

## FORAMINIFERAL EVIDENCE FOR THE AGE OF THE MISSISSIPPIAN PELLA FORMATION (SOUTHEASTERN IOWA, USA)

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### ABSTRACT

The Pella Formation of southeastern Iowa has been correlated variously with the St. Louis Limestone and the Ste. Genevieve Limestone of the upper Meramecian and lower Chesterian stages, respectively, of the type Mississippian succession. The age of the Pella Formation is of interest because in Keokuk County the Pella immediately overlies a fossil tetrapod deposit that is the oldest of its kind in North America. It sits above Romer's Gap in the fossil record of early tetrapod evolution. Occurrences of the foraminifer *Asteroarchaediscus rugosus* indicate that the Pella Formation can be no older than the upper part of the Ste. Genevieve Limestone. Foraminifers are not useful in constraining the upper age limit of the Pella, but previously reported conodonts assignable to the *Gnathodus bilineatus*–*Cavusgnathus charactus* Assemblage Zone (=Lower *bilineatus* Zone; Faunal Unit 9) suggest that the unit can be no younger than mid-Renault Limestone of the Chesterian reference area. The foraminifer *Holkeria avonensis* occurs abundantly in the Pella Formation. This is the youngest occurrence of the genus and species anywhere in the world, as *Holkeria* spp. previously were known only from the Holkerian–lower Asbian stages (lower Upper Visean) in Britain, and from the lower St. Louis Limestone (=Salem Limestone equivalent) in the upper Meramecian of midcontinental North America.

### INTRODUCTION

The Pella Formation is the youngest Mississippian rock unit in Iowa. Its patchy surface distribution in the southeastern part of the state is controlled both by modern erosion and deep incision associated with the pre-Pennsylvanian unconformity. Bain (1895) named the “Pella beds” as the uppermost of three stratal units assigned to the St. Louis Limestone, later elevated to formation rank by Van Tuyl (1925). The type area is near the town of Pella in Marion County, with scattered outcrops also in Mahaska, Wapello, Van Buren, Lee, Henry, Jefferson, Washington, Keokuk, Poweshiek and Webster counties (Fig. 1; Rexroad and Furnish, 1964). In the northwestern (type) part of its distribution, the Pella consists of a lower, thin (1–2 m), bioclastic and oolitic limestone and an upper, thicker (~7 m), highly fossiliferous marl. The combined limestone and marl strata locally reach a thickness of 15 m in the subsurface. In the southeastern outcrop area, the Pella is a 3–5 m thick limestone with no overlying marl (Witzke, 2004).

There has been some confusion regarding the placement of the lower boundary of the Pella Formation. Van Tuyl

(1925), Rexroad and Furnish (1964), Johnson (1967), and Johnson and Vondra (1969) included within the Pella a sequence of non-marine limestones, *Stigmaria*-bearing sandstones, and carbonaceous shales beneath bioclastic and oolitic limestones of unquestioned marine origin. Witzke (1987) redefined the Pella Formation to exclude non-marine lithologies below the lowest brachiopod- and(or) bivalve-bearing limestones. He reassigned the non-marine units to the Waugh Member of the “St. Louis” Formation, while noting that the “St. Louis” in Iowa is lithologically distinct from the type St. Louis and probably should receive a new name (see also Witzke and others, 1990; Witzke, 2004). According to Witzke's (1987) definition, followed herein, the base of the Pella Formation is developed on a regional disconformity, and the lowest limestones of the Pella are marine transgressive deposits.

Correlation of the Pella Formation to equivalents in the type Mississippian succession has been somewhat controversial. Like Bain (1895), Worthen (1858) and White (1870) regarded the then-unnamed “Pella beds” as part of the St. Louis Limestone. Nickles and Bassler (1900) and Weller (1909) were the first to suggest a correlation between the “Pella beds” and the Ste. Genevieve Limestone. Weller and Van Tuyl (1915) reported field observations to further support this correlation, so that equivalence between the Pella and the Ste. Genevieve was accepted by Lees and Thomas (1919), Van Tuyl (1925), Moore (1935) and most subsequent workers. Conodonts from the Pella Formation were studied by Youngquist and Miller (1949) and Rexroad and Furnish (1964). Both studies demonstrated close similarity between the faunas of the Pella Formation and the Ste. Genevieve Limestone, although the former authors regarded only the upper marl facies as the Pella Formation while referring the lower marine limestone to the St. Louis Limestone. Witzke (1987) and Witzke and others (1990) reviewed additional evidence for correlating the Pella Formation with the Ste. Genevieve Limestone. In the earlier of the two papers, Witzke (1987) outlined three possible correlations between the “St. Louis”–Pella interval in Iowa and the standard Mississippian section (Fig. 2). He favored an interpretation that equated the Pella with the lower Ste. Genevieve, and the Iowa “St. Louis” with the type St. Louis (Fig. 2, case C). In the second paper, largely on the basis of new transgressive–regressive cycle correlations, Witzke and others (1990) adopted an alternative interpretation in which they regarded the Verdi and Waugh members of the Iowa “St. Louis” as lower Ste. Genevieve equivalents, and the Pella as an upper Ste. Genevieve equivalent (Fig. 2, case B).

The Pella Formation has been assigned variously to the Meramecian and Chesterian stages of the Mississippian Subsystem. These contrasting chronostratigraphic assignments mainly reflect instability with respect to the position of the Meramecian–Chesterian boundary itself in the type

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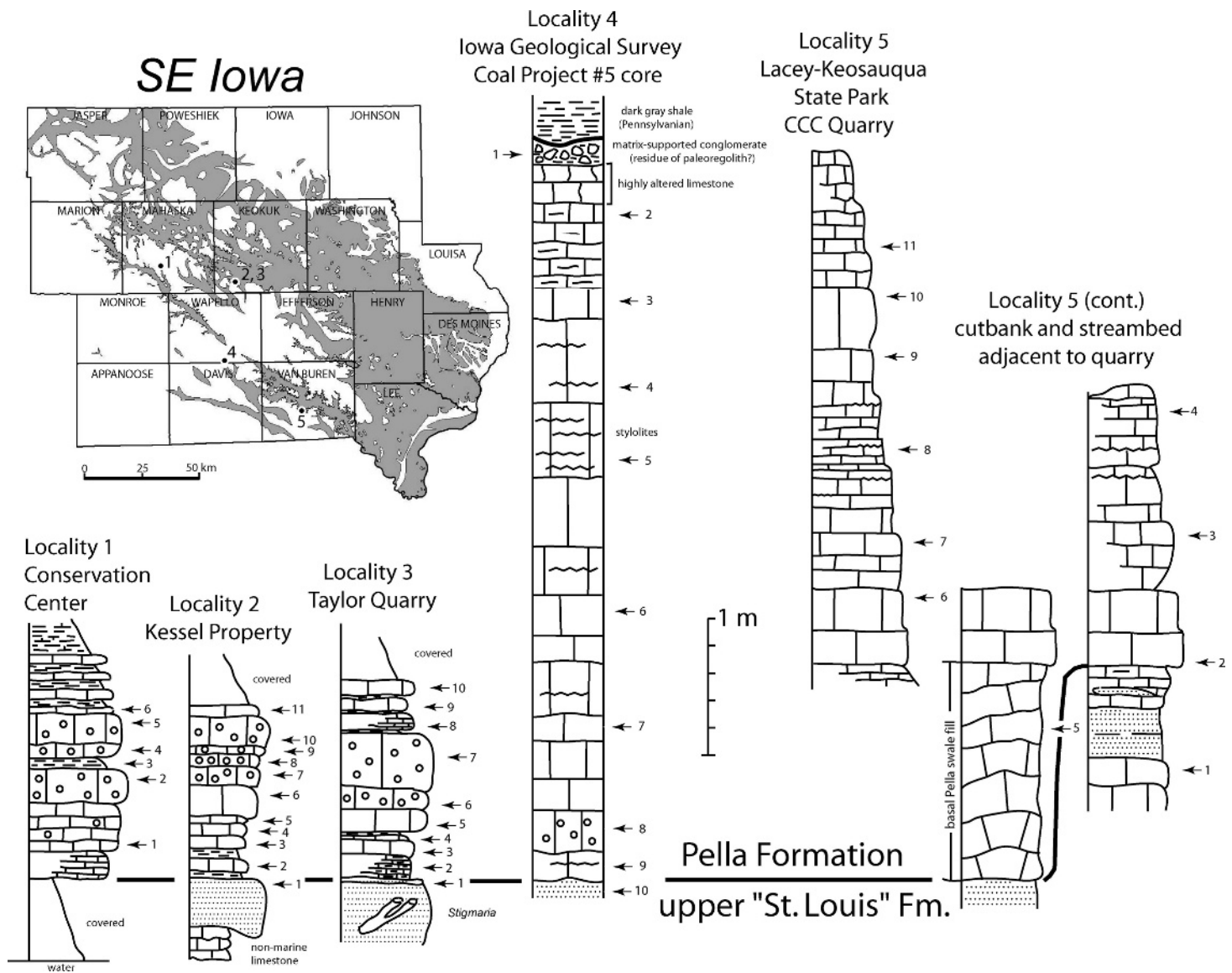


FIGURE 1. Index map to southeastern Iowa, with surface distribution of Mississippian units shaded; and columnar stratigraphic sections showing positions of microfossil samples. Localities as follows: locality 1, SW NE NW sec. 30, T76N, R15E, Mahaska County; locality 2, NW SE SE sec. 14, T74N, R13W, Keokuk County; locality 3, NW SW sec. 13, T74N, R13W, Keokuk County; locality 4, SW SE SE sec. 36, T71N, R13W, Wapello County; locality 5, NW NE SW sec. 1, T68N, R10W, Van Buren County. Map provided by B. J. Bunker (Iowa Geological Survey). Columnar section for locality 5 redrawn after Witzke (2004).

Mississippian succession. Although the Ste. Genevieve Limestone was not included in the original definition of the Meramec Group by Ulrich (1904), it was placed in the Meramecian Series (now Stage) by Weller (1920) and subsequent authors, including those with U. S. Geological Survey. Maples and Waters (1987) reviewed evidence for excluding the Ste. Genevieve Limestone from the Meramecian Stage. They advocated placing the Meramecian–Chesterian boundary at the base of the Ste. Genevieve Limestone, a level that is both historically justifiable and coincident with biostratigraphically-important changes in conodont and foraminiferal faunas (Lane and Brenckle, 2005).

Interest in the age of “St. Louis” and Pella strata in southeastern Iowa increased dramatically upon the 1985

discovery of a fossil vertebrate deposit in the Waugh Member of the “St. Louis” Formation at Heimstra Quarry near the town of Delta in Keokuk County (McKay and others, 1987). The so-called “Delta Amphibian Site” is remarkable for containing primitive tetrapods in addition to a variety of bony fish and sharks (Bolt and others, 1988; Lombard and Bolt, 1995; Bolt and Lombard, 2000, 2006). The oldest known tetrapods are Late Devonian, but the study of early tetrapod evolution is compromised because specimens of Tournaisian–early Viséan age are extremely rare (Clack, 2002, 2006), an unfortunate deficiency in the fossil record known as Romer’s Gap. The Delta site contains one of the world’s oldest tetrapod assemblages from immediately above Romer’s Gap, and it is the oldest well-preserved tetrapod assemblage in North America.

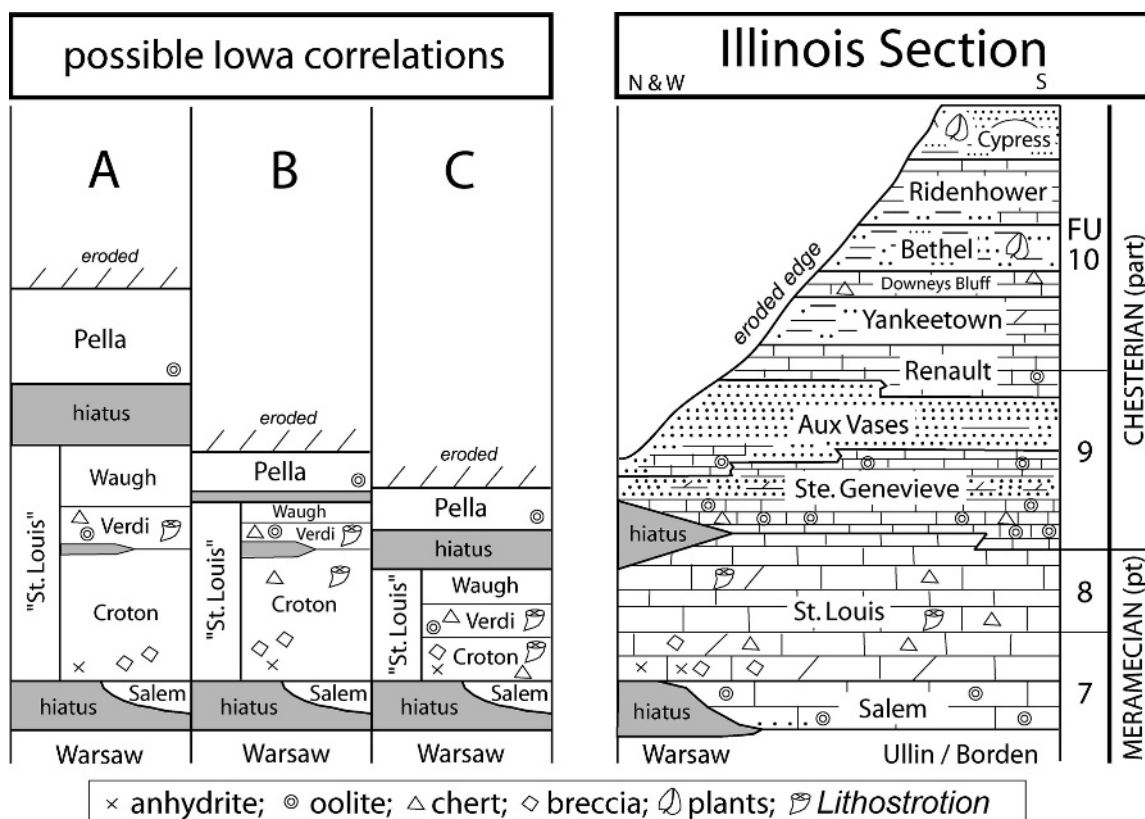


FIGURE 2. Possible correlations of the upper Warsaw-Pella interval in southeastern Iowa with the standard Mississippian section in Illinois (modified from Witzke, 1987). Conodont faunal units (FU) as follows: FU 7 = *texanus* Zone; FU 8 = *scitulus-scalenusus* Zone; FU 9 = Lower *bilineatus* Zone; FU 10 = Upper *bilineatus* Zone [see Lane and Brenckle (2005) for discussion]. Witzke and others (1990) erected the Yenruogis Member of the "St. Louis" Formation in Iowa between the Croton and Verdi members, but for simplicity it is not shown here.

Efforts to establish the precise age of the "St. Louis" beds at Heimstra Quarry include Woodson's (1987) study of foraminifers from the Verdi Member. Although the Verdi foraminiferal fauna is fairly diverse, it lacks diagnostic taxa and was interpreted tentatively as early Chesterian (early Ste. Genevieve) largely on the absence of typical St. Louis forms such as *Eoendothyranopsis* Reitlinger and *Rostovtseva* in Reitlinger, 1966, *Eoforschia* Mamet, 1970, *Globoendothyra* Reitlinger in Voloshinova and Reitlinger, 1959, and the problematicum *Koninckopora* Lee, 1912. Separately, Riley and others (1999) reported the foraminifer *Holkeria* Strank, 1982 from an unspecified section of the Pella Formation near the tetrapod site. Because *Holkeria* is a short-ranging genus in Western Europe, they suggested a correlation between the Pella and the Holkerian to lower Asbian stages of Britain (=Livian to lower Warnantian stages of Belgium). According to correlations presented by Lane and Brenckle (2005), the Holkerian-lower Asbian interval is equivalent to the upper Warsaw-St. Louis interval of the type Mississippian, a level that is slightly older than the Ste. Genevieve with which the Pella Formation has been correlated in recent years. In order to resolve this and other problems in Iowa's Mississippian stratigraphy, Witzke and Bunker (2005) included a study of foraminifers from the Pella Formation in their list of important projects for further research.

#### LOCALITIES AND SAMPLING

Samples for this study were collected at five localities in Mahaska, Keokuk, Wapello and Van Buren counties (Fig. 1). The stratigraphy of the Pella Formation at the localities in Mahaska and Keokuk counties is remarkably similar: in both areas the formation consists of a thin, basal limestone overlain by a thicker marl. Six samples were taken from the lower limestone unit along the north wall of an abandoned quarry immediately south of the Mahaska County Conservation Center (Fig. 1, loc. 1). Ten and nine samples, respectively, were collected from the lower limestone at two localities in Keokuk County (Fig. 1, locs. 2 and 3) situated just a few kilometers south of the vertebrate-bearing Heimstra Quarry. Both of the Keokuk County localities were described in detail by McKay and others (1987). The first (loc. 2) is a section exposed in the cutbank and streambed of an unnamed tributary to Waugh Branch on the Kessel family property, approximately 180 m upstream from the nearest road crossing. The second (loc. 3) is at the southwest corner of the abandoned Taylor Quarry about 0.5 km northeast of the Kessel property site. Eight core samples from southern Wapello County (Fig. 1, loc. 4) were obtained from an Iowa Geological Survey coal exploration well that penetrated the Pella Formation at depths of 43.5–48.9 m beneath the surface. The Pella in this

well consists entirely of limestone, with the marl facies absent because of non-deposition or pre-Pennsylvanian erosion. Ten samples were collected from the 4.5-m-thick Pella Formation at an abandoned Civilian Conservation Corps quarry in Lacey-Keosauqua State Park in Van Buren County (Fig. 1, loc. 5). No marl is present at this section, which was described in detail by Witzke (2004).

FORAMINIFERAL BIOSTRATIGRAPHY

Occurrences of calcareous foraminifers, algae, and problematica at each of the five localities are shown in Figure 3. Representative specimens are illustrated in Plates 1 and 2. Upper Meramecian–Chesterian foraminiferal occurrences in the midcontinent region that form a basis for comparison with the Pella assemblage have been documented by E. J. Zeller (1950), D. E. N. Zeller (1953), Browne and Pohl (1973), Browne and others (1977), Baxter and Brenckle (1982), Brenckle (1991), and Lane and Brenckle (2005). Composite stratigraphic ranges of taxa occurring in the St. Louis Limestone–Beech Creek Limestone interval of the type Mississippian succession are shown in Figure 4.

The Pella Formation contains a low-diversity assemblage of calcareous microfossils including certain long-ranging forms of minimal biostratigraphic utility such as *Earlandia* spp. (Pl. 1, Figs. 27, 28), *Asphaltinella* sp. (Pl. 1, Figs. 24, 26), and salebrids (Pl. 1, Figs. 23, 25, 29, 32). Encrusting foraminifers (calcitornellids and calcivertellids; Pl. 1, Figs. 14, 15) also occur in the Pella, and they have been observed elsewhere as low as the upper Salem Limestone–lower St. Louis and as high as the Permian. Their occurrence in the Pella Formation indicates only a late Meramecian or younger age. *Endothyra* ex gr. *E. bowmani* Phillips, 1846 emend. Brady, 1876 (Pl. 1, Figs. 33–36) and *Endostaffella discoidea* (Girty, 1915) (Pl. 1, Figs. 16–22) are relatively minor elements of the Pella assemblage. Neither is known below the upper St. Louis Limestone of the type Mississippian area, further constraining the lower age limit of the Pella Formation. The most significant foraminiferal occurrence in the Pella is that of *Asteroarchaediscus rugosus* (Rausser-Chernousova, 1948) (Pl. 1, Figs. 1–9). This and other *Asteroarchaediscinae* (e.g., *Asteroarchaediscus* spp. and *Neoarchaediscus* spp.) have not been observed elsewhere below the upper Ste. Genevieve Limestone (Lane and Brenckle, 2005), and they range upward into the lower part of the Middle Pennsylvanian. Thus, on the basis of *A. rugosus*, the Pella can be no older than upper Ste. Genevieve.

The upper age limit of the Pella is less well constrained because all of the recovered taxa are known to range upward into the Pennsylvanian Subsystem or higher. Moreover, post-Ste. Genevieve strata of the lower and middle part of the type Chesterian succession are difficult to characterize foraminiferally because few new taxa appeared before the Menard Limestone of late Chesterian age (Lane and Brenckle, 2005). Conodonts from the Pella Formation were assigned by Rexroad and Furnish (1964) to the *Gnathodus bilineatus*–*Cavusgnathus charactus* Assemblage Zone, which was equated by Lane and Brenckle (2005) with the Lower *bilineatus* Zone (=Faunal Unit 9). This suggests

LOCALITY	SAMPLE NO.	FORAMS							ALGAE & INCERTAE			
		<i>Asteroarchaediscus rugosus</i>	<i>Earlandia</i> spp.	calcitornellids / calcivertellids	<i>Pseudoglomospira</i> spp.	<i>Endothyra</i> ex gr. <i>E. bowmani</i>	<i>Endostaffella</i> aff. <i>E. discoidea</i>	<i>Holkeria avonensis</i>	<i>Holkeria avonensis</i> (uncoiled form)	<i>Principia donbassica</i>	<i>Asphaltinella</i> sp.	salebrid central tube
Manaska Co. Conservation Center	6				X							
	5			X	X							
	4				X							
	3											
	2											
Kessel Property	11	X									X	
	10				X							
	9				X							
	8											
	7											
	6											X
	5		X						X			
	4		X		X							
	3		X		X							X
	2	?							X			
Taylor Quarry	10		X		X			X	X			X
	9			X	X			X				X
	8			X	X							
	7				X							
	6											
	5											X
	4											
	3				X							
	2											
	IGS Coal Project #5 core	2										
3												
4												
5		X				X	X	X	X			X
6												
7					X	?						
8												
9												
Lacey-Keosauqua State Park CCC Quarry		11	X	X		X	X	X	X	X		X
	10	X	X			X	X	X	X			
	9				X		?					
	8				X							
	7				X							
	6		X		X							
	5											
	4				X							
	3		X		X							
	2				X							

FIGURE 3. Calcareous microfossil occurrence chart.

that the Pella is no younger than mid-Renault, where the boundary between the Lower and Upper *bilineatus* zones occurs (Lane and Brenckle, 2005). The conodont evidence is somewhat equivocal, however, because the base of the Upper *bilineatus* Zone (Faunal Unit 10) is defined by the disappearance of *Rhachistognathus* n. sp. (= *Spathognathodus muricatus* of Thompson, 1972), and further characterized by the disappearances of *Geniculatus claviger* (Roundy, 1926) and *Cavusgnathus charactus* Rexroad, 1957, none of which has been reported from the Pella. Thus, the Pella is

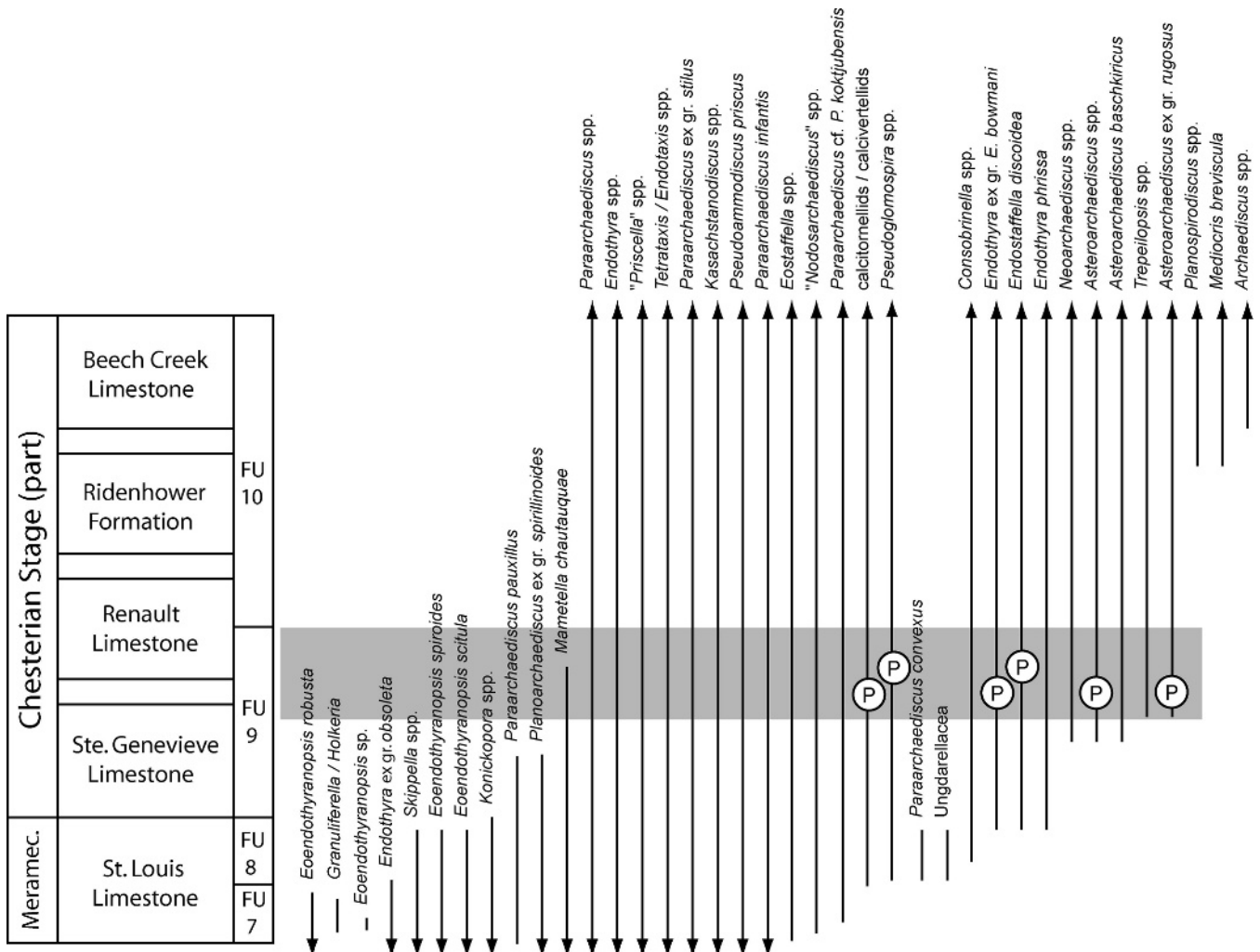


FIGURE 4. Composit stratigraphic ranges of uppermost Meramecian through lower Chesterian calcareous microfossils of the type Mississippi succession [not all lithostratigraphic units shown; redrawn from figures 55 and 56 in Lane and Brenckle (2005)]. Taxa denoted by the letter “P” are those recovered from the Pella Formation. Age of the Pella (shaded rectangle) is no older than upper Ste. Genevieve on the basis of foraminifers, and probably no younger than mid-Renault on the basis of conodonts.

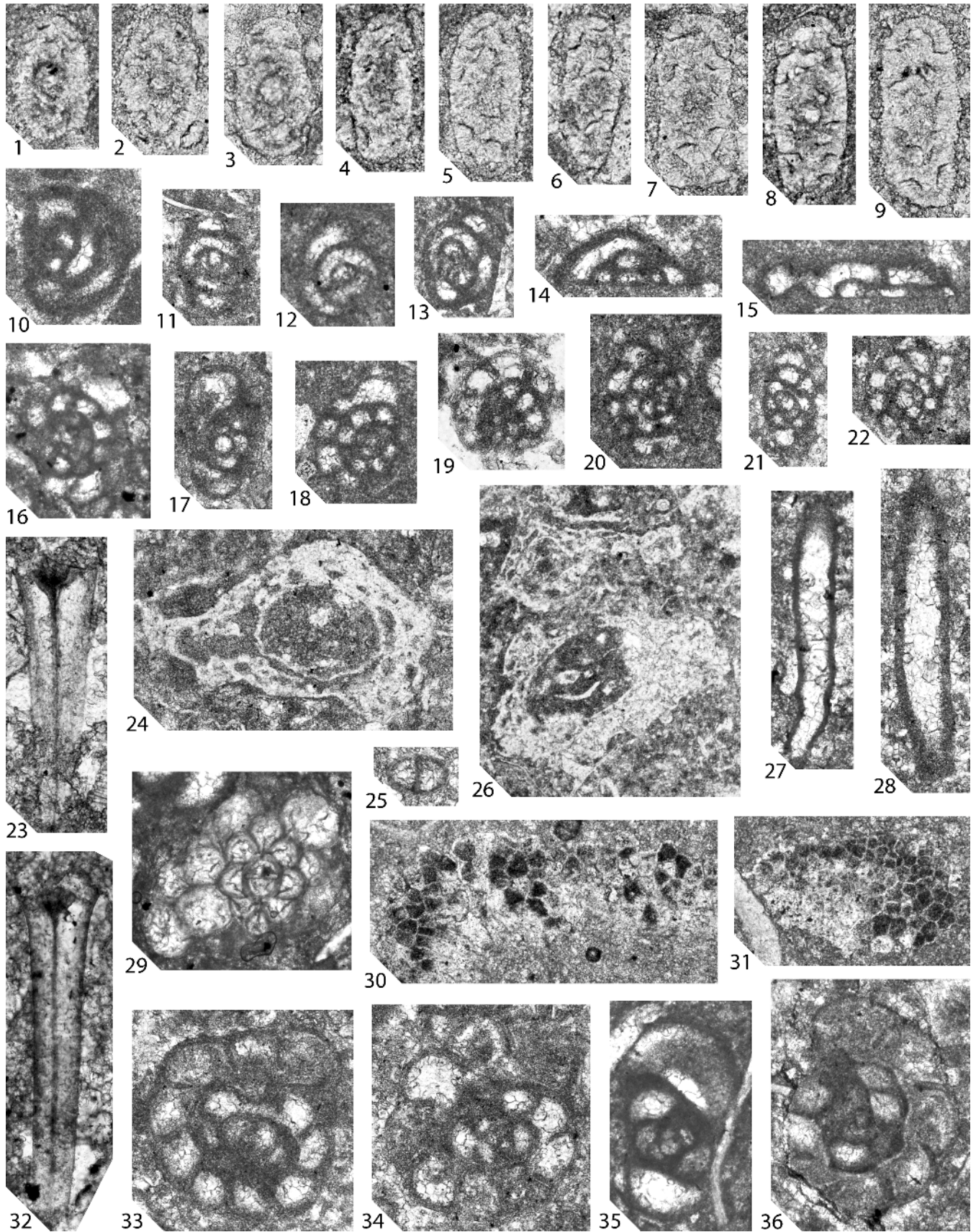
regarded as pre-Upper *bilineatus* Zone partly on negative evidence.

Specimens assigned to *Holkeria avonensis* (Conil and Longersaey in Conil and others, 1980) are by far the most abundant foraminifers in the Pella assemblage. Their occurrence is not central to the present biostratigraphic interpretation, but it requires discussion insofar as *Holkeria* spp. are generally rare in North America and previously have not been observed above the lower part of the St. Louis Limestone of the type Mississippian (Lane and Brenckle, 2005, fig. 55). The genus and all of its constituent species are known from Britain where they are biostratigraphically useful in shelf carbonates of the Holkerian and lower Asbian stages (Conil and others, 1980; Fewtrell and others, 1981; Strank, 1982; Ebdon and others, 1990; Riley, 1993; Barclay and others, 1994). Correlations by Lane and Brenckle (2005) equated the Holkerian–lower Asbian interval with the Meramecian Stage of the North American midcontinent. If these correlations are correct, then the

Pella occurrences of *H. avonensis* represent not only an upward range extension of the genus and species in North America, but also the youngest known occurrences in the world.

TAXONOMIC NOTES

Strank (1982) designated *Rhodesina avonensis* Conil and Longersaey in Conil and others, 1980 as type species of the genus *Holkeria*. Her original diagnosis reads as follows (Strank, 1982, p. 145): “Thick undifferentiated agglutinated wall, droplet shaped chambers; cribrate aperture in final one or two chambers.” On the basis of our examination of the type illustrations and approximately 300 specimens from the Pella Formation, we have observed that the wall is not agglutinated but rather a secreted, microgranular, calcareous layer with scattered adventitious grains (Pl. 2, Figs. 5, 13, 14, 19). The final one or two chambers in specimens with 2–2.5 volutions normally are larger and



more inflated than earlier chambers, and in some specimens both the apertural face and the final septum are cribrate (Pl. 2, Figs. 11, 12). The Pella Formation includes many specimens in which two or more uniserial chambers are added to the last part of the coiled test to produce a rectilinear, uncoiled, final growth stage. The aperture in the uncoiled chambers is reduced to a single circular or ovate opening in the center of the apertural face (Pl. 2, Figs. 15, 16). Furthermore, the bimorphic tests differ from the more typical ones in the apparent absence of cribration in the final few septa of the coiled stage. Uncoiled specimens of *H. avonensis* have not been reported previously. Nevertheless, we assign these specimens to *H. avonensis* because they occur in samples along with unquestioned *H. avonensis* (Fig. 3), and because the coiled portion of the bimorphic tests generally resembles the tests of typically coiled *H. avonensis*. The bimorphic specimens also resemble *Granuliferelloides naliwkini* (Malakhova, 1956) from upper Kinderhookian to lower Osagean strata in North America, and from upper lower to upper Tournaisian strata in Europe (Brenckle and Hance, 2005). Specimens referable to *Granuliferelloides* McKay and Green, 1963 have never been observed above the lower Osagean in cratonic North America (Lane and Brenckle, 2005). If our uncoiled specimens are in fact assignable to *Granuliferelloides* and not *Holkeria*, then the known range of *Granuliferelloides* would be extended upward quite significantly.

The Pella Formation contains some very small endothyroideans with an initial skew-coiled volution followed by two planispiral or nearly planispiral whorls (Pl. 1, Figs. 16–22). These specimens exhibit an undifferentiated microgranular wall without secondary deposits. They closely resemble specimens described and illustrated by Rich (1980) as *Priscella* sp. B from Chesterian strata in the southern Appalachians. The genus *Priscella* Mamet, 1974 is probably a junior synonym of *Endothyra* Phillips, 1846 emend. Brady, 1876 because its type species, *Endothyra prisca* Rauser-Chernousova and Reitlinger in Rauser-Chernousova and others, 1936, possesses secondary floor deposits (Brenckle, 2005, p. 27). Accordingly, we refer our specimens to *Endostaffella* aff. *E. discoidea*. The Pella specimens are generally smaller and possess fewer volutions than the types of *E. discoidea* from the lower Chesterian Batesville Sandstone of Arkansas, but these differences may be ecophenotypic.

## ACKNOWLEDGMENTS

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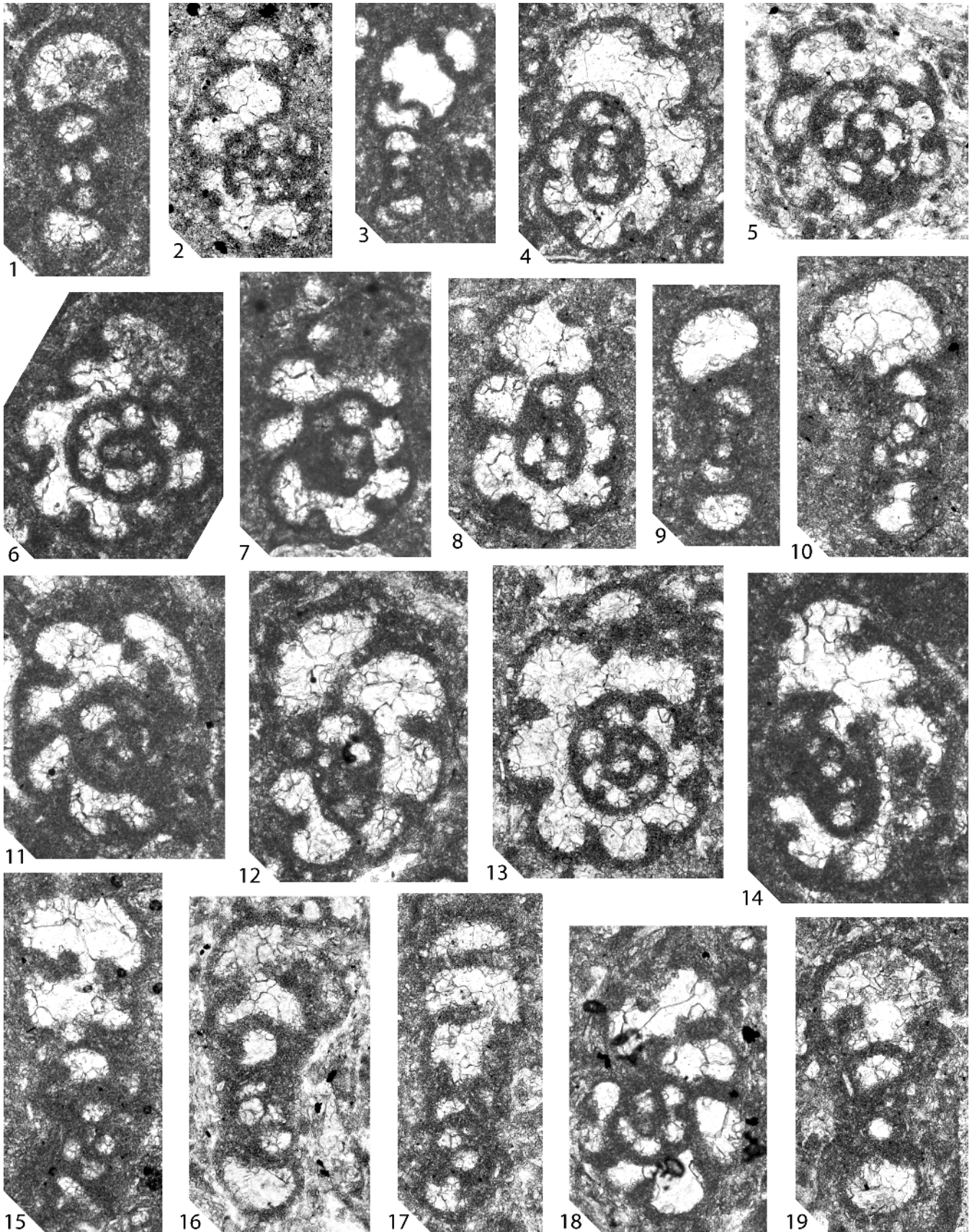
## REFERENCES

- BAIN, H. F., 1895, Central Iowa section of the Mississippian Series: *American Geologist*, v. 15, p. 317–325.
- BARCLAY, W. J., RILEY, N. J., and STRONG, G. E., 1994, The Dinantian rocks of the Sellafeld area, west Cumbria: *Proceedings of the Yorkshire Geological Society*, v. 50, p. 37–49.
- BAXTER, J. W., and BRECKLE, P. L., 1982, Preliminary statement on Mississippian calcareous foraminiferal successions of the Mid-continent (USA) and their correlation to western Europe: *Newsletters on Stratigraphy*, v. 11, p. 136–153.
- BOLT, J. R., and LOMBARD, R. E., 2000, Palaeobiology of *Whatcheeria deltae*, in Heatwole, H., and Carroll, R. L. (eds.), *Amphibian Biology*. Surrey Beatty: Chipping Norton, p. 1044–1052.
- , and LOMBARD, R. E., 2006, *Signournea multidentata*, a new primitive amphibian from the Upper Mississippian of Iowa, USA: *Journal of Paleontology*, v. 80, p. 717–725.
- BRADY, H. B., 1876, A Monograph of Carboniferous and Permian Foraminifera (the genus *Fusulina* excepted): *Palaeontographical Society*, London, 166 p.
- BRECKLE, P. L., 1991, Foraminiferal division of the Lower Carboniferous/Mississippian in North America, in Brenckle, P. L., and Manger, W. L. (eds.), *Intercontinental correlation and division of the Carboniferous System*: *Courier Forschungsinstitut Senckenberg*, v. 130, p. 65–78. (Imprinted 1990)
- , 2005, A compendium of Upper Devonian–Carboniferous type foraminifers from the former Soviet Union: *Cushman Foundation for Foraminiferal Research*, Special Publication, no. 38, 153 p.
- , and HANCE, L., 2005, New and revised Tournaisian (Early

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## PLATE I

1–9, *Asteroarchaediscus rugosus* (Rauser-Chernousova, 1948). 1, oblique axial section, loc. 5, spl. 11 (SUI 102657); 2, axial section, loc. 5, spl. 11 (SUI 102656); 3, axial section, loc. 4, spl. 5 (SUI 102665); 4, tangential axial section, loc. 5, spl. 11 (SUI 102657); 5, tangential axial section, loc. 5, spl. 11 (SUI 102656); 6, axial section, loc. 5, spl. 11 (SUI 102655); 7, tangential axial section, loc. 5, spl. 11 (SUI 102655); 8, axial section, loc. 5, spl. 11 (SUI 102657); 9, tangential axial section, loc. 5, spl. 11 (SUI 102655). 10–13, *Pseudoglomospira* spp., randomly oriented sections. 10, loc. 1, spl. 5 (SUI 102678); 11, loc. 5, spl. 11 (SUI 102655); 12, loc. 5, spl. 3 (SUI 102638); 13, loc. 5, spl. 11 (SUI 102657). 14, 15, encrusting foraminifers, randomly oriented sections. 14, loc. 1, spl. 5 (SUI 102678); 15, loc. 3, spl. 9 (SUI 102703). 16–22, *Endostaffella* aff. *E. discoidea* (Girty, 1915). 16, sagittal section, loc. 4, spl. 5 (SUI 102664); 17, axial section, loc. 5, spl. 11 (SUI 102657); 18, sagittal section, loc. 5, spl. 10 (SUI 102653); 19, oblique sagittal section, loc. 4, spl. 5 (SUI 102665); 20, oblique sagittal section, loc. 5, spl. 10 (SUI 102653); 21, oblique axial section, loc. 5, spl. 11 (SUI 102657); 22, sagittal section, loc. 5, spl. 11 (SUI 102655); 23, 25, 32, salebrid central tubes. 23, oblique longitudinal section, loc. 3, spl. 5 (SUI 102697); 25, transverse section, loc. 1, spl. 1 (SUI 102671); 32, longitudinal section, loc. 2, spl. 6 (SUI 102686); 24, 26, *Asphaltinella* sp., randomly oriented sections, loc. 5, spl. 11; 24, (SUI 102655); 26, (SUI 102656); 27, 28, *Earlandia* spp., longitudinal sections; 27, loc. 2, spl. 3 (SUI 102683); 28, loc. 5, spl. 11 (SUI 102655); 29, *Salebra* sp., oblique transverse section, loc. 4, spl. 5 (SUI 102664); 30, 31, *Principia donbassica* (Kossenko, 1972), randomly oriented sections, loc. 2, spl. 2 (SUI 102682); 33–36, *Endothyra* ex gr. *E. bowmani* Phillips, 1846 emend. Brady, 1876, loc. 5, spl. 11; 33, tangential sagittal section (SUI 102657); 34, tangential sagittal section (SUI 102655); 35, axial section (SUI 102654); 36, tangential sagittal section (SUI 102654). 1–9, ×184; 10–25, 27–36, ×92; 26, ×46.





- Mississippian) foraminiferal taxa from Belgium: *Rivista Italiana di Paleontologia e Stratigrafia*, v. 111, p. 197–214.
- BROWNE, R. G., and POHL, E. R., 1973, Stratigraphy and genera of calcareous foraminifera of the Fraileys Facies (Mississippian) of central Kentucky: *Bulletins of American Paleontology*, v. 64, no. 280, p. 173–243.
- , BAXTER, J. W., and ROBERTS, T. G., 1977, The Archaediscidae of the Fraileys Facies (Mississippian) of central Kentucky: *Bulletins of American Paleontology*, v. 72, no. 298, p. 171–228.
- CLACK, J., 2002, An early tetrapod from Romer's Gap: *Nature*, v. 418, p. 72–76.
- , 2006, The emergence of early tetrapods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 232, p. 167–189.
- CONIL, R., LONGERSTAEY, P. J., and RAMSBOTTOM, W. H. C., 1980, Matériaux pour l'étude micropaléontologique du Dinantien de Grande-Bretagne: *Mémoires de l'Institut Géologique de l'Université de Louvain*, v. 30, p. 1–197. (Imprinted 1979)
- EBDON, C. C., FRASER, A. J., HIGGINS, A. C., MITCHENER, B. C., and STRANK, A. R. E., 1990, The Dinantian stratigraphy of the East Midlands: A seismostratigraphic approach: *Journal of the Geological Society, London*, v. 147, p. 519–536.
- FEWTRELL, M. D., RAMSBOTTOM, W. H. C., and STRANK, A. R. E., 1981, Carboniferous, in Jenkins, D. G., and Murray, J. W. (eds.), *Stratigraphical Atlas of Fossil Foraminifera: British Micropalaeontological Society Series*, p. 15–69.
- GIRTY, G. H., 1915, The fauna of the Batesville Sandstone of northern Arkansas: *U. S. Geological Survey Bulletin*, v. 593, 170 p.
- JOHNSON, G. D., 1967, Stratigraphy of the Pella Formation (Mississippian) of Iowa: Unpublished Masters Thesis, Iowa State University, 136 p.
- , and VONDRA, C. F., 1969, Lithofacies of Pella Formation (Mississippian), southeastern Iowa: *American Association of Petroleum Geologists Bulletin*, v. 53, p. 1894–1908.
- KOSSENKO, Z. A., 1972, New calcareous algae from Ukraine and western Siberia, in Zanina, I. E. (ed.), *New Species of Fossil Plants and Invertebrates of the USSR: Akademiya Nauk SSSR, Izdatel'stvo "Nauka," Moskva*, p. 293–295. (In Russian)
- LANE, H. R., and BRECKLE, P. L., 2005, Type Mississippian subdivisions and biostratigraphic succession, in Heckel, P. H. (ed.), *Stratigraphy and Biostratigraphy of the Mississippian Subsystem (Carboniferous System) in its Type Region, the Mississippi River Valley of Illinois, Missouri, and Iowa: Illinois State Geological Survey, Guidebook 34*, p. 76–105.
- LEE, G. W., 1912, *The British Carboniferous Trepostomata: Great Britain Geological Survey, Memoir*, v. 1, no. 3, p. 135–195.
- LEES, J. H., and THOMAS, A. O., 1919, The Ste. Genevieve marls near Fort Dodge and their fauna: *Proceedings of the Iowa Academy of Science*, v. 25, p. 599–616.
- LOMBARD, R. E., and BOLT, J. R., 1995, A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa: *Palaeontology*, v. 38, p. 471–494.
- MALAKHOVA, N. P., 1956, Upper Tournaisian foraminifera from the western slope of the northern and middle Urals: *Akademiya Nauk SSSR, Ural'skiy Filial, Trudy Gorno-Geologicheskogo Instituta, Sbornik po Voprosam Stratigrafii No. 3, vypusk 24*, p. 72–155. (In Russian)
- MAMET, B., 1970, Carbonate microfacies of the Windsor Group (Carboniferous), Nova Scotia and New Brunswick: *Geological Survey of Canada, Paper 70–21*, 121 p.
- , 1974, Taxonomic notes on Carboniferous Endothyraea: *Journal of Foraminiferal Research*, v. 4, p. 200–204.
- MAPLES, C. G., and WATERS, J., 1987, Redefinition of the Meramecian/Chesterian boundary (Mississippian): *Geology*, v. 15, p. 647–651.
- MCKAY, R. M., WITZKE, B. J., and MCADAMS, M. P. (eds.), 1987, Early tetrapods, stratigraphy, and paleoenvironments of the upper St. Louis Formation, western Keokuk County, Iowa: *Geological Society of Iowa, Guidebook 46*, 74 p.
- , and ———, 1988, A new Lower Carboniferous tetrapod locality in Iowa: *Nature*, v. 333, p. 768–770.
- MCKAY, W., and GREEN, R., 1963, Mississippian foraminifera of the southern Canadian Rocky Mountains, Alberta: *Research Council of Alberta, Bulletin 10*, 77 p.
- MOORE, R. C., 1935, Mississippian System in the upper Mississippi Valley region: *Kansas Geological Society Guidebook, 9<sup>th</sup> Annual Field Conference*, p. 239–245.
- NICKLES, J. M., and BASSLER, R. S., 1900, A synopsis of American fossil bryozoa including bibliography and synonymy: *U. S. Geological Survey Bulletin*, v. 173, p. 1–663.
- PHILLIPS, J., 1846, On the remains of microscopic animals in the rocks of Yorkshire: *Proceedings of the Geologic and Polytechnic Society of the West Riding of Yorkshire*, v. 2, p. 274–285.
- RAUSER-CHERNOUSOVA, D. M., 1948, Materials on the foraminiferal fauna of the Carboniferous deposits of central Kazakhstan: *Akademiya Nauk SSSR, Trudy Instituta Geologicheskikh Nauk, Geologicheskaya Seriya 21, vypusk 66*, p. 1–25. (In Russian)
- , BELYAEV, G., and REITLINGER, E. A., 1936, Upper Paleozoic foraminifera of the Pechora region: *Akademiya Nauk SSSR, Trudy Iolyarnoy Komissii, vypusk 28*, p. 159–232. (In Russian)
- REITLINGER, E. A., 1966, Some questions on the classification and evolution of endothyrids and primitive fusulinids: *Akademiya Nauk SSSR, Geologicheskii Institut, Voprosy Mikropaleontologii*, v. 14, p. 39–67. (in Russian)
- REXROAD, C. B., 1957, Conodonts from the Chester Series in the type area of southwestern Illinois: *Illinois Geological Survey, Report of Investigations*, v. 199, p. 1–43.
- , and FURNISH, W. M., 1964, Conodonts from the Pella Formation (Mississippian), south-central Iowa: *Journal of Paleontology*, v. 38, p. 667–676.
- RICH, M., 1980, Carboniferous calcareous foraminifera from northeastern Alabama, south-central Tennessee, and northwestern Georgia: *Cushman Foundation for Foraminiferal Research, Special Publication No. 18*, 62 p.
- RILEY, N. J., 1993, Dinantian (Lower Carboniferous) biostratigraphy and chronostratigraphy in the British Isles: *Journal of the Geological Society, London*, v. 150, p. 427–446.
- , MCKAY, R. M., and WITZKE, B. J., 1999, The foraminiferan *Holkeria* and its bearing on correlation of the Mississippian of Iowa, USA with the Dinantian of Europe: *XIV International Congress on the Carboniferous and Permian, University of Calgary and Canadian Society of Petroleum Geologists, Calgary, Alberta, Abstracts*, p. 123.
- ROUNDY, P. V., 1926, Introduction, the micro-fauna, in Roundy, P. V., Girty, G. H., and Goldman, M. I. (eds.), *Mississippian Formations of San Saba County, Texas: U. S. Geological Survey Professional Paper 146*, p. 1–17.

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## PLATE 2

1–19, *Holkeria avonensis* (Conil and Longerstaey in Conil and others, 1980). 1, axial section, loc. 5, spl. 10 (SUI 102653); 2, sagittal section of uncoiled morphotype, loc. 3, spl. 10 (SUI 102704); 3, tangential axial section of uncoiled morphotype, loc. 5, spl. 10 (SUI 102653); 4, 13, sagittal sections, loc. 5, spl. 11 (SUI 102655); 5, tangential sagittal section, loc. 4, spl. 5 (SUI 102665); 6, tangential sagittal section of uncoiled morphotype, loc. 6, spl. 10 (SUI 102652); 7, tangential sagittal section of uncoiled morphotype, loc. 5, spl. 11 (SUI 102654); 8, tangential sagittal section, loc. 3, spl. 10 (SUI 102704); 9, tangential axial section, loc. 5, spl. 10 (SUI 102653); 10, axial section, loc. 3, spl. 10 (SUI 102704); 11, tangential sagittal section, loc. 5, spl. 10 (SUI 102650); 12, tangential sagittal section, loc. 5, spl. 11 (SUI 102657); 14, oblique sagittal section, loc. 5, spl. 10 (SUI 102653); 15, oblique and tangential axial section of uncoiled morphotype, loc. 3, spl. 10 (SUI 102704); 16, tangential axial section, loc. 4, spl. 5 (SUI 102665); 17, tangential axial section of uncoiled morphotype, loc. 5, spl. 11 (SUI 102655); 18, tangential sagittal section of uncoiled morphotype, loc. 4, spl. 5 (SUI 102665); 19, tangential axial section, loc. 5, spl. 11 (SUI 102656). 1, 2, 4–19, ×92; 3, ×46.

- STRANK, A. R. E., 1982, *Holkeria* gen. nov., a foraminifer characteristic of the Holkerian Stage of the British Dinantian: Proceedings of the Yorkshire Geological Society, v. 44, p. 145–151.
- THOMPSON, T. L., 1972, Conodont biostratigraphy of Chesterian strata in southwestern Missouri: Missouri Geological Survey and Water Resources, Report of Investigations, v. 50, 46 p.
- ULRICH, E. O., 1904, Preliminary notes on classification and nomenclature of certain Paleozoic rock units in eastern Missouri, in Buckley, E. R., and Buehler, H. A. (eds.), *The Quarrying Industry in Missouri*: Missouri Bureau of Geology and Mines, 2<sup>nd</sup> Series, v. 2, p. 109–111.
- VAN TUYL, F. M., 1925, The stratigraphy of the Mississippian formations of Iowa: Iowa Geological Survey, Annual Reports, v. 30, p. 33–349.
- VOLOSHINOVA, N. A., and REITLINGER, E. A., 1959, Order Endothyrida, in Rauser-Chernousova, D. M., and Fursenko, A. V. (eds.), *Fundamentals of Paleontology, General Part—Protozoa*: Izdatel'stvo Akademii Nauk SSSR, Moskva, p. 190–201. (In Russian)
- WELLER, S., 1909, Correlation of the middle and upper Devonian and the Mississippian faunas of North America: *Journal of Geology*, v. 17, p. 257–285.
- , 1920, The geology of Hardin County and the adjoining part of Pope County: Illinois State Geological Survey Bulletin, v. 41, p. 1–416.
- , and VAN TUYL, F. M., 1915, The Ste. Genevieve Formation and its stratigraphic relations in southeastern Iowa: Proceedings of the Iowa Academy of Science, v. 22, p. 241–247.
- WHITE, C. A., 1870, Report on the geological survey of the state of Iowa, v. 1, 391 p.
- WITZKE, B. J., 1987, Pella stratigraphy, paleontology, and correlation problems of the “St. Louis”–Pella interval, in McKay, R. M., Witzke, B. J., and McAdams, M. P. (eds.), *Early Tetrapods, Stratigraphy and Paleoenvironments of the Upper St. Louis Formation, Western Keokuk County, Iowa*: Geological Society of Iowa, Guidebook 46, p. 29–34.
- , 2004, Bedrock geology of Lacey-Keosauqua State Park, in Anderson, R. R., and Langel, R. J. (eds.), *The Natural History of Lacey-Keosauqua State Park, Van Buren County, Iowa*: Geological Society of Iowa, Guidebook 76, p. 55–65.
- , and BUNKER, B., 2005, Comments on the Mississippian stratigraphic succession in Iowa, in Heckel, P. H. (ed.), *Stratigraphy and Biostratigraphy of the Mississippian Subsystem (Carboniferous System) in its Type Region, the Mississippi River Valley of Illinois, Missouri, and Iowa*: Illinois State Geological Survey, Guidebook 34, p. 63–75.
- , MCKAY, R. M., BUNKER, B. J., and WOODSON, F. J., 1990, Stratigraphy and Paleoenvironments of Mississippian Strata in Keokuk and Washington Counties, Southeastern Iowa: Iowa Department of Natural Resources, Guidebook Series No. 10, 105 p.
- WOODSON, F. J., 1987, Calcareous microfossils from the “St. Louis” Formation, Keokuk County, Iowa, in McKay, R. M., Witzke, B. J., and McAdams, M. P. (eds.), *Early Tetrapods, Stratigraphy and Paleoenvironments of the Upper St. Louis Formation, Western Keokuk County, Iowa*: Geological Society of Iowa, Guidebook 46, p. 35–36.
- WORTHEN, A. H., 1858, Geology of the Des Moines Valley; geology of certain counties: Iowa Geological Survey, Annual Reports, v. 1, p. 147–258.
- YOUNGQUIST, W. L., and MILLER, A. K., 1949, Conodonts from the late Mississippian Pella beds of south-central Iowa: *Journal of Paleontology*, v. 23, p. 617–622.
- ZELLER, D. E. N., 1953, Endothyroid foraminifera and ancestral fusulinids from the type Chesterian (Upper Mississippian): *Journal of Paleontology*, v. 27, p. 183–199.
- ZELLER, E. J., 1950, Stratigraphic significance of Mississippian endothyroid foraminifera: *University of Kansas Paleontological Contributions*, Article 4, p. 1–23.

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