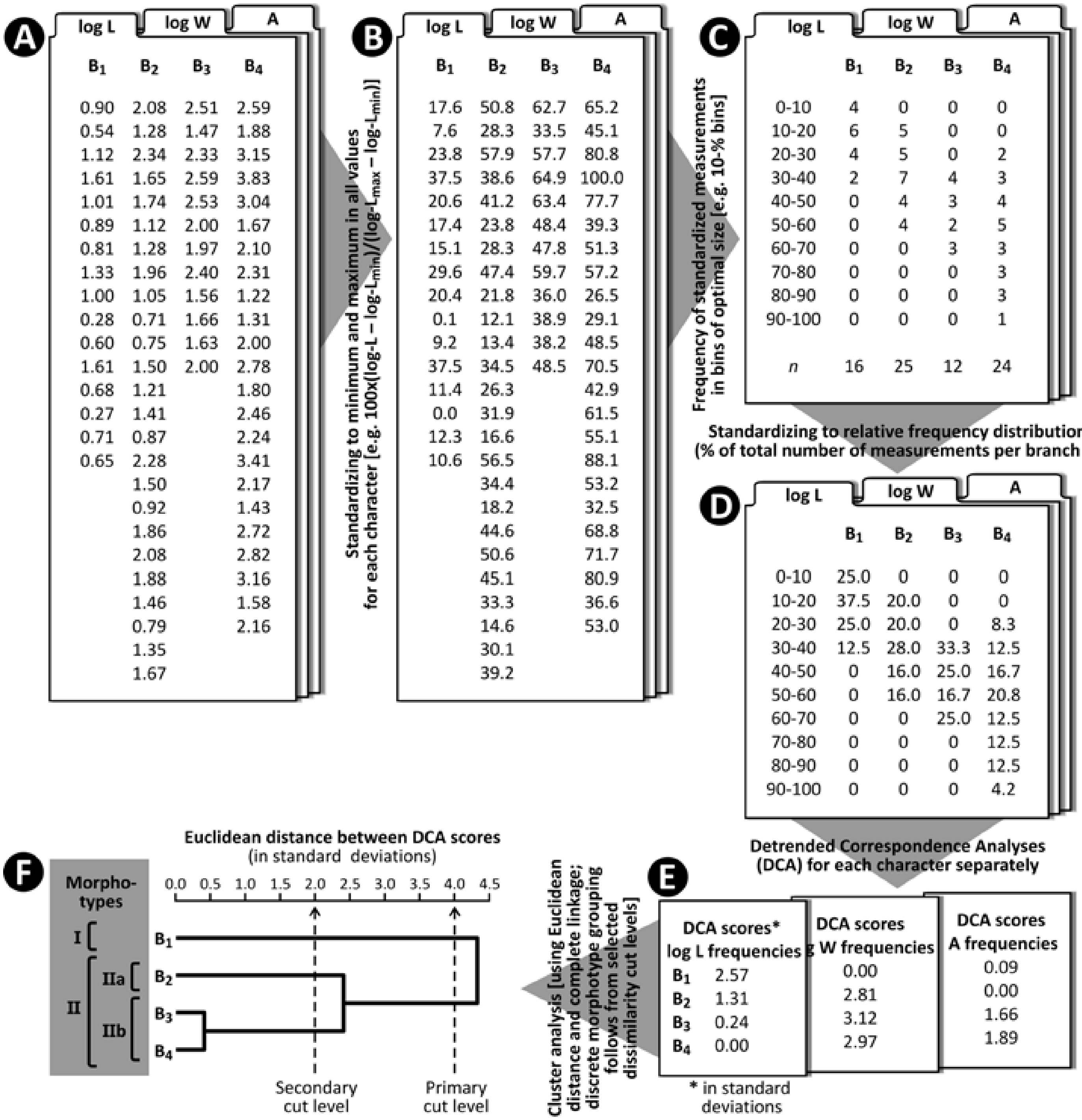
Clustering of the DCA scores revealed an agglomerative hierarchical grouping of branch systems with increasingly dissimilar morphometric distributions as we go up the hierarchy (Fig. 5). In the employed complete-linkage method joins two clusters are joined at the level of the maximum dissimilarity of any pair of members of the two clusters. We therefore picked a cut-off level at a relatively great distance (6 SD) for our initial division in leaf-shape morphotypes. This resulted in four distinct clusters of increasing leaf size with increasing Roman numeral (I-IV). At a level of 5 SD, the clusters III and IV were each divided in two subclusters (IIIa-b, IVa-b). Clusters I and II on the one hand, and III and IV on the other were very dissimilar – grouping at circa 14 SD. To give an idea of the cluster sizes and distance: the mean within-cluster distance (in the twelve-dimensional morphospace used) was 2.69 SD, while the mean distance between the centroid of a cluster and that of its nearest neighbor was 3.24 SD. See Table 2 for a summary of mean, median and maximum within-cluster leaf dimensions and angles.

Plotting the DCA scores on the dominant first ordination axes of the three morphometric data sets, together with the morphotype grouping, provides us with a graphical summary of the numerical rationale for the six different types (Fig. 6). The primary division of the branch systems in groups I-IV was clearly based on differences in leaf size, while the secondary split within group III and IV was brought about by distinct differences in the distribution of leaf angle values.

DISCUSSION

Leaf-morphotype Classification Method

The DCAs used in our classification method were capable of capturing and expressing various aspects of variation between all 90 frequency distributions of log-length, log-width and angle. Rather than the one-dimensionality of metrics such as branch-system mean, median or mode values, the shape of the frequency distributions was used in this analysis. That being said, the Euclidean distances in the twelve-dimensional DCA morphospace were overwhelmingly dominated by the first axes. For example, the mean distance between branch systems was 4.9, a three-dimensional DCA-morphospace that consisted of only the first axes. This was only 5% shorter than the mean distance of 5.1 in the full twelve-dimensional DCA-morphospace. Axes 2-4 in the three DCAs had much shorter lengths of gradients, i.e., distance between the outermost samples on the axis expressed in standard deviations. These axes therefore contributed much less to the distance between branch systems.



A — log L

B1	B2	B3	B4
0.90	2.08	2.51	2.59
0.54	1.28	1.47	1.88
1.12	2.34	2.33	3.15
1.61	1.65	2.59	3.83
1.01	1.74	2.53	3.04
0.89	1.12	2.00	1.67
0.81	1.28	1.97	2.10
1.33	1.96	2.40	2.31
1.00	1.05	1.56	1.22
0.28	0.71	1.66	1.31
0.60	0.75	1.63	2.00
1.61	1.50	2.00	2.78
0.68	1.21		1.80
0.27	1.41		2.46
0.71	0.87		2.24
0.65	2.28		3.41
	1.50		2.17
	0.92		1.43
	1.86		2.72
	2.08		2.82
	1.88		3.16
	1.46		1.58
	0.79		2.16
	1.35		
	1.67		

B — log L

B1	B2	B3	B4
17.6	50.8	62.7	65.2
7.6	28.3	33.5	45.1
23.8	57.9	57.7	80.8
37.5	38.6	64.9	100.0
20.6	41.2	63.4	77.7
17.4	23.8	48.4	39.3
15.1	28.3	47.8	51.3
29.6	47.4	59.7	57.2
20.4	21.8	36.0	26.5
0.1	12.1	38.9	29.1
9.2	13.4	38.2	48.5
37.5	34.5	48.5	70.5
11.4	26.3		42.9
0.0	31.9		61.5
12.3	16.6		55.1
10.6	56.5		88.1
	34.4		53.2
	18.2		32.5
	44.6		68.8
	50.6		71.7
	45.1		80.9
	33.3		36.6
	14.6		53.0
	30.1		
	39.2		

C — log L

	B1	B2	B3	B4
0-10	4	0	0	0
10-20	6	5	0	0
20-30	4	5	0	2
30-40	2	7	4	3
40-50	0	4	3	4
50-60	0	4	2	5
60-70	0	0	3	3
70-80	0	0	0	3
80-90	0	0	0	3
90-100	0	0	0	1
n	16	25	12	24

D — log L

	B1	B2	B3	B4
0-10	25.0	0	0	0
10-20	37.5	20.0	0	0
20-30	25.0	20.0	0	8.3
30-40	12.5	28.0	33.3	12.5
40-50	0	16.0	25.0	16.7
50-60	0	16.0	16.7	20.8
60-70	0	0	25.0	12.5
70-80	0	0	0	12.5
80-90	0	0	0	12.5
90-100	0	0	0	4.2

E

	DCA scores* log L frequencies	DCA scores log W frequencies	DCA scores A frequencies
B1	2.57	0.00	0.09
B2	1.31	2.81	0.00
B3	0.24	3.12	1.66
B4	0.00	2.97	1.89

* in standard deviations

FIGURE 3. Fictitious numerical example of steps in our morphotype classification method. B1-B4 refer to individual branch systems. Log L, log W and A to the measured log-length, log-width and angles of leaves, and n is the number of observations for a branch system.

In turn, the first axes in the DCAs were dominated by the location aspect of the frequency distributions along the full range of values in the three morphometric data sets. Hence, the first axis scores are in fact tightly correlated to simple metrics such as mean or median branch system values. The correlation coefficients for log-length, log-width and angle were respectively -0.999, -0.998 and 0.999 for correlations between mean values and first DCA axis scores, and -0.979, -0.976 and 0.996 for median value and axis-1 scores.

Apparently, in our data set, the second to fourth DCA axes did not contribute very much to the clustering of the branch systems, and the scores on the very influential first axis were near-perfectly proportional to mean or median values. As a result, one might get the impression that in our classification method the DCA step had little added value. However, a critical advantage of DCA scores over, for example, mean values is that the former take the degree of overlap between individual frequency distributions into account. Just by glancing over Fig. 4, it is easy to recognize that distributions of angle values have a far greater degree of overlap than those of log-length and log-width. In the DCA of the angle data set, this higher degree of overlap prevents a better separation of the "species" along the DCA axes, resulting in shorter lengths of gradients. Thus, the length of gradient can in most cases also be interpreted as a measure of the diagnostic potential of a morphometric parameter in the

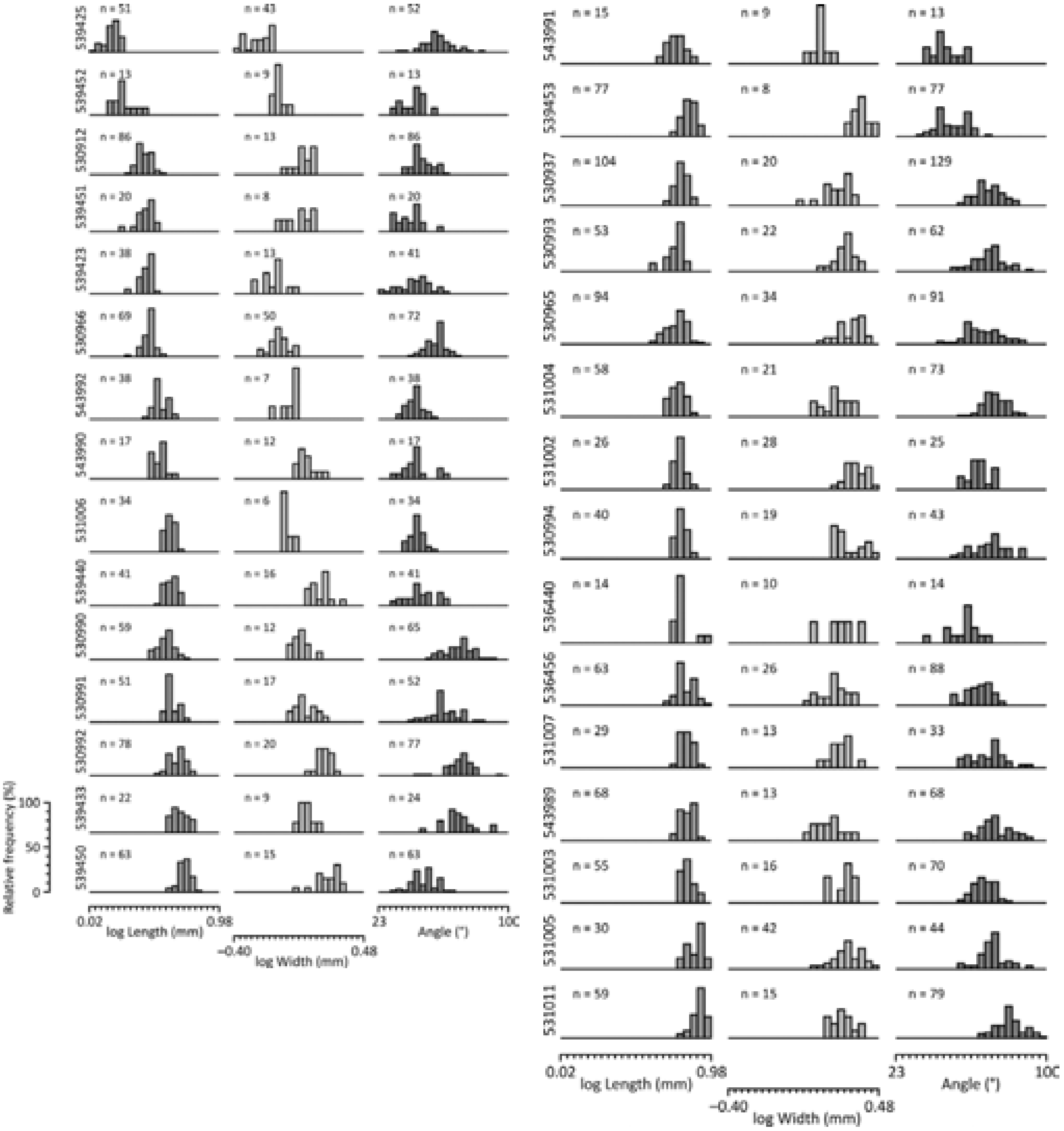


FIGURE 4. Relative frequency distributions of values of log-length, log-width and angle of ultimate leaves for each branch system, enumerated in 22 equal-sized bins between minimum and maximum values for each parameter. The corresponding USNM specimen numbers are shown next to each set of histograms.

identification of distinct morphotypes. Since we directly used DCA scores in the cluster analysis, implicitly a higher weight was given to branch scores based on frequency distributions of the more diagnostic characters with a higher morphotype-differentiating capacity.

Validation of Morphotype Clustering

A first-order estimate of the validity of the clusters chosen based on the cluster analysis can be inferred from post-hoc analysis, using statistical methods that interpret the data in the light of a priori defined groups. Canonical Variate Analysis (CVA) or Fisher's linear discriminant analysis (Fisher, 1938) is such a method (in our case the version of CVA that is used in PAST; Hammer et al., 2001). In CVA, axes consist of linear combinations of variables in the data set (in this case the branch-system scores on twelve DCA axes). The first CVA axis is the particular linear combination of variables that maximizes the spread of the centroids of

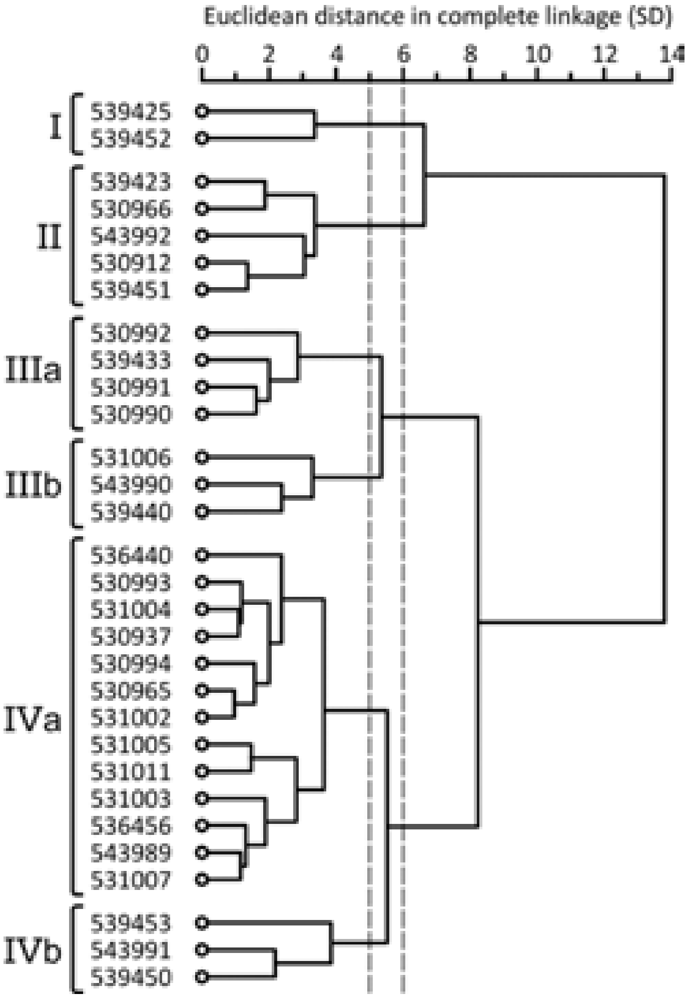


FIGURE 5. Agglomerative hierarchical clustering of DCA scores of branch systems (in the analyses of Log-ength, Log-width and angle frequency distributions within ultimate leaves). Euclidean distances were calculated as index of dissimilarity (thus preserving the SD-units in the three DCAs). The algorithm employed to construct this tree was a complete linkage, or farthest neighbor method.

the a priori defined clusters. A second axis can be obtained by finding the second best linear combination of variables for the separation of cluster centroids, and must be independent of the first axis, etc. Although a very different method than our interpretation of the cluster analysis, the CVA of our twelve-dimensional DCA morphospace confirms a robust separation of the morphotypes (Fig. 7). In addition, it illustrates the preeminence of the first axes in the DCAs compared to the other nine axes. This is even more than expected based on the difference in lengths of gradients alone. Moreover, when applied to the same data set, the “Classifier” tool in PAST (Hammer et al., 2001) – assigning data points to the group that gives minimal Mahalanobis distance to the group mean – produced six clusters identical to our cluster-analysis-based classification.

In a complex, multi-tiered data analysis with consecutive data-reduction steps, it is difficult to evaluate whether the reduced output of each step does justice to the patterns in the input data. Therefore it is important to return full circle and reveal how the original raw data relates to the final classification end-product. For that reason we have presented the distribution of all 3885 measurements in the context of the suggested classification framework (Fig. 8). The near-symmetric spread of length and width values on the logarithmic axis in Fig. 8, illustrate the skewed distribution of these measured dimensions. This confirms that the used log-transformed data was indeed better suited for our analysis than the original raw values.

TABLE 1. Basic statistics for the Detrended Correspondence Analyses (DCA; detrended by segments).

	DCA axes, Log-Length				DCA axes, Log-Width				DCA axes, A			
	1	2	3	4	1	2	3	4	1	2	3	4
Length of gradient	11.5	1.6	1.2	2.0	8.1	1.8	1.6	1.3	5.0	1.2	1.1	0.8
% of variance explained	24.4	3.0	1.8	1.2	25.9	5.0	1.9	1.5	46.6	5.4	2.5	1.7

TABLE 2. Summary of within-morphotype mean, median and maximum leaf dimensions and angle.

	Leaf length (mm)			Leaf width (mm)			Leaf angle (°)		
Morphotype	Mean	Median	Max.	Mean	Median	Max.	Mean	Median	Max.
I	1.74	1.73	2.61	0.70	0.71	0.96	50.9	51.3	83
II	2.93	2.88	4.50	0.97	0.98	1.44	47.2	47.6	70
IIIa	4.44	4.40	6.05	1.30	1.30	1.93	68.4	68.4	94
IIIb	3.97	3.99	5.09	1.23	1.21	2.11	46.4	46.0	63
IVa	6.46	6.54	9.47	1.87	1.85	2.96	69.6	69.8	100
IVb	5.98	5.89	8.55	1.83	1.78	2.99	49.9	49.7	70

CONCLUSIONS

The natural classification of late Paleozoic conifers is for a large part based on the organization of ovuliferous dwarf shoots, vegetative morphology and epidermal characteristics (e.g., Clement-Westerhof, 1988; Rothwell et al., 2005). In the absence of preserved reproductive structures and epidermal features, the gross morphology of ultimate leaves is used to assign conifer remains to taxonomic groups (e.g., Florin, 1939-1945; Broutin and Kerp, 1994). With the exception of few studies (e.g., Hernandez-Castillo, 2001; Rothwell et al., 2005), the variability of these features is generally not explicitly described or graphically summarized. As a consequence, they are also not sufficiently taken into account during classification. Our study provides a methodological framework to define discrete branch system morphotypes that is capable of utilizing the frequency-distribution characteristics of simple leaf parameters, in addition to the position aspect of the distributions along morphological axes (e.g., median or mean values). In general, in studies that deal with variability in biological data sets, the variability is often summarized by the mean and standard deviation. The latter, however, assumes normal distribution of deviations around the mean. Notwithstanding the fact that DCA is related to a unimodal response curves, our method has the advantage that it can also deal with non-normal variability as it is essentially non-parametric.

The developed multivariate classification method can be used to categorize vegetative remains of walchian and other conifers when only compression fossils of ultimate shoots are available. Of course, this morphotype classification method of gross leaf morphology constitutes a purely phenetic approach, rather than a cladistic one. Therefore its value as a proxy for taxonomic position and disparity remains to be seen. The first step was to develop a method that aims to maximize the diagnostic value of general leaf morphology in the absence of apomorphic character states. The next one will be to assess the taxonomic proxy value of the walchian conifer morphotypes in a more comprehensive taxonomic analysis of Colwell Creek Pond branch systems that is based on different characters.

ACKNOWLEDGMENTS

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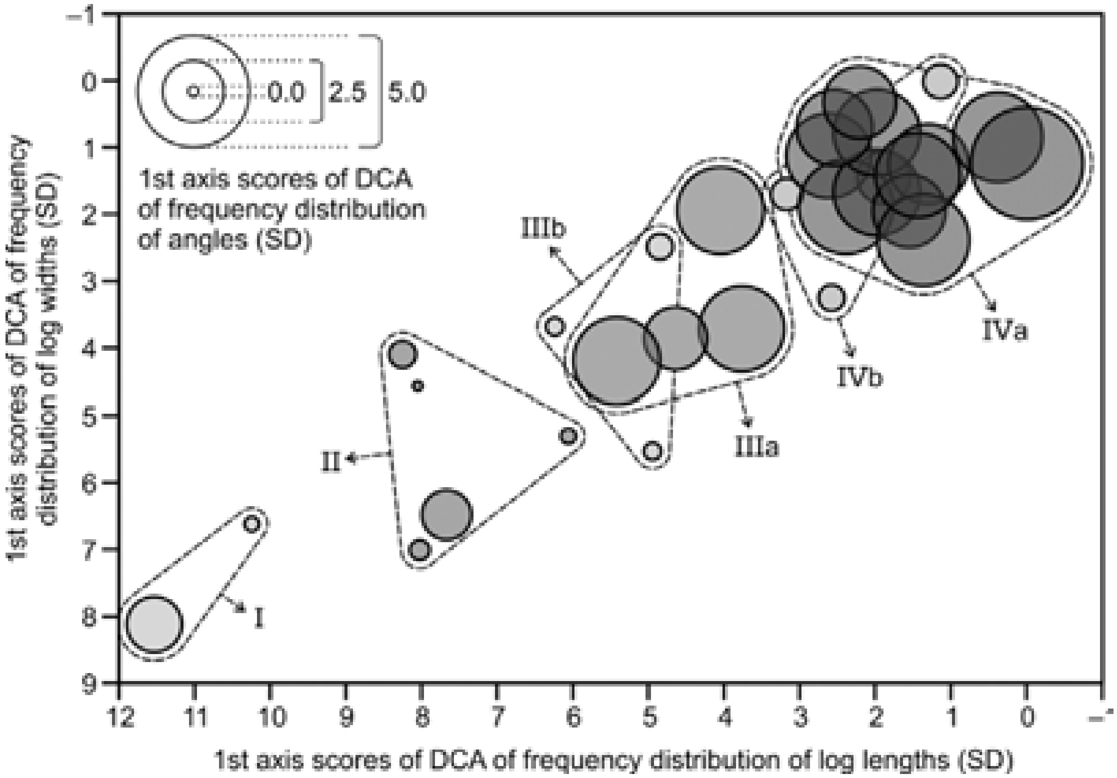

FIGURE 6. First axis scores of branch-system ultimate leaf morphology in Detrended Correspondence Analyses (DCAs) of respectively log-length, log-width and angle measurements. The DCA scores based on log-length are plotted on the horizontal axis. Those of log-width distributions are on the vertical axis, and the bubble sizes reveal DCA scores based on frequency distributions of angle. The morphotype classification of the branch systems is indicated In Roman numerals (the result of clustering of scores on the first four axes of each of the three DCAs; see Figure 5).

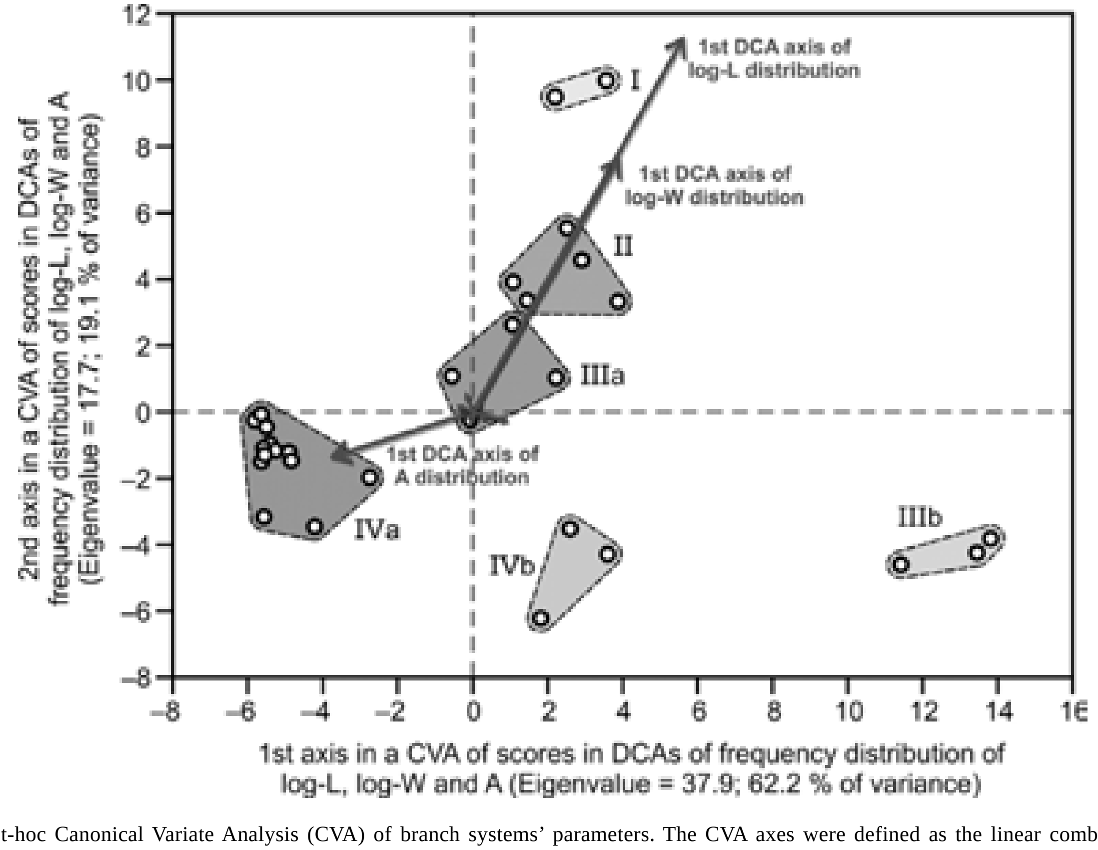

FIGURE 7. Post-hoc Canonical Variate Analysis (CVA) of branch systems' parameters. The CVA axes were defined as the linear combinations of DCA scores (in the analyses of log-length, log-width and angle distributions) that maximize the separation of a priori defined clusters. Only the first two CVA axes are shown, together explaining 82.1 % of the total variance in the DCA data set.

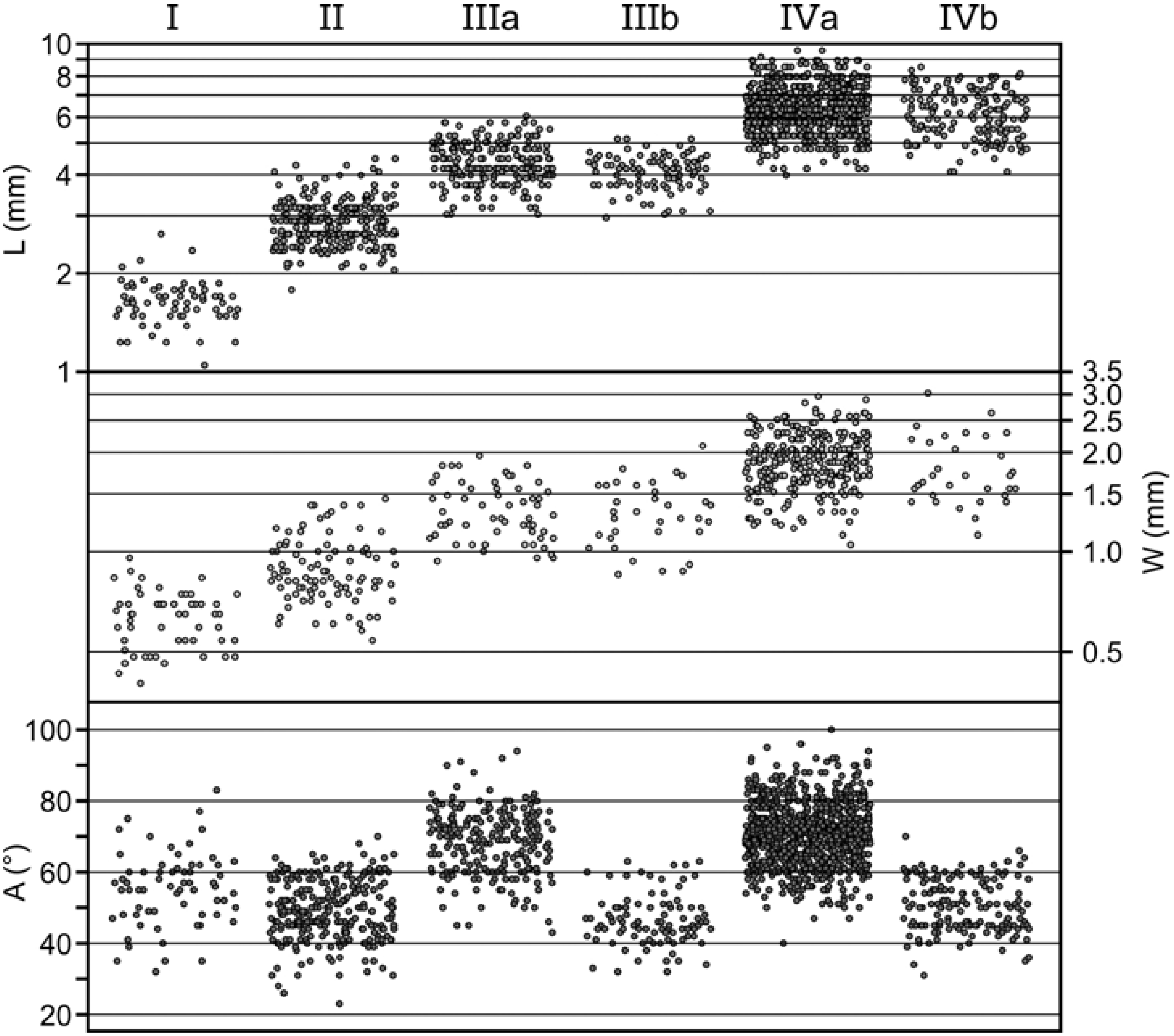

FIGURE 8. Jitter plot of all the raw morphometric data (leaf length, width and angle) within each defined morphotype cluster.

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THE PERMIAN PERIOD ENDED WITH THE IMPACT OF A “SIBERIA” COMET ON EARTH

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Abstract—The Permian Period came to an end with the Permian-Triassic crisis, the largest in the geological history of Earth. Analysis of the continental biota of the East European Platform at the P-T boundary documents a major ecological crisis. It is shown that the crisis of the continental biota preceded the marine one. The assumption is made that the impact of a large comet “Siberia” and processes following it could have acted as the main cause of the crisis. Carbonaceous balls, found in the Nedubrovo Member of the Vokhmian Horizon, are tentatively considered remains of the comet. The Permian-Triassic crisis was in many respects similar to the Cretaceous-Paleogene one, caused by cosmic reasons. The authors provide new evidence in favor of the hypothesis of an impact driver for the Permian-Triassic crisis and designate a possible impact area. The viewpoint on the priority of the historical lower boundary of the Triassic System, instead of the base of the *Hindeodus parvus* conodont zone, as currently accepted, is substantiated.

INTRODUCTION

The extinction of organisms at the Permian-Triassic boundary, usually referred to as the Permian-Triassic crisis or great mass extinction (Alexeev, 1998), was the most considerable in the history of Earth, surpassing in its extent the widely known Cretaceous-Paleogene extinction, which led to the disappearance of dinosaurs. At this boundary, about 90% of all animate beings, both marine and continental, died out (Benton, 2005). Among marine forms, mainly benthonic, typically Paleozoic groups of tabulate and rugose corals, trilobites, numerous orders of brachiopods, bryozoans, crinoids, blastoids, fusulinids, etc., became extinct. Equally important but less known in the literature are changes within the continental biota (vertebrates, invertebrates and flora), which can be explained by the lack of complete sections, characterized by all groups of Permian as well as Triassic terrestrial biota: some sections are characterized mainly by terrestrial vertebrates (South Africa), others (Western Europe) contain full complexes of conchostracans, whereas vertebrates and other invertebrate groups are only sporadically found.

The East European Platform section stands out from others by its exceptional completeness and faunal diversity, and therefore justly claims the first place. Close to it ranks the section of the Tarim Platform (Dalongkou), studied by Chinese researchers and repeatedly highlighted in the literature (see Lozovsky and Esaulova, 1998; Kuchtinov et al., 2011; Kozur, and Weems, 2011, etc.).

CHANGES OF THE CONTINENTAL BIOTA ON THE EAST EUROPEAN PLATFORM AT THE PERMIAN-TRIASSIC BOUNDARY

According to existing schemes, the Permian-Triassic boundary on the East European Platform is placed between the Vjaznikovian Horizon of the Vjatkian stage (Lozovsky and Kuchtinov, 2007) and the Nedubrovo Member of the Vokhmian Horizon (Lozovsky et al., 2011). Changes of continental fauna and flora at this boundary have been well studied and documented for the first time based on tetrapod fauna and other groups of fauna and flora (Ivakhnenko et al., 1997; Lozovsky and Esaulova, 1998), and were subsequently supplemented by data on the youngest Permian and the oldest Early Triassic horizons, established later (Lozovsky et al., 2001, etc.). This question is discussed in detail by Lozovsky (2013). The principal conclusion is that the important changes within the continental biota (including extinction of whole groups of organisms, sharp reduction of faunal and floristic complexes, etc.) can be considered an ecological crisis.

CORRELATION OF THE EAST EUROPEAN PLATFORM SECTION WITH OTHER SECTIONS OF LAURASIA

As shown above, the East European platform section stands out from other Laurasian ones by the best characterization by various groups of fauna and flora. We will try to correlate it with other sections of this region and, first of all, with the classic section of the Germanic Basin, which served as the stratotype area for von Alberti’s establishment of the Triassic System in 1834.

Here, the Permian-Triassic boundary passes between the Fulda Formation (characterized by Zechstein flora), and the colored sandstone (Buntsandstein) Calvörde Formation. This is subdivided into several lithological units (formations). For biostratigraphic subdivision of the Buntsandstein, Kozur (1993) had proposed the definition of biozones based on Conchostraca as, in his opinion, the most reliable and widely distributed group of fauna.

During the last years this researcher published several articles dedicated to the correlation of the conchostracan scheme of the Germanic basin with the global scale, based on conodont and ammonite scales (Kozur, 2003; Kozur and Bachman, 2005, etc.). For this purpose he successfully used a combination of biostratigraphic data and abiotic events, such as palaeomagnetic inversions, changes of carbon isotopic content, and the abundance of microspherical particles (Kozur and Weems, 2011, p.23). This correlation, demonstrated in the right part of Figure 1, is well-founded and confirmed by the data presented in this article.

Conchostracans (determined by N.I Novozhilov) have been used by H. Kozur together with V.R. Lozovsky, E.V. Movshovich and A.J. Lopato (1983) for correlation of the Krasnobakovskaja Subformation of the Vokhmian Horizon with coeval units of Germany, based on the presence of characteristic forms with spines on larval carapaces, *Vertexia tauricornis* (= *Cornia germari* in Kozur’s scheme) (Kozur et al., 1983). This correlation is in good agreement with a change from normal to inverse magnetization at the appearance level of these conchostracans, both in Russia and in Germany. Further support comes from the Nedubrovo Member, containing a Zechstein flora (Krassilov et al., 1999, etc.) and inversely magnetized, and the lower part of the Fulda Formation (Lozovsky, 2010). The same correspondence is given by Kozur as well (Kozur and Weems, 2011, p. 37). The Vjaznikovian Horizon containing archosaurs corresponds to the Zechstein, where thecodont finds are known from lower horizons (Lozovsky and Esaulova, 1998, p.142). A general synthesis of the schemes of the East European basin and Germanic Basin has been given by the author (Lozovsky, 2010).

The section of the Tunguska syneclise is crucial for understanding the problem of the Permian-Triassic crisis. Here, coal-bearing deposits,

FIGURE 1. Map of Nedubrovo locality.

containing a Palaeophytic flora (Gagariy Ostrov Horizon), are overlain by a thick volcano-sedimentary succession, consisting of a lower (tuffogenous) and an upper (lava) part. The dispute about its age has lasted for many years and is far from being resolved. The Permian-Triassic boundary is set by various authors within a range from the basis of the tuffogenous part of the succession (Tutonchana Horizon), containing Mesophytic flora (Mogucheva, Betechtina, 1998), its upper part (Korvunchana Horizon), up to the roof of the Putoranian lava horizon (Sadovnikov and Orlova, 1994). For biostratigraphic subdivision of the volcanic complex these authors successfully used a conchostracan zonation similar to that applied by Kozur in the Germanic Basin. The scheme developed by them has recently been specified and refined (Kozur and Weems, 2011). As a result, it has become possible to confidently correlate the section of Siberia with that of the Germanic Basin, and thus with the East European Platform (Fig.1).

Consideration of this correlation scheme leads to very interesting conclusions, on which we will focus below. In the transitional zone from the Permian to the Triassic in this region three levels are clearly distinguishable, which were initially proposed by the author for the Moscow syneclise (Lozovsky, 2010). Kozur's merit is the exact linking of these levels with conchostracan schemes of sections from Germany, Siberia and China and their relationship to the global scale (Kozur and Weems, 2011).

The first level corresponds to the base of the Fulda Formation in Germany, the base of the Nedubrovo Member in the Moscow syneclise and the Verchnetunguktinian Horizon in Siberia. It is characterized by a mass extinction of continental organisms. For the East European Platform, this has been discussed by Lozovsky (2013), and the data available from the Siberian Platform allow us to speak confidently of the disappearance of pelecypods and the extinction of conchostracans in sections of Germany as well as Siberia (Kozur and Weems, 2011). On this boundary is placed the base of the Vokhmian horizon, considered here the lower boundary of the Triassic. This corresponds to the lower limit of the *Clarkina changingensis-C.deflecta* zone on the global scale. On the palaeomagnetic scale of Germany, here the boundary lies between a zone of normal polarization On and a zone of inverse polarization ?r. On the East European Platform this is the base of zone R0, where an unconformity occurs.

The second level corresponds to the boundary of the Calvörde Formation (the lower part of thje Buntsandstein) and the Bröckelschiefer (Fulda Formation), which is the historical Permian-Triassic boundary in Germany, the base of the Astashiha Member, and the base of the Putorana Formation of Siberia. This equals the boundary of the *Falsisca eotriassica* and *F.postera* zones in the conchostracan scheme. It is characterized by the appearance of Gondwanan *Lystrosaurus* on the East European Platform and in Western China (Xinjiang), and the start of the extrusion of the Putoranian basalts in Siberia, in which *Lystrosaurus* is also found. The main phase of extinction of marine organisms ends. On the global scale, this boundary corresponds to the appearance of *Otoceras boreale*, which usually is taken for the beginning of Triassic (Tozer, 1984). This boundary is extremely significant on the conodont scale, marking the beginning of the *Clarkina meishanensis-Hindeodus praeparvus* (formerly called *H.latidentatus*, and erroneously taken for *H. parvus* by some researchers [Mei S.]) zone: here first occurs the genus *Hindeodus*, characteristic of the Early Triassic! In the paleomagnetic scales of Germany and Russia, it passes through normal zones 1n and N1, respectively.

The third boundary passes within the Calvörde Formation in Germany, the base of the Riabi Member on the East European Platform, between the Marininski and Putorana horizons of the Siberian Platform. On the conchostracan scale, it separates the *Falsisca verchojanica* and *F. postera* zones. By comparison of these levels with the global scale, this is the boundary where the conodont *Hindeodus parvus* occurs – the officially accepted lower border of the Triassic system. On the paleomagnetic scale, it lies within the same normal zone as the previous one, but accordingly higher. It corresponds to a d13? minimum.

The main conclusion from the above is the following: the extinction of continental organisms preceded that of marine ones. Already, Lucas (2009) and Kozur and Weems (2011) wrote about this phenomenon. In the article I try to offer an explanation of this phenomenon, presenting some facts that shall shed light on the solution of this problem.

CHARACTERISTICS AND THE FLORA OF THE NEDUBROVO MEMBER – A KEY TO THE SOLUTION OF THE PERMIAN-TRIASSIC CRISIS PROBLEM

According to the accepted stratigraphic scheme (Lozovsky et al., 2011), the Nedubrovo Member forms the basis of the Early Triassic Vokhmian Horizon. Its stratotype lies near the village Nedubrovo on the left bank of the Kitchmenga river (left tributary of the river Yug) (Figs. 2-3), and a detailed description of the member is given in Lozovsky et al. (2001). It differs from overlying beds of the Vokhmian Horizon by the presence, in its lower part, of a characteristic greenish-gray layer, consisting of thinly interbedded clay- and siltstones (up to 2 m thickness), which resemble ashfall deposits in macroscopic view. Microscopic observations confirmed this fact: the light green shade of the rock is caused by the clay mineral smectite of ferruginous-calciferous composition with a small alloy of potassium (Eroshchev-Shak et al., 2002), whose formation is connected to eolian-ashfall pyro-volcaniclastics. The authors advanced the assumption that the pyroclastites have been transported from the Timan-Petchora region, which represents a marginal zone of the world's largest field of trap extrusions of the Siberian Platform.

The Nedubrovo Member contains abundant floral remains, marked by numerous anomalies of epidermal structure of the cuticles, and also the presence of abnormal pollen grains (Krassilov et al., 2000; Lozovsky et al., 2001; Eroshchev-Shak et al., 2002). These authors suppose that the main reason for such alterations consists in intense ultraviolet radiation caused by the destruction of stratospheric ozone. This could be a consequence of pollution of the atmosphere by products of volcanic emissions (particles, acid gases), especially active during eruptions.

We propose that the main reason for the destruction of the ozone layer and the formation of a huge ozone gap could have been the impact of a large comet that we name "Siberia," or its explosion in the atmosphere. In our opinion, traces of this comet are the numerous carbonaceous microspherules about 10 microns in diameter, which have been found in the Nedubrovo Member (Fig. 4). They contain from 58 to 73% carbon, from 26 to 40% oxygen, and insignificant alloys of Mg (0.21-

FIGURE 2. Exposure of Nedubrovo member on the left bank of the Kichmenga river. Arrows show the layer 2 with carbon spherules and floristic remains.

0.35%), K (from 0.28-0.87%), and Si (0.08-0.12%). These spheroids differ from megaspores by their considerably smaller size (10 microns against 200 microns), and from endofullerenes (C60 –carbonaceous balls) and by the presence of oxygen and their considerably larger size (10 microns against 1 micron).

In this context it should be noted that a similar horizon of carbonaceous balls is documented in Late Pleistocene deposits of North America, aged 12000-13000 years, coinciding with one of the most significant extinctions of large biota – the mammoths. The origin of carbonaceous balls in North America is problematic, linked according to one of the assumptions to the action of insects in mushrooms, and according to another that appears most probable to us, to the impact of a comet on Earth and subsequent fires.

Possible Scenario for the Permian-Triassic Boundary

As stated above, carbonacerous microspheres and spheroids of the Nedubrovo Member, in our opinion, represent remains of a large comet that impacted or exploded in the air, which caused a vast geological disaster. The most probable place of the impact, in our opinion, is the Tunguska syneclise on the Siberian Platform, ironically the same area where in 1908 the world-famous Tunguska meteorite impacted.

The Tunguska syneclise belongs to a special type of platform depression that Muratov (1975) called amphiclise. It is a huge amphitheater with a rather flat bottom surrounded by steep flanks, with a large number of marginally rimming and trans-secting faults. Amphiclises are characterized by huge amounts of volcanic products (lavas and tuff), extruded along the faults and forming very thick accumulations. The reason for the formation of such platform depressions, as writes Muratov with reference to the opinion of various authors (from Shatsky to Subbotin), is seen in processes occurring under the Earth's crust because of the efflux or consolidation of subcrustal material. Generally agreeing with this concept, we suppose that consolidation could be a consequence of impact events connected with the impact of a very large comet or its explosion near the surface.

We shall add to the indirect data confirming this assumption a small iridium anomaly in bed 26 (black clay) together with an enrichment in siderophile elements (Co, Ni and Au) and the increased content of chalcophile elements (As, Se, Sb and Mo) in bed 25 (white clay) of the famous Meishan section below the assumed Permian-Triassic boundary (Yin, 1996, p.85). The small anomaly values are easily explained by the distance of this section from the impact area of comet "Siberia.".Further support is given by the numerous iron-nickel microspherules of cosmic origin, observed in this section (Yin, 1996; Korchagin, 2010, etc.), as well as in continental sections of the Germanic Basin in the same stratigraphic position (Kozur and Bachmann, 2005, etc.) (Fig. 1).

Now we will try to restore the course of events. Approximately 252.8 Ma, the impact of a large comet on Earth occurred, which either impacted directly in the Tunguska river basin or exploded in air. The ozone gap formed as a result of this explosion allowed an unrestricted reach of ultraviolet radiation on Earth's surface, causing the sudden death of most of the terrestrial organisms. On territories located on the periphery of the ozone gap, the mortal radiation was somewhat reduced.

Thus, in the Karoo Basin of South Africa a large extinction of land organisms and appearance of others, adapted to the new conditions, mainly amphibians, is observed at the boundary of the *Dicynodon* and *Lystrosaurus* zones. Only a few forms (the procolophonid *Owenetta,* the therocephalians *Tetracynodon* and *Moschorhinus*) could survive the disaster and still occur for some time in *Lystrosaurus* zone deposits

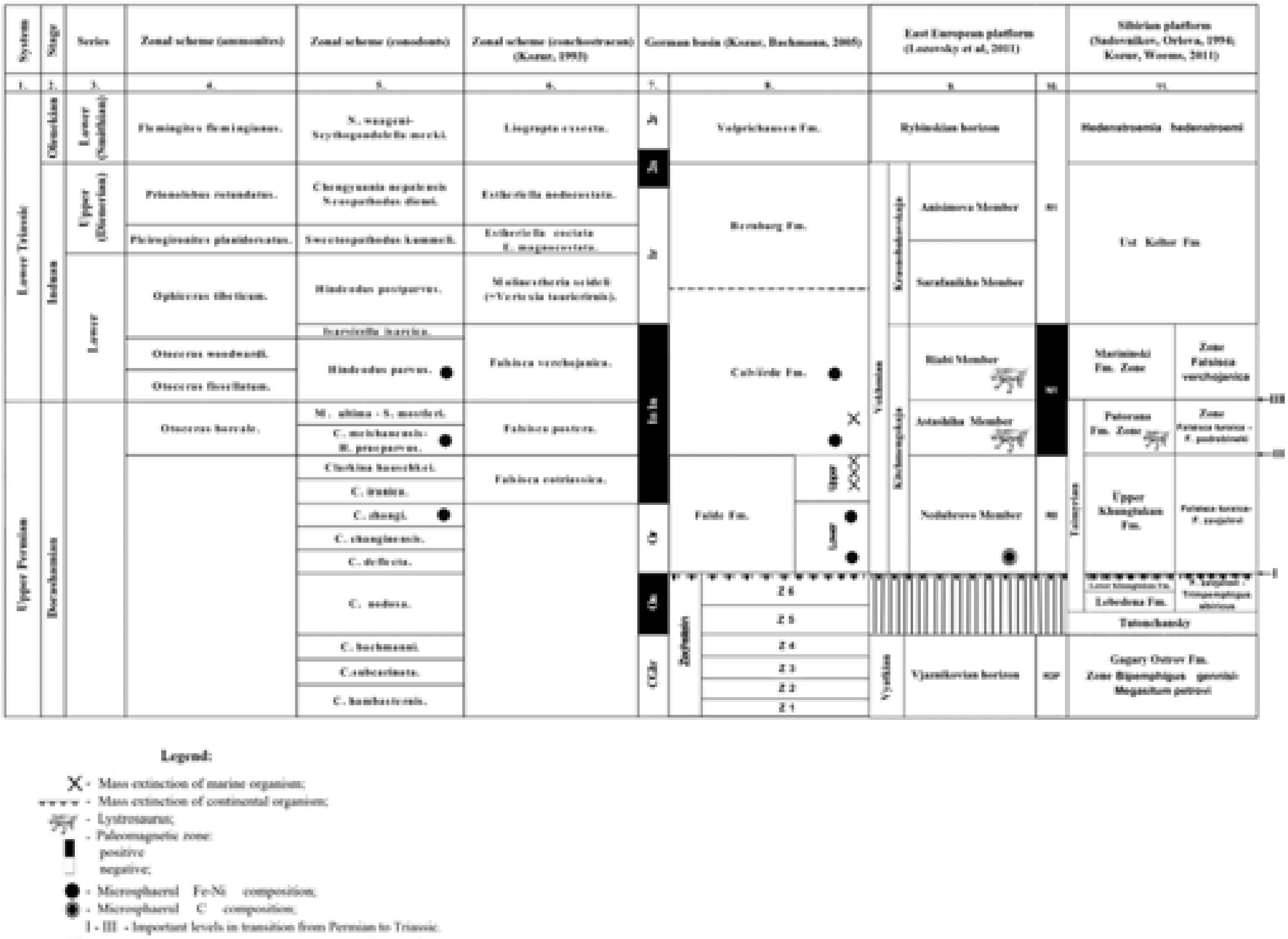

FIGURE 3. Correlation of stratigraphic schemes of the German basin, East European basin and the Siberian platform (using the data of Kozur and Bachmann, 2005; Kozur and Weems, 2011; Lozovsky et al., 2011).

(Rubidge, 1995). Similarly, Permian Dicynodontia that completely died out in Russia by the end of the Permian continue to occur together with *Lystrosaurus* for some time in the Xinjiang Basin of China and disappear later (Kozur and Weems, 2011; Kuchtinov et al., 2011).

The volcanic activity on the Siberian Platform was rather low in Tutonchana and Lebedeva times, and tuffitic sandstones, tuffitic siltstones and tuffitic claystones with rare intercalations of tuffs accumulated here; occasionally, singular basalt covers are observed. The Tunguska event induced a rapid intensification of volcanic activity and a rise of tuff eruption, which was accelerated by the formation of numerous cracks and faults. The upper part of the tuff succession (Utchama Fm.) was deposited, which has a coarser-grained composition than the lower part (tuff breccia, tuffitic conglomerates, etc.), with rare intercalations of basalts.

Eruption of large amounts of ash material in the air led to the excessive distribution of dust in the atmosphere and the fallout of these products in the seas and oceans that, together with acid rains and the intense ultraviolet radiation penetrating into water depths of several tens of meters, was the main cause for the quite rapid extinction of the marine, mainly benthonic organisms. In Early Triassic deep-water deposits, characterized by the absence of radiolarites, the crisis expressed itself through the mass extinction of Radiolaria due to a rapid decline of the siliceous plankton (Bragin, 2000). The sea waters of that time were typically saturated with green algae *Tympanicysta* (*Reduviasporonites*) *stoschiana* Balme, making them similar to the modern Sargasso Sea.

Following the eruption of tuffs, the effusion of the Putorana lavas, as well as the Emeishan volcanism on the Chinese Platform, had no substantial influence directly on the Permian-Triassic crisis. The phenomenon of the global stop of peat formation and, hence, the accumulation of coal at the Permian-Triassic boundary (Retallack et al., 1996) is in good agreement with the scenario described.

At the end of the consideration of the Permian-Triassic crisis it has to be pointed out that, in our opinion, its principal cause was a cosmic or galactic (after the classification of Alekseev, 1998) one, imposed by the impact of a large comet on Earth. The subsequent events (intensification of volcanism on the Siberian and Chinese Platforms, extinction of terrestrial organisms due to ultraviolet radiation, extinction of marine, mainly benthonic organisms and decline of marine plankton) were just its consequence.

WHERE TO PLACE THE PERMIAN-TRIASSIC BOUNDARY?

The accepted GSSP of the P-T boundary, defined by the occurrence of the conodont *Hindeodus parvus*, is, although easy to determine in marine sections, extremely unlucky for continental deposits. The Triassic subcommission of the ICS recognized the choice of this level as unfortunate, and a global correlation of this level is hardly applicable (Oleinikov and Gavrilova, 2008). The author of present article (Karaulov and Lozovsky, 2002) and many other experts previously sharply criti-

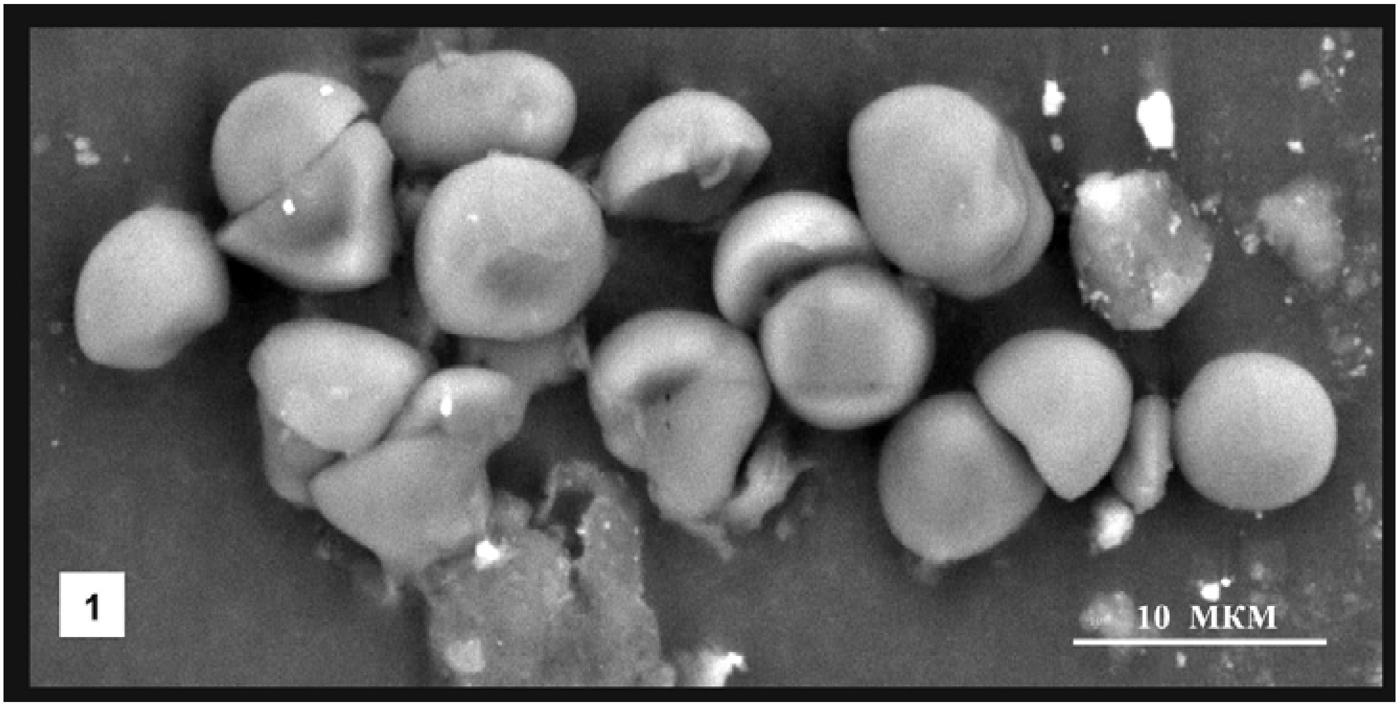

FIGURE 4. Carbon spherules under the electronic microscope.

cized it. The correlation of continental sections by conchostracans (Kozur and Weems, 2011), surprisingly for Kozur, who is an imperturbable supporter of this level, has led to the opposite result: the second correlation level, mentioned above, has wondrously coincided with the historical level of the lower Triassic System boundary, designated by von Alberti in 1834!

In the well-known section of Dalongkou it exactly matches the boundary level assumed by Chinese and American researchers (Lucas, 1993; Kuchtinov et al., 2011) at the base of bed 24 where the first *Lystrosaurus* occurs. With this interpretation of the boundary, the Alpine Tesero Member, the Blind Fjord Formation and the Wordie Creek Formation of East Greenland (Lozovsky et al., 2001, fig.3) will entirely remain within Triassic. On the ammonite scale, the Triassic *Otoceras boreale* will return, to its original system (Tozer, 1984), and the Permian-Triassic GSSP will be moved on the conodont scale slightly downward, to the more distinct level of the first occurrence of genus *Hindeodus*, with the species *H. praeparvus*. It will not be necessary either to destroy the PTGSSP monument erected in the Meishan Province at the location of the known section, but just to specify that the ?-? boundary is placed at the base of bed 25. This will conclude all heated debates on this problem.

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RECONSIDERATION OF THE BASE OF THE PERMIAN SYSTEM

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For more than 70 years, the base of the Permian was recognized globally by a fusulinid biostratigraphic datum, the first occurrence (FO, which operationalizes its FAD = first appearance datum) of "*Schwagerina*," which to many authors meant the FO of the inflated schwagerinids (e.g., Beede and Kniker, 1924). However, in 1998 the base of the Permian was defined by the FO of the conodont *Streptognathodus isolatus* at the GSSP located at Aidaralash Creek in western Kazakstan more or less coeval with the FO of the fusulinid *Sphaeroschwagerina fusiformis* (Davydov et al., 1998), a proposal ratified by the International Commission on Stratigraphy. The FO of *S. isolatus* at Aidaralash was posited to be "an arbitrarily-chosen point within a single conodont chronocline" (Davydov et al., 1998, p. 15). This chronocline supposedly represented the evolution of an "isolated nodular" morphotype of *Streptognathodus* (*S. isolatus*) from a non-isolated nodular morphotype as part of the "*S. wabaunensis*" chronocline (Chernykh and Ritter, 1997; Chernykh et al., 1997). At the time of definition, it was claimed that this point could also be recognized in sections in Russia (Usolka) and North America (Kansas). However, since ratification of this GSSP, it has become clear that with respect to longstanding fusulinid biostratigraphy, the FO of *S. isolatus* is diachronous, with the GSSP being among the youngest known FOs of the species, and that the taxonomy and evolution of *S. isolatus* is not agreed on. These developments call into question the utility of the conodont-based definition of the base of the Permian and indicate that the definition of base of the Permian and its current stratotype needs to be re-evaluated.

As noted above, during the 1990s the FO of *Streptognathodus isolatus* at the Aidaralash section was posited to represent a globally synchronous evolutionary event in a single chronocline. The first explicit effort to document this chronocline appeared seven years after the definition of the boundary. Chernykh (2005; also 2010) outlined the qualitative proposal of the lineage *S. bonus*-*S. wabaunensis*-transitional form-*S. isolatus*-*S. russoflangulatus*-*S. glenisteri* based on material from sections in the Urals. Later, however, Boardman et al. (2009) posited, again qualitatively, a different polytomy of descendants of *S. wabaunensis*, in part through *S. binodosus*, based on material from successive cyclothems in Midcontinent North America (Kansas and Oklahoma). Indeed, Boardman et al. (2009) concluded that the original definition of *S. isolatus* included specimens that were assignable to the previously named *S. invaginatus* and *S. minacutus*. Their model shows a polytomy of three similar species arising from *S. binodosus* (*S. isolatus*, *S. invaginatus* and *S. minacutus*) that possess the same FO in the Midcontinent region. To preserve the name *S. isolatus* from older potential synonyms, its species concept had to be narrowly restricted to a range of morphology that excluded the types of *S. invaginatus* and *S. minacutus*. Thus, there are now two schemes of the phylogeny of *S. isolatus* and two taxonomic definitions of *S. isolatus*--a polymorphic original definition and a revised definition that restricts the species to a single morphotype--and these have been presented in a qualitative way, without apparent rigorous analysis. This calls into question both the originally proposed chronocline leading to *S. isolatus* and the ability to unambiguously recognize *S. isolatus*.

In North America, the base of the Permian had been identified as the base of the Wolfcampian Series since about 1939, based on the FO of *Schwagerina* in the North American sense (e.g., Adams et al., 1939; Thompson, 1954; Wilde, 1990). However, longstanding and widely accepted fusulinid correlations indicate that the new Permian base at the Aidaralash GSSP is younger than the Wolfcampian base, and corresponds closely to the early-middle Wolfcampian boundary (e. g., Ross, 1963; Wilde, 1990; Baars et al., 1994; Wahlman, 1998; Wahlman and King, 2002; Henderson et al., 2012). This has created much confusion with respect to the base of the Permian in North America, particularly with regard to a vast literature that was developed for an oil industry understanding of the greater Permian basin. It also fueled an unnecessary debate over whether a new stage, "Bursumian," was needed in the North American provincial chronostratigraphy to equal early Wolfcampian time, so that the system boundary would not be within a provincial "stage," but correspond to a "stage" boundary (Wilde, 2002).

Well documented and published records of *Streptognathodus isolatus* are few, and there are also several records mentioned but not documented in the literature. Most significant is its well documented record in the Kansas, USA, section, where the FO of *S. isolatus* is at the base of the Bennett Shale Member of the Red Eagle Limestone (Sawin et al., 2006; Boardman et al., 2009). This record is overlain and/or underlain by early Wolfcampian fusulinids (e.g., small species of *Leptotriticites*, large *Triticites* and small *Schwagerina*), which are older than the fusulinids associated with the FO of *S. isolatus* at Aidaralash (Thompson, 1954; Douglass in Mudge and Yochelson, 1962; Wahlman and West, 2010). It could be argued that the fusulinid records are diachronous, but this seems unlikely given that this same succession of early-middle Wolfcampian fusulinids has been documented for nearly a century from numerous sections over a broad area, and within resolution indicates synchrony of the appearance of the inflated schwagerinids (i.e., *Pseudoschwagerina sensu lato*) that mark the beginning of the middle Wolfcampian (e. g., Beede and Kniker, 1924;Thompson, 1954; Ross, 1963; Wahlman and King, 2002; Wilde, 2006; Stevens and Stone, 2007). What seems more likely is that the FO of *S. isolatus* is diachronous; it was based on a hypothetical conodont chronocline, only posited since the 1990s, that is little documented and now problematic.

Other undocumented reports of *Streptognathodus isolatus* from the USA include records from Texas (Pueblo Formation, gray limestone of Gaptank Formation) that are associated with early Wolfcampian fusulinids (though some workers consider the Gaptank fusulinids to be Virgilian: Ross, 1963) and a record from the Horquilla Formation of New Mexico associated with the FO of inflated schwagerinids (Barrick et al., 2012) . Other young FOs of *S. isolatus* have been reported, coeval (within resolution) with the FO at Aidaralash, and include at least some records from China (Wang, 2000). The oldest known *S. isolatus* are in the USA, so the species may have originated in North America and immigrated to Eurasia, with a detectable diachroneity.

It is also important to remember that there was no basis in priority for defining a GSSP for the Permian base at Aidaralash Creek or, indeed, anywhere in the former Soviet Union. Murchison's type Permian only included rocks of Kungurian age and younger, and Soviet extension of the Permian downward (to the base of the Asselian) largely was based on the work of Ruzhentsev on ammonoids. Aidaralash Creek is not the stratotype of the Asselian Stage, and the conodont-based definition redefined the Asselian to include older strata than did the original definition of Ruzhentsev.

Based on the above considerations, I conclude that we should reconsider the position of the base of the Permian and its current GSSP, and reposition the base of the Permian so as to respect longstanding usage and produce the most correlateable boundary. No conodont-based definition obviously meets these criteria, but a fusulinid-based definition does. Two choices are available---the LO of North American *Schwagerina* s. str. (= *Thompsonites* Bensh), which defines the base of the Wolfcampian, or the LO of an inflated schwagerinid taxon, which defines the beginning of the middle Wolfcampian and is closer to the original base of the Asselian. I favor using the FO of North American *Schwagerina sensu stricto* because it also marks a major biological event—the beginning of the explosive diversification of schwagerinids (Ross, 1995)--and it retains longstanding and extensive North American usage that equates the base of the Wolfcampian with the base of the Permian. Several North American locations can provide an excellent GSSP, including sections in New Mexico, Texas and Kansas. Such a fusulinid-defined base of the Permian has the advantages of respecting longstanding usage and produces a correlateable Permian base that is synchronous within current levels of biostratigraphic resolution.

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ALFRED KING'S PENNSYLVANIAN TETRAPOD FOOTPRINTS FROM WESTERN PENNSYLVANIA

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Abstract—In 1844-1846, Alfred T. King (1813-1858) gave ichnotaxonomic names to what he believed to be fossil footprints from the Pennsylvanian strata of Westmoreland County in western Pennsylvania. In 1846, the famous British geologist Charles Lyell examined these footprints and some of their localities and concluded that most were manmade artifacts (Native American carvings = petroglyphs), though Lyell did consider one record to be of bona fide Pennsylvanian tetrapod footprints. The ichnotaxa King named have either slipped into obscurity (*Ornithichnites*) or been considered the footprints of pelycosaurs (*Spheropezium*) or of amphibians (*Thenaropus*). A voucher collection of King's tracks in the Beneski Natural History Museum at Amherst College allows a re-evaluation of his ichnotaxa that demonstrates that his ichnospecies of *Ornithichnites* and *Spheropezium* are based on Native American carvings, not ichnofossils, as Lyell had originally concluded. One specimen in the Amherst College collection is of Pennsylvanian tetrapod footprints properly deemed the lectotype of *Limnopus heterodactylus* (King, 1845). This is the oldest named ichnospecies of *Limnopus*.

INTRODUCTION

The discovery of Carboniferous tetrapod footprints in North America took place during the 1840s. The earliest report was from Nova Scotia, in 1841, by W. E. Logan (Sarjeant and Mossman, 1978). Soon thereafter, King (1844, 1845a, b, c, 1846) reported footprints from the coal-bearing Pennsylvanian strata near Greensburg in Westmoreland County, Pennsylvania (Fig. 1). Lea (1849) followed with the discovery of what are now known to be Mississippian tracks from near Pottsville in eastern Pennsylvania (Fillmore et al., 2012).

Much is now known about the Nova Scotian tracks (Sarjeant and Mossman, 1978), as well as the original discoveries of Lea (Fillmore et al., 2012). But, little has been known of King's discoveries, largely because a collection of some of the tracks (or casts of them) he described, that resides in Amherst College, has long been overlooked. Here, we recount King's discoveries, describe the relevant collection and re-evaluate its ichnotaxonomic significance. In this article, ACM refers to specimens in the Beneski Museum of Natural History, Amherst College, Amherst, Massachusetts.

ALFRED T. KING AND HIS FOOTPRINT DISCOVERIES

Alfred T. King (1813-1858) was a physician who practiced medicine, primarily in Westmoreland County, Pennsylvania. Born in Galway, New York, King was apprenticed to a doctor and later studied medicine in Philadelphia. In about 1838, he took up a medical practice in Pleasant Unity in Westmoreland County, Pennsylvania, and ultimately moved to Greensburg. King was characteristic of many early American scientists in being a polymath who studied, collected and/or wrote about various fields, including astronomy, botany, medical forensics, microscopy, mineralogy, paleontology and zoology. He evidently was self taught in most of these sciences. In 1856, King was appointed a professor at the Medical College of Philadelphia.

In 1844, King began to discover what he believed to be fossil footprints in the Pennsylvanian strata exposed in Westmoreland County. King published articles on these footprints in late 1844, early 1845 and early 1846, in both the *Proceedings of the Academy of Natural Sciences of Philadelphia* and the *American Journal of Science*. In his first published article, King (1844) proposed the new ichnotaxonomic names *Ornithichnites gallinuloides*, *O. culbertsonii*, *Thenaropus leptodactylus*, *T. pachydactylus*, *T. sphaerodactylus* and *T. ovoidactylus*. He provided illustrations (line drawings: Fig. 2) and brief descriptions, and he even

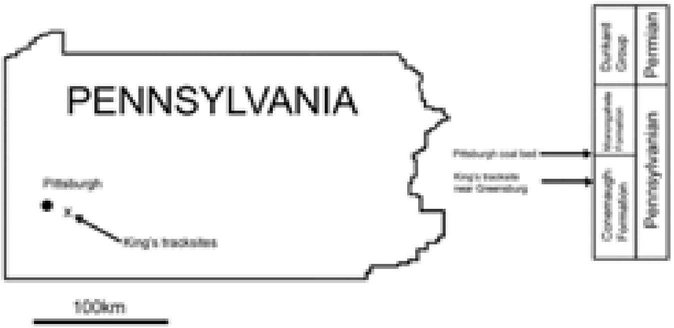

FIGURE 1. Map showing location of Westmoreland County, Pennsylvania and simplified stratigraphy of part of the Pennsylvanian-Permian section, showing stratigraphic level of King's type of *Thenaropus heterodactylus* in the Upper Pennsylvanian (Virgilian) Conemaugh Formation.

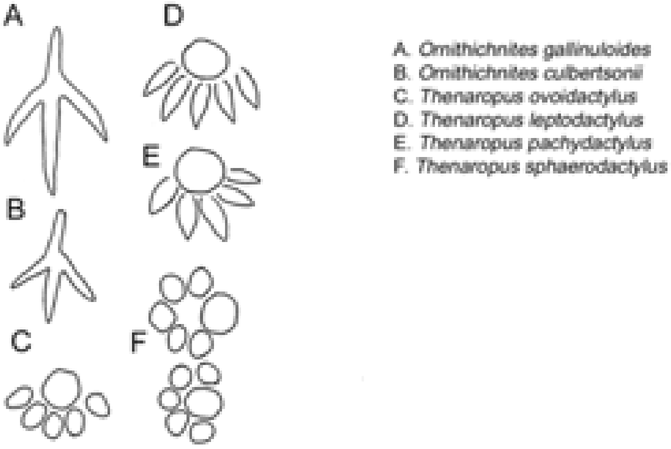

FIGURE 2. King's (1844) line drawings of the new ichnotaxa he named from the locality near Derry in western Pennsylvania.

explicitly distinguished the ichnotaxa from each other, statements equivalent to diagnoses. Thus, like previous workers (e.g., Kuhn, 1963; Haubold, 1971), we regard King's ichnotaxonomic names as available *sensu* the *International Code of Zoological Nomenclature*.

In the next publication, King (1845a) presented a longer version of his first article. An editorial note at the beginning of the article acknowledges the similarity in content and also noted that King desired to change the name *Thenaropus*, restricting it to a trackway slab not illustrated or described in the earlier article. He proposed to use the new name *Spheropezium* for the tracks he had previously called *Thenaropus*. The editor also noted that King wished to use the name *Spheropezopus*, but the editor changed this, "abbreviating his proposed name *Spheropezopus* to *Spheropezium*" (p. 343). The editorial note also suggested using a new name for *Thenaropus heterodactylus*: "we would suggest the propriety of his [King] adopting some new name, as a new use of his word [Thenaropus] will only create increased confusion." Indeed, we agree with the editor's comments.

More importantly, King (1845a) included illustrations of footprints not illustrated in his earlier article. King deemed these footprints to be "batrachian" in origin and gave them the name *Thenaropus heterodactylus*. These footprints were preserved as parts of multiple trackways (Fig. 3). King (1845a) also changed, without mention, the ichnospecies name *Thenaropus sphaerodactylus* to *Spheropezium thaerodactylum*.

King (1845b) mentioned two new footprint sites, one about 5 km from Greensburg preserving large ovoid tracks and another about 43 km from Greensburg that preserved tracks of "ruminants." None of these tracks was illustrated.

King (1845c) published a drawing of the "trackway surface" that included the types of his ichnospecies of *Ornithichnites* and *Spheropezium* (Fig. 4). The text says it is a "slab of limestone containing some of the tracks in series, which were described in the last number of this journal" (p. 216). However, King (1844, p. 178) had already described the track-bearing rock as a "coarse grained sandstone." In this short text King (1845c) again proposes the name *Thenaropus heterodactylus* for the "batrachian" tracks described and illustrated by King (1845a).

King (1845b, 1846) described tracks from a locality 53 km from Greensburg on Chestnut Ridge, in a coarse-grained sandstone. His illustrations clearly are of the track of a cervid and of an unusual track he called "batrachian" (Fig. 5). The "batrachian" track may be a Carboniferous tetrapod footprint, but the location of the original is not known, so it cannot be examined. The fact that it apparently was on the same surface as "artiodactyl tracks" reduces the likelihood it is a Carboniferous fossil footprint.

In 1845-1846, one of the great British founders of modern geology, Charles Lyell (1797-1875) visited the United States, one of four such visits (Lyell, 1849; Wilson, 1998). Lyell was interested in the authenticity of King's tracks because at the time it was believed that no tetrapods lived on land during the Carboniferous. Thus, in April of 1846, Lyell arrived in Pittsburgh and almost immediately left for Greensburg, to examine the footprints that King had published. King and one of his associates, the reverend Mr. Hackney, took Lyell into the field to visit the footprint localities.

King had reported footprints from three localities, which Lyell (1846a, b) described: (1) a stone quarry ~ 8 km southeast of Greensburg in Westmoreland County, Pennsylvania (this is the locality of the "batrachian" tracks reported by King, 1845a); (2) about 1. 6 km (no direction given) from the town of Derry in Westmoreland County (the various ichnospecies of *Ornithichnites* and *Spheropezium* in King, 1844, 1845a are based on specimens from the track surface at this locality illustrated by King, 1845c); and (3) about 53 km from Greensburg on the summit of Chestnut Ridge (King's 1846a track locality). Lyell visited the first two of these localities, and confirmed that the site 8 km southeast of Greenburg is in Carboniferous strata ~ 30 m below the Pittsburgh coal bed (Fig. 1).

However, Lyell (1846a, b) considered the footprints from near

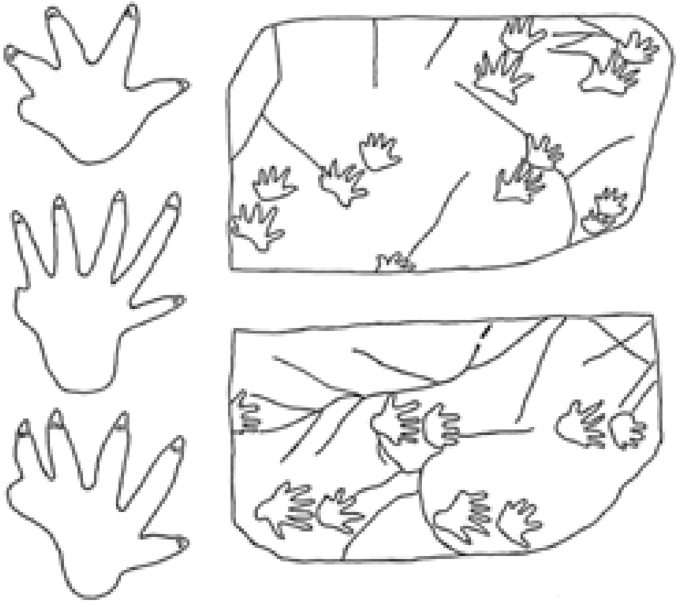

FIGURE 3. King's (1845a) line drawings of the "batrachian" footprints he named *Thenaropus heterodactylus* from a locality in the Conemaugh Formation near Greensburg, Pennsylvania (Fig. 1).

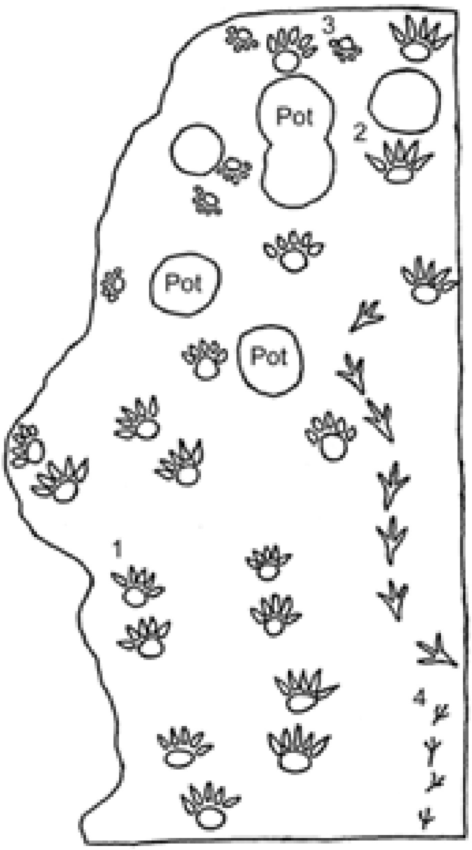

FIGURE 4. King's (1854c) drawing of the trackway surface that produced his type material of ichnospecies of *Ornithichnites* and *Spheropezium* from a locality near Derry, Pennsylvania. Note the very regular trackway patterns that do not resemble actual trackways of animals. In the drawing "Pot" refers to potholes. The numbers appear to indicate specific ichnotaxa: **1**, *Spheropezium pachydactylum*; **2**, *S. leptodactylum*; **3**, *S. thaerodactylum*; **4**, *Ornithichnites culbertsonii* (below) or *O. gallinuloides* (above).

FIGURE 5. King's (1846) drawing of footprints he found 53 km from Greensburg, Pennsylvania. The upper footprint is that of an artiodactyl mammal, and the lower may be of a Carboniferous tetrapod. However, these specimens and the locality have not been subsequently located or documented, so they cannot be further evaluated.

Derry (these were the footprints that were the types of the ichnospecies of *Ornithichnites* and *Spheropezium*) to have been manmade, because of their sharp-edged preservation in coarse sandstone on a very uneven surface where the tracks were registered on different bedding planes. In making this argument, Lyell (1846a, b) drew attention to other, obviously manmade tracks that had appeared in the literature of American geology as fossil tracks, such as the human footprints first reported by Schoolcraft (1822) as natural but later convincingly argued by Owen (1842) to have been carved. Lyell (1849) later published a book on his 1845-1846 visit to North America, and discussed the footprints reported by King over the course of 10 pages (p. 304-314), repeating the conclusions of his 1846 articles, and included a woodcut of one of the track slabs that Lyell regarded as authentic (Fig. 6).

SUBSEQUENT USE OF KING'S ICHNOTAXONOMIC NAMES

Many (or all) of King's ichnotaxonomic names were subsequently listed by bibliographers and compilers (Hay, 1902, 1930; Hickling, 1909; Kuhn 1958, 1963; Haubold, 1971). Matthew (1903a, b, 1904) considered the species of *Thenaropus*/*Spheropezium* named by King as valid (he assigned all to the ichnogenus *Thenaropus*) and even named a new ichnospecies, *Thenaropus mcnaughtoni*, from the Pennsylvanian of Nova Scotia.

Kuhn (1963), in his compendium of all tetrapod footprint ichnotaxa, listed *Thenaropus* (= *Spheropezium*), although he did note (on p. 45) that Lyell considered it an "Artefact!" Kuhn (1963) also noted that Schmidt (1959) and Baird (no citation) regarded King's ichnospecies of *Ornithichnites* to have been based on Native American carvings.

Baird (1952), in an important review of late Paleozoic amphibian footprints from the United States, did not mention King's ichnotaxa. However, Baird (1965, p. C47) later noted that "a slab at Amherst College (Hitchcock colln. 26/14) demonstrates that *Thenaropus heterodactylus* King (1845) from the Conemaugh Group (early Virgil?) near Greensburg, Pa., is a valid species of *Limnopus* and closest in form to *L. littoralis* (Marsh) from the Virgil of Kansas."

Haubold (1971, p. 36, figs. 21.3-7) considered *Spheropezium* King, 1845 (= *Thenaropus*, = *Spheropezopus*, = *Sphaeropezium*) to be a valid ichnogenus of pelycosaur footprint. He diagnosed the ichnogenus as "footprints of a quadruped that are plantigrade, pentadactyl with a round sole mark, only distal imprints of the digits are preserved, isolated from the sole and radiate outward, trackway unknown." The last remark is an oversight, as King did publish an apparent trackway (Fig. 4). Haubold (1971, p. 17) followed Baird (1965) in regarding *Thenaropus heterodactylus* as an ichnospecies of *Limnopus*, as did Voigt (2005, p. 73).

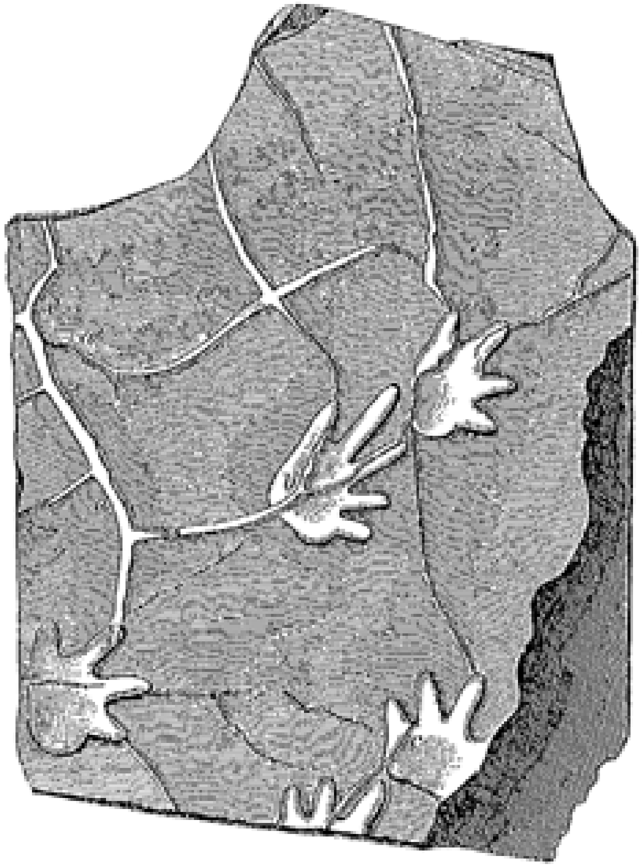

FIGURE 6. Lyell's (1849) woodcut of some of the "batrachian" footprints found by King near Greensburg, Pennsylvania. The match is not exact, but this may be an illustration of the same specimen illustrated in Figure 11, if the woodcut is a reversed image of a larger slab that includes the piece illustrated in Figure 11.

Cotton et al. (1995) briefly reviewed King's work and regarded only *Limnopus heterodactylus* as a valid ichnotaxon named by him. They noted that "several of the 'footprints' described by King (1845, 1846) were later determined by Lyell (1846) to have been carved by Indians, a revelation missed by some later workers" (Cotton et al., 1995, p. 200).

ICHNOTAXONOMY

Introduction

We have concluded that the ichnotaxonomic names introduced by King meet the criteria of availability of the *International Code of Zoological Nomenclature* (see Chapter 4 of the Code, especially Article 12). Importantly, the replacement names King proposed are available nomina nova by the standards of Article 12.2.3. These replacement generic names have the same type species as the original names (e.g., *Thenaropus* and *Spheropezium* have the same type ichnospecies).

Kuhn (1963, p. 45) designated the first named ichnospecies of *Thenaropus, T. leptodactylus,* as the genotypic species. This means it is the genotypic species of *Spheropezium* as well. *Thenaropus heterodactylus* is clearly not the same ichnogenus as the material originally named *Thenaropus* (see below), so this ichnospecies needs to be assigned to a different ichnogenus. This, as Baird (1952) noted, is *Limnopus*, as *L. heterodactylus* (King, 1845), which makes it the oldest named ichnospecies of *Limnopus* (see below).

Ornithichnites

King (1844) used Hitchcock's (1836) ichnogeneric name *Ornithichnites* for what he took to be fossil bird tracks (Fig. 7). The supposed bird tracks named by King are tetradactyl and fall into two size groups: (1) larger tracks named *Ornithichnites gallinuloides*, total footprint length ~ 23 cm; and (2) smaller tracks named *O. culbertsonii*, length ~ 11 cm. These ichnotaxa are based on specimens from the locality near Derry (see above) that were regarded by Lyell to be Native American carvings (see above).

In the ACM collection, four specimens voucher King's "bird track" ichnotaxa--two casts and two marks preserved in coarse, brown sandstone (Fig. 8). The track cast next to the catalogue number ACM 31/67 (Fig. 8A) is a good match for King's drawing of *Ornithichnites gallinuloides*. It may be a cast of the specimen he illustrated, so we consider it to represent the "lectotype" of *O. gallinuloides*.

There are two tracks and one cast of a track in the Amherst College collection that are the right size to be considered *O. culbertsonii*. Of these, the cast ACM 31/68 (Fig. 8B) is the best match for King's illustration—note the relatively equal-sized digits and asymmetry in size and divarication angle of digits II and IV. This can be considered the "lectotype" of *O. culbertsonii*. Specimen ACM 31/63 (Fig. 8C) has too long of a digit III, and the third specimen, ACM 31/62 (Fig. 8D), also has too long of a digit III and more symmetrical digits II and IV than King's illustrations.

These tracks were proclaimed human (Native American) carvings (petroglyphs) by Lyell (1846a, b, 1849), and we concur. Note that they bear a strong resemblance to modern tracks of North American birds such as quail, crow and heron (Elbroch et al., 2001). The actual specimens are marks registered in coarse sandstone, which, as Lyell argued, is a substrate unlikely to preserve such track forms. And, of course, no bona fide bird fossils or tracks are known before the Jurassic. Thus, like previous workers, we can reject King's ichnospecies of *Ornithichnites* as being based on manmade carvings, not on biogenic trace fossils.

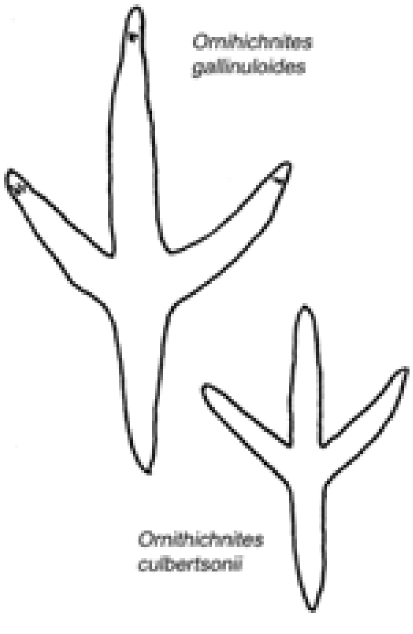

FIGURE 7. King's drawings of the *Ornithichnites* track types he named (from King, 1845a, figs. 1-2).

Spheropezium

King (1845a) named four ichnospecies of *Spheropezium* (Fig. 9). *S. lepodactylum* has five digits, ~ 5 cm long, that fan out over ~ 90 degrees. The digit imprints are separate from the round, sole imprint. The digit imprints are meniscate and have pointed distal tips.

Spheropezium pachydactylum is similar to *S. leptodactylum* but with thicker digits (Fig. 9). It is supposedly larger, but no measurements were given, so there is no way to compare sizes based on King's publications. *S. thaerodactylum* has five digits as round imprints, either directly around or in front of the larger, round sole imprint. *S. ovoidactylum* is like *S. thaerodactylum*, but with widely spread toes.

Six specimens---two in coarse sandstone, four plaster casts—in the ACM collection voucher King's *Spheropezium* ichnospecies (Fig. 10). One cast (Fig. 10D) matches well to his drawing of *S. leptodactylum*, another (Fig. 10E) matches his drawing of *S. pachydactylum*, two match *S. ovoidactylum* (Fig. 10A, F) and two match *S. thaerodactylum* (Fig. 10B-C). We therefore consider them the source of lectotytpes of his ichnospecies. Thus, we regard ACM 31/64 (Fig. 10D) as a cast of the lectotype of *S. leptodactylum*; ACM 31/70 (Fig. 10E) as a cast of the lectotype of *S. pachydactylum*; ACM 31/16 (Fig. 10A) as the lectotype of *S. ovoidactylum*; and ACM 31/60 (Fig. 10C) as the lectotype of *S. thaerodactylum*.

However, these tracks bear no resemblance to any known Carboniferous tetrapod footprints (cf. Haubold, 1971, 1984). They are certainly not those of pelycosaurs, which are pentadactyl and typically have long, ovoid or bean-shaped sole imprints well connected to long digits of varied length (e.g., Haubold, 1971). We concur with Lyell that the *Spheropezium* tracks are likely Native American carvings (petroglyphs). Like the *Ornithichnites* tracks, the *Spheropezium* "tracks" are in coarse sandstone. They are sharply cut, do not form biologically plausible trackways (Fig. 4) and are remarkably simple and symmetrical in form. They strongly resemble the footprints of some modern mammals, especially procyonids and mustelids (Murie, 1974).

Thenaropus

The only bona fide Carboniferous footprints King described are those to which he attached the name *Thenaropus heterodactylus* (Figs. 3, 6, 11). Only one extant specimen is known of the multiple footprints that were parts of multiple trackways illustrated by King (Fig. 3). This is ACM 26/14, which is a manus-pes pair and part of a manus imprint preserved in convex hyporelief (Fig. 11). This is the lectotype of *T. heterodactylus* (Haubold, 1970; Voigt, 2005).

These tracks show diagnostic features of *Limnopus* Marsh, 1894, including: a pentadactyl pes and tetradactyl manus; pes digits that increase in length from I to IV, with digit V subequal in length to digit II; relatively thick pes and manus digits with blunt/rounded distal tips; broad and rounded sole imprints; manus just in front of pes; manus digits I-III obliquely set (turned) toward the trackway midline; and manus digits that increase in length from I to III, with digit IV subequal in length to digit II (cf. Baird, 1952; Haubold, 1970, 1971; Voigt, 2005). Clearly, as earlier workers have concluded, ACM 26/14 is a specimen of *Limnopus* and it is sufficient material to diagnose the first named ichnospecies of the genus.

Most authors use the type species name *Limnopus vagus* Marsh, 1894 as the oldest name to refer to specimens of *Limnopus* (e.g., Haubold, 1971; Voigt, 2005). However, we see little to differentiate *L. vagus* from *L. heterodactylus* and believe these ichnospecies are synonymous. Pending a revision of *Limnopus*, we suggest that *L. heterodactylus* is the name that should be in common use as the oldest valid name of an ichnospecies of *Limnopus*.

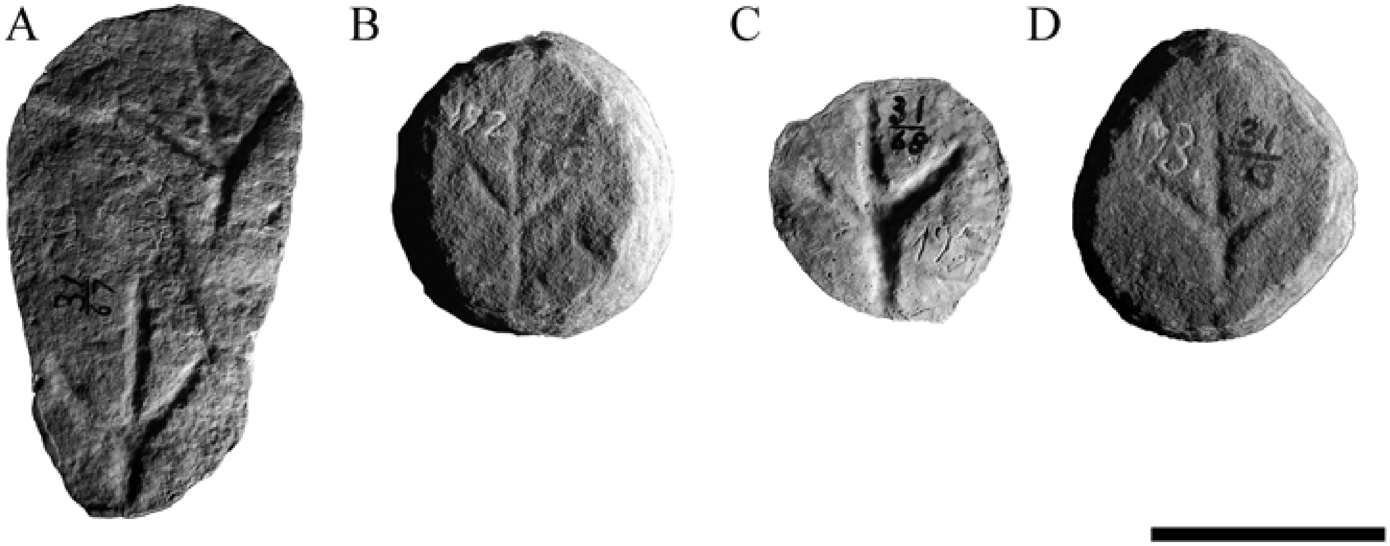

FIGURE 8. Specimens in the Amherst College collection that voucher King's ichnospecies of *Ornithichnites*. **A**, ACM 31/67, plaster cast of two footprints in concave epirelief. **B**, ACM 31/62, specimen in concave epirelief. **C**, ACM 31/68, plaster cast of one footprint in concave epirelief. **D**, ACM 31/63, specimen in concave epirelief.

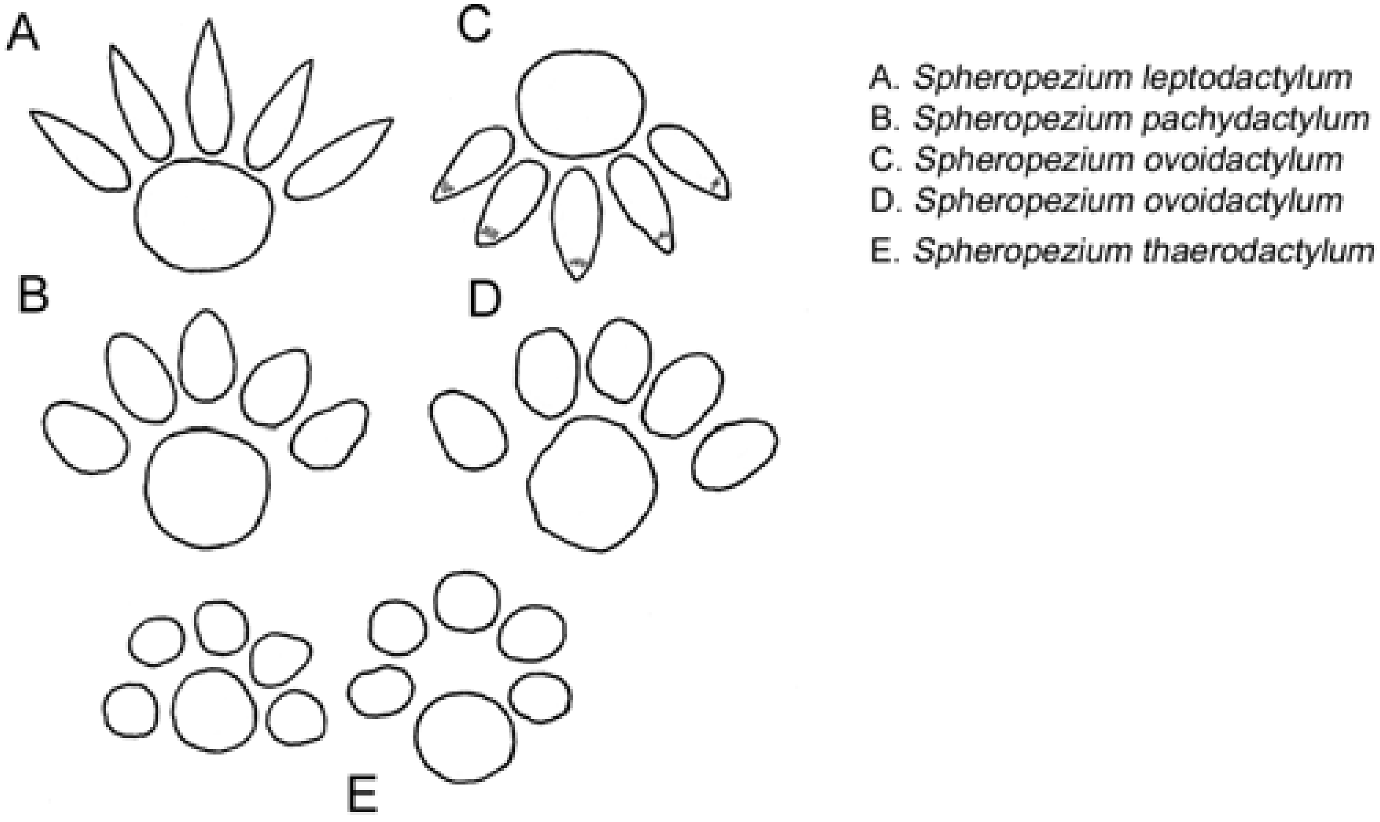

FIGURE 9. King's (1844) line drawings of the ichnospecies of *Spheropezium* he named from western Pennsylvania.

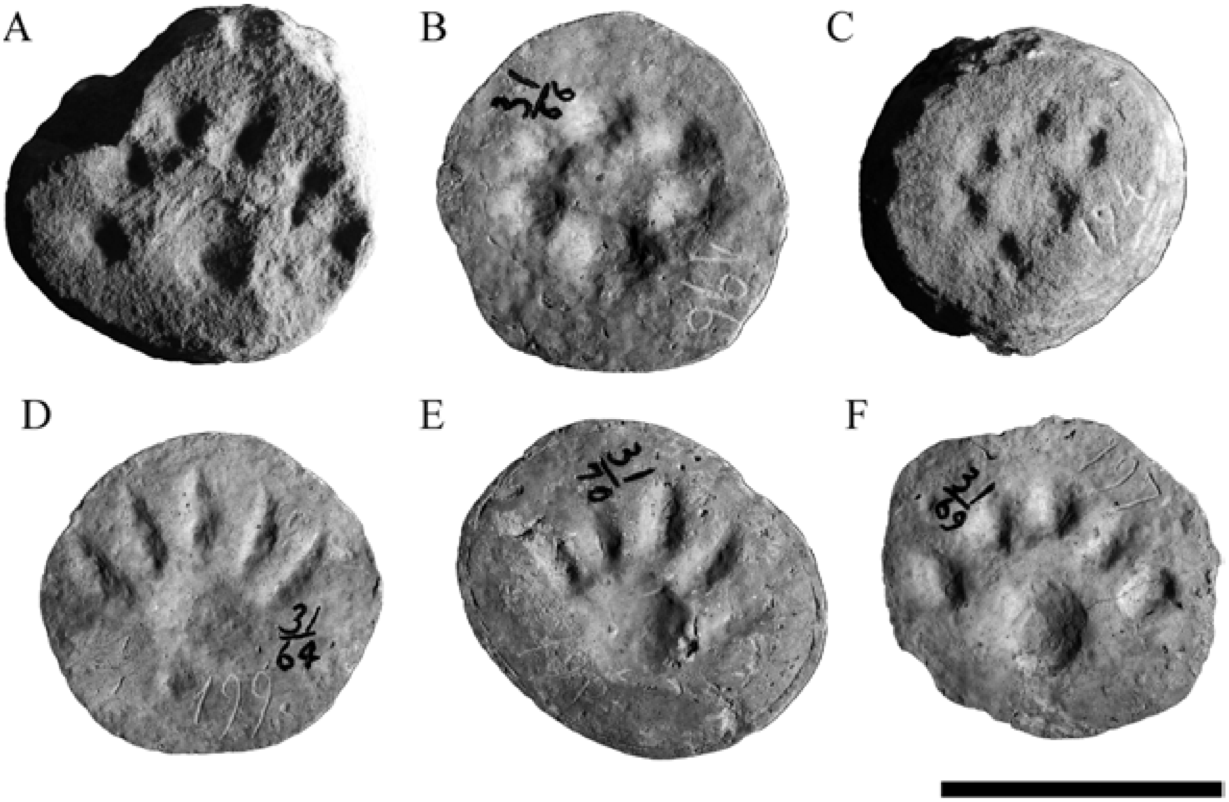

FIGURE 10. Specimens in the Amherst College collection that voucher King's ichnospecies of *Spheropezium*. **A**, ACM 31/16, Specimen in concave epirelief. **B**, ACM 31/66, Plaster cast in concave epirelief. **C**, ACM 31/60, Specimen in concave epirelief. **D**, ACM 31/64, Plaster cast in concave epirelief. **E**, ACM 31/70, Plaster cast in concave epirelief. **F**, ACM 31/69, Plaster cast in concave epirelief.

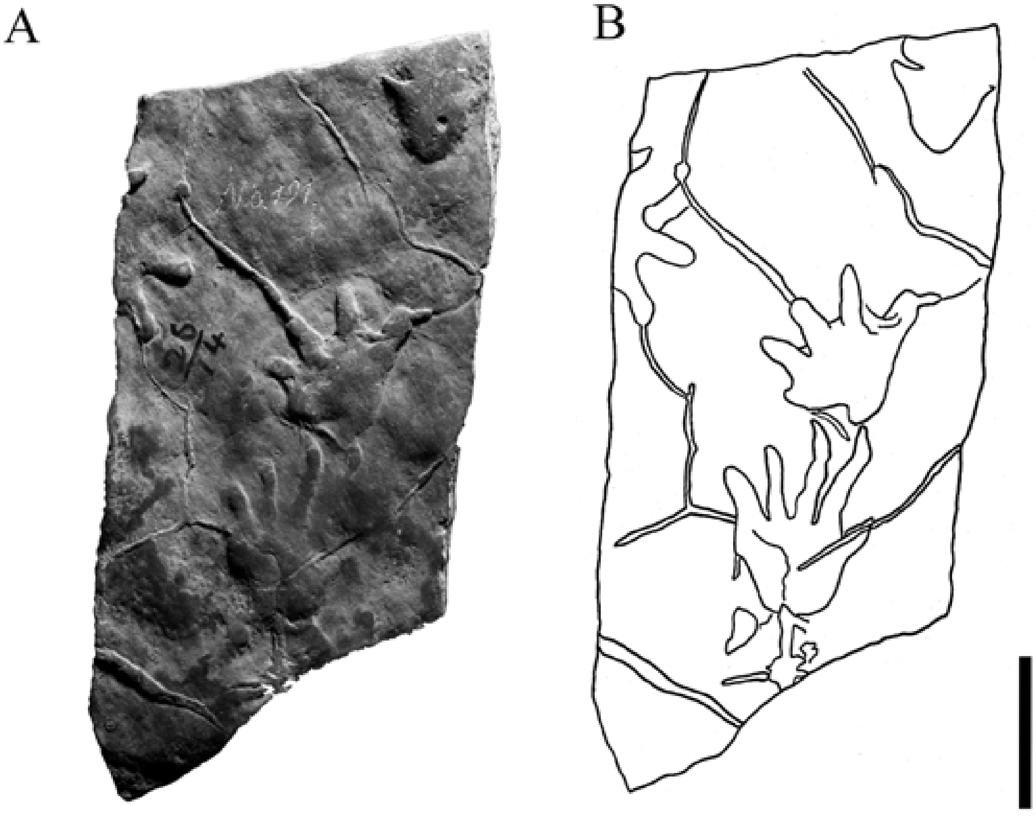

FIGURE 11. ACM 26/14, The lectotype of *Limnopus heterodactylu*s (King, 1845), manus and pes set in convex hyporelief, from the upper Virgilian Conemaugh Formation near Greensburg, Pennsylvania.

CONCLUSIONS

We offer the following conclusions:

1. King's ichnospecies of "bird tracks"—*Ornithichnites gallinuloides* and *O. culbertsonii*—are based on Native American carvings (petroglyphs), not on trace fossils.

2. King's ichnospecies of *Spheropezium*—*S. leptodactylum*, *S. pachydactylum*, *S. thaerodactylum* and *S. ovoidactylum*—are also based on Native American carvings (petroglyphs), not on trace fossils.

3. The type species of *Thenaropus* and its replacement name *Spheropezium* is *T. leptodactylus*.

4. *Thenaropus heterodactylus* is the only name proposed by King for bona fide Carboniferous tetrapod footprints. However, it is not the same ichnogenus as the type species (or other species) assigned to *Thenaropus*/*Spheropezium*.

5. An extant lectotype of *Thenaropus heterodactylus* in the ACM collection has properly been reassigned to *Limnopus*.

6. *Limnopus heterodactylus* (King, 1845) is the oldest valid ichnospecies name of that ichnogenus and probably should be considered a senior subjective synonym of *L. vagus* Marsh, 1894, the type ichnospecies of *Limnopus*.

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ROMER'S GAP REVISITED: CONTINENTAL ASSEMBLAGES AND ICHNO-ASSEMBLAGES FROM THE BASAL CARBONIFEROUS OF BLUE BEACH, NOVA SCOTIA , CANADA

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Abstract—The Lower Mississippian Horton Bluff Formation at Blue Beach, Nova Scotia, is known to yield a rich fossil record including the earliest terrestrial tetrapod fauna, several groups of associated fishes, nonmarine and marine invertebrates, and an early flora containing nearshore and terrestrial plants. A co-occurring ichnological record parallels the body fossil record, and includes the earliest pentadactyl/tetradactyl footprints on earth, and diverse invertebrate traces. The ichnoassemblage represents one of the earliest occurrences of the *Scoyenia* ichnofacies. A new and large collection of these fossils is now curated and stored in the Blue Beach Museum, located at the site. The fossil assemblage recovered encompasses numerous important discoveries, including, but not limited to: (1) fossil charcoal (fusain) is now recognized in the deposit, suggesting ancient wildfires were common occurrences, further implying atmospheric oxygen levels were not significantly reduced as proposed by recent studies; (2) several partially-complete examples of stem tetrapods, and a rare millipede-like form have now been recovered; (3) articulated fish material, plus additional taxa of fish have been recovered; and (4) the only known neurocranium of a large palaeoniscoid that can provide new data on phylogenetic links between older Devonian groups, and on the origins of modern fishes. The new Blue Beach Museum collections merit reporting for a number of significant reasons: (1) the fossils are currently the oldest known material from "Romer's gap," an interval during which many important groups of vertebrates and invertebrates remain virtually unknown; (2) the various lines of new fossil evidence show that by the end of Early Mississippian time, significant increases had occurred in the biotic diversity of early continental settings, compared with those of Devonian age, suggesting there is a significant fossil record yet unfound; (3) some questions about the nature of Romer's gap are surfacing as a result of the new information from Blue Beach; (4) the newly-discovered "marine band" is the first confirmation of fully marine conditions, and probably represents a major transgression event in the Tournaisian of the Maritimes Basin; (5) a newly-discovered marine fauna may help synchronize correlations of the poor continental- and better-known marine-records of the Tournaisian, especially those in western Europe; and (6) there are no recent reviews of the paleontology at Blue Beach.

INTRODUCTION

In the terrestrial realm, an approximately 25 million-year long interval known as "Romer's gap" follows the end of the Devonian period. Encompassing the entire Tournaisian stage, and the approximate first half of the Viséan stage, this interval has a notoriously-poor continental fossil record. It was named after Alfred Sherwin Romer, who first noted its particular absence of tetrapod fossils (Romer, 1941). At the time of his research, and for many years thereafter, not a single tetrapod body fossil was collected from strata deposited during the gap.

The type section of the Horton Bluff Formation, on the western side of the Avon River Estuary at Blue Beach (Figs. 1-5), is known to yield a fossil biota that dates to the middle of Romer's gap. A rich body fossil assemblage includes terrestrial and nearshore plants, non-marine invertebrates, marine invertebrates, and a vertebrate fauna of fish and early tetrapods (Table 1). An unusually diverse, co-occurring ichnofossil assemblage is also present, and includes tracks, trails, burrows, resting traces, and bromalites (coprolites and cololites) (Table 2).

The principal purpose of this article is to provide an up-to-date review of the fossil biota found at Blue Beach. New fossil evidence from Blue Beach necessitates revisions to some of the previous taxonomic nomenclature. In addition, recent finds are nearly correlative with important new finds being made in Scotland (Smithson and Wood, 2009; Smithson et al., 2012). The new material under consideration at Blue Beach will also serve an important role in providing comparative material for those studies and others.

One final purpose of this paper is to demonstrate that the new evidence proposed here does not support the model proposed by Ward et al. (2006) regarding an oxygen crisis during the time of Romer's gap. In their scenario, declining atmospheric oxygen levels (Berner, 2006) hypothetically led to a biotic crisis, which in turn constrains the timing of terrestrial adaptations, effectively postponing the initial evolution of terrestrial vertebrates and invertebrates.

THE BLUE BEACH FOSSIL MUSEUM AND COLLECTION

The Blue Beach Fossil Museum sits atop the classic Early Carboniferous fossil locality of Blue Beach (Fig. 2). During the past two decades, a very large collection of fossils has been amassed, almost all of which has been recovered from the beach. The Blue Beach Fossil Museum is a unique entity that was born out of unique circumstances. A charitable, non-profit society is looking to build a new museum, but the museum is still privately owned and receives no significant contributed funding. All of the museum's sustainability and development have been incurred by the owners. The home-based museum is staffed on a volunteer basis.

The Blue Beach fossil biota is represented by a collection at the Blue Beach Fossil Museum of more than 2800 vertebrate bone specimens, more than 2000 slabs of rock with tetrapod footprints and trackways, more than 400 rock slabs with other assorted traces (including invertebrate traces, fish trails, and bromalites), and the flora by more than 570 fossil plant specimens. At least 3000 additional bone specimens (less interesting or fragmentary) remain in a partially-catalogued state. The total collection is estimated to weigh over 40 tons, most of

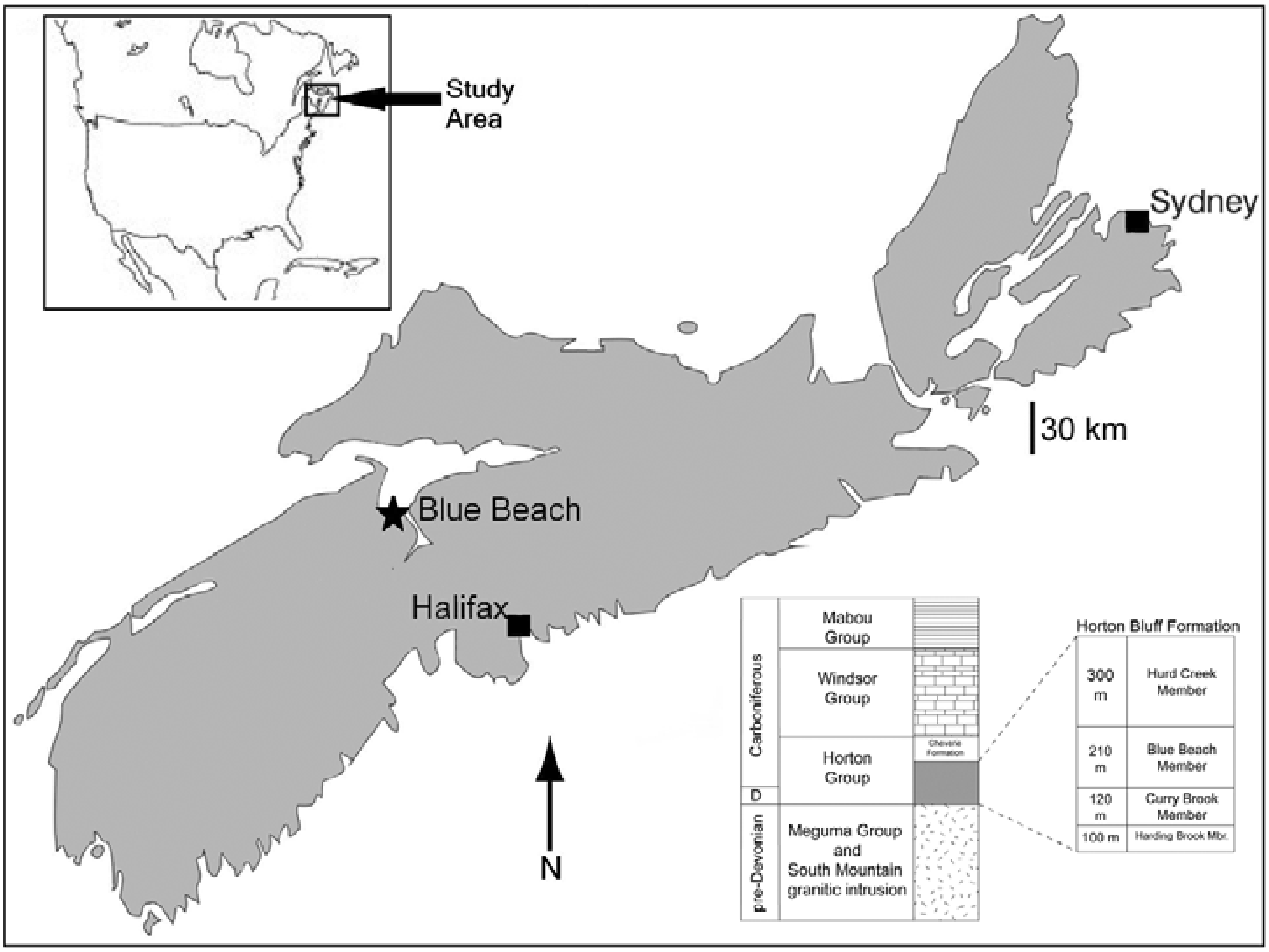

FIGURE 1. Index map of Nova Scotia showing location of Horton Bluff/Blue Beach and inset showing general stratigraphy of the Horton Bluff Formation and adjacent rocks with insert showing lithostratigraphic nomenclature.

which is undescribed, and the collection is in need of a dedicated on-site storage facility.

Almost all of the critical vertebrate fossil specimens in the Blue Beach collections require further preparation. Among the unprepared fossils are dozens of examples where there exists a strong potential for partially articulated skeletons that are rarely reported from the site (Clack and Carroll, 2000; Anderson et al., 2009; Smithson et al., 2012; Mansky et al., 2012). Even without further preparation, the collection is large enough, and contains enough information, to shed considerable light on a virtually unknown Early Mississippian terrestrial fossil record.

INSTITUTIONAL ABBREVIATIONS

The following list of abbreviations are used to denote institutions that are referred to in the text of this report: BWC, Barry Cameron Collection, at the Blue Beach Museum; CM, Chris Mansky Collection, at the Blue Beach Museum; NSM, Nova Scotia Museum Collection, at the Blue Beach Museum; and YPM-PU, Yale Peabody Museum, Princeton University Collection.

LOCALITY DESCRIPTION

The coastal exposure at Blue Beach is almost 5 km in length, with relatively undisturbed sedimentary strata forming wide, wave-cut benches and tall cliffs that are prone to collapse when twice daily the tides on the Bay of Fundy lap at their bases (Fig 6). The larger-than-average tidal range in the area can exceed 17 m, and it is this powerful combination of moving water and waves that work to regularly expose most of the new fossil material.

The classic Horton Bluffs section of the type area (Fig. 2) is referred to as “Blue Beach” and “Blue Beach North” (Martel and Gibling, 1991). The southern arm of the sequence is Blue Beach proper, and is rich in fossils. Its approximate total length is 2 km, from the Blue Beach road access point to about midway along the exposure, to a point just below the Horton Bluff lighthouse. Strata from the upper part of the Blue Beach Member and the lower part of the Hurd Creek Member are exposed in the southern arm (Fig. 4). The northern arm is much shorter, at about 1.5 km in length: it has much lower cliffs, and produces fewer fossils than the southern section. The strata exposed in the northern arm are a repeat of the upper Hurd Creek Member beds seen in the southern section (Fig. 5). To the north, about 600 m beyond these main sections, a small outlier in the intertidal zone marks where the Horton Bluff Formation unconformably is overlain by the Upper Triassic Wolfville Formation (Dawson, 1868). To the south of the main sequence, the strata are sharply folded and faulted, and after a traverse of about 500 m come into disconformable contact with the overlying Cheverie Formation, of slightly younger Mississippian age (Martel, 1990). The two arms show a slight difference in character, but are very similar overall. The oldest strata are those located at the southern end of the sequence at Blue Beach Road, with gently inclining strata of the two arms becoming progressively

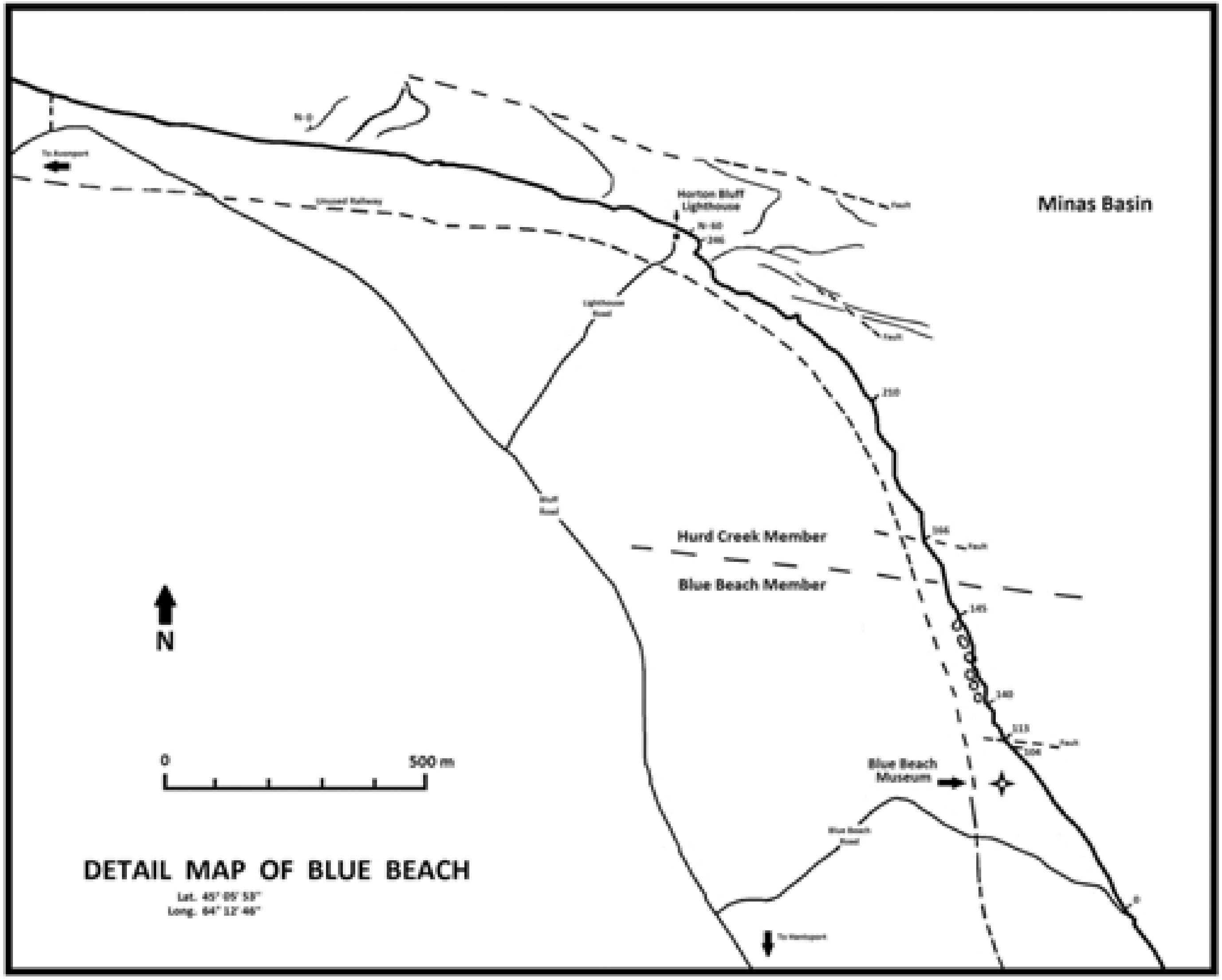

FIGURE 2. Map of the Blue Beach locality. See Figure 1 for location. Numbers correspond to meters in the Blue Beach section (Fig. 4). Numbers prefixed with the letter "N" correspond to meters in the Blue Beach North section (Fig. 5) (after Martel, 1990).

younger as they approach the middle, where they meet directly beneath the Horton Bluff lighthouse in a sharp synclinal axis (Bell, 1913).

GEOLOGICAL CONTEXT

At Blue Beach, strata of the Horton Bluff Formation are exposed along the western side of the Avon estuary (Dawson, 1868), with a total thickness of almost 250 m (Martel and Gibling, 1996). These strata are assigned to the shale-dominated Blue Beach Member, overlain by the sandier Hurd Creek Member (Fig. 3). These are strata of Tournaisian age (Utting et al., 1989). The depositional setting and paleoenvironmental conditions at the time of sedimentation are important considerations, as they influenced the preservation of the fossil record at the deposit. In order to understand scenarios leading to the preservation of these fossils, a review of the geological context is given here.

REGIONAL SETTING

In eastern Canada, the Horton Group was deposited in a series of east-west trending pull-apart basins that together form a larger composite basin, the Maritimes Basin (Martel, 1990). Deposition took place in half-grabens that had formed during a period of tectonic extension after the Acadian orogeny (Martel and Gibling, 1996). The subbasins occupy remnant lowlands separated by intervening highlands of basement rocks (Martel, 1990). The continental Horton Group of the Windsor subbasin (Fig. 3) is subdivided into the basal Horton Bluff Formation, which consists of conglomerates, sandstones, and shales, and the unconformably overlying Cheverie Formation of slightly younger age, composed of arkosic sandstones and pale green and chocolate-colored shales. The oldest Horton Bluff Formation strata in the Windsor subbasin were dated using miospores as Upper Devonian in age, and represent some of the oldest sediments in the Maritimes Basin (Martel et al., 1993).

The Horton Group of the Windsor subbasin rests unconformably on the Cambro-Ordovician basement rocks of the Meguma Group, which are composed of gray slates and light brown metagraywackes, which have been intruded by granites of the South Mountain batholith (dated to about 370 Ma: Worth, 1969), and is in turn overlain by the marine Windsor Group, mainly composed of evaporites and carbonates of Viséan age.

The present day Windsor subbasin is bounded on the north by the Cobequid-Chebucto fault, a large dextral strike-slip fault that formed between the Meguma and Avalon terranes after the Acadian orogenic event; and bounded on the south by the Meguma landmass. The maximum thickness of the Horton Bluff Formation is about 1025 m (Martel and Gibling, 1991), but the formation thins as it approaches the southern

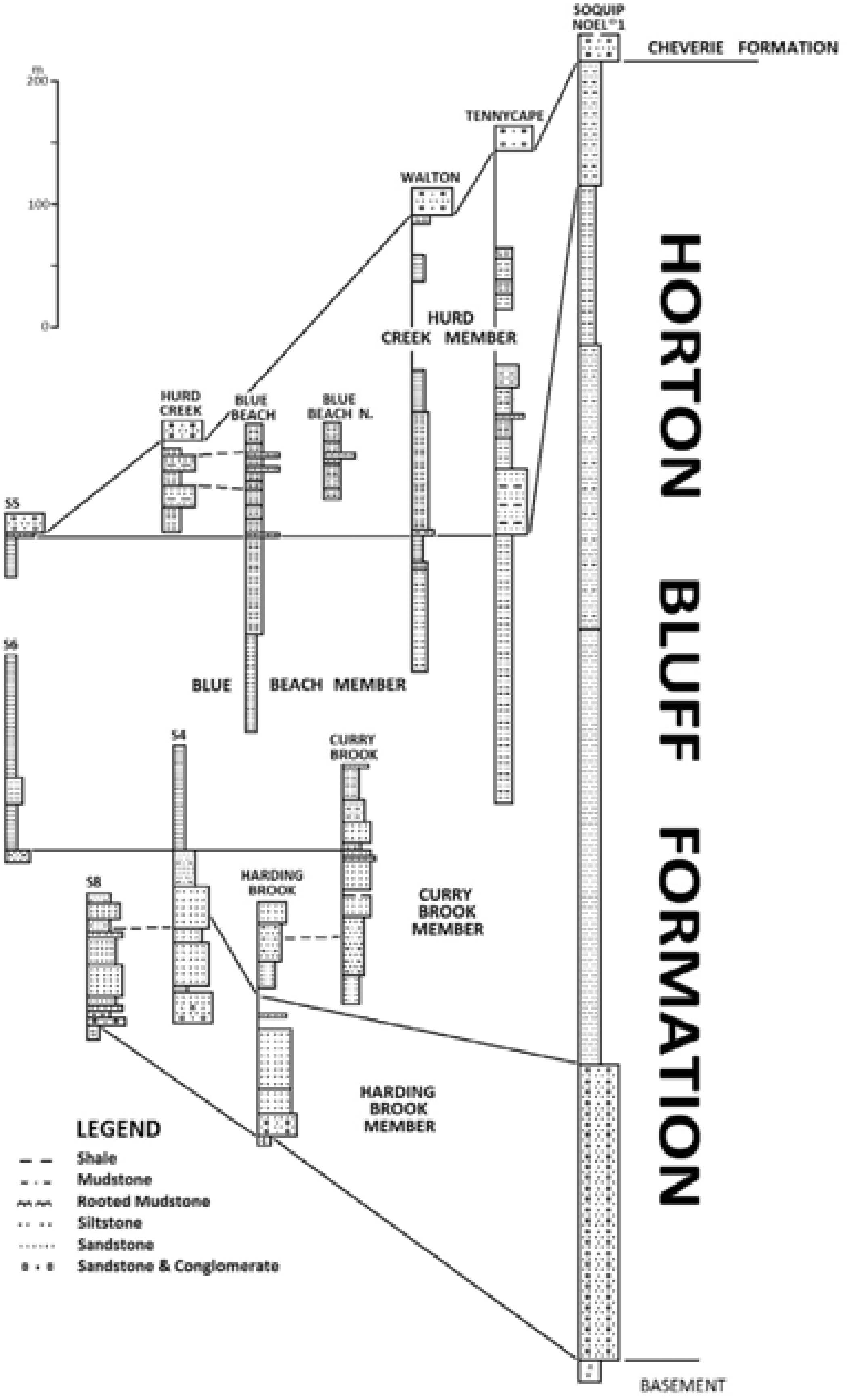

FIGURE 3. Geological cross-section of the Horton Bluff Formation in the Windsor subbasin. Saarburg drill holes S4, S5, S6 and S8 are located just west of Upper Falmouth (see Moore and Ferguson, 1986), while the Soquip #1 well is northeast of Kennetcook (after Martel and Gibling, 1996).

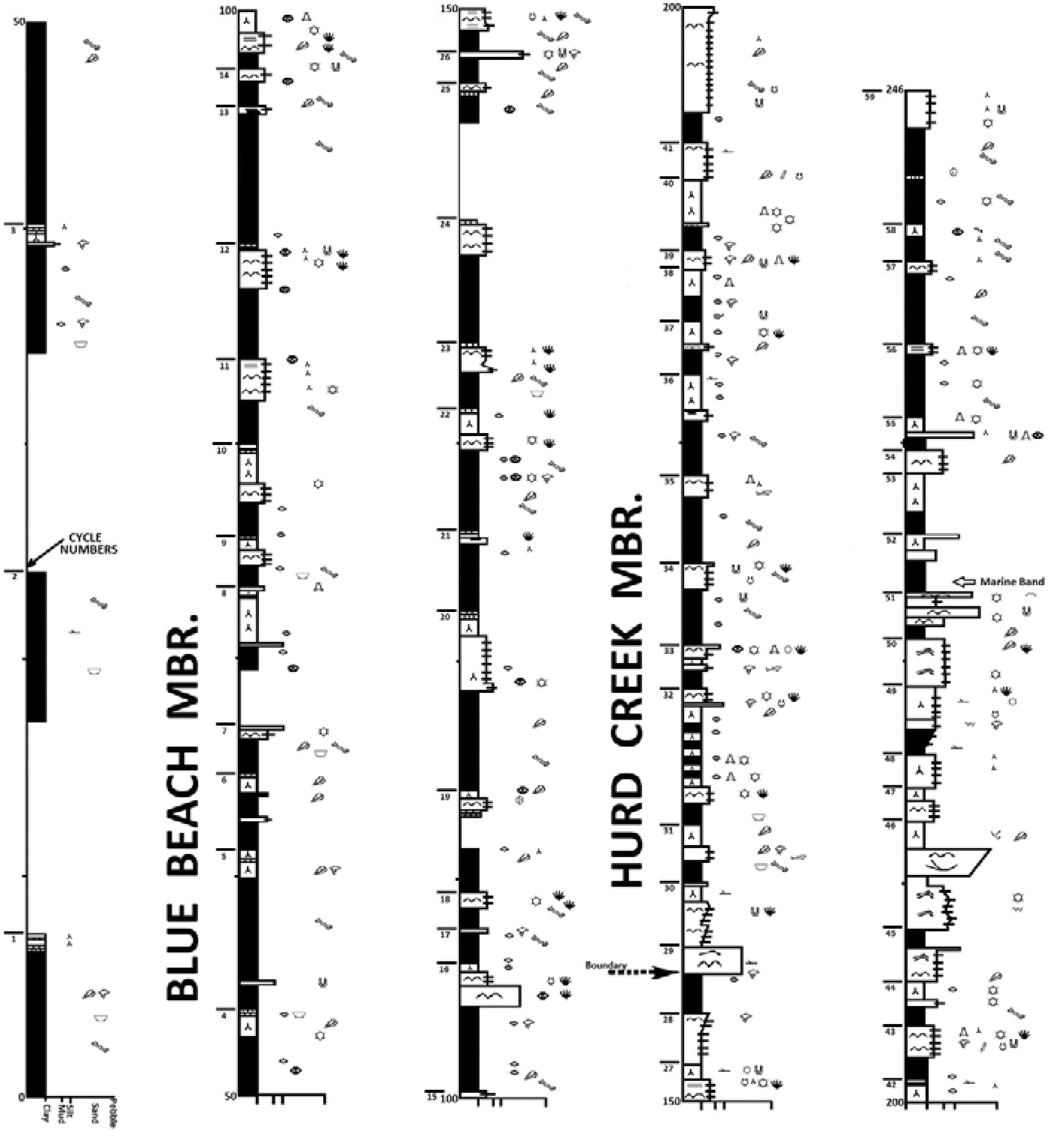

FIGURE 4. Lithologic log of the Blue Beach section. See Figure 2 for location and Figure 5 for legend (modified after Martel and Gibling, 1996).

margin of the subbasin to about 730 m in the type area (Tibert and Scott, 1999), where it unconformably overlies the Meguma highlands just south of Blue Beach. Most of the Horton Group sediments were deposited within intermontane valleys; however, the Blue Beach deposits formed on the continental margin of the Meguma (Gondwanan) terrane, in nearshore settings of a large, open body of water (Martel, 1990).

LITHOSTRATIGRAPHY

Important studies on the sedimentology and stratigraphy of the Horton Bluff Formation at Blue Beach have been completed by Bell (1921, 1929, 1960), Hesse and Reading (1978), Martel (1990), Martel and Gibling (1991, 1994, 1996) and by Tibert and Scott (1999). A number of theses and dissertations on the stratigraphy of certain parts of the map area also appeared (Crosby, 1951; Murray, 1960; Worth, 1969; MacDonald, 1973), but conflicting results necessitated the thorough reassessment by Martel (1990). A reappraisal of the earlier stratigraphic studies is beyond the scope of the present article: unless otherwise noted, the following interpretations are taken from Martel and Gibling (1991, 1994, 1996).

The Horton Bluff Formation was long believed to be strictly

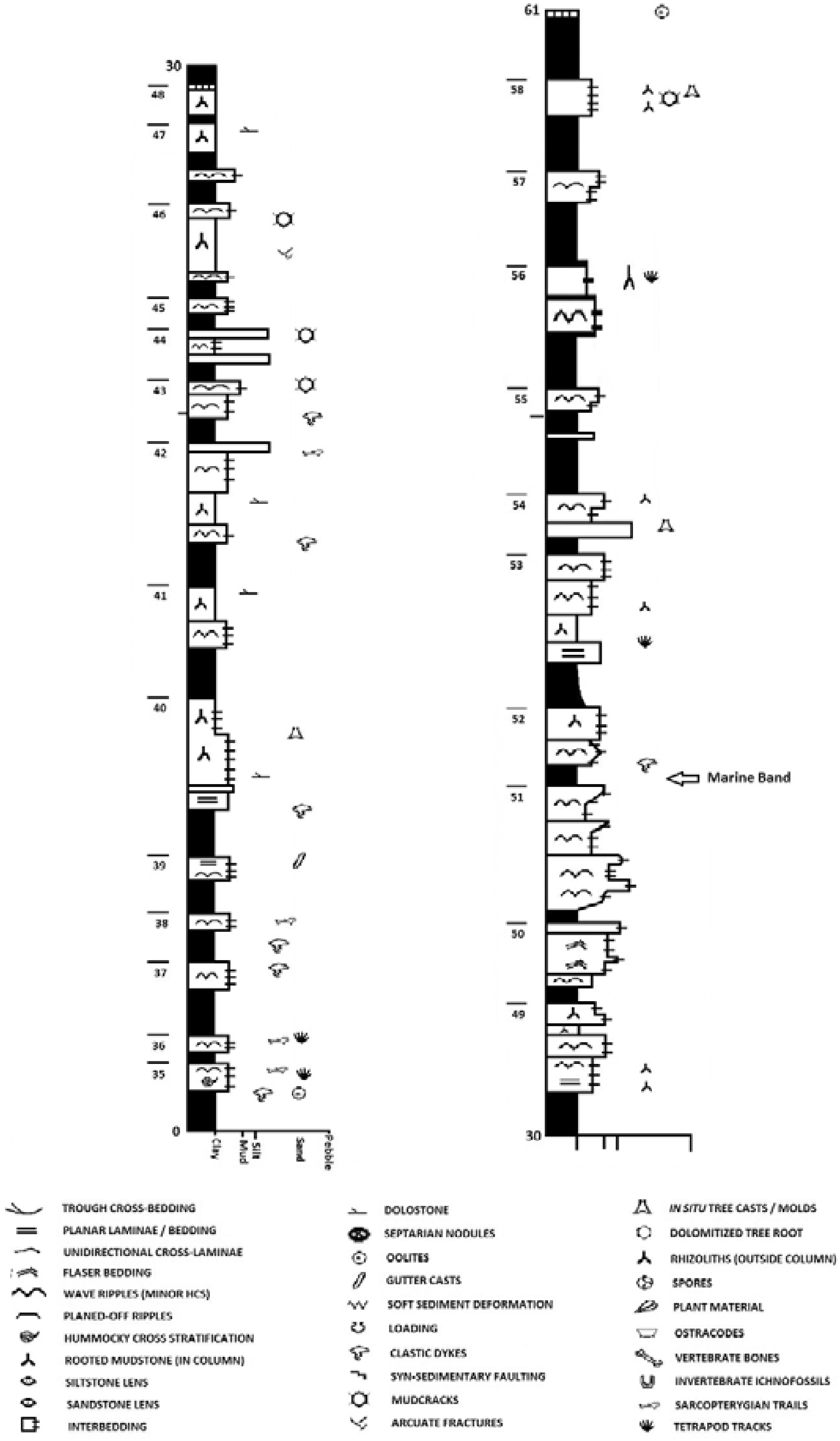

FIGURE 5. Lithologic log of Blue Beach North section. See Figure 2 for location (modified after Martel, 1990).

lacustrine in origin (i. e., a freshwater lake – Bell, 1929, 1960; Hesse and Reading, 1978; Martel, 1990; Martel and Gibling, 1991), but then was understood to have been at least periodically brackish; either a sizeable lagoon or a restricted marine bay with periodic connections to the sea (Tibert and Scott, 1999). A newly-discovered "marine band" (reported here) is the first confirmation of fully marine conditions, and probably represents a major transgression event in the Tournaisian of the Maritimes Basin.

FACIES DESCRIPTIONS

The Horton Bluff Formation strata (Figs. 3-5) consist of upward-coarsening cycles, representing repeated sedimentation and subsidence (Martel, 1990; Martel and Gibling, 1991, 1996) in the Windsor subbasin of the larger Maritimes Basin (Williams, 1974; Martel, 1990). The cycles contain four facies: (1) gray clay shales, overlain by (2) gray planar siltstones and wave-rippled planar sandstones, which, in turn are usually overlain by (3) greenish mudstones that are heavily pedoturbated, and contain a large number of *in-situ* tree casts and detached stems (Bell, 1960; Martel and Gibling, 1991). The greenish mudstones are often overlain by (4) nodular or bedded dolomitic beds, marking the top of "one cycle" (Martel and Gibling, 1991). Cycles are asymmetrical and range from 1-12 m thick in the Blue Beach Member, and 1-6 m thick in the Hurd Creek Member (Martel, 1990). The facies descriptions outlined by Martel and Gibling (1991) are modified here, with revisions of the associated ichnotaxonomy.

Facies 1, gray shales: mainly clay-rich, gray to black, evenly-splitting fissile clayshales and claystones. Less common mudstones typically alternate with the clayshale intevals. Units can contain occasional medium-coarse lags of sandstone grains, and rich fossiliferous interbeds of plant material, ostracods, conchostracans, fish scales and bones, coprolites, or reworked duricrust fragments. Units also occasionally contain siltstone or sandstone lenses. Cycles typically begin with intensely bioturbated strata (*Palaeophycus*), and coarsen upwards. Uncommon *Taenidium* are associated with the *Palaeophycus* beds.

Facies 1 beds are interpreted as having formed from suspension clouds of sediment deposited in a quiet environment. The low organic content suggests aerobic conditions existed periodically, but anaerobic or dysaerobic conditions prevailed. Occasional fossil-rich beds are viewed as storm-related reworked material. Deposition is inferred to have occurred in moderately deep water (Martel and Gibling, 1991).

Facies 2, alternating sandstone, siltstone and clayshale: mainly siltstone and sandstone beds, often forming composite bed sets up to 60 cm thick, with beds commonly separated by thin clayshale interbeds and/or erosional surfaces. Siltstones and sandstones are fine-grained, quartzose, and moderately well sorted. Shallow-water and subaerial structures are common, including desiccation cracks, raindrop imprints, wave ripples, scratch circles, rhizoliths, and a variety of vertebrate and invertebrate ichnofossils.

Subfacies 2a, hummocky cross-stratified siltstone (HCSS): mostly siltstone, with some sandstone beds occurring in single beds or thin bedsets; many of which contain hummocky cross-stratification (HCS) up to 40 cm thick. HCSS beds generally contain parting laminae consisting of thin clayshale and/or mica that are neither flat nor wave rippled. Beds and bedsets typically occur deposited in elongate, low-angle scours and contain tool marks, loads, major or minor lags of fossil material, and rare gutter casts. Some of the siltstone and sandstone beds occur as regularly spaced hummocks up to 600 cm long by 300 cm wide, connected by thin beds (at most) between other lenses at the same stratigraphic level. Otherwise, clayshale beds separate most of the beds and bedsets. The most continuous and coarsest sediments in subfacies 2a occur rarely, and consist of relatively thick (up to 10 cm) beds of fine-grained planar-laminated sandstone. Clastic dikes are usually present, and subaerial features are rarely seen. Ichnofossils in subfacies 2a are predominantly preserved as convex hyporeliefs on the undersides of siltstone and sandstone beds, and include *Rusophycus*, *Cruziana*, *Kouphichnium*, *Limulicubichnus* and *Planolites*.

HCS is generally believed to form under storm conditions where waves interact with the underlying substrate. The high-energy flows and subsequent rapid deposition produced by storms are reflected by the presence of tool marks and gutter casts, and by the increased bioturbation associated with the HCS beds (Gluszek, 1995). The laminated sandstones are seen to represent high energy flows or deposition from upper regime flows. Deposition is inferred to have occurred proximal to the wave-attenuated zone in medium-depth water (Martel and Gibling, 1991).

Subfacies 2b, wave-rippled sandstone: Very fine to fine sandstone and siltstone bedsets (5-20 cm thick) forming continuous layers. Beds may vary laterally in number and thickness throughout the deposit; lenticular-bedding or wavy bedding with complex erosional bases are characteristic. Beds themselves can vary in thickness, averaging 1 to 5 cm thick, and are fairly continuous to discontinuous. Siltstone and sandstone bedsets are typically separated by 2-10 cm thick clayshale-rich bedsets, often interbedded with thin siltstone lenses and layers. Rare planar-laminated, fine-grained sandstone beds up to 10 cm thick are the thickest beds in the subfacies. Wave ripples, desiccation cracks, bio-and pedo-turbation are common, especially near the tops of units. Ichnofossils include *Cruziana*, *Diplichnites*, *Diplopodichnus*, *Gordia*, *Kouphichnium*, *Limulicubichnus*, *Palaeophycus*, *Paleohelcura*, *Planolites*, *Rusophycus*, and moderately abundant tetrapod footprints.

Subfacies 2b sedimentation patterns are attributed to decreasing deposition as storm conditions calmed, with the coarser rippled and lenticular beds deposited beneath relatively high-energy waves, followed by clayshale intervals representing significant periods of deposition by suspended sediments (Martel and Gibling, 1991). Deposition is inferred to have occurred in shallow water.

Subfacies 2c, planar-bedded siltstone: Predominantly composed of tabular siltstones (10-60 cm thick) and less frequent sandstones (1-15 cm thick), that are typically continuous for long distances; the thickness of individual beds generally undergoes only slight variation. Planar-stratified sandstone beds (3-15 cm thick) also occur rarely. Clayshale beds averaging 2-5 cm thick separate the siltstones and sandstones. In general, most of the siltstone and sandstone beds display planar laminae and minor cross laminae internally; most tend to fine upwards, but in rare cases some coarsen upwards. Some beds grade into bioturbated clayshale at their tops, and have associated shallow water de-watering structures or wave ripples. Many of the bedsets contain subaerial features in their top few beds, including desiccation cracks, mini-ripples, rhizoliths, tree casts, plant debris, or rooted *Archaeocalamites*. Ichnofossils include *Cruziana*, *Diplichnites*, *Diplopodichnus*, *Kouphichnium*, *Palaeophycus*, *Paleohelcura*, *Planolites*, *Rusophycus*, abundant tetrapod footprints, and *Undichna*.

Subfacies 2c is interpreted as shallow water to subaerial conditions, with deposition of siltstones and sandstones under storm conditions, mainly by wave trains shoaling over low-relief beaches, and with later suspension clouds depositing the common clayshales (Martel and Gibling, 1991). The development of plant communities near the tops of bedsets may have acted to reduce incoming wave energy, leading to increased sedimentation, usually resulting in clayshale development immediately after plant colonization.

Facies 3, greenish mudstones: Mostly olive-gray to greenish-gray mudstone and silty mudstone. Units with laminated calcareous siltstone and sandstone beds are usually present. Erect tree stem molds and casts, and root casts of *Lepidodendropsis* and *Archaeocalamites* are common. Pedoturbation and desiccation cracking are more intense near the tops of units.

Facies 3 is interpreted as deposition within a coastal marsh where subaerial conditions prevailed, with siltstones and sandstones deposited during the larger storms (Martel and Gibling, 1991; Tibert and Scott, 1999).

Facies 4, nodular or bedded dolomites: Not including minor nodular or lenticular dolomites in the deposit, three subfacies can be seen within this facies: (4a) continuously-bedded, vertically-splitting planar

TABLE 1. Floral and faunal list for the Horton Bluff Formation (most of the following derived from Brazeau, 2004; Mamet, 1995; Martel, 1990; Tibert and Scott, 1999; Utting et al., 1989, and from the collections of the Blue Beach Museum).

PLANTS (excluding miospores)

- *Lepidodendropsis corrugata*
- *Lepidophyllum* (*Lepidostrobophyllum*) *fimbriatum*
- *Archaeocalamites* (*Asterocalamites*) *scrobiculatus*
- *Aneimites acadica*
- *Diplotnema patentissimum*
- *Carpolithus tenellus*
- *Genselina* sp. (Pat Gensel, pers. comm. 2005)
- Unidentified lycopsid(s)

ALGAE

- *Hortonella uttingi*

NON-MARINE INVERTEBRATES

- *Spirorbis avonensis*
- *Copelandella novascotica*
- *Shemonaella scotoburdigalensis*
- *Shemonaella tatei*
- *Chamishaella* sp.
- *Cavallina scalpellus*
- *Cavallina* sp.
- *Carbonita rankiniana*
- *Carbonita scalpellus*
- *Bairdiacypris striatiformis*
- *Bairdia* sp.
- *Geisina* sp.
- *Youngiella* sp.
- *Paraparchites* sp.
- *Carbonita* cf. *subdula*
- *Eoleaia leaiaformis*
- *Eoleaia leavicostata*
- *Trochammina* sp.
- *Ammotium* sp.
- *Ammobaculites* sp.
- *Ammodiscus* sp.
- reticulated spheres (encysted eggs?)
- algal Bodies
- bivalves?
- *Euproops* sp.
- Possible diplopod (millipede)

MARINE INVERTEBRATES

- indet. trilobite
- indet bivalve / brachiopod
- indet. ?ammonoid ?cf. *Gonioceras*

FISH

- *Elonichthys* cf. *brownii*
- *Rhadinichthys* sp.
- *Canobius* sp.
- *Letognathus* (*Strepsodus*) *hardingi*
- ?*Ctenodus* sp.
- *Gyracanthides* sp.
- *Gyracanthus* sp.
- ?*Climatius* sp.
- Acanthodidae sp. indet.
- ?*Ctenacanthus* sp.
- ?indet. ctenacanthid

TETRAPODS

(1) unnamed *Acanthostega*-like tetrapod
(2) unnamed crassigyrinid
(3) unnamed colosteid
(4) unnamed *Eoherpeton*-grade embolomere
(5) unnamed whatcheeriid

dolomite (5-10 cm thick), sometimes containing peloids, and some beds with layers rich in organic material; (4b) continuously bedded massive dolomites (10-40 cm thick) that fracture randomly; rhizoliths are fairly common; this subfacies is usually associated with either facies 1 or some shallow-water sediments of facies 2; and (4c) nodular dolomites, which occasionally form almost continuous layers, generally occurring near the top of facies 3 beds; rhizoliths are common; laminations are rare and have an algal-like morphology.

Subfacies 4b and 4c are believed to have formed within the muds by carbonate precipitation through the porous sediments (Martel and Gibling, 1991). Subfacies 4a is associated mainly with shallow-water strata, but offshore, probably in the groundwater zone. Subfacies 4c nodular formations are interpreted as pedogenic duricrusts, typically forming in the vadose zone.

DEPOSITIONAL ENVIRONMENT

The sedimentology and cycle-stratigraphy of the Blue Beach section suggest that it exposes nearshore sediments that formed on the continental margin of a large, hydrologically open body of water. Storm-generated wave energy is believed to have transported most of the sediment into the vicinity of Blue Beach, a mode of deposition that clearly influences the style and content of sedimentation (Martel and Gibling, 1991, 1994). The source of the sediment was from the south to southeast, confirmed by both the paleocurrent data and the heavy-mineral studies, indicating the sediment was derived from the Central Meguma platform of Nova Scotia (Worth, 1969). Relatively few deltaic sequences are present, mostly occurring in the Hurd Creek Member. The sediments otherwise appear to have been usually supplied by nearby, large deltaic systems (Martel and Gibling, 1991). These sediments were transported

TABLE 2. Ichnofaunal list for the Horton Bluff Formation (most of the following information derived from Lucas et al., 2004, 2010a, b; Mansky et al., 2012).

INVERTEBRATE ICHNOFOSSILS

Arborichnus
Cruziana problematica
Diplichnites gouldi
Diplopodichnus biformis
Gordia
Kouphichnium
Limulocubichnus
Palaeophycus
Paleohelcura tridactyla
Planolites
Protichnites
Rusophycus carbonarius
Skolithos

INCERTAE SEDIS ICHNOFOSSILS

Taenidium

VERTEBRATE ICHNOFOSSILS

Attenosaurus
Batrachichnus
Ctenerpeton
Hylopus
Palaeosauropus
Pseudobradypus
Undichna britannica
Undichna isp. (lg. form)
unnamed sarcopterygian traces

BROMALITES

unnamed large cololites
Coprolites
  (1) ovoid pellets
  (2) elongate pellets
  (3) twisted pellets
  (4) regular 'wrinkled' masses
  (5) irregular flattened masses
  (6) irregular non-flattened masses

laterally along the shore by the wave-generated currents, or longshore-drift. The cumulative evidence of the sedimentology, with the lack of articulated remains, led to the conclusion that vertebrate material was mainly deriving from nearby habitats and that the majority of the vertebrate remains had been reworked (Dilkes et al., 1995). The relatively unworn condition of the fossil bones in this scenario suggested the initial burial sites were not far from Blue Beach, while the completeness of their disarticulation implied decomposition and the work of scavengers prior to transport.

However, we find shortfalls in this model used to explain vertebrate bone accumulations in the Blue Beach section. The above scenario presumes the vertebrates decomposed, disaggregated, and their isolated or partially articulated remains were later transported to burial sites like Blue Beach. However, cumulative ichnological evidence from many of the sequences demonstrates that vertebrate and invertebrate animals were often present at Blue Beach, with ichnofossils and bone beds occasionally mere centimetres apart. While some of the bones could have been derived from nearby deltaic settings, this adjacent ichnological evidence suggests that localized populations also supplied some of these bones, so normal opportunities for the preservation of articulated skeletal remains should have occurred more frequently. Sedimentological evidence demonstrates the shoreline sediments were often eroded and winnowed in the initial phases of large storms (Martel and Gibling, 1991), which could in part help explain the organic-rich and disturbed nature of the storm-produced bedsets, without implying that all of their organic content was derived from distant sources. The dominantly storm-generated sedimentary environment at Blue Beach was not a gentle place of deposition, which may have helped to ensure most of the skeletal remains eventually became disarticulated.

Supportive evidence of storm activity can also be seen to have influenced the biodiversity and biodensity of ichnoassemblages, as precipitation leads to increased nutrient influx from the land, which enters the main body of water, which is being re-oxygenated by larger-than-normal waves. The subsequent increase in biotic activity can be detected by increased ichnoassemblages in the intervals immediately following the storm sequences (Gluszek, 1995).

MACROFLORA

The Horton Bluff Formation macroflora is a typically Tournaisian paleoflora, with the plants mainly preserved as compression/impression fossils. Plant macro-fossils from the Horton Bluff Formation were originally studied by Dawson (1863, 1868, 1873a), and later by White (1913) and Bell (1929, 1960). Ongoing studies on the forested wetlands have been added by Melrose and Gibling (2003) and Rygel et al. (2006). The lycopsid *Lepidodendropsis corrugata* (CM 20300: Fig. 7A) is the most common form – with abundant bark impressions, pith-casts and erect stems, or as scarce fructifications or foliated branches. Somewhat less common, *Archaeocalamites* (CM 20200: Fig. 7B), proto-*Stigmaria* (CM 20217: Fig. 7C), and *Diplotnema* (CM 20258: Fig. 7D) were also important floral components.

The new collection of plant fossils from Blue Beach encompasses several forms not described by Bell (1960). These include bark morphotypes that appear not to belong to the genus *Lepidodendropsis* (CM 20208: Fig. 7E), a few unreported small pteridosperms and sphenophytes, and several unreported fructifications. Also, the presence of minor quantities of coal and several beds containing small pieces of fossilized charcoal (fusain) have been largely ignored by previous studies. Further investigation of this paleoflora will doubtless prove rewarding, as these are amongst the earliest *in-situ* forested wetlands known in the fossil record.

The fusain appears to represent the wood of burnt gymnosperms, and these presumably grew in dryer upland areas (Chaloner and Cope, 1982; Scott and Jones, 1994). The implications of the fusain occurrence are important for several reasons. Fusain is known to preserve discrete cellular structures, and to provide details on plant-tissue morphology not typically preserved in compression floras (Scott, 1989). Fusain is known from the Devonian onwards, and the reason for the plant material to have become burnt is generally accepted as ancient wildfires (Chaloner and Cope, 1982; Cope and Chaloner, 1980, 1985; Scott and Jones, 1994; Scott and Glasspool, 2006). However, to sustain wildfires, oxygen concentration in the atmosphere could not have dropped below 60-percent of what it is today (Cope and Chaloner, 1980). Evidence of fusain occurrences from the Devonian onwards thus is increasingly in conflict with models depicting a significantly reduced Early Carboniferous concentration of atmospheric oxygen (Cope and Chaloner, 1985; Berner, 2006; Ward et al., 2006; Smithson et al, 2012).

FIGURE 6. One view of some of the shoreline exposures at Blue Beach of part of the Hurd Creek Member of the Horton Bluff Formation.

MICROFLORA

Plant miospores of the Horton Bluff Formation have been studied by Hacquebard (1957, 1972), Playford (1963), Utting (1987), Utting et al. (1989), Martel et al. (1993), and Glasspool and Scott (2005). The miospore assemblage has also been reviewed in the context of other global occurrences of Lower Carboniferous assemblages (Clayton, 1985). The rich miospore assemblage of the Windsor subbasin indicates a far greater diversity of plants were present than the Horton Bluff Formation macrofossil record would suggest (Glasspool and Scott, 2005).

Some confusion now exists, however, regarding the affinities of the putative miospore *Triletes glaber* (Dawson, 1868). Recent inspection has cast doubt on these being actual plant spores (CM 21002: Fig. 7F): they do not have the correct morphology for megaspores (E. L. Zodrow, pers. comm. 2011), and their petrographic signature is not consistent with that of plant life, but may be closer to those given by invertebrate fossils (A. C. Scott, pers. comm. 2010); though no particular invertebrate group has been suggested. At Blue Beach, the *Triletes* are very abundant, sometimes occurring in countless numbers within certain beds. There appear to be at least five morphotypes, and these commonly occur "similarly-oriented" (either "convex side up" or "concave side up") (A. C. Scott, pers. comm., 2010). Suspicion that these may be egg-cases or ovules has subsequently been raised by one of the authors (CFM).

Numerous algal bodies have also been found in some of the cycles (Tibert and Scott, 1999), and one report of a new genus and species of green algae in a thin-section from Blue Beach has surfaced (Mamet, 1995), but no detailed study of algal bodies or structures has been done. Newly-recognized stromatoporoid mounds at Blue Beach are now being studied, as are some of the microbially-induced sedimentary structures and algal mats (M. Gibling, pers. comm.; 2010, 2012).

NONMARINE INVERTEBRATES

Ostracods are by far the most common invertebrates in the Horton Bluff Formation (CM 40052: Fig. 8A), and were first discussed by Jones and Kirkby (1884), and by Dawson (1897). The first formal descriptions came much later (Bell, 1929, 1960; Bless and Jordan, 1971), who assigned the ostracods to several taxa, which are revised in light of some lingering problems with the Carboniferous ostracod nomenclature (Tibert and Scott, 1999). Dawson (1868) noted problems with the interpretation of the Horton Bluff ostracods as strictly lacustrine, because many of the same species occur alongside marine microfossils in the British and Scottish Carboniferous strata. Bell noted the resemblance of the Blue Beach ostracods to brackish-marine assemblages of western Europe (Bell, 1929), but nonetheless believed the Horton Bluff ostracods represented forms that were specially adapted to fresh water. Bell (1960) went on to describe an invertebrate fauna that included *Spirorbis*, ostracodes, and estheriids from Blue Beach.

Carroll et al. (1972) added the limuloid *Euproops* to the assemblage, and speculated that the formation may possibly have been brackish occasionally. The discovery of foraminifers (i.e., *Trochammina*, *Ammotium*, *Ammobaculites* - coastal-marsh indicators) in facies 3 strata among numerous erect tree stems signaled marginal-marine conditions; that the deposition at Blue Beach was probably at the shores of a large lagoon or sheltered marine bay, with periodic connections to the sea (Tibert and Scott, 1999). Besides the forams, Tibert and Scott reassessed and identified a rich assemblage of ostracods and estheriids (Table 1). They found large populations of species with brackish or marginal-marine affinities, and correspondingly low numbers of typical lacustrine species, further suggesting unstable salinities controlled the ostracod populations at times.

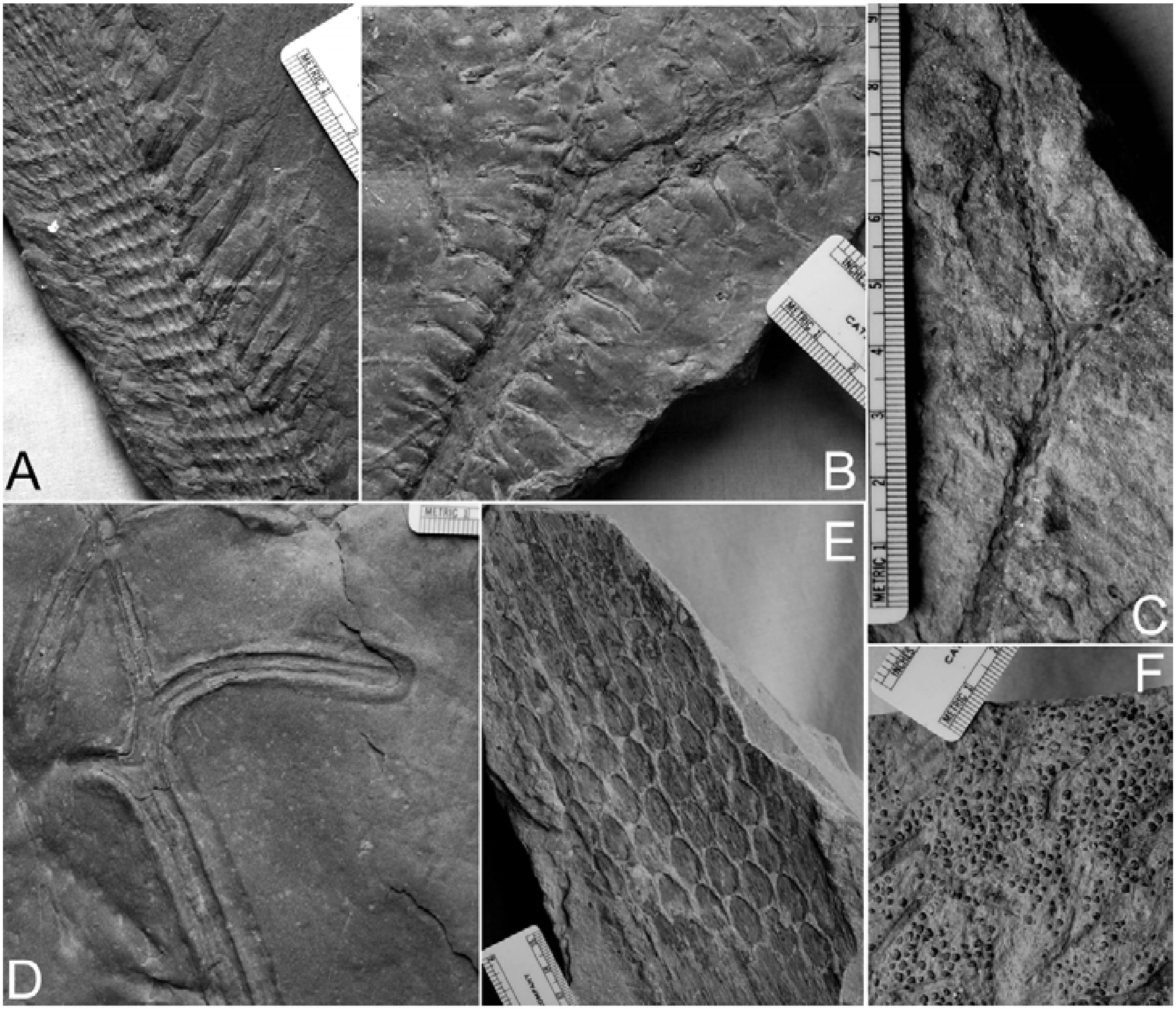

FIGURE 7. Fossil Flora. **A**, CM 20300, *Lepidodendropsis corrugata* (in black silty-shale) from Horton Bluff Formation, Lockartville, NS. **B**, CM 20200, *Archaeocalamites* sp.; Blue Beach Member, in greenish-gray planar-bedded siltstone ("Horizon 33b") (coll. by Ronnie Van Domelin). **C**, CM 20217, Natural mold of proto-*Stigmaria*; Hurd Creek Member, in pale quartzose sandstone. **D**, CM 20258, Impression of rooted-*Diplotnema* sp.; Blue Beach Member, in gray, fine-grained siltstone. **E**, CM 20208, Impression of an undetermined lycopsid; Blue Beach Member, in pale quartzose sandstone. **F**, CM 21002, "*Triletes glaber*" in association with carbonized plant fragments; Blue Beach Member, in greenish, silty-mudstone.

Newly discovered invertebrate fossils in the collections of the Blue Beach Museum can help to broaden our understanding of early terrestrial ecosystems, as some constitute the only examples in the continental Tournaisian record. The only macroinvertebrate body-fossils known from the deposit were those of limulids (CM 9483: Fig. 8C) referable to the genus *Euproops* (Carroll et al., 1972). Large terrestrial arthropods are usually rare fossils at any Carboniferous deposit, but they are especially so at Blue Beach. An impression of a possible millipede (CM 10089: Fig. 8B) has now been recovered (Lerner et al., this volume). Large examples of the arthropod trackways *Diplichnites* and *Diplopodichnus* have been seen in the collections for many years; which suggested millipede-like arthropods were present at Blue Beach. The ichnoassemblage indicates yet more invertebrate taxa await discovery. The ichnofossil *Paleohelcura* is present, potentially indicating terrestrially-adapted scorpionids; while *Rusophycus* and *Arborichnus* are also present and indicate short-bodied trace makers.

Millipedes (Diplopoda) are very rare in the Early Carboniferous fossil record (Rolfe, 1980). They are seen as fully-terrestrial herbivores (Scott, 1984), therefore they occupied important roles in early terrestrial ecosystems. If the fairly large millipede-like finds from the Scottish and Canadian Tournaisian sites actually belong to millipeds, that would bring additional doubt upon the idea that atmospheric oxygen levels had decreased significantly during Romer's gap (Berner, 2006; Ward et al., 2006).

The fine degree of preservation of the invertebrate remains at Blue Beach, however, suggests that acidification or other destructive influences were not responsible for the absence of fossils, so alternative reasons exist for the apparent paucity of macroinvertebrates. Aside from fluctuating water quality, less than optimal depositional circumstances in the wave-dominated environment probably contributed to the scarceness of macroinvertebrate body fossils in the deposit. Alternately, their preferred habitats may have been somewhat distant, meaning they were

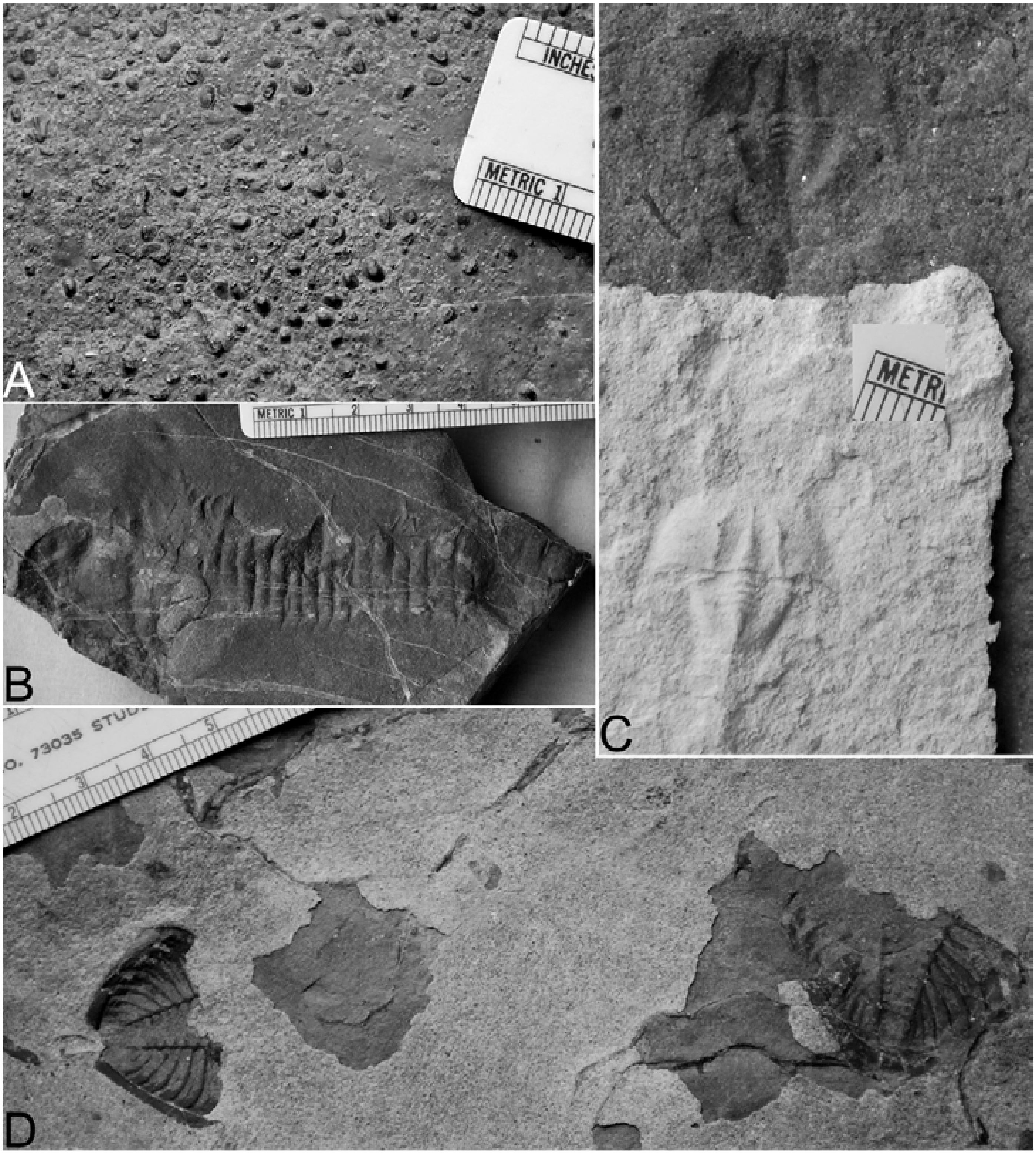

FIGURE 8. Invertebrates. **A**, CM 40052, Numerous ostracods; Blue Beach Member, in facies 1 gray siltstone. **B**, CM 10089, Impression of possibly a millipede in dorsal aspect, Blue Beach Member, in gray siltstone (coll. by Erin Fanning). **C**, CM 9483, Natural mold of *Euproops* sp. shown with its white latex rubber peel; Blue Beach Member, in pale quartzose sandstone (coll. by Ryan Hutt). **D**, CM 40072, Two trilobites in ventral aspect; Hurd Creek Member, in gray silty-mudstone (the "marine band," with thin, greenish-sandstone drape).

only occasionally transported into this area. Ichnological evidence of their presence on the Blue Beach strata suggests the latter scenario is unlikely.

MARINE INVERTEBRATES

We have collected a series of trilobite pygidia from a silty-mudstone bed in the Hurd Creek Member (CM 40072: Fig. 8D), very high within the Blue Beach sequence. The bed is very fine-grained and massive, about 20 cm thick. Associated shelly-fragments are also present. The close association of the trilobite molts, together with their fine state of preservation, does not appear to represent reworking, but rather implies the trilobites were at least temporarily occupying the region. Prior to this, no marine invertebrates were known from the Horton Bluff Formation. We refer to the thin horizon of the Hurd Creek Member that produces trilobite fossils as the "marine band" (Figs. 4-5).

The implied temporary colonization of the region by marine organisms is seen to represent a marine transgression, as the tectonic model of basin development (Martel and Gibling, 1991) does not explain a sudden shift to fullmarine conditions. Many other Horton Bluff Formation deposits contain deep-water sediments at the base of each shallowing-upwards cycle. Because it has proven so difficult to locate marine fossils in the formation anywhere before this, the isolated nature of the marine bed in the otherwise nonmarine beds probably represents a short-lived but maximum stage of transgression in the Tournaisian of the Maritimes Basin.

The Maritimes Basin has no record of a Late Tournaisian transgression (Martel, 1990, p. 4-5), but broader evidence indicates major transgression elsewhere (i. e., Roberts, 1985; Aisenverg et al., 1985). The "marine band" thus is important in helping to correlate the Maritimes Basin history with global models. The marine band may also prove invaluable for correlating the Horton Bluff Formation with better-known marine-Tournaisian records elsewhere, especially with those of Western Europe.

VERTEBRATE PALEONTOLOGY

Introduction

Fish fossils from Blue Beach were described in the past by several workers (Dawson, 1863, 1868, 1877, 1878; Woodward, 1890; Lambe, 1908, 1909, 1910; Zidek, 1977), and amphibian fossils by Carroll et al. (1972). New information on the Horton Bluff vertebrates has begun to emerge (Dilkes et al.,1995; Clack and Carroll, 2000; Cameron et al., 2000; Brazeau and Parker, 2004; Brazeau, 2005; Anderson et al., 2005, 2009; Scott et al., 2005; Brazeau and Jeffery, 2006), and the Horton Bluff material is often commented on as a comparison in other studies (i. e., Lebedev and Coates, 1995; Thulborn et al., 1996; Johanson et al., 2000; Warren and Turner, 2004; Clack and Finney, 2005; Parker et al., 2005; Turner et al., 2005; Smithson et al., 2012), but, most of the newly-collected material at the Blue Beach Museum is in need of review. Several new morphotypes of tetrapods are now known, albeit very incompletely, mainly from isolated bones. The fish fauna can also be seen to contain previously undescribed types.

The vertebrate fauna of the Horton Bluff Formation contains numerous taxa, including the earliest terrestrial tetrapods, whose association can been characterized as belonging to the "Mississippian Tetrapod Province" (Milner, 1993; Warren and Turner, 2004), but appears more transitional in containing both "Devonian-grade" tetrapods and obvious Carboniferous groups (Clack and Carroll, 2000). The fossil record of Mississippian tetrapods is very poor, most of it is of Late Mississippian-age and from nonmarine to marginal-marine environments of Eastern North America and Western Europe (Warren and Turner, 2004), and mostly restricted to an equatorial belt along the southern part of Euramerica (Milner, 1993; Thulborn et al., 1996). Milner's (1993) assessment of Mississippian tetrapod occurrences was made at a time when very few tetrapods or arthropods were known from the second half of the Mississippian, and absolutely none from the first half – "Romer's gap."

The less-understood Mississippian vertebrate assemblages are seen as distinct from assemblages of Devonian and Pennsylvanian deposits. The characteristic groups in such faunas usually include certain bony fishes (palaeoniscoids and sarcopterygians, especially dipnoans), Early Carboniferous freshwater sharks (elasmobranchs), acanthodian fishes (especially large gyracanthiids), and early tetrapods. Typical associated nonmarine invertebrates include ostracodes, spirorbid worms, and estheriids.

Tetrapod Fauna

After the Devonian-Carboniferous boundary, an approximately 25 million-year long interval has been referred to as "Romer's gap" (Romer, 1956; Coates and Clack, 1995). Encompassing the entire Tournaisian Stage, and the approximate first half of the Viséan, this interval has a notoriously-poor continental fossil record. It was named after Alfred Sherwin Romer, who first noted its particular absence of tetrapod fossils (Romer, 1941). At the time of his research, and for many years thereafter, not a single tetrapod body fossil was discovered within the gap.

The discovery of tetrapod bones at Blue Beach in 1966 by Donald Baird was the first indication of tetrapods within Romer's gap (Carroll et al., 1972). Tetrapod fossils are rare at Blue Beach, and these initial finds were just a few isolated bones (YPM-PU 19872, 20103, 20754). Field teams over the next three decades, mainly those from McGill University's Redpath Museum, contributed to the slowly growing collection of Blue Beach tetrapod fossils (Dilkes et al., 1995). In a short paragraph, a few of these Redpath collection tetrapod bones were discussed, and then almost as if to say farewell, the following pronouncement was made: "the nature of deposition is such that it may never yield more than tantalizing, disarticulated remains" (Clack and Carroll, 2000). This has proven not to be the case. A new collection of Blue Beach fossils, one that dwarfs other registered collections of Blue Beach material, includes dozens of important, articulated specimens (i. e., Figs. 10A, B, E).

None of the tetrapod material from the Horton Bluff Formation has received formal identification. Initial finds were believed at first to belong to "anthracosaurian"-grade tetrapods (Carroll et al., 1972), and later simply referred to as "reptiliomorphs" (Clack and Carroll, 2000). The first indication of tetrapod diversity in the Tournaisian was a second morphotype of humerus (discovered at Cambridge Flats, another locality in the same formation) later attributed to an early colosteid (Dilkes et al., 1995; Clack and Carroll, 2000). A third taxon was implied by the discovery of a scapulocoracoid that compares in some aspects with the Devonian tetrapod *Ichthyostega* (Clack and Carroll, 2000), a characterization later shifted to "an *Acanthostega*-like tetrapod" in consideration of additional limb elements (Anderson et al., 2009). Other isolated bones in the Redpath Museum, and readily-comparable whatcheeriid remains from Australia, led to suggestions that at least some of the "reptiliomorph" material from Blue Beach is probably whatcheeriid (Warren and Turner, 2004). But, with so few bones it soon became clear that progress in understanding the Blue Beach tetrapods was going to be very slow.

The eventual recovery of the first complete pelvis (Anderson et al., 2005), displaying several diagnostic traits of the Whatcheeridae (NSM 005.GF.045.001), confirmed their existence. These are the earliest reported whatcheeriid remains (Bolt et al., 1988; Bolt and Lombard, 2000; Lombard and Bolt, 1995; Warren and Turner, 2004; Clack and Ahlberg, 2005), slightly older than *Pederpes* from Scotland (Clack and Finney, 1997, 2005). The most recent report (Anderson et al., 2009) gives a preliminary analysis of tetrapod limb, girdle, and jaw material (including a number of specimens from the Blue Beach Museum collection). The tetrapod fauna is characterized as having an Acanthostega-like tetrapod, early colosteids, an *Eoherpeton*-grade embolomere, a whatcheeriid, and possibly a baphetid or *Crassigyrinus*-like tetrapod. Also, the first of several "associated" tetrapod fossils from the deposit was announced as belonging to an embolomere. The full analyses of these studies have not

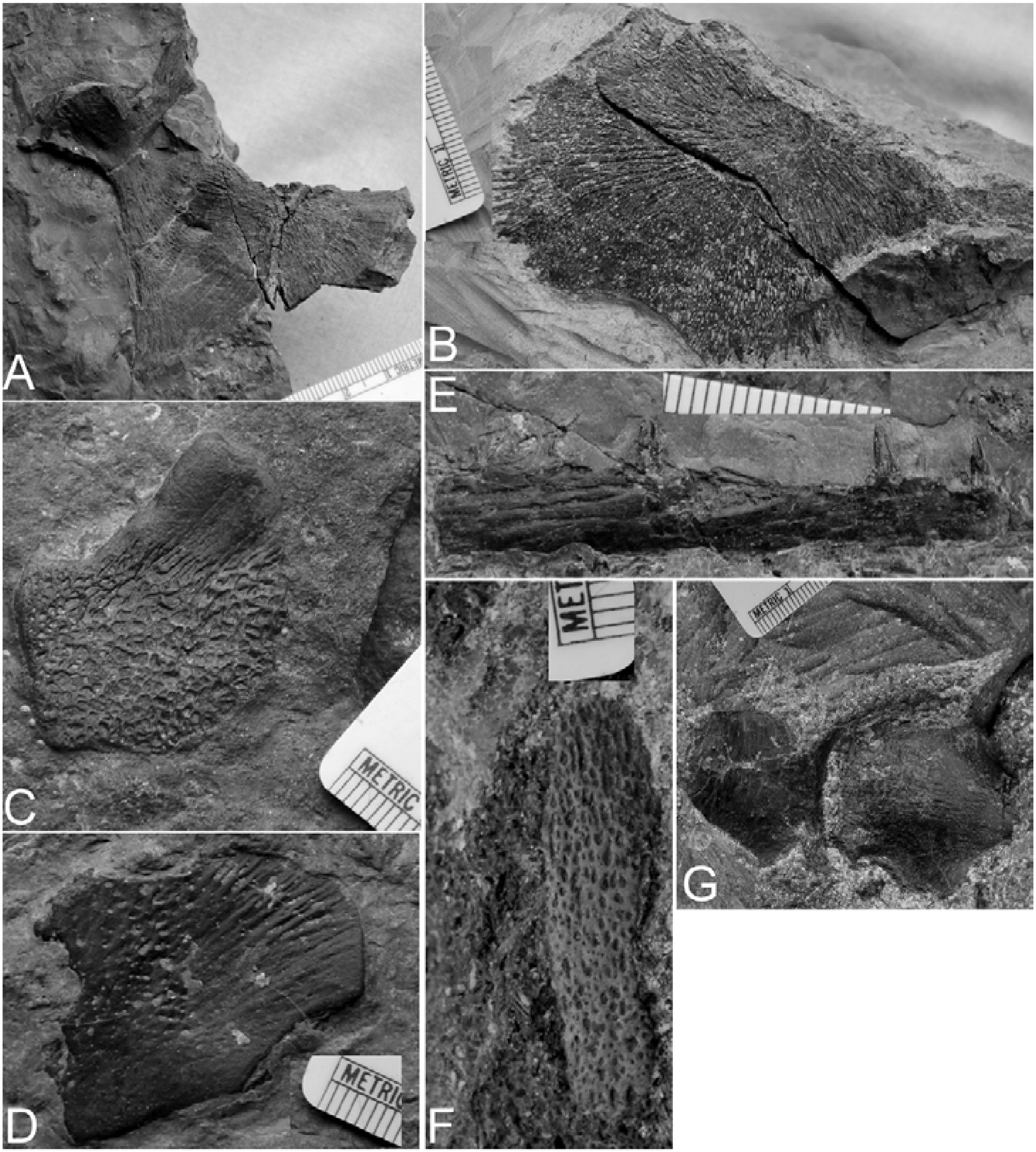

FIGURE 9. Stem tetrapods. **A**, CM 10071.1, Crassigyrinid tetrapod pelvis in medial view; Hurd Creek Member, in silty-sandstone. **B**, NSM 005.GF.045.310-A, Interclavicle of crassigyrinid tetrapod in ventral view; Hurd Creek Member, in gray siltstone. **C**, NSM 005.GF.045.321, Tetrapod cranial bone in dermal view, showing ornament of prominent pits; Hurd Creek Member, dark quartzose sandstone ("theta bonebed"). **D**, CM 10134, Tetrapod cranial bone in dermal view, showing smooth ornament of pits and ridges; Hurd Creek Member, greenish facies 3 mudstone ("alpha bonebed"). **E**, CM 9148, Tetrapod dentary in labial view; Hurd Creek Member, in dark silty-sandstone. **F**, NSM 007.GF.004.531, Tetrapod cranial bone in dermal view showing ornament of fine pits; Hurd Creek Member ("lighthouse-sandstone"). **G**, CM 9678, Neurocranium (basioccipital) of indeterminate tetrapod; Hurd Creek Member ("lighthouse sandstone").

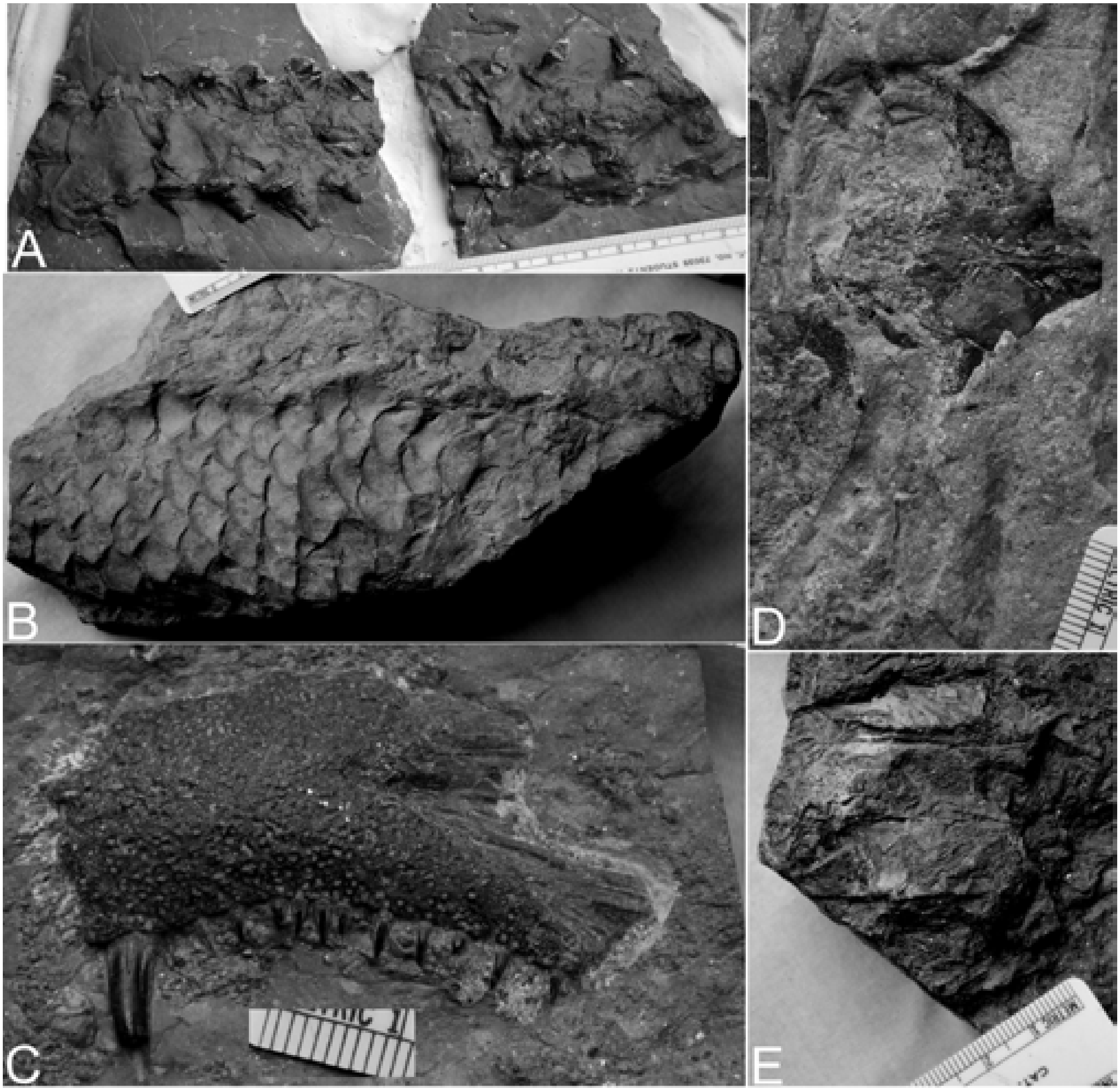

FIGURE 10. Sarcopterygians. **A**, NSM 005.GF.045.162, Rhizodontid vertebral column here reveals a series of neural- and haemal-spines in full articulation with unossified vertebral centra, verifying the notochord was unconstricted; Blue Beach Member, in dark gray siltstone. **B**, NSM 005.GF.045.163, Articulated rhizodontid in lateral view showing squamation and impressions of the neural-spines; Hurd Creek Member, in dark silty-sandstone (coll. by Robert Godfrey). **C**, NSM 007.GF.004.1085, Rhizodontid premaxilla in labial view; Hurd Creek Member, in dark quartzose sandstone (coll. by Barry Cameron). **D**, NSM 007.GF.004.653, Dipnoan parasphenoid in ventral view; Hurd Creek Member, in dark fine-grained sandstone (coll. by Alysha Wood). **E**, CM 10041, Natural mould of dipnoan cranial material in articulation, in internal view; Blue Beach Member, in dark gray siltstone.

been published, and these results will still only reflect a small portion of the vertebrate record, as only fully-prepared and portable specimens have been included in the study sample. The current collection of tetrapod bones at the Blue Beach Museum has more than doubled since the last major viewing in 2005, and contains new tetrapod associations in large-slab form, and many new isolated elements, none of which have yet been prepared to reveal their full extent or identity.

Among the more informative new tetrapod finds is a pelvis collected in 2012, which is here tentatively attributed to a crassigyrinid (CM 10071.1: Fig. 9A). The Crassigyrinidae were previously known to occur in the late Viséan and Namurian, but have also recently been identified from the Tournaisian of Scotland (Smithson et al., 2012). The Blue Beach crassigyrinid material probably encompasses a suite of fossils, including an interclavicle (NSM 005.GF.045.310-A: Fig. 9B) and limb elements, all of which compare well with previously illustrated specimens of *Crassigyrinus* (Panchen, 1985, figs. 20, 23; Panchen and Smithson, 1990).

It is also clear that further additional species of tetrapods were present in the Blue Beach assemblage. Besides a broader range of postcranial evidence, new discoveries including jaw and cranial elements (Figs. 9C-F) and part of a neurocranium (CM 9678: Fig. 9G) can contribute new information on their characters, and on some of the initial patterns and processes underlying stem-tetrapod diversification. The various tetrapod bones display a wide range of external ornamentation, and themselves suggest a wide range of tetrapod morphologies. Many of the isolated fossil bones show fine preservation of discrete structures, so even studying these will positively impact understanding of their biology and functionality. However, any reconstruction of isolated postcranial and cranial material remains problematic for the time being. There is also no basis for fitting the collection of isolated tetrapod remains together into skeletal reconstructions because multiple morphotypes are found mixed in the same beds. Unless more complete remains are found, this will remain the case.

Two additional morphotypes are, however, implied by the ichnofossil record, in the tracks of *Batrachichnus* and *Attenosaurus*. These large and small tracks (Figs. 13A, B) cannot be attributed to the size-range of currently-recognized tetrapod bones, as they are either far too small or too large. Including these two forms, we estimate a minimum of seven different tetrapods present in the assemblage (Anderson et al., 2009; and this paper), possibly double that documented from approximately coeval Scottish sites (Smithson et al., 2012), and far more diverse than the earlier Devonian tetrapod faunas. Maximum diversity documented thus far in Devonian tetrapod records include up to two taxa (E. Greenland: Coates and Clack 1990; Coates, 1996) or possibly three (Pennsylvania: Daeschler et al., 1994; Daeschler, 2000; Shubin et al., 2004).

Fish Fauna

Sarcopterygii

Lobe-fin fish are among the top predators in the fauna, with a large rhizodont (possibly up to 6 m long) as the most common species at Blue Beach (Figs. 10A-C). Dawson (1868) originally gave the name *Rhizodus hardingi* to some isolated scales and teeth, and a fragment of a dentary with teeth. Woodward (1890) transferred Dawson's material to the genus *Strepsodus* on the belief that the former species was solely from the British Isles. Several unique features in the lower jaw are now recognized as distinct, which led to its renaming as *Letognathus hardingi* (Brazeau and Parker, 2004; Brazeau, 2005; Brazeau and Jeffery, 2006), which translates to "jaws of death, annihilation, or ruin."

Rhizodont bones in the Blue Beach Museum collections outnumber the combined bones of both tetrapods and lungfishes by more than ten-to-one. Because rhizodont bones can easily resemble bones from these groups quite closely, and have been mistaken for them in the past (i. e., Andrews, 1972; Clack, 2002a), a cautious approach needs to be employed before diagnosing the material from Blue Beach. With the discovery of better known rhizodonts in the last 15 years (Clack, 2002a; Daeschler and Shubin, 1998; Garvey et al., 2005; Jeffery, 2001, 2003, 2006; Johanson, 2005; Johanson and Ahlberg, 1998, 2001; Johanson et al., 2000; Long and Ahlberg, 1999; Parker et al., 2005; Vorobyeva, 2000), our understanding of their anatomy has so improved that identification of a large portion of the Blue Beach rhizodont bone material is now feasible. In particular, Jeffery (2006) expelled numerous localities and species and sorted out over 150 years of nomenclatural confusion surrounding *Strepsodus*, thereby clearing the way for rhizodont research. There is now a very large Blue Beach Museum collection of *Letognathus* material, and this sample will lead to *Letognathus* eventually becoming one of the best known rhizodonts.

There is also co-occurring trace fossil evidence of rhizodont activity at Blue Beach, (Lucas et al., 2004), which provides vital clues in the reconstruction of rhizodont ecology. Two cololites that were recently described (Mansky et al., 2012) are examples of initial progress made in this direction, providing new information on aspects of rhizodont paleobiology, such as preferences in their diets, body size, and species/facies relationships.

Sarcopterygians are commonly found associated with most early tetrapod faunas, typically including several cosmopolitan groups such as osteolepiforms, rhizodonts, and especially lungfishes (Dipnoi). At Blue Beach there seems to be an overwhelming dominance by the rhizodonts at the apparent expense of these other groups, implying that the rhizodonts may have had some natural advantage. The reasons for this are not very hard to imagine. The Devonian and Carboniferous Rhizodontida were very large sarcopterygian fishes (up to 8 m long) that are now considered to be basal tetrapodomorphs (Ahlberg and Johanson, 1998; Jeffery, 2001, 2006). Their anatomy and physiology are perhaps the mostly poorly understood of any lobe-finned group, as they are mostly known from fragmentary fossils (Johanson and Ahlberg, 1998; Brazeau and Parker, 2004). Rhizodonts are believed to have been ambush predators with feeding strategies in many ways similar to those of modern alligators. Prey typically would have either been swallowed whole or reduced to manageable pieces with violent shaking motions, reminiscent of modern alligator attacks (Andrews, 1985).

The record of lungfishes at Blue Beach is very sparse (Carroll et. al., 1972), quite possibly due to intense competition from the large rhizodontid populations. The first report of a lungfish in the fauna was of a single parasphenoid (Carroll et al., 1972), tentatively attributed to the Mississippian genus *Ctenodus*. New material, including additional parasphenoids (NSM 007.GF.004.653: Fig. 10D) and other elements in the Blue Beach Museum, confirm that there was a large lungfish in the fauna (~2 m long). One of the new specimens shows a portion of an articulated skull (CM 10041: Fig. 10E), and represents the most complete lungfish remains known from the locality. Many additional elements of the lungfish postcranial skeleton still need to be separated from the tetrapod and rhizodont material in the sample. An analysis of new lungfish material now coming out of similar-aged sites in Scotland (J. Clack pers. comm., 2012) is readily comparable to the Blue Beach lungfish, and is expected to help with these identifications.

Actinopterygii

Scales and dermal bones of palaeoniscoid fish are very numerous in the Blue Beach sequence, occasionally preserved as dense accumulations or "bone beds" that can cover entire surface bedding-planes. The palaeoniscids were first noted by Dawson (1868), who referred jaw and scales to *Acrolepis hortonensis*, and much smaller scales to "probably *Palaeoniscus*," noting their similarity with the Albert Formation fishes of New Brunswick. He further noted that fully-articulated fishes were numerous in the Albert Formation, but the same species were completely disarticulated at Blue Beach. Dawson later reviewed the coeval Albert fish fauna of New Brunswick, and identified five species of *Palaeoniscus* (*Rhadinichthys*) without specifically indicating all five species occurred also in the Horton strata (Dawson, 1877, 1878). Woodward (1902) later considered the Albert and Horton fishes better referred to *Elonichthys*, but does not mention Dawson's genus *Acrolepis*, which is almost certainly *Elonichthys*. "*Acrolepis hortonensis*" Dawson (1868) should probably refer only to Dawson's type specimen, not to any of the fish material subsequently collected. Lambe (1908) verified the presence of *Rhadinichthys* in the Blue Beach fauna from isolated scales, and assigned the material to many of the same species as are known from the Albert Formation of New Brunswick (Table 1). Lambe (1909) also transferred Dawson's *Palaeoniscus modulus* to the genus *Canobius*, noting that one of the type specimens is "from Horton."

There are significant examples of articulated and fragmentary palaeoniscoids in the collections of the Blue Beach Museum, including at least one uncharacteristically large form that is probably a new taxon (CM 9827: Fig. 11A), and an unidentified tall-bodied form (BWC 1029: Fig. 11B). A neurocranium of a large palaeoniscoid (BWC 536: Fig. 11C), is the only known large palaeoniscoid neurocranium. The undescribed neurocranium can provide new data on the phylogenetic links between Devonian groups and the origins of modern fishes.

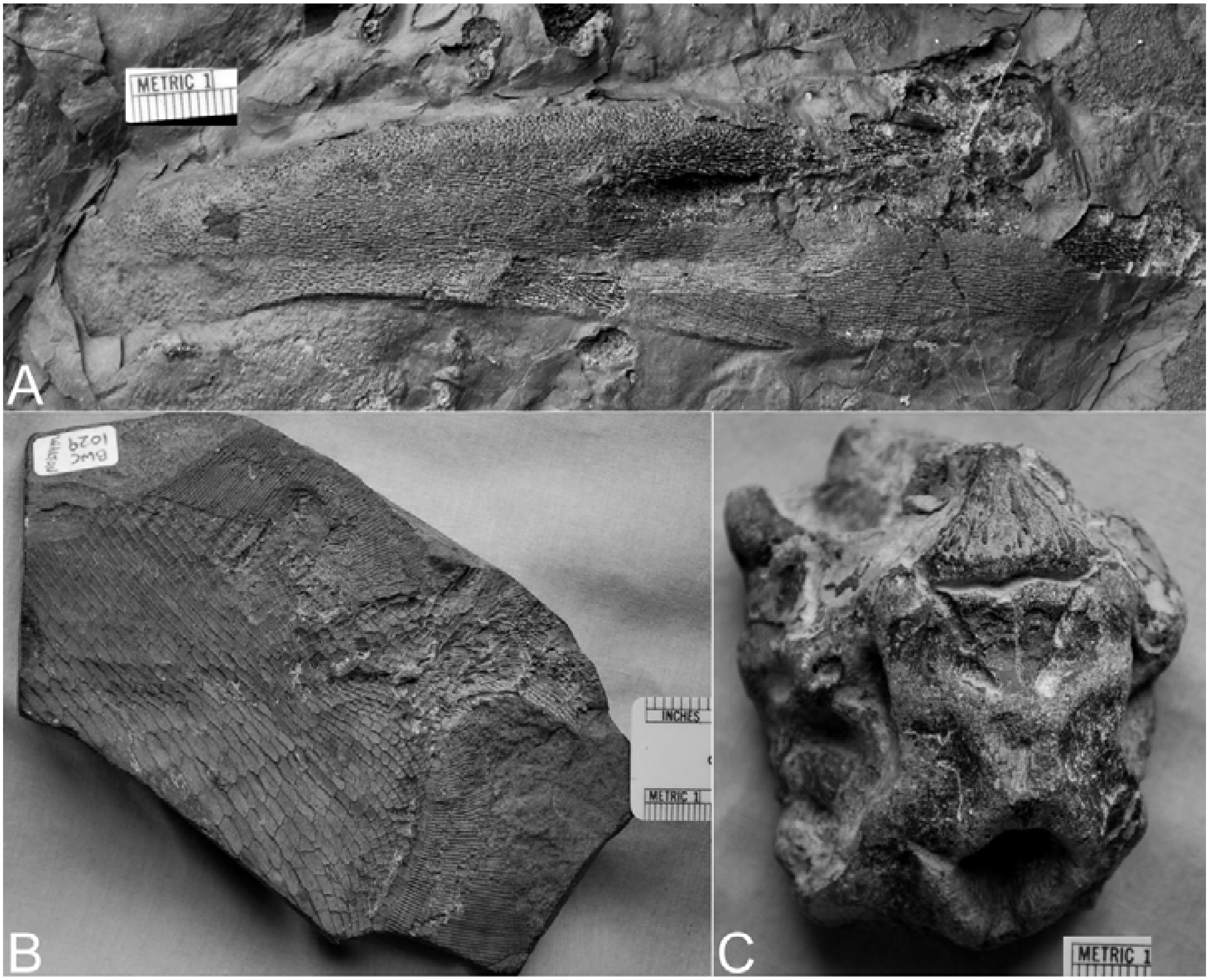

FIGURE 11. Actinopterygians. **A**, CM 9827, Mandible of large-form palaeoniscoid in labial view; Hurd Creek Member (“Gully-slide bonebed”). **B**, BWC 1029, Articulated “tall-bodied” palaeoniscoid in lateral view showing fins and fin-rays; Horton Bluff Formation at Walton, NS (coll. by anonymous student). **C**, BWC 536, Neurocranium of large-form palaeoniscoid in ventro-posterior aspect; Blue Beach Member, in concretion (coll. by Paul White).

Chondrichthyes

Fin spines from Blue Beach tentatively attributed to the chondrichthyan (elasmobranch) genus *Ctenacanthus* (CM 7995: Fig. 12A) were first discussed and illustrated by Dawson (1868), and there have been no formal contradictions to that placement, except it was felt that Dawson’s figure possibly showed a gyracanthid-spine instead (Carroll et al., 1972). Based on the new sample of the Blue Beach Museum, we conclude Dawson was correct, and that the chondrichthyan spines are far more abundant at the deposit than are remains of gyracanthids. In Bell’s (1929, p. 35) report he makes a speculative reference to the possibility of *Stethacanthus* occurring in the Blue Beach assemblage, a statement that has been taken further so that *Stethacanthus* was included in later faunal lists (i. e., Calder, 1998). The cumulative evidence of hundreds of fin spines in the Blue Beach Museum fails to reveal a single specimen of *Stethacanthus*, and we conclude Bell’s reference to that genus was incorrect.

Newly recovered chondrichthyan material in the Blue Beach Museum collections includes at least one additional morphotype of spine, and also some new jaw elements (NSM 005.GF.045.244-A: Fig. 12B). One impressive specimen (CM 9562: Fig. 12C) is fragmentary, and shows the base of a spine which could have been up to 200 cm long in entirety, whereas a maximum normal length of 20 cm for *Ctenacanthus* spines is all we have observed. This much larger spine is not sufficiently preserved to know if it belonged to a true elasmobranch, like *Ctenacanthus*, or to a large acanthodian like *Gyracanthides* (see below), for which it is uncharacteristically large. Aside from the spines, likely postcranial material of elasmobranchs exists in the form of numerous un-ornamented rod-like and plate-like bones that do not seem to belong to other groups.

Acanthodii

In his report on the fishes of Blue Beach, Woodward (1890) noted that there were large numbers of small fin spines he referred to the genus *Acanthodes*. Carroll et al. (1972) mentioned that the small spines resemble the genus *Acanthodes*, and far outnumber all other species of spines in the deposit (CM 5672: Fig. 13A). Zidek (1977) described a Blue Beach scapulocoracoid and pectoral fin-spine, in near articulation, as belonging to the Acanthodidae, thus extending the known geologic range of the group. Additional undescribed acanthodidid elements are

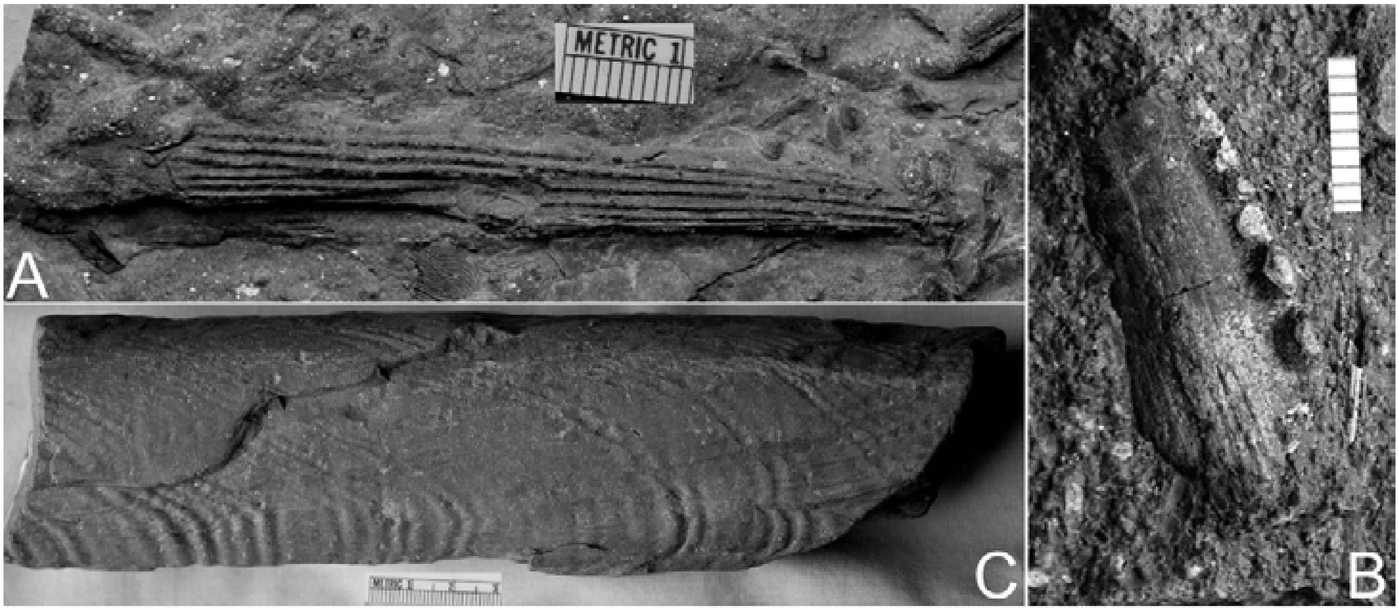

FIGURE 12. Chondrichthyans. **A**, CM 7995, Dorsal fin-spine of *Ctenacanthus* sp, with fragmental palaeoniscoid remains; Blue Beach Member, in gray siltstone. **B**, NSM 005.GF.045.244-A, Dentigerous element of an ?elasmobranch; Hurd Creek Member ("lighthouse sandstone"). **C**, CM 9562, Natural cast of the basal portion of a very large fin-spine; Blue Beach Member, in gray siltstone (coll. by Bruce Blades).

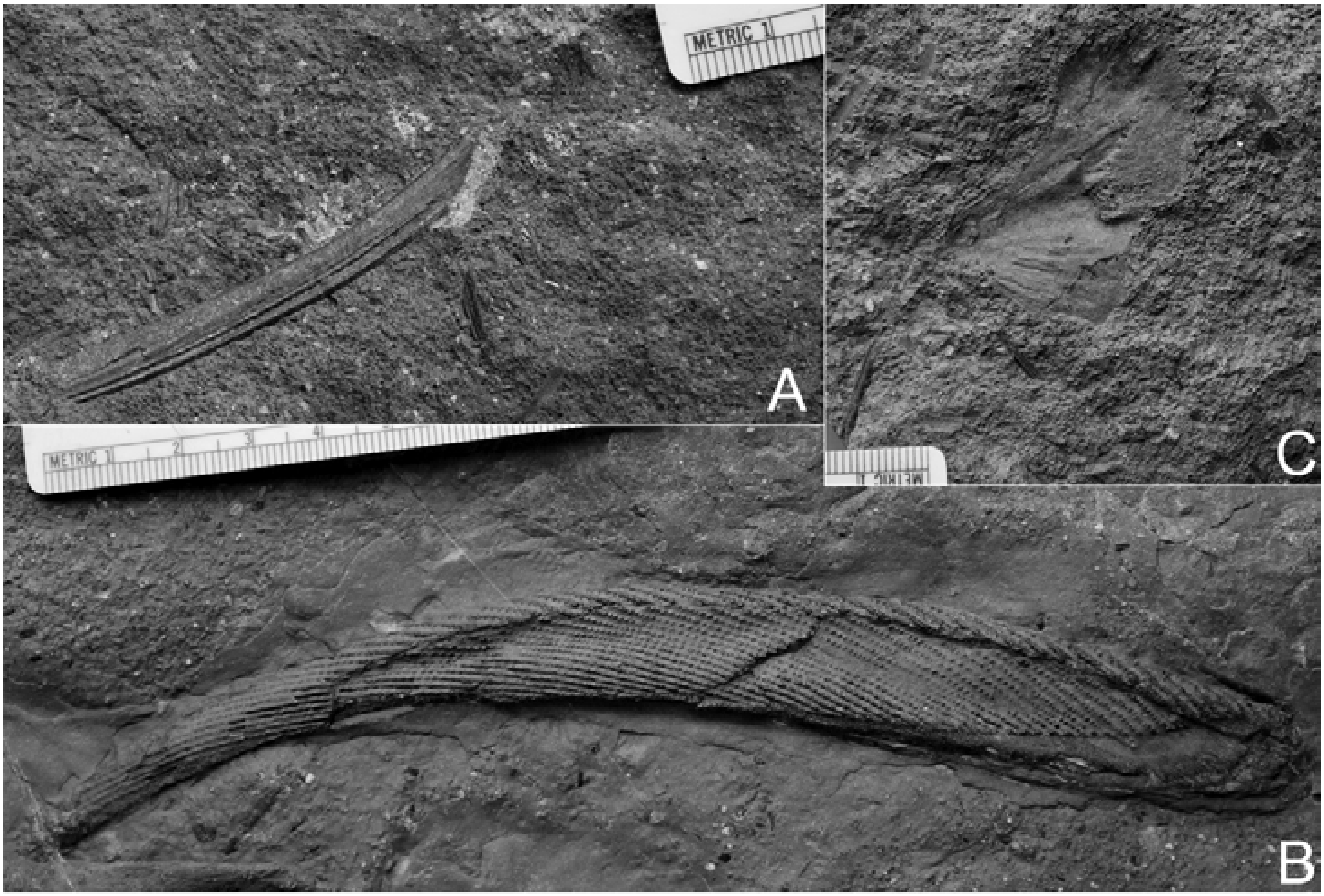

FIGURE 13. Acanthodians. **A**, CM 5672, Acanthodidid pectoral fin-spine; Hurd Creek Member ("lighthouse sandstone"). **B**, NSM 005.GF.045.236, Pectoral fin-spine of *Gyracanthides*; Hurd Creek Member ("shale steps bonebed"). **C**, NSM 07.GF.004.1214.1, Gyracanthid scapulocoracoid; Hurd Creek Member ("lighthouse sandstone").

recognized in the Blue Beach Museum collections. The most diagnostic examples are fairly common mandibular rami, and rare articulated squamation.

A second morphotype of pectoral fin spine has been attributed to *Gyracanthus* (Carroll et al., 1972). In a recent review of known Carboniferous gyracanthids (Turner et al., 2005), the Blue Beach material was identified as *Gyracanthides* (NSM 005.GF.045.236: Fig. 13B), as were numerous *Gyracanthus* records from the Lower Carboniferous. A recent survey of pectoral fin spines in the Blue Beach Museum collections indicates both *Gyracanthus* and *Gyracanthides* are present (Daniel Snyder, pers. comm., 2010). Fin spines from the pectoral and posterior regions of gyracanthids are uncommon, while examples of corresponding prepectoral plates and girdle elements are rare (NSM 007.GF.004.1214.1: Fig. 13C).

Rare examples of fin spines belonging to a fourth acanthodian, provisionally referred to *Climatius*, are in the collections of the Blue Beach Museum (Fanny Couzaris, pers. comm., 2003), and can be distinguished by their different external ornamentation and proportions. There may also be a fifth genus if the very large, previously discussed fin spine (CM 9562, Fig. 12c) proves not to belong to a chondrichthyan.

Implications

The presence of certain Carboniferous tetrapods and fishes, especially sarcopterygians, palaeoniscoids and acanthodians, has generally been taken to signify lacustrine settings. We should not, however, over interpret ichnological and body-fossil evidence from non-lacustrine strata as signifying such faunas freely-tolerated saline environments. While collateral evidence of faunas occurring in marginal-marine strata elsewhere (i. e., Sydney, NS; Wightman et al., 1994) strongly suggests such faunas may have been saltwater tolerant, a precise determination of salinity levels during times of occupation is not possible, which leads to difficulties in arguing about tolerances to salinity at any time. Until we can establish more accurate depositional contexts for the fossils themselves, through detailed taphonomic studies, it may remain difficult to understand the salinity preferences of the once-living faunas they represent.

ICHNOLOGY

Invertebrate Traces

Introduction

The invertebrate ichnofossils of the Horton Bluff Formation have proven to be unusually diverse considering the low diversity of Devonian continental ichnofossil assemblages (Gevers et al., 1971; Miller, 1979; Allen and Williams, 1981; O'Sullivan et al., 1986; Gordon, 1988; Morrissey and Braddy, 2004). The invertebrate traces include various burrows (*Palaeophycus*, *Planolites*, *Skolithos*, *Gordia*), arthropod resting traces (*Rusophycus*, *Limulicubichnus*, *Arborichnus*), and diverse arthropod trails (*Diplopodichnus*, *Diplichnites*, *Kouphichnium*, *Protichnites*, *Paleohelcura*, *Cruziana*). Large burrows attributable to *Taenidium* are also locally present in small numbers. The trace makers of these burrows are not known, although they may have been either large invertebrates, or more possibly, small lungfishes, (a rare component of the Blue Beach fauna). The majority of the invertebrate traces occur as two separate, facies-controlled ichnoassemblages (a *Palaeophycus* assemblage, and a *Rusophycus* assemblage).

The first foray into invertebrate ichnology at Blue Beach was by Sir John W. Dawson (1820-1899), one of Canada's most impressive pioneering scientists. Among his works were landmark articles on the arthropod resting trace *Rusophycus*, and various other surface markings (Dawson, 1864, 1868, 1873b), showing he was a competent, intuitive ichnologist. Numerous ichnological treatments of Blue Beach in recent years have added a large number of ichnotaxa to the record, but there are now many discordant pieces to this picture (Carroll et al., 1972; Martel, 1990; Martel and Gibling, 1991, 1996; Cameron et al., 1991a, b; Wood, 1999; Weir, 2002; Scott et al., 2005). These studies generally give very little review of the earlier studies, and a synthesis of the ichnology has not been attempted. Previous ichnological studies were constrained by small sample sizes, by biases in their specimen-selection method, and by their common lack of appreciation of extramorphological variability and the phenomenon of underprinting.

The Blue Beach invertebrate ichnology is the focus of two back-to-back thesis dissertations (Wood, 1999; Weir, 2002). Wood (1999) studied surficial trace fossils, giving a very detailed treatment to some of these. Arthropod trails were, however, mostly avoided, with the exception of *Cruziana* and *Paleohelcura*, which are well discussed. Wood identified a *Rusophycus* ichnofacies-association, recognizing co-occurring *Rusophycus*, *Cruziana*, diverse arthropod trails, tetrapod footprints, and *Undichna*. Because the study was mainly concerned with surficial ichnofossils, the infaunal burrows were not dealt with. A list of ichnofossils and body fossils that were considered during the study recognizes a diverse invertebrate ichnoassemblage in the sample.

Based on a much larger study sample, including many specimens used by Wood's study, we find the following invertebrate ichnotaxa are erroneous reports that require revision: *Calycraterion* (not figured = diagenic shrinkage structures in concretion); *Conchlichnus* (fig. 7.1 = tool-marks with pull-along wrinkles, microbial mats?); *Cosmorhape* (fig. 7.2 = groove cast); *Gyrichnites* (fig. 4.5a = tool marks); *Laevicyclis* (not figured = "scratch circles"); *Margaritichnus* (figs. 7.4a, b = *Rusophycus* isp.; fig. 7.4c = cast of raindrop impressions); *Phycodes* (not figured = *Palaeophycus*); *Protichnites* (fig. 5.8 = *Kouphichnium*).

In Weir's (2002) thesis a collection of ichnofossils from Blue Beach housed at the Nova Scotia Museum in Halifax is described. Some identifications are incorrect (i.e., pith-casts of *Lepidodendropsis*, misidentified as large invertebrate burrows). The study sample was very small, involving none of the common ichnofossils at Blue Beach, but it is still a curious selection. *Diplopodichnus* is recognized, and a second arthropod trail was erroneously identified as *Isopodichnus*, but is here reassigned to *Diplichnites*. The rationale for choosing an insect-based ichnotaxon was based on the belief these were lacustrine sediments.

We are now studying an important collection of ichnofossils amassed during over 20 years of fieldwork at Blue Beach. The large sample of ichnofossils allows us to confirm the identification of many of the ichnofossils at this time. Our survey reveals numerous unreported ichnotaxa, (Lucas et al., 2010a, b; Mansky et al., 2012), and the above treatment of Blue Beach ichnofossils is meant to remedy some of the earlier ichnotaxonomy, and to provide a basic framework for understanding the inferred paleoecology. The new assessment of the invertebrate ichnoassemblage is based almost entirely on collections at the Blue Beach Museum. A detailed report on this ichnoassemblage will be given elsewhere.

Invertebrate Ichnofacies

The cyclic sedimentation and fine-grained sediments of the Blue Beach section favor preservation of a diverse assemblage of traces in a variety of contexts. The repeating cycles contain hundreds of productive nearshore trace fossil beds. The shallowing-upward trend of the cyclic sedimentation changes at the cycle boundaries as slow basin infilling was repeatedly followed by sudden basin subsidence (Martel, 1990; Martel and Gibling, 1991, 1996). There are over 60 repeated cycles in the Blue Beach section (Figs. 3, 4). A wide range of facies are represented, including periods of transgression, of sedimentation, and of tectonic activity. Storm-related influences and taphonomic biases also played important roles in the ichnofacies-relationships sampled. The abundant preservation of traces in these various facies contexts clearly provides many opportunities for further paleoecological and ichnological investigation.

Invertebrate ichnofossils occur in two separate facies-controlled assemblages, a *Palaeophycus* assemblages and a *Rusophycus* assemblage. The *Palaeophycus* assemblage is abundant near the base of facies 1, mainly preserved as convex hyporeliefs on the undersides of overlying sandstone or siltstones. The *Palaeophycus* assemblage is low in ichnodiversity and has a high ichnofabric. The *Rusophycus* assemblage is best seen in facies 2 where conditions for preservation of diverse ichnofaunas were optimal.

The *Rusophycus* assemblage is characterized by a mixture of invertebrate and vertebrate ichnofossils, including the very common Rusophycus, diverse arthropod trails, fish trails (*Undichna*) and tetrapod footprints. The apparent associations of tracemakers are all the product of various depths of underprinting, and as such they also show a typically wide range of extramorphological variation. No verified example was found to demonstrate the makers of the ichnofossils were occupying the same stratigraphic levels. Therefore, the ichnologic record at Blue Beach shows no direct evidence of predation or group behavior.

Implications

The Horton Bluff Formation invertebrate ichnoassemblage has previously been interpreted as belonging to the relatively low-diversity *Rusophycus* ichnofacies (Wood, 1999). Recent work shows that the ichnofacies assemblage is more advanced and diverse than *Rusophycus* ichnofacies assemblages, reflected by an increase in ecospace utilization, with deep and complex burrowing forms evident (i.e., *Taenidium*). Combined with the *Taenidium*, the wide range of invertebrate traces, fish traces, and tetrapod traces indicate the Horton ichno-assemblage represents the *Scoyenia* ichnofacies (Buatois et al., 1998; Lucas et al., 2010a). Traditional examples of the *Scoyenia* ichnofacies were strictly Permian or younger, but recent evidence from the Lower Carboniferous of Pennsylvania (Fillmore et al., 2010, 2012) has significantly extended this record. The Horton Bluff ichnofossil assemblage now extends this record even further, confirming continental invertebrate communities had achieved an essentially modern aspect in terrestrial nearshore settings far earlier than was once believed.

Additionally, the relative large body-size implied by some of the ichnotaxa, together with the diverse characteristic of the *Scoyenia* association itself, form a strong basis for questioning atmospheric oxygen levels that have been depicted as reduced (Berner, 2006), as the absence of fossil evidence used to rationalize the existence of an oxygen-related biotic crisis during Romer's gap (Ward et al., 2006) no longer exists.

Vertebrate Ichnology

Introduction

Vertebrate ichnofossils from the Horton Bluff Formation have been mentioned in scientific publications for well over a century, with increasing frequency in recent years (Logan, 1842; Lyell, 1843, 1845; Dawson, 1863, 1868, 1882, 1895; Matthew, 1903a, b, 1904, 1905; Sternberg, 1933; Kuhn, 1963; Haubold, 1970, 1971; Carroll et al., 1972; Sarjeant and Mossman, 1978a, b; Mossman and Sarjeant, 1980; Martel, 1990; Martel and Gibling, 1991, 1994, 1996; Cameron et al., 1991b, 2000; Wood, 1999; Hunt et al., 2004a, b; Lucas et al., 2004, 2010a, b; Scott et al., 2005; Carroll and Green, 2003; Mossman and Grantham, 2008). Newly collected material currently being studied by the authors reveals several previously unreported ichnotaxa are present, and numerous revisions to the previous nomenclature will be required (Lucas et al., 2004, 2010a, b; Mansky et al., 2012).

The significant sample of vertebrate traces at the Blue Beach Museum includes more than one ichnospecies of the fish swimming trace *Undichna*, unnamed traces of large, "crawling" sarcopterygian fishes, five ichnogenera of tetrapod footprints and trackways (*Batrachichnus*, *Palaeosauropus*, *Hylopus*, *Pseudobradypus*, *Attenosaurus*) and rare examples of the tetrapod resting-trace *Ctenerpeton* (*sensu* Aldrich and Jones, 1930). In addition to this there are diverse bromalites (Hunt and Lucas, 2012), which consist of six morphotypes of coprolites plus cololites (Mansky et al., 2012). Although invertebrates may have been responsible for some of the bromalites, the majority are attributable to fish, especially to chondrichthyans. Tetrapods may have also produced at least some of the small pellet coprolites.

Undichna

The ichnoassemblage contains a significant record of fish swimming traces belonging to more than one ichnospecies of the ichnogenus *Undichna* (Cameron et al., 1991b; Wood, 1999; Lucas et al., 2010b; Mansky et al., 2012). They occur closely associated with tetrapod footprints and various arthropod traces. None of the associations can be shown to have occurred on the same exact lithological horizon, and the interpretation is that these "associated" trace fossils were made by organisms on separate occasions. There is therefore no evidence of predation. *U. britannica* (CM 1487: Fig. 14A) is the most common form (Wood, 1999). Several specimens exhibit long trails and fine preservation. Attributed ichnospecies are *U. britannica* (Wood, 1999), and a large form that resembles *U. britannica* from Blue Beach (CM 12311: Fig. 14B), but is far larger. The large form may be distinct from *U. britannica*, as drag-marks left by the fins are shallow and wide in contrast to the narrow, sharp markings of *U. britannica*.

The latter ichnospecies was almost certainly produced by palaeoniscoids, numerous components of the fauna. The different character of the large form *Undichna* may signify that a fish of different affinities was the producer, in this case possibly a sarcopterygian. Furthermore, major observable differences between the large form *Undichna* and much larger trails of crawling sarcopterygians (discussed below) suggest that rhizodonts were not making these large form *Undichna*. In addition to morphological differences, the sarcopterygian crawling trails also do not occur in the same facies as the *Undichna* material. A better candidate for the tracemaker of the large form *Undichna* might be a lungfish (Dipnoi), a known component in the Blue Beach fauna.

Two additional ichnospecies were cited by Wood (1999), and we find these to be erroneous interpretations. Based on our study sample, valid examples of *U. bina* do not occur in the Horton Bluff Formation. One of the referred specimens is actually an underprint of *Diplopodichnus*, meandering slightly in its course; several others are recurved tool-marks. Secondly, "*U. septemlineatum*" was erected as a new ichnotaxon that we find invalid. Examination of the referred material, along with additional segments from the same stratigraphic level, show these are also tool-marks.

Unnamed Sarcopterygian Crawling Trails

A remarkable series of impressions preserved *in situ* at Blue Beach North were originally assigned to the tetrapod footprint ichnogenus *Baropezia* (Sarjeant and Mossman, 1978a), but our reinterpretation is that they represent the crawling-trail of a very large sarcopterygian fish (Fig. 15). Some of the individual impressions are over 30 cm long, and at the time of their discovery ran more-or-less in a straight line for over 60 m. The trail has been eroded to one segment about 13 m long, and a second segment about 15 m. The trail was discovered in 1964, photographed in 1974, and briefly described in 1978. In addition, a fiberglass-cast of the trail was prepared in 1979 for the Nova Scotia Museum in Halifax, where it resides today. Additional (but less-organized) markings on these and other strata are not part of the same trail; but appear to be very similar to the longer trail. These disorganized traces have not been formally described.

In two published descriptions (Mossman and Sarjeant, 1980; Sarjeant and Mossman, 1978a) there are no figures showing the trail viewed from directly above, so the authors personally re-examined it in 2004 (Lucas et al., 2004). The impressions are usually deep, and the trail is highly-disorganized and exhibits significant extramorphological variation throughout its length. In addition, the authors examined *in-situ* the numerous disorganized trails and resting-traces on several different beds of apparently-similar facies. The impressions occur in several different

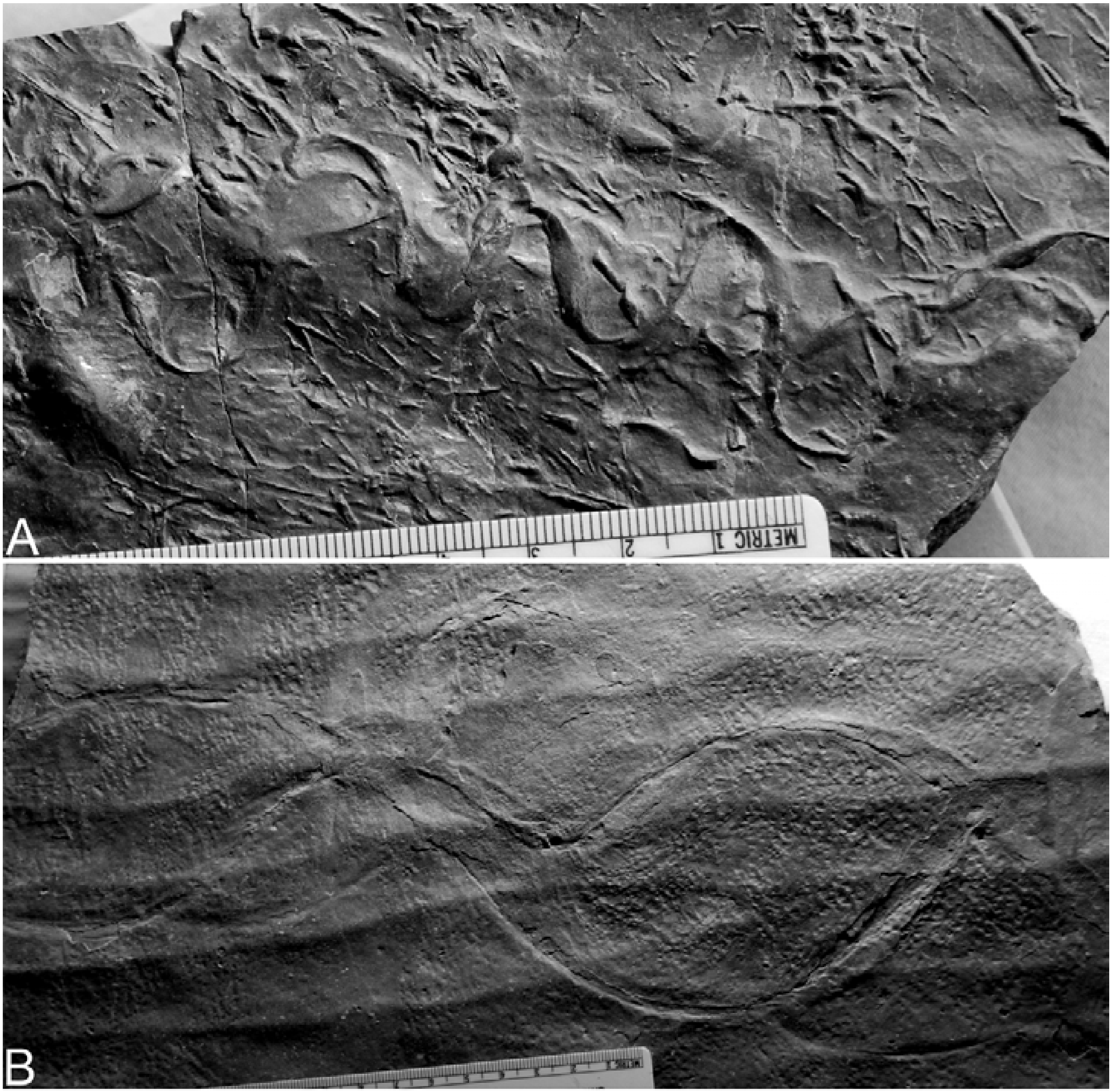

FIGURE 14. *Undichna*. **A**, CM 12311, Large-form *Undichna*; Blue Beach Member, on gray wave-rippled planar-bedded siltstone (“Horizon 7a”, concave). **B**, CM 1487, *Undichna britannica*; on Blue Beach Member, on gray planar-bedded siltstone (“Horizon 8b”, convex).

characteristic shapes, some of which may be resting traces and drags; (1) deep and sub-oval impressions; (2) deep and semi-triangular impressions; (3) deep and u-shaped impressions; (4) deep elongated scratches; and (5) long, shallow, elliptical troughs.

On the basis of three inconsistencies we find it impossible to assign these trails to quadrupedal makers:

1. The trail is highly disorganized, and the pattern of its gait is unlike that of any quadruped. The midline sweeps left and right in wide arcs along the length of the trail, making any attempt to reconstruct the gait impossible. The conclusion is that two main appendages only were used in locomotion.

2. The initial description of the trail stated there were four toes in both the manus and the pes (Sarjeant and Mossman, 1978a), and that the creature was travelling 70o east of north. Based on clear evidence of “sand-wedges,” or “push-ups” in the northeastern portion of the impressions, we conclude that the locomotion was opposite to that described, towards the southwest, so the toes would have to be seen at the back of the foot. There are no signs of digits in any of the impressions when direction of travel is correctly interpreted.

3. The provisional assignment of the trail to a large temnospondyl is not supported by the body fossil record. Large amphibians of this size are not known until the Permian, so at least 50 million years separates these two records. The body fossil record of Blue Beach, however, informs us that large rhizodonts were plentiful in the fauna. The conclu-

FIGURE 15. (Not collected). Sarcopterygian crawling-trail looking northeast; Hurd Creek Member, in gray tabular siltstone (“Horizon 71 minus 1”, concave).

sion is obvious that these trails represent the activities of large sarcopterygians. Also, their impressive size ensures the trails and related traces are almost certainly those of the huge rhizodont *Letognathus*. We will present a more detailed analysis of these trails elsewhere.

Tetrapod Resting Traces

One curious form is neither footprint nor trail: the chevron-shaped ichnofossil *Ctenerpeton*, represented by *C. alveolatum* (Cope), later transferred to *C. primum* based on specimens from near Carbon Hill, Alabama (Aldrich and Jones, 1930). The Blue Beach Museum collection has several very similar examples, including one that is associated with *Palaeosauropus* tracks (NSM 007.GF.004.358), which helps validate *Ctenerpeton* as a valid ichnogenus. The usage of the name *Ctenerpeton* may need to be reconsidered, however, as the name *Ctenerpeton* is already occupied by a body fossil, a nectridean genus (i.e., *C. remex* (Cope) from the Pennsylvanian of Ohio: Bossy, 1976).

Tetrapod Footprints

The vertebrate ichnoassemblage from Blue Beach occurs very near the base of the Carboniferous Period, but is surprisingly diverse considering the low diversity of known Devonian vertebrate ichnoassemblages (Clack, 1997).

The Horton Bluff tracks in particular are of unique importance, as they comprise the oldest diverse assemblage of tetrapod footprints known (Lucas et al., 2004, 2010b). The tracks are seen to represent the earliest diverse community of pentadactyl/tetradactyl tetrapods, and the earliest-known tetrapods capable of fully terrestrial locomotion (Lucas et al., 2004, 2010b; Carroll and Green, 2003). The Blue Beach footprint assemblage is one of only two substantial tetrapod footprint assemblages of Mississippian age, with the other in the Mauch Chunk Formation in Pennsylvania, USA (Lucas et al., 2010b; Fillmore et al., 2012).

The Blue Beach Museum collection includes over 2000 specimens of vertebrate tracks, which is the largest collection of Mississippian tetrapod tracks (Mansky et al., 2012). The vertebrate tracks are known to occur at more than 80 different stratigraphic horizons in the sequence, more than known for any other Carboniferous locality. Most of the tracks are preserved as underprints and display typically wide ranges of extramorphological variation. The density of tracks and productive horizons indicate long-standing, stable populations of tetrapods must have existed very near to Blue Beach throughout much of its Early Mississippian depositional history.

***Attenosaurus*:** Some of the largest and least common Blue Beach tracks closely resemble the ichnogenus *Attenosaurus* (NSM 007.GF.004.348, Fig. 16a) from the Early Pennsylvanian Pottsville Formation of Alabama (Aldrich and Jones, 1930; Hunt et al., 2004; Haubold et al., 2005). Before this, *Attenosaurus* had been considered an endemic ichnogenus, so the Blue Beach occurrence is important in establishing its ichnotaxonomic validity. The footprints of *Attenosaurus* are distinguished by a number of traits: (1) footprints are large (pes width/length ~ 80/70

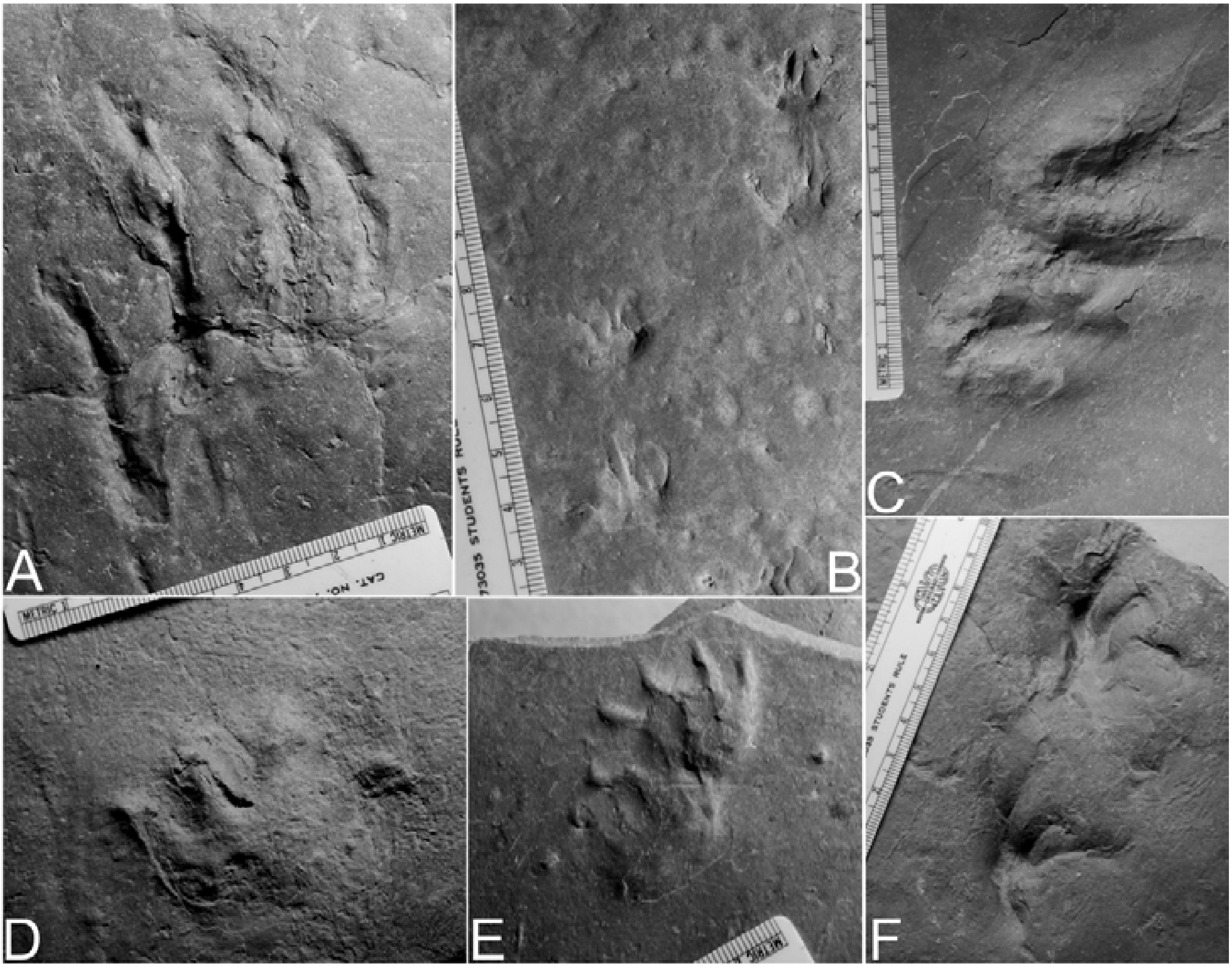

FIGURE 16. Tetrapod footprints. **A**, NSM 007.GF.004.348, *Attenosaurus* isp., preserved as a deep underprint; Hurd Creek Member, on gray planar-bedded siltstone (concave). **B**, NSM 007.GF.004.185, *Batrachichnus* trackway; Blue Beach Member, on tan colored planar bedded siltstone ("Horizon 36a", concave). **C**, CM 18245, Large-form *Palaeosauropus* underprint with associated trails of Diplichnites; Blue Beach Member, on gray planar-bedded siltstone ("Horizon 29a", concave). **D**, NSM 007.GF.004.115, *Palaeosauropus* manus underprint; on pale gray planar-bedded siltstone ("Horiz. 28b", convex). **E**, NSM 007.GF.004.279, *Hylopus* underprints; Hurd Creek Member, on pale blue-gray planar-bedded siltstone ("Horizon 62b to 64b", convex) (coll. by Barry Cameron). **F**, NSM 007.GF.004.098, *Pseudobradypus* underprints; Blue Beach Member, on gray planar-bedded siltstone ("Horizon 18a", concave).

mm), exhibit an extremely narrow sole, and possess a bean-shaped posterior extension resembling the heel-bone often seen in amniote tracks; (2) digits are long and narrow; (3) trackways are proportionately quite narrow, and there is no median drag; (4) tracks are evenly spaced and are not usually overstepped; and (5) manus and pes imprints are of similar size and often hard to differentiate from one another.

***Batrachichnus*:** In the collections of the Blue Beach Museum a modest number of diminutive trackways exist, and these are the earliest known *Batrachichnus* (i.e., NSM 007.GF.004.185: Fig. 16B). In later ichnoassemblages, *Batrachichnus* is often one of the most abundant track morphotypes present, but low numbers in the Tournaisian imply small tetrapods were present, but probably not in dominant numbers. In the later Mississippian (Chesterian) they progressively begin to dominate tetrapod footprint ichnoassemblages (Fillmore et al., 2012). The confirmation of small tetrapod morphotypes in the middle of Romer's gap is important as it suggests the radiation of terrestrial tetrapods was well underway, as highly-specialized small forms are important elements in later tetrapod faunas.

The tetrapods that produced these *Batrachichnus* footprints were most likely terrestrially-adapted. Their small size would have provided no advantages in aquatic scenarios, as they would be defenceless prey. The only logical haven, one the larger species would have trouble colonizing, was microhabitats within the early forests. The small size and agility of diminutive tetrapods would have allowed them to negotiate tight undergrowth, hollow tree stems, crevasses, and other likely refuges where larger tetrapods could not follow. Small body size would also have other advantages: (a) small size meant small metabolic needs, so less food would be required to survive; (b) small invertebrates were already terrestrial and diverse, and would make good prey for small tetrapods; large forms adapted to catching large aquatic prey on the other hand are ill-suited to such diets as they would need to catch large numbers of invertebrates to satisfy their needs, yet would be poorly-suited to catching such prey; and (c) water loss via skin exposure to sun and air would have posed a problem for the first terrestrial tetrapods, but smaller surface area of skin would have reduced water loss significantly, allowing small tetrapods to remain out of water for longer periods of time.

The preservation of the *Batrachichnus* specimens in the study sample is not optimal, most being somewhat faint and difficult to discern. This is in large part because the smaller trackmakers would have left shallower impressions, which were quickly lost as underprints. In part, the smaller sample size for *Batrachichnus* may be thus be a taphonomic artifact.

***Hylopus*:** The first footprint discovery at Blue Beach came in mid-September, 1841, by Sir William E. Logan (1798-1875). Logan was a respected Canadian-born scientist, and would the following year be appointed the first Director of the Geological Survey of Canada. The story of their discovery and subsequent plunge into obscurity is well-documented (Dawson, 1863, 1868; Sarjeant and Mossman 1978a), so it will not be elaborated on here. The tracks received cursory mentions in a series of short reports (Logan, 1842; Lyell, 1843, 1845), but seemed to attract no great attention at the time (Sarjeant and Mossman, 1978a), though their discovery marked "the dawn of vertebrate palaeontology in Canada" (Lambe, 1905). The poorly-preserved tracks, which are deep underprints, were eventually named *Hylopus logani* (Dawson, 1882). The type specimen was much later recognized as not one track, but parts of two parallel tracks with the outermost rows of footprints absent beyond the edges of the broken slab (Sternberg, 1933). The poorly-preserved impressions show as only scratches left by the digits, and nothing of the remainder of the autopods, causing Dawson to choose *Hylopus hardingi* as the type for the ichnogenus, even though the Horton Bluff tracks were the first occurrences found (Dawson, 1863). In the years after Dawson's work, a number of reports discussing *Hylopus* emerged (Matthew, 1903a, b, 1904, 1905; Sternberg, 1933; Kuhn, 1963; Haubold, 1970, 1971), but only the original 1841 specimen is discussed. No further Blue Beach specimens or discoveries are ever mentioned as belonging to *Hylopus*.

In the Blue Beach Museum sample there are many underprints that resemble Logan's undertracks, but collateral evidence from numerous corresponding "lower" underprint levels demonstrate that *Hylopus*, *Palaeosauropus*, and *Pseudobradypus* underprints can all grade together (also see Fillmore et al., 2012). On these terms, we regard the type of *Hylopus logani* (Dawson, 1882) as an indeterminate track, and not clearly diagnostic of an ichnotaxon.

However, tracks assignable to *Hylopus* do occur as a fairly scarce morphotype in the Blue Beach collections (i. e., NSM 007.GF.004.279: Fig. 16E). On the whole, the *Hylopus* tracks resemble those of the similar-sized morphotypes *Palaeosauropus* and *Pseudobradypus*. Very well-preserved *Hylopus* tracks also do show a few distinguishing traits that set them apart from the others: (1) manus tetradactyl, unlike *Pseudobradypus* but agreeing with *Palaeosauropus*; (2) digits long, thin, and curved, unlike *Palaeosauropus*, but agreeing with *Pseudobradypus*; (3) manus and pes of nearly equal size, unlike *Palaeosauropus*, in which the manus is distinctly smaller than the pes; and (4) digits of the pes are directed forwards (in well-preserved *Pseudobradypus* tracks, digits of the pes commonly appear laterally directed, whereas those of *Palaeosauropus* and *Hylopus* are forwardly directed).

In order to confidently identify the distinguishing traits of Hylopus, well-preserved examples are needed. Because the three medium-sized morphotypes are seen to grade into similar forms as deep underprints, there is doubt in identifying many of the imperfectly-preserved examples. These imperfect forms are at best referred to as medium-sized tracks – ichnogenus indeterminate.

***Palaeosauropus*:** In the collections of the Blue Beach Museum, the second-most abundant tracks are assigned to the ichnogenus *Palaeosauropus* (Lucas et al., 2004, 2010b). Many different stratigraphic horizons in the Blue Beach section contain tracks of this type. *Palaeosauropus* can be distinguished by several traits: (1) tetradactyl manus and a larger pentadactyl pes; (2) digits are short and broad; (3) the sole of the foot is wider than long; (4) the tracks are commonly overstepped; and (5) the trackways are relatively wide and often show median drags. There are two distinct size-ranges in the Blue Beach ichnoassemblage: a common medium-sized form (i.e., NSM 007.GF.004.115: Fig. 16D) and a rare large-form (i. e., CM 18245: Fig. 16C). Tracks of the large-form *Palaeosauropus* do not occur in the same stratigraphic intervals as the small-form, and each appear to occupy a different facies, the smaller form apparently preferring slightly shallower conditions. A similar ichnoassemblage with two size-ranges of *Palaeosauropus* has recently been reported from the Mississippian Mauch Chunk formation of Pennsylvania (Lucas et al., 2006; Fillmore et al., 2012), which is the only other large assemblage of Mississippian-age tracks. Two very different sizes of *Palaeosauropus* trackmakers may be one characteristic that distinguishes Mississippian tetrapod communities.

Dawson refers to a very different, much larger form he names *Megapezia pineoi* (Dawson, 1882). Although tracks assigned to "*Megapezia*" are figured, Dawson provides little description, and unfortunately does not designate a type specimen, so the record is vague. Based on our current study sample, we believe Dawson's "*Megapezia*" is probably a junior synonym of *Palaeosauropus*. There is a lesser chance Dawson was referring to a large example attributable to *Pseudobradypus*. We have no way of knowing what the actual tracks look like; depending on the state of preservation, degree of underprinting, and even upon Dawson's interpretive drawing-skills; the two forms are easily confused because as underprints they "grade" into very similar extramorphological forms. The actual ichnofossil Dawson was referring to would have to be examined in order to resolve this question.

***Pseudobradypus*:** The first new tracks discovered at Blue Beach in over 135 years were described as a new ichnogenus and species, *Anticheiropus bishopi* (Sarjeant and Mossman, 1978a). These were quickly renamed after the authors realized the name was preoccupied by a Triassic footprint morphotype, the specimen becoming *Peratodactylopus bishopi* (Sarjeant and Mossman, 1978b). Both names are references to the thumb-like impression of digit V of the pes, which is directed away from the midline laterally. The description identified a tetradactyl manus, but subsequent inspections revealed a fifth-digit in the manus of the type specimen (Wood, 1999; Mansky, pers. obs., 1998). Though the diagnosis was emended, with a new paratype illustrated and described (BWC 159 - Wood, 1999, fig. 6.4), its taxonomic validity was not questioned, despite the fact the numbers of the toes are one of the main criteria used in the classification of tracks (Matthew, 1903b; Haubold et al., 2005). There is little doubt that *Peratodactylopus* is a synonym of *Pseudobradypus*.

To add further confusion, one more new trackway was then described as yet another new ichnotaxon, *Eochelysipus hornei* (Mossman and Grantham, 2008), but these too are reassigned to *Pseudobradypus*. The 1978 and 2008 specimens are almost identical and both derive from the same stratigraphic horizon. In fact, they show so many taphonomic similarities they are almost certainly segments of the very same trackway, each collected on different dates. This is a classic example of how the footprint ichnotaxonomy has been oversplit to the point of chaos, with phantom taxa created mainly because of a failure to appreciate the extramorphological variation in tracks (Peabody, 1948: Lucas, 2007). Another problem stems from the use of small sample-sizes, with individual biases toward well-preserved tracks, especially the practice of using only one or a few prints in descriptions and giving each separate and new names (Haubold et al., 2005b). These difficulties are now resolvable because of the large number of vertebrate tracks in the Blue Beach Museum sample.

Pseudobradypus is the most abundant tetrapod track ichnogenus in the collections of the Blue Beach Museum (i. e., NSM 007.GF.004.098: Fig. 16F), represented by hundreds of specimens. These occur at numerous stratigraphic horizons and often vastly outnumber all other ichnospecies in the same beds. They tend to dominate the planar-bedded intervals, where at times their trackways are so plentiful as to cross one another on every slab.

Comparison to the Blue Beach Tetrapod Body Fossil Record

The co-occurrence of tetrapod tracks and bones in the same deposit, as is the case for Blue Beach, is an uncommon luxury for those trying to correlate vertebrate tracks to trackmakers. However, a significant understanding of the skeletal morphology of contemporaneous tetrapod groups is essential before inferences can be made about who the trackmakers were. Since almost nothing is known about Tournaisian tetrapod groups, nor their skeletal particulars, the comparisons cannot realistically be made. However, some general observations are worth considering, as the disarticulated collections of bones do give useful clues about local faunas: (i.e., the number of different morphotypes, their relative populations, size, and something of their functional morphology). According to the osteological evidence, there are at least five unequivocal morphotypes of medium-sized tetrapods in the Blue Beach fauna. The ichnological evidence also recognizes five morphotypes, of which one is too large (*Attenosaurus*), and one too small (*Batrachichnus*) for us to suggest any of the bone morphotypes as the makers. The three track types that match the size ranges of the Blue Beach bones are *Hylopus*, *Palaeosauropus*, and *Pseudobradypus*.

In later Carboniferous occurrences, the tracks of *Batrachichnus*, *Hylopus*, and *Palaeosauropus* are considered to have been produced by amphibians, especially temnospondyls. As no tetradactyl tetrapods are yet known from the Tournaisian the assignment would be speculative.

The inferred *Pseudobradypus* trackmakers are normally believed to have been amniotes, but the body fossil record of amniotes extends no further down than the beginning of the Pennsylvanian (Westphalian A). In a recent series of papers dealing with *Pseudobradypus* tracks from New Brunswick (Falcon-Lang et al., 2007; Falcon-Lang and Benton, 2008) the geologic range of the amniotes was questioned, and an attempt to use *Pseudobradypus* tracks as a proxy for amniotes was advanced. However, Keighley et al. (2008) cogently questioned the supposed age of the New Brunswick tracksite and the conclusion that only amniotes made the trackway called *Pseudobradypus* (also see Fillmore et al., 2012). The New Brunswick tracksite is not geographically far from the Westphalian A deposits of Joggins, where the earliest amniote *Hylonomus* is known from body fossils (Carroll, 1991). Since the Carboniferous strata at both localities were initially believed to be roughly coeval, the implication is that early amniotes were the trackmakers responsible for *Pseudobradypus*.

However, in considering the abundance of *Pseudobradypus* tracks and their Early Mississippian age at Blue Beach, we conclude there is no support for an assignment of these to amniotes. Rather, we suggest there was a high degree of homeomorphy in the foot structure of early tetrapods, and some of these resembled later amniotes. Based on the body fossil record at Blue Beach we suggest whatcheeriid tetrapods are a good candidate for the trackmaker of *Pseudobradypus* tracks in the Mississippian. Whatcheeriids were fully pentadactyl, were terrestrially-adapted forms, and like the tracks of *Pseudobradypus*, are the most common tetrapods in our study sample.

Attenosaurus tracks have previously been reported from the Early Pennsylvanian Pottsville Formation of Alabama (Aldrich and Jones, 1930; Hunt et al., 2004; Haubold et al., 2005). Pelycosaurs are considered to be the possible Early Pennsylvanian trackmakers, which agrees with the body fossil record showing pelycosaurs had originated in the Pennsylvanian. The Blue Beach *Attenosaurus* trackmakers, however, are characterized as stem tetrapods from the Mississippian Tetrapod Province, an ecosystem nearly 40 million years before body fossil records of amniotes. In light of this we cannot assign the Blue Beach *Attenosaurus* tracks to pelycosaurs. Instead, they must have been made by larger stem tetrapods, or by very early anthracosaurs, and any resemblance to the tracks of pelycosaurs is thus homeomorphic.

Tetrapod Ichnofacies

At Blue Beach, facies controls appear to have dictated the preservation of tracks, which mostly occur in facies 2b and 2c. Scarce examples near the tops of facies 2a beds and parts of facies 3 are also seen. The fine-grained planar beds from facies 2c, in particular, contain the highest observed track densities, and include some of the best-preserved examples. One sequence of these contains more than 10 productive horizons separated by less than a meter. Some horizons containing very few tracks apparently represent times of low traffic. On busy layers, trackways often cross each other in every direction, yet no verified examples were found demonstrating these trackmakers were walking on the same stratigraphic levels. As with the apparent associations of invertebrate ichnofossils, the different tracks appear to have been made on separate occasions, so neither predation nor herding behaviors can be inferred.

DISCUSSION

Transgressions

At Blue Beach, transgressions were highly stressful to the Mississippian terrestrial floras and faunas. Rapidly rising sea levels at times of transgression limited the amount of sediment coming into the system, and caused a drop in surface-water oxygen levels. Evidence for this stress can be seen in the high number of ostracods with brackish, or even shallow marine shelf affinities, combined with low numbers of characteristic lacustrine ostracod species, suggest unstable salinities at times controlled the populations (Tibert and Scott, 1999), but that true lacustrine environments were not distant. Oxygen levels could change rapidly as storm conditions aerated the water after the nutrient influx was enriched by increased detrital material, which resulted in an increase of benthic life and activity in the area, seen in the attendant “enrichment” of trace fossil activity within the storm sequences (Gluszek, 1995). Evidence for frequent storms and associated trace fossil assemblages at Blue Beach (Lucas et al., 2010a) further support the model of transgression as put forth by Tibert and Scott (1999).

In one scenario, continental faunas were forced to seek “refugium” habitats as the rising seas encroached on the land, moving into intramontane valleys during the “great marine colonization” of the major transgressions (Preobrazhensky et al., 1997). During this time the continental faunas are mainly represented by a “relict” assemblage, as significant amounts of low-lying areas are lost, crowding both terrestrial floras and faunas into a time of shock and stress: only more stable forms survive. During regression, the flora in turn re-colonizes the low-lying areas and marine faunas seek refuge habitats (Preobrazhensky et al., 1997).

The recent discovery of a “marine band” in the Hurd Creek Member at Blue Beach confirms the terminal point of a major transgression had occurred, indicating a time of maximum sea level. This confirms transgressions were significant threats to mid-Tournaisian continental habitats, and as such the Blue Beach ecosystem may have experienced all of the above mentioned impacts. Transgressions likely played a major role in the faunal changes that occurred during Romer’s gap, an idea that has not been questioned.

Atmospheric Oxygen Levels

Fusain (fossil charcoal) is fairly common from the Carboniferous onwards (Scott and Jones, 1994), and the source of heat leading to the combustion of plants was usually wildfires – but to sustain wildfires, atmospheric oxygen levels could not have dropped below 60-percent of what they are today (Cope and Chaloner, 1980). Evidence of fusain occurrences from the Carboniferous onwards is increasingly in conflict with models depicting the Early Carboniferous as a time of significantly reduced oxygen (Cope and Chaloner, 1985; Berner, 2006; Smithson et al., 2012). The occurrence of fusain in the Tournaisian of the Canadian and Scottish sites ultimately questions the idea put forth by Ward et al. (2006) and Berner (2006) that oxygen levels had fallen significantly.

Furthermore, global transgression and regression is seen to represent eustacy from polar glacial fluctuations. The occurrence of a "marine band" in the Hurd Creek member at Blue Beach implies glaciers were already advancing in the South pole, and that certainly reflects higher oxygen levels in the atmosphere (Matt Stimson, pers. comm).

Known Tournaisian faunas also help confirm oxygen levels were not critically reduced. The Tournaisian occurrence of large terrestrial myriapods (Smithson et al., 2012) is not easily explained in an oxygen-deficient system as proposed by Ward et al. (2006) and Berner (2006). The presence of terrestrial arthropods with large-bodies in the middle of Romer's gap helps confirm oxygen levels were probably not significantly reduced during this stage, strengthening the position taken by Anderson et al. (2009) that the diverse tetrapod fauna at Blue Beach effectively ruled-out atmospheric oxygen levels as a possible mechanism delaying the arrival of Mississippian tetrapod faunas. Models depicting fluctuating levels of atmospheric oxygen during the Early Carboniferous are otherwise very difficult to confirm, but should be resolvable if more effort in future is put towards gathering the appropriate data (Smithson et al., 2012).

Romer's Gap

The first tetrapods (stem tetrapods) were aquatic and very likely marine (Coates and Clack, 1995), and existed approximately 25 million years prior to the first known terrestrial tetrapod faunas. The 15-20 million-year long interval between the two apparently different lineages spans from the Devonian-Carboniferous boundary, across the entire Tournaisian and first half of the Viséan stages of the Lower Carboniferous (Romer, 1941, 1956; Clack, 2002a). The interval has been given the name Romer's gap (Coates and Clack, 1995), and is crucial to our understanding of the conquest of land. Terrestrialization is seen as two significant events. In the first stage, a few stem tetrapods began turning terrestrial. In the second stage, stem tetrapods gave rise to the crown-group lineages (Warren and Turner, 2004). The origins and early interrelationships of the crown-group tetrapods remain unresolved, with no consensus or resolution in their phylogeny (Anderson, 2003; Wiens, 2003).

Romer's gap has been cited as key to our understanding of crown-group origins. If we can clarify the primitive character states and evolutionary patterns leading to the crown-group origins, we can begin to resolve their phylogeny, and better understand the ascent of all later land vertebrates. Resolution of these unknown origins is expected to positively impact all studies in later terrestrial-vertebrate biology (Clack, 2002b).

There are numerous lines of evidence to now identify that Romer's gap was mostly an artifact of the available fossil sample (Anderson et al., 2009; Smithson et al., 2012) and that by improving our sample we improve some of our poorly resolved view of early tetrapod relationships. The importance of Blue Beach as a source of information was long underappreciated (J. Anderson, pers. comm., 2010), and clearly underutilized, as there has been no major support for its research over the years. In the past, sporadic and temporary fieldwork at the site turned up a few results, whereas year-round patrolling of the same beach has proven to be exponentially productive. An intensive multidisciplinary paleontological approach at Blue Beach will be necessary if we are to gather the most complete and accurate information possible.

The hypothesis explaining Romer's gap as a biotic crisis due to low atmospheric oxygen levels is no longer supportable in the light of new finds that suggest other processes (such as transgressions) may have played a role instead. Secondly, evidence for wildfires contradicts the assumption that atmospheric oxygen had been depleted. Finally, results of analyses of fossil assemblages now known from the gap strongly support an early timeframe for the diversification and terrestrialization of (at least some) important groups of vertebrates and invertebrates, and their presence in Tournaisian assemblages raise further doubt with respect to the proposed oxygen crisis during Romer's gap (Ward et al., 2006). Special attention to the preparation of additional vertebrate material in the Blue Beach Museum can significantly further the aims of the Scottish studies (Smithson et al., 2012), with the common goal of understanding the earliest-known terrestrial stem tetrapods, and their ecological surroundings, by direct comparison of new fossil evidence.

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LITHOSTRATIGRAPHY OF THE LOWER PERMIAN (LEONARDIAN) CLEAR FORK FORMATION OF NORTH-CENTRAL TEXAS

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Abstract—Rocks known as Clear Fork (Leonardian Series, Lower Permian) are a well-known source of vertebrate fossils in north-central Texas and a celebrated producer of oil and gas in West Texas. In the former region, the Clear Fork is a continental redbed sequence nearly 400 m thick that accumulated on the landward side of the Eastern Shelf of the Midland Basin, where the name Clear Fork is applied to a thick marine interval. Approximately 200 km south of these redbed outcrops, Clear Fork exposures composed of alternating and intertonguing shallow-marine carbonates and paralic to terrestrial mudrocks were divided by early workers into the Arroyo (oldest), Vale, Bullwagon Dolomite, and Choza formations; these rocks grade into the entirely terrestrial sequence of north-central Texas. Although vertebrate paleontologists historically have used the marine-based formation divisions in the redbeds, such terms cannot be applied formally, and the Clear Fork is herein classified as a single formation in the northern terrestrial region.

Following the recent discovery of prolific fossil plant deposits in the Clear Fork of north-central Texas, extensive field work and subsurface studies were initiated to better understand the depositional origin of the formation. The Clear Fork is dominated by mudstone (80-85%) but also contains several fluvial sandstone units. The largest is located in the lower part of the Clear Fork and represents a braided bed-load system that is in part correlative to a regionally persistent shale that petroleum geologists have named Big Red or Vale Shale in the subsurface; this unit marks the most widespread influx of terrigenous clastic material on the Eastern Shelf during the Leonardian. Other fluvial systems that originated as high-sinuosity, suspended-load rivers contain abundant fossils in abandoned or restricted channel segments. An absence of fossil occurrences upwards in the Clear Fork corresponds to diminished fluvial sedimentation and the development of coastal sabkhas characterized by red mudstone, thin dolomites, and abundant gypsum.

INTRODUCTION

Since their initial description by W.F. Cummins in 1890, Lower Permian rocks of north-central Texas called Clear Fork have been inextricably linked to terrestrial vertebrate fossils. Cummins, who provided collections to the prolific paleontologist E.D. Cope, established the “Clear Fork beds” as a thick sequence of mainly nonmarine rocks, and Cope established the Clear Fork as a rich source of amphibian and reptile remains (Cummins, 1908; Craddock and Hook, 1989). Late in his life, the remarkable Cummins (1840-1931) also saw the name Clear Fork applied to major oil discoveries in Permian rocks of West Texas. This dual notoriety has resulted in the appearance of the name Clear Fork in hundreds of papers that range in topic from descriptive paleontology to petroleum geology, as well as dozens of maps and cross sections. The present paper seeks to summarize our understanding of the Clear Fork on the basis of field mapping and subsurface studies in north-central Texas and to use these findings to evaluate some previous paleoenvironmental interpretations of these rocks. As such, it is a companion paper to Nelson and Hook (2005), which applied similar treatment to the Pease River Group overlying the Clear Fork.

Our work was prompted by the discovery of numerous plant compression assemblages in the lowermost Clear Fork of north-central Texas in 1994 (Chaney and DiMichele, 2007) (Fig. 1). Although E.C. Olson, Nicholas Hotton, III, and other vertebrate paleontologists had collected extensively in this region since the 1940s, a general lack of geological data necessitated a multi-year field investigation to obtain stratigraphic and sedimentologic information required for the interpretation of depositional environments and paleoecological conditions. Olson’s published work and unpublished field notes were invaluable in the early stages of our investigation because he made cogent observations throughout the Clear Fork outcrop belt, despite the fact that nonmarine sedimentology was still in its infancy and reliable base maps did not exist at the time.

Much like Olson’s pioneering work in the field, regional stratigraphic investigations undertaken previously by L.F. Brown, Jr. were a welcomed starting point for a concurrent subsurface study of the Clear Fork. Although Brown’s published maps and cross sections address rocks below the Clear Fork (e.g., Brown et al., 1987), his large collection of annotated well logs includes thousands of Clear Fork records. These and other wireline and sample logs held by the Texas Bureau of Economic Geology, as well as additional logs obtained from the Texas Railroad Commission and private sources, were used to create structure maps and cross sections that were used to check both surface and subsurface correlations.

TECTONIC SETTING

Clear Fork sediments accumulated on the Eastern Shelf of the Midland Basin (Fig. 2). Throughout the Permian, the Eastern Shelf was a tectonically stable platform of extremely low relief. Sources of terrigenous sediment during Early Permian time included the Wichita-Arbuckle uplifts in southern Oklahoma, the Llano uplift in central Texas, and the newly formed Ouachita orogenic belt. The Wichita-Arbuckle uplift is a Pennsylvanian-age product of the Ancestral Rocky Mountains (ARM) orogeny, the Llano uplift is a long-lived cratonic upwarp comparable to the Ozark dome, and the Ouachita belt is a product of the continental collisions that created the supercontinent of Pangea during Middle and Late Pennsylvanian time (King, 1937; Houseknecht, 1983). Younger rocks now conceal the Ouachita deformed belt in Texas, except in the Big

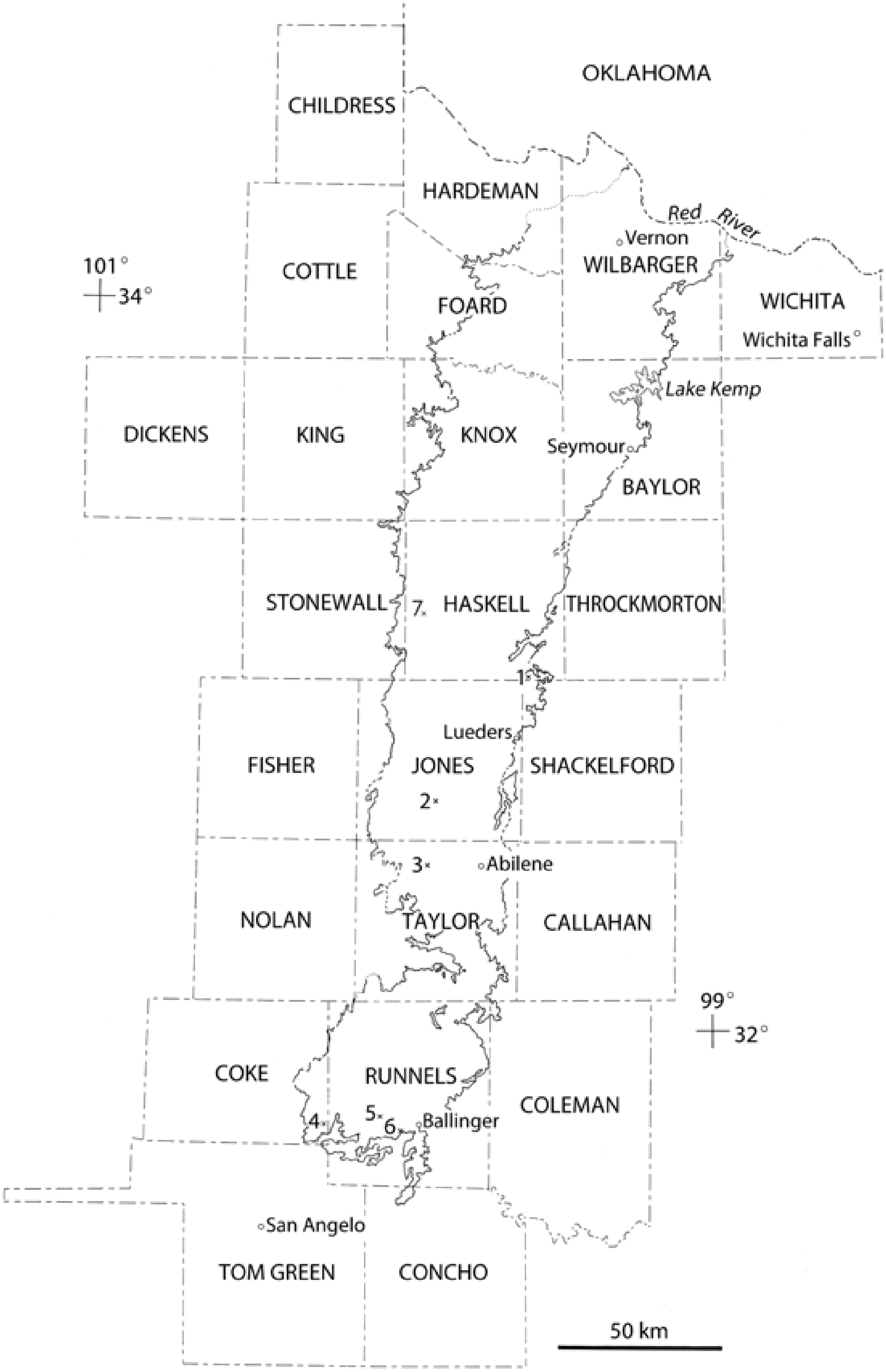


FIGURE 1. Map of part of Texas with generalized outcrop belt of the Clear Fork and localities mentioned in text: **1**, area of Cummins (1890) Clear Fork-Wichita contact; **2**, area of Cummins (1890) descriptions along the Clear Fork of the Brazos River; **3**, Bull Wagon Creek area of Wrather (1917); **4**, “Choza Mountain” area of Beede and Waite (1918); **5**, Vale area of Beede and Waite (1918); **6**, Los Arroyo area of Beede and Waite (1918), **7**, Double Mountain Fork area of Wrather (1917). Small or isolated Clear Fork outcrops south of Runnels County not depicted. Outcrop adapted from Geologic Atlas of Texas (Brown and Goodson, 1972; Eifler et al., 1993, 1994; Eifler, 1976; Hentz and Brown, 1987). For location within Texas, see Fig. 2.

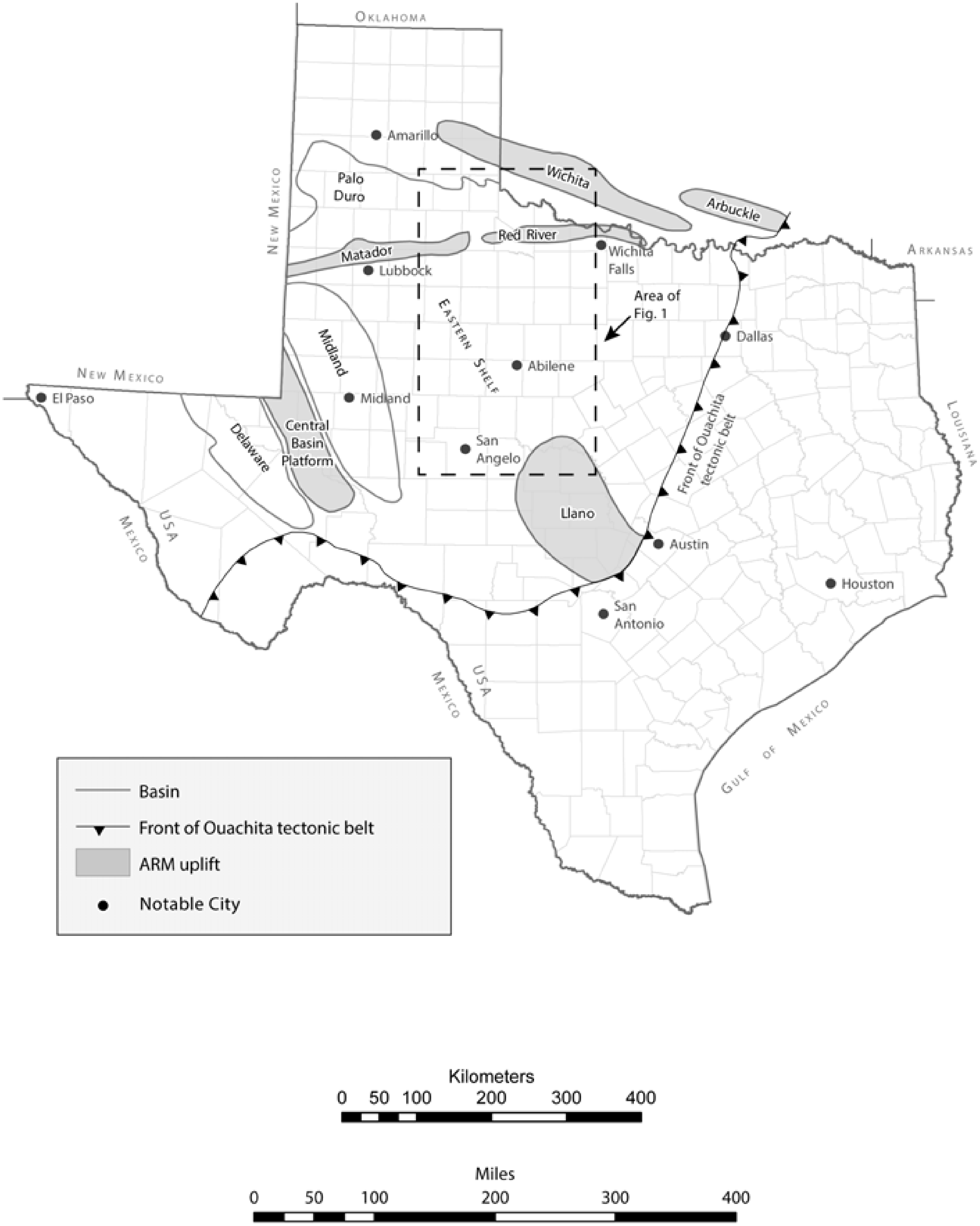


FIGURE 2. Map of major Lower Permian tectonic features of the southern U.S. Midcontinent, after Renfro et al. (1973).

Bend region to the far west. North of the Midland Basin, localized deformation took place along the Matador-Red River uplift during Permian time (Regan and Murphy, 1986a; Budnik, 1989; Brister et al., 2002), but this feature was not a significant source of sediment. The Palo Duro basin, which abuts our field area to the northwest, was a shallow trough on the north side of the Matador-Red River structure. Permian rocks of the Palo Duro basin were the focus of extensive studies by the Texas Bureau and Stone & Webster Engineering Corporation from the middle 1970s to middle 1980s.

A structure contour map (Fig. 3) illustrates elevation of the base of the Coleman Junction Limestone (Wolfcampian, base of Albany Group) in part of north-central Texas. The Coleman Junction is the youngest unit that can be identified consistently on wireline logs throughout the study area. It approximates Clear Fork structure, which is on average 300 m higher in the section. All well locations and elevations were verified with reference to topographic and other maps at the Texas Railroad Commission. Figure 3 also incorporates information from published and unpublished oil-field reports too numerous to list. The maps of Phonogprayoon (1972), Gunn (1976), and Altum (1990) addressed structure in the northern part of the area, although these authors did not map the Coleman Junction or other Permian units.

The Matador arch/Red River uplift (Figs. 2, 3) is the most prominent tectonic feature in the study area. The northwest-trending, en echelon arrangement of domes and anticlines supports an element of wrench faulting (Budnik, 1989; Ewing, 1990; Brister, 2002). South of the Matador/Red River, the Coleman Junction exhibits nearly uniform homoclinal dip, with a gradual eastward rotation of strike trend. North of the uplift, dip is more irregular, but overall dips are northward into the Hardeman basin. Clear Fork outcrops examined for this study lie south of the Matador/Red River structure, except in southern Hardeman County, where we observed upper Clear Fork outcrops north of the structural axis.

AGE

Biostratigraphers agree that the Clear Fork lies entirely in the Leonardian Series. On the international time scale, it falls into the middle part of the Kungurian Stage (Wardlaw, 2005; Lucas, 2006). Others have correlated the Lueders and lower Clear Fork with the older Artinskian Stage (e.g., Montañez et al., 2007).

Plummer and Scott (1937) described ammonites from the Arroyo Formation of the Clear Fork Group on the east side of Abilene and from the upper part of the Choza Formation in western Runnels County (Fig. 4). Faunal lists are short, but include forms characteristic of the type Leonardian Series. The fusulinid *Schubertella melonica* from well cuttings in the upper Clear Fork of Tom Green and Irion Counties matches the upper part of the Hess Formation, which is well below the top of the type Leonardian Series in the Glass Mountains of West Texas (King, 1937; Skinner, 1946). The same fusulinid occurs in limestone within the San Angelo Formation (Fig. 4), overlying the Clear Fork (Skinner, 1946, p. 1863). Finally, limestone directly overlying the San Angelo in wells from Ector County, Texas contains *Parafusulina fountaini*, which is known from outcrops only in the uppermost Bone Spring Formation (top of Leonardian) in the Delaware Basin (Mear, 1984).

Vertebrates and plants of the Clear Fork have limited value for correlation at this time. Taxa are either too long ranged, too few, or too poorly understood for critical assessment.

LITHOSTRATIGRAPHY

As noted in a previous synopsis (Nelson et al., 2001), a recurring problem in the Permian of Texas is the practice of applying the same name to rocks of widely differing lithology. The name Clear Fork has been attached to mixed limestone and mudstone in central Texas, redbeds in northern Texas, evaporites in the Panhandle, and dolomite on the Central Basin platform. Moreover, vertebrate paleontologists have persistently sought to apply the constituent Arroyo, Vale, and Choza Formations of the marine-influenced southern Clear Fork to the predominantly terrestrial collecting areas of north-central Texas (Romer, 1928; Olson, 1958; Murry and Johnson, 1987). Hentz (1988) addressed a similar issue in describing rocks immediately below the Clear Fork in north-central Texas. His solution was to apply separate formation and group names for the southern mixed marine-nonmarine lithofacies of the Albany Group and the northern redbed lithofacies of the correlative Wichita Group (Fig. 4). A similar bipartite classification for Clear Fork rocks would be welcome but never has been proposed, perhaps because the name is entrenched solidly in the literature and any attempt to change it would achieve little. Moreover, subsurface terminology used in the petroleum industry, has acquired legal status in settings such as well permits and production reports.

In this paper, and in conformity with the North American Stratigraphic Code (2005), the Clear Fork is retained as a group in central Texas and as a formation in north-central Texas (Fig. 4). Here we depart from our own earlier practice (Nelson et al., 2001) of calling the Clear Fork a group even where it is not divided into formations. Also in this report, we treat subsurface unit names as informal, except in cases where they have been explicitly formalized via publication. Informal usage is denoted by lower-case type for the generic parts of names, such as "upper Clear Fork formation" and "Fullerton member."

Name

Cummins (1890) first used the term "Clear Fork beds" in reference to strata overlying the Wichita and underlying the Double Mountain (now Pease River) in central Texas. The name refers to the Clear Fork of the Brazos River, which flows across the outcrop north of Abilene (Fig. 1). Wrather (1917) continued use of "Clear Fork beds" and presented two measured sections, one along the Texas & Pacific Railroad west from Abilene and the other along the Double Mountain Fork of the Brazos River in Haskell County. Beede and Waite (1918) described "Clear Fork stage" in Runnels County, including in it the newly named Vale (oldest), Bullwagon Dolomite, and Choza formations (Fig. 4). These authors assigned their newly named Arroyo Formation, below the Vale, to the Wichita stage. Sellards et al. (1932) transferred the Arroyo to the Clear Fork Group, establishing the present classification for central Texas.

No Clear Fork type section has been proposed. Given the paucity of outcrops in the type area, a meaningful reference section would be difficult to establish. The Clear Fork is mapped as an undivided group in the Geologic Atlas of Texas sheets, although the formation names Arroyo, Vale, and Choza are included in accompanying schematic stratigraphic columns as "alternative formational classifications used by earlier workers" (Brown and Goodson, 1972; Hentz and Brown, 1987).

Extent and Thickness

The north-south elongated outcrop of the Clear Fork extends for nearly 400 km from the Oklahoma border to central Texas (Fig. 1). Over much of the outcrop, and particularly at both north and south ends, Quaternary deposits obscure exposures, and a constriction of the outcrop belt south of Abilene reflects overlap by Cretaceous rocks. The unit continues northward into Oklahoma, where it is mapped with approximate equivalence as the Hennessey Group, a term based upon poor exposures in central Oklahoma and presented originally as the "Hennessey shale" (Aurin et al., 1926). Like the Clear Fork, the Hennessey lacks a type section.

In the shallow subsurface on the Eastern Shelf, the Clear Fork ranges from about 300 to 400 m thick, becoming thicker toward the north. These figures are based on our own interpretation of well logs, combined with those taken from published logs and cross sections (Conley et al., 1949; Day and Cheney, 1949; Hann et al., 1949; Noland et al., 1949; Cannon et al., 1953). The regional north-south section of Cannon et al. (1953) shows the Clear Fork increasing from a minimum of about

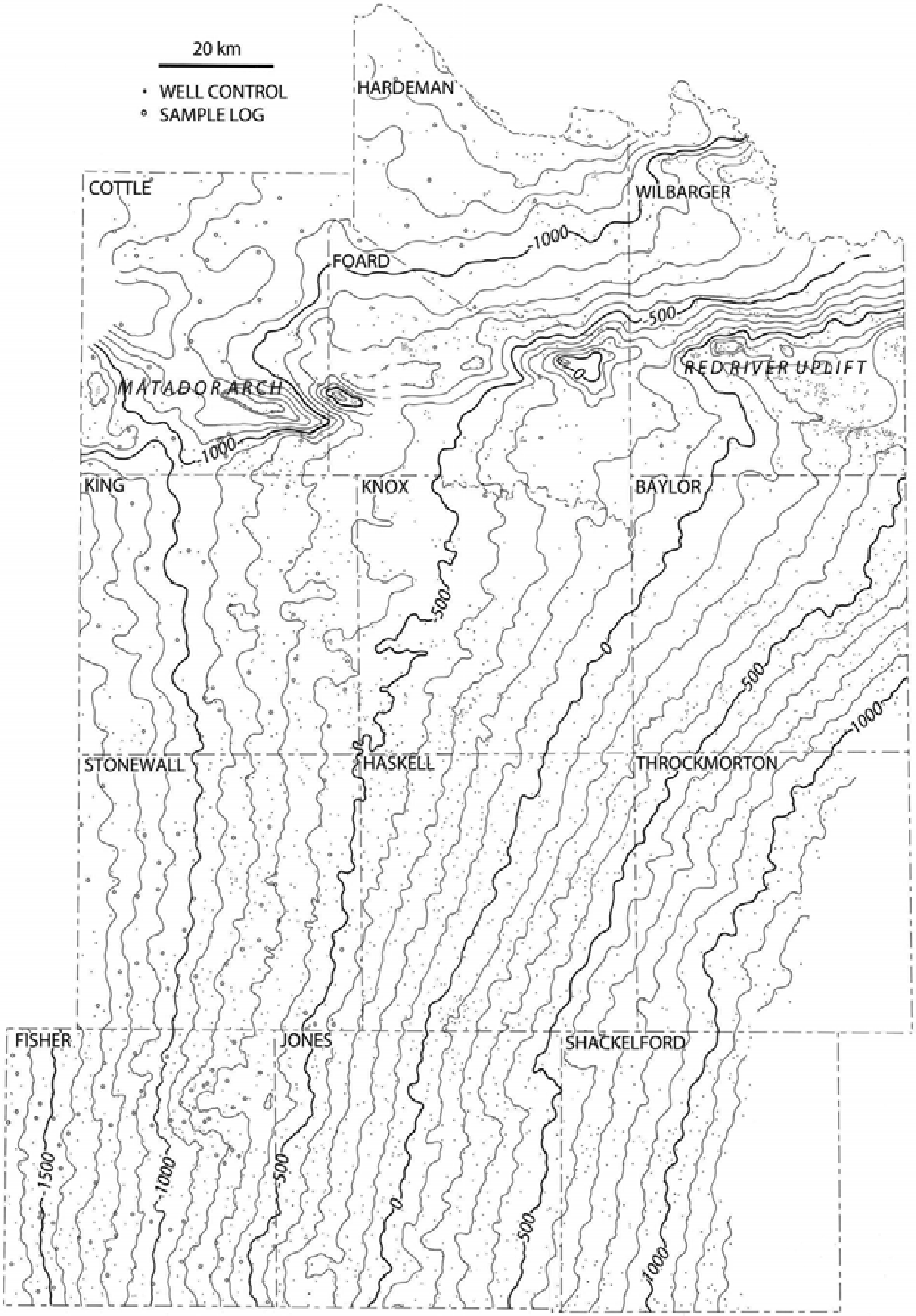


FIGURE 3. Structure map of part of north-central Texas, contoured on the base of the Coleman Junction Limestone (base of Wichita and Albany groups). Contour interval is 100 feet. In addition to the marked well control points, this map incorporates oil field data obtained from the open files of the Texas Railroad Commission.

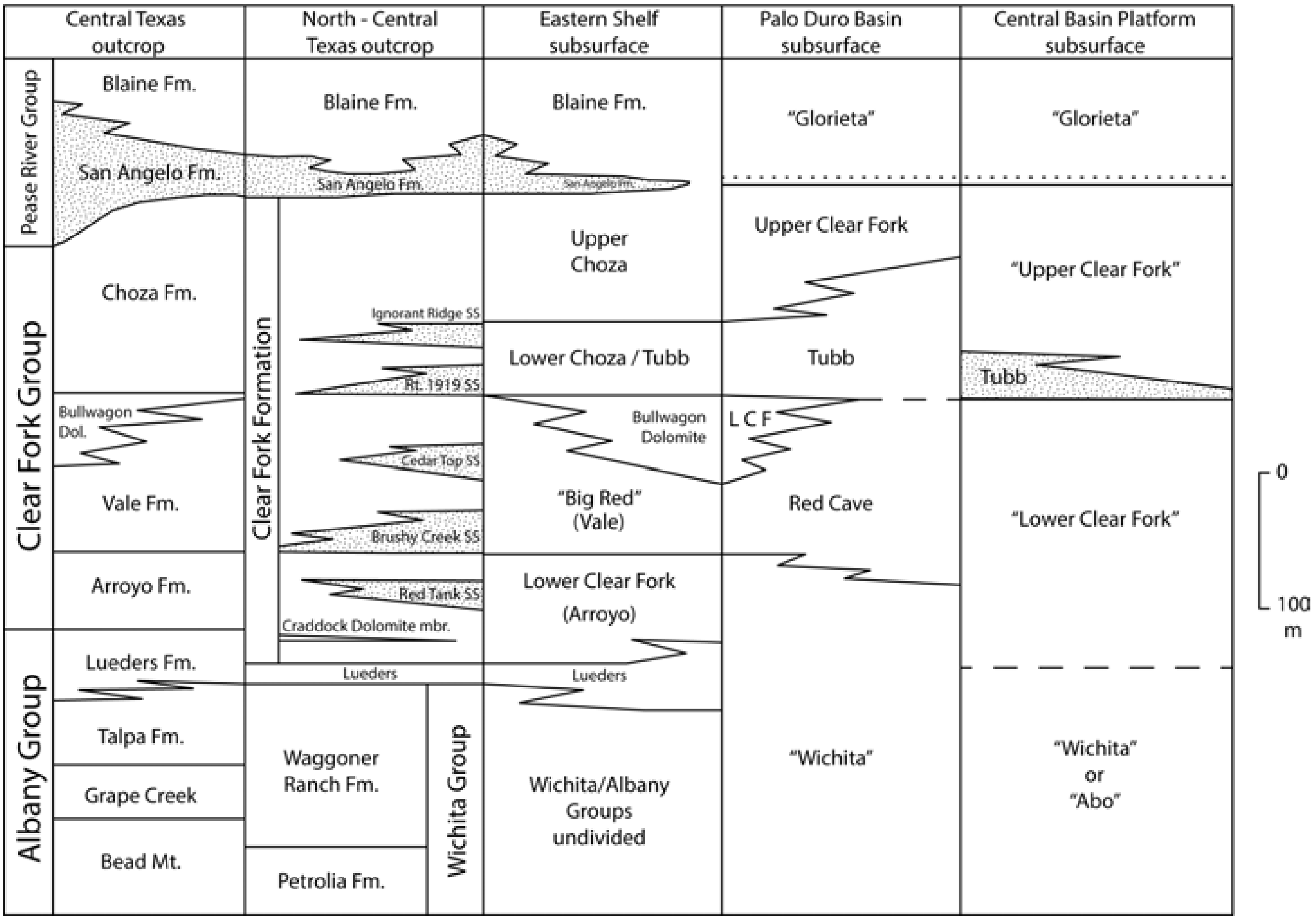


FIGURE 4. Correlation chart of the upper Albany/Wichita groups, Clear Fork Formation/Group, and Pease River Group from outcrop to subsurface of the Eastern shelf, Palo Duro basin, and Central Basin platform. **Abbreviation: LCF**, lower Clear Fork.

340 m in Tom Green County on the south to about 395 m in Childress County on the north. Thicknesses reported in the Geologic Atlas of Texas also indicate that the Clear Fork substantially thickens northward along the outcrop belt (Brown and Goodson, 1972; Eifler, 1976; Hentz and Brown, 1987). The most extensive Clear Fork exposures lie in modest breaks of the Wichita River drainage in the northern part of the outcrop in Baylor, Knox, Foard, and Wilbarger Counties, the classic vertebrate-producing redbed area.

The Coleman Junction structure map (Fig. 3) shows a homoclinal structure with a west-northwest dip that averages about 5 m per kilometer south of the Matador-Red River uplift. Because thickness of the Albany Group is consistent in the study area, this map provides a fair representation of Clear Fork structure. Dip estimates obtained from outcrop observations in the Clear Fork and underlying Lueders Formation agree closely with Coleman Junction structure in subsurface.

Contact Relationships

In north-central Texas, the Clear Fork is underlain conformably by interbedded mudstone and dolomite of the Lueders Formation (Albany Group), except in the northeastern corner of the outcrop, where Hentz and Brown (1987) established a stratigraphic cutoff between upper Albany and upper Wichita rocks in southern Wilbarger County. In the field, the contact between the uppermost carbonate bed of the Lueders and the basal mudstone of the Clear Fork is sharp and planar. Although the Lueders is not known to crop out in Oklahoma, the formation can be traced on a wireline log cross section that extends across the Red River (McGee et al., 1962), thus extending the base of the Clear Fork. At the latitude of Baylor County, the top of the Lueders can be traced confidently in the subsurface as far west as Dickens County. Cross sections and composite logs farther south, however, show an increase in limestone in the lower Clear Fork (Conley et al., 1949; Hann et al., 1949; Noland et al., 1949; Cannon et al., 1953); as noted by Cheney (1940, p. 97), this increase makes distinction between upper Albany and lower Clear Fork carbonates difficult.

In outcrops, the Clear Fork is overlain by the San Angelo Formation (Pease River Group). In north-central Texas, this contact is well exposed in numerous areas and generally regarded as conformable, although locally erosional (Nelson and Hook, 2005). In some exposures, the upper 2 m or less of the Clear Fork consist of a coarsening-upward, mudstone to sandstone sequence in which the sandstone develops channel features. Because the basal sandstones of the overlying San Angelo usually are coarser grained, recognizing the contact is not difficult. However, where the San Angelo pinches out down dip, abruptly and roughly perpendicular to the strike of the outcrop (Smith, 1974), differentiating the Clear Fork from the Pease River Group is problematic. Further subsurface study of this interval, particularly the regional continuity of dolomites close to the contact in the uppermost Clear Fork of central Texas, is needed.

Lithology

North-Central Texas

The Clear Fork Formation of Baylor, Knox, Foard, Hardeman, and Wilbarger Counties is a 350 m to 365 m thick terrestrial redbed sequence that consists of 80% to 85% mudstone, 10% to 15% sandstone, and less than 5% limestone, dolomite, and gypsum. Sandstone occurs mostly in the lower to middle part, whereas bedded gypsum and carbonate rocks are largely confined to the upper 120 m.

Nelson et al. (2001) divided the Clear Fork of north-central Texas into three informal units – lower (55-75 m thick), middle (125-160 m thick), upper (165-180 m thick) – and recognized several informal beds and members. The accompanying graphic column (Fig. 5) was measured along the breaks of the Wichita River from Lake Kemp westward, with thicknesses adjusted to well logs.

Informal lower Clear Fork division

Although the lower division of the Clear Fork Formation is significantly thinner than the middle and upper units, it is the most diverse in depositional terms. The following description provides sedimentologic information in ascending stratigraphic order and represents a baseline for subsequent descriptions of the middle and, to a lesser extent, upper divisions. Additional details on fossil plant occurrences are included because we have only alluded to these data in previous papers.

The basal 14 to 17 m of the Clear Fork Formation in the Lake Kemp area (Figs. 1, 5) consist mainly of multiple mudstone-dominated coarsening-upward sequences that have been overprinted pedogenically. This is the only part of the formation in which coarsening-upward deposits occur in succession or over broad, mappable areas. Paleosol features include blocky structure, peds, slickensides, rhizoliths, pedogenic carbonate nodules and stringers, and vertical sequences related to pedogenic processes (DiMichele et al., 2006). Overall, pedogenic carbonate nodules are rare to absent in basal exposures and increase in abundance and size upward, but nodule-bearing horizons lack the higher degree of lateral continuity common in overlying Clear Fork deposits. In the upper part of the basal unit, large carbonate stringers follow listric slip surfaces (Fig. 6). A sandstone deposit exposed in a borrow pit ("Harmel Quarry" of DiMichele et al., 2006) represents an erosive-based fining-upward channel that includes a basal conglomerate of grain-supported rounded carbonate pebbles, overlain by fine to very fine grained noncalcareous sandstones with planar and low-angle trough crossbeds, ripple bedding, mudstone streaks, and fine organic debris ("organic hash"), followed by interbedded very fine-grained sandstones and mudstones. Basal scours and lateral accretion bedding indicate two to four cut-and-fill episodes or stories. Plant compressions and fusain fragments occur in very thin (< 3 cm) mudstone-dominated beds of the second story. The maximum observed channel depth is nearly 2 m, and the interval to the base of the Clear Fork is estimated at less than 2 m on the basis of nearby Lueders dolomite exposures. A second diverse plant assemblage was found at the same stratigraphic position some 3.8 km distant ("Pony Creek" of DiMichele et al., 2006); fossils were preserved in a fusain-rich gray claystone associated with small-scale trough crossbeds. However, the depositional context could not be determined because of very limited exposure. Other channels in the basal 14 to 17 m of the lower Clear Fork generally are smaller than the Harmel Quarry example and finer grained, with greater amounts of mudstone in lateral accretion beds.

The informally named Craddock dolomite member, approximately 15 m above the base of the Clear Fork, has been traced for at least 32 km along strike from the south side of Lake Kemp to the northern limit of outcrops in Wilbarger County (Fig. 7). The Craddock has a maximum thickness of 1.1 m and consists of one to four layers of light gray, microgranular dolomite separated by beds of greenish to purplish-gray mudstone. Algal lamination (Fig. 7), mud cracks, and nodular to brecciated texture are common. Raindrop impressions, fossil plants, and tetrapod trackways also have been documented (Lucas et al., 2011).

At an exposure south of Lake Kemp where the Craddock dolomite is locally indistinct, numerous carbonate nodules that contain semi-articulated skeletons of the small lysorophoid amphibian *Brachydectes* were found weathered-out of a variegated mudstone over an area of approximately 400 m^2. Such deposits occur sporadically upward for approximately 200 m in the Clear Fork and downward into the Lueders Formation and are believed to represent failed aestivation assemblages (Wellstead, 1991; DiMichele et al., 2006). Skeletons of the lungfish *Gnathorhiza* also occur in burrow deposits (Olson and Bolles, 1975) but only rarely in association with *Brachydectes*.

A predominantly red, mudstone-dominated interval ranging from 12 to 20 m in thickness separates the Craddock dolomite from the next informal member, the Red Tank sandstone (Fig. 5). Like other mudstone sequences in the overlying lower two-thirds of the Clear Fork Formation, this interval contains abundant pedogenic features (Fig. 8), and four paleosol varieties or pedotypes have been identified (DiMichele et al., 2006). Exposures in the Lake Kemp area and in north-central Wilbarger County include small to moderate (< 6 m maximum thickness) channel deposits, some of which eroded through the underlying Craddock member and contain generally thin basal conglomerates of dolomite pebbles. Lateral accretion beds composed of very fine-grained sandstone and mudstone are common. The uppermost part of the interval below the Red Tank sandstone includes sharp-based, fining-upward tabular sandstones less than 0.8 m thick that are very fine grained, calcareous, ripple bedded, and overlain by thinly to very thinly interbedded sequences of very fine sandstone and siltstone, some of which show dessication cracks. Although the lateral extent of these deposits cannot be determined in most exposures, some continue for tens of meters before grading into pedogenically modified mudstones; others appear to be laterally equivalent to resistant outliers of poorly sorted, massive conglomerate up to approximately 0.5 m in thickness.

Small but conspicuous lenses of gray clay-rich mudstones associated with some channels between the Craddock dolomite and Red Tank sandstone contain fragmentary to well-preserved plants, fusain, and cuprified wood, as well as xenacanth shark teeth and small palaeoniscoid fishes ("Craddock dolomite localities" of DiMichele et al., 2006). Although the renowned Craddock Bonebed (Broili, 1904; Williston, 1910, 1911) occurs in the middle part of this interval and is related to channel activity (Behrensmeyer, 1988), its origin is difficult to assess because the locality is topographically isolated and partially obscured. The varied preservational states and wide range of vertebrate taxa reported from this deposit, from freshwater sharks (*Orthacanthus*) to obligatory aquatic amphibians (*Diplocaulus*, *Trimerorhachis*, *Isodectes*) to fully terrestrial amphibians (*Dissorophus*, *Seymouria*) and higher tetrapods (*Diadectes*, *Dimetrodon*, *Edaphosaurus*, *Secondontosaurus*, *Varanosaurus*, *Araeoscelis*), suggest a multifaceted taphonomic history.

The overlying informal Red Tank sandstone member is known from low but extensive exposures that were mapped south and north of Lake Kemp, a distance of approximately 20 km along a north-northeast outcrop strike (Figs. 1, 5). As the name indicates, this unit contains much more sandstone than older Clear Fork rocks, and the sand is almost always very fine grained. In thickness, the interval ranges up to approximately 12 m and varies depending primarily upon the depth of basal scour. The main part of the unit is a fining-upward channel sequence characterized by one or more stories of lateral accretion sets that are broadly colored in alternating hues of contrasting reds and grays (Fig. 9). These beds show depositional dip as steep as 25° and usually fine upwards and laterally upwards within each story. The upward increase in mudstone within each accretion set is accentuated by weathering to produce a characteristic ridge-and-swale topography, which also reveals cross-cutting channel sequences in some areas. Continuous sandstone intervals up to 9 m thick occur, but most stories contain a fine-grained basal sandstone approximately 1 to 2.5 m thick that may be conglomeratic. This typically grades upwards into fine to very fine-grained sandstone with siltstone interbeds, silty mudstone, and if not removed by subsequent channeling, claystone. Medium-scale trough crossbeds and planar beds are limited to the lower, coarsest (though still fine to very fine grained) beds and, therefore, are not widespread. Very fine ripple bedding predominates, and massive beds are all but absent. Large slump

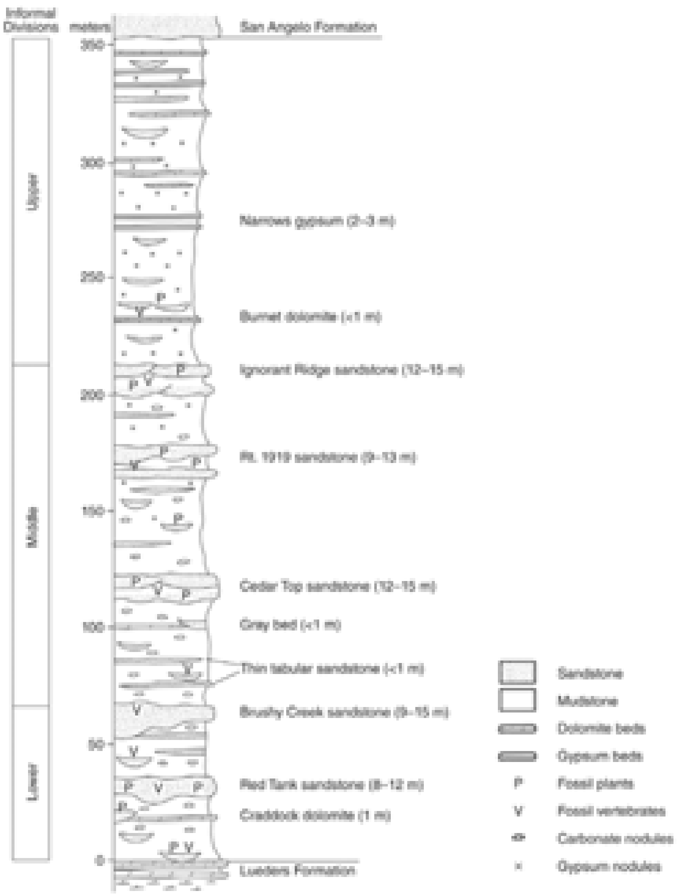


FIGURE 5. Composite section of the Clear Fork Formation along the Wichita River in Baylor, Foard, and Knox Counties based upon outcrop measurements with thicknesses adjusted to well logs.

blocks are common (15 to 30 m in length, 3 to 6 m in width, 3 to 4.5 m in thickness) and occur within multistory deposits or, more typically, along the margins (Fig. 10). Paleocurrent measurements, based chiefly on trough crossbeds, diverge widely from approximately S35°E to N70°W and average a south-southwesterly trend roughly parallel to general outcrop strike. One large channel unit that was mapped for approximately 1.6 km parallel to flow varied from 7.6 to 10.6 m in thickness and had an estimated width of 300 m, with steep, locally slumped, margins.

A tabular, fining-upward conglomerate and sandstone less than 2.1 m thick overlies the channel lithofacies of the Red Tank sandstone on both sides of Lake Kemp and can be traced for up to a kilometer in some areas. The base of this unit is sharp and in places erosive. Most conglomerate clasts are pebble-size carbonate nodules derived from paleosols and have a winnowed appearance where the rock is clast-supported.

The Red Tank sandstone hosts most of the classic vertebrate localities enumerated in the "Kemp Lake" area by Romer (1928) and has more recently been discovered as a source of abundant and well-preserved plant compressions (DiMichele et al., 2006; Chaney and DiMichele, 2007). Plants are preserved in various shaly mudstones, but most prolifically in thinly laminated claystones to very thinly bedded siltstones that are characteristically banded and/or variegated in shades of maroon to greenish gray; yellow-brown limonite nodules usually accompany the plants and add to the spectrum. On outcrop, these fossil-bearing units occur within thicker shale sequences that are several tens of meters wide and have broadly U-shaped lower contacts in lateral perspective. These shales are directly underlain by non-fossiliferous channel lithofacies, abutting laterally accreted sandstones or basal conglomerates in a remarkably sharp contrast of grain sizes. Although most shale deposits are truncated by subsequent channels, more complete examples coarsen upward into mudstones that have weakly developed pedogenic features. Individual plant beds range up to 0.6 m in thickness and may occur at multiple horizons within a single shale or mudstone deposit. Excavations at several localities revealed a recurring suite of internal bedding features, including primary and penecontemporaneous features (ripple and contorted bedding, millimeter-scale slumping and faulting) and secondary (related to loading, compaction, and/or dewatering), but no clear evidence of bioturbation. Conchostracans, myriapods (Baird, 1958), palaeoniscoid fish scales, shark cartilage fragments, and heteropolar coprolites all rarely accompany fossil plants; other vertebrates occur in separate parts of the shale sequences. The most completely exposed shale unit is 5.7 m thick and can be traced in intermittent exposures for over 900 m. With observed widths averaging approximately 57 m and concave-up cross sections, these deposits have distinctive channel geometries within the Red Tank member.

The 12 to 18 m thick interval between the Red Tank sandstone and the next informal unit, the Brushy Creek sandstone member (Fig. 5), is not well exposed because it consists primarily of slope-forming, reddish gray to reddish brown mudstones that are usually vegetated, talus covered, or both. Near the southwest side of Lake Kemp, fining-upward mudstone-dominated sequences from 2.5 to 4.5 m thick have thin (< 0.6 m) lenticular very fine-grained, calcareous, basal sandstone, overlain by calcareous siltstone and claystone. The mudstones have well-developed pedogenic features, including carbonate masses along slickensided planes and abundant carbonate nodules. Other thin but more tabular calcareous sandstones in the middle part of the unit extend for over 1.5 km, commonly show desiccation cracks, and include local algal-like, finely crenulated laminations and abrupt gradations into silty limestone. Partially to poorly exposed channel deposits up to 6 m thick occur at the top of the interval and consist largely of siltstone with few sandstone beds in lateral accretion sets and thin basal conglomerates. Although some of these channels are associated with gray or variegated limonitic shales similar to those of the Red Tank member, they did not yield plant remains.

Numerous sedimentary criteria serve to distinguish deposits of the Brushy Creek sandstone member from all other Clear Fork sandstones: (1) it is thicker and more deeply incised; (2) it contains a higher percentage of sand and larger grains (fine as opposed to very fine); (3) it features a predominance of grain-supported mudstone-pebble conglomerates instead of carbonate-pebble conglomerates; and (4) it exhibits larger scale bedforms (Fig. 11). An additional difference doubtlessly related to these attributes is that despite a dedicated search effort, the Brushy Creek did not yield any significant plant assemblages.

The Brushy Creek sandstone was mapped in the field for more than 30 km from the general area of Lake Kemp to southern Wilbarger County (Fig. 1). The informal Clear Fork sandstone units ss4, ss5, and ss6, mapped by Hentz and Brown (1987) largely on the basis of aerial photographs, partly correspond to our Brushy Creek member. Two to three successive sandstone bodies that total 9 to 15 m in thickness typically comprise the Brushy Creek. Mudstone interbeds occur primarily in the upper part of these sandstone bodies and are a minor component overall. Lateral thickness variations in these sandstone units account for uneven tops and en echelon as well as vertical stacking patterns. Lateral accretion bedding is present, but far less prevalent and less steeply inclined than in the other Clear Fork channel lithofacies. Sandstones of the Brushy Creek have planar and trough crossbedding in sets as thick as 2.5 m in the lower part, and planar, ripple, and cross lamination in the upper part. Conglomerates are not limited to basal scours and commonly recur upward within individual sandstone bodies, but some exposures consisting of large-scale trough crossbeds all but lack conglomerates. Channels observed in modern-day river bluffs are as deep as 9 m and have nearly flat bottoms and steep, locally vertical margins. No paleoslumps were observed,. Limited paleocurrent data indicate a southwestward flow, roughly parallel to the strike of the outcrop. Toward the northeast, the sandstone becomes coarser grained (medium-coarse as opposed to fine) and increasingly arkosic, implying that the primary

FIGURE 6. Paleosol beneath Craddock dolomite, showing large listric carbonate stringers. Gray Creek, Baylor County. Rock hammer is 41 cm long.

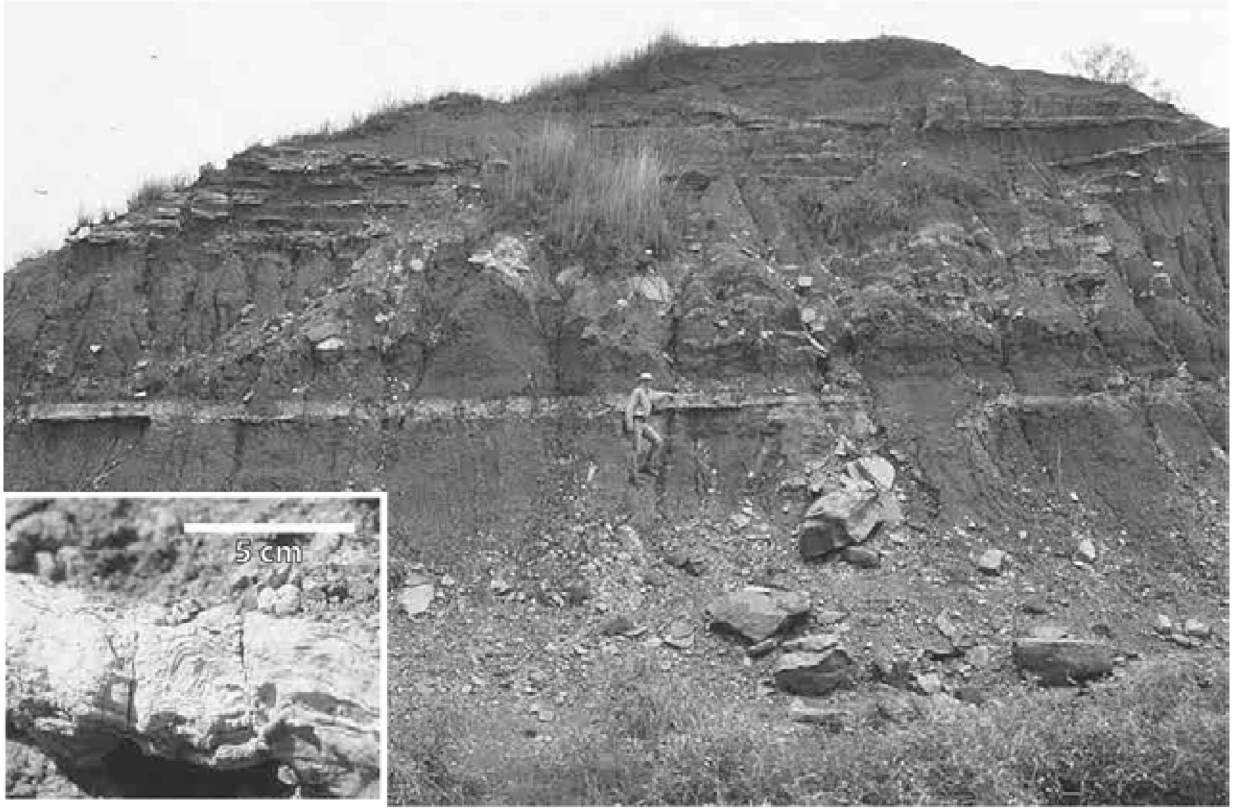


FIGURE 7. Craddock dolomite, a conspicuous bed encased by paleosols at the hand level of W.J. Nelson. A single-story channel forms the upper part of the exposure. Inset shows algal laminations in dolomite. Beaver Creek area, Wilbarger County.

FIGURE 8. Paleosol features as exposed on outcrop below the Red Tank sandstone, Baylor County. **A**, Network of dikes filled with very fine-grained, light-colored sandstone; pick is 66 cm long. **B**, Calcareous rhizolith; rock hammer is 28 cm long.

FIGURE 9. Red Tank sandstone member, Baylor County. **A**, Multiple fining-upward, mudstone-dominated lateral accretion beds typical of upper point-bar deposits. **B**, Cross beds in the lower part of the Red Tank sandstone; hammer is 28 cm long.

sediment source was in the Wichita Mountains. Work in the underlying Wichita Group (Hentz, 1988) and subsurface mapping of sandstone bodies in the upper part of the deeper Cisco/Bowie groups (Brown et al., 1990) indicate the Wichita Mountains had long been the main sediment source for this area.

Informal middle Clear Fork division

Field study of the middle division of the Clear Fork Formation extended westward from the Wichita River drainage of west-central Baylor County into the drainages of the North and South Forks of the river in southeastern Foard and northeastern and central Knox Counties (Fig. 1). The division extends from the top of the prominent Brushy Creek sandstone upward for approximately 125 to 160 m to the top of the informal Ignorant Ridge sandstone member (Fig. 5). Although the Ignorant Ridge sandstone and the two lower informal members, the Rt. 1919 and Cedar Top, are very similar and can be characterized by a single description, the mudstone-dominated intervals of the middle Clear Fork change in character upward through the section. In general, however, the mudstones are dark reddish brown silty claystones to reddish brown siltstones that exhibit abundant pedogenic features in multiple fining-upward sequences; thick mudstone deposits range upward to approximately 7.2 m and represent compound or cumulative paleosols (DiMichele et al., 2006).

A thick (43 to 46 m), predominantly mudstone interval represents the basal middle Clear Fork (Fig. 5). Three thin tabular beds within the interval are widespread and facilitate correlations. The mudstone sequence immediately above the Brushy Creek changes in thickness (3 to 7.6 m) according to variations in the underlying sandstone and contains numerous small to large carbonate nodules and stringers. An overlying thin (< 1.5 m), light colored, very fine-grained, calcareous sandstone is the lowest laterally persistent bed (lower "Thin tabular sandstone" in the middle Clear Fork of Figure 5). This bed commonly exhibits planar, wavy, and ripple lamination, as well as local crossbedding, desiccation cracks, and few poorly preserved plant impressions and tetrapod footprints. The second marker bed (upper "Thin tabular sandstone" in the middle Clear Fork of Figure 5) is a similarly widespread but thinner (< 0.4 m), very fine-grained, tabular, calcareous sandstone that occurs on average 10 m higher in the section and contains desiccation cracks and small gypsum crystals. Between these two marker beds in an area of poor exposure north of the west end of Lake Kemp, the eroded tops of lateral accretion beds record a multistory, mudstone-rich channel lithofacies that locally cuts-out the lower tabular sandstone bed; a vertebrate collecting site (Baa of Olson, 1958, p. 435-437) occurs in this particular area, and a low-diversity plant assemblage was found nearby in a thin (0.24 m), limonitic, clay-streaked siltstone. With the exception of another occurrence that was even less productive, this is the only noteworthy plant deposit found below the level of the Cedar Top sandstone in the middle Clear Fork.

In the upper half of the interval between the Brushy Creek and Cedar Top sandstones, a thin (0.6 - 0.9 m) but distinctive and persistent, gray, calcareous claystone layer represents the third marker bed (Fig. 5); it grades downward into a maroon to dark reddish brown claystone up to 2.4 m thick that has well-developed slickensides and peds but no carbonate nodules and is overlain by a layer of pebble-size silty limestone and dolomite nodules. The 11 to 15 m thick interval above this uppermost marker bed is a succession of fining-upward mudstone-dominated channel deposits that exhibit lateral accretion bedding. Although these deposits produced only fragmentary plant material, they are the source of several vertebrate collections reported by Olson (1958, localities Bz, Bw, possibly Bx).

The informal Cedar Top sandstone member is an approximately 12 to 15 m thick unit overlying the basal mudstone sequence of the middle Clear Fork (Fig. 5). Like the Rt. 1919 and Ignorant Ridge sandstones, the Cedar Top is characterized by scour-based, fining-upward, multistory channel deposits that consist of an intraformational basal conglomerate, fine- to very fine-grained sandstone, siltstone, and claystone. Individual stories range from about 3 to 6.5 m in thickness. The basal conglomerates are usually grain supported and include pedogenic nodules up to 3 cm across and subrounded to subangular red mudstone pebbles; beds range up to 2 m in thickness and are massive, crudely layered or interbedded with thin sandstone and siltstone beds, or crossbedded. Sandstones are typically very fine grained, but beds lower in a channel sequence are fine grained and exhibit small (< 0.25 m) low-angle trough and planar crossbeds. Ripple lamination is prevalent, and climbing ripples are common. Trace fossils, including simple horizontal burrows, vertical and inclined escape burrows, and myriapod trackways, along with rill marks and desiccation cracks are present in the upper part of lateral accretion beds. The lateral accretion beds themselves resemble those of the Red Tank sandstone in having steep depositional dips that approach 25° and in comprising one- to four-story sequences. Slump blocks are present but far less common than observed in association with Red Tank exposures. The channel lithofacies of the Ignorant Ridge sandstone member is between 750 and 800 m wide. Paleocurrent indicators for, and map expression of, all three middle Clear Fork sandstones (Cedar Top, Rt. 1919, Ignorant Ridge) evidence a south-southwesterly transport direction. Edwards et al. (1983) illustrated the ridge-and-swale topography and arcuate-to-semicircular plan view of eroded lateral accretions beds in the Rt. 1919 sandstone; however, their roadcut-based calculation of bank-full channel depth (2.6 m) is less than can be discerned readily from adjacent natural exposures.

Local channel-form mudstone deposits within the three sandstone members of the middle Clear Fork contain significant plant accumulations (Fig. 12). These deposits resemble the fossiliferous coarsening-upwards shale deposits of the Red Tank sandstone in that they occur in the finest grained portion of the channel deposits, yet they differ from the Red Tank in several aspects. In the middle Clear Fork sandstone members, well-preserved plant compressions occur in a greater variety of rock types: fissile red claystones; thinly interlaminated limonitic red claystones and variegated gray-green siltstones; blocky to massive clayey red siltstones with minor gray-yellow limonitic mottling; and sandy, rippled, red siltstones (see Chaney et al., 2009, for color photographs of material from the Rt. 1919 sandstone member). Overall, most of the plant-bearing beds are siltier, even though the most well-preserved specimens usually occur in clay-rich laminae. At the base of the plant beds, a juxtaposition of grain sizes occurs within an abrupt (< 0.5 cm) fining-upwards transition, which differs from the knife-edge contacts found below most Red Tank plant deposits. Individual plant beds range up to 1.4 m in thickness and generally have limited lateral continuity, but multiple plant beds may occur within one deposit. In addition to the sedimentary and structural features noted above in the Red Tank examples, some of the middle Clear Fork plant deposits have a wavy fabric that resulted from foliage accumulating in densely overlapping mats. Whereas myalinid pelecypods, coprolites, fragmentary shark remains, palaeoniscoid fishes, and amphibians (e.g., Anderson et al., 2008) occur rarely with the plants, a wide diversity of vertebrates is known from associated deposits discovered by Olson (mostly termed middle and upper Vale in Olson, 1958). The plan-view dimensions and shape of fossiliferous deposits in the middle Clear Fork is less well defined than those in the Red Tank sandstone because of differences in exposure; apparent widths range up to 32 m with a longer dimension of 71 m, but some examples may be more linear if neighboring fossiliferous exposures were formerly contiguous.

Another thick (24 – 30.5 m) mudstone-dominated interval occurs above the Cedar Top sandstone and separates it from the Rt. 1919 sandstone member (Fig. 5), which in turn is separated from the Ignorant Ridge sandstone member (Fig. 13) by a thinner (4.6 – 13.7 m) mudstone-dominated interval. The differences between the two mudstone sequences are subtle and involve color and the relative abundances of carbonate and gypsum: the lower sequence of reddish brown mudstones contains abundant pedogenic carbonate nodules and small amounts of gypsum, and the

FIGURE 10. Red Tank sandstone member paleoslumps, Baylor County. **A**, Paleoslump composed of steeply dipping sandstone and conglomerate (at level of hammer), underlain by paleosol (left and below) and overlain by horizontal sandstone showing lateral accretion beds and fossiliferous channel fill (upper right); rock hammer is 41 cm long. **B**, Paleoslump in multistory channel. Slumped beds dipping very steeply to right are truncated by horizontal sandstone at level of Nicholas Hotton's head.

FIGURE 11. Brushy Creek sandstone in bluff of Wichita River west of Lake Kemp, Baylor County. R.W. Hook in middle is at base of Brushy Creek, which appears massive from a distance but shows large-scale trough crossbedding on close inspection. Below the Brushy Creek are upward-fining point-bar deposits of a precedent channel.

upper mudstone sequence is reddish gray to reddish brown with gray to greenish gray mottling and contains increased amounts of gypsum and diminished carbonate nodules. In this respect, the lower mudstone more closely resembles deposits in the basal middle Clear Fork, while the upper mudstone has similarities with the gypsum-rich upper Clear Fork. The gypsum of the middle Clear Fork occurs as rosettes, veins, and dikes. Both mudstone sequences include minor amounts of sandstone in small channels and restricted, thin, tabular beds that commonly show dessiccation cracks. Neither sequence has produced significant plant remains.

Informal upper Clear Fork division

At over 165 m thick, the upper division of the Clear Fork Formation is the thickest and most widespread of our field area (Fig. 5). In contrast to the sedimentologically diverse lower and middle Clear Fork, the much thicker upper Clear Fork has been characterized as "monotonous" because of its relatively homogeneous character (Nelson et al., 2001). Exposures continuous with those of the middle Clear Fork were examined in southeastern Foard and northeastern and central Knox Counties, and outcrops of the uppermost part of the Clear Fork and overlying San Angelo Formation were studied over a wide area from south-central Hardeman County in the north to southeastern Stonewall County in the south (Fig. 1). Additional control was achieved through use of well logs, on which thin but laterally persistent markers can be identified in the upper Clear Fork.

In general, the upper Clear Fork is composed of reddish brown blocky mudstone and claystone with thin but persistent layers of greenish gray siltstone and very fine-grain sandstone. Gypsum is abundant and occurs as thin layers as well as in flattened spheroids, nodules, and dikes; bedding plane exposures reveal distinctively configured gypsum deposits, including polygonal patterns known as "chicken wire." Beds of gypsum range up to 0.3 m, and thinly interbedded units of gypsum, dolomite, and mudstone approach a meter in thickness. Pedogenic carbonate nodules are absent except in the basal few meters, and paleosols are only weakly developed overall. Silty dolomite is present as nodules in mudstone, large flattened concretions, and semi-continuous beds a few cm thick.

Layering is highly tabular, and even thin (< 10 cm) units are traceable for over a kilometer in some areas. The two informally named beds shown on Figure 5 are examples of laterally persistent units in the upper Clear Fork. The Burnet dolomite occurs approximately 15 to 22 m above the top of the Ignorant Ridge sandstone and includes one to three, thin (< 10 cm) yet widespread microgranular dolomites. A second tabular unit, the Narrows couplet, is present approximately 40 m higher in the section, consists of two thin beds of interlaminated gypsum and dolomite separated by 1 to 2 m of mudstone (Fig. 14), and can be traced for several kilometers. Other thin continuous dolomites occur in the top of the interval but their extent has not been determined. Tabular clastic beds have a lower degree of lateral continuity and consist of very fine- grained sandstone to siltstone. Some are laterally equivalent to small (< 3 m

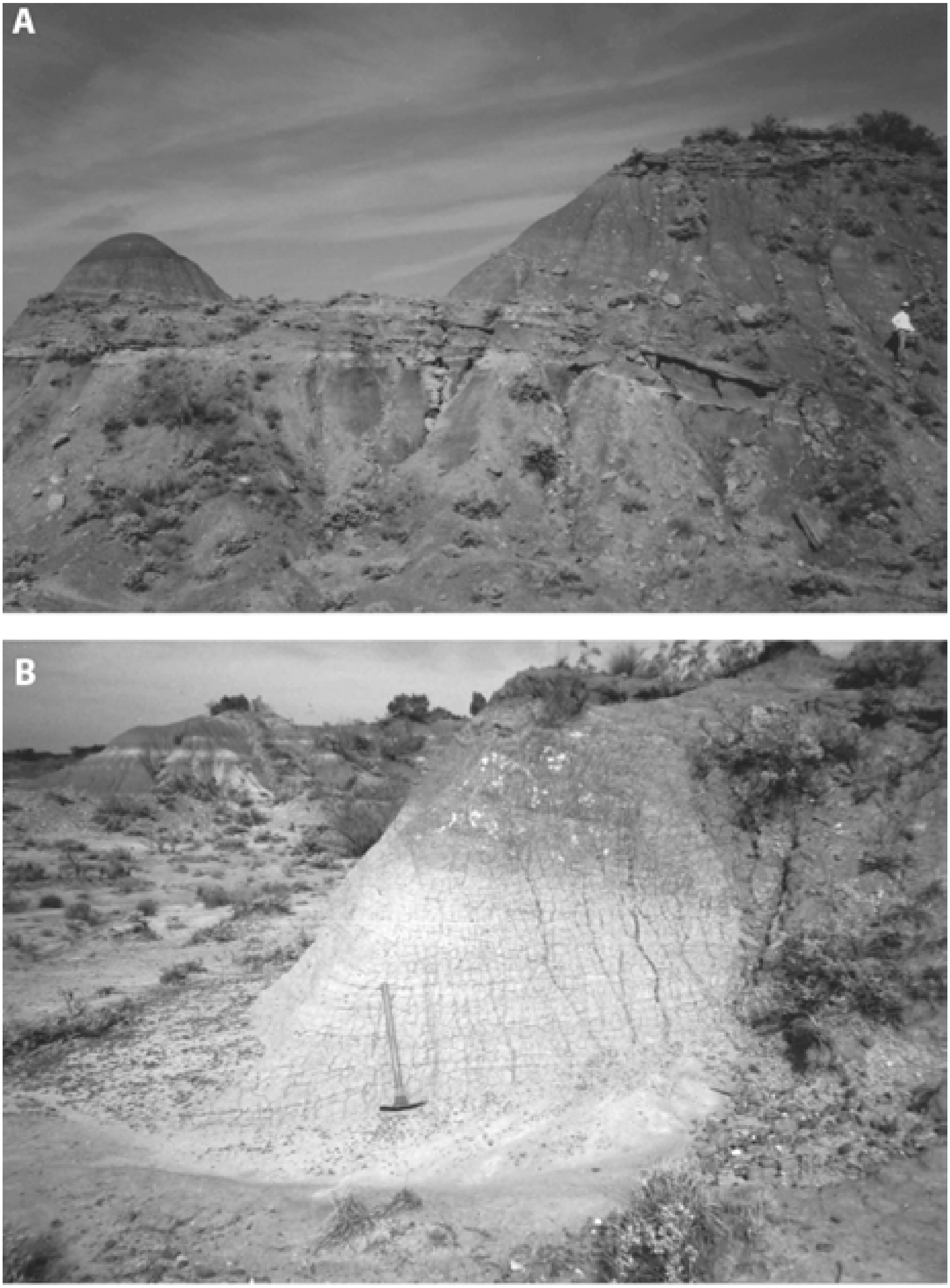


FIGURE 12. Middle Clear Fork exposures of Baylor and Knox Counties. **A**, Multistory channel and U-shaped fossiliferous channel fill in Cedar Top sandstone member; D.S. Chaney stands above second channel story to right; clay-rich channel fill forms knob to left. **B**, Fossiliferous fine-grained, laminated channel-fill deposit in Ignorant Ridge member; Pick is 66 cm long.

FIGURE 13. Mudstone-dominated, multi-story channel deposits, Ignorant Ridge sandstone member, Knox County. Note lateral accretion in second story above R.W. Hook.

thick), single story channel deposits that have gently inclined lateral accretion beds; because of the discontinuous nature of limited exposures, it is not possible to demonstrate a certain depositional relationship.

The uppermost occurrence of a multistory channel lithofacies comparable to those of the middle and lower Clear Fork occurs immediately above the Burnet dolomite in southeast Foard County. This is the only example known from the upper Clear Fork, which otherwise lacks substantial sandstone deposits, and also is the source of the youngest well-preserved plant remains from the formation. This same area and approximate stratigraphic level represent the highest occurrence of Clear Fork vertebrates reported by Olson (1958). Subsequent field work by Murry and Johnson (1987) and continued collecting efforts by Gary D. Johnson into the mid-1990s did not produce vertebrates in the upper 120 m or more of the upper Clear Fork formation.

Gypsum dikes and masses occur in the multistory channel facies much as they do throughout this area. Although gypsum is pervasive in the upper Clear Fork, it is not ubiquitous, and comparison of geographically separated but correlative intervals shows that gypsum abundance varies laterally and, in fact, is nearly absent in some exposures. These variations did not appear to be related to dissolution and may reflect subtle differences in host sediments.

Central Texas

In central Texas, the Clear Fork is ranked as a group comprising the Arroyo (oldest), Vale, Bullwagon Dolomite, and Choza formations (Fig. 4). Where the Bullwagon is thin, it may be classified as a member of the Vale. None of these units have specific type sections. Low topographic relief and a paucity of outcrops characterize this region; therefore, our efforts were limited to a reconnaissance of previously reported and/or available exposures. Descriptions that follow are largely taken from county mapping reports of the early 20th century. Detailed sedimentologic and paleoecological investigations of these rocks have not been undertaken.

Beede and Waite (1918) named the Arroyo Formation for a stream called Los Arroyo (Los Arroyos on current maps), about 3 km west of Ballinger in Runnels County (Fig. 1). In this and adjacent counties, the Arroyo is about 45 to 80 m thick and consists of limestone and shale or mudstone in roughly equal proportions (Fig. 15). Limestone yields a varied fauna of brachiopods, pelecypods, gastropods, cephalopods, ostracods, spirorbids, and fish and shark remains (Beede and Waite, 1918; Henderson, 1928; Coryell and Rogatz, 1932; Moore, 1949; Olson, 1989). Interbedded fissile shale and non-fissile mudstone are variegated in greenish, bluish, olive, and reddish gray. These rocks are commonly calcareous and contain nodules of limestone. Mud cracks, root traces, and other paleosol features are present. Northward into Taylor and Jones Counties, mudstone becomes prevalent at the expense of limestone, red colors become more common, and sandstone appears. The Rainey (oldest), Lytle, Kirby Lake, and Standpipe Limestone members have been named (Cheney, 1929; Lloyd and Thompson, 1929). In these, marine fossils give way northward to brackish-water and terrestrial forms, including linguloid brachiopods, mollusks, serpulid worms, fishes, sharks, amphibians, and *Dimetrodon* (Olson, 1989). As limestone members pinch out farther north in Haskell County, the Arroyo Formation loses its identity.

The Vale Formation (Beede and Waite, 1918) takes its name from a post office that formerly stood about 12 km northwest of Ballinger. This unit is a succession 15 to 130 m thick red to brown mudstonemudstone with very minor sandstones 15 to 130 m thick. The mudstone is largely non-fissile and contains both thin, tabular sandstone bodies and channel-form sandstone bodies. Fossils consist of terrestrial plants along with a variety of sharks, bony fishes, amphibians, and reptiles (Wilson, 1953; Dalquest and Mamay, 1963; Olson and Mead, 1982).

Overlying the Vale mudstone is the Bullwagon Dolomite, which Wrather (1917) named for Bull Wagon Creek in Taylor County, west of Abilene. The dolomite thins northward from more than 50 m in Tom

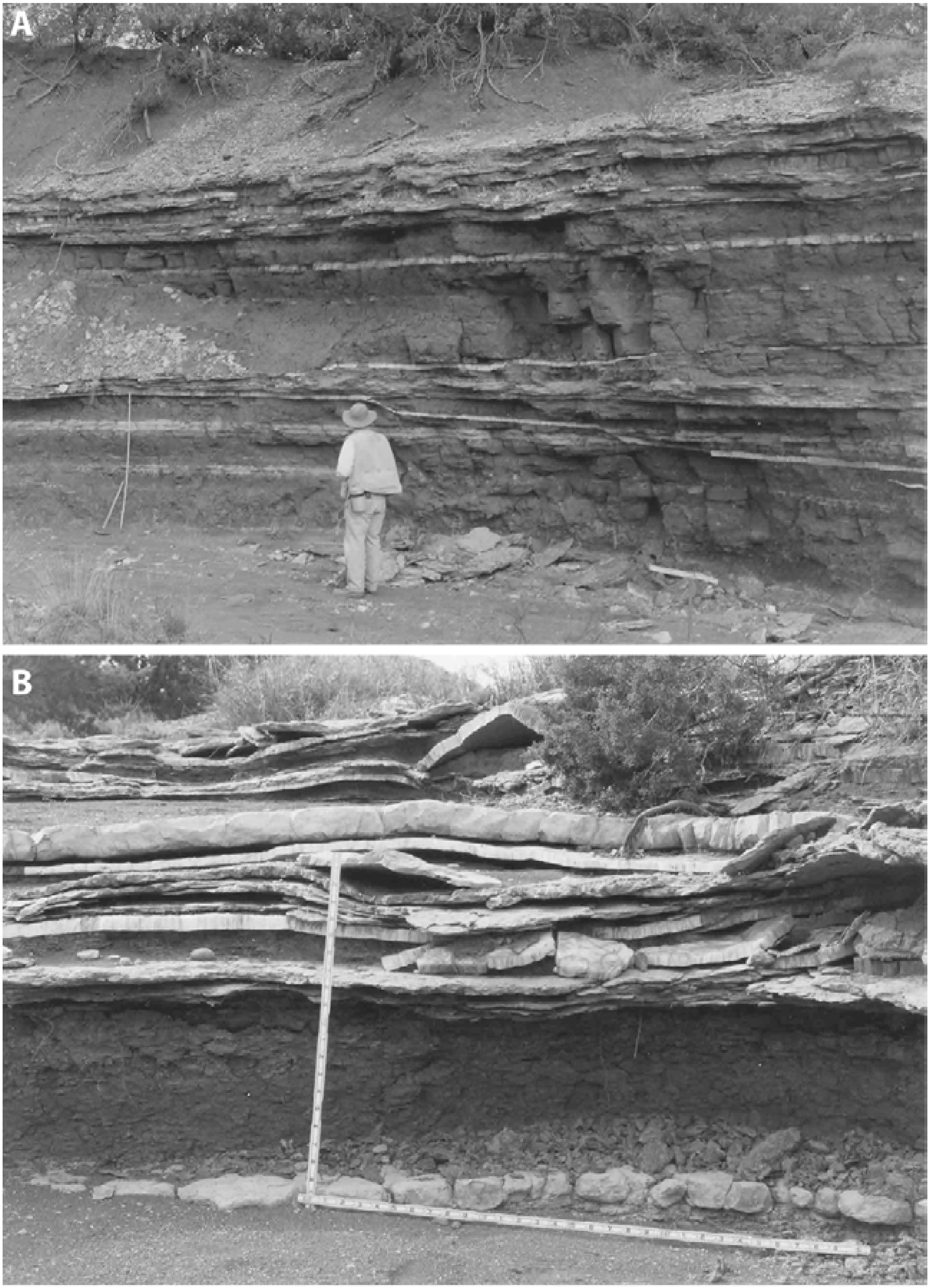


FIGURE 14. Marker beds of the upper Clear Fork in Knox County. **A**, “Narrows couplet” in upper Clear Fork, Knox County. Lower couplet of dolomite and gypsum at shoulder level of R.W. Hook, upper couplet approximately 1.75 m higher. **B**, Upper unit of “Narrows couplet,” consisting of satin spar gypsum interbedded with red mudstone, and thin dolomite at base. Knox County. Ruler graduated in feet and tenths.

FIGURE 15. Interbedded marine limestone and mudstone on Los Arroyo, lower Clear Fork, nominal area of type Arroyo Formation, Runnells County.

Green County to a feather-edge in central Haskell County, where it grades into "evenly bedded, pastel sediments" (Olson and Mead, 1982, p. 6). Sellards et al. (1932) observed that the Vale and Bullwagon exhibit a reciprocal thickness relationship. Our own data collected from well logs, along with information published by Day and Cheney (1949) and Hann et al. (1949), confirm this observation and indicate that Vale mudstone and Bullwagon carbonate beds intertongue, with the youngest beds of the Bullwagon extending farthest up the Eastern Shelf. Published descriptions of the Bullwagon are incomplete. Dolomite and dolomitic limestone are white to light gray, "fine grained," and locally sandy. Wrather (1917) observed small ripple marks, mud cracks, and raindrop impressions in outcrops near the northern limit of the unit. Henderson (1928) reported a fauna of cephalopods, pelecypods, and gastropods in Tom Green County. Interbedded with the carbonate rocks are calcareous mudstone, siltstone, and fine sandstone ranging in color from gray to green, yellowish gray, and red.

Overlying the Bullwagon-Vale succession is the Choza Formation, which takes its name from Choza Mountain (Beede and Waite, 1918). This is problematic because the feature has never appeared on a map to our knowledge. When Beede subsequently published a report on Coke County (Beede and Bentley, 1920), he did not illustrate the location of "Choza Mountain" on his county geologic map (other topographic eminences are included), nor did he elaborate the location in text. As best as we can determine, Beede based this unit upon very modest outcrops approximately 4.5 km east of of Tennyson, an area that lacks extensive exposures. Because unit thicknesses reported by Beede cannot be confirmed and do not agree with subsurface records, they should be dismissed. In the shallow subsurface, thickness ranges from 90 to 195 m, but typically is 150 to 180 m. The thinnest Choza occurs near the southern end of the outcrop belt, where the San Angelo Formation appears to downcut the unit. Otherwise, a gradual northward thickening trend can be discerned (Conley et al., 1949; Day and Cheney, 1949; Hann et al., 1949; Cannon et al., 1953).

At its southernmost outcrops in Tom Green County, the lower Choza is largely reddish-brown sandy mudstone containing lenses of sandstone and a few thin dolomite beds. The upper Choza consists of numerous thick dolomite layers that alternate with mostly gray to green mudstone and shale (Henderson 1928). Northward in Coke and Runnells Counties, redbeds become more prevalent as carbonate beds become thinner and fewer (Beede and Waite, 1918; Beede and Bentley, 1918). Exposures are poor in Jones and Taylor Counties, where the formation appears to be largely red mudstone with lesser sandstone and a single dolomite layer, the Merkel Member (Wrather, 1917). Dolomite of the Choza contains ammonoids, nautiloids, bivalves, gastropods, scaphopods, and bryozoans (Henderson, 1928). A local mudstone deposit near the top of the Choza in Tom Green County yielded the fossil plants *Delnortea abbottiae*, *Brachyphyllum*(?), *B. densum*, *Taeniopteris* sp., and a calamitalean stem (DiMichele et al., 2000, fig. 1, locality 4). Henderson (1928) reported an impure, thin coal and shale containing *Pecopteris* in the same area; we were unable to locate the outcrop and are unaware of any other reports of coal in the Clear Fork outcrop belt. No vertebrate remains are on record, but the well-known Castle Peak site in western Taylor County yields well-preserved trackways of small tetrapods along with a variety of other trace fossils (Sarjeant, 1971; Haubold and Lucas, 2001).

In summary, the entire Clear Fork Group of central Texas comprises intercalated shallow-marine, paralic, and terrestrial strata. Marine rocks are most prevalent in the southernmost exposures, gradually giving way northward to non-marine deposits. The northernmost carbonate beds pinch out in Haskell County, leaving an entirely terrestrial succession.

Eastern Shelf Subsurface

The area of subsurface study extends west from the eastern side of the outcrop through the counties shown on Figure 1, including Tom Green and Concho Counties to the south. The stratigraphic interval extends through and below the Clear Fork to the base of the Coleman Junction Limestone, a regionally persistent unit that marks the base of the Albany Group. These rocks were included because the Albany and Clear Fork share many lithofacies and because the Coleman Junction is the uppermost unit in a large cross section network that features the Cisco Group (Brown et al., 1987).

Correlation within the Clear Fork from outcrop to subsurface on the Eastern Shelf is straightforward (Figs. 4, 16). Carbonate and evaporite rocks increase toward the south and west at the expense of redbeds. The Arroyo Formation is 60 to 75 m thick along a traverse from Childress to Coke County (Cannon et al., 1953). The Arroyo abruptly thickens to 120 m in Tom Green County before losing its identity, as the entire Clear Fork changes to dolomite and limestone. Anhydrite or gypsum occurs in the basal portion of the Clear Fork as far up-shelf as eastern Stonewall, King, and Cottle Counties, continuing a depositional trend observed in the middle to upper Albany Group in the same area (Day and Cheney, 1949; Cannon et al., 1953). The Red Tank sandstone member can be traced down depositional dip into southeastern Knox County. To the west in the same county, the interval is mudstone, and farther west (72 km) in eastern King County, sample logs show multiple thin beds of dolomite and anhydrite with red mudstone.

The descriptive name "Big Red" has been applied to the Vale Formation mudstone in the subsurface (Conley et al., 1949; Day and Cheney, 1949; Noland et al., 1949; Cannon et al., 1953). "Big Red" intertongues with the overlying Bullwagon Dolomite in reciprocal fashion (Figs. 4, 16) and, as noted above, the youngest dolomite beds extend farthest up the shelf. On the far south in Tom Green County, the Vale pinches out entirely. Approaching the Palo Duro basin on the north, interbeds of anhydrite appear in the Bullwagon. The Brushy Creek sandstone can be followed southwestward down depositional dip into at least southern Haskell County. Farther west where sandstone disappears, this interval correlates to the lower part of "Big Red," which also includes the thick (43-46 m) mudstone-dominated interval between the Brushy Creek and Cedar Top sandstones. The latter sandstone is correlative to the Bullwagon Dolomite, which sample logs in eastern King County show to be approximately 30 m thick with thin anhydrite beds.

Overlying the Bullwagon is an interval of mudstone 20 to 60 m thick, containing few or no carbonate beds. Hann et al. (1949) called this mudstone "Fullerton," but that term has fallen into disuse, possibly to avoid confusion with the Fullerton sand, a lower Clear Fork oil field term from West Texas (Moore, 1944). In this report, we use the term "lower Choza mudstone" or Tubb formation (informal; Figs 4, 16). The lower contact of this unit appears to be planar, whereas the upper contact intertongues to some extent with limestone and dolomite of the upper Clear Fork (Fig. 4). Carbonate rocks progressively replace the upper Choza mudstone southward to its pinch-out near the Coke-Tom Green county line (Cannon et al., 1953).

The upper Choza (above the Tubb) also changes from dominantly red mudstone on the northeast to limestone and dolomite on the west and south. Thickness decreases from 170 m on the north to 90 m on the south, where erosion at the base of the overlying San Angelo Formation may come into play. Significant amounts of anhydrite occur in Cottle and Childress Counties in the Palo Duro Basin (Cannon et al., 1953), and salt beds occur near the King-Cottle county line along the Matador Arch (McGookey et al., 1988). The uppermost plant-bearing multistory channel deposit is located approximately 35 km east of well sites that produced such sample logs.

Palo Duro Basin

The Palo Duro is a shallow cratonic basin that was outlined by Ancestral Rocky Mountain uplifts during the Carboniferous (Fig. 2). By Permian time, the basin had coalesced with the Hardeman basin to the east and had become a very shallow shelf or sabkha, the scene of redbed and evaporite deposition. A series of reports, maps, and cross sections enable correlation between the Palo Duro and Midland basins, Central Basin platform, and Eastern shelf (Gustavson et al., 1980; Handford and Fredericks, 1980; Handford, 1981; Handford et al., 1981; Presley, 1981; Presley and McGillis, 1982; Page, 1986; Regan and Murphy, 1986a, 1986b; Rose 1986).

Stratigraphic terminology in the Palo Duro basin is a confusing mix of formal and informal names. The name "Wichita" is applied to a succession of dolomite and anhydrite that is partly equivalent to lower Clear Fork (Arroyo Formation) and Wichita Group redbeds (Fig. 4). Overlying the "Wichita" is the informal Red Cave formation, named for its color and tendency to cave in boreholes. The Red Cave averages about 130 m thick and is composed of brick-red to greenish gray mudstone and siltstone, with interbeds of dolomite and anhydrite. A cross section through King County shows that the Red Cave correlative to the combined Arroyo and Vale mudstone (Regan and Murphy, 1986a, their fig. 32). However, Handford and Fredericks (1980) illustrated widespread intertonguing between "Wichita" and Red Cave. These same authors interpreted the Red Cave as sabkha deposits bounded on the north and west by wadi plain or distal alluvial fans derived from source areas in northern New Mexico.

The Bullwagon Dolomite, confusingly identified as "Lower Clear Fork" on most published cross sections, extends into the Palo Duro basin. Gypsum, anhydrite, and halite become important constituents. As it does farther south, the Bullwagon intertongues with the Red Cave below, the youngest carbonate beds extending farthest northeast (Handford et al., 1981; Presley, 1981; Regan and Murphy, 1986a). In the northwestern part of the Texas Panhandle, the Bullwagon pinches out amid continuous redbeds. Conversely, toward the west and south, the Red Cave terminates due to facies change.

The Tubb formation or sand (see next section) has been extended from the Central Basin platform into the Panhandle and adjacent parts of Oklahoma and New Mexico (Gustavson et al., 1980; Handford et al., 1981; Rose, 1986; Regan and Murphy, 1986a). Here the Tubb directly overlies the Bullwagon Dolomite, in the position of the lower Choza mudstone. The Tubb consists of red mudstone, siltstone, and fine-grained sandstone with lesser interbeds of dolomite, anhydrite, and halite. Overall thickness is about 60 to 75 m.

The Clear Fork above the Tubb is about 100 to 180 m of limestone and calcareous dolomite, with numerous shale interbeds. Proportions of anhydrite, halite, and mudstone increase northward through the Palo Duro basin. Strata overlying the Clear Fork have been termed "Glorieta Formation," although in most places the rocks differ markedly from the outcropping Glorieta Sandstone in New Mexico. Picking the top of the Clear Fork becomes increasingly problematic northward (Regan and Murphy, 1986a, b).

Central Basin Platform

The Central Basin platform (CBP) is a fault-bounded uplift that separates the Midland and Delaware basins (Fig. 2). Throughout Early Permian time, the CBP was a carbonate bank or shoal between two deep (circa 300 m) ocean basins. At times, portions of the CBP were emergent, as shown by terrestrial plant fossils described from drill cores (DiMichele et al., 2000).

Lower Permian rocks on the CBP are predominantly dolomite, with minor limestone, shale, siltstone, and nodular and bedded anhydrite (DiMichele et al., 2000; Ruppel, 2002). Since the 1960s (if not earlier),

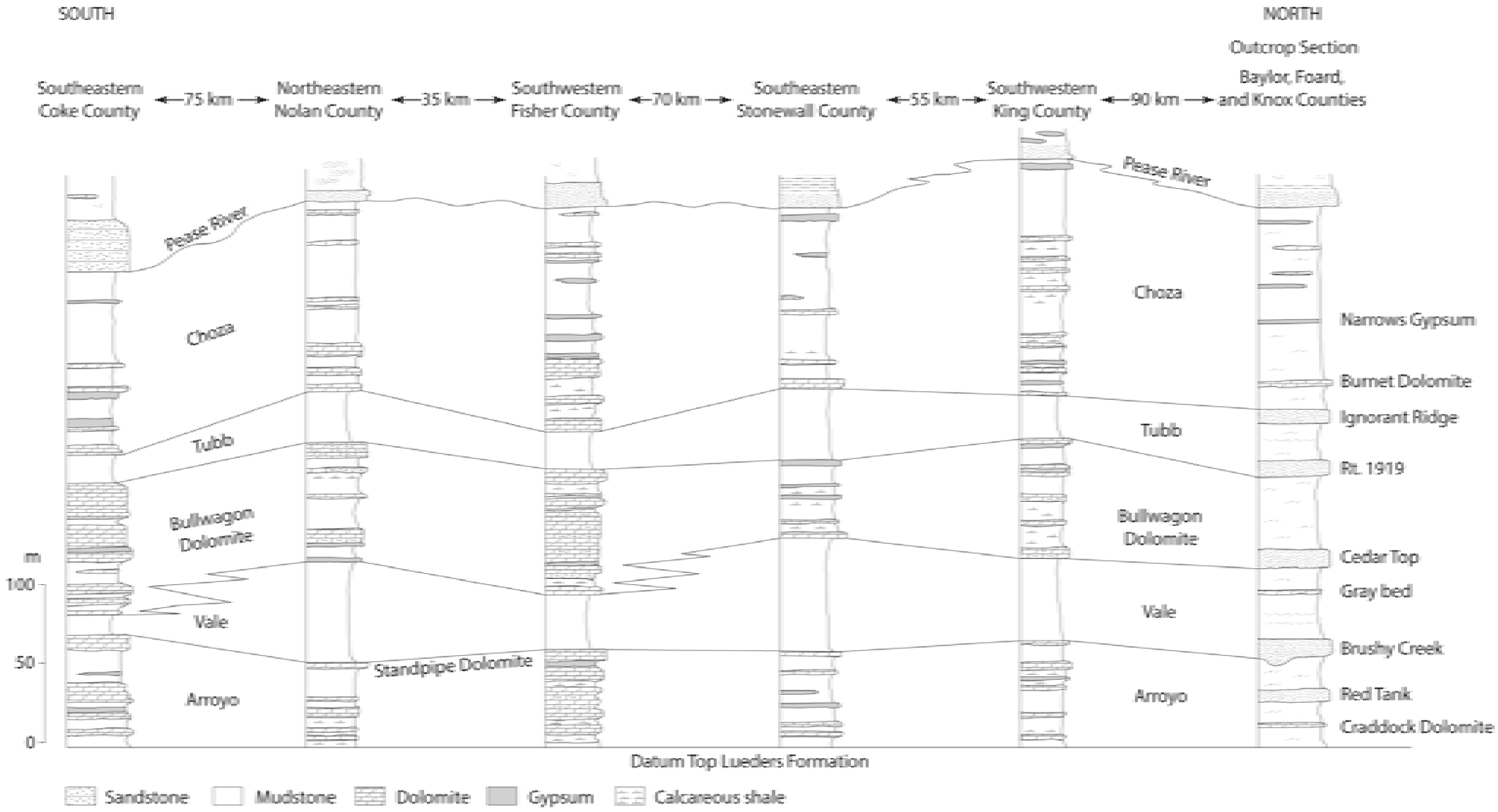


FIGURE 16. Cross section from shallow subsurface on the Eastern Shelf to outcrops in the Wichita Valley. The right-hand column is from the same source as Figure 5. The King County column is based on our interpretation of well logs; the other four columns are modified from Hann et al. (1949).

petroleum geologists have applied a mix of stratigraphic names derived from outcrops on the Eastern shelf (Wichita, Clear Fork) and from central and northern New Mexico (Abo, Yeso, Glorieta). Lithologies of all of these units contrast markedly between the CBP and their type areas. We have found no explanations as to how these unit names came to be used on the CBP. Presumably, they are based on geophysical log characteristics and rough time equivalence. Thus, we enclose "Clear Fork" of the CBP in quotation marks (Fig. 4).

One unit that is well defined is the informally named Tubb sand, which takes its name from the Tubb lease in the Sand Hills oil field of Crane County. Discovered in 1930, the Sand Hills field was the scene of the first "Clear Fork" production on the CBP. No type or reference log has been published, although Powers (1940) identified the "Tubb pay" as a sandy carbonate zone 4,250 to 4,420 feet (1,296 to 1,346 m) below the surface at Sand Hills. The Tubb is widespread, although not ubiquitous, on the CBP. It is typically 10 to 35 m thick and consists of silty shale, siltstone, and very fine to fine-grained sandstone interbedded with silty and sandy dolomite. Mazzullo (1982) reported oolitic dolomite, variegated mudstone, and frosted sand grains, suggesting shallow water and intermittent subaerial exposure. Clastic layers stand out on most wireline logs, especially gamma ray-neutron logs. The Tubb generally lies a short distance above the middle of the "Clear Fork" which ranges from about 270 to 375 m thick.

Some workers correlated the Tubb with the "Big Red" or Vale Formation on the Eastern Shelf (Hann et al., 1949; Hills, 1972; Mazzullo, 1982). However, reference logs of McLennan and Bradley (1951) and Herald (1957) and regional grids of cross sections (Presley, 1981; Handford et al., 1981; Bebout and Meador, 1985; Regan and Murphy, 1986a) lead us to conclude that the Tubb correlates with the lower mudstone unit of the Choza Formation on the Eastern Shelf.

Midland Basin

No generally accepted formal stratigraphy has come into use for Permian rocks in the Midland Basin. Clear Fork equivalents are dark-colored, micritic limestone with intervals of siltstone to very fine sandstone commonly interpreted as submarine fans. Among sandstone units, the Dean and Spraberry sands are most widely recognized. Although McLennan and Bradley (1951) formally named the Dean and described a type section from a well, the name seems to have devolved into informal usage. The Dean is about 25 to 40 m thick and consists of interbedded very fine to fine sandstone and tan to brown, dense limestone and dark shale. Shelf-to-basin correlation is not straightforward because of rapid thickness and facies changes at basin margins. However, most authors correlate the Dean with the Tubb sand (Jeary, 1978; Mazzullo, 1982; Galloway et al., 1983; Matchus and Jones, 1984; Regan and Murphy, 1986a; Hamlin and Baumgardner, 2012).

Regional Lithostratigraphic Relationships

Considering interval thicknesses and overall lithology, the most likely position of the Arroyo-Vale contact in the northern redbeds is at the base of the Brushy Creek sandstone (Figs. 4, 16). This appears to be the same horizon that Olson (1958) and Olson and Mead (1982) selected. Olson's map shows the Arroyo-Vale contact close to the base of the Brushy Creek near the west end of Lake Kemp, where this contact is best exposed. Olson and Mead (1982, p. 5) placed the boundary "at the base of a complex of coarse channel fills which eroded into a persistent red shale about 15 m thick." As noted above, the Brushy Creek sandstone and overlying mudstone of Baylor County are the landward correlatives of Vale mudstone, which extends across much of the Eastern Shelf in the subsurface. This correlation is based on interval thickness and the logical relation of fluvial sand of the alluvial and coastal plain with fine mud of the shelf.

Also as stated above, we correlate the Tubb sand of the CBP and Palo Duro Basin with the lower Choza ("Fullerton"), a mudstone-dominated interval overlying the Bullwagon Dolomite. Considering interval thickness and lithology, the interval bracketed by the Rt. 1919 and Ignorant Ridge sandstones in north-central Texas probably represents the Tubb (Fig. 4). We place the Vale-Choza contact horizon lower than Olson (1958, p. 400-401), who described a transition from "highly channeled section, typical of the upper Vale, to the evenly bedded red and green shales, which have few channel deposits, called basal Choza." Apparently, Olson's Vale-Choza contact is the top of Ignorant Ridge sandstone.

DISCUSSION

Depositional Environments

The following section provides a framework for considering depositional environments represented by Clear Fork rocks based primarily on characteristics observed on outcrop (Table 1). Further studies doubtlessly will contribute a more refined paleoenvironmental picture, especially in the case of floodplain deposits that comprise over half the section in north-central Texas. The term "floodplain" as used here refers to alluvial environments that received sediment from river sources during periodic flooding. Although these would have been adjacent or proximal to fluvial channels, no significant channel deposits are preserved in direct association with floodplain sequences in many cases. Basinward, floodplains would have interfaced with coastal plain environments, but a division between these two categories is arbitrary in the Clear Fork of north-central Texas because there is no evidence of tidal sedimentation, invertebrate fossils are generally lacking, and interpretation of various shark, fish, and even some amphibian remains as marine, brackish, or freshwater indicators is open to debate. Therefore, coastal plain environments are defined somewhat by default – these are rocks that lack evidence of fluvial influence as commonly seen in floodplain sequences.

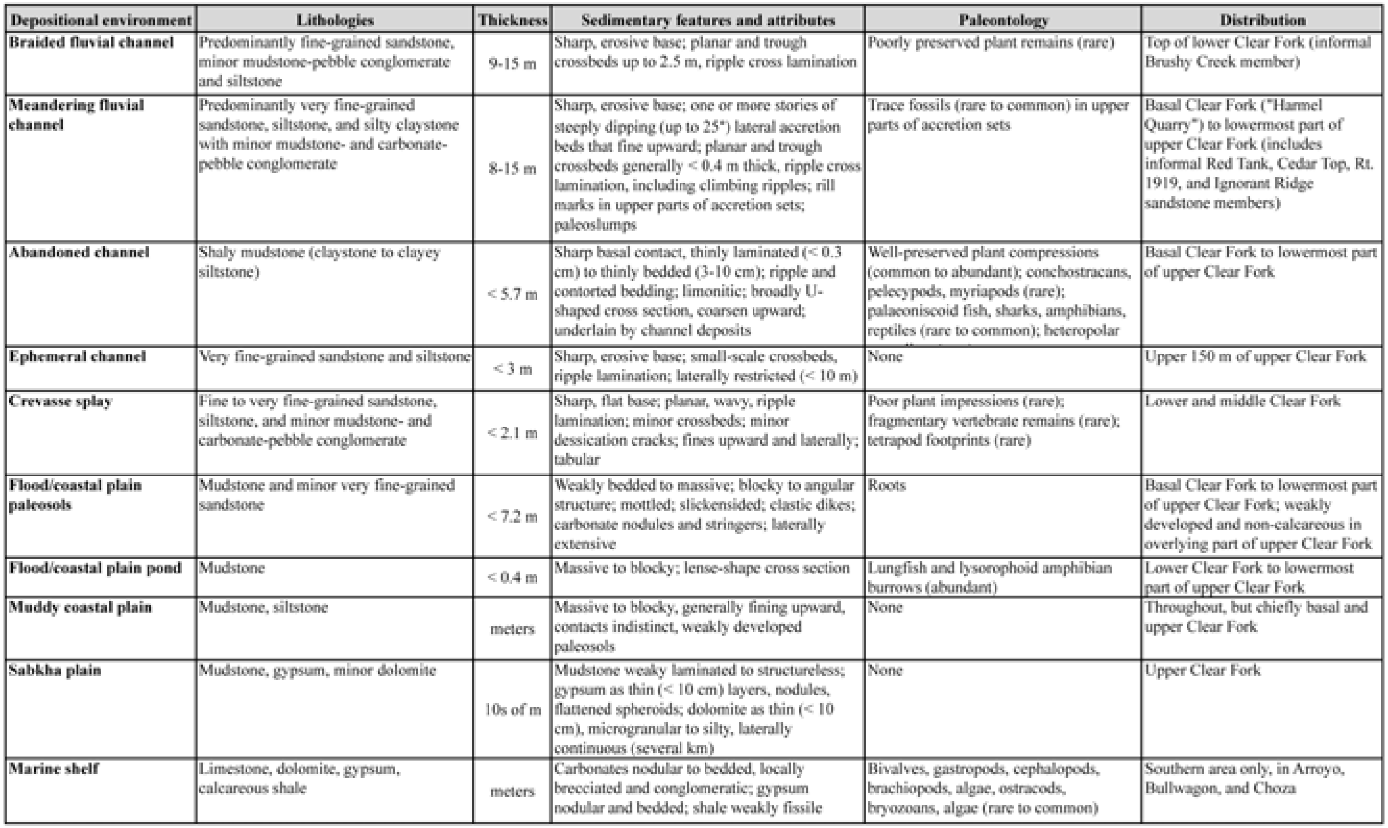
Fluvial Environments

The coarsest grained interval of the entire Clear Fork Formation is the Brushy Creek sandstone. All of the sedimentary attributes described above indicate that this sandstone originated as a mixed to bed-load braided fluvial system that deposited fine to very fine sand and locally derived gravel. The common occurrence of medium- to large-scale planar and trough crossbeds combined with a general absence of lateral accretion bedding with well-defined fining-upward sequences suggests multiple, broad, channels that flowed rapidly. This system may have been preceded by fluvial deposits similar to other Clear Fork sandstones, because some exposures consist of finer grained, multistory channel deposits that are partially eroded by the Brushy Creek member. A similar lithofacies relationship occurs in the underlying Bowie Group of north-central Texas, in which Hentz (1988) described contemporaneous braided and meandering systems.

All characteristics of the Red Tank, Cedar Top, Rt. 1919, and Ignorant Ridge sandstones, as well as the fossil-bearing sandstone at the level of the Burnet dolomite, indicate that they originated as meandering fluvial channels that deposited mud and very fine sand within vertically aggrading channel belts. Such channels are well known from numerous studies of modern as well as ancient streams and rivers. Active channel deposits consist mainly of fining-upward point-bar deposits, which are often termed scroll bars because of their arcuate plan-view appearance. Although Edwards et al. (1983) concluded that sedimentary features of the Rt. 1919 sandstone indicate large fluctuations in discharge, Jackson (1978) demonstrated that discharge rates and other hydraulic criteria of modern channels rarely fit the paleohydraulic model proposed by Brown (1973).

Shale-dominated deposits that form in abandoned, cutoff, or intermittently restricted segments of the meandering channels are curvilinear in plan view and U-shaped in cross section. Abandoned channel deposits frequently contain exceptional organic accumulations and can range from fossiliferous mudstones to carbonaceous shales to carbonates to sapropels depending on the larger environmental setting (Behrensmeyer

TABLE 1. Depositional environments of the Clear Fork outcrop.



Depositional environment	Lithologies	Thickness	Sedimentary features and attributes	Paleontology	Distribution
Braided fluvial channel	Predominantly fine-grained sandstone, minor mudstone-pebble conglomerate and siltstone	9-15 m	Sharp, erosive base; planar and trough crossbeds up to 2.5 m, ripple cross lamination	Poorly preserved plant remains (rare)	Top of lower Clear Fork (informal Brushy Creek member)
Meandering fluvial channel	Predominantly very fine-grained sandstone, siltstone, and silty claystone with minor mudstone- and carbonate-pebble conglomerate	8-15 m	Sharp, erosive base; one or more stories of steeply dipping (up to 25°) lateral accretion beds that fine upward; planar and trough crossbeds generally < 0.4 m thick, ripple cross lamination, including climbing ripples; rill marks in upper parts of accretion sets; paleoslumps	Trace fossils (rare to common) in upper parts of accretion sets	Basal Clear Fork ("Hannel Quarry") to lowermost part of upper Clear Fork (includes informal Red Tank, Cedar Top, Rt. 1919, and Ignorant Ridge sandstone members)
Abandoned channel	Shaly mudstone (claystone to clayey siltstone)	< 5.7 m	Sharp basal contact, thinly laminated (< 0.3 cm) to thinly bedded (3-10 cm); ripple and contorted bedding; limonitic; broadly U-shaped cross section, coarsen upward; underlain by channel deposits	Well-preserved plant compressions (common to abundant); conchostracans, pelecypods, myriapods (rare); palaeoniscoid fish, sharks, amphibians, reptiles (rare to common); heteropolar	Basal Clear Fork to lowermost part of upper Clear Fork
Ephemeral channel	Very fine-grained sandstone and siltstone	< 3 m	Sharp, erosive base; small-scale crossbeds, ripple lamination; laterally restricted (< 10 m)	None	Upper 150 m of upper Clear Fork
Crevasse splay	Fine to very fine-grained sandstone, siltstone, and minor mudstone- and carbonate-pebble conglomerate	< 2.1 m	Sharp, flat base; planar, wavy, ripple lamination; minor crossbeds; minor dessication cracks; fines upward and laterally; tabular	Poor plant impressions (rare); fragmentary vertebrate remains (rare); tetrapod footprints (rare)	Lower and middle Clear Fork
Flood/coastal plain paleosols	Mudstone and minor very fine-grained sandstone	< 7.2 m	Weakly bedded to massive; blocky to angular structure; mottled; slickensided; clastic dikes; carbonate nodules and stringers; laterally extensive	Roots	Basal Clear Fork to lowermost part of upper Clear Fork; weakly developed and non-calcareous in overlying part of upper Clear Fork
Flood/coastal plain pond	Mudstone	< 0.4 m	Massive to blocky; lense-shape cross section	Lungfish and lysorophoid amphibian burrows (abundant)	Lower Clear Fork to lowermost part of upper Clear Fork
Muddy coastal plain	Mudstone, siltstone	meters	Massive to blocky, generally fining upward, contacts indistinct, weakly developed paleosols	None	Throughout, but chiefly basal and upper Clear Fork
Sabkha plain	Mudstone, gypsum, minor dolomite	10s of m	Mudstone weaky laminated to structureless; gypsum as thin (< 10 cm) layers, nodules, flattened spheroids; dolomite as thin (< 10 cm), microgranular to silty, laterally continuous (several km)	None	Upper Clear Fork
Marine shelf	Limestone, dolomite, gypsum, calcareous shale	meters	Carbonates nodular to bedded, locally brecciated and conglomeratic; gypsum nodular and bedded; shale weakly fissile	Bivalves, gastropods, cephalopods, brachiopods, algae, ostracods, bryozoans, algae (rare to common)	Southern area only, in Arroyo, Bullwagon, and Choza

and Hook, 1992; Hotton et al., 2002). The Clear Fork channel fills are especially noteworthy because they span a stratigraphic interval of approximately 240 m, and each of the major sandstones contain multiple plant-bearing deposits. As noted previously, an absence of plants in most of the upper Clear Fork reflects diminished fluvial activity (DiMichele et al., 2006), and specifically a lack of multistory channel deposits. This pattern reflects the distribution of exposures relative to depositional environments: the composite stratigraphic section (Fig. 5) embodies an environmental transect that moves from east to west, or basinward, over a distance of some 50 km.

Smaller channel deposits that include lateral accretion bedding but lack the multistory architecture of other sandstone bodies occur throughout most of the lower and middle Clear Fork. A few of these lateral to tabular sandstone deposits probably represent small crevasse channels, but others more commonly appear to have been short-lived or ephemeral streams with no connection to larger channels. These types of small deposits are the only channels found in the upper 150 m of the formation.

Floodplain Environments

Thick mudstone sequences of the Clear Fork represent a mosaic of floodplain environments that has only recently been addressed. Tabor (in DiMichele et al., 2006) recognized four types of paleosols in the Clear Fork. Three of these soil types (F, G, and H) indicate semi-arid to arid environments. Type E paleosols, which may be interpreted as Entisols (Tabor and Montañez, 2004), indicate the presence of an elevated water table on the floodplain, while providing little information on the distribution of rainfall through the year. According to Cecil and Dulong (2003, fig. 5), modern Entisols and Inceptisols develop across a wide range of annual precipitation. Most Clear Fork vegetation was associated with Entisols in "wet spots" where ground water was close to the surface (DiMichele et al., 2006). Additional evidence of seasonally dry floodplain conditions is provided by failed aestivation assemblages, which preserve lungfish and/or lysorophoid amphibians (Olson and Bolles, 1975; Hembree et al., 2004), and by desiccation features exhibited by thin tabular sandstones that occur locally in mudstone sequences.

In the lower to middle Clear Fork, direct evidence of crevasse splays and other flooding episodes is muted by the narrow size range of available sediment (mostly mud and very fine sand) and subsequent pedogenesis. Restricted beds of crudely stratified conglomerate within mudstone sequences probably represent proximal splay deposits, and thin sandstone sheets that grade laterally into siltstones likely are distal parts of alluvial splays, not unlike some modern examples (O'Brien and Wells, 1986; Tooth, 2005). Otherwise, the multiple fining-upward aspect of stacked paleosol sequences suggests that soil formation was punctuated by, if not abandoned after, influxes of mud-laden floodwaters (Smith, 1990).

Coastal Plain Environments

The lower coastal plain is poorly represented in Clear Fork outcrops of north-central Texas, as few transgressions extended this far inland. The Craddock dolomite member near the base of the Clear Fork provides the most obvious example. Thin but widespread, laminated siltstone and mudstone suggest non-channelized (sheet) flow on a muddy coastal plain. Intercalated multi-colored mudstones are typical floodplain overbank deposits. Vertebrate trackways, mud cracks, raindrop impressions, algal mats, and land plant impressions place the Craddock in the intertidal to supratidal realm (Lucas et al., 2011).

Features similar to those described for the Craddock occur in two thin but laterally extensive layers of calcareous sandstone in the lower part of the informal middle Clear Fork division. They are also closely similar to modern sands forming in the Ranns of Kutch, coastal flats or sabkhas of northwestern India. These sands are deposited during annual monsoons, when prevailing winds drive the sea onshore (Glennie and Evans, 1976).

In a similar vein, gypsum-rich mudstones and thin, tabular dolomites of the upper Clear Fork in our field area have characteristics in common with Lower Permian sequences attributed to a mud-rich coastal to continental sabkha system in the subsurface of King, Cottle, and Childress Counties (Handford and Fredericks, 1980; Handford, 1981; Handford et al., 1981; McGookey et al., 1988) (Fig. 1). The outcrop area would have represented a slightly up dip, arid coastal setting in which dolomites were thinner and sediment transport was limited to low-gradient, ephemeral streams. The model proposed by Handford also suggests that much of the siltstone may have originated as wind-blown silt and that eolian processes influenced sediment accumulation, as in modern sabkhas (Glennie and Evans, 1976).

Neither observed during our field work nor reported by other authors are any features indicative of tidal activity, such as bidirectional current indicators or rhythmic lamination bearing a neap-spring signature. Specifically, shallow channels intercalated with dolomite of the Craddock member and Lueders Formation lack any evidence of tidal flux. Also, storm deposits such as the conglomerates that Hentz (1988, fig. 21a) documented in the Wichita Group have not been encountered in the Clear Fork. Evidently, the nearly landlocked Midland Basin had minimal tides (if any), and its broad, extremely shallow shelf buffered storm waves.

Marine Environments

Fully marine Clear Fork strata are confined to the poorly exposed outcrop of Central Texas and to the subsurface of north-central Texas. Because no petrographic or paleoecological investigations have been carried out, only general remarks may be offered. Not surprisingly, the invertebrate fauna exhibits a northward decline in diversity and abundance. Southern Arroyo, Bullwagon, and Choza carbonates contain largely a molluscan fauna that includes several genera of bivalves, gastropods, and cephalopods. Articulate brachiopods have been reported only from the Arroyo; bryozoans only from the Choza. Corals and echinoderms, major elements of many Late Paleozoic platform carbonates, are scarce or absent. Northward along the outcrop belt, limestone changes to microgranular dolomite and the fauna becomes increasingly restricted. Lists of fossils from this area are limited to a few taxa of bivalves, nautiloids, and ammonoids; along with linguloid brachiopods, serpulids, and remains of sharks, bony fishes, amphibians, and reptiles.

The combination of arid climate indicators, lack of large coastal rivers, and associated evaporites indicates that Clear Fork faunal restriction relates to excessive salinity. Elevated solar heating of extremely shallow water close to shore may have been an added factor.

Depositional History of the Clear Fork in North-Central Texas

The lower Clear Fork division exposed in Baylor County is an overall coarsening-upward sequence that records the progradation of terrigenous clastics from northeastern source areas, primarily the Wichita uplift (Fig. 2), onto coastal lowlands. A roughly north-south coastline adjoined an expansive coastal plain that was tens of kilometers wide. Tidal influence was minimal, and the broad, shallow Eastern Shelf appears to have buffered the effects of sea-based storms. Coastal muds graded basinward into dolomite and anhydrite some 70 km to the west, where mud-rich coastal sabkha complexes had developed first in the early Leonardian. Climate was seasonal, hot, and semi-arid with extended dry periods. Open marine conditions prevailed down the shelf to the south and west.

In the initial stages of the lower Clear Fork, mud and very fine sand were transported in high-sinuosity meandering streams and rivers. As the coastal plain became alluviated, higher energy braided channels occupied parts of a former meander belt and deposited mainly fine to very fine sand with subordinate amounts of mud and locally derived gravels in the last phase of the lower Clear Fork. Development of this fluvial system was accompanied regionally by a thick accumulation of mud over former coastal sabkhas to the west and offshore carbonates to the south. This would be the greatest advance of terrigenous materials on the Eastern Shelf during the Leonardian until the appearance of the Duncan Sandstone of the San Angelo fluvial system. Floodplains before and after the major channel were well-drained and periodically exposed during dry periods.

The middle Clear Fork in western Baylor and adjoining parts of Knox and Foard Counties represents a basinward shift on the landscape. High-sinuosity suspended-load rivers similar to those of the lower Clear Fork returned, and distal floodplains began to take on aspects of mud-rich sabkha environments. About 50 km west of the south-southwest flowing channel belts, dolomite and anhydrite accumulated in shallow, near-shore settings. The last fluvial system of the middle Clear Fork was associated with a second phase of widespread mud deposition over the shelf.

In the upper Clear Fork, from Hardeman County in the north to as far south as Stonewall County, extensive coastal sabkhas are encountered in many of the same areas that hosted evaporite deposition early in the Leonardian. In nearby parts of Cottle and Childress Counties, halite beds began to develop for the first time. As shown by an impoverished soil record, few plants lived in these harsh settings, and streams and rivers were all but absent. Dolomites and anhydrites become less abundant towards the top of the formation near the level of the Duncan Sandstone, a braided fluvial channel that carried sand and gravel south-southwest into North-Central Texas to mark the end of Clear Fork sedimentation.

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FLORA FROM THE LÍNĚ FORMATION (CZECH REPUBLIC) AS AN EXAMPLE OF FLORISTIC DYNAMICS AROUND THE CARBONIFEROUS/PERMIAN BOUNDARY

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Abstract—The latest Pennsylvanian (late Gzhelian-?early Asselian) Líně Formation is the youngest unit in the continental basins of the central and western Czech Republic. It consists dominantly of fluvial red beds intercalated with several tens of meters of thick gray-colored strata, locally bearing poorly developed coals. The significant part of these gray strata was deposited in lacustrine environments. Lithological climatic indicators (e.g. calcic vertisols, freshwater limestones and cherts, silicification of stems, etc.) suggest seasonal climate with variations in degree of seasonality throughout the formation. Floristic and palynological records indicate presence of at least 40 plant taxa. Macrofloral remains include common sphenopsids, mainly calamites, herbaceous ferns and tree ferns, pteridosperms, rare arborescent and herbaceous lycopsids, and also cordaites and conifers. Data from boreholes suggest the existence of two ecologically different and probably spatially separated plant assemblages representing wetland and dryland floras, the former preserved usually as coalified plant compressions in gray-colored to variegated mudstones or lacustrine limestones and the latter preserved as plant impressions in red mudstones or silicified stems in coarse-grained channel facies. The wetland assemblage is dominated by calamites and tree and herbaceous ferns with subdominant medullosan and callystophytalean pteridosperms and rare herbaceous and arborescent lycopsids. Some palynomorph assemblages from thin coals intercalated with nearshore/offshore lacustrine strata are dominated by the miospore genus *Lycospora*. The dryland assemblage occurs in red mudstones and is composed of conifers and cordaitalean impressions; silicified stems of these plants occur in coarse-grained fluvial sediments associated with the red mudstones. Rare conifers and cordaitaleans, as well as their spores, occur in gray lacustrine strata, however, suggesting occasional coexistence of both assemblages, possibly within the basin lowland. It is assumed that the "wetland" flora is largely the assemblage of the lake margin, whereas cordaitaleans and conifers lived away from the margin, in the more xeric soils.

INTRODUCTION

The Late Pennsylvanian to Early Permian is a period that in western and central equatorial Pangea is marked by a transition from humid wetlands to a seasonally dry landscape accompanied by inter-biome floristic dominance and diversity change (e.g., DiMichele and Aronson, 1992; DiMichele et al., 2008, 2009). These coupled climatic-floristic changes in the equatorial region are in phase with changes of ice volume in high latitude glaciated areas of southern Gondwana, which varied on several time scales as an interplay of orbitally driven cyclicity and probable, but still not well-understood, variations in atmospheric pCO2 (Montañez et al., 2007; Tabor and Poulsen, 2008). The floristic response to increasing seasonality is marked by the general contraction of wetland habitats in basinal lowlands, accompanied by a transition from dominance by spore-producing vegetation accompanied by primitive seed plants to dominantly seed-bearing vegetation rich in conifers and peltasperms (Broutin et al., 1990; Kerp, 1996; DiMichele et al., 2005, 2008, 2009). Both types of vegetation can occur in different horizons but can be observed even within the same outcrop (Kerp and Fichter, 1985; DiMichele et al., 2007). This floristic turnover is recorded in a number of spatially disconnected sedimentary basins across North America and Europe. Among these basins are those of the central and western Czech Republic, where there is a complex of continental basins bearing several red bed units, the youngest one being the Líně Formation of latest Pennsylvanian to possibly Early Permian age. As with many other red bed units, this formation has attracted only marginal attention from geologists and paleontologists because of a very poor fossil record and hence has a poorly constrained biostratigraphy. Nevertheless, borehole exploration in the second half of the 20th century produced large amounts of data, including paleontological. These are only partly published and in any case need a taxonomic revision and paleoecological reinterpretation based on new interpretations of the sedimentological and paleogeographical context, topics that are currently being addressed in ongoing projects. This paper presents a brief summary of the current knowledge of the flora of this dominantly red bed unit.

LATE PALEOZOIC BASINS OF THE BOHEMIAN MASSIF

The territory of the Czech Republic is encompassed by a major part of the Bohemian Massif, a complex tectonic unit composed of small terranes located between Baltica and Gondwana and amalgamated during the Variscan Orogeny in Late Devonian and Mississippian times (e.g., Franke, 2006). In the Pennsylvanian, waning orogenic processes resulted in normal and/or wrench faulting, producing basin and range-like topography with numerous continental basins (Cortesogno et al., 1998). The main complex of basins consists of a wide belt ranging from the western to the northern part of the Czech Republic up to the boundary with Poland, and covers an area of about 10,000 km^2 (Fig. 1a). In the central and western Bohemian (= central and western part of the Czech Republic) part of the basin complex, deposition started in early Bolsovian (early Moscovian) times and included several hiatuses lasting until the end of Carboniferous and very probably into the Early Permian (Pešek et al., 1998; Zajíc, 2010). Basin fill, up to 1.4 km thick, is divided into four formations based on basin-wide alternation of several-hundred-meter-thick, gray-colored, coal-bearing and red, coal-barren strata (Fig. 1b) (Weithofer, 1896, 1902; Pešek, 1994). The youngest of these units is the Líně (Upper Red) Formation. It is assigned to the Stephanian C (late Gzhelian) by Pešek (1994) because it lacks clear floristic and palynological data indicating an Early Permian age. Zajíc (2010) and Holub et al. (1981) assign the upper part of this unit to the Early Asselian, based, respectively, on either vertebrate faunal biozonation or borehole correlations to a neighboring basin complex with biostratigraphically proven Permian strata. The youngest unit of this formation is preserved only in

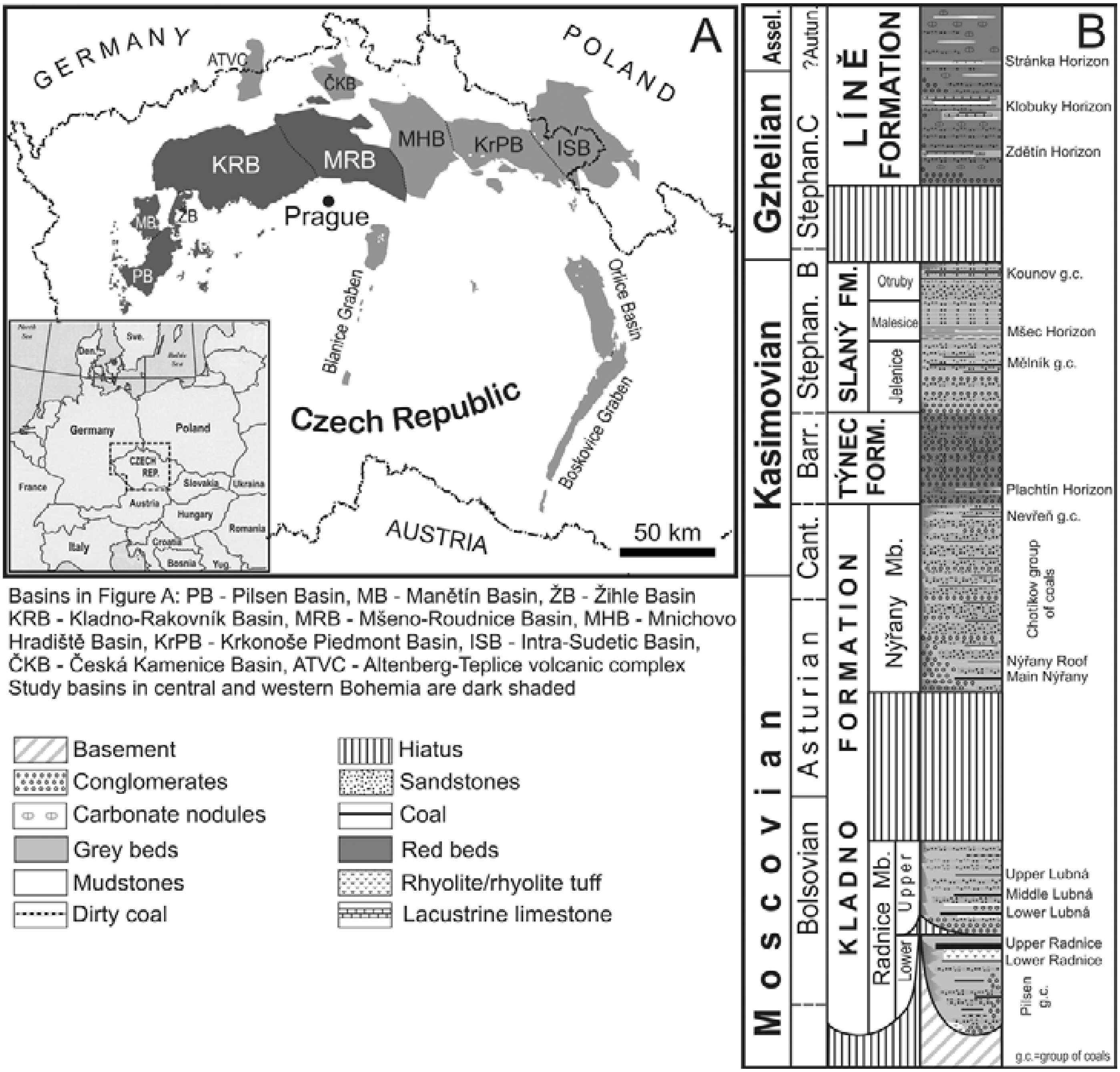

FIGURE 1. **A**, Distribution of the Late Palaeozoic continental deposits in the Czech Republic and their subdivision into basins (After Pešek 2004). **B**, Lithostratigraphic units in the basin complex of the central and western part of the Czech Republic. Composed from data in Pešek (1994).

erosional thickness, up to 800-1000 m, in the northern part of the basin complex, namely in the Kladno-Rakovník and Mšeno-Roudnice basins (KRB and MRB in the following text-see Fig. 1a for the location of these basins). In the Pilsen Basin in western Bohemia only the basal part of the formation, less than 100 m thick, is preserved.

THE LÍNĚ FORMATION AND CURRENT STATE OF ITS INVESTIGATION

The Late Paleozoic continental basins in central and western Bohemia underwent an intensive exploration for coal and other raw materials (e.g., kaoline, refractory claystone or copper and uranium mineralization) in the second half of the 20th century. During a period of 40 years more than one thousand, mostly fully cored, boreholes were drilled into the basement. About 250 of them penetrated the whole preserved thickness of the Líně Formation. The boreholes were explored by a complex of geophysical, petrological, geochemical, mineralogical and paleontological methods. This effort has generated vast amounts of data archived in final reports of exploration companies. Published outputs include litho- and biostratigraphy, basic sedimentary environment and paleogeographic interpretations, lists of flora, palynomorphs and fauna of major lithostratigraphic units as well as a variety of qualitative geochemical and technological parameters of coal seams and accompanying rocks (for an overview see Mašek, 1973; Šetlík, 1977; Pešek, 1994, 2004; Pešek et al., 2001). Although complete borehole cores are no longer available, existing collections of rock and paleontological samples taken from boreholes and a few outcrops or quarries, as well as archived or published data (graphic documentation of logged boreholes, laboratory data) provide a reasonably good platform for a revision of palynomorphs, macroflora and fauna in a context of sedimentary environment, as a baseline for further paleoecological and biostratigraphic studies. These topics are being addressed in currently on-going projects focused on revision of the flora, including silicified stems, interpretation of sedimentary environments, radiometric dating and study of climatic indicators, especially paleosols, applying petrological and geochemical methods. This contribution is therefore mainly an overview of the current state of understanding of the biostratigraphy, sedimentology and paleoecology of this unit, representing the very early results of these projects.

LITHOSTRATIGRAPHY AND SEDIMENTARY ENVIRONMENTS OF THE LÍNĚ FORMATION

Although sediments of the Líně Formation, in a general overview, can be characterized as continental red beds, they are usually not continuously red throughout the section (Fig. 2). Instead, monotonous alternation of red mudstones and sandstones can be interrupted at any level by gray, green-gray or variegated mudstones and/or fine-grained sandstones. Most of the non-red units, however, are concentrated into three distinct lithostratigraphic horizons traceable over various parts of the basin complex in central and western Bohemia (e.g., Pešek, 1994, 2004). These gray to variegated horizons are, in stratigraphic order, the Zdětín, Klobuky and Stránka (Fig. 1b), and are interpreted as mostly lacustrine sediments deposited during prolonged humid periods (Pešek, 1994; Šimůnek et al., 2009). Besides mudstones and sandstones, the non-red units contain fresh water limestones, cherts, carbonaceous or bituminous claystones, thin coals and volcaniclastics, i.e., lithologies that are absent or rare in the dominant red parts of the formation. In contrast, the red-colored strata are dominantly composed of red to purple or carmine mudstones with fine-grained sandstone intercalations ranging in thickness from centimeters to a few meters. Coarse-grained sandstones to conglomerates are subordinate although locally, especially close to the former basin margin, they can attain a thickness of up to several tens of meters (Pešek et al., 1998).

In the northern part of the KRB and MRB, poorly sorted and massive deposits containing clasts of local provenance are locally present, interpreted as cohesive debris flows (Pešek, 1994). Sandstones of the Líně Formation are cemented by calcite and less often by dolomite (Pešek and Skoček, 1999). In the western part of the KRB, Valín (1971) described medium- to coarse-grained cross-bedded bimodal sandstones in the borehole Op-4 (Oplty) composed of well-rounded grains and interpreted as eolian deposits, although this facies seems to be spatially restricted. Mudstones are usually poorly bedded. Paleosol horizons are vertisols, calcic vertisols and locally even calcisols (Skoček, 1993). Root haloes penetrating deeply into the sediment are locally common. Subaerial plant remains are, however, very rare, which excludes further stratigraphic subdivision of this formation by means of flora.

Palaeogeographically the basin complex in central and western Bohemia as well as its continuation to the Sudetic area farther ENE formed during Gzhelian times as a single large basin. The area of maximum subsidence in the KRB and MRB was located along the northern margin, resulting in a half-graben architecture of these particular basins (Pešek, 1994). The depocenter had the character of a wide lowland with minimal topographic elevation, drained by a system of rivers running generally northwards. Pešek et al. (1998) interpret the predominance of mudstones and fine-grained sandstones throughout the section in the area of maximum subsidence, in the northern part of the KRB and MRB, as indicative of the formation of temporary lakes, which changed in extent as the climate and/or tectonic subsidence varied through time. The maximum extent of these lakes is assumed to have occurred during the deposition of gray to variegated horizons with freshwater limestones, cherts and local bituminous shales. Limestones are usually bedded, muddy, without features suggesting sub-aerial exposure and often contain drifted remains of wetland vegetation. Cherts are often massive, laminated and brecciated. Associated thin and high ash coals or carbonaceous mudstones are interpreted to reflect localized wetlands either with clastic or mixed peat-clastic substrates located along lake shallows or in poorly drained floodplains or deltaplains. Dominantly red sediments between these gray to variegated horizons are assumed to have been deposited under generally drier (seasonal) climate in fluvial settings. In marginal parts of the basins there commonly are conglomeratic to coarse-grained cross-bedded sandstone bodies up to several tens of meters thick, with only subordinate mudstones and fine-grained sandstone intercalations. This lithology probably indicates the presence of amalgamated channels, which is typical of braided fluvial styles. However, the proportion of coarse-grained facies decreases toward the basin center, where mudstones become the dominant lithologies. Root horizons and mudcracks are locally present in mudstones, and paleosols are common, basically vertisols, mostly with carbonate nodules or even calcrete horizons. Sandstones are confined to isolated bodies, often decimeters thick but locally even thicker. This change in dominant lithology from the marginal part of the basin complex to its center is interpreted as a transition of fluvial styles from braided to meandering rivers with well developed floodplains. Sediments of localized, shallow, temporary ponds can be present.

CLIMATIC INDICATORS

The red color of sediments itself is indicative of well-drained conditions, which can occur in a wide spectrum of climates (Sheldon, 2005). This is evidenced by lateral transitions of red to gray sediments observed within a single basin, which has nothing to do with a climatic change (e.g., Calder, 1994; Pešek and Skoček ,1999). However, the basin-wide extent of red beds, in combination with the presence or absence of other climate sensitive lithologies, can provide unequivocal information on paleoclimate. In the Líně Formation these climatic indicators include absence or scarcity of coal, paleosol characteristics, fossilization patterns of plant remains and the presence of chemogenic rocks, otherwise rare or absent in major coal-bearing units.

Coal is generally absent in red fluvial sediments of the Líně Formation, and only thin high-ash coals of local extent are known from some gray lacustrine horizons. This indicates climatically unfavorable conditions for peat accumulation except during periods of increased humidity, represented by lake horizons. However, even in these periods the humidity did not reached the level required for long-term peat accumulation of the kind resulting in economically important regional coals, such as those present in the underlying Slaný Formation of middle Late Pennsylvanian age.

Paleosols associated with the red fluvial strata of the Líně Formation are vertisols, often with nodules of precipitated pedogenic carbonates (Opluštil and Cleal, 2007). These nodules often coalesce and occasionally can form continuous calcrete horizons (Skoček, 1993; Pešek and Skoček, 1999). Vertisols with pedogenic carbonates are regionally quite persistent in the Líně Formation (Skoček, 1993). Their formation requires climates with strongly seasonally moisture deficits (Cecil, 2003; Driese and Ober, 2005; Nordt et al., 2006). Under such conditions plant remains are commonly fully oxidized in dry sediments, and only their impression is preserved. Absence of coalified plant compressions is therefore a typical feature of fluvial red beds of the Líně Formation.

In addition, an alkaline environment during deposition of the fluvial red beds favored silicification of woods in porous, coarse-grained sediments, mostly cross bedded feldspatic sandstones or conglomerates (Skoček 1970). These prostrate silicified stems, some of them >10 m long, lack bark, branches and roots, which together with the absence of paleosols in the deposequences in which these fossils are found, is a good indicator of transport prior to final burial. Silicified woods are considered to be indicative of seasonal climates since a fluctuating water table is supposed to be a prerequisite for wood silicification in alluvial sediments (Skocek, 1970; Matysová et al., 2008, 2010). According to Skoček (1970),

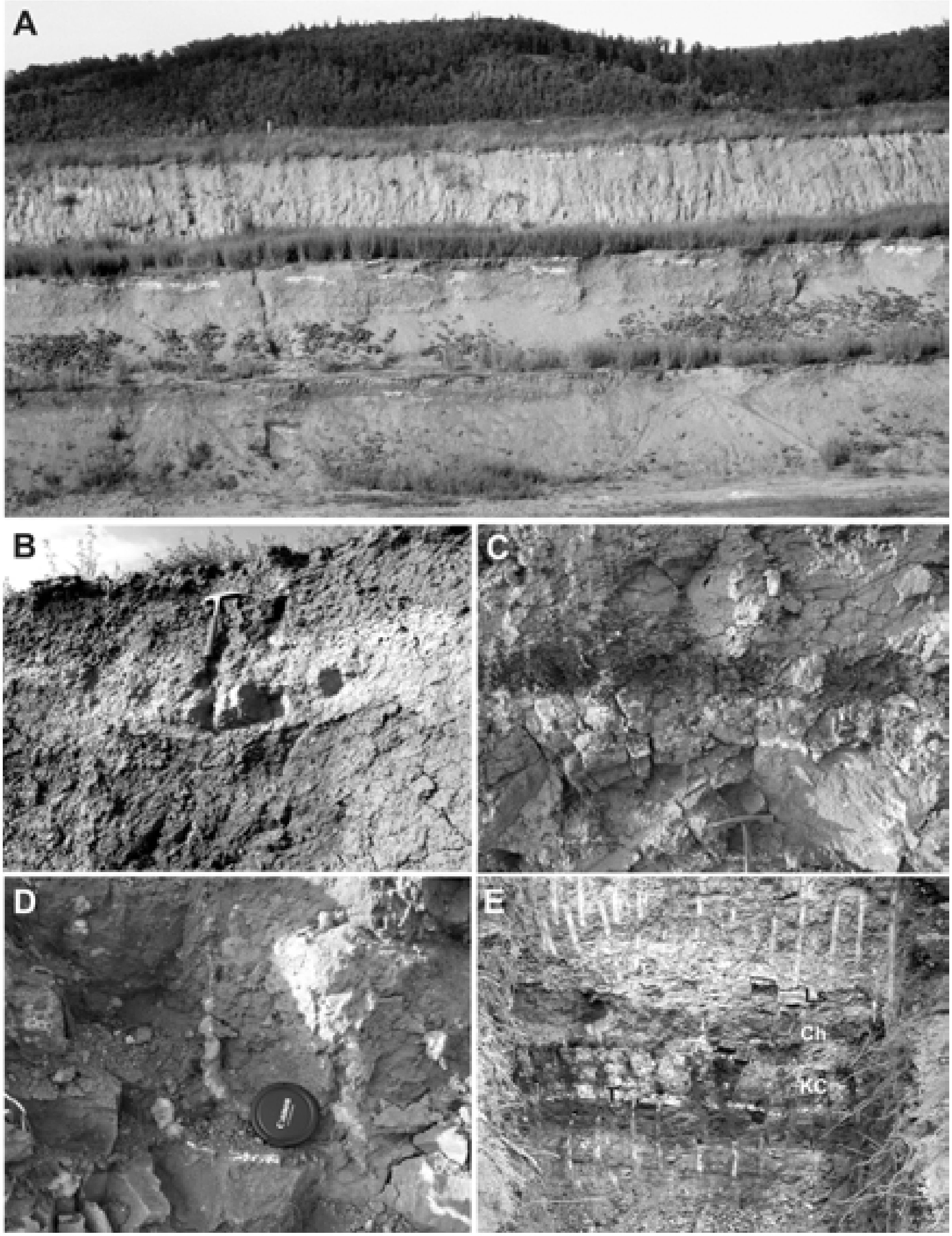

FIGURE 2. **A**, Red beds exposed in a brick-pit near the village of Kryry in the Kladno-Rakovník Basin. Note the discontinuous whitish horizon, which indicates position of pedogenic calcretes. **B**, Detail of calcrete horizon from Fig. 2A. **C**, Part of paleosol (calcisol to calcic vertisol) section in the brickpit near Kryry. Silty mudstone with medium angular blocky structure, rare carbonate nodules and rhizoliths and tubules filled with calcium carbonate at the base is overlain by greenish gray massive to weak angular blocky mudstone with common carbonate nodules. Above is a dark red mudstone with well developed slickensides and fine-medium wedge-shaped aggregate structure. **D**, Vertical to sub-vertical rhizoliths in red angular blocky mudstone with disseminated carbonate nodules. Brickpit near Kryry. **E**, Part of the lacustrine succession exposed near the village of Klobuky in the Kladno-Rakovník Basin. Rusty and poorly laminated nearshore mudstones followed by thin high-ash the Klobuky Coal (**KC**) containing tonstein (**T**) in its lower part. The roof of the coal consists of chert (**Ch**) succeeded by bedded muddy limestone (**Ls**), both interpreted as offshore facies and further followed by nearshore mudstones. Drifted flora was collected especially from mudstones and bedded muddy limestones.

two types of silicified woods occur in the Late Paleozoic basins of the BM: (1) black silicified woods containing coalified organic matter occurring mostly in weakly porous sediments of gray, coal-bearing units and (2) silicified woods without organic matter, which occur in red beds. The latter are indicative of a strongly seasonal climate, which enhances formation of weak SiO_2 solutions migrating throughout the porous sediments. Precipitation of silica in woods is promoted by lowered pH due to CO_2 released by bacterial decomposition of stems (e.g., Soliman, 1962).

The presence of lacustrine cherts and limestones also is considered to be indicative of relatively dry and seasonal climate (Pešek and Skoček, 1999). It is also evidenced by lateral transitions from nonmarine limestones into calcic vertisols in Carboniferous basins of North America (DiMichele et al., 2010; Cecil et al., 2011). In the Líně Formation cherts are relatively common in some lacustrine deposits rich in organic matter, like in the roof of the Klobuky Coal formed in lake shallows. Probably even drier climate is indicated by bimodal eolian sandstones described by Valín (1971) and Pešek and Skoček (1999), indicating the absence of a dense vegetation cover.

All the mentioned indicators commonly point to the existence of seasonal climate during the deposition of the Líně Formation. The climate, however, was not uniformly seasonal all the time. Some level of seasonality existed, even during the deposition of gray-colored horizons, which are assumed to represent the wettest parts of climatic oscillations because of peat accumulation, even though of limited extent, whereas calcic vertisols to calcisols, associated with fluvial redbeds between gray horizons, indicate strongly seasonal conditions. The climate under which deposition of the formation took place thus probably varied from moist subhumid to dry subhumid (Cecil, 2003). The time scale of these oscillations is currently difficult to estimate from existing data. If these climatic cycles in low latitudes are coupled with changes of continental ice as suggested by some authors (e.g., Cecil and Dulong, 2003; Driese and Ober, 2005; DiMichele et al., 2010), than they could correspond to medium-term intervals of glacial advance and retreat identified in glacial deposits of former Gondwana. These cycles lasted from about a hundred thousand to about a million years (Birgenheier et al., 2009). Moreover, there seems to be a hierarchically overriding trend of increasing aridity recorded by the decreasing occurrence of gray-colored sediments in upper half of the Líně Formation.

FOSSIL RECORD OF THE LÍNĚ FORMATION

The fossil record of the Líně Formation is generally very poor, especially in red fluvial sediments where only a limited number of determinable plant remains have been found in boreholes (Šetlík, 1970, 1977). This scarcity is assumed to be a result of a drier climate, less favorable for plant growth, and oxidative conditions in dry soils promoting fast decomposition of plant or faunal remains. From over 250 boreholes examined for macroflora only 33 provided plant fossils (Šetlík, 1970). In all, about 50 morphotaxa have been reported from the formation (Pešek, 2004; Šimůnek et al., 2009). These are estimated to represent at least 40 biological species.

Distribution of flora is irregular throughout the formation. In its lower part (the Zdětín Horizon and associated red beds above and below it) only several root horizons and sporadic remains of *Sphenopteris* sp., *Pecopteris cyathea*, *Neuropteris nervosa*, *Cordaites* sp., *Poa-Cordaites* sp., and *Walchia piniformis* have been found in various levels.

The richest flora of the Líně Formation has been obtained from the 5-100 m thick Klobuky Horizon, about 300-330 m above the base of the formation (Fig. 3). This horizon has been collected from various stratigraphic levels and lithologies accessible in a number of exploration boreholes (Šetlík, 1970, 1977). An even larger collection of plant fossils has been, however, obtained from the outcrops of the Klobuky Horizon near the village of Klobuky (Němejc, 1946, 1953; Jindřich, 1963; Havlena, 1964; Obrhel, 1965; Šimůnek et al., 2009). The locality has provided 38 morphotaxa, which represent about 34 biological plant species (Šimůnek et al., 2009). This clearly drifted and fragmentary allochtonous flora is preserved in lake nearshore and offshore sediments (mudstones, muddy siltstones and limestones). The assemblage is dominated by ferns (*Pecopteris cyathea*, *P. arborescens*, *Sphenopteris* spp.) and sphenopsids (e.g., *Calamites* spp., *Sphenophyllum angustifolium*), and co-dominated by cordaitaleans (*Cordaites* sp., *Poacordaites* sp.) and pteridosperms (e.g., *Odontopteris schlotheimii*, *Alethopteris zeilleri*, *Dicksonites plueckenetii*). Also present is *Taeniopteris jejunata*, considered to be a fern by Němejc (1963), and a pteridosperm by Remy and Remy (1959). Subordinate or rare in lacustrine strata are lycopsids (*Asolanus camptotaenia*, *Lepidostrobus* sp.), whereas conifers (*Walchia* sp., *Ernestiodendron filiciforme*) are even less common.

The upper half of the Líně Formation is up to 500 m thick and contains the Stránka Horizon in its middle part. Determinable plant remains are concentrated in the basal part of this horizon, including *Pecopteris cyathea*, *P. polymorpha*, *Callipteridium pteridium* and *Alethopteris zeilleri*. Roots and plant axes are much less common here than in the older units because of the reduced extent of lacustrine sediments. On the other hand, the conifers (*Walchia* sp.) are more common in this part of the formation, especially in red mudstones.

Šetlík (1970), who searched for flora of the Líně Formation in tens of boreholes, was the first to note the preferential occurrence of particular species in certain lithologies of the formation. Consequently he distinguished three types of deposits, which contain different plant associations that possess different modes of preservation. He observed that red mudstones associated with paleosols provided only a few plant fossils, mostly non-stigmarian roots and unidentifiable plant axes. The most commonly identifiable remains were walchian shoots and cordaitalean (*Cordaites* and *Poa-Cordaites*) leaf impressions. Poorly preserved remains of sphenopsids, ferns and pteridosperms are exceptional, and lycopsids are completely absent from this type of sediment. In coarse-grained or conglomeratic sandstones associated with the red mudstones between gray horizons, silicified stems of gymnosperms are locally common, predominantly walchian conifers, which are more common than cordaitaleans (Bureš 2011). In variegated mudstones Šetlík (1970) found drifted plant fragments (mostly cordaitalean leaves and axes and *Calamites* with subordinate ferns and also walchian conifers) and disarticulated faunal remains as well as common roots of non-stigmarian affinity. However, the most common plant remains he found in gray mudstones were preserved as coalified compressions. Šetlík (1970) interpreted gray mudstones as “wetland” deposits colonized by “hygrophilous” elements dominated by calamites and marattialean ferns.

Sediments of the Líně Formation are not favorable for preservation of palynomorphs. In all, only about 50 miospore taxa have been reported so far from this lithostratigraphic unit (Pešek, 2004). The richest spore assemblages have been obtained only from gray mudstones or thin coals, whereas in red mudstones and claystones spores are present/preserved only very rarely. One of the richest assemblages was obtained from the gray nearshore mudstones of the Klobuky locality. Here the assemblage is dominated by the genus *Cyclogranisporites* followed by the genera *Laevigatosporites*, *Latosporites* and *Punctatisporites*, whereas representatives of the genera *Convolutispora*, *Microreticulatisporites*, *Leiotriletes*, and *Verrucosisporites* are rare (Šimůnek et al. 2009). The genera *Calamospora*, *Cadiospora* (*Sigillaria brardii*), *Cirratriradites* (herbaceous lycopsids), *Florinites* (*Cordaites*), *Potonieisporites* (conifers) and *Schopfipollenites*, *Vesicaspora*, *Wilsonites* and *Vittatina*, which represent pteridosperms, all are found very rarely. This assemblage contrasts with those isolated previously from thin coals and dominated by representatives of the genus *Lycospora* (Kalibová, 1970; Valterová, 1983, 1985).

The scarcity of determinable plant remains and palynomorphs throughout the formation does not allow for internal stratigraphic subdivision of this formation by means of macroflora and miospores. The presence of some key taxa (e.g., *Sphenophyllum angustifolium*) in the Zdětín and Klobuky horizons suggests that the lower half of the forma-

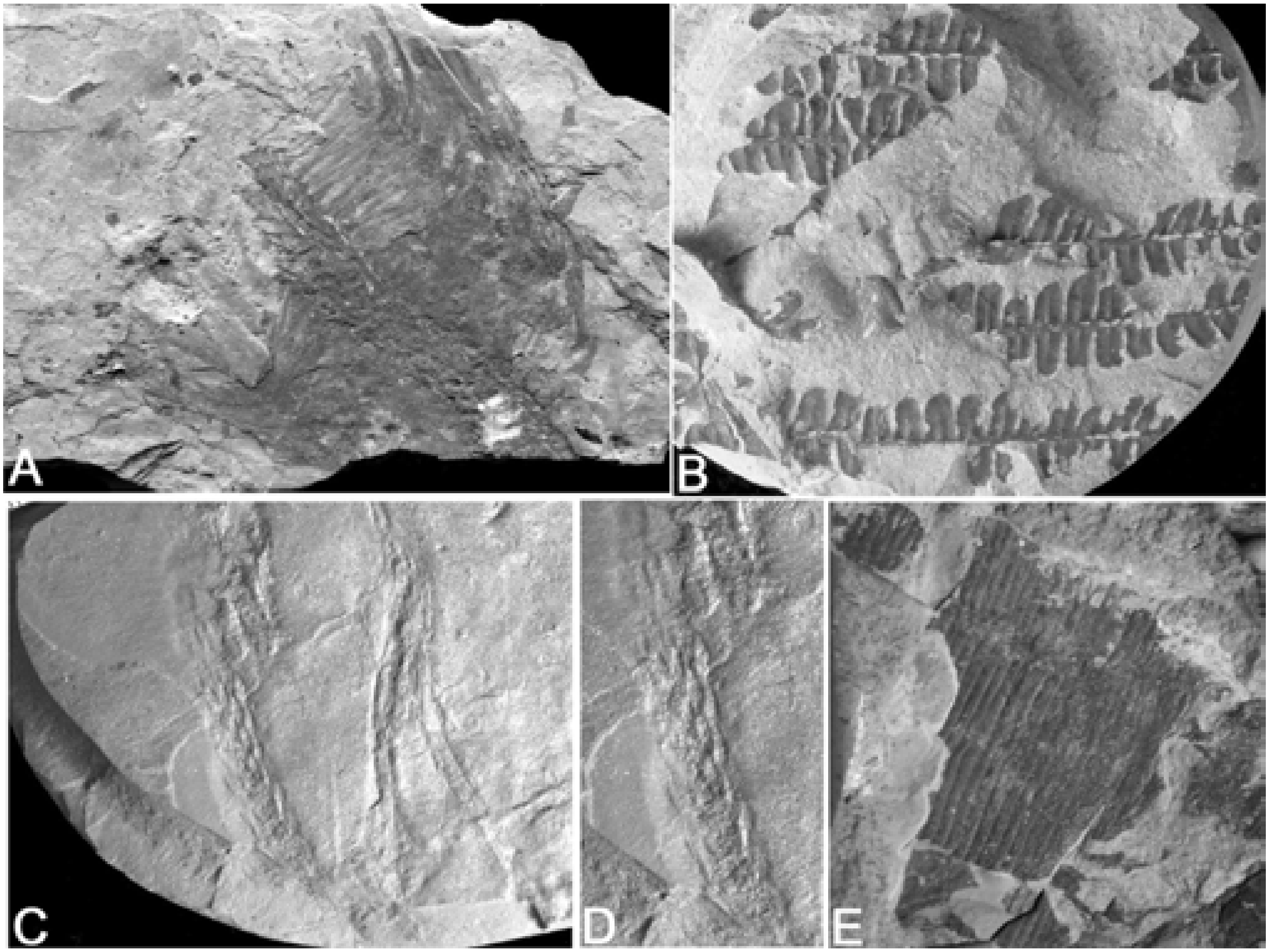

FIGURE 3. **A**, Fragment of a lycopsid cone *Lepidostrobus* cf. *sternbergii* (Corda) from bedded muddy limestone above the Klobuky Coal. Outcrop behind the sugar factory in Klobuky. **B**, *Callipteridium pteridium* (Gutbier) preserved as coalified compression in a grayish mudstone. Borehole Semčice (Sč1), depth 1249.4 m. Mnichovo Hradiště Basin. **C**, *Walchia* sp. in brick-red mudstone preserved as an impression. Borehole Semčice (Sč1), depth 894.4 m. **D**, Detail of the Figure 3C. **E**, *Calamites* cf. *cistii* Brongniart preserved in gray and thin bedded silty claystone covered by a thin layer of iron oxides (?hematite). Borehole Sazená (Sz1), depth 67.3 m. Kladno-Rakovník Basin.

tion correlates with the *S. angustifolium* biozone of Wagner (1984), indicating a latest Pennsylvanian age (upper Gzhelian). The age of up to several hundred meters of sediments above the Klobuky Horizon cannot be constrained on the basis of the floristic record. However, the local vertebrate *Acanthodes gracilis* biozone suggests an Early Permian (Asselian) age of the upper part of the formation (Zajíc, 2010). Surprisingly, no peltasperm remains have been so far reported from this assumed Permian part of the section (Šetlík, 1977).

SUMMARY AND CONCLUSIONS

Sediments of up to about 1 km thick comprise the Líně Formation in basins of central and western Bohemia. These sediments consist dominantly of a fluvial red bed succession interrupted by horizons of gray to variegated and mostly lacustrine strata, tens of meters thick. Both lacustrine and fluvial sediments contain lithological indicators suggesting the existence of seasonality, the intensity of which probably varied through time. Fluvial sediments containing vertisols to calcic vertisols were deposited under a dry subhumid climate, whereas deposition of dominantly gray to variegated parts of the succession fall within the interval of relatively wet subhumid conditions (Cecil, 2003), although even during this time the climate was not completely everwet (humid to perhumid) as indicated by the presence of cherts, lacustrine limestones and only thin high-ash coals of local areal extent.

The fossil record of the formation is generally very poor. In all, only about 50 morphotaxa have been identified, which are estimated to represent about 40 biological species at a minimum. They include very rare arborescent lycopsids, common sphenopsids (both calamites and sphenophylls), ferns (small herbaceous and tree ferns), pteridosperms (both Callystophytales and Medullosales), cordaitaleans and walchian conifers. Peltasperms are completely absent. Palynomorph diversity approximates the number of estimated floristic species and basically reflects the composition of macroflora found in the formation. Domination of *Lycospora* miospores in some samples (Kalibová, 1970; Valterová, 1983, 1985) is noteworthy, and represents a major difference from west-central and western Pangean deposits, where plants producing these spores disappeared around the Middle/Upper Pennsylvanian boundary (e.g., Peppers, 1996).

Plants of the Líně Formation represent floras of two different and ecologically separated wetland and dryland biomes, the former represented by lycopsids, calamites, ferns and pteridosperms, the latter composed dominantly of conifers and cordaitaleans. These biomes occupied different habitats as indicated by preferential occurrence of their remains in different types of sediments. Drifted wetland plant remains are common in gray to variegated sediments deposited mostly in lakes. Red-colored mudstones associated often with pedogenic horizons provided nearly exclusively conifer and cordaitalean remains. Whether they are (para)utochtonous is difficult to estimate from current data, although sub-vertically oriented roots occasionally found in paleosol horizons indicate that the dryland assemblage very probably colonized the basinal lowland during the periods of drier (dry subhumid) climate. In that time, wetland plant elements probably survived in localized wetlands in/along small ponds scattered across the basinal lowland as corroborated by very rare findings of fern and calamite remains in some variegated mudstones associated with fluvial strata. Vice versa, in sediments deposited during wetter periods, very rare findings of conifers and cordaitalean remains in gray lacustrine strata associated with wetland plants indicate temporary, spatially close coexistence of both ecologically contrasting assemblages, even during the wetter (wet subhumid) periods. Whether also during these wetter periods the dryland plant assemblage colonized basinal lowlands or the remains of its component plants were drifted from remote extrabasinal uplands is not completely clear. However, it is assumed that the wetland plant assemblage colonized lake margins while, at the same time, cordaitaleans and conifers lived in the more xeric soils away from lakes.

Biostratigraphically, the flora of the lower half of the Líne Formation indicates a position within the *Sphenophyllum angustifolium* biozone, of the late Stephanian C (upper Gzhelian) age. The upper part of the formation has not provided a biostratigraphically important flora but vertebrate biozonation (*Acanthodes gracilis*) indicates a possible Asselian (Cisuralian) age (Zajíc 1990), although peltaperms are absent in the fossil record.

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LATE DEVONIAN, CARBONIFEROUS, AND PERMIAN SEQUENCES OF SONORA STATE (MEXICO)

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INTRODUCTION

The Late Paleozoic sequences of Sonora (Mexico) were revised principally in five important field sections, the cumulated thickness of which measures approximately 4000 m: (1) Cerros El Tule (NNE of Cananea town); (2-3) Cerro los Abajeños and Cerro El Palmar in the Sierra Agua Verde (near the village San Pedro de la Cueva); (4) Cerro El Yugo (near Arivechi village); and (5) Cerro La Morita (NE of Cananea town). This study (Palafox, 2011) was supported by the Projects ECOS-Nord-ANUIES, UNISON-PROMEP, UNAM-PAPIIT Project IN105012, and CONACYT Project 165826.

GEOLOGICAL SETTING

The classic lithostratigraphic scheme of Ransome (1904), established near the Arizona-Sonora border, can be used in Sonora, with the following formations: Martin Fm (Devonian), Escabrosa Fm (Tournaisian-Viséan-Serpukhovian?) and Horquilla Fm (Bashkirian-Gzhelian). The El Palmar outcrop displays the most complete Martin Fm, with interesting Frasnian and Famennian strata, as well as the base of the Mississippian series. The sequences of Los Abajeños exhibit a relatively thick Escabrosa Fm with micropaleontologically characterized Tournaisian and early Viséan beds. El Yugo shows an especially interesting Martin Fm with well-developed Frasnian reefs as well as a complete Escabrosa Fm, without conspicuous stratigraphic gaps, although the Famennian is probably tectonically reduced, in comparison with its thickness in El Palmar. In El Tule, the Escabrosa Fm and Horquilla Fm are exposed and display all their fossiliferous stages. At La Morita, we found only Moscovian and Kasimovian beds; the other parts of the Pennsylvanian are either devoid of fossils or tectonically absent. Even in El Tule, the richest of our sections, the assemblages of fusulinids are less diversified than those of the outcrops of New Mexico, for example Big Hatchet and Newwell Peaks.

BIOSTRATIGRAPHY

From early Frasnian to middle Viséan times, the following biostratigraphic subdivisions were found in all sections: (1) *Nanicella gallowayi* Zone; (2) *Eogeinitzina devonica* Zone; (3) undetermined moravamminids Zone; (4) *Granuliferella* Zone; (5) *Laxoendothyra parakosvensis* and *Granuliferelloides* Zone; (6) *Tuberendothyra* and *Inflatoendothyra* Zone; and (7) *Endothyra prisca* and *Stacheoides tenuis* Zone. All Pennsylvanian subdivisions (from Bashkirian to Gzhelian; i.e., regionally, from Morrowan to Virgilian) are exposed in the biostratigraphic column of the Cerros El Tule (Buitrón et al., 2012), with rich fossiliferous assemblages in M2, A4, DS1, DS2, MC1/2, VC2/3, PW1/2 biozones of Wilde (1990). The biozones A3, DS1 and MC4 were identified in the Sierra Agua Verde. In this area, the Morrowan and Atokan strata need to be studied more accurately.

In Cerros El Tule, the characteristic foraminiferal zones contain successively: *Inflatoendothyra parainflata*, *Tuberendothyra safonovae* and *Urbanella*? sp. (late Tournaisian = Osagean); *Millerella pressa* (Bashkirian = Morrowan); *Fusulinella famula* (Kashirian/Podolskian = latest Atokan); *Wedekindellina euthysepta*, *Beedeina arizonensis*, *B. pattoni*, *B.* cf. *distenta*, *B. rockymontana* (Myachkovian = early-middle Desmoinesian); *Triticites canyonensis* and *T. acutuloides* (Kasimovian = Missourian); *Triticites* ex gr. *beedei* (middle Virgilian); *Leptotriticites eoextentus* (late Virgilian) and *Geinitzina* first global appearance (Lower Permian). These successsions and appearances (first global and regional appearances) are similar to those of the North American craton; as well as those of South America, during and after the Bashkirian. In Sonora, the most common algae are *Komia* cf. *eganensis*, *K.* sp., *Paraepimastopora kansasensis* and *Epimastopora alpina*. The first ones are common in North America; the last species is cosmopolitan. For the first time, we report the presence of the alga *Gyroporella* aff. *microporosa* and the FAD of *Permocalculus* near the Pennsylvanian-Permian boundary in Cerros de Tule.

GLOBAL EVENTS

The Kellwasser and Hangenberg events (Frasnian-Famennian and Devonian-Carboniferous transition intervals, respectively) were not exactly identified in Sonora but they are easy to approximately locate, thanks to faunal extinctions (reef disappearances) and/or lithofacies changes (sandy limestone passing to criquinite). The different episodes of the LPIA (Late Palaeozoic Ice Age) were not characterized in Sonora, neither sequentially nor faunistically; the classical U.S. cyclothems have not been observed, but some alternations of slightly indurated with very indurated limestones can be their equivalents. These cryptocyclothems (Palafox, 2011) need additional investigation.

PALAEOBIOGEOGRAPHY AND PALAEOGEOGRAPHY

The Atokan of Sonora field sections is characterized by two species of *Fusulinella*, whereas the Desmoinesian is characterized by three species of *Beedeina*; all these fusulinids are unknown in the Tethys. Inversely, all transitional genera of the Tethyan domain, like *Staffellaeformes*, *Moellerites* or *Kamaina*, are unknown in North America. This datum indicates that the connections between the Tethyan shelves and the North American platforms were often interrupted, and that the migrations of microfaunas were sporadic and episodic.

Our results also confirm the palaeogeographic limit, already suggested in Mexico, between the North American craton and the suspect terranes located southwards within the Rheic Ocean (Gómez-Espinosa et al., 2008). Some terranes previously identified in Sonora as derived from the craton, or the Caborca terrane, did not exist during the Carboniferous-Permian. Evidence is also lacking to confirm the existence of the Mojave-Sonora megashear in this period. The Cerros El Tule and La Morita are located on the platform classically assigned to the "basin" of Pedregosa. The Pedregosa basin as well as the Orogrande basin in the U.S.A. were traditionally interpreted as a lateral equivalent of a depocenter corresponding to the flysch deposit of the Chihuahua basin in Mexico. This deep-water Chihuahua basin is probably independent of the shelf reconstructed by us and most probably belonged to the Rheic Ocean. The Pedregosa and Orogrande basins might represent northward, narrow extensions in the U.S.A. of the large platform that extends over the greater part of the Mexican states of Sonora, Chihuahua, Coahuila and Tamaulipas. This platform is probably located in a foreland. Beyond this platform, the lateral equivalents are the deep basins encountered in the Mexican States of Nuevo Léon, Sinaloa, San Luis Potosi and Durango. These flyschoid deposits constitute, with the Central Mexican Acatlán Complex, the sediments of the bottom of the Rheic Ocean and/or its submarine canyon fillings. Some islands and microplates are scattered within this oceanic bottom, e.g., Oaxaquia, Mixteco, Chortis, and Maya. By dispersal routes along these islands and microplates, the Sonora shelf distributed the fusulinid microfaunas through South America (Colombia, Ecuador, Peru-Bolivia). Consequently, the geology of Sonora during the Carboniferous can be correlated with that of the North American craton bordering either the Marathon-Ouachita or Antler deep basins. The Sonora platform received several migrations of foraminiferal faunas, coming from Tethys and passing through the Urals-Canadian Arctic-ancestral Rocky Mountains and Nevada, but possibly also passing through Panthalassa. Receiving the migrations of new taxa that radiated in the Tethys, the Sonora platform, in turn, dispatched these microfaunas through the Rheic Ocean and the intercontinental seas of the U.S. Midcontinent.

CONCLUSION AND PERSPECTIVES

Due to the social context in the northernmost area of Sonora (including Tule), our perspectives are currently re-centered around the Sierra Agua Verde (El Palmar, Cerro El Azogue, etc.) and El Bisani area (near Caborca town). In Cerro El Palmar, our principal topic will be the characterization of the Famennian and the study of the sedimentological and paleontological context of the Kellwasser event (Frasnian-Famennian boundary interval), as well as the Hangenberg event (Devonian-Carboniferous boundary interval), not precisely located but relatively easy to identify lithostratigraphically in the field. These topics could be investigated also in Cerro El Yugo, a more fossiliferous but otherwise more tectonically complicated section.

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TRACES OF HERBIVORY IN THE CARBONIFEROUS – PERMIAN TRANSITION FROM ARGENTINA: BAJO DE VÉLIZ FORMATION

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Arthropods and plants comprise the major source of terrestrial biodiversity. Direct evidence of plant–insect associations is relatively common in the Permian record of Gondwana, but little is known about herbivory from the Carboniferous of Gondwana. In Gondwanaland, the Carboniferous-Permian transition can be recognized in the Bajo de Véliz Formation, Paganzo Basin, Argentina. The upper part of the Bajo de Véliz Formation outcrops in the San Luis Province, which contains a rich flora of glossopteridales, cordaitales, lycopsids, sphenopsids and seeds. In total, 231 specimens from Bajo de Véliz were analyzed. Evidence of insect-plant interactions was present in only eight of these specimens (3.46%), in impressions/compressions belonging to *Glossopteris* sp., *Gangamopteris obovata* (Carruthers) White 1908 , cf. *Eryphyllum* sp. and *Botrychiopsis plantiana* (Carruthers) Archangelsky Arrondo, 1971. Four types of leaf feeding traces are observed: leaf margin feeding traces, hole feeding traces, slot feeding traces and oviposition scars. The feeding traces found in the Bajo de Véliz outcrops are comparable to damage types (DTs) described by Labandeira et al. (2007). The leaf margin feeding traces are similar to DT12 (margin feeding: cuspate excisions of leaf edge). The hole feeding traces are comparable to DT01 (circular perforations < 1 mm in diameter) and DT02 (circular perforations; 1 to 5 mm in diameter). The slot feeding traces can be comparable to DT08 (parallel sided, rectilinear or curvilinear; length/ width ratio > 2.5), but the slot has a V-shape and sometimes is connected to the leaf margin. In the same locality we also find eight species of insects: *Spherocorydaloides lucchesei* Pinto, 1994; *Diaphpterum* sp.; *Philiasptilon huenickeni* Pinto and Ornellas, 1978; *Velizoptera taschi* Pinto and Adami-Rodrigues, 1997; *Rigattoptera ornellasae* Pinto, 1996; *Paranarkemina velizensis* Pinto and Ornellas, 1981; *Paranarkemina amosi* Pinto, 1992; and *Paranarkemina kurtzi* Pinto and Ornellas, 1980. The insects from the Bajo de Véliz are clearly Carboniferous, but the plant assemblage is similar to Lower Permian floras. The feeding traces are typical Late Paleozoic, with an increase in functional feeding groups, like oviposition. The plant and insect assemblages are changing, but the functional feeding groups persist through time, indicating a stability of plant-insect associations during the Carboniferous-Permian transition.

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THE OLDEST FLORA FROM THE SOUTHERN ALPS (ITALY): THE VAL SANAGRA PENNSYLVANIAN FLORA REVISED

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Within the scope of the mission of IGCP 575, a careful revision of the rich Late Carboniferous fossil flora from the Val Sanagra outcrops in Western Lombardy (Southern Alps, Italy) was carried out. All fossil plant remains come from extensive collections housed in the Museo Civico di Storia Naturale (Milan) and also in the Museo Etnografico e Naturalistico Val Sanagra (Grandola ed Uniti, Como). In spite of the large outcrop area between W Lombardy and Canton Ticino (Switzerland), Carboniferous terrestrial deposits crop out only at sparse localities, which often have been tectonically displaced, and lack clear stratigraphic and paleogeographic context. Nonetheless, the Pennsylvanian flora of NW Italy could play an important role when reconstructing Late Carboniferous environments and paleogeography of this part of Europe, even though partly masked by a strong Alpine tectonic overprint.

The first report of Carboniferous macrofloras from the Val Sanagra (Alpe Logone) locality came from Magnani (1946), who discovered impressions and casts of *Calamites* Suckow, *Sigillaria* Brongniart and *Lepidodendron* Sternberg. In the mid 20th century, Venzo and Maglia (Venzo and Maglia, 1947; Venzo, 1951) collected more than 2000 leaf compressions and impressions from those anthraciferous and silicified beds. The high number of species identified by Venzo, however, could not be confirmed by our revision. The main problem is generally poor preservation of plant remains, which makes their identification problematic. Due to this fact, the number of species (especially from lycopsid and sphenopsid groups) described by the above-cited authors, was reduced after a careful revision. Nevertheless, some of the species originally mentioned by these authors are included in the present revision.

The species identified by us in common with previous descriptions are the following: *Sigillaria rugosa*, *Sigillaria tessellata*, *Lepidodendron aculeatum*, *Lepidocarpon* cf. *majus*, *Stigmaria ficoides*, *Calamites* (*Crucicalamites*) *cruciatus*, *Calamites* (*Stylocalamites*) *cisti*, *Annularia radiata*, *Asterophyllites equisetiformis*, *Lobatopteris miltonii*, *Senftenbergia plumosa* and *Linopteris obliqua*. In contrast, the following species are described here for the first time from the locality: *Sigillaria* cf. *inferior*, *Sigillaria* cf. *ovata*, *Asolanus camptotaenia*, *Lepidodendron* cf. *acutum*, *Bothrodendron* sp., *Calamites* (*Diplocalamites*) *carinatus*, *Asterophyllites longifolius*, *Calamostachys* cf. *tuberculata*, *Lobatopteris* cf. *simonii*, *Pecopteris microphylla*, *Corynepteris* (*Alloiopteris*) sp., *Eusphenopteris* cf. *neuropteroides*, *Mariopteris* cf. *lobatifolia*, *Mariopteris* cf. *sauveurii*, *Karinopteris dernoncourti*, *Alepthopteris* cf. *grandinioides* var. *grandinioides*, *Neuralethopteris* cf. *larischii*, *Paripteris linguaefolia* or *Hexagonocarpus* sp.

Zygopterids, as a group of ferns, have never been mentioned from the Val Sanagra locality to date. We discovered only two poorly preserved specimens of the genus *Corynepteris* but it is clear evidence of the presence of this type of fern in the plant assemblage.

Dominance of the assemblage by particular remains of certain plant taxa (e.g., isolated sigillarian leaves or *Linopteris* pinnules) indicates the existence of partitioned habitats colonized by various plant assemblages dominated by pteridosperms and calamitaleans or by arborescent lycopsids, mostly by sigillarias or less common lepidodendrids (mostly *Paralycopodites*). Such ecological differentiation of vegetation is a common feature described from many coalfields and we assume it existed also in the case of the Val Sanagra locality (e.g. DiMichele and Philips, 1994, Bashforth et al. 2011). Carboniferous sediments in Val Sanagra are only a thin tectonic slice of a once thicker sedimentary complex. It is therefore difficult to draw any serious conclusions about the basin type and its development. However, absence of marine fauna in the locality suggests this is a part of a formerly continental basin. This is also in agreement with the relative abundance of feldspathic sandstones, indicating close proximity of a feldpar source. In other European coalfields the feldspathic sandstones are more typical for continental basins than for paralic ones. We therefore assume that the Val Sanagra sediments represent a part of the section deposited in a continental setting in a fluvial environment with a well-developed and vegetated floodplain, within which clastic swamps locally/occasionally transitioned into peat swamps.

As a whole, predominance of rhytidolepis sigillarias and species typical for the Duckmantian or Bolsovian stages suggest that the flora of the Val Sanagra locality spans the interval between the Duckmantian and Bolsovian (middle Moscovian). The Val Sanagra flora thus represents the oldest Pennsylvanian flora of the entire Southern Alps.

The Val Sanagra flora also can be compared biostratigraphically with that found in the Manno locality (Canton Ticino, Switzerland), since the age-attribution of both has, for a long time, been a matter of debate. Sordelli (1896) recognized 13 species from Manno, ten of which are in common with the flora from the Alpe Logone/Val Sanagra, including five species of *Sigillaria*, and another five species among the genera *Calamites*, *Lepidodendron* and *Cordaites*. He attributed the Manno flora to the early Stephanian, but with many Westphalian elements. Venzo and Maglia (1947) compared their taxonomic list with the one of Sordelli (1896) and considered the Val Sanagra flora (Westphalian C) to be older than that from Manno. Only some years later, Venzo (1951) changed his opinion/interpretation and ascribed the flora from Manno to the transition between the Westphalian B and C, thus suggesting it to be slightly older than the flora from Alpe Logone. Jongmans (1950) related the floras of various Swiss localities (including Manno) first to the Westphalian B-C, due to the presence of some elements such as *Linopteris neuropteroides*, cf. *Pecopteridium*, *Sigillariaephyllum*, and *Cordaites* cf. *borassifolius*, but later considered it to be slightly younger, most likely Westphalian C (Jongmans, 1960).

The present taxonomic revision, together with the lithostratigraphical similarities of the two localities, permits a clear litho- and biostratigraphic correlation to be made, denying any age-differences between them. Conversely, the Val Sanagra flora is significantly more recent than the Bèdero palynomorph associations (Luino, eastern side of Maggiore Lake, W Lombardy), which are referred to a late Westphalian-early Stephanian age (Pittau et al., 2008).

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THE *IDIOGNATHODUS TURBATUS* CONODONT LINEAGE IN THE NAQING SECTION, SOUTH CHINA, AND THE BASE OF THE GLOBAL KASIMOVIAN STAGE

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The base of the global Kasimovian Stage is to be raised to approximately the level of the base of the Khamovnikian Substage in the Moscow Basin of Russia. This new level is one substage higher than the traditional base of the Kasimovian Stage at the base of the Krevyakinian Substage, but it will facilitate global correlation. The first appearance datums (FADs) of the conodont species *Idiognathodus sagittalis* Kozitskaya, 1978, and *I. turbatus* Rosscoe and Barrick, 2009, are the two potential biostratigraphic events being currently investigated for selection and correlation of the level of the GSSP for the base of the Kasimovian Stage. *Idiognathodus sagittalis* is a Eurasian species based on material from the Donets Basin (Ukraine), and a possible ancestor-descendent lineage from "*I. nikitini*" to *I. sagittalis* has been reported from the Moscow Basin. *Idiognathodus sagittalis* is poorly known outside of the Donets and Moscow basins. *Idiognathodus turbatus* is a Midcontinent North American species that is also not well known from other regions. A lineage from *I. swadei* Rosscoe and Barrick, 2008 to *I. turbatus* has been described from Midcontinent North America. The lineages and the FADs of *I. sagittalis* and *I. turbatus* need further investigation to document their distribution in all geographic regions for identification of potential GSSP candidates.

Abundant conodonts have been obtained from across the proposed Moscovian-Kasimovian boundary interval in the Naqing section, South China. In these collections occur many morphotypes that represent the rapid morphological transformation from *I. swadei* (no groove) to a transitional form (complete eccentric groove) to *I. turbatus* (medial nodosity). Therefore, the important North American Midcontinent conodont evolutionary lineage from *I. swadei* to *I. turbatus* has been replicated in the South China region. Further work is needed to confirm the presence of the lineage, or at least the occurrence of *I. turbatus*, in the Moscow and Donets basins, the southern Urals, northern Spain, and other regions.

At this time, the species in the lineage leading to *Idiognathodus turbatus* show the greatest potential to serve as the biostratigraphic marker for the base of the Kasimovian Stage. The demonstration of this lineage in the Naqing section, an apparently continuous, condensed section of deep-water marine carbonates, makes the Naqing section a major contender for the GSSP for the base of the Kasimovian Stage.

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MULTIPLE TRANSITIONAL CONODONT MORPHOLOGIES DEMONSTRATE DEPOSITIONAL CONTINUITY IN THE BASHKIRIAN-MOSCOVIAN BOUNDARY INTERVAL, NAQING SECTION, GUIZHOU, SOUTH CHINA

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Abstract—A succession of conodont chronomorphoclines occurs through the Bashkirian-Moscovian boundary interval at the Naqing section in South China. They demonstrate that deposition was remarkably continuous through the boundary interval, a major criterion for selecting a Global Stratotype Section and Point (GSSP). This paper describes the current state of knowledge for several of these chronomorphoclines, and also provides an updated range chart of conodonts recovered from the Naqing section and their correlation with other regions. The taxon that best matches the current concept for the base of the Moscovian Stage in its type region is the phylogenetic first occurrence of *Diplognathodus ellesmerensis*. An ancestral form with most of the characteristics of *D. ellesmerensis* occurs at Naqing. More specimens are needed to completely document the chronomorphocline, but because *D. ellesmerensis* is found worldwide—including at the base of the type Moscovian—its evolutionary first occurrence would provide an almost ideal biostratigraphic level for GSSP definition.

INTRODUCTION

One of the major criteria for selecting a Global Stratotype Section and Point (GSSP) is to demonstrate depositional continuity. Depositional continuity is most often accepted where a complete transitional morphocline from an ancestral species to its descendent can be recognized through the strata under consideration. The stratigraphic level for the GSSP can then be selected to correspond with the phylogenetic first occurrence of the descendent species. Ideally, strata elsewhere are subsequently correlated with the GSSP using the local first appearance of the descendent species, or by using other taxa associated with the GSSP that provide supplementary biostratigraphic data. Any other stratigraphic methods (paleomagnetism, geochemistry, etc.) can be used for correlation once the GSSP has been ratified by the International Union of Geological Sciences Commission on Stratigraphy.

This paper briefly discusses a succession of transitional conodont morphoclines through the traditional Bashkirian-Moscovian boundary interval at the Naqing section in South China. We wish to emphasize the remarkable depositional continuity through the entire boundary section. We also introduce an updated, taxonomically more rigorous range chart for that part of the section (Fig. 1).

The Naqing section is located along a major road cut that exposes Devonian through Permian strata in the mountains between Loudian and Wangmo in Guizhou Province, South China (Fig. 2). It was formerly known as the Nashui section. The general setting of the Naqing section represents a platform margin to slope depositional environment. The Carboniferous part of the section is composed of continuous carbonate deposits from the upper Visean through Gzhelian stages. Conodonts are abundant through much of the section, and there are beds that represent allochthonous flows, which brought in fauna from shallower water shelf settings. These characteristics make the Naqing section ideal for correlation with facies from various depositional settings. That potential is strengthened by two newly discovered sections nearby that include the Bashkirian-Moscovian boundary interval. One is the Loukun section, composed of upper slope to platform edge deposits with relatively abundant fusulinid and non-fusulinid foraminifers, and the other is the Dianzishang section, composed of coarse-grained normal platform carbonates with abundant foraminifers.

The stratigraphic succession in the Bashkirian-Moscovian boundary interval at Naqing consists mainly of gray thin- to medium-bedded wackestone and packstone beds intercalated with chert beds. These beds dip at approximately 60-70 degrees, are 100 per cent exposed, and are easily accessible along the extended road cut. Conodonts are very abundant in the boundary interval, with more than 45 species representing 11 genera. All of the numerous samples that have been collected have produced conodonts.

Conodonts in the Bashkirian-Moscovian boundary interval at Naqing have most recently been studied by Wang and Qi (2003), Qi et al. (2007, 2009, 2010a, 2010b, 2011), Qi (2008), and Wang et al. (2008, 2011). Most of these papers have focused on characterizing the section as a possible GSSP for the base of the Moscovian Stage. Earlier conodont studies that in part covered this interval at Naqing include Rui et al. (1987), Wang et al. (1987), and Wang and Higgins (1989). Specimens from the Bashkirian-Moscovian boundary interval are illustrated among the numerous plates in these older papers.

CONODONT ZONATION AND IMPORTANT FUSULINID FIRST APPEARANCES AT NAQING

Four conodont zones have been distinguished in the Bashkirian-Moscovian boundary interval at Naqing (Qi et al., 2007). In ascending order, they are the "*Streptognathodus*" *expansus*, *Diplognathodus coloradoensis*, *Diplognathodus ellesmerensis*, and *Mesogondolella donbassica-M. clarki* zones, which cover a stratigraphic interval of approximately 25 m (from 161.00 m to 186.22 m). Qi et al. (2007) proposed a provisional level for the base of the Moscovian Stage at the FAD (First Appearance Datum) of *D. ellesmerensis* at 173.0 m above the base of the Naqing section. Subsequent work has shown that the lower specimens then considered to be *D. ellesmerensis* are in fact morphologies transitional to *D. ellesmerensis sensu stricto*, which first appears at 176.9 m. *Diplognathodus ellesmerensis* had a cosmopolitan distribution, is easily identified, and has a restricted and well-defined stratigraphic range (Grayson, 1984; Nemyrovska, 1999; Nemyrovska et al., 1999; Makhlina et al., 2001; Groves and Task Group, 2006; Qi et al., 2007, 2011; Qi, 2008; Wang et al., 2011). Therefore, we consider the first occurrence of *D. ellesmerensis* to be the best biostratigraphic marker for the base of the Moscovian in the Naqing section.

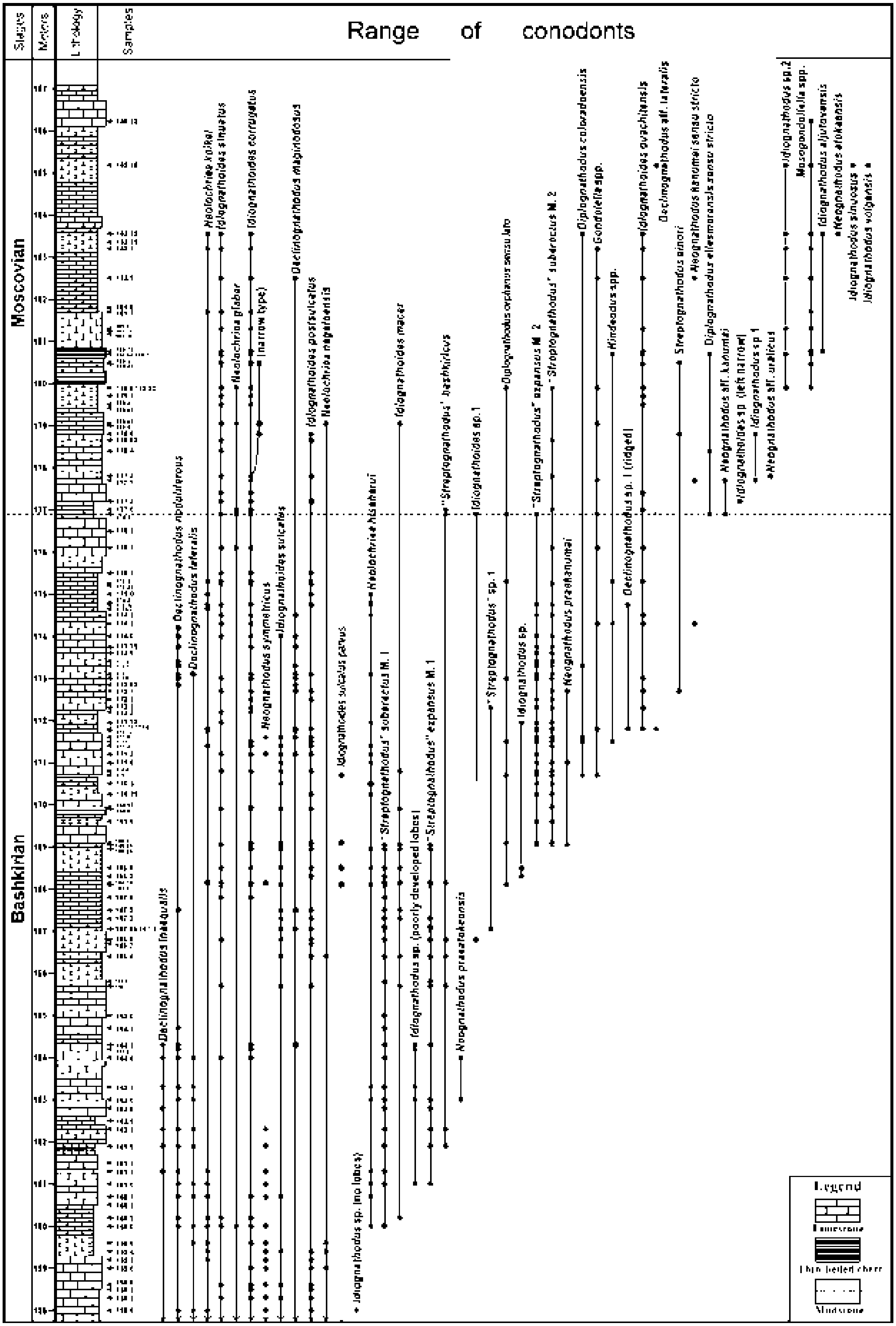

FIGURE 1. Range chart for the conodonts discussed in this paper with regard to the Bashkirian-Moscovian boundary interval at Naqing.

The fusulinid *Profusulinella* occurs at 162.8 m at Naqing, low in the interval of study. Katsumi Ueno (personal communication) suggests that the FAD of *Profusulinella* is probably somewhat lower in the section. The fusulinid *Eofusulina* has been recovered at 183.45 m (Groves and Task Group, 2009; Groves, 2010). Also noteworthy is the first definite occurrence of *Neognathodus atokaensis* at 183.55 m, just above that of *Eofusulina*. Both *Eofusulina* and *N. atokaensis* are considered as definite Moscovian indices in current task group discussions, and the near co-occurrence marks the upper part of the interval of study.

Further work has shown that the lower part of the interval of study might be better characterized at Naqing as the zones of "*Streptognathodus preexpansus*" ("*S.*" *expansus* Morphotype 1 in this paper), and "*S.*" *expansus* ("*S.*" *expansus* Morphotype 2 in this paper), because specimens of these morphotypes are a major component of the conodont fauna (Qi et al., 2011). The resolution of taxonomic questions must await re-examination of the "*S.*" *expansus* holotype and its associated topotype material. Whatever zonal name is used, this lower portion of the Naqing section is equivalent in part to the *Declinognathodus marginodosus* Zone (and in cases preceding zones) in other parts of the world.

TRANSITIONAL CONODONT MORPHOLOGIES AT NAQING

Multiple conodont lineages with transitional, chronoclinal morphologies characterize the Bashkirian-Moscovian boundary interval in the Naqing section. The presence of these chronoclines demonstrates depositional continuity at the Naqing section, and provides numerous possible conodont-based levels that are available for selecting a GSSP for the base of the Moscovian. *Diplognathodus* provides the lineage we favor for ease of identification and widespread correlatability. "*Streptognathodus*" *expansus sensu lato* is also easy to identify and found worldwide, and it could provide a common and easily recognizable mid-Bashkirian marker, if it is considered too low to mark the base of the Moscovian. There are additional transitions in "*Streptognathodus*," and in lineages of *Idiognathodus*, *Gondolella*, and *Mesogondolella*. Other genera at Naqing show a potential for chronomorphoclines with additional study.

Currently Recognized Chronomorphoclines

Diplognathodus ellesmerensis

Diplognathodus first appears in the section at 168.1 m with a *D. orphanus*-type morphology bearing a denticulated "spatula" that slopes to the posterior and is here referred to as *Diplognathodus* aff. *D. orphanus*. It is joined at 170.7 m by a *D. coloradoensis*-type morphology with a distinctively elongated "spatula." Specimens previously referred to *D. ellesmerensis* at 173.0 m have characteristics more in common with *D. orphanus sensu lato*. At 174.3 m a morphotype appears with a *D. ellesmerensis*-like blade (denticle tops fan out and posteriormost denticles point to the posterior), but with a denticulated "spatula" and cup that is arched rather than delineating a flat aboral surface. It ranges through 175.3 m. This morphology could be transitional from *Diplognathodus* aff. *D. orphanus*, but more importantly the only character it lacks to evolve into *D. ellesmerensis* is flattening of the cup. Additional specimens with an intermediate cup morphology are needed to document the transition to *D. ellesmerensis*. *Diplognathodus ellesmerensis sensu stricto* first occurs at 176.9 m and ranges up through 178.4 m. The probable highest occurrence of *D. ellesmerensis*, based on a fragmentary specimen, is at 180.7 m.

The appearance of *Diplognathodus ellesmerensis* has previously been proposed to mark the base of the Moscovian Stage at Naqing (Qi et al., 2007, 2009; Wang et al., 2008, 2011). A potential GSSP level based on the first occurrence of *D. ellesmerensis* in a transitional morphocline will be a stronger candidate if the recovery gap between the transitional form at 175.3 m and the first occurrence of *D. ellesmerensis sensu stricto* at 176.9 m can be filled in with more specimens. The appropriate samples to do this have already been collected bed by bed, and are currently being processed.

"Streptognathodus" expansus sensu lato

"*Streptognathodus*" *expansus* does not belong to the Kasimovian genus *Streptognathodus*, but like *Swadelina* represents a separate clade of conodonts bearing troughed P_1 elements (Sweet, 1988; Barrick and Boardman, 1989; Lambert and Heckel, 1999; Lambert et al., 2003). The different "*Streptognathodus*" *expansus sensu lato* morphologies described below should be recognized formally at the species level, but these taxonomic decisions await re-examination of the holotype and associated specimens.

"*Streptognathodus*" *expansus* Morphotype 1 bears short, straight, parallel adcarinal ridges through ontogeny. It is first recovered at 161.00 m, near the base of the boundary interval, and ranges up through 168.10 m. Another morphotype with only an inner adcarinal ridge occurs low within that range, but it appears to be only a rare variant among the abundant Morphotype 1 specimens.

"*Streptognathodus*" *expansus* Morphotype 2 bears distinctly longer parallel adcarinal ridges that "drape" off the platform towards the anterior. Distinctively, it develops a dimorphic posterior platform expressed on adult forms that are either a) more "thin and pointed," or b) more "broad and rounded." Morphotype 2 is distinct from Morphotype 1 by 169.05 m, and develops from 167.10 m through 169.05 m by incremental extension of the adcarinal ridges. This incremental morphocline strongly supports an interpretation that deposition was continuous at Naquing through these strata. That is one reason why Qi et al. (2010a) suggested that it be considered as a possible biostratigraphic index for the base of the Moscovian Stage. Morphotype 2 continues up through 176.9 m. Morphotype 2 appears to match the morphology of the holotype as drawn in Igo and Koike (1964), but because it is a drawing, visual re-examination of the holotype is required for taxonomic confirmation.

Within the range of Morphotype 2 is a subtle change from predominantly parallel adcarinal ridges to a morphology with adcarinal ridges that "pinch" inward toward the carina on most specimens; instead of being entirely parallel they converge, then diverge toward the anterior. The morphology then changes subtly back to sub-parallel adcarinal ridges. The "pinched" adcarinal ridges are dominant at 171.5 m and are rare by 172.3 m. Concurrent with the "pinched" adcarinal ridges, an inner node or small accessory lobe becomes common and continues through the rest of the range to 176.9 m. Whether the "pinched" and/or noded forms should be recognized as distinct morphotypes or dimorphs will also require further study. If regarded as distinct morphotypes, there are multiple gradational transitions in the "*Streptognathodus*" *expansus* lineage.

"Streptognathodus" suberectus

"*Streptognathodus*" *expansus* is a sinistral P_1 element. Dunn (1970) first proposed that "*Streptognathodus*" *expansus* might be paired with the entirely dextral "*Streptognathodus*" *suberectus* as a Type IIIb symmetry pair (Lane, 1968). Other workers prefer to keep these taxa as separate Type IV entities (e.g., Lane and Straka, 1974; Nemyrovska, 1999).

"*Streptognathodus*" *suberectus*, ranges from 160.0 m through 179.9 m at Naqing. Through that range, the platform becomes more complexly ornamented by an increase in the size and degree of development on the "elongate lobe of several nodes aligned parallel to long axis and situated along inner anterior portion of platform….," as described by Dunn (1966). Specimens from sequential samples appear to develop the ornamentation slightly more fully than the previous sample, providing a complete chronomorphocline. However, because that increasing degree of ornamentation might also reflect an ontogenetic pattern, more specimens at different growth stages are needed from parts of the transition before

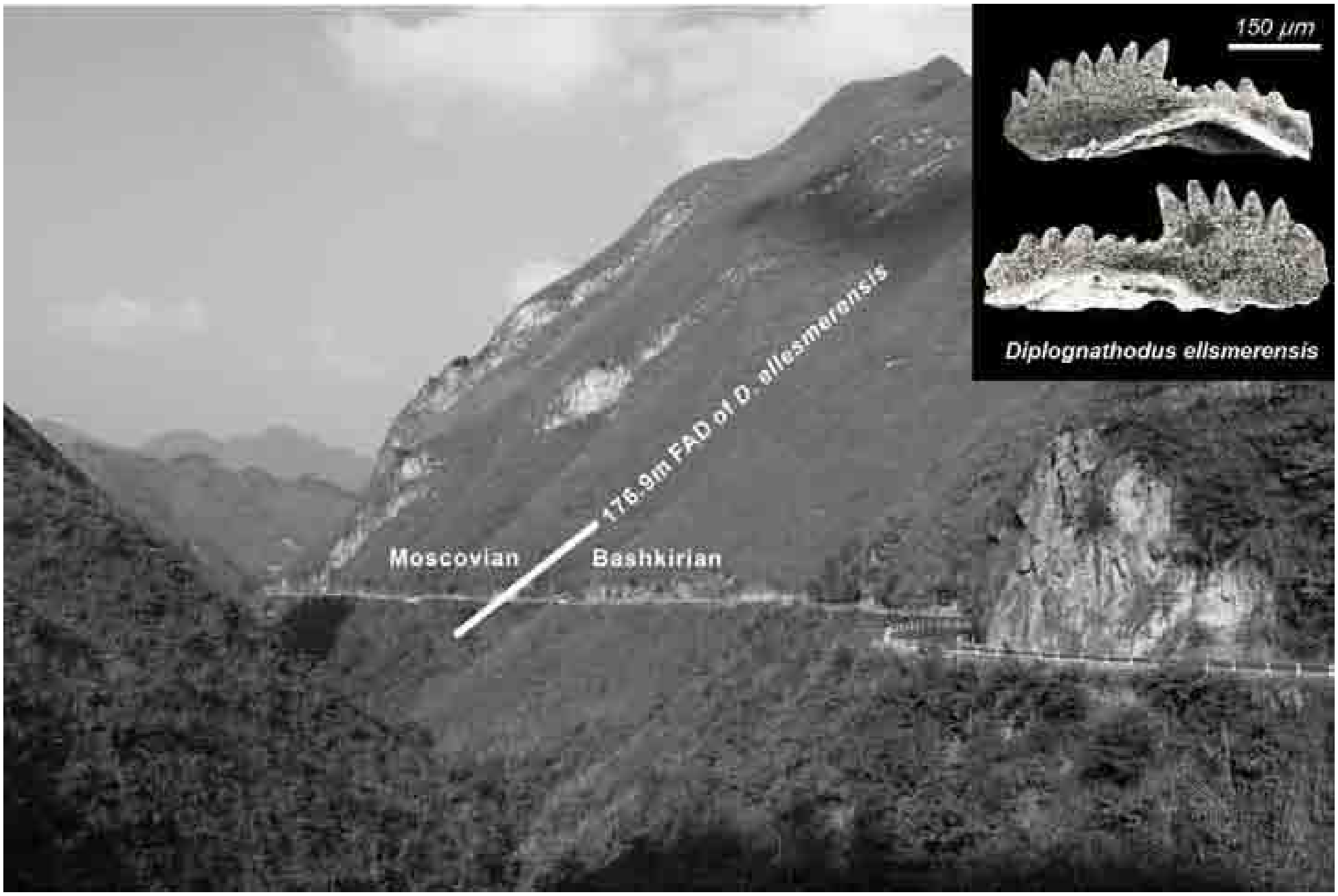

FIGURE 2. Overview photograph of the Naqing section roadcut. Vantage point is from the Devonian part of the section; view is up section. Inset are images of two *Diplognathodus ellesmerensis* P_1 elements from 176.9 m.

"*Streptognathodus*" *suberectus* can be confidently subdivided into potentially different early and late species with a clinal transition in-between.

Idiognathodus species

Many of the *Idiognathodus* P_1 elements through the Naqing section resemble those reported by Nemyrovska (1999) for the Donets Basin, but their occurrences are seldom in successive samples at Naqing. The lower part of the studied interval, from 161.0 m to 164.3 m, contains species with poorly developed lobes. The upper part of the studied interval contains advanced species of *Idiognathodus* with well-developed lobes and regular transverse ridges. These include occurrences of *I. aljutovensis* at 180.68 m, and both *I. volgensis* and *I. sinuosus* at 185.18 m. These species are known from the Bashkirian-Moscovian boundary interval in the Donets Basin and Ural Mountains as well as from the lower Moscovian deposits of the Moscow Syncline (Alekseev et al., 1994; Nemyrovska, 1999; Makhlina et al., 2001; Pazukhin et al., unpubl.).

One well-represented transition between undescribed *Idiognathodus* species could be recognized relatively high in the section. *Idiognathodus* n. sp. 1 occurs at 177.7 m and is characterized by transverse ridges that are thickened or "overdeveloped" on the platform edges. Through successive samples these exaggerated transverse ridge terminations become increasingly nodose, and the mid-platform portion of the transverse ridges becomes increasingly reduced. By 179.9 m the platform has no transverse ridges, but instead is ornamented by parallel nodes that trend down the platform where transverse ridges normally occur, a morphology designated as *Idiognathodus* n. sp. 2. The best correlation horizon based on *Idiognathodus* would thus be at the end of the clinal transition from *I.* n. sp. 1 to *I.* n. sp. 2, at 179.9 m.

Gondolella species

Gondolella is represented only by species with P_1 elements that lack a fully developed platform. Formal taxonomic assignments will require further study, particularly to better circumscribe concepts already used widely in the literature (e.g., *G. laevis*). These P_1 elements evolved through the boundary interval of the Naqing section with continuous trends that can be subdivided into recognizable morphologies. At this time there is one well-represented, but subtle, morphocline. It begins with a morphology that bears a posterior thickening that can be considered a rudimentary platform near the cusp, and the P_1 element always has a small posterior process bearing a few small denticles. The platform denticles are vertical (not bowed), and are either not declined, or barely declined. This morphology ranges from 174.3 m through 176.1 m, and within that range is a transition through which the rudimentary platform becomes increasingly pronounced, and the denticles become increasingly adpressed.

Mesogondolella species

Like *Gondolella*, *Mesogondolella* at Naqing evolved through the boundary interval with continuous mosaic trends. Formal taxonomic assignments will require further study, especially a thorough review of previously described holotypes (e.g., *M. donbassica*, *M. clarki*). Recoveries are very good beginning with the first occurrence of *Mesogondolella* at 179.9 m, which marks the base of the *Mesogondolella donbassica-G.*

clarki Zone of previous Naqing reports. Specimens of the genus occur in almost every overlying sample through the boundary interval and above.

At 179.9 m the mesogondolellids have discrete, round denticles that generally decrease in height toward a relatively small cusp at the posterior platform termination. A small "free blade" is present at the anterior. By 180.5 m, a brim is present at the posterior of some specimens. By 181.3 m the platform has extended anteriorly and the "free-blade" is lost; at the same time the posterior denticles are more closely spaced. That transition can be considered the first distinct mesogondolellid morphocline.

Beginning at 182.5 m, juvenile specimens have more oval denticles that are more compressed, whereas the adult specimens have denticles that are discreet and mostly round. By 183.2 m the denticles begin to compress in adults, and by 183.55 m they are completely compressed in adults. Recoveries are good enough to show that compressed adult denticles occur first in dextral elements, then slightly later in sinistral elements. By 186.14 m, the denticles are equally compressed in both dextral and sinistral elements. This heterochronocline describes the second distinct mesogondolellid morphocline.

Specimens at 183.2 m are the first elements where there is a clear adcarinal trough in adult specimens, and there is a well-developed buttress that encloses the cusp. This combination of characters along with the initial denticle compression in adult specimens makes the forms at 183.2 m distinctive, and these could form the basis of a correlation horizon for offshore settings. It occurs just below the first unequivocal occurrence of *Neognathodus atokaensis* at Naqing, recovered from 183.55 m.

Other Faunal Components at the Naqing Section

Neognathodus is relatively rare in the Naqing section, but its occurrences are relevant to correlation and the overall biostratigraphy. The first *Neognathodus* recovered is *N. symmetricus*, which is abundant at 160.20 m. The next specimens are from 169.05 m and 171.40 m, and resemble coarsely ornamented, triangular morphologies that are characteristic of the Trace Creek Member of the Atoka Formation in Arkansas (Grayson collections, unpubl.). Overlapping that range at 171.2 m are interesting specimens, including both a juvenile and a large adult, that appear to be a direct precursor to *N. kanumai*. All these specimens are assigned on the range chart to *N.* "*praekanumai*," but so far we do not have enough specimens to document a *N.* "*praekanumai*" chronomorphocline to *N. kanumai*.

Neognathodus kanumai sensu stricto first occurs at 174.3 m, and ranges through 182.5 m. Within that range, a similar form, *Neognathodus* aff. *N. kanumai*, is recovered from 176.9 m-177.7 m. This form occurs in midcontinent North America (e.g., Sutherland and Grayson, 1992, plate 2, figs. 16, 17) and possibly Spain (J. Sanz-Lopez and S. Blanco-Ferrera, per. comm.), and was previously referred mistakenly to *N. nataliae*. *Neognathodus* aff. *N. uralicus*, known from the lower Moscovian of the Ural Mountains, was recovered at 177.8m. *Neognathodus* becomes very rare above 177.8m at Naqing, although we note again that at 183.55m, a large specimen of *N. atokaensis* has been recovered just above the first occurrence of the fusulinid *Eofusulina* (Groves, 2010).

Idiognathoides is abundant in the study interval of the Naqing section, where it dominates the conodont fauna as in most of the Bashkirian and lower Moscovian faunas of Europe and Asia. *Idiognathoides sinuatus* first occurs below the interval of study, and ranges up through most of it. *Idiognathoides sinuatus* is the sinistral form-species associated with both *Id. corrugatus* and *Id. ouachitensis*. The latter species is characteristic of the upper Bashkirian of Eurasia, and is also common in North America. *Idiognathoides tuberculatus*, the last member of the *Id. sinuatus* (*corrugatus*) – *Id. ouachitensis* – *Id. tuberculatus* lineage, has not yet been found at Naqing. *Idiognathoides corrugatus* is first recovered at 160.0 m, and *Id. ouachitensis* is first recovered at 171.8 m.

All of the species that make up the *Idiognathoides sulcatus* group in other areas of Europe and Asia are present at Naqing. *Idiognathoides macer*, known from the lower Bashkirian of the Cantabrian Mountains and Western Pyrenees, Spain (Wirth, 1967; Nemyrovska et al., 2011), and the Fergana Valley, Central Asia (Nemyrovska, unpubl.), enters the section at Naqing at 160.2 m. *Idiognathoides sulcatus*, with equal noded parapets, first occurs at 161.0 m. *Idiognathoides postsulcatus* appears next at 165.0 m. Higher in the section *Id. sulcatus parvus*, with one reduced parapet, first appears at 167.5 m.

Several other *Idiognathoides* morphologies are present in the Naqing section. Further study will be required to determine which of these should be referred to as variants, and which should be formally recognized as new species.

Declinognathodus is also quite abundant in the study interval of the Naqing section, represented by *De. lateralis*, *De. inaequalis*, *De. noduliferus*, and *De. marginodosus*. The *De. inaequalis – De. noduliferus – De. marginodosus – De. donetzianus* lineage, already described from the other areas (e.g., Donets Basin and Ural Mountains; Nemyrovska, 1999; Pazukhin et al., 2006; Nemyrovska et al., 2010) is also recognized at Naqing, with the exception of *De. donetzianus*. *Declinognathodus lateralis*, *De. inaequalis*, and *De. noduliferous* first occur below the study interval and range well into it, with *De. marginodosus* first appearing at 164.3 m and ranging much higher.

Forms that we still refer to *Declinognathodus lateralis* at 173.4 m on the range chart resemble those from the early Moscovian of the Ural Mountains (Nemirovskaya and Alekseev, 1994; Kulagina et al., 2009). Also within the study interval, there are *Declinognathodus* morphotypes with transverse ridges developed on the parapets instead of nodes. In some forms these transverse ridges fill the sulcus between the parapets. All of these morphotypes are younger than *De. noduliferous* and *De. marginodosus*, and with further work will most likely become recognized as new species. This peculiar *Declinognathodus* fauna in the Naqing section requires additional careful study.

Neolochriea is relatively abundant and diverse through much of the boundary interval. All of the specimens recovered from the Naqing section are assigned to species described from the lower Bashkirian deposits of Japan (Mizuno, 1997; Mizuno and Ueno, 1997). *Neolochriea hisaharu* has also been recovered from lower Bashkirian deposits of the Ural Mountains (Pazukhin et al., unpubl.). One widespread species of this genus, *Neolochriea glaber*, is common in the lower Bashkirian rocks of Europe and Asia (Cantabrian Mountains, Spain [Nemyrovska et al., 2011; Sanz-Lopez and Blanco-Ferrera, 2012]; Pyrenees, France [Perret, 1993]; Graz Mountains, Austria [Ebner, 1977]; Ural Mountains, Russia [Pazukhin et al., unpubl.]; South Fergana, Kyrghyzstan [Nemyrovska, unpubl.]). Its range in the Naqing section—as with the other *Neolochriea* species—is significantly greater than it is in the other regions. At Naqing it ranges up section into the *Diplognathodus ellesmerensis* zone. The phylogenetic relationships and possible morphocline transitions in *Neolochriea* will require considerable further study to understand.

Idioprioniodus is present in almost every sample, while in contrast *Hindeodus* occurs only rarely (at 171.5 m, 174.3 m, 175.3 m, and 180.7 m)—and then as only one or two specimens among a much larger fauna. No attempt was made to recognize transitional morphologies within either genus. Following the distributional model of Heckel (e.g., Heckel and Baesemann, 1975; Heckel, 1999), the near ubiquity of *Idioprioniodus* and rarity of *Hindeodus* support the petrographic interpretation that the Naqing section represents open marine waters through the entire Bashkirian-Moscovian boundary interval.

COMPARISON WITH RELEVANT STANDARD REGIONAL ZONATIONS

Type Moscovian, Moscow Basin

The Moscow Basin provides the working stage terminology and the name of the corresponding SCCS task group. However, the base of the type Moscovian is unconformable, with marine strata sitting on basal alluvial deposits (Alekseev, 2009). The conodont zonation generally follows that of the Donets Basin (see below), with the *Declinognathodus donetzianus* Zone representing the base of the section, succeeded by the *Idiognathoides ouachitensis* and the "*Streptognathodus*" *transitivus* zones. Kabanov and Alekseev (2011; citing also Barskov et al., 1980) recently suggested that moving the base of the Moscovian stage up to the overlying *Neognathodus bothrops* Zone would facilitate a better potential level for global correlation, if an acceptable defining lineage can be found. However, *Diplognathodus ellesmerensis* occurs at the base of the Moscovian as it is currently defined (e.g., Makhlina et al., 2001), and would provide a much less disruptive GSSP horizon.

Donets Basin

The Donets Basin conodont zonation goes successively from the *Declinognathodus marginodosus* Zone (youngest Bashkirian) to the *De. donetzianus* Zone (which provincially defines the basal Moscovian), followed by the "*Streptognathodus*" *transitivus-Neognathodus atokaensis* Zone. Although the Donets and Moscow basin zonations are similar, they are not identical (Nemyrovska, 2011). *Declinognathodus donetzianus* is a distinctive, easily identifiable form suggested as a potential GSSP marker, but it is a rare faunal component with a distribution primarily limited to the Donets and Moscow basins. The illustrated specimen from a Panthalassan suspect terrane in northwest North America (Savage and Barkeley, 1985, figs. 10, 1-4) look very similar to *De. donetzianus*. A specimen from eastern Kentucky (Work et al., 2012, fig. 8, 1) looks like it could be an intermediate form between *De. marginodosus* and *De. donetzianus*. In describing the *De. donetzianus* Zone, Nemyrovska (2011, p. 59) states "The entry of *Diplognathodus ellesmerensis* is characteristic for this zone." If the base of the Moscovian is instead placed at the level of the evolutionary first occurrence of *D. ellesmerensis*, the result will entirely match the *De. donetzianus* Zone (which could still be used regionally in eastern Europe), plus can be more widely correlated using the marker taxon, since *D. ellesmerensis* is found worldwide.

North America

The stage nomenclature used in North America is based on Andean Realm fusulinid zones (Moore and Thompson, 1949; Ross, 1967), with little direct connection to Paleotethyan chronostratigraphy in much of that section (Groves et al., 2007). A regional conodont zonation has been developed for Midcontinent North America (see Barrick et al., 2004, 2013). Both *Diplognathodus ellesmerensis* and "*Streptognathodus*" *expansus* are commonly reported in North America, but have not been included in the Midcontinent zonation. A GSSP for the base of the Moscovian Stage that corresponds to the level of the *D. ellesmerensis* FAD would fall within the Atokan regional stage. North American geologists should have little problem adapting to a worldwide standard, considering the many problems associated with the Atokan Stage (e.g., Sutherland and Manger, 1983, 1984; Lane and West, 1984; Shaver, 1984) and its boundary definitions (e.g., Douglas and Nestell, 1984; Lambert and Heckel, 1990; Lambert, 1992).

CONCLUSIONS

The succession of transitional conodont morphoclines at the Naqing section demonstrates that deposition was continuous through the Bashkirian-Moscovian boundary interval. The section has complete, bed-by-bed exposure of strata that represent open marine, offshore depositional environments. Conodont diversity is high, and every bed in the boundary interval has been productive. The multiple transitional morphoclines there provide many possible candidates to characterize a level for the GSSP of the Moscovian Stage. The one that best matches the current concept for the base of the Moscovian Stage in its type region, and with the greatest potential for intercontinental correlation, is the phylogenetic first occurrence of *Diplognathodus ellesmerensis*.

Diplognathodus ellesmerensis is easily recognized by conodont workers and has been recovered from China, Europe, boreal Canada (from where it was named; Bender, 1980), North America, and South America. That makes it one of the most widely recovered conodont species in the Upper Carboniferous. It has consistently been associated with the lower Moscovian and its equivalents. Notably, it is found in the basal marine units of the type Moscovian. If a morphologic chronocline can be demonstrated from the ancestral species to *D. ellesmerensis* at Naqing, it would provide an almost ideal level for the GSSP.

The major drawback of a GSSP based on *D. ellesmerensis* lies not with the species, but with the general occurrence typical for the genus *Diplognathodus*. *Diplognathodus* is commonly recovered as a minor faunal constituent, and specimens are usually small. That means that first recoveries away from its phylogenetic FAD will not necessarily be precise first occurrences. However, the diverse, continuous conodont faunas at Naqing would enhance correlations with numerous successive supplementary species occurrences that could help pinpoint where the boundary correlation should be placed. The widely cited characteristic entry of *D. ellesmerensis* at the base of the Moscovian in the Moscow and Donets basins demonstrates that it is already used in that manner.

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PENNSYLVANIAN-PERMIAN HERMOSA GROUP OF THE PARADOX BASIN, USA

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The Hermosa Group is explicitly all of the strata between the regional Leonardian (Kungurian) angular unconformity, at the base of the Organ Rock or White Rim formations (depending on location), and the regional Pennsylvanian Morrowan (Bashkirian) angular unconformity at the top of older rocks (Mississippian, Devonian, Cambrian or Precambrian, depending on location). The most important characters of the Hermosa Group are the angular unconformity surfaces at the top and base, and the included cyclic carbonates, evaporites, siliciclastics and mudstones. The Hermosa Group includes strata of the Cedar Mesa, Halgaito, Elephant Canyon, Honaker Trail, Paradox and Lower Hermosa formations, and all of those strata previously included in the Rico, Lower Cutler, Pinkerton Trail and Molas formations. Of the 83 fourth-order cycles, 72 have evaporites, 41 have halite intervals, and 37 have potash intervals. There are 12 cycles in the Lower Hermosa Fm, 36 in the Paradox Fm, 14 in the Honaker Trail Fm, and 21 in the Elephant Canyon Fm (which intertongues with the Cedar Mesa and Halgaito). Continuous uninterrupted deposition of cycles in the Paradox Basin starts in the Morrowan Lower Hermosa Fm and continues through the Atokan and Desmoinesian (Moscovian) Paradox Fm and Missourian (Kazimovian) Honaker Trail Fm, and possibly through the Virgilian and Wolfcampian (Gzhelian into early Cisuralian) Elephant Canyon Fm. All of the cycles within the Hermosa Group have a basal “shale” (mudstone) transgressive systems tract interval (TST), which in most areas is a black laminated mudstone (BLM), but on the basin margins can vary from gray to green shales or to red beds (oxic), or in the basin center to a highly organic-rich silty dolostone (anoxic) that resembles soft coal. The TST strata are the most widespread strata in the basin and were deposited when there was “maximum” transgressive flooding. All of the cycles contain a highstand systems tract (HST) marine carbonate portion and/or a fluvial siliciclastic portion, and through time, the carbonate distribution among the cycles varied from limited to widespread in the basin, with the widest distribution during the Desmoinesian and Missourian. The top of each HST interval is marked by a disconformity or hiatus (sequence boundary). Above the TST strata and below the HST strata is a distinct transgressive highstand systems tract (THST) interval that is sometimes unintentionally included within the TST BLM strata because of their strong similarity of lithofacies. However, the THST strata are usually thicker and may include interbedded lithologies that can vary from fluvial siliciclastic wedges to thin normal marine (normal salinity) carbonates. The TST and THST strata within each individual cycle are considered parts of a single chronostratigraphic unit, of which the base of the TST forms the ultimate time boundary with the underlying cycle. Most of the cycles contain evaporites (evaporitic lowstand systems tract - ELST) with halite beds present within the Lower Hermosa, Paradox and Honaker Trail formations. Halite deposition (often with an associated potash facies) was greatest during Late Morrowan, Atokan and Desmoinesian, with a total cumulative thickness of up to 8000 ft (2400 m) in the Deep Fold and Fault Belt - DFFB (including all of the interbedded strata within the gross salt interval). Anhydrite beds within the ELST first appear in Morrowan Lower Hermosa cycles within the DFFB, and their final occurrence is in the much younger Wolfcampian Elephant Canyon cycles in the northwestern portion of the basin. Siliciclastics are present in all of the cycles within the Paradox Basin (mainly in the transgressive lowstand systems tract portion of each cycle - TLST); however, for some cycles the thick TLST siliciclastics were confined (“ponded”) within the DFFB which had unfilled accommodation space from the more rapid subsidence in front of the rising Uncompahgre Uplift. Massive wedges of siliciclastics first appear in the DFFB in the latter part of the Desmoinesian and caused the first significant movement of underlying salt beds in the DFFB into salt rolls, anticlines and diapirs, but the first significant deposition of siliciclastics outside of the DFFB was not until the end of the Desmoinesian. During the Missourian, Virgilian and Wolfcampian, siliciclastics were the dominant sediment type during deposition within cycles of the later Hermosa Group. Commercial hydrocarbons occur in HST bioherms, reefs and grainstones, in TST and THST mudstones, and in TLST siliciclastics. Commercial brines and potash occur in the ELST evaporites.

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A NEW PERMINERALIZED *ALETHOPTERIS* FROM THE KALO FORMATION AND A SIMPLE METHOD FOR DISTINGUISHING PERMINERALIZED *ALETHOPTERIS* SPECIES

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Abstract—Coal balls from the Kalo Formation of Iowa contain two new species of permineralized *Alethopteris* pinnules, which can be differentiated from each other, and from other permineralized *Alethopteris* species using shape analysis. The two new species never occur on the same rachis. One of the Kalo alethopterids appears to be *A. ambigua* (Lesquereux) White. The other, *A.* sp. 1, belongs to the *Alethopteris ambigua – A. friedeli – A. grandini – A. lesquereuxi – A. leonensis* morphological continuum, but cannot be assigned to a particular adpressed species. Shape analysis is a useful tool to identify permineralized *Alethopteris* species. In broadly attached medullosan pinnules, lamina thickness/pinnule width is a proxy for leaf mass per area (LMA), enabling investigation of the leaf longevity and metabolic cost of medullosan pinnules preserved as permineralizations. Alethopterids tend to have thick lamina for their width, suggesting that most had metabolically expensive, long-lived foliage relative to other mire seed ferns. Of mire alethopterids, members of the *Alethopteris ambigua* morphological continuum have the thickest pinnules for their width. Neuropterids tend to have thin lamina for their width, suggesting that most had metabolically inexpensive, short-lived foliage relative to other mire medullosans.

INTRODUCTION

Four alethopterids with narrow, pecopteroid pinnules (*A. ambigua* (Lesquereux) White, *A. friedeli*, P. Bertrand, *A. leonensis*, and *A. lesquereuxi*) form a morphological continuum, which also includes the highly variable *A. grandini* (Zodrow and Cleal, 1998; Wagner and Ávarez-Vázquez, 2008, Šimunek, 1996). Surprisingly, two of the five species in this continuum (*A. ambigua* (Lesquereux) White and *A. lesquereuxi*) also occur in the coal-ball record, suggesting that these alethopterids flourished in peat-accumulating mires and on siliciclastic soils (Baxter and Willhite, 1969; Reihman and Schabilion, 1976). Here we report a sixth *Alethopteris* species belonging to the *A. ambigua* morphological continuum, *A.* sp. 1, from the Kalo Formation (mid Moscovian, Pennsylvanian) of Iowa.

MATERIALS AND METHODS

Alethopteris sp. 1 occurs commonly in coal balls from the Williamson No. 3 Mine, the Urbandale Mine and the Shuler Mine. The specimens illustrated in this contribution come from the Williamson No. 3 Mine in Lucas County, Iowa. The Shuler and Urbandale Mines exploited the Cliffland coal, which is the upper coal in the Kalo Formation (Fig. 1; Raymond et al., 2010). The Williamson No. 3 Mine exploited one of the two Kalo Formation Coals, the Blackoak coal or the Cliffland coal; however the exact Kalo Formation coal mined in this location remains unknown (Raymond et al., 2010).

Six measurements of pinnules in orthogonal cross-section serve to differentiate permineralized *Alethopteris* species (Figs. 2.1, 2.2): 1, pinnule width at the margin of the lamina, or edge-to-edge width (EEW); 2, width of the pinnule at its widest point (MaxW); 3, the depth of the midrib below the upper surface of the lamina, at the crest of the vault for vaulted pinnules, or sunkenness (S); 4, midrib width (MidW); 5, the depth of the midrib plus lamina, or midline depth (MidD); 6, the width of the midrib at the midrib-lamina junction. When possible, we chose EEW and MaxW to be parallel lines; however, because the cross-sectional shape of *Alethoperis* may not be symmetric, this was not always possible (Fig. 2.1). We identify orthogonal sections using the following criteria: 1, the ratio of the lamina width on both sides of the midrib is close to 1:1; and 2, the lamina has either one or no lateral veins perpendicular or nearly perpendicular to the midrib (Figs. 2.1, 2.2).

Decay may alter the shape of pinnules by increasing sunkenness and shrinking the width of the midrib-lamina junction, causing the midrib to appear more circular in cross-section (Fig. 2.3). Thus, we exclude pinnules with shriveled parenchyma cells from the shape analysis.

Since we seek to differentiate pinnules based on shape rather than shape and size, we use maximum pinnule width to standardize our measures of pinnule shape. The ratio of edge-to-edge width to maximum width (EEW/MaxW) provides a measure of enrolling (enrolling ratio). Sunkenness and midrib width, each divided by pinnule width, respectively indicate relative sunkenness (S/MaxW) and relative midrib width (MidW/MaxW). Midline depth, divided by pinnule width, indicates relative midline depth (MidD/MaxW) (Figs. 2.1, 2.2).

The population of *Alethopteris* sp. 1 pinnules investigated for this contribution consists of 32 pinnules in orthogonal cross-section and 7 pinnules in paradermal section (Figs. 2.3, 2.4). We compare the shape of *A.* sp. 1 to the shape of *A. ambigua* (Lesquereux) White, also from the Williamson No. 3 Mine of the Kalo Formation, using a population of 22 pinnules in orthogonal cross-section (Fig. 2.1); we compare the shape of *A.* sp. 1 to *A. lesquereuxi* from the Lovilia deposit of Iowa (equivalent in age to the Houchin Creek (No. 4) Coal of the Illinois Basin: Brotzman, 1971) using a population of 31 pinnules in orthogonal cross-section (Fig. 2.5).

In modern land-plants, leaf mass per area (LMA), obtained by dividing leaf mass by leaf area, serves as a proxy measurement for the nutrient content and longevity of leaves (Wright et al., 2004). Leaves with low LMA tend to have high amounts of nitrogen and phosphorous per unit area, high photosynthetic capacity, low dark respiration rates, and short life spans; such leaves are metabolically inexpensive and vulnerable to herbivory (Wright and Cannon, 2001; Wright et al., 2004). Leaves with high LMA tend to have low amounts of nitrogen and phosphorous per unit area, low photosynthetic capacity, high dark respiration rates, and long life spans; such leaves are metabolically expensive and tend to have effective defenses against herbivory (Wright and Cannon, 2001; Wright et al., 2004). Royer et al. (2007) measured the surface area of fossil leaves and used petiole width to estimate ancient leaf mass, allowing them to estimate LMA for fossil angiosperms.

In broadly attached medullosan pinnules, midrib width cannot be used to estimate pinnule mass because the ultimate rachis and subsidiary

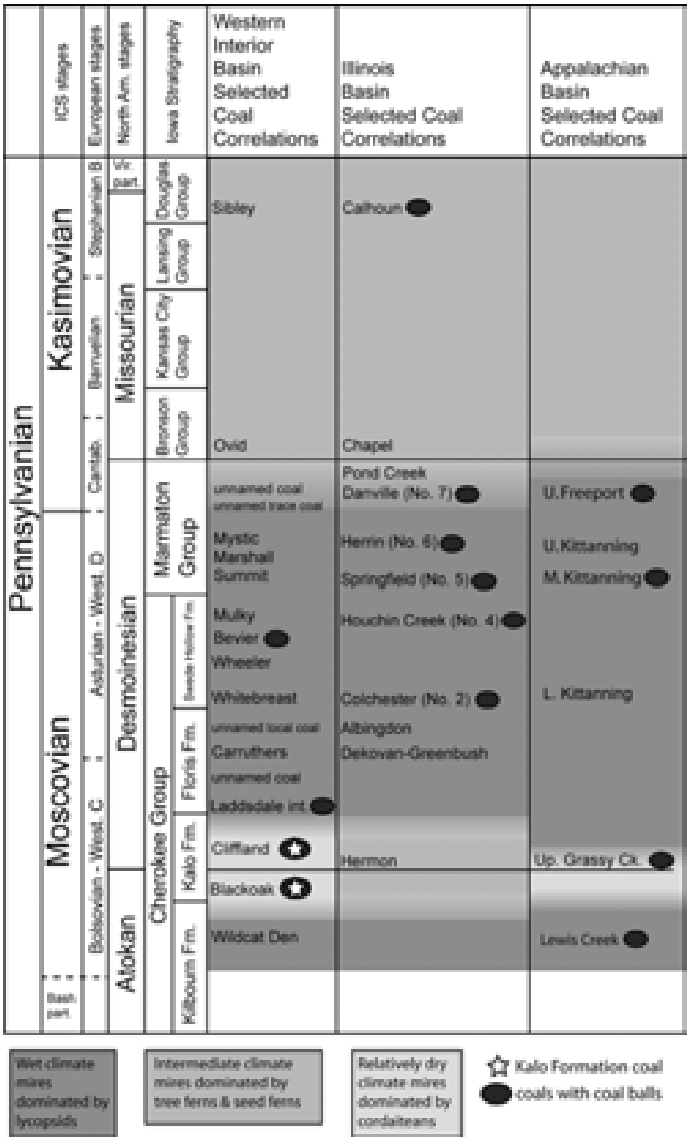

FIGURE 1. Stratigraphy of the Kalo Formation Coals after Raymond et al. (2010).

veins as well as the midrib support the photosynthetic lamina. Thus, we use lamina thickness/pinnule width (LT/MaxW) as a proxy for LMA in broadly attached, permineralized pinnules. In modern leaves, leaf width correlates significantly with leaf area (Wilson et al., 1999). In coal balls, measures of both pinnule width and lamina thickness can be obtained from orthogonal cross sections of pinnules. In modern land plants, both leaf thickness and leaf density correlate significantly with leaf mass, or its inverse, specific leaf area (SLA: Witkowski and Lamont, 1991; Wilson et al., 1999; Wright and Cannon, 2001). However, leaf density and thickness are not significantly correlated to one another and often respond independently along resource gradients (Witkowski and Lamont, 1991; Wilson et al., 1999; Wright and Cannon, 2001; Prior et al., 2003). Using leaf thickness as a proxy for leaf mass per area (LMA) ignores the economic cost of dense tissues (fibers, sclerids, vascular tissue) and related overall size of fronds, which could vary considerably in medullosans (Laveine, 1986; Cleal et al., 1998).

We use a bivariate plot of average lamina thickness versus pinnule width to investigate the longevity and economic cost of permineralized medullosan pinnules. We compiled data on the average lamina thickness and pinnule width of *Alethopteris* sp. 1, *A. ambigua* (Lesquereux) White, *A. lesquereuxi* from the Lovilia, Iowa deposit, and *A. pennsylvanica* from the Berryville locality in Illinois (Calhoun Coal) for this study; data on the average lamina thickness and pinnule width of other *Alethopteris* populations and neuropterid populations come from the published literature.

RESULTS

The new *Alethopteris* species, *A.* sp. 1, has narrow, enrolled, pecopteroid pinnules with blunt apices, averaging 2.7 mm in width (range = 1.9-3.4 mm, N = 32: Figs. 2.3, 2.4). The pinnules range from 5.5 mm to 8.5 mm in length (average = 7.8 mm, N = 11: Fig. 2.4) and have insertion angles close to 90^o. The pinnules are relatively flat with a thick lamina (av. 390 μm) and a broad rectangular midrib, averaging 1.1 mm in width and 0.9 mm in depth (Fig. 2.3). The lateral veins are straight and divide once, or remain simple; there are approximately 40-45 lateral vein endings per cm. (N = 15: Fig. 2.4). When compared to adpressed species, *Alethopteris* sp. 1 is most similar in size, lateral venation, and insertion angle to *A. ambigua* (Lesquereux) White (White, 1899). However, when adpressed, well-preserved *A.* sp. 1 pinnules would not have had midrib flanges, which Cridland (1968) described for *A. ambigua* (Lesquereux) White. The circular shape of the *Alethopteris ambigua* (Lesquereux) White midrib in cross section causes midrib flanges to form during compression. Because the widest part of the midrib lies below the midrib-lamina junction in this species (Figs 2.1; 2.2), compression during fossilization would have resulted in adpressed specimens with midrib flanges. The difference between the diameter of the midrib and the width of the midrib-lamina junction divided by two (Fig. 2.2) would determine the width of the flange on each side of the midrib. In *A. lesquereuxi* (Fig. 2.5) and *A.* sp. 1 (Fig. 2.3), the widest part of the midrib is usually the midrib-lamina junction. Other members of the *Alethopteris ambigua* continuum, *A. friedeli*, *A. grandini*, *A. lesquereuxi*, and *A. leonensis* are wider (*A. lesquereuxi*: 4-5 mm, *A. grandini*: 3.5-6 mm: Wagner, 1968) or have lateral veins that divide once or twice, and that do not remain simple (*A. friedeli*, *A. lesquereuxi*, *A. leonensis*: Bertrand, 1932; Wagner, 1968; Wagner and Ávarez-Vázquez, 2010).

Alethopteris sp. 1 appears to be confined to the Kalo Formation of Iowa (latest Atokan-earliest Desmoinesian, mid Moscovian, Pennsylvanian). It co-occurs with permineralized *Alethopteris ambigua* (Lesquereux) White pinnules (Fig. 2.1). However, permineralized specimens of the two species can be distinguished based on the shape of the midrib in cross-section, which is broadly rectangular in *A.* sp. 1 (Fig. 2.3) and circular in *A. ambigua* (Lesquereux) White (Fig. 2.1), and by the presence of a deeply sunken midrib in *A. ambigua* (Lesquereux) White (Fig. 2.1, Table 1). In addition, these two Kalo Formation alethopterids never occur together on the same rachis. Both Kalo species can be distinguished from *A. lesquereuxi* based on the shape of the midrib, which is semi-circular in *A. lesquereuxi* (Fig. 2.5), and on the presence of prominent, parenchymatous vascular bundle sheath extensions in *A. lesquereuxi* (Fig. 2.5, arrow). The plot of relative midrib width (MidW/MaxW) versus relative sunkeness (S/MaxW) illustrates the different shapes of these three permineralized species (Fig. 2.6).

Taphonomy may alter pinnule shape. As decomposition proceeds, differential loss of parenchyma causes *Alethopteris* sp. 1 pinnules to shrink at the midrib lamina junction (Fig. 2.3, left pointing arrow); differential loss of parenchyma above the midrib during decomposition can also increase the relative shrunkeness of this species, causing the lamina to appear vaulted (Fig. 2.3 downward pointing arrow). For this reason, we eliminated pinnules with shriveled parenchyma cells from our shape analysis.

DISCUSSION

Scheihing and Pfefferkorn (1980) introduced the concept of a morphological continuum to describe species of adpressed seed-fern pinnules that have very similar morphologies and may be geographical or

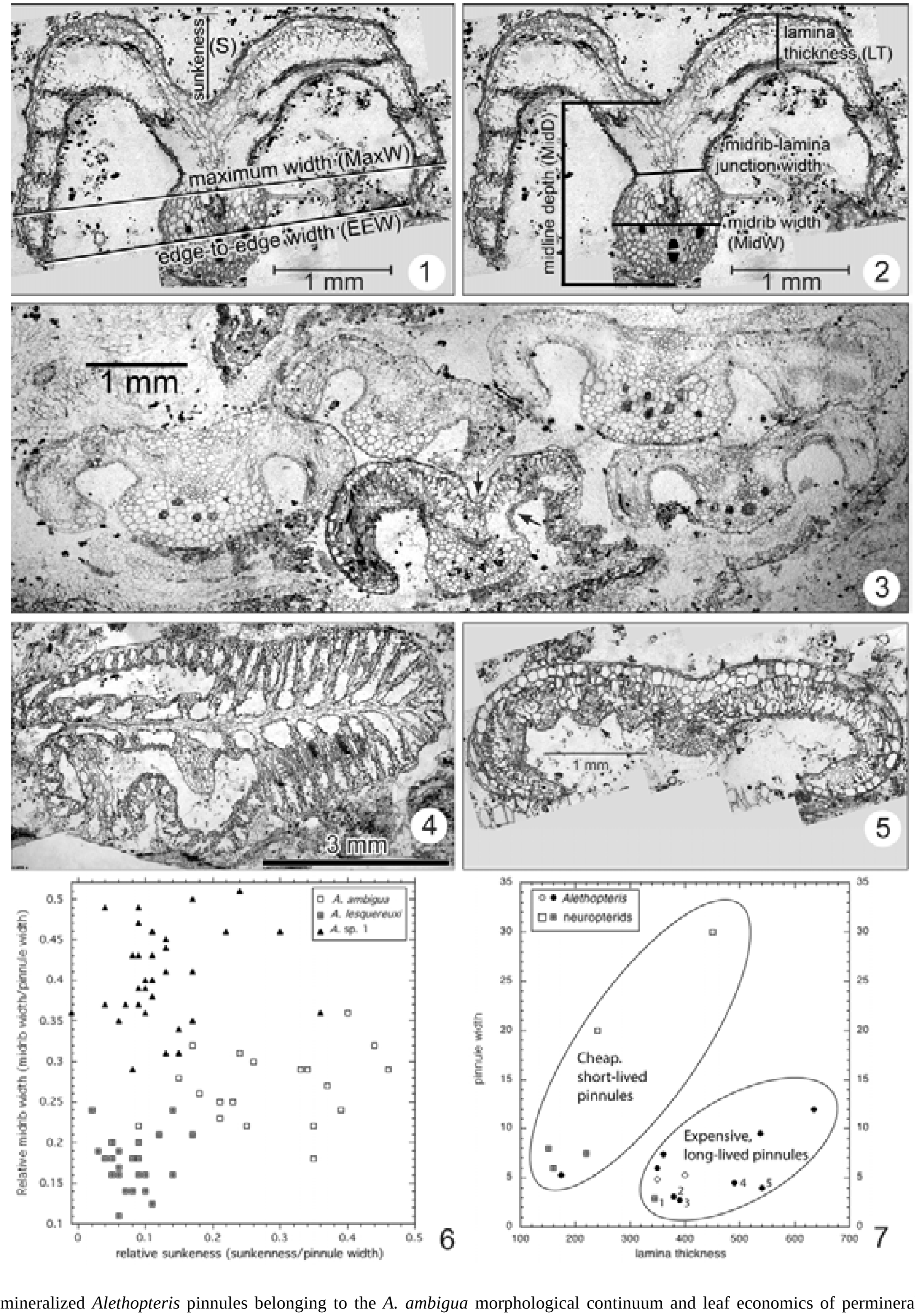

FIGURE 2. Permineralized *Alethopteris* pinnules belonging to the *A. ambigua* morphological continuum and leaf economics of permineralized medullosan pinnules. **2.1-2.2**, *A. ambigua* (Lesquereux) White pinnule in cross-section showing shape measurements. Williamson No. 3 Mine, Kalo Formation (mid-Moscovian, Pennsylvanian), HU64711. **2.3**, *A.* sp. 1 pinnules in cross-section, HU64865. In the decayed pinnule, the downward pointing arrow indicates increased sunkenness; the left pointing arrow indicates a narrower midrib-lamina junction. **2.4**, *A.* sp. 1 ultimate pinnule in paradermal section, Williamson No. 3, Kalo Formation (mid-Moscovian, Pennsylvanian) HU64887. **2.5**, *A. lesquereuxi* pinnule in cross-section, Lovilia, Iowa (equivalent in age to the Houchin Creek (No. 4) Coal, late Moscovian, Pennsylvanian). Arrow indicates a parenchymatous vascular bundle sheath extension. **2.6**, Relative midrib width versus relative sunkeness for *A. ambigua* (Lesquereux) White, *A.* sp. 1 and *A. lesquereuxi*. **2.7**, Lamina thickness versus pinnule width for permineralized medullosan pinnules. **Point 1**, *Laveineopteris rarinervis*, Illinois (Oestry-Stidd, 1979); **Point 2**, *A. ambigua* (Lesquereuxi) White, Kalo Fm, Iowa; **Point 3**, *A.* sp. 1, Kalo Fm., Iowa; **Point 4**, *A. lesquereuxi*, Lovilia Iowa, Reihman and Shabilion, 1976; **Point 5**, *A. lesquereuxi*, Kansas, Baxter and Willhite, 1969.

TABLE 1. Comparison of the new permineralized Kalo *Alethopteris* to permineralized *A. ambigua* (Lesquereux) White and *A. lesquereuxi*.

Species: Trait:	*A.* sp. 1	*A. ambigua* (Lesquereux) White	*A. lesquereuxi*
Pinnule Length (range)	5.5 – 8.5 mm	9 – 12 mm	8 – 10 mm
Av. Pinnule Width	2.7 mm	3.1 mm	4.5 mm
Midrib shape (cross-section)	Broad rectangle	Circular	Semi-circular
Av. Midrib width	1100 µm	840 µm	680 µm
Av. Midline depth	900 µm	1350 µm	730 µm
Lamina thickness	390 µm	380 µm	490 µm (IA) 540 µm (KS)
Enrolling ratio	0.65	0.95	0.72
Relative sunkeness	0.27	0.11	0.08

chronological variants of a single species (see also Wagner, 1968; Zodrow and Cleal, 1998). Most taxa placed into morphological continua have been described as distinct species. In the case of the *Alethopteris densinervosa* continuum, the documentation of transitional forms suggests that the original species descriptions were too narrow (Scheihing and Pfefferkorn, 1980; Zodrow and Cleal, 1998; Wagner and Ávarez-Vázquez, 2008, 2010). In the case of the *A. ambigua* continuum, there is no consensus as to which members of the continuum are distinct species and which are geographical or chronological variants (Zodrow and Cleal, 1998; Wagner and Ávarez-Vázquez, 2008, 2010) .

The new *Alethopteris* species from the Kalo Formation (*A.* sp. 1) clearly belongs to the *A. ambigua* morphological continuum; it is very similar to *A. ambigua* (Lesquereux) White. However, in adpression, *A.* sp. 1 would not have the cuticular midrib flanges described for *A. ambigua* by Cridland (1968), because its midrib does not widen below the midrib-lamina junction (Fig. 2.3). Accordingly, we reserve the name *A. ambigua* (Lesquereux) White for permineralized pinnules having a midrib that is circular in cross section and widens below the midrib-lamina junction (Fig. 2.2).

Permineralized *A.* sp. 1 appears most similar to *A. ambigua* var. *gibsonii*, described by Wagner (1968) from Point Aconi, Nova Scotia. Pinnules of this taxon have blunt apices, a larger proportion of simple veins than most *A. ambigua* (Lesquereux) White populations, and prominent compression rims bordering the pinnule lamina, which could result from the adpression of enrolled pinnules having thick lamina (Wagner, 1968). However, some of the original specimens of adpressed *A. ambigua* (Lesquereux) White discussed in White (1899) also have compression rims. Because compression rims conceivably could result from the adpression of stiff, highly vaulted pinnules that are not enrolled, i.e., permineralized *A. ambigua* (Lesquereux) White (Fig. 2.1), we hesitate to sort populations of adpressed *A. ambigua* (Lesquereux) White based on the presence or absence of compression rims.

Species belonging to the *Alethopteris ambigua* morphological continuum have a complex taxonomic history, especially *A. ambigua*, *A. friedeli*, *A. grandini*, and *A. lesquereuxi* (White, 1899; Bertrand, 1932; Wagner, 1968; Šimunek, 1996; Zodrow and Cleal, 1998; Wagner and Ávarez-Vázquez, 2008, 2010). The best resolution may be to consider *A.* sp. 1 as a member of the *A. ambigua* morphological continuum that has probably been identified as *A. ambigua* (Lesquereux) White when found in adpression, but which is certainly a distinct species based on features seen in permineralized preservation.

Zodrow and Cleal (1998) viewed *Alethopteris lesquereux* and *A. ambigua* (Lesquereux) White as the same species. These authors placed permineralized *A. lesquereuxi* in synonomy with *A. ambigua*, although they did not synonomize adpressed *A. lesquereuxi* with adpressed *A. ambigua*. Clear differences between *A. lesquereuxi* (Fig. 2.5) and the two Kalo Formation species, *A. ambigua* (Lesquereux) White (Fig. 2.1) and *A.* sp. 1 (Figs. 2.3, 2.4), in permineralized preservation indicate that all three are distinct species.

Although adpressed *Alethopteris ambigua* persists in floodplain deposits throughout the Laddsdale coal interval (Cridland, 1968, Fig. 1), and perhaps throughout the Moscovian (Wagner, 1968), this species has not been found in peat-accumulating mires (i.e., coal balls) above the mid-Moscovian Kalo Formation. Permineralized *A. ambigua* and *A.* sp. 1 appear to be confined to the diverse cordaitean community of the Kalo Formation. The earliest known permineralized *A. lesquereuxi* pinnules occur in the Laddsdale coal interval (What Cheer deposit), which overlies the Kalo Formation (Baxter and Willhite, 1969: Fig. 1).

All three pinnules, *A.* sp. 1, *A. ambigua* (Lesquereux) White, and *A. lesquereuxi*, have extremely thick photosynthetic lamina for their size compared to other permineralized medullosan pinnules, consistent with the interpretation that these species were adapted for growth in sunny habitats (Arens, 1997). A bivarate plot of pinnule width against lamina thickness indicates two populations of pinnules (Fig. 2.7, Table 2). Most alethopterids and *Laveineopteris rarinervis* from the Illinois Basin (Oestry-Stidd, 1979) have thick lamina relative to pinnule width, suggesting that these were metabolically expensive, long-lived leaves relative to other mire medullosans. Within this group, *L. rarinervis* from the Illinois Basin and members of the *Alethopteris ambigua* morphological continuum (*A. ambigua*, *A. lesquereuxi*, and *A.* sp. 1) have the thickest lamina for their pinnule width. Most neuropterids, and *Alethopteris* sp. from the Lewis Creek deposit in Kentucky have thin lamina for their pinnule width, suggesting that these were metabolically inexpensive, short-lived pinnules relative to other mire medullosans.

CONCLUSIONS

Two permineralized *Alethopteris* pinnules, which could be assigned to adpressed *A. ambigua* (Lesquereux) White, occur in the coals of the Kalo Formation of Iowa. One of these pinnules has a midrib with a round cross section, which would produce midrib flanges in adpressed specimens; we assign this permineralized *Alethoperis* to *A. ambigua* (Lesquereux) White based on Cridland's (1968) discovery of cuticular flanges in that species. We consider the second species, *A.* sp. 1, to be a member of the *A. ambigua* morphological continuum, which has probably been identified as *A. ambigua* (Lesquereux) White when encountered in adpression. Shape analysis enables us to distinguish all three permineralized members of the *A. ambigua* morphological continuum. Most permineralized alethopterids have relatively thick photosynthetic lamina for their pinnule width, suggesting that they produced metabolically expensive, long-lived foliage relative to other mire medullosans. Among alethopterids, permineralized members of the *A. ambigua* con-

TABLE 2. Pinnule populations used in the economic analysis of medullosan foliage.

Species and Population (source)	Av. Lamina Thickness (LT)	Av. Pinnule Width (MaxW)
Alethopteris ambigua Kalo Fm, IA (this contribution)	380 µm	3.1 mm
A. lesquereuxi KS (this contribution)	540 µm	4.5 mm
A. lesquereuxi IA (Reihman and Schabilion, 1976)	490 µm	4.5 mm
A. pennsylvanica IL (Mickle and Rothwell, 1982)	358 µm	7.4 mm
A. pennsylvanica OH (Mickle and Rothwell, 1982)	350 µm	6 mm
A. sullivantii KS, IA ~Floris Fm. (Leisman, 1960)	635 µm	12 mm
A. sullivantii IA, Lovilia (Reihman and Schabilion, 1976)	537 µm	9.5 mm
A. zeilleri Grand Croix (Doubinger et al., 1995)	400 µm	5.3 mm
A. zeilleri Autun (Franks, 1963)	375 µm	4.9 mm
A. sp. Lewis Creek, KY (this contribution)	180 µm	5.3 mm
Laveineopteris rarinervis IL (Oestry-Stidd, 1979)	345 µm	2.9 mm
L. rarinervis IA (Reihman and Schabilion, 1978)	160 µm	6 mm
Macroneuropteris scheuchzeri OH (Beeler, 1983)	240 µm	20 mm
M. scheuchzeri IA (Schabilion and Reihman, 1985)	450 µm	30 mm
Neuropteris ovata (Beeler, 1983)	220 µm	7.2 mm
Reticulopteris muensteri (Reihman and Schabilion, 1978)	150 µm	8 mm

tinuum have extremely thick photosynthetic lamina for their pinnule width, suggesting that these had extremely long-lived, metabolically expensive foliage compared to other mire medullosans. Most neuropterids had thin photosynthetic lamina for their pinnule width, suggesting that these produced metabolically inexpensive, short-lived pinnules relative to other mire medullosans.

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BRYOPHYTES ASSOCIATED WITH PENNSYLVANIAN PERIGLACIAL ENVIRONMENTS IN SOUTHERN GONDWANA (SÃO PAULO STATE, ITARARÉ GROUP, PARANÁ BASIN, BRAZIL)

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Abstract—This study involves bryophyte fossils from the Itararé Group (Pennsylvanian) collected at three localities in the state of São Paulo, southern Brazil. One new species is proposed, *Dwykea araroii* sp. nov. This species included a possible lateral sporophyte that was organically attached to a gametophyte. The samples of bryophytes studied here are the only genus described so far of Pennsylvanian age from the Paraná and Karoo basins, where periglacial conditions occur in both basins.

INTRODUCTION

The bryophytes, despite having fragile structures, inhabit environments inhospitable to other plants, such as periglacial regions. However, preservation, and fossilization are significantly compromised under such conditions, which makes the study of bryophyte fossils challenging but of significance (Cortez et al., 2012). The bryophyte samples that form the basis of this study come from sedimentary rocks derived from the glaciation of southern Gondwana during the Pennsylvanian, a key climate event that had a significant effect on the evolution of plants. Specimens come from the Paraná Basin in southern Brazil within the sedimentary sequence known as the Itararé Group. The Paraná Basin is a huge intracratonic basin (Milani and De Wit, 2008) that during the Late Paleozoic occupied territories located today in the southern parts of the continents of South America (Paraná and Sauce Grande basins) and a correlated area in Africa (Karoo Basin). During the study period, due to the movement of Gondwana from high to low latitudes, the Paraná Basin went from a cold climate zone to a warm one. This was associated with the retreat of the ice caps to the south, while, at the same time, Gondwana moved to the north. The sedimentary rocks of the Itararé Group record numerous major glacial/interglacial cycles generated during an interval of 30-35 million years (Santos et al., 1996; Blakey, 2008).

The gametophyte and sporophyte bryophyte fossils studied were collected from three outcrops in the state of São Paulo, at the former edge of the basin, a sedimentary sequence fairly representative of the climate events that occurred regionally during this time.

The Itararé Group presents a great variety of lithofacies, including claystones, sandstones and conglomerates (diamictites). The presence of varvites, turbidites and carbonaceous beds indicates different environments from marine to continental and transitional, very often associated with glacial, periglacial and interglacial conditions (Longhim, 2003). The pebbles and blocks of rock have multiple source areas, highlighting the large volume of sediments that were carried by glaciers. In São Paulo state, the rocks from the Itararé Group crop out along a narrow strip in a NE-SW direction, and are in direct contact with the crystalline basement (Longhim, 2003). The three outcrops studied expose turbidite deposits associated with periglacial conditions, sometimes with drop stones at particular levels. Given the lithological characteristics of the rocks within which the bryophytes are found, the specimens probably survived short-distance transport and can be considered allochthonous, despite their fragile structures. The plant fossils collected are small and are mainly bryophytic gametophytes, megaspores (*Sublagenicula brasiliensis*) and scattered cuticles, accompanied by unidentified plant debris. The entire assemblage is preserved as carbonizations and includes a low diversity assemblage of pollens and spores (Longhim, 2003; Amaral et al., 2004; Souza et al., 2006).

The outcrops from Campinas are close to one another, both approximately 34 km from the outcrop located near the city of Salto (Fig. 1) as follows:

- The Salto Outcrop, located in the municipality of Salto, km 101.7, Mayor H. Steffen highway/ SP-75 (excerpt Itu-Salto, coordinates UTM 23K 262095 E / 7432774 N);
- The Delta Landfill Outcrop in the city of Campinas-SP (coordinates UTM 23K 0279328 E / 7464284 N);
- The Bandeirantes Outcrop located in Campinas, km 96 of Bandeirantes highway/ SP-348 (excerpt São Paulo-Campinas, coordinates UTM 23K 281430 E / 7463529 N).

MATERIALS AND METHODS

The samples are housed in the Paleobotany Scientific Collection (CP1) of IG-UNICAMP, numbers CP1/411, 412, 415, 416, 419-422, 427-431, 434-437 and 508 for those from Salto outcrop, and numbers CP1/509-563, for those collected from Delta landfill outcrop.

The gametophytes from the Salto and Delta Landfill outcrops were analyzed with a ZeissStemi 2000-C stereoscopic microscope. Specimen images were captured with a digital camera attached to the microscope and processed by using the AxioVisionZeiss software. After the specimens were microscopically examined and photographed, botanical descriptions were made, and the samples were assigned to a fossil genus. Finally, the analysis of samples CP1/416, 421 and 427 was performed by SEM to identify the microstructure and chemical composition.

The samples from the Campinas Outcrop were the subject of previous studies (Amaral et al., 2004), and comprise samples GP/3T

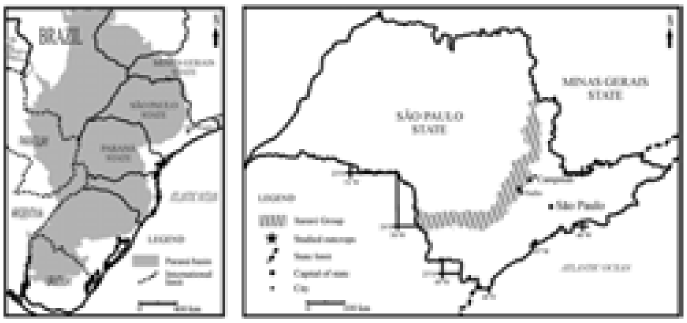

FIGURE 1. Geographic and geological map showing location of studied outcrops.

2284 A and B in the Paleobotany Collection (3T) of the Laboratory of Paleontological Systematics at the Department of Environmental and Sedimentary Geology-Geosciences Institute/USP.

SYSTEMATIC PALEONTOLOGY

BRYOPHYTA Schimper, 1879

Dwykea Anderson and Anderson, 1985

Type species: *Dwykea goedehoopensis* Anderson and Anderson, 1985.

Dwykea araroii sp. nov.

Figures 2 and 3

Holotype: CP1/422.

Referred material: CP1/411, 412, 415, 416, 419-422, 427-431, 434-437, 508- 509 and GP/3T 2284.

Repository: Paleobotany Scientific Collection, Geosciences Institute/ UNICAMP and Paleobotany Collection, Geosciences Institute/ USP.

Horizon and locality: Itararé Group, Salto Outcrop (UTM 23K 262095 E/ 7432774 N), The Bandeirantes highway (UTM 23K 281430 E/7463529 N) and Delta Landfill (UTM 23K 0279328 E/7464284N).

Etymology: From *araroi* (cold) in the Tupi-Guarani language.

Synomyms: aff. *Dwykea* sp. Amaral et al., 2004, Tropical Bryology, 25: 106, plate 1; holotype No. GP/3T 2284.

Diagnosis: Erect gametophytes; erect-patent-leaves in spiral, more tightly closed near the apex of the stem, lamina lanceolate, with acute tip; margin entire, base decurrent. Pleurocarp growth of the sporophyte.

Description: Gametophytes with erect stems at most 9.89 mm in length (fragments varying from 8.08 to 12.00 mm) and variable thickness along stem with an average of 0.87 mm (0.27 to 1.12 mm). The leaves are erect-patent with phyllotaxis in spiral, more tightly closed near the apex of the stem, with average length of 2.92 mm (1.40 to 4.19 mm) and average width near the base of 0.20 mm (0.11 to 0.38 mm) and average width near the tip 0.07mm (0.01 to 0.11). Laminae lanceolate with acute tip; margin entire and base decurrent (Table 1). As described in Amaral et al. (2004), the young sporophyte shows pleurocarpic growth, with a seta with 0.6 mm in length and 0.04 mm in width and bearing a capsule 0.2 mm long and 0.08 mm wide.

Discussion: All samples studied (Table 2) belong to the genus *Dwykea* (Anderson and Anderson, 1985), originally described from the Dwyka Group of the Karoo Basin (South Africa). The Dwyka Group is considered correlative with the Itararé Group consisting of periglacial environments similar to those of the Paraná basin in the Pennsylvanian (Milani and De Wit, 2008). In earlier work (Amaral et al., 2004) a gametophyte with associated sporophyte, aff. *Dwykea* sp., was described for the km 96 Outcrop on Bandeirantes Highway/ SP; this specimen is very similar to those gametophytes described for the Salto and Delta Landfill outcrops. Once a greater number of samples was assembled the bryophyte specimens were placed into a new species, which comprises both the gametophytes and their possible sporophyte.

DISCUSSION

There are very few reports in the literature of fossil bryophyte gametophytes from the end of the Carboniferous, and even fewer from Gondwana (Ricardi-Branco et al., 2011; Cortez et al., 2012). The samples studied here belong to the only genus described so far of Pennsylvanian age from the Paraná and Karoo basins, where periglacial conditions occur in both basins (Anderson et al., 1999; Milani and De Wit, 2008). Moreover, the presence of well preserved bryophytes and low diversity megaspore assemblages, associated with lycopsids, found in rhythmites without other fossil plants, suggests that the plant diversity in fact was low, probably not a reflection of taphonomic biases (Longhim, 2003; Amaral and Ricardi-Branco, 2004). Thus, it is quite likely that mosses and lycopsids belonged to a tundra vegetation type, developed in low-lying areas near water bodies, as in current Patagonia examples. On the other hand, other kinds of plants inhabited places where the soil was not permanently frozen, as recorded by palynomorphs (Longhim, 2003; Amaral et al., 2004).

TABLE 1. Dimensions of *Dwykea araroii* sp. nov. Measurements in mm. The symbol ± indicates standard deviations.

Samples	Stems	Leaves		
	Dimensions (length and width)	Length	Width near the base	Width at tip
CP1/508	8.08 x 1.04	3.03	0.38	0.11
CP1/429	11.28 x 0.93	3.31	0.29	0.08
CP1/430	9.15 x 1.10	3.77	0.14	0.09
CP1/435A	9.03 x 0.73	3.28	0.19	0.08
CP1/434	- x 0.66	2.71	0.18	0.06
CP1/436	8.79 x 0.55	4.19	0.24	0.09
CP1/431	11.27 x 1.12	2.77	0.18	0.09
CP1/419	10.14 x 0.89	1.40	0.15	0.03
CP1/437	12.00 x -	1.75	0.13	0.07
CP1/422		3.42	0.26	0.01
CP1/420	10.60 x 0.27	2.96	0.24	0.08
CP1/421	8.44 x 0.29			
CP1/412		2.94	0.11	0.05
CP1/428		2.86	0.12	0.07
CP1/415		2.54	0.24	0.05
CP1/416	9.97 x 0.79			
Average	9.89 x 0.87 ± 0.001	2.92 ± 0.001	0.20 ± 0.001	0.07 ± 0.001

TABLE 2. Characteristics of similar bryophyte fossil taxa. Measurements in mm.

Characteristics	Gametophyte						Sporophyte
Taxa	Stems	Leaf					
	Dimensions (length)	Dimensions (length x width)	Disposition	Base	Apex	Margin	
Dwykea goedehoopensis	25 mm	5.0 x 0.15		Decurrent	Acute	Entire	
aff. *Dwykea* sp.	17 mm	5.2 x 0.2	Spiral	Decurrent	Acute	Entire	
Dwykea araroii	12 mm	3.0 x 0.2	Spiral	Decurrent	Acute	Entire	Pleurocarpic

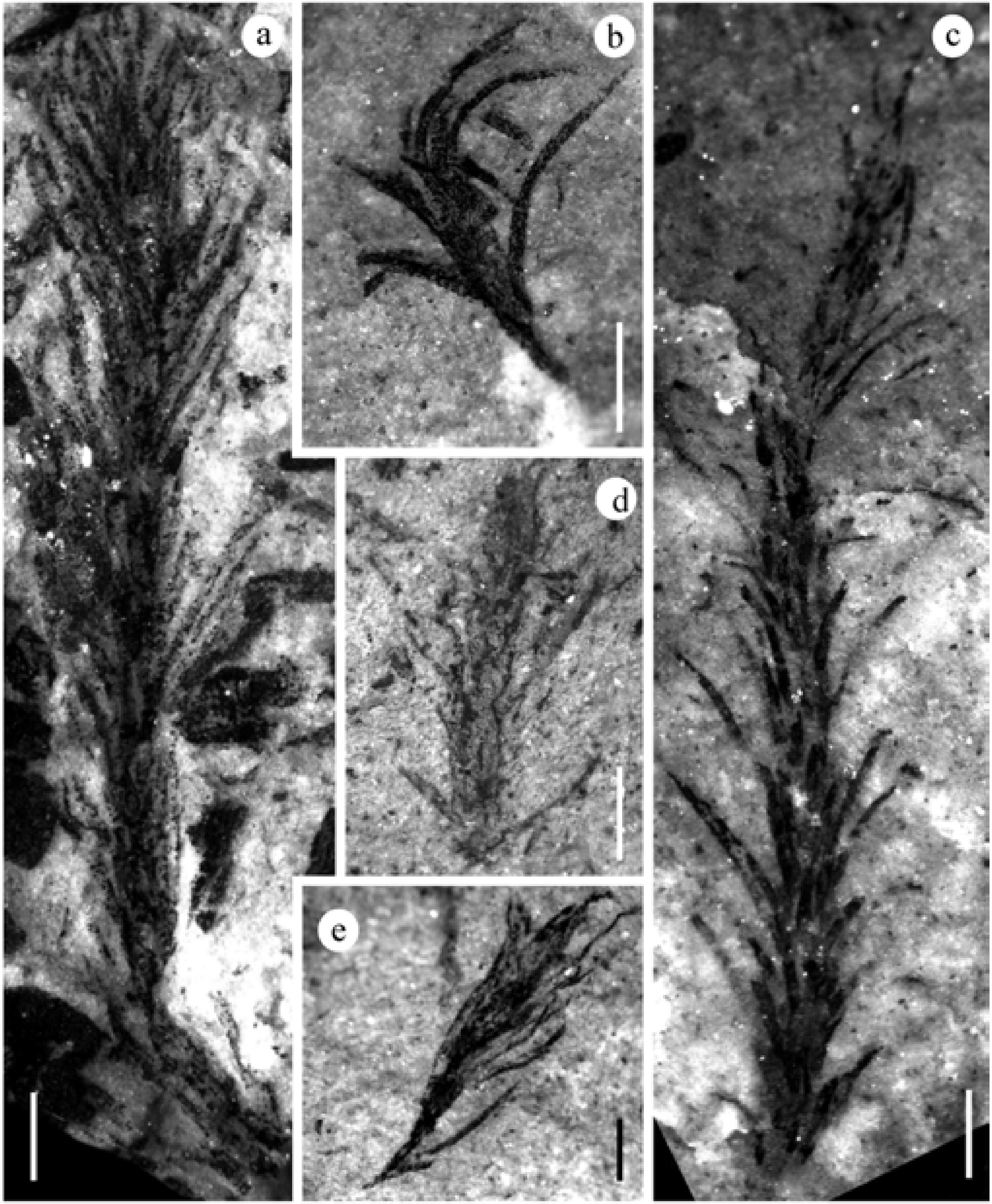

FIGURE 2. *Dwykea araroii* sp. nov. **A**, Stem with erect-patent-leaves in spiral. Holotype CP1/422. **B**, Detail of the upper part of gametophyte with leaves displayed in spiral, CP1/ 434. **C**, Base of the gametophyte, showing decurrent bases of leaves, CP1/ 422. **D**, Gametophyte showing the arrangement of leaves along branch, CP1/ 509. **E**, Detail of the upper part of gametophyte with leaves displayed in spiral, CP1/ 412. Scale bars represent 1 mm.

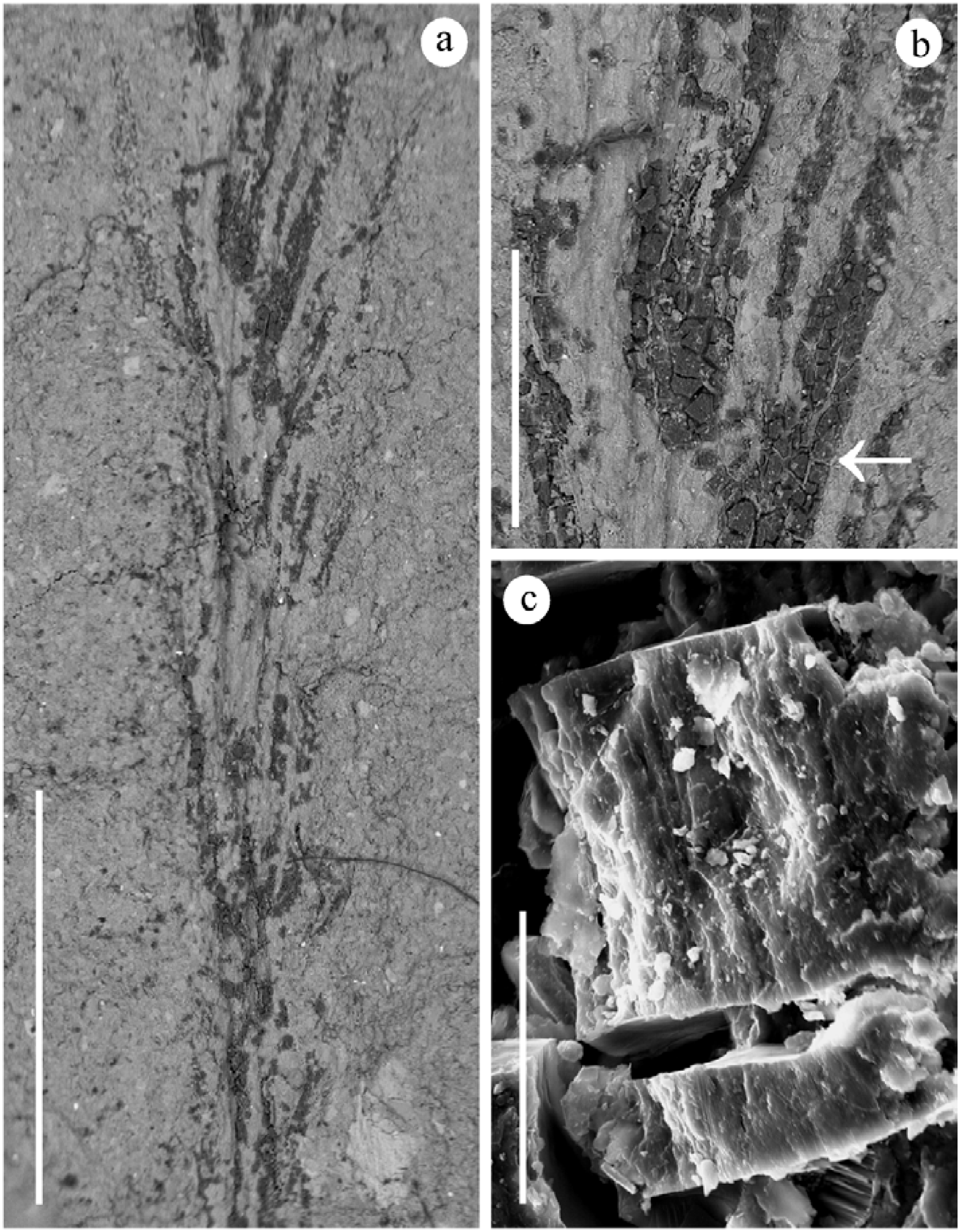

FIGURE 3. *Dwykea araroii* sp. nov. **A**, SEM images of anatomy of gametophyte with erect-patent-leaves in spiral, CP1/ 427. **B**, Upper portion of gametophyte, arrow showing lamina cells. **C**, Detail of **B**, lamina cells. Scale bars represent **A**, 2 mm, **B**, 500 microns or **C**, 50 microns.

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CURRENT STATUS OF THE INTERNATIONAL CARBONIFEROUS TIME SCALE

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The Carboniferous System comprises the Mississippian and Pennsylvanian subsystems and Tournaisian, Viséan, Serpukhovian, Bashkirian, Moscovian, Kasimovian and Gzhelian stages in ascending order (Figs. 1-2). The first use of the name Carboniferous for the rock succession to which it now applies is attributed to William Conybeare and William Phillips in 1822 for coal-bearing strata in England and Wales and was referred to as the Carboniferous System by Phillips in 1835 (Ramsbottom, 1984). This system is unique by comprising two subsystems, the Mississippian (name proposed by Winchell in 1870 for predominantly marine rocks in the upper Mississippi Valley, USA) and overlying Pennsylvanian (name proposed by Stevenson in 1888 for coal measures and terrigenous clastics in the state of Pennsylvania, USA), each of which was proposed as an independent system by Williams (1891). A vote by the International Commission on Stratigraphy (ICS) in 1999 resulted in approval of the names Mississippian and Pennsylvanian together with a reconfirmation of the previous decisions of the ICS Subcommission on Carboniferous Stratigraphy (SCCS) to regard their rank as global subsystems.

In 2003, the SCCS voted to divide the two subsystems into Lower, Middle, and Upper Mississippian series and Lower, Middle, and Upper Pennsylvanian series. This vote, with its implicit acceptance of the stage names used in Russia as the global stage names for the Carboniferous now provides the Carboniferous with its official global series and stage names (Heckel and Clayton, 2006a, b), and all effort by the SCCS is now focused on selecting events and GSSPs for the stage boundaries. In 2013 at the 34th International Geological Congress in Brisbane, Australia, the ICS voted in favor of the formal recognition of global substages. Global substages have not been selected for the Carboniferous, and there are several suites of regional names in use. Figures 1 and 2, the accompanying stratigraphic charts for the Carboniferous, are based on figure 8.5 of Heckel et al. (2008), with radiometric dates updated from Davydov et al. (2012) and the 2013 version of the ICS international stratigraphic chart by Cohen et al. (2013).

A GSSP defines the base of the Carboniferous System (358.9 ± 0.4 Ma), which is co-incident with the Mississippian–Devonian (D-C) boundary and bases of the Lower Mississippian Series and Tournaisian Stage. Studies by Ji et al. (1989) and subsequent analysis (Kaiser, 2009) demonstrated severe problems exist with the D-C boundary GSSP (Paproth et al., 1991) at La Serre Hill, southern France. At La Serre the boundary is defined by the first appearance datum (FAD) of the conodont *Siphonodella sulcata* (Huddle, 1934) in the lineage *Siphonodella praesulcata* Sandberg, 1972-*S. sulcata*, but both the definition and section are considered deficient. Current search for a better boundary index is focused on conodonts and the geochemical-sedimentologic events in the multi-phase Hangenberg Event (Kaiser et al., 2008). Since 2008, the *S. praesulcata-S. sulcata* lineage used to define the boundary has been re-evaluated by several scientists, including Kaiser and Corradini (2011), and the protognathodids, the other conodont group that had shown potential for boundary definition, is being re-studied (Corradini et al., 2011). The conodont studies have been disappointing because it appears that neither the siphonodellid lineage nor the protognathodids are ideal for D-C boundary definition, and other appropriate taxa have not been discovered.

The FAD of the foraminifer *Eoparastaffella simplex* Vdovenko, 1954 in the lineage *Eoparastaffella ovalis* Vdovenko, 1954-*E. simplex* defines the Tournaisian–Viséan boundary GSSP (346.7 ± 0.4 Ma) in the Chinese Pengchong section (carbonate turbidites), which is coincident with the base of the Middle Mississippian Series. Gosselet (1860) introduced Etage du Calcaire de Tournai and Etage du Calcaire de Visé after the towns of Tournai and Visé in Belgium, but Dupont (1861) recognized the units in the Dinant area of Belgium, and in 1883 introduced the terms Tournaisian Stage and Viséan Stage (Devuyst et al., 2003). Using the FAD of *E. simplex* for boundary definition, Devuyst et al. (2003) proposed the Pengchong section in Guangxi Province, south China, for the GSSP, and Devuyst et al. (2004) provided supplementary information on correlating that position into regions where the defining index does not occur. The SCCS task group appointed to establish the boundary voted unanimously to approve the Pengchong GSSP in 2004 and presented the proposal to the SCCS for ballot in late November 2007. The proposal was unanimously approved by the SCCS and ratified by the ICS and IUGS; a final report is in preparation.

The base of the Serpukhovian Stage (330.9 ± 0.2 Ma), coincident with the base of the Upper Mississippian Series, is not defined by a GSSP; however, the SCCS task group appointed to establish this boundary has located a suitable index for boundary definition and is preparing a proposal for SCCS and ICS approval. Nikitin (1890) proposed the name Serpukhovian for a carbonate-dominant succession in the Moscow Basin near the city of Serpukhov. For boundary definition, the SCCS task group is using the FAD of the conodont *Lochriea ziegleri* Nemirovskaya, Perret and Meischner, 1994 in the lineage *Lochriea nodosa* (Bischoff, 1957)-*Lochriea ziegleri*. *L. ziegleri* appears in the upper Venevian Substage somewhat below the current base of the Serpukhovian as defined by its lectostratotype in the Zaborie quarry by Serpukhov in the Moscow Basin, Russia (Kabanov, 2004; Kabanov et al., 2012). Nikolaeva et al. (2002) reported that in Zaborie quarry *L. ziegleri* appears with *Lochriea senckenbergica* Nemirovskaya, Perret and Meischner, 1994 in the basal bed of the lectostratotype but not as a first evolutionary appearance. At the nearby Novogurovsky quarry, the FAD of *L. ziegleri* is in the uppermost Venevian Substage Kabanov et al. (2012) of the Viséan rather than in the lowermost Tarusian Substage of the Serpukhovian as reported for the Zaborie quarry.

Work is well advanced at the two prime GSSP candidates for the lower boundary of the Serpukhovian: the Verkhnyaya Kardailovka section in the southern Ural Mountains of Russia (Nikolaeva et al., 2009; Pazukhin et al., 2010) and the Nashui section in southern Guizhou Province, China (Qi and Wang, 2005; Qi, 2008; Groves et al., 2012). Both are deep-water carbonate-dominant sections containing the selected lineage, but the Kardailovka section has abundant ammonoids in addition to conodonts (Nikolaeva et al., 2009).

The mid-Carboniferous boundary (323.2 ±0.4 Ma), co-incident with bases of the Lower Pennsylvanian Series and Bashkirian Stage, is fixed with a GSSP in the lower Bird Spring Formation at Arrow Canyon, Nevada, U.S.A. (Lane et al., 1999). Semikhatova (1934) proposed the Bashkirian Stage and its stratotype is on the Yuruzan River in the Russian Urals. In Arrow Canyon, the basal Pennsylvanian GSSP is defined by the FAD of the conodont *Declinognathodus noduliferus* (Ellison and Graves, 1941) *sensu lato* in the chronocline *Gnathodus girtyi simplex* Dunn, 1966-*D. noduliferus* and lies in neritic lime grainstone (Richards et al., 2002). When *D. noduliferus sensu lato* was chosen as the index at the 10th International Congress of Carboniferous Geology and Stratigraphy in Madrid (1983), the taxon included the subspecies *D. noduliferus noduliferus* (Ellison and Graves, 1941), *D. noduliferus inaequalis* (Higgins, 1975), and *D. noduliferus japonicus* (Igo and Koike, 1964). But several conodont experts now separate those forms into discrete species, and many biostratigraphers (e.g. Sanz-Lopez et al., 2006) use the FAD of *D. noduliferus inaequalis* (*D. inaequalis*) for boundary definition because

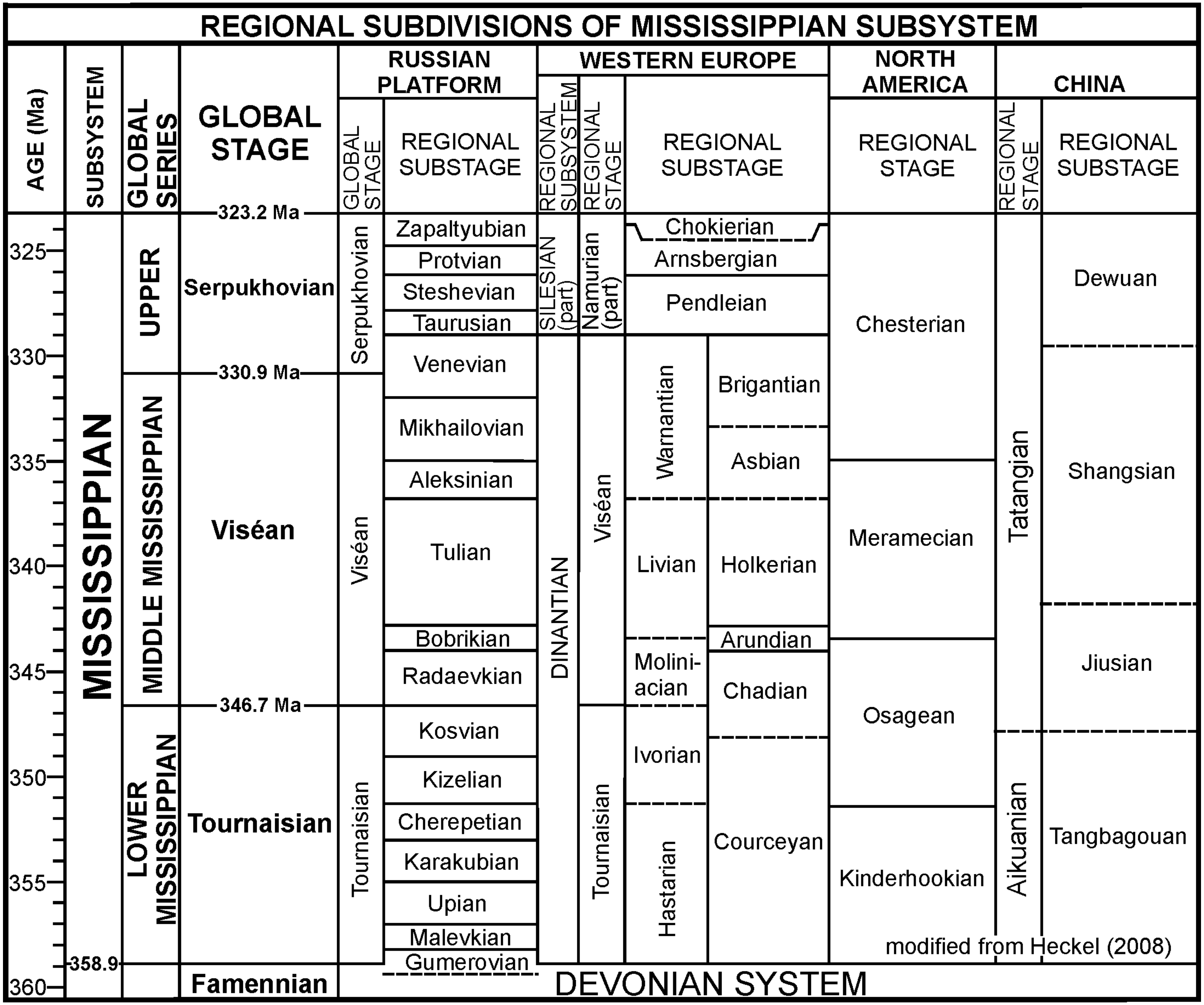

FIGURE 1. Global and regional subdivisions of the Mississippian Subsystem of the Carboniferous System.

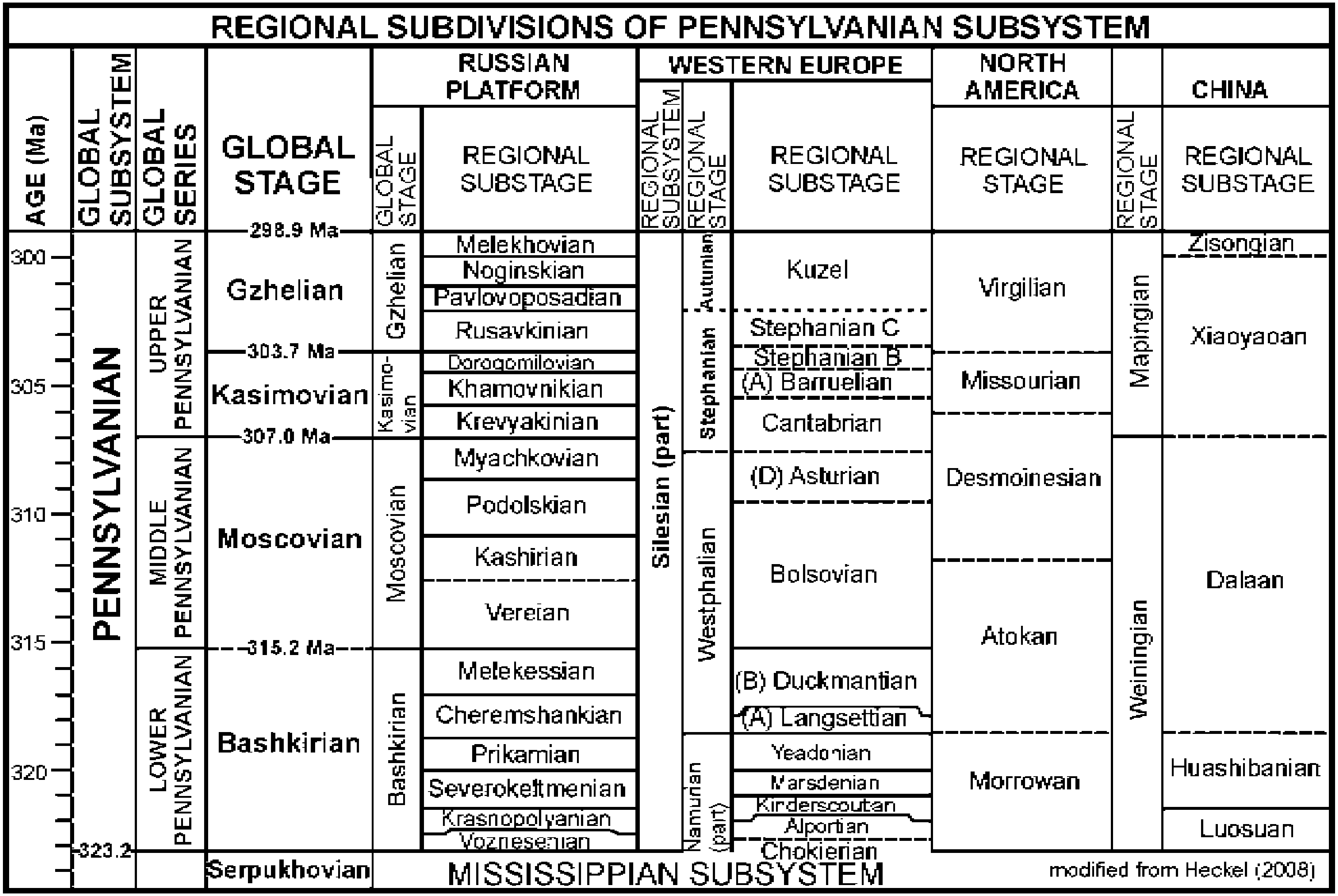

FIGURE 2. Global and regional subdivisions of the Pennsylvanian Subsystem of the Carboniferous System.

the lowest stratigraphic occurrence of *Declinognathodus* in the bed containing the GSSP at Arrow Canyon (Brenckle et al., 1997, pl. 1, figs. 2-4) is apparently *D. noduliferus inaequalis* (Nemyrovska et al., 2011).

The base of the Moscovian Stage (315.2 ± 0.2 Ma), coincident with the base of the Middle Pennsylvanian Series, is not defined by a GSSP, and an index for the boundary definition has not been selected. Nikitin (1890) proposed the name Moscovian for deposits in the Moscow Basin, Russia. A carbonate-dominant section in the Domodedovo quarry southeast of Moscow has been designated as the neostratotype because the stratotype by the village of Myachkovo was covered by the urban spread of Moscow (Goreva et al., 2009). Several conodonts and fusulinids have been recently proposed as potential indices for the GSSP, but only two--*Diplognathodus ellesmerensis* Bender, 1980 and *Declinognathodus donetzianus* Nemirovskaya, 1990--have received substantial support from the SCCS task-group members. Data from the Nashui section in Guizhou Province, South China (Qi et al., 2007; 2010; Groves, 2011) indicate that the FAD of *D. ellesmerensis* in the lineage *Diplognathodus coloradoensis* Murray and Chronic, 1965-*D. ellesmerensis* is one of the best potential boundary markers. *D. ellesmerensis* is easy to identify, the species has a wide geographic distribution (China, Russia, North America), and it occurs in the lowermost Moscovian strata (Alyutovo Formation; Kashirian Russian regional Substage) in the type Moscovian area (Makhlina et al., 2001). The FAD of *D. donetzianus* has long been consider as a potential index, but its apparent absence in North America prevented it from being an ideal candidate; however, Work et al. (2012) recently found the species in the Appalachian Basin, U.S.A. Goreva and Alekseev (2012) proposed moving the lower boundary of the Moscovian one substage higher than the position discussed above; that is from the base of the Vereian regional Substage (lowermost Moscovian substage) to the base of Kashirian regional Substage. A proposed marker for the new level is the FAD of *Neognathodus bothrops* Merrill, 1972 evolving from its ancestor *Neognathodus atokaensis* Grayson, 1984; both species are widely distributed (Goreva and Alekseev, 2012). Several successions, including slope carbonates in the Nashui section, are being intensively studied as potential GSSP candidates.

The base of the Kasimovian Stage (307.0 ± 0.1 Ma), coincident with the base of the Upper Pennsylvanian Series, is not defined by a GSSP, but the SCCS task group studying this boundary has located two conodont taxa that have good potential for boundary definition and are developing a proposal. Originally included in the Moscovian by Nikitin (1890), the Kasimovian is the last Pennsylvanian Stage established in the Moscow Basin (Teodorovich, 1949) and its neostratotype is in the Afansievo quarry in the Moscow Basin southeast of Moscow (Makhilina et al., 2001a).

The SCCS task group responsible for defining the base of the Kasimovian has concluded that the FADs of *Idiognathodus sagittalis* Kozitskaya, 1978 and *Idiognathodus turbatus* Rosscoe and Barrick, 2009a have good potential as markers for the base of the Kasimovian (Ueno et al., 2011). Their occurrence (near base of Khamovnikian regional Substage, the second substage of the Kasimovian in current definition) is approximately one substage higher than the traditional base of the Kasimovian (base of Krevyakinian Substage), but raising the boundary level would facilitate global correlation, and most task-group members consider it appropriate. If the FAD of *I. turbatus* is used for boundary definition, the Nashui section (by village of Naqing) in southern Guizhou Province, China is an excellent candidate for the GSSP (Barrick et al., 2010), preserving the transition from *I. swadei* to *I. turbatus* without interruption.

The base of the Gzhelian Stage (303.7 ± 0.1 Ma) has not been anchored by a GSSP, but an index for boundary definition has been approved by the SCCS and ICS. Its historical stratotype lies in the abandoned Gzhel quarry in the Moscow Basin east of Moscow (Alekseev et al., 2009). The SCCS task group appointed to establish the Kasimovian–Gzhelian boundary selected the FAD of the conodont *Idiognathodus simulator* (Ellison, 1941) *sensu stricto* in its potential lineage *Idiognathodus eudoraensis* Barrick, Heckel and Boardman 2008-*I. simulator* as the event marker for the base of the Gzhelian (Heckel et al., 2008; Villa et al., 2009) and is directing research toward selecting a suitable section for the GSSP. To date the only section that has been formally proposed as a candidate for the GSSP is the Usolka section, a deep-water turbidite-dominated succession in the southern Ural Mountains, Russia (Chernykh et al., 2006; Davydov et al., 2008) but other proposals are being developed. Because the Moscow Basin provides good sections through the Kasimovian-Gzhelian boundary level, Alekseev and his colleagues plan to prepare a proposal for the GSSP at base of the Gzhelian based on either the Rusavkino quarry section or the stratotype of the Gzhelian Stage in the Gzhel quarry (Ueno et al., 2012).

A GSSP defines the top of the Carboniferous (298.9 ± 0.15 Ma), coincident with the base of the Permian System and tops of the Upper Pennsylvanian Series and Gzhelian Stage. The Carboniferous-Permian boundary GSSP lies in northern Kazakstan above the north side of Aidaralash Creek (Davydov et al., 1998). The FAD of the conodont *Streptognathodus isolatus* Chernykh, Ritter and Wardlaw, 1997 in the *Streptognathodus wabaunsensis* Gunnell, 1933-*Streptognathodus isolatus* chronocline defines the Gzhelian- Permian Boundary GSSP in the Aidaralash section (clastic-dominant marine shelf deposits), northern Kazakstan.

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NORTH AMERICAN SPECIES OF THE CONODONT GENUS *IDIOGNATHODUS* FROM THE MOSCOVIAN-KASIMOVIAN BOUNDARY COMPOSITE SEQUENCE AND CORRELATION OF THE MOSCOVIAN-KASIMOVIAN STAGE BOUNDARY

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Abstract—Species of the conodont genus *Idiognathodus* diversified rapidly through the Moscovian-Kasimovian boundary interval in North American Midcontinent basins after the late Desmoinesian extinction event. Reduction of lobes, appearance of eccentric grooves, and formation of medial nodosity appear in successive species, probably through paedomorphosis from *I. swadei* Rosscoe and Barrick 2009a, which replaced the extinct Moscovian idiognathodid morphotypes. The morphologic trends documented in the North American Moscovian-Kasimovian Boundary Composite Sequence (MKBCS) occur in equivalent strata elsewhere in the world, but in different, provincial lineages. The development of a complete, continuous eccentric groove in species of *Idiognathodus* is the best faunal event for demarcation of the boundary between the Moscovian and Kasimovian stages. In North America, this evolutionary step is marked by the rise of *I. heckeli* n. sp. from *I. swadei* and *I. eccentricus* (Ellison, 1941) from *I. harkeyi* Gunnell, 1933 in the Exline intermediate cyclothem. Because the Exline lies in the lower part of the transgressive systems tract of the MKBCS, this faunal level can be readily correlated using both biostratigraphic and sequence stratigraphic analyses, even in the absence of a common globally distributed species. Strata of the overlying highstand systems tract of the MKBCS shows some communication between conodont faunas of the Midcontinent and Eurasian basins, but the apparently diachronous first appearances of these species in the different regions may be a result of sequence architecture, as well as changes in eustatic sea level.

INTRODUCTION

Conodont faunas that span the interval from the Checkerboard-South Mound minor cyclothem to the Swope major cyclothem (latest Desmoinesian to early Missourian) in Midcontinent North America, have proven to be important in the correlation of potential levels for the boundary between the Moscovian and Kasimovian Global Stages of the Middle and Upper Pennsylvanian Series. Villa and the Task Group to Establish the Moscovian/Kasimovian Boundary and the Kasimovian/Gzhelian Boundary (2008) significantly narrowed the stratigraphic window of interest to just a few cyclothems in regions being studied in the United States, Russia, China, and Spain. North American workers focused on one potential marker species, *Idiognathodus turbatus* Rosscoe and Barrick 2009a, whereas Eurasian workers concentrated on another species, *I. sagittalis* Kozitskaya, 1978 (in Kozitskaya et al., 1978). We follow the Task Group recommendation and use a provisional base of the Kasimovian near the level where these two species first appear. However, Davydov et al. (2012) argued strongly for the retention of the Moscovian-Kasimovian boundary near its traditional level, which lies well below the conodont faunas considered here.

Rosscoe and Barrick (2009a) employed a method of taxonomic evaluation relying on functionally significant features of the *Idiognathodus* P_1 element to revise *Idiognathodus* species from the latest Desmoinesian to early Missourian Checkerboard-South Mound to Hertha cyclothems in the North American Midcontinent region. Minor changes were presented later with regard to the lineage leading to *I. turbatus* in Rosscoe and Barrick (2009b). This method of taxonomic revision was applied to *Idiognathodus* species from the Appalachian Basin (Heckel et al., 2012) and is now used for the next higher Swope major cyclothem in the Midcontinent. This paper summarizes our current understanding of the evolution of *Idiognathodus* through the proposed Moscovian-Kasimovian boundary interval in Midcontinent North America and gives some recommendations for placement of the boundary of the base of the Kasimovian Stage and Upper Pennsylvanian Series.

THE MOSCOVIAN-KASIMOVIAN BOUNDARY COMPOSITE SEQUENCE IN MIDCONTINENT NORTH AMERICA

The Moscovian-Kasimovian Boundary Composite Sequence (MKBCS) is the stratigraphic framework within which the evolution of *Idiognathodus* can be evaluated in Midcontinent North America (Fig. 1). Heckel (1992) and Heckel and Watney (2002) presented detailed revisions of the lithostratigraphic nomenclature of uppermost Desmoinesian and Missourian strata of the Northern Midcontinent Shelf (Oklahoma, Kansas, Missouri, and Nebraska). Heckel (2002, 2013) resolved the pattern of cyclothems in the Midcontinent region, and his hierarchy of major, intermediate, and minor cyclothems is followed here. Heckel and Weibel (1991) and Heckel et al. (2012) discussed the correlation of cyclothems eastward from the Northern Midcontinent Shelf into the adjacent Illinois and Appalachian basins. The general stratigraphy of the Northern Midcontinent Shelf and approximate areal extent of the Midcontinent Sea are illustrated in Figure 2.

The basin-restricted, lowstand system tract (LST) of the MKBCS consists of the Hepler Formation, Checkerboard Limestone, and the South Mound Shale. The lower sequence boundary is a large unconformity in which erosional channels have been scoured. Channel-fill deposits on the shelf in central and southern Kansas are an amalgam of sands and terrestrial shales known collectively as the Hepler Formation. In Oklahoma, basinal sands equivalent in age are called the Seminole Sandstone. The Checkerboard Limestone is a fossiliferous limestone centered on the northern slope of the basin. The Checkerboard splits into a lower and upper unit; the upper unit caps the sparsely fossiliferous and lower calcareous South Mound Shale northward. The Checkerboard-South Mound minor cyclothem represents the first transgression of the Midcontinent Sea above the lower sequence boundary, but it is entirely restricted to the basin.

The first marine transgression onto the Northern Midcontinent Shelf is recorded by the deposition of the Exline Limestone. The Exline overlies the transgressive surface marking the start of the transgressive system tract (TST) of the MKBCS. The fossiliferous Exline Limestone

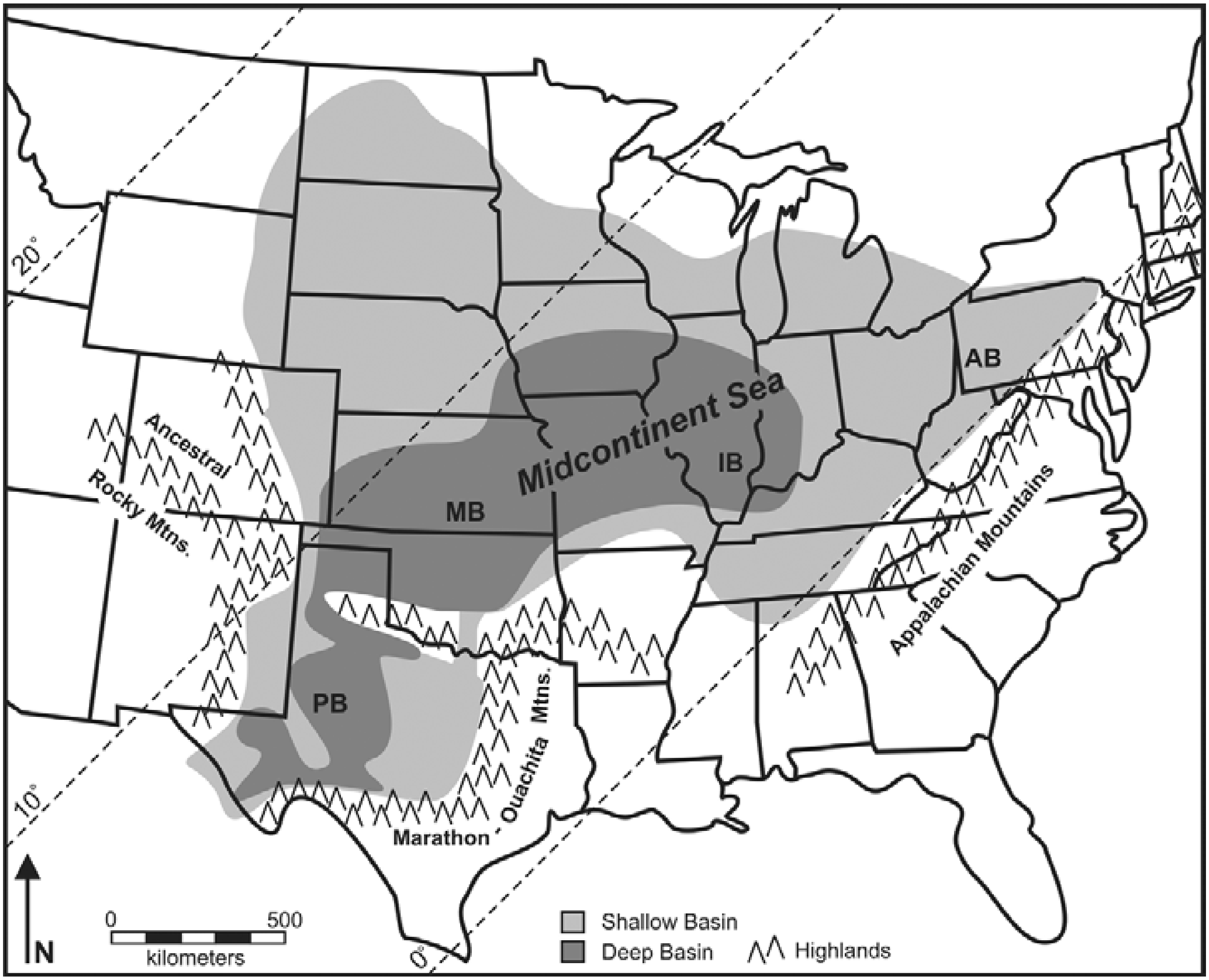

FIGURE 1. General scope and size of the Midcontinent Sea at highstand during the Pennsylvanian. **Abbreviations: AB**, Appalachian Basin; **IB**, Illinois Basin; **MB**, Midcontinent Basin; **PB**, Permian Basin.

is overlain by the sparsely fossiliferous, gray Mantey Shale and these units comprise the intermediate Exline cyclothem. The skeletal Critzer Limestone, a minor cyclothem, overlies the Mantey Shale and underlies the mostly unfossiliferous Guthrie Mountain Shale. As a group, the Exline, Mantey, Critzer, and Guthrie Mountain are known as the Shale Hill Formation (Heckel and Watney, 2002). The Shale Hill Formation represents the lower TST of the MKBCS. The deposits of the lower TST extended into the adjacent Illinois Basin where the Scottville cyclothem correlates with the Exline cyclothem (Heckel and Weibel, 1991).

The Hertha Limestone consists of the organic-rich, dark gray to black Mound City Shale and overlying fossiliferous Sniabar Limestone. These units comprise the major Hertha cyclothem and represent the largest flooding of the TST of the MKBCS. On the Northern Midcontinent Shelf, the Hertha cyclothem represents deeper water conditions than the overlying Swope cyclothem. This major flooding event extended into the Illinois Basin as the Trivoli/Cramer cyclothem (Heckel and Weibel, 1991).

The Elm Branch Shale is the fossiliferous shale with interbedded argillaceous limestone that overlies the Sniabar Limestone. The Elm Branch Shale is succeeded by the fossiliferous Middle Creek Limestone, which underlies the Swope Limestone. The Swope Limestone consists of the lower fissile, organic-rich, black Hushpuckney Shale and the upper thick, fossiliferous Bethany Falls Limestone. These four units comprise the major Swope cyclothem. The base of the Hushpuckney Shale marks the maximum flooding surface and the start of the highstand system tract (HST) of the MKBCS. During this highstand the Northern Midcontinent Shelf and Illinois Basin (Macoupin cyclothem), already connected by the Midcontinent Sea, finally joined with the Appalachian Basin (Lower Brush Creek Shale; Heckel et al. 2012).

LATE DESMOINESIAN - EARLY MISSOURIAN EVOLUTIONARY TRENDS IN *IDIOGNATHODUS* IN THE MKCBS

Midcontinent North America

The morphological diversity of idiognathodid conodonts in the uppermost major Desmoinesian cyclothem in Midcontinent North America, the Lost Branch major cyclothem, is relatively high. Two species of *Idiognathodus* have been recognized; at least two species of *Swadelina* and a minimum of four species of *Neognathodus* are also present (Rosscoe, 2008). The P_1 elements of both *Idiognathodus* species possess the typical flat oral surface bearing continuous transverse ridges,

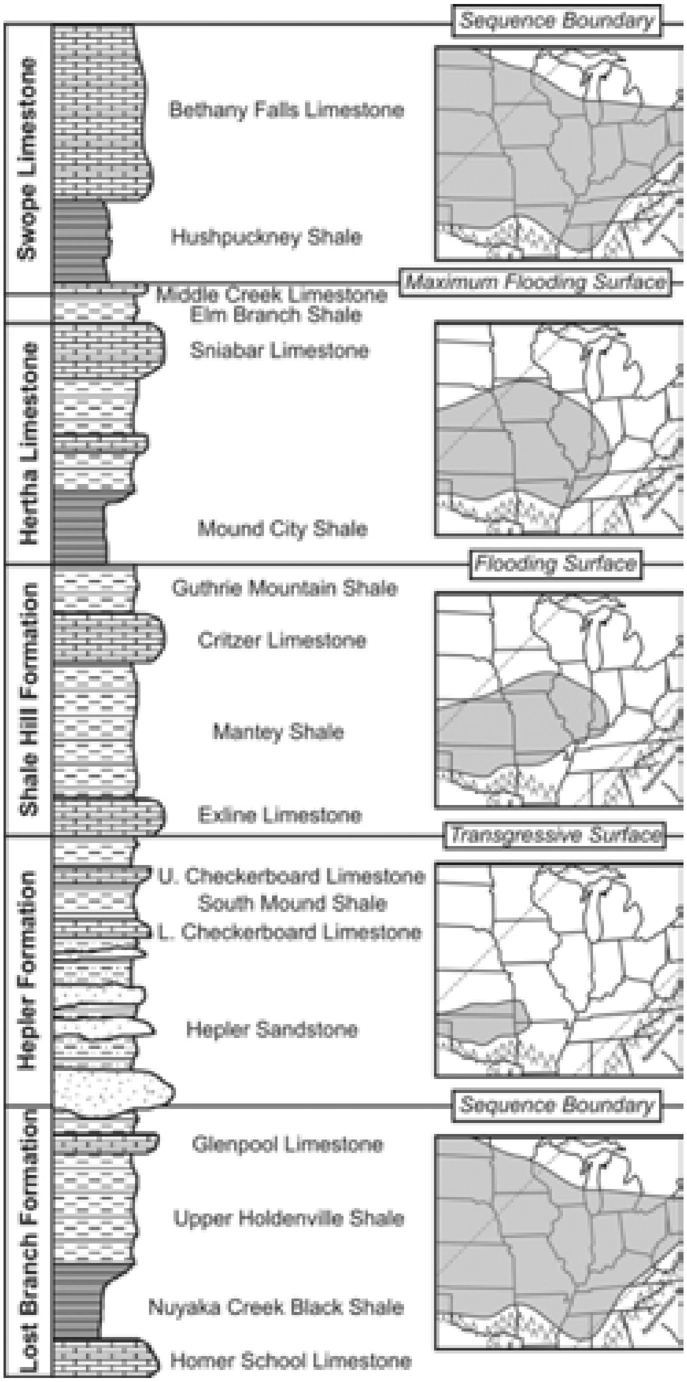

FIGURE 2. General stratigraphy of the Midcontinent region with maps showing the extent of the Midcontinent Sea at the time of deposition for each formation. Important surfaces for sequence stratigraphy are included for the Moscovian-Kasimovian Boundary Composite Sequence.

but differ in the extent of the rostral lobe (Rosscoe and Barrick, 2009a). *Idiognathodus expansus* Stauffer and Plummer, 1932, which ranges up from older cyclothems, has a restricted rostral lobe, whereas *I. swadei* Rosscoe and Barrick 2009a, which appears in the Lost Branch cyclothem, has a robust, expanded rostral lobe. *Swadelina nodocarinata* (Jones, 1941), a polymorphic group that probably includes at least three species, has a deep medial groove on the P_1 element, a characteristic not found in *Idiognathodus* species during the late Desmoinesian. *Neognathodus* species are characterized by P_1 elements with high medial carina and variable development of elevated margins (parapets). The Lost Branch cyclothem represents the last major highstand of the Midcontinent Sea in the late Desmoinesian.

A significant extinction event occurred after the deposition of the Lost Branch cyclothem and before deposition of the marine units of the overlying MKBCS. This North American late Desmoinesian extinction event is characterized by the loss of the brachiopod genus *Mesolobus*, the fusulinid genus *Beedina*, the ammonoid genera *Gonioglyphioceras*, *Wewokites*, *Eothalassoceras*, and *Wellerites*, and numerous conodonts (Boardman et al., 1991; Heckel et al., 2002). The typical Desmoinesian conodont genera *Neognathodus* and *Swadelina* disappear, as well as *Idiognathodus expansus*. *Idiognathodus swadei* is the only idiognathodid to have survived into the MKBCS. The extinctions of *Swadelina* and *Neognathodus* species removed two characteristic P_1 element morphotypes from the conodont faunas: P_1 elements with deep medial troughs and P_1 elements characterized by a high medial carina extending the length of the platform flanked by parapets. The subsequent evolutionary radiation of the one surviving idiognathodid species, *I. swadei*, into these unoccupied morphospaces is the major evolutionary event during the uppermost Desmoinesian and lower Missourian MKBCS in Midcontinent North America (Fig. 3).

In the LST of the MKBCS, two new species arose from *Idiognathodus swadei*, each with relatively simple modification and restriction of the lobes: *Idiognathodus harkeyi* Gunnell, 1933, which has a restricted rostral lobe with a robust caudal lobe, and *I. sulciferus* Gunnell, 1933, characterized by a moderately restricted rostral lobe with a normal caudal lobe. Juvenile forms of all three species are virtually indistinguishable from each other owing to their close relationship. Each species became the founder of three independent lineages, the *I. swadei* lineage, the *I. sulciferus* lineage, and the *I. harkeyi* lineage.

In the lower TST of the MKBCS, the transverse platform ridges of some P_1 elements become disrupted by a narrow, continuoue groove in line with the caudal adcarinal groove, a complete eccentric groove, in all three lineages of *Idiognathodus*. These features appear by the level of the Exline cyclothem. The development of this complete eccentric groove likely represents the first step in replacing grooved morphotypes lost during the end-Desmoinesian extinction event. In the *I. swadei* lineage, the modification results in a complete eccentric groove and forms the species, *I. heckeli* n. sp. In the *I. sulciferus* lineage, a complete eccentric groove appears and forms the more common species *I. eccentricus*. Specimens of all members of the *I. harkeyi* lineage exhibit an incomplete, discontinuous groove at the dorsal and ventral ends of the platform, but the groove does not extend through the central platform. This feature is characteristic of all younger forms of *I. harkeyi*.

Morphological diversification within all three lineages occurs during the widespread and deep flooding of the Northern Midcontinent Shelf of the Hertha transgression, the upper TST of the MKBCS. The *Idiognathodus sulciferus* and *I. harkeyi* lineages follow a path of lobe reduction and narrowing of the platform. *Idiognathodus corrugatus* Gunnell, 1933 (*I. sulciferus* lineage) reduces its rostral lobe almost completely, and the less common *I. gemmiformis* Gunnell, 1933 (*I. harkeyi* lineage) has lobes that are reduced and restricted to only the most ventral portion of the platform. The *Idiognathodus swadei* lineage adds the new species, *I. turbatus* Rosscoe and Barrick, 2009a, which developed a medial row of nodes extending from the end of the medial carina to the dorsal margin of the platform. *Idiognathodus turbatus* is the descendent of *I. heckeli*, as the caudal eccentric groove is an excellent starting point for creating a medial carina, with only the development of a rostral eccentric groove needed to isolate the medial row of nodes. The nodose central platform mimics the medial trough by removal of the former continuous transverse ridges and lowering the platform surface adjacent to the node row. The *I. swadei* lineage is the only lineage in which expansion of the platform remains a trend. *Idiognathodus vorax* Rosscoe and Barrick 2009a has a rostral lobe that extends along the entire length of the platform and is ornamented with nodes. In the Hertha Limestone, *I. swadei* remains the dominant morphotype, *I. turbatus* is less common, and fewer *I. vorax* are present.

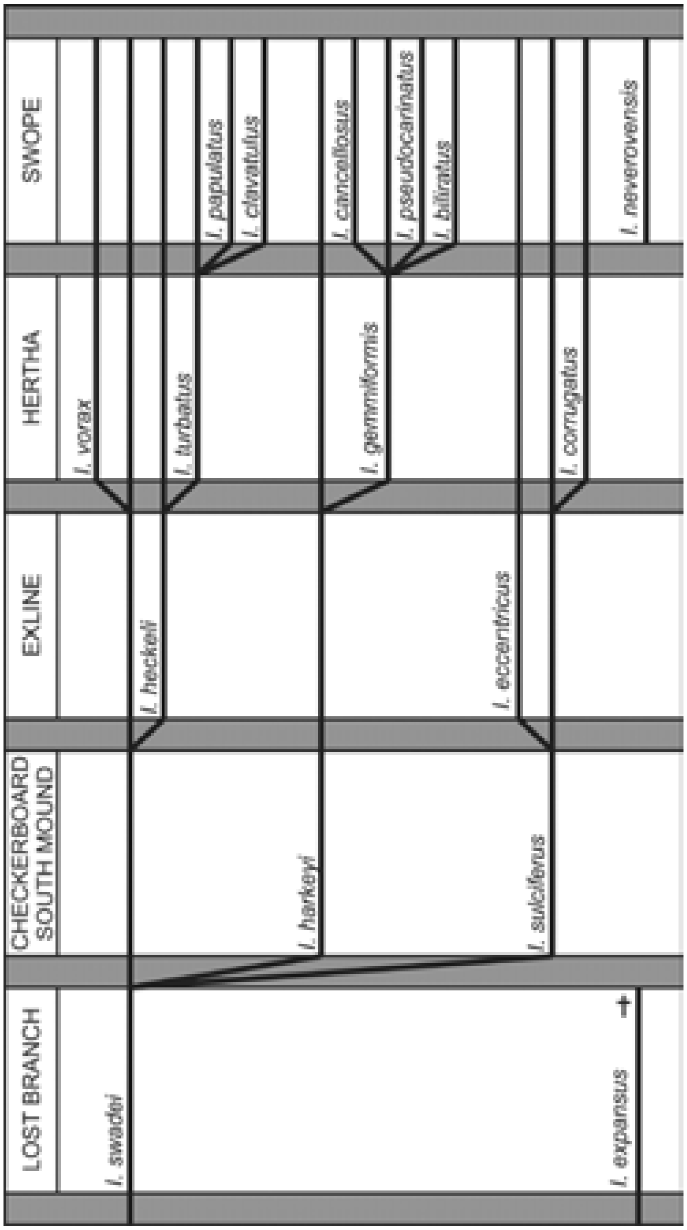

FIGURE 3. *Idiognathodus* species ranges in upper Moscovian and lower Kasimovian strata of central and eastern North America. Cross denotes extinction. Gray regions separating major cyclothems indicate bounding unconformities.

The HST of the MKBCS, represented by the Swope major cyclothem, shows the last stages of diversification in the MKBCS. *Idiognathodus* species continue the trends toward formation of a medial groove and central platform modification, replicating the morphology of the extinct *Swadelina* species. The *I. swadei* lineage develops two new grooved species. *Idiognathodus clavatulus* (Gunnell, 1933) is weakly troughed with reduced lobes and a medial carina reminiscent of the medial carina in *I. turbatus*, its likely ancestor. *Idiognathodus papulatus* n. sp. is relatively rare and represents a near complete conversion of the central platform to nodes that grade into the expanded rostral lobe. In the Swope cyclothem, *I. swadei* becomes significantly less common. In the *I. harkeyi* lineage, the new species *I. cancellosus* (Gunnell, 1933) retains reduced lobes, develops a slight trough, and has a nodose medial platform surface. While the *I. sulciferus* lineage does not see the development of new species in the Swope cyclothem, reduction of the rostral lobe in *I. corrugatus* becomes increasingly more complete. In younger deposits, the rostral lobe is completely absent.

During the MKBCS highstand, new modifications to the P_1 element within the *Idiognathodus harkeyi* lineage began to mimic the medial carina and parapet margins of the extinct genus *Neognathodus*. *Idiognathodus pseudocarinatus* n. sp. develops a short medial carina and has a medial node row that runs the entire length of the platform. Both lobes are exceptionally reduced, and the platform triangular in shape. In *I. biliratus* (Gunnell, 1933), the medial carina extends at least one half the length of the platform and deep featureless grooves separate the carina from elevated platform margins. The platform ornamentation at the margins is so reduced that the margins appear nodose. This species closely approaches the morphology of *Neognathodus*. In addition to the Midcontinent species, *I. neverovensis* (Goreva and Alekseev, 2006), an immigrant from the Moscow Basin, appears during the MKBCS highstand. This Eurasian species also mimics *Neognathodus* where the medial node row fuses ventrally to form a partial medial carina and truncated transverse ridges rise sharply at the margins to form parapets.

The origin of eccentric grooves, medial troughing, and elongation of the medial carina appears to be paedomorphosis acting on *Idiognathodus swadei* and its descendents that survived the end-Desmoinesian extinction event in Midcontinent North America, (Barrick et al., 1999). Small, presumably juvenile, latest Desmoinesian P_1 elements of *I. swadei* are characterized by a long medial carina that is set off from the margins by variably developed grooves. Retention of one or both of the marginal grooves and retention of the medial carina and nodes into adult sizes allowed the early Missourian descendants of *I. swadei* to replicate the morphologies seen in the extinct Desmoinesian taxa *Swadelina* and *Neognathodus*.

Late Moscovian-Early Kasimovian *Idiognathodus* Evolution in Other Regions

In the Moscow and Donets basins, morphological transitions in *Idiognathodus* comparable to those in the North American Midcontinent lineages occurred. Heckel et al. (2007) proposed cycle-by cycle correlations from Midcontinent North America to the Donets Basin and Moscow Basin based on *Idiognathodus* species and cycle-matching (Fig. 4), but the accuracy of these correlations is uncertain. A recent analysis of the stratigraphic sequences and transgressive events in the Donets and Moscow basins appears to support most of these correlations (Alekseev et al., 1996; Eros et al., 2012).

In the Donets Basin, low diversity faunas occur in uppermost Moscovian and lower Kasimovian strata above the disappearance of typical Moscovian species. The most characteristic species is *Idiognathodus sagittalis* (Kozitskaya, 1978, in Kozitskaya et al., 1978). *Idiognathodus sagittalis* is similar to *I. swadei*, but differs in some details of the rostral lobe and platform surface (Rosscoe and Barrick, 2009a). As currently illustrated, the development of medial nodosity on the P_1 element of *I. sagittalis* is strongly variable, ranging from forms with a weak, incomplete eccentric groove on only one side and minor medial protrusions that rise above the transverse ridge to forms in which weak grooves flank both sides of a row of poorly defined medial nodes. These features are somewhat like those observed in the transition from *I. swadei* to *I. heckeli* to *I. turbatus* in Midcontinent North America. Although some potential ancestral forms have been identified in the Moscow Basin (e.g., Goreva et al. 2009), the lineage leading to *I. sagittalis* has not yet been reconstructed, nor has its first appearance level been reliably determined.

A wider range of *Idiognathodus* species has been described from uppermost Moscovian and lowermost Kasimovian beds in the Moscow Basin (Alekseev and Goreva, 2001, 2007; Goreva and Alekseev, 2001, 2006, 2010; Alekseev et al., 2009; Goreva et al., 2009). *Idiognathodus trigonolobatus* Barskov and Alekseev, 1976, which occurs with species of *Swadelina* in upper Moscovian strata, may display some incomplete marginal grooving. Above the extinction level of *Swadelina mahklinae* (Alekseev and Goreva, 2001) in the basal Khamovnikian, a variety of idiognathodids occur in which variable, often incomplete eccentric grooves and medial nodes appear. *Idiognathodus sagittalis* occurs in the Middle Member of the Neverovo Formation, as well as specimens tentatively

MIDCONTINENT	ILLINOIS	APPALACHIAN	MOSCOW	DONETS
Swope *I. cancellosus* *I. neverovensis*	**Macoupin** *I. cancellosus*	**L. Brush Creek** *I. cancellosus* *I. neverovensis*	**Mid-Neverovo** *I. neverovensis* *I. sagittalis I. turbatus*	**O1** *I. sagittalis*
Hertha *I. turbatus* *I. swadei I. sulciferus*	**Trivoli/Cramer** *I. turbatus* *I. swadei I. sulciferus*	***no marine equivalent***	**Lower Neverovo** *I. sagittalis* *I. neverovensis*	**N5/1** *I. sagittalis* *I. cf. eccentricus*
Exline *I. eccentricus* *I. swadei I. sulciferus*	**Scottville** *I. eccentricus* *I. swadei I. sulciferus*	***no marine equivalent***	**Basal Neverovo** *I. aff. eccentricus* *I. aff. trigonolobatus*	***poorly known***
Checkerboard *I. sulciferus* *I. swadei*	***no marine equivalent***	***no marine equivalent***	***no marine equivalent***	***no marine equivalent***

FIGURE 4. Equivalency of units and distinctive conodont occurrences for the Moscovian-Kasimovian Boundary Composite Sequence in major North American and Eurasian basins. Modified from Heckel et al. (2007) and Heckel et al. (2012).

referred to some North American species. *Idiognathodus* aff. *I. eccentricus*, with a caudal eccentric groove, appears earlier, in the basal Neverovo Formation and *I. turbatus*, with a medial row of nodes, is reported from the Middle Neverovo Member. The Eurasian species with a long medial carina that best mimics the appearance of the extinct genus *Neognathodus*, *I. neverovensis*, first appears in the basal Neverovo Formation. The Moscow Basin also has an abundance of forms with reduced lobes as is seen in North America. It is difficult to ascertain how many of these forms are conspecific with the North American species, but the same morphological trends are certainly present. The correlations of Heckel et al. (2007) and Eros et al. (2012) suggest that the appearance of these morphologic features is approximately coeval in North America and Eurasia.

Less is known about early Kasimovian faunas elsewhere in the world. Méndez (2002, 2006) reported small, but comparable early Kasimovian examples of *Idiognathodus* from northern Spain. Barrick et al. (2010) described P_1 elements comparable to the transition from *I. swadei* to *I. heckeli* and to *I. turbatus* from the deep-water limestones of the Naqing section in South China (Nashui section of Wang and Qi, 2003, 2007). Work in progress suggests that a complete, continuous record of this transition may be present in the Naqing section.

Conodont Provincialism and Faunal Interchange

Conodonts, like fusulinids, were extraordinarily provincial during the late Moscovian to early Kasimovian (Charpentier, 1984; Barrick et al., 2000). The interconnectivity of basins around the world was poor and the varying magnitudes of eustatic sea-level events restricted the distribution of conodonts further, because few sea level events were high enough to permit mixing of conodont populations among basins. The potential for species exchange would have occurred only during the longer high stands of major eustatic events.

The HST deposits of the MKBCS can be easily correlated across the Midcontinent, Illinois, and Appalachian basins, as well as into north-central Texas (Boardman and Heckel, 1989), south-central and south-western New Mexico (Barrick, et al. 2012; Barrick et al. 2013), and the Paradox Basin in Utah (Ritter et al. 2002). The large-scale transgression associated with the Hertha cyclothem likely represents the earliest interval where communication may have been established between the conodont faunas of North America and Eurasia. The most likely time of interconnection between global basins and the most likely time for mixing of conodont populations was later, at the level of the Hushpuckney Shale of the Swope cyclothem, which, according to Heckel et al. (2007), would correlate with the Middle Neverovo in the Moscow Basin and the O1 Limestone in the Donets Basin. This is supported by the occurrence of the Eurasian species *I. neverovensis* in the Hushpuckney Shale and Lower Brush Creek Shale of the Appalachian Basin, as well as the report of the North American species *I. turbatus* in the Middle Neverovo. However, both species appeared earlier in their basin of origin than their first occurrences elsewhere, based on the correlations of Heckel et al. (2007).

THE MOSCOVIAN-KASIMOVIAN BOUNDARY

It is recommended that, in line with earlier findings of the Task Group to Establish the Moscovian-Kasimovian and Kasimovian-Gzhelian Boundaries (Villa and Task Group, 2008), the Moscovian-Kasimovian Global Stage boundary be placed considering the following criteria:

1. The chronostratigraphic boundary should lie above the major sequence boundary that overlies strata bearing the last occurrences of *Neognathodus* and *Swadelina*. This is the lower sequence boundary of the MKBCS in Midcontinent North America. This level is well above the traditional level of the base of the Kasimovian and would shorten the duration of the Kasimovian relative to that of the Moscovian (Davydov et al., 2012, p. 616-617). However, the extinction events of these two genera represent a widespread and obvious break in the conodont succession that has been identified in all regions.

2. The boundary should be placed in either the lowstand systems tract (LST) or near the base of the transgressive system tract (TST) of a sequence. Barrick and Männik (2005) discussed the problems of placing chronostratigraphic boundaries in stratigraphic sequences and the corresponding offsets in the species ranges, especially first occurrences, across shelf sections because of sequence architecture and facies patterns. Because most Paleozoic sedimentary sections are shelf successions, the sections include only the TST and HST, and time represented by the LST lies at the unconformity beneath the TST. If the boundary were placed in the LST, or the lower TST of a sequence, then the TST and HST on the shelf would be higher in the sequence and thus younger than the chronostratigraphic boundary. The overlying stage could be identified even in the absence of the characterizing fossil for the boundary. The underlying sequence would belong to the Moscovian, and the overlying sequence to the Kasimovian. Placement of the boundary within the upper TST to HST and its accurate correlation within a sequence, however, would be plagued by the significant range offsets related to shifting facies patterns and migrations, as shown by Holland (2000). This already appears to be the case with *Idiognathodus turbatus* in Eurasia and *I. neverovensis* in North America.

3. The biostratigraphic marker to indicate the level of the base of

the Kasimovian should be the appearance event of either (a) a complete eccentric groove or (b) medial nodosity in *Idiognathodus* in the LST to TST deposits of the MKBCS. Heckel et al. (2002) proposed that the base of the regional North American Missourian Stage be placed at the base of the Exline Limestone, where *I. eccentricus* and now *I. heckeli* n. sp., the species of *Idiognathodus* with an eccentric groove, first appear. This level, in the lower TST of the MKBCS, represents the first evolutionary innovation in *Idiognathodus* above the end-Desmoinesian extinction event. This level is just slightly younger than the long-recognized abrupt floral turnover at the base of the MKBCS that corresponds to the paleofloral break that is considered to be the traditional Westphalian-Stephanian boundary in North America (Peppers, 1996; Heckel, 2013).

The appearance of distinct medial nodosity, in the form of *Idiognathodus turbatus*, occurs higher in the MKBCS in the Hertha cyclothem, but within the upper TST. However, this level is higher than the easily recognized major marine extinction and floral break that lies at the base of the MKBCS. The higher Swope cyclothem is the correlated position of the first occurrence of *I. sagittalis* in the Moscow Basin as well as the N5/1 Limestone, the inferred correlative of the Swope cyclothem (Heckel et al., 2007; Eros et al., 2012).

4. The strong provincialism, which was most obvious during the LST and TST of the MKBCS, will likely prevent direct biostratigraphic correlation among all regions in the lower MKBCS. During the time of the HST, the greater degree of connectivity among basins should allow for migration of species between basins and from one biogeographic region to another, permitting biostratigraphic confirmation of the correlation of the basal Kasimovian sequence. However, the underlying TST of the MKBCS would also be Kasimovian age based on sequence architecture, if the defining boundary level is placed in the LST or low in the TST.

Integration of our understanding of the evolution of *Idiognathodus* across the boundary interval in Midcontinent North America with stratigraphic architecture of the MKBCS, suggests that using the appearance of a complete eccentric grooves in the *Idiognathodus swadei-I. heckeli* lineage, the FAD of *I. heckeli* n. sp., may be the better option for biostratigraphic characterization of the boundary and determination of its stratigraphic placement. This level could also be correlated using the appearance of *I. eccentricus* in the *I. sulciferus* lineage, and perhaps similar morphotypes now included within *I. sagittalis* and *I. trigonolobatus*. Where marine LST deposits are absent and lower marine TST strata are poorly developed or absent, slightly younger species like *I. turbatus*, and *I. neverovensis*, in upper TST and HST deposits would permit recognition of the MKBCS, the lowermost beds of which would lie above the boundary level. The apparent match of stratigraphic sequences in the Donets Basin (Ka III and Ka IV; Eros et al., 2012) and the Moscow Basin (Alekseev et al., 2006; Eros et al., 2012) with the MKBCS suggests that placement of the boundary at a level corresponding to the LST/early TST units is a practical solution.

Because of the hiatal surface at the base of the MKCBS and range offsets related to sequence architecture and facies, shelf sections and offlap sections in which the LST and lower TST are non-marine must be excluded from consideration for the GSSP. The conodont faunas from deeper water successions, ones in which the LST and lower TST deposits are represented by marine facies, need to be better documented. The Naqing section in China is one possibility (Barrick et al., 2010), but the conodont faunas from deeper water successions in other regions should also be investigated.

SUMMARY

This revision of North American Midcontinent *Idiognathodus* species from the stratigraphic interval through the proposed Moscovian-Kasimovian stage boundary level indicates that no single species of conodont can be easily used to designate and correlate the boundary. A distinctive evolutionary pattern does appear to be common among the major basins, and may be approximately synchronous in these basins. Using the first appearance of a complete eccentric groove in species of *Idiognathodus* in LST to early TST strata of the MKBCS or equivalent sequence as a marker permits correlation of the boundary globally. In those regions where the North American Midcontinent fauna dominates, the boundary can be indicated by the first appearance of *I. heckeli* n. sp.; in Eurasian sections the appearance of eccentrically grooved morphotypes of *I. sagittali*, or *I. trigonolobatus* may serve. In stratigraphic intervals where this evolutionary event is absent or lies within the major hiatus at the base of the MKBCS, the development of medial nodosity can be used as a secondary biostratigraphic indicator (e.g., *I. turbatus* in North America).

SYSTEMATIC PALEONTOLOGY

Species from the level of the Swope cyclothem (Hushpuckney Shale) of the Midcontinent area and the equivalent Lower Brush Creek Shale of the Appalachian Basin are emphasized here. See Rosscoe and Barrick (2009a) for more complete description and discussion of most species from the underlying Exline and Mound City cyclothems. The descriptive terminology used in the following section is discussed in Rosscoe and Barrick (2009a). Illustrated specimens reposited in the paleontology collections at the University of Iowa are designated by SUI numbers.

Genus *Idiognathodus* Gunnell, 1931

Type species: *Idiognathodus delicatus* Gunnell, 1931.

Idiognathodus biliratus Gunnell 1933

Fig 5a-d

1933	*Idiognathodus biliratus* n. sp. - Gunnell, p. 276, pl. 31, fig. 59.
1933	*Idiognathodus rugulatus* n. sp. - Gunnell, p. 272, pl. 31, fig. 24.
1941	*Idiognathodus* ? sp. - Ellison, p. 137-138, pl. 23, fig. 11.
1971	*Streptognathodus cancellosus* Gunnell - Lane et al., p. 401, pl. 1, fig. 33.
2002	*Streptognathodus cancellosus* Gunnell - Ritter et al., p. 508, figs. 8.13, 8.16, 8.17.
2009	*Streptognathodus neverovensis* Goreva and Alekseev - Goreva et al., p. 107, fig. 6I (only).
2009b	*Idiognathodus biliratus* Gunnell - Rosscoe and Barrick, 2009b, p. 22, fig. 12.

Diagnosis: P_1 element with ridged marginal platform parapets and elongate medial carina.

Description: The platform of the P_1 element is elongate and triangular in shape. The rostral and caudal margins of the platform are highly elevated parapets ornamented with short transverse ridges or broad nodes. The most dorsal portion of the platform is crossed by one or two complete transverse ridges connecting the marginal parapets that may exhibit weak disruption along the caudal margin. The medial carina is between one-half and three-quarters the length of the platform. Weak denticulation of the medial carina is present up to one-half the length of the platform in most specimens. The medial carina and platform margins are equal in elevation; the remaining platform area is predominantly unornamented.

The ventral caudal margin is high in elevation and deflects in the caudal direction. The point of caudal deflection is associated with the development of one or two nodes on the inside of the marginal ridge in dextral specimens. In sinistral specimens, the caudal marginal ridge is more pronounced and lacks any accessory ornamentation. The ventral rostral margin is similar in elevation to the remainder of the rostral margin. In dextral specimens, the rostral margin is unornamented. In sinistral specimens, the rostral margin can develop a few internal nodes. The rostral adcarinal ridge is much shorter than the caudal adcarinal ridge and both turn inward, toward the blade of the element.

Remarks: The triangular shape of the platform of *Idiognathodus*

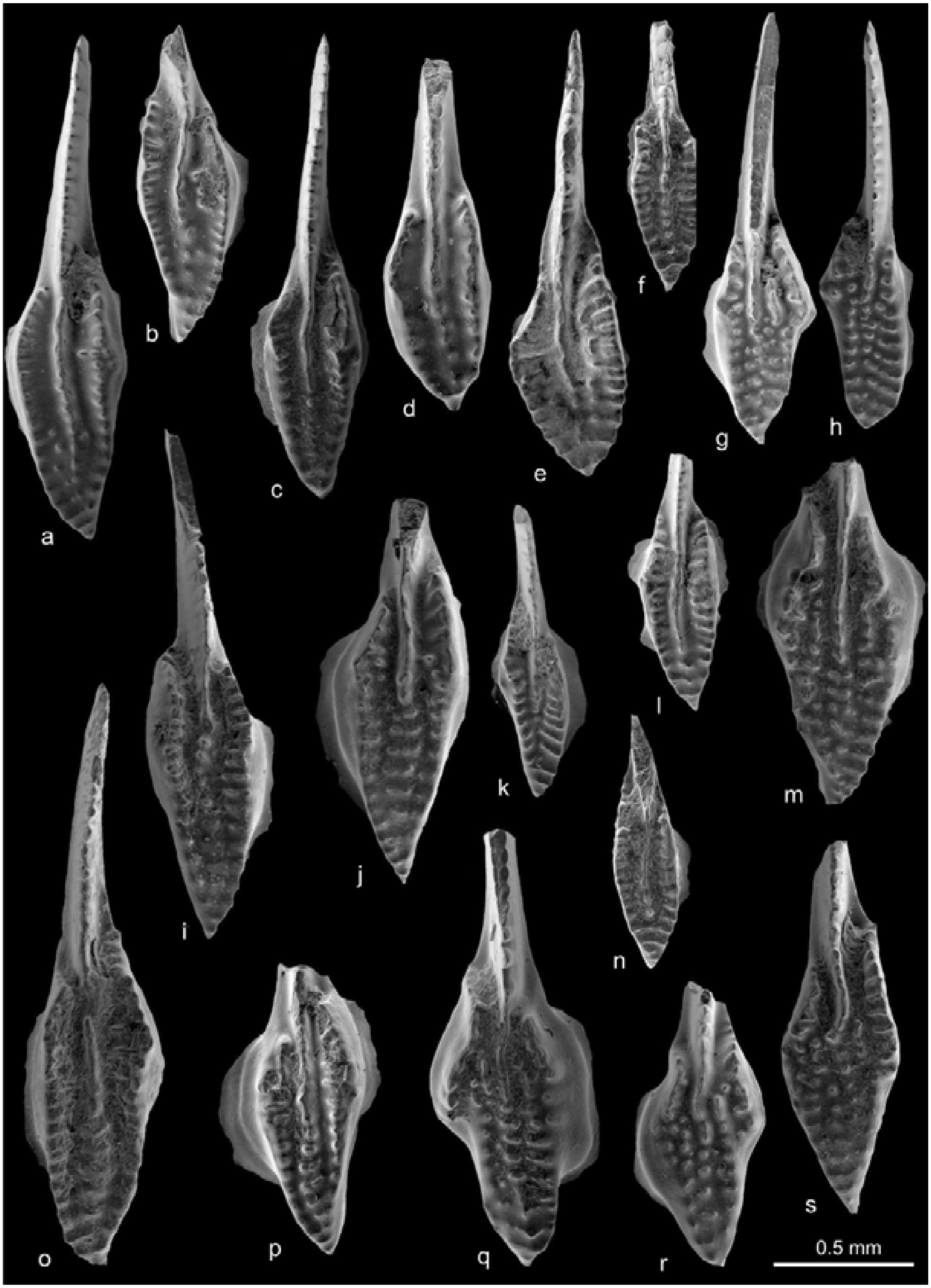

FIGURE 5. P_1 elements of *Idiognathodus* species lacking well developed accessory lobes. Scale bar = 0.5 mm (X50). **a-d**, *Idiognathodus biliratus* Gunnell 1933. **a-b**, SUI 134539, 134540, Hushpuckney Shale, Jingo, KS. **c**, SUI 134541, Hushpuckney Shale, Clear Creek, OK. **d**, SUI 134542, Lower Brush Creek Shale, Cmb1, OH. **e**, **f**, **k**, **l**, **n**, *Idiognathodus neverovensis* (Alekseev and Goreva, 2006). **e**, **f**, **l**, **n**, SUI 134543, 134544, 131087, 131085, Lower Brush Creek Shale, Pgh5, PA. **k**, SUI 134545, Hushpuckney Shale, Fort Calhoun, NE. **g**, **h**, **m**, **q-s**, *Idiognathodus cancellosus* (Gunnell, 1933). **g**, SUI 134546, Hushpuckney Shale, PWA Quarry, NE. h, **r**, SUI 134547, 134548, Hushpuckney Shale, Fort Calhoun, NE. **m**, **s**, SUI 134549, 134550, Hushpuckney Shale, Clear Creek, OK. **q**, SUI 131093, Lower Brush Creek Shale, Stb1, WV. **i**, **j**, **o**, **p**, *Idiognathodus pseudocarinatus* n. sp. **i**, **j**, **o**, SUI 134551-134553, Hushpuckney Shale, Clear Creek, OK. **p**, SUI 131095, Lower Brush Creek Shale, Stb1, WV.

biliratus suggests an affinity to members of the *I. harkeyi* group. *Idiognathodus pseudocarinatus* n. sp., found in both the Midcontinent and Appalachian basins, has a similar triangular shape, a media carina that is mimicked by dual grooves segregating the transverse ridges of the central platform, and lacks the parapets that define *I. biliratus*. *Idiognathodus biliratus* may be descendent of *I. pseudocarinatus* or both may share a common ancestor with *I. harkeyi*. *Idiognathodus biliratus* can be distinguished from *I. cancellosus* as the former lacks a rostral lobe and has a longer medial carina. *Idiognathodus neverovensis*, recognized in the Moscow Basin, is strikingly similar to *Idiognathodus biliratus*. Some illustrated specimens of *I. neverovensis* are examples of *I. biliratus*, whereas typical *I. neverovensis* differs with its broader and more ridged platform margins, as opposed to discrete parapets of *I. biliratus*.

Occurrence: Lower Brush Creek Shale of the Appalachian Basin and the Hushpuckney Shale and Stark Shale (Rosscoe, 2008) in the Midcontinent Basin.

Idiognathodus cancellosus (Gunnell, 1933)
Fig. 5g, h, m, q-s

1933	*Streptognathodus cancellosus* n. sp. - Gunnell, p. 270, pl. 31, fig. 10.
1941	*Streptognathodus cancellosus* Gunnell - Ellison, p.131-132, pl. 22, figs. 23, 26.
1978	*Streptognathodus cancellosus* Gunnell - Kozitskayaet al., p. 90-91, pl. XXVI, figs. 11-14, pl. XXVII, figs. 8, 10 (in Kozitskaya et al., 1978).
1989	*Streptognathodus cancellosus* Gunnell - Barrick and Boardman p. 185, pl. 1, figs. 11, 18.
1989	*Idiognathodus clavatulus* (Gunnell) - Barrick and Boardman, p. 185, pl. 1, fig. 10.
1999	*Streptognathodus cancellosus* Gunnell - Barrick and Walsh, p. 155, fig. 7.3 (reillustration of holotype).
2001	*Streptognathodus cancellosus* Gunnell - Stevens et al., p. 120, fig. 13.10.
2003	*Streptognathodus oppletus* Ellison - Wang and Qi, p. 393, pl. 3, fig. 20.
2004	*Streptognathodus cancellosus* Gunnell - Barrick et al., p. 241, pl. 4, fig. 1 (reillustration of holotype).
2007	*Streptognathodus cancellosus* Gunnell - Alekseev and Goreva, pl. 1, figs. 19, 20.
2009b	*Idiognathodus cancellosus* (Gunnell) - Rosscoe and Barrick, p. 22, figs. 1.10, 1.11.
2012	*Idiognathodus cancellosus* (Gunnell) - Heckel et al., p. 263, pl. 1, figs.15, 17, 18, 20, 27.

Diagnosis: P_1 element with reduced rostral and caudal lobes and distinctive medial nodosity.

Description: The dorsal platform of the P_1 element is split roughly equally along the medial axis with a row of medial nodes. Medial nodes range from discrete small nodes, partially merged nodes, to ridges in larger specimens. The dorsal margin is rounded to subrounded in shape. The caudal accessory lobe is limited to a single row of poorly defined to fused nodes in line with the caudal adcarinal ridge. The rostral accessory lobe is reduced, extending about one third the length of the platform. The rostral lobe is ornamented with only a few nodes where the lobe is expanded the most, in smaller specimens. In larger specimens, a row of nodes along the rostral margin of the lobe is visible.

The caudal adcarinal ridge is well developed and merges with the ornamentation of the caudal accessory lobe. The caudal ridge is a high ridge that stands above all other features of the platform. The rostral ridge is less pronounced than the caudal ridge and extends out onto the platform where it separates the rostral lobe from the central platform. The adcarinal ridges terminate dorsal of the termination of the medial carina. The medial carina terminates near the ventral margin of the platform and does not exceed one-quarter the length of the platform.

Remarks: *Idiognathodus cancellosus* can be distinguished from *I. biliratus* because the former has a shorter medial carina and a more developed rostral lobe. *Idiognathodus cancellosus* can be distinguished from *I. pseudocarinatus* as the medial carina of the former is shorter and more nodose in nature and it has better developed rostral and caudal accessory lobes. *Idiognathodus cancellosus* can be distinguished from *I. clavatulus*, which has a medial groove and a well-developed caudal accessory lobe. Small specimens of *Idiognathodus cancellosus* do have a medial carina that extends the entire length of the platform, but the dorsal portions of the medial carina become separated into nodes with age. Overall, platform nodosity increases with size, with extremely nodose platforms common in the largest specimens.

Ellison (1941) assigned *Idiognathodus cancellosus* to the genus *Streptognathodus*. *Streptognathodus* comprises a clade of species that appears later in time, in which the P_1 has a deeply troughed platform (Rosscoe, 2008). Although the nodosity, medial carina, and raised adcarinal ridges give the impression of a troughed platform in *I. cancellosus*, the platform is actually quite flat and all relief is an effect of ornamentation.

Occurrence: Hushpuckney Shale and Stark Shale (Rosscoe, 2008) of the Midcontinent Basin and the Lower Brush Creek Shale in the Appalachian Basin.

Idiognathodus clavatulus (Gunnell, 1933)
Fig. 8l, p, t-v

1933	*Streptognathodus clavatulus* n. sp. - Gunnell, p. 280, pl. 31, fig. 9.
1999	*Streptognathodus clavatulus* Gunnell - Barrick and Walsh, p. 153, fig. 5.1 (reillustration of holotype).
2004	*Idiognathodus clavatulus* (Gunnell) - Barrick et al., p. 241, pl. 4, fig. 12 (reillustration of holotype).

Diagnosis: P_1 element with a reduced, elongate rostral lobe and an oral surface ornamented with closely spaced transverse ridges bisected by a medial groove.

Description: The platform of the P_1 element is split asymmetrically by a medial groove. The platform is ornamented with closely spaced transverse ridges that deflect ventrally along the medial groove. The dorsal margin is subrounded to rounded in shape. The robust, normal caudal lobe is ornamented with nodes. The rostral lobe is reduced and elongate, forming a narrow lobe with a single row of nodose ornamentation. The rostral lobe extends between one-half and three-quarters the length of the platform.

The caudal adcarinal ridge is the most pronounced and flares outward at the ventral margin of the platform. The caudal margin of the platform merges with the caudal adcarinal ridge and separates the caudal lobe from the central platform. The rostral adcarinal ridge is shorter than the caudal and merges with the rostral margin of the central platform. The medial carina is short and is followed by one to three closely spaced nodes at the dorsal termination. In larger specimens these nodes become fused with the medial carina.

Remarks: Specimens of *Idiognathodus clavatulus* show substantial variation with increase in size. A well-developed medial groove is most common in large specimens. Intermediate and smaller specimens exhibit medial nodosity that is filled with an increase in size to complete the longer transverse ridges on the rostral side of the platform. Rostral lobe ornamentation starts as a single node and nodes are added dorsally in larger specimens. Caudal lobe nodes are most discrete in smaller specimens and become partially fused with increase in specimen size. The best way to distinguish *Idiognathodus clavatulus* from similar species like *I. biliratus* and *I. cancellosus* is by the well-developed caudal lobe and elongate rostral lobe of the former. The elongate rostral lobe helps to distinguish *I. clavatulus* from all species in the *I. harkeyi* and *I. sulciferus* lineage and almost all species in the *I. swadei* lineage.

As originally defined by Gunnell (1933), *Idiognathodus clavatulus* belonged to the genus *Streptognathodus*. *Streptognathodus* comprises a clade of species that appears later in time, in which the P_1 has a deeply troughed platform (Rosscoe, 2008). While the medial groove gives the impression of a troughed platform, the platform is actually quite flat.

Occurrence: Specimens of *Idiognathodus clavatulus* have only been recovered from the Hushpuckney Shale of the Midcontinent Basin.

Idiognathodus corrugatus Gunnell, 1933

Fig. 6a-e, h-k

1933 *Idiognathodus corrugatus* n. sp. - Gunnell, 1933, p. 277, pl. 32, fig. 6.
1933 *Idiognathodus lanceolatus* n. sp. - Gunnell, p. 273-274, pl. 31, fig. 31.
1933 *Idiognathodus liratus* n. sp. - Gunnell, p. 273, pl. 31, fig. 27.
1941 *Idiognathodus antiquus* Stauffer and Plummer - Ellison, p. 136, pl. 23, figs. 1, 8 (only).
2002 *Streptognathodus confragus* Gunnell - Ritter et al., p. 510, fig. 9.14 (only).
2002 *Streptognathodus excelsus* Stauffer and Plummer - Ritter et al., p. fig. 9.15 (only).

Diagnosis: P_1 element has an exceptionally reduced to absent rostral lobe and a reduced caudal lobe. The elongate medial carina is up to one-quarter the length of the platform.

Description: The platform of the poorly lobed P_1 element is ornamented by complete transverse ridges. Specimens may exhibit an incomplete caudal eccentric groove. The groove is most apparent at the more ventral and more dorsal portions of the platform, but not present in the central platform. All specimens exhibit a ventral deflection of the transverse ridges dorsal of the medial carina. The dorsal margin of the platform is subrounded and in some cases angular. The caudal lobe is reduced and ornamented with a fused ridge rather than discrete nodes. The rostral lobe is absent in most specimens, but may be present as an unornamented expansion on the rostral margin of the platform.

The adcarinal ridges form parallel features on the ventral surface of the platform. The caudal adcarinal ridge merges with the central platform to form a distinct division between the central platform and the caudal accessory lobe. The rostral adcarinal ridge is shorter in the ventral direction and merges with the rostral margin of the element. The medial carina is elongate, typically extending around one-quarter the length of the platform. The medial carina is longest in smaller specimens.

Remarks: *Idiognathodus corrugatus* first appears in the Hertha Limestone of the Midcontinent and quickly becomes one of the most abundant idiognathodid conodonts in subsequent strata. Early specimens of *I. corrugatus* are more likely to have a remnant, unornamented rostral lobe; specimens from stratigraphically higher units do not exhibit this remnant lobe. *Idiognathodus corrugatus* is readily distinguished from all other species due to its lack of a rostral lobe and the normal caudal lobe.

Occurrence: The first appearance of *Idiognathodus corrugatus* is in the Mound City Shale of the Hertha Limestone and it is found stratigraphically higher to at least the level of the Quivira Shale in the Midcontinent Basin (Rosscoe, 2008).

Idiognathodus eccentricus (Ellison, 1941)

Fig. 6s

Remarks: For a complete synonymy, diagnosis, description, and discussion, see Rosscoe and Barrick (2009a).

Occurrence: Exline Limestone through the Hushpuckney Shale of the Midcontinent Basin (Rosscoe and Barrick, 2009a).

Idiognathodus gemmiformis Gunnell, 1933

Fig. 8a-c, f-h, j, k, m-o, q-s

1933 *Idiognathodus gemmiformis* n. sp. - Gunnell, p. 275, pl. 31 fig. 44.
1933 *Idiognathodus cicatricosis* n. sp. - Gunnell, p. 274, pl. 31, fig. 34.
1933 *Idiognathodus folium* n. sp. - Gunnell, p. 274, pl. 31, fig. 33.
1933 *Idiognathodus lobatus* n. sp. - Gunnell, p. 271, pl. 31, figs. 17, 18
1933 *Idiognathodus modulatus* n. sp. - Gunnell, p. 271, pl. 31, fig. 15.
1933 *Idiognathodus semipapulatus* n. sp. - Gunnell, p. 273, pl. 31, fig. 29.
1933 *Idiognathodus spathodus* n. sp. - Gunnell, p. 273, pl. 31, fig. 28
1941 *Idiognathodus delicatus* Gunnell - Ellison, pl. 22, fig. 33 (only).
1989 *Idiognathodus lobatus* Gunnell - Barrick and Boardman, p. 185, pl. 1, figs. 7, 9, 24;
1999 *Idiognathodus lobatus* Gunnell - Barrick and Walsh, p. 154, fig. 6.4 (reillustration of holotype).
2002 *Idiognathodus sulciferus* Gunnell - Ritter et al., 2002, p. 508, figs. 8.8, 8.21.

Diagnosis: P_1 element with a rostro-caudally reduced expanded rostral lobe and a reduced high elevation caudal lobe.

Description: The platform of the P_1 element is rostro-caudally compressed and elongate in the dorso-ventral direction. The platform is ornamented with coarsely spaced transverse ridges. In some smaller specimens the transverse ridges exhibit a weak medial disruption. The dorsal margin of the platform is subrounded to subangular in shape. The caudal accessory lobe has a ventral termination that extends beyond the ventral termination of the rostral accessory lobe. The caudal accessory lobe is small and reduced with room for a few discrete nodes in smaller specimens. In larger specimens the ornamentation is fused into the caudal adcarinal ridge. The rostral accessory lobe is expanded, extending up to one half the length of the platform, but it is reduced in width. The rostral accessory lobe is ornamented with a single row of moderately sized nodes. In some specimens the lobe may be ornamented with a clump of a few small nodes rather than a row of larger nodes.

The rostral adcarinal ridge is short and merges with the rostral accessory lobe. The caudal adcarinal ridge is higher in elevation than the rostral adcarinal ridge and extends further in the dorsal direction. The high elevation caudal adcarinal ridge runs along the outside margin of the caudal accessory lobe often merging with the nodose ornamentation of the lobe in larger specimens. Most specimens exhibit a short medial carina, some followed by a small nodes in smaller specimens.

Remarks: *Idiognathodus swadei* has more a robust rostral accessory lobe and more equal ventral terminations of both accessory lobes than *I. gemmiformis*. *Idiognathodus clavatulus* can be distinguished from *I. gemmiformis* by the well-developed medial groove in the former. *Idiognathodus harkeyi* can be distinguished from *I. gemmiformis* by the highly restricted rostral accessory lobe of the former. *Idiognathodus gemmiformis* is the likely ancestor of the important species, *Idiognathodus confragus* Gunnell, which first appears in the stratigraphically higher Stark Shale.

Occurrence: Hushpuckney Shale and Stark Shale of the Midcontinent Basin (Rosscoe, 2008) and the Lower Brush Creek Shale in the Appalachian Basin.

Idiognathodus harkeyi Gunnell, 1933

Fig. 6f, g, l-n, p, v

1932 *Idiognathodus magnificus* Stauffer and Plummer, p. 197, pl. IV, fig. 20 (only).
1933 *Idiognathodus harkeyi* n. sp. - Gunnell, p. 270, pl. 31, fig. 11.
1933 *Idiognathodus cuneiformis* n. sp. - Gunnell, p. 270, pl. 31, fig. 8.
1933 *Idiognathodus erodus* n. sp. - Gunnell, p. 275, pl. 31, fig. 48.
1933 *Idiognathodus fusiformis* n. sp. - Gunnell, p. 276, pl. 31, fig.

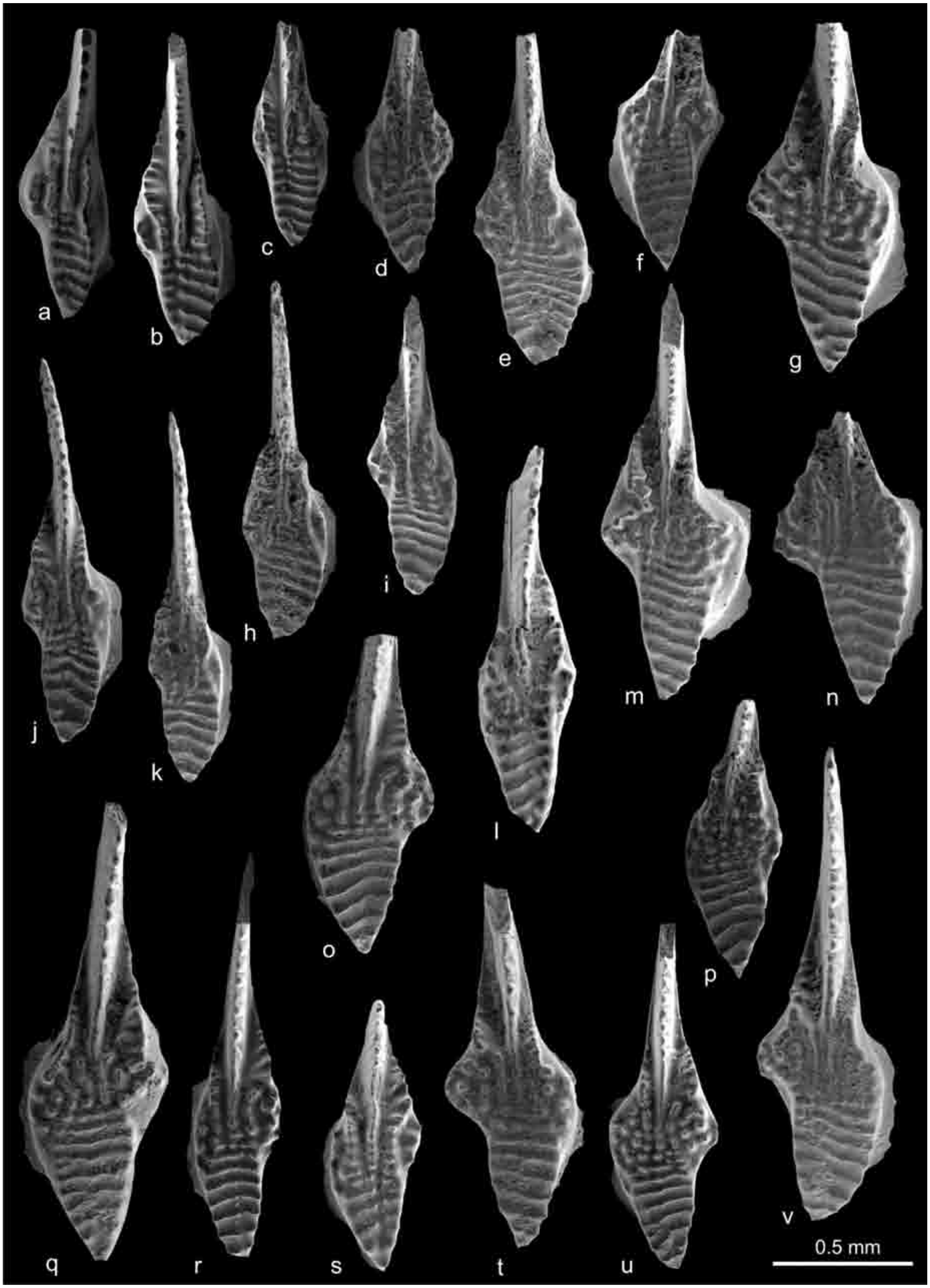

FIGURE 6. P_1 elements of *Idiognathodus* species with reduced rostral accessory lobes. Scale bar = 0.5 mm (X50). **a-e**, **h-k**, *Idiognathodus corrugatus* Gunnell, 1933. SUI 134554-134562, Hushpuckney Shale, Jingo, KS. **f**, **g**, **l-n**, **p**, **v**, *Idiognathodus harkeyi* Gunnell, 1933. **f**, **n**, **p**, **v**, SUI 134563-134566, Hushpuckney Shale, Jingo, KS. **g**, **m**, SUI134567, 134568, Hushpuckney Shale, East Peru, IA. **l**, SUI 134569, Lower Brush Creek Shale, Pgh5, PA. **o**, **q**, **r**, **t**, **u**, *Idiognathodus sulciferus* Gunnell, 1933. **o**, **q**, **r**, SUI 134570-134572, Hushpuckney Shale, Fort Calhoun, NE. **t**, SUI 134573, Hushpuckney Shale, Clear Creek, OK. **u**, SUI 134574, Hushpuckney Shale, East Peru, IA. **s**, *Idiognathodus eccentricus* (Ellison, 1941). SUI 134575 Hushpuckney Shale, Fort Calhoun, NE.

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1933	*Idiognathodus jugosus* n. sp. - Gunnell, p. 270-271, pl. 31, fig. 13.
1933	*Idiognathodus strigillatus* n. sp. - Gunnell, p. 274-275, pl. 31, fig. 37, pl. 32, fig. 8.
1933	*Idiognathodus vadosus* n. sp. - Gunnell, p. 275, pl. 31, fig. 45.
1933	*Idiognathodus wintersetensis* n. sp. - Gunnell, p. 274, pl. 31, fig. 36.
1999	*Idiognathodus harkeyi* Gunnell - Barrick and Walsh, p. 153, fig. 5.3 (reillustration of holotype).
1999	*Idiognathodus cuneiformis* Gunnell - Barrick and Walsh, p. 153, fig. 5.2 (reillustration of holotype).
1999	*Idiognathodus jugosus* Gunnell - Barrick and Walsh, 1999, p. 150, fig. 3.4 (reillustration of holotype)
2001	*Idiognathodus magnificus* Stauffer and Plummer - Stevens et al., p. 120, fig. 13.9, 13.15, 13.16.
2002	*Idiognathodus magnificus* Stauffer and Plummer - Ritter et al., p. 510, figs. 9.20-9.23 (only).
2009a	*Idiognathodus sulciferus fusiformis* Rosscoe and Barrick, p. 128, pl. 3, figs. 2-6, 11.
2009a	*Idiognathodus sulciferus harkeyi* Rosscoe and Barrick, p. 128-129, pl. 3, figs. 1, 7-10.

Diagnosis: A species with an asymmetric pair of triangular P_1 elements. The sinistral P_1 element has ventrally robust moderately restricted rostral lobe, whereas the dextral P_1 element has more restricted rostral lobe.

Description: The overall shape of the platform is triangular. The P1 element is ornamented with complete transverse ridges that are disrupted on the caudal side of the platform. The adcarinal ridges are very short. Both the rostral and caudal adcarinal ridges terminate at the same position along the dorsal portion of the blade. The caudal adcarinal ridge merges with the nodose margin, separating the caudal lobe from the transverse ridges of the central platform. The rostral adcarinal ridge truncates at the first transverse ridge. The remainder of the margin between the rostral lobe and the central platform is marked by the rostral truncation of the transverse ridges. The medial carina is short and is truncated by the first transverse ridge.

The platform of the sinistral P_1 element forms a triangular, almost arrowhead shape. The dorsal margin of the platform is pointed. The caudal lobe is normal in shape, but reduced in overall size from the normal lobes of similar-sized species. The rostral lobe is moderately restricted with only one or two nodes forming the dorsal-most expansion of the lobe beyond the first transverse ridge.

The platform of the dextral P_1 element has a robust and ornamented caudal lobe with discrete hemispherical nodes. In some cases, these nodes may be partially fused or even ridge-like. The rostral lobe is moderately restricted and ornamented with well-defined nodes.

Remarks: *Idiognathodus harkeyi* can be recognized as distinct from *I. sulciferus* because of the much more restricted rostral lobes in *I. harkeyi*. While moderately restricted, the lobes of *I. harkeyi* extend only beyond one transverse ridge. The overall triangular shape of *I. harkeyi* is also distinctive when compared to the more shovel-like shape of *I. sulciferus*. *Idiognathodus swadei* can be distinguished readily by its expanded rostral lobe and the overall robust size of the accessory lobes.

The asymmetry between sinistral and dextral P_1 elements is primarily recognized in that the sinistral elements appear to be narrower while dextral elements appear to be wider. This is the first recognition of asymmetric pairs in species of *Idiognathodus* in this time interval. The subsequent asymmetric species *I. magnificus* is likely a descendent of *I. harkeyi*. Several variations occur within the species through time. Ventral deflection of transverse ridges and even a weak eccentric disruption are common in specimens found from the Exline Limestone and higher, whereas the ridges are continuous in lower strata. The caudal lobe protrudes at a very sharp angle along its dorsal margin, appearing as almost ninety degrees is some early specimens. In specimens from stratigraphically higher units, the lobe margins are also more rounded.

Occurrence: Checkerboard, Exline, Hertha limestones (Rosscoe and Barrick 2009a), and Hushpuckney Shale of the Midcontinent Basin; Lower Brush Creek Shale of the Appalachian Basin.

Idiognathodus heckeli n. sp.
Fig. 7f, g, j-l, n-p

2009a	*Idiognathodus turbatus* n. sp. - Rosscoe and Barrick, p. 142, pl. 4, figs. 3, 4, 5, 11 (only).
2009b	*Idiognathodus swadei* n. ssp. 1 - Rosscoe and Barrick, p.22, figs. 1.3, 1.4.

Diagnosis: P_1 element with an expanded rostral lobe and a well-defined, complete caudal eccentric groove that runs from the ventral margin to the dorsal tip of the element.

Description: The P_1 element is broad along the rostro-caudal axis due to the well-developed accessory lobes. The platform is ornamented with transverse ridges that are cut by a caudal eccentric groove to the dorsal tip of the platform. The dorsal tip is typically pointed to subrounded in shape. The caudal accessory lobe is well developed and rounded. It is ornamented with discrete hemispherical nodes. The rostral accessory lobe is expanded and robust, extending between one-half and three-quarters the length of the platform. The rostral lobe is ornamented with evenly spaced hemispherical nodes.

The rostral adcarinal ridge is short and low in elevation, whereas the caudal adcarinal ridge is ventrally extended and flares away from the blade. In most specimens the caudal adcarinal ridge is the highest elevation feature on the platform. Some ornamental nodes on the caudal lobe may become partially fused with the platform extension of the caudal adcarinal ridge. The medial carina is short, and does not extend beyond the ventral margin of the element.

Remarks: *Idiognathodus heckeli* has a complete eccentric groove, which distinguishes it from other members of the *I. swadei* lineage. *Idiognathodus eccentricus* has a restricted rostral lobe, unlike the expanded rostral lobe of *I. heckeli*. Specimens of *I. heckeli* were originally included in *I. turbatus* by Rosscoe and Barrick (2009a), and later designated as a subspecies of *I. swadei* by Rosscoe and Barrick (2009b). As in the case of *I. eccentricus* the development of a complete eccentric groove is considered to be species level in *I. heckeli*.

Type Specimen: SUI 108263 (Rosscoe and Barrick, 2009a, pl. 4, fig. 4). Exline Limestone, Road cut along east side of US Highway 69, NW-NW-SW sec. 19, T. 22 S., R. 25 E., south of Pleasanton, Linn County, Kansas (Heckel and Watney, 2002, figs. 7, 8).

Etymology: Named in honor of Philip H. Heckel, for his tireless pursuit of global correlation of Pennsylvanian cyclothems, the use of conodonts to effect local to global Pennsylvanian correlations, and his work on the Moscovian-Kasimovian Stage Boundary.

Occurrence: Specimens of *Idiognathodus heckeli* occur in the Exline and Hertha limestones (Rosscoe and Barrick, 2009a, 2009b), and the Hushpuckney Shale in the Midcontinent Basin; the Lower Brush Creek Shale of the Appalachian Basin

Idiognathodus neverovensis (Goreva and Alekseev, 2006)
Fig. 5e, f, k, l, n

2006	*Streptognathodus neverovensis* n. sp. - Goreva and Alekseev, p. 195-196, pl. 10, figs. 1-6 (see for further synonymy).
2009	*Streptognathodus neverovensis* Goreva and Alekseev - Goreva et al., p. 107, figs. 6G, 6H, 6J, 6K.
2012	*Idiognathodus* cf. *cancellosus* - Heckel et al., p. 263, pl. 1, figs. 19, 21, 23.

Diagnosis: P_1 element lacks both rostral and caudal accessory lobes and an elongate medial carina separates elevated ridged margins.

Description: The P_1 element is narrow and elongate. The plat-

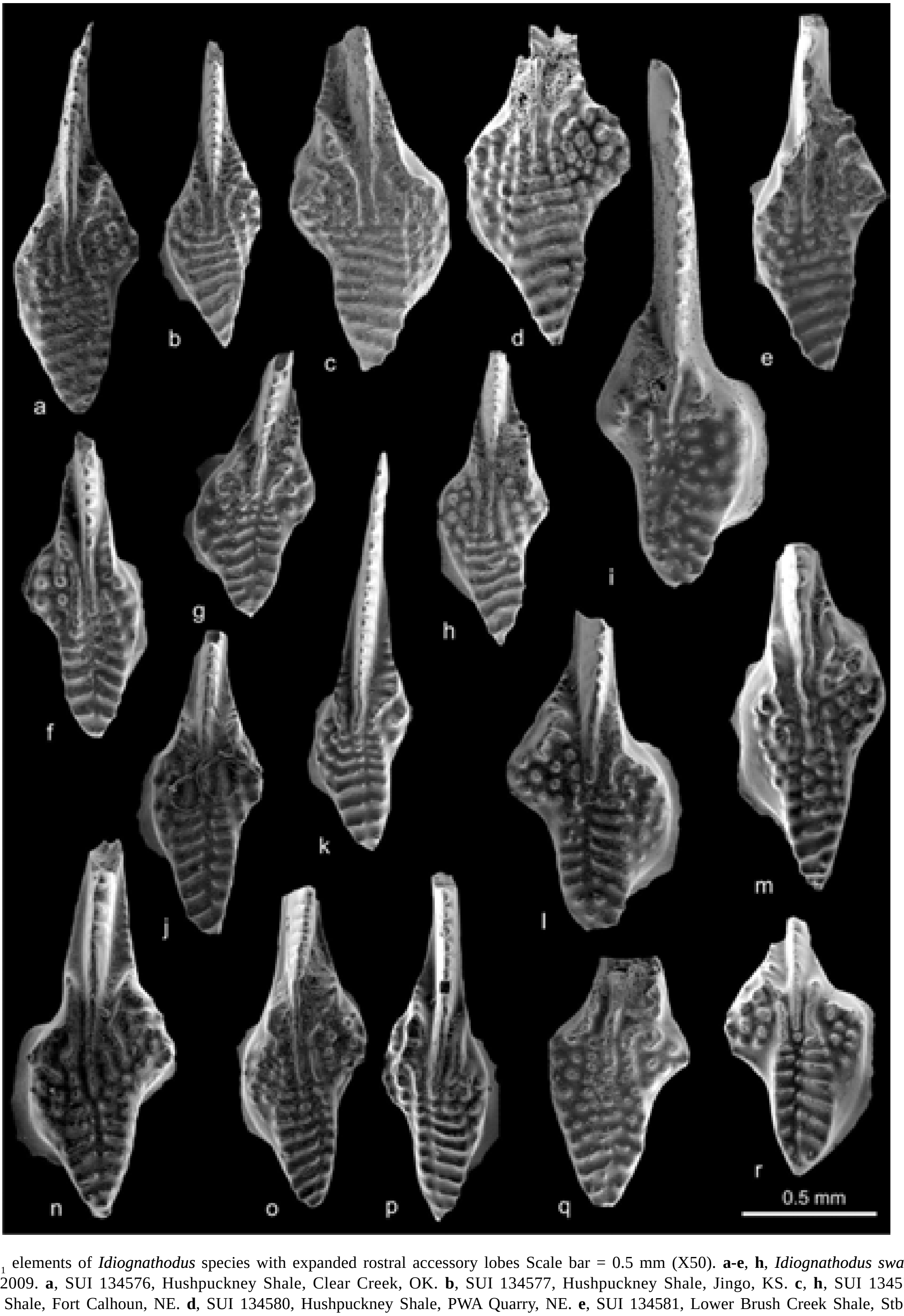

FIGURE 7. P_1 elements of *Idiognathodus* species with expanded rostral accessory lobes Scale bar = 0.5 mm (X50). **a-e**, **h**, *Idiognathodus swadei* Rosscoe and Barrick, 2009. **a**, SUI 134576, Hushpuckney Shale, Clear Creek, OK. **b**, SUI 134577, Hushpuckney Shale, Jingo, KS. **c**, **h**, SUI 134578, 134579, Hushpuckney Shale, Fort Calhoun, NE. **d**, SUI 134580, Hushpuckney Shale, PWA Quarry, NE. **e**, SUI 134581, Lower Brush Creek Shale, Stb1, WV. **f**, **g**, **j-l**, **n-p**, *Idiognathodus heckeli* n. sp. **f**, **k**, SUI 134582, 134583, Hushpuckney Shale, Fort Calhoun, NE. **g**, SUI 134584, Hushpuckney Shale, Jingo, KS. **j**, **n**, SUI 134585, 134586, Hushpuckney Shale, Mason, OK. **l**, SUI 134587, Hushpuckney Shale, Clear Creek, OK. **o**, SUI 131092, Lower Brush Creek Shale, Stb1, WV. **p**, SUI 134588, Lower Brush Creek Shale, Cmb1, OH. **i**, **m**, **q**, *Idiognathodus papulatus* n. sp. **i**, SUI 134589, Hushpuckney Shale, Fort Calhoun, NE. **m**, SUI 131094, Lower Brush Creek Shale, Cmb1, OH. **q**, SUI 134590, Hushpuckney Shale, Mason, OK. **r**, *Idiognathodus turbatus* Rosscoe and Barrick, 2009. **r**, SUI 134591, Hushpuckney Shale, East Peru, IA.

form lacks both caudal and rostral accessory lobes. The crenulated margins of the platform are formed by the transverse ridges that ornament the high margins of the platform. Deep adcarinal grooves separate the elongate medial carina from the ridged platform margins. The medial carina extends at least one half the length of the platform and nears but does not reach the dorsal tip of the platform with a row of medial nodes. The adcarinal ridges are ornamented with short transverse ridges and merge directly with the lobe-less margins of the platform.

Remarks: *Idiognathodus neverovensis* is easy to distinguish from similar species because of the combination of its ridged margins and medial carina with trailing medial nodosity. *Idiognathodus biliratus* has a nodose margin rather than a ridged margin. *Idiognathodus pseudocarinatus* has a distinctive row of medial transverse ridges. All other species in this study have accessory lobes that readily distinguish them from *I. neverovensis*.

As originally defined by Goreva and Alekseev (2006) *Idiognathodus neverovensis* belonged to the genus *Streptognathodus*. The diagnostic character of *Streptognathodus* is a deeply troughed platform. While the medial groove filled with medial carina and elevated platform margins gives the impression of a troughed platform, the platform is flat. All relief is an effect of ornamentation. As the platform is flat, the better fit is within the genus *Idiognathodus*.

Occurrence: The Hushpuckney Shale of the Midcontinent Basin and the Lower Brush Creek Shale of the Appalachian Basin.

Idiognathodus papulatus n. sp.
Fig. 7i, m, q

2009a *Idiognathodus turbatus* n. sp. - Rosscoe and Barrick, pl. 4, fig. 9 (only).

2009b *Idiognathodus* n. sp. Z – Rosscoe and Barrick, p. 21, fig. 1.7.

Diagnosis: P_1 element with expanded rostral lobes and robust caudal lobes in which a majority of the ventral platform is nodose.

Description: The P_1 element is nearly equal in width and length where the accessory lobes are most pronounced. The platform has only a few transverse ridges present near the dorsal margin, however they are not continuous across the platform. The central and ventral portions of the platform are chaotically ornamented with a mixture of discrete nodes, partially fused nodes, and short truncated transverse ridges along the rostral margin. The caudal accessory lobe is well developed, with a semi-pointed to rounded margin. In most specimens ornamentation of the caudal lobe is with numerous hemispherical nodes. The rostral accessory lobe is elongate and ornamented with a single row of nodes along most of its length. The ventral portion of the rostral lobe is wide enough to be ornamented by two rows of nodes.

The adcarinal ridges are short and do not extend dorsally onto the platform. Both adcarinal ridges merge with the interior margins of their respective accessory lobes. The medial carina is short, truncating almost immediately upon merging with the platform. Medial nodes are difficult to distinguish on the ventral platform due to the high number of nodes ornamenting the platform.

Remarks: *Idiognathodus papulatus* was originally included within the broad definition of *I. turbatus* in Rosscoe and Barrick (2009a). Rosscoe and Barrick (2009b) later restricted the definition *I. turbatus* to only those specimens with medial nodosity and assigned the heavily nodose forms to *I.* species Z, which are now included in *I. papulatus*. *Idiognathodus papulatus* can be distinguished from other highly nodose species because of the expanded rostral lobe and normal caudal lobe. *Idiognathodus cancellosus* has reduced rostral and caudal lobes. *Idiognathodus clavatulus* has a reduced elongate rostral lobe. *Idiognathodus vorax* has a rostral lobe that is robust and elongate extending the entire length of the platform.

Type Specimen: SUI 134590, Figure 7q from the Hushpuckney Shale at the Mason, Oklahoma section of the Midcontinent Basin

Etymology: Named using the Latin word "*papula*" meaning pimple or pustule. The name reflects the pimple-like ornamentation of the ventral platform with nodes of varying size.

Occurrence: The Hushpuckney Shale of the Midcontinent Basin and the Lower Brush Creek Shale of the Appalachian Basin.

Idiognathodus pseudocarinatus n. sp.
Fig. 5i, j, o, p

2012 *Idiognathodus* cf. *cancellosus* Heckel et al., p. 263, pl. 1, figs. 14, 16, 22, 29, 30.

Diagnosis: P_1 element with two adcarinal grooves separating the platform into three distinct transverse ridged regions; a rostral marginal region, a caudal marginal region, and a central region mimicking medial nodes.

Description: The P_1 element has a triangular shape in outline. The margins of the platform are slightly elevated above the central platform. Rostral and caudal lobes are essentially absent. At the merger between the caudal and rostral adcarinal ridges with their respective margins there is a slight lobe formed giving room for a few nodes commonly merged with the adcarinal ridges. The caudal adcarinal ridge is highly elevated compared to the rest of the element and extends further in the ventral direction than the caudal adcarinal ridge. The platform is ornamented with transverse ridges that are disrupted twice by eccentric grooves extended across the length of the platform from adcarinal grooves. The result of this disruption is broad platform margins ornamented with laterally short transverse ridges separated from a flat central platform ornamented with truncated transverse ridges in line with those on the margins.

Remarks: *Idiognathodus pseudocarinatus* is readily distinguished from all species in this study because of the unique presence of two grooves on the platform. *Idiognathodus biliratus*, and *I. neverovensis* are similar, but have either a row of medial nodes or a medial carina down the center of the platform, where *I. pseudocarinatus* has a row of truncated transverse ridges. Species like *I. cancellosus* and *I. clavatulus* are readily distinguished owing to their distinctive accessory lobes, whereas *I. pseudocarinatus* has none.

Type Specimen: SUI 134552, Figure 5j, from the Hushpuckney Shale at Clear Creek, Oklahoma.

Etymology: Named using the Latin word "*carina*" meaning keel or ridge. The name reflects the mimicry of a true medial carina through groove truncated transverse ridges along the medial axis of the platform.

Occurrence: The Hushpuckney Shale in the Midcontinent Basin and the Lower Brush Creek Shale of the Appalachian Basin.

Idiognathodus sulciferus Gunnell, 1933
Fig. 6o, q, r, t, u

1933 *Idiognathodus sulciferus* n. sp. - Gunnell, p. 271, pl. 31, fig. 16.

1933 *Idiognathodus chiriformis* n. sp. - Gunnell, p. 272, pl. 31, fig. 23.

1989 *Idiognathodus sulciferus* Gunnell - Barrick and Boardman, p. 185, pl. 1, figs. 9, 23, 24.

1999 *Idiognathodus sulciferus* Gunnell - Barrick and Walsh, p. 154, fig. 6.1 (reillustration of holotype).

2002 *Idiognathodus sulciferus* Gunnell - Ritter et al., p. 508, fig. 8.25.

2003 *Idiognathodus magnificus* Stauffer and Plummer – Wang and Qi, p. 395, pl. 4, fig. 23.

2004 *Idiognathodus sulciferus* Gunnell - Barrick et al., p. 241, pl. 4, fig. 13 (reillustration of holotype);

2009a *Idiognathodus sulciferus sulciferus* Gunnell - Rosscoe and Barrick, p. 139, pl. 3, figs. 12-17.

Diagnosis: P_1 element with a moderately restricted, continuous rostral lobe, normal caudal lobe and a platform ornamented with com-

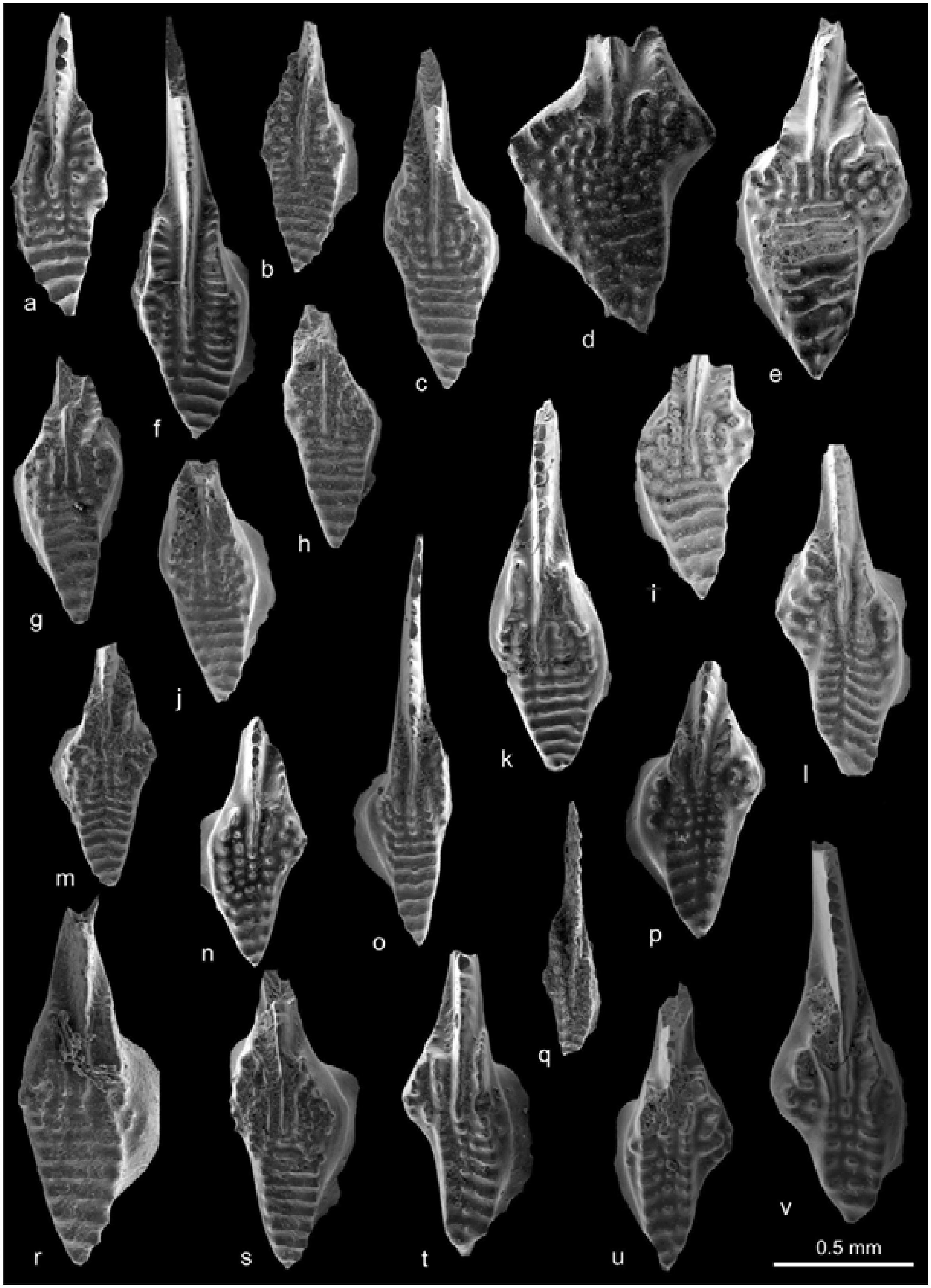

FIGURE 8. P_1 elements of *Idiognathodus* species with robust rostral accessory lobes. Scale bar = 0.5 mm (X50). **a-c**, **f-h**, **j**, **k**, **m-o**, **q-s**, *Idiognathodus gemmiformis* Gunnell 1933. **a**, SUI 134592, Hushpuckney Shale, Fort Calhoun, NE. **b**, **f**, SUI 134593, 134594, Hushpuckney Shale, Clear Creek, OK. **c**, **g**, **h**, **j**, **m**, **o**, **s**, SUI 134595-134601, Hushpuckney Shale, Jingo, KS. **k**, SUI 134602, Lower Brush Creek Shale, Cmb1, OH. **n**, SUI 131086, Lower Brush Creek Shale, Pgh5, PA. **q**, **r**, SUI 134603, 134604, Hushpuckney Shale, Mason, OK. **d**, **e**, **i**, *Idiognathodus vorax* Rosscoe and Barrick 2009. **d**, SUI 134605, Hushpuckney Shale, Fort Calhoun, NE. **e**, **i**, SUI 134606, 134607, PWA Quarry, NE. **l**, **p**, **t-v**, *Idiognathodus clavatulus* Gunnell 1933. **l**, SUI 134608, Hushpuckney Shale, PWA Quarry, NE. **p**, SUI 134609, Hushpuckney Shale, Mason, OK. **t**, SUI 134610, Hushpuckney Shale, Clear Creek, OK. **u**, **v**, SUI 134611, 134612, Hushpuckney Shale, Jingo, KS.

plete transverse ridges that exhibit minor caudal deflection in the ventral direction.

Description: The platform of the P_1 element is ornamented with complete transverse ridges. The transverse ridges are deflected ventrally along the medial axis in some specimens. The dorsal platform margin is subrounded in shape. The caudal accessory lobe is normal in shape and ornamented with large discrete nodes. In smaller specimens, the caudal lobe is more reduced in shape. The rostral lobe is moderately expanded, but is not robust, and does not protrude from the ventral margin of the element. The rostral lobe is ornamented by discrete nodes that lose some definition at the margin of the lobe.

The adcarinal ridges are moderate in length, with the caudal adcarinal ridge extending further in the ventral direction than the rostral adcarinal ridge. The caudal adcarinal ridge merges with the margin separating the caudal lobe from the central platform. The rostral adcarinal ridge forms a ventral ridge on the ventral margin of the rostral lobe. The medial carina does not extend beyond one-quarter the length of the platform.

Remarks: *Idiognathodus sulciferus* is one of the first species to be derived following the Late Desmoinesian extinction. It is closely related to and co-occurs with *I. swadei*, *I. harkeyi*, *I. eccentricus*, and *I. corrugatus*. *Idiognathodus swadei* has an expanded rostral lobe that distinguishes it from *I. sulciferus*. *Idiognathodus eccentricus* has a restricted rostral lobe and a caudal eccentric groove that distinguishes it from *I. sulciferus*. *Idiognathodus corrugatus* does not have rostral lobe. *Idiognathodus harkeyi* has more restricted rostral lobes that are more robust and protruding than the continuous rostral lobe of *I. sulciferus*.

Occurrence: The Checkerboard, Exline, and Hertha limestones (Rosscoe and Barrick, 2009a, 2009b), and the Hushpuckney Shale of the Midcontinent Basin.

Idiognathodus swadei Rosscoe and Barrick, 2009a
Fig. 7a-e, h

1941 *Idiognathodus delicatus* Gunnell - Ellison, pl. 22, fig. 35 (only).
1985 *Idiognathodus* species 1 - Swade, p. 55, figs. 18.4, 18.5, 18.11 (only).
1989 *Idiognathodus clavatulus* (Gunnell) - Barrick and Boardman, p. 185, pl. 1, fig. 14.
1989 *Idiognathodus lobatus* Gunnell - Barrick and Boardman, p. 185, pl. 1, fig. 23.
2002 *Idiognathodus* sp. - Méndez, pl. 2, fig. 5.
2002 *Idiognathodus sulciferus* Gunnell - Ritter et al., p. 508, figs. 8.8, 8.24.
2006 *Idiognathodus* sp. - Méndez, p. 250, fig. 5.5.
2009a *Idiognathodus swadei* n. sp. - Rosscoe and Barrick, p. 138, pl. 2, figs. 1-18.
2009b *Idiognathodus swadei* Rosscoe and Barrick - Rosscoe and Barrick, p. 22, figs. 1.1, 1.2.
2012 *Idiognathodus swadei* Rosscoe and Barrick - Heckel et al., p. 263, pl. 1, figs. 25, 26, 28.

Diagnosis: P_1 element with an expanded and highly developed rostral accessory lobe that is ornamented with discrete hemispherical nodes and is at the same level as the platform surface.

Description: The P_1 element is longitudinally arched and transversely flat. The rostral lobe is elongate with the rostro-caudal extent of the lobe reaching a maximum of half the dorso-ventral dimension. In mature specimens the rostral lobe is ornamented with two to three rows of discrete, hemispherical nodes. The caudal lobe shows the greatest development in the rostro-caudal direction. The dorsal extent of the caudal lobe is typically one half the length of the platform with rostro-caudal extent of the lobe reaching nearly the same length. The caudal lobe is a protruding, slightly triangular feature, decorated with discrete nodes aligned with the curvature of the caudal adcarinal ridge. The dorsal platform is crossed by coarse transverse ridges that are deflected in the ventral direction or disrupted in alignment with the caudal adcarinal groove.

Adcarinal ridges are equal in length to the medial carina, extending one-quarter to one-third the length of the platform. Adcarinal ridges form a short, slightly flared collar around the dorsal blade. The constriction of the adcarinal ridges around the medial carina is tight, leaving a very shallow adcarinal groove that in most cases is the same elevation of the surrounding platform. The adcarinal ridges typically form a fused ridge ending ventrally with a few discrete nodes at an elevation no higher than the surrounding platform ornamentation.

Remarks: *Idiognathodus swadei* can be distinguished from all other idiognathodid conodonts in the study interval by its flat undisrupted dorsal platform ornamented with transverse ridges and its protruding rostral lobe. *Idiognathodus swadei* can be distinguished from *I. turbatus* by the presence of medial nodosity and a shallow trough in *I. turbatus*. Specimens of *I. sagittalis* that exhibit weak medial nodosity can be confused with *I. swadei*. *Idiognathodus swadei* has a more dorsally elongate rostral lobe than *I. sagittalis*. The rostral lobe of *I. swadei* is at the same elevation as the main body of the platform as opposed to the lower elevation discretely bounded rostral lobe of *I. sagittalis*.

Idiognathodus swadei is the only member of the genus that survives the Late Desmoinesian extinction in the Midcontinent region. Juvenile elements that show both rostral and caudal lobes, slight troughing and a long medial carina, are the only juvenile forms encountered immediately above the extinction level. All early Missourian forms of *Idiognathodus* in the Midcontinent region are derived from *I. swadei*.

Occurrence: Lost Branch Formation, Checkerboard, Exline, and Hertha limestones (Rosscoe and Barrick, 2009a and 2009b), and the Hushpuckney Shale of the Midcontinent Basin; the Lower Brush Creek Shale of the Appalachian Basin.

Idiognathodus turbatus Rosscoe and Barrick, 2009a
Fig. 7r

1941 *Idiognathodus claviformis* Gunnell - Ellison, pl. 23, fig. 14 (only).
1989 *Idiognathodus sagittalis* Kozitskaya - Barrick and Boardman, 1989, p. 185, pl. 1, figs. 10, 14.
2002 *Idiognathodus* species A of Barrick et al., 1996 - Ritter, et al., p. 508, fig. 8.10-8.12, 8.15, 8.20.
2003 *Idiognathodus cancellosus* (Gunnell) – Wang and Qi, p. 395, pl. 4, fig. 21.
2004 *Idiognathodus* species A of Barrick et al., 1996 - Barrick et al., p. 241, pl. 4, fig. 11.
2007 *Idiognathodus sagittalis* Kozitskaya – Wang and Qi, pl. 1, fig. 7.
2009a *Idiognathodus turbatus* n. sp. - Rosscoe and Barrick, p. 142, pl. 4, figs. 1, 2, 5-8, 11-15 (only).
2009b *Idiognathodus turbatus* Rosscoe and Barrick - Rosscoe and Barrick, p. 22, figs. 1.5, 1.6.
2009 *Idiognathodus turbatus* Rosscoe and Barrick - Goreva et al., p. 107, fig. 6L.

Diagnosis: P_1 element with a robust and protruding expanded rostral accessory lobe (at the same level as the platform surface) and a ventral platform with medial nodosity and shallow medial trough.

Description: The platform of the P_1 element is flat with a slight troughing along the medial axis. Most specimens exhibit a weak eccentric groove to the caudal side of a medial node row extending almost to the dorsal tip of the element. The dorsal tip ranges from pointed to subrounded. Both the caudal and rostral lobes are extremely well developed and ornamented with discrete hemispherical nodes. The caudal lobe is ornamented in a concentric pattern around the center of the lobe. The rostral lobe is longer in the dorsal direction than in the rostral direction. In large specimens, where the protruding rostral lobe is especially robust, the ornamentation forms as rays of nodes that begin aligned with a transverse ridge and curve ventrally to the ventral margin of the element.

The adcarinal ridges are longer than most of the ridges seen in other species of the study interval. The caudal adcarinal ridge can be twice as long as the rostral adcarinal ridge. On the platform both adcarinal ridges and the medial carina form a series of dorso-ventrally aligned low-elevation ridges. The caudal adcarinal ridge flares off the platform. The caudal margin of the element sits at a slightly higher elevation than the rostral margin due to the flaring, high-elevation caudal adcarinal ridge.

Remarks: *Idiognathodus turbatus* has medial nodosity by which it can be distinguished from *I. swadei*. *Idiognathodus turbatus* can be distinguished from *I. vorax* by the shorter and more protruding rostral lobe of *I. turbatus*. *Idiognathodus turbatus* is close in appearance to the Eurasian conodont *I. sagittalis*, but can be distinguished by the relationship of the rostral lobe to the central platform. In *I. sagittalis*, the central platform is distinctively separated from the lower elevation rostral lobe. In *I. turbatus*, the central platform and rostral lobe are not distinctively separate and are equal in elevation. *Idiognathodus* species A of Barrick et al. (1996) is included in this species as it represents those specimens with the most clearly defined medial nodosity.

Occurrence: The Hertha Limestone (Rosscoe and Barrick, 2009a, 2009b) and the Hushpuckney Shale of the Midcontinent Basin.

Idiognathodus vorax Rosscoe and Barrick, 2009a
Fig. 8d, e, i

2009a *Idiognathodus vorax* n. sp. - Rosscoe and Barrick, p. 145, pl. 5, figs. 1, 3, 4.

Remarks: For a complete synonymy, diagnosis, description, and discussion, see Rosscoe and Barrick (2009a).

Occurrence: The Hertha Limestone (Rosscoe and Barrick, 2009a) and the Hushpuckney Shale of the Midcontinent Basin.

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APPENDIX – LOCALITIES

Additional information about Hushpuckney Shale localities in Kansas, Oklahoma, and Nebraska can be found in Rosscoe (2008). Lower Brush Creek localities in Ohio and Pennsylvanian are discussed in Heckel et al. (2012).

HUSHPUCKNEY SHALE

East Peru: Road cut east of East Peru, Madison County, Iowa, 41º13.560’N; 93º54.750’W.

Jingo, KS: Road cut along US Highway 69 near Jingo, Miami County, Kansas, 38º25.968’N; 94º41.122’W.

Clear Creek, OK: Bank of Clear Creek on the bend south of the EW145 crossing, southwest of Sasakwa, Seminole County, Oklahoma, 34º55.546’N; 96º34.894’W.

Mason, OK: Stream cut on Buckeye Creek adjacent to Mason Road, Okfuskee County, Oklahoma, 35º33.963’N; 96º17.300’W.

Fort Calhoun, NE: Fort Calhoun Quarry, Washington County, Nebraska, 41º27.654’N; 96º00.773’W.

PWA, NE: Richfield PWA Quarry, Sarpy County, Nebraska, 41º04.250’N; 96º04.850’W.

LOWER BRUSH CREEK

Ath2: Exposure near foot of bluff just north of Gibson Road, just east of junction with Ohio Route 56, ~0.4 mile south of intersection with Route 682, southwest of Whites Mill, Ohio.

Cmb1: Road cut along southeast side, near northeast end of exit ramp from northbound I-77 onto eastbound I-70, ~2.5 miles southeast of Cambridge, Guernsey County, Ohio.

Pgh5: Small pit north of US Route 22, just east of Allegheny-Westmoreland County line on west side of Murrysville, east of Pittsburgh, Pennsylvania.

Stb2: Railroad cut on south side of Weirton, ~0.5 mile southwest of southbound WV Route 2 onramp to US Route 22 west, in Brooke County, West Virginia.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

NONMARINE-MARINE CORRELATION OF EUROPEAN AND NORTH AMERICAN LATE CARBONIFEROUS AND EARLY PERMIAN DEPOSITS

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The spiloblattinid insect zonation combined and cross-correlated with the branchiosaurid amphibian zonation of the European, North American and North African Late Carboniferous and Early Permian has delivered so far a very applicable and reliable tool for the correlation of nonmarine deposits in the numerous continental basins of this time in this area. Links to the global marine scale were thus far based on rare and ambiguous isotopic ages only. Here, for the first time, five co-occurrences of spiloblattinid zone species with marine index fossils in North America and the East European Donets basin are used for the construction of a robust biostratigraphical framework for the direct correlation of continental deposits to the Late Pennsylvanian (Kasimovian and Ghzelian) up to the Early Permian (Asselian). This correlation indicates that the base of the Central European regional stage Stephanian is the earliest Kasimovian, the Stephanian B straddles the Late Kasimovian to Early Gzhelian, and the Stephanian C ranges from about the middle to later Gzhelian. The top of the Stephanian (or the base of the lithostratigraphical Rotliegend) is tentatively set at 300 Ma in the Late Gzhelian. The base of the Rotliegend is marked by the base of the *Sysciophlebia ilfeldensis* zone and slightly higher base of the *Apateon dracyiensis-Melanerpeton sembachense* amphibian zone. The *Sysciophlebia ilfeldensis* zone stretches across the Ghzelian/Asselian boundary, which is supported by an occurrence in New Mexico in *Streptognathodus nevaensis* conodont zone, which is early to middle Asselian in age. The West European regional stages can be redefined by insect zone fossils for the here proposed Hermundurian (replacing the interminable and confusing Autunian) and the Saxonian, and by conodonts for the Thuringian. Future syntheses of insect zones with land-vertebrate faunachrons, as well as conchostracan and tetrapod track biostratigraphy will extend the combined marine nonmarine biostratigraphy up to the Permian/Triassic boundary.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

THE PALEOENVIRONMENT AT THE TRANSITION FROM PISCINE TO TETRAPOD SARCOPTERYGIANS

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Abstract—The transition from piscine to tetrapod sarcopterygians is now accepted to have occurred in a coastal margin environment. For most of the last century, a transition in a freshwater paleoenvironment was proposed and accepted. An origin in a freshwater paleoenvironment cannot be explained physiologically as has been shown 50 years ago by comparison with extant fishes. Like the piscine sarcopterygians the first tetrapods were living in a coastal marine to brackish environment. Thus arises the question, when did the early tetrapods lose the tolerance to a salty marine environment? Mapping of paleoecologies on a cladistic analysis may be the way to approach the problem. It has been shown that that was the prior way to reach the conclusion that the fish/tetrapod transition in the Devonian occurred in a coastal marine environment. Many Carboniferous tetrapods may have been salt water tolerant, including the earliest amniotes, as now demonstrated by the reinterpretation of Joggins as deposits in a coastal marine environment.

INTRODUCTION

The transition of vertebrates from aquatic to terrestrial environment, the origin of tetrapods, is a major event in the evolution of vertebrates. Thus there are multiple publications on the subject. These repeat – since Barrell (1916) – the idea that the development of legs was favored in a freshwater environment where these transitional sarcopterygians could leave a drying-out pond to reach another pond. This idea was propounded by Romer (1933, 1945, 1966), even though it had been shown that this is physiologically impossible (Inger, 1957). There are also good extant examples, which show the transition in a coastal marine environment (e.g., Harms, 1929, 1935; Eggert, 1929). Recently, fossil evidence (trackways) has been used to argue for a transition in a marine environment (Niedzwiedzki et al., 2010, George and Blieck, 2011). Clack (2012, p. 132) admits the possibility of a coastal environment based on the worldwide distribution of early tetrapods. I will assemble arguments in the first part of this paper to show that the origin of tetrapods occurred most likely in a coastal marine environment (Schultze, 1997).

As for the origin of tetrapods in the Devonian, a freshwater paleoenvironment is favored for tetrapods in the Carboniferous and Permian especially for the occurrences in Europe (e.g., Boy, 1994; Clausing and Boy, 2000; Boy and Schindler, 2000; Lucas, 2006; Roscher and Schneider, 2006; Štamberg, 2006; Schoch, 2009; and many others). Marine indicators are denied. I will try to show that these are valid, and that tetrapods are salt water tolerant in the Permo-Carboniferous (Laurin and Soler-Gijón, 2001; Schultze and Soler-Gijón, 2004; Laurin and Soler-Gijón, 2010; Laurin, 2010).

STARTING REMARKS

An aquatic paleoenvironment can only be deduced from animals or plants, which lived in that environment; that means aquatic forms. Terrestrial forms (most tetrapods, insects, most plants) cannot be used to identify an aquatic environment; also, the lack of any forms cannot be used to indicate an environment (for a more detailed discussion see Cunningham et al., 1993; Schultze, 1996; Boy, 2003). The occurrence of terrestrial forms may show that they lived close by, but wind or other transport possibilities have to be considered. A difficulty to characterize Paleozoic environments is the lack of clear freshwater indicators (Schultze, 2009). Freshwater indicators (see Gray, 1988 and the discard of the criteria by Schultze, 1996, 2009) are proposed often on present day environmental preference of related animals. One has to take into consideration that there is a time lag between today and the Carboniferous and Devonian of more than 300 million years, so that the current environmental preference of an animal or plant is not the same as 300 million years ago. A better indicator is the environmental preference of closely related contemporaneous forms.

Another argument often used is the lack of marine shelly fossils to support a freshwater environment. Lack of anything does not prove anything. In addition there is the observation that phosphatic and chitinous remains occur often together with plant remains. I do not know any explanation for this chemical preference in diagenetic processes, but the absence of calcitic fossils in connection with phosphatic and chitinous fossils can be observed frequently.

Sedimentological arguments depend on the size of the water body, in which the sediments are deposited, and not primarily from the chemistry of the water. In addition there is little difference between river deposits in the lowlands and those in the intertidal zone (Reineck and Singh, 1973). It is surprising that the intertidal zone (e.g., Kvale et al., 1999) is omitted in the comparison to the extent that clear intertidal markers like couplet-lamination are interpreted as unique freshwater indicators (Lojka et al., 2010). Rootlets, often used to argue for soil formation, are also typically found in intertidal and supratidal environments (DiMichele and Falcon-Lang, 2011; Archer and Greb, 2012).

Chemical analyses may help to identify a paleoenvironment. Whereas chemical analysis of sediments may give ambiguous results, the content of rare elements in phosphatic skeletal parts, preferably enamel, can give more reliable indications (e.g. Schmitz et al., 1991; Matton et al., 2012).

I prefer faunal comparisons of aquatic forms – in most cases fishes – to identify an environment (see also Lebedev, 2004) because I had the best experiences with it. For example, the Upper Devonian locality Miguasha, which was interpreted as a freshwater environment (Dineley and Williams, 1968), contrary to my interpretation as marine based on faunal comparisons (Schultze, 1972; Schultze and Arsenault, 1985; Schultze and Cloutier, 1996), is now accepted as coastal marine based on different data (see Cloutier et al., 1996). Upper Carboniferous localities in Kansas have been shown to be coastal marine (Sawin et al., 1985; Schultze, 1996); some localities in Nova Scotia (Sydney basin: Wightman et al., 1994; Archer et al.,1995; Joggins: Falcon-Lang et al., 2006) have been shown to be coastal marine. Of course one has to take into consideration that fishes migrate, enter estuaries and fluvial environments and vice-versa. Nevertheless, geographically widely distributed fishes need to use a marine route and thus represent an indication that there is a connection of the specific locality to the marine environment.

Plant fossils may indicate closeness of land. Often fossil plants are fractioned in small pieces in coastal deposits, whereas they could be excellently preserved in farther distant localities, where they are imbedded in quietly deposited sediments like in the deep sea in front of the Orinoco delta or in tidal influenced areas (Scheihing and Pfefferkorn, 1984). Recently Falcon-Lang (2005) described Carboniferous trees growing in a coastal marine environment; that was accepted earlier only for angiosperms like mangroves, even though plants had conquered the terrestrial realm only in the Late Silurian and Early Devonian so that one can expect saltwater tolerance.

In this paper I will rely on two criteria to interpret the paleoenvironment:

1. Tidal marks in the sediments, but much more important the evidence of tidal cyclicity in the growth marks preserved in skeletal hard tissues.
2. Comparison with the environment of contemporaneous forms.

PALEOENVIRONMENT AT THE TRANSITION

Freshwater Origin

Devonian Fossil Beds

The origin of tetrapods is connected with and mostly presented as a freshwater event. To say it bluntly: The fish developed the legs to get from a drying pool to the next pool. That was based on the idea that the Devonian red beds are freshwater deposits of a dry and hot climate (Barrell, 1916; Romer, 1933, 1945, 1958, 1966).

Problems: There are problems with that interpretation:

1. There are no invertebrate fossils indicating freshwater environment together with Devonian fossil fish. We find occasionally ichnofossils, traces of trilobites, which are indicative of marine environment (Goujet, 1984).
2. The fish fauna of the Old Red Sandstone is similar and often identical with contemporary marine fish faunas (e.g. Blieck, 1985; Mark-Kurik, 1991).
3. It has long been shown that extant fishes never leave a drying pond because outside it is even drier, and they would die immediately. Extant fish move from one water body to another in a wet environment only (Inger, 1957).

Example: Miguasha/*Eusthenopteron*/elpistostegids – Until the 1980s, *Eusthenopteron* was the sarcopterygian fish taken as focal point of the transition from fish to tetrapod, and especially *Eusthenopteron foordi* from the Upper Devonian deposits in Miguasha, Quebec, Canada (for overview see Jarvik, 1980, 1996). The deposits of Miguasha were interpreted as freshwater deposits (Dineley and Williams, 1968; Carroll et al., 1972), even though Dineley and Williams (1968, p. 252) compared the Escuminac Formation of Miguasha with Upper Devonian sediments of south-central New York State ("Chemung" rocks), which represent marine deposits based on their invertebrate content (crinoids, cephalopods, brachiopods etc.). Schultze (1972) pointed out that the fish fauna compares with that of marine deposits of Kokenhusen (Koknese), Latvia, Bergisch-Gladbach, Germany and Gogo, Western Australia, of the same age. In addition he cited the conchostracan "*Estheria*" (*Asmusia membranacea*: Martens, 1996) as having a co-occurrence in the marine Koknese deposits of Latvia. Further indications that the deposits of Miguasha were marine/coastal marine were published by Schultze and Arsenault (1985), Vézina (1991), Schmitz et al. (1991), Schultze (1996), Chidiac (1996), and Schultze and Cloutier (1996). Still, the freshwater interpretation persisted (Bjerring, 1987; Gray, 1988) until Cloutier et al. (1996) published the occurrence of acritarchs in the Escuminac Formation of Miguasha. In the Escuminac Formation, an elpistostegid sarcopterygian, *Elpistostege watsoni*, occurs. It is closely related to *Panderichthys rhombolepis*, an elpistostegid from marine deposits in Latvia, so that it may be justified to argue that *Elpistostege* was at least tolerant to a marine environment. Elpistostegids still had fins, and thus were not adapted to a terrestrial life style. Recent detailed sedimentological and taphonomic studies of the Escuminac Formation by Cloutier et al. (2011) indicate a wave-dominated estuarine depositional environment. Additionally, the geochemical (rare earth elements) and isotopic (Rb-Sr, Nd-Sm) analyses of bioapatites of fossil fishes and sediment (Matton et al., 2012) reach two important results: a) the vertebrates were living in a brackish to marine environment and, b) there was a connection between waters of the Devonian Rheic Ocean and the Escuminac basin. These results support the paleobiogeographic connections (see Matton et al., 2012, fig. 9) and indicate that the "interconnected marginal environments bording Euramerica witnessed the diversification of the elpistostegalians and the emergence of the first tetrapods" (Matton et al., 2012, p. 80).

Marine Origin

Recent Analog

It has long been shown that extant fish never leave a drying pond because it is even drier outside, so that they would die immediately. Freshwater fish, which move from one water body to another do that in a wet environment. Inger (1957) has published on it, but that was not accepted or even ignored.

Around 1930, Harms (1929, 1935) and Eggert (1929) used the mudskipper (*Boleophthalmus* and *Periophthalmus*) to show the transformation of adaptation from water to land in a tidal area. Eyes are moved high up on the skull so that their fields of vision overlap to permit three-dimensional vision (Schultze, 1997). This is an adaptation to a tidal environment, but it is not unique to the tidal area: one can find it in freshwater forms too like hippopotamus or crocodiles swimming close to the water surface with only the eyes sticking out. Oxygen is taken from water kept in mouth sacs in mudskippers, so that they are always forced to replenish the water to be able to extract oxygen. A change of behavior goes along or enhances the transformation – from species fleeing back to the sea to species fleeing towards land (from *Gobius*, to *Boleophthalmus*, and to *Periophthalmus*). The mudskipper or other teleosts leaving the water did not adapt to tetrapod-like forms for two obvious reasons: lack of lungs and the internal structure of fins. In teleosts the internal elements (radials) of the paired fins are shortened, so that the mudskipper moves on the fin rays. A transmission of forces form the ground to the shoulder or pelvic girdle is not possible.

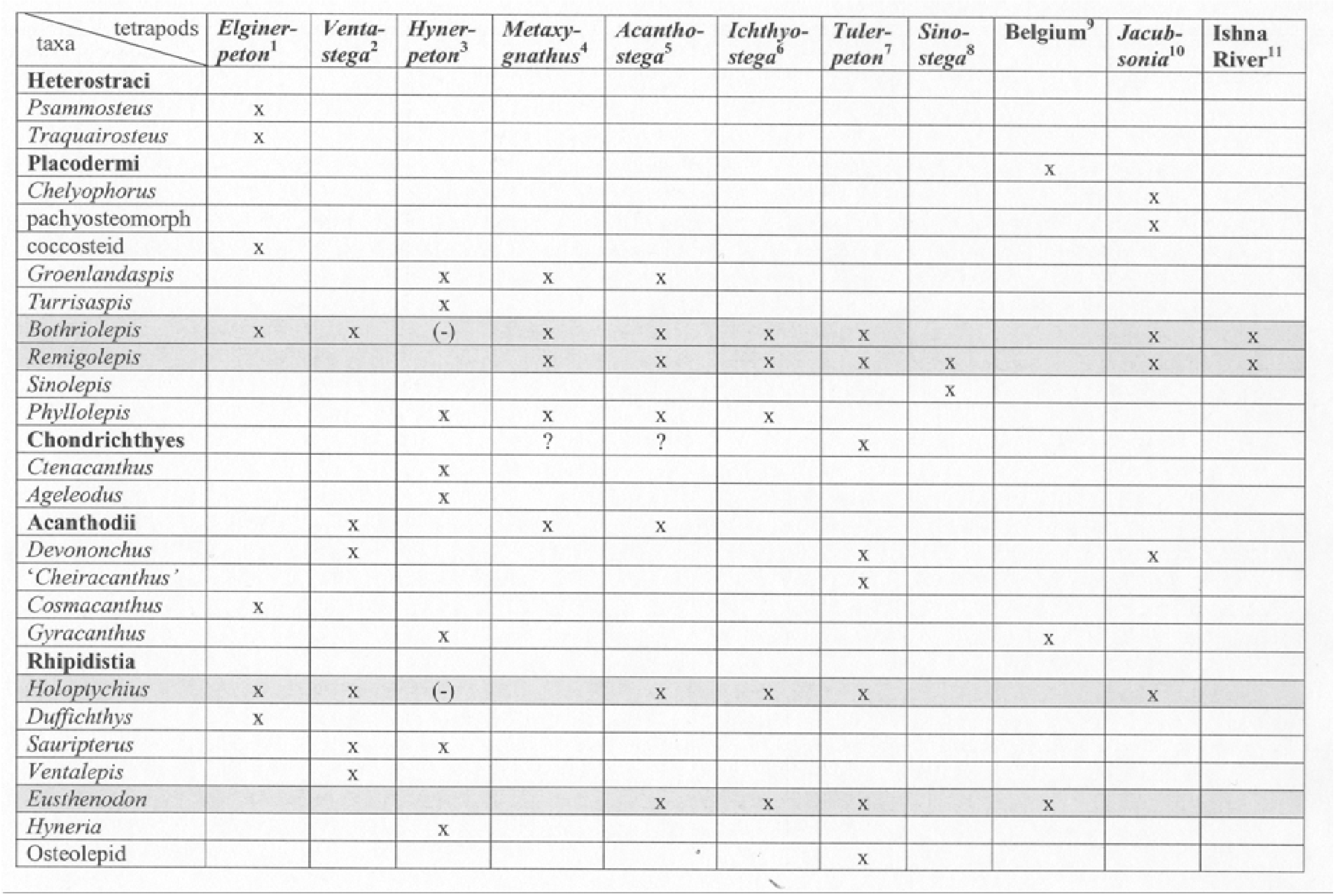
Though morphological structures are unreliable to characterize the environment of an animal, there are histological structures, which indicate growth in tidal environment as shown in bones of the lungfish *Sagenodus* from Robinson, Kansas (Schultze, 1998). The growth of an animal in the tidal area is correlated with cyclical (tidal) fluctuations of environmental parameters such as temperature, salinity and food availability. The tidal cyclicity is shown in the skeletal hard tissues and otoliths of vertebrates by a complex pattern of growth marks (i.e., several periodicities superimposed over each other) different from the growth pattern corresponding to seasonal (annual/semiannual) cyclicity (Soler-Gijón, 1999, and references therein).

PALEOENVIRONMENT OF DEVONIAN TETRAPODS

Table 1, Fig. 1

Concerning the origin of tetrapods, we focus today not anymore on fishes like the tristichopterid *Eusthenopteron*, but on sarcopterygians between the tristichopterids and the tetrapods – the Elpistostegalia (*Panderichthys*, *Elpistostege*, *Tiktaalik*, *Tinirau*). These forms occur in a near-shore environment or in a fully marine environment like *Tinirau*. That was never the question for the occurrences of *Eusthenopteron* and *Panderichthys* in the Baltic. The occurrence of *Eusthenopteron* and *Elpistostege* in the Frasnian of Miguasha, was despite contrary evidence, interpreted as fresh water until acritarchs were discovered in 1996 (Cloutier et al., 1996). Comparing the accompanying faunas of fishes

TABLE 1. Devonian tetrapods and their associated biota.

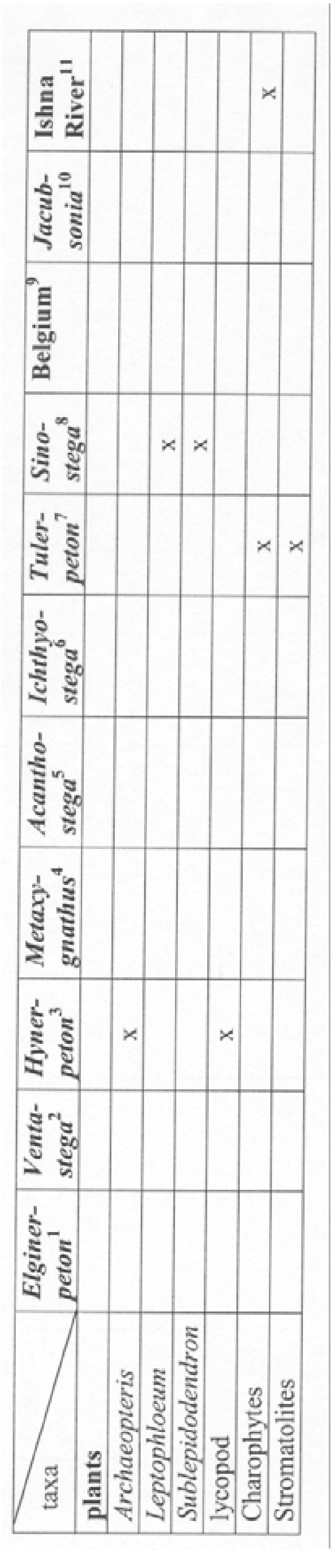


tetrapods / taxa	*Elginerpeton*[1]	*Ventastega*[2]	*Hynerpeton*[3]	*Metaxygnathus*[4]	*Acanthostega*[5]	*Ichthyostega*[6]	*Tulerpeton*[7]	*Sinostega*[8]	**Belgium**[9]	*Jacubsonia*[10]	**Ishna River**[11]
Heterostraci											
Psammosteus	x										
Traquairosteus	x										
Placodermi									x		
Chelyophorus										x	
pachyosteomorph										x	
coccosteid	x										
Groenlandaspis			x	x	x						
Turrisaspis			x								
Bothriolepis	x	x	(-)	x	x	x	x			x	x
Remigolepis				x	x	x	x	x		x	x
Sinolepis								x			
Phyllolepis			x	x	x	x					
Chondrichthyes				?	?		x				
Ctenacanthus			x								
Ageleodus			x								
Acanthodii		x		x	x						
Devononchus		x					x			x	
‘*Cheiracanthus*’							x				
Cosmacanthus	x										
Gyracanthus			x						x		
Rhipidistia											
Holoptychius	x	x	(-)		x	x	x			x	
Duffichthys	x										
Sauripterus		x	x								
Ventalepis		x									
Eusthenodon					x	x	x		x		
Hyneria			x								
Osteolepid							x				

TABLE 1. Continued. Devonian tetrapods and their associated biota.

taxa	***Elginerpeton***^{1}	***Ventastega***^{2}	***Hynerpeton***^{3}	***Metaxygnathus***^{4}	***Acanthostega***^{5}	***Ichthyostega***^{6}	***Tulerpeton***^{7}	***Sinostega***^{8}	**Belgium**^{9}	***Jacubsonia***^{10}	**Ishna River**^{11}
megalichthyid			x						x		
Megapomus										x	
Glyptopomus		x								x	
Cryptolepis		x									
Rhizodont									x		
Strunius							x				x
Dipnoi											x
Soederberghia			x	x	x	x					
longsnouted dipn.	x										
Nielsenia						x					
Oervigia					x	x					
Jarvikia					x	x					
Andreyevichthys							x				
Orlovichthys		x									
Conchodus	x									x	
Dipterus										x	
Holodipterus										x	
Actinopterygii											
Moythomasia							x				
Limnomis			x								
Palaeoniscoidea		x									
invertebrates											
arachnid			x								
scorpionid			x								
myriapod			x								
ostracodes							x				
bivalves							x				
Serpula							x				
rhynchonellid										x	

TABLE 1. Continued. Devonian tetrapods and their associated biota.



taxa	*Elginer-peton*[1]	*Venta-stega*[2]	*Hyner-peton*[3]	*Metaxy-gnathus*[4]	*Acantho-stega*[5]	*Ichthyo-stega*[6]	*Tuler-peton*[7]	*Sino-stega*[8]	Belgium[9]	*Jacub-sonia*[10]	Ishna River[11]
plants											
Archaeopteris			x								
Leptophloeum								x			
Sublepidodendron								x			
lycopod			x								
Charophytes							x				x
Stromatolites							x				

Legend: x = present, (-) = present in nearby localities, ? = uncertain identification, gray = ubiquitous taxa indicating marine connection.

Sources: [1] Miles (1968), Ahlberg (1998); [2] Luksevics and Zupins (2004); [3] Daeschler et al. (2003), Tetrapods: *Hynerpeton*, *Densignathus*; Cressler et al. (2010); [4] Campbell and Bell (1982); [5,6] Bendix-Almgren (1976), Bendix-Almgren et al. (1990), Larsen et al. (2008); [7] Alekseev et al. (1994); [8] Zhu et al. (2002); [9] Clément (2004); [10] Lebedev (2004); [11] Ahlberg et al. (2010).

Note: The genus *Tinirau* (Elpistostegale) is not generally accepted as a tetrapod so it is not listed her. However, *Tinirau* is associated with marine taxa: Porifera: nine genera and 3 tufts; Conulariida: *Paraconularia*; tabulate coral; dacryoconarid tentaculites; Pelecypoda: 4 genera; Ammonoidea: ?clymenids; Brachiopoda: inarticulate (indet.) and articulate (3 genera); Echinodermata indet.; Conodonta (5 genera); Vertebrata: Placodermi: *Asterolepis*, and arthrodires (coccosteid, plourdosteid, pachyosteine); Acanthodii: *Machaeracanthus*, *Persacanthus*; Actinopterygii: *Cheirolepis*, palaeoniscoid; Sarcopterygii: Onychodontida indet.; Dipnoi: *Griphognathus*, *Soederberghia*, dipterid indet.; Rhipidistia: osteolepidid, tristichopterid *Bruehnopteron*. Schultze (2010), Swartz (2012), Schultze and Reed (2012).

between piscine and tetrapod sarcopterygians shows that all these faunas are connected with each other (Schultze and Cloutier, 1996; Schultze, 1997; Lelièvre, 2002; Lebedev, 2004; Blieck et al., 2007) and none restricted to freshwater could be found (Schultze and Cloutier, 1996; Schultze, 1997).

Still, the old idea of the drying pond continued to persist. That – I hope – will change with the publication of Niedzwiedzki et al. (2010) and George and Blieck (2011). Both used trackways in marine deposits of Poland (Zachelmie) and Australia (Glenista). Swartz (2012) published a sarcopterygian, *Tinirau clackae*, from the marine Middle Devonian Red Hill locality (based on invertebrates: Schultze, 2010) in Nevada. *Tinirau* is placed at the base of all Elpistostegalia, which include all tetrapods after Swartz (2012). In Swartz's cladogram of basal tetrapodomorphs, the basal taxa *Tinirau*, *Platycephalichthys*, *Panderichthys*, *Elpistostege*, *Elginerpeton* and *Ventastega* are marine forms, whereas *Tiktaalik*, *Acanthostega*, *Ichthyostega* and *Hynerpeton* (e.g., Clack, 2002, 2012) are frequently cited as freshwater inhabitants (Astin et al., 2010). The latter assignment is questionable considering the faunal assemblage of these localities. Astin et al. (2010) compared East Greenland deposits with present day central Australian desert deposition, where also fish and tetrapods occur. These central Australian fishes are endemic and do not show worldwide distribution as do the fishes in Devonian deposits (Schultze and Cloutier, 1996; Lebedev, 2004). The East Greenland formations, Aina Dal, Brita Dal and Stensiö Bjerg formations, which contain the tetrapods *Ichthyostega* and *Acanthostega*, commonly interpreted as inland basin with fluviatile or lacustrine deposition, yielded also the ubiquitous *Bothriolepis*, *Remigolepis*, *Holoptychius*, and *Eusthenodon*; in addition they share *Soederberghia* and *Phyllolepis* (see Blom et al., 2005 or Larsen et al., 2008 for biostratigraphic distribution) with the Australian Devonian locality of *Metaxygnathus* (Table 1). The occurrence of *Soederberghia* in the fully marine locality of Red Hill, Nevada, together with *Tinirau* supports a marine migration of *Soederberghia* from East Gondwana (Australia) to Laurasia (East Greenland, North America: Pennsylvania, Nevada). The Red Hill locality, Pennsylvania, of *Hynerpeton* and *Densignathus* is part of the Catskill Formation, which is known for its marine invertebrate fossils except at the tetrapod locality. The Red Hill locality is part of the Catskill delta or the intertidal/supratidal portion of the epicontinental sea to the west and northwest of the locality (Walker and Harms, 1971; Cressler et al., 2010). In addition, *Holoptychius* and *Bothriolepis* have been found close by in the formation.

The worldwide occurrences of similar fishes (Table 1: *Bothriolepis*, *Remigolepis*, *Holoptychius*, *Eusthenodon*, *Soederberghia* and *Phyllolepis*) requires capability of these fishes to bridge the distances and to enter the tetrapod localities. One can argue that the paleogeographic reconstructions are incorrect as done for the distribution of *Soederberghia* by Campbell and Bell (1982) and Ahlberg et al. (2001), and the continents were closer to each other. Nevertheless, even then the fishes have to cross the sea. It is much more plausible that these fishes were salt water tolerant and entered the tetrapod localities from the sea, thus indicating that the early tetrapods were normal marine (*Tulerpeton*) or brackish water tolerant. The occurrences of these fishes require a connection to the sea at least.

Placing the paleoenvironment on a cladogram of early tetrapods (Schultze, 1997; Fig. 1) indicates that Devonian tetrapods are salt water tolerant. The basal elpistostegale *Tinirau* occurs in unquestionable marine deposits (Schultze, 2010) and *Elpistostege* and *Panderichthys* in marginal marine or deltaic sediments (Schultze and Cloutier, 1996). The tetrapods *Obruchevichthys* and *Ventastega* are found in coastal marine deposits. Based on the co-occurrence of world-wide distributed fishes, I would postulate a marginal marine paleoenvironment or at least connection to the sea for *Elginerpeton*, *Metaxygnathus*, *Acanthostega*, *Ichthyostega* and *Hynerpeton* (half filled circles in Fig. 1). *Tulerpeton* is marine, so that the transition from Devonian to Carboniferous tetrapods occurs with saltwater tolerant forms.

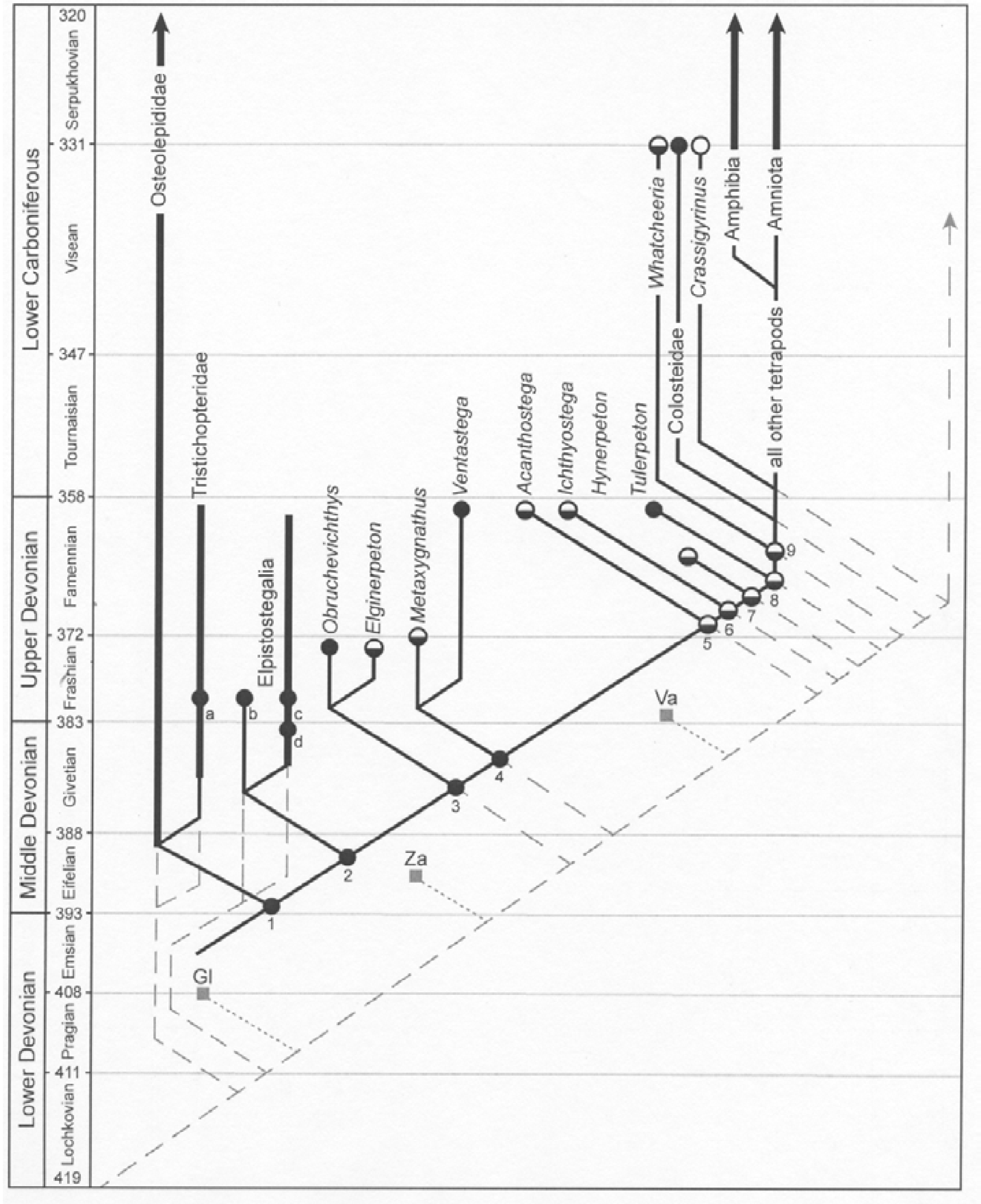


FIGURE. 1. Distribution in time and interrelationship of Devonian sarcopterygians, after Schultze (1997). **Explanations: a**, *Eusthenopteron foordi*, Escuminac Formation, Miguasha, Canada; **b**, *Elpistostege watsoni*, Escuminac Formation, Miguasha, Canada; **c**, *Panderichthys rhombolepis*, Gauja beds, Lode, Latvia; **d**, *Tinirau clackae*, upper Givetian, Northern Simpson Range, Nevada, U.S.A.; **open circle** = fresh water, **half open circle** = brackish (often interpreted as fresh water), **filled circle** = marine; explanation of numbers see Schultze (1997, fig. 1); **GI** = Glenista, Australia, **Va** = Valentia, Ireland, **Za** = Zachelmie, Poland.

The integration of trackways in the cladogram is shown by broken lines. The trackways indicate an earlier first appearance of tetrapods either early Middle Devonian (Niedzwiedzki et al., 2010) or even early Early Devonian (George and Blieck, 2011). These trackways are coastal marine and would support the environmental interpretation based on faunal comparison, if they were produced by tetrapods. I cannot see the skeletal structure superimposed on one track in Niedzwiedzki et al. (2010, fig. 4). Clack (2012) takes a very careful interpretation; she refers especially to the large size of the tracks. Swartz (2012) refers to the same kind of gait in other sarcopterygians (King et al., 2011; Pridmore, 1995); even sharks may produce such trackways (Pridmore, 1995).

PALEOENVIRONMENT OF PERMO-CARBONIFEROUS TETRAPODS

Many tetrapod localities are known in the Permo-Carboniferous. Here I will restrict myself to only a few and use the somewhat artificial division between North American and European localities. The two continents are far apart today, but they were close to each other in the Late Paleozoic.

North America

Table 2

I will restrict myself to a few Carboniferous North American tetrapod localities, which I have seen personally.

Greer, Virginia and other localities with *Greererpeton*

The colosteid genus *Greererpeton* occurs in two Lower Carboniferous localities, Greer and Goreville. Both localities appear to be coastal marine. In Greer, the tetrapodomorphs are associated with a diverse fish fauna (Elliott and Taber, 1982; Schultze and Bolt, 1996: *Greererpeton*, *Proterogyrinus*, *Crassigyrinus*?, *Eoherpeton*?, rhachitomous ?*Eryops*, rhizodont, *Tranodis*, ?*Ganopristodus*, palaeoniscoids, *Gyracanthus*, *Ctenacanthus* and *Cynopodius* in marine Bluefield Formation; Table 2), whereas in Goreville only the lungfish *Tranodis* in large numbers is found in association with *Greererpeton* and microsaurs in a lens of clay between two limestones with marine invertebrates (Schultze and Bolt, 1996). The holotype of *Tranodis* was found also in southern Illinois in a marine limestone (Thomson, 1965). The lungfish *Tranodis* occurs in a third locality in Iowa (Delta) in a little older rocks (upper Viséan) in a sinkhole on a supra-intertidal flat together with *Whatcheria*, an embolomere, a colosteid, large rhizodonts, osteolepidids, palaeoniscoids, *Gyracanthus*, *Orthacanthus*, hybodont and *Cynopodius* (Schultze and Bolt, 1996). The co-occurrence with marine forms like *Ctenacanthus* and *Cynopodius* and with forms, which are found occasionally in marine environment but are not exclusive marine forms (rhizodonts, *Tranodis*, palaeoniscoids, *Gyracanthus*, *Orthacanthus*), suggest that the tetrapods (colosteids, *Whatcheria*, and microsaurs) are also salt water tolerant like the fish fauna.

Joggins, Nova Scotia

Since Archer et al. (1995) published the occurrence of agglutinated foraminifers in the deposits of Joggins, we are back to the early interpretation of Joggins as a coastal intertidal environment of Dawson (1856). The occurrence of spirorbiform microconchids (“*Spirorbis*”) and of fish scales (coelacanths) in the tree stumps together with tetrapods should have always cautioned against a terrestrial interpretation. Falcon-Lang et al. (2006) even argued that some of the trees have grown in a coastal environment (their coastal plain environment). Most tetrapods are found in the coastal plain association within the trees (DiMichele and Falcon-Lang, 2010, fig. 14) or in the open water association (*Baphetes*). From Joggins are reported the temnospondyl *Dendrerpeton*, the microsaurs *Hylerpeton*, *Leiocephalikon*, *Ricnodon*, *Tachystegos* and *Asaphestera*, and the amniotes *Archerpeton*, *Hylonomus*, and the pelycosaur *Protoclepsydrops* (Table 2). These tetrapods should have been at least partly salt water tolerant if they could venture onto the tidal flats and feed on the saltwater fishes. That tolerance should be comparable to that of the microsaur in the southern Illinois (Goreville) locality (see above) and the early microsaur from the Mississipian/Pennsylvanian locality Lehi, Utah (Carroll et al., 1991; see Mickle, 2011, for paleoenvironment).

Mazon Creek, Illinois

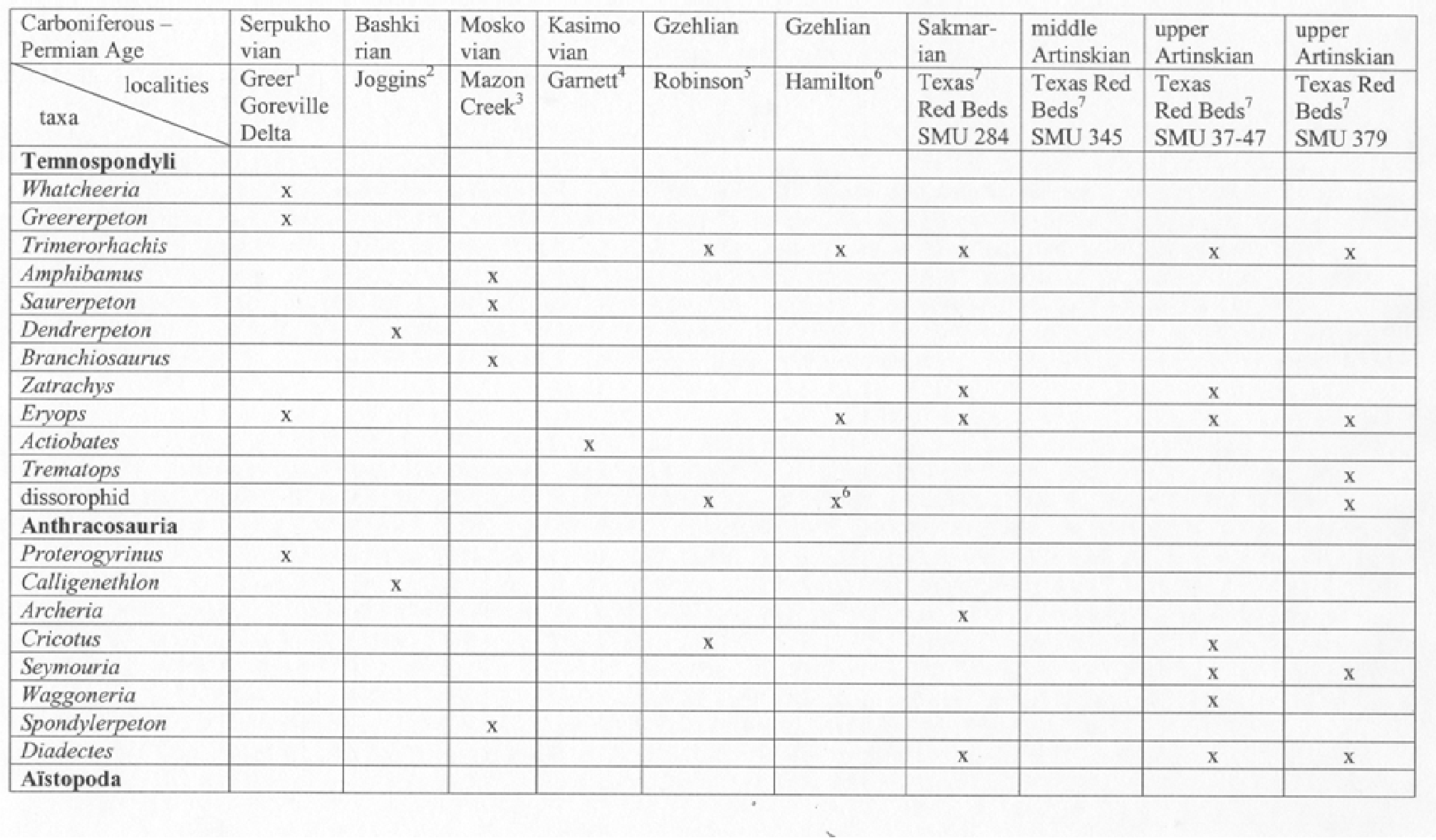
The well-known Upper Carboniferous Mazon Creek locality, Illinois, was originally considered as a freshwater deposit because of the frequent occurrence of plant fossils. Terrestrial plants are no environmental indicator in an aquatic environment (Schultze, 1996). With the discovery of marine fossils in the open-air mine Pit 11 the picture changed. Johnson and Richardson (1966) draw a line between the marine Essex fauna and the freshwater Braidwood fauna. This is an arbitrary line, and more marine fossils have been found in the Braidwood fauna, so that Baird (1997) considered it as brackish to fresh water. In my view the Mazon Creek area represents a typical coastal marine environment with many deltas. The high number of juvenile forms indicates that it is a coastal marine area, where marine forms reproduce as they do today in similar environment. Some tetrapods (Table 2) occur in the marine Essex fauna only (temnospondyl *Saurerpeton*, aistopod *Ophiderpeton*), others in both faunas (temnospondyl *Amphibamus*, lysorophid *Brachydectes*) and some only in the brackish/freshwater Braidwood fauna (temnospondyl ?*Branchiosaurus*, anthracosaur *Spondylerpeton*, aistopod *Aornerpeton*, nectridid *Ptyonius*, captorhinid *Cephalerpeton*). For all tetrapods at Mazon Creek and not only for those of the Essex fauna, one has to expect tolerance of salt water (Schultze, 2009).

Kansas

There are four famous tetrapod localities in the Upper Carboniferous of Kansas (Robinson, Garnett, Hamilton, Eskridge), three of them were originally interpreted as freshwater deposits because of plants, tetrapods and lungfish, but it has been shown otherwise in the mean time. The Robinson locality in NE-Kansas contains stromatolites, which were formed on an elevation in the shallow Pennsylvanian midcontinental sea (Sawin et al., 1985). There was no land nearby. The tetrapods, lungfish and other vertebrates occur in the stromatolites associated with marine shark remains and a broad variety of marine invertebrates (silicified so that they show up in the acetic preparation; see Sawin et al., 1985 and Schultze, 1995, table 1). Two lungfish, *Sagenodus* and *Gnathorhiza*, and a trimerorhachid amphibian (Chorn, 1984) occur in the Robinson locality at about the same frequency. Another unquestionable occurrence in marine sediments of *Gnathorhiza* is recorded from the Texas Arroyo Formation (Olson, 1989). Besides the trimerorhachid, other tetrapods are recorded from Robinson locality: dissorophid (cf. *Platyhystrix*), nectridean (*Diplocaulus*), lysorophid, anthracosaur (*Cricotus*), protorothyridid and pelycosaur (Chorn and Schultze, 1990; Table 2). All these tetrapods should have been salt water tolerant (Laurin, 2010) or washed in from a long distance. There is no indication for a long transport. In contrast the histology of the bones of *Sagenodus* indicates that the lungfish lived in a tidal environment (Schultze, 1998).

Gnathorhiza is the Pennsylvanian/Permian lungfish, which forms burrows, e.g., at Eskeridge but not at Robinson or Hamilton. The burrows of *Gnathorhiza* are compared frequently with burrows of the extant African lungfish *Protopterus* since Romer and Olson (1954). Today two species of *Protopterus* form burrows to survive droughts in inland lakes far away from the coast. The burrows in Kansas and Oklahoma are close to the sea in the intertidal zone. The Speiser Shales give a nice example, because we have here along the highways nearly continuous exposures, which were investigated by invertebrate paleontologists (Hattin, 1957; Cuffey, 1967; Lutz-Garihan, 1976; Lutz-Garihan and Cuffey, 1979) and interpreted as to depositional environment from shallow marine to supratidal (Schultze, 1985). There are no fossils in the

TABLE 2. North American Carboniferous-Permian localities and their fauna.



Carboniferous – Permian Age	Serpukhovian	Bashkirian	Moskovian	Kasimovian	Gzehlian	Gzehlian	Sakmarian	middle Artinskian	upper Artinskian	upper Artinskian
localities / taxa	Greer[1] Goreville Delta	Joggins[2]	Mazon Creek[3]	Garnett[4]	Robinson[5]	Hamilton[6]	Texas[7] Red Beds SMU 284	Texas Red Beds[7] SMU 345	Texas Red Beds[7] SMU 37-47	Texas Red Beds[7] SMU 379
Temnospondyli										
Whatcheeria	x									
Greererpeton	x									
Trimerorhachis					x	x	x		x	x
Amphibamus			x							
Saurerpeton			x							
Dendrerpeton		x								
Branchiosaurus			x							
Zatrachys							x		x	
Eryops	x					x	x		x	x
Actiobates				x						
Trematops										x
dissorophid					x	x[6]				x
Anthracosauria										
Proterogyrinus	x									
Calligenethlon		x								
Archeria							x			
Cricotus					x				x	
Seymouria									x	x
Waggoneria									x	
Spondylerpeton			x							
Diadectes							x		x	x
Aïstopoda										

TABLE 2. Continued. North American Carboniferous-Permian localities and their fauna.

Carboniferous – Permian Age	Serpukhovian	Bashkirian	Moskovian	Kasimovian	Gzehlian	Gzehlian	Sakmarian	middle Artinskian	upper Artinskian	upper Artinskian
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Aornerpeton			x							
Ophiderpeton			x							
Nectridia										
Diplocaulus					x		x	x	x	x
Ptyonius			x							
Lysorophia										
Lysorophus					x				x	
Brachydectes			x							
Microsauria	x		x						x	
Asaphestra		x								
Hylerpeton		x								
Leiocephalikon		x								
Ricnodon		x								
Tachystegos		x								
Euryodus									x	
Ostodolepis									x	
Amniota										
Hylonomus		x								
Protoclepsydrops		x								
Captorhinus							x		x	x
Cephalerpeton			x							
Labidosaurus									x	
Petrolacosaurus				x						
Spinoaequalis						x				
araeoscelid									x	x

TABLE 2. Continued. North American Carboniferous-Permian localities and their fauna.

Carboniferous – Permian Age	Serpukhovian	Bashkirian	Moskovian	Kasimovian	Gzhelian	Gzhelian	Sakmarian	middle Artinskian	upper Artinskian	upper Artinskian
localities / taxa	Greer[1] Goreville Delta	Joggins[2]	Mazon Creek[3]	Garnett[4]	Robinson[5]	Hamilton[6]	Texas[7] Red Beds SMU 284	Texas Red Beds[7] SMU 345	Texas Red Beds[7] SMU 37-47	Texas Red Beds[7] SMU 379
Archerpeton		x								
protorothyrid						x				
Pelycosauria				x[4]		x[6]				
Varanops									x	
Varanosaurus										x
Novascoticus		x								
Dimetrodon							x	x	x	x
Edaphosaurus									x	
ichnofossils		x[2]		x[4]						
“Rhipidistia”										
rhizodont	x	x	x							
osteolepidid		x	x		x	x				
Ectosteorhachis							x			
Actinistia		x			x	x				
Rhabdoderma		x	x							
Synaptotylus				x						
Spermatodus							x			
Dipnoi										
Tranodis	x									
Sagenodus		x			x	x		x		
Megapleuron			x							
Ctenodus			x							
Ganopristodus	x									
Comchopoma			x							
Gnathorhiza					x	x	x	x	x	

TABLE 2. Continued. North American Carboniferous-Permian localities and their fauna.

Carboniferous – Permian Age	Serpukhovian	Bashkirian	Moskovian	Kasimovian	Gzehlian	Gzehlian	Sakmarian	middle Artinskian	upper Artinskian	upper Artinskian
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Palaeophichthys			x							
Actinopterygii										
palaeoniscoid	x	x	x[3]		x	x	x	x	x	x
Platysomus			x				x			
Haplolepiformes		x[2]	x[3]							
Acanthodii										
Acanthodes			x		x	x	x	x		
Gyracanthus	x	x								
Iniopterygia							x			
Jimpohlia			x							
Polysentor			x							
Similihariotta			v							
Elasmobranchii			x[3]				x			
Xenacanthimorpha									x	
Orthacanthus	x				x	x	x	x	x	x
Barbclabornia							x	x	x	
Xenacanthus		x					x	x		
Expleuracanthus						x				
Trichorhipis			x							
Cladodontimorphi										
Glikmanius								x		
Cladodus					x					
Ctenacanthus	x	x								
Homacanthus	x									
Euselachii										

TABLE 2. Continued. North American Carboniferous-Permian localities and their fauna.

Carboniferous – Permian Age	Serpukhovian	Bashkirian	Moskovian	Kasimovian	Gzehlian	Gzehlian	Sakmarian	middle Artinskian	upper Artinskian	upper Artinskian
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Polyacrodus							x	x		
Acrodus								x		
Lissodus							x	x		
hybodont	x				x	x	x	x		
Euchondrocephali										
Helodus							x		x	
deltodontid					x					
Petalodus					x					
Janassa								x		
Ctenoptychius		x								
Ageleodus		x								
Cynopodius	x									
Petromyzontida										
Mayomyzon			x							
Myxinida										
Myxinikela			x							
Enteropneusta										
Mazoglossus			x							
Foraminifera		x[2]				x[6]	x		x	
Coelenterata			x[3]							
coral					x					
Pelecypoda		x[2]	x[3]	x[4]	x	x[6]				
Gastropoda		x[2]	x[3]		x	x[6]				
Cephalopoda			x[3]							

Legend: x = present, grey = marine forms.

Sources: [1] Greer, Virginia, Goreville, Illinois, Delta, Iowa: Elliott and Taber (1982), Schultze and Bolt (1996).

[2] Joggins, Nova Scotia: Falcon-Lang et al. (2006): Additional taxa from the coastal plain (most Tetrapoda) and open water:
Foraminifera: *Ammobaculites*, *Ammotium*, *Trochammina*, cf. *Textularia*; **Mollusca:** Pelecypoda: *Curvirimula*, *Naiadites* (2), Gastropoda: *Dendropupa*, *Pupa*, *Protodiscus*; **Annelida:** traces: *Arenicolites*, *Cochlichnus*, *Gordia*, *Haplotichnus*, *Plangtichnus*, *Treptichnus*; **Arthropoda:** Ostracoda: *Carbonita* (7 sp.), *Candona* (2 sp.), *Hilboldtina*, *Velatomorpha*, Malacostraca: *Pygocephalus*, Myriapoda: *Archiulus*, *Xyloiulus*, Arthropleurida: *Hastimima*, *Amynilyspes*; Arachnida: *Coryphomartes*, *Graeophonus*; Eurypterida: *Belinurus*, cf. *Mycterops*; traces: *Kouphichnium*, cf. *Limulocubichnus*, *Siskemia*; **Actinopterygii**: Haplolepiformes: *Haplolepis*; **Tetrapoda:** trace fossils: *Limnopus*, *Matthewichnus*, *Dromillopus*, *Ornithoides*.

[3] Mazon Creek, Illinois: Shabica and Hay (1997): Additional taxa: **Coelenterata:** different Cubozoa (2 sp), Scyphozoa (4 sp), Hydrozoa (2), and Anthozoa (?12 sp); **Nemertea** (1 sp);

TABLE 2. Continued. North American Carboniferous-Permian localities and their fauna.

Carboniferous – Permian Age	Serpukhovian	Bashkirian	Moskovian	Kasimovian	Gzehlian	Gzehlian	Sakmarian	middle Artinskian	upper Artinskian	upper Artinskian
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Brachiopoda			x[3]	x[4]	x	x[6]				
Bryozoa					x	x[6]				
Echinodermata										
Crinoidea			x		x	x				
Echinoidea					x	x				
Holothuroidea			x							
Annelida			x[3]							
spirorbiform		x[2]	x			x	x		x	
serpulid						x				
Arthropoda			x[3]							
Trilobita					x					
Arthropleurida		x[2]								
Eurypterida		x[2]	x[3]			x[6]				
Scorpionida		x	x[3]	x[4]		x[6]				
Ostracoda		x[2]	x[3]		x	x[6]				
Malacostraca		x[2]	x[3]							
Myriapoda		x[2]	x[3]			x				
Insecta		x	x[3]	x[4]		x[6]				

Nematoda (1 sp); **Priapulida** (1 sp); **Chaetognatha** (1 sp); **Annelida:** many Polychaeta (16); Echiura (1 sp); Onychophora (1 sp); **Arthropoda:** Eurypterida: *Adelophthalmus*; Xiphosura (5), Arachnida (25 sp), Scorpionida (4 sp); Myriapoda (15 sp); Insecta (18 sp); Crustacea: Remipedia (1 sp), Malacostraca (16 sp), Phyllopoda (4 sp), Maxillopoda: Ostracoda: Geisina, Paraparchites, Cirripedia (1 sp), Halicyna (3 sp),Thylacocephala (2 sp); **Mollusca:** Polyplacophora: *Glaphurochiton*; Gastropoda: *Euphemites*, *Hypselentoma*, *Straparollus*, *Naticopsis*, *Strobeus*; Pelecypoda: "*Solemya*," *Myalinella*, *Anthraconia*, *Leptodesma*, *Posidonia*, *Aviculopecten*, *Acanthopecten*, *Euchondria*, *Dunbarella*, *Palaeolima*, *Permophorus*, *Astartella*, *Schizodus*, *Edmondia*, *Sedwickia*, *Grammysioidea*; Cephalopoda: *Bactrites*, *Wiedeyoceras*, schistoceratid, Nautiloidea: *Stearoceras*, *Titanoceras*, *Paleocadmus*; Teuthoidea: *Pohlsepia*, *Jeletzkya*; Brachiopoda: *Lingula*, *Orbiculoidea*, chonetoid; **Elasmobranchii:** *Bandringa*, *Dabasacanthus*, *Holmacanthus*; **Actinopterygii:** Palaeonisciformes: *Illinichthys*, "*Elonichthys*," *Amphicentrum*; Haplolepiformes: *Pyritocephalus*, *Parahaplolepis*, *Microhaplolepis*.

[4] Garnett, Kansas: Reisz et al. (1982), Reisz (1990): Additional taxa: **Pelecypoda:** *Myalina*, *Yoldia*; **Brachiopoda:** *Lingula*; **Arthropoda:** Scorpion: *Garnettius*; Insecta: blattoids, megasecopteran; **Tetrapoda:** Pelycosauria: *Haptodus*, *Ianthasaurus*, *Ophiacodon*, *Xyrospondylus*; ichnofossils: *Megabaropus*, *Notalacerta*.

[5] Robinson, Kansas: Chorn and Schultze (1990): Additional taxa: **Pelecypoda:** *Phestia bellistriata*, *Permophorus*?, *Aviculpecin*; **Gastropoda:** *Euphemites*, *Trepospira*?, *Euconospira*?, *Glabrocingulum* (*Ananias*)?, *Straparollus* (*Amphiscapha*)?; **Brachiopoda:** *Crurithyris*, *Neochonetes*, punctate brachiopod.

[6] Hamilton, Kansas: Cunningham (1990): Additional taxa: **Foraminifera:** *Triticites*, *Globivalvina* and encrusting forms; **Ostracoda:** *Amphissites*, *Bairdia*, *Carbonita*, *Darwinula*, *Geisina*, *Pseudobythocypris*, *Whipplella*; **Pelecypoda:** *Anthraconaia*, *Myalinella*, *Permophorus*, *Phestia*, *Schizodus*; Gastropoda: *Bellerophon*?, *Euphemites*; **Brachiopoda:** *Antiquatonia*, *Juresania*, *Kozlowskia*, *Neochonetes*, *Neospirifer*, *Punctospirifer*, productid; **Bryozoa:** fenestrate and ramose; **Arthropoda:** Eurypterida: *Adelophthalmus*; Scorpionida: *Archaeoctonous*; Insecta: Blattaria, Odonata, Palaeodictyopetra, Protorthoptera; **Elasmobranchii:** hybodont: *Hamiltonichthys*; **Tetrapoda:** Pelycosauria: edaphosaur, ophiacodont, varanopid *Archaeovenator* Reisz and Dilkes, 2003; dissorophid: *Eoscopus* Daly, 1994.

[7] southwest of Wichita Falls, Texas: Johnson (2011).

supratidal zone; the burrows are formed in the intertidal zone. The formation of fish burrows is a common phenomenon within the tidal zone today (see Bhatt et al., 2009, and references therein), only lungfish do not occur, because extant lungfish are restricted to fresh water. The occurrence of tetrapods, lysorophids (*Brachydectes*), in burrows besides burrows of *Gnathorhiza* indicates that both are adapted to the same environment. The geological section at Eskridge (Cunningham, 1989; Hembree et al., 2004, fig. 4) shows rootlets (rhizoliths) mostly separate from the burrows. The rootlets are typical of intertidal and tidal sediments (Dörjes, 1970) as are burrows (Reineck and Singh, 1973). Both are indication of subaerial exposure. Nevertheless there is no indication of a longer exposure to dry conditions or soil formation. The geological position and the similarity to intertidal sedimentation indicate coastal marine conditions without any evidence of seasonality (contra Hembree et al., 2004). Thus the lysorophids must have been salt water tolerant like the lungfish in this locality and like both in the somewhat older locality of Robinson.

Garnett is a coastal marine locality (estuarine after Reisz et al., 1982; see Schultze, 1995, table 3 for the large number of marine invertebrates) with tetrapod tracks and actinistians in the upper part of the section and complete tetrapods in the lower part of the section (Reisz et al., 1982; Table 2). The trackways indicate that the tetrapods were able to enter the brackish to normal marine environment, but there is no indication that they lived in that environment. The diapsid *Petrolacosaurus*, pelycosaurs cf. *Edaphosaurus*, *Haptodus*, cf. *Clepsydrops*, and *Xyrospondylus* are interpreted as terrestrial and as "washed in" by Reisz et al. (1982), whereas Peabody (1952) considered *Petrolacosaurus* as an aquatic form.

In contrast Hamilton, a tidal channel with marine fossils (crinoids, brachiopods, marine ostracods and foraminifera; Cunningham et al., 1993; Cunningham, 1993; Schultze, 1995, table 2; Table 2), preserves an aquatic reptile with deep propulsive caudal organ, the diapsid *Spinoaequalis* (deBraga and Reisz, 1995) besides amphibians (Daly, 1994); both must have been salt water tolerant, to live in the channel environment like the co-occurring lungfishes *Sagenodus* and *Gnathorhiza*. The specimen of *Gnathorhiza* has been found in the lower part of the channel closer to the sea. The amphibian *Eoscopus* is, after juvenile *Acanthodes*, the most common vertebrate and must have lived in the channel. An additional synapsid tetrapod is interpreted as terrestrial (Reisz and Dilkes, 2003) and as drifted into the deposits contrary to its perfect preservation like the complete lungfish specimens (the only known complete *Sagenodus* specimen originates from that locality: Schultze and Chorn, 1997).

The Kansas localities are the strongest indication that Carboniferous tetrapods were salt water tolerant. The pelycosaur *Archaeovenator* could have been terrestrial and transported into the Hamilton channel as suggested by Reisz and Dilkes (2003). Reisz et al. (1982) argued the same for the tetrapods of Garnett. That cannot be the case for the other tetrapods (*Eoscopus* and *Spinoaequalis*) of Hamilton, and it cannot be the case for the tetrapods and lungfish in the Robinson locality. These vertebrates must have lived in normal marine to brackish waters based on the paleogeography. Thus arises the question, if the same tetrapod can be at one locality salt water tolerant and not at the other.

Kinney Brick Company Quarry, New Mexico

Another tetrapodomorph locality, the Kinney Brick Company Quarry in central New Mexico, represents an estuarine environment (Feldman et al., 1992) with many different fish and few tetrapods (amphibamid, trimerorhachid *Lafonius*, saurerpetonid) (Hunt et al., 1992). The vertebrates are concentrated in the lower part of the section – in the marine section. They don't occur in the less marine to freshwater environment in the upper part of the section. Hunt et al. (1992) interpreted the tetrapods as washed in. The preservation of very delicate structures of the three juvenile, complete specimens speaks against transport.

North American Carboniferous localities with lungfish fossils show that the lungfish *Sagenodus* (Schultze and Chorn, 1997, table 1) occurs in clearly marine localities (Robinson, Hamilton, Kinney Brick Company Quarry, Mazon Creek) and in addition in brackish to near shore localities (e.g., Point Edward near Sydney and Joggins, Nova Scotia with agglutinated foraminifers and spirorbiform microconchids, '*Spirorbis*'). These localities contain a variety of tetrapods, so that one has to accept that these tetrapods were at least salt water tolerant.

Texas Red Beds

Tetrapods (e.g., pelycosaurs) and fishes (e.g., xenacanth sharks) are found together in the some locality in the same horizon of the Texas red beds near Wichita Falls (Table 2). *Sagenodus* occurs here, too. Nevertheless, these deposits are interpreted as freshwater deposits (Sander 1989; Olson, 1989; with the exception of Parrish 1978) without any example of freshwater fossils. To the contrary, the few invertebrate fossils in those deposits (Johnson, 2011) are marine indicators like foraminifers and euryhaline forms like spirorbiform microconchids (Vinn, 2010, p. 219). Even teeth of actinopterygians (platysomid) and of elasmobranchs (*Cladodus*, *Helodus*, *Janassa* clearly marine, and *Polyacrodus*, *Lissodus* and hybodonts are not uncommon in marine deposits) are recorded (Table 2). Thus one has to place these deposits in a coastal marine environment. That is supported by the presence of the sea south of the area (Olson, 1989), where lingulid brachiopods and marine pelecypods (after E. Yochelson and J. Pojeta in Olson, 1989, p. 8) are present. The occurrence of *Sagenodus* and of *Gnathorhiza* burrows suggests an interpretation as intertidal phenomenon (Parrish, 1978), like in Kansas (Schultze, 1985). That interpretation is supported by the occurrence of *Gnathorhiza* jaws farther south in the marine Arroyo Formation (Olson, 1989). The Arroyo Formation changes its sedimentology from limestones in the south to silt- and sandstone in the north. That is not a change from marine to terrestrial (Olson, 1989) but a change in lithology from open marine to a coastal marine environment, accompanied by an impoverishment of the invertebrate fauna, but a constancy of the vertebrate fauna. It follows that the co-occurring tetrapods (temnospondyls like *Trimero-rhachis*, anthracosaurs like *Archeria*, *Diadectes*, Nectridia like *Diplocaulus*, *Lysorophus*, microsaurs like *Euryodus*, *Archerpeton*, pelycosaurs like *Dimetrodon*, see Table 2) are salt water tolerant tetrapods (Parrish, 1978). Again that is supported by the occurrence of these groups in fragmentary form in the Arroyo sea further south (Olson, 1989).

Olson (1989) listed many tetrapods (*Diplocaulus*, trimerorhachids, eryopids, microsurs, *Lysorophus*, and pelycosaurs) from many horizons of the marine Arroyo Formation in Texas (Yochelson in Olson, 1989, p. 8); in addition, Yochelson (ibid.) placed doubts on the interpretation of widespread transportation.

Europe

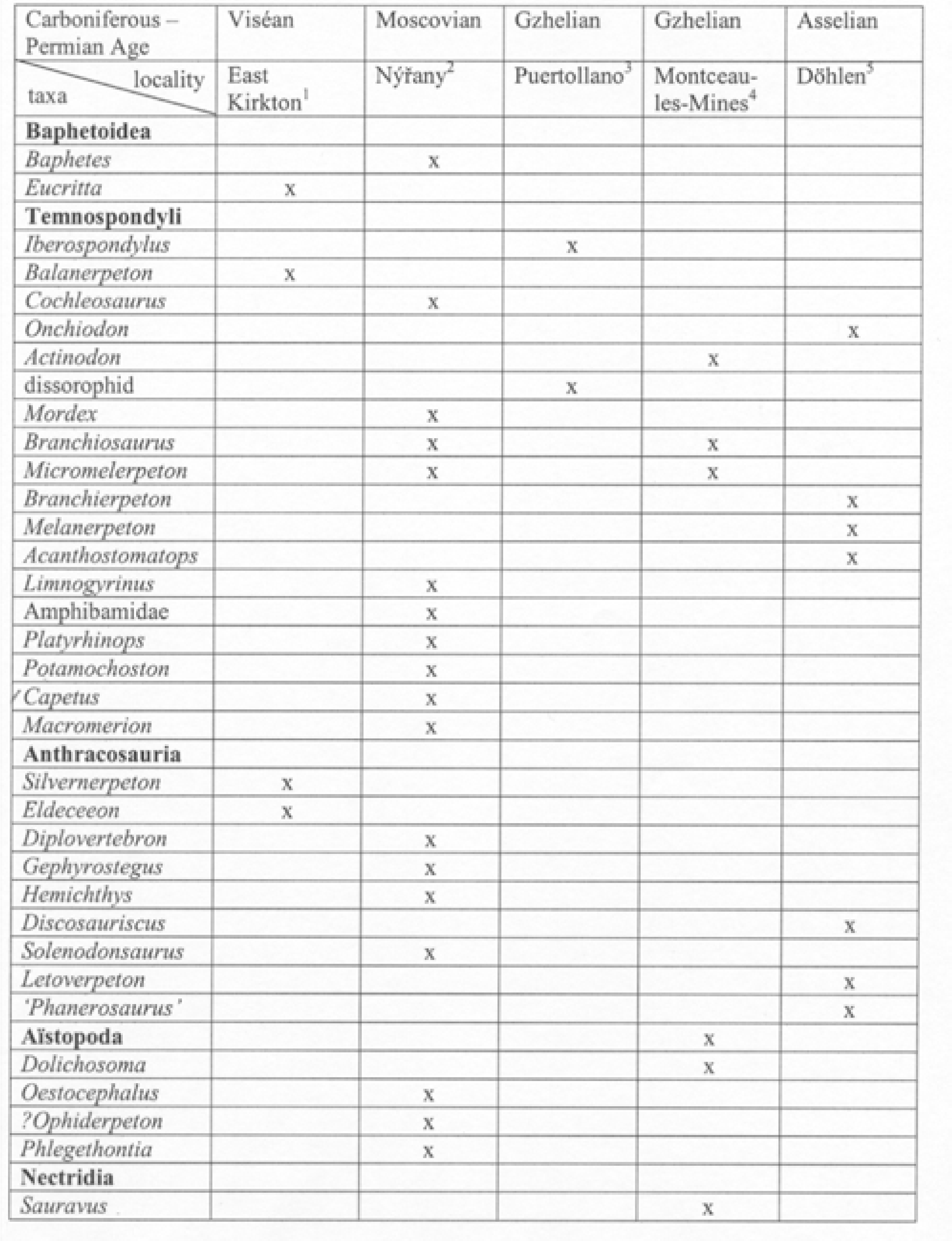
Table 3

A comparison of North American and European Upper Carboniferous localities shows close similarities of the vertebrate faunas as seen in the lower similarity dendrogram (Maples and Schultze, 1989; Schultze and Maples, 1992; Schultze and Soler-Gijón, 2004). Montceau, France, and Nýrany, Czech Republic, cluster within North American localities. And concerning the environment: all localities appear to be marine, starting with the Kansas localities; Kinney, New Mexico, is coastal marine, and the European, French locality Montceau les Mines clusters in between Nýrany close to Garnett, a coastal marine locality and Linton. It could indicate that the last three have less marine influence. The Mazon Creek faunas cluster separately because of their great similarity and the number of identical forms.

East Kirkton, Scotland

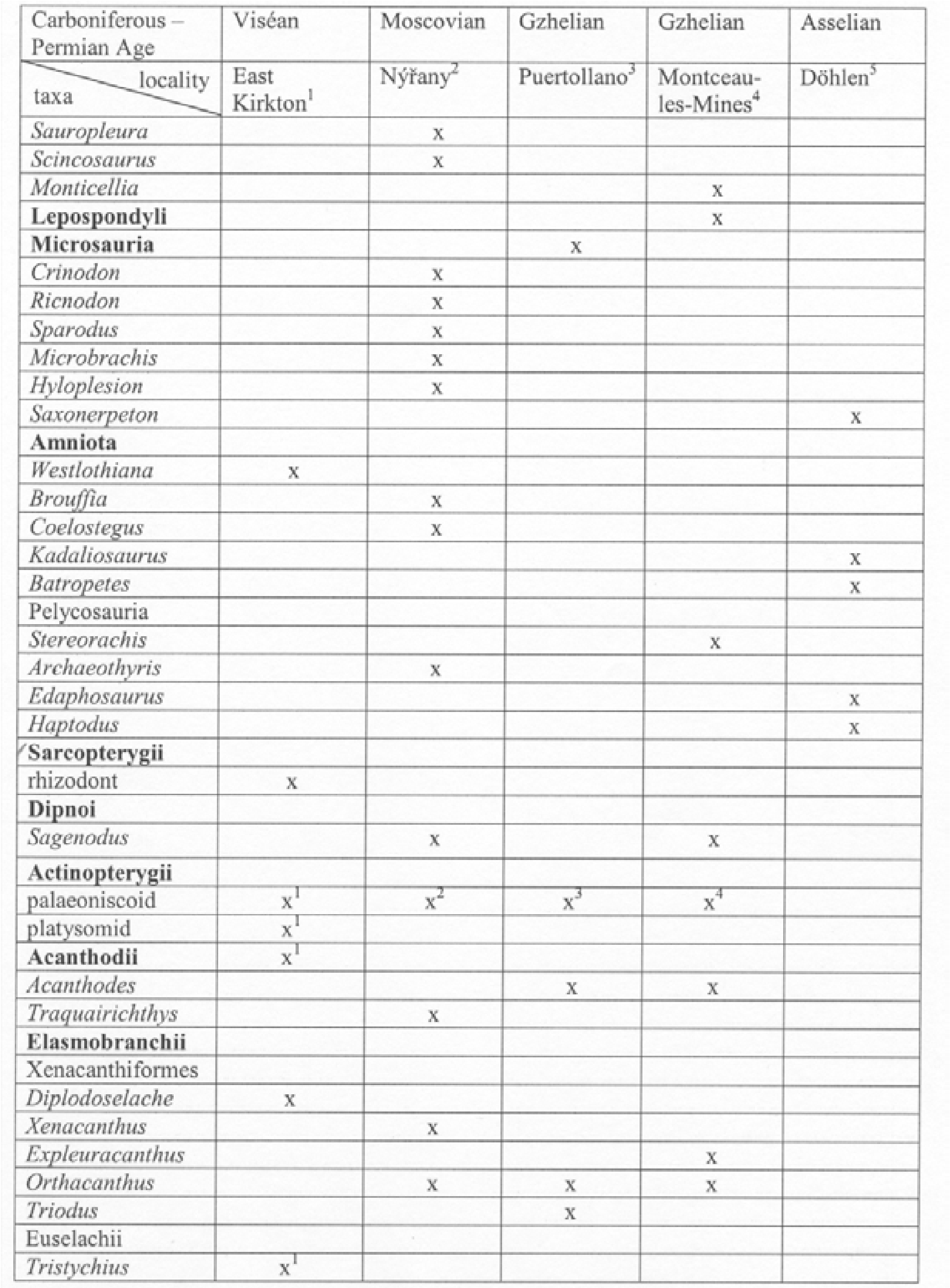
The conventional interpretation of the Lower Carboniferous locality East Kirkton, Scotland, is that of a freshwater lake (Clack, 2012, fig. 8.2) even though the fauna does not support such an interpretation

TABLE 3. European Carboniferous-Permian localities and their fauna.



Carboniferous – Permian Age	Viséan	Moscovian	Gzhelian	Gzhelian	Asselian
locality / taxa	East Kirkton[1]	Nýřany[2]	Puertollano[3]	Montceau-les-Mines[4]	Döhlen[5]
Baphetoidea					
Baphetes		x			
Eucritta	x				
Temnospondyli					
Iberospondylus			x		
Balanerpeton	x				
Cochleosaurus		x			
Onchiodon					x
Actinodon				x	
dissorophid			x		
Mordex		x			
Branchiosaurus		x		x	
Micromelerpeton		x		x	
Branchierpeton					x
Melanerpeton					x
Acanthostomatops					x
Limnogyrinus		x			
Amphibamidae		x			
Platyrhinops		x			
Potamochoston		x			
Capetus		x			
Macromerion		x			
Anthracosauria					
Silvernerpeton	x				
Eldeceeon	x				
Diplovertebron		x			
Gephyrostegus		x			
Hemichthys		x			
Discosauriscus					x
Solenodonsaurus		x			
Letoverpeton					x
'Phanerosaurus'					x
Aïstopoda				x	
Dolichosoma				x	
Oestocephalus		x			
?Ophiderpeton		x			
Phlegethontia		x			
Nectridia					
Sauravus				x	

TABLE 3. Continued. European Carboniferous-Permian localities and their fauna.

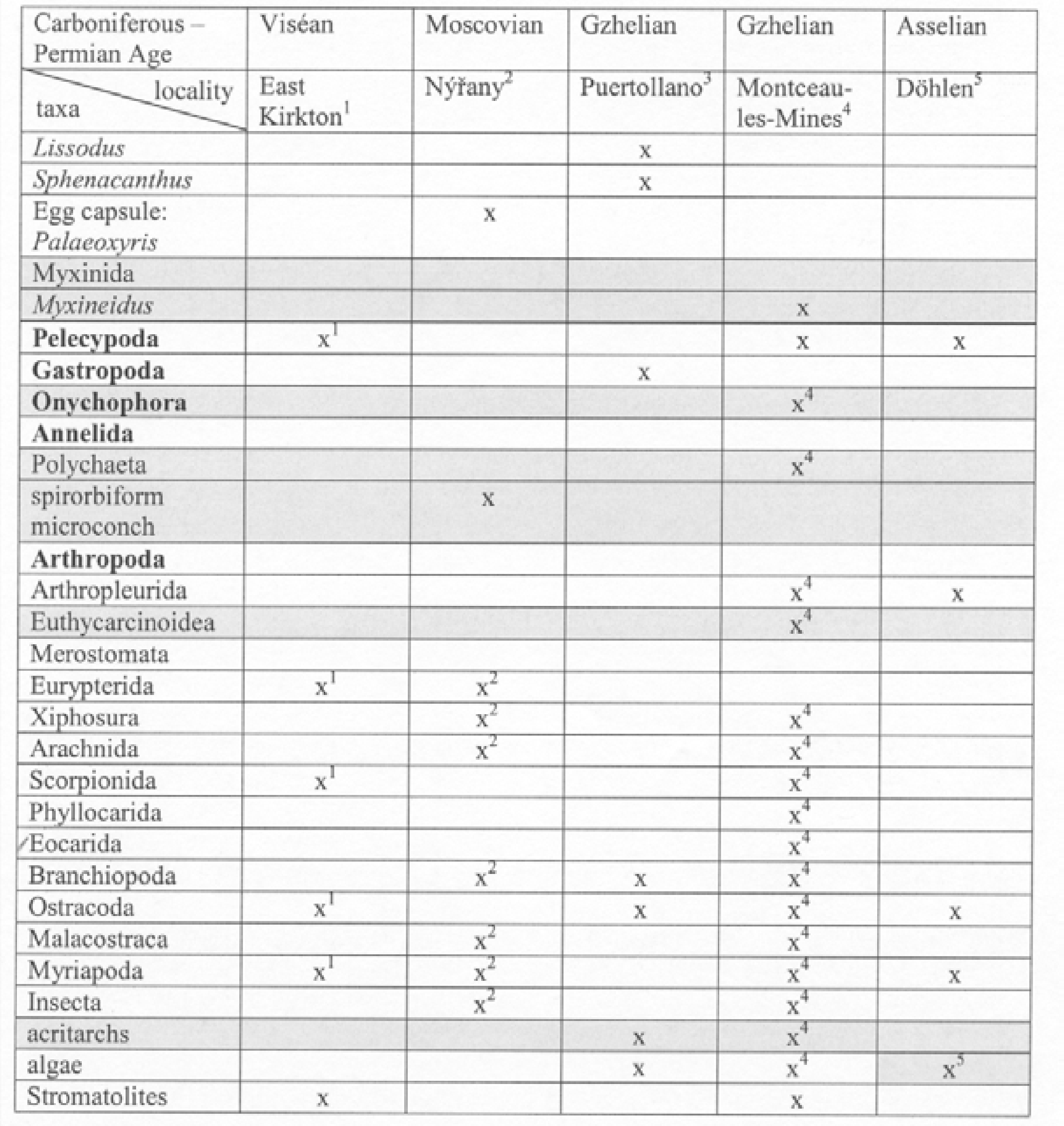


Carboniferous – Permian Age	Viséan	Moscovian	Gzhelian	Gzhelian	Asselian
taxa / locality	East Kirkton[1]	Nýřany[2]	Puertollano[3]	Montceau-les-Mines[4]	Döhlen[5]
Sauropleura		x			
Scincosaurus		x			
Monticellia				x	
Lepospondyli				x	
Microsauria			x		
Crinodon		x			
Ricnodon		x			
Sparodus		x			
Microbrachis		x			
Hyloplesion		x			
Saxonerpeton					x
Amniota					
Westlothiana	x				
Brouffia		x			
Coelostegus		x			
Kadaliosaurus					x
Batropetes					x
Pelycosauria					
Stereorachis				x	
Archaeothyris		x			
Edaphosaurus					x
Haptodus					x
Sarcopterygii					
rhizodont	x				
Dipnoi					
Sagenodus		x		x	
Actinopterygii					
palaeoniscoid	x[1]	x[2]	x[3]	x[4]	
platysomid	x[1]				
Acanthodii	x[1]				
Acanthodes			x	x	
Traquairichthys		x			
Elasmobranchii					
Xenacanthiformes					
Diplodoselache	x				
Xenacanthus		x			
Expleuracanthus				x	
Orthacanthus		x	x	x	
Triodus			x		
Euselachii					
Tristychius	x[1]				

Legend: x = present, grey = marine forms.

Sources: [1] East Kirkton, Scotland: Rolfe et al. (1994), Jeram and Selden (1994), Coates (1994), Paton (1994), Clack (2012): **Actinopterygii:** cf. *Elonichthys*, cf. *Cosmoptychius*, cf. *Rhadinichthys*, cf. *Mesopoma*, *Eurynotus*; **Elasmobranchii:** *Diplodoselache*, *Tristychius*; **Pelecypoda:** *Curvirimula*; **Merostomata: Eurypterida:** *Hibbertopterus*, *Dunsopterus*, *Cyrtoctenus*; **Scorpionida:** *Pulmoscorpius*; **Ostracoda:** paraparchitids, *Carbonita*; **Myriapoda:** indet.

TABLE 3. Continued. European Carboniferous-Permian localities and their fauna.



Carboniferous – Permian Age	Viséan	Moscovian	Gzhelian	Gzhelian	Asselian
taxa / locality	East Kirkton[1]	Nýřany[2]	Puertollano[3]	Montceau-les-Mines[4]	Döhlen[5]
Lissodus			x		
Sphenacanthus			x		
Egg capsule: *Palaeoxyris*		x			
Myxinida					
Myxineidus				x	
Pelecypoda	x[1]			x	x
Gastropoda			x		
Onychophora				x[4]	
Annelida					
Polychaeta				x[4]	
spirorbiform microconch		x			
Arthropoda					
Arthropleurida				x[4]	x
Euthycarcinoidea				x[4]	
Merostomata					
Eurypterida	x[1]	x[2]			
Xiphosura		x[2]		x[4]	
Arachnida		x[2]		x[4]	
Scorpionida	x[1]			x[4]	
Phyllocarida				x[4]	
Eocarida				x[4]	
Branchiopoda		x[2]	x	x[4]	
Ostracoda	x[1]		x	x[4]	x
Malacostraca		x[2]		x[4]	
Myriapoda	x[1]	x[2]		x[4]	x
Insecta		x[2]		x[4]	
acritarchs			x	x[4]	
algae			x	x[4]	x[5]
Stromatolites	x			x	

[2] Nýrany, Czech Republic: Štamberg and Zajíc (2008): **Actinopterygii:** Palaeoniscoids: "*Elonichthys*," *Sceletophorus*, *Spinarichthys*, *Pyritocephalus*; **Merostomata:** Xiphosura: *Prolimulus*; Eurypterida: indet.; Arachnida (10): *Eopholcus*, *Pyritaranea*, *Pleurolycosa*, *Geratarbus*, *Orthotarbus*, *Isobuthus*, *Promygale*, *Brachylycosa*, *Oomartus*, *Nyranytarbus*; Branchiopoda: *Euestheria*, Leaiidae indet.; Malacostraca: Syncarida: *Nectotelson*; Myriapoda: Chilognatha (14): *Euphoberia*, *Acantherpetes*, *Isojulus*, *Pleurojulus*, *Amynilyspes*, *Glomeropsis*, *Purkynia*, *Xyloiulus*, *Nyranius*, *Archiscudderia*, *Archicarabides*, *Hemiphoberia*, *Heterovorhoeffia*, *Sandtneria*; Insecta (9): Apterygota: Neoptera: Blattida: *Kinklidoptera*, *Friciella*, *Flabellites*, *Metaphyloblatta*, *Apotypoma*, *Gongyloblatta*, *Phyllobatta*, *Necymylacris*, "*Gerablattina*?."

[3] Puertollano, Spain: Schultze and Soler-Gijón (2004), Laurin and Soler-Gijón (2006): **Actinopterygii:** *Progyrolepis*, *Elonichthys*, *Palaeoniscum*, *Paramblypterus*, *Puertollanichthys*, ?*Bourbonella*; **Branchiopoda:** *Euestheria*.

[4] Montceau-les-Mines, France: Poplin and Heyler (1994), Schultze and Soler-Gijón (2004), Olive et al. (2012): **Actinopterygii** (8): *Blanzychthys*, *Igornichthys*, *Aeduella*, *Palaeoniscum*, *Paramblypterus*, *Bourbonella*, *Platysella*, *Blanzyhaplolepis*; **Pelecypoda:** *Anthraconaia*; **Onychophora:** *Ilyodus*; **Annelida:** Polychaeta: *Palaeocampa*, indet.; **Arthropoda:** Arthropleurida: *Arthropleura*; Euthycarcinoidea: *Schramixerxes*, *Sottyxerxes*; **Merostomata:** Xiphosura: Xiphosura indet., *Pringlia*; Phyllocarida: *Archaeostraca*; Eocarida (5): *Palaeopalemon*, *Eocaris*, *Crangopsis*, Pygocephalomorph indet., Palaeostomatopod indet.; Branchiopoda: *Estheria*, *Palaeolimnadiopsis*; Ostracoda: *Carbonita*; Malacostraca: Syncarida: *Palaeocaris*, Isopoda: *Paleocrangon*; **Arachnida:** indet.; Scorpionida: *Allobuthus*, *Coseleyscorpio*; Myriapoda (5): *Blanziulus*, Helminthomorpha indet., Oniscomorpha indet., Chilopoda indet., *Amynilyspes*; Insecta (at least 9): Apterygota: Monura, Paleoptera; Ephemoptera, Paleodictyoptera, "Megasecoptera," Neoptera: Mioptera, Caloneurodea genus *Apsidoneura*, Protoptera, Blattida; **Algae:** *Brotrycoccus*; **Acritarchs:** *Michrystridium*.

[5] Döhlen, Saxonia, Germany: Schneider (1994): no fishes (no osteichthyans nor chondrichthyans); marine calcareous algae (10): *Eolithoporella*, *Heteroporella*, *Macroporella*, *Clavaporella*, (?)*Anthracoporella*, (?)*Epimastopora*, *Nuia*, *Girvanella*, *Succodium*, *Saxonia*.

(Table 3). "The East Kirkton limestone is one of a number of horizons … referred to as 'fresh-water' limestones" (Whyte, 1994, p. 239). " … the environmental interpretation of the fresh-water limestones has been based on negative evidence – the absence of distinctive marine fossils -.." (Whyte, 1994, p. 246). As I pointed out above, negative evidence is no evidence (Schultze, 1996, 2009). Therefore Whyte (1994, p. 246) wrote logically that the ostracods, spirorbiform microconchids and fishes are also found in brackish or schizohaline environment. Spirorbiform microconchids occur in marine to brackish environment, not only in freshwater environment (Taylor and Vinn, 2006). They occur together with foraminifera (see above: e.g., Joggins). The most common fossil at East Kirkton (Clack, 2012: p. 304: "…are crowded with …") is a paraparchitid ostracod (Rolfe et al., 1994). Paraparchitid ostracods are worldwide distributed at the beginning of the Carboniferous, they are interpreted as brackish to marine (Olempska, 2008). The fishes (acanthodians, actinopterygians, chondrichthyans) are common Carboniferous forms and occur in different environments; the platysomid is a marine form, occurring in Kinney Brick Quarry and Mazon Creek (Zidek 1992). Coates (1994) compared them with the fishes in Kinney Brick Company Quarry (see above), where they are deposited in coastal marine or deltaic environment. The bivalve *Curvirimula* occurring with the fishes in East Kirkton fits into such environment. Fishes associated with ostracods and sometimes eurypterids occur in the upper part of the East Kirkton sequence, whereas the tetrapods occur in the lower part together with ostracods and eurypterids. Even though Clack (2012) characterized the tetrapods of East Kirkton as terrestrial, still she argued that the complete preservation indicates that they died or even lived in the water. In the final paper in the on the special volume on East Kirkton, Clarkson et al. (1994) argued for deposition in a shallow lake avoiding the evidence of marine actinopterygians, ostracods (they cite only the rare *Carbonita*) and marine bivalves, and the lack of freshwater evidence ("fresh-water" limestone of Whyte, 1994). In conclusion, there is no evidence for a freshwater lake at East Kirkton. On the contrary, the fauna indicates a shallow marine environment, in which the terrestrial forms like scorpionid and myriapodous arthropods and plants have fallen in. It may be difficult to separate the tetrapods, which were exclusive terrestrial, from those which lived in the brackish to normal marine environment and were salt water tolerant.

Bohemia, Czech Republic

In the northern part of Czech Republic a series of Permo-Carboniferous basins occur, they are interpreted as freshwater deposits ("lakes," see e.g., Štamberg, 2006) with a north-south stretching Boskovice Graben, which forms the connection to the Paleotethys in the south after Schultze and Soler-Gijón (2004). The locality Nýrany in the Kladno-Rakovnik basin (Westphalian D) is here taken as an example of the occurring fauna (Table 3). Only spirorbiform microconchs and possibly the xiphosuran and eurypterid can be taken as direct indication of marine influenced environment. The similarity in the fish fauna with German, French and Spanish Permo-Carboniferous basins is accepted as indication of connection of these basins with each other through rivers. In contrast Schultze and Soler-Gijón (2004, fig. 4) proposed a connection to the south, the Paleotethys, which explains the similarities with North American basins containing the same fishes, too. Recently Lojka et al. (2010) described laminated sediments in the Central and Western Bohemian basins (Mšec Member, Stephanian B), which show the couplet-lamination double lines typical for tidal sedimentation, even though the authors compare only with freshwater lacustrine deposits and argue that this is the first occurrence of laminae couplets in freshwater sediments. Tidal rhythmites showing couplet-lamination and neap-spring sedimentary cycles are very well known fom modern and ancient localities (Archer, 1994; Archer and Feldman, 1994; Tessier, 1993; Tessier et al., 1995; Conghenour et al., 2009; Longhitano et al., 2012). The lamination in tidal rhythmites are different from the wavy, interrupted lamination described from an inner Australian lake (Ainsworth et al., 2012), which are attributed to "daily changes in wind direction and velocity, along with weekly to monthly discharge variations in the feeder river system" (Ibid., p. 607). The faunal similarities with Spain and North America through the Paleotethys contradict an interpretation as intra-mountainous lakes. The description of the double lamination is the clearest indication of tidal (estuarine or coastal marine) environment in the Czech Permo-Carboniferous basins (Lojka et al., 2010).

Puertollano, Spain

The Stephanian basin of Puertollano, well known for the coal and bituminous shales, was interpreted as an endorheic basin (Wagner, 1985, and references therein). However, recent paleontological, sedimentological and geochemical studies (see review in Schultze, 2009), demonstrate sedimentary deposition in a paralic environment (coastal, estuarine or lagoonal). The Puertollano coal and bituminous shale field only represents a remnant of a much more extensive basin which opened eastwards in the direction of the open sea (Wagner, 1989; Wagner and Alvarez-Vázquez, 2010). Sedimentological (Soler-Gijón and López-Martínez, 2008) and paleoichnological (Soler-Gijón and Moratalla, 2001) analyses indicate tidal conditions in the basin and consequently a direct connection with the Paleotethys in agreement with the paleobiogeographic results of the comparison of the faunas of Puertollano and other Permo-Carboniferous localities (Schultze and Soler-Gijón, 2004; Table 3). In addition the discovery of acritarchs (Fonollá, 1988; Soler-Gijón and Moratalla, 2001) and several geochemical indicators of marine influence (García-Molla, 1994; Alastuey et al., 2001) support an interpretation of Puertollano as a marine to brackish paleoenvironment despite contrary interpretation as fresh water by Fischer and Schneider (2008), also based on organic geochemistry of the sediments. Only three tetrapods are recorded from that locality, nevertheless the authors (Laurin and Soler-Gijón, 2001, 2006) argue that the temnospondyls are adapted to a near shore marine environment.

Montceau-les-Mines, France

Montceau-les-Mines, France, was compared to Mazon Creek in 1982 (Rolfe et al., 1982), but thereafter considered fresh water because it is interpreted to be an intramontaneous basin. In contrast, the aeduellid *Bourbonella* (Gottfried, 1987; Mickle, 2011) and xiphosurids indicate a marine connection with basins in North America (see for detailed comparison with North American localities: Maples and Schultze, 1989; Schultze and Maples, 1992; Schultze, 2009). And more important, stenohaline marine organisms occur in the basin of Montceau-les-Mines: acritarchs (Doubinger, 1994), polychaetes (Pacaud et al., 1981; Poplin et Heyler, 1994, p. 119-120: *Palaeocampa* "jusqu'à present seulement connu dans la faune marine de Mazon Creek," Pleijel et al. 2004), onychophorans (Poplin et Heyler 1994, p. 121-122: "Il pourrait s'agir de la même forme que celle de Mazon Creek"); euthycarcinoid arthropods (Schram and Rolfe, 1994, p. 139: "These species bear clear affinities to the euthycarcinoids found in the Middle Pennsylvanian Mazon Creek faunas of Illinois…") and myxinids (Table 3; see Schultze and Soler-Gijón, 2004, for detailed analysis of the fauna, and Schultze, 2009, p. 130-131). All these forms occur in contemporaneous marine localities. Myxinids are clear stenohaline marine indicators; they are known today and in the Carboniferous (marine Mazon Creek and Bear Gulch faunas) only from a marine environment (their body fluid is isotonic with sea water). The lungfish *Sagenodus* has recently been described from Montceau-les-Mines (Olive et al., 2012), which makes the fauna even more comparable to North American basins (e.g., Robinson, Hamilton) and requires marine tolerance of the faunal elements for the migration and a connection of the basin to the sea in the south. Olive et al. (2012) agree with Schultze and Chorn (1997) that *Sagenodus* has a worldwide distribution, is found in marine to freshwater environments and therefore euryhaline. It adds another fish, which requires at least a connection of the Montceau-les-Mines basin to the sea, whereas acritarchs, polychaetes, onychophorans, euthycarcinoid arthropods and myxinids are the direct indication of a saltwater environment. Still, most authors interpret Montceau-les-Mines as a freshwater basin, because "the closest Upper

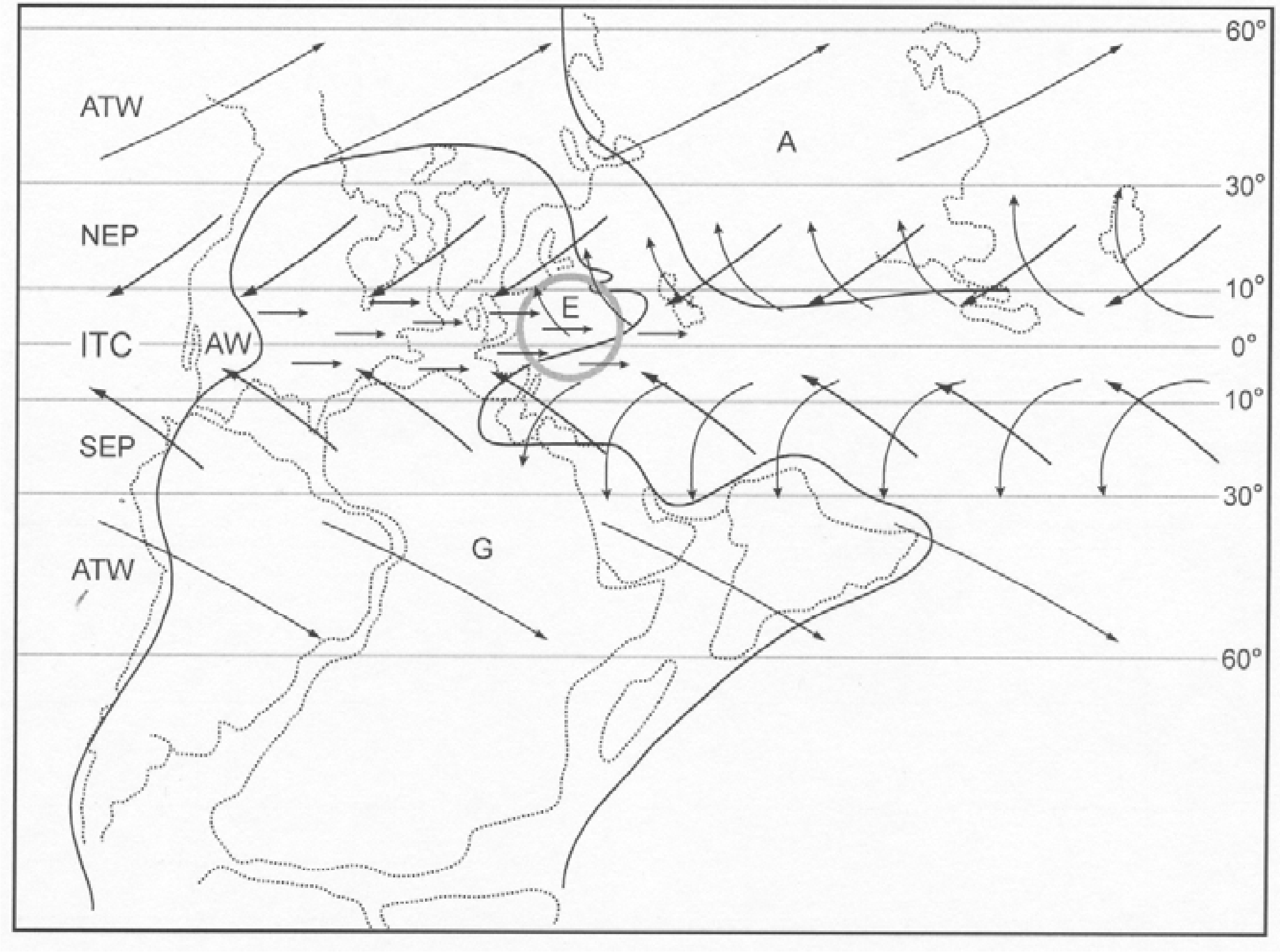


FIGURE. 2. Late Carboniferous/Early Permian global paleowind system changed after Schneider (1994, fig. 11). **Abbreviations: A**, Asia; **ATW**, westerlies; **E**, Europe; **G**, Gondwana; **NEP**, **SEP**, northern and southern trade winds; **ITC**, Inter-Tropical Convergence. Position of Döhlen in the middle of **E**; in the circle, the northern trade winds are moved down to the equator to get the marine algae transported from the northern shelf of the Paleotethys to the Döhlen basin.

Carboniferous marine deposits were located at least several hundred kilometers SW of Montceau" (Racheboeuf et al., 2008, p. 3). Consequently "the genus *Alanops* was possibly the first xiphosuran freshwater representative" (Ibid. p. 3). That is the paleogeographic argument of Gray (1988), which is not an acceptable argument (see Schultze, 1995, 2009) and has been proven wrong in many cases, particularly in both examples used by Gray (1988), Lower Devonian Beartooth Formation and the Upper Devonian Escuminac Formation (Schultze, 1996, 2009).

Döhlen, Germany

In Saxonia, the Lower Permian Döhlen basin is unique as it furnished a rich tetrapod fauna and no fish. Nevertheless, marine algae occur together with pelecypods and ostracods. That is a clear indication that the basin is marine, at least filled with salt water. Schneider (1994) postulated a chemocline between fresh water at the surface and salt water with the algae at the bottom; the tetrapods are terrestrial and/or forms which lived in the fresh water of the upper part of the water column after Schneider (1994). Schneider explained the presence of marine algae by wind transport of their cysts from the northern shelf of the Paleotethys over 200 some km. Looking at the reconstruction of the paleowind system (Fig. 2), it is difficult to imagine such transport. Döhlen lay in the inter-tropical convergence zone (ITCZ) with eastern directed winds in the Early Permian. The source of the marine algae lay at the equator south of Döhlen. Schneider (1994) moved here freely the northern trade wind zone to the equator. It seems to me impossible that ten different marine species of algae or their cysts could have been transported by wind over a distance of more than 200 km within the calm equatorial zone. The possible seasonal migration of the ITCZ (cf. Tabor and Poulsen, 2008) or cyclones (Schneider, 1994) could have allowed the wind dispersal to the continent. However, there are no sedimentological/mineralogical data (e.g., analyses of eolian silt- and sandstones; see Loope et al., 2004, and references therein) supporting the paleowind direction in Döhlen or in other close Permian localities as suggested by Schneider (1994). His conclusions are based only on a global climatic model of atmospheric circulation without any detailed analysis of the regional parameters. As an alternative hypothesis, it seems to be much simpler to argue that the Döhlen basin was marine or connected with the open sea, and that the aquatic tetrapods must have been salt water tolerant like the pelecypods and ostracods because they lived together with the algae on the bottom. Pelecypods, ostracods and algae are the organic portion of the limestone, which cannot be lacustrine containing marine algae, because these organisms must have lived together. Schneider (1994) postulated wind transport for the ostracods (no direction given) and "a specific, very high active and passive migration potential, as evidenced by their appearance in nearly all basins and different facies types" (Ibid., p. 463) for the pelecypods. That could be interpreted as adaptation of both groups from freshwater to marine, or that all the basins are saltwater basins because of the co-occurrence of pelecypods (no identification given) and marine algae. Schultze and Soler-Gijón (2004) postulated a marine connection through the Permo-Carboniferous basins in the Czech Republic. Schneider (1994) interpreted reptiliomorph amphibians as immigrants from the south. Döhlen is not different from other small Permian European basins. The best comparative example is Weissig, 15 km away from Döhlen. Despite the actual dimension and isolated condition of the Weissig basin, a "connection to paralic biotops" (Barthel et al., 2010) has to be admitted because of the presence of shark egg capsules (*Fayolia*) and fish skeletal remains (palaeonisciforms and xenacanth sharks). Döhlen and Weissig may be parts of a large inter- to supratidal (deltaic/estuarine) system, where even neighboring ponds could have different salinities and different faunas (Schultze, 2009, p. 132).

These are only a few of many North American and European Permo-Carboniferous basins, which were interconnected. Here I have selected specific faunal elements, which indicate marine paleoenvironment whereas most authors do not separate the faunal elements and use an overall similarity of the whole fauna and flora (e.g., Olive et al., 2012). The overall similarity is misleading because one has to separate aquatic elements, which alone can define the depositional environment of the deposits in question. Thus, terrestrial elements, plants (as long as they did not grow in a coastal environment, see Falcon-Lang, 2005), insects, most tetrapods etc., are not indicative. The tetrapods are taken by most authors as terrestrial, and it is not easy to support that they have lived in the same environment except for some. Clack (2012) argued for some tetrapods in East Kirkton, that their superb preservation down to details, favors an interpretation that their place of fossilization was their place of life. Schoch (2009) proposed aquatic adaptation for most Carboniferous tetrapods. For tetrapods, which are found far away from land like those in Robinson, Kansas (*Trimerorhachis*, a dissorophid, *Cricotus*, *Diplocaulus*, and *Lysorophus*) or those occurring only in the marine Essex fauna of Mazon Creek, Illinois (temnospondyl *Saurerpeton*, aistopod *Ophiderpeton*), it is easy to accept saltwater tolerance. That is also possible for tetrapods, which occur in the marine Essex and brackish Braidwood fauna (temnospondyl *Amphibamus*, lysorophid *Brachydectes*). For all other tetrapods, which occur in marine influenced environments, it is nevertheless difficult to deduce if they were salt water tolerant or terrestrial. Presence of a lateral line system (*Ichthyostega*, *Acanthostega*, *Greererpeton*, etc.) or of branchial apparatus (e.g., *Micromelerpeton*) indicates aquatic life only. Freshwater adaptation is in most cases a postulate based on comparison with recent amphibians because they are fossilized in sediments, which were deposited in a limestone with marine algae as in Döhlen.

Laurin and Soler-Gijón (2010) reviewed the literature on interpretation of Paleozoic tetrapod localities and the adaptation of early tetrapods. They gave probable explanations why early tetrapods are usually considered creatures of fresh water. First, the dipnoans are taken as their closest sister group; and extant dipnoans are living in fresh water, so that one accepted that the Devonian tetrapods were freshwater dwellers (but see above). Second, Carboniferous tetrapods are compared with extant amphibians, which again are nearly exclusively restricted to fresh water, even though the ancestral Devonian forms were living in a marine environment (Thomson, 1980). Laurin and Soler-Gijón (2010) used a cladistic approach with the result that Carboniferous tetrapods are salt water tolerant (Laurin and Soler-Gijón, 2010, fig. 4, see also Milner, 1987). The change from marine to freshwater environment occurred in an estuarine environment after Parker and Webb (2008). The restriction to fresh water occurred only later.

CONCLUSIONS

The transition from fish-like to tetrapod-like sarcopterygians occurred in the Devonian in a coastal marine to estuarine environment.

In the Permo-Carboniferous, the analysis of different localities points in one direction: saltwater tolerance of early tetrapods (Laurin and Soler-Gijón, 2010). Nevertheless there are problems:

1. If marine indicators are present, then the interpretation is clear. That is not always the case, so that we are faced with the situation that there are no clear freshwater and only few marine indicators in the aquatic Permo-Carboniferous system. Gray (1988) gave a list of criteria to recognize freshwater in the fossil record; none of them holds up (Schultze, 1996, 2009).

2. We cannot use the environment of living organisms as a citerion for an environment in the Paleozoic, more than 250 million years ago. We should take the environment of faunal elements living in the same or close time period (see myxinids or the dipnoan *Sagenodus* above).

3. Often paleosols are mentioned as terrestrial indicators. These are not paleosols in the sense a soil scientist would accept. In most cases these are rootlets as occur in tidal sediments.

4. Red sediments are not necessarily formed in a freshwater or terrestrial environment. That has been shown by faunal comparison between Old Red fish faunas with faunas outside the Old Red and trace fossils in the Old Red of Spitsbergen. Here the Permian Texas Red Beds have been given as example where only marine indicators are present (see above).

The data indicate that early tetrapods were able to live in marine waters. Arguments in favor of saltwater tolerance were proposed earlier by Thomson (1980), Schultze (1985), Milner (1987) and others. A full survey of literature by Laurin and Soler-Gijón (2010) came to the general conclusion that all Devonian and Permo-Carboniferous tetrapods with very few exceptions are salt water tolerant. Even though it appears that early tetrapods are aquatic and salt water tolerant, nevertheless one should not use them as a saltwater indicator. It is prudent to use them first as outside the aquatic depositional system except forms with a lateral line system (*Ichthyostega*, *Acanthostega*, *Greererpeton*, *Trimerorhachis*, *Dendrerpeton*, *Micromelerpeton*, *Branchierpeton*, *Microbrachis*, *Proterogyrinus*, *Archeria*) or gills (*Branchiosaurus*) as terrestrial forms until the opposite has been proven.

Thus I see only two clear environmental indicators:

1. Tidal evidence (sedimentological, paleoichnological, histological) indicate a coastal marine condition or at least an environment with a direct connection with the sea (estuaries, lagoons). Given the possibility of a freshwater tidal environment (e.g., inner part of estuaries, close to the fluvial zone; Dalrymple and Choi, 2007), the sedimentological evidence (tidal rhythmites) does not always imply saline water (Archer and Greb, 2012). Consequently the salinity in the environment has to be ascertained by paleontological studies (Coughenour et al., 2009) and especially by the geochemical and isotopic analyses of the bioapatites of skeletal hard tissues (see Cloutier et al., 2011, Matton et al., 2012 for the Escuminac Formation as a very good example).

2. Only comparison with the environment of the contemporaneous taxa in a clearly proven marine environment can be used. As example I may cite here *Sagenodus*, a lungfish, which is clearly marine in NE-Kansas; it follows that all localities where the genus occurs must be reachable by marine forms. The tetrapods (trimerorhachoid, dissorophid, *Cricotus*, *Diplocaulus*, *Lysorophus*) co-occurring with *Sagenodus* at that locality are then to be interpreted as salt water tolerant, too.

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CARBONIFEROUS-PERMIAN BOUNDARY IN THE HALGAITO FORMATION, CUTLER GROUP, VALLEY OF THE GODS AND SURROUNDING AREA, SOUTHEASTERN UTAH

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Abstract—Carboniferous-Permian strata of southeastern Utah lack evidence of volcanism or local reversals in the magnetostratigraphic record. Although radiometric dating using Halgaito Formation sediments has been attempted, it has not been successful. Additionally, the Carboniferous-Permian Boundary (CPB) lacks any large extinction or speciation events, thus most avenues of radiometric and relative dating are barred. Marine biostratigraphy has recently redefined the Carboniferous-Permian Global Stratotype Section and Point as the first occurrence of the conodont *Streptognathodus isolatus*, but if a terrestrial deposit lacks a marine influx or if this species of conodont is not encountered then it cannot be dated by these means. Temporally significant fusulinids include *Ultradaixina* and *Schellwienia*, which nearly disappear at the CPB, and the fusulinid *Sphaeroschwagerina*, which appears 6 meters (m) above the CPB. Nonmarine extinction and speciation events of this time period are present but are not numerous. Fossils and stratigraphic data collected from 1960 to 2010 in southeastern Utah allow for biostratigraphic analysis in this region. Temporally significant taxa recovered to date from the Halgaito Formation near Mexican Hat, southeastern Utah that occur at or near the CPB include: the gastropod *Euphemites* cf. *E. graffhami*, the brachiopod *Hystriculina wabashensis*; the xenacanth shark *Orthacanthus texensis*; and the tetrapods assignable to *Archeria*, *Seymouria*, *Limnoscelis*, Limnoscelidae, *Edaphosaurus*, *Ophiacodon*, *Dimetrodon*, and *Sphenacodon*. Of these, only *O. texensis* appears either at or very shortly after the CPB in the Wolfcampian. Limnoscelids have previously been considered extinct prior to the CPB, but there are very few known from the geologic record. A specimen of *Limnoscelis* is known from 10 m above the base of the section along with specimens of *O. texensis* and *Ophiacodon*. Additional material assigned to ?Limnoscelidae has been recovered between 65 and 70 m above the base of the section. Based on the paucity of previously recovered limnoscelids outside of the study area and the questionable identity of the ?Limnoscelidae material between 65 and 70 m above the base of the section, it is suggested that at least in southeastern Utah, *Limnoscelis* survives to just beyond the CPB and exists concurrently with *O. texensis*. The ?limnoscelid material between 65 and 70 m above the base of the Halgaito Formation is only questionably assigned to Limnoscelidae and should not be included in this analysis. The proposed range of *Orthacanthus texensis* is not questioned, as is the range for the family Limnoscelidae, as *O. texensis* is much more common in the fossil record. Based on this analysis, there appears to be a disconformity between the Shafer Limestone and the first fossiliferous locality 10 m above the base of the Halgaito Formation where *Orthacanthus texensis* first occurs. The CPB is placed within the first 10 m of the Halgaito Formation and before the first appearance of *Orthacanthus texensis*. Although one specimen of ?*Seymouria* has been reported from the Halgaito Formation, more material should be recovered prior to making any definitive age correlations for this portion of the section.

GEOLOGICAL SETTING

In the Four Corners area of the United Sates, the Carboniferous-Permian Cutler Group is underlain by the thick marine carbonates of the Pennsylvanian Honaker Trail Formation, the uppermost formation of the Pennsylvanian Hermosa Group (Fig. 1). Here, the sediments of the Honaker Trail Formation consist of deep and shallow marine carbonates interbedded with siltstones and sandstones from a coastal plain (Achtley and Loope, 1993). At the top of the Honaker Trail Formation, cycles of terrestrial red beds and marine sandy carbonates are capped by the fossiliferous Shafer Limestone as uplift in the region transitioned the area from a marine to a nonmarine environment (Wengerd, 1955; Wengerd and Matheny, 1958; O'Sullivan, 1965; Ritter et al., 2002).

In the study area at the Valley of the Gods (VOG), in John's Canyon, and near Mexican Hat, San Juan County, Utah, the Cutler Group consists of (from base to top) the Carboniferous-Permian Halgaito Formation, and the following Permian units: the Cedar Mesa Sandstone, the Organ Rock Shale, and the DeChelly Sandstone. Historically, the upper Honaker Trail Formation beds above the first occurrence of terrestrial sediments, and the Halgaito Formation below the McKim Limestone, were assigned to the Pennsylvanian "Rico Formation" (Wengerd, 1950). Named by Cross and Spencer (1900) for exposures near Rico, Colorado, the terminology was expanded from the Paradox Basin into southeastern Utah (Baker and Reeside, 1929; Baker, 1933, 1936, 1946; McKnight, 1940). Condon (1997) provided a review of the history and issues of the assignments of the "Rico" and Halgaito formations.

Because the "Rico Formation" consists of temporally and lithologically transgressive beds, it is no longer recognized as a valid unit. These beds have been considered part of both the Cutler and Hermosa groups by multiple authors (Wengerd and Strickland, 1954; Turnbow, 1955; Herman and Sharps, 1956; Baars, 1962; Loope et al., 1990; Condon, 1997). In the Monument Valley area the Shafer Limestone provides an excellent marker bed, and for this study the contact between the basal Halgaito Formation and upper Honaker Trail Formation is considered to be the top of the distinct Shafer Limestone as per Baker (1936), Condon (1997, p. 13), and Ritter et al. (2002) (Fig. 2).

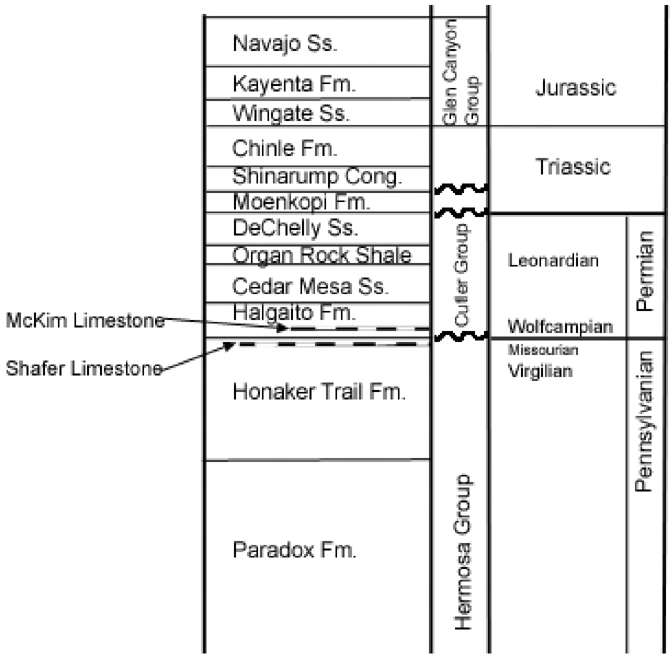

FIGURE 1. Large scale stratigraphy in the Valley of the Gods and Monument Valley area, Utah and Arizona.

The Halgaito Formation is a red-brown, lithified desert loessite deposit with other terrestrial and some marine facies interfingering. Although there is currently contention among several authors as to the standing of the Halgaito Formation (Loope, 1984; Loope et al., 1990; Dubiel et al., 1996; Condon, 1997), it does constitute a lithologically recognizable unit in the study area and will be treated as a distinct formation here. Interfingering with the Halgaito Formation to the north of the study area in the Canyonlands region is the marine Elephant Canyon Formation, which has been assigned to the Virgilian and Wolfcampian (Vaughn, 1962; Loope, pers comm. in Murphy, 1987; Sanderson and Verville, 1990 as per Condon, 1997, p. 20; Baars, 1991, 1995; Davydov et al., 1995; Chernykh et al., 1997; Sumida et al., 1999a, 1999b, 1999c).

To the west of Monument Valley, Arizona and east of the study area in the area of Comb Wash, the Halgaito Formation interfingers with and grades into the Cedar Mesa Sandstone, a well-indurated unit of eolian sands (Baars, 1962, 1979). To the east and southeast of the study area, both the Halgaito Formation and the Cedar Mesa Sandstone are subsumed into the undifferentiated Cutler Formation. Here the undifferentiated Cutler Formation occurs as a wedge of arkosic alluvial fan sediments originating from the rising Uncompahgre highlands to the east of the study area (Baars, 1979). In the Monument Valley area, the Cedar Mesa Sandstone is not present, and the Halgaito Formation is not distinguishable from the nearly identical Organ Rock Formation above (Gregory, 1938).

CONDITIONS PRESENT IN UTAH AT THE TIME OF DEPOSITION

Just prior to the deposition of the Halgaito Formation, southeastern Utah consisted of shallow oceans with the Piute platform (formerly the Emery uplift) to the north, the Defiance and Zuni uplifts to the southwest, and the large Uncompagre highlands to the east (Fig. 3). The upper Honaker Trail and lower Halgaito formations record the uplift of the Uncompaghre highlands and the retreat of the ocean from the miogeocline. The withdrawal of the ocean provided a relatively flat lowland topography and exposed carbonate-rich sands just west of the ocean (Baars, 1962; Huffman and Condon, 1993; Eberth and Berman, 1993; Baars, 1995; Dubiel et al., 1996; Condon, 1997; Tabor et al., 2008).

During the time of the Halgaito Formation's deposition, southeastern Utah was located just north of the equator and trade winds were from the north (Fig. 4). The trade winds shaped the carbonate-rich sands into the eolian deposits of the Cedar Mesa sand ergs. Southeastern Utah was at the tropical-arid boundary with an arid regime to the north (Scotese, 2002; Tabor et al., 2008). As the paleoclimate over the ocean was arid, considerable evaporation occurred and the water vapor was carried to the south by trade winds and seasonal monsoons (Robinson, 1973; Parrish et al., 1986; Scotese, 2002; Tabor et al., 2008). The Halgaito Formation is a desert loess deposited downwind of the Cedar Mesa sand erg from the silts and fine sands blown off the erg (Baars, 1962; Blakey, 1979; Murphy, 1987; Johansen, 1988; Stanesco and Campbell, 1989; Huffman and Condon, 1993; Eberth and Berman, 1993; Baars, 1995; Dubiel et al., 1996; Condon, 1997; Tabor et al., 2008).

The most recent review and interpretation of the deposition of the Halgaito Formation (Scott, 2005) interpreted deposition of the Halgaito Formation to have been aided by the presence of vegetation interrupting wind flow off the erg. This inferred vegetation decreased the wind velocity and brought the silts and fine sands out of suspension. Water on the ground and on the surface of the vegetation from onshore flow and rains helped to entrap the silt. Numerous paleosols are present, and rhizoliths are common within them, supporting the presence of a good amount of vegetation at least in the lower half of the formation.

The continuing rise of the Uncompagre highlands to the east filled the Paradox Basin with alluvial fan and flood plain sediments. Rivers traced westward to the area of Halgaito Formation loess. Eventually the Cedar Mesa erg that surrounded the Halgaito Formation covered over the small depositional low.

Because the Halgaito Formation is derived from the Cedar Mesa Sandstone and interfingers with it on both the eastern and western margins of the study area (Baars, 1962, 1979), it is necessary to consider the deposition of the Cedar Mesa Sandstone. Much of the basal Cedar Mesa Sandstone has been interpreted as a nearshore marine deposit (Baars, 1962; Mack, 1979; Stanesco and Campell, 1989), whereas many of the upper beds have been identified as being eolian in origin (Stanesco and Campell, 1989). To the southeast of the study area in Utah, a lagoonal or sabkha facies has also been recognized in the Cedar Mesa Sandstone (Blakey, 1979; Stanesco and Campell, 1989; Huffman and Condon; 1993; Nuccio and Condon, 1996; Condon, 1997). To the east of the study area, Soreghan (1992a, b) recognized ergs, sabkhas, and mudflats in the arid to semi-arid fluvial systems of the Cedar Mesa Sandstone and the undifferentiated Cutler Formation.

The Cedar Mesa Sandstone has numerous marine fossil fragments, however these may have been reworked from the carbonate-rich Honaker Platform. Tetrapod tracks, some wood, and some tetrapod fossils are known from the Cedar Mesa Sandstone, however their relationship to the Halgaito-Cedar Mesa boundary is not known (Stanesco and Campbell, 1989; Sumida et al., 1999b; this study: trackway). It is also notable that the wood and tetrapod fossils from the Cedar Mesa Sandstone were from a stream bed in the east of Canyonlands National Park, however, the locality has since been destroyed (Sumida et al., 1999b). Structures of the Cedar Mesa Sandstone just above the Halgaito-Cedar Mesa boundary in the VOG and in Johns Canyon are eolian dune crossbedding and not marine. Based on observations in the study area, an eolian origin for at least this portion of the Cedar Mesa Sandstone is more probable. Although there may be some marine facies, it is also possible that the marine interpretation of the Cedar Mesa Sandstone was due to the basal sands originating from the carbonate-rich sands of the recently exposed miogeocline. As time passed, these sands were refined into typical dune particles, giving the appearance of a transition from marine to nonmarine.

HALGAITO STRATIGRAPHY AND BIOSTRATIGRAPHY

Detailed stratigraphic columns were measured in the VOG and John's Canyon (Figs. 5-6). Stratigraphy was recorded using a Jacob's

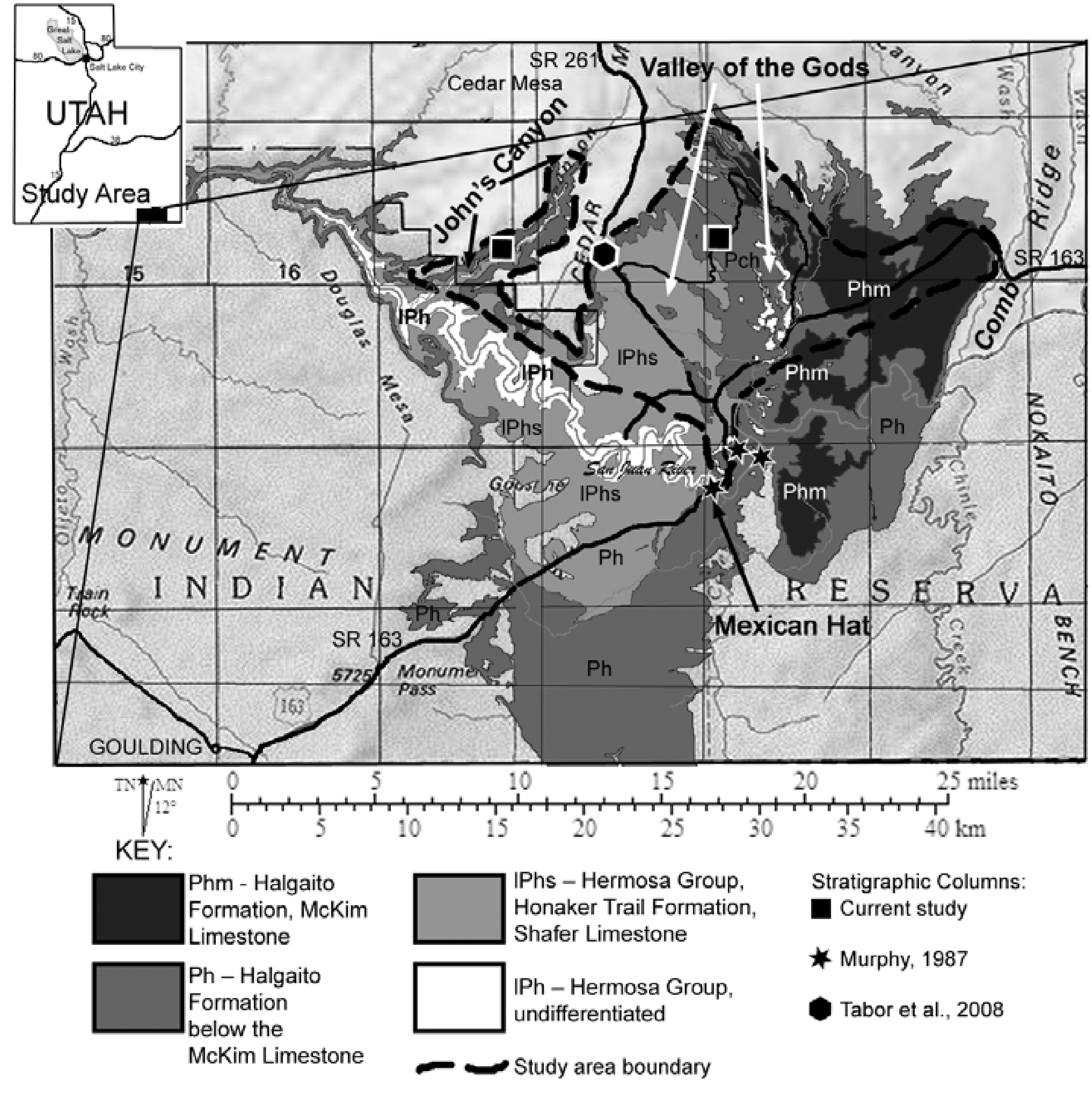

FIGURE 2. The location of the study area in southeastern Utah including: Valley of the Gods, John's Canyon, and Mexican Hat. Mapped exposures of the Halgaito Formation and the Hermosa Group in and near to the study area are modified from Haynes et al. (1972), and Hackman and Wyatt (1973). Within the study area stratigraphic columns are from the current study, Murphy (1987), and Tabor et al. (2008).

staff and a Brunton compass to measure thickness (following Compton, 1985). Lithology was recorded using a Geological Society of America Rock-Color Chart (GSA, 1991) and standard sediment grain size measurements followed Pettijohn (1975, p. 29 as per Compton, 1985). Paleosol descriptions followed Mack et al. (1993). Lithologically distinct beds were photographed and sampled for thin sectioning.

The base of the Cedar Mesa Sandstone seemed to be relatively constant over the study area, whereas access to the base of the Halgaito Formation was often problematic. Measurements were taken for all major fossil localities to determine how far below the base of the Cedar Mesa Sandstone each locality occurred.

GEOLOGY OF THE HALGAITO FORMATION

In John's Canyon the Halgaito Formation above the Shafer Limestone has been measured at 142 m (466 ft) thick (Gregory, 1938) and 159.64 m (523.75 ft) thick (this study). In the VOG the Halgaito Formation above the Shafer Limestone has been measured as 147.81 m (484.94 ft) thick (this study). Near Mexican Hat the Halgaito Formation above the McKim Limestone, which is approximately 47 m above the Shafer Limestone in the VOG, was measured as 125 to 126 m (410 to 413 ft) thick (Murphy, 1987). Because the Halgaito Formation was deposited on a recently exposed miogeocline with no significant features, the nonchannelized beds are remarkably parallel.

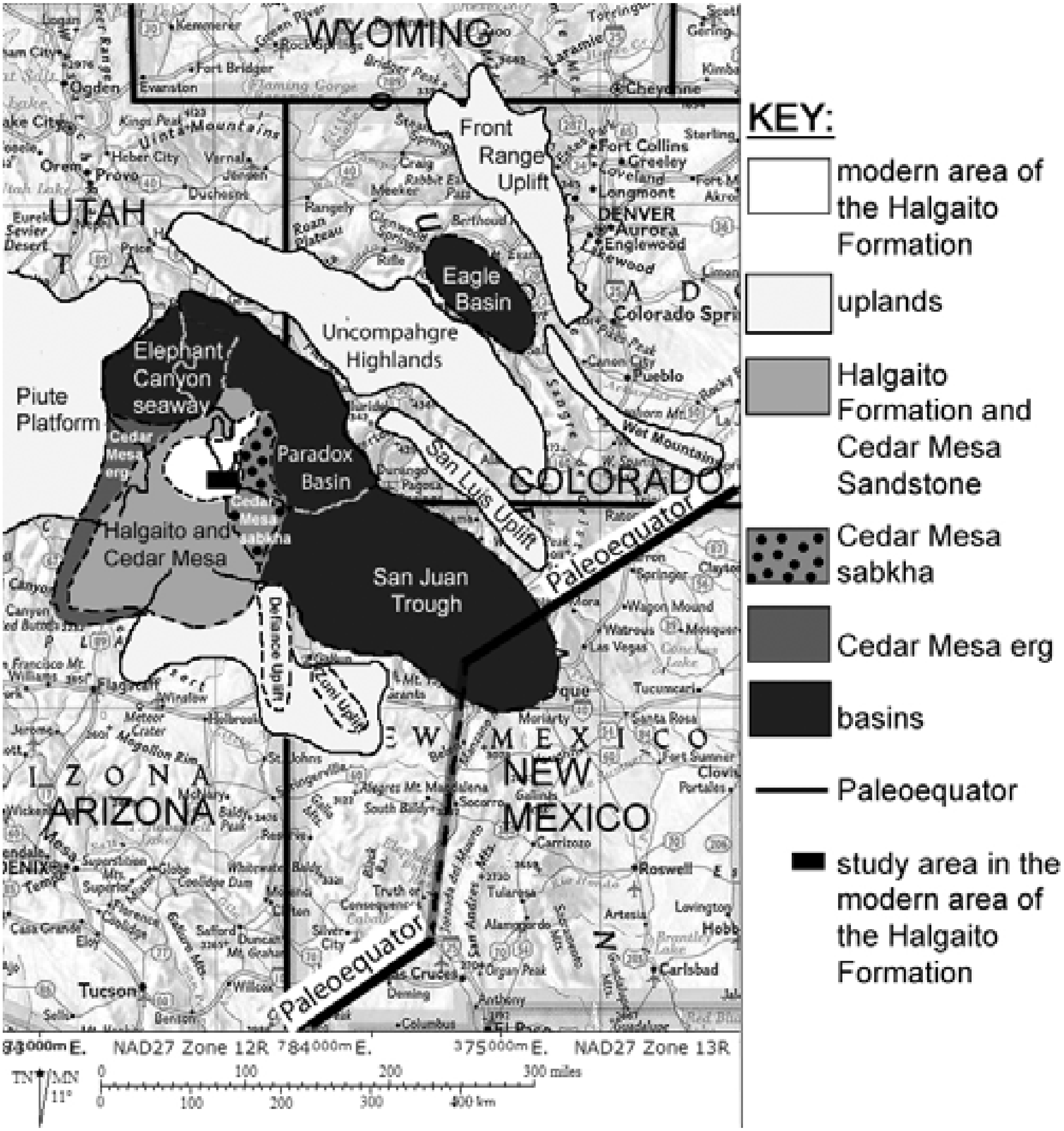

FIGURE 3. Carboniferous-Permian structures and depositional regimes in the Four Corners area. Paleoequator is for 300 Ma and jog is due to later compression of the region. Modified from Baars (1962), Huffman and Condon (1993), Eberth and Berman (1993), Baars (1995), Dubiel et al. (1996), Condon (1997) and Tabor et al. (2008).

The Halgaito Formation is comprised of primarily reddish-brown eolian siltstones to fine- grained sandstones, paleosols, and rare fluvial conglomerates grading into fluvial sands, and some nearshore marine sands in the lower third of the unit. In the field, many of the eolian deposits appear massive due to weathering and/or low grade diagenesis. When structures are present, the siltstone beds show normal grading, planar lamination and small trough crossbeds. In the upper half of the unit, eolian deposits become more common, and there is a chromatic change to a lighter hue in these beds.

Paleosols are primarily Calcisols, but Gleysols and Protosols are also present (Murphy, 1987; Mack et al., 1993; Soreghan et al., 2002; Tabor et al., 2008; this study). Primary soil modifications include bioturbation associated with gleying, reduction spots, and calcium carbonate nodules that can accumulate to Stage II or III levels (Murphy, 1987; Mack et al., 1993; this study). Because of the local topography, much of the upper half of the formation is not readily accessible, but where it has been explored there are fewer paleosols and more eolian sandstones in this part of the section.

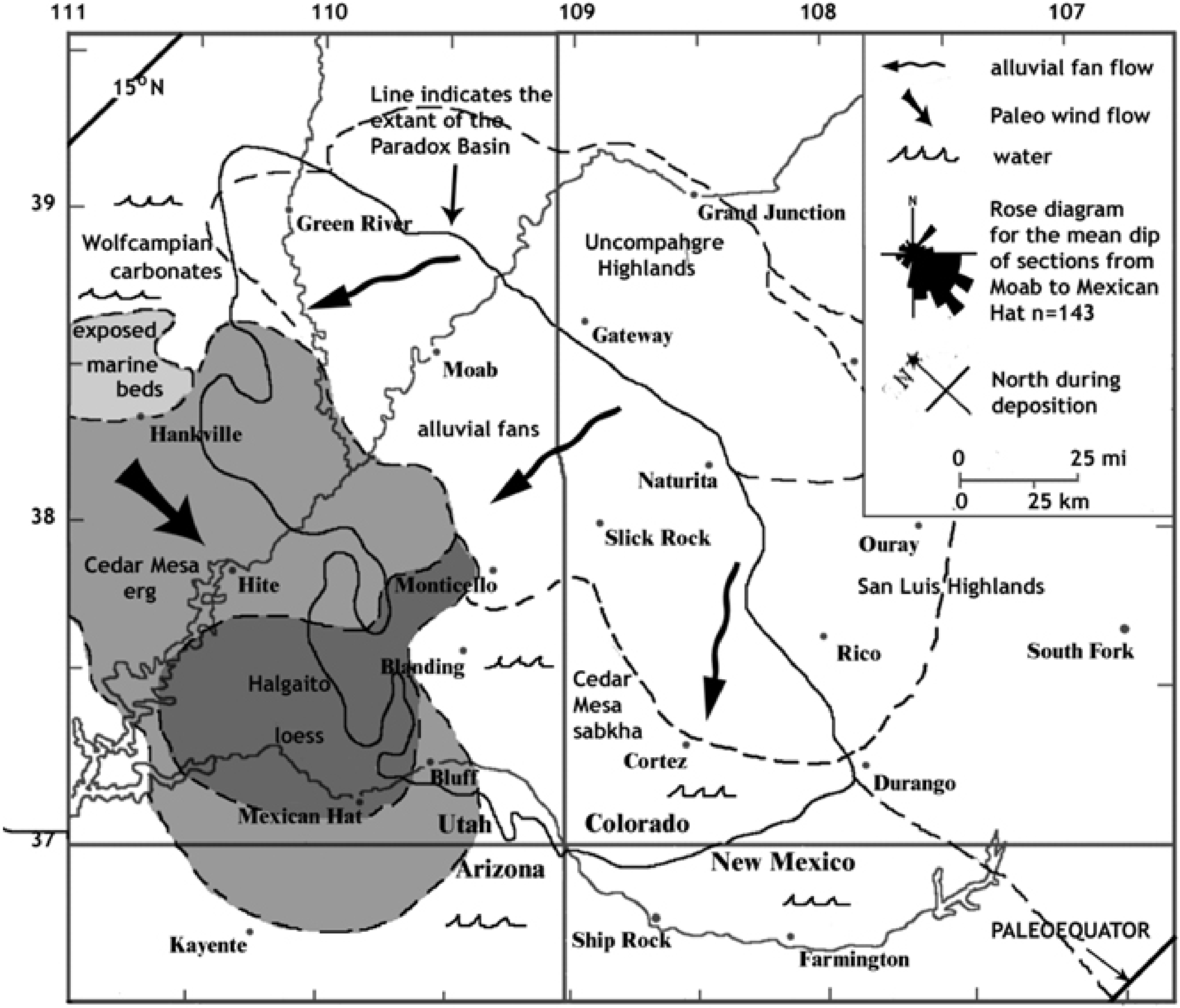

FIGURE 4. Paleoenvironment of the Halgaito Formation during deposition. Although there were other uplifted areas in the region, the Uncompahgre highlands to the east had the largest influence on the local topography. Modified from Baars (1962), Blakey (1979), Stanesco and Campbell (1989), Huffman and Condon (1993), Dubiel et al. (1996) and Condon (1997).

Fluvial channels are rare, and these consist primarily of algal-covered, grey, fluvial, pebble conglomerates that grade into fluvial sands (Murphy, 1987; this study). Within the channels, scoured bases and crossbedding are common. Vertebrate fossils of the Halgaito Formation are primarily recovered from these channels and their associated sands, although one pond deposit has been recognized (Vaughn, 1962, 1966, 1969, 1973; Frede et al., 1993; Sumida et al., 1999a, b, c). Most of the fluvial channels identified to date are in the lower half of the formation.

Marine beds occur only in the lower 50 m (164 ft) of the Halgaito Formation and are primarily gray, calcium carbonate-rich sandstones or limestones. Certain parts of the Shafer and McKim limestones in the study area are fossil rich and include corals, gastropods, bivalves, crinoids, brachiopods, and conodonts (O'Sullivan, 1965; Ritter et al., 2002; this study). The uppermost marine deposit in the VOG is the McKim Limestone.

AVENUES FOR DATING THE HALGAITO FORMATION

Radiometric Dating

No igneous deposits have been found by any of the authors doing detailed mapping or stratigraphy of the Halgaito Formation, removing the possibility of ^{40}K-^{40}Ar, ^{40}Ar-^{39}Ar , and ^{87}Rb-^{87}Sr dating (Murphy, 1987; Soreghan et al., 2002; Tabor pers. comm., 2007; this study).

Rasbury et al. (1997) were able to date Carboniferous-Permian sediments in Texas from ^{238}U-^{207}Pb present within brown paleosol calcite. This technique requires rapid sedimentation to minimize contamination by later influxes of ^{238}U-^{207}Pb into the system. The paleosol calcite of the Halgaito Formation within the study area has been similarly sampled for this method of dating, unfortunately with negative results (Tabor pers. comm., 2007).

Relative Dating-Magnetostratigraphy

Even though silts and very fine grained sands such as those found within the Halgaito Formation preserve excellent records of magnetostratigraphy, the Halgaito Formation of the Cutler Group lies within the Carboniferous-Permian Reverse Super Chron. This enormous segment of reversed magnetism spans from the Middle Pennsylvanian to the Middle Permian, between 320 to 262 Ma ago. Although some beds with normal magnetism have been recognized in Europe and questionably in North America just below the CPB, studies that include the Honaker Trail and Halgaito formations in the VOG and Moab areas have not revealed any such normal magnetism (Gose, 1970; Gose and Hensley, 1972; Scott, 1975; Opdyke and Channell, 1996; Davydov et al., 1998).

Relative Dating-Biostratigraphy

The full fauna and elements recovered will be described in a later publication. Here only taxa relevant to dating the CPB are discussed. Unlike many geologic time boundaries, the CPB is not punctuated by any large extinction or speciation events, so there are few taxa available for dating the CPB, making biostratigraphy a difficult task. Age assignments for the Halgaito Formation based on terrestrial vertebrate fossils have until recently presumed a Wolfcampian age (Vaughn, 1962, 1966, 1969, 1973; Baars, 1979). Baars (1995) placed the Halgaito Formation in the latest Pennsylvanian (Virgilian) because of changes to the age of the CPB to 290 Ma at that time. Davydov et al. (1998) identified the Global Stratotype Section and Point (GSSP) of the CPB and dating of these sediments has moved the date back to 298.9 + 0.15 Ma (Gradstein and Ogg, 2004; Gradstein et al., 2004).

The most recent reviews of the vertebrate paleontology of the Cutler Group of south-eastern Utah and northern Arizona (Sumida et al., 1999a, b, c) followed Baars (1995), placing the group in the Virgilian. However, these reviews were not products of a systematic analysis of the actual biostratigraphy of the area.

Plants

Pollen analysis of the Honaker Trail Formation and in the Halgaito Formation has had little success for dating because the pollen grains have proven to be poorly preserved or lacking in the strata (Urban pers. comm. in Scott, 1975; this study). Although there are excellent Pennsylvanian and Permian floral records in North America, plant remains from the Halgaito Formation are minimal, including only remains of the lycopod *Calamites* (Equisetopsida, Equisetales, Calamitaceae) and some as yet unidentified ferns.

Fusulinids

The fusulinids *Ultradaixina* and *Schellwienia* nearly disappear at the CPB boundary, whereas the lowest occurrence of the fusulinid *Sphaeroschwagerina* is located 6 m (19 ft) above the base of the CPB in the type section in Kazakstan. The proximity of the initial record of this taxon makes *Sphaeroschwagerina* a near match for the CPB Global Stratotype Section and Point (GSSP). Taxa that cross the CPB include *Schwagerina*, *Dutkevitchia*, *Rugosochusenella*, and *Ocellina* (Davydov et al., 1998, 2004). Limitations of fusulinids as a biostratigraphic indicator include that they are benthic organisms that are somewhat provincial, that they are mostly confined to shallow water carbonate facies, and their taxonomy is in flux with variable regional interpretations.

The marine “Elephant Canyon Formation,” which interfingers the Halgaito Formation approximately 70 miles to the north of the study area (Canyonlands area in east-central Utah), was dated by Baars (1962) as lower to middle Wolfcampian based on the presence of the fusulinids *Schwagerina*, *Triticites*, *Dunbarinella*, *Pseudoschwagerina* and *Paraschwagerina*. However, Loope (pers. comm. Murphy, 1987) identified Pennsylvanian fusulinids up to 91 m above the base of the “Elephant Canyon Formation,” and Sanderson and Verville (1990 as per Condon, 1997, p. 20) confirmed the lower part of the “Elephant Canyon Formation” to be Virgilian in age. Baars (1991, 1995) suggested that the basal portion of the Halgaito Formation spanned the CPB based on the interfingering of the Halgaito and “Elephant Canyon” formations. Due to the distance between the VOG and the Canyonlands, the large span of the “Elephant Canyon Formation” where Pennsylvanian fusulinids occur, as well as the time transgressive nature of the lower Cutler Group beds, confident dating of the Halgaito Formation in the study area is not possible on basis of the two formations in east-central Utah. No fusulinids have been identified from the Halgaito Formation.

Marine invertebrates

Gastropods resembling *Euphemites graffhami* (Gastropoda, Bellerophontida, Euphemitidae), but two-thirds larger than E. graffhami fossils recovered from the Late Pennsylvanian, Red Tanks Formation in New Mexico (Kues, 2004b) were recovered from the Shafer Limestone. These snails have been identified as *Euphemites* sp. cf. *E. graffhami*, which indicates a latest Virgilian age, but may extend into the Wolfcampian (Kues, 2004b).

The brachiopod *Hystriculina wabashensis* (Strophomenata, Productida, Productellidae) crosses the Virgilian-Wolfcampian boundary in New Mexico and the mid-continent (Kues, 2004a, b). Specimens of *Hystriculina* sp. cf. *H. wabashensis* were recovered from the Shafer Limestone and from approximately 45 m above the base of the Halgaito Formation (Figs. 5-6).

Nontetrapod Vertebrates

Conodonts: The GSSP of the base of the Permian has recently been redefined as the lowest occurrence of the conodont *Streptognathodus isolatus* (Conodonta, Conodontophorida, Polygnathidae) within the *S.* "*wabaunsensis*" conodont chronocline in the southern Ural Mountains of northern Kazakstan (Davydov et al., 1995, 1998; Chernykh et al., 1997; Wardlaw et al., 2004). Morphotypes of *Streptognathodus isolatus* include *S. invaginatus* and *S. nodulinearis*, both of which have initial occurrences that nearly coincide with the boundary and can be used as proxies for *S. isolatus* (Davydov et al., 1998). This conodont cline is also seen in the mid-continental United States and in West Texas (Ritter, 1995; Boardman et al., 1998; Wardlaw and Davydov, 2000; Sawin et al., 2006). Radiometric dating of the Usolka Section in the southern Ural Mountains of Kazakhstan has also redated the CPB to 299+0.8 Ma (Davydov et al., 2002). Previous to the redefinition of the CPB, the boundary was set at 290 Ma (GSA, 1999).

Based on the most recent conodont studies for the area, the Shafer Limestone at the top of the Honaker Trail Formation is near the Missourian-Virgilian boundary (~305 Ma) (Ritter et al., 2002). The presence of *Streptognathodus firmus* in the Shafer Limestone indicates that this bed is at least 303.4 Ma (Ritter et al., 2002; Gradstein et al., 2012), and very close in age to the CPB at 299+0.8 Ma.

Although the Shafer Limestone has as many as 30 conodont elements per kilogram (Ritter et al., 2002) McKim Limestone conodonts are rarer. Using the buffered acetic acid solution method described by Stone (1987), Jeppsson et al. (1999) and Green (2001), an initial 20 pounds (9.1 kilograms) produced only 3 fragments of small vertebrate bone, however there was not enough material to identify them.

Xenacanthidae: The freshwater shark *Orthacanthus* (Chondrichthyes, Xenacanthida, Xenacanthidae) is the best represented vertebrate of the Halgaito Formation and has been found in every fluvial channel from 10 m above the base to about half way up the section (Figs. 5-6). *Orthacanthus texensis* spans from the Wolfcampian to the Leonardian stages, however one specimen questionably identifiable as *O. texensis* is recorded from the Virgilian Towle Shale (Admire Group, Nebraska) (Johnson, 1999). At this locality 92 other specimens were assigned to *O. compressus*, making the one specimen identified as *O. texensis* dubious (Johnson, 1999). Based on this, *O. texensis* is considered to be a Permian species.

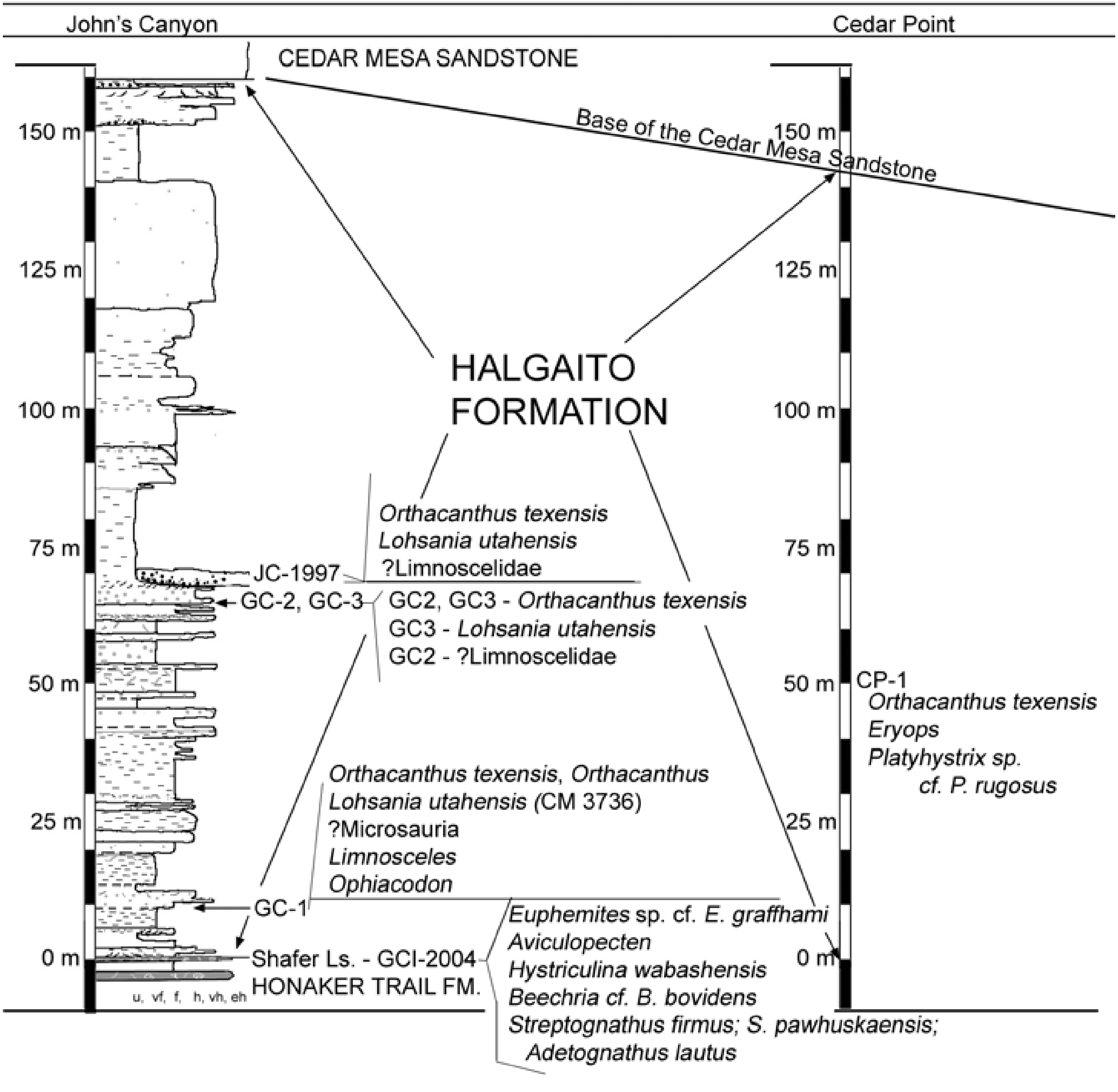

FIGURE 5. Stratigraphy and biostratigraphy of the Halgaito Formation, John's Canyon (Vaughn, 1962; Sumida et al., 1999a, b, c, 2005; this study).

Orthacanthus compressus is a little more problematic. *O. ?compressus* found in the Archer City Formation, Bowie Group (Asselian), may be the precursor to *O. texensis*, and yet in the Permian the two taxa and perhaps *O. compressus* appears to be temporally if not geographically contemporary (Johnson, 1999, 2012). Some specimens assigned to *O. compressus* are very similar to *O. texensis*; in fact the two species can be difficult to tell apart (Hotton, 1952; Lund, 1976; Johnson, 1999, 2012). *O. compressus* is reported to range from the Demoinesian to the Leonardian (Newberry, 1856; Smith, 1927; Simpson, 1976). *O. compressus* does not appear to exist in western North America except from the Upper Carboniferous and lowest Permian in Kansas (Schultze, 1985; Schultze and Chorn, 1988; Chorn and Schultz, 1990; Johnson, 1979, 1999), and the in the Upper Pennsylvanian to Lower Permian (middle Leonardian) of Oklahoma (Johnson, 1979, 1999; Czaplewski et al., 1994).

Although Frede et al. (1983) aided by Gary Johnson reported *Orthacanthus compressus* from the Halgaito Formation, the material was fragmentary and Johnson gave it only a tentative identification (Sumida pers. comm., 2013). All other sharks previously identified from the Halgaito Formation and all material since presented to Johnson have been identified as *O. texensis* (Frede et al., 1983, Sumida et al., 1999, Johnson pers. comm., 2005). Until a positive identification of *O. compressus* can be made from the Halgaito Formation, all material is considered to be *O. texensis* or *O.* sp.

Osteolepidae: *Ectosteorhachis* (Osteichthyes, Crossopterygii, Rhipidistia, Osteolepidae) was previously recorded from the Halgaito

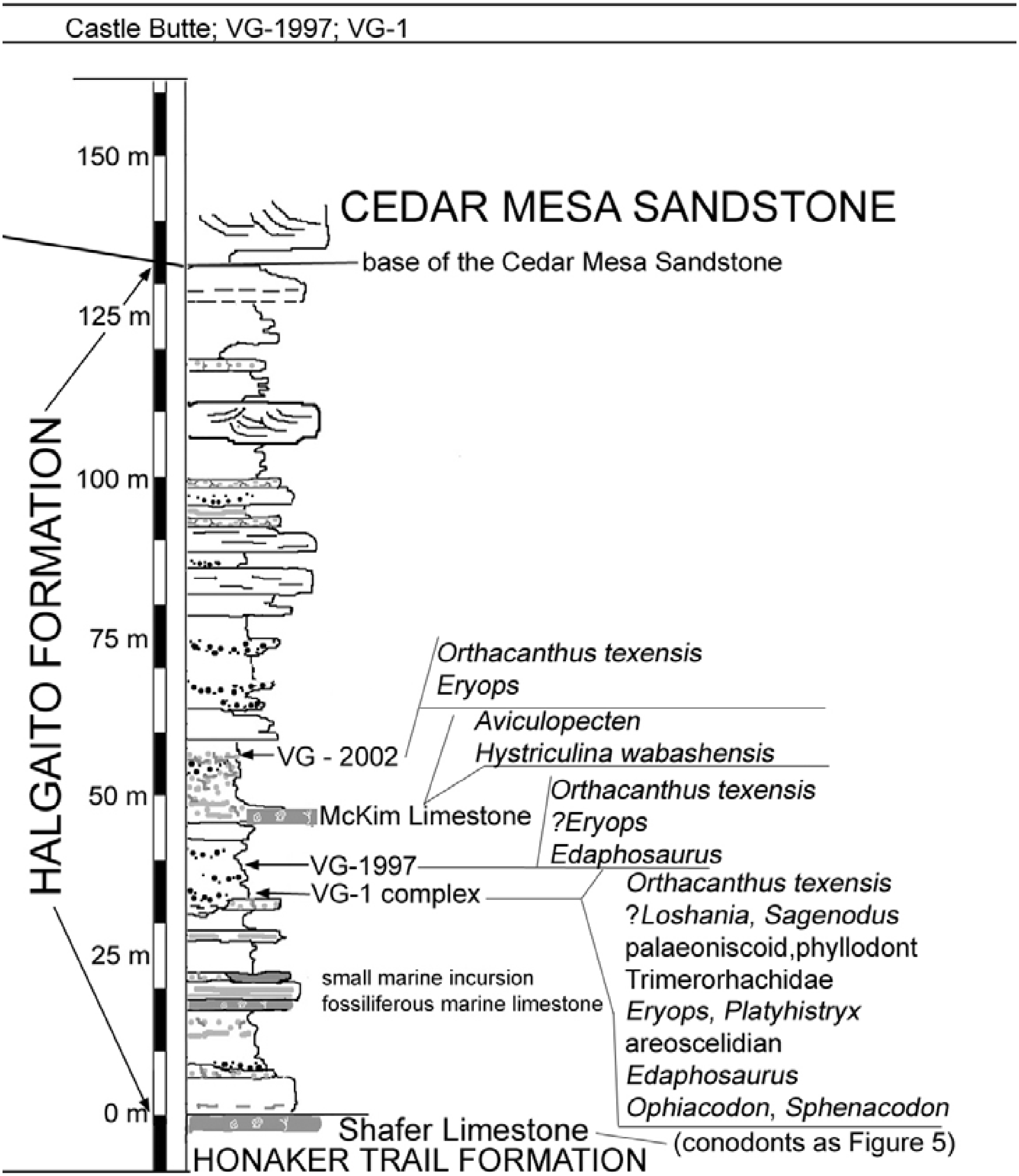

FIGURE 6. Stratigraphy and biostratigraphy of the Halgaito Formation, central Valley of the Gods (Vaughn, 1962; Sumida et al., 1999a, b, c, 2005; this study).

Formation based solely on the presence of crossopterygian scales. These reports now may be in error as only bones from *Lohsania utahensis* (taxonomy as *Ectosteorhachis*) have been found to date (Thomson and Vaughn, 1968; Sumida et al., 1999a, 2005). The scales of the two species appear identical, and without other elements, *Lohsania* appears to be the only crossopterygian present in the section. Although *Ectosteorhachis* is generally considered to be an Early Permian taxon, *Lohsania* is an unknown quantity for biostratigraphy. It is known from bone from between 10 and 75 m above the base of the Halgaito Formation (Figs. 5-6).

Tetrapods

Based on studies in New Mexico and Texas, Lucas (1998, 2005) suggested several terrestrial vertebrate faunochrons for the latest Pennsylvanian and the Permian. The late Pennsylvanian to early Permian Coyotean faunochron begins with the first appearance of the pelycosaur *Sphenacodon* and ends with the first appearance of the seymouriamorph amphibian *Seymouria* along with the microsaur *Pariotichus*, the pelycosaurian-grade synapsid *Secodontosaurus*, the captorhinomorph eureptile *Protocaptrorhinus*, and the aerosclidian diapsid *Areoscelis*. Index fossils for the period include the temnospondyls *Brevidorsum*, *Edops*, and *Neldasaurus*, and the captorhinids *Romeria* and *Proterothyris* (Lucas, 1998, 2002, 2005). Lucas (1998, 2002) noted that the temnospondyl *Eryops*, the anthracosaurs *Archeria* and *Neopteroplax*(?), the diadectomorph *Diadectes*, and the pelycosaurs *Edaphosaurus* and *Stereophallodon* cross the CPB in Texas and the southwestern United States. Additionally, members of the diadectomorph family Limnoscelidae are considered to be extinct by the end of the Pennsylvanian (Sumida et al., 2004). Other tetrapods included in the Coyotean that appear long after the CPB are the temnospondyls *Brevidorsum*, *Neldasaurus*, *Parioxys*, *Tersomius*, *Trimerorachis*, and *Zatrachys*, the microsaur *Pantylus*, the nectridian *Diplocaulus*, the pelycosaurs *Lupeosaurus*, *Ophiacodon* and *Dimetrodon*, and the captorhinid reptiles *Romeria* and *Proterothyris*. However, only the nectridian *Diplocaulus* and the pelycosaurs *Ophiacodon* and *Dimetrodon* have a broad enough distribution to be useful in biochonology in North America (Sumida et al., 2004).

Eryopidae: *Eryop*s (Labyrinthodontia, Temnospondyli, Eryopoidea, Eryopidae) is known from two localities, one 35 m above the base and one 55 m above the base of the Halgaito Formation (Fig. 6). *Eryops* ranges from the Upper Pennsylvanian and throughout most, if not all, of the Lower Permian (Vaughn, 1958; Lucas, 1998, 2002). This makes *Eryops* only an indicator of the time period and not the CPB.

Archeriidae: A single vertebral centrum with the characteristic shape of *Archeria* (Amphibia, Anthracosauria, Archeriidae) was recovered from about 30 m above the base of the Halgaito Formation (Fig. 6). Holmes' (1989) study of the genus is based entirely on specimens presumed to be from Lower Permian sediments. It is notable that the specimen recovered from the VOG is significantly smaller than those studied by Holmes (1989). There is the slim possibility that the VOG specimen could represent a different species, but suggesting that on the basis of a single centrum is here considered to be irresponsible. *Archeria* is generally considered to be an Early Permian taxon, however Lucas (1998, 2002) suggests that *Archeria* crosses the CPB.

Seymouridae: A small vertebra assignable to ?*Seymouria* (Amphibia, Anthracosauria , Seymouridae) is known from approximately 70 m above the base of the Halgaito Formation (Sumida et al., 1999 b) (Fig. 5). Lucas (2005) used *Seymouria* to define the end of the Coyotean and the start of the Seymourian faunochron. This single specimen questionably assigned to ?*Seymouria* is not enough to make a definitive age correlation for this portion of the section.

Limnoscelidae: *Limnoscelis* (Amniota?, Diadectomorpha, Limnoscelidae) is known from a fragment of maxilla approximately 10 m above the base of the Halgaito Formation (Fig. 5). This fragment is identical in shape and size of that seen above the caniniform region of the right maxilla of *Limnoscelis dynatis* described from the Late Pennsylvanian Sangre de Cristo Formation of central Colorado (Berman and Sumida, 1990). A segment of bone thought to be a right pterygoid from the same locality is tentatively assigned to ?*Limnoscelis* sp. based on size compared to *Limnoscelis dynatis*, and the fact that the specimen is not assignable to the pelycosaurs *Ophiacodon* or *Edaphosaurus* (Berman and Sumida, 1990). A well preserved left scapulocoracoid was recovered from approximately 65 m above the base of the section is tentatively assigned to ?Limnoscelidae. The scapulocoracoid also shares some attributes with *Ophiacodon*, however it cannot be confidently assigned to that genus (Fig. 5). Members of the family Limnoscelidae are rare and are known with certainty from only two other locations, the Upper Pennsylvanian of El Cobre Canyon, New Mexico, and the Upper Pennsylvanian Sangre de Cristo Formation of Central Colorado (Vaughn, 1969; Berman and Sumida, 1990). Sumida et al. (2004) suggested that despite this limited data set, Limnoscelidae may be indicative of Late Pennsylvanian-age deposits. Wideman et al. (2005) supported this hypothesis when she established the family as monogeneric with only two known Late Pennsylvania age species.

***Diadectes*:** Previously reported from the study area (Vaughn, 1962; Frede et al., 1993; Sumida et al., 1999c) these specimens have since been reidentified as an unidentifiable tetrapod and potentially a limnoscelidaen, however more work needs to be completed on this second specimen to confirm this identification.

Ophiacodontidae: *Ophiacodon* cf. *O. navajovicus* (Synapsida, Eupelycosauria, Ophiacodontidae) was recovered from approximately 55 m above the base of the Halgaito Formation (Figs. 5-6). Another specimen of *Ophiacodon* is known from 10 m above the base of the section. Although Lucas (2005) placed the first appearance of *Ophiacodon* after the CPB but in the Coyotean, this genus is also known from the following Upper Pennsylvanian formations: the Rock Lake Shale of Garnett Kansas (Kissel and Reisz, 2004), the Ada Formation of Oklahoma (Kissel and Lehman, 2002) and the Sangre de Cristo Formation of central Colorado (Sumida and Berman, 1993). *Ophiacodon* is also known from numerous localities through the Early Permian of North America (Romer and Price, 1940; Reisz, 1986). Given its broad stratigraphic range, its presence does not help determine the exact placement of the CPB.

Sphenacodontidae: *Sphenacodon* (Synapsida, Eupelycosauria, Sphenacodontidae) was recovered from approximately 35 m above the base of the Halgaito Formation (Fig. 6). Lucas (2005) placed the first appearance of Sphenacodon before the CPB at the start of the Coyotean and this taxon is known from the Virgilian-Wolfcampian Cutler Formation in El Cobre Canyon New Mexico, from the Wolfcampian Abo Formation in New Mexico, and from the Wolfcampian-Leonardian Organ Rock Shale, Cutler Group, southeastern Utah (Romer, 1937; Vaughn, 1964; Paton, 1974; Reisz, 1986). Given its broad stratigraphic range, its presence does not help determine the exact placement of CPB.

Edaphosauridae: The eupelycosaurian genus *Edaphosaurus* (Synapsida, Eupelycosauria, Edaphosauridae) is known to span the CPB. On the other hand, the more primitive *Ianthasaurus* is generally considered to be a Late Pennsylvanian taxon. *Ianthasaurus* has a more primitive skull construction and the cross-bars typical of its elongate neural spines are not present on all vertebrae (Reisz and Berman, 1986; Modesto and Reisz, 1990). The partial sail recovered from 35 m above the base of the Halgaito Formation is rolled up in a "scroll-like" manner. Fragments of neural spines of a small edaphosauid are also known from 40 m above the base of the Halgaito Formation (Fig. 6). Whereas these specimens are small like *Ianthasaurus*, it is not clear that they demonstrate the pattern of distribution of the cross bars as in *Ianthasaurus.* A conservative assignment would be to designate these specimens as a small *Edaphosaurus* as opposed to *Ianthasaurus*. If this is correct, then this locality is not necessarily constrained to the Upper Pennsylvanian.

DISCUSSION

The Shafer Limestone at the top of the Honaker Trail is known to be near the Missourian-Virgilian boundary at 305 Ma based on the conodont, *Streptognathodus firmus*. The gastropod *Euphemites* cf. *E. graffhami*, indicates a Virgilian age, but it may extend into the Wolfcampian. Vertebrate taxa previously presumed to have died out before the CPB but present in the Halgaito Formation include *Limnoscelis* and questionably Limnoscelidae. The brachiopod *Hystriculina wabashensis*, and the tetrapods *Eryops*, *Archeria*, *Edaphosaurus*, *Ophiacodon* and *Sphenacodon* all cross the CPB. As *Ophiacodon* crosses the CPB it should not be used as an indicator that a given assemblage is beyond the CPB. *Orthacanthus texensis* questionably appears in the Virgilian based on one specimen and all other specimens have been recovered from the Wolfcampian to the Leonardian. *Seymouria* appears after the CPB.

It is suggested here that there is a disconformity between the Shafer Limestone and the first fossiliferous locality 10 m above the base of the Halgaito Formation where *Orthacanthus texensis* and *Ophiacodon* are present. Based on the paucity of previously recovered limnoscelids material outside of the study area it is suggested that *Limnoscelis* survives beyond the CPB at least in southeastern Utah. The ?Limnoscelidae material between 65 and 70 m above the base of the Halgaito Formation is only questionably assigned and should not be considered an age expansion for the group at this time. The proposed range of *Orthacanthus texensis* is not questioned, as is the range for the family Limnoscelidae, as *O. texensis* is much more common in the fossil record (Johnson, 1999, table 1).

Based on this analysis, the CPB is placed within the first 10 m of the Halgaito Formation and before the first appearance of *Orthacanthus texensis*. Although one specimen of ?

has been reported from the Halgaito Formation, more material should be recovered prior to making any definitive age correlations for this portion of the section.

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SYNCHRONOUS COLLAPSE OF THE LATE PERMIAN TROPICAL TERRESTRIAL AND MARINE ECOSYSTEMS

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The collapse of rainforests at the end-Permian and delayed recovery, until the Middle Triassic, is a proxy for the terrestrial ecosystem changes across the Paleozoic-Mesozoic boundary. This has been interpreted as a consequence of northward motion of Tethyan blocks through paleoclimatic zones. However, an investigation of Permian-Triassic sections on the eastern slope of the Emeishan volcanic plateau and other sections in South China reveals that the die-off of the rainforest-type *Gigantopteris* flora was dramatic. The disappearance was associated with sharp depletions of both $\delta^{13}C_{carb}$ and $\delta^{13}C_{org}$, charcoal-rich layers due to frequent wildfires, catastrophic soil erosion and prevalence of red beds. This event is coincident with marine extinction, the negative anomalies of both $\delta^{13}C_{carb}$ and soot-rich beds in the GSSP section at Meishan based on high-resolution biostratigraphic, geochemical and geochronologic constraints. This suggests that global warming reached its climax at the end-Permian, eliminated rainforests and rapidly transitioned the ever-wet biome to a seasonally dry climate in equatorial regions.

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THE INTERNATIONAL PERMIAN TIMESCALE: MARCH 2013 UPDATE

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Abstract—The Subcommission on Permian Stratigraphy is concentrating its efforts to establish the remaining three GSSPs in the Cisuralian as well as refining the Permian timescale for global correlation, including into the terrestrial realm. In this paper, we provide a brief overview on recent progress of Permian timescale development based on new biostratigraphic, geochemical and geochronologic data. The Permian Period was from 298.9 Ma to 252.17 Ma based on the latest U-Pb ages in the southern Urals and South China. The Cisuralian, Guadalupian and Lopingian have durations of 26.6 Myr, 12.5 Myr and 7.63 Myr, respectively.

INTRODUCTION

The international Permian timescale has been significantly improved during the past five years although no new GSSPs have been formally ratified since 2005. The Permian System is composed of three series (Cisuralian, Guadalupian and Lopingian in ascending order) and nine stages, among which significant progress has been made on the GSSPs and GSSP candidates. New data for several stages are now available. Three GSSPs (base-Sakmarian, base-Artinskian and base-Kungurian) remain to be proposed and ratified. We present here a brief summary and an updated timescale (Fig. 1) to show recent advances on each stage of the Permian System. This timescale is updated from Henderson (2005). A more comprehensive paper on the Permian timescale is presented by Henderson et al. (2012a), but some important data have been updated since then. The current chart provides the latest high-precision geochronologic dates for each stage, high-resolution biostratigraphic data based on multiple fossil groups including terrestrial tetrapods (Lucas, 2006), sea-level changes and paleomagnetic reversal zones. The Cisuralian Working Group has formally published the proposal for the candidates for the base-Kungurian GSSP (Henderson et al., 2012b; Chernykh et al., 2012), and the proposals for the base-Sakmarian and base-Artinskian are in preparation. High-resolution conodonts are from Henderson and Mei (2003) and Chernykh (2006) for the Cisuralian; from Glenister et al. (1999), Wardlaw (2000) and Jin et al. (2006a) for the Guadalupian; and from Jin et al. (2006b), Mei and Henderson (2004) and Shen and Mei (2010) for the Lopingian.

CISURALIAN

The base of the Permian System (also the base of the Asselian Stage) was defined by the First Appearance Datum (FAD) of *Streptognathodus isolatus* Chernykh, Ritter and Wardlaw at Aidaralash Creek, Aktöbe (formerly Aktyubinsk) region, northern Kazakstan (Davydov et al., 1998). Biostratigraphic data from this GSSP have been rarely updated since it was defined. Geochemical and geochronologic data are not available. However, some progress was made from the Usolka section on the north bank of the Usolka River that was defined as an auxiliary section for the Carboniferous–Permian boundary (CPB) (Davydov et al., 1998; Schmitz and Davydov, 2012).The CPB is recognized in the Usolka section at the first occurrence of *Streptognathodus isolatus* associated with multiple ash beds, and the radiometric calibration and biostratigraphy for this part of the section has been published (Ramezani et al., 2007). Those radiometric ages were recently confirmed by new dating of ash beds above and below those ash beds dated by Ramezani et al. (2007). Thus, the CPB is interpolated as 298.9±0.15Ma (Schmitz and Davydov, 2012). In addition, high-resolution carbon isotopic data were analyzed from the Usolka section. A gradually increasing trend in $\delta^{13}C_{carb}$ from -4.8‰ at the base of the Asselian upward to 4.2‰ within Bed 22 in the *Sweetognathus expansus* Zone occurs at the Usolka section based on whole rock samples, although the lower values may have some diagenetic influence. This is followed by an interval with high values around 4‰ from Beds 22 to 24 in the upper Asselian (Zeng et al., 2012).

The base of the Sakmarian was previously considered as the FAD of *Sweetognathus merrilli* Kozur at the Kondurovsky section in the southern Urals (Chuvashov et al., 2002b). However, subsequent studies indicate that the conodont lineage to define the base-Sakmarian GSSP at the Kondurovsky section proposed by the Cisuralian Working Group (Chuvashov et al., 2002b) was rare or absent in samples processed by different labs. Thus, the Kondurovsky section is no longer being considered, and the Usolka section is now under consideration as the candidate for the base-Sakmarian GSSP. Two alternative possibilities for defining the base of the Sakmarian Stage are under consideration. One is the FAD at 54.3 mab of *Sweetognathus merrilli* Kozur within the chronomorphocline *Sweetognathus expansus–S. merrilli* (Chernykh, 2005). However, results from the Apillapampa section in Bolivia, which yields abundant conodonts, interbedded with zircon-rich ash beds, demonstrates that forms comparable to *Sweetognathus merrilli* were present already in the mid-Asselian (Henderson and Kotlyar, 2009).The second option is the FAD at 51.6 mab of *Mesogondolella uralensis* Chernykh within the chronomorphocline of *M. pseudostriata–M. arcuata–M. uralensis* (Chernykh, 2006). The latter lineage is considered acceptable by the Cisuralian Working Group because a similar lineage has been found from Nevada, SE Alaska and possibly in Arctic Canada (Henderson and Kotlyar, 2009). This lineage has not been confirmed yet in South China, which is an important area for global correlation. The estimated age of the base of the Sakmarian Stage is 295.0 Ma (Schmitz and Davydov, 2012). An excursion with double negative shifts in $\delta^{13}C_{carb}$ value is documented around the Asselian/Sakmarian boundary in both the Usolka and Kondurovsky sections, which may have potential to serve as chemostratigraphic markers for intercontinental correlation (Zeng et al., 2012). However, more work in different areas is necessary to confirm this pattern.

The base of the Artinskian Stage is best represented in the Dalny Tulkas section, which was proposed as the GSSP for the base of the Artinskian (Chuvashov et al., 2002a). The base is proposed to be defined by the FAD in Bed 4 of *Sweetognathus* "*whitei*" (Rhodes *sensu* Chernykh) within the chronomorphocline *S. binodosus–S. anceps–S.* "*whitei*". Three ash beds in the Dalny Tulkas section closely constrain the age of the base of the Artinskian to 290.1 Ma (Schmitz and Davydov, 2012). The $\delta^{13}C$ and $\delta^{18}O$ curves in the DalnyTulkas section are characterized by a rapid

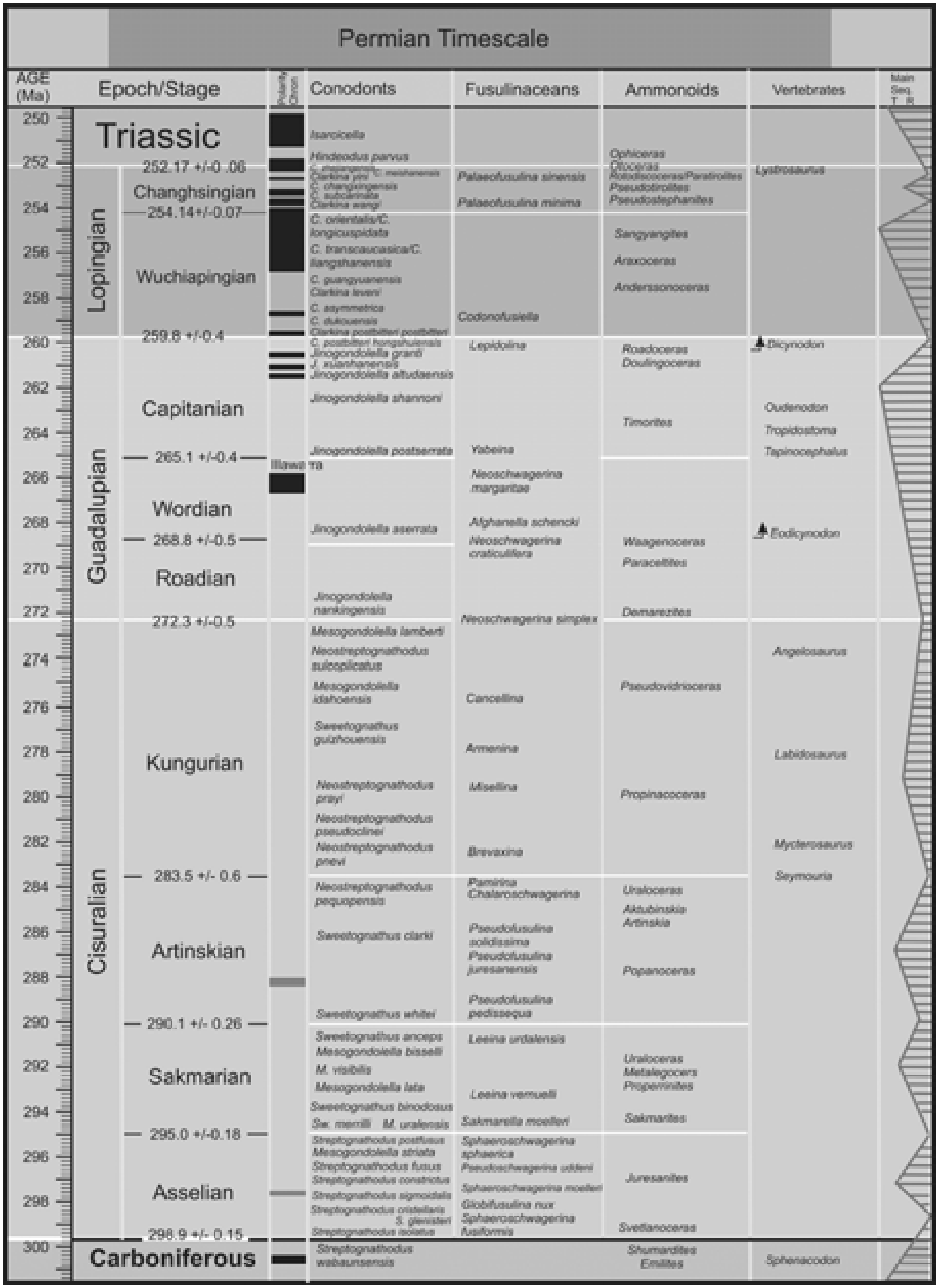

FIGURE 1. Updated Permian timescale. Geochronologic ages are combined from Shen et al. (2011) for the Lopingian; Schmitz and Davydov (2012) for the Cisuralian, Henderson et al. (2012a) for the GLB and Henderson et al. (2012b) for the base of Kungurian. Tetrapod biochronology is after Lucas (2006). Biostratigraphic columns are a work in progress and comments are invited.

and sharp drop around the Sakmarian/Artinskian boundary and a long-term deep depletion stage in the following Artinskian interval, which was interpreted as a diagenetic signature or a result of enhanced organic carbon burial and subsequent isotopic refractionation by microbial chemosynthetic processes (Zeng et al., 2012). The strontium isotopic composition of seawater at the base of the Artinskian Stage is $^{87}Sr/^{86}Sr = 0.70767$ (Chernykh et al., 2012).

The base of the Kungurian Stage was proposed for the Mechetlino section exposed along the right bank of the Yuryuzan River downstream (Chuvashov et al., 2002a). However, subsequent studies indicated that samples collected to test reproducibility of the index conodont species *Neostreptognathodus pnevi* FAD did not produce any conodonts; the section is also too heavily weathered to carry out any chemostratigraphic analysis. Therefore, the Rockland section in the Pequop Mountains of Nevada, USA, with the same chronomorphocline from *Neostreptognathodus pequopensis* to *N. pnevi* was proposed as a potential new candidate for the base-Kungurian GSSP by SPS (Henderson et al., 2012b). Meanwhile, a new section called the Mechetlino Quarry section, which is about 600 m east of the previous Mechetlino section, was also proposed as a new candidate for the base-Kungurian GSSP (Chernykh et al., 2012). This section contains fusulinaceans, ammonoids, conodonts, and presumably some layers of volcanic ash beds. Unfortunately, there are no U-Pb ages for late Artinskian to Kungurian strata at both the Mechetlino and Rockland sections. However, strontium isotopic analysis of conodonts yielded reproducible values of $^{87}Sr/^{86}Sr = 0.70743$ to 0.70739. Projecting these compositions onto the interpolated seawater curve yields an apparent age for the boundary of 283.5 ± 0.5 Ma (Chernykh et al., 2012). This is much older than the age of 279.3 Ma for the base of Kungurian in GTS 2012 (Henderson et al., 2012a).

GUADALUPIAN

The Cisuralian/Guadalupian boundary (CGB) is defined by the FAD of *Jinogondolella nankingensis* within the conodont chronomorphocline from *Mesogondolella idahoensis lamberti* to *Jinogondolella nankingensis* that can be readily distinguished by the appearance of the distinctly characteristic serration on the anterior part of the *Jinogondolella* platform. However, the correlation between the fusulinacean-based Tethyan and the conodont-based international timescales of the Permian System has become one of the most disputed issues among the Permian community during the past two decades; this uncertainty is reflected in Figure 1. The main problem was derived from the appearance of Murgabian fusulinids including *Neoschwagerina simplex* in a horizon about 150 m below the first appearance of the serrated conodont *Jinogondolella nankingensis* at the Luodian section in Guizhou, South China. This point may actually be close to the base of the Roadian if the first occurrence of serrated conodonts is diachronous at the section. The co-occurrence of *Neoschwagerina simplex* with some Kungurian conodonts has been confirmed recently based on the collection from Hatahoku, Japan (Shen et al., in press). However, preliminary results from SE Pamir suggest that in the Tethyan stratotypes, *N. simplex* co-occurs with conodonts that straddle the Kungurian-Roadian boundary and range up into the Roadian. Geochronologic constraints for the CGB are interpolated as 272.3 Ma in GTS 2012 (Henderson et al., 2012a). Recently, U-Pb ages from two volcanic ash beds around the CGB at Chaohu, South China were dated as 272.0±5.5 Ma (MSWD=2.6) and 271.5±3.3 Ma (MSWD=1.7) (Zhu et al., in press).

The three Guadalupian GSSPs were defined more than 10 years ago (Glenister et al., 1999), but little has been updated since then. Although they are the earliest GSSPs defined in the Permian, the GSSP papers have not yet been published, and conodonts from the actual GSSP levels have yet to be figured. Furthermore, high-resolution chemostratigraphy for the whole Guadalupian Series is not available. Only one numerical age, of 265.3 Ma from an ash bed, which lies 2 m above the top of the Hegler Member, 20 m below the base of Capitanian Stage, is available (Bowring et al., 1998). The interpolated ages are 265.1 Ma for the base Capitanian Stage and 268.8 Ma for the base of the Wordian (Henderson et al., 2012), but many more control points are needed. The Illawarra Reversal during the late Wordian (ca 266 Ma) is a mark for time correlation among different regions. This reversal represents a remarkable change in geomagnetism following the long-term stable Kiaman Reverse Superchron (throughout the Late Carboniferous and Early-Middle Permian) and marks the beginning of the Permian–Triassic Mixed Superchron with frequent polarity changes during the Late Permian and Triassic (Embleton et al., 1996; Isozaki, 2009; Jin et al., 1999; Vozarova and Tunyi, 2003). This reversal has not yet been found in South China due to a serious Mesozoic magnetic overprint. Another useful marker in chemostratigraphic correlation of the Late Guadalupian is the late Capitanian minimum of $^{87}Sr/^{86}Sr$ ratio (ca. 0.7068–0.7069; ~260.4 Ma), which represents one of the most significant features in Phanerozoic seawater $^{87}Sr/^{86}Sr$ history (Kani et al., 2013; Liu et al., 2013; McArthur et al., 2012; Veizer et al., 1999).

Carbon isotope chemostratigraphy around the GLB has been extensively studied in different sections, but the results are controversial. A large negative shift was reported from the late Capitanian *Jinogondolella xuanhanensis*/*J. prexuanhanensis* zones in Guizhou, South China (Wignall et al., 2009), but this negative excursion is not confirmed at the Penglaitan GSSP section (Chen et al., 2011). A negative excursion with minor magnitude at GLB was reported by Wang et al. (2004) and Jin et al. (2006a), but may have little significance. A significant positive excursion of carbon isotopic values during the late Capitanian was documented as the Kamura event by Isozaki (2007), but the precise horizon with this event based on conodonts is still unclear.

LOPINGIAN

The Guadalupian/Lopingian boundary (GLB) is defined by the chronomorphocline from *Clarkina postbitteri hongshuiensis* to *C. postbitteri postbitteri* at the Penglaitan section in Laibin, Guangxi Province of South China. Conodonts reported from other sections (Lambert et al., 2002, 2010; Nishikane et al., 2011; Xia et al., 2006; Zhang et al., 2007) as representing this chronomorphocline are mostly questionable in terms of taxonomy. This boundary was associated with the Emeishan volcanism and the largest regression during the Phanerozoic. A widespread distinct disconformity is present in most areas around the world. Only a few areas, such as South China, Iran, and SE Pamir possess continuous deposits around the GLB. The age of the GLB is much discussed and still uncertain. Although widespread volcanism was present around the GLB and numerous dating of the Emeishan basalt has been carried out, high-precision ages are still not available. Some new zircon CA–TIMS U–Pb ages were obtained from intrusive rocks of the Panxi region (Inner Zone) of the Emeishan Large Igneous Province, which yielded a wide range of ages between >257 Ma and ~260 Ma (Shellnutt et al., 2012). An age of about 259 Ma is suggested by Shenet al. (2010) and 259.8 Ma is provided in GTS 2012 (Henderson et al., 2012a). A combined study of mineralogy, geochemistry and geochronology on six layers of claystone around the GLB at the Penglaitan GSSP section indicate that the Penglaitan claystones are not suitable for age determination of the GLB (Zhong et al., 2013).

The Wuchiapingian/Changhsingian boundary (WCB) has been well constrained within the conodont chronomorphocline from *Clarkina longicuspidata* to *C. wangi* at the Meishan GSSP section (Jin et al., 2006b). This same conodont succession was also confirmed at the Shangsi section in Sichuan province, South China. High-precision CA–TIMS U–Pb ages are available from both the Meishan and Shangsi sections. The WCB is bracketed by two ash beds at Shangsi and constrained by a few ages above the WCB at the Meishan GSSP section; it is estimated as 254.14 Ma (Shen et al., 2011) and 254.2 Ma (Henderson et al., 2012a).

The Permian-Triassic boundary (PTB) is very well dated because of a concentrated effort to understand the largest mass extinction in Earth history that occurred immediately below the PTB (Shen et al., 2011). This boundary, defined by the FAD of *Hindeodus parvus*, has been well dated by two ash beds at the Meishan GSSP section. Bed 25 is 252.28±0.08 Ma and Bed 28 is 252.10±0.06 Ma. An interpolated age for the PTB of 252.17±0.06 Ma is suggested from Meishan section data (Shen et al., 2011). The high-precision CA–TIMS U–Pb ages offer far greater resolution at this level than that based on conodont zones.

MARINE-TERRESTRIAL CORRELATION

The Permian time scale is based on the marine record, and, although a few problems and issues are outstanding, it is essentially established. The next major direction for SPS research is to build a rich record of terrestrial correlation proxies including insects, fresh water invertebrates, vertebrates, palynology, paleobotany, magnetostratigraphy, chemostratigraphy and especially geochronology. Figure 1 provides a preliminary assessment of appearances of key vertebrate taxa during the Permian (Lucas, 2006). The latter gives a very rough time frame for the continental Permian and its correlation to the marine global scale. Besides the vertebrate zonation of continental deposits, several other tools have been developed for detailed stratigraphic subdivisions and correlations of continental deposits in the different Euramerican non-marine basins. Most detailed and reliable are the insect (spiloblattinid) and amphibian (branchiosaurid) zonations (Schneider, 1982; Werneburg, 1989; Schneider and Werneburg, 2006; Werneburg and Schneider, 2006). But, neither epoch nor stage boundaries are really directly correlated by co-occurring marine and nonmarine zone fossils or reliable isotopic ages thus far (e.g., Menning et al., 2006; Roscher and Schneider, 2005; Lützner et al., 2007).

Recently, most promising for direct marine–non-marine correlations are ongoing investigations in mixed marine-continental Late Pennsylvanian/Early Permian deposits in New Mexico and brand new discoveries of insect zone species in similar deposits of the Donets Basin, which provide for the first time direct links between conodont and foraminifer zones as well as insect zones for the Late Pennsylvanian and earliest Permian (Schneider et al., 2004; Lerner et al., 2009; Lucas et al., 2011, 2013). An updated version of the current state for the Carboniferous/Permian transition is given by Schneider et al. (2013, this volume). The focus of future work on marine–non-marine correlations should be set for the Cisuralian and Guadalupian mainly on mixed marine-terrestrial deposits on the East European platform and in the North American Midcontinent basins and the East European platform (Sennikov and Golubev, 2006, 2012; Sherbakov, 2008). Most importantly, there needs to be more intensified cooperation by SPS with stratigraphers working in the huge nonmarine basins of Gondwana. The correlation of the Lopingian Series based on marine-terrestrial transitional deposits in South China (Shen et al., 2011) and the vertebrate assemblages in the Middle and Late Permian in the Karoo Basin, South Africa, which is precisely calibrated by a set of new CA-TIMS U-Pb ages (Rubidge et al., 2013), are both excellent examples of how to develop an integrated marine and non-marine time scale.

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AEDUELLID FISHES (ACTINOPTERYGII) OF THE BOHEMIAN MASSIF (CZECH REPUBLIC) ACROSS THE CARBONIFEROUS-PERMIAN BOUNDARY

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Abstract—A collection of well-preserved isolated bones and one partly preserved specimen are newly described from the freshwater sediments of the Early Permian of the Krkonoše Piedmont Basin (Bohemian Massif). Described osteological remains belong to one species closely related to the genera *Aeduella* and *Bourbonnella*. The following overview concerns itself with other aeduellids recently described from the Bohemian Massif: *Spinarichthys dispersus* from the Late Carboniferous and *Neslovicella rzehaki*, *Neslovicella elongata* and *Bourbonnella hirsuta* from the Early Permian. Their relationships to other actinopterygians and their stratigraphical position are discussed.

INTRODUCTION

The Bohemian Massif is notable for widely distributed Late Carboniferous and Early Permian freshwater sediments, with rich faunal content. The list of faunas contains around 400 species, and many specimens have yet to be determined (Štamberg and Zajíc, 2008). The Central and West Bohemian late Paleozoic basins, the Krkonoše Piedmont Basin, the Intra-Sudetic Basin and the Boskovice Graben are the most significant continental basins containing actinopterygians in the Bohemian Massif. Actinopterygians usually comprise a significant portion of the vertebrate fauna in the sediments of the Late Carboniferous (Westphalian-Stephanian), as well as in the Early Permian (Lower Rotliegend). Twenty-one species of actinopterygians are currently known from these sediments. Actinopterygians in the Late Carboniferous are less numerous, but more diverse, and genera of the following families occur: Elonichthyidae Aldinger, 1937, Pygopteridae Aldinger, 1937, Acrolepidae Aldinger, 1937, Trissolepidae Fritsch, 1893, Sceletophoridae Štamberg, 2006, Igornichthyidae Heyler, 1977 and Haplolepidae Westoll, 1944. Actinopterygians in Early Permian sediments are the most numerous vertebrate fauna, and members of the family Amblypteridae Romer, 1945 predominate. Representatives of the families Igornichthyidae Heyler, 1977 and Elonichthyidae Aldinger, 1937 are much rarer. Fishes of the family Aeduellidae Romer, 1945 are known from sediments of the Late Carboniferous as well as from the Early Permian Lower Rotliegend, but they were only discovered during the last 20 years.

The family Aeduellidae was erected by Romer (1945) on the basis of the genus *Aeduella* Westoll, 1937. *Aeduella* are numerous in the Early Permian of the French Massif Central, and several other genera and species of Aeduellidae were described later from the Late Carboniferous and Early Permian of the French Massif Central (Heyler, 1969; Heyler and Poplin, 1983). It later turned out that radiation of Aeduellidae was much more extensive, and they were subsequently described from additional basins of Europe and North America (Poplin and Dutheil, 2005). Although a close relationship between actinopterygians and other fauna of the Bohemian Massif and the French Massif Central basins was described (Heyler, 1969, 1971), the occurrence of Aeduellidae in the Bohemian Massif had not been proven at that time. Štamberg described the first representative of the family Aeduellidae from the Bohemian Massif in 1986, and subsequently, the author worked intensively in several localities. Voluminous material, including several species of Aeduellidae, was recovered, primarily from the Early Permian. The aim of this paper is to present new finds of Aeduellidae from the Early Permian of the Krkonoše Piedmont Basin, and review all currently described fishes of the Aeduellidae from the Carboniferous and Permian of the Bohemian Massif.

DESCRIPTION

Material from the collection of the Museum of Eastern Bohemia (MHK) was used for the description.

New material originates from the Klášterská Lhota locality (Lower Rotliegend, Prosečné Formation) of the Krkonoše Piedmont Basin (Fig. 1). The first isolated bones of aeduellids were discovered at the locality several years ago (Štamberg, 2002), and numerous isolated bones, along with one partly preserved specimen, were collected last year. A specimen (MHK 81765) missing anterior region of the head reached about 18 cm in length. It has a well-preserved operculum and fragment of suboperculum on the head. The operculum is dorsoventrally elongate, and twice as tall as it is long, with its dorsal region curving anteriorly. The anterior margin of the operculum forms an angle of 157 degrees. This bone is longest in its ventral region. The operculum is rounded along its dorsal and posterior edges (Fig. 2H). The ventral edge is straight or sinusoidally curved, whereas the ventro-anterior and ventro-posterior corners are acute. Molding of the ventral edge of the operculum is similar to the modern bowfin *Amia calva* (Grande and Bemis, 1998, fig. 51). Two concentrically arranged ribs running parallel to the dorso-posterior edge form a sculpture in the dorsal region of the lateral surface; the rest of the lateral surface is smooth. The center of ossification of the bone is close to the anterior margin of the bone, at the bend.

The bones of the skull roof and the bone which Heyler (1969) described as the nasal on aeduellids are partly preserved. I consider Heyler's nasal in our case to be the anterior supraorbital. This bone lies anterior to the orbit, and is also present in other aeduellids (Štamberg, 2007). Fragments of the anterior supraorbital and the bones of the skull roof are conspicuously sculptured, with many ridges and tubercles. Smooth, but very stout scales cover the body of the fish. Their posterior edge is straight, not serrate. The scales are relatively large, and there are only 8 scale rows above the lateral sensory line (counted directly before the base of the dorsal fin). There are 25 scale rows between the supracleithrum and beginning of the dorsal fin. The number of the scale rows anteriorly from the dorsal fin is moderately higher than Heyler (1969) showed on *Aeduella blainvillei* (Agassiz, 1833). Four ridge-like scales are present anteriorly from the base of the dorsal fin. The dorsal fin contains about 26 segmented lepidotrichia. Segments are very stout, short and numerous, which indicates an adult specimen. The field of small scales on the base of the dorsal fin was not observed, but this may be the result of imperfect preservation of the specimen.

Beside the above described specimen, numerous isolated bones were found. The most abundant are operculum bones. The basic shape of the bones is the same as in the above described specimen MHK 81765. The dorsal part of the operculum is always orally bent, and dorsal and ventral parts of the anterior edge make an angle of 157–160 degrees (Figs.

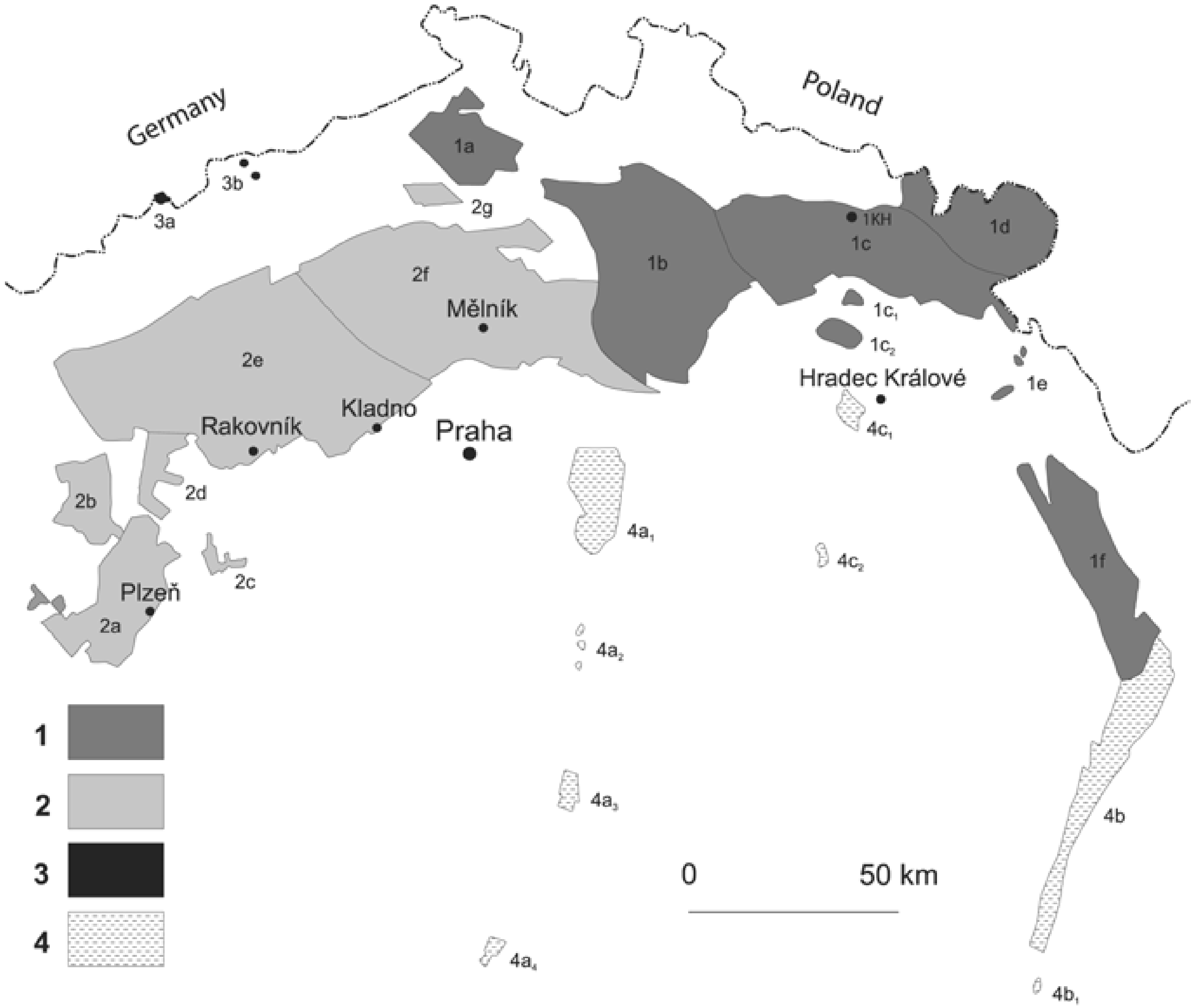

FIGURE 1. Distribution of the freshwater Carboniferous-Permian basins in the Czech Republic. Modified after Holub and Pešek (1994). **1**, Sudetic Area: **1a**, Česká Kamenice Basin; **1b**, Mnichovo Hradište Basin; **1c**, Krkonoše Piedmont Basin (**1c**$_1$, occurrence near Zvičina; **1c**$_2$, occurrence at the Hořice elevation; **1K.H.**, locality Klášterská Lhota); **1d**, Intra-Sudetic Basin (Czech part); **1e**, Permian occurrences in the Orlické hory Mts.; **1f**, Orlice Basin; **2**, Central and West Bohemian late Palaeozoic basins: **2a**, Plzeň Basin; **2b**, Manětín Basin; **2c**, Radnice Basin; **2d**, Žihle Basin; **2e**, Kladno-Rakovník Basin; **2f**, Mšeno-Roudnice Basin; **2g**, occurrence near Kravaře; **3**, Krušné hory Mts. Area: **3a**, occurrence near Brandov; **3b**, occurrences between Moldava and Teplice; **4**, Graben Area: **4a**, Blanice Basin (**4a**$_1$, northern part near Český Brod; **4a**$_2$, central part, occurrences near Vlašim; **4a**$_3$, central part, occurrences near Tábor; **4a**$_4$, southern part near České Budejovice); **4b**, Boskovice Basin (**4b**$_1$, occurrence near Miroslav); **4c**, occurrences in the Železné hory Mts. and near Hradec Králové (**4c**$_1$ RFFXUUHQFH LQ WKH ‡HOH]Qp KRU 0 W **4c**$_2$, occurrence near Hradec Králové).

2G-I). The highest opercula are 18 mm high, which corresponds to specimens of length 20-25 cm. Operculum MHK 81765 (Fig. 2H) is thickened anteriorly, with numerous pores on the anterior edge. The ventral edge is sinusoidally curved and corresponds with the same configuration of the dorsal edge of the suboperculum. The suboperculum is dorsoventrally elongate and exhibits a conspicuous posterodorsal process (Figs. 2E, F). The anterior part of the bone is very narrow, compared to the posterior part. The height of the suboperculum, including its posterodorsal process, is about twice its length.

The maxilla has already been described from this locality (Štamberg, 2002). It has a typical triangular shape, gradually increasing in height posteriorly. The height of the maxillary plate in its posterior region is 2.4 times the length of the maxilla (Fig. 2D). The small, sharp, pointed teeth on tubules are also readily distinguishable.

The well-preserved frontal can be seen in samples MHK 81732 and MHK 81906. This bone is relatively wide, with a length/width ratio of 1.6. The interfrontal suture is not straight, but moderately curved (Figs. 2A, B). Ornamentation on the dorsal surface of the bone consists of short, flat ridges sparsely distributed, close to the anterior and posterior margins of the bone. The supraorbital canal passes the frontal from the anterior margin of the bone; it traverses an arch latero-posteriorly. Frontal shape (length/width ratio, interfrontal suture moderately curved, ornamentation on the dorsal surface) is very close to the frontal shape of *Bourbonnella hirsuta*.

An isolated supracleithrum is dorsoventrally elongated, but it is not so high as the supracleithrum of *Paramblypterus*. A conspicuous process projects dorsally onto the supracleithrum (Fig. 2C), which articulates with the posttemporal. The lateral sensory canal passes ob-

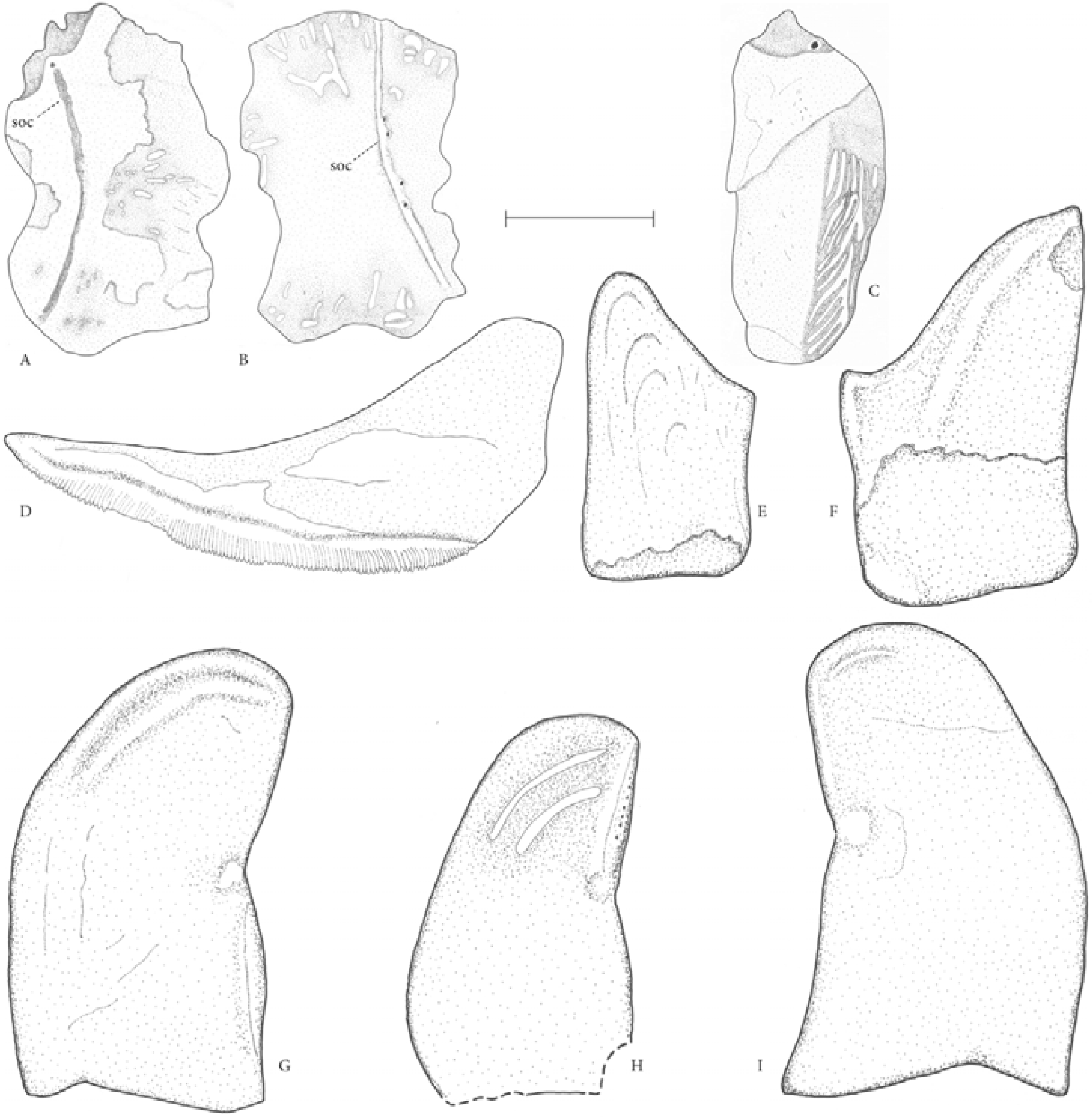

FIGURE 2. Isolated bones of aeduellids from the locality Klášterská Lhota (Krkonoše Piedmont Basin, Early Permian, Lower Rotliegend, Prosečné Formation). **A**, MHK 81732, right frontal in medial view, the sculpture of the dorsal side of the frontal is partly preserved on the counterpart. **B**, MHK 81906, right frontal in dorsal view. **C**, MHK 81758, right supracleithrum in lateral view. **D**, MHK 62441, left maxilla in lateral view. E, MHK 81718, right suboperculum in lateral view. **F**, MHK 81724, left suboperculum in lateral view. **G**, MHK 81720, right operculum in lateral view. **H**, MHK 81765, right operculum in lateral view. **I**, MHK 81905, left operculum in lateral view. Scale bar represents 5 mm. **Abbreviation: soc**, supraorbital canal.

liquely across the supracleithrum in the dorsal third of the bone with one large pore visible below the dorsal process. The anterior third of the lateral surface of the bone is conspicuously ornamented with ridges.

The above-mentioned finds of partially preserved whole specimens and sets of isolated bones represent typical aeduellid fish. Some features similar to those in *Aeduella blainvillei* include an operculum with a sinusoidally curved ventral edge and anteriorly bent dorsal region of the bone, suboperculum with a sinusoidal dorsal edge of the bone with the high dorsal process in the posterior region of the bone, and low-rising anterior region of the bone. The described condition of the operculum is typical for the small aeduellids *Neslovicella rzehaki* and *Neslovicella elongata* (Štamberg, 2007, 2010). Smooth scales posteriorly not denticulated is another feature of *Aeduella blainvillei*. The number of the scale rows between the supracleithrum and the beginning of the dorsal fin is more numerous than on *Aeduella blainvillei*. Typical aeduellid wide frontals with moderately curved interfrontal sutures are similar to the frontal of *Bourbonnella hirsuta*, instead of the frontal with a straight interfrontal suture seen in *Aeduella blainvillei* from the French Massif Central or Saar-Nahe Basin. The maxilla is one of the most typical bones of aeduellids; its length/height ratio of 2.4 indicates closer similarity to *Bourbonnella* than to *Aeduella*, which has this ratio between three and four (Heyler, 1969).

Summarizing the above described specimens, they represent relatively large aeduellid fish of length 20-25 cm, and important anatomical features place this fish in the range of the genera *Aeduella* and *Bourbonnella*. Due to the incompleteness of the newly described osteological fragments of aeduellid fish from the Klášterská Lhota locality, they cannot currently be assigned to one of above mentioned species, and some additional material will be necessary.

OVERVIEW OF THE AEDUELLIDAE IN THE BOHEMIAN MASSIF

Spinarichthys dispersus (Fritsch, 1894) was the first aeduellid fish described from the Bohemian Massif. This species, initially assigned by Fritsch (1894) to the genus *Acentrophorus*, shows typical aeduellid features, like a triangular maxilla with small, sharp, pointed teeth connected with long tubules, a high operculum and suboperculum, and a small number of branchiostegal rays. These characters put the species in Aeduellidae (Štamberg, 1986). *Spinarichthys dispersus* (Fig. 3A) is a small fish not exceeding 8-10 cm in length. It occurs in the Late Carboniferous (Stephanian B) of the Central and West Bohemian late Paleozoic basins. Numerous isolated scales occur in the Stephanian B, C of the Krkonoše Piedmont Basin. This species is not known from Permian sediments so far.

Other aeduellid fishes occur in the Early Permian sediments of the Krkonoše Piedmont Basin and Boskovice Graben. The first, *Neslovicella elongata* Štamberg, 2010 (Fig. 3B), is present in the oldest Permian sediments of the Krkonoše Piedmont Basin (Lower Rotliegend, Asselian, Vrchlabí Formation, Rudník Horizon). *Neslovicella elongata* was frequently recovered in several localities of the Krkonoše Piedmont Basin, and the occurrence of this species was documented in the Lower Rotliegend (Early Asselian, Schneider and Werneburg, 2006) Weissig Basin near Dresden, Germany (Štamberg, 2010). Numerous pieces of *Neslovicella rzehaki* Štamberg, 2007 (Fig. 3C) were recovered from the Boskovice Graben (Lower Rotliegend, Padochov Formation, Říčany Horizon; Early Asselian, Schneider and Werneburg, 2006). Both species of *Neslovicella* represent small fish, not exceeding 10 cm. They have sharpened aeduellid features, like the upper jaw increasing in height gradually posteriorly, without a boundary between the narrow anterior region and high posterior part, increasing their operculum and suboperculum in height, and reduction of the number of branchiostegal rays, in contrast to *Spinarichthys dispersus*. *Bourbonnella hirsuta* Štamberg, 2007 (Fig. 3D) is the third aeduellid fish from the Permian of the Bohemian Massif. It is known from one locality of Early Permian sediments of the Boskovice Graben (Lower Rotliegenden, Letovice Formation, Kochov Horizon, Sakmarian, Schneider and Werneburg, 2006). The species reaches 15 cm in length, with characters similar to the species of *Bourbonnella* described from the French Massif Central, but is distinguished mainly by its pectinated flank scales, numerous suborbitals, which are also pectinated, and the presence of the anterior supraorbital.

BIOSTRATIGRAPHICAL AND GEOGRAPHICAL REMARKS

Fishes of the family Aeduellidae occur in the freshwater basins of the Czech Massif from the Stephanian to Early Permian. The Stephanian species *Spinarichthys dispersus* occurs together with another actinopterygian, *Sphaerolepis kounoviensis* Frič, 1876, as in the Central and West Bohemian late Paleozoic basins and the Krkonoše Piedmont Basin. Neither species continues to the Permian. In addition to *Neslovicella rzehaki*, the Permian species of aeduellids are accompanied by actinopterygians of the family Amblypteridae: *Paramblypterus*. *Paramblypterus* is anatomically clearly distinguishable from the aeduellids in the course of the supraorbital sensory canal, shape of the frontals, shape of the maxilla, shape of the operculum, suboperculum, number of branchiostegal rays, scale count and several other characters. However, both groups are consistent in the type of dentition, presence of the anterior supraorbital and basic morphology of the body. It is obvious that the diet of Aeduellidae and Amblypteridae was identical. I presume that in the main their food was small crustaceans like conchostracans, which are common at all Carboniferous-Permian localities with Aeduellidae and *Paramblypterus*. Aeduellids and paramblypterids were certainly food competitors in the basins of the Bohemian Massif.

Uhl (1997) records the absence of paramblypterids in the localities where the aeduellids occur in the Saar-Nahe Basin. He interprets it as a result of expulsion of paramblypterids from the environment occupied by aeduellids, but he also outlines the possibility that the environment was somehow suitable only for aeduellids, where paramblypterids were absent. The circumstances are diverse in the basins of the Bohemian Massif. *Neslovicella rzehaki* is abundant, but entirely isolated in one locality of the Boskovice Graben. No other actinopterygian, acanthodian, xenacanthid or amphibian species accompany it, and its occurrence is bound to one small and time-limited lake. Other Permian aeduellids did exist together with paramblypterids and other faunas. Small *Neslovicella elongata* shared lakes together with paramblypterids that reached lengths up to 25 cm. Paramblypterids were present as a majority, but aeduellids occur in the same layer, and some samples demonstrate *Paramblypterus rohani* together with *Neslovicella elongata*. *Bourbonnella hirsuta* is very rare (only three specimens are known) and nearly of the same size as the paramblypterids that shared the environment of a large lake in the Boskovice Graben. Also, the above described aeduellid bones from the Klášterská Lhota locality from the Krkonoše Piedmont Basin occur together with isolated bones of *Paramblypterus*. For that reason, it is not possible to confirm conjecture of Uhl (1997) and Boy (1998) that Aeduellidae and Amblypteridae substitute one another, and that they do not occur together.

Aeduellidae occur in several fossiliferous horizons in the Early Permian of the Krkonoše Piedmont Basin and in the Boskovice Graben. Correlation of these horizons is usually very difficult, due to the paleogeographic and tectonic situation. In particular, the sediments of the Boskovice Graben are tectonically faulted, so that the originally continuous units are broken into smaller blocks. Correlation of the numerous separate fossiliferous horizons is further complicated by the gradual shift of the depocenter from the south to the north. The presence of actinopterygians, especially of aeduellids in the Early Permian sediments, can serve for biostratigraphic correlation of some horizons in the basins, and for correlation of basins in Central and Western Europe, supporting the amphibian and insect biostratigraphy of Schneider and Werneburg (2006, 2012). Aeduellidae are particularly suitable for these purposes, due to their clearly distinguishable bones. The *Neslovicella*

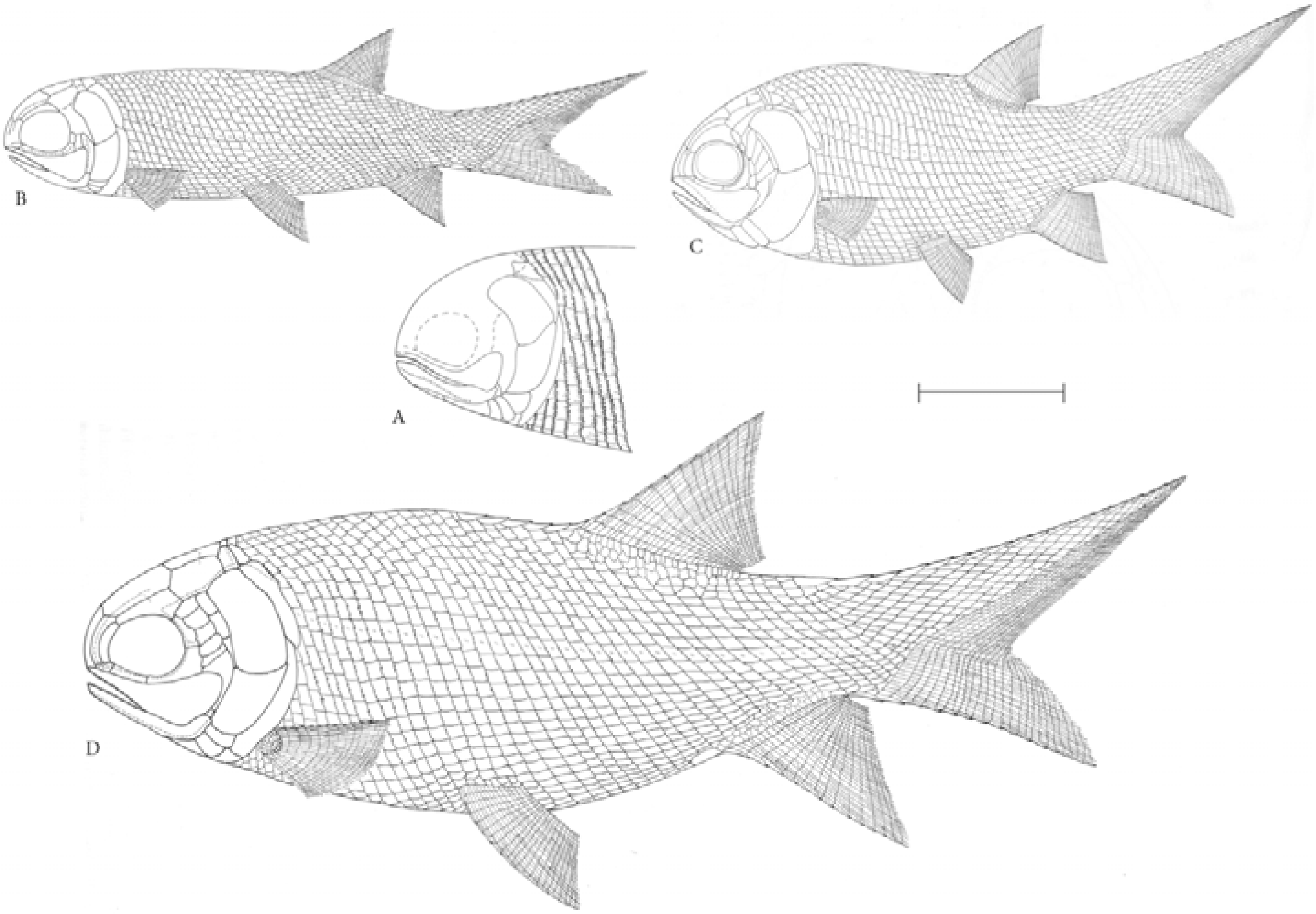

FIGURE 3. Reconstruction of aeduellids from the Bohemian Massif. **A**, *Spinarichthys dispersus* (after Štamberg, 1986). **B**, *Neslovicella elongata* (after Štamberg, 2010). **C**, *Neslovicella rzehaki* (after Štamberg, 2007). **D**, *Bourbonnella hirsuta* (after Štamberg, 2007). Scale bar represents 20 mm.

genus is interesting in this respect. The two species, *N. rzehaki* from the Říčany Horizon of the Boskovice Graben and *N. elongata* from the Rudník Horizon of the Krkonoše Piedmont Basin, are very closely related. Their presence in both basins attests to an approximately equivalent age of the horizons. *Neslovicella elongata* was additionally recorded (Štamberg, 2010) in the Weissig Basin (Early Permian, Weissig formation; Schneider et al., 2005) near Dresden, Germany. The *Neslovicella elongata*-bearing beds of the Weissig Formation and Rudník Horizon may be of identical age, and document the interconnection of the Krkonoše Piedmont Basin in the Bohemian Massif and the Weissig Basin in Germany through fluvial and lacustrine drainage systems linked to the Elbe lineament (Schneider and Reichel, 1989; Schneider and Zajíc, 1994).

CONCLUSION

Newly described isolated bones and body fragments from the Early Permian of the Krkonoše Piedmont Basin belong to one species of Aeduellidae. The body of the fish is 20-25 cm long, with stout, smooth scales, similar to *Aeduella*, but it differs in some anatomical features of the skull and in squamation, which are closer to *Bourbonnella*. *Spinarichthys dispersus* from the Late Carboniferous, and the recently described *Neslovicella rzehaki*, *Neslovicella elongata* and *Bourbonnella hirsuta* from the Early Permian of the Bohemian Massif, illustrate a large paleogeographic distribution area of Aeduellidae across the Carboniferous-Permian boundary, and indicate in this way a Central European basin system intesively interconnected by river systems. More precise knowledge of the aeduellid species will make them a valuable tool for biostratigraphy and especially for the reconstruction of drainage systems that interconnect the Central European continental basins among each other and with the sea.

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RECONSTRUCTION OF THE FLIGHT CHARACTERISTICS OF THE WINGED SEEDS OF AN EARLY PERMIAN CONIFER

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A voltzian conifer from the late Early Permian (~270 million years ago) from north-central Texas is the earliest known that produces one-winged seeds. The winged seeds of this conifer are exceptional in that they have variable morphology. They bear either one or two wings on the chalazal end of the seed, with the second wing ranging in size from a stub to a wing equal in size to that of the primary wing. To examine the aerodynamics of the different wing types, their flight performance and their implications for dispersal potential, we constructed same-scale models based on the geometric-morphometric consensus of three seed morphotypes. To test the validity of such modeling as an inferential tool, descent patterns of the models and extant analogs were captured with high-speed video. The flight characteristics of the models were compared to morphologically similar winged seeds of extant *Agathis* as well as to *Agathis* models created of similar materials and in a similar fashion to the models of the fossil seeds. Based on our observations, we infer ranges of descent speeds, auto-rotational stability, possible descent patterns, and dispersal potentials for the voltzian seeds. Reconstruction of these early forms of seed flight provides insight into why the single winged seeds are prevalent in extant taxa.

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ON THE DISCOVERY OF A NEW INVERTEBRATE ICHNOFOSSIL ASSEMBLAGE FROM DOYLES COVE, PRINCE EDWARD ISLAND

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A newly discovered ichnofossil of invertebrate walking traces from Doyles Cove, Prince Edward Island, has initiated a renewed interested in the paleoichnology of Prince Edward Island. The geological and paleontological history of the Upper Carboniferous-Lower Permian age Pictou Group of Prince Edward Island is well understood. Work conducted by previous researchers has unearthed abundant specimens of macroflora (i.e., *Wachia* and *Tylodendron*), vertebrate remains (i.e., *Bathignathus*) and vertebrate trace fossils (i.e., *Gilmoreichnus*, *Notalacerta*, *Limnopus*). A lesser known aspect of the Island's paleontology is the invertebrate paleoichnology. We present the first example of invertebrate walking traces from Prince Edward Island discovered by one of us (CP). Discoveries of invertebrate trace fossils have previously been restricted to burrows, and have been discussed briefly in previous works as fucoid-like trace fossils, worm borings and ferruginized root tubes, although none have been studied in detail. The specimen was observed within the upper fine-grained facies of the Orby Head Formation (megacycle 4) of the Pictou Group at Doyles Cove (46° 28' 24.79N, 63° 18' 09.40W). Preliminary assessments of the invertebrate ichnofauna exhibit a low diversity ichnofossil assemblage. Invertebrate walking traces include a single ichnospecies (Diplichnites gouldi), while invertebrate burrows include: *Cochlichnus*, *Treptichnus*, *Taenidium*, *Haplotichnus*, and *Planolites*. The ichnofossils are associated with greenish gray reduction zones at the bases of individual fluvial cycles, which are overlain by oxidized trough cross-bedded fluvial channel sequences. The Permian (Artinskian) sediments have been interpreted as being deposited under arid conditions with a declining biodiversity based on micro- and macropaleofloral assemblages. We assign the trace fossil *Diplichnites gouldi* described here to myriapods, which seemed to be present in this arid climate. The burrows seen at Doyles Cove reflect a low diversity suite of surface or near surface grazing and feeding structures, as well as infaunal feeding structures of primarily annelids or other small invertebrates. Depositional environments that yield the trace fossils are interpreted as shallow-water floodplains or ephemeral ponds/lakes adjacent to fluvial channels.

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NEW DISCOVERIES OF TETRAPOD-BEARING FOSSIL FORESTS AT JOGGINS, NOVA SCOTIA: IMPLICATIONS FOR TETRAPOD ENTOMBMENT AND ECOLOGICAL PERSISTENCE

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The classic Carboniferous section at Joggins is most famous for the discovery of standing fossil lycopsid trees that bear a terrestrial fauna within their once hollowed out stumps. The first discovery of this diverse entombed fauna was made by Sir John William Dawson and Sir Charles Lyell in 1852. Dawson's extensive explorations of a single fossil forest at Coal Mine Point, Joggins continued throughout the latter half of the nineteenth century. Fifteen of 25 trees explored were productive in tetrapod remains; these trees yielded 12 species of tetrapods and 6 species of terrestrial arthropods. Dawson's Coal Mine Point site at Joggins remains the most productive cache of Carboniferous tetrapods in the world. Among the disarticulated skeletal remains was the world's oldest known reptile (amniote) named *Hylonomous lyelli*. Only two subsequent tetrapod-bearing trees have been discovered between Dawson's death in 1899, and our recent work (1994-present). Walter Bell, noted by Sternberg, discovered two tetrapod- bearing stumps during the early twentieth century that are now housed at the Ottawa Museum of Natural History in Ottawa, Ontario, Canada. The original stratigraphic horizons from which they were recovered remains enigmatic.

The development of a search strategy, informed by Dawson's writings, and an extensive study of his specimens in London and Montreal, has resulted in the discovery of new tetrapod- bearing trees at Joggins. Eight additional fossil tree stumps of interest from seven new stratigraphic horizons, other than Dawson's Coal Mine Point fossil forest, have been recovered since 1994. Seven of these trees have yielded tetrapod bones, one has yielded ostacods and fish bones, and one has yet to produce animal remains. Three modes of tree stump infill have been noted. Most of the fossiliferous trees discovered in recent years conform to the general model described by Dawson, with tetrapods occurring throughout the upper basal carbonaceous and charcoal sediment infill that records evidence of wildfires. One tree has demonstrated interbedded mudstone and charcoal-carbonaceous sediments with bones and myriapods preserved thoughout the basal infill and *Dendropupa* land snails in the upper sandstone infill together with detrital plant remains. One tree preserves a true bituminous coal horizon within the stump, and is the only tree at Joggins to cross cut two coal seams.

Three of these productive trees derive from a sequence of upright lycopsids underlying the Forty Brine coal seam. The Forty Brine tetrapod-bearing trees demonstrate the persistence of ecological conditions in successive lycopsid forests, wherein entire forest stands were charred by repeated wildfire disturbance, and in at least one case, resulted in the formation of an unequivocal basal fire scar. These, in addition to the other five tetrapod-bearing forests, confirm that Dawson and Lyell's forest was not unique or unusual, but that similar paleoecological conditions recurred. It is unlikely these conditions were exclusive to Joggins, and as yet undiscovered tetrapod-bearing forests doubtless occurred in wetlands of the tropical biome where seasonality promoted disturbance and wildfire.

Experimental computed tomography (CT) scanning shows promise in revealing the distribution of bone material within the tree fills, most of which is concentrated in the basal 15 cm in association with charred plant material. Tetrapod bones from the trees are presently being analyzed by electron microprobe and for stable isotopes to determine whether their geochemistry records evidence of thermal history and consequently details about the chronology of their entombment as it relates to wildfire events and tree burial. Challenges to this process have included the presence of diagenetic mineralization in the form of calcite and gypsum skewing the goechemical data. The ability to study the taphonomy of the tree hollow fauna also permits evaluation of various scenarios of their entombment, in particular the long held pitfall theory and the newer hypothesis of a hollow tree guild (denning). Our recent discoveries not only provide a clearer understanding of the role of wildfires in the development of the ecological niche inhabited by the earliest amniotes, but also unveil a rich new source of tetrapod skeletal material from this pivotal moment in vertebrate evolution.

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BATRACHICHNUS SALAMANDROIDES FROM THE CARBONIFEROUS OF JOGGINS, NOVA SCOTIA, CANADA: THE SMALLEST KNOWN TETRAPOD FOOTPRINTS

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A new trackway of *Batrachichnus salamandroides* from the classic Carboniferous section at Joggins, Nova Scotia, represents the smallest example of tetrapod footprints known in the fossil record. The track maker was a juvenile, quadrupedal temnospondyl or microsaur with a trunk length of 3.55 mm and an estimated body length of 8 mm (skull, presacral vertebrae and caudal vertebrae). The most conservative measurements, which include extramorphological features (i.e., toe drags), measure the manus and pes to have an average length and width of 1.58 mm x 1.65 mm and 2.38 mm x 2.54 mm, respectively. When the relative size of this trackway is compared with other previously described examples of *Batachichnus salamandroides* and other small vertebrate ichnotaxa from Joggins, the trackway described here is substantially smaller than previously described specimens. The 48-mm-long trackway preserves a high degree of extramorphological variation along its course, including a gait change associated with a change in direction together with an increased stride and pace, and the appearance of overstepped imprints, in the latter portion of the trackway. These morphological changes suggest the tetrapod changed from a walking gait to a running gait.

Based on previous work, the case for a temnospondyl (branchiosaur, *Eryops*, or *Dendrerpeton*) track maker of *Batrachichnus* is strong. More than 100 fragmentary remains of *Dendrerpeton* have been prepared from the tree stumps recovered by Dawson in the late 19th century, and one articulated skeleton was collected and prepared from a siderite nodule. Previous work by Haubold compared skeletal reconstructions of the manus and pes anatomy of *Dendrerpeton* to that of *Batrachichnus* and made a compelling case for their similarity. Given the size ranges of *Limnopus* and *Batrachichnus* at Joggins, and the known skeletal remains, *Dendrerpeton* (or some other, similar temnospondyl) is a strong candidate for the track maker of both ichnogenera at Joggins. Body proportion measurements, taken from the only known articulated temnospondyl represented at Joggins, and adult temnospondyl *Dendrerpeton*, were used as a model to estimate the skull and body lengths of the track maker for the recently discovered *Batrachichnus* specimen.

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A PENNSYLVANIAN TETRAPOD TRACKWAY FROM JOGGINS, NOVA SCOTIA: THE SIZE CONTINUUM OF *BATRACHICHNUS SALAMANDROIDES*

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Abstract—A tetrapod trackway from the Lower Pennsylvanian at the historic section at Joggins, Nova Scotia, preserves 13 pairs of impressions with a possible partial tail drag. Although overstepping and poor preservation obscure many of the diagnostic features, the pes is plantigrade to semi-plantigrade and distinctly pentadactyl, with digit length increasing sequentially I-III. The manus may be tetradactyl, but no single impression allows this to be stated confidently. The size of the tracks is within the known range of *Batrachichnus salamandroides*, which is known from the same location, and so these tracks are assigned to this ichnospecies. The trackmaker was a small temnospondyl, although multiple candidates are known from body fossils in this section.

INTRODUCTION

The stratigraphic section at Joggins, Nova Scotia, is one of the best-exposed and most widely studied Carboniferous sections in the world. The locale has long been famous for the preservation of lycopsid trees in growth position, and more so for the diversity of tetrapod fossils, particularly those preserved within the stumps of those trees (Lyell and Dawson, 1853; Owen, 1862; Dawson, 1862, 1863, 1870, 1876, 1882, 1891a, 1891b, 1892a, 1892b, 1894, 1895; Steen, 1933; Carroll, 1964, 1966, 1967, 1972, 1988, 2009). These remains are an important record of tetrapod evolution, and include a demonstration of the diversity of temnospondyl amphibians, microsaurs, anthracosaurs (Carroll, 1966; Holmes et al, 1998; Holmes et al., 2010), and the oldest known amniotes (*Hylonomus lyelli*; Dawson, 1895; Carroll, 1970, 1972, 1988, 2009). Most of the tetrapod body fossils at Joggins are small, due in part, undoubtedly, to the preferential mode of preservation, i.e., within tree stumps (Carroll, 1988).

The section at Joggins also produces a rich ichnofauna, with approximately a dozen tetrapod ichnogenera named thus far (Hunt et al., 2004; Lucas et al., 2005). Most recently, Stimson et al. (2012) described a trackway of *Batrachichnus salamandroides* from this site that they present as the smallest tetrapod tracks yet discovered. This paper describes a similar trackway from the same location in which the tracks are also quite small, although not so small as documented by these authors.

SETTING

The 1.5 km-thick section of the Joggins Formation at Joggins, Nova Scotia, is one of the best-known exposures of non-marine Carboniferous strata. The Joggins Formation, Cumberland Group, was deposited during the Namurian through Stephanian stages (Pennsylvanian) in the Maritimes Basin, Atlantic Canada, a region well known for its Pennsylvanian-age coal deposits, including the historically important location of Joggins,. The Maritimes Basin is a complex of depocenters centered over the Bay of Fundy and Gulf of Saint Lawrence that includes the Cumberland, Minas, Moncton, and Sydney basins. It originated in the Middle Devonian as a structural and erosional remnant of an earlier depocenter of unknown size (Gibling et al., 1992).

The Devonian and Lower Carboniferous basin fill comprises alluvial and lacustrine deposits of the Horton and Canso groups and evaporitic marine deposits of the Windsor Group. Alluvial deposition dominated from Namurian to Early Permian time during accumulation of the Riversdale, Cumberland, and Pictou groups. Sedimentation was notably rapid during deposition of the Joggins Formation as withdrawal from the underlying Windsor Group (Mississippian) evaporites accelerated sediment accomodation (Waldron and Rygel, 2005). Deposition of the Joggins Formation was characterized by cyclical sequences of coastal wetland deposits, including coastal plain, deltaic plain and distributary channel facies comprising fine-grained siliciclastics, sandstones, coals and limestones. Cyclicity was potentially controlled by eustatic changes (parasequences: Davies and Gibling, 2003).

MATERIAL AND PROVENANCE

The slab studied here was collected from the backshore of the beach at Joggins immediately below the cliff about 250 m north of the access from Main Street (Fig. 1). Matching the lithology and bedding of the slab to the cliff face suggests that it derived from just below a channel-fill sandstone at about 597 m above the formation base, between coals 16 and 17 in cycle 9 (after Davies et al., 2005); this is approximately the same location that produced the trackway described by Stimson et al. (2012). The specimen described herein was collected in the summer of 1988 (before passage of the Nova Scotia Special Places Protection Act) while the author conducted graduate research elsewhere in the province. The specimen is housed in the Department of Biological Sciences fossil collection at Le Moyne College, in Syracuse, New York.

The material is a single trackway preserved on a roughly triangular-shaped slab, 15 cm by 24 cm, consisting of light brown, rippled siltstone with gray clay drapes (Fig. 2). The upper and lower surfaces of the slab are thin claystone coatings of the siltstone. The upper surface

FIGURE 1. Location of the sample collection site on the shore of Chignecto Bay, Bay of Fundy, by the village of Joggins, Nova Scotia, Canada (image adapted from Google Earth®.

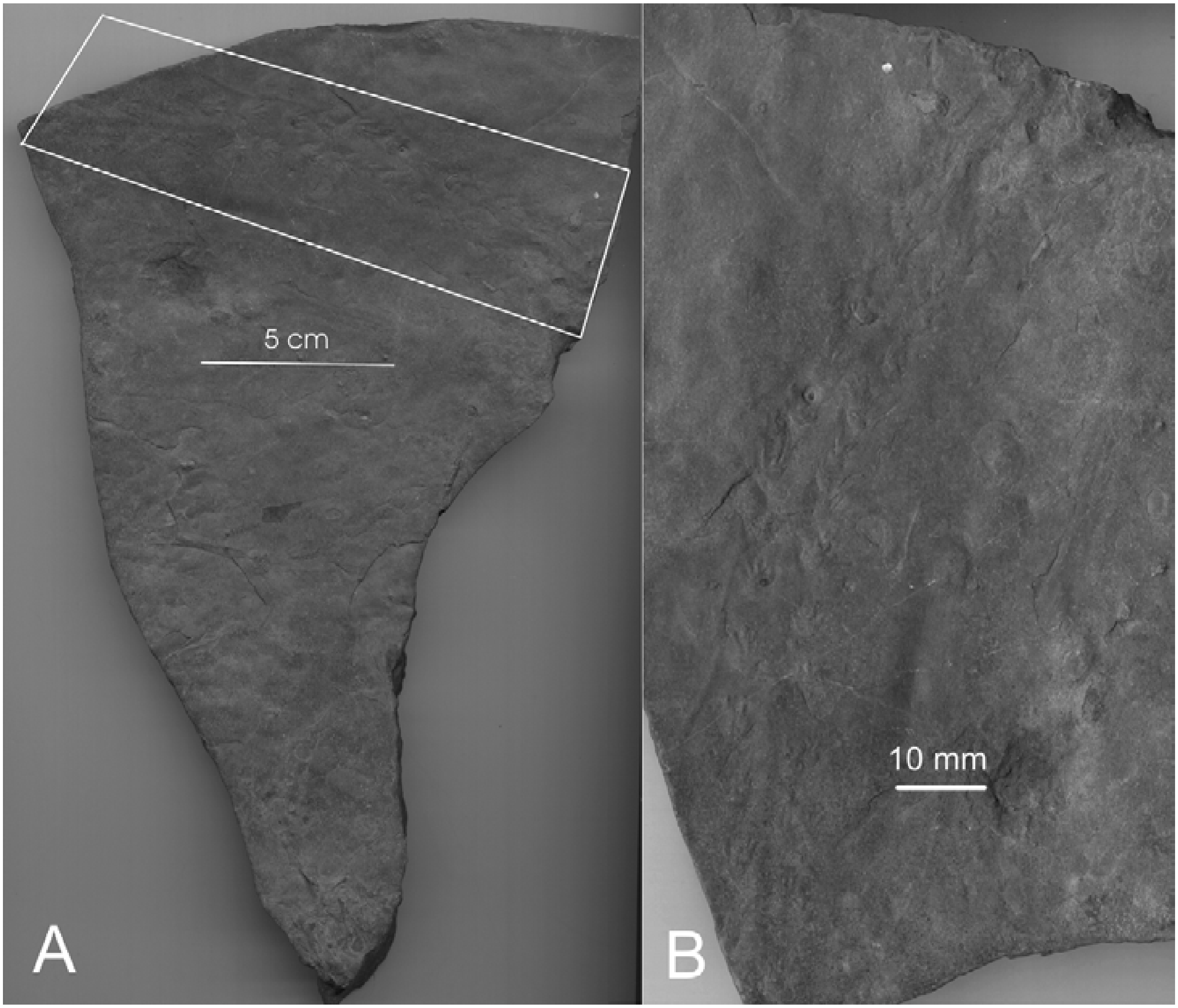

FIGURE 2. Specimen slab collected at Joggins. **A**, View of the underside of the entire slab, with **B**, detail of the trackway (view rotated with proximal end of trackway at bottom).

preserves circular impressions, presumably of raindrops. The trackway described below is preserved on the lower surface of the slab.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Batrachichnus* Woodworth, 1900
Ichnospecies *Batrachichnus salamandroides* (Geinitz, 1861)

Diagnosis: This ichnospecies is represented by quadrupedal trackways that are typically small and narrow, and commonly show alternating manus-pes sets with little divergence of manus and pes axes, and a pace angulation that rarely exceeds 90°. The individual impressions are elongate, the distal ends of the soles and digits are rounded, and the soles narrow posteriorly. Pes prints are pentadactyl and plantigrade to semi-plantigrade, with lengths up to 35 mm long (Voigt, 2005). Digits I - III are grouped closely together and increase in length sequentially, digit IV is the longest and somewhat separated from the others and digit V is directed laterally and set somewhat posteriorly. Manus prints are tetradactyl and semi-plantigrade; they are smaller than the pes prints and digits increase from I – III; digit IV diverges outward from the grouping of I – III. A tail or body drag may be present (Haubold, 1971, 1996; Melchor and Sarjeant, 2004; Lucas et al., 2011; Stimson et al., 2012).

Description: The trackway consists of 27 impressions arranged as roughly 13 left-right pairs. All tracks are preserved as undertracks in convex hyporelief. The entire trackway is 149 mm long and has a mean width (=outer left pes to outer right pes) of 13 mm. The proximal end of the trackway is straight, but bends 23^o to the right (relative to the direction of travel) after 70 mm (Figs. 2A, 3). There is no distinct tail drag, although there is a subdued convex linear feature between the left and right sides of the trackway at the proximal end extending to about 50 mm from the trackway start that suggests a tail or body drag impression (Fig. 4).

In general, preservation is better for the proximal tracks, particularly 2 through 6, in which features of individual tracks are more clearly recognizable. However, consistent partial overstepping severely comprises the ability to measure these quantitatively. Among the proximal tracks, the best preserved pes (e.g. LP5; Fig. 4) is pentadactyl, measuring 5.2 mm long by 5.0 mm wide. On this print, digits I -III are seen to increase serially and IV-V diverge from the first three. Only one manus

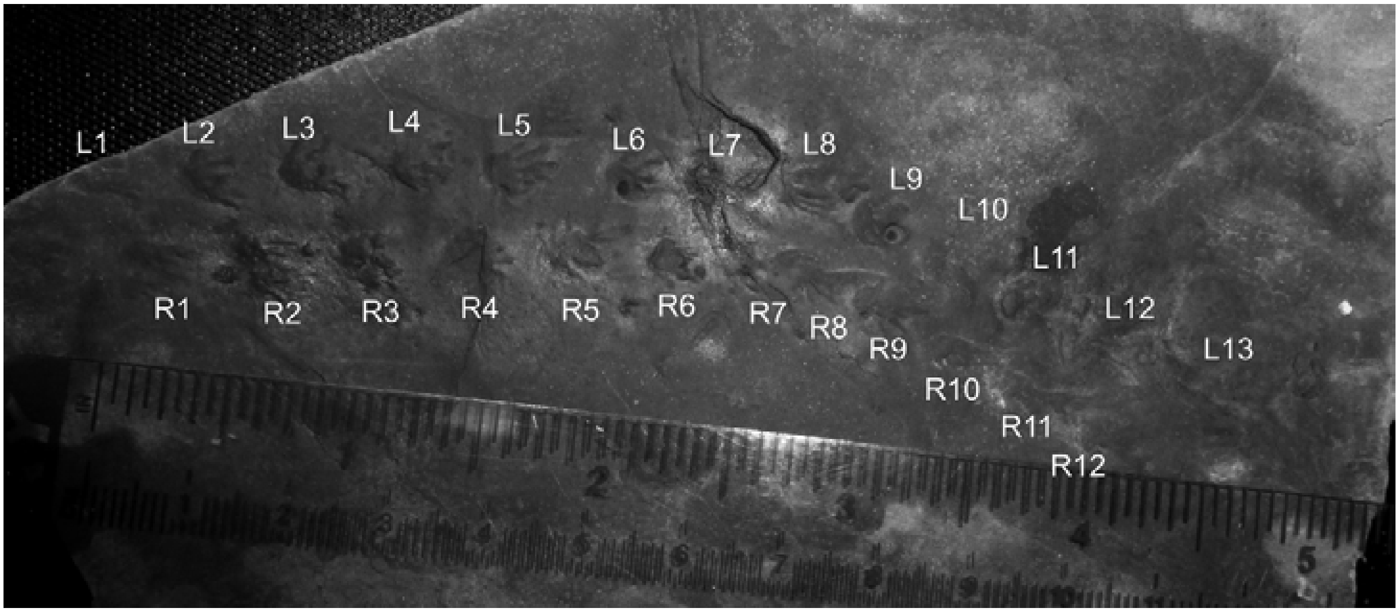

FIGURE 3. Detail of trackway with tracks numbered serially from proximal to distal.

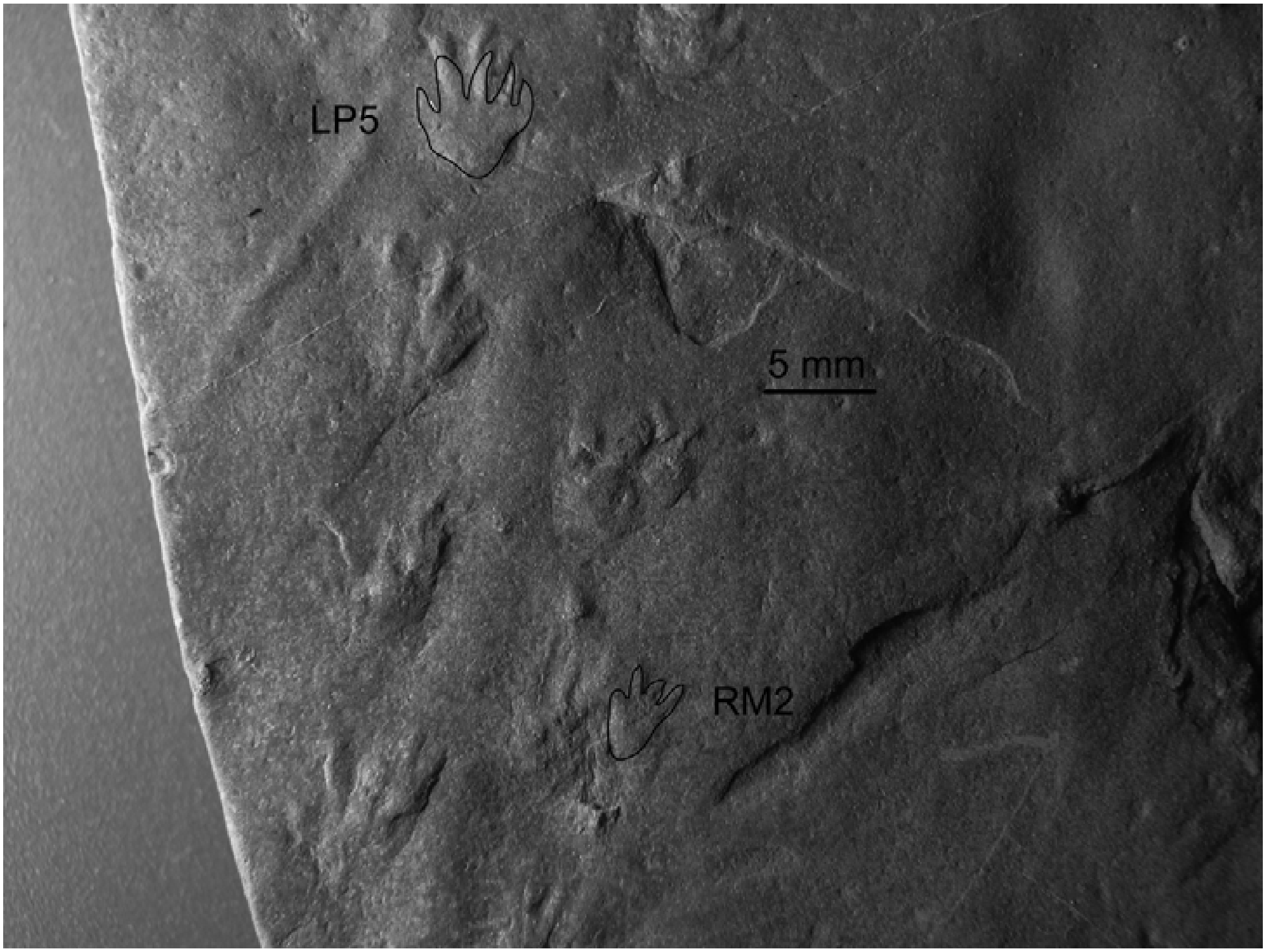

FIGURE 4. Detail of the proximal portion of the trackway, illustrating potential tail drag impression between left and right prints. Partial overstepping of pes on manus present in most tracks, with lateral offset between manus and pes visible in tracks. LP5 and RM2 discussed in text.

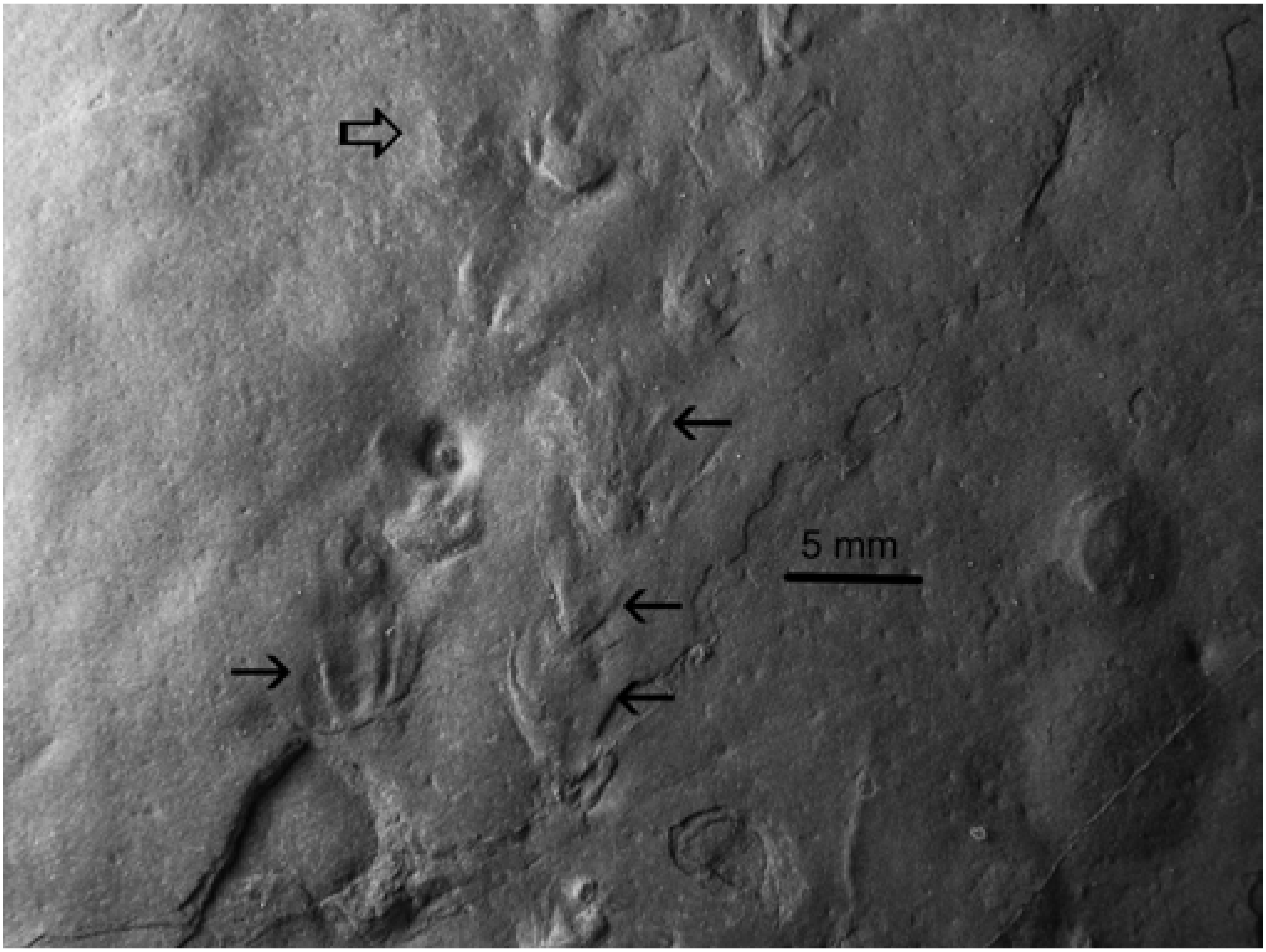

FIGURE 5. Distal portion of the trackway exhibits poorer detail. Elongated digits (*Gracilichnium* preservation) visible in some tracks, indicated by closed arrows. An isolated tridactyl impression appears to the left of the trackway near the top of the photograph (open arrow).

(RM2) approximates a tetradactyl morphology, measuring 4.5 mm long by 4.2 mm long, but this impression is not sufficiently distinct to assess confidently. All other manus impressions have reduced digits (typically three), where the digits are distinct from the overstepping pes impression. The impressions (pes and manus) in the proximal trackway are mostly plantigrade to semi-plantigrade, with posteriorly rounded soles and rounded to pointed digits. The direction of overstepping of the manus by the pes varies from directly in-line (e.g., LP5 over LM5 in figure 3), to offset, with the manus to the right of the pes in both right and left pairs (LM2, LM3, RM2, RM3). The pace measures 4.7 to 6.0 mm, and stride length varies from 9 to 11 mm. Pace angulation varies from 61^o to 74^o.

The distal section of the trackway differs from the proximal in the generally indistinct preservation of the tracks (Figs. 3,5), most likely due to a change in substrate; the clay layer containing the tracks is less than 1 mm thick at the edge of the slab on the proximal end, but about 2 mm thick at the distal edge. Thus, the track maker walked across a firmer substrate initially and encountered deeper, softer material farther on. The distal tracks are mainly semi-plantigrade, and the digits are typically too indistinct to count or measure. Several of the distal impressions exhibit "*Gracilichnium*-type" preservation (Fig. 5; *sensu* Haubold, 1970), consistent with a deeper, softer substrate.

Two isolated impressions occur exterior to the distal portion of the trackway, 2 to 3 mm to the left of the outer edge of the nearest impression (Fig. 5). These appear to be semi-digitigrade impressions displaying at most three digits. The relief and clarity differ from the adjacent impressions of the trackway, and therefore represent tracks made at a different time.

Remarks: As well-reviewed by Stimson et al. (2012), the ichnospecies *Batrachichnus plainvillensis*, erected by Woodworth (1900), is a junior synonym of *Saurichnites salamandroides*, initially erected by Geinitz (1861). Because small trackways are readily subject to significant extramorphological variations, due in part to differences in grain size and water content of the substrate, as well as mode of preservation (Melchor and Sarjeant, 2004), multiple ichnotaxa were introduced to account for the variable morphologies of small temnospondyl footprints, but these were recognized as junior synonyms of *B. delicatulus* (Lull, 1918). Subsequent comparisons of *Anthichnium salamandroides* indicated that it also conforms to the ichnogenus *Batrachichnus* (Woodworth, 1900). Tucker and Smith (2004), in contrast, synonymized *Batarachichnus* and *Limnopus* based on similarities of morphology and the size continuum, but Falcon-Lang et al. (2010) retained *Batrachichnus* to describe the traces at the smaller end of the size range. The present work follows Lucas et al. (2011) in recognizing *Batrachichnus* as a monospecific ichnogenus that includes only *B. salamandroides*.

DISCUSSION

Assignment of the described specimen to *B. salamandroides* is based on the presence of most of the diagnostic features described above, in combination with the size of the individual impressions. In clear specimens, the pentadactyl pes and tetradactyl manus, with distinct separation between digits I-III and IV, are considered diagnostic. The specimen described here does not present a manus sufficiently clear to describe as tetradactyl, due largely to overstepping, although at least one impression suggests this morphology. Otherwise, the tracks conform to the general features of *B. salamandroides*. Haubold et al. (1995) present 20 mm as the typical pes length for *Batrachichnus delicatulus*, with smaller impressions (4 to 5 mm) referred to *B. obscurus*. Lucas et al. (2011), however, suggest 20 mm as the upper range of size of *Batarchichnus*, and describe pes lengths of 5 to 15 mm as typical for the ichnogenus. Falcon-Lang et al. (2010), for example, described tracks of *Batrachichnus* sp. from the Lower Pennsylvanian of New Brunswick (equivalent to the Joggins Formation) and measured manus lengths of 5 to 8 mm. Stimson et al. (2012) extend the size range of this ichnogenus significantly, measuring pes lengths of 1.7 to 3.2 mm. Consequently, size and morphological conformity of the herein described tracks is consistent with attribution to *B. salamandroides*.

Haubold (1971, 1996) favored a small temnospondyl as the *Batrachichnus* trackmaker, possibly a juvenile eryopid, but as noted by others (Yates and Warren, 2000; Ruta et al., 2003; Falcon-Lang et al., 2006), there are no synapomorphies of the manus and pes other than the four-digit manus. Falcon-Lang et al. (2006) suggest the temnospondyl *Dendrerpeton*, known from body fossils in the Joggins Formation, as a likely candidate. Stimson et al. (2012), in comparing the tracks they describe with potential trackmakers, acknowledge *Dendrerpeton* as one possibility, but also acknowledge other temnospondyls (branchiosaur, *Eryops*) that might produce similar tracks.

SUMMARY

The Lower Pennsylvanian tetrapod trackway collected at Joggins displays many of the features typical of the ichnogenus *Batrachichnus*, such as a pentadactyl pes and the size distribution of the digits on the pes. Overstepping and lack of detailed preservation prevent confident description of the manus as tetradacyl, however. The size of the tracks is within the range known for the ichnospecies *B. salamandroides*, which is well-described from this locality, and so these tracks are assigned to this ichnospecies. Potential trackmakers known from body fossils at this section include a variety of small temnospondyls.

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THE PALEOFLORA OF FRANKENBERG/GEISMAR (NW-HESSEN, GERMANY) – A LARGELY UNEXPLORED “TREASURE CHEST’” OF ANATOMICALLY PRESERVED PLANTS FROM THE LATE PERMIAN (WUCHIAPINGIAN) OF THE EURAMERICAN FLORAL PROVINCE

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Abstract—At the locality Frankenberg/Geismar in NW-Hessen (Germany), anatomically preserved plant remains can be found in different modes of preservation. Besides pyritized remains, charred plant fragments as well as “mummified” leaves also occur, which can be studied by means of “classical” light microscopic techniques as well as Scanning Electron Microscopy. These remains can provide new and additional anatomical information for a number of Late Permian plants. In contrast to the few other known Late Permian localities from Euramerica that provided plants in anatomical preservation, this locality is still accessible and thus it is possible to collect new material. Additionally, abundant material that was collected mostly during the 19th century is available in many natural history museums worldwide. However, so far only a few studies have dealt with the anatomically preserved material from this locality. This makes the Frankenberg/Geismar locality unique in the entire Late Permian of the Euramerican floral province, as this material can possibly provide data from a number of important taxa from this period. The (preliminary) results from leaves and megasporophylls of *Peltaspermum martinsii* presented here provide the first data on the internal anatomy of this taxon.

INTRODUCTION

Middle and Late Permian plant-bearing localities are extremely rare in the entire Euramerican floral province (Rees, 2002). Whereas the few Middle Permian localities are scattered throughout North America and Europe, almost all Late Permian sites are restricted to the marine Zechstein facies or its marginal marine equivalents in Europe (e.g., Schweitzer, 1986; Uhl 2004, and citations therein). Most of the Zechstein localities only yield impression fossils of plants; remains with cuticles or internal anatomy preserved are absent at most localities (Uhl and Kerp, 2002). Localities with cuticular preservation are mostly restricted to marginal marine or terrestrially-influenced facies deposited at or near the borders of the Zechstein Sea (e.g., Ullrich, 1964; Poort and Kerp, 1990; Uhl and Kerp, 2002, 2005), whereas at most fully marine localities cuticles are absent due to diagenetic alterations (Haubold and Schaumberg, 1985; Uhl, 2006b). One of the few exceptions are localities in W-Germany in the Lower Rhine area, and here not only cuticles have been preserved, but also remains (permineralized with calcite) with some degree of internal anatomy (Schweitzer, 1962, 1963). Other localities with anatomically-preserved Late Permian plant remains are Ilmenau in Thuringia and Frankenberg/Geismar in NW-Hessen (Solms-Laubach, 1884; Uhl and Kerp, 2002). Although Ilmenau can be regarded as a “classical” locality for Late Permian paleobotany (three widely distributed conifer taxa have been described from here: *Ullmannia frumentaria* (Schlotheim) Göppert, *Quadrocladus solmsii* (Gothan and Nagalhard) Schweitzer and *Quadrocladus orobiformis* (Schlotheim) Schweitzer), no systematic study has so far been conducted at this locality since a first survey on anatomically preserved plant remains was published by Solms-Laubach (1884). However, this study was technically “hampered” by size restrictions of thin sections at that time. Recent tests utilizing the acetate peel technique have demonstrated that material from this locality probably has a large potential for further anatomical studies (Uhl and Kerp, 2002). Unfortunately, the Ilmenau locality (former spoil tips of copper mines) is long gone and there is only a relatively small chance to collect new material. Thus, future studies of that site have to rely on material already present in various museum collections.

Comparable to Ilmenau, only a few studies have dealt so far with anatomically preserved plant remains from Frankenberg/Geismar, but here the great potential for anatomical studies has repeatedly been demonstrated. Göppert (1850) mentioned the fact that some specimens of his new taxon *Ullmannia bronnii* Göppert showed traces of anatomically preserved tissues, which were visible on broken and weathered surfaces of a few specimens. Following this the most extensive study on the anatomy of material from Geismar (and Ilmenau) was done by Solms-Laubach (1884), who was only able to produce and figure rather small thin-sections of this material and it was only possible to get anatomical information from non-permineralized parts of woody tissues. Further studies on the wood of *Ullmannia bronnii* (Lemoigne and Schaarschmidt, 1968) and *Brachyoxylon* Hollick and Jeffrey (Uhl, 2004) had to deal with the same problems, although it is possible to supplement the information from thin sections with data from polished sections of the same specimen as demonstrated by Uhl (2004).

Only recently studies of thin sections have been supplemented by data from SEM studies, leading to the identification of so far unrecognized modes of preservation (i.e., charcoal: Uhl and Kerp, 2003) and to new data about the taphonomy and diagenesis of pyritized plant remains at this locality (Uhl, 2006a). All in all, three different types of anatomically preserved plant remains occur at Frankenberg/Geismar:

1) pyritized plant remains (Figs. 5, 6, 7F-G),
2) “mummified” plant remains (Fig. 7A-D), and
3) charred plant remains (Figs. 8-10; Uhl and Kerp, 2002).

Knowledge about these types of preservation is briefly summarized here and some new anatomical data are presented for two taxa (i.e., the conifer *Ullmannia* sp. and the peltasperm *Peltaspermum martinsii* (Germar) Poort et Kerp).

GEOLOGICAL SETTING

The plant remains investigated here come from the Late Permian (Wuchiapingian) locality Frankenberg/Geismar in NW-Hessen (Germany) (Fig. 1). The sediments, which yield abundant plant remains in different modes of preservation (Uhl and Kerp, 2002), represent a marginal marine facies of the Zechstein Sea known as the Geismar Formation (German Stratigraphic Commission, 2002). The fossiliferous sediments belong to the so-called “Geismarer Kupferletten-Flöz“ (Fig. 2), a 20 to 200 cm thick marly horizon that was mined for copper and other metals from

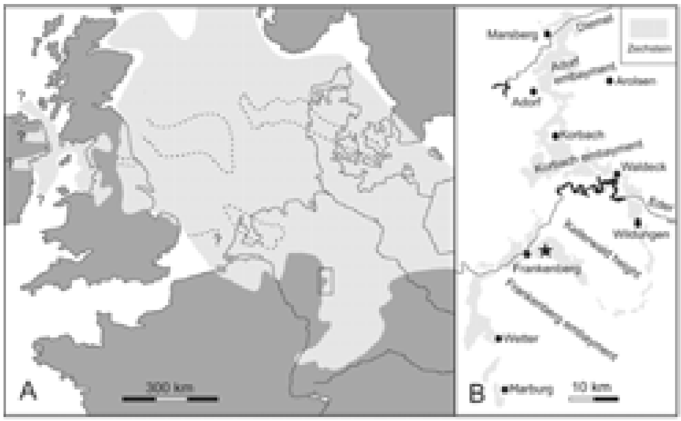

FIGURE 1. **A**, Map of Europe showing the maximum extent of the Zechstein Sea (light grey) (modified from Schweitzer, 1986). **B**, Map of the Zechstein outcrops in NW-Hessen (light grey); the position of the Frankenberg/Geismar locality is marked by the star (modified from Kulick and Paul, 1987).

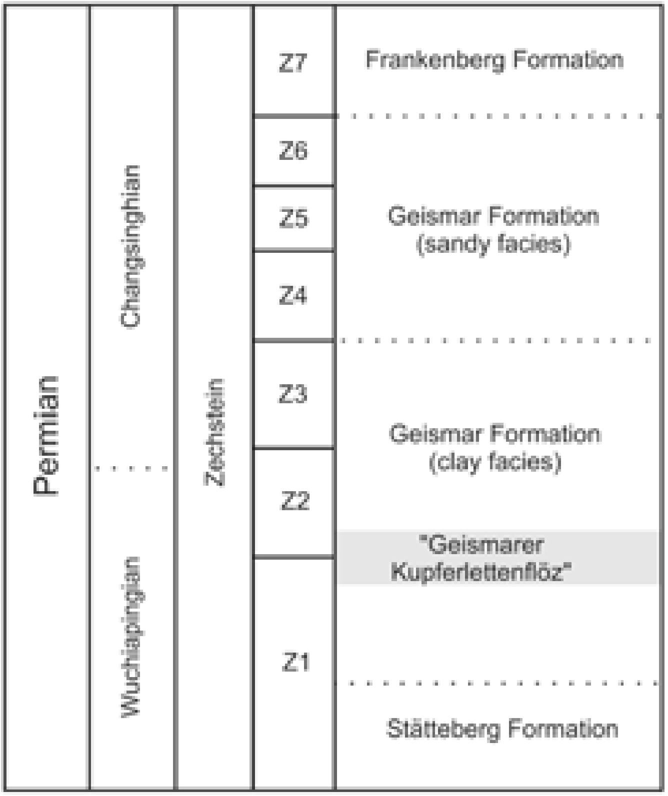

FIGURE 2. Stratigraphic column of the marginal-marine Zechstein in NW-Hessen; plant remains described in this contribution come from the "Geismarer Kupferlettenflöz" (marked in light gray), which corresponds to the transition zone from cycles Z1 to Z2 (based on Kulick, 1987, and German Stratigraphic Commission (ed.), 2002).

FIGURE 3. Photograph of a spoil tip of a former copper mine near Frankenberg/Geismar. Even decades after the mining stopped, vegetation is still scarce on this spoil tip due to the relatively high concentrations of copper in the sediment.

the 16th to the 19th centuries (Kulick, 1987). To isolate mineralized portions of the sediments, which are always linked to organic remains (Kulick, 1987), large pieces of the marly sediment were stirred together with water in large barrels. During this procedure the non-mineralized parts of the marls were dissolved in water and what remained were the mineralizations around plant remains (Ullmann, 1803). Many of these, which were identifiable by the miners as fossils, found their way into a large number of museum collections world-wide (often known as the so-called "Frankenberger Kornähren" [grain ears from Frankenberg]). Fossil specimens can still be collected in great abundance, weathering from the sediment, on former spoil tips of some of these copper mines (Fig. 3). This material not only includes anatomically preserved plants, but also compressions (Fig. 4).

The "Geismarer Kupferletten-Flöz" is equivalent to the top part of the marine Zechstein cycle Z1 (Werra Formation), transitional zone to Zechstein cycle Z2 (Stassfurt Formation) (Fig. 2; Kulick, 1987). The geology and stratigraphy of this area have been discussed in detail by Richter-Bernburg (1955), Sauer (1964), Kulick and Richter-Bernburg (1987) and Kulick (1987).

The Frankenberg area represents an embayment of the Central European Zechstein Basin. A review of the facies development of this and adjacent embayments along the margins of the Central European Zechstein basin has been given by Paul (1982). Specimens investigated here are stored in the collections of the Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universiät Münster, the Department of Geology, University of Marburg (now at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt), and the Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen (all Germany).

PYRITIZED PLANT REMAINS

Plant fragments that have been (at least partly) permineralized with pyrite and other minerals like chalcopyrite are abundant at Frankenberg/Geismar, as in many other Paleozoic, Mesozoic and Ceno-

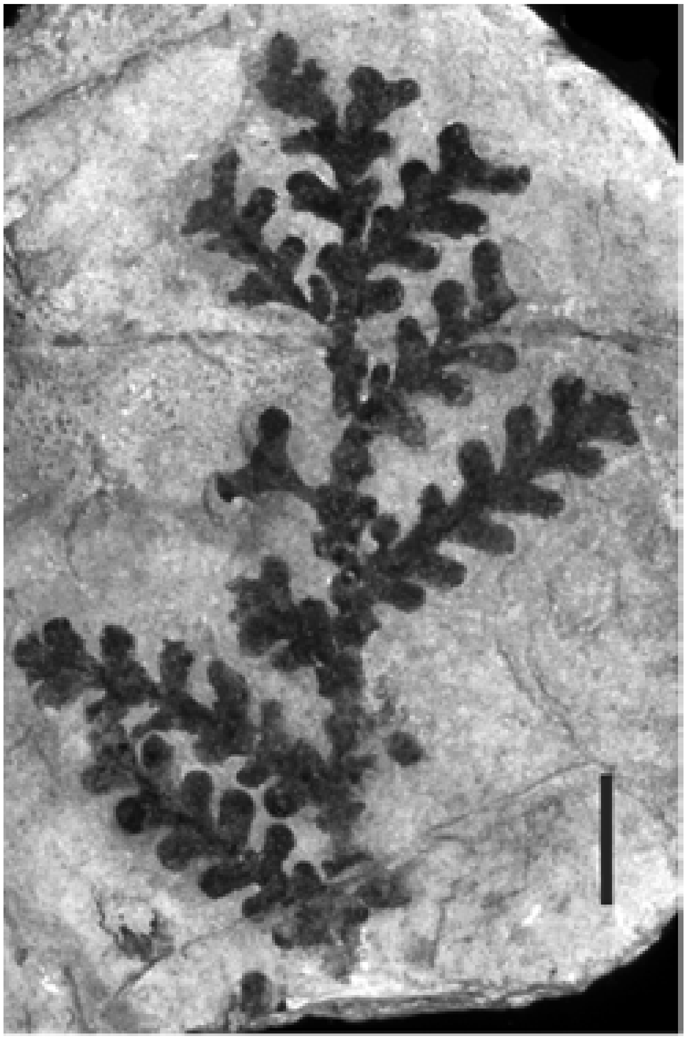

FIGURE 4. Compression fossil of *Peltaspermum martinsii* (Germar) Poort and Kerp (orig. Althaus, 1846; Pl. I, fig. 3) from Frankenberg/Geismar (scale bar = 1 cm; coll. University of Marburg, Germany, Inv.-Nr. MBG 1794; now in the collection of the Senckenberg Research Institute and Natural History Museum, Frankfurt/Main, Germany).

zoic deposits (e.g. Allison, 1988; Kenrick and Edwards, 1988; Canfield and Raiswell, 1991; Brown et al., 1994; Grimes et al., 2001, 2002; Tibbs et al., 2003; Uhl and Lepper, 2006). Both minerals can often be found in the outermost tissues of these plants and in mechanically damaged areas, where cracks and voids may have acted as pathways for bacterial migrations into the plant remains (Uhl, 2006a). Such remains were the basis of a number of publications dealing with plants from this flora (e.g., Waldin, 1778; Ullmann, 1803; Bronn, 1828; Göppert, 1850) during the 18th and 19th century; with the exception of Solms-Laubach (1884), however, these works were almost exclusively based on observations and descriptions of the outer morphology of such fossils (as well as compressions, which also occur at this locality), neglecting potentially permineralized tissues. Recently Uhl (2006a) expressed some concern about the usability of such morphological data from this material, and demonstrated that a large number of such pyritized remains from Frankenberg/Geismar are, in fact, covered by a thin, but extremely robust layer of pyritized sediments. This layer obscures at least some morphological details in many specimens investigated by previous authors (e.g., Göppert, 1850). However, in some cases cuticles, still attached to pyritized specimens, can be used to verify the taxonomic affiliation of pyritized material (Uhl, 2006a).

So far different techniques have been used to extract anatomical information from such pyritized specimens from Frankenberg/Geismar:

1. The most widely used technique is thin sectioning of specimens. In a strict sense it is not possible to investigate pyritized areas with this technique, as pyrite is first deposited in cell lumina (e.g., Grimes et al., 2001, 2002; Uhl, 2006a) and thus only a few anatomical data may be visible in pyritized areas in transmitted light. However, pyrite mechanically stabilizes these plant remains, and very often anatomically preserved areas without pyrite infillings can be found between pryitized areas (Fig. 5C) (Lemoigne and Schaarschmidt, 1968; Uhl, 2004).

2. Areas with pyrite within cell lumina of cell walls in organic preservation and occasionally also completely pyritized areas of specimens can be investigated by means of polished sections (Figs. 6-7; Uhl, 2004). In the case of mere infillings there is mostly a good contrast between organic cell walls and the pyrite (Fig. 6), enabling the observation of anatomical features. Completely pyritized areas may also provide certain information on selected anatomical features like cell size, form and patterns and the distribution of different tissues (Fig. 7F), but in most cases the pyrite obscures the anatomical information. This depends probably on the occurrence of only a single or more than one phase of pyritiziation, leading to pyrite phases with different crystal structure and thus different optical properties (e.g., Grimes et al., 2001, 2002; Uhl, 2006a). Examples are shown in Figure 6B-C where granular pyrite occurs in the position of former cell walls and fine-grained pyrite within the cell lumina.

3. Broken surfaces of completely pyritized areas can be investigated with scanning-electron microscopy (SEM) (Fig. 6). In some cases these broken surfaces provide information about the size, form and position of cells and tissues (Fig. 6), supplementing the information from other techniques. This is best done in specimens with different pyrite phases in cell lumina and cell walls (e.g., granular and fine grained pyrite; cf. Fig. 6B-C). Experience has shown that in such specimens it is also possible to enhance the result by careful etching with diluted HCl to remove calcite (which is ubiquitous at this locality). Small anatomical details of cell walls cannot be revealed by this approach at this locality, as the original cell walls are replaced by pyrite.

To get an idea about the validity of the taxonomic and paleoecological information provided by such pyritized remains, it is necessary to understand their formation. Based on light microscopy and SEM data, together with data from the literature on other localities with pyritized plants as well as on experimental pyritization of plants (e.g., Allison, 1988; Kenrick and Edwards, 1988; Canfield and Raiswell, 1991; Brown et al., 1994; Grimes et al., 2001, 2002; Tibbs et al., 2003; Uhl and Lepper, 2006), two slightly different scenarios have been proposed by Uhl (2006a) for the pyritization of woody and non-woody remains from Frankenberg/Geismar, respectively. In both cases pyritization occurred probably under anaerobic conditions and certainly involved microbial decay of the plant material (e.g., Grimes et al., 2001, 2002). In both cases pyrite formation started within cell lumina. In a second step, the cell walls must have been degraded and pyritized. In woody remains the tracheids may have acted as entranceways for the microbes (i.e., bacteria), whereas in non-woody remains mechanically damaged tissues and stomata may have acted as the most likely entranceways. This has probably led to a less uniform pyritization of smaller areas of tissues in such non-woody remains.

As an example to demonstrate that pyritized specimens from Frankenberg/Geismar can still add new data about the anatomy of fossil plants, a partly pyritized megasporophyll belonging to *Peltaspermum martinsii* has been chosen. Although such pyritized megasporophylls have been known at least since the end of the 18th century (e.g., Waldin, 1778), these remains have never been investigated to search for remnants of anatomically preserved internal tissues. The main reason for this was probably the unwillingness of most museum curators to sacrifice the megasporophylls, which were mostly collected during the latter part of the 18th and the first half of the 19th century, while a number of mines were still working in the Geismar area.

Most of the umbrella-shaped megasporophylls have been com-

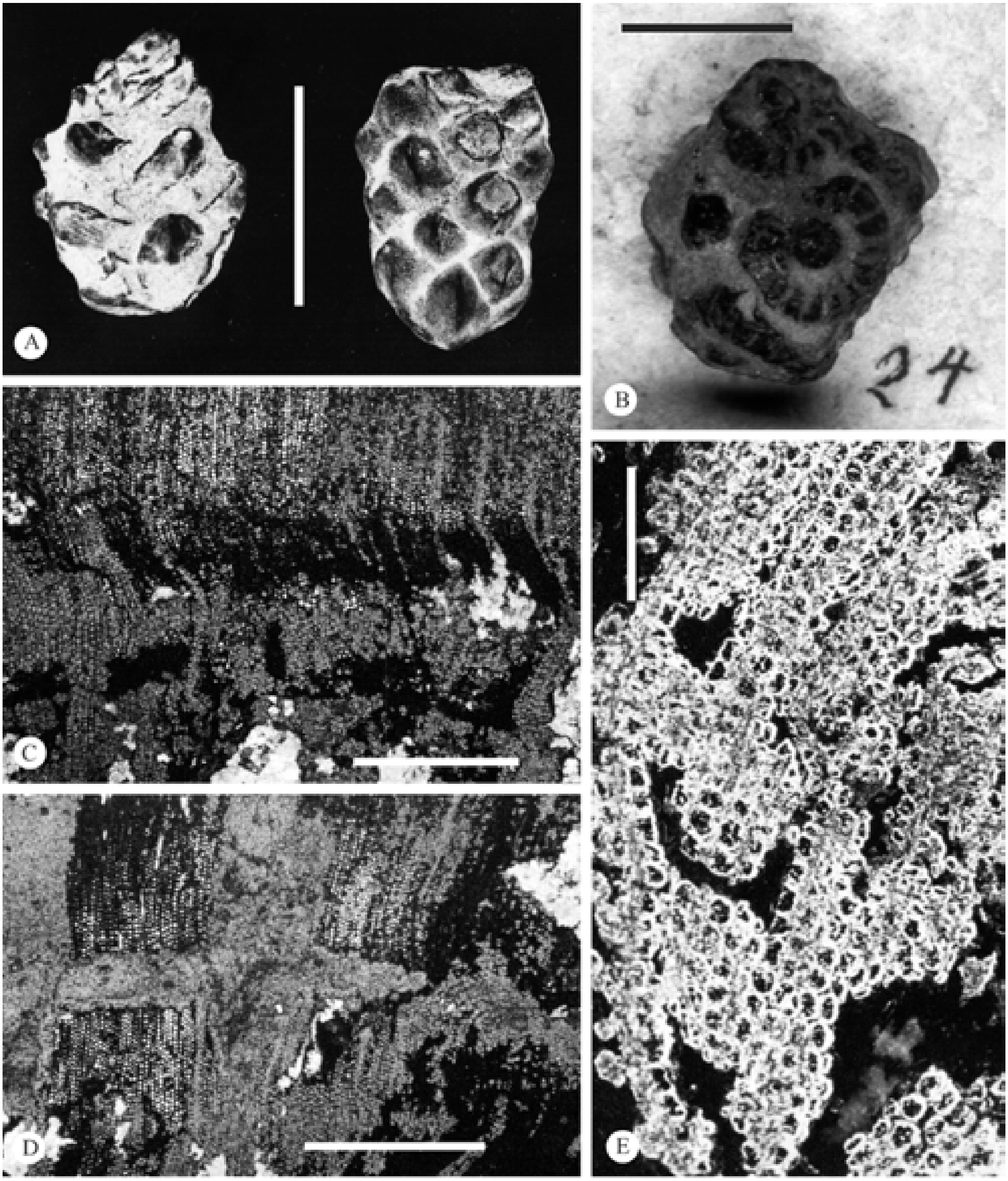

FIGURE 5. **A**, Pyritized remains of *Ullmannia bronnii* (coll. Museum Schleusingen, Germany; scale bar = 10 mm). **B**, Three-dimensionally preserved (pyritized) 'cluster' of megasporophylls of *Peltspermum martinsii* from Frankenberg/Geismar; originally figured by Göppert (1850; plate 20, fig. 24) as incompletely preserved seed cone of the conifer *Ullmannia bronnii* (scale bar = 1 cm; coll. Museum für Naturkunde Berlin, Germany). **C**, Thin section (cross-section) showing pyritized and non-pyritized parts of the wood of *Brachyoxylon* sp. (scale bar = 1 mm; coll. Paläobotanik Münster, Germany). **D**, Thin section (cross-section) showing pyrite filled crack in the wood of *Brachyoxylon* sp. (scale bar = 1 mm; coll. Paläobotanik Münster, Germany). **E**, Polished surface of completely pyritized wood (scale bar = 100 µm; coll. Schweitzer at the Universität Jena, #363; now at the Naturhistoriska Riksmuseet Stockholm Schweden) (**A**, **C**-**E** from Uhl, 2004).

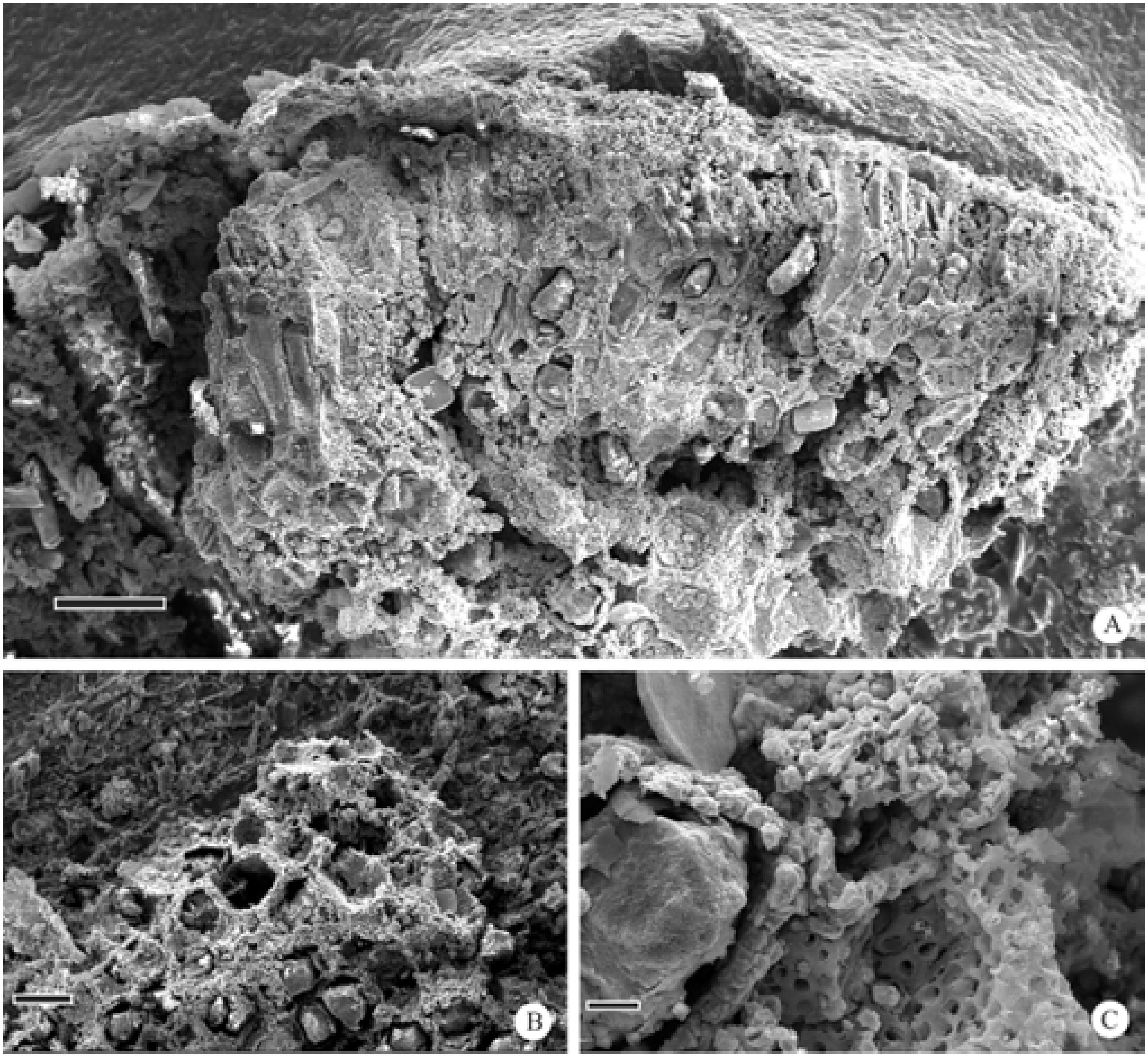

FIGURE 6. **A**, Fragment of a pyritized needle of *Pseudovoltzia liebeana* (Geinitz) Florin showing palisade parenchyma and spongy parenchyma (scale bar = 90 µm). **B**, Pyritized part of spongy parenchyma (scale bar = 60 µm); **C**, Detail from **B** with fine-grained pyrite in cell lumina and granular pyrite replacing former cell walls (scale bars = 10 µm) (A-C from Uhl, 2006a).

pressed, and no details of the internal anatomy are visible in these specimens. Only a single megasporophyll has been sectioned so far in which parts are permineralized, preserving at least some aspects of the internal anatomy of these plant organs (Fig. 7E-G). In this specimen the "stalk" has been partly pyritized (Fig. 7F), whereas the umbrella shows no signs of pyritization (Fig. 7E). In the "stalk" remains of pyritized parenchyma consisting of almost isodiametric cells, as well as remains of a central vascular strand, consisting of spirally thickened tracheids, are visible (Fig. 7G). The black regions in both sections (Fig. 7E-F) consist probably of compressed and coalified remains of the original tissues.

SEM studies of this material have been restricted thus far to secondary electron imaging techniques. Other SEM techniques that may be suitable for the study of pyritized plant remains like backscatter electron imaging or electron backscattered diffraction (cf. Poole and Lloyd, 2000) have so far not been used with material from Frankenberg/Geismar.

"MUMMIFIED" PLANT REMAINS

This peculiar type of preservation has only rarely been observed at Frankenberg/Geismar (Uhl and Kerp, 2002). It seems that in some leaves not only the cuticle, but also parts of the inner tissues are preserved (Fig. 7A-C). These remains exhibit no evidence of charring prior to fossilization, but tissues may be stabilized against mechanical stress by (early diagenetic?) permineralization with calcite (Fig. 7D). The good 3-dimensional anatomical preservation of this material indicates that it did not experience strong microbiological decay nor any significant physical alteration (e.g., temperature increase, compression) (Uhl and Kerp, 2002). It is not clear at the moment whether these remains represent truly mummified leaves, or just excellently preserved organic remains of calcitic permineralizations. Thus the term "mummified" leaf is used here to characterize the excellent anatomical preservation without stabilizing

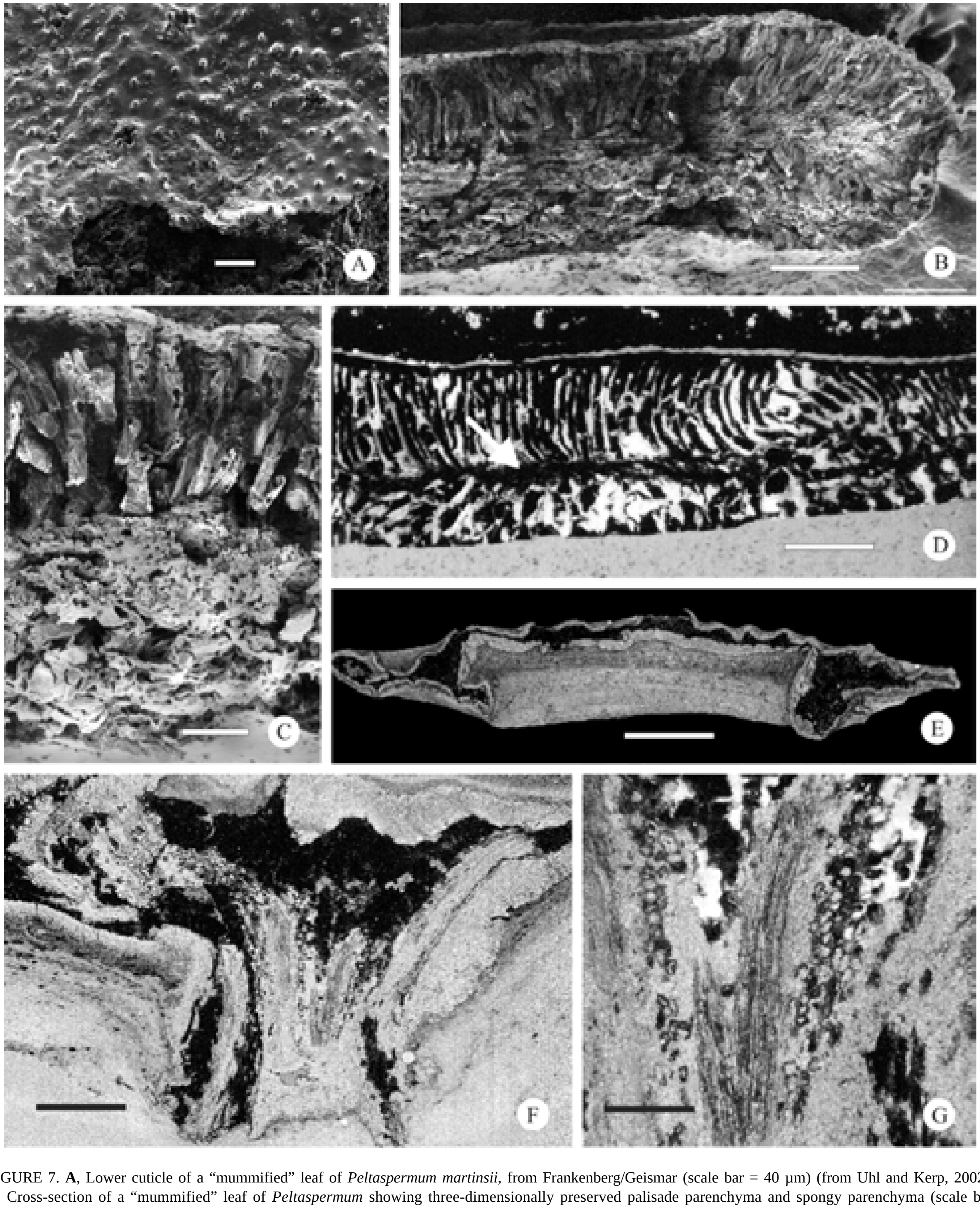

FIGURE 7. **A**, Lower cuticle of a "mummified" leaf of *Peltaspermum martinsii*, from Frankenberg/Geismar (scale bar = 40 µm) (from Uhl and Kerp, 2002). **B**, Cross-section of a "mummified" leaf of *Peltaspermum* showing three-dimensionally preserved palisade parenchyma and spongy parenchyma (scale bar = 100 µm). **C**, Detail of the same leaf showing details of three-dimensionally preserved parenchyma (scale bar = 40 µm, from Uhl and Kerp, 2002). **D**, With calcite permineralized 'mummified' leaf of *Peltaspermum*, showing palisade and spongy parenchyma as well as transfusion tissue in the center of the leaf (scale bar = 100 µm). **E**, Polished section through the "umbrella" of a megasporophyll of *Peltaspermum martinsii* without pyritized tissues, but surrounded by pyritized sediment layer (scale bar = 2 mm; from Uhl, 2006a). **F**, Polished section through the 'stalk' of a megasporophyll with completely pyritized tracheids and surrounding parenchymatous tissue (scale bar = 1 mm; from Uhl, 2006a). **G**, Detail of **F** showing tracheids surrounded by parenchymatous tissue (scale bar = 300 µm).

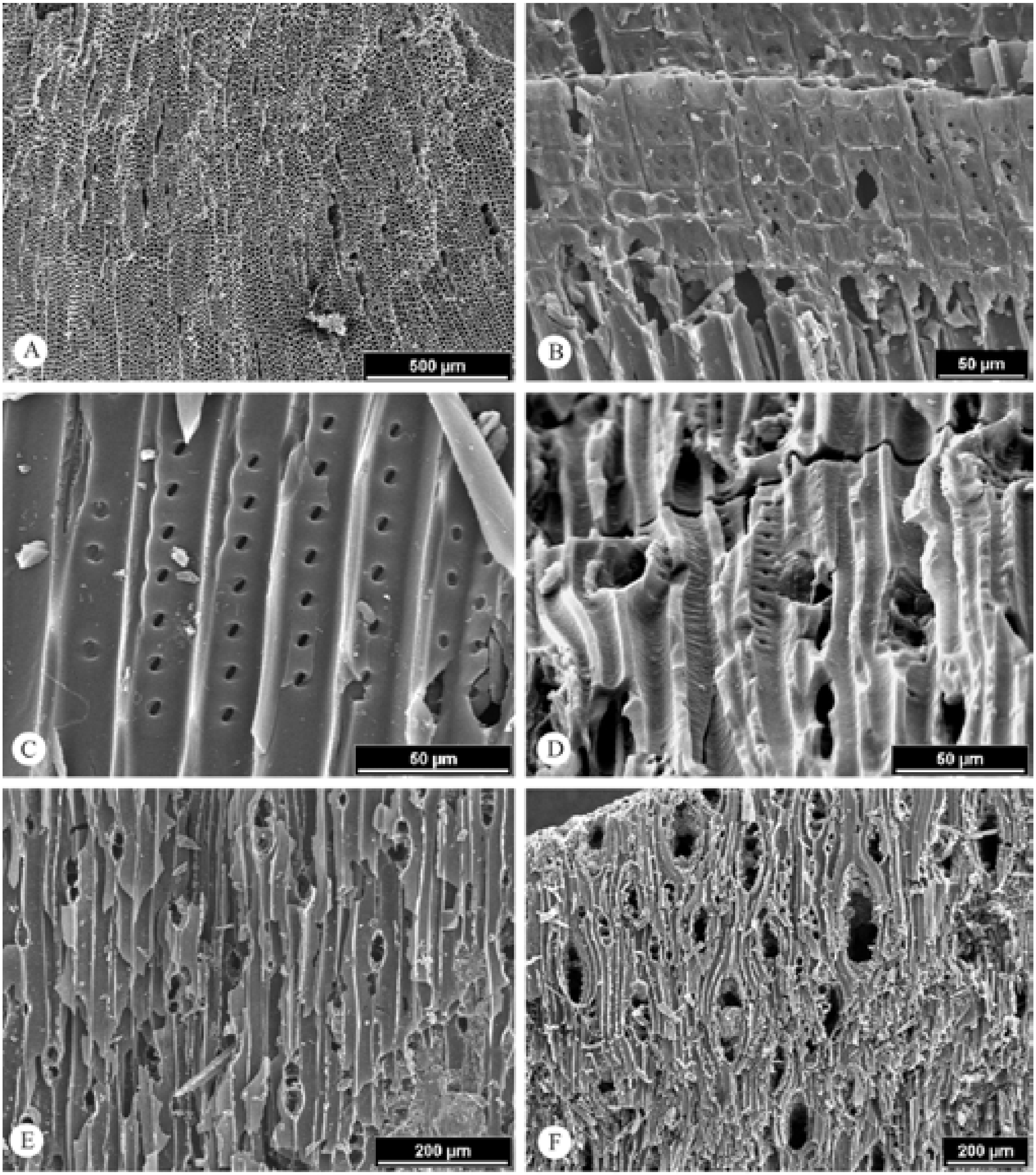

FIGURE 8. Charred wood from Frankenberg/Geismar (**A**-**F** from Uhl and Kerp, 2003). **A**, Cross section (wood type 3). **B**, Radial section showing araucarioid cross-field pitting (wood type 1). **C**, Radial section, showing pitting of tracheids (wood type 2). **D**, Tangential section showing pitting of tracheids and homogenized cell walls (wood type 3). **E**, Tangential section, showing abundant rays (wood type 4). **F**, Tangential section, showing two types of rays (wood type 2).

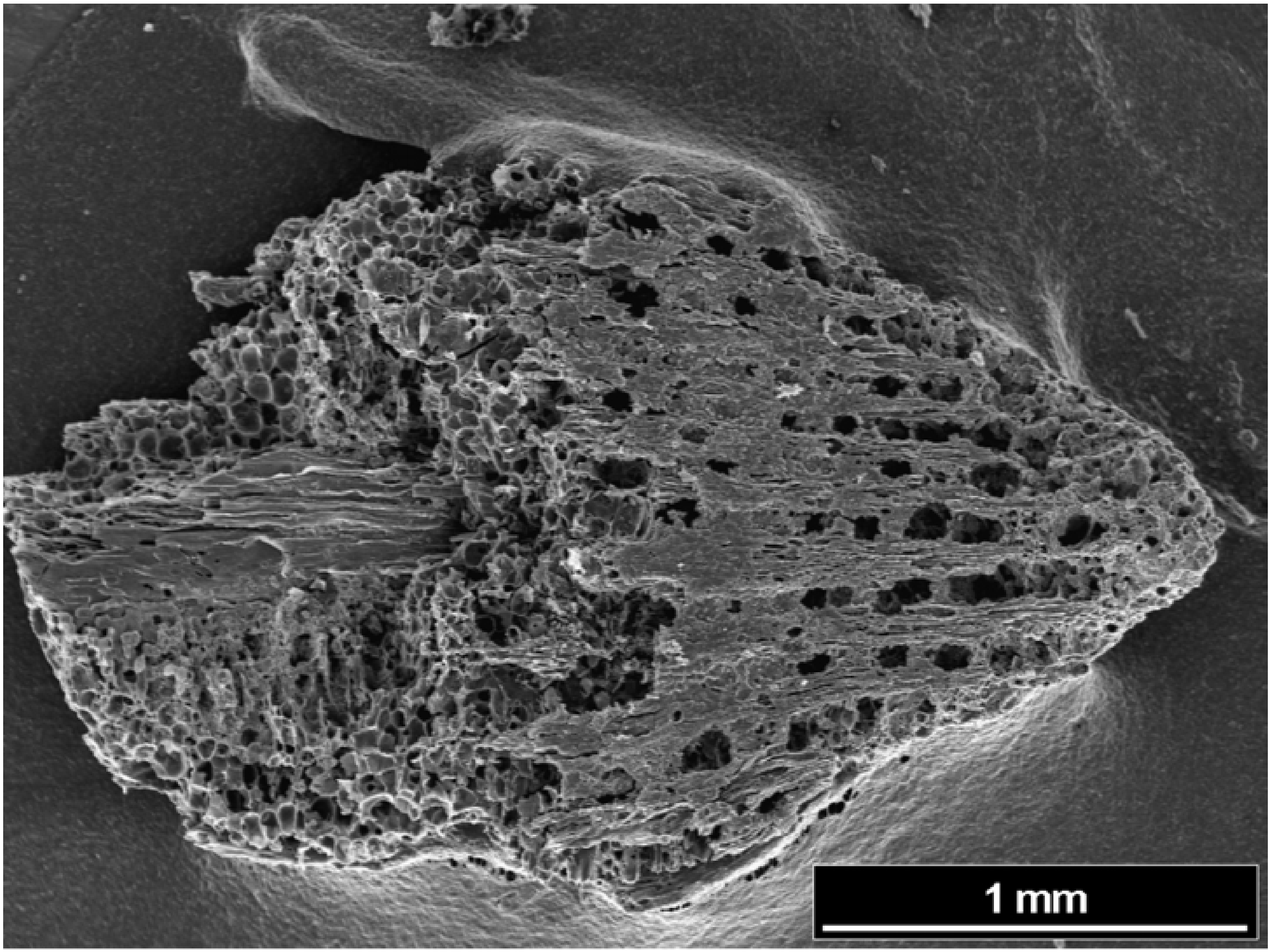

FIGURE 9. Tip of a charred needle of *Ullmannia* sp. (from Uhl and Kerp, 2003).

calcite (or other minerals) within cell lumina and not as a process-based description of how these remains were fossilized.

These remains can be investigated either by means of thin sections (Fig. 7D), or by isolating the remains by carefully dissolving sediments by hydrochloric acid or (preferably) acetic acid (Fig. 7A-C). This has accidentally been discovered on the etched surfaces of sediment samples during bulk-maceration to extract cuticles. Etching should be done very carefully, and experience has shown that it may be advisable not to isolate such remains completely from the sediment, as they are really fragile after removing the calcite. Etched remains can subsequently be investigated by SEM, like dried modern plant remains.

On Figure 7A-D two "mummified" leaves of *Peltaspermum martinsii* are shown. In cross-section epidermal cells are badly preserved, possibly collapsed. The mesophyll is differentiated into an adaxial palisade parenchyma that makes up to 50-60% of the remaining lamina thickness (Fig. 7B-D). Abaxial spongy parenchyma is less well preserved and its thickness before fossilization cannot be determined reliably. In thin sections of anatomically preserved non-pyritized leaves of *Peltaspermum* (representing calcitic permineralizations of "mummified" leaves) remains of a transfusion layer are visible between the palisade parenchyma and the spongy parenchyma (Fig. 7D).

As stated above these "mummified" leaves have only been discovered "by accident" during bulk-maceration of sediments (to extract cuticles) and during a test series of thin sections, mostly of pyritized plant remains. It seems likely that further careful etching of sediments and sectioning of material from this locality may result in additional discoveries of "mummified" plant remains.

CHARRED PLANT REMAINS

Charred plant remains (i.e., charcoal) exhibiting excellently preserved anatomical features occur frequently at this locality, and most specimens recovered so far represent charred remains of gymnospermous secondary xylem (Fig. 8; Uhl and Kerp, 2003). These remains, belonging to at least six different types of wood (Uhl and Kerp, 2003), can provide a wealth of information about paleoecology and taxonomy. However, besides wood, other plant organs can also be charred, and at Frankenberg/Geismar such remains have occasionally been found.

One charred needle (Fig. 9), which can be attributed to the widely distributed conifer *Ullmannia* Göppert, provides the first data on the internal anatomy of the needles of this taxon. On the surface of the charred needle the pattern of epidermal cells is visible (Fig. 10A), which corresponds to the general cellular patterns seen in *Ullmannia bronnii* and *Ullmannia frumentaria* (Uhl and Kerp, 2003). The internal tissues consist of a palisade parenchyma with elongated cells located below the epidermis (Fig. 10D), probably two types of spongy parenchyma, one type with relatively small, isodiametric cells (Fig. 10B) and one with relatively large, isodiametric (?) cells (Fig. 10C), transfusion tissue of elongated parenchymatic cells (Fig. 10E), as well as scalariform tracheids (Fig. 10F).

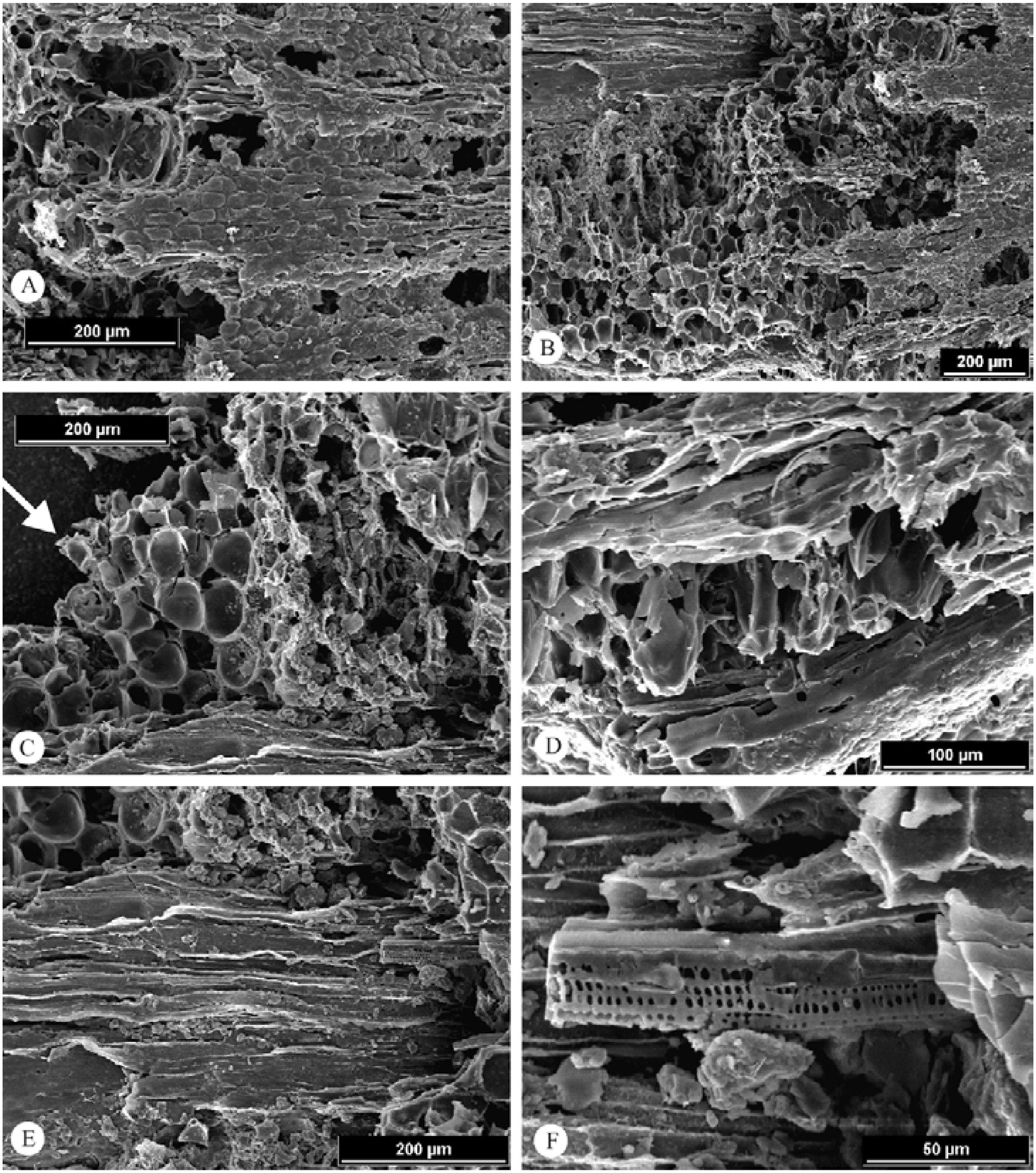

FIGURE 10. Anatomical details of charred needle of *Ullmannia bronnii* Göppert. **A**, Pattern of epidermal cells on surface of the needle. **B**, Spongy parenchyma with relatively small, isodiametric cells. **C**, Spongy (?) parenchyma with relatively large, isodiametric (?) cells. **D**, Palisade parenchyma with elongated cells. **E**, Transfusion tissue with elongated parenchymatous cells. **F**, Tracheid with scalariform pitting on cell walls (**A**, **C**, **E**, **F** from Uhl and Kerp, 2003).

Considering the fact that so far all discoveries of fossil charcoal at Frankenberg/Geismar have been the by-products of bulk-maceration of sediments to extract cuticles, it seems likely that a more intensive and focused search for such remains would yield a considerable amount of new data about the internal anatomy of a number of additional taxa and plant organs.

CONCLUSIONS AND OUTLOOK

A number of Euramerican localities yielding anatomically preserved plant remains is known from the Early and even the Middle Permian (e.g. Rößler, 2000; DiMichele et al., 2004; Looy, 2007; Uhl et al., 2004; Rößler and Noll, 2010), whereas such localities from the Late Permian are extremely rare. The Late Permian locality Frankenberg/ Geismar in NW-Hessen (Germany) is probably unique as it can provide new and additional anatomical information from a number of Late Permian plant taxa in different modes of preservation (i.e., pyritized, charred, “mummified”). Whereas most other known Late Permian localities from Euramerica that produce plant remains in anatomical preservation are inaccessible today, it is still possible to collect new material at this locality to supplement the available, but so far largely neglected, museum specimens. The (preliminary) results from leaves and megasporophylls of *Peltaspermum martinsii* provide the first data on the internal anatomy of this genus. Anatomical knowledge about the entire family Peltaspermaceae is scarce. So far anatomical data have only been published for the midvein of a leaf of the putative peltasperm *Auritifolia waggoneri* Chaney, Mamay, DiMichele and Kerp (Chaney et al., 2009).

Major tasks for the future are to acquire more material for anatomical studies, which may enable us to give a more detailed account of the anatomy of different organs belonging to a number of Late Permian taxa. This can probably be done by collecting new material from the numerous spoil tips near Frankenberg/Geismar, although most of these are currently protected as Natural Heritage, or by convincing museum curators that it may be necessary to sacrifice some of their precious specimens to enable further scientific progress.

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CARBONIFEROUS-PERMIAN TETRAPOD FOOTPRINT BIOCHRONOZONATION

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Tetrapod footprints are among the most common fossil remains in continental strata of post-Devonian age. They have been used for Paleozoic biostratigraphy since the late 19th century. However, the ichnotaxonomy of Carboniferous and Permian tetrapod footprints has long been choatic, mainly due to the naming of incomplete tracks or trackways and the failure to appreciate extramorphological variants. About two decades ago, German vertebrate ichnologist Hartmut Haubold firmly insisted upon the need to identify tetrapod ichnotaxa that are solely based on anatomically controlled characters of the imprint morphology and trackway pattern. This was a turning point, when Haubold himself and a few advocates of his proposals began to delineate general morphotypes of Paleozoic vertebrate footprints by careful revision of previously collected material as well as additional finds and could demonstrate that there was an essentially uniform Carboniferous-Permian tetrapod ichnofauna in equatorial to subequatorial regions of Pangea. Such broad geographic distribution is a precondition for the use of vertebrate tracks in biostratigraphy.

Currently, we can propose five tetrapod footprint biochrons that are based on the first appearance of the ichnogenera *Hylopus* (Early Carboniferous), *Notalacerta* (Late Carboniferous), *Dromopus* (latest Carboniferous), *Erpetopus* (late Early Permian), and *Paradoxichnium* (Late Permian). Tracks of these taxa are referred to anthracosaurs (*Hylopus*), “captorhinomorphs” (*Notalacerta*, *Erpetopus*), basal diapsids (*Dromopus*) and archosauromorphs (*Paradoxichnium*). There are several other ichnotaxa under study that may allow a much more refined palichnostratigraphic subdivision of the Late Paleozoic in the near future. Nevertheless, two more things should be mentioned here: (1) The Carboniferous-Permian boundary (CPB) is not reflected by changes in the tetrapod ichnofauna. Almost all "typical" early Early Permian (Asselian, Sakmarian) tetrapod ichnotaxa are also known from Late Carboniferous beds of Kasimovian and Gzhelian age. Another significant change apparently coincides with the Artinskian-Kungurian boundary. (2) The Late Paleozoic tetrapod footprint record is strongly taphonomically/collectively biased inasmuch as approximately 90% of all specimens comprise the Late Carboniferous and Early Permian record, whereas the Early Carboniferous, Middle and Late Permian tetrapod ichnofaunas are still relatively poorly known.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

ROBLEDOPUS MACDONALDI, A NEW KIND OF BASAL EUREPTILE FOOTPRINT FROM THE EARLY PERMIAN OF NEW MEXICO

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Abstract—A new kind of reptilian footprint, *Robledopus macdonaldi* n. igen. and n. isp., is introduced based on well-preserved tracks and trackways from late Early Permian (Artinskian) redbeds of the Robledo Mountains in south-central New Mexico. Imprint morphology and trackway pattern exhibit a unique set of characters among late Paleozoic tetrapod ichnotaxa. The predominance of features that characterize footprints of Pennsylvanian non-diapsid eureptiles supports interpretation of *Robledopus* as the track of "protorothyridids." Among the very few post-Pennsylvanian records of these small insectivorous reptiles, the New Mexican tracks might be the youngest one. Considering the abundance of insect traces associated with tetrapod footprints in the tidally influenced redbeds of the Robledo Mountains tracksite we suggest that "protorothyridids" preferentially survived into the Permian along tropical shorelines.

INTRODUCTION

During the last two decades, great effort has been made to consolidate the abundant record of Early Permian tetrapod footprints on the premise of a skeleton-based ichnotaxonomy (Lucas and Heckert, 1995; Haubold, 1996, 2000; Voigt, 2005; Lucas, 2007; Voigt et al., 2007). As a result, the several hundred parataxa that were available in the literature for vertebrate tracks of this period has been reduced to less than 15 valid ichnogenera representing footprints of various groups of anamniotes (*Amphisauropus* Haubold, 1970; *Batrachichnus* Woodworth, 1900; *Ichniotherium* Pohlig, 1892; *Limnopus* Marsh, 1894; *Matthewichnus* Haubold, 1970), pelycosaurian-grade synapsids (*Dimetropus* Romer and Price, 1940; *Tambachichnium* Müller, 1954), parareptiles (*Dromopus* Marsh, 1894), and eureptiles (*Dromopus* Marsh, 1894; *Erpetopus* Moodie, 1929; *Hyloidichnus* Gilmore, 1927; *Notalacerta* Butts, 1891; *Varanopus* Moodie, 1929). Based on previously and recently collected material from North America (Lucas and Heckert, 1995; Lucas et al., 2001; Haubold and Lucas, 2003; Van Allen et al., 2005), Europe (Voigt, 2005, 2007, 2012; Gand and Durand, 2006), and Northwest Africa (Hmich et al., 2006; Voigt et al., 2011a, b), a picture emerges of an essentially uniform Early Permian tetrapod ichnofauna in low-latitude areas of the Euramerican part of Pangea (Lucas and Hunt, 2006). This idea, however, is challenged by a new kind of amniote footprint described here that is only known from a single Early Permian locality in the American Southwest.

The tetrapod tracks in question, named *Robledopus macdonaldi* n. igen. and n. isp., occur in reddish-brown to grayish-green, muddy siltstone in the upper part of the Robledo Mountains Formation of the Hueco Group, in the Robledo Mountains, south-central New Mexico (Fig. 1). The Robledo Mountains Formation is an approximately 120 m thick succession of mixed carbonate-siliciclastic rocks representing deposition along a late Early Permian (late Wolfcampian, Artinskian) tropical coast (Lucas et al., 1995, 1998; Voigt et al., 2013). As an outstanding source of Paleozoic invertebrate and vertebrate traces the Robledo Mountains have been recognized as an ichnofossil Lagerstätte of global interest (e.g., Lucas et al., 1995, 1998; Minter and Braddy, 2009) now protected by the U.S. Government as the Prehistoric Trackways National Monument (PTNM; Lucas et al., 2010). Considering the abundance of trace fossils preserved in and collected from the Permian redbeds of the PTNM, one is tempted to ascribe the occurrence of unique finds such as *Robledopus macdonaldi* to the vast number of encountered specimens. Our analysis, however, suggests that the recovery of this ichnotaxon in the Robledo Mountains is instead due to evolutionary ecological constraints of the supposed trackmakers rather than an effect of large sample size. The purpose of this paper thus is to introduce an unusual new kind of tetrapod footprint and to demonstrate the significance of paleoichnology for the reconstruction of vertebrate evolution by providing further evidence of the Permian presence of a group of rare and predominantly Pennsylvanian amniotes.

Ichnological abbreviations: A, distance between manus and pes; B, width of pace; C, apparent body length; L, left manus-pes couple; m, manus imprint; mb, width of manus imprint; ml, length of manus imprint; mI to mV, length of digit I to V of the manus imprint; P, length of pace; p, pes imprint; pb, width of pes imprint; pl, length of pes imprint; pI to pV, length of digit I to V of the pes imprint; R, right manus-pes couple; S, length of stride; a, pace angulation; ß, deviation of manus or pes from midline, plus ß outward rotation, minus ß inward rotation; [illegible], interdigital angle I–V; I–II–III–IV–V, first to fifth digit, numbered from medial to lateral side of imprint.

Institutional abbreviations: NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEOICHNOLOGY

Ichnogenus *Robledopus* new ichnogenus

Type ichnospecies: *Robledopus macdonaldi* new ichnospecies.

Other ichnospecies: Only known from the type ichnospecies.

Diagnosis: Trackway of a quadrupedal tetrapod with pentadactyl, semiplantigrade footprints; relative length of digit impressions I<II<III~V<IV (pes) and I<II~V<III~IV (manus), all digit impressions have distinct claw marks. Trackways consist of alternating sets of manus and pes impressions with outwardly rotated pes and inward- or forward-directed manus; continuous tail/body traces common. Most similar to *Notalacerta*, *Varanopus*, *Hyloidichnus*, *Erpetopus* and *Amphisauropus*. Differs from *Notalacerta* in the outward-directed pes imprint with relatively short digit IV (non-lacertoid track). Differs from *Varanopus* by manual digit impression III long relative to IV, the outward-directed pes imprint and the presence of a body/tail trace. Differs from *Hyloidichnus* by the relatively much longer pedal digit impression V, significantly diverging pes and manus imprints and the presence of a body/tail trace. Differs from *Erpetopus* in the relatively short manus and

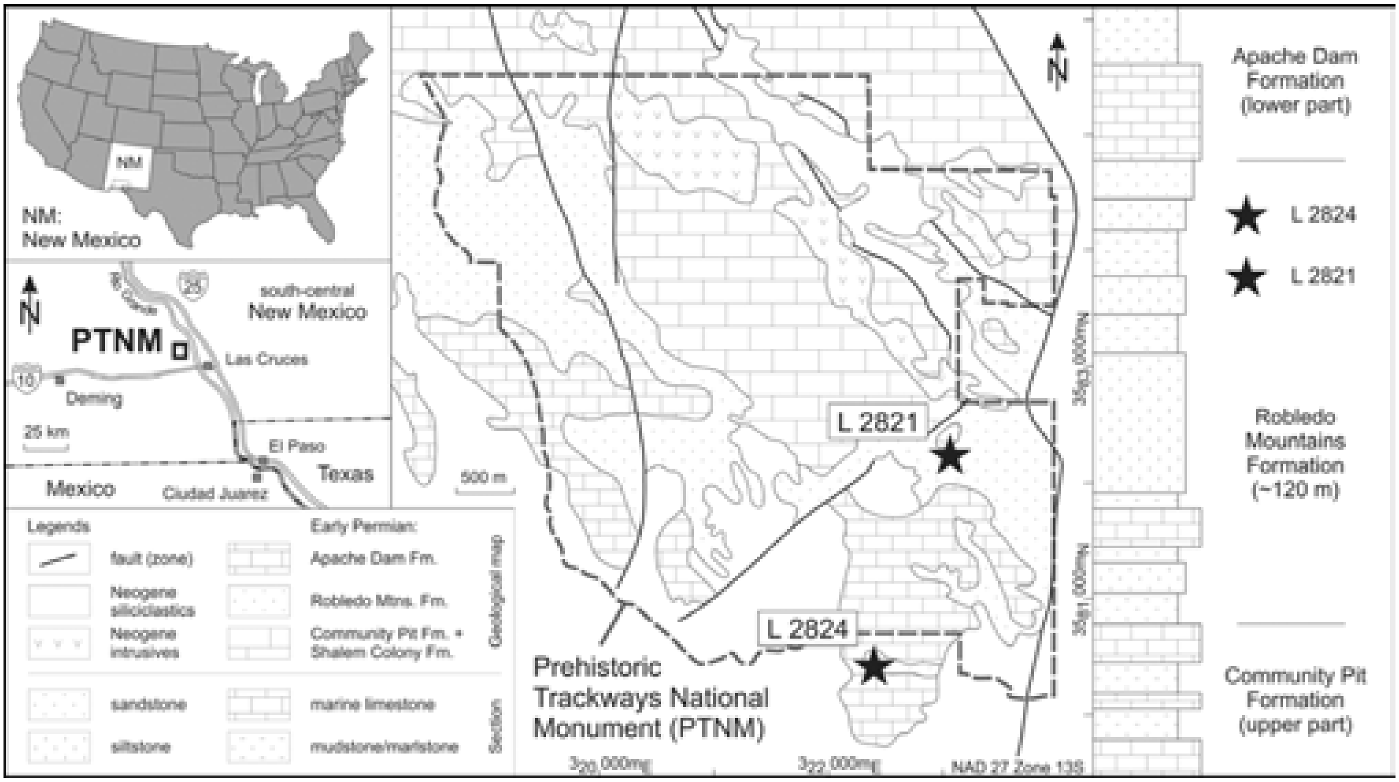

FIGURE 1. Geology of the Prehistoric Trackways National Monument, Robledo Mountains, south-central New Mexico (after Lucas et al., 1995, 1998; Voigt et al., 2013). Localities of *Robledopus macdonaldi* n. igen. and n. isp. are indicated by an asterisk.

pes digit impression IV, relatively long pedal digit impression V, lack of partial overstepping of manus imprint by the pes and presence of a body/tail trace. Differs from *Amphisauropus* in having relatively longer and thinner digit imprints with claw marks at the tips.

Etymology: After the type locality in the Robledo Mountains, Doña Ana County, New Mexico, U.S.A.

Occurrence: Early Permian Robledo Mountains Formation, Robledo Mountains, Doña Ana County, New Mexico.

Ichnospecies *Robledopus macdonaldi* new ichnospecies
Figures 2, 3; Appendix 1

cf. *Gilmoreichnus hermitanus* HAUBOLD, HUNT, LUCAS AND LOCKLEY, 1995, p. 149, fig. 21A.

Gilmoreichnus sp. HAUBOLD, HUNT, LUCAS AND LOCKLEY, 1995, p. 149, fig. 22A, B.

Erpetopus cf. *E. willistoni* HUNT, LUCAS, HAUBOLD AND LOCKLEY, 1995, p. 172, fig. 3A.

Hyloidichnus bifurcatus or *Gilmoreichnus hermitanus* MINTER AND BRADDY, 2009, p. 12, fig. 6A.

Diagnosis: As for the ichnogenus.

Description: Trackway of a small quadrupedal tetrapod with pentadactyl manus and pes imprints that range from 9 to 25 mm in length; manus and pes as long as wide or slightly wider than long; pes about one fourth longer than the manus; digit impressions straight, and slightly tapering distally to terminate in hook-like claw imprints. Manus imprints: Digits increase in length from I to III, IV about as long as III, and V as long as II; without heel impression, proximal margin of sole indistinctly concave; sole approximately one third of imprint's total length; imprint evenly and deeply impressed mediolaterally. Pes imprints: Mediolaterally decrease in relief, digits IV and V missing or as tip marks only; digits increase in length from I to IV, V about as long as III; all tips except V commonly with drag marks; no heel impression, proximal margin of sole indistinctly concave or straight, sole less than one third as long as the entire imprint. Trackways exhibit alternating sets of manus and pes imprints; pes outwardly rotated (ß = 18–53°); manus inwardly- or forward-directed (ß = –25–7°). Width of pedal pace slightly exceeds that of the manus; apparent trunk length ranges from 49 to 111 mm. Continuous, straight to slightly sinuous tail/body traces are common; some trackways (NMMNH P–23120, P–23322) exhibit double-lined traces either well separated from each other (Figs. 2A, 2B, 2G) or superimposed (Fig. 3B).

Etymology: After the discoverer of the type material, Jerry P. MacDonald, Las Cruces, New Mexico, U.S.A., to honor his many contributions to ichnology.

Types: Holotype, NMMNH P–23120 (including specimens formerly numbered NMMNH P–23424, –23425, and –23679; Fig. 2), two trackways with 38 tracks in total, preserved as part and partial counterpart from NMMNH locality 2824 (map coordinates of all NMMNH localities are on file at the NMMNH) from the Early Permian (late Wolfcampian) Robledo Mountains Formation of the Robledo Mountains, Dona Aña County, New Mexico.

Other referred material: NMMNH P–23072 (Fig. 3A), 32 imprints of five mainly faint trackways preserved as concave epirelief; NMMNH P–23322 (Fig. 3B), a single trackway consisting of 15 distinct imprints and two sets of faint manus and pes impressions of another trackway both preserved as part and counterpart.

Occurrences: NMMNH P–23072, –23322 from NMMNH locality 2821 and NMMNH P–23120 from NMMNH locality 2824, all from the Early Permian (late Wolfcampian) Robledo Mountains Formation of the Robledo Mountains, Dona Aña County, New Mexico.

Discussion: Haubold et al. (1995) noted that the digit proportions and the continuous tail trace of *Robledopus macdonaldi* n. igen. and n. isp. are unusual for Early Permian tetrapod footprints, but assigned the tracks to existing ichnotaxa, i.e., *Gilmoreichnus* sp. (NMMNH P–23072, –23222) and cf. *Gilmoreichnus hermitanus* (Gilmore, 1927) (NMMNH P–23120). Similarly, Hunt et al. (1995) and Minter and Braddy (2009) assigned tracks of *R. macdonaldi* to cf. *Erpetopus willistoni*

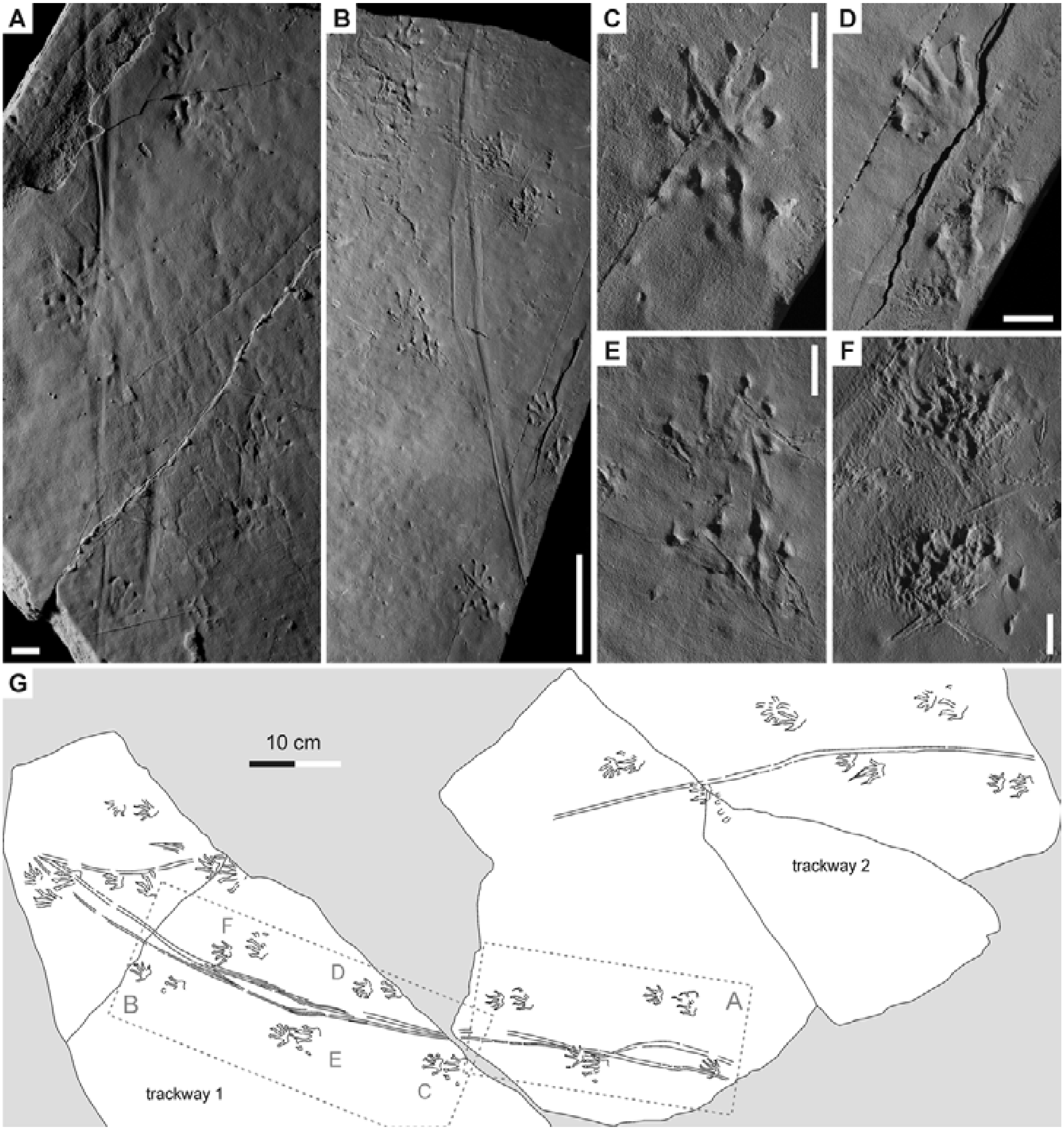

FIGURE 2. Holotype of *Robledopus macdonaldi* n. igen. and n. isp., NMMNH P–23120, preserved as convex hyporelief. **A-F**, Best preserved tracks; **G**, General view indicating position of close-up photos. Scale bars equal 1 cm in **A**, **C**-**F**, and 5 cm in **B**.

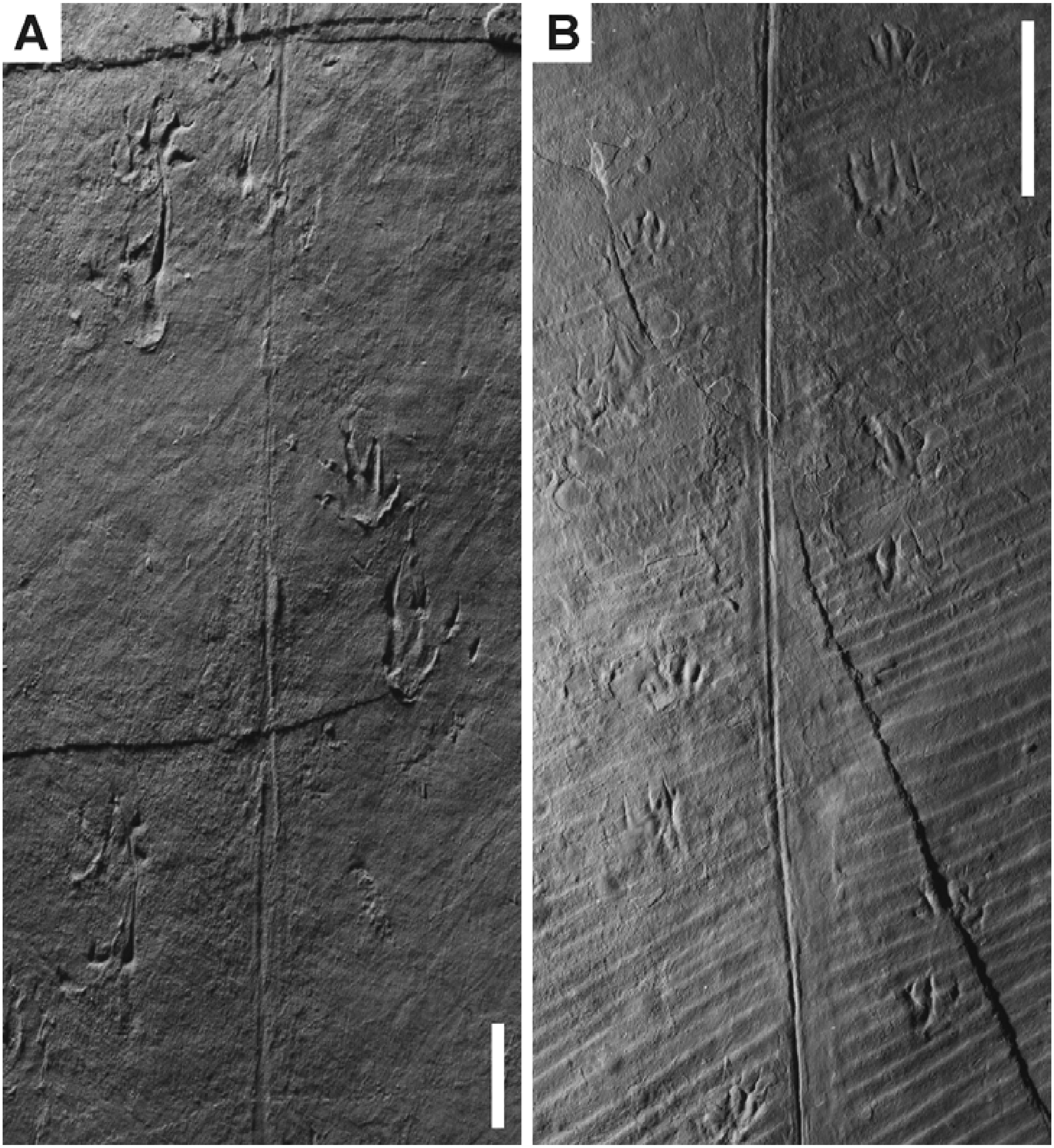

FIGURE 3. *Robledopus macdonaldi* n. igen. and n. isp., best preserved trackways of additional material. **A**, NMMNH P–23072; **B**, NMMNH P–23322, note superimposed, wide and narrow tail/body traces. Scale bar equals 1 cm in **A**, and 5 cm in **B**.

Moodie, 1929, *Hyloidichnus bifurcatus* Gilmore, 1927 and *Gilmoreichnus hermitanus*.

Gilmoreichnus was introduced by Haubold (1971) as an ichnogenus to unify material of *Hylopus hermitanus* Gilmore, 1927 from the Early Permian Hermit Shale, Grand Canyon, Arizona, and material of *Ichnium brachydactylum* Pabst, 1900, from the Early Permian Goldlauter Formation, central Germany. With an increased knowledge of the taphoseries of Pennsylvanian-Permian tetrapod footprints, *Gilmoreichnus* (*Hylopus*) *hermitanus* and *Gilmoreichnus* (*Ichnium*) *brachydactylus* were recognized as preservational extremes of *Varanopus* Moodie, 1929 and *Amphisauropus* Haubold, 1970, respectively, which reduced *Gilmoreichnus* to a junior subjective synonym of these ichnogenera (Voigt, 2005). Our analysis suggests that *R. macdonaldi* is largely a mosaic of characters of five well-established Late Paleozoic tetrapod ichnogenera. While its imprint morphology is most similar to tracks of *Notalacerta* Butts, 1891, *Hyloidichnus* Gilmore, 1927, *Varanopus* Moodie, 1929, and *Erpetopus* Moodie, 1929, the trackway pattern resembles that of *Amphisauropus* Haubold, 1970 (Fig. 4).

Robledopus macdonaldi and *Notalacerta missouriensis* Butts, 1891 (the type ichnospecies of *Notalacerta*) share a superficially similar imprint morphology and a continuous tail/body trace, but differ in the orientation of the pes imprint (outward-directed in *R. macdonaldi*; forward-directed in *N. missouriensis*) and the relative length of pes digit IV (short in *R. macdonaldi*; long in *N. missouriensis*). Some trackways of *Notalacerta* from the Early Pennsylvanian of the United States (Chesnut et al., 1994; Haubold et al., 2005) have pes imprints that point outward as in *R. macdonaldi*, but they all differ from the latter by the more lacertoid morphology of the tracks (relatively elongate digit IV) and the forward-directed manus imprint. *R. macdonaldi* and *Varanopus curvidactylus* Moodie, 1929 are similar in most characters of the imprint morphology, including the length-width ratio of the imprints, the digit proportions, and the asymmetric relief of the pes imprint. However, *Varanopus* is missing a tail/body trace, the manual digit impression III is distinctly shorter than that of digit IV, and the pes imprint is never directed outward.

Robledopus macdonaldi and *Hyloidichnus bifurcatus* are generally similar with regard to the length-width ratio of the manus and pes imprints, with isolated manus imprints of the two ichnotaxa being almost indistinguishable. But, *Hyloidichnus* exhibits a much shorter pedal digit V impression, pes and manus imprints that are parallel to each other, and there is no tail trace. *R. macdonaldi* and *Erpetopus willistoni* Moodie, 1929 are similar with respect to the length-width ratio of the manus and pes imprint and common drag marks of the pedal digits I–III. However, the digit IV of the manus and the pes imprints in *Erpetopus* are relatively longer, pedal digit V is much shorter, there is no continuous tail trace, and the trackway pattern often exhibits partial overstepping of the manus imprint by the pes. *R. macdonaldi* and *Amphisauropus kablikae* (Geinitz and Deichmüller, 1882) share trackways with distinctly outward-directed pes imprints and inwardly rotated manus imprints, but differ in many aspects of the imprint morphology, e.g., the relatively short and thick digits that lack claw marks in *Amphisauropus* (Voigt, 2005).

The tracks of *Robledopus* have a unique set of characters for Late Paleozoic tetrapod footprints, particularly the relatively long digit III of the manus imprint (mIII~mIV), the relatively long digit V of the pes imprint (pIII~pV), the outwardly-directed pes and inwardly-rotated manus imprints, and the presence of continuous tail/body traces. As anatomically- and functionally-controlled features of the imprint morphology and trackway pattern, these characters justify the creation of a new ichnotaxon, at least at the ichnospecies level (Haubold, 1996; Billon-Bruyat and Mazin, 2003). Mandatory criteria for the definition of ichnogenera do not exist in skeleton-based ichnotaxonomy, and we discount as implausible and not feasible the recommendation of Haubold (1996, 2000) that ichnogenera should correspond to the family level of potential trackmaker biotaxa. The tracks of *Robledopus macdonaldi* share about as many characters with *Notalacerta*, *Varanopus*, *Hyloidichnus*, *Erpetopus*, and *Amphisauropus* as separate each of these ichnotaxa from each other. A new ichnogenus is introduced here because graded similarity does not provide a conclusive result on this taxonomic issue.

Using the terminology of Platt and Hasiotis (2008), tail/body traces of *Robledopus macdonaldi* (Figs. 2-3) can be classified as protracted, simple, low sinuous, low percent interruption metric traces. This pattern indicates an animal whose tail has been in continuous contact with the ground surface, and experienced no vertical and only a small amount of lateral movement. We interpret the double-lined trace of some trackways (Figs. 2A, 2B, 3B) as evidence that parts of the belly and tail touched the ground simultaneously during locomotion.

STATISTICAL ANALYSIS

Methods: In addition to the descriptive diagnosis of the new ichnotaxon we carried out principal component analyses (PCA) and linear discriminant analyses on the basis of 9 specimens and a total of 39 step cycles (57 imprint pairs) in order to demonstrate that *Robledopus macdonaldi* n. igen. and n. isp. is distinct from other described ichnotaxa assigned to basal eureptilian trackmakers (*Notalacerta missouriensis*, *Varanopus microdactylus*, *Hyloidichnus bifurcatus*, *Erpetopus willistoni*) in its imprint and trackway measures (Appendices 4 and 5).

Variations in toe proportion are illustrated here by means of PCA, and we depict biplots of the most important principal components (PC 1 to 3, see Fig. 5A-C). In the first PCA run we used the unchanged lengths of manual and pedal digits I to V as input variables. To eliminate body size effects, which may hide proportion differences, we have carried out a second PCA run with normalized toe lengths. Thereby the average length of the pedal digits II to IV has been taken as a basis for normalization. We regard such an average as a reasonable proxy for trackmaker body size. Unlike the total imprint length the toe lengths are not much influenced by substrate properties. Our average measure includes only the middle toes because they are more often and better preserved than lateral toes. We consider pedal imprints rather than manual imprints because the latter show more often the tendency to preserve movements on the ground that obscure the actual hand size of its producer.

In the next step, linear discriminant analyses on the basis of the same dataset of uncorrected and normalized toe lengths have been carried out. Given the small sample size only two classes are considered ("*Robledopus*" and "non-*Robledopus*" = all other basal eureptilian tracks), and the number of variables is reduced to seven (see Appendix 5). Two of the resulting measures, Mahalanobis distance and percentage of misclassification in a cross-validation test, are used here as criteria for the quality of separation between the two classes.

Following our observation that *Robledopus* is deviant in its imprint orientations we have used the rotation angles of manual and pedal imprints (ßm, ßp) towards the trackway midline as input variables for a further linear discriminant analysis whose results illustrate how well *Robledopus* is separated from other eureptilian trackmakers in these particular trackway measures (Fig. 5D).

Results: According to the first PCA run, PC 1 accounts for most of the variance (88.2%) and reflects differences between small and large tracks, whereas PC 2 (5.3% of variance) comprises proportion differences of manual digit V and pedal digit V (loadings in Appendix 6A). In biplot PC 1 versus PC 2 the cluster *Notolacerta-Robledopus-Varanopus* is well separated from *Hyloidichnus* and *Erpetopus* (Fig. 5A). PC 3 (3.5% of variance) covers proportion differences of manual digit I and pedal digit IV. These allow for a distinction between *Notalacerta*, *Robledopus*, and *Varanopus* (see Fig. 5B). The second PCA run with normalized toe length values yields a fair separation between *Robledopus* and other eureptilian tracks in the first two principal components (Fig. 5C), which account for 71.5% of the total variance and reflect differences in the relative size of pedal digital IV (PC 1) and differences in the size ratios of pedal digits II-IV as well as manual digits III-V (PC 2; loadings in Appendix 6B).

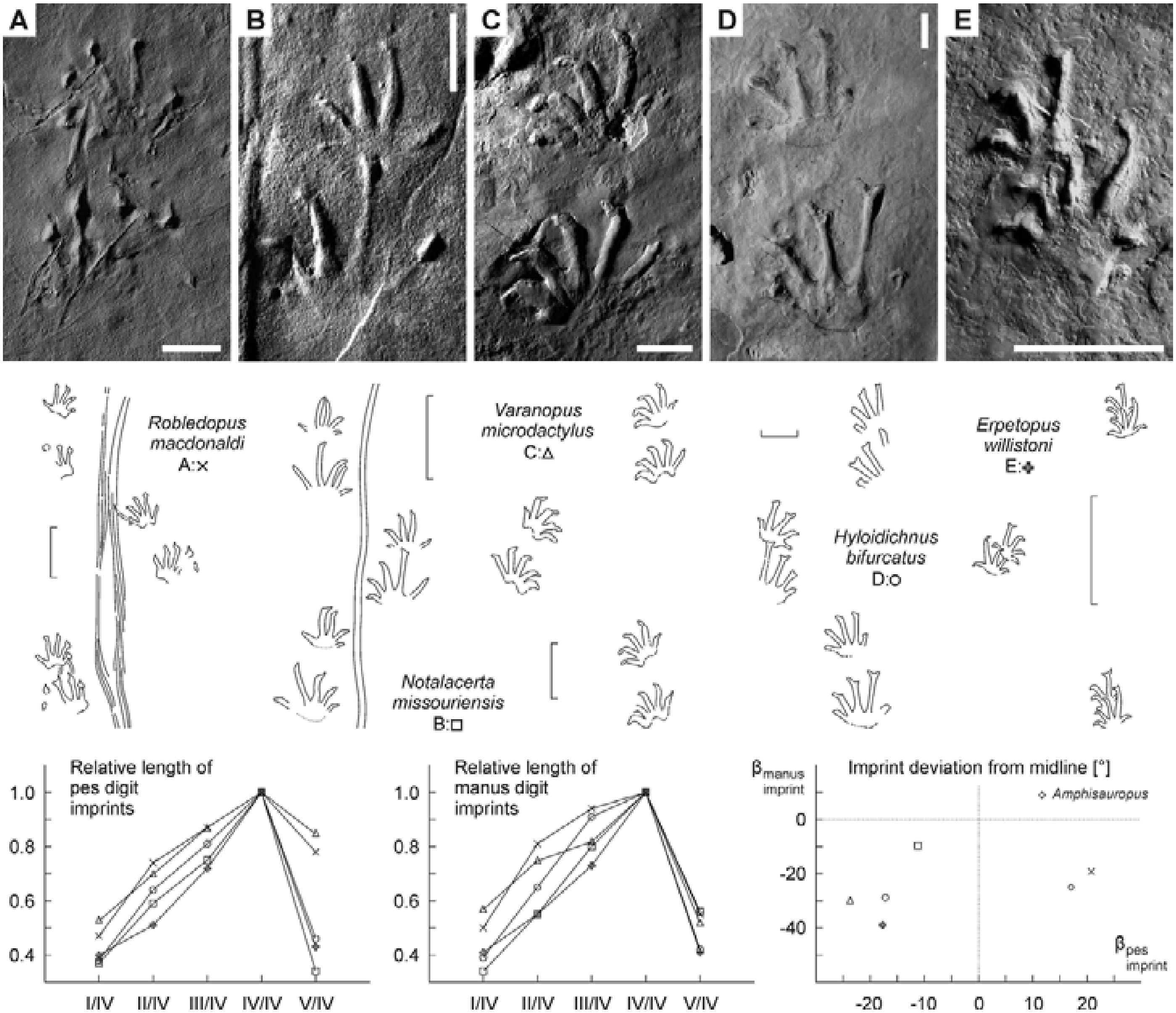

FIGURE 4. *Robledopus macdonaldi* n. igen. and n. isp. in comparison with similar Early Permian tetrapod footprints. **A**, NMMNH P–23120, *Robledopus macdonaldi* n. igen. and n. isp. **B**, NMMNH P–31746, *Notalacerta missouriensis* Butts, 1891. **C**, NMMNH P–32391, *Varanopus curvidactylus* Moodie, 1929. **D**, USNM 11518, *Hyloidichnus bifurcatus* Gilmore, 1927 (Photo Copyright Smithsonian Institution, all rights reserved). **E**, NMMNH P–32411, *Erpetopus willistoni* Moodie, 1929. See Appendices 2–3 for data specification; values of *Amphisauropus* (ßp = 17.1°, ßm = –25.0°) from Voigt, 2005 (appendix 24). Scale bar equals 1 cm in photographs, and 3 cm in drawings.

According to the linear discriminant analysis of toe lengths and normalized toe lengths, *Robledopus* is readily distinguished from the other sampled eureptilian tracks (no misclassification according to cross validation tests; Mahalanobis distances of 32.63 and 27.30, respectively). Furthermore, the discrimination of *Robledopus* and "non-*Robledopus*" is also possible on the basis of imprint orientations (no misclassification according to cross validation test, Mahalanobis distance of 12.97), even though the distributions of manual imprint orientation angles (ßm) of the two classes display a large overlap (Fig. 5D).

DISCUSSION

Potential trackmaker: Pentadactyl manus and pes imprints with distinct claw marks suggest an amniote trackmaker of *Robledopus macdonaldi*. Synapsida and Parareptilia can be excluded because their supposed Early Permian tracks, i.e., *Dimetropus* Romer and Price, 1940, *Tambachichnium* Müller, 1954, and (in part) *Dromopus* Marsh, 1894 (Haubold, 2000; Voigt, 2005), significantly differ from *Robledopus*. While *Dromopus* also seems to represent the principal imprint morphology of Pennsylvanian-Early Permian diapsids (Haubold, 1996, 2000; Haubold and Lucas, 2003; Voigt, 2005), all tracks most similar to *Robledopus* have been previously referred to non-diapsid eureptiles. This includes *Notalacerta* as the supposed track of "Protorothyrididae" (Chesnut et al., 1994; Calder et al., 2004; Haubold et al., 2005), *Varanopus* as that of basal Captorhinidae (Haubold and Lucas, 2003; Voigt, 2005; Voigt et al., 2009), *Hyloidichnus* as that of derived Captorhinidae (Voigt et al., 2009, 2010), and *Erpetopus* as the track of small captorhinids of uncertain affinity (Haubold and Lucas, 2003; Minter et al., 2007). The results of principal component and linear discriminant analyses demonstrate that toe proportions as well as the orientation of the pedal imprints towards the trackway midline are feasible quantitative criteria to distinguish *Robledopus macdonaldi* from the basal eureptilian tracks *Notalacerta missouriensis*, *Varanopus microdactylus*, *Hyloidichnus bifurcatus* and

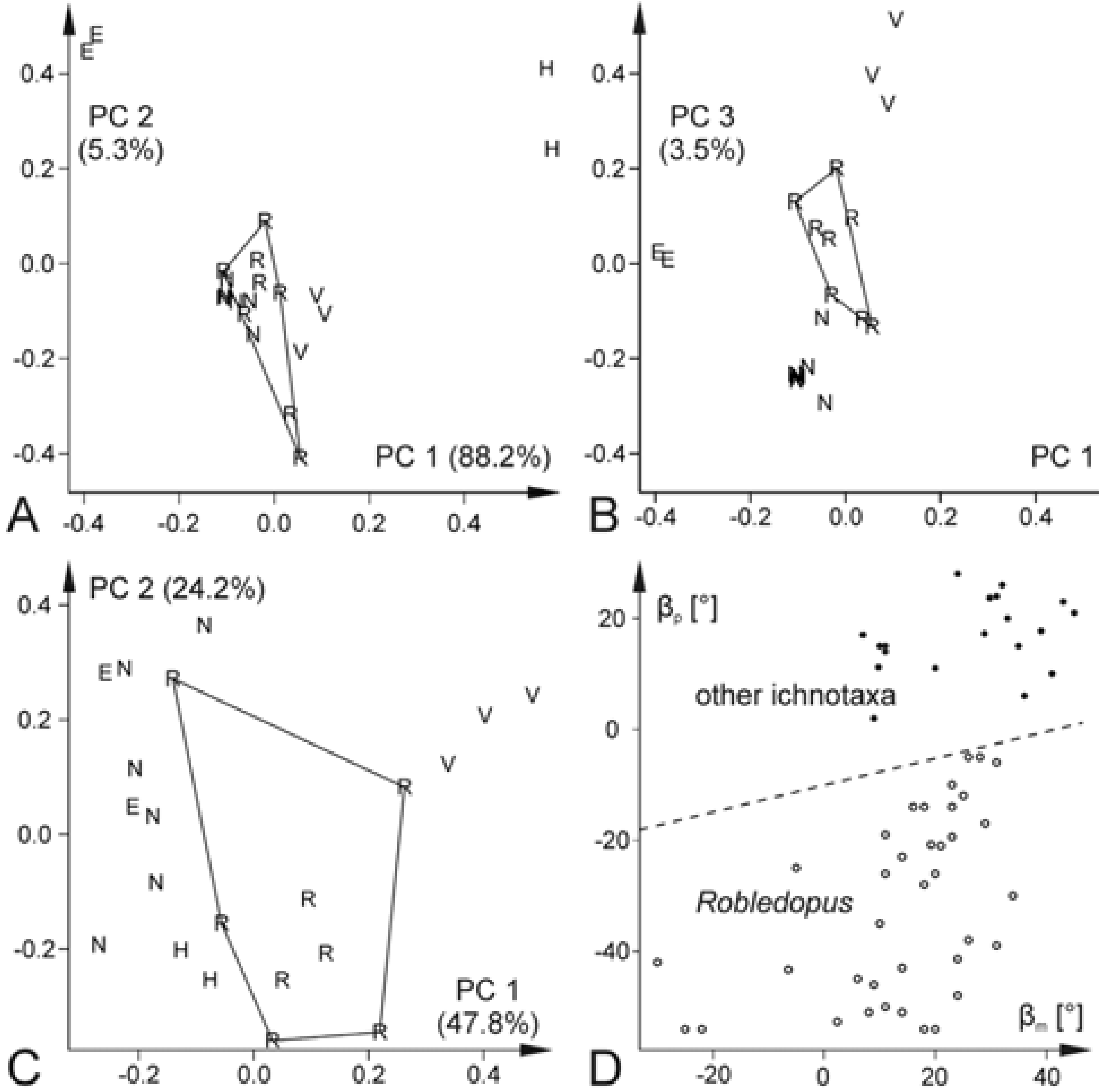

FIGURE 5. Results of principal component analysis (PCA) and linear discriminant analysis. **A**, Biplot of principal components (PC) 1 and 2 for a PCA including 10 toe lengths. **B**, Biplot of PC 1 and 3 for the same PCA. **C**, Biplot of PC 1 and 2 for a PCA including 10 normalized toe lengths. **D**, Plot of pedal imprint orientation (ßp) against manual imprint orientation (ßm) and discriminant function (hashed line) according to linear discriminant analysis. **Labels: E**, *Erpetopus willistoni*; **H**, *Hyloidichnus bifurcatus*; **N**, *Notalacerta missouriensis*; **R**, *Robledopus macdonaldi* n. igen. and n. isp.; **V**, *Varanopus microdactylus*. Polygons represent the convex hull for the *Robledopus* sample.

Erpetopus willistoni. *Robledopus* shares a number of characters with tracks of basal amniotes, such as the continuous tail/body trace, the outward-directed pes and inward-directed manus imprint, and the relatively long digit V of the pes imprint, whereas the reduced length of the digit IV imprint does not occur in the basal amniote ichnotaxa considered here and may be a derived feature. Based on this specific character mosaic in relationship to the most similar Paleozoic amniote tracks, we suggest that *Robledopus macdonaldi* was produced by a Permian representative of basal non-diapsid eureptiles ("Protorothyrididae").

Stratigraphic distribution: The biotaxon "Protorothyrididae," introduced by Price (1937), refers to small, lightly built Paleozoic amniotes (Carroll, 1982, 1988) that are now considered to be a paraphyletic group within Eureptilia (Müller and Reisz, 2006). The majority of "protorothyridid" skeletal remains come from Pennsylvanian strata in Canada, the United States, and the Czech Republic (Carroll and Baird, 1972). There are only three occurrences of Permian "protorothyridid" body fossils: (1) *Protorothyris* from the Archer City Formation of Texas (Price, 1937); (2) *Protorothyris* (=*Melanothyris*) from the Washington Formation of the Dunkard Group in West Virginia (Romer, 1952); and (3) an indeterminate "protorothyridid" from the Early Permian Richards

FIGURE 6. Hypothetical trackmaker of *Robledopus macdonaldi* n. igen. and n. isp. showing a basal eureptile hunting wingless insects on an Early Permian tidal flat.

Spur locality of Oklahoma (Reisz, 1980). Lucas (2006) considered *Protorothyris* an index taxon of the Coyotean land-vertebrate faunachron, which means it could range in age from Asselian to late Artinskian. Based on a U-Pb age of 289±0.68 Ma from a speleothem at the Richards Spur locality, Woodhead et al. (2010) suggested the site is Sakmarian in age, but Lucas (2006) advocated a biostratigraphic assignment to the Mitchellcreekian land-vertebrate faunachron, which is of Leonardian (Kungurian) age. "Protorothyridid" footprints, most likely represented by the ichnogenus *Notalacerta*, are mainly known from Pennsylvanian strata of North America (Butts, 1891; Chesnut et al., 1994; Monks, 2002; Lucas et al., 2004; Haubold et al., 2005; Monks and Kvale, 2006; Lucas, 2007; Getty et al., 2010). Calder et al. (2004) described a single slab with *Notalacerta* from supposed Early Permian (Asselian-Artinskian) redbeds of Nova Scotia, Canada.

The majority of "protorothyridid" body and trace fossils thus come from Pennsylvanian strata of North America interpreted as coastal plain or tidal flat deposits (Butts, 1891; Carroll and Baird, 1972; Chesnut et al., 1994; Monks, 2002; Monks and Kvale, 2006; Lucas et al., 2004; Haubold et al., 2005; Lucas, 2007). Remains from Permian strata are extremely rare and restricted to the early part of the period (Price, 1937; Romer, 1952; Reisz, 1980; Calder, 2004). If the trackmaker assignment is correct, the late Wolfcampian (late Artinskian) tracks of *Robledopus macdonaldi* n. igen. and n. isp. from the Robledo Mountains represent one of the youngest records of "protorothyridids," suggesting that this kind of amniote thrived on tropical marine shores at least to the late Early Permian. As insectivorous animals (Carroll, 1982), the survival of "protorothyridids" might have been favored by the abundant and diverse arthropod fauna of these environments (Minter and Braddy, 2009; Fig. 6). Considering the lack of knowledge about such ecosystems of Early Permian age, the PTNM of south-central New Mexico is developing into a unique taphonomic window on the early evolution of eureptiles.

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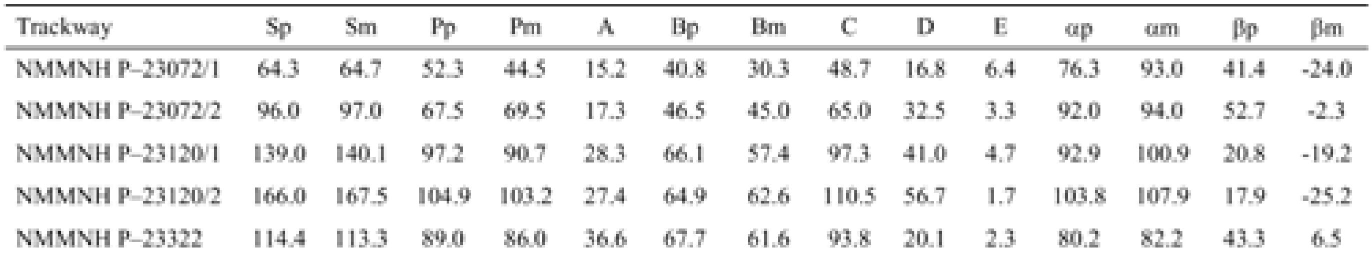
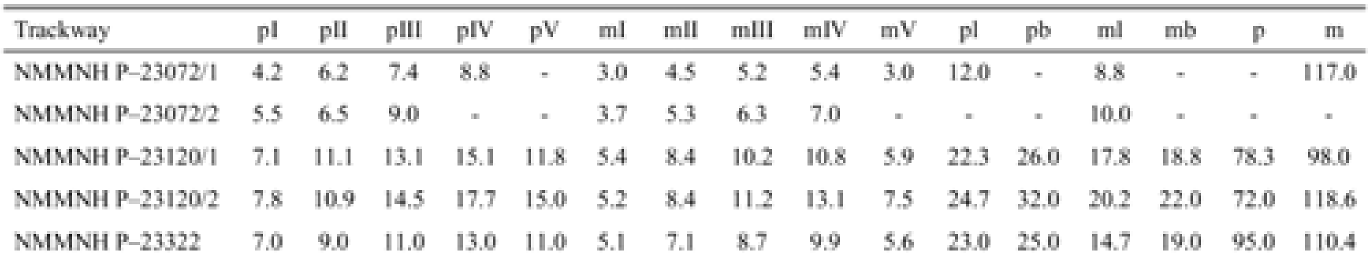
APPENDIX 1

Trackway and imprint parameters of *Robleodpus macdonaldi* n. igen. and n. isp. from the Early Permian Robledo Mountains Formation (in mm and degrees).



Trackway	Sp	Sm	Pp	Pm	A	Bp	Bm	C	D	E	αp	αm	βp	βm
NMMNH P–23072/1	64.3	64.7	52.3	44.5	15.2	40.8	30.3	48.7	16.8	6.4	76.3	93.0	41.4	-24.0
NMMNH P–23072/2	96.0	97.0	67.5	69.5	17.3	46.5	45.0	65.0	32.5	3.3	92.0	94.0	52.7	-2.3
NMMNH P–23120/1	139.0	140.1	97.2	90.7	28.3	66.1	57.4	97.3	41.0	4.7	92.9	100.9	20.8	-19.2
NMMNH P–23120/2	166.0	167.5	104.9	103.2	27.4	64.9	62.6	110.5	56.7	1.7	103.8	107.9	17.9	-25.2
NMMNH P–23322	114.4	113.3	89.0	86.0	36.6	67.7	61.6	93.8	20.1	2.3	80.2	82.2	43.3	6.5



Trackway	pI	pII	pIII	pIV	pV	mI	mII	mIII	mIV	mV	pl	pb	ml	mb	p	m
NMMNH P–23072/1	4.2	6.2	7.4	8.8	-	3.0	4.5	5.2	5.4	3.0	12.0	-	8.8	-	-	117.0
NMMNH P–23072/2	5.5	6.5	9.0	-	-	3.7	5.3	6.3	7.0	-	-	-	10.0	-	-	-
NMMNH P–23120/1	7.1	11.1	13.1	15.1	11.8	5.4	8.4	10.2	10.8	5.9	22.3	26.0	17.8	18.8	78.3	98.0
NMMNH P–23120/2	7.8	10.9	14.5	17.7	15.0	5.2	8.4	11.2	13.1	7.5	24.7	32.0	20.2	22.0	72.0	118.6
NMMNH P–23322	7.0	9.0	11.0	13.0	11.0	5.1	7.1	8.7	9.9	5.6	23.0	25.0	14.7	19.0	95.0	110.4

APPENDIX 2

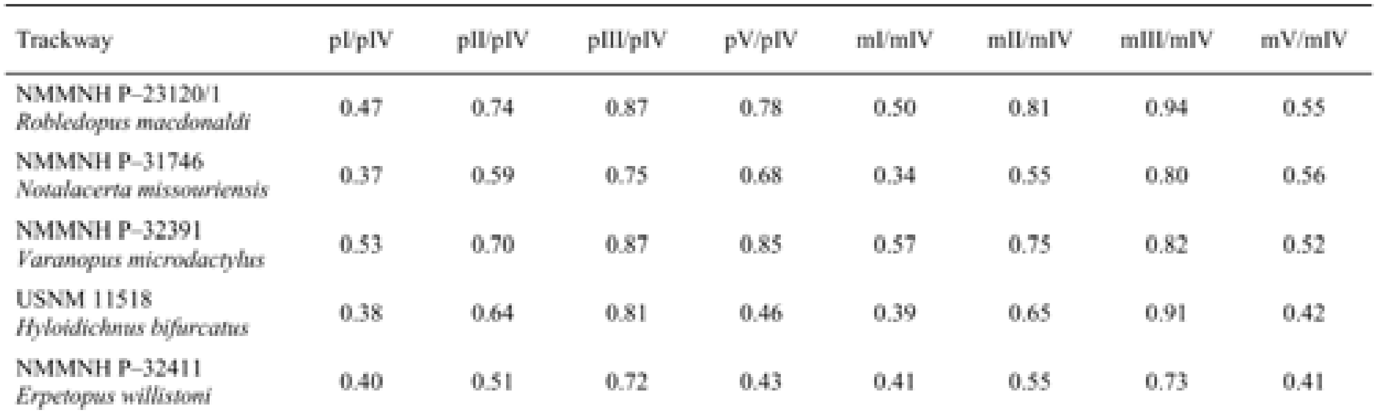
Trackway and imprint parameters of selected non-diapsid eureptile footprints from Pennsylvanian-Early Permian strata of the United States (in mm and degrees). Material: NMMNH P–23120, Robledo Mountains Formation, Early Permian, New Mexico; NMMNH P–31746, McAlester Formation, Middle Pennsylvanian, Oklahoma; NMMNH P–23411 and NMMNH P–32391, Choza Formation, Early Permian, Texas; USNM 11518, Hermit Formation, Early Permian, Arizona.

Trackway	Sp	Sm	Pp	Pm	A	Bp	Bm	C	D	E	αp	αm	βp	βm
NMMNH P–23120/1 *Robledopus macdonaldi*	139.0	140.1	97.2	90.7	28.3	66.1	57.4	97.3	41.0	4.7	92.9	100.9	20.8	-19.2
NMMNH P–31746 *Notalacerta missouriensis*	74.3	77.2	45.0	48.5	21.4	26.8	29.0	58.7	16.2	-0.2	107.3	103.4	-11.2	-9.7
NMMNH P–32391 *Varanopus microdactylus*	136.0	119.0	101.5	84.8	30.7	74.0	60.0	96.0	29.3	6.0	102.0	90.0	-23.7	-29.8
USNM 11518 *Hyloidichnus bifurcatus*	169.3	151.0	114.0	110.0	54.0	73.8	71.0	136.5	25.7	8.0	95.7	105.0	-17.2	-28.8
NMMNH P–32411 *Erpetopus willistoni*	85.0	84.0	57.0	52.5	5.3	37.0	30.0	48.0	37.0	3.0	98.0	109.0	-17.7	-39.0

Trackway	pI	pII	pIII	pIV	pV	mI	mII	mIII	mIV	mV	pl	pb	ml	mb	p	m
NMMNH P–23120/1 *Robledopus macdonaldi*	7.1	11.1	13.1	15.1	11.8	5.4	8.4	10.2	10.8	5.9	22.3	26.0	17.8	18.8	78.3	98.0
NMMNH P–31746 *Notalacerta missouriensis*	5.8	9.3	11.8	15.8	10.8	4.2	6.7	9.7	12.2	6.8	21.0	23.8	15.0	16.2	101.6	117.8
NMMNH P–32391 *Varanopus microdactylus*	8.0	10.5	13.0	15.0	12.7	8.8	11.6	12.6	15.4	8.0	21.3	33.7	21.8	27.0	84.0	95.7
USNM 11518 *Hyloidichnus bifurcates*	12.3	21.0	26.6	32.8	15.0	9.8	16.5	23.0	25.3	10.7	43.0	44.0	33.3	36.3	104.0	116.3
NMMNH P–32411 *Erpetopus willistoni*	3.7	4.7	6.7	9.3	4.0	3.0	4.0	5.3	7.3	3.0	11.0	11.3	9.0	10.0	129.3	143.3

APPENDIX 3

Lengths of digit imprints of selected non-diapsid eureptile footprints from Pennsylvanian-Early Permian strata of the United States relative to imprint length of digit IV. For material specification, see Appendix 2.



Trackway	pI/pIV	pII/pIV	pIII/pIV	pV/pIV	mI/mIV	mII/mIV	mIII/mIV	mV/mIV
NMMNH P–23120/1 *Robledopus macdonaldi*	0.47	0.74	0.87	0.78	0.50	0.81	0.94	0.55
NMMNH P–31746 *Notalacerta missouriensis*	0.37	0.59	0.75	0.68	0.34	0.55	0.80	0.56
NMMNH P–32391 *Varanopus microdactylus*	0.53	0.70	0.87	0.85	0.57	0.75	0.82	0.52
USNM 11518 *Hyloidichnus bifurcatus*	0.38	0.64	0.81	0.46	0.39	0.65	0.91	0.42
NMMNH P–32411 *Erpetopus willistoni*	0.40	0.51	0.72	0.43	0.41	0.55	0.73	0.41

APPENDIX 4A

Individual toe lengths and ß angles used for multivariate analysis (in mm and degrees).

Specimen	Ig*	pI	pII	pIII	pIV	pV	mI	mII	mIII	mIV	mV	m	p
NMMNH_P_23072_F1	R	5	7	8	9	NA	NA	NA	5	6	3	-30	34
NMMNH_P_23072_F1	R	4	5	7	NA	NA	3	5	6	5	NA	-46	9
NMMNH_P_23072_F1	R	5	7	8	9	NA	3	4	5	5	3	-39	31
NMMNH_P_23072_F1	R	3	6	7	9	NA	3	5	5	5	3	-54	20
NMMNH_P_23072_F1	R	4	6	7	8	NA	3	4	5	6	NA	-38	26
NMMNH_P_23072_F1	R	4,2	6,2	7,4	8,8	NA	3	4,5	5,2	5,4	3	-41,4	24
NMMNH_P_23072_F2	R	5	6	9	NA	NA	4	6	7	8	NA	-54	18
NMMNH_P_23072_F2	R	6	7	9	NA	NA	3	5	5	6	NA	-54	-22
NMMNH_P_23072_F2	R	NA	NA	NA	NA	NA	4	5	7	NA	NA	-50	11
NMMNH_P_23072_F2	R	5,5	6,5	9	NA	NA	3,7	5,3	6,3	7	NA	-52,7	2,3
NMMNH_ P_23120_F1	R	NA	NA	NA	NA	NA	5	9	11	12	6	NA	24
NMMNH_ P_23120_F1	R	NA	NA	NA	NA	NA	NA	9	10	10	6	-23	14
NMMNH_ P_23120_F1	R	7	11	13	15	11	5	8	11	11	7	-10	23
NMMNH_ P_23120_F1	R	7	10	13	15	NA	NA	7	9	9	5	-26	11
NMMNH_ P_23120_F1	R	7	11	13	16	12	6	10	12	11	7	-14	16
NMMNH_ P_23120_F1	R	7	11	13	NA	NA	5	9	9	9	NA	-14	23
NMMNH_ P_23120_F1	R	7	13	13	16	13	NA	8	10	11	6	-26	20
NMMNH_ P_23120_F1	R	8	11	13	14	11	6	9	10	12	6	-5	26
NMMNH_ P_23120_F1	R	8	10	13	15	NA	6	8	10	11	5	-48	24
NMMNH_ P_23120_F1	R	7	12	14	15	NA	5	7	10	12	5	-19	11
NMMNH_ P_23120_F1	R	6	11	13	NA	NA	NA	NA	NA	NA	NA	-23	NA
NMMNH_ P_23120_F1	R	7,1	11,1	13,1	15,1	11,8	5,4	8,4	10,2	10,8	5,9	-20,8	19,2
NMMNH_ P_23120_F2a	R	8	10	13	15	NA	4	8	10	13	8	-21	21
NMMNH_ P_23120_F2a	R	7	12	15	NA	NA	4	8	11	12	6	-28	18
NMMNH_ P_23120_F2a	R	7	10	14	16	NA	NA	NA	10	12	6	-12	25
NMMNH_ P_23120_F2a	R	7	10	13	19	14	6	8	12	13	9	-43	14
NMMNH_ P_23120_F2a	R	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-14	18
NMMNH_ P_23120_F2a	R	6	10	13	18	NA	6	10	11	11	6	-17	29
NMMNH_ P_23120_F2b	R	NA	11	15	20	16	6	9	11	14	8	-6	31
NMMNH_ P_23120_F2b	R	10	11	13	16	NA	4	6	NA	NA	NA	-29	NA
NMMNH_ P_23120_F2b	R	7	12	18	19	NA	6	10	12	NA	NA	-5	28
NMMNH_ P_23120_F2	R	7,4	10,8	14,3	17,6	15,0	5,1	8,4	11,0	12,5	7,2	-19,4	23,0
NMMNH_P_23322	R	NA	NA	NA	NA	NA	5	7	9	10	NA	NA	-30
NMMNH_P_23322	R	NA	NA	NA	NA	NA	6	7	8	9	5	-25	-5
NMMNH_P_23322	R	NA	NA	NA	NA	NA	4	7	8	9	6	-51	8
NMMNH_P_23322	R	NA	NA	NA	NA	NA	6	6	8	9	4	-51	14
NMMNH_P_23322	R	NA	NA	NA	NA	NA	5	8	9	10	6	-45	6
NMMNH_P_23322	R	NA	NA	NA	NA	NA	5	7	9	10	NA	-54	-25
NMMNH_P_23322	R	7	9	11	13	11	5	8	10	12	7	-35	10
NMMNH_P_23322	R	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-42	-30
NMMNH_P_23322	R	7	9	11	13	11	5,1	7,1	8,7	9,9	5,6	-43,3	-6,5
NMMNH_ P_31746	N	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	16
NMMNH_ P_31746	N	NA	NA	NA	NA	NA	4	6	9	12	NA	NA	4
NMMNH_ P_31746	N	5	9	12	15	10	4	7	9	11	7	2	9
NMMNH_ P_31746	N	5	8	11	16	10	4	7	10	12	7	15	10
NMMNH_ P_31746	N	6	10	12	17	12	4	7	11	13	7	17	7
NMMNH_ P_31746	N	6	10	12	16	11	4	6	9	11	6	14	11
NMMNH_ P_31746	N	6	9	11	16	11	5	7	11	14	7	15	11
NMMNH_ P_31746	N	7	10	13	15	11	NA	NA	NA	NA	NA	4	NA
NMMNH_ P_31746	N	5,8	9,3	11,8	15,8	10,8	4,2	6,7	9,7	12,2	6,8	11,2	9,7
NMMNH_P_32391	V	NA	NA	NA	NA	NA	9	11	13	16	NA	NA	21
NMMNH_P_32391	V	NA	NA	NA	NA	NA	10	14	12	15	NA	NA	20
NMMNH_P_32391	V	9	NA	13	15	12	9	12	13	16	9	26	32
NMMNH_P_32391	V	7	10	13	15	14	8	10	12	14	7	21	45
NMMNH_P_32391	V	8	11	13	15	12	8	10	13	16	8	24	31
NMMNH_P_32391	V	8	10,5	13	15	12,7	8,8	11,6	12,6	15,4	8	23,7	29,8
USNM_11518	H	15	21	26	31	NA	10	16	22	26	13	6	36
USNM_11518	H	NA	NA	26	32	NA	NA	NA	NA	NA	NA	28	NA
USNM_11518	H	13	21	26	32	15	11	17	23	24	9	11	20
USNM_11518	H	9	17	27	34	NA	9	14	22	24	10	15	35
USNM_11518	H	12	25	28	35	NA	9	19	25	27	NA	28	24
USNM_11518	H	12,3	21	26,6	32,8	15	9,8	16,5	23	25,3	10,7	17,2	28,8
NMMNH_P_32411	E	4	5	7	9	4	3	4	6	8	NA	23	43
NMMNH_P_32411	E	3	4	6	9	4	3	4	5	7	3	20	33
NMMNH_P_32411	E	4	5	7	10	4	NA	4	5	7	NA	10	41
NMMNH_P_32411	E	3,7	4,7	6,7	9,3	4	3	4	5,3	7,3	3	17,7	39

*Ichnogenera: R, *Robledopus*; N, *Notalacerta*; V, *Varanopus*; H, *Hyloidichnus*, E, *Erpetopus*

APPENDIX 4B

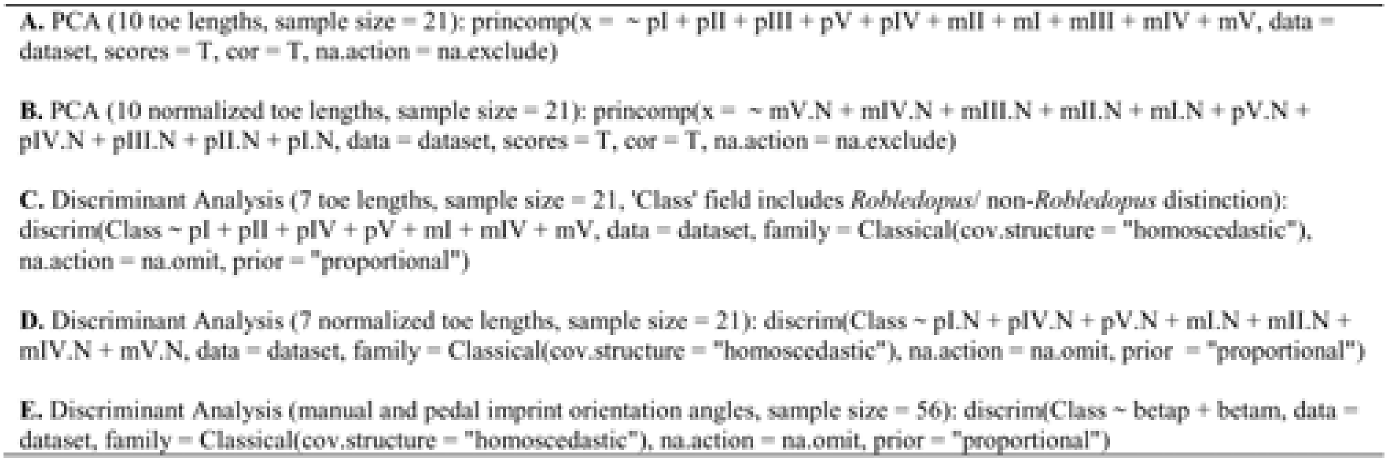
Normalized individual toe lengths (dimensionless) used for multivariate analysis.

Specimen	imprint	pMV†	pIn	pIIn	pIIIn	pIVn	pVn	mIn	mIIn	mIIIn	mIVn	mVn
NMMNH_P_23072_F1	right1	8,0	0,625	0,875	1,000	1,125	NA	NA	NA	0,625	0,750	0,375
NMMNH_P_23072_F1	left1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23072_F1	right2	8,0	0,625	0,875	1,000	1,125	NA	0,375	0,500	0,625	0,625	0,375
NMMNH_P_23072_F1	left2	7,3	0,409	0,818	0,955	1,227	NA	0,409	0,682	0,682	0,682	0,409
NMMNH_P_23072_F1	right3	7,0	0,571	0,857	1,000	1,143	NA	0,429	0,571	0,714	0,857	NA
NMMNH_P_23072_F1	average	7,5	0,563	0,830	0,991	1,179	NA	0,402	0,603	0,696	0,723	0,402
NMMNH_P_23072_F2	right1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23072_F2	left1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23072_F2	right2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23072_F2	average	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_23120_F1	left1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_23120_F1	right1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_23120_F1	left2	13,0	0,538	0,846	1,000	1,154	0,846	0,385	0,615	0,846	0,846	0,538
NMMNH_ P_23120_F1	right2	12,7	0,553	0,789	1,026	1,184	NA	NA	0,553	0,711	0,711	0,395
NMMNH_ P_23120_F1	left3	13,3	0,525	0,825	0,975	1,200	0,900	0,450	0,750	0,900	0,825	0,525
NMMNH_ P_23120_F1	right3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_23120_F1	left4	14,0	0,500	0,929	0,929	1,143	0,929	NA	0,571	0,714	0,786	0,429
NMMNH_ P_23120_F1	right4	12,7	0,632	0,868	1,026	1,105	0,868	0,474	0,711	0,789	0,947	0,474
NMMNH_ P_23120_F1	left5	12,7	0,632	0,789	1,026	1,184	NA	0,474	0,632	0,789	0,868	0,395
NMMNH_ P_23120_F1	right5	13,7	0,512	0,878	1,024	1,098	NA	0,366	0,512	0,732	0,878	0,366
NMMNH_ P_23120_F1	left6	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_23120_F1	average	13,1	0,542	0,847	1,000	1,153	0,901	0,412	0,641	0,779	0,824	0,450
NMMNH_ P_23120_F2a	left1A	12,7	0,632	0,789	1,026	1,184	NA	0,316	0,632	0,789	1,026	0,632
NMMNH_ P_23120_F2a	right1A	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_23120_F2a	left2A	13,3	0,525	0,750	1,050	1,200	NA	NA	NA	0,750	0,900	0,450
NMMNH_ P_23120_F2a	left2A	14,0	0,500	0,714	0,929	1,357	1,000	0,429	0,571	0,857	0,929	0,643
NMMNH_ P_23120_F2a	left3A	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_23120_F2a	right3A	13,7	0,439	0,732	0,951	1,317	NA	0,439	0,732	0,805	0,805	0,439
NMMNH_ P_23120_F2b	left1B	15,3	NA	0,717	0,978	1,304	1,043	0,391	0,587	0,717	0,913	0,522
NMMNH_ P_23120_F2b	right1B	13,3	0,750	0,825	0,975	1,200	NA	0,300	0,450	NA	NA	NA
NMMNH_ P_23120_F2b	left2B	16,3	0,429	0,735	1,102	1,163	NA	0,367	0,612	0,735	NA	NA
NMMNH_ P_23120_F2	average	14,2	0,523	0,758	1,004	1,238	1,057	0,362	0,594	0,775	0,881	0,505
NMMNH_P_23322	right1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23322	left1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23322	right2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23322	left2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23322	right3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23322	left3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23322	right4	11,0	0,636	0,818	1,000	1,182	1,000	0,455	0,727	0,909	1,091	0,636
NMMNH_P_23322	left4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_23322	average	11,0	0,636	0,818	1,000	1,182	1,000	0,464	0,645	0,791	0,900	0,509
NMMNH_ P_31746	left1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_31746	right1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_ P_31746	left2	12,0	0,417	0,750	1,000	1,250	0,833	0,333	0,583	0,750	0,917	0,583
NMMNH_ P_31746	right2	11,7	0,429	0,686	0,943	1,371	0,857	0,343	0,600	0,857	1,029	0,600
NMMNH_ P_31746	left3	13,0	0,462	0,769	0,923	1,308	0,923	0,308	0,538	0,846	1,000	0,538
NMMNH_ P_31746	right3	12,7	0,474	0,789	0,947	1,263	0,868	0,316	0,474	0,711	0,868	0,474
NMMNH_ P_31746	left4	12,0	0,500	0,750	0,917	1,333	0,917	0,417	0,583	0,917	1,167	0,583
NMMNH_ P_31746	right4	12,7	0,553	0,789	1,026	1,184	0,868	NA	NA	NA	NA	NA
NMMNH_ P_31746	average	12,3	0,472	0,756	0,959	1,285	0,878	0,341	0,545	0,789	0,992	0,553
NMMNH_P_32391	left1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_32391	right1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_32391	left2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NMMNH_P_32391	right2	12,7	0,553	0,789	1,026	1,184	1,105	0,632	0,789	0,947	1,105	0,553
NMMNH_P_32391	left3	13,0	0,615	0,846	1,000	1,154	0,923	0,615	0,769	1,000	1,231	0,615
NMMNH_P_32391	average	12,8	0,623	0,818	1,013	1,169	0,990	0,686	0,904	0,982	1,200	0,623
USNM_11518	right1	26,0	0,577	0,808	1,000	1,192	NA	0,385	0,615	0,846	1,000	0,500
USNM_11518	left1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
USNM_11518	right2	26,3	0,494	0,797	0,987	1,215	0,570	0,418	0,646	0,873	0,911	0,342
USNM_11518	left2	26,0	0,346	0,654	1,038	1,308	NA	0,346	0,538	0,846	0,923	0,385
USNM_11518	right3	29,3	0,409	0,852	0,955	1,193	NA	0,307	0,648	0,852	0,920	NA
USNM_11518	average	26,8	0,459	0,784	0,993	1,224	0,560	0,366	0,616	0,858	0,944	0,399
NMMNH_P_32411	right1	7,0	0,571	0,714	1,000	1,286	0,571	0,429	0,571	0,857	1,143	NA
NMMNH_P_32411	left1	6,3	0,474	0,632	0,947	1,421	0,632	0,474	0,632	0,789	1,105	0,474
NMMNH_P_32411	right2	7,3	0,545	0,682	0,955	1,364	0,545	NA	0,545	0,682	0,955	NA
NMMNH_P_32411	average	6,9	0,536	0,681	0,971	1,348	0,580	0,435	0,580	0,768	1,058	0,435

†The mean value of pedal toe lengths II, III, and IV (in mm) was used as divisor for normalization of all toe lengths listed in the following columns.

APPENDIX 5

Commands for principal component and discriminant analyses in S-PLUS 2000.



A. PCA (10 toe lengths, sample size = 21): `princomp(x =  ~ pI + pII + pIII + pV + pIV + mII + mI + mIII + mIV + mV, data = dataset, scores = T, cor = T, na.action = na.exclude)`

B. PCA (10 normalized toe lengths, sample size = 21): `princomp(x =  ~ mV.N + mIV.N + mIII.N + mII.N + mI.N + pV.N + pIV.N + pIII.N + pII.N + pI.N, data = dataset, scores = T, cor = T, na.action = na.exclude)`

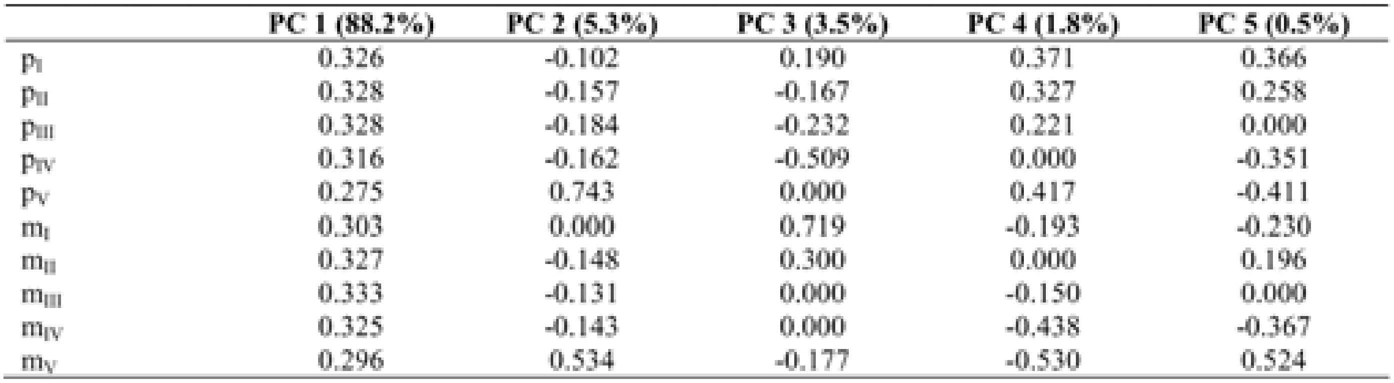
C. Discriminant Analysis (7 toe lengths, sample size = 21, 'Class' field includes *Robledopus*/ non-*Robledopus* distinction): `discrim(Class ~ pI + pII + pIV + pV + mI + mIV + mV, data = dataset, family = Classical(cov.structure = "homoscedastic"), na.action = na.omit, prior = "proportional")`

D. Discriminant Analysis (7 normalized toe lengths, sample size = 21): `discrim(Class ~ pI.N + pIV.N + pV.N + mI.N + mII.N + mIV.N + mV.N, data = dataset, family = Classical(cov.structure = "homoscedastic"), na.action = na.omit, prior  = "proportional")`

E. Discriminant Analysis (manual and pedal imprint orientation angles, sample size = 56): `discrim(Class ~ betap + betam, data = dataset, family = Classical(cov.structure = "homoscedastic"), na.action = na.omit, prior = "proportional")`

APPENDIX 6A

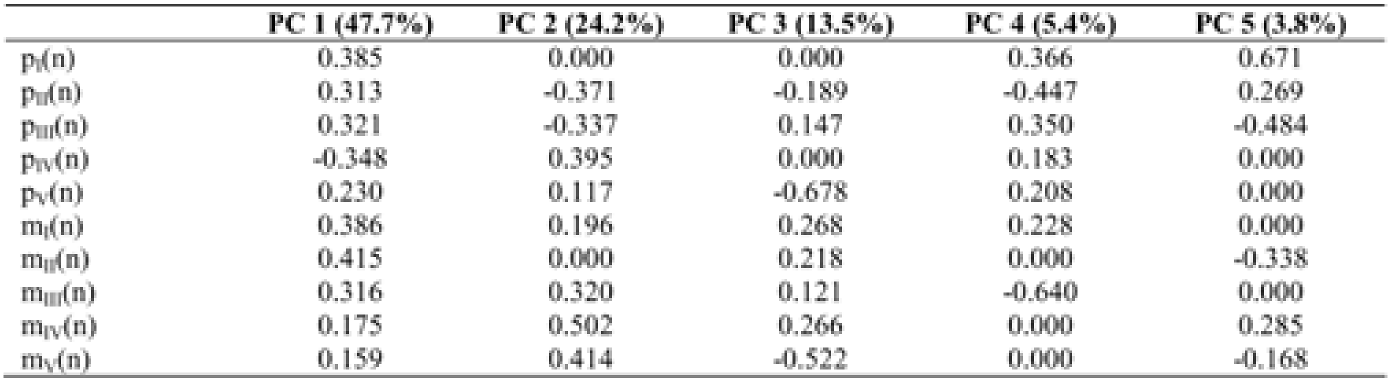
PCA based on (uncorrected) toe lengths: loadings for principal components 1 to 5.



	PC 1 (88.2%)	**PC 2 (5.3%)**	**PC 3 (3.5%)**	**PC 4 (1.8%)**	**PC 5 (0.5%)**
p_{I}	0.326	-0.102	0.190	0.371	0.366
p_{II}	0.328	-0.157	-0.167	0.327	0.258
p_{III}	0.328	-0.184	-0.232	0.221	0.000
p_{IV}	0.316	-0.162	-0.509	0.000	-0.351
p_{V}	0.275	0.743	0.000	0.417	-0.411
m_{I}	0.303	0.000	0.719	-0.193	-0.230
m_{II}	0.327	-0.148	0.300	0.000	0.196
m_{III}	0.333	-0.131	0.000	-0.150	0.000
m_{IV}	0.325	-0.143	0.000	-0.438	-0.367
m_{V}	0.296	0.534	-0.177	-0.530	0.524

APPENDIX 6B

PCA based on normalized toe lengths: loadings for principal components 1 to 5.



	PC 1 (47.7%)	**PC 2 (24.2%)**	**PC 3 (13.5%)**	**PC 4 (5.4%)**	**PC 5 (3.8%)**
$p_{I}(n)$	0.385	0.000	0.000	0.366	0.671
$p_{II}(n)$	0.313	-0.371	-0.189	-0.447	0.269
$p_{III}(n)$	0.321	-0.337	0.147	0.350	-0.484
$p_{IV}(n)$	-0.348	0.395	0.000	0.183	0.000
$p_{V}(n)$	0.230	0.117	-0.678	0.208	0.000
$m_{I}(n)$	0.386	0.196	0.268	0.228	0.000
$m_{II}(n)$	0.415	0.000	0.218	0.000	-0.338
$m_{III}(n)$	0.316	0.320	0.121	-0.640	0.000
$m_{IV}(n)$	0.175	0.502	0.266	0.000	0.285
$m_{V}(n)$	0.159	0.414	-0.522	0.000	-0.168

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

EXPLORATION OF POSSIBLE CORRELATIONS OF THE INTERSTELLAR MEDIUM (IM) OVER TIME WITH THE CARBONIFEROUS-PERMIAN BOUNDARY (CPB)

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We undertake an initial and incremental cyclostationary hydrologic test of a physical model of paleoclimate change that has in various forms been explored in the peer-reviewed literature. This model describes the Interstellar Medium (IM) scale energy and momentum drivers associated with the environments experienced over one period of solar revolution around the Milky Way galaxy. We review the underlying principles of a hydrologic-focused global energy approximation, including ocean levels and ice volumes. We apply that perspective to the emerging exploration of longitudinal IM compression-decompression waves (IMCD) that might have passed through the Sun's trajectory over the limited period of Pleistocene Glacial Oscillations (PGO).

The CPB and the PGO are known to coarsely approximate two end points of a full cycle of galactic revolution (the “galactic cycle”). Ocean levels are a primary proxy metric for the hydrologic potential state over the Earth at any given time, and they reached cyclic minima at those endpoints. Significant glaciation episodes and ocean chemistry changes have also been recognized to correspond. This paper explores additional parallels between the PGO and CPB in regard to the as yet unproven proposition of similar Galactic local environments over those two transitions. The exploration is advanced to consider what similarities in the IM might account for the paleohydrologic signatures.

A limited sampling of the key parameters that are believed to help guide climate models is conducted. We ‘work from literature sources to’ develop a draft first order frequency spectrum of IMCDs that the solar system may have traversed over the PGO, and compare that to literature-based time series and related frequency spectrums for ocean levels over the PGO and the CPB. Our discussion closes with consideration of other related aspects, including orbital parameters, ocean chemistry, and galactic cosmic rays.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

THE FUSULINES NEAR THE ARTINSKIAN-KUNGURIAN BOUNDARY IN SOUTHERN GUIZHOU, SOUTH CHINA

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The Kungurian is one of the Permian stages that has received the least study during the last decade. Though the stratotype section has not been established, the base of the stage was proposed to be defined by the first appearance datum (FAD) of the conodont species *Neostreptognathodus pnevi* (Kozur, 1979), which was commonly recognized in North America, but has never been reported in South China. Its correlation with the shallow marine fossils, the fusulines, has been difficult because of their different living conditions and preservation. Recent studies of the Yangchang and Luodian sections in southern Guizhou, South China, found for the first time the boundary marker *N. pnevi*. Besides well-preserved conodonts, the fusulines were found to be abundant in the intercalated debris flows. It is observed that the fusuline genera *Pamirina* and *Brevaxina* are a few meters above *N. pnevi* at both the Yangchang and Luodian sections. The lower boundary of the Luodianian is thus a few meters higher than that of the Kungurian.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

REVISED CONODONT TAXONOMY AND SUCCESSION FROM THE CHANGHSINGIAN STAGE (PERMIAN) AT THE MEISHAN SECTION, SOUTH CHINA, WITH SAMPLE POPULATION APPROACH

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The Changhsingian Stage and Permian-Triassic transitional sequence that crops out in a series of quarries at Meishan, Zhejiang Province, SE China have been studied for more than three decades, and the Permian-Triassic boundary and the Wuchiapingian/Changhsingian boundary GSSPs were established at the Meishan Section D in Changxing, Zhejiang Province, south China. Thus, the Meishan section D has become a unique body stratotype of the Changhsingian Stage. Conodonts are one of the most important and abundant fossil groups at the Meishan sections and provided a high-resolution biostratigraphic framework for the Changhsingian Stage and the end-Permian mass extinction across the Permian-Triassic boundary. We collected samples from Meishan Sections C and D based on a continuous sampling strategy from the uppermost Lungtan Formation to the basal Triassic and adopted the sample-population approach to establish the conodont succession based on different *Clarkina* and *Hindeodus* species. Eight conodont zones are recognized in this study. They are, in ascending order, the *Clarkina longicuspidata* Zone, *C. wangi* Zone, *C. subcarinata* Zone, *C. changxingensis* Zone, *C. yini* Zone, *C. meishanensis* Zone, *C. zhejiangensis-Hindeodus changxingensis* Zone and *H. parvus* Zone. The evolutionary relationships of Changhsingian conodont species are discussed. This high-resolution conodont-based biostratigraphic framework as well as the geochemical and sequence stratigraphy data from the Meishan section can serve as a standard for global correlation of the Changhsingian Stage.

Lucas, S.G., et al. eds., 2013, The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science, Bulletin 60.

PRESERVATION CHEMISTRY OF COALIFIED OVULES (*TRIGONOCARPUS GRANDIS*), SEED-FERN, CANTABRIAN, CANADA

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Abstract—Arnold (1938; 1948a, b) had the leading edge on studying North American coalified ovules of Carboniferous age, including *Trigonocarpus* Brongniart. We continue with such studies on coalified *Trigonocarpus grandis* (Lesquereux) Cleal et al. 2010 from the Sydney Coalfield, Canada (Fig. 1), investigating what structural aspects are preserved and why in terms of biochemistry. To this effect, we intensively used Nomarski phase-contrast microscopy (invented in the mid 1950's), and spectrochemistry: Fourier transform infrared (FTIR) spectroscopy and pyrolysis gas chromatography with mass spectrometry (Py-GC/MS, cf. Zodrow et al., 2012). The latter two methods are powerful tools for solving problems in palaeophtychemistry, palaeochemotaxonomy/systematics, diagenesis of organic matter, and molecular taphonomy. A general problem, unlike with sectioned petrified seeds (Hoskins and Cross, 1946; Taylor, 1965), is keeping track of the original sequence of the structural components when preparing slides from the macerated coalified ovules, which we successfully did.

Ovule 2-336 (Fig. 2A), ca. 1500 microns thick, separated into three distinct parts for reasons not understood (Fig. 2B). After further maceration (four days) each could be teased apart for a total of at least 15 structure/tissue layers (E.L. Zodrow, J.A. D'Angelo, and R. Helleur, unpubl., 2012). These layers are identified as 3 megaspore membranes with granulose exine surfaces, e.g., Fig. 2C; 2 nucellar cuticles, e.g., Fig. 2D; 7 integumentary epidermises, cuticles, e.g., Fig. 2E; and 3 structured, diaphanous layers or what we call tecta, e.g., Fig. 2F. Each megaspore membrane is covered with a coarse nucellar cuticle, which is individually covered with tecta, as are the integumentary epidermises, though only tectal fragments have been recovered because they are very difficult to see in water.

In proposing a coalified model, two preservation biases are recognized. One is in respect to the three megaspore membranes which should be four for double-layered membranes of trigonocarpalean seeds (Darrah, 1968; Pettitt, 1966); the other is that integumentary epidermises cannot be odd numbered. This assumes correlation with ad- and abaxial surfaces, in reference to an imaginary medial plane axis (cf. Truernit and Haseloff, 2008, fig. 2).

The model, assuming the telomic concept (Herr, 1995), can then conveniently be described in terms of inner and outer integuments and double-layered nucellus with granulose exine. What remains unresolved is the question of stomata on the outer abaxial epidermis. We found that preservation of the nucellus and epidermis correlates with the "oily" (aliphatic) contents, as revealed by the spectrochemistry used, and infer that this applies as well to the tectum and nucellar cuticle. Variation in the local Eh-pH paleoenvironment (Krumbein and Garrels, 1952) probably limited preservation of the "oily" tissues to a certain degree during early diagenesis (Berner, 1980). In general, we believe that the limit of what can be expected in terms of preservation from coalified ovules world-wide has been reached with the Sydney ovules.

Important implications include that continued separation of *Pachytesta* from *Trigonocarpus* is deemed untenable, that "oily" chemistry has potential for the systematics of medullosalean ovules, ultimately for biostratigraphy, and that the large number of dispersed ovules is probably a Carboniferous kerogen source (Arnold, 1938).

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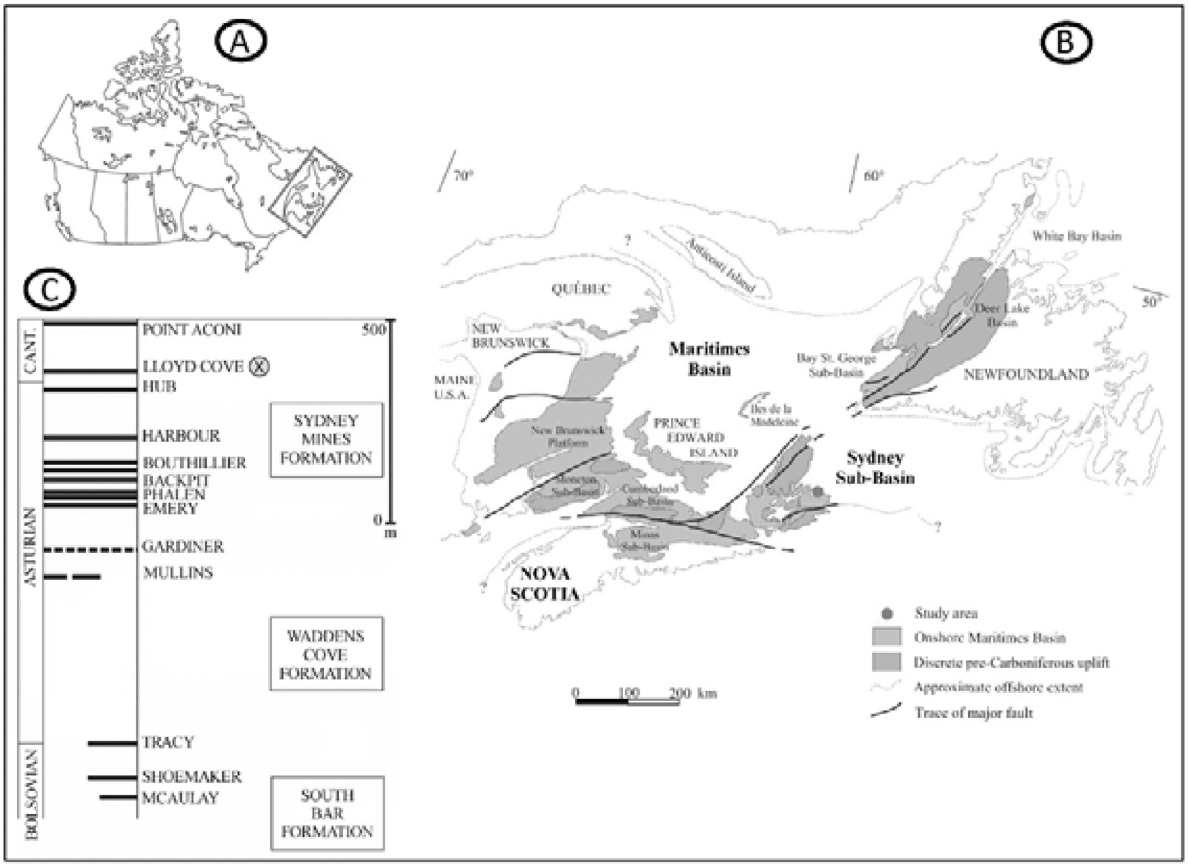

FIGURE 1. Sample location **A**, in Canada, **B**, in the Maritimes Basin and **C**, from the ca. 1-m thick Pennsylvanian-age shale stratum that was exposed by open-pit coal mining, marked X, Sydney Coalfield, Nova Scotia.

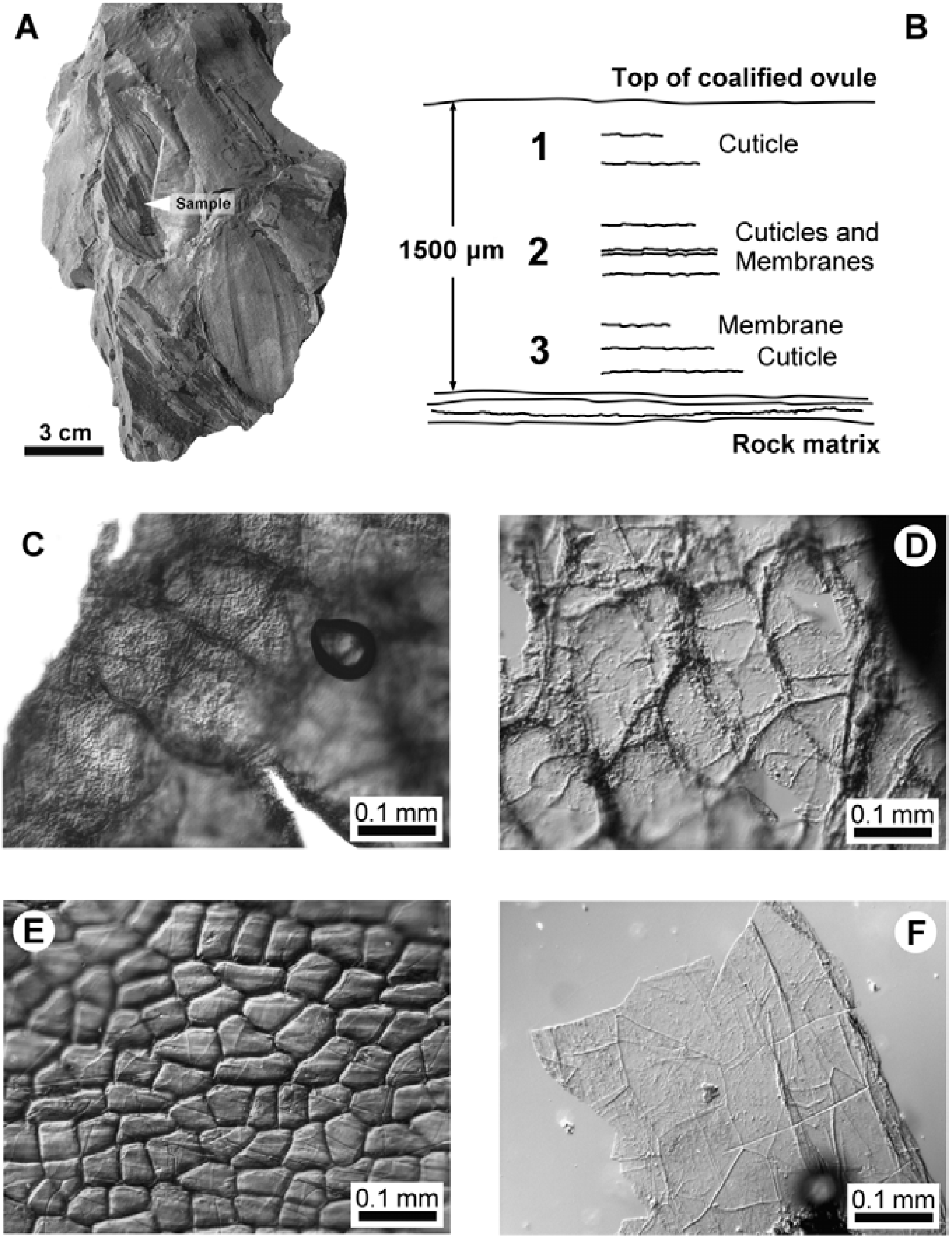

FIGURE 2. *Trigonocarpus grandis*, 2-336 ovule. **A**, Impression with compression material used for analyses, arrowed. **B**, Schematic sketch of the tripartite (1 to 3) separation of the sample A. **C**, Megaspore membrane with granulose exine surface. Slide 2-336/6 2(1). **D**, Nucellar cuticle with attached tectum (see **F**). Slide 2-336COVER. **E**, Integumentary epidermis, cuticle. Slide 2-336/4 3(3). **F**, Single-layered tectum with cell walls ca. one micron wide. Slide 2-336/5aCOVER.