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Facies distribution and taphonomy of echinoids from the Fort Payne Formation (late Osagean, early Viséan, Mississippian) of Kentucky

Jeffrey R. Thompson[1] and William I. Ausich[2]

[1]Department of Earth Science, Zumberge Hall of Science, University of Southern California, 3651 Trousdale Parkway, Los Angeles, California 90089, USA ⟨thompsjr@usc.edu⟩
[2]School of Earth Sciences, 125 South Oval Mall, The Ohio State University, Columbus, Ohio 43210, USA ⟨ausich.1@osu.edu⟩

Abstract.—Paleozoic echinoids are exceptionally rare, and little is known of their paleoenvironmental distribution. The echinoid fauna of the Fort Payne Formation (Late Osagean, Early Viséan) of south-central Kentucky is documented. Four genera, ?*Archaeocidaris*, *Lepidocidaris,* ?*Lepidesthes*, and an unidentified lepidocentrid, were recovered and represent three different families. This fauna, and their associated paleoenvironments, give important new insights into the facies distribution of Paleozoic echinoids and the taphonomic biases that affect this distribution. *Lepidocidaris* is known from the green shale facies, which comprises the core of Fort Payne's carbonate buildups. ?*Archaeocidaris* and the lepidocentrid are known from the wackestone buildups and crinoidal packstone buildups. ?*Lepidesthes* is also known from crinoidal packstone and wackestone buildups, which argues against a semi-infaunal life mode for this taxon. All relatively semiarticulated echinoids were known from autochthonous facies, whereas the only echinoids from the allochthonous facies were disarticulated hemipyramids. Furthermore, deeper-water carbonate buildups were apparently capable of supporting diverse echinoid faunas during the Viséan.

Introduction

Although their fossil record extends back to the Late Ordovician (Smith and Savill, 2001), Paleozoic echinoids are rarely preserved. Because Paleozoic echinoids presumably lack the stereomic interlocking present in many post-Paleozoic echinoids (Smith, 1980, 1984), they have a relatively low preservation potential and, if present, are commonly encountered as disarticulated bioclasts (Schneider, 2008). Echinoids reached their peak species richness during the Mississippian (Kier, 1965; Smith, 1984) and were likely important members of Late Paleozoic ecosystems (Schneider, 2008). Although Paleozoic echinoids were most diverse during the Mississippian, the relationship between the environments in which they lived and the echinoids themselves is understudied. Echinoids occur from a number of different paleoenvironmental settings in the Mississippian (e.g., Kier, 1958; Chestnut and Ettensohn, 1988; Mottequin et al., 2015), but the precise facies in which certain taxa occur has not been examined rigorously. Post-Paleozoic echinoids are known to display a high level of substrate specificity, with irregular echinoids preferentially inhabiting sandy and muddy substrates and regular echinoids inhabiting hard or rocky substrates (e.g., Kier and Grant, 1965; Greenstein, 1993; Nebelsick, 1996). In addition, the differential preservation potential of post-Paleozoic echinoid families is not only dependent on morphologic factors, such as degree of stereomic interlocking, but also on breadth of facies distribution (Nebelsick, 1996). It is unknown whether any of the echinoid families from the Paleozoic display substrate specialization similar to post-Paleozoic echinoids, and the effect of differing facies on Paleozoic echinoid taphonomy is also little known. The Fort Payne Formation is an ideal location in which to examine paleoenvironmental preferences among Paleozoic echinoids and to compare echinoid and crinoid taphonomy because a number of different paleoenvironments are recorded, representing both allochthonous and autochthonous facies (Ausich and Meyer, 1990; Meyer et al., 1995; Greb et al., 2008). Four genera representing three families were collected from the Fort Payne Formation: ?*Archaeocidaris*, *Lepidocidaris*, ?*Lepidesthes*, and an unidentified lepidocentrid. Their paleoenvironmental preference and the taphonomic overprint on their facies distribution in the Fort Payne Formation is discussed herein.

Facies and faunal assemblages from the Fort Payne Formation

The Fort Payne Formation of south-central Kentucky was deposited in an epicontinental basin during the early Viséan (late Osagean; Ausich and Meyer, 1990; Leslie et al., 1996; Greb et al., 2008; Krivicich et al., 2013). The Fort Payne Formation is a mixed siliciclastic-carbonate sequence that includes basinal to toe-of-slope facies. These facies were deposited along a clinoform that prograded westward filling the basin during the early Viséan (Ausich and Meyer, 1990; Khetani and Read, 2002; Krause and Meyer, 2004; Greb et al., 2008). The Fort Payne sequence comprises myriad facies, including both autochthonous and allochthonous facies (Pryor and Sable, 1974; Lewis and Potter, 1978; Ausich and Meyer, 1990). Autochthonous facies include fossiliferous green shales, wackestone buildups, and crinoid packstone buildups; allochthonous facies include the siltstone ‘background sedimentation,’ sheetlike packstones, and the Jabez Sandstone. A channelform packstone facies also exists. Whereas the fill of this latter facies was composed of allochthonous sediment, this facies supported a distinct, autochthonous fauna.

As demonstrated by Ausich and Meyer (1990), Meyer et al. (1995), and Greb et al. (2008), the autochthonous interpretation of the carbonate buildups are a function of the buildups being geographically and stratigraphically circumscribed carbonate accumulations deposited contemporaneously with turbidite facies and siltstone facies as the background sedimentation of the basin. Both buildup types have a core facies and flank beds. Maximum stratigraphic thickness of individual mounds exceeds 15 m, and the diameter of the areal extent of an individual mound may exceed 400 m laterally.

Both mound types were cored by fossiliferous green shale. A green shale core remained present through the entire existence of a crinoid packstone mound. Mature mounds had a core of interbedded green fossiliferous shale and packstones and large packstone flanking beds (Ausich and Meyer, 1990). By contrast, although wackestone buildups also originated above a fossiliferous green shale mound, once carbonate mud production began on a wackestone buildup, green shale deposition ceased. On very large wackestone buildups, packstone flank beds may be present. The Fort Payne Formation wackestone buildups share many characteristics with classical Waulsortian mounds (Meyer et al., 1995). Precise water depth is difficult to determine, but based on stratigraphic evidence, the Fort Payne basin floor was positioned within the lowest portion of storm wave base (Ausich and Meyer, 1990). Judging from the distribution of microendolithic borings, Hannon and Meyer (2014) interpreted the Fort Payne basin floor to have been largely below the photic zone.

The autochthonous nature of these facies is further demonstrated because each supported a statistically distinct crinoid and blastoid assemblage (Krivicich et al., 2014). Dominant camerates on wackestone buildups were *Agaricocrinus americanus* (Roemer, 1854 in Roemer, 1851–1856), *Thinocrinus* sp., and *Alloprosallocrinus conicus* Casseday and Lyon, 1862; whereas on packstone buildups, dominant camerates were *Eretmocrinus magnificus* Lyon and Casseday, 1859, *Actinocrinites gibsoni* (Miller and Gurley, 1893), and *Alloprosallocrinus conicus* (Krivicich et al., 2014). Each facies also had distinct assemblages of disparid crinoids and blastoids. The fossiliferous green shale was dominated by disparid and cyathocrine cladids, and the channels had abundant dendrocrine cladids and *Elegantocrinus hemisphaericus* (Meek and Worthen, 1865). Because of contrasting faunas, different facies have different taphonomic signatures (Meyer et al., 1989). Both of the carbonate buildups were dominated by camerate crinoids.

In areas well studied, the autochthonous facies and the channelform facies are geographically clustered (Fig. 1). This may be explained as follows: (1) the channelform facies represent submarine facies on the Fort Payne clinoform; (2) prior to fill of these canyons, carbonate buildups thrived near the mouth of canyons where food- and oxygen-rich waters were funneled into what was otherwise a largely dysaerobic basin; and (3) the channels were filled with sediment during the advancement of the Fort Payne clinoform, which also buried the carbonate buildups.

Distribution of Fort Payne echinoids

These echinoids were collected over the course of 27 years, from numerous research and class field trips spanning June of 1985 to October of 2012. Relatively few echinoids are known from the Fort Payne Formation, but all echinoids from autochthonous facies are preserved as a scattering of disarticulated plates in close proximity (Table 1). Most of these disarticulated specimens also contain associated hemipyramids. Lepidocentrid genus unknown, ?*Archaeocidaris* sp. and ?*Lepidesthes* sp. are all from the crinoidal packstone buildup facies. ?*Lepidesthes* is also present in the wackestone facies. Isolated, unidentifiable hemipyramids are known from both autochthonous and allochthonous facies (Table 1). With the exception of *Leipidocidaris* (USNM 609803), all echinoids associated with carbonate buildups were collected from the flank facies.

Systematic paleontology

Class Echinoidea Leske, 1778
Family Archaeocidaridae M’Coy, 1844
Genus *Archaeocidaris* M’Coy, 1844

Type species.—*Cidaris urii* Fleming, 1828, p. 478; by monotypy (Fell, 1966, p. U317); Mississippian of northwestern Europe.

Occurrence.—Mississippian–Permian of North America, South America, Russia, Europe, Australia, China.

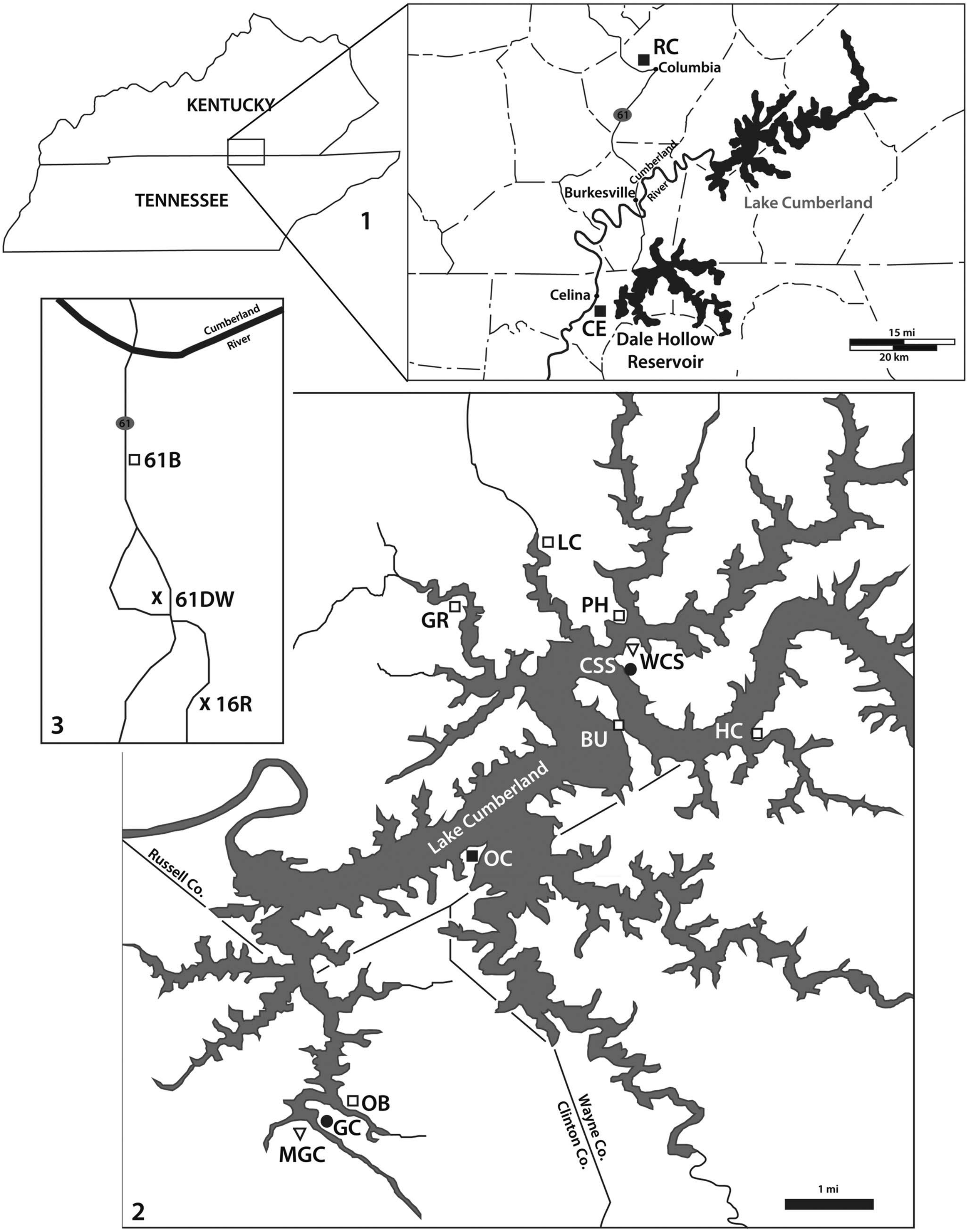
Remarks.—This is arguably the most abundant echinoid genus in the Paleozoic. For a thorough list of species excluding those based solely on disarticulated spines, see Lewis and Donovan (2005).

?*Archaeocidaris* sp.
Figure 2.1

Description.—Test disarticulated but likely small. Plating is imbricate. Apical system is not present. Peristome and perignathic girdle are unknown.

Width of interambulacral plates is 1.3 to 1.7 times their height (Table 2). Plates hexagonal to subhexagonal. Distinction

Figure 1. Location map illustrating occurrences of echinoids from the Fort Payne and distribution of autochthonous carbonate buildups in relation to locations of channelform facies exposed along shore of Lake Cumberland. (**1**) General location map; (**2**) Lake Cumberland localities; (**3**) localities along Kentucky Highway 61 south of Burkesville, Kentucky. Key: squares = carbonate wackestone buildups; circles = carbonate packstone buildups; inverted triangles = channelform facies; filled symbols = locality with known echinoid fossils; X = echinoid occurrences from allochthonous facies. CE = Celina Buildup; RC = Russell Creek Buildup; BU = Bugwood Buildup; CSS = Cave Springs South Buildup; GC = Gross Creek Buildup; GR = Greasy Creek Buildup; HC = Harmon Creek Buildup; LC = Lily Creek Buildup; MGC = Mouth of Gross Creek; OB = Owens Branch Buildup; OC = Otter Creek Buildup; PH = Pleasant Hill Buildup; WCS = Wolf Creek South; 61B = Highway 61 Buildup; 61DW = Highway 61 D West; 61R = Highway 61 Ramp. See Appendix for locality coordinates.


KENTUCKY
TENNESSEE
1
RC
Columbia
61
Cumberland River
Burkesville
Lake Cumberland
Celina
CE
Dale Hollow Reservoir
15 mi
20 km
Cumberland River
61
61B
X 61DW
X 16R
3
LC
GR
PH
CSS
WCS
BU
HC
Lake Cumberland
OC
Russell Co.
OB
GC
MGC
Wayne Co.
Clinton Co.
1 mi
2

between adambulacral and adradial plates unknown. Single row of scrobicular tubercles along edge of plates, but the details of this row are unclear.

Primary tubercle large, perforate, noncrenulate, located centrally on the plate (Fig. 2.1). Boss is about 0.4 to 0.5 times as high as plate and about 0.3 times as wide as plate. Basal terrace present, about 0.5 times as wide as plate and 0.7 times as high as plate. Mamelon not undercut and sunken area present between mamelon and raised parapet (Fig. 2.1). Radial plications absent and details of scrobicular tubercles unknown.

Primary spines all fragmentary, but the longest spine fragment is 20.2 mm long. Spines are circular in cross section; very finely striate; and, due to crushed nature of some spines, were likely hollow. Most proximal end of spines smooth, but numerous spinules present otherwise. Spinules projecting distally and appear to be present along all shaft.

Lantern disarticulated, but with some elements present. One hemipyramid is preserved, about 9.1 mm high. One rotula is also present and is about 6.7 mm high and 1.9 mm wide across the upper surface. It is slightly eroded, thus details are obscured. The condyles are present; however, they are slightly obscured by matrix.

Material.—USNM 609801.

Occurrence.—Cave Springs South, Lake Cumberland, Fort Payne Formation (Fig. 1 and Appendix).

Remarks.—Within the Archaeocidaridae, the genera *Archaeocidaris* and *Polytaxicidaris* have interambulacral plates that are morphologically similar. Because of this, as pointed out by Kier (1958, 1965), without intact interambulacral areas, it is unadvisable to confidently assign disarticulated archaeocidarid plates to *Archaeocidaris* as has been done consistently since the genus was erected. Therefore, the material herein described cannot be confidently assigned to *Archaeocidaris*, thus it is designated ?*Archaeocidaris* sp.

Genus *Lepidocidaris* Meek and Worthen, 1873

Type species.—?*Eocidaris squamosa* Meek and Worthen, 1869, p. 79; by original description and monotypy (Fell, 1966, p. U319) from the Tournaisian of Iowa.

Occurrence.—Tournaisian–Viséan of North America and the United Kingdom.

Lepidocidaris sp.
Figure 2.2

Description.—Test probably small. Plating likely imbricate. Peristome, perignathic girdle, and lantern unknown.

Details of interambulacral and interambulacral plating unknown, but disarticulated ambulacral and interambulacral plates are present. Ambulacral plate is about 2.0 mm wide and 1.2 mm tall. It is fairly thick and irregularly polygonal in outline (Fig. 2.2).

Interambulacral plates are about 0.8 times as wide as high (Table 2). Plate outlines are slightly obscured, thus plate shape is unclear. Scrobicular tubercles present on raised ridge surrounding tubercle.

Table 1. Locality and facies data for Fort Payne echinoids.

Specimen number	Taxon	Locality	Facies	Description	Lithology
USNM 609800	?*Lepidesthes*	Cave Springs South Buildup	Crinoidal Packstone Buildup	Disarticulated test with teeth and hemipyramids	Packstone
USNM 609801	?*Archaeocidaris*	Cave Springs South Buildup	Crinoidal Packstone Buildup	Disarticulated test with spines and hemipyramids	Wackestone
USNM 609802	Unidentified hemipyramids and disarticulated plates	Cave Springs South Buildup	Crinoidal Packstone Buildup	Lantern complete with disarticulated plates	Wackestone
USNM 609803	*Lepidocidaris*	Cave Springs South green shale facies	Crinoidal Packstone Buildup	Disarticulated plates and spines	Green shale
USNM 609804	Lepidocentrid genus unknown	Gross Creek Buildup	Crinoidal Packstone Buildup	Disarticulated test with hemipyramids	Packstone
USNM 609805	?*Lepidesthes*	Russell Creek Buildup	Wackestone Buildup	Disarticulated test with hemipyramids	Calcareous siltstone or silty limestone
USNM 609806	?*Lepidesthes*	Otter Creek	Wackestone Buildup	Disarticulated lantern with few scattered plates	Wackestone
USNM 609807	Unidentified hemipyramids	Salina Buildup	Wackestone Buildup	Disarticulated hemipyramids	NA
USNM 609808	Unidentified hemipyramid	61 D West low middle	Shale interbedded with sheetlike packstones	Disarticulated hemipyramid	NA
USNM 609809	Unidentified hemipyramid	61 D ramp	Green shale	Disarticulated hemipyramid	NA

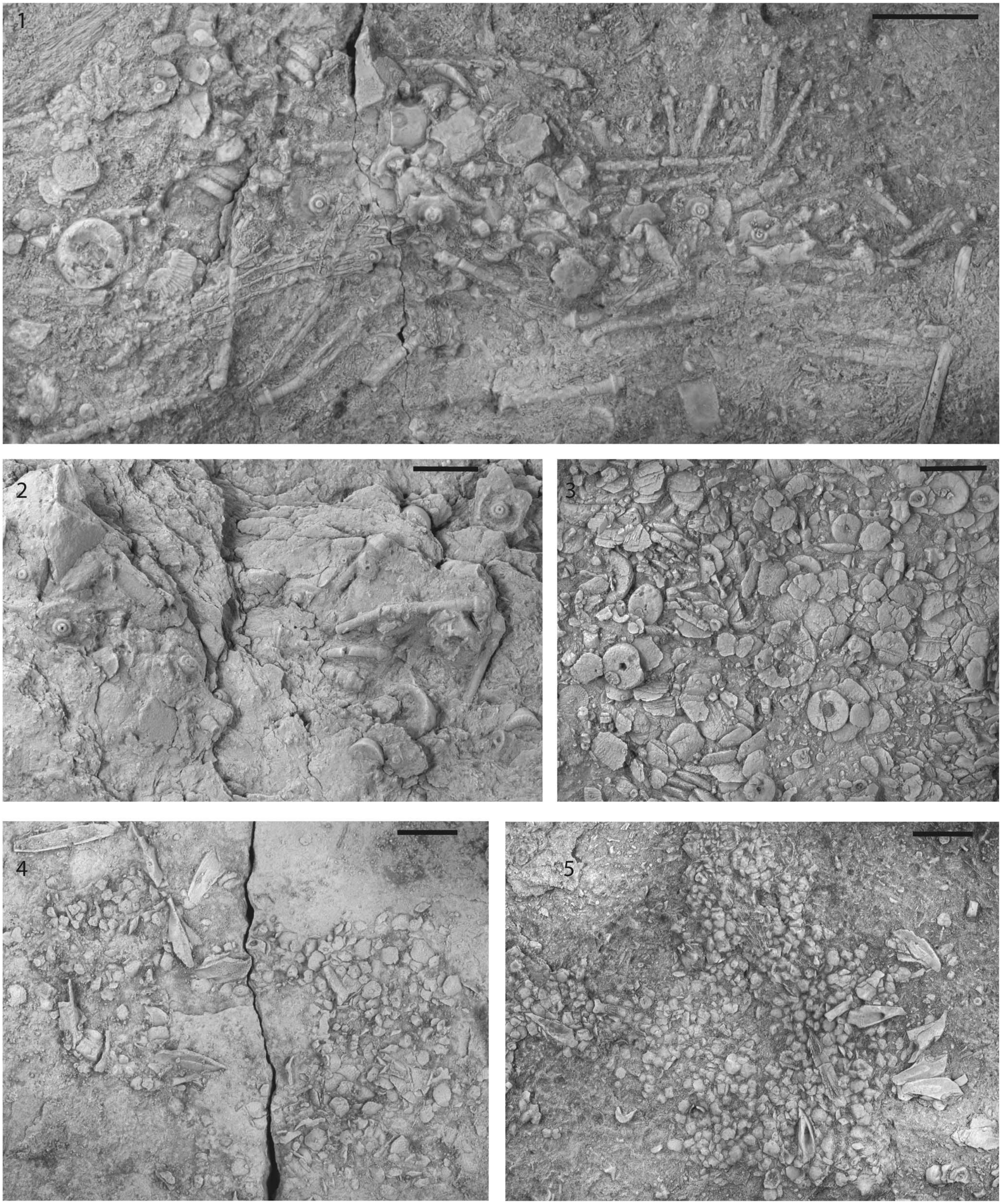


Figure 2. Archaeocidarids, lepidesthids, and lepodocentrids from the Fort Payne Formation. (**1**) ?*Archaeocidaris* specimen USNM 609801. (**2**) *Lepidocidaris* specimen USNM 609803. (**3**) Lepidocentrid specimen USNM 609804. (**4**) ?*Lepidesthes* specimen USNM 609805. (**5**) ?*Lepidesthes* specimen USNM 609800. (**1, 3–5**) Scale bars = 10 mm; (**2**) scale bar = 5 mm.

Primary tubercle large, perforate, noncrenulate. Boss is about 0.3 times as wide as plate and 0.2 times as high as plate. Tubercle sunken, and it is unclear whether a basal terrace is present. Radial plications absent. Scrobicular tubercles are imperforate and irregularly distributed along plate margin (Fig. 2.2).

Table 2. Measurements of Fort Payne echinoids.

	?Archaeocidaris sp.			*?Lepidesthes* sp.	
Measure parameter	Plate 1	Plate 2	*Lepidocidaris* sp.	Plate 1	Plate 2
Interamb width (mm)	5.07	5.85	4.59	2.57	1.95
Interamb height (mm)	3.66	3.43	5.47	2.49	1.83
Ratio of width to height	1.39	1.71	0.84	1.03	1.07
Boss width (mm)	1.7	1.65	1.32	—	—
Boss height (mm)	1.45	1.44	1.2	—	—
Basal terrace width (mm)	3.2	2.92	?	—	—
Basal terrace height (mm)	?	2.3	?	—	—

Primary spines elongate, coarsely striate (Fig. 2.2). Longest spine is 12.6 mm in length. Milled ring present and spine striate for entire length.

Material.—USNM 609803.

Occurrence.—Cave Springs South, Lake Cumberland, Fort Payne Formation (Fig. 1 and Appendix).

Remarks.—*Lepidocidaris* is recognized for its distinctive tubercle morphology with high plates and sunken tubercles. In addition, the smooth, striate spines of this taxon are similar to those of the other known species, *Lepidociaris squamosa* (Meek and Worthen, 1873). This specimen is too disarticulated and incomplete to confidently assign to a known or new species of *Lepidocidaris*; thus, it is designated as *Lepidocidaris* sp. *Lepidocidaris squamosa* is known from the Lower Burlington Limestone of Iowa (Meek and Worthen, 1869); the subspecies *Lepidocidaris squamosa anglica* Hawkins, 1935 is known from the Tournaisian and Viséan of the United Kingdom (Hawkins, 1935; Donovan et al., 2003, Donovan et al., 2014). This is the first occurrence of *Lepidocidaris* from the Viséan of North America, which indicates that the range of the genus is Tournaisian to Viséan in both North America and Europe. *Lepidocidaris squamosa anglica* is subdivided from *Lepidocidaris squamosa* because of the slenderness of its spines and its occurrence in the United Kingdom as opposed to North America. Jackson (1912) adequately described and figured complete spines of *Lepidocidaris squamosa* from North America, and they also appear slender. Thus, the validity of the subspecies *Lepidocidaris squamosa anglica* based strictly on morphological differences is questionable; however, taxonomic revision is beyond the scope of this project.

Family Lepidocentridae Lovén, 1874
Lepidocentrid indet.
Figures 2.3, 3.4

Description.—Test presumably large. Plating imbricate. Peristome and perignathic girdle unknown due to disarticulation. Ambulacral plates 4 to 6 mm wide, with flange. Interambulacral plates variably polygonal, flat, thin; up to 8 mm wide. Plates about 1 mm thick. No primary tubercles are present on ambulacral plates, and most plates are too eroded to clearly preserve secondary tubercles; however, some may be present on a few plates (Fig. 2.3).

Disarticulated lantern elements are present (Fig. 3.4). Hemipyramids about 16 mm tall. Tooth coming to distal point with three distinct serrations.

Material.—USNM 609804.

Occurrence.—Gross Creek, Lake Cumberland, Fort Payne Formation (Fig. 1 and Appendix).

Remarks.—This specimen is assigned to the Lepidocentridae because of its thin interambulacral plating and lack of distinct primary tubercles. Palaechinids also lack primary tubercles; however, they have thick plates that are tessellate and are not similar to the thin, presumably overlapping, plates present here. The state of preservation of this specimen is not good enough to allow for assignment at the generic level; thus, it is left unidentified. The size of the plates does allow for comparison with other lepidocentrid taxa. Judging from the size of the plates, this taxon may be similar to *Pholidechinus brauni* Jackson, 1912 from the Tournaisian Edwardsville Formation of Crawfordsville, Indiana, or *Elliptechinus kiwiaster* Schneider, Sprinkle, and Ryder, 2005 from the Pennsylvanian Winchell Formation of Central Texas. These taxa display distinct minute secondary tubercles, which appear similar to those present on a few of the better-preserved plates of this specimen (Fig. 2.3). The taxon described herein is not well enough preserved, however, to determine whether similar tubercles were present on all interambulacral plates.

Family Lepidesthidae Jackson, 1896
Lepidesthes Meek and Worthen, 1868

Type species.—*Lepidesthes coreyi* Meek and Worthen, 1868, p. 522; by original designation.

Occurrence.—Mississippian–Pennsylvanian of North America; Mississippian of Morocco, England; ?Pennsylvanian of Russia.

Remarks.—This genus consists of numerous species and has a wide geographic and temporal distribution. Species included in the genus are *L. wortheni* Jackson, 1896, *L. colletti* White, 1878, *L. carinata* Jackson, 1912, *L. alta* Kier, 1958, *L. grandis* Kier, 1958, *L. formosa* Miller, 1879, *L. extremis* Jackson, 1912, *L. howsei* Jackson, 1926, *L. caledonica* Jackson, 1912, and *L. laevis* Trautschold, 1879.

?*Lepidesthes* sp.
Figures 2.4, 2.5, 3.1–3.3

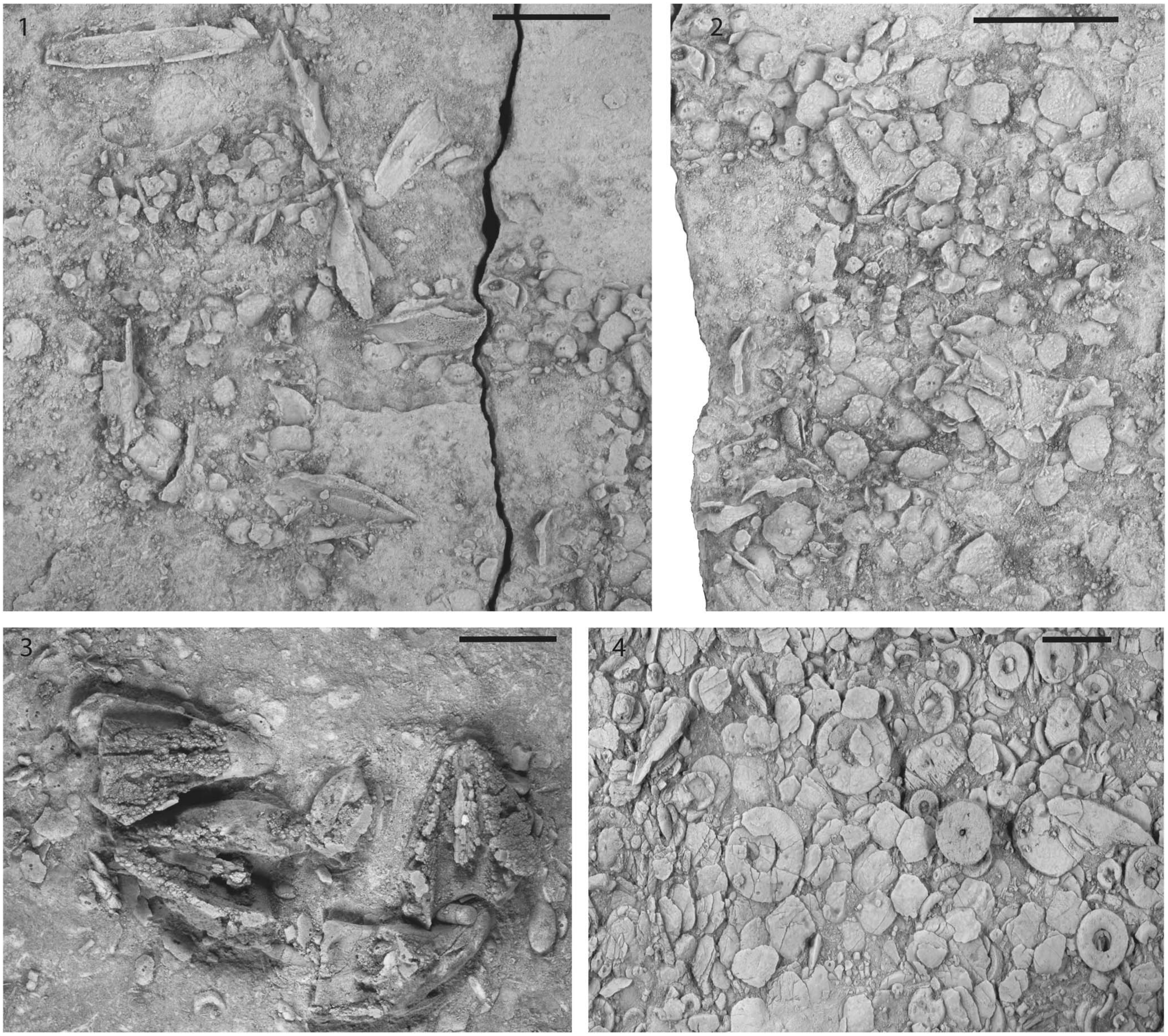


Figure 3. Lepidesthid and lepidocentrid specimens. (**1**) Close-up of ?*Lepidesthes* specimen USNM 609805; note disarticulated lantern elements and teeth. (**2**) Close-up of ?*Lepidesthes* specimen USNM 609805; note interambulacral and ambulacral plates. (**3**) ?*Lepidesthes* specimen USNM 609806; note tightly associated lantern elements. (**4**) Close-up of lepidocentrid specimen USNM 609805. (**1, 2, 4**) Scale bars = 10 mm; (**3**) scale bar equals 5 mm.

Description.—Test small. Plating imbricate. Peristome and perignathic girdle unknown.

Although plating is unknown due to disarticulation of the test, there are far more ambulacral plates than interambulacral plates, which indicates that there are likely numerous columns of ambulacral plates (Fig. 2.4, 2.5).

Ambulacral plates small, wider than high. About 2.3 mm at their widest and 1.3 mm at their highest. Variably polygonal in shape. Each plate pierced by one pore pair with each pore about 0.2 mm apart (Figs. 2.4, 2.5, 3.1, 3.2).

Interambulacral plates are about as wide as high. Specific widths and heights of two plates are recorded in Table 2. They are, on average, larger than ambulacral plates. Faint, small, imperforate secondary tubercles are present on interambulacral plates (Fig 3.2).

Numerous lantern elements are preserved on all three specimens. Hemipyramids about 12.6 mm high. Hemipyramids on specimen USNM 609800 and USNM 609806 have clear indentation, and the foramen magnum on specimens is 0.2 times as shallow as hemipyramids are tall (Fig. 3.1, 3.3). In addition, a poorly preserved rotula is present on specimen USNM 609805 (Fig. 2.5), although the details of the rotula are not clear. All specimens also contain teeth, which come to a single point distally and do not appear to be serrated (Figs. 2.5, 3.1).

Material.—USNM 609800, USNM 609805, and USNM 609806.

Occurrence.—Cave Springs South and Otter Creek, Lake Cumberland; Russell Creek, Fort Payne Formation (Fig. 1 and Appendix).

Remarks.—*Lepidesthes* is widely known from the Carboniferous of North America. The specimens present, however, are in such a state of disarticulation that identification to the generic level is tenuous. Four species of *Lepidesthes, L. colletti, L. wortheni, L. coreyi*, and *L. carinata* are known from siliciclastic facies of the Edwardsville Formation of Montgomery County, Indiana. These strata are coeval with those of the Fort Payne Formation; however, the Edwardsville Formation represents a delta platform environment (Ausich et al., 1979) as opposed to the deeper basinal to toe-of-slope environments represented by the Fort Payne Formation (Ausich and Meyer, 1990). Thus, *Lepidesthes* species may have had a fairly wide environmental tolerance.

Discussion

Paleozoic echinoid taphonomy.—Fort Payne autochthonous facies are the sole environments to preserve semiarticulated, or associated, echinoid tests (Table 1). Furthermore, the only facies that preserve these echinoids are the two carbonate buildup facies. Paleozoic echinoids appear to have disarticulated rapidly after death, presumably due to the lack of stereomic interlocking between abutting coronal plates (Smith, 1980, 1984) and their imbricate test plating. Although all of the Paleozoic families present within this study are extinct, the best taphonomic analogs to Paleozoic echinoids are the basal euechinoids of the clades Echinothurioidea and Diadematoida and the cidaroids. These taxa have limited stereomic interlocking and, in the case of the echinothurioids and diadematoids, more flexible tests (Smith, 1980, 1984; Greenstein, 1991, 1993) than all other extant echinoids. Although no experimental taphonomic studies have been performed on the echinothurioids, the taphonomies of one diadematoid and one cidaroid are well understood (Greenstein, 1991, 1993). These two taxa display more stereomic interlocking than was presumably present in Paleozoic echinoids, especially Paleozoic taxa with imbricate plating. Thus, these are the best known, albeit less easily disarticulating, taphonomic analogues to Paleozoic echinoids. Taphonomically, these Mississippian echinoids also have a preservational potential comparable to dendrocrine cladid and flexible crinoids, which completely disarticulate relatively rapidly after death (Meyer et al., 1989). To be preserved articulated, dendrocrine crinoids and the Fort Payne echinoids needed to have been buried very rapidly, perhaps even buried when still alive. If a specimen lay on the sea floor for a short time, the specimen would disarticulate, and in this stage, any transportation would scatter the plates. Thus, the specimens of clustered plates with hemipyramids (Figs. 2.1, 2.4, 2.5, 3.1, 3.2, 3.4) were likely dead specimens whose tests had disarticulated but not been scattered. This is interpreted as parautochthonous preservation and is similar to that of cladid and flexible crinoids also preserved in the Fort Payne carbonate buildups. Both cidaroid and diadematoid echinoids are known to lose their Aristotle's lantern and apical system within seven days following death (Greenstein, 1991). Given the even higher rates of disarticulation of Paleozoic echinoids relative to the more derived diadematoids and cidaroids, the association of lantern elements with coronal plates in these specimens also supports the interpretation of rapid burial.

Judging from the specimens recovered for this study, it appears that all of the families represented in the Fort Payne Formation displayed similar likelihoods of preservation. Representatives of three families, archaeocidarids, lepidesthids, and lepidocentrids, are preserved as disarticulated and nondissociated coronal plates and associated lantern elements. The lantern elements are clearly associated with coronal plates in all specimens assignable at the familial level except for the specimen of *Lepidocidaris* sp. (USNM 609803); however, it is unclear in this specimen whether the lantern elements have been transported from the test or are obscured by rock matrix. Because the spines are still associated with the test, it is likely that the lantern elements have not been lost, as spines usually disarticulated prior to lantern disarticulation in numerous clades of echinoids (Kidwell and Baumiller, 1990; Greenstein, 1991; Allison, 1990). The archaeocidarids are all preserved with primary spines, further suggesting limited transport and rapid burial (Allison, 1990; Kidwell and Baumiller, 1990; Greenstein, 1991). Of interesting note is specimen USNM 609806 of ?*Lepidesthes* sp., which consists of four closely associated hemipyramids and some scattered coronal plates (Fig. 3.4). In this specimen, many of the coronal plates are scattered and appear to have been transported, leaving the lantern elements essentially where the organism began to disarticulate. It is highly unlikely that the lantern has simply 'dropped out' of the test through the peristome following decay of the peristomial membrane, as can be the case in many post-Paleozoic echinoids. This is because the lantern of lepidesthids is significantly smaller than the diameter of their peristome (Jackson, 1912, plate 68, fig. 3). Because of its differential preservation of corona and lantern, this specimen of ? *Lepidesthes* provides important insight into Paleozoic echinoid taphonomy and disarticulation. Whereas in modern echinoids, the lantern is known to disarticulate well before coronal plates (Kidwell and Baumiller, 1990; Greenstein, 1991), it appears that in some Paleozoic echinoids, specifically the lepidesthids, coronal plates may have disarticulated more rapidly relative to lantern disarticulation than in post-Paleozoic taxa. This rapid coronal disarticulation is almost certainly due to the lack of stereomic interlocking between coronal plates and could explain the presence of single, relatively articulated lanterns known from the Paleozoic echinoid fossil record (Jackson, 1912, plate 12, figs. 1–6, 1929, plate 1, figs. 1–3).

Although mass accumulations of echinoids are well known from the Cenozoic rock record (see Nebelsick and Kroh, 2002 and references therein for a thorough treatment of clypeasteroid mass accumulations), there are no such mass accumulations from the Fort Payne. This is likely due simply to the low abundance of echinoids in the Fort Payne Formation, whose dominant bioclasts are crinoidal in origin. Although mass accumulations comprising entire tests and spine beds are known from the Pennsylvanian of North America (e.g., Schneider et al., 2005; Schneider, 2008; Thompson et al., 2015), to date, no such mass accumulations have been identified in the Mississippian. Although Paleozoic echinoid diversity is highest in the Mississippian (Kier, 1965), it may be possible that echinoids were actually more abundant during the Pennsylvanian, as evidenced by their heightened occurrence in spine beds and mass accumulations. This hypothesis, however, requires further testing.

Autochthonous facies.—The autochthonous facies contain four genera from three families. The Cave Spring South Buildup preserves the most taxa, including *Lepidocidaris* sp., ?*Archaeocidaris,* and ?*Lepidesthes* sp. The specimen of

Lepidocidaris sp. was preserved in the interbedded green shale and packstone core of this packstone buildup, indicating a tolerance for siliciclastics. Given that other North American occurrences of *Lepidocidaris* are from the Lower Burlington Limestone (Meek and Worthen, 1869), this taxon, at least at the generic level, appears to inhabit both carbonate and siliciclastic substrates. The other archaeocidarid present, ?*Archaeocidaris* sp., occurs on crinoidal packstone buildup flank beds. Given the occurrence of *Archaeocidaris* and *Polytaxicidaris* in a variety of substrates (e.g. Kier, 1958, 1965; Schneider et al., 2005), it is not surprising that this taxon was present on the crinoidal packstone buildups. In addition, the lepidesthid specimens are known from the autochthonous crinoidal packstone buildup flank beds and wackestone buildups. Lepidesthids are abundant and diverse in the siliciclastic delta shelf environments of the Edwardsville Formation at Crawfordsville (Lane, 1973) and the soft-bottomed lagoonal environments of the Sloan's Valley Member of the Pennington Formation (Chestnut and Ettensohn, 1988). Their occurrence on the Fort Payne buildups indicates that in North America, they are not limited to soft-bottomed, primarily siliciclastic environments. Their occurrence on the Fort Payne buildups also argues against a semi-infaunal interpretation for their autecology, as suggested by Chestnut and Ettensohn (1988), because a semi-infaunal lifestyle would not have been likely on either the coarse-grained, poorly sorted substratum of flank beds or the firm, presumably microbially bound wackestone buildups.

As discussed in the preceding, a counterintuitive aspect of Fort Payne deposition is that carbonate buildups formed in a siliciclastic basin with siltstone background sediments. Carbonate buildups were eventually buried by the siltstone and sheetlike packstone facies. The siltstone facies is nearly devoid of fossils, with the primary indication of a faunal presence being trace fossils (Ausich and Meyer, 1990). The sheetlike packstones are interpreted to be from turbidite deposition (Ausich and Meyer, 1990; Greb et al., 2008), and their faunal content is a mixture of elements from the autochthonous faunas (Krivicich et al., 2014). The fact that Fort Payne echinoid preservation on carbonate buildups was parautochthonous and that these mounds were surrounded by a largely unfossiliferous siltstone facies supports the interpretation that the Fort Payne echinoids lived and were preserved on the carbonate buildups. Given that these echinoids were likely capable of living on firmer, more coarse-grained substrates, such as the flank beds of Fort Payne buildups, it indicates that echinoids had begun to inhabit coarse-grained environments by the Mississippian. Although the colonization of these coarse-grained environments may have corresponded with certain morphological innovations, there are no obvious morphological innovations associated with the colonization of the Fort Payne buildups. All the genera that inhabit the Fort Payne buildups are also known from fine-grained environments (Lane, 1973; Chestnut and Ettensohn, 1988; Mottequin et al., 2015) and, thus, were likely not restricted to specific substrates, at least on the genus level.

Echinoids are known from other mud-mound facies in the Mississippian. The Waulsortian mounds of Clitheroe, England (Miller and Grayson, 1972), supported a diverse echinoid fauna (Hawkins, 1935; Donovan et al., 2003), and echinoids are also known from the Waulsortian facies of Belgium (Jackson, 1929). These deposits were also interpreted to be from a relatively deepwater environment (Miller and Grayson, 1982; Lees, 1997), similar to the Fort Payne buildups. That echinoids were capable of inhabiting these deeper-water environments, likely below the photic zone (Hannon and Meyer, 2014), indicates that by the Viséan, numerous families of echinoids had successfully inhabited deeper-water environments. Evidence from the Fort Payne Formation and comparative evidence from the Mississippian of Europe indicate that carbonate mound-type facies were apparently capable of supporting diverse and abundant (relative to Paleozoic standards) echinoid faunas.

Allochthonous facies.—No articulated echinoids were found in the allochthonous facies (Table 1), and the only echinoid material recovered from these facies were disarticulated hemipyramids. This can be explained by both preservational biases and worker bias. Hemipyramids have been shown to be relatively robust to laboratory tumbling experiments, remaining fairly intact and recognizable even after 100 hours of tumbling (Greenstein, 1991). In addition, hemipyramids are relatively recognizable, even to nonechinoid workers, as echinoid fragments. Most of the scientific collecting done in the Fort Payne Formation over the course of the past 30 years has been carried out by crinoid workers. Whereas lantern elements and archaeocidarid interambulacral plates are easily recognizable as belonging to echinoids, many disarticulated coronal plates would be very difficult to distinguish from pelmatozoan thecal and arm plates in the crinoidal limestones that are prevalent in the Fort Payne and other Mississippian strata, which dominate the rocks in which they are found. Therefore, it is not surprising that only hemipyramids have been found in allochthonous facies as they are likely to be preserved and recognizable as echinoid fragments, even after extensive transport.

Conclusions

This is the first study to systematically describe the different facies inhabited by echinoids in the Paleozoic. The Fort Payne Formation yields a relatively diverse echinoid fauna, by Paleozoic standards, containing four genera representing three different families. ?*Archaeocidaris* sp., *Lepidocidaris* sp., ?*Lepidesthes* sp., and an unidentified lepidocentrid are known from the fauna, and all are known from the autochthonous facies. The results of this study indicate that echinoids in the Viséan of North America inhabited carbonate mound facies. Echinoids are also known to inhabit the carbonate Waulsortian mounds of Clitheroe, United Kingdom, and Belgium; and thus, carbonate mud mounds appear to have supported diverse echinoid faunas in the Mississippian of both North America and Europe. All relatively well-preserved echinoids were known from autochthonous facies, whereas only disarticulated lantern elements were recovered from allochthonous facies. This is likely due to taphonomic processes.

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Appendix. Locality information

Cave Springs South Buildup, on shores of Lake Cumberland; 36°56'22"N; 85°0'20"W; Jamestown 7.5' Quadrangle, Russell County, Kentucky.

Celina Wackestone Buildup; 36°32'43"N; 85°30'0"W; Columbia 7.5' Quadrangle, Clay County, Tennessee.

Gross Creek Buildup, on shores of Lake Cumberland; 36°47'27"N; 84°59'37"W; Cumberland City 7.5' Quadrangle, Clinton County, Kentucky.

Otter Creek Buildup, on Shores of Lake Cumberland; 36°51'39"N; 85°2'53"W; Cumberland City 7.5' Quadrangle, Russell County, Kentucky.

Russell Creek Buildup; 37°7'24"N; 85°17'56"W; Columbia 7.5' Quadrangle, Adair County, Kentucky.

Otter Creek Buildup, on Shores of Lake Cumberland; 36°51'39"N; 85°2'53"W; Cumberland City 7.5' Quadrangle, Russell County, Kentucky.

Celina Wackestone Buildup; 36°32'43"N; 85°30'0"W; Columbia 7.5' Quadrangle, Clay County, Tennessee.

61D-West along KY HWY 61; 36°42'55"N; 85°21'52"W; Frogue 7.5' Quadrangle, Cumberland County, Kentucky.

61 Ramp along KY HWY 61; 36°42'50"N; 85°21'49"W; Frogue 7.5' Quadrangle, Cumberland County, Kentucky.