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THE MIDDLE EOCENE BONY FISH FAUNA OF CALIFORNIA, USA, RECONSTRUCTED BY MEANS OF OTOLITHS

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Keywords: Teleost otoliths; new genera; new species; middle Eocene; southern California; Ophidiiformes.

Abstract: Large and diverse Eocene otolith assemblages have been described from the US Gulf and Atlantic coastal plains, various basins in Europe, and New Zealand. Here we described a highly diverse otolith association from the middle Eocene (Lutetian and Bartonian) strata of southern California, San Diego County, which was retrieved from the heritage of John E. Fitch (1918-1982) in the archives of the Ichthyology Department of the Natural History Museum of Los Angeles County, Los Angeles, Califronia. The collection represents the first Eocene otolith assemblage described from the Northeastern Pacific and stems from two localities: the Ardath Shale at Black's Beach in the Torrey Pines Park just south of Black's Canyon Road and north of the Salk Fault on the Pacific shore face, and the MissionValley Formation from the west-facing graded hill just east of the Miramar Water Treatment Plant near the southern shore of Miramar Reservoir. The Ardath Shale was deposited on the deep shelf and continental slope while the Mission Valley Formation represent an inland, nearshore environment during times of the maximum transgression.

A total of more than15,000 otoliths were found representing 96 species of which 53 are described as new and 12 remain in open nomenclature. The fauna of the Ardath Shale is distinctly richer containing 88 species while the one from the Miramar Reservoir site yielded 38 species. The low diversity at the Miramar Reservoir site is thought to be related to the shallow-water environment in which it was deposited whereas the high diversity at Black's Beach reflects a mixture of shelf and bathyal fishes. In addition, 24 new otolith-based genera are established, four of which are in the category "incertae sedis". Furthermore, five new species are described from a comparative otolith collection from the US Gulf Coast Eocene and one new species from a comparative collection from the Lutetian of Balegem in Belgium.

The Eocene otolith-based fish fauna from California is assessed for its paleoecological, paleobiogeographic and evolutionary significance. Particular emphasis is directed towards the elucidation of the evolution of the early Ophidiiformes, which during the early Paleogene were predominantly adapted to warm, clastic shallow-water environments and there were competing in abundance and diversity with other percomorphs (e.g., perciforms s.l.). A warm Eocene paleobioprovince is proposed for the Californian fish fauna which is not related to today's endemic Northwest Pacific fish fauna along the regime of the cold-water California Current.

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INTRODUCTION

The otoliths described in the following were found in the heritage of John Fitch in the archives of the fish section of the Ichthyology Department of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, during two visits of the senior author in 2015 and 2017. The collection also contained a few notes and letters from John Fitch detailing where the otoliths have been collected and that he planned to publish about them which however never occurred due to his untimely early death in 1982. Actually, most of the material was collected by the late Mark Roeder (San Diego) in the late 1960's and early 1970's who donated the otoliths to John Fitch. The material recovered came from two localities as described by him: 1) at the face of the sea cliff at Black's Beach just south of Black's Canyon Road (Fig. 1) and 2) from the west-facing graded hill just east of the Miramar Water Treatment Plant near the southern shore of Miramar Reservoir (Fig. 1). Fitch also mentioned a third location from which he collected otoliths, a north facing road cut on Ardath Road near its junction with interstate, but this material was not found.

The collection contained 10,753 identifiable otoliths from Black's Beach and 4,375 from The Miramar Reservoir site representing together 96 species of which 53 are new to science and 12 remain in open nomenclature. The collection also represents the first substantial record of an otolith-based fish fauna from the Eocene of the northern Pacific. Only two specimens of *Eomyctophum cyrano* (Nolf, 1988) have previously been reported by Fitch (1969; as *Diaphus* sp.). The otolith assemblage from the Eocene of California thus represents an important element in the picture to reconstruct the teleost fauna of the world during that time. Comparable Eocene otolith-based faunas are known from the US Gulf Coast and US East Coast containing 101 taxa (Lin & Nolf 2022), and in the Pacific realms from New Zealand with 96 species (Schwarzhans 2019a), and Indo-West Pacific (Pakistan, India, Indonesia) with about 53 taxa (Vorstman 1927; Nolf & Bajpai 1992). The two Californian Eocene localities that yielded the studied otoliths represent remarkably different paleoenvironments, with the Miramar Reservoir site in a shallow-water nearshore environment and the Black's Beach location in a continental slope environment with potential submarine channel and fan deposition associated.

Furthermore, a substantial collection of Eocene otoliths from three classical US Gulf Coast localities were made available for comparison, namely from Brazos River in Texas (Garvie 2021), Moodys Branch in Jackson, Mississippi (S. Kiel, Stockholm, personal communication) and the Yazoo Clay in Cynthia, Mississippi (Haasl & Hanse 1996). This material was made available by S. Kiel and T. Mörs (Stockholm) from the collection of the Swedish Museum of Natural History. This material contained five additional new species not recorded by Lin & Nolf (2022), and which are also described here.

GEOLOGY AND LOCATIONS

The Eocene section exposed at San Diego consists of more than 700 m of intertonguing marine and nonmarine mudstones, siltstones, sandstones, and conglomerates deposited during two major transgressive-regressive cycles (Kennedy 1975). These strata are interpreted to represent from east to west, fluvial, lagoonal, nearshore marine, shelf, and submarine-canyon depositional environments (Boyer & Warme 1975; Kennedy 1975; Link et al. 1979; May 1985). Generally, terrestrial fossils are confined to the eastern nonmarine deposits, and marine fossils to the western, marine deposits.

The Eocene stratigraphy as defined by Kennedy and Moore (1971), recognized the La Jolla Group, which they subdivided into six formations, including the Mount Soledad, Delmar, Torrey Sandstone, Ardath Shale, Friars, and Scripps, and the overlying Poway Group, which they subdivided into the Stadium Conglomerate and Mission Valley Formations (Fig. 1). Later, Peterson and Kennedy (1974) added a new formation, the Pomerado Conglomerate, to the Poway Group. Formations of both of these groups interfinger with other formations and are partly coeval. The La Jolla Group lies stratigraphically below and generally west of the Poway Group, and is generally finer grained.

The Black's Beach site (Natural History Museum of Los Angeles County (LACM 59708) is located at Black's Beach, which stretches 1.8 km along the sea cliffs south from Torrey Pines State Beach to north of the pier at the Scripps Institu-

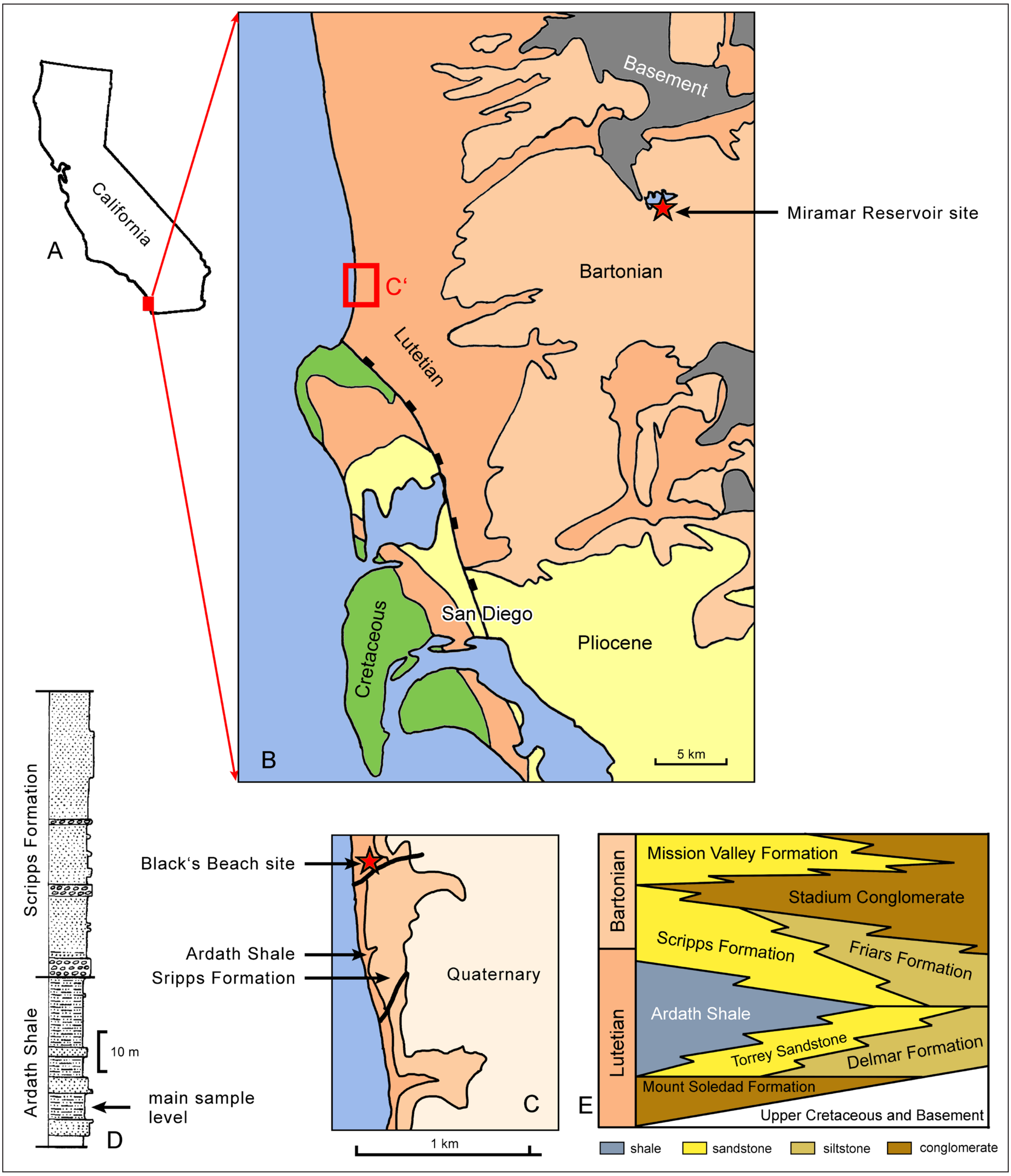


Fig. 1 - Location plate and schematic stratigraphic sequence after Kennedy & Moore (1971). A) Index map of California showing the location of the geological map. B) Geological map of San Diego coastal area; Quaternary deposits not shown. Star indicates location of the Miramar Reservoir site. Red quadrangle indicates detail map shown in C. C) Locality map of Black's Beach, outcrops of Ardath Shale and Scripps Formation. Star indicates location of the sampled Black's Beach site. D) Type section of the Scripps Formation from Kennedy & Moore (1971) taken about 1 km south of the sampled Black's Beach site. E) Stratigraphic and facies model of Eocene rocks in San Diego coastal area.

tion of Oceanography. This region was interpreted to have been located off the continental shelf on the slope between 200 and more than 1000 m water depth during the middle Eocene and the time of the deposition of the Ardath Shale (Lohmar & Warme 1978, 1979; May 1982, 1985; Stright et al. 2014). May (1985) described the setting as "a well-integrated Eocene submarine-canyon complex that dissected coeval slope, shelf, and nearshore deposits of the San Diego Embayment." The fossils were collected from thin-bedded sandstones, siltstones and mudstones near the base of the sea cliffs just south of Black's Canyon Road (Fig. 1). The sandstones and siltstones in the Ardath Shale in this area at beach level have been noted by May (1982) as typical overbank (interchanneling) depositon from diluted density currents and to be the proximal part of a submarine-fan complex (see above, Lohmar et al. 1979; May 1985; Stright et al. 2014). The Ardath Shale has been been assigned to the early Lutetian (early middle Eocene) calcareous nannofossil Subzone CP12b (Bukry and Kennedy 1969; Kennedy and Moore 1971; Okada and Bukry 1980). The Ardath Shale has yielded well documented assemblages of marine microfossils (Bukry and Kennedy 1969; Gibson 1971; Steineck et al. 1972) and macroinvertebrates (Hanna 1927; Givens and Kennedy 1979; Teichert and Stanley 1975; Squires 1998; Schweitzer et al. 2002). Vertebrate remains reported by Golz and Lillegraven (1977) from the Ardath Shale were actually collected from the Scripps Formation (Squires & Deméré 1991).

The Miramar Reservoir site (Natural History Museum of Los Angeles County (LACM 56322) is located in the west-facing graded hill above the parking lot of the Miramar Water Treatment Plant and is near the southern shore of Miramar Reservoir. The fossil bearing horizon is a 10 m thick greenish, sandy siltstone containing molluscan fragments, casts of pelecypods and gastropods. The fossiliferous siltstones are underlain by a massive sandstone and overlain by sandstones and conglomerates (Roeder 1991). The Mission Valley Formation, part of the Poway Group, is predominantly composed of light olive-gray, soft and friable, fine to medium grained marine and nonmarine sandstone containing cobble conglomerate tongues (Kennedy and Moore 1971). The maximum thickness of the formation is 60 m and was named for exposures along the south wall of Mission Valley on the west side of State Highway 163 (Kennedy and Moore 1971). The eastern exposures are nonmarine, and the westernmost exposures are largely of marine origin, with the marine portion interpreted as representing a brief marine transgression within the regressive and predominantly nonmarine Poway Group (Kennedy and Moore 1971; Kennedy 1975). Because of its transgressive origin this formation is different ages in different places (Kennedy and Moore 1971; Gibson 1971; Steineck et al. 1972; Frederickson 1991; Walsh et al. 1996), thus the formation appears to range in age from middle to late middle Eocene. At the Miramar Reservoir site, Thompson (1965) recovered a small benthic foraminiferal assemblage and assigned it to the upper Eocene Narizian Stage of Mallory (1959). Bukry and Kennedy (1969) reported a small coccolith flora and assigned it a late middle to late Eocene age. Givens and Kennedy (1979) describe a limited molluscan fauna assignable to the upper part of the Tejon Molluscan Stage and the Bartonian Stage of Europe, which are considered late middle Eocene in age. Thompson (1965) considered the environment of deposition at the Miramar Reservoir site to be a sheltered, possibly wide-mouthed bay of normal salinity indicated by benthic foraminifera. At a nearby site in the same fossil-bearing horizon, Demere et al. (1979) based on molluscan species, determined deposition under normal marine conditions in a shallow, near-shore and protected series of habitats, such as a bay, estuary mouth, or marine lagoon. No brackish-water species were reported.

Material and Methods

The otolith specimens for this investigation were obtained from the Ichthyology Department of the LACM, California, USA. Although the specimens are middle Eocene in age, they are housed in the Ichthyology Department with extant fishes. The late John Fitch donated his extensive collection of fish otoliths of modern and fossil specimens, including notes, correspondence, and library, to the Ichthyology Department at the LACM. Approximately 15,000 Middle Eocene otoliths were studied from the Ardath Shale and the Mission Valley Formation. A total of 10,708 otolith specimens from the lowermost layer of the early middle Eocene (early Lutetian) Ardath Shale (LACM 59708) were examined, while 4,375 from the middle Eocene (Bartonian) Mission Valley Formation (LACM 56322) were analyzed. Since all of the otoliths are from the collections of the LACM, all figured otolith specimens are reposited there. The locations of LACM 59708 and LACM 56322 are provided in the Geology and Locations section. These LACM sites compare to sample localities 2 and 9, respectively, of the magnetostratigraphy study of Bottjer et al. (1991). The otolith assemblage of the Mission Valley Formation is considered highly significant since the formation is the only Eocene rock unit in southern California to have a radiometric date directly associated with fossil mammal localities (City of San Diego, 2007).

Otoliths from the Eocene of the US Gulf Coast were made available for this study by S. Kiel and T. Mörs (Stockholm) from the following localities: from the Brazos River upstream of bridge of State Highway 21 in Texas (Bartonian, Stone City Member); from the Moodys Branch Formation (Bartonian) of Jackson, Mississippi; the Cynthia pit in Mississippi (Priabonian, Yazoo Formation). These otoliths were used for comparison purposes, but some yet unrecorded species are included in the descriptions. Further comparative Eocene otoliths were studied from the collections of GS and WS and from the Natural History Museum of UK (London).

One of the authors (Schwarzhans) photographed the figured otoliths from the Ardath Shale and the Mission Valley Formation using a Canon EOS mounted on the phototube of a Wilde M400 photomacroscope. All of the figured otoliths were photographed at different focus levels utilizing a computer to ensure clarity in the depth of field. The individual photographs from each focus level were merged using the Helicon Focus software of Helicon Soft. The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast or balance or retouch small inconsistences, e.g., adhered sand grains, as far as possible without altering the otolith morphology in any manner (Schwarzhans & Stringer 2020). During the photographic process, the central portion of the inner and outer faces of the otoliths are carefully positioned to be level in order to avoid any distortion that would occur in strongly bent specimens. The same principle is applied for lateral views, in which the otoliths are oriented in an upright position either along the horizontal or vertical axis depending dorsal/ventral and anterior/posterior views respectively. It has been found that these standardized photographic techniques vastly improve the comparison of specimens for research purposes (Schwarzhans et al. 2018; Stringer et al. 2020; Schwarzhans & Stringer 2020, Stringer and Schwarzhans 2021; Schwarzhans et al. 2022). The most effective method of achieving the desired results is fixing the otoliths in plasticine.

All of the figured specimens illustrate otoliths from the right side (right labyrinth) of the fish. There are cases where right otoliths are not available (none recovered and poor preservation). In that case, left otoliths are utilized, but the specimens are mirror imaged to ensure standardized orientations and comparisons. When this procedure is necessary, the otoliths are annotated in the figure captions as "reversed." The individual otolith specimens are typically shown from the inner face view. However, the otoliths may also be shown from other views such as the outer face, dorsal, ventral, anterior, or posterior views as noted in the figure explanations.

In the systematics, the morphological terminology of the sagittal otoliths (the otolith found in the sacculus of the labyrinth) adheres to the work of Koken (1884) with revisions from Weiler (1942) and Schwarzhans (1978). The various measurements utilized in the taxonomic descriptions were achieved using a camera lucida mounted on the microscope or from photographs obtained from the photomacroscope. The following abbreviations are used in otolith descriptions: OL = otolith length, OH = otolith height, OT = otolith thickness, CaL = cauda length, CaH = cauda height, CCL = length of the caudal colliculum, CCH = height of caudal colliculum, OsL = ostium length, OsH = ostium height, OCL = length of ostial colliculum, OCH = height of ostial colliculum. The OsL is measured from the anterior tip of the ostium to an inflection point at the ventral margin of the ostium marking its termination, which may differ in cases from the posterior inflection of the dorsal margin of the ostium or the termination of the ostial colliculum. The CaL is measured from the same inflection point at the ventral margin of the sulcus to the termination of the cauda. The measures relating to OsL and CaL were taken when the sulcus margins were better-defined than the margins of the colliculi. Conversely, OCL and CCL were measured if the colliculi margins were clearer than the sulcus margins. Inclination angles were measured with the otolith oriented along its long axis, or in the case of high bodied otoliths along the sulcus axis. The above-described abbreviations are utilized in descriptive ratios, e.g., OL:OH (ratio of the length of the otolith to the height of the otolith). It should be noted that length is a horizontal measurement, while height is a vertical measurement usually at a 90^0 angle to the length. Unless otherwise specifically noted, the terms "wide," "wider," and "width" in otolith morphological descriptions refer to a vertical measurement. For example, the statement that the ostium is 2.5 times wider than the cauda means that the height of the ostium is 2.5 times greater than the height of the cauda.

Fossil and extant comparative otolith collections and references were utilized for the identification of the specimens from the Ardath Shale and the Mission Valley Formation. The classification scheme follows that of Nelson et al. (2016), which was greatly influenced by the molecular investigations of Betancur-R. et al. (2013). Any deviation from this classification is noted. Ordinal names typically follow Wiley and Johnson (2010), while the family-group names and authors of modern fishes follow Van der Laan et al. (2014, 2017, 2018). Authors for genera and species depend greatly upon Eschmeyer's Catalog of Fishes: Genera, Species, References (Fricke et al. 2019). Extant and fossil genera were used when possible, and the recommendations of Janssen (2012) were employed when the generic designation was not evident. This is accomplished by placing the unknown genus in the type genus of the family followed by a question mark indicating that the taxon might belong to any other of the known (or as yet unknown) genera in that family.

This published work and the nomenclatural acts it contains have been registered in ZooBank: https://zoobank.org/14DAA391-5F8A-4E67-A4DC-46945B7FB7BE.

SYSTEMATIC PART

Remarks. The systematics follow Nelson et al. (2016), except for the Ambassidae being placed in the Perciformes. The sequence of orders departs from Nelson et al. (2016) in Carangiformes placed after Pleuronectiformes, Spariformes and Caproiformes placed before Scorpaeniformes and Blenniiformes moved to the back of the sequence. This rearrangement of sequence follows aspects of convenience and does not reflect any change in phylogenetic understanding. Full descriptions of species are only provided for new species and for species with pertinent new information.

Division **Teleostei** Müller, 1846
Order **Albuliformes** Jordan, 1923
Family Pterothrissidae Gill, 1893
Genus *Pterothrissus* Hilgendorf, 1877

Pterothrissus umbonatus (Koken, 1884)

Fig. 2A–C

1884 Otolithus (*inc. sed.*) *umbonatus* - Koken: pl.12, fig.12.
1891 Otolithus (*inc. sed.*) *minor* - Koken: figs.23-24.
1906 Otolithus (*inc. sed.*) *dubius* - Priem: figs.9-10.
1916 Otolithus (*Berycidarum*) *bartonensis* - Schubert: pl.7, figs.18-20.

1975 *Pterothrissus cristatus* - Stinton: pl.1, figs.11-12.
1994a *Pterothrissus umbonatus* (Koken, 1884) - Schwarzhans: fig. 3-7 (see there for further references)
2010 *Pterothrissus umbonatus* (Koken, 1884) - Schwarzhans: pl. 1, fig. 1-4.
2022 *Pterothrissus umbonatus* (Koken, 1884) - Lin & Nolf: fig. 8I-L.

Material: 1 specimen, Mission Valley Formation, Miramar Reservoir site, LACM 60084.

Discussion. The single otolith of 7.2 mm in length is considered as diagnostically mature. Schwarzhans (2010) noted that *P. umbonatus* otoliths can reach up to 15 mm in length and then considered diagnostically maturity to occur at approximately 8 mm in length. *Pterothrissus umbonatus* is a widely distributed species with a long stratigraphic range from middle Eocene to Middle Miocene (34 mya), one of the longest known for an otolith-based species. The species has been recorded from various European basins, the US East Coast and Gulf Coast and now also from California. Very similar otoliths have been described as *P. pervetustus* by Stinton (1957) from the Oligocene of Australia and it is possible that these otoliths represent the same species (see Schwarzhans 1981a, 1985).

Pterothrissus sp.

Fig. 2D–E

Material: 2 fragments of otoliths, Mission Valley Forma-tion, Miramar Reservoir site, LACM 60085.

Discussion. The two otolith fragments lack the anterior portion. The larger of the two (Fig. 2A, C) is 12.3 mm in length and when complete must have been in the range of 13.5+ mm. It differs from *Pterothrissus umbonatus* in being more slender with a relatively shallow dorsal rim and may represent a different species.

Family Albulidae Bleeker, 1859
Genus *Albula* Scopoli, 1777

Albula bashiana (Frizzell, 1965)

Fig. 2G–L

1965 *Metalbula bashiana* - Frizzell: pl. 4, fig. 4.
?1993 *Albula* cf. *bashiana* (Frizzell, 1965) - Nolf & Dockery: pl. 1, fig. 1-2.
?2020 *Albula* cf. *bashiana* (Frizzell, 1965) - Schwarzhans & Stringer: fig. 3A-D.
2021 *Albula bashiana* (Frizzell, 1965) - Stringer & Schwarzhans: fig. 4A-D.

Material: 41 specimens: 28 specimens, Ardath Shale, Black's Beach, LACM 60134; 13 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60086.

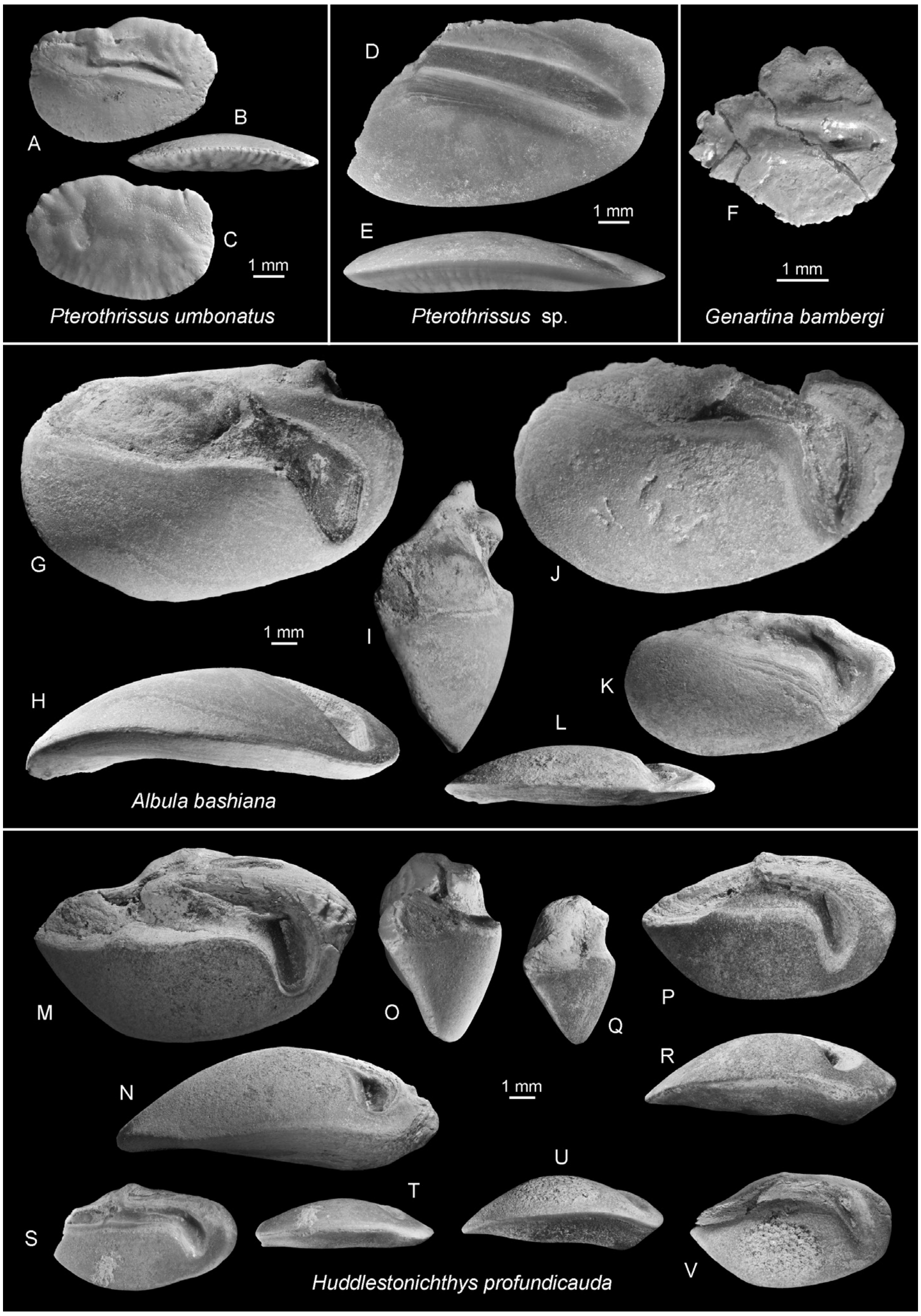
Diagnosis (update based on Fig. 2G–I)**:** OL:OH = 1.65; OH:OT = 2.3. Anterior rim broadly rounded. Inner face strongly convex; outer face flat to concave. CaL:OsL = 1.0. Cauda steeply curved at about 80°, moderately deep.

Description. Large, robust, oval otoliths reaching 15 mm in length (Fig. 2J). Dorsal rim often eroded and well preserved only in one specimen (Fig. 2G–I); shallow, anteriorly nearly horizontal, posteriorly irregularly undulating, sometimes with postdorsal knob-like feature. Ventral rim deeply and regularly curved, its deepest point distinctly anterior of rim's middle point. Anterior rim broadly and regularly rounded; posterior rim rounded, dorsally pronounced, in smaller specimens (Fig. 2K–L) with short dorsal projection. All rims smooth except postdorsal rim.

Inner face distinctly convex. Sulcus wide, strongly supramedian positioned, shallow to moderately deepened, inclined at average 10°. Ostium widened dorsally and ventrally but with indistinct mark at junctions with cauda, anterior-dorsally widely opened to dorsal otolith rim, about as long as cauda. Ostial colliculum distinct, with inclined margin towards junction with cauda. Cauda steeply inclined at mid-section at about 80–85° against otolith axis, slightly widened dorsally at point of bend, terminating very close to postventral rim. Wide ventral field smooth, without ventral furrow; dorsal field very narrow, without dorsal depression. Outer face flat to slightly concave, smooth.

Discussion. *Metalbula bashiana* was established on a single otolith specimen of 8.8 mm in length from the Eocene Wilcox Group ("Bashi Marl") from Mississippi. The unique holotype figured by Frizzell (1965) is eroded along the dorsal otolith rim, but otherwise shows all the diagnostic characters observed in our specimens from California. The erosion of the dorsal rim is a common preservation problem in albulid otoliths and may have led researchers to only tentatively associate other records to this species. We found one large and well preserved specimen in the Californian Eocene (Fig. 2G–I) and use it for updating of the diagnosis and description. The expansion of the posterior rim was considered a key diagnostic character ("postcaudal keel") for *Metalbula bashiana* and *Metalbula*. In general, it appears to be an ontogenetic

Fig. 2 - A–C) *Pterothrissus umbonatus* (Koken, 1884), Miramar Reservoir site, LACM 60084 (reversed), B ventral view, C outer face.
D–E) *Pterothrissus* sp., Miramar Reservoir site, LACM 60085 (reversed), E ventral view.
F) *Genartina bambergi* (Priem, 1913), Black's Beach, LACM 60136.
G–L) *Albula bashiana* (Frizzell, 1965); G–I, L–K Miramar Reservoir site, LACM 60086 (6 reversed), H, L ventral views, I anterior view; J Black's Beach, LACM 60134.
M–V) *Huddlestonichthys profundicauda* n. gen., n. sp.; M–O holotype, Miramar Reservoir site, LACM 60087 (reversed), N ventral view, O anterior view; P–R, U–V paratypes, Miramar Reservoir site, LACM 60088 (8 reversed), R, U ventral views, Q anterior view; S–T paratype, Black's Beach, LACM 60135, T ventral view.



feature in specimens up to about 10 mm in length (Fig. 2K–L), possibly enhanced by erosion, that is not evident anymore in in larger specimens (Fig. 2G–J). The steeply curved cauda and the long ostium lead us to follow the view of Nolf & Dockery (1993) to place the species in the extant genus *Albula*. *Albula bashiana* has been recorded from the late Masstrichtian to the Middle Miocene in North America and hence represents one of relatively few species considered survivors of the K/Pg boundary extinction event (Schwarzhans & Stringer 2020).

Genus *Huddlestonichthys* n. gen.

Type species: *Huddlestonichthys profundicauda* n. sp.

Etymology: In honor of our late colleague Richard Huddleston (Los Angeles) who passed away in 2021.

Diagnosis: An otolith-based genus of the family Albulidae characterized by a short ostium (CaL:OsL = 2.0–2.2, measured in relation to the notch at the junction of ostium and cauda on the ventral margin), a distinctly inclined junction of ostium and cauda of 45–55° and a steeply inclined cauda at 70–80° whereby the downturned part of the cauda is strongly deepened. In addition the otoliths are remarkable for a nearly straight preventral rim and a thick and massive appearance (OH:OT = 1.7–2.0, decreasing with size).

Discussion. *Huddlestonichthys* combines derived features typical for the persistent, extant genus *Albula* like the steeply inclined cauda with plesiomorphic traits like the short ostium with its strongly inclined junction with the cauda and a perceived autapomorphic feature, the strongly deepened downturned part of the cauda. We consider it as a sister-clade to the extant clade that diverged after the separation from the various earlier albulid groups that all show a much less strongly inclined caudal tip which is considered plesiomorphic.

Species: *Huddlestonichthys* is a monospecific genus with *H. profundicauda* from the middle Eocene of California.

Huddlestonichthys profundicola n. sp.

Fig. 2M–V

Holotype: Fig. 2M–O, LACM 60087, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 10 specimens: 1 specimens same data as holotype, LACM 60088; 9 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60135.

Etymology: From profundiclus (Latin) = profound, deep, referring to the deep downturned part of the cauda.

Diagnosis: See generic diagnosis (monospecific genus).

Description. Large, compact, oval otoliths up to 12.5 mm in length (holotype). OL:OH = 1.65–1.8; OH:OT = 1.7–2.0, both decreasing with size. Dorsal rim shallow, slightly and irregularly curved posteriorly, slightly depresses and inclined anteriorly along ostial opening. Ventral rim deeply curved, its deepest point distinctly before middle of rim, its anterior part steeply inclined at 40–50°, relatively straight, central part slightly curved, posterior part well rounded. Anterior rim with blunt rostrum; posterior rim broadly rounded or straight and slanted, slightly dorsally pronounced. All rims smooth.

Inner face strongly convex. Sulcus moderately wide, strongly supramedian positioned, not inclined. Ostium slightly widened its junction with cauda strongly inclined and well marked along ventral sulcus margin. Ostium somewhat deepened, broadly open to anterior-dorsal rim of otolith along its entire length. Cauda steeply inclined at mid-section at about 70–80° against otolith axis, the downturned part strongly deepened, terminating moderately close to postventral rim. Wide ventral field smooth, without ventral furrow; dorsal field very narrow, without dorsal depression. Outer face flat to slightly convex, smooth.

Family indet.
Genus *Genartina* Frizzell & Dante, 1965

Genartina bambergi (Priem, 1913)

Fig. 2F

1913 *Hoplostethus bambergi* - Priem: fig. 5
1915 *Otolithus* (inc. sed.) *hampshirensis* - Schubert: pl. 7, fig. 23.
2019a *Genartina bambergi* (Priem, 1913) - Schwarzhans: fig. 13.5 (see there for further references).
2022 *Genartina bambergi* (Priem, 1913) - Lin & Nolf: fig. 14B-E.

Material: 10, mostly fragmented specimens, Ardath Shale, Black's Beach, LACM 60136.

Discussion. *Genartina bambergi* is the last species of the enigmatic fossil otolith-based genus *Genartina* known since Late Cretaceous times. It is widely distributed, possibly cosmopolitan during middle and late Eocene known from Europe, North America and New Zealand.

Order **Anguilliformes** Regan, 1909
Family Heterenchelyidae Regan, 1912
Genus *Pythonichthys* Poey, 1868

Pythonichthys texanus (Dante & Frizzell, 1965)

Fig. 3A–D

1965 *Eosolea texana* - Dante & Frizzell (in Frizzell & Dante): pl. 88, fig. 15, 20.
?1965 *Eosolea claibornensis* - Dante & Frizzell (in Frizzell & Dante): pl. 88, fig. 13, 14, 18, 22.
1999 "genus aff. *Panturichthys*" *colei* - Müller: fig. 20/5, ?20/4, pl. 16, fig. 2.
?1999 "genus aff. *Panturichthys*" sp. - Müller: fig. 20/6-7.
2003 "genus Heterenchelyidarum" *colei* (Müller, 1999) - Nolf & Stringer: pl. 1, fig. 3-8.
2008 "genus Heterenchelyidarum" aff. *colei* (Müller, 1999) - Girone & Nolf: fig. 2A1-4.
2019 *Pythonichthys colei* (Müller, 1999) - Ebersole, Cicimurri & Stringer: fig. 69.
2022 *Pythonichthys colei* (Müller, 1999) - Stringer, Parmley & Quinn: fig. 3.
2022 *Pythonichthys colei* (Müller, 1999) - Lin & Nolf: fig. 8E-H.

Material: 4 specimens, Ardath Shale, Black's Beach, LACM 60137.

Discussion. Heterenchelyid otolith offer very little morphological characteristics for identifications, as has been commented by most previous researchers as well. The two species described by Dante & Frizzell (1965) who thought that they might represent an extinct soleid genus which they described as *Eosolea*, were usually considered too poorly preserved for diagnosis. In our opinion, *P. texanus* is based on a reasonably preserved specimen and the species was accepted as valid in Nolf (2013) and even considered as potential synonym in the original description of *Panturichthys colei* by Müller (1999). We believe that most of these specimens from the middle Eocene of the USA represent one species for which *P. texanus* (Dante & Frizzell 1965) has priority.

The otoliths described by Dante & Frizzell (1965) as *Eosolea claibornensis* differ from those of *P. texanus* in showing a straight sulcus. This feature may indicate that a second species of *Pythonichthys* lived in the Gulf during the middle Eocene. However, this situation requires a detailed review of available specimens for verification.

Family Ophichtidae Rafinesque, 1815

Genus *Eophichthus* n. gen.

Type species: *Eophichthus ardathensis* n. sp.

Etymology: A combination of Eo from Eocene and the genus name *Ophichthus* in order to indicate the stratigraphic occurrence of the genus.

Diagnosis: An otolith-based genus of the family Ophichthidae characterized by the combination of a rather strongly sinuate sulcus, which fades towards the sulcus opening, a short ostium (CaL:OsL = 1.6–2.0), a strongly convex inner face and a relatively thick appearance (OH:OT = 1.8–2.2). The ostium is only slightly wider than the cauda and not or only slightly deepened.

Discussion. The family Ophichtidae is very rich in species and genera today and otoliths are only known from a fraction of those (see Lombarte et al. 2006; Nolf 2013; Schwarzhans 2019b). None of the known extant otoliths show this combination of a strongly convex inner face and a sinuate sulcus with a relatively narrow ostium. Therefore we consider it appropriate to establish a fossil otolith-based genus for these forms. Ophichthid otoliths are generally rare in the fossil record. The high degree of diversity and relative abundance of ophichthid otoliths in the Eocene of California therefore represents a significant addition for our knowledge of early records in this family.

Species. Three species: *Eophichthus ardathensis* n. sp. and *Eophichthus gracilis* n. sp., both from the middle Eocene of California. *Conger brevior* Koken, 1888 from the middle to upper Eocene Jackson Group and Oligocene Vicksburg Group of the US Gulf Coast is also tentatively referred to *Eophichthus* subject to review. A further, possibly related species has been described from the middle Eocene of England and France as *Echelus contractus* Stinton, 1975.

Eophichthus ardathensis n. sp.

Fig. 3G–S

Holotype: Fig. 3G–I, LACM 60089, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 6 specimens, Ardath Shale, Black's Beach, LACM 60139.

Name: After the Ardath Shale, the type formation.

Diagnosis: OL:OH = 1.4–1.6. Dorsal rim shallow, nearly straight and horizontal. CaL:OsL = 1.6–1.7.

Description. Small, oval, compact otoliths up to 2.5 mm in length (holotype). OH:OT = 1.8–2.2. Dorsal rim shallow, nearly flat and horizontal; ventral rim deeply and regularly curved. Anterior and posterior rims broadly rounded; anterior rim sometimes with blunt rostrum. All rims smooth.

Inner face strongly convex with slightly supramedian sulcus. Sulcus moderately wide, shallow, slightly sinuate, moderately long; OL:SuL = 1.25–1.45. Ostium slightly wider than cauda and distinctly shorter, its anterior opening indistinct, fading, slightly deepened. Ventral field smooth, without ventral furrow; dorsal field smooth, without or with indistinct dorsal depression. Outer face flat, smooth.

Discussion. *Eophichthus ardathenis* at first is a rather indistinct otolith, but its compressed shape distinguishes it well from other coeval ophichthid otoliths. It differs from *E. gracilis* n. sp. in being more compressed (OL:OH = 1.4–1.6 vs. 1.65–1.8) and the lower index CaL:OsL of 1.6–1.7 (vs 1.75–2.0).

Eophichthus gracilis n. sp.

Fig. 3T–AA

Holotype: Fig. 3T–V, LACM 60140, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 10 specimens, same data as holotype, LACM 60141.

Etymology: From gracilis (Latin) = slender, referring to slender shape of the otolith distinguishing it from its congener.

Diagnosis: OL:OH = 1.65–1.8. Dorsal rim shallow, nearly straight and horizontal; ventral rim shallow. CaL:OsL = 1.75–2.0.

Description. Small, elongate otoliths up to 2.15 mm in length (holotype). OH:OT = 1.85–2.15. Dorsal rim shallow, slightly bent or nearly flat and horizontal; ventral rim shallow and regularly curved. Anterior and posterior rims rounded; anterior rim with blunt, inferior rostrum; posterior rim variable. All rims smooth.

Inner face strongly convex with axial to slightly supramedian sulcus. Sulcus narrow, shallow, sinuate, moderately long; OL:SuL = 1.25–1.35. Ostium slightly wider than cauda and distinctly shorter, its anterior opening indistinct, slightly deepened. Ventral field smooth, without ventral furrow; dorsal field smooth, without dorsal depression. Outer face flat to slightly concave, smooth.

Discussion. For distinction from *E. ardathensis* see above.

Genus *Ipaimuraena* n. gen.

Type species: *Ipaimuraena californiensis* n. sp.

Eymology: A combination of Ipai, the name of the Indian first nation living near the type location and the genus name *Muraena*.

Diagnosis: An otolith-based genus of the family Ophichthidae characterized by the combination of an elongate, slender otolith with a straight sulcus, which clearly opens anteriorly, a moderately large and widened ostium (CaL:OsL = 1.1–1.5), a moderately convex inner face and a thin appearance (OH:OT = 2.3–2.8). The postdorsal portion is usually extended and the dorsal rim usually very shallow, nearly flat.

Discussion. *Ipaimuraena* differs from the coeval *Eophichthus* described above in the relatively slender shape, the clearly anteriorly open and distinctly widened ostium. The ostium is particularly dorsally widened. The otoliths are also thinner and more fragile than *Eophichthus*. Among extant ophichthids, *Ipaimuraena* resembles *Pisodonophis* in otolith shape but differs in the wide and open ostium. *Ipaimuraena* also resembles otoliths of the extant *Brachysomophis* (see Schwarzhans 2019b) in otolith shape but differs in the relatively long sulcus (OL:SuL = 1.4–1.5 vs 1.7). The strong dorsal widening of the ostium is particularly characteristic and not comparable to patterns observed in extant ophichtid otoliths.

Species. Two species, *Ipaimuraena californiensis* n. sp. from the middle Eocene of California and *Ipaimuraena fusiformis* n. sp. from the middle Eocene of California and Mississippi.

Ipaimuraena californiensis n. sp.

Fig. 3AB–AF

Holotype: Fig. 3AD–AF, LACM 60142, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 2 specimens, same data as holotype, LACM 60143.

Etymology: After the state of California.

Diagnosis: OL:OH = 2.25–2.45. Dorsal rim shallow, nearly straight or slightly undulating; ventral rim shallow; rostrum distinct; posterior tip expanded. OL:SuL = 1.4–1.5. Ostium dorsally widened, anteriorly open.

Description. Small, slender, thin otoliths up to 3.4 mm in length (holotype 2.35 mm). OH:OT = 2.4–2.6. Dorsal rim shallow, slightly higher anteriorly than posteriorly or horizontal, smooth or slightly undulating; ventral rim shallow and regularly curved, deepest slightly anterior of middle. Anterior tip with rather distinct rostrum of up to 12% of OL, broad excisura and knob-like antirostrum very weak. Posterior rim strongly expanded postdorsally. All rims smooth except for occasionally slightly undulating dorsal rim.

Inner face slightly convex with slightly supramedian sulcus. Sulcus narrow, moderately deepened, short. CaL:OsL = 1.4–1.5. Ostium distinctly wider than cauda and distinctly shorter, its anterior opening distinct, slightly deepened. Dorsal margin of ostium strongly bent, nearly vertical; ventral margin of ostium moderately widened. Ventral field smooth, without ventral furrow; dorsal field smooth, with very short dorsal depression. Outer face slightly concave, smooth.

Discussion. *Ipaimuraena californiensis* differs from *I. fusiformis* n. sp. in being more slender (OL:OH = 2.25–2.45 vs 1.95–2.1), thinner in thickness, and in showing a somewhat stronger expansion of the posterior tip. The ratio CaL:OsL is higher than in *I. fusiformis* n. sp. (1.4–1.5 vs 1.1–1.3).

Ipaimuraena fusiformis n. sp.

Fig. 3AG–AK

Holotype: Fig. 3AG–AI, LACM 60144, upper Lutetian, Ardath Shale, Black's Beach.

Paratype: 1 specimen, Bartonian, Moodys Branch Formation, Jackson, Mississippi, NRM PZ P.19050.

Etymology: From fusiformis (Latin) = fusiform, referring to the shape of the holotype specimen.

Diagnosis: OL:OH = 1.95–2.1. Dorsal rim shallow, gently curved; ventral rim shallow, regularly curved; rostrum distinct, short; posterior tip moderately expanded. OL:SuL = 1.4–1.45. Ostium dorsally widened, anteriorly open.

Description. Small, fusiform, moderately slender, and moderately thin otoliths up to 2.9 mm in length (holotype). OH:OT = 2.2–2.3. Dorsal rim shallow, gently curved or nearly horizontal, slightly undulating; ventral rim shallow and regularly curved, deepest at its middle. Anterior tip with blunt rostrum up to 12% of OL, broad excisura and knob-like antirostrum very weak. Posterior rim expanded, tapering. All rims smooth or slightly undulating.

Inner face distinctly convex with axial sulcus. Sulcus narrow, moderately deepened, short.

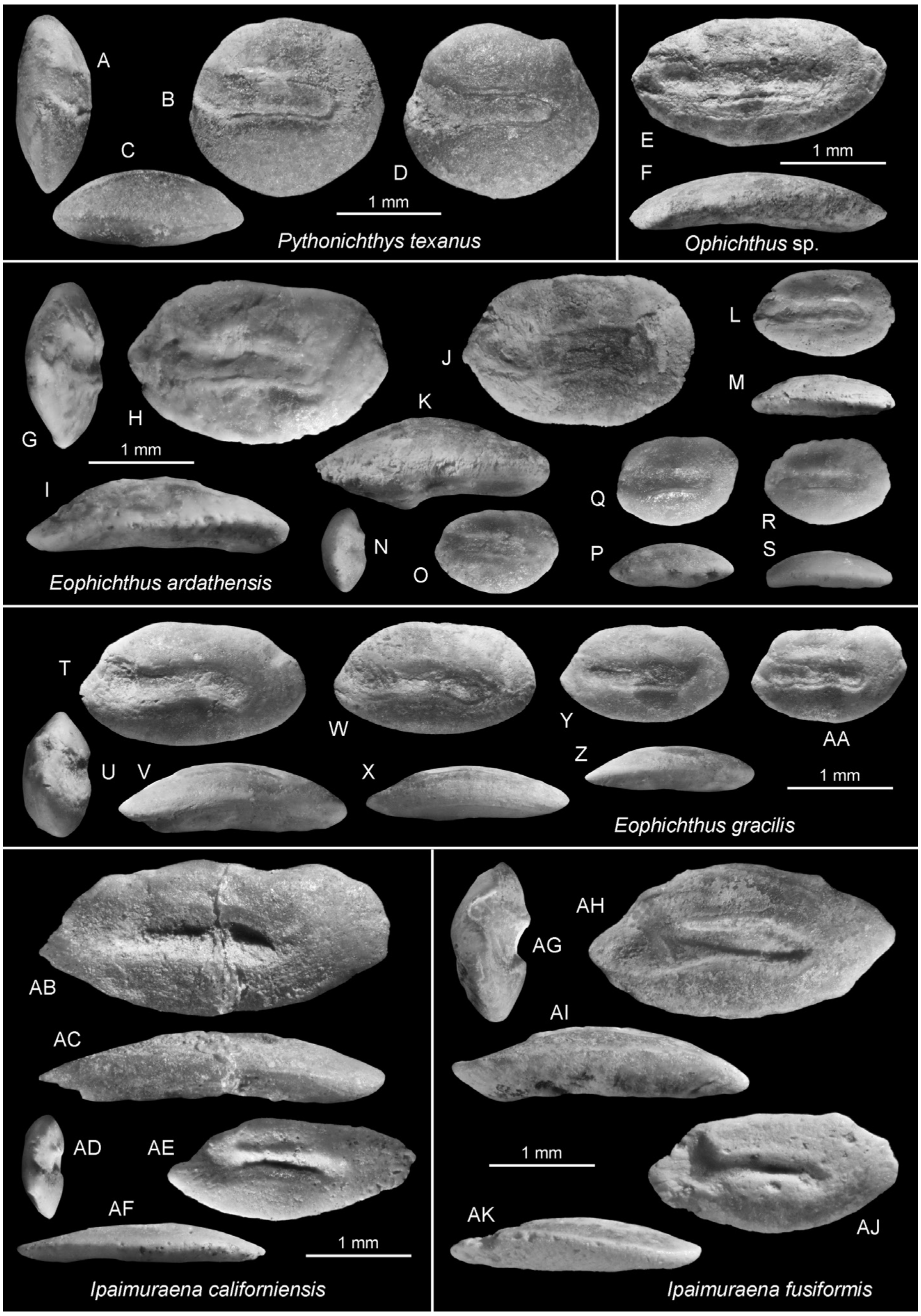


Fig. 3 - A–D) *Pythonichthys texanus* (Dante & Frizzell, 1965), Black's Beach, LACM 60137, A anterior view, C ventral view.
E–F) *Ophichthus* sp., Black's Beach, LACM 60138, F vetral view.
G–S) *Eophichthus ardathensis* n. gen., n. sp.; G–I holotype, Miramar Reservoir site, LACM 60089, G anterior view, I ventral view; J–S paratypes, Black's Beach, LACM 60139 (J–K reversed), K, M, P, S ventral views, N anterior view.
T–AA) *Eophichthus gracilis* n. gen., n. sp.; T–V holotype, Black's Beach, LACM 60140, U anterior view, V ventral view; W–AA paratypes, Black's Beach, LACM 60141 (W–X reversed), X, Z ventral views.
AB–AF) *Ipaimuraena californiensis* n. gen., n. sp.; AD–AF holotype, Black's Beach, LACM 60142, AD anterior view, AF ventral view; AB–AC paratype, Black's Beach, LACM 60143 (reversed), AC ventral view.
AG–AK) *Ipaimuraena fusiformis* n. gen., n. sp.; AG–AI holotype, Torres Pines, LACM 60144. AG anterior view, AI ventral view; AJ–AK paratype, Moodys Branch, Bartonian, Mississippi, NRM PZ P.19050 (reversed), AK ventral view.

CaL:OsL = 1.1–1.3. Ostium distinctly wider than cauda and slightly shorter, its anterior opening distinct, slightly deepened. Dorsal margin of ostium strongly bent upward; ventral margin of ostium moderately widened. Ventral field smooth, without ventral furrow; dorsal field smooth, with very short dorsal depression. Outer face flat or slightly concave, smooth.

Discussion. *Ipaimuraena fusiformis* is recorded from the middle Eocene of California and Mississippi. For distinction from its coeval congener *I. californiensis* see above.

Genus *Ophichthus* Ahl, 1789

***Ophichthus* sp.**

Fig. 3E–F

Material: 1 specimen, Ardath Shale, Black's Beach, LACM 60138.

Discussion. The single otolith of 2.45 mm in length is moderately well preserved and resembles extant *Ophichthus* otoliths in otolith and sulcus shape and proportions (for extant otoliths see Lombarte et al. 2006; Nolf 2013; Schwarzhans 2019b).

In the light of only a single specimen being available we refrain from a specific identification.

Family Muraenesocidae Bleeker, 1864
Genus *Muraenesox* McClelland, 1843

Muraenesox websteri (Frost, 1933)

Fig. 4A–F

1933 Otolithus (*Congridarum*) *websteri* - Frost: pl. 12, fig. 10.
2007 genus *Congridarum websteri* Frost, 1933 - Schwarzhans: fig. 4H-M (see there for further references).
2013 "*Congrida*" *websteri* Frost, 1933 - Nolf: pl. 27.
2022 "*Conger*" *websteri* (Frost, 1933) - Lin & Nolf: fig. 13A-C.

Material: 11 specimens: 8 specimens, Ardath Shale, Black's Beach, LACM 60145; 3 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60090.

Discussion. *Muraenesox websteri* was originally described from the middle Eocene of England (Frost 1933; Stinton 1975) and subsequently from the middle Eocene of Belgium, northern Germany (Schwarzhans 2007), and northeastern America (Virginia) (Lin & Nolf 2022). The species has been described under multiple synonymies for which reference is made to Schwarzhans (2007) and Nolf (2013). Recently, Lin & Nolf (2022) described a further species as "*Muraenesox*" *barrytownensis* Lin & Nolf, 2022 from the middle Eocene of Alabama which differs in the more compressed shape and the slightly bent caudal tip. Lin & Nolf (2022) also commented to *M. websteri* and considered it a congrid because of "the narrower sulcus and more pronounced ventral area". We believe that the narrow sulcus is an ontogenetic feature and large specimens at about 10 mm in length (Fig. 4A) have a much wider sulcus. Other features more typical for muraenesocids are the massive postdorsal projection and the steeply inclined sulcus. We therefore consider this species as a muraenesocid - *Muraenesox websteri*. Other supposed Eocene *Muraenesox* species are all from Europe: *Muraenesox cymbium* Stinton, 1966 from the early Eocene, *M. fissura* (Stinton & Nolf 1970) and *M. furcatus* Schwarzhans, 2007 both from the middle Eocene.

Otoliths of the genus *Conger* look similar in many aspects such as the general otolith outline, the inclined sulcus, and the ostium closely approaching the anterior rim of the otolith. They differ from muraenesocid otoliths in the less strongly developed postdorsal projection, a tapered posterior tip forming a blunt point and the colliculum being somewhat reduced towards the termination of the cauda (for extant otoliths see Schwarzhans 2019b). Like *Muraenesox*, *Conger* otoliths are well known since Eocene times but have not been identified yet from California. For comparison we have figured a specimen of *Conger vetustus* Frizzell & Lamber, 1962 from the Yazoo Clay (Fig. 4G–H; NRM PZ P.19051).

Family Congridae Kaup, 1856
Subfamily Bathymyrinae Böhlke, 1949

Genus *Protanago* n. gen.

Type species: *Otolithus* (*Platessae*) *sector* Koken, 1888.

Etymology: Combination of protos (Greek) = first and anago (Japanese) = eel and word stem found in several congrid genera, referring to the early occurrence of the genus in respect to the stratigraphy and the phylogenetic position in bathymyrins.

Diagnosis: An otolith-based genus of the subfamily Bathymirinae that shows the typical rounded diamond-shaped shape outline of the otoliths of this subfamily, whereby the long axis is longer than the vertical axis (OL:OH = 1.1–1.45). The well-developed dorsal lobe is usually positioned at the middle of the dorsal rim; the posterior tip is usually sharper than the anterior tip. The inner face is strongly convex and smooth with a shallow, slightly supramedian positioned sulcus. The sulcus is typical for bathymyrine otoliths. Its ostium is short with a backward oriented ostial channel that does not reach the predorsal rim of the otolith. The cauda is long with gently curved dorsal margin and a wavy ventral sulcus margin (see Schwarzhans, 2019b, for terminology). The caudal tip is tapered or rounded. The ventral field is smooth, and the dorsal field without depression.

Discussion. *Protanago* resembles otoliths of the extant *Ariosoma* Swainson, 1838, which is known since at least early Miocene (Schwarzhans 2019b; Agiadi et al. 2021), in general habitus but differs in the lack of the s-shaped sulcus, which is considered to represent a diagnostic autapomorphic character of *Ariosoma* (Schwarzhans 2019b). Otoliths of other bathymyrine genera differ from *Protanago* in the flat inner face (*Bathymyrus*, *Parabathymyrus*), the shortened sulcus (*Chiloconger*), the anteriorly shifted dorsal lobe (*Paraconger*), and the simpler sulcus shape which is also deepened (*Congriscus*) (for extant otoliths of these genera see Schwarzhans 2019b). We consider *Protanago* an extinct genus near the base of the bathymyrine clade, possibly related to *Congriscus* and *Paraconger*.

Species. Most otolith-based species now placed in *Protanago* have in the past been considered as species of *Ariosoma* or *Paraconger*, whereby the latter is also known with several species since Eocene times. Here, we consider the following 6 species to belong to *Protanago*: *Protanago brazosensis* (Dante &

Frizzell 1965) from the middle Eocene of the US Gulf Coast and California, *Protanago miramarensis* n. sp. from the middle Eocene of California, *Protanago nonsector* (Nolf & Stringer, 2003) from the middle Eocene of the Gulf Coast and the late Eocene of Italy (Girone & Nolf 2008) being the only species of the genus recorded outside of North America, *Protanago sector* (Koken, 1888) from the middle Eocene of the Gulf Coast and the US East Coast, *Protanago solidus* (Müller, 1999) middle Eocene of the US East Coast, and *Protanago wechesensis* (Lin & Nolf, 2022) from the middle Eocene of the Gulf Coast.

Protanago brazosensis (Dante & Frizzell, 1965)

Fig. 4I–N

1965 *Parbatmya brazosensis* - Dante & Frizzell (in Frizzell & Dante): pl. 86, fig. 5, 6, 11-13.
2022 *Paraconger brazosensis* (Dante & Frizzell, 1965) - Lin & Nolf: fig. 11G-L.

Material: 550 specimens: 534 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60146; 16 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60091.

Discussion. Otoliths of *Protanago brazosensis* are recognized by their rather regularly rounded outline and the wide and shallow sulcus. The otoliths are also relatively compressed (OL:OH = 1.2–1.35). More compressed are only the otoliths of *Protanago nonsector* and *Protanago solidus* (OL:OH = 1.05–1.2). Otoliths of *Protanago nonsector* also have a narrower sulcus (for comparison see Fig. 4X–AB; Moodys Branch Formation, NRM PZ P.19052-53).

Protanago miramarensis n. sp.

Fig. 4O–W

Holotype: Fig. 4Q–S, LACM 60092, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 20 specimens: 19 specimens same data as holotype, LACM 60093; 1 specimen, Ardath Shale, Black's Beach, figured specimens LACM 60147.

Referred specimens: 74 specimens, same data as holotype, LACM 60094 and collection WWS and GLS.

Etymology: Referring to the type location, Miramar Reservoir site, San Diego County, southern California.

Diagnosis: OL:OH = 1.3–1.4. Dorsal rim with relatively narrow middorsal lobe. Anterior rim rounded; posterior tip tapering. Sulcus narrow, slightly deepened, relatively short; OL:SuL = 1.5–1.55. Cauda very narrow with tapering tip.

Description. Relatively small, relatively slender otoliths seemingly not exceeding 3.2 mm in length (holotype 2.55 mm). OH:OT = 2.7–3.1. Dorsal rim high, with distinct and relatively narrow mid-dorsal lobe; ventral rim deep and regularly curved, deepest slightly in front of its midpoint. Anterior tip broadly rounded, posterior tip slightly expanded, tapering or rounded. All rims smooth.

Inner face distinctly convex with slightly supramedian sulcus. Sulcus narrow, slightly deepened throughout, relatively short. Distinction of ostium and cauda marked by notch on ventral margin of sulcus; CaL:OsL = 1.45–1.85. Ostium with short vertical to slightly backward inclined ostial channel. Cauda narrow, its dorsal margin very slightly bent and its ventral margin wavy; caudal tip tapering. Ventral field smooth, without ventral furrow; dorsal field smooth, without discernable dorsal depression. Outer face flat or slightly concave, smooth.

Discussion. *Protanago miramarensis* apparently was a relatively small species compared to the other known species of the genus. It resembles most *P. sector* in its slender shape and relatively high ratio OL:OH >1.3 but differs in the very narrow and short sulcus (OL:SuL = 1.5–1.55 vs 1.3–1.4) and the tapering caudal tip. Otoliths are figured of *P. sector* from Moodys Branch and Brazos River (Fig. 4AC–AF; NRM PZ P.19054-55) for comparison.

For further comparison otoliths are figured from another fossil, otolith-based genus and species from the late Eocene of the Gulf Coast: *Parbatmya fornicata* (Frizzell & Lamber, 1962) from the Yazoo Clay of Cynthia, Mississippi (Fig. 5A–D; NRM PZ P.19056-57). This species was selected as type species for *Parbatmya* Frizzell, Lamber & Dante, 1965 (in Frizzell & Dante 1965). *Parbatmya* differs from the otolith-based genus *Alaconger* Schwarzhans, 2010 from the Maastrichtian to Eocene in the shallower sulcus and the lack of a dorsal depression.

Subfamily Congrinae Kaup, 1856
Genus *Acromycter* Smith & Kanazawa, 1977

Acromycter gratus n. sp.

Fig. 5X–AA

Holotype: Fig. 5X–Z, LACM 60148, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 2 specimens, same data as holotype, LACM 60149.

Etymology: From gratus (Latin) = grateful, acceptable, referring to the systematic allocation of the species.

Diagnosis: OL:OH = 1.35–1.45. Predorsal rim broadly expanded; ventral rim shallow; posterior rim blunt. Inner face nearly flat. Sulcus very small and narrow, nearly horizontal; OL:SuL = 2.4–2.5; no ostial channel. Broad dorsal depression.

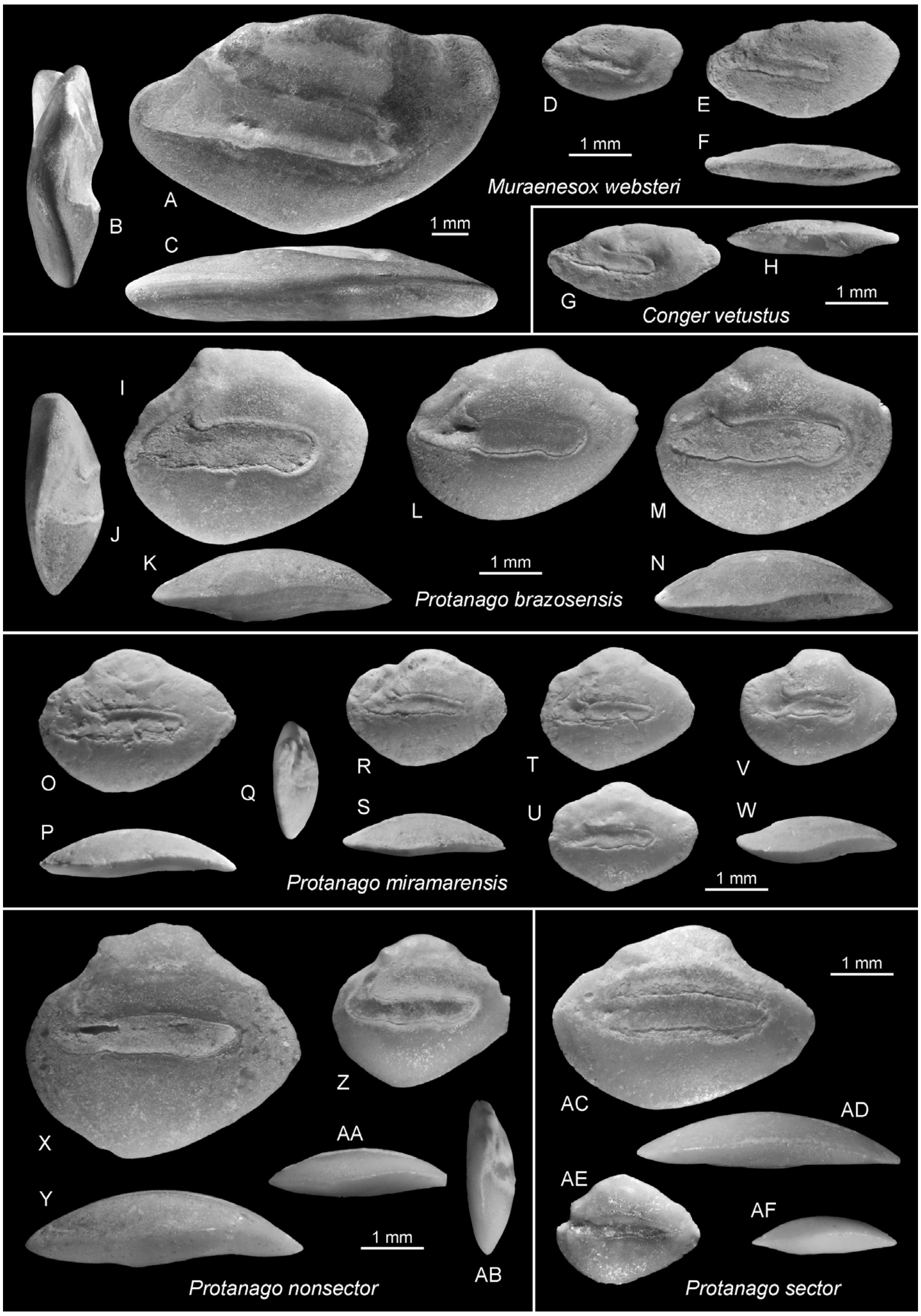


Fig. 4 - A–F) *Muraenesox websteri* (Frost, 1933), Black's Beach, LACM 60145 (D reversed), B anterior view, C, F ventral views.

G–H) *Conger vetustus* Frizzell & Lamber, 1962, Yazoo Clay, Priabonian, Mississippi, NRMZ PZ P.19051 (reversed), H ventral view.

I–N) *Protanago* n. gen. *brazosensis* (Dante & Frizzell, 1965), Black's Beach, LACM 60146 (reversed), J anterior view, K, N ventral views.

O–W *Protanago miramarensis* n. gen., n. sp.; Q–S holotype, Miramar Reservoir site, LACM 60092 (reversed), Q anterior view, S ventral view; O–P, T–W paratypes, Miramar Reservoir site, LACM 60093 (reversed), P, W ventral views.

X–AB *Protanago* n. gen. *nonsector* (Nolf & Stringer, 2003), Moodys Branch, Bartonian, Mississippi, NRM PZ P.19052-53 (reversed), AB anterior view, Y, AA ventral views.

AC–AF *Protanago* n. gen. *sector* (Koken, 1888); AC–AD Moodys Branch, Bartonian, Mississippi, NRM PZ P.19054 (reversed), AD ventral view; AE–AF Brazos River, Bartonian, Texas, NRM PZ P.19055 (reversed), AF ventral view.

Description. Small, oval, robust otolith up to 2.0 mm in length (holotype). OH:OT = 2.6. Dorsal rim with broad, rounded predorsal angle and low, rounded postdorsal angle. Ventral rim shallower than dorsal rim, deepest anterior of its middle. Anterior rim broadly rounded, inferior; posterior rim blunt. All rims smooth.

Inner face nearly flat, with very small and narrow, undivided, uniform sulcus on center of inner face. Sulcus filled by uniform, slightly deepened colliculum. Sulcus nearly horizontal, inclined at about 2° against otolith axis. No ostial channel present but possible remnants seen vertical at tip of sulcus. Ventral field smooth, without ventral furrow; dorsal field with distinct cup-shaped depression.

Discussion. *Acromycter gratus* is based on relatively small specimens and it is possible that larger ones could be expected. However, these otoliths are highly diagnostic, despite the overall rather reduced morphology that a description is warranted. We know of no other Eocene congrid otolith with such a reduced sulcus morphology in combination with a distinct dorsal depression. The pattern thus is phylogenetically advanced like the one found in extant otoliths of *Acromycter nezumi* (Asano, 1958) (see Schwarzhans 2019b for otolith figures).

Genus *Gnathophis* Kaup, 1859

Gnathophis frizzelli n. sp.

Fig. 5E–O

Holotype: Fig. 5G–I, LACM 60095, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 40 specimens: 20 specimens same data as holotype, LACM 60096; 20 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60150.

Referred specimens: 1539 specimens: 993 specimens same data as holotype, LACM 60097 and collection WWS and GLS; 546 specimens, Ardath Shale, Black's Beach, LACM 60151 and collection WWS and GLS.

Etymology: In memory of Don L. Frizzell for his contributions to the knowledge of fossil otoliths from the USA.

Diagnosis: OL:OH = 1.4–1.6. Dorsal rim with well-developed predorsal angle or small lobe. Posterior tip expanded, tapering. Sulcus narrow, short, distinctly deepened, inclined at 10–12°, relatively short; OL:SuL = 1.7–1.75. Ostial channel broad. Inner face strongly convex. No or indistinct dorsal depression.

Description. Relatively large, moderately slender otoliths up to 7.3 mm in length (holotype 6.3 mm). OH:OT = 2.4–2.8, decreasing with size. Dorsal rim high, with distinct and high predorsal angle, sometimes developed as lobe; ventral rim deep and regularly curved, deepest in front of its middle. Anterior tip with rounded median projection, posterior tip distinctly expanded, tapering. All rims smooth, except dorsal rim irregularly undulating.

Inner face distinctly convex with slightly supramedian sulcus. Sulcus narrow, distinctly deepened throughout, relatively short, inclined against otolith axis. Distinction of ostium and cauda marked by notch on ventral margin of sulcus (Fig. 5E); CaL:OsL = 1.4–1.7. Ostium reaching close to anterior rim of otolith, with broad vertical to slightly backward inclined ostial channel filled by collicular matter. Cauda with nearly straight dorsal rim; ventral sulcus margin wavy; caudal tip rounded. Ventral field smooth, without ventral furrow; dorsal field smooth, without discernable dorsal depression. Outer face flat or slightly concave, often with shallow central umbo, smooth.

Discussion. *Ganthophis frizzelli* is inconspicuous at first, but there are only few species in the Eocene which combine this morphotype of sulcus, the strongly convex inner face, the broad ostial channel and the absence or very weak development of a dorsal depression. These are *G. meridies* Frizzell & Lamber, 1962 from the early to middle Eocene USA Gulf Coast and *G, yazooensis* (Nolf & Stringer, 2003) from the late Eocene of the USA Gulf Coast. *Gnathophis frizzelli* differs from both of them in the strongly expanded posterior tip and from *G. yazooensis* in addition in the mostly more elongate shape (OL:OH = 1.4–1.6 vs 1.3–1.45) and the distinct wavy ventral margin of the sulcus. Frizzell & Lamber (1962) figured otoliths as *"Conger" brevior* (Koken, 1888) from the Oligocene of the USA Gulf Coast which according to the review of Koken's type material by Nolf (2003) represents a different species than described by Koken and probably of the genus *Gnathophis.* It appears to have a very steeply inclined sulcus (+20°) and therefore probably represents a different species.

Genus *Rhynchoconger* Jordan & Hubbs, 1925

Rhynchoconger eocenicus (Shepherd, 1916)

Fig. 5P–U

1916 *Otolithus* (*Apogonidarum*) *eocenicus* - Shepherd: fig. 154.4.
2019a *Rhynchoconger eocenicus* (Shepherd, 1916) - Schwarzhans: fig. 15.1–7 (see there for further references).

Material: 461 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60152, also LACM 60153 and collection WWS and GLS.

Discussion. *Rhynchoconger eocenicus* is recognized by the simple, straight cauda, the broad, vertical ostial channel, a rather regular oval shape with slightly pointed anterior and posterior tips and the presence of a distinct, somewhat rectangular-shaped dorsal depression. It appears to have been a cosmopolitan species during the early and middle Eocene known from numerous locations in Europe, New Zealand, Maryland (USA) and now from California. Lin & Nolf (2022) described *Rhynchoconger* sp. from the middle Eocene of the Gulf Coast, which seems to represent a different species characterized by a more elongate shape and, at least sometimes, concave postdorsal section. *Rhnychoconger sanctus* (Frizzell & Lamber, 1962) from the Oligocene of the Gulf Coast is also more slender and thinner than *R. eocenicus* (see Nolf 2013, plate 25 for figure). Furthermore, *R. sanctus* has a round to irregular-shaped dorsal depression.

Genus *Uroconger* Kaup, 1856

Uroconger priscus n. sp.

Fig. 5V–W

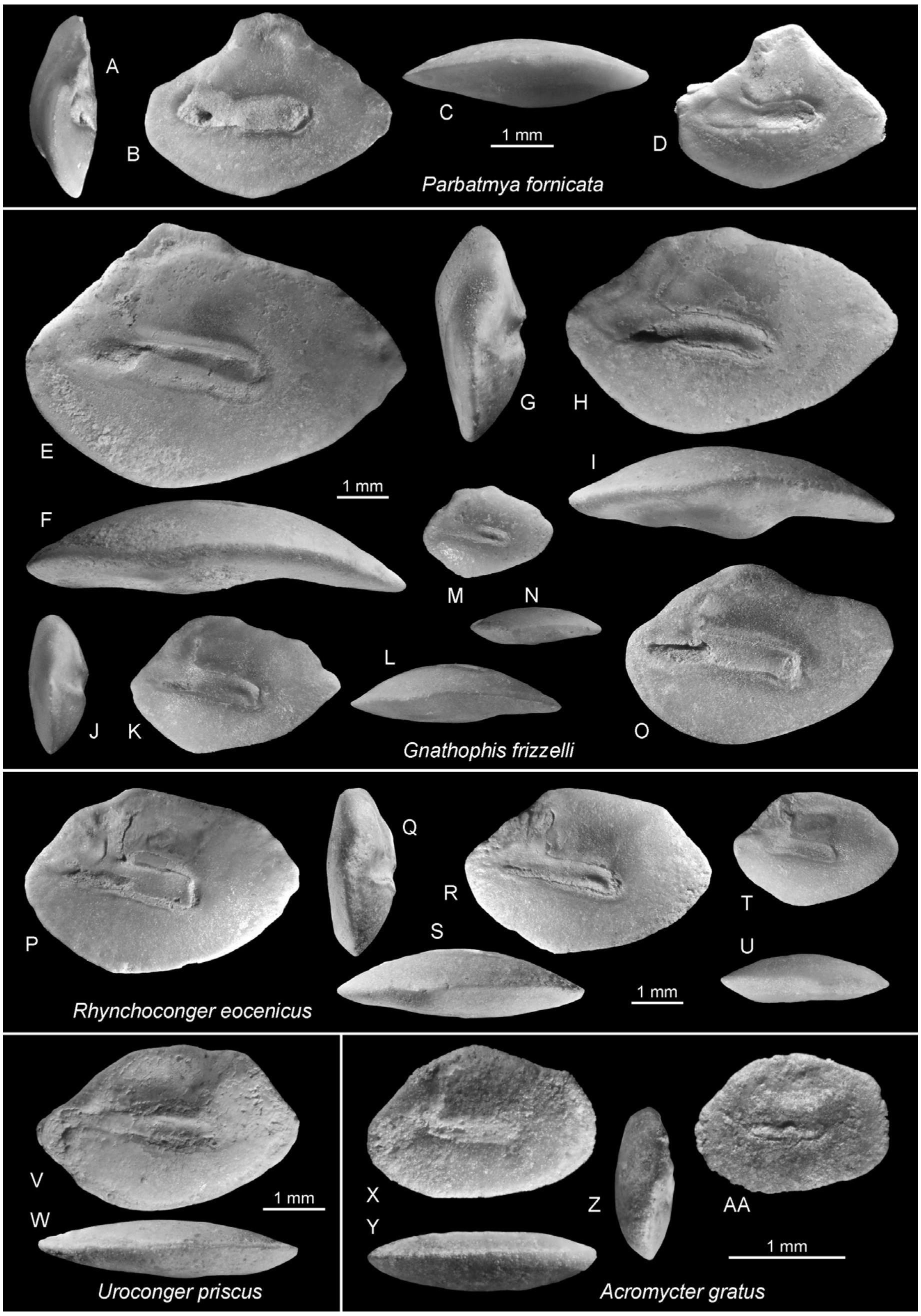


Fig. 5 - A–D) *Parbatmya fornicata* (Frizzell & Lamber, 1962), Yazoo Clay, Priabonian, Mississippi, NRMZ PZ P.19056-57 (reversed), A anterior view, C ventral view.
E–O) *Gnathophis frizzelli* n. sp.; **G–I** holotype, Miramar Reservoir site, LACM 60095 (reversed), G anterior view, I ventral view; E–F, M–N paratypes, Miramar Reservoir site, LACM 60096 (M–N reversed), F, N ventral views; J–L, O paratype, Black's Beach, LACM 60151 (O reversed), J anterior view, L ventral view.
P–U) *Rhynchoconger eocenicus* (Shepherd, 1916), Black's Beach, LACM 60152 (T–U reversed), Q anterior view, S, U ventral view.
V–W) *Uroconger priscus* n. sp., holotype, Miramar Reservoir site, LACM 60278 (reversed), W ventral view.
X–AA) *Acromycter gratus* n. sp.; X–Z holotype, Black's Beach, LACM 60148 (reversed), Y ventral view, Z anterior view; AA paratype, Black's Beach, LACM 60149.

Holotype (and unique specimen): Fig. 5V–W, LACM 60278, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Etymology: From priscus (Latin) = ancient, referring to the early stratigraphic occurrence of the species.

Diagnosis: OL:OH = 1.6. Dorsal rim with pre- and postdorsal angles equally strongly developed. Anterior and posterior tips slightly pointed, but with rounded tips. Sulcus straight, anteriorly narrowing with fading opening; no ostial channel. Colliculum straight extending into narrowing anterior section of sulcus and reaching close to anterior rim of otolith. Ventral furrow very close to ventral rim of otolith; dorsal depression large and distinct.

Description. The single otolith is well preserved and 4.15 mm in length. OH:OT = 2.8. Dorsal rim high, with distinct, rounded pre- and postdorsal angles on equal height and section in-between nearly straight and horizontal; pre- and postdorsal rims straight and inclined. Ventral rim deep and regularly curved, deepest in front of its midpoint. Anterior tip with moderately pointed median projection, posterior tip nearly symmetrical but more strongly rounded. All rims smooth, except dorsal rim slightly undulating at its middle.

Inner face slightly convex with central sulcus. Sulcus narrow, uniform, shallow, straight, inclined against otolith axis at 5°. OL:SuL = 1.55. Sulcus anteriorly narrowing, without ostial channel. Shallow, uniform colliculum filling most of sulcus, somewhat narrowing anteriorly into narrowed sulcus and reaching close to anterior rim of otolith. Ventral field smooth, with distinct ventral furrow close to ventral rim of otolith; dorsal field with wide, rather distinct dorsal depression. Outer face slightly convex similar to inner face, smooth.

Discussion. This is a typical otolith of the genus *Uroconger* characterized by the colliculum extending into the narrowing anterior part of the sulcus, presence of a wide dorsal depression and absence of an ostial channel. It differs from the extant species (otoliths are known from two of the three extant species; see Schwarzhans, 2019b for figures) in the more compressed shape (OL:OH = 1.6 vs 1.7–1.85), the shape of the dorsal rim, the ostial colliculum extending further towards the anterior rim of the otoliths, i.e., being less reduced, and the slightly inclined sulcus. *Uroconger*? sp. was noted from the Eocene Yazoo Clay in Louisiana, USA, by Nolf & Stringer (2003; pl. 2, figs 7–8). However, these otoliths are here not considered to represent the genus *Uroconger* since they have a distinct, vertical ostial channel. Therefore, *Uroconger priscus* represents the first known fossil record of the genus.

Family Nettastomatidae Bleeker, 1864
Genus *Hoplunnis* Kaup, 1859

Hoplunnis diagonalis n. sp.

Fig. 6A–F

Holotype: Fig. 6A–B, LACM 60154, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 7 specimens, same data as holotype, LACM 60155.

Etymology: From diagonalis (Latin) = diagonal, referring to the step inclination of the sulcus.

Diagnosis: OL:OH = 1.8–2.05. Dorsal and ventral rims nearly straight; posterior rim blunt; anterior dorsally pronounced. Sulcus with flat ventral and curved dorsal rim, small, distant from anterior rim of otolith, steeply inclined at 25–30°. OL:SuL = 2.4–2.6.

Description. Slender, small and relatively thin otoliths up to 2.5 mm in length (holotype). OH:OT = 2.0–2.35. Dorsal and ventral rims both very shallow, nearly horizontal; dorsal rim very slightly undulating; ventral rim deepest far anterior of its midpoint. Anterior rim steeply inclined, dorsally pronounced in rounded angle at junction of anterior and dorsal rims; posterior rim blunt, nearly vertical.

Inner face almost flat, with steeply inclined, slightly anteriorly shifted sulcus terminating far from anterior rim of otolith. Sulcus-shape very characteristic with flat ventral margin and distinctly bent dorsal margin; filled by single undivided, shallow to slightly deepened colliculum. No ventral furrow or dorsal depression but slight depression posterior to sulcus.

Discussion. *Hoplunnis diagonalis* his highly characteristic because of its peculiar sulcus which is similar to *H. ariejansseni* Nolf, 1988 from the Eocene of the Aquitaine Basin in France and northern Italy (Girone & Nolf, 2008) but differs in the longer sulcus (OL:SuL = 2.4–2.6 vs 3.0–4.7), the lack of a ridge connecting the sulcus with the anterior tip of the otolith and the steep inclination of the sulcus (25° vs <20°). These traits also distinguish *H. diagonalis* from extant species of the genus (see Schwarzhans, 2019b for figures).

Family Protanguillidae Johnson, Ida & Miya, 2012
Genus indet.

Protanguilla? glaber (Koken, 1888)

Fig. 6G–N

1888 *Otolithus* (*Soleae*) *glaber* - Koken: pl. 18, fig. 3.
1999 "genus aff. *Pseudophichthys*" *oviformis* - Müller: fig. 21/3-4.
1999 ?"genus aff. *Pseudophichthys*" *laevis* - Müller: fig. 21/5-6.
2003 "*genus* aff. *Pseudophichthys*" *glaber* (Koken, 1888) - Nolf: pl. 1, fig. 4.
2003 "*genus* aff. *Pseudophichthys*" *glaber* (Koken, 1888) - Nolf & Stringer: pl. 1, fig. 13-18.
2019 ?*Pseudophichthys* sp. - Ebersole, Cicimurri & Stringer: fig. 69k-l.
2022 *Pseudophichthys glaber* (Koken, 1888) - Lin & Nolf: fig. 9G-K.

Material: 5 specimens: 4 specimens, Ardath Shale, Black's Beach, LACM 60156; 1 specimen, Mission Valley Formation, Miramar Reservoir site, LACM 60098.

Discussion. This species and similar elongate otoliths with a distinctly inclined, small, centrally positioned, undivided, uniform sulcus with a shallow colliculum standing far from the anterior rim of the otolith have traditionally been placed in the genus *Pseudophichthys*. Other species referred to *Pseudophichthys* in Nolf (2013) are *P. elongatus* (Sulc, 1932) from the late Eocene of the Aquitaine Basin in France, *P. guttulus* (Stinton, 1975) from the middle Eocene of England and France, *P. lenticularis* (Koken, 1884) from the Oligocene of the North Sea Basin and *P. sincerus* (Schwarzhans, 2010) from the Miocene of the North Sea Basin. They all differ substantially from the extant *Pseudophichthys splendens*

(Lea, 1913) (for otolith figures see Schwarzhans, 2019b) in the way that otoliths of *P. splendens* are more compressed. Otoliths of *Pseudophichthys splendens* show a small, nearly horizontal colliculum in a sulcus with an anterior, horizontal ostial channel connecting to the anterior tip of the otolith. *Pseudophichthys* today is a monospecific genus with a single species, *P. splendens*, in tropical West Africa. A very similar otolith-based species has been described from the Early Pliocene of southern France as *Pseudophichthys escaravatierensis* Nolf & Cappetta, 1989.

Schwarzhans (2019a) established a fossil otolith-based genus for similar otoliths in appearance from the Eocene and Oligocene of New Zealand with a small, centrally positioned colliculum but a distinct dorsally directed ostial channel as *Notoconger hesperis* Schwarzhans, 2019 and *N. devexus* Schwarzhans, 2019. A third species possibly belonging to this genus is *N. acer* (Schwarzhans, 1985), originally placed in *Pseudophichthys*, from the late Eocene of Australia. The above-mentioned species, however, cannot be placed in *Notoconger* because of the lack of a vertical ostial channel and not in *Pseudophichthys* because of the steeply inclined sulcus and the lack of a horizontal ostial channel. So far, we have identified only one otolith pattern combining all the features observed in these enigmatic fossil otoliths, and that is in the extant, basal anguilliform genus *Protanguilla* (see Schwarzhans 2019b for figures). However, the otoliths of the extant *Protanguilla palau* show a nearly horizontal sulcus while in the fossil species discussed above the sulcus is distinctly inclined. We therefore allocate *Protanguilla*? *glaber* and related fossil otolith-based species to the Protanguillidae as incertae sedis. Most likely, they represent an extinct genus of the family, which today contains but a single species.

Order **Clupeiformes** Bleeker, 1859
Family Clupeidae Rafinesque, 1810
Genus and species indet.

Clupeidae indet.
Fig. 6O–P

Material: 21 otolith fragments, Ardath Shale, Black's Beach, LACM 60157.

Discussion. None of the specimens are preserved in a way that would allow any further identification. The figured specimen being the best one currently available. It does not represent *Neoopisthopterus weltoni* Lin & Nolf, 2022, described from the Bartonian of Texas, but it could possibly represent the same or a similar species as their *Sardinops* sp. recorded from the same location.

Order **Siluriformes** Cuvier, 1817
Family Ariidae Bleeker, 1862
Genus indet.

Arius*? *planus Frost, 1934
Fig. 6Q–AA

1934 *Arius planus* - Frost: pl. 14, fig. 14.
1977 *Tachysurus planus* (Frost, 1934) - Stinton: pl. 5, fig. 7-8.

Material: 1135 specimens: 532 specimens Ardath Shale, Black's Beach, figured specimens LACM 60158 and collection WWS and GLS; 603 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60099 and collection WWS and GLS.

Discussion. *Arius*? *planus* is among the most common otoliths in both locations; ranked fifth in abundance at the Miramar Reservoir site and ranked seventh at Black's Beach. The population is dominated by large specimens, mostly in the range of 8 to 11 mm in length but smaller specimens in the range of 5.5 mm (Fig. 6Y–AA) and smaller exist as well. However, relatively few specimens are preserved well enough for documentation.

Ariids are represented by lapilli otoliths which show a much lower level of diagnostic valuable characters than sagittae otoliths. Most of the Paleogene ariid otoliths belong to a group characterized by a narrow pseudocauda positioned on the smooth ventral face close to the distal projection of the otolith. In the case of *Arius*? *planus* it does not extend along the mesial edge (for lapilli terminology see Aguilera et al. 2013). A mesial inward curvature is absent. The smooth ventral face is slightly less convex than the sculptured dorsal face. This otolith pattern cannot be connected with any of the extant ariid otolith patterns as depicted by Aguilera et al. (2013, 2020) and likely represents an extinct group or genus within ariids.

Order **Stomiiformes** Regan, 1909
Family Gonostomatidae Gill, 1893
Genus *Progonostoma* Schwarzhans, 2012

Progonostoma torreyensis n. sp.
Fig. 7A–H

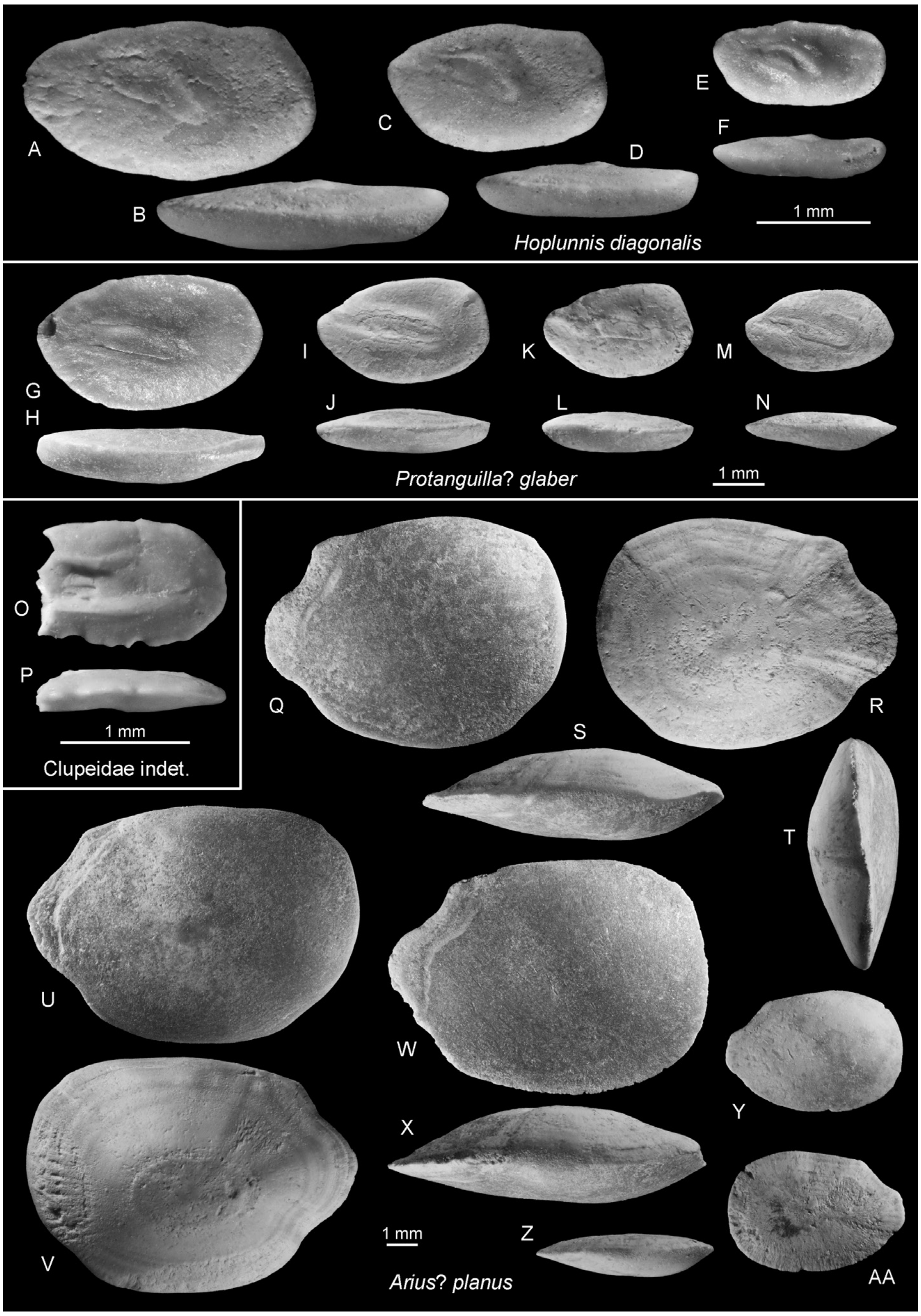


Fig. 6 - A–F) *Hoplunnis diagonalis* n. sp.; A–B holotype, Black's Beach, LACM 60154, B ventral view; C–F paratypes, Black's Beach, LACM 60155 (E–F reversed), D, F ventral views.
G–N) *Protanguilla*? *glaber* (Koken, 1888); G–J Black's Beach, LACM 60156 (reversed), H, J ventral views; K–L Miramar Reservoir site, LACM 60098 (reversed), L ventral view; M–N Brazos River, Bartonian, Texas, NRM PZ P. 19077 (reversed), N ventral view.
O–P) Clupeidae indet., Black's Beach, LACM 60157, P ventral view.
Q–AA) *Arius*? *planus* Frost, 1934; Miramar Reservoir site, LACM 60099 (Q–T, W–AA reversed), Q, U, W, Y ventral views, R, V, AA dorsal views, T anterior view, S, X, Z lateral views.

Holotype: Fig. 7A–C, LACM 60159, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 5 specimens, same data as holotype, LACM 60160.

Referred specimens: 24 specimens, same data as holotype.

Etymology: Referring to the type location, Black's Beach in the Torrey Pines Park.

Diagnosis: OL:OH = 1.3–1.4. Dorsal rim with pronounced postdorsal angle; ventral rim shallow. Rostrum length 15–20% of OL. Sulcus deep, narrow, straight, long, with ostium about as wide as cauda.

Description. Small, thin, delicate otoliths reaching at least 1.95 mm in length (holotype 1.88 mm). Dorsal rim short with pronounced postdorsal angle and depressed or rounded predorsal section. Ventral rim relatively shallow, usually less deep than dorsal rim high. Rostrum rarely fully preserved (Fig. 7G) and moderately long and with pointed tip. Posterior rim oblique, with rounded obtuse angle at about level of caudal tip or below. All rims smooth.

Inner face flat to slightly convex with long, narrow, deepened sulcus reaching close to posterior rim. Ostium slightly deeper than straight cauda, not or only slightly dorsally widened, about half the length of cauda. No colliculi discernable. Dorsal depression indistinct; no ventral furrow. Outer face slightly convex, smooth.

Discussion. The otoliths of *P. torreyensis* resemble the two Paleocene species from Bavaria where the genus was first described – *P. primordialis* Schwarzhans, 2012 and *P. hagni* Schwarzhans, 2012. *Progonostoma torreyensis* differs from *P. primordialis* in the pronounced postdorsal angle and the shallow ventral rim. From *P. hagni* it differs in the longer rostrum and the pronounced postdorsal angle.

Family Sternoptychidae Dumeril, 1806

Genus *Platygonostoma* n. gen.

Type species: *Danaphos gibbsi* Nolf, 1988.

Etymology: A combination of platy (Greek) = wide, referring to the wide ostium and the genus name *Gomostoma*.

Diagnosis: A fossil otolith-based genus of the family Sternoptychidae characterized by the combination of a high-bodied otolith shape (OL:OH = 0.95–1.0), short rostrum (10–15% of OL) and a short, strongly widened ostium (CaL:OsL = 1.7–2.2; OsH:CaH = 1.7–2.5). The otolith size is small up to 1.9 mm in length (holotype of *Danaphos gibbsi* figured in Nolf, 1988).

Discussion. Otoliths of *Platygonostoma* resemble in their high-bodied appearance and the short rostrum otoliths of the extant genera *Danaphos* and *Argyripnus* but differ in the distinctly widened ostium. The combination of a wide ostium and short rostrum and high-bodied otolith shape is unique in Stomiiformes and therefore warrants the recognition of a distinct fossil otolith-based genus.

Species. *Platygonostoma* is monospecific with *P. gibbsi* (Nolf, 1988) known from the late middle Eocene and late Eocene of Europe and California indicating a wide oceanic or bathypelagic distribution pattern.

Paltygonostoma gibbsi (Nolf, 1988)

Fig. 7I–R

1988 *Danaphos gibbsi* - Nolf: pl. 3, fig. 15-16.

Material: 22 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60161.

Genus *Polyipnus* Günther, 1887

Polyipnus apicalis n. sp.

Fig. 7S–AA

Holotype: Fig. 7S–U, LACM 60162, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 5 specimens, same data as holotype, LACM 60163.

Referred specimens: 60 specimens, same data as holotype.

Etymology: From apicalis (Latin) = apical (peak or pinnacle of a mountain top), referring to the sharply pointed dorsal spine.

Diagnosis: OH:OT = 3.0–3.5. Dorsal rim with sharply pointed, high, middorsal spine; predorsal rim steeply inclined and concave above anterior part of cauda; ventral rim deeply and regularly curved. Rostrum relatively short, about 30% of OL, blunt, not extended. Cauda long, reaching close to posterior rim of otolith, with distinct ventral colliculum margin; ostium extremely short. No or feeble posterior furrow. Outer face with massive vertical bulge near posterior rim of otolith.

Description. Small, extremely high-bodied otoliths with a massive posterior part and a thin anterior section reaching about 2.6 mm in length (holotype). OL:OH about 0.7–0.8 (rostrum reconstructed). Dorsal rim high with strongly pointed middorsal spine; predorsal rim steeply inclined, near vertical, with distinct concavity at base; postdorsal rim steep but regularly curved and contingent with half-moon-shaped posterior rim. Ventral rim deep and relatively regularly curved. Rostrum mostly incomplete or damaged but reconstructed to be relatively short (Fig. 7X). No antirostrum or excisura discernable. All rims smooth or slightly undulating.

Inner face flat, with centrally or slightly supramedian sulcus consisting almost entirely of cauda. Cauda long, wide, deepened, reaching close to posterior rim of otolith, its colliculum well marked ventrally. Ostium only at tip of rostrum, very short, not widened and barely distinguishable from cauda. Dorsal field without depression but with steeply inclined furrow connecting postdorsal rim behind middorsal spine with central part of cauda. No or very weak posterior furrow close to posterior rim of otolith. Outer face with massive vertical bulge and rapidly thinning rostral portion, smooth.

Discussion. Otoliths of *Polypnus* and *Ichthyococcus* of the Phosichthyidae are unique amongst teleost otoliths in their high-bodied shape, the thick bulge on the outer face close to the posterior rim of the otolith and the thin, slender rostrum. The latter is usually broken off in fossil specimens, but in the case of *P. apicalis* it appears to have been relatively short. Until now, four fossil otolith-based species of *Polyipnus* have been described from Oligocene and Miocene rocks (see Nolf 2013 and Schwarzhans 2019a). *Polyipnus apicalis* represents the earliest record so far and is readily recognized by the strongly pointed middorsal spine and the relatively long cauda reaching close to the posterior rim of the otolith leaving only a narrow space for an indistinct posterior furrow.

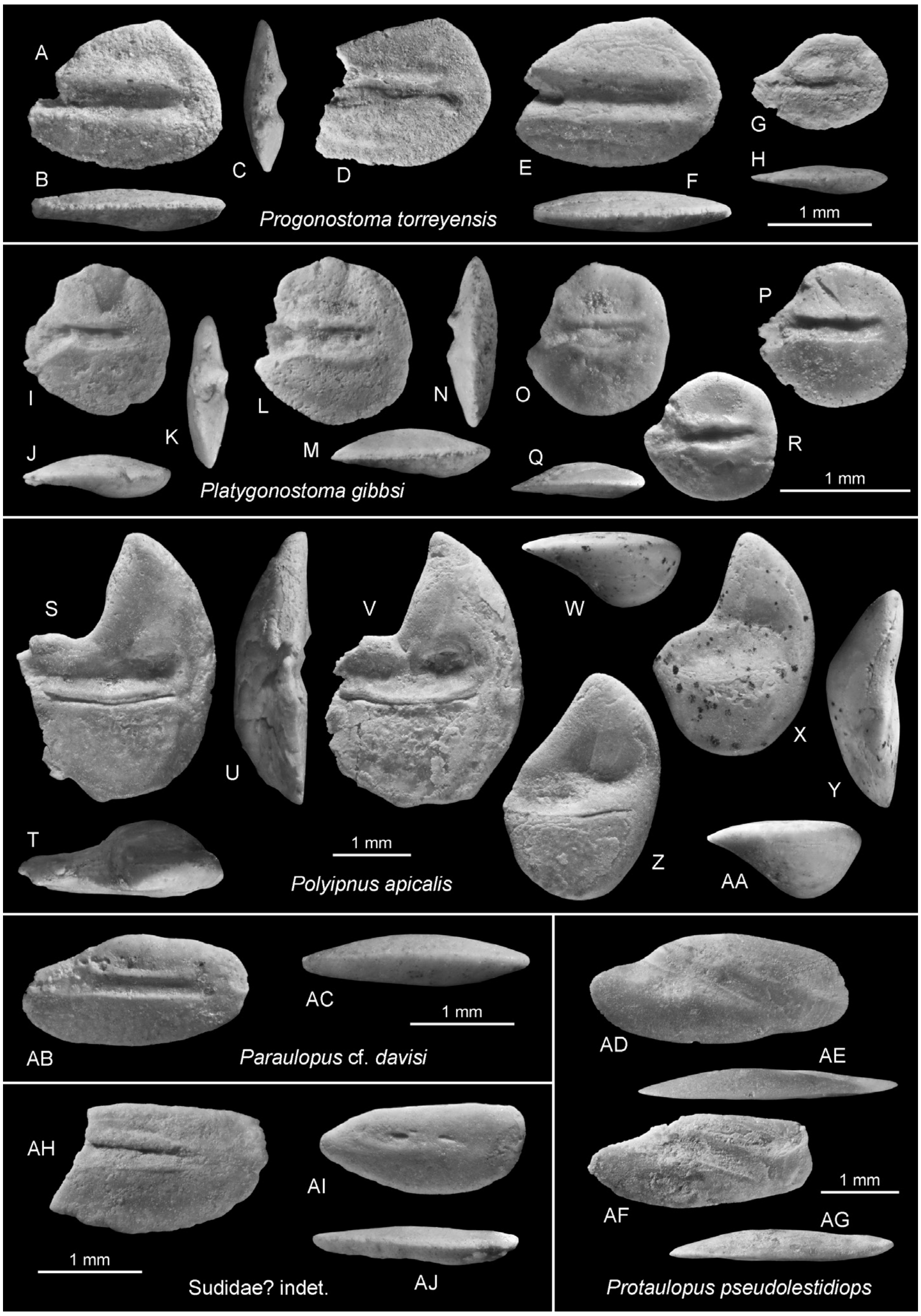


Fig. 7 - A–H) *Progonostoma torreyensis* n. sp.; A–C holotype, Black's Beach, LACM 60159 (reversed), B ventral view, C anterior view; D–H paratypes, Black's Beach, LACM 60160 (D–F reversed), F, H ventral views.
I–R) *Platygonostoma* n. gen. *gibbsi* (Nolf, 1988), Black's Beach, LACM 60161 (P–R reversed), K anterior view, N posterior view, J, M, Q ventral views.
S–AA) *Polyipnus apicalis* n. sp.; S–U holotype, Black's Beach, LACM 60162 (reversed), U anterior view, T dorsal view; V–AA paratypes, Black's Beach, LACM 60163, Y anterior view, W, AA ventral views.
AB–AC) *Paraulopus* cf. *davisi* (Frost, 1925), Black's Beach, LACM 60164 (reversed), AC ventral view.
AD–AG) *Protaulopus* n. gen. *pseudolestidiops* (Nolf, 1988), Black's Beach, LACM 60165, AE, AG ventral views.
AH–AJ) Sudidae? indet., Black's Beach, LACM 60166 (AI–AJ reversed), AJ ventral view.

Order **Aulopiformes** Rosen, 1973
Family Paraulopidae Sato & Nakabo, 2002
Genus *Paraulopus* Sato & Nakabo, 2001

Paraulopus cf. ***davisi*** (Frost, 1925)

Fig. 7AB–AC

1925 Otolithus *Clupeidarum davisis* - Frost: pl. 10, fig. 5.
2007 *Paraulopus* aff. *davisi* (Frost, 1925) - Schwarzhans: fig. 7 E-F (see there for further references).

Material: 1 specimen, Ardath Shale, Black's Beach, figured specimens LACM 60164.

Discussion. Otoliths of *Paraulopus* are common and widespread in the Late Cretaceous and the Paleogene. The differentiation of the various species is difficult, particularly of small specimens like the one of about 2.2 mm of length found in the Ardath Shale. A comprehensive revision of the otolith-based fossil species of this group is necessary before several of the species can be properly defined or, as the case may be, become synonymized.

Family Aulopidae Bonaparte, 1831
Genus *Protaulopus* n. gen.

Type species: "genus Percoideorum" *pseudolestidiops* Nolf, 1988.

Etymology: A combination of proto (Greek) = first, primordial, referring to the early occurrence of this otolith morphology and the genus name *Aulopus*.

Diagnosis: A fossil otolith-based genus of the family Aulopidae characterized by the combination of an elongate, subrectangular otolith shape with nearly straight dorsal rim and orthogonal postdorsal angle and massive, broad rostrum; OL:OH = 2.0–2.3; rostrum length 30% of OL in average. Sulcus straight, distinctly inclined against otolith axis at 15° in average; ostium slightly widened; cauda slightly longer than ostium (CaL:OsL = 1.2–1.4), with indistinct termination close to postventral rim.

Discussion. Otoliths of *Protaulopus* are highly characteristic and their allocation with the Aulopidae is primarily based on the shape and proportions of the sulcus. Nolf (1988) also noticed a certain similarity to aulopiform otoliths for instance of the genus *Lestidiops* (hence the species name) but considered it superficial. The prime differences are the steeply inclined, straight sulcus and the subrectangular otolith outline with the nearly straight dorsal rim and orthogonal postdorsal angle. The inclination measurement, however, depends on the orientation of the otolith. We have shown it here with the long axis from rostral tip to middle part of posterior rim horizontal against which the sulcus is inclined at 15° on average, whereas Nolf (1988) showed it with the sulcus-axis horizontal. However, this produces an atypical orientation of the rostrum.

Species. *Protaulopus* is monospecific with *P. pseudolestidiops* (Nolf, 1988) known from the late middle Eocene and late Eocene of Europe and California indicating a wide oceanic distribution pattern.

Protaulopus pseudolestidiops (Nolf, 1988)

Fig. 7AD–AG

1988 "genus Percoideorum" *pseudolestidiops* - Nolf: pl. 12, fig. 19-21.
2016 "*Perca*" *pseudolestidiops* (Nolf, 1988) - Lin, Nolf, Steurbaut & Girone: fig. 10 I-K.

Material: 7 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60165.

Family Synodontidae Gill, 1861
Genus *Synodus* Scopoli, 1777

Synodus moodyensis n. sp.

Fig. 8A–H

2003 *Synodus* sp. - Nolf & Stringer: pl. 3, fig. 1.
2022 *Synodus* sp. - Lin & Nolf: fig. 14A.

Holotype: Fig. 8A–B, NRM PZ P.19058, Bartonian, Moodys Branch Formation, Jackson, Mississippi.

Paratypes: 12 specimens: 10 specimens same data as holotype, NRM PZ P.19059; 1 specimen, NRM PZ P.19060, Bartonian, Stone City Member, Brazos River upstream of bridge of State Highway 21, Texas; 1 specimen, NRM PZ P.19061, Priabonian, Yazoo Formation, Cynthia pit, Mississippi.

Etymology: Named after the type formation, Moodys Branch Formation.

Diagnosis: OL:OH = 1.85–2.05. Rostrum sharply pointed; dorsal rim irregularly undulating; posterior rim variably cut or blunt. Cauda narrow, slightly flexed at rear. Crista superior distinct above anterior part of sulcus abruptly terminating above middle of cauda.

Description. Small, delicate otoliths reaching 2 mm in length (holotype 1.9 mm). OH:OT = 2.0–2.2. Dorsal rim shallow, irregularly undulating without distinct angles or projections. Ventral rim likewise relatively shallow, regularly curved and smooth. Rostrum sharply pointed, moderately long at 17–25% of OL, positioned at central axis of otolith. Excisura and antirostrum minute or absent. Posterior rim vertically cut or blunt and oblique.

Inner face markedly convex both in horizontal and vertical direction with axial to slightly supramedian sulcus. Ostium slightly and gradually widened against narrow cauda and deepened in v-shaped junction; CaL:OsL = 1.1–1.4. Cauda slightly wavy and slightly flexed towards its end, terminating relatively far from posterior tip of otolith; OL:SuL = 1.1–1.22. Crista superior distinct above anterior half of sulcus, abruptly terminating above midpoint of sulcus. Dorsal depression shallow, only above region with developed crista superior. Ventral field smooth, without ventral furrow. Outer face flat, smooth or slightly irregularly sculptured.

Discussion. The subtle shape of the cauda and the abruptly terminating crista superior are characteristic features of *Synodus* otoliths. Nolf & Stringer (2003) and Lin & Nolf (2022) had only a single specimen available for investigation and found it not sufficient for specific identification. Now, with several well-preserved specimens of different sizes specific diagnostic features can be recognized (see diagnosis). *Synodus moodyensis* and *S. diadematus* n. sp. described below represent the earliest records of the genus, the only other confirmed fossil record being *S. occidentalis* Steurbaut, 1984 from the Early Miocene of South-West France.

Synodus diadematus n. sp.

Fig. 8I–N

Holotype: Fig. 8I–K, NRM PZ P.19062, Bartonian, Moodys Branch Formation, Jackson, Mississippi.

Paratypes: 2 specimens same data as holotype, NRM PZ P.19063.

Etymology: From diadema (Latin) = crown, referring to the predorsal expansion of the dorsal rim.

Diagnosis: OL:OH = 1.55–1.65. Rostrum short, pointed, inferior; dorsal rim with predorsal expansion; posterior rim vertically cut. Cauda narrow, slightly flexed at rear. Crista superior distinct above anterior part of sulcus abruptly terminating above middle of cauda.

Description. Small, delicate otoliths reaching 1.3 mm in length (holotype). OH:OT = 1.9–2.2. Dorsal rim irregularly undulating with distinct predorsal expansion. Ventral rim shallower than dorsal rim, regularly curved and smooth. Rostrum pointed, relatively short at 8–12% of OL, positioned inferior of central axis of otolith. Excisura and antirostrum indistinct. Posterior rim vertically cut.

Inner face markedly convex both in horizontal and vertical direction with axial sulcus. Ostium slightly and gradually widened against narrow cauda and deepened in v-shaped junction; CaL:OsL = 1.1–1.15. Cauda slightly wavy and slightly flexed towards its end, terminating relatively far from posterior tip of otolith; OL:SuL = 1.25. Crista superior distinct above anterior half of sulcus, abruptly terminating above midpoint of sulcus. Dorsal depression shallow, only above region with developed crista superior. Ventral field smooth, without ventral furrow. Outer face flat to slightly convex, smooth.

Discussion. The largest otolith of *S. diadematus* of 1.3 mm in length shows sufficient diagnostic characters to distinguish it from *S. moodyensis*. The key differences are the predorsal expansion, the lower ratio OL:OH (1.55–1.65 vs. 1.85–2.05) and the short and inferior rostrum (8–12% of OL vs. 17–25%). The two smaller paratypes show the same proportions as the holotype, but the predorsal expansion is less prominently developed, which probably indicates that they represent juvenile specimens.

Family Sudidae Regan, 1911
Genus indet.

Sudidae? indet.

Fig. 7AH–AJ

Material: 3 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60166.

Discussion. Three fragmentary or eroded specimens resemble extant sudid and notosudid otoliths but their identification remains highly tentative, mainly because of their poor preservation.

Order **Myctophiformes** Regan, 1911
Family Myctophidae Gill, 1893
Subfamily Eomyctophinae Prokofiev, 2006
Genus *Eomyctophum* Daniltchenko, 1947

Eomyctophum cyrano (Nolf, 1988)

Fig. 8Z–AF

1969 *Diaphus* sp. - Fitch: fig. 4 A, B.
1988 *Diaphus cyrano* - Nolf: pl. 4, fig. 24-27.
2016 *Diaphus cyrano* Nolf, 1988 - Lin, Nolf, Steurbaut & Girone: fig. 6 N-P.

Material: 55 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60275.

Discussion: When Nolf (1988) described this species he named it for the shape of the antirostrum resembling the large nose of the famous Cyrano de Bergerac. It was described from the middle Eocene of South-West France and was considered to belong to a lineage also including the earlier *E. rhinoceros* (Nolf, 1988) from the early Eocene. The specimens from the late Lutetian of California perfectly match the specimens of *E. cyrano* from France indicating a wide, possibly oceanic distribution of the species.

Subfamily Diaphinae Paxton, 1972
Genus *Diaphus* Eigenmann & Eigenmann, 1890

Diaphus roederi n. sp.

Fig. 8O–Y

Holotype: Fig. 8O–Q, LACM 60167, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 9 specimens same data as holotype, LACM 60168.

Referred specimens: 96 specimens, same data as holotype.

Etymology: Named in memory of Mark Roeder, who described the fossil locality of the Miramar Reservoir site and collected most otoliths from there.

Diagnosis: OL:OH = 1.25–1.3. Dorsal rim with moderately developed predorsal lobe and denticle-like postdorsal angle. 7 to 8 denticles along ventral rim, anteriorly less well-developed than posteriorly. Rostrum relatively long, 10–14% of OL.

Description. Moderately large otoliths with oval shape reaching at least 3.25 mm in length (ho-

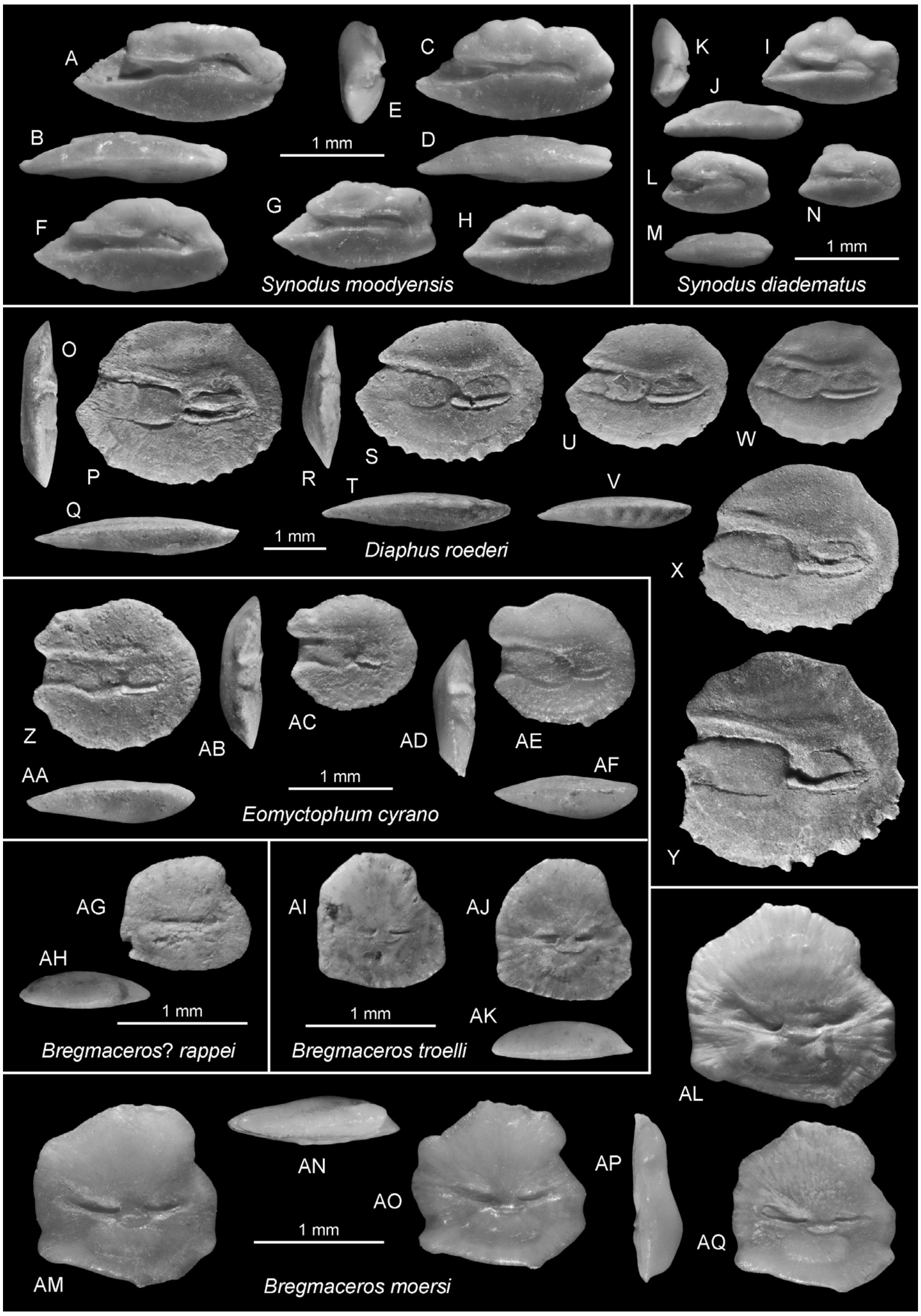


Fig. 8 - A–H) *Synodus moodyensis* n. sp.; A–B holotype, Moodys Branch, Bartonian, Mississippi, NRM PZ P.19058, B ventral view; C–H paratypes, Moodys Branch, Bartonian, Mississippi, NRM PZ P.19059 (reversed), E anterior view, D ventral view.
I–N) *Synodus diadematus* n. sp.; I–K holotype, Moodys Branch, Bartonian, Mississippi, NRM PZ P.19062, K anterior view, J ventral view; L–N paratypes, Moodys Branch, Bartonian, Mississippi, NRM PZ P.19063, M ventral view.
O–Y) *Diaphus roederi* n. sp.; O–Q holotype, Black's Beach, LACM 60167, O anterior view, Q ventral view; R–Y paratypes, Black's Beach, LACM 61068 (R–T, W–Y reversed), R anterior view, T, V ventral views.
Z–AF) *Eomyctophum cyrano* (Nolf, 1988), Black's Beach, LACM 60275 (Z–AA, AD–AF reversed), AB, AD anterior views, AA, AF ventral views.
AG–AH) *Bregmaceros*? *rappei* Nolf, 1988, Black's Beach, LACM 60169, AH dorsal view.
AI–AK) *Bregmaceros troelli* (Dante & Frizzell, 1965), Brazos River, Bartonian, Texas, NRM PZ P. 19078, AK dorsal view.
AL–AQ) *Bregmaceros moersi* n. sp.; AN–AP holotype, Yazoo Clay, Priabonian, Mississippi, NRMZ PZ P.19064 (reversed), AN dorsal view, AP posterior view; AL–AM, AQ paratypes, Yazoo Clay, Priabonian, Mississippi, NRMZ PZ P.19065 (AM, AQ reversed).

lotype) but probably more than 4 mm (Fig. 8Y). OH:OT = 3.8–4.5. Dorsal rim regularly curved, slightly lobate anteriorly, with denticle-like postdorsal angle and short, steeply inclined, slightly concave postdorsal section. Ventral rim regularly curved, with 7 to 8 sharp denticles, posterior ones stronger than anterior ones, the latter often eroded. Rostrum moderately long, bluntly pointed; posterior rim gently rounded. Antirostrum and excisura small but mostly distinct.

Inner face slightly convex with slightly supramedian sulcus. Sulcus slightly bent; ostium with straight or slightly curved dorsal rim. Ostium longer than cauda and ostial colliculum distinctly wider than caudal colliculum; OCL:CCL = 1.7–2.0; OCH:CCH = 1.9–2.2. Caudal pseudocolliculum distinct and long. Dorsal depression broad, ventrally marked by crista superior, dorsally indistinct; ventral furrow weak, moderately close to ventral otolith rim. Outer face flat, anteriorly slightly concave, posteriorly with shallow umbo, smooth with few short radial furrows.

Discussion. *Diaphus* otoliths are among the earliest myctophid otoliths recognized in the fossil record. Several *Diaphus* otolith-based species have been described from the Eocene (see Schwarzhans

& Carnevale 2022), the most relevant being *D. quadrangularis* (Sulc, 1932), a long-ranging species in Europe from the Ypresian to Bartonian and *D. marambionis* Schwarzhans, Mörs, Engelbrecht, Reguero & Kriwet, 2017 from Antarctica. Both species differ from *D. roederi* in the expanded predorsal rim and depressed postdorsal rim. Furthermore, *D. roederi* is distinguished by a relatively longer rostrum and the narrow caudal colliculum.

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

Bregmaceros? rappei Nolf, 1988

Fig. 8AG–AH

1988 "genus Bregmacerotidarum" *rappei* - Nolf: pl. 6, fig. 12.

Material: 2 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60169.

Discussion. *Bregmaceros*? *rappei* was originally described from the early Eocene of South-West France and is characterized by a rounded outline and a narrow sulcus with small colliculi. Its inner face is completely flat and the outer face uniformly convex. This otolith pattern may indeed represent a fossil lineage separate from the extant *Bregmaceros*. Similar morphotypes are also known from the Eocene of the Gulf Coast – *B. troelli* (Dante & Frizzell, 1965) – and the Oligocene of Germany – *B. oblongus* Schwarzhans, 1977. All these species are characterized by a flat inner face and small colliculi in a narrow sulcus. One of us (WS) had the opportunity to inspect the holotype of *B. troelli* (USNM 23374) from the Lutetian Weches Formation of Texas, which is congruent with the specimens figured by Lin & Nolf (2022; fig. 15 A-D). We have several otoliths with the same pattern from the Brazos River (Fig. 8AI–AK), Moodys Branch and Yazoo Clay of the Gulf Coast (late Lutetian to Priabonian). However, the ones from the Bartonian (Moodys Branch) and Priabonian (Yazoo Clay) tend to be more compressed than the earlier ones and could represent a different species subject to a review of a broad representation of specimens.

Bregmaceros moersi n. sp.

Fig. 8AL–AQ

Holotype: Fig. 8AN–AP, NRM PZ P.19064, Priabonian, Ya-zoo Formation, Cynthia pit, Mississippi.

Paratypes: 14 specimens same data as holotype, NRM PZ P.19065.

Referred specimens: 92 specimens: 85 specimens, same data as holotype; 5 specimens, NRM PZ P.19066, Bartonian, Moodys Branch Formation, Jackson, Mississippi; 2 specimens, NRM PZ P.19067, Bartonian, Stone City Member, Brazos River upstream of bridge of State Highway 21, Texas.

Etymology: Named in honor of Thomas Mörs, Stockholm, who made the collection of Eocene otoliths from the USA Gulf Coast available for our study.

Diagnosis: OL:OH = 0.93–1.02. Preventral lobe distinct; midventral denticle small. Dorsal projection broad, distinctly backward inclined. Inner face slightly convex; outer face with inferior umbo. Colliculi narrow, deepened, relatively long.

Description. Relatively thin and delicate otoliths reaching a size of about 2 mm in length (holotype 1.35 mm). OH:OT = 3.5–4.0. Otolith shape characterized by being about as long as high, with nearly vertical anterior margin, distinct preventral lobe and broad, backward inclined dorsal lobe. Ventral rim shallow, anteriorly straight, inclined until small, obtuse midventral denticle, thereafter broadly rounded. Dorsal rim anteriorly inclined; steep concavity behind dorsal lobe. Posterior rim broadly rounded below postdorsal concavity. Rims smooth or slightly crenulated.

Inner face slightly convex with slightly inframedian, narrow concave, fairly evenly curved sulcus. Ostial colliculum slightly longer than caudal colliculum (OCL:CCL = 1.4–1.65), both distinctly deepened. Collum narrow, with small ventral pseudocolliculum and no bulge of inner face below collum. No discernable dorsal depression; ventral field with broad, indistinct furrow below central part of sulcus. Many indistinct radial furrows visible on dorsal field and along anterior and posterior rims. Outer face with shallow and broad umbo near ventral otolith rim.

Discussion. *Bregmaceros moersi* belongs to the modern morphotype in the Bregmacerotidae found in otoliths of all extant species. Several bregmacerotid species are known with a similar pattern from the Eocene, i.e., *B. brihandensis* Nolf, 1988 from the Priabonian of South-West France, *B. antiquus* Schwarzhans, 1980 from the late middle and late Eocene of New Zealand and *B. minimus* (Frost, 1934) from the Bartonian of England. *Bregmaceros moersi* differs from *B. minimus* in the narrower dorsal lobe and the inclined anterior-dorsal rim and the longer caudal colliculum. From *B. antiquus* it differs in the less compressed shape (OL:OH = 0.93–1.02 vs. 0.88–0.94) and the narrower dorsal lobe. *Bregmaceros bri-*

handensis is similar in otolith shape but differs from *B. moersi* in the wider and shorter colliculi. *Bregmaceros moersi* differs from all its Eocene congeners in the presence of a distinct preventral lobe and a small midventral denticle. It furthermore differs in the very narrow colliculi.

Order **Ophidiiformes** Berg, 1937
Family Ophidiidae Rafinesque, 1810
Subamily Carapinae Jordan & Fowler, 1902
Genus *Alienocarapus* n. gen.

Type species: *Alienocarapus banana* n. sp.

Etymology: A combination of alienus (Latin) = strange, referring to the unusual otolith morphology and the genus name *Carapus*.

Diagnosis: A fossil otolith-based genus of the family Carapidae characterized by the combination of a compressed, high-bodied otolith (OL:OH = 1.05–1.1) with a smooth but not entirely flat inner face. The dorsal rim shows the typical carapid projection but positioned just anterior to midpoint. The sulcus is large, very shallow almost level with the rest of the inner face, filled with a single undivided colliculum showing a convex dorsal and a concave ventral margin; its anterior tip is tapered, the posterior tip rounded.

Discussion. *Alienocarapus* is a highly diagnostic and unmistakable otolith. The smooth inner face, lobed dorsal rim and large undivided sulcus with the dorsal margin strongly convex and the ventral margin being slightly concave is typical for carapid otoliths. The semblance of the sulcus to the shape of a banana and the very compressed otolith shape are, however, very distinct from any extant carapid otolith morphology.

Species. *Alienocarapus* is monospecific with *A. banana* known from the middle Eocene of California.

Alienocarapus banana n. sp.

Fig. 9A–E

Holotype: Fig. 9A–C, LACM 60100, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 3 specimens: 2 specimens same data as holotype, 60101; 1 specimen, Ardath Shale, Black's Beach, LACM 60170.

Etymology: From banana because of the resemblance of the sulcus to the shape of a banana.

Diagnosis: See diagnosis of genus (monospecific genus).

Description. Compressed, high-bodied and compact otoliths reaching 2.95 mm in length (holotype). OL:OH = 1.05–1.1; OH:OT = 2.6–2.7. Dorsal rim high with rounded but distinct nearly middorsal expansion. Ventral rim regularly curved, slightly and irregularly serrated. Anterior rim steep, slightly tapered; posterior rim broadly rounded.

Inner face smooth, nearly flat but slightly bent along horizontal axis, particularly anterior-ventral region, best seen in anterior views (Fig. 9A, E). Dorsal margin with dorsal expansion just anterior to midpoint and bent outward. Sulcus large, shallow, with single undivided flat colliculum, banana shaped with slightly concave ventral and distinctly convex dorsal margin; its anterior tip tapering and posterior tip rounded. OL:SuL = 1.25–1.35; SuL:SuH = 2.35–2.65. No dorsal depression or ventral furrow. Outer face moderately convex, smooth.

Genus *Encheliophis* Müller, 1842

Encheliophis transversalis n. sp.

Fig. 9F–J

Holotype: Fig. 9F–H, LACM 60171, upper Lutetian, Ardath Shale, Black's Beach.

Paratype: 1 specimen same data as holotype, LACM 60172.

Etymology: From transversalis (Latin) = transverse, referring to the distinctly inclined sulcus.

Diagnosis: OL:OH = 1.85–2.05. Dorsal rim regularly curved without predorsal lobe. Ventral rim shallow. Inner face flat; outer face moderately convex, thickest at its middle. Sulcus long, narrow, with nearly parallel dorsal and ventral margins, inclined at 5–8° against otolith axis.

Description. Elongate otoliths with nearly oval outline up to 5.2 mm in length (holotype). OH:OT = 2.0–2.3. Dorsal rim regularly curved, highest near its middle, without predorsal lobe. Ventral rim shallow, regularly curved. Anterior rim broadly rounded; posterior rim tapering with rounded tip. All rims smooth.

Inner face flat with long, narrow, shallow, distinctly inclined sulcus, filled with undivided colliculum. OL:SuL = 1.4–1.5; SuL:SuH = 6. Weak and indistinct dorsal depression; no ventral furrow. Dorsal rim only slightly thicker than ventral rim. Outer face moderately convex, smooth, thickest at its middle.

Discussion. *Encheliophis transversalis* is characterized by the distinctly inclined and very narrow sulcus and the lack of a predorsal lobe. It is placed in the genus *Encheliophis* because of the flat inner face, the not significantly thickened dorsal rim, and the relatively low ratio OL:SuL of 1.4–1.5. *Encheliophis crassidorsalis* from the Lutetian of Germany

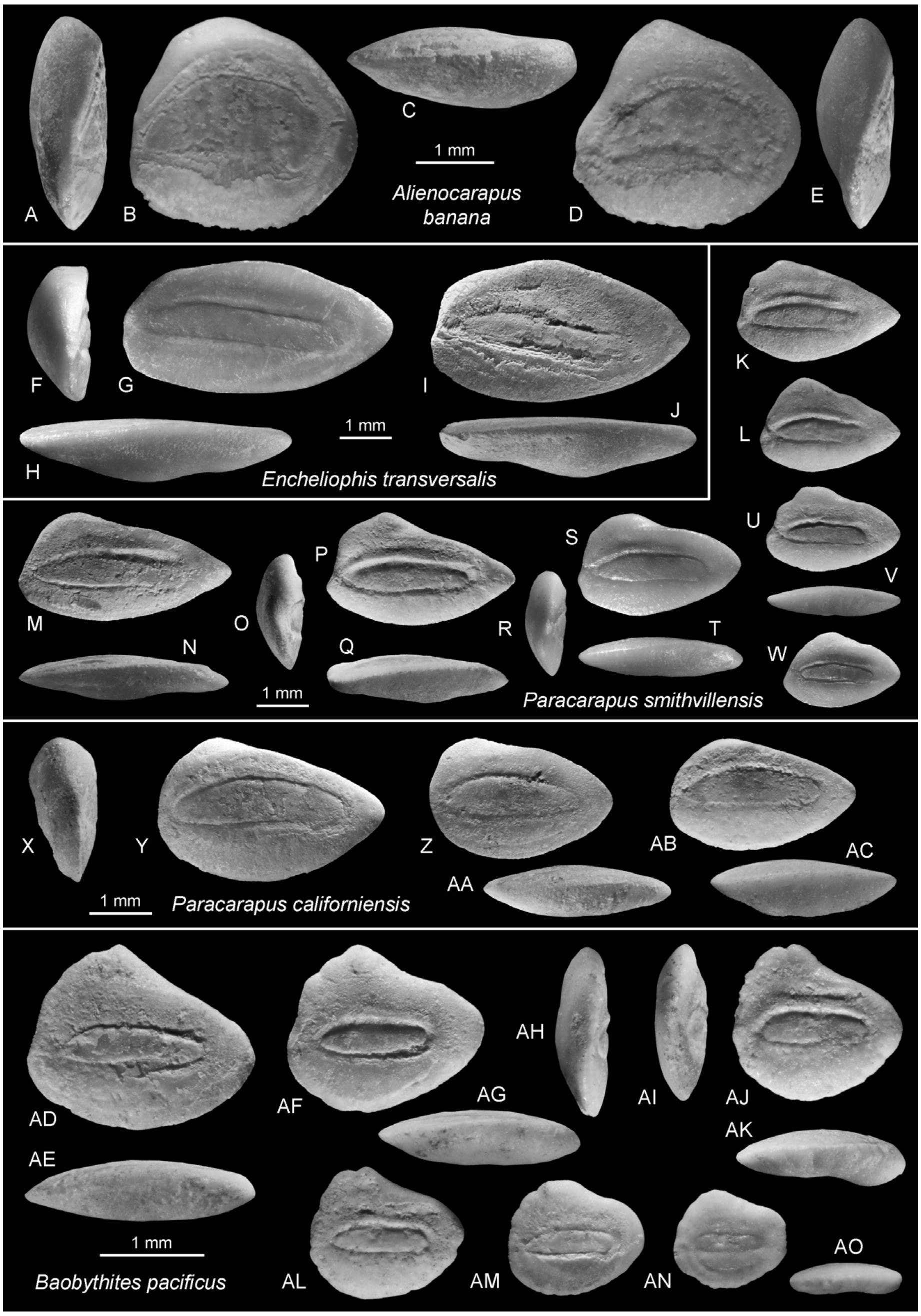


Fig. 9 - A–E) *Alienocarapus banana* n. gen., n. sp.; A–C holotype, Miramar Reservoir site, LACM 60100, A anterior view, C ventral view; D–E paratype, Black's Beach, LACM 60170, E anterior view.
F–J) *Encheliophis transversalis* n. sp.; F–H holotype, Black's Beach, LACM 60171 (reversed), F anterior view, H ventral view; I–J paratype, Black's Beach, LACM 60172, J ventral vew.
K–W) *Paracarapus smithvillensis* (Dante & Frizzell, 1965), Black's Beach, LACM 60175 (O–W reversed), O, R anterior views, N, Q, T, V ventral views.
X–AC) *Paracarapus californiensis* n. sp.; Z–AA holotype, Black's Beach, LACM 60173, AA ventral view; X–Y, AB–AC paratypes, Black's Beach, LACM 60174 (reversed), X anterior view, AC ventral view.
AD–AO) *Baobythites pacificus* n. gen., n. sp.; AF–AH holotype, Black's Beach, LACM 60178, AH anterior view, AG ventral view; AD–AE, AI–AO paratypes, Black's Beach, LACM 60179 (AD–AE, AI–AM reversed), AI anterior view, AE, AK, AO ventral views.

is thicker with a distinctly thickened dorsal rim and a predorsal expansion. *Carapus lisus* (Nolf, 1973), a widespread species in the European middle Eocene, is similarly thin overall but with a slightly thickened dorsal rim and a predorsal expansion. The distinctly inclined sulcus is shared with *Onuxodon kiriakoffi* Nolf, 1980 from the early Eocene of South-West France, but *E. transversalis* differs from this species in the more elongate shape (OL:OH = 1.85–2.05 vs. 1.5–1.6) and the lack of a predorsal expansion (vs. present).

Genus *Paracarapus* Schwarzhans & Nielsen, 2021

Paracarapus californiensis n. sp.

Fig. 9X–AC

Holotype: Fig. 9Z–AA, LACM 60173, upper Lutetian, Ardath Shale, Black's Beach.

Paratype: 6 specimens same data as holotype, LACM 60174.

Etymology: Named after California, the state where the investigated otoliths were collected.

Diagnosis: OL:OH = 1.5–1.7. Dorsal rim with broad predorsal lobe. Ventral rim moderately deep. Inner face distinctly convex, smooth; outer face strongly convex, thickest near its dorsal margin. Sulcus long, moderately wide, its dorsal margin more strongly curved than its ventral margin.

Description. Moderately elongate and massive otoliths up to 3.6 mm in length (holotype 2.9

mm). OH:OT = 2.0–2.3. Dorsal rim with broad, relatively weak predorsal lobe; postdorsal rim regularly inclined downwards toward not strongly pointed posterior tip. Ventral rim moderately deep, regularly curved, deepest anterior of its middle. Anterior rim broadly rounded; posterior rim tapering. All rims smooth.

Inner face distinctly convex in horizontal and vertical directions with long, moderately wide, shallow sulcus, filled with undivided colliculum. OL:SuL = 1.3–1.35; SuL:SuH = 3.2–3.7. No dorsal depression and no ventral furrow. Dorsal rim thicker than ventral rim. Outer face moderately to strongly convex, smooth, thickest close to dorsal rim.

Discussion. The fossil otolith-based genus *Paracarapus* was established by Schwarzhans & Nielsen (2021) to accomplish carapid otoliths with a convex inner face, a sulcus where the ventral margin is curved, and an outer face with not thickened or moderately thickened dorsal rim. *Paracarapus californiensis* is morphological intermediate to the modern morphotype of *Carapus* otoliths with the shape of the sulcus and the thickened dorsal rim approaching that status. However, the distinctly convex inner face precludes *P. californiensis* to be placed in *Carapus*.

Paracarapus californiensis also resembles the parallel occurring *P. smithvillensis* but differs in being less elongate (OL:OH = 1.5–1.7 vs. 1.6–2.0) and thicker (OH:OT = 2.0–2.3 vs. 2.3–2.5) and a wider sulcus (SuL:SuH = 3.2–3.7 vs. 4–5).

Paracarapus smithvillensis (Dante & Frizzell, 1965)

Fig. 9K–W

1965 "*Carapus*" *smithvillensis* - Dante & Frizzell in Frizzell & Dante: pl. 86, fig. 32-33, pl.87, fig. 7-8.

2022 *Carapus smithvillensis* Dante & Frizzell, 1965 - Lin & Nolf: fig. 15 L–M.

Material: 385 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60175.

Discussion. *Paracarapus smithvillensis* is the most common carapid in the Eocene of North America, both from the Gulf Coast and California. We allocate it with the extinct *Paracarapus* because of the slightly convex inner face and the lack of a thickened dorsal rim.

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

Ampheristus turgidus n. sp.

Fig. 10O–S

Holotype: Fig. 10O–N, LACM 60176, upper Lutetian, Ardath Shale, Black's Beach.

Paratype: 5 specimens same data as holotype, LACM 60177.

Referred specimens: 20 specimens same data as holotype.

Etymology: From turgidus (Latin) = swollen, inflated, referring to the strongly convex inner face of the otolith.

Diagnosis: OL:OH = 1.6–1.7. Dorsal rim with low, obtuse predorsal lobe. Ventral rim moderately deep and regularly curved. Inner face distinctly convex; outer face concave. Ostium distinctly longer than cauda (OCL:CCL = 2.35–2.65). Cauda narrow, ventrally constricted and downward oriented, not or only slightly deepened.

Description. Moderately elongate otoliths up to 4 mm in length (holotype). Dorsal rim with low, broad, obtuse predorsal lobe and gently inclined, almost straight or slightly rounded posterior section; postdorsal angle weak and low or absent. Ventral rim moderately deep, gently curved, deepest slightly in front of middle. Anterior rim broadly rounded; posterior tip tapering, moderately pointed and extended. All rims smooth.

Inner face strongly convex in horizontal and vertical direction. Sulcus slightly supramedian, long, shallow; ostium much longer than cauda, reaching very close to anterior rim of otolith. OL:SuL = 1.25–1.35. Ostium shallow, filled with well-defined shallow, elongate colliculum; cauda narrow, short, ventrally much constricted, slightly bent downwards, not or only slightly deeper than ostium. Dorsal depression indistinct; ventral furrow feeble and very close to ventral rim of otolith. Outer face flat to concave, smooth.

Discussion. *Ampheristus* is an extinct basal neobythitine genus close to the extant *Hoplobrotula*. The main difference in otoliths between the two genera is the very narrow, ventrally restricted and often somewhat deepened cauda in *Ampheristus* while in *Hoplobrotula* it is not deepened, less ventrally constricted and wider. *Ampheristus* contains several otolith-based species in the Late Cretaceous and Paleogene, and we have therefore figured representatives of *Ampheristus* species from the European Eocene: *Ampheristus toliapicus* König, 1825, from the Ypresian of England (Fig. 10A–D), *Ampheristus lerichei* (Stinton & Nolf, 1970) from the Lutetian of Belgium (Fig. 10J–K) and *Ampheristus waltoni* (Schubert, 1916) from the Bartonian of England (Fig. 10L–M). *Ampheristus turgidus* differs from all of them except *A. lerichei* and *A. toliapicus* in the very convex inner face and the low predorsal lobe. Also its cauda is less deepened than in most of its cogeners.

Genus *Baobythites* n. gen.

Type species: *Baobythites pacificus* n. sp.

Etymology: A combination of bao, a Chinese type of buns similar to the sulcus shape, in combination with the genus name *Bythites*.

Diagnosis: A fossil otolith-based genus of the family Ophidiidae characterized by the combination of a compressed, high-bodied shape (OL:OH = 1.1–1.3) with a massive predorsal expansion and a bao or sausage-shaped uniform, undivided sulcus filled with a single shallow colliculum. The sulcus is distinctly wider than the colliculum leaving a distinct furrow encircling the latter. The ventral field shows a mostly distinct ventral furrow near the ventral otolith rim that curves upward and away from the otolith rim along its posterior part to closely approach the posterior tip of the sulcus.

Discussion. *Baobythites* appears inconspicuous at first sight but in the combination of the otolith shape and the shape of the sulcus is rather unmistakable. It resembles most *Aequalobythites* with which it shares the general outline and undivided sulcus but differs in being more compressed, showing a stronger predorsal expansion and a longer sulcus. A third morphotype is represented by "*Glyptophidium*" *polli* (Casier, 1946) from the Ypresian of England, France and Belgium that differs from *Baobythites* only in showing a separated minute caudal colliculum. This morphotype may represent the predecessor of both *Aequalobythites* and *Baobythites* and probably also represents a separate fossil genus. It would furthermore indicate that in this generic complex the undivided colliculum was not a result of the fusion of originally separated ostial and caudal colliculi but rather of the loss of a tiny caudal colliculum.

Species. Three species are allocated in *Baobythites*: *B. pacificus* n. sp. from the Lutetian and Bartonian of California, *B. stringeri* (Lin & Nolf, 2022) (originally described as "aff. *Glyptophidium*" *stringeri*) from the Lutetian and Bartonian of the Gulf Coast and *B. biarritzense* (Sulc, 1932) (originally described as ?*Ophidium biarritzense*) from the Priabonian of South-West France.

Baobythites pacificus n. sp.

Fig. 9AD–AO

Holotype: Fig. 9AF–AH, LACM 60178, upper Lutetian, Ardath Shale, Black's Beach.

Paratype: 10 specimens same data as holotype, LACM 60179.

Referred specimens: 90 specimens: 84 specimens same data as holotype; 6 specimens Mission Valley Formation, Miramar Reservoir site.

Etymology: Referring to the occurrence of the species in the paleo-northeast Pacific in California.

Diagnosis: OL:OH = 1.1–1.2. Dorsal rim with strongly projecting broad predorsal lobe. Ventral rim regularly curved, deepest slightly before middle, anteriorly broadly rounded to almost vertical. Posterior tip rounded. Sulcus short, simple sausage-shaped; OL:SuL = 1.55–1.65. Ventral furrow asymmetrical as if shifted towards anterior.

Description. Small, compressed otoliths up to 2.2 mm in length (holotype 1.8 mm). Dorsal rim with high, pronounced, broad and somewhat crenulated predorsal lobe followed by slight concavity on sloping postdorsal rim; no postdorsal angle. Ventral rim moderately deep, gently curved, deepest slightly in front of middle. Anterior rim broadly rounded, ventrally very regularly curved; posterior rim tapering with rounded tip. Rims smooth or slightly crenulated or undulating.

Inner face mildly convex. Sulcus axial to slightly supramedian, short, shallow, undivided with sausage-shaped colliculum surrounded by relatively broad groove from sulcus margin. OL:SuL = 1.55–1.65. Dorsal depression variable, usually a narrow groove above crista superior; ventral furrow mostly weak, anteriorly close to ventral rim of otolith, posteriorly shifted away from it leading up to posterior tip of sulcus. Outer face slightly convex, smooth.

Discussion. *Baobythites pacificus* are small otoliths that differ from *B. stringeri* in the broader predorsal expansion, in being more compressed (OL:OH = 1.1–1.2 vs. 1.2–1.3) and the shorter sulcus (OL:SuL = 1.55–1.65 vs. 1.3–1.55). *Baobythites pacificus* shares the short sulcus with *B. biarritzense* but differs again in the broader predorsal expansion and the broadly rounded ventral part of the anterior rim (vs. straight to concave).

Genus *Hoplobrotula* Gill, 1863

Hoplobrotula panicula n. sp.

Fig. 10T–AC

Holotype: Fig. 10T–V, LACM 60102, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratype: 5 specimens: 3 specimens same data as holotype, LACM 60103; 2 specimens, Ardath Shale, Black's Beach, LACM 60180.

Referred specimens: 411 specimens: 301 specimens same data as holotype; 110 specimens Ardath Shale, Black's Beach.

Etymology: From panicula (Latin) = tuft, referring to the relatively strong predorsal expansion.

Diagnosis: OL:OH = 1.45–1.55. Dorsal rim with narrow, strongly projecting predorsal lobe. Ventral rim relatively shallow and regularly curved. Inner face convex; outer face flat to slightly concave. Ratio OCL:CCL = 2.4–2.7. Cauda narrow, ventrally constricted and more or less straight, not deepened.

Description. Moderately elongate otoliths up to 5.8 mm in length (holotype 5.7 mm). Dorsal rim with pronounced, high, narrow, tuft-like predorsal lobe followed by deep concavity and nearly straight postdorsal rim slanted slightly toward posterior; postdorsal angle broadly rounded. Ventral rim shallow, gently curved, deepest slightly in front of middle. Anterior rim ventrally rounded, dorsally straight and inclined; posterior rim tapering, with short pointed tip. Rims smooth except anterior-dorsal and posterior-ventral sections sometimes slightly undulating.

Inner face convex in horizontal and less bent in vertical direction. Sulcus axial to slightly supramedian, moderately long, shallow; ostium substantially longer than cauda, reaching close to anterior rim of otolith. OL:SuL = 1.4–1.45. Ostium shallow, filled with well-defined shallow, elongate colliculum; cauda narrow, short, ventrally constricted, more or less straight, not as deep as ostium. Dorsal depression indistinct, long, narrow; ventral furrow not well defined, very close to ventral rim of otolith turning inward posteriorly. Outer face flat to slightly concave, smooth.

Discussion. *Hoplobrotula panicula* is a typical member of the genus. It differs from the coeval *H. robusta* Nolf, 1980 (see below) in the more pronounced, narrower, higher predorsal expansion, the slightly more compact shape (OL:OH = 1.45–1.55 vs. 1.65–1.85) and the lower ratio OCL:CCL of 2.4–2.7 (vs. 3.2–3.9). *Hoplobrotula panicula* shares the strong predorsal expansion with *H. biscaica* (Sulc, 1932) from the Priabonian of South-West France but differs in the narrowed cauda and the usually more strongly pointed posterior tip. Specimens of the extinct genus *Bauzaia* Dante & Frizzell, 1965,– *B. melrosensis* Dante & Frizzell, 1965, *B. lamberi* Dante & Frizzell, 1965 and *B. mucronata* (Koken, 1888) (see Lin & Nolf, 2022 for figures) – which are common in the Gulf Coast Eocene show a similarly strong predorsal expansion, but are characterized by a much narrower, belt-like sulcus and a cauda that is as wide as the ostium and without ventral constriction.

Hoplobrotula panicula is more common in the Miramar than in the Black's Beach and is represented by mostly large specimens in Miramar and smaller ones in Black's Beach. This could indicate that the species lived in schools whereby the large ones lived in shallower water and closer to the shore than the small ones.

Hoplobrotula robusta Nolf, 1980

Fig. 10AD–AI

1980 *Hoplobrotula robusta* - Nolf: pl. 16, fig. 8-11.
2007 *Hoplobrotula robusta* Nolf, 1980 - Schwarzhans: fig. 15 F-J.

Material: 2093 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60181.

Discussion. *Hoplobrotula robusta* is the most common species in the Ardath Shale. Interestingly, it has not been found at the Miramar Reservoir site. This could be an indication of the two species having been ecologically separated with *H. robusta* having preferred deeper shelf environments as compared to *H. panicula*. For distinction of the two species see *H. panicula* above.

Genus *Pseudaequalobythites* Schwarzhans, 2019

Pseudaequalobythites biplex Schwarzhans, 2019

Fig. 10AQ–AY

2019a *Pseudaequalobythites biplex* - Schwarzhans: fig. 26.1-8.

Material: 457 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60182.

Discussion. The genus *Pseudaequalobythites* contains two species: *P. biplex* described from the early and middle Eocene of New Zealand and *P. hilgendorfi* (Koken, 1891) from the middle and late Eocene of Europe. The two species differ primarily in the presence of two separate albeit closely spaced colliculi (*P. biplex*) and a fused single colliculum (*P. hilgendorfi*). The specimens from California show separated colliculi and also match in all other parameters *P. biplex* from New Zealand very well. *Pseudaequalobythites biplex* thus represents one of only few species in the Eocene known diagonally across the Pacific from the southwest to the northeast. The otoliths of *P. biplex* are also known for a pronounced ontogenetic allometry in otolith proportions and ornamentation of the otolith rims, which is likewise reflected in the specimens from California.

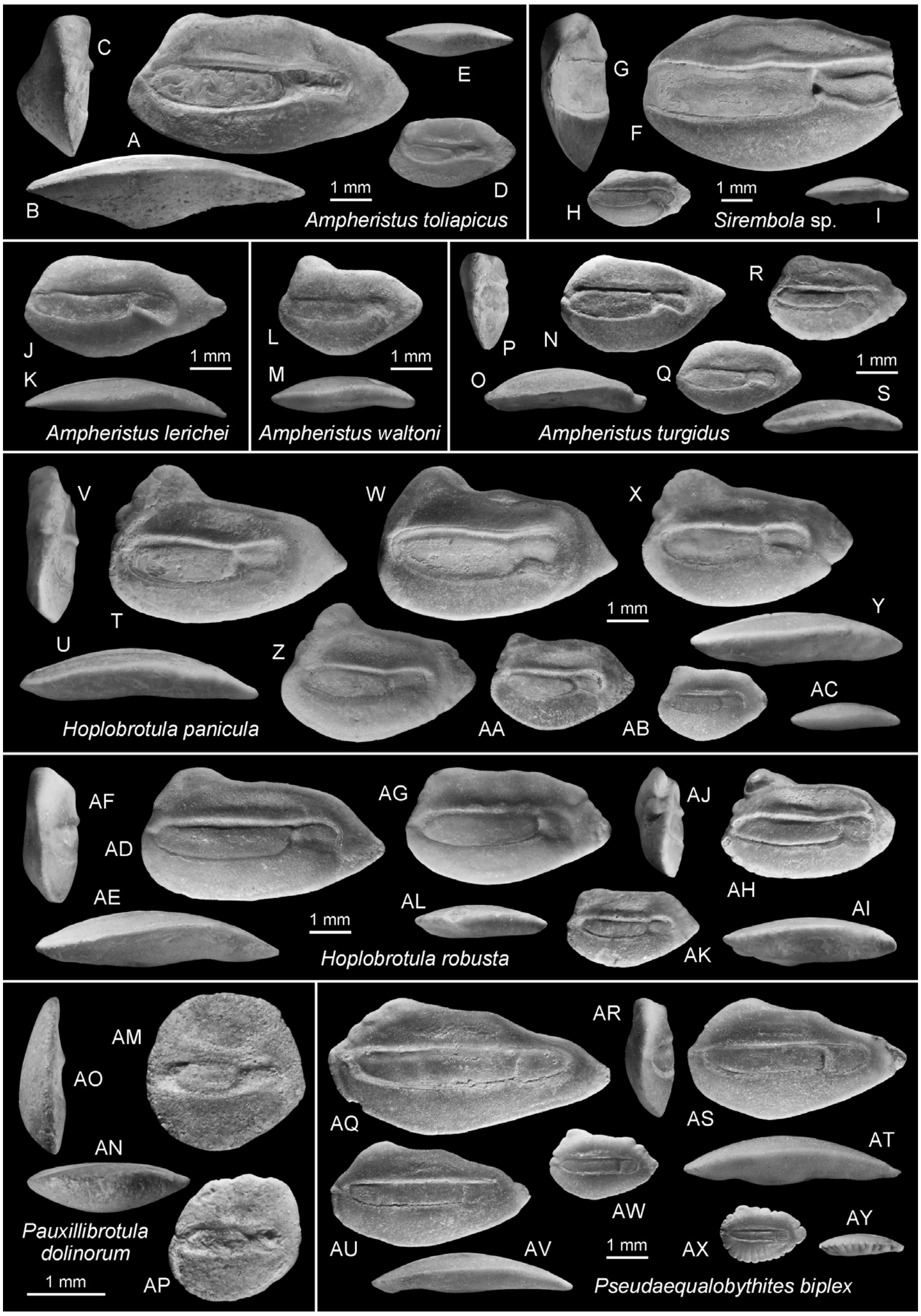


Fig. 10 - A–D) *Ampheristus toliapicus* König, 1825, Ypresian, London Basin, England (D–E reversed), C anterior view, B, E ventral views.
G–I) *Sirembola* sp.; G–F Miramar Reservoir site, LACM 60104 (reversed), G anterior view; H–I Black's Beach, LACM 60183 (reversed), I ventral view.
J–K) *Ampheristus lerichei* (Stinton & Nolf, 1970), Lutetian, Balegem, Belgium, K ventral view.
L–M) *Amphersitus waltoni* (Schubert, 1916), Bartonian, Hampshire, England (reversed), M ventral view.
O–S) *Ampheristus turgidus* n. sp.; O–N holotype, Black's Beach, LACM 60176, P anterior view, O ventral view; Q–S paratypes, Black's Beach, LACM 60177, S ventral view.
T–AC) *Hoplobrotula panicula* n. sp.; T–V holotype, Miramar Reservoir site, LACM 60102, V anterior view, U ventral view; W–Z paratypes, Miramar Reservoir site, LACM 601043 (X–Z reversed), Y ventral view; AA–AC paratypes, Black's Beach, LACM 60180 (reversed), AC ventral vew.
AD–AI) *Hoplobrotula robusta* Nolf, 1980, Black's Beach, LACM 60181 (AE–AG reversed), AF, AJ anterior views, AE, AI, AL ventral views.
AM–AP) *Pauxillibrotula* n. gen. *dolinorum* (Nolf, 1988), Black's Beach, LACM 60184, AO anterior view, AN ventral view.
AQ–AY) *Pseudaequalobythites biplex* Schwarzhans, 2019, Black's Beach, LACM 60182 (AR–AT, AW reversed), AR anterior view, AV, AT, AY ventral views.

Genus *Sirembola* Schwarzhans, 1981

Sirembola sp.

Fig. 10G–I

Material: 2 specimens: 1 specimen, Ardath Shale, Black's Beach, LACM 60183; 1 specimen, Mission Valley Formation, Miramar Reservoir site, LACM 60104.

Discussion. One specimen is large (8.3+ mm; Fig. 10F–G), well preserved but lacks the posterior tip while the other specimen is small and complete (3.25 mm; Fig. 10H–I). The almost certainly represent an undescribed species but neither of the specimens is adequate to serve as holotype. The two otoliths resemble the only known species of the genus – *S. arcuata* (Stinton, 1966) from the middle Eocene of England and Belgium – in the distinctly convex and smooth inner face, the long and narrow sulcus that almost opens anteriorly, and the cauda with its oscillating ventral margin and the separated colliculum. They differ in the sulcus proportions whereby the ostium is shorter than in *S. arcuata* (OCL:CCL = 2.1–2.2 vs. 2.4) and the lack of a thickened dorsal rim of the otolith.

Subfamily Brotulotaeniinae Cohen & Nielsen, 1978

Genus *Pauxillibrotula* n. gen.

Type species: "genus Neobythitinorum" *dolinorum* Nolf, 1988.

Etymology: A combination of pauxillis (Latin) = very small in reference to the size of the otoliths, in combination with the genus name *Brotula.*

Diagnosis: A fossil otolith-based genus of the family Ophidiidae, subfamily Brotulataeniinae with small otoliths up to about 2.5 mm in length with a compressed, high-bodied shape (OL:OH = 1.0–1.03), combined with blunt anterior and posterior rims and broadly expanded dorsal and ventral rims. The inner face is flat and the outer face convex. The sulcus is positioned along the center of the inner face, reaching close to the anterior and posterior rims of the otolith and divided in a relatively long ostium and a short, slightly deepened cauda (OL:SuL = 1.2–1.3; OCL:CCL = 2.4–3.0).

Discussion. *Pauxillibrotula* has a highly characteristic otolith pattern that is unique in extant and fossil ophidiiform otoliths. The otolith shape resembles that of the extant *Brotulataenia* but differs in the long sulcus (OL:SuL = 1.2–1.3 vs. 1.8–2.5) and the clearly distinct ostial and caudal colliculi (vs. indistinctly separated or fused). *Brotulataenia* otoliths are, nevertheless, the only extant ones showing some resemblance with *Pauxillibrotula* and therefore we tentatively place the latter in the subfamily Brotulataeniinae, making it the only known fossil record in this monogeneric extant group.

Species. A monospecific genus with *Pauxillibrotula dolinorum* (Nolf, 1988).

Pauxillibrotula dolinorum (Nolf, 1988)

Fig. 10AM–AP

1988 "genus Neobythitinorum" *dolinorum* - Nolf: pl. 7, fig. 16.
2016 *Glyptophidium dolinorum* (Nolf, 1988) - Lin, Nolf, Steurbaut & Girone: fig. 7 W-Y.

Material: 4 specimens, Ardath Shale, Black's Beach, LACM 60184.

Discussion: *Pauxillibrotula dolinorum* so far has been known from only 3 specimens from the Eocene of South-West France; the holotype from the Ypresian (Nolf 1988) and two specimens from the Lutetian (Lin et al. 2016). In Black's Beach, too, it is a rare species and represents the latest record. The disjunctive distribution indicates that the species may have had an oceanic life style similar to *Brotulataenia* today. Lin et al. (2016) related these otoliths to the genus *Glyptophidium* but the lack of a predorsal lobe, an ubiquitous characteristic in extant *Glyptophidium* otoliths precludes such an allocation in our assessment. It is interesting to note that a true species of *Glyptophidium* occurred in parallel in the Lutetian of France described by Lin et al. (2016) as *G. major* (Schubert, 1905). However, *G. major* is a species of the Miocene of the Tethys and Paratethys and the Lutetian specimens likely represent an undescribed species differentiated by a lower predorsal lobe and an anteriorly expanded ventral rim (compare figures in Lin et al. 2016 and Schwarzhans 2022).

Subfamily Brotulinae Swainson, 1838

Genus *Brotula* Cuvier, 1829

Brotula aquitanica Nolf, 1980

Fig. 11A–F

1980 *Brotula aquitanica* - Nolf: pl. 15, fig. 14.
1988 *Brotula aquitanica* Nolf, 1980 - Nolf: pl. 6, fig. 6-7.
2003 *Brotula aquitanica* Nolf, 1980 – Nolf and Stringer: pl. 7, fig. 12.

Material: 12 specimens, Ardath Shale, Black's Beach, LACM 60185.

Discussion. *Brotula aquitanica* is another species shared between the Eocene of South-West France and California indicating a wide geographical distribution and probably a more open marine life style.

Genus *Sirembrotula* n. gen.

Type species: *Sirembrotula mediator* n. sp.

Etymology: A combination of the genus names *Sirembo* and *Brotula* indicating the morphological resemblance to otoliths of the two genera.

Diagnosis: A fossil otolith-based genus of the family Ophidiidae, subfamily Brotulinae with elongate, fusiform otoliths of 4 mm in length (holotype of the type species) with smooth and gently curved dorsal and ventral rims and moderately pointed anterior and posterior tips (OL:OH = 1.9). The inner face is strongly convex and the outer face flat. The relatively narrow, long and shallow sulcus is characterized by a long ostium and a shorter, narrower cauda that is constricted along its anterior ventral rim (OL:SuL = 1.2; OCL:CCL = 1.9; OCH:CCH = 1.45).

Discussion. *Sirembrotula* resembles many of the extinct Paleogene Sirembini genera (see Schwarzhans 1981 and Lin & Nolf 2022) in the strongly convex and smooth inner face and the shallow sulcus while the overall shape and the shape of the cauda has more in common with *Brotula* otoliths. *Sirembrotula* differs from early *Brotula* otoliths, i.e., *B. aquitanica*, in the proportions of the sulcus with the ostium being distinctly longer than the cauda

(OCL:CCL = 1.9 vs. 1.05–1.1). We therefore consider *Sirembrotula* to represent a basal, stem member of the subfamily Brotulinae.

Species. A monospecific genus with *Sirembrotula mediator* n. sp.

Sirembrotula mediator n. sp.

Fig. 11G–J

Holotype: Fig. 11G–J, LACM 60186, upper Lutetian, Ardath Shale, Black's Beach.

Etymology: From mediator (Latin) = mediator, intermediary, referring to the intermediate morphology between otoliths of the Sirembini and Brotulinae.

Diagnosis: See genus diagnosis (monospecific genus).

Description. The unique holotype is 4.1 mm in length. OL:OH = 1.9; OH=OT = 2.5. Otolith shape fusiform with gently and regularly curved dorsal and ventral rims without prominent angles. Anterior and posterior tips moderately pointed, positioned at otolith axis, symmetrical. All rims smooth.

Inner face strongly convex in horizontal and vertical direction, smooth. Sulcus slightly supramedian, long reaching relatively close to anterior and posterior rims of otolith, shallow, clearly differentiated in a long and wider ostium and a shorter and narrower cauda (OL:SuL = 1.2; OCL:CCL = 1.9; OCH:CCH = 1.45). Ostium slightly bent; cauda ventrally constricted, particularly at collum. Colliculi well-defined and clearly separated, shallow. Dorsal field smooth without dorsal depression; ventral field smooth without ventral furrow. Outer face flat with faint irregular ornamentation.

Discussion. See above discussion to genus (monospecific genus).

Family Bythitidae Gill, 1861

Genus *Calamopteryx* Böhlke & Cohen, 1966

Calamopteryx? moelleri (Schwarzhans, 2007)

Fig. 11K–P

2007 genus *Bythitidarum moelleri* - Schwarzhans: fig. 20 A-G.

Material: 8 specimens, Ardath Shale, Black's Beach, LACM 60187.

Discussion. The otoliths of many extant bythitid genera have a rather reduced morphology both in terms of the otolith shape and the shape of the sulcus that is often simple and oval in outline and filled with a uniform colliculum. Then, small differences in outline as well as size and orientation of the sulcus are often the only characters that can be used for distinction of species and genera. *Calamopteryx* is one of the genera with such a reduced otolith pattern. Its otoliths are relatively slender with pointed anterior and posterior tips and the sulcus is usually small, short and slightly inclined. *Calamopteryx? moelleri* fits these characteristics but because of the vague nature of the features is only tentatively associated with the extant genus. The otoliths from the Lutetian of California match well the morphological characteristics of the coeval specimens described from Germany.

Genus *Eobidenichthys* n. gen.

Type species: Otolithus (Ophidiidarum) *symmetricus* Frost, 1934.

Etymology: A combination of eos (Greek) = early and the genus names *Bidenichthys* to which the species here referred to have often been described.

Diagnosis: A fossil otolith-based genus of the family Bythitidae characterized by separated colliculi. The shape of the otoliths is elongate, fusiform, anteriorly and posteriorly moderately pointed (OL:OH >1.8). Inner and outer faces about equally convex. The sulcus is centrally positioned and terminating relatively far from the anterior tip of the otolith. The cauda is much smaller than the ostium and marked by a recession of the ventral rim. Ostium and cauda are filled by clearly separated, shallow colliculi. A ridge-like connection of the ostial tip with the tip of the otolith is often discernable. The ventral furrow is usually well-developed.

Discussion. *Eobidenichthys* is characterized as a bythitoid otolith because of the drop-like to fusiform otolith shape and the sulcus being positioned distant from the anterior rim of the otolith. Such otoliths are found in several extant genera of the family Dinematichthyidae and few extant genera of the Bythitidae, notably *Bidenichthys* and *Melodichthys*. Dinematichthyid otoliths usually show a more asymmetrically positioned sulcus that is closer to the anterior tip of the otolith than in the species of *Eobidenichthys* and also tend to have a more convex inner face and flat to concave outer face (see Møller et al. 2004, 2005, Møller & Schwarzhans 2006, 2008 and Schwarzhans et al. 2005, Schwarzhans & Møller 2007 for extant otoliths). Otoliths of *Melodichthys* Nielsen & Cohen, 1986 are distinctly more compressed where the ostium is more than twice the width of the tiny cauda. Thus the closest resemblance is with otoliths of the extant *Bidenichthys capensis* Barnard, 1934 (see Nolf 1980; Schwarzhans 1981; Møller et al. 2021 for extant otoliths) and therefore many fossil otoliths have been allocated in that genus. However, the otolith morphology found in extant *Bidenichthys* species is diverse and only the type species *B. capensis* showing clearly separated colliculi while in all other species the sulcus is widened, the colliculi connected and the caudal separation from the ostium only marked by a slight inward bend of the ventral sulcus margin (see Møller et al. 2021 for figures). These otoliths may warrant recognition of a separate genus for which *Fiordichthys* Paulin, 1995 had been introduced. In *Bidenichthys capensis*, however, the colliculi are deepened, particularly the caudal one, and the ostium is relatively short when compared to the fossil species. In a molecular analysis of the viviparous brotulas, Møller et al. (2016) indicated that the many fossil otolith-based species from the late Cretaceous and Paleogene that are placed in the genus *Bidenichthys* in fact are more likely to represent a plesiomorphic otolith pattern of an early stem-bythitid clade. We now follow this argumentation and erect the fossil genus *Eobidenichthys* for these taxa.

Species. *Eobidenichthys* is common and widespread in the Late Cretaceous and Paleogene and contains the following species: *Eobidenichthys crepidatus* (Voigt, 1926) from the Campanian and Maastrichtian of Germany and Netherlands, *Eobidenichthys lapierrei* (Nolf, 1978) from the Paleocene and early Eocene of France, Germany and Ukraine, *Eobidenichthys midwayensis* (Nolf & Dockery, 1993) from the Paleocene of Alabama (USA), *Eobidenichthys symmetricus* (Frost, 1934) from the Eocene of England and Belgium and *Eobidenichthys boscheineni* (Schwarzhans, 1994a) from the Oligocene of Germany.

Eobidenichthys symmetricus (Frost, 1934)

Fig. 11Q–AB

1934 Otolithus (Ophidiidarum) *symmetricus* - Frost: pl. 12, fig. 8.
1934 Otolithus (Ophidiidarum) *sagittalis* - Frost: pl. 12, fig. 7.
1934 Otolithus (Pleuronectidarum) *tenuis* - Frost: pl. 14, fig. 10.
1957 Otolithus (Ophidiidarum) *symmetricus* Frost, 1934 - Stinton: pl. 2, fig. 23.
1966 *Brosmophycis sagittalis* (Frost, 1934) - Stinton: pl. 67, fig. 2.
1970 *Brosmophycis sagittalis* (Frost, 1934) - Nolf: pl. 14, fig. 7.
1977 *Brosmophycis sagittalis* (Frost, 1934) - Stinton: text-fig. 21d.
1980 "genus *Dinematichthyinorum*" *symmetricus* (Frost, 1934) - Nolf: pl. 18, fig. 11-15.

Material: 94 specimens: 88 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60188; 6 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60105.

Discussion. *Eobidenichthys symmetricus* is a well-known species in the European Eocene. The specimens from the Eocene of California show the same characters and proportions as the European ones and are therefore interpreted to represent the same species. Nolf (1980) reviewed the holotypes of Ot. (Ophidiidarum) *sagittalis* and *symmetricus* and found that they represent the same species. However, the holotype of *symmetricus* is well-preserved and the holotype of *sagittalis* is eroded and incomplete. Nolf (2013; p. 130) proposed to use *symmetricus* as valid species name and we follow his assessment.

Genus *Pseudobrotulina* n. gen.

Type species: *Pseudobrotulina fitchi* n. sp..

Etymology: A combination of pseudo (Greek) = false and the genus names *Brotulina*.

Diagnosis: A fossil otolith-based genus of the family Bythitidae with a uniform oval sulcus and colliculum. The shape of the otoliths is elongate, fusiform, anteriorly and posteriorly moderately pointed (OL:OH = 1.8-2.2). Inner face nearly flat, outer face slightly convex. The sulcus is centrally positioned, long, not or only very slightly inclined and terminating relatively far from the anterior tip of the otolith (OL:SuL = 1.8–2.0; SuL:SuH = 2.8–3.5). A ridge-like connection of ostial tip with the anterior tip of the otolith is often discernable. The dorsal depression is relatively distinct; the ventral furrow is usually well-developed and curves upward and backward posteriorly to meet the posterior tip of the sulcus.

Discussion. *Pseudobrotulina* has relatively few characteristics for recognition which mainly owes to the simple, uniform sulcus and colliculum. There are several extant genera with similar looking otoliths such as *Cataetyx* or *Saccogaster* and several fossil otolith-based species from the Eocene sharing the overall appearance. *Pseudobrotulina* differs from all of them in the relatively long and nearly horizontal sulcus. Similar in otolith shape and sulcus orientation are *Saccogaster*? *torpidus* Schwarzhans, 1985 from the late Eocene of South Australia and *Grammonus*? *argutus* (Stinton, 1966) from the early Eocene of England, but both have a distinctly shorter sulcus (OL:SuL = 2.1–2.3 vs. 1.8–2.0) and also a usually somewhat inclined sulcus (5–10° vs. <3°). Another similar species is *Brosmophyciops tongarewae* Schwarzhans, 2019 from the early Eocene of New Zealand, but that species differs from *Pseudobrotulina* in a mostly longer sulcus (OL:SuL = 1.7–1.8 vs. 1.8–2.0) and the lack of the inward curvature of the posterior end of the ventral furrow. We therefore currently consider only *P. fitchi* n. sp. to represent *Pseudobrotulina*.

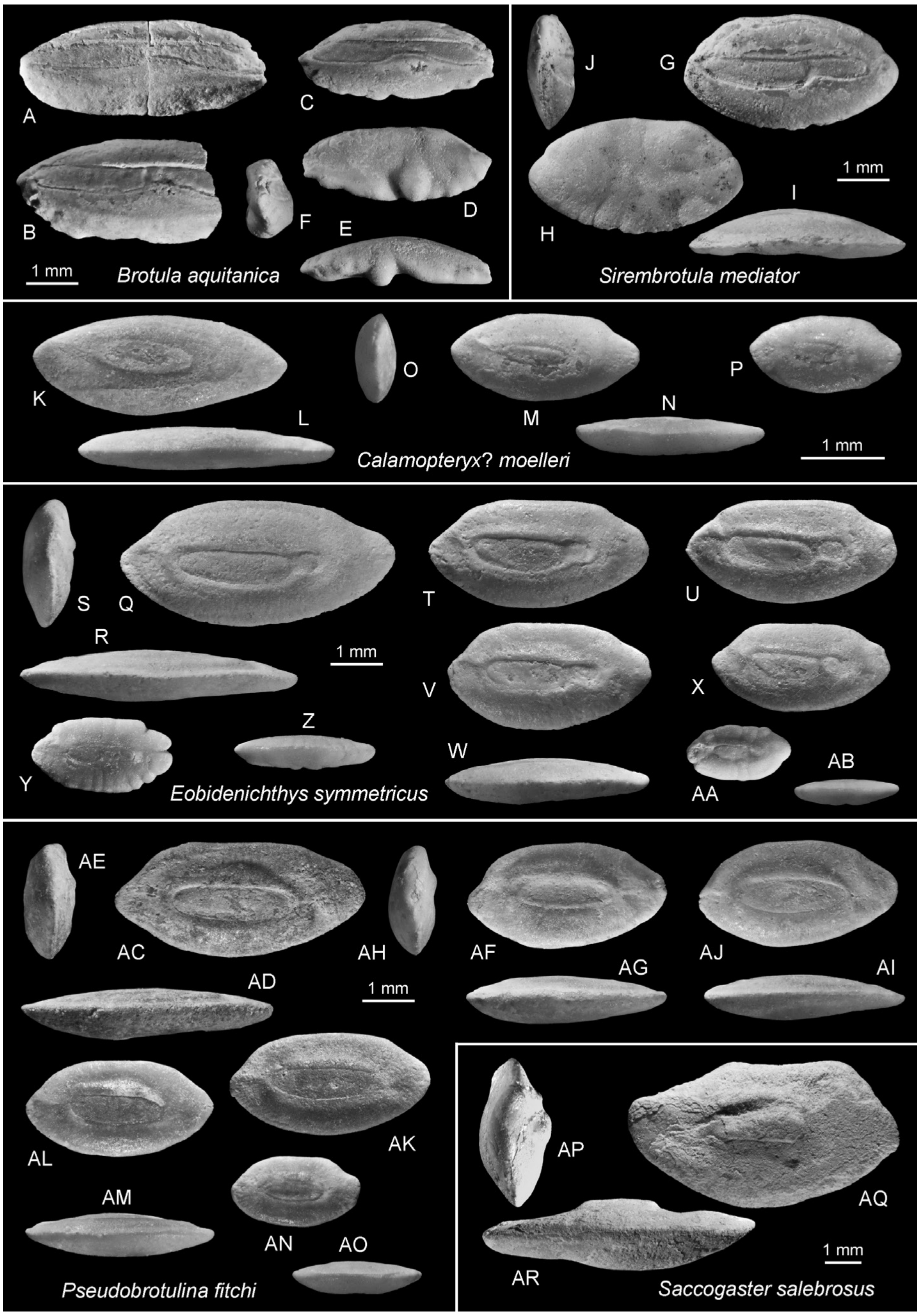


Fig. 11 - A–F) *Brotula aquitanica* Nolf, 1980, Black's Beach, LACM 60185 (A reversed), F anterior view, D outer face, E ventral view.
G–J) *Sirembrotula mediator* n. gen., n. sp., holotype, Black's Beach, LACM 60186 (reversed), H outer face, I ventral view, J anterior view.
K–P) *Calamopteryx*? *moelleri* (Schwarzhans, 2007), Black's Beach, LACM 60187 (O–P reversed), O anterior view, L, N ventral views.
Q–AB) *Eobidenichthys* n. gen. *symmetricus* (Frost, 1934), Black's Beach, LACM 60188 (V reversed), S anterior view, R, W, Z, AB ventral views.
AC–AO) *Pseudobrotulina fitchi* n. gen., n. sp.; AC–AE holotype, Black's Beach, LACM 60189 (reversed), AE anterior view, AD ventral view; **AF–AO** paratypes, Black's Beach, LACM 60190 (AF–AI, AN–AO reversed), AH anterior view, AG, AI, AM, AO ventral views.
AP–AR) *Saccogaster salebrosus* n. sp., holotype, Black's Beach, LACM 60192, AP anterior view, AR ventral view.

Species. A monospecific genus with *Pseudobrotulina fitchi* n. sp.

Pseudobrotulina fitchi n. sp.

Fig. 11AC–AO

Holotype: Fig. 11AC–AE, LACM 60189, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 5 specimens same data as holotype, LACM 60190.

Referred specimens: 76 specimens same data as holotype, LACM 60191.

Etymology: In memory of the John Fitch (Long Beach, California) who contributed so much to the knowledge and understanding of otoliths of extant fishes and generously supported the authors in the early days of their research.

Diagnosis: See genus diagnosis (monospecific genus).

Description. Elongate, fusiform and relatively thin otoliths up to 4.65 mm in length (holotype). OL:OH = 1.8–2.2; OH=OT = 2.0–2.3. Otolith shape fusiform with gently curved, centrally flattened dorsal rim without prominent angles and regularly curved ventral rim. Anterior and posterior tips moderately pointed, positioned at otolith axis, symmetrical or anterior tip sharper. All rims smooth.

Inner face slightly convex with centrally positioned sulcus. Sulcus relatively long positioned at equal distance from anterior and posterior tips of otolith, shallow, with uniform, elongate sulcus and colliculum. Sulcus inclined at less than 3° against otolith axis. Ridge-like connection of ostial tip with anterior tip of otolith often discernable. Colliculum well-defined and clearly separated, shallow. Dorsal field with distinct, narrow dorsal depression; ventral field with ventral furrow close to ventral rim of otolith but turning upwards and inwards posteriorly to nearly meet tip of sulcus and posteriormost portion of dorsal depression. Outer face about as strongly convex as inner face or slightly stronger, smooth.

Discussion. See above discussion to genus (monospecific genus).

Genus *Saccogaster* Alcock, 1889

Saccogaster salebrosus n. sp.

Fig. 11AP–AR

Holotype: Fig. 11AP–AR, LACM 60192, upper Lutetian, Ardath Shale, Black's Beach.

Etymology: From salebrosus (Latin) = rugged, uneven, referring to the elevated nature of the colliculum.

Diagnosis: OL:OH = 1.85. Inner face nerly flat. Sulcus short (OL:SuL = 2.7) with small, undevided, elevated colliculum.

Description. The unique specimen is 7.3 mm in length. OH:OT = 2.0. Dorsal rim relatively shallow with small predorsal lobe and slightly concave rims before and behind and distinct, broad, rounded postdorsal angle followed by steeply inclined straight postdorsal rim. Ventral rim deeper than dorsal rim, deepest near center of rim, and regularly curved. Anterior tip dorsal to otolith axis, moderately pointed; posterior tip positioned at otolith axis, angular. All rims smooth.

Inner face nearly flat in horizontal direction and slightly bent in vertical direction. Sulcus outline poorly defined but sulcus marked by small, clearly defined, centrally positioned and elevated colliculum (elevation best seen in lateral view; Fig. 11AR. OL:SuL = 2.7. No dorsal depression or ventral furrow discernable. Outer face convex, smooth.

Discussion. The single, large otolith is characterized by the distinct shape of the dorsal rim and the small, centrally positioned and elevated colliculum. This pattern is shared with otoliths of some extant species of the genus *Saccogaster* for instance *S. tuberculata* (Chan, 1966) (see Nielsen et al. 2012).

Order **Holocentriformes** Patterson, 1993

Family Myripristidae Nelson, 1955

Genus *Weileria* Frizzell & Lamber, 1961

Weileria cajun Frizzell & Lamber, 1961

Fig. 12A–F

1961 *Weileria cajun* - Frizzell & Lamber: fig. 6, 18–19.
?1999 "genus Myripristinarum" *cajun* (Frizzell & Lamber, 1962) - Müller: fig. 29/22.
2003 "genus Myripristidarum" *cajun* (Frizzell & Lamber, 1961) - Nolf & Stringer: pl. 4, fig. 1-2.
non 2022 "*Myripristis*" *cajun* (Frizzell & Lamber, 1961) - Lin & Nolf: fig. 15I-K (*Stintonia brazosia* Frizzell & Lamber, 1961).

Material: 59 specimens: 58 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60193; 1 specimen, Mission Valley Formation, Miramar Reservoir site, LACM 60106.

Discussion. Otoliths of the fossil otolith-based genus *Weileria* differ from the extant genera *Myripristis* and *Ostichthys* in the shallow ventral lobe of the ostium. A similar character status is observed in *Plectrypops* (for otoliths of *Plectrypops lima* see Smale et al. 1995 and Rivaton & Bourret 1999), but the otoliths of *Weileria* are more compressed and show a shorter ostium. The latter is interpreted to be a plesiomorphic character with the caveat, however, that otoliths of the most plesiomorphic extant genus *Corniger* are not known.

Frizzell & Lamber (1961) placed three species from the Eocene and Oligocene of the Gulf Coast and two species from the Oligocene and Miocene of Europe in *Weileria*. They also established a second fossil otolith-based species - *Stintonia* - in which they placed three species from the Oligocene and Eocene of the Gulf Coast and four species from Europe. *Stintonia* otoliths are even more plesiomorphic than *Weileria* otoliths with a more regular shape of the otolith, a regularly curved ventral rim, and an even less expanded ventral margin of the ostium. Distinction of myripristid species by means of otoliths is notoriously difficult and depends on often very subtle differences. Unfortunately, myripristid otoliths also have the tendency to be easily affected by erosion along the anterior tip of the otoliths and the dorsal rim, and therefore, few fossil myripristid otoliths are usually preserved well enough for identification. Because of this, several of the species established in past literature, including the ones described by Frizzell & Lamber (1961), are in need of revision. This may also be a reason for the predominant record of *W. cajun* from the Eocene of the USA (see above synonymy listing).

However, some of them may indeed represent different taxa. Müller figured a well preserved and relatively slender myripristid otolith with a moderately developed ventral ostial lobe from the Eocene of Virginia which might represent an undescribed species of *Weileria*. Lin & Nolf (2022) figured otoliths from the Stone City beds of the Brazos River that show a regularly curved ventral rim and a very low ventral rim of the ostium. These otoliths stem from the type locality of *Stintonia brazosia* Frizzell & Lamber, 1961 and probably represent the same species. Lin & Nolf (2022) considered the genus *Weileria* as invalid because the type species, *W. louisiana* Frizzell & Lamber, 1961, was "based on an eroded holotype without true features" (p. 47; thereby citing Nolf, 2013). Judging from Frizzell & Lamber's drawing of the holotype, we do not follow this assessment and regard *W. louisiana* as a valid species, and therewith the genus as valid too, differing from *W. cajun* in a more compressed shape.

Order **Trachichythiformes** Moore, 1990
Family Trachichthyidae Bleeker, 1859
Genus *Trachichthys* Shaw, 1799

Trachichthys melamphaoides (Nolf, 1988)

Fig. 12K–N

1988 "genus Epigoninarum" *melamphaoides* - Nolf: pl. 11, fig.7-8.
2016 *'Epigonus' melamphaoides* (Nolf, 1988) - Lin, Nolf, Steurbaut & Girone: fig. 11R-T.

Material: 2 specimens, Ardath Shale, Black's Beach, LACM 60194.

Discussion. *Trachichthys melamphaoides* is morphologically intermediate between otoliths of the genera *Trachichthys* and *Paratrachichthys*. The species resembles the *Trachichthys anomalopsoides* Schwarzhans, 2012 from the Paleocene of Austria and differs in the more pronounced rostrum, the nearly horizontal middorsal and midventral rims, and the well-developed postdorsal angle. *Trachichthys melamphaoides* probably derived from *T. anomalopsoides*. It is possible that both species represent an extinct genus positioned in-between *Trachichthys* and *Paratrachichthys*.

Another similar species in the European Eocene is *Gephyroberyx hexagonalis* (Leriche, 1905), which differs in the wider sulcus and the presence of a postventral denticle.

Family Diretmidae Gill, 1896
Genus *Diretmus* Johnson, 1863

Diretmus fidelis n. sp.

Fig. 12G–J

Holotype: Fig. 12G–I, LACM 60195, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 3 specimens same data as holotype, LACM 60196.

Etymology: From fidelis (Latin) = faithful, referring to the allocation of these otoliths to the genus *Diretmus*.

Diagnosis: OL:OH = 0.75. Dorsal and ventral rims broad, resulting in a nearly rectangular otolith shape. CaL:OsL = 0.95–1.05. Ostium and cauda deepened.

Description. Very high-bodied, robust otoliths with nearly rectangular outline reaching 3.5 mm in length (holotype). OH:OT = 3.5. Dorsal rim broad, its central portion flattened; ventral rim deep, broad, its central portion flattened. Pre- and postdorsal and pre- and postventral angles rounded. Anterior rim nearly vertical with very short and blunt rostrum; posterior rim blunt, its broadly rounded tip above caudal tip, ventrally slightly inclined. All rims smooth.

Inner face bent in horizontal direction, straight in vertical direction. Sulcus slightly supramedian, relatively wide and deepened. Ostium and cauda about equally long. Ostium strongly widened ventrally, oriented at 33–43° ascending towards anterior; ostial colliculum anteriorly closed. Cauda deeper than ostium and narrower, oriented at 15° ascending towards the dorsal posterior rim; caudal colliculum poorly defined except for its ventral margin. Dorsal depression large, wide, somewhat oblong in shape; ventral field smooth, occasionally with feeble ventral furrow across central region. Outer face convex, smooth.

Discussion: *Diretmus fidelis* shows a number of characteristic features which are typical for the genus and distinguish it from other diretmid genera (see Schwarzhans, 2010 for figures of otoliths of the three extant genera). These features are the high body shape, the inclination of ostium and cauda, the shape of the ostium and the anteriorly closed ostial colliculum, and the sulcus proportions. *Diretmus fidelis* differs from the Late Cretaceous *D. primus* Schwarzhans, 2010 in being higher bodied (OL:OH = 0.75 vs. 0.8), having a relatively shorter cauda (CaL:OsL = 0.95–1.05 vs. 1.2–1.8), and the ostial colliculum being anteriorly closed (vs. open). *Diret-*

mus semicompletus Nolf & Steurbaut, 2004 from early Oligocene bathyal sediments of Piedmont, Italy, shows an anteriorly open ostium and a cauda that closely approaches the posterior rim of the otolith. This character status suggests an allocation of the species to *Diretmoides*. The same is true for *Diretmus* sp. from the Lutetian of the Aquitaine Basin figured by Nolf (2013). The status of a variety of other high-bodied otoliths that are commonly associated with the Diretmidae remains unresolved: *Argyroberyx dentatus* (Liebus, 1927) and *Beauryia medialis* Schwarzhans, 2010, both from the Maastrichtian of Bavaria, Germany, and *Diretmus*? *serratus* (Müller, 1999).

Order **Beryciformes** Regan, 1909
Family Berycidae Lowe, 1839
Genus *Centroberyx* Gill, 1862

Centroberyx eocenicus (Frost, 1933)

Fig. 12O–W

1933 Otolithus (*Polymixia*) *eocenicus* - Frost: pl. 12, fig. 20.
1978 *Centroberyx lemoinei* (Priem, 1906) - Stinton: text-fig. 26f (see there for further references).
1988 *Centroberyx eocenicus* Frost, 1933 - Nolf: pl. 8, fig. 19-21.
2007 *Centroberyx ingens* (Koken, 1884) - Schwarzhans: fig. 24 A-C.

Material: 145 specimens: 1 specimen from the syntype series of Frost from the London Clay figured by Frost (pl. 12, fig. 20), here selected as the lectotype (Fig. 12S), NHMUK PV P 22496; 106 specimens, Ardath Shale, Black's Beach, LACM 60197; 38 specimens, Ardath Shale middle layer, Black's Beach, LACM 60198.

Diagnosis (based on lectotype)**:** OL:OH = 1.3. Ventral rim with narrowly spaced pre- and postventral angles. Inner face more strongly convex than outer face. CaL:OsL = 1.15. Caudal tip pointed.

Description (based on all available specimens)**.** Moderately large, relatively thin otoliths up to at least 6.5 mm in length (lectotype 5.4 mm). OL:OH = 1.2–1.3; OH:OT = 3.3–3.8. Dorsal rim gently curved without prominent angles, undulating, becoming lobate in large specimens (Fig. 12O). Ventral rim relatively regularly curved with rounded pre- and postdorsal angles and short middorsal section. Anterior rim with moderately strong rostrum, less prominent antirostrum, and mostly sharp excisura. Posterior rim somewhat projecting, angular tip, positioned at about level of caudal tip. All rims smooth except for dorsal rim.

Inner face distinctly convex with slightly supramedian sulcus. Ostium slightly shorter than cauda and about twice as wide due to the deep ventral ostial margin. Ostium narrowing towards opening with clearly defined and slightly deepened colliculum. Cauda relatively narrow, slightly bent upwards, with tapering, pointed tip that is very near the posterior rim. Caudal colliculum well marked, particularly ventrally. CaL:OsL = 1.15–1.3. Dorsal depression wide, ventrally marked by distinct crista superior towards sulcus. Ventral field smooth, rarely with feeble ventral furrow close to ventral rim of otolith. Outer face less convex than inner face to almost flat, mostly smooth.

Discussion. The distinction of the various described otolith-based species of the genus *Centroberyx* is not always well defined. Several nominal species have been regarded as synonyms of other species, particularly in the European Paleogene. Unfortunately, the situation had been complicated by Schwarzhans (1980) who postulated a significant ontogenetic morphological allometry based on extant otoliths, which later turned out to represent different species (Schwarzhans 2019a), which in turn led to the rehabilitation of several previously synonymized species. However, much revision work still remains to be done. Here, we redefine a rarely reported species, *C. eocenicus*, by establishing a lectotype from the original series representing the specimen figured in the original description. The distinction of *C. eocenicus* from *C. ingens* (Koken, 1884) and *C. subrotundus* (Koken, 1884) from the late Eocene and early Oligocene for instance remains to be verified. Schwarzhans & Jagt (2021) placed *C. eocenicus* in the *Centroberyx integer* Group, but with the new review data now available, the species is more likely to belong to the *Centroberyx fragilis* Group.

Among the many problematical Eocene species of *Centroberyx* is also *C. pattersoni* (Nolf, 1975) from the Lutetian of Belgium. We have here figured several well-preserved specimens from Balegem in Belgium (Fig. 12 AL–AQ) for comparison. *Centroberyx pattersoni* differs from *C. eocenicus* in the somewhat more compressed shape with a slightly lower OL:OH ratio (1.05–1.15 vs. 1.2–1.3) and the narrow and slightly flexed cauda.

Centroberyx predorsalis n. sp.

Fig. 12X–AB

Holotype: Fig. 12X–Y, LACM 60107, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 10 specimens same data as holotype, LACM 60108.

Referred specimens: 66 specimens: 65 specimens same data as holotype, LACM 60109; 1 specimen, upper Lutetian, Ardath Shale middle layer, Black's Beach, LACM 60199.

Etymology: Referring to the pronounced predorsal angle observed in these otoliths.

Diagnosis: OL:OH = 1.1–1.15. Dorsal rim with forward positioned predorsal expansion. Ventral rim relatively regularly curved. Inner face more strongly convex than outer face. CaL:OsL = 1.05–1.2. Caudal tip pointed.

Description. Moderately large, relatively thin otoliths up to 8.8 mm in length (holotype). OH:OT = 3.6–4.0. Dorsal rim with broad, distinct, forward positioned predorsal expansion and gently sloping downwards thereafter, slightly undulating. Ventral rim relatively regularly curved without prominent angles. Anterior rim bluntly rounded with short rostrum, weak or no antirostrum, and excisura. Posterior rim somewhat projecting, rounded tip, positioned at about level of caudal tip. All rims smooth except for dorsal rim.

Inner face distinctly convex with distinctly supramedian sulcus. Ostium slightly shorter than cauda and about twice as wide due to deep ventral ostial margin. Ostium slightly narrowing towards opening, with clearly defined and slightly deepened colliculum. Cauda relatively narrow, slightly bent upwards, with tapering, pointed tip. Caudal colliculum well marked, particularly ventrally. Dorsal depression wide, ventrally marked by distinct crista superior towards sulcus. Ventral field smooth, without ventral furrow. Outer face slightly convex or flat, smooth.

Discussion. *Centroberyx predorsalis* is characterized by the distinct predorsal expansion and sloping rim thereafter and the deeply and gently rounded ventral rim. However, when the predorsal rim has been eroded the species is difficult to be distinguished from *C. eocenicus*. *Centroberyx predorsalis* is the most common *Centroberyx* species in the Bartonian Mission Valley Formation but has not been found in the upper Lutetian Black's Beach (except a single specimen from the middle level) where it is replaced by *C. eocenicus*. The distribution pattern of these two species may reflect one of very few instances of a stratigraphic signal between the otolith communities of Black's Beach and the Miramar Reservoir sites.

Centroberyx pseudopulcher n. sp.

Fig. 12AC–AK

Holotype: Fig. 12AC–AE, LACM 60200, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 10 specimens same data as holotype, LACM 60201.

Referred specimens: 144 specimens: 123 specimens same data as holotype, LACM 60202; 21 specimens, Bartonian Ardath Shale middle layer, Black's Beach, LACM 60203.

Etymology: Referring to the similarity with *C. pulcher* Schwarzhans, 1980, from the Eocene of New Zealand.

Diagnosis: OL:OH = 1.05–1.15. Ventral rim with widely separated pre- and postventral angles; rim horizontal between angles straight. Inner and outer face about equally strong convex. CaL:OsL = 1.25–1.4. Caudal tip slightly tapered and rounded.

Description. Relatively small and thick otoliths up to 4.5 mm in length (holotype 4.25 mm). OH:OT = 3.3–3.7. Dorsal rim shallow, regularly curved or with broadly rounded pre- and postdorsal angles. Ventral rim deep, with distinct widely spaced pre- and postdorsal angles and straight, horizontal midventral section. Anterior rim blunt, steeply inclined from short rostrum to preventral angle. Antirostrum and excisura weak. Posterior rim blunt, steeply inclined, posterior tip angular, positioned above caudal tip. All rims smooth except dorsal rim slightly undulating.

Inner face mildly convex with distinctly supramedian sulcus. Ostium distinctly shorter than cauda and about twice as wide as high due to a deep ventral ostial margin. Ostium slightly narrowing towards opening, with clearly defined and slightly deepened colliculum. Cauda relatively wide, slightly upward directed toward postdorsal, with slightly tapered and rounded tip. Caudal colliculum well marked, particularly ventrally. Dorsal depression wide, ventrally marked by distinct crista superior towards sulcus. Ventral field smooth, without ventral furrow. Outer face somewhat more convex than inner face, smooth.

Discussion. Otoliths of *C. pseudopulcher* do not achieve the sizes of the parallel occurring *C. eocenicus* and differ in the slightly more compressed shape (OL:OH = 1.05–1.15 vs. 1.2–1.3), the outer face being as convex as the inner face (vs. inner face more strongly convex than outer face), and the shape of the ventral rim and the cauda. Distinction of the two species is not always easy with the otolith proportions and the shape of the ventral rim being the most reliable traits. *Centroberyx pseudopulcher* also resembles *C. pulcher* (Schwarzhans, 1980) from the early and middle Eocene of New Zealand but differs in the relatively smooth otolith rims (vs. intensely crenulated) and the wider ostium. Both species may represent vicariant species across the Eocene Pacific.

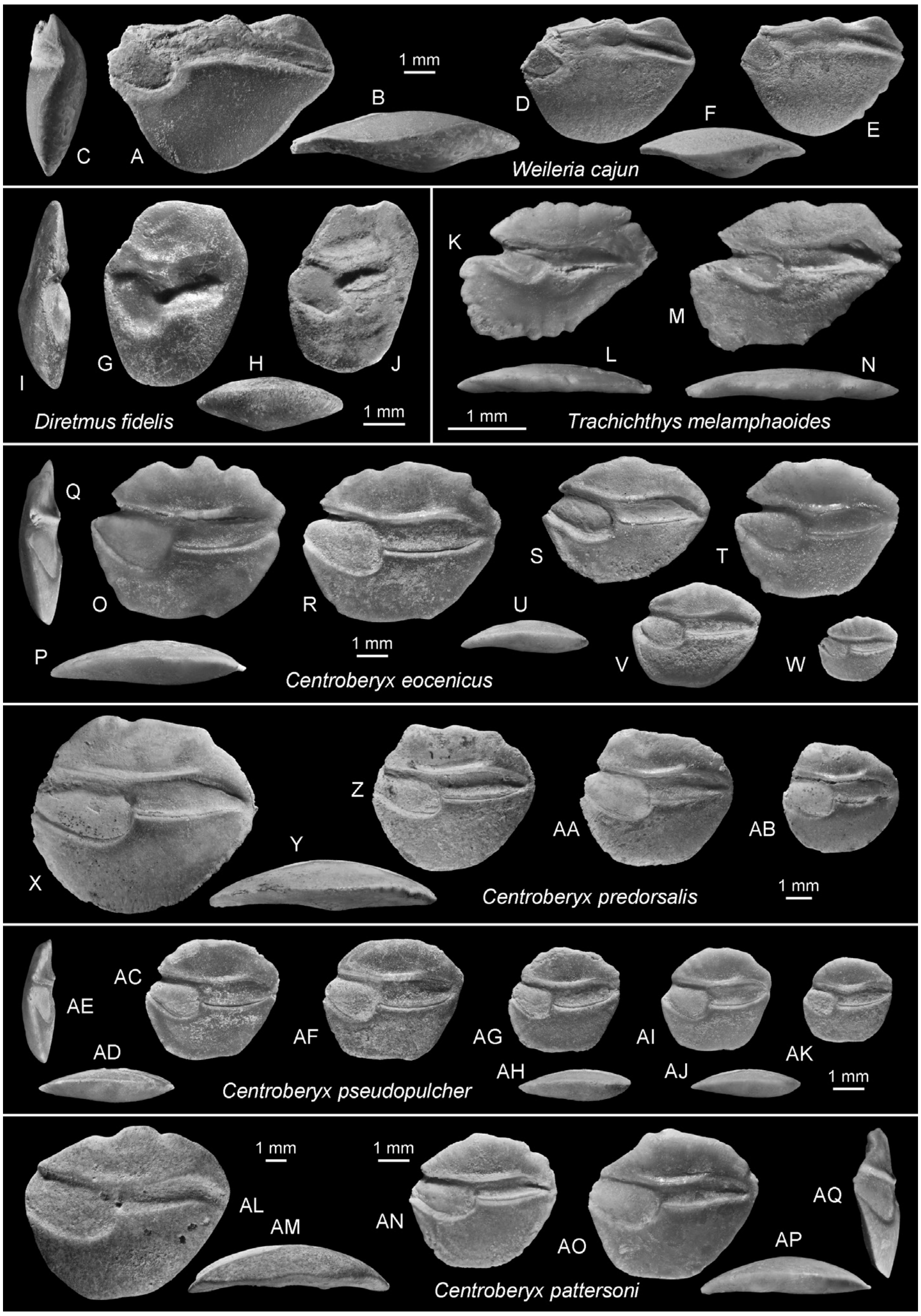


Fig. 12 - A–F) *Weileria cajun* Frizzel & Lamber, 1961, Black's Beach, LACM 60193, C posterior view, B, F ventral view.
G–J) *Diretmus fidelis* n. sp.; G–I holotype, Black's Beach, LACM 60195 (reversed), I anterior view, H ventral view; J paratype, Black's Beach, LACM 60196.
K–N) *Trachichthys melamphaoides* (Nolf, 1988), Black's Beach, LACM 60194 (M–N reversed), L, N ventral views.
O–W) *Centroberyx eocenicus* (Frost, 1933); **S** lectotype, Ypresian, London Clay, England, NHMUK PV P22496 (reversed); O–R, Z–W Black's Beach, LACM 60197 (T–W reversed), Q anterior view, P, U ventral views.
X–AB) *Centroberyx predorsalis* n. sp.; X–Y holotype, Miramar Reservoir site, LACM 60107 (reversed), Y ventral view; Z–AB paratypes, Miramar Reservoir site, LACM 60108 (reversed).
AC–AK) *Centroberyx pseudopulcher* n. sp.; AC–AE holotype, Black's Beach, LACM 60200, AE anterior view, AD ventral view; AF–AK paratypes, paratypes, LACM 60201 (AG–AH, AK reversed), AH, AJ ventral views.
AL–AQ) *Centroberyx pattersoni* (Nolf, 1975), Lutetian, Balegem, Belgium (AO–AQ reversed), AM, AP ventral views, AQ anterior view.

Order **Mugiliformes** Regan, 1909
Family Mugilidae Risso, 1827
Genus *Avitamugil* n. gen.

Type species: *Avitamugil scrippsi* n. sp.

Etymology: A combination of avitus (Latin) = ancient and the genus names *Mugil*.

Diagnosis: A fossil otolith-based genus of the family Mugilidae characterized by regularly curved ventral and dorsal rims. The dorsal rim is not depressed in any way. The otoliths are elongate with a ratio OL:OH of 1.5–1.8. The cauda is long, narrow, entirely straight and horizontal. The ratio CaL:OsL ranges from 3.2 to 4.0. The tip of the cauda is bent downwards at an angle of 40–50° in a sharp bent.

Discussion. The characteristic shape and proportions of the sulcus characterize *Avitamugil* as a typical member of the family Mugilidae. *Avitamugil* differs from the otoliths of all known modern mugilid genera in the regularly curved dorsal rim and the horizontal, straight cauda with the sharply bent tip (for otoliths of modern mugilids see e.g., Smale et al. 1995; Rivaton & Bourret 1999; Lin & Chang 2012). We consider it a plesiomorphic "archaetype" of modern mugilid otoliths as they are known since Oligocene times.

Apart from the two species listed below, a number of similar looking otoliths have been described from European Eocene as members of the family Toxotidae (*Toxotes arcuatus* Stinton, 1984, *T. eximius* Stinton, 1984, *T. pentagonalis* Stinton, 1984 and *T. wheeleri* Nolf & Lapierre, 1979). The family Toxotidae today contains a single genus (*Toxotes*) with seven species living in brackish and freshwater from India to Philippines and Australia and Polynesia (Nelson et al. 2016) and is known for its capability to eject squirts of water from their mouth to shoot down and eat insects. Their otoliths indeed show some striking similarity with mugilid otoliths because of their long and narrow sulcus and the short and funnel-shaped ostium. As far as the fossil forms from the European Eocene are concerned, it should be mentioned that they more than likely represent an extinct mugilid genus close to *Avitamugil*. They differ from otoliths of *Avitamugil* in the more compact shape, the only slightly bent caudal tip, and a longer rostrum when preserved.

Species. *Avitamugil scrippsi* n. sp. from the middle Eocene of California and *Avitamugil constrictus* (Stinton, 1984) from the early Eocene of England, originally described as *Pentanemus constrictus* by Stinton (1984) with *Pentanemus rotundus* Stinton, 1984 as a synonym.

Avitamugil scrippsi n. sp.

Fig. 13A–J

Holotype: Fig. 13A–C, LACM 60204, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 24 specimens: 18 specimens same data as holotype, LACM 60205; 6 specimens, Bartonian, Mission Valley Formation, Miramar Reservoir site, LACM 60109.

Etymology: Referring to the Scripps Research Institute located on the Black's Beach Road just above the outcrops.

Diagnosis: OL:OH = 1.65–1.8. Dorsal rim shallow, irregularly undulating. Ventral rim regularly curved, slightly crenulated. CaL:OsL = 3.2–3.5.

Description. Thin, slender, and relatively large otoliths up to 6.3 mm in length (holotype). Dorsal rim shallow, regularly curved, with variably developed but mostly well rounded postdorsal angle, irregularly undulating. Ventral rim deeper, evenly curved, slightly and finely crenulated or smooth. Anterior tip of otoliths rarely well-preserved, with short, rounded rostrum and minute antirostrum and excisura. Rostrum length 10–18% of OL. Posterior rim blunt to slanted; posterior tip rounded, inferior.

Inner face distinctly convex with distinctly supramedian sulcus. Sulcus composed of a long, narrow, straight, horizontal, deepened cauda with sharply bent tip at angle of 40–50°, and a short, only slightly widened ostium. Dorsal depression narrow, indistinct; ventral field smooth, somewhat crenulated along the ventral margin, sometimes with very faint ventral furrow distant from ventral rim. Outer face concave, with some faint radial ornamentation.

Discussion. *Avitamugil scrippsi* differs from its congener *A. constrictus* from the early Eocene of England in the more elongate shape and a slightly lower index CaL:OsL (3.2–3.5 vs. 3.6–4.0 measured from figures in Nolf, 2013). *Avitamugil scrippsi* shows some variation in the expression of the postdorsal angle and posterior rim which can be relatively strong and blunt (Fig. 13A, D, E, I) or more depressed and slanted (Fig. 13F, G). These small variations do not appear to be consistent or supported by any other character and, therefore, are thought to reflect intraspecific variability.

Order **Pleuronectiformes** Bleeker, 1859
Family Citharidae Hubbs & Hubbs, 1945
Genus *Rhombocitharus* Schwarzhans, 1994

Rhombocitharus nanus (Müller, 1999)

Fig. 13K–R

1999 "genus Bothidarum" *nanus* - Müller: fig. 42/7-10, pl. 17, fig. 10.
2022 *Brachypleura nana* (Müller, 1999) - Lin & Nolf: fig. 23A-D.

Material: 50 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60206.

Discussion. Lin & Nolf (2022) recognized these otoliths as representing a citharid and placed it in the genus *Brachypleura*. However, we consider a placement with the extinct citharid otolith-based genus *Rhombocitharus* more appropriate based on the nearly pentagonal outline of the otolith and the lack of predorsal expansion, which is typical for *Brachypleura* (for figures of extant citharid otoliths see Schwarzhans 1999).

Rhombocitharus nanus is a small species barely exceeding 2 mm in length characterized by a deep ventral rim and a shallow, nearly flat dorsal rim. The ratio OL:OH is very variable ranging from 1.3 to 1.65 whereby right otoliths are slenderer than left otoliths.

Family Paralichthyidae Regan, 1910
Genus indet.

Paralichthyidae indet.

Fig. 13S–Z

Material: 5 specimens: 3 specimens, Ardath Shale, Black's Beach, figured specimens LACM 60207; 2 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60110.

Discussion. A few small specimens not exceeding 1.7 mm in length (Fig. 13S–U, X–Z) are characterized by a compressed rectangular shape in combination with a convex inner and flat to concave outer face (OL:OH 1.15–1.25; OH:OT about 3.0). The ostium opens to the anterior rim of the otoliths and is distinctly longer and slightly wider than the cauda (OsL:CaL = 1.9–2.1). The rostrum is short in the small specimens, but a single larger, eroded specimen of 2.8 mm in length shows a distinct rostrum (Fig. 13V–W) and is thought to represent the same species. Due to the limited material with mostly small and one larger, eroded specimens, neither genus nor a specific identification is possible.

Family Soleidae Bonaparte, 1835
Genus *Praearchirolithus* Schwarzhans, 1999

Praearchirolithus altus n. sp.

Fig. 13AA–AK

Holotype: Fig. 13AC–AE, LACM 60111, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 11 specimens: 5 specimens same data as holotype, LACM 60112; 6 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60208.

Referred material: 635 specimens: 20 specimens same data as holotype, LACM 60113; 615 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60209.

Etymology: From altus (Latin) = high, referring to the high-bodied shape of the otoliths.

Diagnosis: OL:OH = 0.77–0.95. Inner and outer faces moderately convex. Sulcus long, almost opens anteriorly; OL:SuL = 1.1–1.2; OsL:CaL = 1.8–2.4. Cauda reaching close to posterior rim of otolith. Dorsal and ventral furrows wide, not connected behind cauda.

Description. Compressed, high-bodied otoliths with a ratio OL:OH <1.0, reaching 2.4 mm in length (holotype); OH:OT = 2.6–3.0. Dorsal rim shallow, nearly flat and horizontal or very slightly ascending towards anterior; ventral rim deeply and regularly curved. Anterior rim blunt, dorsally vertical, ventrally broadly rounded; posterior rim nearly vertical. All rims smooth or slightly undulating.

Inner face distinctly convex with distinctly supramedian positioned sulcus. Sulcus long, slightly inclined downwards towards anterior at 5–15°, moderately wide and slightly deepened. Ostium distinctly longer than cauda (nearly twice as long), and almost open to anterior rim of otolith. Cauda terminating close to posterior rim of otolith, slightly deeper and narrower than ostium. Dorsal depression a well-defined wide furrow just above sulcus; ventral furrow wide, mostly distinct and deep, running across middle of ventral field. Dorsal depression and ventral furrow not connected around posterior tip of cauda and thus not forming a continuous circumsulcal furrow. Outer face convex, about as strongly as inner face or slightly less, smooth.

Side dimorphism. Side dimorphism is very weakly developed. Right otoliths appear to have a less convex inner face than left otoliths and tend to have a slightly lower ratio OL:OH than left otoliths.

Discussion. The moderately convex inner face, the high ratio OsL:CaL, and the relatively wide ventral furrow are characteristic for the fossil otolith-based genus *Praearchirolithus* and distinguish them from the coeval *Pseudopardarchirolithus* Schwarzhans, 1999. So far, *Praearchirolithus* was known from a single species, *P. schultzei* (Nolf & Lapierre, 1979) from the late Eocene of France. *Praearchirolithus altus* differs from *P. schultzei* in the longer sulcus reaching close to the posterior rim of the otolith (OL:SuL = 1.1–1.2 vs. 1.35–1.4), the lack of a connection of the ventral furrow with the dorsal depression behind the cauda, and the relatively wide ventral furrow.

Praearchirolithus altus is very common in Black's Beach, but represented mostly by small specimens. At the Miramar Reservoir site, it is relatively rare but represented by distinctly larger specimens. This indicates that *P. altus* may have changed habitat during ontogeny from further offshore and deeper to nearshore and shallower.

Praearchirolithus confusus n. sp.

Fig. 13AL–AW

Holotype: Fig. 13AO–AQ, LACM 60114, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 12 specimens: 5 specimens same data as holotype, LACM 60115; 7 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60210.

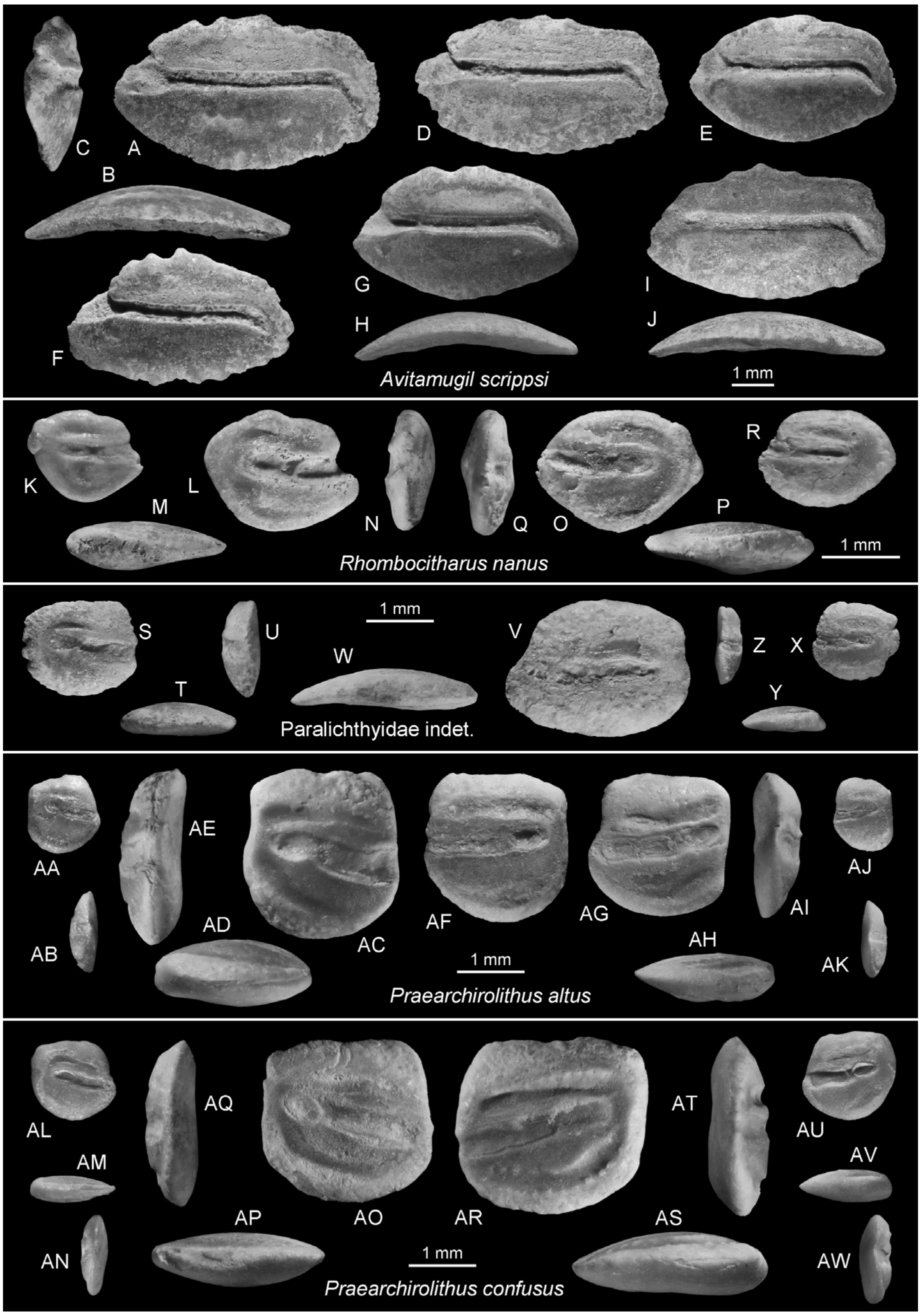


Fig. 13 - A–J) *Avitamugil scrippsi* n. gen., n. sp.; A–C holotype, Black's Beach, LACM 60204, C anterior view, B ventral view; D, E, I–J paratypes, Black's Beach, LACM 60205 (reversed), J ventral view; F–H paratypes, Miramar Reservoir site, LACM 60109 (G–H reversed), H ventral view.
K–R) *Rhombocitharus nanus* (Müller, 1999), Black's Beach, LACM 60206, M, P ventral views, N, Q anterior views.
S–Z) Paralichthyidae indet.; S–U, X–Z Black's Beach, LACM 60207, U, Z anterior views, T, Y ventral views; V–W Miramar Reservoir site, LACM 60110, W ventral view.
AA–AK) *Praearchirolithus altus* n. sp.; AC–AE holotype, Miramar Reservoir site, LACM 60111, AE anterior view, AD ventral view; AF–AH paratypes, Miramar Reservoir site, LACM 60112, AI anterior view, AH ventral view; AA–AB, AJ–AK paratypes, Black's Beach, LACM 60208, AB, AK anterior views.
AL–AW) *Praearchirolithus confusus* n. sp.; AO–AQ holotype, Miramar Reservoir site, LACM 60114, AQ anterior view, AP ventral view; AR–AT paratype, Miramar Reservoir site, LACM 60115, AT anterior view, AS ventral view; AL–AN, AU–AW paratypes, Black's Beach, LACM 60210, AM, AV ventral views, AN, AW anterior views.

Referred material: 531 specimens: 422 specimens same data as holotype, LACM 60116; 109 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60211.

Etymology: From confusus (Latin) = confused, perplexed, referring to the remarkable variability of the features of the otoliths.

Diagnosis: OL:OH = 1.05–1.1. Inner and outer faces moderately convex. Sulcus long, almost opens anteriorly; OL:SuL = 1.2–1.25; OsL:CaL = 1.9–2.1. Cauda reaching close to posterior rim of otolith. Dorsal and ventral furrows wide, not connected behind cauda.

Description. Moderately compressed, nearly round otoliths with a ratio OL:OH >1.0, reaching 2.9 mm in length (holotype); OH:OT = 2.8–3.2. Dorsal rim shallow, nearly flat and horizontal with orthogonal angles at joint with anterior and posterior rims; ventral rim moderately deep and regularly curved. Anterior rim blunt, vertical, very slightly curved; posterior rim nearly vertical. All rims smooth or slightly undulating.

Inner face distinctly convex with slightly supramedian positioned sulcus. Sulcus long, inclined downwards towards anterior at 10–15°, moderate in height and slightly deepened. Ostium distinctly longer than cauda (almost 2.5 times as long), and almost opens to anterior rim of otolith. Cauda terminating moderately close to posterior rim of otolith, slightly narrower than ostium. Dorsal depression a well-defined wide furrow just above sulcus; ventral furrow wide, distinct and deep, running across middle of ventral field. Dorsal depression and ventral furrow not connected around posterior tip of cauda and thus not forming a continuous circumsulcal furrow. Outer face flat to convex, about as strongly as inner face or slightly less, smooth.

Side dimorphism. No side dimorphism is discernable in these otoliths.

Discussion. *Praearchirolithus confusus* differs from *P. altus* in being less compressed (OL:OH >1.0 vs. <1.0) and the cauda not reaching as far backward towards the posterior rim of the otoliths (OL:SuL = 1.2–1.25 vs. 1.1–1.2). These differences, however, are subtle and well discernable in large specimens but multiple transitional forms exist in small specimens below 1.5 mm in length. Like *P. altus*, *P. confusus* too shows a separation of large specimens found predominantly at the Miramar Reservoir site (Mission Valley Formation) and smaller ones at Black's Beach (Ardath Shale). Different from *P. altus*, *P. confusus* is much more common at the Miramar Reservoir site than Black's Beach.

Order **Carangiformes** Jordan, 1923
Family Menidae Fitzinger, 1873
Genus *Mene* Lacepède, 1803

Mene sp.

Fig. 14A–C

Material: 1 specimen, Mission Valley Formation, Miramar Reservoir site, LACM 60117.

Discussion. Today, the family Menidae contains a single species, *Mene maculata* (Bloch, 1801) from the Indo-West Pacific, but in the fossil record, several species have been described from Paleogene rocks based on skeletons (e.g., Friedman & Johnson 2005) and otoliths (e.g., Nolf 2013). Recently, *Mene graviei* Lin & Nolf, 2022 was described from the Bartonian of the Gulf Coast. The single specimen from the Bartonian of California resembles *M. graviei* in the hooked cauda and the general appearance but differs in the knob-like expansion of the posterior part of the ventral rim, the strongly convex outer face, and the more compressed shape. It likely represents a further fossil species of the family. However, the preservation of the single specimen prevents any further identification.

Family Carangidae Rafinesque, 1815
Genus indet.

Carangidae indet.

Fig. 14D–E

Material: 1 specimen, Mission Valley Formation, Miramar Reservoir site, LACM 60118.

Discussion. A single, rather eroded otolith with smoothened rims and lacking rostrum of 2.5 mm in length resembles carangid otoliths in the slender, thin shape of the sagitta and the shape and proportions of the sulcus. No further identification is possible.

Order **Scombriformes** Bleeker, 1859
Family Stromateidae Rafinesque, 1810
Genus *Peprilus* Cuvier, 1829

Peprilus*? *muelleri n. sp.

Fig. 14F–G

Holotype (and unique specimen)**:** Fig 14F–G, LACM 60276, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Etymology: In honor of Arnold Müller (Leipzig, Germany) in recognition of his contribution to the knowledge of the fossil otoliths from the middle Atlantic Coastal Plain of the USA.

Diagnosis: OL:OH = 1.6. Dorsal rim highest at predorsal angle; ventral rim shallow, nearly flat. Rostrum long, 30% of OL, with blunt tip; excisura wide; antirostrum sharp. Cauda slightly bent at tip terminating close to posterior rim of otolith; CaL:OsL = 1.45.

Description. The unique holotype is a thin, fragile otolith of 4.15 mm in length. OH:OT = 3.4. Dorsal rim triangular in shape with elevated, broad predorsal angle slightly in front of center of otolith and just behind antirostrum. Postdorsal rim slanted, with indistinct, broadly rounded postdorsal angle. Ventral rim shallow, nearly straight and horizontal, smooth. Rostrum long, with blunt tip; antirostrum sharp, less than half the length of rostrum; excisura deep and wide. Posterior rim rounded with inferior tip. Dorsal and posterior rims undulating.

Inner face strongly convex, with relatively wide and moderately deep, slightly supramedian sulcus. Ostium wide, its dorsal part excavated by deep excisura. Cauda downward inclined at 8°, narrower than ostium with slightly bent rear part and rounded tip terminating close to posterior rim of otolith. Dorsal depression small, narrow; ventral field smooth with faint ventral furrow near ventral rim of otolith turned upwards posteriorly towards caudal tip. Outer face concave, smooth.

Discussion. *Peprilus*? *muelleri* is a highly characteristic otolith that resembles otoliths of extant *Peprilus* species but differs in the more compressed shape and the deep and wide excisura. It is therefore only tentatively associated with the genus.

Family Nomeidae Günther, 1860
Genus *Cubiceps* Lowe, 1843

Cubiceps lautus n. sp.

Fig. 14H–K

Holotype (and unique specimen)**:** Fig. 14H–K, LACM 60212, upper Lutetian, Ardath Shale, Black's Beach.

Etymology: From lautus (Latin) = fine, elegant, referring to the delicate ornamentation of the otolith.

Diagnosis: OL:OH = 1.85. Dorsal rim shallow, highest at middorsal angle; ventral rim regularly curved. All rims delicately crenulated. Rostrum long, 22% of OL; excisura and antirostrum minute. Cauda relatively short but about the same length as ostium, slightly bent at tip; CaL:OsL = 1.05.

Description. The unique holotype is a thin, fragile otolith of 3.0 mm in length. OH:OT = 3.3. Dorsal rim low, with broad, rounded middorsal angle. Ventral rim deeper than dorsal rim and more regularly curved. Rostrum long, with moderately pointed tip; antirostrum and excisura minute. Posterior rim rounded with superior tip. All rims delicately crenulated, dorsal and posterior rims more intense than ventral rim.

Inner face distinctly convex, with relatively narrow and moderately deep, distinctly supramedian sulcus. Ostium slightly greater in height anteriorly, about 1.5 times height of cauda. Cauda only slightly longer than ostium, with slightly bent posterior and rounded tip terminating moderately close to posterior rim of otolith; OL:SuL = 1.2. Dorsal depression narrow and linear, with many radial furrows ingressing from marginal crenulation; ventral field without ventral furrow and some ornamentation ingressing from ventral rim. Outer face concave, with many moderately long radial furrows ingressing from marginal crenulations.

Discussion. *Cubiceps lautus* resembles in shape and proportions of the sulcus extant *Cubiceps* otoliths (see e.g., Smale et al. 1995). Particularly the relatively narrow ostium, only slightly bent cauda, and the nearly equal length of ostium and cauda are typical for *Cubiceps* otoliths as well as the thin and mildly bent characteristics of the otoliths.

Order **Trachiniformes** Bertin & Arambourg, 1958
Family Uranoscopidae Bonaparte, 1831
Genus indet.

Uranoscopus*? *lini n. sp.

Fig. 14L–Q

Holotype: Fig. 14P–Q, LACM 60213, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 7 specimens same data as holotype, LACM 60214.

Etymology: In honor of Chien-Hsiang Lin (Taipei, Taiwan) in recognition of his contributions to the knowledge of fossil otoliths.

Diagnosis: OL:OH = 1.7–1.75; OH:OT = 1.8–2.2. Dorsal rim shallow with distinct postdorsal angle positioned above center of cauda. Sulcus strongly supramedian, almost straight, narrow, shallow. Ostium longer than cauda; OsL:CaL = 1.4–1.9.

Description. Robust, thick, lenticular otoliths up to 4.7 mm in length (holotype). Dorsal rim anteriorly depressed with distinct but low postdorsal angle positioned relatively far forward above center of cauda and gently curved postdorsal rim. Ventral rim deeper than dorsal rim, regularly curved, its deepest point usually shifted towards anterior. Anterior tip blunt, angular, marking an indistinct rostrum positioned slightly above horizontal axis of otolith; posterior tip slightly projecting, rounded, positioned on horizontal axis. All rims smooth.

Inner face strongly convex with distinctly supramedian, shallow, almost straight and narrow sulcus. Ostial opening relatively small and indistinct; caudal termination relatively far from posterior tip of otolith; OL:SuL = 1.35–1.4. Ostium distinctly longer than cauda but not greater in height. Colliculi moderately well defined. Dorsal depression large, well marked ventrally towards sulcus; ventral field smooth, with feeble ventral furrow very close to ventral rim of otolith. All rims thick except for anterior tip. Outer face flat to mildly convex, smooth.

Discussion. Lin & Nolf (2022) described two uranoscopid otolith-based species from coeval strata of the Gulf Coast - *Astroscopus compactus* Lin & Nolf, 2022 and *A. fusiformis* (Müller, 1999) - which both resemble *Uranoscopus*? *lini*. *Uranoscopus*? *lini* differs from both species in the distinctly longer ostium compared to the cauda (OsL:CaL >1.4 vs. <1.0) and the forward positioned and characteristic postdorsal angle. It differs further from *A. compactus* in the more elongate shape.

The differentiation of uranoscopid genera by means of otoliths is not easy. Otoliths of *Astrosco-*

pus and *Ichthyscopus* do indeed show some similarity in outline and sulcus organization (see Schwarzhans 2019c for extant trachiniform otoliths), but we consider it premature to allocate the fossil otolith-based species mentioned above to an extant genus. We therefore maintain a view to place them in an incertae sedis generic position and believe that they most likely represent an extinct lineage/genus.

Family Trichonotidae? Bleeker, 1859

Remark. The family Trichonotidae has long been placed in the Trachinoidei (later Trachiniformes; see Mooi & Johnson, 1997; Nelson et al., 2016) but in a recent molecular study has been interpreted as the sister-group of the Gobioidei (Thacker et al. 2015). We here follow the assessment based on otoliths by Schwarzhans (2019c) and retain their allocation with the Trachiniformes. Irrespective of this, the otoliths described below have been associated with different groups such as the Platycephaloidei, Platycephalidae (Stinton & Nolf 1970), and Trachinidae (Nolf & Stringer 2003).

Genus *Protobembrops* n. gen.

Type species: *Trachinus laevigatus* Koken, 1888.

Etymology: A combination of protos (Greek) = ancient, first and the genus names *Bembrops*.

Diagnosis: A fossil otolith-based genus tentatively placed in the family Trichonotidae with a fusiform otolith shape characterized as follows. The otoliths are elongate with a ratio OL:OH of 1.6–2.25. The rostrum is pointed, and the posterior tip not quite as pointed, while the dorsal and ventral rims are regularly and symmetrically curved giving the otoliths the fusiform shape. The ostium is the same length or slightly longer than the cauda and very slightly greater in height. The cauda is straight. The sulcus is short (OL:SuL = 1.35–1.6), narrow, and straight or very slightly oriented upwards towards posterior. The inner face is strongly convex, the outer face flat or slightly concave. The smooth ventral field shows a faint ventral furrow that runs close to the ventral margin of the otolith but turns upwards and inwards at the rear to approach the caudal tip.

Discussion. The systematic allocation of these otoliths has been enigmatic in the past (see above). The narrow ostium, which is only slightly wider than the cauda, the straight cauda, and the upward turning of the rear of the ventral furrow are considered indicative for a trachiniform. The straight sulcus and its proportions resemble extant otoliths of *Trichonotus* (see Schwarzhans 2019c for figures), and that is the reason why *Protobembrops* is placed in the Trichonotidae. An alternative placement in the Bembropidae as a plesiomorphic member would also be possible. Ultimately, the phylogenetical placement of these otoliths can only be resolved by the finding of an articulated skeleton with otoliths in situ of that type.

Species. *Protobembrops laevigatus* (Koken, 1888) from the middle and late Eocene of the Gulf Coast, *Protobembrops janeti* (Priem, 1911) (originally described as *Trachinus janeti*, with *Platycephalus aculeatus* Stinton & Nolf, 1970 as junior synonym according to Nolf, 2013) from the Eocene of Belgium, England, and France, and *Protobembrops ascensus* n. sp. from the middle Eocene of California.

Protobembrops ascensus n. sp.

Fig. 14U–Z

Holotype: Fig. 14U–V, LACM 60215, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 9 specimens same data as holotype, LACM 60216.

Referred specimens: 6 specimens: 28 specimens same data as holotype, LACM 60217; 8 specimens, Bartonian, Mission Valley Formation, Miramar Reservoir site, LACM 60277.

Etymology: From ascensus (Latin) = ascending, referring to the upward directed sulcus.

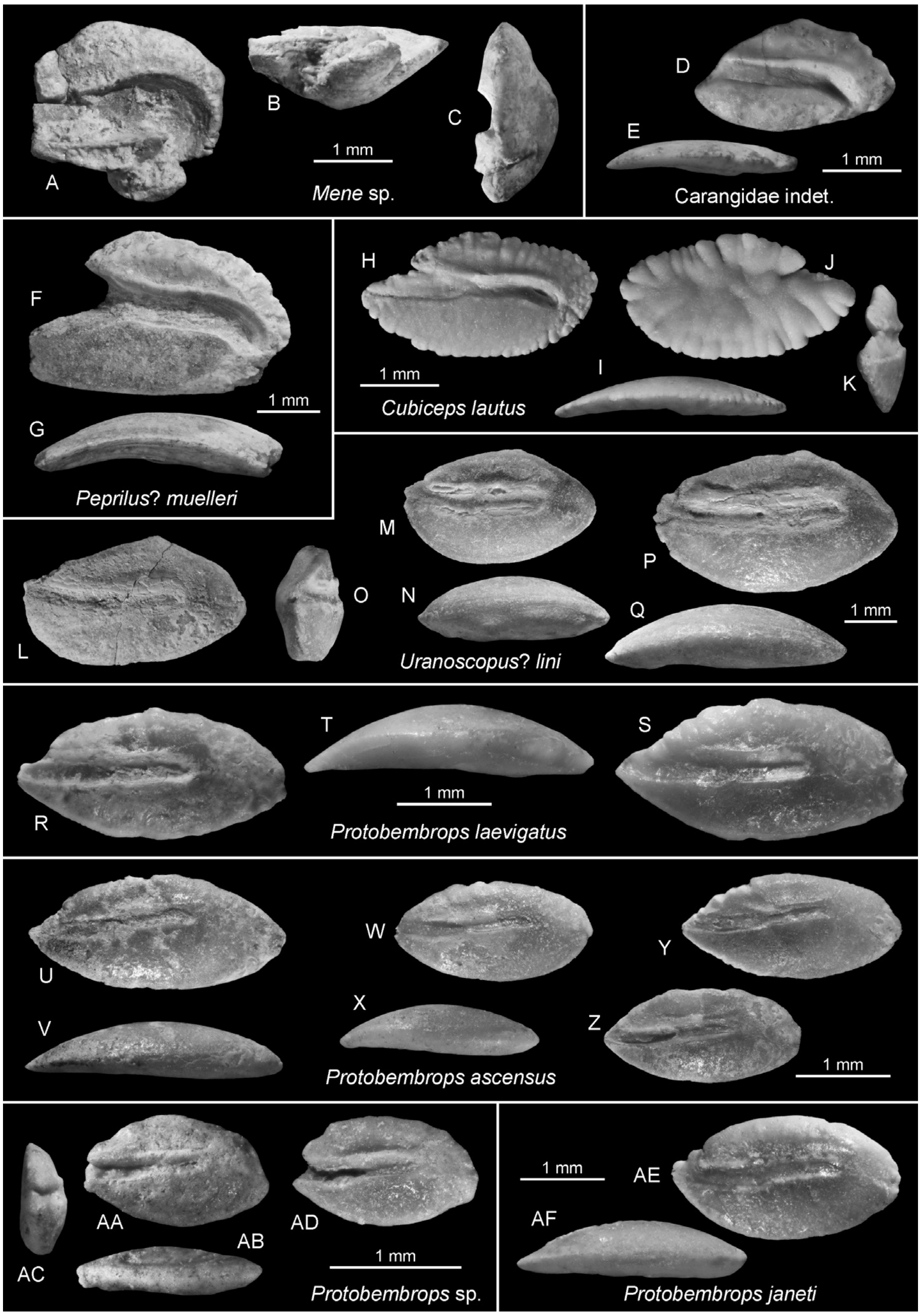
Diagnosis: OL:OH = 2.0–2.25. Sulcus slightly but noticeable ascending toward postdorsal rim at 4–7°. OL:SuL = 1.5–1.6; OsL:CaL = 1.1–1.3.

Description. Slender, fusiform otoliths up to 2.7 mm in length (holotype). OH:OT = 2.0–2.1. Dorsal and ventral rims regularly curved without angles, symmetrical; dorsal rim slightly undulating. Anterior tip (rostrum) pointed, and posterior tip slightly rounded to moderately pointed, both along horizontal axis of otolith.

Inner face strongly convex with distinctly supramedian and slightly upward oriented cauda. Sulcus relatively short, narrow, shallow, anteriorly open, posteriorly terminating far from posterior rim of otolith; ostium very slightly greater in height and longer than cauda. Colliculi discernable and slightly deepened. Dorsal depression small, narrow; ventral field smooth with very faint ventral furrow close to ventral rim of otolith, turning upwards towards caudal tip posteriorly. Outer face flat, smooth.

Discussion. *Protobembrops ascensus* resembles *P. laevigatus* from the Eocene Gulf Coast but has a more strongly upward oriented sulcus and a relatively longer ostium (OsL:CaL = 1.1–1.3 vs. 1.3–1.5). *Protobembrops janeti* from the European Eocene is similar in sulcus proportions but more compressed than *P. ascensus* (OL:OH = 1.8–1.9 vs.

Fig. 14 - A–C) *Mene* sp., Miramar Reservoir site, LACM 60117 (reversed), B ventral view, C posterior view.
D–E) Carangidae indet., Miramar Reservoir site, LACM 60118 (reversed), E ventral view.
F–G) *Peprilus*? *muelleri* n. sp., holotype, Miramar Reservoir site, LACM 60276 (reversed), G ventral view.
H–K) *Cubiceps lautus* n. sp., holotype, Black's Beach, LACM 60212 (reversed), I ventral view, J outer face, K anterior view.
L–Q) *Uranoscopus*? *lini* n. sp.; P–Q holotype, Black's Beach, LACM 60213 (reversed), Q ventral view; L–O paratypes, Black's Beach, LACM 60214 (L reversed), N ventral view, O anterior view.
R–T) *Protobembrops* n. gen. *laevigatus* (Koken, 1888), Moodys Branch, Bartonian, Mississippi, NRM PZ P.19068-69 (S–T reversed), T ventral view.
U–Z) *Protobembrops ascensus* n. gen., n. sp.; U–V holotype, Black's Beach, LACM 60215, V ventral view; W–Z paratypes, Black's Beach, LACM 60126, X ventral view.
AA–AD) *Protobembrops* n. gen., sp., Black's Beach, LACM 60218, AB ventral view, AC anterior view.
AE–AF) *Protobembrops* n. gen. *janeti* (Priem, 1911), Lutetian, Balegem, Belgium (reversed), AF ventral view.



2.0–2.25). For comparison otoliths are figured of *P. laevigatus* from the Bartonian of the Gulf Coast (Moodys Branch; Fig. 14R–T, NRM PZ P.19068-69) and of *P. janeti* from the Lutetian of Belgium (Balegem; Fig. 14AE–AF).

Protobembrops sp.

Fig. 14AA–AD

Material: 5 specimens, Ardath Shale, Black's Beach, LACM 60218.

Discussion. A few small, juvenile specimens of sizes slightly larger than 1 mm in length differ from *P. ascensus* in a much more compressed shape (OL:OH = 1.6–1.7 vs. 2.0–2.25) and a very short rostrum. They may represent an additional species of *Protobembrops*, however, that designation would require larger and adult specimens.

Order **Perciformes** Bleeker, 1859
Family Ambassidae Klunzinger, 1870
Genus *Ambassis* Cuvier, 1828

Ambassis californiensis n. sp.

Fig. 15A–M

Holotype: Fig. 15A–C, LACM 60219, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 10 specimens same data as holotype, LACM 60220.

Referred specimens: 1090 specimens same data as holotype, LACM 60221.

Etymology: Referring to the State of California.

Diagnosis: OL:OH = 1.05–1.12. Rostrum broad, relatively short, 15–20% of OL. Sulcus long; cauda reaching close to posterior rim of otolith; OL:SuL = 1.05. CaL:OsL = 1.3–1.5.

Description. High-bodied, nearly round and compact otoliths up to 5 mm in length (holotype). OH:OT = 2.8–3.8. Dorsal rim moderately high, with mostly well-developed predorsal angle and broadly rounded postdorsal angle, smooth or slightly and irregularly undulating. Ventral rim deep, deepest anterior of its middle, regularly curved and smooth. Rostrum broad, blunt, relatively short; excisura and antirostrum distinct, antirostrum about one third the length of rostrum. Posterior rim bluntly rounded, smooth or slightly and irregularly undulating.

Inner face distinctly bent in horizontal direction and nearly flat in vertical direction. Sulcus relatively wide, moderately deepened, distinctly supramedian and long, reaching close to posterior rim of otolith. Ostium distinctly shorter than cauda (approximately one-half) and about twice as wide, particularly ventrally widened; ostial colliculum well-marked. Cauda very slightly upward directed and tapering with ventrally positioned tip; caudal colliculum well-marked, particularly its ventral margin. Dorsal depression wide, ventrally well-marked towards sulcus; ventral furrow distinct, running close to ventral rim of otolith. Outer face flat or with more or less strongly developed postcentral umbo, smooth.

Discussion. The Ambassidae today are a species-rich family in marine, brackish, and freshwater realms in and adjacent to the Indo-West Pacific. In the fossil record of the Paleogene and early Neogene, however, they were more widely distributed. *Ambassis antipodus* (Schwarzhans, 1980) and *A. simesi* Schwarzhans, 2019 have been described from the Eocene of New Zealand and *A. meldertensis* (Nolf, 1973) from the Eocene of Belgium. The extinct ambassid genus *Dapalis* Gistl, 1848 is known with several species from freshwater and brackish water sediments of the Oligocene and Miocene of Europe.

Ambassis californiensis resembles both *A. antipodus* and *A. meldertensis* but differs from both species in being more compressed (OL:OH 1.05–1.12 vs. 1.15–1.3), the massive and blunt rostrum, bluntly rounded posterior rim, and the cauda reaching very close to the posterior rim of the otolith (OL:SuL = 1.05 vs. 1.1–1.15). Even though these differences are rather subtle, they are nevertheless consistent and based on a large sample size.

Family Lactariidae Fowler, 1904
Genus *Lactarius* Cuvier & Valenciennes, 1833

Lactarius kokeni (Dante & Frizzell, 1965)

Fig. 15N–U

1965 *Brazosiella kokeni* - Dante & Frizzell (in Frizzell & Dante): pl. 87, fig. 25, 30, 32-34, 36.

2022 *Lactarius kokeni* (Dante & Frizzell, 1965) - Lin & Nolf: fig. 28F-J (see there for further references).

Material: 1006 specimens: 42 specimens, Ardath Shale, Black's Beach, LACM 60222; 964 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60246.

Discussion. *Lactarius kokeni* is a common species in the Gulf Coast as well as the Californian middle Eocene. A second common *Lactarius* species, *L. amplus* Stinton, 1978 is common in the middle Eocene of the Gulf Coast and Europe (Ebersole et al. 2019; Lin & Nolf 2022). *Lactarius primigenius* Schwarzhans, 2019, has been recorded from the middle Eocene of New Zealand, *L. caraibeus* (Casier, 1958) from the middle Eocene of Barbados and *L. concavus* (Frost, 1926) from the Eocene of Nigeria. *Lactarius kokeni* was made the type species of the fossil otolith-based genus *Brazosiella* Dante & Frizzell, 1965, which they considered a beryciform of uncertain family position and which contained another species, *B. moseleyi* Dante & Frizzell, 1965 that is represented by a poorly preserved lactariid specimen in their published figure. Nolf (1985) placed *Brazosiella kokeni* in the genus *Lactarius,* and we follow this assessment. The abundance and diversity of otolith-based species of the genus *Lactarius* during the Eocene contrasts with the single *Lactarius lactarius* (Bloch & Schneider, 1801) today, which is widespread in the Indo-West Pacific.

Family Acropomatidae Gill, 1891
Genus *Parascombrops* Alcock, 1889

Parascombrops fragilis n. sp.

Fig. 15V–AC

Holotype: Fig. 15X–Y, LACM 60223, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 9 specimens same data as holotype, LACM 60224.

Referred specimens: 50 specimens same data as holotype, LACM 60225.

Etymology: From fragilis (Latin) = fragile, referring to delicate nature of these thin otoliths.

Diagnosis: OL:OH = 1.55–1.65. Dorsal rim highest at obtuse predorsal angle. Ventral rim deepest before middle. Ostium ventrally widened forming orthogonal angle below joint with cauda, its axis slightly upward directed towards anterior at 5-10° against the horizontal otolith axis. Cauda slightly flexed and dorsally widened at flexure. OL:SuL = 1.1–1.15. CaL:OsL = 1.2–1.45. Ventral furrow distant from ventral rim of otolith.

Description. Slender, thin and fragile otoliths up to at least 4 mm in length (holotype 3.4 mm). OH:OT = 3.8–4.2. Dorsal rim relatively shallow, highest at broadly rounded or obtuse predorsal angle positioned above ostial/caudal joint; postdorsal region depressed with low and feeble postdorsal angle. Ventral rim deeper, regularly curved, deepest before its center. Rostrum thin and often broken, moderately long when preserved; antirostrum and excisura weak. Posterior rim rounded or angular, its tip at level of caudal tip. All rims smooth or faintly undulating.

Inner face moderately convex with slightly supramedian sulcus. Sulcus relatively wide, moderately deepened, reaching close to posterior rim of otolith. Ostium slightly shorter than cauda, ventrally widened with sharp angle, its axis inclined upwards towards opening at 5-10° against otolith axis and about twice as wide as cauda; ostial colliculum well-marked. Cauda slightly inclined downwards towards posterior at about 2°, posteriorly slightly flexed, its dorsal margin slightly widened at flexure point, its tip ventrally pointed; caudal colliculum usually not discernable. Dorsal depression narrow, ventrally well-marked by crista superior; ventral furrow moderately distinct, running far from ventral rim of otolith across center of ventral field and swinging upwards towards caudal tip. Outer face flat to slightly concave, relatively smooth.

Discussion. *Parascombrops fragilis* is a typical otolith of the genus characterized by the shape of the ostium and its orientation, the course of the ventral furrow and the slender and fragile appearance. The otoliths resemble extant *Parascombrops* otoliths as depicted in Schwarzhans & Prokofiev (2017), differing primarily in the more pronounced inclination of the sulcus against the otolith axis. A number of fossil otolith-based species have been placed in *Parascombrops* (see Nolf, 2013) and while most of them represent acropomatids only few have been accepted as representatives of the genus *Parascombrops* (see Schwarzhans & Prokofiev 2017). These are: *Parascombrops*? *brzobohatyi* Nolf, 1988 from the late Eocene of South-West France, *P. epigonoides* Nolf & Brzobohaty, 2002 from the Early Miocene of South-West France, and more recently *P. giganteus* Schwarzhans, 2019 from the early Eocene of New Zealand and *P. schwarzhansi* van Hinsbergh & Helwerda, 2019 from the Late Pliocene of Philippines. *Parascombrops yanceyi* Lin & Nolf, 2022 recently described from the middle Eocene of Texas differs from the typical morphotype of otoliths of the genus in the ventral furrow being very close to the ventral rim of the otolith. This species certainly represents an acropomatid but probably an extinct lineage.

Genus *Verilus* Poey, 1860

Verilus lajollaensis n. sp.

Fig. 15AD–AM

Holotype: Fig. 15AE–AG, LACM 60226, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 9 specimens same data as holotype, LACM 60227.

Referred specimens: 145 specimens same data as holotype, LACM 60228.

Etymology: After La Jolla, California, the community closest to the type location of Black's Beach.

Diagnosis: OL:OH = 1.4–1.6. Dorsal rim highest at obtuse predorsal angle and with marked postdorsal angle. Ventral rim deepest distinctly shifted towards anterior. Ostium ventrally more widened than dorsally, its axis inclined upwards towards opening at 3-7° against otolith horizontal axis. Cauda nearly straight, with ventrally pointed tip. OL:SuL = 1.05–1.1. CaL:OsL = 1.2–1.4. Ventral furrow close to ventral rim of otolith, posteriorly more distant, straight inclined and widened.

Description. Moderately slender, robust otoliths up to 10.5 mm in length (holotype 8.35 mm). OH:OT = 3.0–3.8. Dorsal rim moderately high, highest at broadly rounded or obtuse predorsal angle positioned above or slightly behind ostial/caudal joint; postdorsal region nearly horizontal with distinct postdorsal angle. Ventral rim deeper, deepest much before its center and usually also before predorsal angle. Rostrum massive, moderately long, 15–20% of OL; antirostrum and excisura weak. Posterior rim blunt, rounded, can be almost vertical, its weakly defined tip below level of caudal tip. Dorsal rim irregularly undulating, other rims smooth.

Inner face moderately convex with slightly supramedian sulcus. Sulcus relatively wide, moderately deepened, reaching close to posterior rim of otolith. Ostium shorter than cauda, ventrally more widened than dorsally, its axis inclined upwards to wards opening at 3-7° against otolith horizontal axis and about twice as wide as cauda; ostial colliculum well-marked. Cauda horizontal, straight except for ventrally pointed tip, deeper than ostium; caudal colliculum usually not discernable except for its ventral margin. Dorsal depression narrow, distinct, ventrally well-marked by crista superior; ventral furrow distinct, running close to ventral rim of otolith, posteriorly departing from otolith rim at about 45°, and this section straight, widened, and deepened. Outer face flat to slightly concave, relatively smooth.

Discussion. The concept of the genus *Verilus* was reviewed in Schwarzhans & Prokofiev (2017) and was further detailed in Schwarzhans (2019a) and Schwarzhans et al. (2020). As a consequence, *Verilus* now contains several extant and otolith-based fossil species. *Verilus lajollaensis* is a typical representative of the genus and is best distinguished by the unique development of the rear part of the ventral furrow.

Family Scombropidae Gill, 1862
Genus Scombrops Temminck & Schlegel, 1845

Scombrops americanus n. sp.

Fig. 15AN–AS

Holotype: Fig. 15AN–AQ, LACM 60229, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 2 specimens same data as holotype, LACM 60230.

Etymology: After the geographical continent America.

Diagnosis: OL:OH = 1.55–1.65. Dorsal rim with broad middorsal angle. Ventral rim deepest distinctly shifted towards anterior. Sulcus flat-lying s-shaped with ostium slightly upward directed and cauda gently curving with rounded tip. Cauda relatively wide.OL:SuL = 1.05–1.1. CaL:OsL = 1.5.

Description. Slender, relatively thin otoliths up to 9.3 mm in length (holotype). OH:OT = 4.0. Dorsal rim relatively low, highest at broad, obtuse middorsal angle positioned slightly anteriorly; pre- and postdorsal rims slightly inclined, straight; obtuse postdorsal angle. Ventral rim deeper, deepest at or slightly before its center. Rostrum massive, moderately long, with rounded tip, 13–15% of OL; anti-rostrum and excisura weak. Posterior rim angular (in holotype) or rounded (in smaller specimens), its tip slightly below level of caudal tip. All rims intensely crenulated in the figured paratype of 4.7 mm in length (Fig. 15AR–AS), smooth to slightly undulating in large holotype (Fig. 15AN–AQ), which is probably an expression of ontogenetic change.

Inner face moderately convex with slightly supramedian sulcus. Sulcus relatively long, moderately deepened, reaching close to posterior rim of otolith. Sulcus weakly flat-lying s-shaped (more strongly developed in large holotype). Ostium shorter than cauda, ventrally moderately widened, its axis inclined upwards towards opening at about 10° against otolith axis. Cauda slightly upward bent anteriorly and regularly downward bent at low angle posteriorly with rounded tip. Colliculi deepened, moderately well-marked. Dorsal depression narrow, moderately distinct, ventrally marked by crista superior; ventral furrow not discernable. Outer face slightly concave, intensely ornamented in figured small paratype (Fig. 15AS), relatively smooth with ostial furrow and few short radial furrows postdorsally in large holotype (Fig. 15AO).

Discussion. *Scombrops americanus* is the first fossil record of the genus and family (*Scombrops* sp. reported from the early Eocene of the Aquitaine Basin by Nolf (1988) is here regarded as an unidentifiable juvenile perciform). The low flat-lying sulcus is considered characteristic for *Scombrops*. *Scombrops americanus* differs from the extant *S. boops* (see Lin & Chang 2012 for figure), in the wider cauda and the lower ratio OL:SuL (1.05–1.1 vs. 1.15) and the less strongly bent caudal tip.

Family Serranidae Swainson, 1839
Genus *Paralabrax* Girard, 1856

Paralabrax nolfi n. sp.

Fig. 16C–E

Holotype (and unique specimen)**:** Fig. 16C–E, SMF PO 101.341, Sands of Lede, Lutetian, Balegem, Belgium.

Etymology: In honor of Dirk Nolf (Bruges, Belgium), in recognition of his many contributions to the knowledge of fossil otoliths.

Diagnosis: OL:OH = 2.35. Dorsal and ventral rims shallow; dorsal rim with postdorsal depression. Ostium spatulate, large, with short upper margin. Cauda long, narrow, distinctly bent posteriorly at 40°. CaL:OsL = 1.55.

Description. The unique holotype is very slender, large (11 mm in length) and well preserved except for the postventral tip of the otolith. OH:OT

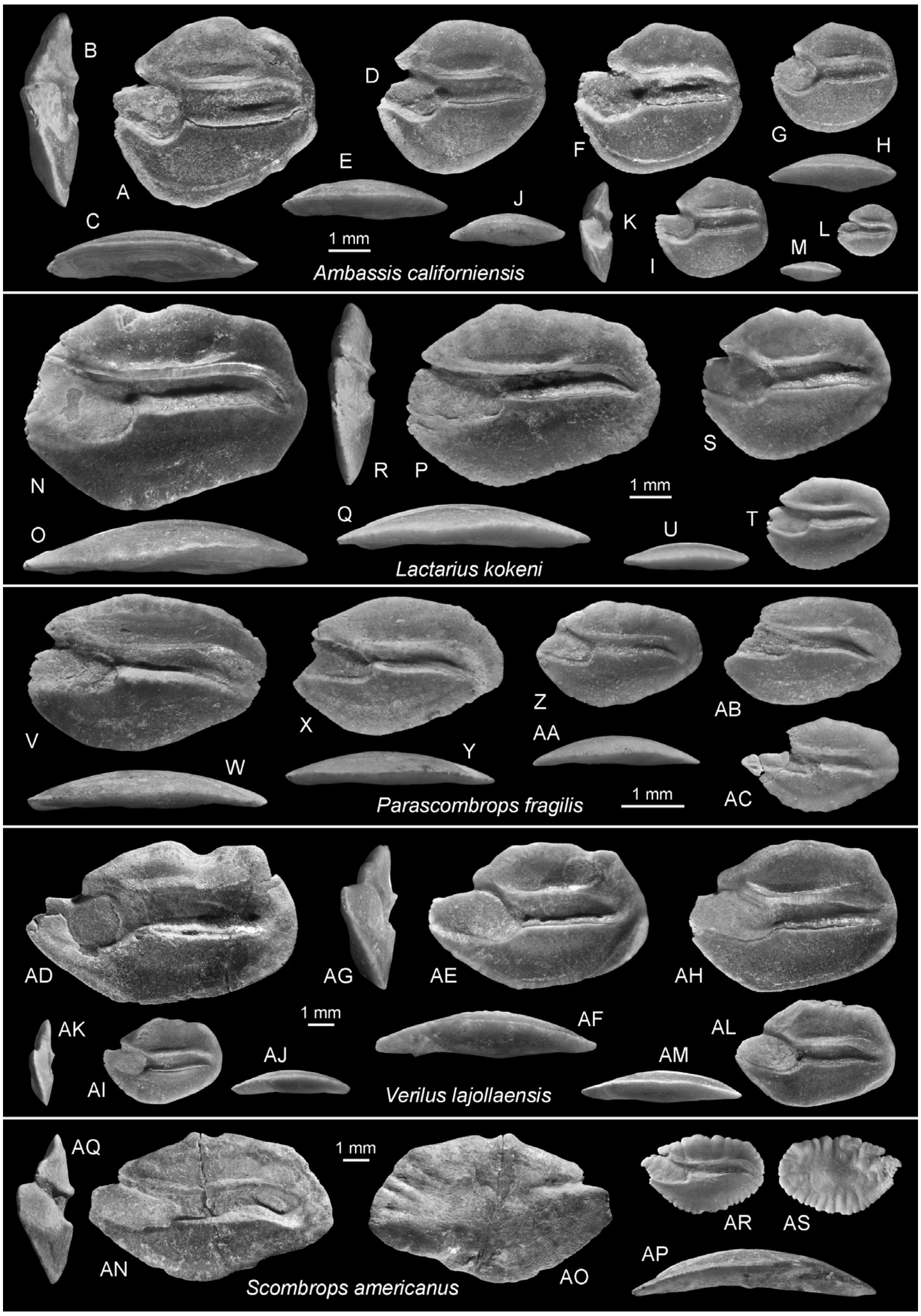


Fig. 15 - A–M) *Ambassis californiensis* n. sp.; A–C holotype, Black's Beach, LACM 60219 (reversed), B anterior view, C ventral view; D–M paratypes, Black's Beach, LACM 60220 (I–K, L–M reversed), K anterior view, E, H, J, M ventral views.
N–U) *Lactarius kokeni* (Dante & Frizzell, 1965); N–R, T–U Miramar Reservoir site, LACM 60246 (P–R, T–U reversed), R anterior view, Q, U ventral views; S Black's Beach, LACM 60222 (reversed).
V–AC) *Parascombrops fragilis* n. sp.; X–Y holotype, Black's Beach, LACM 60223 (reversed), Y ventral view; V–W, Z–AC, paratypes, Black's Beach, LACM 60224 (AB reversed), W, AA ventral views.
AD–AM) *Verilus lajollaensis* n. sp.; AE–AG holotype, Black's Beach, LACM 60226 (reversed), AG anterior view, AF ventral view; AD, AH–AM paratypes, Black's Beach, LACM 60227 (AD, AH reversed), AK anterior view, AJ, AM ventral views.
AN–AS) *Scombrops americanus* n. sp.; AN–AQ holotype, Black's Beach, LACM 60229 (reversed), AO outer face, AP ventral view, AQ anterior view; AR–AS paratype, Black's Beach, LACM 60230, AS outer face.

= 3.3. Dorsal rim low, anteriorly slightly lobate followed by mild concavity and regularly curved, inclined postdorsal section without angle. Ventral rim very shallow, regularly curved, smooth. Rostrum long, broad, with rounded tip, 25% of OL; antirostrum and excisura indistinct. Posterior rim tapering, its tip missing. All rims smooth.

Inner face distinctly convex with slightly supramedian sulcus. Sulcus long, moderately deepened, reaching close to posterior rim of otolith. Ostium shorter than cauda, distinctly widened dorsally and ventrally, its upper margin short. Cauda narrow, about one third the of ostium, anteriorly straight, posteriorly moderately bent at 40° and slightly widened. Ostial colliculum marked, caudal colliculum not discernable. Dorsal depression very narrow, indistinct; no ventral furrow. Outer face distinctly concave, smooth.

Discussion. *Paralabrax nolfi* strongly resembles otoliths of the extant *P. clathratus* (Girard, 1854) as figured by Nolf (2013, pl. 213). It differs in the wider ostium and the mild concavity of the middorsal rim. We included the description of *P. nolfi* here for comparison purposes with the rich serranid assemblage in the middle Eocene of California. We further figure a specimen of *Epinephelus*? *postangula-*

tus Nolf, 1973 (Fig. 16A–B) from the same location as *P. nolfi*.

Genus *Pseudolabrax* n. gen.

Type species: *Pseudolabrax missionis* n. sp.

Etymology: A combination of pseudo (Greek) = wrong and the genus names *Labrax*.

Diagnosis: A fossil otolith-based genus placed in the family Serranidae with a fusiform otolith shape characterized as follows. The otoliths are elongate with a ratio OL:OH of 2.1–2.3. The rostrum is relatively short (10–17% of OL) and rounded, and the posterior tip is variable (tapered, pointed, and sometimes projecting). The fusiform otolith shape is a result of the symmetrical position of rostrum and posterior tip together with the low and regularly curved dorsal and ventral rims. Both ostium and cauda are relatively narrow in height. The cauda is slightly longer than the ostium (CaL:OsL = 1.2–1.5) and only slightly bent at its tip (25–30° from the horizontal). The sulcus is moderately short (OL:SuL = 1.2–1.3). The inner face is strongly convex, most strongly bent at its anterior region; the outer face is distinctly concave.

Discussion. Otoliths of *Pseudolabrax* are relatively easy to recognize because of the combination of a narrow ostium and cauda and the strongly convex inner and concave outer faces with the anterior part of the otolith being most strongly bent. The allocation in the Serranidae is tentative since the otoliths of all extant serranid genera are not known, and similar otoliths are also known from other perciform families, which is a general problem when identifying fossil perciform otoliths.

Species. *Pseudolabrax* is a monospecific genus with *Pseudolabrax missionis* n. sp. from the middle Eocene of California.

Pseudolabrax missionis n. sp.

Fig. 16F–L

Holotype: Fig. 16F–G, LACM 60119, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 13 specimens: 12 specimens same data as holotype, LACM 60120; 1 specimen, upper Lutetian, Ardath Shale, Black's Beach, LACM 60231.

Etymology: After the type formation, the Mission Canyon Formation.

Diagnosis: See generic diagnosis (monospecific genus).

Description. Small, elongate and thin specimens up to 3.5 mm in length (holotype 3.45 mm). OH:OT = 2.6–3.0. Otolith shape fusiform with shallow, symmetrical dorsal and ventral rims and often symmetrical, pointed anterior and posterior tips. Dorsal rim irregularly undulating, with rounded postdorsal angle. Ventral rim regularly curved, posteriorly straight, generally smooth with some variability. Rostrum relatively short and rounded; antirostrum and excisura minute or absent. Posterior tip more sharply pointed than rostrum and sometimes strongly projecting.

Inner face strongly convex, most strongly bent at its anterior region. Sulcus narrow, relatively short, terminating far from posterior tip of otolith, slightly supramedian. Ostium distinctly shorter than cauda and narrow, only slightly wider than cauda. Cauda very narrow, straight, with slightly bent caudal tip at 25–30° from the horizontal axis. Dorsal depression narrow, indistinct; ventral furrow weakly expressed, close to ventral rim of otolith, terminating below caudal tip. Outer face strongly concave, smooth.

Genus *Torreyichthys* n. gen.

Type species: *Torreyichthys speciosus* n. sp.

Etymology: Named after the type locality in Torrey Pines Park.

Diagnosis: A fossil otolith-based genus placed in the family Serranidae characterized as follows. The otoliths are moderately elongate with a ratio OL:OH of 1.8–2.1. The rostrum is massive and moderately long (17–20% of OL). The dorsal rim shows a strong postdorsal angle well posterior and a low pre- and middorsal region, which is depressed in large specimens. The posterior tip is massive, angular and with its tip at or below the caudal tip. Ostium and cauda are relatively wide. The cauda is slightly to moderately longer than the ostium (CaL:OsL = 1.2–1.5), which is possibly an ontogenetic effect, and only slightly bent at its tip (20–25° from the horizontal axis). The sulcus is relatively short (OL:SuL = 1.2–1.3). The inner face is moderately convex; the outer face is flat to slightly concave.

Discussion. Otoliths of *Torreyichthys* are relatively easy to recognize in large specimens (>10 mm in length) due to the deeply depressed pre- and middorsal rims. In smaller specimens, the massive posterior rim with the strong and well posterior postdorsal angle and the sulcus proportions may be considered the most reliable characters. The allocation in the Serranidae is tentative since the otoliths of all extant serranid genera are not known, and similar otoliths are also known from other perciform families, which is a general problem when identifying fossil perciform otoliths.

Species. *Torreyichthys* is a monospecific genus with *Torreyichthys speciosus* n. sp. from the middle Eocene of California.

Torreyichthys speciosus n. sp.

Fig. 16M–S

Holotype: Fig. 16N–O, LACM 60232, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 15 specimens same data as holotype, LACM 60233.

Etymology: From speciosus (Latin) = notable, referring to the depressed dorsal rim in large specimens.

Diagnosis: See generic diagnosis (monospecific genus).

Description. Robust, moderately elongate otoliths achieving large sizes (12 mm in length; holotype 7.2 mm). OH:OT = 2.9–3.2. Dorsal rim shallow, nearly straight and horizontal in specimens up to about 10 mm in length; pre- and middorsal section strongly depressed in the largest specimen of 12 mm in length (Fig. 16M). Postdorsal angle massive, at junction with posterior rim. Ventral rim regularly curved, deepest anterior of its middle, smooth. Rostrum massive, moderately long; antirostrum and excisura indistinct. Posterior rim massive, oblique, its tip at or below level of caudal tip.

Inner face moderately convex with relatively wide and short sulcus terminating at some distance from posterior tip of otolith. Ostium wide and ventrally strongly widened, shorter than cauda, oriented upwards towards anterior at about 15° from horizontal axis. Cauda deeper and narrower than ostium, with only slightly bent posterior at 20–25° from horizontal axis, with rounded tip. Dorsal depression narrow, indistinct; ventral furrow weak, close to ventral rim of otolith, terminating below caudal tip. Outer face flat to slightly concave, smooth.

Remarks. The single large otolith of 12 mm in length is not well enough preserved for all measurements and therefore does not qualify as holotype. It is, however, highly diagnostic because of the development of the dorsal rim. The smaller specimens including the holotype do show a nearly straight and horizontal dorsal rim. We assume that the depression of the dorsal rim observed in the large specimen of Fig. 16M reflects a late ontogenetic development.

For further comparison, a specimen is figured of the middle Eocene European *Serranus*? *pectinoides* (Stinton & Nolf, 1970) (Fig. 16W–X). This otolith shows some overall similarity with our species but the ostium is horizontally oriented. Also, it does not show any indication of a dorsal depression up to sizes of 8.5 mm in length (see figures in Nolf 2013 as *Lithognathus pectinoides*). Its generic allocation, here tentatively placed in the Serranidae, remains uncertain.

Genus indet.

Remarks. The following three species are considered to represent taxa of the Serranidae but their otolith morphology does not show sufficient diagnostic characters of potential generic value. Therefore, they are placed in the form-genus *Serranus*? indicating their uncertain position.

***Serranus*? *fongeri* n. sp.**

Fig. 16Y–AC

Holotype: Fig. 16Y–Z, LACM 60234, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 18 specimens: 14 specimens same data as holotype, LACM 60235; 4 specimens, Bartonian, Mission Valley Formation, Miramar Reservoir site, LACM 60121.

Etymology: In honor of George Fonger of Maryland, USA, for his years of extensive collecting of Mesozoic and Cenozoic otoliths in the US Atlantic Coastal Plain.

Diagnosis: OL:OH = 1.65–1.75. Dorsal rim broadly rounded with low postdorsal angle. Rostrum moderately long, massive; posterior rim broadly rounded. Ostium moderately widened, shorter than cauda. Cauda slightly bent at tip at 27–32° from horizontal axis. OL:SuL = 1.15. CaL:OsL = 1.4–1.5.

Description. Slender, relatively thin otoliths up to 4.6 mm in length (holotype). OH:OT = 3.0–3.3. Dorsal rim relatively low, highest middorsal, regularly curved, with low and rounded postdorsal angle. Ventral rim deeper, regularly curved, deepest slightly before center. Rostrum massive, moderately long, with blunt tip (tip missing in holotype), about 17% of OL; antirostrum and excisura weak. Posterior rim broadly rounded, its tip slightly below level of caudal tip. All rims irregularly crenulated, more visible in smaller specimens as well as better-preserved specimens.

Inner face distinctly convex with slightly supramedian sulcus. Sulcus is fairly long, narrow, moderately deepened, terminating at some distance from posterior rim of otolith. Ostium shorter than cauda in length, ventrally moderately widened, its colliculum well-marked. Cauda regularly downward bent posteriorly at 27–32°, with rounded tip. Caudal colliculum deepened, poorly marked. Dorsal depression narrow, moderately distinct, ventrally marked by crista superior; ventral furrow weak and close to ventral rim of otolith or not discernable. Outer face slightly concave, slightly ornamented.

Discussion. *Serranus*? *fongeri* is a relatively inconspicuous otolith, which is best defined by its low and gently curved dorsal rim, the broadly rounded posterior rim, the crenulation of the rims, and the relatively short and narrow ostium. For distinction from *Serranus*? *moratus* n. sp. and *S.*? *strigosus* n. sp. see below.

***Serranus*? *moratus* n. sp.**

Fig. 16T–V

Holotype: Fig. 16U–V, LACM 60236, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 7 specimens: 5 specimens same data as holotype, LACM 60237; 2 specimens, Bartonian, Mission Valley Formation, Miramar Reservoir site, LACM 60122.

Etymology: From moratus (Latin) = mannered, referring to the delicate and easy breakable nature of the otoliths.

Diagnosis: OL:OH = 1.9–2.0. Dorsal rim shallow, anteriorly highest and rounded, posteriorly depressed. Rostrum moderately long, with rounded tip; posterior rim expanded, with inferior tip. Ostium moderately widened, shorter than cauda. Cauda slightly bent at tip at about 30° from horizontal axis. OL:SuL = 1.25. CaL:OsL = 1.8–1.9.

Description. Slender, thin, and fragile otoliths up to 5.4 mm in length (holotype 3.8 mm). OH:OT = 3.5. Dorsal rim low, broadly rounded and highest anteriorly and slightly depressed posteriorly with weak postdorsal angle. Ventral rim shallow, regularly curved, deepest at about its middle. Rostrum moderately long, with rounded tip (tip missing in holotype and broken off in largest specimen); antirostrum and excisura very weak. Posterior rim expanded, oblique, with angular inferior tip. Dorsal rim slightly undulating, ventral rim smooth or slightly crenulated anteriorly and posteriorly, posterior rim irregularly crenulated.

Inner face distinctly convex with slightly supramedian sulcus. Sulcus is fairly long, narrow, moderately deepened, terminating at some distance from posterior rim of otolith. Ostium much shorter than cauda, moderately widened, its colliculum poorly marked. Cauda slightly downward bent posteriorly at about 30° from horizontal, with tapering tip. Caudal colliculum deepened, poorly marked. Dorsal depression narrow, indistinct, ventrally marked by crista superior; no ventral furrow discernable. Outer face distinctly concave, slightly ornamented.

Remarks. The best preserved and largest specimen (Fig. 16T) unfortunately broke during cleaning operations for preparing for photographing. The tip of the rostrum was lost. Some measurements had been done, but the specimen was not considered to be adequate as a holotype, and therefore, the somewhat smaller specimen of Fig. 16U–V was selected.

Discussion. *Serranus*? *moratus* is a characteristic and easily recognizable species because of its distinct shape, particularly of the dorsal rim, and the thin, strongly bent appearance in ventral view.

***Serranus*? *strigosus* n. sp.**

Fig. 16AD–AI

Holotype: Fig. 16AE–AF, LACM 60123, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 13 specimens: 6 specimens same data as holotype, LACM 60124; 7 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60238.

Etymology: From strigosus (Latin) = lean, featureless, referring to the generalized shape of the otoliths.

Diagnosis: OL:OH = 1.9–2.0. Dorsal rim regularly curved, highest at its middle, without prominent angles. Rostrum and posterior tip nearly symmetrical in larger specimens, inferior. Ostium distinctly widened and shorter than cauda. Cauda slightly bent at tip at 25–32° from horizontal axis. OL:SuL = 1.2–1.25. CaL:OsL = 1.05–1.25.

Description. Slender, moderately thin otoliths up to 6 mm in length (holotype 5.5 mm). OH:OT = 2.7–3.0. Dorsal rim very regularly curved, slightly undulating, highest at its middle, without prominent angles except sometimes a broadly rounded postdorsal angle (Fig. 16AG). Ventral rim shallow, regularly curved, deepest at about its middle, smooth. Rostrum moderately long, with pointed inferior tip, about 20% of OL; antirostrum and excisura weak. Posterior tip expanded in larger specimens, angular or pointed, inferior, often symmetrical in shape and expansion to rostrum, especially in larger specimens. All rims smooth except finely crenulated in small specimens (Fig. 16AH).

Inner face moderately convex with slightly supramedian sulcus. Sulcus fairly long, moderately wide and deepened, terminating at some distance from posterior rim of otolith. Ostium shorter than cauda, but distinctly wider, its colliculum moderately well-marked. Cauda slightly downward bent posteriorly at 25–32° from horizontal axis, with somewhat tapered, rounded tip. Caudal colliculum deepened, poorly marked. Dorsal depression narrow, distinct and rather deep, ventrally marked by crista superior; ventral furrow very close to ventral rim of otolith. Outer face flat to slightly concave, smooth.

Discussion. *Serranus*? *strigosus* is best characterized by the regularly curved dorsal rim, the, usually expanded and pointed inferior posterior tip that is symmetrical to the rostrum, mainly in larger specimens, and the low index CaL:OsL.

Family Haemulidae Gill, 1885
Genus *Micropomadasys* n. gen.

Type species: *Micropomadasys granulosus* n. sp.

Etymology: A combination of micro (Greek) = small and the genus name *Pomadasys*.

Diagnosis: A fossil otolith-based genus placed in the family Haemulidae characterized as follows. The otoliths are relatively small (up to 3 mm in length) and fusiform in shape with a ratio OL:OH of 1.65–1.75. The rostrum is relatively short and pointed (10–17% of OL), and antirostrum and excisura are not developed. The dorsal and ventral rims are regularly and symmetrically curved without prominent angles. The posterior tip is pointed and symmetrical to the rostrum and positioned at the level of the otolith axis. The ostium is narrow, shallow, and spatulate. The cauda is narrow, and only slightly bent in its rear part at 25–30°. OL:SuL = 1.15–1.25; CaL:OsL = 1.4–1.5. The inner face is strongly convex; the outer face is slightly concave.

Discussion. Haemulid otoliths are characterized by a spatulate, often relatively wide and shallow ostium, strongly convex and smooth inner face and a cauda, which is usually strongly bent at its tip, but morphotypes with a less strongly bent caudal tip exist as well. Small, plesiomorphic looking haemulid otoliths are a common occurrence in Eocene sediments of Europe and North America. They are mostly placed in an extant genus of which otoliths appear to be similar in morphology or recoded as pertaining to the formal genus *Haemulon*?, i.e., as Haemulidae incertae sedis. The otoliths from the Eocene of California, however, show specific characters that allow for a generic definition.

Micropomadasys belongs to the relatively few haemulid morphotypes with an only moderately bent and short caudal tip. Another one is *Allomorone* Dante & Frizzell, 1965 that was originally thought to represent a Serranidae and was regarded as a junior synonym of the haemulid genus *Orthopristis* Girard, 1858 by Nolf (2013). We consider *Allomorone* as distinct from *Orthopristis* because of the much shorter downward bent section of the cauda that terminates far from the postventral rim of the otolith. *Micropomadasys* differs from *Allomorone* in the narrow ostium and the low bend of the caudal tip (25–30° vs. 50–60°). For comparison, otoliths are figured from *Allomorone americana* (Koken, 1888) (Fig. 17I–J) from the middle Eocene of the Gulf Coast and *A. trewavasae* (Nolf & Lapierre, 1979) (Fig. 17K–L) from the middle Eocene of the Paris Basin, France. For the difference to another haemulid genus with low caudal curvature, *Strongylauris* n. gen., see below.

Species. *Micropomadasys* is a monospecific genus with *Micropomadasys granulosus* n. sp. from the middle Eocene of California.

Micropomadasys granulosus n. sp.

Fig. 16A–H

Holotype: Fig. 16A–B, LACM 60239, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 12 specimens same data as holotype, LACM 60240.

Referred specimens: 100 specimens same data as holotype, LACM 60241.

Etymology: From granulosus (Latin) = granular, referring to the small size of the otoliths resembling grains.

Diagnosis: See generic diagnosis (monospecific genus).

Description. Small, relatively robust, fusiform-shaped otoliths up to 3 mm in length (holotype 2.85 mm). OL:OH of 1.65–1.75; OH:OT = 2.5–2.7. Dorsal and ventral rims regularly curved without prominent angles and highest at the middle; ventral rim deeper than dorsal rim. Rostrum short, pointed; posterior tip symmetrical; both centrally positioned along otolith axis. Dorsal rim slightly undulating; ventral rim smooth or anteriorly crenulated.

Inner face strongly convex, smooth, with distinctly supramedian sulcus. Sulcus narrow, moderately long, and terminating at some distance from posterior rim of otolith. Ostium less than half as long as cauda, narrow, about twice as wide as cauda, and spatulate in shape with long, horizontal ventral and dorsal margins, shallow, with poorly defined colliculum. Cauda narrow, moderately long, and only slightly bent in its rear part at 25–30°. Caudal colliculum indistinct. OL:SuL = 1.15–1.25; CaL:OsL = 1.4–1.5. Dorsal depression very shallow, indistinct; ventral furrow mostly indistinct, rarely visible and very close to ventral rim of otolith. Outer face slightly concave, smooth.

Discussion. *Micropomadasys granulosus* is the most common haemulid at Black's Beach but has not been found at the Miramar Reservoir site. This distribution may indicate that it was a deeper living species.

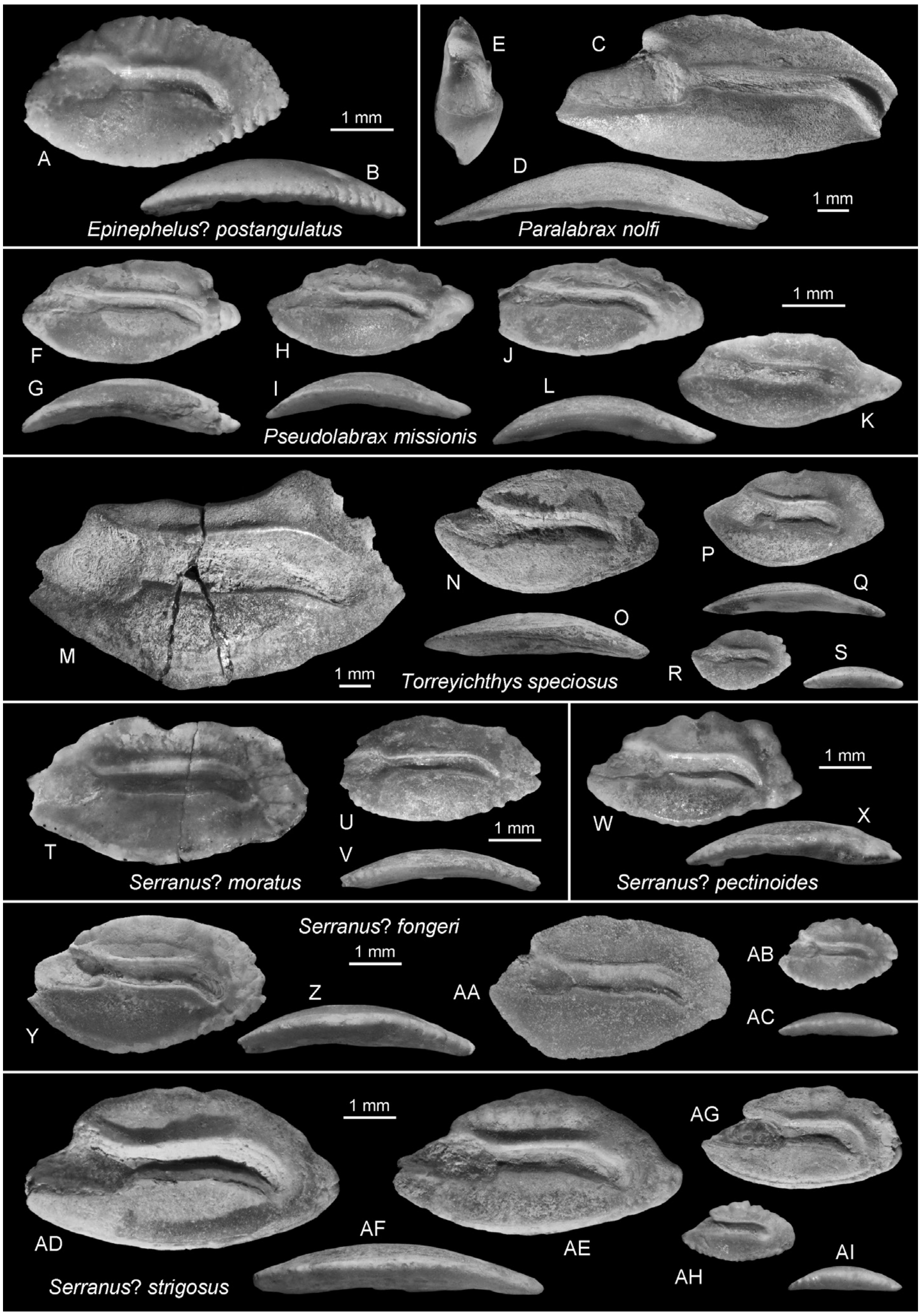


Fig. 16 - A–B) *Epinephelus*? *postangulatus* Nolf, 1973, Lutetian, Balegem, Belgium (reversed), B ventral view.
C–E) *Paralabrax nolfi* n. sp., holotype, Lutetian, Balegem, Belgium, SMF PO 101.341 (reversed), D ventral view, E anterior view.
F–L) *Pseudolabrax missionis* n. gen., n. sp.; F–G holotype, Miramar Reservoir site, LACM 60119 (reversd), G ventral view; H–L paratypes, Miramar Reservoir site, LACM 60231 (K–L reversed), I, L ventral views.
M–S) *Torreichthys speciosus* n. gen., n. sp.; N–O holotype, Black's Beach, LACM 60232, O ventral view; M, P–S paratypes, Black's Beach, LACM 60233 (R–S reversed), Q, S ventral view.
T–V) *Serranus*? *moratus* n. sp.; U–V holotype, Black's Beach, LACM 60236 (reversed), V ventral view; T paratype, Black's Beach, LACM 60237.
W–X) *Serranus*? *pectinoides* (Stinton & Nolf, 1970), Lutetian, Balegem, Belgium, X ventral view.
Y–AC) *Serranus*? *fongeri* n. sp.; Y–Z holotype, Black's Beach, LAC 60234, Z ventral view; AA–AC paratypes, Black's Beach, LACM 60235 (reversed), AC ventral view.
AD–AI) *Serranus*? *strigosus* n. sp.; AE–AF holotype, Miramar Reservoir site, LACM 60123, AF ventral view; AD paratype, Miramar Reservoir site, LACM 60124 (reversed); AG–AI paratypes, Black's Beach, LACM 60238, AI ventral view.

Genus *Protopomadasys* n. gen.

Type species: *Protopomadasys fitchi* n. sp.

Etymology: A combination of protos (Greek) = first and the genus name *Pomadasys*.

Diagnosis: A fossil otolith-based genus placed in the family Haemulidae characterized as follows. The otoliths are moderately sized (up to 7.2 mm in length) with a ratio OL:OH of 1.3–1.7. The dorsal rim is considerably shallower than the deep ventral rim. The rostrum is relatively short and blunt (12–15% of OL), and antirostrum and excisura are not developed. The posterior tip is broadly rounded to somewhat tapered (Fig. 17O). The ostium is more than half the length of the cauda, wide, shallow, and spatulate in shape. The cauda is less than half the width of the ostium, relatively long and longer than the ostium, and only distinctly bent in its rear part at 40–65°, but the downturned section is short and terminates at some distance from the postventral margin of the otolith. OL:SuL = 1.1–1.25; CaL:OsL = 1.5–1.7. The inner face is strongly convex; the outer face is slightly concave.

Discussion. *Protopomadasys* is more similar to modern haemulid otoliths than *Micropomadasys* or even *Allomorone* in the shape of the otolith as well as the proportions of the sulcus, in particular the width of the ostium. It differs from otoliths of extant haemulid genera such as *Haemulon, Pomadasys*, or *Orthopristis* mainly in the shorter downturned part of the cauda terminating relatively far from the postventral rim of the otolith.

Species. *Protopomadasys* contains two species from the middle Eocene of California: *P. fitchi* n. sp. and *P. pacificus* n. sp.

Protopomadasys fitchi n. sp.

Fig. 17M–S

Holotype: Fig. 17M–N, LACM 60125, Bartonian, Mission Valley Formation, Miramar Reservoir site.

Paratypes: 20 specimens: 19 specimens same data as holotype, LACM 60126; 1 specimen, upper Lutetian, Ardath Shale, Black's Beach, LACM 60242.

Etymology: Named in honor of the late John Fitch (Long Beach, California) for his many contributions to the knowledge of otoliths.

Diagnosis: OL:OH = 1.65–1.7. Dorsal rim relatively shallow with somewhat moderate to slight middorsal concavity. Ventral rim moderately deep. Posterior rim irregularly rounded, dorsally shifted. OL:SuL = 1.2–1.25. Curvature of caudal tip 60–65°. Ventral furrow only discernable at rear below caudal tip forming a terrace.

Description. Relatively large, robust otoliths up to 7.2 mm in length (holotype). OH:OT = 2.7–3.0. Dorsal rim relatively shallow, with rounded predorsal region, shallow middorsal depression and rounded, slightly depressed postdorsal region. Ventral rim moderately deep and regularly curved, deepest slightly in front of its middle. Rostrum relatively short, blunt, or rounded, 12–15% of OL; no or minute antirostrum and excisura; posterior rim irregularly rounded with supramedian tip. Dorsal rim slightly undulating; ventral rim smooth.

Inner face strongly convex, smooth, with distinctly supramedian sulcus. Sulcus relatively long, moderately wide, and terminating at a moderate distance from posterior rim of otolith. Ostium wide, about three times as wide as cauda, spatulate, moderately shallow, with well-defined colliculum. Cauda is longer than ostium, narrower than ostium, deepened, relatively steeply bent posteriorly at 60–65° but downward bent section short and terminating fairly far from postventral rim of otolith. Caudal colliculum indistinct. CaL:OsL = 1.5–1.6. Dorsal depression shallow, indistinct; ventral furrow mostly indistinct, very close to ventral rim of otolith, becoming prominent below caudal tip and there bending away from ventral rim otolith and forming a terrace with a small postventral region of the ventral field being depressed. Outer face slightly concave, smooth.

Discussion. *Protopomadasys fitchi* differs from *P. pacificus* n. sp. described below in being more elongate (OL:OH = 1.65–1.7 vs. 1.3–1.4), the more steeply downturned posterior of the cauda (60–65° vs. 40–50°) and the depressed part of the ventral field below the rear part of the ventral furrow (vs. not depressed). The abundance of *P. fitchi* at the Miramar Reservoir site and rarity at Black's Beach indicates that the species was probably shallow living (see discussion later).

Protopomadasys pacificus n. sp.

Fig. 17T–AC

Holotype: Fig. 17T–U, LACM 60243, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 10 specimens: 9 specimens same data as holotype, LACM 60244; 1 specimen, Bartonian, Mission Valley Formation, Miramar Reservoir site LACM 60127.

Referred material: 49 specimens: 34 specimens, Ardath Shale, Black's Beach, LACM 60245; 15 specimens, Mission Valley Formation, Miramar Reservoir site LACM 60128.

Etymology: Referring to the Pacific Ocean.

Diagnosis: OL:OH = 1.2–1.4. Dorsal rim shallow irregularly undulating. Ventral rim deep. Posterior rim blunt, dorsally shifted. OL:SuL = 1.1–1.15. Curvature of caudal tip 40–50° from horizontal axis. Ventral furrow only discernable at rear below caudal tip but not forming a terrace.

Description. Relatively large, robust and compressed otoliths up to 6.8 mm in length (holotype). OH:OT = 2.7–3.4. Dorsal rim shallow, undulating, highest at obtuse predorsal angle, postdorsal angle distinct, rounded. Ventral rim deep and regularly curved, deepest at its middle, smooth. Rostrum short, blunt, and rounded, 12–13% of OL; no antirostrum and excisura; posterior rim blunt to bluntly rounded, dorsally shifted.

Inner face strongly convex, smooth, with distinctly supramedian sulcus. Sulcus long, moderately wide, and terminating relatively close to posterior rim of otolith. Ostium wide, about three times as wide as cauda, spatulate, moderately shallow, with well-defined colliculum. Cauda narrower than ostium, deepened, bent posteriorly at 40–50°, downward bent section short and terminating at moderate distance from postventral rim of otolith. Caudal colliculum indistinct. CaL:OsL = 1.6–1.7. Dorsal depression shallow, mostly indistinct; ventral furrow mostly indistinct, very close to ventral rim of otolith, becoming prominent below caudal tip and there bending away from ventral rim otolith towards caudal tip. Outer face flat to slightly concave, smooth.

Discussion. *Protopomadasys pacificus* is more common in Black's Beach than at the Miramar Reservoir site and thus shows the opposite distribution to *P. fitchi* described above. For the differentiation of the two species, see above.

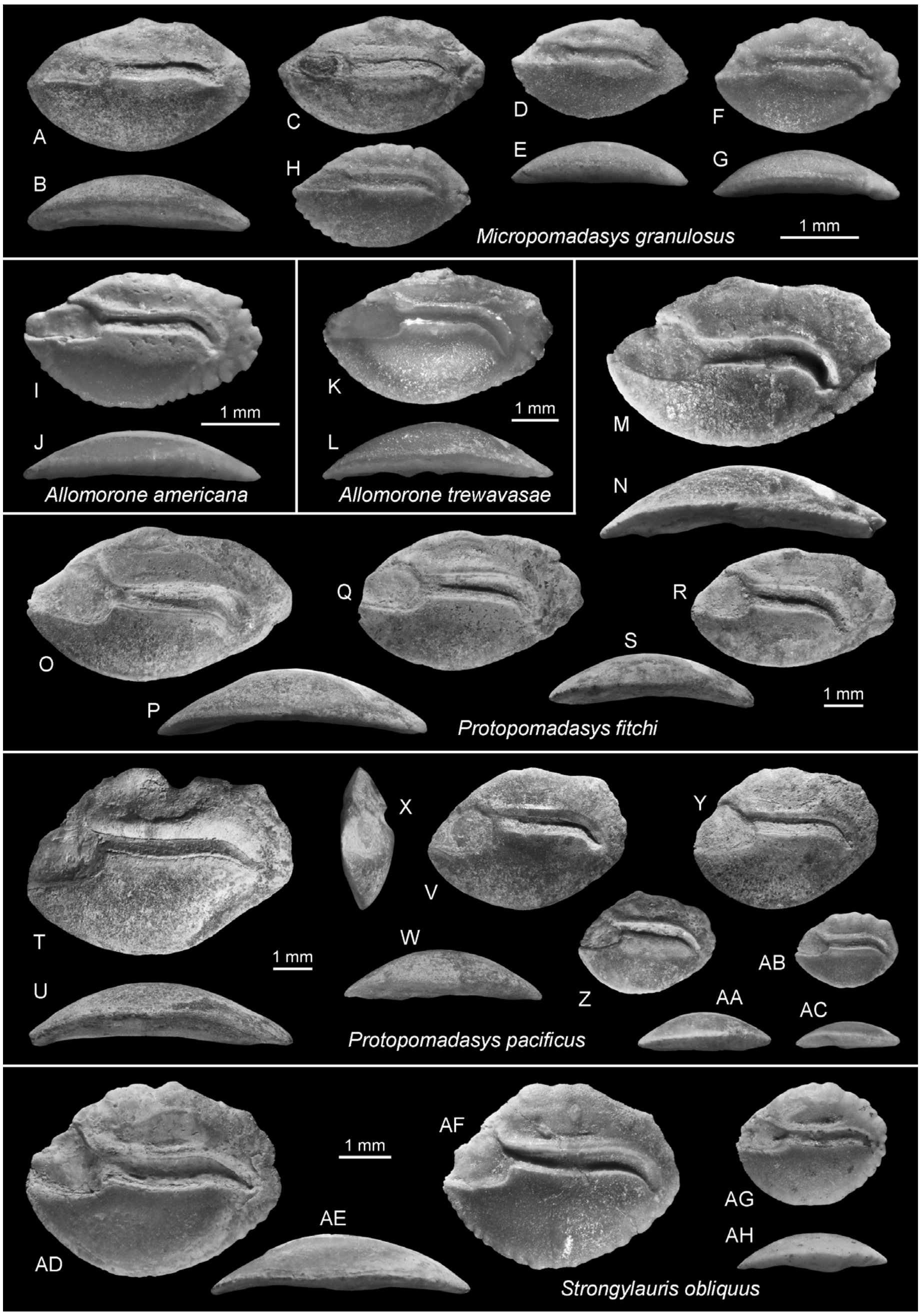


Fig. 17 - A–H) *Micropomadasys granulosus* n. gen., n. sp.; A–B holotype, Black's Beach, LACM 60239 (reversed), B ventral view; C–H paratypes, Black's Beach, LACM 60240 (C, F–H reversed), E, G ventral views.
I–J) *Allomorone americana* (Koken, 1888), Moodys Branch, Bartonian, Mississippi, NRM PZ P.19079, J ventral view.
K–L) *Allomorone trewavasae* (Nolf & Lapierre, 1979), Lutetian, Paris Basin, L ventral view.
M–S) *Protopomadasys fitchi* n. gen., n. sp.; M–N holotype, Miramar Reservoir site, LACM 60125 (reversed), N ventral view; O–S paratypes, Miramar Reservoir site, LACM 60126, P, S ventral views.
T–AC) *Protopomadasys pacificus* n. gen., n. sp.; T–U holotype, Black's Beach, LACM 60243, U ventral view; V–Y, AB–AC paratypes, Black's Beach, LACM 60244 (V–X, AB–AC reversed), X anterior view, W, AC ventral views; Z–AA paratype, Miramar Reservoir site, LACM 60127, AA ventral view.
AD–AH) *Strongylauris* n. gen. *obliquus* (Müller, 1999); AD–AE Miramar Reservoir site, LACM 60130, AE ventral view; AF–AH Black's Beach, LACM 60129, AH ventral view.

Genus *Strongylauris* n. gen.

Type species: genus aff. *Xenistius obliquus* Müller, 1999

Etymology: A combination of strongylos (Greek) = round and auris (Latin) = ear, referring to the round shape of the otoliths ("ear-stone").

Diagnosis: A fossil otolith-based genus placed in the family Haemulidae characterized as follows. The otoliths are moderately sized (up to 5 mm in length), nearly round in shape with a ratio OL:OH of 1.2–1.3. All rims are gently rounded and variably ornamented. The rostrum is relatively short and bluntly rounded (8–15% of OL), and antirostrum and excisura are not developed. The sulcus is long extending across a majority of the inner face. The ostium is noticeably short, wide, shallow, and spatulate. The ostium is equally strongly widened dorsally and ventrally and its dorsal margin is much shorter than the ventral margin. The cauda is approximately twice as long as the ostium, about a third the height of the ostium or less, and a slightly bent posterior at 30–45°; the downturned section is short and terminates close to the posterior rim of the otolith. OL:SuL = 1.07–1.1; CaL:OsL = 1.9–2.2. The inner face is strongly convex; the outer face is flat to slightly concave.

Discussion. *Strongylauris* is a haemulid otolith-based genus with a low caudal curvature index, similar to the extant *Brachydeuterus* Gill, 1862 (see Schwarzhans 2013 for figures) or *Haemulopsis* Steindachner, 1869 (see Nolf 2013 for figure). *Strongylauris*, however, differs from the otoliths of the two extant genera by the rounded shape and the short ostium. We consider *Strongylauris* as a basal member of the Haemulidae with plesiomorphic features.

Species. *Strongylauris* is a monospecific genus with *Strongylauris obliquus* (Müller, 1999) from the middle Eocene of California and the US Gulf Coast. It is, however, possible that further Paleogene haemulid otolith-based species could also be associated with this genus, but we would see this as subject to a dedicated review.

Strongylauris obliquus (Müller, 1999)

Fig. 17AD–AH

1999 genus aff. *Xenistius obliquus* - Müller: fig. 30/24–25.

Material: 71 specimens: 8 specimens LACM 60129, upper Lutetian, Ardath Shale, Black's Beach; 63 specimens Mission Valley Formation, Miramar Reservoir site LACM 60130.

Diagnosis: See generic diagnosis (monospecific genus).

Description. Moderately sized compressed otoliths up to 5 mm in length (holotype 4.5 mm). OH:OT = 3.1–3.4. Dorsal rim relatively high, regularly curved, irregularly undulating, without prominent angles. Ventral rim deep and regularly curved, deepest at its middle, delicately crenulated or smooth. Rostrum short, rounded, 8–15% of OL; no antirostrum and excisura; posterior rim broadly rounded, crenulated.

Inner face strongly convex, smooth, with distinctly supramedian sulcus. Sulcus is long extending nearly across the inner face and terminating close to posterior rim of otolith. Ostium wide, at least three times as wide as cauda, spatulate, its dorsal margin much shorter than its ventral margin, moderately shallow, with well-defined colliculum. Cauda narrower than ostium, deepened, slightly bent posteriorly at 30–45°, downward bent section short. Caudal colliculum indistinct. CaL:OsL = 1.9–2.2. Dorsal depression moderately developed, narrow, marked by crista superior towards sulcus; ventral furrow mostly indistinct, very close to ventral rim of otolith when discernable. Outer face flat to slightly concave, with shallow central umbo, smooth.

Family Malacanthidae Günther, 1861
Genus indet.

Malacanthus*? *rugosus n. sp.

Fig. 18E–M

Holotype: Fig. 18E–G, LACM 60248, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 15 specimens same data as holotype, LACM 60249.

Referred material: 490 specimens same data as holotype, LACM 60250.

Etymology: From rugosus (Latin) = rugose, referring to the strongly sculptured inner face.

Diagnosis: OL:OH = 1.5–1.75. Dorsal rim regularly rounded, lobate. Cauda straight, its posterior part deepened and slightly widened. Ostium slightly widened, with nearly parallel dorsal and ventral margins. Ventral furrow distinct. Outer face flat to slightly concave.

Description. Moderately sized, robust otoliths up to 4 mm in length (holotype 3.3 mm). OH:OT = 2.7–3.0. Dorsal rim moderately high, regularly curved, lobate or irregularly undulating, without prominent angles. Ventral rim regularly curved, deepest at its middle, relatively smooth. Rostrum moderately long, with pointed tip, 15–18% of OL; antirostrum short; excisura shallow. Posterior rim rounded or slightly projecting, irregularly ornamented.

Inner face strongly convex, rugose, with axial positioned sulcus. Sulcus moderately wide, deep and terminating relatively close to posterior rim of otolith. Ostium slightly wider than cauda, with nearly parallel dorsal and ventral margins, usually well-defined colliculum not opening to anterior rim. Cauda about the same length as ostium, slightly narrower than ostium, almost straight, deepened, with rounded tip. Caudal colliculum deepened, with indistinct margins. CaL:OsL = 1.0–1.15. Dorsal depression distinct, small, with distinct crista superior towards central part of sulcus; ventral furrow distinct, close to ventral rim of otolith, slightly turning upward and away from ventral sulcus margin anteriorly and posteriorly. Outer face flat to slightly concave, smooth.

Discussion. *Malacanthus*? *rugosus* is common in Black's Beach but not present at the Miramar Reservoir site. This may indicate a preference for deeper water (see discussion below). Another malacanthid otolith is known from the shallow-water environments of the Gulf Coast Eocene: *Malacanthus*? *sulcatus* (Koken, 1888), of which two specimens from Brazos and Moodys Branch are figured for comparison (Fig. 18A–D, NRM PZ P.19070-71). *Malacanthus*? *rugosus* differs from *M.*? *sulcatus* in being somewhat less elongate (OL:OH = 1.5–1.75 vs. 1.75–2.0), the outer face being flat (vs. distinctly concave), and the only slightly widened and straight caudal tip (vs. more strongly widened and slightly bent downward).

Otoliths are known from all five extant malacanthid genera (two genera in Malacanthinae and three in Latilinae acc. to Nelson et al. 2016) (for figures see Nolf 2013). The general appearance of *M.*? *rugosus* resemble otoliths of *Branchiostegus*, *M.*? *sulcatus*, *Lopholatilus*, and *Malacanthus*. However, we agree with Lin & Nolf (2022) that these Eocene otoliths cannot be readily attributed to one of the five extant genera, and therefore, leave it in the form-genus *Malacanthus*?, indicating they may possibly belong to an extinct genus.

Order **Spariformes** Bleeker, 1876
Family Sparidae Rafinesque, 1810
Genus indet.

Remarks. The following two species are considered to represent taxa of the Sparidae but their otolith morphology does not show sufficient diagnostic characters of potential generic value. In fact, extant sparid otoliths and those of the related families Nemipteridae and Lethrinidae show few morphological features that can be used for distinction of genera. Paleogene otoliths attributed to any of these families usually exhibit a very generalized morphology, which is also the case here. Therefore, we place the two species described in the following in the form-genus *Sparus*? indicating their uncertain position. This protocol was also followed in Ebersole et al. (2021) and Stringer et al. (2020) regarding otoliths of the Sparidae.

Sparus*? *esseri (Müller, 1999)

Fig. 18N–S

1999 *Dentex esseri* - Müller: fig. 33/1–4.
2022 *Pagrus esseri* (Müller, 1999) - Lin & Nolf: fig. 39G.

Material: 1085 specimens, upper Lutetian, Ardath Shale, Black's Beach, figured specimens LACM 60251.

Description (of Californian specimens). Moderately sized thin otoliths up to 4.5 mm in length. OL:OH = 1.5–1.6; OH:OT = 2.7–3.0. Dorsal rim moderately high, irregularly curved, intensely undulating, without prominent angles. Ventral rim regularly curved, relatively deep, deepest slightly in front of its middle, slightly undulating. Rostrum moderately long, with rounded tip, 15–18% of OL; antirostrum short; excisura shallow. Posterior rim tapering, slightly projecting, irregularly undulating, with tip at otolith axis and symmetrically positioned to rostrum.

Inner face distinctly convex, with slightly supramedian sulcus. Sulcus fairly long comprising over 90% of the length of the inner face, moderately wide, deep and terminating at some distance from posterior rim of otolith. Ostium about twice as wide as cauda, with parallel dorsal and ventral margins, with well-defined colliculum. Cauda narrow, deepened, posterior part inclined downward at 25–35°, with tapering tip. Caudal colliculum with indistinct margins. CaL:OsL = 1.3–1.4. Dorsal depression indistinct, but well marked by crista superior towards central part of sulcus; dorsal field with radial furrows ingressing from ornamentation of dorsal rim; ventral furrow indistinct, close to ventral rim of otolith. Outer face flat to slightly concave, with little ornamentation.

Discussion. *Sparus*? *esseri* was originally described by Müller (1999) as *Dentex esseri* based on seven specimens from the middle Eocene of Virginia. Lin & Nolf (2022) did not identify this species from the Gulf Coast Eocene but instead found common *Sparus*? *elegantulus* (Koken, 1888), which differs from *S.*? *esseri* in being more compressed (OL:OH = 1.35–1.45 vs. 1.5–1.6). Interestingly, *Sparus*? *esseri* is very common in Black's Beach, i.e., the most common sparid and one of the most common species overall but absent from the Miramar Reservoir site. Because of its abundance and geographic distance, we have here provided a detailed description of the Californian specimens. Another similar species in appearance is known from the middle Eocene of Belgium: *Sparus*? *joneti* (Stinton & Nolf, 1970) (Fig. 18T–U) originally described as *Oblada joneti*.

Sparus*? *sparsus n. sp.

Fig. 18V–AB

Holotype: Fig. 18V–W, LACM 60252, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 30 specimens same data as holotype, LACM 60253.

Etymology: From sparsus (Latin) = sparse, referring to this species being much rarer than *Sparus*? *esseri* at Black's Beach.

Diagnosis: OL:OH = 1.65–1.75. Dorsal rim low, intensely and irregularly crenulated, without prominent angles. Ventral rim low, gently curved. Cauda narrow, moderately bent in posterior part at 40–45° (except one paratype at 30°). CaL:OsL = 1.35–1.5. Outer face slightly concave.

Description. Moderately sized, thin otoliths up to 5 mm in length (holotype). OH:OT = 3.5–3.8. Dorsal rim low, intensely and irregularly crenu-

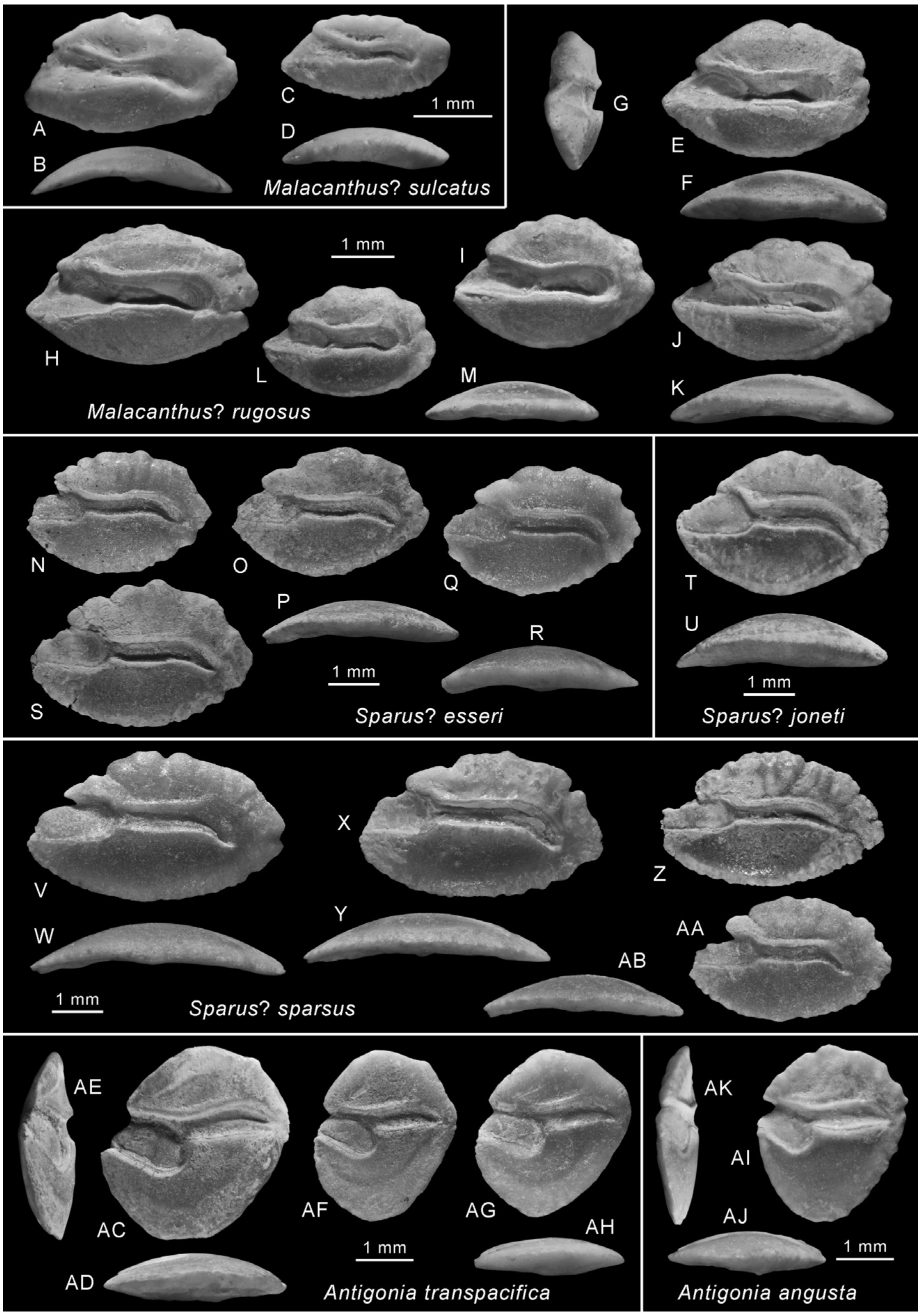


Fig. 18 - A–D *Malacanthus*? *sulcatus* (Koken, 1888); A–B Brazos River, Bartonian, Texas, NRM PZ P.19070 (reversed), B ventral view; C–D Moodys Branch, Bartonian, Mississippi, NRM PZ P.19071, D ventral view.
E–M) *Malacanthus*? *rugosus* n. sp.; E–G holotype, Black's Beach, LACM 60248 (reversed), F ventral view, G anterior view; H–M paratypes, Black's Beach, LACM 60249 (H, I, L–M reversed), K, M ventral views.
N–S) *Sparus*? *esseri* (Müller, 1999), Black's Beach, LACM 60251 (N, S reversed), P, R ventral views.
T–U) *Sparus*? *joneti* (Stinton & Nolf, 1970), Lutetian, Balegem, Belgium, U ventral view.
V–AB) *Sparus*? *sparsus* n. sp.; V–W holotype, Black's Beach, LACM 60252 (reversed), W ventral view; Z–AB paratypes, Black's Beach, LACM 60253 (AA–AB reversed), AB ventral view; X–Y referred specimen, Moodys Branch, Bartonian, Mississippi, NRM PZ P.19080, Y ventral view.
AC–AH) *Antigonia transpacifica* n. sp.; AC–AE holotype, Black's Beach, LACM 60254 (reversed), AD ventral view, AE anterior view; AF–AH paratypes, Black's Beach, LACM 60255, AH ventral view.
AI–AK) *Antigonia angusta* Stinton & Nolf, 1970, Lutetian, Balegem, Belgium, AJ ventral view, AK anterior view.

lated, without prominent angles. Ventral rim regularly curved, shallow, deepest at about its middle, slightly undulating. Rostrum moderately long, with rounded tip, 15–20% of OL; antirostrum short; excisura sharp, moderately deep. Posterior rim tapering, slightly projecting, irregularly undulating, with tip slightly below otolith axis and below rostrum rostrum.

Inner face distinctly convex, with slightly supramedian sulcus. Sulcus moderately long, deep, and terminating at some distance from posterior rim of otolith. Ostium about twice the width of cauda, with parallel dorsal and ventral margins, its dorsal margin much shorter than ventral margin, with well-defined colliculum. Cauda long (almost twice the length of ostium), narrow, deepened, pos-terior part inclined downward relatively steeply at 40–45° but only 30° in one specimen (Fig. 18Z), with tapering tip. Caudal colliculum with indis-tinct margins. CaL:OsL = 1.35–1.5. Dorsal depres-sion indistinct, but well marked by crista superior towards central part of sulcus; dorsal field with ra-dial furrows ingressing from ornamentation of dorsal rim; ventral furrow indistinct, moderately close to ventral rim of otolith. Outer face slightly concave, with some radial furrows.

Discussion. *Sparus*? *sparsus* differ from the parallel occurring *S.*? *esseri* in being slenderer (OL:OH = 1.65–1.75 vs. 1.5–1.6) and in having a, usually, more steeply downturned caudal tip (40–45° but 30° in one specimen vs. 25–35°).

Sparidae indet.

Remarks. About 27 sparid otoliths from Black's Beach are too poorly preserved to be attributable to one of the two species described above.

Order **Caproiformes** Rosen, 1984
Family Antigoniidae Jordan & Evermann, 1898
Genus *Antigonia* Lowe, 1843

Antigonia transpacifica n. sp.

Fig. 18AC–AH

Holotype: Fig. 18AC–AE, LACM 60254, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 25 specimens same data as holotype, LACM 60255.

Referred material: 60 specimens same data as holotype, LACM 60256.

Etymology: Referring to the putative transpacific relationship of the species with *Antigonia artata* Schwarzhans, 2019 from the early and middle Eocene of New Zealand.

Diagnosis: OL:OH = 0.85–0.95. All rims smooth; dorsal rim with broad postdorsal denticle; ventral rim broadly rounded. CaL:OsL = 0.95–1.0. Ventral furrow distinct, far from ventral rim of otolith.

Description. High-bodied, delicate otoliths reaching 3.25 mm in length (holotype). Dorsal rim relatively high with broad middorsal lobe and stubby postdorsal denticle. Ventral rim deeply and broadly curved. Rostrum blunt, short, slightly longer than antirostrum; antirostrum blunt; excisura broad, shallow. Posterior rim ventrally slanting, dorsally rounded with tip at level of caudal tip. All rims smooth.

Inner face moderately convex, with distinctly supramedian sulcus. Ostium and cauda about equally long. Ostium about three times as high as cauda, ventrally strongly lobate, inclined at about 15–20°. Cauda narrow, with slightly flexing and pointed tip close to posterior rim of otolith. Dorsal depression small, ventrally well marked; ventral furrow far from ventral rim of otolith across middle of ventral field. Outer face flat, smooth.

Discussion. *Antigonia* otoliths are easy to recognize as such, but the species are difficult to distinguish from each other. Eighteen extant species are currently considered valid of which 10 have ben described by Parin & Borodulina in 1986, 2005, and 2006. Otoliths are not known of any of those. Of the remainder, otoliths of six species are known and four of them figured in Lombarte et al. (2006). In the fossil record, there is *Antigonia alta* (Weiler, 1950) and *A. postangusta* Holec, 1975 (*Antigonia* sp. in Schwarzhans 2010) known from the European Miocene and two species from the Eocene: *Antigonia angusta* Stinton & Nolf, 1970 from the middle Eocene of Europe (Fig. 18AI–AK) and *A. artata* Schwarzhans, 2019 from the early and middle Eocene of New Zealand.

Antigonia transpacifica differs from its two Eocene congeners in ostium and cauda being equal in length (CaL:OsL ≤1.0 vs. >1.1) and the stubby postdorsal denticle. From *A. angusta* (Fig. 18AI–AK), it differs furthermore in the rostrum being longer than the antirostrum (vs. equally long with very short rostrum), the less deeply curved ventral rim, the less steeply inclined ostium (15–20° vs. >30°) and the smooth rims (vs. crenulated or undulating). From *A. artata* (pl. 28, figs. 15–18, in Schwarzhans 2019a), it differs additionally in the higher index OL:OH (0.85–0.95 vs. 0.8–0.85), the less steeply inclined and not narrowed anteriorly ostium (15–20° vs. 30–40°), and the ventral furrow running across the middle of the ventral field (vs. close to the ventral rim of the otolith). These findings confirm that *Antigonia* is an old, long-ranging, diverse genus since Eocene times.

Order **Scorpaeniformes** Garman, 1899 Suborder Scorpaenoidei Garman, 1899
Family Scorpaenidae Risso, 1827
Genus *Scorpaenodes* Bleeker, 1857

Scorpaenodes acronis n. sp.

Fig. 19A–I

Holotype: Fig. 19A–B, LACM 60257, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 21 specimens same data as holotype, LACM 60258.

Referred material: 50 specimens same data as holotype, LACM 60259.

Etymology: From acronis (Latin) genitive of acro = stem, referring to the putative stem position of the taxon within the genus.

Diagnosis: OL:OH = 2.0–2.1. Dorsal rim regularly curved, highest at its middle, without prominent angles. Rostrum long, pointed. Ostium distinctly widened and slightly longer than cauda. Cauda nearly straight, terminating far from posterior rim of otolith. OL:SuL = 1.3–1.45. CaL:OsL = 0.85–0.95.

Description. Small, slender, moderately thick otoliths up to 3.1 mm in length (holotype). OH:OT = 2.0–2.3. Dorsal rim regularly curved, irregularly undulating, highest at its middle, without prominent angles. Ventral rim shallow, regularly curved, deepest at its middle, smooth. Rostrum moderately long, with pointed tip in axial position, 15–22% of OL; antirostrum and excisura weak or absent. Posterior tip expanded, angular or pointed but not as sharp as rostrum, inferior, often symmetrical in position to rostrum.

Inner face distinctly convex with slightly supramedian sulcus. Sulcus extends only about 75% of the length of the inner face, moderately wide and deepened, terminating at considerable distance from posterior rim of otolith. Ostium slightly longer than cauda, distinctly wider, its colliculum poorly marked. Cauda almost straight, with rounded tip. Caudal colliculum poorly marked. Dorsal depression wide but short above anterior part of cauda, distinct, ventrally marked by crista superior; ventral furrow very close to ventral rim of otolith. Outer face flat to slightly convex, smooth.

Discussion. *Scorpaenodes acronis* is distinguished from its coeval congeners (see below) by the short and nearly straight cauda and the shape of the dorsal rim. For comparison, otoliths of two extant species are figured: *S. guamensis* (Quoy & Gaimard, 1824) (Fig. 19Z–AA) and *S. evides* (Jordan & Thompson, 1914) (Fig. 19AB–AC). Furthermore, we figure for comparison an otolith of an early Eocene species from England that we allocate with the genus: *S. colletti* (Nolf & Lapierre, 1979) (Fig. 19X–Y), which was originally described as *Haliophis colletti* of the family Pseudochromidae. Indeed, scorpaenid otoliths are difficult to distinguish from otoliths of the family Serranidae, Pseudochromidae, and related families. All otolith allocations in the fossil record to these families, particularly in the Paleogene, bear a certain uncertainty.

Scorpaenodes huddlestoni n. sp.

Fig. 19J–O

Holotype: Fig. 19J–K, LACM 60260, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 20 specimens: 10 same data as holotype, LACM 60261; 10 specimens, Tortonian, Mission Valley Formation, Miramar Reservoir site, LACM 60247.

Referred material: 819 specimens: 168 specimens same data as holotype, LACM 60262; 651 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60131.

Etymology: Named in honor of the late Richard Huddleston (Los Angeles), who participated originally in the evaluation of the fauna and made many contributions to the study of otoliths, especially in California, USA.

Diagnosis: OL:OH = 1.75–1.95. Dorsal rim regularly curved, highest at its middle, without prominent angles. Rostrum long, pointed. Ostium distinctly widened and slightly shorter than cauda. Cauda flexed at tip with abrupt bent at 20–30°, terminating moderately far from posterior rim of otolith. OL:SuL = 1.2–1.3. CaL:OsL = 1.1–1.15.

Description. Small, slender, relatively thick otoliths up to 4 mm in length (holotype 3.65 mm). OH:OT = 2.0–2.5. Dorsal rim regularly curved, slightly undulating or smooth, highest at its middle, without prominent angles. Ventral rim moderately deep, regularly curved, deepest at its middle, smooth. Rostrum moderately long, with moderately pointed or rounded tip in axial position, 15–22% of OL; antirostrum and excisura weak or absent. Posterior tip expanded, rounded or moderately pointed, symmetrical in position to rostrum.

Inner face distinctly convex with distinctly supramedian sulcus. Sulcus extends for slightly more than 80% of the length of the inner face, deepened, terminating at moderate distance from posterior rim of otolith. Ostium slightly shorter than cauda, distinctly wider, its colliculum moderately well marked. Cauda somewhat greater in length, distinctly flexed at tip in relatively abruptly bent; inclination angle 20–30°. Caudal colliculum poorly marked. Dorsal depression small, narrow, mostly weak, ventrally marked by crista superior; ventral furrow distinct, very close to ventral rim of otolith, posteriorly turning upward and inward towards caudal tip. Outer face flat to slightly convex, smooth.

Discussion. *Scorpaenodes huddlestoni* is the most common scorpaenid in the middle Eocene of California, and the only one of the three *Scorpaenodes* species known from both locations, Black's Beach and the Miramar Reservoir site. In fact, it is more common in the Miramar Reservoir site than Black's Beach. *Scorpaenodes huddlestoni* differs from the two coeval congeners in the cauda being longer than the ostium (CaL:OsL = 1.1–1.15 vs. 0.85–1.0) and the robust appearance. From *S. acronis* it differs additionally in the distinctly bent cauda (vs. nearly straight) and the lower ratio OL:SuL of 1.2–1.3 (vs. 1.3–1.45). The differentiation of *S. huddlestoni* from *S. starnesi* n. sp. (see below) is more subtle. *Scorpaenodes huddlestoni* is less elongate than *S. starnesi* (OL:OH = 1.75–1.95 vs. 1.95–2.1), has a less pointed rostrum, the dorsal rim is smooth to slightly undulating (vs. crenulated), and the caudal tip is more abruptly bent downward (vs. gently curved).

Scorpaenodes starnesi n. sp.

Fig. 19P–W

Holotype: Fig. 19P–Q, LACM 60263, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 31 specimens same data as holotype, LACM 60264.

Etymology: Named in honor of James Starnes, Director of the Geologic Mapping and Surface Geology for the Mississippi Office of Geology (Jackson, MS). Has made important contributions to paleontology and geology through his research and publications.

Diagnosis: OL:OH = 1.95–2.1. Dorsal rim low regularly curved, irregularly crenulated, highest at its middle, without prominent angles. Rostrum long, pointed. Ostium distinctly wider than cauda and slightly shorter than cauda. Cauda gently flexed at tip with abrupt bent at 20–30°, terminating moderately far from posterior rim of otolith. OL:SuL = 1.2–1.3. CaL:OsL = 0.85–1.0.

Description. Small, slender, relatively thin and delicate otoliths up to 3.4 mm in length (holotype 3.25 mm). OH:OT = 2.1–2.4. Dorsal rim regularly curved, irregularly crenulated or undulating, highest at its middle, without prominent angles. Ventral rim shallow, regularly curved, deepest at its middle, smooth or finely crenulated. Rostrum long, with pointed tip in axial position, 20–23% of OL; antirostrum and excisura weak or absent. Posterior tip expanded, rounded or moderately pointed, symmetrical in position to rostrum.

Inner face distinctly convex with slightly supramedian sulcus. Sulcus extending across approximately 75% of the length of the inner face, deepened, terminating at moderate distance from posterior rim of otolith. Ostium approximately same length as cauda, distinctly wider, its colliculum moderately well marked. Cauda distinctly flexed at tip in relatively gentle curve; inclination angle 20–30°. Caudal colliculum poorly marked. Dorsal depression small, somewhat elongated, well-developed, ventrally marked by crista superior; ventral furrow distinct, very close to ventral rim of otolith, posteriorly turning upward and inward towards caudal tip. Outer face flat to slightly convex, smooth.

Discussion. *Scorpaenodes starnesi* resembles *S. acronis* in shape and the pointed rostrum but differs in the longer sulcus (OL:SuL = 1.2–1.3 vs. 1.3–1.45) and the distinctly bent caudal tip (vs, straight cauda). For distinction from *S. huddlestoni* see above.

Genus *Eopterois* n. gen.

Type species: *Eopterois bandeli* n. sp.

Etymology: A combination of Eo from Eocene and the genus name *Pterois* in order to indicate the stratigraphic occurrence of the genus.

Diagnosis: A fossil otolith-based genus placed in the family Scorpaenidae characterized as follows. The otoliths are small (up to about 2 mm in length), and fusiform shape with a ratio OL:OH of 1.8–1.9. The rostrum is relatively long, pointed, and slightly inferior (15–20% of OL), and antirostrum and excisura are not developed. The ostium is distinctly wider and longer than the cauda. The cauda is slightly slanted and very short, with an indistinct posterior tip. OL:SuL = 1.6; CaL:OsL = 0.7. The cauda is connected with the posterior rim of the otolith through a long postcaudal depression extending along the axis of the cauda. The inner face is irregularly convex and somewhat rugose; the outer face is flat. The ventral furrow is distinct and relatively short, i.e. turns upward well before rostrum and posterior tip; the section of the ventral field above the ventral furrow is bulged.

Discussion. *Eopterois* is the first fossil record of the tribe Pteroini in the family Scorpaenidae. The otoliths of the Pteroini are characterized by the strongly reduced caudal length and the continuation of the cauda in the form of a postcaudal depression reaching the posterior rim of the otolith over a relatively long distance. The latter is a character so far only known from the Pteroini. Other typical features for otoliths of the Pteroini concern the development of the ventral furrow and the ventral field above the furrow. *Eopterois* differs from the extant Pteroini in the more compact and thicker appearance and the more compressed shape with a ratio OL:OH <2.0 (vs. >2.0). Both are probably plesiomorphic features within the tribe. An otolith of the extant *Pterois antennata* (Bloch, 1787) is figured for comparison (Fig. 19AH–AI).

Species. *Eopterois* is a monospecific genus with *Eopterois bandeli* n. sp. from the middle Eocene of Mississippi.

Eopterois bandeli n. sp.

Fig. 19AD–AG

Holotype: Fig. 19AD–AE, NRM PZ P.19072, Bartonian, Moodys Branch, Jackson, Mississippi.

Paratype: 1 specimen same data as holotype, NRM PZ P.19073.

Etymology: Named in honor of paleontologist Klaus Bandel (Hamburg), who collected most of the material studied here from Mississippi and Texas.

Diagnosis: See generic diagnosis (monospecific genus).

Description. Small, fusiform otoliths up to 1.8 mm in length (holotype). OH:OT = 2.3–2.5.

Dorsal rim regularly curved, irregularly undulating, highest at its middle, without prominent angles. Ventral rim shallow, regularly curved, deepest at its middle, slightly undulating. Rostrum moderately long, with pointed, slightly inferior tip, 15–20% of OL; no antirostrum or excisura. Posterior tip expanded, rounded, symmetrical in position to rostrum.

Inner face rugose, slightly convex, posterior part distinctly convex, anterior part slightly convex. Sulcus axially positioned, relatively short, slightly deepened, not extending backwards further than central part of inner face. Ostium distinctly longer than cauda, significantly wider, funnel-shaped, its colliculum poorly marked. Cauda very small and short, terminating far from posterior rim of otolith. Cauda connected with posterior rim of otolith through long postcaudal depression extending along axis of cauda. Dorsal depression small, indistinct; ventral furrow distinct, short, more strongly bent than ventral rim of otolith and thus not reaching to anterior and posterior parts of ventral field; area of ventral field above ventral furrow bulged. Outer face flat, smooth.

Discussion. The two specimens of *Eopterois bandeli* are rather small. The smaller one of 1.2 mm in length shows a simpler morphological pattern than the larger one at 1.8 mm, which indicates that the smaller one stems from a juvenile fish and is not fully morphologically mature. However, the characters are still distinctive enough to align it with the lager specimen which appears morphologically mature despite its still small size. We conclude from this observation that *E. bandeli* was probably a smaller species than today's Pteroini.

Suborder **Cottoidei** Bleeker, 1859
Family Cottidae Bonaparte, 1831
Genus indet.

Cottidae indet.

Fig. 19AJ–AL

Material: 3 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60265.

Discussion. These otoliths are thick, oval/fusiform with a short, narrow and supramedian sulcus with about equally long ostium and cauda. They don't show useful diagnostic characters for identification and may probably stem from juvenile fishes. We have figured the largest specimen that is about 1.6 mm in length.

Family Liparidae? Scopeli, 1777
Genus *Liparomorphus* n. gen.

Type species: *Liparomorphus gerringerae* n. sp.

Etymology: A combination of the genus name *Liparis* and morphus (Latin) = morph, mutate, reflecting the putative allocation to the family Liparidae.

Diagnosis: A fossil otolith-based genus tentatively placed in the family Liparidae and characterized as follows. The otoliths are small (up to about 2 mm in length) and have a parallelogram-like shape whereby dorsal and ventral rims are horizontal and the anterior and posterior rims parallel inclined between 45 and 55°. The ratio OL:OH is 1.55–1.65. The rostrum is long, moderately pointed and very inferior (20–25% of OL), and the posterior rim shows a strong projection at the junction with the dorsal rim. The sulcus only comprises approximately 65% of the length of the inner face. The ostium is slightly wider and shorter than the cauda. The cauda is straight, with a rounded tip, terminating far from the posterior rim of the otolith. OL:SuL = 1.55–1.65; CaL:OsL = 1.3–1.4. The inner face is distinctly convex and the outer face flat.

Discussion. *Liparomorphus* has characteristic otoliths despite its relatively simple sulcus morphology. So far, fossil liparids are extremely scarce. Possible unspecified liparid otoliths have been figured by Nolf (2013) from the Early Miocene of Washington State, USA, and otolith-based species have been described as *Liparis*? *minusculus* Nolf, 1977 from the early Oligocene of Belgium and *Liparis*? *hampdenensis* Schwarzhans, 2019 from the middle Eocene of New Zealand. The short sulcus with the short ostium and simple cauda of *Liparomorphus* resembles many extant liparid otoliths (see Lombarte et al. 2006 and Knudsen et al. 2007 for figures of extant otoliths). Also the shape of the otolith and its size is typical for liparid otoliths, but the convex inner and flat outer face distinguishes it from known extant liparid otoliths. Because of remaining uncertainties concerning the characterization of liparid otoliths we place *Liparomorphus* only tentatively in the family.

Species. *Liparomorphus* is a monospecific genus with *Liparomorphus gerringerae* n. sp. from the middle Eocene of California.

Liparomorphus gerringerae n. sp.

Fig. 19AM–AP

Holotype: Fig. 19AM–AO, LACM 60266, upper Lutetian, Ardath Shale, Black's Beach.

Paratype: 1 specimen same data as holotype, LACM 60267.

Etymology: Named in honor of Mackenzie Gerringer (State University of New York at Geneseo, USA) for her contribution to the knowledge of the biology of hadal fishes.

Diagnosis: See generic diagnosis (monospecific genus).

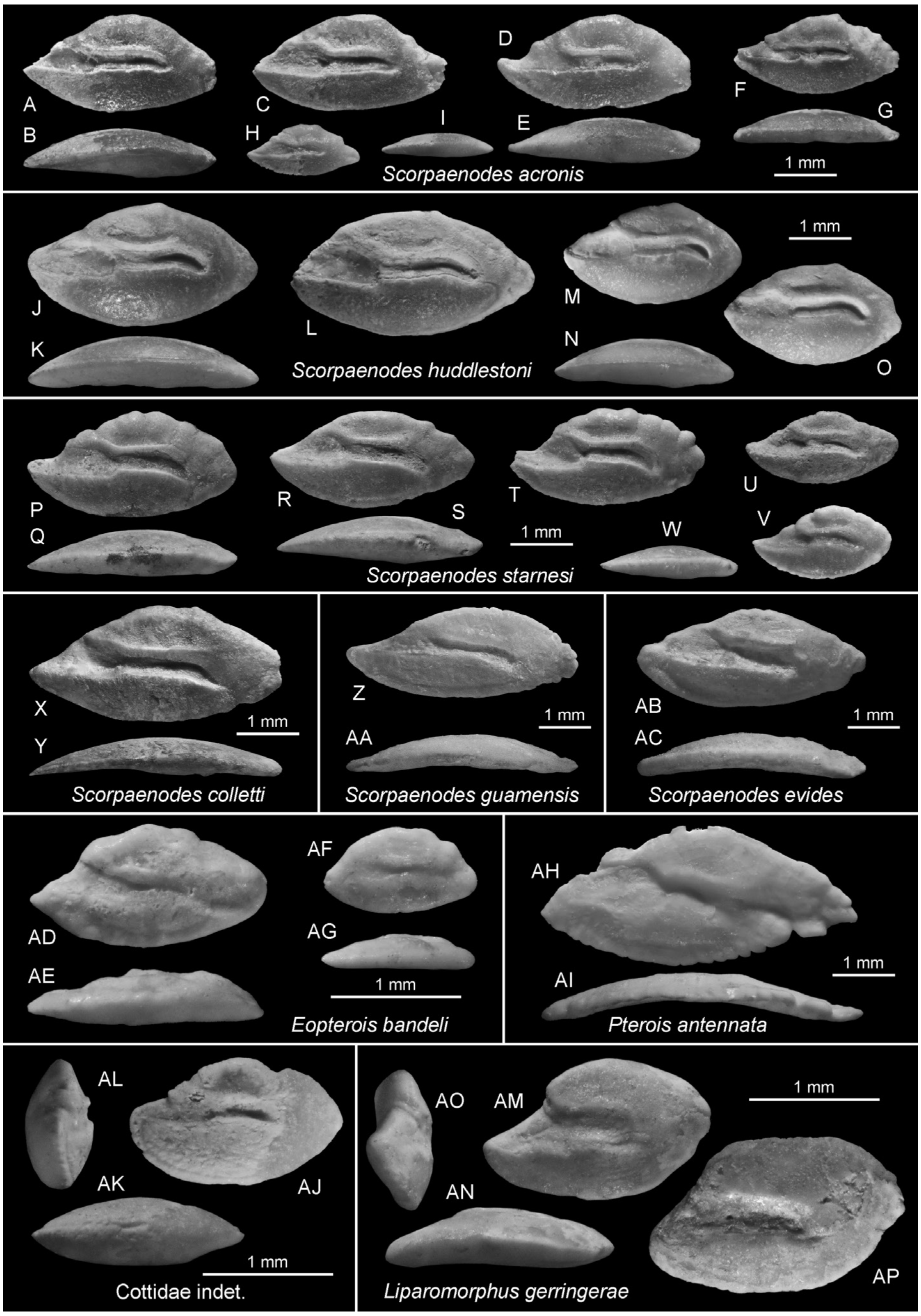


Fig. 19 - A–I) *Scorpaenodes acronis* n. sp.; A–B holotype, Black's Beach, LACM 60257 (reversed), B ventral vew; C–I paratypes, Black's Beach, LACM 60258 (C–E, H–I reversed), E, G, I ventral views.
J–O) *Scorpaenodes huddlestoni* n. sp.; J–K holotype, Black's Beach, LACM 60260, K ventral view; L–O paratypes, Black's Beach, LACM 60261 (reversed), N ventral view.
P–W) *Scorpaenodes starnesi* n. sp.; P–Q holotype, Black's Beach, LACM 60263, Q ventral view; R–W paratypes, Black's Beach, LACM 60264 (U–W reversed), S, W ventral views.
X–Y) *Scorpaenodes colletti* (Nolf & Lapierre, 1979), Ypresian, London Clay, Isle of Sheppey, England, Y ventral view.
Z–AA) *Scorpaenodes guamensis* (Quoy & Gaimard, 1824), Recent, NSMT-P.115497, Kagoshima, SL 58 mm, AA ventral view.
AB–AC) *Scorpaenodes evides* (Jordan & Thompson, 1914), Recent, WAM 33056.009, 08°48'S, 115°35'E, AC ventral view.
AD–AG) *Eopterois bandeli* n. gen., n. sp.; AD–AE holotype, Bartonian, Moodys Branch, Jackson, Mississippi, NRM PZ P.19072 (reversed), AE ventral view; AF–AG paratype, same data as holotype, NRM PZ P.19073 (reversed), AG ventral view.
AH–AI) *Pterois antennata* (Bloch, 1787), Recent, aquarium specimen, AI ventral view.
AJ–AL) Cottidae indet., Black's Beach, LACM 60265 (reversed), AK ventral view, AL anterior view.
AM–AP) *Liparomorphus gerringerae* n. gen., n. sp.; AM–AO Holotype, Black's Beach, LACM 60266 (reversed), AN ventral view, AO anterior view; AP paratype, Black's Beach, LACM 60267 (reversed).

Description. Small, parallelogram-shaped otoliths up to 2 mm in length (holotype 1.75 mm). OH:OT = 2.4–2.5. Dorsal rim shallow, slightly curved or flat, horizontal. Ventral rim nearly flat, horizontal. Rostrum long, with moderately pointed and very inferior tip (20–25% of OL). Antirostrum and excisura very weak or absent. Inclination angle of anterior rim 45–55°. Posterior rim straight or slightly curved, inclined at about 50°, forming strong projection at junction with dorsal rim. All rims smooth.

Inner face distinctly convex, with short, axial positioned sulcus. Sulcus fairly short, moderately wide, slightly deepened, anteriorly open, posteriorly terminating far from posterior rim of otolith. Ostium slightly shorter than cauda, slightly deeper, its dorsal margin very short. Collum poorly marked and hence differentiation of ostium and cauda poor. Colliculi indistinct. Dorsal depression not discernable; ventral furrow very feeble and close to ventral rim of otolith. Outer face flat, smooth.

Suborder **Platycephaloidei** Nelson, 2006
Family Triglidae Rafinesque, 1810
Genus *Prionotus* Lacepède, 1801

Prionotus kieli n. sp.

Fig. 20A–E

Holotype: Fig. 20C–D, NRM PZ P.19074, Priabonian, Yazoo Clay, Cynthia, Mississippi.

Paratypes: 2 specimens same data as holotype, NRM PZ P.19075.

Etymology: Named in honor of Steffen Kiel (Stockholm), who has sampled many of the fossil otoliths from Mississippi and Texas described here.

Diagnosis: OL:OH = 1.65–1.7. Dorsal rim low, highest slightly anterior of its middle, postdorsal rim straight, inclined at 25–30°. Rostrum moderately long, blunt. Sulcus horizontal, extending across 75% of length, somewhat s-shaped. Ostium slightly widened and about same length as cauda. Collum narrow, long. OL:SuL = 1.3–1.4. Outer face distinctly concave.

Description. Relatively large and slender, and relatively thin and delicate otoliths up to 4 mm in length (holotype). OH:OT = 3.4– Dorsal rim low, highest slightly anterior of its middle, postdorsal rim straight, inclined at 25–30°. Ventral rim shallow, regularly curved, deepest at its middle. Rostrum moderately long, blunt, slightly inferior, 12–15% of OL; antirostrum and excisura weak. Posterior tip expanded, broad, positioned slightly higher than rostrum. All rims slightly undulating.

Inner face strongly convex with slightly supramedian, horizontal somewhat s-shaped sulcus. Sulcus is moderately long, wider away from collum, and relatively deep, terminating at moderate distance from posterior rim of otolith. Ostium and cauda of about equal length, separated by a narrow, relatively long collum. Ostium slightly wider than cauda slightly upward directed towards anterior. Cauda slightly widened and deepened and slightly downward inclined. Ostial and caudal coliculi relatively well-marked and separated by long collum. Dorsal depression small, well-developed, somewhat oval in shape, ventrally marked by crescent-shaped crista superior; ventral furrow indistinct, very close to ventral rim of otolith, positioned on outward bent lower margin. Outer face strongly concave, relatively smooth.

Discussion. *Prionotus* otoliths are relatively rare in the fossil record and are never abundant when present. For example, Schwarzhans (2010) described two *Prionotus* species from the Miocene of the North Sea Basin and van Hinsbergh & Hoedemakers (2022) from the Pliocene of the Mediterranean, which were both considered short-lived migrations from North America. *Prionotus* today is restricted to the seas around America and therefore reports of fossil *Prionotus* otoliths are naturally much more common in North America than in other parts of the world. Fitch first noted *Prionotus* otoliths from two different Pleistocene sites in California (Fitch 1966; 1970). Fitch and Lavenberg (1983) identified *Prionotus* from the Pliocene Yorktown Formation from the Nutrien phosphate pit (commonly referred to as Lee Creek) in North Carolina. *Prionotus* sp. was reported by Nolf and Stringer (1992) from the Mio-Pliocene of the Dominican Republic and by Stringer (1992) from the Late Pleistocene mudlump islands in Louisiana. Stringer (1998) reported *Prionotus* from the Bowden shell bed (Layton Formation, Pliocene) of Jamaica. Müller (1999) described several *Prionotus* morphotypes in open nomenclature from the Neogene of the southeastern Atlantic Coast of the USA. More recently, Stringer and Shannon (2019) described *Prionotus* from the Pliocene of southern North Carolina, while Stringer et al. (2022) reported *Prionotus* from two inland localities of the Pliocene Yorktown Formation in North Carolina. Stringer et al. (2020) noted the occurrence of *Prionotus* in the Pliocene Graham Ferry Formation on Dauphin Island in Alabama. Most of the reports in North America have been as *Prionotus* sp. or *Prionotus* cf. *P. carolinus*. However, *Prionotus kieli* of this investigation easily represents the oldest fossil record of the genus based on otoliths.

Prionotus? sp.

Fig. 20F–G

?2022 Triglidae indet. - Lin & Nolf: fig. 29F-G.

Material: 2 specimens, Mission Valley Formation, Miramar Reservoir site, LACM 60132.

Discussion. The two specimens are incompletely preserved or were broken and partly retrieved and reconstructed like the one figured (Fig. 20F–G) and thus do not warrant specific identification. They do, however, represent a rather different morphotype from *P. kieli* and are therefore only tentatively associated with *Prionotus*. Similarly incompletely preserved otoliths figured by Lin & Nolf (2022) as unspecified triglids from the middle Eocene of Texas may represent the same species.

Order **Blenniiformes** Bleeker, 1859

Family Labrisomidae Hubbs, 1952

Genus indet.

Labrisomus*? *eocenicus Müller, 1999

Fig. 20H–I

1999 "genus Labrisomidarum" *eocenicus* - Müller: fig. 42/12-14.
2022 "*Labrisomus*" *eocenicus* (Müller, 1999) - Lin & Nolf: fig. 21E-G.

Material: 1 specimen, Bartonian, Mission Valley Formation, Miramar Reservoir site, LACM 60133.

Discussion. The single, moderately preserved specimen resembles the ones described by Müller (1999) and Lin & Nolf (2022) from the Atlantic middle Eocene in otolith and sulcus shape, particularly as far as the "hooked" caudal tip is concerned. This is also the main differences to otherwise similar looking triglid otoliths. For further comparison, we have figured representatives of other Eocene otoliths described at one time as blenniiforms: *Blennius*? *cor* (Koken, 1888) (Fig. 20J–K, NRM PZ P.19076) from the middle Eocene of Texas and *Blennius*? *vectensis* (Nolf, 1973) (Fig. 20L–M) from the middle Eocene of Belgium.

Incertae sedis

Remarks. In this category of teleost taxa of unresolved systematic position, we place the family Bathyclupeidae, which has seen a variety of different placements in past literature and otolith morphologies that are highly characteristic but cannot be related to any known extant or fossil teleost groups. The latter are likely to represent extinct teleost families or higher systematic units of which otoliths are not known. Only finds of otolith in situ will eventually be able to resolve their systematic position.

Family Bathyclupeidae Gill, 1896
Genus *Bathyclupea* Alcock, 1891

Bathyclupea arribaoutensis Nolf, 1988

Fig. 20N–U

1988 *Bathyclupea arribaoutensis* - Nolf: pl. 12, fig. 3.
2016 *Bathyclupea arribaoutensis* Nolf, 1988 - Lin, Nolf, Steurbaut & Girone: fig. 13F-H.

Material: 13 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60268; several otolith fragments from the middle layer of the Ardath Shale.

Remarks. Bathyclupeid otoliths are highly distinctive in their outline. They are usually shown with a horizontally oriented sulcus, which gives them a high-bodied, skewed parallelogram-like shape. However, radiographs of various extant specimens can be seen on the webpage of the National Museum of Natural History (USNM), Washington D.C. or in Prokofiev (2014), and these show that the in vivo position of the otoliths is very different in a way that the dorsal rim of the otolith is horizontal. We have therefore arranged the *Bathyclupea* otoliths from the Californian Eocene accordingly and base our description on this orientation. In fact, the steeply inclined sulcus (>40°) means that also the macula acustica, which is attached to the sulcus must be steeply inclined as well. This pattern is unique in teleosts and certainly autapomorphic for the Bathyclupeidae. The only other family from which steeply inclined sulci are known is the Pterothrissidae, but in that family, the inclination does not exceed 30°.

Description. Thin, rectangular otoliths up to 9 mm in length (Fig. 20N). When oriented with horizontal dorsal rim following values are eminent. OL:OH = 1.7–1.9; OH:OT = 3.8–4.8. Anterior rim nearly vertical, straight or slightly bent. Dorsal rim nearly straight, horizontal, with sulcus opening towards anterior-dorsal rim; dorsal positioned rostrum and antirostrum short, excisura shallow. Posterior rim straight, slanting at 70–75° from the horizontal axis. Ventral rim straight, slightly inclined at 10–15° toward the anterior rim. Angles at junction of ventral rim with anterior and posterior rims sharp, orthogonal, or acute; angles at junction of dorsal rim with anterior and posterior rims somewhat rounded, orthogonal, or obtuse. Anterior and posterior rims slightly crenulated or smooth, dorsal rim slightly undulating, ventral rim smooth.

Inner face nearly flat, slightly convex in anterior view (Fig. 20Q, T). Sulcus steeply inclined at 42–48° and extending from anterodorsal to almost posteroventral, deepened, relatively wide, straight, anteriorly open, posteriorly reaching very close to postventral rim and often extended by postcaudal depression. Ostium slightly wider than cauda, distinctly shorter; CaL:OsL = 1.45–1.85, measured along sulcus axis.

Discussion. *Bathyclupea arribaoutensis* so far represents one of very few otolith-based fossil species in the family together with a possible bathyclupeid from the Paleocene of Mississippi (Nolf & Dockery 1993) and an unspecified bathyclupeid from the lower Miocene of Trinidad (Nolf 1976). *Bathyclupea arribaoutensis* has been described on a unique holotype from the Eocene of South-West France by Nolf (1988) and was recorded by two further specimens from the region by Lin et al. (2016). The relative abundance in the middle Eocene of California is thus perhaps surprising but also documents a wide distribution of the species.

Family indet.

Genus *Electolapis* n. gen.

Type species: *Ambassis electilis* Stinton & Nolf, 1970

Etymology: Formed as a partial tautology from the name of the type species in combination with lapis (Latin) = stone.

Diagnosis: A fossil otolith-based genus of unknown familial relationships with the following characteristics. The otoliths are small (up to about 3 mm in length), with a roundish shape and a short, pointed rostrum. The rims are typically crenulated, the ventral rim finer than the dorsal rim. The ratio OL:OH is 1.2–1.4. The ostium is distinctly wider than the cauda and about equal in length. The cauda is straight except for a slightly flexed and postero-ventrally pointed tip. OL:SuL = 1.2. The ventral furrow runs relatively distant from the ventral rim of the otolith and separates an ornamented section below from a smooth section above the ventral furrow. The inner face is distinctly convex, and the outer face slightly concave, strongest anteriorly.

Discussion. *Electolapis* resembles a number of "lower" perciform otoliths such as for example from the Ambassidae, in which their otoliths have originally been placed, or certain Epigonidae but also certain Atheriniformes. They represent a well-defined otolith morphology and in the light of their uncertain relationships are here placed in Teleostei incertae sedis. It is hoped that eventually otoliths will be found in situ and will then resolve the relationship of this group.

Species. Two species - *Electolapis electilis* (Stinton & Nolf, 1970) from the middle Eocene of Belgium, England, and the Paris Basin of France (Fig. 20V–X), *Electolapis aquitanicus* (Nolf, 1988) (originally described as "genus Gerreidarum" *aquitanicus*) from the Eocene of the Aquitaine Basin in France and a potential third species from the middle Eocene of California (see below).

Electolapis sp.

Fig. 20Y–Z

Material: 1 specimen, upper LutetianArdath Shale, Black's Beach, LACM 60269.

Discussion. The single specimen from the Californian Eocene closely resembles *E. electilis* but differs in the distinctly concavity of the predorsal rim, which resembles *E. aquitanicus*, and the slightly stronger bent caudal tip. It probably represents a third species of this enigmatic genus, which, however, cannot be conclusively identified based on the unique specimen with a broken rostrum.

Genus *Fitchichthys* n. gen.

Type species: *Fitchichthys placidus* n. sp.

Etymology: In memory of the late John Fitch (Long Beach, California), who was instrumental in the scientific study of otoliths and emphasized the importance of the knowledge of extant taxa.

Diagnosis: A fossil otolith-based genus of unknown familial relationships with the following characteristics. The otoliths are small (up to about 2.7 mm in length), with a roughly triangular shape caused by a high dorsal rim with its highest point at the middle, an inferior rostrum and nearly symmetrical posterior tip, and a relatively low ventral rim. The rims are typically relatively thick and irregularly undulating. The ratio OL:OH is 1.0–1.1. The ostium is narrow, only slightly wider than the cauda, relatively short, anteriorly open and deepened. The cauda is long, straight, occasionally slightly bent upward at its tip and reaches very close to the posterior rim of the otolith or opens to it. CaL:OsL = 1.3–2.0. The ventral furrow runs at variable distance from the ventral rim of the otolith. The inner face is distin-ctly convex, and the outer face likewise distinctly concave.

Discussion. *Ftichichthys* is a highly characteristic otolith of unknown relationships, and one of the two congeners has in the past be related with the Macroramphosidae (Schwarzhans 2007). However, this relationship, albeit possible, is not supported by potential synapomorphous otolith characters (see also Bratishko et al. 2023). It appears prudent at this stage to consider *Fitchichthys* as a Teleostei incertae sedis until otoliths have been found in situ.

Species. Two species: *Fitchichthys placidus* n. sp. from the middle Eocene of California and *Fitchichthys testuliformis* (Schwarzhans, 2007) (originally described as *Macroramphosidarum testuliformis*) from the middle Eocene of Germany.

Fitchichthys placidus n. sp.

Fig. 20AA–AG

Holotype: Fig. 20AA–AC, LACM 60270, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 21 specimens same data as holotype, LACM 60271.

Etymology: From placidus (Latin) = gentle, placid, referring to the memory of John Fitch after whom the genus has been named.

Diagnosis: OL:OH = 1.0–1.1. Dorsal rim high, highest at center. Rostrum inferior, relatively sharp; posterior tip symmetrical, less sharp. Ventral rim shallower than dorsal rim, gently curved. Cau-

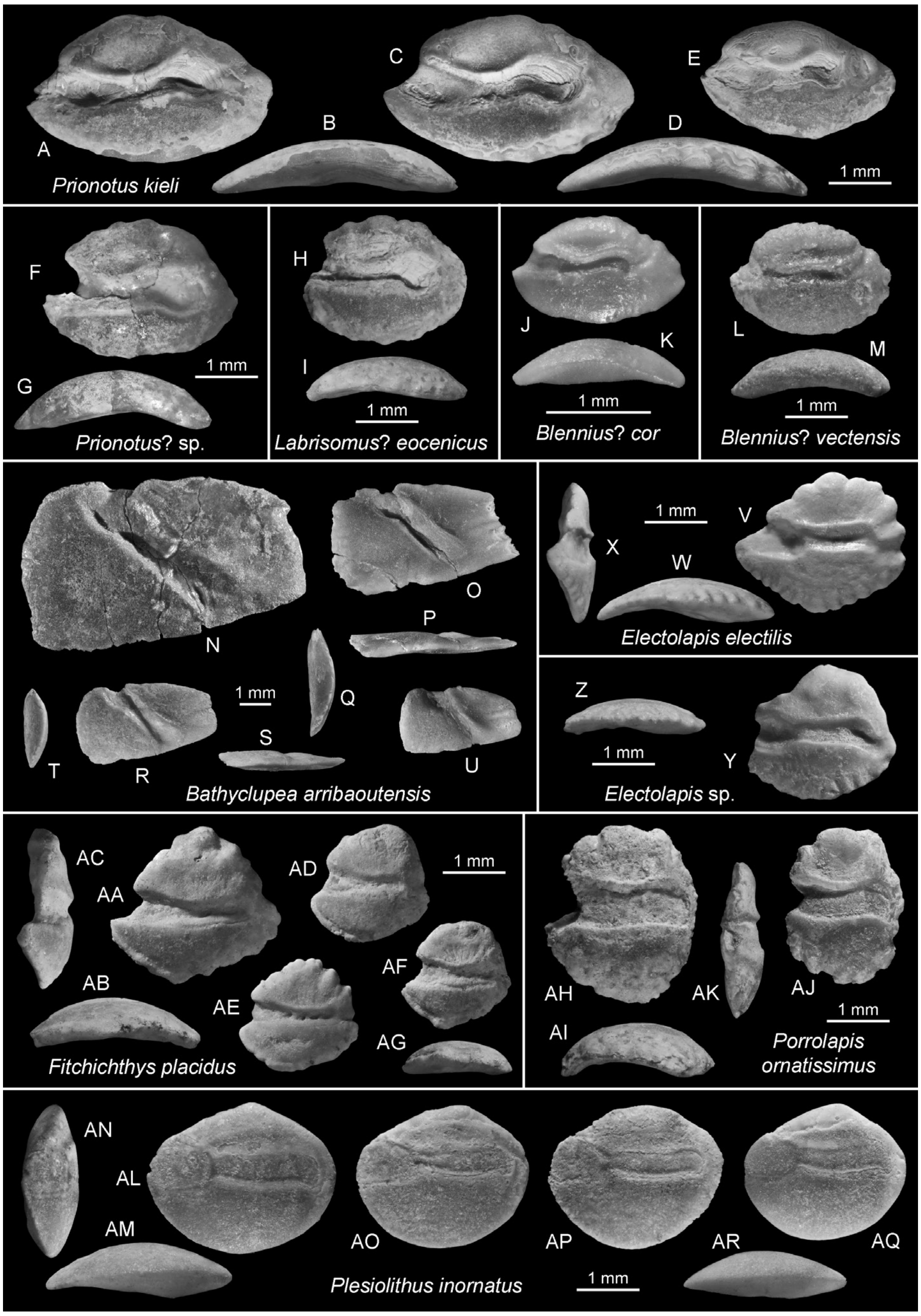


Fig. 20 - A–E) *Prionotus kielei* n. sp.; C–D holotype, Yazoo Clay, Priabonian, Mississippi, NRMZ PZ P.19074 (reversed), D ventral view; A–B, E paratypes, same data as holotype, NRM PZ P.19075 (A–B reversed), B ventral view.
F–G) *Prionotus*? sp., Miramar Reservoir site, LACM 60132, G ventral view.
H–I) *Labrisomus*? *eocenicus* Müller, 1999, Miramar Reservoir site, LACM 60133 (reversed), I ventral view.
J–K) *Blennius*? *cor* (Koken, 1888), Brazos River, Bartonian, Texas, NRM PZ P.19076 (reversed), K ventral view.
L–M) *Blennius*? *vectensis* (Nolf, 1973), Lutetian, Balegem, Belgium, M ventral view.
N–U) *Bathyclupea arribaoutensis* Nolf, 1988, Black's Beach, LACM 60268 (N–T reversed), P, S ventral views, Q, T anterior views.
V–X) *Electolapis* n. gen. *electilis* (Stinton & Nolf, 1970), Lutetian, Balegem, Belgium (reversed), W ventral view, X anterior view.
Y–Z) *Electolapis* n. gen., sp., Black's Beach, LACM 60269, Z ventral view.
AA–AG) *Fitchichthys placidus* n. gen., n. sp.; AA–AC holotype, Black's Beach, LACM 60270, AB ventral vew, AC anterior view; AD–AG paratypes, Black's Beach, LACM 60271, AG ventral view.
AH–AK) *Porrolapis* n. gen. *ornatissimus* (Nolf, 1988), Black's Beach, LACM 60274 (reversed), AI ventral view, AK anterior view.
AL–AR) *Plesiolithus inornatus* n. gen., n. sp.; AL–AN holotype, Black's Beach, LACM 60272, AM ventral view, AN anterior view; AO–AR paratypes, Black's Beach, LACM 60273 (AP–AR reversed), AR ventral view.

da not reaching posterior rim of otolith. Ventral furrow relatively close to ventral rim of otolith.

Description. Small, roughly triangular, robust otoliths up to 2.7 mm in length (holotype). OH:OT = 3.0–3.8. Dorsal rim high, with angular, rounded or broad central part. Ventral rim much shallower, relatively regularly bent but occasionally with preventral angle. Rostrum moderately long, sharp, inferior (12–18% of OL). Antirostrum short but mostly sharp; excisura broad, moderately deep. Posterior rim dorsally straight or slightly curved, inclined at about 55–70°; posterior tip slightly inferior, symmetrically positioned to rostrum but less pointed. All rims tend to be irregular with some rather intensely crenulated.

Inner face distinctly convex, with long, axial to slightly infarmedian positioned sulcus. Sulcus extends across approximately 85–90% of length of inner face, narrow, distinctly deepened, anteriorly open, posteriorly terminating close to posterior rim of otolith. Ostium shorter than cauda, slightly deeper and slightly wider. Cauda is less wide than ostium and not as deep. Caudal colliculum with mostly distinct ventral margin. CaL:OsL = 1.3–1.6. Dorsal depression indistinct; ventral furrow distinct and relatively close to ventral rim of otolith. Outer face slightly to distinctly concave, relatively smooth.

Discussion. *Fitchichthys placidus* differs from its European congener *F. testuliformis* in the higher dorsal rim (vs. flattened at center), the cauda being closed posteriorly (vs. reaching the posterior rim of the otolith), the ratio CaL:OsL (1.3–1.6 vs. 2.0) and the ventral furrow being relatively close to the ventral rim of the otolith (vs. relatively distant).

Genus *Plesiolithus* n. gen.

Type species: *Plesiolithus inornatus* n. sp.

Etymology: A combination of plesio from plesiomorph (evolved trait that is shared by some or all members of a phylogenetic group but not unique to that group) and lithus (stone) from Otolithus.

Diagnosis: A fossil otolith-based genus of unknown familial relationships with the following characteristics. The otoliths are small (up to about 3 mm in length), with a gently rounded outline without conspicuous angles, tips, or incisions except for an obtuse middorsal angle. The ratio OL:OH is 1.18–1.28. The sulcus is shallow (lightly impressed) with a spatulate ostium and a narrower, longer cauda with the slightly bent tip terminating close to the posterior rim of the otolith. CaL:OsL = 1.4–1.5. The inner face is distinctly convex and very smooth because of the shallow sulcus and the indistinct dorsal depression.

Discussion. *Plesiolithus* is an easy recognizable otolith despite its apparent simple and plesiomorphic structure. We know of no extant otoliths that shows any resemblance. Likely, these otoliths represent an extinct family or even higher unit which will only be identified once otoliths have been found in situ.

Species. *Plesiolithus* is a monospecific genus with *Plesiolithus inornatus* n. sp. from the middle Eocene of California.

Plesiolithus inornatus n. sp.

Fig. 20AL–AR

Holotype: Fig. 20AL–AN, LACM 60272, upper Lutetian, Ardath Shale, Black's Beach.

Paratypes: 29 specimens same data as holotype, LACM 60273.

Etymology: From inornatus (Latin) = unsculptured, referring to the smooth appearance of the inner face of the otoliths.

Diagnosis: See generic diagnosis (monospecific genus).

Description. Small, roundish, robust otoliths in thickness up to 3 mm in length (holotype). OH:OT = 3.0. All rims gently and regularly curved except low, obtuse middorsal angle; no rostrum, antirostrum or excisura. All rims smooth.

Inner face strongly convex, smooth, with long, shallow, supramedian sulcus. Ostium spatulate, anteriorly open, distinctly wider and shorter than cauda. Cauda long, reaching close to posterior rim of otolith, slightly swinging posteriorly, with broadly rounded tip. Dorsal depression very indistinct; ventral furrow indistinct, close to ventral rim of otolith. Outer face flat, posteriorly with shallow umbo, anteriorly slightly concave, smooth.

Genus *Porrolapis* n. gen.

Type species: "genus Cyprinodontoideorum" *ornatissimus* Nolf, 1988.

Etymology: A combination of porro (Latin) = furthermore and lapis (Latin) = stone.

Diagnosis: A fossil otolith-based genus of unknown familial relationships with the following characteristics. The otoliths are small (up to about 2.5 mm in length), with a high-bodied outline characterized by a high dorsal rim with a flattened central part, a deeply curved ventral rim, a near vertical, blunt posterior rim and an anterior rim with a blunt, short rostrum and a broad, moderately deep excisura. All rims are intensely crenulated or irregularly lobed. The ratio OL:OH is 0.75–0.85. The sulcus is slightly supramedian, relatively shallow and extends across the length of the inner face with a slightly oscillating, long cauda reaching close to the posterior rim of the otolith, and an almost indiscernible, very small ostium. CaL:OsL = 1.4–1.5. The inner face is strongly convex; the outer face strongly concave in ventral view.

Discussion. The strange morphological pattern of the otoliths of *Porrolapis* has in the past been associated with the Cyprinodontidae (Nolf 1988) and the Menidae (Nolf 2013; Lin et al. 2016). However, both associations are not convincing and cannot be substantiated by any synapomorphies. In fact, we know of no extant otoliths that shows any significant resemblance. Likely, these otoliths represent an extinct family or even higher unit that will only be identified once otoliths have been found in situ.

Species. *Porrolapis* is a monospecific genus with *Porrolapis ornatissimus* (Nolf, 1988) from the early and middle Eocene of the Aquitaine Basin in France and the middle Eocene of California.

Porrolapis ornatissimus (Nolf, 1988)

Fig. 20AH–AK

1988 "genus Cyprinodontoideorum" *ornatissimus* - Nolf: pl. 8, fig. 11.
2016 '*Mene*' *ornatissima* (Nolf, 1988) - Lin, Nolf, Steurbaut & Girone: fig. 12M-N.

Material: 7 specimens, upper Lutetian, Ardath Shale, Black's Beach, LACM 60274.

Discussion. This unusual otolith originally described from the Eocene of the northeast Atlantic Aquitaine Basin in France has now also been identified from the middle Eocene of California.

Faunal reconstruction

Diversity of fishes based on otoliths from the Ardath Shale and Mission Valley Formation

The diversity of the fish taxa in the Ardath Shale and the Mission Valley Formation, both middle Eocene, is directly related to the paleoecological conditions and the resulting paleoenvironment. Species diversity includes the number of species (richness) and the relative abundance of each species present (evenness). A myriad of factors affected the richness and evenness of the two middle Eocene formations including temperature, water depth, dissolved oxygen, salinity, substrate conditions, sediment input, biological productivity, and other parameters. Additionally, the diversity was likely affected by the presence of the Tropical American Seaway, especially between the eastern Pacific and the western Atlantic region. The influence of an interoceanic central America seaway corridor would have been present during the deposition of the middle Eocene Ardath Shale and the Mission Valley Formation. The number of species (richness) and their relative abundance (evenness) were determined based on Supplementary Tab. 2 for the Ardath Shale and the Mission Valley Formation.

The number of species present (richness) in the otolith assemblage of the early middle Eocene (early Lutetian) Ardath Shale is extremely prolific with at least 83 taxa identified to either genus or species level as well as five groups identified only to the family (Supplementary Tab. 1). For comparison, the middle Eocene (Bartonian) Clinchfield Formation in Georgia, USA (Gulf Coastal Plain), only produced 14 otolith-based taxa although 4,768 specimens were examined (Stringer et al. 2022). It should be noted that the paleoenvironment of the Clinchfield Formation was interpreted as subtropical, soft substrate, mainly normal marine to slightly reduced, and indications of proximal continental coastlines. Another middle Eocene otolith assemblage from the Lutetian Stone City Member in Texas, USA (Gulf Coastal Plain) yielded 23 otolith-based taxa. Paleoenvironments ranged from possible tidal channels emptying into nearshore marine for the lower assemblage to a nearshore, fully marine setting of 25 m or less for the upper assemblage (Bread & Stringer 1999). These Eocene examples from the Gulf Coastal Plain clearly indicate the richness of taxa in the Ardath Shale.

The relative abundance or evenness of the taxa present in the Ardath Shale is also obtained from the data in Supplementary Tab. 3. Examination of the relative abundance of the otolith assemblage indicates that no individual species represents more than 19.55% of the total assemblage. Further examination of the assemblage shows that three congrids represent 4.31–5.29%, an ariid represents 4.97%, a sparid represents 10.13%, a soleid accounts for 5.8%, a presumed ambassid represents 10.28%, and ophidiids account for 3.60–19.56%. These examples and other percentages of the taxa in the Ardath Shale are compelling evidence for the evenness of the otolith assemblage with no strongly dominant taxon or taxa. This is in stark contrast to the evenness, or lack thereof, of the younger Yazoo Clay Formation (primarily Priabonian but lowermost portion appears to be Bartonian) of Louisiana, USA (Nolf & Stringer 2003; Lin & Nolf 2022). The Yazoo Clay Formation otolith assemblage is not as rich with 44 taxa, but a 450-kg sample yielded 5,293 specimens. One species, *Symmetrosulcus meyeri* (previously identified as *Preophidion meyeri* in numerous studies of Gulf Coast otoliths) accounted for 58.94% of the total assemblage.

The Mission Valley Formation has a richness of 37 taxa as well as one group identified only to the family level. This is a fairly diverse number of species in the formation, but the Ardath Shale has approximately 56% more taxa. Therefore, the Ardath Shale is much richer in the number of species. However, the Mission Valley Formation is less even than the Ardath Shale but not greatly. There are only two taxa in the Mission Valley Formation that are greater than 20% (a congrid at 23.18% and a lactariid at 22.03%). In summary, the species diversity of the Ardath Shale is significantly richer with 83 taxa, but the evenness of the Ardath Shale and the Mission Valley Formation are not greatly different.

Comparison of the otolith assemblages of the two middle Eocene formations

A meaningful analysis of the otolith assemblages of the Ardath Shale and the Mission Valley Formation is to compare their similarity (or lack thereof). An appropriate tool for analyzing the two localities is the percentage similarity measurement, which allows a comparison of assemblages from different localities (Reitz & Wing 1999; Stringer et al. 2016; Stringer et al. 2018; Stringer & Schwarzhans 2021).

The percentage similarity measurement between the Ardath Shale and the Mission Valley Formation was calculated using data from Supplementary Tab. 2. The analysis indicated that there were 29 shared taxa between the two formations, which might appear significant. However, 24 of the shared taxa each represented less than 1% of the total assemblages of the two formations. Therefore, the percentage similarity is only 17.18% between the Ardath Shale and the Mission Valley Formation. This is further evidence that the two formations are not significantly similar. The percentage similarity, which indicates a lack of similarity in this case, could be related to numerous factors and may be indicative of significant differences in the paleoenvironments of the two formations, which are examined below.

Otolith-based paleoenvironmental reconstruction

The utilization of fossil teleostean otoliths to reconstruct ancient environments has been discussed at length by many studies including Nolf and Brzobohaty (1992), Schwarzhans (2019a, and references therein), Stringer et al. (2020), and Stringer and Schwarzhans (2021, and references therein). Several, detailed analyses of modern fish otoliths in ocean sediments in the last ten years have validated their accuracy and use (Lin et al. 2016a, 2017, and 2018, and references therein). The use of fossil otolith assemblages to interpret paleoenvironments has been utilized for nearly 60 years in the USA (Fitch 1964). Studies of fossil otoliths in California that contain some discussion of paleoecology and paleobiogeography include Carnevale et al. (2008), Firestine et al. 2012, Fitch (1964, 1966, 1967, 1968, 1969a, 1969b, 1970), Fitch and Barker (1970), Fitch and Reimer (2007), Huddleston and Takeuchi (2007), and Takeuchi and Huddleston (2008a, 2008b). However, this study is the first use of otoliths for paleoenvironmental interpretation for the US Pacific Coast Paleogene.

Numerous studies in North America (Nolf & Stringer 1992; Stringer & Bell 2018; Stringer & Hulbert 2020; Stringer & Starnes 2020; Stringer et al. 2020a; Stringer et al. 2022; Stringer et al. 2023) have demonstrated that Neogene otoliths can produce very precise paleoenvironmental determination based upon specific fish taxa with detailed fisheries data on their range, habitat preference and distribution, life mode, abundance, and age distribution (based upon the size of the sagittae). The vast majority of otoliths from Neogene strata may be assigned to extant species and increase their value in producing very accurate insight into paleoenvironmental conditions.

The primary hypothesis in employing fish otoliths to perform paleoecological analysis is to obtain detailed information on the preferred habitats of extant fishes as comparable analogues (a uniformitarian approach). In the Neogene, this hypothesis performs extremely well as the analogues are either the same species or closely related, comparable species. However, this becomes more difficult and tenuous in older geologic strata. The overarching concern of the uniformitarian approach and the use of fossil otoliths, actually with all fossils, is the limitations that must be considered and evaluated as the process is extended into deeper geologic time. It must be carefully addressed to determine at what point or age does this principle cease to be accurate. Although the age of the Ardath Shale and Mission Valley Formation otolith assemblages is middle Eocene, the authors believe that it is still possible to ascertain generalized paleoecological parameters based on the otoliths. The paleoecological interpretations must be made within limitations and with the recognition that the accuracy will not match that possible in the Neogene. Furthermore, interpretations of paleoenvironments should be scrutinized and compared to other paleoecological parameters, such as foraminifera, ostracodes, and various types of invertebrates, as well as paleogeographical (i.e., maps) and sedimentological data. This type of protocol has been utilized with fossil otoliths as old as the Late Cretaceous as demonstrated in Stringer et al. (2016), Stringer et al. (2018), Stringer et al. (2020b), and Stringer & Schwarzhans (2021). It should also be noted that the classification of environments for paleoecological studies has been utilized for almost 60 years in the USA and was based initially on studies of extant foraminifers and ostracodes. The major environments included nonmarine (continental), transitional (high tide to low tide), inner shelf (0–20 m), middle shelf (20–100 m), outer shelf (100–200 m), upper slope (200–500 m), lower slope (500–2000 m), and abyssal (>2000 m) (Tipsword et al 1966). Unless otherwise indicated, these designations will be utilized in the discussion of paleoenvironments.

Investigations have shown that the families of bony fish families as discerned by otoliths can also be valuable in ascertaining general paleoenvironmental parameters. This has been demonstrated in the the Gulf and Atlantic coastal plains (Stringer et al. 2020b; Stringer & Schwarzhans 2021; Stringer & Sloan 2023). While species may show changes in their preferred habitats with time, changes at the family level appears to be more stable as far as general habitats (freshwater, brackish, and marine). The analysis of the families in a formation as indicated by otoliths is based on the distribution and ecological preferences of extant fish families as well as climatic data and bottom sediments.

An analysis of the otolith-based fishes represented in the Ardath Shale indicates that 44 families are present. However, many of these families compose an extremely small percentage of the total assemblage. Therefore, adjustments were made to mitigate the effect of the otoliths with extremely small numbers in the general interpretation of major habitats. Only the families that constituted 0.1% or greater were considered in the interpretation. With this guideline, 26 of the 44 families were eligible for the evaluation of possible general environments (fresh water, brackish, and marine). However, it should be noted that one family indeterminate met the guidelines to be considered, but obviously, no information is available. So, the actual number of families employed was 25 and are shown in Supplementary Tab. 3. In addition to the general distribution of the families, general climatic ranges are also included for each family. Pertinent information on the habitats and climatic preferences of extant families were obtained from a variety of sources including Robins and Ray (1986), Cohen et al. (1990), Hoese and Moore (1998), McEachran and Fechhelm (1998, 2005), Nelson et al. (2016), and Froese and Pauly (2023).

The same procedure was employed with the families of fishes represented by otoliths in the Mission Valley Formation. There were a total of 23 families indicated by otoliths in the Mission Valley Formation. However, only 13 of these families met the criteria of constituting at least 0.1% of the total otolith assemblage for the formation. The analysis of the fish families in the Ardath Shale and the Mission Valley Formation reveals that the two formations appear to represent paleoenvironments that were quite different from one another. It could be presumed that since the two formations had 29 shared taxa that the paleoenvironments were probably similar. However, as pointed out in the percentage similarity analysis, 24 of the shared taxa each represented less than 1% of the total assemblage. The resulting percentage similarity between the two formations was only 17.18%. Therefore, the two formations representing different paleoenvironments is expected.

In the Ardath Shale, all of the fish families represented by otoliths have representatives in the marine habitat, and it appears to represent a fully marine environment. There are notably less families with representatives in fresh water and brackish. This most likely indicates that the Ardath Shale is fully marine. The Mission Valley Formation also has fish families that are all found in the marine habit. However, in contrast to the Ardath Shale, the fish families in the Mission Valley Formation have, except for one, representatives found in brackish habitats (92% of the families have brackish-water forms). This is an indication that the Mission Valley Formation is a shallower marine environment possibly influenced by nearby brackish conditions during its time of deposition.

Comparison of the fish families represented by otoliths in the Ardath Shale to fishes described by Page et al. (2013) as presently occurring in the United States (both Atlantic and Pacific), Canada, and Mexico (marine species to a bottom depth of 200 m), there are ten families in the Ardath Shale that are not reported. Examination of these families indicates two primary reasons for their absence from Page et al. (2013). Five of the families' distributions do not include the US, Canada, or Mexico (Protanguillidae, Citharidae, Trichnotidae, Lactariidae, and Scombropidae). For example, the Scombropidae is found in the Eastern Atlantic and the Indo-West Pacific (Nelson et al. 2016). The other four families (Gonostomiatidae, Sudidae, Diretmidae, and Bathyclupeidae) appear to be deep water in distribution and found deeper than 200 m (outer shelf) and are not included in Page et al. (2013). However, when the otoliths of the Mission Valley Formation are compared to Page et al. (2013), only three families are not reported (Protanguillidae, Menidae, and Lactariidae). These three families are absent due to their present-day geographic distributions. It is important to note that none of the Mission Valley Formation are absent due to being found deeper than 200 m. The Mission Valley Formation shows more similarity to present-day families in the Atlantic, Gulf Coast, and Pacific along the coasts of the USA and Mexico according to Page et al. (2013).

One of the most compelling differences in the Ardath Shale and Mission Valley Formation otolith assemblages are the families that appear to represent deeper-water conditions in the Ardath Shale. These families, which are totally absent in the Mission Valley Formation, are the Gonostomatidae, Sternoptychidae, Myctophidae, Trachichthyidae, Bathyclupeidae, and tentatively the Diretmidae. The extant representatives of these fish families are meso- to bathypelagic. However, it is important to note that these families are relatively rare in the Ardath Shale as indicated by their percentage of the total assemblage: Gonostomatidae (0.28%), Sternoptychidae (0.83%), Myctophidae (1.50%), Trachichthyidae (0.02%), Bathyclupeidae (0.12%), and possibly the Diretmidae (0.24%). However, there are families in the Ardath Shale that represent fish taxa that are indicative of deep-water marine forms, i.e., greater than 200 m as a minimum depth. Nolf and Brzobohaty (1992) stated that marine assemblages that were free or almost free of myctophids indicate a neritic environment with little open oceanic influence. Therefore, the presence of myctophids in the Ardath Shale, as well as several other deeper-water families indicative of at least outer shelf or deeper depths, points to open oceanic influence (see also below). However, the exact distribution of the Eocene deep-sea families is not fully understood, although progress has been made (Schwarzhans 2019). The impact of the Paleocene-Eocene Thermal Maximum (PETM) and the migration of fishes from the shelf to deep-sea habitats (Thomas et al. 2000; Thomas 2003, 2007) are discussed later in this study.

Generalizations regarding the climatic conditions in the Ardath Shale and the Mission Valley Formation are also possible based on the data from extant fish families. Examination of the Ardath Shale assemblage indicates that all of the families represented by otoliths could be found in tropical conditions. However, all but three of the families could be found in subtropical. So, while the strongest indication is for tropical conditions, there is some evidence for subtropical. The Mission Valley Formation points to a very similar climatic setting with all of its families represented by otoliths found in tropical conditions. Furthermore, like the Ardath Shale, there are suggestions of possible subtropical with all of the families except for two in this climatic range.

Stratigraphic considerations in paleoenvironmental interpretations

The stratigraphic relationships and geologic age of the various Eocene formations in southern California are complex and abstruse. The age and relationship of the Ardath Shale and the Mission Valley Formation are pertinent to a discussion of the differences in the paleoenvironments of the two formations. Samples of a bentonite from the Mission Valley Formation indicated a single-crystal $^{40}Ar/^{39}Ar$ radiometric age of 42.83 ± 0.24 (Walsh et al., 1996). However, the age was given as slightly younger at approximately 42.4 –43.0 Ma in the same publication (fig. 15) based on comparisons to the Geomagnetic Time Scale. Walsh et al. (1996) contends that more credence should be given to the $^{40}Ar/^{39}Ar$ radiometric age of 42.83 ± 0.24. Either of these ages place the formation clearly in the middle to late middle Eocene. Numerous studies including groups such as planktonic foraminifers and coccoliths as well as polarity investigations placed the Ardath Shale in the early middle Eocene (Berggren et al. 1995). In a magnetostratigraphic study, Walsh et al. (1996) placed the Ardath Shale at 47.0–47.5 Ma, which would be in the early middle Eocene. Therefore, based on these studies, the Mission Valley Formation would be approximately 4 million years younger than the Ardath Shale. Although somewhat different in geologic age, the two localities of the Ardath Shale and Mission Valley Formation that produced the otolith specimens for this study are only separated by 14.8 km in an east-west direction and only 2.1 km in a north-south direction in southern California. Therefore, latitudinal separation is not a major consideration in differences of the two localities.

Paleoenvironmental conditions indicated by other fossil groups present

The general paleoenvironmental parameters ascertained from the analysis of the otolith assemblages of the Ardath Shale and the Mission Valley Formation are compared to a variety of other, independently derived paleoecological determinations such as other fossil groups (especially invertebrates), paleogeography, and sedimentological data. Several studies have delineated that the Ardath Shale represents an off-shore shelf facies (Kennedy & Moore 1971; Welton 1979). The formation has yielded diverse and well-preserved assemblages of marine microfossils, macroinvertebrates, and vertebrates (City of San Diego 2007). Gibson (1971) stated that benthic foraminifers indicated paleo-water depths of 500 m to possibly 1500 m. Teichert and Stanley (1975) in a study of a cephalopod mandible from the Ardath Shale reported a variety of fish remains, including shark and ray teeth as well as otoliths. The authors noted that in written communication (1974) that J. Fitch believed the Ardath Shale represented a deeper water environment and was deposited in depths between 300–500 m. Fitch noted that he based his reconstruction on the number of mesopelagic and bathypelagic fishes represented by otoliths in the assemblage.

The literature indicates that paleontological investigations have been more frequent in the Mission Valley Formation. Deméré et al. (1979) recovered a fauna from the Mission Valley Formation 0.33 km south-southeast of LACM 59708 in the same fossil-bearing horizon, that they contended represented a mixture of assemblages derived from two primary habitats. These were a sandy substrate characterized by a moderate- to high-flow regime and dominated by infaunal suspension feeders and a muddy substrate characterized by a low-flow regime and populated largely by infaunal deposit feeders. The composite fauna was interpreted as representing deposition under normal marine conditions in a shallow, near-shore, protected series of habitats. These habitats could include a bay, estuary mouth, or marine lagoon according to Deméré et al. (1979), but the exact habitat could not be determined.

Kern (1978) provided strong evidence of the paleoenvironment of the Mission Valley Formation based on his study of two ichnospecies. He compared the modern distribution of associated foraminifers, ostracodes, and mollusks as well as carbonized algal fragments. He concluded that the associations of the various groups suggested deposition in the inner shelf and possibly as shallow as a few tens of meters. Several factors, primarily shell distribution, suggested moderate current action. The composition and diversity of the invertebrate assemblage in the Mission Valley Formation indicated that salinity and other physical and chemical parameters were within the normal for shallow marine environments. In his study of the fossil fish remains (shark and bony fish) from the Mission Valley Formation, Roeder (1991 and references therein) noted that foraminifers, coccoliths, ostracods, trace fossils, mollusks (primarily bivalves and gastropods), and crustaceans have been recovered and studied from the formation.

Both the Ardath Shale and Mission Valley Formation had strong indications of tropical conditions and possible warm subtropical based on the distribution of the families of fishes represented by otoliths. This agrees well with the projections of Markwick (2007) for southern California for the middle Eocene. Numerous peats and coals are known from this area during this time interval (Markwick, 2007; fig. 40). Modern climate proxy studies found that plant production that could result in peat and/or coal was a function of the percentage of months with mean temperatures > 10^0 C and precipitation of > 40 mm. It also indicated that 80–100% of plant growth occurred within these parameters.

Comparison to previous paleogeographic interpretations

Examination of the paleocoastline map presented by Smith et al. (1994, map 7) for the middle Eocene (Bartonian–Lutetian, 45 Ma) indicates marine conditions but also the proximity of transitional and non-marine environments. Likewise, a scrutiny of Scotese (2014; maps 11–12) demonstrate that marine and terrestrial environments were possible during the late middle Eocene (Bartonian, 38.8 Ma) and the early middle Eocene (Lutetian, 46.6 Ma) for southern California. Thus, the indications of a shallow marine Mission Valley Formation and a deeper Ardath Shale would certainly be feasible. The paleogeographic maps of Blakey (2020) of the Eocene (50 Ma) and Eocene (40 Ma) are also supportive of the paleoenvironment based on otoliths. The Eocene (50 Ma) map, which is closer in age to the Ardath Shale, shows marine waters with indications of deeper waters present at and west of the Black's Beach locality. The Eocene (40 Ma) map, which would be closer in age to the Mission Valley Formation, indicates marine waters but terrestrial (land) is very close to the Miramar Reservoir locality. This would be congruent with the previous findings of Kern (1978) that stated that the Mission Valley Formation is nonmarine in its eastern exposures and marine in its westernmost exposures in southern California (San Diego area). Deméré et al. (1979) described the marine portion of the Mission Valley Formation as a "brief marine transgression with the otherwise regressive and predominantly nonmarine Poway Group."

Comparison of sedimentary compositions of the formations

Another consideration is the difference of the two formations is shown in the sedimentary composition. The Ardath Shale at its type locality consists of a uniform, weakly fissile olive-gray, silty shale (Kennedy & Moore 1971). The composition of the portion of the Mission Valley Formation from which the otoliths were obtained is typically a soft and friable, light olive gray, fine to medium grained sandstone consisting mostly of quartz and potassium feldspar. It is a predominantly marine sandstone unit, but the underlying and overlying formations are non-marine.

Pinet (2014) presents a model prediction of shelf sediments in which the sediments range from sand in the shallow water to mud in the deeper water toward the shelf break. The sand sedimentation begins essentially at the shoreline, while mud sedimentation is shown as beginning at approximately 55 km from land. The composition of the Mission Valley Formation would indicate shallow-water deposition in the inner shelf occurring at less than 15 km from land. The composition of the Ardath Shale would indicate deeper-water deposition in the outer shelf or shelf slope and at least 55 km from land. Obviously, there are a multitude of factors that can influence this model, but it provides general evidence of the depositional paleoenvironments of the two studied formations.

Unlike at the type locality, the Ardath Shale at Black's Beach was deposited in a canyon-fan complex at water depths ranging from 200 to over 1000 m water depth that was cut into the shelf (Lohmar & Warme 1978, 1979; Lohmar et al. 1979; May 1982, 1985; Stright et al. 2014). Collection data communicated by the late M. Roeder and confirmed by the late R. Huddleston indicate that the otoliths were collected from sediments believed to represent a proximal channel fill according to May (1982) or in a shelf-slope position. Shelf currents may have fed the channel system with sediments from the adjacent outer shelf at 100 to 200 m water depth (Lohmar et al. 1979). Such a scenario dominated by the redeposition of sediment and contained fossils from the outer shelf downslope in a mud-rich channel system could explain the dominance of deep neritic fishes in the otolith assemblage, the relatively low percentage of potential meso/bathypelagic fishes, and the nearly complete absence of bathydemersal fishes.

Summary of paleoenvironments for the two formations

A compilation of the parameters enumerated and discussed above indicates that the paleoenvironments of the Ardath Shale and Mission Valley Formation differ. Even the diversity, specifically the richness (number of taxa), hints at the dissimilarity of the formations. The Ardath Shale has 83 taxa identified to at least genus or species, whereas the Mission Valley Formation has only 37 taxa. Furthermore, the three most abundant species in each of the formations are different, which is certainly significant. One of the most telling differences is shown by the percentage similarity measurement that indicates a similarity, or lack thereof, of only 17.18%. This illustrates that in spite of 29 shared taxa between the two formations that the assemblages are really not meaningful similar as 24 of the 29 shared taxa each represent less than 1% of the total number of specimens.

One of the most diagnostic indicators of the general environments of the two formations is the analysis of the distribution and climatic preferences of the fish families represented in each of the formations based on extant fisheries data. Based on 25 utilized families for the Ardath Shale, 100% of them would be found in marine waters, but 32% of them would not be represented in brackish waters. The Mission Valley Formation also has 100% of its families represented in marine water, but all but one of its families could also be found in brackish water, which means that 92% of the families could be found in brackish waters. This would be an indication of much shallower marine waters. Furthermore, there are five families in the Ardath Shale that are reported as deep-water forms (mostly meso/bathypelagic fishes, i.e., Gonostomatidae, Sternoptychidae, Myctophidae, Diretmidae, and Bathyclupeidae) (> 200 m) by Page et al. (2013). Although these families are not abundant in the percentage of specimens, they are still indicative of deeper water oceanic influences. There are no families present in the Mission Valley Formation indicative of deeper waters. A prominent and meaningful indicator of the paleoenvironments is the presence of the Lactariidae. The present-day Lactariidae are found in tropical environments primarily from 15–100 m in depth (inner and middle shelf). The Lactariidae represent well less than 1% of the total assemblage of the Ardath Shale (0.39%). This is in great contrast to the 22.03% of the Lactariidae in the Mission Valley Formation. A lactariid is the second most abundant form in the Mission Valley Formation.

It is proposed that the original paleoenvironment of the Ardath Shale at Black's Beach is at the deeper portions of the outer shelf depths (200 m) and possibly greater than 200 m, perhaps at the upper portion of the upper slope. However, an allochthonous setting in a proximal fan sediment could imply a shallower paleobathymetry of the redeposited fossil content than was actually the case. The salinity is expected to be normal marine. Bottom conditions would most likely be soft and muddy substratum. The climatic conditions would be tropical with some evidence of subtropical. The paleoenvironment of the Mission Valley Formation is believed to be inner shelf to shallow middle shelf (0 –50 m in depth). The number of fish families with brackish water representatives could also indicate nearby brackish water habitats. The salinity is probably normal marine, but some minor fluctuations could have occurred. Bottom conditions consisted of a soft and sandy substratum. The climatic conditions are indicated as clearly tropical with some indications of warm subtropical. These interpretations of the Ardath Shale and the Mission Valley Formation are compatible with paleogeography indicated by Smith et al. (1994), Markwick (2007), Scotese (2014), and Blakey (2020). The proposed paleoenvironment of the Ardath Shale is also similar to that suggested by J. Fitch based on otoliths (300 –500 m in depth) in Teichert and Stanley (1975) description of an Eocene rhyncholite from California.

Comparison with middle Eocene otolith assemblages around the world

Ninety-six species of otoliths have been identified from the middle Eocene of southern California, thereof 84 identifiable to the species level (Supplementary). This compares to 106 species from the Eocene of the US Gulf Coast (Lin & Nolf 2022 and this work), 96 from the Eocene of New Zealand (Schwarzhans 2019a), 163 species from the Eocene of the Aquitaine Basin in South-West France (Nolf 1988; Lin. et al. 2016), more than 200 from the Eocene of northern and central European basins (estimated from Nolf 2013) and about 63 species from the Eocene of Pakistan, India, and Indonesia (Vorstman 1927; Nolf & Bajpai 1992). The otolith assemblage from the Eocene of California shows a relatively high degree of uniqueness when compared to other, equally well-known middle Eocene otolith-based faunas. Twenty-four of the 84 identified species (28.5%) do not show any relationship to taxa known from other regions. This comprises mostly otolith-based fossil genera established here and a few persistent ones: *†Huddlestonichthys* (Albulidae), *†Eophichthus* and *†Ipaimuraena* (Ophichthidae), *Acromycter* and *Uroconger* (Congridae), *†Progonostoma* (Gonostomatidae), *Polypnus* (Sternoptychidae), *†Alienocarapus* (Carapinae, Ophidiidae), *Diretmus* (Diretmidae), *†Avitamugil* (Mugilidae), *Peprilus*? (Stromateidae), *Cubiceps* (Nomeidae), *Scombrops* (Scombropidae), *†Torreichthys* and *†Pseudolabrax* (Serranidae), *†Micropomadasys* (Haemulidae), *Scorpaenodes* (Scorpaenidae), *†Liparomorphus* (Liparidae?) and the enigmatic incertae sedis taxa *†Fitchichthys* and *†Plesiolithus.*

Fifteen species (17.8%) are shared with the Eocene of the US Gulf Coast and another eight (9.5%) are closely related (together 27.3%) (Supplementary Tab. 1, Fig. 21). Across the North Atlantic, 11 species (13.1%) are shared with the Aquitaine Basin (plus another eight related ones amounting to 22.6% together) and 10 species (11.9%) (plus another 13 related ones amounting to 27.4% together) with Eocene Basins in central France, England, Belgium, and Germany (Fig. 21). Across the Pacific three species (3.6%) (plus another eight related ones amounting to 13.1% together) are shared with New Zealand (Fig. 21) and none with the Indo-West Pacific. Of the three shared species with New Zealand, two are widely distributed, probably cosmopolitan (*Genartina bambergi* and *Rhynchoconger eocenicus*) and only *Pseuaequalobythites biplex* has so far only been found in the Pacific arena. This is a clear indication that faunal exchange across the wide Eocene Pacific Ocean was quite restricted.

The correlation of shared species from California with the US Gulf Coast, the Aquitaine Basin

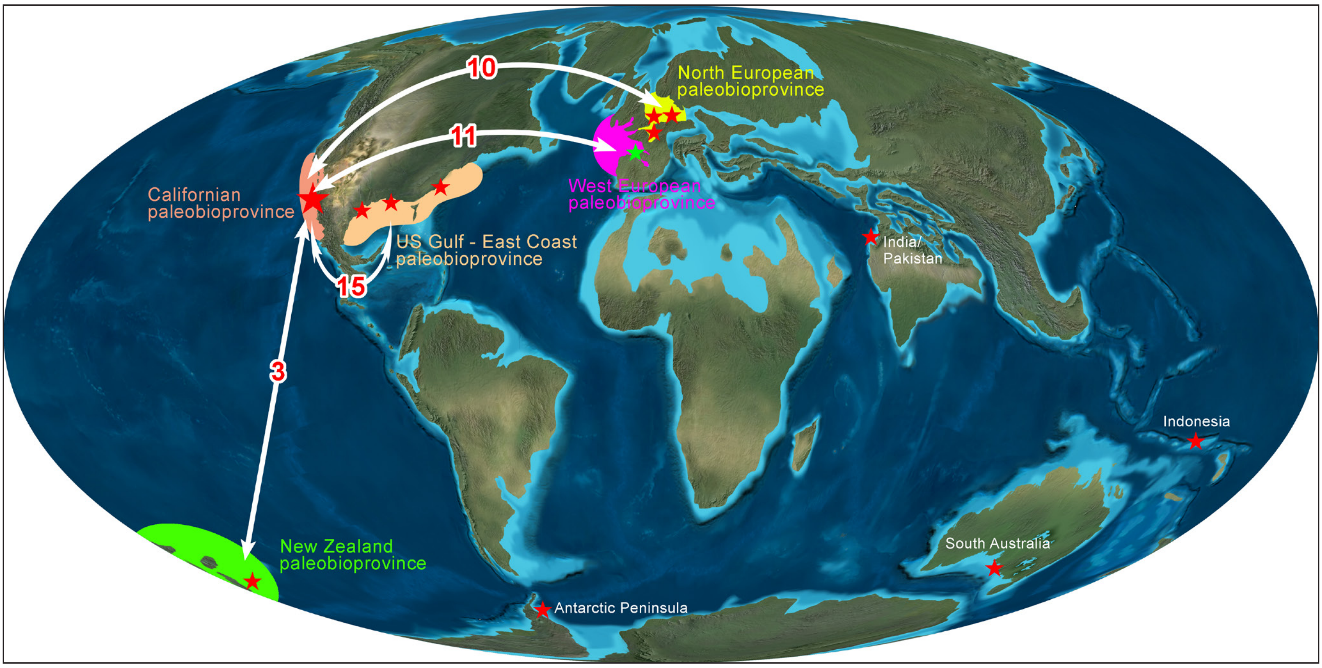


Fig. 21 - Eocene paleobioprovinces of marine fishes based on otolith occurrences (stars). One star can include several localities. Californian localities highlighted. Arrows and numbers indicate number of shared species with Californian Eocene. Paleogeographic map based on Blakey (2021), 40 Ma.

in South-West France, and the northern and central European basins, however, harbours a number of surprises. Only a single species, the ubiquitous *Pterothrissus umbonatus* is shared between all four regions. One species is shared with the US Gulf Coast and the northern European basins (*Muraenesox websteri*), one with the US Gulf Coast and the Aquitaine Basin (*Brotula aquitanica*), and one with the Aquitaine Basin and the northern European basins (*Centroberyx eocenicus*). This documents that in fact all four regions have rather distinct faunal assemblages in teleosts that warrants some closer inspection and analysis.

The US Gulf and Atlantic coastal plains are the nearest region to southern California although already relatively separated from each other by a long southward extending peninsula according to paleogeographic reconstructions (Fig. 21). This fact may already explain a certain degree of faunal differentiation between both areas. However, there must have been some additional aspect having been responsible for such a low correlation since the equally distant US Gulf and Atlantic coastal plains otolith assemblages are much more similar (Lin & Nolf, 2022). Additional aspects at play that may have caused faunal separation could have been different ocean circulation patterns in the North Atlantic and the Northeast Pacific and differences in the environmental setting. Also, the extent and emergence of the Floridian peninsula are major factors that would affect faunal interchange between the Atlantic Coastal Plain and the Gulf Coastal Plain (Stringer et al. 2020) The Eocene sediments onshore of the US Gulf Coast in particular are dominated by a very wide, shallow, gently dipping, clastic and passive shelf with local significant river discharge. The southern Californian Eocene on the other hand was deposited on a narrow shelf with a steep profile from the shore to the base of the continental slope across a rather short distance and intersected by submarine canyons (e.g., Lohmar et al. 1979; Stright et al. 2014). These are fundamentally different macroenvironments that attracted different kinds of fishes. For instance the US Gulf Eocene contains a large variety of the Sirembini (Ophidiidae) and Sciaenidae, which are both totally lacking in California. Conversely, the Californian Eocene contains a number of presumably open marine and bathyal fishes like Stomiiformes, Myctophidae, and Bathyclupeidae that are not known from the Eocene of the US Gulf Coast. Interestingly, even in shallow-marine neritic fishes, there are many significant differences. For example, very few of the many Californian species of the Congridae, Ophidiidae, Serranidae, or Haemulidae are shared with the US Gulf Coast Eocene.

The position of the Black's Beach site on the continental edge and slope is comparable to that of certain localities in the Aquitaine Basin of South-West France from which Lin et al. (2016) described a rich time-equivalent otolith association (Fig. 21). The following taxa are exclusively shared between the two areas: *Platygonostoma gibbsi, Protaulopus pseudolestidiops, Eomyctophum cyrano, Bregmaceros*? *rappei, Pauxillibrotula dolinorum, Trachichthys melamphaoides, Bathyclupea arribaoutensis*, and *Porrolapis ornatissimus*. None of them occur at the Miramar Reservoir site. This distribution pattern indicates that the species in question might have been oceanic/pelagic fishes with a wide regional distribution since they were missing from shallow-water environments. Also, these species represented clades that today live meso- to bathypelagic, with the exception of *Pauxillibrotula* and *Porrolapis* of which the relationships are tentative or unresolved. Conversely, there are no obvious shallow-water species exclusively shared between the Eocene of California and the Aquitaine Basin, and the remaining three shared species (*Pterothrissus umbonatus, Brotula aquitanica*, and *Centroberyx eocenicus*) are also known from other basins. Lin et al. (2016), however, recorded a significantly larger number of potential oceanic/pelagic fishes from the Aquitaine Basin, e.g., of the families Opisthoproctidae, Sternoptychidae, Phosichthyidae, Scoeplarchidae, Evermannellidae, Alepisauridae, Neoscopelidae, Melamphaidae and Zeniontidae. These are all meso- to bathypelagic groups today and it is possible that they were already living in similar environments during the Eocene. No representatives of any of these families have been found in the Californian Eocene. Furthermore, Lin et al. (2016) also described otoliths of several families that today occur bathydemersal, e.g., Macrouridae, Bathygadidae, Trachyrinchidae, Chaunacidae, and Ogcocephalidae. It is not known in as much representatives of these families were already adapted to a bathybenthic live style like they are today, and there are instances where species of these families have been found commonly in shallow water nearshore environments during the Eocene (Schwarzhans et al. 2017a). Nevertheless, it is notable that no fishes of these families have been found in the Californian Eocene and there are no indications of any potentially bathydemersal fishes being represented in the Ardath Shale. The following demersal fish groups are dominant in the Californian Eocene: Congridae, Ariidae, Ophidiidae, Bythitidae, Berycidae, Soleidae, several perciforms, spariform, and scorpaeniform families. Even though several of those today contain bathydemersal fishes, e.g., the Congridae, Ophidiidae and Bythitidae, they were common and highly diverse groups on the shallow warm shelf environments during the Eocene (see below), and it is not known at present if and which taxa in these groups may have already migrated into the deep sea.

The number of fish species exclusively shared between the Eocene of California and in the shallow-water central and northern European basins is expectedly small (Fig. 21): *Arius*? *planus*, *Paraulopus* cf. *davisi, Hoplobrotula robusta, Calamopteryx*? *moelleri*, and *Eobidenichthys symmetricus*. The absence of these species in the shallow-water environments of the Eocene in southern and eastern USA could be related to environmental adaptations not met in the sampled localities there. It would otherwise be difficult to explain their punctuated distribution. There are no shared species with other, leaner Eocene otolith assemblages known from further distant regions, such as South Australia (Schwarzhans 1985) or Antarctica (Schwarzhans et al. 2017a).

Middle Eocene paleobiogeographic analysis of otolith assemblages

As discussed above in more detail, middle Eocene otolith associations are now known from several widely separated regions on Earth, namely various basins in Europe, basins along the US east and south coasts, California, various basins in the Indo-West Pacific (Pakistan, India, Indonesia), New Zealand, South Australia, Antarctica and a few isolated finds in the Caribbean (Casier 1958) and West Africa (Frost 1926). A picture is emerging from these otolith assemblages of a highly regionalized fish fauna at least in the neritic zone of the oceans, like today. Thus, each of the regions listed above characterizes a specific middle Eocene paleobioprovince (Fig. 21). The exchange of shallow-water fish species along the American and North Atlantic shores apparently must have been rather restricted despite the presumably more even latitudinal temperature distribution during the middle Eocene warm-house and the closer paleogeographic situation and connection (Fenton et al. 2023). It must be noted though that the otolith associations cannot be compared with fish faunas based on articulated skeletons because of the scarcity of otolith in situ finds in Eocene fossils. This is particularly important in respect to the largest known Eocene skeleton-based fish fauna from the Monte Bolca Lagerstätte in northern Italy (see below), which represents a reef-associated environment that so far has not been represented in otolith assemblages.

The middle Eocene fish fauna from California described here shows only a moderate correlation of today's highly endemic Californian fish fauna. Typical present day endemic groups like the Embiotocidae and many of the scorpaeniform families Bathymasteridae, Hexagrammidae, Stichaeidae or Zaniolepididae have not been found. In fact, the Scorpaeniformes represent one of the most diverse clades today in the North Pacific and along the Northwest American coast. They are typical cold-water fishes, and their present distribution in the North Pacific is governed by water temperature and the cold California Current off California (Millar 2012). The California Current probably originated during the Mid-Miocene Climate Transition after 15 Ma and strengthened during the Late Miocene-Early Pliocene Biogenic Bloom between 7 to 4 Ma (Millar 2012). Pleistocene otolith assemblages recorded from California are very similar to today's fauna (e.g., Fitch 1966, 1970). However, the Californian Eocene fish fauna described here contains only a few scorpaeniforms, albeit more than any of the other middle Eocene otolith-based faunas known so far, and in general bears very little semblance to the present-day fauna in the region. The middle Eocene Californian otolith-based fish fauna is a typical warm-water association similar in its principal composition with those from the southern and eastern USA or the European basins with abundant shallow-water ophidiiforms, and a rich anguilliform and perciform s.l. component. The differences between the individual regions is mainly on the species and to a lesser degree on the genus level. The Californian Eocene contains a reasonable proportion of taxa related to other taxa in those other regions which we take as an indication of allopatric, geographically separated speciation. Only 30 species (31%) find no equivalents in faunas of any of the other regions. We therefore propose a Californian paleobioprovince of fishes during the (middle) Eocene that was related to a Northeast American, Aquitanian, and North European paleobioprovince during the time but was unrelated to the present-day Californian bioprovince (Fig. 21).

PHYLOGENETIC ANALYSIS AND EVOLUTIONARY INTERPRETATION

Comparison of middle Eocene otolith and skeleton data of teleosts

Articulated skeletons and isolated otoliths are subject to different taphonomic boundary conditions relevant for their fossilization. The preservation of articulated skeletons depends on specific and rather rare taphonomic settings preventing the complete decay of the carcasses due to biological, chemical, or physical factors. Preferential conditions for the fossilization of articulated fish skeletons are, for instance, in the presence of anoxic conditions at the sea bottom, rapid sedimentation, or mass mortality events. These conditions favor fossilization of neritic fishes as articulated skeletons and is disadvantageous for demersal fishes. Otoliths on the other hand are thought to have mainly entered sediments through excretion of predators and scavengers having feasted on fish (Nolf 1985; Schwarzhans 2019a). In addition, otoliths are primarily preserved in sediments deposited under well-oxygenated conditions. Therefore, the fossil otolith record is dominated by small "prey fish" and demersal fishes. As a result, the fossil record of articulated skeletons and isolated otoliths overlaps only to a certain extent and in fact complements each other in a rather large proportion.

Based on these observations and assumptions, it is clear that there is a limited amount of Lagerstätten with articulated fish skeletons known from the Eocene which can be compared with the otolith-based fauna from the middle Eocene of California. The most prolific such Lagerstätte rich in articulated skeletons is the one from the late early Eocene of Monte Bolca in Italy (Bannikov 2014; Carnevale et al. 2014). Since no otoliths in situ are known from any Monte Bolca fishes, and in fact, the knowledge of otolith in situ is generally poor for the Eocene (Schwarzhans et al. 2018) any comparison can only be based on genus or family level.

When comparing the 217 taxa of teleosts listed by Carnevale et al. (2014) from Monte Bolca based on articulated skeletons with the 96 otolith-based taxa from the middle Eocene of California a number of observations can be made, which are mostly not geographically related. First of all, there are species-rich groups in Monte Bolca, which are totally missing in California, e.g. Osteoglossiformes (3 species), Clupeiformes (3 species), Lophiiformes

(6 species), Atheriniformes (4 species), Beloniformes (3 species), Syngnathiformes (28 species), and Tetraodontiformes (15 species), totaling 62 taxa or 28.5% of the fauna of Monte Bolca not represented in any way by otoliths in California. The reason for this is manifold. In the case of the Syngnathiformes it is probably related to their otoliths being extremely small and therefore generally lacking in the fossil record. Clupeiform and tetraodontiform otoliths are small and fragile and therefore usually underrepresented in otolith-based assemblages. In fact, there are a few fragmentary clupeiform otoliths known from the Black's Beach site, which, however, cannot be identified even to family level. Conversely, there are a number of groups represented in the otolith assemblage of California that are missing from the skeleton-based fauna of Monte Bolca or are very rare, e.g. Albuliformes (5 species), Stomiiformes (3 species), Myctophiformes (3 species), and Ophidiiformes (17 species versus 1 species). The discrepancy in respect to Albuliformes, Stomiiformes and Myctophiformes is probably environmentally related (open marine versus near reef), but the Ophidiiformes is related to differences in the taphonomic boundary conditions (see above) and is subject of chapter "the flourishing of the Ophidiiformes in the Eocene" below.

Therefore, we now focus on those groups where there is a considerable overlap and potential for parataxonomy. Such groups are primarily the Anguilliformes (16 species in Monte Bolca and 15 species in California) and the Perciformes sensu latu (sensu Nelson 2006) with 119 species in Carnevale et al., 2014 and 33 species in California (orders Carangiformes, Scombriformes, Trachiniformes, Perciformes, Spariformes, Caproiformes, Scorpaeniformes, Blenniiformes, and Bathyclupeidae). The match in Anguilliformes is the closest. In Monte Bolca, nine anguilliform families and one group of Anguilliformes incertae sedis are represented (Carnevale et al. 2014). Five of the nine anguilliform families are considered extinct; the most diverse family is the Congridae with four species. The otoliths of the Californian Eocene are placed in six families, none of which are extinct, and again the Congridae are the most diverse with six species. Thus, the diversity of the Congridae is congruent between both data sets. The difference of no fossil family recognized in the Californian Eocene is a reflection of otolith researchers not nominating fossil fish families purely on otolith evidence. In fact, some of the fossil genera described from otoliths from the Californian Eocene could represent extinct anguilliform families, but this will only be possible to identify when otoliths in situ become available.

A very special case is the diversity of the Perciformes s.l. in Monte Bolca. The Monte Bolca Lagerstätte was deposited in a lagoon not far from a reef according to Papazzoni et al. (2014) although no direct evidence of a reef is found in outcrops. Nevertheless, the perciform s.l. composition contains a significant number of morphotypes pointing to a nearby reef environment, and Bellwood (1996) and Bellwood & Wainwright (2002) considered the teleosts from Monte Bolca to represent "the earliest clearly defined evidence of a coral reef fish assemblage." It is therefore not surprising that the majority of the perciform families observed in Monte Bolca are not mirrored in the clastic shelf environment of the middle Eocene of California. The shared families are Acropomatidae, Carangidae, Menidae, Sparidae, and Caproidae/Antigoniidae. Even among those, only the Sparidae match in diversity and abundance whereas the Acropomatidae are much more important in the Californian Eocene than in Monte Bolca. Families with a significant diversity in Monte Bolca such as Apogonidae, Lutjianidae, Pomacentridae, Labridae, Siganidae, Acanthuridae, or Scombridae are missing in the Californian Eocene. Conversely, families common in the Californian Eocene seem to be missing in Monte Bolca, such as Ambassidae, Serranidae, Haemulidae, Malacanthidae, and Scorpaenidae. However, some of these representatives are poorly defined as members of the respective extant families and in the light of the many extinct acanthomorph families recorded from Monte Bolca could potentially relate to some of those. Nevertheless, we postulate that much of the difference in the composition of the perciform s.l. community in Monte Bolca and the California Eocene is related to differences in the paleoenvironment.

Another aspect of difference between the two Lagerstätten is the fact that almost all fishes described from Monte Bolca are allocated to fossil genera even though in general they exhibit a rather modern appearance (Carnevale et al. 2014). This compares to 40 recognized extant genera in the Californian Eocene (of 76), i.e., 53%. Many of those, however, are of tentative nature representing a system of quasi-open generic nomenclature as suggested by Janssen (2012). In fact, 36 genera (47%) observed in the Californian Eocene are reliably considered related to extant genera. However, this may still be too large a percentage owing to the prevailing conservative concept in otolith research regarding defining new fossil genera.

Otoliths of deep-water fishes in the Middle Eocene

Our knowledge of otoliths from deep-water sediments of middle Eocene age or earlier is limited. The earliest otolith assemblages of true bathyal fish faunas have been recorded from the late middle Eocene (Bartonian) of New Zealand (Schwarzhans 2019a) and Italy (Schwarzhans & Carnevale 2022), the terminal Eocene (Priabonian) of New Zealand (Schwarzhans 2019a), and the early Oligocene (Rupelian) of Italy (Nolf & Steurbaut 1988, 1990, 2004). A small otolith association from late early Eocene bathyal environment has recently been studied from Denmark (Schwarzhans & Nielsen 2023). It includes a myctophid, a bregmacerotid, and an extinct ophidiid genus (Supplementary Tab. 4). There are, however, a number of otolith-based fish faunas that have been described from lower shelf to upper slope environments of Paleocene to middle Eocene age. These faunas undoubtedly contain otoliths of deep-water fishes of the time but in a mixture with shelf components. It is possible to some extent to recognize deep-water elements by comparison with lateral-time-equivalent shallow-water faunas where such fishes were missing. Such outer shelf/upper slope faunas have been described from the Paleocene of Austria (Schwarzhans 2012), and the early to middle Eocene of the Aquitaine Basin in South-West France (Nolf 1988; Lin et al. 2016). The fish fauna described here from the Ardath Shale falls in the same category. It was probably deposited on the upper continental slope in the vicinity of submarine canyon and fans, not far from the shelf break and therefore contains putatively bathyal elements that are missing from the shallow shelf environment of the Miramar Reservoir site, with a strong admixture of lower shelf elements.

The following species present in the Black's Beach site assemblage and missing in the Miramar Reservoir site that indicate deeper water are as follows: *Progonostoma torreyensis* (Gonostomatidae), *Platygonostoma gibbsi*, *Polyipnus apicalis* (both Sternoptychidae), *Eomyctophum cyrano*, *Diaphus roederi* (both Myctophidae), *Bathyclupea arribaoutensis* (Bathyclupeidae), *Trachichthys melamphaoides* (Trachichthyidae), and perhaps *Diretmus fidelis* (Diretmidae). These are all fish families that today live in meso- to bathypelagic environments. There are, however, no clear bathybenthic elements indicating that the water depth or paleoenvironment during sedimentation of the Ardath Shale was probably not suitable for them. The middle Eocene assemblage from the Aquitaine Basin described by Lin et al. (2016) is richer in putative offshore faunal elements such as Opisthoproctidae (2 species), Sternoptychidae (2 species), Phosichthyidae, Scopelarchidae (2 species), Evermannellidae, Neoscopelidae, Myctophidae (5 species), Macrouridae (genera *Bathygadus* and *Trachyrincus*), Melamphaidae, Diretmidae, and Bathyclupeidae. The small bathyal association of Italy described by Schwarzhans & Carnevale (2022) contained one Congridae, one Sternoptychidae, one Bregmacerotidae, and four Myctophidae. The late Eocene bathyal faunas of New Zealand (Schwarzhans 2019a) contained one Gonostomatidae, two Sternoptychidae, one Myctophidae, one Bregmacerotidae, one Macrouridae, two Ophidiidae of the genus *Neobythites*, one putative deep-water Platycephalidae, one putative Liparidae, and one putative deep-water Hemerocoetidae.

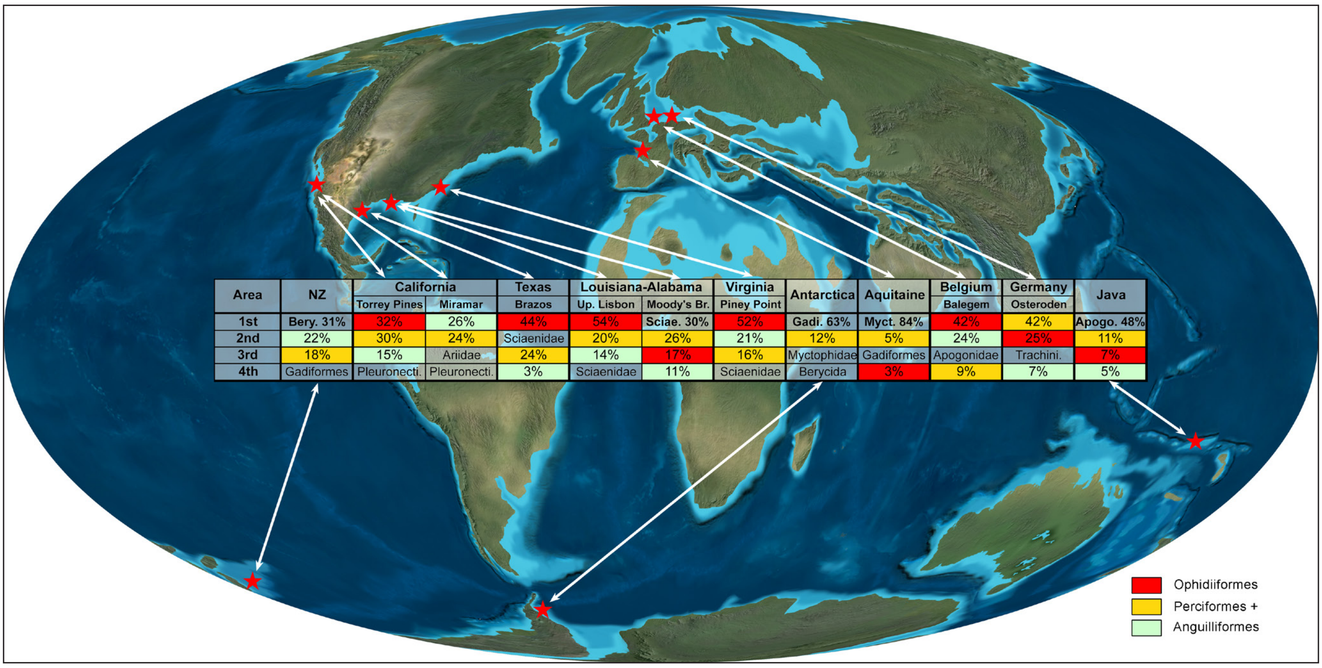
It is of course not entirely certain that fishes identified on the continental slope sediments from the Black's Beach site or the Aquitaine Basin were really deep-water fishes at the time like their modern counterparts. The correlation with relatively limited data from true bathyal environments, however, suggests that a good proportion may have been deep-water fishes already in the Eocene. Some fishes known from localities far apart in California and Europe and from deep shelf to offshore environments may be categorized as genuine deep-water fishes, e.g., *Platygonostoma gibbsi*, *Eomyctophum cyrano, Trachichthys melamphaoides, Bathyclupea arribaoutensis* or even *Pauxillibrotula dolinorum*. There are also numerous indications that certain fish groups that today live in deep water were living on the shelf during the Eocene. This is particularly evident in today's iconic mesopelagic Myctophidae or dominant bathybenthic Macrouridae and Ophidiidae (Schwarzhans et al. 2017a; Schwarzhans & Carnevale 2021). It was shown in late Eocene and Oligocene otolith assemblages of different depth environments in New Zealand how migration into depth occurred as a speciation event with related species one on the shelf and another one in the bathyal environment (Schwarzhans 2019a). It was also shown in the same study that during the late Eocene fish families ventured into deep water that were not able to successfully establish themselves there and presently contain only shelf fishes (e.g., Platycephalidae, Hemerocoetidae).

Evidence is accumulating that the migration of several groups of fishes began after the Paleocene-Eocene Thermal Maximum (PETM) which was thought to have had a severe impact on the composition of the deep-sea fauna (Thomas et al. 2000; Thomas 2003, 2007). The beginning of new recruits into the deep-sea during late early to late Eocene is in line with observations made with benthic foraminifera (Miller et al. 1992; Thomas 2007). Fish groups that began migrating into the deep-sea during the Eocene apparently were certain Myctophidae, Neoscopelidae, Bregmacerotidae, certain Macrouridae and Ophidiidae, Bathyclupeidae, and some Beryciformes. How many of those groups already populated the deep-sea prior to the PETM is unknown since the otoliths of many of them have not yet been found in the Paleocene, e.g., Myctophidae, Bregmacerotidae, and Bathyclupeidae. Neoscopelid and macrourid otoliths have been found in mid- to outer shelf deposits of Western Greenland (Schwarzhans 2004) and Denmark (Schwarzhans 2003; Schwarzhans et al. 2021). Ophidiiforms appear to have been almost exclusively shallow-water fishes during the early to middle Paleogene. Their rich and diverse appearance in the Black's Beach site for a good part is considered derived downslope from shallower environments since most of them are also known from shallow-water localities like the Miramar Reservoir site, the US Gulf Coastal Plain (Nolf & Stringer 2003; Lin & Nolf 2022), or European basins (Nolf 1971, 1973a, b). The rich deep shelf fauna from the Paleocene of Kroisbach, Bavaria, contains several stomiiform otoliths as well as rare *Trachichthys* and diretmid otoliths (Schwarzhans, 2012), which could qualify as deep-water elements. Stomiiforms indeed seem to have been adapted to deep water already in the Late Cretaceous (Carnevale & Rindone 2011) and may thus constitute the earliest persistent deepwater teleost fish group. The strongest recruitment phase of deep-water fishes seems to have taken place with the change of the halothermal to the termohaline deep ocean circulation leading to a better ventilation and oxygen supply in the deep-sea (Thomas 2007; Schwarzhans & Carnevale 2022). This was the time of many lineages of bathybenthic ophidiiforms and macrourids to migrate into the deep sea and the Myctophidae to move to a high-oceanic lifestyle (Nolf & Steurbaut 2004; Schwarzhans 2019a; Schwarzhans & Carnevale 2022). Supplementary Tab. 4 summarizes our current understanding of the migration phasing of fishes into the deep sea as interpreted from fossil otoliths.

THE FLOURISHING OF THE OPHIDIIFORMES IN THE EOCENE

The abundance of ophidiiform otoliths in the fossil record was recognized from the very early days in otolith research by Koken (1891). Subsequent studies, e.g., by Schubert (1916), Frost (1925, 1934), Stinton & Nolf (1970), Nolf (1971, 1973a, b, 1974), and Stinton (1977) have significantly increased the number of otolith-based ophidiiform species particularly in the Eocene. On the other hand, otoliths of extant ophidiiforms were poorly known. Today, ophidiiform fishes live mostly bathybenthic or cryptic, which has led to relatively few catches and a limited number of specimens housed in institutional collections. In the light of the tremendous diversity of extant Ophidiiformes with about 135 nominal genera (82 of them were considered valid) and 300 to 400 species reported by Cohen & Nielsen (1978), the meager knowledge of their otoliths triggered the interest of otolith researchers with the aim to better relate their fossil finds. These efforts resulted in two parallel conducted studies and publications documenting a large database of extant ophidiiform otoliths by Nolf (1980) and Schwarzhans (1981). Since then, numerous revisions of extant ophidiiform groups have led to the recognition of currently about 115 genera and more than 500 species (e.g., Nielsen 2002; Nielsen et al. 1999, 2009, 2012; Møller et al. 2004, 2005; Møller & Schwarzhans 2006, 2008; Schwarzhans et al. 2005; Schwarzhans & Møller 2007, 2011, 2021).

Nolf (2013) listed 139 fossil otolith-based ophidiiform species considered as valid. Since then, the number has risen to about 200, with nine new ophidiiform species alone described here from the



Area	NZ	California		Texas	Louisiana-Alabama		Virginia	Antarctica	Aquitaine	Belgium	Germany	Java
		Torrey Pines	Miramar	Brazos	Up. Lisbon	Moody's Br.	Piney Point			Balegem	Osteroden	
1st	Bery. 31%	🟥 32%	🟩 26%	🟥 44%	🟥 54%	Sciae. 30%	🟥 52%	Gadi. 63%	Myct. 84%	🟥 42%	🟨 42%	Apogo. 48%
2nd	🟩 22%	🟨 30%	🟨 24%	Sciaenidae	🟨 20%	🟨 26%	🟩 21%	🟨 12%	🟨 5%	🟩 24%	🟥 25%	🟨 11%
3rd	🟨 18%	🟩 15%	Ariidae	🟨 24%	🟩 14%	🟥 17%	🟨 16%	Myctophidae	Gadiformes	Apogonidae	Trachini.	🟥 7%
4th	Gadiformes	Pleuronecti.	Pleuronecti.	🟩 3%	Sciaenidae	🟩 11%	Sciaenidae	Berycida	🟥 3%	🟨 9%	🟩 7%	🟩 5%

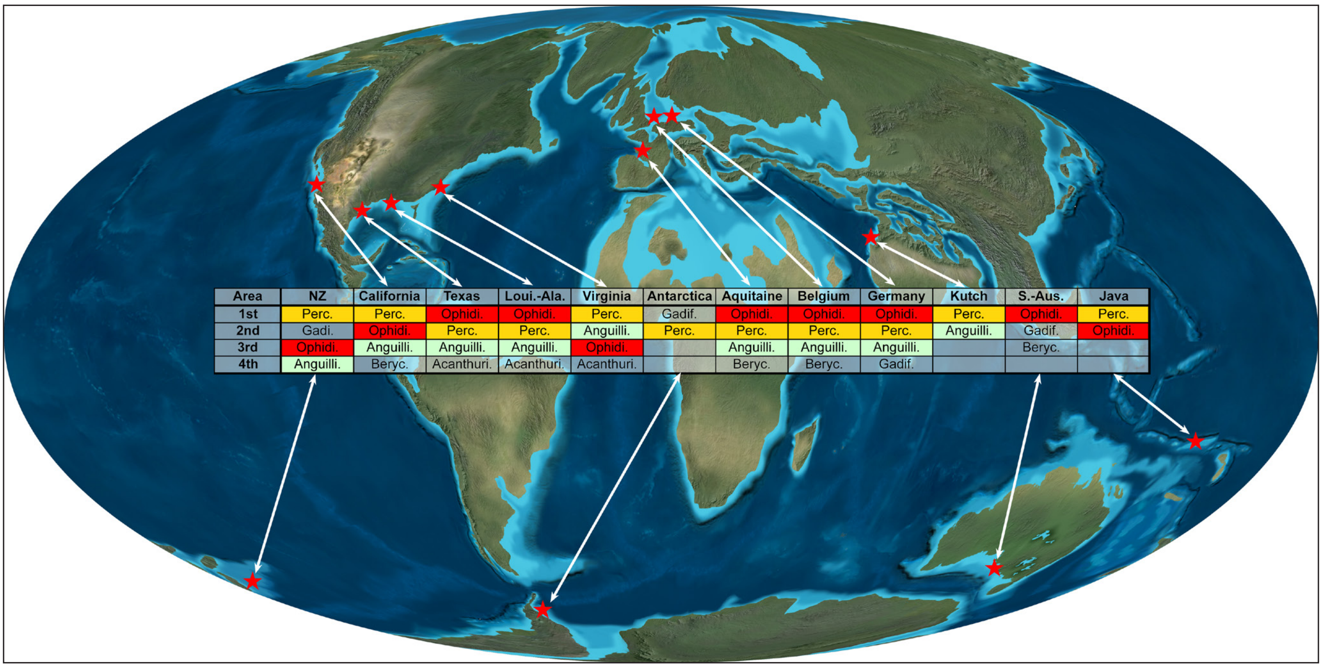
🟥 Ophidiiformes
🟨 Perciformes +
🟩 Anguilliformes

Fig. 22 - Abundance of otoliths in selected middle Eocene locations (stars), highlighting Ophidiiformes, Perciformes s.l. (sensu Nelson, 2006) and Anguilliformes. Only the four most common groups shown. Abbreviations used: Bery. = Berycida, Sciae. = Sciaenidae, Gadi. = Gadiformes, Myct. = Myctophidae, Pleuronecti. = Pleuronectiformes, Trachini. = Trachinoidei, Apogo. = Apogonidae. Paleogeographic map based on Blakey (2021), 40 Ma.

Californian Eocene. The earliest ophidiiform otoliths are known from the Campanian (Voigt 1926, reviewed in Schwarzhans 2010), but the most diverse species number is from the Eocene. The 200 otolith-based ophidiiform species compare to less than 10% of that amount in skeleton-based species, several of which are in need of review. The earliest skeleton- and otolith-based records, however, both occur in the Campanian with a basal bythitoid in each: *Pastorius methenyi* Carnevale & Johnson (2015) in the skeletal record and *Eobidenichthys crepidatus* (Voigt, 1926) in otoliths. The discrepancy in the abundance of otoliths versus articulated skeletons is mainly thought to be related to different taphonomic boundary conditions relevant for the fossilization of them (see above). The preservation of articulated skeletons is disadvantageous for demersal fishes like the Ophidiiformes, while it is advantageous for its otoliths (see above).

The peak of the abundance of ophidiiform otoliths appears to have been during the middle Eocene. When comparing the faunal composition of otolith-based taxa during the middle Eocene in 12 regions of the Earth spanning from New Zealand and Antarctica to California, the US Gulf Coast, the US East Coast to the various basins in Europe, it can be seen that ophidiiform taxa are the most common in five of them and are among the top four most common groups in another four regions (Fig. 22). The otoliths of their closest competitors, the Perciformes (s.l.), are the most common in only one location, but are amongst the top four in all other regions. In a third position are the otoliths of the Anguilliformes. When it comes to species diversity, ophidiiforms and perciforms (s.l.) are nearly equally dominant (Fig. 23). In all these regions, otoliths were primarily sampled from clastic environments in warm shallow seas. Nolf (1980) and Schwarzhans (1981) also recognized that in the Eocene ophidiiform otoliths were not only very common compared to their perceived current abundance but also occurred predominantly in shallow-water sediments while many of the extant ophidiiforms are bathydemersal fishes. They concluded that the extant species may represent relicts of a formerly much larger group.

However, it was also assumed that several Paleogene ophidiiform otoliths represent extinct lineages and Schwarzhans (1981) established a number of fossil otolith-based ophidiiform genera to accommodate this observation. The principle of the usage of fossil otolith-based genera versus open generic nomenclature was a matter of controversial viewpoints in the past (compare Schwarzhans



Area	NZ	California	Texas	Loui.-Ala.	Virginia	Antarctica	Aquitaine	Belgium	Germany	Kutch	S.-Aus.	Java
1st	Perc.	Perc.	Ophidi.	Ophidi.	Perc.	Gadif.	Ophidi.	Ophidi.	Ophidi.	Perc.	Ophidi.	Perc.
2nd	Gadi.	Ophidi.	Perc.	Perc.	Anguilli.	Perc.	Perc.	Perc.	Perc.	Anguilli.	Gadif.	Ophidi.
3rd	Ophidi.	Anguilli.	Anguilli.	Anguilli.	Ophidi.		Anguilli.	Anguilli.	Anguilli.		Beryc.	
4th	Anguilli.	Beryc.	Acanthuri.	Acanthuri.	Acanthuri.		Beryc.	Beryc.	Gadif.			

Fig. 23 - Diversity of otolith-based species in selected middle Eocene locations (stars), highlighting Ophidiiformes, Perciformes s.l. (sensu Nelson, 2006) and Anguilliformes. Only the four most common groups shown. Abbreviations used: Ophidi. = Ophidiiformes, Perc. = Perciformes s.l., Anguilli. = Anguilliformes, Gadi. = Gadiformes, Beryc. = Berycida, Acanthuri. = Acanthuriformes (in the sense of Sciaenidae). Paleogeographic map based on Blakey (2021), 40 Ma.

2012 and Nolf 2013) but otolith-based genus and species names are now more commonly used. Also, otoliths are now available for study from all extant ophidiiform genera and the majority of species so that the risk of establishing fossil taxa because of insufficient knowledge of extant taxa is negligible (a comprehensive comparative study of these otoliths is in progress by WS). Likewise, the risk of parataxonomy between skeletal and otolith taxa is minimal in the case of the Ophidiiformes because of the rarity of articulated ophidiiform skeletons in the fossil record.

In any case, the concept that the extant ophidiiforms are merely a relict of a much larger ophidiiform fauna during the Paleogene may be so for few clades (e.g., Sirembini, *Hoplobrotula* and *Bidenichthys* groups) but must be revised for the majority of the extant ophidiiforms (Figs. 24–25). Extant ophidiiforms comprise an amazing variety in environmental adaptations including shallow-water demersal fishes (Ophidiinae), fishes living commensal in holothurians or large clams (Carapinae), cryptic in euphotic reefs (and rocky shore environments) from 0 to 40 m water depth (Dinematichthyidae), on the continental slopes (most Bythitidae), neotenic bathydemersal fishes (*Aphyonus* group), and bathydemersal to abyssal demersal fishes including some of the deepest-living teleosts (Neobythitinae) (Fig. 24–26). It is difficult to explain all these highly adapted environmental specializations as a relict of a former shallow-water fauna that lived in warm clastic shelf seas.

A new, revised picture of the evolution of the Ophidiiformes is now emerging (Fig. 26). The earliest records are from the Late Cretaceous (Campanian and Maastrichtian); *Pastorius* and *Eobidenichthys* in Bythitoidei and *Ampheristus* and *Protobythites* in Ophidioidei (Figs. 24–26). All three families have been identified prior to the K/Pg boundary extinction event (Carnevale & Johnson 2015; Schwarzhans 2010; Schwarzhans & Milàn 2017; Schwarzhans & Stringer 2020; Stringer & Sloan 2023) (Figs. 24–26). However, abundance and diversity was relatively low. It is not known, how far back in time the origin of the Ophidiiformes may have reached, but a Late Cretaceous origination appears likely. The Ophidiiformes were among the survivors of the K/Pg boundary extinction event and seem to have benefited from the disappearance of a number of widespread and diverse clades of teleosts of the Maastrichtian time (Schwarzhans et al. 2024). During the Paleocene, they further diversified and several new clades have materialized like the Sirembini, Carapinae, some probably extinct bythitid clades, and the

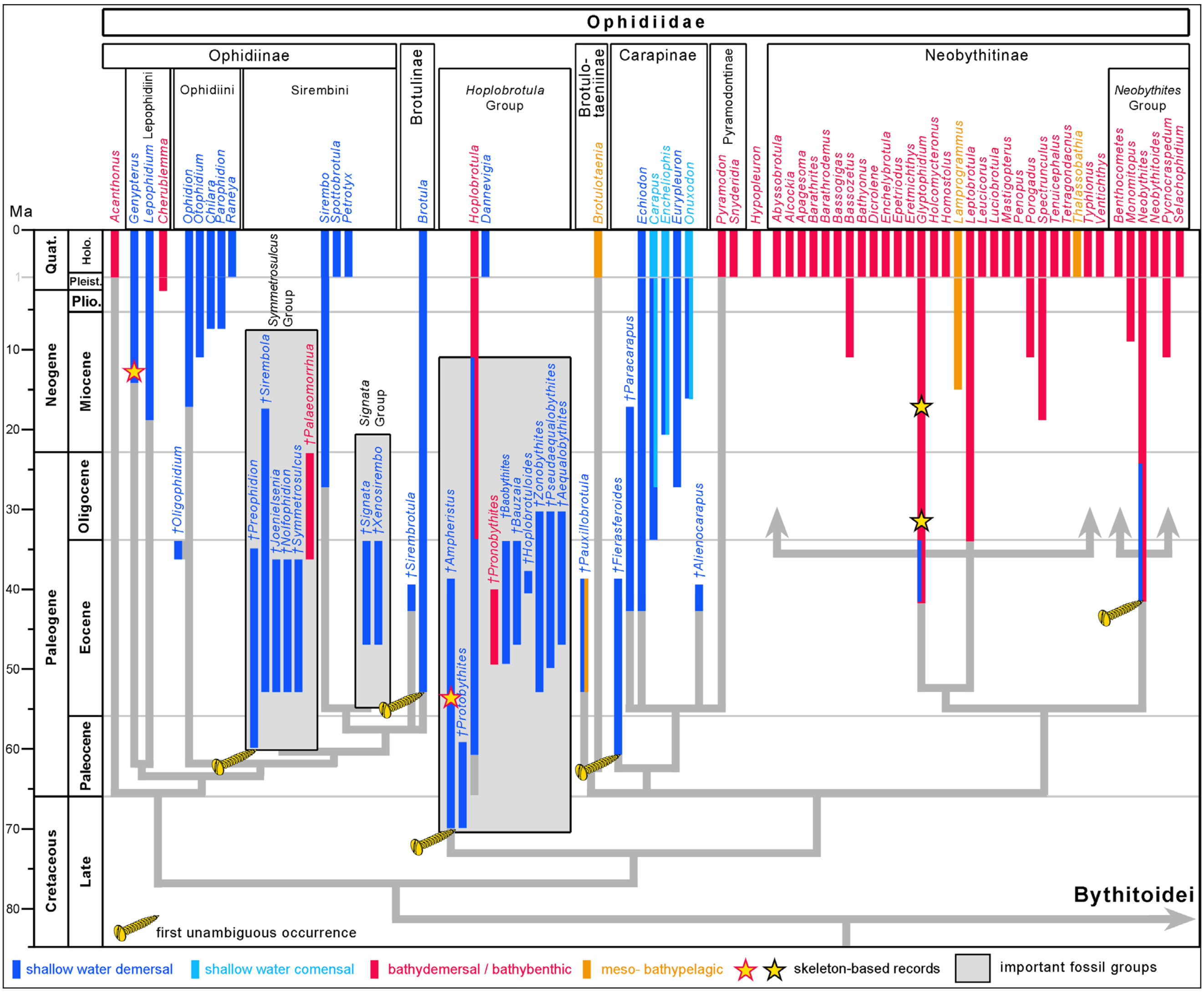


Fig. 24 - Phylogram of the Ophidiidae with fossil occurrences. Phylogram based on classifications of Cohen & Nielsen (1978), Schwarzhans (1981), Nielsen et al. (1999) and Møller et al. (2016); skeletal data after Carnevale & Johnson (2015) and personal information by Carnevale (2023); taxa shown to genus level, phylogram shown to group level.

Ogilbia group in the Dinematichthyidae (Fig. 25). Ophidiiforms also increased in abundance but were not yet dominating in any environment.

The "warm house" period that followed the PETM during the Eocene obviously generated beneficial conditions for a rapid radiation and diversification of ophidiiform fishes in the warm shallow seas (Nolf 1980, 2013; Schwarzhans 1981) (Figs. 24–26). As demersal fishes, they thrived particularly well on sandy to muddy sea bottom for instance in the Belgian (Stinton & Nolf 1970; Nolf 1971, 1973a,b), English (Stinton 1977) and German (Schwarzhans 2007) basins of Europe as well as in the US Gulf Coastal Plain (Lin & Nolf 2022 and literature cited therein) and Californian (this study) basins and in New Zealand (Schwarzhans 2019a). Their diversification peaked during middle Eocene where they were competing with perciforms s.l. in a variety of environments (Figs. 24–26). Primarily taxa putatively related to the *Hoplobrotula* group in Neobythitinae, the Sirembini of the Ophidiinae, and certain difficult to relate bythitid genera constituted the bulk of Eocene ophidiiform radiation. Of these, the Sirembini were particularly diverse in the US Gulf Coast Eocene (Lin & Nolf 2022) while the Neobythitinae and Bythitidae were the most common in all other basins. Apart from this amazing radiation in the warm, shallow clastic seas, it is furthermore notable that otolith size suggests a dominance of small fishes. Many of the Eocene ophidiiform otoliths appear to indicate fish sizes of 5 to 15 mm SL when compared to extant otoliths,

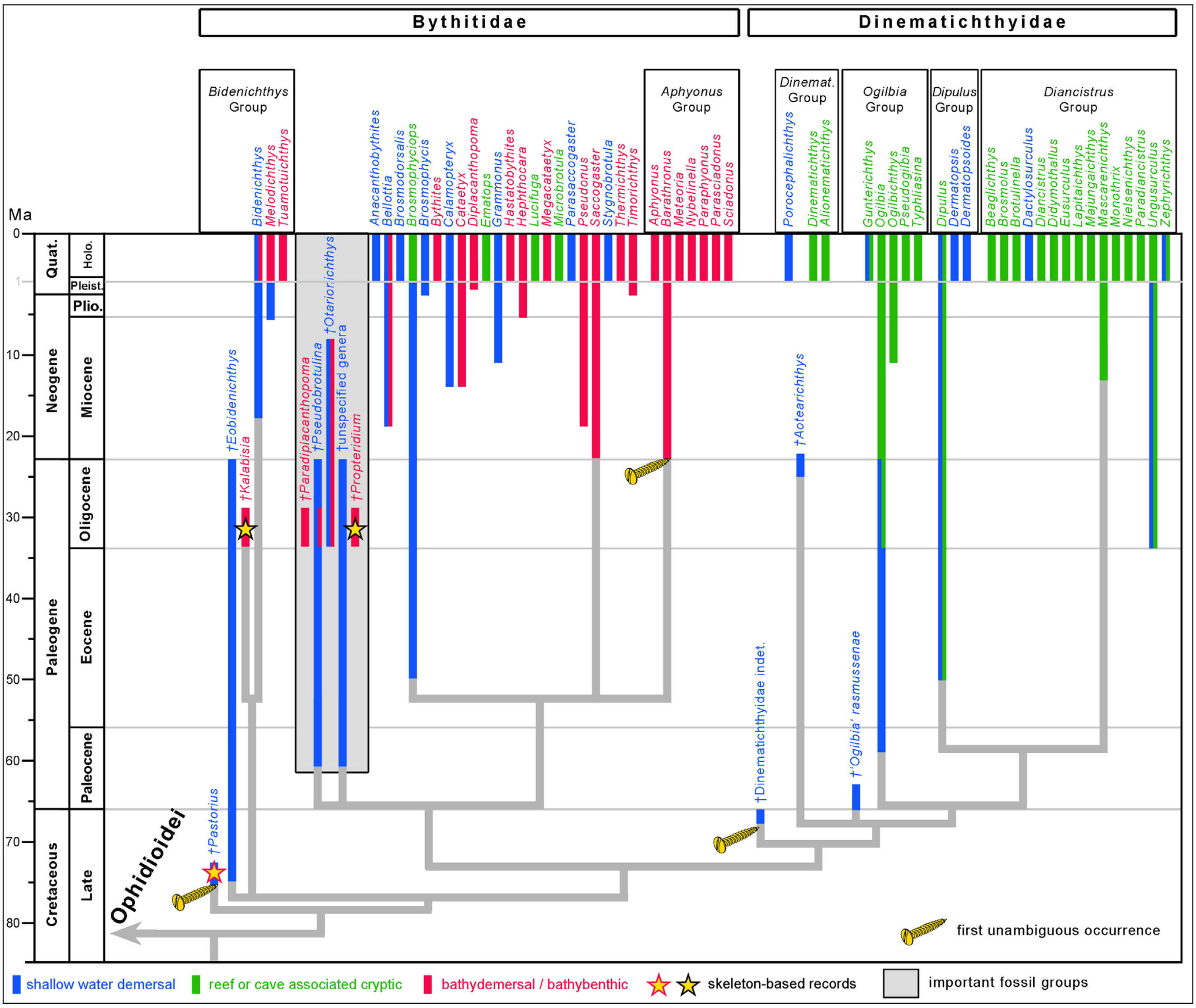


Fig. 25 - Phylogram of the Bythitidae and Dinematichthyidae with fossil occurrences. Phylogram based on classifications of Cohen & Nielsen (1978), Schwarzhans (1981), Nielsen et al. (1999) and Møller et al. (2016); skeletal data after Carnevale & Johnson (2015) and personal information by Carnevale (2023); taxa shown to genus level, phylogram shown to group level.

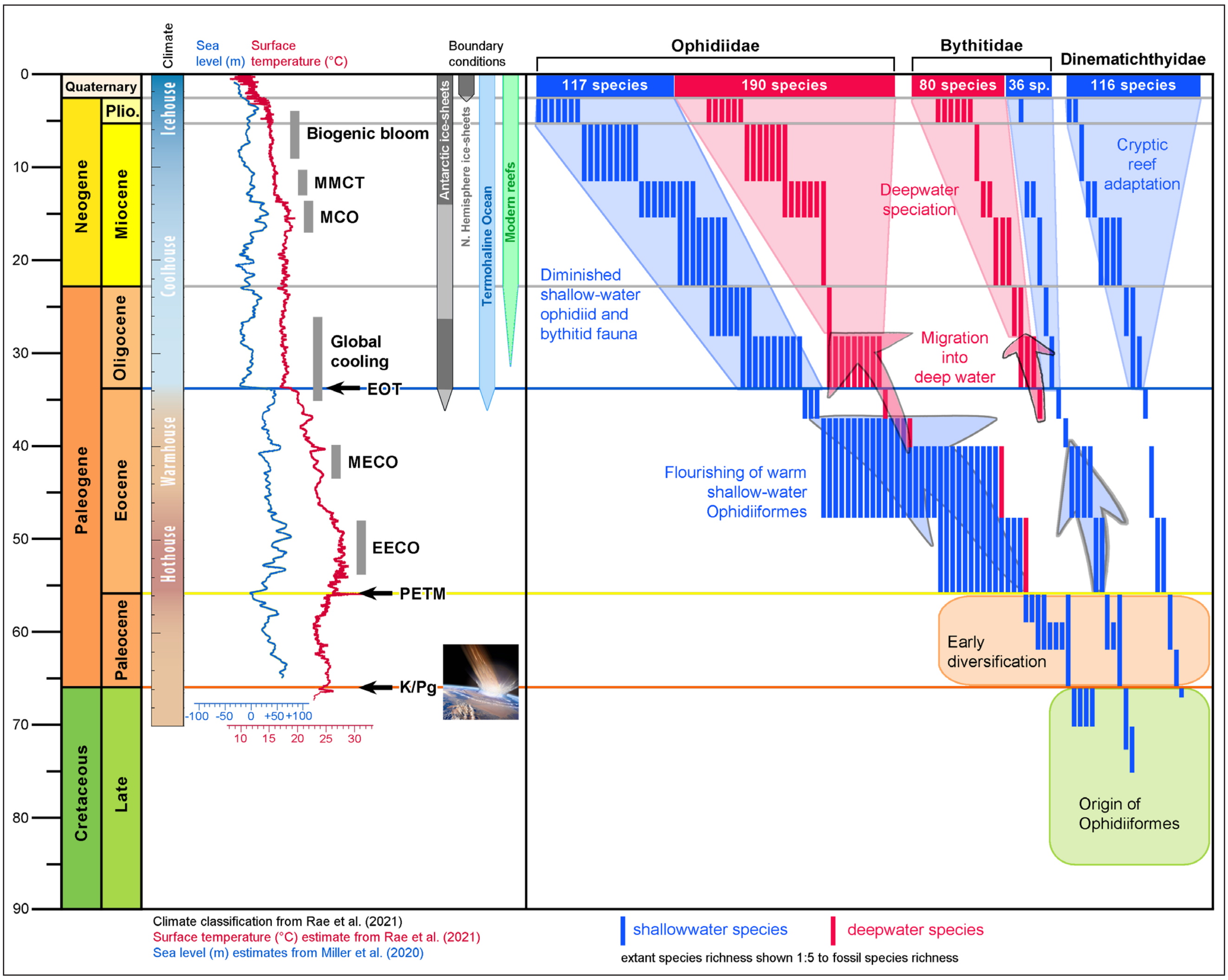
for example of the Dinematichthyidae, which are generally of similar sizes. Only a few larger ophidiiforms seem to have existed during the middle Eocene, predominantly in the genera *Ampheristus* and *Pseudaequalobythites*. This differs from the much larger sizes of most extant fishes in the Neobythitinae or Ophidiinae. It is possible that the many small, shallow-water ophidiiforms occupied environmental niches in the Eocene that later became a domain for the Gobiidae. In this context, it is interesting to note that gobioids are extremely scarce in the Eocene, both in the skeletal and otolith record. However, they have become the dominant group in nearly all warm shallow seas since the Miocene (Nolf 2013; Bratishko et al. 2023; Schwarzhans & Aguilera 2024). However, gobies today span a wider ecological terrain extending into brackish and freshwater environments, which apparently were never effectively populated by the Ophidiiformes.

These Eocene shallow-water ophidiiform lineages rapidly diminished during late Eocene and early Oligocene and, with few exceptions in Chile (Schwarzhans & Nielsen 2021) supposedly became extinct at the turn of the Oligocene to the Miocene (Fig. 24). Interestingly, it is also the early Oligocene were the first locally abundant shallow-water goby communities have been observed in the Aquitaine Basin of France (Steurbaut 1984) and Japan (Schwarzhans et al. 2017b). Only a few ophidiiform groups remain in the shallow water, particularly in Ophidiinae, Carapinae, and the Dinematichthyidae. Some of the Ophidiinae (*Lepophidium* and *Ophidion* groups) successfully diversified in the seas around America (Nielsen et al. 1999; Schwarzhans & Aguilera 2016; Schwarzhans & Nielsen 2021). The Dinematichthyidae are generally rare in the fossil record because of their reef associated cryptic live-style, which is unfavorable for the fossilization of their otoliths. However, the relatively few records of dinematichthyid otoliths that have been recovered in Oligocene and Neogene sediments suggest that they inhabited shallow and secretive environments during that time. We postulate that this was the time when their remarkable ecological specialization and adaptation began (Fig. 26).

Today, ophidiiforms are best known for their many and diverse deep-water species, some of them being among the deepest-living fishes (Schwarzhans & Gerringer 2023). So when did the various deep-water lineages in the Ophidiiformes actually migrated into deep water? A rich bathyal ophidiiform assemblage was found in true deep-water sediments of early Oligocene (Rupelian) age in Italy (Nolf & Steurbaut 2004). This fauna contained otoliths that were unambiguously placed in extant deep-water ophidiid genera such as *Hoplobrotula, Leptobrotula*, and *Neobythites*. A deepwater fauna from the late Eocene of New Zealand yielded commonly a species of *Neobythites* that is believed to expose sexual dimorphism in otolith morphology (Schwarzhans 2019a). Sexual dimorphism in the otolith morphology of certain extant *Neobythites* species is a rather unique development and was thought to represent some sort of functional adaptation of these fishes to living preferentially at the depth of the optimal sound transmission in the ocean (Schwarzhans 1994b). In addition there are two species of *Neobythites* in the Oligocene of New Zealand, one in shallow water, the other in deep water, which was considered as an expression of ongoing depth-related speciation during an active phase of migration into deep-water (Schwarzhans 2019a). The earliest deep-water ophidiid is an undefined species of *Neobythites* from the Bartonian of New Zealand (Schwarzhans 2019a; Tab. 4). Finds by Lin et al. (2016) and recently published data from bathyal sediments in Denmark (Schwarzhans & Nielsen 2023) suggest that certain ophidiid taxa already started to venture into deep water during the late early and middle Eocene, but this lineage apparently was not successful and does not persist today (*Pronobythites*, Fig. 24). Other bathybenthic ophidiiform fishes are *Glyptophidium* (Neobythitinae) known from the Oligocene skeletal record (Świdnicki 1988; Přikryl & Carnevale 2018), *Saccogaster* (Bythitidae) and *Barathronus* (Bythitidae, *Aphyonus* group) since at least Early Miocene (Schwarzhans 2019a). A number of extinct bathybenthic genera are recorded from the latest Eocene and Oligocene. In the skeletal record these are *Kalabisia* (Bythitidae, *Bidenichthys* group) and *Propteridium* (Bythitidae) (Přikryl & Carnevale, 2018); and in otoliths *Palaeomorrhua* (Sirembini) and *Paradiplacanthopoma* (Bythitidae) (Schwarzhans, 1981). The stratigraphic ranges are shown in Figs. 24–25. It now seems that the first lineages of the Ophidiidae began to migrate into the deep sea during the middle Eocene or even the latest early Eocene, but these were few and they didn't succeed in establishing in that environment. Migration into the deep sea accelerated during the latest Eocene and early Oligocene with clades of the Neobythitinae; and these were successful and formed the base of the current deep water neobythitine stock (e.g., *Glyptophidium*, *Hoplobrotula*, *Leptobrotula* and *Neobythites*) (Figs. 24–26; Tab. 4). The change of the deep ocean circulation from halothermal to termohaline that occurred during this time may have triggered the establishment of a new deep-water community caused by a better ventilation and oxygen supply into the deep sea and an increase of the biogenic pump (Miller et al. 1992; Thomas 2007; Katz et al. 2011). The otolith record suggests that the Oligocene and Miocene were times of a further diversification of the deep-water clades of the Neobythitinae and Bythitidae, while at the same time the shallow-water ophidiid and bythitid composition diminished (Fig. 26).

Early acanthomorph diversity in otoliths

A continuous rise in acanthomorph otolith diversity has been observed since the Late Cretaceous. However, a large proportion of that diversity documented in many skeleton records (Patterson 1993) and highly derived otolith morphologies (Schwarzhans & Stringer 2020) became extinct at the K/Pg boundary (Schwarzhans et al. 2024). It is as if much of the acanthomorph diversity was reset with the K/Pg boundary extinction event and restarted anew in the Paleogene. It is thus naturally of interest for palichthyologists to investigate which acanthomorph lineages survived the extinction event and how they fared and radiated in the recovery phase thereafter (see Cavin 2001, 2008;



Climate classification from Rae et al. (2021)
Surface temperature (°C) estimate from Rae et al. (2021)
Sea level (m) estimates from Miller et al. (2020)

Fig. 26 - The evolution and evolutionary events of the Ophidiiformes, mainly deduced from fossil otoliths, and shown in the context of major changes in the Earth's history. Abbreviations used: K/Pg = Createceous/Paleogene boundary, PETM = Paleocene-Eocene thermal maximum, EECO = early Eocene climate optimum, MECO = middle Eocene climate optimum, MCO = Miocene climate optimum, MMCT = Middle Miocene climate optimum.

Schwarzhans & Stringer 2020). The remarkably high morphological diversity in Maastrichtian acanthomorph otoliths (Schwarzhans & Stringer 2020) gives way to a low diversity in the Paleocene where acanthomorph otoliths are characterized by very generalized patterns that are difficult to allocate (Schwarzhans 2010, 2012). Many of the Paleocene acanthomorph otolith morphotypes just allow for a general placement in a specific perciform (s.l.) family but do not show sufficient diagnostic character to define a generic allocation. These forms are often placed in the kind of open generic nomenclature proposed by Janssen (2012) whereby the species in question is placed in the name-giving genus of the family followed by a "?" indicating that it could belong to an undefined fossil genus. It goes without saying that the degree of phylogenetic information that can be retrieved from such forms is rather limited. Attempts in some past literature to place such forms in extant genera should be met with skepticism.

Similar to the situation of the perciform s.l. fish fauna found in Monte Bolca, the Eocene perciform s.l. otoliths also show a considerably advanced morphological diversification when compared to that of their Paleocene counterparts, and some morphologies already resemble modern faunal elements. However, the articulated acanthomorph fauna from Monte Bolca also documents that the vast majority of species belong to fossil genera probably representing extinct or stem lineages. Furthermore, the fish fauna of Monte Bolca includes a considerable number of extinct families. Unfortunately, otoliths are not preserved in the fishes of Monte Bolca. Therefore, in the absence of a suitable calibration of isolated otoliths with in situ finds, it is pertinent to apply a careful approach in the allocation of Eocene perciform s.l. otoliths. We therefore believe that one should be very careful when comparing these morphologies with those of extant fishes and placing such fossil otoliths in extant genera with which the otoliths show the seemingly best resemblance. Such an approach is feasible for instance in Berycida where many of the lineages that survived the K/Pg boundary extinction apparently haven't changed much morphologically until today, e.g. in the genera *Centroberyx* or *Trachichthys*. In the case of the Perciformes s.l., however, a significant evolutionary development took place during the Eocene, and therefore, rather diverse otolith morphologies are found as well. Here we take the approach of allocating the middle Eocene Californian otoliths 1) to extant genera when we consider such as reasonably justified, but still applying a rather broad morphological concept, 2) place them in fossil genera (often established as new here) where we consider sufficient diagnostic valid characters to be manifest, and 3) place them in open generic nomenclature in the way suggested by Janssen (2012) where neither 1) or 2) are justifiable and where the otolith morphology is considered plesiomorphic.

1) Taxa allocated in extend genera: *Mene* (Menidae) is one of the few genera recognized in skeletons and otoliths from the Eocene (Carnevale et al. 2014). Other families with stable otolith morphologies since middle Eocene times are the Ambassidae (*Ambassis*), Acropomatidae (*Acropoma*, *Parascombrops*), Lactariidae (*Lactarius*), Scombropidae (*Scombrops*), Antigoniidae (*Antigonia*), Triglidae (*Prionotus*), Scorpaenidae (*Scorpaenodes*), Nomeidae (*Cubiceps*), and the enigmatic Bathyclupeidae (*Bathyclupea*). Otoliths of the Ambassidae, Acropomatidae, Lactariidae and Scombropidae exhibit a relatively plesiomorphic otolith morphology within the Perciformes (s.l.), and it is therefore not surprising that they occur early in the fossil record. Those of the Triglidae, Scorpaenidae, and Nomeidae are more advanced, and it is therefore less expected to find otoliths of these families in the Eocene that can be relatively comfortably allocated in persistent lineages. Some special mentioning, however, is necessary for *Mene, Antigonia*, and *Bathyclupea*, which are all highly advanced fishes. Particularly *Antigonia* and *Bythclupea* exhibit a distinctive and specialized otolith morphology that has remained practically unaltered since Eocene times, and probably earlier in the case of *Antigonia* (see Schwarzhans 2010). The unique otolith morphotype is evident since middle Eocene. Otoliths described by Schwarzhans (2012) as *Diretmus serrativenter* from the late Paleocene of Austria might rather be considered a bathyclupeid as well. Such an old and consistent occurrence may not be congruent with a placement in the Perciformes as shown in Nelson et al. (2016).

2) Taxa allocated in fossil genera: in this category we observe in the middle Eocene of California a number of otolith morphologies that can be reasonably placed in persistent families but also show certain diagnostic features that indicate that they may not be part of any lineage leading to extent genera. Here, we count a putative Trichonotidae (*Protobembrops*), two Serranidae (*Torreichthys* and *Pseudolabrax*), three Haemulidae (*Micropomadasys, Protopomadasys,* and *Strongylauris*), and a putative early liparid (*Liparomorphus*). Perhaps the most unexpected occurrence is the diversity of haemulids, which combine plesiomorphic characters such as a low caudal curvature and a relatively narrow ostium with other, derived features that exclude them from a direct relationship to any of the extant haemulid genera from which otoliths are known. This high degree of diversity contrasts with few species of the fossil otolith-based haemulid *Allomorone* in the Eocene of the US Gulf Coastal Plain.

3) Taxa in open generic position: This category remains the largest in perciforms s.l. in the Californian middle Eocene comprising species in the Carangidae, Stromateidae, Uranoscopidae, Serranidae, Malacanthidae, Sparidae, and Cottidae. They are mostly otolith morphologies characterized by plesiomorphic, generalized patterns that do not allow placement in any extant genus nor definition of a fossil one because of the lack of diagnostic features at a higher than species level. This uncertainty in systematic allocation could only change in our opinion if any of these morphotypes could be found in situ. The high percentage of taxa in this category also indicates that the diversification in many perciform s.l. groups was still at its early stages in the Eocene.

First occurrences in otoliths and tip-point qualifications

Otoliths can also help to identify minimum ages (tip-points) for the calibration of phylogenies. However, the use of otolith data for minimum age determinations of teleost clades comes with a major caveat because the taxonomy of isolated otoliths is primarily based on morphological comparison with otoliths extracted from extant fishes. This practice becomes increasingly problematic the deeper in time otoliths are obtained for obvious reasons related to evolutionary changes or extinction of lineages. Therefore, calibration of isolated otoliths with otoliths found in situ in articulated skeletons would be crucial in those deep-time finds, but unfortunately these finds are rarely observed in the Paleogene (see Schwarzhans et al. 2018a; Fig. 1). Consequently, the use of Eocene and older otoliths for this purpose must be interpreted using a rigorous quality control (Schwarzhans et al. 2024). We have therefore focused in our assessment on occurrences that we consider unambiguous for a defined systematic level. Also, otoliths are much more common in the fossil record, and therefore, allow for a more continuous assessment of teleost evolution in time and space.

Otolith associations are relatively well-known from Eocene strata, particularly from Europe (Nolf 1988, 2013), US Gulf Coast (Nolf & Stringer 2003; Lin et al. 2022; Stringer et al. 2022 and references therein) and New Zealand (Schwarzhans 2019a). It is therefore not surprising that the middle Eocene otolith association from California described here contained only few new deepest time records on a higher systematic level. In fact, it appears that the principal composition and evolutionary level of the various Eocene otolith assemblages are relatively similar to each other on family level and to lesser degree also on genus level reflecting a kind of a common phase in the evolution of teleosts during the Eocene. On the family level, the only novel record is that of the Scombropidae (no other fossil record; *Scombrops* sp. from the early Eocene of SW-France [Nolf 1988] is here regarded as an unidentifiable juvenile perciform). On the genus level, however, there are a few additions of interest. In Congridae, the genus *Acromycter* is reported for the first time in the fossil record and for *Uroconger*, it is the earliest record. The California middle Eocene assemblage has yielded the first Eocene record of the genera *Polyipnus* (Sternoptychidae), *Cubiceps* (Nomeidae), *Peprilus*? (tentative; Stromateidae), and *Scorpaenodes* (first records of the genus in Scorpaenidae). *Eopterois*, described here from the Bartonian of Mississippi represents the first fossil record of the tribe Pteroini in the family Scorpaenidae.

CONCLUSIONS AND OUTLOOK

The middle Eocene otolith association of the Ardath Shale and Mission Valley Formation from southern California, San Diego County, described here is exceptionally rich and diverse, comparable only to the Eocene otolith assemblages of the US Gulf and Atlantic coastal plains (Nolf & Stringer 2003; Lin & Nolf 2022; Stringer et al. 2022), the Aquitaine Basin in South-West France (Nolf 1988; Lin et al. 2016), the northern and central European Basins (e.g., Nolf 1971, 1973a,b, 1975; Schwarzhans 2007; Stinton 1975, 1977, 1978, 1980, 1984) and New Zealand (Schwarzhans 2019a). Furthermore, it is the first record of Eocene otoliths from the North Pacific and thus represent an important piece of the puzzle in the understanding of the Eocene fish fauna. The main conclusions are as follows:

1) The middle Eocene otolith-based fish fauna from California (Ardath Shale and Mission Valley Formation) resembles in its general composition that of the other mentioned regions characterized by a diverse assemblage of anguilliforms (primarily Congridae), shallow-water ophidiiforms and often difficult to interpret, plesiomorphic percomorphs (in the sense of perciforms s.l.). Such a faunal composition seems to reflect the status of teleost evolution during the Eocene.

2) At the species level and partly also on the genus level, however, the Eocene Californian fish fauna differs greatly from those of the other regions, particularly the US Gulf and Atlantic coastal plains, which may be due to different current regimes and differences in the environment and topography of the continental shelf (steep relief, active continental margin in California versus wide, shallow, low relief passive continental margin at the US Gulf Coast) as well as paleogeographic constraints.

3) As a consequence of point 2, we propose a Californian paleobioprovince of fishes for the Eocene, which was governed by a much warmer sea temperature than today, and therefore, is unrelated

to the present-day cold California Current driven endemic fish fauna.

4) The two sampled localities differ greatly in their paleoenvironmental conditions (continental edge to slope at the Black's Beach site, possibly dominated by redeposition from a lower neritic shelf environment and shallow-water near-shore at Miramar Reservoir site), which is reflected in the faunal composition with the Black's Beach site containing 89 species while the Miramar Reservoir site yielded 38 species. Several species at the Black's Beach site indicate open ocean influence.

5) The two sampled localities are also considered to differ stratigraphically (early to middle Lutetian for the Black's Beach site versus late Lutetian to early Bartonian for the Miramar Reservoir site), which does not find any significant reflection in the composition of the otolith taxa. However, the otolith assemblages of the two localities show large significant differences in species diversity (richness), the percentage similarity measurement (the two are significantly different in abundance of taxa) and the percentage of the most abundant species.

Our study of the middle Eocene otoliths from California demonstrates how much new information is still to be gained regarding fossil otolith-based fish faunas once new regions are sampled and carefully studied. We believe that future research in Eocene otoliths has the potential to significantly increase our understanding of teleost evolution further. We would anticipate that many understudied or not studied regions of the world can yield important new otolith associations. One particularly understudied terrain is deep-water sediments. Only a few true Paleogene bathyal otolith communities have so far been recovered, the largest one from the early Oligocene of Italy (e.g., Nolf & Steurbaut 2004) and smaller ones from the late and middle Eocene of Italy and New Zealand (Schwarzhans 2019a; Schwarzhans & Carnevale 2022). The continental margin associations from the Aquitaine Basin in France (Lin et al. 2016) and from California described here no doubt contain pelagic and bathyal elements, but a reliable assessment of those will only become possible once true and sizeable bathyal faunas have been found for comparison. Finally, we hope that future efforts will also be directed to finding otoliths in situ in articulated skeletons of Eocene age in order to connect the two important data sets and calibrate isolated otoliths. Unfortunately, fish skeletons from the famous Monte Bolca Lagerstätte in Italy do not contain recoverable otoliths, but other less prolific localities may.

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