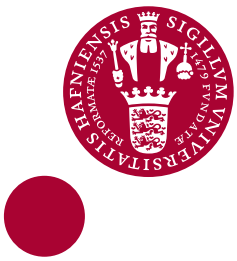

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A LATE SANTONIAN FISH-FAUNA FROM THE EUTAW FORMATION OF ALABAMA RECONSTRUCTED FROM OTOLITHS

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Keywords: Late Cretaceous, Albuliformes, Stomiiformes, Beryciformes, USA.

Abstract. The otoliths described here from the Late Santonian of the Eutaw Formation of Alabama, represent one of the earliest association of teleost otoliths known from North America and it is remarkable for its good preservation and species diversity. They were collected by the late C.K. Lamber in 1969 from a road cut on the Hurtsboro-Marvyn highway south of Marvyn in Russell County, eastern Alabama. It contains 18 taxa based on sagittae otoliths, of which 14 are identifiable to the species level, 10 species are new to science and five new genera. The new otolith-based genera are: *Allogenartina* n. gen. (Stomiiformes family indet.), *Pseudotrichiurus* n. gen. (Aulopiformes family indet.), *Eutawichthys* n. gen. (Beryciformes family indet.), *Cowetaichthys* n. gen. (Polymixiidae) and *Vox* n. gen. (Teleostei family indet.); the new species are: *Elops eutawanus* n. sp., *Genartina cretacea* n. sp., *Allogenartina muscogeei* n. sp., *Pseudotrichiurus sagax* n. sp., *Apateodus? assisi* n. sp., *Eutawichthys compressus* n. sp., *Eutawichthys stringeri* n. sp., *Cowetaichthys alabamae* n. sp., *Cowetaichthys lamberi* n. sp. and *Vox thlotlo* n. sp. In addition, 8 different morphologies are recognized based on lapilli otoliths, which however cannot be identified to a distinct taxonomic level except for a species of the Ariidae. Two taxa can be related to otoliths recently recorded in situ, pertaining to the genera *Osmeroides* and *Apateodus*.

The otolith association bears much similarity with those of the Campanian to Maastrichtian of the USA described previously as indicated by the dominance of otoliths of the genera *Eutawichthys* and *Osmeroides*. Differences with those faunas are on the species level as well as in the accessory components. The abundance of otoliths of the albuliforms (*Osmeroides*), putative stomiiforms (*Allogenartina*), beryciform (*Eutawichthys*) and polymixiids (*Cowetaichthys*) characterizes a rather stable faunal composition through the entire Late Cretaceous of locations studied in the USA.

The conundrum of interpreting the systematic position of isolated Late Cretaceous otoliths is discussed and the findings are correlated with the rich fish fauna known from articulated skeletons of the coeval Niobrara Formation. We consider the taxonomic position of the majority of isolated otoliths to be more or less consistent with the skeletal findings, but there are also a few otolith morphologies, which do not seem to have a skeletal equivalent in the Niobrara Formation, e.g. in osteoglossiforms, clupeiforms, stomiiforms and Ariidae.

Introduction

Fossil otoliths are commonly recorded from Cenozoic strata, where they represent a well established means to reconstruct fossil teleost fish faunas (Nolf 2013). Since otoliths are composed of metastable aragonite, their fossil record becomes increasingly sparse with stratigraphic age. Only a handful of sizeable otolith associations have so far been described from Late Cretaceous rocks (Huddleston & Savoie 1983; Liebus 1927; Nolf 2003, 2016; Nolf & Dockery 1990; Nolf & Stringer 1996; Schwarzhans 2010; Stringer et al. 2016; Voigt 1926). Four of these publications dealt with Late Cretaceous otoliths from North America (Huddleston & Savoie 1983; Nolf & Dockery 1990; Nolf & Stringer 1996; Stringer et al. 2016). With this comparatively scarce record, every new otolith association discovered in Late Cretaceous sediments is likely to contribute a substantial gain in knowledge. The Santonian assemblage described here contains 14 identifiable taxa, 10 of which are new. It also represents the earliest substantial otolith assemblage known from the USA.

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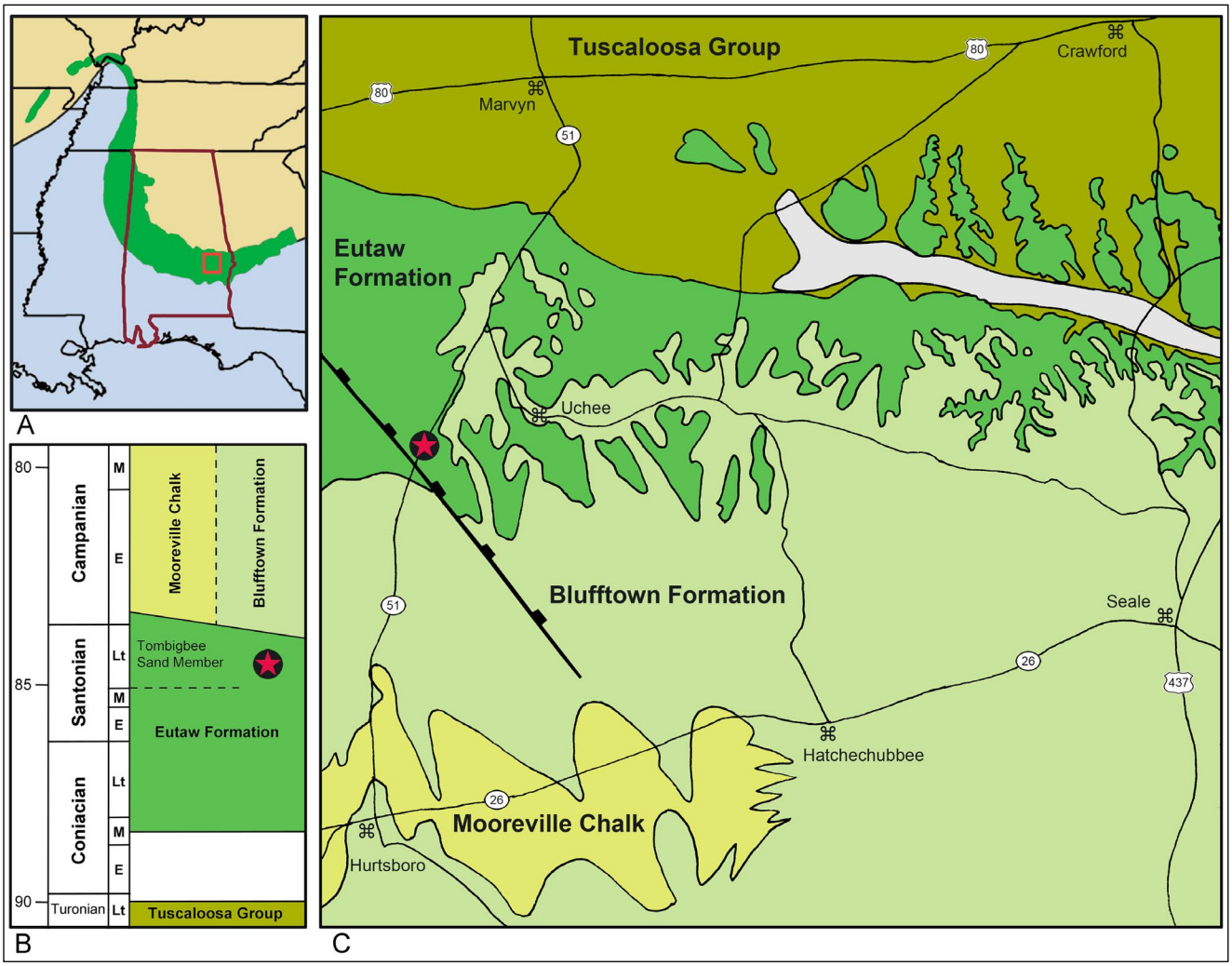

Fig. 1 - Location and generalized stratigraphy. A, index map with state of Alabama and detailed location area highlighted overprinted on Late Cretaceous paleogeographic map (after Ikejiri et al., 2013), blue = marine, light tan = land, green = Late Cretaceous outcrops. B, generalized stratigraphy after Mancini & Puckett (2005), chronostratigraphy after Gradstein et al. (2012), star marks approximate stratigraphic position of sampled interval. C, geological map part of Russell County, Alabama, after Scott (1962), star marks outcrop location at road cut of Alabama highway 51, color-coding consistent with generalized stratigraphy. Map not to scale; northing vertically up.

Location and geological setting

The otolith material was collected by C.K. Lamber on August 21st 1969 south of Marvyn, Alabama. The label that accompany the otoliths read "Eutaw Fm (late Santonian stage?), Road cut eastside of Alabama Hwy 37, 7.8 miles south of Marvyn from junction with Hwy 80." Highway 37 was replaced in 1995 when Highway 51 was extended northward from Hurtsboro to Marvyn. Although more precise stratigraphic placement is not possible, examination of the geological map for Russell County, Alabama shows the entire exposure of the nearby road cut is mapped as the Eutaw Formation (Scott 1962).

The Upper Cretaceous Eutaw Formation (Santonian) crops out in the eastern Gulf coastal plain in an arcute belt that extends through northeast Mississippi, across Alabama, into western Georgia (see Mancini & Soens 1994). In eastern Alabama, the Eutaw lies disconformably above fluvial deposits of the Cenomanian to Turonian Tuscaloosa Formation and below the marginal marine deposits of the Blufftown Formation (Reinhart et al. 1994). The upper contact of the Eutaw with the overlying Blufftown Formation is not well defined and forms a gradational transition from carbonate to clastic sediment deposition. The Eutaw Formation is 30-45 m thick and is undifferentiated (Reinhardt & Donovan 1986). The middle and upper parts of the Eutaw Formation consists chiefly of gray sand calcareous fossilerous clay interbedded with thin indurated beds of fossilerous and, in the outcrop, are locally referred to as

"shell reefs" or "oyster banks" (Scott 1962; Smith 2001). Further to the west the upper Eutaw Formation is referred to as the Tombigbee Sand Member (Mancini & Puckett 2005). This is consistent with the detailed descriptions of outcrops of the Eutaw Formation as described by Stephenson (1956) and located in direct vicinity of the location sampled by Lamber. Stephenson described two road cut sections along the same Hurtsboro-Marvyn highway close to Utchee mentioning 'dark grey sands containing many shell fragments, particularly in the upper half'. He mentioned sampling from the Eutaw Formation to be made from the *Ostrea cretacea* Biozone, which he stated as typical for the upper Eutaw Tombigbee Sand Member (p. 239).

The Eutaw Formation is heterolithic, reflecting deposition in various shallow and marginal marine settings (Eargle 1955; Frazier 1987, 1997; Frazier & Taylor 1980; King 1990, 1993; Savrda & Nanson 2003; Stephenson 1956). In Eastern Alabama it is attributed to deposition in estuarine settings variably influenced by tides and storms (Frazier 1996, 1997) and its position above the Tuscaloosa Formation indicates marine transgression.

Material and methods

The otolith-material described here was obtained from sediment samples that were collected by C.K. Lamber and were not studied. This collection passed on to the late John E. Fitch sometime in the mid-1970's and was incorporated into his large collection of Recent and fossil otoliths. Unfortunately, Fitch never formally described the otolith from the Eutaw Formation before his untimely death in 1982. His entire collection of Recent and fossil otolith, including notes, correspondence, and library were donated to the Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM) and are housed in the Department of Ichthyology. They were located by WS during a visit in 2015.

It is not known, how much rock was processed in order to extract the large amount of about 500 otoliths studied, nor how this was achieved. The generally good preservation of the specimens, however, speaks for a careful operation.

All otoliths are deposited in the collection of the Department of Ichthyology, (LACM), under the collection registration LACM 58469-1 to 58469-46.

The terminology for the morphological description of the sagittal otoliths follows Koken (1891), Weiler (1942) and Schwarzhans (1978). The following abbreviations are used in morphometric measurements: otolith length = OL; otolith height = OH; otolith thickness = OT; ostium length = OsL; ostial colliculum length = OCL; cauda length = CaL; caudal colliculum length = CCL; sulcus length = SuL. The terminology of the morphological description of the utricular (lapilli) otoliths follows Assis (2005).

All otoliths are shown as if from the right side in order to facilitate easier comparison. Left otoliths are mirror imaged and annotated accordingly in the figure captions.

Systematic paleontology

Remarks. Fossil skeletons of teleost fishes from the Late Cretaceous contain many taxa belonging to families and higher systematic levels that are extinct or which represent stem groups of modern systematic units, and only a limited amount of taxa is continuously connected to living groups in a more direct manner. The identification of otoliths is almost entirely dependent on comparison with extant specimens for systematic allocation, when not calibrated by finds of fossil skeletons with otoliths in situ. The latter is rare and only very recently have otoliths in situ been recorded from Cretaceous fishes (Schwarzhans, Beckett, Schein & Friedman 2018, in press). For these reasons, otolith research in the (Late) Cretaceous has the dilemma that only few morphotypes can be convincingly attributed to extent groups while most represent morphologies, which are difficult to relate. In many instances even the attribution to a suborder or order is uncertain, as is also reflected in the following systematic part. On the other hand the otolith morphologies in question are often highly specific, with a certain degree of advanced features that do allow a reliable taxonomic definition. In such a situation, we consider that defining and describing of fossil otolith-based genera for those distinct morphologies serves the purpose of taxonomic handling and citing best. Of course we hope that further Cretaceous fishes with otoliths in situ will be identified in the future, which will allow a better allocation of these formal taxa, and we are aware of the risk that can ultimately lead to a fusion of otolith and skeleton based names in certain taxa.

The following descriptive part is arranged in two distinct parts. The first part contains identifications and descriptions of sagittal otoliths, the ones usually studied in the fossil record. The second part covers utricular (lapilli) otoliths, which except for an ariid species cannot be identified to any meaningful systematic level at this stage. For optimal comparison purposes, all figures show otoliths from the right side. Photos of left otoliths have been mirror imaged and are marked as 'reversed'.

The classification of the systematic part follows Nelson, Grande & Wilson (2016).

Sagittae otoliths

Class **OSTEICHTHYES** Huxley, 1880
Subclass **ACTINOPTERYGII** Klein, 1885
Division **Teleostei** Müller, 1846
Order **Osteoglossiformes** Regan, 1909
Family indet.
Genus *Kokenichthys* Schwarzhans, 2010

Kokenichthys ensis (Nolf & Dockery, 1990)

Fig. 2A-C

1983 Albuloidei - Huddleston & Savoie: fig. 1F-G
1990 "genus ?Albulidarum" *ensis* Nolf & Dockery - pl. 4, fig. 7
1996 "genus ?Albulidarum" *ensis* Nolf & Dockery, 1990 - Nolf & Stringer: pl. 1, fig. 5
2010a *Kokenichthys ensis* (Nolf & Dockery, 1990) - Schwarzhans: figs. 1-2
2013 "? *Albulida" ensis* Nolf & Dockery, 1990 - Nolf: pl. 13
2016 *Kokenichthys ensis* (Nolf & Dockery, 1990) - Stringer, Oman & Badger: pl. 1, fig. 5

Material: 5 specimens from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM., LACM 58469-1.

Discussion. Otoliths of *Kokenichthys ensis* are very peculiar in their blade-like appearance and the morphology of the inner face that carries a wide, shallow sulcus covering almost the entire upper half of the inner face but depicting very feeble, often indistinct sulcus margins. The outer face is flat and the inner face mildly convex. The wide sulcus is completely in level with the reminder of the inner face and basically unstructured. It opens broadly anterior-dorsally, while further back a very narrow rim remains between sulcus and dorsal rim of the otolith. The short portion located behind the sulcus on the inner face is sometimes slightly elevated.

We do not know of any Recent fishes with only moderately similar otoliths. *Kokenichthys* has been associated with Albuliformes or Osteoglossiformes (as is the case here), but both designations must be considered speculative and tentative, and it is as much possible that these otoliths represent an extinct group of fishes from which otoliths obviously are not yet know.

Order **Elopiformes** Jordan, 1923
Family Elopidae Bonaparte, 1832
Genus *Elops* Linnaeus, 1766

Elops eutawanus n. sp.

Fig. 2D-G

Etymology: Referring to the Eutaw Formation, Late Santonian of Alabama, from which the otoliths have been obtained.

Holotype: LACM 58469-2 (Fig. 2D-G); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Diagnosis: Inner face slightly convex, markedly twisted along the long axis. Outline regularly oval. Dorsal rim with very slightly expanded middorsal section. Ostium incomplete, short, wider than cauda. Cauda very slightly bent and inclined backwards. Outer face intensely ornamented with numerous short, radial, delicate furrows.

Description. The unique holotype is well preserved except for the missing rostral tip. Otolith elongate, with nearly oval shape, 4 mm long. Dorsal rim with broad, only slightly expanded and rounded middorsal region, followed by a short, slightly depressed postdorsal region and then a regularly curved posterior region. Ventral rim very regularly curved. Anterior rostral tip probably short judging from fracture face; very short and backward positioned antirostrum and small excisura. Posterior tip tapering, rounded, positioned at level with caudal tip.

Inner face slightly convex, twisted along long axis with anterior portion curved upwards and outwards and posterior portion downwards and outwards (best seen in figure 2F). Sulcus moderately deep, with (presumably) short and moderately wide ostium and long, very slightly end gently bent and downward inclined cauda. Short dorsal margin of ostium curved upwards. Caudal tip rounded, terminating close to posterior tip of otolith. Very shallow and indistinct dorsal depression; no ventral furrow. Outer face flat, with many short, delicate radial furrows along the ventral and posterior margins and some irregular undulations along the middorsal margin.

Discussion. The shape of the sulcus with the short dorsal margin of the ostium being curved upwards and the slightly bent and inclined cauda, and the outline of the otolith resemble well otoliths of extant species of *Elops* as depicted by Schwarzhans (1986) and Nolf (2013). The most closely resembling species is *Elops ramaekersi* Schwarzhans, 1986 from the Paleocene / Lower Eocene of Ellesmere, Canada. *Elops eutawanus* differs in the very shallower middorsal expansion (vs strong postdorsal expansion) and the slight bending of the cauda.

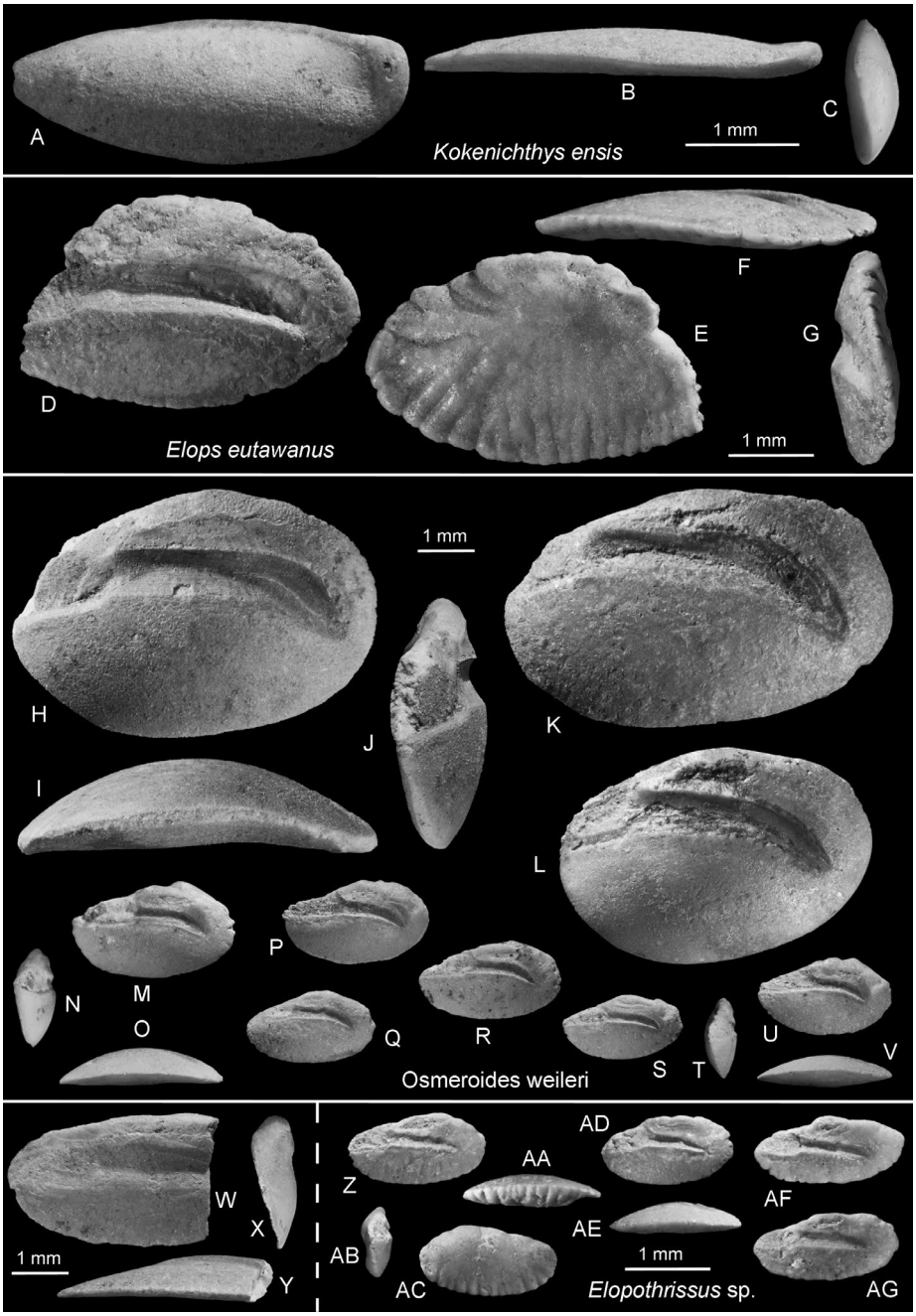

Fig. 2 - A-C) *Kokenichthys ensis* (Nolf & Dockery, 1990), LACM 58469-1, reversed, A inner face, B ventral view, C anterior view; D-G) *Elops eutawanus* n. sp., holotype, LACM 58469-2, reversed, D inner face, E outer face, F ventral view, G posterior view; H-V) *Osmeroides weileri* (Frizzell, 1965), LACM 58469-3 (M-O, R-S reversed); H, K, L, M, P, Q, R, S, U inner faces, I, O, V ventral views, J, N, T anterior views; W-AG) *Elopothrissus* sp., LACM 58469-4 (W-Y, AD-AE reversed), W, Z, AD, AF, AG inner faces, AC outer face, Y, AA, AE ventral views, X, AB anterior views.

Stringer et al. (2016) figured a slightly smaller otolith from the Campanian of New Jersey as Megalopidae indet. This otolith is distinctly more compressed than *Elops eutawanus*.

Order **Albuliformes** Jordan, 1923
Suborder **Albuloidei** Jordan, 1923
Family Osmeroididae Forey, 1973
Genus *Osmeroides* Agassiz, 1837

syn. *Prealbula* Frizzell, 1965 (type-species: *Prealbula weileri* Frizzell, 1965) [otolith-based genus and species]
syn. *Archaealbula* Frizzell, 1965 (type-species: *Archaealbula alabamae* Frizzell, 1965) [otolith-based genus and species]

Osmeroides weileri (Frizzell, 1965)

Figs 2H-V

1965 *Praealbula weileri* Frizzell - pl. 4, fig. 1
1996 "genus Albulidarum" *weileri* Frizzell, 1965 - Nolf & Stringer: pl. 1, fig. 7

Material: 19 large and many juvenile and fragmented specimens from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, LACM 58469-3. Frizzell's holotype (LACM 33735-1) was inspected, but not refigured.

Description. Otoliths growing up to at least 7 mm length (largest figured specimen, Fig. 1K, is 6.9 mm long). OL:OH = 1.45-1.65 in specimens larger than 4 mm length, 1.65-1.80 in specimens

smaller than 4 mm length; OH:OT = 2.3-2.7, decreasing with size. Otolith shape elongate, oval. Anterior and posterior rims broadly rounded. Dorsal rim shallow, regularly curved, somewhat undulating in small specimens, with broad postdorsal angle in large specimens. Ventral rim very regularly curved, smooth, deeper in larger specimens.

Inner face distinctly convex. Sulcus way supramedian positioned with ostium opening on anterior-dorsal rim. CaL:OsL = 1.4-2.0, decreasing with size. Ostium narrow, dorsally more widened than ventrally, shallow. Cauda narrow, deeper than ostium, slightly bent, inclined at about 10-15° against ostium, terminating moderately close to posterior rim of otolith. Dorsal depression narrow, very indistinct. Ventral field smooth without ventral furrow. Outer face slightly concave in large specimens, flat to slightly convex in small specimens, smooth.

Ontogeny. *Osmeroides weileri* exhibits a rather distinct allometric ontogenetic growth as can be seen when comparing specimens between 5.5 and 7 mm length (Figs 1H-L) with those between 3 and 2 mm length (Figs 1M-V). Few intermediate specimens found were too poorly preserved for figuring. The smaller specimens differ from the larger ones in being more elongate, mostly caused by the rather shallow ventral rim, and the dorsal rim being slightly undulating and highest at its middle without a clear postdorsal angle. They also show a somewhat more protruding rostrum and therewith longer ostium, which is expressed in a smaller ratio CaL:OsL. If found in isolation and not linked through an ontogenetic sequence, they could easily be understood as representing two different species.

Discussion. Frizzell described the species based on the holotype of 6.9 mm length and 9 juvenile paratypes of 2.4 to 2.8 mm length which were not figured, all from the Eutaw FM of Alabama like our specimens and probably from a location very close by. They were collected by N.F. Sohl on April 14th, 1958 on the Marvyn-Hurtsboro road, 8.1 miles south of Marvyn, whereas Lamber's location was 7.8 miles south of Marvyn. References by Nolf & Stringer were to the same specimens as described by Frizzell. Frizzell's holotype was damaged anterior-dorsally, but otherwise perfectly resembles our specimens. His list of measurements suggests a similar degree of allometric ontogenetic growth.

Similar otoliths that can be attributed to *Osmeroides* are common in the Late Cretaceous and Paleocene of North America (Schwarzhans et al. 2018 in press), i.e. *Osmeroides griffini* (Nolf & Dockery, 1990) and *O. campanianus* (Nolf & Dockery, 1996), both from the Campanian and *O. alabamae* (Frizzell, 1965) from the Paleocene. Also an otolith figured as Pterothrissidae indet. by Stringer et al. (2016, pl. 1, fig. 8) could in fact represent a further representative of the genus *Osmeroides* judging from its mildly bent cauda.

Family Pterothrissidae Gill, 1893
Genus *Elopothrissus* Schwarzhans, 1981

Remark. *Elopothrissus* is a fossil otolith-based genus established with *Pterothrissus protensus* Stinton, 1973 from the Eocene of England as type species, characterized by very elongate otoliths with a pterothrissid pattern.

Elopothrissus sp.

Figs 2W-AG

Material: 27 small, juvenile specimens and two fragments of large specimens from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, LACM 58469-4.

Discussion. Most specimens studied are small, in the range of 1.5-1.75 mm length and represent truly juvenile specimens. The largest specimen is an anterior half of about 3.6 mm length probably representing a specimen well in the range 5 to 5.5 mm length (Fig. 1W). The small specimens resemble small specimens of *Osmeroides weileri* in many aspects of their outline and sulcus morphology, but are slightly more elongate (OL:OH = 1.9-2.2 vs 1.65-1.8), show a completely straight cauda and a rugged ornamentation on the ventral margin of the inner and outer face, which is typical for small pterothrissid otoliths. The large specimen indicates a possibly antithetic allometric ontogenetic growth in becoming even more elongate, not more compressed as in *Osmeroides weileri*. These otoliths represent an undescribed species, but formal taxonomic action should wait for well preserved adult specimens. A similar small otolith has been figured as *Pterothrissus* sp. 2 by Stringer et al. (2016, pl. 1, fig. 2).

Order **Anguilliformes** Regan, 1909
Suborder **Congroidei** Nelson, 1984
Family and Genus indet.

Anguilliform indet.
Fig. 2A-C

Material: One small, juvenile specimen from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Eutaw FM, LACM 58469-5.

Discussion. The single, very small specimen is only 1 mm long. It shows a triangular outline with a mediodorsal angle, a median and somewhat pointed anterior tip and a ventrally shifted and rounded posterior tip. The oval, elongate, shallow and undivided sulcus does not clearly open anteriorly. We interpret this small, probably juvenile otolith as an anguilliform representative of unknown affinities.

Order **Clupeiformes** Bleeker, 1859
Family and Genus indet.

Clupeiform indet.
Fig. 3D-L

Material: 13 specimens, LACM 58469-6 to 58469-8; from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. The rostrum is missing in all specimens available and thus preventing formal establishment of a new species, but the remainder is well enough preserved to allow allocation with the Clupeiformes. The otoliths are small, rarely exceeding 1 mm in length (without rostrum reconstruction), fragile, thin and flat (OH:OT = 3.5-4.25). The dorsal rim shows a broad, obtuse mediodorsal angle. The ventral rim is regularly curved posteriorly, and anteriorly with a marked indentation at the beginning of the (broken) rostrum. The antirostrum is moderately sharp and long; the excisura is deep and sharp. The posterior tip of the otolith is blunt.

The inner face is flat, with the sulcus positioned along the central axis. The sulcus is anteriorly open, with a slightly widened and deepened (incomplete) ostium and a narrow, less deep, tapering cauda terminating at moderate distance from the posterior tip of the otolith. The dorsal field is marked with a narrow depression ventrally bound by a distinct crista superior above the anterior part of the cauda. The ventral field exhibits no ventral furrow but a distinct narrow depression below the entire length of the cauda and marked by a sharp crista inferior.

Discussion. These otoliths strikingly resemble typical extant clupeid otoliths in the delicate morphology with the ostium only slightly wider than the cauda, a distinct rostrum (incomplete), antirostrum and excisura, the distinct crista inferior and the indentation of the ventral rim of the otolith at the beginning of the rostrum. The main distinguishing character from all known Recent clupeid otoliths is the rather shallow and narrow cauda, but apart from this character the otolith conveys a surprisingly modern morphological pattern. Unfortunately, none of the specimens is preserved well enough for formally describing a new species and genus, which undoubtedly would have to be expected once better preserved specimens become available.

Order **Stomiiformes** Regan, 1909
Suborder **Gonostomatoidei** Weitzman, 1974
Family indet.
Genus *Allogenartina* n. gen.
Type species: *Allogenartina muscogeei* n. sp.

Etymology: A composition of allos (Greek) = strange and the genus name *Genartina* symbolizing the enigmatic nature of this otolith morphology.

Diagnosis: A fossil otolith-based genus of unknown familial relationships of the order Stomiiformes. Otoliths very compressed (OL:OH = 0.85-1.05) with high dorsal and deep, regularly curved ventral rim. Otoliths rather thin (OH:OT = 4.0-4.5) with flat inner face. Rostrum short, broad, spatulate; no antirostrum or excisura. Posterior rim blunt. Sulcus straight, horizontal, positioned along horizontal axis of otoliths. Ostium short, widened, extending onto rostrum, its colliculum not reaching the anterior rim. Cauda narrow, terminating close to posterior rim of otolith. CaL:OsL = 1.3-1.7.

Comparison and discussion. *Allogenartina* resembles certain Paleocene otolith-based putative gonostomiatid genera such as *Progonostoma* Schwarzhans, 2012 and particularly *Cyclogonostoma* Schwarzhans, 2012. It differs from *Progonostoma* in the very compressed shape (OL:OH = 0.85-1.05 vs 1.25-1.5), which is accentuated by the high, blunt posterior rim and the short and spatulate rostrum, and the wider ostium. *Cyclogonostoma* is nearly as compressed (OL:OH = 1.1.-1.15), which however is caused by a very short, minute rostrum and has a very short ostium (CaL:OsL = 2.2-2.7 vs 1.3-1.7). Similar otoliths are also found in the

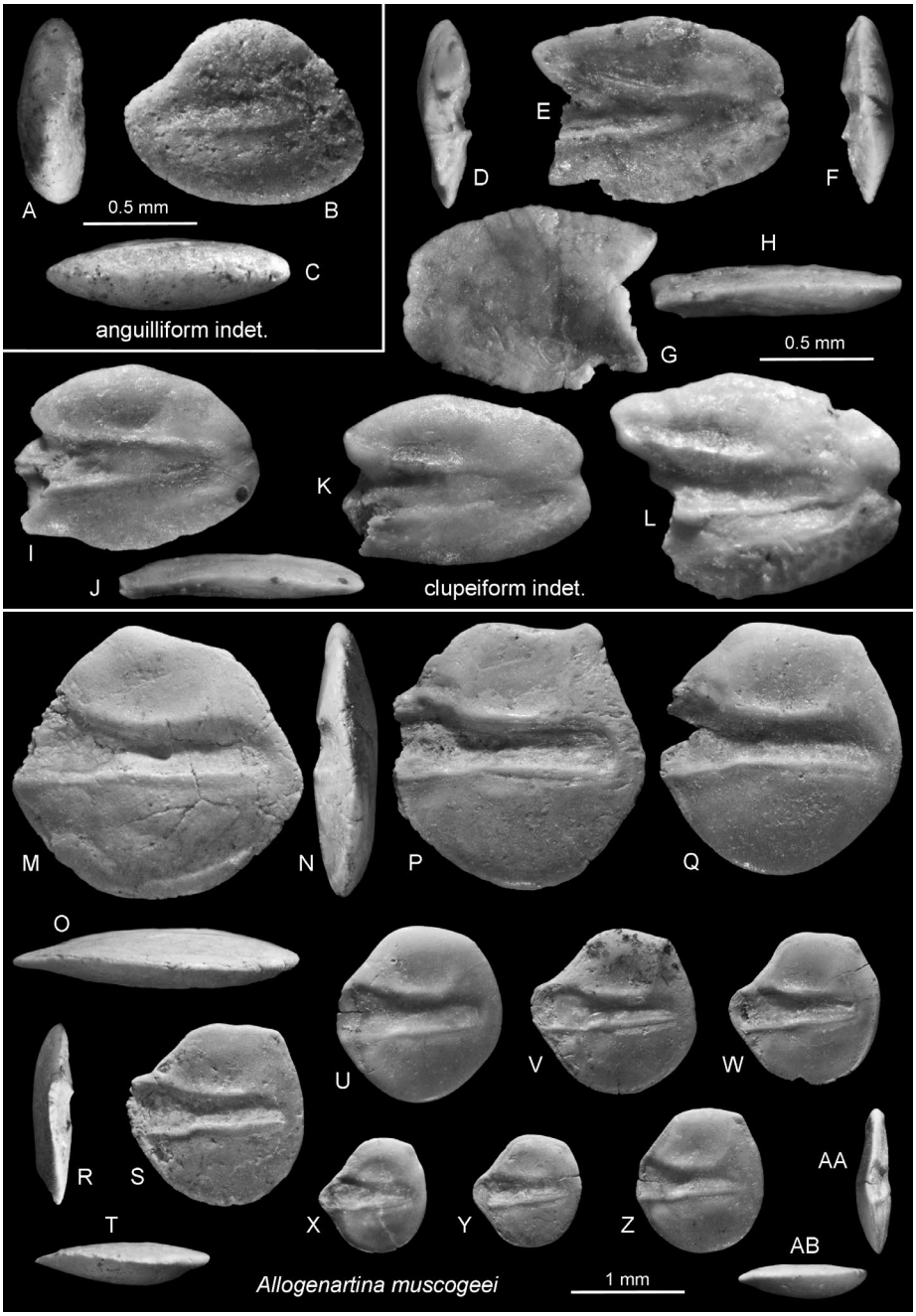

Fig. 3 - A-C) anguilliform indet., LACM 58469-5, reversed, A anterior view, B inner face, C ventral view; D-L) clupeiform indet., D-H LACM 58469-6, reversed, I-L (I, J, L reversed), LACM 58469-7, E, I, K, L inner faces, G outer face, H, J ventral views, D anterior view, F posterior view; M-AB) *Allogenartina muscogeei* gen. n. et n. sp., R-T holotype, LACM 58469-9, reversed, P-Q, U-AB paratypes, LACM 58469-10 (P, Q, W, Y reversed), M-O tentatively assigned specimen, LACM 58469-12, reversed, M, P, Q, S, U-Z inner faces, O, T, AB ventral views, R, AA anterior views, N posterior view.

enigmatic genus *Genartina* Frizzel & Dante (1965) known from few species ranging from Late Cretaceous to Eocene, which reaches larger sizes up to about 4 mm (vs 2.5 mm). *Genartina* is diagnosed by a very specific development of the dorsal rim with a deep indentation anteriorly just above the beginning of the ostium. *Allogenartina* in contrast shows a predorsal expansion of the dorsal rim and no such deep indentation. The systematic position of *Genartina* is obscure and the genus has been associated with Osteoglossidae (Frizzell & Dante 1965), Argentinidae (Stinton 1965), Osmeridae (Nolf 1985), Elopiformes indet. (Schwarzhans 2003 and 2012), Harpodontinae (Nolf 2013) and Synodontidae (Stringer et al. 2016). Because of the similarity of *Genartina* with *Allogenartina* we place both tentatively within Stomiiformes, but we are aware that this otolith morphology may represent an extinct group, which will only become unambiguously resolved once otoliths in situ have been found.

Species. A single species, *Allogenartina muscogeei* n. sp. from the Late Santonian of Alabama and the Campanian of New Jersey.

Allogenartina muscogeei n. sp.

Fig. 3M-AB

2016 Gonostomatidae indet. - Stringer, Oman & Badger: pl. 1, fig. 9

Etymology: Named after the Muscogee, the tribe of the First Nation inhabiting the general area; name used in apposition.

Holotype: LACM 58469-9 (Fig. 3R-T); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 8 specimens, LACM 58469-10 (Figs. 3P-Q, U-AB); same data as holotype.

Further material: 58 specimens, LACM 58469-11; same data as holotype.

Tentative assigned specimen: 3 specimens, LACM 58469-12 (Figs. 3 M-O); same data as holotype.

Diagnosis: Same as for genus (monospecific genus).

Description. Small, high bodied otoliths reaching about 2.5 mm length (holotype 1.55 mm). OL:OH = 0.85-0.95. Dorsal rim high, with rounded pre- and postdorsal angles; predorsal angle often more pronounced; postdorsal angle sometimes lobed; anterior and posterior dorsal rim steeply inclined, middorsal rim straight or only slightly inclined backwards. Ventral rim deep, gently and regularly curved. Posterior rim blunt, broadly rounded. Anterior tip with short, broad, spatulate rostrum without excisura or antirostrum. All rims smooth.

Inner face flat with straight, horizontally positioned, moderately narrow and moderately deep sulcus. Ostium distinctly wider and shorter than cauda, extending with its anterior half onto rostrum, with its ostial colliculum not reaching anterior rim. Cauda ventrally pointed at tip, reaching close to posterior rim of otolith, with marked crista inferior. Large dorsal depression with clear margin only ventrally towards middle portion of sulcus. Ventral field smooth, sometimes with indistinct ventral furrow close to ventral rim of otolith and with furrow below crista inferior. Outer face slightly convex and smooth.

Variability. *Allogenartina muscogeei* shows a moderate degree of variability expressed mainly in variations of the dorsal rim and the strength of the protrusion of the rostrum. One large specimen (Fig. 3M-O) differs in a more strongly pronounced predorsal angle and slightly shallower ventral rim, which also finds its expression in an index OL:OH of slightly above 1 (1.05). This specimen is only tentatively referred to *A. muscogeei*.

Discussion. The otoliths described here as *Allogenartina muscogeei* were first described from the Campanian of New Jersey and recognized as gonostomatoid representatives by Stringer et al. (2016).

Genus *Genartina* Frizzel & Dante, 1965

Remark. *Genartina* is a fossil otolith-based genus relationships that was established by Frizzel & Dante (1965) as a putative osteoglossiform with *G. hamphirensis* (Schubert, 1916) as type species, which is considered as a junior synonym of *G. bambergi* (Priem, 1913) by Nolf (2013). It is hear considered as a tentative stomiiform for reasons explained above.

Genartina cretacea n. sp.

Figs 4A-F

Etymology: Named after its occurrence in the Cretaceous.

Holotype: LACM 58469-13 (Fig. 4C-F); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 8 specimens, LACM 58469-14 (Fig. 4A-B); same data as holotype.

Diagnosis: OL:OH = 0.85. Ventral rim very deep, deepest anterior of its middle. Rostrum very short, almost indistinct, without concavity of ventral rim below. Dorsal rim moderately high, with broad anterior-dorsal lobe, anteriorly vertically cut down to minute horizontal stretch towards anterior tip. Cauda long, posteriorly widened, terminating very close to posterior rim of otolith. Ostium very short; CaL:OsL = 3.5.

Description. Moderately sized, very high bodied and thin otoliths up to about 2.5 mm length (holotype 1.9 mm), OH:OT = 5.0-5.5. Ventral very deep; dorsal rim high; both rims with their respective balance points well before middle of otolith. Anterior rim nearly vertical with minute, blunt rostrum and rectangular indentation above ostium. Posterior rim broadly rounded, somewhat pronounced at tip of cauda. All rims smooth. Short rostrum thin and slightly bent outwards, often damaged.

Inner face flat, with long, moderately deep, straight, supramedian sulcus. Ostium slightly widened and very short; cauda long and slightly widened towards the tip, terminating close to posterior rim of otolith. Wide dorsal depression with indistinct margins occupying most of dorsal field; ventral field smooth, sometimes with indistinct ventral furrow close to ventral margin of otolith. Outer face slightly convex, smooth.

Discussion. So far three species have been described that can be assigned to *Genartina*: *G. bambergi* (Priem, 1913) (syn. *G. hampshirensis* (Schu-

bert, 1916)) from the Eocene of France and England, *G. abbatiae* (Stinton, 1965) (syn. *G. hauniensis* Schwarzhans, 2003) from the Paleocene of Denmark and England, and *G. texana* Dante & Frizzell, 1965 from the Eocene of Texas. Recently, Stringer et al. (2016) have also figured a *Genartina* sp. from the Campanian of New Jersey.

The holotype is the only specimen with a completely preserved rostrum, which otherwise is often damaged because of its delicate nature. This extremely short and blunt rostrum and the nearly vertical anterior rim are the main characters distinguishing *G. cretacea* from the other species mentioned above. The species of *Genartina* fall into two morphotypes, one with a rather long rostrum and a distinct concavity at the ventral rim below it and an OL:OH of 1.1-1.25 comprising *G. bambergi, G. abbatiae* and *Genartina* sp. from Stringer et al. (2016), and the other with a more compressed shape (OL:OH = 0.85-1.05) and a minute rostrum with a nearly vertically cut anterior rim comprising *G. texana* and *G. cretacea*. *Genartina cretacea* differs from *G. texana* in the even shorter rostrum and the higher dorsal rim. From *Genartina* sp. of Stringer et al. (2016), *G. cretacea* differs additionally to the short rostrum without concavity of the ventral rim in the much higher dorsal rim. It is interesting that *Genartina* is present with two distinct species in the Late Cretaceous simultaneously, which also seem to represent the two distinct lineages observed in the genus.

Order **Aulopiformes** Rosen, 1973
Family indet.
Genus *Pseudotrichiurus* n. gen.

Type species: *Pseudotrichiurus sagax* n. sp.

Etymology: A combination of pseudo (Greek) = wrong, false and the genus name *Trichiurus* refering to the superficial resemblance of these otoliths with extant trichiurid otoliths.

Diagnosis: A fossil otolith-based genus of unknown familial relationships of the order Aulopiformes. Otoliths very elongate (OL:OH = 2.5) with pointed rostrum and posterior tip. Otoliths thin (OH:OT = 2.5-3.0) with inner face markedly curved along vertical axis. Sulcus straight, horizontal. Ostium short, widened, particularly dorsally. Cauda narrow, terminating far from posterior rim of otolith. CaL:OsL about 1.0-1.2.

Comparison and discussion. Otoliths of *Pseudotrichiurus* resemble certain aulopiform otoliths, such as of the families Aulopidae, Chlorophthalmidae and Paraulopidae, in the distinctly dorsally widened ostium with the ostium margin sometimes being curving backwards and the ostial colliculum not expanded in combination with the short cauda and slender otolith shape. It differs in the regular fusiform otolith shape, the completely straight cauda terminating at considerable distance from the posterior tip of the otolith and the inner surface being markedly convex in the vertical direction. Some of these characters like the bending of the inner face, the fusiform shape and the straight cauda resemble Recent otoliths of the scombriform family Trichiuridae. The peculiar upper margin of the ostium, however, is a distinctive character so far exclusively observed in aulopiform otoliths. There are also several extinct Cretaceous aulopiform families recorded from the fossil record (Nelson et al. 2016), some of which entertained similar ecological environments and trophic levels as did the scombriforms later in the Cenozoic (Friedman 2009; Miya et al. 2013) and therefore we assume that the apparent similarities in otoliths between these two groups may in fact represent a certain degree of functional adaption.

Species. A single species, *Pseudotrichiurus sagax* n. sp. from the Late Santonian of Alabama.

Pseudotrichiurus sagax n. sp.
Figs 4G-M

Etymology: From sagax (Lat.) = acute, sharp, referring to the sharply pointed rostrum and posterior tip of the otolith.

Holotype: LACM 58469-15 (Fig. 4G-I); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 6 specimens, LACM 58469-16 (Figs. 4J-M); same data as holotype.

Diagnosis: Same as for genus (monospecific genus).

Description. Small, slender otoliths reaching > 3 mm length (holotype without broken rostrum 2.9 mm). Shape fusiform, with dorsal and ventral rim shallow and regularly curved, dorsal rim with somewhat irregular middorsal angle. Rostrum and posterior tip sharply pointed, nearly symmetrical.

Inner face slightly bent in horizontal direction and more distinctly convex in vertical direction. Sulcus narrow, slightly supramedian, divided in about equally long ostium and cauda. Ostium slightly widened ventrally and considerably widened dorsally with recurving dorsal margin. Ostial colliculum not expending as much upwards as dorsal margin of ostium. Cauda narrow, moderately deep, straight, terminating far from posterior otolith rim. Dorsal depression distinct above cauda; cauda with distin-

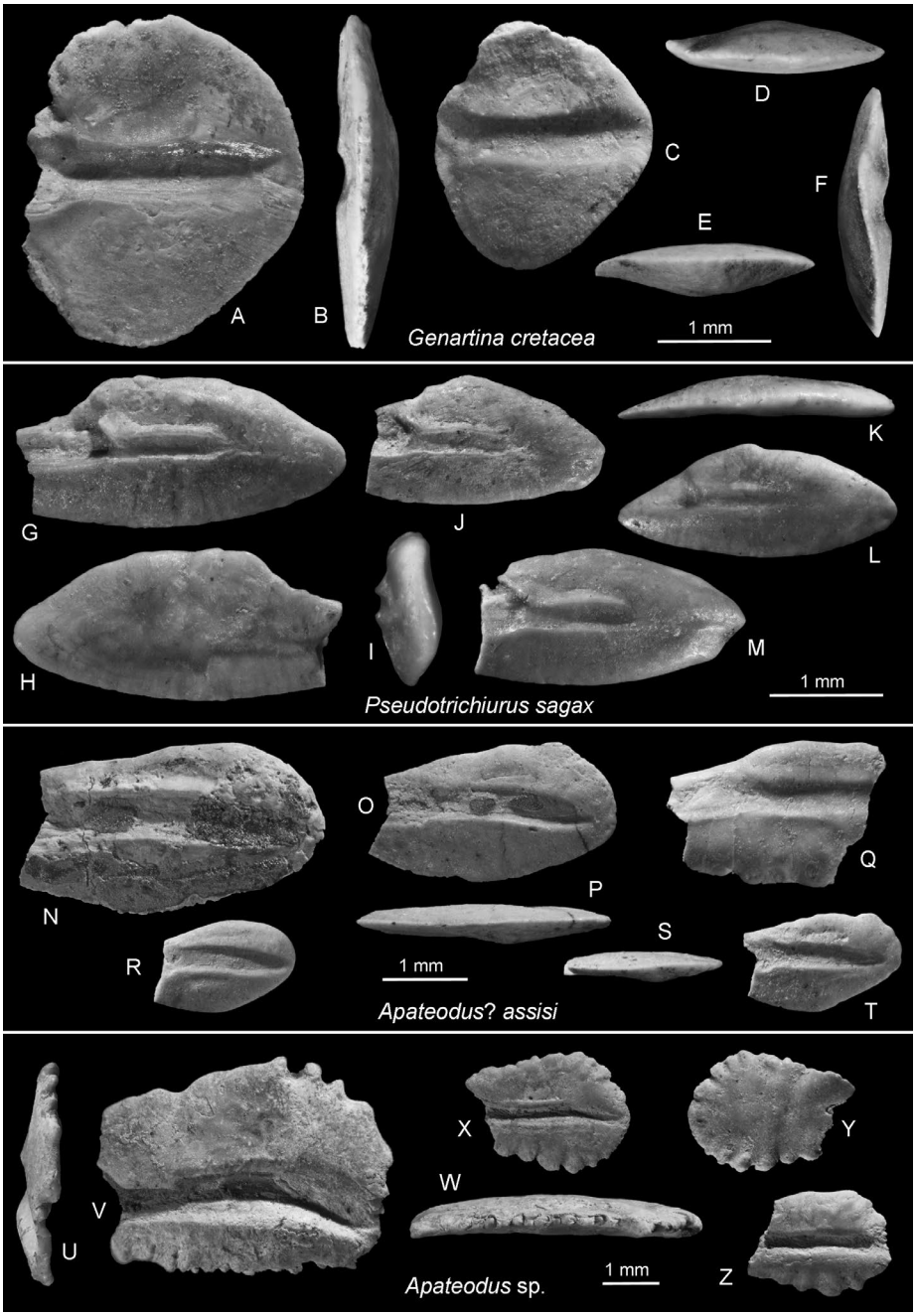

Fig. 4 - A-F) *Genartina cretacea* n. sp., C-F holotype, LACM 58469-13, reversed, A-B paratype, LACM 58469-14, reversed, A, C inner faces, B posterior view, D dorsal view, E ventral view, F anterior view; G-M) *Pseudotrichiurus sagax* gen. n. et n. sp., G-I holotype, reversed, LACM 58469-15, J-M paratypes, LACM 58469-16 (K-L reversed), G, J, L, M inner faces, H outer face, K ventral view, I posterior view; N-T) *Apateodus*? *assisi* n. sp., O-P holotype, 58469-17, reversed, N (reversed), Q-T paratypes, LACM 58469-18, N, O, Q, R, T inner faces, P, S ventral views; U-Z) *Apateodus* sp., LACM 58469-20, reversed, V, X, Z inner faces, Y outer face, W ventral view, U posterior view.

ct crista superior. Ventral field smooth or with few vertical furrows, without ventral furrow. Outer face flat to slightly concave, smooth.

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

Remark. The allocation of the following otoliths to the fossil skeleton-based family Ichthyotringidae and genus *Apateodus* is based on otoliths found in situ by CT-micro scanning in *Apateodus cor-neti* (Forir, 1847) (Schwarzhans et al. 2018 in press).

Apateodus*? *assisi n. sp.

Figs 4N-T

Etymology: Named in honor of Carlos A. Assis, Lisbon, for his contribution to the better understanding of utricular and lagenar otoliths..

Holotype: LACM 58469-17 (Fig. 4O-P); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 4 specimens, LACM 58469-18 (Figs. 4N, Q-T); same data as holotype.

Further material: 23 specimens, LACM 58469-19; same data as holotype.

Diagnosis: Slender and fragile otoliths with flat inner and outer faces. Rostral tip unknown; dorsal rim with broad postdorsal expansion. Ventral rim shallow, deepest at its middle. Cauda long, almost straight, with very faint bending at rear and tapering tip closely reaching to posterior tip of otolith.

Description. Elongate otoliths, largest fragment 3.5 mm long (holotype 2.9 mm). OH:OT = 3.3-3.7. Dorsal rim anteriorly inclined, low, rising to gentle, broadly rounded postdorsal angle. Ventral rim shallow, regularly curving, deepest at its middle. Rostrum not completely preserved, no antirostrum or excisura. Posterior rim broadly rounded, posterior tip at level of caudal tip. Rims smooth or slightly undulating.

Inner face flat with slightly supramedian, moderately deep sulcus. Ostium incomplete, moderately widened, its dorsal margin short and curving upward to anterior-dorsal rim. Cauda long, straight, except for a very slight bending toward rear accompanied by a slight expansion of its ventral margin, with tapering tip close to posterior tip of otolith. Indistinct, narrow depression above anterior half of cauda; no ventral furrow. Outer face flat, smooth.

Discussion. Otoliths of *Apateodus*? *assisi* resemble slender argentinoid otoliths in the form of the ventral otolith rim and the straight, long cauda and the otolith found in situ in *Apateodus corneti* in the shape of the dorsal rim and the very slender outline. It differs from *A. corneti* in the shape of the ventral rim with its deepest point at the middle and the rear part of the cauda not being expanded dorsally as well as the less deepened sulcus. We therefore assign these otoliths only tentatively to *Apateodus* being aware that they might in fact represent yet another, possibly related fossil ichthyotringid genus of which otoliths are not yet known.

Apateodus sp.

Figs 4U-Z

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
2017 *Apateodus* sp. - Schwarzhans, Beckett, Schein & Friedman: fig. 10B-C

Material: 8 specimens, LACM 58469-20, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Otolith fragments of 2.5 to 5.2 mm length, all of which are lacking the rostrum. OH:OT = 5.5. Dorsal rim with broadly rounded postdorsal angle, anteriorly inclined. Ventral rim shallow, in small specimens expanded and rounded postventrally. Posterior rim broadly rounded. Antirostrum distinct, moderately sharp, excisura present, but difficult to evaluate without preserved rostrum. All rims intensely and coarsely crenulate.

Inner face very slightly convex. Ostium missing. Cauda deep, straight, somewhat expanded posteriorly towards its tip and terminating very close to posterior tip of otolith. Indistinct dorsal depression above anterior part of cauda. No ventral furrow, instead several radial furrows ingressing from marginal crenulation. Outer face flat, smooth, except for marginal furrows ingressing from crenulation of otolith rims.

Discussion. As can be seen from the synonymy list, these enigmatic otoliths have been associated with a variety of different teleost groups in the past. It was only Schwarzhans et al. (2018 in press) who could relate it to the then described otoliths in situ found by CT micro scanning in *Apateodus corneti*. It is not a rare otolith in the Santonian to Maastrichtian rocks of North America, but so far no complete otolith has been found to warrant species definition.

Order **Beryciformes** Regan, 1909
Suborder **Berycoidei**, Regan 1909
Family indet.
Genus *Eutawichthys* n. gen.

Type species. E*utawichthys stringeri* n. sp.

Etymology: Named after the (upper) Eutaw Formation, Santonian, from which these otoliths were obtained.

Diagnosis: A fossil otolith-based genus of unknown familial relationships of the order Beryciformes, suborder Berycoidei. Otoliths compact, oval in outline (OL:OH = 1.15-1.55) with short, upward directed rostrum and broadly rounded posterior rim. Inner face slightly convex to nearly flat. Ostium and cauda of about equal length. Ostium oriented upwards towards anterior, widened, with clearly outlined colliculum. Cauda narrower, oriented upwards towards posterior, with colliculum restricted ventrally and separated from ridge like caudal pseudocolliculum. Distinct ventral furrow present.

Comparison and discussion. These enigmatic otoliths have commonly been associated with the perciform family Apogonidae (now in Kurtiformes in Nelson et al. 2016) by Huddle-

ston & Savoie (1983) and Nolf & Stringer (1996) or Beryciformes by Schwarzhans (2010a) and Stringer et al. (2016). There are indeed many characters, superficially or not, that resemble apogonid otoliths, such as the outline, the clear-cut ventral furrow, the round dorsal depression, the large ostium and the shallow cauda with its rounded tip, but there are also significant differences like the lack of the expanded dorsal margin of the ostium, which is typical for extant apogonid otoliths, the upward oriented cauda, which is about as long as the ostium (vs distinctly shorter than the ostium) and the presence of a clear caudal pseudocolliculum that amongst extant otoliths is only know from the Myctophidae. In our assessment, the characters of the sulcus speak against an assignment with the Apogonidae. While the shape of the ostium or the length of the cauda could be considered plesiomorphic compared to modern apogonid otoliths, the other characters associated with the cauda like its upward orientation and the presence of a pseudocolliculum are probably apomorphic and would exclude such arrangement. The placement within Berycoidei matches with the outline and orientation of ostium and cauda in *Eutawichthys*, but not with the presence of a caudal pseudocolliculum. Therefore, we also consider the assignment with the Berycoidei and Beryciformes as provisional and it might well turn out that *Eutawichthys* in reality represents an extinct teleost group of which otoliths are not yet known.

Species. Four species: *Eutawichthys compressus* n. sp. from the Santonian of Alabama, *E. maastrichtiensis* (Nolf & Stringer, 1996) (originally described as "genus Apogonidarum" *maastrichtiensis*) from the Campanian of New Jersey and the Maastrichtian of Mississippi, Maryland and Tenessee, *E. stringeri* n. sp. from the Campanian of New Jersey and the Santonian of Alabama, *E. zideki* (Nolf & Stringer, 1996) (originally described as "genus Apogonidarum" *zideki*) from the Campanian of New Jersey, the Santonian of Alabama and the Maastrichtian of Mississippi and Maryland.

Eutawichthys compressus n. sp.

Figs 5A-L

Etymology: From compressus (Lat.) = compressed, referring to the compressed outline of these otoliths.

Holotype: LACM 58469-25 (Fig. 5C-F); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 6 specimens, LACM 58469-26 (Figs. 5A-B, G-L); same data as holotype.

Further material: 23 specimens, LACM 58469-27; same data as holotype.

Diagnosis: Compact otoliths, OL:OH = 1.15-1.3. Dorsal rim with broad and much expanded middorsal region, often higher than ventral rim deep. Rostrum very blunt. Otolith rims commonly crenulate.

Description. Moderately small, compressed otoliths apparently not reaching larger sizes than 2.7 mm length (holotype 2.4 mm). OH:OT = 2.8-3.3. Dorsal rim broadly expanded middorsally, anteriorly concave and posteriorly broadly rounded. Ventral rim moderately deep, gently curved, often almost flat at its middle. Anterior rim with massive, dorsally shifted rostrum with convex ventral margin and almost horizontal short dorsal margin. Excisura and antirostrum minute or absent. Posterior rim broadly rounded, its tip shifted dorsally to a position at level with caudal tip. All rims finely crenulated or almost smooth.

Inner face slightly convex, with slightly supramedian, rather shallow and moderately wide sulcus. Ostium curved upwards towards anterior, opening towards dorsal rim of rostrum, moderately widened, particularly ventrally and with clearly defined shallow colliculum. Cauda nearly as long as ostium (CaL:OsL = 0.85-1.0), oriented upwards towards posterior, with rounded tip terminating at moderate distance from posterior rim. Caudal colliculum slightly deepened, ventrally reduced and separated from ridge-like, long pseudocolliculum. Dorsal depression broad, round, above central portion of oblique v-shaped sulcus and marked by clear crista superior against sulcus. Ventral furrow variably expressed, often feeble, close to ventral rim of otolith. Outer face slightly convex like inner face, mostly smooth except for short furrows near otolith rims.

Discussion. *Eutawichthys compressus* is a relatively rare species of the genus in the Eutaw FM and not know so far from younger Late Cretaceous strata. It differs from the other species of the genus by its compressed shape, except for *E. maastrichtiensis*, which however differs from *E. compressus* in the ventral furrow positioned much further inwards from the ventral rim of the otolith and the short, posteriorly reduced caudal pseudocolliculum. The specimens described as *E. maastrichtiensis* from the Campanian of New Jersey by Stringer et al. (2016); however appear to be slightly more elongate than those from the Maastrichtian.

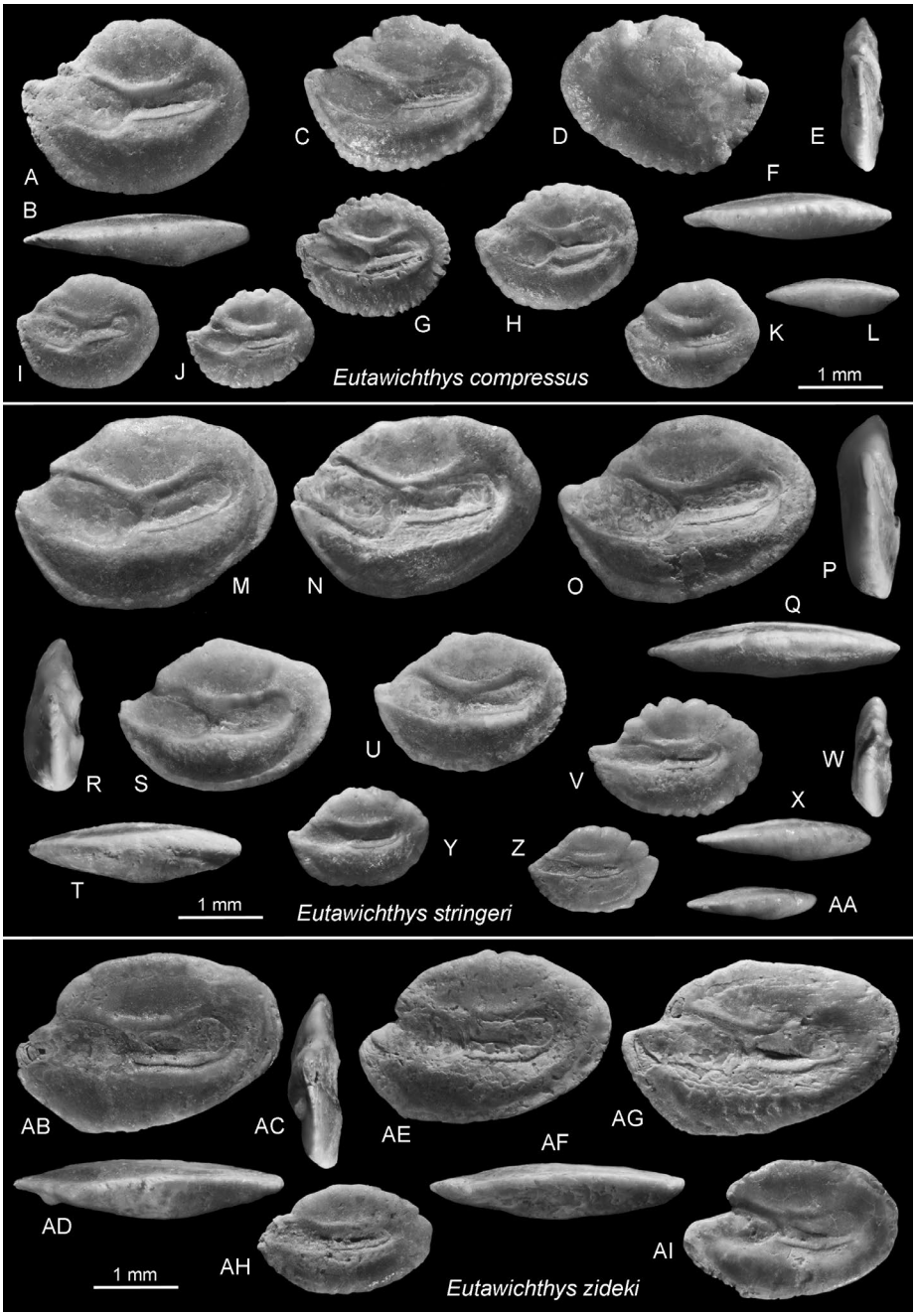

Fig. 5 - A-L) *Eutawichthys compressus* gen. n. et n. sp., C-F holotype, LACM 58469-25, reversed, A-B, G-L paratypes, LACM 58469-26 (G-H, J-K reversed), A, C, G-K inner faces, D outer face, B, F, L ventral views, E anterior view; M-AA) *Eutawichthys stringeri* gen. n. et n. sp., O-Q holotype, LACM 58469-22, reversed, M-N, R-AA paratypes, LACM 58469-23 (M, S, U reversed), M-O, S, U, V, Y, Z inner faces, Q, T, X, AA ventral views, P, R, W anterior views; AB-AI) *Eutawichthys zideki* (Nolf & Stringer, 1996), LACM 58469-21 (AB-AG reversed), AB, AE, AG, AH, AI inner faces, AD, AF ventral views, AC anterior view.

Eutawichthys stringeri n. sp.

Figs 5M-AA

2016 Berycidae indet. - Stringer, Oman & Badger: pl. 2, fig. 6

Etymology: Named in honor of Gary L. Stringer (Monroe, Louisiana) in recognition to his contribution to the knowledge of fossil otoliths in the USA.

Holotype: LACM 58469-22 (Fig. 5O-Q); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 7 specimens, LACM 58469-23 (Figs. 5M-N, R-AA); same data as holotype.

Further material: Many specimens, LACM 58469-24; same data as holotype.

Diagnosis: Moderately compact otoliths, OL:OH = 1.35-1.45. Dorsal rim regularly curved. Rostrum moderately long, often pointed. Ventral furrow distinct, close to ventral rim of otolith. Otolith rims smooth, crenulate in small specimens of 3 mm length and less.

Description. Moderately small, and moderately compressed otoliths reaching sizes up to 3.0 mm length (holotype). OH:OT = 2.6-3.5. Dorsal rim broadly rounded, without distinct angles except for sometimes a small postdorsal angle. Ventral rim moderately deep, gently and regularly curved, deepest anterior of its middle. Anterior rim with broad, dorsally shifted rostrum with pointed tip, convex ventral margin and slightly inclined short dorsal margin. Excisura and antirostrum minute (Fig. 5M)

or absent. Posterior rim broadly rounded, its tip shifted dorsally to a position at level with caudal tip. All rims smooth, finely crenulated in small specimens.

Inner face slightly convex, with slightly supramedian, rather shallow and moderately wide sulcus, somewhat deeper in small specimens. Ostium curved upwards towards anterior, opening towards dorsal rim of rostrum, moderately widened, particularly ventrally and with clearly defined shallow colliculum. Cauda about as long as ostium (CaL:OsL = 0.95-1.0), oriented upwards towards posterior, with rounded tip terminating at moderate distance from posterior rim. Caudal colliculum slightly deepened, ventrally reduced and separated from ridge-like, long pseudocolliculum. Dorsal depression broad, short, round, above central portion of oblique v-shaped sulcus and marked by clear crista superior against sulcus. Ventral furrow mostly well developed, close to ventral rim of otolith. Outer face slightly convex like inner face or more convex, relatively smooth.

Discussion. *Eutawichthys stringeri* is by far the most common species in the otolith association of the Eutaw FM and was also recorded by Stringer et al. (2016) in smaller numbers from the Campanian of New Jersey. It is intermediate in the OL:OH ratio between *E. compressus* and *E. maastrichtiensis* on one side (OL:OH = 1.15-1.3) and *E. zideki* on the other (OL:OH = 1.45-1.55). It additionally differs from *E. compressus* in the more regularly curved and shallower dorsal rim, the lack of intense crenulation in adults and the distinct ventral furrow. From *E. maastrichtiensis* it differs additionally in the ventral furrow located close to the ventral rim of the otolith and long caudal pseudocolliculum (vs short and posteriorly reduced). From *E. zideki* it differs additionally in the wider ostium, the sometimes anteriorly reduced caudal colliculum and the more v-shaped sulcus margins.

Eutawichthys zideki (Nolf & Stringer, 1996)

Figs 5AB-AI

1983 Apogonidae-A - Huddleston & Savoie: figs. 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, Oman & Badger: pl. 2, fig. 5

Material: 14 specimens, LACM 58469-21; from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Moderately small, and moderately elongate otoliths reaching sizes up to 3.7 mm length (according to Nolf & Stringer, 1996). OL:OH = 1.45-1.55; OH:OT about 3.0. Dorsal rim shallow, gently curved, without distinct angles. Ventral rim moderately deep, gently curved, deepest distinctly anterior of its middle. Anterior rim with broad, median rostrum with blunt tip, convex ventral margin and inclined short dorsal margin. No or very feeble excisura or antirostrum. Posterior rim rounded, its tip shifted dorsally to a position at or above caudal tip. All rims smooth.

Inner face nearly flat, with slightly supramedian, rather shallow and moderately wide sulcus. Ostium slightly curved upwards towards anterior, opening towards dorsal rim of rostrum, only slightly widened in comparison to cauda, with clearly defined shallow colliculum. Cauda about as long as ostium (CaL:OsL = 0.95-1.0), oriented slightly upwards towards posterior, with rounded tip terminating at moderate distance from posterior rim. Caudal colliculum not deepened, ventrally reduced and anteriorly reduced leaving anteriorly collum-like space towards ostial colliculum and ventrally separated from ridge-like, long pseudocolliculum. Dorsal depression small, rather narrow, above central portion of sulcus and marked by clear crista superior against sulcus. Ventral furrow mostly well developed, close to ventral rim of otolith. Outer face more convex than inner face, smooth.

Discussion. *Eutawichthys zideki* is readily recognized by the more elongate shape of the otolith (OL:OH = 1.45.1.55 vs 1.15-1.4), the almost straight sulcus, the narrow ostium and the anteriorly reduced caudal colliculum. It appears to be a stratigraphically log reaching species ranging from Late Santonian to Late Maastrichtian.

Order **Polymixiiformes** Patterson, 1964
Family Polymixiidae Bleeker, 1859
Genus *Cowetaichthys* n. gen.

Type species: *Cowetaichthys alabamae* n. sp.

Etymology: Named after the historic township Coweta of the first nation located in the greater region.

Diagnosis: A fossil otolith-based genus of the family Polymixiidae. Otoliths compact, OL:OH = 0.9-1.45. Ventral rim deepest anterior of middle; dorsal rim highest posterior of middle. Inner face distinctly convex. Ostium ventrally widened, distinctly shorter than cauda. Cauda narrower, slightly oscillating but not bent downwards at tip, which terminates close to posterior tip of otolith. Ventral field wide, smooth, without ventral furrow.

Comparison and discussion. Otoliths of *Cowetaichthys* resemble much extant *Polymixia* otoliths in outline, smooth and wide ventral field and sulcus shape, differing primarily in the lack of a down turning caudal tip. The downturned caudal tip however is shared by all known extant *Polymixia* otoliths as well as *Polymixia polita* Schwarzhans, 2012 from the Paleocene of Bavaria and the Maastrichtian specimens described as Polymixiidae indet, by Huddleston & Savoie (1983) and Nolf & Dockery (1996). We consider this a derived character separating *Polymxia* from the Late Cretaceous / Paleocene *Cowetaichthys*, which sometimes however shows a distal dorsal widening of the cauda, which is not observed in extant *Polymixia* otoliths. Another fossil otolith-based polymixiid genus was recently established from the Early Oligocene of Japan - *Namicauda* Schwarzhans, Ohe & Ando, 2016 - which is characterized by a very specific style of the oscillation of the cauda and a continuous colliculum throughout ostium and cauda.

Similar compressed otoliths with a heterosulcoid sulcus without bent caudal tip are found in certain Percoidei (of Perciformes), for instance Ambassidae or Priacanthidae and in Sparidae of the Spariformes. The distinction of polymixiiform otoliths from such perciform and spariform otoliths is difficult, and has led in the past of such otoliths having been described as percoids incertae sedis (Stringer et al. 2016). Polymixiiform otoliths generally lack a ventral furrow on the inner face, while this character is well developed in otoliths of those perciform and spariform families. This, and the abundance of skeleton-based polymixiiform fishes in the Late Cretaceous as opposed to the sparsity of perciform fishes in the same time interval are our main arguments for placement of *Cowetaichthys* in the Polymixiiformes.

Species. Five species: *Cowetaichthys alabamae* n. sp. from the Santonian of Alabama, *C. beauryi* (Schwarzhans, 2010a) (originally described as genus Polymixiidarum *beauryi*) from the Maastrichtian of Bavaria, *C. groenlandicus* (Schwarzhans, 2004) (originally described as genus Veliferidarum *groenlandicus*) from the Paleocene of West-Greenland, *C. harderi* (Schwarzhans, 2003) (originally described as genus Veliferidarum *harderi*) from the Paleocene of Denmark and *C. lamberi* n. sp. from the Santonian of Alabama.

Cowetaichthys alabamae n. sp.

Figs 6A-M

2016 Percoidei sp. 1 - Stringer, Oman & Badger: pl. 2, fig. 9

Etymology: Named after the state Alabama, USA, in which the type-locality is located.

Holotype: LACM 58469-28 (Fig. 6A-C); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 6 specimens, LACM 58469-29 (Figs. 6D-M); same data as holotype.

Further material: 25 specimens, LACM 58469-30; same data as holotype.

Diagnosis: OL:OH = 0.9-1.1, increasing with size. Dorsal rim deeply and coarsely lobed. Rostrum short, blunt, pointed in small specimens. Ventral rim regularly curved, broad. Cauda widened dorsally near caudal tip.

Description. Compressed otoliths reaching about 3 mm length (holotype 2.6 mm). OH:OT = 3.6-4.0. Dorsal rim high, highest slightly behind its middle, deeply and irregularly lobed in adults. Ventral rim much deeper than dorsal rim high, gently and regularly curved, deepest anterior of its middle below collum. Rostrum short, rounded in adults, pointed in small specimens. Variably deep excisura and expanded antirostrum. Posterior rim blunt, rounded, its tip shifted dorsally to level of caudal tip or above. Rims rather smooth in adults, intensely crenulated in juveniles.

Inner face strongly convex with distinctly supramedian, deep sulcus. Ostium shorter than cauda and much wider, but only ventrally widened, anteriorly open. Ostial colliculum deepened. Sulcus with small ventral notch at collum. Cauda straight, slightly oscillating, but without downward bent tip. Cauda dorsally widened towards tip, terminating very close posterior tip of otolith. CaL:OsL = 1.5-1.6. Dorsal depression broad, only above central part of sulcus, ventrally marked by distinct crista superior against sulcus. Dorsal field narrower and shorter than ventral field. Ventral field smooth, without ventral furrow. Outer face flat, smooth or with few radial furrows.

Ontogeny. Otoliths of *C. alabamae* show a distinct ontogenetic change. Small otoliths of sizes of 0.9-1.4 mm length differ from large ones of sizes from 2.2-3.0 mm length in a much stronger crenulation of the otolith rims and ornamentation on the outer face, a higher and laterally more confined dorsal rim resulting in a smaller index OL:OH of 0.9-1.0 (vs 1.05-1.1) and a somewhat pointed rostrum (vs rounded). Also excisura and

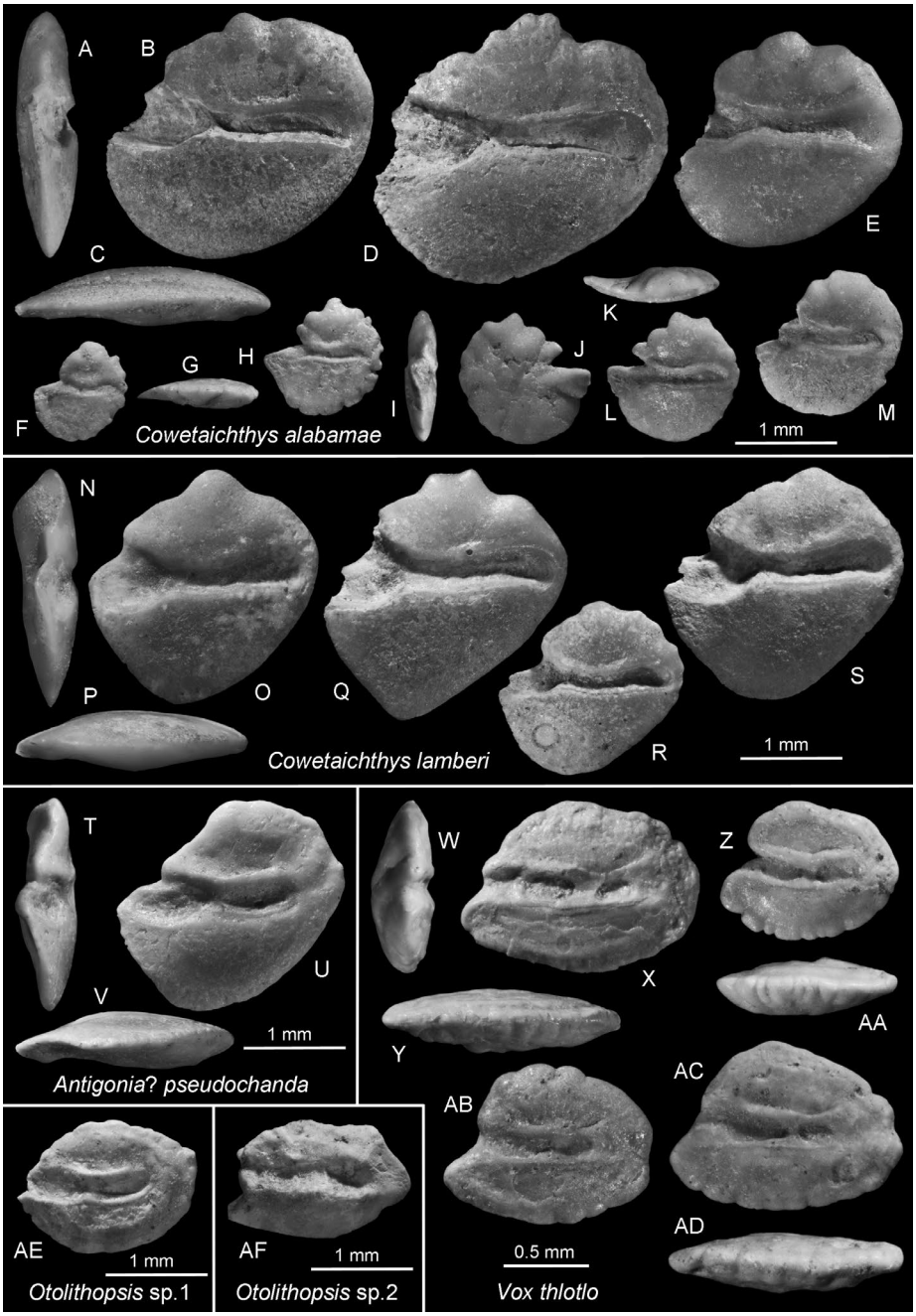

Fig. 6 - A-M) *Cowetaichthys alabamae* gen. n. et n. sp., A-C holotype, LACM 58469-28, reversed, D-M paratypes, LACM 58469-29 (E, H-M reversed), B, D, E, F, H, L, M inner faces, J outer face, C, G ventral view, K dorsal view, A, I anterior view; N-S) *Cowetaichthys lamberi* gen. n. et n. sp., N-P holotype, LACM 58469-31, Q-S paratypes, LACM 58469-32 (R reversed), O, Q-S inner faces, P ventral view, N anterior view; T-V) *Antigonia*? *pseudochanda* (Nolf & Dockery, 1990), LACM 58469-34, U inner face, V ventral view, T anterior view; W-AD) *Vox thlotlo* gen. n. et n. sp., W-Y holotype, LACM 58469-35, Z-AD paratypes, LACM 58469-36 (Z-AA, AC-AD reversed), X, Z, AB, AC inner faces, Y, AA, AD ventral views, W anterior view; AE) *Otolithopsis* sp. 1, LACM 58469-45, inner face; AF) *Otolithopsis* sp. 2, LACM 58469-46, reversed, inner face.

antirostrum are often more pronounced. We have very few and poorly preserved otoliths of intermediate sizes, but they do indicate a gradual change from the juvenile to the adult morphology (Fig. 6M). Stringer et al. (2016) figured an otolith of 2.4 mm length from the Campanian of New Jersey as Percoidei sp. 1, which is morphologically intermediate between the small and the large specimens here described and which we therefore assign to *C. alabamae* as well.

Discussion. *Cowetaichthys alabamae* differs from *C. lamberi* n. sp. described in the following by the gently rounded ventral rim (vs with a deep v-shaped angle) and the higher dorsal field. Specimens of similar sizes of *C. lamberi* are more compressed (at OL 1.8-2.9; OL:OH = 1.0-1.1 in *C. alabamae* vs 0.95-1.0 in *C. lamberi*) and show a rounded rostrum (vs pointed). The Paleocene species *C. groenlandicus* and *C. harderi* do not show a postdorsally widened cauda, a narrower dorsal field and a longer ostium (CaL:OsL = 1.1-1.3 vs 1.5-1.6). *Cowetaichthys groenlandicus* differs further in being more elongate (OL:OH = 1.2-1.25 vs 0.9-1.1). *Cowetaichthys beauryi* is the most elongate species with an index OL:OH of 1.3-1.45, and shows a regularly curved, broadly crenulate dorsal rim.

Cowetaichthys lamberi n. sp.

Figs 6N-S

?2016 Percoidei sp. 4 - Stringer, Oman & Badger: pl. 2, fig. 10

Etymology: Named in honor of the late Chet Kurt Lamber (1938-2004), who collected this unique material.

Holotype: LACM 58469-31 (Fig. 6N-P); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 4 specimens, LACM 58469-32 (Figs. 6Q-S); same data as holotype.

Further material: 20 specimens, LACM 58469-33; same data as holotype.

Diagnosis: OL:OH = 0.9-1.0. Dorsal rim broadly lobed. Rostrum moderately projecting and moderately pointed. Ventral rim with deep, v-shaped angle at preventral position. Cauda widened dorsally near caudal tip.

Description. Compressed otoliths reaching about 2.5 mm length (holotype 2.2 mm). OH:OT = 4.0. Dorsal rim moderately high, highest slightly behind its middle, broadly lobed and rather smooth. Ventral rim much deeper than dorsal rim high, with distinct v-shaped angle and deepest anterior of its middle below collum. Rostrum moderately short, and moderately pointed. Excisura and antirostrum feeble. Posterior rim rounded, its tip shifted far dorsally to level of caudal tip or above. Rims smooth and somewhat undulating at dorsal rim and upper part of posterior rim.

Inner face strongly convex with distinctly supramedian, deep sulcus. Ostium shorter than cauda and much wider, but only ventrally widened, anteriorly open. Ostial colliculum deepened. Sulcus with small ventral notch at collum. Cauda straight, slightly oscillating, but without downward bent tip. Cauda dorsally widened towards tip, terminating very close posterior tip of otolith. CaL:OsL = 1.6-1.8. Dorsal depression broad, only above central part of sulcus, ventrally marked by distinct crista superior against sulcus. Dorsal field narrower and shorter than ventral field. Ventral field smooth, without ventral furrow. Outer face flat, smooth.

Discussion. *Cowetaichthys lamberi* resembles the parallel occurring *C. alabamae*. See discussion for the latter for differences.

Order **Zeiformes** Regan, 1909
Family Antigoniidae Jordan & Evermann, 1898

Remark. We follow Stinton (1967) and Schwarzhans (2010b) in recognizing Antigoniidae as a family separate from Caproideae and continue to associate it with Zeiformes, while Caproidae are now placed in an order of their own, Caproiformes of the Percomorpha (Nelson et al. 2016).

Genus *Antigonia* Lowe, 1843

Antigonia? pseudochanda
(Nolf & Dockery, 1990)

Fig. 6T-V

1990 "genus Percoideorum" *pseudochanda* - Nolf & Dockery: pl. 3, figs. 5-6

1996 "genus Percoideorum" *pseudochanda* Nolf & Dockery, 1990 - Nolf & Stringer: pl.6, figs. 8-9

Material: 1 specimen, LACM 58469-34, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Incertae sedis
Genus *Vox* n. gen.

Type species: *Vox thlotlo* n. sp.

Etymology: Vox (Latin) = voice, an allegory to the enigmatic relationships of the genus.

Diagnosis: A fossil otolith-based genus of unknown familial relationships. Otoliths small, oval in outline (OL:OH = 1.25-1.4) with short rostrum and feeble excisura and antirostrum. Inner face slightly convex. Sulcus narrow; sulcus margins confluent without distinction into ostium and cauda. Ostial and caudal colliculi distinctly deepened with sharp margins, much shorter than ostium or cauda, terminating far from anterior and posterior tips of sulcus, with distinct collum in between. OsL:CaL = 1.5-2.0; OCL:CCL = 1.1-1.5. Sharp crista superior.

Comparison and discussion. These small otoliths have a very distinctive morphology characterized by the peculiar deepened colliculi, which are also so much shorter than the ostium and cauda in which they are located, while otherwise the sulcus shows little distinction in ostium and cauda. Such a pattern is not observed in Recent otoliths. One is hard-pressed to locate even vaguely resembling extant or fossil otoliths, to which these forms show some similarity, may be certain putative batrachoidiforms like *Batrachoidiformis trapezoidalis* Nolf, 1988 from the Early Eocene of France, or *Percopsiformis resonus* Schwarzhans, 2004 and *P. enigmaticus* Schwarzhans, 2003 from the Paleocene, or extant zoarcids. We do not postulate, however, a relationship to any of these, although a representative of an extant paracanthopterygian group may seem a possible candidate.

Species. A single species, *Vox thlotlo* n. sp. from the Late Santonian of Alabama.

Vox thlotlo n. sp.

Figs 6W-AD

Etymology: From thlotlo, the Muscogeean word for fish, used as noun in apposition.

Holotype: LACM 58469-35 (Fig. 6W-Y); from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Paratypes: 6 specimens, LACM 58469-36 (Figs. 6Z-AD); same data as holotype.

Diagnosis: Same as for genus (monospecific genus).

Description. Small, robust otoliths barely reaching 1.4 mm in length (holotype 1.4 mm). OH:OT = 2.6-3.0. Dorsal and ventral rims rather regularly curved; dorsal rim anterior-dorsally expanded, otherwise without angles. Rostrum short, rounded; antirostrum and excisura feeble. Posterior rim broadly rounded. All rims slightly crenulated or undulating.

Inner face slightly convex with median sulcus. Sulcus narrow, straight, its margin not indicating a distinction into ostium and cauda. Within sulcus two sharply rimmed and deepened colliculi; ostial colliculum terminating far from sulcus opening; caudal colliculum very small, terminating at some distance from posterior tip of sulcus; in between a narrow collum. Dorsal depression wide, distinct, with sharp crista superior towards sulcus margin. Ventral field with indistinct ventral furrow moderately close to ventral rim of otolith and few furrows ingressing from otolith rim until ventral furrow. Outer face moderately convex, smooth at its center, with irregular radial furrows towards the rims.

Collective genus *Otolithopsis* Huddleston, 1983

Otolithopsis sp. 1

Fig. 6AE

Material: 1 specimen, LACM 58469-45, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Discussion. A small, oval otolith of 1.75 mm length that resembles *Eutawichthys* otoliths, but with a much smaller rostrum and a much narrower ostium. The upward bent cauda suggests a berycoid affinity.

Otolithopsis sp. 2

Fig. 6AF

Material: 2 specimens, LACM 58469-46, Marvyn, Russell Co., Alabama; Eutaw FM, Late Santonian.

Discussion. Two fragmented small otoliths, the more complete figured one is 1.75 mm long and lacks the rostrum. The thin dorsal rim shows a prominent and sharp postdorsal angle, while the thick ventral rim is shallow and regularly curved. The posterior tip is pointed slightly inferiorly. The sulcus is deep, with a, partly preserved, rather narrow ostium and a cauda exhibiting a slightly widened and deepened terminating at some distance from the posterior tip of the otolith. The habitus resembles extant scorpaeniform otoliths, but the preservation is too poor to justify any substantiated interpretation.

Lapilli otoliths

Remark. The collection of otoliths from the Eutaw FM is remarkable for the abundance and diversity of lapilli otoliths, totaling 28 specimens. There is a total of 8 different lapillus morphotypes, one representing an Ariidae, a group commonly recorded as fossils and commonly described and 7 others, which cannot be allocated systematically with any degree of confidence for the time being, mainly because still too little is known of extant lapilli and also our knowledge of fossil lapilli other than ariids is extremely sparse. The description of these morphotypes and the discussion about their semblance has been generously provided by C. A. Assis. The description of lapilli otoliths follows the morphological terminology established by Assis (2005), except for ariid lapilli follows the long term established procedure for their description in order to avoid confusion.

Order **Siluriformes** Cuvier, 1817
Family Ariidae Bleeker, 1862
Genus *Arius* Valenciennes, 1840

Arius danicus Koken, 1891

Figs 7A-H

1891 *Arius danicus* - Koken: pl. 81, fig. 1
1930 *Arius rotundus* - Roedel: pl. 1, fig. 17

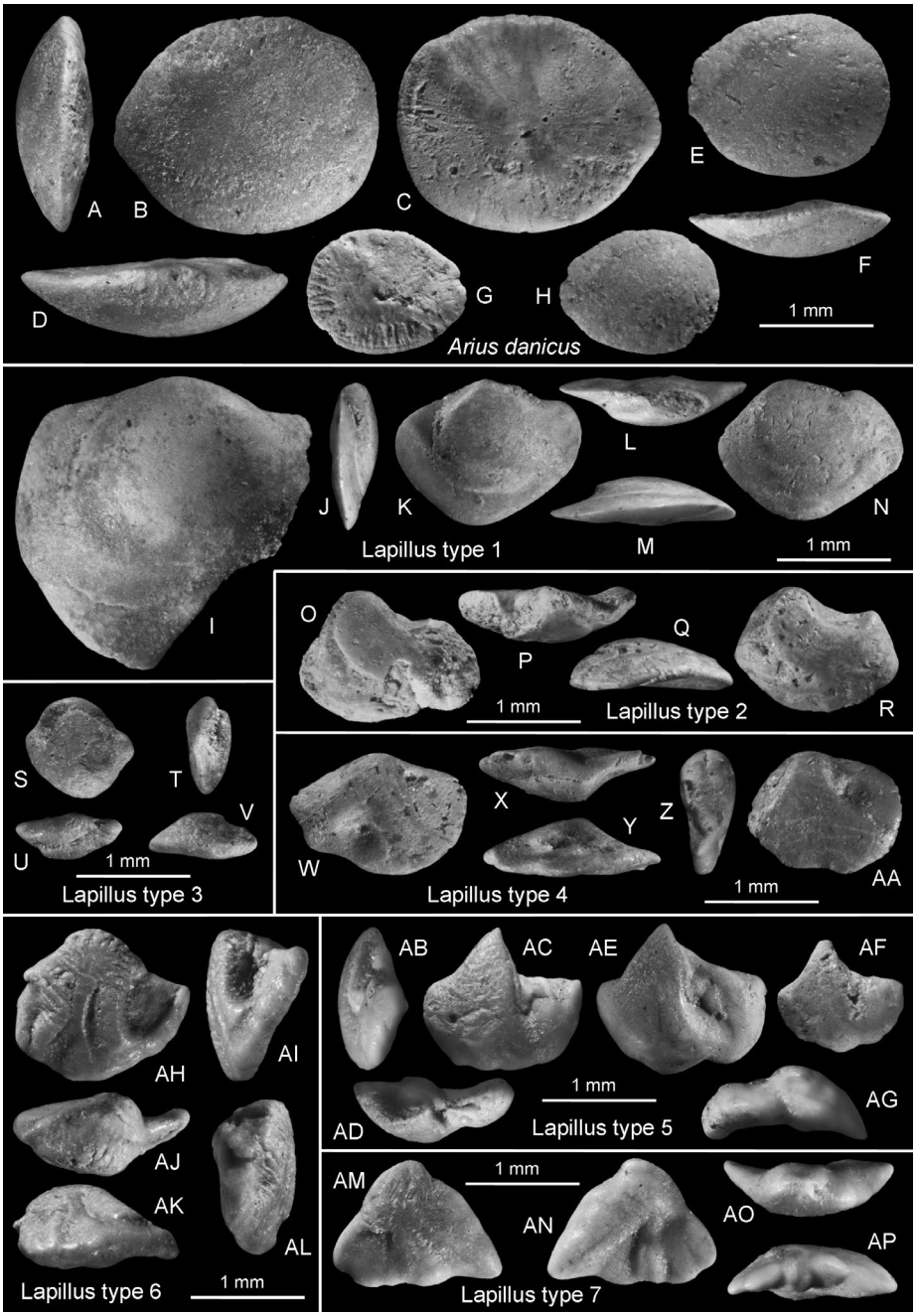

Fig. 7 - A-H) *Arius danicus* Koken, 1891, LACM 58469-37 (E-H reversed), B, E, H inner faces, C, G outer faces, A posterior view, D, F dorsal views; I-N) lapillus type 1, LACM 58469-38 (I reversed), I, K, N ventral views, J anterior view, L, M lateral views; O-R) lapillus type 2, LACM 58469-39 (O, P reversed), O, R ventral views, P, Q lateral views; S-V) lapillus type 3, LACM 58469-40, reversed, S ventral view, T anterior view, U-V lateral views; W-AA) lapillus type 4, LACM 58469-41, W, AA ventral view, Z anterior view, X-Y lateral views; AB-AG) lapillus type 5, LACM 58469-42 (AB-AD reversed), AC, AE, AF ventral views, AB anterior view, AD, AG lateral views; AH-AL) lapillus type 6, LACM 58469-43, AH ventral view, AI posterior view, AL anterior view, AJ-AK lateral views; AM-AP) lapillus type 7, LACM 58469-44, AM ventral view, AN dorsal view, AO-AP lateral views.

2003 *Arius danicus* Koken, 1891 - Schwarzhans: fig. 11J-K
2004 *Arius danicus* Koken, 1891 - Schwarzhans: fig. 3A-F
2010a *Arius danicus* Koken, 1891 - Schwarzhans: figs. 31-32
2011 *Arius danicus* Koken, 1891 - Schwarzhans & Bratishko: fig. 4A-E
2012 *Arius danicus* Koken, 1891 - Schwarzhans: figs. 48-51

Material: 7 specimens, LACM 58469-37, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Discussion. These are almost circular, round otoliths with only a small postdorsal projection, a flat outer face and mildly convex and smooth inner face with a faint sulcus like feature (confluentia gibbi maculae) running oblique along the dorsal rim. *Arius danicus* is regularly found in Maastrichtian and Paleocene rocks. Our finds from the Santonian represent the earliest of this apparently long ranging species. Huddleston & Savoie (1983) and Nolf & Dockery (1996) figured ariid otoliths from the Maastrichtian, which differs in being slightly more elongate. It resembles *Arius subtilis* Schwarzhans & Bratishko, 2011 from the European Paleocene. Interestingly, *A. danicus,* and possibly *A. subtilis* too, are amongst the very few otolith-based species persistent across the Cretaceous-Paleogene border event.

Unidentified lapilli morphotypes (descriptions and assessment provided by C. Assis)

Lapillus type 1
Figs 7I-N

Material: 5 specimens, LACM 58469-38, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Otolith longer than wide; elliptical asymmetrical, with longer axis much closer to apex of lateral margin. Lateral margin convex in median region and slightly concave both anteriorly and posteriorly. Medial margin curved, asymmetrical with premedian apex. Dorsal face flat. Ventral face convex. Gibbus maculae large, round and almost symmetrical. Prominentia marginalis coincident with apical curvature of gibbus maculae. Confluentia gibbi maculae narrow and superficial. Linea basalis conspicuous and continuous. Incisura lineae basalis absent.

Discussion. This is an unusually large lapillus for a non-Ostariophysi. The symmetry of its gibbus maculae resembles extant gadiform lapilli.

Lapillus type 2
Figs 7O-R

Material: 2 specimens, LACM 58469-39, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Otolith longer than wide, elongate. Anterior region wide, round or oval with median apex. Posterior region round or inflected with apex towards medial. Medial margin regularly curved, symmetrical with median apex. Lateral margin convex anteriorly until apex of prominentia marginalis, and concave posteriorly until a posterior-lateral protuberance. Dorsal face slightly concave. Ventral face convex. Gibbus maculae large and well marked; apical region long and tilted in anterior-lateral direction, from middle of otoliths slightly curving towards lateral direction, with parallel sides and round apex coincident with prominentia marginalis; basal region divided into two branches, posterior one wide and directed to posterior margin, anterior one slender and directed towards apex of curvature of anterior margin. Prominentia marginalis with round premedian apex, its anterior region continuous with curvature of anterior margin, posterior region marked by broad concavity between apex and posterior-lateral protuberance. Confluentia gibbi macula narrow and shallow. Linea basalis continuous. Incisura lineae basalis angular and deeply incisive, oriented antero-laterally in post-median position.

Discussion. This morphotype resembles lapilli of perciforms in the shape of the gibbus maculae, the linea basalis and its incisura.

Lapillus type 3
Fig. 7S-V

Material: 1 specimen, LACM 58469-40, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Otolith very small, rhomboidal, as long as wide. Anterior and posterior margins with round median apices. Medial margin round, asymmetrical with post-median apex. Lateral margin round, symmetrical, with median apex. Dorsal face slightly convex with apex in lateral region above prominentia marginalis. Ventral face convex. Gibbus maculae large and well-marked laterally, asymmetrical, with median apex and slightly tilted in anterior lateral direction. Prominentia marginalis conspicuous, with regularly rounded median apex, limited anteriorly and posteriorly by shallow broad concavities. Confluentia gibbi maculae wide and excavated in anterior and posterior regions. Linea basalis inconspicuous. Incisura lineae basalis absent.

Discussion. This morphotype resembles myctophiform lapilli, particularly of the family Myctophidae.

Lapillus type 4
Figs 7W-AA

Material: 2 specimens, LACM 58469-41, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Otolith longer than wide. Anterior region wide, round with median apex. Posterior region angular with round, median to slightly lateral apex. Medial margin regularly curved, asymmetrical with pre-median apex and shallow, median to slightly post-median shallow concavity defining a post-median angle. Lateral margin regularly rounded, with slightly post-median apex. Dorsal face flat. Ventral face concave anteriorly, convex posteriorly, with an inflection at the anterior mar-

gin of the gibbus maculae. Gibbus maculae triangular with anterior and posterior lateral sides concave and deep incisura lineae basalis; apical region short and round; basal region long and wide with two morphologically similar branches converging towards apical region. Prominentia marginalis with slightly pos-median apex, continuous with curvature of lateral margin. Confluentia gibbi maculae narrow and shallow. Linea basalis inconspicuous. Incisura lineae basalis triangular, angular, wide and very deep, reaching center of otolith, with apex pointing in direction of apex of gibbus maculae.

Discussion. These lapilli resemble those of certain scorpaeniforms and perciforms.

Lapillus type 5
Figs 7AB-AG

Material: 5 specimens, LACM 58469-42, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Otolith longer than wide. Anterior region oval, asymmetrical, with concave lateral margin and convex medial margin, converging to a lateral, more or less angular apex, and an irregular, large depression on surface close to anterior margin of gibbus maculae. Posterior region oval, asymmetrical, with concave lateral margin and convex medial margin, converging to a lateral round apex. Medial margin semi-elliptical, symmetrical with irregularly distributed, small and shallow grooves. Lateral margin concave both anteriorly and posteriorly in relation to apex of prominentia marginalis, anterior concavity deeper than posterior. Dorsal face concave. Ventral face convex. Gibbus maculae triangular, completely post-median, with sharp, pointed apex at level of its anterior margin, directed laterally. Prominentia marginalis triangular with post-median, sharp apex, usually completely covered by gibbus maculae. Confluentia gibbi maculae wide and excavated anteriorly and posteriorly of apex. Linea basalis visible, marked by a change in surface texture. Incisura lineae basalis presence uncertain.

Discussion. This is probably the most spectacular morphotype observed in the lapilli of the Eutaw FM and there are no Recent lapilli known which would resemble to any reasonable extend.

Lapillus type 6
Fig. 7AH-AL

Material: 1 specimen, LACM 58469-43, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Otolith as long as wide, rhomboidal with round corners. Anterior region wavy, asymmetrical, curved in dorsal direction, with concave lateral margin and convex medial margin, converging to lateral, more or less angular apex, and round arch shaped, large and deep depression on most of ventral surface, stressing the anterior margin of the gibbus maculae. Posterior region round, symmetrical, with small protuberance on posterior margin of gibbus maculae. Medial margin semi-elliptical, asymmetrical, slightly flattened posteriorly. Lateral margin concave anteriorly, straight posteriorly with round medial apex. Dorsal face concave. Ventral face convex. Gibbus maculae wavy; apical region rounded asymmetrical, with pre-median apex inclined in anterior lateral direction, and posterior end forming a protuberance in outline of otolith; basal region rectangular, narrower than apical region, concave anteriorly and straight posteriorly. Prominentia marginalis round, asymmetrical, with round, median apex, posteriorly continuous with curvature of lateral margin, but anteriorly marked by concave round incursion. Confluentia gibbi maculae narrow and shallow posteriorly and around prominentia marginalis, but wide and deep anteriorly. Linea basalis conspicuous, marked by rounded step and change in surface texture. Incisura lineae basalis poorly defined, triangular.

Discussion. This spectacular morphotype resembles that of type 5 in many aspects being distinguished primarily by the broad, rounded apex of the gibbus maculae. Again, there are no extant lapilli known to resemble this morphology.

Lapillus type 7
Fig. 7AM-AP

Material: 5 specimens, LACM 58469-44, from a section in a road cut on the Hurtsboro-Marvyn highway, 12.6 km south of Marvyn, Alabama; Eutaw FM, Late Santonian.

Description. Otolith triangular, longer than wide. Anterior region parabola-shaped with round medial apex. Posterior region triangular, angular with round, medial apex. Medial margin straight from anterior to the posterior apices, with irregular, wavy margin. Lateral margin triangular with round, asymmetrical median apex. Dorsal face slightly con-

vex with an irregular depression at medial anterior region. Ventral face convex. Gibbus maculae with round apical region, inclined towards lateral anterior direction. Prominentia marginalis triangular, continuous with sides of otolith. Confluentia gibbi maculae narrow and shallow. Linea basalis inconspicuous. Incisura lineae basalis absent.

Discussion. This morphotype structurally resembles certain gadiform lapilli, for instance the Merlucciidae, but differs significantly in its triangular outline.

Faunal analysis

Late Cretaceous otoliths have not been recorded very commonly in the past. The publications of Voigt (1926) about Senonian otoliths from erratic boulders of north-eastern Germany and Liebus (1927) about Campanian to Maastrichtian otoliths of Austria (originally believed to be of Eocene age) represent the first major contributions to the subject. Otoliths from Campanian to Maastrichtian rocks of Maryland, Mississippi, New Jersey and other localities in the eastern USA have been the subject of monographic studies by Huddleston & Savoie (1983), Nolf & Dockery (1990), Nolf & Stringer (1996) and Stringer, Oman & Badger (2016). Nolf (2003) described a Santonian otolith assemblage from Spain and Schwarzhans (2010a) from the Maastrichtian of Bavaria, Germany. These studies provide for a reasonable comparison despite the general paucity of our knowledge about Cretaceous otoliths. The Campanian otolith associations from Mississippi (Nolf & Dockery 1990) and New Jersey (Stringer et al. 2016) and the one from the Maastrichtian of Maryland (Huddleston & Savoie 1983; Nolf & Stringer 1996) resemble closest. Seven species are shared with the association described from the Campanian of New Jersey and three and four from the Campanian of Mississippi and Maastrichtian of Maryland respectively. Except for the enigmatic *Kokenichthys ensis* and for *Arius danicus* no species from the Santonian of Alabama is known from Europe. This indicates a relatively stable teleost faunal community in North-East America during Santonian and Campanian, which becomes even more obvious when comparing on the genus level. Nine of the 14 genera recognized in Alabama are likewise observed in the slightly younger formations of New Jersey. The otolith association of the Santonian of Alabama is distinguished from those slightly younger associations by the complete absence of trachichthyid otoliths and the occurrence of certain previously unrecorded morphotypes here considered to represent putative stomiiforms incertae sedis (*Allogenartina*), aulopiforms incertae sedis (*Pseudotrichiurus*) and a teleost incertae sedis (*Vox*). [In the introductory remarks to the systematic part, we have explained our rational for the establishment of fossil otolith-based genera.] The faunal composition is quite diverse with 18 taxa based on about 500 otolith specimens. The two most common species are *Eutawichthys stringeri* and *Osmeroides weileri*, which together account for about two-thirds of all specimens. Other fairly common species are *Allogenartina muscogeei, Elopothrissus* sp. (only juvenile specimens), *Apateodus assisi*, *Eutawichthys compressus, Cowetaichthys alabamae* and *C. lamberi*.

As already stated, the nature of the faunal composition of the teleost otoliths is not easily accessible in pre-Cenozoic times without some calibration through otolith finds in situ. So far, the identification of fossil otoliths relies heavily on comparison with extant material due to the current paucity of described articulated fossil skeletons with otoliths in situ. The reliability of such comparison of course decreases with increasing geological age of the otoliths, also because of the abundance of many extinct families or higher taxa during the Late Cretaceous, of which we do not know the otoliths. First studies from Cretaceous fishes with otoliths in situ retrieved by micro-CT scanning (Schwarzhans et al. 2018 in press) have revealed varying results. An otolith found in the *Osmeroides* sp., a fossil albuliform genus, matches well with isolated otoliths usually described as pterothrissids of an unresolved genus. On the other hand, otoliths sometimes described as representing a gempylid of some sort (Nolf & Stringer 1996) have been shown to belong to the genus *Apateodus*, a genus of the unrelated extinct suborder Ichthyotringoidei. This case may serve as an example of the pitfalls of systematic otolith allocation from Mesozoic strata when correlation has to be based on extant otoliths only. In recent literature about Cretaceous otoliths there has been a dispute concerning a number of morphotypes, which seem to resemble extant acanthopterygian otoliths. They are considered to represent perciforms (sensu Nelson 2006) by some (Nolf & Dockery 1990 or Nolf

& Stringer 1996) or as beryciforms and polymixiiforms of some kind (Schwarzhans 2010a). Most recently, Nolf (2016) extended the stratigraphic reach of otoliths interpreted as percoids and apogonids down to Cenomanian times. Three of the genera used here (*Apateodus, Eutawichthys, Cowetaichthys*) have also been associated with perciforms in the past (Nolf & Stringer 1996). Unambiguous articulated perciform skeletons, however, are rare in the uppermost Cretaceous (Patterson, 1993; Arratia et al. 2004; Carnevale & Johnson 2015). In our assessment, the otoliths in question show features that are not consistent with a placement in perciforms or apogonids. In our view it is more likely that they belong to extinct higher taxa of Cretaceous fishes known from skeletons and from which otoliths are not yet known. Some of the apparent similarities between such otolith morphotypes and extant otoliths of presumably unrelated fishes could well be an expression of functional morphology of fishes adapted to similar environments. This for instance appears to be the case for the similarity between *Apateodus* otoliths and extent gempylids (Schwarzhans et al. 2018 in press).

The Eutaw Formation is also unusually rich in highly diverse lapilli. The association of isolated lapilli from the Late Cretaceous is, however, even more tentative than that of sagittal otoliths, because much less is known of their morphology in the Recent, and in the fossil record there is essentially a recording gap throughout except for ariid otoliths. Nevertheless, some of the lapillus morphologies observed looks similar to gadiform, myctophiform and perciform morphologies, of which there are no coeval equivalents in the skeletal record. It is, however, also possible that certain lapilli could belong to stem teleosts or fossil holosteans. Anyway, we do not take these vague similarities at face value, but they still indicate that the diversity of the otolith-based faunal assemblage may have been larger than deduced from the sagittal otoliths only.

With all the restrictions in the systematic assessment of the otoliths studied here, it is difficult to reach any meaningful paleoecological conclusions. If the otoliths of *Allogenartina* indeed represent an early stomiiform, then this might reflect a moderately deep or a lower shelf environment with access to deeper water. This, however, contrasts with the shallow marine environment interpreted from other fossil groups (Smith 2001; Stephenson 1956).

Comparison with the skeleton-based fish fauna of the Niobrara Formation

The Eutaw Formation spans the time interval from Coniacian to Santonian in the states Tennessee, Mississippi, Alabama and Georgia. It represents the time equivalent section covered by the Niobrara Formation of the eastern Interior Basin, in particular of the Smoky Hill Chalk Member lagerstätte, known for its superbly preserved articulated vertebrate skeletons (Blakey 2014; Hattin 1982; Ikejiri et al. 2013; Shimer 1934). A total of 50 skeleton-based teleost species have been described from the Coniacian to early Campanian of the Niobrara Formation from Kansas, Colorado and South Dakota, ranking it as one of the richest Late Cretaceous fish faunas known to date (Cope 1878; Fielitz & Shimada 2009; Shimada & Fielitz 2006). They represent a large number of extinct Late Cretaceous families and higher taxonomic units such as Ichthyodectiformes, Tselfatiformes, Urenchelyidae of Anguilliformes, Crossognathiformes, Enchodontoidei and Ichthyotringoidei of Aulopiformes as well as certain taxa of acanthomorph or unknown affinities (Ferrifronsidae, *Laminospondylus* and *Aethocephalichthys*). Of these, otoliths in situ are only known of *Apsopelix* (Crossognathiformes) and *Apateodus* (Ichthyotringoidei) (Schwarzhans et al. 2018 in press). Representatives of families still persistent today are few in the Smoky Hill lagerstätte: Elopidae, Albulidae, Polymixiidae and Holocentridae. The fish fauna from the Smoky Hill Chalk is dominated by top-end predators and other large and robust fishes, for instances of the families Ichthyodectidae, Plethodidae, Pachyrhizodontidae, Enchodontidae and Holocentridae, while small "prey fishes" appear to be largely missing. Otolith assemblages on the other hand are typically dominated by those small "prey fishes", while crown predators are rare (see Nolf 1985, p. 19). The phenomenon is best documented by the abundance of small ophidiiform otoliths in practically all Eocene shallow water sediments, while their skeletal counterparts are largely missing. Those ophidiiforms represented an extinct branch of small shallow water fishes which may have preferred well aerated clastic environments, which are suitable for otolith fossilization. Articulated skeletons of fishes are more commonly preserved in carbonates or anoxic shales, which may not have been preferred environments for those small ophidiiform

Tab. 1 - Family level comparison chart of the Niobrara Formation skeletal teleost record and the Eutaw Formation otolith record.

Skeletal record from Niobrara Formation		Otolith based record from Eutaw Formation	
Order Family and genera	comment	**Order** Family and genera	comment
† Crossognathiformes			
† Crossognathidae († *Apsopelix*)	otoliths known in situ		
† Pachyrhizodontidae († *Pachyrhizodus*)	otoliths unknown		
† Ichthyodectiformes			
† Ichthyodectidae (with three genera)	otoliths unknown		
† Saurodontidae (with three genera)	otoliths unknown		
† Tselfatiiformes			
† Plethodidae (with 12 genera)	otoliths unknown		
Elopiformes		**Elopiformes**	
Elopidae († *Paleolops*)		Elopidae (*Elops*)	
Albuliformes		**Albuliformes**	
Albulidae (with one albulid gen. indet.)		† Osmeroididae († *Osmeroides*)	otoliths known in situ
		Pterothrissidae († *Elopothrissus*)	otolith-based genus
Anguilliformes		**Anguilliformes**	
† Urenchelidae	otoliths unknown	family indet.	
		Osteoglossiformes	
		family indet. († *Kokenichthys*)	otolith-based genus
		Clupeiformes	
		family indet.	
		Siluriformes	
		Ariidae (*Arius*)	
		Stomiiformes	
		family indet. († *Genartina*, † *Allogenartina*)	otolith-based genera
Aulopiformes		**Aulopiformes**	
† Cimolichthyidae († *Cimolichthys*)	otoliths unknown		
† Dercetidae (with three genera)	otoliths unknown		
† Enchodontidae († *Enchodus*)	otoliths unknown		
† Ichthyotringidae († *Apateodus*)	otoliths known in situ	† Ichthyotringidae († *Apateodus*)	otoliths known in situ
		family indet. († *Pseudotrichiurus*)	otolith-based genus
Beryciformes		**Beryciformes**	
Holocentridae († *Kansius*)		family indet. († *Eutawichthys*)	otolith-based genus
Polymixiiformes		**Polymixiiformes**	
Polymixiidae († *Omosoma*)		Polymixiidae († *Cowetaichthys*)	otolith-based genus
		Zeiformes	
		Antigoniidae (*Antigonia*)	
Acanthomorpha indet.			
† Ferrifronsidae († *Ferrifrons*)	otoliths unknown		
incertae sedis		**incertae sedis**	
† *Laminospondylus*	otoliths unknown		
† *Aethocephalichthys*	otoliths unknown	† *Vox*	otolith-based genus

fishes (see Schwarzhans 2010a, p. 89). A similar distinction is apparent between the carbonatic Smoky Hill Chalk and the sandy Eutaw Formation. Against this background, one would naturally expect a good degree of correlation between the fish fauna of the Niobrara Formation and the otolith assemblage of the Eutaw Formation, at least for fishes of a high trophic level. At the same time, we might expect some faunal complementation similar to observations previously made and resulting from differences in the paleoenvironment and the taphocoenosis.

A direct correlation is only possible in those rare instances of otoliths in situ or in the case of the persistent families. Relevant otoliths in situ have recently become known from the following Cretaceous genera: *Apateodus* (Ichthyotringidae), *Apsopelix* (Crossognathidae), *Hoplopteryx* (Trachichthyidae) and *Osmeroides* (Osmeroididae, Albuliformes) (Schwarzhans et al. 2018 in press). Of these, *Apateodus* is present in both skeleton record of the Smoky Hill Chalk and otolith record in the Eutaw Formation, *Apsopelix* is only present in the skeleton record, and *Osmeroides* only in the otolith record, although it could relate to an unspecified albulid in the Niobrara Formation (Shimada & Fielitz 2006). Other family level taxa occurring in the otolith records and possibly shared with the skeleton record (Tab. 1) are Elopidae, Anguilliformes family indet., Aulopiformes family indet., Polymixiidae and Beryciformes family indet. The large proportion of otolith morphologies not assigned to a specific family reflects of course the likelyhood of them representing extinct Cretaceous taxa of which otoliths are not yet known. There are, however, also a fair proportion of the otoliths from the Eutaw Formation, which cannot be compared to the skeleton record from Niobrara. For instance we have interpreted representatives of the Osteoglossiformes family indet., Clupeiformes family indet., Stomiiformes family indet. and Ariidae (Siluriformes). Of these, the ariid record can be considered as very reliable, while the other three are only tentatively assigned and could experience review once more otoliths in situ have become known from Cretaceous fishes.

In summary, we observe a relatively good correlation between the skeletal record from the Niobrara Formation and the otolith record from the Eutaw Formation, hampered by the still scarce record of otoliths in situ. The abundance of taxa in each taphocoenosis, however, differs widely. While the skeletal record is dominated by top predators and other large fishes, the otolith record is dominated by osmeroidids, pterothrissids, polymixiids and the genus *Eutawichthys,* an enigmatic morphology interpreted here as representing an extinct beryciform of some sort. Complementation is likely the cause for such otolith morphologies like *Allogenartina* (Stomiiformes family indet.), a Clupeiformes indet., *Arius*

(Ariidae) and *Vox* (incertae sedis). Table 1 summarizes the correlation between the skeleton record of the Niobrara Formation and the otolith record of the Eutaw Formation.

In 1919, Cockerell described a total of 21 morphotypes of scales from various Late Cretaceous rocks ranging geographically from California to Montana and New Jersey to Texas and gave them taxonomic names. Of course fish scales are easier to correlate with articulated fish skeletons than otoliths and Cockerell did so quite extensively according to his publication. Nevertheless, he only recognized two species as belonging to described skeletal remains, both belonging to the ichthyodectid genus *Xiphactinus* (as *Hypsodon* in Cockerell), and established new species and several new genera based on isolated scales. On family or higher level, his findings were rather consistent with the skeletal record, except for a new family (Erythrinolepidae) which he established based on isolated scales. Isolated fossil scales are apparently not used anymore for taxonomical purposes in paleontology, similar in most cases to isolated bones or teeth of teleosts. In our opinion we consider this an adequate practice since (sagittal) otoliths really are the only isolated teleost remains which are morphologically sufficiently diverse and taxonomically stable to be of practicable use.

Conclusions and Outlook

The otolith assemblage described here from the Eutaw Formation of Alabama represents the earliest otolith association recovered from the USA and is remarkable for its good preservation and diversity. The faunal composition shows a high degree of continuity with the younger otolith assemblages described from Campanian and Maastrichtian formations of the region. Many otolith morphologies are interpreted as representing extinct Late Cretaceous families or higher systematic units, as indicated by coeval skeletal finds, and therefore restrict comparison with otoliths of Cenozoic age or from Recent fishes. We interpret most otolith morphologies to represent teleost groups consistent with skeletal finds from the coeval Niobrara Formation lagerstätte, but there are also indications of the presence of complementary data in otoliths, such as from ariids and putative stomiiforms and clupeiforms of unresolved relationships.

The Late Cretaceous strata of the eastern USA have proven to be unusually rich in otoliths when compared internationally, probably because of an abundance of fine clastic sediments. In our view this indicates that many more otolith bearing strata could be discovered in the USA and many more and diverse otolith-based faunal assemblages could be found. With the rich record of Late Cretaceous articulated fish skeletons, particularly from the Niobrara Formation of the Interior Basin, we consider that the USA also represents a prime opportunity to prospect for otoliths in situ. Recovery of otoliths in situ represents an eminent goal for the calibration of isolated fossil otoliths, particularly from Cretaceous times, and will be the only viable solution in our view to resolve ongoing disputes concerning the interpretation of certain Cretaceous otolith morphologies.

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References

Arratia G., López-Arbarello A., Prasad G.V.R., Parmar V. & Kriwet J. (2004) - Late Cretaceous-Paleocene percomorphs (Teleostei) from India - Early radiation of Perciformes. In: Arratia G., Wilson M.V.H. & Cloutier R. (Eds) - Recent Advances in the Origin and Early Radiation of Vertebrates: 635-663. Verlag Dr. Friedrich Pfeil, München.

Assis C.A. (2005) - The utricular otoliths, lapilli, of teleosts: their morphology and relevance for species identification and systematics studies. *Scientia Marina*, 69: 259-273.

Blackey R.C. (2014) - Paleogeography and paleotectonics of the Western Interior Seaway, Jurassic-Cretaceous of North America. *Search and Discovery Article* #30392, posted Dec. 29, 2014.

Carnevale G. & Johnson G.D. (2015) - A Cretaceous cusk-eel (Teleostei, Ophidiiformes) from Italy and the Mesozoic diversification of percomorph fishes. *Copeia,* 103: 771-791.

Cockerell T.D.A. (1919) - Some American Cretaceous fish scales, with notes on the classification and distribution of Cretaceous fishes. *Bull. U.S. Geol. Serv.,* for 1918: 165-202.

Cook M.R, Smith K.M. & Rogers A.L. (2013) - Hydrogeological characterization and groundwater source devel-

opment asessment for the south Bullock County water authority. *Geol. Surv. Alabama, Open-file rep.,* 1309: 1-26.

Cope E.D. (1878) - Descriptions of fishes from the Cretaceous and Tertiary deposits west of the Mississippi River. *Bull. U.S. Geol. & Geogr. Surv.*, 4: 67-77.

Eargle D.H. (1955) - Stratigraphy of the outcropping Cretaceous rocks of Georgia. *U.S. Geol. Surv. Bull.* 1014: 1-101.

Fielitz C. & Shimada K. (2009) - A new species of *Apateodus* (Teleostei: Aulopiformes) from the upper Cretaceous Niobrara Chalk of western Kansas, U.S.A. *J. Vert. Paleontol.*, 29: 650-658.

Frazier W.J. (1996) - Estuarine deposits in the Eutaw and Blufftown formations (Santonian and Campanian) of southwestern Georgia and adjacent Alabama and their sequence stratigraphie significance. *Geol. Soc. America*, Abstracts with Programs, 28(2): 12.

Frazier W.J. (1997) - Upper Cretaceous strata in southwestern Georgia and adjacent Alabama. *Atlanta Geol. Soc. Field Trip Guidebook, Atlanta Geological Society, Atlanta*: 1-22.

Frazier W.J. & Taylor R.S. (1980) - Facies changes and paleogeographic interpretation of the Eutaw Formation (Upper Cretaceous) from western Georgia to central Alabama. In: Tull J.F. (Ed.) - Field Trips for the Southeastern Section of Geological Society of America, Birmingham, AL: 1-27.

Friedman M. (2009) - Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. *Proc. Nat. Acad. Sci.*, 106: 5218-5223.

Frizzell D.L. (1965) - Otolith-based genera and lineages of fossil bonefishes (Clupeiformes, Albulidae). *Senckenbergiana Lethaea*, 46a: 85-110.

Frizzell D.L. & Dante J.H. (1965) - Otoliths of some early Cenozoic fishes of the Gulf Coast. *J. Paleontol.*, 39: 687-718.

Gradstein M.G., Ogg J.G., Schmitz M.D. & Ogg G.M. (2012) - The geologic time scale. Elsevier, 1144 pp.

Hattin D.E. (1982) - Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (upper Cretaceous) of the type area, western Kansas. *Univ. Kansas publ.*, *Bull.* 225: 1-108.

Huddleston R.W. (1983) - *Otolithopsis*, nom. nov., new name for Otolithus Koken, 1884, non Cuvier, 1829 (Pisces: family incertae sedis). *J. Paleontol.*, 57: 601-602.

Huddleston R. & Savoie K. (1983) - Teleostean otoliths from the late Cretaceous (Maastrichtian age) Severn Formation of Maryland. *Proc. Biol. Soc. Washington*, 96: 657-663.

Ikejiri T., Ebersole J.A., Blewitt H.L. & Ebersole S.M. (2013) - An overview of Late Cretaceous vertebrates from Alabama. *Bull. Alabama Mus. Nat. Hist.*, 31: 46-71.

King D.T. (1990) - Facies stratigraphy and relative sea-level history - Upper Cretaceous Eutaw Formation, central and eastern Alabama. *Trans. Gulf Coast Assoc. Geol. Soc.*, 40: 381-387.

King D.T. (1993) - Eustatic and tectonic effects within sequence stratigraphy of the outcropping paralic-marine section, Upper Cretaceous, Alabama. *Trans. Gulf Coast Assoc. Geol. Soc.*, 43: 157-171.

Koken E. (1891) - Neue Untersuchungen an tertiären Fisch-Otoloithen II. *Z. deut. geol. Ges.*, 43: 77–170.

Liebus A. (1927) - Neue Beiträge zur Kenttnis der Eozänfauna des Krappfeldes in Kärnten. *Jb. geol. Bundesanst.*, 77: 333-393.

Mancini E.A. & Puckett T.M. (2005) - Jurassic and Cretaceous transgressive-regressive (T-R) cycles, northern Gulf of Mexico, USA. *Stratigraphy*, 2: 31-48.

Mancini E.A. & Soens D.D. (1994) - Paleoenvironments of the Tombigbee Sand Member of the Eutaw Formation (upper Cretaceous) of eastern Mississippi and western Alabama. *Gulf Coast Asoc. Geol. Soc. Trans.* 44: 421-430.

Miya M., Friedman M., Satoh T.P., Takeshima H., Sado T., Iwasaki W., Yamanoue Y., Nakatani M., Mabuchi K., Inoue J.G., Poulsen J.Y., Fukunaga T., Sato Y. & Nishida M. (2013) - Evolutionary origin of the Scombridae (tunas and mackerels): members of a Paleogene adaptive radiation with 14 other pelagic fish families. *Plos One*, 8, e73535: 1-19.

Nelson J.S. (2006) - Fishes of the world. 4th ed. Hoboken, John Wiley and Sons.

Nelson J.S., Grande T.C. & Wilson M.V.H. (2016) - Fishes of the world. 5th ed. Hoboken, John Wiley and Sons.

Nolf D. (1985) - Otolithi piscium. In: Handbook of Paleoichthyology, Vol. 10. Stuttgart, Gustav Fischer, 145 pp.

Nolf D. (1988) - Les otolithes de téléostèens éocènes d'Aquitaine (sud-ouest de la France) et leur intérêt stratigraphique. *Mém. Acad. roy. Belg., Cl. Sci.*, 19: 1-147.

Nolf D. (2003) - Fish otoliths from the Santonian of the Pyrenean faunal province, and an overview of all otolith-documented North Atlantic Late Cretaceous teleosts. *Bull. Inst. Roy. Sci. Natur. Belg.*, 73: 155-173.

Nolf D. (2013) - The Diversity of Fish Otoliths, Past and Present. Royal Belgian Institute of Natural Sciences, Brussels, 222 pp.

Nolf D. (2016) - Otoliths of Cenomanian fishes in the Ballon Marl (France). The earliest fossil record of perciform fishes. *Bull. Inform. Géol. Bassin Parisien*, 53: 14-20.

Nolf D. & Dockery D.T. (1990) - Fish otoliths from the Coffee Sand (Campanian of Northeastern Mississippi). *Mississippi Geol.*, 10: 1-14.

Nolf D. & Stringer G.L. (1996) - Cretaceous fish otoliths - a synthesis of the North American record. In: Arratia G. & Viohl G. (Eds) Mesozoic Fishes - Systematics and Paleoecology. 433-459. Verlag Dr. Friedrich Pfeil, Munich.

Patterson C. (1993) - An overview of the early fossil record of acanthomorphs. *Bull. Marine Sci.*, 52: 29-59.

Priem F. (1913) - Sur les otolithes de l'Eocène du Cotentin et de Bretagne. *Bull. Soc. géol. France*, 13: 151-158.

Reinhardt J. & Donovan A.A. (1986) - Stratigraphy and sedimentology of Cretaceous continental and nearshore sediments in the eastern Gulf coastal plain. In: Reinhardt J. (Ed.) - Stratigraphy and Sedimentology of Continental, Nearshore and Marine Cretaceous Sediments of the Eastern Gulf Coastal Plain, Field Trip No.3. *Soc. Econ. Paleontol. Mineral.-Am. Assoc. Pet. Geol. Annu. Meet.*: 3-28.

Reinhardt J., Schindler S. & Gibson T.G. (1994) - Geologic map of the Americus 30‘ X60‘ quadrangle, Georgia and

Alabama. *Department of the Interior, U.S. Geological Survey*, map 1-2174.

Roedel H. (1930) - Fischotolithen aus Palaeozängeschieben. *Z. Geschiebeforsch.*, 6: 49-77.

Savrda C.E. & Nanson L.L. (2003) - Ichnology of fair-weather and storm deposits in an Upper Cretaceous estuary (Eutaw Formation, western Georgia, USA). *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 202: 67-83.

Schubert R.J. (1916) - Obereozäne Otolithen vom Barton Cliff bei Christchurch (Hampshire). *Jahrb. K.u.K. Geol. Reichsanst., Wien*, 65: 277-288.

Schwarzhans W. (1978) - Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. *Meded. Werkgr. Tert. Kwart. Geol,* 15: 167-185.

Schwarzhans W. (1981) - Die Entwicklung der Familie Pterothrissidae (Elopomorpha; Pisces), rekonstruiert nach Otolithen. *Senckenbergeana lethaea*, 62: 77-91.

Schwarzhans W. (1986) - Fish otoliths from the lower Tertiary of Ellesmere Island. *Canadian J. Earth Sci.*, 23: 787-793.

Schwarzhans W. (2003) - Fish otoliths from the Paleocene of Denmark. *Geol. Surv. Denmark Greenland Bull.*, 2: 1-94.

Schwarzhans W. (2004) - Fish otoliths from the Paleocene (Selandian) of West Greenland. *Meddelser om Grønland*, 42: 1-32.

Schwarzhans W. (2010a) - Otolithen aus den Gerhartsreiter Schichten (Oberkreide: Maastricht) des Gerhartsreiter Grabens (Oberbayern). *Palaeo Ichthyologica*, 4: 1-100.

Schwarzhans W. (2010b) - The otoliths from the Miocene of the North Sea Basin. Backhuys Publishers, Leiden; Margraf Publishers, Weikersheim, 350 pp.

Schwarzhans W. (2012) - Fish otoliths from the Paleocene of Kressenberg, Bavaria, and Kroisbach, Austria. *Palaeo Ichthyologica*, 12: 1-88.

Schwarzhans W. & Bratishko A. (2011) - The otoliths from the middle Paleocene of Luzanivka (Cherkasy district, Ukraine). *N. Jb. Geol. Paläontol., Abh.*, 261: 83-110.

Schwarzhans W., Beckett H., Schein J. & Friedman M. (2018 in press) - Computed tomography as a tool for linking the skeleton- and otolith-based records of teleost fishes. *Palaeontology,* DOI 10.1111/pala.12349.

Scott J.C. (1962) - Geological map of Russell County, Alabama. *Geol. Surv. Alabama*, Special Map 24. Scale 1:63,360.

Shimada K. & Fielitz C. (2006) - Annotated checklist of fossil fishes from the Smoky Hill Chalk of the Niobrara Chalk (Upper Cretaceous) in Kansas. *Bull. New Mexico Mus. Nat. Hist.*, 35: 193-213.

Shimer H.W. (1934) - Correlation chart of geologic formations of North America. *Bull. geol. Soc. America*, 45: 909-936.

Smith C.C. (2001) - Implementation assessment for water resources availability, protection, and utilization for the Choctawhatchee, Pea, and Yellow Rivers watersheds. *Geol. Surv. Alabama Open-File Rep.*: 1-148 .

Stephenson L.W. (1956) - Fossils from the Eutaw Formation Chattahoochee River region, Alabama-Georgia. *U.S. Geol. Surv. prof. paper* 274-J: 227-250, plates 38-45.

Stinton F.C. (1965) - Teleost otoliths from the lower London Tertiaries. *Senckenbergiana Lethaea*, 46a: 389-425.

Stinton F.C. (1973) - Fish otoliths from the English Cretaceous. *Palaeontology*, 16: 293-305.

Stinton F.C. & Torrens H.S. (1968) - Fish otoliths from the Bathonian of southern England. *Palaeontology*, 11: 246-258.

Stringer G.L. (1991) - Upper Cretaceous (Maastrichtian) teleostean otoliths from the Ripley Formation, Union County, Mississippi. *Mississippi Geology*, 11: 9-19.

Stringer G.L., Oman L.D. & Badger R.F. (2016) - Woodbury Formation (Campanian) in New Jersey yields largest known Cretaceous otolith assemblage of teleostean fishes in North America. *Proc. Acad. Nat. Sci. Philadelphia*, 165: 15-36.

Voigt E. (1926) - Über ein bemerkenswertes Vorkommen neuer Fischotolithen in einem Senongeschiebe von Cöthen in Anhalt. *Z. Geschiebeforsch.*, 2: 172-187.

Weiler W. (1942) - Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. *Abh. Reichsamt Bodenforsch., N. F.,* 206: 5-140.