Acta Geologica Polonica, Vol. 75 (2025), No. 4, e60
DOI: 10.24425/agp.2025.155954

Additional records of Paleogene fishes (Chondrichthyes and Osteichthyes) from Alabama, USA

DAVID J. CICIMURRI[1], GARY L. STRINGER[2] and JUN A. EBERSOLE[3]

[1] *Geological Survey of Alabama, 420 Hackberry Lane, Tuscaloosa, Alabama 35401, USA;*
e-mail: dcicimurri@gsa.state.al.us
[2] *University of Louisiana at Monroe, 708 University Avenue, Monroe, Louisiana 71209, USA;*
e-mail: stringer@ulm.edu
[3] *McWane Science Center, 200 19th Street North, Birmingham, Alabama, 35203, USA;*
e-mail: jebersole@mcwane.org

ABSTRACT:

Cicimurri, D.J., Stringer, G.L. and Ebersole, J.A. 2025. Additional records of Paleogene fishes (Chondrichthyes and Osteichthyes) from Alabama, USA. *Acta Geologica Polonica*, **75** (4), e60.

The Paleogene deposits in Alabama, USA, contain abundant marine invertebrate and vertebrate fossils that represent diverse paleofaunas, but the fish taxa contained within these units remain understudied. The present work, based primarily on cataloged specimens from museum and university collections, discusses 12 chondrichthyan and 9 osteichthyan taxa that are newly recognized from Paleogene lithostratigraphic units in Alabama. All the chondrichthyan taxa are represented by teeth, whereas the bony fishes were identified by otoliths, teeth, and scales. The fossils we discuss include a previously unreported morphology of *Otodus* sp., as well as *Striatolamia cederstroemi* Siverson, 1995, *Odontaspis substriata* (Stromer, 1910), *Microscyliorhinus leggetti* Case, 1994, *Hemipristis* cf. *intermedia* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025, *Physogaleus* aff. *contortus* Gibbes, 1849, '*Sphyrna*' *robustum* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025, *Galeocerdo* aff. *platycuspidatum* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025, *Casierabatis* cf. *lambrechtsi* Reinecke, Mollen, Gijsen, D'Haeze and Hoedemakers, 2024, *Hypolophities* sp., '*Rhinoptera*' *prisca* Woodward, 1907, and a batoid identified only as Myliobatidae indet. The teleosts include *Pterothrissus conchaeformis* (Koken, 1885), *Synodus* sp., *Holocentrities ovalis* Conrad, 1941, *Arnoglossus* sp., *Centropristis* aff. *priaboniana* Nolf and Stringer, 2003, aff. *Scorpaenopsis* sp., *Aplodinotus distortus* Nolf, 2003, *Lobodus pedemontanus* Costa, 1866, and Lutjanidae indet. These newly recognized taxa provide further insights into Paleogene ecologies in Alabama, as well as the paleobiogeographical distribution and evolutionary history of the species.

Key words: Elasmobranchs; Bony Fishes; Gulf Coastal Plain; Paleocene; Eocene; Oligocene.

INTRODUCTION

The Paleogene surficial deposits in Alabama, USA, have long been known for the abundance and diversity of marine invertebrate fossils (see Conrad 1835; Toulmin 1977) they often yield. Despite the long history of investigation in this state, reports of contemporaneous fish fossils are relatively uncommon and many of the Paleogene units have been only cursorily investigated. The study of Cenozoic fishes in Alabama began in 1833, when Isaac Lea published the earliest report of a Paleogene fish fossil, which was an otolith collected from the town of Claiborne, on the bluffs of the Alabama River in Monroe County. Although Lea (1833) only noted that the fossil was collected from 'Tertiary' deposits, the Claiborne locality is famous for exposures of middle Eocene Claiborne Group strata (Lisbon Formation and Gosport Sand)

and the Moodys Branch Formation (Jackson Group). The fossil illustrated by Lea (1833, pl. 6, fig. 218) was recognized as "bone of a fish," but he was unaware of its exact anatomical location. However, his illustration of the fossil clearly shows a sciaenid otolith that can be assigned to '*Sciaena*' *intermedia* (Koken, 1888), a taxon known from middle Eocene units in Alabama (Ebersole *et al.* 2019). Lea's (1833) report is important because it is the first recognition of a Paleogene otolith from Alabama, and it appears to be the first recognized fossil otolith from the USA.

Gibbes (1849) mentioned the occurrence of several Paleogene elasmobranchs from Alabama, and Alabama's first State Geologist, Michael Tuomey (1858), provided the first published list of Paleogene fishes from the state. Unfortunately, the whereabouts of Gibbes' specimens are unknown, and Tuomey did not describe or figure any of his Cretaceous specimens. Koken (1888) later studied otoliths derived from the Gulf Coastal Plain, which included middle Eocene strata of Mississippi and Alabama, and his report represents the oldest comprehensive study of Paleogene otolith assemblages from Alabama. Meyer (1889, p. 42) subsequently documented fish otoliths of the "southern Old-Tertiary" (= Paleogene) that included specimens from Alabama. Two years later, Woodward (1891) listed several Paleogene fishes from Alabama that were reposited in the British Museum collections in the UK.

During the 20th century, Eastman (1904) reported that Eocene fish otoliths were abundant and diverse in Alabama and Mississippi, and noted that these small, seemingly insignificant fossils were the remains of a flourishing fish fauna in the geologic past. Campbell (1929a) later contended that Koken's (1888) work on Alabama and Mississippi taxa represented the only described otoliths in North America and refigured many of those fossils for his article. Shortly thereafter, Campbell (1929b) included many of the same specimens in his *Bibliography of Otoliths*. Leriche (1942) described and figured several Paleogene fish taxa from Alabama, including a purportedly new galeomorph, *Lamna mediavia*. White (1956) later erected seven new taxa within his larger study of Paleogene elasmobranchs from Alabama, which were originally contained within the private cabinet of Michael Tuomey but shipped to the British Museum in the UK after his death in 1857 (White 1956; Ebersole and Dean 2013).

From other lithostratigraphic units in Alabama, Frizzell and Lamber (1962) investigated Congridae otoliths derived from the Oligocene (Rupelian) Red Bluff Clay exposed at the former Lone Star Cement Quarry in St. Stephens, Washington County, and Frizzell (1965) published a study on Gulf Coast albulid otoliths that included specimens collected from the Paleocene Porters Creek Formation. Frizzell and Dante (1965) produced a seminal work that included Eocene and Oligocene otoliths from Alabama strata (specifically the Gosport Sand at Little Stave Creek in Clarke County, the Lisbon Formation at Claiborne Landing in Monroe County, and the Red Bluff Clay at St. Stephens Quarry in Washington County). Painter (1965) and Salem (1971), two of Frizzell's graduate students, later studied lower Cenozoic Gulf Coast otoliths for their master's theses, and both included specimens derived from Paleogene formations in Alabama.

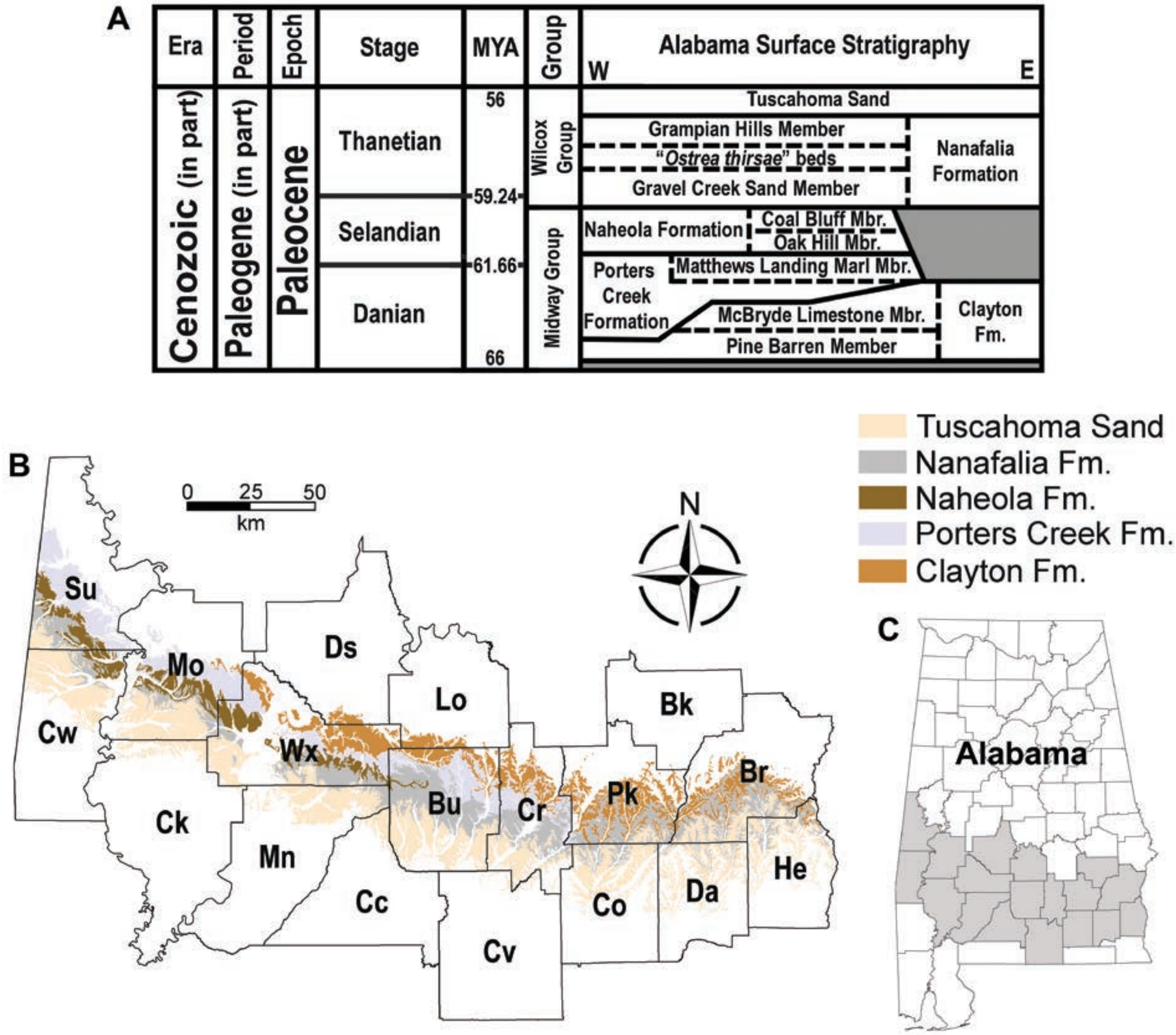
Thurmond and Jones (1981) summarized the previous 150 years of fossil fish study in Alabama, repeating the taxa identified in the works of Koken (1888), Leriche (1942), White (1956), Frizzell and Lamber (1962) (among others), but they also added several shark and bony fish taxa to the Paleogene record of Alabama. Nolf (1985) listed and figured numerous otoliths from the Paleogene strata in Alabama in his *Handbook of Paleoichthyology*, and Holman and Case (1988) provided a short list of middle Eocene tooth-based fish taxa they observed in Conecuh County. Nolf and Dockery (1993) described otoliths from the Paleocene (Danian) Matthews Landing Member of the Porters Creek Formation in Wilcox County, which represents one of the few otolith studies strictly from the Alabama Paleocene. A short while later, Denton *et al.* (1997) reported the first Paleogene chimaeroid from the state.

More recent studies describing Paleocene fish taxa from Alabama include Schein *et al.* (2011), Cicimurri and Ebersole (2015a), Cicimurri *et al.* (2020), and Ebersole *et al.* (2024a). Eocene fishes have received more attention in recent years, with studies by Westgate (2001), Cappetta (2012), Clayton *et al.* (2013), Maisch *et al.* (2014, 2016), Ehret and Ebersole (2014), Cicimurri and Ebersole (2015b), Cappetta and Case (2016), and Ebersole *et al.* (2019). Reports by Manning (2003), Stringer *et al.* (2020a), and Ebersole *et al.* (2021, 2024b) each provided new Oligocene fish records in Alabama, but strata dating to this epoch remain significantly understudied. In his exhaustive book, *The Diversity of Fish Otoliths Past and Present*, Nolf (2013) referenced and illustrated numerous otoliths from Alabama Paleogene strata. Finally, Ebersole *et al.* (2024c) provided an extensive overview of all previously described Paleogene fishes from Alabama.

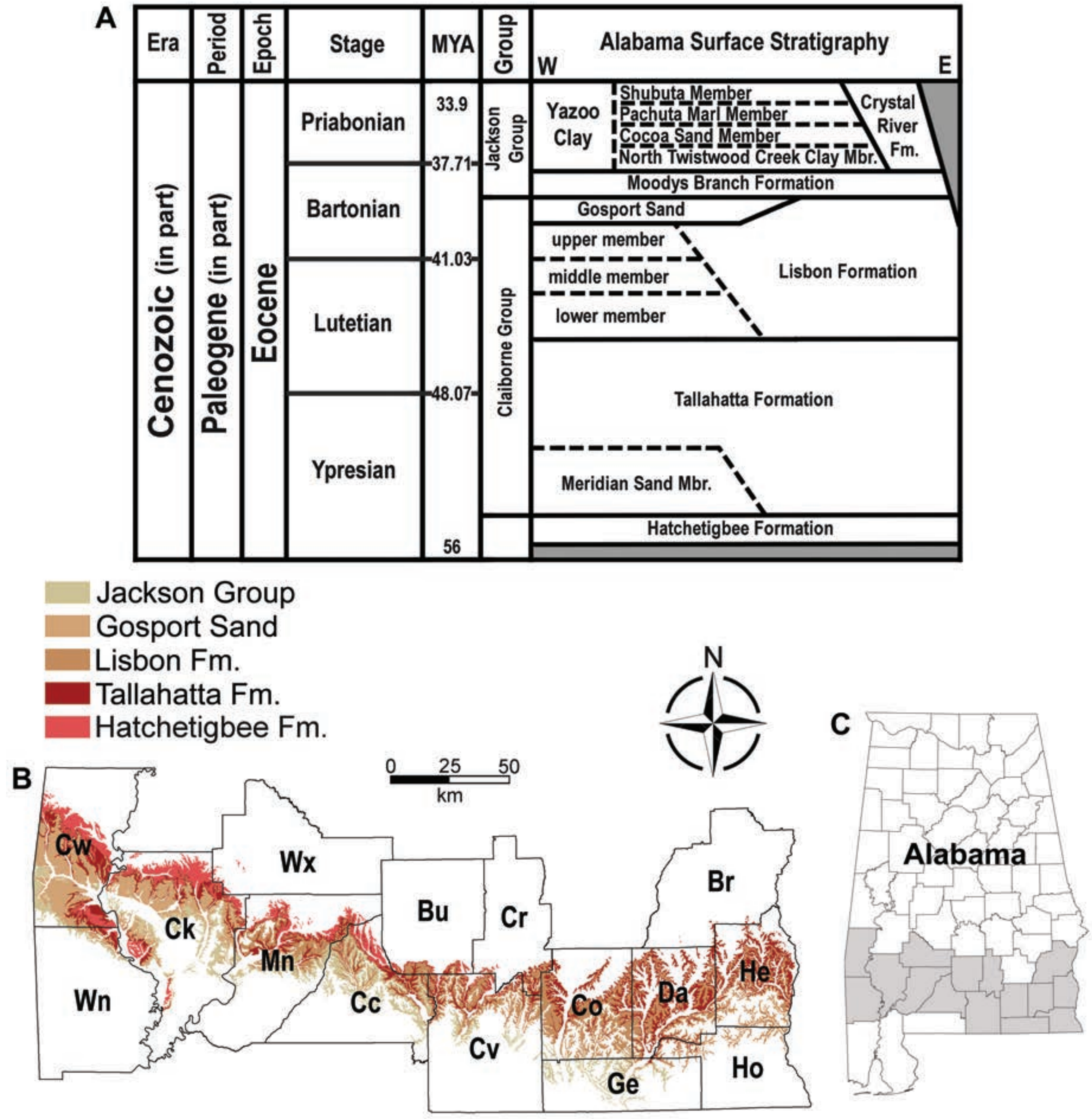
Herein, we describe 21 newly recognized elasmobranch and bony fish taxa from Paleogene units in Alabama. Some of these taxa have been previously reported but were not described or were presented with a different taxonomic assignment. To the latter point, we comment on the morphological criteria used to identify the taxa and discuss related taxonomic issues, and we provide an overview of the temporal and stratigraphic distributions of Paleogene fishes in the state.

GEOLOGICAL SETTING

Surface exposures in Alabama, USA, are numerous throughout the expansive and widespread Paleogene outcrop belt, which extends continuously for approximately 350 km in an essentially east-west oriented band across the southern portion of the state. Paleogene strata generally decrease in age in a southward direction and represent a nearly unbroken lithostratigraphic marine sequence that extends from the K/Pg boundary to the terminus of the Oligocene Epoch (Raymond *et al.* 1988; Text-fig. 1). Paleocene stratigraphic units have been mapped in 18 counties in Alabama, and their outcrop belts comprise approximately 8% of the total surface area of the state (Ebersole *et al.* 2024b; Text-fig. 1). Paleocene lithostratigraphic units in Alabama are placed within the Midway and Wilcox groups, with those in the Midway Group including, in ascending order, the Danian Clayton Formation (with Pine Barren



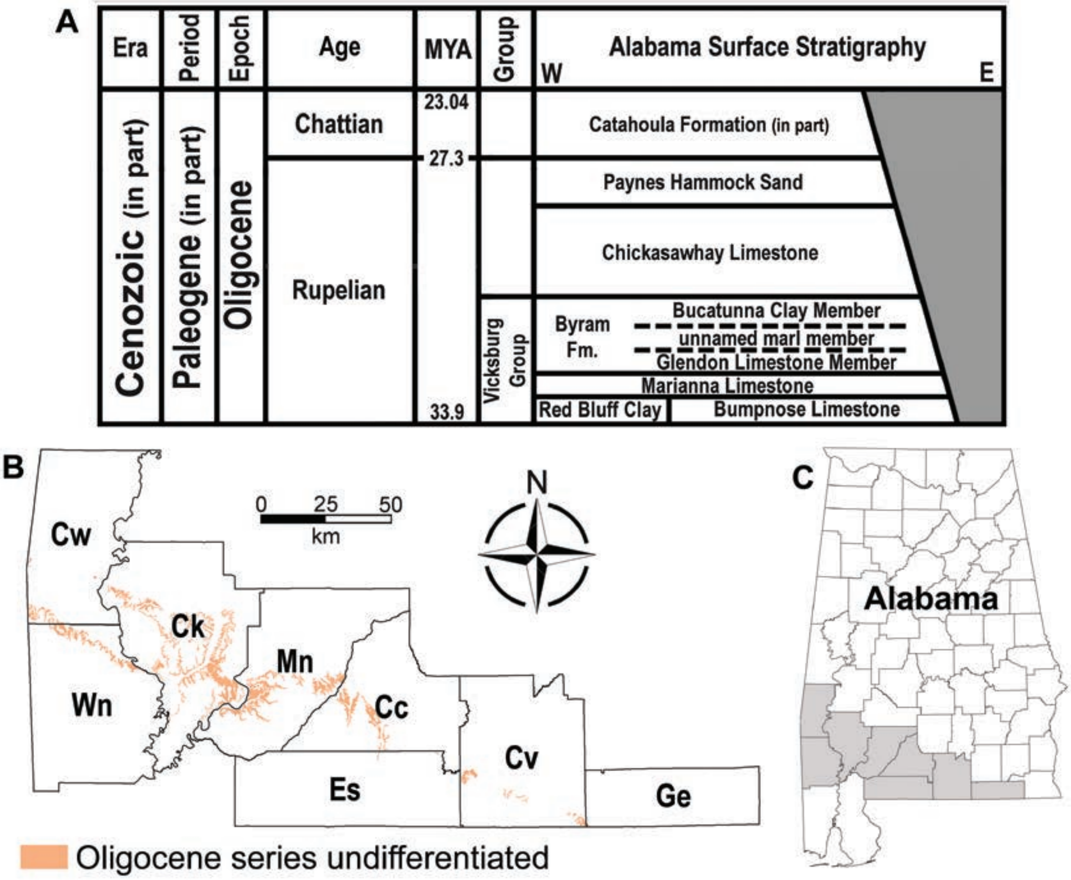
Text-fig. 1. Paleocene surface stratigraphy in Alabama. A – Stratigraphic chart showing Paleocene surface units in Alabama. Gray areas represent unconformities. B – Surface exposures of Paleocene stratigraphic units in Alabama. C – Map of Alabama showing counties containing Paleocene surface exposures. County abbreviations: Bk – Bullock; Br – Barbor; Bu – Butler; Cc – Conecuh; Ck – Clarke; Co – Coffee; Cr – Crenshaw; Cv – Covington; Cw – Choctaw; Da – Dale; Ds – Dallas; He – Henry; Lo – Lowndes; Mn – Monroe; Mo – Marengo; Pk – Pike; Su – Sumter; Wx – Wilcox. Stratigraphic chart modified from Ebersole *et al.* (2025).



Text-fig. 2. Eocene surface stratigraphy in Alabama. A – Stratigraphic chart showing Eocene surface units in Alabama. Gray areas represent unconformities. B – Surface exposures of Eocene stratigraphic units in Alabama. C – Map of Alabama showing counties containing Eocene surface exposures. County abbreviations: Ge – Geneva; Ho – Houston; Wn – Washington; for other abbreviations see caption to Text-fig. 1. Stratigraphic chart modified from Ebersole *et al.* (2025).

and McBryde Limestone members), Porters Creek Formation (with Matthews Landing Marl Member), and the Selandian Naheola Formation (with Oak Hill and Coal Bluff members). In ascending order, the formations and members comprising the Wilcox Group include the Selandian–Thanetian Nanafalia Formation (with Gravel Creek Sand Member, the biohorizon '*Ostrea thirsae* beds', and Grampian Hills Member), and Tuscahoma Sand (with Greggs Landing Marl and Bells Landing Marl members) (Raymond *et al.* 1988; Text-fig. 1).

Eocene units have been mapped in 16 counties in Alabama and comprise approximately 5.61% of the state's land area (Ebersole *et al.* 2024c; Text-fig. 2). The Eocene strata in Alabama are divided into the Wilcox, Claiborne, and Jackson groups, with the lone



Text-fig. 3. Oligocene surface stratigraphy in Alabama. A – Stratigraphic chart showing Oligocene surface units in Alabama. Gray areas represent unconformities. B – Surface exposures of Oligocene stratigraphic units in Alabama. C – Map of Alabama showing counties containing Oligocene surface exposures. County abbreviations: Es – Escambia; Ge: Geneva; Wn – Washington; for other abbreviations see caption to Text-fig. 1. Stratigraphic chart modified from Ebersole *et al.* (2025).

Eocene unit in the Wilcox Group being the Ypresian Hatchetigbee Formation (with Bashi Marl Member). The units within the Claiborne Group include, in ascending order, the Ypresian–Lutetian Tallahatta Formation (with Meridian Sand Member), the Lutetian–Bartonian Lisbon Formation (with 'lower,' 'middle,' and 'upper' members), and the Bartonian Gosport Sand. The Jackson Group is comprised of the Bartonian Moodys Branch Formation, Priabonian Crystal River Formation, and the Priabonian Yazoo Clay Formation (with North Twistwood Creek Clay, Cocoa Sand, Pachuta Marl, and Shubuta members; Raymond *et al.* 1988; Text-fig. 2).

Oligocene surface units have been mapped in eight counties in Alabama and comprise approximately 0.46% of the state's surface (Ebersole *et al.* 2024c; Text-fig. 3). In ascending order, these Oligocene strata include the Rupelian Red Bluff Clay, Bumpnose Limestone Formation, Forest Hill Sand, Marianna Limestone (with Mint Spring Marl Member), Byram Formation (with Glendon Limestone, 'unnamed marl,' and Bucatunna Clay members), Chickasawhay Limestone, Paynes Hammock Sand, and Chattian Catahoula Formation. All the Oligocene units underlying the Chickasawhay Limestone are included within the Vicksburg Group (Raymond *et al.* 1988; Text-fig. 3).

The depositional environments amongst these units vary but mostly represent shallow, nearshore, subtropical to tropical marine environments, nearly all of which are extremely fossiliferous (see references cited herein). Although the Paleogene surface units in Alabama are almost exclusively marine (Whetstone and Martin 1978; Thurmond and Jones 1981; Ehret and Ebersole 2014; Ebersole *et al.* 2019, 2021, 2024b; Stringer *et al.* 2020a), terrestrial vertebrates have been documented from some of the strata (Thurmond and Jones 1981; Westgate 2001).

Number	Taxon	Lithostratigraphic Unit	Age	County	Text-fig.
MSC 45338	*Otodus* sp.	Chickasawhay Limestone	Rupelian	Washington County	Text-fig. 4
MSC 33481.1–2	*Striatolamia cederstroemi*	Porters Creek Formation	Danian	Butler County	Text-fig. 5G–I, R–T
MSC 34829.1–2	*Striatolamia cederstroemi*	Porters Creek Formation	Danian	Butler County	
MSC 35805.1–4	*Striatolamia cederstroemi*	Porters Creek Formation	Danian	Butler County	
MSC 41071	*Striatolamia cederstroemi*	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	
MSC 42514	*Striatolamia cederstroemi*	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 5J–M
MSC 42515	*Striatolamia cederstroemi*	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 5X–Z
MSC 42516	*Striatolamia cederstroemi*	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 5A–C
MSC 42517	*Striatolamia cederstroemi*	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 5N–Q
MSC 42518	*Striatolamia cederstroemi*	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 5U–W
MSC 42519.1–30	*Striatolamia cederstroemi*	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	
MSC 45351.1–2	*Striatolamia cederstroemi*	Clayton Formation	Danian	Dallas County	
MSC 45352.1–3	*Striatolamia cederstroemi*	Clayton Formation	Danian	Wilcox County	
MSC 45353	*Striatolamia cederstroemi*	Clayton Formation	Danian	Wilcox County	
MSC 45354	*Striatolamia cederstroemi*	Clayton Formation	Danian	Wilcox County	Text-fig. 5D–F
MSC 45355	*Striatolamia cederstroemi*	Clayton Formation	Danian	Wilcox County	
MSC 45356	*Striatolamia cederstroemi*	Clayton Formation	Danian	Wilcox County	
MSC 42728.1–3	*Odontaspis substriata*	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 6A–D, E–F
MSC 38262	*Odontaspis substriata*	Hatchetigbee Formation	Ypresian	Butler County	Text-fig. 6G–H
MSC 38477	*Odontaspis substriata*	Tallahatta Formation	Ypresian	Dale County	Text-fig. 6I–K
MSC 37950	*Microscyliorhinus leggetti*	Hatchetigbee Formation	Ypresian	Butler County	Text-fig. 7
MSC 35003	*Hemipristis intermedia*	Pachuta Marl Member of the Yazoo Clay	Priabonian	Washington County	Text-fig. 8A–C
MSC 50819	*Hemipristis intermedia*	Pachuta Marl Member of the Yazoo Clay	Priabonian	Washington County	Text-fig. 8D–F
MSC 44567	*Physogaleus* aff. *contortus*	Yazoo Clay	Priabonian	Washington County	Text-fig. 9
MSC 50034	‘*Sphyrna*’ *robustum*	Red Bluff Clay	Rupelian	Monroe County	Text-fig. 10
MSC 35018	*Galeocerdo* aff. *platycuspidatum*	Chickasawhay Limestone	Rupelian	Washington County	Text-fig. 11A–C
MSC 50815	*Galeocerdo* aff. *platycuspidatum*	Chickasawhay Limestone	Rupelian	Washington County	Text-fig. 11D–F
SC2012.47.10	*Casierabatis* cf. *lambrechtsi*	Lisbon Formation	Lutetian	Covington County	Text-fig. 12
MMNS VP-7297.1	*Hypolophities* sp.	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 13A–E
MMNS VP-8178	*Hypolophities* sp.	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 13F–J
MMNS VP-7298	Myliobatidae indet.	Pine Barren Member of the Clayton Formation	Danian	Lowndes County	Text-fig. 14
MSC 2996	‘*Rhinoptera*’ *prisca*	Clayton Formation	Danian	Lowndes County	Text-fig. 15A–E
MSC 3001.1–2	‘*Rhinoptera*’ *prisca*	Clayton Formation	Danian	Lowndes County	
MSC 3022	‘*Rhinoptera*’ *prisca*	Clayton Formation	Danian	Dallas County	Text-fig. 15F–J
MSC 3074.1–2	‘*Rhinoptera*’ *prisca*	Clayton Formation	Danian	Dallas County	Text-fig. 15K–O
MSC 34783	‘*Rhinoptera*’ *prisca*	Porters Creek Formation	Danian	Butler County	
MSC 34823	‘*Rhinoptera*’ *prisca*	Porters Creek Formation	Danian	Butler County	
MSC 38241	*Pterothrissus conchaeformis*	Hatchetigbee Formation	Ypresian	Butler County	Text-fig. 16
MSC 42228	*Synodus* sp.	Red Bluff Clay	Rupelian	Clarke County	Text-fig. 17
ALMNH:Paleo:681	*Holocentrities ovalis*	Marianna Limestone	Rupelian	Clarke County	Text-fig. 18A
ALMNH:Paleo:682	*Holocentrities ovalis*	Marianna Limestone	Rupelian	Clarke County	Text-fig. 18B
MSC 42232	*Arnoglossus* sp.	Red Bluff Clay	Rupelian	Clarke County	Text-fig. 19

Number	Taxon	Lithostratigraphic Unit	Age	County	Text-fig.
MSC 42231	*Centropristis* aff. *priaboniana*	Red Bluff Clay	Rupelian	Clarke County	Text-fig. 20
MSC 35778.1–2	Lutjanidae indet.	Tallahatta Formation	Ypresian	Dale County	Text-fig. 21A–C
MSC 37242	Lutjanidae indet.	Lisbon Formation	Lutetian	Covington County	
MSC 37307.1–2	Lutjanidae indet.	Lisbon Formation	Lutetian	Covington County	Text-fig. 21H, I
MSC 37515	Lutjanidae indet.	Gosport Sand	Bartonian	Clarke County	Text-fig. 21F, G
MSC 38109	Lutjanidae indet.	Hatchetigbee Formation	Ypresian	Washington County	
MSC 38349.1–2	Lutjanidae indet.	Hatchetigbee Formation	Ypresian	Washington County	
MSC 38443	Lutjanidae indet.	Contact of the Tallahatta and Lisbon formations	Lutetian	Covington County	
MSC 38444	Lutjanidae indet.	Contact of the Tallahatta and Lisbon formations	Lutetian	Covington County	Text-fig. 21D, E
MSC 38488	Lutjanidae indet.	Lisbon Formation	Lutetian	Covington County	
MSC 38532	Lutjanidae indet.	Tallahatta Formation	Ypresian	Dale County	
MSC 42225	aff. *Scorpaenopsis* sp.	Matthews Landing Marl Member of the Porters Creek Formation	Danian	Wilcox County	Text-fig. 22
MSC 42203	*Aplodinotus distortus*	Chickasawhay Limestone	Rupelian	Washington County	Text-fig. 23
MSC 2402	*Lobodus pedemontanus*	Gosport Sand	Bartonian	Choctaw County	Text-fig. 24I–L
MSC 34991	*Lobodus pedemontanus*	Pachuta Marl Member of the Yazoo Clay	Priabonian	Washington County	Text-fig. 24A–D
MSC 35001	*Lobodus pedemontanus*	Pachuta Marl Member of the Yazoo Clay	Priabonian	Washington County	
MSC 40447	*Lobodus pedemontanus*	Marianna Limestone	Rupelian	Washington County	Text-fig. 24E–H
MSC 42055	*Lobodus pedemontanus*	Yazoo Clay	Priabonian	Washington County	
MSC 42543	*Lobodus pedemontanus*	Tallahatta/Lisbon formation contact	Lutetian	Covington County	
MSC 45581	*Lobodus pedemontanus*	Pachuta Marl Member of the Yazoo Clay	Priabonian	Clarke County	
MSC 45582	*Lobodus pedemontanus*	Pachuta Marl Member of the Yazoo Clay	Priabonian	Washington County	

Table 1. Paleogene specimens from Alabama, USA, examined in this study.

METHODS

The vast majority of the fossils we discuss herein were collected by one or more of the current authors, but specimens that were historically collected were also examined. Unfortunately, historically collected specimens did not always have detailed information associated with them, and it was often not clear if the specimens were surface collected or obtained through bulk sampling. However, the minute size of some of the historically collected Paleogene fish specimens examined in this study do indicate they were likely obtained through bulk sampling and subsequent processing with microscopic examination. Bulk sampling employed by the present authors involved wet screening in nested sieves down to a 0.25 mm mesh (US Standard Sieve No. 60), which ensured that micro-vertebrate remains were recovered. A majority of fish specimens separated out in the 0.50 mm (US Standard Sieve No. 35) or larger mesh sizes, and specimens (typically otoliths) smaller than 0.5 mm often represented plesiomorphic juveniles. The residue from the wet screening was air dried to prevent damage from heating. Concentrates from the different sieve sizes were sorted with the use of binocular microscopes.

The non-otolith fossils we examined were compared to extant specimens within the neontological skeletal collections at McWane Science Center and South Carolina State Museum, whereas fossil otoliths were compared to material within the reference collections of one of the present authors (GLS). The fossil specimens discussed herein are listed in Table 1. Figured specimens exceeding 5.0 mm in greatest dimension were photographed at MSC with a Nikon D-80 camera with Tamron macro-lens, and those smaller than 5.0 mm in greatest dimension were photographed with a Wild Photomakroskop M400 microscope with mounted Canon EOS R50 camera. To account for depth of field, specimens were photographed from several focal lengths, and the resulting photographs were stacked and merged in Helicon

Focus 8 software. The final figures and plates were produced in Adobe Photoshop v. 22.5.9.

The higher taxonomic rankings for elasmobranchs and bony fishes generally adhere to Nelson *et al*. (2016), whereas we typically follow Wiley and Johnson (2010) for ordinal names and Van der Laan *et al.* (2024) for family-group names. We utilized Fricke *et al.* (2024) and Froese and Pauly (2024) for attribution of naming authors of extant genera and species. Descriptive terms for elasmobranch teeth largely follow Shimada (2002) and Cappetta (2012), whereas the tooth group terminology follows Siverson (1999) and Cicimurri *et al.* (2020). We adhere to the work of Koken (1884), with revisions from Weiler (1942) and Schwarzhans (1978), for morphological terminology of the sagittal otoliths (the otolith found in the sacculus of the labyrinth).

Institutional abbreviations

ALMNH – Alabama Museum of Natural History, Tuscaloosa, Alabama, USA;
MMNS VP – Mississippi Museum of Natural Science, Jackson, Mississippi, USA;
MSC – McWane Science Center, Birmingham, Alabama, USA;
SC – South Carolina State Museum, Columbia, South Carolina, USA.

SYSTEMATIC PALEONTOLOGY

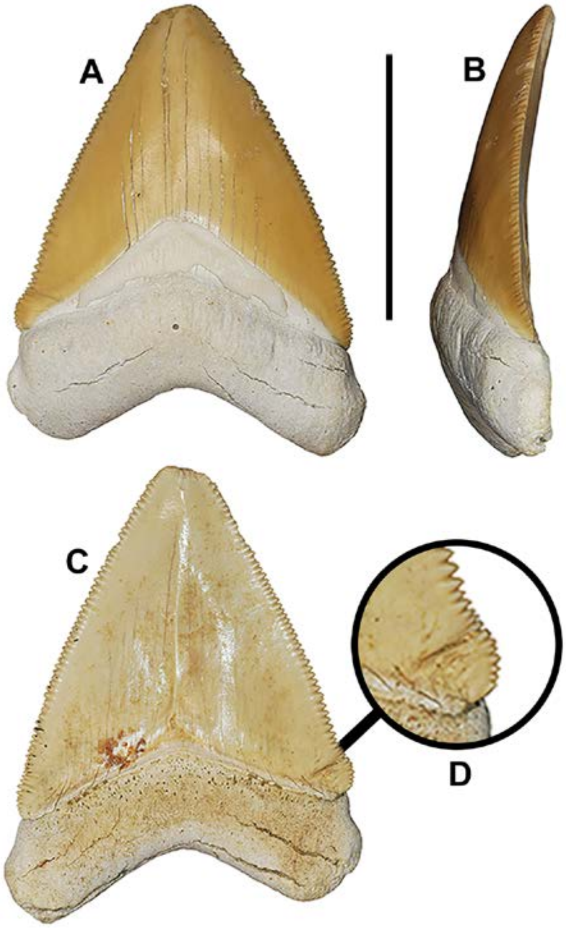
Class Chondrichthyes Huxley, 1880
Subclass Euselachii Hay, 1902
Infraclass Elasmobranchii Bonaparte, 1838
Division Selachii Cope, 1871
Order Lamniformes Berg, 1937
Family Otodontidae Glückman, 1964
Genus *Otodus* Agassiz, 1838
Otodus sp.
(Text-fig. 4)

MATERIAL: MSC 45338.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Oligocene (upper Rupelian, NP24) Chickasawhay Limestone.

DESCRIPTION: MSC 45338 is a tooth measuring roughly 5.5 cm in apico-basal height and 4 cm in mesio-distal width. The crown is broadly triangular with convex mesial and distal cutting edges. Both cutting edges are coarsely serrated, with serrations being triangular, pointed, and rather evenly developed along the edge. The serrations are simple, with one or two serrae being incompletely subdivided into smaller serrations. Although the cutting edges are complete to the crown foot, there is a very slight constriction near the crown base and a barely perceptible convexity where the edges meet the root. Within the constricted portion of the mesial cutting edge, the serrations are noticeably smaller and more closely spaced compared to the rest of the cutting edge. This phenomenon also occurs on the distal side, but the enamel is also folded, and these structures result in a very inconspicuous cusplet. The labial crown face is flat and smooth, whereas the lingual face is broadly convex but also smooth. In profile view, the crown has a uniform labial curvature. In lingual view, the crown and root are separated by a chevron-shaped dental band. The root is massive, with relatively short but widely spaced, sub-rectangular mesial and distal lobes (the mesial lobe is slightly narrower and more elongated). The interlobe area is deep and U-shaped. There is a conspicuous foramen positioned on a weak lingual protuberance.

REMARKS: The lateral cusplets on this specimen are very inconspicuous, being entirely united to the base of the main cusp and barely raised beyond the general trend of the mesial and distal cutting edges (Text-fig. 4D). This tooth morphology is unusual compared to other specimens recovered from the Chickasawhay Limestone in Alabama and neighboring Mississippi, all of which (n=4) exhibit distinct lateral cusplets that are clearly separated from the main cusp by a conspicuous notch. Although it is possible that the varied morphologies indicate the co-occurrence of two distinct otodontid sharks within the Chickasawhay Limestone, the teeth may also represent heterodonty within a single species. Gottfried and Fordyce (2001) reported an associated *O.* (*C.*) *angustidens* Agassiz, 1843 dentition from the Chattian of New Zealand that exhibits significant variation in lateral cusplet morphology, with some teeth having distinct cusplets, others reduced cusplets, and still other teeth lacking cusplets altogether. The New Zealand specimen indicates that the various Chickasawhay Formation teeth could belong to the same taxon. We note here that the biconvex cutting edges on the crown of MSC 45338 differ from those on the teeth discussed by Gottfried and Fordyce (2001), all of which have a much narrower crown, suggesting the Chickasawhay Formation specimen does not represent the same taxon as the New Zealand specimen, or *O.* (*C.*) *an-*



Text-fig. 4. *Otodus* sp., upper right anterior tooth, MSC 37844, Rupelian, Chickasawhay Limestone, Washington County, Alabama, USA, in lingual (A), mesial (B) and labial (C) views, and (D) close-up of distal cusplet. Scale bar equals 3 cm.

gustidens dentitions are even more variable than previously known.

Otodus teeth with highly reduced lateral cusplets like those on the Alabama specimen are comparable to those described by Agassiz (1839) as *Carcharodon subauriculatus*, a taxon he based on three anterior teeth derived from an unknown locality and stratum. Gemmellaro (1857) later suggested that *C. subauriculatus* teeth were a variety of *Otodus* (*Megaselachus*) *megalodon* (Agassiz, 1843) and Leriche (1926) subsequently concluded that the *subauriculatus* and *megalodon* morphologies were from one and the same taxon. Based on an associated dentition derived from the Miocene of North Carolina, Purdy *et al.* (2001) resurrected use of the *subauriculatus* name (therein referring it to the genus *Carcharodon*) and included within their paradigm several teeth that Leriche (1926) identified as *Otodus* (*Megaselachus*) *chubutensis* (Ameghino, 1901). However, Perez *et al.* (2019) later referred Purdy *et al.* (2001)'s North Carolina specimen to *O.* (*M.*) *chubutensis*, despite the former having priority. Although Leriche (1926) and Perez *et al.* (2019) considered *C. subauriculatus* and *O.* (*M.*) *chubutensis* to be conspecific, the latter is primarily known from Neogene deposits elsewhere (Ameghino 1901; Cappetta 2012). Interestingly, Purdy *et al.* (2001) utilized the *subauriculatus* species name for numerous isolated teeth from the upper Oligocene (Chattian) Chandler Bridge Formation in South Carolina. If the species is valid, the temporal range of the taxon extends at least into the late Oligocene (i.e., Chattian). Complicating the matter, Miller *et al.* (2021) assigned all the teeth collected from the Ashley Formation (upper Rupelian) and Chandler Bridge Formation (Chattian) to *O.* (*C.*) *angustidens* based on the specimen reported by Gottfried and Fordyce (2001). The teeth illustrated by Miller *et al.* (2021, figs 3–5), as well as many Chandler Bridge Formation specimens in the SC collection, demonstrate the same variability in lateral cusplet morphology as observed by Gottfried and Fordyce (2001).

Following Cappetta (2012), unserrated *Otodus* teeth are generally referred to the subgenus *Otodus* (*Otodus*), serrated teeth with lateral cusplets to *Otodus* (*Carcharocles*), and serrated teeth with reduced to absent lateral cusplets to *Otodus* (*Megaselachus*). However, the referral of MSC 45338 to one of these subgenera is complicated based on our available Chickasawhay Formation sample. If all the Chickasawhay Formation teeth represent the same taxon, the morphologies overlap with those of *O.* (*C.*) *angustidens* as identified by Gottfried and Fordyce (2001) and Miller *et al.* (2021). However, assuming ancestor-descendent relationship between *O.* (*C.*) *angustidens* and *O.* (*M.*) *chubutensis*, the evolutionary timing of the divergence of these two taxa is unclear, and the latter taxon apparently exhibits a comparable variation in cusplet development, bringing into question when the latter first occurs in the fossil record. Due to our limited sample size and the taxonomic complexities outlined above, MSC 45338 is herein not assigned to a subgenus or species. Although several *Otodus* species have previously been reported from Alabama (Woodward 1889; Leriche 1942; Thurmond and Jones 1981; Feldmann and Portell 2007; Clayton *et al.* 2013; Ehret and Ebersole 2014; Maisch *et al.* 2014; Cappetta and Case 2016; Ebersole *et al.* 2019, 2024b), MSC 45338 is included herein because it is the first otodontid tooth exhibiting such convex cutting edges and highly reduced cusplet size.

Family Mitsukurinidae Jordan, 1898
Genus *Striatolamia* Glückman, 1964
Striatolamia cederstroemi Siverson, 1995

(Text-fig. 5)

MATERIAL: MSC 33481 (2 teeth), MSC 34829 (2 teeth), MSC 35805 (4 teeth), MSC 41071, MSC 42514, MSC 42515 (Text-fig. 5X–Z), MSC 42516, MSC 42517 (Text-fig. 5N–Q), MSC 42518, MSC 42519 (30 teeth), MSC 45351 (2 teeth), MSC 45352 (3 teeth), MSC 45353–45356.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Paleocene (Danian) Pine Barren Member of the Clayton Formation (NP1/2) and the Porters Creek Formation (NP3/4).

DESCRIPTION: All of the teeth available to us range between 1.0 to 2.5 cm in apico-basal height. The teeth consist of a crown and bilobate root, with the crown being developed into a rather narrow main cusp. The main cusp can be tall and nearly vertical or weakly to strongly distally inclined. The labial crown face is slightly convex and smooth, whereas the very convex lingual face can bear very fine longitudinal ridges that do not reach the crown apex. The cutting edges are smooth and continuous across the main cusp and onto a single pair of lateral cusplets. The mesial and distal cusplets are poorly separated from the main cusp, wide but very low, and bluntly pointed to weakly denticulated. The root lobes are divergent and elongated, with the mesial lobe generally being narrower and slightly longer than the distal lobe, and their extremities can be rounded to somewhat pointed. The interlobe area is wide and can be U-shaped or V-shaped. A lingual boss is bisected by a narrow nutritive groove.

REMARKS: The specimens in our sample exhibit some morphological variation, which we interpret as representing heterodonty within a single taxon. For

Text-fig. 5. Teeth of *Striatolamia cederstroemi* Siverson, 1995, Danian, Alabama, USA. A–C – MSC 42516, Pine Barren Member, Clayton Formation, Lowndes County, in lingual (A), labial (B) and mesial (C) views. D–F – MSC 45354, Clayton Formation, Wilcox County, in lingual (D), labial (E) and mesial (F) views. G–I – MSC 33481.2, Porters Creek Formation, Butler County, in lingual (G), labial (H) and mesial (I) views. J–M – MSC 42514, Pine Barren Member, Clayton Formation, Lowndes County, with (J) close-up of distal cusplet, and lingual (K), labial (L) and mesial (M) views. N–Q – MSC 42517, Pine Barren Member of the Clayton Formation, Lowndes County, with (N) close-up of distal cusplet, and lingual (O), labial (P) and mesial (Q) views. R–T – MSC 33481.1, Porters Creek Formation, Butler County, in lingual (R), labial (S) and mesial (T) views. U–W – MSC 42518, Pine Barren Member of the Clayton Formation, Lowndes County, in lingual (U), labial (V) and mesial (W) views. X–Z – MSC 42515, Pine Barren Member of the Clayton Formation, Lowndes County, in lingual (X), labial (Y) and mesial (Z) views. Scale bars equal 5 mm.

example, MSC 42515 (Text-fig. 5X–Z) appears to be an upper right third anterior tooth based on the mesial curvature of the cusp and the short but widely separated root lobes. MSC 42514 and MSC 42517 (Text-fig. 5N–Q) are upper right lateral teeth (monognathic heterodonty) based on their labio-lingually thinner cusp that is distally directed, whereas MSC 33481.2 is a lower left lateral based on the more erect stature of the main cusp (dignathic heterodonty).

These teeth can be differentiated from coeval *Mennerotodus mackayi* Cicimurri, Ebersole and Martin, 2020, by the wide but very low and blunt lateral cusplets and lack of denticulation between the main cusp and lateral cusplets. Siverson (1995) distinguished *S. cederstroemi* from *S. macrota* based in part on the comparatively weaker lingual ornamentation and low and blunt morphology of the lateral cusplets. In Alabama, the latter taxon is rather common in middle Eocene strata (Ebersole *et al.* 2019), but *S. cederstroemi* appears to be restricted to lower Paleocene strata, as the specimens described herein were recovered from the Danian Pine Barren Member of the Clayton Formation and the Porters Creek Formation (see Text-fig. 1).

Text-fig. 6. Teeth of *Odontaspis substriata* (Stromer, 1910), Paleogene, Alabama, USA. A–D – MSC 42728.1, Danian, Pine Barren Member, Clayton Formation, Lowndes County, in lingual (A), labial (C) and mesial (D) views, and (B) close-up of lingual crown ornamentation. E–F – MSC 42728.2, Danian, Pine Barren Member, Clayton Formation, Lowndes County, in lingual (E) and labial (F) views. G–H – MSC 38262, Ypresian, Hatchetigbee Formation, Butler County, in lingual (G) and labial (H) views. I–K – MSC 38477, Ypresian, Tallahatta Formation, Dale County, in lingual (I), labial (J), and mesial (K) views. Scale bars equal 2.5 mm (A–D, G, H) and 5 mm (E, F, I–K).

Family Odontaspididae Müller and Henle, 1839

Genus *Odontaspis* Agassiz, 1838

Odontaspis substriata (Stromer, 1910)

(Text-fig. 6)

MATERIAL: MSC 38262 (Text-fig. 6G, H), MSC 38477 (Text-fig. 6I–K), MSC 42728.1–3 (Text-fig. 6A–D, E, F).

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Paleocene (lower Danian) Pine Barren Member of the Clayton Formation (NP1/2), lower Eocene Hatchetigbee Formation (lower Ypresian, NP10) and Tallahatta Formation (upper Ypresian, NP12).

DESCRIPTION: Our sample consists of anterior and lateral teeth. The anterior teeth range between 9 to 11 mm in apico-basal height and 6 to 7 mm in mesio-distal width. The main cusp is tall and either erect or slightly distally inclined. The labial face of the main cusp is slightly convex, whereas the lingual face is strongly convex. The labial crown face is smooth, but the lingual crown face is ornamented with a series of faint longitudinal ridges extending up to two-thirds the height of the main cusp. The main cusp is flanked by one or two pairs of tall, narrow, and conical lateral cusplets. On teeth with two pairs of cusplets, the lateral-most pair is less than half the height of the larger, more medial pair. The lateral cusplets vary from erect to divergent, are lingually bent, and are ornamented with faint lingual ridges. The main cusp is slightly sigmoidal in mesial or distal views. The root is robust and has short and divergent root lobes with rounded extremities. A conspicuous nutritive groove occurs on a robust lingual root protuberance. The interlobe area is deep and U-shaped.

The single lateral tooth in our sample (MSC 42728.1; Text-fig. 6A–D) measures 4.5 mm in mesio-distal width and 5 mm in apico-basal height. The crown consists of a tall, narrow, sharply pointed main cusp that is flanked by two pairs of lateral cusplets. The main cusp has a weakly sigmoidal profile. The labial face of the main cusp is nearly flat and has smooth enameloid, whereas the lingual face is very convex and bears fine longitudinal ridges that extend to roughly one-half the cusp height. The longitudinal ridges are coarser and more readily apparent than those on the anterior teeth. The cutting edges are smooth and continuous. A lingual dental band is conspicuous. The tooth has two pairs of lateral cusplets that are tall, vertical, and needle-like, with the primary pair being more than twice the size of the secondary pair. In profile view, the cusplets are roughly conical, but the primary cusplets are crossed by smooth cutting edges. The lingual face of all cusplets bears conspicuous longitudinal ridges that extend nearly to the apex. The bilobate root has rather elongated, labio-lingually thin, highly diverging lobes with rounded extremities. There is a deep nutritive groove bisecting a thickened medial portion of the root. The interlobe area is wide and V-shaped.

REMARKS: Stromer (1910, p. 495) originally named this morphology as *Odontaspis elegans* var. *substriata* based on three teeth from the "early Tertiary of southern Togo". Arambourg (1952) later elevated this morphology to species status based on his analysis of teeth derived from the Danian of Morocco. Cicimurri *et al.* (2020) was the first to note the occurrence of *Odontaspis substriata* in Alabama, but these specimens were neither figured nor described. Two *Odontaspis* species are known from Alabama Paleogene strata, including *O. substriata* and *O. winkleri* Leriche, 1905. The teeth of these taxa are easily distinguished from one another by the presence of distinct lingual ornamentation on the main cusp and lateral cusplets of *O. substriata*, whereas crown enameloid on *O. winkleri* teeth is smooth.

Our analysis of Paleogene *Odontaspis* teeth from Alabama corroborates the identification of multiple species based on the presence or absence of crown ornamentation, which is not related to heterodonty because its presence/absence is consistent across all tooth positions and sizes. Based on this phenomenon, one specimen from the upper Ypresian Tallahatta Formation identified as *O. winkleri* by Ebersole *et al.* (2019) is herein considered *O. substriata* because under magnification it exhibits distinct lingual crown ornamentation. In Alabama, *O. substriata* specimens have been confirmed from the Danian Pine Barren Member of the Clayton Formation, Ypresian Hatchetigbee Formation and lower component of the Tallahatta Formation. Interestingly, the upper Ypresian to lower Lutetian Tallahatta Formation is the only unit in Alabama from which these two morphologies co-occur, as only smooth-crowned teeth occur in units below the Tallahatta Formation and only ornamented teeth occur above it. This further corroborates our assertion that *O. substriata* and *O. winkleri* are not conspecific, and the latter appears to have supplanted the former during the depositional history of the Tallahatta Formation.

Order Carcharhiniformes Compagno, 1973
Family Scyliorhinidae Gill, 1862
Subfamily Scyliorhininae Gill, 1862
Genus *Microscyliorhinus* Case, 1994
Microscyliorhinus leggetti Case, 1994
(Text-fig. 7)

MATERIAL: MSC 37950.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Eocene (lower Ypresian, NP10) Hatchetigbee Formation.

DESCRIPTION: The single specimen available to us measures roughly 3 mm in apico-basal height. In labial view, the crown is broad basally but narrows quickly to a distally directed cusp with a sharply pointed apex, the crown foot extends onto the mesial and distal root lobes, and the weakly convex face has some very weak longitudinal ridges at the distal crown foot. In contrast, the lingual face is very convex and has very fine longitudinal ridges extending at least two-thirds crown height (Text-fig. 7A). Mesial and distal cutting edges are smooth and largely restricted to the medial portion of the crown. The root has a prominent lingual boss, and the lobes are divided by a deep nutritive groove. The mesial lobe is more elongated than the distal lobe, and the extremities of both lobes are rounded. The lobes are rather closely spaced and the interlobe area is V-shaped. The basal attachment surface is flat.

REMARKS: MSC 37950 was recovered from the Ypresian (Zone NP10) Hatchetigbee Formation, and it appears to be conspecific with the type material of *Microscyliorhinus leggetti* described by Case (1994) from the Bashi Formation in Lauderdale County, Mississippi, USA. In Alabama, the Bashi is included as the lower member of the Hatchetigbee Formation, whereas in Mississippi, the Bashi is thicker and more

Text-fig. 7. Tooth of *Microscyliorhinus leggetti* Case, 1994, MSC 37950, Ypresian, Hatchetigbee Formation, Butler County, Alabama, USA, in lingual (A), mesial (B) and labial (C) views. Scale bar equals 1 mm.

detrital and considered a distinct lithological formation (Dockery and Thompson 2016). The small size and morphology of the MSC 37950 is unique and will not be confused with other Eocene shark taxa previously reported from Alabama (i.e., Ebersole *et al.* 2019).

Family Hemigaleidae Hasse, 1878
Genus *Hemipristis* Agassiz, 1835
Hemipristis cf. *intermedia* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025

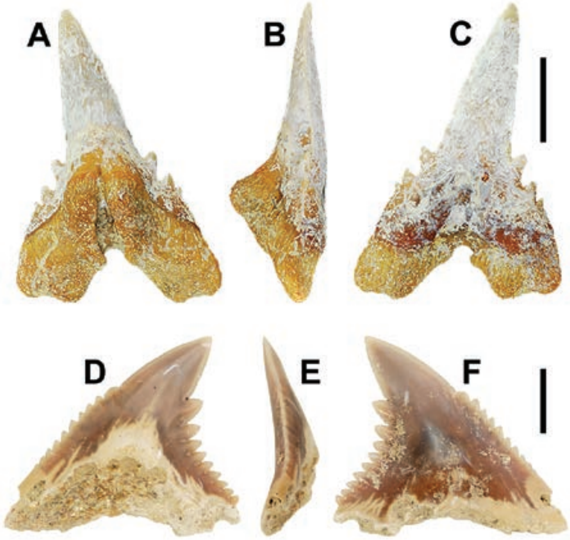
(Text-fig. 8)

MATERIAL: MSC 35003 (Text-fig. 8A–C), MSC 50819 (Text-fig. 8D–F).

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Upper Eocene (upper Priabonian, NP19/20) Pachuta Marl Member of the Yazoo Clay.

DESCRIPTION: MSC 35003 measures 1.4 cm in mesio-distal width and nearly 2 cm in apico-basal height. The tooth consists of a crown and bilobate root. The crown is tall, narrowly triangular, and slightly distally directed. In labial view, the crown foot is thickened, medially concave, and the mesial and distal sides appear to extend onto the root lobes. The lower one-third of the crown bears four denticles, but the upper two-thirds is developed into a narrow and sharply pointed cusp. The denticles decrease in size basally, with the apical denticle on each side being well separated from the cusp and succeeding denticle. The tertiary denticle is very small and situated close to the secondary denticle, whereas the quaternary denticle on each side is barely perceptible. The cusp is tall and narrow and has sharp, smooth mesial and distal cutting edges. In mesial view, the labial face is moderately convex and the lingual face is strongly convex. The crown enameloid appears to be smooth but there is a significant amount of ablation from plant roots. The root has rather short, wide, labio-lingually thin lobes that have scalloped extremities. The lobes are diverging and the interlobe area is narrow and V-shaped. A robust lingual boss is bisected by an elongated, narrow, and deep nutritive groove.

MSC 50819 measures 1.8 cm in crown width and 1.4 cm in crown height. The mesial cutting edge is elongated, distally directed, and very weakly convex. The basal two-thirds is heavily denticulated, but the apical one-third is smooth. The distal cutting edge is also elongated and deeply concave. The basal two-thirds of the distal edge bears nine very large denticles that decrease in size basally. The upper one-third of the edge is weakly convex and smooth. The smooth portions of the mesial and distal edges intersect apically to form a triangular and distally inclined cusp. The denticles on the mesial cutting edge are apically directed, whereas those on the distal edge are oblique to the crown height, and there are no accessory serrations. In mesial view, the labial face is somewhat convex, the lingual face is very convex, and enameloid is smooth. Additionally, the crown curves labially, particularly at the base. The root is not well preserved.



Text-fig. 8. Teeth of *Hemipristis* cf. *intermedia* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025, Ypresian, Alabama, USA. A–C – MSC 35003, Pachuta Marl Member, Yazoo Clay, Washington County, in lingual (A), mesial (B) and labial (C) views. D–F – MSC 50819, Yazoo Clay, Washington County, in lingual (D), mesial (E) and labial (F) views. Scale bars equal 5 mm.

REMARKS: Based on the gross morphologies of the specimens, MSC 50819 (Text-fig. 8D–F) is an upper left lateral tooth and MSC 35003 (Text-fig. 8A–C) is a lower left anterolateral tooth. Several Paleogene species of *Hemipristis* have been reported, including *H. curvatus* Dames, 1883, *H. intermedia*, *H. serra* Agassiz, 1835, and *H. tanakai* Tomita, Yabumoto and Kuga, 2023. Of these species, *H. curvatus* occurs in middle Eocene strata of Alabama (Ebersole *et al.* 2019). However, *H. curvatus* teeth are easily distinguished from the material described above by the smaller overall tooth size, much reduced development of denticles, and larger proportion of cusp in relation to overall crown size. In contrast, Oligocene–Miocene *H. serra* teeth are even larger than the teeth in our sample, have much more extensive crown denticulation, and a relatively small cusp with respect to overall crown size.

MSC 35003 and MSC 50819 appear to fall within the morphological range of *H. intermedia* as described by Cicimurri *et al.* (2025) based on specimens derived from the basal Catahoula Formation (lower Chattian) of Mississippi. The Alabama teeth are of comparable size, have a similar number (and size) of mesial and distal denticles, and cusp size with respect to overall crown size is analogous. However, the limited sample size (n=2) and older geologic age of the Alabama material leads us to only tentatively regard the teeth as conspecific to the Mississippi taxon. Cicimurri *et al.* (2025) indicated that *H. intermedia* may occur in the upper Rupelian Ashley Formation of South Carolina, an occurrence that could bridge the temporal gap between the Mississippi and Alabama occurrences. If it is later shown that MSC 35003 and MSC 50819 indeed belong to *H. intermedia*, it would indicate this species co-occurs with *H. curvatus* in the Priabonian Yazoo Clay in Alabama, and that the latter supplanted the former.

With respect to *H. tanakai*, the species is based on limited material that is either incompletely preserved or collected from disparate global localities, and it is difficult to accurately compare the Alabama material to those specimens. However, Cicimurri *et al.* (2025) considered the likelihood that *H. tanakai* is a *nomen dubium*.

Family Carcharhinidae Jordan and Evermann, 1896
Genus *Physogaleus* Cappetta, 1980
Physogaleus aff. *contortus* Gibbes, 1849

(Text-fig. 9)

MATERIAL: MSC 44567.

Text-fig. 9. Tooth of *Physogaleus* aff. *contortus* Gibbes, 1849, MSC 37844, Rupelian, Chickasawhay Limestone, Washington County, Alabama, USA, in lingual (A), mesial (B) and labial (C) views. Scale bar equals 5 mm.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Upper Eocene (Priabonian) Yazoo Clay.

DESCRIPTION: The isolated tooth in our sample measures 1.1 cm in apico-basal height and 2.2 cm in mesio-distal width. The main cusp is broadly triangular and distally inclined. Its mesial cutting edge is very elongated, highly sinuous and finely serrated nearly to the apex. The sinuosity results in a highly convex medial portion, and in mesial view the cutting edge above this area has a twisted appearance. The distal cutting edge is shorter but also finely serrated along its basal two-thirds. These cutting edges intersect to form a sharply pointed apex. The labial and lingual crown faces are convex and smooth, and the enameloid at the labial crown foot is essentially flush with the root. The elongated distal heel bears a series of large denticles that decrease in size distally. Interestingly, the serrations of the distal cutting edge extend via a curved line onto the distal heel, such that the first (and largest) denticle is well separated from the base of the main cusp. The next denticle is also well separated from, and only approximately one-half the size of, the first denticle, and there is a diminutive denticle in between these structures. Only two additional denticles are large enough to see with the naked eye, and the remaining ones (2–3) are barely perceptible. The root is bilobate with rather short but highly diverging lobes that have rounded extremities. The robust lingual boss bears a conspicuous nutritive groove.

REMARKS: Two Eocene *Physogaleus* species have been reported from Eocene (Ypresian to Bartonian) strata in Alabama, including *Physogaleus secundus* (Winkler, 1874) and *P. alabamensis* (Leriche, 1942) (see Ebersole *et al.* 2019). These older species are easily distinguished from the Priabonian taxon by their unserrated mesial and distal cutting edges, straight mesial cutting edge, and transition from distal cutting edge to heel via a deep notch. The Yazoo Clay specimen differs from teeth recently reported from the slightly younger (Oligocene, lower Rupelian) Red Bluff Clay of Alabama (Ebersole *et al.* 2024b) by having a much more sinuous mesial crown edge and serrated (as opposed to smooth) mesial and distal cutting edges.

MSC 44567 possesses a twisted crown apex (Text-fig. 9B) and curving, serrated transition from distal cutting edge to heel (Text-fig. 9C), features also occurring on teeth identified as *Physogaleus contortus* (Gibbes, 1849). Cicimurri *et al.* (2025) recently commented that the type specimens of *P. contortus* may be those Gibbes (1849) collected from Oligocene (Rupelian) strata of South Carolina, rather than Neogene deposits of Virginia, USA. The Yazoo Clay tooth is more similar to Rupelian and Chattian specimens of *P. contortus* from South Carolina (Cicimurri and Knight 2009 and Cicimurri *et al.* 2022, respectively) rather than to specimens occurring in the Miocene–Pliocene elsewhere in the Atlantic Coastal Plain (i.e., Purdy *et al.* 2001). These latter specimens attain much larger size, have more evenly serrated mesial and distal cutting edges with serrations extending nearly to the apex, and the distal heel is usually coarsely to finely serrated rather than denticulated. Although there are morphological similarities between MSC 44567 and Oligocene teeth identified as *P. contortus* from South Carolina, additional specimens from the Yazoo Clay are necessary to help make more meaningful comparisons. Although MSC 44567 is tentatively assigned herein to *P. contortus*, it is also included because it is a *Physogaleus* morphology not previously encountered in Alabama.

Family Sphyrnidae Bonaparte, 1840
Genus *Sphyrna* Rafinesque, 1810
‘*Sphyrna*’ *robustum* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025

(Text-fig. 10)

MATERIAL: MSC 50034.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Upper Oligocene (lower Rupelian, NP21) Red Bluff Clay.

DESCRIPTION: The single specimen in our sample measures 9 mm in mesio-distal width and 5 mm in apico-basal height. This tooth has a short and triangular main cusp that is distally inclined. The cutting edges are smooth, with the elongated mesial edge being slightly sinuous and the shorter distal edge slightly concave. The distal crown base is represented as a short and slightly convex heel. The intersection of the distal heel and distal cutting edge forms a nearly 90º angle. Crown enameloid is smooth. The labial face of the crown is rather flat but the lingual face is convex. The tooth has a slight labial curve in profile view. The intersection of the root and crown is straight labially but triangular on the lingual face. The mesial and distal root lobes are rounded, and there is a low and rounded lingual protuberance. A shallow nutritive groove forms a conspicuous basal notch on the otherwise straight root base. At least two conspicuous nutritive foramina are visible within the lingual nutritive groove.

Text-fig. 10. Tooth of ‘*Sphyrna*’ *robustum* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025, MSC 50034, Rupelian, Red Bluff Clay, Monroe County, Alabama, USA, in lingual (A), mesial (B) and labial (C) views. Scale bar equals 5 mm.

REMARKS: This tooth was previously identified as ‘*Sphyrna*’ sp. by Ebersole *et al.* (2024b), being left in open nomenclature because of the single specimen available for evaluation. However, Cicimurri *et al.* (2025) later examined a large number of sphyrnid teeth from the lowermost Catahoula Formation (lower Chattian) in Mississippi that they referred to two new taxa, including ‘*Sphyrna*’ *robustum* and ‘*Sphyrna*’ *gracile*. MSC 50034 is comparable to the type specimens from Mississippi and therefore herein referred to ‘*Sphyrna*’ *robustum*. This identification theretofore extends the biostratigraphic range of this species into the Rupelian and the paleobiogeographic range slightly eastward to Alabama. Following Ebersole *et al.* (2024b) and Cicimurri *et al.* (2025), the genus name is included in quotation marks to indicate its affinity to extant *Sphyrna* and denote that it may belong to a different, presently unknown, genus as is indicated by molecular divergence estimates (i.e., Lim *et al.* 2010).

Family Galeocerdonidae Poey, 1875
Genus *Galeocerdo* Müller and Henle, 1837

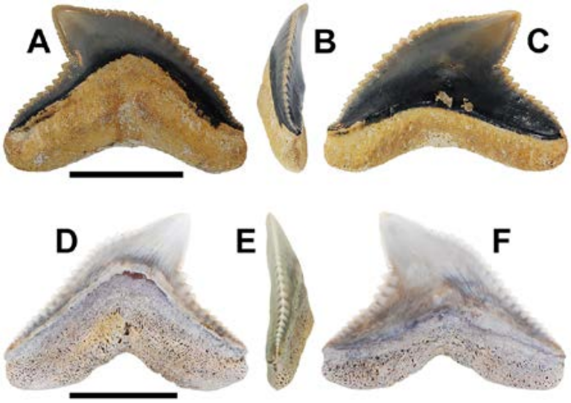
Galeocerdo aff. *platycuspidatum* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025
(Text-fig. 11)

MATERIAL: MSC 35018 (Text-fig. 11A–C), MSC 50815 (Text-fig. 11D–F).

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Oligocene (upper Rupelian, NP24) Chickasawhay Limestone.

DESCRIPTION: MSC 35018 measures 2.1 cm in mesio-distal width and 1.4 cm in apico-basal height. The crown consists of a main cusp and distal heel. The mesial cutting edge is very elongated and generally strongly and evenly convex, although there is a weakly concave portion near the apex. This edge is very coarsely serrated, with the largest serrations occurring medially and decreasing in size basally and apically. The distal cutting edge is much shorter, lingually inclined, and finely serrated to the apex. The mesial and distal cutting edges intersect apically to form a broad and distally inclined cusp. The high, elongated distal heel is oblique to crown height and bears 11 denticles that decrease in size towards the distal crown margin. The intersection of the distal cutting edge and distal heel is a sharp oblique angle (>120º) marked by a deep notch. The serrations are compound, with the large serrae of the mesial cutting edge bearing finer serrae on the apical edge and often the basal edge. The distal heel denticles also bear serrations on the apical edges. The labial crown face is rather flat but basally convex such that it slightly overhangs the root, and in mesial view the apical region is distinctively labially curved. The lingual face is uniformly convex. The crown enameloid is smooth. The root is very low in labial view but high lingually, and bilobate with widely diverging lobes that extend only a short distance beyond the crown margins. The lobe extremities are rounded, and the interlobe area is shallow and U-shaped. There is a wide and shallow, medially located lingual nutritive groove.

MSC 50815 is a slightly larger tooth measuring 2.5 cm in mesio-distal width and 1.9 cm in apico-basal height. The mesial cutting edge is elongated and exhibits a significant convexity on the apical part. The edge is serrated, with the largest serrations being located on the most convex portion. The serrations are slightly smaller on the basal one-half but are of uniform size nearly to the crown foot. The apical serrations on the mesial edge are smaller and decrease in size to the apex. The distal cutting edge is much shorter, weakly convex, and finely serrated, with serrations being of the same size as those on the apical portion of the mesial cutting edge. The mesial and distal cutting edges intersect apically to form a broad distally inclined cusp. The high distal heel is oblique to the crown height, elongated, and bears 13 denticles that decrease in size towards the distal crown margin. The intersection of the distal cutting edge and distal heel is an acute angle (<80º) marked by an abrupt transition from serrated distal cutting edge to the distal heel. The serrations are compound, with the large serrae of the mesial cutting edge bearing finer serrae on the apical and basal edges. The distal heel denticles also bear serrations on the apical and basal edges. In mesial view, the crown is labially curving. The lingual face is convex and the crown enameloid is smooth. The labial crown foot is thickened and overhangs the root. The bilobate root is very low in labial view but high in lingual view, and lobes are widely diverging and do not extend beyond the crown margins. The distal and basal lobe extremities are rounded, and the interlobe area is deep and V-shaped. There is a wide and shallow, medially located lingual nutritive groove.



Text-fig. 11. Teeth of *Galeocerdo* aff. *platycuspidatum* Cicimurri, Ebersole, Stringer, Starnes and Phillips, 2025, Rupelian, Chickasawhay Limestone, Washington County, Alabama, USA. A–C – MSC 35018 in lingual (A), mesial (B) and labial (C) views. D–F – MSC 50815 in lingual (D), mesial (E) and labial (F) views. Scale bars equal 1 cm.

REMARKS: Two Eocene *Galeocerdo* species have been verified from Eocene strata of Alabama, including *G. eaglesomei* White, 1955 and *G. clarkensis* White, 1956 (Ebersole *et al.* 2019). The former taxon is easily distinguished from MSC 35018 and MSC

50815 by the very high crown with comparatively small cusp, and simple serrations (i.e., no serrae on primary serrations). The two teeth in our sample were both derived from the uppermost Chickasawhay Limestone (upper Rupelian) and differ from White's (1956) *G. clarkensis* holotype (which was derived from the Priabonian Yazoo Clay in Clarke County, Alabama) by their wider cusp and more complexly serrated cutting edges. The mesial cutting edge of the two Chickasawhay Formation teeth is also more convex than on specimens from the Bartonian Gosport Sand that were identified as *G. clarkensis* by Ebersole *et al.* (2019), and the serrations of the former specimens are also more complex.

Two *Galeocerdo* sp. teeth recently reported from the lower Rupelian Red Bluff Clay in Monroe County, Alabama (Ebersole *et al.* 2024b), are rather small and have very narrow main cusps compared to those of MSC 35018 and MSC 50815. Additionally, the distal heel of the Red Bluff Clay specimens is comparatively shorter with far fewer (five), albeit much larger, denticles. With respect to the main cusp, that of MSC 35018 (Text-fig. 11A–C) represents only 40% of the total crown width (cusp width measured from the distal notch to the opposite side on the mesial cutting edge), and that of MSC 50815 (Text-fig. 11D–F) is 47% of crown width. The cusp widths of these specimens are less than those of a species recently described from the stratigraphically younger Catahoula Formation (lower Chattian) of Mississippi (Cicimurri *et al.* 2025). This taxon, *Galeocerdo platycuspidatum* Cicimurri *et al.*, 2025 has a cusp width averaging 51% of total crown width. Other than this discrepancy, the gross morphology of the Chickasawhay material in terms of number of denticles and serration complexity, are also consistent with *G. platycuspidatum*. However, our sample consists only of two specimens that are slightly older in age (late Rupelian *vs.* early Chattian) and we only tentatively assign these teeth to *G. platycuspidatum*. A larger number of specimens is needed to confirm if the Chickasawhay Limestone taxon indeed represents *G. platycuspidatum*, as the possibility exists that the two teeth represent an intermediate taxon between this species and the temporally older *G. clarkensis*.

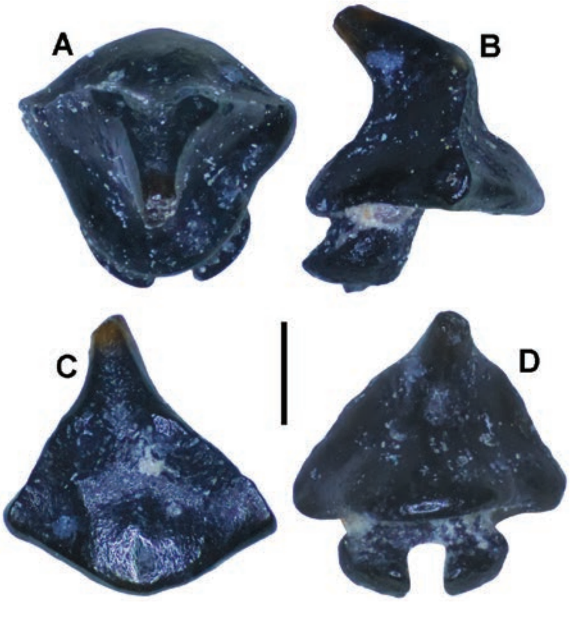
Division Batomorphi Cappetta, 1980
Order Myliobatiformes Compagno, 1973
Suborder Myliobatoidei Compagno, 1973
Family Dasyatidae Jordan and Gilbert, 1879
Genus *Casierabatis* Reinecke, Mollen, Gijsen, D'Haeze and Hoedemakers, 2024

Casierabatis cf. *lambrechtsi* Reinecke, Mollen, Gijsen, D'Haeze and Hoedemakers, 2024
(Text-fig. 12)

MATERIAL: SC2012.47.10.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Upper Eocene (lower Lutetian, NP15) Lisbon Formation.

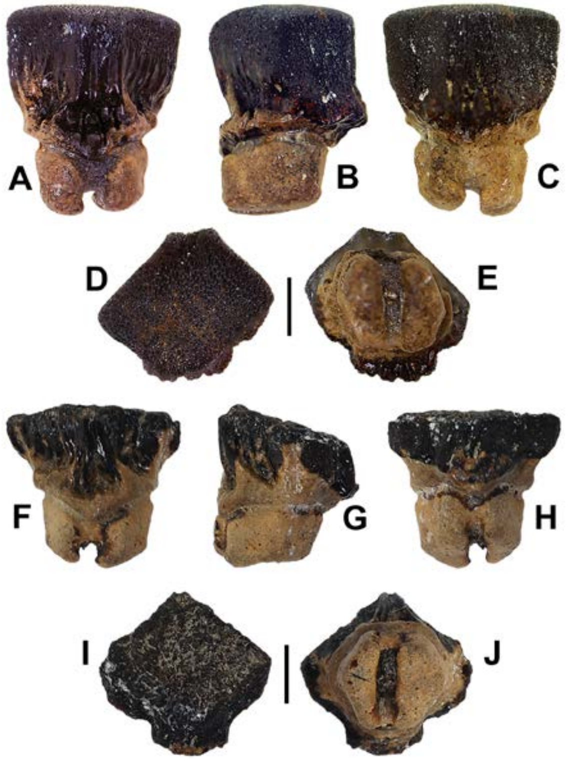
DESCRIPTION: Our sample consists of a single small tooth that measures less than 1.5 mm in apicobasal height. This tooth is distinctive by having a cuspidate crown that, in mesial or distal views, has a cusp that is lingually angled near the apex (Text-fig. 12B). A sharp transverse crest divides the crown into larger lingual and smaller labial parts, both of which have triangular crown faces. The lingual crown margin is strongly concave in mesial or distal views. Conversely, the labial margin is strongly sinuous and the upper third of the crown is conspicuously angled lingually. The upper third of the labial crown face is distinctively concave towards the apex, whereas the lower two-thirds is slightly convex. The main cusp is evenly tapered and terminates at a blunt apex. Both the labial and lingual visors are convex in occlusal view and have laterally projected mesial and distal edges at the junction where the transverse crest meets



Text-fig. 12. Male tooth of *Casierabatis* cf. *lambrechtsi* Reinecke, Mollen, Gijsen, D'Haeze and Hoedemakers, 2024, SC 2012.47.10, Lutetian, Lisbon Formation, Covington County, Alabama, USA, in occlusal (A), distal (B), labial (C) and lingual (D) views. Scale bar equals 0.5 mm.

the crown foot. The crown foot is slightly concave in mesial or distal views but is straight in labial or lingual views. A robust medial ridge divides the lingual crown face into unequal mesial and distal sides. The medial portion of the labial crown face has a weak pitted ornamentation, whereas the remainder of the crown enameloid is smooth. The root is only half the height of the crown and constricted just below the crown foot. The root lobes are weakly divergent, lingually projected, and have rounded extremities that extend beyond the lingual crown foot. The root lobes are separated by a deep U-shaped interlobe area.

REMARKS: Ebersole *et al.* (2019, fig. 40u–x) figured a male tooth that was derived from the basal Lisbon Formation in Covington County, Alabama, that they thought represented a high-crowned, male breeding variant of '*Dasyatis*' *jaekeli* (Leriche, 1905). However, based on a large sample of teeth derived from lower Eocene (Ypresian) deposits in Belgium, Reinicke *et al.* (2024) commented that this tooth may belong to their newly erected genus, *Casierabatis*, and possibly to their new species *Casierabatis lambrechtsi*. We concur that SC2012.47.10 is assignable to *Casierabatis*, but because it is younger in age than the type specimens from Belgium (Lutetian *vs.* Ypresian) and exhibits weaker labial crown ornamentation, we only tentatively assign it to *C. lambrechtsi*.



Text-fig. 13. Teeth of *Hypolophities* sp., Danian, Pine Barren Member, Clayton Formation, Lowndes County, Alabama, USA. A–E – MMNS VP-7297.1 in lingual (A), mesial (B), labial (C), occlusal (D) and basal (E) views. F–J – MMNS VP-8178 in lingual (F), profile (G), labial (H), occlusal (I) and basal (J) views. Scale bars equal 2 mm.

Genus *Hypolophities* Stromer, 1910
Hypolophities sp.
(Text-fig. 13)

MATERIAL: MMNS VP-7297.1 (Text-fig. 13A–E), MMNS VP-8178 (Text-fig. 13F–J).

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Paleocene (lower Danian, NP1/2) Pine Barren Member of the Clayton Formation.

DESCRIPTION: MMNS VP-8178 is a pristine tooth measuring 7 mm in total apico-basal height. The crown height measures 5 mm and represents 71% of the total tooth height. In occlusal view, the crown has a six-sided outline that is slightly wider (6 mm) than long (5 mm). Of the labial and lingual faces, there is a narrow medial portion, but the mesio-labial/lingual and disto-labial/lingual portions are more extensive. These faces are straight and ornamented basally with a network of sinuous longitudinal ridges that grade apically into a reticulated network of finer ridges. In labial/lingual views, the crown margins are vertical but taper basally, whereas in profile view the crown margins are vertical and roughly parallel. The crown foot is rather smooth and in labial/lingual views there is a slight constriction just apical to the crown base. In profile view, there is a slight labial projection extending from the crown foot, whereas the lingual crown foot is developed into a short and rounded transverse ridge. The medial portion of the lingual crown foot extends basally as a short uvula. The crown overhangs the root labially and laterally but is even with the lingual root face. The bilobate root has short lobes that are separated by a relatively shallow and narrow nutritive groove. In basal view, the root attachment surfaces are convex, pentagonal but with a sub-triangular outline, and the mesial lobe has a larger surface area compared to the distal lobe.

MMNS VP-7297.1 (Text-fig. 13A–E) is a highly worn specimen (through *in vivo* use), but the remaining portion is morphologically comparable to MMNS VP-8178 (Text-fig. 13F–J). This tooth measures 5.5 mm in greatest apico-basal height. The crown of MMNS VP-7297.1 is worn such that, in lingual view, the occlusal surface is flat and perpendicular to crown height. However, in profile view the surface is flat and oblique to crown height (i.e., lingually inclined). Additionally, the occlusal outline is more diamond-shaped compared to that of MMNS VP-8178.

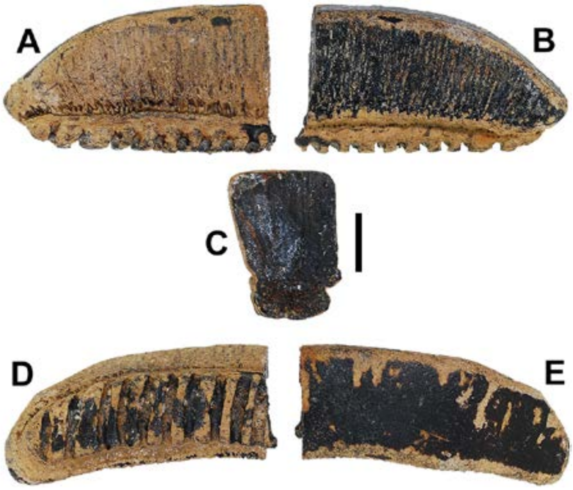
REMARKS: Two species of *Hypolophites* have been reported from Paleocene deposits of the USA, including *H. hutchinsi* Case, 1996 from the Hornerstown Formation of New Jersey and *H. beckeri* Maisch, 2020 from the Clayton Formation of Arkansas. Unfortunately, the legitimacy of each of these species is debatable because both appear to be based on poorly preserved specimens (i.e., highly worn through *in vivo* use) and possibly a mixture of multiple, distinct taxa. MMNS VP-7297.1 is a highly worn (*in vivo*) tooth that compares well to the worn specimens of *H. hutchinsi* and *H. beckeri* that have been reported. No pristine specimen of either of these species has been described and we therefore cannot know how these compare to MMNS VP-8178 (Text-fig. 13A–E). We consider the two Alabama specimens available to us to be conspecific, but for the reasons outlined above we do not speciate them.

Family Myliobatidae indet.
(Text-fig. 14)

MATERIAL: MMNS VP-7298.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Paleocene (lower Danian, NP1/2) Pine Barren Member of the Clayton Formation.

DESCRIPTION: The specimen is a partial upper symphyseal tooth that was wider than long. In occlusal view, the labial margin is concave but the lingual is margin convex, and the complete tooth would have had a U-shaped appearance. Furthermore, the preserved distal end exhibits an obtuse angle, with the rounded vertex being located closer to the labial margin. The profile at the broken end shows a very high crown with a weakly concave labial face that is rather vertical, a nearly straight lingual face that is lingually inclined, and flat and straight occlusal surface. Additionally, the labial crown foot is developed into a weak transverse shelf, and there is a thick, rounded, but relatively short transverse ridge at the lingual crown foot. This lingual ridge is separated from the remainder of the crown by a conspicuous but shallow transverse furrow. The labial and lingual faces bear numerous closely spaced, rather fine longitudinal ridges that extend from the crown foot nearly to the occlusal margin. These ridges are coarsest basally but become finer apically. In labial and lingual views, the thickest part of the crown is at the broken medial end, where it measures roughly 7 mm in height. Crown thickness is relatively consistent towards the distal end, where the occlusal surface abruptly curves basally toward the root, and the crown height is only approximately 2.5 mm. The root is very low, at less than 2 mm in height, and is overhung by the crown labially and distally. The lingual root face reaches the crown foot but does not extend beyond this structure. In basal view, the root is polyaulocorhize with 11 parallel and rather closely spaced lamellae separated by nutritive grooves. The lamellae have a slightly curved appearance and are of variable width.



Text-fig. 14. Upper sympnyseal tooth of Myliobatidae indet., MMNS VP-7298, Danian, Pine Barren Member, Clayton Formation, Lowndes County, Alabama, USA, in lingual (A), labial (B), profile (C), basal (D) and occlusal (E) views. Scale bars equal 5 mm.

REMARKS: Based on the morphology of the specimen, symphyseal teeth articulated with each other within the dentition by the lingually inclined lingual face of one tooth overlapping the lingually inclined labial face of the succeeding tooth. The longitudinal ridges on these faces would have interfingered with each other. Additionally, the labial transverse ridge would have fit into the lingual transverse furrow and overlapped the transverse ridge at the crown foot of the preceding tooth.

Although represented by a single tooth, this morphology appears to differ from that of ‘*Rhinoptera*’ *prisca* Woodward, 1907, described below. For example, the crown ornamentation of MMNS VP-7298 is finer than what we observed on all the ‘*Rhinoptera*’ specimens, even considering the moderate to extensive *in vivo* wear on the teeth of the latter. Also, the labial and lingual faces of MMNS VP-7298 are not as lingually inclined as the ‘*Rhinoptera*’ teeth, again taking into account the state of wear exhibited by the latter specimens. Furthermore, neither the labial crown foot nor the lingual transverse furrow is as pronounced as the equivalent features on the ‘*Rhinoptera*’ teeth. Lastly, the lingual transverse ridge of MMNS VP-7298 is straight rather than crenulated as on the ‘*Rhinoptera*’ teeth.

The single specimen in our sample represents the first tooth known from Alabama with this distinct morphology. With respect to its taxonomic placement, the overall morphology is consistent with upper symphyseal teeth of extant Myliobatidae like *Aetomylaeus* and *Myliobatis*, and to apparent Eocene relatives of these genera (i.e., Ebersole *et al.* 2019). Symphyseal teeth of Aetobatidae (*Aetobatus* and extinct relatives) lack lateral angles due to the absence of lateral files within the dentition, and the straight distal ends did not articulate with lateral teeth. Symphyseal teeth of Rhinopteridae (*Rhinoptera* and extinct relatives) have a relatively consistent thickness across tooth width, and the lateral angles are sharp and medially located. One feature consistent between MMNS VP-7298 and Rhinopteridae is the low root height and its abrupt termination at the lingual crown foot. In contrast, the root of Myliobatidae and Aetobatidae typically extend lingually well beyond the crown foot, although some *Myliobatis* and *Myliobatis*-type teeth exhibit a root morphology similar to that of the fossil specimen. For the purposes of this report, we assign the fossil to Myliobatidae based on its thick crown that abruptly thins at the distal end.

Family Rhinopteridae Bonaparte, 1835
Genus *Rhinoptera* Cuvier, 1829
‘*Rhinoptera*’ *prisca* Woodward, 1907

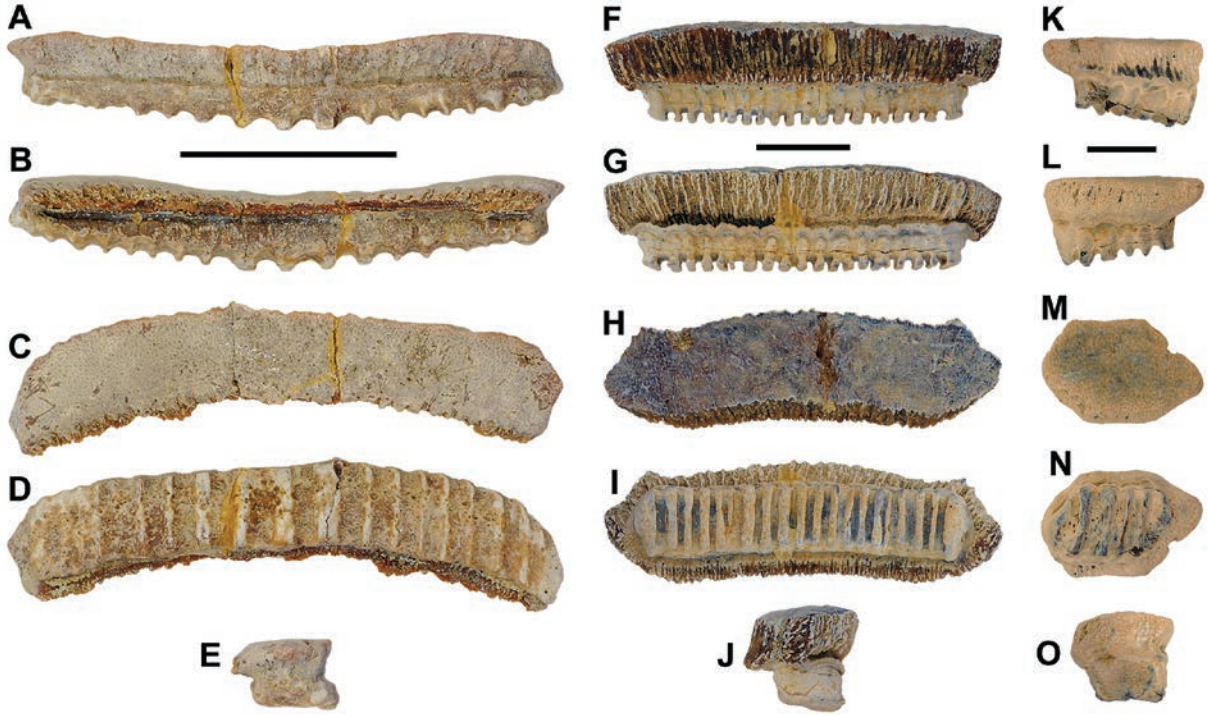
(Text-fig. 15)

MATERIAL: MSC 2996 (Text-fig. 15A–E), MSC 3001.1–2, MSC 3022 (Text-fig. 15F–J), MSC 3074.1–2 (Text-fig. 15K–O), MSC 34783, MSC 34823.1–3.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Paleocene Clayton Formation (lower Danian, NP1/2), Danian–Selandian (NP3/4) Porters Creek Formation,

DESCRIPTION: Three specimens, MSC 3001.1, MSC 3001.2, and MSC 3022 (Text-fig. 15F–J), are similar to each other in that they are roughly three times wider (mesio-distal) than long (labio-lingual) and have a sigmoidal occlusal outline. The largest of these three teeth, MSC 3022, measures 3.8 cm in mesio-distal width, 8 mm in labio-lingual depth, and 9 mm in apico-basal height. In profile view, the labial and lingual crown faces are lingually inclined, with the labial face being concave and lingual face convex. The labial crown foot is developed into a sharp shelf-like projection, and the crown face bears numerous prominent closely spaced, sharp-edged ridges extending from the crown foot and intersecting with the occlusal margin. The lingual crown ornamentation is similar but can be overlapped by a finer reticulated network of ridges near the occlusal surface. In occlusal view, the crown margin is highly irregular, and the acute lateral angles are medially located. In labial view, the occlusal surface of MSC 3001.1 and MSC 3001.2 is flat and straight, whereas that of MSC 3022 is weakly convex. The lingual crown foot bears a thick, rounded, and crenulated transverse ridge. This ridge is separated from the remainder of the crown by a deep furrow and from the root by a shallow irregular furrow. The high root (3–4 mm) has straight and vertical labial and lingual faces, and the basal surface is flat. In basal view, the root is polyaulocorhize with up to 19 closely spaced lamellae of variable width being separated by deep nutritive grooves. Lamellae are perpendicular to crown width. In lingual view, the nutritive grooves are keyhole-shaped, and the crenulations of the transverse ridge reflect the locations of root lamellae. The crown overhangs the root labially and laterally, but the root lamellae extend to the margin of the lingual transverse ridge.

MSC 2996 (Text-fig. 15A–E) is a large, highly worn (*in vivo*) and ablated (weathering) tooth that is 16 times wider than long. It measures 5 cm in mesio-distal width, 8 mm in labio-lingual depth, and 6 mm in apico-basal height. In occlusal view, the crown has a U-shaped outline due to the concave labial margin and convex lingual margin, and these margins are highly irregular. The distal end of one side is developed into a medially located lateral angle, whereas the opposite side is more uniformly convex and labially pointed. In profile view, the labial and lingual crown faces are lingually directed, and the lingual face is conspicuously higher than the labial face. In labial view, the occlusal surface is medially concave where it is worn nearly to the crown foot. The labial crown foot conspicuously overhangs the root, and the lingual transverse ridge is highly



Text-fig. 15. Teeth of '*Rhinoptera*' *prisca* Woodward, 1907, Danian, Clayton Formation, Alabama, USA. A–E – lower symphyseal tooth, MSC 2996, Lowndes County, in labial (A), lingual (B), occlusal (C), basal (D) and profile (E) views. F–J – upper symphyseal tooth, MSC 3022, Dallas County, in labial (F), lingual (G), occlusal (H), basal (I) and profile (J) views. K–O – lateral tooth, MSC 3074.1, Dallas County, in labial (K), lingual (L), occlusal (M), basal (N) and mesial (O) views. Scale bars equal 2 cm (A–E), 1 cm (F–J) and 5 mm (K–O).

ablated but still evident. The root is thickest medially but thins laterally, resulting in a convex basal surface. In basal view, at least 19 root lamellae are developed, but their width and height have been altered through post-mortem erosion. Root lamellae do not extend beyond the transverse ridge at the base of the lingual face.

MSC 3074.1 (Text-fig. 15K–O) is a much smaller tooth with a crown that is roughly twice as wide as long. This tooth measures 1.3 cm in mesio-distal width, 8 mm in labio-lingual depth, and 7 mm in apico-basal height. In occlusal view, the crown is six-sided and has sharp, medially located lateral angles. Interestingly, the distal angle is acute, more elongated, and sharper than the obtuse mesial angle. In profile view, the labial and lingual faces are lingually inclined. In labial view, the mesial side of the crown is higher than the distal side. Although the labial and lingual faces are ablated the bases of robust vertical ridges are preserved. The lingual transverse ridge is inconspicuous due to erosion. In basal view, the crown significantly overhangs the root labially and distally, less so mesially, and the root lamellae extend to the edge of the transverse ridge at the lingual crown foot. The root is polyaulacorhize and subdivided into six lamellae of varying width by nutritive grooves. Root lamellae are oriented oblique to crown width.

MSC 3704.2 is a small tooth having a crown that is nearly as long as it is wide. This tooth measures 8 mm in mesio-distal width, 6 mm in labio-lingual depth, and 6 mm in apico-basal height. In occlusal view, the six-sided crown has a highly irregular outline, and the sharp lateral angles are unevenly located (medially on the mesial side, labially on the distal side). In profile view, the labial and lingual faces are lingually inclined, and both faces bear large, narrow, closely spaced longitudinal ridges that extend to the occlusal surface. On the labial face, these ridges extend from the labial crown base, but lingually they originate above a basal transverse ridge. This transverse ridge is separated from the remainder of the crown by a deep furrow, and from the root by a shallower furrow. The ridge is also crenulated in the area of the root lamellae. In basal view, the root is subdivided into three lamellae by two nutritive grooves. The lateral lamellae have a sub-triangular appearance, with the mesial one being much larger than the distal one. The crown substantially overhangs the root distally and labially, less so mesially, and root lamellae extend to but not beyond the transverse ridge at the lingual crown foot. The root lamellae are oblique to the crown width. The remaining specimens in our sample, MSC 34783 and 34823.1–3, are represented by broken teeth that match the general morphology of the specimens described above.

REMARKS: Although there is variation in the available sample, we believe this reflects heterodonty within a single taxon rather than multiple species. The orientation of the labial and lingual crown faces, nature of crown ornamentation, morphology of the lingual transverse crown ridge, and morphology of the root are comparable among the specimens. The various shapes reflect monognathic and dignathic heterodonty, with specimens like MSC 2996 (Text-fig. 15A–E) representing a lower symphyseal file based on the basally convex root (root thick medially but thin laterally) and concave medial wear surface on the crown. In contrast, teeth like MSC 3022 (Text-fig. 15F–J) are from upper symphyseal files based on their great width, convex occlusal surface, and flat basal attachment surface (root equally thick across tooth width) with lamellae perpendicular to crown width. Teeth like MSC 3704.1 and MSC 3704.2 represent lateral files, as crowns are roughly equidimensional or only twice as wide as long, the mesial side of the crown is higher than the distal side, and root lamellae are oblique to crown width. The difference in crown width between MSC 3704.1 (Text-fig. 15K–O) and MSC 3704.2 could further indicate that tooth width gradually decreased towards the commissure, rather than abruptly changed from symphyseal to lateral files.

Based on their morphology, the teeth articulated with each other within the dentition to form a tightly packed dental pavement. The labial face of a tooth was overlapped by the lingual face of the preceding tooth, and the vertical ridges on both faces served to interlock the teeth. Additionally, the labial crown foot fit into the furrow near the lingual crown foot and also overlapped the lingual transverse ridge of the preceding tooth.

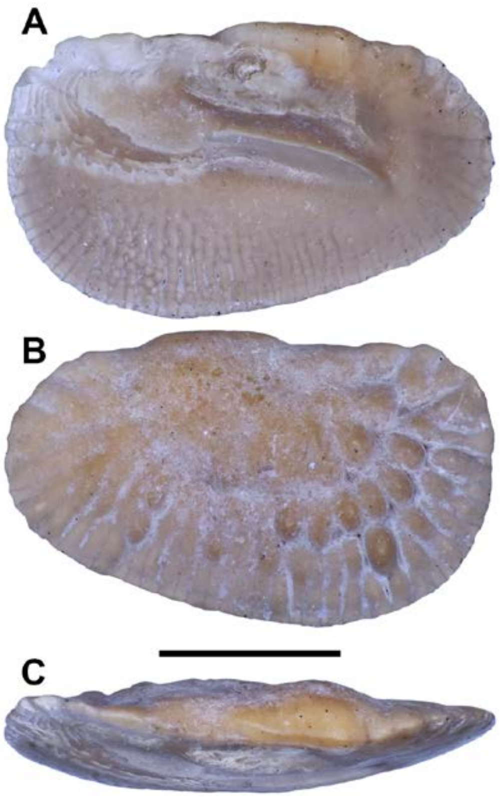
The tooth morphology and our hypothetical arrangement of the dentition are consistent with what we observed in dentitions of extant *Rhinoptera* that we examined (MSC 42598, SC88.120.1), and it is possible that this Danian taxon is related to modern Cownose rays. Although molecular divergence estimates indicate that Rhinopteridae diverged from Myliobatidae sometime during the Miocene (Villalobos-Segura and Underwood 2020), *Rhinoptera*-like teeth were found to be quite common in Eocene strata (Ypresian to Bartonian) of Alabama (Ebersole *et al.* 2019). The Alabama specimens are comparable to material that Woodward (1907) named as a new species, *Rhinoptera prisca*, from Danian deposits of Brazil. Although the fossils from these locations appear to be conspecific, it is likely they represent a taxon other than *Rhinoptera*. However, for the purposes of this report, we provisionally maintain the *prisca* morphology within this genus. This morphology appears to be restricted to the lower Paleocene of Alabama.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii *sensu* Goodrich, 1930
Unranked Neopterygii Regan, 1923
Division Teleosteomorpha Arratia, Scasso and Kiessling, 2004
Subdivision Teleostei Müller, 1845
Supercohort Teleocephala de Pinna, 1996
Cohort Elopomorpha Greenwood, Rosen, Weitzman and Myers, 1966
Order Albuliformes Greenwood, Rosen, Weitzman and Myers, 1966
Family Albulidae Bleeker, 1849
Subfamily Pterothrissinae Gill, 1893
Genus *Pterothrissus* Hilgendorf, 1877
Pterothrissus conchaeformis (Koken, 1885)
(Text-fig. 16)

MATERIAL: MSC 38241.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Eocene (lower Ypresian, NP10) Hatchetigbee Formation.

DESCRIPTION: The single sagitta available to us is primarily oval in shape (*sensu* Smale *et al.* 1995). The margins are mostly smooth, although some small lobes occur along the dorsal margin. The anterior margin is almost vertical and slightly rounded. The antero-dorsal margin is rounded and includes the ostial opening. The dorsal margin is almost horizontal with very slight undulations. The postero-dorsal margin is rounded to various degrees and forms a postero-dorsal angle with the posterior margin. The posterior margin is slightly convex but the postero-ventral margin is fairly straight. The ventral margin is very slightly convex and slants ventrally toward the expanded antero-ventral margin, which is rounded. The sagitta is characterized by a slightly convex in-



Text-fig. 16. Right sagitta of *Pterothrissus conchaeformis* (Koken, 1885), MSC 38241, Ypresian, Hatchetigbee Formation, Butler County, Alabama, USA, in inner (A), outer (B), and dorsal (C) views. Scale bar equals 2 mm.

ner face with a prominent sulcus that extends across approximately 85% of the length. The sulcus is primarily located dorsal of the median horizontal axis; however, the posterior portion of the cauda extends below the horizontal axis. The ostium opens on the antero-dorsal margin and is greater in height than the cauda. The cauda is approximately twice the length of the ostium and flexed downward slightly. The cauda is more excavated and is tapered at its tip. There is a slightly depressed area above the anterior of the cauda, and there is no ventral furrow. The outer face is relatively flat, has numerous oval rugosities, and has radial lines extending inward from the margins.

REMARKS: *Pterothrissus conchaeformis* sagittae have been reported from Europe and North America under various taxonomic names for over 100 years (Koken 1885, pl. 5, fig. 25; Roedel 1930, pl. 1, fig. 14). Schwarzhans (2003) identified specimens from the Paleocene of Bavaria and Austria as *Pteralbula conchaeformis*, but he later (Schwarzhans 2004) assigned this species to *Pterothrissus* based on his study of Paleocene specimens from Greenland. Schwarzhans and Stringer (2020) reported *P. conchaeformis* as being common in the Upper Cretaceous Kemp Clay of Texas and the Paleocene (Danian) Clayton Formation of Arkansas. Stringer and Schwarzhans (2021) later reported this species from the Upper Cretaceous Severn Formation in Maryland. This taxon appears to have been widely geographically distributed, but MSC 38241 represents the first published occurrence in Alabama.

Unranked Clupeocephala Patterson and Rosen, 1977
Cohort Euteleostei Rosen, 1985
Superorder Cyclosquamata Rosen, 1973
Order Aulopiformes Rosen, 1973
Suborder Aulopoidei *sensu* Nelson, Grande and Wilson, 2016
Family Synodontidae Gill, 1861
Subfamily Synodontinae Gill, 1861
Genus *Synodus* Scopoli, 1777
Synodus sp.
(Text-fig. 17)

MATERIAL: MSC 42228.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Oligocene (lower Rupelian, NP21) Red Bluff Clay.

DESCRIPTION: The sagitta is ablated, particularly on the anterior margin and the sulcus, and due to this erosion, its outline is best described as elliptic (*sensu* Smale *et al.* 1995). The margins range from smooth to irregular and undulating. The anterior margin is tapered and characterized by a sharply pointed rostrum and what may be a very small antirostum (it appears to be affected by erosion). The excisura is essentially straight and extends from the rostrum to the antirostrum at a 45º angle from the horizontal axis. The antero-dorsal margin is straight and slants at approximately 45º toward the dorsal margin. The dorsal margin is shallowly rounded and undulates. The postero-dorsal margin is rounded and does not form a distinct angle with the posterior margin. The posterior margin is rather evenly rounded with little taper. The postero-ventral margin is smoothly rounded and short. The ventral margin is shallow and broadly rounded. The antero-ventral margin is also shallow and rounded and tapers near the anterior margin and the rostrum.

The inner face is gently convex in both the hor-

Text-fig. 17. *Synodus* sp., right sagitta MSC 42228 (reversed), Rupelian, Red Bluff Clay, Clarke County, Alabama, USA, in inner (A) and dorsal (B) views. Scale bar equals 2 mm.

izontal and vertical directions. There is a heterosulcoid-type sulcus that extends from the anterior/antero-dorsal margins for approximately 85% of the length of the inner face. The ostium is only about one-half the length of the cauda. The height of the ostium appears to be slightly greater than the height of the cauda, but this is difficult to ascertain because of erosion. The ostium/cauda junction is V-shaped. The cauda is wavy and is slightly flexed towards its tip. The caudal tip is separated from the posterior margin. There is a distinct crista superior above the anterior half of the sulcus, but it terminates near the midpoint of the sulcus. There is a shallow dorsal depression that occurs above the crista superior, and there is an indication of a weak crista inferior. The ventral field is essentially smooth, and no ventral furrow is discernible. The outer face is primarily flat and smooth but there are some very slight, irregularly shaped sculptures.

REMARKS: *Synodus* sp. appears to be a rare component of the otolith assemblages across the Gulf Coastal Plain of the USA. For example, only one specimen of *Synodus* sp. was identified by Nolf and Stringer (2003, pl. 3, fig. 1a, b) among a sample of 5,599 otoliths they examined from the Yazoo Clay (Eocene, mainly Priabonian) in northeastern Louisiana. Their specimen represented one of the first reports of this genus in the fossil record. Lin and Nolf (2022) also reported a single *Synodus* specimen from the Moodys Branch Formation (Bartonian) in Mississippi, which was noted as being similar to the specimen reported by Nolf and Stringer (2003). Unfortunately, both specimens lacked sufficient diagnostic features for identification beyond the generic level. Schwarzhans *et al.* (2024) recognized two new species of *Synodus* based on 16 specimens derived from two different formations in Mississippi and one formation in Texas. The Alabama specimen appears to compare most favorably with *Synodus moodyensis* Schwarzhans, Stringer and Takeuchi, 2024, but this cannot be determined unequivocally until better preserved specimens are obtained.

Superorder Acanthopterygii Greenwood, Rosen, Weitzman and Myers, 1966
Series Berycida *sensu* Nelson, Grande and Wilson, 2016
Order Holocentriformes Betancur *et al.*, 2013
Family Holocentridae Bonaparte, 1833
Subfamily Myripristinae Nelson, 1955
Genus *Holocentrites* Conrad, 1941
Holocentrities ovalis Conrad, 1941
(Text-fig. 18)

MATERIAL: ALMNH:Paleo:681 (Text-fig. 18A), ALMNH:Paleo:682 (Text-fig. 18B).

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Oligocene (Rupelian, NP22) Marianna Limestone.

DESCRIPTION: Our sample consists of two groups of associated scales. The individual scales are strongly overlapped so that the lateral angles of any given scale are covered by those of adjacent scales. For most of the exposed scales, only the apical one-half to one-third is visible. The scales vary in size but can reach up to 2.0 cm in width and 1.5 cm in height. The individual scales are broader than deep and have an apical margin that is lined with straight ‘comb-like’ radii. The apical margin is broadly convex, and the basal margin is straight to slightly convex. The apical and basal margins converge at sharp lateral angles. The lateral surfaces of the scales are ornamented with distinctive parallel radii that extend to the apical margin. In contrast, the basal margin is mostly smooth, unornamented, and has no radii.

REMARKS: Groups of scales similar to those described herein have been observed by one of the present authors (JAE) within private collections that were derived from the Marianna Limestone in Conecuh County, AL. These scales appear to be identical to those on the type specimen of *Holocentrites ovalis* collected from the upper Eocene (Priabonian) deposits in Florida, USA (Conrad 1941). Subsequent reports have demonstrated that this taxon has a biostra-

Text-fig. 18. Articulated scales of *Holocentrities ovalis* Conrad, 1941, Rupelian, Marianna Limestone, Clarke County, Alabama, USA. A – ALMNH:Paleo:681; B – ALMNH:Paleo:682. Scale bars equal 2 cm.

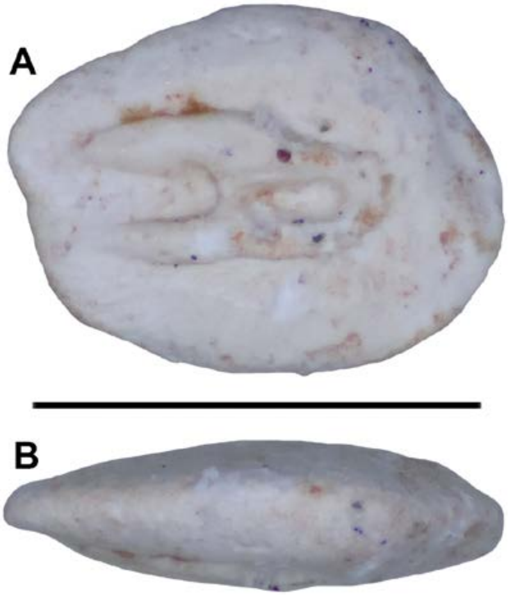
tigraphic range that extends into the early Oligocene, being collected from the Marianna Limestone and Glendon Limestone in Florida and Mississippi, respectively (Dunkle and Olsen 1959; Stewart 1992; Dockery and Thompson 2016). Herein we follow Stewart (1992) in assigning this genus to the Myripristinae.

Series Percomorpha *sensu* Nelson, Grande and Wilson, 2016
Subseries Ovalentaria Smith and Near in Wainwright *et al.*, 2012
Order Pleuronectiformes Nelson, Grande and Wilson, 2016
Suborder Pleuronectoidei Nelson, Grande and Wilson, 2016
Superfamily Pleuronectoidea Nelson, Grande and Wilson, 2016
Family Bothidae Smitt, 1892
Genus *Arnoglossus* Bleeker, 1862
Arnoglossus sp.
(Text-fig. 19)

MATERIAL: MSC 42232.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Oligocene (lower Rupelian, NP21) Red Bluff Clay.

DESCRIPTION: The sagitta has a discoid outline (*sensu* Smale *et al.* 1995) but is elongated in length. The margins are primarily smooth, but a few small undulations are present. The anterior margin is small, very slightly tapered on the dorsal and ventral edges, and rounded. The antero-dorsal margin is straight and slants toward the postero-dorsal margin at an approximately 25º angle. The dorsal margin is almost horizontal and slightly convex. The postero-dorsal, postero-ventral, and ventral margins are evenly rounded. The antero-ventral margin is almost straight and slants dorsally to the anterior margin. Both the outer and inner faces are convex. The inner face has a pleuronectid-type sulcus that extends from the anterior margin to about 70% of the length of the inner face. A circumsulcal depression is evident, as are the ostial and caudal collicula. The sulcus terminates well away from the posterior margin. The sulcus is slightly inframedian. The ostium appears greater in



Text-fig. 19. *Arnoglossus* sp., right sagitta MSC 42232, Rupelian, Red Bluff Clay, Clarke County, Alabama, USA, in inner (A) and dorsal (B) views. Scale bar equals 1 mm.

height and length than the cauda (although difficult to determine due to preservation). The cauda and caudal colliculum are shorter in length than the ostium and ostial colliculum. The caudal tip is rounded and appears to flex slightly dorsally. There is no depressed dorsal area, and no ventral furrow is present. The outer face is primarily smooth.

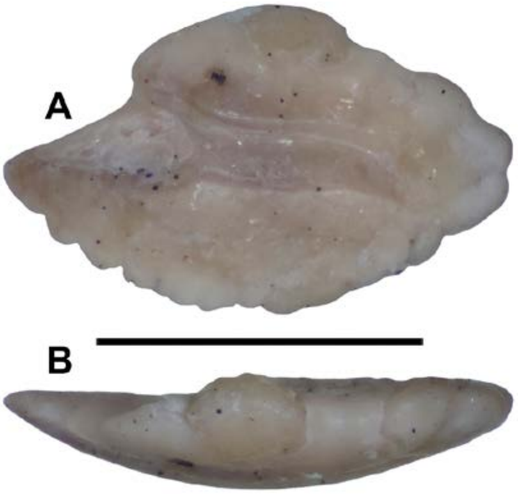
REMARKS: *Arnoglossus* is an extant taxon, with the type species being *Pleuronectes arnoglossus* Bloch and Schneider, 1801. In his treatise on fossil and extant Pleuronectiformes otoliths, Schwarzhans (1999) reported ten otolith-based fossil *Arnoglossus* species that range in age from the Eocene to the Pliocene. Although the inner face of MSC 42232 is somewhat eroded, the ostial and caudal collicula and the circumsulcal depression are evident. The degree of sulcus inclination of *Arnoglossus* sagittae ranges from almost horizontal to steeply inclined toward the antero-ventral margin, and Schwarzhans (1999) noted that small specimens of *Arnoglossus* (generally those less than 1.5 mm in length) are often very generalized in their morphological features, making even related species difficult to distinguish. Due to these factors and the preservation of our singular specimen, MSC 42232, is herein identified only to the genus level.

Order Perciformes *sensu* Nelson, Grande and Wilson, 2016
Family Serranidae Swainson, 1839
Subfamily Serraninae Swainson, 1839
Genus *Centropristis* Cuvier, 1829
Centropristis aff. *priaboniana* Nolf and Stringer, 2003
(Text-fig. 20)

MATERIAL: MSC 42231.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Oligocene (lower Rupelian, NP21) Red Bluff Clay.

DESCRIPTION: The outline of the sagitta is primarily oval (*sensu* Smale *et al.* 1995), but the outline is affected by its prominent rostrum. The margins range from sinuate to irregularly lobed. However, this is likely related to the presumed juvenile age of this specimen, which measures only 1.45 mm in length. The anterior margin is tapered and characterized by a well-developed and pointed rostrum, and the opening of the ostium onto the margin. The dorsal portion of the anterior margin is straight and slants at approximately 60º toward the dorsal margin. The antero-dorsal margin is rounded, whereas the dorsal margin is rounded and convex. The postero-dorsal margin is slightly rounded and characterized by numerous undulations and irregular lobes. The posterior margin is tapered and also has irregular lobes. The postero-ventral margin is slightly rounded with irregular lobes. The ventral margin is evenly rounded, convex, and has irregular lobes. The antero-ventral margin is slightly convex, and the lobes are more sinuate in nature.



Text-fig. 20. *Centropristis* aff. *priaboniana* Nolf and Stringer, 2003, right sagitta MSC 42231, Rupelian, Red Bluff Clay, Clarke County, Alabama, USA, in inner (A) and dorsal (B) views. Scale bar equals 1 mm.

The inner face is evenly convex and characterized by a rather prominent heterosulcoid-type sulcus that is medially horizontal in orientation. The sulcus extends from the anterior margin for approximately 80% of the length of the inner face. There is notable space between the termination of the sulcus and the posterior margin. The ostium extends nearly to the tip of the rostrum. The dorsal margin of the ostium is shorter and slants toward the antero-dorsal margin, whereas the ventral margin of the ostium is almost horizontal. The height of the ostium is slightly greater than the height of the cauda. The cauda is mainly horizontal with a small downturned component at the tip. The length of the cauda is approximately 1.25 times greater than that of the ostium. The outer face is nearly flat to slightly concave. The outer face is fairly regular.

REMARKS: *Centropristis priaboniana* was first identified by Nolf and Stringer (2003) based on 28 specimens recovered from the lower portion of the upper Eocene Yazoo Clay in northeast Louisiana. These represented a very small percentage (0.5%) of the 5,599 otoliths that were obtained from 465 kg of processed matrix. Other species of *Centropristis* also appear to be rather uncommon in otolith assemblages reported from elsewhere in the USA (Fitch and Lavenberg 1983; Müller 1999; Stringer and Bell 2018; Stringer *et al.* 2022).

MSC 42231 is thus far the only representative of the genus known from Alabama, and it appears to represent a juvenile individual because its length is only 1.45 mm and it has sinuate and lobed margins (*sensu* Smale *et al.* 1995). The specimen displays many of the characteristics of *Centropristis priaboniana* as illustrated by Nolf and Stringer (2003, pl. 1, figs 3–5 and especially fig. 6), but it differs by the presence of a large lobe on the antero-dorsal and dorsal margins (which may be related to the juvenile stage of the sagitta). The specimen is herein tentatively assigned to *C. priaboniana* until more and better-preserved specimens are recovered from Alabama, but if correctly identified the Red Bluff Clay occurrence represents a temporal range extension into the early Rupelian.

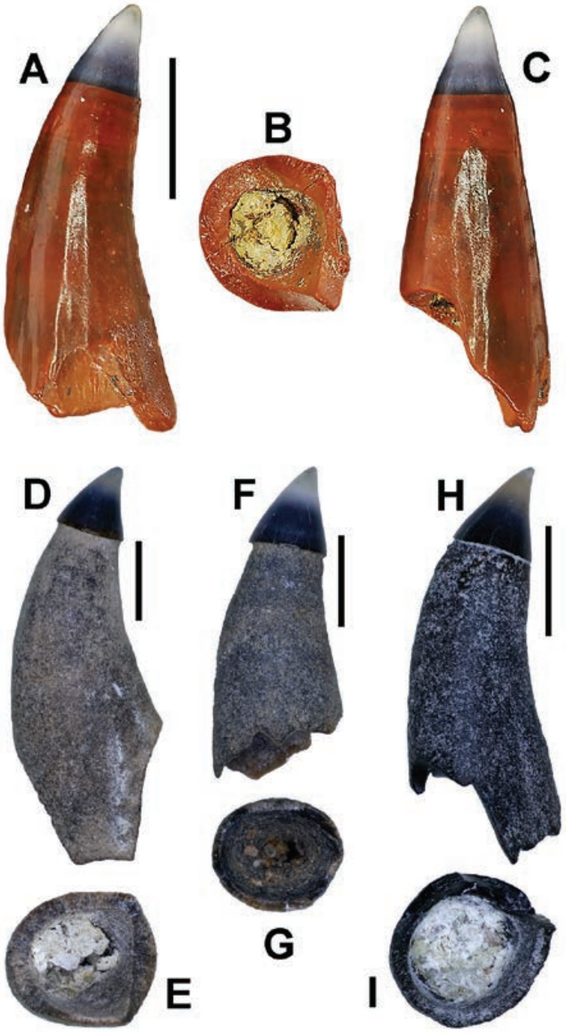
Family Lutjanidae Gill, 1861
Gen. et. sp. indet.
(Text-fig. 21)

MATERIAL: MSC 35778.1–2 (Text-fig. 21A–C), MSC 37242, MSC 37307 (Text-fig. 21H, I, MSC 37515 (Text-fig. 21F, G), MSC 38109, MSC 38349.1–2, MSC 38443, MSC 38444 (Text-fig. 21D, E), MSC 38488, MSC 38532.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower-to-middle Eocene Wilcox and Claiborne Group strata, including the Hatchetigbee (Ypresian, NP10), Tallahatta (Ypresian, NP12), and Lisbon (Lutetian, NP15) formations and the Gosport Sand (Bartonian, NP17).

DESCRIPTION: Our sample consists of 12 isolated teeth that measure less than 1.0 cm in apico-basal height. The teeth are conical with lateral edges that taper to a sharp point. The teeth are lingually recurved and lack carinae. The crown enameloid is smooth and lacks ornamentation. The enameloid at the apex of many specimens is translucent or often a different color than that covering the rest of the tooth. The enameloid on the main portion of the crown is extremely thin and eroded from most specimens, exposing the interior dentine (although the enameloid apex remains). The teeth are circular in basal view and have a large basal pulp cavity.

REMARKS: The teeth in our sample were originally assigned by Ebersole *et al.* (2019) to Osteoglossidae indet. based on their similarities to Eocene taxa like *Brychaetus* Woodward, 1901, *Phareodus* Leidy, 1873 and *Ridgewoodichthys* Taverne, 2004. However, evaluation of similar teeth from the Oligocene of Mississippi led Cicimurri *et al.* (2025) to conclude that they were likely derived from a Paleogene member of the Lutjanidae based on their identical shape



Text-fig. 21. Teeth of Lutjanidae indet., Eocene, Alabama, USA. A–C – MSC 35778.1, Ypresian, Tallahatta Formation, Dale County, in labial (A), basal (B) and mesial (C) views. D–E – MSC 38444, Lutetian, contact of the Tallahatta and Lisbon formations, Covington County, in labial (D) and basal (E) views. F–G – MSC 37515, Bartonian, Gosport Sand, Clarke County, in labial (F) and basal (G) views. H–I – MSC 37307.1, Lutetian, Lisbon Formation, Covington County, in labial (H) and basal (I) views. Scale bars equal 3 mm (A–C) and 2 mm (D–I).

to the canine teeth of extant *Lutjanus jocu* (Bloch and Schneider, 1801) that they examined (MSC 49315). Although extant osteoglossids are restricted to freshwater, marine representatives have been described from the Cretaceous and Paleogene of the U.K. (Casier 1966). However, it is more parsimonious that the teeth described above belong to Lutjanidae, a marine family that is common in Alabama waters today (Hoese and Moore 1998), rather than to a family of teleost that does not have an extant biogeographic range in this area.

Order Scorpaeniformes *sensu* Nelson, Grande and Wilson, 2016
Suborder Scorpaenoidei *sensu* Nelson, Grande and Wilson, 2016
Family Scorpaenidae Risso, 1827
Subfamily Scorpaeninae Risso, 1827
Tribe Scorpaenini *sensu* Nelson, Grande and Wilson, 2016
Genus *Scorpaenopsis* Heckel, 1837
aff. *Scorpaenopsis* sp.
(Text-fig. 22)

MATERIAL: MSC 42225.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Paleocene (Selandian, NP4) Matthews Landing Marl Member of the Porters Creek Formation.

DESCRIPTION: The outline of the sagitta is best described as oblong (*sensu* Smale *et al.* 1995), but with significantly more pointed anterior and posterior margins. The sagitta is significantly elongated and measures 3.1 mm in length and only 1.2 mm in height, resulting in a length-to-height ratio of 2.58. The greatest thickness (0.6 mm) occurs at the posterior portion of the sagitta. The margins vary from smooth, undulating, to irregularly lobed. The dorsal margin is significantly more undulating and irregularly lobed, whereas the ventral margin is primarily smooth. The anterior margin is greatly tapered and has a well-developed, pointed rostrum. The ventral portion of the ostium opens onto the anterior margin, whereas the dorsal portion opens on the antero-dorsal margin. The antero-dorsal margin is convex and rounded. The dorsal margin is higher than the antero-dorsal margin but is similarly rounded. The midpoint of the dorsal margin is conspicuously undulated. The postero-dorsal margin is characterized by numerous undulations and irregular lobes. The posterior margin is tapered with a slightly rounded tip. The postero-ventral margin is slightly rounded and shallow. The ventral margin is smooth, shallow, and convex. The antero-ventral margin is shallow, slightly convex, and smooth.

Text-fig. 22. aff. *Scorpaenopsis* sp., right sagitta MSC 42225, Danian, Matthews Landing Marl Member, Porters Creek Formation, Wilcox County, Alabama, USA, in inner (A) and dorsal (B) views. Scale bar equals 2 mm.

The inner face is evenly convex and characterized by a fairly prominent heterosulcoid-type sulcus that is medially horizontal in orientation. The sulcus is essentially straight except for the slightly downturned caudal tip. The sulcus extends from the anterior margin for approximately 75% of the length of the inner face. There is a conspicuous space between the termination of the sulcus and the posterior margin. The ostium extends to the tip of the pointed rostrum. The length of the ostium is approximately 87% of the length of the cauda, whereas the height of the ostium is slightly greater than that of the cauda. The cauda is mainly horizontal with a small downturned component at the tip. The caudal tip is tapered but rounded. There is an indication of a slight dorsal depression mainly above the cauda, and there is a ridge-like crista superior. There are slight indications of a ventral furrow. The outer face ranges from nearly flat at the anterior and posterior but is noticeably concave just anterior to the midpoint. The outer face is mainly smooth with some small undulations.

REMARKS: MSC 42225 exhibits morphological characteristics consistent with sagttae of the family Scorpaenidae, including the pointed and prominent rostrum, the shape, type, and orientation of the sulcus, the pointed posterior, and the elongated outline. These features commonly occur in extant and fossil Scorpaenidae (Nolf 2013, pls. 176–179) otoliths, including extant genera such as *Scorpaenodes* Bleeker, 1857, *Pontinus* Poey, 1960, *Scorpaena* Linnæus, 1758, and *Scorpaenopsis.* Roedel (1930) reported some of the first fossil scorpaenids based on specimens from the Paleocene erratic deposits in Germany. Shortly after, Frost (1934) noted Scorpaenidae otoliths from lower Eocene strata of England. Nolf and Stringer (1992) identified several Scorpaenidae indet. otoliths from Miocene–Pliocene deposits of the Dominican Republic, and Stringer (1998) later reported the same taxon from the Pliocene Bowden Shell Bed in southeast Jamaica. Schwarzhans (2003) named a new species of Paleocene *Scorpaena* based on otoliths collected from five localities in Denmark, and he later (Schwarzhans 2019) recovered Scorpaenidae indet. specimens from Miocene strata of New Zealand. Schwarzhans *et al.* (2024) subsequently recovered several scorpaenids from middle Eocene strata of California. To our knowledge, the only previously reported fossil Scorpaenidae otolith from the Gulf Coastal Plain of the USA, derived from a lower Pliocene deposit at a site in Georgia, was a single sagitta referred by Stringer and Bell (2018) to Scorpaenidae indet.

Several salient characteristics of MSC 42225 indicate it is more closely related to *Scorpaenopsis* rather than to some other scopraenid genus. For example, the antero-dorsal and postero-dorsal margins of the species of *Scorpaena*, *Pontinus*, *Neosebastes* Guichenot, 1867, *Sebastes* Cuvier, 1829, and *Scorpaenodes* tend to be noticeably lower than the dorsal margin. The midpoint of the dorsal margin is typically the region with the greatest height of the sagitta (see examples in Nolf 1985; Smale *et al.* 1995; Schwarzhans 2003, 2010; Nolf *et al.* 2009; Lowry 2011; Conversani *et al.* 2017; Haimovici *et al.* 2024; Schwarzhans *et al.* 2024). The Alabama specimen assigned to aff. *Scorpaenopsis* sp. has a primarily horizontal dorsal outline with the postero-dorsal margin being slightly higher than the dorsal margin. This can be observed on sagittae of many *Scorpaenopsis* species. For examples, see *Scorpaenopsis oxycephala* (Rivaton and Bourret 1999, pl. 16, figs 25, 26) and *Scorpaenopsis gibbosa* and *S. venosa* (Smale *et al.* 1995, pl. 50, figs b1, b2 and c1, c2).

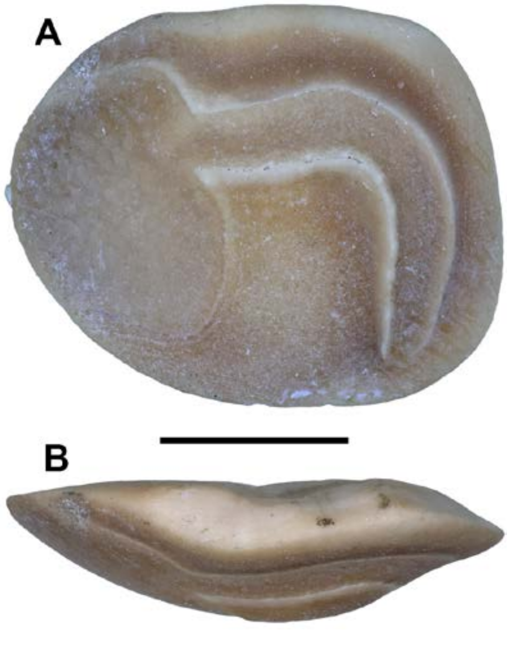
Order Acanthuriformes *sensu* Nelson, Grande and Wilson, 2016
Suborder Sciaenoidei Betancur *et al.*, 2013
Family Sciaenidae Cuvier, 1829
Genus *Aplodinotus* Rafinesque, 1819
Aplodinotus distortus Nolf, 2003
(Text-fig. 23)

MATERIAL: MSC 42203.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Lower Oligocene (upper Rupelian, NP24) Chickasawhay Limestone.

DESCRIPTION: This sagitta measures approximately 5.3 mm in length. The outline can be described as somewhat rectangular (*sensu* Smale *et al.* 1995), but there is a marked antero-dorsal to postero-ventral distortion that affects the shape. The margins of the otolith are smooth. The anterior margin is slightly convex and almost vertical, whereas the antero-dorsal margin is rounded. The dorsal margin is almost horizontal and slightly convex. The postero-dorsal margin has a pronounced post-dorsal angle of nearly 90º. The posterior margin is vertical and very slightly convex. The postero-ventral margin is rounded and convex and forms a nearly 90º angle with the posterior and ventral margins. The ventral margin is slightly rounded and almost horizontal. The antero-ventral margin is evenly convex.

The inner face is unevenly convex and is characterized by a very large, prominent heterosulcoid-type sulcus. The ostium extends from near the antero-dorsal margin to well into the ventral field. The postero-ventral portion of the ostium extends underneath the cauda. A wide space occurs between the postero-ventral portion of the ostium and the downturned portion of the cauda. The height of the cauda is



Text-fig. 23. *Aplodinotus distortus* Nolf, 2003, right sagitta (reversed) MSC 42203, Rupelian, Chickasawhay Limestone, Washington County, Alabama, USA, in inner (A) and dorsal (B) views. Scale bar equals 2 mm.

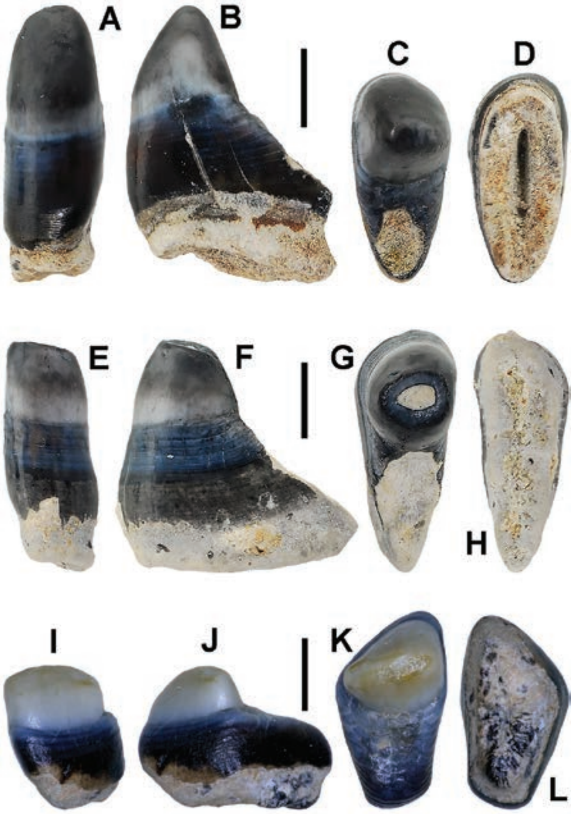
slightly over 20% of the height of the ostium, and the cauda has both a horizontal and downturned component. The outer face is convex, with the greatest convexity occurring in the posterior portion. The outer face is less convex than the inner face.

REMARKS: Nolf (2003) published a revision of the American otolith-based fish species originally described by Koken (1888). Although Koken (1888) did not describe *Aplodinotus distortus*, the species occurred with three other sciaenids he had collected from the Oligocene (Rupelian) Byram Formation in Mississippi. Due to their coeval association, Nolf (2003) included the taxon as a new species, *Aplodinotus distortus*, and based his type series on specimens derived from the Byram Formation in Mississippi and the Oligocene Rosefield Formation in Louisiana, USA. *Aplodinotus distortus* is distinguished from coeval and similar sciaenids in Alabama by the long distance between the posterior of the ventral portion of the ostium and the downturned portion of the cauda, and by the conspicuous distortion along the antero-dorsal to poster-ventral axis (which is most obvious in larger specimens). *Aplodinotus distortus* differs from the similar *Sciaena radians* by the absence of an infra median tip on the posterior margin, a notable characteristic that is found on the latter. Although *A. distortus* was present in the western part of the Mississippi Embayment during the Oligocene (i.e., Louisiana and Mississippi, see Stringer and Miller 2001; Nolf 2003; Stringer and Worley 2003; Worley 2004; Stringer *et al.* 2020b; Fuelling *et al.* 2022; Cicimurri *et al.* 2025), MSC 42203 represents an eastward range extension into Alabama.

Order Tetraodontiformes Berg, 1940
Suborder Balistoidei Rafinesque, 1810
Family Balistidae Rafinesque, 1810
Genus *Lobodus* Costa, 1866
Lobodus pedemontanus Costa, 1866
(Text-fig. 24)

MATERIAL: MSC 2402, MSC 34991 (Text-fig. 24A–D), MSC 35001, MSC 40447 (Text-fig. 24E–H), MSC 42055, MSC 42543, MSC 45581, MSC 45582.

STRATIGRAPHIC OCCURRENCE AND AGE IN ALABAMA: Upper Eocene (Lutetian, NP15) contact zone of the Tallahatta and Lisbon formations, Upper Eocene (Bartonian, NP17) Gosport Sand, Upper Eocene (Priabonian, NP19/20) Yazoo Clay (including Pachuta Marl Member), Lower Oligocene (lower Rupelian, NP22) Marianna Limestone, Lower Oligocene (Rupelian, NP22/23) Glendon Limestone Member of the Byram Formation.



Text-fig. 24. Incisiform teeth of *Lobodus pedemontanus* Costa, 1866, Eocene, Alabama, USA. A–D – MSC 34991, Priabonian, Yazoo Clay, Washington County, in anterior (A), profile (B), occlusal (C) and basal (D) views. E–H – MSC 40447, Priabonian, Yazoo Clay, Washington County, in anterior (E), profile (F), occlusal (G) and basal (H) views. I–L – MSC 2402, Bartonian, Gosport Sand, Choctaw County, in anterior (I), profile (J), occlusal (K) and basal (L) views. Scale bars equal 2 mm.

DESCRIPTION: Our sample is comprised of isolated incisiform teeth. These teeth are mesio-distally compressed and antero-posteriorly longer than wide. The largest tooth in our sample measures 6.8 mm in apicobasal height, 5.1 mm in antero-posterior length, and 2.6 mm in mesio-distal width. In occlusal view, the anterior and posterior margins are strongly convex, whereas the lateral margins range from straight to slightly convex. The teeth have a teardrop-shaped occlusal outline, with the anterior half of the tooth being mesiodistally wider than the posterior half. In apical view, the mesial and distal surfaces of the crown range from straight to convex. The anterior margin is convex in profile view, whereas the posterior margin is concave and slopes toward the edge of the crown. A cusp is developed at the anterior end of the crown, and depending on the amount of *in vivo* wear the cusp can range from sub-triangular to bluntly rounded. The crown is covered by thick enameloid, and fine growth lines are often visible on the edges of the crown. The enameloid on the cusp is often a conspicuously different color than the remainder of tooth. The tooth base lacks enameloid on the lateral edges and a deep and elongated pulp cavity extends anteroposteriorly across the basal face.

REMARKS: Ebersole *et al.* (2019) were the first to identify a Paleogene balistid in the USA when they reported an Eocene tooth from Chocktaw County, Alabama, and Ebersole *et al.* (2021) later reported a Rupelian specimen from Washington County, Alabama. Although these prior studies referred these teeth to Balistidae indet., this obscure tooth morphology had previously been named by Costa (1866) as *Lobodus pedemontanus* for specimens derived from the Eocene of Gassino Torinese, Italy. Costa (1866) believed that his new taxon was a species of the Sparidae, but we follow Ebersole *et al.* (2019, 2021) in assigning this morphology to the Balistidae. Additional specimens from the MSC collection confirm the occurrence of *L. pedemontanus* within several other lithostratigraphic units in Alabama (see above).

DISCUSSION

Despite nearly 200 years of paleontological investigations in Alabama, it is evident that more detailed and comprehensive investigations of the Paleogene fish record are needed. During our study we examined 110 Paleogene fossil teeth, otoliths, and skeletal elements and determined that they represent 21 fish taxa that had not been previously confirmed as occurring in Alabama. Among these taxa are 12 elasmobranchs and nine teleosts that belong to 11 distinct orders, 20 families, and 19 genera (with two additional taxa that could not be identified beyond the family level).

Although numerous prior studies have documented *Otodus* (*Carcharocles*) sp. in Alabama (i.e., Woodward 1889; Leriche 1942; Thurmond and Jones 1981; Feldmann and Portell 2007; Clayton *et al.* 2013; Ehret and Ebersole 2014; Maisch *et al.* 2014; Cappetta and Case 2016; Ebersole *et al.* 2019, 2024b), the tooth we examined (MSC 45338) is morphologically dissimilar to those within the entirety of the northern Gulf Coastal Plain of the USA. Additional specimens are needed to further elucidate the taxonomy of this tooth morphology.

Striatolamia cederstroemi was named by Siverson *et al.* (1995) based on specimens derived from Danian deposits of Sweden. Subsequent studies have since reported this species from Belgium (Jagt *et al.* 2013), Denmark (Adolfssen and Ward 2015), the Netherlands (Jagt 2013), New Zealand (Adolfssen 2012), Russia (Yarkov and Popov 1998), and Scandinavia (Adolfssen *et al.* 2017). Our examination of 53 teeth confirms the purported occurrence of *S. cederstroemi* in Alabama, corroborating the only record of this taxon in the Western Hemisphere.

Odontaspis substriata was erected by Stromer (1910) based on specimens derived from Eocene deposits in West Africa. Leriche (1942) later described this morphology from North Dakota in the USA, and more recently Case (1994) identified this taxon within the upper Thanetian Tuscahoma Sand in Mississippi. The specimens in our sample represent the first to be confirmed from Alabama, and new lithostratigraphic records include the Pine Barren Member of the Clayton Formation, Hatchetigbee Formation, and Tallahatta Formation. These occurrences provide a bracketed biostratigraphic range for this taxon that extends from the lower Danian to the upper Ypresian.

Case (1994) named *Microscyliorhinus leggetti* for teeth recovered from the Ypresian Bashi Formation in Mississippi. The only other published identification of this taxon appears to have been by Mustafa and Zalmout (2002) from Ypresian deposits in Jordan, although Adnet *et al.* (2020) more recently considered those specimens conspecific with their new taxon, *Leptocharias tunisiensis*. The single *M. leggetti* specimen identified in our sample represents just the second unequivocal published occurrence of this taxon, and its occurrence within the Hatchetigbee Formation represents a new lithostratigraphic record and the first occurrence of the species in Alabama.

Two teeth (MSC 35003, MSC 50819) tentatively extend the temporal and biogeographic range of *Hemipristis intermedia* from the early Chattian (Oligocene) Catahoula Formation in Mississippi to the Priabonian (Eocene) Yazoo Clay of Alabama. Additional specimens are needed to confirm the identification or determine if an unrecognized transitional taxon between the Eocene *H. curvatus* and Oligocene *H. intermedia* exists.

A single tooth (MSC 44567) is tentatively assigned to *Physogaleus contortus* based on its morphology, but temporally older age compared to specimens from the Atlantic Coastal Plain. Teeth with this unique crown morphology were recently described within the Gulf Coastal Plain of the USA by Cicimurri *et al.* (2025) based on specimens derived from the Chattian Catahoula Formation in Mississippi. If the Alabama specimen belongs to this taxon, it would represent a range extension for this species into the Priabonian Yazoo Clay. More specimens are necessary to corroborate our interpretation, or determine if the specimen represents a transitional species between Oligocene *P. contortus* and middle Eocene species like *P. secundus* and *P. alabamensis*.

The single sphyrnid tooth (MSC 50034) we examined was originally referred by Ebersole *et al.* (2024b) to '*Sphyrna*' sp. However, a large sample of '*Sphyrna*' *robustum* teeth from the Chattian Catahoula Formation in Mississippi (Cicimurri *et al.* 2025) allowed us to refine the taxonomic identity and extend the biostratigraphic range of '*S.*' *robustum* into the Rupelian Red Bluff Clay.

Two teeth in our sample, MSC 35018 and MSC 50815, are tentatively assigned to *Galeocerdo platycuspidatum*, a taxon recently erected for teeth from the Chattian Catahoula Formation in Mississippi. Additional specimens are needed to solidify our identification, which would extend the biostratigraphic range of this species to the upper Rupelian Chickasawhay Limestone. Slight morphological differences between the Alabama and Mississippi specimens do not allow us to rule out the possibility that the Alabama teeth represent an intermediate taxon between *G. clarkensis* and *G. platycuspidatum*.

Ebersole *et al.* (2019) identified a specimen (SC2012.47.10) from the Lutetian Lisbon Formation in Alabama as a male tooth of '*Dasyatis*' *jaekeli.* Reinicke *et al.* (2024) noted that this specimen could belong to their new genus, *Casierabatis*, and perhaps to their new species, *C. lambrechtsi*. Although we conclude that the tooth is more appropriately identified as *Casierabatis*, the single specimen available to us is stratigraphically younger in age (Lutetian *vs.* Ypresian) and exhibits weaker crown ornamentation and is therefore only tentatively referred to *C. lambrechtsi*. Nevertheless, SC2012.47.10 is the only (and youngest) *Casierabatis* tooth identified outside of the type region.

Two teeth (MMNS VP-7297.1 and MMNS VP-8178) from the lower Danian Pine Barren Member of the Clayton Formation are herein referred to *Hypolophities* sp. Of the two Paleocene *Hypolophities* species described in North America, both are based on poorly preserved specimens as well as teeth that appear to represent other taxa. These realities make it impossible to speciate the two teeth, but MMNS VP-7297.1 and MMNS VP-8178 nevertheless represent the first Alabama record of the genus.

A single tooth (MMNS VP-7298) is referred to Myliobatidae indet. because it exhibits the salient features of teeth of fossil and extant members of this family. However, it is morphologically distinct from any of the Paleogene myliobatids previously described from the state (see Ebersole *et al.* 2019). Additional teeth are needed to elucidate the taxonomy of this specimen.

A total of 11 teeth in our sample have been referred to '*Rhinoptera*' *prisca*. This species was originally named by Woodward (1907) for teeth derived from the Danian of Brazil, and the specimens in our sample represent the first occurrence of the taxon in North America, demonstrating its extensive biogeographic distribution during the Danian.

A single sagitta in our sample (MSC 38241) is referred to the otolith-based species *Pterothrissus conchaeformis* (Koken, 1885). This taxon has been reported from both Cretaceous and Paleocene deposits in Europe, Greenland, and the USA (Schwarzhans 2003, 2004; Stringer and Schwarzhans 2021), but the Alabama specimen represents the first early Eocene (Ypresian) occurrence of this species. Another sagitta in our sample, MSC 42228, has been referred to *Synodus* sp. Previously documented North American occurrences of this taxon include Eocene deposits in Louisiana, Mississippi, and Texas. The Alabama specimen represents the first occurrence of the taxon in this state, as well as the first early Oligocene (Rupelian) occurrence of the genus.

The enigmatic teleost, *Holocentrities ovalis*, has been previously reported from the Rupelian Marianna Limestone in Florida (including the type locality) and Mississippi. Two sets of articulated teleost scales from this lithostratigraphic unit in Alabama are identified as *H. ovalis*, and the Alabama specimens bridge the paleobiogeographic gap that previously existed between the Florida and Mississippi records.

The teleost taxa *Arnoglossus* sp. (MSC 42232), *Centropristis* aff. *priaboniana* (MSC 42231), aff. *Scorpaenopsis* sp. (MSC 42225), and *Aplodinotus distortus* (MSC 42203) are each identified by a single otolith specimen. Each represents the first Paleogene record in Alabama, and with respect to MSC 42231, the fossil extends the biostratigraphic range of *C.* aff. *priaboniana* from the Priabonian Yazoo Clay into the Rupelian Red Bluff Clay. Regarding MSC 42225, this otolith represents the first (albeit tentative) Paleocene occurrence of *Scorpaenopsis* sp. in North America.

Ebersole *et al.* (2019) referred several middle Eocene teeth from Alabama to Osteoglossidae indet. based on morphological similarities to European taxa. However, Cicimurri *et al.* (2025) concluded that the teeth more likely belong to an extinct representative of the Lutjanidae, which we follow herein. The teeth therefore represent the first non-otolith records of this family from the Gulf Coastal Plain of the USA. Lastly, Paleogene teeth from Alabama previously identified only as Balistidae indet. (Ebersole *et al.* 2019, 2021) are herein identified as *Lobodus pedemontanus* Costa, 1866, a species previously known only from Eocene deposits in Italy. Thus, the Alabama specimens represent the first recognition of this species in the Western Hemisphere.

CONCLUSIONS

We examined numerous Paleogene fish fossils from Alabama and documented 21 taxa that were previously not known or recognized as occurring in the state. This report demonstrates that, despite the number of prior studies that have focused on Paleogene sharks and bony fishes in the state, much work remains to be done. However, research currently underway aims to continue increasing our understanding of the Paleogene fish assemblages in Alabama. This includes investigation of the early Paleocene (Danian) batoids from the southeastern USA, a comprehensive evaluation of the Bashi and Hatchetigbee lithostratigraphic units, a detailed study of the Priabonian Yazoo Clay, and a study of the lower Oligocene (Rupelian) Chickasawhay Limestone. Based on preliminary investigations, we expect that the number of Paleogene taxa occurring in Alabama will significantly increase.

Acknowledgements

Kimberly A. Johnson (National Marine Fisheries Service, Southeast Fisheries Science Center, Pascagoula, MS, USA), Ron Taylor (formerly of the Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, USA), Joseph Read Hendon (Center for Fisheries Research and Development, Gulf Coast Research Laboratory, University of Southern Mississippi, Ocean Springs, MS, USA), and Dirk Nolf (Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium) generously provided modern fishes and otoliths. Drew Gentry, Lloyd Glawe, James Lowery, George Martin, Loni Parker, David Phillips, and Lindsay and Tom Stallworth are thanked for contributing specimens that were included in this study. Werner Schwarzhans (Natural History Museum of Denmark, Zoological Museum, Copenhagen, Denmark) made valuable and insightful suggestions on the identity and taxonomy of specimens. George Phillips is thanked for his loan of specimens from the MMNS collections, and Adiël Klompmaker is thanked for granting access to the ALMNH collections. Sandy Ebersole and Irene Burgess (Geological Survey of Alabama) reviewed a version of this manuscript prior to formal submission. We thank Nicolae Trif (Brukenthal National Museum, Romania) and an anonymous reviewer for their critical evaluation of an earlier version of this manuscript. Lastly, the editorial staff at AGP are thanked for their time and effort in publishing this article.

REFERENCES

Adolfssen, J. 2012. Palaeoenvironment and Shark Evolution across the K/T-boundary on Southern Zealand, 250 pp. Unpublished PhD Thesis, Faculty of Science, University of Copenhagen; Denmark.

Adolfssen, J., Milàn, J. and Friedman, M. 2017. Review of the Danian vertebrate fauna of southern Scandinavia. *Bulletin of the Geological Society of Denmark*, **65**, 1–23.

Adolfssen, J. and Ward, D.J. 2015. Neoselachians from the Danian (Early Paleocene) of Denmark. *Acta Palaeontologica Polonica*, **60**, 313–338.

Adnet, S., Miravaux, L., Cappetta, H., Charruault, A.-L., el Mabrouk, E., Jiquel, S., Ammar, H.K., Marandat, B., Marzougui, W., Merzeraud, G., Temani, R., Vainey-Liaud, M. and Tabuce, R. 2020. Diversity and renewal of tropical elasmobranchs around the Middle Eocene Climatic Optimum (MECO) in North Africa: New data from the lagoonal deposits of Djebel el Kebar, Central Tunisia. *Palaeontologia Electronica*, **23**, a38.

Agassiz, L. 1835. Recherches sur les poissons fossiles, 5 livraison (June 1835), vol. 3, 46 pp. Petitpierre et Prince (text) and H. Nicolet (plates); Neuchâtel.

Agassiz, L. 1838. Recherches sur les poissons fossiles, 11 livraison (November 1838), vol. 3, 73–140. Petitpierre et Prince (text) and H. Nicolet (plates); Neuchâtel.

Agassiz, L. 1839. Recherches sur les poissons fossiles, 13 livraison, vol. 4, 109–204. Imprimerie de Petitpierre; Neuchâtel.

Agassiz, L. 1843. Recherches sur les poissons fossiles, 15 et 16 livraisons (Mardi 1843), vol. 3, 157–390. Jent and Gassmann (text) and H. Nicolet (plates); Soleure and Neuchâtel.

Ameghino, F. 1901. L'age des formations sédimentaires de Patagonie. *Anales de la Sociedad Cientifica Argentina*, **51**, 65–91.

Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Notes et Mémoires du Service Géologique du Maroc*, **92**, 1–372.

Arratia, G., Scasso, R.A. and Kiessling, W. 2004. Late Jurassic fishes from Longing Gap, Antarctic Peninsula. *Journal of Vertebrate Paleontology*, **24**, 41–55.

Berg, L.S. 1937. A classification of fish-like vertebrates. *Izve-*

stiya Akademii Nauk SSSR, Seriya Biologicheskaya, **4**, 1277–1280.

Berg, L.S. 1940. Classification of fishes, both recent and fossil. *Trudy Zoologicheskogo Instituta, Akademia Nauk SSSR*, **5** (2), 85–517. [In Russian]

Betancur, R.R., Broughton, R., Wiley, E., Carpenter, K., López, J., Li, C., Holcroft, N., Arcila, D., Sanciangco, M., Cureton II, J., Zhang, F., Buser, T. Campbell, M., Ballesteros, J., Roa-Varon, A., Willis, S., Borden, W., Rowley, T., Reneau, P., Hough, D., Lu, G., Grande, T., Arratia, G. and Ortí, G. 2013. The Tree of Life and a New Classification of Bony Fishes. PLOS Currents Tree of Life. 2013 Apr 18, Edition 1. Available at: 10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288.

Bleeker, P. 1849. Bijdrage tot de kennis der ichthyologische fauna van het eiland Madura, met beschrijving van eenige nieuwe soorten. *Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen*, **22** (8), 1–16.

Bleeker, P. 1857. Tweede bijdrage tot de kennis der ichthyologische fauna van het eiland Madura. *Acta Societatis Regiae Scientiarum Indo-Neêrlandicae*, **2**, 1–114.

Bleeker, P. 1862. Sur quelques genres de la famille des Pleuronectoïdes. *Verslagen en Mededeelingen der Koninklijke Akademie van Wetenschappen*, **13**, 422–429.

Bloch, M. and Schneider, J. 1801. Systema Ichthyologiae Iconibus CX Illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit, 584 pp. Sumtibus Auctoris Impressum et Bibliopolio Sanderiano Commissum; Berolini.

Bonaparte, C.L. 1833. Iconografia della fauna italica per le quattro classi degli animali vertebrati. Tomo III, 7–28. Pesci; Roma.

Bonaparte, C.L. 1835. Prodromus systematis ichthyologiae. *Nuovi Annali delle Scienze naturali Bologna (Ser. 1)*, **2** (4), 181–196, 272–277.

Bonaparte, C.L. 1838. Selachorum tabula analytica. *Nuovi Annali delle Science Naturali Bologna*, **1** (2), 195–214.

Bonaparte, C.L. 1840. Iconografia della fauna italica per le quattro classi degli animali vertebrati. Tomo III. Fasc. 27–29, 136–154. Pesci; Roma.

Campbell, R. 1929a. Fish otoliths, their occurrence and value as stratigraphic markers. *Journal of Paleontology*, **3**, 254–279.

Campbell, R. 1929b. Bibliography of otoliths. *Society of Economic Paleontologists and Mineralogists in conjunction with the American Association of Petroleum Geologists Special Contribution*, **1**, 1–31.

Cappetta, H. 1980. Modification du statut générique de quelques espèces de sélaciens crétacés et tertiaires. *Palaeovertebrata*, **10** (1), 29–42.

Cappetta, H. 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Schultze, H.-P. (Ed.), Handbook of Palaeoichthyology 3E, 1–512. Dr. Friedrich Pfeil; Munich.

Cappetta, H. and Case, G.R. 2016. A selachian fauna from the middle Eocene (Lutetian, Lisbon Formation) of Andalusia, Covington County, Alabama, USA. *Palaeontographica Abt. A*, **307** (1–6), 43–103.

Case, G.R. 1994. Fossil fish remains from the late Paleocene Tuscahoma and early Eocene Bashi formations of Meridian, Lauderdale County, Mississippi. Part I – Selachians. *Palaeontographica Abteilung A*, **230** (4–6), 97–138.

Case, G.R. 1996. A new selachian fauna from the lower Hornestown Formation (early Paleocene/Montian) of Monmouth County, New Jersey. *Palaeontographica Abt. A*, **242** (1–3), 1–14.

Casier, E. 1966. Faune ichthyologique du London Clay, 496 pp. Trustees of the British Museum; London.

Cicimurri, D.J. and Ebersole, J.A. 2015a. Paleocene chimaeroid fishes (Chondrichthyes: Holocephali) from the eastern United States, including two new species of *Callorhinchus*. *PaleoBios*, **32**, 1–29.

Cicimurri, D.J. and Ebersole, J.A. 2015b. Two new species of *Pseudaetobatus* Cappetta, 1986 (Batoidei: Myliobatidae) from the southeastern United States. *Palaeontologia Electronica*, **18.1.15A**, 1–17.

Cicimurri, D.J., Ebersole, J.A. and Martin, G. 2020. Two new species of *Mennerotodus* Zhelezko, 1994 (Chondrichthyes: Lamniformes: Odontaspididae), from the Paleogene of the southeastern United States. *Fossil Record*, **23** (2), 117–140.

Cicimurri, D.J., Ebersole, J.A., Stringer, G.L., Starnes, J.E. and Phillips, G.E. 2025. Late Oligocene fishes (Chondrichthyes and Osteichthyes) from the Catahoula formation in Wayne County, Mississippi, USA. *European Journal of Taxonomy*, **984** (1), 1–131.

Cicimurri, D.J. and Knight, J.L. 2009. Late Oligocene sharks and rays from the Chandler Bridge Formation, Dorchester County, South Carolina, USA. *Acta Paleontologica Polonica*, **54** (4), 627–647.

Cicimurri, D.J., Knight, J.L. and Ebersole, J.A. 2022. Early Oligocene (Rupelian) fishes (Chondrichthyes, Osteichthyes) from the Ashley Formation (Cooper Group) of South Carolina, USA. *PaleoBios*, **39**, 1–38.

Clayton, A.A., Ciampaglio, C.N. and Cicimurri, D.J. 2013. An inquiry into the stratigraphic occurrence of a Clabornian (Eocene) vertebrate fauna from Covington County, Alabama. *Bulletin Alabama Museum of Natural History*, **31**, 60–73.

Compagno, L.J.V. 1973. Interrelationships of living elasmobranchs. *Zoological Journal of the Linnean Society*, **53** (Supplement 1), 15–61.

Conrad, T.A. 1835. Fossil shells of the Tertiary formations of North America: Eocene fossils of Claiborne, with observations on this formation in the United States, and a geological map of Alabama, 29–56. Philadelphia.

Conrad, G.M. 1941. A fossil squirrel-fish from the upper Eocene of Florida. *Contributions to Florida Vertebrate Paleontology, Florida Geological Survey Bulletin*, **22**, 1–41.

Conversani, V.R.M., Brenha-Nunes, M.R., Santificetur, C., Giaretta, M.B., Siliprandi, C.C. and Rossi-Wongtschowski, C.L. del B. 2017. Atlas of marine bony fish otoliths (sagittae) of Southeastern-Southern Brazil Part VII: Atheriniformes, Beloniformes, Beryciformes, Zeiformes, Syngnathiformes, Scorpaeniformes and Tetraodontiformes. *Brazilian Journal of Oceanography*, **65** (3), 400–447.

Cope, E.D. 1871. Contribution to the ichthyology of the Lesser Antilles. *Transactions of the American Philosophical Society*, **14** (3), 445–483.

Costa, O.G. 1866. Nuove osservazioni intorno ai fossili di Gassino, ed illustrazione di alcune nouve specie, 41 pp. Antonio Cons tipografo; Napoli.

Cuvier, G. 1829. Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée, Tome II, 2nd edition, 406 pp. Chez Dêterville; Paris.

Dames, W. 1883. Über eine tertiäre Wirbelthierfauna von der westlichen Insel der Birket-EI-Qrûn im Fajum (Aegypten). *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, **6**, 129–153.

Denton, Jr., R.K., Dobie J.L. and Parris, D.C. 1997. The marine crocodilian *Hyposaurus* in North America. In: Callaway, J.M. and Nichols, E.L. (Eds), Ancient Marine Reptiles, 375–397. Academic Press; San Diego.

Dockery, D. and Thompson, D. 2016. The Geology of Mississippi, 751 pp. Office of Geology, Mississippi Department of Environmental Quality. University Press of Mississippi; Jackson.

Dunkle, D.H. and Olsen, S.J. 1959. Description of a Beryciform fish from the Oligocene of Florida. *Contributions to Florida Vertebrate Paleontology, Special Publication*, **2**, 1–20.

Eastman, C. 1904. Pisces. In: Clark, W., Shattuck, G. and Hall, W. (Eds), The Miocene Deposits of Maryland (Maryland Geological Survey), 71–93. The John Hopkins Press; Baltimore.

Ebersole, J.A., Cicimurri, D.J. and Harrell Jr, T.L. 2024a. A new species of *Palaeohypotodus* Glückman, 1964 (Chondrichthyes, Lamniformes) from the lower Paleocene (Danian) Porters Creek Formation, Wilcox County, Alabama, USA. *Fossil Record*, **27** (1), 111–134.

Ebersole, J.A., Cicimurri, D.J., Stallworth, L.M. and Gentry, A.D. 2024b. Preliminary report on the fishes (Chondrichthyes & Teleostei) from the lower Oligocene (Rupelian) Red Bluff Clay at site AMo-9, Monroe County, Alabama, USA. *Palaeovertebrata*, **47** (2), 1–24.

Ebersole, J.A., Cicimurri, D. J. and Stringer, G.L. 2019. Taxonomy and biostratigraphy of the elasmobranchs and bony fishes (Chondrichthyes and Osteichthyes) of the lower-to-middle Eocene (Ypresian to Bartonian) Claiborne Group in Alabama, USA, including an analysis of otoliths. *European Journal of Taxonomy*, **585**, 1–274.

Ebersole, J.A., Cicimurri, D.J. and Stringer, G.L. 2021. Marine fishes (Elasmobranchii, Teleostei) from the Glendon Limestone Member of the Byram Formation (Oligocene, Rupelian) at site AWa-9, Washington County, Alabama, USA, including a new species of gobiid (Gobiiformes: Gobiidae). *Acta Geologica Polonica*, **71**, 481–518.

Ebersole, J.A., Cicimurri, D.J., Stringer, G.L., Jacquemin, S.J. and Ciampaglio, C.N. 2024c. Fossil Fishes of Alabama. McWane Science Center; Birmingham, Alabama. Available at: https://doi.org/10.69737/GGLE1724

Ebersole, J.A., Cicimurri, D.J., Stringer, G.L., Jacquemin, S.J. and Ciampaglio, C.N. 2025. Paleogene Fishes of Alabama: Introduction version 2. In: Ebersole J.A. (Ed.), Fossil Fishes of Alabama, 4 (1), 1–5. McWane Science Center; Birmingham, Alabama.

Ebersole, J.A. and Dean, L.S. 2013. The history of Late Cretaceous vertebrate research in Alabama. *Bulletin Alabama Museum of Natural History*, **31** (1), 3–45.

Ehret, D.J. and Ebersole, J.A. 2014. Occurrence of the megatoothed sharks (Lamniformes: Otodontidae) in Alabama, USA. *PeerJ*, **2**, e625.

Feldmann, R.M. and Portell, R.W. 2007. First report of *Costacopluma* Collins and Morris, 1975 (Decapoda: Brachyura: Retroplumidae) from the Eocene of Alabama, U.S.A. *Journal of Crustacean Biology*, **27** (1), 90–96.

Fitch, J. and Lavenberg, R. 1983. Teleost fish otoliths from Lee Creek mine, Aurora, North Carolina (Yorktown Formation, Pliocene). In: Ray, C.E. (Ed), Geology and Paleontology of the Lee Creek Mine, North Carolina, I, 509–529. Smithsonian Institution Press; Washington D.C.

Fricke, R., Eschmeyer, W. and Van der Laan, R. 2024. Eschmeyer's Catalog of Fishes: Genera, Species, References. Available at: https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Accessed 20/11/2024

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

Frizzell, D. and Dante, J. 1965. Otoliths of some early Cenozoic fishes of the Gulf Coast. *Journal of Paleontology*, **39**, 687–718.

Frizzell, D. and Lamber, C. 1962. Distinctive "congrid type" fish otoliths from the lower Tertiary of the Gulf Coast (Pisces: Anguilliformes). *Proceedings of the California Academy of Science Series* (*4*), **32**, 87–101.

Froese, R. and Pauly, D. 2024. FishBase. World Wide Web electronic publication. www.fishbase.org. Accessed 9/12/2025.

Frost, E. 1934. Otoliths of fishes from the Lower Tertiary formations of southern England. III. Percomorphi, Scleroparei. *Annals and Magazine of Natural History*, **13**, 380–386.

Fuelling, L., Jacquemin, S., Stringer, G., Smith, A. and Ciampaglio, C. 2022. Phylogeography and biogeography of the ubiquitous and unique sciaenid genus *Aplodinotus* in North America. *Historical Biology*, **35** (3), 1–12.

Gemmellaro, G. 1857. Ricerche sui pesci fossili della Sicilia. *Atti dell'Accademia nat. Catania*, **13** (series 2), 279–328.

Gibbes, R.W. 1849. Monograph of the fossil Squalidae of the United States. *Journal of the Academy of Natural Sciences of Philadelphia*, **1** (series 2), 191–206.

Gill, T.N. 1861. Catalogue of the fishes of the eastern coast of North America, from Greenland to Georgia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **13**, 1–63.

Gill, T.N. 1862. Analytical synopsis of the order of Squali; and revision of the nomenclature of the genera. *Annals of the Lyceum of Natural History of New York*, **7** (32), 367–370, 371–408.

Gill, T.N. 1893. Families and subfamilies of fishes. *Memoirs of the National Academy of Science*, **6** (6), 127–138.

Glückman, L.S. 1964. Sharks of Paleogene and their stratigraphic significance, 229 pp. Issledovaniye Nauka; Moskva. [In Russian]

Goodrich, E.S. 1930. Studies on the structure & development of vertebrates, 837 pp. Macmillan; London.

Gottfried, M.D. and Fordyce, R.E. 2001. An associated specimen of *Carcharodon angustidens* (Chondrichthyes, Lamnidae) from the Late Oligocene of New Zealand, with comments on *Carcharodon* interrelationships. *Journal of Vertebrate Paleontology*, **21** (4), 730–739.

Greenwood, P.H., Rosen, D.E., Weitzman, S.H. and Myers, G.S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, **131** (4), 341–455.

Guichenot, A. 1867. Notice sur le Néosébaste nouveau genre de poissons de la famille des scorpènoides, et description d'une nouvelle espèce. *Mémoires de la Société Impériale des Sciences Naturelles de Cherbourg*, **13**, 83–89.

Haimovici, M., Rodrigues, L., Lucato, S., Freire, M., Fishcher, L. and Cardoso, L. 2024. Otolith atlas for marine fishes of the southwestern Atlantic occurring along southern Brazil (28ºS-34ºS). *Marine and Fishery Science*, **37** (1), 1–155.

Hasse, J.C.F. 1878. Das natürliche System des Elasmobranchier auf Grundlage des Baues und der Entwickelung des Wirbelsäule. *Zoologischer Anzeiger*, **1** (7–8), 144–172.

Hay, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. *Bulletin of the United States Geological Survey*, **179**, 1–868.

Heckel, J.J. 1837. Ichthyologische Beiträge zu den Familien der Cottoiden, Scorpaenoiden, Gobioiden und Cyprinoiden. *Annalen des Wiener Museums der Naturgeschichte*, **2** (1), 143–164.

Hilgendorf, F.M. 1877. *Pterothrissus*, eine neue Clupeidengattung. *Leopoldina, Amtliches Organ der Kaiserlich Leopoldinisch-Carolinisch-Deutschen Akademie der Naturforscher*, **13** (15–16), 127–128.

Hoese, H.D. and Moore, R.H. 1998. Fishes of the Gulf of Mexico, second edition, 422 pp. Texas A&M University Press; College Station.

Holman, J.A. and Case, G.R. 1988. Reptiles from the Eocene Tallahatta Formation of Alabama. *Journal of Vertebrate Paleontology*, **8** (3), 328–333.

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*, **1880**, 649–662.

Jagt, J.W.M. 2013. Rijke fauna's uit het Laat-Krijt en Vroeg-Paleoceen van Geulhem (zuidelijk Limburg). *GEA*, **2013** (4), 100–108.

Jagt, J.W.M., Van Bakel, B.W.M., Cremers, G., Deckers, M.J.M., Dortangs, R.W., Van Es, M., Fraaije, R.H.B., Kisters, P.J.M., Van Knippenberg, P.H.M., Lemmens, H., Nieuwenhuis, E., Severijns, J. and Stroucken, J.W. 2013. Het Vroeg Paleoceen (Danien) van zuidelijk Limburg en aangrenzend gebied – nieuwe fauna's en nieuwe inzichten. *Afzettingen*, **34** (4), 198–230.

Jordan, D.S. 1898. Description of a species of fish (*Mitsukurina owstoni*) from Japan, the type of a distinct family of lamnoid sharks. *Proceedings of the California Academy of Sciences, Series 3 Zoology*, **1** (6), 199–204.

Jordan, D.S. and Evermann, B.W. 1896. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. *Bulletin of the United States National Museum*, **47**, 1–1240.

Jordan, D.S. and Gilbert C.H. 1879. Notes on the fishes of Beaufort Harbor, North Carolina. *Proceedings of the United States National Museum*, **1** (55), 365–388.

Koken, E. 1884. Ueber Fisch-Otolithen, insbesondere ueber diejenigen der norddeutschen Oligocän Ablagerungen. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **36**, 500–565.

Koken, E. 1885. Otolithen. In: von Koenen, A.V. (Ed.), Ueber eine Paleocaene Fauna von Kopenhagen. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Goettingen*, **32**, 113–116.

Koken, E. 1888. Neue Untersuchungen an tertiären fisch-otolithen. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **40**, 274–305.

Lea, I. 1833. Tertiary Formation of Alabama. In: Lea, I. (Ed.), Contributions to Geology, 9–208. Carey, Lea, and Blanchard; Philadelphia.

Leidy, J. 1873. Notice of remains of fishes in the Bridger Tertiary Formation of Wyoming. *Proceedings of the Academy of Natural Science of Philadelphia*, **25**, 97–99.

Leriche, M. 1905. Les poissons éocènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **3** (11), 49–228.

Leriche, M. 1926. Les poissons Nêogènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **32**, 367–472.

Leriche, M. 1942. Contribution à l'étude des faunes ichthyologiques marines des terrains tertiaires de la Plaine Côtière Atlantique et du centre des Etats-Unis. Les synchronismes des formations tertiaires des deux côtés de l'Atlantique. *Mémoires de la Société géologique de France*, **45** (2–4), 1–110.

Lim, D.D., Motta, P.J., Mara, K. and Martin, A.P. 2010. Phylogeny of hammerhead sharks (Family Sphyrnidae) inferred from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, **55** (2), 572–579.

Lin, C.-H. and Nolf, D. 2022. Middle and late Eocene fish otoliths from the eastern and southern USA. *European Journal of Taxonomy*, **814**, 1–122.

Linnæus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Editio Decima, Reformata, 1384 pp. Impensis Direct, Laurentii Salvii; Holmiae.

Lowry, M. 2011. Photographic catalog of California marine fish otoliths: prey of California sea lions (*Zalophus californianus*). *National Oceanic and Atmospheric Administration Technical Memorandum National Marine Fisheries Service Southwest Fisheries Science Center*, **483**, 1–250.

Maisch IV, H.M., Becker, M.A., Raines, B.W. and Chamberlain Jr., J.A. 2014. Chondrichthyans from the Tallahatta-Lisbon Formation contact (Middle Eocene), Silas, Choctaw County, Alabama. *Paludicola*, **9** (4), 183–209.

Maisch IV, H.M., Becker, M.A., Raines, B.W. and Chamberlain Jr., J.A. 2016. Osteichthyans from the Tallahatta–Lisbon Formation contact (middle Eocene–Lutetian) Pigeon Creek, Conecuh-Covington counties, Alabama with comments on transatlantic occurrences in the Northern Atlantic Ocean Basin. *PalArch's Journal of Vertebrate Palaeontology*, **13** (3), 1–22.

Maisch IV, H.M. 2020. A new species of *Hypolophites* (Chondrichthyes, Myliobatiformes) from the Lower Clayton Limestone Unit of the Midway Group (Paleocene), near Malvern, Arkansas, USA. *Journal of Paleontology*, **94** (3), 548–556.

Manning, E.M. 2003. Chapter 21: The Eocene/Oligocene transition in marine vertebrates of the Gulf Coastal Plain. In: Prothro, D.R., Ivany, L.C. and Nesbitt, E.A. (Eds), From Greenhouse to Icehouse: The Marine Eocene–Oligocene Transition, 366–385. Columbia University Press; New York.

Meyer, O. 1889. Fish otoliths of the southern Old-Tertiary. *American Naturalist*, **23**, 42–43.

Miller, A.E., Gibson, M.L. and Boessenecker, R.W. 2021. A megatoothed shark (*Carcharocles angustidens*) nursery in the Oligocene Charleston Embayment, South Carolina, USA. *Palaeontologia Electronica*, **24** (2), a19.

Müller, A. 1999. Ichthyofaunen aus dem atlantischen Tertiär der USA. *Leipziger Geowissenschaften*, **9/10**, 1–360.

Müller, J. 1845. Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. *Archiv für Naturgeschichte*, **11** (1), 91–141.

Müller, J. and Henle, F.G.J. 1837. Über die Gattungen der Haifische und Rochen nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. *Berichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin*, **1837**, 111–118.

Müller, J. and Henle, J. 1839. Systematische Beschreibung der Plagiostomen, 29–102. Veit und Comp.; Berlin.

Mustafa, H.A. and Zalmout, I.S. 2002. Elasmobranchs from the late Eocene Wadi Esh-Shallala Formation of Qa'Faydat ad Dahikiya, east Jordan. *Tertiary Research*, **21** (1–4), 77–94.

Nelson, E.M. 1955. The morphology of the swim bladder and auditory bulla in the Holocentridae. *Fieldiana Zoology*, **37**, 121–130.

Nelson, J.S., Grande, T.C. and Wilson, M.V.H. 2016. Fishes of the World, 707 pp. John Wiley & Sons, Inc.; New York.

Nolf, D. 1985. Otolithi Piscium. In: Schultze, H. (Ed.), Handbook of Paleoichthyology (10), 1–145. Gustav Fischer Verlag; Stuttgart, Germany and New York, United States.

Nolf, D. 2003. Revision of the American otolith-based fish species described by Koken in 1888. *Louisiana Geological Survey Geological Pamphlet*, **12**, 1–19.

Nolf, D. 2013. The diversity of fish otoliths, past and present, 581 pp. Operational Directorate "Earth and History of Life" of the Royal Belgian Institute of Natural Sciences; Brussels, Belgium.

Nolf, D., De Potter, H. and LaFond-Grellety, J. 2009. Homage to Joseph Chaine and Jean Duvergier: The diversity and variability of fish otoliths, 59 pp. Palaeo Publishing and Library; Mortsel, Belgium.

Nolf, D. and Dockery, D. 1993. Fish otoliths from the Matthews Landing Marl Member (Porters Creek Formation), Paleocene of Alabama. *Mississippi Geology*, **14**, 24–39.

Nolf, D. and Stringer, G. 1992. Neogene paleontology in the northern Dominican Republic: otoliths of teleostean fishes. *Bulletins of American Paleontology*, **102**, 45–81.

Nolf, D. and Stringer, G. 2003. Late Eocene (Priabonian) fish otoliths from the Yazoo Clay at Copenhagen, Louisiana. *Louisiana Geological Survey Geological Pamphlet*, **13**, 1–23.

Painter, G. 1965. Taxonomic study of fossil and recent otoliths of certain cusk-eels. Unpublished Master's thesis, 89 pp. University of Missouri at Rolla, Missouri, USA.

Patterson, C. and Rosen, D. 1977. Review of the ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History*, **158**, 83–172.

Perez, V.J., Godfrey, S.J., Kent, B.W., Weems, R.E. and Nance, J.R. 2019. The transition between *Carcharocles chubutensis* and *Carcharocles megalodon* (Otodontidae, Chondrichthyes): lateral cusplet loss through time. *Journal of Vertebrate Paleontology*, e1546732.

Pinna, M.C.C. de. 1996. Teleostean monophyly. In: Stiassny, M.L.J., Parenti, L.R. and Johnson, G.D. (Eds), Interrelationships of Fishes, 147–162. Academic Press; San Diego, California.

Poey, F. 1860. Memorias sobra la historia natural de la Isla de Cuba, acompañadas de sumarios Latinos y extractos en Francés, 422 pp. Imprenta de Barcina; La Habana.

Poey, F. 1875. Enumeratio piscium cubensium. *Anales de la Sociedad Española de Historia Natural*, **4**, 75–161.

Purdy, R.W., Schneider, V.P., Applegate, S.P., McLellan, J.H., Meyer, R.L. and Slaughter, B.H. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. In: Ray, C.E. and Bohaska, D.J. (Eds), Geology and Paleontology of the Lee Creek Mine, North Carolina, III. *Smithsonian Contributions to Paleobiology*, **90**, 71–202.

Rafinesque, C.S. 1810. Indice d'ittiologia siciliana; ossia, catalogo metodico dei nomi latini, italiani, e siciliani dei pesci, che si rinvengono in Sicilia disposti secondo un metodo naturale e seguito da un appendice che contiene la descrizione de alcuni nuovi pesci siciliani, 70 pp.. Presso Giovanni del Nobolo; Messina.

Rafinesque, C.S. 1819. Prodrome de 70 nouveaux genres d'animaux découverts dans l'intérieur des États-Unis d'Amérique, durant l'année 1818. *Journal de Physique, de Chimie et d'Histoire Naturelle*, **88**, 417–429.

Raymond, D.E., Osborne, W.E., Copeland, C.W. and Neathery, T.L. 1988. Alabama Stratigraphy. *Geological Survey of Alabama Circular*, **140**, 1–97.

Regan, C.T. 1923. The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. *Proceedings of the Zoological Society of London*, **1923** (1–2), 445–461.

Reinecke, T., Mollen, F.H., Gijsen, B., D'Haeze, B. and Hoedemakers, K. 2024. Batoids (Elasmobranchii: Rajiformes, Rhinopristiformes, Torpediniformes, Myliobatiformes) of the middle to late Ypresian, early Eocene, in the Anglo-Belgian Basin (south-western North Sea Basin) – a review and description of new taxa. *Palaeontos*, **35**, 1–171.

Risso, A. 1827. Histoire naturelle des principales productions de l'Europe méridionale, et particulièrement de celles des environs de Nice et des Alpes maritimes Tome 3, 480 pp. F.G. Levrault; Paris.

Rivaton, J. and Bourret, P. 1999. Les otolithes des poissons de l'Indo-Pacifique. *Documents Scientifiques et Techniques, special volume: Sciences de la mer*, **II2**, 1–372.

Roedel, H. 1930. Fischotolithen aus Palaeozängeschieben. *Zeitschrift für Geschiebeforschung*, **6**, 49–77.

Rosen, D.E. 1973. Interrelationships of higher euteleostean fishes. In: Greenwood, P.H., Miles, R.S. and Patterson, C. (Eds), Interrelationships of Fishes, 397–513. Academic Press; London.

Rosen, D.E. 1985. An essay on euteleostean classification. *American Museum Novitates*, **2827**, 1–57.

Salem, M. 1971. Fossil otoliths of some lower Cenozoic perciforms fishes of the Gulf Coast, 111 pp. Unpublished Master's thesis, University of Missouri at Rolla, Missouri, USA.

Schein J.P., Grandstaff, B.S., Gallagher W.B., Poole, J.C. and Lacovara, K.J. 2011. *Paralbula* in North America, revisiting an enigmatic Campanian–Late Paleocene teleost with hope for new insights. *The Geological Society of America Abstracts with Programs*, **43** (1), 87.

Schwarzhans, W. 1978. Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. *Mededelingen van de werkgroep voor tertiaire en kwartaire geologie*, **15** (4), 167–185.

Schwarzhans, W. 1999. A comparative morphological treatise of Recent and fossil otoliths of the order Pleuronectiformes, Piscium Catalogus, Otolithi Piscium 2, 245 pp. Verlag Dr. Freidrich Pfeil; Munich, Germany.

Schwarzhans, W. 2003. Fish otoliths from the Paleocene of Denmark. *Geological Survey of Denmark and Greenland Bulletin*, **2**, 1–94.

Schwarzhans, W. 2004. Fish otoliths from the Paleocene (Selandian) of West Greenland. *Medddelelser om Grønland Geoscience*, **42**, 1–32.

Schwarzhans, W. 2010. The otoliths from the Miocene of the North Sea Basin, 352 pp. Backhuys Publishers; Leiden.

Schwarzhans, W. 2019. Reconstruction of the fossil marine bony fish fauna (Teleostei) from the Eocene to Pleistocene of New Zealand by means of otoliths. With studies of Recent congroid, morid and trachinoid otoliths. *Memorie della Società Italiana di Scienze Naturali e Museo di Storia Naturale di Milano*, **46**, 1–392.

Schwarzhans, W. and Stringer, G. 2020. Fish otoliths from the late Maastrichtian Kemp Clay (Texas, USA) and the early Danian Clayton Formation (Arkansas, USA) and an assessment of extinction and survival of teleost lineages across the K-Pg boundary based on otoliths. *Rivista Italiana di Paleontologia e Stratigrafia*, **126** (2), 395–446.

Schwarzhans, W., Stringer, G. and Takeuchi, G. 2024. The middle Eocene bony fish fauna of California, USA, reconstructed by means of otoliths. *Rivista Italiana di Paleontologia e Stratigrafia*, **130** (2), 373–473.

Scopoli, J.A. 1777. Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae, 506 pp. Apud Wolfgangum Gerle; Prague.

Shimada, K. 2002. Dental homologies of lamniform sharks (Chondrichthyes: Elasmobranchii). *Journal of Morphology*, **215**, 38–72.

Siverson, M. 1995. Revision of the Danian cow sharks, sand tiger sharks, and goblin sharks (Hexnchidae, Odontaspididae, and Mitsukurinidae) from southern Sweden. *Journal of Vertebrate Paleontology*, **15** (1), 1–12.

Siverson, M. 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. *Transactions of the Royal Society of Edinburgh*, *Earth Sciences*, **90**, 49–66.

Smale, M., Watson, G. and Hecht, T. 1995. Otolith atlas of southern African marine fishes. *Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology*, **1**, 1–253.

Smitt, F.A. 1892. A history of Scandinavian fishes (second edition), 566 pp. P.A. Norstedt & Söner; Stockholm.

Stewart, J.D. 1992. First Mississippi records of *Holocentrites* (Beryciformes, Holocentridae), and confirmation of its Myripristine affinities. *Journal of Vertebrate Paleontology*, **12** (3), 53A.

Stringer, G. 1998. Otolith-based fishes from the Bowden shell bed (Pliocene) of Jamaica: Systematics and Paleoecology. *Contributions to Tertiary and Quaternary Geology*, **35**, 147–160.

Stringer, G. and Bell, D. 2018. Teleostean otoliths reveal diverse Plio-Pleistocene fish assemblages in coastal Georgia (Glynn County). *Bulletin of the Florida Museum of Natural History*, **56** (3), 83–108.

Stringer, G.L., Ebersole, J.A. and Ebersole, S.M. 2020a. First description of the fossil otolith-based sciaenid *Equetulus silverdalensis* in the Gulf Coastal Plain, USA, with comments on the enigmatic distribution of the species. *PaleoBios*, **37**, 1–12.

Stringer, G. and Miller, M. 2001. Paleoenvironmental interpretations based on vertebrate fossil assemblages: an example of their utilization in the Gulf Coast. *Transactions of the Gulf Coast Association of Geological Societies*, **51**, 329–338.

Stringer, G., Parmley, D. and Quinn, A. 2022. Eocene teleostean otoliths, including a new taxon, from the Clinchfield Formation (Bartonian) in Georgia, USA, with biostratigraphic, biogeographic, and paleoecologic implications. *Palaeovertebrata*, **45** (1), e1.

Stringer, G. and Schwarzhans, W. 2021. Upper Cretaceous teleosteans otoliths from the Severn Formation (Maastrichtian) of Maryland, USA, with an unusual occurrence of Siluriformes and Beryciformes and the oldest Atlantic coast Gadiformes. *Cretaceous Research*, **125** (1), 104867.

Stringer, G., Starnes, J., Leard, J. and Puckett, M. 2020b. Taphonomic and paleoecologic considerations of a phenomenal abundance of teleostean otoliths in the Glendon Limestone (Oligocene, Rupelian), Brandon, Mississippi. *Journal of the Mississippi Academy of Sciences*, **65** (1), 101.

Stringer, G. and Worley, L. 2003. Implications of recently discovered marine Oligocene vertebrates from the Rosefield Formation of Louisiana. *Texas Academy of Sciences Abstracts with Programs*, **106**, 67.

Stromer, E. 1910. Reptilien und Fischreste aus dem marinen Alttertiär von Südtogo (West Africa). *Monatsbericht der Deutschen Geologischen Gesellschaft*, **62** (7), 478–505.

Swainson, W. 1839. On the natural history and classification of fishes, amphibians & reptiles, or monocardian animals, Volume II, 452 pp. Spottiswoode & Co.; London.

Taverne L. 2009. *Ridgewoodichthys*, a new genus for *Brychaetus caheni* from the marine Paleocene of Cabinda (Africa): re-description and comments on its relationships within the Osteoglossidae (Teleostei, Osteoglossomorpha). *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, **79**, 147–153.

Tomita, T., Yabumoto, Y. and Kuga, N. 2023. A new snaggletooth shark species, *Hemipristis tanakai* sp. nov. from the Ashiya Group (Oligocene), Northern Kyushu, Japan. *Paleontological Research*, **28** (3), 273–278.

Toulmin, L.D. 1977. Stratigraphic distribution of Paleocene and Eocene Fossils in the Eastern Gulf Coast Region. *Geological Survey of Alabama Monograph*, **13**, 1–602.

Tuomey, M. 1858. Second Biennial Report of the Geology of Alabama, 256 pp. N.B. Cloud, State Printer; Montgomery, Alabama.

Thurmond, J. and Jones, E. 1981. Fossil vertebrates of Alabama, 244 pp. The University of Alabama Press; Tuscaloosa.

Van der Laan, R., Eschmeyer, W. and Fricke, R. 2024. Eschmeyer's Catalog of Fishes: Family-Group names. Available at: www.calacademy.org/scientists/catalog-of-fishes-family-group-names. Accessed 20/11/2024.

Villalobos-Segura, E. and Underwood, C.J. 2020. Radiation and divergence times of Batoidea. *Journal of Vertebrate Paleontology*, **40** (3), e1777147.

Wainwright, P.C., Smith, W.L., Price, S.A., Tang, K.L., Sparks, J.S., Ferry, L.A., Kuhn, K.L., Eytan, R.I. and Near, T.J. 2012. The evolution of pharyngognathy: a phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. *Systematic Biology*, **61** (6), 1001–1027.

Weiler, W. 1942. Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. *Abhandlungen des Reichsamts für Bodenforschung, Neue Folge*, **206**, 1–140.

Westgate, J.W. 2001. Chapter 11: Paleoecology and biostratigraphy of marginal marine Gulf Coast Eocene vertebrate localities. In: Gunnell, G.F. (Ed.), Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats, 263–297. Kluwer Academic/Plenum Publishers; New York.

Whetstone, K. and Martin, L. 1978. An Oligocene (Orellan) sirenian from the Bucatunna Formation of Alabama. *Tulane Studies in Geology and Paleontology*, **14** (4), 161−163.

White, E.I. 1955. Notes on African Tertiary sharks. *Bulletin of the Geological Society of Nigeria*, **5** (3), 319–325.

White, E.I. 1956. The Eocene fishes of Alabama. *Bulletins of American Paleontology*, **36** (156), 123–150.

Wiley, E. and Johnson, G. 2010. A teleost classification based on monophyletic groups. In: Nelson, J, Schultze, H.-P. and Wilson, M. (Eds), Origin and phylogenetic interrelationships of teleosts, 123 –182. Verlag Dr. Friedrich Pfeil; Munich.

Winkler, T.C. 1874. Deuxième mémoire sur des dents de poissons fossiles du terrain bruxellien. *Archives du Musée Teyler*, **4** (1), 16–48.

Woodward, A.S. 1889. Catalogue of the fossil fishes in the British Museum. Part. I, 474 pp. British Museum (Natural History); London.

Woodward, A.S. 1891. Notes on some fish remains from the Lower Tertiary and Upper Cretaceous of Belgium: collected by Monsieur A. Houzeau de Lehaie. *Geological Magazine*, **11891**, 1–14.

Woodward, A.S. 1901. Catalogue of the Fossil Fishes in the British Museum (Natural History). Part IV, 636 pp. British Museum (Natural History); London.

Woodward, A.S. 1907. Notes on some Upper Cretaceous fish-remains from the Provinces of Sergipe and Pernambuco, Brazil. *Geological Magazine*, **5** (4), 193–197.

Worley, L. 2004. Paleoecologic and evolutionary implications of bony and cartilaginous fishes from Oligocene sites of the Rosefield Formation in northwestern Catahoula Parish, Louisiana. Unpublished Master's thesis, 103 pp. University of Louisiana at Monroe; Monroe.

Yarkov, A.A. and Popov, E.V. 1998. A new chondrichthyan fauna from the Beriozovaya beds (lower Paleocene) of the Volgograd Volga River Basin, preliminary data. *Voprosy paleontologii i stratigrafii*, **1998** (1), 59–65. [In Russian]

Manuscript submitted: 25th July 2025
Revised version accepted: 10th October 2025