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Early Eocene fish otoliths from the eastern and southern USA

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Abstract. A collection of 1149 otoliths of the Ypresian and Ypresian–Lutetian transition (early Eocene) from 18 sites across five states in the eastern and southern regions of the USA was analyzed. In total, 33 otolith-based taxa are documented, of which 27 are identified at the species level. Nine of these are introduced as new species: "*Conger*" *biaculeatus* sp. nov., *Bauzaia gibbosa* sp. nov., *Ampheristus brevicaudatus* sp. nov., *Symmetrosulcus virginicus* sp. nov., *Neobythites longesulcatus* sp. nov., "*Neobythites*" *pamunkeyensis* sp. nov., "*Neobythites*" *stringeri* sp. nov., *Waitakia dorsogibbosa* sp. nov., and "*Haemulon*" *ypresiensis* sp. nov. The assemblages are distinct when compared to their younger Eocene counterparts in America. This distinction is primarily characterized by the high proportion of the newly introduced species or exclusive Ypresian species. Additionally, we highlight the presence of 10 amphi-Atlantic species originally described in European deposits. Significantly, the composition of the otolith collection supports the interpretation of a shallow-water environment for the sampled sites during the Ypresian. This ecological setting appears to persist into the subsequent middle and late Eocene within the same geographic region.

Keywords. Paleodiversity, Eocene, paleoecology, faunal comparison.

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Introduction

In a previous monograph (Lin & Nolf 2022), we provided a comprehensive account of all available knowledge on middle and late Eocene otoliths from the Atlantic side of the USA, encompassing both the Atlantic and Gulf Coastal Geologic plains. In the present study, we present the early Eocene counterpart of this work, which focuses on the Ypresian otoliths. Both studies combined provide a comprehensive

picture of the whole otolith-based fish fauna of the Eocene Gulf Coastal Plain allowing for a more thorough understanding of the diversity and distribution of these fossils in both time and space.

The study of fossil American fish otoliths dates back to the late 19th century, with early works by Koken (1888). Since then, various researchers have contributed to our understanding of otoliths from the Eocene formations along the Gulf Coast, including Frizzell & Lamber (1961, 1962), Frizzell (1965), Frizzell & Dante (1965), Stringer (1977, 1979, 1986, 2016), Stringer & Breard (1997), Ebersole *et al*. (2019), Stringer *et al*. (2022), and Lin & Nolf (2022). In addition, Müller (1999) provided a comprehensive monograph on shark teeth and otoliths from the Atlantic Coastal Plain.

Previously published papers have documented only five Ypresian taxa. They are, in the here adopted nomenclature: *Albula bashiana* (Frizzell, 1965), *Albula meridiana* (Frizzell, 1965), *Paraconger meridies* (Frizzell & Lamber, 1962), *Symmetrosulcus meyeri* (Koken, 1888), and a worn sciaenid otolith (Nolf 1995). With the exception of *S. meyeri*, reported from the Tallahatta Formation in Alabama (Ebersole *et al*. 2019), the remaining four species were reported from the Bashi Formation in Mississippi (Frizzell & Lamber 1962; Frizzell 1965; Nolf 1995).

Thanks to multiple sampling campaigns conducted by one of us (D. Nolf), whose results are discussed herein, we now possess additional data from the Ypresian deposits of the Atlantic Coastal Plain in Virginia and Maryland, where otoliths have never been mentioned for this age. These campaigns also provided additional information from the Gulf Coastal Plain in Alabama, Mississippi, and Texas, including specimens from the Reklaw Formation.

Material and methods

Sampling and otolith preparation

The primary source of the materials used in this study consists of the otoliths collected by D. Nolf during six field campaigns conducted between 1987 and 2007. The otoliths were obtained from sediment samples taken from the Ypresian (early Eocene) Atlantic and Gulf coastal plains. The geographic distribution is five states: Texas, Mississippi, Alabama, Virginia, and Maryland (Fig. 1). These samples were collected from eighteen different locations (described alphabetically by state) across Texas, Mississippi, Alabama, Virginia, and Maryland (Fig. 1), with the formations yielding otoliths indicated in Figure 2.

The bulk sediment samples were dried and then soaked in water before being screen-washed over a 0.75 mm mesh. Otoliths from fractions above 2 mm were handpicked at the site, while fractions between 2 and 0.75 mm were transported to the laboratories of the Institut royal des Sciences naturelles de Belgique (IRSNB) in Brussels, Belgium, where they were picked out using a Wild M5 stereo microscope. In addition, the collection includes isolated otoliths that were surface-collected and donated by D. Dockery, C. Garvie and G. Stringer. Whenever possible, the otoliths were identified at the species level. All material used in this study is deposited in the IRSNB under the code IRSNB P for figured specimens, unfigured specimens are kept unnumbered in the collection.

Comments on the age of the Reklaw Formation

The three otolith-bearing samples from the Reklaw Formation studied herein (1 from the locality Ridge Creek and 2 from the locality Taylor's Branch of Two Mile Creek, see below) are devoid of calcareous nannofossils (studied by E. Steurbaut), hindering a precise age assessment. No other samples from this unit were available to us for calcareous nannofossil dating. Consequently, the biostratigraphic and age-related considerations on the otolith association of the Reklaw Formation are exclusively based on literature. Jiang (1998) re-evaluated the ages of the Eocene and Oligocene sequences in 49 wells across the Western Gulf Coast region using the standard calcareous nannofossil markers as outlined in Perch-

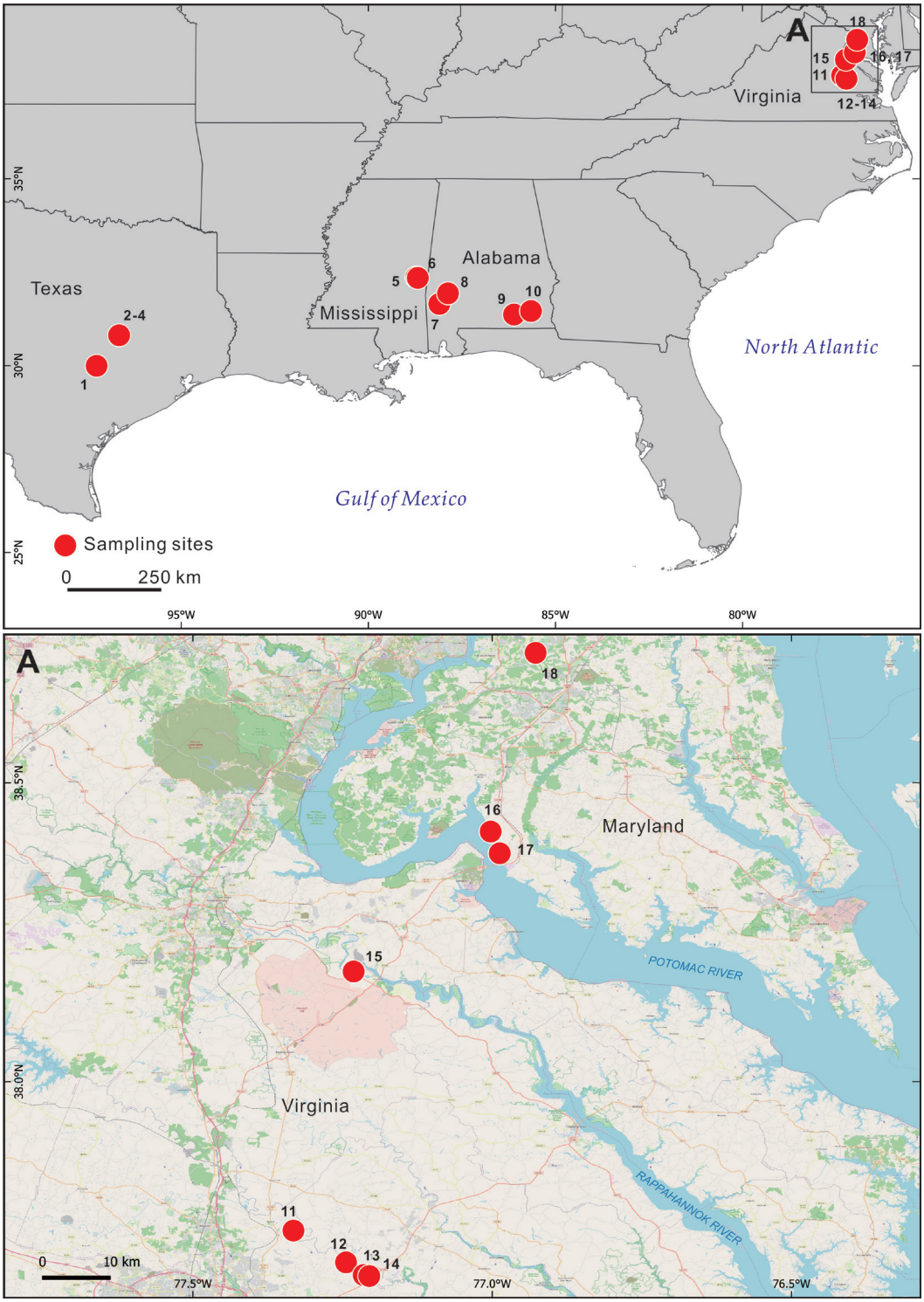

Fig. 1. Maps showing the sampling sites on the US Gulf Coastal Plain (Texas, Mississippi, and Alabama) and Atlantic Coastal Plain (A = Virginia and Maryland). **1**. Ridge Creek. **2–4**. Taylor's Branch of Two Mile Creek, samples 1–3. **5**. Meridian, Gallagher Creek. **6**. Meridian, Red Hot Truck Stop. **7**. Hatchetigbee Bluff. **8**. Cave Branch. **9**. Elba Dam on Pea River. **10**. Ozark. **11**. Pamunkey River, E of Hanover School for boys. **12**. Pamunkey River, Hanovertown. **13**. Pamunkey River, 1 km W of Hunters Club. **14**. Pamunkey River, Hunters Club. **15**. Rappahannock River. **16**. Loyola Retreat House, N of Popes Creek. **17**. Popes Creek, South. **18**. Piscataway Creek, Thrift Road ravine.

Nielsen (1985) (later updated in Agnini *et al*. 2014). He concluded that the lowest occurrence of the calcareous nannofossil species *Blackites inflatus* (Bramlette & Sullivan, 1961) is at the top of the lower third of the Reklaw Formation (Jiang 1998: 859, fig. 2). This nannofossil event marks the base of the Lutetian Stage as originally defined by the Global Stratotype Section and Point (GSSP) at Gorrondatxe (Spain) (Molina *et al*. 2011; Speijer *et al*. 2020). This means that only the lower portion of the Reklaw Formation belongs to the Ypresian, but that the main part of it is Lutetian in age. (Fig. 2). Jiang (1998: fig. 2) also suggested that it took about 1.7 Myr to deposit the Reklaw Formation, from about 48.4 Ma to about 46.7 Ma, if the data are converted to the time scale of Speijer *et al.* (2020). However, it must be noted that this indicative timeframe is difficult to assess on the basis of the available information. Sams & Gaskell (1998: figs 4–5) noticed around the same time that the lithostratigraphy of the Reklaw Formation is very complex. There is an increasing complexity in basinward direction, due to a series of distinct sand bodies which developed within the predominantly silty succession. The conclusions of a calcareous nannofossil dating of four separate locations by Sams & Gaskell (1998: 315) (among which the Bastrop County area where the Ridge Creek sample was collected) were far from decisive, as it suggested a possibly assignment to nannofossil zones CP11, CP12 or even CP 13. This nannofossil interval covers a very large time span (about 4 Myr according to Agnini *et al.* 2014, from about 50 Ma to 46 Ma), which extends far below and above the Ypresian/Lutetian boundary, dated at 47.84 Ma according to Payros *et al.* (2015). As to date we are unable to clarify the exact position of the studied otolith samples, we prefer to consider the Reklaw Formation as part of the Ypresian-Lutetian transition.

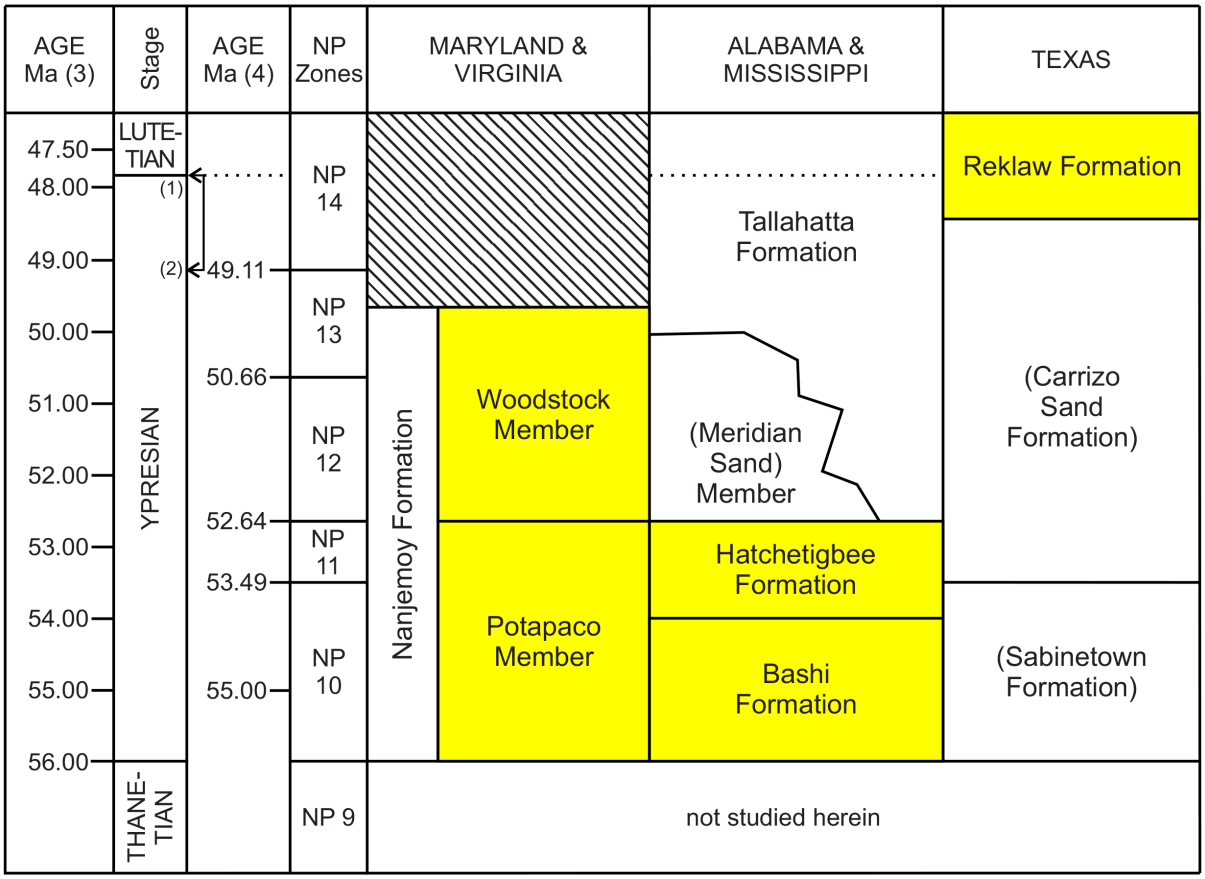

Fig. 2. Stratigraphic overview of the studied American Ypresian deposits. The studied formations are indicated in yellow. (1) GSSP for the base of the Lutetian as originally defined by Molina *et al*. (2011): 47.76 Ma, corrected to 47.84 Ma by Payros *et al*. (2015). (2) Age of the base of the historical Lutetian stratotype sensu Steurbaut & Nolf (2021): 49.11 Ma. (3) Speijer *et al*. (2020). (4) Agnini *et al*. (2014).

However, on top of these uncertainties arises the question of the placement of the GSSP for the base Lutetian, which was recently contested by Steurbaut & Nolf (2021) (see caption of Fig. 2). Based on a high-resolution biostratigraphic comparison between the GSSP at Gorrondatxe (Spain), Belgium and the historical Lutetian stratotype in the Paris Basin, they suggested that the golden spike had been placed 130 m too high at Gorrondatxe. It should be lowered down to a level predating the internationally accepted GSSP by about 1.3 Myr, estimated at about 49.11 Ma (Steurbaut & Nolf 2021), instead of the 47.76 Ma date initially proposed by Molina *et al.* (2011).

Locality data

ALABAMA

Cave Branch (Clarke County) (Fig. 1, site 8)
Alabama, Bashi 1/24 000 quadrangle, x = 418.175, y = 3533.525. GPS 31°56′04.9″ N, 87°51′56.4″ W.

Stratigraphy: Bashi Formation, Ypresian.

Sediment: coquina with grey green sandy matrix.

Available material: bulk samples collected by D. Nolf (ca 30 kg).

Elba Dam on Pea River (Coffee County) (Fig. 1, site 9)
Alabama, Ino 1/24 000 quadrangle, x = 586.300, y = 3470.100. GPS 31°21′43.9″ N, 86°05′33.3″ W. About 5 km S of Elba.

Identical locality: Loc. ACof-1 in Toulmin (1977: 372; see also Dockery & Thompson 2016: 330–331, figs 506–510).

Stratigraphy: Bashi Formation, Ypresian.

Sediment: fine-to medium-grained dark-greenish glauconitic sand, calcareous, with well preserved molluscs.

Available material: additional otoliths provided by C. Garvie.

Hatchetigbee Bluff (Washington County) (Fig. 1, site 7)
Alabama, Tattersville 1/24 000 quadrangle, x = 396.500, y = 3502.600. GPS 31°39′14.3″ N, 88°05′29.9″ W. Bluff section on W bank of Tombigbee River, about 7.5 km SW of Tattersville.

Identical locality: Loc. AWa-1 in Toulmin (1977: 380; see also Dockery & Thompson 2016: 331–332, figs 511–514).

Stratigraphy: type locality of the Hatchetigbee Formation, Ypresian.

Sediment: the Hatchetigbee Bluff section shows a very heterogeneous lithological succession. The lowest visible part at the time of the visit consisted of brownish-green, clayey sand with a *Venericardia* Lamarck, 1801 coquina, followed by (in ascending order): 2.3 m of finely stratified organic clay; about 1.20 m of green sand, the lower part of which protrudes markedly from the bluff; at least 2 m (upper part not well exposed) of organic clay; and, finally, a layer of green clayey sand with coquina levels of broken shell material.

Available material: *sample 13a* (ca 100 kg, sampled by D. Nolf in 1987) from the upper coquina in green clayey sand and some additional separate otoliths from the same level, provided by G. Stringer; *sample 13b* (ca 50 kg, sampled by D. Nolf in 1987) from the middle protruding sand bed; *sample 13c* (ca 50 kg, sampled by D. Nolf in 1987) from the *Venericardia* coquina, which was devoid of otoliths, but was used for calcareous nannofossil analysis.

Ozark (Dale County) (Fig. 1, site 10)
Alabama, Ozark 1/24 000 quadrangle, x = 628.800, y = 3482.475. GPS 31°28′11.6″ N, 85°38′39.1″ W. Railroad cut beneath overpass on old US Highway 231.

Identical locality: Loc. ADa-1 in Toulmin (1977: 375).

Stratigraphy: Bashi Formation, Ypresian.

Sediment: sand, greenish grey, fine- to medium-grained with well preserved shells of molluscs.

Available material: bulk samples collected by D. Nolf (ca 30 kg).

MARYLAND

Loyola Retreat House, N of Popes Creek (Charles County) (Fig. 1, site 16)
Maryland, Mathias Point 1/24 000 quadrangle, x = 325.300, y = 4254.050. GPS 38°25′03.5″ N, 77°00′04.0″ W.

Stratigraphy: Nanjemoy Formation, Woodstock Member, Ypresian.

Sediment: green glauconitic sand with mollusc shells.

Available material: bulk samples collected by D. Nolf (ca 150 kg).

Piscataway Creek, Thrift Road ravine (Prince George's County) (Fig. 1, site 18)
Maryland, Piscataway 1/24 000 quadrangle, x = 332.450, y = 4287.100. GPS 38°43′00.1″ N, 76°55′37.9″ W.

Stratigraphy: Nanjemoy Formation, Potapaco Member, Ypresian.

Sediment: glauconitic sand with mollusc shells, sampled near the top of the exposure.

Available material: bulk samples collected by D. Nolf in 1997 (ca 30 kg).

Popes Creek, South (Charles County) (Fig. 1, site 17)
Maryland, Colonial Beach North 1/24 000 quadrangle, x = 326.500, y = 4249.900. GPS 38°22′49.8″ N, 76°59′10.9″ W.

Identical locality: Loc. 68 in Ward (1985).

Stratigraphy: Nanjemoy Formation, Woodstock Member, Ypresian.

Sediment: glauconitic sand with small shells.

Available material: only sampled for nannoplankton (by D. Nolf in 1997); no otoliths encountered.

MISSISSIPPI

Meridian, Gallagher Creek (Lauderdale County) (Fig. 1, site 5)
Mississippi, Meridian 1/24 000 quadrangle, x = 338.125, y = 3582.125. GPS 32°21′51.7″ N, 88°43′13.8″ W. See also photographs in Dockery & Thompson (2016: 327, figs 489–491).

Stratigraphy: Bashi Formation, Ypresian.

Sediment: unweathered marls with many molluscs, shark teeth and other vertebrate remains.

Available material: additional otoliths provided by D. Dockery.

Meridian, Red Hot Truck Stop (Lauderdale County) (Fig. 1, site 6)
Mississippi, Meridian 1/24 000 quadrangle, x = 341.400, y = 3580.800. GPS 32°21′10.4″ N, 88°41′07.7″ W. Bluff behind the parking lot of the "Red Hot Truck Stop" restaurant. See also photograph in Dockery & Thompson (2016: 326, figs 483–486).

Identical locality: Mississippi Geological Society (MGS) Loc. No. 19.

Stratigraphy: Bashi Formation, Ypresian.

Sediment: coarse grey to reddish-brown glauconitic sand with many shells, exposed below a well marked level of large sandstone concretions.

Available material: bulk samples collected by D. Nolf in 1987 (ca 25 kg) and additional otoliths provided by D. Dockery.

TEXAS

Ridge Creek (Bastrop County) (Fig. 1, site 1)
Texas, Rosanky 1/24 000 quadrangle, x = 668.400, y = 3319.900. GPS 29°59′54.5″ N, 97°15′14.9″ W.

Stratigraphy: Reklaw Formation, unnamed member at top of Marques Shale Member, Ypresian–Lutetian transition (see Material and methods).

Available material: additional surface collecting otoliths provided by C. Garvie.

Taylor's Branch of Two Mile Creek (Milam County) (Fig. 1, sites 2–4)
Texas, Gause 1/24 000 quadrangle.

Stratigraphy, sampling and available material:

– *Sample 1*: Texas, Gause 1/24 000 quadrangle, x = 725.600, y = 3410.850. GPS 30°48′33.6″ N, 96°38′30.7″ W. Curve in the river, C. Garvie's best point for mollusc collecting; no otolith sample.
– *Sample 2*: Texas, Gause 1/24 000 quadrangle, x = 724.900, y = 3410.675. GPS 30°48′28.4″ N, 96°38′57.1″ W. About 200 m downstream from access to the river. Stratigraphy: Reklaw Formation, Ypresian–Lutetian transition (see Material and methods). Sediment: Clayey facies. Available material: bulk samples collected by D. Nolf (ca 30 kg).
– *Sample 3*: Texas, Gause 1/24 000 quadrangle, x = 724.800, y = 3410.700. GPS 30°48′29.3″ N, 96°39′00.9″ W. About 30 m downstream from access to the rivier. Stratigraphy: Reklaw Formation, Ypresian–Lutetian transition (see Material and methods). Sediment: sand facies. Available material: additional otoliths provided by C. Garvie.

VIRGINIA

Pamunkey River, E of Hanover School for boys (Hanover County) (Fig. 1, site 11)
Virginia, Hanover 1/24 000 quadrangle, x = 294.700, y = 4180.700. GPS 37°45′02.1″ N, 77°19′49.1″ W.

Identical locality: Loc. 13 in Strickland (1985).

Stratigraphy: Nanjemoy Formation, Potapaco Member, Bed B, Ypresian.

Sediment: olive-grey, very clayey glauconitic sand, burrowed, with many *Venericardia* shells.

Available material: 30 kg from lowest *Venericardia* level, taken by D. Nolf in 1989; no otoliths, but the sample was used for calcareous nannofossil analysis.

Pamunkey River, Hanovertown (Hanover County) (Fig. 1, site 12)
Virginia, Manquin 1/24 000 quadrangle, x = 302.200, y = 4174.450. GPS 37°41′45.4″ N, 77°14′36.7″ W

Identical locality: Loc. 51 in Ward (1985).

Stratigraphy: Nanjemoy Formation, Potapacco Member, Bed B, Ypresian.

Available material: bulk samples collected by D. Nolf in 1989 and 2000 (ca 100 kg).

Pamunkey River, Hunters Club (Hanover County) (Fig. 1, site 14)
Virginia, Manquin 1/24 000 quadrangle, x = 305.400, y = 4172.050. GPS 37°40′30.1″ N, 77°12′23.9″ W.

Identical locality: Loc. 30 in Strickland (1985) and Loc. 74 in Ward (1985).

Stratigraphy: Nanjemoy Formation, Woodstock Member, Ypresian.

Sediment: sand, olive-black, silty, very fine with large numbers of well-preserved molluscs, scattered throughout, large *Venericardia* concentrated in several thin bands.

Available material: 100 kg of sediment, taken by D. Nolf, 1989; no otoliths, but the sample was used for calcareous nannofossil analysis.

Pamunkey River, 1 km W of Hunters Club (Hanover County) (Fig. 1, site 13)
Virginia, Manquin 1/24 000 quadrangle, x = 304.825, y = 4172.150. GPS 37°40′32.9″ N, 77°12′47.4″ W.

Identical locality: Loc. 61 in Ward (1985).

Stratigraphy: Nanjemoy Formation, Potapaco Member, Bed D, Ypresian.

Sediment: sand, olive-black, silty, very fine, burrowed.

Available material: 30 kg of sediment, taken by D. Nolf, 1989; no otoliths, but the sample was used for calcareous nannofossil analysis.

Rappahannock River (Caroline County) (Fig. 1, site 15)
Virginia, Port Royal 1/24 000 quadrangle, x = 304.600, y = 4228.600. GPS 38°11′03.0″ N, 77°13′51.7″ W. Right bank of the Pamunkey River, in front of Goat Island.

Identical locality: Loc. 31 in Ward (1985).

Stratigraphy: Nanjemoy Formation, Potapaco Member, Ypresian.

Sediment: olive grey, very clayey fine sand.

Available material: bulk samples collected by D. Nolf (ca 180 kg).

Systematics

The classification system used in this paper is based on Nelson *et al*. (2016), while the authorships for higher taxa follow Van Der Laan *et al*. (2014). To maintain consistency, we only use existing generic names for fossil species belonging to extinct genera and restrict the use of exclusively otolith-based generic names. Fossil species that cannot be allocated to a specific genus are assigned to the type genus of the corresponding family or subfamily and presented between inverted commas (see Lin *et al*. 2017a, 2017b).

We first describe new species and then provide comments on rare or important taxa wherever necessary. Each identified taxon is accompanied by at least one otolith image (Figs 3–10). Diagnoses of new species include morphometrics and are limited to otolith length (OL), otolith height (OH), ostium length (OsL), and cauda length (CaL). A comprehensive list of all collected taxa and their abundance is presented in Table 1. Readers can refer to Lin & Nolf (2022) for detailed descriptions that are not repeated herein.

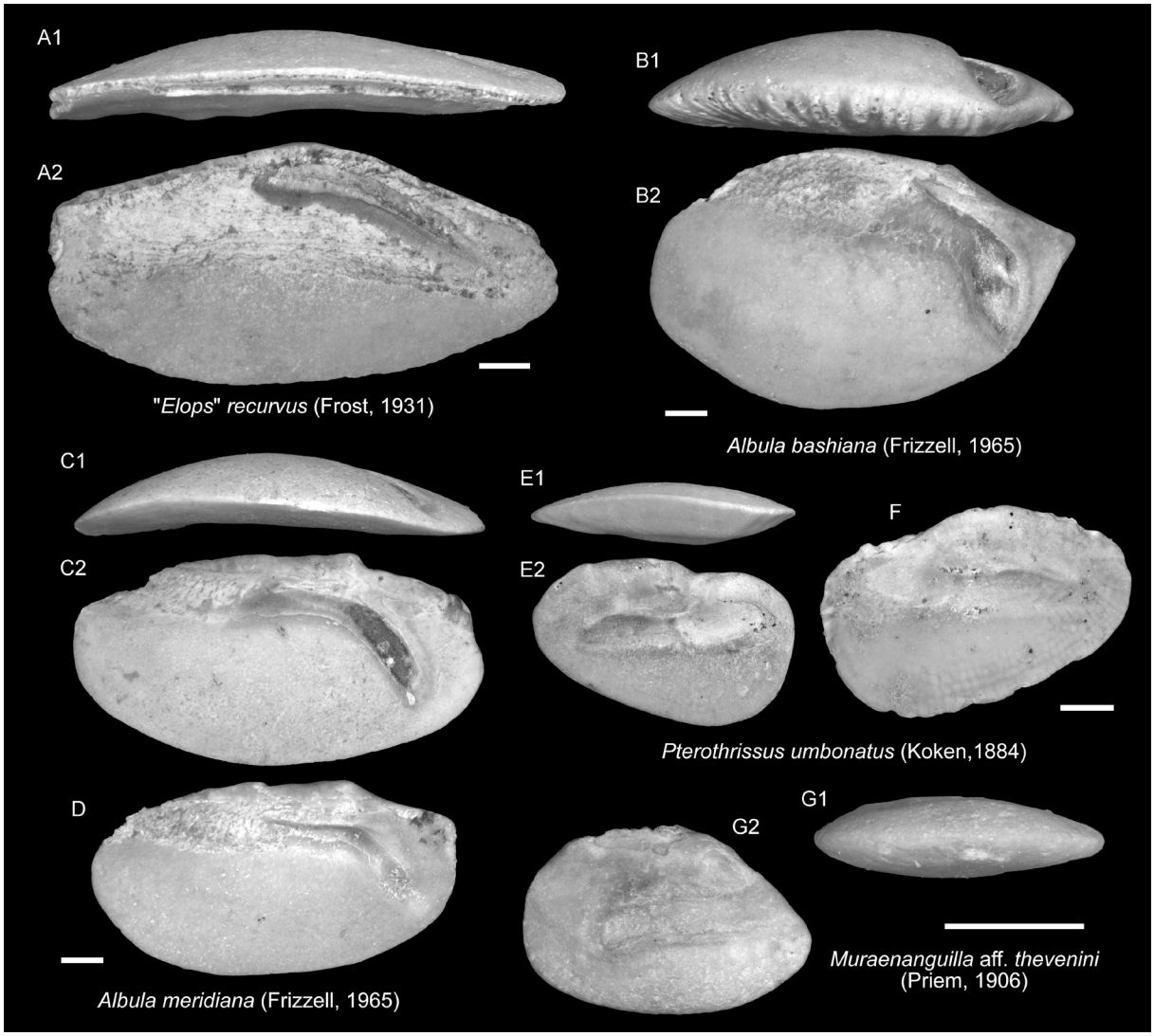

Fig. 3. Fish otoliths from the US lower Eocene formations. **A**. "*Elops*" *recurvus* (Frost, 1931), Hatchetigbee Bluff, Hatchetigbee Fm., Alabama (IRSNB P 10710). **B**. *Albula bashiana* (Frizzell, 1965), Meridian, Gallagher Creek, Bashi Fm., Mississippi (IRSNB P 10711). **C–D**. *Albula meridiana* (Frizzell, 1965), Meridian, Gallagher Creek, Bashi Fm., Mississippi (IRSNB P 10712, P 10713). **E–F**. *Pterothrissus umbonatus* (Koken,1884), Taylor's Branch of Two Mile Creek, Reklaw Fm., Texas (IRSNB P 10714, P 10715). **G**. *Muraenanguilla* aff. *thevenini* (Priem, 1906), Pamunkey River, Hanovertown, Potapaco Member, Virginia (IRSNB P 10716). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Table 1 (continued on next page). An overview of otolith-based fish taxa from the Ypresian (early Eocene) of the Atlantic and Gulf coastal plains. Fossil genera are underlined. Number of identified specimens are indicated in each studied stratum.

Fish otolith taxa from the early Eocene of eastern and southern USA	Mississippi	Alabama		Virginia	Maryland		Texas
	Bashi Fm.	Bashi Fm.	Hatchetigbee Fm.	Nanjemoy Fm.	Nanjemoy Formation		Reklaw Fm.
				Potapaco M.	Potapaco M.	Woodstock M.	
"*Elops*" *recurvus* (Frost, 1931)	3		1				
Albula bashiana (Frizzell, 1965)	13						
Albula meridiana (Frizzell, 1965)	3						
Pterothrissus umbonatus (Koken,1884)				3			15
Muraenanguilla aff. *thevenini* (Priem, 1906)				1			
Ariosoma sp.	1						
Paraconger meridies (Frizzell & Lamber, 1962)	195	64	24	14	2	2	
"*Conger*" *biaculeatus* sp. nov.		14					
"*Conger*" *websteri* (Frost, 1933)	2	1	16	1			1
Ariidae indet.		1					6
Saurida sp.		1					
Genartina bambergi (Priem, 1913)	3						
Myripristinae indet.							6
"*Merluccius*" *papillosus* (Stinton, 1966)				1			
Bauzaia gibbosa sp. nov.						3	
Bauzaia mucronata (Koken, 1891)							52
Ampheristus brevicaudatus sp. nov.		1		13		1	
Glyptophidium polli (Casier, 1946)		3	12	3			4
Symmetrosulcus virginicus sp. nov.			3	45	3	1	
Neobythites longesulcatus sp. nov.				1		3	
"*Neobythites*" *constrictus* Stinton, 1977				1			

Table 1 (continued). An overview of otolith-based fish taxa from the Ypresian (early Eocene) of the Atlantic and Gulf coastal plains. Fossil genera are underlined. Number of identified specimens are indicated in each studied stratum.

Fish otolith taxa from the early Eocene of eastern and southern USA	Mississippi	Alabama		Virginia	Maryland		Texas
	Bashi Fm.	Bashi Fm.	Hatchetigbee Fm.	Nanjemoy Fm.	Nanjemoy Formation		Reklaw Fm.
				Potapaco M.	Potapaco M.	Woodstock M.	
"*Neobythites*" *pamunkeyensis* sp. nov.				1			
"*Neobythites*" *stringeri* sp. nov.			4				
Preophidion arcuatus (Stinton, 1966)	4	39	180				
Centroberyx sp.	2	1	1				
Bothidae indet.							1
Waitakia dorsogibbosa sp. nov.				1	1		
Lactarius amplus Stinton, 1978			1	2			4
Lactarius kokeni (Dante & Frizzell, 1965)							17
Anisotremus rambo Lin & Nolf, 2022							1
Orthopristis burlesonis (Dante & Frizzell, 1965)	36	153	1	63	2		
"*Haemulon*" *ypresiensis* sp. nov.	46	18	2	6		1	
Ekokenia eporrecta (Koken, 1888)			1				17
Total	308	296	246	156	8	11	124

Results

Description of new species

Order Anguilliformes Regan, 1909
Suborder Congroidei Nelson, 1984
Family Congridae Kaup, 1856
Genus incertae sedis

"*Conger*" *biaculeatus* sp. nov.
urn:lsid:zoobank.org:act:644AE8C1-D8E8-471A-B0AC-054551C98BF0
Fig. 4D–H

Diagnosis

OL/OH = 1.8–1.9, OsL/CaL = 0.4–0.9. Small oval otoliths with salient and pointed rostrum and posterior rim. Wide sulcus, ostium opens widely to the antero-dorsal rim, cauda straight. Large colliculum visible in cauda.

Etymology

The species name *biaculeatus* alludes to the acuminated anterior and posterior rims of the otoliths.

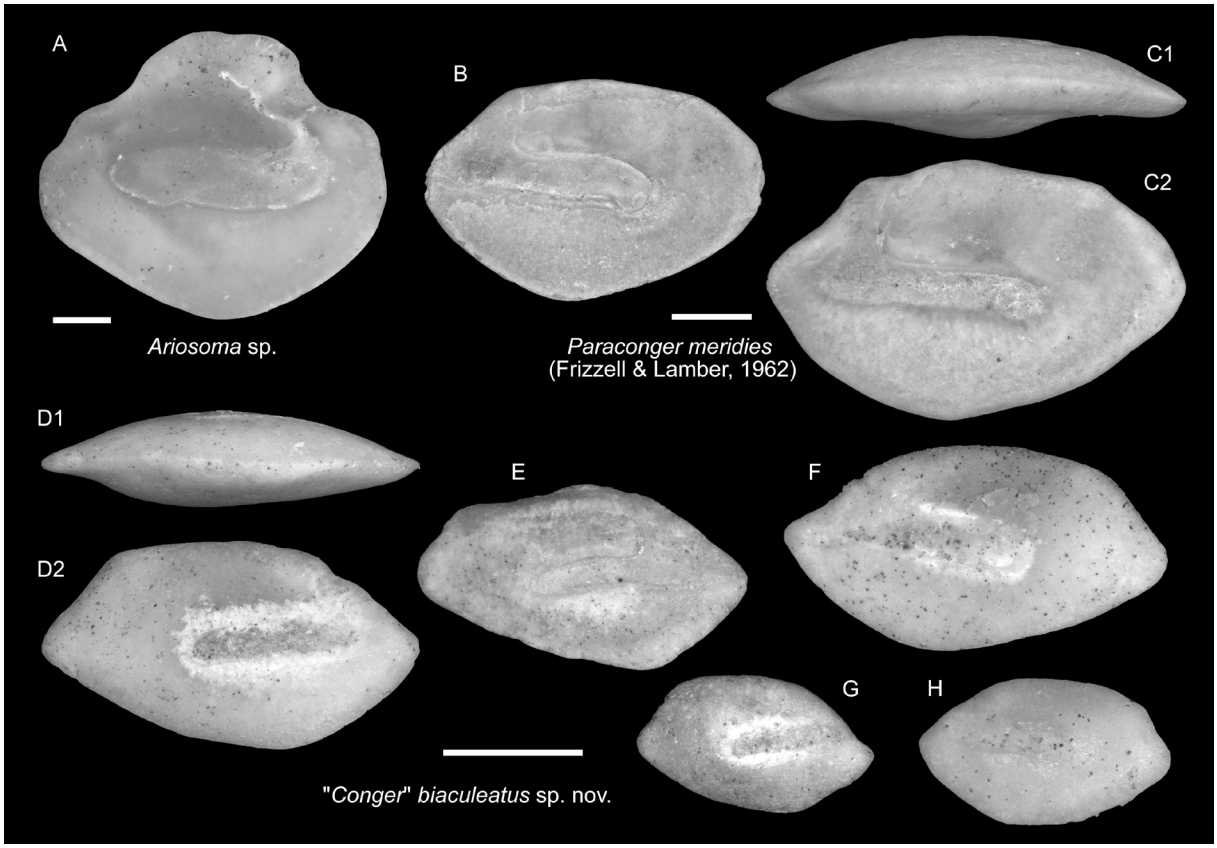

Fig. 4. Fish otoliths from the US lower Eocene formations. **A**. *Ariosoma* sp., Meridian, Red Hot Truck Stop, Bashi Fm., Mississippi (IRSNB P 10717). **B–C**. *Paraconger meridies* (Frizzell & Lamber, 1962), Rappahannock River, Potapaco Member, Virginia (IRSNB P 10718, P 10719). **D–H**. "*Conger*" *biaculeatus* sp. nov., Ozark, Bashi Fm., Alabama. **D**. Holotype (IRSNB P 10720). **E–H**. Paratypes (IRSNB P 10721 to P 10724). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Type material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Alabama, Ozark, Bashi Formation; Fig. 4D; IRSNB P 10720.

Paratypes (13 in total)

UNITED STATES OF AMERICA • 13 otoliths of which four are figured: Fig. 4E–H; same collection data as for holotype; IRSNB P 10721 to P 10724.

Type locality and horizon

United States of America, Ozark (Alabama), Bashi Formation.

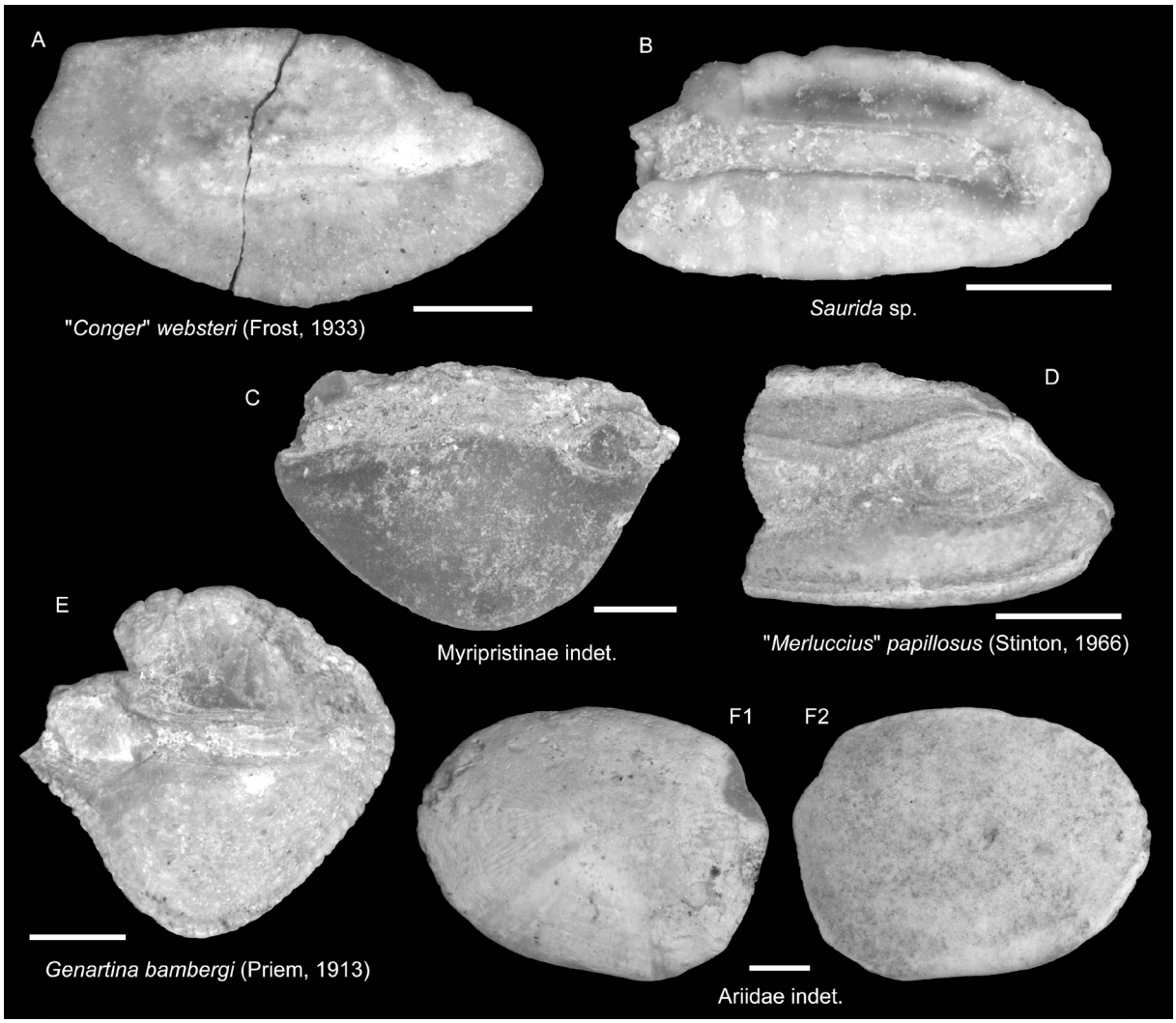

Fig. 5. Fish otoliths from the US lower Eocene formations. **A**. "*Conger*" *websteri* (Frost, 1933), Meridian, Red Hot Truck Stop, Bashi Fm., Mississippi (IRSNB P 10725). **B**. *Saurida* sp., Cave Branch, Bashi Fm., Alabama (IRSNB P 10726). **C**. Myripristinae indet., Ridge Creek, Reklaw Fm., Texas (IRSNB P 10727). **D**. "*Merluccius*" *papillosus* (Stinton, 1966), Rappahannock River, Potapaco Member, Virginia (IRSNB P 10728). **E**. *Genartina bambergi* (Priem, 1913), Meridian, Red Hot Truck Stop, Bashi Fm., Mississippi (IRSNB P 10729). **F**. Ariidae indet., Ridge Creek, Reklaw Fm., Texas (IRSNB P 10730). 1 = dorsal view; 2 = ventral view. Scale bars = 1 mm.

Dimensions of the holotype

Length = 2.69 mm; height = 1.47 mm; thickness = 0.69 mm.

Description

The newly described species "*C.*" *biaculeatus* sp. nov. is characterized by oval-shaped otoliths with pointed anterior and posterior rims. The otoliths are moderately thick and have smooth margins, with slightly convex inner and outer faces. The deepest part of the otoliths is in their central part, where the ventral rim is slightly angled. The sulcus is wide and not well-divided into ostium and cauda, opening antero-dorsally on the anterior rim. A large colliculum fills the sulcus, which is more visible in the cauda. The ostial crista superior curves markedly upwards, and the caudal cristae are well-developed. The cauda is short, straight, and ends well before the posterior rim, while the crista inferior is almost straight without constriction. The size of the ventral area is comparable to the dorsal one.

Remarks

The sulcus type of "*C.*" *biaculeatus* is similar to that of other species under the incertae sedis genus, such as "*C.*" *prolatus* and "*C.*" *websteri* in Lin & Nolf (2022: figs 12d–g, 13a–c), which suggests that it may belong to an extinct taxon within the family Congridae.

Stratigraphic and geographic distribution

Ypresian: Bashi Formation, Alabama.

Order Ophidiiformes Berg, 1937
Suborder Ophidioidei Berg, 1937
Family Ophidiidae Rafinesque, 1810
Subfamily Ophidiinae Rafinesque, 1810
Genus *Bauzaia* Dante & Frizzell, 1965

Bauzaia gibbosa sp. nov.
urn:lsid:zoobank.org:act:6C930371-0974-49BC-B693-778E70E26798
Fig. 6A

Diagnosis

OL/OH = 1.5, OsL/CaL = 2.8. Large, oval otoliths with salient and pointed posterodorsal angle. Straight, wide, well-divided sulcus; ostium large, elongate; cauda short, rectangular. Ventral area markedly large.

Etymology

'*Gibbosus*, *a*, *um*' = 'hump bearing'. Alludes to the very convex inner face of the otoltihs.

Type material examined

Holotype

UNITED STATES OF AMERICA • Right otolith; Maryland, Loyola Retreat House, N of Popes Creek, Woodstock Member; Fig. 6A; IRSNB P 10731.

Paratypes (2 in total)

UNITED STATES OF AMERICA • 2 otoliths very badly preserved, not figured; Maryland, Loyola Retreat House, N of Popes Creek, Woodstock Member; IRSNB.

Type locality and horizon

United States of America, Loyola Retreat House, N of Popes Creek (Maryland), Woodstock Member.

Dimensions of the holotype

Length = 3.77 mm; height = 2.56 mm; thickness = 1.00 mm.

Description

The otoliths are thick and rounded, with a salient, pointed posterior end. The inner face is convex and the outer face is strongly concave. The margins are smooth. The sulcus is straight, broad, and reaching, but not opening, to the margins of both anterior and posterior rims. It is divided into an elongate ostium and a very short cauda, which is rectangular and slightly pointing downwards. The ventral area is markedly large, semicircular and forming the general shape of the otoliths.

Remarks

The otolith characters of the new species, *Bauzaia gibbosa* sp. nov., display a mix of those seen in the other two congeneric species, *B. mucronata* (Koken, 1891), and *B. lamberi* Dante & Frizzell, 1965, but differ from them by lacking the notable antero-dorsal bulging expansion of the dorsal rim. The appearance and shape of the otoliths of *B. gibbosa* are most similar to those of *B. lamberi*, but the former has a sulcus type resembling that of *B. mucronata*, especially the rectangular shape of the cauda. The new species is very rare and only known from the type locality.

Stratigraphic and geographic distribution

Ypresian: Woodstock Member, Maryland.

Subfamily Neobythitinae Radcliffe, 1913
Genus *Ampheristus* König, 1825

Ampheristus brevicaudatus sp. nov.
urn:lsid:zoobank.org:act:4ACB919D-6809-44FF-AE33-560D58E9276B
Fig. 6D–G

Diagnosis

OL/OH = 1.8–2.1, OsL/CaL = 2.0–3.1. Otoliths with notable pointed or protruding posterior rim. Sulcus straight, elongate, well-divided into ostium and cauda, both filled with colliculum. Cauda short, oblong, ventrally oriented posteriorly.

Etymology

'*Brevicaudatus*, *a*, *um*' = 'having a short cauda'. Refers to the very small and short cauda.

Type material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Virginia, Rappahannock River, Potapaco Member; Fig. 6D; IRSNB P 10734.

Paratypes (14 in total)

UNITED STATES OF AMERICA • 12 otoliths of which three are figured: Fig. 6E–G; same collection data as for holotype; IRSNB P 10735 to P 10737 • 1 otolith; Alabama, Cave Branch, Bashi Formation; IRSNB • 1 otolith; Maryland, Loyola Retreat House, N of Popes Creek, Woodstock Member; IRSNB.

Type locality and horizon

United States of America, Rappahannock River (Virginia), Potapaco Member.

Dimensions of the holotype

Length = 3.85 mm; height = 1.84 mm; thickness = 0.79 mm.

Description

This species has fusiform otoliths with a postero-ventral angle that is extended. While the holotype has a pointed angle (Fig. 6D), it is typically blunt in other specimens (probably a result of abrasion). The margins are smooth, but may be slightly lobated in some specimens along the anterior and postero-dorsal rims (Fig. 6F). The antero-dorsal rim is slightly elevated, but not protruding dorsally, while the anterior rim forms a large, obtuse rostrum. The inner face is slightly convex; the outer face is concave posteriorly, but may be slightly convex anteriorly. The sulcus is well-divided into an elongate ostium and a very short, much narrower cauda that points downwards. Both the ostium and cauda are filled with a colliculum each. The ventral area is of similar size to the dorsal area. There is a shallow, elongate dorsal depression above the crista superior.

Remarks

Otoliths of *Ampheristus* are mainly known from Paleogene European deposits (Nolf 2013), with two species from the Lutetian of New Zealand (Schwarzhans 2019). The first record of the genus from the New World region is *Ampheristus americanus* Schwarzhans & Stringer, 2020, a recently described

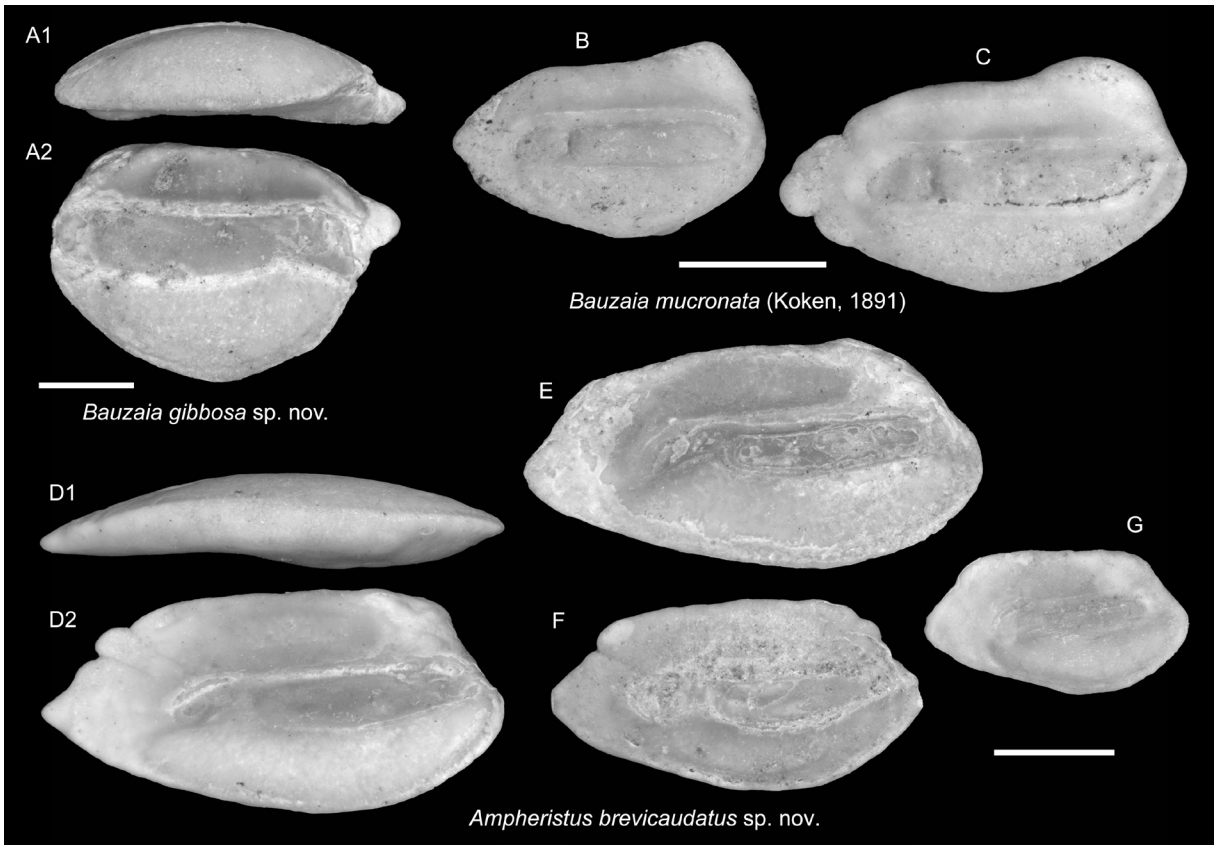

Fig. 6. Fish otoliths from the US lower Eocene formations. **A**. *Bauzaia gibbosa* sp. nov., Loyola Retreat House, N of Popes Creek, Woodstock M., Maryland (IRSNB P 10731). **B–C**. *Bauzaia mucronata* (Koken, 1891), Taylor's Branch of Two Mile Creek, Reklaw Fm., Texas (IRSNB P 10732, P 10733). **D–G**. *Ampheristus brevicaudatus* sp. nov., Rappahannock River, Potapaco Member, Virginia. **D**. Holotype (IRSNB P 10734). **E–G**. Paratypes (IRSNB P 10735 to P 10737). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Maastrichtian–Danian species from the southern USA (Schwarzhans & Stringer 2020; Stringer & Schwarzhans 2021). The cauda of *A. brevicaudatus* sp. nov. is much shorter than that of *A. americanus*. The posterior rim of *A. brevicaudatus* also appears to be more pointed than the truncated rim of *A. americanus*. The occurrences of the new species and *A. americanus* indicate a much wider geographic distribution and longer stratigraphic range of *Ampheristus*.

Stratigraphic and geographic distribution

Ypresian: Bashi Formation, Alabama; Potapaco Member, Virginia; Woodstock Member, Maryland.

Genus *Symmetrosulcus* Schwarzhans, 1981

Symmetrosulcus virginicus sp. nov.
urn:lsid:zoobank.org:act:72E254E4-1823-4F6B-9E38-3C7F45389634
Fig. 7C–F

Diagnosis

OL/OH = 1.7–1.8, OsL/CaL = 1.0–1.4. Elliptic otoliths with angled posterior rim. Concave postero-ventral rim. Dorsal and ventral rims gently curved. Anterior rim blunt. Sulcus very wide and elongate. Ostium slightly longer than cauda, similar width, each filled with colliculum.

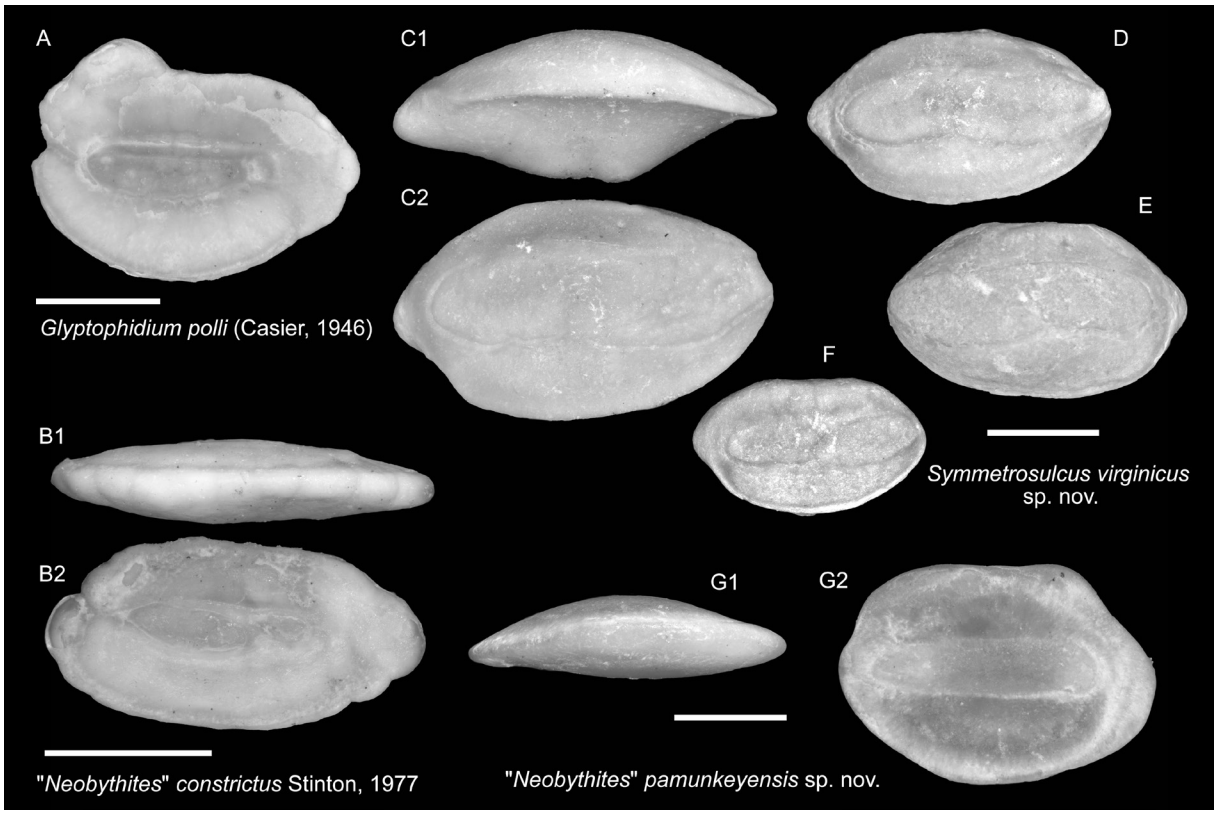

Fig. 7. Fish otoliths from the US lower Eocene formations. **A**. *Glyptophidium polli* (Casier, 1946), Pamunkey River, Hanovertown, Potapaco Member, Virginia (IRSNB P 10738). **B**. "*Neobythites*" *constrictus* Stinton, 1977, Rappahannock River, Potapaco Member, Virginia (IRSNB P 10739). **C–F**. *Symmetrosulcus virginicus* sp. nov., Pamunkey River, Hanovertown, Potapaco Member, Virginia. **C**. Holotype (IRSNB P 10740). **D–F**. Paratypes (IRSNB P 10741 to P 10743). **G**. "*Neobythites*" *pamunkeyensis* sp. nov., Pamunkey River, Hanovertown, Potapaco Member, Virginia, holotype (IRSNB P 10744). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Etymology

'*Virginicus*, *a*, *um*' = 'from Virginia'. The name alludes to the state, where the holotype was collected.

Type material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Virginia, Pamunkey River, Hanovertown, Potapaco Member; Fig. 7C; IRSNB P 10740.

Paratypes (51 in total)

United States of America • 44 otoliths of which three are figured: Fig. 7D–F; same collection data as for holotype; IRSNB P 10741 to P 10743 • 3 otoliths; Alabama, Hatchetigbee Bluff, Hatchetigbee Formation; IRSNB • 1 otolith; Maryland, Loyola Retreat House, N of Popes Creek, Woodstock Member; IRSNB • 3 otoliths; Maryland, Piscataway Creek, Thrift Road ravine, Potapaco Member; IRSNB.

Type locality and horizon

United States of America, Pamunkey River, Hanovertown (Virginia), Potapaco Member.

Dimensions of the holotype

Length = 3.41 mm; height = 1.96 mm; thickness = 1.38 mm.

Description

The otoliths of this new species are elliptical in shape, with a blunt anterior rim and a well-marked posterior angle. The dorsal and ventral rims are gently curved, and their deepest part is in the middle of the otoliths, giving them a regular, rounded appearance. All margins are smooth, and the otoliths are considerably thick, with both the inner and outer faces being convex (Fig. 7C1). A straight, wide, and well-divided sulcus occupies nearly the entire length of the inner face and is located in the central zone of the otoliths. The ostial and caudal parts are each fully filled by a colliculum. The ostium reaches the anterior margin, while the cauda extends backward to the origin of the posterior angle but does not reach the posterior margin. The cauda is slightly shorter than the ostium. The ventral area is of similar size as the dorsal one.

Remarks

The general shape of the otoltihs and the caudal type of this new species are similar to those of *Symmetrosulcus meyeri* (Koken, 1888) (see Lin & Nolf 2022: fig. 18a–f), whereas the thickness of the otoliths is similar to that of the otoliths of *Preophidion*, such as *P. elevatus* (Koken, 1888) and *P. granus* (Müller, 1999). However, the otoliths of the new species exhibit a concavity on the postero-ventral rim, and its sulcus is much wider than that of *S. meyeri*. On the other hand, the cauda of the new species does not bend as strongly as that of *Preophidion*. The sulcus of the new species suggests that it is more similar to *Symmetrosulcus* than to *Preophidion*.

Stratigraphic and geographic distribution

Ypresian: Hatchetigbee Formation, Alabama; Potapaco Member, Virginia and Maryland; Woodstock Member, Maryland.

Genus *Neobythites* Goode & Bean, 1885

Neobythites longesulcatus sp. nov.
urn:lsid:zoobank.org:act:E7434385-3EEF-4F21-B545-519B63B9EA49
Fig. 8A–C

Diagnosis

OL/OH = 1.8–1.9, OsL/CaL = 2.5–2.8. Fusiform otoliths with angled posterior rim. Rounded antero-dorsal bulge on dorsal rim. Anterior rim largely blunt. Sulcus very wide and elongate. Ostium markedly elongate, very slightly narrower than rectanglar cauda.

Etymology

'*Longesulcatus*, *a*, *um*' = 'provided with a long sulcus'. Refers to the notably elongate sulcus of the species.

Type material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Virginia, Pamunkey River, Hanovertown, Potapaco Member; Fig. 8A; IRSNB P 10745.

Paratypes (3 in total)

UNITED STATES OF AMERICA • 3 otoliths of which two are figured: Fig. 8B–C; Maryland, Loyola Retreat House, N of Popes Creek, Woodstock Member; IRSNB P 10746, P 10747.

Type locality and horizon

United States of America, Pamunkey River, Hanovertown (Virginia), Potapaco Member.

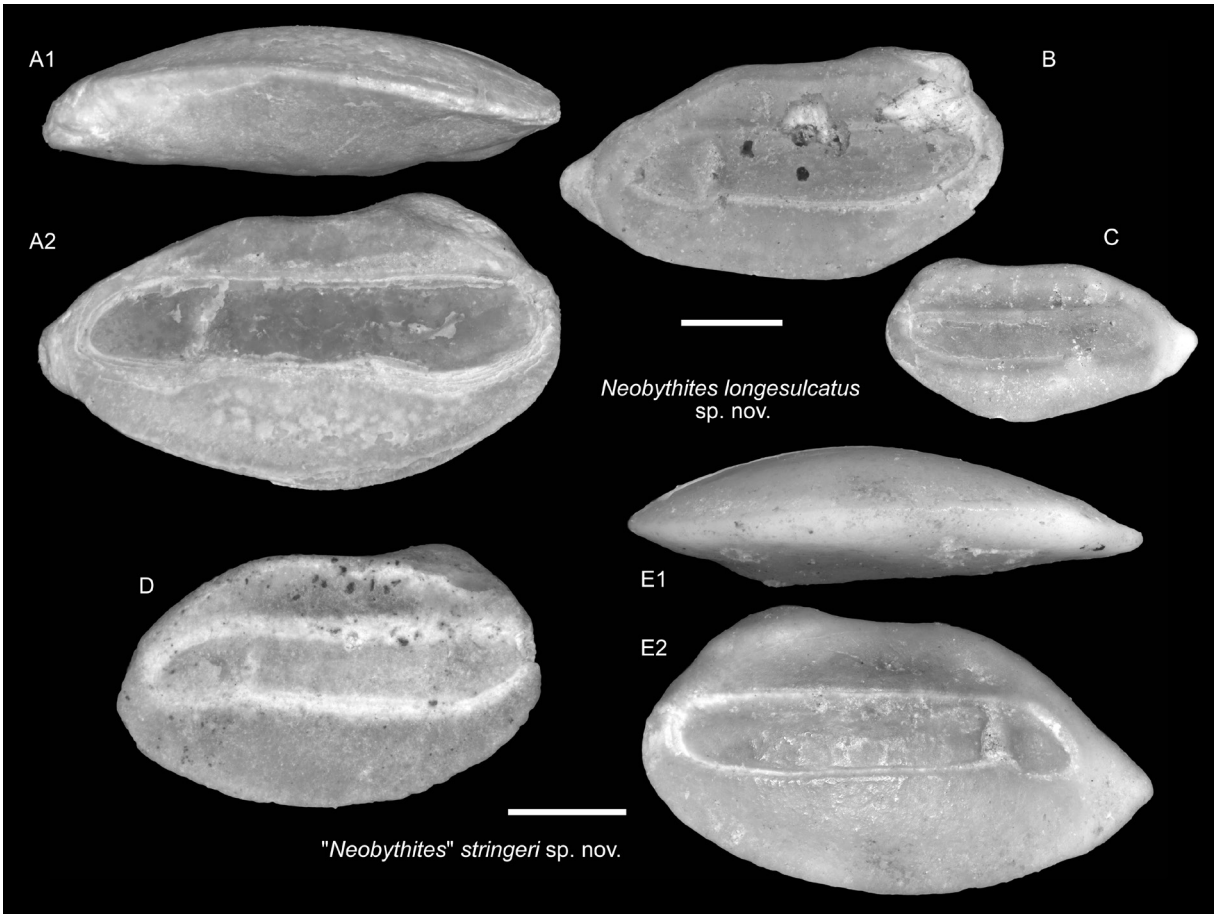

Fig. 8. Fish otoliths from the US lower Eocene formations. **A–C**. *Neobythites longesulcatus* sp. nov. **A**. Pamunkey River, Hanovertown, Potapaco Member, Virginia, holotype (IRSNB P 10745). **B–C**. Loyola Retreat House, N of Popes Creek, Woodstock M., Maryland, paratypes (IRSNB P 10746, P 10747). **D–E**. "*Neobythites*" *stringeri* sp. nov., Hatchetigbee Bluff, Hatchetigbee Fm., Alabama. **D**. Paratype (IRSNB P 10748). **E**. Holotype (IRSNB P 10749). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Dimensions of the holotype

Length = 4.99 mm; height = 2.81 mm; thickness = 1.50 mm.

Description

The species is identifiable by its fusiform otoliths, which have a largely blunt anterior rim and a well-marked posterior angle. The dorsal rim is elevated and possesses a blunt antero-dorsal bulge, forming the highest point of the otoliths. The ventral rim is gently curved, and all margins are smooth. The otoliths are thick and possess convex inner and outer faces (Fig. 8A1). A straight, wide, and well-divided sulcus occupies nearly the entire length of the inner face in the central region of the otoliths. The sulcus does not open to the margins. The ostium is notably elongate and extends over one-third of the sulcus length, and it is very slightly narrower than the short, rectanglar cauda. Above the crista superior, there is a shallow, elongate dorsal depression.

Remarks

The massive, robust otoliths of this new species share many characters with those of "*Neobythites*" *auribatianus* Lin *et al*., 2017, from the Lutetian of the Aquitaine Basin (Lin *et al*. 2017b: fig. 9a–g), indicating a possible close relationship. Nevertheless, the American species is distinguished by its less pronounced blunt antero-dorsal bulge, more rounded anterior rim, less tapered posterior rim, and somewhat broader sulcus. Moreover, the high resemblance of the sulcus shape and proportions (e.g. OL/sulcus length, OsL/CaL) and the overall configuration with otoliths of *Neobythites* allow us to assign this new species to this extant genus (see Lin & Chang 2012: pl. 81).

Stratigraphic and geographic distribution

Ypresian: Potapaco Member, Virginia; Woodstock Member, Maryland.

Genus incertae sedis

"*Neobythites*" *pamunkeyensis* sp. nov.
urn:lsid:zoobank.org:act:3CC19923-220B-4A62-A48E-D0791BC2486B
Fig. 7G

Diagnosis

OL/OH = 1.5. Squarish otoliths with postero-dorsal angle. Anterior rim rounded, posterior rim largely blunt. Sulcus elongate, not divided, slightly wider posteriorly.

Etymology

'*Pamunkeyensis*, *is*, *e*' = 'from the Pamunkey River'. Refers to the river area, where the specimens have been collected.

Type material examined

Holotype

UNITED STATES OF AMERICA • Right otolith; Virginia, Pamunkey River, Hanovertown, Potapaco Member; Fig. 7G; IRSNB P 10744.

Type locality and horizon

United States of America, Pamunkey River, Hanovertown (Virginia), Potapaco Member.

Dimensions of the holotype

Length = 2.82 mm; height = 1.98 mm; thickness = 0.77 mm.

Description

The otolith of this species is characterized by an oval to squarish outline with a prominent postero-dorsal angle. The dorsal rim is nearly flat, and and the ventral rim is gently curved. The anterior rim is rounded, and the posterior rim is largely blunt. All margins are smooth. The otoliths are thick, with both the inner and outer faces convex (Fig. 7G1). A straight, elongate, and undivided sulcus sits in the central zone of the otolith. The sulcus does not open to the margins. The posterior part of the sulcus is slightly wider than the anterior part and very slightly bent downward at the tip. The ventral area is of similar size as the dorsal one.

Remarks

This species is solely represented by a single specimen from the type locality. The bizarre outline and undivided sulcus are a unique character combination that does not resemble any known otolith-based species.

Stratigraphic and geographic distribution

Ypresian: Potapaco Member, Virginia.

"*Neobythites*" *stringeri* sp. nov.
urn:lsid:zoobank.org:act:A1E1BA6B-78E3-4FCC-BAE7-35737F87131D
Fig. 8D–E

Diagnosis

OL/OH = 1.6–1.8, OsL/CaL = 2.9–4.1. Fusiform otoliths with blunt antero-dorsal bulge and pointed posterior rim. Anterior rim largely blunt. Sulcus wide, elongate, well-divided. Ostium markedly elongate; cauda oval, pointing downward.

Etymology

This species is dedicated to Gary L. Stringer (University of Louisiana at Monroe) for his major contributions to the knowledge of the fossil otoliths from the USA.

Type material examined

Holotype
UNITED STATES OF AMERICA • Right otolith; Alabama, Hatchetigbee Bluff, Hatchetigbee Formation; Fig. 8E; IRSNB P 10749.

Paratypes (3 in total)
UNITED STATES OF AMERICA • 3 otoliths of which one is figured: Fig. 8D; same collection data as for holotype; IRSNB P 10748.

Type locality and horizon

United States of America, Hatchetigbee Bluff (Alabama), Hatchetigbee Formation.

Dimensions of the holotype

Length = 4.36 mm; height = 2.43 mm; thickness = 1.21 mm.

Description

This species is characterized by robust and fusiform otoliths that bear a blunt antero-dorsal bulge, forming the highest and thickest part of the otoliths in the anterior portion (Fig. 8E1). The otoliths taper in the posterior part and end with a pointed tip. The ventral rim is regularly curved. The inner face is convex; the outer face is essentially flat, becoming thinner towards the ventral and posterior rims. The

sulcus occupies nearly the entire length of the inner face and is constituted by a long, horizontal ostium and a very short, downward-bent cauda. A shallow dorsal depression is observed above the central part of the crista superior. The ventral area is slightly larger than the dorsal one.

Remarks

At first glance, the otoliths of "*N.*" *stringeri* sp. nov. are very similar to those of *N. longesulcatus* sp. nov. (see above), but they can be distinguished by the short, strongly bent cauda and larger ventral area in the former species. "*Neobythites*" *stringeri* is only known form the type locality.

Stratigraphic and geographic distribution

Ypresian: Hatchetigbee Formation, Alabama.

Order Trachiniformes Rafinesque, 1810
Family Percophidae Swainson, 1839
Subfamily Hemerocoetinae Kaup, 1873
Genus *Waitakia* Schwarzhans, 1980

Waitakia dorsogibbosa sp. nov.
urn:lsid:zoobank.org:act:946D0B8E-FDC0-4DA4-8A24-44CBBE0F9BA0
Fig. 9F–G

Diagnosis

OL/OH = 1.4–1.6, OsL/CaL = 0.9–1.1. Trapezoid to triangular otoliths with strong postero-dorsal angle. Anterior and posterior rims pointed. Sulcus well-divided. Ostium wide, arrow-like with low ostial lobe tilting towards antero-ventral rim. Cauda rod-like, horizontal.

Etymology

'*Dorsogibbosus*, *a*, *um*' = 'hump bearing on the dorsal part'. Refers to the angulous and humpy dorsal part of the otoliths.

Type material examined

Holotype

United States of America • Left otolith; Virginia, Pamunkey River, Hanovertown, Potapaco Member; Fig. 9F; IRSNB P 10755.

Paratype

UNITED STATES OF AMERICA • 1 otolith: Fig. 9G; Maryland, Piscataway Creek, Thrift Road ravine, Potapaco Member; IRSNB P 10756.

Type locality and horizon

United States of America, Pamunkey River, Hanovertown (Virginia), Potapaco Member.

Dimensions of the holotype

Length = 2.13 mm; height = 1.37 mm; thickness = 0.55 mm.

Description

This species is characterized by small, trapezoid to triangular otoliths, with dorsal and ventral rims approximately parallel to each other and oblique anterior and posterior rims. The dorsal rim is very short, bears a strong postero-dorsal angle, and its anterior part is inclined downwards. The ventral rim is gently curved and bears an angle at each end. The thickness of the otoliths is most considerable in the middle, with both the inner and outer faces being convex (Fig. 9F1). The sulcus is well-divided into

ostium and cauda, marked by a constriction of the cristae in the central zone of the sulcus. The ostium is wide, arrow-like, with a low ostial lobe expanding ventrally and tilting towards the antero-ventral rim, and its anterior tip nearly reaches the anterior rim of the otolith. The cauda is rod-like, horizontal, and shows a rounded posterior end. There is no trace of a swollen collicular crest on the caudal crista inferior like in gobiids. A dorsal depression is observed above the well-developed caudal crista superior.

Remarks

The otoliths of *W. dorsogibbosa* sp. nov. resemble most to those of *Waitakia beelzebub* Lin & Nolf, 2022 from the middle to late Eocene (Lutetian-Bartonian) of the southern USA and other congeners from the Eocene of New Zealand. The thick profile and sulcus morphology are characteristics for assigning the new species to the fossil genus *Waitakia*. However, *W. dorsogibbosa* has the shortest dorsal rim exhibiting a triangular outline. The species may represent one of the earliest records of this extinct lineage. It is extremely rare with only two specimens in our material.

Stratigraphic and geographic distribution

Ypresian: Potapaco Member, Virginia and Maryland.

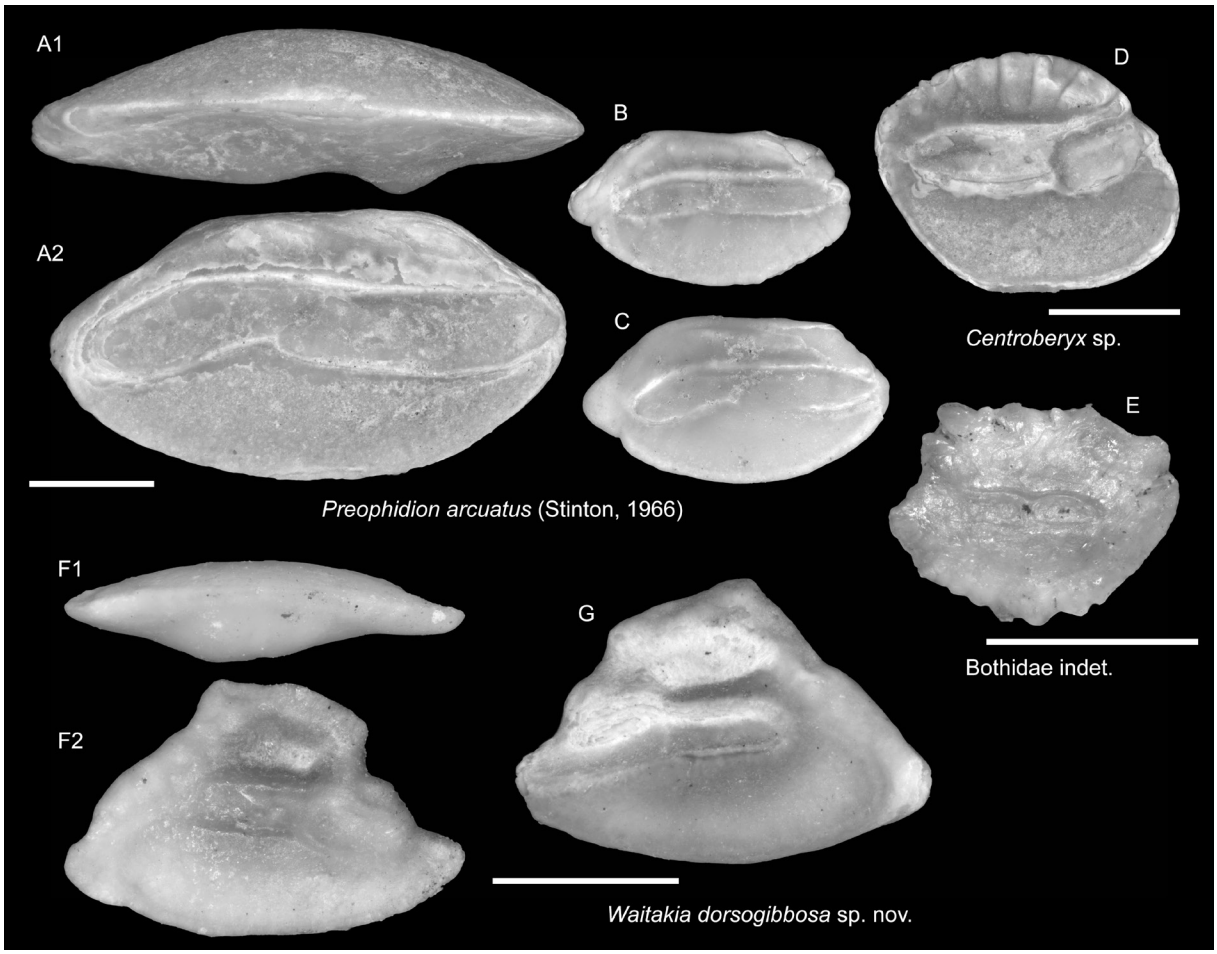

Fig. 9. Fish otoliths from the US lower Eocene formations. **A–C**. *Preophidion arcuatus* (Stinton, 1966), Cave Branch, Bashi Fm., Alabama (IRSNB P 10750 to P 10752). **D**. *Centroberyx* sp., Hatchetigbee Bluff, Hatchetigbee Fm., Alabama (IRSNB P 10753). **E**. Bothidae indet., Ridge Creek, Reklaw Fm., Texas (IRSNB P 10754). **F–G**. *Waitakia dorsogibbosa* sp. nov. **F**. Pamunkey River, Hanovertown, Potapaco Member, Virginia, holotype (IRSNB P 10755). **G**. Piscataway Creek, Thrift Road ravine, Potapaco Member, Maryland, paratype (IRSNB P 10756). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Order Perciformes Bleeker, 1859
Suborder Percoidei Bleeker, 1859
Family Haemulidae Gill, 1885
Genus incertae sedis

"*Haemulon*" *ypresiensis* sp. nov.
urn:lsid:zoobank.org:act:AA387688-D529-4AF7-B3DA-C6E3C2A82413
Fig. 10G–H

Diagnosis

OL/OH = 1.3–1.5, OsL/CaL = 0.4–0.7. Oblong otoliths with weak postero-dorsal angle. Margins crenulated. Sulcus well-divided. Ostium wide, opens antero-dorsally. Cauda elongate, straight, but strongly bent ventrally at posterior.

Etymology

'*Ypresiensis*, *is*, *e*' = 'from the Ypresian'. Refers to the geological stage from where the fossils were collected.

Type material examined

Holotype
UNITED STATES OF AMERICA • Left otolith; Virginia, Pamunkey River, Hanovertown, Potapaco Member; Fig. 10G; IRSNB P 10766.

Paratypes (72 in total)
UNITED STATES OF AMERICA • 2 otoliths of which one is figured: Fig. 10H; same collection data as for holotype; IRSNB P 10767 • 10 otoliths; Mississippi, Meridian, Gallagher Creek, Bashi Formation; IRSNB • 36 otoliths; Mississippi, Meridian, Red Hot Truck Stop, Bashi Formation; IRSNB • 13 otoliths; Alabama, Cave Branch, Bashi Formation; IRSNB • 1 otolith; Alabama, Elba Dam on Pea River, Bashi Formation; IRSNB • 4 otoliths; Alabama, Ozark, Bashi Formation; IRSNB • 2 otoliths; Alabama, Hatchetigbee Bluff, Hatchetigbee Formation; IRSNB • 3 otoliths; Virginia, Rappahannock River, Potapaco Member; IRSNB • 1 otolith; Maryland, Loyola Retreat House, N of Popes Creek, Woodstock Member; IRSNB.

Type locality and horizon

United States of America, Pamunkey River, Hanovertown (Virginia), Potapaco Member.

Dimensions of the holotype

Length = 3.33 mm; height = 2.19 mm; thickness = 0.76 mm.

Description

This species is distinguished by oblong otoliths with crenulated margins and a moderately thick build. The inner face is convex and the outer face is concave. The sulcus is clearly devided with crest-like cristae forming a deep incised sulcus. The ostium opens widely and antero-dorsally, and an expansion is present at the ostial lobe. The junction of the ostial and caudal crista inferior is located more posteriorly with respect to the same junction in the crista superior. The cauda is straight for about two-thirds of its length and markedly bent ventrally at the posterior end. The dorsal area is narrower than the ventral one. There is a shallow dorsal depression located just above the crest-like caudal crista superior.

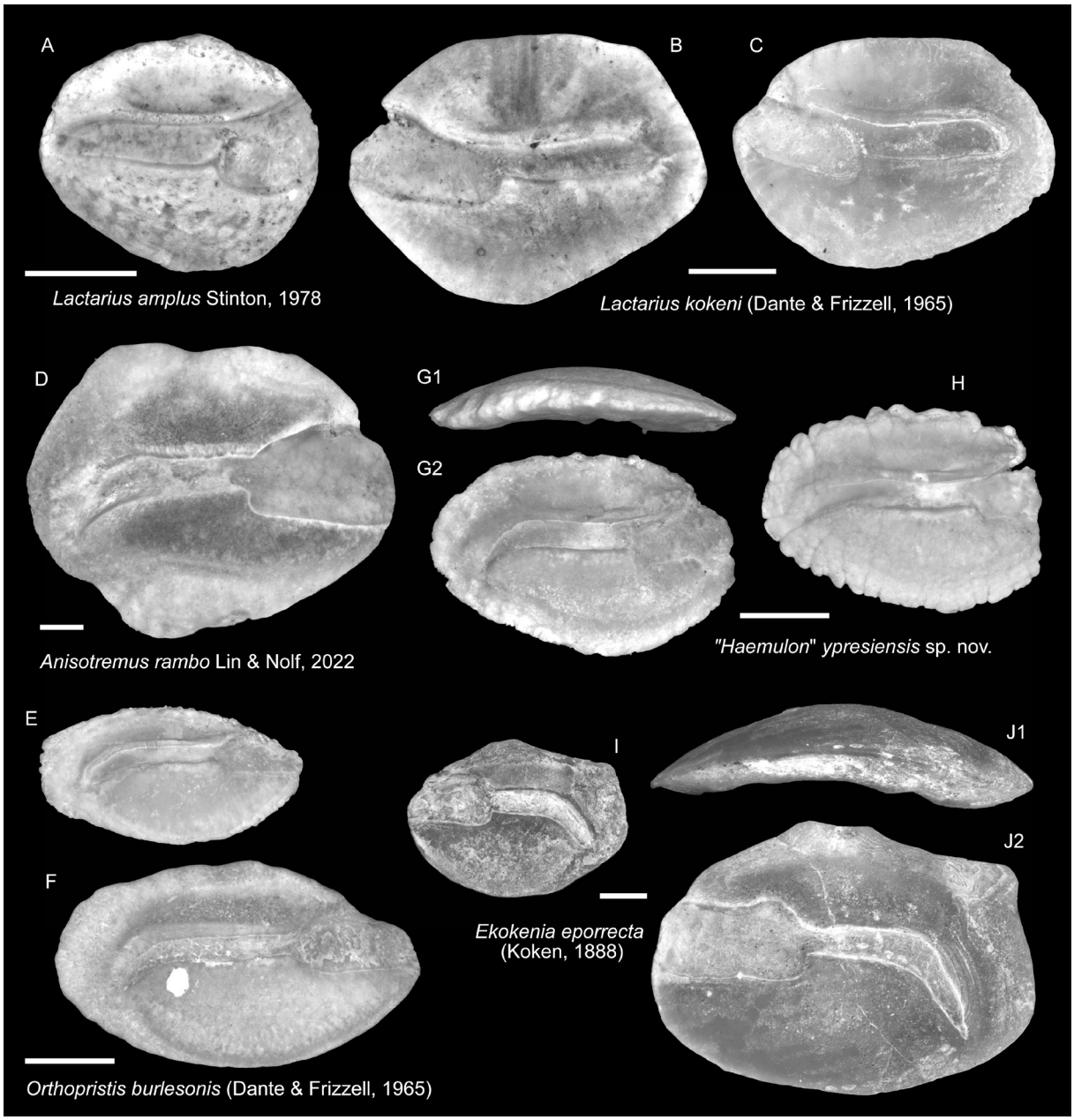

Fig. 10. Fish otoliths from the US lower Eocene formations. **A**. *Lactarius amplus* Stinton, 1978, Taylor's Branch of Two Mile Creek, Reklaw Fm., Texas (IRSNB P 10757). **B–C**. *Lactarius kokeni* (Dante & Frizzell, 1965), Taylor's Branch of Two Mile Creek, Reklaw Fm., Texas (IRSNB P 10758, P 10759). **D**. *Anisotremus rambo* , 2022, Taylor's Branch of Two Mile Creek, Reklaw Fm., Texas (IRSNB P 10763). **E–F**. *Orthopristis burlesonis* (Dante & Frizzell, 1965), Pamunkey River, Hanovertown, Potapaco Member, Virginia (IRSNB P 10764–10765). **G–H**. "*Haemulon*" *ypresiensis* sp. nov., Pamunkey River, Hanovertown, Potapaco Member, Virginia. **G**. Holotype (IRSNB P 10766). **H**. Paratype (IRSNB P 10767). **I–J**. *Ekokenia eporrecta* (Koken, 1888), Taylor's Branch of Two Mile Creek, Reklaw Fm., Texas (IRSNB P 10768, P 10769). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Remarks

The otoliths of "*H.*" *ypresiensis* sp. nov. are most similar to those of "*Haemulon*" *pulchrum* (Frost, 1934) and "*Haemulon*" *obliquum* (Müller, 1999), based on their sulcus and outline shape. "*Haemulon*" *pulchrum* is a widely distributed Eocene European species, and the otoliths of the new species resemble those from the Lutetian of Osteroden, Germany (see Schwarzhans 2007: fig. 32; Lin *et al*. 2017b: fig. 12h–l). However, the dorsal rim of the new species is flat, whereas in "*H.*" *pulchrum*, it is notably elevated and forms the highest part of the otoliths. On the other hand, "*H.*" *obliquum*, a middle to late Eocene American species (see Lin & Nolf 2022), has otoliths that are more similar to the new species, with the largest difference being that the cauda tip extends further backwards and is more markedly bent, reaching almost to the posterior rim of the otoliths.

Stratigraphic and geographic distribution

Ypresian: Bashi Formation, Mississippi and Alabama; Hatchetigbee Formation, Alabama; Potapaco Member, Virginia and Maryland.

Remarks on taxa requiring comments

Ariosoma sp.
Fig. 4A

A single *Ariosoma* otolith was recovered from the Bashi Formation, Mississippi (Table 1). The otolith differs from the common species of *Ariosoma*, *A. nonsector* Nolf & Stringer, 2003, by having a flatter dorsal rim, but we retain our identification due to the lack of sufficient specimens.

Albula meridiana (Frizzell, 1965)
Fig. 3C–D

The otoliths are elongate to rectangle in shape, with a cauda that is bent downward and a nearly flat dorsal rim that ends with a weak postero-dorsal angle. *Albula meridiana* was originally described as *Eoalbula meridiana* by Frizzell (1965), and later assigned to the "*genus Albulidarum*" by Nolf (1985) and remained as such in the following literature (Müller 1999). However, the species remains doubtful (Nolf 2013) and requires further study as suggested by Nolf & Dockery (1993). Frizzell's taxonomic acts were questionable, as they were mainly based on poorly-preserved or juvenile specimens, and his otolith-based genera were forced to reveal tentative evolutionary lineages. Despite this, based on their distinct characters, the three better-preserved otoliths described in this study can be confidently assigned to this species. *Albula meridiana* is only known from the Bashi Formation of Mississippi.

Ariidae indet.
Fig. 5F

Based on the poor preservation and lack of distinct features, the ariid otoliths in the collection could not be confidently identified to the species level and are therefore assigned as Ariidae indet. The lack of common occurrence of ariid otoliths in the studied localities could indicate a low abundance of ariids.

"*Merluccius*" *papillosus* (Stinton, 1966)
Fig. 5D

We assign a medium-sized otolith from the Rappahannock River, Virginia, to "*M.*" *papillosus* based on distinct features, including an obtuse rostrum, relatively flat dorsal and ventral rims, a wide and pince-nez-shaped sulcus, and an upward-oriented ostium. Although about one-third of its posterior part is not preserved, we deem these characteristics to be sufficient for identification. The species is known from

Lutetian European deposits, including the English Hampshire Basin, Belgian Basin, and NW Germany (Osteroden) (Lin *et al*. 2017b). This specimen represents the first occurrence of "*M.*" *papillosus* in the Americas.

"*Neobythites*" *constrictus* Stinton, 1977
Fig. 7B

An oblong otolith from the Rappahannock River locality in Virginia possesses an obtuse, moderately protruding rostrum and a sulcus type most similar to "*N.*" *constrictus* from the Ypresian London Clay of southern England. The more compact outline of the otolith and flatter inner face are considered as size-related intra-specific variability.

Preophidion arcuatus (Stinton, 1966)
Fig. 9A–C

Otoliths belonging to this species are commonly found in the Bashi and Hatchetigbee formations and share several distinctive characteristics with those of *P. arcuatus* from the Ypresian London Clay, as described by Stinton (1966) under the name *Brotula arcuatus*. The general outline of the otoliths, as well as the downward-bent cauda, suggest that this species can be assigned to the fossil genus *Preophidion*.

Discussion

The otolith collection described here consists of 1149 otolith specimens, which were assigned to 33 different taxa from 17 families (Table 1). Of these taxa, nine species were newly described. The highest number of otoliths were found in the Bashi Formation in Mississippi (308 otoliths) and Alabama (296 otoliths), each containing 11 taxa. The Potapaco Member in Virginia had the highest taxonomic richness with 15 taxa and 156 otoliths, including several new ophidiid species. The Hatchetigbee Formation in Alabama (246 otoliths) and the Reklaw Formation in Texas (124 otoliths) also yielded moderately rich and abundant assemblages with 12 and 11 taxa, respectively. Although the otolith assemblages from the Potapaco and Woodstock members in Maryland were small (only eight and 11 otoliths, respectively), they still contained four and six taxa, respectively (Table 1).

The dominant taxa within the collection are the Ophidiidae, Congridae, and Haemulidae (Table 1). The collection lacks any representation of mesopelagic and bathybenthic fishes, which strongly implies that the sampled sites were situated in shallow-water environments. This finding is consistent with the notion of a persistent shallow, neritic environment that likely prevailed in the younger middle and late Eocene of America (Lin & Nolf 2022).

Figure 11 shows the stratigraphic distribution of the currently known 28 nominal otolith-based species recorded from the American Ypresian and Ypresian–Lutetian transition (27 identified herein and one, namely *Symmetrosulcus meyeri*, mentioned by Ebersole *et al.* 2019). Among these, nine newly described species are exclusively known from the early and middle Ypresian, specifically occurring in Zones NP 10 to base NP 13. Notably, the stratigraphic range of *Orthopristis burlesonis*, originally documented from Burleson Bluff (Lutetian), has now been extended downward to the early Ypresian, persisting until the Bartonian. Furthermore, we have identified 10 amphi-Atlantic species, initially described from European deposits, and their American range is shown (Fig. 11). This further contributes to the understanding of trans-Atlantic faunal connections during this period.

In the Reklaw Formation, representing the Ypresian–Lutetian transition, the emergence of certain species is evident, and these persist in subsequent deposits where they become more distinctly characteristic. Specifically, we have identified small specimens that appear to be juveniles of *Bauzaia*

mucronata, *Lactarius kokeni*, and *Anisotremus rambo*, species of which the adults have been found in a large number of Lutetian and Bartonian deposits (Lin & Nolf 2022). Within the Hatchetigbee Formation in Alabama, we have recovered a single otolith of the sciaenid species *Ekokenia eporrecta*, marking one of the earliest confirmed records of the Sciaenidae family with species assignment. *Ekokenia eporrecta* is a common to abundant species across all Claibornian localities in the southern USA (Frizzell & Dante 1965; Ebersole *et al.* 2019; Lin & Nolf 2022). Its common occurrence in the Reklaw Formation, representing the Ypresian–Lutetian transition, is not unexpected given its abundance and wide geographic distribution in the Claibornian (? top Ypresian to middle Priabonian). But, its early appearance in lower-Ypresian strata is quite surprising, although entirely in line with the paleogeographic distribution pattern of *Ekokenia eporrecta*, which is restricted to the US Atlantic and Gulf coastal plains. Additionally, Nolf (1995) reported a worn sciaenid otolith from the slightly older Bashi Formation in Mississippi, which could not be identified to the species level. These findings collectively suggest the initial presence of Sciaenidae in the early Eocene, and the potential for additional records in lower Eocene strata. It is noteworthy that sciaenids gradually increase in importance in Lutetian deposits of America and become a dominant group in Bartonian and subsequent younger strata (Lin & Nolf 2022). Interestingly, sciaenids are conspicuously absent from the European Eocene record and their occurrences only becomes widespread in the Neogene.

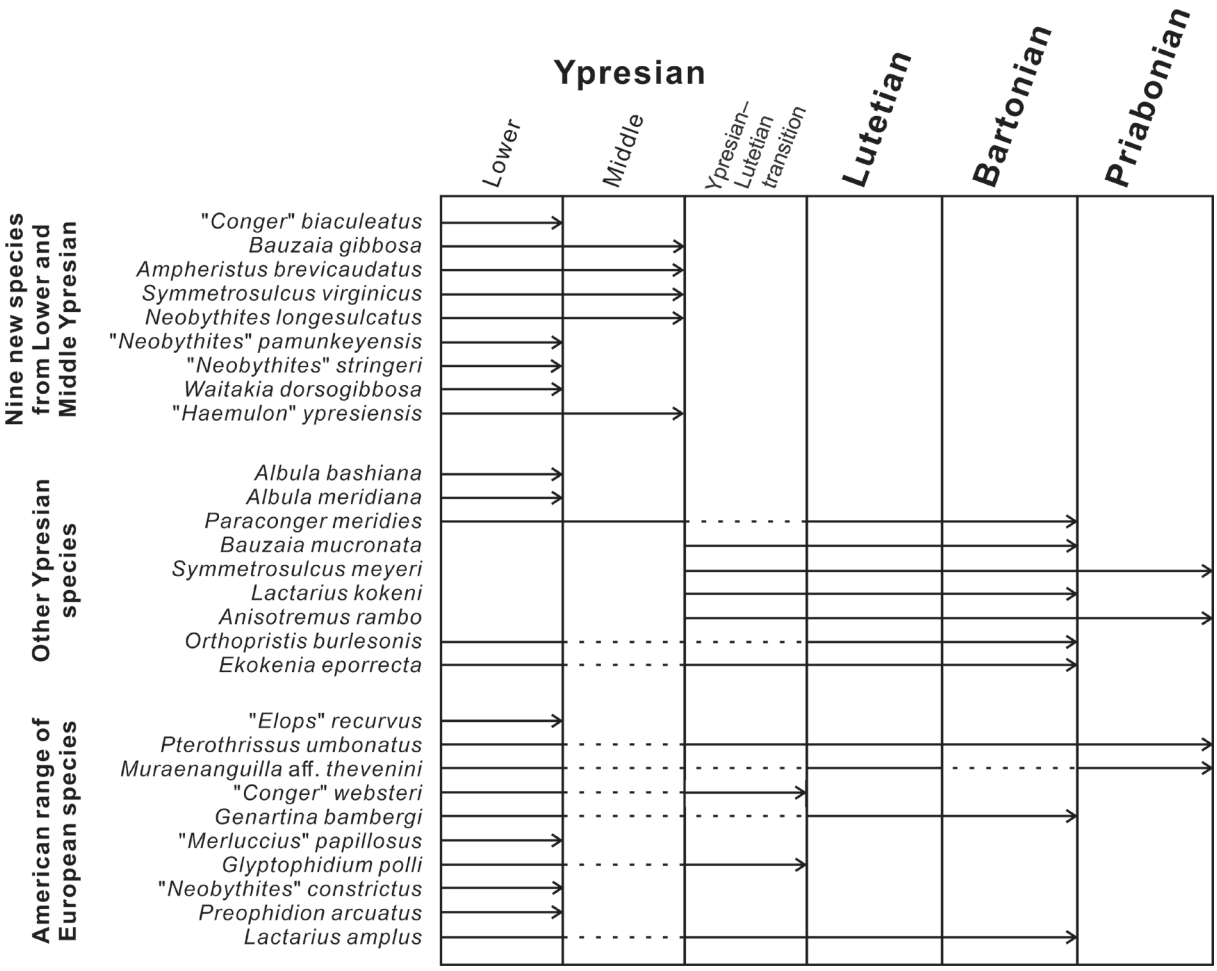

Fig. 11. Distribution of the currently known 28 nominal otolith-based species from the Ypresian and Ypresian–Lutetian transition of the eastern and southern USA, arranged according to their first appearance and stratigraphic ranges. This includes *Symmetrosulcus meyeri* (Koken, 1888) from the Tallahatta Formation (Ebersole *et al*. 2019) and 27 nominal species described in the present study.

In Appendix 1, we present a comprehensive dataset indicating the presence or absence of nominal otolith-based species from the American Eocene. This dataset allows for a broader-scale comparison of otolith-based fauna between the Atlantic and Gulf coastal plains, encompassing a total of 99 known species to date. In comparison to the extensive collection documented in middle and upper Eocene deposits by Lin & Nolf (2022), it is evident that the Ypresian collection appears relatively smaller both in terms of abundance and species diversity due to lower sampling effort (Table 1). However, the Ypresian collection remains noteworthy due to the substantial proportion of unique taxonomic composition it possesses. To be precise, out of the 28 nominal species identified, a remarkable 15 of them are either newly described or confined exclusively to the lower and middle Ypresian strata. This distinctive characteristic sets these assemblages apart from the otolith-based faunas found in the younger Eocene deposits.

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The field work for the present paper was achieved by Dirk Nolf during several periods, between 1987 and 2007 and it is a pleasure for him to express his heartfelt gratitude to his wife Dora, who always supported his activities with enthusiasm, ensuring a lot of logistic help, and driving thousands of kilometers. In 1989, many sites in Mississipi and Alabama were visited and sampled. For this work, the Nolf family received a lot of help from David Dockery (Mississippi Geological Survey, Jackson). This collaboration continued for several subsequent trips during later years. Moreover, the publication of Dockery & Thompson's (2016) book on the Geology of Mississippi also provided a precious actualized overview work for the whole eastern Gulf coast area. For the exploration in eastern Mississippi and Alabama, the Nolf family camped for a long period in Quitman, where they found an excellent opportunity for screenwashing samples in the Archusa Water Park, and where they also profited from the support of All Vowell for several logistic issues. For their exploration in Alabama, they were also guided by Andy Rindsberg. Exploration in Texas started in 2001. On this trip and several later ones, the Nolf family enjoyed the generous hospitality of Christopher and Shirley Garvie. In the surroundings of Washington and in Virginia, they had easy access to literature and cartography through the efforts of James Tyler, Robert Purdy, and Dave Bohaska in the Department of Paleontology of the Smithsonian Institution. Dave Johnson (Recent fish division of the USNM) allowed access to the collection of Recent fishes, and provided fundings for Dirk Nolf's stay in 2000. Lauck Ward (Virginia Museum of Natural History, Martinsville) took the Nolf family on a boat trip on the Pamunkey River, what provided easy access to several river side exposures. Also, Ward's (1985) overview paper provided a very clear view on the stratigraphy and topography of the area. Besides the own otolith collecting, which was almost exclusively by screenwashing, a lot of material, mainly surface collected, was provided by Chistopher Garvie, David Dockery and Bruce Welton. The authors thank Angela Girone (Dipartimento di Scienze della Terra and Geoambientali, Università degli Studi di Bari Aldo Moro, Italy) for her logistic assistance to Chien-Hsiang Lin between 2013 and 2017 during his PhD studies. For all the colleagues who helped us, we hope that they are still enjoying the kind of work that we have done together, and that they will accept our sincere gratitude for the help that they have generously given to us. Travel to Belgium and research fundings are provided by the National Science and Technology Council, Taiwan (MOST-FNRS Bilateral Cooperation Programme, 112-2927-I-001-505, 112-2116-M-001-017-MY3) and Academia Sinica, Taipei, Taiwan to Chien-Hsiang Lin in 2023. We thank Gary Stringer, Werner Schwarzhans, and an anonymous reviewer for their constructive reviews.

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Appendix 1 (continued on next five pages). An overview of the nominal otolith-based fish species from the American Eocene. Presence (+) of the species is indicated. Fossil genera are underlined. Data source: Frizzell & Lamber (1961, 1962), Frizzell & Dante (1965), Müller (1999), Nolf (1995, 2003), Stringer (2016), Ebersole *et al*. (2019), Stringer *et al*. (2022: table 3), Lin & Nolf (2022), and this study.

Fish otolith-based species from the Eocene of the eastern and southern USA	Texas					Louisiana		Mississippi					Alabama							Virginia		Maryland	
	Reklaw Formation	Weches Formation	"Stone City beds"	Wheelock Marl M.	Landrum Shale M.	Moodys Branch F.	Yazoo Clay	Bashi Formation	Dobys Bluff Tongue	Archusa Marl M./ Potterchitto M.	Moodys Branch F.	Shubuta Clay M.	Bashi Formation	Hatchetigbee F.	Tallahatta Formation	"Lower-Middle" Lisbon Formation	"upper" Lisbon F.	Gosport Sand	Moodys Branch F.	Potapaco Member	Piney Point Fm.	Potapaco Member	Woodstock Member
"*Elops*" *recurvus* (Frost, 1931)								+						+									
Albula bashiana (Frizzell, 1965)								+															
Albula meridiana (Frizzell, 1965)								+															
Elopothrissus bernardlemorti Lin & Nolf, 2022			+														+						
Pterothrissus umbonatus (Koken, 1884)	+	+	+	+	+		+			+		+					+			+	+		
Muraenanguilla aff. *thevenini* (Priem, 1906)							+													+	+		
Pythonichthys colei (Müller, 1999)			+	+	+	+	+				+	+					+		+		+		
"*Ophichthus*" *brevior* (Koken, 1888)											+												
"*Muraenesox*" *barrytownensis* Lin & Nolf, 2022			+														+						
Alaconger fornicata (Frizzell & Lamber, 1962)							+					+											
Conger vetustus Frizzell & Lamber, 1962						+	+				+						+						
Gnathophis dissimilis (Frizzell & Lamber, 1962)						+	+																
Pseudophichthys glaber (Koken, 1888)		+	+	+	+	+	+					+					+		+		+		
Pseudophichthys texanus Lin & Nolf, 2022		+							+	+							+				+		
Heteroconger ovatus (Müller, 1999)																					+		
Ariosoma nonsector Nolf & Stringer, 2003			+	+		+	+		+	+	+					+	+		+				
Paraconger brazosensis (Dante & Frizzell, 1965)		+	+	+	+				+														
Paraconger meridies (Frizzell & Lamber, 1962)								+					+	+			+			+	+	+	+

Appendix 1 (continued). An overview of the nominal otolith-based fish species from the American Eocene. Presence (+) of the species is indicated. Fossil genera are underlined. Data source: Frizzell & Lamber (1961, 1962), Frizzell & Dante (1965), Müller (1999), Nolf (1995, 2003), Stringer (2016), Ebersole *et al*. (2019), Stringer *et al*. (2022: table 3), Lin & Nolf (2022), and this study.

Fish otolith-based species from the Eocene of the eastern and southern USA	Texas					Louisiana		Mississippi					Alabama							Virginia		Maryland	
	Reklaw Formation	Weches Formation	"Stone City beds"	Wheelock Marl M.	Landrum Shale M.	Moodys Branch F.	Yazoo Clay	Bashi Formation	Dobys Bluff Tongue	Archusa Marl M./ Potterchitto M.	Moodys Branch F.	Shubuta Clay M.	Bashi Formation	Hatchetigbee F.	Tallahatta Formation	"Lower-Middle" Lisbon Formation	"upper" Lisbon F.	Gosport Sand	Moodys Branch F.	Potapaco Member	Piney Point Fm.	Potapaco Member	Woodstock Member
Paraconger sector (Koken, 1889)						+	+			+	+					+	+	+	+		+		
Paraconger solidus Müller, 1999																					+		
Paraconger wechesensis Lin & Nolf, 2022		+																					
Paraconger yazooensis Nolf & Stringer, 2003						+	+																
"*Conger*" *biaculeatus* sp. nov.													+										
"*Conger*" *prolatus* (Müller, 1999)																					+		
"*Conger*" *websteri* (Frost, 1933)	+							+		+			+	+						+	+		
"*Osteoglossum*" aff. *rhomboidalis* (Stinton, 1977)			+																				
Neoopisthopterus weltoni Lin & Nolf, 2022			+		+																		
Genartina bambergi (Priem, 1913)			+	+	+			+									+						
Genartina texana Dante & Frizzell, 1965		+	+	+													+						
"*Merluccius*" *papillosus* (Stinton, 1966)																				+			
Bregmaceros troelli (Dante & Frizzell, 1965)		+	+	+	+	+	+			+	+	+					+		+				
"*Myripristis*" *cajun* (Frizzell & Lamber, 1961)		+	+	+		+	+			+	+						+				+		
"*Diretmus*" *serratus* (Müller, 1999)		+	+	+	+				+								+				+		
Carapus smithvillensis Dante & Frizzell, 1965		+	+													+	+						
Brotula aquitanica Nolf, 1980						+	+																

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Bauzaia gibbosa sp. nov.																							+
Bauzaia lamberi Dante & Frizzell, 1965		+	+													+	+						
Bauzaia mucronata (Koken, 1888)	+	+	+	+	+				+	+						+	+				+		
Signata nicoli Dante & Frizzell, 1965		+															+						
Signata stenzeli Dante & Frizzell, 1965			+	+	+				+								+						
Aequalobythites aequaloides (Nolf & Stringer, 2003)							+																
Ampheristus brevicaudatus sp. nov.													+							+			+
Glyptophidium polli (Casier, 1946)	+												+	+						+			
"aff. *Glyptophidium*" *stringeri* Lin & Nolf, 2022			+	+	+				+								+						
Hoplobrotula melrosensis (Dante & Frizzell, 1965)		+	+													+	+						
Symmetrosulcus dockeryi Lin & Nolf, 2022		+								+						+							
Symmetrosulcus meyeri (Koken, 1888)			+	+		+	+			+	+	+			+	+	+	+	+		+		
Symmetrosulcus stintoni (Dante & Frizzell, 1965)		+	+																				
Symmetrosulcus virginicus sp. nov.														+						+		+	+
Neobythites longesulcatus sp. nov.																				+			+
"*Neobythites*" *constrictus* Stinton, 1977																				+			
"*Neobythites*" *pamunkeyensis* sp. nov.																				+			
"*Neobythites*" *rotundus* (Müller, 1999)																					+		

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"*Neobythites*" *stringeri* sp. nov.														+									
"*Neobythites*" *virginicus* Müller, 1999														+							+		
Preophidion arcuatus (Stinton, 1966)								+					+	+									
Preophidion elevatus (Koken, 1888)										+						+	+	+			+		
Preophidion granus (Müller, 1999)						+	+				+	+					+	+	+		+		
Preophidion petropolis (Dante & Frizzell, 1965)		+	+	+	+	+				+							+						
Xenosirembo decipiens (Koken, 1888)																+	+	+					
"*Apogon*" *americana* (Dante & Frizzell, 1965)		+	+	+																			
"*Gobius*" *vetustus* (Nolf & Stringer, 2003)						+	+																
"*Blennius*" *cor* (Koken, 1888)						+	+				+						+		+		+		
"*Labrisomus*" *eocaenicus* (Müller, 1999)																					+		
"*Atherina*" *debilis* (Koken, 1888)			+			+	+				+								+				
Mene garviei Lin & Nolf, 2022					+																		
Psettodes trapeziformis Müller, 1999																					+		
Brachypleura nana (Müller, 1999)																					+		
"*Citharus*" *hoffmani* (Nolf & Stringer, 2003)						+	+																
"*Citharus*" *varians* Lin & Nolf, 2022			+	+	+												+						
Citharichthys altissimus Nolf & Stringer, 2003						+	+																
Waitakia beelzebub Lin & Nolf, 2022																	+				+		

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<u>Waitakia</u> *dorsogibbosa* sp. nov.																				+		+	
"*Trachinus*" *laevigatus* (Koken, 1888)		+	+				+				+						+		+		+		
Astroscopus compactus Lin & Nolf, 2022										+							+						
Astroscopus fusiformis (Müller, 1999)																					+		
Parascombrops yanceyi Lin & Nolf, 2022			+	+	+																		
Centropristis priaboniana Nolf & Stringer, 2003						+	+				+												
Lactarius amplus Stinton, 1978	+	+	+	+	+				+	+		+					+			+	+		
Lactarius kokeni (Dante & Frizzell, 1965)	+	+	+	+	+				+	+						+	+	+			+		
Pseudopriacanthus obliquus (Nolf & Stringer, 2003)						+	+																
"*Latilus*" *sulcatus* (Koken, 1888)						+	+				+						+		+				
Anisotremus rambo Lin & Nolf, 2022	+		+	+			+										+						
Orthopristis americana (Koken, 1888)						+	+				+								+				
Orthopristis burlesonis (Dante & Frizzell, 1965)		+	+	+	+			+	+	+			+	+			+	+		+	+	+	
"*Haemulon*" *obliquum* (Müller, 1999)		+	+	+		+	+				+						+		+		+		
"*Haemulon*" *ypresiensis* sp. nov.								+					+	+						+			+
Owstonia comes (Koken, 1888)											+												
<u>Ekokenia</u> *eporrecta* (Koken, 1888)	+	+	+	+	+				+	+				+		+	+				+		
<u>Eosciaena</u> *ebersolei* Stringer *et al*., 2022							+																

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<u>*Jefitchia*</u> *copelandi* Dante & Frizzell, 1965		+	+	+	+				+			+				+	+	+					
Sciaena pseudoradians (Dante & Frizzell, 1965)				+		+	+				+	+							+				
"*Sciaena*" *claybornensis* (Koken, 1888)					+	+	+			+	+	+					+	+	+				
"*Sciaena*" *eanes*i (Müller, 1999)		+	+	+						+							+	+			+		
"*Sciaena*" *intermedia* Koken, 1888			+	+	+				+								+	+					
"*Sciaena*" *livesayi* (Müller, 1999)			+	+	+					+							+				+		
Pagellus pamunkeyensis Lin & Nolf, 2022																					+		
Pagrus esseri (Müller, 1999)																					+		
"*Sparus*" *elegantulus* (Koken, 1888)		+	+	+	+	+	+			+	+						+		+		+		