

## HIGHLY DIVERSIFIED LATE CRETACEOUS FISH ASSEMBLAGE REVEALED BY OTOLITHS (RIPLEY FORMATION AND OWL CREEK FORMATION, NORTHEAST MISSISSIPPI, USA)

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To cite this article: Stringer G.L., Schwarzhans W., Phillips G. & Lambert R. (2020) - Highly diversified Late Cretaceous fish assemblage revealed by otoliths (Ripley Formation and Owl Creek Formation, Northeast Mississippi, USA). *Riv. It. Paleontol. Strat.*, 126(1): 111-155.

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*Keywords:* Beryciformes; Holocentriformes; Aulopiformes; otolith; evolutionary implications; paleoecology.

*Abstract.* Bulk sampling and extensive, systematic surface collecting of the Coon Creek Member of the Ripley Formation (early Maastrichtian) at the Blue Springs locality and primarily bulk sampling of the Owl Creek Formation (late Maastrichtian) at the Owl Creek type locality, both in northeast Mississippi, USA, have produced the largest and most highly diversified actinopterygian otolith (ear stone) assemblage described from the Mesozoic of North America. The 3,802 otoliths represent 30 taxa of bony fishes representing at least 22 families. In addition, there were two different morphological types of lapilli, which were not identifiable to species level. The large number of otolith specimens as well as the preservation contributed to the recognition of 4 new genera and 13 new species. The otoliths supplied information regarding the presence of bony fishes not available solely on the basis of osteological remains, and the Late Cretaceous bony fish assemblage at the sites would be underestimated and misinterpreted without an examination of the otoliths. The otoliths also contributed evidence on the evolutionary development of teleosts in North America, especially the diversity of the beryciforms in the Late Cretaceous, and provided indications of the paleoecology during the Maastrichtian. The Ripley Formation (Coon Creek Member) otolith assemblage, which accounted for 3,718 of the specimens, is compared to other Cretaceous otolith assemblages in North America that meet certain criteria (employed bulk-sampling techniques, had well-preserved specimens, and possessed a substantial number of specimens and taxa for analysis). These sites were in Alabama, Maryland, Mississippi (two localities), New Jersey, North Carolina, North Dakota, Tennessee, and Texas. Systematic surface collecting at the Blue Springs locality proved to be very beneficial in supplying otoliths specimens from maturer fishes. Many of the surface-collected otoliths represent older adult fishes that assist with the identification of several forms with greater specificity.

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## INTRODUCTION

The usefulness of otoliths in interpreting and determining bony fish assemblages has been unquestionably corroborated in numerous studies such as Breard & Stringer (1995), Girone (2003), Huddleston & Savoie (1983), Lin (2016), Lin et al. (2016), Nolf (1985, 2003b, 2013), Nolf & Brzobohaty (1994), Nolf & Stringer (1996), Schwarzhans (1993, 1996, 2003, 2010), Schwarzhans et al. (2018a, 2018b), Stringer (1992, 1998a), Stringer et al. (2016, 2018) as well as many other references contained in the aforementioned publications. For example, Breard & Stringer (1995) in a study of the late Eocene Yazoo Clay in Louisiana reported 12 actinopterygians based on skeletal remains (primarily teeth). This is in stark contrast to the 43 taxa of bony fish identified from the same locality

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Received: July 25, 2019; accepted: September 27, 2019

using otoliths (Nolf & Stringer 2003). The diversity of the bony fishes is more fully understood when osteological elements and otoliths are both considered and analyzed. This, of course, is predicated by the presence of skeletal remains and otoliths in the strata.

The importance of otoliths for identifying and understanding the diversity of actinopterygians in the Ripley Formation at the Blue Springs locality is demonstrated by the number of bony fishes identified based on skeletal remains. Since there are no publications on the osteological remains of bony fishes from the site, various collections were utilized to ascertain this information including the holdings in the Paleontology Section at the Mississippi Museum of Natural Science and specimens held by the North Mississippi Gem and Mineral Society. These two entities possess some of the most extensive collections from the site. Yet, there is strong evidence for only five taxa of bony fishes from the Ripley Formation at the Blue Springs locality based on skeletal remains (*Enchodus ferox*, *Enchodus gladius*, *Apateodus ghyphodus*, *Paralbula casei*, and *Anomoeodus sp.*). There are several unidentified specimens that may represent a couple of additional taxa. The collection and analysis of otoliths from the Ripley Formation increased the bony fish assemblage at least fivefold and identified taxa that would have otherwise gone unrecognized in the ichthyological fauna. The otoliths from the Owl Creek Formation type locality also increased the known taxa at the site but not as pronounced as at the Blue Springs locality. Obviously, the best scenario is to analyze both the skeletal material and otoliths in order to gain a better understanding of the Late Cretaceous fish fauna.

The actinopterygians represented by otoliths from Ripley Formation at the Blue Springs locality described here and the Owl Creek Formation at the Owl Creek type locality have not been scientifically described, although other Cretaceous sites have been. An overview of the fishes identified on the basis of otoliths from the site is presented, and the systematic paleontology for the taxa is described. The evolutionary and paleoecological significance indicated by the otoliths from the sites are also addressed. Finally, the Ripley Formation bony fish assemblage represented by otoliths is compared to otolith assemblages from other Late Cretaceous localities in the U.S.

## LOCATION OF THE INVESTIGATED SITES

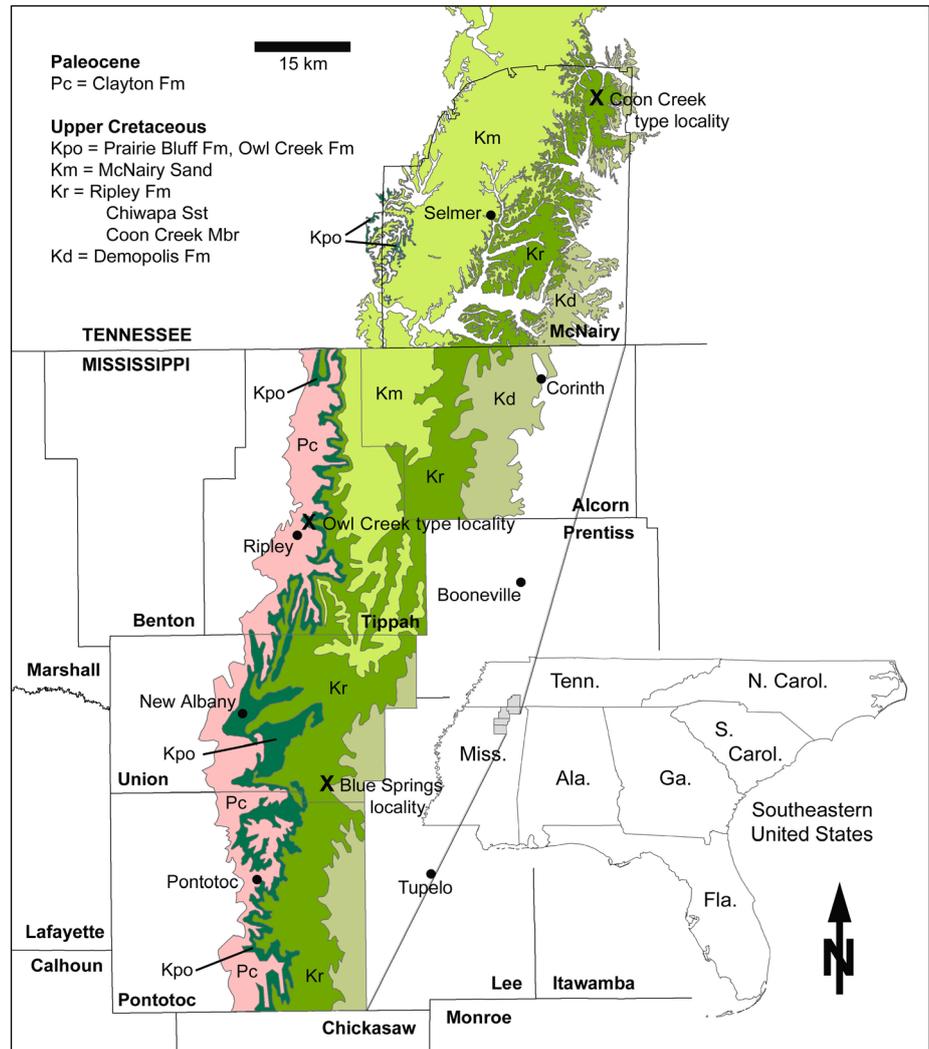
The Blue Springs site is located at approximately 34.25° N, 88.5° W in Union County in northeast Mississippi, USA (Fig. 1), and the name of the locality is in reference to a nearby village. The locality is northeast and southeast of the intersection of Mississippi Highway 9 South and Mississippi County Road 209 (approximately 130 m northeast of intersection of Mississippi Highway 9 South and Highway 178 South). Exposures are present on the east and west side of Highway 9 and are quite extensive (over 300 m long and 250 m wide). Exposures on the west side of Highway 9 are considerably larger in extent and contain a more complete section. The exposures are the result of highway construction in the area. It should be noted that the Blue Springs site is not the same as the one referred to by the same name in Bishop (1983; 1985), Stringer (1991) and Nolf & Stringer (1996). The present site is north of the one in the aforementioned studies and is referred to as the Blue Springs site in this study. If reference is made to the previous site, it is noted as the Blue Springs site (Bishop 1983).

The type locality for the Owl Creek Formation is just northeast of Ripley, Mississippi, in Tippah County in northeast Mississippi (Fig. 1) and is designated as MMNS locality MS.70.002. The Owl Creek Formation type locality is located approximately 44 km almost due north of the Blue Springs locality and is approximately 78 km southwest of the Coon Creek type locality in McNairy County, Tennessee. The exposures of the formation are in the sides and bottom of Owl Creek (Dockery & Thompson 2016; Larina et al. 2016). The material for this study was collected in the Owl Creek Formation within the vicinity of a prominent bed of *Exogyra costata* Say (Ostreidae: Gryphaeidae) lying approximately 10 m below the K-Pg boundary (Paleocene Clayton Formation).

## STRATIGRAPHY OF THE LOCALITIES

The Blue Springs locality is an extensive, unprecedented exposure of the Upper Cretaceous Coon Creek Member in Mississippi (Fig. 2). These very fossiliferous clays, sandy clays, and calcareous clays form the bulk of the Ripley Formation. As at

Fig. 1 - Surface geologic map of northeastern Mississippi and adjoining Tennessee showing relevant published Maastrichtian (uppermost Cretaceous) localities. The Blue Springs locality, as used herein, is stratigraphically equivalent to Bishop's (1983, 1985) "Blue Springs Locality" (GAB 37), which is now covered and was located south of the present study. The Owl Creek locality to the north exposes the younger (latest Maastrichtian) Owl Creek Formation (e.g. Stephenson 1955; Sohl 1960). Even further north is the Coon Creek type locality of Wade (1926). The insert map shows the counties of interest (shaded) detailed in the larger map.



the type locality, this interval in Mississippi exhibits exceptional biodiversity due to aragonite preservation. At the type locality, the mollusk-rich layers of the Coon Creek are regarded as late Campanian based on the presence of *Exogyra cancellata* (Stephenson & Monroe 1940) and ammonite biostratigraphy (Cobban & Kennedy 1994; Larson 2012, 2016). The otolith samples of Stringer (2016b) are of this age. However, the Coon Creek Member exposed in Union County is early Maastrichtian (Cobban 1974; Landman et al. 2019). The Coon Creek otolith samples analyzed herein are from these younger sediments.

The Owl Creek Formation exposed at the type locality represents the highest unit of the Upper Cretaceous (upper Maastrichtian) in the northern Mississippi Embayment. The Owl Creek Formation is composed of glauconitic, variably micaceous, fine-grained beds ranging from sandy clay

to clayey sand that become increasingly calcareous to the south (Stephenson & Monroe 1940; Sohl 1960). At least 9.5 m of Owl Creek Formation are exposed at the type locality near Ripley, Mississippi (Phillips, pers. obs.), where the present otolith samples were collected. Almost all of the specimens were collected in the bed of Owl Creek at the base of the main section (a bluff), just above an *Exogyra costata* Say biostrome. Larina et al. (2016) most recently measured the type locality (the bluff section) but did not include the *E. costata* bed, which lies just below the base of their measured section. Most of the Owl Creek otoliths studied are derived from a washed bulk sample taken from one of the "fossiliferous pods...scattered throughout the section" and interpreted as large burrows (Larina et al. 2016: 130). The sediments above the *E. costata* bed at the type locality belong to nannofossil subzone CC26b and are thus latest Maastrichtian (Larina et al. 2016).

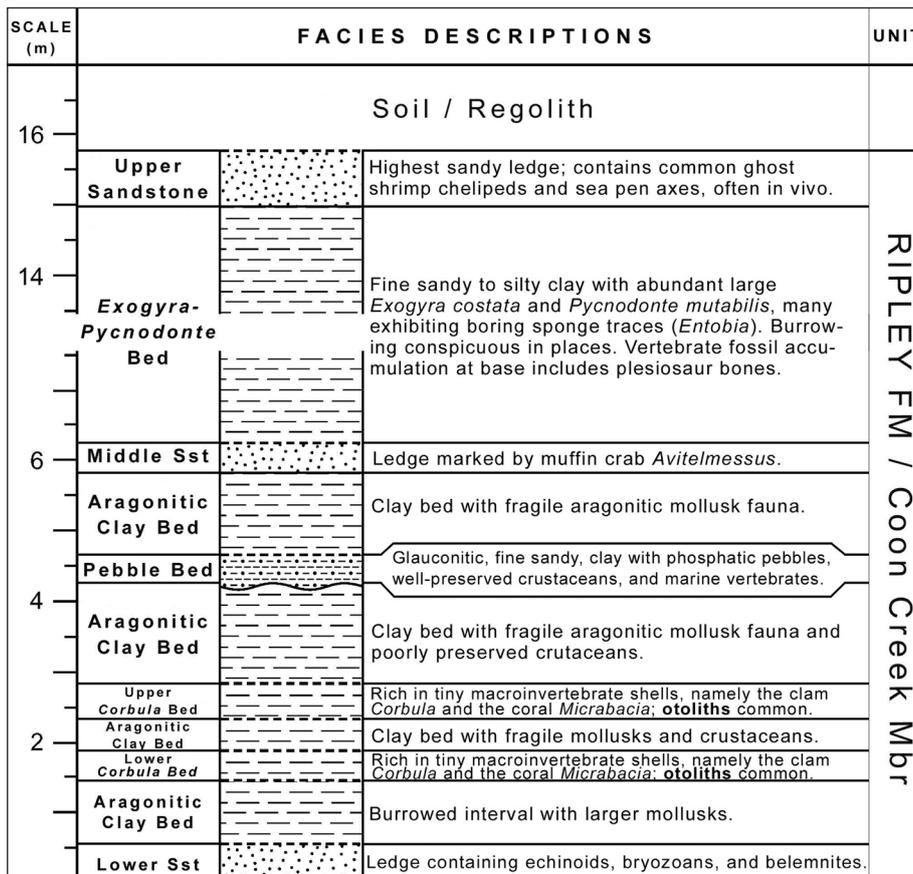


Fig. 2 - Composite section of the Blue Springs locality. Three different stations were measured in 2010 to produce the illustrated section, which lies entirely within the Coon Creek Member of the Ripley Formation. Otoliths were concentrated in the *Corbula* beds.

The lower contact of the Owl Creek Formation with the McNairy Sand or Chiwapa Member of the Ripley Formation represents a transgressive surface. The higher beds in the Owl Creek Formation represent sediments associated with a transgressive systems tract followed by progradation beds of a highstand system tract according to Mancini et al. (1995). Therefore, the Owl Creek Formation at the type locality indicates a nearshore, marine environment that was below wave base. Microfaunal and macrofaunal analysis as well as sedimentological studies point to a paleowater depth of about 20–30 m. As the Owl Creek Formation was deposited in the Late Cretaceous Mississippi Embayment, it was probably in a warm temperate to subtropical climate (Larina et al. 2016). A comprehensive summary of the stratigraphic relationships of the Coon Creek Member of the Ripley Formation and the Owl Creek Formation including European stratotypes, planktonic foraminiferal zonation, nannofossil zonation, Gulf Coast ammonite zones, Tethyan ammonite zones, and North American western interior ammonite zones is shown in Fig. 3.

## PREVIOUS STUDIES OF CRETACEOUS OTOLITHS IN NORTH AMERICA

In his *Otolithi Piscium* in 1895, Nolf reported less than 20 valid species represented by otoliths for the Cretaceous worldwide. While the number of Cretaceous species has increased substantially over the last three decades (Nolf 2013), there is still a paucity of investigations of Cretaceous otoliths, although Late Cretaceous rock have proven to be particularly prone for otoliths in North America due to the common deposition of sandy and clayey sediments. The relatively low level of previous research increases the importance of this study of the Ripley Formation at the Blue Springs locality otoliths and the Owl Creek Formation at the Owl Creek type locality. North American Cretaceous otoliths have been obtained primarily from Campanian and Maastrichtian strata although there are isolated reports from other ages such as Cenomanian (Huddlestone 1981) and Santonian (Frizzell 1965a; Schwarzahans et al. 2018b). Although Koken completed the first scientific description of Cretaceous otoliths in 1891 on otoliths from Europe, studies

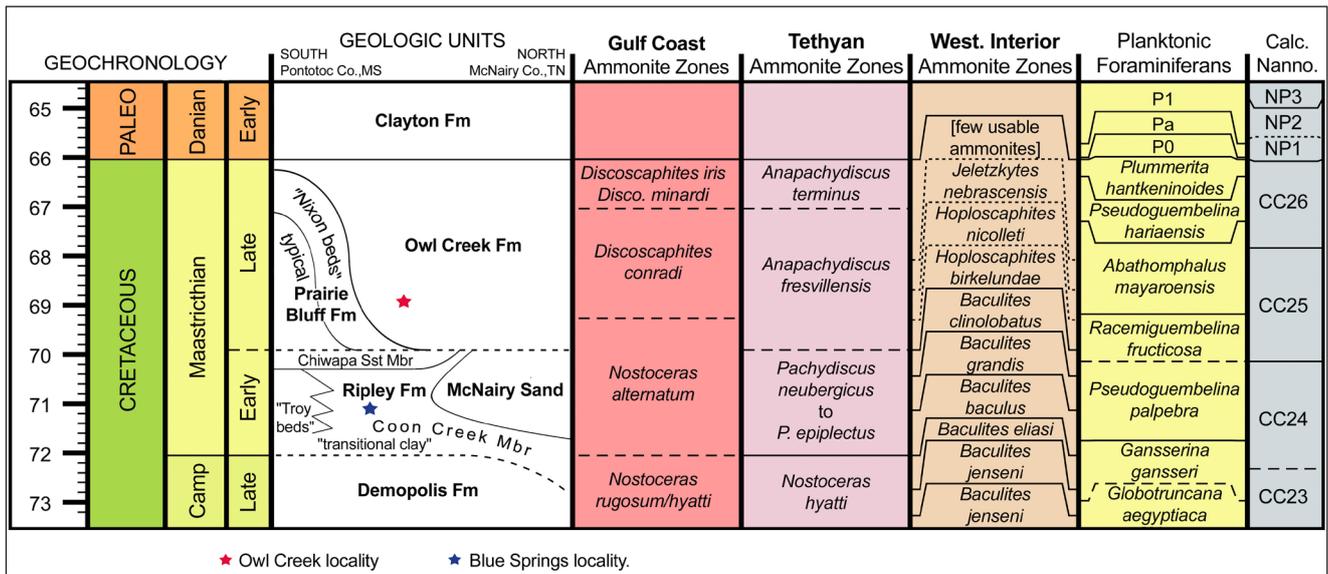


Fig. 3 - Stratigraphic chart of Upper Cretaceous deposits exposed at the surface in northeastern Mississippi and adjoining Tennessee. The chronostratigraphy and most of the biostratigraphic columns were produced using TS (TimeScale) Creator 7.3 (© 2005-2018 Geologic TimeScale Foundation), which is based on Ogg et al. (2016). The planktonic foram and nannoplanktonic biozones of Ogg et al. (2016) are in turn based (in part) on Hardenbol et al. (1998) and Foucher & Monteil (1998). The stratigraphic data used in TS Creator represent standards as ratified by the International Commission on Stratigraphy and the International Union of Geological Sciences. The Gulf Coastal Plain (GCP) ammonite zones and their correlative ages are based primarily on Cobban (1974), Cobban & Kennedy (1991a,b, 1993,1995), and Larina et al. (2016). Support for a more certain placement of an ammonite-based Campanian-Maastrichtian boundary in the eastern GCP is in progress. The correlation of geologic unit contacts as related to the stage and substage boundaries is based, in part, on the work of Sohl and Koch (1986). The informal member units “Nixon beds,” “Troy beds,” and “transitional clay” were introduced by Phillips (2010), Swann & Dew (2008, 2009), and Sohl (1960), respectively. The Coon Creek beds are time transgressive, the Campanian-Maastrichtian boundary being located higher in the section in the northern part of the outcrop belt (e.g. Larson, 2016) than in the southern part (e.g., Cobban 1974).

of North American Cretaceous otoliths were not to occur until much later.

One of the earliest reports on the occurrence of otoliths from the Cretaceous of North America was from the Coon Creek site in southwest Tennessee by Wade (1926), who figured a single otolith from the Coon Creek type locality. The otolith was mentioned in a section entitled “Class Pisces” (p. 192) that was actually written by J. Gidley of the United States National Museum. The otolith was figured on Plate LXXI (figs. 9 and 10) and was labeled as simply “otolith” in the plate description. The figured specimen appears to be a lapillus (utricular) otolith from a marine ariid (sea catfish), which are known from several other Cretaceous formations in North America (Huddleston & Savoie 1983; Stringer 1991; Nolf & Stringer 1996). Although only one otolith is discussed in the section on fishes by J. Gidley and figured in the plates, Wade used the term “otoliths” in his table entitled “The Coon Creek fauna and its range” (pp. 22–26). Otoliths are listed, but they are not discussed. It is unclear if the “otoliths” in the table represent one taxon and how many otoliths were actually recovered by Wade

from Coon Creek.

Almost thirty years after Wade (1926) figured an otolith from the Coon Creek type locality in Tennessee, Tychsen & Vorhis (1955) noted the occurrence of otoliths in the Fox Hills Sandstone (Maastrichtian) of South Dakota but did not describe any of the otolith specimens. Frizzell completed the first descriptions of Cretaceous otoliths from North America in two different publications in 1965. Frizzell (1965a) described fossil bonefish sagittae, which included *Prealbulula weileri* (Santonian Eutaw Formation in Alabama) and *Protoalbulula sobli* (Campanian Blufftown Formation in Alabama). He also published the first description of *Vorbisia vulpes* based on isolated lapilli of this siluriform from the Fox Hills Sandstone (Maastrichtian) of South Dakota (Frizzell 1965b). Waage (1968) also noted the occurrence of ariid otoliths in his studies of the stratigraphy and paleoenvironments of the Fox Hills Sandstone. Frizzell & Koenig (1973) reported on asterisci from the same formation in South Dakota and assigned the asterisci to *Vorbisia vulpes*, but there has been considerable disagreement on this identification (Huddleston & Savoie 1983).

Huddleston (1981) described a new Cretaceous genus and species, *Bernardichthys zorraquinosi*, from a single well-preserved otolith from the Bernard Formation (early Cenomanian) of Oregon. This represents the oldest reported occurrence of an otolith in North America at approximately 99.6 million years old. Huddleston & Savoie (1983) conducted a study of 1086 otoliths from the Severn Formation (early-middle Maastrichtian) of Maryland, and Nolf & Dockery (1990) reported on the otoliths from the Tupelo Tongue of the Coffee Sand (Campanian) in Mississippi.

Patterson (1993) published a thorough and extensive overview of the early fossil record of acanthomorphs based primarily on skeletal remains. However, he also discussed the fossil record of otoliths, including the Cretaceous. In addition, he compared the differences in findings based on osteological remains and otoliths. Patterson stated, “the Cretaceous otoliths record is still very poor,” which at that time was certainly true. Nolf & Stringer (1996) conducted one of the most extensive investigations of Cretaceous otoliths in North America. They reported 43 teleost taxa and otoliths from several new localities (the Late Cretaceous Ripley Formation at Lake, Mississippi and the Late Cretaceous Severn Formation at Brightseat, Maryland).

Stringer (2016b) summarized otolith investigations at the Late Cretaceous Coon Creek type locality in Tennessee as part of a monograph on the site. Woodward (2003) reported on a large otolith assemblage from the Late Cretaceous (Maastrichtian) Kemp Clay from the South Sulfur River in Hunt County, Texas. A 27-kg bulk sample produced a prolific number of specimens (1202). More recent investigations of Campanian otoliths in North America are Stringer et al. (2016) and Stringer et al. (2018). Stringer et al. (2016) reported on the early-middle Campanian Woodbury Formation in New Jersey, while Stringer et al. (2018) described otoliths from the early Campanian Tar Heel Formation in North Carolina. The most recent publication on North American Cretaceous otoliths is that of Schwarzghans et al. (2018b) of the late Santonian Eutaw Formation of Alabama. This research presented major changes to the taxonomy of Cretaceous otoliths based on several factors including *in situ* otoliths in skeletal remains. In addition, four taxa based on otoliths are reported from the extensive study of the chondrichthyan and osteichthyan

faunas of the Cretaceous (late Maastrichtian) Fox Hills Formation of North Dakota based primarily on skeletal remains (Hoganson et al. 2019).

## METHODOLOGY AND TERMINOLOGY

This study included material that was collected by various researchers who utilized different techniques at the two localities. George Phillips initially investigated the Ripley Formation at the Blue Springs site for several reasons including the discovery of dinosaur remains (a hadrosaur femur) and the presence of aragonitic micromollusks. Aragonitic micromollusks, especially gastropods, indicated that leaching most likely had not destroyed the otoliths. Phillips collected three bulk samples (54 kg) from the *Corbula* beds (Fig. 2) and made a surface collection primarily for micromollusks, but it also included otoliths. Stringer processed Phillips' Ripley Formation bulk samples for otoliths, and subsequently, collected additional bulk samples (85 kg) at the four sections of Phillips. Stringer made a small surface collection of otoliths while collecting bulk samples. Robert Langford (North Mississippi Gem and Mineral Society) collected and processed the largest bulk samples (approximately 296 kg) from the aragonitic clay *Corbula* beds. Nancy Roberts (North Mississippi Gem and Mineral Society) provided access to her surface collection of otoliths. J. C. Sloan, geologist with the Arkansas Department of Transportation, also supplied specimens from the Blue Springs site. Otolith specimens from the Ripley Formation at the Blue Springs locality were borrowed from the McWane Science Center, Birmingham, Alabama. Roger and Matthew Lambert (North Mississippi Gem and Mineral Society) independently conducted exhaustive, systematic surface collecting at the site over a six-year span.

There was some variation in the bulk sample preparation by different researchers, primarily sieve size, but all of the sediment was wet screened using plain water. All residue from the Phillips and Stringer bulk samples from the Ripley Formation that was retained on a U.S. Standard Sieve #30 was air-dried and kept for study. U.S. Standard sieves (#5 to #30) were employed to separate the residue into similar-sized material for microscopic examination using an Olympus binocular microscope (6.7x to 40x). The Phillips and Stringer bulk samples (139 kg) yielded 742 otoliths or 5.34 otoliths/kg of sediment. This ratio is almost identical to that of Stringer et al. (2016) from the Late Cretaceous (Campanian) Woodbury Formation of New Jersey (5.22 otoliths/kg of sediment). The ratio of otoliths to kg of sediment at the Blue Springs locality is exponentially better than otoliths from the Late Cretaceous (Campanian) Coffee Sands studied by Nolf & Dockery (1990) that yielded only 0.08 otoliths/kg of sediment. The Late Cretaceous (Campanian) Tar Heel Formation (Stringer et al. 2018) yielded a much greater ratio (14.3 otoliths/kg of sediment), but unfortunately, the preservation of the otoliths was not nearly as good. In contrast, the bulk samples collected by Phillips from the Owl Creek Formation were not nearly as prolific. One 26-kg Owl Creek Formation bulk sample produced only 15 otoliths or 0.58 otoliths per kg of bulk sample. Additional Owl Creek bulk samples yielded similar results.

This investigation also included otoliths specimens that were collected on the surface. By far, the most extensive surface collecting was conducted by Lambert, who utilized a systematic approach to collect the specimens. The large areal extent of the Blue Springs locality made it conducive to systematic surface collecting. Initial investigations were conducted to determine specific beds with aragonitic remains such as gastropods. Following this, Lambert followed the bed along the outcrop collecting otoliths that could be seen with

the naked eye. All surface-collected specimens (Phillips and Lambert) were sent to Stringer for analysis as were all specimens from the bulk samples. The Owl Creek Formation type locality is located in a narrow creek with very steep sides. As such, the areal extent of the locality is very small, and surface collecting was greatly limited and contributed little to the study of the otoliths at that site. Only otolith specimens from bulk samples were utilized for statistical purposes.

All of the figured otolith specimens in this study have been repositied in the Mississippi Museum of Natural Science (MMNS) located at 2148 Riverside Drive, Jackson, Mississippi 39202. The MMNS is the official repository for all scientific specimens collected in the State of Mississippi and is accredited by the American Alliance of Museums. In addition to the figured specimens, several thousand unfigured otolith specimens recovered from the Ripley and Owl Creek formations are also repositied in the MMNS. A few specimens that are non-types and not figured have remained in the comparative private collections of the authors. All otolith specimens are housed in the Paleontology Collection at the museum and are designated by a MMNS collection number (e.g., MMNS VP 6382). Typically if specimens are part of a single collection obtained at the same time at the same location, the collection numbers will be consecutive. However since the otoliths were collected at different times (over several years) and by different collectors, the collection numbers are not consecutive.

Photographs were made by Schwarzahns with a Canon EOS mounted on the phototube of a Wild M400 photomicroscope. They were taken at regular focus levels for each view remotely controlled from a computer. The individual photographs of each view were stacked with Helicon Focus software of Helicon Soft. The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast or balance exposition or retouch small inconsistencies such as sand grains, incrustations or pigmentation spots, as far as possible without altering the otolith morphology. Specific care was taken to photograph inner and outer otolith faces with the central portion of the respective faces positioned at level in order to avoid distortions that otherwise occur in strongly bent specimens (for an explanation, see fig. 3.9 in Lombarte & Tuset 2015). The same principle has been applied for lateral views, in which the otoliths were oriented in upright position either along the horizontal or vertical axis depending on dorsal/ventral and anterior/posterior views respectively. Such standardized display techniques are essential for comparison with other research work. Fixing otolith in plasticine has proven to be the most effective method of achieving adequate results.

All figures show right otoliths. Left otoliths have been mirror imaged to facilitate better comparison and are annotated in the captions as “reversed.” Individual specimens are shown from the inner face, and, in some cases, are shown from other views as well such as outer face, ventral, dorsal, anterior or posterior views. These other views are shown without specific annotation since their orientation can be easily deduced from the figure of the accompanying inner face.

The morphological terminology of sagittae otoliths (“otolith” hereinafter) follows Koken (1884) with amendments by Weiler (1942) and Schwarzahns (1978). Measurements were done either using a *camera lucida* mounted on the microscope or from photographs obtained from the photomicroscope. The following abbreviations are used for expressing ratios: OL = otolith length, OH = otolith height, OT = otolith thickness, CaL = cauda length, CaH = cauda height, CCL = length auf caudal colliculum, CCH = height of caudal colliculum, OsL = ostium length, OsH = ostium height, OCL = length of ostial colliculum, OCH = height of ostial colliculum. The OsL is measured from the anterior tip of the ostium to an inflection point at the ventral margin of the ostium marking its

termination, which may differ in cases from the posterior inflection of the dorsal margin of the ostium or the termination of the ostial colliculum. The CaL is measured from the same inflection point at the ventral margin of the sulcus to the termination of the cauda. The measures relating to OsL and CaL were taken when the sulcus margins were better-defined than the margins of the colliculi. Conversely, OCL and CCL were measured when the colliculi margins were clearer than the sulcus margins. Inclination angles were measured with the otolith oriented along its long axis, or in the case of high bodied otoliths along the sulcus axis.

## SYSTEMATIC PALEONTOLOGY

The taxa represented by otoliths in the Ripley Formation (Blue Springs locality) and the Owl Creek Formation (Owl Creek type locality) are presented in Table 1 and shown in Figures 4 – 13. The systematic paleontology of these taxa is provided. Fossil and Recent comparative otolith collections and references were utilized for the identification of the specimens. Unless otherwise noted, classification follows that of Nelson et al. (2106), which was greatly influenced by the work of Betancur-R. et al. (2013). Ordinal names follow Wiley & Johnson (2010), while the family-group names and authors of Recent fishes follow van der Laan et al. (2014). Recent 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.

### Order Elopiformes Jordan, 1923

#### Family Megalopidae Jordan & Gilbert, 1883

#### Genus *Megalops* Lacepède, 1803

#### *Megalops? nolfi* Schwarzahns & Stringer n. sp.

Fig. 4 O-U

- 1990 ? Megalopidae – Nolf & Dockery: pl. 1, fig. 1.  
 1991 Megalopidae – Stringer: pl. 1, fig. 1.  
 1996 ? Megalopidae – Nolf & Stringer: pl. 1, figs. 3-4.  
 2016 Megalopidae ind. – Stringer, Oman & Badger: pl. 1, fig. 1.

**Etymology:** In honor of Dirk Nolf (Bruges, Belgium) for his contributions to the knowledge of fossil otoliths from the U.S.A.

**Holotype:** MMNS VP 6382 (Fig. 4 O-Q), Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 2 specimens, MMNS VP 6382.1 and 6382.2, same data as holotype.

**Further specimens:** 6 specimens, same data as holotype.

**Diagnosis:** Oval otolith with long, but not well demarcated rostrum of nearly half the length of otolith (rostrum length 40-45% OL). OL:OH = 1.75-1.9. Sulcus distinctly archaesulcoid without marked colliculi. Ostium much wider and slightly longer than cauda. OsL:CaL = 1.45-1.65; OsH:CaH = 1.9-2.0.

**Description.** Thin, oval and rather inconspicuous otoliths up to 5.3 mm length (holotype 4.8 mm long). OH:OT = 3.6. Dorsal rim shallow, regularly curved with broad mediadorsal angle its anterior 40 to 45% corresponding to length of ostium and length of rostrum. Ventral rim shallow, regularly curved. Anterior and posterior tips median, rounded, posterior tip more blunt than anterior tip (rostrum). No or very feeble excisura and antirostrum. All rims relatively sharp and variably crenulated.

Inner face slightly convex with slightly supra-median sulcus. Sulcus archaesulcoid without colliculi, slightly deepened, with wide ostium and narrow, straight cauda terminating relatively close to posterior rim of otolith. Ostium about twice as wide as cauda, usually with indistinct opening along its entire dorsal margin (sometimes only anterior half of ostium; see Fig. 4 R). Dorsal depression very small, only above cauda; no ventral furrow. Outer face flat, slightly ornamented.

**Discussion.** *Megalops? nolfi* represents a 'primitive' sulcus morphology similar to many Jurassic and Early Cretaceous teleost otoliths (Schwarzhans 2018). This type of morphology has become rare in the Late Cretaceous and today is only found in a very few extant teleosts considered closest to stem teleosts, e.g., in the basal Elopiformes such as the Megalopidae. We therefore follow Nolf & Dockery (1990) and Nolf & Stringer (1996) in tentatively allocating these otoliths with the Megalopidae. So far, only relatively small otoliths have been described of sizes of less than 3 mm length, which are considered to stem from juveniles and do not show sufficient pertinent characters for species definition. Now, two larger and morphologically mature specimens are available warranting description. Recent specimens do not have the very slight downward flex found in the fossil specimens. Fossil megalopid otoliths are rare in all reported assemblages.

Order **Albuliformes** Jordan, 1923  
Family **Albulidae** Bleeker, 1859  
genus indet.

Albulidae indet.

Fig. 4 I-J

**Material:** 11 specimens: 10 specimens Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimen MMNS VP 6384). 1 specimen Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Discussion.** A number of poorly or incompletely preserved specimens represent an albulid of unresolved relationships. It is characterized by a short, ventrally little widened ostium, a strongly and regularly bent cauda, a strongly convex inner face with a very narrow dorsal field marked by a low dorsal rim and a wide, smooth ventral field. The outer face is almost flat to slightly concave. The OL/OH ratios are less than 2.0. Several of the specimens are quite large (exceed 12 mm in length). Although the specimens show some sulcal features that are more typical of Recent albulids such as *Albula vulpes* from the Gulf of Mexico (Hoese and Moore 1998; McEachran and Fechhelm 1998), the exact relationship cannot be determined because of poor preservation.

Family **Osmeroididae** Forey, 1973

Genus *Osmeroides* Agassiz, 1837

***Osmeroides mississippiensis*** Schwarzhans &

Stringer n. sp.

Fig. 4 A-H

**Etymology:** Referring to the state Mississippi, where the type location is located.

**Holotype:** MMNS VP 8894 (Fig. 4 A-D), Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 4 specimens, MMNS VP 8894.1-4 same data as holotype.

**Further specimens:** 65 specimens: 63 specimens same data as holotype; 2 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Diagnosis:** Moderately elongate, oval otolith with deep ventral and shallow dorsal rim. OL:OH = 1.75-1.9. Ostium wide, dorsally open; cauda distinctly flexed downward, diagonally positioned at 15-22° angle. CaL:OsL = 1.7-1.9. Inner face strongly convex.

**Description.** Large, oval otoliths up to 18.3 mm length (holotype). OH:OT = 2.0-2.3. Dorsal rim shallow, without prominent angles, irregularly undulating. Ventral rim deeply and very regularly curved, smooth. Anterior rim broadly rounded, with dorsally shifted, broadly rounded rostrum. Posteri-

Tab. 1 - Taxa represented by otoliths from the Ripley Formation (Blue Springs locality; 3,718 specimens from bulk samples and surface collections) and Owl Creek Formation (type locality; 84 specimens from bulk and surface collections) and corresponding figure numbers.

Order (uppercase letters and bold), family (lowercase and bold) and Taxon (based primarily on Nelson et al. 2016)	Ripley Formation Specimens	Owl Creek Formation Specimens	Figure numbers
<b>ELOPIFORMES</b>			
<b>Megalopidae</b>			
<i>Megalops? nolfi</i>	9		Fig. 4 O-U
<b>ALBULIFORMES</b>			
<b>Albulidae</b>			
Albulidae indeterminate	10	1	Fig. 4 I-J
<b>Osmeroididae</b>			
<i>Osmeroides mississippiensis</i>	68	2	Fig. 4 A-H
<i>Osmeroides</i> sp.	10	2	Fig. 4 K-L
<b>Pterothrissidae</b>			
<i>Pterothrissus</i> sp.	28	1	Fig. 4 M-N
<b>ANGUILLIFORMES</b>			
<b>Anguillidae</b>			
<i>Anguilla? chickasawae</i>	2		Fig. 5 A-E
<b>Family indeterminate</b>			
<i>Muraenanguilla unionensis</i>	33	2	Fig. 5 F-L
<b>OSTEOGLOSSIFORMES</b>			
<b>Family Osteoglossidae</b>			
<i>Osteoglossum? tavernei</i>	7		Fig. 6 J-K
<b>Family indeterminate</b>			
<i>Kokenichthys navis</i>	69	4	Fig. 6 A-F
<i>Kokenichthys ripleyensis</i>	1		Fig. 3 G-I
<b>AULOPIFORMES</b>			
<b>Ichthyotringidae</b>			
<i>Apateodus crenellatus</i>	107	4	Fig. 7 G-N
<i>Thrax acutus</i>	1		Fig. 7 O-R
<b>Paraulopidae</b>			
<i>Paraulopus pseudoperca</i>	210	10	Fig. 7 A-F
<b>PARACANTHOPTERYGII</b>			
<b>Order and family indeterminate</b>			
<i>Choctawichthys cepoloides</i>	4		Fig. 8 A-E
<b>POLYMIXIIFORMES</b>			
<b>Polymixiidae</b>			
<i>Cowetaichthys alabamiae</i>	33	6	Fig. 8 F-K
<i>Cowetaichthys carnevalei</i>	52		Fig. 8 L-S
<b>HOLOCENTRIFORMES</b>			
<b>Family indeterminate</b>			
<i>Tippaha cavata</i>	4		Fig. 11 A-F
<i>Tippaha mythica</i>	1	18	Fig. 11 I-X
<b>TRACHICHTHYIFORMES</b>			
<b>Trachichthyidae</b>			
<i>Hoplopteryx langfordi</i>	108		Fig. 9 I-O
<i>Hoplopteryx oscitans</i>	2548	3	Fig. 9 A-H
<b>BERYCIFORMES</b>			
<b>Family indeterminate, type 1</b>			
<i>Eutawichthys choctawae</i>	1		Fig. 9 U-W
<i>Eutawichthys maastrichtiensis</i>	43		Fig. 9 P-T
<i>Eutawichthys zideki</i>	31		Fig. 9 X-AA
<b>Family indeterminate, type 2</b>			
<i>Argyroberyx? dockeryi</i>	11	6	Fig. 10 A-E
<b>Family indeterminate, type 3</b>			
<i>Ossulcus labiatus</i>	3		Fig. 9 F-K
<b>PERCIFORMES s.l.</b>			
<b>Pempferidae s.l.</b>			
<i>Pempferis? huddlestoni</i>	38		Fig. 12 A-F
<b>Serranidae s.l.</b>			
<i>Serranus? severnensis</i>	1		Fig. 12 G-H
<b>INCERTAE SEDIS</b>			
<i>Otolithopsis cumatilis</i>	4		Fig. 12 I-L
<b>LAPILLI SILURIFORMES</b>			
<b>Ariidae</b>			
<i>Arius subtilis</i>	114	11	Fig. 13 A-E
<b>Family indeterminate</b>			
<i>Vorhisia vulpes</i>	142		Fig. 13 F-L
<b>LAPILLI INDETERMINATE</b>			
Lapillus 1	12		Fig. 13 M-V
Lapillus 2	1		Fig. 13 W-Z
Otolith fragments, unfigured specimens	15	14	
<b>Total number of specimens</b>	<b>3,718</b>	<b>84</b>	

or rim likewise with dorsally shifted, rounded tip.

Inner face strongly convex with strongly subpramedian positioned sulcus. Ostium wide, anteriorly and dorsally opened, shallow. Cauda deepened, flexed downward, diagonally positioned at 15-22°

angle, terminating close to posterior ventral rim of otolith. Dorsal depression very narrow, only above cauda; ventral field smooth, without ventral furrow. Outer face flat to slightly concave, smooth in large specimens.

**Ontogeny.** A complete ontogenetic sequence is available of *O. mississippiensis* from about 3 mm length (Fig. 4 G-H) to the holotype of 18.3 mm length. Small specimens if less than 5 mm length show an intense, fine ornamentation on the ventral field of the inner face and outer face. The downward flexure of the cauda increases with size, the outer face becomes concave, and the postdorsal rim flatter with size. These are all common ontogenetic observations in osmeroidid and pterothrissid otoliths and require truly large and morphologically mature otoliths like the holotype for adequate definition.

**Discussion.** *Osmeroides mississippiensis* resembles *O. griffini* (Nolf & Dockery, 1990) and *O. weileri* (Frizzell, 1965a), which are slightly older (Santonian and Campanian respectively) but readily differs in the more elongate shape (OL:OH = 1.75-1.9 vs 1.4-1.65). *Osmeroides alabamiae* (Frizzell, 1965a) from the Paleocene is more elongate (OL:OH = 2.0) with a relatively shallow ventral rim and an expanded posterior tip. Schwarzhans et al. (2018b) have shown from *in situ* otoliths in skeletal remains using computed tomography that the otolith-based genus *Prealbula* Frizzell (1965a) is a junior synonym of *Osmeroides*.

### *Osmeroides* sp.

Fig. 4 K-L

**Material:** 12 specimens: 10 specimens Blue Springs, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimen MMNS VP 6404); 2 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Discussion.** A number of mostly small and rarely well preserved otoliths strongly resemble *Osmeroides mississippiensis* but differ in the thinner appearance (OH:OT = 3.5), the sharper rostrum, and a less strongly inclined and bent cauda (<10°). The figured specimen of 7 mm length is very well preserved, but we feel unable at this stage to properly define this potential additional species because of the lack of further well-preserved specimens.

Family Pterothrissidae Gill, 1893

**Remarks.** We follow the arguments of Nolf (2013) and remain keeping the family Pterothrissidae separate from the Albulidae.

Genus *Pterothrissus* Hilgendorf, 1877

### *Pterothrissus* sp.

Fig. 4 M-N

**Material:** 29 specimens: 28 specimens Blue Springs, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimen MMNS VP 6387); 1 specimen Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Discussion.** A number of mostly poorly preserved and small specimens may possibly represent a further albuliform species, probably of the Pterothrissidae. It differs from *Osmeroides mississippiensis* in the blunt, nearly vertically cut anterior rim and the nearly straight, inclined cauda (about 10°). It can, however not be excluded that these otoliths represent only variants of the same species, which will only be possible to evaluate once larger and well preserved specimens have become available.

Order **Anguilliformes** Regan, 1909

Suborder **Anguilloidei** Regan, 1909

Family Anguillidae Rafinesque, 1810

Genus *Anguilla* Schrank, 1798

### *Anguilla?* *chickasawae* Schwarzhans & Stringer

n. sp.

Fig. 5 A-E

1983 Anguilloidei-B – Huddleston & Savoie: fig. 2C.

**Etymology:** Referring to the Native American Chickasaw, who resided near the collection locations.

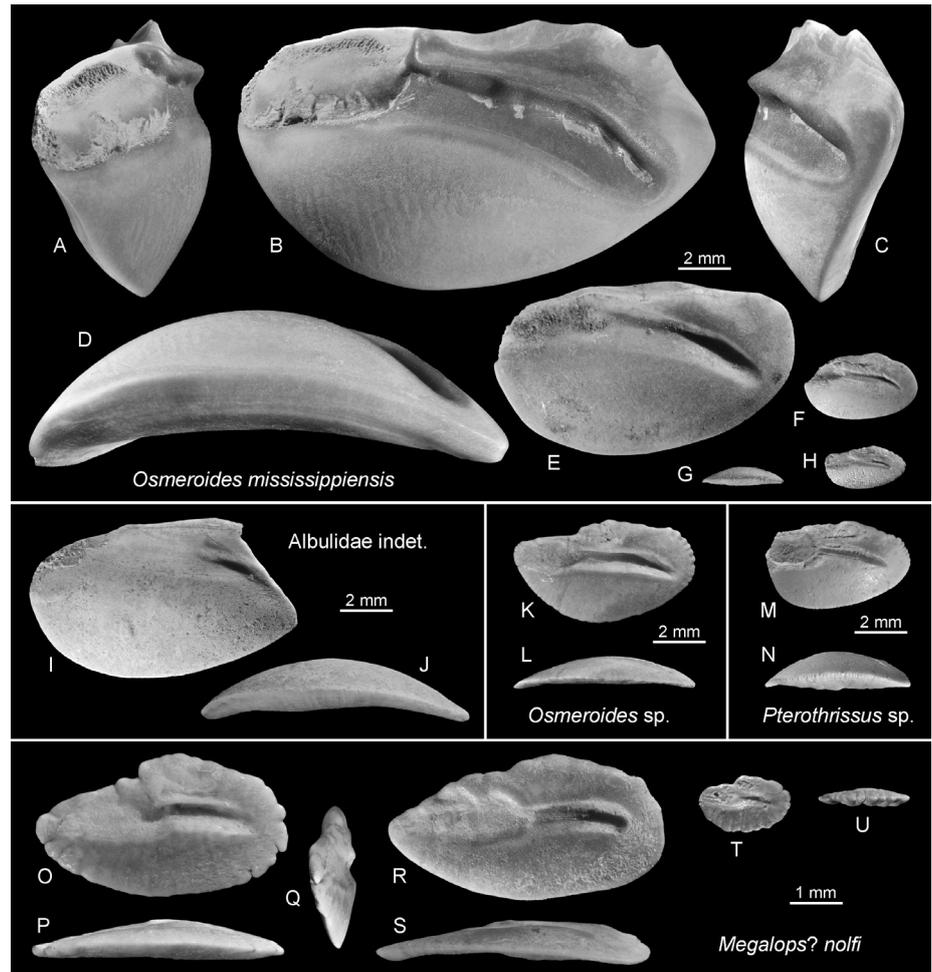
**Holotype:** MMNS VP 6391 (Fig. 5 C-E), Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 1 specimen, MMNS VP 6391.1, same data as holotype.

**Diagnosis:** Otolith with roughly rectangular outline with inferior rostrum and blunt posterior rim with three lobes. OL:OH = 1.5. Ostium slightly shorter than cauda and slightly wider, its dorsal margin curving upwards close to opening. CaL:OsL = 1.1-1.4.

**Description.** Small, robust otoliths, with nearly rectangular outline reaching 1.65 mm length (holotype 1.8 mm long). OH:OT = 2.3-2.5. Dorsal and ventral rims shallow, somewhat irregularly shaped; dorsal rim highest in broad mediodorsal angle. Anterior rim with short, rounded, inferior rostrum. Posterior rim nearly vertical, with two regular incisions resulting in a three-lobed appearance.

Fig. 4 - A-H) *Osmeroides mississippiensis* n. sp., Blue Springs; A-D holotype, MMNS VP 8894; E paratype (reversed), MMNS VP 8894.1; F paratype (reversed), MMNS VP 6385; G-H paratype (reversed), MMNS VP 6386. I-J) *Albulidae* indet., Blue Springs, MMNS VP 6384 (reversed). K-L) *Osmeroides* sp., Blue Springs, MMNS VP 6404 (reversed). M-N) *Pterothrissus* sp., Blue Springs, MMNS VP 6387. O-U) *Megalops? nolfi* n. sp., Blue Springs; O-Q holotype (reversed), MMNS VP 6382; R-U paratypes (R-S reversed), MMNS VP 6382.1 and 6382.2.



Inner face convex with slightly suprmedian and deepened, relatively narrow sulcus. Ostium and cauda poorly distinguished by slightly narrowed column; ostium slightly shorter and wider than cauda. Ostium slightly bent downward, its dorsal margin bent upward to vertical or even backward inclined position very close to ostial opening. Cauda with widened, rounded tip terminating far from posterior rim of otolith. Outer face less strongly convex than inner face, smooth.

**Discussion.** *Anguilla? chickasawae* resembles extant otoliths of *A. anguilla* (see Nolf, 2013 for figures) except for the slight indication of a differentiation of ostium and cauda. Similar in respect to the development of the sulcus are the fossil *A. rectangularis* Stinton & Nolf, 1970 from the Middle Eocene, *A.? angulosus* Nolf & Rundle, 2013 (in: Nolf 2013) from the Late Paleocene and *A. rouxi* Nolf, 1977 from the Early Oligocene. In all these species, however, the ostium is distinctly shorter than the cauda by a factor of more than 2 (vs 1.1-1.4). We consider *A.? chickasawae* to represent a fossil genus of the

family Anguillidae or a related fossil family of which otoliths are not yet known.

Family indet.

Genus *Muraenanguilla* Schwarzhans, 2019

*Muraenanguilla unionensis* Schwarzhans & Stringer n. sp.

Fig. 5 F-L

- 1983 Anguilloidei-A – Huddleston & Savoie: fig. 1D-E.
- 1991 Congridae – Stringer: pl. 1, fig. 6.
- 1996 “genus Congridarum” aff. *diagonalis* (Stinton & Nolf, 1970) – Nolf & Stringer: pl. 2, figs. 7-8.
- 2016 “*Congrida*” aff. “*C.*” *thevenini* (Priem, 1906) – Stringer: fig. 1C.

**Etymology:** Referring to Union County, Mississippi, where the type locality is located.

**Holotype:** MMNS VP 6388 (Fig. 5 F-G), Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 2 specimens, MMNS VP 6388.1 and 6388.2, same data as holotype.

**Further specimens:** 32 specimens; 30 specimens same data as holotype, 2 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Diagnosis:** Otolith with oval outline with median rostrum and posterior tip. OL:OH = 1.45-1.65. Dorsal rim shallow with rounded, broad middorsal angle. Sulcus inclined at about 10°. Tip of cauda very slightly flexed and tapering.

**Description.** Oval, robust otoliths reaching 5.6 mm length (holotype 3.9 mm long). OL:OH = 1.45-1.65, distinctly increasing with size; OH:OT about 2.5. Dorsal rim irregularly curved, relatively shallow, with broadly rounded mediodorsal angle, sometimes located in front of middle of dorsal rim. Ventral rim deeply and regularly curved, smooth. Broadly rounded rostrum positioned along axis of otolith; broadly rounded posterior tip axial or slightly superior.

Inner face convex with slightly supramedian and deepened, moderately narrow sulcus. Ostium and cauda poorly distinguished but ostium apparently much shorter than cauda. Ostium slightly widened anterior-dorsally at ostial opening. Cauda with tapering, slightly flexed tip terminating moderately far from posterior rim of otolith. Outer face less strongly convex than inner face, smooth.

**Discussion.** The fossil otolith-based genus *Muraenanguilla* has recently been introduced by Schwarzahans (2019) for the widely known Eocene species *Otolithus (Trachini) thevenini* Priem, 1906 (syn. *Gymnothorax diagonalis* Stinton & Nolf, 1970) and has been shown to be more species rich than hitherto recognized. *Muraenanguilla unionensis* differs from the three known Paleogene species (see Schwarzahans, 2019) in the low dorsal rim resulting in a relatively high ratio OL:OH of 1.45-1.65 (vs 1.1-1.45) and the broadly rounded middorsal angle. *Muraenanguilla* probably represents a fossil skeleton-based family of the Anguilloidei from which otoliths are not yet known. *Muraenanguilla* otoliths are also known from the Late Cretaceous Coon Creek type locality in southeastern Tennessee (Stringer 1999; Stringer 2016b) and from the Maastrichtian Severn Formation in Maryland (Huddleston & Savoie 1983).

Order **Osteoglossiformes** Regan, 1909  
Family **Osteoglossidae** Bonaparte, 1846  
Genus indet.

*Osteoglossum? tavernei* Nolf & Stringer, 1996

Fig. 6 J-K

1991 Gadidae – Stringer: pl. 2, fig. 4.

1996 “genus *Osteoglossidarum*” *tavernei* – Nolf & Stringer: pl. 1, figs. 1-2.

2003b “genus *Arapaimidarum*” *tavernei* (Nolf & Stringer, 1996) – Nolf: table 1

2008 “genus *Heterotidinarum*” *tavernei* (Nolf & Stringer, 1996) – Nolf, Rana, & Prasad: p. 249

**Material:** 7 specimens, Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimen MMNS VP 6381).

**Discussion.** Only relatively poorly preserved eroded specimens are available from this characteristic species, which is recognized by its elongate shape in combination with the wide, long, unstructured sulcus. We follow Nolf & Stringer (1996) in allocating it to the Osteoglossiformes, but this has to be considered as tentative until such otoliths are found *in situ*. Nolf (2003b) in his overview of otolith-documented North Atlantic Late Cretaceous teleosts referred to the form as “*Arapaimidarum*” *tavernei* (Table 1, p. 158). Then, Nolf, Rana, and Prasad (2008) in their revision of Late Cretaceous otoliths from the Deccan Traps in India denoted the taxon as “*Heterotidinarum*” *tavernei* (p. 249). Present-day osteoglossids or bonytongues are exclusively freshwater in distribution (Nelson et al., 2016), but there is ample fossil evidence of several extinct representatives in various marine deposits in Europe and Africa (Nolf 1985; Nolf 2013).

Family indet.

Genus *Kokenichthys* Schwarzahans, 2010

*Kokenichthys navis* Schwarzahans & Stringer n. sp.

Fig. 6 A-F

**Etymology:** From *navis* (Latin = ship), referring to the shape of the otolith resembling a bottom of a ship.

**Holotype:** MMNS VP 8900 (Fig. 6 A-D), Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

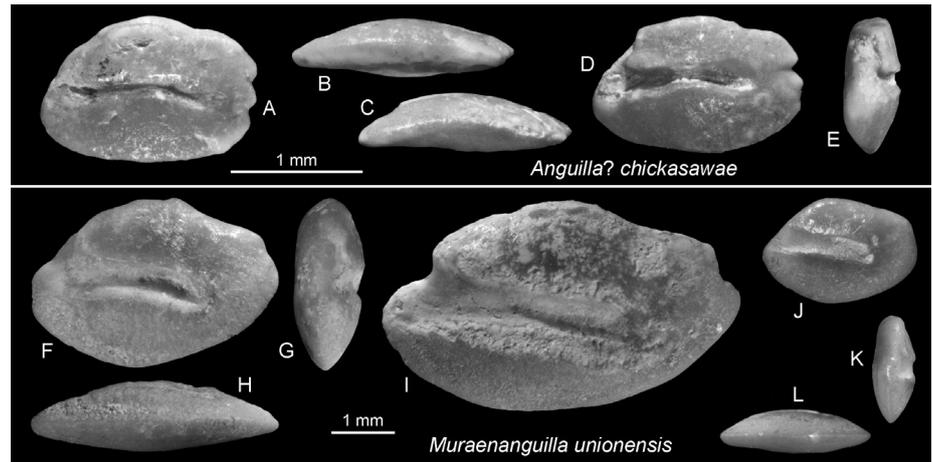
**Paratypes:** 2 specimens, MMNS VP 8900.1 and 8900.2, same data as holotype.

**Further specimens:** 70 specimens; 66 specimens same data as holotype; 4 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Diagnosis:** OL:OH = 1.7-1.9. Ventral rim deep and regularly curved; dorsal rim shallow. Sulcus wide, poorly defined, dorsally open until postdorsal angle (70-75% of length of dorsal rim). Ventral margin of cauda slightly flexed downward at tip. Height of ventral field 55-60% of OH.

**Description.** Thin otolith with a deep and regularly curved ventral rim and a shallow dorsal rim reaching a size of about 9 mm length (holotype 8.1 mm long). OH:OT = 3.2. Dorsal rim broadly and

Fig. 5 - A-E) *Anguilla? chickasawae* n. sp., Blue Springs; A-B paratype, MMNS VP 6391.1; C-E holotype, MMNS VP 6391. F-L) *Muraenanguilla unionensis* n. sp., Blue Springs; F-H holotype (reversed), MMNS VP 6388; I-L paratypes, MMNS VP 6388.1 and 6388.2.



very shallow curved, with notch at location where dorsal sulcus margin meets dorsal rim (70-75% from anterior tip of otolith), with postdorsal angle near joint with posterior rim. Anterior tip strongly superior, rounded; posterior tip even more strongly shifted dorsally. All rims sharp, smooth or very finely crenulated.

Inner face distinctly convex and very smooth and even throughout except slight deepening of the posterior-most part of sulcus. Sulcus very shallow, unstructured, with nearly straight, slightly inclined ventral margin (7-10°), slightly flexing downward at posterior tip. Sulcus open along dorsal margin for about 70-75% of length of dorsal rim starting at anterior tip. No clear colliculum, but narrow growth marks visible along ventral section of sulcus. Ventral field very wide (55-60% of OH), completely smooth. Outer face flat to slightly concave, smooth.

**Discussion.** *Kokenichthys navis* is less slender than the type species *K. ensis* (Nolf & Dockery, 1990) (OL:OH 1.7-1.9 vs 2.4-2.8), which ranges from Santonian to Maastrichtian, has a wider ventral field (55-60% of OH vs 43-48%), and a more distinct downward bend of the ventral margin of the sulcus near its termination. The coeval *K. ripleyensis* (Nolf & Stringer, 1996) (see below) is more compressed (OL:OH = 1.25-1.3 vs 1.7-1.9) and has an even wider ventral field (63-65% of OH vs 55-60%). The relationships of *Kokenichthys* with its unique otolith morphology remains obscure and is only tentatively related to the Osteoglossiformes.

***Kokenichthys ripleyensis*** (Nolf & Stringer, 1996)

Fig. 6 G-I

1991 Albulidae – Stringer: pl. 1, fig. 3.

1996 “genus *Albulidarum*” *ripleyensis* – Nolf and Stringer: pl. 1, fig. 8

**Material:** 1 specimen (MMNS VP 9100), Blue Springs, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Short description.** *Kokenichthys ripleyensis* is almost rhomboidal in shape (sensu Smale et al. 1995). Sagitta quite high with smooth margins. Both the dorsal and ventral margins sharp. Rostrum blunt. The inner face slightly convex with broad sulcus located almost entirely in upper portion of otolith. The sulcus shows considerable erosion, but it is possible to discern that it opens onto the dorsal rim. It is not possible to distinguish the ostial and caudal areas of the sulcus. Posterior portion of sulcus downwardly curved and more deeply excavated.

**Discussion.** A single, relatively small and somewhat eroded specimen of 3.5 mm length is accounted for *K. ripleyensis*. It is readily distinguished from the coeval *K. navis* (see above) by the compressed shape expressed in the low ratio OL:OH (1.25-1.3) and the deeply bent, anteriorly pronounced ventral rim. This species is known only from a few Maastrichtian localities in the USA and is very rare when present.

Order **Aulopiformes** Rosen, 1973

Family **Paraulopidae** Sato & Nakabo, 2002

Genus ***Paraulopus*** Sato & Nakabo, 2002

***Paraulopus pseudoperca*** (Nolf & Dockery, 1990)

Fig. 7 A-F

1990 “genus Synodontidarum” *pseudoperca* – Nolf & Dockery, pl. 2, figs. 12-16.

1991 “genus Synodontidarum” *pseudoperca* Nolf & Dockery, 1990 – Stringer: pl. 2, fig. 2.

1996 “genus Chlorophthalmidarum” *pseudoperca* (Nolf & Dockery, 1990) – Nolf & Stringer: pl. 2, figs. 14-18.

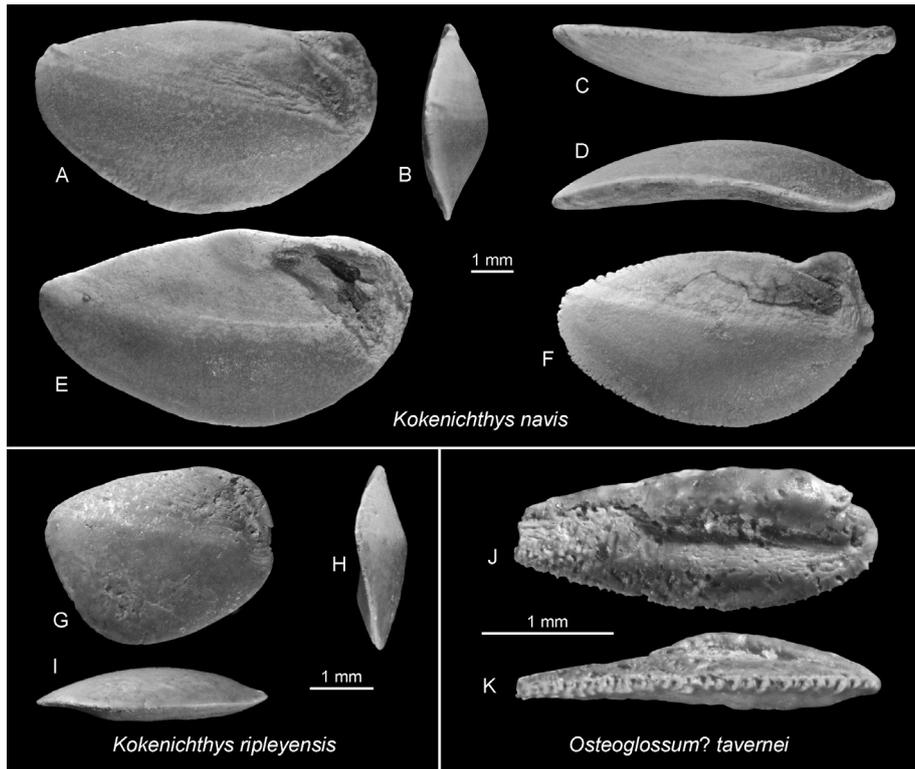


Fig 6 - A-F) *Kokenichthys navis* n. sp., Blue Springs; A-D holotype, MMNS VP 8900. E-F paratypes, MMNS VP 8900.1 and 8900.2. G-I) *Kokenichthys ripleyensis* (Nolf & Stringer, 1996), Blue Springs, MMNS VP 9100. J-K) *Osteoglossum? tavernei* Nolf & Stringer, 1996, Blue Springs, MMNS VP 6381 (reversed).

- 1996 Chlorophthalmidae indet. – Nolf & Stringer: pl. 4, figs. 1-5.  
 2016 *Paraulopus pseudoperca* (Nolf & Dockery, 1990) – Stringer, Oman & Badger: pl. 2, fig. 1.

**Material:** 220 specimens; 210 specimens Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6393, 6393.1, 6393.2, and 6400); 10 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Discussion.** *Paraulopus* otoliths are a common element in sediments of the Late Cretaceous and the Paleogene on a global scale. The distinction of species is often difficult and relying on subtle characteristics, which has led Nolf & Stringer (1996) to adopt a very conservative approach. We largely follow their recommendation and consider the common Late Cretaceous *P. pseudoperca* to be defined by a slightly more strongly flexure of the caudal tip in comparison to the Paleocene *P. postangulatus* (Nolf & Dockery 1993). The otoliths of *P. pseudoperca* from the Ripley Formation and the Owl Creek Formation appear to be very similar or identical to specimens from the Late Cretaceous Coon Creek type locality in southwest Tennessee (Stringer 2016b), the Coffee Sand (Campanian) of northeastern Mississippi (Nolf and Dockery 1990), and the Woodbury Formation of New Jersey (Stringer et al. 2016). Most of the specimens of *P. pseudoperca* from the Ripley Formation and the Owl Creek Formation are small and recovered from bulk samples. It is the second

most abundant species in the Ripley Formation bulk sample (25.34%).

Family Ichthyotringidae Jordan, 1905  
 Genus *Apateodus* Woodward, 1901

*Apateodus crenellatus* Schwarzghans & Stringer n.

sp.

Fig. 7 G-N

- 1990 Salmoniformes – Nolf & Dockery: pl. 2, figs. 10-11.  
 1991 Argentinidae – Stringer: pl. 1, fig. 9.  
 1996 Gempylidae indet. – Nolf & Stringer: pl. 6, figs. 3-5.  
 2016 Aulopiformes indet. – Stringer, Oman & Badger: pl. 1, fig. 10.  
 2018 Aulopiformes indet. – Stringer, Clements, Sadorf & Shannon: pl. 2, fig. 2  
 2018 *Apateodus* sp. – Schwarzghans, Beckett, Schein & Friedman: fig. 7 D-G.  
 2018 *Apateodus* sp. – Schwarzghans, Huddleston & Takeuchi: fig. 4 U-Z.

**Etymology:** From crenellatus (Latin = crenellate), referring to the shape of the ventral rim of the otolith.

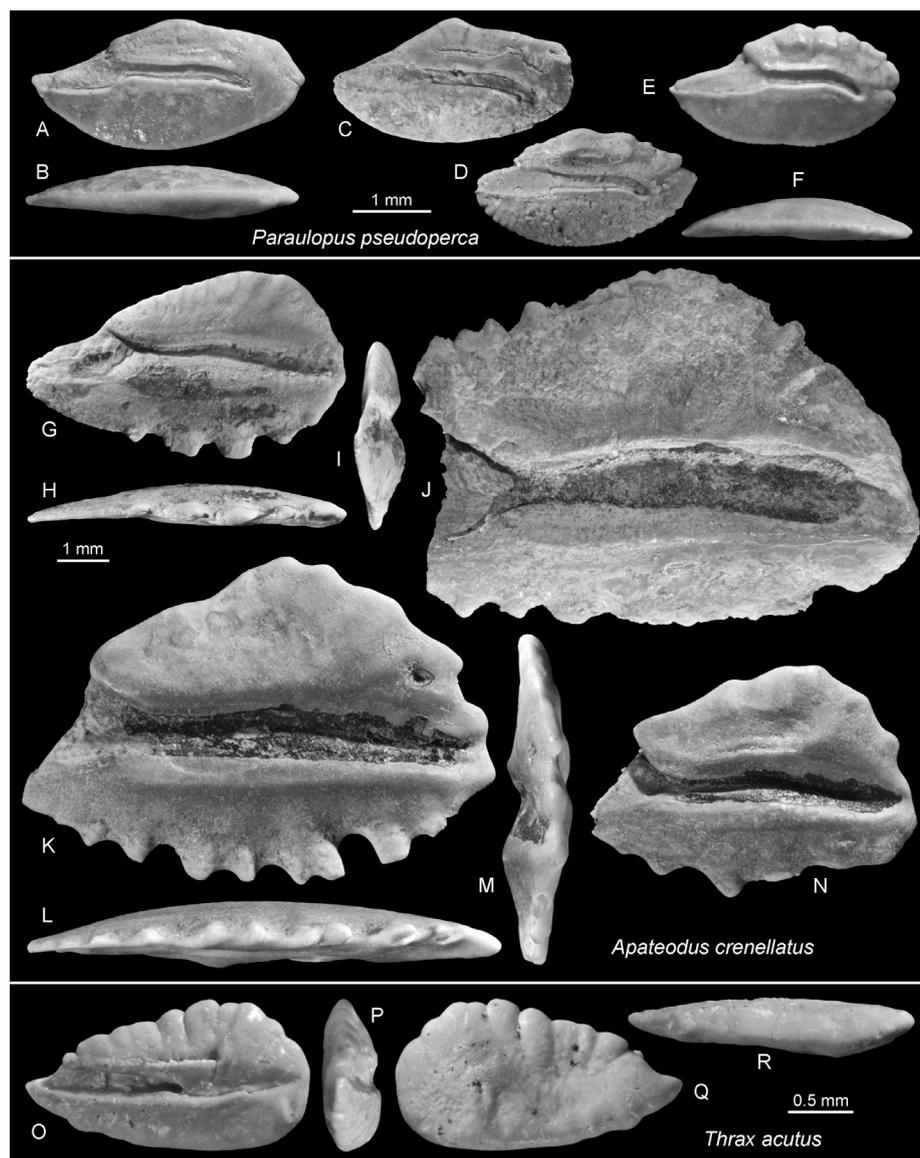
**Holotype:** MMNS VP 6411 (Fig. 7 G-I), Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 3 specimens, MMNS VP 6411.1, 6411.2, and 6411.3, same data as holotype.

**Further specimens:** 107 specimens; 103 specimens same data as holotype; 4 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Diagnosis:** OL:OH = 1.7. Otoliths very thin and fragile. Dorsal rim with distinct postdorsal angle. Ventral rim shallow, with intense crenellation. Rostrum long, moderately pointed, 25% of OL. Sulcus with shorter, slightly widened ostium and narrow, long, poste-

Fig. 7 - A-F) *Paraulopus pseudoperca* (Nolf & Dockery, 1990), Blue Springs; A-D MMNS VP 6393 (A-C reversed), E-F MMNS VP 6393.1, 6393.2, and 6400 (reversed). G-N) *Apateodus crenellatus* n. sp., Blue Springs; G-I holotype, MMNS VP 6411; J-N paratypes, MMNS VP 6411.1, 6411.2, and 6411.3 (J reversed). O-R) *Thrax acutus* n. gen. et n. sp., Blue Springs, MMNS VP 8893 (reversed).



riorly slightly widened cauda reaching close to posterior tip of otolith.  $CaL:OsL = 1.8$ . Ventral field with edge close to ventral margin of cauda.

**Description.** Elongate, thin and fragile otolith reaching at least 12 mm length (reconstructed with broken rostrum; holotype 6.1 mm long).  $OH:OT = 4.5-5.0$ . Dorsal rim straight, inclined at about  $20^\circ$  up to broad, massive, rounded postdorsal angle; thereafter declining at steep angle of  $45-60^\circ$ ; irregularly undulating and crenulated. Ventral rim shallow, only slightly bent, with intense crenellation particularly at its middle section. Rostrum long, moderately pointed, slightly inferior, symmetrical, 25% of OL. Posterior rim inclined at  $45-60^\circ$  (see above) with inferior angular tip.

Inner face slightly convex. Sulcus median to slightly inframedian, long, slightly deepened. Ostium distinctly shorter than cauda and slightly widened;

its dorsal margin very short. Cauda straight, narrower and deeper than ostium, its dorsal margin slightly convex, its tip reaching very close to posterior tip of otolith. No distinct dorsal depression; no ventral furrow, but faint edge running close to cauda. Outer face flat and almost smooth.

**Discussion.** The relationships of this peculiar otolith morphology has long been unclear which is easily seen from the allocations in the synonymy list ranging from salmoniforms to scombroids. Finally, an otolith *in situ* was found by CT micro-scanning in *Apateodus corneti* (Forir, 1887) in Schwarzhans et al. (2018) that has resolved the systematic allocation and demonstrates how environmental and habitat functionality can effect convergence in otolith morphology. The revised taxonomic assignment is in better agreement with several molecular-based phylogenetic and dating studies (Near et al. 2012;

Betancur-R. et al. 2013; Near et al. 2013). Furthermore, the Ripley Formation otoliths provide the first time a complete specimen with a preserved thin rostrum has been retrieved and therefore now allows for definition and description of the species. *Apateodus crenellatus* differs from *A. corneti* primarily in the shallow, intensely crenellated ventral rim (vs gently curved and smooth) and the more forward reaching dorsal rim.

### Genus *Thrax* Schwarzhans & Stringer n. gen.

**Type species:** *Thrax acutus* Stringer & Schwarzhans, n. sp.

**Etymology:** From thrax (Latin = gladiator, secutor), referring to the pointed, forward projecting sharp anterior portion of the otolith.

**Diagnosis:** Elongate otolith with sharp but short rostrum (15% of OL) and far backward positioned widest point of otolith. OL:OH = 1.9. Dorsal rim with massive, broadly rounded postdorsal angle and intensely crenulated. Posterior rim broadly rounded. Sulcus deep, long, narrow, reaching close to posterior tip of otolith. Ostium and cauda poorly differentiated, about equally long and wide; caudal tip pointed.

**Discussion.** *Thrax* resembles otoliths of *Apateodus* but differs in the sulcus proportions and the short rostrum. It also resembles certain scombroid otoliths from the Cenozoic and Recent, particularly of the family Trichiuridae, but this must be considered again as a convergence due to functional morphological adaptation. For these reasons, it is placed in the Ichthyotringidae along with *Apateodus*.

**Species.** Monospecific genus with *Thrax acutus* n. sp. from the Maastrichtian of Mississippi.

### *Thrax acutus* Schwarzhans & Stringer n. sp.

Fig. 7 O-R

**Etymology:** From acutus (Latin = pointed, sharp), referring to the pointed rostrum.

**Holotype:** MMNS VP 8893 (Fig. 7 O-R), Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Diagnosis:** See generic diagnosis (monospecific genus).

**Description.** Elongate, thin, relatively small otolith of 2.15 mm length. OL:OH = 1.9; OH:OT = 2.7. Anterior two thirds of dorsal rim regularly ascending to broad, massive, rounded postdorsal angle at 20°. Dorsal rim coarsely and intensely crenulated. Ventral rim shallow, smooth, regularly curving and deepest far behind middle at about level of postdorsal angle. Anterior rim with short but sharply pointed rostrum (15% of OL) positioned at axis of

otolith, shallow excisura and very small antirostrum. Posterior rim broadly and regularly rounded.

Inner face almost flat in horizontal direction but markedly convex in vertical direction. Sulcus deep, long, straight, rather narrow and poorly structured. Differentiation of ostium and cauda only marked by small incursion of ventral sulcus margin. Ostium about as long and wide as cauda. Cauda tapering with pointed tip reaching very close to posterior tip of otolith. Dorsal field with many radial furrows and deep, narrow depression above central part of sulcus underpinned by distinct crista superior. Ventral field without ventral furrow. Outer face flat, smooth except for few long radial furrows dorsally.

### Superorder **Paracanthopterygii** Greenwood, Rosen, Weitzman & Myers, 1966 Order and Family indet.

### Genus *Choctawichthys* Schwarzhans & Stringer n. gen.

**Type species:** “genus Perciformorum” *cepoloides* Nolf & Dockery, 1990.

**Etymology:** Referring to the Native American Choctaw, who resided historically near the two studied localities in Mississippi.

**Diagnosis:** Oval otoliths with a homosulcoid sulcus pattern where the ostium is slightly larger and longer than the cauda and both being oval in shape and separated by a wide and narrow collum. Ostial and caudal colliculi shallow, oval in shape, the ostial colliculum being larger than the caudal colliculum and both colliculi being closed. OCL:CCL = 1.2; OCH:CCH = 1.15-1.3. Collum narrow, about half as long as ostial colliculum, containing pseudocolliculum. Sulcus opening pseudoostial to pseudobiostial (see Schwarzhans 1978). Dorsal depression v-shaped above central part of sulcus; ventral furrow broad, moderately close to ventral rim of otolith.

**Discussion.** These small otoliths barely reaching 2 mm length represent the earliest truly homosulcoid sulcus patterns so far observed. The proportions of the sulcus, the sulcal opening, the shape of the colliculi, and the presence of a pseudocolliculum in the collum are all typical traits for gadiform otoliths. Therefore, we tentatively allocate these otoliths with the Paracanthopterygii.

### *Choctawichthys cepoloides* (Nolf & Dockery, 1990)

Fig. 8 A-E

- 1990 “genus Perciformorum” *cepoloides* – Nolf & Dockery: pl. 3, figs. 8-11.  
1996 “genus Perciformorum” *cepoloides* Nolf & Dockery, 1990 – Nolf & Stringer: pl. 6, figs. 3-5.  
2016 “*Perciformis*” *cepoloides* Nolf & Dockery, 1990 – Stringer: fig. 1H.

**Material:** 4 specimens, Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6412, 8895).

**Remarks.** For diagnosis see above (mono-specific genus).

**Discussion.** This taxon was first described from the Late Cretaceous Coffee Sand in Mississippi by Nolf and Dockery (1990; pl. 3, figs. 8–11) and is also known from the Late Cretaceous Coon Creek type locality in southwest Tennessee (Nolf & Stringer 1996; Stringer 2016). In all occurrences of the species, the specimens are small at approximately 2 mm (Nolf & Stringer 1996; pl. 5, figs. 5a–8).

Order **Polymixiiformes** Patterson, 1964

Family Polymixiidae Bleeker, 1859

Genus *Cowetaichthys* Schwarzahns, Huddleston & Takeuchi, 2018

*Cowetaichthys alabamae* Schwarzahns,  
Huddleston & Takeuchi, 2018

Fig. 8 F-K

- 1990 Percoidei sp. 1 – Nolf & Dockery: pl. 2, fig. 7.  
 2016 Percoidei sp. 1 – Stringer, Oman & Badger: pl. 2, fig. 9.  
 2018 Percoidei sp. 1 – Stringer, Clements, Sadorf & Shannon: pl. 2, fig. 7.  
 2018 *Cowetaichthys alabamae* – Schwarzahns, Huddleston & Takeuchi: fig. 6 A-M.

**Material:** 39 specimens; 33 specimens Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6394, 6394.1, 6394.2, 6409); 6 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Discussion.** This form was first recognized as Percoidei sp. 1 from the Late Cretaceous (Campanian) Coffee Sand of Mississippi by Nolf and Dockery (1990) based on a single sagitta, which was broken along the anterior and posterior margins. The specimens from the Ripley Fm. and the Owl Creek Fm. have juvenile and adult forms represented and are better preserved than the specimens referred to as Percoidei sp. 1 by Nolf and Stringer (1996), Stringer et al. (2016), and Stringer et al. (2018).

*Cowetaichthys carnevalei* Schwarzahns  
& Stringer n. sp.

Fig. 8 L-S

1996 Percoidei sp. 4 – Nolf & Stringer: pl. 6, fig. 6.

**Etymology:** In honor of Giorgio Carnevale (Torino, Italy) for his many contributions to the knowledge of fossil fishes.

**Holotype:** MMNS VP 6407 (Fig. 8 L-O), Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 2 specimens, MMNS VP 6407.1 and 6410, same data as holotype.

**Further specimens:** 49 specimens, same data as holotype.

**Diagnosis:** High bodied, parallelogram-like shape. OL:OH = 1.05-1.15. Anterior rim nearly straight from rostrum to predorsal angle, inclined at 45-50°. Sulcus wide, deep; cauda with slightly convex dorsal margin anteriorly and downturned tip reaching very close to posterior rim of otolith. Dorsal field very high.

**Description.** Otoliths large, high bodied, with skewed parallelogram-like outline, reaching sizes of 7.0 mm length (holotype). OH:OT = 3.3-4.5. Dorsal rim very high with distinct, near orthogonal pre- and postdorsal angles; straight middorsal section in between inclined at 12-18°. Anterior rim nearly straight from short, blunt, sometimes pointed rostrum to predorsal angle and inclined at 45-50°; excisura and antirostrum very weak or absent. Posterior rim inclined almost parallel to anterior rim, but more gently curved, less straight. Ventral rim regularly rounded, shifted anteriorly. Rims sharp, smooth except dorsal rim slightly undulating; dorsal rim and anterior ventral rim finely crenulated in small specimens (Fig. 8 Q-S).

Inner face distinctly convex with more or less centrally positioned, relatively wide and deep sulcus, slightly inclined at 5-8°. Ostium slightly wider than cauda, primarily ventrally widened, and somewhat shorter. CaL:OsL = 1.2-1.4; OsH:CaH = 1.1-1.2. Ostium widely open anteriorly. Cauda anteriorly with sagging ventral and slightly expanded dorsal margin; posteriorly reaching very close to posterior rim of otolith or even connected to it, with rounded, somewhat downturned tip. Dorsal field wide, narrow, smooth, without discernable depression; ventral field smooth, without ventral furrow. Outer face flat and smooth or irregularly ornamented in small specimens.

**Discussion.** The parallelogram-like shape of the otolith and unusual widening of the anterior part of the cauda (which however is sometimes obliterated; Fig. 8 P) are the most obvious characters of distinction to the other two Cretaceous species of the genus: *C. alabamae* and *C. lamberi*. It appears that *Cowetaichthys* was a species rich genus of the Polymixiidae during Late Cretaceous and Paleocene (Schwarzahns et al. 2018b).

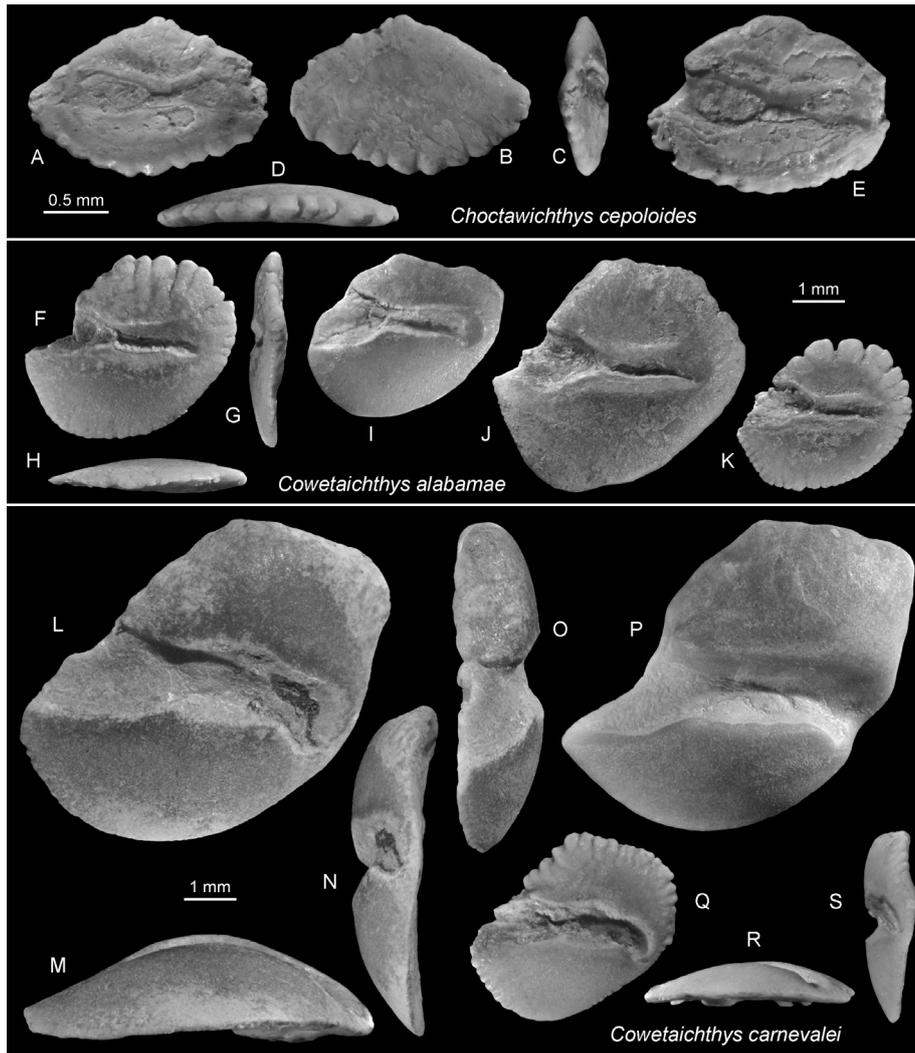


Fig. 8 - A-E) *Choctawichthys cepoloides* (Nolf & Dockery, 1990), Blue Springs; A-D MMNS VP 8895 (reversed), E MMNS VP 6412. F-K) *Cowetaichthys alabamiae* Schwarzhans, Huddleston & Takeuchi, 2018, Blue Springs; F-I MMNS VP 6394 and 6394.1 (F-H reversed), J-K MMNS VP 6394.2 and 6409. L-S) *Cowetaichthys carnevalei* n. sp. Blue Springs; L-O holotype, MMNS VP 6407 (reversed); P-S paratypes, MMNS VP 6407.1 and 6410 (P reversed).

Order **Trachichthyiformes** Bleeker, 1856  
 Family **Trachichthyidae** Bleeker, 1856  
 Genus *Hoplopteryx* Agassiz, 1838

*Hoplopteryx langfordi* Stringer  
 & Schwarzhans n. sp.

Fig. 9 I-O

**Etymology:** In honor of Robert Langford, a geologist and member of the North Mississippi Gem and Mineral Society, who was instrumental in the collection of numerous specimens for this study.

**Holotype:** MMNS VP 6398 (Fig. 9 I-K), Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 3 specimens, MMNS VP 6398.1, 6398.2, and 6398.3, same data as holotype.

**Further specimens:** 104 specimens, same data as holotype.

**Diagnosis:** High bodied otoliths, OL:OH = 0.9-0.95. Specimens larger than 5 mm long with relatively smooth rims except anterior-dorsal incision. Ostium deeply expanded ventrally, resulting in an angle of about 100° at collum. Cauda shorter than ostium (OL:CaL = 1.1-1.35); caudal tip widened, particularly dorsally.

**Description.** Large, high bodied otolith reaching sizes of nearly 9 mm length (holotype 6.9 mm long). OH:OT = 4.0-4.5. Dorsal rim high, highest at postdorsal angle above caudal tip, with deep incision anterior-dorsally above collum. Ventral rim deep, much deeper than dorsal rim, its deepest position much anteriorly shifted below anterior section of ostium; posteriorly with broadly rounded postventral angle. Anterior rim nearly vertical, with short, blunt rostrum and short, small antirostrum and shallow excisura. Posterior rim steeply inclined at 72-80° with angular posterior tip located high above caudal tip. All rims smooth or irregularly undulating in specimens larger than 5 mm length, crenulated in smaller specimens.

Inner face flat in vertical direction, moderately bent along horizontal axis. Sulcus distinctly supramedian with wide and moderately deep sulcus. Ostium much wider and slightly longer than cauda, ventrally much widened resulting in a sharp

collum with an ostial/caudal intersection angle of about  $100^\circ$ . OsL:CaL = 1.1-1.35; OsH:CaH = 1.6-1.9. Ostium with well-marked deepened colliculum; cauda slightly upward bent, with widened, cut tip terminating at some distance from posterior rim of otolith. Dorsal field with distinct, ventrally well-marked depression above central part of sulcus. Ventral field smooth except for ventral furrow close to ventral rim of otolith and some occasional deeply ingressing radial furrows anteriorly below ostium. Outer face slightly convex, thickest below its central position, smooth with some radial furrows near rims.

**Discussion.** *Hoplopteryx langfordi* differs from the much more common *H. oscitans* in the wider ostium, the sharper collum, the shorter cauda with the widened, cut posterior tip, and the less intense ornamentation of the otolith rims in large specimens.

***Hoplopteryx oscitans*** (Nolf & Stringer, 1996)

Fig. 9 A-H

- 1991 “genus Trachichthyidarum” *coffeesandensis* Nolf & Dockery, 1990 – Stringer: pl. 2, fig. 5 (non Nolf & Dockery, 1990).  
 1996 “genus Trachichthyidarum” *oscitans* – Nolf & Stringer: pl. 3, figs. 1-4.  
 1999 “Trachichthyida” *oscitans* Nolf & Stringer, 1996 – Stringer: fig. 1F.

**Material:** 2551 specimens: 2548 specimens Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6397, 6397.1, 6397.2); 3 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Discussion.** *Hoplopteryx oscitans* is by far the most common species encountered in the Ripley Formation with 2548 specimens. It is the most abundant otolith from both the bulk and systematic surface collections in the Ripley Fm. at the Blue Springs locality. *Hoplopteryx oscitans* comprised 36.5% of the bulk sampling of the Ripley Formation. Interestingly, the species is represented by only three specimens from the Owl Creek Fm. (3.6%). It differs in four main characters from *H. langfordi* described above: the oval shaped, less wide ostium (OsH:CaH = 1.3-1.45 vs 1.6-1.9), the ostial/caudal inception angle at the collum (average  $135^\circ$  vs  $100^\circ$ ), the longer cauda (OsL:CaL = 0.85-1.05 vs 1.1-1.35), and the not widened, rounded caudal tip (vs widened and cut). The distinction from *H. coffeesandensis* (Nolf & Dockery, 1990) from the late

Campanian is less clear depending on subtle differences like the shape of the dorsal margin of the ostium (expanded vs flat) and the more pronounced preventral and postdorsal angles. Differentiation of the many *Hoplopteryx* species is difficult with juvenile specimens. The tremendous number of *Hoplopteryx oscitans* otoliths from the Ripley Fm. and the larger size of the surface-collected specimens allowed for the recognition of growth series that clearly illustrate the ontogeny of this taxon. Otoliths of *Hoplopteryx oscitans* of sizes larger than 6 to 7 mm reflect several diagnostic features not discernible in smaller specimens. It became evident that prior identifications had been based primarily on immature, small and often worn specimens. One of the diagnostic features is the development of a prominent, deeply incised dorsal margin, like in the Recent *Hoplostethus*. Equally important is the substantial change in the shape of the otolith. There is a marked elongation along an axis from the anteroventral to the postero-dorsal to the extent that the otolith became almost v-shaped.

Order **Beryciformes?** Regan, 1909

Family indet. type 1

Genus *Eutawichthys* Schwarzahns, Huddleston & Takeuchi, 2018

***Eutawichthys choctawae*** Stringer  
& Schwarzahns n. sp.

Fig. 9 U-W

**Etymology:** Referring to the Native American Choctaw, who resided near the collecting localities.

**Holotype:** MMNS VP 8899 (Fig. 9 U-W), Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Diagnosis:** OL:OH = 1.6. Dorsal rim shallow, with distinct predorsal lobe. Ventral rim shallow. Inner face flat; outer face convex. Ostium anteriorly closed.

**Description.** A single large and elongate oval otolith of 9.2 mm length. OH:OT = 2.7. Dorsal rim broadly shallow, with horn-like predorsal lobe and without distinct angles. Ventral rim shallow, gently and regularly curved, deepest anterior of its middle. Anterior rim broadly rounded, positioned at otolith axis, no rostrum, antirostrum or excisura developed. Posterior rim broadly rounded, distinctly dorsally shifted. All rims smooth, dorsal rim slightly crenulated at its middle section.

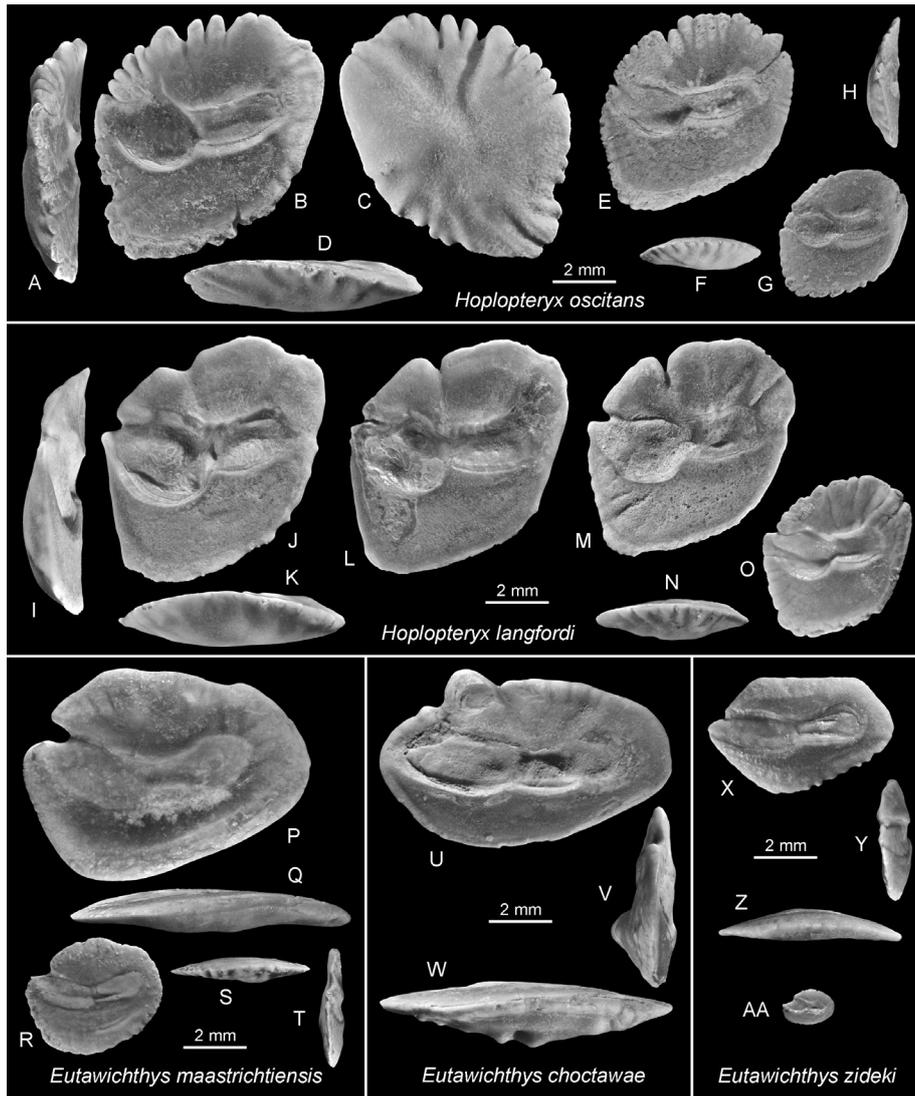


Fig. 9 - A-H) *Hoplopteryx oscitans* (Nolf & Stringer, 1996), Blue Springs, MMNS VP 6397, 6397.1, and 6397.2 (A-D reversed); I-O) *Hoplopteryx langfordi* n. sp. Blue Springs; I-K holotype, MMNS VP 6398 (reversed); L-O paratypes, MMNS VP 6398.1, 6398.2, and 6398.3 (L reversed). P-T) *Eutawichthys maastrichtiensis* (Nolf & Stringer, 1996), Blue Springs, MMNS VP 6401 and 6401.1 (R-T reversed). U-W) *Eutawichthys choctawae* n. sp., holotype, Blue Springs, MMNS VP 8899. X-AA) *Eutawichthys zideki* (Nolf & Stringer, 1996), Blue Springs, MMNS VP 6402 and 6402.1.

Inner face almost flat, with axial, rather shallow and moderately wide sulcus. Ostium straight, slightly ascending anteriorly and closed, slightly longer and wider than cauda.  $CaL:OsL = 0.8$ ;  $OsH:CaH = 1.2$ . Cauda oval in shape with rounded tip terminating at moderate distance from posterior rim. Ostial colliculum shallow, oval; caudal colliculum shallow, only developed at posterior region, anterior-ventrally reduced and separated with deepened section from ridge-like, long pseudocolliculum. Dorsal depression large, shallow, poorly marked. Ventral furrow feeble, very close to ventral rim of otolith. Outer face more strongly convex than inner face, smooth except for few irregular tubercles.

**Discussion.** *Eutawichthys choctawae* differs from its congeners in the presence of a predorsal lobe, the ostium being anteriorly closed, and the

straight sulcus with an oval ostium. It additionally differs from *E. compressus*, *E. maastrichtiensis*, and *E. stringeri* (see Schwarzhans et al. 2018b) by being more elongate ( $OL:OH = 1.6$  vs 1.15-1.45) and from large specimens of *E. zideki* (Fig. 9 X-Z) in the inner face being almost flat and the outer face being convex (vs inner face convex and outer face flat). Huddleston & Savoie (1983) and Nolf & Stringer (1996) related this eye-catching otolith morphology to the family Apogonidae (then a family of the Perciformes, now Gobiiformes). However, Stringer (2016) and Stringer, Oman & Badger (2016) recognized its features as being related to the beryciforms. Then, Schwarzhans et al. (2018b) also found arguments against a close relationship with the Apogonidae and instead considered *Eutawichthys* to represent an extinct group of Late Cretaceous beryciforms.

***Eutawichthys maastrichtiensis*** (Nolf & Stringer,

1996)

Fig. 9 P-T

- 1983 Apogonidae-B – Huddleston & Savoie: fig. 3C.  
 1991 Apogonidae sp. 1 – Stringer: pl. 2, fig. 7.  
 1996 “genus Apogonidarum” *maastrichtiensis* – Nolf & Stringer: pl. 5, figs. 9-10.  
 2016 *Beryx?* *maastrichtiensis* (Nolf & Stringer, 1996) – Stringer: fig. 1G.  
 2016 *Beryx?* *maastrichtiensis* (Nolf & Stringer, 1996) – Stringer, Oman, & Badger: pl. 2, fig. 4.  
 2019 “Apogonidarum” *maastrichtiensis* Nolf & Stringer, 1996 – Hoganson, Erickson & Holland: fig. 12.61, 12.63, 12.64.

**Material:** 43 specimens, Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6401 and 6401.1).

**Discussion.** *Eutawichthys maastrichtiensis* appears to be replacing *E. compressus* and *E. stringeri* from the Santonian, from which it differs in the more crenulated rims (eroded in the specimen figured in 9 P-Q), the short rostrum, and anterior-ventrally reduced caudal colliculum. It shares with the other two species the compressed appearance (OL:OH = 1.2-1.35). *Eutawichthys maastrichtiensis* was extremely abundant in the Campanian Woodbury Fm. of New Jersey and represented 2,990 specimens of the total 3,550 otoliths whereas *E. stringeri* was represented by only 22 specimens (Stringer, Oman & Badger 2016).

***Eutawichthys zideki*** (Nolf & Stringer, 1996)

Fig. 9 X-AA

- 1983 Apogonidae-A – Huddleston & Savoie: fig. 3F, 3H.  
 1991 Apogonidae sp. 2 – Stringer: pl. 2, fig. 8.  
 1996 “genus Apogonidarum” *zideki* – Nolf & Stringer: pl. 5, figs. 11-13.  
 2016 *Beryx?* *zideki* (Nolf & Stringer, 1996) – Stringer: fig. 1H.  
 2016 *Beryx?* *zideki* (Nolf & Stringer, 1996) – Stringer, Oman & Badger: pl. 2, fig. 5.

**Material:** 31 specimens, Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6402 and 6402.1).

**Discussion.** *Eutawichthys zideki* ranges from the Santonian to Maastrichtian. It is characterized by a rather elongate shape, which it shares with *E. choctawae* (OL:OH = 1.5-1.6). For differences between the two species see above.

Family indet. type 2

Genus *Argyroberyx* Schwarzhans, 2010***Argyroberyx?* *dockeryi*** (Nolf & Stringer, 1996)

Fig. 10 A-E

- 1983 Stomioidei – Huddleston & Savoie: fig. 3D.  
 1991 Sternoptychidae – Stringer: pl. 2, fig. 1.  
 1996 “genus Caproideorum” *dockeryi* – Nolf & Stringer: pl. 4, figs. 15-17.  
 2013 “?Caristiida” *dockeryi* (Nolf & Stringer, 1996) – Nolf: pl. 245.

**Material:** 17 specimens; 11 specimens, Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6403 and 6403.1); 6 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm..

**Discussion.** *Argyroberyx?* *dockeryi* is an easy recognizable otolith morphology characterized by the extremely high body (OL:OH = 0.65-0.7), the regularly rounded ventral rim and the high dorsal rim with a sharp mediodorsal angle (approximately 90°), and sometimes a small denticle at a post-dorsal position in well-preserved specimens. Rostrum and antirostrum are very blunt and short but the excisura is wide and rather deep. The sulcus is very slender with a short ostium (CaL:OsL = 1.6). The dorsal depression is wide and the ventral furrow runs far from the ventral rim of the otolith. These otoliths resemble *Argyroberyx dentatus* (Liebus, 1927) from the Maastrichtian of Bavaria and Austria, but differ in the sharp middorsal angle, the cauda being straight and not bent upward, and the ventral furrow running very distant from the ventral rim of the otolith. Therefore, *A.?* *dockeryi* is only tentatively allocated to *Argyroberyx* and could in fact represent yet another fossil genus in this group. The relationships of *Argyroberyx* and the related *Beaurymia* are unresolved. Nolf & Stringer (1996) related *A.?* *dockeryi* to the percomorph suborder Caproidei, and Nolf (2013) placed it in the family Caristiidae. Schwarzhans (2010) related the European species to the Diretmidae of the Beryciformes. We consider these unique and unusual otolith morphologies of *Argyroberyx?* *dockeryi* to represent an extinct Late Cretaceous family or higher taxon within or related to the Beryciformes primarily because of the many specialized beryciforms that populated the Late Cretaceous seas (Patterson 1964).

Family indet. type 3

Genus *Ossulcus* Schwarzhans & Stringer n. gen.**Type species:** *Ossulcus labiatus* Stringer & Schwarzhans, n. sp.

**Etymology:** From os (Latin = mouth) in combination with ‘sulcus’ as a term from the morphology of otoliths, referring to the anteriorly wide opened sulcus resembling the opening of a mouth.

**Diagnosis:** Highly diagnostic otoliths with a unique set of

morphological characters. Otolith body distinctly higher than long (OL:OH = 0.75). Sulcus horizontal, deepened; at middle axis of otolith; distinctly widening towards its anterior opening, posteriorly fading, closed; ostium much wider than cauda but without clear separation or collum, and with undivided, dorsally reduced colliculum. Crista superior and crista inferior elevated and prominent at ostium, more leveling around cauda. Antirostrum strong, very distinct, more distinct than equally long rostrum, dorsally set off from dorsal rim by deep incision which joins with dorsal depression. Inner face slightly convex; outer face flat.

**Discussion.** This spectacular otolith morphology does not compare to any known extant otolith morphologies. Particularly the sulcus opening and the development of the cristae and the antirostrum are unparalleled in the Recent. Therefore, the systematic position of *Ossulcus* remains obscure until such time that this otolith morphology has been found in situ with an identifiable articulated skeleton. In the light of the many specializations that occurred within the Beryciformes s.l. during the Late Cretaceous we have tentatively placed *Ossulcus* in a family indet. of this order.

**Species.** Monospecific genus with *Ossulcus labiatus* n. sp. from the Maastrichtian of Mississippi, USA.

***Ossulcus labiatus*** Schwarzahans & Stringer n. sp.

Fig. 10 F-K

**Etymology:** From labiatus (Latin = lipped), referring to the elevated crista superior and crista inferior at the ostium resembling lips.

**Holotype:** MMNS VP 8896 (Fig. 10 F-K), Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 2 incompletely preserved specimens, MMNS VP 8896.1 and 8896.2, same data as holotype.

**Diagnosis:** See generic diagnosis (monospecific genus).

**Description.** High bodied, delicate and rather thin otoliths reaching a size of 4.25 mm length (holotype); OL:OH = 0.75; OH:OT = 6. Dorsal rim high, highest behind its middle, anteriorly with very deep incision above massive antirostrum. Ventral rim likewise deep, deepest anterior of its middle, otherwise regularly curved and smooth. Posterior rim high, bluntly rounded, smooth. Anterior rim with massive antirostrum and much less strongly developed, equally long rostrum. Excisura distinct, wide, but not very deep. Ventral part of ostial opening very thin and not entirely complete in holotype.

Inner face distinctly convex in horizontal axis, less in vertical axis. Anterior part of dorsal field

particularly strongly bent outwards as can best be seen in dorsal view (Fig. 7 H). Sulcus axial, central, somewhat deepened, with strongly widened ostium and narrow cauda. Ostium and cauda of about equal length but not distinctly separated except for slight step change of dorsal sulcus margin above perceived collum. Ostium continuously widening towards opening; cauda narrow, straight, termination somewhat fading and close to posterior rim of otolith. Crista superior very prominent, particularly above ostium, which occupies entire antirostrum, fading above rear half of cauda. Crista inferior distinct only below anterior section of ostium and there underpinned by short furrow joining anterior rim of otolith below rostrum. Dorsal depression deep, well marked above crista superior, anteriorly joining into deep incision of anterior-dorsal rim, dorsally and posteriorly with no clear demarcation. Ventral field smooth, without ventral furrow except for under crista inferior.

Outer face flat to slightly concave; smooth except few short radial furrows in postdorsal region and distinct furrows along margins of antirostrum. Otolith rims sharp, often very thin, for instance within rostrum, but thickened at antirostrum and anterior-dorsal rim.

**Order Holocentriformes** Patterson, 1993

Family indet.

Genus *Tippaha* Schwarzahans & Stringer n. gen.

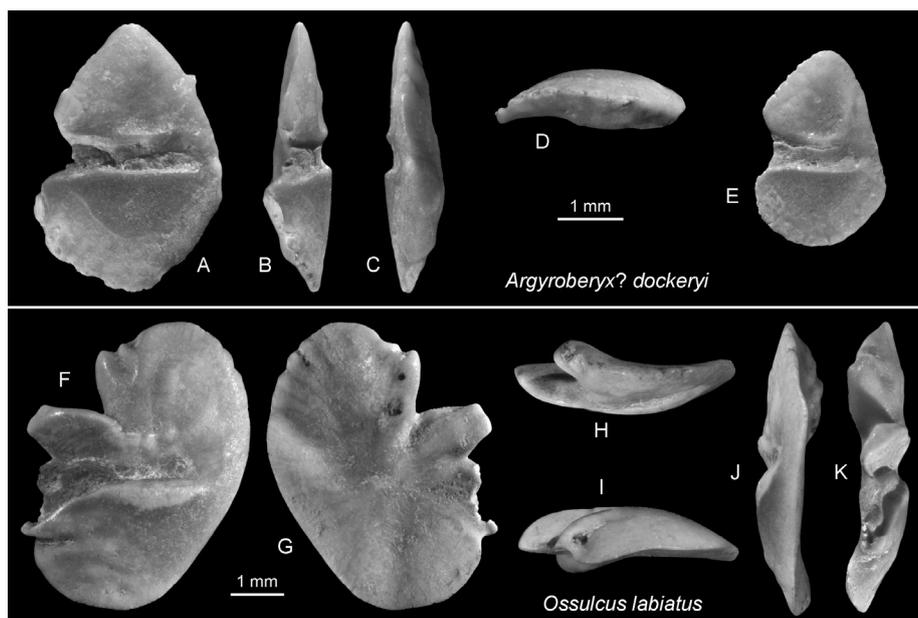
**Type species:** *Tippaha mythica* Stringer & Schwarzahans, n. sp.

**Etymology:** Referring to the county Tippah in Mississippi, where the fossil localities are located. Tippah is a word of the Chickasaw language, one of the first Native American tribes originally inhabiting the area.

**Diagnosis:** Highly diagnostic otoliths with a unique set of morphological characters. Otolith body massive, elongate, with blunt inferior anterior tip and tapering median posterior tip; OL:OH = 1.4-1.7, OH:OT = 1.5-2.2. Dorsal rim with predorsal lobe or prominent predorsal projection. Sulcus horizontal, relatively shallow; anteriorly and posteriorly closely approaching otolith rims, but not clearly opened (pseudobiostial); ostium much wider than cauda and shorter; CaL:OsL = 1.1-1.7, OsH:CaH = 1.5-2.0. Dorsal margin of anterior section of cauda indistinct, appearing as connected to the well-marked dorsal depression. Posterior part of ventral field strongly depressed and separated from inner face by sharp, curved hinge line. Inner face distinctly convex.

**Discussion.** *Tippaha* otoliths are truly spectacular in shape and sulcus organization and do not relate to any known otolith morphology of extant teleosts. The most eye-catching features are

Fig. 10 - A-E) *Argyroberyx?* *dockeryi* (Nolf & Stringer, 1996), Blue Springs, MMNS VP 6403 and 6403.1 (A-D reversed). F-K) *Ossulcus labiatus* n. gen et n. sp., holotype, Blue Springs, MMNS VP 8896.



the pseudobiostial sulcus opening, the massive depression of the posterior part of the ventral field, and the predorsal projection, which is most spectacularly developed in the type species. *Tippaha cavata* has originally been described as an ophidiid of unresolved relationships (Nolf & Stringer 1996). While some overall features such as the convex inner face, the relatively shallow sulcus and its characterization in a wider ostium, and a nearly straight narrower cauda indeed resembles certain ophidiiform otoliths, there are also significant differences. These are the ostium being distinctly shorter than the cauda, a character only matched with the specialized otolith morphology found in *Brotula* within ophidiiforms, the pseudobiostial opening of the sulcus, and the strange fading of the dorsal margin of the anterior section of the cauda towards the dorsal depression. The latter is an unusual feature otherwise only known from the Myripristidae of the Holocentriformes, where it is connected with an area of specific supporting cells of the macula (Popper 1977). *Myripristis* is known for its enhanced auditory capability for very high frequencies (Coombs & Popper 1979). Other strange features such as the depressed posterior ventral field or the massive predorsal projection (in *T. mythica* n. sp.) may point to some kind of connectivity of the otic capsule to the swim bladder in these fishes, as has been observed in extant morid otoliths which show similar morphological effects (Deng et al. 2011).

We conclude that *Tippaha* represented a

highly derived extinct teleost during terminal Cretaceous times, which probably had developed some kind of specialized auditory capabilities expressed in a spectacular otolith morphology. Certain overall similarities with myripristid (or morid) otoliths may very well have a functional morphological background, but we are still unable to understand its meaning. *Tippaha* is not connected to any teleost lineage persisting into Cenozoic times. Therefore, its systematic allocation is highly tentative. The feature of the sulcus resembling that found in myripristid otoliths may be biased by functional morphology, but considering the variety of extinct holocentriform fish skeletons known from the Late Cretaceous (Patterson 1964) appears to be the most plausible at this moment in time. This interpretation is consistent with the allocation of certain other otolith-based taxa from the Maastrichtian of Bavaria, Germany, which have also been tentatively allocated with holocentriforms (Schwarzahns 2010). From these, *Pfeilichthys* Schwarzahns, 2010 is the most closely resembling with a similar sulcus organization, but without the fading of the dorsal margin of the cauda, and a similar overall shape, thickness, and curvature of inner face, but without the massive depression of the posterior ventral field or the spectacular predorsal projection.

**Species.** Two species from the Maastrichtian of the U.S.A.: *Tippaha cavata* (Nolf & Stringer 1996), originally described as “genus Ophidiidarum” *cavatus*, and *Tippaha mythica* n. sp.

*Tippaha cavata* (Nolf & Stringer, 1996)

Fig. 11 A-H

1996 "genus Ophidiidarum" *cavatus* – Nolf & Stringer: pl. 4, fig. 6

**Material:** 4 specimens (figured specimens MMNS VP 6395 and 6395.1), Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Description.** Oval, elongate, thick otoliths reaching a size of about 5.5 mm length; OL:OH = 1.7; OH:OT = 1.5. Dorsal rim shallow with blunt predorsal expansion above ostium, regularly declining and straight posteriorly (10-15°), steeply inclining anteriorly (50-60°); obtuse postdorsal angle located close to posterior tip of otolith. Ventral rim regularly curved, thin and irregularly undulating posteriorly, gently rounded and smooth anteriorly. Anterior rim rounded, with inferior rostrum-like projection below level of ostium. Posterior rim tapering, with median tip.

Inner face distinctly convex with slightly supramedian sulcus. Sulcus shallow, except for slightly deepened posterior half of cauda, anteriorly closely approaching anterior rim of otolith and posteriorly reaching closely to posterior tip of otolith, but without clear opening. Ostium oval in shape, slightly shorter than cauda but twice as wide, with distinct ostial colliculum. CaL:OsL = 1.1; OsH:CaH = 2.0. Collum marked with deep ventral rectangular incision at ostial-caudal joint. Cauda narrow, slender, almost straight, with tapering tip, its anterior half with fading dorsal margin towards dorsal depression. Dorsal depression moderately deep, well marked, oval in outline, positioned above posterior half of ostium and anterior half of cauda. Predorsal projection set off from inner face at a hinge line. Ventral field without ventral furrow, anteriorly smooth, posteriorly strongly depressed with a distinct curved hinge line starting at ventral rim of otolith below collum, then closely running below cauda and posteriorly reaching posterior tip of otolith. Postventral depression best visible in inner face and ventral views (Fig. 11 A and 11 G).

Outer face very irregular, nearly flat towards anterior and posterior tips, distinctly convex in its central portion with large, irregular humps but no distinct umbo. Predorsal projection thickest. Dorsal otolith rim thick; other otolith rims sharp, postventral rim thin in area of postventral depression of inner face.

*Tippaha mythica* Schwarzahans & Stringer n. sp.

Fig. 11 I-X

**Etymology:** From mythicus (Latin = mythical), in reference to the long, narrow, slightly forward inclined predorsal projection which vaguely resembles the horn of the mythical unicorn.

**Holotype:** MMNS VP 8887 (Fig. 11 I-L), Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Paratypes:** 4 specimens: 3 specimens MMNS VP 9015.1, 9015.2, and 9015.3, same data as holotype; 1 specimen MMNS VP 6396 Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Further specimens:** 14 specimens, same data as holotype.

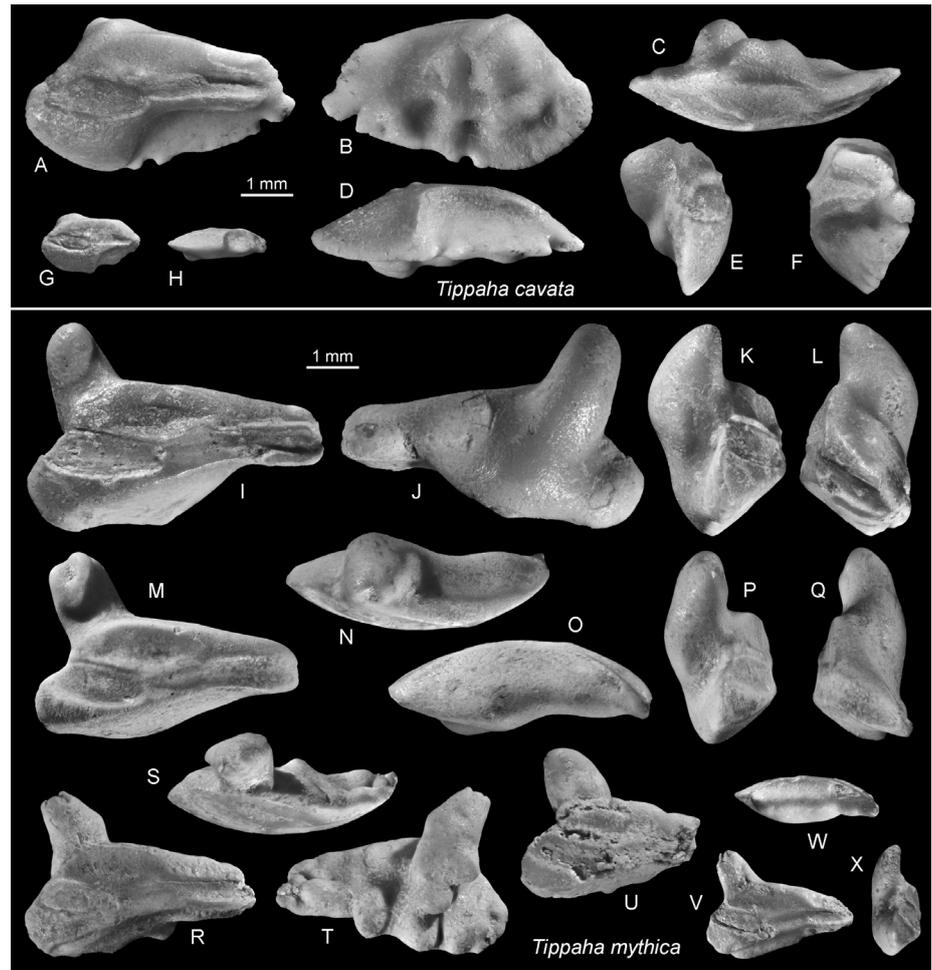
**Diagnosis:** Very long, slender predorsal projection resembling a horn, inclined forward at 65-75°, its length 25-30% of OL. Ventral depression very long, starting below anterior tip of ostium and extending until posterior tip; postventral field much narrowed, particularly below cauda. Sulcus clearly pseudobioistial with slightly widened caudal tip; CaL:OsL = 1.7; OsH:CaH = 1.5.

**Description.** Elongate, moderately thick otoliths reaching a size of 5.7 mm length (holotype); OL:OH = 1.4; OH:OT = 1.9-2.2. Dorsal rim with long, slender, horn-like slightly forward leaning predorsal projection at anterior tip, straight and slightly declining posteriorly (10-12°). Ventral rim shallow, anteriorly irregularly bent, posteriorly straight or concave. Anterior rim rounded, with distinctly inferior rostrum-like projection below level of ostium. Posterior rim tapering, with blunt, median tip.

Inner face distinctly convex with axial sulcus. Sulcus shallow, except for slightly deepened posterior half of cauda, anteriorly and posteriorly reaching otolith rims but without clear opening (pseudobioistial). Ostium oval in shape, slightly shorter than cauda and about 50% wider, with distinct ostial colliculum. CaL:OsL = 1.7; OsH:CaH = 1.5. Collum marked with deep ventral rectangular incision at ostial-caudal joint. Cauda narrow, slender, almost straight, with slightly widening, cut tip, its anterior half with fading dorsal margin towards dorsal depression. Dorsal depression moderately deep, well marked, oval in outline, positioned above posterior half of ostium and anterior half of cauda. Predorsal projection set off from inner face at a hinge line. Ventral field without ventral furrow, strongly depressed along most of its course, with a distinct hinge line starting just below rostrum, and closely running below posterior part of ostium and cauda to posterior tip of otolith.

Outer face irregular, nearly flat except for thickened predorsal projection, rather smooth. Otolith rims thick, even along postventral depression of inner face.

Fig. 11 - A-H) *Tippaha cavata* (Nolf & Stringer, 1996), Blue Springs, MMNS VP 6395 and 6395.1 (A-F reversed). I-X) *Tippaha mythica* n. sp.; I-L holotype, Owl Creek, MMNS VP 8887 (reversed); M-T, V-X paratypes, Owl Creek, MMNS VP 9015.1, 9015.2, and 9015.3 (M-T reversed); U. paratype, Blue Springs, MMNS VP 6396 (reversed).



**Discussion.** *Tippaha mythica* is probably the most spectacular and unique otolith morphology so far known from the Cretaceous. It looks like *T. cavata* taken to extremes concerning the horn-like pre-dorsal projection and the very extensive depression of the ventral field.

Order **Perciformes** s.l. Bleeker, 1859  
 Family Pempheridae Gill, 1862  
 Genus indet.

***Pempheris? huddlestoni*** Nolf & Stringer, 1996

Fig. 12 A-F

- 1983 Pempheridae – Huddleston & Savoie: fig. 2A.
- 1991 Pempheridae – Stringer: pl. 2, fig. 9.
- 1996 “genus Pempheridarum” *huddlestoni* – Nolf & Stringer: pl. 5, figs. 1-3.
- 2016 “*Pempherida*” *huddlestoni* Nolf & Stringer, 1996 – Stringer: fig. 11.
- 2016 *Pempheris? huddlestoni* Nolf & Stringer, 1996 – Stringer, Oman & Badger: pl. 2, fig. 8.
- 2018 *Pempheris? huddlestoni* Nolf & Stringer, 1996 – Stringer, Clements, Sadorf & Shannon: pl. 2, fig. 6.

**Material:** 38 specimens, Blue Springs, 34.25°N, 88.5°W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6405 and 6405.1).

**Short description.** Otoliths oval in outline with angular ostium and slightly pointed posterior tip. Size up to 4.5 mm length. OL:OH = 1.45; OH:OT = 5.5. All rims sharp and finely crenulated, dorsal rim somewhat coarser than ventral rim.

Inner face convex. Sulcus long extending nearly across inner face, divided into ostium and cauda (heterosulcoid). Ostium almost twice as wide as cauda, mainly ventrally widened, shallow, with clearly marked ostial colliculum. Cauda narrow, slightly deepened, with its posterior end flexed slightly downward. CaL:OsL = 1.3-1.4; OsH:CaH = 1.7-2.0. Dorsal depression narrow; no ventral furrow. Outer face concave with many radial furrows along otolith margins.

**Discussion.** *Pempheris? huddlestoni* represents approximately 1% of the total otoliths from the Ripley and was not found in the Owl Creek Formation. It has been identified as a Pempher-

ridae and was described from the Ripley Formation by Nolf & Stringer in 1996. Previously, it has been mentioned from the Severn Formation in Maryland by Huddleston & Savoie (1983) and from the Ripley Formation in Mississippi by Stringer (1991). Subsequently, Stringer (1999; 2016) recognized this species at the Coon Creek Site in Tennessee. More recently, the species was noted from the Woodbury Formation in New Jersey (Stringer et al. 2016) and the Tar Heel Formation in North Carolina (Stringer et al. 2018). We follow the view expressed by Nolf & Stringer (1996) that these otoliths truly represent a percid s.l. and resembles otoliths of the family Pempheridae. It is likely to represent a fossil genus of the family or a related fossil family, but its otolith morphology does not provide sufficient characteristics for definition.

Family Serranidae Swainson, 1839  
Genus indet.

*Serranus? severnensis* (Nolf & Stringer, 1996)

Fig. 12 G-H

1996 “genus Percoideorum” *severnensis* – Nolf & Stringer: pl. 4, fig. 13.

?1996 Moronidae indet. – Nolf & Stringer: pl. 4, fig. 10-12.

**Material:** 1 slightly eroded specimen, MMNS VP 6408, Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Short description.** Small, thin, elongate otoliths up to 3.3 mm length, with an aculeate anterior and a rounded posterior tip. OL:OH = 2.2; OH:OT = 2.5. Dorsal and ventral rims regularly curved; dorsal rim more shallow than ventral rim.

Inner face moderately convex, with narrow, slightly suprmedian sulcus. Ostium shorter than cauda, relatively narrow and somewhat wider than cauda. CaL:OsL = 1.4; OsH:CaH = 1.6. Cauda narrow, slightly deepened, slightly flexed towards its tip and terminating close to posterior tip of otolith. Dorsal depression indistinct, small; no ventral furrow. Outer face flat, smooth.

**Discussion.** This otolith displays a very generalized percomorph morphology, similar for instance to the pattern found in the Serranidae and Scorpaenidae. It is therefore tentatively placed in the Serranidae without generic allocation.

**Otoliths incertae sedis**

Collective genus *Otolithopsis* Huddleston, 1983

**Remarks.** The collective group name *Otolithopsis* was introduced by Huddleston (1983) in compliance with the ICZN rules for all those instances where a given fossil otolith-based species could not be associated with any teleost group. It replaces the previously used name *Otolithus* Koken, 1884 which was preoccupied by *Otolithus* Cuvier, 1829 (syn. *Otolithes* Oken, 1817), a genus of the family Sciaenidae.

*Otolithopsis cumatilis* Schwarzhans & Stringer n. sp.

Fig. 12 I-L

1996 Euteleostei indet. – Nolf & Stringer: pl. 4, fig. 7.

**Etymology:** From *cumatilis* (Latin = blue, water-colored), an allusion to the name of the type location Blue Springs.

**Holotype:** MMNS VP 9101 (Fig. 12 I-K), Blue Springs, 34.25° N, 88.5° W, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr.

**Paratypes:** 1 specimen, MMNS VP 9101.1, same data as holotype.

**Further specimens:** 2 specimens, same data as holotype.

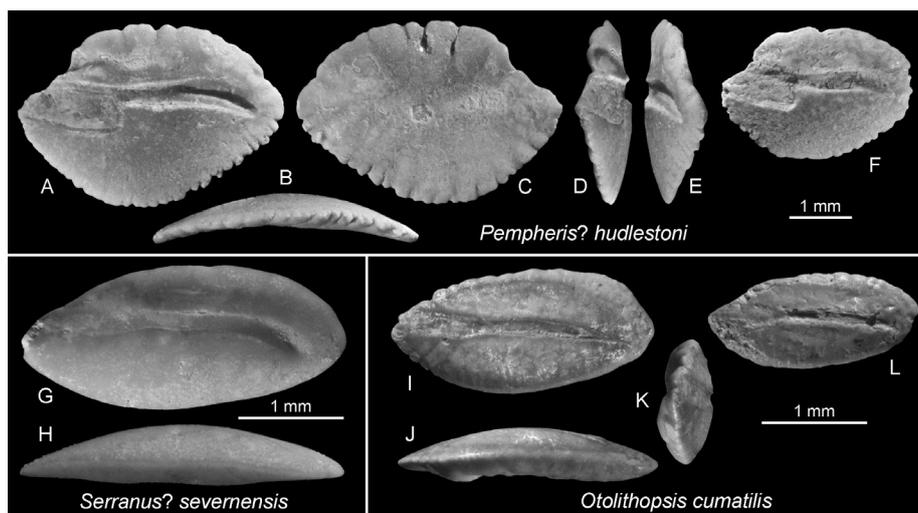
**Diagnosis:** Elongate, oval outline; OL:OH = 2.1-2.2. Sulcus narrow, straight, slightly inclined at 3-5° with ostium only slightly wider than cauda; cauda with tapering, sharply pointed tip. Caudal colliculum likewise with tapering and pointed tip, but distinctly before caudal tip.

**Description.** Small, elongate, oval otolith up to 3.0 mm length (in Nolf & Stringer, 1996; holotype 2.5 mm length). OH:OT = 2.5. Dorsal rim regularly curved, slightly expanded postdorsally, without prominent angles and finely undulating. Ventral rim regularly curved and smooth. Rostrum and posterior tip rounded angular, positioned along axis of otolith. No clear excisura or antirostrum.

Inner face convex with narrow, straight, slightly inclined sulcus at 3 to 5°. Ostium shorter and shallower than cauda, anteriorly open and with well-marked colliculum, slightly wider than cauda. CaL:OsL = 1.5; OsH:CaH = 1.3-1.5. Cauda straight with tapering, pointed tip, its colliculum fairly distinct and also with tapering pointing tip but terminating distinctly earlier than caudal tip. Dorsal depression very large and wide, but with indistinct margins. Ventral furrow indistinct, close to ventral rim of otolith. Outer face flat, with some irregular ornamentation.

**Discussion.** This otolith-based species is easily recognized by the specific development of

Fig. 12 - A-F) *Pempheris? huddlestoni* Nolf & Stringer, 1996, Blue Springs, MMNS VP 6405 and 6405.1 (A-E reversed). G-H) *Serranus? severnensis* (Nolf & Stringer, 1996), Blue Springs, MMNS VP 6408 (reversed). I-L) *Otolithopsis cumatilis* n. sp. Blue Springs; I-K holotype, MMNS VP 9101 (reversed); L paratype, MMNS VP 9101.1.



the cauda and the slightly inclined position of the sulcus, but there is no extant otolith morphology known in which this pattern could be placed comfortably. Hence it is left with the collective group *Otolithopsis*.

### Lapilli otoliths

**Remarks.** The collection of Maastrichtian otoliths described from the Ripley and Owl Creek formations contains a few lapilli or utricular otoliths. Sagittae or saccular otoliths typically occur most commonly in the fossil record, but there are assemblages where lapilli are very abundant (Huddleston & Savoie 1983; Schwarzhans et al. 2018b). Two morphotypes have been described from the Ripley and Owl Creek that represent siluriforms, and two further morphotypes represent unknown teleosts and are not placed in any specific taxon. It should be noted that Assis (2005) in an exhaustive study of lapilli of modern fishes (183 species from Portuguese coastal waters, estuaries, and rivers) contended that lapilli could be used for the purpose of identification in Recent and fossil teleosts. However, he also stated that lapilli possessed a limited number of useable morphological features for taxonomy and that no clear tendencies in the character distribution of lapilli have so far been determined for teleosts. Lapilli from the Santonian of Alabama, USA (Schwarzhans et al. 2018b) were identified as lapillus types 1–7 (except for *Arius danicus*). We suggest that until more definitive and conclusive work is performed, most fossil lapilli should be identified as morphotypes without specific taxonomy.

### Order Siluriformes Cuvier, 1817

#### Family Ariidae Bleeker, 1862

#### Genus indet.

### *Arius? subtilis* Schwarzhans & Bratishko, 2011

Fig. 13 A-E

- 1926 Otolith – Wade: pl. LXXI, figs 9 – 10.  
 1983 Ariidae – Huddleston & Savoie: fig. 2, D – E.  
 1996 Ariidae – Nolf & Stringer: pl. 2, fig. 10  
 2011 *Arius subtilis* – Schwarzhans & Bratishko: fig. 4, F – H.

**Material:** 125 specimens: 114 specimens Blue Springs, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6390 and 6390.1); 11 specimens Owl Creek, Tippah County, Mississippi, USA, late Maastrichtian Owl Creek Fm.

**Short description.** The lapillus of *Arius? subtilis* have an oval-shaped outline with smooth margins. It is essentially plano-convex. There are few prominent, diagnostic features. In well-preserved specimens, a lightly impressed sulcal area may be present. The specimens appear to be the same as *Arius subtilis* identified by Schwarzhans and Bratishko (2011, fig. 4 f–h) in the Paleocene (Selandian) of the Ukraine.

**Discussion.** *Arius? subtilis* is not uncommon in the early Paleocene of Europe (see Schwarzhans & Bratishko 2011 and Schwarzhans 2012) and has now also been found in the Maastrichtian. It thus represents the second ariid otolith-based species known to stratigraphically extend across the K-Pg boundary along with *Arius? danicus* Koken, 1891, from which it differs in being thinner and slightly more elongated (see Schwarzhans 2010 and 2012 for comparison). The specimens of *Arius? subtilis* from the Ripley and Owl Creek formations are probably

the same as the one figured by Wade (1926) from the Coon Creek type locality as well as the ariid otoliths known from several Campanian and Maastrichtian localities in North America (Huddleston & Savoie 1983; Nolf & Stringer 1996).

Family indet.

Genus *Vorbisia* Frizzell, 1965b

*Vorbisia vulpes* Frizzell, 1965b

Fig. 13 F-L

1965b *Vorbisia vulpes* – Frizzell: fig. 2.

1973 *Vorbisia vulpes* Frizzell, 1965 – Frizzell & Koenig: fig. 3 (figs. 1 and 4 depict asterisci which have also been assigned to *Vorbisia vulpes*, but are here considered of questionable identity).

1983 *Vorbisia* sp. – Huddleston & Savoie: fig. 2 F-G.

1996 “genus *Ariidarum*” *vulpes* (Frizzell, 1965) – Nolf & Stringer: pl. 2, figs. 11-12.

2003 *Vorbisia vulpes* Frizzell, 1965 – Carpenter, Erickson & Holland: fig. 2, a-d.

2019 *Vorbisia vulpes* Frizzell, 1965 – Hoganson, Erickson & Holland: fig. 12.62

**Material:** 142 specimens Blue Springs, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6389 and 6389.1).

**Short description.** Lapilli of *Vorbisia vulpes* can be large and massive. Many of the specimens from the Ripley Formation exceeded 10 mm in length with several longer than 12 mm. The lapillus is unequally biconvex, and the outline is subangular in shape. The sulcal area is located on the outer face along the dorsal margin extending down the posterior margin. These margins are nearly straight. In well-preserved specimens, the sulcal area is characterized by numerous, closely spaced, radial lines. The anterior margin is broadly rounded, and the ventral margin has a centrally located broad notch or indentation. The inner face is convex and typically smooth and slightly undulating.

**Discussion.** A highly characteristic and large otolith reaching at least 12 mm length. The species has been extensively described and discussed in Frizzell (1965b) and Frizzell & Koenig (1973) who concluded that *Vorbisia* lived in mostly brackish to marine environments in South Dakota but not in freshwater. Its common occurrence in the Severn Formation of Maryland (Nolf & Stringer, 1996) and now in Mississippi supports a marine habitat. Interestingly, *Vorbisia vulpes* is not present in the Owl Creek Formation although it is abundant in the Ripley Formation. At the time of the

original description, Frizzell (1965b) placed *Vorbisia vulpes* in the cypriniforms, but it is now interpreted as a siluriform believed to be in the family Ariidae (sea catfishes). Nolf & Stringer (1996) reported it (as “genus *Ariidarum*” *vulpes*) only from the Fox Hills Sandstone of South Dakota and the late Maastrichtian Severn Formation of Maryland. Since that time, Woodward (2003) reported this species from the late Maastrichtian Kemp Clay of Texas. All finds so far have been confined to the Maastrichtian of the U.S.A.

## Unidentified lapilli morphotypes

### Lapillus type 1

Fig. 13 M-V

1996 Utricular otolith – Nolf & Stringer: pl. 6, fig. 12.

**Material:** 12 specimens Blue Springs, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 8897, 8898).

**Short description.** The utricular otoliths designated as Lapillus type 1 are small (many around 2 mm but reaching up to 5 mm and more). The specimens have a conspicuous gibbus maculae and a well-defined confluentia gibbi maculae on the ventral or macular side. The specimens are rounded on several of the edges, which give the otoliths a lobe-like appearance.

**Discussion.** A highly characteristic slender, thin otolith up to about 5 mm length of unknown relationships. Nolf & Stringer (1996) cited a single utricular otolith from the Late Cretaceous Ripley Formation in northeast Mississippi. This utricular otolith was not found at any of the other Cretaceous localities reported by Nolf & Stringer (1996). However, ten utricular otoliths that appear to be the same as the one figured in Nolf & Stringer (1996) were recovered from bulk samples of the Ripley Formation in this study.

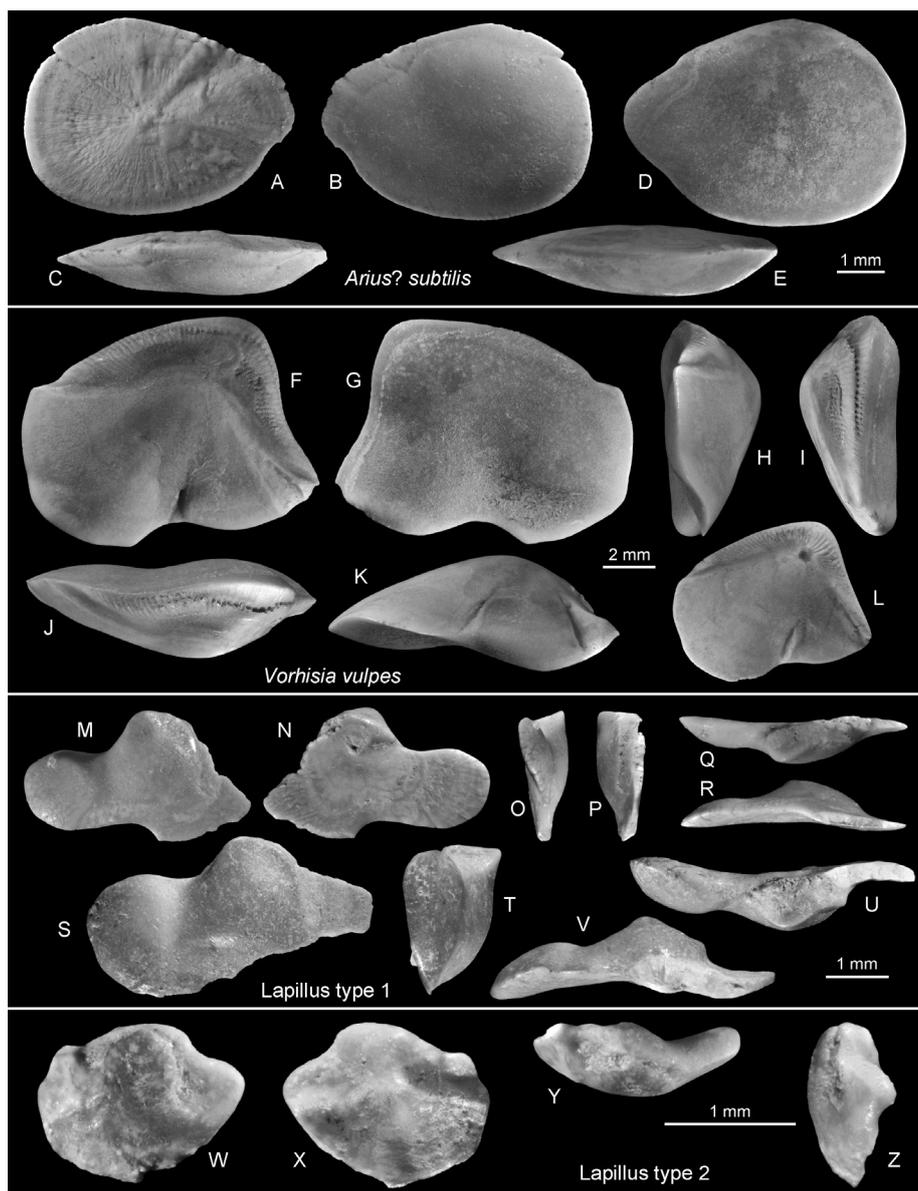
### Lapillus type 2

Fig. 13 W-Z

**Material:** 1 specimen Blue Springs, Union County, Mississippi, USA, early Maastrichtian Ripley Fm., Coon Creek Mbr. (figured specimens MMNS VP 6414).

**Discussion.** A single, nearly round and moderately thick, small otolith of 1.55 mm length that resembles in size and morphology many utricular

Fig. 13 - A-E) *Arius? subtilis* Schwarzahns & Bratishko, 2011, Blue Springs, MMNS VP 6390 and 6390.1 (D-E reversed); F-L) *Vorbisia vulpes* Frizzell, 1965b, Blue Springs, MMNS VP 6389 and 6389.1 (L reversed). M-V) Lapillus type 1, Blue Springs, MMNS VP 8897-8898 (S-V reversed). W-Z) Lapillus type 2, Blue Springs, MMNS VP 6414 (reversed).



otoliths of extant teleosts (see Assiz 2005). Lapillus type 2 is the smallest of any of the lapilli recovered from the Ripley and Owl Creek formations.

### EVOLUTIONARY IMPLICATIONS OF THE OTOLITHS

The fish fauna of the Ripley and Owl Creek formations as indicated by otoliths provides information regarding the evolutionary development of the teleosts during the Late Cretaceous. In 1985, Nolf cited less than 20 valid species of bony fish as indicated by otoliths for the entire Cretaceous worldwide. Even a decade later, Schwarzahns noted less than 100 species worldwide (Schwarzahns 1996). However, investigations of Late Cretaceous

unconsolidated glauconitic sands, clays, and marls in the U.S. Gulf and Atlantic coasts since the 1990s have provided otoliths that have shown the presence of additional species (Nolf & Dockery 1990; Stringer 1991; Nolf & Stringer 1996; Stringer 1999; Nolf 2013; Stringer 2016b; Stringer et al. 2016; Stringer et al. 2018; Schwarzahns et al. 2018b). Nolf & Stringer (1996) reported 43 teleost taxa in the Late Cretaceous of North America alone. Thus, the 30 Blue Springs taxa are important and pertinent in furthering the understanding Late Cretaceous fish assemblages and their evolutionary development.

Since fossil otoliths are found in a wide range of paleoenvironments, they can provide a plenitude of information for investigating the origin and geological distribution of fish families (Nolf 1995). Friedman & Sallan (2012: 707) verified the signif-

icance and usefulness of fish analysis in the paleontological record 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.” According to Nolf (2013), one of the most important data that fossil otolith studies can provide is regarding the evolutionary history of teleostean fishes and the geological extension of records compared to osteological remains. The fossil record for many teleostean families is extended considerably by otoliths, and otoliths play a primary role in tracing the history of modern teleost taxa. Certainly, the Ripley and Owl Creek otoliths as well as otoliths from other North American Late Cretaceous studies confirm the usefulness of otoliths in determining the geological range of fishes and insight into their evolution. Furthermore, the discovery of 4 new otolith-based genera and 13 new species provides evidence of the evolutionary development and diversification of the bony fishes prior to the Cretaceous/Paleogene extinction event.

The systematic interpretation of Late Cretaceous otoliths, however, meets certain challenges and restrictions. Their morphological diversity is much broader than during the preceding Jurassic and Early Cretaceous periods (Schwarzhans et al. 2017) and shows a number of rather spectacular specializations, e.g., *Tippaba* or *Ossulcus*, but many of these morphological patterns do not continue into Paleogene times or are difficult to associate with Cenozoic otolith patterns. One has to bear in mind that many teleost groups existed during the Late Cretaceous that became extinct around the K-Pg boundary as evidenced by the articulated skeleton record (Patterson 1964, 1993; Friedman 2010, 2012). Otoliths in situ have only been found in very few instances so far (Schwarzhans et al. 2018a), and these have already shown the conundrum of systematic allocation of Cretaceous otoliths (see discussion to *Apateodus*). There are otolith morphologies that relate well to Cenozoic taxa such as of the Elopiformes, Albuliformes, Paraulopidae, or Trachichthyidae, but many others will likely belong to extinct groups known from articulated skeletons. Therefore, the actualistic principle of comparing Late Cretaceous otolith morphologies with those of extant fishes does not work as well as with Ce-

nozoic otoliths. This has led to controversial views in past publications about the allocation of a number of fossil Late Cretaceous otoliths, particularly in respect to their relationships to the Perciformes (compare Nolf & Dockery 1990; Nolf & Stringer 1996; Nolf 2013; and Schwarzhans 2010, 2012; Schwarzhans et al. 2018b). The record of Late Cretaceous articulated teleost skeletons is rich in beryciforms, polymixiiforms, and holocentriforms but scarce in perciforms (Patterson 1993; Carnevale & Johnson 2015). There are no morphological characters in otoliths that would unequivocally distinguish perciform otoliths from those of the Beryciformes, Polymixiiformes, or Holocentriformes, although at family level clear synapomorphies can be identified in some instances. In the light of the scarcity of perciform skeletons in the Late Cretaceous, we have here allocated only otolith finds to that order which we regard as undisputable. As a result, the systematic allocation of several Late Cretaceous otolith morphologies remains unresolved until such morphologies have been found in situ. We consider those to represent extinct groups mostly of beryciform or holocentriform affinities but are aware of the tentative nature of these allocations.

One of the most significant findings regarding the evolution of the Late Cretaceous fishes is the diversification and specialization observed in otolith morphologies which are here interpreted to represent extinct Beryciformes. This is especially true in the genus *Eutawichthys*, which is now known to have been represented by at least five species (*E. compressus*, *E. stringeri*, *E. maastrichtiensis*, *E. zideki*, and *E. choctawae*) in the Late Cretaceous. Furthermore, the otoliths of the Ripley and Owl Creek formations appear to indicate that *E. maastrichtiensis* and *E. zideki* were replacing *E. compressus* and *E. stringeri*, known primarily from the Santonian. Another form, tentatively placed in the Beryciformes, *Ossulcus labiatus*, exhibits one of the most spectacular otolith morphologies recognized in fossil otoliths. The sulcus opening and the development of the crista superior, crista inferior, and antirostrum are unparalleled in known Recent otoliths. The morphology of *Ossulcus labiatus* does not compare to any known extant otoliths and, most probably, serves as further evidence of the specialization occurring in the Late Cretaceous.

Equally intriguing and spectacular are the otoliths of *Tippaba*, which do not relate to any known

otolith morphology of extant teleosts. One of the most unique features is the fading of the dorsal margin of the anterior section of the cauda towards the dorsal depression. This unusual feature is known from the Myripristidae (Holocentriformes), where it is connected with an area of specific supporting cells of the macula (Popper 1977). Coombs & Popper (1979) indicated that *Myripristis* possessed an enhanced auditory capability for very high frequencies. The extremely depressed posterior ventral field and the massive predorsal projection (in *T. mythica*) may point to a connection of the otic capsule to the swim bladder, as has been observed in extant morid otoliths (Deng et al. 2011). It appears that *Tippaha* represented a highly derived extinct teleost during the latest Cretaceous that probably had developed specialized auditory capabilities that were reflected in the spectacular otolith morphology. *Tippaha* certainly does not appear to be related to any teleostean lineage persisting into the Cenozoic, and the taxonomic assignment therefore is highly tentative. However, considering the resemblance to myripristid otoliths and the variety of extinct holocentriform fish skeletons from the Late Cretaceous (Patterson 1964), the assignment seems plausible. The taxonomic assignment also agrees with holocentriform otoliths described from the Maastrichtian of Germany (Schwarzahns 2010).

Other otolith taxa from the Ripley and Owl Creek supply evidence of evolutionary developments during the Late Cretaceous. For example, specimens of *Choctawichtys cepoloides* with their homosulcoid sulcus pattern represent the earliest occurrence of this feature, which is primarily known from the superorder Paracanthopterygii. Homosulcoid sulcus patterns occur not only in Gadiformes of the Paracanthopterygii but also certain Alepisauriformes and Zeiformes, albeit differing in detail (Schwarzahns et al. 2017). Therefore, we regard the homosulcoid sulcus pattern found in *Choctawichtys* as supporting the synapomorphy of this pattern for gadiform otoliths. *Covetaichthys* with at least three species (*C. alabamiae*, *C. lamberi*, and *C. carnevalei*) is indicative of a species-rich genus of the family Polymixiidae during the Late Cretaceous. Larger specimens of *Hoplopteryx oscitans* (greater than 6 to 7 mm), which were recovered primarily from the systematic surface collecting of the Ripley Formation, displayed prominent, deeply incised dorsal margins unlike the smaller specimens. The deeply

incised dorsal margins are very similar to Recent trachichthyids such as of *Hoplostethus* (Brzobohaty 1978, pl. 1, figs. 1-7; Schwarzahns 1980, figs. 348–351; Campana 2004, p. 41; Nolf 2013, pl. 165).

The Ripley and Owl Creek formations otolith assemblages included limited representatives of the order Perciformes (see above), one of the most diversified of all extant fish orders (Nelson et al. 2016). Perciform families have long been considered as modern in their affinities by the Eocene (Carroll 1988; Alfaro et al. 2009; Wiley & Johnson 2010; Near et al. 2013). The perciform taxa represented by otoliths in the Ripley and Owl Creek formations (*Pempheris? buddlestoni* and *Serranus? severnensis*) represent a very small percentage of the assemblage and are typically small, but they do provide confirmation of the early development of modern perciform lineages in the Late Cretaceous. An extensive review of Late Cretaceous vertebrates from Alabama by Ikejiri et al. (2013), which entailed over 8,000 skeletal specimens from 12 institutions, indicated the presence of no perciform fishes. However, a Paleogene fish assemblage from Alabama studied by Clayton et al. (2013) showed that well over half of the lower to middle Eocene skeletal remains of osteichthyans represented perciforms. Nolf (2013) pointed out almost exactly the same trend based on skeletal remains of perciforms in Europe, and perciforms comprised almost 25% of a middle Paleocene (Selandian) fauna of the Ukraine (Schwarzahns and Bratishko 2011). Friedman (2010) noted that the fossil record patterns reveal an explosive morphological diversification of percomorphs in the aftermath of the end of the Cretaceous extinction, and Schwarzahns (2012) refers to the Paleocene percoid radiation. There have been molecular studies that have noted the development of the Percomorpha, which includes the Perciformes, in the Late Cretaceous (Santini et al. 2009), and Near et al. (2012, fig. 2A) indicated molecular age estimates of just over 100 Ma for the percomorphs.

The large-scale, exhaustive research of Betancur-R. et al. (2013) indicated that the major lineages within the Percomorphaceae, which contains the Perciformes, originated between 132 Ma and 82 Ma, well before the end of the Cretaceous. Quental & Marshall (2010) asserted that while molecular phylogeny research can provide details and statistics on changes in diversification rates, it

is still essential to access paleontological remains (“embrace the fossil record”) to fully understand the evolution and diversity of Recent species. This seems applicable to the Late Cretaceous evolution of the Perciformes as indicated by molecular studies and the otoliths of the Ripley and Owl Creek formations. Friedman (2010) indicated that important phylogenetic splits within the Percomorpha occurred by the Late Cretaceous, but members of this clade remained infrequent throughout the time interval. The very limited perciforms of the Ripley and Owl Creek formations is consistent with this observation and are probably rare examples of the percomorph lineages that began in the early part of the Late Cretaceous.

## PALEOECOLOGICAL DETERMINATIONS

An essential taphonomic consideration in the utilization of otoliths for paleoecological interpretations is whether the otoliths accurately represent the fishes that inhabited the area during a specific interval of geologic time. Multiple strands of evidence certainly indicate that otoliths represent fish that are autochthonous in nature and represent part of the biocoenosis or life assemblage. It appears that the 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 of piscivorous vertebrates such as sharks, predatory fish, and whales (Fitch 1967; Schäfer 1972; Stringer 1992). Nolf (1985; 2013) believed that predation and subsequent excretion are the commonest method by which otoliths become part of the sediment. Remains from the Ripley Formation indicated that otoliths were on the ocean bottom during the taphonomic process as several were recovered with invertebrates, such as cnidarians and bivalves, attached and using the otoliths as a stratum for growth. However, the number of specimens with evidence of invertebrate settlement, encrusting, and boring constitute a very small percentage as was found in Stringer (2016a). Stringer et al. (2016) also reported a small percentage of otoliths from the Campanian Woodbury Formation with invertebrate evidence and even less examples of invertebrate activity on the otoliths from the Campanian Tar Heel Formation (Stringer et al. 2018).

There are a number of studies of otoliths from modern sediments that have indicated that otoliths generally reflect fishes that are found in an area (Gaemers 1978; Wigley & Stinton 1973; Stringer 1992; Fierstine, Huddleston & Takeuchi 2012; Schwarzhans 2013; Lin 2016; Lin et al. 2016; Lin et al. 2017). Investigations of the otoliths of Recent sea bottoms sediments have been greatly facilitated by taxonomic studies of modern fish otoliths or include modern fish otoliths such as those by Schwarzhans (1993), Schwarzhans (1999), Smale et al. (1995), Rivaton & Bourret (1999), Campana (2004), Veen & Hoedemakers (2005), Furlani et al. (2007), Florida Fish and Wildlife Conservation Commission (2007), Tuset et al. (2008), McBride et al. (2010), Lin & Chang (2012), Nolf (2013), Schwarzhans (2013), and Schwarzhans & Aguilera (2013, 2016). There seems to be a consensus that a strong correlation exists between otolith associations in modern bottom sediments in specific environments and the expected fishes. Although various taphonomic processes may affect the otoliths, such as time-averaged and spatial-averaged (Lin et al. 2017), the otoliths appear to remain part of the biocoenosis and can be interpreted as such in the fossil record.

Evidence of the reliability of otoliths in paleoenvironmental interpretation is illustrated in numerous studies, especially in the Cenozoic of the Gulf of Mexico and Caribbean (Nolf & Stringer 1992; Stringer 1992, 1998a; Breard & Stringer 1995; Stringer & Breard 1997; Nolf & Aguilera 1998; and Aguilera & Aguilera 1999). These studies utilized foraminifera and ostracodes to determine the paleobathymetry as well as other paleoenvironmental parameters for various localities. Fish otoliths were also used independently to derive the paleoenvironmental parameters for each of the locations. Results indicated close agreement between the paleoecology indicated by the microfossils and the otoliths. The foraminifera provided greater detail and reliability about paleoenvironmental conditions, but the otoliths appeared to be reliable indicators of general paleoecological parameters. Other studies, which were international in scope, have also demonstrated the value of otoliths for interpreting paleoenvironments including Schwarzhans (1980), Nolf & Brzobohaty (1992), Nolf & Brzobohaty (1994; 2009), Reichenbacher & Cappetta (1999), Girone (2003), Schwarzhans (2008), and Agiadi et al. (2018; 2019). Studies seem to indicate that an otolith as-

Tab. 2 - Taxa represented by otoliths (n = 742 specimens) in the Ripley Formation bulk samples of Phillips and Stringer (139 kg) at the Blue Springs locality with number of specimens and percentage of total. The five shaded taxa are the most abundant and represent approximately 75% of the total otoliths in the bulk samples.

Family (all capital letters) and Taxon	Number in Bulk Sample	Percentage of Total
MEGALOPIDAE		
<i>Megalops? nolfi</i>	3	0.40
ALBULIDAE		
Albulidae indet.	7	0.94
OSMEROIDIDAE		
<i>Osmerooides mississippiensis</i>	14	1.89
<i>Osmerooides</i> sp.	4	0.53
PTEROTHRISSIDAE		
<i>Pterothrissus</i> sp.	6	0.81
ANGUILLIDAE		
<i>Anguilla? chickasawae</i>	2	0.27
FAMILY INDET.		
<i>Muraenanguilla unionensis</i>	19	2.56
OSTEOGLOSSIDAE		
<i>Osteoglossum? tavernei</i>	4	0.53
FAMILY INDET.		
<i>Kokenichthys navis</i>	7	0.94
<i>Kokenichthys ripleyensis</i>	1	0.13
ICHTHYOTRINGIDAE		
<i>Apateodus crenellatus</i>	42	5.66
<i>Thrax acutus</i>	1	0.13
PARAULOPIDAE		
<i>Paraulopus pseudoperca</i>	190	25.61
FAMILY INDET.		
<i>Choctawichthys cepoloides</i>	2	0.27
POLYMIXIIDAE		
<i>Cowetaichthys alabamiae</i>	9	1.21
<i>Cowetaichthys carnevalei</i>	3	0.40
TRACHICHTHYIDAE		
<i>Hoplopteryx oscitans</i>	278	37.47
<i>Hoplopteryx langfordi</i>	11	1.48
FAMILY INDET., type 1 (Beryciiformes)		
<i>Eutawichthys maastrichtiensis</i>	15	2.02
<i>Eutawichthys zideki</i>	24	3.23
FAMILY INDET., type 2 (Beryciiformes)		
<i>Argyroberyx? dockeryi</i>	2	0.27
FAMILY INDET., type 3 (Beryciiformes)		
<i>Ossulcus labiatus</i>	3	0.40
FAMILY INDET. (Holocentriformes)		
<i>Tippaha cavata</i>	1	0.13
<i>Tippaha mythica</i>	1	0.13
PEMPHERIDAE		
<i>Pempheris? huddlestoni</i>	29	3.91
SERRANIDAE		
<i>Serranus? severnensis</i>	1	0.13
INCERTAE SEDIS		
<i>Otolithopsis cumatilis</i>	4	0.54
Percoidei sp.	3	0.40
<b>LAPILLI</b>		
ARIIDAE (Siluriformes)		
<i>Arius? subtilis</i>	13	1.75
FAMILY INDET. (Siluriformes)		
<i>Vorhisia vulpes</i>	2	0.27
FAMILY INDET.		
Lapillus type 1	7	0.94
Lapillus type 2	1	0.13
Non-identifiable (broken, eroded, worn)	33	4.45

sociation will reflect with reasonable certainty the teleostean fauna inhabiting an area during a certain interval of geological time.

As noted earlier, taxonomic identification of fossil otoliths is accomplished primarily by comparison to Recent otoliths. The basic premise in paleoenvironmental analysis is to utilize the identified otoliths to obtain data on the preferred habitats of comparable modern fishes for analogues. Some

would argue that Late Cretaceous otoliths are too old to apply uniformitarian parameters, and there is certainly merit to that argument. Several groups of fishes that are extremely useful in paleoenvironmental interpretations, such as the sciaenids (Stringer & Shannon 2019), have not evolved and are not available. Obviously, the Late Cretaceous otolith assemblage cannot provide the precision and accuracy of paleoecological interpretation possible with

Plio-Pleistocene otoliths. However, we contend that it is still possible to ascertain general paleoenvironmental conditions with Late Cretaceous otoliths within limitations. Also, interpretations suggested by the otoliths will be carefully scrutinized and compared to other paleoenvironmental evidence such as foraminifera, invertebrates such as cnidarians, bivalves, and gastropods, and skeletal remains. In addition, the paleoecology suggested by the otolith taxa will be evaluated on the basis of paleogeographical considerations for the Late Cretaceous (see below).

Only the otoliths recovered from the Ripley Formation bulk samples of Stringer and Phillips (139 kg) were used for paleoecological interpretations (742 specimens) since the techniques were exactly the same. Other bulk samples were prepared, but the techniques varied slightly (e.g., sieve sizes). To avoid any bias due to differences in techniques, those samples were not used for paleoecological interpretations. Surface collections were not employed for statistical analysis in paleoecology because of potential statistical bias (e.g., otolith size). Examination of the otoliths from the bulk samples (Table 2) revealed the absence of representatives that are indicative of deep waters only (greater than outer shelf or 200 m). The otolith assemblage seems to indicate a neritic environment with little open ocean influence. Many of the teleost taxa or similar modern analogues represented by otoliths from the site are presently found in shore waters of the continental United States on or above the continental shelf (less than 200 m) according to Page et al. (2013). Therefore as a general interpretation, the bony fishes represented by otoliths indicate a marine environment no deeper than outer shelf and probably shallower.

If the bony fishes represented by otoliths in the Ripley Formation are compared to the modern ichthyological fauna from the Gulf of Mexico and the Atlantic Ocean (Hoese & Moore 1998; McEachran & Fechhelm 1998; McEachran & Fechhelm 2005; Nelson et al. 2016), the fossil otoliths represent fish that are mainly tropical, subtropical, and warm temperate in nature. Furthermore, most of the otoliths represent fish expected in normal marine salinity although a few of the forms could tolerate reduced salinities. In order to ascertain general paleoenvironmental conditions at the Blue Springs locality, special attention is given to the most abundant taxa in the bulk samples. Five taxa

account for approximately 75% of the total specimens. The trachichthyids or roughies are by far the most common forms at Blue Springs as they represent over one-third of the bulk sample assemblage (37.47%) and were certainly very abundant at the locality during the Late Cretaceous. The paleoenvironmental setting at Blue Springs was conducive to roughies, and their presence is indicative of ancient conditions there. According to Nelson et al. (2016), all modern members of the family Trachichthyidae are marine. McEachran & Fechhelm (1998) listed the distribution of the trachichthyids as tropical to warm temperate and quite widespread being found in the Atlantic, Indian, and Pacific. McEachran & Fechhelm further noted that roughies are generally found in depths from 70 m to 500 m and are found on or near the bottom or demersal. The depth distribution for the family presented by Nelson et al. (2016) is slightly deeper at about 100 m to 1,500 m with most species occurring in deeper water. However, Masuda & Allen (1993) noted that the young roughies of some species occur nearer the coast, which had also been previously reported by Kotlyar (1980). As noted previously, the size and number of the Blue Springs trachichthyid otoliths (many around 1–2 mm) certainly seem to indicate many juveniles. There are three species in two genera in the present Gulf of Mexico according to McEachran & Fechhelm (1998), and all species feed on crustaceans, such as small shrimp, and on small fish, which would have been readily available at the Blue Springs locality and the Owl Creek type locality during the Late Cretaceous.

The second most abundant form in the otolith assemblage from the bulk samples is *Paraulopus pseudoperca*, which comprised 25.34%. Recent representatives of the family Paraulopidae or cucumber fishes are found exclusively in marine environments, primarily in the Indian and Pacific oceans. They are mainly benthic and found in tropical and temperate environments (Nelson et al. 2016). Paraulopids are usually found in fairly deep water on the outer continental shelf to the upper continental slope, but some species of *Paraulopus*, such as *P. nigrippinis*, are commonly found in water depths as shallow as 50 m on sandy to muddy bottoms (McMillan et al. 2011). The paraulopids appear to have been much more widely distributed in the Mesozoic than today. There are no extant species known from the Gulf of Mexico or Caribbean.

The aulopiform *Apateodus crenellatus* represented the third most abundant form in the Blue Springs bulk samples (5.66%). *Apateodus* is one of the few extinct Late Cretaceous genera which has been found with otoliths in situ (Schwarzshans et al. 2018a). Fielitz & Shimada (2009) described a skeleton find from the early Campanian from the Niobrara Chalk of western Kansas, which is the closest in space and time. *Apateodus* was a slender, medium sized fish of c. 40 cm total length with elongate jaws and a slender head. Fielitz & Shimada (l.c.) concluded that it likely was a pelagic fish that was probably capable of fast swimming. From its dentition they deduced that they could have been feeding on small soft-bodied macro-invertebrates such as squids.

One representative from the family Pempheridae (*Pempheris? huddlestoni*) is the fourth most abundant species and constitutes 3.91% of the bulk sample specimens. The pempherids or sweepers are found in marine and brackish waters in the western Atlantic, Indian, and Pacific oceans (Nelson et al. 2016). Pempherids are found mainly in tropical to subtropical in shallow marine waters (less than 100 m) and are also common on coral reefs (Tominaga 1968; Mooi & Jubb 1996). Most remain hidden in structures, such as reefs or other protective areas, during the day and feed on crustaceans and polychaete worms at night. The sweepers, like modern ariids in the Gulf of Mexico, probably indicate marine waters generally no deeper than 100 m.

One of the three berycid taxa, *Eutawichthys zideki*, accounts for 3.23% and is the fifth most abundant species from the Blue Spring locality. This is a significant component of the assemblage. Unfortunately, it is not possible to relate *Eutawichthys zideki* (an otolith-based fossil genus and species) to a modern analogue, which inhibits its use in paleoecological determinations.

Despite the limitations, especially the age of the otolith assemblage, it is still possible to deduce some general paleoecological parameters utilizing the most abundant taxa as well as the other species. In summary, the fishes represented by otoliths in the Ripley Formation at the Blue Springs locality indicate a paleowater depth in the middle-shelf range (20–100 m). Most of the forms are exclusively marine and are found in tropical, subtropical, and warm temperate environments. There are several forms, such as the sea catfishes (ariids) and sweepers (pempherids), which are not normally found

at depths greater than 100 m. There is very little indication of very shallow or brackish waters. The preponderance of evidence suggested by the otoliths is that of a normal marine salinity. Conditions were most likely tropical and subtropical, but there are some suggestions of warm temperate. There are several taxa indicated by otoliths that may have preferred mud and clay bottoms, and forms such as the pempherids (sweepers) suggested the possibility of a reef or reef-like structures or conditions in the vicinity. Many of the fishes fed on various types of crustaceans and worms, and there is evidence of these food sources based on the invertebrate fauna at the locality.

The paleoenvironment suggested by the actinopterygians based on otoliths compares well with the paleogeography suggested by Smith et al. (1994), Sampson et al. (2010), and Blakey (2014). Furthermore, the bony fish agree quite well with the environment indicated by the various invertebrate fossil groups collected from the locality by one of the authors (GP). Earl Manning of Davenport, Iowa, examined a small collection of Blue Springs skeletal material consisting of sharks, rays, and bony fishes. Manning (pers. comm.) identified *Chiloscyllium greeni* (Cappetta, 1973), *Borodinopristis* cf. *schwimmeri* Case, 1987, *Hadrodus priscus* Leidi, 1857, *Enchodus petrosus* Cope, 1874, and *Paralbula casei* Estes, 1969. He believed that the Blue Springs skeletal remains indicated moderately deep, marine waters, perhaps 80 m (outer middle shelf). He further noted that there were no fluvial indicators, only one possible estuarine/inner shelf form, and that the bulk of the fauna is likely of moderately deep water. Therefore, numerous independent criteria also seem to corroborate the paleoenvironmental conditions indicated by the otoliths.

## COMPARISONS TO OTHER NORTH AMERICAN MESOZOIC TELEOSTEAN OTOLITH ASSEMBLAGES

Comparison of the Late Cretaceous Ripley Formation and Owl Creek Formation bony fishes indicated by otoliths to other North American Cretaceous otoliths provides data on distributional differences. However, the comparison is not really meaningful or relevant to some of the other reported North American Cretaceous otoliths. For exam-

ple, Frizzell (1965a) reported only one siluriform taxon from the Maastrichtian Fox Hills Sandstone of South Dakota, and Huddleston (1981) described a single otolith from the early Cenomanian Bernard Formation of Oregon. To reliably differentiate between otolith assemblages, it is recommended that the studies employ bulk sampling techniques, that there is similar preservation of specimens in the sediments, and that there are a substantial number of specimens and taxa for analysis. Based upon these criteria, there are a number of North American otolith assemblages available for comparison to the Ripley Formation and Owl Creek otoliths. These include the late Santonian Eutaw Formation of Alabama (Schwarzhans et al. 2018b), Campanian Coffee Sand of Mississippi (Nolf & Dockery 1990), early Campanian Tar Heel Formation of North Carolina (Stringer et al. 2018), early-middle Campanian Woodbury Formation of New Jersey (Stringer et al. 2016), the early Maastrichtian Coon Creek type locality of Tennessee (Nolf & Stringer 1996; Stringer 1999; Stringer 2016b), the early Maastrichtian Ripley Formation of Mississippi (Stringer 1991; Nolf & Stringer 1996), early-middle Maastrichtian Severn Formation of Maryland (Huddleston & Savoie 1983), the late Maastrichtian Fox Hills Formation of North Dakota (Hoganson et al. 2019), and the late Maastrichtian Kemp Clay of Texas (Woodward 2003).

#### Late Santonian Eutaw Formation of Alabama

Schwarzhans et al. (2018b) examined approximately 500 otoliths that were collected from the late Santonian Eutaw Formation in Alabama by C. K. Lamber in 1969. The exact weight of the bulk sample is not known, but preservation of the specimens is quite good. The Eutaw Formation otoliths represent the oldest assemblage of otoliths from North America. The assemblage consisted of 18 taxa as well as 8 different morphotypes based on lapilli. The assemblage is dominated by beryciforms such as *Eutawichthys* and albuliforms such as *Osmeroides*. In fact, the berycid *Eutawichthys stringeri* was noted as by far the most common species in the Eutaw Formation (Schwarzhans et al. 2018b). The Eutaw Formation assemblage is quite similar to Campanian and Maastrichtian assemblages previously described from the U.S., but there are notable differences in the abundance of taxa (e.g., the absence of trachichthyids).

The Ripley Formation assemblage has more species, perhaps related to the much larger number of specimens. One of the most obvious differences in the assemblages is the dominance of the trachichthyids and much smaller percentage of beryciforms in the Ripley Formation material. The beryciform *Eutawichthys stringeri*, which was the most abundant otolith in the Eutaw Formation, is not even represented in the Ripley Formation assemblage at the Blue Springs locality although other species of *Eutawichthys* are present. This significant contrast is most likely related to differences in the paleoenvironment, very likely water depth, or to evolutionary changes from the late Santonian to early Maastrichtian.

#### Campanian Coffee Sand of Mississippi

Nolf & Dockery (1990) processed over 3,000 kg of sediment from the early Campanian Coffee Sand, but the residue only produced 117 otoliths. Although the number of specimens was quite small compared to the Ripley Formation (3,718 otoliths), 20 taxa were identified from the Coffee Sand, which is quite substantial for such a small number of specimens but still much less diverse than the Ripley Formation. There were similar taxa, but there were also noticeable differences. The most significant variance in the assemblages is probably in the relative abundances of the taxa. Although Nolf & Dockery (1990) did not provide a table with the percentages, the number of specimens for different taxa was given in the “Systematics” section. The Coffee Sand assemblage was dominated by albuliforms (about 38% of total) and by paraulopids (about 27% of total), which were originally classified as synodontids by Nolf & Dockery (1990) and changed to paraulopids in Nolf (2013). Although the Ripley Formation assemblage shares a similar abundance of paraulopids with the Coffee Sand, there is a significant difference in the abundance of albuliforms. Albuliforms represented 38% of the total Coffee Sand specimens but constituted less than 6% of the Blue Springs otoliths. Nolf & Dockery interpreted the Coffee Sand as a shallow neritic environment (probably inner shelf), and it does not appear to have experienced much influence of fresh or brackish water. However, the Ripley Formation assemblage with its preponderance of trachichthyids probably indicated deeper marine conditions (middle shelf) and is significantly younger (evolutionary changes).

### Early Campanian Tar Heel Formation of North Carolina

Although not an especially large number of otoliths ( $n = 866$ ), Stringer et al. (2018) described 28 taxa (13 families) of fishes from two localities in the early Campanian Tar Heel Formation of North Carolina. The Albuliformes dominate the Tar Heel Formation assemblage both in the number of taxa (9) and the number of specimens (640 specimens, which is 73.9% of the total assemblage). The beryciforms are also well represented in the Tar Heel Formation otoliths in terms of taxa (3) and number of specimens (96 specimens or 11.09% of the total). Therefore, almost 85% of the Tar Heel Formation assemblage is represented by albuliforms and beryciforms. Paraulopids are entirely absent, and trachichthyids and ariids are very rare. The Tar Heel Formation otoliths indicate inner to middle neritic depths, but there are some species that may have ecological ranges that extend into brackish or fresh water.

Although the species and the total number of taxa in the Tar Heel Formation assemblage and the Ripley Formation assemblage are fairly similar, the percentages of taxa are in stark contrast to one another. The Ripley Formation otolith assemblage is dominated by trachichthyids, ariids, and paraulopids, which are all rare or absent in the Tar Heel Formation. These dramatic differences in the two assemblages may be related to several factors. The Ripley Formation otolith assemblage does appear to represent a deeper paleo-water depth and has very little indications of brackish or fresh water. The latitudinal difference in the two locations does not seem large enough to be significant. However, the age differences of the sites allows for evolutionary developments.

### Early-Middle Campanian Woodbury Formation of New Jersey

Stringer et al. (2016) reported on teleostean otoliths from the upper portion of the Woodbury Formation (early-middle Campanian) at the Stone Bridge locality in southern New Jersey. The number of otoliths obtained from the Woodbury Formation is unprecedented with 3,555 specimens, which represented the largest Cretaceous otolith assemblage ever described in North America prior to the current study and one of the largest ever reported worldwide. The Woodbury Formation with its early-middle Campanian age (approximately  $83.6 \pm 0.2$

Ma to  $77.9 \pm 0.2$  Ma) is significantly older than the Ripley Formation at the Blue Springs locality. Otoliths from the Stone Bridge locality indicated the presence of probably at least 29 teleostean taxa representing 14 families. Families included megalopids, albuliforms including pterothrissids, stomiiforms, paraulopids, trachichthyids, beryciforms, and several percomorphs, but specimens of beryciforms (e.g. *Eutawichthys* spp.) numerically dominated the assemblage (88.02% of the total specimens).

There are notable differences in the assemblages of the Stone Bridge locality and the Blue Springs locality. Two of the most significant are the percentage of trachichthyids (more than 37% at Blue Springs and 0.06% at Stone Bridge), and the percentage of beryciforms (less than 7% at Blue Springs and more than 88% at Stone Bridge). While the Stone Bridge Woodbury has albuliforms (nine taxa) and stomiiforms, it has no anguilliforms or siluriforms. The dissimilarity of the two localities may be related to paleoenvironmental differences (possibly paleo-water depth, specialized niches, and latitude) as well as evolutionary changes related to the age differences.

### Early Maastrichtian Coon Creek type locality of Tennessee

Nolf & Stringer (1996) reported only six taxa from the analysis of residue from the Coon Creek type locality and noted the site as rather sparse in otoliths. Additional bulk sampling by Stringer (1999) resulted in ten taxa representing eight families from the Coon Creek type locality, which is much less diverse than the Ripley Formation at the Blue Springs locality. Although the number of taxa at Coon Creek is much smaller, the taxa present there are essentially the same species found at the Blue Springs locality. The albuliforms, paraulopids, beryciforms, trachichthyids, and pempherids at the Coon Creek site appear to be the same species present in the Ripley Formation at the Blue Springs locality. The Coon Creek type locality has been interpreted as a neritic environment with little open ocean influence. The two localities are quite close geographically (southwestern Tennessee and northeast Mississippi), but the much greater diversity and difference in relative abundance of certain taxa at the Blue Springs locality are believed to indicate significant differences in the two localities with deeper, middle shelf conditions at Blue Springs.

### Early Maastrichtian Ripley Formation of Mississippi

The otoliths of this northeast Mississippi location (early Maastrichtian Ripley Formation) were first reported by Stringer (1991) and revised by Nolf & Stringer (1996). Bulk sampling produced 257 otoliths that represented 23 taxa. While the number of specimens is substantially smaller than the present study, the number of taxa is quite significant and similar. It should be noted that this locality (Bishop, 1983) was located just south of the present study and is from the same formation. Therefore, it is not unexpected that the otolith assemblages are very similar and strikingly alike. The three most abundant taxa of the Ripley Formation in the study by Nolf & Stringer (1996) were trachichthyids (37%), paraulopids (22%), and aulopiforms (4%, *Apateodus* otoliths were originally noted as gempylids). These three taxa are also the most abundant in the present study with almost identical percentages (37%, 25%, and 6% respectively based on the bulk sample results). Stringer (1991) originally proposed that the paleoenvironment for the Ripley locality was a marine shelf, possibly middle to outer shelf, with tropical to subtropical conditions, which is very similar to the middle shelf environment postulated for the present study. This is not unexpected with the close geographical proximity of the sites. While every taxa reported from the Ripley locality by Nolf & Stringer (1996) are found in the current study, the otolith assemblage of this study contains many additional taxa.

### Early-middle Maastrichtian Severn Formation of Maryland

Huddleston & Savoie (1983) analyzed 1086 otoliths from the early-middle Maastrichtian Severn Formation (LACM Locality 4425) in Maryland and identified at least 14 taxa representing 8 families. It should be noted that a majority of the taxa were identified only to the family level. Although there are some similar taxa in the assemblages of the Severn and Blue Springs Site, there are pronounced and significant differences between the two faunas. The Blue Springs fauna is much more diverse in the number of taxa (35). The Severn otoliths are dominated by one siluriform species, *Vorbisia vulpes*, which comprised almost 55% of the total specimens. Including the family Ariidae, siluriforms accounted for over 62% of the spec-

imens. Two beryciforms (*Eutawichthys* spp., originally identified as apogonids) comprised slightly over 27% of the total for the Severn otoliths. This is in stark contrast to the Ripley Formation assemblage at the Blue Springs locality (bulk samples), which is dominated by *Hoplopteryx oscitans* (37%), *Paraulopus* sp. (26%), and *Apateodus crenellatus* (6%). The latter two taxa, which comprise over 32% of the Blue Springs assemblage, are not even present in LACM Locality 4425. The marked differences in the assemblages are believed to be related to paleoenvironmental conditions, primarily water depth. The Severn assemblage is interpreted as occurring in a very shallow marine environment (inner shelf, 0–20 m) with brackish water influences, whereas the Ripley Formation at the Blue Springs locality represents a deeper marine environment (middle shelf, 20–100 m) with little brackish or freshwater influences.

### Late Maastrichtian Fox Hills Formation of North Dakota

Hoganson et al. (2019) conducted an in-depth study and analysis of the chondrichthyan and osteichthyan faunas of the late Maastrichtian Fox Hills Formation of North Dakota. The study included 48 sites in the Fox Hills Formation in western and central North Dakota. While the study concentrated primarily on skeletal remains (52 of the 56 described taxa), four species based on 266 otoliths were identified. The otolith-based taxa were *Pollerspoeckia siegsdorfensis* (4 specimens), *Vorbisia vulpes* (78 specimens), cf. *Bathylagus* sp. (176 specimens; identification problematical but cannot be evaluated based on the published figures), and *Eutawichthys maastrichtiensis*, which was reported as “*Apogonidarum*” *maastrichtiensis* (8 specimens). The Fox Hill Formation has a wide variety of paleoenvironments including deep and shallow marine, brackish water, and fresh water. Although 266 otolith specimens were recovered, the diversity is very low with only 4 taxa, while the Ripley and Owl Creek formations have much greater diversity. It is important to note that two of Fox Hills otolith taxa (*Pollerspoeckia siegsdorfensis* and cf. *Bathylagus* sp.) were collected at the same locality, but the other two taxa (*Vorbisia vulpes* and *Eutawichthys maastrichtiensis*) were collected at different and separate localities. Two species from the Fox Hills Formation are also found in the Ripley and

Owl Creek formations, and these are *Vorbisia vulpes* and *Eutawichthys maastrichtiensis*. Since the Fox Hills Formation has a wide range of habitats and the otoliths came from different sites, it is difficult to make any further comparisons with the Ripley and Owl Creek formations.

#### Late Maastrichtian Kemp Clay of Texas

Stringer (1998b and 1998c) conducted preliminary studies on the otoliths of the Maastrichtian Kemp Clay while Woodward (2003; unpublished MS thesis) completed the most extensive work to date on the Kemp Clay otoliths. Woodward reported 27 taxa representing 15 families based on 1,202 specimens, which represents a very diverse assemblage. There are some similarities in the taxa of the bony fish assemblages of the Kemp Clay and the Ripley Formation at the Blue Springs locality, but the differences are notable and meaningful. While the most abundant taxon in the Ripley Formation at the Blue Springs locality is *Hoplopteryx oscitans* at approximately 37%, this species is totally absent from the Kemp Clay. Another trachichthyid is present in the Kemp Clay, but it is not nearly as abundant comprising less than 5% of the total specimens. An ophidiid, *Ampheristus* sp., that is present in the Kemp Clay is completely absent from the Ripley Formation at the Blue Springs locality. Furthermore, the ophidiid *Ampheristus* sp. makes up almost 11% of the Kemp Clay otoliths. Other taxa listed by Woodward (2003) from the Kemp Clay and missing from the Ripley Formation at Blue Springs include *Albula* cf. *campaniana*, Heterenchelyidae indeterminate, *Genartina* sp., aff. *Dinematichthys* sp., Merlucciidae indeterminate, Gadidae indeterminate, and aff. *Centroberyx* sp. The relative abundances of taxa vary greatly between the Kemp Clay and the Ripley Formation at the Blue Springs locality. The paraulopids, which are very abundant at Blue Springs and comprise over 25% of the total specimens, represent less than 1% of the Kemp Clay otolith specimens. Siluriforms comprise less than 3% of the total specimens at Blue Springs but account for almost 57% of the Kemp Clay bony fishes. Some of the differences in taxa and relative abundances between the two assemblages may be attributed to paleoenvironmental parameters. More detailed investigations of the Kemp Clay otoliths will be necessary to ascertain more definitive reasons for the conspicuous differences in the two assemblages.

#### CONCLUSIONS

The Ripley and Owl Creek formations from two localities in northeast Mississippi, USA, have produced the most highly diversified actinopterygian and largest otolith assemblage described from the Mesozoic of North America. The 3,802 otoliths represent 30 taxa of bony fishes from at least 22 families as well as two different morphological types of lapilli. The large number of otolith specimens as well as the preservation contributed to the recognition of 4 new otolith-based genera and 13 new species.

The Ripley and Owl Creek formation otoliths point to significant evolutionary developments in the Late Cretaceous bony fishes. This includes highly specialized otolith morphologies which document a high level of diversity already during the Late Cretaceous. Some of these are here recorded for the first time and are distinctly spectacular, e.g., *Ossulcus* and *Tippaba*. Many of these highly specialized morphotypes apparently became extinct with the K-Pg boundary crisis and therefore cannot be related to persistent extant teleost lineages. We interpret certain morphologies to represent extinct Beryciformes, especially in genera such as *Eutawichthys* and *Ossulcus*. The spectacular pattern of the genus *Tippaba* is interpreted to represent an extinct holocentriform. The early development of the homosulcoid sulcus pattern is indicated by *Choctawichthys cepoloides*, which is known primarily in the superorder Paracanthopterygii. Other specializations and diversifications are reflected in the species-rich genera *Cowetaichthys* in the Polymixiidae; early, but very limited, indications of the Perciformes in taxon such as *Pempheris? huddlestoni*; and the acquisition of morphological features more similar to modern forms in the trachichthyids (prominent, deeply incised dorsal margins). Many of the specialized extinct otolith morphologies will only be conclusively allocated in the systematics once their otolith have been found in situ, like this has for instance been the case for *Apateodus* or *Hoplopteryx*.

The Ripley Formation otoliths also provided general paleoenvironmental data including a paleowater depth in the middle-shelf range (20-100 m) with little indication of very shallow or brackish waters, primarily marine taxa found in tropical, subtropical, and warm temperate settings with most likely normal marine salinity. The Ripley and Owl

Creek otolith assemblages were compared and contrasted with nine other Late Cretaceous (Santonian to late Maastrichtian) otolith assemblages from eight U.S. states. There were some remarkable similarities as well as notable dissimilarities in the assemblages, which were believed to be related to paleoenvironmental differences as well as evolutionary developments. The authors believe that this study clearly indicates the potential for more Cretaceous otolith assemblages with diverse faunas of bony fishes in the USA, especially in the Gulf and Atlantic coastal plains.

*Acknowledgments:* M. Lambert collected at the Blue Springs locality on numerous occasions and furnished a large number of otoliths. R. Langford of the North Mississippi Gem and Mineral Society provided specimens from his extensive bulk sampling of the Blue Springs locality and donated specimens to be figured for this study. N. Roberts, also of the North Mississippi Gem and Mineral Society, provided surface-collected specimens and donated specimens to be used in figures. J. C. Sloan, geologist with the Arkansas Department of Transportation, supplied specimens from the site. J. Ebersole, Director of Collections at the McWane Science Center, Birmingham, Alabama, arranged for loans of specimens collected by P. Atkinson and J. Baldwin from the Blue Springs locality. We thank the Mississippi Museum of Natural Science in Jackson, Mississippi, for its assistance, especially J. Rushing who extracted otoliths from residue. K. A. Johnson (National Marine Fisheries Service, Southeast Fisheries Science Center), J. Tunnell (Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute), R. Taylor (formerly of the Florida Fish and Wildlife Conservation Commission), and J. R. Hendon (Center for Fisheries Research and Development, Gulf Coast Research Laboratory, University of Southern Mississippi) generously provided Recent fishes and otoliths from the Gulf of Mexico. The localities' landowners, J. Young and S. Coffey, allowed researchers access for collecting. D. Stringer assisted the senior author with field work (bulk sampling, surface collecting, and photography) at the Blue Springs locality on several trips. P. Kuchirka, J. Rushing, R. Horne, and C. Baird assisted with measuring sections at the site. D. Nolf of the Institut Royal des Sciences Naturelles de Belgique in Brussels, Belgium, supplied Recent and fossil otolith specimens. E. Manning of Davenport, Iowa, identified skeletal remains of bony fishes. The two anonymous reviewers are thanked for their constructive reviews of the manuscript.

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