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Gary L. STRINGER & James Carson SLOAN (2023). First Cretaceous teleostean otolith assemblage (Arkadelphia Formation, upper Maastrichtian) from Arkansas, USA, early Gadiformes, and the Western Interior Seaway.

Cover: Drilling rig used in the geotechnical investigations at Cabot, Lonoke County, Arkansas, USA, by the Arkansas Department of Transportation that produced subsurface samples of the Arkadelphia Formation (Upper Cretaceous, upper Maastrichtian) that contained teleostean otoliths. Inset is the holotype of *Palaeogadus? belli*, a new species of gadiform fish recovered from the project. Scale bar=1mm.

Citation: Stringer, G.L., and J.C. Sloan. 2023. First Cretaceous teleostean otolith assemblage (Arkadelphia Formation, upper Maastrichtian) from Arkansas, USA, early Gadiformes, and the Western Interior Seaway. *PaleoBios* 40(3): 1-39.

DOI: <https://doi.org/10.5070/P940361192>.

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First Cretaceous teleostean otolith assemblage (Arkadelphia Formation, upper Maastrichtian) from Arkansas, USA, early Gadiformes, and the Western Interior Seaway

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The fortuitous discovery of Cretaceous (late Maastrichtian) teleostean otoliths in boring samples (17–31 m below ground level) from the Arkadelphia Formation near Cabot, Arkansas, USA, has consequential and overarching ramifications. The otolith assemblage, which is relatively large with 2,109 specimens, represents the first Mesozoic otolith assemblage described from Arkansas and one of the largest Cretaceous assemblages from a single USA site. The diversity of the assemblage is fairly large with a richness of 19 species with three additional taxa in open nomenclature and one unknown lapillus, which more than doubles the known actinopterygians from the Arkadelphia Formation. The otolith assemblage is extremely uneven in its diversity with one species, a putative siluriform *Vorhisia vulpes* Frizzell (1965b), accounting for approximately 73% of the total. The most unique feature of the otolith assemblage is the presence of cool-water gadiforms, which represent approximately 7.6% of the total assemblage. The presence of the gadiforms is related to the effects of the Western Interior Seaway and paleogeography during the Late Cretaceous in the western Gulf Coastal Plain. The gadiforms may represent relicts of a greater population and distribution in the early Maastrichtian. Percentage similarity measurements of the otolith assemblage indicate that the Arkadelphia Formation is more closely related to the Severn Formation in eastern Maryland (57.86%) and the Kemp Clay Formation in northeast Texas (35.77%) than to the Ripley Formation in northeastern Mississippi (5.34%). The similarity measurements and other factors indicate that the Arkadelphia Formation otolith assemblage belongs to the Western Interior Seaway community (bioprovince). The Arkadelphia Formation otolith assemblage also contains several taxa that become extinct, such as the ubiquitous *V. vulpes*, at the K-Pg extinction event. The otoliths point to a very shallow marine environment (possibly inner shelf; less than 20 m in depth) with estuarine and freshwater input nearby and may be utilized for refinement of paleoshorelines for the southern reaches of the Western Interior Seaway during the Late Cretaceous.

Keywords: fish otoliths, Cretaceous, Arkadelphia Formation, gadiforms, Western Interior Seaway

INTRODUCTION

No assemblages of Mesozoic teleostean otoliths have ever been described from Arkansas. Furthermore, the studies of Mesozoic otolith assemblages in the USA Gulf Coastal Plain have been limited to a few studies from Texas, Tennessee, Mississippi, and Alabama. This lack of investigation increases the importance of this study of Cretaceous otoliths from the upper Maastrichtian

Arkadelphia Formation. Equally important are the paleogeographical and paleoecological implications of the Arkadelphia Formation otolith assemblages and the occurrence of some of the earliest representatives of the family Gadiformes and the influence of the Western Interior Seaway.

Numerous studies, including Huddleston and Savoie (1983), Nolf (1985, 2003, 2013), Stringer (1992, 1998), Schwarzhans (1993, 1996, 2003, 2010), Nolf and Brzobohaty (1994), Nolf and Stringer (1996), Lin (2016), Lin

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LSID: urn:lsid:zoobank.org:pub:3B70D32F-9BF0-4595-AF4B-45ADEE03B204

et al. (2016), Stringer et al. (2016, 2020), Schwarzhans et al. (2018a, b), Stringer and Bell (2018), and Stringer and Shannon (2019), as well as many other references contained in the aforementioned publications, have corroborated the value of otoliths in determining and interpreting bony fish fossil assemblages. In their long-term study of the upper Eocene Yazoo Clay in Louisiana, Breard and Stringer (1995) recovered 12 actinopterygians based on skeletal remains (primarily teeth). Whereas, Nolf and Stringer (2003) and Stringer and King (2010) reported 44 taxa of bony fish identified from the same locality using otoliths. Obviously, bony fish diversity is more fully comprehended when osteological elements and otoliths are both considered and analyzed. This, of course, is dependent upon the presence of skeletal remains and otoliths in the strata, and unfortunately, the aragonitic otoliths are susceptible to leaching.

The importance of otoliths for identifying and understanding the diversity of actinopterygians in the Arkadelphia Formation at the Cabot locality is shown by recovered bony fish osteological remains (primarily teeth). Skeletal remains of bony fishes from the boring samples indicated four taxa identified to at least genus level [*Enchodus ferox* Leidy (1855), *Hadrodus priscus* Leidy (1857), *Xiphactinus audax* Leidy (1870), and *Lepisosteus* sp. Lacépède (1803)] and two to the family level [Phyllodontidae indeterminate Darteville and Casier, (1943) and Albulidae indeterminate Bleeker (1859)]. Unidentifiable bony fish remains were common (E. Manning, personal communication, 2020). The otoliths from the Arkadelphia Formation made it possible to identify bony fish taxa that would have otherwise gone unrecognized. Since the actinopterygians represented by otoliths from the Arkadelphia Formation have not been scientifically described, an overview of the bony fishes identified on the basis of otoliths from the site is presented. The systematic paleontology for each taxon is briefly described. The significance of some of the earliest Gadiformes known in the paleontological record is discussed. Finally, the otoliths are utilized to interpret paleogeographical and paleoecological conditions during the Late Cretaceous in this portion of the Gulf Coastal Plain and to assess the influence of the Western Interior Seaway on the teleosts of the Arkadelphia Formation.

MATERIALS AND METHODS

Geologic setting

The Arkadelphia Formation is primarily a dark-gray to black marl or marly clay. However, there is also some

limy, gray sandstone, gray sandy clay, sandy limestone, concretionary limestone, and white to light brown impure chalk present in the formation. The sandy marls and limestones are found mainly at or near the base, while the impure chalks are found closer to the top of the formation (McFarland 2004, Larina et al. 2016). The thickness of the unit in Arkansas ranges from approximately 36.6 to 48.8 m (Dane 1929, Renfroe 1949). There is a slight unconformity that separates the Arkadelphia Formation from the underlying Cretaceous Nacatoch Sand, while there is a more conspicuous unconformity that separates it from the overlying Paleocene Clayton Formation (Midway) (Fig. 1). The unconformity between the Cretaceous and the Paleocene is consistent across the Gulf Coastal Plain (Hart et al. 2012, 2013). However, it should be noted that based on borings drilled by the Arkansas Department of Transportation (ARDOT), the Arkadelphia Formation northeast of Arkadelphia, Arkansas, to Cabot, Arkansas directly overlies Paleozoic rocks.

The Arkadelphia Formation was first named by Hill (1888) for outcrops at Arkadelphia in Clark County, Arkansas, according to Veatch (1906). A portion of the strata for which Hill first applied the name "Arkadelphia" are no longer considered part of the formation but now considered part of the underlying Nacatoch Formation

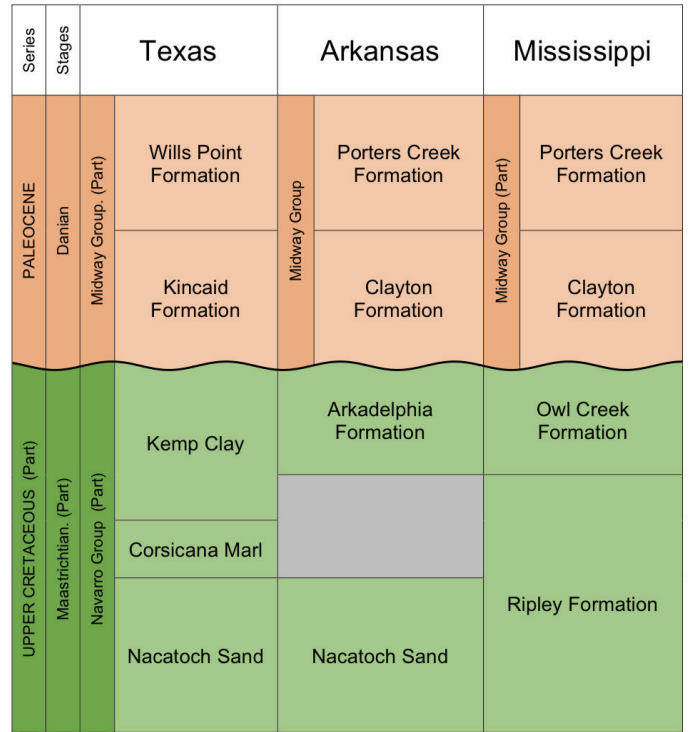


Figure 1. Stratigraphy of the Arkadelphia Formation and other formations discussed in the text based primarily on McFarland (2004). The gray-shaded area represents an unconformity.

(McFarland 2004). One of the only references to Cretaceous strata in the Cabot area is from the Annual Report of the Geological Survey of Arkansas for 1892 (Harris 1894). The age of the Arkadelphia Formation is Late Cretaceous, and outcrops of the formation are recognized in the Gulf Coastal Plain in Clark, Nevada, and Hempstead counties in southwestern Arkansas. Studies indicate that the Arkadelphia Formation is in the Navarro Group (Renfroe 1949), but this designation is not used in this area of Arkansas (see discussion in Stephenson et al. 1942 and McFarland 2004). Several lines of evidence point to the late Maastrichtian age of the Arkadelphia Formation including paleomagnetic studies (Liddicoat et al. 1981), ammonite studies (M. Garb of Brooklyn College, Brooklyn, New York, personal communication, 2020), dinoflagellates (Dastas et al. 2014), combined study of ammonites, dinoflagellates, and nannofossils (Larina et al. 2016), and ostracodes (M. Puckett, University of Southern Mississippi, Hattiesburg, Mississippi).

As noted previously, no Cretaceous teleostean otoliths have ever been described from Arkansas, and this study represents the first investigation of a Cretaceous otolith assemblage from the state. A review of the literature also clearly indicates that studies of Cretaceous teleostean otoliths are very limited in the entire U.S. Gulf Coastal Plain (Nolf and Stringer 1996, Schwarzhans et al. 2018b, Stringer et al. 2020, Schwarzhans and Stringer 2020a). Although conducted in other states, otolith studies of the Upper Cretaceous Coon Creek in Tennessee (Stringer 2016b), the Upper Cretaceous Ripley and Owl Creek formations in Mississippi (Stringer et al. 2020), and the Upper Cretaceous Kemp Clay in Texas (Schwarzhans and Stringer 2020a) are the nearest described otolith assemblages to the Arkadelphia Formation assemblage at the Cabot site in Arkansas (Fig. 2).

Several studies that concentrated exclusively on vertebrate skeletal remains have been conducted on the surface exposures of the Arkadelphia Formation along the

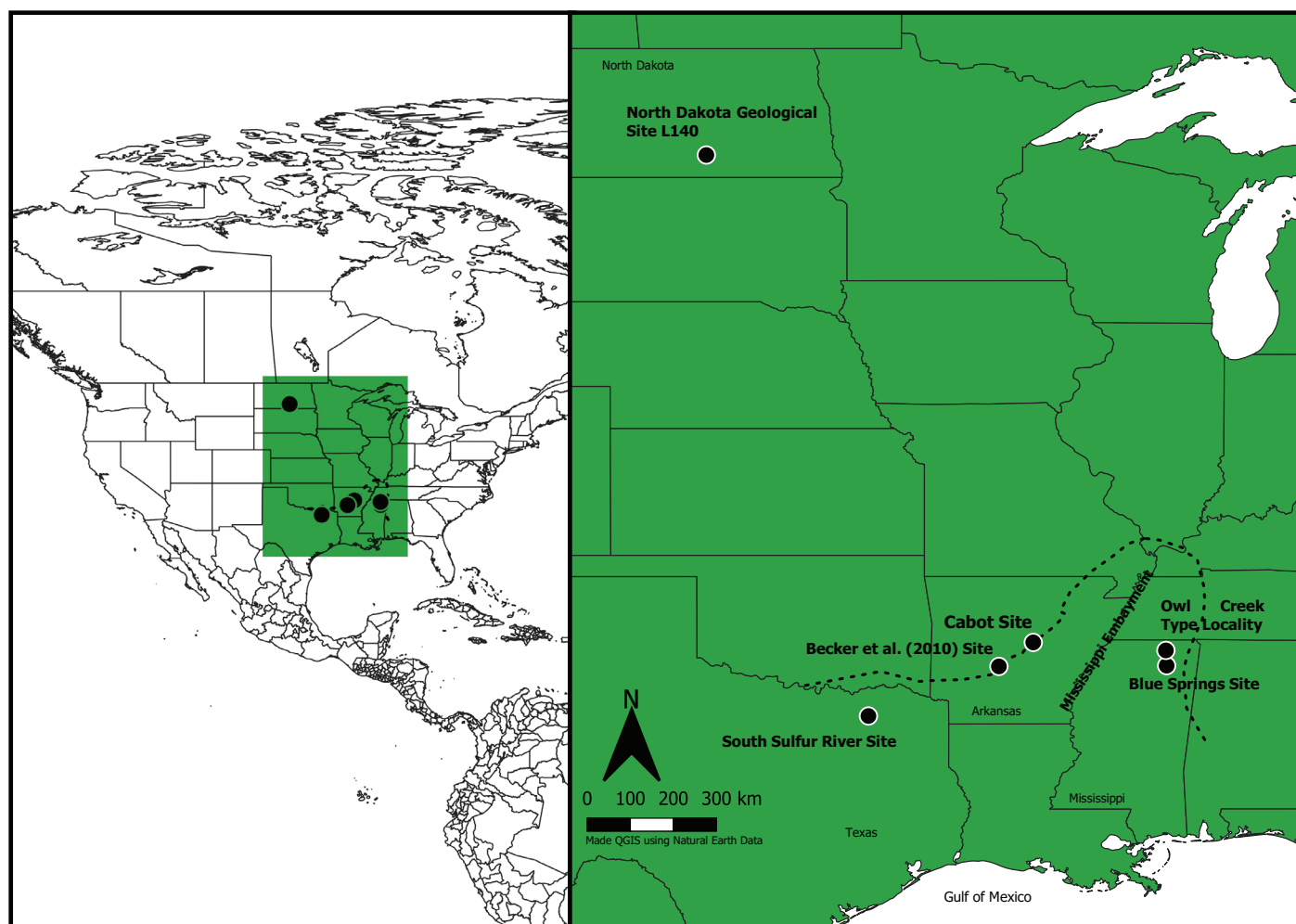


Figure 2. Regional map of otolith-bearing Cretaceous sites mentioned in the text. Dashed line shows approximate shoreline during the late Maastrichtian (Roberts and Kirschaum 1995, Dastas et al. 2014, Stringer and Sloan 2018).

Ouachita River near Malvern in Hot Spring County, Arkansas. Malvern is located approximately 111 km southwest of Cabot, Arkansas, and both of the sites are probably along the strike of the Late Cretaceous shoreline (Roberts and Kirschaum 1995, Dastas et al. 2014, Stringer and Sloan 2018, Schwarzhans and Stringer 2020a). Becker et al. (2006) reported 17 species of chondrichthyans from the Arkadelphia Formation near Malvern based primarily on shark teeth. Becker et al. (2010) described osteichthyans from a lag deposit between the Arkadelphia Formation and the Clayton Formation (same site as 2006 study). The bony fishes were based on teeth, scales, and other skeletal elements. A total of 11 taxa of bony fishes were reported including a *Teleostei incertae sedis* Müller (1845). The authors noted that they were unable to determine whether the lag deposit comprised the uppermost Arkadelphia Formation or a locally preserved

basal unit of the Midway Group containing reworked Late Maastrichtian fossils. Therefore, it is not clear whether all of the bony fishes actually occurred in the Arkadelphia Formation or could have originated in the Midway Group. Maisch (2020) described a new myliobatid from the area, but it was from Clayton Formation (Paleocene) rather than the underlying Cretaceous Arkadelphia Formation.

Methodology

All of the Arkadelphia Formation specimens examined for this study were from material obtained as a byproduct of sampling for a geotechnical investigation by the ARDOT for a bridge feasibility study along Arkansas Highway 321 (Bill Foster Memorial Highway West) in Cabot, Lonoke County, Arkansas, USA. Cabot is located just northeast of the capital Little Rock near the center of the state (Fig. 3). The samples were obtained by one

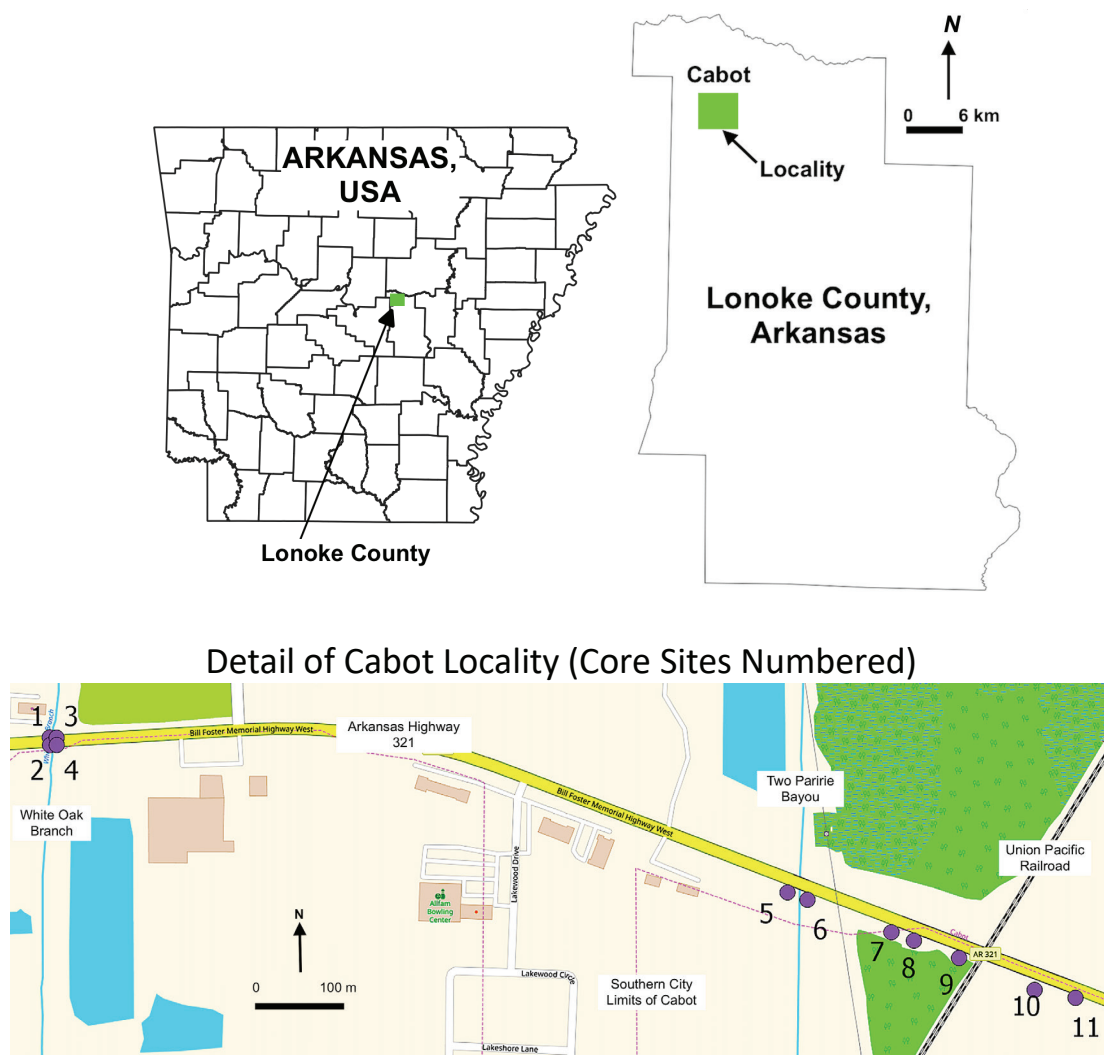


Figure 3. Location of the study area near Cabot, Lonoke County, Arkansas, USA.

of the authors (JCS), who was present during the drilling process. Sample recovery was accomplished utilizing two different methods. The first method was by coring. This method was used in the only borehole encountering the Arkadelphia Formation. Previous borings encountered Quaternary alluvium directly above Paleozoic rock. Once it was observed that Cretaceous/Paleogene sediment was being encountered, subsequent borings were drilled by rotary wash with sampling accomplished by split spoon at 1.52 m intervals to conduct a standard penetration test known as American Association of State Highway and Transportation Officials (AASHTO) T 206-19. Split-spoon sampling involves using an automatic hammer to drive the sampler 0.457 m into the boring wall.

Borings 1 and 3 are on the northern side of the highway, while borings 2 and 4–11 are on the southern side. The first four borings (B1–B4) drilled encountered indurated rock (lower Pennsylvanian Atoka Formation) from 8.5–10.7 m below ground level (bgl). Based on these results, it was decided to core Boring 5 (B5). Subsequent borings, Borings 6 through 11 (B6–B11) were split-spooned in 1.5 m intervals. The only borings of the eleven drilled to produce samples with identifiable Cretaceous otoliths were B5, B6, B8, B9, and B10. The coordinates for the five borings that yielded Cretaceous otoliths are as follows: B5 (34.941292, -92.044155), B6 (34.941187, -92.043788), B8 (34.940683, -92.042295), B9 (34.940450, -92.041533), and B10 (34.940027, -92.040231). The Upper Cretaceous Arkadelphia Formation was present in these five borings and was encountered at depths ranging from 17–27 m. The drilling appears to be essentially along the dip of the Arkadelphia Formation and is probably the reason for the differences in the top of the formation in the different borings. It was approximately 381 m along the roadway between borings B5 and B10. The upper Pennsylvanian Atoka Formation was encountered in B5 through B9 (depths from approximately 23–30 m bgl) but was not encountered in B10.

Aragonitic micromollusks, micrabaciid coral, and fish teeth were first observed in the core occurring in thin, light-colored concentrated layers. One of the authors (JCS) extracted these layers including some of the clay directly above and below for processing. Subsequently, aragonitic fossils, including otoliths, were observed in the split-spoon samples. Any otoliths observed with the naked eye in the split-spoon samples were removed to avoid damage. However, all samples were processed by water screening to obtain otoliths. Each individual sample was dried in a calibrated oven at $110 \pm 5^\circ\text{C}$ and then rewetted to break down the clay. This process was

repeated for some samples to extricate the otoliths from the clay. The samples were then wet-sieved with plain water on a #40 sieve (425 μm). If excess clay was still present after washing, then the sample was dried and washed again. One of the authors (JCS) extracted the otoliths from the residue, and the other author (GLS) identified the otoliths.

Fossil and modern comparative otolith collections and references were utilized for the identification of the specimens. The classification scheme follows that of Nelson et al. (2016), which was greatly influenced by the molecular investigations of Near et al. (2012), Near et al. (2013), and Betancur-R. et al. (2013). Any deviation from this classification is noted. Ordinal names typically follow Wiley and Johnson (2010), while the family-group names and authors of extant fishes follow Van der Laan et al. (2014, 2017, 2018). Authors for genera and species depend greatly upon Eschmeyer's Catalog of Fishes: Genera, Species, References (Fricke et al. 2019) and FishBase (Froese and Pauly 2019). Extant and fossil genera were used when possible, and the recommendations of Janssen (2012) were employed when the generic designation was not evident. This is accomplished by placing the unknown genus in the type genus of the family followed by a question mark indicating that the taxon might belong to any other of the known (or as yet unknown) genera in that family. All type and figured specimens from this investigation are deposited in the Perot Museum of Nature and Science (DMNH) located at 2201 North Field Street, Dallas, Texas 75201, under the catalog numbers 2021-09-01–2021-09-31. Remaining material is in the comparative collection of one of the authors (GS).

RESULTS

Late Cretaceous otoliths were obtained from 16 samples in the Arkadelphia Formation from the borings drilled by the ARDOT at Cabot, Arkansas. The number of samples (shown in parentheses) obtained from each of the borings was as follow: B-5 (7), B-6 (1), B-8 (3), B-9 (2), and B-10 (3). A geologic section with the formations, approximate depth at which samples with otoliths were found, and the number of otoliths from each sample are shown in Figure 4. Analysis of the 2,109 specimens revealed a fairly diverse Late Cretaceous otolith assemblage from the Arkadelphia Formation at the Cabot locality in Arkansas with a diversity of 19 taxa (richness), three taxa in open nomenclature, and one unknown type of lapillus representing at least 20 families (several of these families are indeterminate and may represent extinct families).

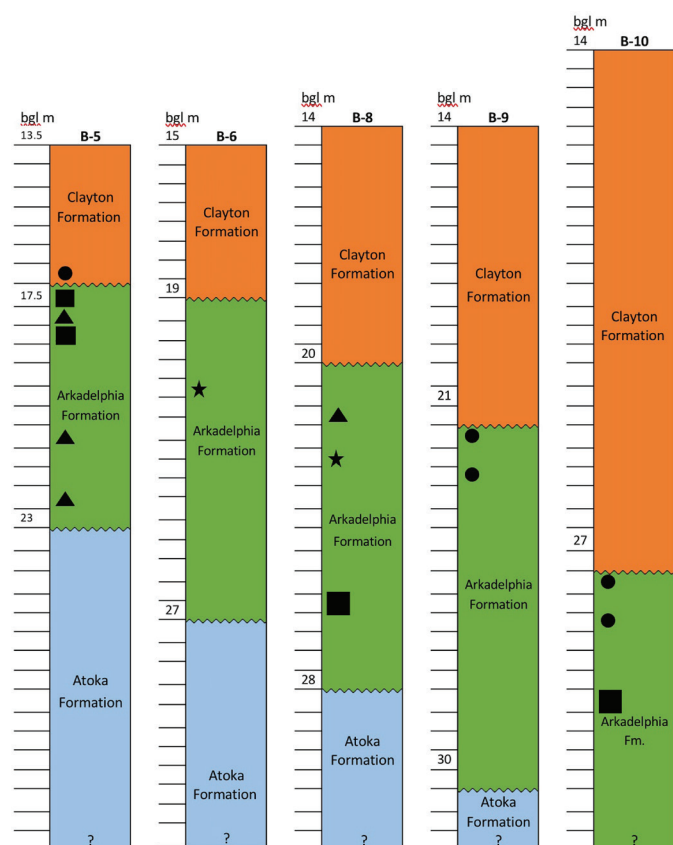


Figure 4. Geologic section of borings B-5, B-6, B-8, B-9, and B-10 at the Cabot site, Lonoke County, Arkansas, USA. Black shapes designate the approximate level at which otoliths were recovered (bgl m=below ground level in meters). The shape is indicative of the number of otoliths recovered at that level: **circle**=less than 10 specimens; **triangle**=11–100 specimens; **rectangle**=101–500 specimens; and **star**=greater than 500 specimens.

SYSTEMATIC PALEONTOLOGY

The taxa represented by the 2,109 otoliths recovered from the Arkadelphia Formation are presented in Table 1. Most of the taxa found in the Arkadelphia Formation, with the exception of a new gadiform, have been described from various other Upper Cretaceous formations in Mississippi (Ripley Formation and Owl Creek Formation), Texas (Kemp Clay), North Dakota (Fox Hills Formation), and Maryland (Severn Formation). The taxa from Mississippi are described in detail by Stringer et al. (2020), from Texas are given in Schwarzhans and Stringer (2020a), from North Dakota are reported by Hoganson et al. (2019) and Schwarzhans and Stringer (2020a), and from Maryland are discussed by Stringer and Schwarzhans (2021). The reader is directed to those works for additional systematic descriptions. Because of the prior descriptions, only those taxa requiring further discussion, such as the new gadiform species, are presented

in detail, while the others are briefly described and discussed. The taxonomic assignment of the Arkadelphia Formation otolith assemblage is extremely relevant as it allows comparisons to other Late Cretaceous assemblages as well as the possible reasons for the uniqueness of the Arkadelphia Formation otoliths.

OSTEICHTHYES HUXLEY, 1880
 ACTINOPTERYGII *SENSU* GOODRICH, 1930
 ELOPIFORMES JORDAN, 1923
 ELOPIDAE VALENCIENNES, 1847
ELOPS LINNAEUS, 1766
ELOPS SP.

FIG. 5A

Material—one small, broken specimen, DMNH 2021-09-01.

Description and Remarks—Although the single, small specimen (2.5 mm) attributed to *Elops* from the Arkadelphia Formation is broken (the anterior portion is missing), there are enough characteristics to assign it to this genus. The overall shape is oval (*sensu* Smale et al. 1995). The dorsal margin is somewhat rounded, while the ventral margin is more broadly and evenly rounded. The inner face is convex. Only a very small portion of the ostium is present, while the cauda is complete. The cauda is fairly wide and has an arching of its dorsal margin near the center. However, the posterior portion of the cauda is slightly downturned. The terminal portion of the cauda is rounded. There is no dorsal depression. The ventral furrow is faint and close to the ventral margin. The outer face is almost flat.

The Arkadelphia Formation specimen shows characteristics comparable to *Elops eutawanus* Schwarzhans, Huddleston, and Takeuki (2018b) from the Cretaceous (Santonian) of Alabama. Like the Arkadelphia Formation specimen attributed to *Elops*, the specimen of *Elops eutawanus* is broken anteriorly (Schwarzhans et al. 2018b, figs. 2D–G). The Arkadelphia Formation *Elops* otolith, especially the cauda and features of the inner face, is similar to the extant *Elops* from the eastern Atlantic off the coast of central Africa (Nolf 2013, Froese and Pauly 2019).

ALBULIFORMES JORDAN, 1923
 ALBULIDAE BLEEKER, 1849
 ALBULIDAE INDETERMINATE

FIG. 5B

Material—four small, eroded specimens, specimen figured, DMNH 2021-09-02 (Fig. 5B).

Description and Remarks—These specimens were

Table 1. Taxa from the Arkadelphia Formation (Cabot locality, Arkansas, USA) with number of specimens, percentage of total, and occurrences in the Cretaceous and Paleocene of North America. Letters in third and fourth columns refer to the following references: **A**=Stringer et al. (2020); **B**=Schwarzahns and Stringer (2020a); **C**=Schwarzahns et al. (2018b); **D**=Hoganson et al. (2019); **E**=Stringer et al. (2018); **F**=Schwarzahns (1985); **G**=Frizzell (1965a). References are not inclusive but provide evidence of the range of the species in North America. **Order=FORMES, Family=idae**

Taxa	No. of specimens	% of total	Known N. Am Cretaceous	Known N. Am Paleocene
ELOPIFORMES				
Elopidae				
<i>Elops</i> sp.	1	0.05	C	F
ALBULIFORMES				
Albulidae				
Albuliformes indeterminate	4	0.19	E	B
<i>Elopothrissus</i> sp.	1	0.05	A	B
ORDER INDETERMINATE				
Family indeterminate				
<i>Genartina</i> sp.	1	0.05	B	B
Osmeroididae				
<i>Osmeroides</i> sp.	3	0.14	A	G
ANGUILLIFORMES				
Anguillidae				
<i>Anguilla?</i> <i>chickasawae</i>	6	0.28	A	B
Ophichthidae				
<i>Echiophis</i> aff. <i>E. semisphaeroides</i>	11	0.52	B	B
Family Indeterminate				
<i>Muraenanguilla?</i> sp.	2	0.09	A	B
OSTEOGLOSSIFORMES				
Family indeterminate				
<i>Kokenichthys navis</i>	2	0.09	A	No
CLUPEIFORMES				
Family indeterminate				
Clupeiform? indeterminate	1	0.05	—	—
SILURIFORMES				
Ariidae				
<i>Arius?</i> <i>subtilis</i>	1	0.05	A	B
Family indeterminate				
<i>Vorhisia vulpes</i>	1,537	72.88	A	No
AULOPIFORMES				
Ichthyotringidae				
<i>Apateodus crenellatus?</i>	3	0.14	A	No
GADIFORMES				
Merlucciidae				
<i>Palaeogadus?</i> <i>belli</i> sp. nov.	148	7.02	No	No
<i>Palaeogadus</i> cf. <i>P. weltoni</i>	1	0.05	B	No

Table 1 (continued). Taxa from the Arkadelphia Formation (Cabot locality, Arkansas, USA) with number of specimens, percentage of total, and occurrences in the Cretaceous and Paleocene of North America. Letters in third and fourth columns refer to the following references: **A**=Stringer et al. (2020); **B**=Schwarzahns and Stringer (2020a); **C**=Schwarzahns et al. (2018b); **D**=Hoganson et al. (2019); **E**=Stringer et al. (2018); **F**=Schwarzahns (1985); **G**=Frizzell (1965a). References are not inclusive but provide evidence of the range of the species in North America. **Order=FORMES, Family=idae**

Taxa	No. of specimens	% of total	Known N. Am Cretaceous	Known N. Am Paleocene
GADIFORMES				
Family indeterminate				
Gadiformes indeterminate	11	0.52	—	—
HOLOCENTRIFORMES				
Family indeterminate				
<i>Tippaha mythica</i>	8	0.38	A	No
BERYCIFORMES				
Family indeterminate				
<i>Eutawichthys maastrichtiensis</i>	21	1.00	A	No
<i>Eutawichthys zideki</i>	287	13.61	A	No
<i>Eutawichthys</i> cf. <i>E. stringeri</i>	48	2.28	C	No
OPHIDIIFORMES				
Ophidiidae				
<i>Ampheristus</i> cf. <i>A. americanus</i>	6	0.28	B	B
Bythitidae				
<i>Protobythites brzobohatyi</i>	4	0.19	B	No
ORDER UNKNOWN				
Family unknown				
Lapillus type 1	1	0.05	A	No
Family unknown				
Unknown sagitta	1	0.05	n/a	n/a
Total	2,109	~100		

assigned to Albulidae indeterminate. They are believed to be closely related to the genus *Albula*, but this determination cannot be made with the existing specimens. The Arkadelphia Formation Albulidae indeterminate are very similar to the Albulidae indeterminate illustrated in Stringer et al. (2020, fig. 4I–J) from the Ripley Formation in northeastern Mississippi. The otoliths are oval in shape (*sensu* Smale et al. 1995) and somewhat elongate (H/L ratios of around 50%). The margins are mainly smooth. The strongly convex inner face has a sulcus that is located primarily supramedially and opens onto the anterodorsal margin. It is difficult to discern the ostium and cauda juncture, but the cauda bends ventrally near its posterior. There is a wide, smooth ventral area with no ventral furrow. The outer face is essentially flat to

slightly concave. The Arkadelphia Formation specimens appear to be different from *Albula* cf. *A. bashiana* (Frizzell, 1965a) reported from the Kemp Clay of Texas by Schwarzahns and Stringer (2020a) in respect to the outline, depth of the cauda, and the down-turned portion of the cauda. The exact taxonomic position and relationship of this albulid is not known presently.

ELOPOTHRISUS SCHWARZHANS, 1981
ELOPOTHRISUS SP.

FIG. 5C

Material—one specimen, DMNH 2021-09-03.

Description and Remarks—The one elongate specimen assigned to *Elopotherissus* has a prominent sulcus clearly divided into an oval ostium opening anteriorly and

anterodorsally, and a narrower, longer more excavated cauda. However, as noted in Schwarzhans and Stringer (2020a) there are significant changes in the H/L ratios with ontogenetic changes in size, which is caused primarily by an increase in the length of the rostrum. There is a slight postdorsal angle as well as some faint marginal crenulation. Like with many other pterothrissids, morphological maturity is only reached when specimens are more than 5 mm long, hence, smaller specimens should not be used for species definition (Schwarzhans 2012). For this reason, DMNH 2021-09-03, which is only 1.83 mm long, is identified only to genus.

Elopothrissus carsonsloani Schwarzhans and Stringer (2020a) was reported from the Danian Clayton Formation but not the Maastrichtian Kemp Clay (Schwarzhans and Stringer 2020a). An unidentified species of *Elopothrissus* was noted by Schwarzhans et al. (2018b) from the Santonian of Alabama. The genus represents an extinct pterothrissid that extends across the K-Pg extinction event and well into the Paleogene (Schwarzhans and Stringer 2020a).

ORDER INDETERMINATE

FAMILY INDETERMINATE

GENARTINA FRIZZELL AND DANTE, 1965

GENARTINA SP. 1 (*SENSU* SCHWARZHANS AND STRINGER, 2020a)

FIG. 5D

Material—one specimen, DMNH 2021-09-04.

Description and Remarks—The one specimen attributed to the fossil otolith-based *Genartina* is similar to *Genartina* sp. 1 reported and illustrated by Schwarzhans and Stringer (2020a). The specimen is high-bodied, somewhat discoid in shape (*sensu* Smale et al. 1995), thin and flat, a gentle and deeply curved ventral margin, and a short, pointed rostrum (which is often broken). The sulcus is slightly dorsal with a much longer, tapering cauda and a somewhat oval ostium. The Arkadelphia specimen resembles *G. abbatiae* (Stinton, 1965) from the European Paleocene and early Eocene (see under “*Harpadontina*” *abbatiae* in Nolf 2013, pl. 58). The specimen also somewhat resembles *G. texana* Dante and Frizzell (1965) described from the Eocene of the USA Gulf Coastal Plain (Frizzell and Dante 1965). Schwarzhans and Stringer (2020) noted that *Genartina* has a relatively large stratigraphic range from Late Cretaceous (Santonian) to middle Eocene (Bartonian). Its taxonomic assignment has been greatly debated and included the Osteoglossiformes Regan (1909) (Frizzell and Dante 1965), Osmeridae Forey (1973) (Nolf 1985), Elopiformes

(including Albuliformes) in Schwarzhans (2003, 2012), Harpodontidae Bleeker (1875) (Nolf 2013), Synodontidae Gill (1861) (Stringer et al. 2016), and Stomiiformes Fink and Weitzmann (1982) (Schwarzhans et al. 2018b). Schwarzhans and Stringer (2020a) proposed that *Genartina* probably belongs to an extinct family and order of bony fishes and placed it after the Albuliformes.

ANGUILLIFORMES REGAN, 1909

OSMEROIDIDAE FOREY, 1973

OSMEROIDES AGASSIZ, 1837

OSMEROIDES SP.

FIG. 5E

Material—three specimens, specimen figured, DMNH 2021-09-05.

Description and Remarks—The three small specimens assigned to *Osmeroides* are slightly oval shaped (*sensu* Smale et al. 1995) with a somewhat irregular dorsal margin and mostly smooth ventral margin. The dorsal field is much smaller than the ventral field. There is a heterosulcoid-type sulcus that is located primarily supramedially with a very slight downturn at the posterior of the slanted cauda. The inner face is convex, while the outer face is concave. The Arkadelphia specimens are similar to the *Osmeroides* sp. described and illustrated from the Ripley Formation in northeastern Mississippi by Stringer et al. (2020). Due to their small size and poor preservation, the assignment is tenuous, and a species determination is not possible.

ANGUILLIDAE RAFINESQUE, 1810

ANGUILLA SCHRANK, 1798

ANGUILLA? CHICKASAWAE SCHWARZHANS AND STRINGER, 2020a

FIG. 5F

Material—six specimens, specimen figured, DMNH 2021-09-06.

Description and Remarks—Distinguishing characteristics of *Anguilla? chickasawae* include a somewhat oval to ovate shape in well preserved specimens (*sensu* Smale et al. 1995) with a H/L ratio of approximately 66%, a convex inner face, a narrow, almost horizontal sulcus with a poorly-defined ostium and cauda. The posterior margin is commonly almost vertical. Stringer et al. (2020, fig. 5A–E) originally described *A.? chickasawae* from the Ripley Formation (Maastrichtian) of Mississippi. *Anguilla? chickasawae* differs from other Late Cretaceous or Paleogene anguillid otoliths by its much longer ostium. Schwarzhans and Stringer (2020a) postulated that *A.? chickasawae* could represent a fossil

genus of the Anguillidae or a closely related fossil family of which otoliths are not known presently.

OPHICHTHIDAE [RAFINESQUE, 1815](#)

ECHIOPHIS [KAUP, 1856](#)

ECHIOPHIS AFF. *E. SEMISPHAEROIDES* ([SCHWARZHANS, 2003](#))

FIG. 5G

Material—11 specimens, specimen figured, DMNH 2021-09-07.

Description and Remarks—These otoliths tend to be primarily circular in shape (*sensu* [Smale et al. 1995](#)). The nearly straight to slightly outwardly curved posterodorsal margin produces a discernible angle. The otolith is thick with mainly smooth margins. The inner face is strongly convex and smooth with a deep sulcus. The sulcus has a long, narrow, and deep cauda, while the ostium is much shorter and shallower. The outer face is flat and relatively smooth. [Schwarzahns \(2003\)](#) originally classified *Echiophis semisphaeroides* in the family Anguillidae. However, [Schwarzahns \(2019\)](#) illustrated the modern *Echiophis brunneus* Castro-Aguirre and Suárez de los Cobos (1983), and examination of the specimen has shown a great similarity in convexity and smoothness of the inner face as well as the shape and depth of the sulcus. There are three extant species of *Echiophis* known from tropical and subtropical America. Modern ophichthid otoliths illustrate significant variability and are still not understood well. In fact, it is often difficult to assign fossil otoliths to genera with very much confidence. However, [Schwarzahns and Stringer \(2020a\)](#) believed that the similarity was significant compared to other known anguilliform otoliths and changed the species to the family Ophichthidae.

FAMILY INDETERMINATE

MURAENANGUILLA [SCHWARZHANS, 2019](#)

MURAENANGUILLA? SP.

FIG. 5H

Material—two worn, broken specimens, specimen figured, DMNH 2021-09-08.

Description and Remarks—The *Muraenanguilla?* specimens from the Arkadelphia Formation are oval in shape (*sensu* [Smale et al. 1995](#)) with a H/L ratio of approximately 66%. The convex inner face has a fairly deep, moderately narrow sulcus. It is difficult to differentiate the ostium and cauda. The dorsal margin tends to be irregularly curved, while the ventral margin appears to be smooth and regularly curved. These specimens resemble *Muraenanguilla unionensis* [Schwarzahns and](#)

[Stringer \(2020b\)](#), which is known from the Ripley and Owl Creek formations (Maastrichtian) of Mississippi ([Stringer et al. 2020](#)). Unfortunately, the specimens are not preserved well enough to make any definitive identification. The genus is also known from the Paleogene of Europe ([Schwarzahns 2019](#)), the Upper Cretaceous Coon Creek type locality in Tennessee ([Stringer 2016b](#)), and the upper Maastrichtian Severn Formation in Maryland ([Huddleston and Savoie 1983](#), [Stringer and Schwarzahns 2021](#)).

OSTEOGLOSSIFORMES [REGAN, 1909](#)

FAMILY INDETERMINATE

KOKENICHTHYS [SCHWARZHANS, 2010](#)

KOKENICHTHYS NAVIS [SCHWARZHANS AND STRINGER, 2020b](#)

FIG. 6A

Material—two eroded, but diagnostic, specimens, specimen figured, DMNH 2021-09-9.

Description and Remarks—The sagitta of *Kokenichthys navis* has several diagnostic features including its very unusual sulcus, which is located almost entirely dorsally. The shape is mainly oval (*sensu* [Smale et al. 1995](#)) with smooth margins. The ventral margins are fairly sharp, and there is a rostrum. The convex inner face has a broad sulcus that appears very shallow and easily eroded. Other specimens of *K. navis* show similar erosion (see fig. 6 A in [Stringer et al. 2020](#), on the specimens from the Ripley and Owl Creek formations of Mississippi). However, the other specimens in [Stringer et al. \(2020, fig. 6C–F\)](#) are much better preserved, and the ostial and caudal regions are clearly visible. In addition to the Arkadelphia Formation in Arkansas, *K. navis* is known from the Ripley Formation in Mississippi and possibly in the Tar Heel Formation in North Carolina ([Stringer et al. 2018](#)). The species is very abundant in the Ripley Formation at the Blue Springs locality in northeastern Mississippi with 69 specimens ([Stringer et al. 2020](#)).

CLUPEIFORMES [GOODRICH, 1909](#)

FAMILY INDETERMINATE

CLUPEIFORM? INDETERMINATE

FIG. 6B

Material—one eroded, broken specimen, DMNH 2021-09-10.

Description and Remarks—Although small and somewhat eroded, this specimen is tentatively assigned to the Clupeiformes and is included because of the rarity of clupeids in the Cretaceous. The outline of the sagitta, the flat inner face, and the shape of the sulcus indicate a possible clupeid. [Schwarzahns et al. \(2018b\)](#) assigned 13

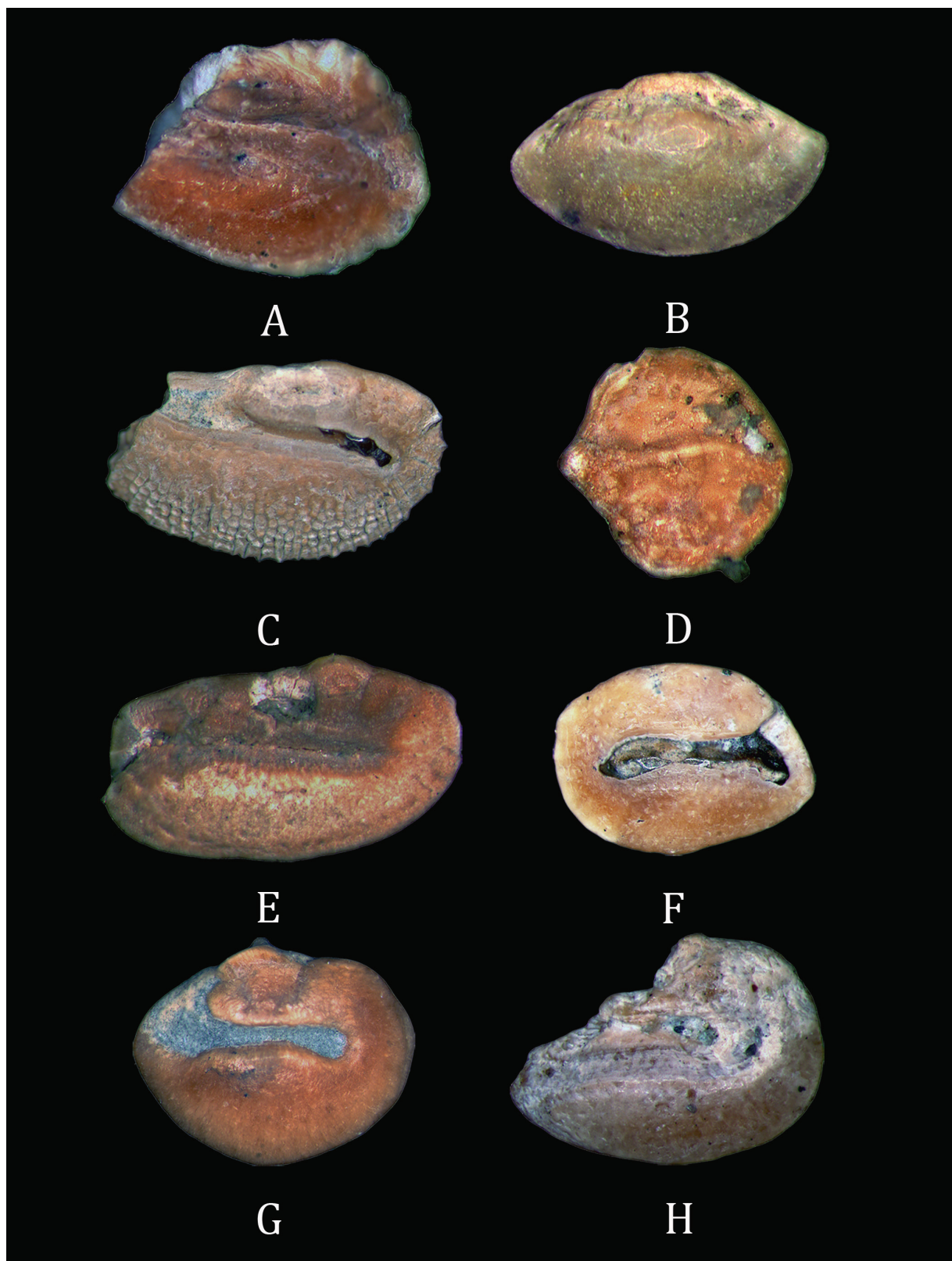


Figure 5. Otoliths from the Cretaceous Arkadelphia Formation. All specimens unless otherwise noted are inner views of right sagittae. Length in mm. **A.** *Elops* sp., DMNH 2021-09-01, 1.89 mm. **B.** *Albuliformes* indeterminate, DMNH 2021-09-02, 1.42 mm. **C.** *Elopothrissus* sp. DMNH 2021-09-03, 1.83 mm. **D.** *Genartina* sp. DMNH 2021-09-04, 0.85 mm. **E.** *Osmeroides* sp. DMNH 2021-09-05, 3.85 mm. **F.** *Anguilla?* *chickasawae* Schwarzhans and Stringer (2020b), DMNH 2021-09-6, 1.90 mm. **G.** *Echiophis* aff. *E. semisphaeroides* Schwarzhans (2003), DMNH 2021-09-07, 3.25 mm. **H.** *Muraenanguilla?* sp. DMNH 2021-09-08, 2.18 mm.

specimens to Clupeiform indeterminate from the Eutaw Formation (upper Santonian) of Alabama.

SILURIFORMES CUVIER, 1817

ARIIDAE BLEEKER, 1862

ARIUS VALENCIENNES, 1840

ARIUS? SUBTILIS SCHWARZHANS AND BRATISHKO, 2011

FIG. 6C

Material—one well preserved specimen, DMNH 2021-09-11.

Description and Remarks—*Arius? subtilis* is represented by the utricular otolith or lapillus rather than the sagitta. The lapillus is oval in outline (*sensu* Smale et al. 1995) and has characteristically smooth margins except for one diagnostic projection. It is typically plano-convex and usually fairly thin. The flat side often has radial growth lines visible, especially in eroded specimens. In some specimens, a very lightly impressed sulcal area may be visible on the convex side. *Arius? subtilis* was first identified in the Paleocene of the Ukraine by Schwarzhans and Bratishko (2011) and is fairly common in the early Paleocene of Europe (Schwarzhans 2012). It is also known from the Clayton Formation (early Paleocene) of the USA (Schwarzhans and Stringer 2020a). However, its range was extended to the Late Cretaceous when it was reported from the Ripley and Owl Creek formations of Mississippi (Stringer et al. 2020), where it was abundant (125 specimens from the two formations). It also occurs in the Coon Creek Formation in Tennessee (as Ariidae indeterminate in Stringer 2016b) and in the Kemp Clay (upper Maastrichtian) of northeast Texas, where it was very abundant with 195 specimens (Schwarzhans and Stringer 2020a). The rarity of *Arius? subtilis* in the stratigraphically equivalent Arkadelphia Formation is enigmatic.

FAMILY INDETERMINATE

VORHISIA FRIZZELL, 1965b

VORHISIA VULPES FRIZZELL, 1965b

FIG. 6D–H

Material—1,537 specimens. Five specimens figured: DMNH 2021-09-12, DMNH 2021-09-13, DMNH 2021-09-14, DMNH 2021-09-15, DMNH 2021-09-16.

Description and Remarks—*Vorhisia vulpes* is one of most ubiquitous Late Cretaceous otoliths known in the USA and has been reported in the Fox Hills Formation (North Dakota), the Kemp Clay (Texas), the Ripley Formation (Mississippi), and the Severn Formation (Maryland) (Hoganson et al. 2019, Woodward 2003, Schwarzhans and Stringer 2020a, Stringer et al. 2020, and Huddleston

and Savoie 1983). It has been classified primarily as an extinct siluriform, or perhaps an ariid, based on the large lapillus and similarities to extant ariid lapilli. One Arkadelphia Formation specimen was extremely large at 19.36 mm in length and 14.02 mm in height (Fig. 6H), which is rare, considering that it was recovered from a bore sample. Stringer et al. (2020) stated that *Vorhisia* probably represents an extinct family of the Siluriformes or Ostariophysi, but there is also the possibility that it could relate to an extinct higher taxonomic group or even a non-teleost fish as some extant Holostei have large lapilli.

To state that *V. vulpes* is the most common species in the upper Maastrichtian Arkadelphia Formation is an understatement. The total specimens in the Arkadelphia Formation assemblage is 2,109, and 1,537 of those (72.88%) are *V. vulpes*. The species is abundant in the Severn Formation (Huddleston and Savoie 1983), but noticeably less at 55%. *Vorhisia vulpes* is the most abundant species in the Kemp Clay, but its percentage is approximately 35% (Schwarzhans and Stringer 2020a). The percentage of *V. vulpes* in the Arkadelphia Formation certainly seems to indicate that the paleoenvironmental parameters were decidedly conducive for its growth and proliferation. *Vorhisia vulpes* has not been found in Europe although Cretaceous otoliths have been investigated in several areas (Nolf 2003, Schwarzhans 2010, Schwarzhans and Jagt 2021). Current studies indicate that the distribution of *Vorhisia vulpes* is limited to the USA. As noted by Schwarzhans and Stringer (2020a), *V. vulpes* was one of the most prominent and widespread teleostean species to succumb to the K-Pg extinction event in North America.

AULOPIFORMES ROSEN, 1973

ICHTHYOTRINGIDAE JORDAN, 1905

APATEODUS WOODWARD, 1901

APATEODUS CRENELLATUS? SCHWARZHANS AND STRINGER, 2020b

FIG. 7A

Material—three specimens, specimen figured, DMNH 2021-09-9.

Description and Remarks—The three Arkadelphia Formation specimens fit the description of *Apateodus crenellatus* presented in Stringer et al. (2020) from the Ripley Formation in northeastern Mississippi. Unfortunately, none of the thin, fragile specimens have a preserved rostrum like the holotype shown in Stringer et al. (2020, fig. 7 G–I). The outline of *A. crenellatus* appears to be more oval (*sensu* Smale et al. 1995), but if the long and

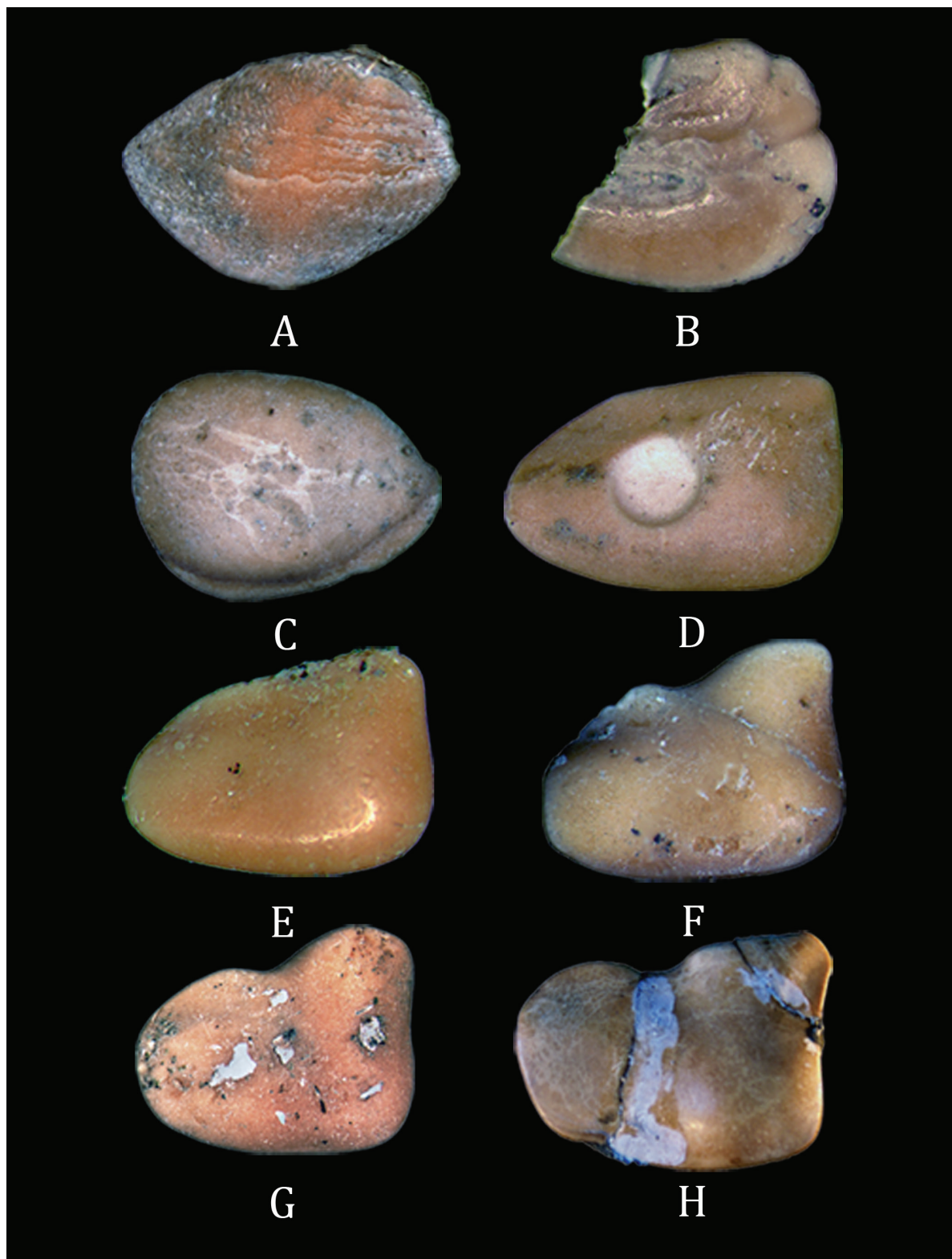


Figure 6. Otoliths from the Cretaceous Arkadelphia Formation. All specimens unless otherwise noted are inner views of right saggittae. Length in mm. **A.** *Kokenichthys navis* Schwarzhans and Stringer (2020b), DMNH 2021-09-9, 4.10 mm. **B.** Clupeiform? indeterminate DMNH 2021-09-10, 1.42 mm. **C.** *Arius subtilis* Schwarzhans and Bratishko (2011), DMNH 2021-09-11, 4.61 mm. **D.** *Vorhisia vulpes* Frizzell (1965b), DMNH 2021-09-13, 2.49 mm. **E.** *Vorhisia vulpes* Frizzell (1965b), DMNH 2021-09-14, 3.06 mm. **F.** *Vorhisia vulpes* Frizzell (1965b), DMNH 2021-09-15, 3.99 mm. **G.** *Vorhisia vulpes* Frizzell (1965b), DMNH 2021-09-16, 7.98 mm. **H.** *Vorhisia vulpes* Frizzell (1965b), DMNH 2021-09-12, 19.36 mm.

moderately pointed rostrum is present, it is more ovate in outline (*sensu* Smale et al. 1995). The margins are variable, which may be related to erosion. The heterosulcoid sulcus appears to be more slightly ventral and extends across essentially the entire inner fac. The outer face is typically flat and smooth.

The classification of *A. crenellatus* has been debated for several decades since its initial discovery by Nolf and Dockery (1990) in the Coffee Sand (Campanian) of north-eastern Mississippi. Its classification as an aulopiform was first suggested by Stringer et al. (2016) and Stringer et al. (2018). Its classification was confirmed when an otolith was discovered *in situ* by CT micro-scanning in *A. corneti* Forir (1887) by Schwarzhans et al. (2018a). This discovery and the subsequent revised taxonomy are also congruent with modern molecular-based phylogenetic and dating studies such as Near et al. (2012), Betancur-R. et al. (2013), Near et al. (2013), and Betancur-R et al. (2017).

GADIFORMES GOODRICH, 1909
MERLUCCIIDAE RAFINESQUE, 1815
PALAEOGADUS RATH, 1859
PALAEOGADUS? BELLI SP. NOV.

Fig. 7B–H

Diagnosis—Moderately compressed, approximately oblong otoliths (*sensu* Smale et al. 1995) with a homosulcoid-type sulcus. The H/L ratio ranges from approximately 47%–62%, which is related to ontogenetic changes. Anterodorsal dome (predorsal expansion) evident on specimens greater than 2.0 mm. Ostium and cauda nearly equal in length. Narrow collum with ostial and caudal colliculi very near. Prominent ventral furrow that curves away from anteroventral and posteroventral margins.

Holotype—*Palaeogadus? belli* sp. nov., DMNH 2021-09-22, 3.13 mm, Arkadelphia Formation (Upper Cretaceous, upper Maastrichtian), Cabot, Lonoke County, Arkansas, USA ; coordinates: 34.941292, -92.044155.

Paratypes—*Palaeogadus? belli* sp. nov., DMNH 2021-09-18, 1.25 mm. *Palaeogadus? belli* sp. nov., DMNH 2021-09-19, 1.78 mm. *Palaeogadus? belli* sp. nov., DMNH 2021-09-20, 2.21 mm. *Palaeogadus? belli* sp. nov., DMNH 2021-09-21, 2.34 mm. Same locality as holotype.

Occurrence—Type locality: Cabot, Lonoke County, Arkansas, USA ; coordinates: 34.941292, -92.044155 (Boring 5; Station 266; 22.86–23.32 m below ground elevation), Arkadelphia Formation, Upper Cretaceous (upper Maastrichtian). The coordinates for the four other borings that yielded *Palaeogadus? belli* sp. nov. are as

follows: B6 (34.941187, -92.043788), B8 (34.940683, -92.042295), B9 (34.940450, -92.041533), and B10 (34.940027, -92.040231).

Etymology—Species named for retired Professor Dennis Bell (Monroe, Louisiana, USA) for his extensive assistance in paleontological vertebrate and invertebrate research, especially in the areas of photography of fossils and preparation of manuscript figures.

Description—Sagitta is moderately compressed. Shape is elongated and is best described as oblong (*sensu* Smale et al. 1995). Larger specimens tend to be more elongated and narrower posteriorly. Margins are crenulated, especially on the dorsal and ventral margins (all specimens were less than 3.5 mm in length). The dorsal margin tends to have more and deeper crenulations. Anterior margin is somewhat compressed but primarily rounded. Dorsal margin is more broadly rounded on smaller specimens, but a diagnostic anterodorsal (predorsal) dome becomes evident in specimens greater than 2.0 mm. Posterior margin is similar to anterior margin but tends to become more compressed and pointed in the larger specimens. The ventral margin is gently but unevenly curved and can be almost horizontal in the center.

The inner face is convex with a long, homosulcoid-type sulcus. The sulcus extends from almost the anterior to very near the posterior to the extent it could be classified as pseudo-ostiocaudal as defined by Smale et al. (1995). There is a fairly narrow collum between the ostium and the cauda. The ostium and cauda are both elongated, compressed ovals in shape and are similar in length. Colliculi are present in the ostium and cauda and approach very closely to the collum. The dorsal depression is found primarily above the collum. The dorsal depression is small, elongated but somewhat irregular, and best defined on its ventral margin. The ventral furrow is present and is very close to the ventral edge in the center. However, the ventral furrow curves strongly away from the anteroventral and posteroventral margins toward the sulcus. The outer face is irregular with a characteristic hollowing in the central dorsal area, especially in the larger of the specimens.

Remarks—*Palaeogadus? belli* sp. nov. has gadiform features that seem to place it into the family Merlucciidae. The species is similar to *Palaeogadus weltoni* Schwarzhans and Stringer (2020a) described from the Upper Cretaceous (upper Maastrichtian) Kemp Clay in northeast Texas (Schwarzhans and Stringer 2020a). Morphological features similar to *P. weltoni* include the nearly equal length of the ostium and cauda, no pseudocolliculum in the collum, and the similar shape of the

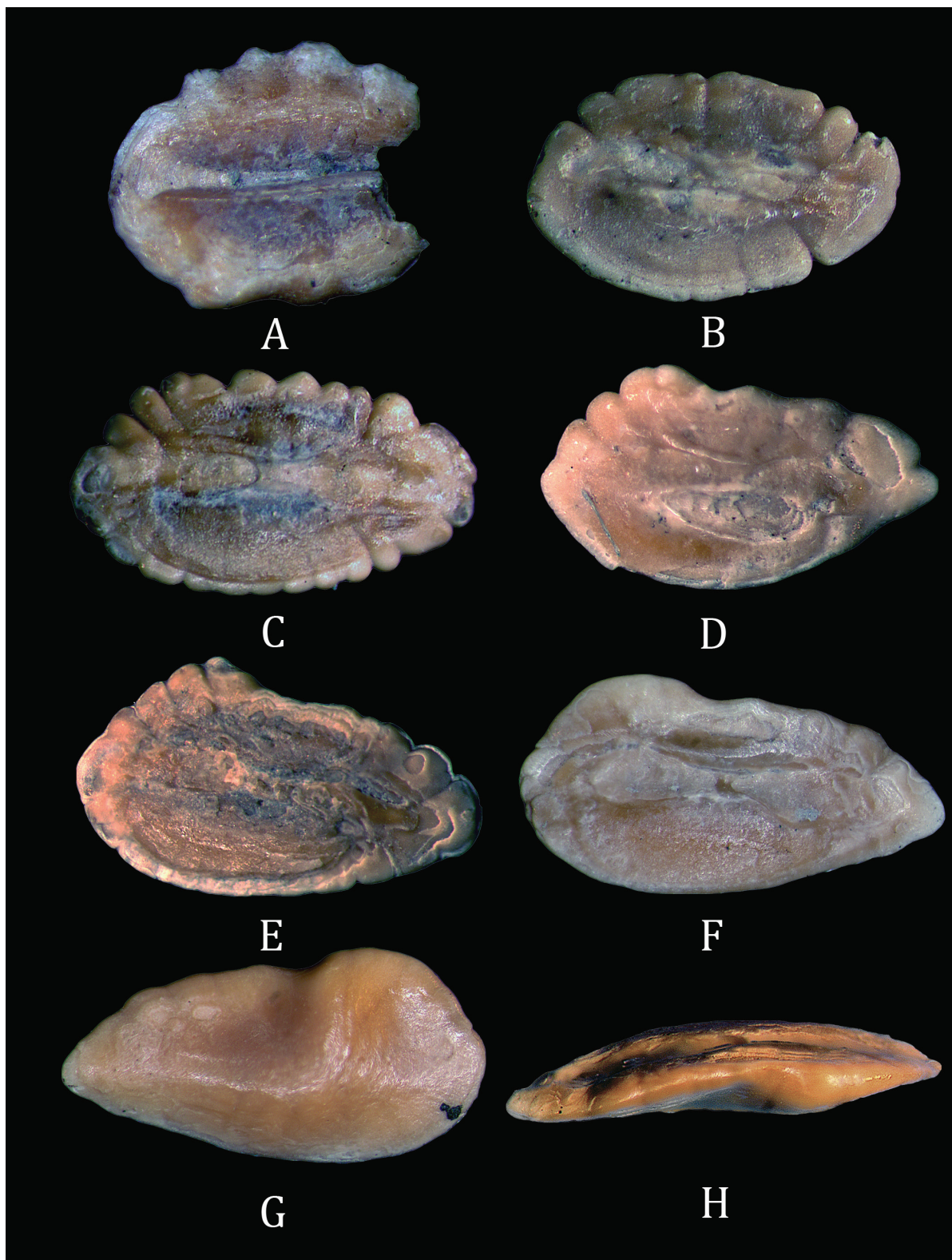


Figure 7. Otoliths from the Cretaceous Arkadelphia Formation. All specimens unless otherwise noted are inner views of right sagittae. Length in mm. **A.** *Apateodus crenellatus?* Schwarzhans and Stringer (2020b), DMNH 2021-09-17, 1.78 mm. **B.** *Palaeogadus? belli* sp. nov., DMNH 2021-09-18, 1.25 mm (paratype). **C.** *Palaeogadus? belli* sp. nov., DMNH 2021-09-19, 1.78 mm (paratype). **D.** *Palaeogadus? belli* sp. nov., 2021-09-20, 2.21 mm (paratype). **E.** *Palaeogadus? belli* sp. nov., DMNH 2021-09-21, 2.34 mm (paratype). **F.** *Palaeogadus? belli* sp. nov., DMNH 2021-09-22, 3.13 mm (holotype). **G.** *Palaeogadus? belli* sp. nov., DMNH 2021-09-22, 3.13 mm (holotype, outer view). **H.** *Palaeogadus? belli* sp. nov., DMNH 2021-09-22, 3.13 mm (holotype, dorsal view).

ventral furrow. However, there are some features that readily distinguish it from *P. weltoni*. These include the development of a fairly prominent anterodorsal dome by specimens greater than 2.0 mm and a narrow collum with the ostial and caudal colliculi situated very near the collum. *Palaeogadus? belli* also shows similarity to *P.? bratishkoi* Schwarzhans (2012) known from Paleocene (Thanetian) of Austria and is especially evident in the holotype (fig. 110a) and two of the paratypes (figs. 112 and 113) as illustrated in Schwarzhans (2012).

Palaeogadus? belli is one of the most common specimens in the Arkadelphia Formation comprising 7.02% of the total assemblage. It is only surpassed by the extremely abundant *Vorhisia vulpes* and *Eutawichthys zideki*. Unfortunately, all of the gadiform specimens from the Arkadelphia are small (around 3.1 mm in length for the best-preserved specimens), and some are poorly preserved. In spite of the size and preservation, there are features that indicate that the otoliths could belong to the merlucciid genus *Palaeogadus* to which it is tentatively assigned. However, it is important to note that there are many primitive features present in the Late Cretaceous *P.? belli*, and there is the distinct possibility that it represents an unknown fossil genus that may also include *P. weltoni* of Schwarzhans and Stringer (2020a) and possibly *P.? bratishkoi* of Schwarzhans (2012). The relatively large percentage of *P.? belli*, a putative cool-water form, in the Arkadelphia Formation at the Cabot site in Arkansas is certainly important in the determination and evaluation of the paleoenvironment and paleogeography in this portion of the Gulf Coastal Plain during the late Maastrichtian. This importance is addressed further and in greater detail in the “Paleoecology and Paleogeography” section.

PALAEOGADUS RATH, 1859

PALAEOGADUS CF. *P. WELTONI* SCHWARZHANS AND STRINGER, 2020a

FIG. 8A

Material—one small, slightly eroded specimen, DMNH 2021-09-23.

Description and Remarks—The one Arkadelphia Formation specimen assigned to *Palaeogadus weltoni* is very small and eroded. However, it was felt that it possessed enough gadid features to compare it to *Palaeogadus* cf. *P. weltoni*. Similarities include the overall oblong shape (*sensu* Smale et al. 1995), the slightly convex inner face; the tapered and rounded anterior and posterior margins that are almost alike; the homosulcoid-type sulcus; a broadly, gently arched dorsal margin; a very shallow ventral margin that approaches horizontal; and

a prominent ventral furrow extending from under the anterior of the ostium to near the posterior of the cauda; the anterior and posterior ends of the ventral furrow appear to turn upwards. It compares very well to the one specimen of *P. weltoni* illustrated by Schwarzhans and Stringer (2020a) from the Kemp Clay in Texas and to the specimens shown by Stringer and Schwarzhans (2021) from the Severn Formation in Maryland. *Palaeogadus* is an extinct genus that is known from otoliths and skeletons from the early Paleogene of Europe (Schwarzhans 2003, fig. 20A–I).

GADIFORMES INDETERMINATE

FIG. 8B

Material—11 very small or broken specimens, specimen figured, DMNH 2021-09-24.

Description and Remarks—The 11 specimens designated as Gadiformes indeterminate are included because of the rarity of the Gadiformes in the Cretaceous. Their occurrence is certainly worth noting even at this taxonomic level. Some of the specimens represent non-diagnostic juveniles or perhaps even larval, while others represent badly eroded specimens. The specimens have typical gadiform characteristics such as a long, homosulcoid-type sulcus with a collum, a convex inner face, a flat or slightly concave outer face, the outline, and extensive crenulations. It is likely that the specimens represent gadiforms already known from the Arkadelphia Formation, but this cannot be determined with certainty. Schwarzhans (2003) used a similar identification of juvenile gadiforms from the Paleocene of Denmark.

HOLOCENTRIFORMES PATTERSON, 1993

FAMILY INDETERMINATE

TIPPAHA SCHWARZHANS AND STRINGER, 2020a

TIPPAHA MYTHICA SCHWARZHANS AND STRINGER, 2020a

FIG. 8C

Material—eight specimens including three complete well-preserved specimens, specimen figured, DMNH 2021-09-25.

Description and Remarks—*Tippaha mythica* is certainly the most unique and impressive otolith in the Arkadelphia Formation assemblage based on its distinctive morphological characteristics. The basic outline is somewhat oblong to elliptic (*sensu* Smale et al. 1995), but there are numerous features that modify the shape. The convex inner face has a distinct and characteristic pseudobiostial sulcus that is primarily shallow except for a slightly deeper posterior portion of the cauda. An exceptional feature of the anterior portion of the cauda

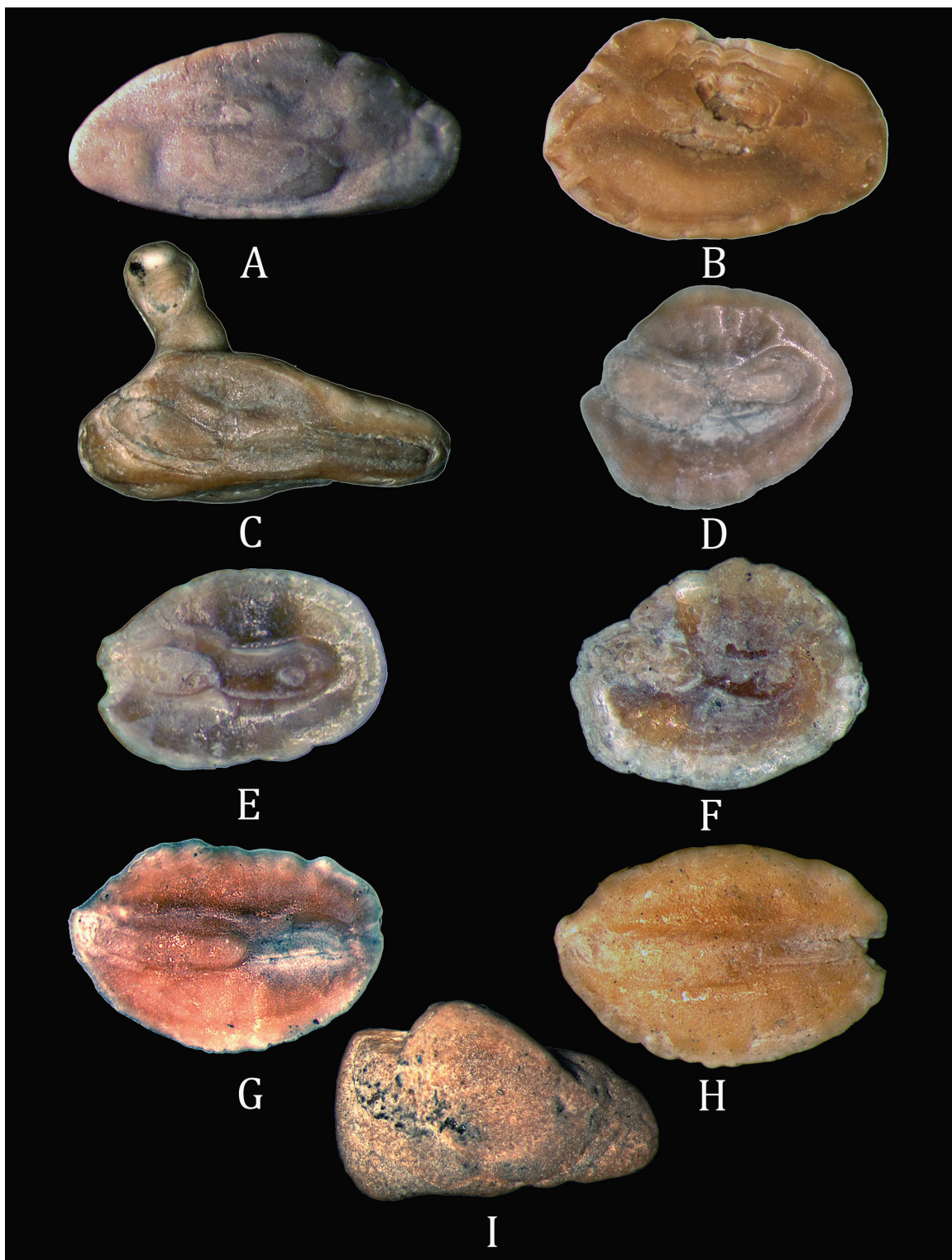


Figure 8. Otoliths from the Cretaceous Arkadelphia Formation. All specimens unless otherwise noted are inner views of right sagittae. Lapilli are macular views. Length in mm. **A.** *Palaeogadus* cf. *P. weltoni* Schwarzhans and Stringer (2020a), DMNH 2021-09-23, 1.46 mm. **B.** Gadiformes indeterminate, DMNH 2021-09-24, 1.56 mm. **C.** *Tippaha mythica* Schwarzhans and Stringer (2020a), DMNH 2021-09-25, 3.85 mm. **D.** *Eutawichthys maastrichtiensis* Nolf and Stringer (1996), DMNH 2021-09-26, 3.93 mm. **E.** *Eutawichthys zideki* Nolf and Stringer (1996), DMNH 2021-09-27, 1.42 mm. **F.** *Eutawichthys* cf. *E. stringeri* Schwarzhans, Huddleston, and Takeuchi (2018b), DMNH 2021-09-28, 1.85 mm. **G.** *Ampheristus* cf. *A. americanus* Schwarzhans and Stringer (2020a), DMNH 2021-09-29, 1.58 mm. **H.** *Protobythities brzobohaty* Schwarzhans (2010), DMNH 2021-09-30, 1.68 mm. **I.** Lapillus type 1, DMNH 2021-09-31, 2.98 mm.

is the fading of its dorsal margin toward the moderately deep, well-marked, oval dorsal depression. There is no ventral furrow, but a long, obvious ventral depression is present under the sulcus. The most prominent feature is a long, fairly narrow predorsal projection that typically leans anteriorly at about 65–75°. The length of this conspicuous protuberance is often 25–30% of the length of the otolith. The outer face is usually irregular and nearly flat except for the massive predorsal protuberance.

Stringer et al. (2020) noted that *T. mythica* is probably the most distinct and remarkable otolith morphology presently known from the Cretaceous. In addition to the eight specimens from the Arkadelphia Formation, *T. mythica* is known from the Ripley Formation and the Owl Creek Formation, both Upper Cretaceous sites in northeastern Mississippi (Stringer et al. 2020) and the Providence Sand in Alabama, according to J. Ebersole, Director of Collections at McWane Science Center, Birmingham, Alabama (personal communication, 2020).

BERYCIFORMES REGAN, 1909

FAMILY INDETERMINATE TYPE 1 (*SENSU* STRINGER AND SCHWARZHANS, 2021)

EUTAWICHTHYS SCHWARZHANS, HUDDLESTON, AND TAKEUCHI, 2018b

EUTAWICHTHYS MAASTRICHTIENSIS (NOLF AND STRINGER, 1996)

FIG. 8D

Material—21 specimens, specimen figured, DMNH 2021-09-26.

Description and Remarks—*Eutawichthys maastrichtiensis* has a nearly circular to slightly oval outline (*sensu* Smale et al. 1995). The dorsal margin is irregular, while the ventral margin can have crenulations that are often obliterated by erosion. The thin sagitta is only slightly convex with a distinctive, long sulcus (heterosulcoid type) that is wide and continuously curved. The cauda curves diagnostically dorsally in its posterior section. There is a depressed area that is fairly distinct above the center of the sulcus.

Eutawichthys maastrichtiensis was designated as an apogonid for many years, and there are certainly resemblances to the apogonids. Its designation as a berycid is discussed at length in Stringer et al. (2016) and is more congruent with molecular studies such as Betancur-R. et al. (2013) that indicate a much later divergence for the apogonids (around 45 Ma). The fossil-based genus *Eutawichthys* was erected by Schwarzhans et al. (2018b). *Eutawichthys maastrichtiensis* is known from several Cretaceous formations including the Severn Formation

of Maryland (Huddleston and Savoie 1983), the Woodbury Formation of New Jersey (Stringer et al. 2016), the Eutaw Formation of Alabama (Schwarzhans et al. 2018a), the Tar Heel Formation of North Carolina (Stringer et al. 2018), the Coon Creek Formation of Tennessee (Stringer 2016b), the Ripley Formation of Mississippi (Stringer et al. 2020), and the Kemp Clay of Texas (Schwarzhans and Stringer 2020a).

EUTAWICHTHYS ZIDEKI (NOLF AND STRINGER, 1996)

FIG. 8E

Material—287 specimens, specimen figured, DMNH 2021-09-27.

Description and Remarks—*Eutawichthys zideki* is the most abundant species of this genus in the Arkadelphia Formation. It is characterized by an oval outline (*sensu* Smale et al. 1995), but larger specimens can become somewhat angular. Although the sulcus (heterosulcoid type) is not deeply impressed, it is distinct and extends for approximately 75% of the length of the inner face. The sulcus is almost horizontal, which is a distinguishing feature of the species. The ostium and cauda are approximately the same length, and the ostium is only slightly wider than the cauda. *Eutawichthys zideki* is geographically widespread in its distribution and has been reported from the Severn Formation of Maryland (Huddleston and Savoie 1983), the Woodbury Formation of New Jersey (Stringer et al. 2016), the Tar Heel Formation of North Carolina (Stringer et al. 2018), the Coon Creek Formation of Tennessee (Stringer 2016b), the Eutaw Formation of Alabama (Schwarzhans et al. 2018b), and the Ripley Formation of Mississippi (Stringer et al. 2020).

EUTAWICHTHYS STRINGERI SCHWARZHANS, HUDDLESTON, AND TAKEUCHI, 2018b

EUTAWICHTHYS CF. *E. STRINGERI*

FIG. 8F

Material—48 specimens, specimen figured, DMNH 2021-09-28.

Description and Remarks—The specimens assigned to *Eutawichthys stringeri* are characterized by an anterior margin with a broad, dorsally shifted rostrum, a broadly rounded dorsal margin, a broadly rounded posterior margin, and a moderately deep, gently and regularly curved convex ventral margin. The inner face is slightly convex with a shallow, moderately wide sulcus divided into an ostium and cauda. The ostium is curved upwards towards the dorsal margin of the rostrum. The cauda is about the same length as the ostium and is oriented

upwards. The cauda has a rounded tip that ends well before the posterior margin.

Excellent figures of the ontogeny of *E. stringeri* are found in Schwarzhans et al. (2018b) and readily illustrate the differences between it and other species of *Eutawichthys*. The distribution of *E. stringeri* is not nearly as widespread as *E. maastrichtiensis* and *E. zideki*. It has only been previously reported from the Woodbury Formation (early–middle Campanian) of New Jersey (Stringer et al. 2016) and the Eutaw Formation (upper Santonian) of Alabama (Schwarzhans et al. 2018b), where it represents the most abundant species.

OPHIDIIFORMES BERG, 1937
OPHIDIIDAE RAFINESQUE, 1810

AMPHERISTUS KÖNIG, 1825

AMPHERISTUS CF. *A. AMERICANUS* SCHWARZHANS AND
STRINGER, 2020a

FIG. 8G

Material—six specimens, specimen figured, DMNH 2021-09-29.

Description and Remarks—The sagitta of *Ampheristus* cf. *A. americanus* is basically oval (*sensu* Smale et al. 1995) with a long, nearly straight, smooth dorsal margin, while the ventral margin is regularly curved, deepest anterior of its middle, and relatively shallow. The inner face is convex horizontally with a long, slightly s-shaped sulcus that is medially located. The sulcus almost reaches the anterior margin but ends well before the posterior margin. *Ampheristus americanus* was first named by Schwarzhans and Stringer (2020a) based on 143 specimens from the Kemp Clay (Maastrichtian) of Texas and the Clayton Formation (Danian) of Arkansas. According to Schwarzhans (1981) the fossil genus *Ampheristus* is considered to be closely related to the extant *Hoplobrotula* Gill (1863).

PROTOBYTHITES SCHWARZHANS, 2010
PROTOBYTHITES BRZOBOHATYI SCHWARZHANS, 2010

FIG. 8H

Material—four specimens, specimen figured, DMNH 2021-09-30.

Description and Remarks—The four Arkadelphia Formation otoliths assigned to *Protobythites brzobohaty* are similar to *Ampheristus*, but they are distinguished from *Ampheristus* in the inner face being distinctly convex in both the horizontal and vertical directions. *Protobythites brzobohaty* also has a relatively smooth inner face except for the slightly deepened sulcus (especially the cauda). The sulcus has a wide, long ostium and a short,

flexed, narrow cauda. There is a very shallow dorsal depression present and a faint ventral furrow on the inner face. The margins are sharp. *Protobythites brzobohaty* has a thin appearance with a nearly flat outer face. The species was based on a single well-preserved otolith from the Maastrichtian of Bavaria (Schwarzhans 2010). It is also known from the Maastrichtian Kemp Clay of Texas (Schwarzhans and Stringer 2020a). Its occurrence is now extended to the Maastrichtian Arkadelphia Formation of Arkansas.

FAMILY INDETERMINATE
GENUS INDETERMINATE

LAPILLUS TYPE 1 (*SENSU* STRINGER ET AL., 2020)

FIG. 8I

Material—one small, slightly eroded specimen, DMNH 2021-09-31.

Description and Remarks—The single utricular otolith identified as Lapillus type 1 from the Arkadelphia Formation is small (around 3 mm) and rounded on several sides, which gives it a lobe-like appearance. The Arkadelphia specimen appears to be identical to specimens identified as utricular otoliths (family and genus indeterminate) from the Ripley Formation (Cretaceous, Maastrichtian) in northeast Mississippi by Stringer (1991), Nolf and Stringer (1996), and Stringer et al. (2020, as Lapillus type 1). It was also noted from the Severn Formation by Stringer and Schwarzhans (2021). Typically, Lapillus type 1 is not numerous, but Stringer et al. (2016) reported 36 of these utricular otoliths from the Woodbury Formation (Cretaceous, early-middle Campanian). Some of the utricular otoliths from Stringer et al. (2016) are preserved especially well (their pl. 2, fig. 11) and show many features not discernible in the Arkadelphia Formation specimen. If the specimens represent the same taxon, then the teleost has a fairly long stratigraphic range from the early-middle Campanian to the late Maastrichtian.

DISCUSSION

The Arkadelphia Formation otoliths and their indications of paleoecology and paleogeography

The otolith assemblage of the Arkadelphia Formation at Cabot, Arkansas, consisted of 19 species, three taxa in open nomenclature, and one unknown type of lapillus representing at least 19 families based on 2,109 specimens. The richness or number of species in the Arkadelphia Formation otolith assemblage is relatively high, but it is considerably less than the Upper Cretaceous

(Maastrichtian) Ripley Formation in Mississippi, which had a richness of 30 species and two morphological types of unknown lapilli representing at least 22 families based on 3,802 specimens (Stringer et al. 2020) and the Severn Formation with 32 taxa with one unknown lapillus representing 24 families based on 2,296 specimens. The richness of taxa in the Ripley Formation and the Severn Formation was approximately 36% and 41%, respectively, more than the Arkadelphia Formation. The Arkadelphia Formation otolith assemblage was closer to the number of taxa in the Upper Cretaceous Kemp Clay in richness (25 species with two in open nomenclature based on 1,202 specimens). The Upper Cretaceous Fox Hills Formation otolith assemblage was extremely diminutive with only four species from four different families (Hoganson et al. 2019). It must be taken into consideration that the otolith specimens of the Arkadelphia Formation were obtained from boring samples (17–31 m bgl), and it is difficult to ascertain the equivalency to bulk samples collected on the surface and weighed. However, even with this caveat, the richness and evenness of the Arkadelphia Formation otolith assemblage provides relevant information for comparison.

Another aspect of diversity, evenness or the percentage of individual species, is meaningful for analyzing the Arkadelphia Formation otolith assemblage and comparing it to other Late Cretaceous assemblages (Fig. 2). The Arkadelphia Formation is extremely uneven with one species, the presumed siluriform *Vorhisia vulpes*, representing almost 73% of the total number of specimens. If the other two most abundant species are included (*Eutawichthys zideki* and *Palaeogadus? belli*), these three species account for almost 94% of the assemblage and are indicative of a very uneven distribution. The Kemp Clay is also uneven in the distribution of species but not as much as the Arkadelphia Formation. The same species that is so abundant in the Arkadelphia Formation, *Vorhisia vulpes*, also represents the greatest percentage in the Kemp Clay (almost 35%). Another siluriform, *Arius? subtilis*, represents around 16% of the Kemp Clay. So, two species account for over 50% of the Kemp Clay. The Fox Hill Formation is also uneven in its diversity with a presumed gadid, *Dakotaichthys hogansoni* Schwarzhans and Stringer (2020a), comprising approximately 66% of the total. The ubiquitous *Vorhisia vulpes* accounts for around 29%. So, two species make up 95% of the assemblage. The Ripley Formation assemblage is somewhat uneven with the two species *Hoplopteryx oscitans* (Nolf and Stringer, 1996) and *Paraulopus pseudoperca* (Nolf and Dockery, 1990) making up about 53% of the total.

However, of the other 28 species in the Ripley Formation, all of them represent less than 6% of the total specimens with many less than 1%. It should also be noted that the exceptionally abundant *Vorhisia vulpes* in the Arkadelphia Formation, Kemp Clay, Severn Formation, and the Fox Hills Formation represents only 0.27% in the Ripley Formation.

An informative and insightful tool for comparing otolith assemblages from various sites is the percentage similarity measurement (Reitz and Wing 1999, Stringer et al. 2018, Stringer and Hulbert 2020, Stringer and Schwarzhans 2021). The percentage similarity measurement allows for a comparison of assemblages from different geographical localities. The measurement, also known as percent similarity or proportional similarity, is calculated using the following equation:

$$P = \sum \text{minimum} (p_{1i}, p_{2i})$$

where:

P = percentage similarity between assemblages 1 and 2

p_{1i} = percentage of species i in assemblage 1

p_{2i} = percentage of species i in assemblage 2

The otolith assemblages from the Fox Hills Formation (NDGS 5597 locality), Kemp Clay (South Sulphur River locality, Texas), Ripley Formation (Blue Springs locality, Mississippi), and Severn Formation (four localities in Maryland of Stringer and Schwarzhans 2021) were selected for comparison to the Arkadelphia Formation assemblage because of their similar age (late Maastrichtian), geographical location (in adjacent states as well as distant states), and relatively large number of specimens. Data for the percentage similarity calculations were obtained from Table 1 for the Arkadelphia Formation, Table 2 for the Fox Hills Formation, the Kemp Clay, and the Ripley Formation, and table 3 of Stringer and Schwarzhans (2021) for the Severn Formation. The results of the percent similarity measurements are presented in Table 3. It should be noted that the species and percentages for the Ripley Formation were based on specimens derived from bulk samples and did not include the specimens collected by systematic surface collecting conducted at the Blue Springs locality.

The percentage similarity measurement for the Arkadelphia Formation (Cabot locality) and Fox Hills Formation (NDGS 5597 locality, North Dakota) was 30.32%. This would indicate that the two either shared a number of species but with low percentages or shared a few species with larger percentages. In this case, three of the four

Table 2. Comparison of the otoliths (taxa and percentage of total) of the Fox Hills Formation (NDGS 5597 locality, near Burnstad, North Dakota, USA), Kemp Clay (South Sulphur River, near Commerce, Texas, USA), and Ripley Formation (near Blue Springs, Mississippi, USA) based on bulk samples. ¹ includes specimens identified as *Pterothrissus* cf. *P. conchaeformis*, ² includes specimens identified as *Ampheristus* cf. *A. americanus*. **Order=FORMES, Family=idae**

Taxa in Fox Hill., Kemp Clay, and Ripley formation sites	Fox Hills Fm., North Dakota		Kemp Clay, Texas		Ripley Fm., Mississippi	
	No. of otoliths	% of total	No. of otoliths	% of total	No. of otoliths	% of total
Megalopidae						
<i>Megalops? nolfi</i>	0	0	0	0	3	0.40
Albulidae						
<i>Albula</i> cf. <i>A. bashiana</i>	0	0	7	0.58	0	0
<i>Pollerspoeckia</i> sp.	4	1.50	0	0	0	0
<i>Pterothrissus conchaeformis</i> ¹	0	0	113	9.33	6	0.81
<i>Pterothrissus</i> cf. <i>P. foreyi</i>	0	0	2	0.17	0	0
<i>Albula</i> sp.	0	0	0	0	7	0.94
<i>Elopothrissus</i> sp.	0	0	0	0	0	0
ORDER INDETERMINATE						
<i>Genartina</i> sp.	0	0	3	0.25	0	0
Osmeroididae						
<i>Osmeroides mississippiensis</i>	0	0	0	0	14	1.89
<i>Osmeroides</i> sp.	0	0	0	0	4	0.53
Anguillidae						
<i>Anguilla chickasawae</i>	0	0	0	0	2	0.27
Ophichthidae						
<i>Echiophis</i> aff. <i>E. semispaeroides</i>	0	0	2	0.17	0	0
Family Ind. (ANGUILLIFORMES)						
<i>Muraenanguilla</i> cf. <i>M. unionensis</i>	0	0	0	0	19	2.56
Heterenchelyidae						
<i>Pythonichthys arkansasensis</i>	0	0	3	0.25	0	0
Congridae						
<i>Rhynchoconger? piger</i>	0	0	38	3.14	0	0
<i>Rhynchoconger brettwoodwardi</i>	0	0	25	2.06	0	0
<i>Congrophichthys transterminus</i>	0	0	3	0.25	0	0
Family ind. (OSTEOGLOSSIFORMES)						
<i>Kokenichthys navis</i>	0	0	0	0	7	0.94
<i>Kokenichthys ripleyensis</i>	0	0	0	0	1	0.13
Family Ind. (CLUPEIFORMES)						
Clupeiform indeterminate	0	0	0	0	0	0
Ariidae						
<i>Arius? danicus</i>	0	0	67	5.53	0	0
<i>Arius? subtilis</i>	0	0	195	16.10	13	1.75

Table 2 (continued). Comparison of the otoliths (taxa and percentage of total) of the Fox Hills Formation (NDGS 5597 locality, near Burnstad, North Dakota, USA), Kemp Clay (South Sulphur River, near Commerce, Texas, USA), and Ripley Formation (near Blue Springs, Mississippi, USA) based on bulk samples. ¹ includes specimens identified as *Pterothrissus* cf. *P. conchaeformis*, ² includes specimens identified as *Ampheristus* cf. *A. americanus*. **Order=FORMES, Family=idae**

Taxa in Fox Hill., Kemp Clay, and Ripley formation sites	Fox Hills Fm., North Dakota		Kemp Clay, Texas		Ripley Fm., Mississippi	
	No. of otoliths	% of total	No. of otoliths	% of total	No. of otoliths	% of total
Family Ind. (SILURIFORMES)						
<i>Vorhisia vulpes</i>	78	29.32	423	34.93	2	0.27
Ichthyotringidae						
<i>Apateodus crennelatus?</i>	0	0	0	0	42	5.66
<i>Thrax acutus</i>	0	0	0	0	1	0.13
<i>Ichthyotringa? tavernei</i>	0	0	0	0	4	0.53
Paraulopidae						
<i>Paraulopus pseudoperca</i>	0	0	4	0.33	190	25.61
Family Ind. (ORDER UNKNOWN)						
<i>Choctawichthys ceploides</i>	0	0	0	0	2	0.27
Polymixiidae						
<i>Cowetaichtys carnevalei</i>	0	0	0	0	3	0.40
<i>Cowetaichthys alabamae</i>	0	0	0	0	9	1.21
Merlucciidae						
<i>Paleogadus weltoni</i>	0	0	2	0.17	0	0
<i>Palaeogadus belli</i>	0	0	0	0	0	0
Gadidae?						
<i>Dakotaichthys hogansoni</i>	177	66.29	16	1.32	0	0
Family Ind. (GADIFORMES)						
<i>Archaemacruroides bratishkoi</i>	0	0	11	0.91	0	0
GADIFORMES Ind.	0	0	0	0	0	0
Family Ind. (HOLOCENTRIFORMES)						
<i>Tippaha mythica</i>	0	0	0	0	1	0.13
<i>Tippaha cavata</i>	0	0	0	0	1	0.13
Trachichthyidae						
<i>Hoplopteryx oscitans</i>	0	0	0	0	278	37.47
<i>Hoplopteryx langfordi</i>	0	0	0	0	11	1.48
<i>Hoplostethus stringeri</i>	0	0	52	4.29	0	0
Berycidae						
<i>Centroberyx apogoniformis</i>	0	0	42	3.47	0	0
Family Ind. (BERYCIFORMES)						
<i>Argyroberyx? dentatus</i>	0	0	1	0.08	0	0
<i>Argyroberyx? dockeryi</i>	0	0	0	0	2	0.27

Table 2 (continued). Comparison of the otoliths (taxa and percentage of total) of the Fox Hills Formation (NDGS 5597 locality, near Burnstad, North Dakota, USA), Kemp Clay (South Sulphur River, near Commerce, Texas, USA), and Ripley Formation (near Blue Springs, Mississippi, USA) based on bulk samples. ¹ includes specimens identified as *Pterothrissus* cf. *P. conchaeformis*, ² includes specimens identified as *Ampheristus* cf. *A. americanus*. **Order=FORMES, Family=idae**

Taxa in Fox Hill., Kemp Clay, and Ripley formation sites	Fox Hills Fm., North Dakota		Kemp Clay, Texas		Ripley Fm., Mississippi	
	No. of otoliths	% of total	No. of otoliths	% of total	No. of otoliths	% of total
Family Ind. (BERYCIFORMES)						
<i>Eutawichthys</i> cf. <i>E. choctawae</i>	0	0	7	0.58	0	0
<i>Eutawichthys maastrichtensis</i>	8	3.00	2	0.17	15	2.02
<i>Eutawichthys zideki</i> ²	0	0	0	0	24	3.23
<i>Eutawichthys stringeri</i>	0	0	0	0	0	0
Family Ind. (BERYCIFORMES)						
<i>Ossulcus labiatus</i>	0	0	0	0	3	0.40
Ophidiidae						
<i>Ampheristus americanus</i> ²	0	0	130	10.73	0	0
Bythitidae						
<i>Bidenichthys?</i> <i>crepidatus</i>	0	0	2	0.17	0	0
<i>Protobythites brzobohaty</i>	0	0	1	0.08	0	0
Pempheridae						
<i>Pempheris?</i> <i>huddlestoni</i>	0	0	0	0	29	3.91
Serranidae						
<i>Serranus?</i> <i>caribbaeus</i>	0	0	12	0.99	0	0
<i>Serranus?</i> <i>severnensis</i>	0	0	0	0	1	0
Incertae sedis						
<i>Otolithopsis cumatilis</i>	0	0	0	0	4	0.54
Percoide sp.	0	0	0	0	3	0.40
ORDER/Family unknown						
Lapillus type 1	0	0	0	0	7	0.94

species found in the Fox Hills Formation (very low diversity) were also found in the Arkadelphia Formation, and one of them, *V. vulpes* represented a large percentage of the Fox Hills Formation assemblage and the Arkadelphia Formation assemblage.

Percentage similarity for the Arkadelphia Formation (Cabot locality) and the Kemp Clay (South Sulphur River) was 35.73%. This would indicate that either there were some of the same species that had somewhat abundant percentages at both sites or more species in common but lower percentages. In this case, there were seven species in common, and six of them were very low percentages. However, one species, *V. vulpes*, represented a large percentage of the Kemp Clay and the Arkadelphia Formation. Although the percentage similarity value (35.73%) is not

that large, it would point to a greater similarity between the Arkadelphia Formation and the Kemp Clay than other assemblages compared except for the Severn Formation.

The Arkadelphia Formation (Cabot locality) and Ripley Formation (Blue Springs locality) pointed to a very small percentage similarity with a value of 5.46%. However, the Arkadelphia and Ripley formations otolith assemblages actually had 11 species in common, but ten of the 11 species were 1% or less similarity except for *Eutawichthys zideki*. So, the assemblages shared species, but they were all low percentages. One of the most telling of the percentage similarity measurements was the one comparing the Kemp Clay (South Sulphur River locality) and Ripley Formation (Blue Springs locality). These two sites had an extremely low percentage similarity with

only 3.33% (Table 3). This would be a clear indication that the two shared few species (5), and the ones that were shared were not abundant (very low percentages). The percentage similarity measurement would indicate that the otolith assemblages of the Kemp Clay and Ripley Formation were not similar and notably different.

It is important to note that three of these percentage similarity measurements were calculated between sites in the Arkadelphia Formation, Kemp Clay, and Ripley Formation that are essentially the same age (Late Cretaceous, late Maastrichtian). Furthermore, these three sites are located in the Gulf Coastal Province, and their present latitudinal differences are small (less than 2° difference in latitude between the three sites), and their geographical separation is not that large (approximately 7° longitude between Commerce, Texas, and Blue Springs, Mississippi, with Cabot, Arkansas, approximately between the two). So, the two very low percentage similarity measurements between the Kemp Clay (South Sulphur River locality)/Ripley Formation (Blue Springs locality) and the Arkadelphia Formation (Cabot locality)/Ripley Formation (Blue Springs locality) are indicative of major differences between the otolith assemblages of the sites. Of course, the question is what factor or factors are causing such significant differences between the otoliths of the sites. This question is addressed later in the discussion of the paleoecology and paleogeography.

Although the Fox Hills Formation assemblage in North Dakota is Maastrichtian in age and has a relatively large number of otoliths, it is certainly not in geographical proximity to the other localities. The Fox Hills Formation locality (NDGS 5597) is located in Logan County, North Dakota, which is in the south-central portion of the state. Presently, the Fox Hills Formation locality (46.3855, -99.6326) is almost 12° latitude further north and over 7° longitude further west than the Cabot locality (34.9745, -92.0165). In addition, the Fox Hills Formation locality in North Dakota is approximately 1,704 km north-northwest of the Arkadelphia Formation site in Cabot, Arkansas. This allowed for comparison to a site that was latitudinally separated from the other sites. During the Late Cretaceous, the Fox Hills Formation locality would have been in the Western Interior Seaway fairly close to the shore of Laramidia (Stringer and Schwarzhans 2021). Although separated by a substantial number of degrees of latitude, the percentage similarity measurement between the Arkadelphia Formation and the Fox Hills Formation was 30.32%. While not a large percentage similarity, it certainly appears unusual that the Arkadelphia Formation and Fox Hills Formation otolith assemblages have a

much greater percentage similarity than the Arkadelphia Formation has with the Ripley Formation. The Arkadelphia Formation (Cabot site) and the Ripley Formation (Blue Springs site) are both Maastrichtian, essentially the same latitude, and only separated by 358 km. Obviously, some factor or factors are affecting the percentage similarity differences.

Equally intriguing and compelling is the percentage similarity analysis of the Arkadelphia Formation and the Severn Formation (Upper Cretaceous, Maastrichtian) based on data from four localities in Maryland from recent studies by Stringer and Schwarzhans (2021). Although the assemblages are widely separated geographically (central Arkansas and eastern Maryland, which are approximately 1426 km apart with a latitudinal difference of about 4°), the percentage similarity between the two is 57.68%. This is much greater similarity than any of the other assemblages that were compared to the Arkadelphia Formation. The percentage similarity between the Severn and Arkadelphia otoliths is unquestionably unexpected and initially baffling. It will be explored further later in this discussion.

The otolith assemblage from the Owl Creek Formation at its type locality northeast of Ripley, Tippah County, Mississippi, was also considered for comparison to the Arkadelphia Formation assemblage. However, the Owl Creek otolith assemblage from the type locality only met two of the criteria applied to the other sites. It is stratigraphically equivalent to the Arkadelphia Formation as both are uppermost Maastrichtian (Larina et al. 2016), and its geographical proximity is close in adjacent Mississippi. However, the number of otolith specimens available from the Owl Creek type locality was less than 100, which is significantly less than the other sites chosen for comparison. In spite of not meeting all three criteria, the percentage similarity was calculated with this proviso noted and was slightly greater than 1.00% (1.08%). The percentage similarity of the Arkadelphia Formation and the Owl Creek type locality was even less than the Arkadelphia Formation and the underlying Ripley Formation (5.46%). The very small percentage similarity between the Owl Creek type locality and Arkadelphia Formation otolith assemblages does serve as ancillary evidence of the dissimilarity of the Arkadelphia otolith assemblages with those to the east in Mississippi.

Schwarzhans and Stringer (2020a) proposed four distinct Maastrichtian fish communities (bioprovinces) based on a correlation of Late Cretaceous otoliths at the genus level (i.e., lineages) including open nomenclature records. The communities (bioprovinces) were the

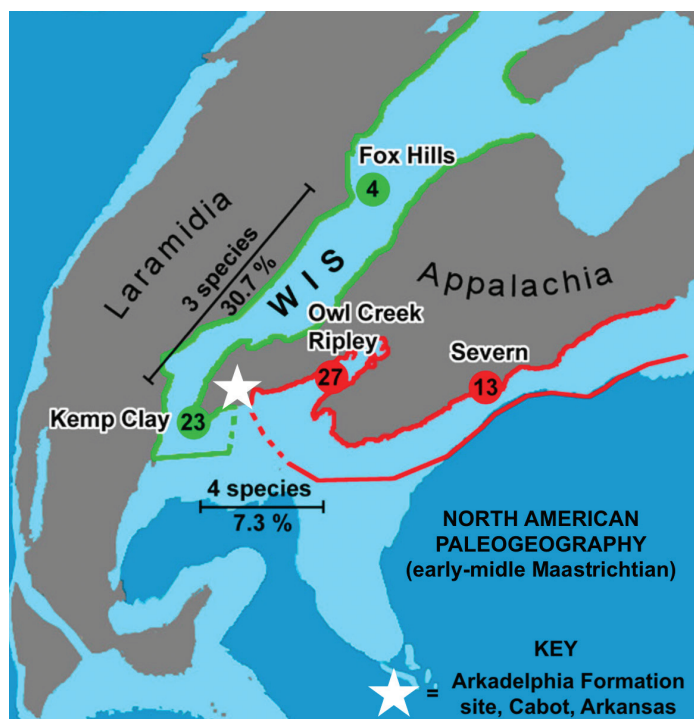


Figure 9. Maastrichtian otolith localities in North America and otolith-based faunal communities (bioprovinces) based on Schwarzhans and Stringer (2020a). The Western Interior Seaway community is outlined in green, and the localities are shown in green circles. The Appalachian community is outlined in red, and the localities are shown in red circles. The number in the circle is the number of species known from the localities. The white star is the Arkadelphia Formation site at Cabot, Arkansas, and the focus of this study. The base paleogeographic map was modified from Blakey (2014) and Scotese (2014).

Appalachian community, the Western Interior Seaway community, the Peninnic community, and the Boreal European community. This investigation is primarily concerned with the Western Interior Seaway community and the Appalachian community (Fig. 9). These communities (bioprovinces) were based on studies of Late Cretaceous otoliths from the USA and Europe, the primary areas in which Cretaceous otoliths have been reported, although Nolf et al. (2008) did report Cretaceous otoliths from India. The Kemp Clay of Texas and the Fox Hills Formation of North Dakota were placed in the Western Interior Seaway (WIS) community (bioprovince) based on the occurrence of common ariids, abundant siluriforms (e.g., *Vorhisia vulpes*), diverse anguilliforms, and the occurrence of gadiform otoliths. Based on the results of this study, the Arkadelphia Formation otolith assemblage matches the criteria of the WIS community (bioprovince) with its characteristic taxa, especially relatively abundant gadiforms, and deposition near the southeastern portion of the Western Interior

Table 3. Percentage similarity measurements for the otolith assemblages from the Arkadelphia Formation (Cabot locality, Arkansas, USA), Fox Hills Formation (NDGS 5597, North Dakota, USA), Kemp Clay (South Sulphur River locality, Texas, USA), Ripley Formation (Blue Springs locality, Mississippi, USA, and Severn Formation (five sites, Maryland, USA). Data for calculations were obtained from this study (Table 1) for the Arkadelphia Formation (Cabot locality), from Hoganson et al. (2019) for the Fox Hills Formation (NDGS 5597 locality), from Schwarzhans and Stringer (2020a) for the Kemp Clay (South Sulphur River locality), from Stringer et al. (2020, table 2) for the Ripley Formation (Blue Springs locality; bulk samples only), and from Stringer and Schwarzhans (2021; table 3) for the Severn Formation (four sites).

Localities compared	Percent similarity
Arkadelphia Formation (Cabot locality, Arkansas) and Fox Hills Formation (NDGS 5597, North Dakota)	30.32%
Arkadelphia Formation (Cabot locality, Arkansas) and Kemp Clay (South Sulphur River locality Texas)	35.73%
Arkadelphia Formation (Cabot locality, Arkansas) and Ripley Formation (Blue Springs locality, Mississippi)	5.46%
Arkadelphia Formation (Cabot locality, Arkansas) and Severn Formation (four sites in Maryland)	57.68%
Kemp Clay (South Sulphur River locality, Texas) and Ripley Formation (Blue Springs locality, Mississippi)	3.33%

Seaway. Some of the most compelling evidence for this categorization may be found in the percentage similarity measurements (Table 3). The Arkadelphia Formation otolith assemblage has a percentage similarity of 30.32% with the Fox Hills Formation and a percentage similarity of 35.73% with the Kemp Clay. Contrast this with a similarity percentage of 5.46% and 1.08% between the Arkadelphia Formation and the Ripley and the Owl Creek formations, respectively (both formations in the Appalachian Community). A seemingly unusual result is the percentage similarity between the Arkadelphia and the Severn formations otoliths (57.68%), which is the most similarity of any of the comparisons made in this study. Schwarzhans and Stringer (2020a) placed the Severn Formation in the Appalachian Community with the Ripley and Owl Creek formations.

However, more detailed study with additional localities indicated the presence of gadiforms (merluccids) in the Severn Formation (Stringer and Schwarzhans 2021). This is not typical of otolith assemblages found in the southern portion of the Appalachian Community. However, it is not unexpected that the Severn Formation would be affected by cooler waters from the northern Atlantic. The influence of cool waters and the similarity of the paleoenvironments of the Severn and Arkadelphia (both probably inner shelf with estuarine influences) could explain the percentage similarity between the two otolith assemblages.

In order for otoliths to be used for paleoenvironmental interpretations, an essential taphonomic consideration is whether the otoliths accurately represent the fishes that inhabited the area during a given interval of geologic time. Evidence from multiple strands indicate that otoliths usually represent fish that are autochthonous in nature, and therefore, represent part of the biocoenosis (life assemblage). Two major taphonomic processes by which otoliths become part of the sediment are death and decay of the fish with the release of the otoliths from the neocranium or skull and the excretion from piscivorous vertebrates such as sharks, predatory fish, and whales (Fitch 1967, Schafer 1972, Stringer 1992). Nolf (1985, 2013) contended that predation and subsequent excretion by bony fishes are the primary means by which otoliths become incorporated into sediment. Only a very small percentage (<1% of the total) of otoliths recovered from the Arkadelphia Formation exhibit evidence of invertebrate boring, settlement, and encrusting that indicate that the otoliths were present on the sea bottom for an extended period. Figure 5L shows the rare occurrence of a gastropod boring on a *V. vulpes* lapillus from the Arkadelphia Formation. This is very similar to what was found by Stringer (2016a) in the otolith assemblage from the Moodys Branch Formation (Eocene, Bartonian). A very small percentage of otoliths with evidence of invertebrate settlement were reported from the Campanian Woodbury Formation (Stringer et al. 2016) and the Campanian Tar Heel Formation (Stringer et al. 2018). The evidence or lack thereof is most likely related to the amount of time exposed on the sea bottom before being incorporated into the substrate (i.e., longer exposure time equates with a greater chance of invertebrate boring or settlement given a similar number of invertebrates).

Studies of fish otoliths from Holocene bottom sediments have indicated that otoliths generally reflect fishes that inhabit an area. Research that support this conclusion includes those of Wigley and Stinton (1973),

Gaemers (1978), Stringer (1992), McBride et al. (2010), Lowry (2011), Firestine et al. (2012), Schwarzhans (2013), Lin (2016), Lin et al. (2016, 2017). Taxonomic studies of extant fish otoliths or that include extant fish otoliths have greatly facilitated investigations of the otoliths of modern sea bottoms sediments. Taxonomic analysis of modern fish otoliths include works such as Schwarzhans (1993, 1999, 2013, 2019), Smale et al. (1995), Rivaton and Bourret (1999), Campana (2004), Veen and Hoedemakers (2005), Florida Fish and Wildlife Conservation Commission (2007), Furlani et al. (2007), Tuset et al. (2008), McBride et al. (2010), Lin and Chang (2012), Nolf (2013), and Schwarzhans and Aguilera (2013, 2016). It appears that a strong correlation exists between otolith associations in modern sea-bottom sediments in particular environments and the expected fishes. Lin et al. (2017) demonstrated that various taphonomic processes, such as time-averaged and spatial-averaged, may affect otoliths, but otoliths seem to remain part of the biocoenosis and can be interpreted as such in the fossil record.

Paleoenvironmental analysis using otoliths is based on the premise that identified otoliths can be utilized to obtain data on the preferred habitats of comparable extant fishes (i.e., analogues). Some contend that Late Cretaceous otoliths are too far removed from modern counterparts to be utilized for uniformitarian application. This contention definitely has its arguments and must be considered. Unquestionably, the Late Cretaceous otolith assemblages cannot provide the accuracy and precision that is possible with Plio-Pleistocene otoliths that represent extant fishes almost exclusively. However, we maintain that general paleoecological parameters within limits are still discernable with Late Cretaceous otoliths. Interpretations based on otoliths are also compared to data from microfossil groups as well as to paleogeographical reconstructions. This use of other fossil groups as well as paleogeography provides essential ancillary data to the use of otoliths in paleoenvironmental reconstructions.

Examination of the otoliths from the Arkadelphia Formation samples recovered from the drilling (Table 1) and comparing them to closely related extant forms when possible revealed the absence of representatives that are indicative of deep waters exclusively (greater than outer shelf or 200 m of the USA) according to Page et al. (2013). A neritic environment with little open ocean influence is indicated by the majority of the taxa of the otolith assemblage (Nolf and Brzobohaty 1992). Therefore as a general interpretation, the bony fishes represented by

otoliths indicate a marine environment no deeper than outer shelf and probably much shallower. Most of the otoliths represent fish families expected in normal marine salinity, but some of the forms could tolerate reduced salinities (brackish) and even fresh water. These salinity ranges would be expected in shallow marine waters close to estuaries and freshwater input.

In geologically younger strata in the Atlantic and Gulf coastal plains, it is possible to compare the families of bony fishes represented by otoliths to the distribution of the modern ichthyological fauna from the Gulf of Mexico and the Atlantic Ocean (Hoese and Moore 1998, McEachran and Fechhelm 1998, 2005, Nelson et al. 2016). However, this is much more difficult when many of the families are unknown (i.e., indeterminate). In the Arkadelphia Formation otolith assemblage, ten of the families are classified as indeterminate primarily because it is not possible to relate them to extant families, and they may also, and probably do, represent extinct families. Many of these taxonomic questions could be answered if skeletal remains of fishes with *in situ* otoliths could be recovered. In spite of this limitation, the Arkadelphia Formation otoliths can be related to nine extant families. Six of these families (Elopidae, Albulidae, Anguillidae, Ophichthidae, Ariidae, and Bythitidae) are listed as fresh water, brackish, and marine by Froese and Pauly (2019). However, this is somewhat misleading since three of the six families (Elopidae, Albulidae, and Bythitidae) are noted as chiefly in marine and rarely in fresh water or brackish. There are three families that are listed as exclusively marine (Macrouridae, Merlucciidae, and Ophidiidae). The general climate range of these families extend from tropical only, subtropical, warm temperate, and temperate. However, there are families with representatives that occur in cold and even Arctic waters. It could be contended that gadiforms that preferred warm waters were present in the Late Cretaceous. However, there is no indication of this occurrence in previous studies of otoliths and related fossil groups, especially microfossils (Huddleston and Savoie 1983, Nolf 2003, Schwarzhans et al. 2018b, Stringer et al. 2018, Hoganson et al. 2019, Stringer et al. 2020, Schwarzhans and Stringer 2020a, Stringer and Schwarzhans 2021).

The occurrence of fish indicative of such diverse climatic ranges is very unusual in otolith assemblages in the Atlantic and Gulf coastal plains, especially in the Gulf Coastal Plain (Fitch and Lavenberg 1983, Huddleston and Savoie 1983, Schwarzhans et al. 2018b, Stringer and Bell 2018; Stringer et al. 2018, Ebersole et al. 2019, Stringer and Shannon 2019, Stringer et al. 2020). This occurrence

would seem to signify atypical and different parameters than what normally occurs in the Gulf and Atlantic coastal plains. A strong consideration for the unusual climatic conditions is the Late Cretaceous paleogeography and the Western Interior Seaway. Numerous studies and the resulting paleogeographic maps have indicated a substantial Western Interior Seaway that linked the Arctic Ocean (sometimes referred to as the Boreal Sea) through central North America with the Gulf of Mexico during much of Cretaceous times. Studies include, but certainly not limited to, Williams and Stelck (1975), Erickson (1978, 1999), Kennedy et al. (1998), Cobban et al. (2006), Boyd and Lillegraven (2011), Landman et al. (2012), Blakey (2014), Scotese (2014), Slattery et al. (2015), and Hoganson et al. (2019). Slattery et al. (2015) noted that the Western Interior Seaway was one of the largest post-Paleozoic epeiric seas and covered a large portion of west-central North America for an estimated 46 Ma. The resulting paleogeography was primarily controlled by the interaction of sea level with the Late Cretaceous physiography.

The paleogeographic configuration of the Western Interior Seaway provided for a unique set of environmental conditions related to atmospheric and oceanographic parameters. Models developed by Kauffman (1975), Eicher and Diner (1985), and others indicated cold, south-flowing currents from the Arctic Ocean through the Western Interior Seaway in a portion of the Late Cretaceous. Wright (1987) conducted a detailed study of the stratification and paleocirculation of the Western Interior Seaway for the early Maastrichtian. Paleotemperatures and salinity profiles were developed using the oxygen and carbon isotopic signatures of shell material (cephalopods, epifaunal bivalves, and infaunal bivalves). Wright's results indicated a reduced salinity surface layer, an intermediate normal salinity layer, and a denser, more saline, warmer bottom layer. Wright noted that the southern part of the Western Interior Seaway was subtropical and would have north-flowing surface currents during part of the year.

Studies such as Landman et al. (2004), Umhoefer and Blakey (2006), Dastas et al. (2014), Scotese (2014), Slattery et al. (2015), DePalma et al. (2019), and Hoganson et al. (2019) indicated a fairly unobstructed interchange between the northern and southern reaches of the Western Interior Seaway throughout most of the Late Cretaceous. Several studies noted the faunal similarity, especially ammonites, of the Arctic Basin, North Dakota, and Texas (Slattery et al. 2015, DePalma et al. 2019, Hoganson et al. 2019). This assertion has been challenged

by some who believe the seaway was closed by late Maastrichtian (Roberts and Kirschbaum 1995, Kennedy et al. 1998, Erickson 1999, Crowell 2011). For example, Roberts and Kirschbaum (1995) indicated an expansive Western Interior Seaway westward from the middle of Wyoming to almost the eastern border of South Dakota and extending northward from the Gulf Coast to northern Canada during the Campanian (fig. 16). However by the late Maastrichtian, they showed the seaway ending in the middle of North Dakota (fig. 22). Blakely (2014) in his paleogeographic map of the Western Interior Seaway at 69.7 Ma (Late Maastrichtian) depicted the seaway completely separated from the Gulf of Mexico. In fact, it indicated that all of central and eastern Oklahoma and western Arkansas were terrestrial.

As noted in the aforementioned studies, there are differences in the timing and geographical location of the closure of the Western Interior Seaway. However, it appears, according to the majority of the investigations, that the seaway remained open until at least the beginning of the Maastrichtian and perhaps later. No matter the exact timing of the closure, the effects of the seaway upon the fishes was profound and would continue even after the closure, which was probably gradual and perhaps even intermittent (due to erosional processes and reopening). Cool-water fishes based on extant forms are assuredly still present in the Arkadelphia Formation during the late Maastrichtian as evidenced by the numerous gadiform otoliths. It does appear that the “Fox Hills-Hell Creek delta” (*sensu* Hoganson et al. 2019) was instrumental in the closure of the seaway by the Paleocene (Danian) and effectively isolating the northern and southern portions (Slattery et al. 2015, fig. 16, Hoganson et al. 2019, text-fig. 14). The Danian otoliths from the overlying Clayton Formation are markedly different from the Maastrichtian otoliths from the Arkadelphia Formation. These differences are believed to be related not only to the closure of the Western Interior Seaway but also the effect of the K-Pg extinction event. An extensive discussion of the effect of the K-Pg boundary event on the marine teleostean fishes based on otoliths can be found in Schwarzhans and Stringer (2020a).

In summary, there is considerable debate over the closure of the Western Interior Seaway, especially in the exact timing and the precise process of the closure as noted in the aforementioned references. However, it should be emphasized that the earlier conditions, i.e., those in the early part of the Maastrichtian, were prerequisite for the occurrence of the cool-water gadiforms. It is postulated that the early Maastrichtian, primarily open

Western Interior Seaway was instrumental in providing an environment suitable for the cool-water gadiforms. Regardless of when the Western Interior Seaway closed completely, the impact on the distribution of fishes would still be present. The Fox Hills Formation (North Dakota) otolith assemblage is older than the Arkadelphia assemblage and considerably further north. The Fox Hills assemblage is dominated by gadiforms (approximately 66.3%), while the Arkadelphia Formation assemblage is approximately 7.6%. The Arkadelphia Formation also lies directly under the Paleocene Clayton Formation. It is postulated that the gadiforms were relicts of the earlier cooler conditions when there was greater interchange with the north. This could explain their more limited abundance in the Arkadelphia Formation and complete disappearance in the overlying Clayton Formation, along with the effects of the K/Pg extinction. Nolf and Stringer (1992) discussed the occurrence of relicts in fossil fish assemblages and their eventual disappearance. One of those noted was the catfish *Plotosus* Lacépède (1803), which is currently an Indo-Pacific form, but is found in numerous assemblages in the Caribbean Neogene but completely absent today in the Gulf of Mexico and Caribbean. It and other taxa are interpreted as relicts of the western Tethys fauna prior to the closure of the Isthmus of Panama. A similar scenario is envisioned for the closure of the Western Interior Seaway and the cool-water gadiforms.

In determining the paleoenvironment of the Arkadelphia Formation at the Cabot site, emphasis can be given to the most abundant taxa since the conditions appear to be most conducive to those groups (i.e., environmental factors favor the growth and proliferation of those taxa). Examination of Table 1 indicates that *Vorhisia vulpes*, *Eutawichthys zideki*, and *Palaeogadus? belli* comprise 93.51% of the total number of otoliths in the Arkadelphia Formation assemblage. Unfortunately, these taxa are problematic in that two of the three most abundant taxa belong to indeterminate families, and their relationship to extant forms is less certain. However, some useful paleoecological and paleogeographical data can still be attained.

Vorhisia vulpes constitutes almost three-fourths (72.88%) of the total otoliths from the Arkadelphia Formation. Most studies consider *V. vulpes* as an extinct ariid, or at the least, a siluriform of some type based on the large lapillus and some features found in extant ariid lapilli (Huddleston and Savoie 1983, Hoganson et al. 2019, Schwarzhans and Stringer 2020a, Stringer et al. 2020). This premise is followed in this study with the

concession that it is possible that it could relate to an extinct higher taxonomic group. However, the taxon is considered presently as most likely some type of Siluriformes in an indeterminate family.

Huddleston and Savoie (1983) noted that *Vorhisia vulpes* comprised approximately 55% of the total otolith assemblage of the early-middle Maastrichtian Severn Formation in Maryland. They interpreted the paleoenvironment as very shallow marine, probably 0–20 m in depth (inner shelf). Stringer and Schwarzhans (2021) reported *V. vulpes* as the most abundant species in the upper Maastrichtian Kemp Clay in Texas (approximately 35%). Again, this environment was interpreted as very shallow marine with estuaries and freshwater input most likely nearby. Hoganson et al. (2019) noted that *V. vulpes* comprised almost 30% of the Fox Hills Formation in North Dakota, which was interpreted primarily as estuarine and shallow marine. *Vorhisia vulpes* was also present in the Ripley Formation, which was interpreted as 20–100 m (middle shelf) by Stringer et al. (2020). However, *V. vulpes* only represented 0.27% of the total specimens of the bulk sample studies. So, there is evidence that a high percentage of *V. vulpes* is indicative of very shallow marine conditions with possible estuarine and freshwater influence. This assertion appears to be supported by the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ analysis of the growth rings of the lapilli of *V. vulpes* in the Fox Hills Formation in North Dakota by Carpenter et al. (2003). Their studies indicated that *V. vulpes* most likely spawned in estuarine waters with the juvenile lapilli showing brackish water influence.

The second most abundant species in the Arkadelphia Formation otolith assemblage was the beryciform and otolith-based genus and species *Eutawichthys zideki* (13.61% of the total specimens). The exact taxonomic position of *Eutawichthys zideki* within the Beryciformes is not known, and the species is assigned to an indeterminate, probably extinct family. Perhaps, like the aulopiform *Apateodus*, *in situ* otoliths in skeletal remains will be discovered and make a more definitive identification possible (Schwarzhans et al. 2018a). The Woodbury Formation in New Jersey was reported as having a tremendous number of beryciforms, primarily *Eutawichthys maastrichtiensis* and *Eutawichthys zideki* with 3,100 beryciforms of the total 3,555 (Stringer et al. 2016). Obviously, conditions were optimum for the beryciforms based upon their abundance. The paleoenvironment was interpreted based on otoliths, foraminifera, and calcareous nannofossils as 0–100 m. A more exhaustive and detailed examination of the site by Oman et al. (2016)

indicated a paleoenvironment of slightly deeper than inner shelf and influenced by major rivers and deltas. The paleoenvironment of the Arkadelphia Formation at Cabot would fit within these ecologic parameters.

The third most abundant species (7.02% of the total specimens) in the Arkadelphia Formation assemblage is a gadiform assigned to *Palaeogadus? belli* in the family Merlucciidae. The presence of gadiforms in the Gulf Coastal Plain is unusual, and 112 specimens are really unique. Schwarzhans and Stringer (2020a) noted that the Gadiformes appear to have been cool-water fishes in the Late Cretaceous and probably since their origin despite the lack of data from the Arctic Basin. Late Cretaceous and early Paleogene gadiform evidence in the boreal province of northern Europe support this premise.

As mentioned previously, ostracodes were also recovered from the samples while extracting otoliths. These ostracodes were sent to M. Puckett at the University of Southern Mississippi for stratigraphic and paleoecologic analysis. All but one of the specimens belonged to *Haplocytheridea everetti* and included male and female forms. The other specimen belonged to *Brachycythere* cf. *B. ovata*. Both of these Late Cretaceous ostracod species are restricted to the North American Coastal Plain and indicate relatively shallow marine paleoenvironment (Puckett, personal communication, 2020).

When the parameters of the paleoecology indicated by the Arkadelphia Formation otoliths at a family level are evaluated, they generally indicate a marine environment no deeper than outer shelf (200 m) and probably much shallower (0–100 m). Many of the families point to a normal marine salinity, but there are representatives of families that could tolerate reduced salinities. The families present denote a wide range of climatic preferences including tropical, subtropical, temperate, subtemperate, and even cold waters. This is extremely unusual, especially in the Gulf Coastal Plain, and it is believed that the Late Cretaceous paleogeography and the Western Interior Seaway were agents for the atypical array of climatic preferences signified by the fishes based on otoliths. Furthermore, the overall cooling trend of the latest Cretaceous could have evoked major climatic impacts on fish distribution (Friedrich et al. 2005, 2012, Thibault et al. 2011, Linnert et al. 2014, Hassan and Nassif, 2018). On a more specific level, the three taxa (*Vorhisia vulpes*, *Eutawichthys zideki*, and *Palaeogadus? belli*) that make up almost 94% of the Arkadelphia Formation otolith assemblage point to a very shallow marine environment (possibly inner shelf; less than 20 m) with estuarine and freshwater input nearby. The high percentage of *Vorhisia*

vulpes is believed to be highly indicative of very shallow marine and accompanying estuaries. The relatively abundant gadiforms testify to the influence of the Western Interior Seaway and possible cool-water currents affecting the Gulf Coast prior to the Late Cretaceous, and most possibly, during the late Maastrichtian as well as the overall cooling trend of the Maastrichtian.

The paleoenvironmental interpretation of the Arkadelphia Formation based on otoliths agrees generally with other lines of evidence. Pitakpaivan and Hazel (1994) interpreted the Upper Cretaceous Arkadelphia Formation in Arkansas to be inner sublittoral zone based on ostracodes, while it was noted that the ostracodes pointed to a relatively shallow marine paleoenvironment (Pucket, personal communication, 2020). Becker et al. (2006) agreed with the assessment of Pitakpaivan and Hazel (1994) and noted that a shallow marine setting had been confirmed by foraminifera, coccoliths, oysters, ostracodes, and chondrichthyans. Manning (personal communication, 2020) noted the occurrence of six bony fishes from the Arkadelphia samples: *Lepisosteus* sp., *Hadrodus priscus* Leidy (1858), Albulidae indeterminate, Phyllodontidae indeterminate, *Enchodus ferox* Leidy (1855), and *Xiphactinus audax* Leidy (1870). He interpreted the fishes as indicative of shallow-water marine with indications of estuarine. Furthermore, the paleoecological parameters suggested by the teleostean otoliths for the Arkadelphia Formation are in general agreement with numerous paleogeographic maps for the Late Cretaceous in central Arkansas including Smith et al. (1994, map 10), Roberts and Kirschbaum (1995, fig. 22); Sampson et al. (2010, fig. 1), Blakey (2014, Mesozoic: NAM_Key-72 Ma_LateK), Scotese (2014, map 17), Slattery et al. (2015, fig. 15), DePalma et al. (2019, fig. 1), and Hoganson et al. (2019, text-fig. 13). It is significant to note that the paleoenvironment for the Arkadelphia Formation based on otoliths is in agreement with paleogeographic maps regardless of an early or late closure of the Western Interior Seaway. Thus, numerous and diverse independent criteria confirm and verify the paleoecological parameters as demonstrated by the otoliths.

Evolutionary implications of the otolith assemblage

The bony fish assemblage of the Arkadelphia Formation as indicated by otoliths provides significant information on teleostean evolution during the terminal portion of the Late Cretaceous. Other studies such as Huddleston and Savoie (1983), Stringer (1991), Nolf and Stringer (1996), Nolf (2013), Stringer (2016b), Schwarzhans and

Stringer (2020a), Stringer et al. (2020), and Stringer and Schwarzhans (2021) demonstrate the importance of otoliths in unraveling and understanding the evolution of the teleosts during the Late Cretaceous in the USA. The occurrence of fossil otoliths in a wide variety of paleoenvironments provides an abundance of data for investigating the origin and geological distribution of modern fish families (Nolf 1995). The significance of fish analysis in the paleontological record was emphasized by Friedman and Sallan (2012:707) in a large-scale diversity patterns study when they stated, “No other vertebrate assemblage encompasses as much taxonomic richness and morphological disparity distributed over such a long geological interval and represented by such a diverse range of preservational styles as fishes.” Certainly, the Arkadelphia Formation otoliths as well as otoliths from other North American Late Cretaceous studies, such as the Severn, Ripley, Owl Creek, Kemp Clay, and Fox Hill formations (Huddleston and Savoie 1983, Nolf and Stringer 1996, Hoganson et al. 2019, Schwarzhans and Stringer 2020a, Stringer et al. 2020), confirm the value of otoliths in ascertaining the geological range of bony fishes and providing insight into their evolutionary history. The otoliths from the Arkadelphia Formation present an opportunity to catch a glimpse of the bony fishes in the marine environment just prior to the K-Pg extinction event and a baseline for discerning their plight subsequently.

The most abundant species in the Arkadelphia Formation based on otoliths is the putative siluriform *Vorhisia vulpes*. The species is incredibly abundant ($n=1,537$) and represents 72.88% of the total otolith specimens in the Arkadelphia Formation assemblage. Yet in the overlying Paleogene Clayton Formation (Danian) in Arkansas, *V. vulpes* is completely absent (Schwarzhans and Stringer 2020a). This scenario is repeated in several other Upper Cretaceous formations in the USA. Huddleston and Savoie (1983) reported that *V. vulpes* was the dominant species (approximately 55% of the total otolith specimens) of the Upper Cretaceous Severn Formation (Maastrichtian) in Maryland. Likewise, *V. vulpes* is not found in any overlying strata. Similar results were obtained in the analysis of five Severn localities in Maryland by Stringer and Schwarzhans (2021) with *V. vulpes* present in four of the five sites and represented 42.47% of the total specimens recovered. Schwarzhans and Stringer (2020a) noted that *V. vulpes* was the most common species in the Kemp Clay and represented 423 of 1,160 otoliths (34.93%). However, the species is not found in any overlying Paleogene strata in Texas. So, evidence indicates that this very

successful, highly adapted, abundant species becomes extinct at the end of the Cretaceous. It is interesting to note that *V. vulpes* is not known from the Cretaceous outside of the U.S. (Koken 1891, Schwarzhans 1996, Schwarzhans 2010, Schwarzhans and Stringer 2020a). The center of evolution for *V. vulpes* surely appears to be in North America, specifically in the US, during the Late Cretaceous (Frizzell 1965b, Waage 1968, Frizzell and Koenig 1973, Huddleston and Savoie 1983; Nolf and Stringer 1996, Hoganson et al. 2019, Schwarzhans and Stringer 2020a, Stringer et al. 2020, Stringer and Schwarzhans, 2021).

The abundant and wide distribution in North America of *V. vulpes*, a putative member of the order Siluriformes (catfishes of Nelson et al. 2016), may appear enigmatic given that Lundberg (1975) reported the first catfishes in North America from the late Paleocene. However, catfishes are known in the southern hemisphere during the Cretaceous (Cione and Prasad 2002, Bogan and Agnolin 2011, Alves et al. 2019). These Late Cretaceous occurrences all occur in non-marine environments. The unusual distribution of the catfishes can partly be explained by differences in skeletal or osteological remains versus otoliths. In the classic work of Patterson (1993), he reported that 224 modern families were known as fossils, and 54 of those were represented exclusively by otoliths. Nolf (2013) reported the number had increased to 78. Nolf also noted that for many families that have a fossil record of both skeletal material and otoliths that the first appearance is documented by otoliths (Nolf 2013, table 1, pp. 8–12). The Paleocene record of catfishes of Lundberg (1975) in North America is based on osteological records, while the Cretaceous record is established on otoliths.

One of the most significant and revealing evolutionary indications regarding modern teleostean groups from the Arkadelphia Formation is the presence and abundance of representatives of the Gadiformes. Schwarzhans (2003) had noted, “Cretaceous gadiforms are not known from otoliths or skeletons,” which was true at that time. Likewise, Kriwet and Hecht (2008) in their investigation of early gadiform evolution and diversification noted that the oldest skeletal record of a gadiform was a macrourid from the Eocene of Antarctica. Like several others, they mentioned the rich and diverse gadiforms known from otoliths in the North Sea Basin since the Paleocene. Nolf (2013) in his extensive survey of fossil otoliths does not indicate any Cretaceous gadiform otoliths. Nelson et al. (2016) reiterated that the oldest Gadiformes are skeletal remains of the Paleocene macrourid from Antarctica.

Schwarzhans and Aguilera (2016) identified unequivocal macrourid otoliths as well as definitive gadoid otoliths in the Antarctica early Eocene. However, evidence and ideas on the evolutionary history of the Gadiformes has changed drastically and rapidly in the last few years.

Schwarzhans and Stringer (2020a) recorded three gadiform otolith-based species based on 29 specimens from the Upper Cretaceous (upper Maastrichtian) Kemp Clay of northeastern Texas. They noted that a form from the Upper Cretaceous Fox Hills Formation in North Dakota reported by Hoganson et al. (2019) as an argentiniform was an undescribed genus of gadiform. These discoveries led to a re-evaluation of an older study by Voigt (1926) in the Campanian of northern Germany. Although the otoliths are poorly preserved (generic identification is not even possible with many), one of them, *Otolithus. Gadidarum erraticus* Voigt (1926) appears to represent a gadiform otolith. Gadiform otoliths have also been reported from the Maastrichtian type area (Netherlands, Belgium). Although it is a very small number of silicified specimens (only 39 identifiable), two gadiforms are present with one of them a typical merluccid (Schwarzhans and Jagt 2021). The first gadiforms have been reported from the eastern coast of the USA from the Upper Cretaceous Severn Formation, although only a small number of specimens (six) were present (Stringer and Schwarzhans 2021).

The Arkadelphia Formation gadiforms of this study supply another important piece of evidence in unraveling the evolution of the Gadiformes. The gadiform otoliths from the Arkadelphia Formation are the largest number of specimens (n=160) from any Cretaceous formation known to date. Two gadiform taxa are present in the Arkadelphia Formation as well as specimens left in open nomenclature. *Palaeogadus* cf. *P. weltoni* adds to the geographic distribution of the species, and the presence of a new species, *Palaeogadus? belli* provides salient data on the development of the gadiforms in the Late Cretaceous. The Arkadelphia Formation gadiforms, along with the above-mentioned records, provide further evidence of the presence of this order and clearly indicate speciation and diversification in the Late Cretaceous as suggested by earlier investigations. Equally important and relevant is the abundance of *Palaeogadus? belli* in the Arkadelphia Formation. The 148 specimens of *Palaeogadus? belli* represent 7.02% of the total assemblage of 2,109 otoliths. Thus, it appears that these early gadiforms were not only present and diversified but also successful and abundant prior to the K-Pg extinction.

The gadiforms in the Arkadelphia Formation, the

Kemp Clay, and the Severn Formation verify the presence and geographical distribution of the order in the Late Cretaceous. However, gadiform otoliths are completely missing from the Santonian Eutaw Formation (Schwarzahns et al. 2018b) of Alabama and from the Campanian Tar Heel Formation of North Carolina (Stringer et al. 2018) and the Campanian Woodbury Formation of New Jersey (Stringer et al. 2016). This is especially evident in the study of the Woodbury Formation in New Jersey by Stringer et al. (2016). Otolith specimens were numerous in the investigation of the Woodbury Formation with 3,555 specimens and were obtained through bulk sampling. If gadiforms were present during this interval of the Late Cretaceous, it would seem that they should have been recovered. Furthermore, New Jersey was located at a more northern latitude and open to the Atlantic realm. Both of these factors would have been conducive to the presence of gadiforms. Yet, no evidence of gadiforms were found. A paramount consideration is that the Woodbury Formation is lower to middle Campanian. Likewise, the Tar Heel Formation is lower Campanian. If the gadiforms evolved in the late Campanian as proposed by Schwarzahns and Stringer (2020a) based on two specimens reported by Voight (1926), then the absence of gadiforms may be related to the timing of their evolutionary development. This premise is also supported by time-calibrated molecular analysis using 15 fossil taxa that suggested the evolution of the Gadiformes at approximately 79.5 Ma (Roa-Varón et al. 2021). This date would indicate that the Gadiformes evolved in the middle Campanian (Cohen et al. 2013) and would be very close to the geological age proposed by Schwarzahns and Stringer (2020a).

As noted by Stringer et al. (2020), the evolution of the Late Cretaceous fishes was characterized by the diversification and specialization in the Beryciformes and was especially notable in the genus *Eutawichthys*. This taxon had at least five species including *E. compressus* Schwarzahns, Huddleston, and Takeuchi (2018b), *E. stringeri*, *E. maastrichtiensis*, *E. zideki*, and *E. choctawae* Stringer and Schwarzahns (2020) during the Late Cretaceous in North America (Stringer et al. 2016, Schwarzahns et al. 2018b, Stringer et al. 2018, Schwarzahns and Stringer 2020a, Stringer et al. 2020). Although *E. maastrichtiensis* and *E. zideki* appear to be replacing *E. compressus* and *E. stringeri* during the Late Cretaceous, *E. stringeri* is present in the Arkadelphia Formation, but its abundance is much less than *E. zideki*. Otoliths of *E. zideki* comprised 13.61% (287 specimens) of the total assemblage in the Arkadelphia Formation and were second only to *Vorhisia*

vulpes in abundance. The genus *Eutawichthys* was abundant and well represented starting in the Santonian and extending through the Campanian and Maastrichtian. However, this diverse beryciform genus became extinct at the K-Pg boundary and appears to be replaced by perciformes in the Paleogene.

One of the most spectacular and striking otolith morphologies to evolve in the Late Cretaceous was *Tippaha mythica*, which is present in the Arkadelphia Formation. The otolith morphology of this species is not comparable to any known extant fishes, and it was provisionally placed in the order Holocentriformes by Stringer et al. (2020; fig. 11, I–X). The species was originally described as an ophidiid by Nolf and Stringer (1996). Some of the more distinctive morphological features of this species are the prominent and large predorsal projection, the unusual shape of the sagitta, the pseudobiostial sulcus opening, and the significant depression of the posteroventral of the sagitta. As noted by Stringer et al. (2020), one of the most distinguishing features is the fading of the dorsal margin of the anterior section of the cauda towards the dorsal depression, which is also known in the extant Myripristidae. This feature connects to an area of specific supporting cells of the macula (Popper 1977). The extant *Myripristis* Cuvier (1829) possesses an enhanced auditory ability for very high sound frequencies (Coombs and Popper 1979). This feature and the prominent predorsal projection could represent a connection of the otic capsule to the swim bladder. This arrangement has also been noted in the otoliths of extant morids (Deng et al. 2011). The basis of the tentative taxonomic assignment of this species by Stringer et al. (2020) was its resemblance to extant myripristid otoliths, the diversity of extinct holocentriform fish skeletons from the Late Cretaceous (Patterson 1964), and holocentriform otoliths from the Maastrichtian of Germany (Schwarzahns 2010). This species with its impressive otolith morphology and possible heightened auditory capabilities became extinct at the K-Pg event (Schwarzahns and Stringer 2020a).

Although the Upper Cretaceous Ripley Formation, Owl Creek Formation, Kemp Clay, and Severn otolith assemblages included very limited, possible representatives of the order Perciformes (Schwarzahns and Stringer 2020a, Stringer et al. 2020, Stringer and Schwarzahns 2021), no perciformes were represented in the Arkadelphia Formation. Possible perciform taxa in the Ripley and Owl Creek formations were *Pempheris? huddlestoni* (Nolf and Stringer, 1996) and *Serranus? severnensis* (Nolf and Stringer, 1996) while *Serranus? caribbaeus* (Nolf and

Dockery, 1990) was present in the Kemp Clay. However, *S. ? severnensis* was tentatively allocated to the fossil genus *Holocentronotus* in the Holocentridae by Stringer and Schwarzhans (2021). Although perciform otoliths represented only a very small percentage of the assemblages in these formations, they do provide evidence of the early percomorph lineage development. The lack of perciforms in the Arkadelphia Formation otolith assemblage does not appear to be related to the paleoenvironment since several of the other formations have similar paleoenvironmental conditions. It also does not seem to be related to the geologic age of the Arkadelphia Formation since it is the same age as other formations that have putative perciforms in their assemblage. For the present, the complete absence of perciforms in the 2,109 otolith specimens of the Arkadelphia Formation may attest to the rarity of the perciforms in the Late Cretaceous.

CONCLUSIONS

Although unexpected, the opportune and propitious finding of teleostean otoliths in boring samples in the Arkadelphia Formation (Cretaceous, upper Maastrichtian) has provided an abundant array of information. The otoliths (2,109 specimens) are the first known from the Mesozoic of Arkansas and represent one of the largest assemblages from a single site in the Gulf Coastal Plain. The otolith assemblage diversity is characterized by a richness of 19 unequivocal taxa and a pronounced unevenness with one species (*Vorhisia vulpes*) accounting for 72.88% of the total specimens. The number of species based on otoliths increases the bony fishes known from the Arkadelphia Formation from 6 to 28 taxa (a very significant change). Both the presence of cool-water gadiforms and their percentage (7.59% of the assemblage) in the Arkadelphia Formation are distinctive and rare for the Gulf Coastal Plain. The gadiforms are associated with the configuration of the Late Cretaceous paleogeography and the Western Interior Seaway. The otoliths of the Arkadelphia Formation were shown to be significantly more closely related to the Kemp Clay Formation (Texas), the Fox Hills Formation (North Dakota), and the Severn Formation (Maryland) than to Upper Cretaceous formations in the central Gulf Coastal Plain (Mississippi) based on percentage similarity measurements. The Arkadelphia Formation otolith assemblage was placed in the WIS Community proposed by Schwarzhans and Stringer (2020a) based on a number of correlative characteristics. A fairly large component of the Arkadelphia Formation otolith assemblage becomes extinct at the K-Pg boundary event. An analysis of the otoliths based

on families and species indicates a very shallow marine environment (possibly inner shelf; less than 20 m) with estuarine and freshwater input nearby. The interpreted paleoenvironment of the Arkadelphia Formation agrees well with other fossil groups, especially microfossils, and generally with paleogeographic maps. However, the Arkadelphia Formation paleoenvironment may necessitate some revisions to the paleogeography for the southern portions of the Western Interior Seaway.

ACKNOWLEDGEMENTS

Special thanks are extended to the drill crew (D. Thornton, D. McCollum, T. Frazier, A. Dillman, S. Bates) for their field assistance and to the ARDOT for allowing the analysis of the drill core samples. K.A. Johnson (National Marine Fisheries Service, Southeast Fisheries Science Center, Pascagoula, MS), R. Taylor (formerly of the Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL), and J.R. Hendon (Center for Fisheries Research and Development, Gulf Coast Research Laboratory, University of Southern Mississippi, Ocean Springs, MS) generously provided modern fishes and otoliths. D. Nolf (Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium) also supplied extant and fossil otolith specimens. W. Schwarzhans (Natural History Museum of Denmark, Zoological Museum, Copenhagen, Denmark) made valuable suggestions regarding the identity and taxonomy of otoliths. E. Manning (Davenport, Iowa) identified osteological remains from the Arkadelphia Formation. Karen Morton, Collections Manager, and R.S. Tykoski, Director of Paleontology and Curator of Vertebrate Paleontology, both of the Perot Museum of Nature and Science, Dallas, Texas, were especially helpful in the repositing of the otolith specimens at their institution. D. Bell graciously provided expertise and assistance in the development of the figures of the otoliths and other figures for the study. Appreciation is extended to J. Ebersole (Director of Collections, McWane Science Center, Birmingham, Alabama) and an anonymous reviewer for their detailed and helpful review of the manuscript. A special word of thanks to D.M. Erwin (Senior Museum Scientist, University of California Berkeley, Museum of Paleontology, Berkeley, California) for her assistance.

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