Geological Society of America
Special Paper 399
2006

The Hancock County tetrapod locality: A new Mississippian (Chesterian) wetlands fauna from western Kentucky (USA)

William J. Garcia
Glenn W. Storrs
Cincinnati Museum Center, Geier Collections and Research Center, 1301 Western Avenue, Cincinnati, Ohio 45203, USA, and
University of Cincinnati, Department of Geology, ML 0013, Cincinnati, Ohio 45221-0013, USA

Stephen F. Greb
Kentucky Geological Survey, 228 MMRB, University of Kentucky, Lexington, Kentucky 40506, USA

ABSTRACT

The earliest tetrapods are known from a handful of Upper Devonian and Lower Carboniferous localities in Europe, North America, and Australia. All Upper Devonian sites and virtually all Early Carboniferous faunas are regarded as predominantly aquatic and most occur within, or are associated with, wetland habitats. A new mid-Carboniferous (Elvirian, Namurian A) fossil locality in Kentucky preserves the first tetrapod fauna from the eastern portion of the Illinois Basin. Four distinct facies at the locality have yielded vertebrate material. Diverse faunas have been found in an abandoned channel/oxbow facies and a floodplain/lake facies.

The abandoned channel/oxbow facies contains Colosteidae, Embolomeri, Rhizodontida, Dipnoi, Xenacanthiformes, Palaeonisciformes, and Gyracanthidae remains. This assemblage is similar to known Mississippian freshwater and brackish-water faunas, providing further evidence of a cosmopolitan tetrapod province during the Mississippian. A different fauna, rich in tetrapods but lacking fish, is associated with granular carbonate masses, rooting structures, and a paleosol in the floodplain/lake facies. Isolated and associated tetrapod elements from this facies exhibit morphological adaptations that may suggest a fauna of more highly terrestrial vertebrates than previously known from the North American Mississippian.

Keywords: tetrapod, Mississippian, wetland, Illinois Basin.

INTRODUCTION

Stem tetrapods are first recorded from the Frasnian (ca. 370 Ma), with their record extending from the Late Devonian into the Early Carboniferous. Fewer than three dozen Upper Devonian (ca. 377–362 Ma) and Lower Carboniferous (ca. 362–323 Ma) tetrapod localities are known worldwide. In the past 20 years, vigorous investigation of these sites and the discovery of new faunas have greatly advanced our knowledge of early tetrapod morphology (Clack, 1988, 1994, 2002; Coates and Clack, 1991; Lombard and Bolt, 1995; Coates, 1996; Milner and Lindsay, 1998; Warren and Turner, 2004) and distribution (Bolt et al., 1988; Ahlberg, 1995; Thulborn et al., 1996). Reassessment of known fossils (Ahlberg, 1991; Daeschler et al., 1994), and new discoveries (Lebedev and Clack, 1993; Lebedev and Coates, 1995; Daeschler, 2000; Zhu et al., 2002; Clement et al., 2004)

Garcia, W.J., Storrs, G.W., and Greb, S.F., 2006, The Hancock County tetrapod locality: A new Mississippian (Chesterian) wetlands fauna from western Kentucky (USA), *in* Greb, S.F., and DiMichele, W.A., Wetlands through time: Geological Society of America Special Paper 399, p. 155–167, doi: 10.1130/2006.2399(08).

have revealed a more diverse array of Devonian taxa than previously suspected.

While the last two decades have seen a great improvement in the quality of the Devonian and Mississippian fossil record, the early record of tetrapods in the Devonian and Carboniferous contains significant gaps. The most notable is a 30-million-year period at the base of the Mississippian that is represented by only two localities (Fig. 1). Known Devonian taxa show numerous adaptations that separate them from their piscine ancestors. However, these forms are clearly distinct from Mississippian tetrapods. The morphological disparity and taxonomic diversity of late Mississippian tetrapods implies that their primary diversification occurred early in the Mississippian, as they adapted to a variety of unoccupied niches.

The origin of terrestrial ecosystems bears directly on the early radiation and diversification of tetrapods, and on the aquatic to terrestrial vertebrate transition. This transition occurred in facies associated with lowland wetland habitats that occupy the transition between aquatic and terrestrial ecosystems. Devonian tetrapods for which extensive material is known were clearly aquatic (Coates and Clack, 1991; 1995; Lebedev and Coates, 1995; Jarvik, 1996; Clack et al., 2003a, 2003b). The presence of lateral line canals, paddle-like limbs, and a caudal fin on the tail argues convincingly that *Acanthostega* and *Ichthyostega* were highly aquatic forms (Coates 1996; Jarvik, 1996; Clack et al., 2003a, 2003b). Additionally, *Acanthostega* appears to have retained functional gills (Coates and Clack, 1991, 1995; Coates, 1996). Although it has been argued that certain morphological features of Devonian forms are associated with terrestrial abilities (Carroll and Green, 2003), the overwhelming morphological evidence indicates that known Devonian tetrapods were highly aquatic. Numerous Carboniferous forms retained aquatic adaptations (lateral line systems in the skull table and cheeks, reduction in vertebral ossification, reduced limbs) but also possessed characters associated with increased terrestriality (Holmes, 1984, 1980; Clack, 2002, 2001). All Devonian and most Carboniferous tetrapods were almost certainly non-amniotes, necessitating placement of eggs in a moist environment. While certain extant lissamphibians have evolved strategies for keeping eggs moist in non-wetland environments, the majority of these taxa are restricted to wetlands (Duellman and Trueb, 1986; Stebbins and Cohen, 1995). Thus, early tetrapods, like modern Lissamphibia, almost certainly possessed physiological constraints that forced them to inhabit wet or moist environments. This apparent duality, adaptations for terrestriality but constraints necessitating access to aquatic environments, explains the great importance of wetland ecosystems for early tetrapods. Environments such as ponds, swamps, small streams, and floodplains provided a wide variety of new ecological niches for early tetrapods to exploit during their diversification in the Early Carboniferous. These niches provided access to both aquatic and terrestrial ecosystems, an important feature for organisms with adaptations to both types of environment. At the same time, the expanding diversity of land plants and arthropods in the Devonian and Carboniferous increased the disparity of wetland niches, providing additional habitats and potential prey for early tetrapods (DiMichele and Hook, 1992; Shear and Selden, 2001; Gensel, 1986; Scheckler, 1986). For these reasons wetland ecosystems are of key importance for understanding the evolution of early tetrapods.

The majority of Early Carboniferous tetrapod localities are located in Great Britain and North America, with the notable exception of the Middle Paddock locality of western Australia. These localities are situated along a belt roughly 20º north and south of the paleoequator (Fig. 2). North American localities are concentrated within the Appalachian and Illinois Basins of the United States and Nova Scotia in Canada, while British localities are predominantly from the Midland Valley of Scotland.

All known Early Carboniferous tetrapod faunas derive from a narrow range of environments that are all wetland ecosystems (Milner et al., 1986; DiMichele and Hook, 1992). Mississippian wetland faunas, typically deposited in paludal, small pond or forest-swamp settings, show a high degree of similarity. Most elements of these faunas are decidedly aquatic in their morphology, and composition of these faunas is broadly comparable (Milner, 1993). One major exception to this pattern is known. The unique thermal pond fauna of East Kirkton, Scotland (Lower Carboniferous, Visean) contains unequivocally terrestrial animals (Fig. 1.) (Milner and Sequeria, 1994; Smithson, 1994; Smithson et al., 1994; Clack, 2001).

These ecological/environmental restrictions are not limited to the Mississippian; they are seen also in the early Pennsylvanian (Westphalian). At this time, most faunas are derived from autochthonous, coal-bearing, fluviodeltaic sequences (Hook and Ferm, 1988; DiMichele and Hook, 1992). These deposits represent tropical lowland wetland ecosystems. Although it has been argued that certain components of these faunas were derived from more upland faunas (Milner, 1980; Boyd, 1984), sedimentological evidence suggests that these species coexisted in a single ecosystem (Hook and Hower, 1988). Additional Westphalian tetrapod faunas derive from more terrestrial assemblages, the best known of which is Joggins, Nova Scotia (Upper Carboniferous, Westphalian A). To date, the earliest known fully terrestrial vertebrates in North America are from Joggins (Fig. 1). Here, early amniotes are found inside *Sigillaria* stumps (Dawson, 1868; Carroll, 1967), a lycopod swamp-forest habitat.

A new Lower Carboniferous (Mississippian, Chesterian) site in Hancock County, Kentucky, records the first known tetrapods in the eastern Illinois Basin (Fig. 3). In this paper we present a preliminary description of the vertebrate fauna from two facies at the Hancock County locality. We compare the fauna from these two facies with other Mississippian freshwater faunas. In addition, we discuss differences in faunal composition and morphological features of tetrapod specimens recovered from a flood plain/lake facies at the Hancock County. These morphological features include terrestrial adaptations in early tetrapods at Hancock County when compared with faunas in lacustrine facies from other Mississippian faunas. The morphological adaptations have implications for the timing of terrestriality in tetrapods.

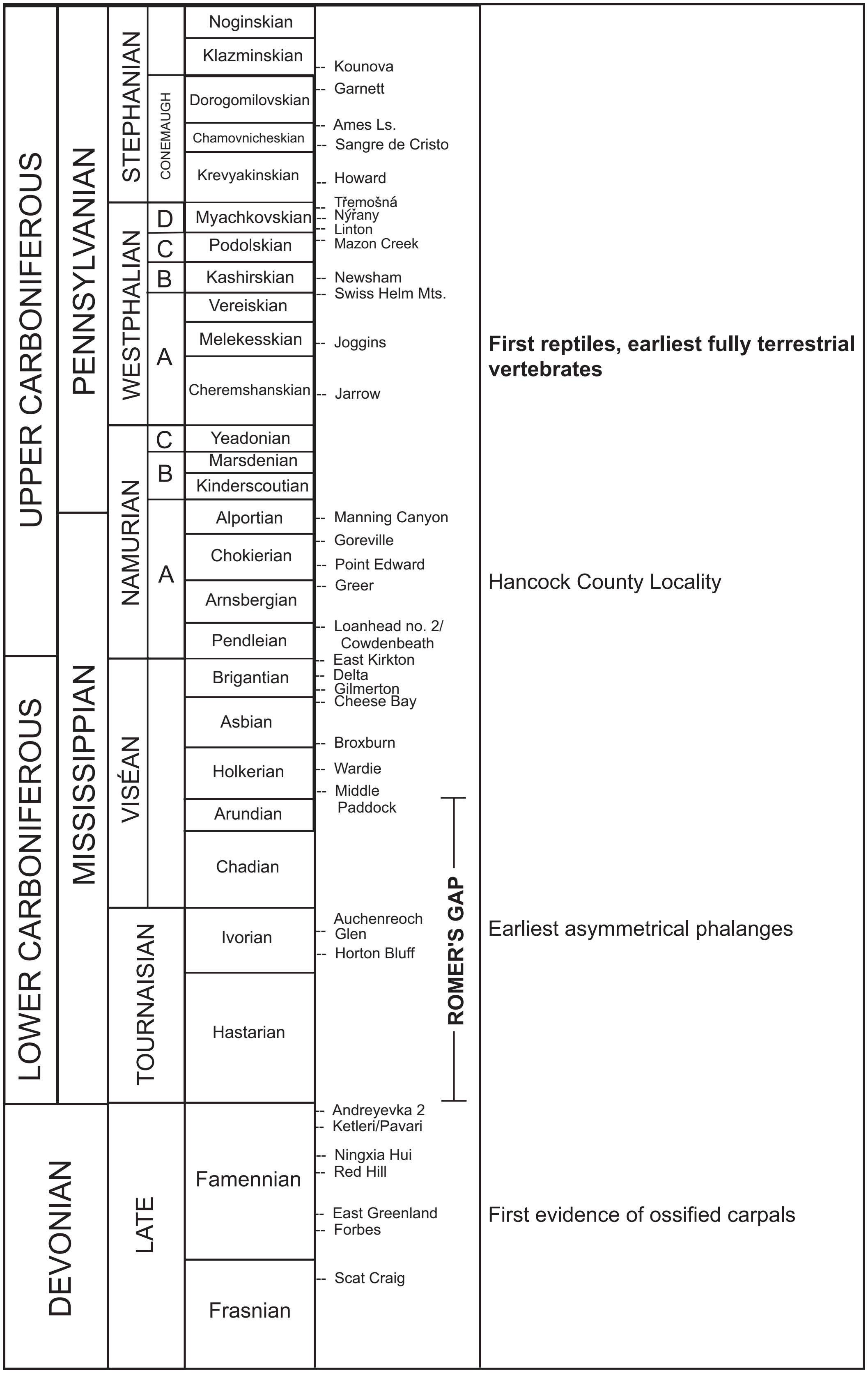

Figure 1. Geological time scale showing occurrences of early tetrapod faunas and timing of major events in the evolution of terrestriality (modified from Clack and Carroll, 2000, and Marshall et al., 1990).

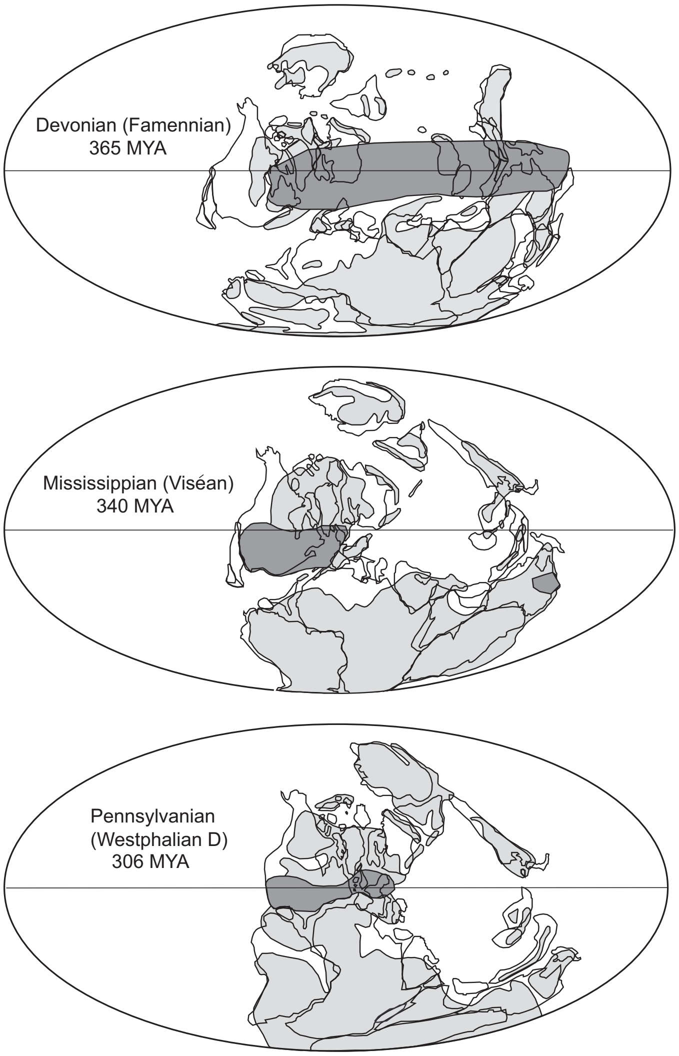

Figure 2. Estimated distribution of tetrapods during the Late Devonian, Early Mississippian, and Pennsylvanian. Gray shading represents terrestrial environments and dark shading represents the distribution of tetrapods. Modified from Scotese, 2000 (Paleomap project) and Milner, 1993.

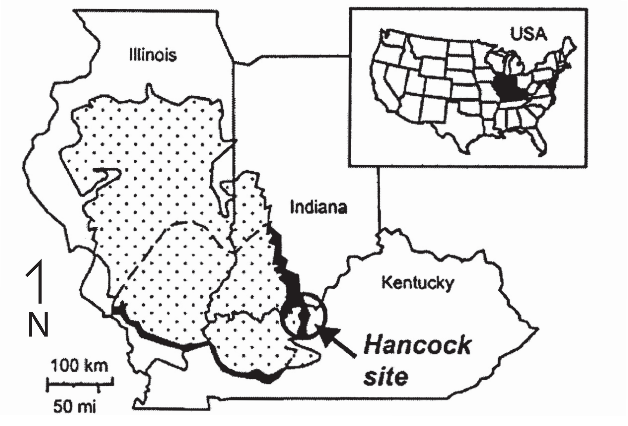

Figure 3. Location of the upper Chesterian, lower Namurian A, Hancock County site in the Illinois (Eastern Interior) Basin of North America.

Stratigraphy and Geologic Setting

The Hancock County site (data on file at Cincinnati Museum Center, CMC) lies on the eastern margin of the Illinois (Eastern Interior) Basin (Fig. 3). Four facies yield well-preserved vertebrate remains. Upper Chesterian rocks in the basin are divided into alternating carbonate and clastic formations, which thin onto the eastern margin of the basin. Along the basin margin in parts of Kentucky, the interval from the base of the Vienna Limestone to the base of Pennsylvanian strata is mapped as the Buffalo Wallow Formation (Weller, 1913; Rice et al., 1979). Some of the carbonate formations that occur basinward are reduced to members or beds within the Buffalo Wallow Formation.

At the Hancock County site, a complex suite of marginal marine and terrestrial rocks above the Menard-equivalent limestone is exposed (Fig. 4). The Clore Limestone is missing here, apparently truncated by the sub-Pennsylvanian unconformity. A heterolithic sandstone above the Menard-equivalent limestones, interpreted as a laterally accreting, fluvial to upper estuarine paleochannel, correlates with the Palestine Sandstone deeper in the basin (personal observation). Carbonaceous shales, cross-cutting paleochannels, and paleosols overlie the Palestine-equivalent sandstone at the Hancock County site (Fig. 4). Some of the facies in this complex are tentatively equated with the upper Palestine because at least one of the cross-cutting channel fills is similar to the underlying heterolithic paleochannel. A pyritic coaly shale drapes a scour and may also be upper Palestine, or mark the beginning of the Clore transgression (personal observation).

At Hancock County, vertebrate material has been found in the Menard Limestone, the heterolithic channel equated to the Palestine Sandstone, a floodplain/lake facies with paleosols above the main heterolithic channel, and the scour-filling carbonaceous shale that may be equivalent to the Clore transgression (Fig. 4, Table 1). Vertebrate material from the lower two facies will be discussed in future papers. Material from the upper two facies is discussed herein.

Rocks from the Hancock site represent distal and near-shore marine, to estuarine and/or lacustrine, to terrestrial/flood-plain paleoenvironments. All have produced vertebrate fossils (Table 1). Two of these fossil-bearing facies preserve wetland environments and will be discussed below. Discussion of the faunas from the remaining two facies (distal and nearshore marine rocks) will be dealt with in future papers.

FACIES AND PALEOENVIRONMENTS

Flood Plain/Lake Facies

One of the facies above the main Palestine-equivalent sandstone is a 3-m-thick, tan to buff, unlaminated to poorly laminated shale and claystone (Fig. 5). The contact between this shale and lateral small channel fills is not well exposed, but the shale appears to be truncated eastward. The top of the

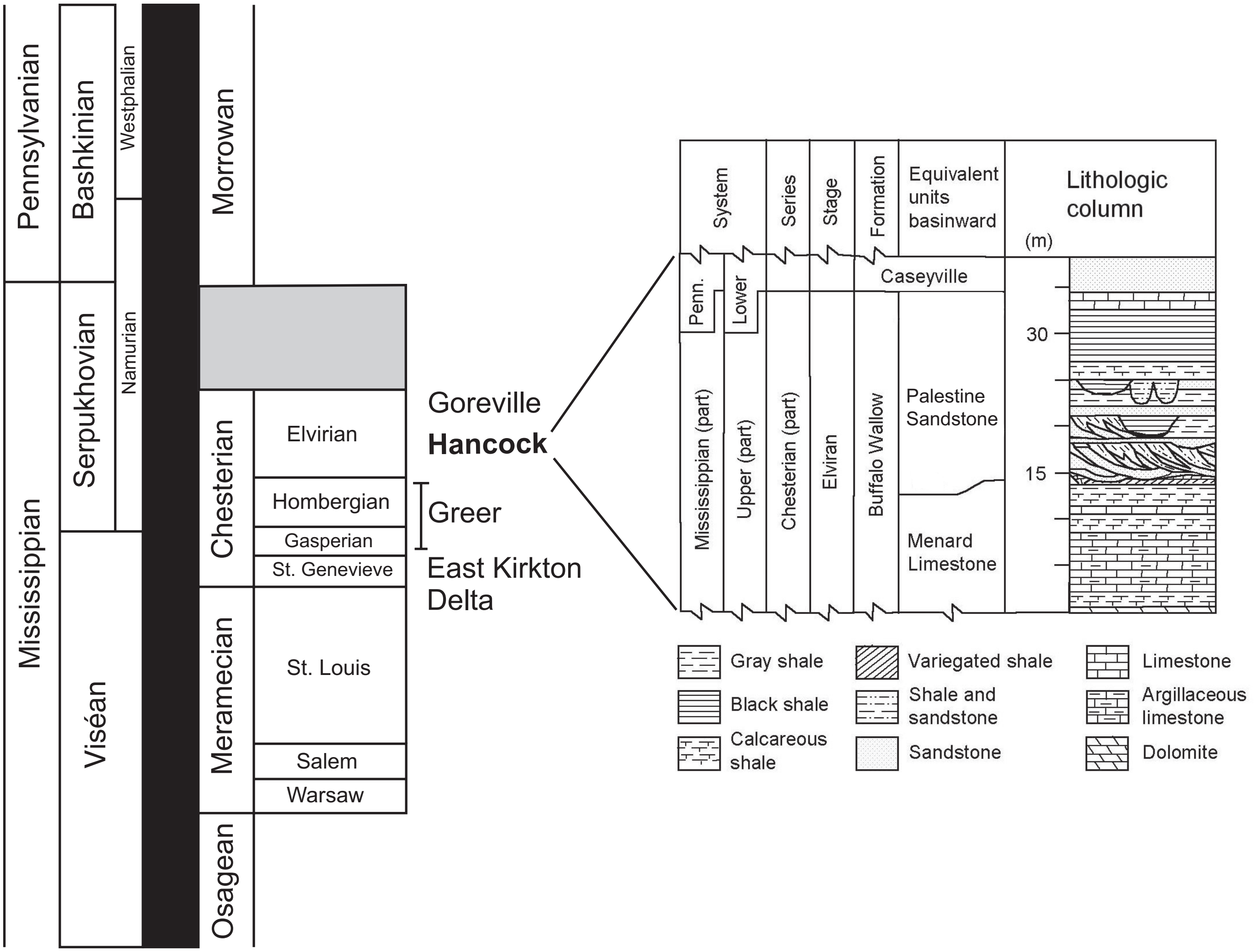

Figure 4. Stratigraphic section at the Hancock County site. Modified from Schultze and Bolt, 1996.

shale is not well exposed, although lateral units are capped by a poorly developed paleosol.

The tan to buff shale contains numerous cross-cutting slickenside surfaces. Siderite nodules and bands (20–35 cm) are concentrated along some slickensides. At least one of the siderite occurrences is bulbous (2–3 cm in diameter) and slightly upward-thickening, as would occur in a root trace. Macroscopic plant remains (carbonaceous fragments on bedding surfaces) occur along semi-continuous, horizontal surfaces in the lower 2 m of the unit but are disrupted by slickensides. The overall concentration of plant remains increases toward the base of the unit.

At least two horizons of well-cemented, granular carbonate masses occur in the lower meter of the unit. The carbonates are laterally discontinuous, up to14 cm thick, and consist of pisolitic and sub-pisolitic (>2 mm) grains, clay fragments, and dark organic debris. Small hollow tubes (0.5–2 mm) and carbonaceous

TABLE 1. DISTRIBUTION OF MAJOR FAUNAL ELEMENTS

	Menard Limestone (Marine)	Palestine Sandstone (Fluvial)	Palestine Paleosol (Flood-plain)	Palestine Shale (Estuarine)
Holocephali	X			
Rhizodontida		X		X
Gyracanthus				X
Xenacanthiformes				X
Dipnoi				X
Embolomeri		X	X	
Colosteidae				X
Temnospondyli			X	
Whatcheeriid			X	

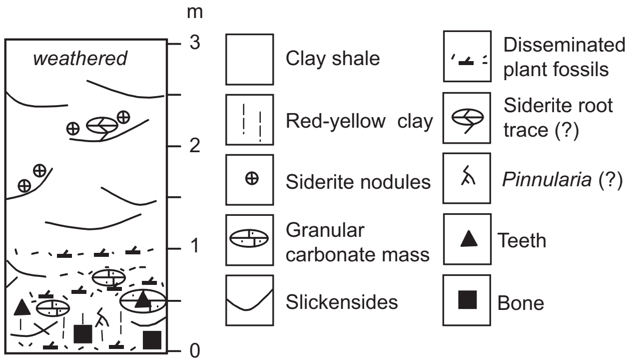

Figure 5. Vertical section through the flood plain/lake facies.

rootlets occur throughout the masses. Pseudolamination is preserved in the carbonate masses but is not preserved in the surrounding shales.

The upper carbonate horizon is overlain by a layer of shale with abundant plant fossil debris and is underlain by a 45–50 cm thick clay-rich horizon. The upper 20 cm of the clay is a mottled tan to yellow in color and contains at least one small, downward-branching feature, similar in appearance to *Pinnularia,* a common Mississippian root structure. The lower 25 cm of the clay-rich interval grades downward from yellow/ochre to red. The lower carbonate horizon is also overlain by thin shale layer with abundant carbonaceous debris.

Disarticulated, associated, and articulated tetrapod bones and teeth are concentrated in a 30 cm interval between the two carbonate horizons. Isolated material, in particular teeth, is found within the upper carbonate horizon.

Interpretation

The shale is situated above a fluvial to fluvio-estuarine channel (personal observation) and is laterally truncated by fluvial facies and an abandoned coaly shale-draped scour. The fine grain size, disseminated plant debris, rooting, and lack of marine trace or body fossils suggest a quiet freshwater environment, such as a distal floodplain or floodplain lake. The possible siderite rootlets and *Pinnularia* indicate intermittent colonization of the flood plain or lake by emergent vegetation. The granular carbonate masses bracket a clay-rich interval. Mottling within the clay indicates mineral leaching and paleosol development. The occurrence of disseminated plant debris and granular carbonates is consistent with an interpretation of a freshwater riparian environment with intermittent or marginal marshes. The unit's fine grain size indicates relative protection from clastic influx. Slickensides suggest seasonal alternations in precipitation (Retallack, 1988), as these features develop from the contraction and expansion of clay-rich substrates in alternating wet and dry seasons. Chesterian paleoclimates in eastern North America are interpreted as alternatively dry and humid (Cecil, 1990; Caudill et al., 1996; Miller and Eriksson, 1999). Seasonal variation in precipitation may have accompanied this dry to humid alternation.

Abandoned channel/oxbow Facies

One of the scours above the Palestine-equivalent heterolithic channel at the Hancock County site truncates the stratigraphic level of the flood plain/lake facies and lateral channel fills (Fig. 4). The channel is 30–50 m wide. A 5–60 cm layer of black, pyritic, carbonaceous shale drapes the base of the scour. This shale contains vitrainous coal streaks that thicken into the scour (Fig. 6). Palynologic analyses indicate that *Lycospora orbicula*, *L. micropapillata,* and *Schulzospora,* with subdominant *Calamospora* are the dominant flora of the carbonaceous shale. *Stigmaria* and sideritic nodules (rootlets) underlie the scour and are continuous onto the limbs of the scour, where the coaly shale thins or is absent. On the limbs of the scour, carbonate concretions encase pyritized stigmarian rootlets, forming "coal balls."

Overlying the coaly shale is 30–45 cm of lighter, dark-gray, carbonaceous shale with common pyrite nodules and pyritized fossil wood fragments ranging in length from 5 to 30 cm. The upper contact of this carbonaceous shale is marked by a horizon of small (0.5–2 cm), marcasite nodules (Fig. 6). The marcasite horizon is overlain by 2 m of gray shale lacking pyrite. Vertebrate remains are restricted to this non-pyritic gray shale interval. Palynologic analyses indicate that this interval is dominated by *L. pusilla*, many of which are broken or abraded. The upper part of the non-pyritic gray shale contains two distinct horizons of carbonate concretions. The lowermost of these horizons consists of irregular carbonate concretions. The upper horizon includes elongate, oval-shaped concretions, which contain Dipnoan (lungfish) fossils. The upper concretion horizon is approximately equivalent to the level of coal balls on the limb of the scour (Fig. 6).

Interpretation

Coal-draped scours are common in Carboniferous strata of Kentucky and represent abandoned scours that developed into peat-forming wetlands (Greb and Chesnut, 1992; Eble and Greb, 1997). The presence of pyrite in the lower part of the fill indicates anaerobic substrates typical of wetland soils, and possible marine influences. Rising base level related to the Clore transgression down paleoslope in the basin may have initiated the accumulation of peat to form the coaly shale and the sulfides contained therein (Greb et al., in review).

Lycospora orbicula and *L. micropapillata* are products of *Paralycopodites*, a small, shrubby lycopod (DiMichele and Phillips, 1994). *Lycospora orbicula* and *L. micropapillata* are common in the basal increments of Carboniferous coals and coals that fill scours or abandoned channels (DiMichele and Phillips, 1994; Eble and Greb, 1997). *Schulzospora* is a product of the pteriodosperm (seed fern) *Lyginopteris*, which was common in Lower Carboniferous wetlands. This seed fern had small stems and is interpreted as vinelike with large plannated frond leaves (form genera of the *Sphenopteris* or *Pecopteris* type) (Stewart and Rothwell, 1993). *Lyginopteris* probably relied upon other plants (in this case, *Paralycopodites)* for support. The sphenopsid (rush) *Calamites*, a common inhabitant of Carboniferous wetlands, capable of growing to treelike stature, produced *Calamaspora* (DiMichele and Phillips, 1994). The palynological assemblage in the basal carbonaceous shale suggests a lacustrine scrub-shrub wetland or small forest swamp, which infilled an abandoned scour.

The marcasite nodules mark a distinct change in water chemistry within the fill. Overlying sediments lack pyrite and are fossiliferous, suggesting deposition in more oxygenated waters as the scour filled. The marcasite nodules themselves may represent coprolites that accumulated on top of the buried peaty shale. The overlying non-pyritic shales contain a diverse freshwater fauna typical of a small oxbow lake or pond. The diversity within the scour, in addition to the large size of certain taxa, suggests intermittent connection to a larger lake or river when it was filled. Modern oxbow lakes and ponds are often successively in-filled by flooding from nearby rivers.

The non-pyritic gray shale contains a palynoflora different from the basal carbonaceous shales. Samples from this part of the fill are dominated by *L. pusilla*, the spores of *Lepidodendron*. This arborescent lycopod is a common constituent of Carboniferous swamp forests (DiMichele and Phillips, 1994). Spores are mostly broken, suggesting transport. *Lepidodendron* needed a wet substrate to survive, but its lack of pneumatophores indicates that the lycopod did not occupy a habitat consisting of standing water. Standing water was necessary to support the large rhizodont fish and other fauna found within the shale. The source of these spores may have been *Lepidodendron* swamp forests situated between the oxbow pond and riverine source area, rather than in or adjacent to the pond itself.

The top of the hill is characterized by carbonate concretions containing dipnoans (Fig. 6). This marks a point at which the pond was nearly filled, and perhaps influenced by seasonal drying. The carbonates containing lungfish are at a stratigraphically similar horizon to the rootlet-coal balls beneath the scour on the scour limbs. Carbonate precipitation across the scour boundary suggests a mechanism that was partly independent of depositional facies, such as a change in groundwater level. Water level fluctuations were common in the seasonal paleoclimates inferred for the Chesterian (Cecil, 1990; Caudill et al., 1996; Miller and Eriksson, 1999).

VERTEBRATE FAUNA

Abandoned Channel/Oxbow Facies Fauna

Tetrapods include a nearly complete colosteid (CMC VP7288), with only the anterior third of the skull and the distal half of the caudal vertebral series missing (Fig. 7A, 7B, Table 1). The body is elongate and the limbs small, indicating highly aquatic habits. The disparity in size between the maxillary and larger dentary teeth, tri-radiate parasphenoid, rhachitomous vertebrae, open palate, absence of an otic notch/temporal embayment, and robust single dorsal process of the ilium indicate its colosteid affinity. This specimen is distinguished from known colosteids by the unusual dorsal osteoderms covering it from just anterior of the pectoral girdle to immediately caudad of the pelvis. The thick, rectangular osteoderms are arranged in diagonal rows of 6–10 elements. Each row is oriented 55º posterolaterally to the axis of the vertebral column. Rows from opposite sides of the column alternate position along its axis. The long axes of individual osteoderms parallel the rows. Each is pitted dorsally, while the smooth lateral and posterior edges are beveled for squamous articulation with adjacent scutes. The dorsal scales of the well-known colosteid *Greererpeton* are subcircular and distinctly thinner (Romer, 1972). The scales of CMC VP7288 most closely resemble those of the Pennsylvanian colosteid *Colosteus* (Hook, 1983). Isolated vertebrae, scales, maxilla fragments, and a lower jaw also represent this taxon.

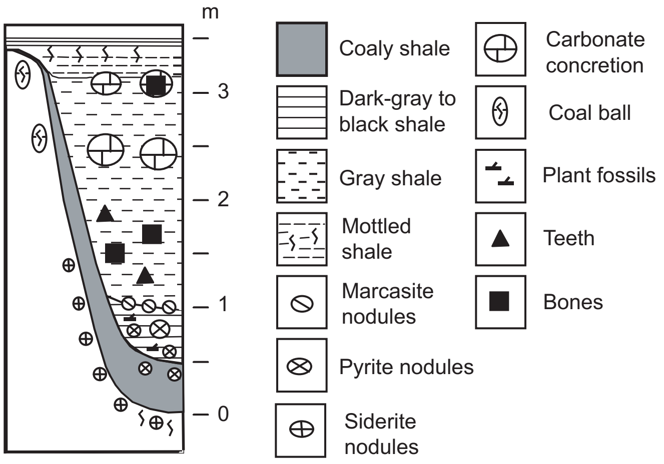

Figure 6. Vertical section through the abandoned channel/oxbow facies.

Dorsal squamation is unusual in early tetrapods but is present in some advanced, presumably terrestrial temnospondyls (e.g., *Peltobatrachus, Cacops, Dissorophus,* and *Broiliellus*). Their large scutes likely served to strengthen the vertebral column (DeMar, 1968). However, the small size and mail-like arrangement of scutes in the Hancock specimen, along with its probable aquatic habit, argue against such a function here. Notably, the occurrence of dermal armor at the Hancock County site coincides with the presence of large, predatory fish in the same deposit (Table 2).

Sarcopterygian rhizodont material is abundant in this facies (Fig. 7D). It includes a partly articulated individual (CMC VP6915) that is the most complete specimen of a giant rhizodont known. It includes skull table and temporal elements, opercular and gular plates, premaxillaries, left maxilla, vomers, complete right mandible, clavicles, cleithra, various fin elements, and numerous scales. Living length of this animal was ~4 m. A second smaller individual is known from an articulated shoulder girdle and partial

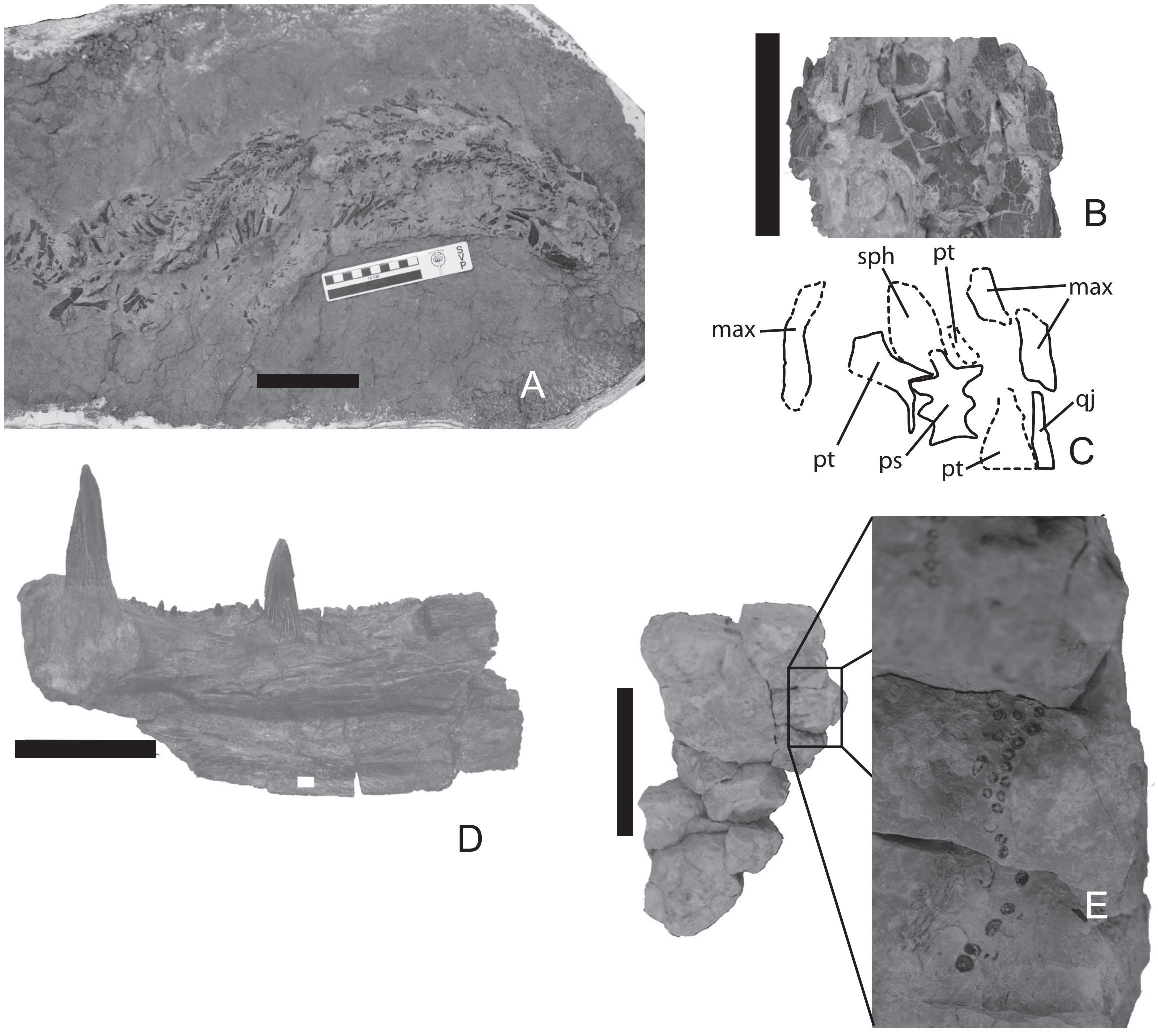

Figure 7. Vertebrate fossils from the abandoned channel/oxbow facies. A. Dorsal view of colosteid. Anterior is to the right. B. Palatal view of colosteid skull. C. Drawing and interpretation of colosteid palatal elements (max = maxillary, ps = parasphenoid, pt = pterygoid, qj = quadratojugal, sph = sphenethmoid) D. Lingual view of rhizodont lower jaw. E. Lungfish burrow with inset of ribs in cross section. All scales are 10 cm.

Table 2. Faunal Comparison of select North American Lower to mid-Mississippian fish and tetrapod localities

Hancock, KY	Goreville, IL	Greer, WV	Delta, IA	Point Edward, NS
Rhizodont		Rhizodont	Rhizodont	*?Strepsodus*
Tranodis	*Tranodis*	*Tranodis*	*Tranodis*	*Sagenodus*
Palaeoniscoids		Palaeoniscoids	Palaeoniscoids	
Xenacanthids				
Gyracanthus		*Gyracanthus*		*Gyracanthus*
Colosteid	*?Greererpeton*	*Greererpeton*	Colosteid	Colosteid
Embolomere	Embolomere	*Proterogyrinus*	Embolomere	Proterogyrinid
		Whatcheeriid		
	Microsaur			
		?Crassigyrinus		
				Spathicephalus

cranial material. Although partial remains are distributed worldwide in Upper Devonian and Carboniferous rocks, Rhizodontida is poorly known with few articulated specimens (Andrews, 1985; Jeffery, 2001). The oldest and, to date, most complete rhizodonts are from Antarctica (Young et al., 1992) and Australia (Johanson and Ahlberg, 1998; Johanson et al. 2000; Long, 1989), leading to speculation that this clade, near the base of Tetrapodamorpha, originated in eastern Gondwana (Cloutier and Ahlberg, 1996). North American material is typically incomplete (Daeschler and Shubin, 1998; Davis et al., 2001).

Putative aestivation burrows of lungfish (cf. *Tranodis*) (Fig. 7E) containing entombed skeletons occur within a 30 cm thick horizon near the top of the upper shale at the Hancock County site. These are the oldest known dipnoan burrow structures with skeletons. Carroll (1965) described apparent burrow traces from the Pennsylvanian of the Michigan Basin and *Gnathorhiza* burrows and skeletons are well known from the Lower Permian of New Mexico, Oklahoma, and Texas (Berman, 1979a, 1979b, 1979c; Olson and Daly, 1972; Romer and Olson, 1954; Vaughn, 1964). Smaller burrows, lacking skeletal material, from the Devonian Catskill Group of Pennsylvania are only questionably attributable to dipnoans. Additional fish fossils from the Hancock County are xenacanth coprolites, some of which contain palaeonisciform scales, and numerous, large gyracanthid acanthodian pectoral and pelvic spines.

Floodplain/Lake Facies Tetrapod Fauna

The interval between the two horizons of granular carbonate masses in the lower part of the floodplain/lake facies preserves more than 100 elements, including skull fragments, jaws, vertebrae, ribs, limb girdle bones, propodials, epipodials, phalanges, and teeth. This represents the oldest known paleosol containing tetrapod fossils. Anthracosaur femora of various sizes, intercentra, and pleurocentra are relatively common. Vertebrae of a large temnospondyl have also been recovered. Numerous limb elements of indeterminate taxa are stout with well-developed condyles, suggesting large, robust limbs compatible with a more terrestrial lifestyle than seen in most other Mississippian tetrapods.

An embolomerous vertebra (CMC VP7279, Figure 8A, 8B) with fused pleurocentrum and neural arch represents a previously unknown form. The pleurocentrum is a complete disc, similar to those from known embolomeres such as *Pholiderpeton* (Clack, 1987), *Archeria* (Holmes, 1989a) and *Calligenethlon* (Carroll, 1967), but there is no evidence of a dorsal suture as in *Proterogyrinus* (Holmes, 1984). It is strongly amphicoelous (possessing concave anterior and posterior faces) with a wide notochordal canal rather than the small perforation typical of *Archeria* and *Pteroplax* (Holmes, 1989a; Boyd, 1980). No intercentral facet is apparent. The transverse processes are unusually tall, with long axes directed sub-vertically. Well-developed zygopophyses are set near the midline, but with sub-horizontal articular faces as in seymouriamorphs. This orientation would resist rotational movement of the body and confine the vertebral column to lateral flexion (Panchen, 1977). A supraneural canal is narrow, relative to other anthracosaurs.

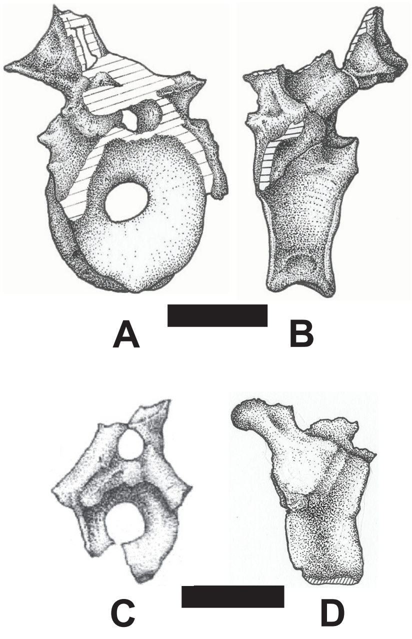

Figure 8. Anterior (A) and left-lateral views (B) of CMC VP 7279 and anterior (C) and left-lateral (D) views of CMC VP 7278. Scale bar = 1 cm

A second pleurocentrum and fused neural arch from an unknown taxon (CMC VP7278, Figure 8C, 8D) exhibits wide buttresses that descend from the neural arch and support short, ventrally directed diapophyses. Here, the zygopophyses lie near the midline with medially inclined articular surfaces (~45º). Highly angled zygopophyses in this specimen may equate with complex trunk motion, namely, lateral flexure coupled with rotation around the spinal axis (Holmes, 1989b). Morphological differences between these vertebral types possess potential taxonomic significance, though these differences could represent variation among vertebrae of the same column. Resolution of these issues must await the collection of more material.

Additional elements exhibiting morphological adaptations to terrestrial locomotion include several ilia recovered from the paleosol. Three ilia represent various sizes of the same taxon. The largest (CMC VP7328) (Fig. 9) displays dorsal and posterior processes somewhat resembling those of *Whatcheeria* and *Pederpes*. The dorsal process is fan shaped and is 2.0 cm at its greatest length. Postdepositional compression appears to have flattened portions of the specimen, including the dorsal process; the narrow fan-shaped appearance may be an artifact of preservation. The posterior process is short and relatively stout, broadening slightly over its posterior half. It is distinctly necked dorsoventrally as it emerges from the body of the ilium. The most notable feature of this specimen is the broad dorsal roof of the acetabulum. The acetabular surface is oval in shape, with its long axis oriented primarily dorso-ventrally. The surface is inclined

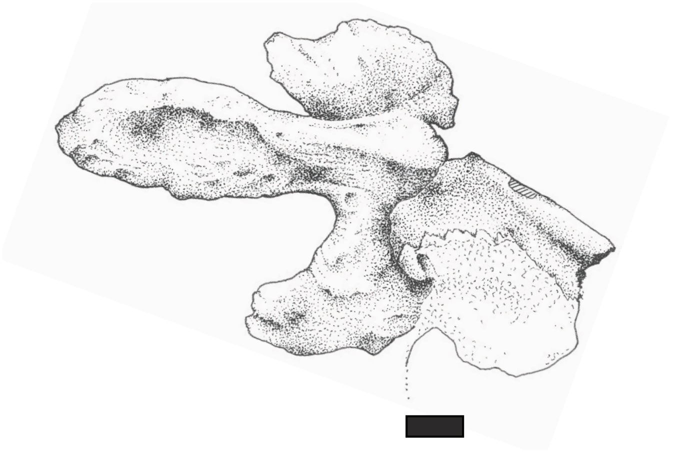

Figure 9. Right lateral view of CMC 7328. Scale bar = 2 cm

such that the articular surface faces ventrolaterally at ~25° to the horizontal plane.

The smaller size class is represented by two left ilia (CMC 7261 and CMC 7664). These specimens also possess a long posterior process and a dorsal process. In neither specimen is the posterior process completely preserved; thus its true length is unknown. A broken rim of bone projecting mediodorsally from the dorsal surface of the ilium indicates the presence of a dorsal process. In both specimens, this projection is broken at its base, suggesting a thin, easily broken process. Like the larger specimen, the acetabulae are oval in shape, but the articular surfaces face more posterior-ventrally in these smaller forms. The ventrally facing dorsal acetabular rim in these specimens provided a surface against which the femoral head would have braced during locomotion. Such a bracing mechanism is unnecessary for aquatic locomotion, as the femur is moved in an anterior/posterior motion when not held against the body. For terrestrial locomotion, this would provide much-needed support.

DISCUSSION

Comparison with Other Mississippian Faunas

Typical Mississippian faunas consist primarily of members of three early tetrapod clades: Embolomeri, Colosteidae, and Baphetidae (Godfrey, 1988). Although other taxa characterize certain Mississippian deposits (*Crassigyrinus*, *Whatcheeria, Eoherpeton*), taxa from these three clades are the dominant and most numerous forms. Dominance of Mississippian faunas is not broadly restricted to the clade level, but certain taxa seem to typify these faunas (Table 2). Milner has used this broad faunal similarity to argue that the Euramerican tetrapod fauna represents a single biogeographical province, termed the Mississippian Tetrapod Province (Milner, 1993). Because of ecological bias and the small number of faunas in the early tetrapod fossil record, robust conclusions cannot be drawn from the comparison of these assemblages. The Hancock County assemblage, however, adds evidence for the validity of this province. Preliminary collecting at Hancock has produced a proterogyrinid and an articulated colosteid specimen.

Early Carboniferous tetrapod assemblages are rare, so little is known about their ecosystem structure. However, nearly all known are of fresh- to brackish-water origin, and some comparisons can be made. Tetrapod taxa typical of a Mississippian Tetrapod Province include colosteids, loxommatids, embolomeres, and the aberrant *Crassigyrinus* (Milner, 1993). The abandoned channel/oxbow facies from the Hancock County site contains a typical Mississippian lacustrine/paludal fish fauna with strong similarity to those previously known from North America and Europe. In particular, the Hancock fish fauna is most similar to those of Greer, West Virginia, and Delta, Iowa (Table 2; Godfrey, 1988; Schultze and Bolt, 1996). The depositional setting of the Greer locality has been debated and it has variably been suggested as fluvial point bar to overbank deposits (Busanus, 1974), or marine with periodic encroachment of nearshore mud (Elliott and Taber, 1982).

The other known Illinois Basin Lower Carboniferous tetrapod locality—Goreville, Illinois—has a similar tetrapod fauna (Schultze and Bolt, 1996). Both the Greer and Goreville faunas contain common dipnoans (cf. *Tranodis*), and each preserves a colosteid and an embolomere. The dominant rhizodonts of Hancock are absent from Goreville, although rhizodont material of distinctly smaller taxa is known from Greer (Godfrey, 1989). In addition, the acanthodians, palaeoniscoids, and xenacanthids known from Hancock are absent from Goreville. Differences between the Goreville locality and other Mississippian vertebrate faunas have been ascribed to the relative lack of marine influence at Goreville. Fossil-bearing strata at Goreville represent clastic sedimentation between marine limestones (Schultze and Bolt, 1996).

Implications for Tetrapod Terrestriality

The most significant aspect of the Hancock County site is the preservation of a riparian flood-plain fauna that contains tetrapod elements with morphological characteristics suggesting terrestrial locomotion. Modern riparian areas provide a critical habitat for amphibians and reptiles, due to the abundance of water and accessible transition between aquatic, wetland, and upland habitats.

The 30-million-year "Romer's Gap" of the basal Carboniferous fossil record hinders knowledge of early tetrapod radiations (Coates and Clack, 1995). Recent discovery of the whatcheeriid tetrapod *Pederpes* (whatcheeriids are stem-tetrapods known from the Mississippian of North America and Great Britain) at the base of this gap suggests that even the earliest Mississippian tetrapods were partially adapted to limited terrestrial locomotion, although they were still primarily aquatic (Clack, 2002). *Pederpes* displays asymmetrical phalanges associated with turning of the manus during walking (Clack, 2002). Finds in the Lower Carboniferous at East Kirkton and elsewhere hint at a radiation much broader in scope than previously suspected. The East Kirkton deposit is atypical of Mississippian faunas in that the pond shales are shales deposited within a hot spring setting and interbedded with volcaniclastic sediments (Rolfe et al., 1990). More significantly, the fauna of East Kirkton shows various morphological adaptations for terrestrial locomotion (Clack, 2001; Milner and Sequeira, 1994; Smithson, 1994; Smithson et al., 1994), and many of the specimens were likely washed into the pond from surrounding habitats (Clarkson et al. 1994). The presence of robust limb elements (femora and humeri) and the ossification of carpals and tarsals indicate that the majority of faunal elements from East Kirkton were capable of terrestrial locomotion. Although some of the taxa bearing these features are of uncertain affinity, representatives of at least three early tetrapod clades (Milner and Sequeira, 1994; Smithson, 1994; Smithson et al., 1994) exhibit terrestrial adaptations. Two other taxa of uncertain taxonomic affinities, *Eucritta* (Clack, 2001) and *Eldeceeon* (Smithson, 1994), also exhibit terrestrial morphological adaptations. An exception to the terrestrially dominated nature of the East Kirkton fauna is *Silvanerpeton*, with morphology suggestive of a more aquatic existence (Clack, 1994).

The taxonomic uncertainty of some East Kirkton taxa does not diminish their importance as indicators of great diversity among terrestrially adapted Carboniferous tetrapods. Rather, this evidence indicates that terrestrially adapted tetrapods may have been widespread by the mid-Mississippian. Evidence of highly terrestrial taxa in the Viséan indicates that a potential ecological bias in preservation of Carboniferous assemblages has obscured a portion of the pattern of early tetrapod diversity and disparity. Prior to the discovery of the East Kirkton site, the oldest known Carboniferous locality to yield terrestrial tetrapod remains was Joggins, Nova Scotia—a gap of ~20 million years. Joggins is lower Pennsylvanian (Langsettian, Westphalian A) in age and represents another unique depositional setting. Vertebrates, including the world's oldest reptiles, are preserved inside fossilized lycopod stumps (Dawson, 1868). The reptiles were originally inferred to have been trapped as pitfalls within the trees; more recently, it has been suggested that the animals were trapped within dens during a forest-swamp fire (Calder et al., this volume). Additional support for an early and more widespread terrestrial fauna in the Mississippian comes from Scotland. A single specimen of the terrestrially adapted taxon *Casineria* is known from the Asbian (Lower Carboniferous, Visean) of Cheese Bay (Paton et al., 1999).

Vertebral elaboration was a major adaptation of advanced tetrapods and distinguishes them from their more aquatic precursors. Elaboration of the vertebral column is associated with increased strength and stability of the axial skeleton, and would have allowed greater access to terrestrial settings. Modifications include increased ossification of the central elements and fusion with the neural arch, reduction of the notochord, and development of zygopophyses. However, the earliest tetrapods typically have multipartite centra with separate neural arches. Even probable terrestrial taxa from East Kirkton (with robust limbs, ossified carpals and tarsals) possess multipartite centra (Clack, 1994; Milner and Sequeira, 1994; Smithson, 1994). Apart from lepospondyls, nearly all early tetrapods that possessed single central elements fused to their neural arches are terrestrial. While microsaurs, nectridians, and aïstopods exhibit fusion/suturing, the vast majority of lepospondyls are of small body size, come from aquatic deposits, and/or possess aquatic adaptations (Carroll, 1997; Carroll et al., 1998). Early temnospondyls, as well as colosteids, lack central element/neural arch fusion. In the derived stereospondyls, the intercentra become the dominant elements of the vertebrae, while the pleurocentra are reduced (Schoch and Milner, 2000). Among known embolomeres, fusion does not appear until the Permian. Advanced tetrapods that are thought to have been highly terrestrial, such as seymouriamorphs and diadectomorphs, also exhibit fusion. Their terrestrial adaptations include the reduction or loss of the intercentrum, consequent stiffening of the vertebral column, and a sub-horizontal orientation of the zygopophyses.

Some of the tetrapod remains from the floodplain/lake facies at Hancock County show attributes typically associated with terrestriality among vertebrates. The fauna is thus advanced in comparison to other Lower Carboniferous tetrapods, except those of East Kirkton. At the Hancock County site, specimen CMC VP7279 (Fig. 8A, 8B) exhibits a sub-horizontal orientation of the zygopophyses. As vertebral fusion is typically associated with terrestriality (with the exception of lepospondyls), the morphology of CMC VP7278 and CMC VP7279 is an indication of a terrestrial habit. Ilial morphology strongly indicates adaptations for terrestrial locomotion, namely the robust acetabular roof, which would have braced the femur during locomotion.

The fauna is associated with a paleosol and floodplain or small flood-plain lake setting. The absence of fish in the floodplain/lake facies is different from other Lower Carboniferous tetrapod assemblages (Table 1). The absence of fish also suggests that the vertebrate material was not likely transported from adjacent or nearby fluvial sources. The robust nature of associated limb elements supports the idea that the paleosol taxa were more terrestrially active than most known early tetrapods. The morphology of these elements does not establish terrestrial habits for these taxa, but the absence of fish remains and the presence of paleosol features is strong secondary evidence for some degree of terrestrial activity.

The Hancock County site provides evidence of a potentially more terrestrial fauna in North America during the Chesterian (Namurian A). In particular, morphological adaptations of CMC VP7279 support the notion that anthracosaurs expanded into more terrestrial niches during the Lower Carboniferous and that members of the clade were more terrestrial than other early tetrapod groups (e.g., loxommatids and whatcheeriids) (Smithson, 1994). Typical anthracosaurs have previously been considered highly aquatic (Smithson, 2000). Significantly, the Hancock County site material exhibits new adaptations (ossification and suturing of the vertebrae and pronounced acetabular roof) relative to those seen at East Kirkton. Addition of the Hancock site fauna to our current knowledge of Mississippian tetrapods supports the notion of a widespread distribution of terrestrial tetrapods in the mid-Carboniferous.

ACKNOWLEDGMENTS

This research was supported by grants from the National Science Foundation (EAR-0309747), the University Research Council of the University of Cincinnati, the Geological Society of America, the Theodore Roosevelt Memorial Fund, the Paleobiological Fund, Chiquita Brands International Inc. Foundation, John M. Tate, the Helen B. Vogel Trust, the Grace M. Harvie Foundation, and the Paul Sanders Award. The paper benefited greatly from reviews by Jenny Clack and Ted Daeschler. Katherine Glover provided helpful editorial advice. E. Mohalski Pence aided in the drafting of figures and G. Hardebeck and M. Milam kindly provided the specimen drawings. Field assistance was provided by E. Kvale, D. Chesnut, J. Devera, D. Williams, C. Eble, J. Nelson, D. Phelps, T. Hendricks, A. Horner, J. Sessa, R. Krause, J. Bonelli, T. Bantel, J. Lundquist, A. Watson, J. Bellan, and K. Houck.

REFERENCES CITED

Ahlberg, P.E., 1991, Tetrapod or near-tetrapod fossils from the Upper Devonian of Scotland: Nature, v. 354, p. 298–301, doi: 10.1038/354298a0.

Ahlberg, P.E., 1995, *Elginerpeton pancheni* and the earliest tetrapod clade: Nature, v. 373, p. 420–425, doi: 10.1038/373420a0.

Andrews, S.M., 1985, Rhizodont crossopterygian fish from the Dinantian of Foulden, Berwickshire, Scotland, with a re-evaluation of this group: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 76, p. 67–95.

Berman, D.S., 1979a, Cranial morphology of the Lower Permian lungfish *Gnathorhiza* (Osteichthyes: Dipnoi): Journal of Paleontology, v. 50, p. 1020–1033.

Berman, D.S., 1979b, Occurrence of *Gnathorhiza* (Osteichthyes: Dipnoi) in aestivation burrows in the Lower Permian of New Mexico with description of a new species: Journal of Paleontology, v. 50, p. 1034–1039.

Berman, D.S., 1979c, *Gnathorhiza bothrotreta* (Osteichthyes: Dipnoi) from the Lower Permian Abo Formation of New Mexico: Annals of the Carnegie Museum, v. 48, p. 211–230.

Bolt, J.R., Mckay, R.M., Witzke, B.J., and McAdams, M.P.A., 1988, A new Lower Carboniferous tetrapod locality in Iowa: Nature, v. 333, p. 768–770, doi: 10.1038/333768a0.

Boyd, M.J., 1980, The axial skeleton of the Carboniferous amphibian *Pteroplax cornutus*: Palaeontology, v. 23, p. 273–285.

Boyd, M.J., 1984, The Upper Carboniferous tetrapod assemblage from Newsham, Northumberland: Palaeontology, v. 27, p. 367–392.

Busanus, J.W., 1974, Paleontology and paleoecology of the Mauch Chunk Group in Northwestern West Virginia [M.S. thesis]: Bowling Green, Ohio, Bowling Green State University, 388 p.

Carroll, R.L., 1965, Lungfish burrows from the Michigan Coal Basin: Science, v. 148, p. 963–964.

Carroll, R.L., 1967, Labyrinthodonts from the Joggins Formation: Journal of Paleontology, v. 41, p. 111–142.

Carroll, R.L., 1997, Limits to knowledge of the fossil record: Zoology (Jena, Germany), v. 100, p. 221–231.

Carroll, R. L., and Green, D., 2003, Origin of terrestrial locomotion in vertebrates: Journal of Vertebrate Paleontology, v. 23, Suppl. to no. 3, p. 39A.

Carroll, R.L., Bossy, K.A., Milner, A.C., Andrews, S.M., and Wellstead, C.F., 1998, Handbuch der Paläoherpetologie: Lepospondyli. Munich, Dr. Friedrich Pfeil, 216 p.

Caudill, M.R., Driese, S.G., and Mora, C.I., 1996, Preservation of paleo-vertisol and an estimate of Late Mississippian precipitation: Journal of Sedimentary Research, v. A66, p. 58–70.

Cecil, C.B., 1990, Paleoclimate controls on stratigraphic repetition of chemical and siliciclastic rocks: Geology, v. 18, p. 533–536, doi: 10.1130/0091-7613(1990)018<0533:PCOSRO>2.3.CO;2.

Clack, J.A., 1987, *Pholiderpeton scutigerum* Huxley, an amphibian from the Yorkshire Coal Measures: Royal Society of London Philosophical Transactions, ser. B, v. 318, p. 1–107.

Clack, J.A., 1988, New material of the early tetrapod *Acanthostega* from the Upper Devonian of East Greenland: Palaeontology, v. 31, p. 699–724.

Clack, J.A., 1994, *Silvanerpeton miripedes*, a new anthracosauroid from the Visean of East Kirkton, West Lothian, Scotland: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 84, p. 369–376.

Clack, J.A., 2001, *Eucritta melanolimnetes* from the early Carboniferous of Scotland, a stem tetrapod showing a mosaic of characteristics: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 92, p. 75–95.

Clack, J.A., 2002, An early tetrapod from 'Romer's Gap': Nature, v. 418, p. 72–76, doi: 10.1038/nature00824.

Clack, J.A., and Carroll, R.L., 2000, Early Carboniferous tetrapods, *in* Heatwole, H., and Carroll, R. L., eds., Amphibian biology, Volume 4, Palaeontology: Chipping Norton, Australia, Surrey Beatty and Sons, p. 1030–1043.

Clack, J.A., Ahlberg, P.A., Finney, S.M., Dominguez, A.P., Robinson, J., and Ketcham, R.A., 2003a, A uniquely specialized ear in a very early tetrapod: Nature, v. 425, p. 65–69, doi: 10.1038/nature01904.

Clack, J.A., Blom, H., and Coates, M.I., 2003b, New insights into the postcranial skeleton of *Ichthyostega*: Journal of Vertebrate Paleontology, v. 23 Suppl., p. 41A.

Clarkson, E.N.K., Milner, A.R., and Coates, M.I., 1994, Palaeoecology of the Visean of East Kirkton, West Lothian, Scotland: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 84, p. 417–425.

Clement, G., Ahlberg, P.E., Blieck, A., Blom, H., Clack, J.A., Poty, E., Thorez, J., and Janvier, P., 2004, Devonian tetrapod from western Europe: Nature, v. 427, p. 412–413, doi: 10.1038/427412a.

Cloutier, R., and Ahlberg, P.E., 1996, Morphology, characters, and the interrelationships of basal sarcopterygians, *in* Stiassny, M. L. J., Parenti, L. R., and Johnson, G. D., eds., Interrelationships of fishes: San Diego, Academic Press, p. 445–479.

Coates, M.I., 1996, The Devonian tetrapod *Acanthostega gunnari* Jarvik: Postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 87, p. 363–421.

Coates, M.I., and Clack, J.A., 1991, Fish-like gills and breathing in the earliest known tetrapod: Nature, v. 352, p. 234–236, doi: 10.1038/352234a0.

Coates, M.I., and Clack, J.A., 1995, Romer's gap: tetrapod origins and terrestriality: Bulletin du Museum National d'Histoire Naturelle (Paris), ser. 4, 17, p. 373–388.

Daeschler, E.B., 2000, Early tetrapod jaws from the Late Devonian of Pennsylvania, USA: Journal of Paleontology, v. 74, p. 301–308.

Daeschler, E.B., and Shubin, N., 1998, Fish with fingers?: Nature, v. 391, p. 133, doi: 10.1038/34317.

Daeschler, E.B., Shubin, N., Thomson, K.S., and Amaral, W.W., 1994, A Devonian tetrapod from North America: Science, v. 265, p. 639–642.

Davis, M.C., Shubin, N.H., and Daeschler, E.B., 2001, Immature rhizodonts from the Devonian of North America: Bulletin of the Museum of Comparative Zoology, v. 156, p. 171–178.

Dawson, J.W., 1868, Acadian geology: The geological structure, organic remains, and mineral resources of Nova Scotia, New Brunswick, and Prince Edward Island (2nd edition): London, Macmillan and Co., 694 p.

DeMar, R.E., 1968, The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae: Journal of Paleontology, v. 42, p. 1210–1242.

DiMichele, W.A., and Hook, R.W., rapporteurs, 1992, Paleozoic terrestrial ecosystems, *in* Behrensmeyer, A. K., Damuth, J. D., DiMichele, W. A., Potts, R., Sues, H.-D., and Wing, S. eds., Terrestrial ecosystems through time: Evolutionary paleoecology of terrestrial plants and animals: Chicago, Chicago University Press, p. 205–325.

DiMichele, W.A., and Phillips, T.L., 1994, Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 106, p. 39–90, doi: 10.1016/0031-0182(94)90004-3.

Duellman, W.E., and Trueb, L., 1986, Biology of amphibians: Baltimore, Johns Hopkins University Press, 670 p.

Eble, C.F., and Greb, S.F., 1997, Channel-fill coals on the western margin of the Eastern Kentucky Coal Field: International Journal of Coal Geology, v. 33, p. 183–207, doi: 10.1016/S0166-5162(96)00048-1.

Elliott, D.K., and Taber, A.C., 1982, Mississippian vertebrates from Greer, West Virginia: Proceedings of the West Virginia Academy of Science, v. 53, p. 73–80.

Gensel, P.G., 1986, Diversification of land plants in the Early and Middle Devonian: University of Tennessee, Department of Geological Sciences, Studies in Geology, v. 15, p. 64–80.

Godfrey, S.J., 1988, Isolated tetrapod remains from the Carboniferous of West Virginia: Kirtlandia, v. 43, p. 27–36.

Godfrey, S.J., 1989, A rhizodontid crossopterygian from the Upper Mississippian at Greer, West Virginia: Acta Musei Reginaehradecensis, ser. A, Scientiae Naturales XXII, p. 89–98.

Greb, S.F., and Chesnut, D.R., Jr., 1992, Transgressive channel filling in the Breathitt Formation (Upper Carboniferous), Eastern Kentucky Coal Field, U.S.A: Sedimentary Geology, v. 75, p. 209–221, doi: 10.1016/0037-0738(92)90093-7.

Holmes, R., 1980, *Proterogyrinus scheelei* and the early evolution of the Labyrinthodont pectoral limb, *in* Panchen, A. L., ed., The terrestrial environment and the origin of land vertebrates, Systematics Association Special Volume 15, p. 351–376.

Holmes, R., 1984, The Carboniferous amphibian *Proterogyrinus scheelei* Romer, and the early evolution of tetrapods: Royal Society of London Philosophical Transactions, ser. B, v. 306, 431–524.

Holmes, R., 1989a, The skull and axial skeleton of the Lower Permian anthracosauroid amphibian *Archeria crassidisca*: Palaeontographica, Abteilung A., v. 207, p. 161–206.

Holmes, R., 1989b, Functional interpretations of the vertebral structure in Paleozoic labyrinthodont amphibians: Historical Biology, v. 2, p. 111–124.

Hook, R.W., 1983, *Colosteus scutellus* (Newberry), a primitive temnospondyl amphibian from the middle Pennsylvanian of Linton, Ohio: American Museum Novitates, v. 2770, p. 1–41.

Hook, R.W., and Ferm, J.C., 1988, Paleoenvironmental controls on vertebrate abandoned channels in the Upper Carboniferous: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 63, p. 159–181, doi: 10.1016/0031-0182(88)90095-8.

Hook, R.W., and Hower, J.C., 1988, Petrography and taphonomic significance of the vertebrate-bearing cannel coal of Linton, Ohio (Westphalian D, Upper Carboniferous): Journal of Sedimentary Petrology, v. 58, p. 72–80.

Jarvik, E., 1996, The Devonian tetrapod *Ichthyostega*: Fossils and Strata, v. 40, 1–213.

Jeffery, J.E., 2001, Pectoral fins of rhizodontids and the evolution of pectoral appendages in the tetrapod stem-group: Biological Journal of the Linnean Society, v. 74, p. 217–236, doi: 10.1006/bijl.2001.0572.

Johanson, Z., and Ahlberg, P.E., 1998, A complete primitive rhizodont from Australia: Nature, v. 394, p. 569–573, doi: 10.1038/29058.

Johanson, Z., Turner, S., and Warren, A., 2000, First East Gondwanan record of *Strepsodus* (Sarcopterygii, Rhizodontida) from the Lower Carboniferous Ducabrook Formation, central Queensland, Australia: Geodiversitas, v. 22, p. 161–169.

Lebedev, O.A., and Clack, J.A., 1993, Upper Devonian tetrapods from Andreyevka, Tula Region, Russia: Palaeontology, v. 36, p. 721–734.

Lebedev, O.A., and Coates, M.I., 1995, The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev: Zoological Journal of the Linnean Society, v. 114, p. 307–348, doi: 10.1006/zjls.1995.0027.

Lombard, E., and Bolt, J.R., 1995, A new primitive tetrapod *Whatcheeria deltae* from the Lower Carboniferous of Iowa: Palaeontology, v. 38, p. 471–494.

Long, J.A., 1989, A new rhizodontiform fish from the Early Carboniferous of Victoria, Australia, with remarks on the phylogenetic position of the group: Journal of Vertebrate Paleontology, v. 9, p. 1–17.

Marshall, J.E.A., Astin, T.R., and Clack, J.A., 1999, East Greenland tetrapods are Devonian in age: Geology, v. 27, p. 637–640.

Miller, D.J., and Eriksson, K.A., 1999, Linked sequence development and global climate change: The Upper Mississippian record in the Appalachian Basin: Geology, v. 27, p. 35–38, doi: 10.1130/0091-7613(1999)027<0035:LSDAGC>2.3.CO;2.

Milner, A.C., and Lindsay, W., 1998, Postcranial remains of *Baphetes* and their bearing on the relationships of the Baphetidae (= Loxommatidae): Zoological Journal of the Linnean Society, v. 122, p. 211–235, doi: 10.1006/zjls.1997.0119.

Milner, A.R., 1980, The tetrapod assemblage from Nyrany, Czechoslovakia, *in* Panchen, A. L., ed., The terrestrial environment and the origin of land vertebrates. Systematics Association Special Volume 15, p. 439–496.

Milner, A.R., 1993, Biogeography of Paleozoic tetrapods, *in* Long, J. A., ed., Paleozoic vertebrate biostratigraphy and biogeography: London, Belhaven Press, p. 324–353.

Milner, A.R., and Sequeira, S.E.K., 1994, The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 84, p. 331–361.

Milner, A.R., Smithson, T.S., Milner, A.C., Coates, M.I., and Rolfe, W.D.I., 1986, The search for early tetrapods: Modern Geology, v. 10, p. 1–28.

Olson, E.C., and Daly, E., 1972, Notes on *Gnathorhiza* (Osteichthyes, Dipnoi): Journal of Paleontology, v. 46, p. 371–376.

Panchen, A.L., 1977, The origin and early evolution of tetrapod vertebrae, *in* Andrews, S. M, Miles, R. S., and Walker, A. D., eds., Problems in vertebrate evolution: London, Academic Press, p. 289–318.

Paton, R.L., Smithson, T.R., and Clack, J.A., 1999, An amniote-like skeleton from the Early Carboniferous of Scotland: Nature, v. 398, p. 508–513, doi: 10.1038/19071.

Retallack, G.J., 1988, Field recognition of paleosols, *in* Reinhardt, J., and Sigleo, W.R., eds., Paleosols and weathering through geologic time: Geological Society of America Special Paper 216, p. 1–20.

Rice, C.L., Sable, E.G., Dever, G.R., Jr., and Kehn, T.M., 1979, The Mississippian and Pennsylvanian (Carboniferous) Systems in the United States—Kentucky: U.S. Geological Survey Professional Paper 1110F, p. F1–F32.

Rolfe, W.D.I., Durant, G.P., Fallick, A.E., Hall, A.J., Large, D.J., Scott, A.C., Smithson, T.R., and Walkden, G.M., 1990, An early terrestrial biota preserved by Visean vulcanicity in Scotland, *in* Lockley, M.G.R., and Boulder, A., eds., Volcanism and fossil biotas: Geological Society of America Special Paper 244, p. 13–24.

Romer, A.S., 1972, A Carboniferous labyrinthodont with complete dermal armor: Kirtlandia, v. 16, p. 1–8.

Romer, A.S., and Olson, E.C., 1954, Aestivation in a Permian lungfish: Breviora, v. 30, p. 1–8.

Scheckler, S.E., 1986, Floras of the Devonian-Mississippian transition, *in* Broadhead, T.W., ed., Land plants: University of Tennessee, Department of Geological Sciences, Studies in Geology, v. 15, p. 81–96.

Schoch, R.R., and Milner, A.R., 2000, Handbuch der Paläoherpetologie 3B: Stereospondyli: Munich, Dr. Friedrich Pfeil, 203p.

Schultze, H.-P., and Bolt, J.R., 1996, The lungfish *Tranodis* and the tetrapod fauna from the Upper Mississippian of North America, *in* Milner, A.R., ed., Studies on Carboniferous and Permian vertebrates: London, Palaeontological Association Special Papers in Palaeontology, v. 52, p. 31–54.

Shear, W.A., and Selden, P.A., 2001, Rustling in the undergrowth: Animals in early terrestrial ecosystems, *in* Gensel. P. G., and Edwards, D., eds., Plants invade the land: Evolutionary and environmental perspectives: New York, Columbia University Press, p. 29–51.

Smithson, T.R., 1994, *Eldeceeon rolfei*, a new reptilomorph from the Visean of East Kirkton, West Lothian, Scotland: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 84, p. 377–382.

Smithson, T.R., 2000, Anthracosaurs, *in* Heatwole, H., and Carroll, R.L., eds., Amphibian biology, Volume 4, Palaeontology: Chipping Norton, Australia, Surrey Beatty and Sons, p. 1053–1063.

Smithson, T.R., Carroll, R.L., Panchen, A.L., and Andrews, S.M., 1994, *Westlothiana lizziae* from the Viséan of East Kirkton, West Lothian, Scotland, and the amniote stem: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 84, p. 383–412.

Stebbins, R.C., and Cohen, N.W., 1995, A natural history of amphibians: Princeton, New Jersey, Princeton University Press, 316 p.

Stewart, W.N., and Rothwell, G.R., 1993, Paleobotany and the evolution of plants: Cambridge, UK, Cambridge University Press, 521 p.

Thulborn, T., Hamley, T., Turner, S., and Warren, A., 1996, Early Carboniferous tetrapods in Australia: Nature, v. 381, p. 777–780, doi: 10.1038/381777a0.

Vaughn, P.P., 1964, Evidence of aestivating lungfish from the Sangre de Cristo Formation, Lower Permian of northern New Mexico: Contributions to Science, Los Angeles County Museum of Natural History, v. 80, p. 1–8.

Warren, A., and Turner, S., 2004, The first stem tetrapod from the Lower Carboniferous of Gondwana: Palaeontology, v. 47, 151–184.

Weller, S., 1913, Stratigraphy of the Chester Group in southwestern Illinois: Transactions of the Illinois State Academy of Science, v. 118, p. 118–129.

Young, G.C., Long, J.A., and Ritchie, A., 1992, Crossopterygian fishes from the Devonian of Antarctica: Systematics, relationships, and biogeographic significance: Records of the Australian Museum, Suppl. 14, p. 1–77.

Zhu, M., Ahlberg, P.E., and Zhao, W.J., 2002, First Devonian tetrapod from Asia: Nature, v. 420, p. 760–761, doi: 10.1038/420760a.

Manuscript Accepted by the Society 28 June 2005

Printed in the USA