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Monograph

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Middle and late Eocene fish otoliths from the eastern and southern USA

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(with a contribution by Etienne STEURBAUT [3,‡])

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‡ This contribution concerns the nannoplankton-based dating of samples from the Yazoo Clay at the Copenhagen site, Louisiana and the Piney Point Formation in the Pamunkey River, Virginia. The results of these analyses are included in the locality list, respectively under the sites "Louisiana: Copenhagen (Caldwell Parish)" and "Virginia: Pamunkey River, Horseshoe".

Abstract. The fossil otoliths of the southern USA have been known for more than 130 years and are among the richest assemblages worldwide. However, previous studies are often scattered and employed outdated systematic scheme. A collection of over 25000 otoliths ranging in age from the Lutetian to the Priabonian from 47 sites in five states in the eastern and southern USA is analysed here. Combined with the earlier described material, at least 101 otolith-based taxa are documented, of which 83 are identified at species level. Fourteen of these are introduced as new species: *Elopothrissus bernardlemorti* sp. nov., "*Muraenesox*" *barrytownensis* sp. nov., *Pseudophichthys texanus* sp. nov., *Paraconger wechesensis* sp. nov., *Neoopisthopterus weltoni* sp. nov., "aff. *Glyptophidium*" *stringeri* sp. nov., *Symmetrosulcus dockeryi* sp. nov., *Mene garviei* sp. nov., "*Citharus*" *varians* sp. nov., *Waitakia beelzebub* sp. nov., *Astroscopus compactus* sp. nov., *Parascombrops yanceyi* sp. nov., *Anisotremus rambo* sp. nov., and *Pagellus pamunkeyensis* sp. nov. The assemblages are distinct from contemporary European faunas by the complete lack of mesopelagic fish otoliths, and by the presence of sciaenids. Dominant taxa in the American Eocene are the Ophidiidae, Sciaenidae, Lactariidae, and Congridae. They indicate shallow-water environments for all the sampled sites. The notable abundance of those taxa suggests that they could have had a higher turnover rate, and provided fundamental nutrition in the local Paleogene marine ecosystem. Further analyses of the species in the stratigraphic succession revealed that a faunal turnover between the Claiborne and Jackson seas was evident in teleosts, and it might be more widespread in other marine organisms in the region.

Keywords. Paleodiversity, Claiborne and Jackson groups, paleoecology, Sciaenidae, faunal comparison.

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Introduction

On the Atlantic side of the USA, Eocene deposits are well represented, both in the eastern Atlantic Coastal Plain and along the Gulf of Mexico Coastal Plain (Gulf Coastal Plain), from Alabama to Texas. On the American side of the Atlantic, the best accessible exposures are found in Virginia, and the monograph of Ward (1985) provides a comprehensive overview of the accessible places and of their molluscan faunas. The Gulf Coastal Plain is renowned for its numerous outcrops and represents one of the best-preserved marine Eocene fossil records in the United States. In Alabama, the work of Toulmin (1977) provides an overview of most Eocene exposures and their mollusc faunas all over the state. Relevant additional data are also provided by Bandy (1949) on the Foraminifera, Ivany (1998) on the sequence stratigraphy, Siesser (1983) on the calcareous nannoplankton, and Mancini & Tew (1991) on the planktonic foraminiferal zones. In Mississippi, locality and stratigraphical data and an overview of the mollusc fauna are available from Dockery & Thompson (2016, and the references therein). For Louisiana, much information can be found in Schiebout & van den Bold (1986). In Texas, Paleogene exposures crop out in a broad band across the state from the Louisiana border to the Rio Grande and provide the best interval for the examination of Cenozoic depositional systems (Yancey & Yancey 1988). Along the Brazos River, excellent Paleogene exposures extend from the Cretaceous/Paleogene boundary (Schulte *et al.* 2006; Hart *et al.* 2012) to the top of the Eocene/Oligocene boundary (Davidoff & Yancey 1993; Yancey *et al.* 2018). Among these exposures is the "Stone City Bluff," a worldwide renowned site for all kinds of shallow marine fossils including molluscs, shark teeth, and teleost otoliths (Stanton & Nelson 1980; Yancey & Yancey 1988; Breard & Stringer 1999; Westgate 2001; Zuschin & Stanton 2002). A detailed section was published by Stenzel *et al*. (1957), and the papers of Fisher *et al*. (1964), and, more recently, Garvie (2013a, 2013b) also provided very useful additional data for Eocene collecting localities in the region.

The occurrence of American fossil fish otoliths has been known since the earliest days of systematic otolith studies, which can be dated back in the late 19th century (Koken 1888). Concerning the source of his fossils, Koken mentioned that he acquired his American material from the collection of Otto Meyer, a German that lived in New York, and who collected and named mollusc species from the Moodys Branch Formation at Jackson, Mississippi. Koken published formal names for 23 species (Meyer 1889; Nolf 2003). Subsequent works include Frizzell & Lamber (1961, 1962), Frizzell (1965), and more importantly, Frizzell & Dante (1965). Stringer (1977, 1979, 1986, 2016), Stringer & Breard (1997), and Stringer *et al*. (2022) reported on the Eocene otoliths. Recently, Ebersole *et al*. (2019) published a monograph on the Eocene ichthyological fauna from the lower to middle Eocene of Alabama, including the fish otoliths treated by Stringer. All these papers concern material from the Gulf Coast.

Regarding the eastern Atlantic coast, an extensive monograph is provided by Müller (1999), treating shark teeth and otoliths from middle Eocene till upper Miocene strata. The relevant part for our study is the association from the middle Eocene Piney Point Formation. Specimens in Müller (1999) were evaluated by Nolf (2013), who also provided some additional pictures.

Despite the long history of research activity that produced several related reports, which are often restricted in geological age and geographical area, much of the otolith-based fish fauna of the whole Eocene Gulf Coast remains unexplored. The present study focuses on the otoliths of teleostean fishes of Lutetian, Bartonian, and Priabonian age (a smaller collection of otoliths from the early Eocene Ypresian will be studied later). Beside extensive taxonomic work, the collection allows us to report this highly diversified otolith-based fauna in a better-controlled stratigraphic context. We then synthesize and review taxa that were previously described and explicitly compare this fauna in time and space.

Geological setting

On the Atlantic Coastal Plain, sediments are characterized by relatively thin deposits, principally marine, with only remnants of very nearshore faunas (Müller 1999). Paleocene and lower Eocene (Ypresian) deposits are represented in nearly all places from New Jersey to Georgia. However, from Virginia to the north, the Piney Point Formation is the only exposed middle Eocene deposit, and it crops out only in Virginia. Late Eocene (Priabonian) sediments occur in the subsurface but are not known to crop out (Ward 1985; Bybell & Gibson 1994). More to the south, sediments of Bartonian and Priabonian age occur, but in most places, these sediments are too lithified to collect otoliths.

Nearly all ages of Cenozoic deposits, ranging from Paleocene to Holocene, can be found in the Gulf Coastal Plain. These massive deposits have been accumulated since the Mesozoic Era and formed the floor for the later Cenozoic sediments (Hosman 1996). The basic structure of the Gulf Coast (Gulf Coast geosyncline and the Mississippi embayment) was formed, however, at the end of the Paleozoic, when the major deformation (downfaulting and downwarping) of the surface was initiated (Murray 1947, 1961; Cushing *et al.* 1964; Hosman 1996). Nonetheless, studies on the pre-Cretaceous geology in the Gulf Coast are scarce, due to limited exposures (Hosman 1996).

Throughout the Paleocene and Eocene, marine and non-marine depositional cycles repeated as the sea alternatively transgressed and regressed. This produced sequences of alternating sand and clay lithologic types. The clay deposits are mainly the result of marine transgressions and often contain abundant marine fossils including fish otoliths. Successive transgressions were gradually smaller in scale since the Paleocene, and the sea did not extend to the Mississippi embayment after the Eocene (Cushing *et al.* 1964; Hosman 1996). Progressive and continuous sediment infills were then restricted to the southern part of the Gulf Coast, resulting in a southward (gulfward) migration of the shoreline and continental shelf boundary during the rest of the Paleogene.

The Eocene Series in the Atlantic and Gulf Coast area is, in ascending order, represented by the upper Wilcox Group, the Claiborne Group, and the Jackson Group. The studied materials from the middle to late Eocene include the Claiborne Group, and almost the entire Jackson Group, except its uppermost part. Weems *et al*. (2004) placed the concerned groups along with other younger calcareous strata into their Trent Supergroup. This carbonate-rich supergroup, ranging in age from the middle Lutetian (base of Claiborne) to the Aquitanian, is lithologically different from the underlying clastic Ancora Supergroup and the overlaying siliciclastic Nomini Supergroup.

Material and methods

Sampling and otolith preparation

The otoliths were collected from the Eocene eastern Atlantic and Gulf Coastal Plain, ranging in age from the Lutetian (middle Eocene) to the Priabonian (late Eocene). The geographic distribution includes five states: Texas, Louisiana, Mississippi, Alabama, and Virginia (Fig. 1). Sampling localities are described below in alphabetical order. The formations yielding otoliths are indicated in Figs 2 and 3. Note that for the terminology of formations and lateral stratigraphic correlation, we follow Dockery (1980, 1986c; Fig. 2A). Figure 2B is based on the detailed correlation table between the stratigraphic units in Mississippi and the international Planktonic Foraminiferal and Calcareous Nannofossil zonations and the numerical time scale published by Dockery & Thompson (2016: 247, and 375 for a discussion and explanation of the Dobys Bluff Tongue). However, alternative views for correlation and local stratigraphy exist; for example, Flis *et al*. (2017) put the Stone City Member as the basal member of the Crockett (Cook Mountain) Formation; in Garvie (2013b), the Stone City Member is above the Sparta Formation and is a member of the Cook Mountain Formation. We judge that regional stratigraphic terminology and correlations exceed the scope of our present monograph. Therefore, Fig. 2 is split in

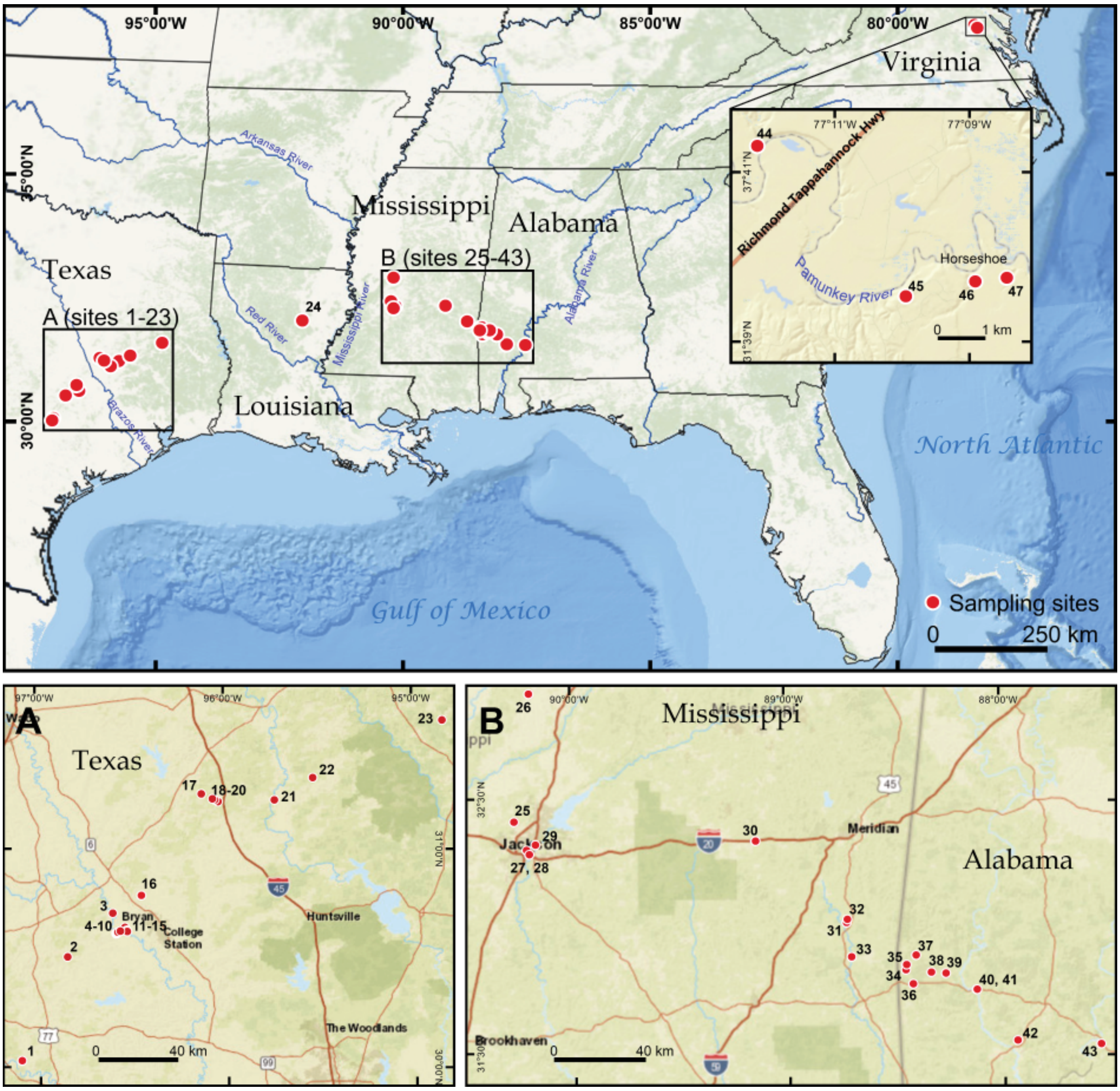


Fig. 1. Maps showing the sampling sites on the US Gulf and eastern Atlantic Coasts (Texas, Louisiana, Mississippi, Alabama, Virginia). **A**. Sites 1–23 from Texas. **B**. Sites 25–43 from Mississippi and Alabama. **1**. Pin Oak Creek. **2**. Hooker Creek. **3**. Burleson Bluff. **4–10**. Rocky Branch, 1.5 miles SW of Stone City Bluff, samples 0–6. **11**. Stone City Bluff, Brazos River. **12**. Little Brazos River, under Highway 21 bridge. **13**. Little Brazos River, Stenzel loc. **14**. Little Brazos River, 1.5 km S of Highway 21 bridge. **15**. Little Brazos River, confluence with Brazos River. **16**. Dunn's Ranch, NNE of Bryan. **17**. Robbins, roadside. **18**. Wall Farm 2. **19**. Wall Farm 1. **20**. Cedar Creek, E of Centerville. **21**. Alabama Ferry, on Trinity River, North. **22**. Crockett. **23**. Nacogdoces Dam. **24**. Copenhagen (after Nolf & Stringer 2003). **25**. Cynthia, Mississippi Lite clay pit. **26**. Midway, Techeva Creek. **27**. Jackson, boring at the corner of Amite and Mill Streets. **28**. Jackson, Town Creek. **29**. Jackson, Riverside Park. **30**. Newton, NE exit off Interstate 20. **31**. Dobys Bluff. **32**. Quitman, Archusa Water Park. **33**. Chickasawhay River, Hunting Lodge. **34**. Evansboro (SE of town). **35**. Puss Cuss Creek. **36**. Isney. **37**. Melvin (SE of town). **38**. Gilbertown. **39**. Barrytown, County Road 21. **40**. Coffeeville Landing, samples A–D. **41**. Coffeeville Landing, sample S. **42**. Little Stave Creek. **43**. Claiborne Bluff, Gosport F. **44**. Pamunkey River, Devil's Hole. **45**. Pamunkey River, 1 km E of Eanes property. **46**. Pamunkey River, Horseshoe, Old Church type locality. **47**. Pamunkey River, SW of Pampatike Landing.

two parts: Fig. 2A shows the correlation of the stratigraphic successions of the southern US states and Fig. 2B the published correlation of the Mississippi units with international zonations. Moreover, we opt for the use of the informal name "Stone City beds" throughout our current text.

The material is mainly based on the otoliths collected by D. Nolf during six field campaigns, each of about one month, between 1987 and 2007. At various periods, about one month was spent for sampling the Eocene of the East Atlantic coast and about five in the Gulf Coast states. Altogether about 6000 kg of sediments were dried, then again soaked in water and screen washed over 0.75 mm mesh. Otoliths from the fractions above 2 mm were directly handpicked at the site, and the fractions between 2 and 0.75 mm were transported to the lab in the Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRSNB) and picked out under a Wild M5 stereo microscope. Moreover, this collection is completed by isolated (surface-collected) otoliths that were donated by local researchers (mainly D. Dockery, C. Garvie and B. Welton), who obtained them as additional material from their sampling for molluscs and/or shark teeth. This provided a highly diverse collection from precisely known stratigraphic levels, which is deposited in the collections of the IRSNB. The inclusion of the surface specimens significantly improved the knowledge of ontogenetic and intraspecific variability of specific taxa, but the specimens were not be considered in statistical studies because of collecting bias. The otoliths, whenever possible, have been identified at the species level. The study material is stored at the IRSNB, registered under the code IRSNB P. Occasionally, some type specimens from other Museums are figured.

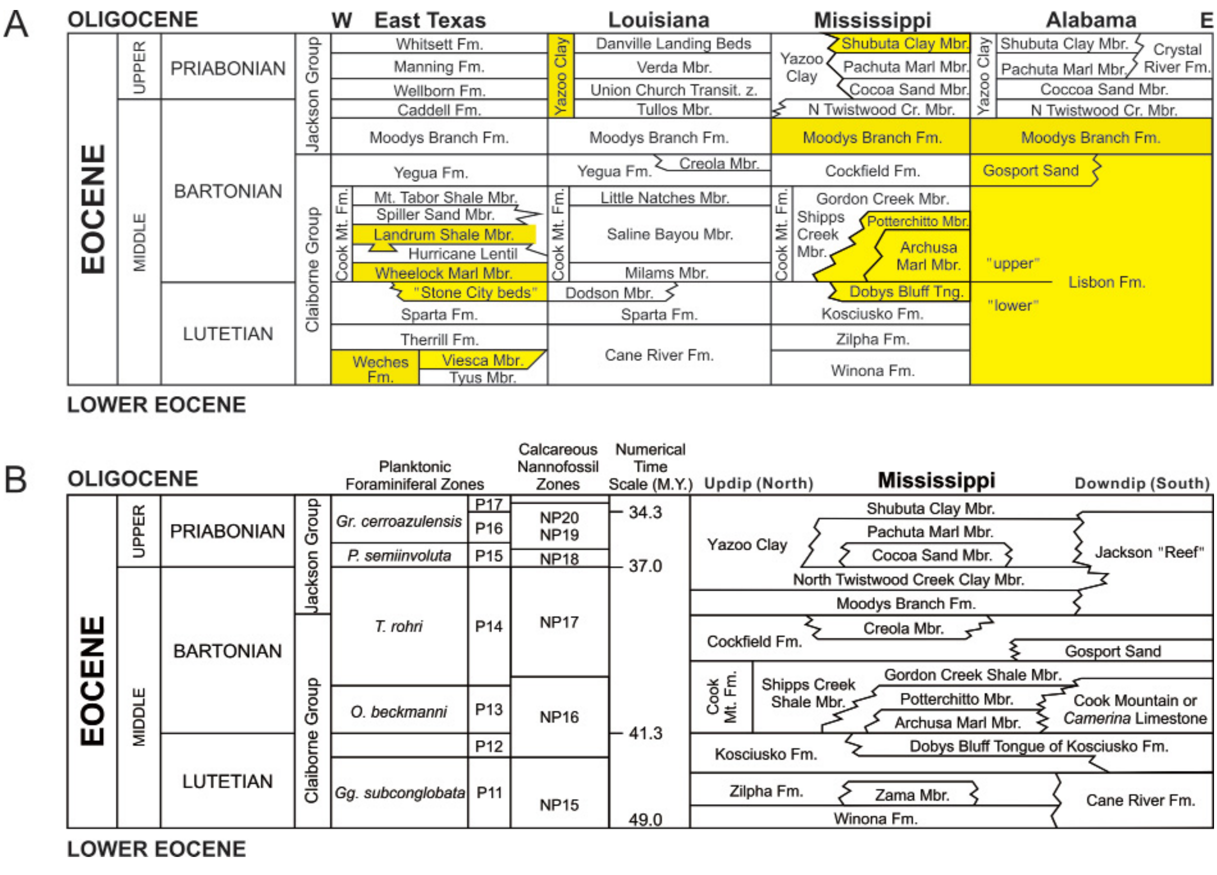


Fig. 2. Stratigraphic position of otolith-bearing strata in the US Gulf Coast middle and upper Eocene. **A**. The studied formations are indicated in yellow (after Dockery 1980, 1986c). **B**. Detailed stratigraphic units and biostratigraphic zonations for the succession in Mississippi (after Dockery & Thompson 2016).

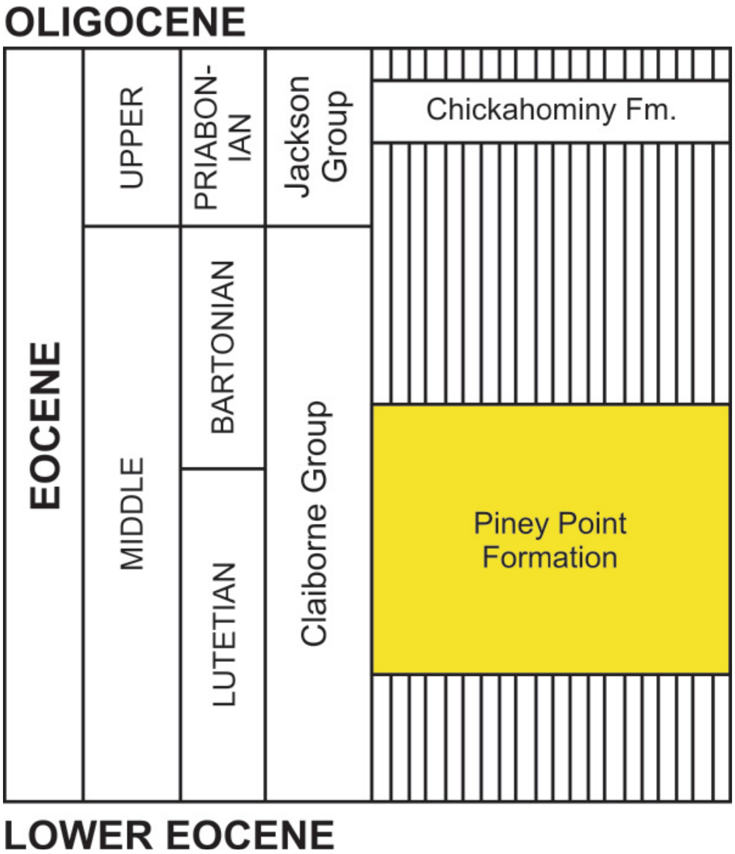


Fig. 3. Stratigraphic position of otolith-bearing stratum in the US eastern Atlantic Coast middle and upper Eocene. The studied formation, the Piney Point Formation, is indicated in yellow (after Ward 1985).

Institutional abbreviations

IRSNB	=	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
USNM	=	US National Museum of Natural History, Smithsonian Institution, Washington DC, USA
ZMB	=	Universität Humboldt Museum für Naturkunde, Berlin, germany

Locality data

ALABAMA

Barrytown, County Road 21 (Choctaw County) (Fig. 1, site 39)
Alabama, Coffeeville Lock and Dam 1/24 000 quadrangle, x = 382.225, y = 3520.800. GPS 31°49′00.1″ N, 88°14′38.4″ W. Road cut on west side of County Road 21, about 2 km south of Barrytown, 350 m south of bridge on Souwilpa Creek.

Identical locality: Loc. ACh-8 in Toulmin (1977: 367) and Ivany (1998: 18).

Stratigraphy: "upper" Lisbon Formation, Bartonian.

Sediment: light gray, slightly gravelly sand with many well-preserved shells.

Available material: bulk samples collected by D. Nolf in 1987 (ca 30 kg) and in 2003 (ca 70 kg).

Claiborne Bluff, Gosport (Monroe County) (Fig. 1, site 43)
Alabama, Claiborne 1/24 000 quadrangle, x = 450.400, y = 3489.525. GPS 31°32′22.6″ N, 87°31′21.0″ W.

Identical locality: Loc. AMo-4 in Toulmin (1977: 379).

Stratigraphy: Gosport Sand, Bartonian.

Available material: otolith specimens picked out by C. Garvie.

Coffeeville Landing (Clarke County) (Fig. 1, sites 40–41, Fig. 4)
Alabama, Coffeeville 1/24 000 quadrangle. East bank of Tombigbee River, from Coffeeville Landing till about 100 m south of the bridge of Highway 84. The landing itself is located about 100 m N of the bridge.

Identical locality: Loc. ACl-3 in Toulmin (1977: 370) and in Ivany (1998: 19). See also Smith & Johnson (1887: 32).

Stratigraphy: "upper" Lisbon Formation, Bartonian.

Sediment: yellowish gray marly sand, very easy to screenwash.

Available material: samples A–D: x = 395.650, y = 3513.750. GPS 31°45′16.2″ N, 88°06′06.5″ W (= near boat ramp, 10 m south of the landing). Sample S: x = 395.725, y = 3513.600. GPS 31°45′11.2″ N, 88°06′03.6″ W. Samples A, B, and C, each about 30 kg, were taken by D. Nolf in 2003; sample D, some 100 kg was taken by D. Nolf in 2002. Sample S was from the highest point of the section (Fig. 4) at about 80 m south of the bridge.

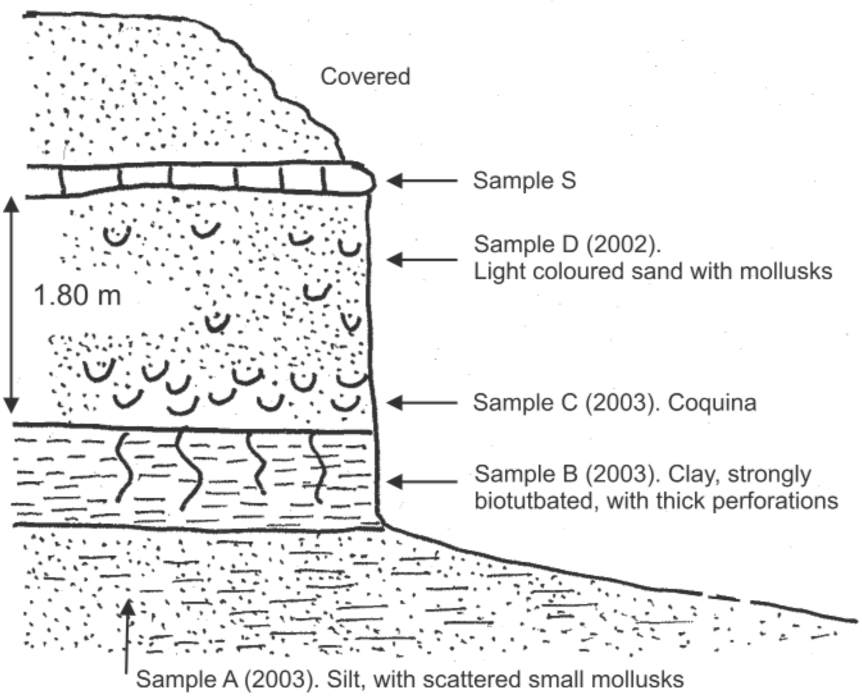


Fig. 4. Measured section at the Coffeeville Landing locality, Alabama (by D. Nolf).

Evansboro (SE of town) (Choctaw County) (Fig. 1, site 34)
Alabama, Isney 1/24 000 quadrangle, x = 364.800, y = 3524.575. GPS 31°50′56.0″ N, 88°25′44.4″ W. Creek-bed and surface exposure at SE end of John Green Pond, on the west side of County Road 39, SE of Evansboro.

Identical locality: loc. ACh-24* in Ivany (1998: 18).

Stratigraphy: "upper" Lisbon Formation, Bartonian.

Gilbertown (Choctaw County) (Fig. 1, site 38)
Alabama, Silas 1/24 000 quadrangle, x = 375.700, y = 3521.150. GPS 31°49′09.1″ N, 88°18′47.9″ W. Exposure on the E side of Highway 17, about 6 km S of Gilbertown.

Stratigraphy: "lower" and "middle" Lisbon Formation, Lutetian.

Sediment: the "lower" Lisbon Formation (sample 16b) consists of gray or weathered reddish brown, coarse sand with large specimens of *Cubitostrea lisbonensis* (Harris, 1919). The "middle" Lisbon Formation (sample 16a) consists of gray, slightly indurated sand with scattered shell material. The base of the "lower" Lisbon Formation is marked by a massive sandstone ledge at about 2m above the lowest part of the exposure.

Available material: both samples (16a, 16b) were collected by D. Nolf in 1987 (ca 25 kg each). Sample 16b is from 2 m above the sandstone ledge.

Isney (Choctaw County) (Fig. 1, site 36)
Alabama, Isney 1/24 000 quadrangle, x = 367.875, y = 3516.100. GPS 31°46′22.1″ N, 88°23′43.1″ W. Road cut on S side of Highway 84, 6 km E of Isney.

Identical locality: loc. ACh-18 in Toulmin (1977: 369) and in Ivany (1998: 18).

Stratigraphy: Moodys Branch Formation, Bartonian.

Sediment: sample A (lower clay) and sample B (upper sand).

Available material: both samples (A, B) were collected by D. Nolf in 2003 (ca 35 kg each).

Little Stave Creek (Clarke County) (Fig. 1, site 42)
Alabama, Jackson 1/24 000 quadrangle, x = 413.725, y = 3491.000. GPS 31°33′02.9″ N, 87°54′32.4″ W. At this classic locality, an almost complete section from near the base of the Claiborne Group to the upper Oligocene can be observed, but many of the facies are inappropriate for otolith collecting. Only the Gosport Sand (Bartonian) has been sampled for otoliths, and our data are based on these samples. See also Bandy (1949) and Toulmin (1977: 370, loc. ACl-4).

Stratigraphy: Gosport Sand, Bartonian.

Sediment and available material: highly fossiliferous coquina, containing very well preserved, dark colored shells. The shell material makes up the major part of the sediment (sample 17a, by D. Nolf, in 1987, ca 35 kg) and an additional otolith sample provided by C. Garvie. The basal part (sample 17b, by D. Nolf, in 1987, ca 20 kg) is gravelly and contains many eroded shark teeth. Our sample 17a corresponds to point 34 of Bandy (1949: figs 1–2) and Sample 17b to point 35.

Melvin (SE of town) (Choctaw County) (Fig. 1, site 37)
Alabama, Melvin 1/24 000 quadrangle, x = 369.000, y = 3529.000. GPS 31°53′21.5″ N, 88°23′06.7″ W. Road cut on N side of Choctaw County Road 14, east of Puss Cuss Creek.

Identical locality: loc. ACh-10 in Toulmin (1977: 368) and in Ivany (1998: 18).

Stratigraphy: Moodys Branch Formation, Bartonian.

Sediment: the sample is from the lower sandy part of the section, below more indurate soft sandstone levels. It is calcareous sandy silt with large glauconite grains.

Available material: sediments of ca 30 kg sampled by D. Nolf in 2002.

Puss Cuss Creek (Choctaw County) (Fig. 1, site 35)
Alabama, Isney 1/24 000 quadrangle, x = 364.800, y = 3522.500. GPS 31°49′48.7″ N, 88°25′43.3″ W. Bluff at waterfall.

Identical locality: loc. ACh-23* in Ivany (1998: 7, 18, fig. 5).

Stratigraphy: "upper" Lisbon Formation, Bartonian.

Sediment: light gray-green fine silty sand with scattered mollusk shell material.

Available material: sediments of ca 30 kg sampled by D. Nolf in 2003. However, this sample only contains badly-preserved, not identifiable otoliths.

LOUISIANA

Copenhagen (Caldwell Parish) (Fig. 1, site 24)
Louisiana, Columbia 1/24 000 quadrangle, x = 591.900, y = 3544.100. GPS 32°01′45.5″ N, 92°01′36.5″ W. See also Nolf & Stringer (2003) for locality data.

Stratigraphy: Yazoo Clay, Priabonian.

Sediment: greenish gray to bluish gray silty, glauconitic, very fossiliferous marl in the lowermost portion of the section and gray to tan clay, calcareous, slightly fossiliferous in the upper part.

Available material: D. Nolf and G.L. Stringer collected small samples in 1982. A large bulk sample (ca 450 kg) was taken by G.L. Stringer and geology students from the University of Louisiana at Monroe in 1989 from the lowermost portion of the section and provided 5293 otoliths, representing 43 taxa (Nolf & Stringer 2003). A sample of ca 15 kg from the upper part, at 8 m above the base of the exposure, provided 266 otoliths, representing 7 taxa.

Nannoplankton analysis (by E. Steurbaut)
Two outcrops of the Yazoo Clay sampled near Copenhagen: one at the basal layer of the exposed clay (see Nolf & Stringer 2003, lower sample) and one at Gibson Landing (Columbia 1/24 000 quadrangle, x = 592.100, y = 3544.520) yielded quasi-identical, well preserved and diversified calcareous nannofossil assemblages. These are dominated by small and medium-sized (D < 10 µm) and large-sized (D > 15 µm) *Coccolithus pelagicus* (Wallich, 1877)Schiller, 1930. The following stratigraphically important Noelaerhabdaceae Jerković, 1970 have also been identified: *Cribrocentrum isabellae* Catanzariti, Rio & Fornaciari, 2010, *Cribrocentrum reticulatum* (Gartner & Smith, 1967) Perch-Nielsen, 1971, *Dictyococcites bisectus* (Hay, Mohler & Wade, 1966) Bukry & Percival, 1971 and *Reticulofenestra*

umbilica (Levin, 1965) Martini & Ritzkowski, 1968 (large forms with D around 21 µm). The assemblages are furthermore marked by the presence of *Braarudosphaera stylifera* Troelsen & Quadros, 1971, *Coccolithus formosus* (Kamptner, 1963) Wise, 1973, *Discoaster barbadiensis* Tan Sin Hok, 1927, *Discoaster saipanensis* Bramklette & Riedel, 1954 and *Pemma papillatum* Martini, 1959. The two marker species *Chiasmolithus oamaruensis* (Deflandre, 1954) Hay, Mohler & Wade, 1966 (defining the base of Martini's nannofossil Zone NP18) and *Isthmolithus recurvus* Deflandre, 1954 (defining the base of Zone NP19 of Martini 1971), which were expected to be found in these assemblages, have not been recorded. The absence of *C. oamaruensis* is believed to be due to the gradual decline of this species throughout Chron C17n.1n (Fornaciari *et al*. 2010), the absence of *I. recurvus* to the particular paleoenvironmental and/or paleogeographical context of the outcrops. The co-occurrence of *Cribrocentrum isabellae* and *C. reticulatum* indicates that the Yazoo Clay at Copenhagen can be attributed to calcareous nannofossil Zone CNE19 of Agnini *et al.* (2014). This, in combination with the fact that the highest occurrence of large-sized *Coccolithus pelagicus* slightly predates the highest occurrence of *Cribrocentrum reticulatum* in the Fayum (Western Desert, Egypt; King *et al.* 2014), may point to the middle part of Zone CNE19 for these Copenhagen outcrops. Cross-correlations with the geological time scale (Agnini *et al*. 2014; Speijer *et al.* 2020) allows the conclusion that this part of the Yazoo Clay belongs to the middle part of the Priabonian, dated at around 35.7 Ma.

MISSISSIPPI

Chickasawhay River, Hunting Lodge (Clarke County) (Fig. 1, site 33)
Mississippi, De Soto 1/24 000 quadrangle, x = 339.986, y = 3530.455. GPS 31°53′55.29″ N, 88°41′31.54″ W, N of Shubuta.

Identical locality: Mississippi Geological Society (MGS) loc. no. 16 (see also Dockery & Thompson 2016).

Stratigraphy: Moodys Branch Formation.

Available material: isolated otoliths provided by D. Dockery.

Cynthia, Mississippi Lite clay pit (Hinds County) (Fig. 1, site 25)
Mississippi, Pocahontas 1/24 000 quadrangle, x = 758.100, y = 3589.500. GPS 32°24′45.7″ N, 90°15′20.2″ W.

Identical locality: MGS loc. no. 15 (see also Dockery & Thompson 2016).

Stratigraphy: Yazoo Clay, Shubuta Clay Member, Priabonian.

Sediment: the sample is from small shell concentration lenses in massive greenish clay.

Available material: sediment sample of ca 35 kg collected by D. Nolf in 1987.

Dobys Bluff (Clarke County) (Fig. 1, site 31, Fig. 5)
Mississippi, Quitman 1/24 000 quadrangle, x = 338.850, y = 3543.500. GPS 32°00′58.3″ N, 88°42′22.7″ W. Bluff exposure on Chickasawhay River (see also Dockery 1986a: 380).

Stratigraphy: Kosciusko Formation, Dobys Bluff Tongue, Lutetian.

Sediment and available material: sample 1: gray, very fossiliferous bed, 60 cm above the basal sandy clay (ca 8 kg); sample 2: gray, fossiliferous sand, sample of ca 120 kg.

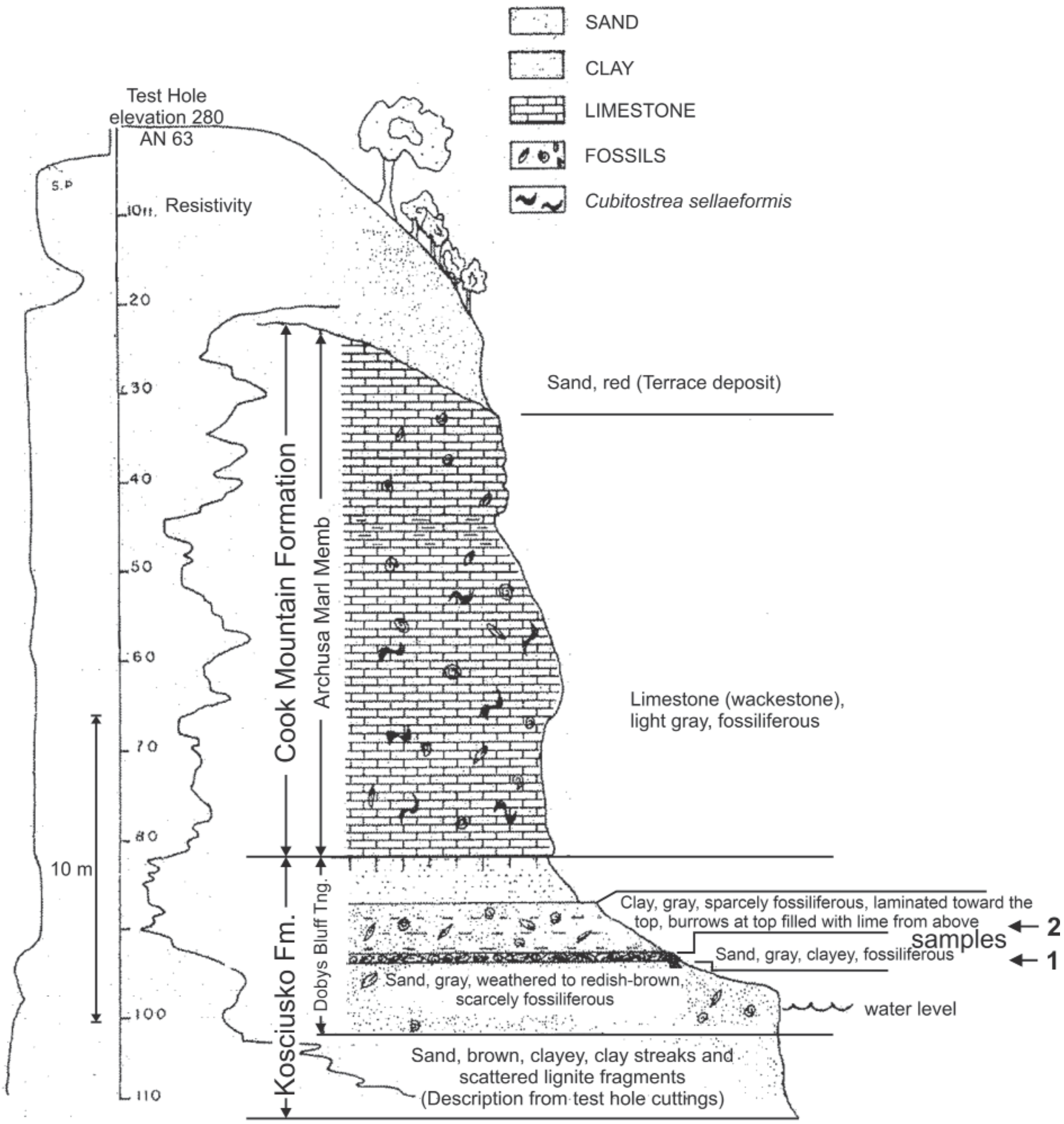


Fig. 5. Measured section at the Dobys Bluff locality, Mississippi (after Dockery 1986a).

Jackson, boring at the corner of Amite & Mill streets (Hinds County) (Fig. 1, site 27)
Mississippi, Jackson 1/24 000 quadrangle, x = 764.550, y = 3577.500. GPS 32°18′11.1″ N, 90°11′25.5″ W.

Stratigraphy: Moodys Branch Formation.

Available material: isolated otoliths provided by D. Dockery.

Jackson, Riverside Park (Hinds County) (Fig. 1, site 29)
Mississippi, Jackson 1/24 000 quadrangle, x = 767.800, y = 3579.700. GPS 32°19′19.6″ N, 90°09′19.1″ W. The "Fossil Gulch", ravine along the valley wall of the Pearl River floodplain at Riverside Park.

Identical locality: MGS loc. no. 2 (Dockery 1977: 18, 196, figs 4–5; 1986b; Dockery & Thompson 2016).

Stratigraphy: Moodys Branch Formation, Bartonian.

Sediment: green glauconitic sand with many mollusks, weathered to reddish-brown in the upper part.

Available material: sample 6a (by D. Nolf in 1987, ca 25 kg) comes from 10–30 cm above the base of the exposure; sample 6b (by D. Nolf in 1987, ca 25 kg) is from 1 m above the base.

Jackson, Town Creek (Hinds County) (Fig. 1, site 28)
Mississippi, Jackson 1/24 000 quadrangle, x = 765.350, y = 3575.300. GPS 32°16′59.2″ N, 90°10′57.0″ W.

Identical locality: MGS loc. no. 1 (Dockery 1977: 196; Dockery & Thompson 2016).

Stratigraphy: Moodys Branch Formation, Bartonian.

Sediment: light gray sand with many well-preserved shells

Available material: sample of ca 5 kg, collected by D. Dockery in 1987.

Midway, Techeva Creek (Yazoo County) (Fig. 1, site 26)
Mississippi, Zeigerville 1/24 000 quadrangle, x = 763.000, y = 3643.750. GPS 32°54′01.4″ N, 90°11′17.9″ W. Exposure in the banks of Techeva Creek, just upstream from the bridge at the intersection of Techeva Creek and Highway 433, about 1.5 km N of Midway.

Identical locality: MGS loc. no. 11 (Dockery 1977: 18–20, 196, figs 6–9; Dockery & Thompson 2016).

Stratigraphy: Moodys Branch Formation, Bartonian.

Sediment: green glauconitic sand with many mollusks and bioturbation.

Available material: sample 5a (by D. Nolf in 1987, ca 15 kg) is from a *Glycymeris* coquina in the upper part of the section; sample 5b (by D. Nolf in 1987, ca 35 kg) comes from sand with scattered mollusks, about 1.5 m below the *Glycymeris* coquina. An additional sample of isolated otoliths from the same site was provided by C. Garvie.

Newton, NE exit off Interstate 20 (Newton County) (Fig. 1, site 30)
Mississippi, Newton 1/24 000 quadrangle, x = 299.175, y = 3579.925. GPS 32°20′17.5″ N, 89°08′01.7″ W.

Stratigraphy: Cook Mountain Formation, Potterchitto Member, Bartonian.

Sediment: gray silty sand with scattered shells

Available material: sediments were sampled by D. Nolf in 1987 (ca 35 kg) and a sample of isolated otoliths was provided by D. Dockery. Near the same point, a sample (ca 60 kg) was also taken in 1987, by a gas station at the SW corner of Highway 15 and Interstate 20 (exit 20). The gas station was already pulled down in 2002, and the place is almost unrecognizable.

Quitman, Archusa Water Park (Clarke County) (Fig. 1, site 32)
Mississippi, Quitman 1/24 000 quadrangle, x = 339.150, y = 3544.750. GPS 32°01′39.0″ N, 88°42′11.9″ W. Roadside exposure, about 100 m S of the entrance of Archusa Creek Water Park.

Identical locality: MGS loc. no. 27 (see also Dockery & Thompson 2016).

Stratigraphy: Cook Mountain Formation, Archusa Marl Member, Bartonian.

Sediment: whitish sandy marl with shell fragments.

Available material: sediments of ca 35 kg were sampled by D. Nolf in 1987.

TEXAS

Alabama Ferry, on Trinity River, North (Houston County) (Fig. 1, site 21)
Texas, Austonio 1/24 000 quadrangle, x = 240.325, y = 3457.700. GPS 31°13′28.6″ N, 95°43′33.6″ W. Approximately 1.4 km N of Alabama Ferry.

Identical locality: Loc. 113-T-36 in Fisher *et al*. (1964)

Stratigraphy: "Stone City beds", Lutetian.

Available material: a sample of isolated otoliths provided by C. Garvie (113-T-36), and three otolith samples provided by B. Welton (BJW 02-IX-14-1; BJW 02-IX-14-4; BJW 02-IX-21-1).

Burleson Bluff (Burleson County) (Fig. 1, site 3)
Texas, Mumford 1/24 000 quadrangle, x = 731.350, y = 3399.700. GPS 30°42′27.7″ N, 96°35′03.5″ W.

Stratigraphy: Weches Formation, transgressive system track, Lutetian.

Sediment: rusty, somewhat clayey glauconitic sand with many scattered shells.

Available material: a sample was taken by D. Nolf in 2001 (ca 60 kg) at about 1 m from the top of the exposure, just below a limestone ledge with siderite.

Cedar Creek, E of Centerville (Leon County) (Fig. 1, site 20)
Texas, Spring Seat 1/24 000 quadrangle, x = 783.425, y = 3457.500. GPS 31°13′02.3″ N, 96°01′30.0″ W. The site is 1.5 km W of the Wall Farm 1 locality (see below).

Stratigraphy: Weches Formation, Viesca Member, Lutetian.

Available material: isolated otoliths provided by C. Garvie.

Crockett (Houston County) (Fig. 1, site 22)
Texas, Porter Springs 1/24.000 quadrangle, x = 260.000, y = 3468.500. GPS 31°19′34.3″ N, 95°31′19.9″ W. W of Crockett, drainage ditch on the N side of Texas FM 2076 road, 1.75 km W of its junction with Bennet Lane.

Stratigraphy: Cook Mountain Formation, Landrum Member, Bartonian.

Available material: sample of isolated otoliths provided by B. Welton (BJW 02-III-4-4).

Dunn's Ranch, NNE of Bryan (Robertson County) (Fig. 1, site 16**)**
Texas, Dunn's Creek 1/24 000 quadrangle, x = 745.085, y = 3408.270. GPS 30°46′55.94″ N, 96°26′20.28″ W.

Stratigraphy: "Stone City beds", Lutetian.

Available material: isolated otoliths provided by C. Garvie.

Hooker Creek (Burleson County) (Fig. 1, site 2)
Texas, Chriesman 1/24 000 quadrangle, x = 708.850, y = 3377.050. GPS 30°30′27.4″ N, 96°49′25.3″ W.

Stratigraphy: Weches Formation (upper part), Lutetian.

Sediment: level with dentaliums between siderite sandy limestone ledges.

Available material: the otoliths are very fragile, sediments were sampled by D. Nolf in 2001 (ca 30 kg).

Little Brazos River, Stenzel loc. (Brazos County) (Fig. 1, site 13)
Texas, Mumford 1/24 000 quadrangle, x = 737.700, y = 3392.600. GPS 30°38′32.6″ N, 96°31′10.9″ W. N of the Highway 21 bridge, near the mouth of a small confluent.

Identical locality: Loc. 21-T-1 in Stenzel *et al*. (1957: 17).

Stratigraphy: Cook Mountain Formation, Wheelock Member, Bartonian.

Sediment: fine gray green silty glauconitic sand with mollusks

Available material: a sample of ca 30 kg sediment by D. Nolf in 2001 and ca 240 kg in 2002.

Little Brazos River, under Highway 21 bridge (Brazos County) (Fig. 1, site 12)
Texas, Mumford 1/24 000 quadrangle, x = 737.600, y = 3392.250. GPS 30°38′21.5″ N, 96°31′14.9″ W.

Stratigraphy: Cook Mountain Formation, Wheelock Member, Bartonian.

Available material: isolated otoliths (sample BJW 02-V-25-2) collected by B. Welton.

Little Brazos River, 1.5 km S of Highway 21 bridge (Brazos County) (Fig. 1, site 14)
Texas, Mumford 1/24 000 quadrangle, x = 738.650, y = 3391.150. GPS 30°37′45.1″ N, 96°30′36.4″ W.

Stratigraphy: Cook Mountain Formation, Wheelock Member, Bartonian.

Available material: otolith samples provided by C. Garvie (sample LB2) and by B. Welton (sample BJW 02-V-25-3).

Little Brazos River, confluence with Brazos River (Brazos County) (Fig. 1, site 15)
Texas, Mumford 1/24 000 quadrangle, x = 738.950, y = 3390.575. GPS 30°37′26.0″ N, 96°30′25.6″ W.

Identical locality: Loc. 21-T-6 in Stenzel *et al*. (1957: 17).

Stratigraphy: Cook Mountain Formation, Wheelock Member, Bartonian.

Available material: otolith samples (sample LB-BR) provided by C. Garvie and B. Welton (sample BJW 02-IX-1-1).

Nacogdoches Dam (Nacogdoches County) (Fig. 1, site 23)
Texas, Lake Nacogdoches South 1/24 000 quadrangle, x = 325.850, y = 3496.175. GPS 31°35′15.0″ N, 94°50′07.4″ W.

Stratigraphy: Weches Formation, Lutetian.

Available material: otolith sample provided by C. Garvie.

Pin Oak Creek (Bastrop County) (Fig. 1, site 1)
Texas, Winchester 1/24 000 quadrangle, x = 686.475, y = 3323.650. GPS 30°01′46.9″ N, 97°03′58.3″ W.

Identical locality: Loc. 11-T-70 in Fisher *et al*. (1964).

Stratigraphy: Cook Mountain Formation, Landrum Member, Bartonian.

Available material: otolith samples (Pin Oak Creek 1 and Pin Oak Creek 2) provided by C. Garvie.

Robbins, roadside (Leon County) (Fig. 1, site 17)
Texas, Robbins 1/24 000 quadrangle, x = 774.850, y = 3461.125. GPS 31°15′07.2″ N, 96°06′50.0″ W. Road side (Private Rd 4080), in front of a pond.

Stratigraphy: Weches Formation, Lutetian.

Sediment: sandy coquina.

Available material: sediments were sampled by D. Nolf in 2001 (ca 30 kg).

Rocky Branch, 1.5 miles SW of Stone City Bluff (Burleson County) (Fig. 1, sites 4-10)
Texas, Tunis 1/24 000 quadrangle.

River section; the numbering of the samples is in descending stratigraphic order. Sediments sampled by D. Nolf in 2002.

Stratigraphy, sampling and available material:

Sample 0 = Cook Mountain Formation, Wheelock Member, Bartonian (x = 733.425, y = 3389.300. GPS 30°36′48.6″ N, 96°33′54.0″ W) = 150 m upstream from waterfall; ca 30 kg.

Samples 1–6 = “Stone City beds”, Lutetian.
- Sample 1 (x = 733.325, y = 3389.450. GPS 30°36′53.6″ N, 96°33′57.6″ W). Just below the top of a waterfall, ca 30 kg;
- Sample 2 (x = 733.375, y = 3389.500. GPS 30°36′55.1″ N, 96°33′55.8″ W). Storm level, sandy, lenticular. Right bank, ca 10 kg;
- Sample 3 (x = 733.550, y = 3389.650. GPS 30°37′00.1″ N, 96°33′49.0″ W). *Cypraea* bed. Left bank, 5 kg;
- Sample 4 (x = 733.900, y = 3389.825. GPS 30°37′05.5″ N, 96°33′35.6″ W). Storm level; somewhat indurate clayey glauconitic sand. Right bank, ca 3 kg;
- Sample 5 (x = 734.100, y = 3389.950. GPS 30°37′09.5″ N, 96°33′28.1″ W). Equivalent of the top of the Main Glauconite (Bed S) in Stone City Bluff, Brazos River (see below). Right bank, coral level (ca 5 kg) and shell gravel level (5 kg);
- Sample 6 (x = 734.200, y = 3390.125. GPS 30°37′14.9″ N, 96°33′24.1″ W). Equivalent of Bed P in Stone City Bluff, Brazos River (see below). Right bank, ca 30 kg.

Stone City Bluff, Brazos River (Burleson County) (Fig. 1, site 11)
Texas, Mumford 1/24 000 quadrangle, x = 735.400, y = 3390.680. GPS 30°37′32.2″ N, 96°32′38.8″ W. This place is also called "Moseley's Ferry", after the location of the old ferry, before the road bridge and railway bridge were built. Letter designations of the beds (levels) are from Stenzel *et al*. (1957). The section is redrawn here (Fig. 6). The lower part of the section (downwards from the middle of Bed M) was under water level at the moment of the visit and could not be sampled, but we have otoliths of

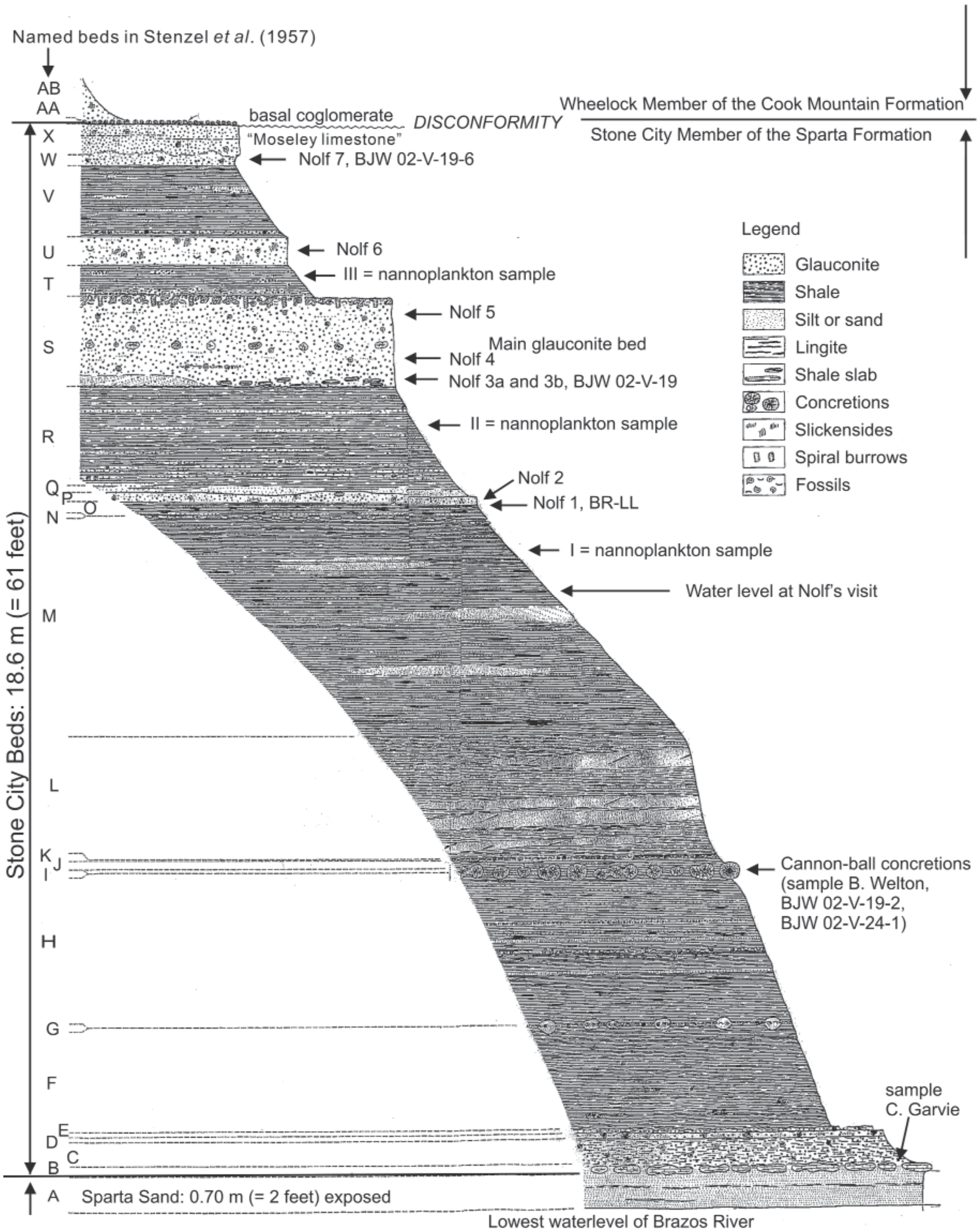


Fig. 6. Measured section at the Stone City Bluff, Brazos River locality, Texas (after Stenzel *et al*. 1957).

Bed I (also known as the "Cannon Ball zone") and the basal part (Bed B) provided by B. Welton and C. Garvie, respectively.

Stratigraphy: "Stone City beds", Lutetian.

Available material:

1. Bed P, sample Nolf 1 = base of the lower glauconitic; ca 30 kg and isolated otoliths provided by C. Garvie (sample BR-LL).
2. Bed P, sample Nolf 2 = middle part of lower glauconitic, ca 60 kg.
3. Bed S, sample Nolf 3a = base of main glauconitic, dominant glauconitic facies, ca 30 kg.
4. Bed S, sample Nolf 3b = base of main glauconitic (Bed S), quartzite-sand facies, storm level. 30 kg (coll. IRSNB) and isolated otoliths provided by B. Welton (BJW 02-V-19).
5. Bed S, sample Nolf 4 = main glauconitic Bed S, just below Septaria level, (ca 30 kg, sampled by D. Nolf in 2002) and isolated otoliths provided by C. Garvie.
6. Bed S, sample Nolf 5 = top main glauconitic (Bed S), 30 kg.
7. Bed U, sample Nolf 6 = glauconitic level, 30 kg.
8. Bed W, sample Nolf 7 = soft basement below Moseley Limestone, ca 30 kg, sampled by D. Nolf in 2001 and isolated otoliths provided by B. Welton (BJW 02-V-19-6).

Additional samples:

1. Bed I (Cannon Ball zone), isolated otoliths provided by B. Welton (BJW 02-V-19-2, BJW 02-V-24-1).
2. Bed B (= at the base of the "Stone City beds"), isolated otoliths provided by C. Garvie.
3. A sample provided by H. von Hacht (not localized in the section).

Nannoplankton samples in coll. IRSNB:

1. sample I = from Bed M, 1 m below glauconitic Bed P.
2. sample II = from Bed R, 70 cm below main glauconitic Bed S.
3. sample III = from Bed T, 30 cm above top of main glauconite Bed S.

Bed P appeared to be excessively rich in otoliths, and because all other beds were sampled in quantities that only provided much scarcer amounts of otoliths, we judged that it was not meaningful to mention quantitative data. Although not detailed in the present study, further sampling and analysis are expected to reveal any faunal differences related to different paleoenvironment among different beds.

Wall Farm 1 (Leon County) (Fig. 1, site 19)
Texas, Spring Seat 1/24 000 quadrangle, x = 781.725, y = 3458.300. GPS 31°13′29.6″ N, 96°02′33.4″ W. Exposure in a creek, E of the road.

Stratigraphy: Weches Formation, above the basis of the Viesca Member, Lutetian.

Available material: ca 30 kg, sampled by D. Nolf in 2001.

Wall Farm 2 (Leon County) (Fig. 1, site 18)
Texas, Spring Seat 1/24 000 quadrangle, x = 780.500, y = 3458.775. GPS 31°13′46.2″ N, 96°03′19.1″ W. "Dunn's Ranch Creek", in the middle of grasslands.

Stratigraphy: Weches Formation, slightly indurated coquina, Lutetian.

Available material: ca 30 kg, sampled by D. Nolf in 2001.

VIRGINIA

Pamunkey River area, Devil's Hole (King William County) (Fig. 1, site 44)
Virginia, Manquin 1/24 000 quadrangle, x = 305.775, y = 4173. 550. GPS 37°41′19.0″ N, 77°12′10.1″ W.

Identical locality: loc. 19 in Müller (1999).

Stratigraphy: Piney Point Formation, Lutetian.

Sediment: calcareous, gray green, medium-sized glauconitic sand.

Available material: sediments were sampled by D. Nolf in 2000 (ca 150 kg).

Pamunkey River, 1 km E of Eanes property (Hanover County) (Fig. 1, site 45)
Virginia, Manquin 1/24 000 quadrangle, x = 308.950, y = 4170.200. GPS 37°39′32.8″ N, 77°09′57.2″ W.

Identical locality: loc. 37 in Strickland (1985).

Stratigraphy: Piney Point Formation, Lutetian.

Sediment and available material: detailed section of this locality is provided in Fig. 7.

Sample 1 = Bed A, 30–150 cm below the sandstone ledge; sample 2 = Bed A, 0–30 cm above the sandstone ledge; sample 3 = Bed B. Sediments of ca 120 kg each from samples 1 and 2, and ca 30 kg from sample 3 were taken by D. Nolf in 1989.

Pamunkey River, Horseshoe, Old Church type locality (Hanover County) (Fig. 1, site 46)
Virginia, Manquin 1/24 000 quadrangle, x = 310.500, y = 4170.450. GPS 37°39′42.1″ N, 77°08′54.2″ W.
Identical locality: loc. 40 (= stop 12) in Strickland (1985) and loc. 85 in Ward (1985).
Stratigraphy and available material:
- Old Church Formation (Chattian/Aquitanian), above concretions. 60 kg of sediments were sampled by D. Nolf in 2000; not studied here, but are mentioned here as a part of the description of the exposure.
- Old Church Formation (Chattian/Aquitanian), below concretions. 100 kg of sediments were sampled by D. Nolf in 2000; not studied here, but are mentioned here as a part of the description of the exposure.
- Piney Point Formation, Lutetian. 2 m below top of the formation. 30 kg of sediments were sampled by D. Nolf in 2000.

Nannoplankton analysis (by E. Steurbaut)
The Piney Point Formation has been sampled at two different points along the Pamunkey River in Virginia: Devil's Hole (see above) and Horseshoe. Devil's Hole only yielded a poorly preserved, very poor and not interpretable calcareous nannofossil assemblage. The assemblage from Horseshoe is moderately preserved and rather well-diversified. It is dominated by small-sized Noelaerhabdaceae and particularly rich in cold-water-preference taxa, such as *Chiasmolithus* Hay, Mohler & Wade, 1966. Warm-water-preference taxa, such as Discoasteraceae Tan Sin Hok, 1927, Sphenolithaceae Deflandre in Grassé, 1952 and *Pemma* Klumpp, 1953 are poorly represented. The assemblage is marked by the co-occurrence of *Chiasmolithus solitus* (Bramlette & Sullivan, 1961)Locker, 1968, *Reticulofenestra umbilica* (D > 14 µm) and *Helicosphaera seminulum* Bramlette & Sullivan, 1961. This, in combination with the absence of *Nannotetrina* spp., *Chiasmolithus gigas* (Bramlette & Sullivan, 1961)Radomski, 1968, *Cribrocentrum reticulatum*, and *Dictyococcites bisectus*, refers to the lower part of calcareous

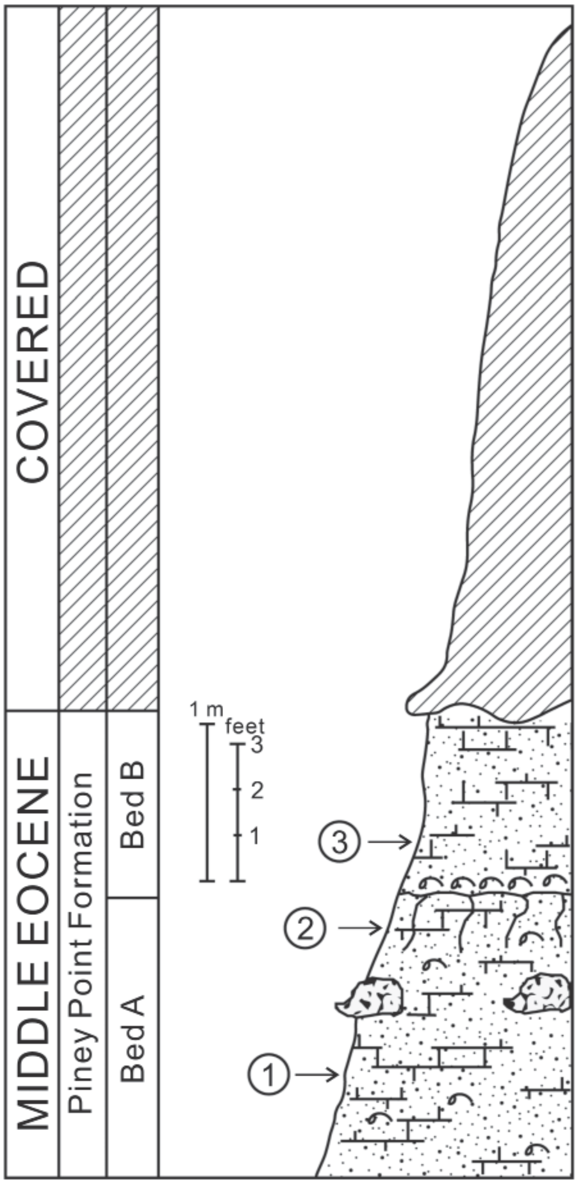


Fig. 7. Measured section at the Pamunkey River, 1 km E of Eanes property, Virginia (after Strickland 1985, loc. 37).

nannofossil Zone CNE13 of Agnini *et al.* (2014). The latter corresponds to the lower middle part of Martini's (1971) nannofossil Zone NP16. Cross-correlations with the geological time scale (Agnini *et al*. 2014; Speijer *et al.* 2020) allows us to conclude that this part of the Piney Point Formation belongs to the lower upper part of the Lutetian, dated at around 42.9 Ma.

Pamunkey River, SW of Pampatike Landing (Hanover County) (Fig. 1, site 47)
Virginia, Manquin 1/24 000 quadrangle, x = 311.175, y = 4170.550. GPS 37°39′45.7″ N, 77°08′26.9″ W.

Stratigraphy: Piney Point Formation, Lutetian.

Sediment: sediments were sampled by D. Nolf in 2000 (30 kg).

Type specimens of Müller (1999)

For comparative purposes, some type and paratype specimens of Müller (1999) were donated by Müller to the IRSNB, and are studied and compiled in the figures for completeness (see below, systematic paleontology). These include images of five species, *Paraconger sector* (Koken, 1888) (as *P. americanus* in Müller), "*Conger*" *prolatus* (Müller, 1999), "*Neobythites*" *rotunda* Müller, 1999, "*Sciaena*" *eanesi* (Müller, 1999), and "*Sciaena*" *livesayi* (Müller, 1999).

Faunal analyses

Since our material includes localities across several states and covers approximately 15 million years, both biogeographical and stratigraphical factors shaped the otolith-based fish associations. To better understand the shift of these associations across time and space, otolith assemblages from each locality were grouped according to the formation where they are collected. Our data matrix (Table 1) includes Frizzell & Lamber (1961, 1962), Frizzell (1965), Frizzell & Dante (1965), Stringer (1979, 1986, 2016), Nolf & Stringer (2003), Ebersole *et al*. (2019), and the present material. Additional data were also extracted from Stringer *et al*. (2022: table 3). A rarely known assemblage from the Cane River Formation of Louisiana was described by Stringer & Breard (1997); however, we did not include this dataset due to its low taxonomic resolution. Multivariate analyses were also performed based on the dataset (see Appendix), but in the text we only list differences and similarities of the taxonomic composition for these associations and discuss their overall trend. Recently, Stringer *et al*. (2022) reported Bartonian otoliths from the Clinchfield Formation (Georgia); this assemblage was incorporated in our systematic paleontology.

Results

Systematic paleontology

The classification follows Nelson *et al*. (2016). For the authorships of higher taxa, we follow Van Der Laan *et al*. (2014). The abbreviation aff. (affinis) is used when well-preserved specimens could not unequivocally be attributed to known species, whereas cf. (conformis) is inserted when the preservation does not allow for a conclusive identification. In the subsequent analyses, however, these taxa are treated like the other ones.

Although we are not in favor of the introduction of exclusively otolith-based generic names (see Nolf 2013), more and more authors use them today, especially because the ICZN Code has compulsorily required valid generic names. Because it is not opportune to fill up the literature with a long-lasting conflicting generic nomenclature (Nolf 2013), we at last decided on the restricted use of exclusively otolith-based generic names for species belonging to extinct genera. This action means that we accept the already existing generic names for the species treated here and the closely related ones when they are represented among our material. For species of uncertain generic position for which such formal names are not available, we follow the system in Lin *et al*. (2017a, 2017b) in order to comply entirely with the ICZN Code. In this approach, fossil species that can only be allocated at the Recent family level (or higher-ranking level), but not attributed to a precise recent genus, are assigned to the type genus of the concerned family (or subfamily, etc.), and the genus name is placed between inverted commas. At least one otolith image is provided for each identified taxon for the present collection (Figs 8–37). Diagnoses of new species include morphmetrics which are restricted to otolith length (OL), otolith height (OH), ostium length (OsL), and cauda length (CaL). Previously described nominal species not found in the newly collected material are also included in this systematic review, and they are redrawn and assembled in Figs 38–39. A list of all the collected taxa and their abundance is presented in Table 1. A list of doubtful and rejected species is provided at the end of the descriptive part, which is mainly derived from Nolf (2013) and incorporated here.

Table 1 (continued on next two pages). An overview of otolith-based fish taxa from the middle and late Eocene of the eastern and southern USA. Fossil genera are underlined. The number of identified specimens is indicated for each studied stratum. The collection of the Yazoo Clay of Louisiana was directly derived from Nolf & Stringer (2003) for comparison. Data sources: a = Frizzell & Lamber (1961); b = Frizzell & Lamber (1962); c = Frizzell & Dante (1965); d = Müller (1999); e = Nolf (2003); f = Stringer (2016); g = Ebersole *et al*. (2019); h = Stringer *et al*. (2022: table 3).

Fish otolith taxa from the middle and late Eocene of eastern and southern USA	Texas				Louisiana		Mississippi				Alabama				Virginia
			Cook Mountain F.				Kosciusko F.	Cook Mountain F.		Yazoo C.	Lisbon F.				
	Weches F.	"Stone City beds"	Wheelock Marl M.	Landrum Shale M.	Moodys Branch F.	Yazoo C. (N. & S. 2003)	Dobys Bluff Tongue	Archusa Marl M./ Potterchitto M.	Moodys Branch F.	Shubuta Clay M.	"Lower-Middle"	"upper"	Gosport Sand	Moodys Branch F.	Piney Point F.
Albula sp.		4				5									
Elopothrissus bernardlemorti sp. nov.		5										1			
Pterothrissus umbonatus (Koken, 1884)	24	105	7	19		1		5		6		4			3
Muraenanguilla aff. *thevenini* (Priem, 1906)						1									d
Pythonichthys colei (Müller, 1999)		6	2	3	h	90			2	4		14		3	10
"*Ophichthus*" *brevior* (Koken, 1888)									e						
"*Muraenesox*" *barrytownensis* sp. nov.		4										1			
Alaconger fornicata (Frizzell & Lamber, 1962)						b				4					
Conger vetustus Frizzell & Lamber, 1962					b	8			b			1			
Gnathophis dissimilis (F. & L., 1962)					b	1									
Pseudophichthys glaber (Koken, 1888)	1	10	3	5	h	54				1		4		1	d, e
Pseudophichthys texanus sp. nov.	8						1	5				9			31
Rhynchoconger sp. 1				4											
Rhynchoconger sp. 2			16												
Heteroconger ovatus (Müller, 1999)															11
Ariosoma nonsector Nolf & Stringer, 2003		12	17		f	582	3	56	62		3	146		87	
Paraconger brazosensis (D. & F., 1965)	c	305	9	50			2								
Paraconger meridies (F. & L., 1962)												g			15
Paraconger sector (Koken, 1889)					h	17		1	28		1	57	4	12	138
Paraconger solidus Müller, 1999															d
Paraconger wechesensis sp. nov.	101														
Paraconger yazooensis N. & S., 2003					f	25									
"*Conger*" *prolatus* (Müller, 1999)															15
"*Conger*" *websteri* (Frost, 1933)								1							11
"*Osteoglossum*" aff. *rhomboidalis* (Stinton, 1977)		2													
Neoopisthopterus weltoni sp. nov.		2		1											
Sardinops sp.				1											
Clupeidae indet.		1		2			1	1				1			
Plotosus sp.		2	5												
Synodus sp.									1						

Table 1 (continued).

Fish otolith taxa from the middle and late Eocene of eastern and southern USA	Texas: Weches F.	Texas: "Stone City beds"	Texas: Cook Mountain F.		Louisiana: Moodys Branch F.	Louisiana: Yazoo C. (N. & S. 2003)	Mississippi: Kosciusko F.	Mississippi: Cook Mountain F.	Mississippi: Moodys Branch F.	Mississippi: Yazoo C.	Alabama: Lisbon F.		Alabama: Gosport Sand	Alabama: Moodys Branch F.	Virginia: Piney Point F.
			Wheelock Marl M.	Landrum Shale M.			Dobys Bluff Tongue	Archusa Marl M./ Potterchitto M.		Shubuta Clay M.	"Lower-Middle"	"upper"			
Bregmaceros troelli (D. & F., 1965)	c	42	122	271	h	259		8	h	6		10		2	
"*Myripristis*" *cajun* (Frizzell & Lamber, 1961)	3	30	23		a, f, h	3		2	h			20			d
"*Diretmus*" *serratus* (Müller, 1999)	1	5	18	15			1					2			7
Carapus smithvillensis D. & F., 1965	3	12									5	4			
Brotula aquitanica Nolf, 1980					h	2									
Bauzaia lamberi Dante & Frizzell, 1965	15	304									5	g			
Bauzaia mucronata (Koken, 1888)	73	148	198	443			91	12			3	82			133
Signata nicoli Dante & Frizzell, 1965	c											g			
Signata stenzeli Dante & Frizzell, 1965		1463	289	43			2					1			
Aequalobythites aequaloides (N. & S., 2003)						8									
"aff. *Glyptophidium*" *stringeri* sp. nov.		222	543	756			26					52			
Hoplobrotula melrosensis (D. & F., 1965)	18	1138									2	7			
Symmetrosulcus dockeryi sp. nov.	166							1			25				
Symmetrosulcus meyeri (Koken, 1888)		807	5		f	3168		15	67	2	3	324	1	74	10
Symmetrosulcus stintoni (D. & F., 1965)	1	168													
"*Neobythites*" *rotundus* (Müller, 1999)															15
"*Neobythites*" *virginicus* Müller, 1999															8
Preophidion elevatus (Koken, 1888)								7			1	387	1		403
Preophidion granus (Müller, 1999)					f	76			8	11		3	1	10	5
Preophidion petropolis D. & F., 1965)	11	315	c	49	h			54				6			
Xenosirembo decipiens (Koken, 1888)											e	e	e		
"*Apogon*" *americana* (D. & F., 1965)	c	171	2												
Apogon sp.		29	2	2											
"*Gobius*" *vetustus* (Nolf & Stringer, 2003)					h	57									
"*Blennius*" *cor* (Koken, 1888)					h	14			1			3		8	3
"*Labrisomus*" *eocaenicus* (Müller, 1999)															7
"*Atherina*" *debilis* (Koken, 1888)		1			h	16			5					7	
Carangidae indet.		19	1				1			1					
Mene garviei sp. nov.				2											
Psettodes trapeziformis Müller, 1999															4
Brachypleura nana (Müller, 1999)															9
"*Citharus*" *hoffmani* (N. & S., 2003)					h	4									
"*Citharus*" *varians* sp. nov.		24	51	22								5			

Table 1 (continued).

Fish otolith taxa from the middle and late Eocene of eastern and southern USA	Texas				Louisiana		Mississippi				Alabama				Virginia
	Weches F.	"Stone City beds"	Cook Mountain F.		Moodys Branch F.	Yazoo C. (N. & S. 2003)	Kosciusko F.	Cook Mountain F.	Moodys Branch F.	Yazoo C.	Lisbon F.		Gosport Sand	Moodys Branch F.	Piney Point F.
			Wheelock Marl M.	Landrum Shale M.			Dobys Bluff Tongue	Archusa Marl M./ Potterchitto M.		Shubuta Clay M.	"Lower-Middle"	"upper"			
Soleidae indet.															2
<u>*Waitakia*</u> *beelzebub* sp. nov.												g			6
"*Trachinus*" *laevigatus* (Koken, 1888)	1	1				4			4			4		16	17
Astroscopus compactus sp. nov.								11				17	1		
Astroscopus fusiformis (Müller, 1999)															14
Parascombrops yanceyi sp. nov.		67	11	6											
Centropristis priaboniana N. & S., 2003					h	28			5						
Serranidae indet.							6					2			3
Lactarius amplus Stinton, 1978	7	597	136	80			17	4				32			40
Lactarius kokeni (Dante & Frizzell, 1965)	20	1625	245	124			38	9			c	76	g		37
Pseudopriacanthus obliquus (N. & S., 2003)					h	44									
"*Latilus*" *sulcatus* (Koken, 1888)					h	57			2			8		2	
Malacanthidae indet.	2														
Anisotremus rambo sp. nov.		11	1			1						g			
Orthopristis americana (Koken, 1888)					h	232			99					124	
Orthopristis burlesonis (D. & F., 1965)	15	46	22	24			4	9				192	3		40
"*Haemulon*" *obliquum* (Müller, 1999)	20	62	1		f	3			1			15		10	46
Triglidae indet.		1		2											
Owstonia comes (Koken, 1888)									e						
<u>*Ekokenia*</u> *eporrecta* (Koken, 1888)	10	2077	232	427			83	7			c	60			d, e
<u>*Eosciaena*</u> *ebersolei* Stringer *et al.*, 2022						1									
<u>*Jefitchia*</u> *copelandi* D. & F., 1965	c	180	50	49			2				c	2	c, g		
Sciaena pseudoradians (D. & F., 1965)			5		f, h	78			16	9				10	
"*Sciaena*" *claybornensis* (Koken, 1888)				1	f, h	649		1	207	3		14	4	50	
"*Sciaena*" *eanesi* (Müller, 1999)	4	17	2					1				7	4		32
"*Sciaena*" *intermedia* Koken, 1888		285	33	4			2					30	g		
"*Sciaena*" *livesayi* (Müller, 1999)		31	22	8				1				1			23
Sciaenidae indet.								1					1		
Pagellus pamunkeyensis sp. nov.															7
Pagrus esseri (Müller, 1999)															d
"*Sparus*" *elegantulus* (Koken, 1888)	2	52	141	30	h	131		1	e			2		2	2
Antigonia sp.						1						1			2
Antennariidae indet.															1
Malthopsis? sp.			2	1					3						
total	508	10429	2220	2462	NA	5628	283	213	512	47	48	1613	20	420	1111

Order Albuliformes Jordan, 1923
Suborder Albuloidei Jordan, 1923
Family Albulidae Bleeker, 1859
Genus *Albula* Scopoli, 1777

Albula sp.
Fig. 8A–B

Remarks

The otoliths of *Albula* are uncommon in our material: only four specimens from the "Stone City beds" were found. These otoliths share many features with those of the extant *Albula*, but unfortunately, they are not well preserved. Additionally, Nolf & Stringer (2003) reported five *Albula* otoliths from the Yazoo Clay of Louisiana and Ebersole *et al*. (2019) four otoliths from the Lisbon Formation of Alabama. A study of albulid otoliths is further provided by Frizzell (1965), but it seems that his otolith-based genera and species were just established to reveal tentative evolutionary lineages. These genera and species have been reviewed by Nolf (2013).

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: "upper" Lisbon Formation, Alabama. Priabonian: Yazoo Clay, Louisiana.

Family Pterothrissidae Gill, 1893 sensu Nolf 2013
Genus *Elopothrissus* Schwarzhans, 1981

Elopothrissus bernardlemorti sp. nov.
urn:lsid:zoobank.org:act:EC4517DA-4346-4D6D-9875-6D79D11AA044
Fig. 8C–D

Diagnosis

OL/OH = 2.21–2.47, OsL/CaL = 0.43–0.55. Otoliths very elongate, thin, higher in the middle. Oval ostium with colliculum. Elongate cauda of about ½ OL with crest like crista superior.

Etymology

This species is named after the owner, Bernard Lemort, of the bar L'Espérance near the IRSNB where many innovative discussions have taken place among researchers, with excellent drinks, continuously inspiring the authors.

Material examined

Holotype

UNITED STATES OF AMERICA • Right otolith; Texas, Alabama Ferry; "Stone City beds"; Fig. 8C; IRSNB P 9959.

Paratypes

UNITED STATES OF AMERICA • 5 otoliths, of which one is figured: Fig. 8D; Texas, Stone City Bluff, Brazos River; "Stone City beds"; IRSNB P 9960.

Type locality and horizon

United States of America, Alabama Ferry (Texas), "Stone City beds".

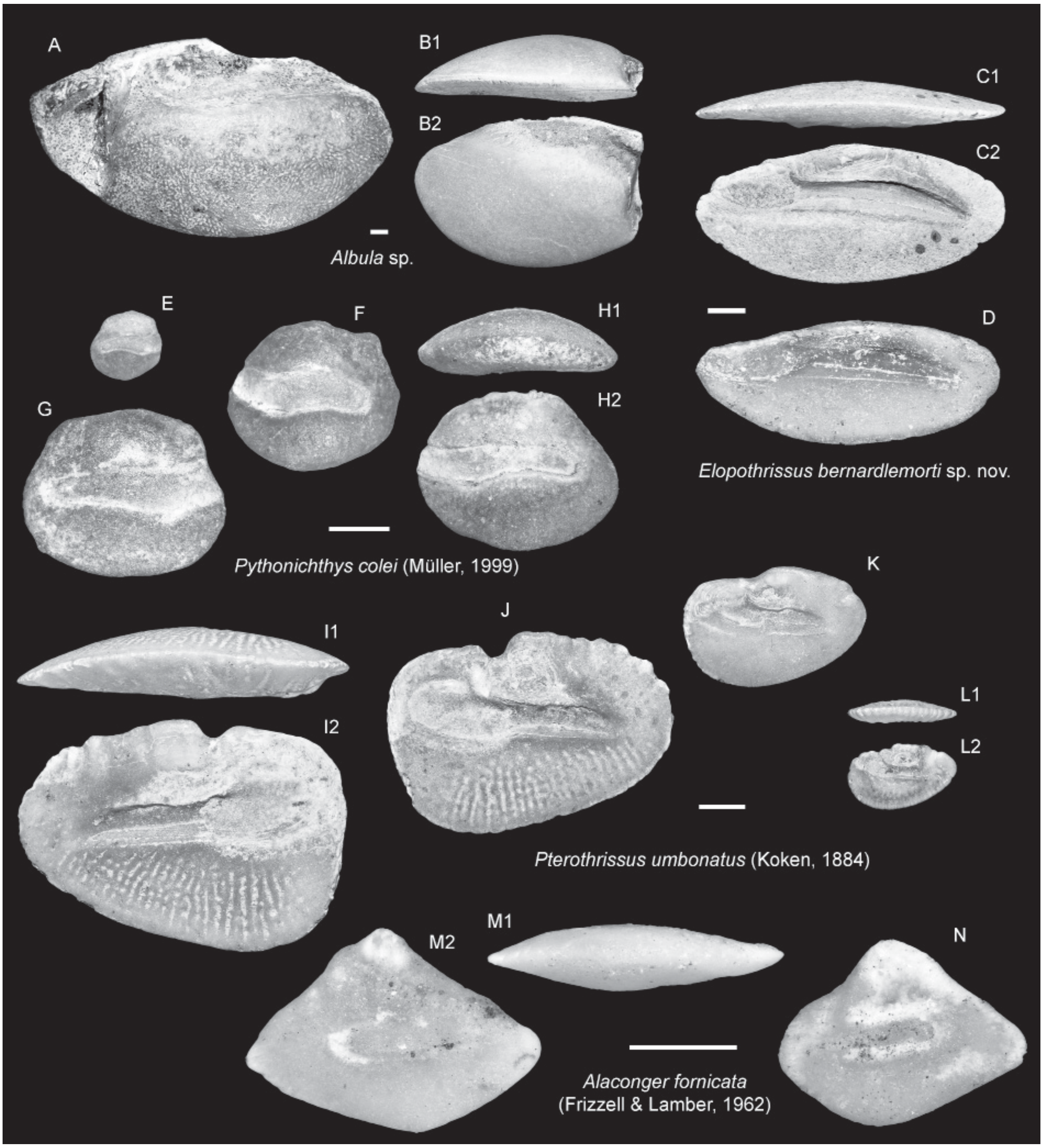


Fig. 8. Fish otoliths from the US middle and upper Eocene. **A–B**. *Albula* sp. (IRSNB P 9957–9958). **A**. Weches F., Wall Farm 2, Texas. **B**. "Stone City beds", Alabama Ferry, on Trinity River, North, Texas. **C–D**. *Elopothrissus bernardlemorti* sp. nov., "Stone City beds", Texas. **C**. Alabama Ferry, on Trinity River, North, holotype (IRSNB P 9959), **D**. Stone City Bluff, Brazos River, sample 2 from bed P, paratype (IRSNB P 9960). **E–H**. *Pythonichthys colei* (Müller, 1999). **E–F**. Landrum M., Pin Oak Creek, Texas (IRSNB P 9961–9962). **G–H**. "Stone City beds", Stone City Bluff, Brazos River, Texas (IRSNB P 9963–9964). **I–L**. *Pterothrissus umbonatus* (Koken, 1884), "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 9965–9968). **M–N**. *Alaconger fornicatus* (Frizzell & Lamber, 1962), Shubuta Clay M., Cynthia, Mississippi Lite clay pit, Mississippi (IRSNB P 10005–10006). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Dimensions of the holotype

Length = 8.20 mm; height = 3.68 mm; thickness = 1.27 mm.

Description

This species is characterized by thin, very elongate otoliths which are obtuse at both ends, but the anterior one is more pointed. The deepest part of the otoliths is in their central part, which feature is most evident in the holotype. All the margins are smooth. The inner face is very slightly convex and the outer face is nearly flat. The sulcus is well-divided into ostium and cauda and opens widely antero-dorsally on the anterior rim. A large and oval ostial colliculum fills the ostium. The ostial crista superior curves markedly upwards. The cauda is long and straight, without colliculum. The caudal crista superior is more developed than the crista inferior and markedly constricted and ventrally bent in the posterior part. The crista inferior is almost straight without constriction. The ventral area is larger than the dorsal one.

Remarks

The otoliths of this new species are clearly different from those of the more commonly co-occurring *Pterothrissus umbonatus* (Koken, 1884) (see below) by their slender appearance. Schwarzhans (1981a) indicated *Pterothrissus protensus* Stinton, 1975, a junior synonym of *Pterothrissus tardinensis* (Leriche, 1908) (see Nolf & Rundle 2018: 19), as the type species of *Elopothrissus*. The otoliths of *E. tardinensis* are thicker and much more convex on the outer face than those of *E. bernardlemorti* sp. nov.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: "upper" Lisbon Formation, Alabama.

Genus *Pterothrissus* Hilgendorf, 1877

Pterothrissus umbonatus (Koken, 1884)
Fig. 8I–L

Otolithus (*incertae sedis*) *umbonatus* Koken, 1884: 557, pl. 12 fig. 12.

Otolithus (*inc. sedis*) aff. *umbonato* – Koken 1888: 294, pl. 17 fig. 12a.
Pterothrissus umbonatus – Weiler 1958: 325, pl. 1 fig. 1. — Nolf 1985: 40 fig. 35d; 2013: 33, pl. 15.
Pterothrissus sp. – Nolf & Stringer 2003: pl. 1 fig. 1.

Remarks

The otoliths of *P. umbonatus* are characterized by a large and elliptic ostium and nearly straight cauda, typical of *Pterothrissus*. These otoliths show a marked ontogenetic change in the development of the ventral area, whose anterior part becomes much deeper in larger specimens. The species can be found in all regions studied here, but is more abundant at the Texas localities (Table 1). In particular, we note that the species also comprised a significant percentage (over 13%) of the Cane River Formation (Louisiana) otolith assemblage (Stringer & Breard 1997). The otoliths show little difference both in time and space. They have a remarkable distribution ranging in age from the middle Eocene to the middle Miocene (Schwarzhans 2010) and can be found at both European and North American localities.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Cane River Formation, Louisiana; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation, Alabama. Priabonian: Yazoo Clay, Louisiana and Mississippi. In Europe, the species is known from the Lutetian till the end of the Oligocene.

Order Anguilliformes Regan, 1909
Family incertae sedis
Genus *Muraenanguilla* Schwarzhans, 2019

Muraenanguilla aff. ***thevenini*** (Priem, 1906)
Fig. 38H

Otolithus (*Trachini*) *thevenini* Priem, 1906: 273, figs 30–31.
Gymnothorax diagonalis Stinton & Nolf, 1970: 220, pl. fig. 3.
Muraenanguilla balegemensis Schwarzhans 2019a: 26–27, fig. 13.13–16.

"genus Congridarum" aff. *diagonalis* – Müller 1999: 84, fig. 21/10.
"genus Congridarum" aff. *thevenini* – Nolf & Stringer 2003: 5, pl. 2 fig. 15.

Remarks

The fossil genus *Muraenanguilla* was recently established by Schwarzhans (2019a) for otoliths that were variously attributed to muraenids, congrids and ophichthids and is based on the type species *Otolithus* (*Trachini*) *thevenini* Priem, 1906. It is known from many European Paleocene and Eocene localities and is probably represented only by a single species in Europe. The taxon was cited often as "genus Congridarum" *diagonalis* but was originally described as a muraenid, under the name *Gymnothorax diagonalis*. It was even considered as possibly belonging to the family Ophichthidae by Nolf & Lapierre (1979: 88). Although the general look of these rather robust otoliths resembles otoliths of congrids, the deep ostium that opens widely on the anterior rim and the crista inferior ending on a little rostrum are not congrid features. Therefore, we agree with Schwarzhans' solution to consider it as an incertae sedis anguilliform. The holotype of *Muraenaguilla thevenini* was considered of doubtful quality by Nolf (1985: 132), but the numerous topotypes from Hérouval that are now available leave no doubt about the identity of the holotype (Nolf 2013). After his discussion on *Muraenanguilla*, Schwarzhans (2019a) also introduced a new species, *M. balegemensis*, based on small specimens. These are no more than the juveniles of *M. thevenini*, and both otolith types are always found together in any sample from the Sands of Lede containing sufficient otoliths (collection IRSNB). An ontogenetic series of *Muraenanguilla thevenini* is figured by Nolf (2013: pl. 27, as "*Congrida*" *thevenini*), and shows that larger otoliths gradually take a more elongate form and a less salient posterodorsal angle.

Stratigraphic and geographic distribution

In the American Eocene, the taxon is only known by a single specimen from the Lutetian Piney Point Formation, mentioned by Müller (1999), and by the single specimen from the Yazoo Clay, mentioned by Nolf & Stringer (2003) and refigured here (Fig. 38H). Some otoliths from the late Cretaceous of Mississippi may belong to the same taxon (Nolf & Stringer 1996: 441). It is also widely distributed in the Eocene of Europe, Pakistan (Nolf 1991), India and Java (Nolf & Bajpai 1992).

Suborder Muraenoidei Nelson, 1994
Family Heterenchelyidae Regan, 1912
Genus *Pythonichthys* Poey, 1868

Pythonichthys colei (Müller, 1999)
Fig. 8E–H

"genus aff. *Panturichthys*" *colei* Müller, 1999: 68, fig. 20/4–5, pl. 16 fig. 2.

"genus Heterenchelyidarum" *colei* – Nolf & Stringer 2003: 5, pl. 1 figs 3–8.
"*Heterenchelyida*" *colei* – Nolf 2013: 33, pl. 17.
Pythonichthys colei – Ebersole *et al*. 2019: 187, fig. 69c–d. — Stringer *et al*. 2022: 4, fig. 3b.

Remarks

Otoliths of the extant *Pythonichthys microphthalmus* (Regan, 1912) and *P. macrurus* (Regan, 1912) were figured by Nolf & Stringer (1992: pl. 9 figs 14 and 15, respectively). This was overlooked in the overview of Nolf (2013), and not mentioned by Ebersole *et al*. (2019), but a comparison with the above-mentioned figures of Nolf & Stringer (1992) suggests that their generic attribution is plausible. This species was represented by 90 specimens in the upper Eocene Yazoo Clay by Nolf & Stringer (2003), but it represented less than 2% of the total assemblage. Although widely distributed in the Claiborne and Jackson groups, it typically represents only a small percentage of the assemblages. The genus is also known from the Paleocene Clayton Formation in Arkansas in unusually large numbers (24% of the total assemblage) according to Schwarzhans & Stringer (2020).

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas; Moodys Branch Formation, Louisiana and Mississippi; "upper" Lisbon Formation and Moodys Branch Formation, Alabama. Priabonian: Yazoo Clay, Louisiana and Mississippi.

Suborder Congroidei Nelson, 1984
Family Ophichthidae Günther, 1870
Genus incertae sedis

"*Ophichthus*" *brevior* (Koken, 1888)
Fig. 38A

Otolithus (*Congeris*) *brevior* Koken, 1888: 293, pl. 18 fig. 7.

"*Conger*" *brevior* – Frizzell & Lamber 1962: 90, figs 4a–b, 10 a–d.
"genus *Ophichthyidarum*" *brevior* – Nolf 1985: 115; 2003: 3, pl. 1 fig. 1.
"*Ophichthida*" *brevior* – Nolf 2013: 34, pl. 19.

Remarks

This species is only known from its holotype, a small left otolith, which was tentatively attributed to an ophichthid by Nolf (1985). The otolith mentioned as "genus Congridarum" aff. *brevior* by Müller (1999: 82, fig. 21/7) shows a different pattern from ophichthid otoliths and probably belongs to a congrid.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Mississippi.

Family Muraenesocidae Bleeker, 1864
Genus incertae sedis

"*Muraenesox*" *barrytownensis* sp. nov.
urn:lsid:zoobank.org:act:8DFE6B71-9C28-4560-BD89-202468E3A97C
Fig. 9A–C

Muraenesocidae indet. – Ebersole *et al*. 2019: 189, fig. 69e–f.

Diagnosis

OL/OH = 1.54. Otoliths triangular, thick, higher in the middle. Sulcus wide, not divided into ostium and cauda, with ostial channel at antero-dorsal corner.

Etymology

This species is named after its type locality.

Material examined

Holotype

UNITED STATES OF AMERICA • Right otolith; Alabama, Barrytown; "upper" Lisbon Formation; Fig. 9C; IRSNB P 9971.

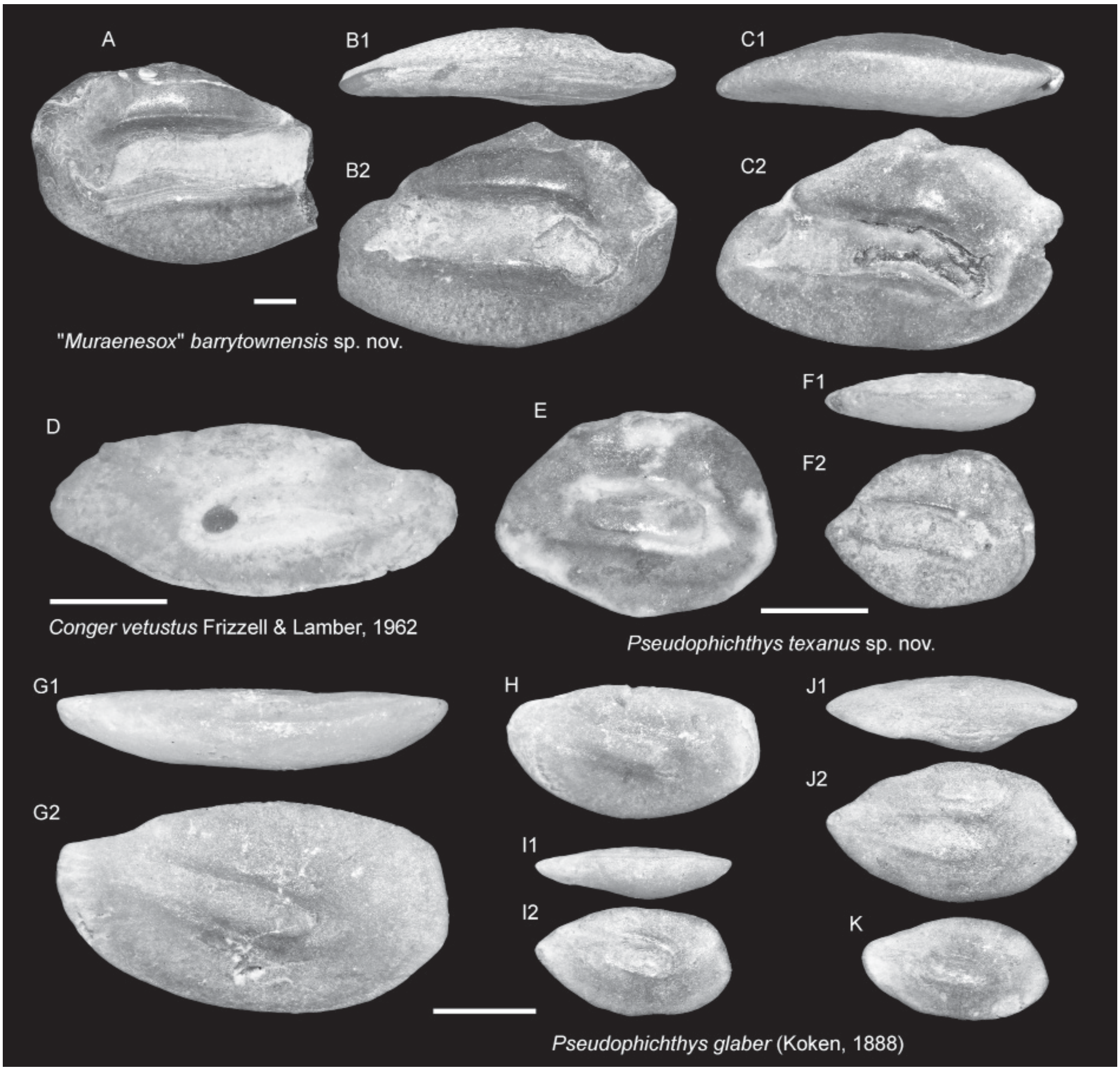


Fig. 9. Fish otoliths from the US middle and upper Eocene. **A–C**. "*Muraenesox*" *barrytownensis* sp. nov. **A–B**. "Stone City beds", Stone City Bluff, Brazos River, Texas, paratypes (IRSNB P 9969–9970). **C**. "Upper" Lisbon F., Barrytown, County Road 21, Alabama, holotype (IRSNB P 9971). **D**. *Conger vetustus* Frizzell & Lamber, 1962, "upper" Lisbon F., Coffeeville Landing, Alabama (IRSNB P 9972). **E–F**. *Pseudophichthys texanus* sp. nov., Weches F., Wall Farm 1, Texas. **E**. Paratype (IRSNB P 9973). **F**. Holotype (IRSNB P 9974). **G–K**. *Pseudophichthys glaber* (Koken, 1888). **G–H**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 9975–9976). **I–K**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 9977–9979). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Paratypes

UNITED STATES OF AMERICA • 4 otoliths of which two are figured: Fig. 9A–B; Texas, Stone City Bluff, Brazos River, “Stone City beds”; IRSNB P 9969–P 9970.

Type locality and horizon

United States of America, Barrytown (Alabama), “upper” Lisbon Formation.

Dimensions of the holotype

Length = 8.40 mm; height = 5.37 mm; thickness = 2.08 mm.

Description

The otoliths are very robust, massive and thickset; they are triangular to trapezoid in shape, with the ventral rim much longer than the dorsal one. Their anterior and posterior parts are straight, and the ventral part is smoothly curved. The highest part of the otolith is in the middle, and is prominently extruding dorsally. The margins are smooth, except for the postero-dorsal rim which is largely undulated and expands dorsally. The inner face is slightly convex, and the outer face is nearly flat, but somewhat convex posteriorly. The sulcus is wide, overall straight and not distinctively divided into ostium and cauda; it opens broadly to the anterior end of the otolith where the crista inferior is not clearly marked. Additionally, there is an ostial channel at the antero-dorsal corner, a feature most evident in the holotype. A single large colliculum fills the entire sulcus, whose posterior end is bent ventrally. The cristae are well-developed but not ridge-like. The dorsal area just above the crista superior swells and the size of the dorsal area is larger than that of the ventral one.

Remarks

These otoliths are assigned to the muraenesocids on the basis of their sulcus configuration, which is extraordinarily wide with a broad ostial part and a ventrally bent caudal end. Although the generic allocation is not certain, the overall similarity is close to genera such as *Cynoponticus* and *Muraenesox* (Nolf 2013: pl. 19; Schwarzhans 2019b: pl. 8 figs 9–13). Otoliths from the Piney Point Formation described as *Muraenesox rhomboideus* by Müller (1999) do not show the aforementioned muraenesocid features. Instead, the narrower sulcus and more pronounced ventral area of this species are typical congrid features, and these otoliths were synonymized with “*Conger*” *websteri* (Frost, 1933) by Nolf (2013) (see below).

Stratigraphic and geographic distribution

Lutetian: “Stone City beds”, Texas. Bartonian: “upper” Lisbon Formation, Alabama.

Family Congridae Kaup, 1856
Genus *Alaconger* Schwarzhans, 2010

Alaconger fornicatus (Frizzell & Lamber, 1962)
Fig. 8M–N

“*Conger*” *fornicatus* Frizzell & Lamber, 1962: 96, figs 3a–b, 9a–d.

“genus *Congridarum*” *fornicatus* – Nolf 1985: 44.
“*Congrida*” *fornicata* – Nolf 2013: 36, pl. 26.

Remarks

The otoliths of *A. fornicatus* are characterized by a salient angle in the middle of both their dorsal and ventral rims. This provides them with a very recognizable overall lozenge shape (rhombus- or diamond-shaped). This feature is not seen in otoliths of any of the extant congrid genera, but a somewhat similar looking shape is seen in the Maastrichtian *Alaconger triquetrus* Schwarzhans, 2010 from the Gerhartsreiter Beds in Bavaria, Germany (Schwarzhans 2010). This Maastrichtian species, however, has a higher dorsal expansion and does not show the very salient anterior and posterior ends seen in *A. fornicatus*.

Stratigraphic and geographic distribution

Priabonian: Yazoo Clay, Louisiana and Mississippi.

Genus *Conger* Bosc, 1817

Conger vetustus Frizzell & Lamber, 1962
Fig. 9D

Conger? *vetustus* Frizzell & Lamber, 1962: 100, figs 6a–b, 8a–d.

Conger vetustus – Nolf 1985: 42; 2013: 35, pl. 22. — Nolf & Stringer 2003: pl. 1 fig. 9.

Remarks

A single otolith of this species was collected from the “upper” Lisbon Formation (Alabama) (Table 1). Despite its poor preservation, the characteristically very elongate otolith shape and the straight but obliquely ventrally oriented sulcus allow a conclusive identification.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana and Mississippi; “upper” Lisbon Formation, Alabama. Priabonian: Yazoo Clay, Louisiana.

Genus *Gnathophis* Kaup, 1859

Gnathophis dissimilis (Frizzell & Lamber, 1962)
Fig. 38B

“*Conger*” *dissimilis* Frizzell & Lamber, 1962: 94, figs 5a–b, 12a–d.

Gnathophis dissimilis – Nolf 1985: 42; 2013: 35, pl. 22. — Nolf & Stringer 2003: pl. 1 fig. 11.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana. Priabonian: Yazoo Clay, Louisiana.

Genus *Pseudophichthys* Roule, 1915

Pseudophichthys glaber (Koken, 1888)
Fig. 9G–K

Otolithus (*Soleae*) *glaber* Koken, 1888: 293, pl. 18 fig. 3.
“genus aff. *Pseudophichthys*” *oviformis* Müller, 1999: 81, fig. 21/3–4.
?”genus aff. *Pseudophichthys*” *laevis* Müller, 1999: 82, fig. 21/5–6.

"*genus* aff. *Pseudophichthys*" *glaber* – Nolf 1985: 43.
Pseudophichthys glaber – Nolf 2003: 4, pl. 1 fig. 5; 2013: 36, pl. 24. — Nolf & Stringer 2003: 5, pl. 1 figs 13–18.
?*Pseudophichthys* sp. – Ebersole *et al*. 2019: 191, fig. 69k–l.

Remarks

Pseudophichthys glaber has elliptic otoliths with a blunt posterior end and a more or less pointed anterior tip. The sulcus is straight but inclined downwards to the posterior end; it opens anteriorly, and a single colliculum occurs more to the end of the cauda. The dorsal rim and the outer face of the otolith show some variability; most specimens have a rather flat outer face, but some individuals have a more elevated one. The otoliths described by Müller (1999) as "genus aff. *Pseudophichthys*" *laevis* lack diagnostic features but likely belong to juveniles of this species. Also, the worn otolith from the "upper" Lisbon Formation in Alabama, figured by Ebersole *et al*. (2019), might belong to this species. The species was found more frequently in the Texas localities, although in relatively low numbers.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas; "upper" Lisbon Formation, Alabama; Moodys Branch Formation, Louisiana and Alabama. Priabonian: Yazoo Clay, Louisiana and Mississippi.

Pseudophichthys texanus sp. nov.

urn:lsid:zoobank.org:act:46DD4BB0-C7AB-4250-96E6-89E32E555091
Fig. 9E–F

Pseudophichthys aff. *elongatus* (Sulc, 1932) – Müller 1999: 80, fig. 21/1–2.

Diagnosis

OL/OH = 1.38–1.42. Otoliths oval, moderately thick, higher in the middle. Sulcus wide, not divided into ostium and cauda, with an oblong colliculum in the center.

Etymology

The species name is derived from 'Texas', the state of the type locality.

Material examined

Holotype

UNITED STATES OF AMERICA • Right otolith; Texas, Wall Farm 1; Weches Formation; Fig. 9F; IRSNB P 9974.

Paratypes

UNITED STATES OF AMERICA • 53 otoliths of which one is figured; same collection data as for holotype; Fig. 9E; IRSNB P 9973.

Type locality and horizon

United States of America, Wall Farm 1 (Texas), Weches Formation.

Dimensions of the holotype

Length = 2.00 mm; height = 1.91 mm; thickness = 1.43 mm.

Description

This species is characterized by oval otoliths, with a rather considerable height. The margins are smooth. The postero-dorsal rim presents a blunt angle. The dorsal rim is flat and straight; the ventral rim is curved, with a somewhat angular central portion. The rostrum is protruding, which feature is most pronounced in the holotype. The inner face is nearly flat; the outer face is convex, and the thickness of the otolith is mainly located in the posterior part. The sulcus is wide, large, and somewhat downwards inclined in its posterior end; there is no division into ostial and caudal part. A large, oblong colliculum is located in the center of the sulcus. The cristae are well delineated in the central part of the sulcus but less developed at both ends. The dorsal area is of similar size as the ventral one.

Remarks

The otoliths of this new species are characterized firstly by their oval, rounded shape, with a height/length ratio exceeding that of most otoliths of other species of *Pseudophichthys*. Specimens from the Piney Point Formation of Virginia were attributed to *Pseudophichthys elongatus* (Sulc, 1932) by Müller (1999), but this congeneric species from the Eocene of the Aquitaine Basin, SW France, has a more elongate shape.

Stratigraphic and geographic distribution

Lutetian: Weches Formation, Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Mississippi; "upper" Lisbon Formation, Alabama.

Genus *Rhynchoconger* Jordan & Hubbs, 1925

Rhynchoconger sp. 1
Fig. 10A–D

Remarks

Four specimens from the Bartonian Landrum Member of the Cook Mountain Formation show a reasonable similarity to those of *Rhynchoconger*? *piger*, a Maastrichtian species that is known from Germany and Texas (see Schwarzhans & Stringer 2020), but our specimens are too small to be completely affirmed.

Stratigraphic and geographic distribution

Bartonian: Landrum Member, Texas.

Rhynchoconger sp. 2
Fig. 10E–F

Remarks

Otoliths of this taxon show a reasonable resemblance to the Maastrichtian (Kemp Clay) *Rhynchoconger brettwoodwardi* Schwarzhans & Stringer, 2020 (Schwarzhans & Stringer 2020), but most of our specimens of *Rhynchoconger* sp. 2 have a slightly hollow upper part of the posterior rim and lack the more prominent expansion of the antero-dorsal portion. Therefore, they probably represent a different species.

Stratigraphic and geographic distribution

Bartonian: Wheelock Member, Texas.

Genus *Heteroconger* Bleeker, 1868

Heteroconger ovatus (Müller, 1999)
Fig. 10G–H

"genus aff. *Paraconger*" *ovatus* Müller, 1999: 74, fig. 20/18.

"*Heterocongrida*" *ovata* – Nolf 2013: 37, pl. 28.

Remarks

These small otoliths show a similar outline to what is seen in those of the congrine genera *Ariosoma* and *Heteroconger*, but otoliths of *Ariosoma* do not exhibit such a strong convexity of the inner face and considerable thickness at their juvenile stage.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Genus *Ariosoma* Swainson, 1838

Ariosoma nonsector Nolf & Stringer, 2003
Fig. 11A–D

Ariosoma nonsector Nolf & Stringer, 2003: 7, pl. 2 figs 1–6.

Otolithus (*Platessae*) *sector* – Koken 1888: 292, pl. 17 figs 15–16, non fig. 14 (= lectotype of *Paraconger sector*).
Ariosoma nonsector – Nolf 2003: 3, pl. 1 figs 3–4; 2013: 35, pl. 21. — Ebersole *et al*. 2019: 189, fig. 69g–h. — Stringer *et al*. 2022: 5, fig. 3c.

Remarks

The otoliths of *A. nonsector* are deep and more compact than those of similar-looking *Paraconger* ones; they also have a much broader but shorter and less incised sulcus.

This taxon is the only species of *Ariosoma* known from the American Eocene.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; "lower" Lisbon Formation, Alabama. Bartonian: Wheelock Member, Texas; Cook Mountain Formation, Mississippi; "upper" Lisbon Formation, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana.

Genus *Paraconger* Kanazawa, 1961

Paraconger brazosensis (Dante & Frizzell, 1965)
Fig. 11G–L

Parabatmya brazosensis Dante & Frizzell *in* Frizzell & Dante, 1965: 698, pl. 86 figs 5–6, 11–13.

"genus aff. *Paraconger*" *brazosensis* – Nolf 1985: 43.
"aff. *Paraconger*" *brazosensis* – Nolf 2013: 36, pl. 23.

Remarks

Otoliths of *Paraconger brazosensis* are very similar to those of *Paraconger sector* (see below). The essential differences are that those of the former are more massive and compact without many extensions of their posterior end, less angled ventrally, and most importantly, their sulcus is wider. The constriction in the posterior part of the crista inferior is less pronounced.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi. Bartonian: Cook Mountain Formation, Texas.

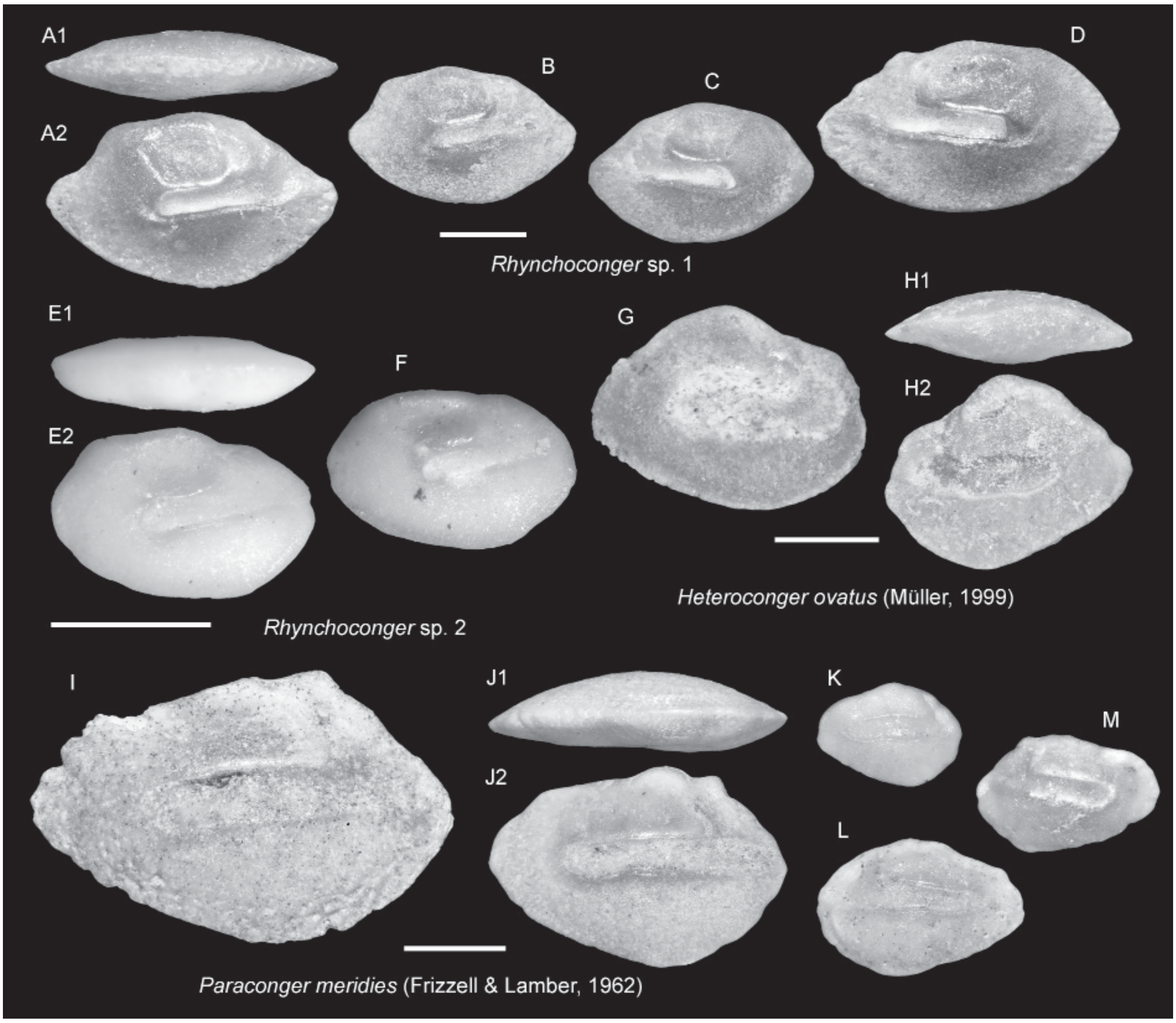


Fig. 10. Fish otoliths from the US middle and upper Eocene. **A–D**. *Rhynchoconger* sp. 1, Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 9980–9983). **E–F**. *Rhynchoconger* sp. 2, Landrum M., Crockett, Texas (IRSNB P 9984–9985). **G–H**. *Heteroconger ovatus* (Müller, 1999), Piney Point F., Pamunkey River, SW of Pampatike Landing, Virginia (IRSNB P 9986–9987). **I–M**. *Paraconger meridies* (Frizzell & Lamber, 1962), Piney Point F., Virginia. **I–L**. Pamunkey River, 1 km E of Eanes property (IRSNB P 9988–9991). **M**. Pamunkey River, SW of Pampatike Landing (IRSNB P 9992). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Paraconger meridies (Frizzell & Lamber, 1962)
Fig. 10I–M

"*Conger*" *meridies* Frizzell & Lamber, 1962: 97, figs 2a–b, 11a–d.

Paraconger meridies – Nolf 1985: 43.
Gnathophis meridies – Nolf 2013: 35, pl. 22. — Ebersole *et al*. 2019: 192, fig. 69o–p.

Remarks

Nolf (2013) and Ebersole *et al*. (2019) allocated this species to *Gnathophis*, but reconsidering for the present study fixed our attention to the affinity with *Paraconger papointi* (Priem, 1906) from the Ypresian Hérouval sands in the Paris Basin (Nolf 2013: pl. 23; compare with the specimens figured as *Gnathophis meridies* in Nolf 2013: pl. 22). *Paraconger meridies* is characterized by relatively elongate otoliths, due to the extended posterior part and a slightly ventrally oriented caudal end. For what concerns the slight depression in the dorsal area of *P. meridies*, this feature is present in the larger specimens of the series figured by Nolf (2013: pl. 22). Based on this combination of features, the species is here assigned to *Paraconger*. Besides the Ypresian type locality of *P. meridies*, Ebersole *et al*. (2019) reported four specimens from the Bartonian "upper" Lisbon Formation of Alabama. Otoliths of this species were absent from our Gulf Coastal assemblages; however, our specimens from the Piney Point Formation of Virginia extend its range to the upper Lutetian of the American side of the Atlantic.

Stratigraphic and geographic distribution

Ypresian: Bashi Marl, Mississippi. Lutetian: Piney Point Formation, Virginia. Bartonian: "upper" Lisbon Formation, Alabama.

Paraconger sector (Koken, 1888)
Fig. 12A–C

Otolithus (*Platessae*) *sector* Koken, 1888: 292, fig. 14, non figs 15–16.
Paraconger americanus Müller, 1999: 70, fig. 20/11–17.

Paraconger sector – Nolf 1985: 43; 2003: 4, pl. 1 fig. 2; 2013: 36, pl. 24. — Nolf & Stringer 2003: 5, pl. 2 figs 9–10. — Ebersole *et al*. 2019: 190, fig. 69i–j. — Stringer *et al*. 2022: 5, fig. 3d.

Remarks

The differences between the otoliths of *P. sector* and *P. brazosensis* are mentioned above. Interestingly, there appears to be a spatial separation in the occurrence of the two species (Table 1): *P. brazosensis* is known mainly from the western part of the Gulf Coast (Lutetian and Bartonian of Texas and the upper Lutetian Dobys Bluff Tongue of Mississippi), whereas *P. sector* is found in the Piney Point Formation of Virginia and throughout the Gulf Coast from Louisiana, Mississippi and Alabama (see Nolf 2003: 4).

Stratigraphic and geographic distribution

Lutetian: "lower" Lisbon Formation, Alabama; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Mississippi; Moodys Branch Formation, Louisiana and Mississippi; "upper" Lisbon Formation, Gosport Sand and Moodys Branch Formation, Alabama. Priabonian: Yazoo Clay, Louisiana.

Paraconger solidus Müller, 1999
Fig. 38C

Paraconger solidus Müller, 1999: 71, fig. 20/8–10.

Paraconger solidus – Nolf 2013: 36, pl. 24.

Remarks

Compared to other otoliths of *Paraconger*, otoliths of *Paraconger solidus* are the most compact and highest-shaped ones. The species seems to be restricted to the Piney Point Formation.

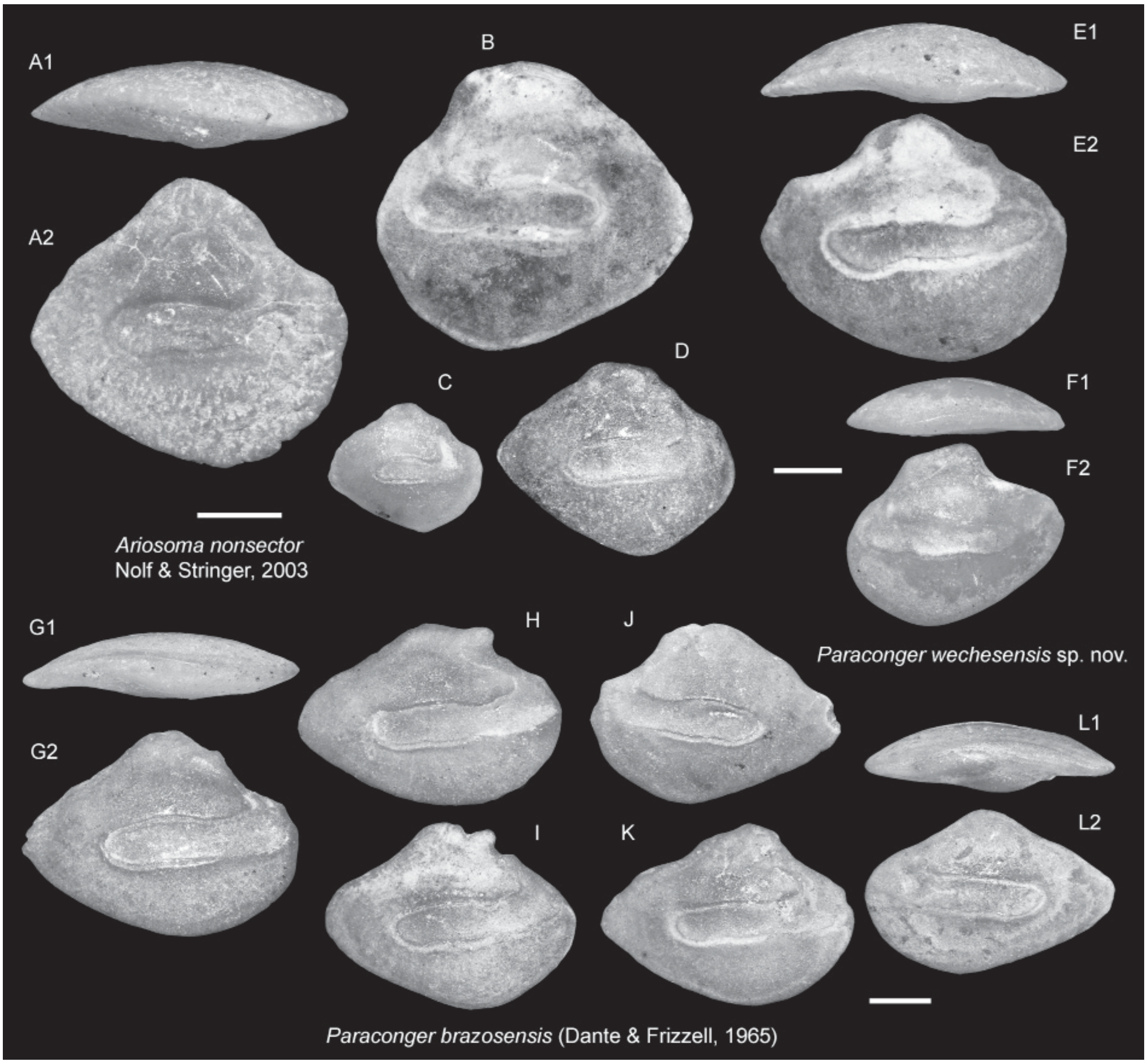


Fig. 11. Fish otoliths from the US middle and upper Eocene. **A–D**. *Ariosoma nonsector* Nolf & Stringer, 2003. **A–C**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 9993–9995). **D**. "Stone City beds", Stone City Bluff, Brazos River, sample 5 from bed S, Texas (IRSNB P 9996). **E–F**. *Paraconger wechesensis* sp. nov., Weches F., Wall Farm 1, Texas. **E**. Holotype (IRSNB P 9997). **F**. Paratype (IRSNB P 9998). **G–L**. *Paraconger brazosensis* (Dante & Frizzell, 1965), "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 9999–10004). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Paraconger yazooensis Nolf & Stringer, 2003
Fig. 38D–G

Paraconger yazooensis Nolf & Stringer, 2003: p.7, pl. 2 figs 11–14.

Paraconger yazooensis – Nolf 2013: 36, pl. 24.

Remarks

The otoliths of *P. yazooensis* appear to be more pointed and acuminate at their posterior end, compared to those of other congeneric species.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana. Priabonian: Yazoo Clay, Louisiana.

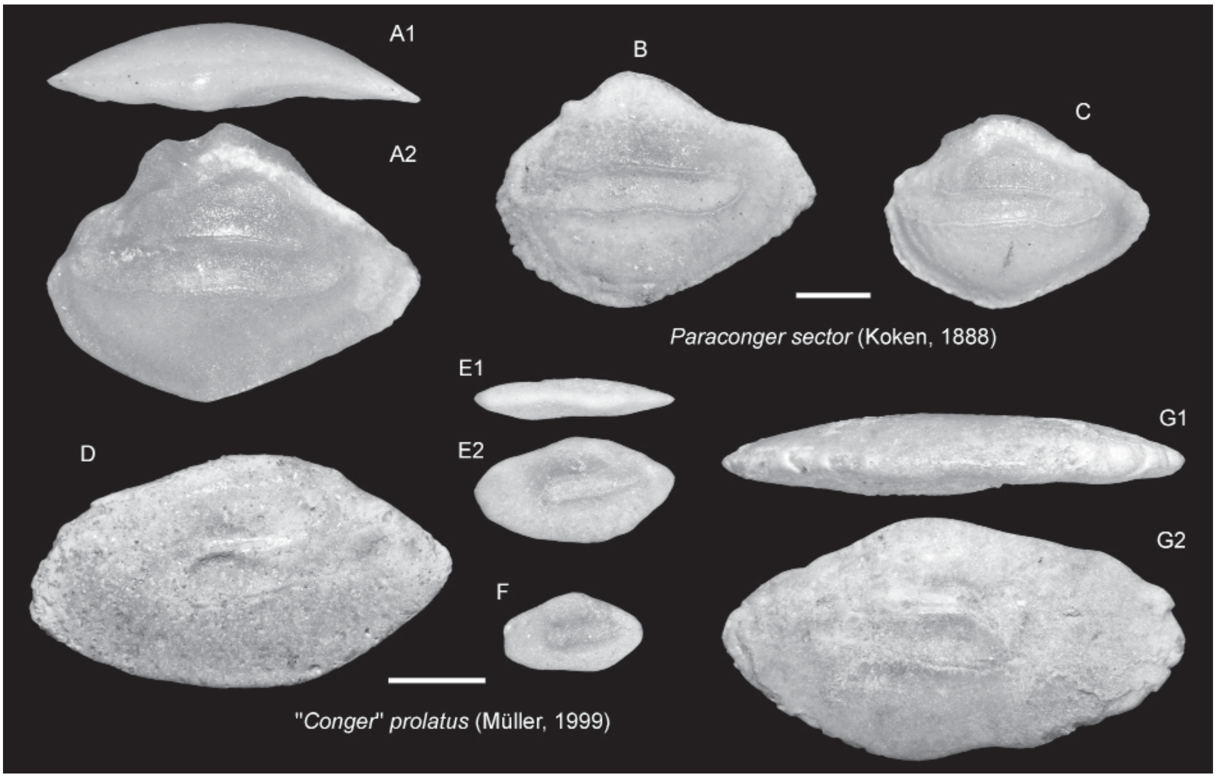


Fig. 12. Fish otoliths from the US middle and upper Eocene. **A–C**. *Paraconger sector* (Koken, 1888). **A**. Moodys Branch F., Jackson, Riverside Park, Mississippi (IRSNB P 10007). **B**. Piney Point F., Pamunkey River, loc. 25 of Müller, Virginia (IRSNB P 10008), paratype of *P. americanus* Müller, 1999. **C**. Moodys Branch F., Midway, Techeva Creek, Mississippi (IRSNB P 10009). **D–G**. "*Conger*" *prolatus* (Müller, 1999), Piney Point F., Virginia. **D**. Sand and gravel pit, Bottoms Bridge, loc. 22 of Müller, paratype (IRSNB P 10010). **E–F**. Pamunkey River, Devil's Hole (IRSNB P 10011–10012). **G**. Pamunkey River, SW of Pampatike Landing (IRSNB P 10013). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Paraconger wechesensis sp. nov.
urn:lsid:zoobank.org:act:5369716F-FDB7-4926-90F4-B28096D37553
Fig. 11E–F

Diagnosis

OL/OH = 1.17–1.25. Elliptic otoliths with protruding dorsal area in the middle. Sulcus wide, long, but not divided into ostium and cauda. Narrow ostial channel present at antero-dorsal corner.

Etymology

The species is named after the formation from which it was collected.

Material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Texas, Wall Farm 1; Weches Formation; Fig. 11E; IRSNB P 9997.

Paratypes

UNITED STATES OF AMERICA • 100 otoliths of which one is figured, Fig. 11F; same collection data as for holotype; IRSNB P 9998.

Type locality and horizon

United States of America, Wall Farm 1 (Texas), Weches Formation.

Dimensions of the holotype

Length = 4.33 mm; height = 3.24 mm; thickness = 1.22 mm.

Description

The species is characterized by massive, more or less elliptic otoliths that are high in the center, with a protruding dorsal rim. This protruding dorsal part of the otoliths is sharply raised, making its anterior rim and particularly the posterior one steep and angled. The anterior and the ventral rims are, overall, smoothly curved. The posterior rim of the otolith is extended and its shape varies; it is angled in the holotype (Fig. 11E) but tapering upwards in many of the smaller specimens (Fig. 11F). The inner face is convex and the outer face is slightly concave but swollen in the center. The sulcus is wide, nearly straight and not distinctively divided into ostium and cauda; it opens very restrictedly to the antero-dorsal rim of the otolith. A single large elevated colliculum fills the entire sulcus. A marked constriction in the posterior part of the crista inferior is followed by a broad ventrally extended posterior end of the cauda.

Remarks

The otoliths of this species are readily distinguished from those of the co-occurring related species, *Paraconger brazosensis* (Dante & Frizzell, 1965), *P. sector* (Koken, 1888), and *P. yazooensis* Nolf & Stringer, 2003, by their more compact outline and wider and rounded ventral area. They have a slightly more extended posterior part than those of *P. solidus* (Fig. 38C) from the Piney Point Formation of Virginia. *Paraconger wechesensis* sp. nov. is currently confined to the Weches Formation; however, the available specimens are not always perfectly preserved; many of them are somewhat worn and surface abraded.

Stratigraphic and geographic distribution

Lutetian: Weches Formation, Texas.

Genus incertae sedis

"*Conger*" *prolatus* (Müller, 1999)
Fig. 12D–G

"genus *Congridarum*" *prolatus* Müller, 1999: 83, fig. 21/11–14.

"*Congrida*" *prolata* – Nolf 2013: 36, pl. 27.

Remarks

The otoliths of "*C.*" *prolatus* are characterized by a relatively elongate shape, a wide sulcus, an ostium opening widely to the antero-dorsal rim, and a small dorsal depression. The combination of these characters may point to an extinct taxon within the family Congridae.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

"*Conger*" *websteri* (Frost, 1933)
Fig. 13A–C

Otolihus (*Congridarum*) *websteri* Frost, 1933: 392, pl. 12 fig. 10.
Muraenesox rhomboideus Müller, 1999: 85, fig. 21/8–9.

"genus *Congridarum*" *websteri* – Nolf 1985: 44.
"*Congrida*" *websteri* – Nolf 2013: 37, pl. 27.

Remarks

The otoliths of "*Conger*" *websteri* show some similarity to those of "*C.*" *prolatus* (see above), which might indicate a relationship. The dorsal rim of the latter species is slightly elevated in the middle, whereas it is flat in "*C.*" *websteri*. The species is also known from the Bartonian (Barton Clay) of Southern England.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Mississippi.

Order Osteoglossiformes Regan, 1909
Family Osteoglossidae Bonaparte, 1846
Genus incertae sedis

"*Osteoglossum*" aff. *rhomboidalis* (Stinton, 1977)
Fig. 13D

Polymixia? *rhomboidalis* Stinton, 1977: 86, pl. 6 fig. 12.

"*genus Osteoglossidarum*" *rhomboidalis* – Nolf 1985: 38.
"*Osteoglossida*" *rhomboidalis* – Nolf 2013: 31, pl. 8.

Remarks

The two otoliths from the "Stone City beds" (Texas), here named "*O.*" aff. *rhomboidalis*, are very similar to those of the "*O.*" *rhomboidalis* from the European Ypresian. The concerned American otoliths are somewhat higher and have a shorter rostrum.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas.

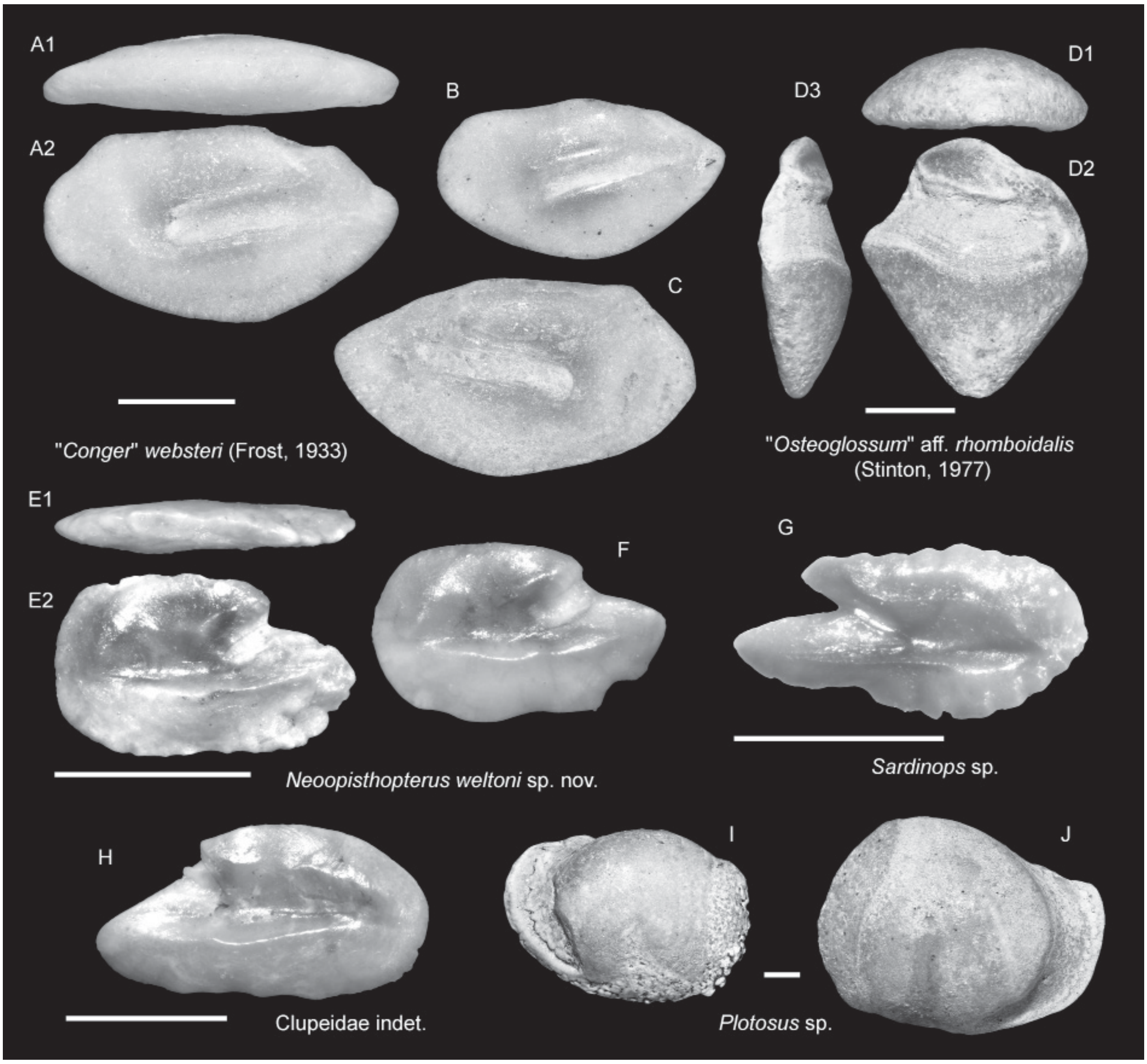


Fig. 13. Fish otoliths from the US middle and upper Eocene. **A–C**. "*Conger*" *websteri* (Frost, 1933), Piney Point F., Pamunkey River, 1 km E of Eanes property, Virginia (IRSNB P 10014–10016). **D**. "*Osteoglossum*" aff. *rhomboidalis* (Stinton, 1977), "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (P 10017). **E–F**. *Neoopisthopterus weltoni* sp. nov. **E**. Landrum M., Crockett, Texas, holotype (IRSNB P 10018). **F**. "Stone City beds", Stone City Bluff, Brazos River, bed I, Texas, paratype (IRSNB P 10019). **G**. *Sardinops* sp., Landrum M., Crockett, Texas (IRSNB P 10020). **H**. Clupeidae indet., Landrum M., Crockett, Texas (IRSNB P 10021). **I–J**. *Plotosus* sp., Wheelock M., Little Brazos River, confluence with Brazos River, Texas (P 10022–10023). 1 = ventral view; 2 = inner view; 3 = anterior view. Scale bars = 1 mm.

Order Clupeiformes Bleeker, 1859
Family Clupeidae Cuvier, 1816
Genus *Neoopisthopterus* Hildebrand, 1948

Neoopisthopterus weltoni sp. nov.
urn:lsid:zoobank.org:act:023E1875-E9C9-4E5A-A087-E1F1DF4FF1C4
Fig. 13E–F

Diagnosis

OL/OH = 1.64–1.68, OsL/CaL = 1.00–1.07. Otoliths trapezoid, thin, with large rostrum. Sulcus wide and shallow. Ostium opens widely. Cauda straight and wide.

Etymology

This species is dedicated to Bruce Welton, who provided us a lot of otoliths, and as an appreciation of his extensive work on the fossil shark teeth from the Gulf Coast area.

Material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Texas, Crockett; Landrum Member of the Cook Mountain Formation; Fig. 13E; IRSNB P 10018.

Paratypes

UNITED STATES OF AMERICA • 2 otoliths, of which one is figured: Fig. 13F; Texas, Stone City Bluff, Brazos River; “Stone City beds”; IRSNB P 10019.

Type locality and horizon

United States of America, Crockett (Texas), Landrum Member of the Cook Mountain Formation.

Dimensions of the holotype

Length = 1.13 mm; height = 0.94 mm; thickness = 0.32 mm.

Description

This species is characterized by rectangular to trapezoid otoliths. The dorsal rim is more or less straight. The posterior rim is gently curved, forming rounded junctions with the dorsal and ventral rims. The ventral rim varies, which partly resulted from its preservation status; it is slightly irregular in the holotype (Fig. 13E), but largely undulated in the figured paratype. The anterior portion is characterized by a large, robust, and extended rostrum with a small but notable excisura. The otoliths are nearly flat on both faces. The sulcus is not deep but very wide and clearly divided into ostium and cauda. No collicula are visible. The ostial crista inferior curves somewhat upwards anteriorly and the ostium opens widely antero-dorsally. The cauda is straight and wide. At its posterior end, the cristae are indistinct. The dorsal area is somewhat hollowed out.

Remarks

Neoopisthopterus weltoni sp. nov. is a rare species; only three specimens are currently known: two from the Cook Mountain Formation and one from the "Stone City beds", both in Texas. The above diagnosis allows us to assign this new species to the Recent genus *Neoopisthopterus* (see Nolf & Aguilera 1998: pl. 2 fig. 11 for an illustration of an otolith of the Recent *N. tropicus*).

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Landrum Member, Texas.

Genus *Sardinops* Hubbs, 1929

Sardinops sp.
Fig. 13G

Remarks

This single otolith from the Landrum Member of Texas can confidently be assigned to the recent genus *Sardinops*, but the single available specimen does not allow any precision at the species level.

Stratigraphic and geographic distribution

Bartonian: Landrum Member, Texas.

Clupeidae indet.
Fig. 13H

Remarks

Clupeid otoliths are rare in the collection in terms of their numeric abundance in the associations, but they were found across different regions and ages. The mentioned specimen is an example of such a small otolith, well recognizable as a clupeid, but it does not allow a more precise assignment.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi. Bartonian: Landrum Member, Texas; Cook Mountain Formation, Mississippi; "upper" Lisbon Formation, Alabama.

Order Siluriformes Cuvier, 1817
Family Plotosidae Bleeker, 1858
Genus *Plotosus* Lacepède, 1803

Plotosus sp.
Fig. 13I–J

Remarks

Utricular otoliths are very rare in the collection. The present ones resemble those of the recent *Plotosus* (see Lin & Chang 2012: pl. 74), and are tentatively allocated to this genus.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Wheelock Member, Texas.

Order Aulopiformes Rosen, 1973
Family Synodontidae Gill, 1861
Genus *Synodus* Scopoli, 1777

Synodus sp.
Fig. 14A

Remarks

This single otolith is very similar to the one reported by Nolf & Stringer (2003: pl. 3 fig. 1), but both lack sufficient diagnostic features and can only be assigned at the generic level.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Mississippi.

Family incertae sedis
Genus *Genartina* Frizzell & Dante, 1965

Genartina bambergi (Priem, 1913)
Fig. 14B–E

Otolithus (*Hoplostethus*) *Bambergi* Priem, 1913: 153, fig. 5.

"*Harpadontina*" *bambergi* – Nolf 2013: 50, pl. 58.

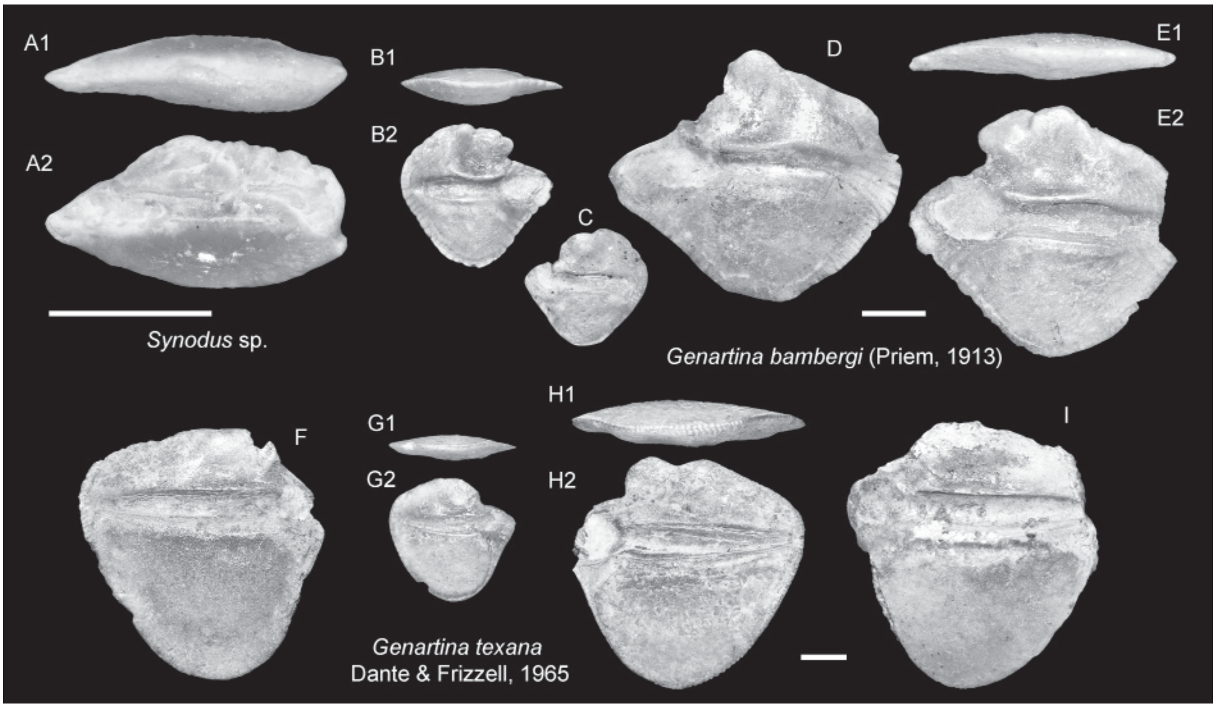


Fig. 14. Fish otoliths from the US middle and upper Eocene. **A**. *Synodus* sp., Moodys Branch F., Jackson, Town Creek, Mississippi (IRSNB P 10024). **B–E**. *Genartina bambergi* (Priem, 1913). **B–C**. Landrum M., Pin Oak Creek, Texas (IRSNB P 10025–10026). **D–E**. "Stone City beds", Stone City Bluff, Brazos River, sample 5 from bed S, Texas (IRSNB P 10027–10028). **F–I**. *Genartina texana* Dante & Frizzell, 1965, "Stone City beds", Stone City Bluff, Brazos River, sample 5 from bed S, Texas (IRSNB P 10029–10032). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Remarks

The otoliths of *Genartina* show a very peculiar pattern, different from other teleost otoliths. Schwarzhans & Stringer (2020) pointed out the indefinite allocation of *Genartina*, indicating it might well belong to an extinct group of higher systematic position. Nolf (2013) placed it within the subfamily Harpadontinae based on its sulcus configuration. We follow Nolf's interpretation but place it as an incertae sedis within the Aulopiformes. Otoliths of *G. bambergi* are high; they are also characterized by a nearly straight and horizontal sulcus, a rounded and largely protruding ostium, and a deep depression in the dorsal area, just above the crista superior. The ventral area is larger than the dorsal one. The dorsal rim may be more ornamented and elevated in large specimens. They are readily distinguished from the presumably congeneric *G. texana* (see below), the latter having a significantly larger ventral area with a rounded outline, and somewhat tapering cauda.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Cook Mountain Formation, Texas; "upper" Lisbon Formation, Alabama.

Genartina texana Dante & Frizzell, 1965
Fig. 14F–I

Genartina texana Dante & Frizzell in Frizzell & Dante, 1965: 696, pl. 86 figs 20–22.

"*Harpadontina*" *texana* – Nolf 2013: 50, pl. 58.

Remarks

Genartina texana is rather rare and found only from Texas in our collection (Weches Formation, till Cook Mountain Formation, but mainly from the "Stone City beds"). Frizzell & Dante (1965) reported its occurrence also in the Lisbon Formation of Alabama. See also above, under *G. bambergi*, for the distinction of the two species.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas. Bartonian: Wheelock Member, Texas; "upper" Lisbon Formation, Alabama.

Order Gadiformes Goodrich, 1909
Family Bregmacerotidae Gill, 1872
Genus *Bregmaceros* Thompson, 1840

Bregmaceros troelli Dante & Frizzell, 1965
Fig. 15A–D

Bregmaceros troelli Dante & Frizzell in Frizzell & Dante, 1965: 699, pl. 87 figs 14–19.

Bregmaceros troelli – Nolf 1985: 59; 2013: 56, pl. 87.
Bregmaceros sp. – Nolf & Stringer 2003: 5, pl. 3 fig. 18.

Remarks

Bregmaceros otoliths are sometimes tricky to identify at the species level (Přikryl *et al*. 2016) due to their often insufficient diagnostic features. Several features, including an enlarged part in the antero-ventral area that forms a conspicuous sharp postero-ventral angle and an evident concavity in the dorsal rim, are very consistent in the investigated specimens, and therefore we have assigned them to *B. troelli* (or a closely related species complex). The species can be very abundant in some of the levels, such as the Landrum Member. In the upper sample of the Yazoo Clay in Louisiana, nearly 92% of the total assemblage was comprised of this species (Nolf & Stringer 2003).

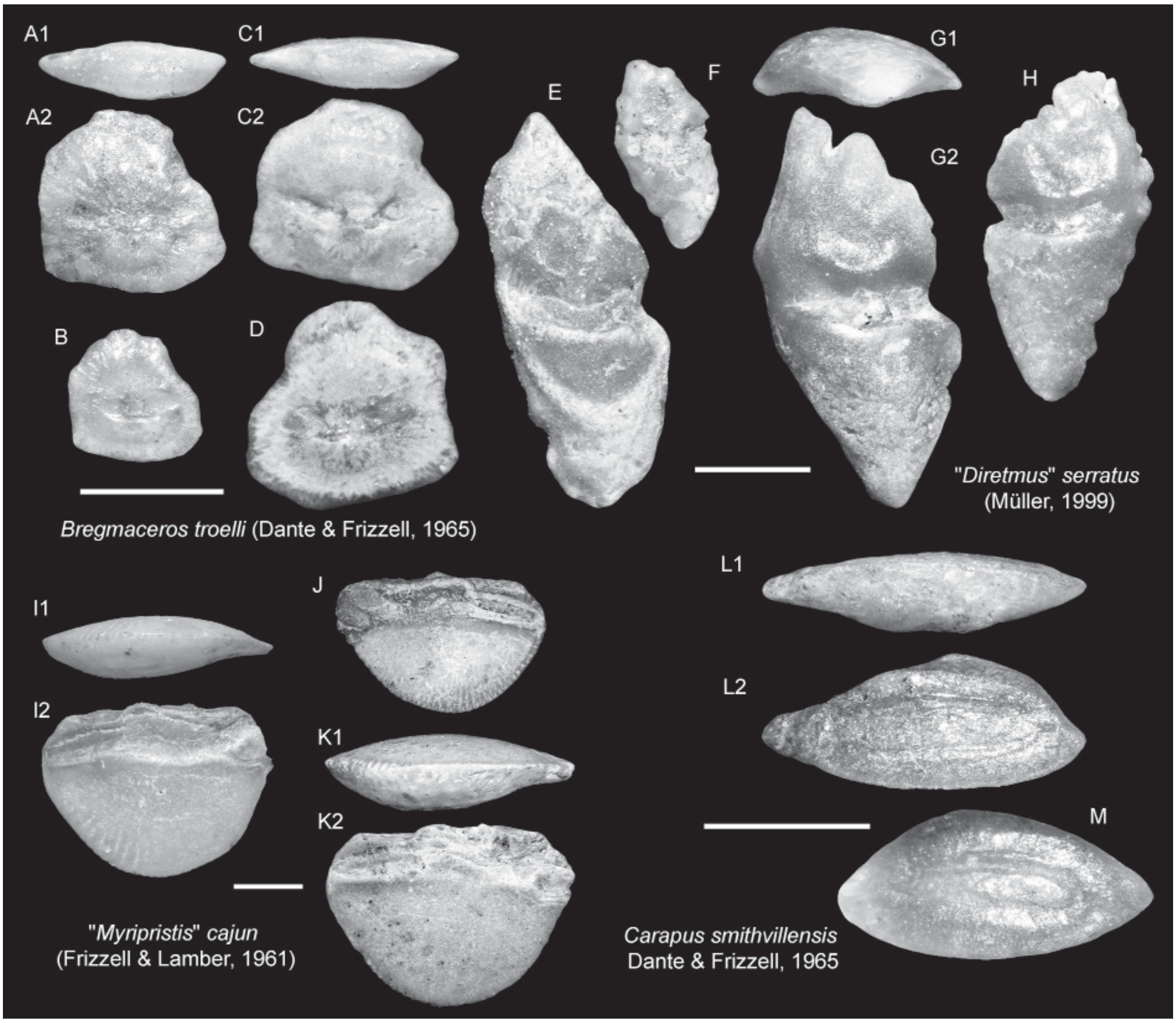


Fig. 15. Fish otoliths from the US middle and upper Eocene. **A–D**. *Bregmaceros troelli* (Dante & Frizzell, 1965). **A–B**. "Stone City beds", Alabama Ferry on Trinity River, North, Texas (IRSNB P 10033–10034). **C–D**. Landrum M., Pin Oak Creek, Texas (IRSNB P 10035–10036). **E–H**. "*Diretmus*" *serratus* (Müller, 1999). **E**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10037). **F**. "Stone City beds", Alabama Ferry, on Trinity River, North, Texas (IRSNB P 10038). **G–H**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 10039–10040). **I–K**. "*Myripristis*" *cajun* (Frizzell & Lamber, 1961). **I**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 10041). **J–K**. "Stone City beds", Stone City Bluff, Brazos River, Texas (IRSNB P 10042–10043). **L–M**. *Carapus smithvillensis* (Dante & Frizzell, 1965), "Stone City beds", Alabama Ferry, on Trinity River, North, Texas (IRSNB P 10044–10045). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Cane River Formation, Louisiana. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana and Mississippi.

Order Holocentriformes Patterson, 1993
Family Holocentridae Bonaparte, 1833
Subfamily Myripristinae Nelson, 1955
Genus incertae sedis

"Myripristis" cajun (Frizzell & Lamber, 1961)
Fig 15I–K

Weileria cajun Frizzell & Lamber, 1961: 20, figs 6, 18–19.

"*genus Myripristinarum*" *cajun* – Nolf 1985: 72. — Müller 1999: 130, fig. 29/22.
"genus Myripristidarum" *cajun* – Nolf & Stringer 2003: 5, pl. 4 figs 1–2.
"*Myripristina*" *cajun* – Nolf 2013: 80, pl. 172.
Myripristis sp. – Ebersole *et al*. 2019: 194, fig. 69q–r.

Remarks

This species was attributed to the extinct genus *Weileria* by Frizzell & Lamber (1961). This doubtful genus cannot be accepted, because its type species, *W. louisiana* from the Moodys Branch Formation of Louisiana, is a doubtful species based on an eroded holotype without true features (Nolf 2013). Otoliths of "*M*." *cajun* have the following combination of features: a small, rounded ostium with restricted anterior extension, a gently curved ventral rim, and a strongly convex outer face that forms a thickset profile in the posterior portion. These features are not seen in the recent genus *Myripristis*. The species was not uncommon but never abundant in our material. Also, many of the myripristine specimens in the collection are rather eroded and do not allow an identification at species level.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Cane River Formation, Louisiana; Piney Point Formation, Virginia. Bartonian: Wheelock Member, Texas; Moodys Branch Formation, Louisiana and Mississippi; Cook Mountain Formation, Mississippi; "upper" Lisbon Formation, Alabama. Priabonian: Yazoo Clay, Louisiana.

Order Trachichthyiformes Moore, 1993
Family Diretmidae Gill, 1893
Genus incertae sedis

"Diretmus" serratus (Müller, 1999)
Fig. 15E–H

"genus *Caproidarum*" *serratus* Müller, 1999: 130, fig. 29/18–21, pl. 16 fig. 8.

"*Diretmida*" *serrata* – Nolf 2013: 78, pl. 163.
?*Diretmus*? cf. *D. serratus* – Ebersole *et al*. 2019: 195, fig. 70a–b.

Remarks

"*Diretmus*" *serratus* has very short and high otoliths; the dorsal and ventral areas are tapering vertically and extremely extended with pointed tips. On the dorsal rim, the pointed tip is located in the posterior portion; the ventral one is more central. A weakly developed colliculum can be detected, especially in the anterior part of the cauda. The posterior end of the crista superior is slightly bent upward. This combination of features allows us to allocate the species to diretmids, but these features are not found in the recent genus, and thus the fossil species cannot be placed in the extant genus.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas; "upper" Lisbon Formation, Alabama.

Order Ophidiiformes Berg, 1937
Suborder Ophidioidei Berg, 1937
Family Carapidae Poey, 1867
Genus *Carapus* Rafinesque, 1810

Carapus smithvillensis Dante & Frizzell, 1965
Fig. 15L–M

"*Carapus*" *smithvillensis* Dante & Frizzell in Frizzell & Dante, 1965: 715, pl. 86 figs 32–33, 35, pl 87 figs 7–8.

Carapus smithvillensis – Schwarzhans 1981b: 113. — Nolf 1985: 64; 2013: 65, pl. 123.

Remarks

The otoliths are characterized by an enclosed and elongated sulcus, which is almost completely filled by a single, large colliculum. The features are almost identical to those of Recent otoliths of *Carapus*. The degree of extension in the posterior part and the thickness of the otoliths seem to vary intra-specifically, which can also be observed in other recent carapid species such as *Echiodon dentatus* (Nolf 2013: pl. 122).

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; "lower" Lisbon Formation, Alabama. Bartonian: "upper" Lisbon Formation, Alabama.

Family Ophidiidae Rafinesque, 1810
Subfamily Brotulinae Swainson, 1838
Genus *Brotula* Cuvier, 1829

Brotula aquitanica Nolf, 1980
Fig. 38K

Brotula aquitanica Nolf, 1980: 104, pl. 15 fig. 14.

Brotula aquitanica – Nolf 1985: 64; 1988: 59, pl. 6 figs 6–7; 2013: 65, pl. 124. — Nolf & Stringer 2003: 5, pl. 7 fig. 12.

Remarks

As already mentioned by Nolf & Stringer (2003), two specimens from the Priabonian Yazoo Clay of Louisiana look almost identical to those of *Brotula aquitanica* from the Ypresian Gan Clay in Aquitaine, SW France (see Nolf 2013: pl. 124 for an iconography of the specimens from Aquitaine).

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana. Priabonian: Yazoo Clay, Louisiana.

Subfamily Ophidiinae Rafinesque, 1810
Tribe Lepophidiini Robins, 1961
Genus *Bauzaia* Dante & Frizzell, 1965

Bauzaia lamberi Dante & Frizzell, 1965
Fig. 16F–H

Bauzaia lamberi Dante & Frizzell in Frizzell & Dante, 1965: 711, pl. 86 figs 27–28, 30–31, 41.

"genus *Lepophidiinorum*" *lamberi* – Nolf 1980: 103, pl. 20 fig. 1; 1985: 64.
Bauzaia lamberi – Schwarzhans 1981b: 112.
"*Lepophidiinus*" *lamberi* – Nolf 2013: 65, pl. 125.

Remarks

The extinct genus *Bauzaia* is characterized by rather thickset otoliths with a very strong but rounded antero-dorsal bulging expansion of their dorsal rim, and a salient, spine-like posterior end. The sulcus is almost straight, rather broad, and is constituted by a long ostium and a very short cauda. The inner face is strongly convex. There are two congeneric species: the type species, *Bauzaia mucronata* (Koken, 1891), and *B. lamberi*. Both can be readily distinguished by their length-height ratio. Otoliths of *B. lamberi* are short and high, whereas those of *B. mucronata* are markedly longer, which gives them a more massive look.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Cane River Formation, Louisiana; "lower" Lisbon Formation, Alabama. Bartonian: "upper" Lisbon Formation, Alabama.

Bauzaia mucronata (Koken, 1888)
Fig. 16I–N

Otolithus (*Gadidarum*) *mucronatus* Koken, 1888: 290, pl. 17 figs 10–11.

Bauzaia mucronata – Frizzell & Dante 1965: 712, pl. 86 figs 43–44.
"genus *Lepophidiinorum*" *mucronatus* – Nolf 1985: 64; 2003: 4, pl. 1 figs 11–13. — Müller 1999: 111, fig. 26/14–20.
"*Lepophidiinus*" *mucronatus* – Nolf 2013: 65, pl. 125.
Lepophidium? *mucronata* – Ebersole *et al*. 2019: 201, fig. 70m–n.

Remarks

See comments under the preceding species, *B. lamberi*.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Cane River Formation, Louisiana; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; "lower" Lisbon Formation, Alabama; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation, Alabama.

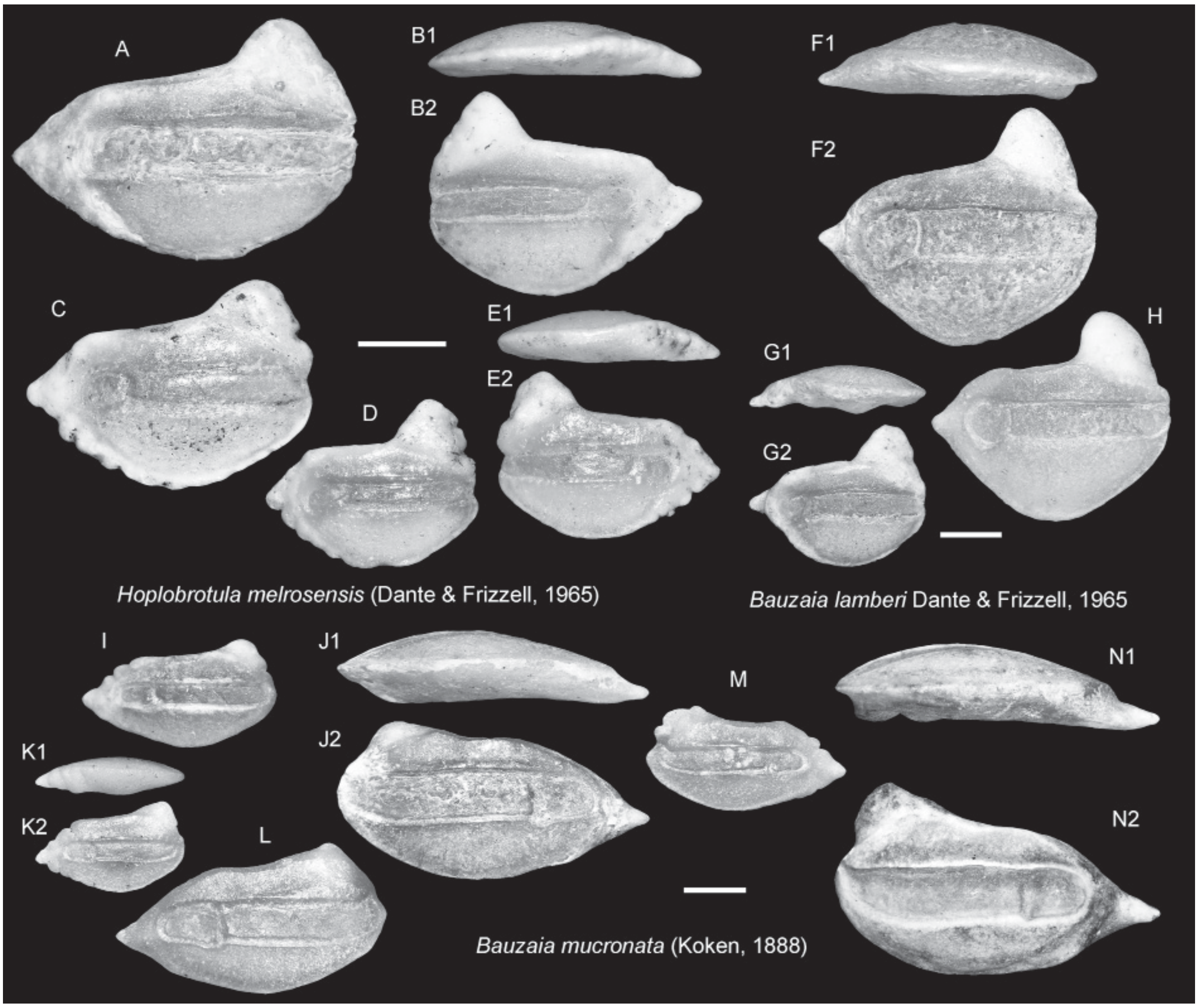


Fig. 16. Fish otoliths from the US middle and upper Eocene. **A–E**. *Hoplobrotula melrosensis* (Dante & Frizzell, 1965), "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10046–10050). **F–H**. *Bauzaia lamberi* Dante & Frizzell, 1965, "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10051–10053). **I–N**. *Bauzaia mucronata* (Koken, 1888). **I–J**. "Stone City beds", Stone City Bluff, Brazos River, sample 6 from bed U, Texas (IRSNB P 10054–10055). **K–N**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 10056–10059). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Subfamily incertae sedis
Genus *Signata* Dante & Frizzell, 1965

Signata nicoli Dante & Frizzell, 1965
Fig. 38I

Signata nicoli Dante & Frizzell in Frizzell & Dante, 1965: 709, pl. 88 figs 3–4, 21, 25.

Signata nicoli – Schwarzhans 1981b: 113. — Ebersole *et al*. 2019: 200, fig. 70i–j.
"genus *Ophidiidarum*" *nicoli* – Nolf 1985: 67.
"*Ophidiida*" *nicoli* – Nolf 2013: 65, pl. 124.

Remarks

Signata represents yet another extinct taxon within Ophidiidae. The otoliths have a very wide sulcus that is filled only with a very flat, undivided colliculum. This sulcus has a somewhat *Sirembo*-like aspect, but the stronger convexity of the inner face and the more extended and thinner posterior part are never seen in *Sirembo* or any other related otolith type. Also, in otoliths of *Signata*, the areas above and below the sulcus are very restricted. Otoliths of *Signata* are very well characterized by autapomorphic features, but do not provide any indication for affinities with other ophidiid groups. Two species are included in the genus: *S. nicoli* and *S. stenzeli*. The holotype of *S. nicoli* has smoothly curved cristae, with just an angle on the crista superior, while the otoliths of *S. stenzeli* have a more elevated angle on the crista superior and two notable undulations in their crista inferior. The holotype of *S. nicoli* is from the Weches Formation (Lutetian) of Texas, but we did not find additional specimens among our present collection. Ebersole *et al*. (2019), however, reported a specimen from the "upper" Lisbon Formation (Bartonian) of Alabama.

Stratigraphic and geographic distribution

Lutetian: Weches Formation, Texas. Bartonian: "upper" Lisbon Formation, Alabama.

Signata stenzeli Dante & Frizzell, 1965
Fig. 17A–F

Signata stenzeli Dante & Frizzell in Frizzell & Dante, 1965: 709, pl. 88 figs 12, 16–17.

Signata stenzeli – Schwarzhans 1981b: 113. — Ebersole *et al*. 2019: 199, fig. 70g–h.
"genus *Ophidiidarum*" *stenzeli* – Nolf 1985: 67.
"*Ophidiida*" *stenzeli* – Nolf 2013: 65, pl. 124.

Remarks

See under *S. nicoli* for the distinction of both species of *Signata*.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi. Bartonian: Cook Mountain Formation, Texas; "upper" Lisbon Formation, Alabama.

Subfamily Neobythitinae Radcliffe, 1913
Genus *Aequalobythites* Schwarzhans, 1981

Aequalobythites aequaloides (Nolf & Stringer, 2003)
Fig. 38L–O

"genus Neobythitinarum" *aequaloides* Nolf & Stringer, 2003: 7, pl. 3 figs 11–14.

"*Neobythitina*" *aequaloides* – Nolf 2013: 68, pl. 134.

Remarks

Otoliths of this species are only known by specimens from the Yazoo Clay (Priabonian) of Louisiana. They are closely related to those of the species originally described as *Lepophidium aequalis* Stinton & Nolf, 1970 from the Belgian Lede Formation (Lutetian), that Schwarzhans (1981b) placed in the extinct genus *Aequalobythites*. Other related species are *A. regularis* (Priem, 1911) from the Lutetian and Bartonian of the Paris Basin, Belgium and southern England, and *A. hilgendorfi* (Koken, 1891) from the German lower Oligocene.

Stratigraphic and geographic distribution

Priabonian: Yazoo Clay, Louisiana.

Genus *Glyptophidium* Alcock, 1889

"aff. *Glyptophidium*" *stringeri* sp. nov.
urn:lsid:zoobank.org:act:B65B9A77-A733-41EB-9AEA-61F744665C4B
Fig. 17G–N

Diagnosis

OL/OH = 1.11–1.32. Otoliths with a large protruding antero-dorsal expansion and a pointed posterior rim. Sulcus wide, oblong, and not divided into ostium and cauda; it is filled with a large colliculum.

Etymology

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

Material examined

Holotype

UNITED STATED OF AMERIA • Right otolith; Texas, Alabama Ferry; "Stone City beds"; Fig. 17G; IRSNB P 10066.

Paratypes

UNITED STATES OF AMERICA • 221 otoliths, of which five are figured: Fig. 17H–L; same collection data as for holotype; IRSNB P 10067–10071 • 543 otoliths, of which two are figured: Fig. 17M–N; Texas, Little Brazos River, Stenzel loc.; Wheelock Member; IRSNB P 10072–10073 • 756 otoliths; same locality as for preceding; Landrum Shale Member.

Type locality and horizon

United States of America, Alabama Ferry (Texas), "Stone City beds".

Dimensions of the holotype

Length = 2.75 mm; height = 2.23 mm; thickness = 0.59 mm.

Description

The otoliths of this species are especially characterized by a large protruding antero-dorsal expansion, which is triangular and pointing upward, and by their acuminated posterior end. The anterior rim of the dorsal expansion can be smooth or undulated. The anterior rim of the otolith is almost vertical, forming a blunt rostrum. The posterior part of the otolith shows a triangular shape; it tapers strongly after a well-marked postero-dorsal angle. The ventral rim is smoothly curved and its deepest part is located in the middle of the otolith. This rim may be crenulate in smaller specimens (Fig. 17L). The inner face is slightly convex; the outer face is nearly flat, but may be slightly convex anteriorly (Fig. 17G). A long

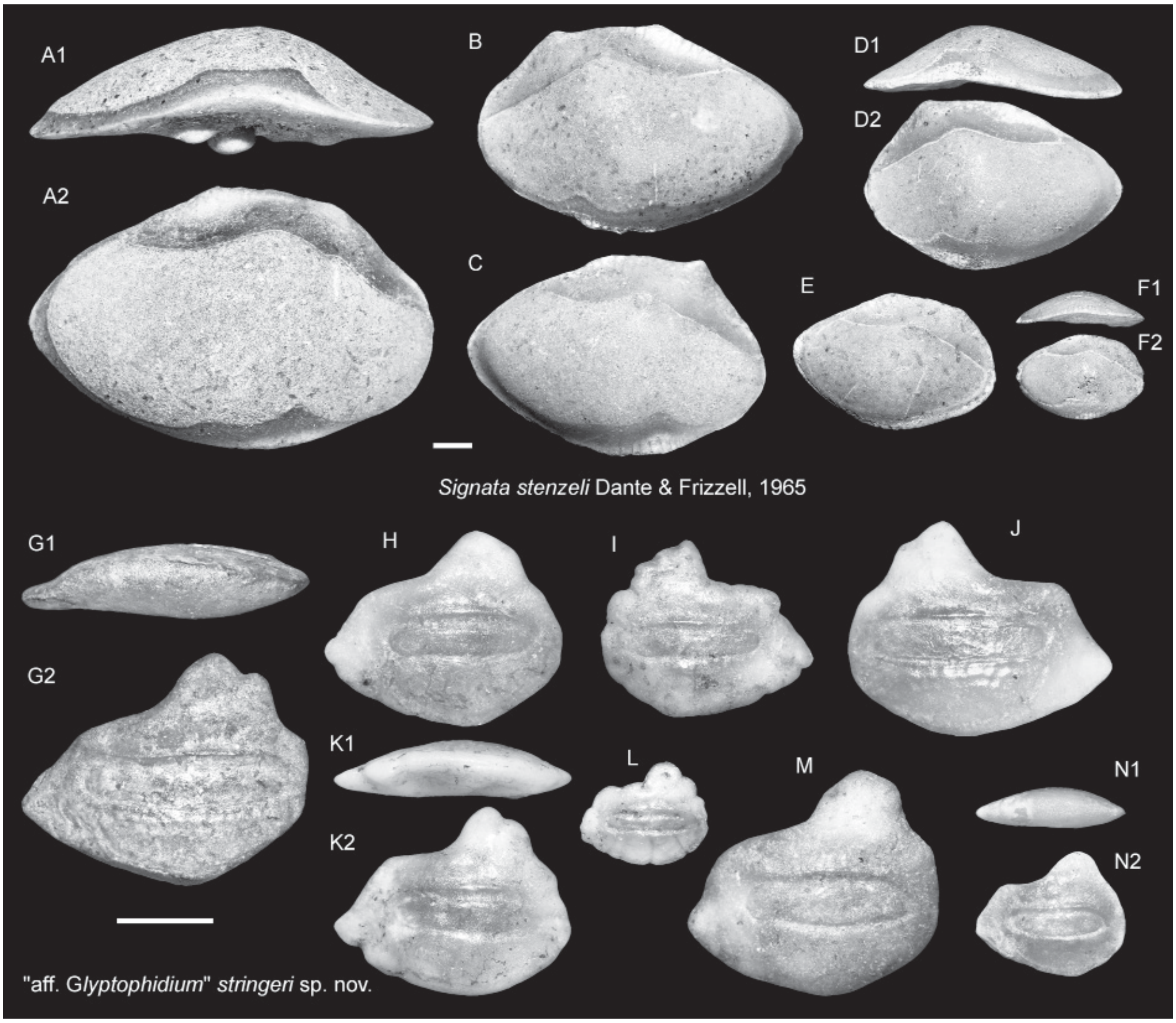


Fig. 17. Fish otoliths from the US middle and upper Eocene. **A–F**. *Signata stenzeli* Dante & Frizzell, 1965, "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10060–10065). **G–N**. "aff. *Glyptophidium*" *stringeri* sp. nov. **G–L**. "Stone City beds", Alabama Ferry, on Trinity River, North, Texas (IRSNB P 10066–10071). **M–N**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 10072–10073). **G**. Holotype (IRSNB P 10066). **H–N**. Paratypes (IRSNB P 10067–10073). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

and wide sulcus occupies nearly the entire length of the inner face. It is located in the middle of that face, and is completely filled by a single colliculum. This sulcus is not clearly divided into ostial and caudal parts. The cristae are well-developed but not ridge-like. The dorsal and the ventral areas are almost equal in size.

Remarks

The otoliths of this new species are somewhat similar looking to those of the co-occurring *Hoplobrotula melrosensis* (Dante & Frizzell, 1965) and also to those of *Bauzaia mucronata* (Koken, 1888), but this similarity is only superficial and restricted to the outline of the otoliths. Firstly, the sulcus of both *H. melrosensis* and *B. mucronata* are clearly divided into an ostium and cauda, and secondly, their posterior end is much more extended and spine-like. The sulcus of "aff. *G.*" *stringeri* sp. nov. is straight, and the posterior tip is located in their lower part. Although the posterior part of the otoliths resembles that of the extant genus *Glyptophidium*, this genus has a sulcus type with distinct ostium and cauda. The lack of a clear division between ostium and cauda in the sulcus of "aff. *G.*" *stringeri* sp. nov. suggests affinities to *Glyptophidium*, but does not imply a certain attribution to that genus. Two related Eocene species with similar features are "aff. *G.*" *biarritzense* (Sulc, 1932) from the Aquitaine Basin and "aff. *G.*" *pseudobiarritzense* Nolf & Bajpai, 1992 from Java (Nolf & Bajpai 1992: pl. 3 fig. 11).

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi. Bartonian: Landrum Member of Cook Mountain Formation, Texas; "upper" Lisbon Formation, Alabama.

Genus *Hoplobrotula* Gill, 1863

Hoplobrotula melrosensis (Dante & Frizzell, 1965)
Fig. 16A–E

Bauzaia melrosensis Dante & Frizzell in Frizzell & Dante, 1965: 711, pl. 86 figs 7, 9.

Hoplobrotula melrosensis – Schwarzhans 1981b: 113. — Nolf 1985: 66; 2013: 67, pl. 132. — Ebersole *et al*. 2019: 200, fig. 70k–l.

Remarks

Hoplobrotula melrosensis has a sulcus with a somewhat downward oriented cauda, a feature typical of the extant *Hoplobrotula*.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; "lower" Lisbon Formation, Alabama. Bartonian: "upper" Lisbon Formation, Alabama.

Genus ***Symmetrosulcus*** Schwarzhans, 1981

Remarks

The *Neobythites*-like otolith group includes three American species that are more closely related to each other than to anything else, and correspond to the extinct genus *Symmetrosulcus* Schwarzhans, 1981 (type species: *Ot.* (*Ophidiidarum*) *dimidiatus* Schubert, 1916). They are: *S. dockeryi* sp. nov., *S. stintoni* (Dante & Frizzell, 1965), and *S. meyeri* (Koken, 1888). The European *S. dimidiatus* (Schubert, 1916) from the Bartonian of southern England and *S. fitchi* Nolf, 1980 from the Ypresian Gan Clay of Aquitaine, SW France are also closely related to this group.

Symmetrosulcus dockeryi sp. nov.
urn:lsid:zoobank.org:act:124FFDA6-FA7C-442E-AC9E-88BE08F77445
Fig. 18G–K

Diagnosis

OL/OH = 1.47–1.57, OsL/CaL = 1.43–1.73. Elliptic otoliths with angled posterior rim. Ventral rim deepest in the middle. Sulcus wide, oblong, but narrow. Ostium longer than cauda, each filled with a colliculum.

Etymology

The species is named in honor of David T. Dockery III (Mississippi Bureau of Geology) who provided major support during our field work.

Material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Texas, Wall Farm 1; Weches Formation; Fig. 18G; IRSNB P 10090.

Paratypes

UNITED STATES OF AMERICA • 191 otoliths of which four are figured: Fig. 18H–K; same collection data as for holotpye; IRSNB P 10091–10094.

Type locality and horizon

United States of America, Wall Farm 1 (Texas), Weches Formation.

Dimensions of the holotype

Length = 3.16 mm; height = 2.11 mm; thickness = 0.93 mm.

Description

This species is characterized by elliptical otoliths with blunt, but well-marked antero- and postero-dorsal angles. The rim between those two angles is almost horizontal, but may be very slightly undulated in the smaller individuals (Fig. 18I). The posterior portion of the otoliths forms a tapering triangle. The ventral rim is smoothly curved with its deepest part in the middle of the otolith, providing it a regular rounded appearance. The anterior part of the otolith is slightly oblique and largely blunt at its lower, most prominent part. All the margins are smooth. The otoliths are moderately thick, with both the inner and outer faces convex. The thickness may be slightly more considerable near the posterior end, which is the case in the holotype (Fig. 18G). A straight sulcus occupies nearly the entire length of the inner face and is located in the central zone, but does not open to the margins of the otolith. There is a clear division into ostial and caudal parts, each fully filled by a colliculum. The cauda is about twice as long as the ostium. The cristae are clearly marked, but not ridge-like. They are almost horizontal, but the crista inferior may be slightly constricted at the collum, which is well visible in the holotype (Fig. 18G).

Comparison

The otoliths of this species can be distinguished from the co-occurring related species, *S. meyeri* (Koken, 1888), *S. stintoni* (Dante & Frizzell, 1965), "*N.*" *rotundus* (Müller, 1999), and "*N.*" *virginicus* Müller, 1999, by the combination of the following features: a more rectangular outline, a nearly flat dorsal rim, a more vertical anterior rim, a less extended posterior rim, and a dorsal area of similar width as the ventral one. See below for a detailed discussion on other ophidiid otoliths.

Stratigraphic and geographic distribution

Lutetian: Weches Formation, Texas; "lower" Lisbon Formation, Alabama. Bartonian: Cook Mountain Formation, Mississippi.

Symmetrosulcus meyeri (Koken, 1888)
Fig. 18A–F

Otolithus (*Gadidarum*) *Meyeri* Koken, 1888: 289, pl. 18 figs 8–9.
"genus *Sirembinorum*" *pamunkeyanus* Müller, 1999: 124, fig. 28/24–27.

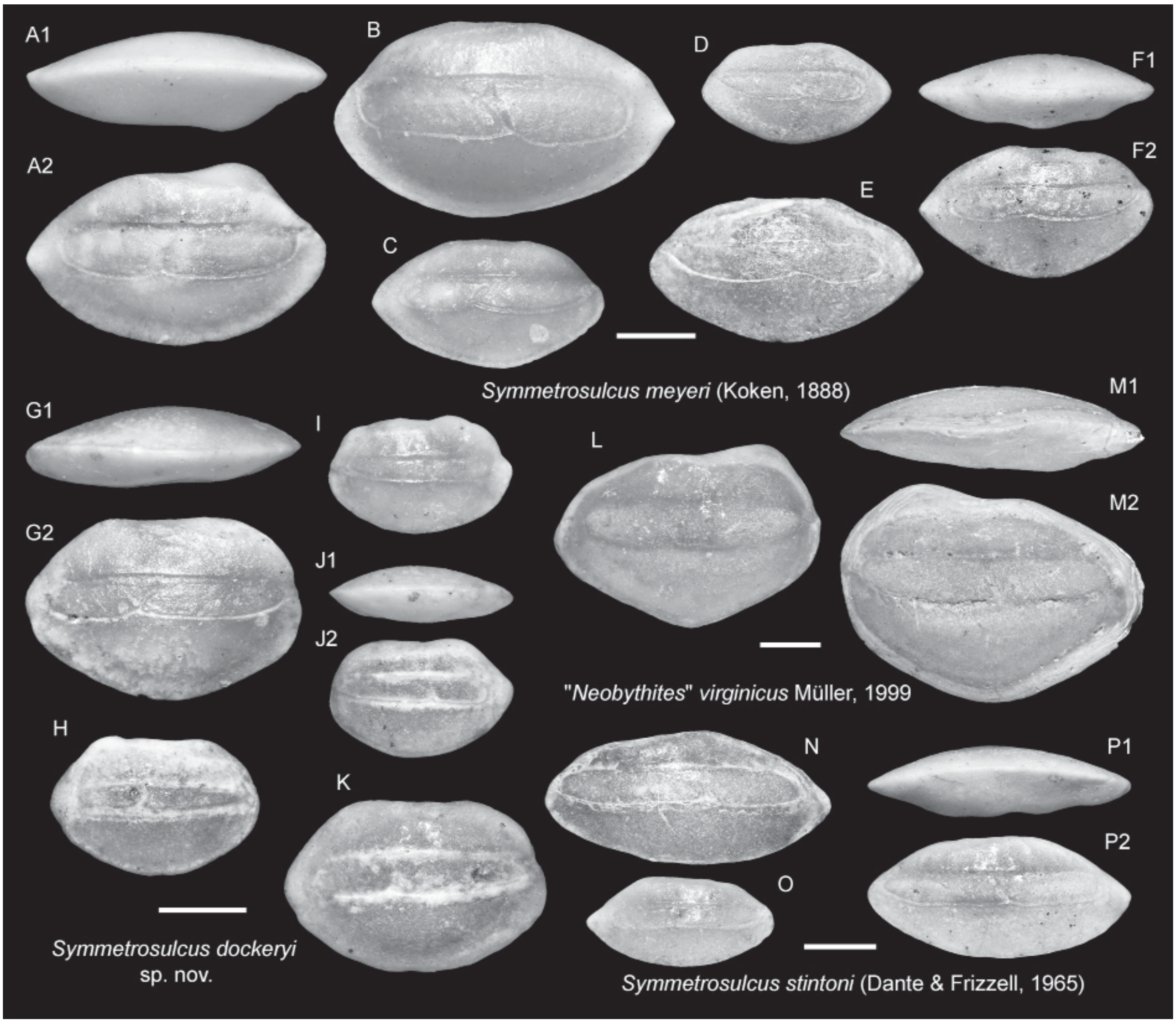


Fig. 18. Fish otoliths from the US middle and upper Eocene. **A–F**. *Symmetrosulcus meyeri* (Koken, 1888). **A–C**. Yazoo Clay, Copenhagen, Louisiana (IRSNB P10084–10086). **D–F**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10087–10089). **G–K**. *Symmetrosulcus dockeryi* sp. nov., Weches F., Wall Farm 1, Texas. **G**. Holotype (IRSNB P 10090). **H–K**. Paratypes (IRSNB P 10091–10094). **L–M**. "*Neobythites*" *virginicus* Müller, 1999, Piney Point F., Pamunkey River, 1 km E of Eanes property, Virginia (IRSNB P 10095–10096). **N–P**. *Symmetrosulcus stintoni* (Dante & Frizzell, 1965), "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10097–10099). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

"genus *Neobythitinarum*" *meyeri* – Nolf 1980: 111, pl. 18 fig. 16; 1985: 67; 2003: 5, pl. 1 fig. 9. — Nolf & Stringer 2003: 5, pl. 3 figs 3–10.
Symmetrosulcus meyeri – Schwarzhans 1981b: 75, 113.
"*Neobythitina*" *meyeri* – Nolf 2013: 68, pl. 136.
Preophidium meyeri – Ebersole *et al*. 2019: 197, fig. 70c–d. — Stringer *et al*. 2022: 6, fig. 3f.

Remarks

See remarks under the genus *Symmetrosulcus*.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas; Cane River Formation, Louisiana; "lower" Lisbon Formation, Alabama; Piney Point Formation, Virginia. Bartonian: Wheelock Member, Texas; Cook Mountain Formation, Mississippi; "upper" Lisbon Formation and Gosport Sand, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana and Mississippi.

Symmetrosulcus stintoni (Dante & Frizzell, 1965)
Fig. 18N–P

Preophidion stintoni Dante & Frizzell in Frizzell & Dante, 1965: 714, pl. 86 figs 36–37, 42.

"genus *Neobythitinarum*" *stintoni* – Nolf 1980: 137, pl. 20 fig. 9; 1985: 67.
Symmetrosulcus stintoni – Schwarzhans 1981b: 75, 113.
"*Neobythitina*" *stintoni* – Nolf 2013: 68, pl. 137.

Remarks

See remarks under the genus *Symmetrosulcus*.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas.

Genus **incertae sedis**

Remarks

"*Neobythites*" *rotundus* (Müller, 1999) and "*N.*" *virginicus* Müller, 1999, two species that are known from the Atlantic Coastal Plain only (Piney Point Formation), are incertae sedis Neobythitinae that are not clairly related to other living or fossil genera of Neobythitinae. Otoliths of "*Neobythites*" *virginicus* have a deep ventral area and a small but well-marked antero-dorsal angle. Those of "*N.*" *rotundus* are easily recognizable by their height which is more considerable than their length, their important thickness, which is essentially located in their posterior portion, and by a salient antero-dorsal angle.

"*Neobythites*" *rotundus* (Müller, 1999)
Fig. 20A–C

"genus Neobythitinarum" *rotundus* Müller, 1999: 127, fig. 29/1–16.

"*Neobythitina*" *rotunda* – Nolf 2013: 68, pl. 137.

Remarks

See remarks under the genus.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

"*Neobythites*" *virginicus* Müller, 1999
Fig. 18L–M

"genus Neobythitinarum" *virginicus* Müller, 1999: 126, fig. 28/21–23.

"*Neobythitina*" *virginica*– Nolf 2013: 69, pl. 138.

Remarks

See remarks under the genus.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Genus ***Preophidion*** Frizzell & Dante, 1965

Remarks

Preophidion is an extinct genus with otoliths resembling those of the extant *Sirembo*. We here place *P. elevatus* (Koken, 1888), *P. granus* (Müller, 1999), and *P. petropolis* (Dante & Frizzell, 1965) in this genus. "*Neobythites*" *meyeri* and "*N.*" *stintoni* were initially also assigned to *Preophidion* by Frizzell & Dante (1965), and this was followed as such in Ebersole *et al*. (2019), but here we reassign the former two species to the *Symmetrosulcus* (see above). The most significant distinctive feature between otoliths of *Symmetrusulcus* and *Preophidion* consists in the cleavage between the ostial and caudal collicula, which is vertical and short in otoliths of *Symmetrosulcus*, whereas it is more oblique and inclined in an anterodorsal-posteroventral direction in the more *Sirembo*-like otoliths of *Preophidion*. Additionally, *Sirembo*-like otoliths usually have a wider sulcus, a sharply restricted collum on the crista inferior, a more considerable thickness and a more convex inner face.

Preophidion elevatus (Koken, 1888)
Fig. 19A–C

Otolithus (*Gadidarum*) *elevatus* Koken, 1888: 290, pl. 18 figs 4–5.
"genus Sirembinorum" *crassus* Müller, 1999: 120, fig. 28/3–18, pl. 16 figs 13–14 (erroneously mentioned as valid in Nolf 2013: 175, but not in his list of valid Sirembini on p. 66).

"*genus* aff. *Sirembo*" *elevatus* – Nolf 1980: 110, pl. 17 fig. 5; 1985: 66; 2003: 5, pl. 1 fig. 6.
Joenelsenia elevatus – Schwarzhans 1981b: 112 (*Joenielsenia* is a synonym of *Preophidium*).
"aff. *Sirembo*" *elevatus* – Nolf 2013: 66, pl. 127.

Remarks

The otoliths of *P. elevatus* are very similar to those of *P. granus*, but the anterior portion of their cauda is shorter and broader, and their outline is less elongated.

Stratigraphic and geographic distribution

Lutetian: "lower" Lisbon Formation, Alabama; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Mississippi; "upper" Lisbon Formation and Gosport Sand, Alabama.

Preophidion granus (Müller, 1999)
Fig. 19D–F

"genus Sirembinorum" *granus* Müller, 1999: 122, fig. 28/19–20, pl 16 fig. 15.

"genus Sirembinorum" *granus* – Nolf & Stringer 2003: pl. 3 figs 15–17.
"*Sirembinus*" *granus* – Nolf 2013: 66, pl. 128.
Sirembo? *granus* – Stringer *et al*. 2022: 6, fig. 3g.

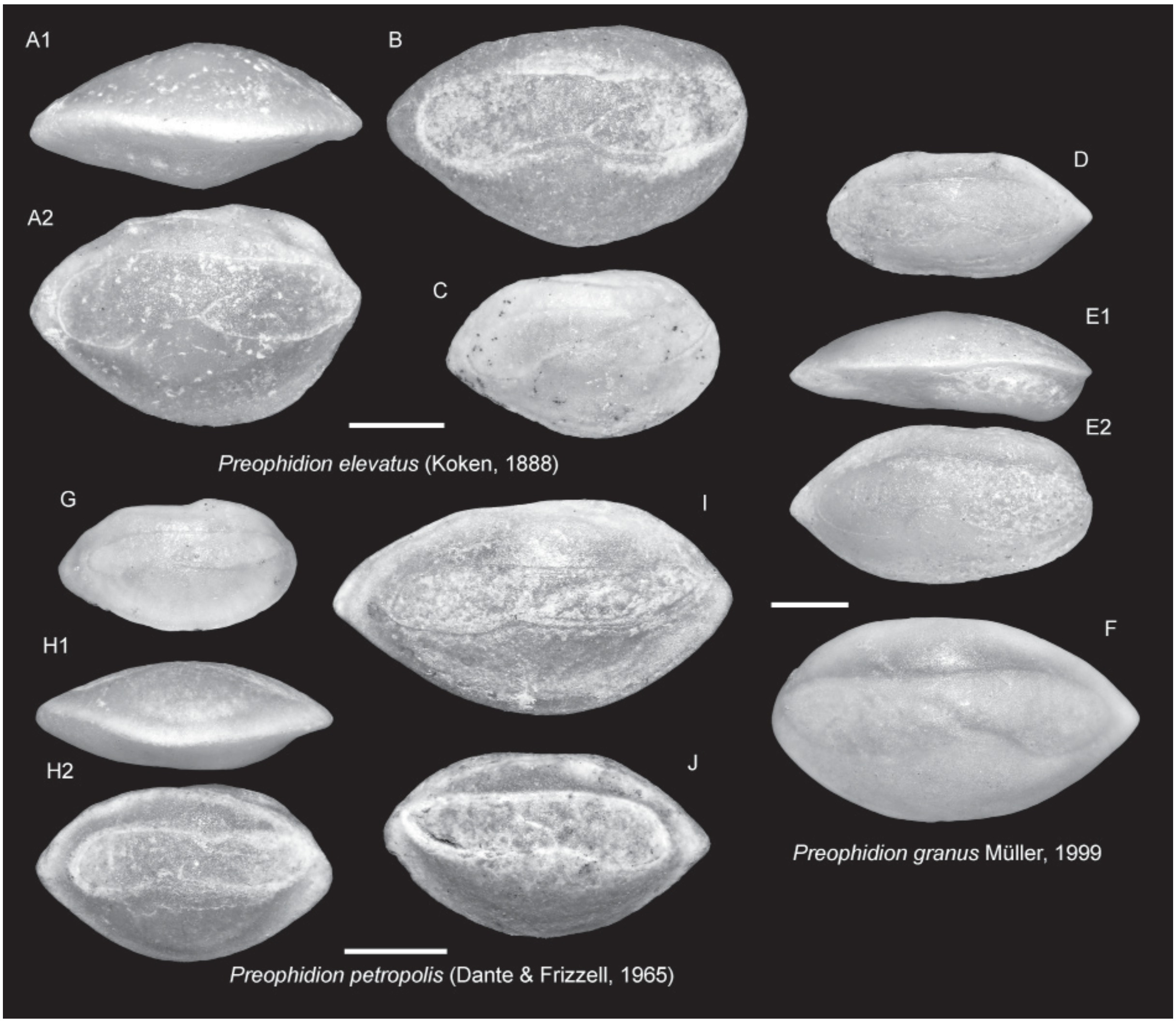


Fig. 19. Fish otoliths from the US middle and upper Eocene. **A–C**. *Preophidion elevatus* (Koken, 1888). **A–B**. "upper" Lisbon F., Coffeeville Landing, Alabama (IRSNB P 10074–10075). **C**. Potterchitto M., Newton, NE exit off Interstate 20, Mississippi (IRSNB P 10076). **D–F**. *Preophidion granus* Müller, 1999. **D–E**. Moodys Branch F., Jackson, Riverside Park, Mississippi (IRSNB P 10077–10078). **F**. Shubuta Clay M., Cynthia, Mississippi Lite clay pit, Mississippi (IRSNB P 10079). **G–J**. *Preophidion petropolis* (Dante & Frizzell, 1965). **G**. Potterchitto M., Newton, NE exit off Interstate 20, Mississippi (IRSNB P 10080). **H–J**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10081–10083). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Remarks

The otoliths of *P. granus* are easily distinguished from those of *P. elevatus* and *P. petropolis* by their having a clearly angular junction of the ostial and caudal crista inferior, a narrow anterior part of the cauda, and a posterior portion of the cauda that is bent in a ventral direction. But the most striking feature of *P. granus* is apparently that in a ventral view the otoliths show a very marked thickening of their anterior portion.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia. Bartonian: "upper" Lisbon Formation and Gosport Sand, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana and Mississippi.

Preophidion petropolis (Dante & Frizzell, 1965)
Fig. 19G–J

Preophidion petropolis Dante & Frizzell in Frizzell & Dante, 1965: 713, pl. 86 figs 34, 39.

Preophidion petropolis – Schwarzhans 1981b: 80.
"*genus* aff. *Sirembo*" *petropolis* – Nolf 1980: 137; 1985: 66.
"aff. *Sirembo*" *petropolis* – Nolf 2013: 66, pl. 128.

Remarks

The otoliths of *P. petropolis* are easily distinguished from those of *P. elevatus* and *P. granus* by their cauda, which is almost straight and is nearly the same length as the ostium.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas. Bartonian: Cook Mountain Formation, Texas and Mississippi; Moodys Branch Formation, Louisiana; "upper" Lisbon Formation, Alabama.

Genus *Xenosirembo* Schwarzhans, 1981

Xenosirembo decipiens (Koken, 1888)
Fig. 38J

Otolithus (*Sciaenidarum*) *decipiens* Koken, 1888: 285, pl. 19 figs 5–6.

"genus *Sirembinorum*" *decipiens* – Nolf 1980: 137, pl. 16 fig. 13; 1985: 66; 2003: 5, pl. 1 fig. 7.
Xenosirembo decipiens – Schwarzhans 1981b: 80, fig. 27.
"*Sirembinus*" *decipiens* – Nolf 2013: 66, pl. 128.

Remarks

Based on the convexity of the inner face and configuration of the cauda, Nolf (1980) indicated a possible relationship of this species with *Sirembo* and placed it within the Sirembini. The species is only known from Koken's original collection (Nolf 2003), and no otoliths of *X. decipiens* were found in our newly collected material.

Stratigraphic and geographic distribution

This species is only known from the "Clayborne Beds", probably from Claiborne Bluff, "upper" Lisbon Formation, Gosport Sand, Bartonian, Alabama.

Order Kurtiformes Jordan, 1923
Family Apogonidae Günther, 1859
Genus incertae sedis

"*Apogon*" *americanus* (Dante & Frizzell, 1965)
Fig. 20F–J

"*Myctophum*" *americanum* Dante & Frizzell in Frizzell & Dante, 1965: 696, pl. 86 figs 14–16.

"*Apogonida*" *americana* – Nolf 2013: 96, pl. 230.

Remarks

This species is characterized by the nearly equal length of the ostium and cauda and by the large ostial colliculum. Therefore, it reasonably aligns with the features of apogonid otoliths. However, the massive and protruding rostrum and compact posterior part of the otolith is not seen in any of the Recent apogonid genera. We here follow Nolf's (2013) interpretation and place it as an incertae sedis genus

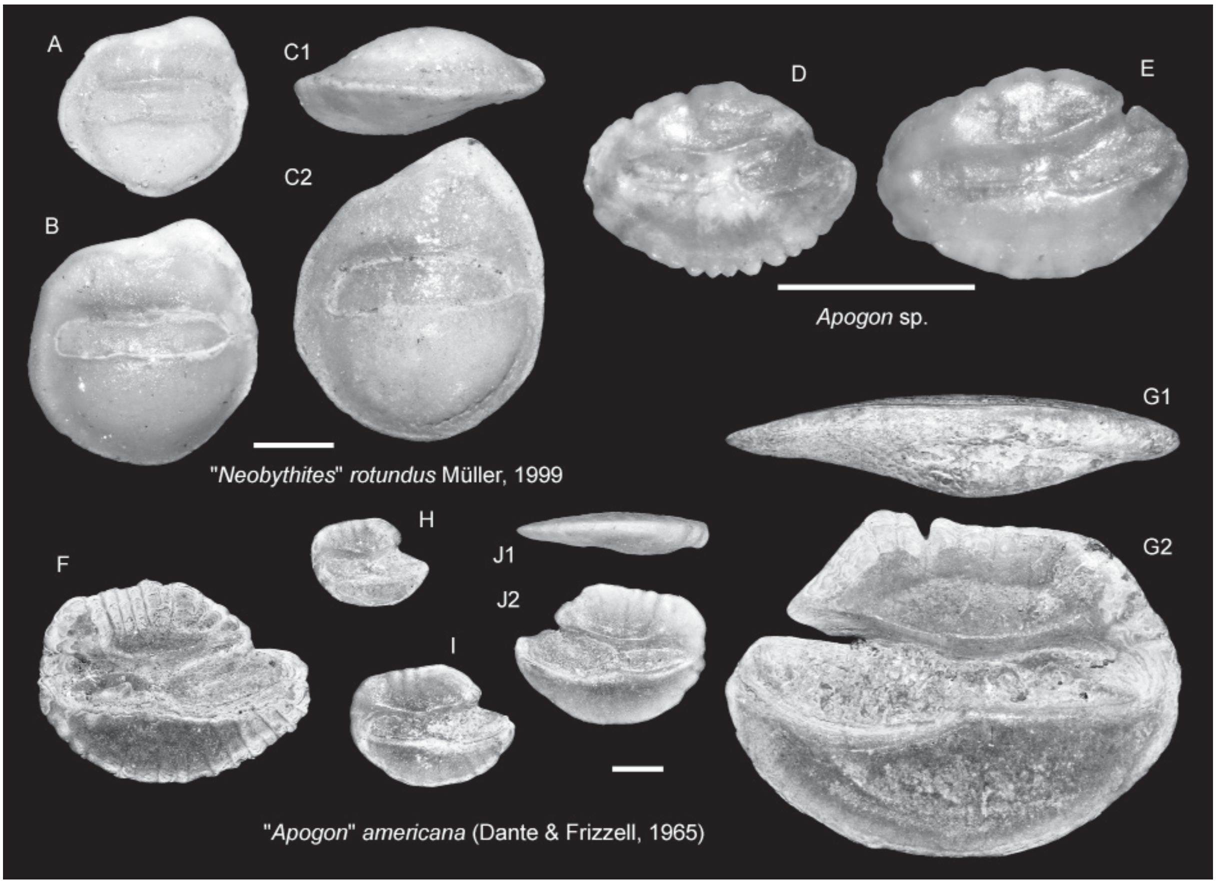


Fig. 20. Fish otoliths from the US middle and upper Eocene. **A–C**. "*Neobythites*" *rotundus* Müller, 1999, Piney Point F., sand and gravel pit, Bottoms Bridge, loc. 22 of Müller, Virginia (IRSNB P 10100–10102). **D–E**. *Apogon* sp., "Stone City beds", Stone City Bluff, Brazos River, Texas (IRSNB P 10103–10104). **F–J**. "*Apogon*" *americanus* (Dante & Frizzell, 1965), "Stone City beds", Texas. **F–G**. Stone City Bluff, Brazos River, sample 2 from bed P (IRSNB P 10105–10106). **H–J**. Alabama Ferry, on Trinity River, North (IRSNB P 10107–10109). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

within Apogonidae. A very large specimen (9 mm length) was collected at the Stone City Bluff (Texas) (Fig. 20G), expanding the range of otolith ontogeny of the species.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas. Bartonian: Wheelock Member, Texas.

Genus *Apogon* Lacepède, 1801

Apogon sp.
Fig. 20D–E

Remarks

Several small otoliths (n = 33) from localities in Texas are here assigned to *Apogon.* These likely belong to juveniles, and their non-diagnostic morphology does not allow further assignment.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Cook Mountain Formation, Texas.

Order Gobiiformes Günther, 1880
Family Gobiidae Cuvier, 1816
Genus incertae sedis

"*Gobius*" *vetustus* (Nolf & Stringer, 2003)
Fig. 39I–N

"genus Gobiidarum" *vetustus* Nolf & Stringer, 2003: 9, pl. 7 figs 6–11.

"*Gobiida*" *vetusta* – Nolf 2013: 119, pl. 325.

Remarks

As stated in Nolf & Stringer (2003) in the introduction of the species, these otoliths from the Priabonian Yazoo Clay of Louisiana likely represent an early, rare record of an extinct form of the diverse gobioid group. The species was not found among our newly collected material from other localities.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana. Priabonian: Yazoo Clay, Louisiana.

Order Blenniiformes Bleeker, 1860
Family Blenniidae Rafinesque, 1810
Subfamily Blenniinae Rafinesque, 1810
Genus incertae sedis

"*Blennius*" *cor* (Koken, 1888)
Fig. 21A–D

Otolithus (*Triglae*) *cor* Koken, 1888: 287, pl. 18 fig. 10.
"genus Blenniidarum" *curvatus* Müller, 1999: 205, fig. 42/3–6, pl. 16 fig. 19.

"genus Blenniidarum" *cor* – Nolf & Stringer 2003: 6, pl. 8 figs 2–4. — Nolf 2003: 10, pl. 3 fig. 1.
"*Blenniida*" *cor* – Nolf 2013: 116, pl. 313.

Remarks

Two species, "*Blennius*" *cor* and the labrisomid "*Labrisomus*" *eocaenicus* (Müller, 1999), share many otolith features and look very similar in appearance. However, some critical differences exist: "*B.*" *cor* has a larger ostium with a wider opening and a high dorsal rim, resulting in a somewhat triangular shape of the upper part of the otoliths, while in the latter species, the ostium is shorter and its anterior opening is more restricted. Also, "*L.*" *eocaenicus* has almost elliptic otoliths. Other differences include a slightly stronger constriction at the collum in "*B.*" *cor* and a more ventrally-oriented caudal end in "*L.*" *eocaenicus*. Both species are not common, and "*L.*" *eocaenicus* is only known from the Piney Point Formation of Virginia (Table 1).

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia. Bartonian: "upper" Lisbon Formation, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana.

Family Labrisomidae Clark Hubbs, 1952
Genus incertae sedis

"*Labrisomus*" *eocaenicus* (Müller, 1999)
Fig. 21E–G

"genus Labrisomidarum" *eocaenicus* Müller, 1999: 205, fig. 42/12–14.

"*Labrisomida*" *eocaenica* – Nolf 2013: 116, pl. 314.

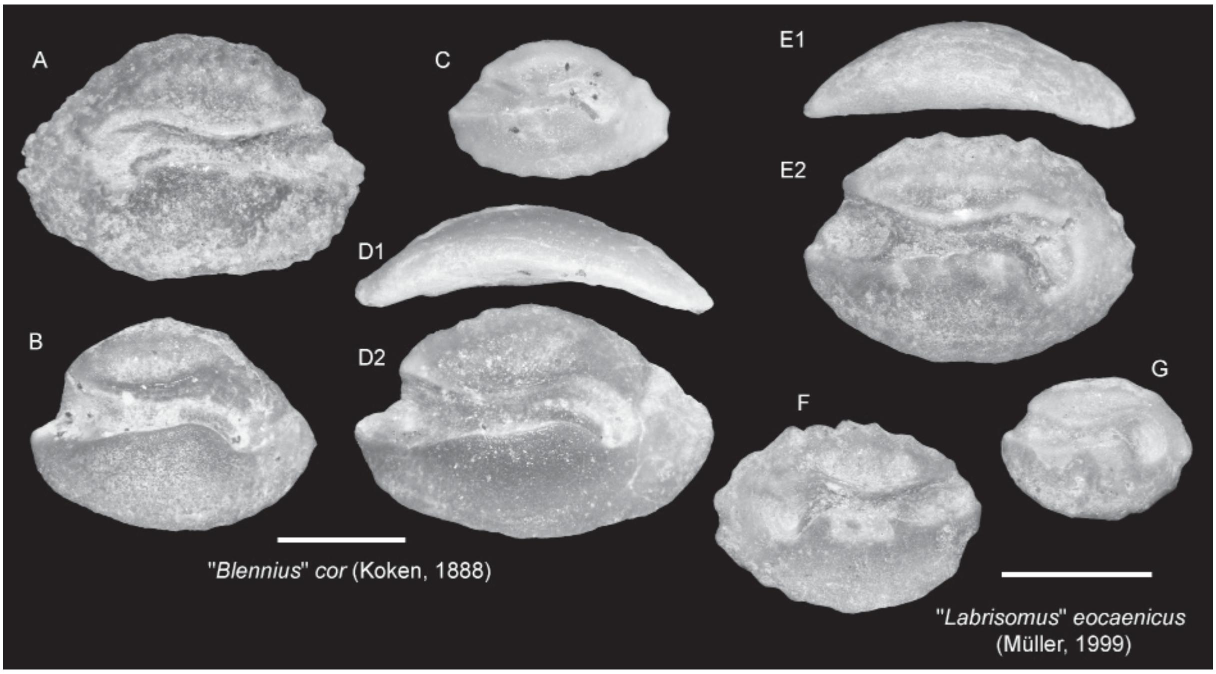


Fig. 21. Fish otoliths from the US middle and upper Eocene. **A–D**. "*Blennius*" *cor* (Koken, 1888). **A**. Piney Point F., Pamunkey River, Devil's Hole, Virginia (IRSNB P 10110). **B–D**. Moodys Branch F., Melvin (SE of town), Alabama (IRSNB P 10111–10113). **E–G**. "*Labrisomus*" *eocaenicus* (Müller, 1999), Piney Point F., Virginia. **E–F**. Pamunkey River, Devil's Hole (IRSNB P 10114–10115). **G**. Pamunkey River, 1 km E of Eanes property (IRSNB P 10116). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Remarks

See under "*Blennius*" *cor* for the distinctive features of "*B.*" *cor* and "*L.*" *eocenicus*.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Order Atheriniformes Rosen, 1964
Family Atherinidae Risso, 1827
Genus incertae sedis

"*Atherina*" *debilis* (Koken, 1888)
Fig. 22A–C

Otolithus (*Mugilidarum*) *debilis* Koken, 1888: 288, pl. 17 fig. 8.

"genus? *Mugilidarum*" *debilis* – Nolf 1985: 124.
"genus Atherinidarum" *debilis* – Nolf & Stringer 2003: pl. 3 figs 20–21. — Nolf 2003: 5, pl. 1 fig. 10.
"*Atherinida*" *debilis* – Nolf 2013: 73, pl. 150.

Remarks

Otoliths of "*A.*" *debilis* have a cauda with a very long anterior portion and a restricted ostium. They show some plesiomorphic features that make both allocations, either to Atherinidae or Mugilidae, plausible. The close relationship of both families is supported by a number of features (Stiassny 1993; Datovo *et al*. 2014). However, the inner face showing only a weak convexity and the deeper ventral area seem to be more typical of atherinid otoliths. The New Zealandian middle Eocene (Bortonian) species *Thoroatherina toroa* Schwarzhans, 2019 shows some similarity to "*A.* " *debilis*, especially in the morphology of the cauda, and was placed in the same genus in the original description of Schwarzhans (2019a: 61). However, we prefer not to include the American species in the same genus because otoliths of *T. toroa* have a much deeper ventral portion, and a very considerable convexity and thickness.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana.

Order Carangiformes Jordan, 1923
Family Carangidae Rafinesque, 1815

Carangidae indet.
Fig. 22H–I

Remarks

Several otoliths (n = 22) are only assigned to the family level. They lack the diagnostic morphology for a more precise assignment.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Wheelock Member, Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi. Priabonian: Yazoo Clay, Mississippi.

Family Menidae Fitzinger, 1873
Genus *Mene* Lacepède, 1803

Mene garviei sp. nov.
urn:lsid:zoobank.org:act:A654012A-47FF-4478-9462-310422D160AA
Fig. 22D–E

Diagnosis

OL/OH = 1.63. Pyriform otoliths with large rostrum curving towards outer face at anterior tip. Sulcus wide, oblong. Ostium opens widely anteriorly. Cristae in cauda ridge-like, curving ventrally at posterior.

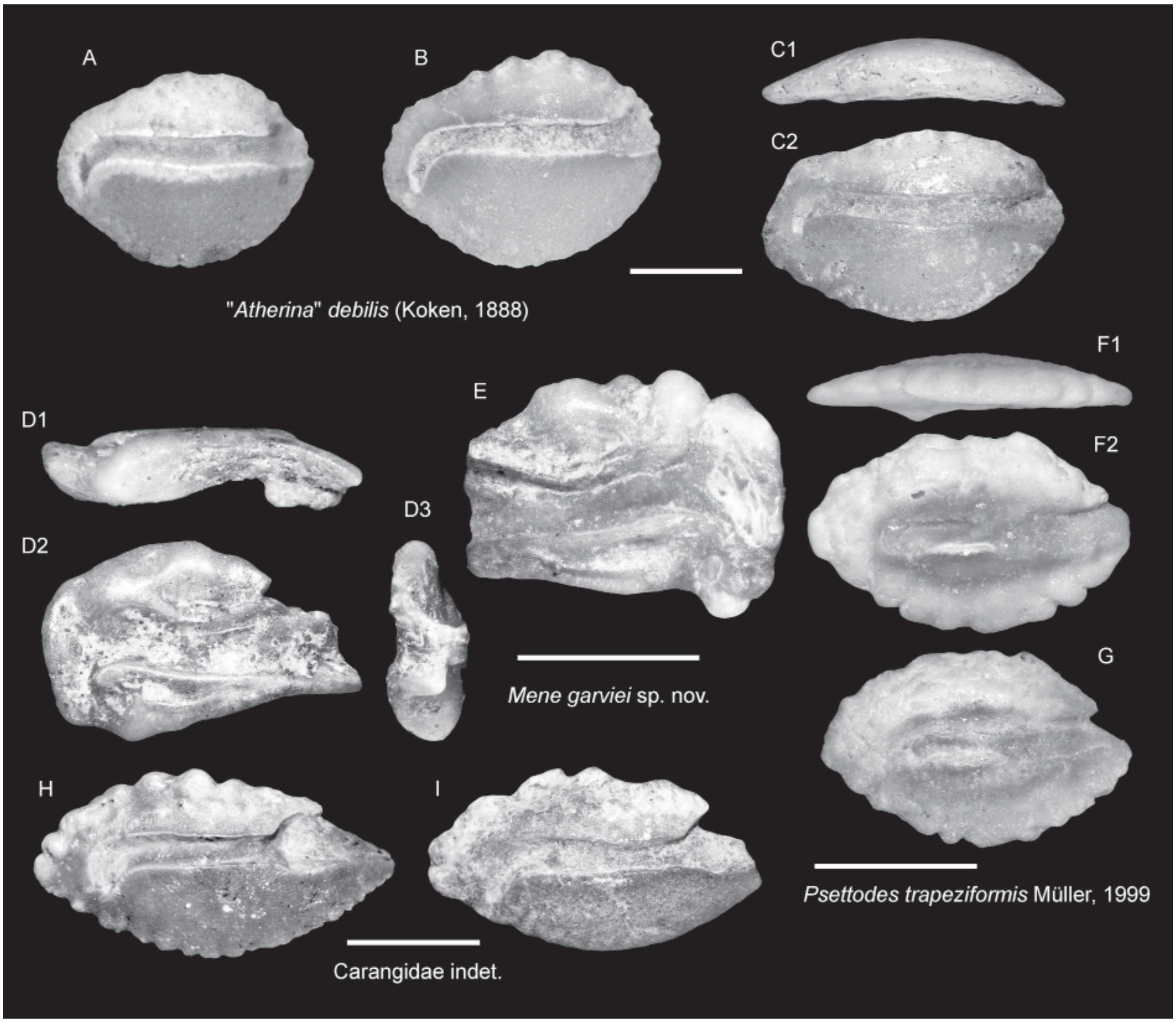


Fig. 22. Fish otoliths from the US middle and upper Eocene. **A–C**. "*Atherina*" *debilis* (Koken, 1888). **A**. "Stone City beds", Stone City Bluff, Brazos River, sample 6 from bed U, Texas (IRSNB P 10122). **B–C**. Moodys Branch F., Jackson, Riverside Park, Mississippi (IRSNB P 10123–10124). **D–E**. *Mene garviei* sp. nov., Landrum M., Pin Oak Creek, Texas. **D**. Holotype (IRSNB P 10125). **E**. Paratype (IRSNB P 10126). **F–G**. *Psettodes trapeziformis* Müller, 1999, Piney Point F., Virginia. **F**. Pamunkey River, 1 km E of Eanes property (IRSNB P 10127). **G**. Pamunkey River, Devil's Hole (IRSNB P 10128). **H–I**. Carangidae indet. **H**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 10129). **I**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10130). 1 = ventral view; 2 = inner view; 3 = anterior view. Scale bars = 1 mm.

Etymology

This species is dedicated to Christopher Garvie for his very substantial help during our field work and for the donation of many otoliths that he collected.

Material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Texas, Pin Oak Creek 1; Landrum Member of the Cook Mountain Formation; Fig. 22D; IRSNB P 10125.

Paratype

UNITED STATES OF AMERICA • 1 otolith; same collection data as for holotype; Fig. 22E; IRSNB P 10126.

Type locality and horizon

United States of America, Pin Oak Creek 1 (Texas), Landrum Member of the Cook Mountain Formation.

Dimensions of the holotype

Length = 1.76 mm; height = 1.11 mm; thickness = 0.44 mm.

Description

The otoliths of this species have a pyriform to elongate triangular outline, with the most considerable length in the antero-posterior direction. The posterior rim is almost vertical; it bears a rounded postero-dorsal angle and a ventrally enlarged postero-ventral angle, which is accentuated by a notch at the junction with the ventral rim. This notch is most evident in the paratype. The margin of the dorsal rim is smooth in the holotype, but lobate in the paratype. The otoliths are thin and fragile, especially for what concerns the anterior portion; the posterior part is more robust and thickset. The inner face is convex and strongly curved towards the outer face at the anterior side. The outer face is concave, and in the holotype, a tubercle is seen near the rostrum. The sulcus is well-developed, deeply incised, and wide. In the crista superior, a constriction of the middle part marks the collum. The cristae are ridge-like, except at the posterior end, which is less delineated. The ostium widens gradually to the anterior end. The cauda is rather short and strongly curved in ventral direction. In the dorsal area, there is a small depression just above the central part of the crista superior. The ventral area is slightly larger than the dorsal one.

Remarks

Mene garviei sp. nov. is very rare (two specimens only); they were found only in the Landrum Member of the Cook Mountain Formation, Texas. A single otolith of *Mene* from the Yazoo Clay, Louisiana figured by Nolf & Stringer (2003: 6, pl. 4 fig. 16a–b) has a much shorter rostrum and higher posterior part, and likely represents another undescribed menid species.

Stratigraphic and geographic distribution

Bartonian: Landrum Member, Texas.

Order Pleuronectiformes Bleeker, 1859
Family Psettodidae Regan, 1910
Genus *Psettodes* Bennett, 1831

Psettodes trapeziformis Müller, 1999
Fig. 22F–G

Psettodes trapeziformis Müller, 1999: 211, fig. 42/17–18, pl. 17 fig. 8.

Psettodes trapeziformis – Nolf 2013: 124, pl. 339.

Remarks

Otoliths of *P. trapeziformis* can be readily distinguished by their elliptic shape with about similar dorsal and ventral areas, a sulcus without colliculum and a nearly straight cauda with a very slightly downwards bent end.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Family Citharidae de Buen, 1935
Genus *Brachypleura* Günther, 1862

Brachypleura nana (Müller, 1999)
Fig. 23A–D

"genus Bothidarum" *nanus* Müller, 1999: 212, fig. 42/7–10, pl. 17 fig. 10

"aff. *Brachypleura*" *nana* – Nolf 2013: 124, pl. 340.

Remarks

The otoliths of this species seem most similar to those of Recent *Brachypleura* (see Schwarzhans 1999: 87, figs 105–110 for otoliths of the Recent *B. novaezeelandiae* Günther, 1862), and therefore, were assigned to that genus by Nolf (2013).

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Genus incertae sedis

"*Citharus*" *hoffmani* (Nolf & Stringer, 2003)
Fig. 39O–P

"genus Citharidarum" *hoffmani* Nolf & Stringer, 2003: 9, pl. 8 figs 9–11.

"*Citharida*" *hoffmani* – Nolf 2013: 124, pl. 341.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana. Priabonian: Yazoo Clay, Louisiana.

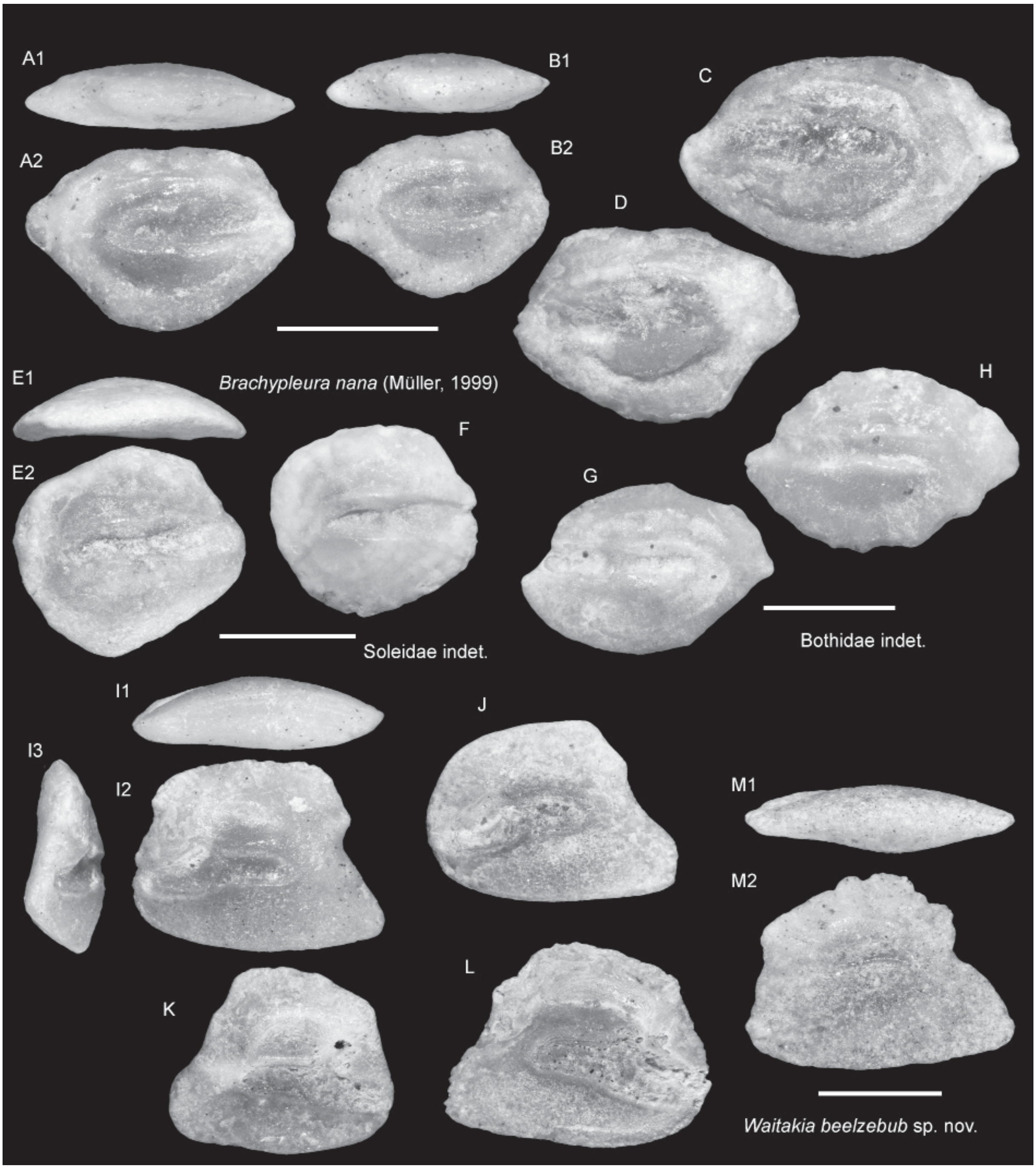


Fig. 23. Fish otoliths from the US middle and upper Eocene. **A–D**. *Brachypleura nana* (Müller, 1999), Piney Point F., Virginia. **A–C**. Pamunkey River, Devil's Hole (IRSNB P 10131–10133). **D**. Pamunkey River, SW of Pampatike Landing (IRSNB P 10134). **E–F**. Soleidae indet., Piney Point F., Pamunkey River, Devil's Hole, Virginia (IRSNB P 10135–10136). **G–H**. Bothidae indet., Moodys Branch F., Melvin (SE of town), Alabama (IRSNB P 10137–10138). **I–M**. *Waitakia beelzebub* sp. nov., Piney Point F., Virginia. **I–L**. Pamunkey River, 1 km E of Eanes property (IRSNB P 10117–10120). **M**. Pamunkey River, Devil's Hole (IRSNB P 10121). **I**. Holotype (IRSBN P 10117). **J–M**. Paratypes (IRSNB P 10118–10121). 1 = ventral view; 2 = inner view; 3 = anterior view. Scale bars = 1 mm.

"*Citharus*" *varians* sp. nov.
urn:lsid:zoobank.org:act:88394BA7-3F94-45EC-A7E4-B3903364E0ED
Fig. 24

Diagnosis

OL/OH = 1.03–1.33, OsL/CaL = 0.83–1.20. Circular otoliths with small, pointed but well-developed rostrum and antirostrum. Shape of posterior rim varies markedly among specimens. Sulcus well divided into ostium and cauda.

Etymology

The name alludes to the considerable intraspecific variability of the otoliths.

Material examined

Holotype

UNITED STATES OF AMERICA • Right otolith; Texas, Little Brazos River, Stenzel loc.; Wheelock Member; Fig. 24G; IRSNB P 10145.

Paratypes

UNITED STATES OF AMERICA • 51 otoliths of which six are figured: Fig. 24A–F; Texas, Little Brazos River, Stenzel loc.; Wheelock Member; IRSNB P 10139–10144 • 24 otoliths; Texas, Stone City Bluff, Brazos River; "Stone City Beds" • 22 otoliths; Pin Oak Creek; Landrum Member.

Type locality and horizon

United States of America, Little Brazos River, Stenzel loc. (Texas), Wheelock Member of the Cook Mountain Formation.

Dimensions of the holotype

Length = 2.28 mm; height = 2.03 mm; thickness = 0.83 mm.

Description

This species is characterized by globally circular otoliths, but with a marked rostrum, antirostrum, and a postero-dorsal angle. The dorsal and ventral rims are smoothly curved and raised in the center. The curvature is most pronounced in the ventral rim. The dorsal rim may be irregular but it is usually smooth. The configuration of the posterior rim varies greatly. It may be vertically straight (Fig. 24D), or pointed and extended at the lower part, as in the holotype (Fig. 24G). The rostrum and the antirostrum are both small, short and pointed at their tips. The tip of the rostrum is directed upwards. The excisura is not very incised, but always well-marked with its hollow shape. The inner face is more or less flat but notably elevated in the sulcus area. The outer face varies from convex to strongly convex (Fig. 24F1). The sulcus has ridge-like cristae; it is deeply incised and with elevated collum, well divided into ostium and cauda. Both are oblong, straight, and of nearly similar length. The shape of the cauda varies in left and right otoliths; in the left ones it is somewhat shorter and more rounded; in the right ones, the posterior end is very slightly inclined ventrally.

Remarks

The otoliths of this species demonstrate the great intra-specific variation in flatfishes already mentioned by Schwarzhans (1999). The dissymmetric look of the left and right otoliths further increases this variability. Furthermore, a high variability in otolith can also be observed in many of the extant pleuronectiforms illustrated in the various papers of Chaine (see Nolf *et al.* 2009: pls 133–149).

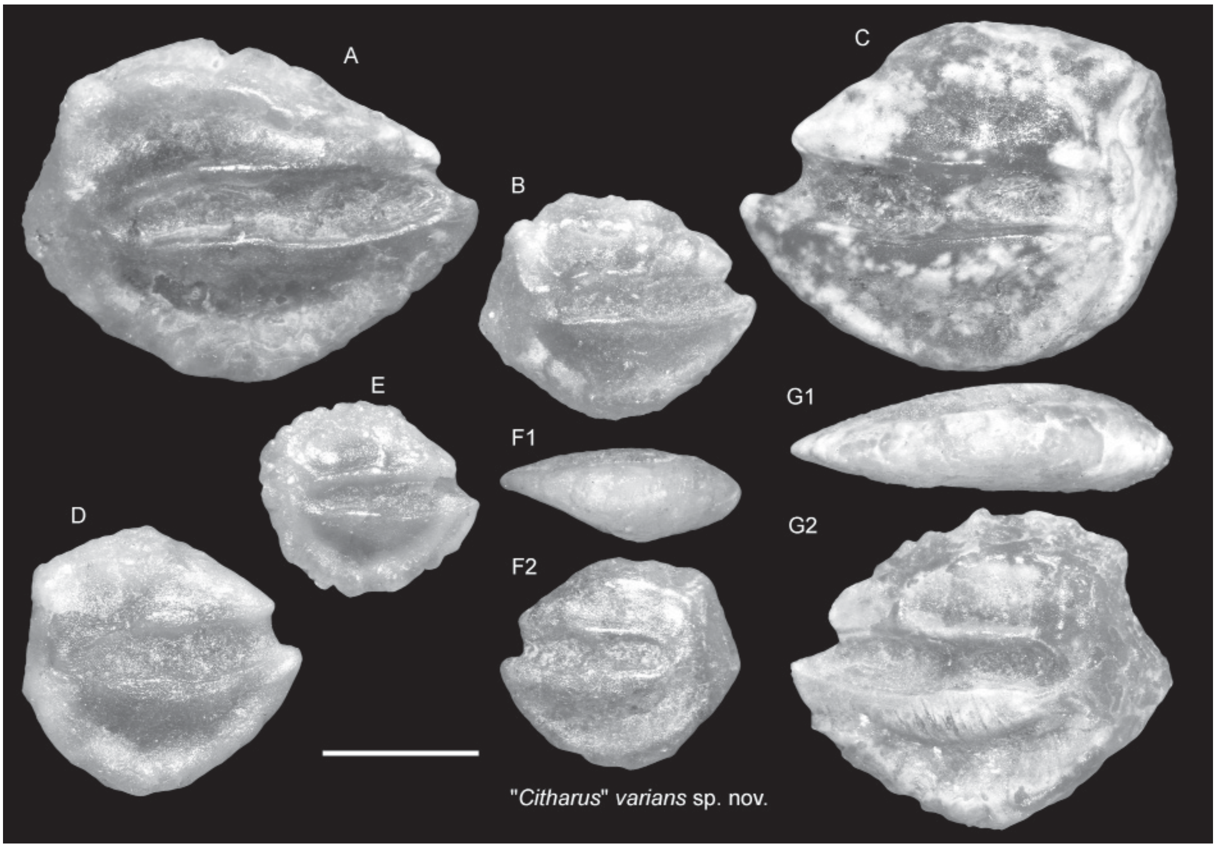


Fig. 24. Otoliths of "*Citharus*" *varians* sp. nov. from the US middle and upper Eocene; Wheelock M., Little Brazos River, Stenzel loc., Texas. **A–F**. Paratypes (IRSNB P 10139–10144). **G**. Holotype (IRSNB P 10145). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Cook Mountain Formation, Texas; "upper" Lisbon Formation, Alabama.

Family Paralichthyidae Regan, 1910
Genus *Citharichthys* Bleeker, 1862

Citharichthys altissimus Nolf & Stringer, 2003
Fig. 39Q–R

Citharichthys altissimus Nolf & Stringer, 2003: 10, pl. 8 figs 7–8.

Citharichthys altissimus – Nolf 2013: 125, pl. 344.

Remarks

This species is only known from the holotype and seven paratypes described by Nolf & Stringer (2003).

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana. Priabonian: Yazoo Clay, Louisiana.

Family Bothidae Smitt, 1892

Bothidae indet.
Fig. 23G–H

Remarks

Several otoliths (n = 13) are here assigned to the family Bothidae, but cannot be defined with more precision, due to their poor preservation. Ebersole *et al*. (2019: 204, fig. 70q–r) reported a somewhat similar looking bothid otolith from the "upper" Lisbon Formation of Alabama, but more and better specimens are required for good taxonomic work.

Stratigraphic and geographic distribution

Lutetian: Weches Formation, Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; Piney Point Formation, Virginia. Bartonian: "upper" Lisbon Formation, Alabama; Moodys Branch Formation, Mississippi and Alabama.

Family Soleidae Bonaparte, 1833

Soleidae indet.
Fig. 23E–F

Remarks

Although exhibiting typical soleid features, we judge that the only, two very small specimens from the Piney Point Formation are not appropriate for further description and taxonomic evaluation.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

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

Waitakia beelzebub sp. nov.
urn:lsid:zoobank.org:act:37227549-BE44-47BF-B1F7-58508E5D72FE
Fig. 23I–M

Gobiidae indet. – Ebersole *et al*. 2019: 204, fig. 70o–p.

Diagnosis

OL/OH = 1.19–1.37, OsL/CaL = 1.10–1.29. Trapezoid otoliths with blunt anterior rim. Posterior rim with strong postero-ventral angle. Sulcus well divided into ostium and cauda. Ostium tilting towards antero-ventral rim; wider and longer than cauda.

Etymology

Refers to the locality Devil's Hole, where one of the paratypes was collected.

Material examined

Holotype

UNITED STATES OF AMERICA • Right otolith; Virginia, Pamunkey River, 1 km E of Eanes property; Bed A, sample 1; Fig. 23I; IRSNB P 10117.

Paratypes

UNITED STATES OF AMERICA • 4 otoliths of which three are figured: Fig. 23J–L; same collection data as for holotype; IRSNB P 10118–10120 • 1 otolith: Fig. 23M; Virginia, Pamunkey River, Devil's Hole; Piney Point Formation; IRSNB P 10121.

Type locality and horizon

United States of America, Pamunkey River, 1 km E of Eanes property (Virginia), Bed A, sample 1 (Fig. 7); see also Strickland (1985), loc. 37, Piney Point Formation.

Dimensions of the holotype

Length = 2.04 mm; height = 1.56 mm; thickness = 0.59 mm.

Description

The shape of the otoliths is trapezoid, with their dorsal and ventral rims approximately parallel to each other and with oblique anterior and posterior rims. The ventral rim is much longer than the dorsal one. There is a well-incised notch in the middle of the posterior rim. Below this notch, there is a conspicuous large and strong postero-ventral angle at the junction with the ventral rim, and extending far backwards below the upper portion of the posterior rim. The anterior part of the dorsal rim is slightly inclined towards the junction with the anterior rim. The margins are smooth, but somewhat more irregular on the dorsal rim of the holotype. The thickness of the otoliths is considerable; both the inner and outer faces are clearly convex in the dorso-ventral direction. The sulcus has well-developed cristae and there is a clear division into an ostial and caudal part, which is marked by a constriction of the cristae in the central zone of the sulcus. The ostium is large and expanded ventrally. The ostial crista superior is sharply inclined and directs ventrally. The anterior end of the ostium nearly reaches the anterior rim of the otolith. The cauda is narrower than the ostium; it is horizontally directed and shows a rounded posterior end; also, there is no trace of a swollen collicular crest like in gobiids. The dorsal area is wider than the ventral one because the sulcus is located more ventrally.

Remarks

At a first glance, the conspicuous shape of these otoliths suggests a possible relationship with gobiiforms, but there is no gobiiform with a strong dorso-ventral convexity of the inner face and also, the sulcus does not match with that taxon. Finally, we opted for hemerocoetids because of some similarity with the sulcus pattern of *Bembrops* Steindachner, 1876, and also with otoliths that Schwarzhans (2019a: figs 95, 97) described from New Zealand as the apparently extinct genera *Krebsiella* and *Waitakia* and classified in the family Hemerocoetidae, which Nelson *et al*. (2016) consider as a subfamily of the Percophidae. See also Nolf (2013: pls 306–307) and Schwarzhans (2019c: pl. 3), where various otoliths of recent and fossil hemerocoetids are figured. Ebersole *et al*. (2019: fig. 70o–p) reported a single similar otolith from the "upper" Lisbon Formation, Alabama, which we believe also belongs to this new species, based on the above description. The species is rare: only six specimens were found in our material.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia. Bartonian: "upper" Lisbon Formation, Alabama.

Family Trachinidae Rafinesque, 1815
Genus incertae sedis

"*Trachinus*" *laevigatus* (Koken, 1888)
Fig. 25A–B

Otolithus (*Trachini*) *laevigatus* Koken, 1888: 286, pl. 18 figs 13–14.

"genus Trachinidarum" *laevigatus* – Nolf & Stringer 2003: 6, pl. 8 fig. 1. — Nolf 2003: 10, pl. 3 fig. 12.
"*Trachinida*" *laevigata* – Nolf 2013: 115, pl. 310.

Remarks

The otoliths of this species show typical features of trachinid otoliths and seem to be closely related to those of the genus *Trachinus*, which is presently distributed in the eastern Atlantic. It should be noted, however, that there is a fossil Western Atlantic species (*Trachinus unus* Müller, 1999) from the upper Oligocene Old Church Formation of Virginia.

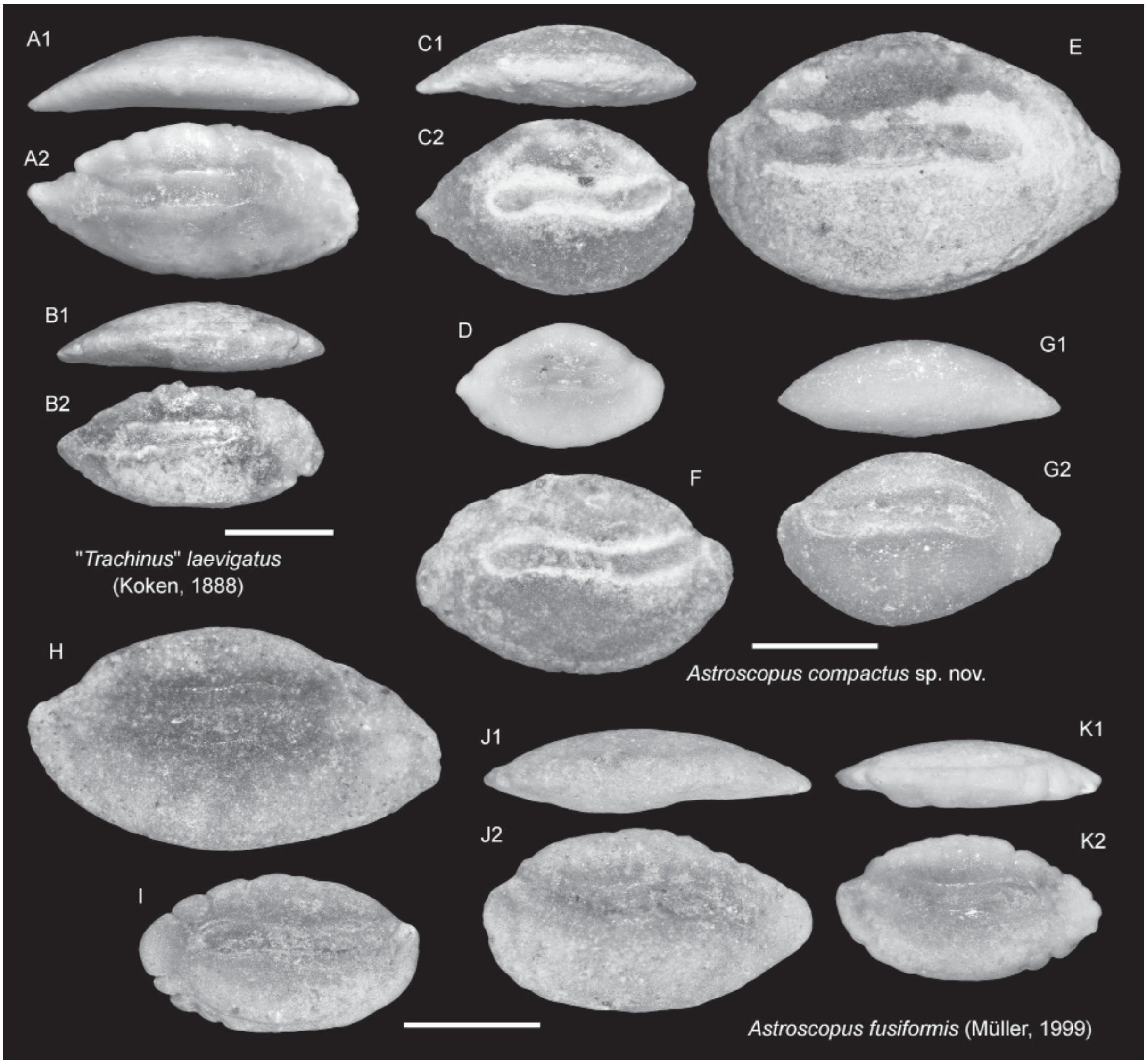


Fig. 25. Fish otoliths from the US middle and upper Eocene. **A–B**. "*Trachinus*" *laevigatus* (Koken, 1888). **A**. Moodys Branch F., Midway, Techeva Creek, Mississippi (IRSNB P 10146). **B**. "Stone City beds", Rocky Branch, 1.5 miles SW of Stone City Bluff, Texas (IRSNB P 10147). **C–G**. *Astroscopus compactus* sp. nov. **C**. Gosport Sand, Little Stave Creek, Mississippi, holotype (IRSNB P 10148). **D–E**. Potterchitto M., Newton, NE exit off Interstate 20, Mississippi, paratypes (IRSNB P 10149–10150). **F–G**. "Upper" Lisbon F., Evansboro (SE of town), Alabama, paratypes (IRSNB P 10151–10152). **H–K**. *Astroscopus fusiformis* (Müller, 1999), Piney Point F., Pamunkey River, 1 km E of Eanes property, bed A, Virginia (IRSNB P 10053–10156). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and “Stone City beds”, Texas; Piney Point Formation, Virginia. Bartonian: “upper” Lisbon Formation, Alabama; Moodys Branch Formation, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana.

Family Uranoscopidae Bonaparte, 1831
Genus *Astroscopus* Brevoort, 1860

Astroscopus compactus sp. nov.
urn:lsid:zoobank.org:act:D6BFE465-59DD-4A7A-8965-9EED7217997D
Fig. 25C–G

Diagnosis

OL/OH = 1.55–1.67. Fusiform otoliths with blunt anterior and extended posterior rims. Sulcus narrow, long and divided into ostium and cauda. Ostium gently curving upwards and cauda curving ventrally at posterior.

Etymology

From the Latin adjective ‘*compactus*, *-a*, *-um*’, meaning ‘compact, massive’ and alluding to the thick and robust aspect of the otoliths.

Material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Alabama, Little Stave Creek; Gosport Sand; Fig. 25C; IRSNB P 10148.

Paratypes

UNITED STATES OF AMERICA • 10 otoliths, of which two are figured: Fig. 25D–E; Mississippi, Newton, NE exit off Interstate 20; Poterchito Member; IRSNB P 10149–10150 • 17 otoliths, of which two are figured: Fig. 25F–G; Alabama, Evansboro (SE of town); “upper” Lisbon Formation; IRSNB P 10151–10152 • 1 otolith; Mississippi, Quitman, Archusa Water Park; Archusa Marl Member.

Type locality and horizon

United States of America, Little Stave Creek (Alabama), Gosport Sand.

Dimensions of the holotype

Length = 2.23 mm; height = 1.41 mm; thickness = 0.67 mm.

Description

This species is characterized by robust, fusiform otoliths. Both the anterior and posterior rims are tapering but the posterior rim is more extended than the anterior one. The tip of the posterior rim varies; it may show none (Fig. 25F), one (Fig. 25C) or two undulations (Fig. 25G). The dorsal and ventral rims are of equal length and markedly curved, with the highest part of the otolith in the middle. The otoliths are thick; they have a strongly convex inner face and an outer face that is nearly flat in the antero-posterior direction, but convex dorso-ventrally. The extended part of the posterior rim is the thinnest zone of the otolith. The sulcus is shallow, narrow and located very slightly at the base of the dorsal part of the otolith. There is no division into ostium and cauda by the constriction of the cristae, but the entire sulcus is rather undulated, with a long transitional zone connecting the ostium and cauda. The ostium is filled with a long colliculum and is slightly curved upwards, with its highest part at the anterior end, which opens dorsally. The cauda is slightly bent downwards in ventral direction, and ends at the lowest level of the sulcus. The cristae are not very salient, but they are sufficiently marked to delimit the margins of the sulcus. The ventral area is wide and deeper than the height of the dorsal one.

Remarks

This new species is readily distinguished from the congeneric *Astroscopus fusiformis* (Müller, 1999) (see below) by its more rounded appearance and more considerable thickness profile. *Astroscopus fusiformis* is known from the Piney Point Formation of Virginia only, while *A. compactus* sp. nov. is found in the "upper" Lisbon Formation of Alabama and the Cook Mountain Formation of Mississippi.

Stratigraphic and geographic distribution

Bartonian: Cook Mountain Formation, Mississippi; "upper" Lisbon Formation, Alabama.

Astroscopus fusiformis (Müller, 1999)
Fig. 25H–K

"genus Batrachoididarum" *fusiformis* Müller, 1999: 89, fig. 22/7–8.

Astroscopus fusiformis – Nolf 2013: 116, pl. 310.

Remarks

See under *Astroscopis compactus* sp. nov. for the differences between these two congeneric species.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Order Perciformes Bleeker, 1859
Suborder Percoidei Bleeker, 1859
Family Acropomatidae Gill, 1891
Genus *Parascombrops* Alcock, 1889

Parascombrops yanceyi sp. nov.
urn:lsid:zoobank.org:act:12B10CEA-D774-4789-98B9-4A425D01D565
Fig. 26

Diagnosis

OL/OH = 1.71–1.94, OsL/CaL = 0.77–1.00. Elongate otoliths with large rostrum and blunt posterior rim. Oval ostium with oblong colliculum. Elongate and narrow cauda of over ½ OL, with crest-like crista superior.

Etymology

This species is dedicated to Thomas Yancey for his much appreciated support during our field work in the Brazos River area.

Material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Texas, Alabama Ferry; "Stone City Beds"; Fig. 26A; IRSNB P 10157.

Paratypes

UNITED STATES OF AMERICA • 11 otoliths, of which one is figured: Fig. 26B; Texas, Little Brazos River, confluence with Brazos River; Wheelock Member; IRSNB P 10158 • 66 otoliths, of which six are figured: Fig. 26C–H; Texas, Stone City Bluff; "Stone City beds"; IRSNB P 10159–10164 • 6 otoliths; Texas, Pin Oak Creek; Landrum Member.

Type locality and horizon

United States of America, Alabama Ferry (Texas), "Stone City beds".

Dimensions of the holotype

Length = 6.85 mm; height = 3.85 mm; thickness = 1.01 mm.

Description

This species is characterized by elongated otoliths with a well-marked rostrum and a more blunt posterior end. The dorsal rim bears a marked postero-dorsal angle and a subtle antero-dorsal angle which is located at a slightly raised part of the dorsal rim. The ventral rim is smoothly curved with its deepest part in the middle, or slightly to the anterior part of the otolith. The posterior rim is oblique after the posterior-dorsal angle and provides a sharp to nearly vertical posterior end to the otolith. The anterior rim looks triangular, with a pointed tip which forms an evident rostrum. The margins of the otoliths vary: they are smooth in larger specimens, and lobed in juveniles. The otoliths are thin; the inner face is convex and the outer face is slightly concave. The sulcus is well-developed and moderately incised, with a wide and oblong ostium and long and narrow cauda. The ostium opens widely on the antero-dorsal side and is completely filled with a colliculum. The cauda is straight for about two-thirds of its length, and its posterior part is bent in a ventral direction. The cristae are well-developed and near the collum,

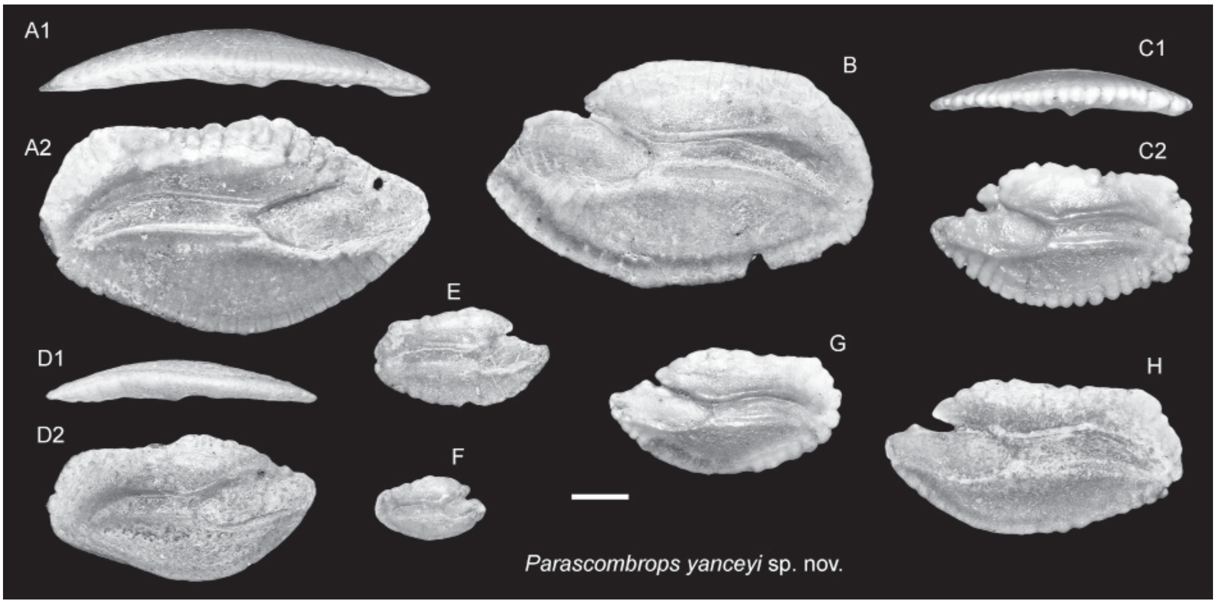


Fig. 26. Otoliths of *Parascombrops yanceyi* sp. nov. from the US middle and upper Eocene. **A**. "Stone City beds", Alabama Ferry, on Trinity River, North, Texas, holotype (IRSNB P 10157). **B**. Wheelock M., Little Brazos River, confluence with Brazos River, Texas, paratype (IRSNB P 10158). **C–H**. "Stone City beds", Stone City Bluff, Brazos River, Texas, paratypes (IRSNB P 10159–10164). **C–D**. Sample 5 from bed S (IRSNB P 10159–10160). **E–H**. Bed P (IRSNB P 10161–10164). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

the crista superior is ridge-like. The ostial crista superior curves towards the dorsal rim. The ventral area is wide and has about the same height as the dorsal one.

Remarks

The shape of the otoliths of the species demonstrate some similarities to those of moronids, but the relatively flat inner face, shorter cauda and slightly upwards oriented ostium strongly suggest that this species must be an acropomatid. A critical review on the taxonomy and the otoliths of acropomatids is provided by Schwarzhans & Prokofiev (2017), in which they also stated that fossil otoliths of acropomatids may have been more widely distributed.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Cook Mountain Formation, Texas.

Family Serranidae Swainson, 1839
Subfamily Serraninae Swainson, 1839
Genus *Centropristis* Cuvier, 1829

Centropristis priaboniana Nolf & Stringer, 2003
Fig. 27A–D

Centropristis priaboniana Nolf & Stringer, 2003: 8, pl. 4 figs 3–6.

Centropristis priaboniana – Nolf 2013: 92, pl. 214.

Remarks

At a first glance, these small otoliths can be confused with the juveniles of "*Sparus*" *elegantulus* (Koken, 1888) (see below). Nevertheless, *C. priaboniana* has a nearly horizontal ostial crista inferior, forming a triangular ostium, while in "*S.*" *elegantulus*, the ostial crista inferior is evenly widened like that of the crista superior and forms an oval ostium. Otoliths of *C. priaboniana* are rare (n = 5), but our specimens from the Moodys Branch Formation, Mississippi expands their record to a lower level than their original type locality from the Yazoo Clay of Louisiana.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana and Mississippi. Priabonian: Yazoo Clay, Louisiana.

Serranidae indet.
Fig. 27E–F

Remarks

Serranid otoliths are uncommon in our samples and more specimens are required to provide more taxonomic precision.

Stratigraphic and geographic distribution

Lutetian: Dobys Bluff Tongue of Kosciusko Formation, Mississippi; Piney Point Formation, Virginia. Bartonian: "upper" Lisbon Formation, Alabama.

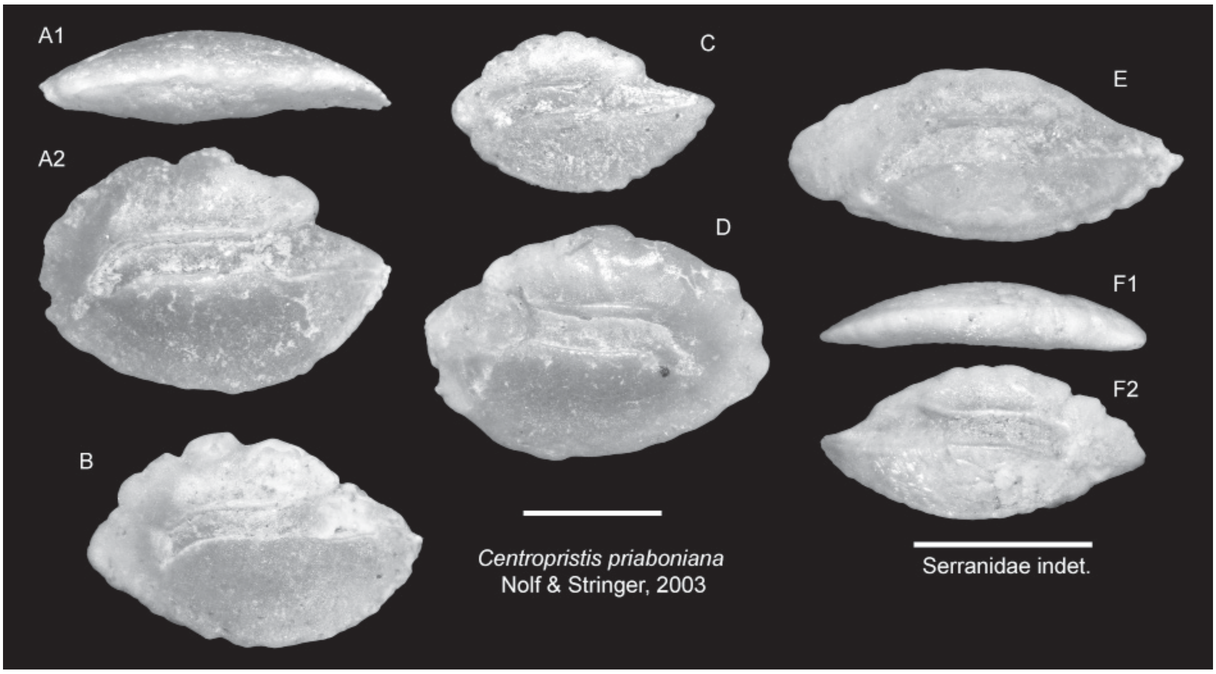


Fig. 27. Fish otoliths from the US middle and upper Eocene. **A–D**. *Centropristis priaboniana* Nolf & Stringer, 2003, Moodys Branch F., Mississippi. **A–B**. Jackson, Town Creek (IRSNB P 10165–10166). **C–D**. Jackson, Riverside Park (IRSNB P 10167–10168). **E–F**. Serranidae indet. **E**. Kosciusko F., Dobys Bluff Tongue, Dobys Bluff, Mississippi (IRSNB P 10169). **F**. "upper" Lisbon F., Coffeeville Landing, Alabama (IRSNB P 10170). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Family Lactariidae Boulenger, 1904

Genus *Lactarius* Valenciennes, 1833

Lactarius amplus (Pomerol, 1973) Stinton 1978

Fig. 28A–E

Lactarius amplus Pomerol, 1973: 122, fig. 8 (figure without description).

Lactarius amplus – Stinton 1978: 181, pl. 12 figs 11–15. — Nolf 1985: 84. — Müller 1999: 152, fig. 32/6–11, pl. 16 fig. 17.— Ebersole *et al*. 2019: 207, fig. 71c–d. — Nolf 2013: 98, pl. 238.

Remarks

Lactarius was one of the most abundant otoliths in the collection. Two species were recognized, *L. amplus* and *L. kokeni* (see below), the latter one being more abundant. Both species can be easily separated by the shape of their otoliths: *L. amplus* has a horizontally more compressed outline (OL/OH = 1.15–1.33), whereas, in *L. kokeni* (OL/OH = 1.35–1.57), the posterior part of the otolith is markedly extended backwards.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation, Alabama.

Lactarius kokeni (Dante & Frizzell, 1965)
Fig. 28F–J

Brazosiella kokeni Dante & Frizzell in Frizzell & Dante, 1965: 700, pl. 87 figs 25, 30, 32–34, 36.

Lactarius kokeni – Nolf 1985: 84; 2013: 98, pl. 238. — Müller 1999: 151, fig. 32/12–16. — Ebersole *et al*. 2019: 205, fig. 71a–b.

Remarks

See under *L. amplus* for the differences between both American *Lactarius* species. The genus name *Brazosiella* Dante & Frizzell in Frizzell & Dante (1965) is a junior synonym of *Lactarius*.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; "lower" Lisbon Formation, Alabama; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation and Gosport Sand, Alabama.

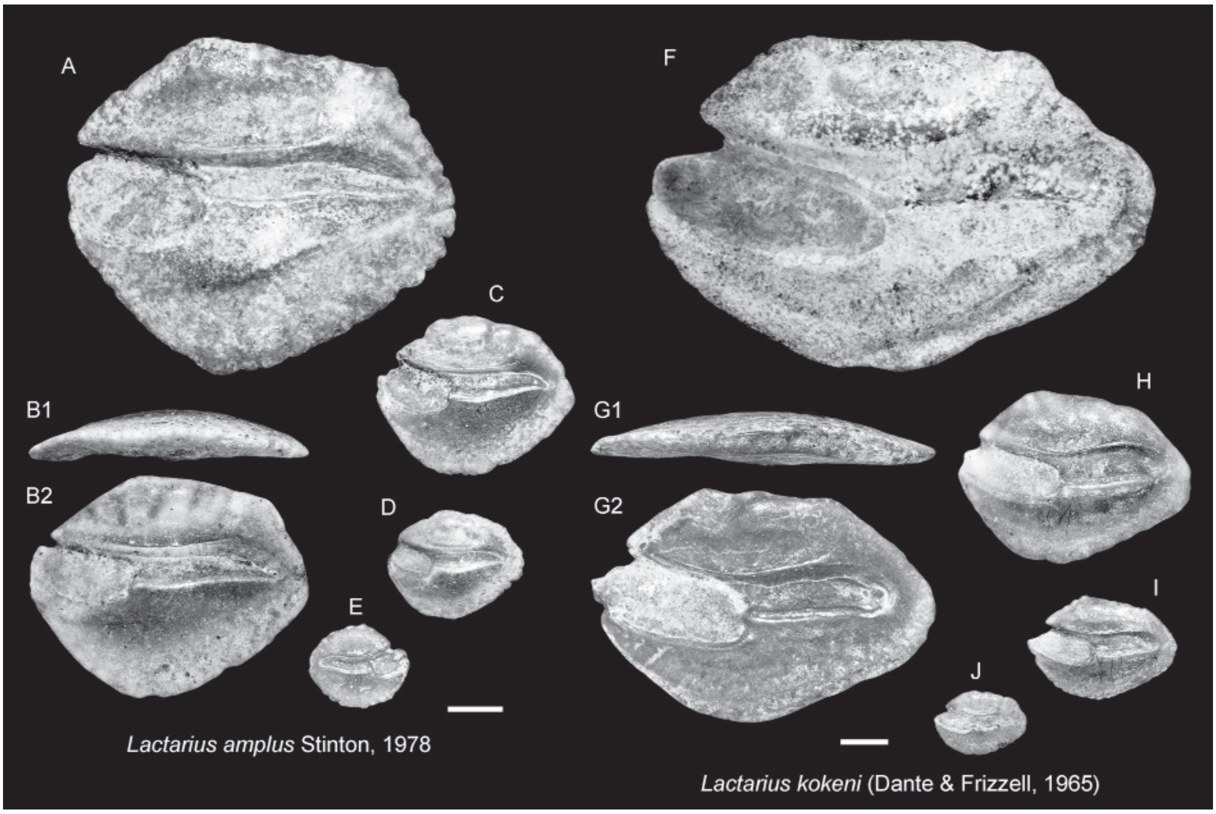


Fig. 28. Fish otoliths from the US middle and upper Eocene. **A–E**. *Lactarius amplus* Stinton, 1978, "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10171–10175). **F–J**. *Lactarius kokeni* (Dante & Frizzell, 1965), "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10176–10180). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Family Priacanthidae Günther, 1859
Genus *Pseudopriacanthus* Bleeker, 1869

Pseudopriacanthus obliquus (Nolf & Stringer, 2003)
Fig. 39A–F

Pristigenys obliquus Nolf & Stringer, 2003: 8, pl. 4 figs 7–12.

Pristigenys obliqua – Nolf 2013: 95, pl. 226.

Remarks

In a reappraisal of the Eocene priacanthid skeleton of *Pristigenys substriata* from Monte Bolca, Italy, Carnevale *et al*. (2017) stated that there is substantial evidence to consider it as generically different from the recent genus *Pseudopriacanthus*, which they also consider as a valid genus including the various Recent species that were synonymized with *Pristigenys*. Two other partially articulated skeletons with associated otoliths are known from the Belgian Lede Formation (Lutetian). They were described by Taverne & Nolf (2010), and compared with the Recent *Pseudopriacanthus hamrur* (Forsskal, 1775). For these two fossil Belgian species, *Ps. rutoti* (Leriche, 1905) and *Ps. hermani* (Taverne & Nolf, 2010), Carnevale *et al*. (2017) also concluded that they cannot be assigned to *Pristigenys*, but both have otoliths associated with the skeletons. These otoliths perfectly match with those of Recent species of *Pseudopriacanthus*. This is also the case for the otoliths of the Priabonian *Ps. obliquus* from the Yazoo Clay of Louisiana, and these three priacanthids are here referred to *Pseudopriacanthus*. For the European *Ps. rutoti* and *Ps. hermani*, the attribution to the genus *Pseudopriacanthus* is also supported by osteological data (see Taverne & Nolf 2010).

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana. Priabonian: Yazoo Clay, Louisiana.

Family Malacanthidae Poey, 1861
Subfamily Latilinae Gill, 1862
Genus incertae sedis

“*Latilus*” *sulcatus* (Koken, 1888)
Fig. 29A–D

Otolithus (*Cottidarum*) *sulcatus* Koken, 1888: 287, pl. 18 fig. 12.

“genus Malacanthidarum” *sulcatus* – Nolf & Stringer 2003: 5, pl. 5 figs 3–8. — Nolf 2003: 6, pl. 1 fig. 14.
“*Malacanthida*” *sulcata* – Nolf 2013: 98, pl. 238.
Malacanthus? *sulcatus* – Ebersole *et al*. 2019: 208, fig. 71e–f.

Remarks

Otoliths of “*L*.” *sulcatus* have much in common with those of latilines, but the sulcus is not as deeply incised as that of their Recent relatives, and the excisura is much less incised. The configuration of the sulcus appears to be the most consistent and can be readily recognized. The dorsal rim of the otoliths shows much intra-specific variability.

Stratigraphic and geographic distribution

Bartonian: "upper" Lisbon Formation, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana.

Malacanthidae indet.
Fig. 29E

Remarks

Two specimens belong to the family Malacanthidae from the Weches Formation of Texas but lack sufficient diagnostic features; however, they have a shorter posterior part and slightly deeper otolith height and might be different from "*L*" *sulcatus*.

Stratigraphic and geographic distribution

Lutetian: Weches Formation, Texas.

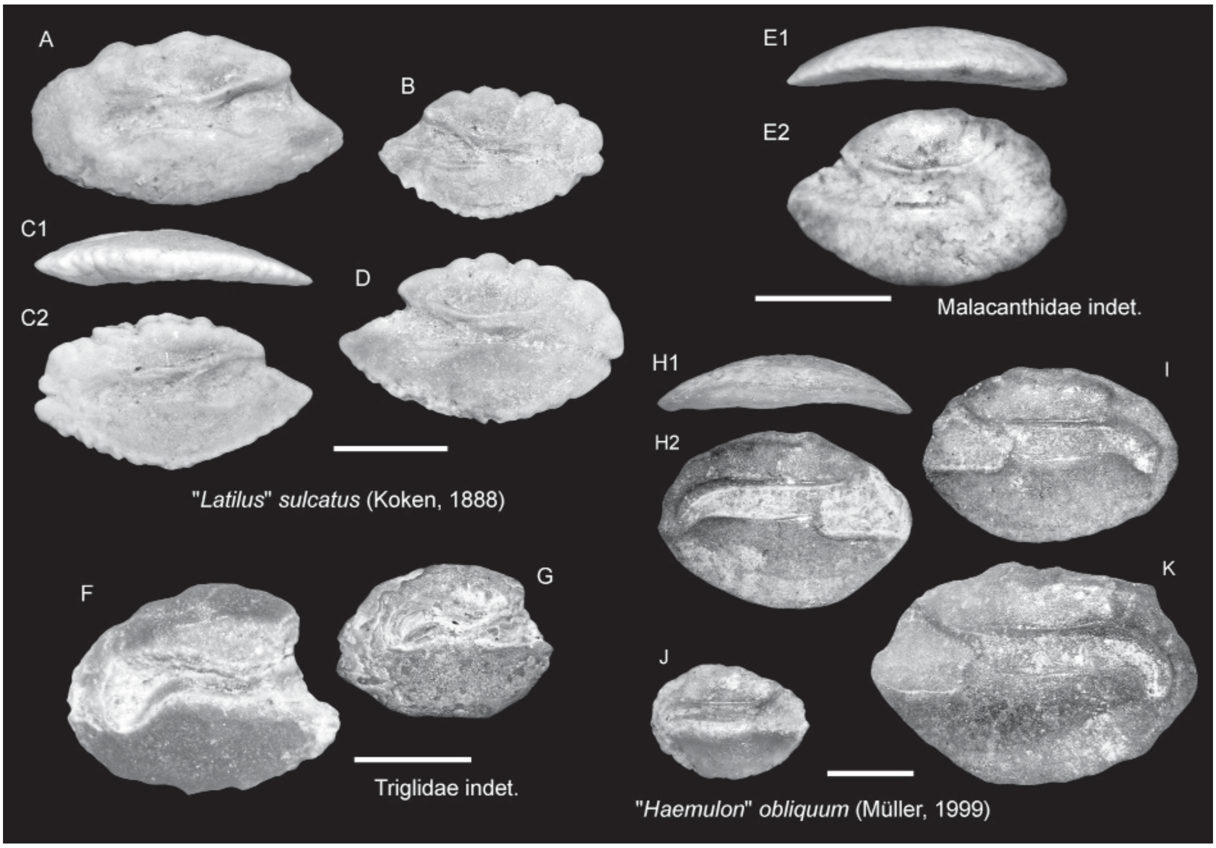


Fig. 29. Fish otoliths from the US middle and upper Eocene. **A–D**. "*Latilus*" *sulcatus* Koken, 1888. **A**. Moodys Branch F., Melvin (SE of town), Alabama (IRSNB P 10181). **B–D**. "Upper" Lisbon F., Barrytown, County Road 21, Alabama (IRSNB P 10182–10184). **E**. Malacanthidae indet., Weches F., Robbins, road side, Texas (IRSNB P 10185). **F–G**. Triglidae indet. **F**. Landrum M., Pin Oak Creek, Texas (IRSNB P 10186). **G**. "Stone City beds", Stone City Bluff, Brazos River, Texas (IRSNB P 10187). **H–K**. "*Haemulon*" *obliquum* (Müller, 1999), "Stone City beds", Stone City Bluff, Brazos River sample 2 from bed P, Texas (IRSNB P 10188–10191). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Family Haemulidae Gill, 1885
Genus *Anisotremus* Gill, 1861

Anisotremus rambo sp. nov.
urn:lsid:zoobank.org:act:AC553D36-02F2-4A77-9408-62895B70C194
Fig. 30

Anisotremus sp. – Nolf & Stringer 2003: 6, pl. 5 fig. 13. — Nolf 2013: 101, pl. 251.
Anisotremus? sp. – Ebersole *et al*. 2019: 211, fig. 71k–l.

Diagnosis

OL/OH = 1.04–1.35, OsL/CaL = 0.67–1.45. Massive otoliths with strongly convex inner face. Large and oblong ostium filled with colliculum. Elongate and narrow cauda of about 1/2 OL.

Etymology

Named after the famous movie 'Rambo', which alludes to the unrestrained, wild, but valiant appearance of the otoliths.

Material examined

Holotype

UNITED STATES OF AMERICA • Left otolith; Texas, Alabama Ferry; "Stone City beds"; Fig. 30A; IRSNB P 10192.

Paratypes

UNITED STATES OF AMERICA • 1 otolith: Fig. 30B; same collection data as for holotype; IRSNB P 10193 • 3 otoliths, of which one is figured: Fig. 30C; Texas, Rocky Branch; "Stone City beds"; IRSNB P 10094 • 1 otolith, Fig. 30D; Texas, Little Brazos River, confluence with Brazos River; Wheelock Member; IRSNB P 10095 • 6 otoliths, of which two are figured: Fig. 30E–F; Texas, Stone City Bluff; Brazos River, sample 2 from bed P; "Stone City beds"; IRSNB P 10196–10197.

Type locality and horizon

United States of America, Alabama Ferry (Texas), "Stone City beds".

Dimensions of the holotype

Length = 15.11 mm; height = 11.40 mm; thickness = 3.90 mm.

Description

The outline of the otoliths of this species changes ontogenetically; from circular in smaller specimens to more oblong and triangular in large individuals, which results from their deeper posterior part and longer rostrum. The postero-dorsal angle becomes prominent in large individuals, but the extension on the postero-ventral part of the otolith already exists in the small specimens. The margins can be considered smooth, but are more irregular at the dorsal rim. The otoliths are rather thin, with their inner face strongly convex and outer face strongly concave. The sulcus is well-developed. The ostium is about as long as the cauda in large specimens but it is shorter in smaller ones. The ostium opens on the anterior rim and is completely filled with a large colliculum. The junction of the ostial and caudal crista inferior is located slightly more caudally with respect to the same junction in the crista superior. In large specimens the cauda is straight for about two-thirds of its length and its posterior part is markedly curved in a ventral direction, but in smaller specimens the cauda widens at the end and is only slightly bent ventrally. The cristae are well-developed, but not ridge-like; the ostial crista superior curves markedly towards the dorsal rim in small specimens. The dorsal area is wide and about of the same height as the ventral one.

Remarks

Anisotremus rambo sp. nov. was first reported from the Yazoo Clay of Louisiana by Nolf & Stringer (2003), who then placed the species in the recent genus *Anisotremus* (see iconography of comparative Recent material therein). The large specimen from the Yazoo Clay further demonstrates the drastic ontogenetic change within the species. Small individuals are rounder in shape and have a shorter downward directed portion of the cauda, whereas larger ones become more elongate both in the ostium and the overall shape of the otolith, and have a longer and more strongly downward inclined portion of the cauda. The sulcus configuration, however, is more or less conservative and not changing ontogenetically. The transition can be observed from the medium-sized specimens (Fig. 30D, F). Ebersole *et al*. (2019) recently reported this species from the "upper" Lisbon Formation of Alabama, expanding its geographical distribution.

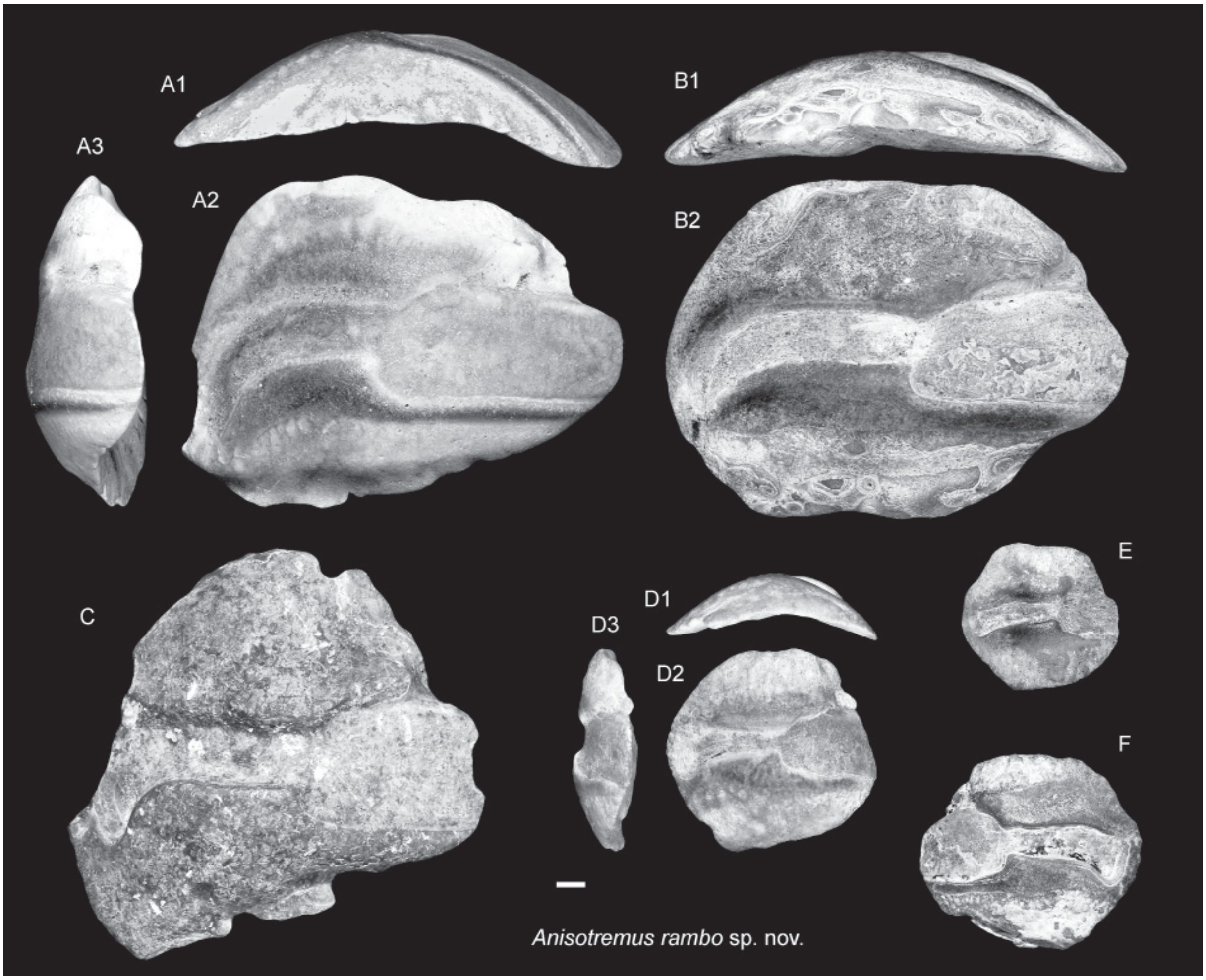


Fig. 30. Otoliths of *Anisotremus rambo* sp. nov. from the US middle and upper Eocene. **A–B**. "Stone City beds", Alabama Ferry, on Trinity River, North, Texas (IRSNB P 10192–10193). **C**. "Stone City beds", Rocky Branch, 1.5 miles SW of Stone City Bluff, sample 2, Texas (IRSNB P 10194). **D**. Wheelock M., Little Brazos River, confluence with Brazos River, Texas (IRSNB P 10195). **E–F**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10196–10197). **A**. Holotype (IRSNB P 10192). **B–F**. Paratypes (IRSNB P 10193–10197). 1 = ventral view; 2 = inner view; 3 = anterior view. Scale bars = 1 mm.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Wheelock Member, Texas; "upper" Lisbon Formation, Alabama. Priabonian: Yazoo Clay, Louisiana.

Genus *Orthopristis* Girard, 1858

Orthopristis americana (Koken, 1888)
Fig. 31A–D

Otolithus (*Carangidarum*) *americanus* Koken, 1888: 277, pl. 17 figs 1–3.

"genus *Pomadasyidarum*" *americanus* – Nolf 1985: 86.
Orthopristis americana – Nolf & Stringer 2003: 6, pl. 4 figs 17–21. — Nolf 2003: 6, pl. 3 figs 13–15; 2013: 101, pl. 252. — Stringer *et al*. 2022: 7, fig. 3i.

Remarks

Two closely related congeneric species, *O. americana* and *O. burlesonis* (Dante & Frizzell, 1965), exist in our collection. However, they are both morphologically and chronologically distinct: *O. americana* has more compact otoliths with a deeper ventral area, whereas the otoliths of the latter species are more elongate, which is due to their extended posterior part. The occurrence of *O. americana* is restricted to the younger Moodys Branch Formation and Yazoo Clay, and *O. burlesonis* is only found in the older Claiborne Group.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana.

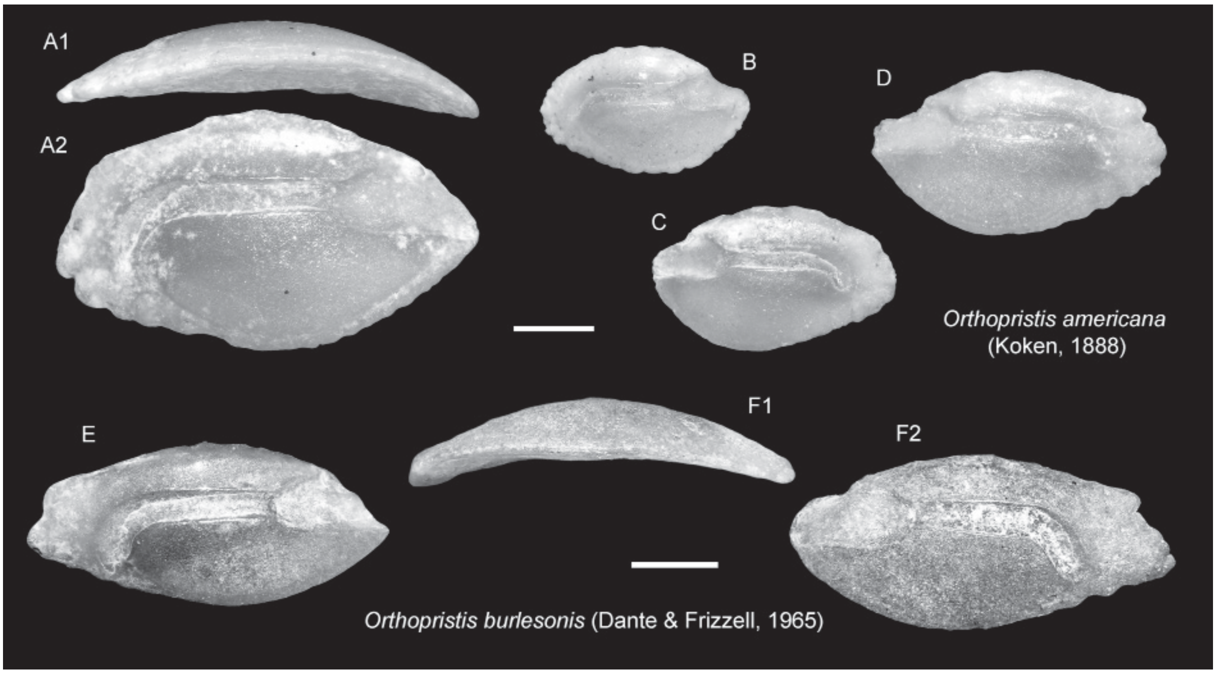


Fig. 31. Fish otoliths from the US middle and upper Eocene. **A–D**. *Orthopristis americana* (Koken, 1888), Moodys Branch F., Jackson, Riverside Park, Mississippi (IRSNB P 10198–10201). **E–F**. *Orthopristis burlesonis* (Dante & Frizzell, 1965), "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10202–10203). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Orthopristis burlesonis (Dante & Frizzell, 1965)
Fig. 31E–F

Allomorone burlesonis Dante & Frizzell in Frizzell & Dante, 1965: 703, pl. 87 figs 5, 10, 15.
"genus aff. *Isacia*" *elongatus* Müller, 1999: 142, fig. 31/6–11

"genus aff. *Parapristipoma*" aff. *kokeni* (Leriche, 1905) – Müller 1999: 143, fig. 31/4–5.
Orthopristis burlesonensis – Nolf 2013: 102, pl. 252.
Orthopristis burlesonis – Ebersole *et al*. 2019: 209, fig. 71g–h.

Remarks

See under *Orthopristis americana* for the distinction of both species of *Orthopristis* and their stratigraphical ranges.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation and Gosport Sand, Alabama.

Genus incertae sedis

"*Haemulon*" *obliquum* (Müller, 1999)
Fig. 29H–K

"genus aff. *Xenistius*" *obliquus* Müller, 1999: 145, fig. 30/24–25.

"genus Haemulidarum" *obliquus* – Nolf & Strnger 2003: 6, pl. 6 figs 1–2.
"*Haemulida*" *obliqua* – Nolf 2013: 102, pl. 254.
Haemulon? *obliquus* – Ebersole *et al*. 2019: 210, fig. 71i–j.

Remarks

Based on the sulcus, particularly the ostium, and on the outline shape, this species seems most closely related to two other Eocene European species, "*H*." *pulchrum* (Frost, 1934) and "*H*." *strascinate* Lin *et al*., 2017 (see Lin *et al*. 2017b: fig. 12), and they might well belong to an extinct genus. The otoliths of "*H*." *obliquum* and "*H*." *pulchrum* seem most similar; both have a thinner profile than "*H*." *strascinate*, and are more elongate, with a stronger postero-dorsal angle. But the dorsal rim of "*H*." *obliquum* is relatively flat, and the cauda is more markedly bent at its end than that of "*H*." *pulchrum*.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Piney Point Formation, Virginia. Bartonian: Wheelock Member, Texas; "upper" Lisbon Formation, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana.

Family Cepolidae Rafinesque, 1815

Subfamily Owstoniinae Jordan *et al*., 1913
Genus *Owstonia* Tanaka, 1908

Owstonia comes (Koken,1888)
Fig. 39H

Otolithus (*Cepolae*) *comes* Koken, 1888: 288, pl. 17 fig. 12.

Cepola comes – Nolf 1985: 91.
Owstonia comes – Nolf 2003: 10, pl. 3 fig. 10; 2013: 111, pl. 295.

Remarks

This species is only represented by a single specimen from the Moodys Branch Formation of Mississippi described by Koken (Nolf 2003). The otolith strongly resembles that of the Recent *Owstonia weberi* (Gilchrist, 1922) (see Nolf 2013: pl. 295) and can be attributed to that genus.

Stratigraphic and geographic distribution

Bartonian: Moodys Branch Formation, Mississippi.

Order Scorpaeniformes Garman, 1899
Suborder Platycephaloidei sensu Nelson 2006
Family Triglidae Rafinesque, 1815

Triglidae indet.
Fig. 29F–G

Remarks

Although these otoliths are not well preserved, they show the typical shape and sulcus pattern of triglid otoliths. Triglid otoliths are rare in the collection; only three specimens from Texas localities were found.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas. Bartonian: Landrum Member, Texas.

Order Acanthuriformes Jordan, 1923 sensu Nelson *et al*. 2016
Suborder Sciaenoidei sensu Betancur-R. *et al*. 2013

Family **Sciaenidae** Cuvier, 1829

Remarks

At least nine sciaenid species are represented in our material, *Ekokenia eporrecta* (Koken, 1888), *Eosciaena ebersolei* Stringer *et al.*, 2022, *Jefitchia copelandi* Dante & Frizzell, 1965, *Sciaena pseudoradians* (Dante & Frizzell, 1965), "*Sciaena*" *claybornensis* (Koken, 1888), "*S.*" *eanesi* (Müller, 1999), "*S.*" *intermedia* (Koken, 1888), "*S.*" *livesayi* (Müller, 1999), and one undescribed species (as Sciaenidae indet.). The relationships of these sciaenids are still obscure and a point of discussion (Schwarzhans 1993; Nolf 2013; Ebersole *et al*. 2019), which is mainly due to plesiomorphic conditions concerning the modern analogs. Using landmark analysis, the geometric morphometrics of these otoliths quantitatively showed at least two clear divisions (Lin, unpublished conference data, Supplementary file 1, not including the recently described *Eosciaena ebersolei*): one with shorter cauda and wider distance between the ostium and the bent part of the cauda, including *E. eporrecta*, "*S.*" *claybornensis*, "*S.*" *eanesi*, and the undescribed species. The other cluster of otoliths, with a relatively long cauda and wide ostium, includes *J. copelandi*, *S. pseudoradians*, "*S.*" *intermedia*, and "*S.*" *livesayi*. Although preliminarily and unresolved, these data indicated that more fossil genera and fossil species are involved and yet to be discovered or described.

Genus *Ekokenia* Dante & Frizzell, 1965

Ekokenia eporrecta (Koken, 1888)
Fig. 32A–G

Otolithus (*Sciaenidarum*) *eporrectus* Koken, 1888: 282, pl. 18 figs 16–17.

Ekokenia eporrecta – Frizzell & Dante 1965: 704, pl. 87 figs 11–12, 16, pl. 88 figs 5, 11.

"genus *Sciaenidarum*" *eporrectus* – Nolf 1985: 88; 2003: 9, pl. 3 figs 6–9. — Müller 1999: 160, fig. 33/10–15.
Eokokenia eporrecta – Schwarzhans 1993: 27, fig. 11.
"*Sciaenida*" *eporrecta* — Nolf 2013: 107, pl. 281.
Ekokenia eporrecta – Ebersole *et al*. 2019: 217, fig. 72e–f.

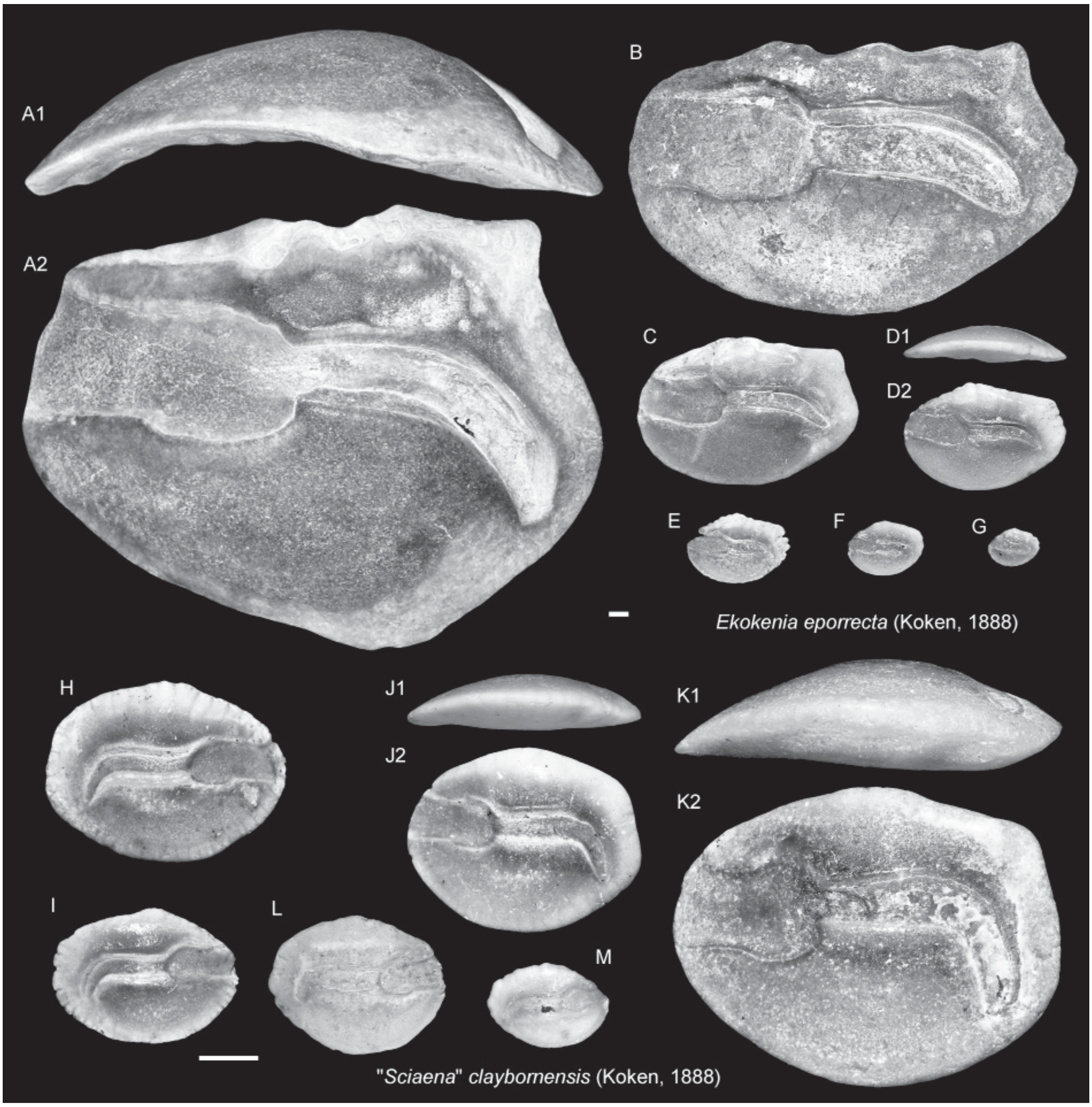


Fig. 32. Fish otoliths from the US middle and upper Eocene. **A–G**. *Ekokenia eporrecta* (Koken, 1888). **A–B**. Wheelock M., Little Brazos River, confluence with Brazos River, Texas (IRSNB P 10204–10205). **C–G**. "Stone City beds", Stone City Bluff, Brazos River, sample 2, bed P, Texas (IRSNB P 10206–10210). **H–M**. "*Sciaena*" *claybornensis* (Koken, 1888). **H–K**. Yazoo Clay, Copenhagen, Louisiana (IRSNB P 10211–10214). **L–M**. Moodys Branch F., Midway, Techeva Creek, Mississippi (IRSNB P 10215–10216). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Remarks

The sulcus type of *E. eporrecta* might imply a close relationship with the family Haemulidae; however, by having exclusive sciaenid features such as a strong postero-dorsal angle and constriction of the ostial cristae (particularly the ostial crista inferior), *E. eporrecta* can be confidently included in the Sciaenidae. The otoliths of *E. eporrecta* are the most abundant sciaenid species in the collection, and with the clear growth series of the species, it can easily be separated from those of other sciaenids by its short cauda and relatively flat inner face. A single, exceptionally large specimen (Fig. 32A) reveals a strong ontogenetic shift towards a much deeper ventral area and strongly convex inner face.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; "lower" Lisbon Formation, Alabama; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation, Alabama.

Genus *Eosciaena* Stringer *et al*., 2022

Eosciaena ebersolei Stringer *et al*., 2022
Fig. 39S

Eosciaena ebersolei sp. nov. Stringer *et al*., 2022: 8, figs 3l–n, 4a.

"genus aff. *Nibea*" sp. – Nolf & Stringer 2003: 6, pl. 6 fig. 12.

Remarks

A single somewhat eroded sciaenid otolith from the Yazoo Clay that doesn't match those of any living or fossil American sciaenid genus was tentatively compared to the extant genus *Nibea* on the basis of its general outline and pattern of its ostium by Nolf & Stringer (2003). When the present manuscript had already been submitted, this species was described by Stringer *et al*. (2022) based on new material from the Clinchfield Formation (Bartonian), Georgia.

Stratigraphic and geographic distribution

Bartonian: Clinchfield Formation, Georgia. Priabonian: Yazoo Clay, Louisiana.

Genus *Jefitchia* Dante & Frizzell, 1965

Jefitchia copelandi Dante & Frizzell, 1965
Fig. 33A–F

Jefitchia copelandi Dante & Frizzell in Frizzell & Dante, 1965: 705, pl. 87 figs 3–4, 9, pl 88 figs 1–2, 6.

Jefitchia copelandi – Schwarzhans 1993: 26, fig. 10. — Ebersole *et al*. 2019: 215, fig. 71q–r.
"*Sciaenida*" *copelandi* – Nolf 2013: 107, pl. 281.

Remarks

The otoliths of this species are characterized by a narrow and straight ostium and a very long cauda that bends strongly downwards, with its end recurved in the anterior direction. There is a rather narrow distance between the ostium and the bent part of the cauda; this distance is only about half as long as the ventrally oriented caudal end. The growth series clearly illustrates that these features already exist at the juvenile stage. During growth, the inner face swells and becomes markedly convex, bulging like a hill at a later stage of the ontogeny.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi; "lower" Lisbon Formation, Alabama. Bartonian: Cook Mountain Formation, Texas; "upper" Lisbon Formation and Gosport Sand, Alabama.

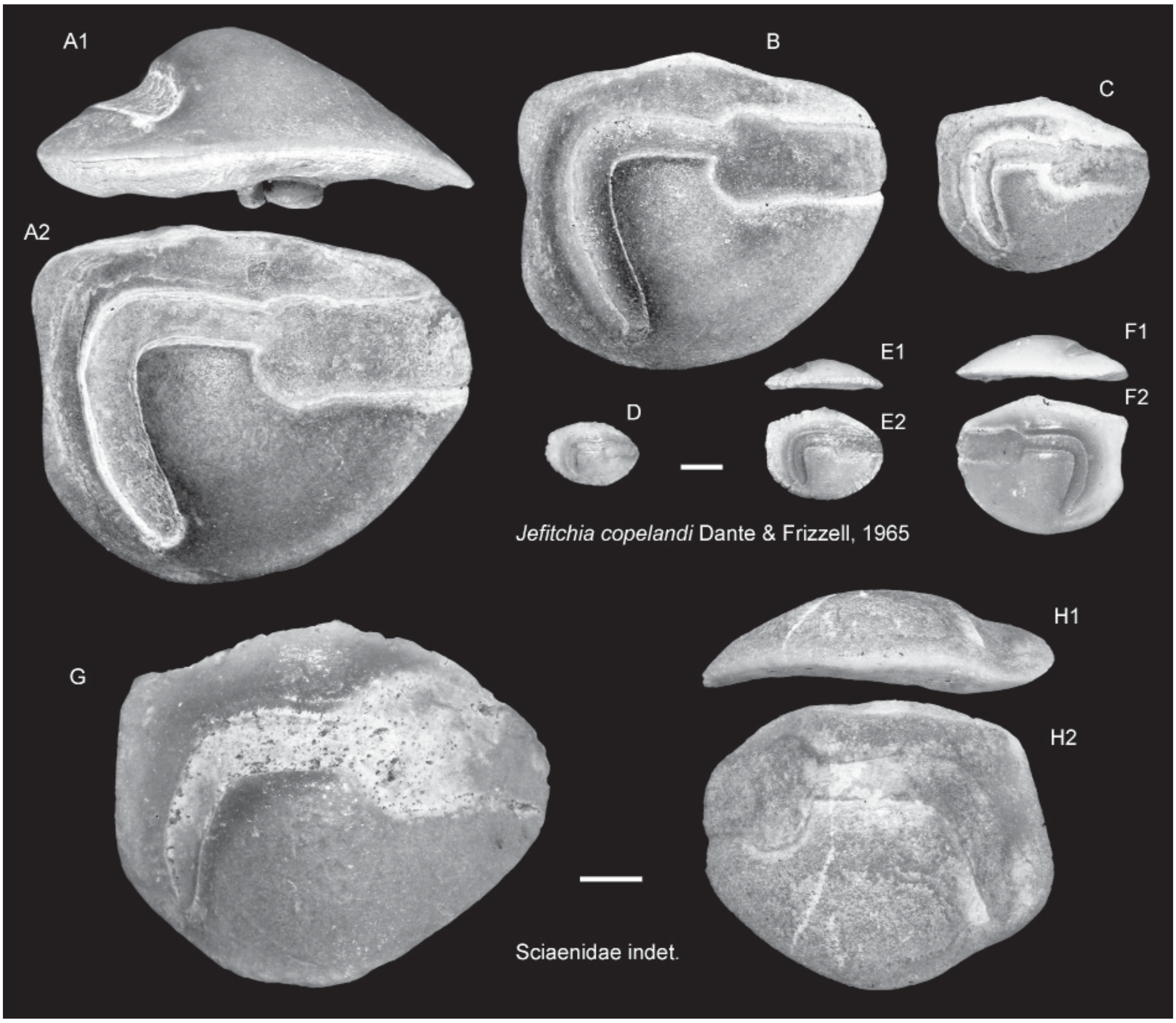


Fig. 33. Fish otoliths from the US middle and upper Eocene. **A–F**. *Jefitchia copelandi* Dante & Frizzell, 1965. **A–B**. Wheelock M., Little Brazos River, confluence with Brazos River, Texas (IRSNB P 10217–10218). **C–F**. "Stone City beds", Stone City Bluff, Brazos River, sample 6 from bed U, Texas (IRSNB P 10219–10222). **G–H**. Sciaenidae indet. **G**. Gosport Sand, Claiborne Bluff, Alabama (IRSNB P 10223). **H**. Potterchitto M., Newton, NE exit off Interstate 20, Mississippi (IRSNB P 10224). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Genus *Sciaena* Linnaeus, 1758

Sciaena pseudoradians (Dante & Frizzell, 1965)
Fig. 34A–E

Corvina pseudoradians Dante & Frizzell in Frizzell & Dante, 1965: 707, pl. 87 figs 31, 35, pl. 88 figs 26, 28.

?*Umbrina pseudoradians* – Schwarzhans 1993: 79, fig. 128.
Sciaena aff. *pseudoradians* – Nolf & Stringer 2003: 6, pl. 6 figs 3–5.
Sciaena pseudoradians – Nolf 2003: 8, pl. 2 figs 3–6; 2013: 106, pl. 277.
Sciaena aff. *S. pseudoradians* – Stringer *et al*. 2022: 9, fig. 4f–k.

Remarks

Otoliths of *S. pseudoradians* have a very wide ostium, which is the widest among the here treated sciaenid species. They are also characterized by a rather short caudal end that does not extend lower than the margin of the ostial crista inferior. These features allow an allocation of the species to the Recent genus *Sciaena*. *Sciaena pseudoradians* is essentially collected from lower Oligocene sites, but some imperfectly preserved otoliths are also known from the Priabonian Yazoo Clay (see Nolf 2003: 8). Our specimens from the Cook Mountain Formation of Texas extend further back their existing age.

Stratigraphic and geographic distribution

Bartonian: Wheelock Member, Texas; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana and Mississippi.

Genus incertae sedis

"*Sciaena*" *claybornensis* (Koken, 1888)
Fig. 32H–M

Otolithus (*Sciaenidarum*) *Claybornensis* Koken, 1888: 283, pl. 19 figs 1, 4.

Jefitchia claybornensis – Frizzell & Dante 1965: 705. — Schwarzhans 1993: 26, figs 5–9. — Ebersole *et al*. 2019: 216, fig. 72a–b, non 72c–d. — Stringer *et al*. 2022: 7, fig. 3j, non 3k
"genus *Sciaenidarum*" *claybornensis* – Nolf 1985: 88; 2003: 8, pl. 3 figs 1–5. — Nolf & Stringer 2003: 6, pl. 7 figs 1–5.
"*Sciaenida*" *claybornensis* – Nolf 2013: 107, pl. 281.

Remarks

Based on the sulcus configuration, particularly the caudal part, "*S*." *claybornensis* and "*S*." *eanesi*, a much rarer species, might be more closely related. Their otoliths are characterized by a narrow ostium and a cauda which is straight in its anterior part. The end of the cauda is bent in a postero-ventral direction, but never curving forward. Admittedly, the differences between the otoliths of the two species are subtle, and Ebersole *et al*. (2019: 217) considered them to be synonyms. However, after examining more specimens in the collection, we recognized that they can still be separated by their outline shape and convexity of the inner face. The otoliths are more rounded and flatter in "*S*." *claybornensis*, while in "*S*." *eanesi*, two pronounced dorsal angles always exist in the middle and posterior part of the dorsal rim, and the latter angle further makes their posterior rim sharp in appearance. The otoliths of "*S*." *eanesi* also have a more convex inner face, which is most evident in their anterior portion. Moreover, otoliths of "*S*." *claybornensis* show an ontogenetic variation in the length of the cauda (Nolf 2003: pl. 3 figs 1–5), which is not seen in "*S.*" *eanesi* (Fig. 34F–J). It is also worth mentioning that Frizzell & Dante (1965) included "*S.*" *claybornensis* in their fossil genus *Jefitchia*, together with the type species *J. copelandi* (see above), and this was followed as such by Schwarzhans (1993) and Ebersole *et al*. (2019). However, based on

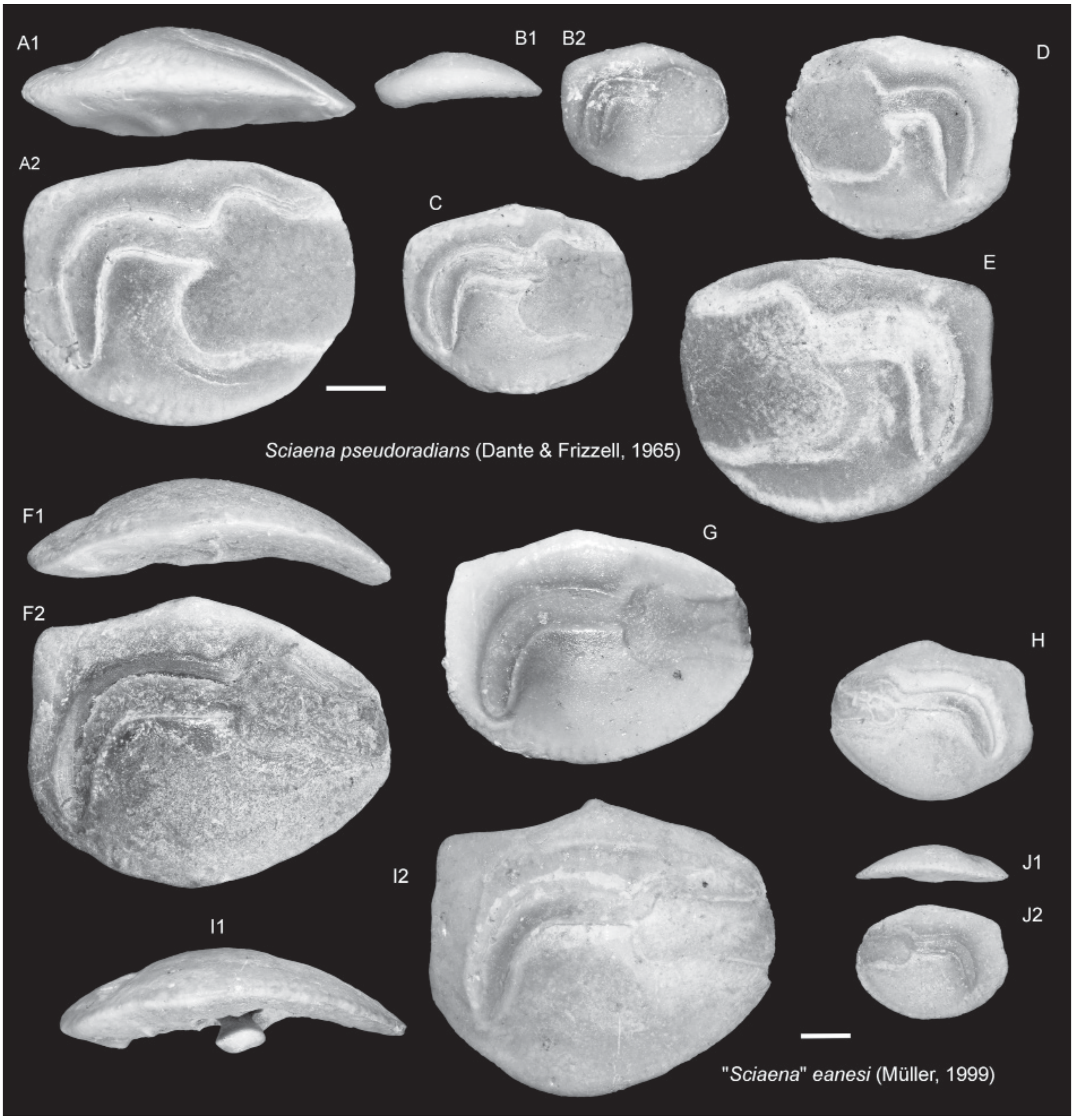


Fig. 34. Fish otoliths from the US middle and upper Eocene. **A–E**. *Sciaena pseudoradians* (Dante & Frizzell, 1965). **A–C**. Yazoo Clay, Copenhagen, Louisiana (IRSNB P 10225–10227). **D**. Yazoo Clay, Shubuta Clay M., Cynthia, Mississippi Lite clay pit, Mississippi (IRSNB P 10228). **E**. Moodys Branch F., Jackson, boring at the corner of Amite & Mill Streets, Mississippi (IRSNB P 10229). **F–J**. "*Sciaena*" *eanesi* (Müller, 1999). **F**. Gosport Sand, Little Stave Creek, Alabama (IRSNB P 10230). **G**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10231). **H–J**. Piney Point F., Pamunkey River, Devil's Hole, Virginia (loc. 19 of Müller), paratypes (IRSNB P 10232–10234). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

the diagnosis of the genus and the marked differences between *J. copelandi* and "*S.*" *claybornensis*, we conclude that "*S.*" *claybornensis* belongs to an unknown clade and *Jefitchia* is currently monospecific.

Stratigraphic and geographic distribution

Bartonian: Landrum Member, Texas; Cook Mountain Formation, Mississippi; "upper" Lisbon and Gosport Sand, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana and Mississippi.

"Sciaena" eanesi (Müller, 1999)
Fig. 34F–J

"genus aff. *Umbrina*" *eanesi* Müller, 1999: 162, fig. 33/16–21.

"*Sciaenida*" *eanesi* – Nolf 2013: 107, pl. 281.
Jefitchia claybornensis – Ebersole *et al*. 2019: 216, fig. 72c–d, non 72a–b. — Stringer *et al*. 2022: 7, fig. 3k, non 3j.

Remarks

See under "*Sciaena*" *claybornensis* for the distinction between the two species.

Stratigraphic and geographic distribution

Lutetian*:* Weches Formation and "Stone City beds", Texas; Piney Point Formation, Virginia. Bartonian: Wheelock Member, Texas; Cook Mountain Formation, Mississippi; "upper" Lisbon Formation and Gosport Sand, Alabama.

"Sciaena" intermedia Koken, 1888
Fig. 35A–I

Otolithus (*Sciaenidarum*) *intermedius* Koken, 1888: 283, pl. 19 figs 2–3.

"genus Sciaenidarum" *intermedius* – Nolf 2003: 9, pl. 2 figs 12–14.
"*Sciaenida*" *intermedia* – Nolf 2013: 107, pl. 282.
Sciaena intermedius – Ebersole *et al*. 2019: 213, fig. 71o–p.

Remarks

The otoliths of "*S.*" *intermedia* and "*S.*" *livesayi* both have a long cauda that strongly bends at about one-third of its length, a similar ostial length and a similar inner face convexity. However, "*S.*" *livesayi* can be distinguished from "*S.*" *intermedia* by having a more antero-posteriorly compressed shape, mostly with a caudal tip directed more anteriorly, and by the much wider ostium, whose ventral part is not constricted on the crista inferior. Ebersole *et al*. (2019) hypothesized a close relationship between "*S.*" *intermedia* and *S. pseudoradians*, and even with *Jefitchia*. It seems to us that otoliths of "*S.*" *intermedia* indeed resemble those of *S. pseudoradians* (Supplementary file 1), but *Jefitchia* (*J. copelandi*) is very distinct and likely represent a different clade.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas; Dobys Bluff Tongue of Kosciusko Formation, Mississippi. Bartonian: Cook Mountain Formation, Texas; "upper" Lisbon Formation and Gosport Sand, Alabama.

"Sciaena" livesayi (Müller, 1999)
Fig. 35J–O

"genus aff. *Umbrina*" *livesayi* Müller, 1999: 163, figs 33/23–30, 34/1–2.

"*Sciaenida*" *livesayi* – Nolf 2013: 107, pl. 283.
Sciaena intermedia – Stringer *et al*. 2022: 9, fig. 4b–e.

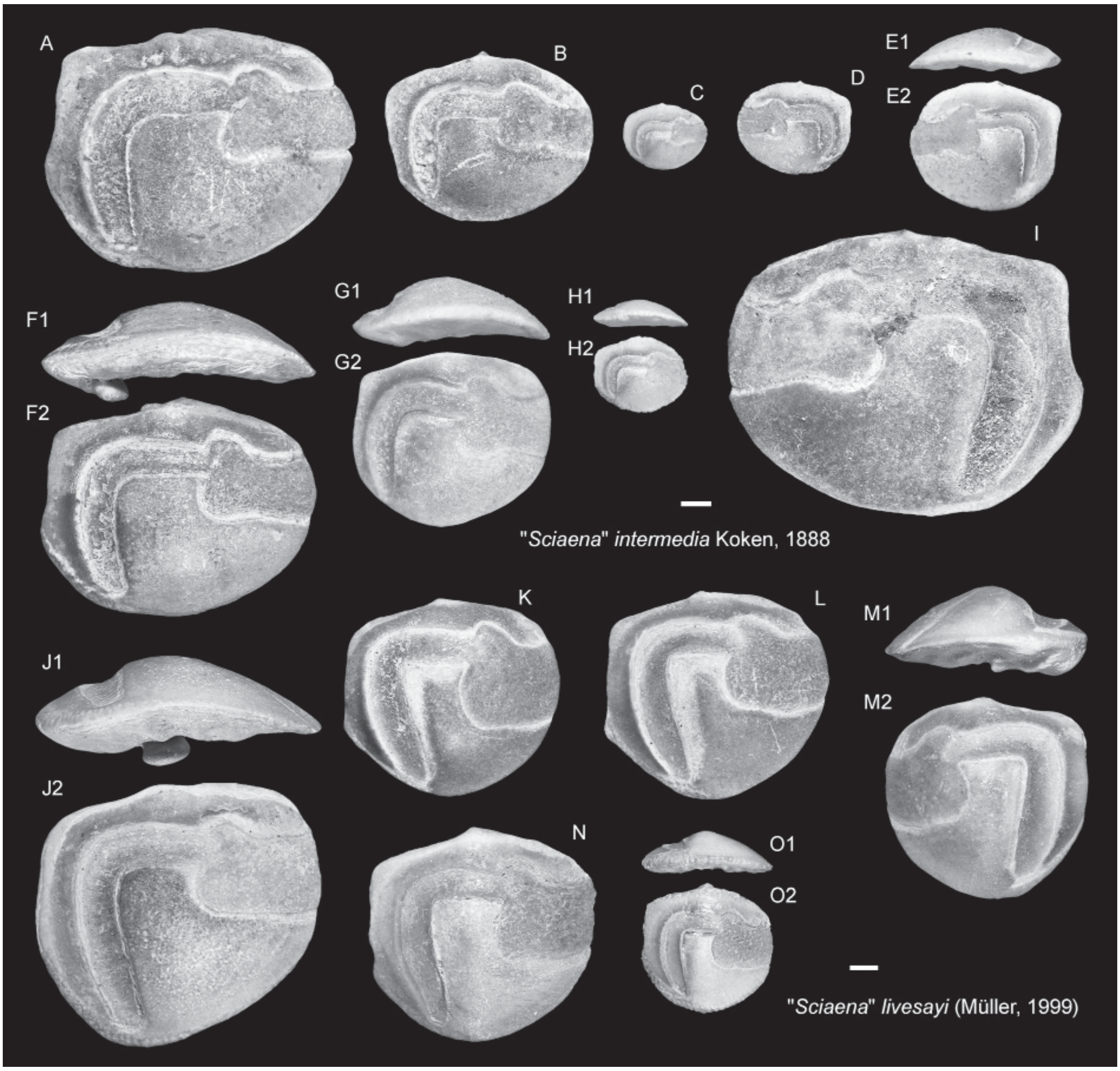


Fig. 35. Fish otoliths from the US middle and upper Eocene. **A–I**. "*Sciaena*" *intermedia* Koken, 1888. **A–F**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10235–10240). **G–H**. "Upper" Lisbon F., Barrytown, County Road 21, Alabama (IRSNB P 10241–10242). **I**. "Stone City beds", Alabama Ferry, on Trinity River, North, Texas (IRSNB P 10243). **J–O**. "*Sciaena*" *livesayi* (Müller, 1999). **J–M**. Wheelock M., Little Brazos River, confluence with Brazos River, Texas (IRSNB P 10244–10247). **N–O**. Piney Point F., sand and gravel pit, Bottoms Bridge, loc. 22 of Müller, Virginia, paratypes (IRSNB P 10248–10249). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Remarks

See remarks under "*Sciaena*" *intermedia*.

Stratigraphic and geographic distribution

Lutetian: "Stone City beds", Texas; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation, Alabama.

Sciaenidae indet.
Fig. 33G–H

Remarks

Two specimens are characterized by a long cauda, whose ventrally bent portion does not exceed 90 degrees, a rather short ostium, and a pointed rostrum. They apparently represent an undescribed species. However, their preservation does not allow a precise characterization.

Stratigraphic and geographic distribution

Bartonian: Cook Mountain Formation, Mississippi; Gosport Sand, Alabama.

Order Spariformes Bleeker, 1876
Family Sparidae Rafinesque, 1818
Genus *Pagellus* Valenciennes, 1830

Pagellus pamunkeyensis sp. nov.
urn:lsid:zoobank.org:act:34C1E623-0612-40A2-9A21-C7A4FAE642B6
Fig. 36C–F

Diagnosis

OL/OH = 1.67–1.74, OsL/CaL = 0.67–0.82. Otoliths oblong, with tapering posterior margin. Inner face strongly convex. Ostium oval, with colliculum. Cauda straight for anterior two-thirds and markedly curved ventrally at posterior.

Etymology

This species is named after its type area, the Pamunkey River, Virginia.

Material examined

Holotype

UNITED STATES OF AMERICA • Right otolith; Virginia, Pamunkey River, 1 km E of Eanes property, Bed A, sample 1, see also Strickland (1985), loc. 37; Piney Point Formation; Fig. 36F; IRSNB P 10255.

Paratypes

UNITED STATES OF AMERICA • 6 otoliths of which three are figured: Fig. 36C–E; same collection data as for holotype; IRSNB P 10252–10254.

Type locality and horizon

United States of America, Pamunkey River, 1 km E of Eanes property (Virginia), Bed A, sample 1 (Fig. 7), see also Strickland (1985), loc. 37, Piney Point Formation.

Dimensions of the holotype

Length = 6.00 mm; height = 3.47 mm; thickness = 1.11 mm.

Description

The otoliths are oblong in shape. The dorsal rim is raised in the centre of the otolith, and the ventral rim is also deeper in the middle or slightly anteriorly. There is a postero-dorsal angle on the dorsal rim, forming an oblique posterior rim after the angle. A much stronger and very pointed angle characterizes the transition of the posterior rim to the ventral one. The ventral rim is smoothly curved. The margins are smooth, but somewhat more irregular on the dorsal rim of the holotype. The otoliths are thin; their inner face is strongly convex and the outer face well concave. The sulcus is clearly divided, well-delineated and deeply incised. The ostium is clearly shorter and wider than the cauda, but unfortunately, none of the available specimens have a complete anterior margin. The ostium is oval, opens widely, and is completely filled by a large colliculum. The cauda is straight for about two-thirds of its length, and its

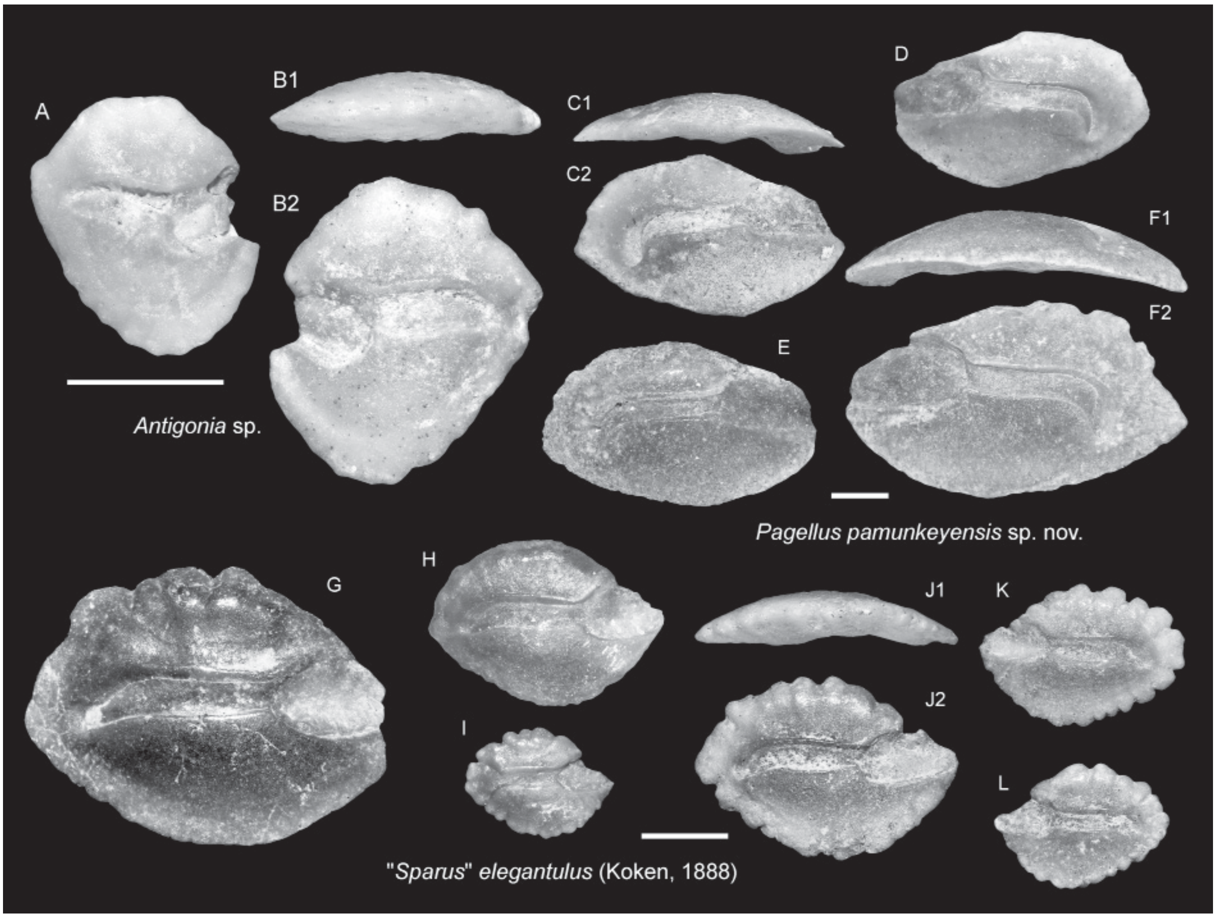


Fig. 36. Fish otoliths from the US middle and upper Eocene. **A–B**. *Antigonia* sp., Piney Point F., Pamunkey River, Virginia. **A**. SW of Pampatike Landing (IRSNB P 10250). **B**. Devil's Hole (IRSNB P 10251). **C–F**. *Pagellus pamunkeyensis* sp. nov., Piney Point F., Pamunkey River, 1 km E of Eanes property, Virginia. **C–E**. Paratypes (IRSNB P 10252–10254). **F**. Holotype (IRSNB P 10255). **G–L**. "*Sparus*" *elegantulus* (Koken, 1888). **G**. Landrum M., Pin Oak Creek, Texas (IRSNB P 10256). **H–I**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 10257–10258). **J–L**. "Stone City beds", Stone City Bluff, Brazos River, sample 2 from bed P, Texas (IRSNB P 10259–10261). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

posterior part is markedly curved in a ventral direction. The cristae are well-developed, and those along the straight part of the cauda are ridge-like. The dorsal area is wide and shows a depression just above the caudal crista superior. In the ventral area, a ventral furrow is present vey near to the ventral rim, but this can only be observed in the holotype, which is the largest and best-preserved specimen.

Remarks

Because of their general shape, their prominent posterodorsal angle and their salient postero-ventral angle, these otoliths seems to match very well with those of the sparid genus *Pagellus*; see Nolf (2018: pl. 56), where an ontogenetic series of the Recent *Pagellus bogaraveo* (Brünnich, 1768) is figured. Also, the ontogenetic series of the Recent taxon, with a more anteriorly located pronounced rounding in the ventral rim of small specimens, matches very well with the ontogenetic changes seen in the fossils.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Genus *Pagrus* Cuvier, 1816

Pagrus esseri (Müller, 1999)
Fig. 39G

Dentex esseri Müller, 1999: 155, fig. 33/1–4.

Pagrus esseri – Nolf 2013: 103, pl. 263.

Remarks

These otoliths seem to show most affinities with those of the genus *Pagrus* and can be attributed to that genus (see Nolf 2018: pl. 57 for iconography of the Recent *Pagrus pagrus* (Linnaeus, 1758)).

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

Genus incertae sedis

"*Sparus*" *elegantulus* (Koken, 1888)
Fig. 36G–L

Otolithus (*Pagelli*) *elegantulus* Koken, 1888: 279, pl. 17 figs 5–6.

"genus *Sparidarum*" *elegantulus* – Nolf 1985: 88; 2003: 6, pl. 2 figs 1–2. — Nolf & Stringer 2003: pl. 6 figs 6–11.
"*Sparida*" *elegantula* – Nolf 2013: 103, pl. 264.

Remarks

Otoliths of "*S.*" *elegantulus* show typical sparid affinities, but allocation to any Recent genus was not satisfactory. Therefore, we here follow Nolf's (1985, 2013) interpretation, considering the taxon as an incertae sedis at the generic level. The dorsal rim of the otoliths of "*S.*" *elegantulus* appears to have the highest variability. See also remarks under *Centropristis priaboniana* for comparative purposes.

Stratigraphic and geographic distribution

Lutetian: Weches Formation and "Stone City beds", Texas; Piney Point Formation, Virginia. Bartonian: Cook Mountain Formation, Texas and Mississippi; "upper" Lisbon Formation, Alabama; Moodys Branch Formation, Louisiana, Mississippi and Alabama. Priabonian: Yazoo Clay, Louisiana.

Order Caproiformes sensu Nelson *et al*. 2016
Family Caproidae Bonaparte, 1835
Subfamily Antigoniinae Jordan & Evermann, 1898
Genus *Antigonia* Lowe, 1843

Antigonia sp.
Fig. 36A–B

Remarks

No well-preserved specimens of this species were found, but affinities of these very high bodied otoliths to the recent genus *Antigonia* are nevertheless clear. Fossil *Antigonia* otoliths are also known from the European Eocene of Belgium, southern England, Paris Basin, and Aquitaine.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia. Bartonian: "upper" Lisbon Formation, Alabama.

Order Lophiiformes Garman, 1899
Suborder Antennarioidei Pietsch, 1981
Family Anrennariidae Jarocki, 1822

Antennariidae indet.
Fig. 37E

Remarks

A single otolith from the Piney Point Formation, Virginia, has the typical sulcus pattern of antennariids. A more precise taxonomic evaluation is not possible just on the basis of that specimen.

Stratigraphic and geographic distribution

Lutetian: Piney Point Formation, Virginia.

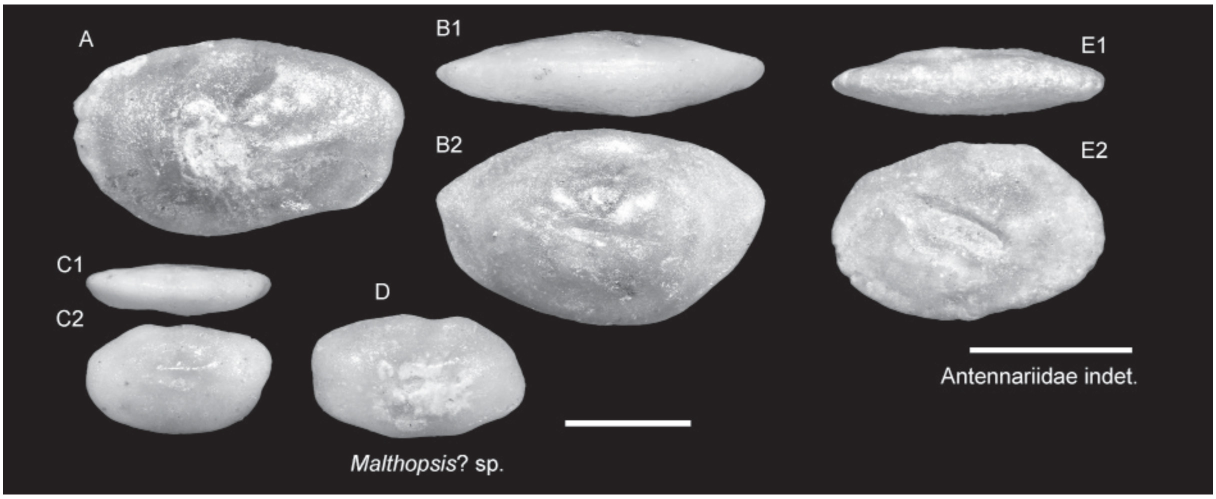


Fig. 37. Fish otoliths from the US middle and upper Eocene. **A–D**. *Malthopsis*? sp. **A**. Landrum M., Pin Oak Creek, Texas (IRSNB P 10262). **B**. Wheelock M., Little Brazos River, Stenzel loc., Texas (IRSNB P 10263). **C–D**. Moodys Branch F., Jackson, Town Creek, Mississippi (IRSNB P 10264–10265). **E**. Antennariidae indet., Piney Point F., Pamunkey River, Devil's Hole, Virginia (IRSNB P 10266). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.

Suborder Ogcocephaloidei Greenwood *et al.*, 1966
Family Ogcocephalidae Gill, 1893
Genus *Malthopsis* Alcock, 1891

***Malthopsis*?** sp.
Fig. 37A–D

Remarks

Six small otoliths were tentatively identified as *Malthopsis*. The otoliths are sub-rectangular, with their dorsal and ventral rims longer than the anterior and posterior ones. The sulcus is very restricted, located in the middle of the otolith, and there is no opening to the margins of the otolith. It is only featured by a limited depression, with the cristae not well-delineated, and it is not separated into ostium and cauda. These otoliths agree very well with those of Recent *Malthopsis*, for example, to those of *M. annulifera* and *M. gigas* (see Lin & Chang 2012: pl. 82), but lacking sufficient material, we prefer to keep these specimens in open nomenclature. Their occurrence, however, is extremely scarce, but may represent one of the oldest fossil records of the family.

Stratigraphic and geographic distribution

Bartonian: Cook Mountain Formation, Texas; Moodys Branch Formation, Mississippi.

Rejected and doubtful species

brandonis Frizzell & Lamber, 1961 (*Weileria*) = doubtful species (eroded holotype).

brazosia Frizzell & Lamber, 1961 (*Stintonia*) = doubtful species (eroded holotype).

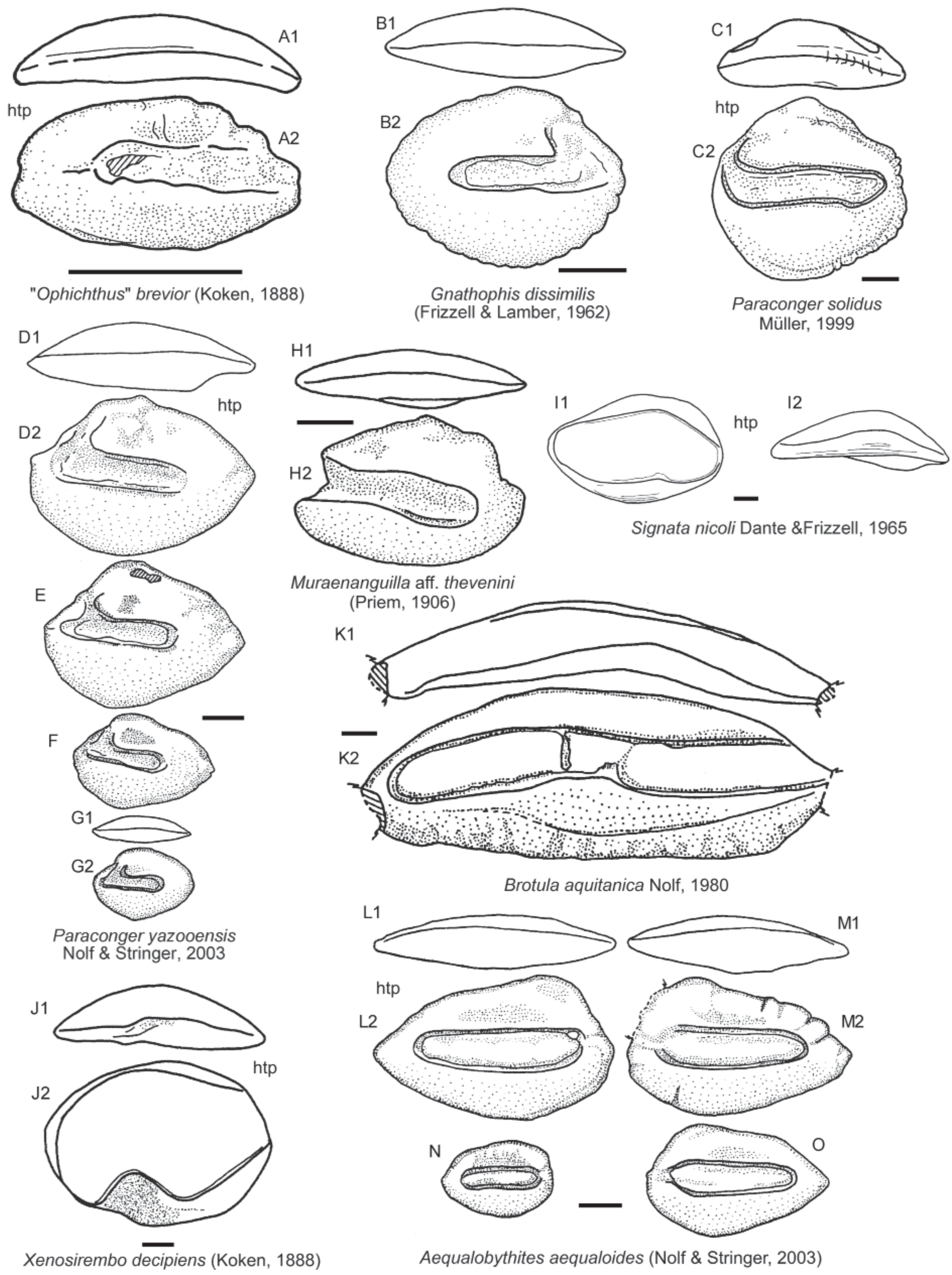
claibornensis Dante & Frizzell in Frizzell & Dante, 1965 (*Eosolea*) = rejected species (eroded holotype, non-diagnostic at species level).

creola Frizzell & Lamber, 1961 (*Stintonia*) = doubtful species; cannot be evaluated on the basis of the iconography (holotype not figured; only an eroded paratype).

gottfriedei Müller, 1999 ("genus aff. *Otophidium*") = doubtful species (based on non-diagnostic juvenile otoliths).

hospes Koken, 1888 (Apogonidarum) = doubtful species (based on an eroded *Centroberyx* otolith, non-diagnostic at species level).

Fig. 38 (opposite page). Fish otoliths from the US middle and upper Eocene. **A**. "*Ophichthus*" *brevior* (Koken, 1888), holotype (ZMB Ot. 26), "Jackson Beds", Mississippi (?). **B**. *Gnathophis dissimilis* (Frizzell & Lamber, 1962), Moodys Branch F., Town Creek, Jackson, Mississippi (IRSNB P 9038). **C**. *Paraconger solidus* Müller, 1999, holotype (coll. Institut für Geowissenschaften, University of Leipzig, Nr. 10/P67), Piney Point F., loc. 24 (Horseshoe) of Müller, 1999, Virginia. **D–G**. *Paraconger yazooensis* Nolf & Stringer, 2003, Yazoo Clay, Tullos M., Copenhagen, Louisiana. **D**. Holotype (IRSNB P 6962). **E–G**. Paratypes (IRSNB P 6963–6965). **H**. *Muraenanguilla* aff. *thevenini* (Priem, 1906), Yazoo Clay, Copenhagen, Louisiana (IRSNB P 6966). **I**. *Signata nicoli* Dante & Frizzell, 1965, Weches F., Pleasanto, Atascosa County, Texas, holotype (USNM 23370). **J**. *Xenosirembo decipiens* (Koken, 1888), lectotype (ZMB Ot. 135), middle Eocene, "Clayborne Group", southern USA. **K**. *Brotula aquitanica* Nolf, 1980, Yazoo Clay, Tullos M., Copenhagen, Louisiana (IRSNB P 7419). **L–O**. *Aequalobythites aequaloides* (Nolf & Stringer, 2003), Yazoo Clay, Copenhagen, Louisiana. **L**. Holotype (IRSNB P 6977). **M–O**. Paratypes (IRSNB P 6978–6980). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.


A1
htp
A2
"Ophichthus" brevior (Koken, 1888)
B1
B2
Gnathophis dissimilis
(Frizzell & Lamber, 1962)
C1
htp
C2
Paraconger solidus
Müller, 1999
D1
htp
D2
H1
H2
I1
htp
I2
Signata nicoli Dante &Frizzell, 1965
E
Muraenanguilla aff. thevenini
(Priem, 1906)
K1
K2
F
G1
G2
Brotula aquitanica Nolf, 1980
Paraconger yazooensis
Nolf & Stringer, 2003
L1
M1
htp
L2
M2
J1
htp
J2
N
O
Xenosirembo decipiens (Koken, 1888)
Aequalobythites aequaloides (Nolf & Stringer, 2003)

insuetus Koken, 1888 (Sparidarum) = rejected species (eroded holotype).

longirostris Müller, 1999 (“*genus Clupeidarum*”) = cannot be evaluated on the basis of the iconography, but apparently based on very small, imperfectly preserved specimens.

louisiana Frizzell & Lamber, 1961 (*Weileria*) = doubtful species (eroded holotype).

minutus Müller, 1999 (“*Bembrops*”) = doubtful species (based on non-diagnostic juvenile otoliths, may be of “*Trachinus*” *laevigatus*).

moseleyi Dante & Frizzell in Frizzell & Dante, 1965 (*Brazosiella*) = cannot be evaluated on the basis of the iconography.

similis Koken, 1888 (Sciaenidarum) = doubtful species (based on non-diagnostic juvenile syntypes).

texana Dante & Frizzell in Frizzell & Dante, 1965 (*Eosolea*) = rejected species (eroded holotype, non-diagnostic at species level). Note that this species was erroneously cited as valid under the name “*Heterenchelyida*” *texana* in Nolf (2013: 205), but was not included in the list of otolith-based fossil heterenchelyds on p. 33 of the same paper.

townsendi Müller, 1999 (“*Platycephalus*”) = doubtful species (based on non-diagnostic juvenile otoliths).

troelli Dante & Frizzell in Frizzell & Dante, 1965 (*Claybornichthys*) = cannot be evaluated on the basis of the iconography.

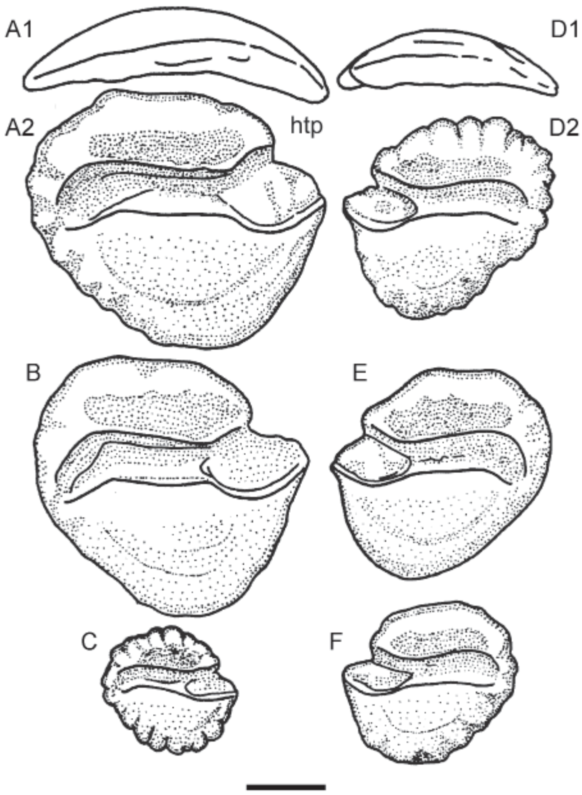
walleri Müller, 1999 (“*Serranus*”) = doubtful species (based on non-diagnostic juvenile perciform otoliths).

Abundance and composition of the assemblages

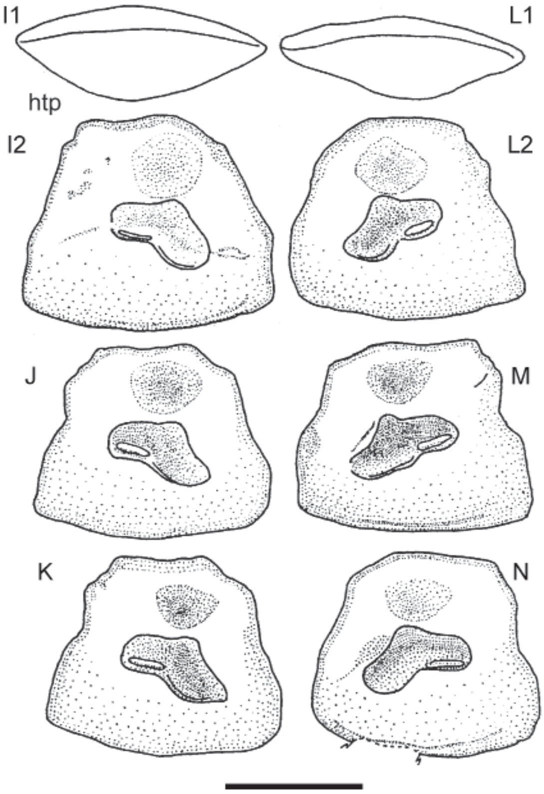
Bulk samples and isolated surface collected otoliths combined produced more than 25 000 specimens for this study. The otoliths are generally well-preserved; they are assigned to 101 taxa distributed over 43 extant families. Furthermore, 14 species were described as new (Table 1).

Both taxonomic richness and abundance are high in the Texas strata (Table 1). Aside from the Louisiana collection previously described by Nolf & Stringer (2003, see also Locality data), samples from the “Stone City beds” are amongst the best represented in the collection (45 taxa and 10429 otoliths). Other rich horizons include the “upper” Lisbon Formation, Alabama (42 taxa and 1613 otoliths) and the

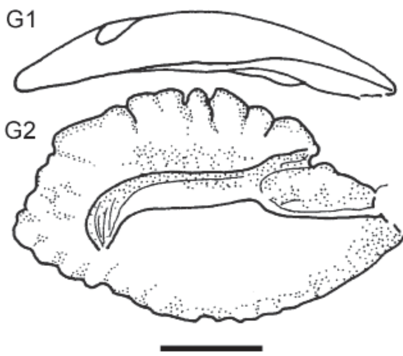
Fig. 39 (opposite page). Fish otoliths from the US middle and upper Eocene. **A–F**. *Pseudopriacanthus obliquus* (Nolf & Stringer, 2003), Yazoo Clay, Tullos M., Copenhagen, Louisiana. **A**. Holoype (IRSNB P6994). **B–F**. Paratypes (IRSNB P 6995–6999). **G**. *Pagrus esseri* (Müller, 1999), Piney Point F., sand and gravel pit, Bottoms Bridge, loc. 22 of Müller, Virginia, holotype (coll. Institut für Geowissenschaften, University of Leipzig, Nr.149/P38). **H**. *Owstonia comes* (Koken, 1888), Moodys Branch F., “Jackson River”, Mississippi, holotype (ZMB Ot. 165). **I–N**. “*Gobius*” *vetustus* (Nolf & Stringer, 2003), Yazoo Clay, Tullos M., Copenhagen, Louisiana. **I**. Holoype (IRSNB P 7413). **J–N**. Paratypes (IRSNB P 7414–7418). **O–P**. “*Citharus*” *hoffmani* (Nolf & Stringer, 2003), Yazoo Clay, Tullos M., Copenhagen, Louisiana. **O**. Holotype (IRSNB P 7424). **P**. Paratype (IRSNB P 7426). **Q–R**. *Citharichthys altissimus* Nolf & Stringer, 2003, Yazoo Clay, Tullos M., Copenhagen, Louisiana. **Q**. Holotype (IRSNB P 7422). **R**. Paratype (IRSNB P 7423). **S**. *Eosciaena ebersolei* Stringer *et al*., 2022, Yazoo Clay, Tullos M., Copenhagen, Louisiana (IRSNB P 7027). 1 = ventral view; 2 = inner view. Scale bars = 1 mm.



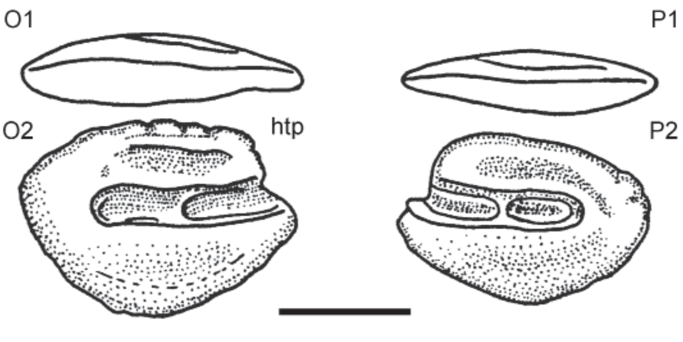
Pseudopriacanthus obliquus (Nolf & Stringer, 2003)



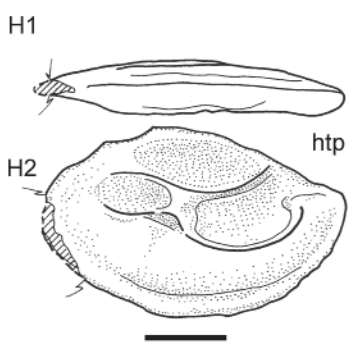
"*Gobius*" *vetustus* (Nolf & Stringer, 2003)



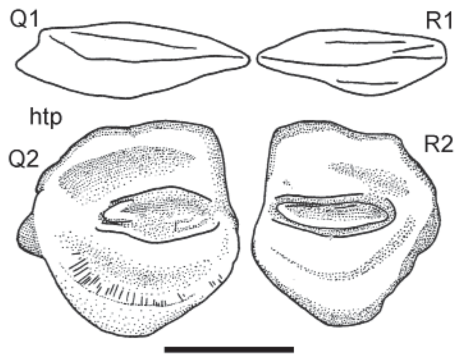
Pagrus esseri (Müller, 1999)



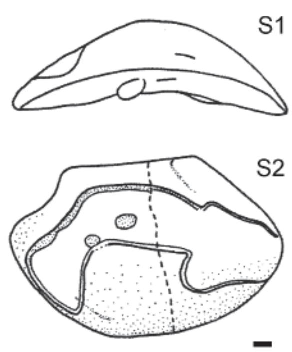
"*Citharus*" *hoffmani* (Nolf & Stringer, 2003)



Owstonia comes (Koken, 1888)



Citharichthys altissimus
Nolf & Stringer, 2003



Eosciaena ebersolei
Stringer *et al.*, 2022

Piney Point Formation, Virginia (35 and 1111 otoliths). The Gosport Sand in Alabama provided only 20 otoliths, but still eight taxa were recognized (Table 1).

The abundance rank of families indicates that the assemblages are strongly dominated by a few taxa (Fig. 40). When all samples are pooled, the Ophidiidae represent the most abundant family in number of specimens and comprise more than 45.4% of the total number of otoliths identified. They are followed by Sciaenidae (20.1%), Lactariidae (15.5%), Congridae (6.2%), and Haemulidae (3.7%). These first five families total over 91.1% of the assemblages. The pooled rank-abundance graph is very similar to that of the middle Eocene Claiborne assemblages both in the proportion and ranking order (Fig. 40). However, samples from the middle–late Eocene Jackson beds have a different pattern. The first four families are, in descending order, Sciaenidae (30.1%), Haemulidae (23.9%), Congridae (19.9%) and Ophidiidae (17.6%), and together, comprise over 91.5% of the assemblages. These families also form different ranking orders relative to the pooled and Claiborne assemblages. On the other hand, samples from the Atlantic Piney Point Formation are dominated by Ophidiidae, which is similar to those of the pooled and Claiborne assemblages; however, more otoliths of Congridae and Haemulidae than Lactariidae and Sciaenidae are found in the Atlantic assemblage.

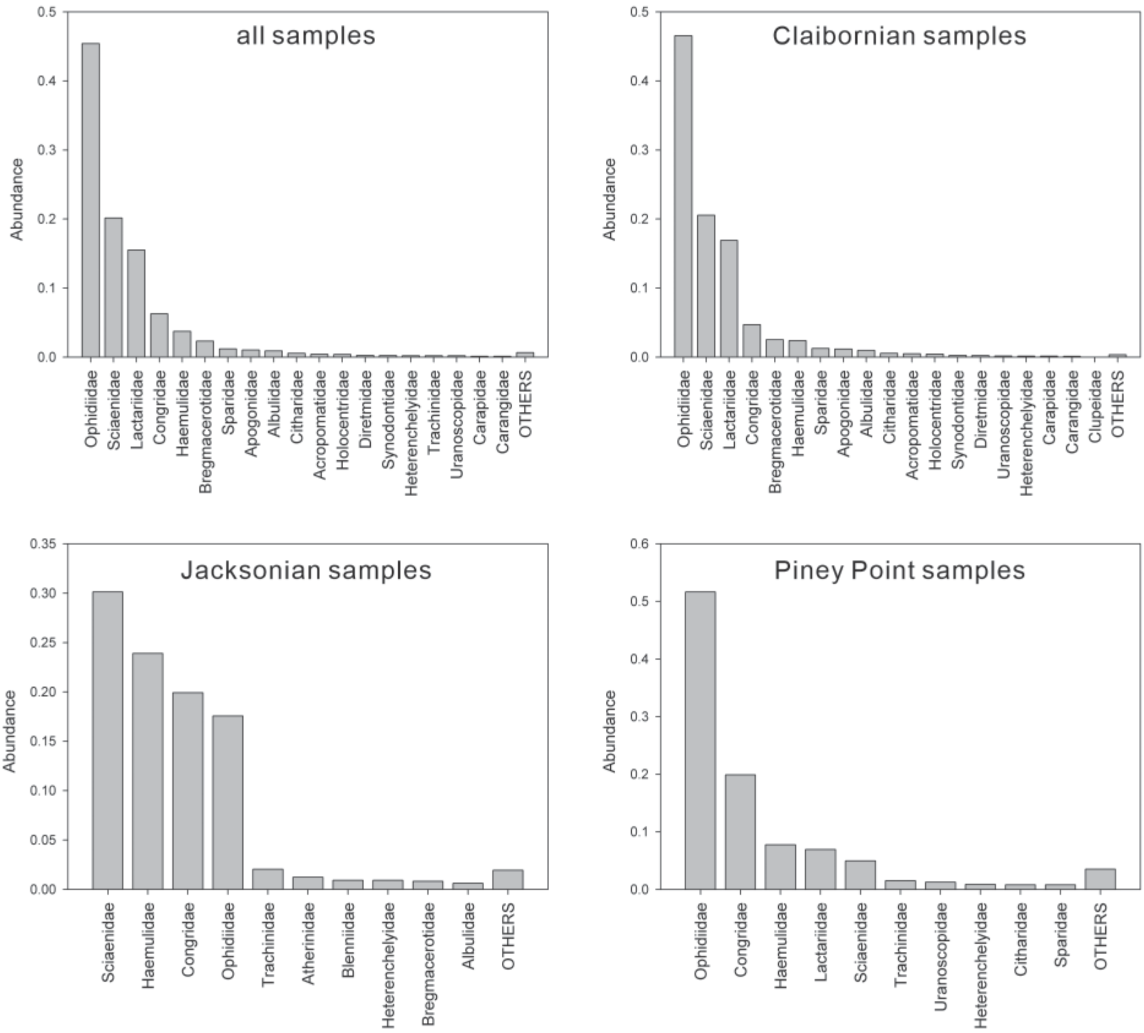


Fig. 40. Rank-abundance of fish families from the middle and late Eocene of the eastern and southern USA otolith assemblages. Previous studies are not included here.

Discussion

Preservation, richness, and distribution

The preservation of the collected otoliths is generally good, allowing for taxonomic recognition. Leaching, abrasion, and marine invertebrate settlement, such as bryozoans, molluscs, and cnidarians, on the surface of the otoliths are rare. Such preservation indicates a relatively stable sedimentary environment, and the lack of invertebrate settlement implies rapid burial postmortem (Stringer 2016), which is contrary to what is observed from modern deep-sea samples where a higher proportion of settlement is evident, which is caused by a prolonged exposure time on the sea bottoms (Lin *et al*. 2017c).

Our material includes both bulk samples and surface collections and therefore the density of otoliths cannot always be clearly assessed. As a general rule, the abundance of otoliths varies greatly from locality to locality (see discussion in Lin & Chien 2022). It usually yields less than 10 otoliths/kg sediments, but in some extremely rich localities (e.g., Stone City Bluff, Brazos River, Sample 2), condensed otolith assemblages of over 100 specimens per kg sediment have been collected. The uneven distribution of otoliths in the sediments is not unusual in fossil records, and aligns with the observations from late Pleistocene–Holocene sea bottom samples (Wigley & Stinton 1973; Lin *et al*. 2016, 2018). Notably, the richness of the material (number of species or taxa) is affected by such abundance. Samples from Texas, the "upper" Lisbon Formation of Alabama, and the Piney Point Formation (Virginia) contain much higher numbers of otoliths and taxa than other regions. Nevertheless, all of the studied horizons contain at least 19 otoliths specimens with a taxonomic richness ranging from 10 to 45 (Table 1).

Our material covers almost the entire middle to late Eocene otolith-based fauna of the Gulf Coast and central eastern Atlantic Plain. It is the most extensively documented fauna in terms of chronologic and geographic coverage in the region. Moreover, several assemblages are described for the first time. For this reason, the records of many of the taxa could be extended into the Weches and Cook Mountain formations in Texas, and also the Kosciusko, Cook Mountain, and Moodys Branch formations, and the Yazoo Clay in Mississippi, and new information on various taxa in Alabama and Virginia became available (Table 1). However, materials from several horizons remain less represented. For example, the otolith assemblage from the Cane River Formation (Stringer & Breard 1997) requires further sampling and review. Moreover, no data are available from the Yegua and Moodys Branch formations in Texas and Louisiana, which would help to elucidate better the faunal differences between the Claiborne and Jackson beds (see below).

Taxonomic representation

The present data are documented by 101 taxa of which 83 are identified at the species level (including 14 new species) and 18 that could only be identified at the genus or higher level. This constitutes the richest yet studied Eocene otolith-based fish fauna in the US. The entire collection is dominated by taxa that are typical of Paleogene shallow-water deposits. Deep-water taxa such as the mesopelagic Gonostomatidae and Myctophidae and bathypelagic Macrouridae are completely absent. This general taxonomic composition is in line with previous studies in the region (e.g., Frizzell & Dante 1965; Nolf & Stringer 2003; Ebersole *et al*. 2019). The major components are the Ophidiidae, Sciaenidae, Lactariidae, Congridae, and Haemulidae (Fig. 40). The other taxa constitute a highly diverse fauna, but numerically they only represent a marginal percentage of the assemblages.

In the modern fauna, *Lactarius* is an Indo-West Pacific, monospecific genus. However, the two extremely abundant species of *Lactarius* in our material indicate that at least in the Eocene, the genus was more diverse and widely distributed, also in Europe. In the present-day oceans, the Ophidiidae and the Congridae are more common in deeper water habitats, but in many Paleogene shallow-water deposits, extinct taxa of the same groups are common (Nolf 1980, 1985; Schwarzhans 1981b, 2019a, 2019b).

Extinct genera and species of the subfamily Neobythitinae (Ophidiidae) were particularly species-rich and abundant in the Eocene shallow-waters of the Anglo-Paris-Belgian Basin (Stinton 1975, 1977, 1978, 1980, 1984; Nolf & Cappetta 1976; Nolf & Lapierre 1979; Nolf 1988; Lin *et al*. 2017b). It is clear that in such cases, a paleobathymetric interpretation based on the depth range of their modern relatives leads to erroneous conclusions. Many of the extinct Eocene neobythitine and congrid taxa do not persist into the Neogene but are replaced there by new groups that acquired a deep-water habitat comparable to that of their modern counterparts (Nolf & Steurbaut 1989; Schwarzhans 2019a).

The many sciaenid otoliths in the collection are of particular interest. Based on otolith morphology, many of the American Eocene marine sciaenids have their closest relationships to present-day freshwater taxa. These successful Paleogene marine sciaenid taxa (*Aplodinotus*, Pachyurinae) were apparently replaced in the marine environment by more successful modern groups (*Sciaena* was already present in the Eocene), but most others only appeared in the Neogene, while some of the Paleogene genera and their relatives survived in freshwater, mainly in the Mississippi and Amazon drainage systems (see Nolf 2013: 105; Aguilera *et al*. 2014). As in the case of Ophidiidae, these are extinct forms that do not persist in marine Neogene deposits. The oldest sciaenid records include a worn otolith from the early Ypresian Bashi Formation, Mississippi (Nolf 1995: fig. 5f) and several otoliths from the late Ypresian Reklaw Formation, Texas (Nolf, unpublished data). Also, teeth of possible sciaenid origin have been reported from the Ypresian strata of Mississippi, South Carolina, and Virginia (Case 1994, as *Albula eppsi*; Cicimurri & Knight 2009), although the taxonomic assignment of these teeth is admittedly very problematic (Cicimurri & Knight 2009). In Neogene strata, sciaenid otoliths are very common worldwide (e.g., Schwarzhans 1993; Nolf & Aguilera 1998; Aguilera *et al*. 2014, 2016; Lin *et al*. 2021; Lin & Chien 2022), as well as in the Atlantic and Gulf coastal plains (Stringer & Bell 2018; Stringer & Shannon 2019; Stringer & Starnes 2020; Stringer *et al.* 2020, 2021). However, skeletal records of this family are scarce. This may be due to preservation and sedimentary environments (Bannikov *et al*. 2009, 2018; Přikryl *et al*. 2021).

Otolith-based fossil records suggest that the Sciaenidae originated in the New World by the early Eocene. Sciaenids with close Recent relationships only appear from the Oligo–Miocene onwards. This transition has been partly supported by molecular data, which indicate a New World origin of the group (Xu *et al*. 2014; Lo *et al*. 2015) and also that their extant lineages experienced waves of radiation in the early Miocene worldwide (Lo *et al*. 2015). However, the origin time of the sciaenid crown group varies drastically in molecular studies (208 Ma in Xu *et al*. (2014) and 27.3 Ma in Lo *et al*. (2015)), and neither are consistent with the fossil records. This incongruent result is most likely due to the complete ignorance of the many earlier otolith records in the Eocene for molecular calibration. Thus, records of otoliths may provide a unique opportunity documenting past fish diversity that otherwise could not be recognized.

Some rare occurrences are also notable. The otoliths of *Mene garviei* sp. nov. are remarkable in their exquisite preservation because isolated otoliths of *Mene* are rather uncommon with respect to their many skeleton records (Friedman & Johnson 2005), a condition contrary to that of sciaenids. The occurrences of *Plotosus* and *Malthopsis*? sp. are unexpected and their otoliths are almost indistinguishable from those of the extant counterparts.

Ecological significance

It appears that the frequency distribution pattern of the taxa shows a restricted number of strongly dominant ones, while all the others are only represented by very low numbers (Fig. 40). This is not uncommon in the otolith-based fossil record in general, and this pattern might imply more profound ecological insights. Recent actuo-paleontological analyses (Schwarzhans 2013; Lin *et al*. 2016, 2017c) and thanatocoenosis surveys (Lin *et al*. 2019) suggest that otoliths in a sediment do not only represent the taxonomic composition of the fish fauna inhabiting a region (Lin *et al*. 2018), but that their abundance also reflects the trophic level of the concerned species in a specific fish community of the past. Dominant taxa likely have a higher turnover rate and shorter life span, delivering nutrition to higher trophic levels and maintaining a stable energetic flow in marine ecosystems. For example, the presence of many Gobiidae and Apogonidae provides fundamental energetic flow in the reef fish communities (Brandl *et al*. 2018; Lin *et al*. 2019). The dominant taxa (Ophidiidae, Sciaenidae, Lactariidae, etc.) in the Eocene of the US Gulf Coast might have played a similar role as Gobiidae and Apogonidae in present day shallow-water settings. Although shifts in the numeric presence of ophidiids and congrids, apparently for similar ecological functioning, are recognized in the Paleogene and Neogene fossil records, compelling evidence is required from detailed studies. It seems beyond the scope of the present study to speculate further on the ecological significance of the otolith-based death assemblages until a rigorous taphonomic process is established, but the hypothesis proposed here is intended to facilitate further studies.

The middle and late Eocene otolith-based faunas in the Atlantic and Gulf Coastal Plain: dynamics in time and space

Comparing Atlantic and Gulf Coastal Plain Eocene otolith associations

Our compiled data matrix from previous studies and the present material (Table 1) provides an opportunity for a larger scale otolith-based faunal comparison of the Atlantic and Gulf Coastal Plains. Besides the taxonomic review, a significant result of the present study is that a transformation from the middle Eocene Claiborne fauna to the middle-late Eocene Jackson bony fish fauna was recognized statistically (see Appendix). This transformation is documented in a broad geographical range including Texas, Louisiana, Mississippi, Alabama, and Virginia. Some aspects of this transformation can be visualized at a first glance in Figure 41, in which the represented nominal species are arranged according to their first appearance and stratigraphic ranges. This shows that among the 82 represented species (excluding *Muraenanguilla* aff. *thevenini*, as this species appeared earlier in the Ypresian of the Paris Basin), there is a massive Lutetian component of 62 species, of which 47 continue no higher into the stratigraphical column of the "Jackson portion" of the Bartonian, and also two of the "Claiborne portion" of the Bartonian don't continue higher up, which brings the total to 49 exclusive "Claiborne species". Several of the species that appeared in the Lutetian continue in the "Jackson portion" of the Bartonian (15 species), and all of those continue into the Prianonian deposits. This Priabonian fauna is completed with seven additional species that are only represented there. In summary, this divides the totality of the represented species in a lower "Claiborne" group of 49 ones and an upper "Jackson" group of 14 different species and 19 species common to both groups (Fig. 41).

The scale of this faunal turnover, however, seems to be rather regional than global, since no large events are known during this geological interval; the boundary between the Claiborne and Jackson groups is only a regional one. A similar pattern was also reported by Stringer *et al.* (2022) based on a rich Bartonian otolith assemblage from Georgia. Although statistically significant (Appendix), the shift in the otolith assemblages does not reflect a drastic change in the composition at family or even genus level. This suggests a mild replacement of the fish fauna. The mechanisms of the faunal shift identified here are distinct from major ones, as observed in large events, such as the one at the K/P boundary (Schwarzhans & Stringer 2020). Further studies will benefit from a detailed investigation and revision of the rich American Oligocene otolith collection that is available in the IRSNB.

Apart from the otolith-based fauna, similar faunal shifts are known in other marine fossils, for example, in the echinoid (Stefanini 1924) and chondrichthyan assemblages (Westgate 2001). The shark assemblages have shown that there is a general diversification of Carcharhiniformes and a reduction of Lamniformes during the early–middle Eocene and late Eocene–early Oligocene transition, as the water temperature dropped from a greenhouse climate to an icehouse climate (Manning 2003; Maisch *et al*. 2014). Westgate

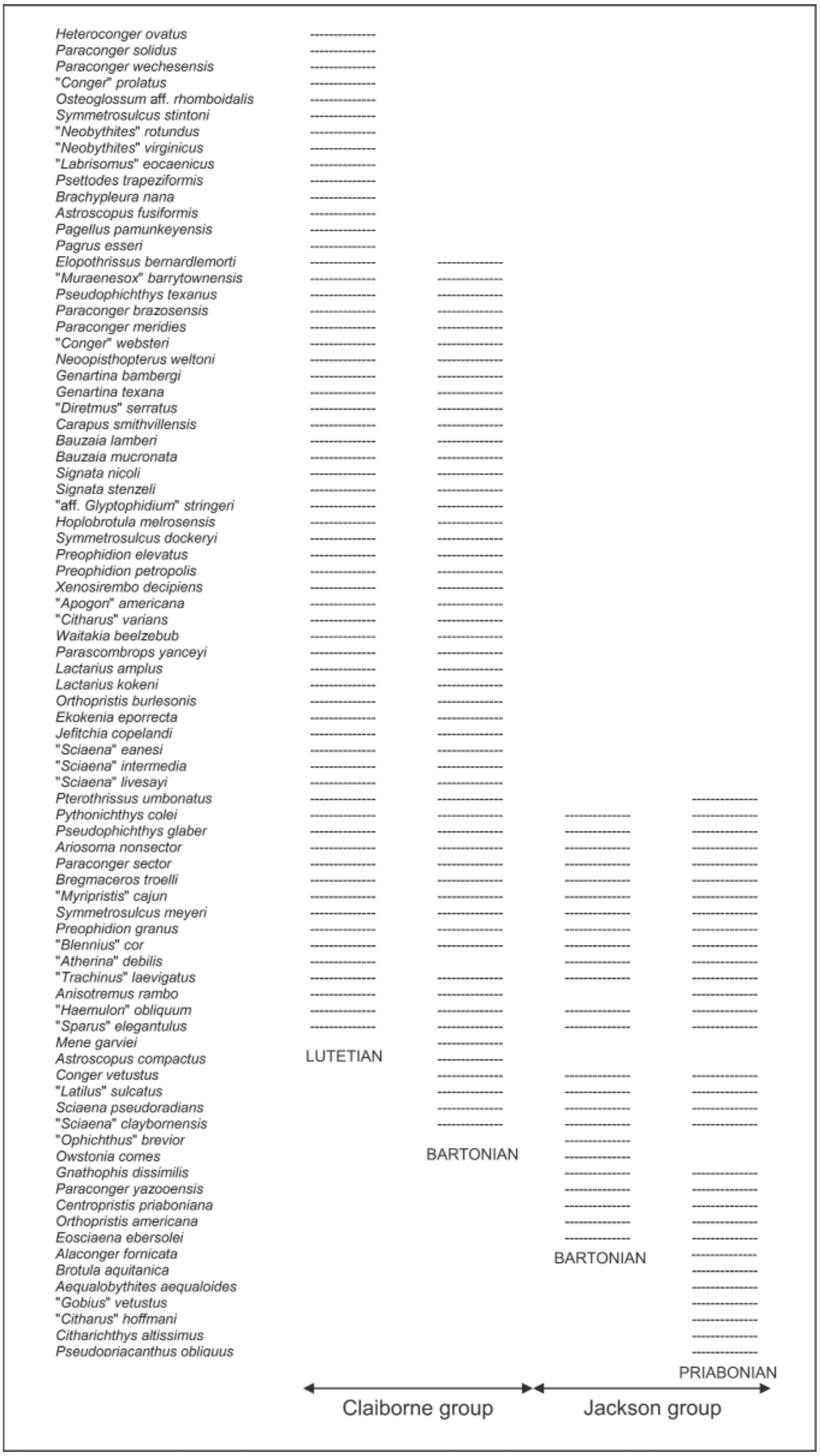


Fig. 41. Distribution of the represented nominal species, arranged according to their first appearance and stratigraphic ranges, illustrating the totality of the represented species in a lower "Claiborne" Group of 68 ones and an upper "Jackson" Group of 32 different species. The Priabonian taxon *Muraenanguilla* aff. *thevenini* (Priem, 1906) is not taken into consideration here, because the type of the nominal species already appeared in the Ypresian of the Paris Basin.

(2001) further assumed that this faunal turnover, also including an increased body size in sharks in the respective Claiborne and Jackson seas, can be correlated with the rise of gigantic whales.

The trigger behind this regional faunal turnover is yet to explore. The result of an oxygen isotope analysis in congrid and ophidiid otoliths has indicated a slight increase (~0.4‰) in the mean $\delta^{18}O$ values at the boundary of the middle and late Eocene (Ivany *et al*. 2000). Although this temperature excursion (a decrease in mean temperature) has not been tested significantly, possible season variation might be involved (Ivany *et al*. 2000). Spatiotemporal dynamics of the fauna, such as a faunal turnover from extended geological age and large-scale paleobiogeography, could indicate a more important evolutionary pattern hidden behind the fossil records.

Comparing western and eastern Atlantic Eocene otolith associations

Extensive otolith-based faunas are known from both the European and the American sides of the Atlantic. Many similarities between them, but also important differences, can be observed and are listed below. All the here described American associations are from upper epicontinental platform sediments, deposited at depths of less than 100 m and completely lacking oceanic components, such as the mesopelagic myctophids and the bathybenthic macrourids (see above). In Europe, the best documented otolith associations are mainly from the southern North Sea Basin and from the Aquitaine Basin. The southern North Sea and its dependencies, the Belgian Basin, the Southern English Hampshire Basin and the Paris Basin, are characterized by similar shallow epicontinental deposits providing only otoliths of fishes from the neritic environment, and are completely devoid of mesopelagic and bathybenthic fishes, as is the case in our Eastern USA sites (see above). In Southern Europe, extensive otolith material was collected in the Aquitaine Basin, SW France (Nolf 1988; Lin *et al*. 2017b). These associations cover a stretch of time ranging from Ypresian to Priabonian, and include several associations from the continental platform, including environments around 100 m and deeper, which were more exposed to the open oceanic environment than the Southern North Sea and dependencies. Consequently, they also contain rich mesopelagic fish associations including gonostomatids and even some bathypelagic macrourids (Nolf 1988; Lin *et al*. 2017b).

Finally, otolith associations containing a mix of neritic associations and some mesopelagic ones are described from northern Italy (Priabonian type area) (Girone & Nolf 2009) and from SE France (Castellane and Saint-André des Alpes area) (Nolf & Girone 2008). A very summary overview of all the taxa described up to 2013 can be found in Nolf (2013), where all European Eocene taxa are listed.

Similarities

Six Eocene species are amphi-Atlantic: *Pterothrissus umbonatus*, *Muraenanguilla thevenini*, "*Conger*" *websteri*, *Genartina bambergi*, *Brotula aquitanica*, and *Lactarius amplus*. *Muraenanguilla thevenini* is known from Ypresian till Priabonian deposits in Europe and is represented by a tentatively identified specimen from the Priabonian of Louisiana; the other five are known from strata of approximately the same age on both sides. The following genera or families are represented on both sides of the Atlantic, but by different species (no stratigraphic levels are mentioned for the European taxa):

1. The pterothrissid genus *Elopothrissus* is known by *E. tardinensis* (Leriche, 1908) in Europe and by *E. bernardlemorti* sp. nov. in the USA.

2. The heterenchelyids are known by two species that cannot be allocated to a precise Recent genus in Europe: "*Heterenchelys*" *circularis* (Shepherd, 1916) and "*H.*" *richardsi* Nolf, 1988. In America, they are represented by *Pythonichthys colei*.

3. Muraenesocids are known by two European species, *Muraenesox cymbium* Stinton, 1966 and *M. fissure* (Stinton & Nolf, 1970); there is an American species that does not show a precise generic affinity: “*Muraenesox*” *barrytownensis* sp. nov.

4. Congrid otoliths are very common on both the European and the American side. Beside the already cited common species “*Conger*” *websteri* Frost, 1933, three genera are represented on both sides. *Pseudophichthys*: two European species (*P. elongatus* (Sulc, 1932) and “aff. *P.*” *guttulus* (Stinton, 1975)) and two American ones (*P. glaber* and *P. texanus* sp. nov.). *Rhynchoconger*: three European species (*R. donzaquensis* (Nolf, 1988), *R. eocenicus* (Shepherd, 1916), and *R. transversus* (Sulc, 1932)) and two American ones (*R*. sp. 1 and *R*. sp. 2). *Paraconger: P. sauvagei* (Priem, 1906) is very common at many Belgian, Paris Basin and Hampshire Basin sites and is also known from the Priabonian of Aquitaine. On the American side, the genus is represented by six different species.

5. The osteoglossid family is represented by “*Osteoglossum*” *rhomboidalis* (Stinton, 1977) in Europe and there is a closely related American taxon that we cited as “*O*” aff. *rhomboidalis*.

6. Eocene clupeid otoliths occur on both sides of the Atlantic, but are too uncommon and too poorly diagnostic below the family level to draw any significant conclusion.

7. Myripristine otoliths are rather scarce in Eocene sediments; they are often poorly preserved, which usually makes their identification at both generic and specific levels hazardous. In Europe, they are represented by “*Myripristis*” *priemi* (Schubert, 1916) in Lutetian and Bartonian deposits of the southern North Sea and dependencies. Among our American material, we identified “*Myripristis*” *cajun* from Lutetian, Bartonian, and Priabonian sites.

8. Ophidiid otoliths were very abundant on both coasts of the Eocene Atlantic. Besides an amphi-Atlantic species, *Brotula aquitanica*, many genera are known from Europe and America by different species. *Aequalobythites aequalis* (Stinton & Nolf, 1970) and *A. hilgendorfi* (Koken, 1891) in Europe and *A. aequaloides* on the American side. “aff. *Glyptophidium*” *biarritzense* (Sulc, 1932) in Europe and “aff. *Glyptophidium*” *stringeri* sp. nov. in America. *Hoplobrotola*, known by *H. biscaica* (Sulc, 1932), *H. greenwoodi* Nolf, 1980, and *H. robusta* Nolf, 1980 in Europe and by *H. melrosensis* in America. *Symmetrosulcus dimidiatus* in Europe, with three American species as counterpart: *S. dockeryi* sp. nov., *S. meyeri*, and *S. stintoni. Preophidium*: *P. convexus* (Stinton, 1977), *P. ringeadei* (Nolf, 1980), *P. spinosus* (Nolf & Cappetta, 1976), and *P. tumidus* (Nolf, 1973) in Europe and *P. elevatus*, *P. granus*, and *P. petropolis* in America.

9. Menids are the next family with both European and American species: *Mene sekharani* Nolf & Cappetta, 1976 and *M. iberica* Brzobohatý & Nolf, 2011 in Europe; *M. garviei* sp. nov. and the *Mene* sp. from the Yazoo Clay in the U.S.

10. The flatfish genus *Psettodes* is known by four European Eocene species, *P. bavayi* Nolf, 1988, *P. collates* Nolf, 1973, *P. oedelemensis* Nolf, 1973, and *P. spinosus* Nolf, 1972, and one American species, *P. trapeziformis*.

11. Trachinids, today a typical eastern Atlantic family, count one European Eocene species, *Trachinus falcatus* Frost, 1934, and an incertae sedis trachinid, “*Trachinus*” *laevigatus*, in America. It is also worthy to mention that *T. unus* Müller, 1999 from the upper Oligocene of Virginia can be confidently attributed to *Trachinus*.

12. The serranid genus *Centropristis* is known by two European Eocene species (*C. europaea* Nolf, 1988 and *C. exsculpta* Stinton & Nolf, 1970) and by the American *C. priaboniana*.

13. The genus *Pseudopriacanthus* counts two European species, *P. rutoti* (Leriche, 1905) and *P. hermani* Taverne & Nolf, 2010, and one American, *P. obliquus*. In the present-day Atlantic fauna, there are two species of *Pseudopriacanthus*, *P. altus* (Gill, 1862) and *P. serrula* (Gilbert, 1891).

14. The haemulid genus *Orthopristis* is quite common at some localities in both European and American Eocene otolith associations. In Europe, it is represented by *O. bartonensis* (Priem, 1912), *O. kokeni* (Leriche, 1905), *O. trewavasae* Nolf & Lapierre, 1979, and by the Ypresian *O. rectangulus* (Frost, 1934); in America by *O. americana* and *O. burlesonis*. Two incertae sedis, but apparently related haemulid species, "*Haemulon*" *pulchrum* (Frost, 1934) and "*H*" *obliquum*, are known on respectively the European and the American side of the Atlantic.

15. Among Eocene owstoniines, *Owstonia brihandensis* (Nolf, 1988) is known on the European side of the Atlantic and *O. comes* on the American side.

16. For Eocene sparids, the genus *Pagellus* is represented by a European species, *P. folletti* Nolf & Lapierre, 1979, and an American species, *P. pamunkeyensis* sp. nov.; the genus *Pagrus* is represented by *P. symmetricus* (Frost, 1934) in Europe and *P. esseri* in America.

17. Another family that is represented by a genus that is common to both sides of the Atlantic is Caproidae: *A. angusta* Stinton & Nolf, 1970 in Europe and unnamed otoliths of *Antigonia* in the American Piney Point Formation and the "upper" Lisbon Formation.

Differences

1. Apogonids: Apogonid otoliths are very scarce in the US American Eocene deposits; in total, only two species represented by 200 otoliths were collected, while in Europe, they are very common in several associations, for example, the Lutetian Calcaire Grossier sites at Fercourt and Châteaurouge in the Paris Basin and the Lede Sands at Balegem (Belgium). The explanation may be that apogonids are more associated with circum-recifal facies and indurated substrates, and therefore are scarce in the American soft bottom neritic Eocene sediments.

2. Gobiids: As a rule, records of Eocene gobiids are rare. Their otoliths are unknown in European Eocene deposits, except for a skeleton-based record from the Priabonian of the Isle of Wight, southern England (Chapelcorner Fish Bed, Osborne Member of the Headon Formation), mentioned by Gaudant & Quayle (1988) as *Pomatoschistus* (?) *bleicheri* (Sauvage, 1883), and skeleton-based species based on a single specimen from Monte Bolca, Italy (*Carlomonnius quasigobius* Bannikov & Carnevale, 2016) (Bannikov & Carnevale 2016). In America, however, one species, "*Gobius*" *vetustus*, is known by 57 specimens from the Priabonian Yazoo Clay of Louisiana (Nolf & Stringer 2003). This only illustrates that, at least in some areas, gobiids or gobiid-like fish started becoming a significant group in late Eocene fish communities.

3. Sciaenids: Sciaenid otoliths are unknown in Europe, but they are very common at many of the investigated American sites. Seven species and one unnamed species have been recorded; they are often represented by many specimens (Table 1). Although some otoliths have been collected from American Ypresian deposits (Nolf 1995: fig. 5f), they only became common since the Lutetian, and are also regular constituents in the associations of the succeeding Bartonian and Priabonian deposits. In the upper Lutetian "Stone City beds" of Texas, we even collected more than 2500 sciaenid otoliths. Apparently, America was a major center for the Eocene radiation of the family (see above). In the modern Atlantic, marine sciaenids are well represented on both the West African and the American sides, but except for the plesiomorphic genus *Umbrina* Cuvier, 1816, all belong to different genera. In America, a detailed study of Oligocene sciaenids is yet in course, but since the Miocene, many Recent sciaenid were already represented, for example, *Bairdiella* Gill, 1861, *Ctenosciaena* Fowler & Bean, 1923, *Equetes* Rafinesque, 1815, *Larimus* Cuvier, 1830, *Nebris* Cuvier, 1830, *Protosciaena* Sasaki,

1989, and *Umbrina* (Müller 1999; Nolf 1976; Nolf & Stringer 1992; Nolf 2013; Aguilera *et al*. 2014, 2016).

Conclusions

The Eocene otolith assemblages in the Gulf Coastal Plain have been known for more than a century, but regional reports on the subject were either scattered, restricted in scale, or based on insufficient knowledge of extant teleostean otoliths. For the first time, the entire middle and late Eocene otolith-based teleost fauna is described and documented by a large number of specimens from many localities and stratigraphic levels, and is presented in an updated classification scheme. The high proportion of newly recorded taxa, including 14 new species, extends our knowledge of the fauna both in time and space. The results also highlight a signature of diversity yet to be discovered: more taxa and new species are likely to be unearthed with a similar extensive sampling in younger and older strata. On the other hand, our analysis suggests a mild replacement of the fish fauna in the late Bartonian (at the boundary between the middle Eocene Claiborne and Jackson groups). Though the general taxonomic composition remains similar at least at the family and genus level, several abundant taxa are confined to either Claiborne or Jackson strata. As a conclusion, we can state that during the Eocene, the coastal teleostean fish fauna was rather similar on both sides of the Atlantic, with several common genera, but these were represented by distinct species. An essential difference, however, consists in the total lack of sciaenids on the European side, and the increasing importance of this group in America since the beginning of the Lutetian.

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Suppl. file 1. A poster entitled "*Establishing Relationships of Fossil Otoliths through Geometric Morphometrics: a Case Study of Sciaenid Otoliths from the Eocene Gulf Coast*", presented by Chien-Hsiang Lin at the Sixth International Otolith Symposium, 2018, Keelung, Taiwan. https://doi.org/10.5852/ejt.2022.814.1745.6571

Appendix

Brief summary and results of the multivariate analyses based on the dataset in Table 1.

Methods

To disentangle the spatiotemporal dynamics of the fauna in the fossil record, the taxonomic component was evaluated using multivariate statistic techniques. Assemblages from each locality were first grouped according to their lithological formation. These formed the basic element of the analysis and were then labelled with corresponding region (state) and age. Our data matrix is presented in Table 1.

A hierarchical cluster analysis with arithmetic mean (UPGMA) algorithm was performed to find out how each element is grouped, and these groupings were further visualized and compared by plotting on a principal coordinate analysis (PCoA) plot. Both analyses were based upon their taxonomic composition with presence/absence (1/0) in the matrix, and performed on the R software (Core Team and others 2013) using the Bray-Curtis similarity index.

A non-parametric one-way analysis of similarity (ANOSIM) with the Bray-Curtis similarity index was then conducted to statistically distinguish the assemblages of interest based on the results of above analyses (cluster and PCoA). Finally, when a significant difference ($p < 0.05$) was detected in ANOSIM, a similarity percentage analysis (SIMPER) was conducted to indicate significant taxa resulting in the observed dissimilarities between each pair of groups. The ANOSIM and SIMPER analyses were performed under the PAST software (Hammer *et al.* 2001).

Results

The result of cluster analysis indicates that the otolith-based fish fauna is rather stratigraphically (chronologically) than geographically structured (Fig. S1). Two well-defined clusters, one with all assemblages belonging to the middle Eocene Claiborne Group, and one belonging to the middle-late Eocene Jackson Group, can be identified. Both clusters contain assemblages from various regions (states). Similarly, PCoA indicated that the Claiborne assemblages were separated from the Jackson ones (Fig. S1). The result of ANOSIM analysis corroborates the above analyses (Global $R = 0.8291$, $p < 0.05$).

The result of SIMPER analysis (Table S1, in descending order) revealed that the Claiborne assemblages are strongly defined by the presence of *Lactarius kokeni*, *Orthopristis burlesonis*, *Bauzaia mucronata*, *Ekokenia eporrecta*, *Jefitchia copelandi*, and *Lactarius amplus*, whereas the occurrences of *Sciaena pseudoradians* and *Preophidion granus* are typical taxa of the Jackson Group.

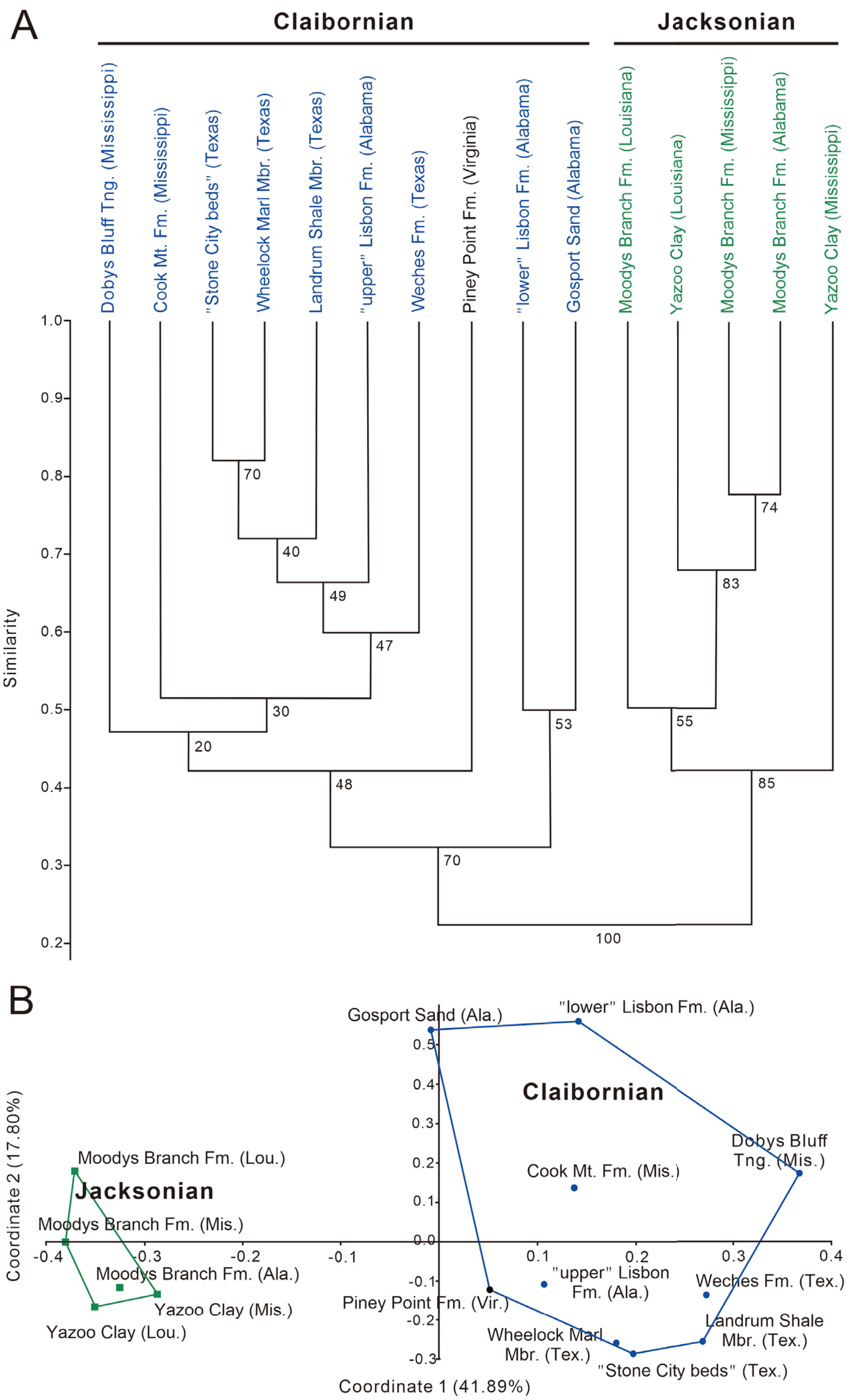

Fig. S1. Comparison of Claibornian and Jacksonian otolith assemblages from the middle and late Eocene of the eastern and southern USA. A cluster analysis (**A**) and a principal coordinate analysis, PCoA (**B**) with Bray-Curtis similarity index were performed based on the taxonomic composition (presence/absence) of each assemblage. Bootstrap values are given at the roots of each cluster in (**A**).

Table S1. Results of the SIMPER analyses between the Claibornian and Jacksonian assemblages. The first eight taxa of contribution to the overall average dissimilarity are listed in decreasing order. sd, standard deviation.

Taxa	Average dissimilarity	sd
Lactarius kokeni	0.0240	0.0080
Sciaena pseudoradians	0.0219	0.0108
Orthopristis burlesonis	0.0208	0.0100
Bauzaia mucronata	0.0205	0.0097
Ekokenia eporrecta	0.0205	0.0097
Jefitchia copelandi	0.0197	0.0125
Lactarius amplus	0.0173	0.0104
Preophidion granus	0.0172	0.0128

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