FISHES AND TETRAPODS IN THE UPPER PENNSYLVANIAN (KASIMOVIAN) COHN COAL MEMBER OF THE MATTOON FORMATION OF ILLINOIS, UNITED STATES: SYSTEMATICS, PALEOECOLOGY, AND PALEOENVIRONMENTS

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ABSTRACT
A newly discovered vertebrate assemblage is reported from the Upper Pennsylvanian (mid- to upper Kasimovian) Cohn Coal Member of the Mattoon Formation of southeast Illinois, United States. Teeth, scales, and spines of xenacanth (Dicentrodus, Orthacanthus, Triodus, Xena- canthus) and euselachian (Sphyrancanthus) sharks dominate the assemblage. Less common are the teeth, scales, and centra of holoccephalan (Helodus) and actinopterygian fishes, together with rare tetrapod (mainly pelycosaur) phalanges and centra. The assemblage occurs within a broad, shallow channel incised into a prominent Vertisol. The channel is interpreted as having been cut during a seasonally dry glacial phase when sea level was low, but filled during a subsequent transgression triggered by deglaciation. We interpret this as a brackish water (estuarine) assemblage, based on the co-occurrence of the vertebrate material with spirobroids (putative microconchids) and paleoecological inferences gleaned from a critical analysis of the literature dealing with Pennsylvanian fish ecology. This interpretation is broadly consistent with taphonomic data and the results of 87Sr/86Sr isotope analysis of shark material. The pelycosaur material may have been reworked from the lowstand Vertisol, however, and these animals occupied dryland niches that developed during glacial phases.

INTRODUCTION
Fish assemblages have been widely reported from the Pennsylvanian of Euramerica (e.g., Agassiz, 1837–1843; Traquair, 1881; Fitsch, 1889; Woodward, 1891; Zidek, 1978; Zangerl, 1981; Schultz, 1985; Soler-Gijón, 1997; Calder, 1998; Hampe, 2003; Johnson and Thayer, 2009), but in many cases relatively little attention has been given to their paleoenvironmental context and paleoecology (see Zangerl and Richardson, 1963; Baird et al., 1985a, 1985b for notable exceptions). Traditionally, Pennsylvanian fishes have been classified either as marine or nonmarine (Calder, 1998), the latter often taken to mean freshwater (Dick, 1998). In very many cases, the mere absence of an associated stenohaline fauna and the co-occurrence of plant fossils have been cited as sure evidence for a freshwater habitat (Hook and Baird, 1988; Hook and Ferm, 1988; Sander, 1989). Many such analyses, however, overlook the importance and widespread distribution of Pennsylvanian brackish water settings, e.g., commonly encountered in estuaries, interdistribu- tory bays, and even certain epicontinental seas (Buatois et al., 1998; Schultz, 1998; Falcon-Lang, 2005). Advances in the understanding of tidal deposits (Kvale et al., 1989), invertebrate salinity tolerances (Calver, 1968; Bennett, 2008), and ichnology (Archer et al., 1995; Buatois et al., 2005) now permit recognition of such brackish facies in the rock record (Schultze, 2009).

Nonetheless, determining paleosalinity for Pennsylvanian fish assemblages is particularly challenging. Cyclothemic patterns of sedimentation are dominant in Pennsylvanian successions in Euramerica (Wanless and Weller, 1932), reflecting coupled fluctuations in climate and sea level (Tandon and Gibling, 1994) linked to Gondwanan glacial–interglacial cycles (Fielding et al., 2008a, 2008b; Falcon-Lang et al., 2009). With paleoenvironments rapidly oscillating between fresh, brackish, and marine conditions in space and time (e.g., Hampson et al., 1999; Falcon-Lang, 2004, 2005), unusually precise geologic control of assemblages is required to determine habitat salinity. Notable examples of such analyses include the classic studies on faunal distribution in vertical profiles through British marine bands (Calver, 1968), or the identification of a salinity gradient from brackish nearshore to marine offshore assemblages in the Mazon Creek estuary (Baird, 1997a, 1997b, 1997c).

In this paper, a new assemblage of Pennsylvanian fishes, together with some rare tetrapods, is reported from the Friendsville Mine of Illinois, United States (Fig. 1). In addition to describing vertebrate systematics, an analysis of the facies context, sequence stratigraphy, taphonomy, and 87Sr/86Sr isotope geochemistry of the vertebrate assemblage is presented. These data, combined with a critical review of the literature concerning the geological context of Pennsylvanian fishes, allow assessment of paleoenvironments and paleosalinity, in particular, and provide a firm basis for interpretation of fish paleobiology and paleoecology.

GEOLOGICAL SETTING
The vertebrate fossil assemblage from the Friendsville Mine comes from an incised channel below the Cohn Coal, a member of the middle Missourian to Virgilian Mattoon Formation (Nance and Treworgy, 1981). In earlier reports, this coal was termed the McCleary’s Bluff Coal (Kosanke et al., 1960). Regional correlation based on borehole cores, however, shows that it is equivalent to the type Cohn Coal in Clark County, Illinois, 110 km north of the Friendsville Mine (W.J. Nelson, unpublished data, 2009). Although the two coals are no longer continuous following erosion across the La Salle Anticlinorium, correlation is beyond reasonable doubt because the prominent Livingston Limestone and Eudora Shale bracket the coals in both areas (Heckel, 2008). As the name Cohn Coal (Newton and Weller, 1937) has priority over McCleary’s Bluff Coal (Kosanke et al., 1960) we use the former stratigraphic term.

The Cohn Coal can be tied precisely to global Carboniferous stratigraphy, based on the biostratigraphy of bracketing marine units (Fig. 2; Gradstein et al., 2004; Heckel, 2008; Davydov et al., 2010; Falcon-Lang et al., 2011). As noted above, the Cohn Coal occurs just above the widespread marine transgressive unit termed the Livingston Limestone (Willman et al., 1975). This unit is positioned two major 400 ka cyclothem groups (Iola Group) below the top of the Missourian regional stage in North America (Heckel, 2008). The Livingston Limestone and its lateral equivalents can be correlated, based on conodont biostratigraphy, throughout the Midcontinent, Illinois, and

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Appalachian basins of North America (Heckel, 2008) and into the Moscow and Donets basins of eastern Europe (Falcon-Lang et al., 2011), where the global stratotypes are defined (Davydov et al., 2010). This correlation suggests that the Livingston Limestone and the overlying Cohn Coal interval is of mid- to upper Kasimovian age (~304 Ma) and may be broadly time-equivalent to the mid-Stephanian (Barruelian) of western Europe.

**GEOLOGY OF FRIENDSVILLE MINE, ILLINOIS**

The Friendsville Mine is located 9 km west northwest of Mount Carmel in Wabash County, southeast Illinois, United States (Latitude 38°26'28"N; Longitude 87°51'47"W; Section 9, T1S, R13W, Wabash County, Mount Carmel 7.5" quadrangle map). Operated by the Vigo Coal Company, it comprises a 1.8-km-long highwall oriented N–S and advancing to the east. We studied the geology in the course of three visits on 14 June 2005, 19 August 2008, and 26 January 2009. In the course of the latter visit the vertebrate remains were discovered.

**Sedimentary Facies**

In the Friendsville Mine, a 19.5-m-thick succession is accessible in multiple benches and comprises part of the lower Mattoon Formation. Five main depositional units were recognizable during our site visits (Fig. 3).

Unit 1: The lowermost unit currently exposed is the 0.7–1.1-m-thick Friendsville Coal, a low pyrite, dull-banded, semibituminous coal with a stigmarian seat earth. This comprises the Vigo Coal Company’s main target coal and forms the floor of the strip mine.

Unit 2: Sharply overlying the Friendsville Coal is a complex body of laterally variable facies about 9 m thick. This succession is dominated over much of the length of the highwall by medium- to dark-gray, heterolithic, rhythmically laminated shale, which coarsens upward. Features include flaser lamination, symmetrical ripples, siderite nodules, and a rich ichnofauna of *Cochlichnus*, *Arenicolites*, and *Lockeia*. Along strike, especially within scoured surfaces, however, sediments may grade up into very fine to fine-grained, thinly bedded, sandstone showing cross ripple lamination, soft-sediment deformation,
Lockeia, and locally, lateral accretion bedforms, 1–2 m thick. Elsewhere, the Friendsville coal may be overlain by dark-gray fossil-rich calcareous shale with channels filled with productid- or crinoid-dominated packstone and grainstone lenses.

Unit 3: The uppermost 1.1 m of Unit 2 marks an abrupt change in facies. Here, the shale exhibits siderite-filled desiccation cracks, networks of tiny fractures, and masses of intergrown calcite and siderite nodules, ≤0.3 m diameter. This hummocky unit grades up into an olive green to medium-gray claystone paleosol, 1.4–2.6 m thick, showing a blocky structure of peds with clay skins, irregular siderite- and calcite-cemented roots, pervasive slickensides, pseudoanticlines, pedogenic calcite nodules, ≤40 mm diameter, and an undulating upper surface. The calcite nodules are in greatest abundance in the upper 0.25–0.5 m of the unit.

Unit 4: Draping the irregular top of Unit 3 is a 0.6-m-thick zone of laminated dark gray, carbonaceous shale containing abundant plant compressions (dominantly Macroneuropteris scheuchzeri pinnules and axes with rare Neuropterus ovata, Alethopteris sp., Pecopteris sp.,
Calamites suckowi, and Cordaites sp.) with spirorbids (putative microconchids) locally encrusting foliage in abundance. These shaley beds contain common, thin coaly intervals, 10–30 mm thick, and are capped by the ~0.3-m-thick Cohn Coal, a pyrite-rich, bright-banded, semibituminous coal. Locally, the Cohn Coal is cut, from base to top, by a series of claystone dykes.

Unit 5: The uppermost strata in the strip mine are ≈6 m thick, but not well exposed. In some areas, they may comprise beds of calcareous shale with thin limestone lenses of brachiopod- and crinoid-dominated wackestone. Elsewhere, they may consist of medium-gray siltstone, showing upward coarsening, convolute lamination, and a prominent layer of ball-and-pillow soft sediment deformation structures immediately above the Cohn Coal.

Incised Channel Fill

Near the southeast corner of the strip mine, a shallowly incised channel is present, cutting down from a horizon within Unit 3, the claystone paleosol below the Cohn Coal, and shallowly eroding into the top of Unit 2. The channel body is 2.1–2.6 m thick at its deepest point and approximately 45 m wide—estimated perpendicular to the approximately N–S oriented channel margins (Fig. 4). The Cohn Coal shows no thickness change where it extends over the top of the channel fill.

The basal channel fill contains a matrix-supported, granular to pebble conglomerate, 0.6 m thick, composed of reworked pedogenic carbonate nodules (presumably derived from Unit 3) and shale clasts, together with a few quartz grains, within a lime mud matrix. Vertebrate skeletal fragments are present in low numbers. Higher in the channel fill are units of dark-gray, laminated shale containing common plant compressions—especially Cordaites sp., Macroneuropteris scheuchzeri, rare calamites, and indeterminate axes—encrusted with spirorbids (Taylor and Vinn, 2006) and a few freshwater to brackish water bivalves. The shale beds thicken toward the deepest part of the channel (Fig. 4).

Several thin lenses, ≤0.1 m thick, of conglomerate identical to that lower in the channel fill are interbedded with the dark shale. These lenses contain highly abundant vertebrate skeletal fragments, including elements ≤0.14 m long. Also present in the conglomerate are abundant specimens of Valvisisporites auritus, the megaspore of the small lycopsid, Chaloneria (Figs. 5A, C; Gastaldo, 1981; Pigg and Rothwell, 1983), other sparse megaspores (Fig. 5B), and two morphotypes of spirorbids (Figs. 5D–F).

Paleoenvironmental Interpretation

The Friendsville Coal (Unit 1) is interpreted as the deposits of long-lived coastal peat mires formed under perhumid tropical conditions (DiMichele et al., 2001, 2007). The overlying complex of rhythmically laminated shales, sandstone channels with lateral accretion and channels infilled with crinoid and brachiopod debris (Unit 2) represents a variety of tidal flat, estuarine, and coastal marine deposits formed following rapid marine transgression (Kvale et al., 1989). The thick claystone paleosol (Unit 3) developed on top is interpreted as a Vertisol, a fossil soil formed under seasonally dry conditions (Driese and Ober, 2005). The associated shallow channel is interpreted as an alluvial drainage incised into this landscape during base-level fall (Falcon-Lang et al., 2009). The channel must have been originally at least 5 m deep, taking into account a minimal ×2 sediment compaction. A conglomerate of pedogenic carbonate nodules in the base of the channel was reworked from the adjacent dryland soil. Dark shales with brackish spirorbids (Schultze, 2009), higher in the channel fill, record the early stages of transgression that started to flood the channel and form an estuary. The thin lenses of pedogenic carbonate conglomerate containing most of the vertebrate remains probably represent a
ravinement surface that reworked channel-floor sediments during transgression to produce a lag deposit rich in vertebrate remains. The Cohn Coal that blankets this surface represented a renewed phase of coal formation in a coastal setting following a switch back to humid climatic conditions (Unit 4). Finally, shallow marine facies of Unit 5 represent further transgression and development of shallow shelf conditions. The presence of a prominent ball-and-pillow soft sediment deformation layer just above the Cohn Coal may imply that co-seismic subsidence contributed to rapid flooding in this coastal setting (Gastaldo et al., 2004).

Cyclothems, Sea Level, and Climate

The cyclic patterns of marine transgression and regression (cyclothems) seen in our study area are generally interpreted as the response of coastal regions to coupled fluctuations in climate and sea level (Tandon and Gibling, 1994) inferred to represent the far-field effects of Gondwanan glacial–interglacial cycles (Felding et al., 2008a, 2008b). The Vertisol (Unit 3) and its associated incised channel likely started to form as sea level was dropping toward, and following, lowstand (glacial maximum) when the region was seasonally dry (Feldman et al., 2005) and coniferopsid vegetation dominated (DiMichele et al., 2009, 2010; Falcon-Lang and DiMichele, 2010). The upper part of the channel, which is filled with brackish spirorbid-bearing shale and contains the vertebrate remains, however, marks a turnaround with sea level rising once again during deglaciation. Being dominated by the megaspores of Chaloneria-type herbaceous lycopsids, the palynoflora of this interval is similar to that seen in early deglaciation deposits from other Pennsylvanian cyclothems (Dolby et al., 2011).

MATERIAL AND METHODS

Approximately 15 kg of bulk samples of rock were obtained from conglomerate lenses associated by dark-gray shales in the upper part of the incised channel fill in the Friendsville Mine. In the laboratory, samples were disaggregated by immersion in 5% acetic acid solution, buffered with tri-calcium di-orthophosphate and calcium acetate (spent acid); the latter was produced by adding a small quantity of sodium carbonate to each freshly mixed batch of acid before the samples were introduced. Each acid cycle lasted 72 hours followed by a 144-hour rinse cycle to neutralize residual acid. The rinse cycle involved acid; the latter was produced by adding a small quantity of sodium carbonate to each freshly mixed batch of acid before the samples were introduced. Each acid cycle lasted 72 hours followed by a 144-hour rinse cycle to neutralize residual acid. The rinse cycle involved a mixture of water, detergent and sodium carbonate. During each acid cycle, the samples were suspended in a plastic sieve to aid acid circulation. After each rinse cycle, any fossils that were visibly protruding ≥5 mm were removed and allowed to dry. These fossils were then coated in a weak, ethanol-based adhesive (Mowital), to prevent breakage during subsequent manual extraction. The residue from each acid cycle was passed through a series of sieves (aperture sizes: 1 mm, 0.5 mm, 0.25 mm) and decanted onto filter paper. After 48 hours drying time, remaining fossils were manually picked under a transmitted light microscope.

A total of 7642 vertebrate specimens were obtained through this process with a size range of 0.25–15 mm (typically 0.5–3 mm). Most specimens either lacked any diagnostic features or were too abraded to permit identification. The 1399 specimens (18.3%) that could be identified to some taxonomic level were subdivided into morphotypes with the aid of a transmitted light microscope and picked into plastic containers. The best specimens of each taxon were then mounted onto 10 mm aluminum stubs, gold coated using a Bio-Rad SC650 sputter coater, and imaged using a Hitachi S-3500N scanning electron microscope.

The vertebrate assemblage is described in systematic detail, dominated by a rich diversity of xenacanth and euselachian sharks (n = 1028; 73.5%) and actinopterygian fish (n = 329; 23.5%), together with the rare remains of chimaeroid fish (n = 5; 0.4%), other indeterminate bony fish (n = 20; 1.4%), and tetrapods (n = 17; 1.2%) (Fig. 6). All figured specimens, and additional material, are stored in the Vertebrate Paleontology collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States (USNM 542530–542560).

SHARKS (FIGS. 7A–F, H–L)

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1832–1841

Sharks are by far the most abundant and diverse component of the fish fauna comprising 73.5% of all the vertebrate specimens (n = 1399), representing at least five recognizable genera.

Order Xenacanthiformes Berg, 1937

The identification of xenacanthid species using teeth alone is problematic, but is often the only option available since preservation of cartilaginous elements is rare (Johnson, 1999). Xenacanths are known to possess graduated, monognathic heterodont dentition (Compagno, 1970), and the morphological variation—particularly the angle of divergence of the lateral cusps, and the numbers of coronal and basal nutritive foramina—can be as great within individual dentitions as between different species (Johnson, 1999). Ontogenetic variation can also be an issue, for example in the development of serrations in Orthacanthus (Soler-Gijón, 1997). Ultimately, there is often no single reliable character to differentiate between closely related species, and a suite of characters must be used in combination. If the specimens are incomplete or poorly preserved, this may be impossible. Xenacanthid tooth components are described here using the terminology of Hampe (2003, fig. 2). In the following, length refers to the distance between anteromedial and posterolateral margins of the base, and is perpendicular to width, which refers to the distance between the labial and lingual margins (Johnson and Thayer, 2009).

Family Xenacanthidae Fritsch, 1889

Triodus sp. (Fig. 7K–L)

Type species: Triodus sessilis Jordan, 1849.
Material: 105 teeth. Figured specimen (USNM 542530), other material (USNM 542546).
Diagnosis: Teeth tricuspid, cusps polygonal in cross section and equipped with straight vertical cristae on labial and lingual surfaces, which may split dichotomously.

Description: The teeth range in length from 0.50 to 2.25 mm. The median cusp is slender and approximately two thirds of the length of the lateral cusps; this size relationship is difficult to judge, however, as the median cusp is incomplete in most specimens. A median foramen is always present, and variable numbers of coronal and basal nutritive foramina are observed, most commonly 3 and 4, respectively. The coronal button is prominent and rounded, and the basal tubercle depressed.

Remarks: The teeth are distinguished from those of the otherwise very similar bransonelliforms Bransonella and Barbclabornia and the xenacanthid Plicatodus by the pattern of cristae. These form characteristic nested, inverted V shapes in all known bransonelliforms (Johnson, 2003, figs. 8A–N; Hampe and Ivanov, 2007, figs. 1A–H), and in Plicatodus follow an "undulating hybodont-like pattern" (Hampe, 2003, p. 225), neither of which patterns are observed here. Most Triodus species are known from the Saar-Nahe Basin, Germany; the only other known occurrence of Triodus in North America is that of Triodus elphia from the Lower Pennsylvanian (upper Bashkirian) of Arizona (Johnson and Thayer, 2009), so our new specimen extends the stratigraphic range of this genus in North America by approximately 10 Ma. Hampe (2003) notes that the reason this genus is so uncommon in many areas may simply be the result of collector bias, as the teeth are typically very small and easily overlooked.

Xenacanthus cf. ossiani Johnson, 1999 (Figs. 7A–B)

Genus: Xenacanthus Beyrich, 1848.
Type species: Xenacanthus decheni Goldfuss, 1847.
Material: 93 teeth. Figure specimen (USNM 542531), other material (USNM 542547).

Diagnosis: Teeth tricuspid, cusps lacking serrations and lanceolate in cross section. Basal surface concave, basal tubercle depressed.

Description: Length ranges from 0.5 to 3 mm. The median cusp is approximately a third of the length and width of the lateral cusps. Variable numbers of coronal and basal nutritive foramina are present, most commonly three and four respectively. Aside from cases where obscuring matrix or incompleteness prevents assessment, a prominent median foramen is present in all specimens. The base is longer than wide, with a flat or slightly concave basal surface. The basal tubercle is depressed, and a shaft extends to the center, although this is not a prominent feature. The coronal button is very prominent and extends beyond the lingual margin, but is isolated from the cusps and medial foramen. The cusps are sometimes spatulate at their tips, and though divergent are generally of similar size.

Remarks: The teeth have many features in common with those of Xenacanthus ossiani (Johnson, 1999, fig. 24)—the base in particular is extremely similar—but lack the labial inclination of the cusps observed in all known specimens of that species. Johnson (1999) speculated that X. ossiani might exhibit a heterodont dentition; if so, this could explain the differences seen here.

Family Diplodoselachidae Dick, 1981

?Orthacanthus cf. compressus (Figs. 7E–F)

Genus: Orthacanthus Agassiz, 1843.
Type species: Orthacanthus cylindricus Agassiz, 1843.
Material: 216 teeth. Figured specimen (USNM 542532), other material (USNM 542548).

Diagnosis: Teeth tricuspid, with lateral cusps much larger than median cusp. Lateral cusps serrated, median foramen always present. Basal tubercle undepressed.

Description: Teeth range in length from 0.5 to 4 mm. The median cusp is frequently minute, and never more than a quarter of the length of the lateral cusps. Coronal button isolated from cusps and flush with lingual margin of the base, which is typically but not always longer than wide and varies greatly in thickness between specimens. Variable numbers of coronal and basal nutritive foramina are present, most commonly two and four respectively.

Remarks: The genera Orthacanthus and Lebachacanthus are indistinguishable based on dental characteristics alone (Soler-Gijón, 1997, 2000). The tentative assignment of the specimens described here to Orthacanthus rests solely on the fact that Lebachacanthus has thus far only been reported from lower Permian strata in the Saar Nahe Basin, Germany (Soler-Gijón, 1997), whereas Orthacanthus is known from Pennsylvanian of North America (Johnson and Thayer, 2009). Our material is closely similar to Orthacanthus compressus, which is the most common Orthacanthus species found in the Pennsylvanian of North America. There is considerable morphological overlap among the four known North American Orthacanthus species, however, i.e., the variation between teeth from a single heterodont dentition can be as great as the variation between species, so the value of specific determination may be limited (Johnson and Thayer, 2009).

Dicentrodus cf. alatus (Fig. 7J)

Genus: Dicentrodus Traquair, 1888.
Type species: Dicentrodus bicuspidatus Traquair, 1888.
Material: Two spine fragments (USNM 542533, USNM 542548)

Diagnosis: Xenacanthid spine with two rows of denticles oriented ventro-laterally.

Description: Straight spines with an elliptical cross section, flattened ventrally, and narrowing distally. Two ventrolateral rows of denticles with slender, pointed cusps are present; the surface of one of the spines is striated, while the other is smooth. The denticles are directed proximally.

Remarks: This material was original placed in Anodontacanthus Davis, 1881 but this taxon was recently synonymized with Dicentrodus (Ginter et al., 2010). The level of striation varies between proximal and distal portions of individual spines, as well as between species (Hampe, 2003, figs. 12a–d); therefore, whether the two incomplete specimens presented here represent different species is not possible to determine.

Xenacanthiformes indet.

Material: 323 teeth (USNM 542550).

Description: Moderately to severely abraded and pitted tricuspid teeth of length (where complete), 0.5–5 mm, with two lateral cusps, flanking one or sometimes two smaller median cusps. The cusps (where present) may be carinated or smooth. In most cases the cusps are broken near the base, and the base itself is also frequently incomplete. The base extends lingually, and possesses a coronal button, basal tubercle, and variable numbers of nutritive foramina on its basal and upper surfaces.

Remarks: From incompleteness and poor preservation, these specimens lack the full suite of diagnostic characters required for further identification.

Elasmobranchii Indet. (Figs. 7C–D)

Material: 318 scales. Figured specimen (USNM 542537), other material (USNM 542553).

Description: Scales comprise distinct base and crown components. The crown is composed of 1–5 recurved lepidomoria-type cusps, equipped with strong vertical ridges that tend to converge distally. The base is circular or ovoid, with a gently to moderately convex basal surface in which one or two small foramina are occasionally present; these do not follow any regular pattern. The scales range in diameter from 0.5 to 3 mm across the widest part of the base.
Remarks: Scales consisting of aggregates of lepidomoria sharing a common base are a common feature of Paleozoic chondrichthians (Zangerl, 1981). In addition, several chondrichthyan taxa are known in which different scale types are found on different parts of the body, e.g., Diplodeloselache (Hampe, 2003, fig. 5), Heterodontus (Reif, 1974), and Orodus (Moy-Thomas and Miles, 1971). Scales are of little taxonomic value because of these factors: Zangerl (1981), on the subject of species specificity, notes that: “many [scales] have been described, but the variation, even in a single individual, is so great that this [species determination] is a hopeless proposition and merely burdens the nomenclature with useless names.” An identical scale was described by Lebedev (1996, fig. 3b) from the Lower Carboniferous of the Northern Urals, Russia, which he also attributed to Elasmobranchii indet.

Euselachii Incertae Sedis

Family Sphenacanthidae Maisey, 1982
Sphenacanthus sp. (Fig. 7H–I)

Genus:  Sphenacanthus Agassiz, 1837.
Type species:  Sphenacanthus serratus Agassiz, 1837.
Material:  62 teeth. Figure specimen (USNM 542534), other material (USNM 542551).
Diagnosis:  Labio-lingually compressed, multi-cusped teeth comprising a large median cusp and one to four pairs of smaller lateral cusps, attached to a distinct base. Cusps and cuspsules bear prominent vertical ridges.
Description:  The base is gently arched along its anteromedial–posterolateral axis, is slightly overhung by the crown on its labial margin and develops a prominent flat shelf on the lingual margin. This shelf contains numerous, strongly developed foramina on its ventral surface, but there is little consistency in the pattern or number of these. The basal surface is sharply divided between a smooth section underlying the lingual shelf, and a recessed groove penetrated by multiple foramina beneath the crown. The cusps or cuspsules are often inclined lingually, and in larger teeth are slightly recurved.
Remarks:  As with many Paleozoic and Mesozoic shark groups, the dentition of Sphenacanthus was heterodont; larger teeth with prominent recurved cusps are likely to have been anteriorly situated, while smaller teeth with cusps less well developed probably represent posterior teeth from closer to the jaw articulation (Dick, 1998).

CHIMAEROID FISH (Figs. 7M–N)

Class Chondrichthyes Huexley, 1880
Subclass Subterbranchialia Zangerl, 1979
Superorder Holoccephali Bonaparte, 1832–1841

Chimaeroid fishes are a very rare component of the fish fauna comprising 0.4% of all the vertebrate specimens (n = 5), representing only one confirmed family, Helodontidae.

Order Helodontiformes Patterson, 1965
Family Helodontidae Patterson, 1965
Helodus sp. (Figs. 7M–N)

Genus:  Helodus Agassiz, 1838.
Type species:  Helodus simplex Agassiz, 1838.
Material:  Four teeth. Figured specimen (USNM 542535), other material (USNM 542552).
Description:  Teeth labiolingually compressed, with a mesiodistally elongated crown, forming a rounded cone at its midpoint. The base is convex, and extends on its labial side to form a prominent shelf containing strongly developed foramina. The lingual portion of the basal surface contains a wide, shallow groove, again containing strongly developed foramina. The mesiodistal length—estimated for the incomplete specimens—ranges from 1.5 to 5 mm.

Remarks:  Some 72 species of Helodus have been named over the last 150 years (Stahl, 1999), many of them based on isolated teeth. The complete dentition is known only from the type species H. simplex, but the available evidence suggests that at least some Helodus species were heterodont, with multiple tooth types in one organism; the discovery of associated dentition of Psephodus (Traquair, 1885) showed that teeth assigned to up to four different species belonged to a single fish (Stahl, 1999). Smith and Patterson (1988) felt that many teeth referred to the family Helodontidae represented generalized bradyodont teeth. Pending the discovery of more complete dentitions, the taxonomy of Helodus must remain uncertain.

Holoccephali indet. (Fig. 7G)

Material:  One scale. Figured specimen (USNM 542536).
Description:  A wide, ovoid base is surmounted by a single, narrow conical cusp, broken at its tip. The base is 2 mm across at its widest point, and folded into gentle ridges radiating from the cusp. Several prominent foramina penetrate the base, but do not appear to follow any regular pattern.
Remarks:  The specimen appears quite similar to one of the scales of Helodus simplex illustrated by Stahl (1999, fig. 1A).

RAY-FINNED FISHES (Figs. 8A, C–E)

Subclass Actinopterygii Cope, 1887

Ray-finned fishes (Actinopterygii) comprise the second most abundant component of the vertebrate assemblage comprising 329 specimens (23.5% of the total) and two morphotypes. Taxonomic determination is only possible at a very general level, however.
Remarks:  Janvier (1996) remarks that, “the determination of isolated actinopterygian remains is extremely difficult”. In particular, there has never been a comprehensive study of the various forms of vertebrae that occur within this group (Arratia et al., 2001).

Actinopterygii indet. A (Figs. 8C–E)

Material:  241 teeth. Figured specimen (USNM 542538), other material (USNM 542554).
Diagnosis:  Teeth equipped with apical caps of acrodin.
Description:  Slender, conical teeth with a gently sigmoidal shape. The translucent apical caps contrast with shafts exhibiting a distinctive cross-hatched surface texture.
Remarks:  The teeth of many actinopterygians are equipped with an apical cap of hypermineralized tissue (acrodin), which is not seen in any other group (Ørvig, 1978). This substance, first noted by Peyer (1968) and subsequently named by Ørvig (1973), is therefore a clear indicator of actinopterygian affinity, although there are several cases in which it is absent, e.g., Cheirolepis (Patterson, 1982), Androlepis (Janvier, 1978), the pachycormids, and some teleosts (Gardiner et al., 2005). This cap is clearly recognizable as distinct from the tooth shaft, with a smooth surface texture and translucent appearance. The specimens described here appear identical to a single tooth reported by Robb (1992, figs. 2A–B) from the Wathena Shale Member, upper Lawrence Formation (Douglass Group, Virgilian), which he assigns without evidence to Paleoniscoidea indet.

Actinopterygii indet. B (Fig. 8A)

Material:  88 centra. Figured material (USNM 542540), other material (USNM 542556).
Description:  Centrally constricted hourglass–shaped, vertebral centra, 0.5–11 mm long. A gently concave, frequently pitted dorsal surface is flanked on either side by longitudinally elongated neural arch sockets; the ventral surface is equipped with a single deep channel, also oriented longitudinally. No attachment points for a hemal arch are evident.
Remarks:  The dorsal and ventral surfaces are distinguished following the guidelines given by Berman (1970). The centra bear a close resemblance to those described by Schultze and Chorn (1986, fig. 4),
which they assign to Palaeoniscoidea indet. Arratia et al. (2001), in their brief overview of actinopterygian vertebrae, state that vertebrae of this type only occur in “some Late Paleozoic palaeonisciformes… and probably in polypteriformes,” apparently referring to the vertebral centra described by Schultze and Chorn (1986).

INDETERMINATE BONY FISHES (Fig. 8B)
Class Osteichthyes Huxley, 1880

Material: Twenty rhomboid scales. Figured specimen (USNM 542539), other material (USNM 542555)

Diagnosis: Rhomboid scales with distinct concentric growth lines.

Description: The scales, where complete, are ≤3 mm along the diagonal long axis and are lacking any kind of superficial covering of the bony base; it seems likely that any enameloid layer has been lost through abrasion.

Remarks: Rhomboid scales are found in both the Sarcopterygii and Actinopterygii during the Pennsylvanian, and thus the state of preservation of the specimens described here precludes more detailed identification.

TETRAPODS (Figs. 9A–D; Figs. 10A–G)
Infraclass Tetrapoda Broili, 1913
Supercohort Amniota Haeckel, 1866
Cohort Synapsida Osborn, 1903

Suborder Eupelycosauria Kemp, 1982
Remarks: Only 13 pelycosaur localities have been reported from the Pennsylvanian of North America to date (Kissel and Lehman, 2002). This includes material described as Milosaurus mccordi from the Mattoon Formation of Illinois (DeMar, 1970), from which our own material originated. That species, however, is clearly dissimilar to the specimens described here; the wide, flattened cross-sectional shape of the terminal phalanges of M. mccordi, typical of more primitive synapsids, contrasts strongly with the triangular cross section seen in our specimens, which is a feature of more advanced sphenacodontid groups.

Family Sphenacodontidae Williston, 1912
Sphenacodontidae Indet. (Figs. 9A–D)

Material: One complete, and twelve incomplete, terminal phalanges. Figured specimen (USNM 542543), other material (USNM 542558).

Description: Specimens whose complete length can be measured range from 7 to 14 mm; the features can best be seen in the largest specimen (Figs. 9A–D). The overall shape is similar to that depicted by Maddin and Reisz (2007, fig. 4E) for *Dimetrodon limbatus*; the dorsal surface is wide proximally and narrows to a point distally; in lateral view, the downward curvature is moderate; in distal view, there is a marked asymmetry, with the lateral edge protruding further on one side; in cross section, the shape is roughly triangular. Blood vessel channels run down each lateral edge, moving to a more ventral position proximally; the channel on the more protruding edge is more prominent. Numerous foramina occupy the area in and around the blood vessel channels, and also appear sporadically on the ventral surface; small, faint, undulating channels are also observed, which may record the presence of small blood vessels. The flexor tubercle is well developed; 1.25 mm ventral projection, 4.5 mm distal placement as measured from the proximal edge of the phalange.

Remarks: Maddin and Reisz (2007) showed that the morphology of Permian–Carboniferous synapsid terminal phalanges follows a clear evolutionary trend. Based on their descriptions and figures (Maddin and Reisz, 2007, fig. 4), the current specimens look most like the claws of derived sphenacodontids such as *Dimetrodon*. This is uncertain, however, as *Dimetrodon* is known exclusively from the lower Permian, specifically the lower Asselian–upper Kungurian, 3–4 myr younger than the Friendsville deposits. Among sphenacodontids, such haptodontines as *Haptodus* were relatively common in the Pennsylvanian (Reisz, 1986).

Amniota Indet. (Figs. 10E–F)

Material: One incomplete vertebra (USNM 542544).

Description: A largely incomplete centrum retaining a partial neural arch with transverse processes, identified as diapophyses based on the rib attachment point visible on the (left) lateral surface.

Remarks: The specimen is insufficiently complete to identify to ordinal level, but it should be noted that there are no features that preclude a sphenacodontid affinity for this specimen; given the presence of other sphenacodontid material in the assemblage, this would not be unexpected.

Tetrapoda Indet. A (Figs. 10A–D)

Material: Two incomplete centra (USNM 543545), other material (USNM 542559).

Description: The first centrum is amphicoelous, longitudinally compressed and distorted, but appears to have been smoothly cylindrical in its original state. The second is less complete, retaining only one articular end (which is also concave), but has a prominent notch in its outer edge, and part of a process (neural or hemal arch) is also preserved. The articulating surfaces are 12–15 mm in diameter at their widest points.

Tetrapoda Indet. B (Fig. 10G)

Material: One caudal vertebra (USNM 543546).

Description: Laterally compressed, amphicoelous centrum, 14 mm long, with no visible rib attachment points and a gently concave dorsal process running along its length.

ABRASION INDEX

In order to assess the taphonomic history of the vertebrate material, the level of abrasion for each specimen was assessed following the abrasion index developed by Behrensmeyer (1978) and modified by Cook (1995). In this scheme, specimens are scored on a scale of 0–4 as follows:

Stage 0. Angular: bone edges and processes, well defined and sharp.
Stage 1. Subangular: bone edges and processes, slightly abraded and polished.
Stage 2. Subrounded: bone edges, well rounded; processes recognizable.
Stage 3. Rounded: bone edges, high degree of rounding; processes, generally remnant.
Stage 4. Highly rounded: fragments often show a high degree of sphericity.

Only those specimens (n = 913) whose pristine morphology could be inferred were measured. This is because determining the level of abrasion relies on knowing the original shape of the element. The analysis is somewhat subjective as it rests on judgments of whether, for example, the bluntness of tooth tips is a natural feature of the tooth, a result of wear through use—although this would typically result in...
distinctive wear facets—or a result of postmortem abrasion. Thus, one major bias is that it is easier to detect abrasion of elements that have a complex morphology; e.g., fine surface ornamentation.

Results

Analysis of the vertebrate assemblage indicates wide variation in the level of abrasion (Fig. 11). While some specimens are not noticeably abraded, others are so rounded as to be hardly recognizable. Overall, data suggest rather minimal abrasion, most specimens either showing no abrasion (23%; Stage 0) or only light abrasion (46%; Stage 1). In addition, when analyzed taxonomically, there is no statistical difference between taxa (range 0.58–1.36; statistical methods performed using Microsoft Excel®), with the exception of a single outlier, *Sphenacanthus* (mean 2.82). This outlier, however, is probably explained by the morphological complexity of *Sphenacanthus* (prominently ridged cusps), which would make it more susceptible to abrasion.

Taphonomic Interpretation

The unimodal abrasion data suggests that our vertebrate material obtained from the ravinement surface originated from a single source. If the material under investigation was from multiple sources, a bimodal or multimodal distribution of abrasion levels might be expected, reflecting the differing transport histories of specimens from different areas; this is not seen in our data. As the abrasion score of most elements is low, this further implies that the assemblage has undergone relatively little reworking and that the environment of deposition—brackish estuary formed during transgression—was probably the environment in which the fishes were living. Although the rare tetrapod remains show similar abrasion scores to the fish material, the dataset is very limited, and it remains an open question as to whether these terrestrial-based animals were living in and around the estuary (Laurin and Soler-Gijón, 2010), or whether their remains were reworked from the seasonally dry Vertisol into which the channel is incised.

STRONTIUM ISOTOPE ANALYSES

To further test the hypothesis that the fishes were residents of the brackish estuary, we conducted 87Sr/86Sr analysis of skeletal remains to determine habitat paleosalinity (Schmitz et al., 1991). We did not perform similar tests on the tetrapods because the 87Sr/86Sr ratio of their skeletal remains would be related to diet rather than paleoenvironment.

The 87Sr/86Sr paleosalinity technique relies on the difference between the 87Sr/86Sr isotopic composition of seawater and river water. The 87Sr/86Sr isotopic ratio of modern riverine environments is highly variable, controlled by the bedrock geology of the drainage area (Schmitz et al., 1991); water passing through old, Rb rich granitic rocks and siliciclastic sedimentary deposits will have a much higher ratio than water passing through calcareous or young basaltic strata (Schmitz et al., 1991). In contrast, the Sr isotopic composition of open oceans is globally uniform at any given time, determined by the relative contribution of oceanic and terrestrial sources (Denison et al., 1993). The slow changes in oceanic Sr composition that have occurred during the Phanerozoic are well constrained (Prokoph et al., 2008). Thus, fossils recording Sr isotopic ratios that are anomalous with respect to contemporaneous oceanic values must logically be from environments with some level of freshwater input (Dasch and Campbell, 1970).
Cleaning, the samples were dissolved in 3 ml 7N HNO₃ ultrasonicated for 3 minutes; this cycle was repeated twice more. After Samples were first cleaned with ultrapure (Milli-Q) water, then possibility that samples have been reequilibrated by groundwater. significance of our measurements because we cannot exclude the case—so bulk samples were submitted for analysis. This weakens the conclusion; isotopic analysis of dentine and enameloid from individual teeth gave conflicting results, and when these signatures were used for radiometric dating only the enameloid gave biostratigraphically consistent results.

There are a number of uncertainties with the application of the fish paleosalinity technique, however. Schmitz et al. (1991) noted that postdepositional isotopic exchange might cause ⁸⁷Sr/⁸⁶Sr ratios of fossil material to reequilibrate with pore waters. Later, Schmitz et al. (1997) confirmed that apatite and dentine are indeed subject to reequilibration, but also showed that more inert substances such as tooth enamel are much more resistant to this process. Further work by Becker et al. (2008) on the teeth of Upper Cretaceous sharks supported this conclusion: isotopic analysis of dentine and enameloid from individual teeth gave conflicting results, and when these signatures were used for radiometric dating only the enameloid gave biostratigraphically consistent results.

Methods

We analyzed five shark samples for ⁸⁷Sr/⁸⁶Sr composition as follows: *Orthacanthus* (n = 1), *Xenacanthus* (n = 2) and elasmobranch scales (n = 2). There was insufficient material to separate enameloid from dentine and apatite—*Orthacanthus* does not possess enameloid in any case—so bulk samples were submitted for analysis. This weakens the significance of our measurements because we cannot exclude the possibility that samples have been reequilibrated by groundwater. Samples were first cleaned with ultrapure (Milli-Q) water, then ultrasonicated for 3 minutes; this cycle was repeated twice more. After cleaning, the samples were dissolved in 3 ml 7N HNO₃, dried, and redissolved in 2 ml 3N HNO₃. This solution was ultrasonicated for 15 minutes, then transferred to a centrifuge for 5 minutes. An aliquot of the solution representing 3 mg of solid was removed, and made up to 0.5 ml using 3N HNO₃. Separation of Sr was achieved with standard ion exchange chromatography using 70 µl of Eichrom Sr specific resin (50–100 µm). The Sr was eluted with 1.5 ml of Milli-Q water. The eluant was dried, and loaded into the ion exchange column using a few µl of 10% HNO₃, onto a single rhenium filament preconditioned with 1µl TaCl₅ solution and 1µl 10% H₃PO₄. The isotopic analysis was conducted with a Thermo Finnigan Triton Ionization Mass Spectrometer. Values were corrected to 0.710248 for the NBS 987 standard. Reproducibility did not exceed 0.000013.

Results

All five samples yielded nearly identical ⁸⁷Sr/⁸⁶Sr ratios in the narrow range from 0.71027 to 0.71033.

Interpretation

The ⁸⁷Sr/⁸⁶Sr ratios are substantially higher than Late Pennsylvanian (Kasimovian) marine values, which are in the range of 0.7080–0.7085 (Veizer et al., 1999; Prokoph et al., 2008). They are lower than those seen in rivers draining granitic cratons such as the Laurentian craton (0.725–0.740), however, that formed the Pennsylvanian hinterland for the Illinois Basin (Aberg and Wickman, 1987). Nonetheless, given that the Sr content of marine water is typically around 100 times greater than that of freshwater, the ⁸⁷Sr/⁸⁶Sr ratios obtained for our samples imply a strong freshwater influence (Schmitz et al., 1991), assuming that they have not reequilibrated.

One important caveat to this interpretation is that the Illinois Basin comprised part of a large, epeiric sea that was poorly mixed and dysaerobic (Heckel, 2008). In such analogous present-day environments as the Baltic Sea where salinity is near marine to brackish, ⁸⁷Sr/⁸⁶Sr ratios are also dominated by freshwater sources. Ratios rise from 0.7092 at the near marine (35.29‰ salinity) end of the system to 0.7097 at the near freshwater end (2.46‰ salinity), and attain values comparable to our specimens within brackish estuaries (Andersson et al., 1992, 1994). Thus, the ratios we have obtained for the xenacanth sharks are more supportive of a brackish salinity rather than freshwater.

FISH SALINITY TOLERANCE INFERRED FROM FACIES

Further verification that the fishes were residents of brackish habitats comes from a critical analysis of their facies context and co-occurring invertebrate assemblages.

Xenacanth Sharks

Although xenacanths have been traditionally considered to be freshwater sharks (Zangerl, 1981; Masson and Rust, 1984; Gray, 1988), recent studies have questioned this interpretation (Calder, 1998; Soler-Gijón, 1999; Schultzze and Soler-Gijón, 2004; Schultzze, 2009). The concept of freshwater xenacanths seems to have arisen from their association with Pennsylvanian plant-bearing Coal Measures (Hampe, 2003), especially in basins lacking such stenohaline fauna as Saar-Nahe, Germany (Boy, 1998) and Joggins, Nova Scotia (Calder, 1998). New data, however, indicate that shark-bearing facies at Joggins were brackish, based on trace fossil assemblages and foraminifera (Archer et al., 1995), or even near-stenohaline based on the co-occurrence of the bivalve, *Curvirimula* (Calver, 1968; Falcon-Lang, 2005; Falcon-Lang et al., 2006), and the recent report of brachiopods and echinoids (Grey et al., 2011), while marine bands with glauconite have now been recognized in shark-bearing units in the Saar-Nahe basin (Krätzschmer and Forst, 2005; Schultzze, 2009).

In addition, many reports have shown that xenacanths are intimately associated with brackish and marine fauna (e.g., Bardack, 1979; Schultzze, 1985, 1995; Thayer, 1985; Calder, 1998; Soler-Gijón, 1999; Schultzze and Soler-Gijón, 2004). For example, 75% of *Xenacanthus* and 35% of *Orthacanthus*—two taxa that we report...
from Friendsville, Illinois—occur in facies association with stenohaline marine invertebrates according to data compilations (Schultze and Chorn, 1997). Further, investigations of growth increments in specimens of *Orthacanthus* from Spain suggest that this shark lived in a coastal environment subject to tidal cyclicity (Soler-Gijón, 1999), which is consistent with brackish to stenohaline salinity, though not indicative.

Thus, the interpretation that best fits these data is that xenacanths were euryhaline, capable of living in marine, brackish, and perhaps, freshwater environments. Ironically, given the former dominance of the freshwater xenacanth concept, the weakest support is for unequivocally freshwater habitats, in part, because it is difficult to positively identify such settings in the geological record (Grey, 1988). Euryhaline capability would explain the cosmopolitan distribution of certain xenacanth groups (Hampe and Ivanov, 2007), and the close similarities that exist between some geographically distant species, e.g., *Orthacanthus compressus* and *O. bohemicus* (Johnson, 1999). If xenacanths were exclusively freshwater taxa, one would expect to see a high degree of endemism—and this is not the case.

In his review, Hampe (2003) showed that most xenacanth taxa (e.g., *Anodontacanthus-Dicentrodus, Triodus* and half of *Orthacanthus and Xenacanthus* species) disappeared from the British Coal Measures during the Bolsovian substage. This stratigraphic level, which coincides with the last stenohaline marine incursion in the British Pennsylvanian (Waters and Davies, 2006), also witnessed the local extirpation of such near-stenohaline bivalves as *Curvirimula* (Calver, 1968). This implies that these xenacanth species were tolerant only of waters of near-stenohaline salinity. The only taxon that diversified after the Bolsovian was *Orthacanthus*, suggesting that it tolerated salinities closer to the freshwater end of the spectrum. This tolerance for fresh- to brackish water is supported, to a limited degree, by the facies context of various *Orthacanthus* species in North America and Europe (Hanson, 1986; Sander, 1989; Johnson, 1999), for example, *O. platypterus* is associated with both marine facies (Olson, 1989) and presumably fresh to brackish alluvial channel deposits (Johnson, 1999) in the Permian of Texas.

**Euselachian Sharks**

The salinity tolerance of *Sphenacanthus*, the only euselachian shark found in our vertebrate assemblage, is less well documented. Dick (1998) described specimens from the Mississippian Oil Shales of the Midland Valley of Scotland, and interpreted the habitat as freshwater or brackish. Subsequent research on the invertebrate fauna and oxygen isotopes, however, has shown that this unit was deposited under brackish to near-stenohaline conditions, at least in part (Guirdham et al., 2003; Williams et al., 2006). Very similar Mississippian oil shale facies in the Horton Group of Nova Scotia and New Brunswick, which also contains euselachian sharks (Calder, 1998), are now considered brackish water deposits (Tibert and Scott, 1999; Rygel et al., 2006). Thus, the likelihood is that these euselachians were euryhaline sharks, though generally preferring lower levels of salinity than xenacanths (Maisey, 1982).

**Elasmobranch Salinity Tolerance**

Today, there are only 43 species of elasmobranchs in ten genera and four families that have a reported tolerance to brackish and freshwater (5% of all elasmobranch species; Helfman et al., 1997), and only a proportion of these are permanent residents of freshwater and brackish water environments (Martin, 2005). This compares to 41% of teleost fishes that have an exclusively freshwater mode of life. The osmoregulatory strategy employed by elasmobranchs is cited as the main barrier that has prevented their more extensive invasion of freshwater and brackish water environments (Ballantyne and Robinson, 2010). In contrast to teleosts, elasmobranchs maintain their osmotic status at a hyposmotic level relative to seawater through urea retention, and this is linked to protein function. Thus, when they encounter freshwater, they must synthesize urea to counteract water absorption.

Ballantyne and Robinson (2010) identify three hypothetical stages in the colonization of freshwater and brackish water environments by elasmobranchs: (1) euryhaline forms that periodically entered brackish to freshwater settings, (2) permanent freshwater and brackish water forms that retained the capability to live in marine settings, and (3) obligate freshwater forms. This transition involves, first, the reduction, and then, the elimination of the urea retention osmoregulatory strategy. All the evidence suggests that Paleozoic xenacanth and euselachian sharks were euryhaline forms (Stage 1); certain species of *Orthacanthus* may have been permanent brackish water residents (Stage 2), though if they were, they clearly inhabited the tidal zone (Soler-Gijón, 1999).

**Other Fishes**

The other fishes in the Friendsville assemblage are generally not known in sufficient systematic detail to allow for analysis of salinity tolerance. Possible exceptions are rare chimaeroid fishes that include helodontids and other indeterminate holocephalans. Holocephalans have traditionally been considered a strictly marine group (Moy-Thomas and Miles, 1971). Helodontids were durophagous bottom dwellers, and upper Paleozoic examples are known from shallow marine deposits (Falcon-Lang, 1998; Trinajstic and George, 2009), including an occurrence in crinoidal limestone in the Lower Missourian Bond Formation of Illinois (Brusatte, 2007), of very similar age and paleogeographic context to our material.

**PALEOECOLOGICAL SYNTHESIS**

Drawing together all these data from systematics, taphonomy, $^{87}$Sr/$^{86}$Sr ratios, and critical literature review, building an understanding of the paleoenvironments and paleoecology of the Friendsville vertebrate assemblage is possible.

**Paleoenvironments**

Sedimentary facies analysis reveals that the incised channel, which contains the vertebrate assemblage, and its associated interfluve Vertisol originated during a glacial lowstand when the tropics were seasonally dry and sea level was low. The incised channel was infilled during subsequent deglaciation when sea level rose and the channel flooded, forming a broad estuary (cf. Falcon-Lang et al., 2009). The vertebrate assemblage contained in the channel is possibly of mixed taphonomic origin with some components derived from seasonally dry, terrestrial settings (reworked from the lowstand Vertisol) and others from brackish coastal waters (transgressive shores containing brackish spirorbids). The fishes almost certainly inhabited the brackish estuary during transgression, based on literature review, abrasion data, and $^{87}$Sr/$^{86}$Sr ratios. What is less certain is whether the tetrapods also lived in, and around, the estuary or whether their remains have been reworked from the lowstand Vertisol. Consequently we show palco-saurs on both lowstand and transgressive reconstructions (Fig. 12).

**Community Ecology**

Although sharks and actinopterygian fish dominate our assemblage (97.0% of specimens), with rare chimaeroids and tetrapsods, it is unlikely that this taphocoenosis accurately reflects original community composition, as a result of taphonomic bias (Korth, 1979; Maas, 1985). In addition, there may be collector bias (250 μm sieve size), resulting in undersampling of smaller members of the fish community—e.g., small
actinopterygians and acanthodians, which may not have been identified because of the minute size of their teeth and scales. Thus, Friendsville assemblage cannot be demonstrated to be an accurate sample of a single original ecosystem. This means that detailed community reconstruction, comparison with other assemblages, and application of quantitative paleoecological measures—e.g., Margalef diversity, x diversity, dominance, relative abundance—are not meaningful for our assemblage (Eberth, 1990; Schulze, 1995; Baird and Maples, 1997). To directly compare the quantitative composition of our assemblage with other localities would require a taphonomic investigation of each site to evaluate the degree of isotaphonomy (Blob and Fiorillo, 1997; Moore and Norman, 2009) and our fragmentary material is not amenable to such an assessment. Nonetheless, at a qualitative level, the faunal assemblage from Friendsville, when compared with those of ten other contemporary Pennsylvanian sites (Kinney Brick Company Quarry, New Mexico; Hamilton Quarry, Kansas; Robinson, Kansas; Garnett, Kansas; Essex, Illinois; Braidwood, Illinois; Linton, Ohio; Montceau-les-Mines, France; Nyhany, Czech Republic; Lawrence, Kansas; summarized in Schulze and Maples, 1992; Robb, 1992) shares most similarities with the Upper Pennsylvanian Hamilton Quarry Lagerstätte, Kansas, United States, which also contains many xenacanth and euselachian sharks, actinopterygian fishes, and rare tetrapods (Schultze et al., 1993) and comprises a similar geological setting—an incised paleovalley drowned by eustatic sea-level rise during deglaciation (Cunningham et al., 1993).

Food Webs

Within the limits imposed by taphonomy, the Friendsville Coal food web can be roughly reconstructed (Fig. 13). The actinopterygians would have mostly fed on such invertebrate prey as arthropods and molluscs, and some perhaps on water plants. The mid-(Triodus) to large-sized (e.g., Orthacanthus, Xenacanthus) sharks, ≤1–2 m long, would have likely fed on such smaller fishes as the actinopterygians (Williams, 1972; Hampe, 1988). Olson (1971) suggested that, in addition to fishes, Orthacanthus might have preyed opportunistically on amphibians and reptiles that came down to drink at the water's edge. Further, the dramatic discovery of a three-step trophic chain, a lower Pennsylvanian xenacanth shark, containing in its stomach two temnospondyl amphibians, one of which had devoured an acanthodian fish (Kriwet et al., 2008), confirms that these sharks had catholic tastes. These predatory fishes, however, did not eat exclusively pelagic prey: coprolites and gut contents of fully marine upper Paleozoic holoccephalans, sharks, and other fishes also contain fragmented brachiopods and crinoid ossicles (Brett and Walker, 2002), and there is no reason to think that shallow marine fishes of these kinds would not also have dined on benthic organisms as part of their diet. The holoccephalan Helodus, with broad tooth plates, is widely regarded as a shell crusher (Brett and Walker, 2002).

The rare tetrapods from Friendsville, including, or exclusively, such sphenacodontid pelycosaurs (amniotes) as Haptodus or Dimetrodon, were fully terrestrial animals (e.g., Olson, 1952, 1971; Olson and Vaughn, 1970). Early amniotes, in general, were dryland adapted as implied by footprint records in red beds (Falcon-Lang et al., 2007, 2010). Further, the origin of amniotes is associated with a break from dependence on the water for egg-laying, and phylogenetic reconstructions of ancestral states suggest low osmotic tolerance, and so dryland and freshwater adaptation, at the base of the clade (Garland et al., 1997). This is consistent with the facies distribution of basal synapsid eupelycosaurs and sphenacodontids, which are interpreted largely as terrestrial red bed deposits, both in the Pennsylvanian and lower Permian of North America and Europe (Reisz, 1986). These inferences lend some support to the hypothesis that our tetrapods may have been reworked from the lowstand Vertisol and inhabited the seasonal drylands that developed during glacial maxima (Falcon-Lang et al., 2009).

Evolutionary Context of Pelycosaurs

Importantly, the finding of likely pelycosaur remains at Friendsville coincides with a dramatic upheaval in continental ecosystems. Olson (1952, 1971) long identified a multistep process of full terrestrialization of Permian–Carboniferous tetrapod ecosystems, with the increasing significance of amniotes (reptiles) as climates and floras became ever more dryland adapted. The first step occurred in the early Kasimovian, toward the end of the Pennsylvanian, when sphenacodontids became relatively abundant, and further steps toward modern-style terrestrial ecosystems happened in the early Permian. This important series of events has now been tied firmly to the rapid disappearance of the luxuriant Coal Forests of the Pennsylvanian (Sahney et al., 2010), and places the Friendsville deposit at a critical time in ecosystem evolution.
CONCLUSIONS

1. A new vertebrate assemblage is reported from the Upper Pennsylvanian (mid- to upper Kasimovian) Cohn Coal Member of the Mattoon Formation of Illinois, United States.

2. The assemblage occurs within a conglomerate-filled channel, incised into a lowstand vertic paleosol. The paleosol and channel was formed during a glacial phase, but the vertebrate assemblage occurs in a transgressive fill, interpreted as a ravinement deposit, formed as deglaciation-driven, sea-level rise created a broad estuary.

3. Xenacanth and euselachian sharks overwhelmingly dominate our vertebrate assemblage (73.5%), which also includes common actinopterygian (23.5%) and rare chimaeroids and tetrapods, especially pelycosaurs (together totalling only 1.6%).

4. Taphonomic and isotopic data, combined with a critical literature, suggest that the fish-dominated assemblage occupied brackish water habitats in the estuary. The presumed ecological tolerance of rare pelycosaurs, however, implies that these specimens may have inhabited seasonal drylands represented by the lowstand paleosol.

5. The findings improve knowledge of the paleoecology of Pennsylvanian vertebrate ecosystems during an evolutionary phase and illustrate the importance of precise facies context for paleoecological studies.

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FIGURE 13—Paleoecological reconstruction of the incised channel during transgressive phase when it was flooded with brackish water (modified from Falcon-Lang et al., 2006). Key to flora and fauna: 1 = Macroneuropteris tree with mangrove habit; 2 = Cordaitalean tree with mangrove habit; 3 = calamites; 4 = herbaceous lycopsids; 5 = spirorbids encrusting living and dead plant matter; 6 = bivalve shoals; 7 = euselachian shark; 8 = palaeoniscid fish; 9 = Dimetrodon-like reptiles. The relative abundance of taxa cannot be determined for our fragmentary assemblage; the intention of the reconstruction is to illustrate the general setting rather than capture details of the community ecology.
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