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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

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Abstract. The Tallahatta Formation, Lisbon Formation, and Gosport Sand are the three lithostratigraphic units that make up the lower-to-middle Eocene Claiborne Group. In Alabama, these marine units are among the most fossiliferous in the state and a long history of scattered reports have attempted to document their fossil diversity. In this study, we examined 20 931 elasmobranch and bony fish elements, including otoliths, derived from Claiborne Group units in Alabama and identified 115 unequivocal taxa. Among the taxa identified, one new species is described, *Carcharhinus mancinae* sp. nov., and *Pseudabdounia* gen. nov. is a new genus erected to include two species formerly placed within *Abdounia* Capatta, 1980. New taxonomic combinations proposed include *Pseudabdounia claibornensis* (White, 1956) gen. et comb. nov., *Pseudabdounia recticona* (Winkler, 1874) gen. et comb. nov., *Physogaleus alabamensis* (Leriche, 1942) comb. nov., and *Eutrichiurides plicidens* (Arambourg, 1952) comb. nov. We also report the first North American paleobiogeographic occurrences of *Aturobatis* aff. *A. aquensis* Adnet, 2006, *Brachycarcharias atlasi* (Arambourg, 1952), *Eutrichiurides plicidens* comb. nov., *Galeorhinus louisi* Adnet & Cappetta, 2008, *Ginglymostoma maroccanum* Noubhani & Cappetta, 1997, *Gymnosarda* sp., *Mennerotodus* sp., *Rhizoprionodon ganntourensis* (Arambourg, 1952), *Stenoscyllium* aff. *S. priemi* Noubhani & Cappetta, 1997, *Trichiurus oshosunensis* White, 1926, and the first North American occurrence for a fossil member of the Balistidae Risso, 1810. Our sample also included 26 taxa that represented first paleobiogeographic occurrences for Alabama, including *Abdounia beaugei* (Arambourg, 1935), *Albula eppsi* White, 1931, *Ariosoma nonsector* Nolf & Stringer, 2003, *Anisotremus*? sp., *Anomotodon* sp., *Brachycarcharias twiggsensis* (Case, 1981), *Burnhamia daviesi* (Woodward, 1889), *Eoplinthicus yazooensis* Capetta & Stringer, 2002, *Galeorhinus ypresiensis* (Casier, 1946), *Gnathophis meridies* (Frizzell & Lamber, 1962), *Haemulon? obliquus* (Müller, 1999), *Hypolophodon sylvestris* (White, 1931), *Malacanthus? sulcatus* (Koken, 1888), *Meridiania* cf. *M. convexa* Case, 1994, *Palaeocybium proosti* (Storms, 1897), *Paraconger sector* (Koken, 1888), *Paralbula* aff. *P. marylandica*

Blake, 1940, *Phyllodus toliapicus* Agassiz, 1844, *Propristis schweinfurthi* Dames, 1883, *Pycnodus* sp., *Pythonichthys colei* (Müller, 1999), *Scomberomorus stormsi* (Leriche, 1905), *Signata stenzeli* Frizzell & Dante, 1965, and *Signata nicoli* Frizzell & Dante, 1965, and the first Paleogene occurrences in Alabama of a member of the Gobiidae Cuvier, 1816. A biostratigraphic analysis of our sample showed stratigraphic range extensions for several taxa, including the first Bartonian occurrences of *Eoplinthicus yazooensis*, *Jacquhermania duponti* (Winkler, 1876), *Meridiania* cf. *M. convexa*, *Phyllodus toliapicus*, and “*Rhinobatos*” *bruxelliensis* (Jaekel, 1894), range extensions into the late Ypresian and Bartonian for *Tethylamna dunni* Cappetta & Case, 2016 and *Scoliodon conecuhensis* Cappetta & Case, 2016, the first late Ypresian records of *Galeorhinus louisi*, the first Lutetian occurrence of *Gymnosarda* Gill, 1862, and a range extension for *Fisherichthys* aff. *F. folmeri* Weems, 1999 into the middle Bartonian. Larger biostratigraphic and evolutionary trends are also documented, such as the acquisition of serrations in *Otodus* spp., possible population increases for the Rhinopterinae Jordan & Evermann, 1896 and Carcharhiniformes Compagno, 1973 in the Bartonian, and the apparent diversification of the Tetraodontiformes Berg, 1940 during the same stage. This study helps better our understanding of early-to-middle Eocene elasmobranch and bony fish diversity, paleobiogeography, and biostratigraphy in the Gulf Coastal Plain of North America.

Keywords. Tallahatta Formation, Lisbon Formation, Gosport Sand, Gulf Coastal Plain, Elasmobranchii, Teleostei.

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Contents

Introduction

The lithostratigraphic units that comprise the lower-to-middle Eocene (upper Ypresian to Bartonian) Claiborne Group in Alabama (USA), the Tallahatta Formation, Lisbon Formation, and Gosport Sand, are three of the most productive geologic units in the state with respect to the diversity of marine fossils. Over the past 150 years, scattered studies have documented a variety of chondrichthyan and teleost taxa from Claiborne Group strata in Alabama. Gibbes (1848), for example, was the first to report a chondrichthyan fossil from the Claiborne Group when he noted that teeth belonging to *Lamna elegans* Agassiz, 1843 were common at Claiborne Bluff (site AMo-4) in Monroe County, AL (the locality for which the Claiborne Group was named). A more comprehensive study of these units was later conducted by Alabama's first state geologist, Michael Tuomey, as part of his first report on the geology of the state (Tuomey 1850). Although Tuomey (1850) noted the presence of abundant fossils within Claiborne Group strata, he did not describe, figure, or list any of them. Tuomey continued to study the Claiborne Group units for several more years, but unfortunately, he passed away in 1857 before he could publish his findings in his second geological report of the state (Ebersole & Dean 2013). However, under a direct order from the Alabama Governor, Tuomey's colleague John Mallet, a chemist and professor at the University of Alabama, was tasked with completing Tuomey's work. In 1858, Mallet published the *Second Biennial Report on the Geology of Alabama* (Tuomey 1858), and incorporated many of the geological notes left behind by Tuomey, including a list of 14 sharks he had identified from Eocene strata in the state. Although this list did not include specific collecting localities or formations, Tuomey (1858) did specifically mention collecting shark teeth along Pigeon Creek (site ACon-6) in Conecuh County, a locality that exposes the contact of the Tallahatta and Lisbon formations. Mallet shipped a subset of Tuomey's vertebrate fossil collection to London in 1859, a fortunate turn of events because the majority of Tuomey's remaining fossil collection was destroyed by fire at the end of the American Civil War (White 1956; Ebersole & Dean 2013).

In 1882, Tuomey's fossils, along with two other Alabama Eocene collections, those of Lord Enniskillen and Sir Philip Grey-Egerton, were accessioned into the permanent collections at the British Museum of Natural History (NHMUK) in London. These specimens were soon after examined by Woodward (1889) who provided an extensive systematic list of the fossils he identified. A year earlier, Koken (1888) pioneered the taxonomic study of North American Paleogene otoliths and named 23 new species from the Vicksburg, Jackson, and Claiborne Groups in Alabama and Mississippi. The specimens Koken (1888) examined were collected by "O. Meyer" of New York, who later gave several otoliths to "O. Boettger" of Frankfurt, Germany. Both Meyer and Boettger later gave these otoliths to Koken for examination. Of these otoliths, Eastman (1904) stated: "The Eocene and Miocene of Virginia combined yield scarcely a half dozen species of bony fishes, and this group is represented in equal meagerness in North and South Carolina. In these states, however, and especially in the Eocene of Alabama and Mississippi, Teleostome otoliths occur in considerable abundance and variety; and it happens that these insignificant appearing objects are the only record that remains of a once flourishing fish fauna, which can be but inadequately reconstructed in imagination."

Campbell (1929a) noted that the 23 species described by Koken (1888) remained the only described fossil otoliths in North America, and later that year Campbell (1929b) included these taxa in his *Bibliography of Otoliths*. Dante (1954) stated that many of the Koken (1888) specimens were indistinguishable from several of the Miocene otoliths he observed in Maryland.

White (1956) re-examined and described the NHMUK specimens originally published by Woodward (1889), ultimately describing seven chondrichthyan taxa and an otolith that were collected from the Gosport Sand at the famous Claiborne Landing in Monroe County. The otolith was collected by "G.H. Harris" and he subsequently donated it, along with several Alabama shark teeth, to the NHMUK in 1892. In 1960 and 1964, Don L. Frizzell visited Claiborne Landing and Little Stave Creek, the latter in Clarke County, Alabama, where he collected several otoliths from the Lisbon Formation and Gosport Sand, respectively. These specimens were subsequently described by Frizzell & Dante (1965) who named 11 new genera, and nine new species, and they recognized a total of 53 otolith-based taxa from Claiborne Group and Oligocene strata in Alabama, Mississippi, and Texas. That same year, Frizzell (1965) described numerous fossil otoliths belonging to the family Albulidae, but this study did not specifically describe any Claiborne Group specimens. Those authors did mention, however, that taxa like *Stintonia* Frizzell & Lamber, 1961 were also known from Claibornian strata in the United States and referenced Claiborne Group exposures in both Alabama and Texas.

Thurmond & Jones (1981) reviewed the known fossil vertebrates from Alabama and included within their descriptions 23 shark and bony fish taxa from the Claiborne Group, most of which were collected from the Tallahatta Formation and Gosport Sand in Clarke and Monroe counties. Oddly, however, Thurmond & Jones (1981) referenced two congrids described by Koken (1888), but failed to mention the many sciaenid otolith taxa Koken (1888) described from the Alabama Lisbon Formation. Later, Manning (2003) mentioned and figured a few additional specimens from the Gosport Sand in Clarke County, and Underwood & Gunter (2012) alluded to an undescribed species of carcharhiniform shark from the same unit. Maisch *et al.* (2014, 2016) later documented chondrichthyan and teleost faunas from two localities in Alabama (sites ACh-14 and ACon-6, respectively) where the contact of the Tallahatta and Lisbon Formations is exposed. In addition, Ehret & Ebersole (2014) documented several Claiborne Group specimens of *Carcharocles auriculatus* (de Blainville, 1818) in their study of otodontid sharks in Alabama, and Cicimurri & Ebersole (2015) reported a new ray from the lower Tallahatta Formation at site ADl-1 in Dale County and provided a brief discussion on other myliobatids occurring within the same unit.

Of the numerous Claiborne Group localities that have been reported in Alabama (see Toulmin 1977, and additional localities cited herein), site ACov-11 in Covington County experienced a surge in scientific attention in recent years. This locality, which exposes the contact of the Tallahatta and Lisbon Formations, has become well known to local hobbyists for the extensive amount of shark and bony fish remains that can be found there. Holman & Case (1988) were the first to document specific vertebrate taxa recovered from site ACov-11, and they provided a preliminary list of 21 elasmobranch and teleost taxa that they identified from the site. Feldmann & Portell (2007) provided their own provisional list of 11 shark and bony fish taxa from the site, and Clayton *et al.* (2013) figured, but did not describe, a total of 31 taxa. Three years later, Cappetta & Case (2016) documented a total of 39 chondrichthyan taxa from the ACov-ll locality, a diversity that is eclipsed only by the current study.

Herein, we present the largest and most comprehensive study of elasmobranch and bony fish taxa from the Claiborne Group of Alabama, USA. The nearly 21 000 specimens in our sample were derived from 16 unique localities across Alabama and span the entire stratigraphic extent of the Claiborne Group. This study includes detailed descriptions and figures of all confirmed taxa, and taxonomic remarks are provided for each. In addition, a review of all prior studies on the Claiborne Group vertebrates was conducted, and whenever possible, the reported specimens were reexamined. Furthermore, detailed stratigraphic and geographic ranges within Alabama are documented for each of the identified taxa, allowing us to compare the faunal compositions within each of the three Claiborne Group formations. This in turn allowed us to conduct a detailed biostratigraphic analysis of the early-to-middle Eocene elasmobranch and bony fish taxa. An in-depth analysis of the Claiborne Group otoliths is also provided, which compliments the list of teleost taxa identified by their teeth and other bony remains.

Material and methods

Collection and examination of specimens

The Claiborne Group dataset studied herein was acquired through a variety of methods, including field collection by the authors, the processing of historically collected bulk samples, direct examination of specimens through visits to collections housed in publicly-accessible scientific institutions, donations of specimens from private collectors, and loans from institutions housing collections of Alabama Claiborne Group specimens. Only specimens that were directly examined by the present authors were included within our dataset.

We examined specimens from a total of 16 distinct Claiborne Group localities in Alabama (Table 1). These localities are spread across the Eocene surface strata in the state, and each have exposures of one or more of the Claiborne Group formations, the Tallahatta and Lisbon formations and the Gosport Sand. Detailed discussions on the exposed units at each of these localities is provided in the 'Geologic Settings' section below. Bulk field samples were processed from seven of the 16 localities reported herein, and at least one large bulk field sample (> 20 kg) was obtained from each of the three Claiborne Group formations. Several of the bulk samples processed were housed at the South Carolina State Museum (SC) in Columbia, USA, Wright State University – Lake Campus (WSU) in Celina, Ohio, USA, and the bulk field sample library at McWane Science Center (MSC) in Birmingham, AL, USA (a collection that houses over 1100 such samples from across the state). Bulk field samples were not obtained from

Table 1. Claiborne Group localities that produced remains examined in this study.

Site	County	Unit(s) exposed	Published reference(s)
ACh-7	Choctaw County	Tallahatta/Lisbon contact zone	Toulmin 1977
ACh-8	Choctaw County	"upper" Lisbon Formation	Toulmin 1977
ACh-14	Choctaw County	Tallahatta/Lisbon contact zone	Toulmin 1977; Maisch *et al.* 2014
ACh-21	Choctaw County	Gosport Sand	This study
ACl-3	Clarke County	"upper" Lisbon Formation	Toulmin 1977; Uhen 2008
ACl-4	Clarke County	Basal Gosport Sand	Jones 1967; Toulmin 1977
ACl-14	Clarke County	Gosport Sand	This study
ACl-15	Clarke County	Gosport Sand	This study
ACl-16	Clarke County	"upper" Lisbon Formation	This study
ACon-6	Covington / Conecuh counties	Tallahatta/Lisbon contact zone	Maisch *et al.* 2016
ACov-1	Covington County	Upper Tallahatta, "lower" Lisbon Formation	Toulmin 1977
ACov-11	Covington County	Upper Tallahatta, "lower" Lisbon Formation	Copeland 1966; Clayton *et al.* 2013
ADl-1	Dale County	Meridian Sand Member, lower Tallahatta Formation	Cicimurri & Ebersole 2016
AMo-4	Monroe County	Lisbon Formation/Gosport Sand contact zone	Toulmin 1977
AMo-8	Monroe County	Tallahatta Formation	This study
AWa-2	Washington County	"upper" Lisbon Formation, Gosport Sand	Toulmin 1977

the remaining eight localities for one of three reasons: 1) the reported locality was based on historically collected specimens and was not visited by the present authors; 2) the reported locality was based on historically collected specimens and the site no longer exists; or 3) the collection of bulk field samples would not be productive at the locality (i.e., chalk deposits with low fossil density).

All bulk field samples were processed in the laboratories at MSC, SC, and WSU. Samples were wet screened down to 0.8 mm mesh (No. 20 USA Standard Testing sieves) to ensure the recovery of macro and micro vertebrate remains. The resulting concentrates were dried and were hand-picked using microscopes. Historically collected bulk samples housed at MSC, SC, ULM, and WSU were processed in the same manner.

Additional Alabama Claiborne Group specimens were documented from within the collections at the following scientific institutions:
ALMNH = Alabama Museum of Natural History, Tuscaloosa, USA
ANSP = Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA
GSA = Geological Survey of Alabama, Tuscaloosa, USA
MMNS = Mississippi Museum of Natural Science, Jackson, USA
MSC = McWane Science Center, Birmingham, Alabama, USA
NHMUK = British Museum of Natural History, London, UK
NJSM = New Jersey State Museum, Trenton, USA

SC	=	South Carolina State Museum, Columbia, USA
ULM	=	University of Louisiana at Monroe, Monroe, USA
USNM	=	United States National Museum, Washington, D.C., USA
WSU	=	Wright State University – Lake Campus, Celina, Ohio, USA

These specimens were either obtained on loan or directly examined by one or more of the authors at the respective institution. If direct examination was not possible, high resolution photographs were obtained of the specimens (which was the case for certain type specimens housed at the NHMUK). Donations of Claiborne Group specimens were also solicited from the members of the Alabama Paleontological Society, Inc. in Birmingham, AL, who frequented many of the localities reported herein. Donated specimens were cataloged into the collections at MSC, and only those for which the provenance was confirmed were included within the dataset. We extend our gratitude to these local collectors, and their contributions to this study are credited herein. Specimens that reside in private collections, rather than publicly accessible repositories, were not included in our dataset.

Data collection, taxonomy, and analysis

All of the specimens we examined were tabulated into an MS Excel spreadsheet and the following data was recorded for each: museum catalog number, specimen identification (to the lowest taxonomic ranking), number of specimens, stratigraphic horizon (including upper or lower position within the formation, if known), locality designation (see Table 1), collector, and date collected. Except for several ray tooth plates, articulated elements belonging to the same individual were completely absent in our sample. Because it was not possible to calculate the minimum number of individuals (MNI) present within our sample, each element was recorded individually in our dataset (except for ray tooth plates with each received an N-value of 1). Specimens with incomplete or unconfirmed stratigraphic horizon and/or locality information were not included in the dataset. The stratigraphic unit(s) exposed at each locality were confirmed by one or more of the following methods: direct investigation by the authors, published accounts, and/or detailed site records and historical field notes. The localities we studied are reported herein using standard Alabama paleontological locality designations and are listed in Table 1. Many of the reported localities reside on Federal Land or private property, and per legal regulations and for ethical reasons their precise geographic locations cannot be made public. However, to ensure the repeatability of this and future studies, this information is permanently filed in the MSC archives and fully available to qualified researchers upon request.

The higher taxonomic rankings and the systematic order presented herein follows that of Nelson *et al.* (2016), a work that incorporated morphological and molecular phylogenies for both fossil and extant taxa. Explanations are provided for any deviation from Nelson *et al.* (2016). Whenever possible, type specimens were examined (either directly or indirectly) to assist with identifications, and recent molecular divergence data was consulted to help determine more refined taxonomic placements for many of the fossil taxa. To better understand heterodonty within living representatives of the fossil species, and therefore further justify taxonomic placements and synonymies, we compared fossil teeth to those within the jaws of extant elasmobranch and osteichthyan taxa housed at MSC, SC and the USNM.

The synonymy listings provided are not all inclusive, but reflect type descriptions, taxonomic revisions, and select specimens from the literature that we enter into synonymy (with a particular focus on those previously reported in Alabama). The stratigraphic and geographic ranges listed were directly derived from our sample and reflect the range of the taxon within the Claiborne Group of Alabama only. Global occurrences obtained from previous peer-reviewed studies are provided when relevant. The biostratigraphic analysis presented herein was derived exclusively from our dataset. To compile this information, the number of specimens identified within each stratigraphic interval and at each locality was tabulated in separate spreadsheets (see Appendices 1 and 2, respectively).

Figured specimens that exceeded 0.5 cm in greatest dimension were photographed with a Nikon D80 camera with Tamron macro lens. Specimens smaller than 0.5 cm were photographed using an AmScope MU1000 camera mounted to an AmScope 3.5×–90× stereo microscope and 10MB images were captured using AmScope Toupview software ver. 3.7. All photographs were rendered in Photoshop CC 2017 software as part of the production of the accompanying figures.

Geologic setting

The lower-to-middle Eocene Claiborne Group is the middle of three groups that comprise the Eocene surface exposures in Alabama, USA. The Wilcox Group is positioned stratigraphically below the Claiborne Group, and the Jackson Group is stratigraphically above (Fig. 1). Together these three groups form a nearly complete Eocene sequence that ranges from the Ypresian to the end of the Priabonian. In Alabama, the Claiborne Group forms an arcuate belt that extends east to west across parts of 14 counties in the southern half of the state. The specimens examined as part of this study were collected from 16 distinct localities spread across seven different counties in southern Alabama. Each of these localities has surface exposures of one or more of the three distinct lithologic formations that comprise the Claiborne Group in Alabama – the Tallahatta Formation, Lisbon Formation, and Gosport Sand. Locality information is summarized in Table 1 but discussed in detail below.

Tallahatta Formation

The Tallahatta Formation (Fig. 2) lies at the base of the Claiborne Group, and a type 1 unconformity separates this unit from the underlying Hatchetigbee Formation of the Wilcox Group (Bybell & Gibson 1985; Mancini & Tew 1991). The aerial extent of the Tallahatta Formation extends from northern and central Mississippi, through Alabama, and into western Georgia. In Mississippi, the Tallahatta Formation is divided into three members, including (in ascending order) the Meridian Sand, Basic City Shale, and

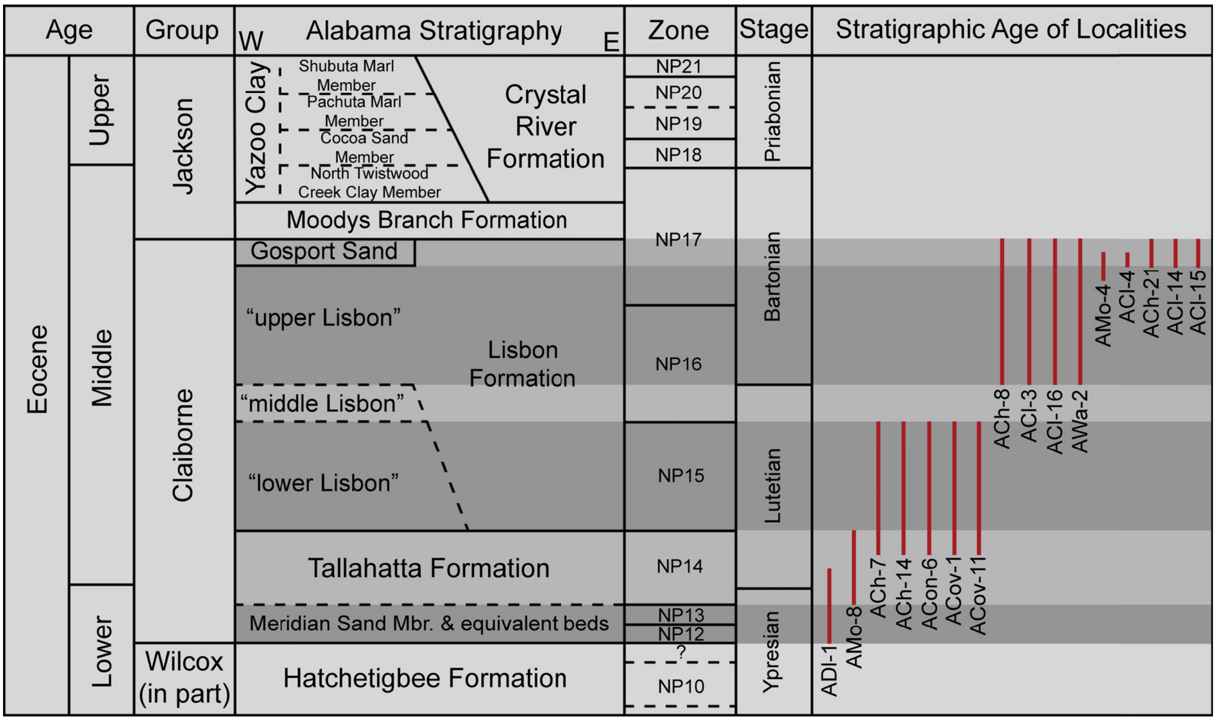

Fig. 1. Eocene surface stratigraphy in Alabama and the stratigraphic age of Claiborne Group localities. Vertical red lines indicate the stratigraphic unit(s) exposed at each locality. Abbreviations: E = east; Mbr. = Member; NP = Nannoplankton Zone; W = west.

Neshoba Sand (Bybell & Gibson 1985). In Alabama, only the Meridian Sand is discernable, as the Tallahatta Formation thins in an easterly direction and is generally not divided into members in the central and eastern parts of the state (Raymond *et al.* 1988; Savrda *et al.* 2010). Although the Meridian Sand Member is formally recognized in the southwestern part of Alabama, Bybell & Gibson (1985) and Cicimurri & Ebersole (2015) identified a unit located at the base of the Tallahatta Formation in the southeastern part of Alabama that they referred to as "Meridian Sand equivalent."

The Meridian Sand Member (and "Meridian Sand equivalent") consists of fine gray, fossiliferous, gravelly, lignitic sand that has been interpreted as representing nearshore and shallow marine deposits (Bybell & Gibson 1985; Cicimurri & Ebersole 2015). The Tallahatta Formation proper consists of claystone, coarse sand and gravel, glauconitic sand, and calcareous matrix containing an abundance of invertebrate fossils, all indicative of deeper inner shelf deposits (Bybell & Gibson 1985). Overall the Tallahatta Formation is thought to represent a single third-order depositional sequence (TE2.1 of Baum & Vail 1988; Mancini & Tew 1991). The biostratigraphic age of both the Meridian Sand Member and Tallahatta Formation has been disputed in the literature. Based on calcareous nannofossils, Bybell & Gibson (1985) placed the entirety of the Meridian Sand Member within Nannoplankton Zone (NP) 12, and the remainder of the Tallahatta Formation within zones NP13 and NP14. Mancini (1989)

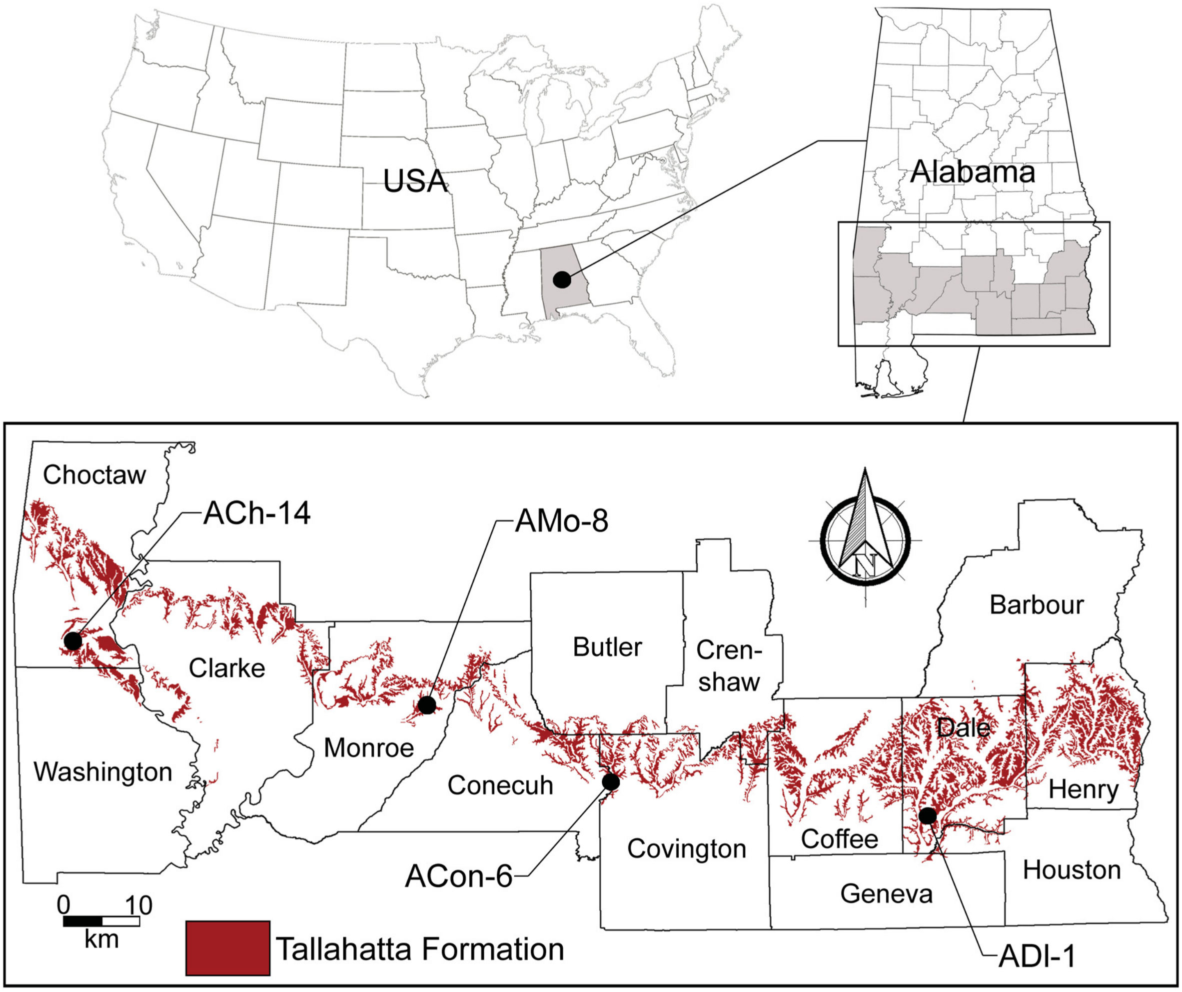

Fig. 2. Tallahatta Formation surface exposures in Alabama, with sampled localities indicated by closed circles.

and Mancini & Tew (1990) showed the Meridian Sand Member within zones NP12 and NP13, and the Tallahatta Formation proper within both Zone NP14 and the lower portion of Zone NP15. Later, Mancini & Tew (1995) and Mancini (2008) showed the Meridian Sand Member within zones NP12 and NP13, and the remainder of the Tallahatta Formation within Zone NP14. Here, we follow the nannoplankton zonations shown by Mancini & Tew (1995) and Mancini (2008) because these represent the most recent interpretations of the biostratigraphic ages of these units.

Our sample of vertebrate remains from the Tallahatta Formation consists of specimens collected from Meridian Sand Member equivalent beds, as well as from the lower and upper portions of the Tallahatta Formation proper. A majority of our Tallahatta samples were derived from site ADl-1 (n = 5689) in Dale County, AL, a stream locality that exposes both Meridian Sand Member equivalent beds and the lower portion of the Tallahatta Formation. The geology at site ADl-1 was described by Cicimirri & Ebersole (2015), who noted that the exposed strata at the locality were barren of calcareous nannoplanktons. This lends further evidence that the exposed strata likely reside within zones NP12–13, and the lower portion of Zone NP14, which were shown by Mancini & Tew (1995) and Mancini (2008) to be devoid of these microfossils. A small historically collected bulk sample (> 0.5 kg) from this site was composed of a fine gray, fossiliferous, gravelly, lignitic sand (Cicimurri & Ebersole 2015). This lithology, indicative of the Meridian Sand Member equivalent beds (see Bybell & Gibson 1985), showed that not only is this basal unit exposed at the site, but that the exposed strata includes the contact between the Meridian Sand equivalent beds and the lower Tallahatta Formation. Several large (> 9 kg), vertebrate-rich bulk samples were historically collected from this locality that were derived from the lower Tallahatta Formation beds within the lower half of Zone NP14. For simplicity, the specimens recovered from the Meridian Sand Member equivalent beds at this locality are referred herein as being derived from the Meridian Sand Member.

853 specimens in our sample were collected from site AMo-8, a road cut locality in Monroe County. Several historically collected bulk samples were examined from this previously unpublished locality, and a stratigraphic profile of this site is on file in the MSC archives (entry 167-01). The lithology at this site suggests the exposed strata fall within the main body of the Tallahatta Formation within Zone NP14. As part of our study we reexamined specimens that were reported by Maisch *et al.* (2014, 2016) from two distinct localities; site ACh-14 in Choctaw County and site ACon-6 on the Conecuh/Covington county line, respectively. Both sites are stream localities, and the strata described at both sites are similar to each other and indicate that the contact between the Tallahatta and overlying Lisbon Formation is exposed. However, in both instances, Maisch *et al.* (2014, 2016) appear to have included specimens collected as float from gravel bars, making the stratigraphic provenance difficult to ascertain. As a result, both of those paleofaunas are herein recorded as being from the contact of the Tallahatta and Lisbon formations, with the material being derived from the uppermost portion of Zone NP14 or the base of Zone NP15.

Lisbon Formation

The Lisbon Formation (Fig. 3) is the middle unit within the Claiborne Group and occurs stratigraphically below the Gosport Sand and disconformably above the Tallahatta Formation (Toulmin 1977; Raymond *et al.* 1988). Surface exposures of the Lisbon Formation can be found in 10 counties within the central and eastern parts of southern Alabama. Surface exposures of the Lisbon Formation also exist in Clarke, Choctaw, and Washington counties in the western part of Alabama, but this unit is often difficult to distinguish from the overlying Gosport Sand because of the similarities in lithologic composition.

In Alabama the Lisbon Formation is divided into three unofficial members, termed “lower,” “middle”, and “upper.” These three units vary slightly in lithologic composition, with the “lower” Lisbon consisting of fossiliferous coarse-grained glauconitic sands, the “middle” Lisbon being composed mostly of carbonaceous sand and carbonaceous silty clay, and the “upper” Lisbon consisting of fossiliferous sandy clay, calcareous sand, and glauconitic, calcareous clayey sand (Raymond *et al.* 1988). The depositional setting of the Lisbon Formation varies by locality, but largely consists of nearshore marine and estuarine deposits (see Bybell & Gibson 1985; Raymond *et al.* 1988; Clayton *et al.* 2013). According to Mancini & Tew (1990, 1991), the Lisbon Formation represents a single third order depositional sequence, with the "lower", "middle", and "upper" members being assigned to TE2.1, TE2.2, and TE2.3 of Baum & Vail (1988), respectively. As noted by Clayton *et al.* (2013), the biostratigraphic age of the Lisbon Formation has been inconsistently reported in the literature. For example, Mancini & Tew (1990, 1991) showed the base of the Lisbon Formation within the lower portion of Zone NP15 and the upper contact within the upper half of Zone NP17. Bybell & Gibson (1985) showed the top of Zone NP14 as representing the base of the Lisbon Formation, a boundary that was later corroborated by Mancini (2008). We follow the interpretations of Bybell & Gibson (1985) and Mancini (2008) and view the base of the Lisbon Formation as falling within the lower part of Zone NP15, with the upper boundary of the formation residing in the middle of Zone NP17 (as suggested by Mancini & Tew 1990, 1991).

The majority of the Lisbon Formation specimens in our sample (n = 6394) were recovered from river site ACov-11 in Covington County. The exposures at this locality are well documented and originally interpreted as belonging to the Tallahatta Formation (see Copeland 1966; Holman & Case 1988; Savrda

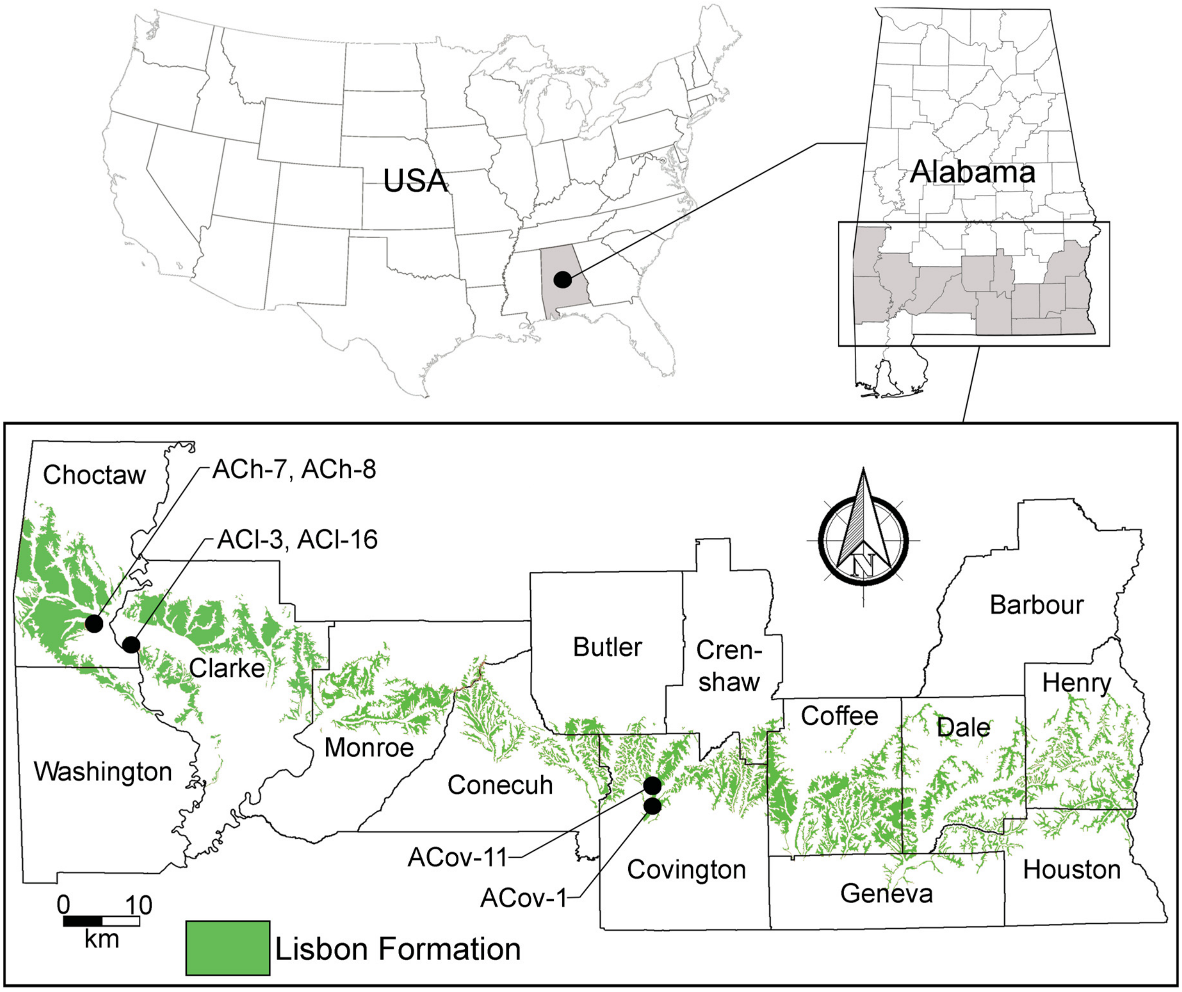

Fig. 3. Lisbon Formation surface exposures in Alabama, with sampled localities indicated by closed circles.

et al. 2010; Feldmann & Portell 2007). Clayton *et al.* (2013), however, described an unconsolidated bluish-green, quartz sand bed at the site that was attributed to the lowermost Lisbon Formation (bed 2 of Copeland 1966; Cappetta & Case 2016), and they showed the base of this bed represented the unconformable contact between the Tallahatta and Lisbon formations. This unconsolidated lens at the base of the Lisbon Formation is prolific in terms of producing vertebrate remains and is likely the source for much of the vertebrate material recovered from the river as float by hobby collectors.

The specimens we examined from the ACov-11 locality were recovered by bulk field sampling and surface collecting. As part of this study, numerous bulk field samples were collected over the course of several years by personnel at MSC and WSU. These samples were specifically excavated from the lower 5.0 cm of bed 2 of Copeland (1966), where the vertebrate density is highest and where the exact stratigraphic position of these specimens is known. The specimens reported by Clayton *et al.* (2013) were derived from this same bed, and their figured specimens were reexamined as part of the present study. These specimens, as well as those recovered from processing bulk field samples at MSC and WSU (some of which were donated to SC), are all assigned to the basal Lisbon Formation and fall within the lower half of Zone NP15.

As part of this study, donations of specimens from the ACov-11 locality, a popular site among amateur collectors, were solicited from members of the Alabama Paleontological Society, Inc. However, because these specimens were obtained via surface collecting and/or screening in the river, it cannot be known for certain whether the specimens were derived from the Tallahatta or Lisbon formations. Further complicating the matter is that Copeland (1966) reported vertebrate remains from two beds positioned stratigraphically above bed 2 at site ACov-11 (his beds 3 and 5), and the senior author (JAE) has observed vertebrate remains within the underlying bed 1. Additionally, specimens derived from further downstream and from along several of the nearby tributaries, where Tallahatta Formation beds are exposed, have been considered by hobby collectors as part of the same locality. As a result, unless the specimens were confirmed to be recovered *in situ* from bed 2 at the ACov-11 locality, they are reported herein as being derived from the contact of the Tallahatta and Lisbon formations. Several historical collections from site ACov-11 were examined at the ALMNH, MSC, MMNS, and the GSA, and they too are assigned to the Tallahatta/Lisbon Formation contact zone (meaning the specimens could have been derived from the uppermost portion of Zone NP14 or the base of Zone NP 15) because the exact unit/bed that produced these specimens is unknown.

Five specimens in our sample were collected from locality ACov-1 in Covington County. The geology at this stream site was investigated by Toulmin (1977), who noted that the exposed beds represented the contact between the Tallahatta and Lisbon formations. Toulmin (1977) also investigated two additional localities recorded in our sample, sites ACh-7 and ACh-8, both in Choctaw County. Although both localities are located along the same shallow stream, each exposes a different stratigraphic unit. A total of three specimens were collected from site ACh-7, a locality that exposes the contact of the Tallahatta and Lisbon Formations (see Toulmin 1977) in the upper part of Zone NP14 and the lower part of Zone NP15. Thirty-three specimens were collected from site ACh-8, a locality that exposes beds from the "upper" member of the Lisbon Formation (see Toulmin 1977) that fall within the upper half of Zone NP16 and the lower half of Zone NP17. One hundred and seven specimens in our sample were collected from site ACl-3 in Clarke County. The geology at this locality was described by Toulmin (1977) and Uhen (2008), who both reported exposures of the "upper" member of the Lisbon Formation, which places the recovered fossils within the upper half of Zone NP16 and the lower half of Zone NP17. Finally, three of the specimens we examined were collected from a previously unpublished locality, site ACl-16. This locality occurs approximately 1.0 km northwest of site ACl-3 and exposes deposits of the "upper" member of the Lisbon Formation.

Gosport Sand

The uppermost formation in the Claiborne Group is the Gosport Sand (Fig. 4). In Alabama, surface exposures of the Gosport Sand are confined to four counties in the southwestern part of the state. The contact between the Gosport Sand and underlying Lisbon Formation is disconformable and this contact is marked with Gosport Sand-filled borings in the top of the Lisbon Formation (Toulmin 1977). The Gosport Sand is not as thick as the other Claiborne Group formations, with the unit not exceeding 9.0 m. The Gosport Sand is composed of fine- to medium-grained sand, glauconitic sand, laminated carbonaceous clays, and occasional lenses of greenish-gray shale (Toulmin 1977; Raymond *et al.* 1988). This formation is recognized for its abundance of invertebrate fossils (see Conrad 1835; Toulmin 1977), and the basal portion of the unit is known to contain quartz pebbles and an extensive lag of vertebrate remains (Toulmin 1977). The Gosport Sand and overlying Moodys Branch Formation are part of the Td supercycle, and Mancini & Tew (1990; 1991) assigned the Gosport Sand to the TE3.1 sequence stratigraphy cycle. As indicated by the presence of leaf-bearing clays (Toulmin 1977) and occasional terrestrial vertebrates (see Westgate 2001, 2012), the Gosport Sand has been interpreted to represent a nearshore environment. On the geologic map of Alabama, the Gosport Sand and underlying Lisbon Formation are often not differentiated because they often appear to have similar lithologies when exposed at weathered outcrops (Causey & Newton 1972). As a result, the true aerial extent of Gosport Sand surface exposures is currently unknown, and what is presented on Fig. 4 is mapped as Lisbon / Gosport Undifferentiated.

The majority of our Gosport Sand specimens (n = 5747) were derived from historically collected bulk samples at site ACl-4 in Clarke County. Field notes associated with these samples indicate they were collected from a 0.3 m thick lens located at the base of the Gosport Sand, a lens that has previously been noted for the abundance of vertebrate remains it contains (Jones 1967; Toulmin 1977). These fossils are reported herein as being derived from the basal Gosport Sand within the lower half of Zone NP17. One hundred and twenty specimens in our sample were historically collected from site AMo-4 in Monroe County. This classic locality, known as Claiborne Bluff, is famous for its abundance of

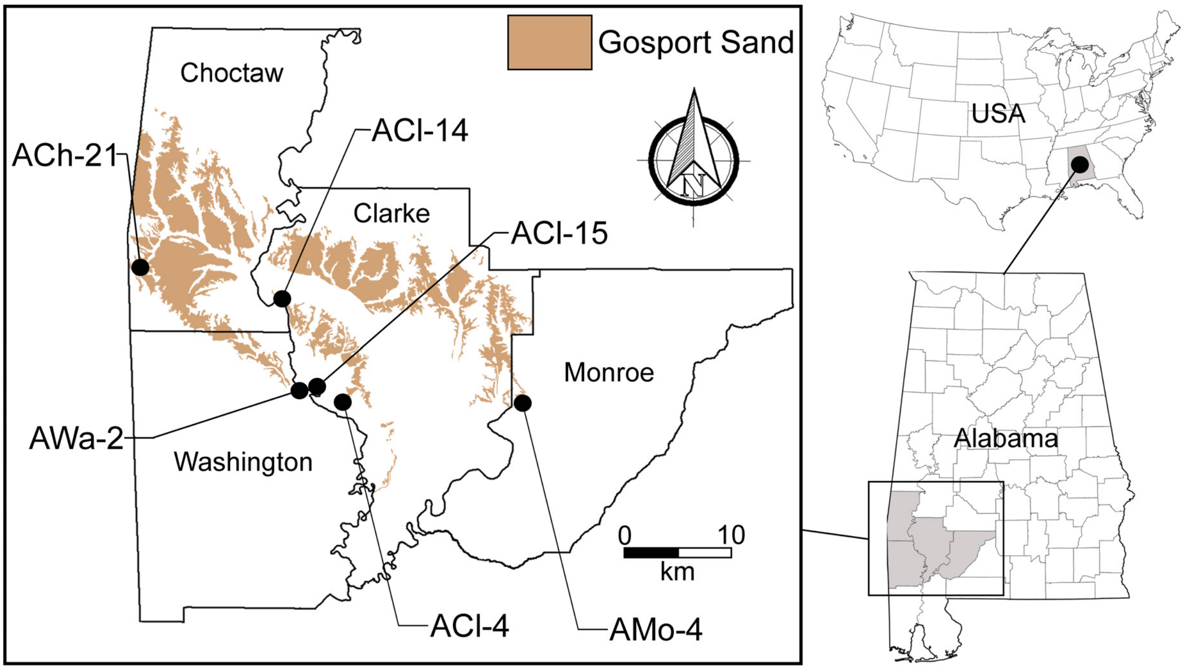

Fig. 4. Gosport Sand surface exposures in Alabama, with sampled localities indicated by closed circles.

pristine invertebrate fossils (Conrad 1835; Smith & Johnson 1887; Toulmin 1977). Toulmin (1977) reported three units exposed at the site including the "upper" Lisbon Formation, the Gosport Sand, and the overlying Moodys Branch Formation. All of the specimens in our sample were derived from the "upper" Lisbon Formation and the Gosport Sand within the upper half of Zone NP16 and the lower half of Zone NP17. A single historically collected specimen in our sample was recovered from site AWa-2 in Washington County. This site was also investigated by Toulmin (1977), who documented "upper" Lisbon Formation and Gosport Sand exposures at the site, placing it within the same NP zones as reported for site AMo-4.

Another historically collected specimen in our sample was collected from site ACl-14 in Clarke County. This previously unpublished locality is located roughly 300 meters downstream from site ACl-3 (see above), and records associated with the specimen indicate it was collected from the Gosport Sand (which is contained entirely within the middle of Zone NP17). Large collections of specimens in our sample were historically collected from two additional unpublished localities, sites ACh-21 in Choctaw County (n = 836) and ACl-15 in Clarke County (n = 497). Records on file at MSC indicate the Gosport Sand as the only formation exposed at these localities, placing all the specimens within the middle of Zone NP17.

Results

Elasmobranch and Teleostean osteological remains from the Claiborne Group of Alabama

Class Chondrichthyes Huxley, 1880
Subclass Euselachii Hay, 1902
Infraclass Elasmobranchii Bonaparte, 1838
Division Selachii Cope, 1871
Superorder Galeomorphii Compagno, 1973
Order Heterodontiformes Berg, 1940
Family Heterodontidae Gray, 1851

Genus ***Heterodontus*** de Blainville, 1816

Type species

Squalus philippi Bloch & Schneider, 1801, Recent.

Heterodontus sp.
Fig. 5

Heterodontus sp. cf. *H. woodwardi* – White 1956: 128. — Thurmond & Jones 1981: 42, fig. 9.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 7 isolated teeth; Claiborne Group; MSC 2394, MSC 37449, MSC 37320, MSC 35769.1–2, SC2012.47.33, SC2012.47.156.

Description

Only lateral teeth were identified in our sample. Lateral teeth are apicobasally compressed and mesiodistally elongated. Teeth range from oval to rectangular to slightly sigmoidal in occlusal outline. Crown is dome-shaped and ranges from non-cuspidate to weakly cuspidate in profile view. Teeth have a medial transverse ridge that extends mesiodistally across the tooth, but not to the lateral margins. The ridge bisects the oral surface into labial and lingual crown faces of unequal size. Crown enameloid ranges from completely smooth to heavily ornamented, with ornamentation consisting of a combination of reticulated, folded, and smooth surfaces. Reticulations and folds often intersect the transverse ridge, but do not reach the crown foot. Transverse furrow at base of lingual face serves as articulation surface for succeeding tooth. Root is thin with flat attachment surface, slightly smaller in area than the crown.

Remarks

Our sample of Claiborne specimens includes seven *Heterodontus* lateral teeth, five of which preserve a complete crown. These teeth include both cuspidate (Fig. 5E, G, I) and non-cuspidate forms (Fig. 5A, C). Of the cuspidate teeth, the central cusp is located either in the center of the crown (Fig. 5G, I) or is offset laterally (Fig. 5E), indicating they are from different tooth positions. On the non-cuspidate teeth, the crown is more dome-shaped in profile view than those with cusps. On all the teeth, the crown ornamentation differs on the lingual and labial surfaces. In general, the lingual crown surface is more ornamented than the labial surface, often consisting of bifurcating ridges or folds that intersect with the transverse ridge but do not reach the edges of the crown. The labial surface on at least one tooth (MSC 37449; Fig. 5I –J) has a reticulated ornamentation, but the ornamentation is nondescript or absent on the other teeth in our sample, likely due to wear.

The teeth of *Heterodontus* in our sample were directly compared to the jaws of two modern members of the genus, *Heterodontus portusjacksoni* (Meyer, 1793) and *Heterodontus zebra* (Gray, 1831). Our observations of these Recent specimens showed that the lateral teeth on the jaws of *H. portusjacksoni* are non-cuspidate, whereas several lateral files on the jaw of *H. zebra* have teeth with cusps. On the jaws of *H. zebra*, the teeth within the first few lateral rows are more cuspidate than those in the remaining lateral files, having the appearance of a low-crowned crushing tooth with a cusp. Within the dentition of *H. zebra*, the teeth were observed to become progressively more cuspidate in the younger replacement

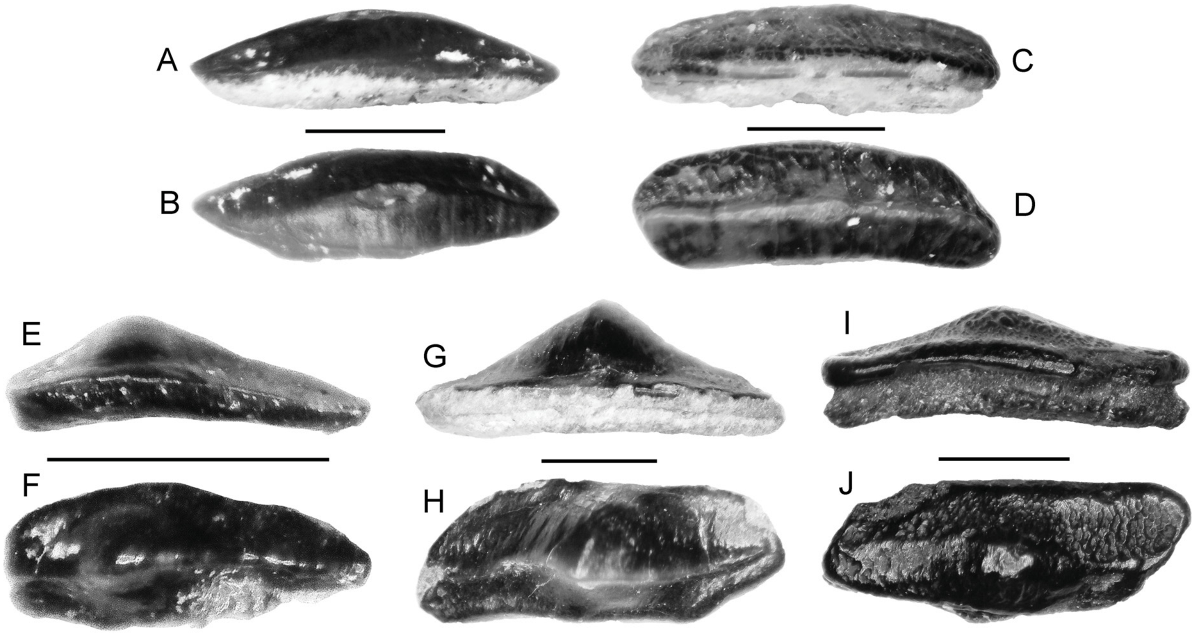

Fig. 5. *Heterodontus* sp. lateral teeth. **A**–**B**. MSC 35769.2, lower Tallahatta Formation. **A**. Lingual view. **B**. Oral view. **C**–**D**. MSC 35769.1, lower Tallahatta Formation. **C**. Lingual view. **D**. Oral view. **E**–**F**. SC2012.47.33, basal Lisbon Formation. **E**. Lingual view. **F**. Oral view. **G**–**H**. MSC 37320, basal Gosport Sand. **G**. Lingual view. **H**. Oral view. **I**–**J**. MSC 37449, basal Gosport Sand. **I**. Labial view. **J**. Oral view. Labial surface at top in oral views. Scale bars = 2 mm.

rows, and the transverse ridges in both species become more robust in these rows. This suggests that the formation of cuspidate teeth and expression of the transverse ridge might be related to ontogeny, and that both features increase in size/robustness as an individual aged. With respect to general morphology and ornamentation, the upper lateral teeth of both species appear to be identical to the lower laterals, making it difficult to distinguish upper and lower files. Furthermore, the teeth of both species appear more worn in the more labial, functional rows, possibly suggesting a longer period of tooth retention in *Heterodontus* than in other shark taxa.

Our observations of dentitions of extant *Heterodontus* suggest that the presence or absence of cuspidate lateral teeth might be a taxonomically useful characteristic, but only when presented with a complete dentition. When isolated teeth are involved, this characteristic is not taxonomically useful because non-cuspidate teeth may simply be from a more laterally positioned file or from a younger individual. Although both cuspidate and non-cuspidate teeth are present in our sample, due to their extremely small size we cannot rule out the possibility that they all belong to the same taxon, and the variation present reflects monognathic and/or ontogenetic heterodonty. Furthermore, the crown ornamentation varies across our suite of teeth and several specimens are ablated, which does not allow us to determine with confidence which species they represent. The combined seven specimens in our sample demonstrates that *Heterodontus* occurs in all three Claiborne Group formations, but at this time we cannot determine if they are conspecific or represent two or more distinct species.

Stratigraphic and geographic range in Alabama

Specimens of *Heterodontus* sp. were collected from the lower Tallahatta Formation at site ADl-1, the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Order Orectolobiformes Applegate, 1972
Suborder Orectoloboidei Applegate, 1972
Superfamily Orectoloboidea Naylor *et al.*, 2012
Family Orectolobidae Gill, 1896

Genus ***Orectolobus*** Bonaparte, 1834

Type species

Squalus barbatus Gmelin, 1789, Recent, Australia.

Orectolobus ziegenhinei Cappetta & Case, 2016
Fig. 6

Orectolobus ziegenhinei Cappetta & Case, 2016: 46–48, pl. 1, figs 1–9.
Squatiscyllium aff. *nigeriensis* Clayton *et al.*, 2013: 16, fig. 2f–g.

Orectolobus sp. – Cappetta 2012: 161, fig. 147.
cf. *Eometlaouia* sp. – Clayton *et al.* 2013: 16, figs 2d–e.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 180 isolated teeth; Claiborne Group; ALMNH PV1992.28.37 (1 specimen), ALMNH PV1992.28.4 (4 specimens), MMNS VP-8216 (3 specimens), MSC 37008.1–2, MSC 37009, MSC 37010, MSC 37056.1–2, MSC 37068.1–2, MSC 37069.1–2, MSC 37070, MSC 37071, MSC 37164, MSC 37181, MSC 37240.1–3, MSC 37250, MSC 37274, MSC 37303,

MSC 37319.1–43, MSC 37673.1–9, MSC 37692.1–2, MSC 38612.1–2, NJSM 24016, SC2012.47.34–35, SC2012.47.36 (13 specimens), SC2012.47.37, SC2012.47.38, SC2012.47.39 (11 specimens), SC2012.47.159 (29 specimens), SC2012.47.244 (3 specimens), SC2012.47.245 (2 specimens), SC2012.47.246 (3 specimens), WSU 19, WSU 4, WSU 5036 (28 specimens).

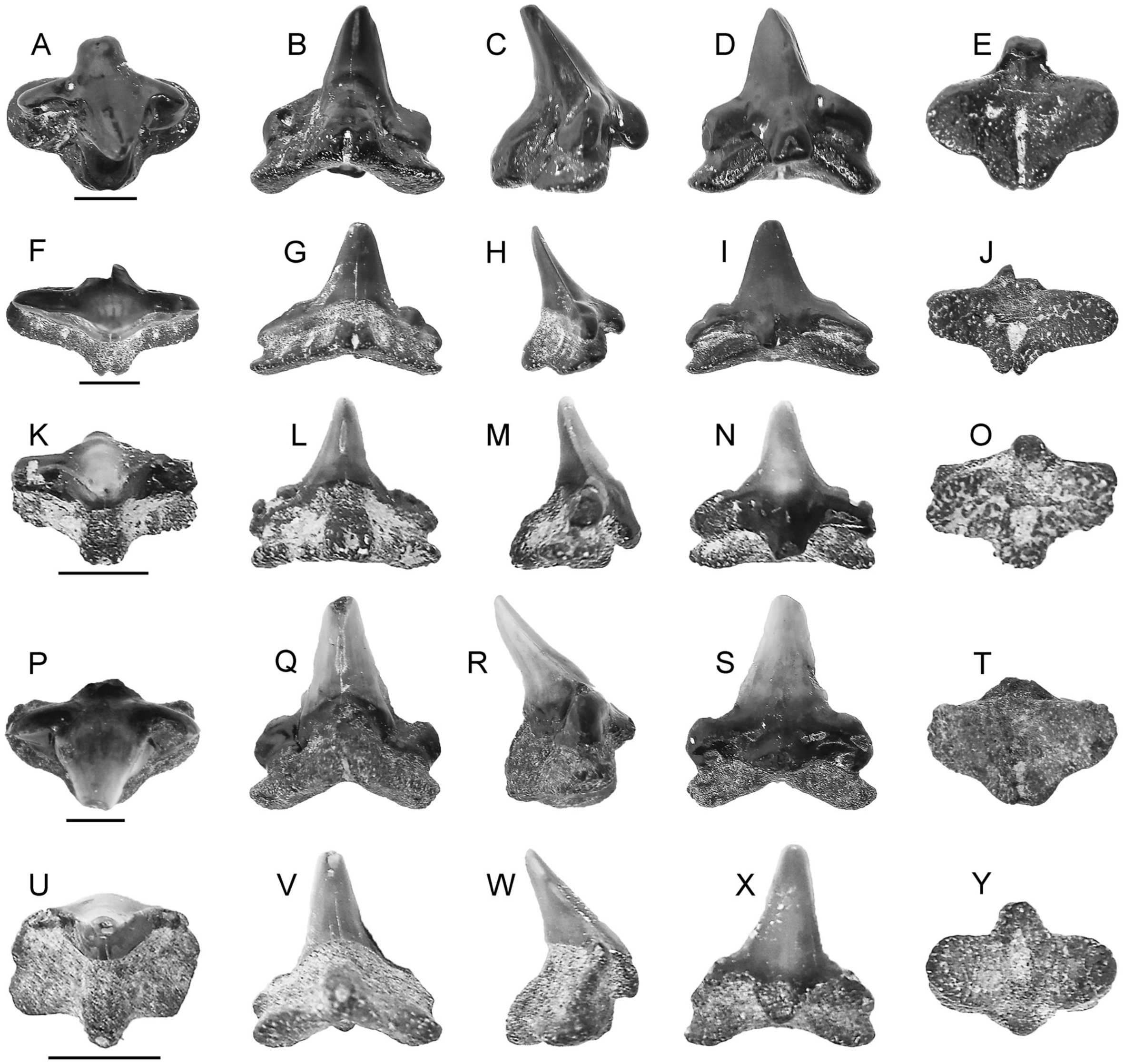

Fig. 6. *Orectolobus ziegenhinei* Cappetta & Case, 2016, teeth. **A**–**E**. MSC 37009, Tallahatta/Lisbon formation contact zone, courtesy of Carl Sloan. **A**. Oral view. **B**. Lingual view. **C**. Distal view. **D**. Labial view. **E**. Basal view. **F**–**J**. MSC 37181, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **F**. Oral view. **G**. Lingual view. **H**. Distal view. **I**. Labial view. **J**. Basal view. **K**–**O**. MSC 37056.1, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **K**. Oral view. **L**. Lingual view. **M**. Distal view. **N**. Labial view. **O**. Basal view. **P**–**T**. MSC 37319.1, basal Lisbon Formation. **P**. Oral view. **Q**. Lingual view. **R**. Mesial view. **S**. Labial view. **T**. Basal view. **U**–**Y**. MSC 37319.3, basal Lisbon Formation. **U**. Oral view. **V**. Lingual view. **W**. Mesial view. **X**. Labial view. **Y**. Basal view. Labial at top in oral and basal views. Scale bars = 2 mm.

Description

Anterior teeth with tall, triangular cusp that is lingually directed and may be very slightly distally inclined. Main cusp flanked by short lateral shoulders that may be oblique or perpendicular to the cusp. A smooth cutting edge extends across the entire crown, dividing it into convex labial and lingual parts. The labial crown foot bears a basally directed protuberance of varying length and width. Lingual crown foot bears a lingually directed protuberance that extends onto the dorsal surface of the root. Root very low with short lobes; heart-shaped in basal view; basal attachment surface is very concave. Root hemiaulocorhizous, with an anterior depression directed towards a large basal foramen. Basal depression located closer to the posterior margin. Posteriorly, the basal foramen is connected to a foramen on the lingual face of the root by a narrow canal; sometimes these foramina are joined by a groove. The dorsal surface of the lingual side of the root bears two or three small foramina, located below the crown foot, on each side of the crown protuberance. Crowns of lateral and posterior teeth are like those in anterior positions except that they are wider (due to more elongated shoulders) and the cusp is lower and more obviously distally inclined. Root is wider, with more elongated lobes, and the number of dorsal foramina on the root varies from three to six. Some lateral teeth have one to two pairs of lateral cusplets. Short longitudinal ridges present on the labial face of lateral shoulders of small teeth (< 5 mm), but only a short medial ridge may occur on large teeth.

Remarks

The *Orectolobus ziegenhinei* teeth in our sample were directly compared to those within two Recent *Orectolobus japonicus* Regan, 1906 jaws, one a presumed adult set measuring 16.5 cm wide and the other a presumed juvenile or subadult set measuring 11 cm wide. Our observations of these two *O. japonicus* jaws indicate that a degree of ontogenetic heterodonty occurs, with older/larger specimens lacking or having a single pair of cusplets on their lateral teeth, whereas lateral teeth of younger/smaller specimens have one-to-two pairs of cusplets. Furthermore, the lower dentition of *O. japonicus* has a single symphyseal tooth that is nearly identical to those in the anterior positions but has mesial and distal shoulders that are equal in length. On the anterior teeth, the distal lobe is slightly elongated and lateral cusplets are absent. Lateral teeth are broader than anterior teeth, and all have lateral cusplets. The first lateral tooth is distinct, as it has a distal cusplet, but no mesial cusplet(s). The right and left sides of the upper and lower dentitions have a single row of anterior teeth, and the upper dentition has a row of minute symphyseal teeth. Upper lateral teeth are more lingually inclined than lower laterals. In profile view, the upper anterior teeth are slightly more sigmoidal than those in the lower jaw. Ornamentation, occurring as striations at the crown foot, is present on the labial crown face of the anterior and lateral teeth in both jaw sets, but is coarser and more conspicuous on the juvenile/subadult specimen.

Comparison of the fossil material to Recent *Orectolobus japonicus* teeth revealed that the ornamentation on the Lisbon Formation specimens generally extends higher on the crown, lateral teeth are not as distally inclined, and the teeth have a shorter crown. These differences aside, the fossil teeth in our sample compare very favorably with those within the extant jaws, allowing us to draw several conclusions regarding the fossil species. Our sample of fossil teeth exhibit a similar degree of monognathic and dignathic heterodonty, as lower symphyseal (symmetrical teeth), anterior (teeth with elongated distal heels), first lateral (teeth with mesial cusplet present, but no distal cusplet), and lateral teeth (teeth with one to two pairs of lateral cusplets) have been identified in our sample. However, the crown on the fossil lateral teeth is less distally inclined than those in the Recent jaw sets we examined; dignathic heterodonty is therefore less apparent because it is difficult to distinguish upper from lower files. We also note a pattern within the fossil teeth in our sample that we interpret as ontogenetic heterodonty based on our observation of the *O. japonicus* jaws, as specimens with single and double pairs of lateral cusplets are present, indicating the presence of both juvenile and adult teeth in our sample.

Our analysis of both the fossil and Recent teeth allows us to emend the species identifications previously made by Clayton *et al.* (2013). These authors identified two species, cf. *Eometlaouia* and *Squatiscyllium* aff. *nigeriensis*, based on the presence (cf. *Eometlaouia*) or absence (*Squatiscyllium*) of lateral cusplets. The figured cf. *Eometlaouia* specimen (Clayton *et al.* 2013: fig. 2: d–e) has an elongated distal heel and distal cusplet, but no mesial cusplet, suggesting it instead belongs to a first lateral tooth of *O. ziegenhinei.* The *Squatiscyllium* aff. *nigeriensis* tooth (Clayton *et al.* 2013: fig. 2: f–g) has mesial and distal shoulders of equal length, indicating it is an *O. ziegenhinei* lower symphyseal tooth. Cappetta (2012: fig. 147) figured three "*Orectolobus* sp." teeth purportedly from the Tallahatta Formation in Mississippi, which Cappetta & Case (2016) later referred to *O. ziegenhinei* while at the same time correcting the error in stratigraphic horizon and geographic location, as the teeth were actually derived from the contact zone of the Tallahatta and Lisbon formations at site ACov-11 in Covington County, AL. According to Cappetta & Case (2016), the *O. ziegenhinei* teeth from site ACov-11 represent the stratigraphically oldest member of this genus.

Stratigraphic and geographic range in Alabama

To date this taxon appears stratigraphically confined to the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, and the basal Lisbon Formation at site ACov-11. Middle Lutetian, zones NP14 and NP15.

Superfamily Hemiscyllioidea Naylor *et al.*, 2012

Family Ginglymostomatidae Gill, 1862

Genus ***Ginglymostoma*** Müller & Henle, 1837

Type species

Squalus cirratus (Bonnaterre, 1788), Recent.

Ginglymostoma maroccanum Noubhani & Cappetta, 1997

Fig. 7A–D

Ginglymostoma maroccanum Noubhani & Cappetta, 1997: 34, pl. 10, fig. 2.

Ginglymostoma serra – Woodward 1889: 348, pl. 16, fig. 9.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 8 isolated teeth; Claiborne Group; MSC 34407.2, MSC 35752.1–7.

Description

Teeth with symmetrical crown and prominent median cusp. Median cusp tall, erect, and triangular, flanked by three pairs of lateral cusplets. Lateral cusplets decrease in size laterally. Labial crown face generally flat and smooth; a pair of low ridges is at times present that extends to the crown base. Labial face distally oriented with a shallow basal apron. Basal edge of the apron generally flat or slightly concave. Lingual crown face convex with a strong medial protuberance. Crown T-shaped in oral view. Lateral edges of the root extend beyond the base of the crown. Root base heart-shaped in basal view. Wide nutritive groove on root base that opens labially. Nutritive foramen is positioned within the lingual half of the nutritive groove. Prominent marginolingual foramen present on lingual root protuberance.

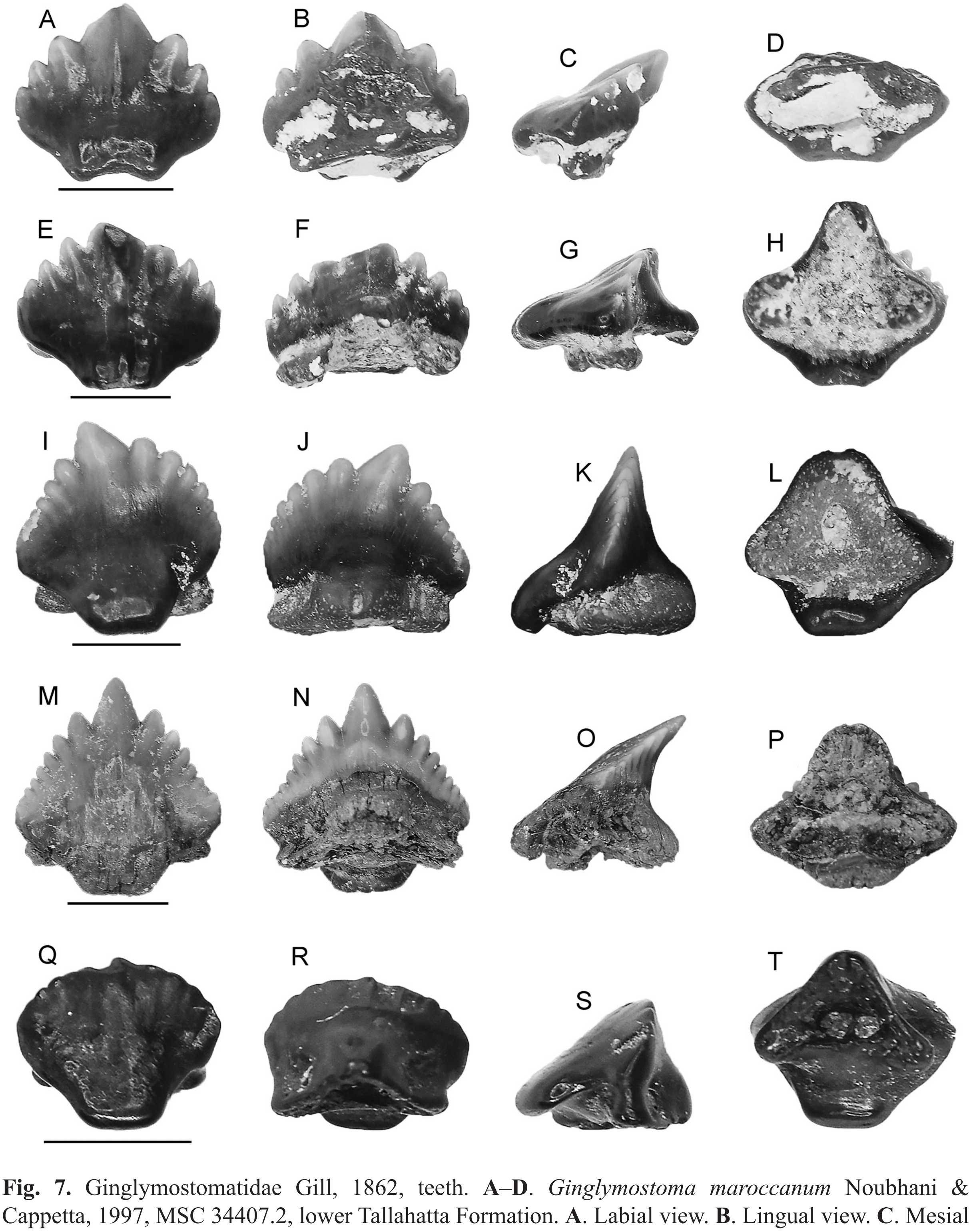

Fig. 7. Ginglymostomatidae Gill, 1862, teeth. **A**–**D**. *Ginglymostoma maroccanum* Noubhani & Cappetta, 1997, MSC 34407.2, lower Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D**. Basal view. — **E**–**H**. *Ginglymostoma* sp., MSC 37548.1, basal Gosport Sand. **E**. Labial view. **F**. Lingual view. **G**. Mesial view. **H**. Basal view. — **I**–**T**. *Nebrius thielensi* (Winkler, 1874). **I–L**. MSC 35755.6, lower Tallahatta Formation. **I**. Labial view. **J**. Lingual view. **K**. Mesial view. **L**. Basal view. **M**–**P**. MSC 37266.1, basal Lisbon Formation. **M**. Labial view. **N**. Lingual view. **O**. Distal view. **P**. Basal view. **Q**–**T**. MSC 37496.1, basal Gosport Sand. **Q**. Labial view. **R**. Lingual view. **S**. Profile view. **T**. Basal view. Labial at bottom in basal views. Scale bars = 3 mm.

Remarks

Noubhani & Cappetta (1997) and Cappetta (2012) recognized five species of Eocene *Ginglymostoma* including *G. angolense* Dartevelle & Casier, 1943; *G. maghrebianum* Casier, 1947; *G. maroccanum* Noubhani & Cappetta, 1997; *G. serra* Leidy, 1877; and *G. sokotoense* White, 1934. The *Ginglymostoma* teeth described above are all assigned to *G. maroccanum* because they have no more than three pairs of lateral cusplets (*G. angolense* = six or more; *G. serra* = five to nine; *G. sokotoense* = five or more; *G. maghrebianum* = two to six). Additionally, the Tallahatta Formation specimens have a pronounced apron that is either flat or slightly concave, as opposed to the shallow and rounded apron on *G. angolense*. These teeth are similar to the Thanetian *G. chenanei* Noubhani & Cappetta, 1997 and Ypresian *G. maghrebianum*, but differ by never having more than three pairs of lateral cusplets (as opposed to up to four pairs on *G. chenanei* and five on *G. maghrebianum*). These teeth also differ from the Thanetian *G. khourbgaense* Noubhani & Cappetta, 1997 by having a shorter, and less triangular, median cusp and can be distinguished from the Danian *G. subafricanum* Arambourg, 1952 by having shorter and wider lateral cusplets. Because there appears to be a lack of variability regarding the number of cusplets on the teeth in our sample (only three pairs), these specimens are most appropriately assigned to *G. maroccanum*.

It should also be noted that although *G. serra* has been reported within the Paleogene by Dartevelle & Casier (1943) and Arambourg (1952), the species was originally erected by Leidy (1877) for teeth collected from South Carolina and is currently considered to be restricted to the Neogene (see Cappetta 2012). Woodward (1889), however, reported two *G. serra* teeth from Alabama that were derived from upper Eocene Jackson Group deposits in Choctaw County. Upon reexamining these teeth, Leriche (1942), and later White (1956), reassigned them to *Ginglymostoma obliquum* (Leidy, 1877) based on the distal inclination of their crowns. Later, Case & West (1991) placed *G. obliquum* within the genus *Nebrius* because it has a crown morphology that is more typical of this latter genus. Thurmond & Jones (1981) compared the tooth illustrated by Woodward (1889: pl. 16: 9) to a suite of *Ginglymostoma* teeth they collected from the Gosport Sand at site ACl-4 in Clarke County, AL. Their analysis concluded with the designation of *G. obliquum* as a junior synonym of *G. serra*, and they stated that crown inclination is not a taxonomically viable characteristic but is instead related to heterodonty. Unfortunately, the identity of the Thurmond & Jones (1981) specimens remain a mystery as the teeth they discussed could not be located and the figures they provided (fig. 10) are reproductions of the original *G. serra* type material illustrated by Leidy (1877), not their specimens from the Gosport Sand.

The *Ginglymostoma* specimens in our sample were collected from the Ypresian portion of the lower Tallahatta Formation at site ADl-1. *Ginglymostoma maroccanum* was originally described from Thanetian and Ypresian deposits in Morocco (Noubhani & Cappetta 1997) and the stratigraphic overlap with our Tallahatta Formation specimens (Fig. 7A–D) supports that they do indeed belong to this species. These specimens differ from a sample of *Ginglymostoma* teeth collected from the Bartonian Gosport Sand at site ACl-4 (Fig. 7E–H), the latter of which has up to four pairs of triangular lateral cusplets. The Bartonian teeth, assigned here to *Ginglymostoma* sp., appear to represent a different species and are discussed in detail below.

Stratigraphic and geographic range in Alabama

Ginglymostoma maroccanum specimens have been recovered only from the lower Tallahatta Formation at site ADl-1. Upper Ypresian, zones NP13 and NP14.

Ginglymostoma sp.

Fig. 7E–H

Material examined

UNITED STATES OF AMERICA – **Alabama** • 21 isolated teeth; Claiborne Group; ALMNH PV1993.2.410 (13 specimens), MSC 37522.1–4, MSC 37548.1–2, MSC 37554, MSC 37704.

Description

Teeth with symmetrical crown and prominent median cusp. Median cusp tall, erect, and triangular, flanked by four pairs of lateral cusplets. Lateral cusplets decrease in size laterally. Distal cusplets are triangular and divergent; mesial cusplets have a slight medial bend. Labial crown face generally flat and smooth; a pair of low ridges is at times present that extends to the crown base. Labial face distally oriented with a shallow basal apron. Basal edge of the apron generally flat or slightly concave. Lingual crown face convex with a strong medial protuberance. Crown T-shaped in oral view. Lateral edges of the root extend beyond the base of the crown. Root base heart-shaped in basal view. Wide nutritive groove on root base that opens labially. Nutritive foramen is positioned within the lingual half of the nutritive groove. Prominent marginolingual foramen present on lingual root protuberance.

Remarks

Unfortunately, only partial and abraded specimens are present in our sample. These teeth (Fig. 7E–H) differ from those of *Ginglymostoma maroccanum* (Fig. 7A–D) by having four pairs of lateral cusplets, as opposed to three, and the cusplets are mesiodistally not as wide. Furthermore, the mesial cusplets on these teeth have a slight medial bend, as opposed to the more divergent cusplets on the teeth of *G. maroccanum*. Due to the poor state of preservation of the teeth in our sample, all are assigned to *Ginglymostoma* sp. These teeth, however, differ from the other known Paleogene *Ginglymostoma* species by having a shorter and less triangular median cusp than on *G. khourbgaense*, they have a much more pronounced labial apron than on *G. maghrebianum*, wider and shorter cusplets than on *G. subafricanum*, and a different number of pairs of lateral cusplets than *G. angolense* (six or more), *G. khourbgaense* (one to three), and *G. serra* (five to nine). These teeth are most similar to the Thanetian *G. chenanei*, which can have up to four pairs of lateral cusplets, however the lateral cusplets and median cusp on the teeth of *G. chenanei* have much straighter mesial and distal edges than those on the teeth in our sample. Furthermore, the *Ginglymostoma* sp. specimens in our sample were recovered from the stratigraphically much younger Bartonian Gosport Sand. It is possible the Bartonian teeth in our sample represent a unique taxon, but better-preserved material is needed to corroborate this hypothesis.

Stratigraphic and geographic range in Alabama

Ginglymostoma sp. specimens have been recovered only from the basal Gosport Sand at site ACl-4. Middle Bartonian, Zone NP17.

Genus ***Nebrius*** Rüppell, 1835

Type species

Nebrius ferrugineus Lesson, 1831, Recent.

Nebrius thielensi (Winkler, 1874)

Fig. 7I–T

Plicodus thielensis Winkler, 1874a: 301, pl. 7, fig. 5.
Acrodobatis obliquus Leidy, 1877: 250, pl. 34, fig. 14.
Ginglymostoma blankenhorni Stromer, 1905b: 34, pl. 1, fig. 6.

Ginglymostoma thielensis – Daimeries 1889: 9.
Ginglymostoma aff. *thielensi* – Casier 1958: 17, pl. 1, fig. 7.
Nebrius thielensi – Herman & Crochard 1977: 133.
Ginglymostoma sp. cf. *G. blankenhorni* – Thurmond & Jones 1981: 45, fig. 11.
Nebrius thielensi – Clayton *et al.* 2013: fig 2b–c.
Nebrius obliquus – Cappetta & Case 2016: 48, pl. 2, figs 1–4.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 170 isolated teeth; Claiborne Group; MSC 38785, ALMNH PV1992.28.36, ALMNH PV1992.28.5 (2 specimens), ALMNH PV2005.6.434, MMNS VP-8211 (2 specimens), MSC 2174.1–2, MSC 2387, MSC 33263, MSC 34407.1–9, MSC 35755.1–20, MSC 37124.1–2, MSC 37175, MSC 37266.1–4, MSC 37272, MSC 37336.1–5, MSC 37341.1–7, MSC 37441.1–6, MSC 37496.1–5, MSC 37652, MSC 37677.1–6, MSC 38502.1–5, MSC 38549.1–3, MSC 38777, NJSM 24017, SC2012.47.40, SC2012.47.41, SC2012.47.42, SC2012.47.43, SC2012.47.44 (20 specimens), SC2012.47.183 (16 specimens), WSU 5013 (3 specimens), WSU 5035 (37 specimens), WSU 6, WSU CC 504 (2 specimens).

Description

Tooth crown with tall median cusp flanked by numerous mesial and distal cusplets that decrease in size towards the crown margins. More cusplets on mesial side of cusp than on distal side, particularly on lateral teeth, resulting in strong crown asymmetry especially when median cusp is distally inclined. Mesial edge of crown strongly convex, whereas distal edge more or less straight. Prominent labial apron present, which is often bifid but can be uniformly rounded. Lingual and labial crown faces smooth, but faint wrinkles may be present on labial apron. Labial edge of apron overhangs the root. Both crown faces convex, but more so lingually. Prominent medial protuberance on lingual face has rounded lingual margin. Root thin with sub-triangular basal outline, and lobes do not extend past the lateral margins of the crown. Root base flat with deep nutritive groove that opens labially. Marginolingual foramina present on lingual root face.

Remarks

Thurmond & Jones (1981: fig. 11) figured a specimen from the Tallahatta Formation at site AMo-8 that they referred to *Ginglymostoma* sp. cf. *blankenhorni.* However, not only was this species later designated a junior synonym of *Nebrius obliquus* (Leidy, 1877) by Noubhani & Cappetta (1997), but a reexamination of the specimen (ALMNH PV 2005.6.434) by the present authors revealed that it belongs to *Nebrius thielensi*. Holman & Case (1988), Feldmann & Portell (2007), and Clayton *et al.* (2013), each reported the recovery of *Nebrius* teeth from site ACov-11 in Covington County, AL, the latter two referring their specimens to *Nebrius thielensi* Winkler, 1874. In contrast, Cappetta & Case (2016) later reported 174 *Nebrius* teeth from the same locality and referred all to *N. obliquus*. In justifying the referral of their teeth to *N. obliquus* as opposed to *N. thielensi*, Cappetta & Case (2016) explained that the teeth of the latter generally have a thicker apron that is less prominent and at times bifid, as seen on the type specimen of Winkler (1874a). On the other hand, Cappetta & Case (2016) noted that on *N. obliquus*, the apron is more prominent and much more oblique on some teeth, as seen in Leidy's (1877) type specimen. Noubhani & Cappetta (1997) had previously stated that *N. obliquus* was typical of Ypresian deposits, whereas *N. thielensi* was of middle Eocene age.

Of the *Nebrius* teeth in our sample (n = 170), we observed that the shape of the labial crown apron varies from rounded, to flat, to bifid. The length of the apron also varies from short and rather narrow on specimens with bifid to flat aprons, to wide and elongate on specimens with rounded aprons. Although this might suggest the presence of two species, this variance in apron morphology is also seen within the dentitions of the Recent *Nebrius ferrugineus* (Lesson, 1831), where the teeth in the more anterior positions have short bifid aprons, but the aprons become more rounded and prominent in the lateral positions. Due to the variation observed within this extant analogue, it is our conclusion that the differences in apron morphology in our sample is not an indication of separate species (in this case *N. obliquus* and *N. thielensi*), but rather a reflection of heterodonty. Noubhani & Cappetta (1997) cited further differences between the teeth of *N. obliquus* and *N. thielensi*, stating that the labial crown profiles on the teeth of *N. thielensi* are less concave than those on *N. obliquus*. However, this characteristic can also be observed on the teeth in the Recent *Nebrius ferrugineus* jaw, as the labial crown face is flatter on the teeth in the anterior positions (i.e., the teeth with bifid aprons) and more concave in the lateral positions (i.e., teeth with rounded aprons). Thus, with a lack of characteristics to sufficiently separate these two taxa, it is our opinion that *N. obliquus* from the Claibornian of Alabama should be considered a junior synonym of *N. thielensi*, and all our Claiborne Group *Nebrius* teeth are therefore assigned to this latter species.

Some of the Claibornian specimens in our sample superficially resemble teeth of *Ginglymostoma angolense*. However, based on a sample from the Thanetian Williamsburg Formation of South Carolina (in the collections of SC), teeth of *G. angolense* have a large main cusp relative to tooth size, and the labial apron is rather narrow and short (see also Dartevelle & Casier 1943; Arambourg 1952; Noubhani & Cappetta 1997). In contrast, the Alabama specimens have a rather small main cusp and the labial apron is wide and elongated.

Stratigraphic and geographic range in Alabama

The specimens in our sample were derived from the Tallahatta Formation at sites ADl-1 and AMo-8, the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at sites ACh-14 and ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Orectolobiformes indet.

Fig. 8

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 isolated tooth; Claiborne Group; SC2012.47.45.

Description

Miniscule tooth measuring 1.2 mm in width and 1 mm in preserved height. Crown with broad-based main cusp flanked by single pair of lateral cusplets. Labial face of main cusp weakly convex and lingual face strongly convex, smooth lateral cutting edges extend from cusp base to broken apical region. Cusplets broad, pointed, with convex labial and lingual faces and smooth lateral cutting edges. Entire

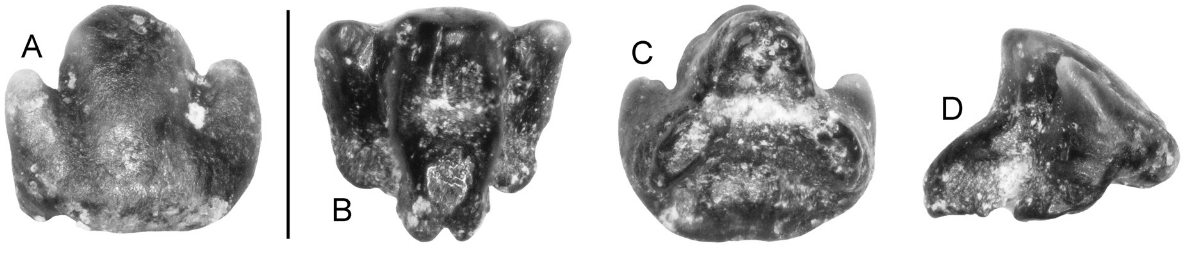

Fig. 8. Orectolobiformes indet., tooth. **A**–**D**. SC2012.47.45, basal Lisbon Formation. **A**. Labial view. **B**. Orolingual view. **C**. Basiolingual view. **D**. Distal view. Scale bar = 1 mm.

labial face weakly convex and lacks ornamentation. Labial crown foot forms basally flattened apron that overhangs the root. Lingual face very convex, with elongated medial basal uvula that extends onto dorsal surface of root. Root largely incomplete, but single pair of large dorsolingual root foramina flank the lingual crown uvula.

Remarks

SC2012.47.45 resembles teeth of *Chiloscyllium* Müller & Henle, 1837 in having a wide, low crown bearing a robust medial cusp that is flanked by a single pair of rather large lateral cusplets, and a broad, somewhat bifid labial apron. In contrast, the similar teeth of *Hemiscyllium* Müller & Henle, 1838 have reduced or absent lateral cusplets and the labial apron is less rounded and more concave in oral view (Herman 1977; Noubhani & Cappetta 1997; Adnet 2006). SC2012.47.45 is also similar to teeth of *Delpitoscyllium africanum* (Leriche, 1927) in that it appears to have had a large main cusp, and the sides of the crown are rather vertical, but the root is largely missing and the main cusp and lateral cusplets are too ablated to be certain (Leriche 1927). The specimen can be distinguished from *Ginglymostoma* and *Nebrius* (see above) in having only a single pair of lateral cusplets, and it lacks the very elongated labial apron of *Nebrius*. Although this specimen clearly differs from the other orectolobiforms in our sample, additional, better preserved material is needed in order to more accurately identify the taxon represented by SC2012.47.45.

Stratigraphic and geographic range in Alabama

The lone specimen in our sample was collected from the basal Lisbon Formation at site ACov-11. Middle Lutetian, Zone NP15.

Order Lamniformes Berg, 1958
Family Otodontidae Glikman, 1964
Genus *Otodus* Agassiz, 1843

Subgenus ***Otodus* (*Otodus*)** (Agassiz, 1843)

Type species

Otodus obliquus Agassiz, 1843, probably Ypresian, United Kingdom.

***Otodus* (*Otodus*)** sp.
Fig. 9A–L

Otodus obliquus – Maisch *et al.* 2014: 189, fig. 3:1–2.
Cretolamna sp. – Cappetta & Case 2016: 55, pl. 6, figs 1–3.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 9 isolated teeth; Claiborne Group; ANSP 23413, MSC 2998.3, MSC 2999.2, MSC 3008.1, MSC 35761.1–2, MSC 38528.1–3.

Description

Our sample includes anterior, lateral, and posterolateral teeth. All teeth have a triangular, unserrated main cusp and single pair of triangular, divergent, lateral cusplets. Labial and lingual crown faces smooth. Labial crown face flat; lingual face convex. Tooth root holaulacorhizous. Root lobes range from rounded to angular and thin basally. One or more nutritive foramina present on lingual root face. Crown taller and more erect in anterior files, but lower, broader, and distally inclined on lateral teeth. Root bilobate, with narrow, elongate, diverging lobes on anterior teeth. Lateral teeth with short, broad, sub-rectangular lobes. Interlobe area U-shaped, deep in anterior files but shallow on lateral teeth. In basal view, anterior teeth have a prominent, box-like, well delineated, lingual boss.

Remarks

Paleogene specimens from Alabama with a similar morphology to the teeth in our sample have traditionally been referred to the genera *Otodus* or *Cretalamna* (see Ehret & Ebersole 2014; Maisch *et al.* 2014; Cappetta & Case 2016). For many years authors have recognized the morphological similarity of *Cretalamna* and *Otodus* teeth, lending strong support to the idea that the two genera are part of a single lineage where *Cretalamna* gives rise to the *Otodus* group. It is readily accepted that the transition from *Cretalamna* to *Otodus* occurred in the Paleocene (Siverson 1992; Zhelezko 2000; Ward 2010; Siversson *et al.* 2015;), but it is unclear as to how late in the Paleogene members of the genus *Cretalamna* persisted. *Cretalamna* specimens have been reported in Ypresian deposits elsewhere (Cappetta 2012) and deposits as young as the Lutetian in Alabama (Cappetta & Case 2016), and often these teeth have been referred to the Late Cretaceous taxon *Cretalamna appendiculata* (Agassiz, 1843) (see Noubhani & Cappetta 1997; Adnet 2006; Carlsen & Cuny 2014; Vasquez & Pimiento 2014). This later species, however, has become a 'waste-basket' taxon, and recent studies have shown that *C. appendiculata* sensu stricto is, at present, stratigraphically and geographically restricted to the Turonian of England (Siverson 1999; Siversson *et al.* 2015). A redescription of the genus by Siversson *et al.* (2015) has shown a good degree of morphological variability among the teeth of the various Late Cretaceous *Cretalamna* species, making it difficult to determine what characteristics can be utilized to separate them from those of the closely related *Otodus*. This lack of disparity can be seen among the unserrated Paleocene and Eocene otodontid teeth recovered in Alabama, as it remains uncertain whether they should be assigned to *Otodus* or *Cretalamna*. Although much more clarity is needed to resolve the taxonomy of these unserrated Paleogene otodontids, it is our opinion that the Claiborne specimens are likely best placed within *Otodus* (*Otodus*) because it seems more parsimonious to extend the Paleocene-derived *Otodus* (*Otodus*) lineage into the middle Eocene, as opposed to further extending the range of the Late Cretaceous-derived *Cretalamna* sensu stricto. Furthermore, we have observed that, towards the commissure, the teeth of several fossil lamniform sharks become broader, low-crowned, more recurved, and with wider lateral cusplets than teeth in more anterior positions. Therefore, Eocene specimens identified as *Cretalamna* could represent more lateral/posterior teeth of *Otodus* (*Otodus*).

Two species of *Otodus* have previously been described from Paleogene deposits in Alabama, *Otodus mediavius* (Leriche, 1942) and *O. obliquus* Agassiz, 1843 (Ehret & Ebersole 2014). The taxonomic validity of *O. mediavius*, however, is in question because Leriche (1942) did not designate a holotype, and his syntypes included a range of morphologies from both the Danian Midway Group of Wilcox County, AL, and the Thanetian Cannonball Formation of North Dakota, USA. Furthermore, Arambourg (1952), Cvancara & Hoganson (1993), and later Müller (1999) considered *O. mediavius* a junior synonym of *O. obliquus*, a species originally described from the Ypresian London Clay in England. As part of this study, the specimens in our sample were compared directly to the *O. mediavius* syntypes at the USNM (USNM 8256, USNM 25957-59, USNM 25961–67, USNM 25970), as well as illustrated *O. obliquus* specimens from the London Clay (i.e., Agassiz 1843: fig. 208a–e; Casier 1966: pl. 6–7). The teeth in our sample (Fig. 9A–L) differ from both of these taxa in being of smaller size (not exceeding 3.0 cm in greatest height for anterior teeth, 1.5 cm for lateral teeth), and by having a main cusp that is not as wide (especially those in the anterior files). Furthermore, the mesial and distal cutting edges on the main cusp on the anterior teeth in our sample (Fig. 9A–F) are concave at the base, as opposed to straight or often bi-convex on the teeth of *O. mediavius* and *O. obliquus*. Moreover, the lateral teeth in our sample (Fig. 9G–L) have a shorter crown and never more than a single pair of lateral cusplets (as opposed the occasional presence of up to two pairs on both *O. mediavius* and *O. obliquus*). Although some of the teeth in our sample may indeed represent a stratigraphically young (upper Ypresian) occurrence of *O. obliquus*, here we choose to remain conservative and assign them to *Otodus* (*Otodus*) sp. as to resolve the taxonomy of middle Eocene *Otodus* specimens in Alabama would require many more specimens than what is currently available. For the purposes of this report, we utilize the subgenus *Otodus* (*Otodus*) to differentiate unserrated *Otodus* teeth from those with serrations (see below).

Stratigraphic and geographic range in Alabama

All of the specimens in our sample were collected from the Tallahatta Formation at sites ACon-6 and ADl-1. Cappetta & Case (2016) reported additional *Otodus* teeth from the contact of the Lisbon and Tallahatta formations at site ACov-11. These specimens were likely derived from the Tallahatta Formation (see our discussion of these specimens below). Upper Ypresian to lower Lutetian, zones NP12 to NP14.

Subgenus ***Otodus*** **(*Carcharocles*)** (Jordan, 1923)

Type species

Squalus auriculatus de Blainville, 1818, middle Eocene, Belgium.

Otodus **(*Carcharocles*)** sp.

Fig. 9M–X

Squalus auriculatus de Blainville, 1818: 80.

Carcharodon auriculatus – Agassiz 1843: 254, pl. 28, figs 17–19.
Procarcharodon auriculatus – Casier 1960: 13.
Carcharocles auriculatus – Keyes 1972: 237.
Otodus (*Carcharocles*) *auriculatus* – Cappetta 2012: 224, fig. 209.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 23 isolated teeth; Claiborne Group; ALMNH PV1985.87.7, ALMNH PV1985.87.8, ALMNH PV1988.29.1, ALMNH PV1989.4.50.2, ALMNH PV1992.28.44.1–2, ALMNH PV2016.4.27 (2 specimens), ALMNH PV2016.4.28 (3 specimens), ANSP 23410, ANSP 23411, ANSP 23412, MMNS VP-8233, MSC 2370, MSC 2371, MSC 37019, MSC 37158, MSC 37170, MSC 37172, MSC 37288, NJSM 24021.

Description

Teeth very large, approaching 10 cm in overall height. Main cusp large, robust, triangular, flanked by a single pair of lateral cusplets. Anterior teeth with erect main cusp; whereas main cusp on lateral teeth broader, lower, with slight distal inclination. Base of main cusp broader on upper anterior teeth than in lower anterior files. Lingual crown face smooth and strongly convex; labial face smooth and nearly flat to moderately convex. Prominent V-shaped dental band present at lingual base of main cusp. Lateral cusplets broad and triangular, variable in overall height and width. Cutting edges of main cusp and lateral cusplets serrated from the base to the apex. Serrations coarse, often varying from regular to irregular along the length of the cutting edge, decreasing in size apically to crown apex. Root robust with well-developed lingual protuberance. Multiple prominent foramina present on lingual root face. Root lobes slightly divergent, with U-shaped or V-shaped interlobe area.

Remarks

The generic placement of teeth with this morphology has been a contentious subject for many years, with the names *Squalus* Linnaeus, 1758, *Carcharodon* Smith in Müller & Henley, 1838, *Procarcharodon* Casier, 1960, *Carcharocles* Jordan & Hannibal, 1923, and *Otodus* Agassiz, 1843 each being used by various researchers (see Agassiz 1843; Jordan & Hannibal 1923; Glikman 1964; Cappetta 1987, 2012; Applegate & Espinosa-Arrubarrena 1996; Zhelezko & Kozlov 1999; Purdy *et al.* 2001; Nyberg *et al.* 2006; Pimiento *et al.* 2010; Ehret *et al.* 2012; Pimiento *et al.* 2013; Ehret & Ebersole 2014). It is believed that this genus is part of an evolutionary lineage that begins with *Otodus* (*Otodus*) *obliquus* and

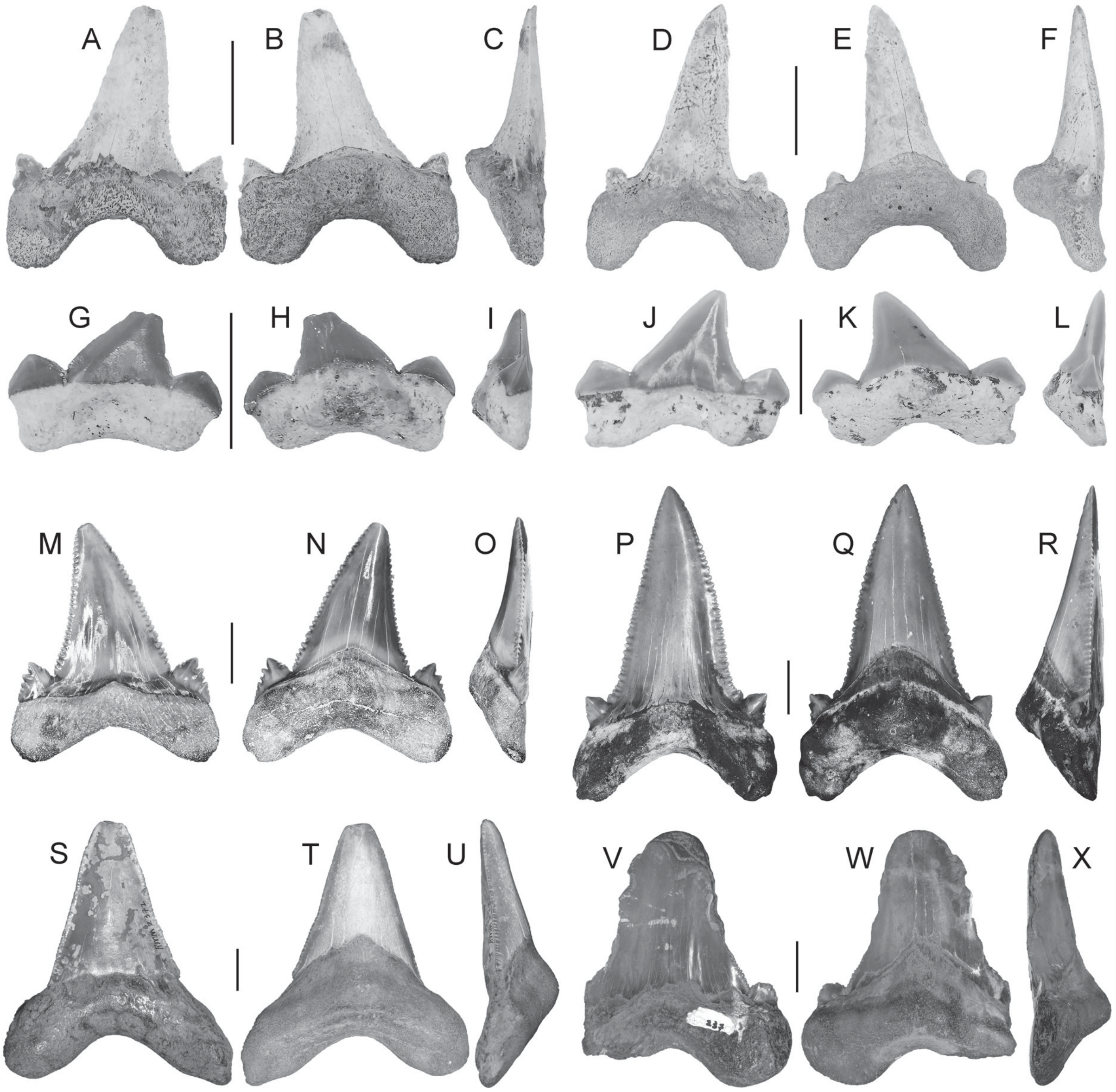

Fig. 9. Otodontidae Glikman, 1964, teeth. **A**–**L**. *Otodus* (*Otodus*) sp. **A**–**C**. MSC 2999.2, lower Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D**–**F**. MSC 3008.1, lower Tallahatta Formation. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G**–**I**. MSC 35761.2, lower Tallahatta Formation. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J**–**L**. MSC 35761.1, lower Tallahatta Formation. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. — **M**–**X**. *Otodus* (*Carcharocles*) sp. **M**–**O**. MSC 37019, basal Lisbon Formation, courtesy of Carl Sloan. **M**. Labial view. **N**. Lingual view. **O**. Distal view. **P**–**R**. MSC 37172, basal Lisbon Formation, courtesy of James Lowery. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S**–**U**. MSC 2371, Gosport Sand. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V**–**X**. MSC 2370, Gosport Sand. **V**. Labial view. **W**. Lingual view. **X**. Distal view. Scale bars: A–F, M–X = 1 cm; G–L = 5 mm.

culminates with *Otodus* (*Megaselachus*) *megalodon* (see Cappetta 2012; Ehret *et al.* 2012; King *et al.* 2013; Malyshkina & Ward 2016). Cappetta (2012) suggested the usage of *Otodus* for all specimens within this lineage and assigned unserrated teeth with cusplets to the subgenus *Otodus* (*Otodus*), those with serrated crowns and cusplets to *Otodus* (*Carcharocles*), and those with serrations and no cusplets to *Otodus* (*Megaselachus*). We follow the recent convention and utilize Cappetta's (2012) taxonomic divisions for the members of Otodonitdae, with *Otodus* (*Otodus*) representing unserrated species and *Otodus* (*Carcharocles*) the serrated species with lateral cusplets.

Taxonomic uncertainty clouds accurate identification of large serrated teeth like those from the Claibornian of Alabama, as numerous nominal *Otodus* (*Carcharocles*) species have been named from Eocene deposits elsewhere (Cappetta 2012). Early-to-middle Eocene teeth like those described above have been assigned to *O.* (*C.*) *angustidens* (Agassiz, 1843), *O.* (*C.*) *auriculatus* (de Blainville, 1818) and *O.* (*C.*) *sokolovi* (Jaekel, 1895), based on tooth size and the nature of serrations. It is unclear, however, if these morphologies represent distinct species because the range of variation within each taxon is insufficiently documented, and type descriptions and figures are far from adequate when differentiating specimens. Agassiz (1843), for example, admitted that he lacked specific characteristics to separate his *C. angustidens* type specimens from *C. auriculatus*, and did so based on tooth size. Case & Cappetta (1990) noted that the teeth of *C. auriculatus* differed from those of *C. sokolovi* by having serrations that are stronger and more irregular, by having lateral cusplets that are more united to the main cusp, and by having root lobes that are more mesiodistally compressed. However, these characteristics are highly variable on the teeth in our Claiborne sample, and they co-occur within the Priabonian Parkers Ferry Formation of South Carolina (DJC, pers. observ.). Diedrich (2013) and Malyshkina & Ward (2016) reported both the *auriculatus* and *sokolovi* morphologies as coeval, and these occurrences suggest that 1) two very similar species of large shark inhabited the same paleoenvironment, or 2) the tooth morphologies represent variation within a single biological species. It is entirely possible that the small teeth Diedrich (2013) identified as *O.* (*C.*) *auriculatus* represent the same species as large teeth he identified as *O.* (*C.*) *sokolovi*. Due to the variability in tooth morphology and limited sample size among the Claibornian units, we refrain from making specific determinations for these specimens. However, we utilize the subgenus *Carcharocles* to differentiate these serrated *Otodus* teeth from unserrated *Otodus* (*Otodus*).

Stratigraphic and geographic range in Alabama

Specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at sites ACov-11, ACh-14, and ACon-6, the basal Lisbon Formation at site ACov-11, and the Gosport Sand at site ACh-21. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Family Mitsukurinidae Jordan, 1898

Genus ***Anomotodon*** Arambourg, 1952

Type species

Anomotodon plicatus Arambourg, 1952, Maastrichtian of Morocco.

Anomotodon sp.
Fig. 10

Material examined

UNITED STATES OF AMERICA – **Alabama** • 6 isolated teeth; Claiborne Group; MSC 35766.1–2, MSC 37497, MSC 37503, MSC 37660, MSC 37683.

Description

Teeth similar in form to those within the Mitsukurinidae and Odontaspididae but lack lateral cusplets. Anterior teeth with tall, slender, erect crown that is sigmoidal in profile view. Lingual crown face strongly convex; labial face flat to slightly convex. Some anterior or anterolateral teeth with short mesial and distal shoulders, but lack cusplets. Crown generally smooth, but faint vertical lingual striations present on some specimens. Anterior teeth narrow, erect, but lateral teeth broader basally, shorter, distally inclined, and labiolingually flattened. Lateral teeth with distinct mesial and distal shoulders, but lack cusplets. Weak striations present at the lingual crown base on some teeth. Root holaulacorhize, bilobate, with thin and rounded lobes and U-shaped interlobe area on anterior teeth. Root lobes of lateral teeth short, strongly divergent, separated by V-shaped interlobe area. Basal face of the root flattened, and nutritive groove present on a prominent lingual root boss.

Remarks

Three Eocene species of *Anomotodon* are currently recognized, including *A. multidenticulatus* Long, 1992, *A. novus* (Winkler, 1876), and *A. sheppeyensis* (Casier, 1966) (see Cappetta 2012; Carlsen & Cuny 2014). In addition, Case (1994a: 113, pl. 7, figs 141–147, text fig. 6) described and figured teeth he referred to "*Anomotodon* sp.", noting they were more robust than any of the previously described forms. Six teeth within our Claiborne sample have been identified as belonging to *Anomotodon*, and they can be separated from *A. multidenticulatus* by the lack of cusplets on the mesial and distal heels. They are not as robust as the unnamed *Anomotodon* teeth figured by Case (1994a: pl. 7, figs 141–147, text fig. 6). One of the main characteristics used to separate *A. novus* from *A. sheppeyensis* is the presence or absence of lingual crown ornamentation (see Casier 1966; Cappetta 1976), which is reportedly absent on the teeth of *A. novus* (Cappetta 1976; Carlsen & Cuny 2014). Ornament is present on the anterior and anterolateral teeth of *A. sheppeyensis* but fades or is absent altogether on the teeth in lateral positions (Casier 1966; Cappetta 1976).

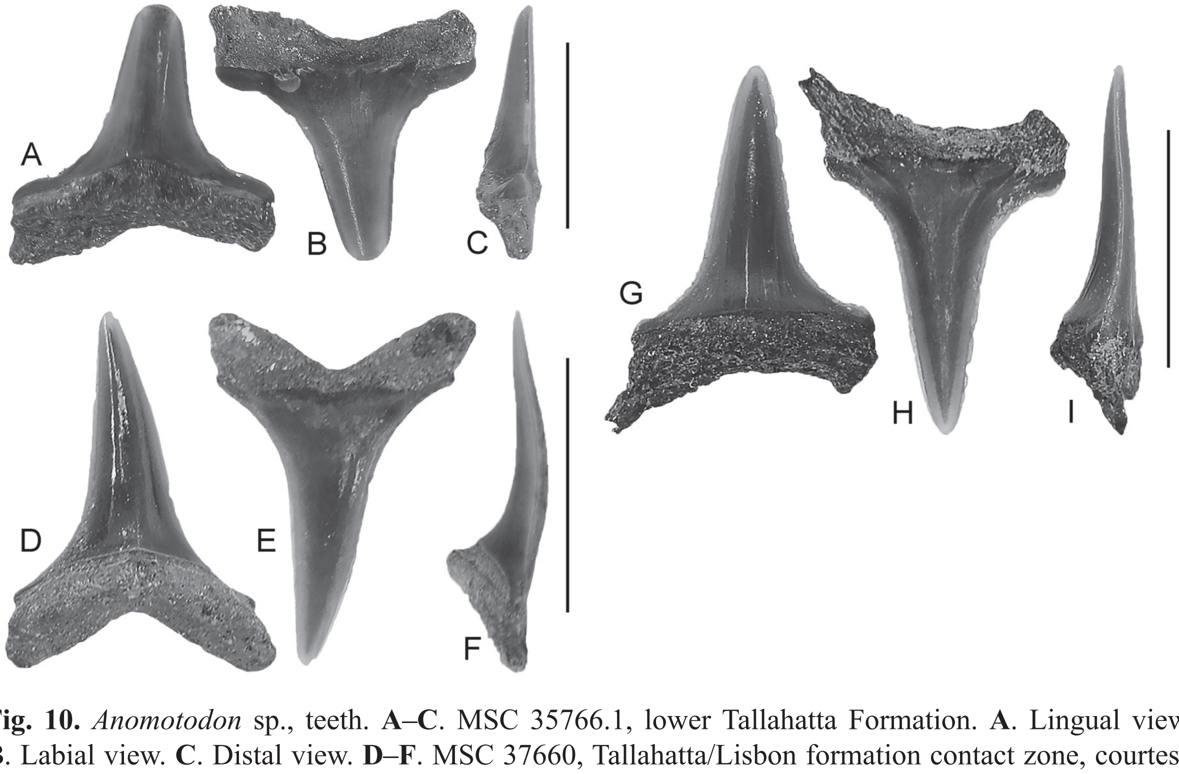

Fig. 10. *Anomotodon* sp., teeth. **A**–**C**. MSC 35766.1, lower Tallahatta Formation. **A**. Lingual view. **B**. Labial view. **C**. Distal view. **D**–**F**. MSC 37660, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **D**. Lingual view. **E**. Labial view. **F**. Mesial view. **G**–**I**. MSC 37503, Gosport Sand. **G**. Lingual view. **H**. Labial view. **I**. Distal view. Scale bars = 5 mm.

Of the six teeth in our sample, three have faint plications on their lingual crown face (MSC 37503, MSC 35766.1, MSC 37683; Fig. 10A, G), and three do not (MSC 35766.2, MSC 37497, and MSC 37660; Fig. 10D). Furthermore, these specimens were derived from all three formations within the Claiborne Group, with one ornamented and one unornamented tooth from each formation. We cannot, however, ascertain if the same species persisted from the Ypresian (Tallahatta Formation) to the Bartonian (Gosport Sand), or if multiple species are present. In terms of speciation, several interpretations can be drawn:

1. The presence of lingual crown ornamentation on half of our sample suggests they may belong to *A. sheppeyensis*. Our teeth, however, are smaller and more gracile than the type suite illustrated by Casier (1966: pl. 5, figs 19–25), and fall more within the size range of *A. novus* (> 1.5 cm in height; see Winkler 1876; Carlsen & Cuny 2014).
2. The small size of these specimens might indicate they represent juvenile teeth of *A. sheppyensis*. However, the absence of larger, adult, representatives is problematic because of the large sample sizes obtained from the localities from which these specimens were derived.
3. The teeth fall within the size range of *A. novus*, but the presence of ornamentation is problematical because ornamentation is supposedly absent on the teeth of this taxon. It is possible that *A. novus* teeth are more variable than previously described, and certain teeth may indeed have lingual ornamentation. Further examination of the type specimen could shed light on this interpretation, as the ornamentation on the specimens in our sample is only visible under magnification.
4. Our teeth could belong to an undescribed, small species of *Anomotodon*, with ornamented anterior and anterolateral teeth and unornamented laterals. Unfortunately, at this time our sample size is too small (n = 6) to substantiate this hypothesis.

Due to our small sample size and the various interpretations of the specimens at hand, we cannot speciate these teeth and assign them to *Anomotodon* sp.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Genus ***Striatolamia*** Glikman, 1964

Type species

Otodus macrotus Agassiz, 1843, Eocene, France.

Striatolamia macrota (Agassiz, 1843)

Fig. 11

Otodus macrotus Agassiz, 1843: 273, pls 32, 27–28, 30.
Lamna elegans Agassiz, 1843: 289, pl. 35, figs 1–5, pl. 37a, figs 58–59.
Otodus striatus Winkler, 1874a: 8, pl. 1, figs 7–9.
Odontaspis macrota striata var. *semistriata* Leriche, 1942: 13–14, pl. 1, figs 6–8.

Odontaspis elegans – Woodward 1889: 361.
Odontaspis macrota var. *rossica* – Jaekel 1895: 11, pl. 1, figs 8–17.
Odontaspis macrota – Eastman 1901: 105, pl. 14, figs 4. — White 1956: 147–148. — Thurmond & Jones 1981: 48.

Lamna striata – Priem 1901: 484, pl. 11, figs 29–30.
Odontaspis (*Synodontaspis*) *macrota* – Casier 1958: 18.
Striatolamia macrota – Applegate 1968: 32–36, pls 1–3.
Odontaspis macrota striata var. *semistriata* – Thurmond & Jones 1981: 48, fig. 14.
Eugomphodus macrotus – Kruckow & Thies 1990: 35.
Striatolamia cf. *striata* – Clayton *et al.* 2013: fig. 2m–o.
Sylvestrilamia teretidens – Clayton *et al.* 2013: fig. 2p–q.
Isurolamna inflata – Cappetta & Case 2016: pl. 6, fig. 5.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 2123 isolated teeth; Claiborne Group; ALMNH PV1989.2.421 (13 specimens), ALMNH PV1989.4.1.2.5 (6 specimens), ALMNH PV1989.4.10.2.5, ALMNH PV1989.4.105.2, ALMNH PV1989.4.118.2 (4 specimens), ALMNH PV1989.4.126b (3 specimens), ALMNH PV1989.4.144.1 (3 specimens), ALMNH PV1989.4.144.4 (6 specimens), ALMNH PV1989.4.15.4, ALMNH PV1989.4.16.1.4 (8 specimens), ALMNH PV1989.4.16.2b (2 specimens), ALMNH PV1989.4.160.1 (5 specimens), ALMNH PV1989.4.161.5 (5 specimens), ALMNH PV1989.4.165 (2 specimens), ALMNH PV1989.4.17.3a (3 specimens), ALMNH PV1989.4.17.4 (4 specimens), ALMNH PV1989.4.173, ALMNH PV1989.4.175b (5 specimens), ALMNH PV1989.4.176.3, ALMNH PV1989.4.177b (2 specimens), ALMNH PV1989.4.182 (2 specimens), ALMNH PV1989.4.20.2 (3 specimens), ALMNH PV1989.4.22.4 (9 specimens), ALMNH PV1989.4.27.3 (8 specimens), ALMNH PV1989.4.31.1, ALMNH PV1989.4.32.1 (2 specimens), ALMNH PV1989.4.33.1 (2 specimens), ALMNH PV1989.4.34.4 (5 specimens), ALMNH PV1989.4.38.4 (4 specimens), ALMNH PV1989.4.52.3, ALMNH PV1989.4.55.2 (4 specimens), ALMNH PV1989.4.6.1.2 (4 specimens), ALMNH PV1989.4.62, ALMNH PV1989.4.63.1.1 (2 specimens), ALMNH PV1989.4.69 (2 specimens), ALMNH PV1989.4.7.2 (2 specimens), ALMNH PV1989.4.71.2, ALMNH PV1989.4.77.1 (7 specimens), ALMNH PV1989.4.77.1.3, ALMNH PV1989.4.86 (3 specimens), ALMNH PV1989.4.94.3 (2 specimens), ALMNH PV1989.4.98 (2 specimens), ALMNH PV1992.28.13 (2 specimens), ALMNH PV1992.28.18a (5 specimens), ALMNH PV1992.28.22, ALMNH PV1992.28.27 (3 specimens), ALMNH PV1992.28.34a (2 specimens), ALMNH PV1992.28.45 (3 specimens), ALMNH PV1993.2.422 (2 specimens), ALMNH PV2000.1.43.1a (4 specimens), ALMNH PV2000.1.43.2a (21 specimens), ALMNH PV2000.1.43.5a, ALMNH PV2000.1.43.5d (9 specimens), ALMNH PV2000.1.44.2, ALMNH PV2000.1.44.5 (2 specimens), ALMNH PV2013.1.388, ALMNH PV2013.3.127, ALMNH PV2013.3.136b (5 specimens), ALMNH PV2013.4.166, ALMNH PV2013.4.53 (2 specimens), ALMNH PV2013.4.55 (2 specimens), ALMNH PV2016.3.262b (10 specimens), ALMNH PV2016.4.26 (5 specimens), ALMNH PV2016.4.29, ANSP 23404, ANSP 23405, ANSP 23406, GSA-V697 (13 specimens), GSA-V700 (2 specimens), GSA-V707, GSA-V708 (4 specimens), GSA-V711, GSA-V712 (4 specimens), GSA-V714 (4 specimens), GSA-V715, GSA-V717 (7 specimens), MMNS VP-8219 (7 specimens), MMNS VP-8228 (85 specimens), MSC 188.2, MSC 188.11–14, MSC 188.16–19, MSC 188.21–22, MSC 188.29, MSC 188.36, MSC 188.39, MSC 188.41–45, MSC 188.49, MSC 188.78, MSC 188.111 MSC 188.121, MSC 188.178, MSC 188.193, MSC 188.202, MSC 188.254, MSC 188.328, MSC 1424.1, MSC 1424.10, MSC 1424.22–25, MSC 2372.1–2, MSC 2372.4, MSC 2372.6–10, MSC 2372.10, MSC 2372.12, MSC 2372.14, MSC 2372.16–19, MSC 2372.22–23, MSC 2373.1–6, MSC 2375.2, MSC 2375.6, MSC 2375.39, MSC 12675.3–4, MSC 12675.7 MSC 12697.1–2, MSC 12708.1–9, MSC 33246, MSC 33248, MSC 33251, MSC 33253, MSC 33254, MSC 33256, MSC 33259, MSC 33261, MSC 33273, MSC 33275, MSC 33276, MSC 33277, MSC 33285, MSC 33286, MSC 33287, MSC 33288, MSC 33289, MSC 33290, MSC 33292, MSC 33297, MSC 33313, MSC 33314, MSC 33325, MSC 33327, MSC 33331, MSC 33335, MSC 33337, MSC 33339, MSC 33341, MSC 33353, MSC 33357, MSC 33365, MSC 33370, MSC 33372, MSC 33379, MSC 33381, MSC 33382, MSC 33385, MSC 33386, MSC 33400, MSC 33401, MSC 33405, MSC 33406, MSC 33409, MSC 33411, MSC 33417, MSC 33418, MSC 33424, MSC 33425, MSC

33426, MSC 33431, MSC 33434, MSC 33435, MSC 33437, MSC 33438, MSC 33440, MSC 33441, MSC 33442, MSC 33443, MSC 33447, MSC 33451, MSC 33453, MSC 33456, MSC 33459, MSC 33460, MSC 33465, MSC 33466, MSC 33468, MSC 33469, MSC 33470, MSC 33472, MSC 33474, MSC 33482, MSC 33486, MSC 33491, MSC 33493, MSC 33501, MSC 33502, MSC 33505, MSC 33506, MSC 33508, MSC 33512, MSC 33522, MSC 33523, MSC 33524, MSC 33531, MSC 33534, MSC 33538, MSC 33539, MSC 33540, MSC 33541, MSC 33545, MSC 33546, MSC 33547, MSC 33555, MSC 33557, MSC 33560, MSC 33562, MSC 33564, MSC 33566, MSC 33569, MSC 33572, MSC 33575, MSC 33577, MSC 33580, MSC 33584, MSC 33585, MSC 33589, MSC 33591, MSC 33592, MSC 33593, MSC 33597, MSC 33598, MSC 33599, MSC 33639, MSC 33640, MSC 33641, MSC 33644, MSC 33645, MSC 33649, MSC 33651, MSC 33652, MSC 33657, MSC 33659, MSC 33660, MSC 33661, MSC 33665, MSC 33667, MSC 33668, MSC 33674, MSC 33675, MSC 33676, MSC 33692, MSC 33694, MSC 33699, MSC 33704, MSC 33710, MSC 33716, MSC 33718, MSC 33724, MSC 33727, MSC 33732, MSC 33734, MSC 33737, MSC 33843, MSC 33859, MSC 33861, MSC 33863, MSC 33867, MSC 33871, MSC 33872, MSC 33876, MSC 33879, MSC 33880, MSC 33885, MSC 33886, MSC 33891.1–11, MSC 33892.1–10, MSC 33893.1–10, MSC 33894.1–10, MSC 33895.1–10, MSC 33896.1–10, MSC 33897.1–10, MSC 33898, MSC 33898.1–10, MSC 33899.1–10, MSC 33900.1–9, MSC 33901.1–10, MSC 33902.1–10, MSC 33903.1–10, MSC 33904.1–10, MSC 33905.1–10, MSC 33906.1–10, MSC 33907.1–10, MSC 33908.1–9, MSC 33909.1–10, MSC 33910.1–10, MSC 33911.1–10, MSC 33912.1–11, MSC 33913.1–10, MSC 33914.1–16, MSC 33915.1–328, MSC 33917, MSC 33920, MSC 33921, MSC 33923, MSC 33936, MSC 33937, MSC 33939, MSC 33940, MSC 33941, MSC 33945, MSC 33946, MSC 33949, MSC 33951, MSC 33954, MSC 34403.1–86, MSC 35739.1–24, MSC 35792, MSC 35793.1–10, MSC 35794.1–10, MSC 35795.1–10, MSC 35796.1–10, MSC 35797.1–10, MSC 35798.1–10, MSC 35799.1–18, MSC 35810, MSC 35890.1–10, MSC 36903, MSC 37118, MSC 37128, MSC 37129, MSC 37140, MSC 37191.1–13, MSC 37202.1–5, MSC 37252.1–18, MSC 37253.1–3, MSC 37267.1–3, MSC 37278.1–2, MSC 37285.1–20, MSC 37314.1–2, MSC 37329.1–19, MSC 37393.1–6, MSC 37400, MSC 37495.1–299, MSC 37511.1–15, MSC 37521.1–25, MSC 37527.1–7, MSC 37537.1–2, MSC 37562.1–34, MSC 37578, MSC 37579, MSC 37580.1–4, MSC 37581.1–5, MSC 37582, MSC 37583, MSC 37585.2, MSC 37599.1–6, MSC 37612.1–4, MSC 37614.1–2, MSC 37615, MSC 37619, MSC 37640.1–2, MSC 37642.1–2, MSC 37644, MSC 37646.1–2, MSC 37668, MSC 37685, MSC 37686, MSC 37697, MSC 38474.1–2, MSC 38499.1–14, MSC 38557.1–2, MSC 38613, MSC 38614, MSC 38615, MSC 38617, MSC 38618, MSC 38619, MSC 38620, MSC 38621, MSC 38622, MSC 38623, MSC 38624, MSC 38625, NJSM 24018 (2 specimens), SC2012.47.163 (10 specimens), SC2012.47.180, SC2012.47.207 (24 specimens), SC2012.47.79, SC2012.47.80 (47 specimens), SC2012.47.81, SC2012.47.82 (17 specimens), SC2012.47.83, SC2012.47.257 (3 specimens), SC2012.47.260, WSU 5, WSU 21, WSU 5025, WSU 5029 (7 specimens), WSU 5033, WSU 5034 (17 specimens), WSU 5043 (59 specimens), WSU CC 447, WSU CC 455, WSU CC 539.

Description

Anterior teeth with a long, slender, pointed crown that is sigmoidal in profile view, with upper anteriors more so than lower anteriors. Lingual crown face strongly convex and bears numerous longitudinal ridges extending to nearly 75% of cusp height. Labial face flat, smooth. Anterior teeth with single pair of minute, often indistinct, lateral cusplets. Root holaulacorhize with deep U-shaped interlobe area separating thin, rounded, and divergent lobes. Shallow nutritive groove located on pronounced lingual root boss. Upper third anterior teeth may have a slight mesial bend. Lateral teeth with broad-based triangular crown that quickly tapers apically; crown labiolingually narrower than on anterior teeth. Lingual crown ornament reduced on lateral teeth, generally very faint and confined to the medial portion of the face. Lateral teeth usually with one pair of low, broadly triangular, diverging lateral cusplets, but reduced second pair occasionally observed. Main cusp on lower lateral teeth erect; those on lower files is distally inclined. Root holaulacorhize and flattened basally. Shallow nutritive groove located on lingual root protuberance. Interlobe area shallow, V-shaped. Root lobes shorter and wider than on anteriors.

Remarks

Clayton *et al.* (2013) referred a large number of specimens in their sample from the basal Lisbon Formation in Covington County (site ACov-11) to *Striatolamia* cf. *striata* (Winkler, 1874) and *Sylvestrilamia teretidens* (White, 1931). Although morphologically similar, the teeth of *Sylvestrilamia teretidens* are described as being smaller in size and not as sigmoidal as those of *Striatolamia* (see Cappetta 2012). A reexamination of these specimens has shown all to belong to *S. macrota*. Clayton *et al.* (2013) referred their *Striatolamia* teeth to *S. striata* because of their small size and coarse lingual ornamentation, which was seen as a contrast to the larger and more finely ornamented *S. macrota*. However, examination of several thousand specimens from the Claiborne Group, as well as a sample from the Bartonian Tupelo Bay Formation (temporally equivalent to the Gosport Sand) of South Carolina (housed at SC), shows that tooth size and crown ornament is highly variable within the formations, with *S. striata*-type teeth occurring with *S. macrota* teeth. Several extremely large (up to 6.0 cm in apicobasal height) *Striatolamia* specimens have been recovered from the Lisbon Formation and Gosport Sand in Alabama (Fig. 11BB–GG), and overall these teeth are more robust than their smaller counterparts, have a wider crown base, and often have conspicuous lingual crown ornamentation. Specimens of this size are rare in Alabama, but they also occur in South Carolina. It appears that, assuming all of the Claibornian teeth represent *S. macrota*, there is an increase in maximum tooth size from the early Eocene to the late-middle Eocene. This phenomenon was also observed by Cappetta (2012), who noted a size increase in *S. macrota* teeth throughout the temporal range of the taxon, and Malyshkina & Ward (2016) also noted size differences between their sample of early and middle Eocene *S. macrota* teeth from Uzbekistan. We attribute the variation we observed within the Claiborne formations of Alabama to ontogeny and phyletic increase in tooth size from stratigraphically older units to younger units.

Cappetta & Case (2016) assigned four teeth from the ACov-11 site to *Isurolamna* aff. *inflata* (Leriche, 1905). This species, however, is considered a *nomen dubium* because Leriche (1905) failed to figure a specimen or designate a holotype. The tooth figured by Cappetta & Case (2016: pl. 6, fig. 5) does bear a superficial resemblance to *Isurolamna affinis* Casier, 1946 by having a thin, lingually bent crown, and a nutritive foramen as opposed to nutritive groove. However, our large sample from the ACov-11 does not contain any material that can unequivocally be identified as *Isurolamna*, but certain ablated *Striatolamia* anterior teeth in our sample resemble the tooth they figured.

Striatolamia was originally placed within the Odontaspididae, with some suggesting that the *macrota*-type morphology should be included within *Carcharias* (see Ward 1980; Welton & Zinsmeister 1980; Long 1992; Purdy 1998). Cappetta & Nolf (1981), however, recognized *Striatolamia* as a distinct genus, citing differences between with the lateral cusplets of *Striatolamia* and the Recent *Carcharias taurus* Rafinesque, 1810. Cappetta & Nolf (1981) placed the taxon within the Mitsukurinidae, a view later followed by Siverson (1995), who suggested *Striatolamia* has an affinity to certain Cretaceous members of this family. Although Long (1992) and Cunningham (2000) illustrated the morphological similarities between *Striatolamia* and *C. taurus*, Siverson (1995) proposed that these similarities could be the result of convergent evolution. Herein we follow Cappetta & Nolf (1981) and Siverson (1995) in placing *Striatolamia* within the Mitsukurinidae.

Stratigraphic and geographic range in Alabama

The specimens in our sample were derived from the Meridian Sand Member of the Tallahatta Formation and the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon Formations at sites ACh-14, ACov-1, ACov-11, and ACon-6, the “upper” Lisbon Formation at sites ACh-8 and ACl-3,

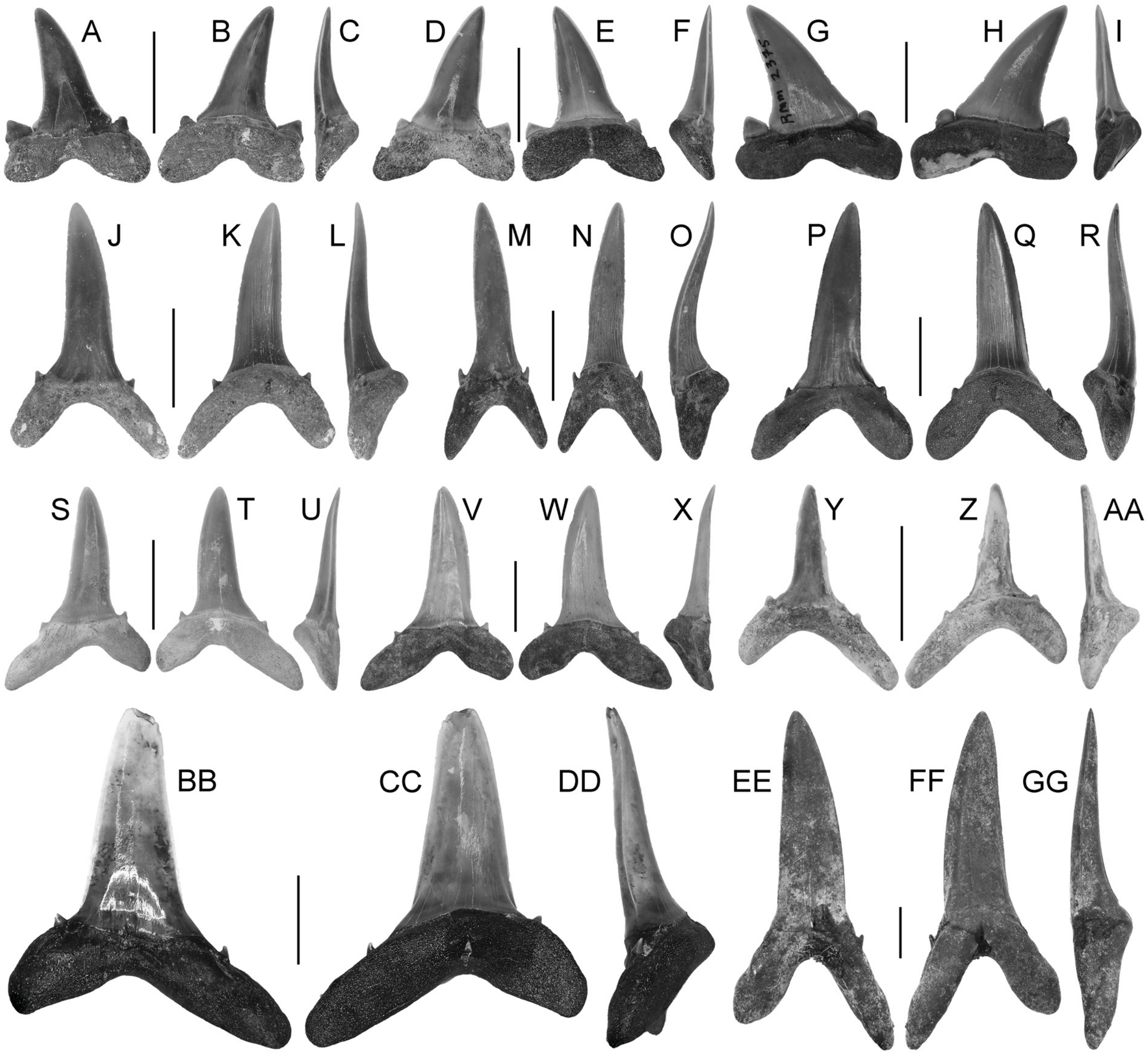

Fig. 11. *Striatolamia macrota* (Agassiz, 1843), teeth. **A**–**C**. MSC 33541, lateral tooth, lower Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D**–**F**. MSC 37191.5, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G**–**I**. MSC 2375.6, lateral tooth, Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J**–**L**. MSC 33591, anterior tooth, lower Tallahatta Formation. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M**–**O**. MSC 37252.15, anterior tooth, basal Lisbon Formation. **M**. Labial view. **N**. Lingual view. **O**. Mesial view. **P**–**R**. MSC 37521.10, anterior tooth, Gosport Sand. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S**–**U**. MSC 33341, tooth, lower Tallahatta Formation. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V**–**X**. MSC 37252.17, tooth, basal Lisbon Formation. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. **Y**–**AA**. MSC 37562.14, tooth, basal Gosport Sand. **Y**. Labial view. **Z**. Lingual view. **AA**. Mesial view. **BB**–**DD**. ALMNH PV2016.4.26, tooth, large morphology, Gosport Sand. **BB**. Labial view. **CC**. Lingual view. **DD**. Mesial view. **EE**–**GG**. MSC 37129, anterior tooth, Tallahatta/Lisbon formation contact zone, large morphology, courtesy of James Lowery. **EE**. Labial view. **FF**. Lingual view. **GG**. Mesial view. Scale bars = 1 cm.

the basal Gosport Sand at sites ACl-4, AMo-4, and AWa-2, and the Gosport Sand at sites ACh-21 and ACl-15. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Family Odontaspididae Müller & Henle, 1839

Genus ***Brachycarcharias*** Cappetta & Nolf, 2005

Type species

Otodus vincenti Winkler, 1876, Eocene, Belgium.

Brachycarcharias atlasi (Arambourg, 1952)
Fig. 12

Odontaspis substriata mut. *atlasi* Arambourg, 1952: 80, pl. 12, text fig. 18.

Odontaspis atlasi – Nolf 1972: 115, pl. 1, figs 4–6.
Carcharias aff. *atlasi* – Tabuce *et al.* 2005: 385.
Brachycarcharias atlasi – Cappetta 2012: 193.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 113 isolated teeth; Claiborne Group; MMNS VP-8220, MMNS VP-8951, MMNS VP-8953 (10 specimens), MSC 37561.1, MSC 37561.16, MSC 37561.25, MSC 37561.30, MSC 37284.19, MSC 37284.20, MSC 37284.23, MSC 37284.24, MSC 37284.33, MSC 37325.12, MSC 37325.13, MSC 37325.25, MSC 37325.27, MSC 37130, MSC 37189.17, MSC 37189.18, MSC 33269, MSC 33310, MSC 33334, MSC 33343, MSC 33373, MSC 33450, MSC 33452, MSC 33495, MSC 33503, MSC 33549, MSC 33567, MSC 33663, MSC 33705, MSC 33882, MSC 33935, MSC 33938, MSC 35626.1, MSC 35627.2, MSC 35627.6, MSC 35628.1, MSC 35629.5, MSC 35629.6, MSC 35632.6, MSC 35632.10, MSC 35633.6, MSC 35635.1–2, MSC 35636.6, MSC 35638.4, MSC 35644.3, MSC 35645.1, MSC 35646.6, MSC 35646.8, MSC 35647.5, MSC 35647.9, MSC 35648.3–4, MSC 35650.6, MSC 35651.4, MSC 35652.7, MSC 35653.8, MSC 35653.11, MSC 35654.7, MSC 35655.1, MSC 35655.8, MSC 35662.1, MSC 35663.1, MSC 35665.8, MSC 35667.3, MSC 35672.2, MSC 35675.1, MSC 35675.8–10, MSC 35676.3, MSC 35676.7, MSC 35677.6, MSC 35678.2, MSC 35678.6, MSC 35741.13, MSC 37199.7, MSC 37077.2, MSC 37077.6, MSC 37650.1, MSC 37685, MSC 37668, SC2012.47.85, SC2012.47.158 (2 specimens), SC2012.47.254, SC2012.47.255 (2 specimens), SC2012.47.256 (3 specimens), SC2012.47.261 (7 specimens), WSU 3, WSU 7, WSU 16.

Description

Teeth small, most measuring less than 1.0 cm in mesiodistal width. Main cusp tall, narrow, triangular. Labial face of main cusp flat to slightly convex; lingual face strongly convex. Main cusp erect in anterior and anterolateral files; with slight distal inclination in lateral files. Coarse vertical ridges occur on lower one-half to two-thirds of lingual face of main cusp of anterior teeth. Ornamentation on lateral teeth less distinct. Anterior teeth generally with single pair of tall, sharply pointed medially curved cusplets; occasionally two pairs present, with second pair incipient. Two pairs lateral cusplets present on most lateral teeth; cusplets wider, lower than on anterior teeth, divergent. All lateral cusplets with slightly convex labial face, strongly convex lingual face; vertical ridges occur on lingual side, particularly on anterior teeth. Cutting edges extend from main cusp apex across lateral cusplets. Root bilobate. Anterior teeth with elongated, strongly divergent lobes having rounded extremities. Lateral tooth root lobes shorter, wider. Prominent lingual root boss bisected by deep nutritive groove. Interlobe area wide, U-shaped.

Remarks

Three species of *Brachycarcharias* were identified within our Claiborne Group sample including *B. atlasi* (Arambourg, 1952); *B. lerichei* (Casier, 1946); and *B. twiggsensis* (Case, 1981). The various *B. atlasi* tooth morphologies identified in our sample appear to be conspecific with many of the syntypes figured by Arambourg (1952: pl. 12, text fig. 18) in having tall and narrow cusplets on the anterior teeth, coarse lingual ornamentation on both the main cusp and lateral cusplets and having two pairs of lateral cusplets on the lateral teeth. In addition to these morphological similarities, the stratigraphic range of Arambourg's (1952) type material overlaps with those in our sample (Ypresian to Bartonian). The

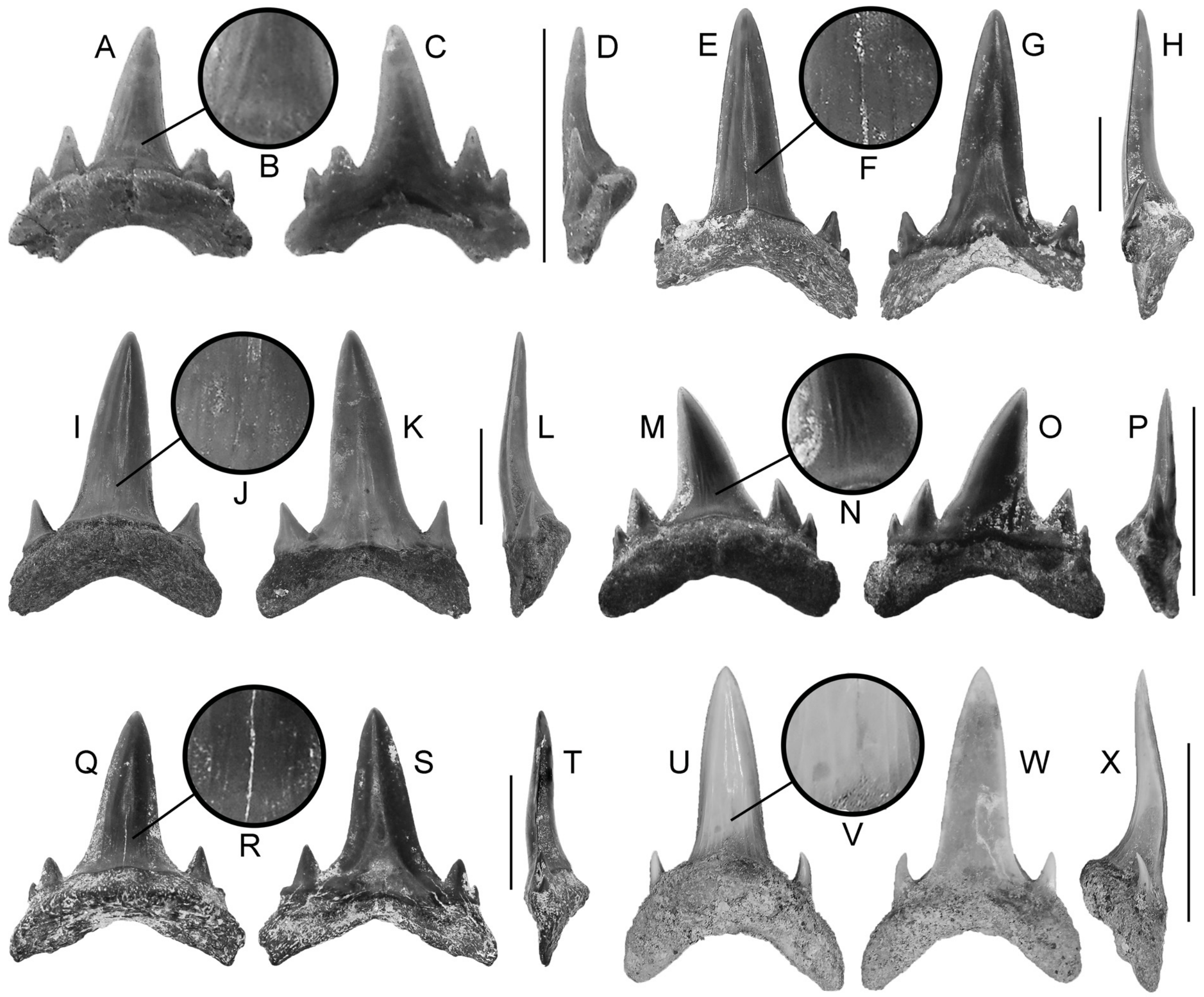

Fig. 12. *Brachycarcharias atlasi* (Arambourg, 1952), teeth. **A**–**D**. MSC 35762.1, lateral tooth, lower Tallahatta Formation. **A**. Lingual view. **B**. Close-up of lingual crown ornamentation. **C**. Labial view. **D**. Mesial view. **E**–**H**. MSC 33450, anterior tooth, lower Tallahatta Formation. **E**. Lingual view. **F**. Close-up of lingual crown ornamentation. **G**. Labial view. **H**. Distal view. **I**–**L**. MSC 37284.19, anterior tooth, basal Lisbon Formation. **I**. Lingual view. **J**. Close-up of lingual crown ornamentation. **K**. Labial view. **L**. Mesial view. **M**–**P**. MSC 37650, lateral tooth, Tallahatta/Lisbon formation contact, courtesy of Bruce Relihan. **M**. Lingual view. **N**. Close-up of lingual crown ornamentation. **O**. Labial view. **P**. Mesial view. **Q**–**T**. MSC 37561.16, lateral tooth, basal Gosport Sand. **Q**. Lingual view. **R**. Close-up of lingual crown ornamentation. **S**. Labial view. **T**. Mesial view. **U**–**X**. MSC 37561.1, anterior tooth, Gosport Sand. **U**. Lingual view. **V**. Close-up of lingual crown ornamentation. **W**. Labial view. **X**. Mesial view. Scale bar: A–D = 4 mm; E–T = 4 mm; U–X = 1 cm.

B. atlasi lateral teeth from Alabama were differentiated from those of *B. lerichei* by the combination of having up to two pairs of lateral cusplets and the presence of coarse striations on the lingual face of the main cusp and on the comparatively larger lateral cusplets. The anterior teeth are similar between the two species, but those of *B. atlasi* have much coarser ornamentation, the lateral cusplets are mesiodistally narrower, more lingually curved, and have a more conical apex. In addition, the tooth root of *B. atlasi* is often more labiolingually compressed than that of *B. lerichei*. *Brachycarcharias atlasi* teeth differ from *B. twiggsensis* by their smaller overall size, having a main cusp that is mesiodistally narrower, and having lingual crown ornamentation. The lingual striations on the teeth of *B. atlasi* are reminiscent of *Striatolamia macrota* teeth, but the species are easily distinguished by the very prominent lateral cusplets on *B. atlasi* compared to *S. macrota* (which are minute on anterior teeth), the lateral teeth are more strongly ornamented, and the anterior teeth have a much shorter and less sigmoidal main cusp. Furthermore, the lingual ornamentation is not present on the lateral cusplets of *S. macrota*. The lateral cusplets also distinguish teeth of *B. atlasi* from those of *Odontaspis winkleri*, whose cusplets are taller, more cylindrical, and lack mesial and distal cutting edges extending across the lateral cusplets.

Stratigraphic and geographic range in Alabama

The *B. atlasi* teeth in our sample were collected from the Meridian Sand Member and lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11, and the basal Gosport Sand at site ACl-4. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Brachycarcharias lerichei (Casier, 1946)
Fig. 13

Otodus vincenti Winkler, 1876: 25.
Lamna lerichei Casier, 1946: 80, pl. 2, figs 7a–b.
Odontaspis substriata var. *atlasi* Arambourg, 1952: pl. 12, text fig. 18.
Odontaspis atlasi Nolf, 1972: 115, pl. 1, figs 4–6.

Lamna vincenti – Woodward 1899: 10, pl. 1, figs 21–22.
Odontaspis vincenti – Arambourg 1952: 85, pl. 85, fig. 19.
Cretolamna lerichei – Case 1994a: 115, pl. 4, figs 62–71, 74–77.
"*Carcharias*" *vincenti* – Baut & Genault 1995: 205, pl. 5, figs 3–4.
Serratolamna lerichei – Kent 1999a: 21, pl. 2.2, figs j–k.
Brachycarcharias lerichei – Cappetta & Nolf 2005: 241, pl. 2.
Isurolamna lerichei – González-Rodríguez *et al.* 2013: 30.
Isurolamna inflata – Cappetta & Case 2016: pl. 6, figs 6–7.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1370 isolated teeth; Claiborne Group; ANSP 23407, ANSP 23408, ALMNH PV1989.4.208b (3 specimens), ALMNH PV1992.28.24, ALMNH PV2000.1.43.1a (2 specimens), ALMNH PV2000.1.43.5b, ALMNH PV2016.3.262a (3 specimens), MMNS VP-8218 (9 specimens), MMNS VP-8229 (116 specimens), MSC 12675.1, MSC 12708.5, MSC 188.32, MSC 2372.2, MSC 2375.1, MSC 2375.3, MSC 2375.5, MSC 33252, MSC 33258, MSC 33260, MSC 33264, MSC 33266, MSC 33267, MSC 33268, MSC 33270, MSC 33271, MSC 33279, MSC 33281, MSC 33282, MSC 33284, MSC 33296, MSC 33298, MSC 33299, MSC 33300, MSC 33301, MSC 33304, MSC 33307, MSC 33308, MSC 33309, MSC 33312, MSC 33320, MSC 33322, MSC 33336, MSC 33346, MSC 33349, MSC 33352, MSC 33354, MSC 33356, MSC 33358, MSC 33359, MSC 33369, MSC 33375, MSC 33376, MSC 33383, MSC 33384, MSC 33387, MSC 33388, MSC 33391, MSC

33392, MSC 33393, MSC 33395, MSC 33397, MSC 33398, MSC 33407, MSC 33410, MSC 33414, MSC 33416, MSC 33419, MSC 33423, MSC 33427, MSC 33428, MSC 33429, MSC 33432, MSC 33439, MSC 33446, MSC 33448, MSC 33454, MSC 33457, MSC 33458, MSC 33462, MSC 33473, MSC 33477, MSC 33478, MSC 33479, MSC 33480, MSC 33484, MSC 33485, MSC 33487, MSC 33488, MSC 33489, MSC 33490, MSC 33492, MSC 33498, MSC 33500, MSC 33504, MSC 33509, MSC 33514, MSC 33517, MSC 33518, MSC 33521, MSC 33527, MSC 33530, MSC 33532, MSC 33533, MSC 33535, MSC 33537, MSC 33542, MSC 33544, MSC 33550, MSC 33551, MSC 33554, MSC 33556, MSC 33561, MSC 33568, MSC 33571, MSC 33576, MSC 33578, MSC 33581, MSC 33582, MSC 33588, MSC 33594, MSC 33595, MSC 33596, MSC 33638, MSC 33642, MSC 33647, MSC 33648, MSC 33654, MSC 33662, MSC 33664, MSC 33669, MSC 33671, MSC 33678, MSC 33679, MSC 33680, MSC 33681, MSC 33683, MSC 33687, MSC 33689, MSC 33690, MSC 33696, MSC 33697, MSC 33698, MSC 33708, MSC 33709, MSC 33711, MSC 33712, MSC 33713, MSC 33714, MSC 33715, MSC 33717, MSC 33719, MSC 33720, MSC 33721, MSC 33722, MSC 33725, MSC 33726, MSC 33730, MSC 33731, MSC 33733, MSC 33735, MSC 33736, MSC 33738, MSC 33857, MSC 33859, MSC 33860, MSC 33862, MSC 33864, MSC 33866, MSC 33868, MSC 33874, MSC 33881, MSC 33884, MSC 33887, MSC 33889, MSC 33892, MSC 33893, MSC 33906, MSC 33918, MSC 33919, MSC 33924, MSC 33927, MSC 33929, MSC 33930, MSC 33942, MSC 33944, MSC 33947, MSC 33953, MSC 33955, MSC 34404.1–29, MSC 35626.2–10, MSC 35627.1, MSC 35627.3–5, MSC 35627.7–10, MSC 35628.2–10, MSC 35629.1–4, MSC 35629.7–10, MSC 35630.1–10, MSC 35631.1–10, MSC 35632.1–9, MSC 35633.1–5, MSC 35633.7–10, MSC 35634.1–10, MSC 35635.3–10, MSC 35636.1–8, MSC 35637.1–10, MSC 35638.1–3, MSC 35638.5–10, MSC 35639.1–10, MSC 35640.1–10, MSC 35641.1–10, MSC 35642.1–10, MSC 35643.1–10, MSC 35644.1–2, MSC 35644.4–10, MSC 35645.2-10, MSC 35646.1–5, MSC 35646.7, MSC 35646.9–10, MSC 35647.1–4, MSC 35647.6–8, MSC 35647.10, MSC 35648.1–2, MSC 35648.5–10, MSC 35649.1–10, MSC 35650.1–5, MSC 35650.7–10, MSC 35651.1–3, MSC 35651.5–10, MSC 35652.1–6, MSC 35652.8–10, MSC 35653.1–7, MSC 35653.9–10, MSC 35654.1–6, MSC 35654.8–10, MSC 35655.2–7, MSC 35655.9–10, MSC 35656.1–10, MSC 35657.1–10, MSC 35658.1–10, MSC 35659.1–10, MSC 35660.1–8, MSC 35661.1–10, MSC 35662.2–10, MSC 35663.2–10, MSC 35664.1–10, MSC 35665.1–7, MSC 35665.9–10, MSC 35666.1–10, MSC 35667.1–2, MSC 35667.4–10, MSC 35668.1–10, MSC 35669.1–10, MSC 35670.1–10, MSC 35671.1–10, MSC 35672.1, MSC 35672.3–10, MSC 35673.1–10, MSC 35674.1–10, MSC 35675.2–7, MSC 35676.1–2, MSC 35676.4–6, MSC 35676.8–10, MSC 35677.1–5, MSC 35677.7–10, MSC 35678.1, MSC 35678.3–10, MSC 35679.1–10, MSC 35680.1–10, MSC 35741.1–12, MSC 35741.14, MSC 35762.1–2, MSC 35782, MSC 37074.3, MSC 37183, MSC 37189.1–29, MSC 37199.1–24, MSC 37261.1–3, MSC 37284.1–18, MSC 37284.21–22, MSC 37284.25–32, MSC 37284.34–39, MSC 37284.40, MSC 37325.1–11, MSC 37325.14–24, MSC 37325.26, MSC 37325.28, MSC 37328, MSC 37401.1–3, MSC 37508.1–4, MSC 37510.2, MSC 37510.4–5, MSC 37561.3–15, MSC 37561.18–24, MSC 37561.26–27, MSC 37561.29, MSC 37561.31–40, MSC 37584.1–6, MSC 37600.1–4, MSC 38531.1–2, NJSM 24019 (3 specimens), SC2012.47.78 (3 specimens), SC2012.47.86, SC2012.47.87, SC2012.47.88 (151 specimens), SC2012.47.89 (2 specimens), SC2012.47.205 (18 specimens), SC2012.47.210 (63 specimens), WSU 5024, WSU 5030 (85 specimens), WSU 9, WSU CC 535.2, WSU CC 537.2, WSU CC 540 (2 specimens), WSU CC 541, WSU CC 542.

Description

Anterior teeth with tall, narrow, weakly to strongly sigmoidal main cusp. Mesial and distal cutting edges sharp, continuous, bi-convex, reaching base of main cusp. Main cusp with flat and smooth labial face, whereas lingual face very convex or may bear faint parallel striations, which are restricted to lower one-third of cusp. Generally, one pair of large and sharply pointed lateral cusplets present, but indistinct second pair observed on some specimens. Root holaulacorhize with deep U-shaped interlobe area separating elongated and rounded lobes. Deep nutritive groove located on prominent lingual root boss. Lateral teeth differ from anterior teeth by having lower, more triangular, and labiolingually thinner main cusp that is also distally inclined. Most lateral teeth devoid of ornamentation, but some specimens show indistinct lingual striations that are restricted to the base of the main cusp. Lateral teeth with one-to-three pairs of triangular lateral cusplets, with first pair the largest. Upper lateral teeth with a distinct distal inclination. Lower lateral teeth with an erect crown and slight lingual bend. Root on lateral teeth holaulacorhize with shallow V-shaped interlobe area separating short, wide, diverging lobes. Shallow nutritive groove occurs on pronounced lingual root protuberance.

Remarks

The *Brachycarcharias lerichei* teeth in our sample were differentiated from those of *B. twiggsensis* by their smaller overall size, narrower main cusp, smaller lateral cusplets compared to main cusp size, and the teeth generally only bear a single pair of lateral cusplets. The *B. lerichei* teeth were distinguished from those of *B. atlasi* by having much less distinct lingual ornamentation on the main cusp and absence of ornamentation on lateral cusplets, by generally having only a single pair of lateral cusplets on lateral teeth, and wider, more triangular cusplets on anterior teeth. In addition, the root is often more labiolingually robust on the teeth of *B. atlasi*. Several other morphologically similar genera that can be found within Claiborne strata in Alabama including *Hypotodus*, *Striatolamia*, *Tethylamna*, and *Jaekelotodus* (see below). *Brachycarcharias lerichei* anterior teeth have cutting edges that reach the base of the main cusp, but edges on *Hypotodus* and *Striatolamia* stop well short of the cusp base. Additionally, anterior teeth of *Striatolamia* are always ornamented, the ornament is always coarser than on *B. lerichei* teeth, and the cusplets are diminutive. Anterior teeth of *Jaekelotodus* are more robust and have smaller lateral cusplets than *B. lerichei*. *Tethylamna* anterior teeth are comparably much larger and robust than those of *B. lerichei* and they are always smooth on their lingual face (*B. lerichei* teeth can, at times, exhibit weak longitudinal ridges). *Tethylamna* lateral teeth are also larger and broader than those of *B. lerichei*, and the lateral cusplets are almost always distally directed (as opposed to diverging on *B. lerichei*). The lateral teeth of *B. lerichei* have larger and more divergent cusplets compared to *Hypotodus*, and the single pair of cusplets on the latter taxon are medially oriented. Lateral teeth of *Jaekelotodus* are conspicuously hooked and have smaller lateral cusplets than those of *B. lerichei*. The lateral teeth of *Striatolamia* are more strongly ornamented than *B. lerichei*, and cusplets are comparatively wider and more blunt, and the root lobes are wider.

The *B. lerichei* teeth in our sample appear to be highly variable with respect to lingual crown ornamentation (as it may be present or absent) and development of lateral cusplets (as two pairs are occasionally present, depending on jaw position and ontogenetic age). This variability has also been documented in the morphologically similar dentitions of the extant *Lamna nasus* (Bonnaterre, 1788), leading some to question whether the placement of the species within *Brachycarcharias* is necessary (see Purdy & Francis 2007). Despite questions regarding the generic placement of this species, the use of *Brachycarcharias* has gained favor and is followed herein.

Cappetta & Case (2016) reported three teeth in their sample from site ACov-11 in Covington County, AL as belonging to *Isurolamna* aff. *inflata* (Leriche, 1905). We did not encounter this genus within our large sample of teeth from the same site, and it is our opinion that those specimens are not *Isurolamna*. Within our Lisbon sample of *B. lerichei*, we did observe several ablated lateral teeth that superficially resemble *Isurolamna*.

Stratigraphic and geographic range in Alabama

The specimens in our sample were derived from the Meridian Sand Member of the Tallahatta Formation and lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at sites ACh-14, ACov-11, and ACon-6, the basal Lisbon Formation at site ACov-11, the “upper” Lisbon Formation at site ACl-3, the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21 and ACl-15. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

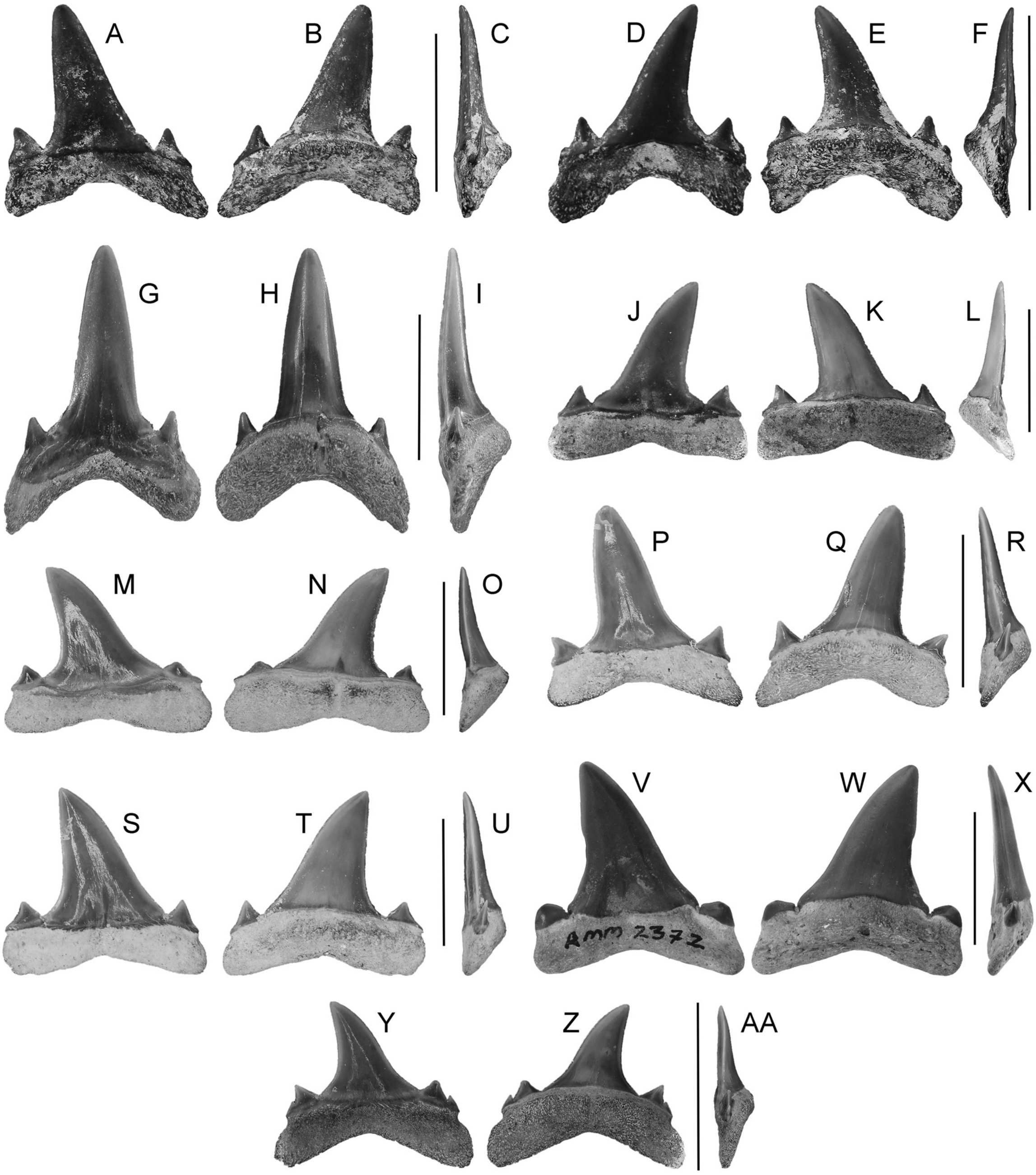

Fig. 13. *Brachycarcharias lerichei* (Casier, 1946), teeth. **A**–**C**. MSC 37199.1, lateral tooth, Meridian Sand Member of the Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D**–**F**. MSC 37199.2, lateral tooth, Meridian Sand Member of the Tallahatta Formation. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G**–**I**. MSC 33918, anterior tooth, lower Tallahatta Formation. **G**. Labial view. **H**. Lingual view. **I**. Distal view. **J**–**L**. MSC 33868, lateral tooth, lower Tallahatta Formation. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M**–**O**. MSC 37183, lateral tooth, Tallahatta/Lisbon formation contact zone. **M**. Labial view. **N**. Lingual view. **O**. Mesial view. **P**–**R**. MSC 37189.2, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S**–**U**. MSC 37189.1, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V**–**X**. 2372.2, lateral tooth, Gosport Sand. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. **Y**–**AA**. MSC 37074.3, lateral tooth, Tallahatta/Lisbon formation contact zone. **Y**. Labial view. **Z**. Lingual view. **AA**. Mesial view. Scale bars = 1 cm.

Brachycarcharias twiggsensis (Case, 1981)

Fig. 14

Lamna twiggsensis Case, 1981: 58–59, pl. 3, figs 4–8, text fig. 3.

Cretolamna twiggsensis – Case & Cappetta 1990: 9–10, pl. 3, figs 40–55.
Brachycarcharias cf. *twiggsensis* – Underwood *et al.* 2011: 52.
Tethylamna twiggsensis – Cappetta & Case 2016: 51.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 21 isolated teeth; Claiborne Group; ALMNH PV1989.4.160.2 (2 specimens), ALMNH PV1989.4.32.4, ALMNH PV1989.4.34.3, ALMNH PV1989.4.47.2 (2 specimens), ALMNH PV1989.4.6.1.3 (3 specimens), ALMNH PV1989.4.63.1.2, ALMNH PV1989.4.94.2, MSC 2372.15, MSC 2375.4, MSC 37510.1, MSC 37510.3, MSC 37561.2, MSC 37561.17, MSC 37561.28, MSC 37561.41, MSC 37561.42, MSC 37645.

Description

Sample includes anterior, anterolateral, and lateroposterior teeth. Anterior teeth with tall, erect, somewhat narrow, symmetrically triangular main cusp. Sharp, sinuous cutting edges extend from cusp base to apex; apex sharply pointed. Labial face nearly flat, lingual face very convex; enameloid smooth. In profile, apex of main cusp curves labially. Single pair of tall lateral cusplets present. Root bilobate with elongated, slightly diverging lobes separated by U-shaped interlobe area. Lingual nutritive groove on medial boss. Anterolateral teeth with slight distal inclination to main cusp; cusp labiolingually thinner than on anterior teeth. In profile, labial curvature of main cusp apex more pronounced than on anterior teeth. Two pairs of diverging lateral cusplets present; first pair large, tall, broadly triangular; second pair diminutive. Root bilobate with more divergent lobes; lobes range from pointed to rounded. Interlobe area shallow, V-shaped to U-shaped. Shallow nutritive groove on triangular lingual root protuberance. One or more large nutritive foramina occur within nutritive groove.

Remarks

The taxonomic history of the *twiggsensis* morphology has been tumultuous, having been assigned to *Lamna* (Case 1981), *Cretalamna* (Case & Cappetta 1990), *Brachycarcharias* (Underwood *et al.* 2011), and more recently *Tethylamna* (Cappetta & Case 2016). As part of their generic diagnosis for *Tethylamna*, Cappetta & Case (2016) referred the Priabonian "*Lamna*" *twiggsensis* Case, 1981 to this genus. However, the lateral cusplets on the teeth of "*L.*" *twiggsensis* differ significantly from those of the type species of *Tethylamna*, *T. dunni* Cappetta & Case, 2016, suggesting the species does not belong to the latter genus. For instance, the anterior teeth of *T. dunni* often have two pairs of lateral cusplets, the larger of which is very narrow and often medially curved. In contrast, there is generally only a single pair of erect cusplets on "*L.*" *twiggsensis* anterior teeth. Additionally, although both *T. dunni* and "*L.*" *twiggsensis* lateral teeth have two pairs of cusplets, those of *T. dunni* are most often both mesially directed, whereas they are diverging on the *twiggsensis* morphology. Also, the first cusplet on the distal crown shoulder of *T. dunni* lateral teeth is conspicuously wider than the corresponding cusplet on the mesial side. In contrast, the equivalent cusplets on "*L.*" *twiggsensis* lateral teeth are roughly of equal size. Underwood *et al.* (2011) placed the *twiggsensis* morphology within *Brachycarcharias* because the degree of ontogenetic heterodonty they observed within their middle-to-late Eocene sample from Egypt suggested a close affinity to this genus, as opposed to *Cretalamna* or *Lamna*. Because the characteristics noted above are more consistent with our observations of *Brachycarcharias* teeth in Alabama, we follow Underwood *et al.* (2011) in assigning the *twiggsensis* morphology to this genus.

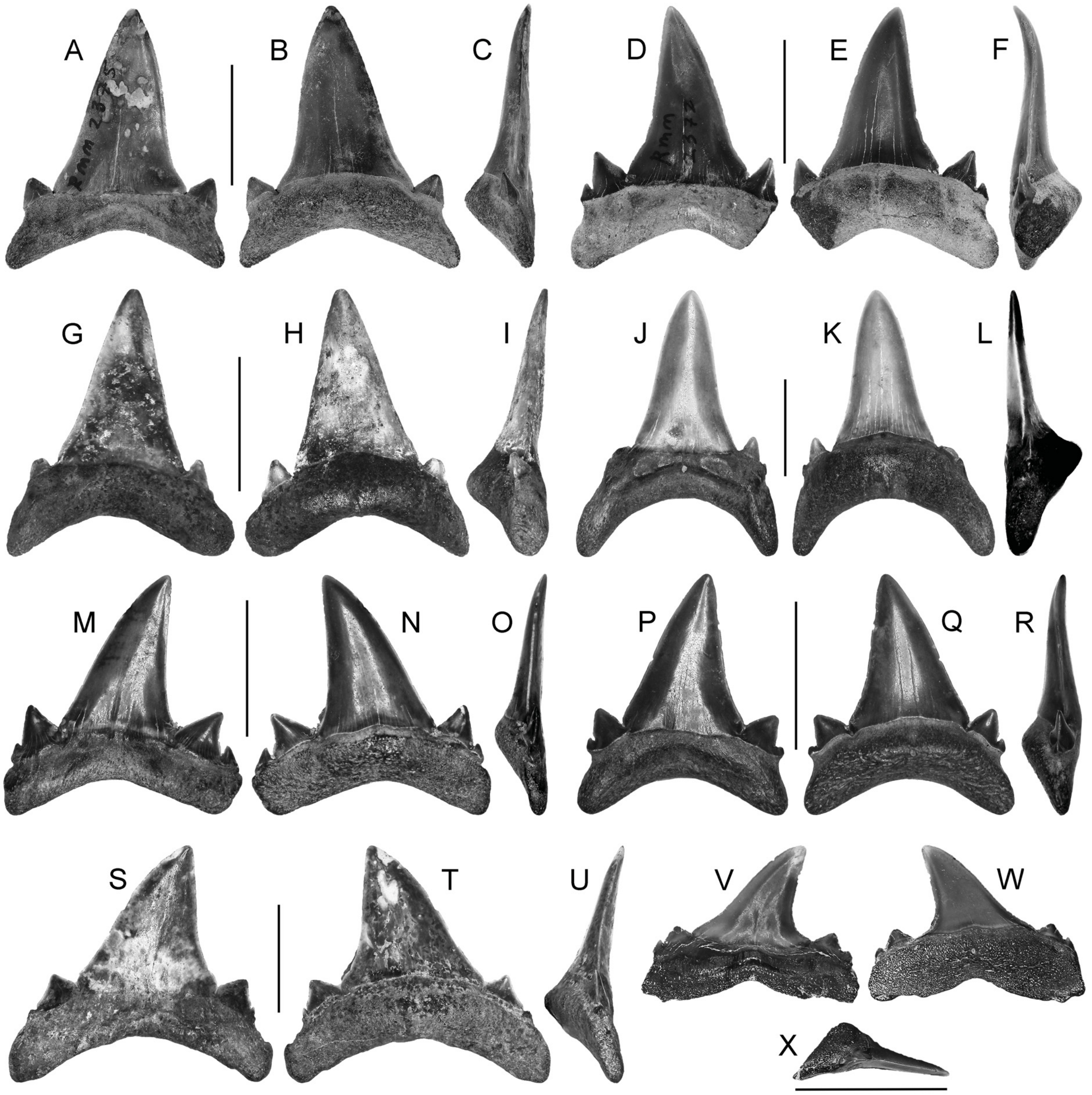

Fig. 14. *Brachycarcharias twiggsensis* (Case, 1981), teeth. **A–C**. MSC 2372.4, anterior tooth, Gosport Sand. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 2372.15, anterolateral tooth, Gosport Sand. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G–I**. ALMNH PV1989.4.47.1, anterior tooth, Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. ALMNH PV1989.4.16.1, anterior tooth, Gosport Sand. **J**. Labial view. **K**. Lingual view. **L**. Distal view. **M–O**. ALMNH PV1989.4.47.2, lateral tooth, Gosport Sand. **M**. Labial view. **N**. Lingual view. **O**. Mesial view. **P–R**. ALMNH PV1989.4.63.1, lateral tooth, Gosport Sand. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S–U**. ALMNH PV1989.4.94, lateral tooth, Gosport Sand. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V–X**. MSC 37561.2, lateroposterior tooth, Gosport Sand. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. Scale bars = 1 cm.

The *B. twiggsensis* teeth in our sample were separated from those of *Brachycarcharias atlasi* by being more robust and larger in overall size, by having a wider crown base, and by lacking coarse lingual ornamentation on the main cusp and lateral cusplets. Similarly, the teeth of *B. twiggsensis* can be differentiated from those of *Brachycarcharias lerichei* by their larger overall size, broader crown, and consistent development of a second pair of lateral cusplets. In contrast, teeth of *B. lerichei* only occasionally exhibit a second lateral cusplet (generally on one side of the tooth, and poorly separated from the larger, first cusplet). There are certain smaller teeth in the Gosport Sand sample that resemble specimens of *B. lerichei* (i.e., Fig 14V–X), but based on larger samples of *B. twiggsensis* teeth from the Clinchfield Formation of Georgia and Tupelo Bay Formation of South Carolina, we regard these teeth as belonging to juvenile individuals of *B. twiggsensis*. In these samples, smaller and more gracile teeth could be identified as *B. lerichei*, but the lateral teeth have a conspicuous second or third lateral cusplet like their larger and more robust *B. twiggsensis* counterparts.

Anterior teeth of *Striatolamia* differ from those of *B. twiggsensis* in their taller but much narrower dimensions, diminutive lateral cusplets, and presence of coarse lingual longitudinal ridges. Lateral teeth of *Striatolamia* differ in having a main cusp with blunted apex and fine lingual ornamentation, the lateral cusplets are rounded with the distal cusplet being much larger in size than the mesial one. In contrast, cusplets of *B. twiggsensis* lateral teeth are sharply pointed and of roughly equal size. Anterior and lateral teeth of *Jaekelotodus* have much smaller lateral cusplets than those of *B. twiggsensis*, and the lateral teeth of *Jaekelotodus* are very conspicuously distally hooked and with a much more sharply apically tapering main cusp.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21 and ACl-15. Middle Bartonian, Zone NP17.

Genus ***Hypotodus*** Jaekel, 1895

Type species

Lamna verticalis Agassiz, 1843, Ypresian, United Kingdom.

Hypotodus verticalis (Agassiz, 1843)
Fig. 15

Lamna hopei Agassiz, 1843: 293, pl. 37a, figs 28, 30.
Lamna verticalis Agassiz, 1843: 294, pl. 37a, fig. 31.
Otodus vincenti Winkler, 1874a: 11, figs 9–10.
Odontaspis hopei affinia Casier, 1946: 64, pl. 2, fig. 9.

Odontaspis verticalis – Casier 1946: 70, pl. 2, fig. 13.
Synodontaspis hopei – Nolf 1988: pl. 25, fig. 8.
Hypotodus verticalis – Nolf 1988: pl. 29, figs 3–7. — Cappetta & Nolf 2005: 244, pl. 4.
Carcharias hopei – Ward 1988: 1, pl. 2, figs 1–17, pl. 6, text-fig. 2.
Eugomphodus verticalis – Kruckow & Thies 1990: 36.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 121 isolated teeth; Claiborne Group; ALMNH PV1992.28.18c, ALMNH PV2016.4.57b, MMNS VP-8954 (37 specimens), MSC 2372.3, MSC 33265, MSC 33305, MSC 33315, MSC 33360, MSC 33367, MSC 33368, MSC 33377, MSC 33399, MSC 33408, MSC 33464, MSC 33467, MSC 33499, MSC 33516, MSC 33543, MSC 33552, MSC

33553, MSC 33558, MSC 33563, MSC 33583, MSC 33586, MSC 33877, MSC 33897, MSC 33899, MSC 33933, MSC 35784.1–3, MSC 36177, MSC 37013, MSC 37014, MSC 37054.1–6, MSC 37055.1–3, MSC 37060.1–4, MSC 37062.1–3, MSC 37063, MSC 37103.1–3, MSC 37114.1–5, MSC 37131, MSC 37143.1–5, MSC 37159, MSC 37295, MSC 37296, MSC 37313, MSC 37535, MSC 38473.1–2, MSC 39012, NJSM 24020 (2 specimens), SC2012.47.162, SC2012.47.76, SC2012.47.77 (2 specimens), SC2012.47.90 (5 specimens), WSU 5003.

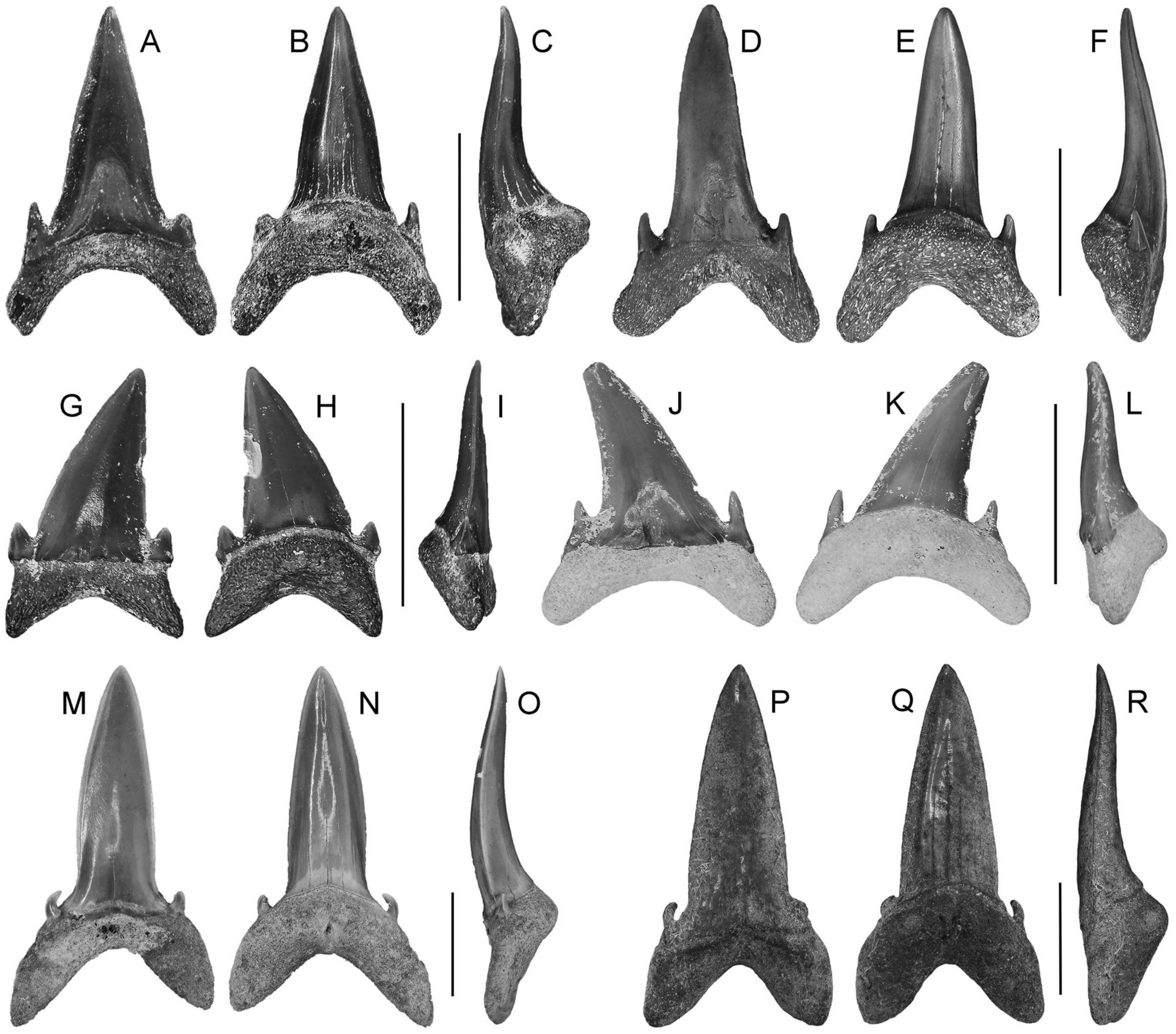

Fig. 15. *Hypotodus verticalis* (Agassiz, 1843), teeth. **A–C**. MSC 37055.1, anterior tooth, Meridian Sand Member of the Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 33908, anterior tooth, lower Tallahatta Formation. **D**. Labial view. **E**. Lingual view. **F**. Distal view. **G–I**. MSC 37296, lateral tooth, basal Lisbon Formation. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. MSC 36177, upper lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M–O**. MSC 37103.1, anterior tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **M**. Labial view. **N**. Lingual view. **O**. Distal view. **P–R**. MSC 37159, anterior tooth, Tallahatta/Lisbon contact zone, courtesy of James Lowery. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. Scale bars = 1 cm.

Description

All teeth with single pair of lateral cusplets that angle medially. Crown faces smooth. Labial crown face flat; lingual face convex. Cutting edges incomplete and never reach the lateral cusplets. Root bilobed with rounded root lobes. Prominent nutritive groove present on lingual root protuberance. Upper anterior teeth with long, slender, and triangular main cusp with a slight distal inclination. Root lobes divergent and elongated mesially. Base of the main cusp wider in upper anterior files. Cusplets more needle-like in anterior files. Apex on upper lateral teeth generally have a slight labial bend. Lower anterior teeth with taller and labiolingually thinner main cusp than on upper anterior files. Root protuberance more pronounced on lower anterior teeth and have a more sigmoidal cusp. Main cusp on upper lateral teeth short and triangular with distinctive distal hook. Base of the main cusp on upper lateral teeth are wider than other tooth positions, the cusplets more triangular, and lingual boss reduced. Root lobes on upper lateral teeth labiolingually compressed. Interlobe area on upper lateral teeth V-shaped; U-shaped on all other files. Main cusp on lower anterolateral teeth more triangular than other files. Main cusp on lower anterolateral teeth more erect and slenderer than on upper anteriors. Main cusp on lower anterolateral teeth with slight distal bend and root with elongated mesial lobe.

Remarks

Agassiz (1843) originally named *Lamna hopei* and *Lamna verticalis*, two taxa that were subsequently placed by Cappetta (1987) within the genus *Hypotodus* Jaekel, 1895. Ward (1988) later questioned the validity of *Hypotodus* and placed *L. hopei* in the genus *Carcharias*. He also argued that *H. verticalis* and *C. hopei* were conspecific, ultimately designating *H. verticalis* a junior synonym of *C. hopei*. Cappetta (1987) and Cappetta & Nolf (2005) later argued that *H. verticalis* was indeed a valid taxon because, as they determined, the presence of two upper anterior teeth separated the species from all the known members of the Odontaspididae and thus warranted placement within its own genus. Currently *Hypotodus* is monospecific and is only represented by the type species, *H. verticalis*. We follow Cappetta & Nolf (2005) in recognizing the validity of *H. verticalis* because all specimens in our sample have incomplete cutting edges that terminate well short of the lateral cusplets. This unique characteristic separates the teeth of this taxon from similar genera in our sample like *Brachycarcharias* and *Jaekelotodus*, both of which have complete cutting edges that extend to the base of the main cusp. Anterior teeth of *Striatolamia* also have incomplete cutting edges, but the presence of longitudinal ridges on the lingual cusp face contrasts with the smooth faces of *Hypotodus* teeth. In addition, *Striatolamia* lateral teeth attain larger sizes, are broader and bear lingual ornamentation, and the cusplets are broader and more closely connected to the main cusp. *Hypotodus* lateral teeth differ from those of *Brachycarcharias* in having a single pair of comparatively smaller lateral cusplets, and from *Jaekelotodus* by having a less hooked main cusp and broader lateral cusplets.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Meridian Sand Member of the Tallahatta Formation and the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, “upper” Lisbon Formation at site ACl-3, and the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Genus ***Jaekelotodus*** Menner, 1928

Type species

Hypotodus trigonalis Jaekel, 1895, Oligocene, Russia.

Jaekelotodus robustus (Leriche, 1921)

Fig. 16

Odontaspis robusta Leriche, 1921: 117.

Odontaspis (*Synodontaspis*) *robusta* – White 1931: 62, figs 75–79.
Hypotodus robustus – Nolf 1986: pl. 28, figs 1–6.
Carcharias robustus – Case 1994a: 111, text-fig. 4.
Jaekelotodus robustus – Cappetta & Nolf 2005: 264, pl. 5.

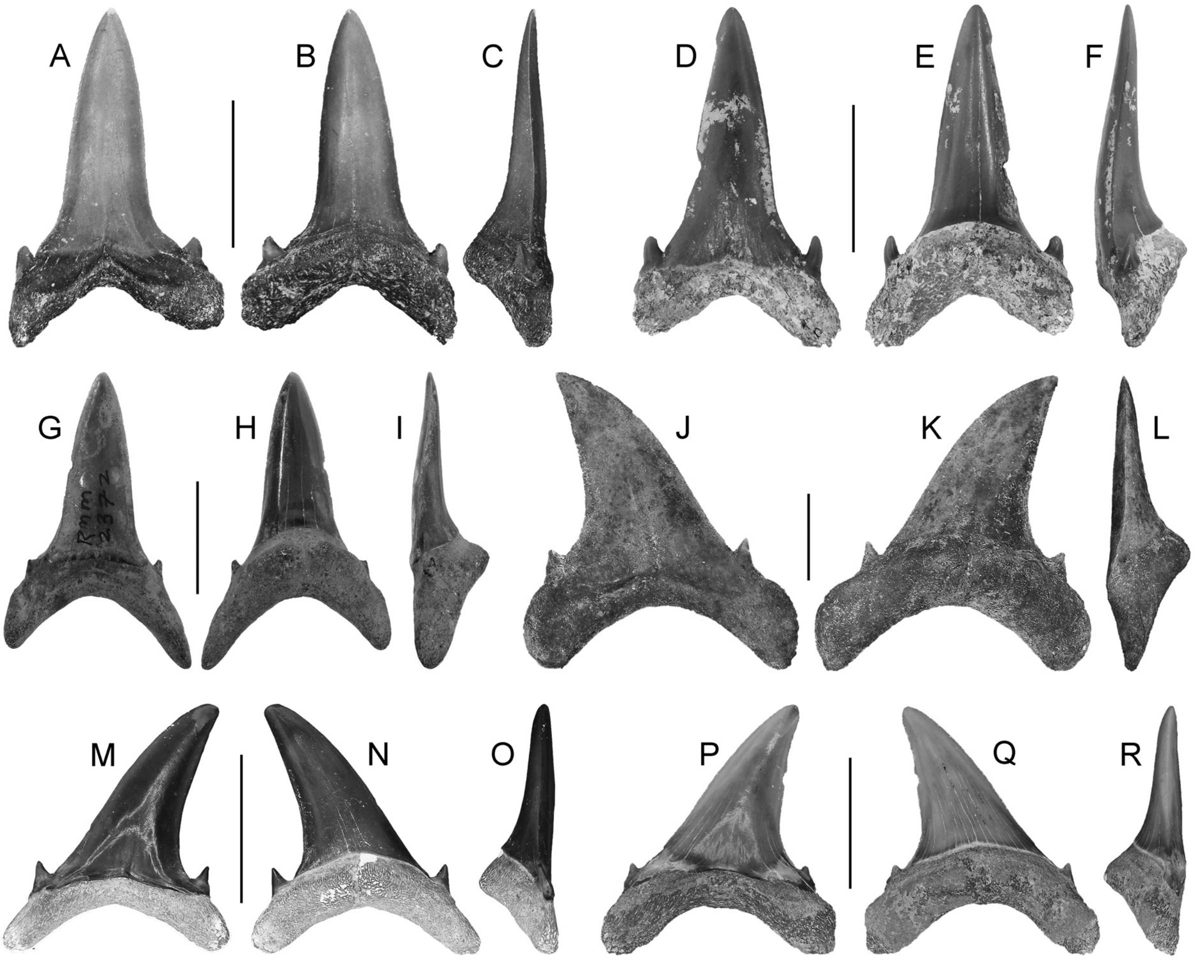

Fig. 16. *Jaekelotodus robustus* (Leriche, 1921), teeth. **A–C**. MSC 35740.1, anterior tooth, Meridian Sand Member of the Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 33371, anterior tooth (lower Tallahatta Formation). **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G–I**. MSC 2372.11, anterior tooth, Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. MSC 37149, upper lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M–O**. MSC 33932, upper lateral tooth, lower Tallahatta Formation. **M**. Labial view. **N**. Lingual view. **O**. Mesial view. **P–R**. MSC 35783.1, upper lateral tooth, lower Tallahatta Formation. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. Scale bars = 1 cm.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 157 isolated teeth; Claiborne Group; ALMNH PV1992.28.18b, ALMNH PV1992.28.34b, ALMNH PV1992.28.53, ALMNH PV2000.1.43.1a (5 specimens), ALMNH PV2000.1.43.5c (4 specimens), ALMNH PV2013.3.136a, ALMNH PV2016.4.30 (2 specimens), ALMNH PV2016.4.31 (4 specimens), GSA-V698 (3 specimens), GSA-V716 (3 specimens), MMNS VP-7495, MMNS VP-8215 (2 specimens), MMNS VP-8230 (61 specimens), MSC 1424.26, MSC 2372.11, MSC 2372.21, MSC 2383, MSC 33371, MSC 33374, MSC 33483, MSC 33656, MSC 33875, MSC 33900, MSC 33926, MSC 33932, MSC 33950, MSC 35738.1–4, MSC 35740.1–2, MSC 35783.1–3, MSC 37061, MSC 37064.1–2, MSC 37108.1–2, MSC 37149, MSC 37171.1–3, MSC 37529, MSC 38282.1–2, SC2012.47.179, SC2012.47.251 (3 specimens), SC2012.47.70, SC2012.47.71 (2 specimens), SC2012.47.72, SC2012.47.73 (11 specimens), SC2012.47.74, SC2012.47.75 (16 specimens), SC2012.47.91, SC2012.47.159.

Description

Anterior teeth with tall triangular main cusp; crown base wide. Main cusp of anterior teeth biconvex in labial/lingual views, sigmoidal in profile view. Lingual face of main cusp very convex; labial face flat to slightly convex; enameloid on both faces smooth. Single pair of very narrow and medially curved lateral cusplets present that are small compared to main cusp size. Lateral teeth with lower, broader, conspicuously distally curved main cusp. Apex on upper lateral teeth with slight labial bend. Generally, a single pair of small, pointed lateral cusplets, that are broader than those of anteriors; some lateral teeth with a secondary pair of vestigial cusplets. Cutting edges of all teeth complete and extend to the base of main cusp, reaching cusplets. Weak lingual dental band occasionally observed at base of the main cusp. All teeth bilobate with rounded, divergent root lobes and U-shaped interlobe area. Interlobe area on anterior teeth deeper than on lateral files, and root lobes less divergent. Prominent lingual boss bears shallow nutritive groove.

Remarks

The teeth of *Jaekelotodus robustus* were separated from those of taxa with similar teeth in our sample by the following combination of features: the main cusp cutting edges extend to the lateral cusplets on all teeth (separating them from *Hypotodus*); the lack of crown ornamentation (separating them from *Striatolamia* and *Brachycarcharias lerichei* and *B. atlasi*); and the anterior teeth have a single pair of lateral cusplets (separating them from *Anomotodon*). *Tethylamna* anterior teeth are similar to those of *Jaekelotodus*, but the cutting edges reach the crown foot and the cusplets are larger and more sharply curved medially. Lateral teeth of *Jaekelotodus* have much smaller lateral cusplets, and a central cusp that is more sharply apically tapered and distally curved than *Tethylamna*. Teeth of *Otodus* (*Otodus*) are robust like those of *Jaekelotodus*, but the lateral cusplets of *Otodus* (*Otodus*) are very broadly triangular and diverging, the lateral teeth are not as sharply tapered and distally curved, and roots lack a lingual nutritive groove.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Meridian Sand Member of the Tallahatta Formation and the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations and basal Lisbon Formation at site ACov-11, the “upper” Lisbon Formation at site ACl-3, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Genus ***Mennerotodus*** Zhelezko, 1994

Type species

Mennerotodus glueckmani Zhelezko, 1994, middle Eocene (Bartonian), Kazakhstan.

Mennerotodus sp.
Fig. 17

Material examined

UNITED STATES OF AMERICA – **Alabama** • 5 isolated teeth; Claiborne Group; ALMNH PV1989.4.16.1.1, ALMNH PV1989.4.17.3.8, ALMNH PV1989.4.20.1, ALMNH PV1989.4.34.1, ALMNH PV1989.4.203.1.

Description

Both anterior and upper lateral teeth present in our sample. Anterior teeth with tall, triangular main cusp with smooth labial and lingual faces. Labial crown face slightly convex; lingual face strongly convex. Main cusp only slightly sigmoidal in profile view. Single pair of short, triangular lateral cusplets present at base of main cusp, with tiny rounded denticulation at the base of the mesial side of the main cusp, just before the first cusplet. Lateral cusplets appear well separated from the main cusp in lingual view. Deep medial depression occurs at base of labial crown face. Root lobes elongate, basally tapering, slightly diverging, sub-rounded. Deep U-shaped interlobe area. Very pronounced lingual protuberance; box-like in basal view, with shallow but wide nutritive groove. Lateral teeth have a shorter, broad-based but apically narrow main cusp that may be erect or distally inclined. Labial face of main cusp flat to slightly convex; lingual face very convex. Crown labially inclined in profile view. Mesial and distal cutting edges do not extend to the lateral cusplets. One-to-two pairs of divergent lateral cusplets present. Secondary pairs of cusplets are smaller and always positioned lateral to the larger, medial pair. Cusplets tend to have a slight medial bend. One or more minute, triangular, denticulations present between the medial pair of cusplets and cutting edges. Up to two denticulations may be present mesially, with no more than one present distally, if present at all. Root lobes triangular with rounded ends, strongly divergent. Interlobe area shallow, V-shaped. Lingual root protuberance inconspicuous but has deep nutritive groove.

Remarks

The five specimens in our sample are morphologically very similar those of the Recent *Carcharias taurus* Rafinesque, 1810, and we used dentitions of this extant taxon to determine hypothetical tooth positions for the *Mennerotodus* teeth in our sample. *Mennerotodus* teeth differ from *C. taurus*, and all the other Claiborne odontasipids in our sample, by the conspicuous presence of distinct denticulations located between the lateral cusplets and mesial cutting edge on the teeth (these denticulations may be present on the distal edge as well but are more prevalent mesially). This feature is not present on teeth within any of the *C. taurus* jaw sets examined at SC and USNM (n = 5) but has been reported on a small number of *Jaekelotodus trigonalis* (Jaekel, 1895) teeth (see Cappetta & Nolf 2005; Van den Eeckhaut & De Schutter 2009). The teeth in our sample, however, are smaller, more gracile, and have a mesiodistally thinner main cusp than those of *J. trigonalis* and are more consistent with the morphology of the middle Eocene *Mennerotodus glueckmani* as described and illustrated by Zhelezko (1994). The specimens in our sample appear to differ from those of the type species, *M. glueckmani*, by having a shorter and more robust main cusp, but a larger sample is needed to make more direct comparisons to previously described species. A more detailed study of the occurrences of this genus in North America is currently being undertaken by the present authors.

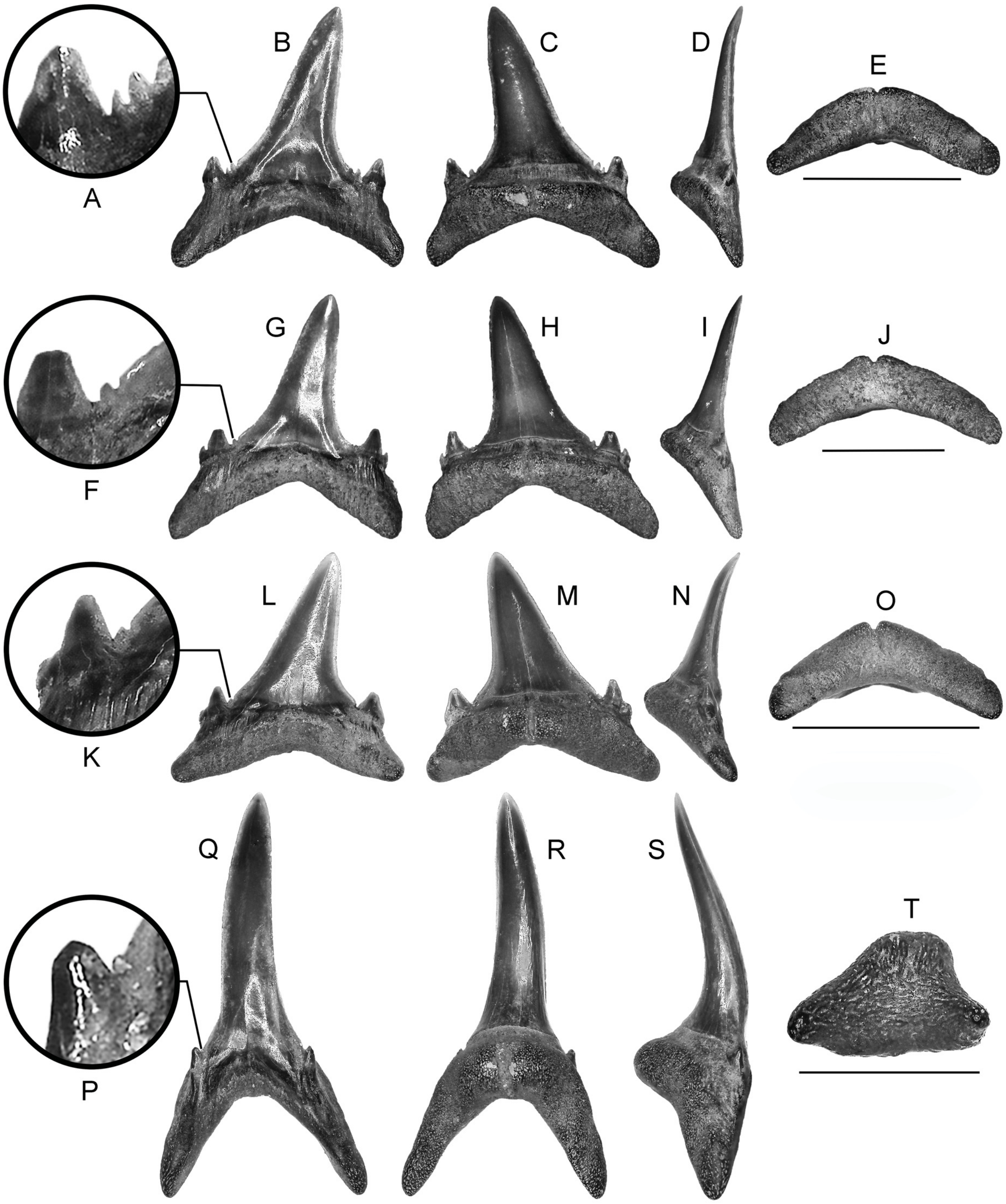

Fig. 17. *Mennerotodus* sp., teeth. **A–E**. ALMNH PV1994.4.16.1, upper right lateral tooth, Gosport Sand. **A**. Close-up of mesial denticulations. **B**. Labial view. **C**. Lingual view. **D**. Mesial view. **E**. Basal view. **F–J**. ALMNH PV1994.4.203.1, upper right lateral tooth, Gosport Sand. **F**. Close-up of mesial denticulation. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J**. Basal view. **K–O**. ALMNH PV1989.4.17.3.8, upper left lateral tooth (reversed for comparison), Gosport Sand. **K**. Close-up of mesial denticulation. **L**. Labial view. **M**. Lingual view. **N**. Mesial view. **O**. Basal view. **P–T**. ALMNH PV1989.4.20, lower left second anterior tooth, Gosport Sand. **P**. Close-up of mesial denticulation. **Q**. Labial view. **R**. Lingual view. **S**. Mesial view. **T**. Basal view. Labial at bottom in basal views. Scale bars = 1 cm.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Gosport Sand at site ACh-21. Middle Bartonian, Zone NP17.

Genus ***Odontaspis*** Agassiz, 1843

Type species

Squalus ferox Risso, 1810, early Pliocene, Italy.

Odontaspis winkleri Leriche, 1905

Fig. 18

Odontaspis winkleri sp. nov. Leriche, 1905: 74, pl. 6, fig. 8.

Odontaspis (*Odontaspis*) aff. *winkleri* – Arambourg 1935: 425, pl. 29, figs 20–22.
Synodontaspis? winkleri – Herman 1977: 245.
Eugomphodus winkleri – Krukow & Thies 1990: 35.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 5 isolated teeth; Claiborne Group; SC2012.47.92, MSC 33380, MSC 35764, MSC 38477, WSU CC 535.1.

Description

Teeth small, generally not exceeding 1.0 cm in overall height. Upper teeth slightly sigmoidal; lower teeth with slight lingual bend. Teeth with tall and thin cusp, with characteristically tall, erect, conical and sharply pointed lateral cusplets. Lingual face of main cusp strongly convex; labial face may be nearly

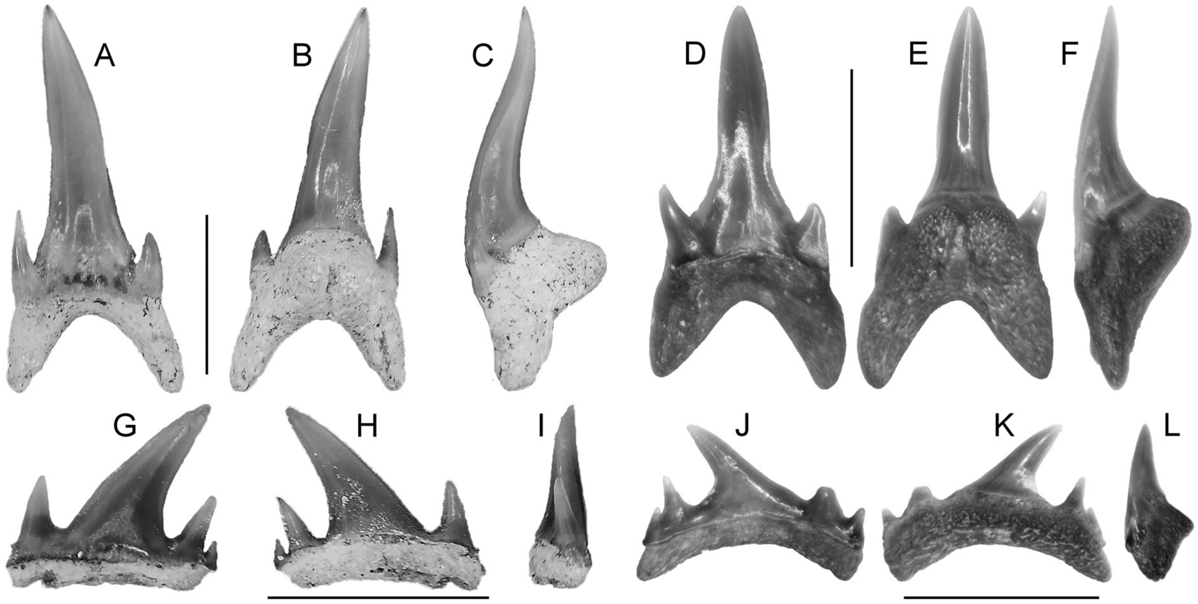

Fig. 18. *Odontaspis winkleri* Leriche, 1905, teeth. **A**–**C**. MSC 33380, anterior tooth, lower Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D**–**F**. SC2012.47.162, anterior tooth, basal Lisbon Formation. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G**–**I**. MSC 35764, lateral tooth, lower Tallahatta Formation. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J**–**L**. WSU CC535.1, lateral tooth, basal Lisbon Formation. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. Scale bars = 5 mm.

flat to convex (particularly at the base). Mesial and distal cutting edges absent or restricted to the upper two-thirds of the main cusp. Lingual and labial cusp faces of anterior teeth smooth, but lateral teeth with distinct folding at labial crown foot. Anterior teeth with single pair of lateral cusplets; lateral teeth with two to three pairs of lateral cusplets. Cusplets divergent and decrease in size laterally. Root bilobate with long, thin, divergent, and rounded lobes; lobes separated by deep U-shaped interlobe area. Deep nutritive groove located on prominent lingual root protuberance.

Remarks

Three species of Paleogene *Odontaspis* have been recognized in North America including *O. carolinensis* Case & Borodin, 2000, *O. speyeri* Dartevelle & Casier, 1943, and *O. winkleri* Leriche, 1905. The *Odontaspis* teeth in our sample differ from those of *O. carolinensis* by having a less robust main cusp on the anterior teeth and cylindrical, not labiolingually flattened, lateral cusplets on the lateral teeth. The teeth of *O. speyeri* are much more robust and have smaller cusplets than those in our sample, and Cappetta (2012) referred this species to *Jaekelotodus*. Although Holman & Case (1988) reported *O. speyeri* from the ACov-11 locality, this was likely a misidentification as no such teeth have been identified within our exceptionally large sample of teeth from this locality, nor have they been reported by Clayton *et al.* (2013) or Cappetta & Case (2016). Furthermore, *O. speyeri* is a taxon that has generally been reported from Paleocene deposits elsewhere (see Siverson 1995; Yarkov & Popov 1998; Adolfssen & Ward 2015). Unfortunately, Holman & Case (1988) did not figure their specimens so the identity of these teeth remains unconfirmed.

The teeth in our sample appear to be conspecific with *Odontaspis winkleri* as originally described by Leriche (1905). These teeth are differentiated from other odontaspids in our sample by their tall, cylindrical lateral cusplets, reduced or absent cutting edges on anterior teeth, and presence of distinctive folds at the base of the labial cusp face on lateral teeth.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1 and the basal Lisbon Formation at site ACov-11. Upper Ypresian to middle Lutetian, zones NP14 and NP15.

Genus ***Tethylamna*** Cappetta & Case, 2016

Type species

Tethylamna dunni Cappetta & Case, 2016, contact of the Lisbon and Tallahatta formations, site ACov-11, Covington County, Alabama, USA.

Tethylamna dunni Cappetta & Case, 2016

Fig. 19

Tethylamna dunni Cappetta & Case, 2016: 51, pl. 5, fig. 21.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 96 isolated teeth; Claiborne Group; ALMNH PV1989.4.126a, ALMNH PV1989.4.175a, ALMNH PV1989.4.177a, ALMNH PV1989.4.204, ALMNH PV1989.4.208a, ALMNH PV1992.28.16 (5 specimens), ALMNH PV1992.28.23, ALMNH PV1992.28.28 (3 specimens), ALMNH PV2000.1.43.1a (3 specimens), ALMNH PV2016.3.262c (2 specimens), ALMNH PV2016.3.264, ALMNH PV2016.3.264, ALMNH PV2016.4.57a, ANSP 23409, MMNS VP-8950 (6 specimens), MMNS VP-8955 (16 specimens), MSC 34624.4, MSC 37072, MSC 37073.1–2, MSC 37074.1–2, MSC 37075.1–3, MSC 37076.1–6, MSC 37077.1, MSC 37077.3–4, MSC 37077.7–8, MSC 37078.1–7, MSC 37112, MSC 37259.1–7, MSC 37294.1–5, MSC 37479, MSC

37585.1, MSC 38526, MSC 38626, SC2012.47.250 (3 specimens), WSU CC 536 (2 specimens), WSU CC 537.1, WSU CC 543.

Description

Anterior teeth with erect triangular, broad-based main cusp. Main cusp bi-convex, with smooth, continuous cutting edges extending from apex to base of crown and across lateral cusplets. Lingual crown face strongly convex, smooth; labial face flat to slightly convex, smooth. Single pair of relatively large, sharply pointed, medially curving cusplets. Anterolateral teeth with less symmetrical main cusp, and cusplets becoming wider and often two pairs developed. Root bilobate, with elongate, rounded, diverging lobes separated by V-shaped interlobe area; deep nutritive groove present on pronounced lingual root boss. Lateral teeth with broadly triangular, distally inclined main cusp that is labiolingually thinner than anterior teeth. Continuous cutting edges along main cusp, extending to main cusp base and across lateral cusplets; mesial edge straight to convex, whereas distal edge straight to slightly concave. Lingual crown face moderately convex, smooth; labial face flat with faint vertical wrinkling at crown base on some specimens. Two pairs of lateral cusplets generally present, with a third vestigial distal cusplet occasionally observed. All cusplets distally inclined, with first pair always larger than second pair, and first distal cusplet usually conspicuously larger than the mesial one. Mesial edge of largest cusplets usually convex, distal edge straight. Base of cusplets on some teeth are positioned labial to the cutting edge of the main cusp. Root lobes short, angular, strongly divergent, separated by shallow V-shaped interlobe area. Conspicuous nutritive groove on lingual root boss.

Remarks

This species was first described by Cappetta & Case (2016) based on specimens derived from the contact of the Tallahatta and Lisbon formations at site ACov-11 in Covington County, AL. These authors noted their provisional placement of the genus within the Odontaspididae. Cappetta & Case (2016: pl. 5: 1–2) figured two specimens that they identified as parasymphyseal teeth, but it is unclear to us as to why they arrived at that conclusion. If these teeth are from the lower dentition, we cannot know if they occurred on the side of the jaw symphysis, adjacent to the first anterior tooth, or if they occurred within the first dental hollow along with the anterior teeth. If the latter case, we believe the "parasymphyseal" teeth would more appropriately be identified as the first anterior position.

Anterior teeth of *Tethylamna dunni* are distinguished from those of *Hypotodus* in having a more robust main cusp with complete cutting edges. Lateral teeth of *Tethylamna* differ from those of *Brachycarcharias*,

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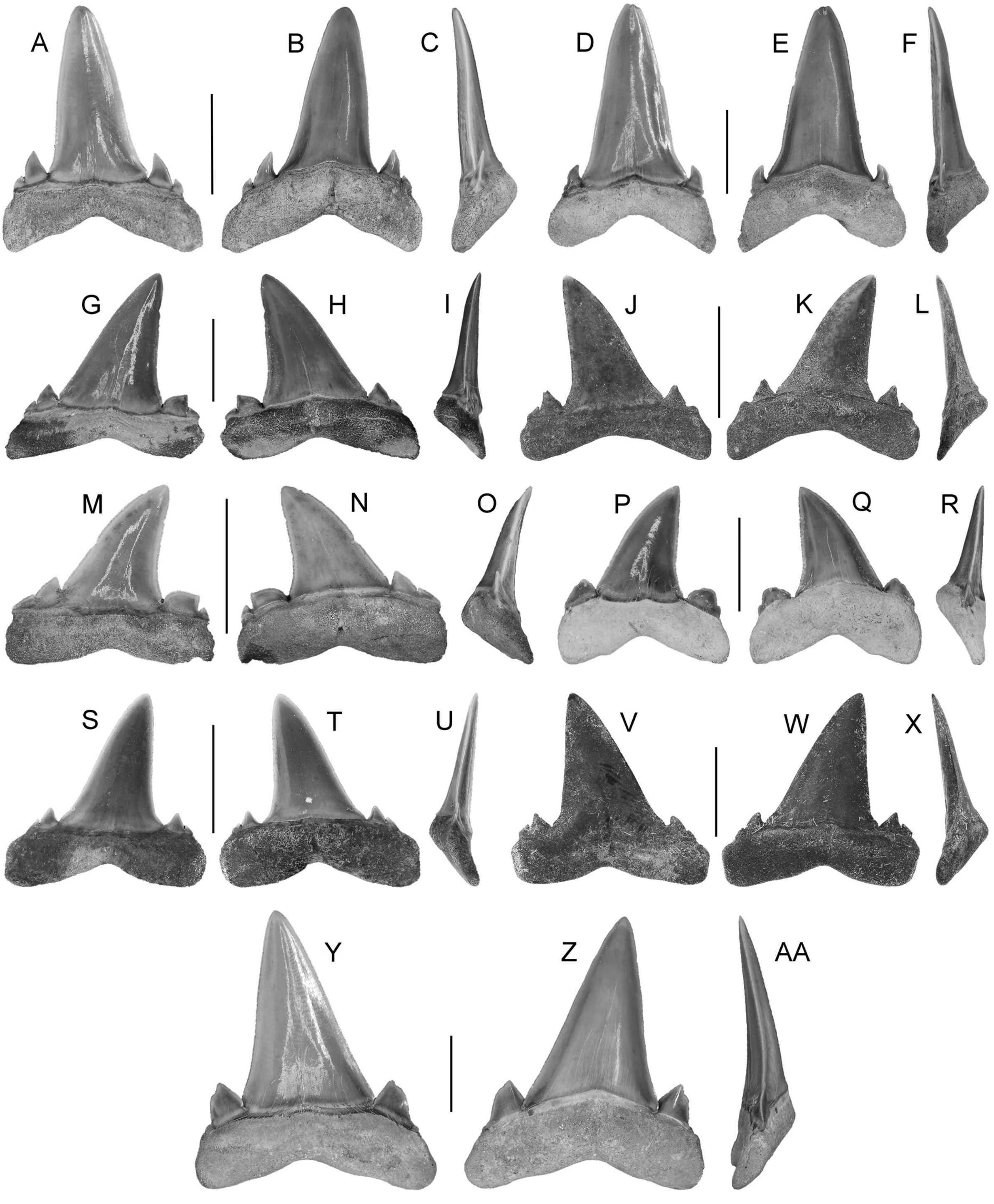
Fig. 19 (opposite page)**.** *Tethylamna* Cappetta & Case, 2016, teeth. **A–X**. *T. dunni* Cappetta & Case, 2016. **A–C**. MSC 37077.1, anterior tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 37077.4, anterior tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G–I**. MSC 37077.8, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. MSC 37078.6, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M–O**. MSC 37077.7, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **M**. Labial view. **N**. Lingual view. **O**. Mesial view. **P–R**. MSC 37585.1, lateral tooth, "upper" Lisbon Formation. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S–U**. MSC 37078.4, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V–X**. MSC 37078.5, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. — **Y–AA**. *Tethylamna* aff. *T. dunni*, MSC 34624.4, anterolateral tooth, "upper" Lisbon Formation. **Y**. Labial view. **Z**. Lingual view. **AA**. Mesial view. Scale bars = 1 cm.

Hypotodus, and *Jaekelotodus* in having larger lateral cusplets that are mesially directed, and the distal cusplet is usually larger than the mesial one. Anterior teeth of *Striatolamia* are much narrower than those of *Tethylamna*, with diminutive lateral cusplets, incomplete cutting edges, and strong lingual ornamentation. The lateral teeth differ from *Tethylamna* in having a single pair of lateral cusplets and faint lingual ornamentation.



One curious specimen in our sample, MSC 34624.4 (Fig. 19Z–AA), is here tentatively assigned to *Tethylamna* sp. Although this specimen appears to have affinities with *T. dunni*, it differs by being nearly 1.5 cm taller and wider than any of the *T. dunni* specimens we observed. This specimen also differs by having a wider crown base, and mesial and distal cusplets that are positioned labially to the main cusp. Although this characteristic has been observed on some of the *T. dunni* teeth in our sample, it generally occurs only on one side, and to a lesser degree, allowing the mesial and distal cutting edge to extend continuously across the lateral cusplets. Due to the labial position of the cusplets on MSC 34624.4, the cutting edge is not continuous across the lateral cusplets. Moreover, although two pairs of lateral cusplets are present on this specimen, the outer pair is greatly reduced compared to those on *T. dunni*, and almost appear vestigial. The more medial, larger, pair of cusplets are also curious as they are lanceolate in shape and have a strong lingual bend. On the teeth of *T. dunni*, the anterolateral and lateral teeth have cusplets that are similar in shape, but they are erect and not lingually bent. Although the cusplets on the anterior teeth of *T. dunni* are often lingually directed (as well as medially), they are cylindrical and not lanceolate such as those on MSC 34624.4. Although the slight morphological differences might suggest MSC 34624.4 represents a distinct species, we refrain from such a distinction as our sample consists of a single isolated tooth. Although we provisionally assign this tooth to *Tethylamna* sp., the collection of additional specimens might show MSC 34624.4 to be taxonomically distinct.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site AD1-1, the contact of the Tallahatta and Lisbon Formations at sites ACov-11 and ACon-6, the basal Lisbon Formation at site ACov-11, the "upper" Lisbon Formation at site ACl-3, the "upper" Lisbon Formation and basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Family Lamnidae Müller & Henle, 1838

Genus ***Macrorhizodus*** Glikman, 1964

Type species

Oxyrhina falcata Rogovich, 1860, Priabonian, Ukraine.

Macrorhizodus praecursor (Leriche, 1905)

Fig. 20

Otodus lawleyi Bassani, 1877: 80, pl. 11, figs 3–5.
Oxyrhina desori praecursor Leriche, 1905: 128.
Oxyrhina praecursor americana Leriche, 1942: 45, pl. 3, figs 6–13.

Isurus desori praecursor – White 1931: 47.
Macrorhizodus praecursor – Zharkov *et al.* 1976: 132.
Isurus praecursor americana – Thurmond & Jones 1981: 55, fig. 21.
Isurus oxyrhincus – Case 1980: 82, 99, pl. 2, figs 4–8.
Cosmopolitodus praecursor – Mustafa & Zalmout 2002: 82, pl. 1, figs 7–11.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 20 isolated teeth; Claiborne Group; ALMNH PV1989.4.32.3, ALMNH PV1989.4.15 (2 specimens), ALMNH PV1989.4.161.4 (2 specimens), ALMNH PV1989.4.6.1.1, ALMNH PV1989.4.97.2, ALMNH PV2013.4.56, ALMNH PV2016.3.142, GSA-V696, GSA-V709 (3 specimens), MSC 2372.25, MSC 2374.1, MSC 2386.1–2, MSC 34585, MSC 35759, MSC 37174, MSC 37500.

Description

All teeth with large triangular crown and lack lateral cusplets. Labial crown face flat; lingual crown face moderately to strongly convex; both crown faces smooth. Main cusp on lower anterior teeth erect and triangular; mesial and distal cutting edges bi-convex. Roots robust with foramina located on large lingual boss (indistinct nutritive groove sometimes observed). Roots on lower anterior teeth slightly higher than the crown. Lower anterior teeth sigmoidal and lingual crown face strongly convex. Lower anterior teeth with robust root protuberance and rounded root lobes; interlobe area deep and U-shaped. Anterolateral teeth with tall triangular crown; height of the crown exceeds the height of the root. Crown on anterolateral teeth have a slight distal inclination and bi-convex mesial and distal cutting edges. Lingual crown face less convex than on anterior files and have a shallower interlobe area. Root lobes on anterolateral teeth range from rounded to angular. Mesial and distal cutting edges on upper lateral teeth distinctly concave. Crown is shorter than those on anterior or anterolateral files, and more triangular. Lateral crown edges slope to the lateral edges of root. Root lobes short, distinctly angular, and flattened basally. Have shallow V-shaped interlobe area.

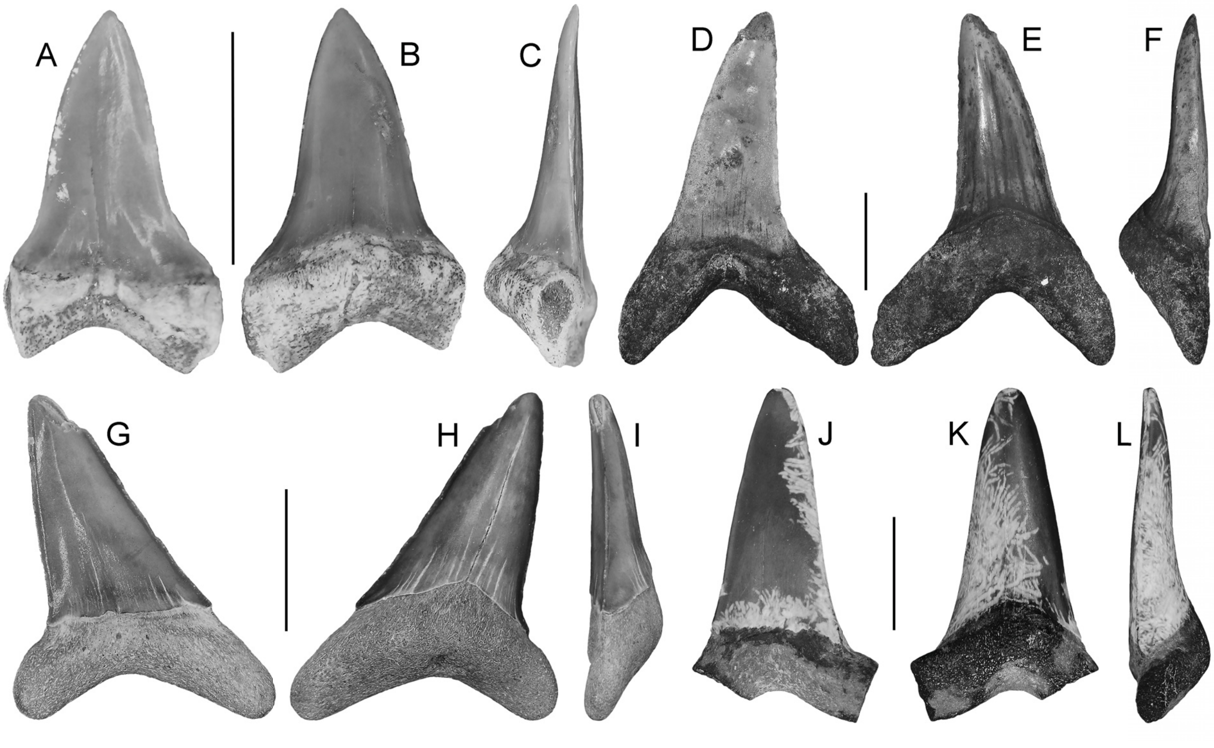


Fig. 20. *Macrorhizodus praecursor* (Leriche, 1905), teeth. **A–C**. MSC 35759, anterior tooth, lower Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Distal view. **D–F**. MSC 37174, anterolateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G–I**. MSC 37500, lateral tooth, Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. MSC 34585, anterior tooth, Gosport Sand. **J**. Labial view. **K**. Lingual view. **L**. Distal view. Scale bars = 1 cm.

Remarks

Leriche (1905) erected *Oxyrhina desori praecursor* for what he believed were Eocene teeth belonging to the stratigraphically younger *O. desori* Agassiz, 1843. Based on specimens from Priabonian deposits in Choctaw County, Alabama, Leriche (1942) later erected *Oxyrhina praecursor americana* for teeth that he thought were similar to the *praecursor* morphology, but differed by having a higher root, narrower crown, and more divergent root lobes. These morphologies were later placed within *Isurus* by White (1931), then referred by Glikman (1964) to a new genus, *Macrorhizodus*. Subsequent authors later recognized both the *praecursor* and *americana* morphologies as distinct species (see White 1956; Ward & Wiest 1990; Zhelezko & Kozlov 1999; Case & Borodin 2000a).

We reexamined the syntypes of *O. praecursor americana* of Leriche (1942: 45, pl. 3, figs 6–13) to determine the validity of this subspecies. A comparison of these eight syntypes (USNM 366462 to USNM 366469) to teeth within recent jaw sets of the extant *Isurus oxyrinchus* (Rafinesque, 1810) suggests to us that Leriche's (1942) differential characteristics (higher root, narrower crown, and more divergent root lobes) can all be attributed to heterodonty (dignathic, monognathic, and ontogenetic) and intraspecific variation. Thus, it is our opinion that the *americana* morphology is a junior synonym of *Macrorhizodus praecursor*, and we dispense with the subspecies name and refer all the specimens in our sample to *M. praecursor*. The specimens in our sample differ from those of *Macrorhizodus nolfi* Zhelezko & Kozlov, 1999 by having smooth enameloid shoulders and by lacking vestigial cusplets (Carlsen & Cuny 2014). Finally, although Glickman (1964) placed *M. praecursor* within its own family, the Lamiostomatidae, we follow Nelson *et al.* (2016) in placing this taxon within the Lamnidae.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at site ACov-11, the "upper" Lisbon Formation at site ACl-3, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, and the Gosport Sand at sites ACl-15 and ACh-21. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Order Carcharhiniformes Compagno, 1973
Family Scyliorhinidae Gill, 1862
Subfamily Premontreinae Cappetta, 1992
Genus *Premontreia* Cappetta, 1992

Subgenus ***Oxyscyllium*** Noubhani & Cappetta, 1997

Type species

Premontreia (*Premontreia*) *degremonti* Cappetta, 1992, Ypresian, France.

Premontreia* (*Oxyscyllium*) *subulidens (Arambourg, 1952)

Fig. 21

Scyliorhinus subulidens Arambourg 1952: 121, figs 5–19.

Premontreia (*Oxyscyllium*) *subulidens* – Noubhani & Cappetta 1997: 55, pl. 21:1–11.
Scyliorhinus sp. – Maisch *et al.* 2014: 192, fig. 3:17–19.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 isolated tooth; Claiborne Group; ANSP 23421.

Description

Small tooth measuring 5.0 mm in total height as preserved. Main cusp narrow, triangular, sharply tapering apically. Labial face flat and smooth, whereas lingual face very convex, smooth. Smooth cutting edges reach base of cusp. Single pair of broad and triangular lateral cusplets that are diverging. Root with very short, reniform lobes that are bisected by deep and elongate nutritive groove. Basal attachment surface flat with heart-shaped outline.

Remarks

The single specimen in our sample, ANSP 23421, was derived from the Tallahatta/Lisbon contact zone and was previously reported by Maisch *et al.* (2014). Although the authors indicated that the tooth was comparable to *Premontreia*, they ultimately identified it as *Scyliorhinus* sp. We reexamined the specimen and believe that it is *Premontreia* and can be referred to the subspecies *Oxyscyllium* due to the large size of the lateral cusplets. ANSP 23421 is virtually identical in size and morphology to specimens of *P.* (*O.*) *subulidens* illustrated by Arambourg (1952) and Noubhani & Cappetta (1997: pl. 21, 5), and we therefore attribute the specimen to this species.

Among the thousands of Claibornian specimens we personally examined, ANSP 23421 is the only tooth that can be identified as *Premontreia*. However, a second specimen reported by Cappetta & Case (2016: pl. 9, fig. 11) was identified by them as *Premontreia* (*Premontreia*) *degremonti* based on the diminutive size of the lateral cusplets. We could only examine the specimen via publication, but the morphology is consistent with the species as described and illustrated by Cappetta (1992), although the tooth does appear to be ablated. It would appear to be serendipitous that two species of *Premontreia* are represented in a total sample size of two teeth from the Tallahatta/Lisbon contact zone, and additional specimens are needed to corroborate these identifications.

Stratigraphic and geographic range in Alabama

ANSP 23421 was collected from the contact of the Tallahatta and Lisbon formations at site ACon-6. Cappetta & Case (2016) reported a specimen from the contact of the Tallahatta and Lisbon formations at site ACov-11 that they referred to *Premontreia* (*Premontreia*) *degremonti*. Lower Lutetian, zones NP 14 and NP15.

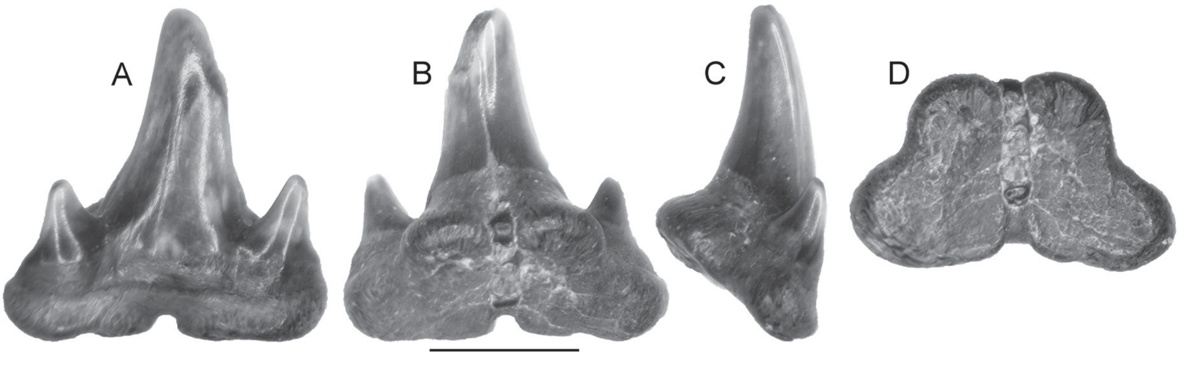


Fig. 21. *Premontreia* (*Oxyscyllium*) *subulidens* (Arambourg, 1952), tooth. **A–D**. ANSP 23421, lateral tooth, Tallahatta/Lisbon contact zone. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D**. Basal view. Scale bar = 2 mm.

Genus ***Stenoscyllium*** Noubhani & Cappetta, 1997

Type species

Stenoscyllium priemi Noubhani & Cappetta, 1997, Ypresian, Morocco.

Stenoscyllium cf. ***S. priemi*** Noubhani & Cappetta, 1997
Fig. 22

Stenoscyllium priemi Noubhani & Cappetta, 1997: 70, pl. 28, figs 8–11, text-fig. 13.

Scyliorhinus subulidens – Arambourg 1952: pl. 23, figs 2–4.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 3 isolated teeth; Claiborne Group; MSC 35760.1–2, MSC 38527.

Description

Teeth distinctively mesiodistally compressed. Tooth crown tall and triangular with a strong lingual bend. Both lingual and labial crown faces convex with smooth enameloid. Prominent mesial and distal cutting edges present on the upper two-thirds of crown, but not reaching the crown base. Basal labial crown face slightly overhangs root. Single pair of cusplets present on some teeth. Root holaulacorhize, with closely spaced, rounded lobes. In lingual view, root height almost equal to crown height. Lingual root face with pronounced protuberance bisected by nutritive groove. Large nutritive foramina present within nutritive groove. Individual foramina located on upper-half of lingual and labial root faces. Lingual, labial, and basal root faces distinctly flat.

Fig. 22. *Stenoscyllium* cf. *S. priemi* Noubhani & Cappetta, 1997, teeth. **A**–**C**. MSC 35760.1, lower Tallahatta Formation. **A**. Labial view. **B**. Mesial view. **C**. Lingual view. **D**–**F**. MSC 35760.2, lower Tallahatta Formation. **D**. Labial view. **E**. Distal view. **F**. Lingual view. Scale bars = 2 mm.

Remarks

In his type suite for *Scyliorhinus subulidens*, Arambourg (1952) included several teeth that he considered to represent anterior jaw positions. Working with new material recovered from lower Eocene deposits in Morocco, Noubhani & Cappetta (1997) erected *Stenoscyllium priemi* to include the teeth Arambourg (1952) thought were anterior teeth of the *subulidens* species. The genus *Stenoscyllium* is currently monospecific, with the only species being *S. priemi*. Although the roots are abraded and the cusplets are not preserved on all the specimens in our sample, their overall morphology matches that of *S. priemi* as figured by Arambourg (1952: pl. 23), Noubhani & Cappetta (1997: pl. 28) and Cappetta (2012: fig. 266). Due to the preservation and limited sample size, our specimens are only tentatively assigned to this species.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1. Upper Ypresian/ lower Lutetian, Zone NP14.

Family Triakidae Gray, 1851

Genus ***Galeorhinus*** de Blainville, 1816

Type species

Squalus galeus Linnaeus, 1758, Recent.

Galeorhinus aff. ***G. duchaussoisi*** Adnet & Cappetta, 2008

Fig. 23A–F, K–M

Galeorhinus duchaussoisi Adnet & Cappetta, 2008: 435, fig. 2.

cf. *Galeorhinus* sp. – Clayton *et al.* 2013: fig. 3k.
Galeorhinus duchaussoisi – Cappetta & Case 2016: 60, pl. 9, figs 7–8.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 10 isolated teeth; Claiborne Group; ALMNH PV1989.4.219d (3 specimens), MSC 35756.1–2, MSC 37353.4, MSC 37691, SC2012.47.56 (3 specimens).

Description

Teeth mesiodistally wider than tall, with elongated mesial cutting edge that is sinuous in anterolateral jaw positions but slightly convex in lateral files. Distal cutting edge short, vertical or inclined, forms triangular cusp with mesial edge. Cusp distally inclined in all tooth positions; apex on some teeth upturned. Distinct distal heel bears one to six triangular distal cusplets. Cusplets decrease in size laterally; largest, most mesial, cusplet well separated from main cusp. Distal cusplets often less conspicuous than the others, often forming an irregular cutting edge. Irregular serrations occur on lower half of mesial cutting edge of anterolateral teeth but absent on lateral files. Labial and lingual crown faces generally smooth, but faint labial folds observed on some teeth. Labial crown face overhangs the root with a pronounced bulge. Roots low with very divergent lobes. Lingual root face distinctly flat, with deep and wide nutritive groove.

Remarks

Five species of Paleogene *Galeorhinus* have been reported in the literature, including *G. duchaussoisi* Adnet & Cappetta, 2008; *G. louisi* Adnet & Cappetta, 2008; *G. mesetaensis* Noubhani & Cappetta, 1997; *G. minutissimus* (Arambourg, 1935); and *G. ypresiensis* (Casier, 1946). Averianov & Udovichenko (1993) erected *Galeorhinus tenius* based on specimens from the Eocene of Uzbekistan, but this species has not been formally described or figured so it is considered as a *nomen nudum*. Cappetta & Case (2016) were the first to report the occurrence of *G. duchaussoisi* in the Eocene of Alabama, and most of the specimens in our sample appear to fit the type description for this taxon in that they range between 5.0 to 7.0 mm in greatest width and have up to six pairs of lateral cusplets. However, one specimen in our sample, MSC 37353.4 (Fig. 23K–M), measures only 2.2 mm in width and has only two distal cusplets. This tooth lacks any labial ornamentation, separating it from *G. louisi* and *G. mesetaensis*, and also lacks any denticulations on its mesial edge, separating it from *G. ypresiensis*. Although this tooth is complete, assigning it to either *G. duchaussoisi* or *G. minutissimus* has proven to be problematic.

MSC 37353.4 appears to correspond well to the *G. minutissimus* specimens described and figured by Noubhani & Cappetta (1997: 81, pl. 43, figs 2–14) as it falls within the size range they provided for this species (1.87 to 3.79 mm in greatest width) and, as claimed by the authors, the teeth of this taxon never

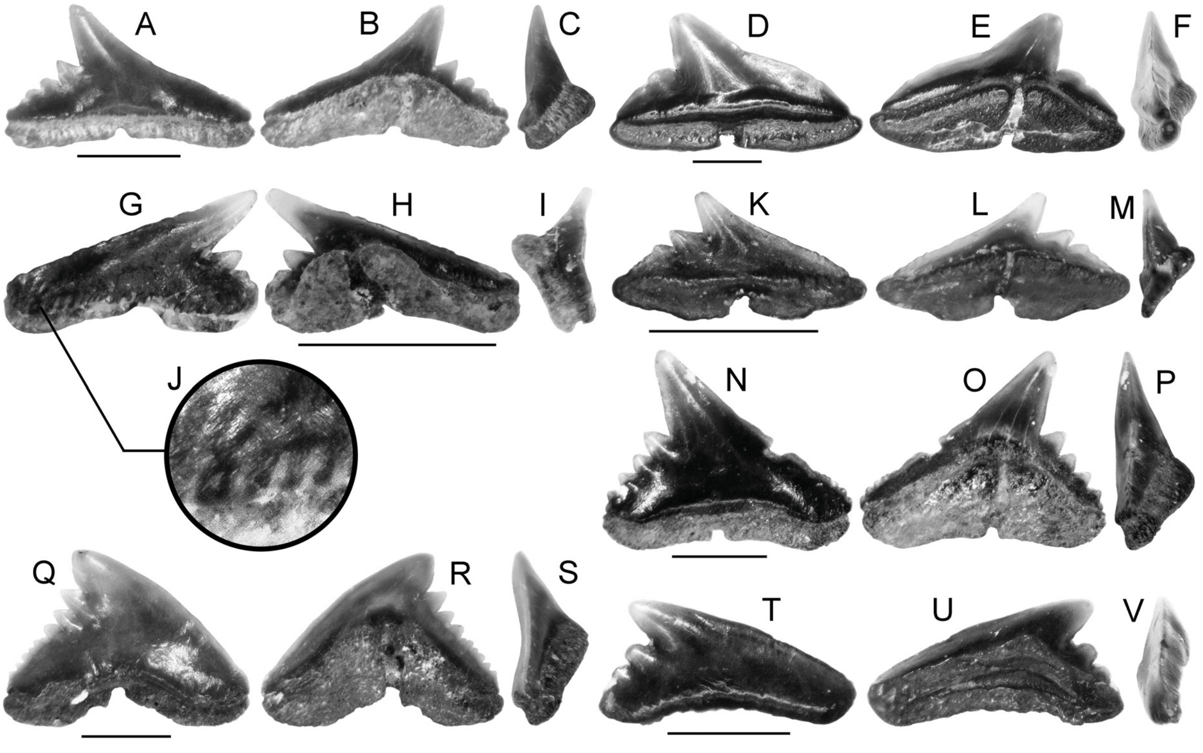


Fig. 23. *Galeorhinus* de Blainville, 1816 and *Pachygaleus* Cappetta, 1992, teeth. **A–F**. *Galeorhinus* aff. *G. duchaussoisi* Adnet & Cappetta, 2008. **A–C**. MSC 35756.1, lower Tallahatta Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 37691, basal Lisbon Formation. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. — **G–J**. *G. louisi* Adnet & Cappetta, 2008, MSC 37353.2, lower Tallahatta Formation. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J**. Close–up of labial wrinkling. — **K–M**. *G.* aff. *G. duchaussoisi*, MSC 37353.4, Tallahatta Formation. **K**. Labial view. **L**. Lingual view. **M**. Mesial view. — **N–P**. *Galeorhinus ypresiensis* (Casier, 1946), MSC 37693.1, Gosport Sand. **N**. Labial view. **O**. Lingual view. **P**. Mesial view. — **Q–V**. *Pachygaleus lefevrei* (Diameries, 1891). **Q–S**. MSC 37688, basal Lisbon Formation. **Q**. Labial view. **R**. Lingual view. **S**. Mesial view. **T–V**. MSC 35763, lower Tallahatta Formation. **T**. Labial view. **U**. Lingual view. **V**. Mesial view. Scale bars = 2 mm.

have more than three distal cusplets. These characteristics, however, contrast with the type description by Arambourg (1935) for *G. minutissimus* in which he described the teeth as not exceeding 5.0 mm in width and having up to five or six distal cusplets. Arambourg (1952: 155–157, pl. 24, figs 29–37) later provided a more complete description of *G. minutissimus* and included additional figures. The two aforementioned characteristics were not only reiterated by Arambourg (1952), but are clearly visible on several of the teeth he figured in both 1935 and 1952. Aside from specimen MSC 37353.4, the remaining teeth in our sample exceed 5.0 mm in width, the maximum size for *G. minutissimus* per Arambourg (1935, 1952).

To further differentiate these species, Adnet & Cappetta (2008) noted that the main cusp on the teeth of *G. minutissimus* are more slender than those on *G. duchaussoisi*. However, aside from size, the characteristics provided by Adnet & Cappetta (2008) to separate *G. duchaussoisi* from *G. minutissimus* appear ambiguous when dealing with specimens smaller than 5.0 mm in width. In a comparison of the type suites and descriptions for both taxa, the number of distal cusplets can vary from between one and six for both taxa depending on tooth position (see Arambourg 1935: pl. 10, figs 13–15, 1952: pl. 24, figs 29–37; Adnet & Cappetta 2008: fig. 2). Furthermore, their size ranges overlap from 2.0 to 5.0 mm for *G. minutissimus* and 2.8 to 6.7 for *G. duchaussoisi*, again depending on tooth position. These characteristics, however, could be a result of ontogenetic heterodonty, as it has been reported that within Recent *Galeorhinus* specimens, the number of distal cusplets on the teeth increases as the teeth become larger and more robust with age (Compagno 1988). Such changes could be the result ontogenetic dietary shifts, which have been well documented in extant populations of *Galeorhinus galeus* (Linneaus, 1758) (see Lucifora *et al.* 2006; Ebert & Stehmann 2013). As a result, there is a distinct possibility that the teeth of *G. minutissimus* represent the juvenile form of *G. duchaussoisi*, thus compounding the difficulty in differentiating smaller specimens. Furthermore, both species have been reported from Ypresian and Lutetian deposits (see Noubhani & Cappetta 1997; Adnet & Cappetta 2008; Cappetta & Case 2016), indicating that they have stratigraphic as well as morphological overlap. Regarding the specimens in our sample, teeth with the morphology described above are provisionally assigned to *Galeorhinus* aff. *G. duchaussoisi* because a majority are wider than 5.0 mm, exceeding the maximum size of *G. minutissimus* as reported by Arambourg (1935, 1952).

White (1956) and Thurmond & Jones (1981) reported the occurrence of *Galeorhinus recticonus claibornensis* White, 1956 from the Gosport Sand from Clarke and Monroe counties in Alabama. This taxon was later placed within the genus *Abdounia* by Cappetta (1980a), and we refer this species to a new genus described in detailed below. White (1956) and Thurmond & Jones (1981) also reported the occurrence of *Galeorhinus* cf. *falconeri* from the Tallahatta Formation and Gosport Sand in Monroe County and the Jackson Group strata in Clarke County. Although neither White (1956) nor Thurmond & Jones (1981) figured their specimens, *G. falconeri* was subsequently referred to *Physogaleus* by Adnet & Cappetta (2008) (see *Physogaleus secundus* below).

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the Tallahatta Formation at site AMo-8, the basal Lisbon Formation at site ACov-11, and the Gosport Sand at site ACh-21. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Galeorhinus louisi Adnet & Cappetta, 2008

Fig. 23G–J

Galeorhinus louisi Adnet & Cappetta, 2008: 438, fig. 4.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 2 isolated teeth; Claiborne Group; MSC 37353.1–2.

Description

Teeth small, not exceeding 2.2 mm in mesiodistal width; distal-most extent of main cusp in line with, or slightly exceeding, distal extent of heel. Mesial cutting edge elongate, ranges from straight to slightly sinuous; distal edge much shorter, slightly convex, forms triangular and distally inclined cusp with mesial edge. Prominent distal heel bears one or two cusplets, which are not well differentiated from the heel itself. Lingual crown face smooth, strongly convex. Labial face with bulbous base that overhangs the root; very short folds and wrinkles at base that coalesce apically to form a transverse ridge (easily seen in profile view). Root high and thick, with highly diverging and rounded lobes; lobes separated by shallow and triangular interlobe area. Lingual root face bisected by deep nutritive groove.

Remarks

The teeth in our sample appear conspecific to the holotype of *G. louisi* Adnet & Cappetta, 2008 in that they have extensive folds and notches present along the entire width of the labial crown base. This ornamentation is indistinct or absent on the teeth of *G. minutissimus*, present only beneath the heels on the teeth of *G. mesetaensis*, and is much less extensive on the teeth of *G. duchaussoisi* (see above) and *G. ypresiensis* (see below).

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Tallahatta Formation at site AMo-8. Lower Lutetian, Zone NP14.

Galeorhinus ypresiensis (Casier, 1946)

Fig. 23N–P

Eugaleus ypresiensis Casier, 1946: 86–89, pl .1, fig. 11a–t.

Galeorhinus ypresiensis – Kemp 1982: pl. 9, fig. 4.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 3 isolated teeth; Claiborne Group; MSC 37693.1–2, MSC 37898.

Description

Teeth do not exceed 4.5 mm in mesiodistal width. Main cusp thin, triangular, and distally inclined. Mesial edge of main cusp ranges from straight to slightly concave. Distal edge of main cusp slightly convex. Large distal heel with four-to-five triangular distal cusplets, which decrease in size distally. A series of weak serrations present on mesial cutting edge, most prominent on the lower third. Labial crown face flat, bulbous basally and overhanging root, with faint wrinkling at the mesial half of the labial crown foot. Lingual crown face strongly convex. Root lobes are divergent and rounded. Interlobe area shallow. Root high and thick lingually and covers much of the crown face. Nutritive grooves deep and wide; forms a basal notch on the root base.

Remarks

The specimens in our sample are similar in overall morphology to those of *Galeorhinus duchaussoisi*, *G. louisi*, and *G. mesetaensis*, but are easily differentiated by having prominent mesial denticulations.

Furthermore, the teeth of *G. ypresiensis* lack heavy crenulations across the labial crown base as seen on the teeth of *G. louisi* (see above). The teeth of *G. ypresiensis* are further differentiated from those of *G. mesetaensis* by the complete absence of ornamentation on the lingual crown face, and teeth of *G. duchaussoisi* (see above) can attain larger overall sizes (up to 6.7 mm in mesiodistal width as opposed to 4.5 mm for *G. ypresiensis*). The teeth of *G. ypresiensis* are similar to some tooth positions of *Physogaleus* (see below) but can be differentiated by having a more convex labial crown face and a more bulbous labial crown base that overhangs the root.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Gosport Sand at site ACl-15. Middle Bartonian, Zone NP17.

Genus ***Pachygaleus*** Cappetta, 1992

Type species

Galaeus lefevrei Daimeries, 1891, Ypresian, Belgium.

Pachygaleus lefevrei (Daimeries, 1891)

Fig. 23Q–V

Galaeus lefeveri Daimeries, 1891: 74.
Eugaleus falconeri White, 1926: 73.

Galeus lefevrei – Leriche 1905: 136, pl. 8, figs 54–58.
Eugaleus lefevrei – Casier 1946: 84, pl. 1, fig. 13a–b.
Galeorhinus lefevrei – Casier 1966: 86, pl. 8, figs 4–6.
Pachygaleus lefevrei – Baut & Genault 1995: 206, pl. 7, figs 5–6, pl. 8, figs 1–2.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 9 isolated teeth; Claiborne Group; MSC 37688, MSC 35758.1–2, MSC 35763, MSC 38289.1–2, MSC 38487, NJSM 24024, WSU 5002.

Description

Teeth mesiodistally wider than tall. Crown labiolingually thick and conspicuously overhangs the root labially. Labial crown face flat to concave; lingual face strongly convex. Main cusp distally directed, formed from intersection of elongate, convex mesial cutting edge and much shorter distal edge. Elongated distal heel often concave, may be flat or slightly sigmoidal on lateral teeth. Distal heel with three-to-10 pronounced cusplets, which are distally directed and decreasing in size away from cusp. Crown enameloid generally smooth, but short longitudinal folds sometimes located at base of labial crown face on extreme lateral teeth or juveniles. Root thick and bulbous, bilobate, with widely diverging and rounded lobes; shallow, U-shaped interlobe area. Wide and deep nutritive groove located on lingual root face; large central foramen occurs within groove. Additional foramina present on basal portion of lingual root face.

Remarks

The genus *Pachygaleus* currently only contains the species *P. lefevrei* (Daimeries, 1891), and all of our specimens are assigned to this taxon. The *Pachygaleus* teeth in our sample were separated from those of *Galeorhinus* by their larger size, more convex labial crown face, wider U-shaped interlobe area and, in the case of the anterolateral teeth, up to 10 cusplets on the distal heel.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at site ACh-14, and the basal Lisbon Formation at site ACov-11. Upper Ypresian to lower Lutetian, zones NP14 and NP15.

Family Hemigaleidae Compagno, 1984

Genus ***Hemipristis*** Agassiz, 1843

Type species

Hemipristis serra Agassiz, 1843, Miocene, Germany.

Hemipristis curvatus Dames, 1883

Fig. 24

Hemipristis curvatus Dames, 1883: 140, pl. 3, fig. 4a–b.
Hemipristis wyattdurhami White, 1956: 134, text-pl. figs 40–47, pl. 11, fig. 4.

Hemipristis serra – Woodward 1889: 451.
Hemipristis wyattdurhami – Thurmond & Jones 1981: 63, fig. 29.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 6 isolated teeth; Claiborne Group; ALMNH PV1989.4.189, ALMNH PV1989.4.220, ALMNH PV1989.4.221, MSC 2376.1–2, MSC 2377.

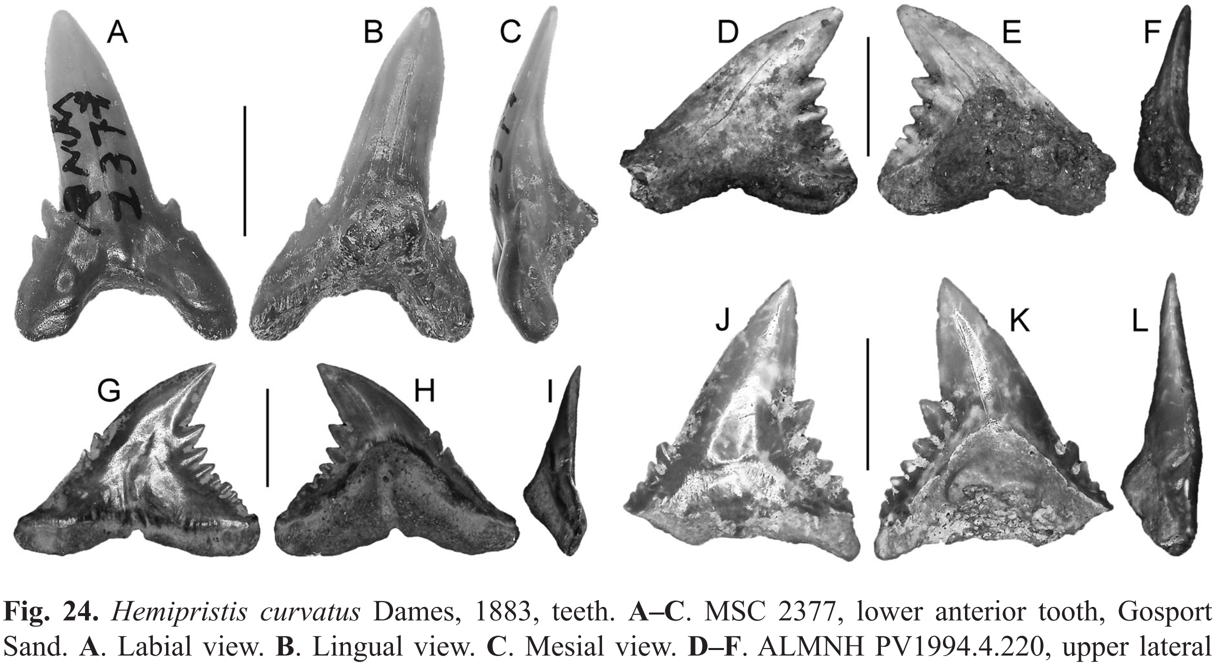


Fig. 24. *Hemipristis curvatus* Dames, 1883, teeth. **A**–**C**. MSC 2377, lower anterior tooth, Gosport Sand. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D**–**F**. ALMNH PV1994.4.220, upper lateral tooth, Gosport Sand. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G**–**I**. ALMNH PV1994.4.221, upper lateral tooth, Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J**–**L**. ALMNH PV1994.4.189, lower lateral tooth, Gosport Sand. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. Scale bars = 5 mm.

Description

Upper anterior teeth have high, triangular crown. Mesial cutting edge elongate, slightly convex, bearing four large serrae basally but otherwise smooth; basal serrae decrease in size towards crown foot. Upper half of the distal edge smooth, vertical, whereas basal half bears five large serrae decreasing in size towards the crown foot. Mesial edge and upper half of the distal edge form conspicuous cusp that is slightly distally inclined. Root has a large lingual boss bisected by a nutritive groove. Upper lateral teeth have broad-based crown bearing distally curving cusp. Mesial cutting edge very convex, smooth except for one-or-two medially located serrae. Apical one-third of distal edge smooth, forms distally inclined cusp along with mesial edge. Lower two-thirds of distal edge formed into heavily serrated oblique heel; five-to-eight serrae present that decrease in size basally. Root bilobate; very short and highly diverging lobes separated by V-shaped interlobe area; wide, shallow lingual nutritive groove.

Remarks

Woodward (1889: 451) originally reported a tooth collected from Eocene deposits in Clarke County, AL as *Hemipristis serra* Agassiz, 1843, noting, however, that the specimen was "doubtfully of this species." This specimen was later reexamined by White (1956) and referred to a new species, *Hemipristis wyattdurhami*, a taxon that Cappetta (1987) later designated as a junior synonym of *H. curvatus* Dames, 1883. Teeth of *H. serra* attain much larger sizes than those of *H. curvatus*, and the mesial cutting edge on the upper teeth and lower lateral teeth of *H. serra* bear more denticles than do teeth of *H. curvatus*. In contrast, the mesial edge on *H. curvatus* teeth in these jaw positions are smooth or with few very weak denticles. *H. serra* is also widely regarded as a Neogene taxon (see Cappetta 2012).

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Gosport Sand at site ACh-21. Middle Bartonian, Zone NP17.

Family Carcharhinidae Jordan & Evermann, 1896

Genus ***Carcharhinus*** de Blainville, 1816

Type species

Carcharhinus melanopterus Quoy & Gaimard, 1824, Recent.

Carcharhinus mancinae sp. nov.

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Figs 25–26

Galeocerdo alabamensis – Thurmond & Jones 1981: 63, fig. 28, left.
Galeocerdo latidens – Manning 2003: 374, fig. 21.3.2.

Etymology

The species name is dedicated to the late Lois Nickey Mancin of Birmingham, Alabama, USA, in honor of her years of volunteer service to MSC and her life-long dedication to science education.

Material examined

Holotype

UNITED STATES OF AMERICA – **Alabama** • upper right lateral tooth; Claiborne Group; MSC 39036. (Fig. 25A–F).

Paratypes

UNITED STATES OF AMERICA – **Alabama** • 1 upper left anterior tooth; same collection data as for holotype; MSC 39037 (Fig. 25G–K) • 1 upper left posterior tooth; same collection data as for holotype; MSC 39038 (Fig. 25V–Z) • 1 lower right anterior tooth; same collection data as for holotype; MSC 39040 (Fig. 25L–P) • 1 lower left lateral tooth; same collection data as for holotype; MSC 39041 (Fig. 25Q–U).

Referred material

UNITED STATES OF AMERICA – **Alabama** • 98 isolated teeth; Claiborne Group; ALMNH PV1993.3.408, ALMNH PV1996.1.9, ALMNH PV2016.3.74, MSC 188.15, MSC 188.27, MSC 188.40, MSC 188.89, MSC 12653, MSC 12728, MSC 36952.1–3, MSC 37448, MSC 37502, MSC 37522.1–3, MSC 37532, MSC 37896, MSC 38416, MSC 38423, MSC 38424.1–9, MSC 38425.1–2, MSC 38426.2–4, MSC 38426.6–20, MSC 38426.22–58, MSC 38503.1–5, MSC 38546, MSC 38558.1–2, MSC 38798, MSC 38863 (6 specimens).

Stratum typicum

Basal Gosport Sand, middle Bartonian, Zone NP17.

Locus typicus

Site ACl-4, Clarke County, Alabama, USA.

Differential diagnosis

This species can be differentiated from most other Claiborne Group chondrichthyans by the presence of compound and/or double serrations, which are absent on all taxa except *Galeocerdo clarkensis* White, 1956 and *Otodus* (*Carcharocles*) sp. Further separated from the carcharhiniforms *Abdounia* Cappetta, 1980, *Galeorhinus*, *Hemipristis*, *Negaprion*, *Pachygaleus*, and *Physogaleus* by the presence of fine mesial and distal serrations that extend to the apex of the main cusp. Differentiated from *Galeocerdo clarkensis* by the presence of erect and triangular upper anterior teeth, lower lateral teeth with a narrower and more erect crown, uniformly concave distal cutting edge with compound serrations medially, and lateral teeth have a more pronounced and 'pinched' lingual root protuberance. This species is separated from the following Paleogene *Carcharhinus* sensu stricto Underwood & Gunter (2012) species: the lower Lutetian *Carcharhinus marçaisi* from northern Africa (Arambourg 1952) by having serrated cutting edges; the middle Eocene *Carcharhinus* sp. from Jamaica (Underwood & Gunter 2012), the middle-to-late Eocene *Carcharhinus* sp. from Egypt (Underwood *et al.* 2011), and the middle-to-late Eocene *Carcharhinus underwoodi* and *Carcharhinus* sp. from Madagascar (Samonds *et al.* 2019) by having compound and/or double serrations and a more 'pinched' and pronounced lingual root boss; the Priabonian *Carcharhinus balochensis* from Pakistan Adnet *et al.* 2007 by having a less concave distal cutting edge, shorter and mesiodistally thinner crown in all anterior and lateral tooth positions, and pointed (as opposed to rounded) serrations on the lower two-thirds of the crown; and the Chattian *Carcharhinus perseus* Adnet *et al.*, 2007 by having compound serrations and mesiodistally narrower crown in all tooth positions.

Description

Upper anterior teeth. Teeth with broad, triangular crown. Crown erect, slightly inclined distally in anterolateral files. Mesial cutting edge elongate, slightly concave medially, slightly convex apically. Distal cutting edge elongate, concave to slightly angular medially, upper half weakly convex but less so than mesial edge. Labial crown face weakly concave medially; lingual face strongly and evenly convex. Base of the labial crown face is slightly bulbous. Crown enameloid smooth. Mesial and distal serrations coarse, weakly compound (by compound we mean one or more additional serrae located on the primary serration) and/or doubly serrate (where a serration is partially divided), extending along entire length of cutting edges. Largest mesial and distal serrations located medially on the cutting edges; serrations decrease in size both apically and basally. Root bilobate, with widely diverging, angular lobes that do not extend past mesial and distal ends of crown; distal root lobe mesiodistally wider than mesial root lobe. Root significantly higher lingually than labially. V-shaped lingual dental band. Lingual root protuberance is not well demarcated, but with wide, shallow nutritive groove.

LOWER ANTERIOR TEETH. Teeth with tall, mesiodistally narrow, triangular main cusp. Crown erect; apex with slight labial bend; cusp distally inclined in anterolateral files. Mesial and distal cutting edges elongate, sinuous, concave medially but convex basally and apically. Labial crown face is flat; lingual face is strongly convex. Mesial and distal cutting edges coarsely serrated along entire length, compound and/or doubly serrate; largest serrations located medially on both edges, reducing in size apically and basally. Root lobes short, rounded, strongly divergent, labiolingually flattened**;** distal root lobe slightly larger than mesial lobe. Interlobe area shallow, U-shaped. Root higher lingually than labially; lobes extend slightly beyond mesial and distal crown margins. Conspicuous but low lingual root protuberance bisected by deep nutritive groove.

UPPER AND LOWER LATERAL TEETH. Teeth with tall, triangular crown; with distally inclined cusp. Labial crown face flat, lingual face convex; both crown faces smooth. Mesial cutting edge elongate, slightly concave near the base but apical half convex. Distal cutting edge elongate, with straight apical half, strongly concave medially, transitioning to straight oblique heel. Medial concavity uniformly curving, not angular; distal heel not distinctively separated from apical half of cutting edge. Cutting edges complete across entire edge, coarsely serrated; serrations compound and/or doubly serrate. Mesially, largest serrations are located on the basal half of cutting edge, becoming finer apically. On distal edge, largest serrations located medially, slightly decreasing in size basally, significantly finer on apical half. First large serration on distal edge always compound. Root lobes short, rounded, strongly divergent. Root higher lingually than labially, with lobes extending slightly past the lateral extent of the crown. Interlobe area shallow and U-shaped. Pronounced lingual root boss bisected by deep nutritive groove.

Lower lateral teeth are similar to those in upper lateral files but differ by the following: main cusp mesiodistally narrower and shorter; mesial edge straighter; upper half of the distal edge of main cusp is more convex; and interlobe area is shallow and V-shaped rather than U-shaped.

UPPER POSTERIOR TEETH. Teeth mesiodistally wider than tall, with short, distally inclined cusp. Mesial cutting edge elongate, uniformly convex, serrated along entire length. Basal two-thirds of the distal cutting edge is weakly convex; apical one-third weakly convex. Mesial serrations generally coarsest medially; much finer basally and apically. Distal cutting edge very short, straight to weakly convex, finely serrated. Distinct distal heel forms notch with distal cutting edge; heel very coarsely serrated; serrations decrease in size distally. Serrations on cutting edges compound and/or doubly serrate. Labial crown face flat to slightly convex; lingual face is more strongly convex; both crown faces lack ornamentation. Root lobes very short, rounded, highly diverging. Very shallow U-shaped interlobe area. Weak lingual protuberance bisected by a deep nutritive groove.

Remarks

The fossil record of *Carcharhinus* (and *Carcharhinus*-like taxa) was reviewed by Adnet *et al.* (2007), Cappetta (2012), and Underwood & Gunter (2012). Although the origins of *Carcharhinus* sensu stricto Underwood & Gunter (2012) have not been resolved, the oldest representative of the genus appears to be the early Lutetian *Carcharhinus marçaisi* (Arambourg, 1952). However, the syntypes for this taxon (Arambourg 1952: pl. 26, figs 31–48) appear better aligned with our definition of *Negaprion* (see below) as they are unserrated, have a narrow main cusp, and have an asymmetrical T-shaped outline.

In contrast, the *mancinae* morphology described herein is appropriately assigned to *Carcharhinus* sensu stricto because it has upper teeth with a broader main cusp than those in the corresponding lower files, and all cutting edges are completely serrated to the apex. When compared to extant *Carcharhinus* jaw sets at MSC, SC, and figured in Voigt & Weber (2011), the teeth in our sample appear most similar to those of *Carcharhinus amboinensis* (Müller & Henle, 1839) and *Carcharhinus leucas* (Müller & Henle, 1839), the two members of the *leucas*-*amboinensis* species group as defined by Garrick (1982). These two extant taxa have similar dentitions that are characterized by having broadly triangular upper teeth, narrower crowned triangular lower teeth that are more erect, and completely serrated cutting edges. The similarities between the *C. mancinae* sp. nov. teeth in our sample and the extant *C. amboinensis* and *C. leucas* led us to place our fossil teeth into the generalized tooth groups described above.

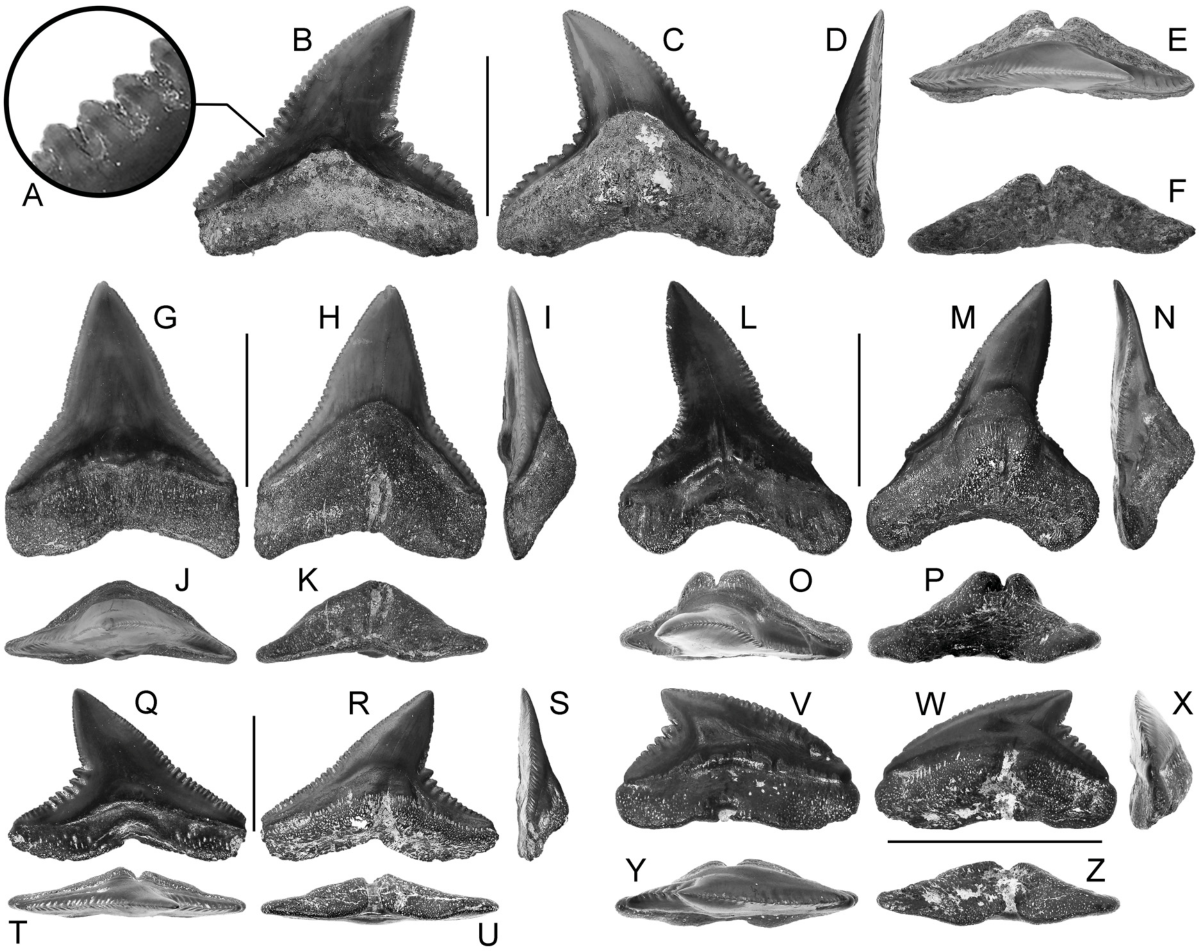


Fig. 25. *Carcharhinus mancinae* sp. nov. hypodigm. **A–F**. MSC 39036, holotype, upper right lateral tooth, basal Gosport Sand. **A**. Close–up of mesial compound serrations. **B**. Labial view. **C**. Lingual view. **D**. Mesial view. **E**. Oral view. **F**. Basal view. **G–K**. MSC 39037, paratype, upper left anterior tooth, basal Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J**. Oral view. **K**. Basal view. **L–P**. MSC 39040, paratype, lower right anterior tooth, basal Gosport Sand. **L**. Labial view. **M**. Lingual view. **N**. Mesial view. **O**. Oral view. **P**. Basal view. **Q–U**. MSC 39041, paratype, lower right lateral tooth, basal Gosport Sand. **Q**. Labial view. **R**. Lingual view. **S**. Mesial view. **T**. Oral view. **U**. Basal view. **V–Z**. MSC 39038, paratype, upper left posterior tooth, basal Gosport Sand. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. **Y**. Oral view. **Z**. Basal view. Labial at bottom in oral and basal views. Scale bars = 1 cm.

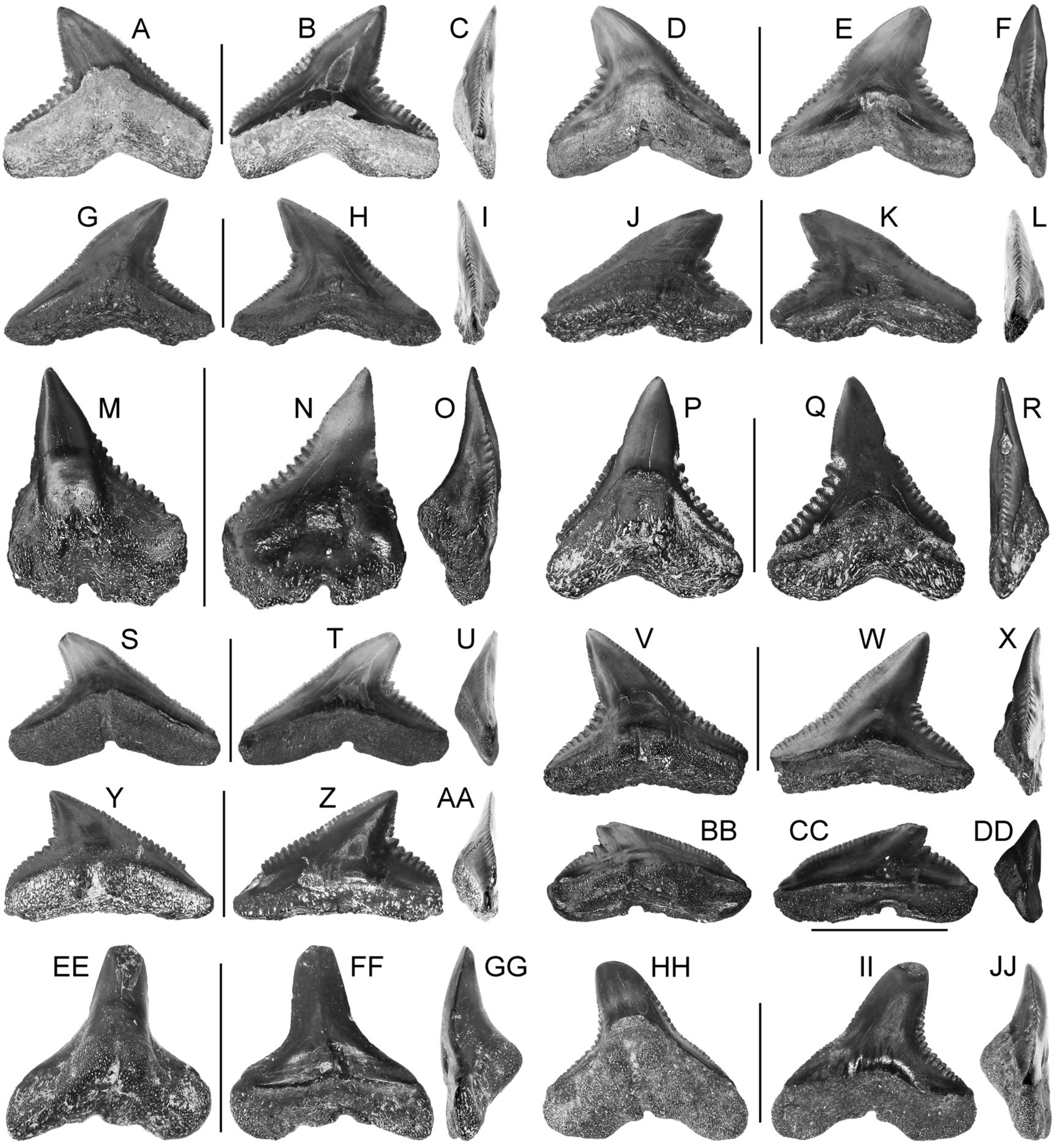


Fig. 26. *Carcharhinus mancinae* sp. nov. referred specimens. **A–C**. MSC 38426.16, upper lateral tooth, basal Gosport Sand. **A**. Lingual view. **B**. Labial view. **C**. Mesial view. **D–F**. MSC 38424.1, upper lateral tooth, basal Gosport Sand. **D**. Lingual view. **E**. Labial view. **F**. Mesial view. **G–I**. MSC 38424.5, upper lateral tooth, basal Gosport Sand. **G**. Lingual view. **H**. Labial view. **I**. Mesial view. **J–L**. MSC 38424.3, upper lateral tooth, basal Gosport Sand. **J**. Lingual view. **K**. Labial view. **L**. Mesial view. **M–O**. MSC 38426.3, symphysial? tooth, basal Gosport Sand. **M**. Lingual view. **N**. Labial view. **O**. Mesial view. **P–R**. MSC 38426.2, lower anterior tooth, basal Gosport Sand. **P**. Lingual view. **Q**. Labial view. **R**. Mesial view. **S–U**. MSC 37522.3, upper lateral tooth, basal Gosport Sand. **S**. Lingual view. **T**. Labial view. **U**. Mesial view. **V–X**. MSC 38424.2, lower lateral tooth, basal Gosport Sand. **V**. Lingual view. **W**. Labial view. **X**. Mesial view. **Y–AA**. MSC 37522.1, lower posterolateral tooth, basal Gosport Sand. **Y**. Lingual view. **Z**. Labial view. **AA**. Mesial view. **BB–DD**. MSC 38426.4, upper lateral tooth, basal Gosport Sand. **BB**. Lingual view. **CC**. Labial view. **DD**. Mesial view. **EE–GG**. MSC 38416, lower anterior tooth, basal Gosport Sand. **EE**. Lingual view. **FF**. Labial view. **GG**. Mesial view. **HH–JJ**. MSC 188.40, lower anterolateral tooth, basal Gosport Sand. **HH**. Lingual view. **II**. Labial view. **JJ**. Mesial view. Scale bars = 1 cm.

Within our sample we identified upper and lower anterior and lateral teeth, and upper posterior teeth. These tooth groups indicate that the dentition of *Carcharhinus mancinae* sp. nov. exhibits monognathic and dignathic heterodonty similar to the dentitions of several extant *Carcharhinus* species. Despite the variations in tooth morphology we observed in the fossil species, all the teeth can be attributed to the same taxon due to the presence of coarse compound and/or double serrations both mesially and distally, by having a tall and triangular main cusp with finer serrations that extend to the apex, and by the lack of a distinct distal notch on all but posterior positions. The combination of these characteristics separates these teeth from those of all other taxa in our Claiborne Group sample. The one taxon in our sample that could be confused with the new species is *Galeocerdo clarkensis*. However, this species lacks the dignathic heterodonty observed in *Carcharhinus mancinae* sp. nov., as the upper and lower teeth of *G. clarkensis* are difficult to differentiate, and the dentition lacks the erect triangular anterior tooth morphologies attributed to the new species. Although the upper posterior teeth of *C. mancinae* sp. nov. are morphologically similar to those of *G. clarkensis*, they can be differentiated by the absence of a distinct distal notch, and by having a distinctive 'pinched' lingual root protuberance that is more pronounced than that on *G. clarkensis*.

Adnet *et al.* (2007), Cappetta (2012), Underwood & Gunter (2012), and Samonds *et al.* (2019) recognized several species of Paleogene *Carcharhinus* sensu stricto. Of these, *C. mancinae* sp. nov. can be differentiated from the early Lutetian *Carcharhinus marçaisi* (Arambourg, 1952) by having a wider crown and completely serrated cutting edges. The presence of compound and/or double serrations differentiates *C. mancinae* sp. nov. from the *Carcharhinus* sp. teeth figured by Underwood *et al.* (2011) from the late Eocene of Egypt and by Underwood & Gunter (2012) from the middle Eocene of Jamaica, both of which have simple serrations. The teeth of *C. mancinae* sp. nov. also differ from those of the Oligocene (Chattian) *Carcharhinus perseus* Adnet *et al.*, 2007 by having compound and/or double serrations and a narrower crown in all tooth positions.

Carcharhinus mancinae sp. nov. closely resembles the Priabonian *C. balochensis* Adnet *et al.*, 2007 from Pakistan. However, the upper lateral teeth of *C. balochensis* differ from those of *C. mancinae* sp. nov. by having a less concave distal cutting edge. Furthermore, the anterior and lateral tooth positions known for *C. balochensis* have a taller and mesiodistally thicker main cusp that is not as basally constricted at the base. Finally, the large serrations on the teeth of *C. mancinae* sp. nov. are more irregular and pointed, and the largest distal serration (located just below the finer apical serrations) projects further distally than that on *C. balochensis.*

Samonds *et al.* (2019) recently named *Carcharhinus underwoodi* based on teeth from middle-to-upper Eocene deposits in Madagascar. As part of their type description, Samonds *et al.* (2019) referred all but one of the syntypes of *C. balochensis* of Adnet *et al.* (2007) to *Galeocerdo eaglesomei*, the lone exception being an upper lateral tooth (fig. 3, 10–11) that the authors suggested corresponded closely to that of *C. underwoodi*. However, according to their type description of *C. balochensis*, Adnet *et al.* (2007) clearly stated that the lower half of the teeth have distinct double serrations, which contrasts with the simple serrations on all the teeth of *C. underwoodi* (D.J. Ward, pers. com.). Also, per Samonds *et al.* (2019), the serrations are simple in form on all middle Eocene *G. eaglesomei* teeth. Although the overall shape of many of the tooth positions within the dentition of *C. mancinae* sp. nov. appear to be shared with *C. underwoodi* and *G. eaglesomei* (see Samonds *et al.* 2019: figs 2–3), the compound and/or double serrations on the teeth of *C. mancinae* sp. nov. clearly separates them from these other taxa. In addition, the distinct 'pinched' morphology of the lingual root protuberance on many of the *C. mancinae* sp. nov. teeth also distinguish them from *C. underwoodi* and *G. eaglesomei*. Within the same assemblage, Samonds *et al.* (2019: figs 3s–t) also figured a tooth they referred to *Carcharhinus* sp. that differed from *C. underwoodi* by having a distinct distal notch and evenly spaced mesial serrae. The teeth of *C. mancinae* sp. nov. can be differentiated from this unspeciated taxon by the absence of a distal notch and by the presence of compound and/or double serrations. Finally, the triangular upper anterior tooth morphology of *C. mancinae* sp. nov. (Fig. 25G–K) is unique and appears absent in the dentitions of *G. eaglesomei* and all the previously described Paleogene *Carcharhinus* sensu stricto species.

Thurmond & Jones (1981: fig. 28, left) illustrated a tooth they referred to *Galeocerdo alabamensis*, but it appears this tooth belongs to *C. mancinae* sp. nov. Manning (2003: fig. 21.3.2) illustrated a tooth from site ACl-4 in Clarke County that he referred to *Galeocerdo latidens*, but this specimen appears to be a lower lateral tooth of *C. mancinae* sp. nov. Citing a personal communication from David Ward, Underwood & Gunter (2012) noted a coarsely serrated species of *Carcharhinus* from the same locality. Photographs of these specimens provided to us by Ward confirmed they also belong to *C. mancinae* sp. nov.

Stratigraphic and geographic range in Alabama

The material in our sample were collected from the "upper" Lisbon Formation at site ACl-3, the basal Gosport Sand at sites ACl-4 and AMo-4, and the Gosport Sand at site ACl-15. Lower-to-middle Bartonian, zones NP16 and NP17.

Genus ***Negaprion*** Whitley, 1940

Type species

Aprionodon acutidens subsp. *queenslandicus* Whitley, 1939, Recent.

Negaprion gilmorei (White, 1956)

Fig. 27

Sphyrna gilmorei Leriche, 1942: 47, pl. 4, fig. 1.
Alopias latidens alabamensis White, 1956: 132–133, text figs 28–32, pl. 2, figs 5–6.
Negaprion gibbesi gilmorei White, 1956: 142, figs 37–66, pl. 2, fig. 9.
Hypoprion greyegertoni White, 1956: 137, figs 50–56, pl. 2, fig. 7.

Aprionodon greyegertoni – Thurmond & Jones 1981: 65, fig. 30.
Negaprion gibbesi gilmorei – Thurmond & Jones 1981: 66, fig. 31.
Carcharhinus greyegertoni – Kruckow & Thies 1990: 51.
Carcharhinus gilmorei – Müller 1999: 49, pl. 7, fig. 1.
Sphyrna sp. – Cappetta & Case 2016: 61, pl. 10, figs 1–4.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1519 isolated teeth; Claiborne Group; ALMNH PV1989.4.13.3 (25 specimens), ALMNH PV1989.4.151.1b, ALMNH PV1989.4.193, ALMNH PV1989.4.196 (21 specimens), ALMNH PV1989.4.6 (2 specimens), ALMNH PV1989.4.8.3 (17 specimens), ALMNH PV1989.4.8.4 (18 specimens), ALMNH PV1993.2.401 (160 specimens), ALMNH PV1993.2.402 (50 specimens), ALMNH PV2016.3.72, ANSP 23422, GSA-V701 (5 specimens), GSA-V704 (2 specimens), GSA-V710, MSC 188.3–5, MSC 188.7–10, MSC 188.14, MSC 188.24–25, MSC 188.28, MSC 188.30, MSC 188.33, MSC 188.35, MSC 188.37, MSC 188.46–48, MSC 188.52–53, MSC 188.55–59, MSC 188.61, MSC 188.63–64, MSC 188.66, MSC 188.69–71, MSC 188.74–77, MSC 188.80–81, MSC 188.83–87, MSC 188.90–93, MSC 188.95, MSC 188.97–100, MSC 188.102–

103, MSC 188.105–106, MSC 188.108–110, MSC 188.113–116, MSC 188.118–119, MSC 188.122, MSC 188.125, MSC 188.127, MSC 188.132–135, MSC 188.137–139, MSC 188.141–144, MSC 188.146–148, MSC 188.150, MSC 188.152–157, MSC 188.160–163, MSC 188.165, MSC 188.167–168, MSC 188.170–173, MSC 188.175, MSC 188.177, MSC 188.180–184, MSC 188.186–187, MSC 188.189–192, MSC 188.194–196, MSC 188.198–201, MSC 188.203, MSC 188.206, MSC 188.208–216, MSC 188.218–224, MSC 188.226–232, MSC 188.234–240, MSC 188.242–244, MSC 188.246–253, MSC 188.256–257, MSC 188.260, MSC 188.264–265, MSC 188.267, MSC 188.269–271, MSC 188.274, MSC 188.277, MSC 188.279, MSC 188.281, MSC 188.284–291, MSC 188.293–296, MSC 188.298–302, MSC 188.304, MSC 188.306, MSC 188.309, MSC 188.312–315, MSC 188.319–322, MSC 188.325, MSC 188.327, MSC 188.329, MSC 188.332–336, MSC 1424.3–8, MSC 1424.13–21, MSC 2171.7, MSC 2173.8, MSC 2175.1–4, MSC 2175.7–8, MSC 2175.10–16, MSC 2175.18, MSC 2175.20, MSC 2175.23–24, MSC 2175.26–29, MSC 2175.31–37, MSC 2175.41–48, MSC 2175.50–54, MSC 2175.56, MSC 2175.58–63, MSC 2175.65–69, MSC 2175.71–73, MSC 2380.1–19, MSC 37161.1–16, MSC 37395, MSC 37431, MSC 37466.1–62, MSC 37469, MSC 37475, MSC 37493.1–552, MSC 37526.1–2, MSC 37539.1–3, MSC 37545, MSC 37593, MSC 37594, MSC 37596.1–134, MSC 37597.1–6, MSC 37649, MSC 37682.1–5, MSC 37914.1–5, MSC 37916.1–2, MSC 38415.1–6, MSC 38429, MSC 38465, MSC 38466.1–29, MSC 38495.1–6, MSC 38506.1–11, MSC 38508.1–10, MSC 38547.1–33, MSC 38547.9, MSC 38556.1–8, NJSM 24029, SC2012.47.165 (4 specimens), SC2012.47.176, SC2012.47.181.

Description

Dentition exhibits strong dignathic heterodonty. Upper anterior teeth with triangular main cusp. Broad-based cusp flanked by short, oblique mesial and distal heels. Lateral teeth mesiodistally wider, cusp distally inclined, shoulders more elongated, becoming horizontal. Posterior teeth wide, short and distally inclined cusp. Cutting edges on cusp smooth; cutting edges on shoulders smooth to weakly and irregularly serrated. Labial crown face flat; lingual face convex; smooth enameloid. Root bilobate; lobes elongated, low, rounded, highly diverging. Interlobe area generally shallow, V-shaped. Attachment surface of lingual face generally flat, bisected by deep nutritive groove. Nutritive groove often forms a distinctive basal notch. Lower anterior teeth with narrow, erect cusp flanked by short, nearly horizontal mesial and distal shoulders. Lateral teeth mesiodistally wider, with distally inclined cusp, elongated lateral shoulders. Posterior teeth with shorter and very inclined cusp. Cutting edges of cusp and shoulders smooth.

Remarks

Woodward (1889) erected the name *Carcharias* (*Aprionodon*) *gibbesii* for 120+ teeth he examined in the NHMUK collections that were derived from Eocene deposits in South Carolina and Clarke County, AL. Although Woodward (1889) did not figure these teeth, with some uncertainty he referred several of those illustrated by Gibbes (1848) to his new taxon, whereas others he identified as *Galeocerdo minor* Agassiz, 1843 (Gibbes 1848: pl. 25, figs 63–65), and a single specimen was assigned to *Oxyrhina minuta* Agassiz, 1843 (Gibbes 1848: pl. 27, fig. 164).

White (1956) later reexamined Woodward’s (1889) *Carcharias* (*Aprionodon*) *gibbesii* teeth and agreed that Gibbes’ (1848: pl. 27, fig. 164) *Oxyrhina minuta* was a lower tooth of the *gibbesii* morphology. However, of Gibbes’ (1848: pl. 25, figs 63–65) *Galeocerdo minor* teeth, White (1956) disagreed with Woodward’s (1889) referral and said they belonged instead to *Sphyrna prisca* (Agassiz, 1843). White (1956) assigned the *gibbesi* morphology to *Negaprion* because he believed that they more closely resembled teeth of the extant Lemon Shark. However, several years prior, Leriche (1942: 47, pl. 4, fig. 1) figured two teeth from the Priabonian Yazoo Clay at Cocoa in Choctaw County, AL that he referred to a new taxon, *Sphyrna gilmorei*, noting their similarity with the extant *Sphyrna prisca*. White (1956) reexamined these teeth and synonymized *S. gilmorei* with *Negaprion gibbesii*. White (1956) also noted slight differences between Woodward's (1889) South Carolina and Alabama teeth and stated that the South Carolina specimens had finer serrations on the upper teeth, and to some extent on the lower teeth, whereas the lower teeth from Alabama were smooth. Because of this, White (1956) referred to the South Carolina teeth as the "typical" form *Negaprion gibbesii*, and assigned the Alabama teeth to a new subgenus, *Negaprion gibbesii gilmorei*. White's (1956) placement of these morphologies within *Negaprion* was later followed by numerous authors, including Case (1980), Thurmond & Jones (1981), Westgate (1984), and Krukow & Thies (1990).

Based on nine teeth from Clarke County, AL, White (1956) erected the taxon *Hypoprion greyegertoni*, which Thurmond & Jones (1981) later placed within *Aprionodon* because this genus lacked the lateral cusplets that occur on the teeth of *Hypoprion*. Thurmond & Jones (1981) also stated that the teeth of *Aprionodon greyegertoni* were very similar to those of *Negaprion gibbesi gilmorei* but differed by being taller than broad and lacking a medial nutritive groove (stating this characteristic was very prominent on the teeth of *N. gibbesi gilmorei*). Müller (1999), however, noted issues with White's (1956) *H. greyegertoni* syntypes and believed that they represented at least three different genera. Müller (1999) designated *H. greyegertoni* as a *nomen dubium*, referred most of White's (1956) syntypes to the genera *Abdounia* and *Physogaleus*, and assigned White's (1956: figs 50–51, 53–54, 56) remaining teeth to the *gilmorei* morphology.

Ward & Wiest (1990) and Müller (1999) both recognized teeth of the *gibbesi* morphology as occurring within the Paleocene-to-Eocene Pamunky Group in Maryland, and Müller (1999) reported both the *gibbesi* and *gilmorei* morphologies from the same deposits in Virginia. Ward & Wiest (1990) and Müller (1999) placed these morphologies within the genus *Carcharhinus*, and between the two, elevated both *C. gibbesi* and *C. gilmorei* to species status. Manning (2003) later suggested that these two species are intergradational, with *C. gilmorei* occurring in both Eocene and Oligocene deposits, whereas *C. gibbesi* was largely confined to the Oligocene.

As part of our study, we examined numerous teeth of the *gilmorei/gibbesi* morphologies that were derived from various middle Eocene (Lutetian) to late Oligocene (Chattian) localities in Alabama. We determined that all these teeth represent the *gilmorei* morphology, as serrations on the upper and lower teeth were either absent or inconspicuous. Although no teeth attributable to the *gibbesi* morphology (those with distinct heel serrations) were identified in our sample, the presence of the *gilmorei* morphology within both Eocene and Oligocene deposits in Alabama corroborates Manning's (2003) observation regarding the stratigraphic range of this species.

To further complicate the matter, Cappetta & Case (2016) identified 40 specimens from the contact of the Tallahatta and Lisbon formations at site ACov-11 in Covington County as belonging to *Sphyrna* sp. and suggested these teeth represented the oldest occurrence of this genus. Cappetta & Case (2016: pl. 10, figs 1–4), however, failed to compare the teeth in their sample to those with the *gilmorei* morphology, even though the specimens they figured are conspecific with the upper teeth of this taxon. Furthermore, our sample consisted of 23 additional specimens from the ACov-11 locality that appear conspecific to those figured by Cappetta & Case (2016), all of which are consistent with the *gilmorei* morphology.

Confusion over the generic placement of teeth with the *gilmorei* morphology stems from the generalized dentition of this shark, which consists of T-shaped lower teeth and upper teeth with a broader triangular main cusp. This generalized dentition strongly resembles those of several representatives within the extant *Carcharhinus*, *Negaprion*, and *Sphyrna*, prompting various authors, at one point or another, to refer the *gilmorei* morphology to each of these genera (see Leriche 1942; White 1956; Müller 1999). To garner insight into the taxonomic placement of teeth with the *gilmorei* morphology, we compared the teeth in our sample to those within the dentitions of extant representatives within all three of the aforementioned genera. Our observations show that the dentitions of the numerous species of *Carcharhinus* are extremely variable in terms of upper and lower tooth morphology, but all members of the genus can be categorized by having distinct dignathic heterodonty with upper teeth having serrated mesial and distal cutting edges, and lower teeth with more slender crowns that may or may not have weak serrations (see Voigt & Weber 2011). A few *Carcharhinus* species have lower teeth that bear fine serrations extending nearly to the apex of the crown (i.e., *C. acronotus*, *C. albimarginatus*, *C. amblyrhynchos*, *C. amboinensis*, *C. borneensis*, *C. brachyurus*, *C. leucas*, *C. longimanus*, and *C. wheeleri*), whereas other species have weak serrations that are confined to the mesial and distal shoulders (i.e., *C. hemiodon*, *C. obscurus*, *C. porosus*, *C. signatus*). However, the upper teeth of all these species have serrated mesial and distal cutting edges, with serrations generally extending nearly to the crown apex.

The Sphyrnidae (*Eusphyra* and *Sphyrna*) jaw sets we examined exhibited varying degrees of dignathic heterodonty (see Compagno 1984) and fall into one the following four categories: 1) those with triangular upper teeth and lower teeth with a narrow crown and a sinuous mesial edge (i.e., *Eusphyra*

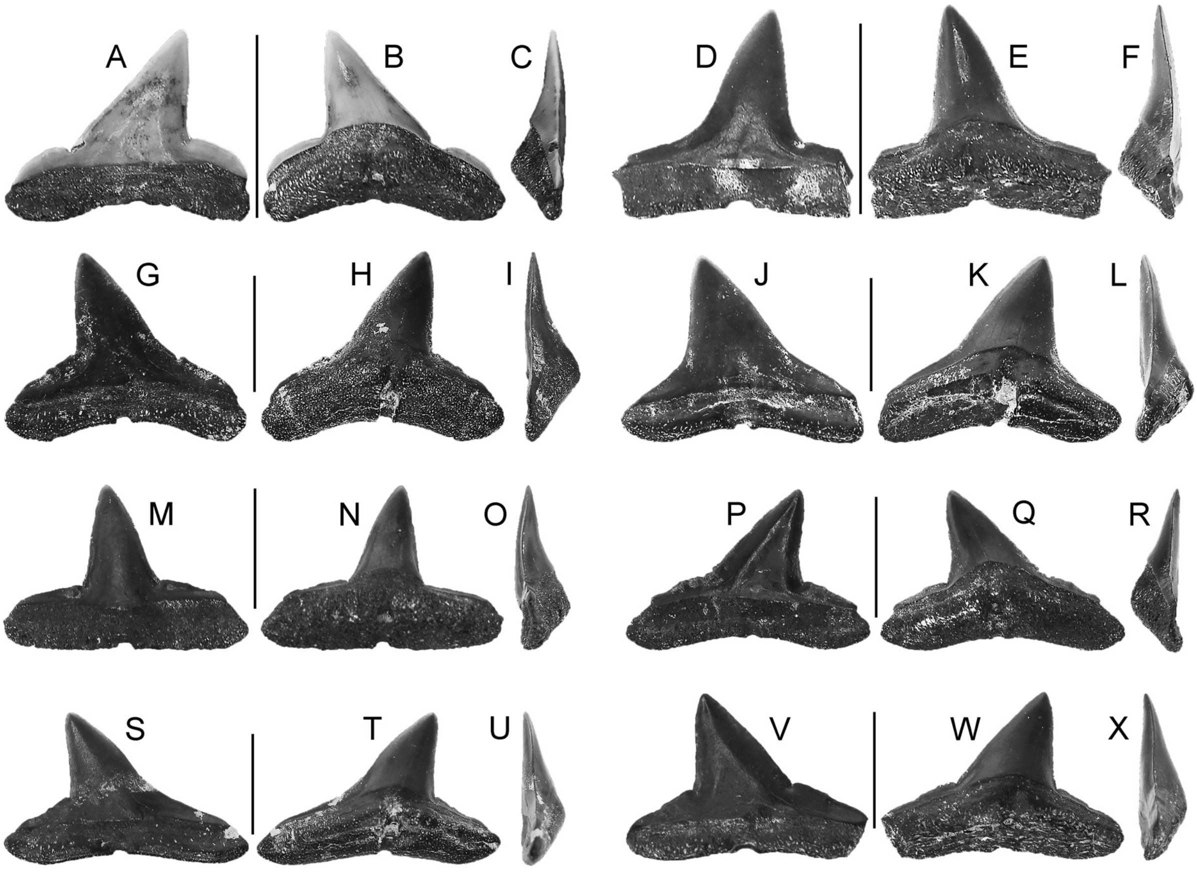


Fig. 27. *Negaprion gilmorei* (White, 1956), teeth. **A–C**. MSC 37682.2, upper lateral tooth, basal Lisbon Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 37596.132, lower anterolateral tooth, basal Gosport Sand. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G–I**. MSC 38466.2, upper lateral tooth, basal Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. MSC 38466.1, upper lateral tooth, basal Gosport Sand. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M–O**. MSC 37596.5, lower anterior tooth, basal Gosport Sand. **M**. Labial view. **N**. Lingual view. **O**. Mesial tooth. **P–R**. MSC 37596.116, upper lateral tooth, basal Gosport Sand. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S–U**. MSC 37596.11, upper lateral tooth, basal Gosport Sand. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V–X**. MSC 37596.121, upper lateral tooth, basal Gosport Sand. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. Scale bars = 5 mm.

blochii and *Sphyrna tiburo*); 2) those with upper and lower teeth with a narrow crown and a sinuous mesial edge (i.e., *Sphyrna corona*); 3) those with triangular upper teeth and T-shaped lower teeth (i.e., *Sphyrna lewini*, *Sphyrna media*, and *Sphyrna tudes*); and 4) those with triangular upper and lower teeth exhibiting little dignathic heterodonty (i.e., *Sphyrna mokarran* and *Sphyrna zygaena*). Of these species, *S. tudes* had serrated cutting edges on its upper teeth but smooth cutting edges on the crowns of lower teeth, and upper and lower teeth of *S. mokarran* are uniformly serrated. All remaining species have upper and lower teeth that lack serrations.

The dentitions of the two extant species of *Negaprion*, *N. acutidens* and *N. brevirostris*, exhibit a similar degree of dignathic heterodonty, consisting of triangular upper teeth and T-shaped lower teeth. Both species also have serrated upper teeth, although to varying degrees. The upper teeth of *N. acutidens* have serrated mesial and distal cutting edges, and the serrations extend almost to the cusp apex. In contrast the serrations on upper teeth of *N. brevirostris* are confined to the mesial and distal shoulders and do not extend onto the central cusp. The cutting edges on the lower teeth of both species are smooth. Examination of teeth from the extinct *N. eurybathodon* show they are more similar to those of *N. brevirostris*, with a difference being the occasional presence of weak serrations on the mesial and distal shoulders on certain lower teeth of the extinct species.

Although early *Carcharhinus* representatives have been recently described from middle and upper Eocene deposits elsewhere (see Adnet *et al.* 2007; Underwood & Gunter 2012; Samonds *et al.* 2019), these species, as well as all the extant species, have upper teeth with serrations on their mesial and distal cutting edges that extend nearly to the apex of the crown. The presence of these mesial and distal serrations appears to be a defining characteristic of *Carcharhinus* (see Underwood & Gunter 2012), suggesting teeth with the *gilmorei* morphology do not belong to this genus. Assigning the *gilmorei* morphology to *Sphyrna* is also problematic because molecular divergence estimates by Lim *et al.* (2010) indicated that the family Sphyrnidae split from *Carcharhinus* during the early-to-middle Eocene (40 to 50 Ma), and that *Sphyrna* only diverged from its sister taxon *Eusphyra* during the early-to-middle Miocene (15 to 20 Ma). These data suggests that true members of *Sphyrna* did not evolve until the early-to-middle Miocene, and any Eocene teeth with a similar morphology should therefore be referred to a different genus. Regarding the use of *Negaprion*, Schultz *et al.* (2008) calculated molecular divergence times for the two extant species of the genus and suggested that they are derived from a cosmopolitan common ancestor, the Oligo–Miocene *Negaprion eurybathodon* (Blake, 1862).

Our analysis showed that extant species of *Carcharhinus*, *Sphyrna tudes*, and *Negaprion acutidens* have teeth with serrations that extend nearly to the apex of the crown in all upper tooth positions. In addition, all the species within the Sphyrnidae (with the exception of *S. tudes* and *S. mokarran*) were observed to have smooth crowns on both the upper and lower teeth. Based on these observations, teeth with the *gilmorei* morphology appear most closely aligned with those of *N. brevirostris* and *N. acutidens* in that they have triangular upper teeth, T-shaped lower teeth, and weak serrations that are limited to the mesial and distal shoulders of certain teeth (as serrations appear on the upper teeth in *N. brevirostris* and both upper and lower teeth in *N. acutidens*). Due to their morphological similarity to the other members of *Negaprion*, we concur with previous assignments of the *gilmorei* morphology to *Negaprion*, making *N. gilmorei* one of the earliest representatives of the genus.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at sites ACh-14, ACov-11 and ACon-6, the basal Lisbon Formation at site ACov-11, the “upper” Lisbon Formation at site ACl-3, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Genus ***Rhizoprionodon*** Whitley, 1929

Type species

Carcharias crenidens Klunzinger, 1880, Recent.

Rhizoprionodon ganntourensis (Arambourg, 1952)
Fig. 28

Scoliodon ganntourensis Arambourg, 1952: 164, pl. 24, figs 49–63; text-fig. 33.

Rhizoprionodon sp. – Thurmond & Jones 1981: 68, fig. 33.
Rhizoprionodon cf. *ganntourensis* – Cappetta & Traverse 1988: 361.
Rhizoprionodon sp. – Clayton *et al.* 2013: fig. 2i.
Sphyrna sp. – Cappetta & Case 2016: 61, pl. 10, figs 2–4.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 156 isolated teeth; Claiborne Group; ALMNH PV1993.2.426 (24 specimens), ALMNH PV1993.2.442 (17 specimens), ALMNH PVPV 2005.6.435, MMNS VP-8212, MSC 188.324, MSC 2173.1–7, MSC 2379.1–5, MSC 35753.1–7, MSC 36178, MSC 37098, MSC 37099, MSC 37264.1–5, MSC 37265, MSC 37355, MSC 37648.1–3, MSC 37674.1–4, MSC 37904.1–3, MSC 37905.1–3, MSC 37906.1–2, MSC 37907.1–2, MSC 38199.1–2, MSC 38486.1–6, MSC 38504.1–10, MSC 38544.1–11, SC2012.47.160, SC2012.47.168 (5 specimens), SC2012.47.172, SC2012.47.52, SC2012.47.53, SC2012.47.54 (9 specimens), SC2012.47.55 (12 specimens), WSU 5017, WSU 5037 (6 specimens).

Description

Teeth small, most not exceeding 0.75 cm in mesiodistal width. Crown wide, with broad-based and distally inclined triangular cusp; apex of cusp not extending past the distal edge of the crown. Mesial cutting edge elongate, continuous, smooth. Distal cutting edge very short, oblique, straight to weakly convex, smooth. Conspicuous distal heel forms acute angle with cusp, separated by distal notch. Cutting edge of distal heel convex to angular, smooth. Labial crown face is flat; lingual face is convex; both crown faces smooth. Root shallow with rounded root lobes. Root lobes extend mesially and distally beyond the base of the root. Tooth base is flat to slightly concave in mesial and distal views. A deep nutritive groove present on lingual root face that often forms a basal notch.

Remarks

Our *Rhizoprionodon* sample exhibits monognathic, dignathic and gynandric heterodonty. Monognathic heterodonty is expressed as a more erect crown on upper and lower anterior teeth when compared to lateral teeth, and lateral teeth are wider than tall with a more inclined main cusp. With regard to dignathic heterodonty, the cusp of upper teeth is taller and more broadly triangular than on lower teeth. Also, lower anterolateral and lateral teeth have a more elongated mesial edge. Male teeth have a mesiodistally thinner crown than those on females, and the distal edge of the crown is often less convex.

Thurmond & Jones (1981: 68, fig. 33) first reported Eocene representatives of *Rhizoprionodon* in North America when they referred teeth to this taxon that were derived from the basal Gosport Sand at site ACl-4 in Clarke County, AL. The presence of this genus within the Claiborne Group of Alabama was confirmed as part of this study by comparing the teeth in our sample to the dentitions of extant *Loxodon* (one species), *Rhizoprionodon* (eight species), and *Scoliodon* (one species) housed at MSC and SC and as illustrated by Springer (1964). Of these taxa, the teeth in our sample most closely resemble those of

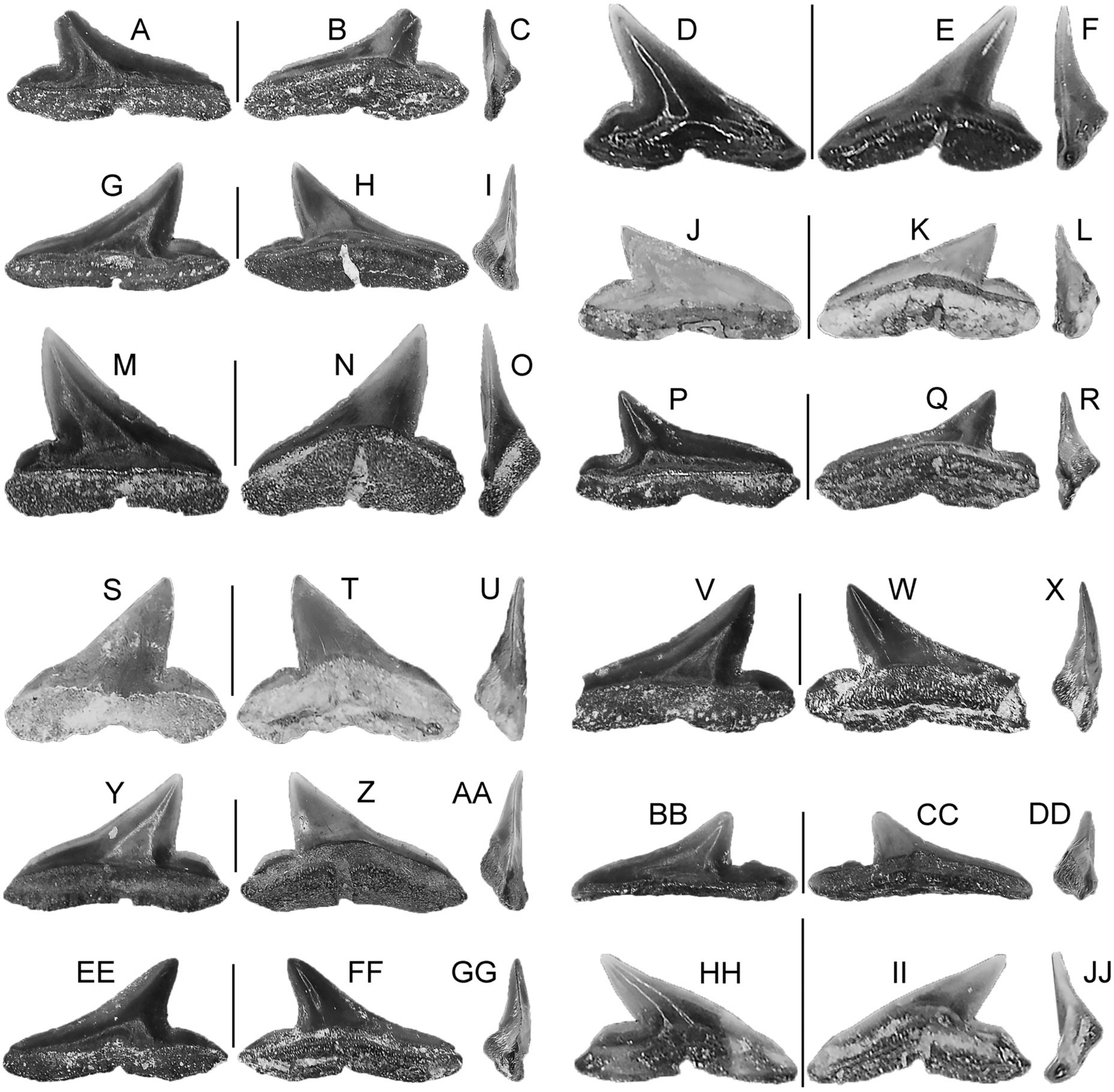


Fig. 28. *Rhizoprionodon ganntourensis* (Arambourg, 1952), teeth. **A–C**. MSC 2173.4, lower lateroposterior tooth, basal Gosport Sand. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 37674.3, lower anterior tooth, basal Lisbon Formation. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G–I**. MSC 2173.5, lower lateral tooth, basal Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. MSC 37907.1, lower lateral tooth, lower Tallahatta Formation. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M–O**. MSC 2173.6, upper anterolateral tooth, basal Gosport Sand. **M**. Labial view. **N**. Lingual view. **O**. Mesial view. **P–R**. MSC 38504.7, lower lateroposterior tooth, basal Gosport Sand. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S–U**. MSC 35753.3, upper anterolateral tooth, lower Tallahatta Formation. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V–X**. MSC 37648.2, lower lateral tooth, basal Gosport Sand. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. **Y–AA**. MSC 37098, lower lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **Y**. Labial view. **Z**. Lingual view. **AA**. Mesial view. **BB–DD**. MSC 37674.1, lower lateroposterior tooth, basal Lisbon Formation. **BB**. Labial view. **CC**. Lingual view. **DD**. Mesial view. **EE–GG**. MSC 37648.1, lower lateral tooth, basal Gosport Sand. **EE**. Labial view. **FF**. Lingual view. **GG**. Mesial view. **HH–JJ**. MSC 37674.4, lower lateral tooth, basal Lisbon Formation. **HH**. Labial view. **II**. Lingual view. **JJ**. Mesial view. Scale bars = 2.5 mm.

extant species of *Rhizoprionodon* with respect to the shape of the mesial and distal edges of the crown, the mesiodistal thickness of the crown base, overall crown height, and the extent of distal inclination.

Examination of the dentitions of Recent female *Rhizoprionodon acutus* (Rüppell, 1837) and *Rhizoprionodon terraenovae* (Richardson, 1836) specimens in the SC collection revealed differences between the distal heels between the two species. The finely serrated distal heel of *R. acutus* teeth are broadly convex, but a single small denticle often provides some angularity, most evident on upper anterior teeth. Teeth in the *R. terraenovae* dentition exhibit a similarly serrated distal heel, but a distinctively large denticle results in a more angular appearance than *R. acutus*, particularly on the upper teeth. We did not observe any significant variation within the Claiborne sample that could indicate multiple species, and we refer all of the material to one taxon. Our Claiborne Group teeth are similar in age and overall morphology to the type specimens of *Rhizoprionodon ganntourensis* as described and figured by Arambourg (1952: pl. 26, figs 49–63), and both samples have teeth with a distal heel that varies in shape from rounded to angular. Due to these similarities, the Claiborne material is assigned to *R. ganntourensis*, currently the only recognized Eocene species within the genus (see Cappetta 2012).

The dentition of extant *Scoliodon laticaudus* Müller & Henle, 1838 exhibits gynandric heterodonty, with tooth crowns on female lateral and posterolateral teeth being much more distally inclined than those in the male dentitions (which instead have a thin crown with an upturned apex and an elongated mesial shoulder). Only two species of extant *Rhizoprionodon* possess gynandric heterodonty (Springer 1964), with male anterolateral teeth having a thinner cusp base than on female teeth. A similar pattern can be observed within our *Rhizoprionodon* sample. Male anterolateral teeth of *Rhizoprionodon* are similar to those of *Scoliodon* (see Cappetta 2012: 300, fig. 283), but can be differentiated by their lack of a lingually twisted cusp apex.

Cappetta & Case (2016) did not identify *Rhizoprionodon* in their sample of teeth from site ACov-11 in Covington County, AL. However, the authors figured three specimens (pl. 10, figs 2–4) they referred to *Sphyrna* sp. that, in our opinion, belong to *Rhizoprionodon*.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the Tallahatta Formation at site AMo-8, the contact of the Tallahatta and Lisbon Formations and the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand and site ACh-21. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Genus **Scoliodon** Müller & Henle, 1838

Type species

Carcharias (*Scoliodon*) *laticaudus* Müller & Henle, 1838, Recent, India.

Scoliodon conecuhensis Cappetta & Case, 2016
Fig. 29

Scoliodon conecuhensis Cappetta & Case, 2016: 59, pl. 9, figs 1–6.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 130 isolated teeth; Claiborne Group; ALMNH PV1993.2.440b (2 specimens), ALMNH PV1993.3.408 (2 specimens), GSA-V702, MSC 188.130, MSC 188.268, MSC 188.323, MSC 2175.17, MSC 2175.38, MSC 2394.2–5, MSC 34405.14, MSC

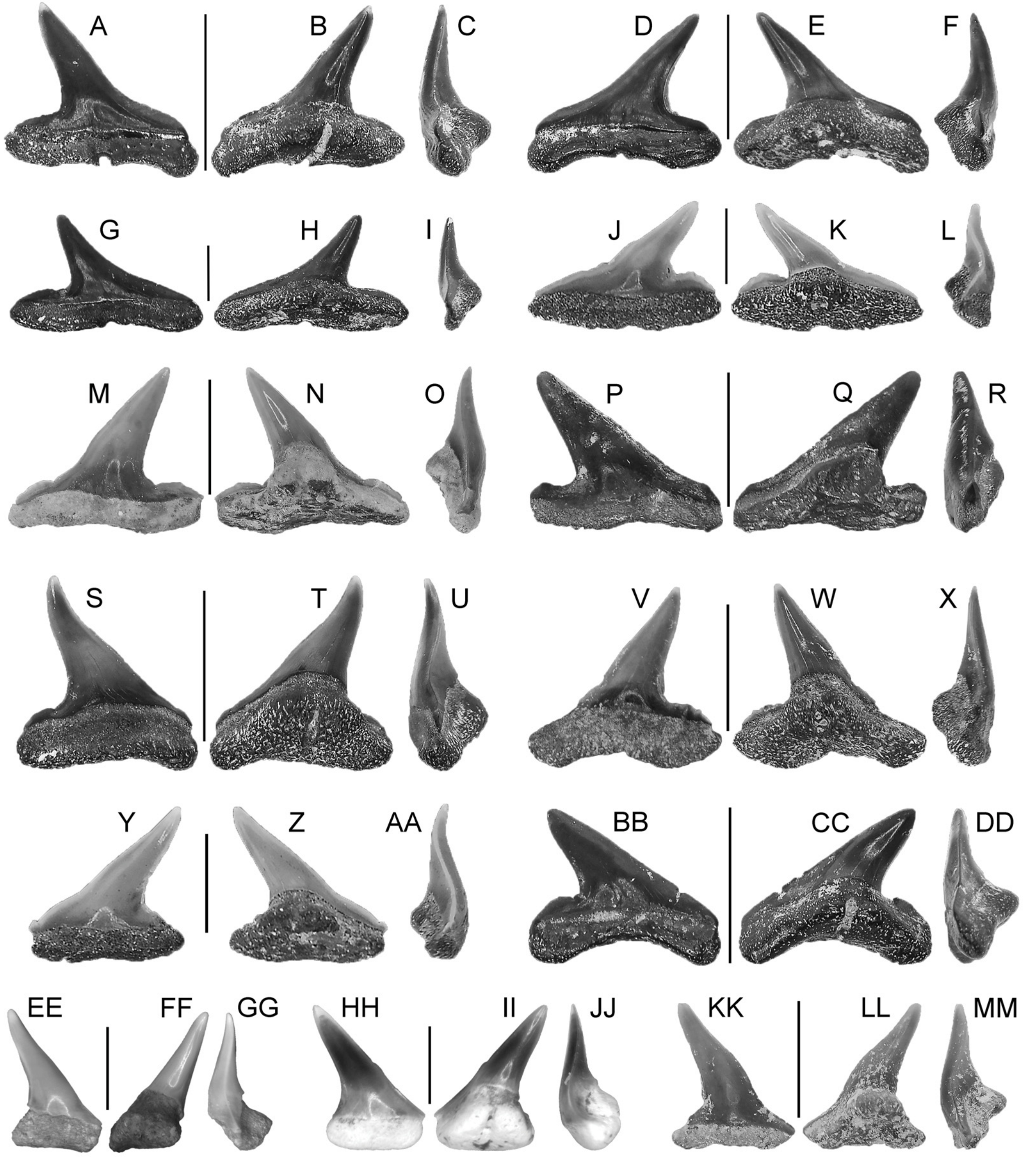


Fig. 29. *Scoliodon conecuhensis* Cappetta & Case, 2016, teeth. **A–C**. MSC 188.130, upper lateral tooth, basal Gosport Sand. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 38498.1, upper lateral tooth, basal Gosport Sand. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G–I**. MSC 188.268, lower lateral tooth, basal Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. MSC 37627, upper lateral tooth, basal Lisbon Formation. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M–O**. MSC 34405.2, lower lateral tooth, lower Tallahatta Formation. **M**. Labial view. **N**. Lingual view. **O**. Mesial view. **P–R**. MSC 37756.1, lateral tooth, lower Tallahatta Formation. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S–U**. MSC 37133, upper anterolateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V–X**. MSC 38490.3, upper lateral tooth, basal Lisbon Formation. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. **Y–AA**. MSC 38490.2, lower lateral tooth, basal Lisbon Formation. **Y**. Labial view. **Z**. Lingual view. **AA**. Mesial view. **BB–DD**. MSC 38498.3, upper lateral tooth, basal Gosport Sand. **BB**. Labial view. **CC**. Lingual view. **DD**. Mesial view. **EE–GG**. MSC 37678.1, male lower anterior tooth, basal Lisbon Formation. **EE**. Labial view. **FF**. Lingual view. **GG**. Mesial view. **HH–JJ**. MSC 37756.3, male lower anterior tooth, lower Tallahatta Formation. **HH**. Labial view. **II**. Lingual view. **JJ**. Mesial view. **KK–MM**. MSC 37756.2, male lower anterior tooth, lower Tallahatta Formation. **KK**. Labial view. **LL**. Lingual view. **MM**. Mesial view. Scale bars for A–F, M–X, BB–DD, KK–MM = 5 mm. Scale bars for G–L, Y–AA, EE–JJ = 2 mm.

34405.2, MSC 37133, MSC 37316.1–4, MSC 37326.1–3, MSC 37627, MSC 37672, MSC 37678.1–7, MSC 37753.1–8, MSC 37754, MSC 37755, MSC 37756.1–19, MSC 37757.1–2, MSC 37758.1–2, MSC 37759.1–2, MSC 37760, MSC 37761.1–5, MSC 37762, MSC 38490.1–5, MSC 38498.1–3, MSC 38523.1–2, MSC 38553.1–4, NJSM 24028, SC2012.47.170 (4 specimens), SC2012.47.247 (2 specimens), SC2012.47.249 (4 specimens), SC2012.47.69 (4 specimens), WSU 5028 (4 specimens), WSU 5038 (10 specimens), WSU 5045 (9 specimens), WSU CC 530.2 (2 specimens), WSU CC 553.

Description

Anterior teeth taller than wide, lateral teeth wider than tall. Teeth with narrow, elongate, triangular, sharply distally inclined crown. Lingual crown face strongly convex; labial face weakly convex; enameloid smooth. Cusp apex with slight lingual flexure; apex extends nearly to, or slightly beyond, distal edge of crown. Mesial cutting edge elongate, smooth, straight, sinuous or convex; straighter on lower teeth. Distal cutting edge short, smooth, oblique. Short, smooth distal heel on all lateral teeth; heel lacking on some anterior teeth. Root very low, bilobate, with highly diverging lobes. Interlobe area lacking to weakly U-shaped. Conspicuous lingual root boss bears narrow, deep nutritive groove.

Remarks

Scoliodon conecuhensis was named by Cappetta & Case (2016) for a series of teeth collected from site ACov-11 in Covington County, AL. The teeth of *S. conecuhensis* are morphologically similar to those of *Physogaleus* and *Rhizoprionodon*. However, *Scoliodon* teeth are easily distinguished from *Physogaleus* by their lack of denticulations on the mesial cutting edge and distal heel. They were separated from *Rhizoprionodon* by having a narrower and more elongated cusp that extends to, or beyond, the distal edge of the crown.

The extant *Scoliodon laticaudus* Müller & Henle, 1838, and some species of *Rhizoprionodon*, exhibit gynandric heterodonty. The extinct species *S. conecuhensis* also appears to have displayed a strong degree of gynandric heterodonty. Male teeth have a cusp that is mesiodistally thinner than those on female teeth, and male upper teeth have a more sinuous crown than do female teeth. In addition, male lower lateral teeth have a shorter, upturned cusp. Also, male lower lateral teeth have an elongated mesial heel, but the heel is very short or absent altogether on anterior teeth. The cusp on *S. conecuhensis* anterior teeth have a lingually twisted apex, which is lacking on equivalent teeth of *Rhizoprionodon ganntourensis*.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at site ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21 and ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Genus ***Abdounia*** Cappetta, 1980a

Type species

Eugaleus beaugei Arambourg, 1935, early Eocene, Belgium.

Abdounia beaugei (Arambourg, 1935)

Fig. 30

Eugaleus beaugei Arambourg, 1935: 430, pl. 14, figs 28–35.

Galeus doncieuxi Leriche, 1936: 391, pl. 27, fig. 9.

Galeorhinus beaugei – Dartevelle & Casier 1943: 154, pl. 12, figs 40–46.
Scyliorhinus beaugei – Arambourg 1952: 123, pl. 23, figs 20–47.
Abdounia beaugei – Cappetta 1980a: 35, fig. 4.
Abdounia biauriculata – Cappetta & Case 2016: 56, pl. 7, fig. 5.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 50 isolated teeth; Claiborne Group; MSC 35754.1–13, MSC 37133, MSC 37318.2, MSC 37318.4, MSC 37570.3–5, MSC 37571.1–21, MSC 37572, MSC 37695.2, SC2012.47.167, SC2012.47.177 (4 specimens), WSU CC 510 (2 specimens).

Description

Anterior teeth with tall erect main cusp; cusp of lateral and lateroposterior teeth becoming shorter, more distally inclined. Anterior teeth with single pair of short, triangular cusplets; cusplets divergent and largely united to main cusp. Lateral teeth with two pairs of lateral cusplets; second pair smaller, vestigial on more distally located teeth. Lingual face of main cusp of anterior teeth strongly convex; less convex on lateral teeth. Labial cusp face flat; all enameloid smooth. Cutting edges of main cusp and lateral cusplets smooth, continuous. Root bilobate with short, diverging lobes. Lingual attachment surface flat; wide and deep nutritive groove.

Remarks

Three species of *Abdounia* have been identified within our sample of Claiborne Group teeth, including *A. beaugei* (Arambourg, 1935), *A. enniskilleni* (White, 1956), and *A. minutissima* (Winkler, 1874). Two additional species previously assigned to *Abdounia* are placed within a new genus and are described in detail below. The *A. beaugei* anterior teeth in our sample have a single pair of lateral cusplets, easily separating them from the latter two species, which have three-to-eight pairs. Anterior teeth of *A. minutissima* have taller triangular cusplets that are less united to the main cusp. Teeth of *A. enniskilleni* are much larger in overall size and generally have fine longitudinal ridges on the lingual cusp face. The

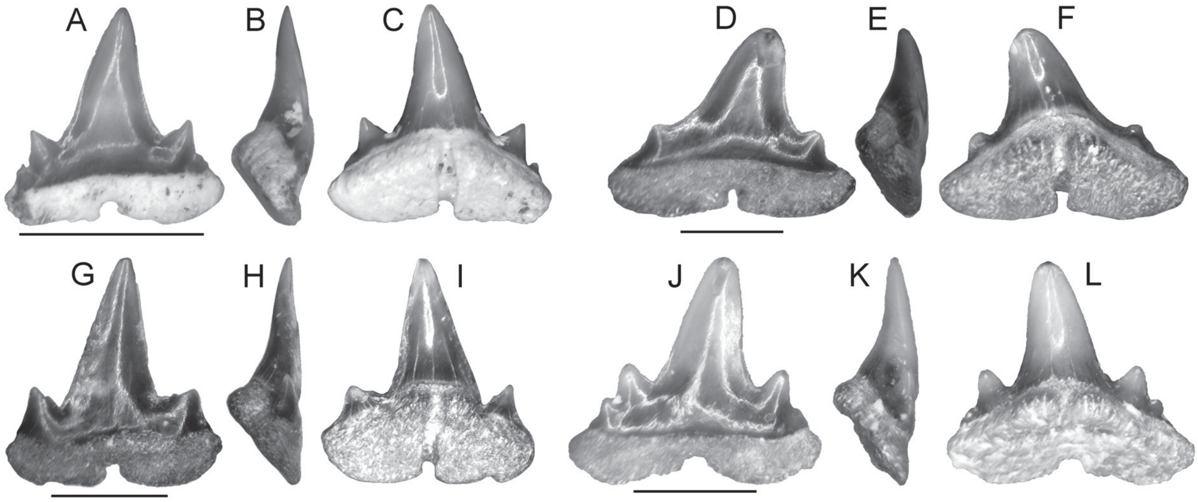


Fig. 30. *Abdounia beaugei* (Arambourg, 1935), teeth. **A–C**. MSC 35754.1, anterolateral tooth, lower Tallahatta Formation. **A**. Labial view. **B**. Mesial view. **C**. Lingual view. **D–F**. MSC 37571.1, lateral tooth, Gosport Sand. **D**. Labial view. **E**. Mesial view. **F**. Lingual view. **G–I**. MSC 37571.2, anterior tooth, Gosport Sand. **G**. Labial view. **H**. Mesial view. **I**. Lingual view. **J–L**. MSC 35754.9, lateral tooth, lower Tallahatta Formation. **J**. Labial view. **K**. Mesial view. **L**. Lingual view. Scale bars for A–L = 2 mm.

lateral teeth of *A. beaugei* have two pairs of lateral cusplets, whereas *A. enniskilleni* and *A. minutissima* have a single pair.

Cappetta & Case (2016) described and figured a single tooth from site ACov-11 that they assigned to *Abdounia biauriculata* (Casier, 1946). Teeth of to this species are very similar in size to those of *A. beaugei*, and anterior teeth of both species have a single pair of cusplets and the lateral teeth two pairs (see Arambourg 1935: text fig. 23, pl., 19, figs 28–35; Casier 1946: pl. 1, 6; Arambourg 1952: pl. 23, figs 20–47; Casier 1966: pl. 3, figs 23–25). Although Casier (1966: fig. 65) stated that the two taxa were “analogous”, he reported that his Ypresian *A. biauriculata* from Belgium differed from Arambourg’s (1952) *A. beaugei* from the Ypresian London Clay and Thanetian to Ypresian strata of Morocco in that the teeth have a less robust root, and the lateral cusplets that are taller, straighter, more pointed, and more separated from the main cusp.

When compared to the teeth in our sample, the *Abdounia biauriculata* specimen figured by Cappetta & Case (2016: pl. 7, fig. 5) appears anomalous as it has two pairs of tall, pointed cusplets that are separated from the main cusp. Although this single tooth could be identified as *A. biauriculata*, the absence of any other specimens in our sample leads us to believe that it may represent an aberrant *A. minutissima.* A few teeth from our sample of Gosport Sand *Abdounia* teeth have similar tall and pointed cusplets. However, in our opinion these teeth still fall within the morphological range of *A. beaugei*. Furthermore, as eluded to by Casier (1966: fig. 65), *A. beaugei* and *A. biauriculata* may be conspecific, with any observed differences being the product of heterodonty and/or intraspecific or geographic variation. Support for this stems from the difficulty, at times, in distinguishing these two morphologies, and the fact that the morphologies appear to be coeval within the same deposits in Belgium (see Noubhani & Cappetta 1997). Based on samples from both Alabama (see below) and Georgia (also Parmley & Cicimurri 2003), the variation we observed in *A. enniskilleni* leads us to believe that Cappetta & Case’s (2016) *A. biauriculata* is synonymous with *A. beaugei*.

Numerous teeth in our sample are assigned to *Abdounia* sp. (see Appendix 1) because of their incomplete preservation, making their specific assignments unclear.

Stratigraphic and geographic range in Alabama

Abdounia beaugei specimens have been recovered from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations and the “lower” Lisbon Formation at site ACov-11, the lower Gosport Sand at site ACl-4, and the Gosport Sand at ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Abdounia enniskilleni (White, 1956)

Fig. 31A–O

Scyliorhinus enniskilleni White, 1956: 128, pl. 11, fig. 1, text-figs 1–9.

Abdounia enniskilleni – Cappetta 1980a: 37.
Scyliorhinus enniskilleni – Thurmond & Jones 1981: 60, fig. 26.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 302 isolated teeth; Claiborne Group; ALMNH PV1989.4.16.2a (6 specimens), ALMNH PV1989.4.23.7, ALMNH PV1989.4.32.2 (2 specimens), ALMNH PV1989.4.38.3, ALMNH PV1989.4.126c, ALMNH PV1989.4.192, ALMNH PV1989.4.194 (2 specimens), ALMNH PV1989.4.205, ALMNH PV1989.4.209 (seven specimens), ALMNH PV1989.4.210, ALMNH PV1993.2.440a (56 specimens), ALMNH PV2000.1.43.2b, ALMNH

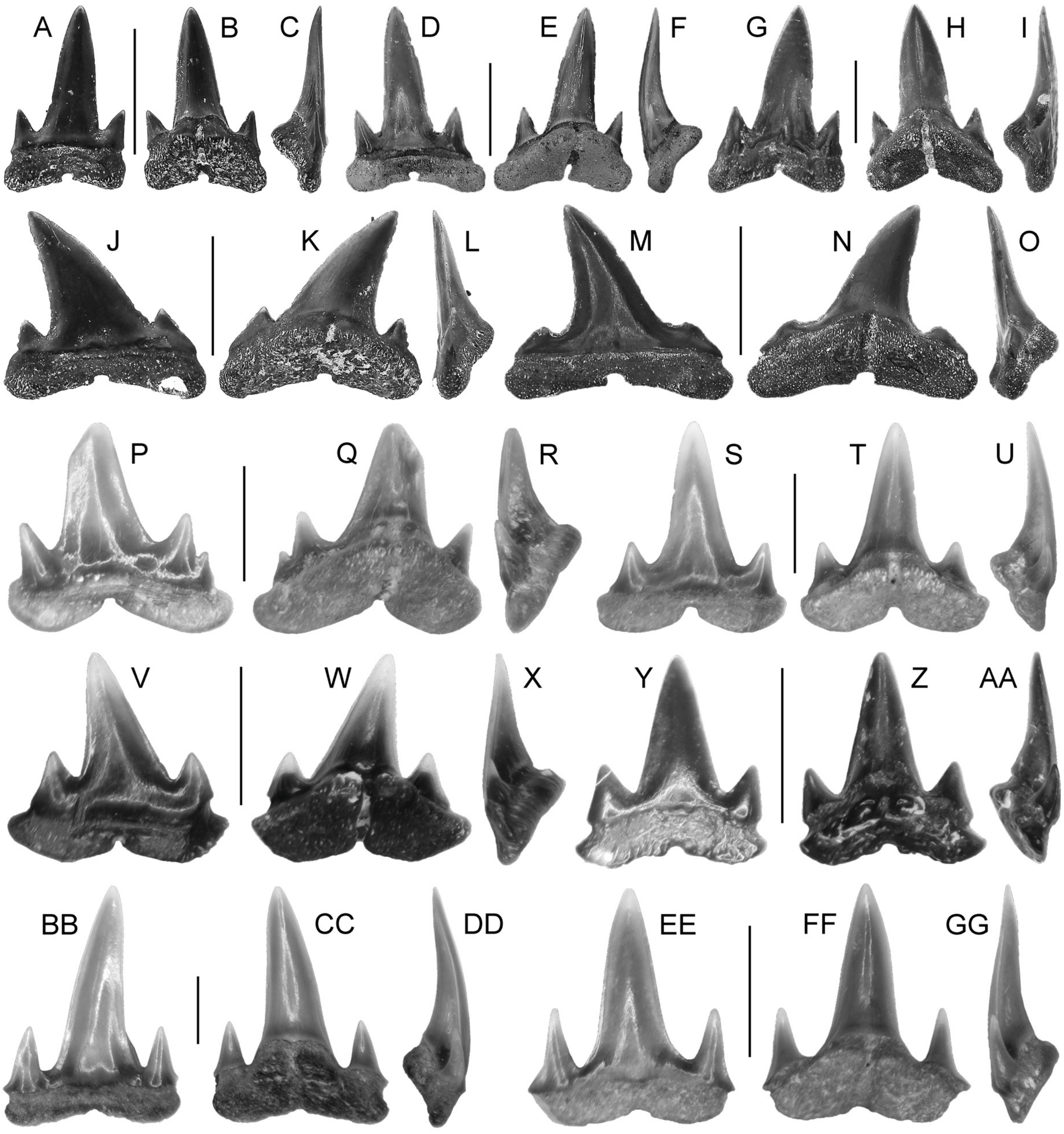


Fig. 31. *Abdounia enniskilleni* (White, 1956) and *A. minutissima* (Winkler, 1874), teeth. **A–O**. *A. enniskilleni*. **A–C**. MSC 2171.8, anterior tooth, basal Gosport Sand. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D–F**. MSC 37620, anterior tooth, "upper" Lisbon Formation, courtesy of James Lowery. **D**. Labial view. **E**. Lingual view. **F**. Mesial view. **G–I**. MSC 37567.1, anterior tooth, basal Gosport Sand. **G**. Labial view. **H**. Lingual view. **I**. Mesial view. **J–L**. MSC 1424.2, lateral tooth, basal Gosport Sand. **J**. Labial view. **K**. Lingual view. **L**. Mesial view. **M–O**. MSC 188.292, lateral tooth, basal Gosport Sand. **M**. Labial view. **N**. Lingual view. **O**. Mesial view. — **P–GG**. *A. minutissima*. **P–R**. MSC 35768.2, lateral tooth, lower Tallahatta Formation. **P**. Labial view. **Q**. Lingual view. **R**. Mesial view. **S–U**. MSC 35768.1, anterior tooth, lower Tallahatta Formation. **S**. Labial view. **T**. Lingual view. **U**. Distal view. **V–X**. MSC 37574.1, lateral tooth, basal Gosport Sand. **V**. Labial view. **W**. Lingual view. **X**. Mesial view. **Y–AA**. MSC 37574.2, anterior tooth, basal Gosport Sand. **Y**. Labial view. **Z**. Lingual view. **AA**. Distal view. **BB–DD**. MSC 37577.1, anterior tooth, basal Lisbon Formation. **BB**. Labial view. **CC**. Lingual view. **DD**. Mesial view. **EE–GG**. MSC 37577.2, anterior tooth, basal Lisbon Formation. **EE**. Labial view. **FF**. Lingual view. **GG**. Mesial view. Scale bars: A–O = 5 mm; P–GG = 2 mm.

PV2000.1.43.5e (2 specimens), ANSP 23416, MSC 188.23, MSC 188.50, MSC 188.94, MSC 188.112.1, MSC 188.129, MSC 188.159, MSC 188.164, MSC 188.169, MSC 188.174, MSC 188.204, MSC 188.233, MSC 188.262–263, MSC 188.278, MSC 188.282–283, MSC 188.292, MSC 188.307, MSC 188.310–311, MSC 188.317–318, MSC 188.330–331, MSC 567, MSC 1424.2, MSC 1424.11, MSC 2171.1–6, MSC 2171.8–13, MSC 2175.49, MSC 2175.64, MSC 2175.70, MSC 2175.75–76, MSC 2372.5, MSC 2372.13, MSC 2384.1–2, MSC 12675.5–11, MSC 12686, MSC 36965, MSC 37405.1–2, MSC 37453, MSC 37513, MSC 37567.106, MSC 37568.1–4, MSC 37569, MSC 37608, MSC 37620, MSC 37696, MSC 37890.1–2, MSC 38412.1–2, MSC 38497.1–6, MSC 38507.1–14, MSC 38533.1–4, MSC 38550.1–8, NJSM 24026, WSU CC 538 (4 specimens).

Description

Anterior teeth with tall, erect main cusp. Lingual crown face convex, often with fine longitudinal ridges extending more than half the cusp height. Labial crown face flat, smooth. Single pair of diverging lateral cusplets. Lateral teeth with broader but lower main cusp; cusp distally inclined. Single pair of divergent lateral cusplets; broader and lower than on anterior teeth. Lateroposterior teeth with more distally curving main cusp. Cutting edges of main cusp and lateral cusplets smooth, continuous. Root high, bilobate with short, rounded, diverging lobes. Lingual attachment surface flat; wide and deep nutritive groove. Interlobe area on teeth shallow and U-shaped.

Remarks

Teeth of *A. enniskilleni* were differentiated from the other *Abdounia* species in our sample by having a single pair of divergent cusplets in all tooth positions, and the lingual face of the main cusp generally bears fine lingual ornamentation. Additionally, this species is the largest of those we assign to *Abdounia*, with anterior teeth reaching upwards of 1.5 cm in overall height. Based on our sample of teeth, and several thousand more from the Clinchfield Formation of central Georgia, the teeth of *A. enniskilleni* appear extremely variable. For example, not all teeth exhibit lingual ornamentation, the main cusp within various files vary in width, and the lateral cusplets, especially in anterior positions, range from tall and narrow to low and wide. *Abdounia enniskilleni* is easily distinguished from two species formerly placed within *Abdounia* (see below), *A. recticona* and *A. claibornensis*, by the presence of a single pair of lateral cusplets, as opposed to three-to-four and four-to-eight, respectively, in the latter two taxa.

Stratigraphic and geographic range in Alabama

The specimens we examined were collected from the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACon-6, the basal Lisbon Formation at site ACov-11, the “upper” Lisbon Formation at sites ACh-8 and ACl-3, basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21 and ACl-15. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Abdounia minutissima (Winkler, 1874)
Fig. 31P–GG

Otodus minutissimus Winkler, 1874a: 23.

Scyllium minutissimus – Daimeries 1891: 73.
Scyllium minutissimum – Leriche 1905: 186, pl. 5, fig. 15.
Scyliorhinus minutissumus – White 1931: 65, fig. 80.
Abdounia minutissima – Cappetta 1980a: 37.
Abdounia minutissimus – Baut & Genault 1995: 226.
Scyliorhinus sp. – Maisch *et al.* 2014: 192, fig. 3, 17–19.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 71 isolated teeth; Claiborne Group; GSA-V706, MMNS VP-8192 (3 specimens), MSC 35757.1–2, MSC 35768.1–5, MSC 37573, MSC 37574.1–2, MSC 37575.1–16, MSC 37576.1–3, MSC 37577.1–12, MSC 37694, MSC 37707, MSC 37900.1–5, SC2012.47.49, SC2012.47.50 (9 specimens), SC2012.47.158, WSU 5014, WSU 5015, WSU 5032 (6 specimens).

Description

Teeth small, most not exceeding 4.0 mm high. Main cusp of anterior teeth tall and triangular; cusp wider, lower, distally inclined on lateral teeth. Cusp flanked by single pair of tall triangular lateral cusplets in all tooth positions. Base of lateral cusplets separated from main cusp; cusplets slender, tall, erect. Cutting edges of main cusp and cusplets smooth, continuous. Lingual crown face convex, less so on lateral teeth; labial crown face flat; enameloid smooth. Root bilobate with short, diverging lobes. Lingual attachment surface flat, bisected by deep nutritive groove.

Remarks

The *A. minutissima* anterior teeth in our sample have a single pair of lateral cusplets in all tooth positions, whereas two species formerly placed within *Abdounia* (see below), *A. claibornensis* and *A. recticona*, have three-to-eight pairs. The anterior teeth of *A. minutissima* were distinguished from those of *A. beaugei* by having lateral cusplets that are taller, more slender, and more conspicuously differentiated from the main cusp. The teeth of *A. minutissima* differ from those of *A. enniskilleni* by their smaller size and more gracile appearance, by having a smooth lingual crown face, and by having narrower lateral cusplets.

Cappetta & Case (2016) referred 120 teeth from the contact of the Tallahatta and Lisbon Formation at site ACov-11 to *Abdounia* sp. and questioned the assignment of teeth to *A. minutissima* by Clayton *et al.* (2013). Cappetta & Case (2016) stated that the 120 teeth were similar to those of *A. minutissima*, but noted that they lack short folds at the base of the labial crown face and have a thicker root. However, the type specimens of *A. minutissima* originally illustrated by Winkler (1874a) lack any labial folds, and the presence of such ornamentation was not mentioned by either Winkler (1874a) or later by Daimeries (1891). The presence of faint labial ornamentation on the teeth of *A. minutissima* was first reported by Leriche (1905), but he noted that these vertical striations are extremely faint, almost invisible to the naked eye, and were extremely susceptible to abrasion. This lack of ornamentation on certain teeth is substantiated by its absence on several figured *A. minutissima* specimens by other authors, at least one of which was derived from the type locality in Belgium (see Van den Eeckhaut & De Schutter 2009: pl. 20, fig. 6). Furthermore, an examination of the *A. minutissima* teeth in our sample suggests that the thickness of the root is variable and can be attributed to heterodonty. Additionally, the presence or absence of labial ornamentation, as well as root thickness and cusplet morphology, is variable in large samples of *A. enniskilleni* teeth from both Alabama and South Carolina that we examined. The taxonomic utility of crown ornamentation may not be significant (Purdy *et al.* 2001), as it is also variable within the various species of *Premontreia* that have been identified (Cappetta 1992; Noubhani & Cappetta 1997).

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the Tallahatta Formation at AMo-8, the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Genus ***Pseudabdounia*** gen. nov.

urn:lsid:zoobank.org:act:AAB3C520-7C1D-4D10-9FB2-7DC604A27A57

Type species

Galeocerdo recticonus Winkler, 1874, Eocene, Belgium.

Etymology

The genus name is composed of the Latin prefix '*pseud*-', meaning 'false' and the generic name *Abdounia*, defining a new genus for certain species formerly placed within *Abdounia*.

Diagnosis

Small teeth generally measuring less than 1.0 cm in mesiodistal width. Labial crown face flat to slightly convex; lingual face strongly convex. Main cusp triangular; erect on anterior teeth, distally inclined on lateral teeth. Apex of main cusp bi-convex. Lateral teeth with unique triangular outline in labial and lingual views. Three-to-eight mesial and distal cusplets present. Cusplets extend one-half to two-thirds the height of mesial and distal cutting edges. Cusplets often more in number mesially than distally. Cusplets triangular and largely united to main cusp. Cusplets decrease in size towards the crown base. Smooth mesial and distal cutting edge extends across main cusp and lateral cusplets. Anterior teeth taller than wide; lateral teeth often wider than tall. Root much higher lingually than labially. Deep nutritive groove on lingual root protuberance. Basal face of root flattened. Basal notch visible on some specimens. Root lobes divergent and rounded. Interlobe area shallow; U-shaped or V-shaped.

Remarks

Two species formerly placed within *Abdounia*, *A. clairbornensis* (White, 1956) and *A. recticona* (Winkler, 1874) are referred to this new genus. These two species appear related to the remaining members of *Abdounia* based on their root morphology, as they have a flat basal face, shallow interlobe area, basal notch on some specimens, deep nutritive groove, and divergent and rounded root lobes. These two taxa can be separated from the various Claibornian species of *Abdounia* by having three-to-eight mesial or distal cusplets (as opposed to no more than two pairs on *Abdounia* spp.) and by having lateral teeth with a unique triangular outline in labial and lingual views. The mesial and distal cusplets also extend much higher onto the main cusp than they do on any of the members of *Abdounia*. The two species placed into *Pseudabdounia* gen. nov. are discussed in detail below.

Pseudabdounia claibornensis (White, 1956) gen. et comb. nov.

Fig. 32A–R

Galeorhinus recticonus claibornensis White, 1956: 148, text-fig. 97, pl. 11, fig. 11.

Galeorhinus recticonus claibornensis – Thurmond & Jones 1981: 67, fig. 11.
Abdounia claibornensis – Müller 1999: 48, text-fig. 17, pl. 5, fig. 10–12.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 89 isolated teeth; Claiborne Group; ALMNH PV1993.2.396, ALMNH PV1993.2.397 (17 specimens), MSC 188.73, MSC 188.88, MSC 188.96, MSC 188.1, MSC 188.131, MSC 188.185, MSC 188.207, MSC 188.245, MSC 188.252, MSC 188.258, MSC 188.273, MSC 188.276, MSC 188.280, MSC 35566.1–12, MSC 37538, MSC 37563.1–33, MSC 37564.1–2, MSC 37570.1–2, MSC 37591, MSC 37603, MSC 37611, MSC 37623.1–2, MSC 37625, MSC 37626, MSC 38548.

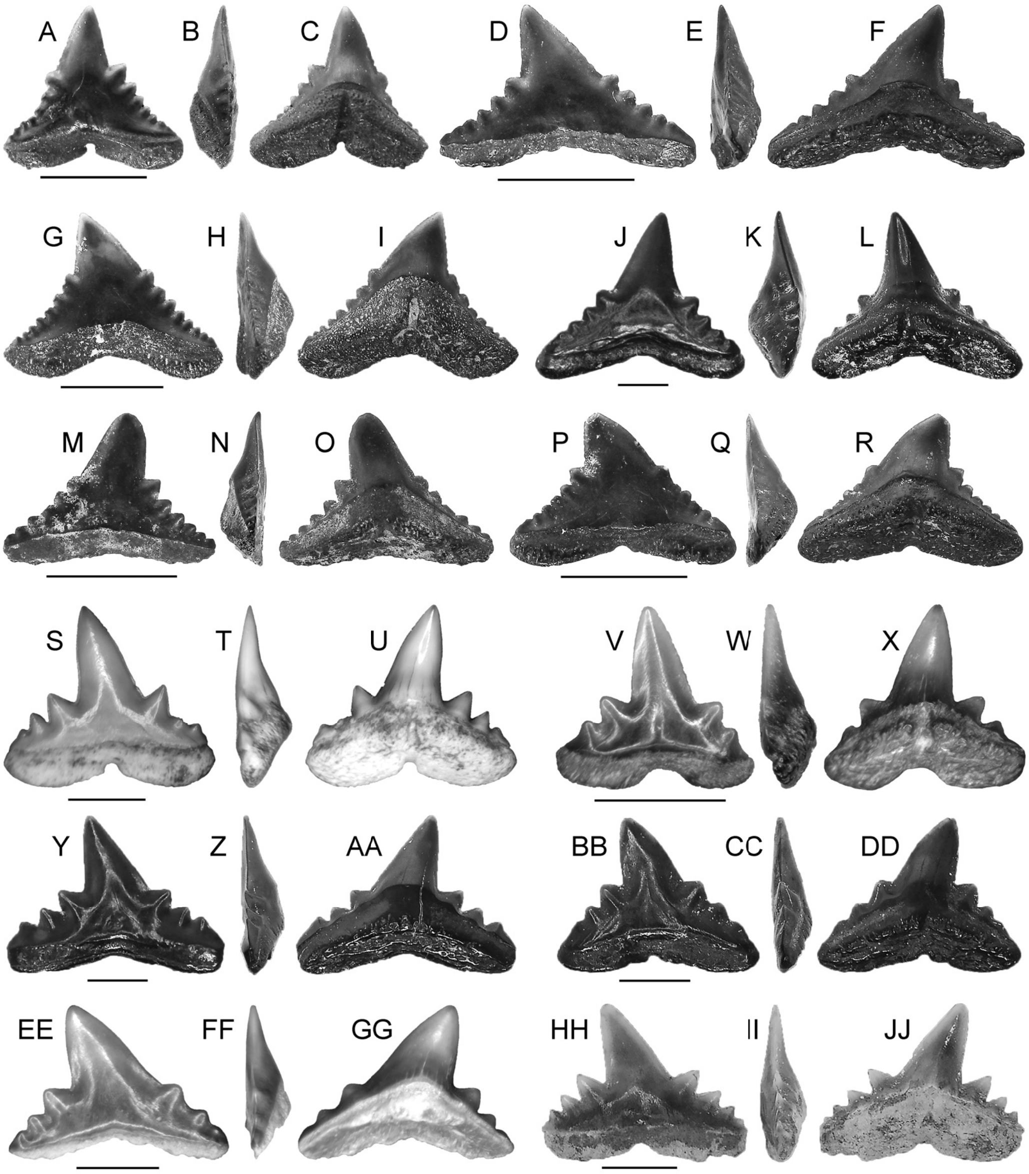


Fig. 32. *Pseudabdounia claibornensis* (White, 1956) gen. et comb. nov. and *P. recticona* (Winkler, 1874) gen. et comb. nov., teeth. **A–R**. *P. claibornensis* gen. et comb. nov. **A–C**. MSC 37591, anterior tooth, basal Gosport Sand. **A**. Labial view. **B**. Mesial view. **C**. Lingual view. **D–F**. MSC 37563.20, lateral tooth, basal Gosport Sand. **D**. Labial view. **E**. Mesial view. **F**. Lingual view. **G–I**. MSC 37563.16, lateral tooth, basal Gosport Sand. **G**. Labial view. **H**. Mesial view. **I**. Lingual view. **J–L**. MSC 188.88, lateral tooth, basal Gosport Sand. **J**. Labial view. **K**. Mesial view. **L**. Lingual view. **M–O**. MSC 37563.28, lateral tooth, basal Gosport Sand. **M**. Labial view. **N**. Mesial view. **O**. Lingual view. **P–R**. MSC 37563.30, lateral tooth, basal Gosport Sand. **P**. Labial view. **Q**. Mesial view. **R**. Lingual view. — **S–JJ**. *P. recticona* gen. et comb. nov. **S–U**. MSC 35767.1, lateral tooth, lower Tallahatta Formation. **S**. Labial view. **T**. Mesial view. **U**. Lingual view. **V–X**. MSC 37318.3, lateral tooth, basal Lisbon Formation. **V**. Labial view. **W**. Mesial view. **X**. Lingual view. **Y–AA**. MSC 37193, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **Y**. Labial view. **Z**. Mesial view. **AA**. Lingual view. **BB–DD**. MSC 37167.1, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **BB**. Labial view. **CC**. Mesial view. **DD**. Lingual view. **EE–GG**. MSC 35767.2, lateral tooth, lower Tallahatta Formation. **EE**. Labial view. **FF**. Mesial view. **GG**. Lingual view. **HH–JJ**. MSC 37167.2, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **HH**. Labial view. **II**. Mesial view. **JJ**. Lingual view. Scale bars: A–R = 5 mm; S–JJ = 2 mm.

Description

Anterior teeth taller than wide or nearly equal in proportion, lateral teeth wider than tall. Teeth with broadly triangular crown; small central cusp flanked by four-to-eight cusplets; distal side usually with one cusplet more than mesial side. Main cusp of anterior teeth erect; distally inclined on lateral and posterior teeth. Cusplets triangular, divergent, decreasing in size towards crown base. Cutting edge of main cusp and cusplets smooth, continuous. Lingual crown face convex; labial face flat; enameloid smooth. Root bilobate with short, diverging lobes. Lingual attachment surface flat; wide and deep nutritive groove. Interlobe area on teeth shallow and U-shaped.

Remarks

White (1956) erected the subspecies *Galeorhinus recticonus claibornensis* based on an isolated tooth collected from the Gosport Sand in Monroe County, AL. Cappetta (1980a) later created the genus *Abdounia* for several species previously assigned to *Scyliorhinus*, including *S. beaugei*, *S. biauriculatus*, *S. minutissimus*, and *S. enniskilleni*, as well as *Galeorhinus recticonus claibornensis*. Based on his analysis of nine teeth from the upper Eocene Piney Point Formation in Virginia, Müller (1999) considered the *claibornensis* morphology distinct enough to elevate it to species status.

Within our sample of Claiborne teeth, those assigned to *Pseudabdounia claibornensis* gen. et comb. nov. appear very similar in overall gross morphology to teeth previously identified as *Abdounia recticona*. The teeth were differentiated by the number of pairs of lateral cusplets, with those assigned to *A. recticona* having three-to-four pairs and those of *P. claibornensis* gen. et comb. nov. having four-to-eight pairs. Although both species can have teeth with four pairs of lateral cusplets, teeth belonging to *P. claibornensis* gen. et comb. nov. can be differentiated by having smaller cusplets relative to the size of the main cusp. An argument could be made that the difference in number of cusplets could be a product of heterodonty, suggesting that teeth with narrower cusps with straight cutting edges are lower teeth, whereas teeth having a broader cusp with convex cutting edges are from the upper dentition. One might also suggest that anterior teeth may be those with fewer pairs of cusplets (three-to-four) that are arranged more in a horizontal row to the main cusp (giving them a T-shaped labial outline). Lateral teeth may be those with five or more cusplets that are oblique to the main cusp (triangular labial outline). However, the teeth in our Claiborne sample suggest that the difference in number of cusplets between *P. claibornensis* gen. et comb. nov. and the *recticona* morphology does not reflect heterodonty within a single species, as teeth from identical tooth positions (monognathic) and sizes (ontogenetic) have been recovered for both morphologies. Furthermore, the specimens in our Claiborne Group sample strongly suggests that the two species are stratigraphically separated, with *P. claibornensis* gen. et comb. nov. being confined to the Gosport Sand and the *recticona* morphology occurring within the stratigraphically older Tallahatta and Lisbon formations. The lack of stratigraphic overlap between these two species strongly suggests that the increase in pairs of cusplets is taxonomically significant and not related to intraspecific heterodonty. This, in turn, indicates that the two morphologies represent distinct taxa, further corroborating Müller's (1999) elevation of the *claibornensis* morphology to species status.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the basal Gosport Sand at site ACl-4 and the Gosport Sand at site ACl-15. Middle Bartonian, Zone NP17.

Pseudabdounia recticona (Winkler, 1874) gen. et comb. nov.

Fig. 32S–JJ

Galeocerdo recticonus Winkler, 1874a: 26.

Galeus recticonus – Leriche 1905: 135, pl. 8, figs 44–53.
Eugaleus recticonus – Casier 1950: 18, pl. 2, fig. 9.
Galeorhinus recticonus – Von der Hocht 1979: 40.
Abdounia recticonus – Cappetta 1980a: 37.
Abdounia recticona – Ward & Wiest 1990: 84.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 168 isolated teeth; Claiborne Group; ANSP 23414, GSA-V694, GSA-V703, MMNS VP-8213 (2 specimens), MSC 34405.4, MSC 35767.1–5, MSC 37115.1–3, MSC 37138, MSC 37155, MSC 37160, MSC 37167.1–4, MSC 37193, MSC 37318.1, MSC 37318.3, MSC 37629.1–5, MSC 37634.1–22, MSC 37635.1, MSC 37647, MSC 37665.1–3, MSC 37679.1–2, MSC 37680.1–3, MSC 38286, MSC 38287.1–2, MSC 38831, MSC 38970, NJSM 24025 (3 specimens), SC2012.47.164 (28 specimens), SC2012.47.178, SC2012.47.46, SC2012.47.47, SC2012.47.48 (27 specimens), WSU 5016, WSU 5018, WSU 5042 (30 specimens), WSU CC 506 (3 specimens), WSU CC 507 (2 specimens), WSU CC 508, WSU CC 509.1, WSU CC 509.2, WSU CC 832.2.

Description

Anterior teeth somewhat taller than wide; lateral teeth mesiodistally wider than tall. Teeth with broadly triangular crown; large, triangular main cusp. Main cusp on anterior teeth erect, flanked by two pairs of cusplets. Main cusp distally inclined on lateral teeth, flanked by three-to-four cusplets; distal side often with one more cusplet than mesial side. Cusplets large compared to overall size of main cusp; triangular, divergent, decreasing in size towards the crown foot; terminal cusplet can be difficult to distinguish from preceding cusplet. Cutting edges on main cusp nearly straight on anterior teeth, more convex on lateral teeth; all cutting edges smooth and continuous. Labial crown face flat; lingual face concave; crown enameloid is smooth. Root bilobate with short, pointed to rounded, diverging lobes. Lingual attachment surface flat, bisected by deep nutritive groove.

Remarks

The teeth of *Pseudabdounia recticona* gen. et comb. nov. have two-to-four pairs of lateral cusplets, distinguishing them from those of *Abdounia enniskilleni* and *Abdounia minutissima*, which have only a single pair. Teeth of *Pseudabdounia claibornensis* gen. et comb. nov. have four-to-eight pairs of cusplets. Although the anterior teeth of *A. beaugei* only have a single pair of lateral cusplets, the lateral teeth have two pairs. These lateral teeth differ from those of *P. recticona* gen. et comb. nov. by having lateral cusplets that are more separated from the main cusp. In contrast, the cusplets on the lateral teeth of *P. recticona* gen. et comb. nov. are joined to the main cusp and the teeth are more broadly triangular in outline.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the Tallahatta Formation at site AMo-8, the contact of the Tallahatta and Lisbon formations at sites ACh-14, ACov-11, and ACon-6, the basal Lisbon Formation at site ACov-11, and the contact of the Lisbon Formation and Gosport Sand at site AMo-4. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Genus ***Physogaleus*** Cappetta, 1980

Type species

Trigonodus secundus Winkler 1876, Lutetian, Belgium.

Physogaleus alabamensis (Leriche, 1942) comb. nov.

Fig. 33

Galeocerdo alabamensis Leriche, 1942: 48, pl. 4, fig. 2.

Galeocerdo alabamensis – Thurmond & Jones 1981: 63, fig. 28, right.
Galeocerdo latidens – Van den Eeckhaut & De Schutter 2009: pl. 20, figs 9–11. — Clayton *et al.* 2013: 68, fig. 3j. — Cappetta & Case 2016: 57, pl. 8, 12–16.
Galeocerdo eaglesomei – Van den Eeckhaut & De Schutter 2009: pl. 20, fig. 8.
Physogaleus sp. – Cappetta & Case 2016: 58, pl. 7, figs 12–13.
Galeorhinus sp. – Pandey *et al.* 2018: fig. 4a–b.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 507 isolated teeth; Claiborne Group; ALMNH PV1989.4.125a (2 specimens), ALMNH PV1989.4.21 (2 specimens), ALMNH PV1989.4.219b (6 specimens), ALMNH PV1992.28.17 (2 specimens), ALMNH PV1992.28.35 (6 specimens), ALMNH PV2000.1.43.3, ALMNH PV2005.6.441, ALMNH PV2016.4.25, MMNS VP-8197 (19 specimens), MMNS VP-8198 (3 specimens), MMNS VP-8199 (122 specimens), MMNS VP-8217 (7 specimens), MMNS VP-8948 (2 specimens), MMNS VP-8949, MSC 2180.1, MSC 2180.3, MSC 2381.2, MSC 2382.1–3, MSC 34405.1–4, MSC 34405.6MSC 34408.8, MSC 34408.10–12, MSC 37020, MSC 37104, MSC 37105.1–4, MSC 37107, MSC 37137.1–3, MSC 37144, MSC 37145, MSC 37154.1–3, MSC 37300, MSC 37344, MSC 37628, MSC 37635.2, MSC 37637.1–2, MSC 37653.1–2, MSC 37655.1–2, MSC 37663.1–2, MSC 37676, MSC 38152, MSC 38153.1–5, MSC 38154.1–10, MSC 38155.1–2, MSC 38156.1–12, MSC 38169, MSC 38170.1–4, MSC 38190.1–2, MSC 38191, MSC 38192.1–32, MSC 38193.1–4, MSC 38195.1–2, MSC 38215, MSC 38216.1–2, MSC 38242.1–3, MSC 38243.1–3, MSC 38244.1–11, MSC 38245.1–9, MSC 38285.1–3, MSC 38288, MSC 38318.1–4, MSC 38319.1–4, MSC 38320, MSC 38321.1–3, MSC 38427.1–13, MSC 38511.1–2, SC2012.47.166 (9 specimens), SC2012.47.174 (9 specimens), SC2012.47.184 (12 specimens), SC2012.47.206 (85 specimens), SC2012.47.252 (9 specimens), WSU 1, WSU 2, WSU 5001, WSU 5039 (17 specimens), WSU CC 527 (2 specimens), WSU CC 533 (2 specimens), WSU CC 832.1 (2 specimens).

Description

Anterior teeth with nearly triangular crown; mesial and distal cutting edges slightly convex. Lingual crown face convex; labial face flat to very weakly convex; crown enameloid smooth. Mesial cutting edge denticulated along lower two-thirds, upper two-thirds smooth. Distal cutting edge similar, contiguous or with slightly differentiated distal heel. Denticulation on distal edge decreases in size basally. Upper part of mesial and distal cutting edges form triangular, nearly erect cusp. Root bulky, bilobate, with low, elongated, highly divergent lobes; pronounced lingual boss bisected by nutritive groove, which contains large nutritive foramen. Lateral teeth wide, with more convex mesial cutting edge, short distal cutting edge, distally directed cusp; conspicuous distal heel separated from cutting edge by pronounced notch; heel with up to 12 serrations, decreasing in size basally. Root wider, more labiolingually compressed than anterior teeth. Root lobes generally rounded, widely diverging; interlobe area weakly concave to absent. Basal root face distinctly flattened. Conspicuous nutritive groove on lingual root boss; multiple foramina located on labial root face. Gynandric heterodonty expressed as male lower anterior teeth with taller, mesiodistally thinner, more sigmoidal crown than female teeth.

Remarks

Numerous teeth in our sample appear to be conspecific with *Galeocerdo alabamensis*, a taxon erected by Leriche (1942) based on a single tooth derived from Jackson Group deposits at Cocoa in Choctaw

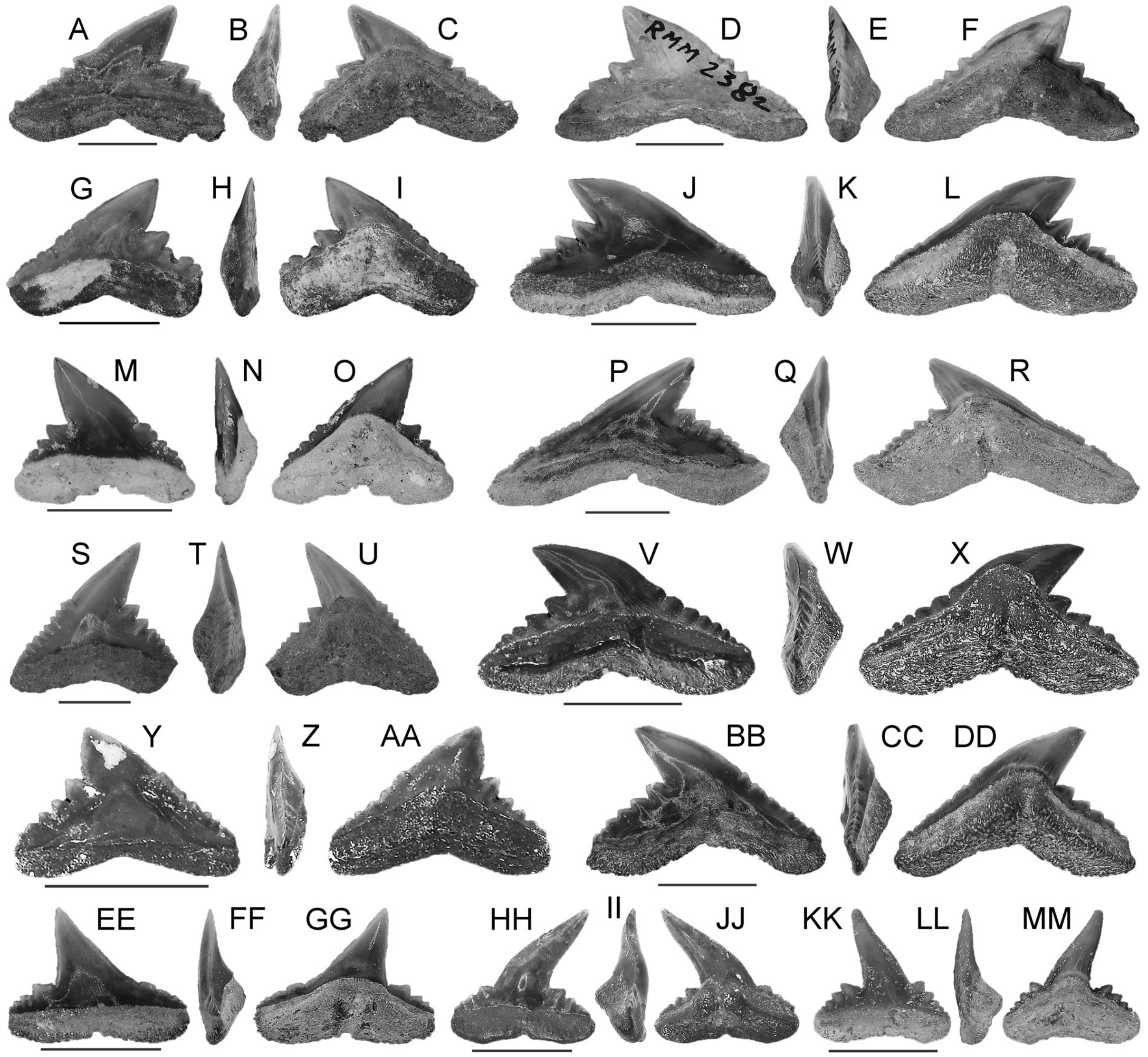


Fig. 33. *Physogaleus alabamensis* (Leriche, 1942) comb. nov., teeth. **A–C**. MSC 2382.1, lateral tooth, Gosport Sand. **A**. Labial view. **B**. Mesial view. **C**. Lingual view. **D–F**. MSC 2382.3, lateral tooth, Gosport Sand. **D**. Labial view. **E**. Mesial view. **F**. Lingual view. **G–I**. MSC 34408.2, lateral tooth, lower Tallahatta Formation. **G**. Labial view. **H**. Mesial view. **I**. Lingual view. **J–L**. MSC 38154.1, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **J**. Labial view. **K**. Mesial view. **L**. Lingual view. **M–O**. MSC 38156.1, anterolateral tooth, lower Tallahatta Formation. **M**. Labial view. **N**. Mesial view. **O**. Lingual view. **P–R**. MSC 38154.3, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **P**. Labial view. **Q**. Mesial view. **R**. Lingual view. **S–U**. MSC 37154.3, anterolateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **S**. Labial view. **T**. Mesial view. **U**. Lingual view. **V–X**. MSC 38485.9, lateral tooth, basal Lisbon Formation. **V**. Labial view. **W**. Mesial view. **X**. Lingual view. **Y–AA**. MSC 38242.2, lateral tooth, basal Gosport Sand. **Y**. Labial view. **Z**. Mesial view. **AA**. Lingual view. **BB–DD**. MSC 38485.2, lateral tooth, basal Lisbon Formation. **BB**. Labial view. **CC**. Mesial view. **DD**. Lingual view. **EE–GG**. MSC 38511.1, lateral tooth, basal Gosport Sand. **EE**. Labial view. **FF**. Mesial view. **GG**. Lingual view. **HH–JJ**. MSC 37144, male anterior tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **HH**. Labial view. **II**. Mesial view. **JJ**. Lingual view. **KK–MM**. MSC 38156.6, male anterior tooth, lower Tallahatta Formation. **KK**. Labial view. **LL**. Mesial view. **MM**. Lingual view. Scale bars = 5 mm.

County, AL. Although Leriche (1942: 11) did not provide more specific details regarding the stratigraphic horizon of this tooth, he noted that the collection of teeth he examined was collected "by C. Schuchert in Alabama and Mississippi, partly in the *Zeuglodon* beds." In Alabama, deposits within the town of Cocoa were designated the type section for the Cocoa Sand Member of the Yazoo Clay of the Jackson Group, the upper portion of which grades into a *Zeuglodon*-bearing bed (Cooke 1933). Thus, it can be said with some certainty that the *G. alabamensis* holotype was collected from the upper portion of the Priabonian Cocoa Sand Member.

Upon reexamination of the holotype of *G. alabamensis*, USNM 8256, we determined that the species name is valid and that it is more appropriately assignable to *Physogaleus*, not *Galeocerdo*. USNM 8256 exhibits several characteristics that better ally it with *Physogaleus*, including a mesiodistally thinner crown that is sinuous in profile view and smooth cutting edges (although cusplets are developed on the base of the mesial edge and on the distal heel). In contrast, mesial cutting edges of all the species of *Galeocerdo* examined, both fossil and extant (for a discussion on the differences between *Physogaleus* and *Galeocerdo*, see *Galeocerdo clarkensis* and *G. eaglesomei* below), have a thick, flat crown, completely (or nearly completely) serrated mesial cutting edge, and serrated distal cutting edge. Furthermore, in a comparison with the teeth in our Claiborne sample, we conclude that USNM 8256 represents an upper lateral tooth, and that the dentition of this species is very similar to that of another Claiborne species, *Physogaleus secundus*. Our sample includes numerous teeth of both species, from all jaw positions, including upper and lower anterior, lateral, and symphyseal positions, as well as male teeth. These two taxa are differentiated from each other by the number of mesial denticulations and distal cusplets present, with teeth of *Physogaleus alabamensis* comb. nov. having well-defined cusplets on the mesial cutting edge that extend up to two-thirds the height of the crown, and up to 12 denticulations on the distal heel. In contrast, *P. secundus* has indistinct, if any, denticulation that is limited to the lower part of the mesial cutting edge, and four or less cusplets on the distal heel. Although these differences could be attributed to ontogeny within a single species, our sample of both morphologies contains teeth ranging in mesiodistal width from 4 mm to 17 mm. This indicates that the number of denticulations does not increase with the age of the animal (ontogeny), but rather that this is a taxonomically useful characteristic that can be used to differentiate these two species.

Several other Eocene species of *Physogaleus* have been described in the literature, including *P. americanus* (Case, 1994), *P. cuvieri* (Agassiz, 1835), *P. latecuspidatus* Müller, 1999, *P. rosehillensis* Case & Borodin, 2000, and *P. secundus* (Winkler, 1876). A comparison to these varied taxa indicates that the *P. alabamensis* comb. nov. morphology is both unique and valid. The differences between *P. alabamensis* comb. nov. and *P. secundus* have been noted above, and *P. rosehillensis* differs by having fewer denticulations than *P. alabamensis* comb. nov. Also, Cappetta & Case (2016) have suggested that the *rosehillensis* morphology should be considered a junior synonym of *P. secundus* because it falls within the morphological range of this latter taxon. Although the teeth of *P. latecuspidatus* Müller, 1999 have more defined mesial denticles than generally observed on *P. secundus*, it still has fewer mesial denticles and distal cusplets than on *P. alabamensis* comb. nov. *Physogaleus latecuspidatus* may also fall within the morphological range, and could be considered a junior synonym of *P. secundus*. The teeth of *P. cuvieri* (Agassiz, 1835) have three-to-five distal cusplets and very few, if any, mesial denticles. Not only do the number of mesial denticles and distal cusplets separate these teeth from those of *P. alabamensis* comb. nov., but Fanti *et al.* (2016) provided a convincing argument that *P. cuveri* instead belongs in *Galeorhinus*. The teeth of *P. alabamensis* comb. nov. differ from those of *P. americanus* by having more mesial denticles and distal cusplets, and by lacking the single large mesial cusplet as seen on the *P. americanus* type specimens (see Case 1994a: figs 214–218).

The *P. alabamensis* comb. nov. teeth in our sample most closely resemble those of the Oligocene and Miocene *Physogaleus latus* (Storms, 1894) as both have distinct mesial and distal cusplets. The teeth of *P. alabamensis* comb. nov., however, can be differentiated from this latter taxon by the number of distal cusplets which Storms (1894) reported never exceeds five on *P. latus*, although as many as 12 can be present on *P. alabamensis* comb. nov. The similarity in morphology between these two species, and the slightly younger stratigraphic age of *P. latus*, suggests that these two taxa might be closely aligned.

Thurmond & Jones (1981) recognized the validity of the *alabamensis* morphology, noting the sinuosity of its crown. Our reexamination of their two figured specimens revealed that one specimen belongs to *P. alabamensis* comb. nov. (fig. 28, right), but the other (fig. 28, left) is *Galeocerdo eaglesomei*. Manning & Standhardt (1986) suggested that *Galeocerdo clarkensis* was a junior synonym of *Galeocerdo alabamensis* and that the former represented the upper teeth of the latter. However, serrations on the teeth of *G. clarkensis* are compound and extend nearly to the cusp apex on the mesial and distal edges (see below), whereas cusplets are not serrated on *P. alabamensis* comb. nov. and cutting edges on the main cusp are smooth. This indicates that the morphologies belong to entirely different taxa. Parmley & Cicimurri (2003) later identified teeth within their sample from the Clinchfield Formation in Georgia as belonging to *Galeocerdo alabamensis*, noting that the teeth were completely serrated and that serrations were compound. Their determination was based on White's (1956) identification of teeth from South Carolina as *G. alabamensis*, but upon our reexamination, it is clear that Leriche's (1942) *alabamensis* holotype is significantly different from the Clinchfield material. Our reexamination of *Galeocerdo* teeth from the Clinchfield Formation suggests that they compare more favorably to *Galeocerdo clarkensis*.

Several teeth in our sample appear conspecific to those illustrated by Van den Eeckhaut and De Schutter (2009: pl. 20, figs 9–11) as *Galeocerdo latidens*. Not only are these teeth similar in overall form to *Physogaleus alabamensis* comb. nov., they also have the same number of cusplets on the mesial and distal cutting edges, and lack serrations above the distal notch and on the upper third of the mesial blade. Van den Eeckhaut & De Schutter (2009: pl. 20, fig. 8) also illustrated a tooth that they assigned to *G. eaglesomei*, but this specimen lacks denticulations on the upper portion of the crown, and it exhibits a pronounced distal notch, a characteristic not well defined on the teeth of *G. eaglesomei*. We believe that the two teeth are more appropriately assigned to *Physogaleus*, and that they are comparable to *P. alabamensis* comb. nov. as described above.

Both Clayton *et al.* (2013: fig. 3j) and Cappetta & Case (2016: pl. 8, figs 12–16) illustrated teeth that they identified as *Galeocerdo latidens* that we herein refer to *P. alabamensis* comb. nov. These teeth all have more than four cusplets on the distal heel, they have well-defined mesial denticles that do not extend to the cusp apex, and serrations are lacking on the cutting edges. Cappetta & Case (2016: 58, pl. 7, figs 12–13) also described teeth that they assigned to *Physogaleus* sp., noting the morphology was common in the Ypresian of Prémontré in the Paris Basin. It is our opinion that these teeth are also conspecific with *P. alabamensis* comb. nov.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Meridian Sand Member of the Tallahatta Formation and the lower Tallahatta Formation at site ADl-1, the Tallahatta Formation at site AMo-8, the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11, the "upper" Lisbon Formation at site ACl-3, the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21 and ACl-15. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Physogaleus secundus (Winkler, 1876)

Fig. 34

Trigonodus secundus Winkler, 1876: 20.
Trigonodus tertius Winkler, 1876: 21.

Physodon secundus – Leriche 1905: 189, pl. 8, figs 6, 17, 18.
Carcharias (*Physodon*) *secundus* – Priem 1908: 109.
Carcharias (*Physodon*) *tertius* – Leriche 1922: 183.
Galeorhinus sp. cf. *G. falconeri* – White 1956: 144–145, fig. 149.
Galeorhinus cf. *falconeri* – Thurmond & Jones 1981: 67–68.
Rhizoprionodon secundus – Bor 1980: 7, pl. 1, fig. 2.
Physogaleus secundus – Cappetta 1980a: 37, pl. 5.
Physogaleus tertius – Cappetta 1980a: 38.
Scoliodon secundus – Kruckow & Thies 1990: 57.
Abdounia recticona – Maisch *et al.* 2014: figs 3, 5–6.

Material examined

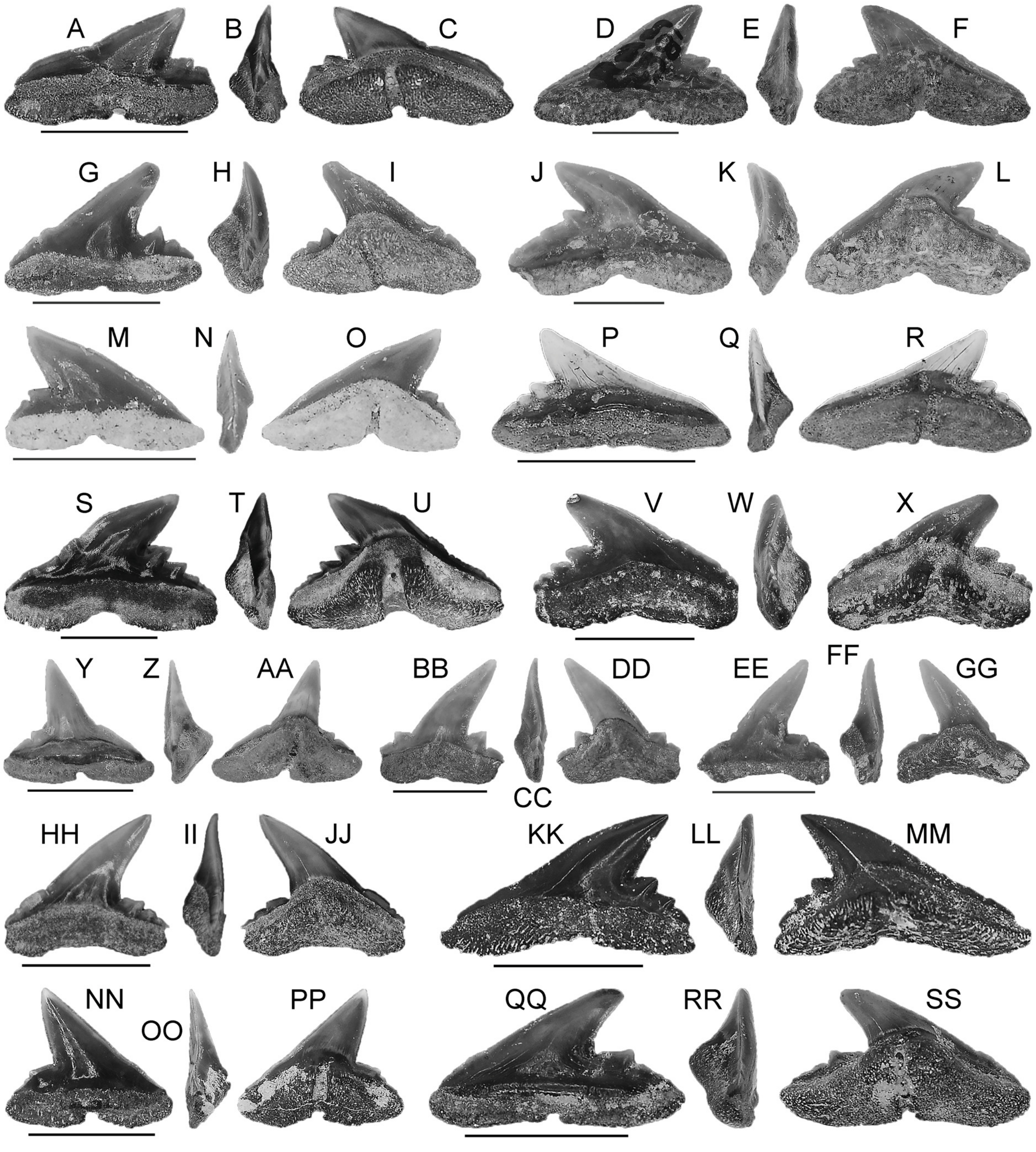
UNITED STATES OF AMERICA – **Alabama** • 786 isolated teeth; Claiborne Group; ALMNH PV1989.4.125b, ALMNH PV1989.4.219c (3 specimens), ANSP 23415, ANSP 23420, GSA-V713, MMNS VP-8191, MMNS VP-8214 (2 specimens), MSC 1424.12, MSC 188.82, MSC 188.128, MSC 188.217, MSC 2381.1, MSC 2381.3, MSC 34405.3, MSC 34405.5, MSC 34405.7–10, MSC 34405.13, MSC 34405.15, MSC 34408.1, MSC 34408.5–7, MSC 34408.9, MSC 34408.11–13, MSC 35736.1–2, MSC 35765.1–21, MSC 35770.1–72, MSC 35771.1–12, MSC 36168, MSC 36179, MSC 37116, MSC 37120.1–4, MSC 37139, MSC 37151, MSC 37156, MSC 37165, MSC 37187.1–5, MSC 37188, MSC 37201, MSC 37245.1–6, MSC 37247.1–8, MSC 37262.1–4, MSC 37275.1–7, MSC 37283, MSC 37298, MSC 37327.1–72, MSC 37353.3, MSC 37456.1–12, MSC 37509.1–17, MSC 37557.1–11, MSC 37610.1–3, MSC 37613.1–4, MSC 37633.1–2, MSC 37639.1–2, MSC 37659.1–2, MSC 37661, MSC 37669.1–6, MSC 37899, MSC 38198.1–3, MSC 38428, MSC 38467.1–2, MSC 38481.1–81, MSC 38510.1–4, MSC 38529, MSC 38545, MSC 38627, MSC 38832, MSC 38861, MSC 38968.1–2, NJSM 24027 (2 specimens), SC2012.47.57, SC2012.47.58, SC2012.47.59 (2 specimens), SC2012.47.60 (56 specimens), SC2012.47.61 (2 specimens), SC2012.47.62 (2 specimens), SC2012.47.63 (2 specimens), SC2012.47.64 (2 specimens), SC2012.47.65 (63 specimens), SC2012.47.66, SC2012.47.67, SC2012.47.68 (8 specimens), SC2012.47.161, SC2012.47.173 (2 specimens),

Fig. 34 (opposite page)**.** *Physogaleus secundus* (Winkler, 1876), teeth. **A**–**C**. MSC 37116, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **A**. Labial view. **B**. Mesial view. **C**. Lingual view. **D**–**F**. MSC 2381.3, lateral tooth, Gosport Sand. **D**. Labial view. **E**. Mesial view. **F**. Lingual view. **G**–**I**. MSC 35770.1, anterolateral tooth, lower Tallahatta Formation. **G**. Labial view. **H**. Mesial view. **I**. Lingual view. **J**–**L**. MSC 35771.1, lateral tooth, lower Tallahatta Formation. **J**. Labial view. **K**. Mesial view. **L**. Lingual view. **M**–**O**. MSC 35770.3, lateral tooth, lower Tallahatta Formation. **M**. Labial view. **N**. Mesial view. **O**. Lingual view. **P**–**R**. MSC 37245.1, lateral tooth, basal Lisbon Formation. **P**. Labial view. **Q**. Mesial view. **R**. Lingual view. **S**–**U**. MSC 37188, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **S**. Labial view. **T**. Mesial view. **U**. Lingual view. **V**–**X**. MSC 37201, lateral tooth, Meridian Sand Member of the Tallahatta Formation. **V**. Labial view. **W**. Mesial view. **X**. Lingual view. **Y**–**AA**. MSC 37245.3, anterolateral tooth, basal Lisbon Formation. **Y**. Labial view. **Z**. Mesial view. **AA**. Lingual view. **BB**–**DD**. MSC 37245.2, lower anterior tooth, basal Lisbon Formation. **BB**. Labial view. **CC**. Mesial view. **DD**. Lingual view. **EE**–**GG**. MSC 35770.2, lower anterior tooth, lower Tallahatta Formation. **EE**. Labial view. **FF**. Mesial view. **GG**. Lingual view. **HH**–**JJ**. MSC 37156, anterolateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **HH**. Labial view. **II**. Mesial view. **JJ**. Lingual view. **KK**–**MM**. MSC 37298, lateral tooth, basal Lisbon Formation. **KK**. Labial view. **LL**. Mesial view. **MM**. Lingual view. **NN**–**PP**. MSC 37557.2, anterolateral tooth, basal Gosport Sand. **NN**. Labial view. **OO**. Mesial view. **PP**. Lingual view. **QQ**–**SS**. MSC 37557.1, anterolateral tooth, basal Gosport Sand. **QQ**. Labial view. **RR**. Mesial view. **SS**. Lingual view. Scale bars = 5 mm.

SC2012.47.182 (9 specimens), SC2012.47.208 (27 specimens), SC2012.47.209 (26 specimens), WSU 5041 (143 specimens), WSU CC 444, WSU CC 511 (2 specimens), WSU CC 529 (3 specimens), WSU CC 530.1 (2 specimens), WSU CC 531 (3 specimens), WSU CC 534 (2 specimens), WSU CC 582 (3 specimens).

Description

Anterior teeth with triangular crown; mesial and distal edges slightly convex. Lingual crown face convex; labial face nearly flat; enameloid smooth. Mesial cutting edge smooth to very weakly denticulated basally. Distal cutting edge smooth apically, denticulated basally. Distal heel contiguous or only weakly differentiated from cutting edge. Up to four denticulations on distal heel that decrease in



size basally. Upper part of mesial and distal cutting edges form triangular, slightly distally directed cusp. Root bulky, bilobate, with low, elongated lobes; pronounced lingual boss bears nutritive groove, which contains large nutritive foramen. Weakly U-shaped interlobe area. Lateral teeth wide, with more convex mesial cutting edge, short distal cutting edge, cusp distally directed. Indistinct denticulation sometimes present at base of mesial edge. Conspicuous distal heel bearing one-to-four denticles, decreasing in size basally; distal heel separated from cutting edge by pronounced notch. Root wider, more labiolingually compressed than on anterior teeth. Root lobes generally rounded, widely diverging; interlobe area from flat to weakly concave. Conspicuous nutritive groove on lingual root boss; multiple foramina located on labial root face. Basal root face flattened. Gynandric heterodonty evident, with male lower anterior teeth being taller, mesiodistally thinner, more sigmoidal than female teeth.

Remarks

Winkler (1876) erected *Physogaleus secundus* and *P. tertius* within the same publication, but Kent (1999a) viewed these two taxa as conspecific because he believed the characteristics distinguishing them (*P. tertius* with taller main cusp and larger overall size) were likely the result of gynandric and/or ontogenetic heterodonty. We agree with Kent (1999a) that the two species are conspecific, and because both taxa were named within the same publication, *P. secundus* has priority because it was listed first.

We assigned Claiborne teeth to *P. secundus* based on the number of denticles on the mesial cutting edge and distal heel cusplets. The anterior teeth of *P. secundus* generally have one-to-two mesial and distal cusplets, lateral teeth generally have up to four on the distal heel, and mesial denticles, if present, lack definition and tend to be restricted to the crown base. In contrast, the lateral teeth of *Physogaleus alabamensis* comb. nov. have up to 12 distal cusplets and well-defined mesial denticles that can extend almost two-thirds the height of the crown. Furthermore, *P. alabamensis* comb. nov. anterior teeth have three or more sets of mesial denticles and distal cusplets. Maisch *et al.* (2014: fig. 3, 5–6) identified an *Abdounia recticona* (recognized here as *Pseudabdounia recticona* gen. et comb. nov.) tooth from the contact of the Tallahatta and Lisbon formations in Choctaw County. Although this tooth has a superficial resemblance to *Pseudabdounia recticona* gen. et comb. nov., we refer it to *Physogaleus secundus* because the denticles are rounded, not triangular and divergent as seen on the former taxon, and the mesial denticles are irregular and not clearly defined.

Although superficially similar to *Galeorhinus*, teeth of *P. secundus* and *P. alabamensis* comb. nov. lack a thickened labial crown base. *Physogaleus* lateral teeth could be confused with *Galeocerdo*, but they can be differentiated by the lack of serrations on the main cusp (see *Galeocerdo clarkensis* and *Galeocerdo eaglesomei* below). On the *P. secundus* and *P. alabamensis* comb. nov. teeth examined, these cusplets are nearly always absent above the distal notch, and denticles rarely extend more than two-thirds the height of the crown on the mesial edge.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Meridian Sand Member of the Tallahatta Formation and the lower Tallahatta Formation at site ADl-1, the Tallahatta Formation at site AMo-8, the contact of the Tallahatta and Lisbon formations at sites ACh-14, ACov-1, ACov-11, and ACon-6, the basal Lisbon Formation at site ACov-11, the “upper” Lisbon Formation at site ACh-8, the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21 and ACl-15. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Family Galeocerdidae Herman *et al.*, 2010

Genus ***Galeocerdo*** Müller & Henle, 1837

Type species

Squalus cuvier Péron & Leseur, 1822, Recent.

Galeocerdo eaglesomei White, 1955
Fig. 35

Galeus latidens Agassiz, 1843: pl. 26, figs 22–23.
Galeocerdo eaglesomei White, 1955: 320, text fig. 1.

Galeocerdo latidens – White 1926: 26, pl. 6, figs 1–21. — Pedroni 1844: 283. — Stromer 1905b: 175, pl. 14, figs 10–15.
Galeocerdo alabamensis – Thurmond & Jones 1981: 63, fig. 28, right.
Galeocerdo eaglesomei – Maisch *et al.* 2014: fig. 3, 9–14.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 38 isolated teeth; Claiborne Group; ALMNH PV1989.4.1.1 (11 specimens), ALMNH PV1989.4.151.1a (3 specimens), ALMNH PV1989.4.219a (2 specimens), ALMNH PV1989.4.90, ALMNH PV2000.1.43.4 (8 specimens), ALMNH PV2000.1.44.3, ANSP 23412, ANSP 23418, ANSP 23419, GSA-V695, MMNS VP-7496 (2 specimens), MSC 2378.1, MSC 36904, MSC 37619.1–2, MSC 39039, NJSM 24023.

Description

Teeth broadly triangular, with distally inclined, narrow triangular cusp. Anterior teeth with elongate, sinuous mesial cutting edge; cutting edge becomes more uniformly convex towards commissure. Lower two-thirds to three-quarters of mesial edge coarsely serrated; remainder of edge with much smaller serrations; serrations simple in form. Distal edge short, weakly convex, finely serrated nearly to apex. Anterior teeth with distal heel not well differentiated from distal cutting edge; heel becoming more conspicuous towards commissure. Distal heel elongate, concave, very coarsely serrated; serrations simple, decreasing in size basally. Labial crown face flat; lingual face convex; enameloid smooth. Root bilobate; lobes short, rounded, highly diverging; narrow to broadly U-shaped interlobe area. Lingual root face high, flat, bisected by shallow nutritive groove.

Remarks

Five species of *Galeocerdo* have been reported from Paleogene deposits in Alabama, including *G. aduncus* (Agassiz, 1843), *G. alabamensis* Leriche, 1942, *G. clarkensis* White, 1956; *G. eaglesomei* White, 1955; and *G. latidens* (Agassiz, 1843). Both *G. aduncus* and *G. latidens* were first reported from the "Tertiary of Alabama" by Tuomey (1858); however, these specimens were never illustrated and were destroyed by fire near the end of the Civil War in 1865 (see Ebersole & Dean 2013). Hence, the identity of his material cannot be corroborated. Woodward (1889) assigned 18 teeth, purportedly from Alabama but housed within various NHMUK collections, to *G. aduncus*. White (1956) reexamined Woodward's (1889) specimens and referred several to a new species, *Galeocerdo clarkensis*, and determined that the remaining teeth were indeed correctly identified as *G. aduncus*, but they instead originated from Malta. A few years prior, Leriche (1942) named *Galeocerdo alabamensis* based on a single tooth derived from Priabonian deposits in Choctaw County, AL. Both *G. eaglesomei* and *G. latidens* have since been reported from various Claiborne Group deposits in the state. Westgate (2001), for example, reported 13 *G. latidens* specimens from the Gosport Sand at site ACl-4 (TMM 43412.2) in Clarke

County. Feldmann & Portell (2007) later reported the occurrence of *G. latidens* from the contact of the Tallahatta and Lisbon formations at site ACov-11 in Covington County. However, because these authors never figured their specimens we cannot confirm or refute their identifications. Clayton *et al.* (2013) and Cappetta & Case (2016) also reported *G. latidens* from site ACov-11, but examination of actual and figured specimens leads us to conclude that they all to belong to *Physogaleus*. Thurmond & Jones (1981: fig. 28, left) figured a tooth from Monroe County, AL that they referred to *Galeocerdo alabamensis*, but our reexamination of this tooth (ALMNH PV 2005.6.448) revealed that it instead belongs to *G. eaglesomei*. Maisch *et al.* (2014: fig. 3, 9–14) described and figured two *G. eaglesomei* teeth from the contact of the Tallahatta and Lisbon formations in Choctaw County, and our analysis confirmed their identification.

As part of this study, teeth of Paleogene *Galeocerdo* species that have been reported from Alabama were compared to those within several Recent jaw sets of *Galeocerdo cuvier* Péron & Leseur, 1822, the only extant member of the genus. The purpose of this analysis was to gain a better understanding of the types and degrees of heterodonty (monognathic, dignathic, ontogenetic) occurring within the jaws of *Galeocerdo*. This analysis allowed us to better define the teeth of this genus, test the validity of published differential characteristics for the various reported species, and ultimately help determine whether these species are valid, nominal, or should belong to a different genus. To test for differences that could be attributed to ontogeny, the fossil *Galeocerdo* teeth in our sample were directly compared to those

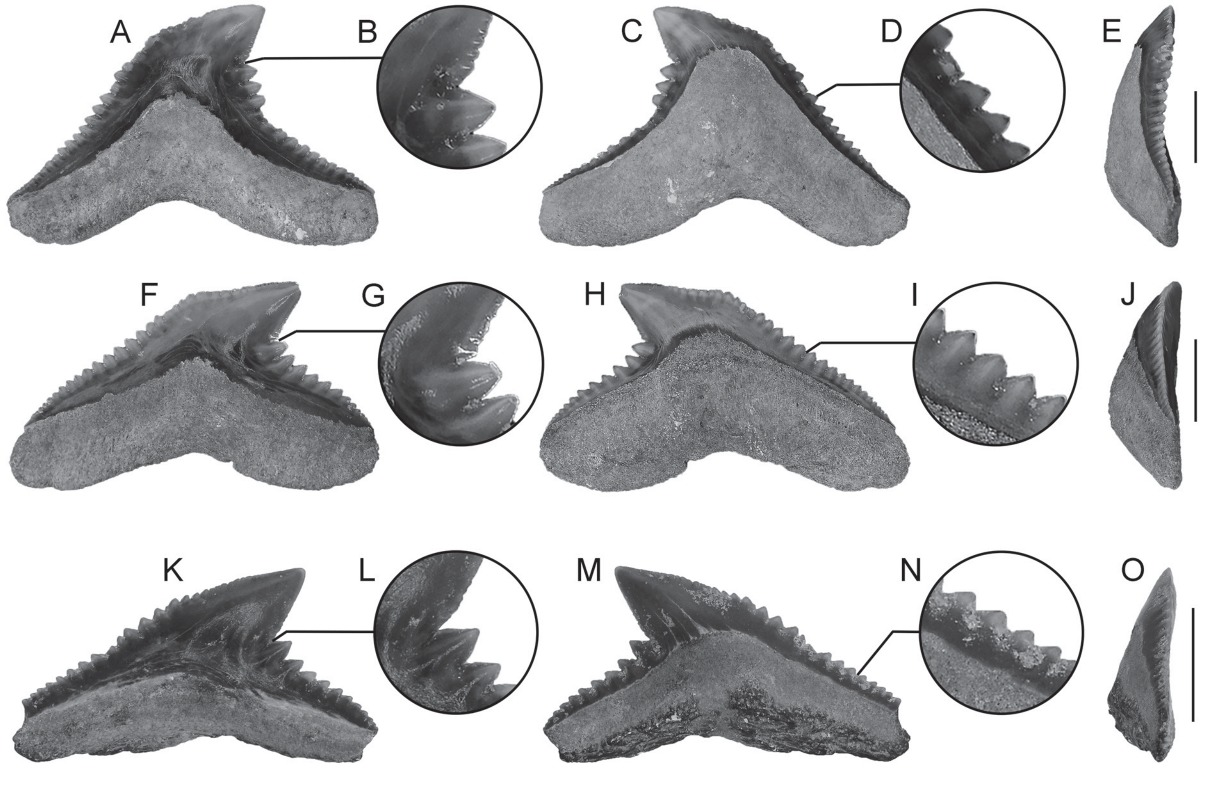


Fig. 35. *Galeocerdo eaglesomei* White, 1955, teeth. **A–E**. MMNS VP–7496.1, anterolateral tooth, “upper” Lisbon Formation. **A**. Labial view. **B**. Close–up of distal notch. **C**. Lingual view. **D**. Close–up of simple mesial serrations. **E**. Mesial view. **F–J**. MMNS VP–7496.2, lateral tooth, “upper” Lisbon Formation. **F**. Labial view. **G**. Close–up of distal notch. **H**. Lingual view. **I**. Close–up of simple mesial serrations. **J**. Mesial view. **K–O**. MSC 37619.1, lateral tooth, “upper” Lisbon Formation, reversed for comparison, courtesy of James Lowery. **K**. Labial view. **L**. Close–up of distal notch. **M**. Lingual view. **N**. Close–up of simple mesial serrations. **O**. Mesial view. Scale bars = 5 mm.

within three sizes of *G. cuvier* jaws. Measured in terms of greatest internal mesiodistal width, the three jaw sizes examined were as follows, small = 11.0 cm; medium = 23.5 cm; and large 40.6 cm. A critical examination and comparison of these three *G. cuvier* jaws provided the following key characteristics that, in turn, helped diagnose the teeth belonging to this genus:

1. Within a jaw, the number of distal heel cusplets decreases the more laterally a tooth is positioned.
2. Among the various jaws, the number of distal heel cusplets on the teeth increases as the shark gets older (presumably because the teeth get larger).
3. Among the various jaws, the tooth serrations become more compound and complex as the shark gets older.
4. Within a jaw, teeth in the anterior and anterolateral files tend to have a mesial edge that is slightly angular. Teeth in the lateral and posterior files have a smoothly concave mesial edge.
5. Within a jaw, teeth in anterior and anterolateral files have a distal edge that is more convex than those in the lateral and posterior positions.
6. Within the jaw, anterior teeth are taller than wide; lateral teeth are wider than tall.
7. Within the jaw, the cusps on the upper teeth are slightly more erect than those in the equivalent position of the lower jaw. This characteristic can only be observed in jaw sets, not on isolated teeth.
8. Within the jaw, the teeth that are about to shed (the oldest teeth) are smaller than the replacement teeth. Furthermore, replacement teeth generally have an additional distal cusplet. This phenomenon was most evident on the smallest jaw, indicating rapid tooth-size increase in juveniles.
9. Within the jaw, serrations on the teeth increase in size apically to the most convex portion of the mesial edge, at which point the serrations decrease in size. Serrations extend nearly to the cusp apex on both the mesial and distal edges.
10. Within the jaw, the serrations on the mesial edge of anterior teeth are larger than those on the distal edge. In the lateral positions, the teeth are more evenly serrated.
11. Among the various jaws, the size difference between the mesial and distal serrations on the anterior teeth was observed on each specimen, suggesting this phenomenon is not related to ontogeny.

Although discernable monognathic heterodonty exists within the dentition of *G. cuvier*, the teeth of this species, regardless of size/age or position, have the following defining characteristics: all have a distally inclined cusp; a conspicuous notch where the distal edge meets the distal heel; a convex mesial edge; serrations that are largest on the medial part of the mesial edge, but much finer serrations on the upper half, extending nearly to the apex; very large serrated cusplets on the distal heel but fine serrations on the distal edge, which extend nearly to the apex.

Galeocerdo eaglesomei exhibits monognathic heterodonty in that the anterior teeth are more erect, whereas lateral teeth have a lower crown with a more distally inclined cusp. Additionally, the distal heel on anterior teeth is not well differentiated from the distal cutting edge but is seen as a transition from very fine serrations on the distal edge to coarse cusplets on the heel. Lateral teeth have a more conspicuous heel, forming more of a notch with the distal cutting edge. Anterior teeth have a more sinuous mesial cutting edge, whereas lateral teeth are more uniformly convex, although basally weakly concave. Upper and lower teeth were difficult to differentiate with certainty, but lower teeth at times have a slight labial bend in profile view.

With regard to *Galeocerdo eaglesomei* and *Galeocerdo latidens*, the latter species was originally erected by Agassiz (1843) based on teeth from an unknown locality and horizon. White (1926) later referred

39 teeth that were derived from Eocene deposits in Nigeria to *G. latidens*. Dartevelle & Casier (1943), however, expressed their opinion that the *G. latidens* teeth figured by White (1926: pl. 6), as well those figured by Stromer (1905b: 175, pl. 14, figs 10–15), differed from the specimens reported by Agassiz (1843: pl. 26, figs 22–23) and possibly represented a new taxon. In agreement with these assessments, White (1955) subsequently assigned the teeth he figured in 1926 to a new species, *Galeocerdo eaglesomei*. White (1955) also referred the teeth figured by Stromer (1905b) to this new taxon and designated a specimen from his 1926 publication (pl. 6: 2) as the holotype. Although we are not certain, White (1926: pl. 6) may have originally referred his specimens to *G. latidens* because the lateral teeth (figs 7–10, 17–21) were wider than tall and appeared conspecific with the type specimen illustrated by Agassiz (1843: pl. 26, figs 22–23), which is a tooth from a lateral or posterior position. It appears that when Dartevelle & Casier (1943) pointed out that several other of White's (1926) teeth did not match Agassiz's (1843) type specimen, White (1955) made the decision to assign his 1926 (pl. 6) teeth, as well as those in Stromer (1905b: pl. 14), to *G. eaglesomei*. However, Stromer's (1905b: pl.14) specimens are of interest because he combined teeth with the *G. eaglesomei* morphology with several lateral teeth (pl. 14, figs 11, 13, 15) that appear to be conspecific with Agassiz's (1843) *G. latidens* holotype. In fact, one of the teeth figured by Stromer (1905b: pl. 14, fig. 15) appears nearly identical to Agassiz's (1843) type specimen, possibly being from the same tooth position (but from the opposite side of the jaw). As part of White's (1955: 320) type description for *G. eaglesomei*, he described how the teeth could be differentiated from those of *G. latidens* by their "greater relative height and shorter base, while the anterior margin is much more convex and posterior emargination less marked owing to the length of the denticles, which also reach nearer to the tip." These characteristics, however, fall within the range of monognathic heterodonty as observed on the Recent jaw sets of *G. cuvier*. Therefore, it is our belief that White (1955) failed to recognize the degree of heterodonty within Recent *Galeocerdo*, leading him to erect a new species, *G. eaglesomei*, for what were instead the anterior teeth of *G. latidens*.

Despite our contention that the *G. eaglesomei* and *G. latidens* morphologies of White (1926, 1955) and Stromer (1905b) are conspecific, the designation of the former as a junior synonym of *G. latidens* is problematic. As explained by Agassiz (1843), his figured holotype was collected from an unknown locality and horizon. Because this likely renders *G. latidens* as a *nomen dubium*, we suggest the usage of *G. eaglesomei* for teeth with this morphology, as it is a name that is available and based on specimens from a known locality and horizon.

It is also our conclusion that many teeth previously referred to "*G. latidens*" (i.e., Thurmond & Jones 1981: fig. 28, right; Van den Eeckhaut & De Schutter 2009: pl. 20, figs 8–11; Clayton *et al.* 2013: fig. 3J; Cappetta & Case 2016: pl. 8, figs 12–16) are misidentified, and instead are lateral teeth belonging to *Physogaleus alabamensis* comb. nov. (Leriche 1942). Teeth of *Galeocerdo* can be differentiated from *P. alabamensis* comb. nov. by the presence of serrated mesial and distal cutting edges, with serrations extending nearly to the cusp apex. Our examination of Recent *G. cuvier* jaws indicates that, these fine serrations are always present (unless taphonomically lost) regardless of tooth size and position, and their presence is therefore not related to heterodonty (monognathic or ontogenetic). On the lateral teeth of both *P. alabamensis* comb. nov. and *P. secundus*, cutting edges are smooth and mesial denticles never reach the main cusp apex.

Although *Galeocerdo* has traditionally been placed within the Carcharhinidae (see Compagno 2005; Cappetta 2012; Nelson *et al.* 2016), recent mitochondrial DNA studies have revealed *Galeocerdo cuvier* to be an outgroup from this otherwise monophyletic family (see López *et al.* 2006; Naylor *et al.* 2012). Furthermore, the dentitions of Recent *G. cuvier* specimens exhibit little dignathic heterodonty, with isolated upper and lower teeth being difficult to distinguish. The presence of strong dignathic heterodonty is a defining characteristic for nearly all members of the Carcharhinidae, as the overall morphology of upper teeth is generally substantially different from that of the lower teeth (see Compagno 1984;

Voigt & Weber 2011). Because of this we follow Herman *et al.* (2010) in placing *Galeocerdo*, and all recognized fossil species, within the monogeneric family Galeocerdidae.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at site ACh-14 and ACon-6, the "upper" Lisbon Formation at site ACl-3, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Galeocerdo clarkensis White, 1956

Fig. 36

Galeocerdo clarkensis White, 1956: 127–128, text figs 24–26, pl. 2, figs 12–14.

Galeocerdo aduncus – Woodward 1889: 446.
Galeocerdo alabamensis – Parmley & Cicimurri 2003: 170–171, fig. 6. — Manning 2003: 374, fig. 21.3.3.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 86 isolated teeth; Claiborne Group; ALMNH PV1993.2.407 (6 specimens), MSC 188.6, MSC 188.26, MSC 188.68, MSC 188.149, MSC 188.255, MSC 188.259, MSC 188.272, MSC 188.308, MSC 2175.21, MSC 2180.2, MSC 2378.2–3, MSC 2382.4, MSC 37402.1–3, MSC 37494.1–49, MSC 37522, MSC 37592, MSC 37604, MSC 37897, MSC 38468, MSC 38469, MSC 38470.1–2, MSC 38509.1–2, MSC 38543.1–5.

Description

Teeth with roughly triangular crown. Mesial cutting edge is uniformly convex, sometimes slightly concave basally. Coarse, weakly compound serrations located at most convex portion of mesial edge; serrations finer basally and apically. Distal cutting edge short, weakly convex, finely serrated nearly to apex, forms distally inclined cusp with mesial edge. Distal heel heavily serrated, separated from distal cutting edge by notch. Heel serrations decrease in size distally; generally, largest serration (just distal to notch) has compound serration pattern on distal side. Labial crown face flat to slightly convex; lingual face convex; enameloid smooth. Root bilobate; lobes short, rounded, divergent; lobes separated by shallow U-shaped interlobe area. Lingual root face high, with weak lingual protuberance bisected by deep nutritive groove.

Remarks

Leriche (1942) erected the species *Galeocerdo alabamensis* based on a single specimen recovered from upper Eocene deposits at Cocoa in Choctaw County, AL. White (1956) later named *G. clarkensis* in part based on specimens that Woodward (1889) reported from the Priabonian Yazoo Clay in Clarke County, Alabama. White (1956) justified his new taxon by stating that the teeth of *G. clarkensis* were evenly serrated on the mesial edge, whereas those on the teeth *G. alabamensis* and *G. latidens* were more coarsely serrated. Thurmond & Jones (1981) recognized the validity and occurrence of both *G. clarkensis* and *G. alabamensis* in Alabama and noted that the two species could be differentiated by the shape of their mesial cutting edge, with that on *G. clarkensis* being smoothly convex and that on *G. alabamensis* being straight, concave, or S-shaped. Manning & Standhardt (1986) later synonymized *G. clarkensis* with *G. alabamensis*, stating, with no justification, that the former were the upper teeth of the latter. This synonymy is in error, as the *alabamensis* morphology is more appropriately assigned to *Physogaleus* (see above).

An examination of high-resolution photographs of White's (1956) syntypes leads us to believe that *Galeocerdo clarkensis* is a valid species that occurs within the Claiborne Group in Alabama. The holotype (NHMUK P.30501) measures 1.3 cm in height and 1.6 cm in mesiodistal width, proportions that suggests it is an anterior tooth. One of syntypes, NHMUK P.30467, measures 1.2 cm in height and 2.0 cm in mesiodistal width, suggesting it is a lateral tooth. The second syntype, NHMUK P.30502, is slightly ablated, but as preserved measures 0.7 cm in height and 1.3 cm in mesiodistal width, suggesting the tooth is from a lateroposterior position. All three of these teeth have compound serrations, an evenly convex mesial edge, and serrations that extend nearly to the apex on both the mesial and distal cutting edges. The presence of an evenly convex mesial edge on all three *G. clarkensis* syntypes indicates that this characteristic is consistent across the tooth row, separating this species from *G. eaglesomei*, whose anterior teeth have a mesial edge that is strongly sinuous. In addition, the development of

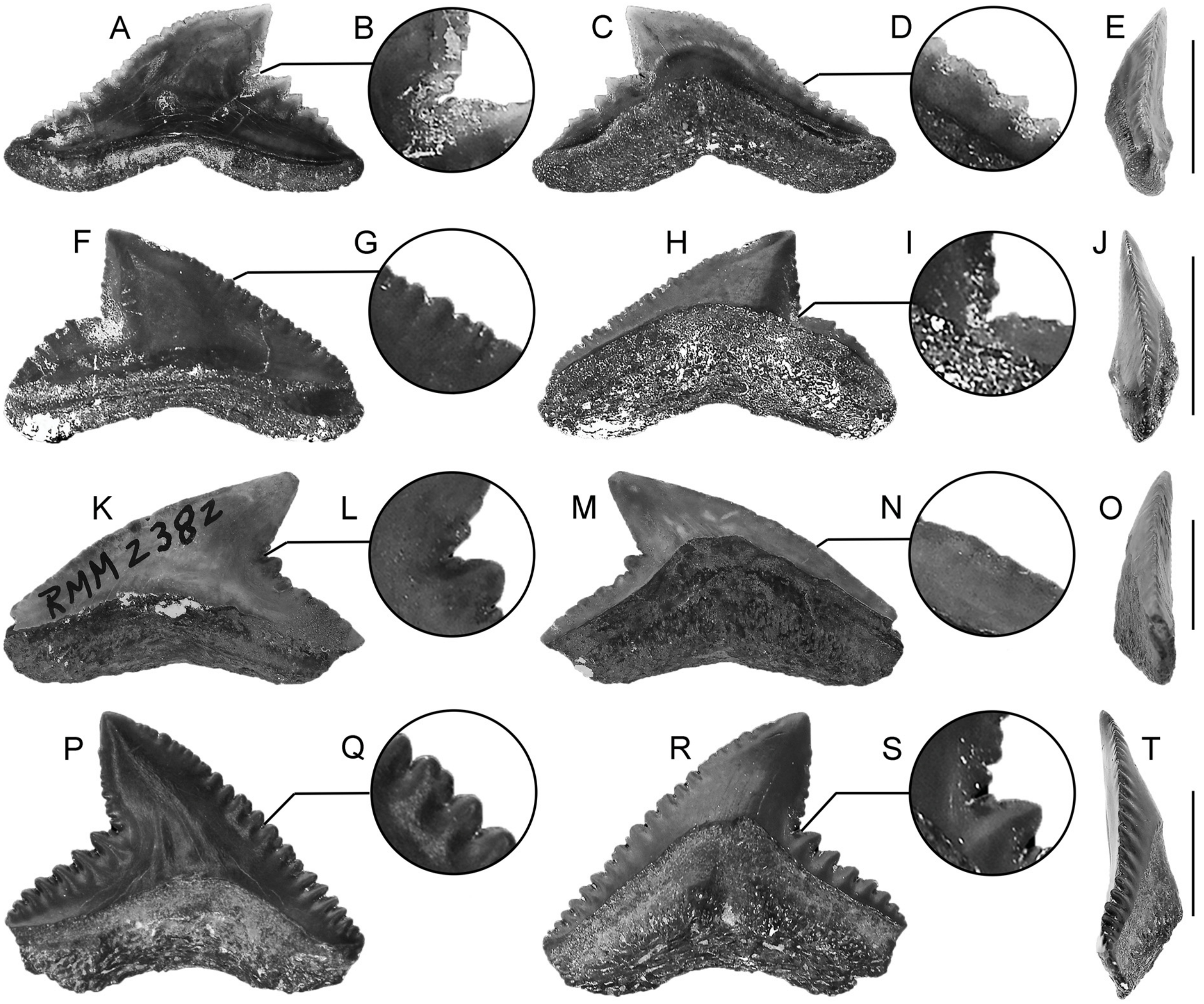


Fig. 36. *Galeocerdo clarkensis* White, 1956, teeth. **A–E**. MSC 188.68, lateral tooth, basal Gosport Sand. **A**. Labial view. **B**. Close–up of distal notch. **C**. Lingual view. **D**. Close–up of mesial compound serrations. **E**. Mesial view. **F–J**. MSC 188.272, lateral tooth, basal Gosport Sand. **F**. Labial view. **G**. Close–up of mesial compound serrations. **H**. Lingual view. **I**. Close–up of distal notch. **J**. Mesial view. **K–O**. MSC 2382.4, lateral tooth, Gosport Sand. **K**. Labial view. **L**. Close–up of distal notch. **M**. Lingual view. **N**. Close–up of mesial serrations. **O**. Mesial view. **P–T**. MSC 37592, anterolateral tooth, basal Gosport Sand. **P**. Labial view. **Q**. Close–up of mesial compound serrations. **R**. Lingual view. **S**. Close–up of distal notch. **T**. Mesial view. Scale bars = 5 mm.

compound serrations on the teeth of *G. clarkensis* is in contrast to *G. eaglesomei*, whose teeth have simple serrations. Our examination of *Galeocerdo* teeth from the Clinchfield Formation in Georgia, identified as *G. alabamensis* by Parmley & Cicimurri (2003), leads us to conclude that they are similar to the *G. clarkensis* teeth reported herein.

We could not confidently differentiate upper and lower teeth for this species. Monognathic heterodonty is expressed as anterior teeth that are nearly as tall as wide, and lateral teeth are much wider than tall with a more inclined cusp. Lateral teeth of *G. clarkensis* could be confused with the lateral teeth of *Carcharhinus mancinae* sp. nov., as both have convex mesial cutting edges and compound serrations. However, the distal notch on the teeth of *C. mancinae* sp. nov. is much less defined and the lingual root protuberance is much more pronounced and “pinched.”

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the basal Gosport Sand at sites ACl-4 and AMo-4, and the Gosport Sand at site ACh-21. Middle Bartonian, Zone NP17.

Galeomorphii indet.

Fig. 37

cf. “*Synechodus*” sp. – Clayton *et al.* 2013: fig. 2a.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 isolated tooth; Claiborne Group; SC2012.47.32.

Description

Tooth fragment consisting of the distal shoulder with three cusplets preserved. Cusplets cylindrical, distally directed, decrease in size laterally. Lingual face of cusplets lack ornamentation, and slight orolingual shelf visible. Labial face with very coarse, oblique ridges that extend from crown base but do not reach apices of cusplets. Labial edge of the crown base overhangs the root, which is incompletely preserved.

Remarks

The single tooth fragment in our sample was picked by one of the present authors (DJC) out of bulk matrix recovered directly from the basal Lisbon Formation (bed 2 of Copeland 1966) at site ACov-11. This specimen was originally figured, but not described, by Clayton *et al.* (2013) who referred the tooth to cf. “*Synechodus*” sp. Cappetta & Case (2016) contested this assignment, simply on the grounds that the specimen fell outside the youngest known occurrence of the family.

SC2012.47.32 possesses a unique combination of having multiple lateral cusplets, a small orolingual shelf, a labial crown face that overhangs the root, heavily folded enameloid ornamentation on the labial

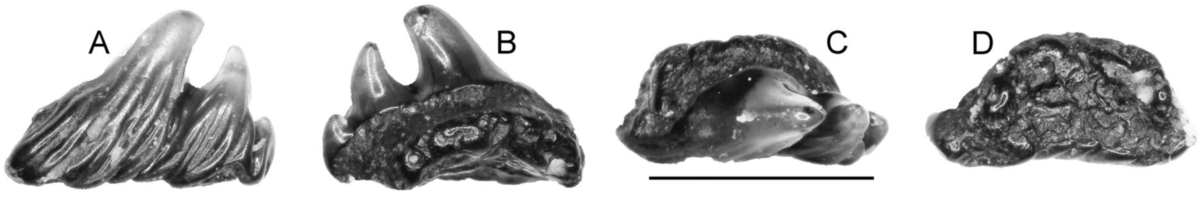


Fig. 37. Galeomorphii indet., tooth fragment. SC2012.47.32, basal Lisbon Formation. **A**. Labial view. **B**. Lingual view. **C**. Oral view. **D**. Basal view. Scale bar = 2 mm.

face (Fig. 37A), and a smooth lingual face (Fig. 37B). Additionally, SC2012.47.32 exhibits a third lateral cusplet, and the lateral two cusplets have a slight medial bend. This combination of characteristics separates this tooth fragment from all the other specimens in our sample and does conform well with the genera represented within the Paleospinacidae, including *Palidiplospinax* Klug & Kriwet, 2008 and *Synechodus* Woodward, 1888 (see Cappetta 2012: figs 304–6). Unfortunately, we scrutinized the specimen but cannot determine what taxon it represents due to its incompleteness, but it is included here for thoroughness.

Stratigraphic and geographic range in Alabama

The lone specimen in our sample, SC2012.47.32, was derived from the basal Lisbon Formation at site ACov-11. Middle Lutetian, Zone NP15.

Division Batomorphii Cappetta, 1980
Order Rhinopristiformes Naylor *et al.*, 2012
Family "Rhinobatidae" Müller & Henle, 1837

Genus **"*Rhinobatos*"** Linck, 1790

Type species

Raja rhinobatos Linneaus, 1758, Recent.

"*Rhinobatos*" *bruxelliensis* (Jaekel, 1894)
Fig. 38

Rhinobatus bruxelliensis Jaekel, 1894: 77, fig. 8.

Rhinobatos bruxelliensis – Cappetta 1976: 564, pl. 4, fig. 7.
Rhinobatos sp. – Holman & Case 1988: 328.
Rhinobatis sp. – Feldmann & Portell 2007: 90.
"Pristidae oral teeth?" – Cappetta & Case 2016: 62, pl. 10, figs 5–8.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 68 isolated teeth; Claiborne Group; ALMNH PV1993.7.490 (5 specimens), MSC 35787.1–3, MSC 37315.1–2, MSC 37550.1–9, MSC 37670.1–2, MSC 37689.1–8, MSC 37902, MSC 37903.1–2, MSC 37903.2, SC2012.47.1, SC2012.47.2, SC2012.47.3 (20 specimens), WSU 10, WSU CC 445, WSU CC 505 (2 specimens), WSU 5049 (10 specimens).

Description

Teeth extremely small, most not exceeding 2 mm in mesiodistal width. Crown has weakly convex, smooth labial face with broadly convex crown foot. Lingual face bearing three uvulae, separated by a transverse crest of varying lengths. Medial lingual uvula is most prominent; being narrow and elongated towards the succeeding tooth. Lateral uvulae are much shorter and divergent. Uvulae extend onto upper surface of root and have rounded extremities. Faint longitudinal ridge may be present on medial uvula. Most teeth lack cusps; some have taller, more cuspidate crown (see Fig. 38Q–T). Root positioned lingually under the crown. Root T-shaped in basal view. Lateral root extremities project below the lateral crown uvulae. Prominent nutritive groove extends labiolingually across the root base. Nutritive foramen present within nutritive groove; additional foramina often visible on lingual root face.

Remarks

The *Rhinobatos* teeth in our sample are conspecific with those of *Rhinobatos bruxelliensis* (Jaekel, 1894) in that the lateral uvulae are divergent, with the medial uvula being more pronounced than the lateral ones, and the uvulae all have rounded extremities. The teeth also have a characteristic apical transverse ridge that separates the crown into labial and lingual faces. Holman & Case (1988) and Feldmann & Portell (2007) each reported specimens they assigned to *Rhinobatos* sp. from the contact of the Tallahatta and Lisbon formations at site ACov-11. Although these specimens were not examined as part of this study, our sample included numerous *Rhinobatos* specimens collected from the same locality, all of which fall within the morphological range of *R. bruxelliensis.* This suggests the Holman & Case (1988) and Feldmann & Portell (2007) specimens also belong to this taxon.

Cappetta & Case (2016) figured four specimens (pl. 10, 5–8) from the ACov-11 locality that have the *R. bruxelliensis* morphology. These authors, however, questioned the identification of the teeth as *Rhinobatos*, suggesting instead they belong to a member of the Pristidae Bonaparte, 1838. Although teeth of these two taxa are similar, Cappetta & Case (2016) appear to argue for a pristid identification simply because their sample included numerous *Pristis* Linck, 1790 rostral spines, but otherwise lacked *Pristis* oral teeth. This interpretation seems problematic, as teeth of very similar morphology, identified as *Rhinobatos*, have been reported from Cretaceous strata, a time well before the first occurrence of the

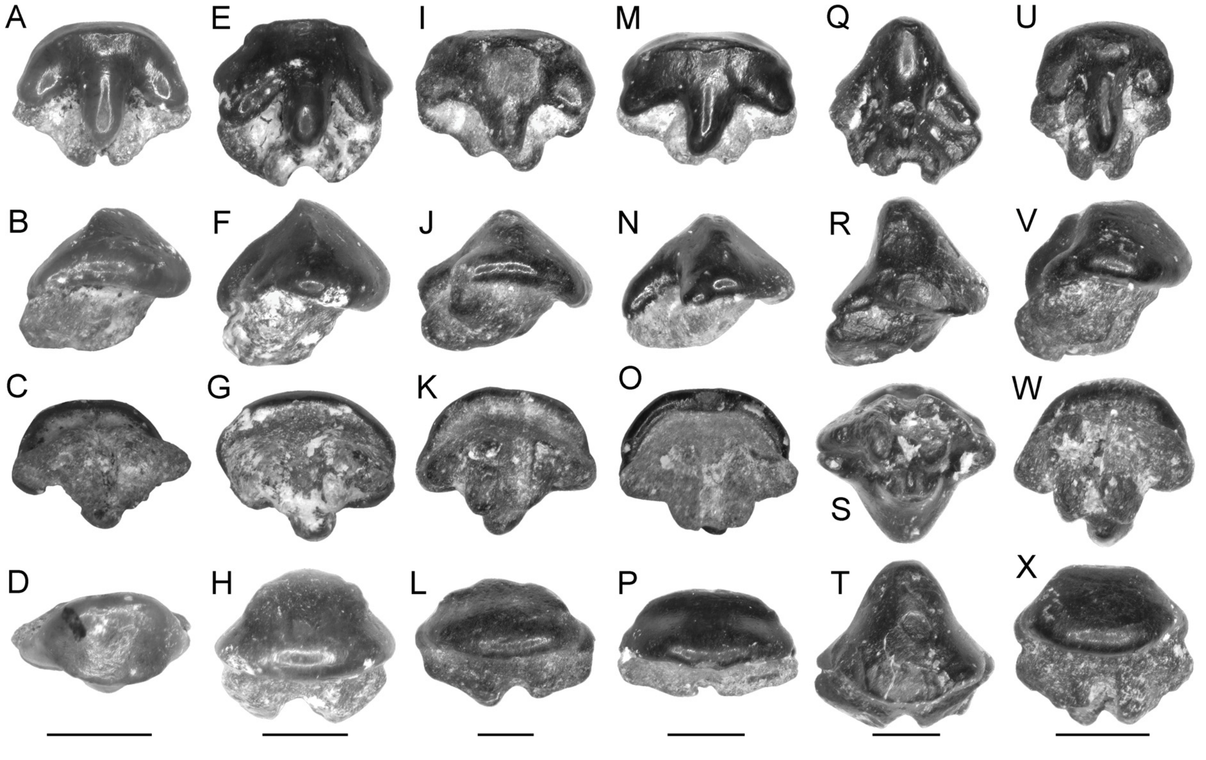


Fig. 38. "*Rhinobatos*" *bruxelliensis* (Jaekel, 1894), teeth. **A–D**. MSC 35787.1, lower Tallahatta Formation. **A**. Orolingual view. **B**. Profile view. **C**. Basal view. **D**. Labial view. **E–H**. MSC 35787.2, lower Tallahatta Formation. **E**. Orolingual view. **F**. Profile view. **G**. Basal view. **H**. Labial view. **I–L**. MSC 37315.1, basal Lisbon Formation. **I**. Orolingual view. **J**. Profile view. **K**. Basal view. **L**. Labial view. **M–P**. MSC 37315.2, basal Lisbon Formation. **M**. Orolingual view. **N**. Profile view. **O**. Basal view. **P**. Labial view. **Q–T**. MSC 37550.1, male tooth, basal Gosport Sand. **Q**. Orolingual view. **R**. Profile view. **S**. Basal view. **T**. Labial view. **U–X**. MSC 37550.2, basal Gosport Sand. **U**. Orolingual view. **V**. Profile view. **W**. Basal view. **X**. Labial view. Labial at top in basal views. Scale bars = 1 mm.

Pristidae in the Paleogene (see Cappetta 2012). Furthermore, *Pristis* teeth have a very elongated medial lingual uvula but lack lateral uvulae (Carrillo-Briceño *et al.* 2015, 2016), which is inconsistent with the teeth in our sample.

We do concur that the teeth of the *bruxelliensis* morphology are dissimilar to those of the extant *Rhinobatos*, and the tooth morphology of living and fossil rhinobatid species should be reviewed. Recent phylogenetic studies have shown *Rhinobatos* to be paraphyletic (see Naylor *et al.* 2012; Claeson *et al.* 2013), calling into question the placement of fossil and living species within this genus, and casting doubt that they can all be placed into the family Rhinobatidae. Thus, we provisionally assign the *bruxelliensis* teeth in our sample to "*Rhinobatos*" and place them tentatively within the Rhinobatidae.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the basal Lisbon Formation at site ACov-11, the "upper" Lisbon Formation at site ACh-8, and the basal Gosport Sand at site ACl-4. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Family Pristidae Bonaparte, 1838

Genus ***Anoxypristis*** White & Moy-Thomas, 1941

Type species

Pristis cuspidatus Latham, 1794, Recent.

Anoxypristis sp.

Fig. 39A–I

Anoxypristis aff. *mucrodens* – Cappetta & Case 2016: 62–63, pl. 10, figs 9–12.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 18 isolated teeth; Claiborne Group; ALMNH PV1985.87.10, ALMNH PV1985.87.9, ALMNH PV1992.56.4 (2 specimens), MMNS VP-8946 (3 specimens), MMNS VP-8952 (3 specimens), MSC 35791, MSC 37289, MSC 37310, MSC 37333, MSC 37422, MSC 37643, MSC 37658, WSU CC 549.

Description

Rostral spines dorsoventrally flattened and symmetrical in either of these views. Spines have a slight ventral bend and weakly convex dorsal and ventral faces. Anterior and posterior edges straight and rounded basally, becoming sharp and tapering gently to a rounded point. No posterior groove present. Spine slightly wider basally, where transverse growth lines visible dorsally and ventrally. Growth lines visible ventrally almost to the spine apex. Faint mediolateral striations visible on ventral face. Spine base ovate and with weak central depression. Entire spine lacks an enameloid covering.

Remarks

The *Anoxypristis* rostral spines in our sample were differentiated from those of *Pristis* by having thin anterior and posterior edges, as opposed to a wide and flat or grooved posterior edge on *Pristis* spines. *Anoxypristis* spines can be differentiated from those of *Propristis* (see below) in being anteroposteriorly narrower and much more elongated, with a correspondingly more pointed apex. *Anoxypristis* spines in our sample are similar to a specimen assigned by Case & Cappetta (1990) to *Anoxypristis* aff. *mucrodens*, but we refrain from speciating these specimens because the range of variation in rostral

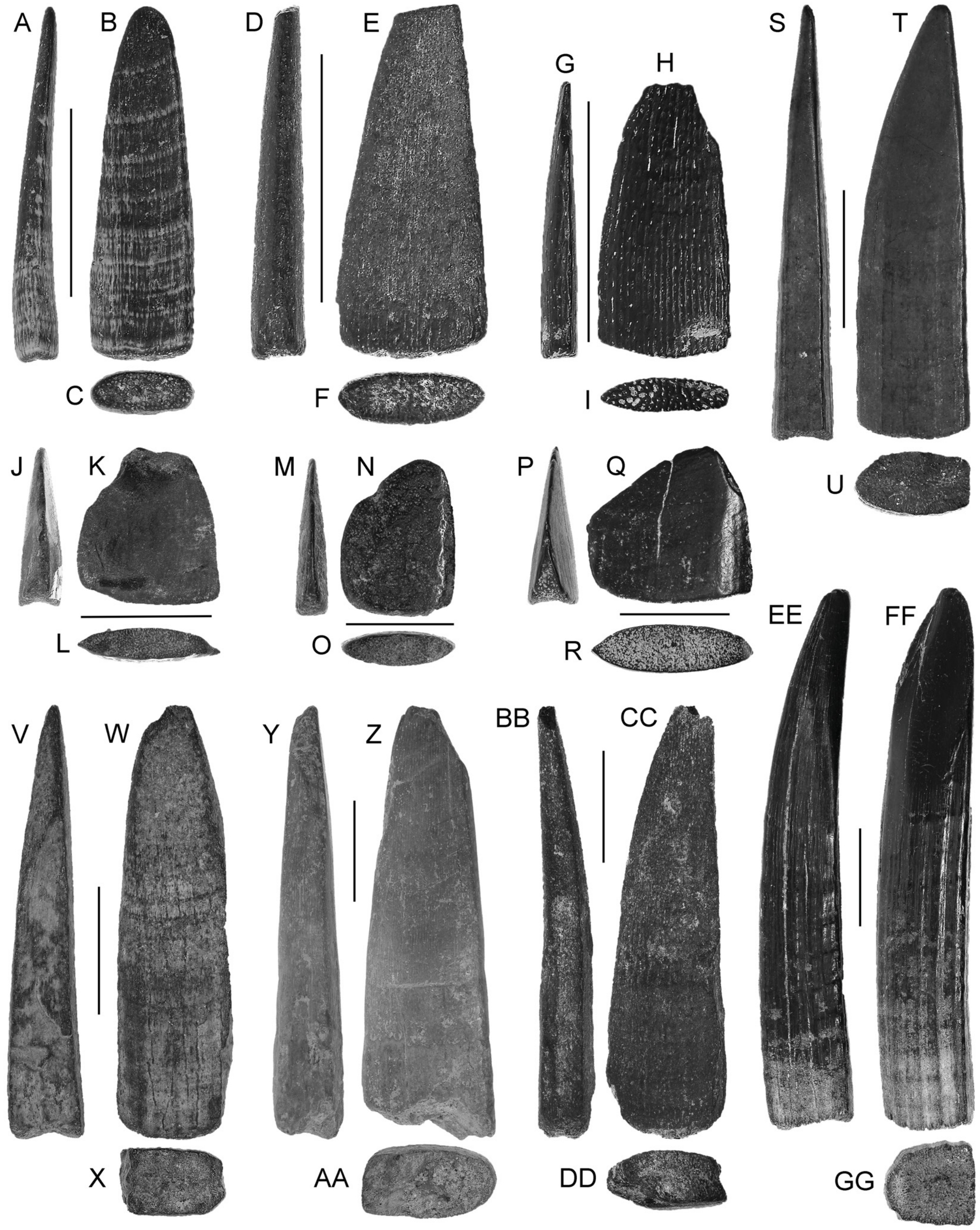


Fig. 39. Pristidae Bonaparte, 1838, rostral spines. **A–I**. *Anoxypristis* sp. **A–C**. MSC 35791, basal Tallahatta Formation. **A**. Anterior view. **B**. Ventral view. **C**. Basal view. **D–F**. MSC 37658, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **D**. Anterior view. **E**. Ventral view. **F**. Basal view. **G–I**. MSC 37643, basal Gosport Sand. **G**. Posterior view. **H**. Dorsal view. **I**. Basal view. — **J–R**. *Propristis schweinfurthi* Dames, 1883. **J–L**. MSC 2392.8, Gosport Sand. **J**. Anterior view. **K**. Dorsal view. **L**. Basal view. **M–O**. MSC 2392.6, Gosport Sand. **M**. Anterior view. **N**. Dorsal view. **O**. Basal view. **P–R**. MSC 37392, basal Gosport Sand. **P**. Anterior view. **Q**. Dorsal view. **R**. Basal view. — **S–GG**. *Pristis* sp. **S–U**. MSC 37169, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **S**. Posterior view. **T**. Dorsal view. **U**. Basal view. **V–X**. MSC 33528, lower Tallahatta Formation. **V**. Posterior view. **W**. Dorsal view. **X**. Basal view. **Y–AA**. MSC 33548, lower Tallahatta Formation. **Y**. Posterior view. **Z**. Ventral view. **AA**. Basal view. **BB–DD**. MSC 35737.1, lower Tallahatta Formation. **BB**. Posterior view. **CC**. Ventral view. **DD**. Basal view. **EE–GG**. MSC 2392.1, Gosport Sand. **EE**. Posterior view. **FF**. Dorsal view. **GG**. Basal view. Scale bars = 1 cm.

spine morphology is inadequately known within the two Eocene species of *Anoxypristis*, including *A. fajumensis* (Stromer, 1905a) and *A. mucrodens* (White, 1926). The spines in our sample differ from those of *Mesopristis osonensis* Farrés, 2003 from the middle Eocene of Spain in their lack a distinctive V-shaped basal concavity. The concavity occurring on *M. osonensis* spines fits over a thin projection emanating from the base of the alveolus of the rostrum, forming a tongue-and-groove articulation.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11, and the basal Gosport Sand at site ACl-4. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Genus ***Pristis*** Linck, 1790

Type species

Squalus pristis Linneaus, 1758, Recent.

Pristis sp.

Fig. 39S–GG

Pristis lathami – Holman & Case 1988: 328. — Cappetta & Case 2016: 63–64, pl. 11, figs 1–2.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 247 isolated teeth; Claiborne Group; ALMNH PV1989.4.108 (36 specimens), ALMNH PV1985.87.11, ALMNH PV1985.87.12, ALMNH PV1985.87.13, ALMNH PV1985.87.14, ALMNH PV1985.87.15, ALMNH PV1985.87.16, ALMNH PV1985.87.17, ALMNH PV1985.87.18, ALMNH PV1985.87.19, ALMNH PV1985.87.20, ALMNH PV1985.87.21, ALMNH PV1985.87.22, ALMNH PV1985.87.23, ALMNH PV1985.87.24, ALMNH PV1985.87.25, ALMNH PV1985.87.26, ALMNH PV1985.87.27, ALMNH PV1985.87.28, ALMNH PV1985.87.29, ALMNH PV1985.87.30, ALMNH PV1985.87.31, ALMNH PV1985.87.32, ALMNH PV1985.87.53, ALMNH PV1985.87.54, ALMNH PV1985.87.6, ALMNH PV1989.4.10.1 (3 specimens), ALMNH PV1989.4.14 (2 specimens), ALMNH PV1989.4.151.2 (4 specimens), ALMNH PV1989.4.17.2 (7 specimens), ALMNH PV1989.4.46, ALMNH PV1989.4.57, ALMNH PV1989.4.75.1, ALMNH PV1989.4.78 (2 specimens), ALMNH PV1989.4.92 (2 specimens), ALMNH PV1990.7, ALMNH PV1992.28.12, ALMNH PV1992.28.20 (2 specimens), ALMNH PV1992.28.8 (2 specimens), ALMNH PV1992.28.8 (2 specimens), ALMNH PV1992.56.4 (22 specimens), ALMNH PV1993.2.488, ALMNH PV2000.1.43.13 (2 specimens), MMNS VP-5640 (23 specimens), MMNS VP-8221 (6 specimens), MSC 2150.2, MSC 2150.4, MSC 2175.30, MSC 2392.1–3, MSC 2392.9, MSC 2395.5, MSC 33249, MSC 33364, MSC 33378, MSC 33390, MSC 33528, MSC 33548, MSC 33570, MSC 33646, MSC 33650, MSC 33666, MSC 33691, MSC 33888, MSC 33890, MSC 33905, MSC 34406.1–5, MSC 34621, MSC 35737.1–3, MSC 35790.1–5, MSC 37134.1–6, MSC 37169, MSC 37182.1–3, MSC 37277, MSC 37334.1–8, MSC 37437.1–25, MSC 37439, MSC 37458, MSC 37525, MSC 37617, MSC 38399, MSC 38628, MSC 38788, NJSM 24030 (2 specimens), SC2012.47.169 (2 specimens), SC2012.47.93 (9 specimens), WSU 5026.

Description

Rostral spines attain large sizes, some reaching 10 cm in length. Rostral spines long, slender. Spines generally straight, may curve ventrally; dorsal and ventral surfaces slightly convex anteroposteriorly. Anterior spine edge rounded; posterior edge generally concave, with sharp dorsal and ventral edges. Apical portion of anterior edge sharp, slightly convex, forms sharp point with posterior edge. Anterior and posterior edges nearly parallel, slightly wider basally. Longitudinal striations sometimes visible on basal portion of the spine. Growth bands perpendicular to spine length visible on some spines. Medial margins of rostral spines flat to slightly concave. Some spines with flat posterior margin. Rostral spines lack enameloid.

Remarks

Cappetta (2012) and Cappetta & Case (2016) recognized the following species of Eocene *Pristis*: *P. amblodon* Cope, 1869; *P. brayi* Casier, 1949; *P. lathami* Galeotti, 1837; *P. olbrechtsi* Dartevelle & Casier, 1959; *P. pickeringi* Case, 1981; and *P. prosulcatus* Stromer, 1905a. Cappetta & Case (2016) noted two morphologies of *Pristis* rostral spines from the ACov-11 locality that they assigned to "*Pristis* sp. 1" and "*Pristis* sp. 2." The two morphologies were differentiated based on supposedly unique ornamentation and by being "thicker", and the authors suggested that a new species may be represented. *Pristis lathami* Galeotti, 1837 is the name most frequently assigned to isolated Eocene *Pristis* rostral spines (see Cappetta 2012; Cappetta & Case 2016), but we refrain from speciating any of the isolated Claiborne spines because of the variation observable on fossil and extant *Pristis* rostral spines, and our lack of knowledge of the post-rostrum skeletal morphology of the extinct species. Variation in spine shape may be the result of several factors, including ontogeny, *in vivo* wear and, potentially, heterodonty. *Pristis* rostral spines are not replaced but instead increase in size over the lifespan of the animal (Slaughter & Springer 1968). Spines of older animals are large, dorsoventrally thicker, have deeper posterior grooves, and are often more worn than their smaller/younger counterparts. There is also potential for heterodonty in our sample based on preserved specimens at MSC and SC, where the spines in the rostra of extant *Pristis* tend to be shorter at the posterior end of the rostrum than those located more anteriorly. Due to this range of variation, it is our opinion that a conservative approach be taken when identifying isolated fossil *Pristis* rostral spines because one or more of the described species are likely nominal. We also believe that the absence of a posterior groove is not related to ontogeny, as the posterior margin of both small and large spines may be flat or slightly concave.

It is interesting to note that certain spines in our sample exhibit faint striations on the dorsal and ventral surfaces, oblique to the anterior/posterior edges, near the spine tip. These are identical to what was described by Cicimurri (2007) on middle Eocene spines from South Carolina and has been observed on spines of extant species (Allen 1999). The sharp anterior edge, pointed tip, and faint dorsal/ventral striations are believed to be the result of the sawfish using the spined rostrum to probe the sea floor in search of prey animals.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at sites ACl-4 and AMo-4, and the Gosport Sand at site ACh-21. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Genus ***Propristis*** Dames, 1883

Type species

Propristis schweinfurthi Dames, 1883, upper Eocene, Fayoum, Egypt.

Propristis schweinfurthi Dames, 1883
Fig. 39J–R

Propristis schweinfurthi Dames, 1883: 136, pl 3, figs 1a–c, 2.
Amblypristis cheops Dames, 1883: 106, text fig.
Pristis schweinfurthi Priem 1905: 636, text-fig. 6.
Pristis (*Eopristis*) *reinachi* Stromer 1905a: 52, pl. 4, figs 15, 15a.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 10 isolated teeth; Claiborne Group; ALMNH PV1989.4.2 (3 specimens), ALMNH PV1989.4.110, ALMNH PV1989.4.118.1 (2 specimens), MSC 2392.6, MSC 2392.8, MSC 37392.1–2.

Description

Rostral spines short, anteroposteriorly wide, dorsoventrally very thin. Spines asymmetrical, with sharp and sinuous anteroposterior cutting edge at spine apex. Dorsal and ventral faces taper to a point anteriorly and posteriorly. Spine base slightly concave in dorsal and ventral views, with faint growth line striations. Striations extend less than halfway up the spine and terminate where the spine is worn. Spine base elliptical in basal view; anterior and posterior edges pointed. Basal edge is granular with a shallow anteroposterior sulcus.

Remarks

The genus *Propristis* contains two species, the Eocene *Propristis schweinfurthi* Dames, 1883 and the Miocene *Propristis mayumbensis* Dartevelle & Casier, 1943. The teeth in our sample appear to be conspecific with those referred to *P. schweinfurthi* (see Dames 1888: 107; Cappetta 2012: fig. 386; Zalmout *et al.* 2012: fig. 5q–r) and are only slightly older (Bartonian) than the type specimens from the Priabonian of Egypt (Dames 1883). *Propristis schweinfurthi* was originally named for a partial rostrum, but later Dames (1888) named the species *Amblypristis cheops* for a number of isolated pristid rostral teeth from the same locality. Stromer (1905a), however, designated *A. cheops* a junior synonym of *P. schweinfurthi*, as he determined that specimens of the former belonged to the rostrum of the latter.

Propristis rostral spines are easily distinguished from *Pristis* and *Anoxypristis* by their wider and shorter dimensions, and more extensive cutting edge. In contrast to the latter two genera, the spines of *Propristis* were set into shallow, closely spaced depressions on the margins of the rostral cartilage, as opposed to deep alveoli formed by broad projections of rostral cartilage. The spines of *Propristis* overlapped each other and formed an irregular, continuous cutting edge (Fraas 1907).

Stratigraphic and geographic range in Alabama

The specimens in our sample are known only from the basal Gosport Sand at site ACl-4 and the Gosport Sand at site ACh-21. Middle Bartonian, Zone NP17.

Order Myliobatiformes Compagno, 1973
Suborder Myliobatoidei Compagno, 1973
Family Dasyatidae Jordan, 1888

Genus ***Dasyatis*** Rafinesque, 1810

Type species

Dasyatis ujo Rafinesque, 1810, Recent.

“***Dasyatis***” aff. ***D. charlisae*** Case, 1981
Fig. 40A–L

Dasyatis charlisae Case, 1981: 69, text-fig. 8, pl. 7, figs 1a–e, 2a–e, 4a–d.

Dasyatis sp. 1 – Clayton *et al.* 2013: fig. 5c–d.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 8 isolated teeth; Claiborne Group; SC2012.47.240, SC2012.47.242, SC2012.47.243, WSU 29, WSU CC 441, WSU CC 448, WSU CC 449, WSU CC 450.

Description

Only low-crowned teeth present. Transverse crest divides crown into labial and lingual halves. Crown is triangular in mesial and distal views; root lingually projected. Crown overhangs the root on all sides; base of labial face well developed, forming a labial shelf. Lingual crown face ranges from flat to slightly concave; labial face concave to convex, depending on tooth position. In occlusal view, labial face ranges from diamond to oval in outline; lingual face triangular and basally elongate. Basal margin of lingual crown face strongly convex. Punctate ornamentation present on entire labial crown face, at times extending just past the transverse ridge onto the periphery of lingual face. Root bilobed; separated from the crown by a shallow groove. Multiple foramina present within the median root furrow.

Remarks

Clayton *et al.* (2013) recognized two *Dasyatis* tooth morphologies within their sample from site ACov-11 in Covington County, AL. Assigned to "*Dasyatis* sp. 1" and "*Dasyatis* sp. 2", these morphologies were differentiated by their overall shape and development of ornamentation on their labial crown face.

To test whether the degree of crown ornamentation is a taxonomically useful characteristic for differentiating these otherwise similar taxa, our sample of "*Dasyatis*" teeth were directly compared to a modern set of dasyatid jaws (genus and species indet.) from the MSC collection. Our observations of this dentition are as follows:

1. Upper anterior teeth have a labial face that is obliquely flat to weakly convex.
2. Upper lateral teeth have a lower crown than anteriors but have a transverse crest that forms a sharper edge.
3. The labial face of the teeth is concave, and the apical one-third to one-half of the labial face is ornamented with vertical wrinkling.
4. The lower portion of the teeth have a reticulated ornamentation.
5. The ornamentation extends to lingual side of transverse crest.
6. Teeth in the lower jaw are similar to those in the upper jaw, but the lower jaw appears to have more lateral rows containing teeth with a concave labial face.

These observations indicate that many of the morphological characteristics cited for the isolated teeth of *Dasyatis* are ambiguous and can be attributed to heterodonty (monognathic, dignathic, and gynandric). However, crown ornamentation appears to be consistent across all tooth files, upper and lower, within a dentition, suggesting the extent and type of ornamentation can be useful in differentiating the various taxa. This lends support to the presence of two species being present within our Claiborne sample.

Cappetta & Case (2016) recognized two *Dasyatis* species from site ACov-11, including *Dasyatis charlisae* Case, 1981 and *Dasyatis jaekeli* (Leriche, 1905). Of these, Cappetta & Case (2016) also referred *Dasyatis* sp. 1 of Clayton *et al.* (2013) to *D. charlisae*. Although several of our Lisbon Formation teeth are similar to *D. charlisae* in that the ornamentation covers the entire labial face, the species is difficult to evaluate because Case (1981) based the species on only five teeth, all of which are slightly different in size, shape, and ornament. We tentatively follow Cappetta & Case (2016) regarding taxonomic assignment of this tooth type. These teeth of *D. jaekeli* are differentiated from *D. charlisae* by having a labial face bearing fine pitting that does not extend to the lingual side of the transverse crest.

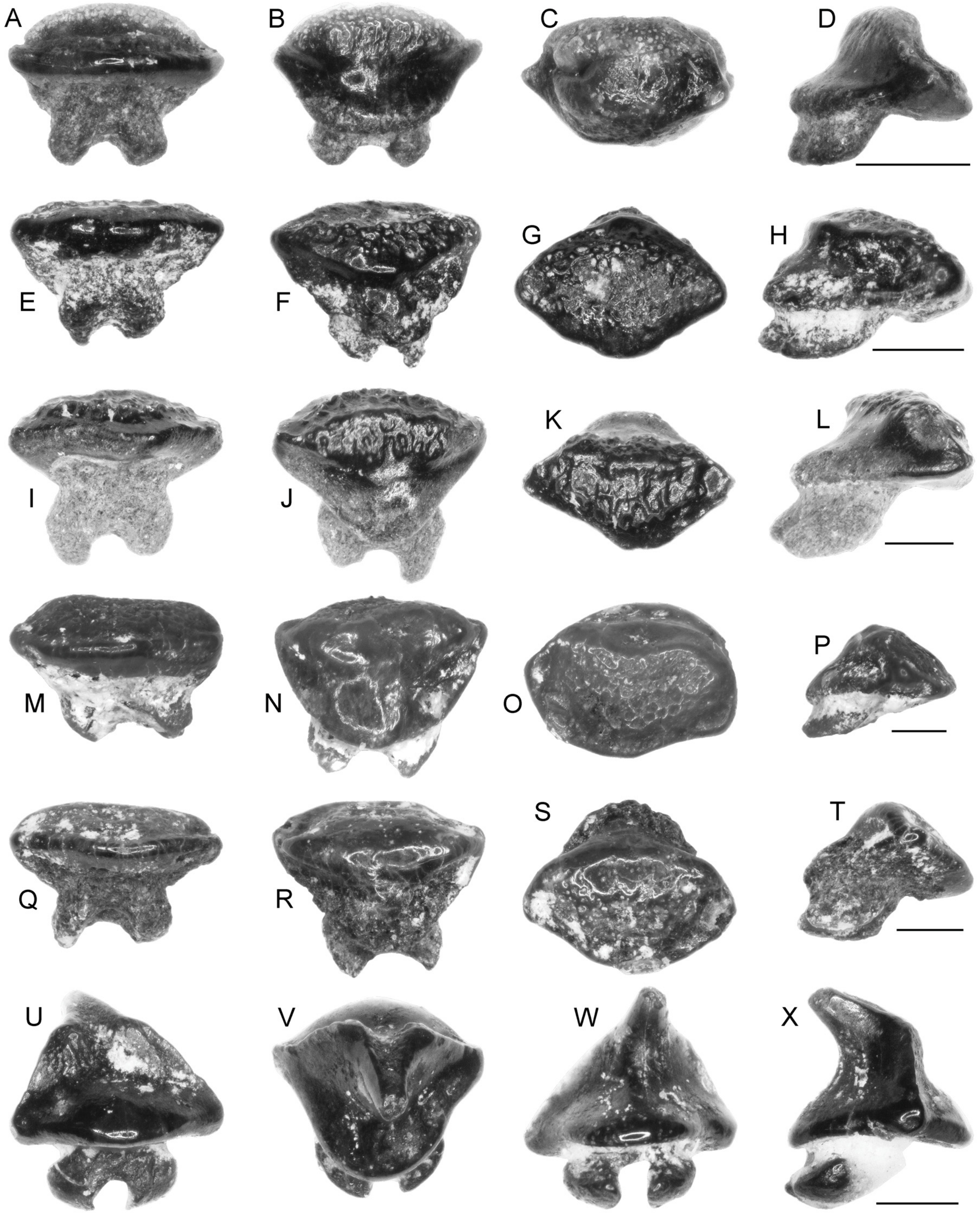


Fig. 40. "*Dasyatis*", teeth. **A–L**. "*Dasyatis*" aff. *D. charlisae* Case, 1981. **A–D**. SC2012.47.242, basal Lisbon Formation. **A**. Basiolabial view. **B**. Oral view. **C**. Labial view. **D**. Profile view. **E–H**. SC2012.47.243, basal Lisbon Formation. **E**. Basiolabial view. **F**. Oral view. **G**. Labial view. **H**. Profile view. **I–L**. WSU CC–449, "upper" Lisbon Formation. **I**. Basiolabial view. **J**. Oral view. **K**. Labial view. **L**. Profile view. — **M–X**. "*Dasyatis*" *jaekeli* (Leriche, 1905). **M–P**. MSC 35785.1, lower Tallahatta Formation. **M**. Basiolabial view. **N**. Oral view. **O**. Labial view. **P**. Profile view. **Q–T**. SC2012.47.9.241, basal Lisbon Formation. **Q**. Basiolabial view. **R**. Oral view. **S**. Labial view. **T**. Profile view. **U–X**. SC2012.47.10, male breeding morphology, basal Lisbon Formation. **U**. Basiolabial view. **V**. Oral view. **W**. Lingual view. **X**. Distal view. Labial at top in oral view. Scale bars = 5 mm.

Placing the two Lisbon Formation morphologies within *Dasyatis* is potentially problematic. Extant Dasyatidae consists of eight genera and at least 88 species (Nelson *et al.* 2016), and a recent phylogenetic analysis organized the species into the subfamilies Dasyatinae, Neotrygoninae, Urogymninae, and Hypolophinae (Last *et al.* 2016). The results presented by Last *et al.* (2016) showed the genera *Dasyatis* and *Himantura* to be paraphyletic, and the authors resorted to using external morphology to ascribe several species to these genera. Because these recent taxonomic revisions were based on genetics and body shape, as opposed to tooth morphology, it is currently unclear how identification of extinct members of the Dasyatidae will be impacted. The difficulty in identifying fossil Dasyatidae teeth was discussed by Ward (1979), who explained that the morphological characteristics used to define extant and fossil *Dasyatis* teeth are shared among several different genera within the family. Due to the lack of taxonomic clarity among the fossil members of this family, we suggest the conservative usage of "*Dasyatis*" for these teeth because they could belong to any number of different genera within the Dasyatidae.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the basal Lisbon Formation at site ACov-11 and the "upper" Lisbon Formation at site ACh-8. Lower Lutetian to middle Bartonian, zones NP15 to NP17.

"*Dasyatis*" *jaekeli* (Leriche, 1905)

Fig. 40M–X

Trygon jaekeli Leriche, 1905: 100, pl. 4, figs 29–32.

Dasyatis jaekeli – Casier 1946: 101, pl. 3, fig. 2a–h.
Dasyatis sp. 2 – Clayton *et al.* 2013: fig. 5e–f.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 16 isolated teeth; Claiborne Group; MSC 35785.1–3, SC2012.47.8, SC2012.47.9 (3 specimens), SC2012.47.10, SC2012.47.11, SC2012.47.12 (5 specimens), SC2012.47.241, WSU 14.

Description

High-crowned and low-crowned morphologies present. Transverse crest on low-crowned teeth divides crown into labial and lingual halves. Crown triangular in mesial and distal views; root projects lingually. Crown overhangs root on all sides; base of labial face well developed forming a labial shelf. Lingual crown face ranges from flat to slightly concave; labial face concave to convex depending on tooth position. In occlusal view, labial face ranges from diamond-to-oval in outline; lingual face triangular and basally elongate. Basal margin of lingual crown face strongly convex. Punctate ornamentation present on labial crown face; ornamentation restricted to the crown base or along the transverse crest. Root bilobed, separated from crown by a shallow groove. Multiple foramina present within the median furrow of the root. High-crowned (male) teeth like the low-crowned morphology, but with more triangular labial crown face. In mesial or distal views, the lingual crown face is concave and the labial face convex; apex of the crown lingually projected.

Remarks

Clayton *et al.* (2013) identified this tooth type as *Dasyatis* sp. 2 and differentiated it from their *Dasyatis* sp. 1 specimens based on the highly convex labial face bearing fine pitting that does not extend to the lingual side of the transverse crest. The *Dasyatis* sp. 1 specimens figured by Clayton *et al.* (2013: pl. 70, figs 5c–d) were later assigned to *D. jaekeli* by Case & Cappetta (2016), and our comparison of the

Lisbon sample to the type suite of *D. jaekeli* (Leriche 1905: pl. 4, figs 29–32) indicates they do indeed belong to this taxon.

Both high-crowned and low-crowned tooth morphologies have been identified within our sample, which we consider to be conspecific due to the shared fine pitting on the labial face. It is important to note that several authors (i.e., Case 1981; Cappetta 2012; Cappetta & Case 2016) have erroneously assumed that because the high-crowned dasyatid teeth can be attributed to males, the low-crowned morphology must belong to female individuals. However, depending on the species, both males and females can have low-crowned teeth, and the males of some species may develop highly cuspidate teeth during the breeding season (Kajiura & Tricas 1996).

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1 and the basal Lisbon Formation at site ACov-11. Upper Ypresian to lower Lutetian, zones NP14 and NP15.

Family *incertae sedis*

Genus ***Aturobatis*** Adnet, 2006

Type species

Aturobatis aquensis Adnet, 2006, middle Eocene, France.

Aturobatis aff. ***A. aquensis*** Adnet, 2006

Fig. 41

Aturobatis aquensis Adnet, 2006: 111, pl. 39, figs 3a–5b.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 2 isolated teeth; Claiborne Group; MSC 37687, MSC 38464.

Description

Large teeth approaching 4.0 mm in mesiodistal width. Occlusal outline of crown is rhomboidal, wider than long, with sharp labial, lingual and lateral angles. Oral surface flat and diamond-shaped, sub-parallel to basal plane of crown. Sharp medial vertical ridge of labial face flanked by concave faces, with indistinct transverse ridge near the crown foot. Crown is weakly concave on each side of the vertical ridge. Lingual crown face slightly higher than labial face, inclined, straight, weakly concave on either side of lingual angle. Lingual crown foot developed into distinctive shelf-like projection, forming acute angle with lingual face. All crown faces smooth. Base of crown overhangs root labially and laterally. Root narrow, distally located under lingual part of crown, bilobed with a shallow medial nutritive groove. Root lobes rather elongate, with oblique labial face, extending just past lingual crown foot.

Remarks

The gross morphology of MSC 37687 and MSC 38464 is similar to other the Dasyatidae teeth in our sample, but the teeth are much larger and lack crown ornamentation. These teeth are also morphologically similar to the lateral teeth of members of the Myliobatidae, however, the lack of labial and lingual ornament on vertical crown faces and narrow, distally located root are inconsistent with our observations of Lisbon Formation Myliobatidae (see below). Teeth of *Aturobatis* are not to be confused with *Hypolophodon*, which has a weakly convex occlusal surface, much less angular appearance in occlusal and profile views, and a wide, centrally located root (Dartevelle & Casier 1959; Murray *et al.* 2010: figs 2c–d; Cappetta 2012: fig. 412).

Adnet *et al.* (2010) and Cappetta (2012) mentioned the occurrence of *Aturobatis* in Ypresian strata in the Atlantic Coastal Plain of the USA, and a younger, potentially new species has been noted from the Priabonian of Morocco (Adnet *et al.* 2010). Only the type species, *A. aquensis*, has been described and illustrated, and the two teeth in our Lisbon Formation sample, although much larger, are comparable to the Lutetian teeth reported by Adnet (2006). However, as *A. aquensis* is based on only four teeth and the range of variation is not known, we tentatively assign our two teeth to this species. Discovery of additional specimens will help determine if the Lisbon taxon is distinct or conspecific with *A. aquensis*.

Stratigraphic and geographic range in Alabama

The two specimens in our sample were collected from the basal Lisbon Formation at site ACov-11. Lower Lutetian, Zone NP15.

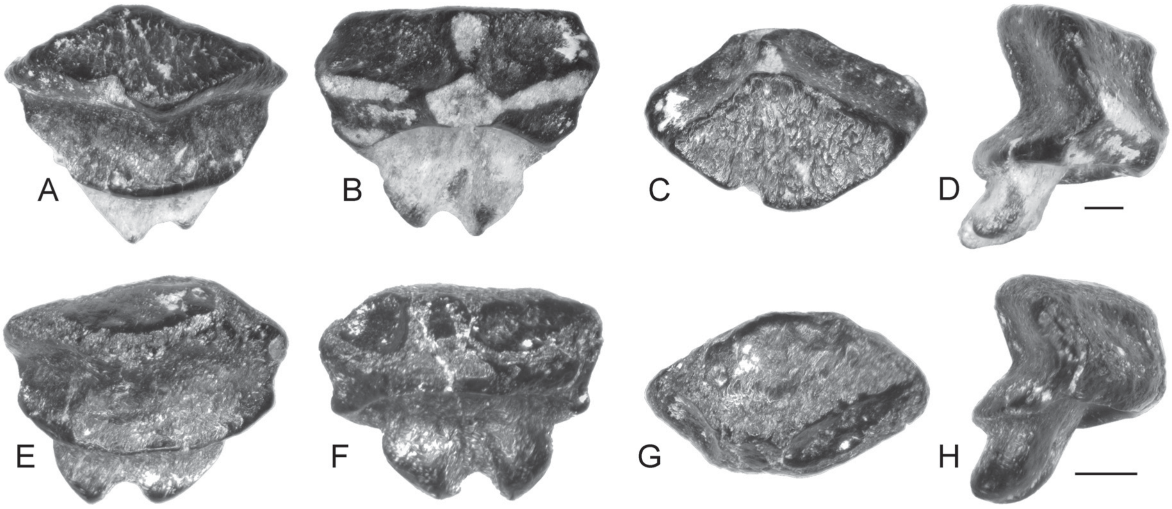


Fig. 41. *Aturobatis* aff. *A. aquensis* Adnet, 2006, teeth. **A–D**. MSC 37687, basal Tallahatta Formation. **A**. Orolingual view. **B**. Labial view. **C**. Oral view. **D**. Profile view. **E–H**. MSC 38464, basal Tallahatta Formation. **E**. Orolingual view. **F**. Labial view. **G**. Oral view. **H**. Profile view. Scale bars = 5 mm.

Genus ***Coupatezia*** Cappetta, 1982

Type species

Coupatezia woutersi Cappetta, 1982, middle Eocene, Belgium.

Coupatezia sp.
Fig. 42A–L

Coupatezia woutersi Cappetta, 1982: 18, pls 2–3.

Coupatezia woutersi – Clayton *et al.* 2013: fig. 5a–b.
Coupatezia sp. – Cappetta & Case 2016: 65, pl. 13, figs 1–6.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 18 isolated teeth; Claiborne Group; MSC 35786, MSC 37309.1–3, MSC 37339, MSC 37671, MSC 38480.1–3, SC2012.47.6, SC2012.47.7 (6 specimens), WSU 22, WSU CC 502.1.

Description

All teeth in our sample low-crowned. Teeth with elliptical outline in oral view. Labial face deeply convex, framed by cingulum-like margin. Base of labial face bears transverse crest that may be simple or appear reticulated; does not reach the sides of the crown. Lingual face of crown convex or sinuous in profile, unornamented. Crown overhangs the root on all sides. Roots bilobate. In labial or lingual views, mesial and distal extent of roots extend slightly beyond the crown foot. In profile the root extends well beyond the lingual crown margin, but labially crown conspicuously overhangs root. Deep nutritive groove bisects the root equally, and basal face of lobes convex with triangular outline.

Remarks

Coupatezia appears to exhibit gynandric heterodonty, with male teeth having a more cuspidate, triangular crown (Cappetta 1982; Noubhani & Cappetta 1997). Unfortunately, the 18 specimens available to us all exhibit the purported female morphology (described above). Clayton *et al.* (2013) assigned their sample of *Coupatezia* teeth from site ACov-11 to *C. woutersi*, a species described from the Lutetian of Belgium (Cappetta 1982), but Cappetta & Case (2016) did not speciate the specimens in their sample from the same site. The latter authors cited morphological differences between the Alabama teeth and *C. woutersi* specimens from the type locality in Belgium, including a less ornamented labial face, more regular labial crown margin, and root lobes that extend further distally on *C. woutersi*. The Alabama specimens differ significantly from female teeth of Lutetian *C. miretrainensis* Adnet, 2006 in having a more rounded occlusal outline, more concave labial face, and nodular labial crown ornament. Female teeth of the Ypresian species *C. boujoi* Noubhani & Cappetta, 1997 appear to have a more concave labial crown margin, and the basiolabial transverse crest is less conspicuous, sometimes merging with the crown margin. With regard to the Alabama specimens, we found that the outline of the labial crown margin varies from concave, straight, to convex, and the crown margin itself can be sharp, nodular, or weakly developed. Also, the basiolabial transverse crest of the labial face may be simple or have a reticulated appearance, and the root lobes vary in distal length. This variation, coupled with the fact that we cannot compare a male tooth with any of the described Eocene species, makes it difficult to ascertain if the Alabama taxon is distinct or conspecific with any of them. Thus, we chose here to refrain from a specific identification.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1 and the basal Lisbon Formation at site ACov-11. Upper Ypresian to lower Lutetian, zones NP14 and NP15.

Genus ***Hypolophodon*** Cappetta, 1980

Type species

Hypolophus sylvestris White, 1931, Ypresian, the United Kingdom.

Hypolophodon sylvestris (White, 1931)

Fig. 42M–X

Hypolophus sylvestris White, 1931: 30, pl. 7, figs 22–23.

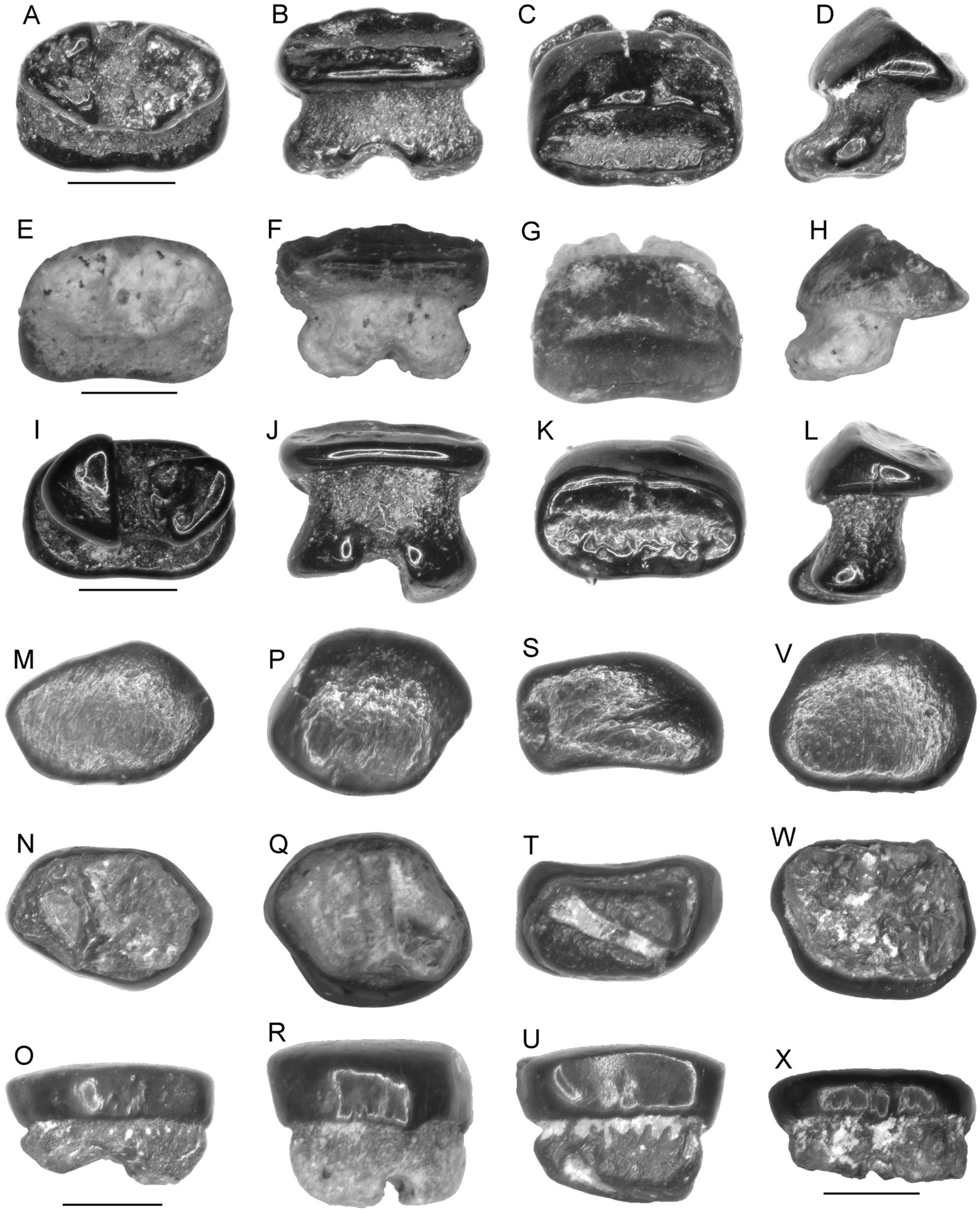


Fig. 42. *Coupatezia* sp. and *Hypolophodon* s*ylvestris* (White, 1931), teeth. — **A–L**. *Coupatezia* sp. **A–D**. MSC 37339, basal Lisbon Formation. **A**. Basal view. **B**. Basiolabial view. **C**. Oral view. **D**. Profile view. **E–H**. MSC 35786.1, lower Tallahatta Formation. **E**. Basal view. **F**. Basiolabial view. **G**. Oral view. **H**. Profile view. **I–L**. MSC 38480.2, basal Lisbon Formation. **I**. Basal view. **J**. Basiolabial view. **K**. Oral view. **L**. Profile view. — **M–X**. *Hypolophodon* s*ylvestris*. **M–O**. MSC 35788.1, lower Tallahatta Formation. **M**. Oral view. **N**. Basal view. **O**. Lingual view. **P–R**. MSC 35788.2, lower Tallahatta Formation. **P**. Oral view. **Q**. Basal view. **R**. Lingual view. **S–U**. MSC 35788.3, lower Tallahatta Formation. **S**. Oral view. **T**. Basal view. **U**. Profile view. **V–X**. MSC 35788.4, lower Tallahatta Formation. **V**. Oral view. **W**. Basal view. **X**. Lingual view. Scale bars: A–L = 1 mm; M–X = 2 mm.

Hypolophodon sylvestris – Cappetta 1980a: pl. 39, fig. 6.
Dasyatis sylvestris – Sahni & Mehrotra 1981: 101, pl. 3, figs 5–7. — Sharma & Patnaik 2013: 175, pl. 6a.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 7 isolated teeth; Claiborne Group; MSC 35788.1–7.

Description

Teeth small, measure up to 5.0 mm in greatest width. Crown may have rounded six-sided outline in occlusal view; more often ovate. Crown of unworn teeth covered with smooth enameloid. Occlusal, labial, and lingual surfaces convex and smooth. Lingual crown face has a small uvula and faint enameloid wrinkling at basal margin. Root low, generally divided by single nutritive groove into two triangular lobes. Root lobes may be equidimensional or of differing size, depending on location of the nutritive groove. Two or more nutritive grooves occasionally observed.

Remarks

Based on morphological and histological criteria, Cappetta (1980b) synonymized some species that had been placed within *Hypolophus* and *Platyrhina* with his newly created genus, *Hypolophodon*. Junior synonyms included the type species, *H. sylvestris* (White, 1931), and Casier's (1946) *P. ypresiensis*. The teeth in our sample appear to be conspecific with those of *H. sylvestris* as described and figured by Cappetta (1980a: pl. 39, fig. 6) in that they have enameloid wrinkling and a small uvula on their lingual crown face. The presence of lingual crown wrinkling separates the teeth in our sample from those of *H. dockeryi* Case, 1994, which apparently lacks this characteristic (Case 1994a; also Case *et al.* 2015: 1132, fig. 7.3). The teeth of *H. malembeensis* Murray *et al.*, 2010 can be separated from those in our sample by having numerous labial foramina on their root, sharper crown edges, and a distinct lingual concavity in profile view (see Murray *et al.* 2010: figs 2c–d). Teeth of *H. farreri* Gurr, 1962 can have a similarly angular six-sided outline, but their crown faces are vertical and flat, and they lack a lingual basal protuberance. It remains to be shown if *H. farreri* is valid, as abraded specimens in our sample lack enameloid on the underside of the crown, as well as a lingual protuberance, and this latter characteristic is also absent from larger adult teeth we examined. Casier (1967) tentatively referred a tooth to *H. farreri*, and to our knowledge this is the only other mention of the species. However, the specimen he illustrated (Casier 1967: pl. VII, fig. 24) is abraded and in our opinion compares more favorably to *H. sylvestris*.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1. Upper Ypresian to lower Lutetian, Zone NP14.

Family Gymnuridae Jordan, 1888

Genus *Jacquhermania* Cappetta, 1982

Type species

Cestracion duponti Winkler, 1876, Lutetian, Belgium.

Jacquhermania duponti (Winkler, 1876)

Fig. 43

Cestracion duponti Winkler, 1876: 17, figs 1–3.
Raja aequilateralis Dartevelle & Casier, 1959: 329, fig. 85, pl. 35, fig. 12.

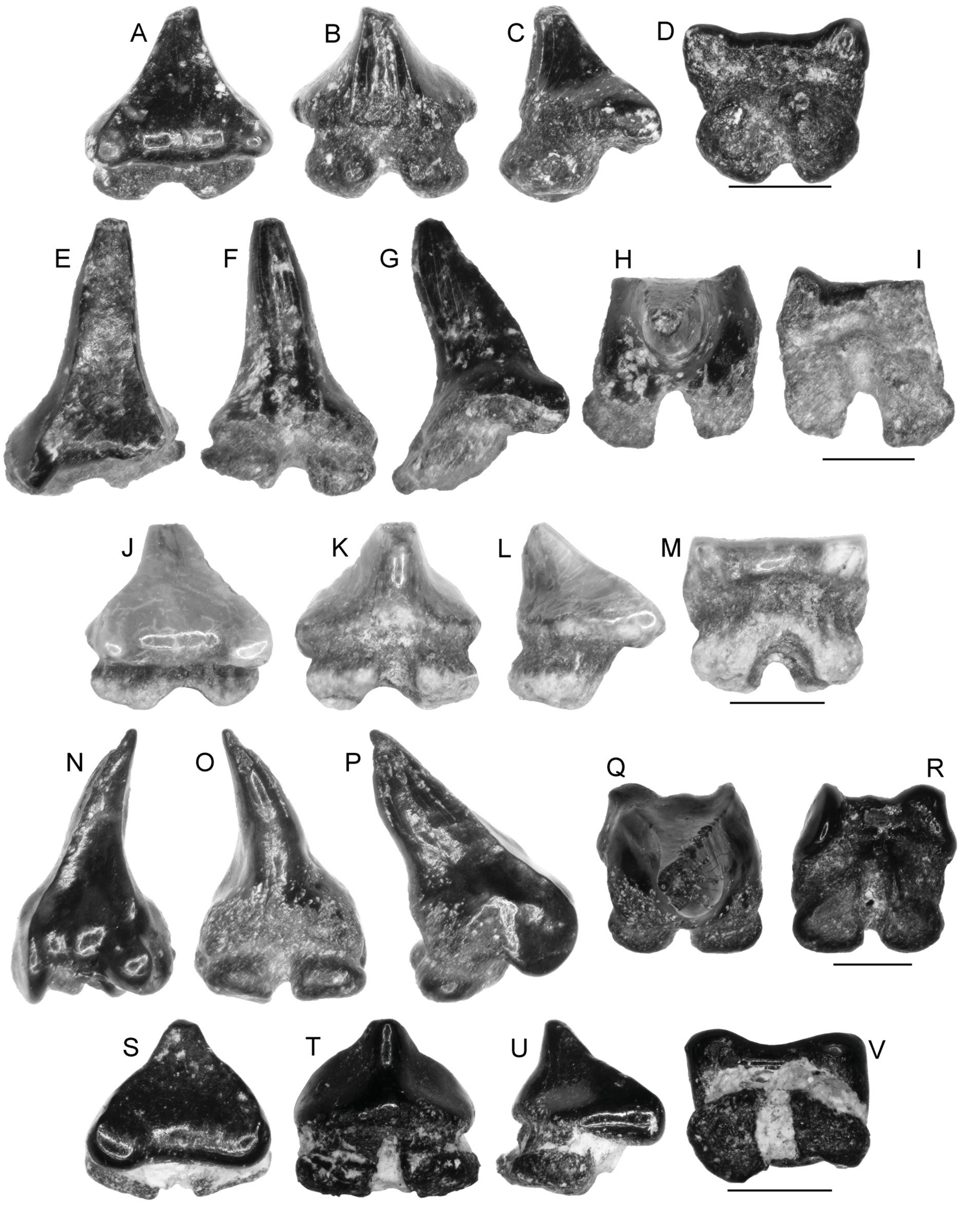


Fig. 43. *Jacquhermania duponti* (Winkler, 1876), teeth. **A–D**. SC2012.47.5, basal Lisbon Formation. **A**. Labial view. **B**. Lingual view. **C**. Mesial view. **D**. Basal view. **E–I**. MSC 38484, basal Lisbon Formation. **E**. Labial view. **F**. Lingual view. **G**. Mesial view. **H**. Oral view. **I**. Basal view. **J–M**. MSC 37519, Gosport Sand. **J**. Labial view. **K**. Lingual view. **L**. Distal view. **M**. Basal view. **N–R**. SC2012.42.4, basal Lisbon Formation. **N**. Labial view. **O**. Lingual view. **P**. Mesial view. **Q**. Oral view. **R**. Basal view. **S–V**. WSU AL15, basal Lisbon Formation. **S**. Labial view. **T**. Lingual view. **U**. Mesial view. **V**. Basal view. Labial at top in oral and basal views. Scale bars = 1 mm.

Raja duponti – Leriche 1905: 100, pl. 4, figs 26–28.
Raja sp. – Dartevelle & Casier 1943: 177, pl. 11, fig. 15.
Dasyatis duponti – Cappetta 1972: 202, pl. 4, figs 11–18.
Jacquhermania duponti – Cappetta 1982: 116, pl. 1, figs 1–10. — Clayton *et al.* 2013: figs 5i–j.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 28 isolated teeth; Claiborne Group; ALMNH PV1993.2.337 (5 specimens), ALMNH PV1993.2.376 (8 specimens), MSC 37519, MSC 37553.1–3, MSC 38463, MSC 38484, SC2012.47.4, SC2012.47.5, SC2012.47.155 (2 specimens), SC2012.47.157, WSU 11, WSU 15, WSU CC 502.2, WSU CC 512.

Description

Teeth do not exceed 1.5 mm in mesiodistal width. Crown cuspidate, triangular in labial, lingual and profile views. In oral view, labial face rather narrow, triangular and flanked by smooth edges; lingual face more extensive and very convex. Labial face concave along tooth height. All enameloid smooth. Crown overhangs the root labially, but root lobes extend beyond crown base laterally and lingually. Root bilobed with deep medial furrow, and convex, sub-triangular basal attachment surfaces.

Remarks

Jacquhermania Cappetta, 1982 is a monospecific genus, with the only named species being *J. duponti* (Winkler, 1876). This species was originally placed within the genus *Cestracion* by Winkler (1876), then later referred to *Raja* and *Dasyatis* by Leriche (1905) and Cappetta (1972), respectively. Cappetta (1982) discussed how the teeth examined by Leriche (1905) as *Raja duponti* actually represented two separate taxa, *Coupatezia woutersi* and *Cestracion duponti*, the latter of which was placed into a new genus, *Jacquhermania*.

Teeth of *Jacquhermania* are generally easy to distinguish from all other coeval batoids within the Lisbon Formation and Gosport Sand. The combination of a very convex lingual face, small and concave labial face flanked by smooth cutting edges, lack of lingual uvulae, smooth enameloid, and cuspidate crown separate *Jacquhermania* from "*Dasyatis*", *Aturobatis*, "*Rhinobatos*", and *Hypolophodon*, as well as the lateral teeth of the various members of the Myliobatidae. Two teeth from the Lisbon Formation, one of which was illustrated by Clayton *et al.* (2013) as *Gymnura* sp., are unusual in being very high high-crowned but otherwise similar to *Jacquhermania* in our sample. These two teeth have a weakly concave labial face flanked by lateral cutting edges, the labial crown foot is drawn out into mesial and distal projections, but there is a conspicuous medial embayment at the lingual crown foot. These specimens (Fig. 43E–I, N–R) could represent anteriorly located teeth and/or potentially a male morphological variant of *Jacquhermania* as indicated by Cappetta (1982).

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACl-15. Lower Lutetian to middle Bartonian, zones NP15 to NP17.

Family Myliobatidae Bonaparte, 1838
Subfamily Myliobatinae Bonaparte, 1835

Genus ***Aetobatus*** de Blainville, 1816

Type species

Raja narinari Euphrasen, 1790, Recent.

Aetobatus sp.
Fig. 44

Aetiobatis sp. cf. *A. irregularis* – Thurmond & Jones 1981: 75, fig. 36b.
Aetobatis sp. – Holman & Case 1988: 328.
Aetobatus irregularis – Cappetta & Case 2016: 66, pl. 14, fig. 1.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 127 isolated teeth; Claiborne Group; GSA-V699, MMNS VP-5642 (2 specimens), MMNS VP-5648, MSC 2389.1–11, MSC 37150 (4 specimens), MSC 37184 (3 specimens), MSC 37244 (2 specimens), MSC 37255 (9 specimens), MSC 37303 (15 specimens), MSC 37330 (7 specimens), MSC 38806 (2 specimens), MSC 38810 (14 specimens), MSC 38830 (3 specimens), MSC 38947, NJSM 24031, NJSM 24032, SC2012.47.23, SC2012.47.24, SC2012.47.25, SC2012.47.26, SC2012.47.27, SC2012.47.28 (4 specimens), SC2012.47.29 (2 specimens), SC2012.47.211 (29 specimens), SC2012.47.212, SC2012.47.213, SC2012.47.214, SC2012.47.215, SC2012.47.216, SC2012.47.217, SC2012.47.218, SC2012.47.219, WSU 5012, WSU 5023.

Description

Upper and lower tooth plates consist of a single median file. In oral view, tooth crowns very wide but narrow. Teeth in upper dentition straight, sinuous, or weakly arcuate (convex labially) in outline. Teeth in lower dentition strongly arcuate or chevron shaped. Distal ends of crown within both dentitions are straight and perpendicular to width, basally curving and slightly lingually directed. The labial crown face overhangs the root; root extends well beyond the lingual side of the crown. Both crown faces ornamented with fine vertical wrinkles; thick and rounded transverse ridge present at lingual crown foot. Root polyaulacorhize; numerous thin lamellae present on basal and dorsal surfaces. Labial root face oblique (basiolingually directed); may bear shallow grooves that are in line with lamellae.

Remarks

Partial teeth of *Aetobatus* could be confused with *Pseudaetobatus* (see below), although there is currently no evidence that the two taxa were coeval within the Claibornian of Alabama. There are no lateral teeth in the *Aetobatus* dentition, and the distal ends of individual teeth are straight and perpendicular to the width, basally curving, and lingually directed. In contrast, distal ends of *Pseudaetobatus* median teeth are angular and form a point of articulation for lateral teeth.

Aetobatus does occur with several other Myliobatinae within Claibornian strata. Tooth crowns of *Aetobatus* lack the thickened, tuberculated enameloid seen on the occlusal surface of *Leidybatis* teeth, and the ornament on the vertical crown faces is only weakly developed. A reticulated pattern of beaded ridges and pitting on the vertical crown faces, angular lateral margins, and the sharp and narrow lingual transverse ridge distinguish *Aetomylaeus* from *Aetobatus*. *Myliobatis* teeth are more similar to *Aetomylaeus* than *Aetobatus*. Although the teeth of both *Aetobatus* and *Rhinoptera* (Rhinopterinae) have a crown with similar ornament and cross section, the labial root face of *Aetobatus* is oblique and the lingual root margin extends well past the crown, whereas the labial root face on *Rhinoptera* teeth is low and vertical, and the lingual margin generally does not extend past the lingual crown foot.

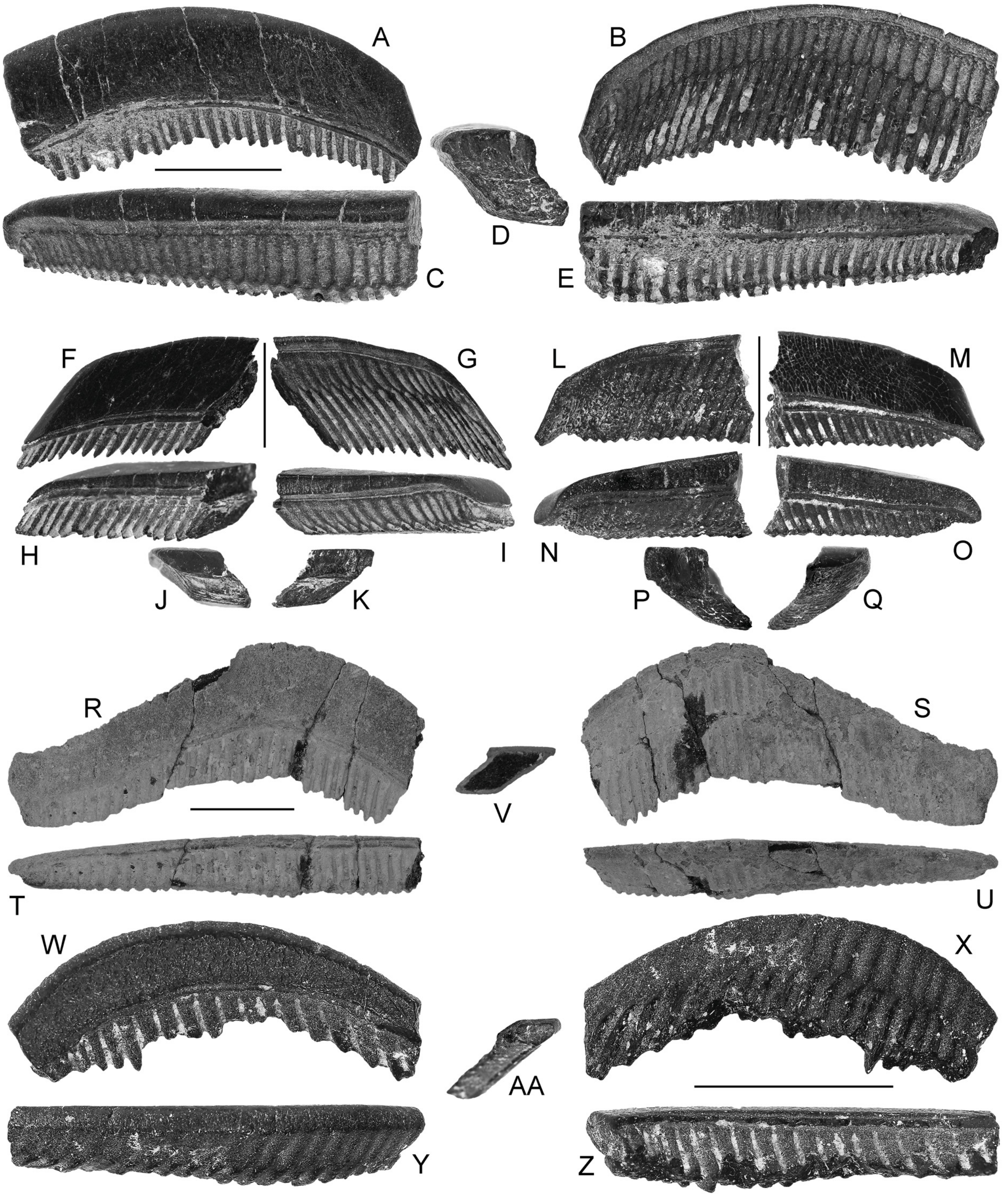


Fig. 44. *Aetobatus* sp., teeth. **A–E**. MSC 37150, lower median tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **A**. Oral view. **B**. Basal view. **C**. Labial view. **D**. Profile view. **E**. Lingual view. **F–K**. MSC 37330.1, median tooth, basal Lisbon Formation. **F**. Oral view. **G**. Basal view. **H**. Lingual view. **I**. Labial view. **J**. Distal view. **K**. Mesial view. **L–Q**. MSC 37330.2, median tooth, basal Lisbon Formation. **L**. Basal view. **M**. Oral view. **N**. Labial view. **O**. Lingual view. **P**. Profile view. **Q**. Distal view. **R–V**. SC2012.47.23, lower median tooth, basal Lisbon Formation. **R**. Oral view. **S**. Basal view. **T**. Lingual view. **U**. Labial view. **V**. Profile view. **W–AA**. SC2012.47.24, lower median tooth, basal Lisbon Formation. **W**. Oral view. **X**. Basal view. **Y**. Labial view. **Z**. Lingual view. **AA**. Profile view. Scale bars = 1 cm.

Eocene specimens of *Aetobatus* are often assigned to *A. irregularis*. However, we could not directly compare the Lisbon material to the type specimens and therefore cannot confidently assign our incomplete specimens to *A. irregularis*. Additionally, Hovestadt & Hovestadt-Euler (2013) demonstrated that dentitions of extant myliobatin taxa exhibit varying degrees of intraspecific variation, and it is difficult to ascertain if the generally fragmentary, globally distributed remains typically identified as *A. irregularis* actually represent a single species.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at site ACh-14, the basal Lisbon Formation at site ACov-11, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, and the Gosport Sand at site ACh-21. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Genus ***Aetomylaeus*** Garman, 1908

Type species

Myliobatus maculatus Gray 1834, Recent.

Aetomylaeus sp.

Figs 45–46

Myliobatis dixoni – Clayton *et al.* 2013: fig. 4.d–f

Material examined

UNITED STATES OF AMERICA – **Alabama** • 392 isolated teeth; Claiborne Group; ALMNH PV1992.28.21, ALMNH PV2000.1.45, ANSP 23425, MMNS VP-8190, MSC 20988.5, MSC 33247, MSC 33274, MSC 33280, MSC 33321, MSC 33324, MSC 33329, MSC 33333, MSC 33403, MSC 33421, MSC 33436, MSC 33445, MSC 33476, MSC 33494, MSC 33600, MSC 33653, MSC 33844.1, MSC 33844.2, MSC 33844.5, MSC 33844.7, MSC 33916, MSC 33931, MSC 33956, MSC 35748 (10 specimens), MSC 37079, MSC 37117 (4 specimens), MSC 37205, MSC 37246, MSC 37293, MSC 37302 (24 specimens), MSC 37403, MSC 37481, MSC 37528, MSC 37910, MSC 38402, MSC 38410, MSC 38778 (8 specimens), MSC 38780 (5 specimens), MSC 38781 (6 specimens), MSC 38782 (5 specimens), MSC 38783, MSC 38789 (8 specimens), MSC 38797 (9 specimens), MSC 38801 (2 specimens), MSC 38807 (5 specimens), MSC 38813 (2 specimens), MSC 38814 (2 specimens), MSC 38819 (4 specimens), MSC 38824 (5 specimens), MSC 38833 (7 specimens), MSC 38836 (3 specimens), MSC 38844 (101 specimens), MSC 38850 (3 specimens), MSC 38851, MSC 38853, MSC 38858 (12 specimens), MSC 38872 (3 specimens), MSC 38882 (35 specimens), MSC 38886, MSC 38942, MSC 38946, MSC 38963 (2 specimens), SC2012.47.13, SC2012.47.14 (4 specimens), SC2012.47.15 (12 specimens), SC2012.47.185, SC2012.47.186 (50 specimens), SC2012.47.187 (3 specimens), SC2012.47.188, SC2012.47.189, SC2012.47.190, SC2012.47.191, SC2012.47.192, SC2012.47.193, SC2012.47.194, SC2012.47.195, SC2012.47.196, WSU 5006, WSU 5007, WSU 5011, WSU 5021, WSU 5027.

Description

Median teeth are wider than long; those in upper dentition have a very convex occlusal surface and sinuous to arcuate (convex labially) occlusal outline. Labial and lingual crown foot straight. Teeth in lower dentition with flat occlusal surface; occlusal outline sinuous or arcuate. In labial and lingual views, crown is thickest medially; crown foot is convex and tapers toward the distal margins. Labial crown face of median teeth weakly concave; generally inclined lingually, but at times near vertical.

Lingual face with reticulated ornamentation; forms network of fine pits across the surface. Less worn teeth show the ornamentation may have longitudinal component apically (that is obliterated as the crown is worn through *in vivo* use). Labial crown face weakly convex, usually lingually inclined, may be nearly vertical. Lingual face ornamented with interconnected beaded ridges. Median teeth with rounded, strongly obtuse lateral angles; intersection of labial and lingual parts of the angle located closer to the anterior or posterior crown margin, depending on tooth position. Labial crown foot overhangs the root; lingual face bears thin and sharp transverse lingual ridge at the boundary between the crown and root. Root is low; labial face strongly inclined basiolingually; lingual margin extends beyond the crown foot. Root of median teeth polyaulocorhize, subdivided into numerous thin lamellae.

Upper and lower lateral teeth longer than wide, six-sided, may have a diamond-shaped occlusal outline due to very narrow labial and lingual faces. Ornamentation on vertical faces the same as observed on median teeth. Root generally bisected by a single nutritive groove (occasionally two).

Remarks

This taxon is represented by several partial to nearly complete upper and lower dentitions. MSC 35808 is an upper dentition consisting of nine articulated median teeth, with the remnants of an additional (tenth) tooth preserved on the labial face of the anterior-most tooth. This specimen, as well as all the available upper dentitions, shows that the entire upper dentition was a convex plate. Median teeth in the labial portion of the dentition have a sinuous occlusal outline, whereas the outline becomes more arcuate towards the back of the mouth. Although teeth are thickest medially, the crown tapers laterally to a very short and thin shelf. Although no complete lateral teeth are preserved on specimen MSC 20988.5, a part of a lateral tooth row is preserved on one side. A second lateral row is indicated by distal articular

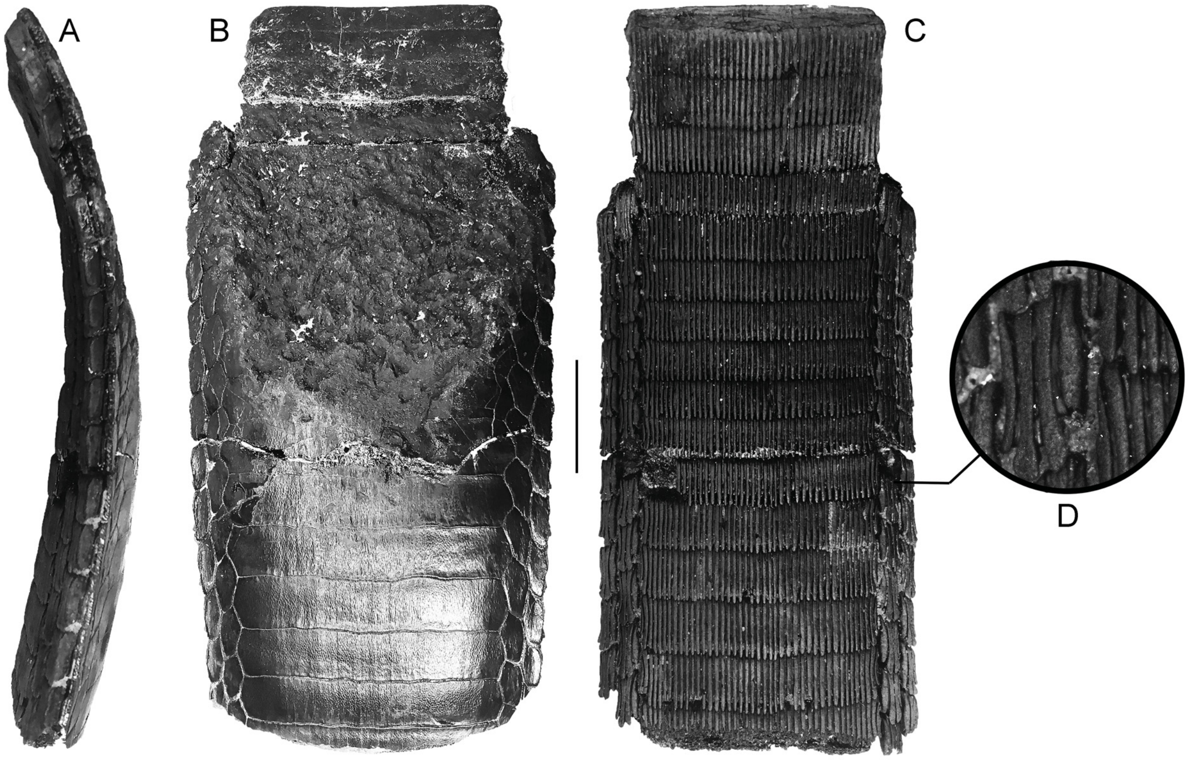


Fig. 45. *Aetomylaeus* sp., tooth plates. **A**–**D**. ALMNH PV2000.1.45, lower tooth plate, “upper” Lisbon Formation. **A**. Lateral view. **B**. Oral view. **C**. Basal view. **D**. Close–up of root lamilae. Labial at top in A–D. Scale bar = 2 cm.

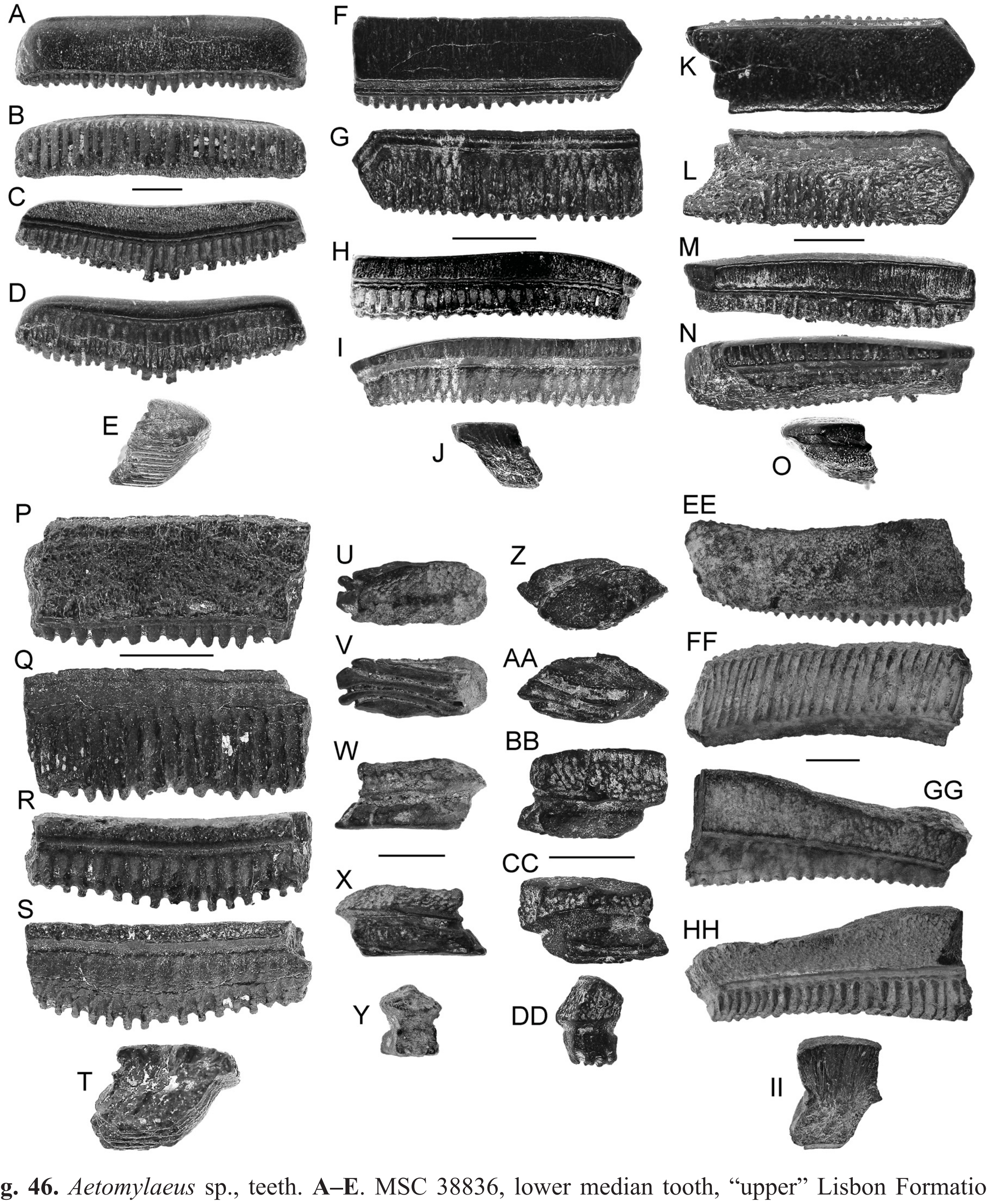


Fig. 46. *Aetomylaeus* sp., teeth. **A–E**. MSC 38836, lower median tooth, “upper” Lisbon Formation. **A**. Oral view. **B**. Basal view. **C**. Lingual view. **D**. Labial view. **E**. Profile view. **F–J**. MSC 199.2, median tooth, basal Gosport Sand. **F**. Oral view. **G**. Basal view. **H**. Lingual view. **I**. Labial view. **J**. Profile view. **K–O**. MSC 199.1, median tooth, basal Gosport Sand. **K**. Oral view. **L**. Basal view. **M**. Lingual view. **N**. Labial view. **O**. Profile view. **P–T**. MSC 38872, lower median tooth, Gosport Sand. **P**. Oral view. **Q**. Basal view. **R**. Lingual view. **S**. Labial view. **T**. Profile view. **U–Y**. MSC 37910, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **U**. Oral view. **V**. Basal view. **W**. Mesial view. **X**. Distal view. **Y**. Labial view. **Z–DD**. MSC 38851, lateral tooth, basal Gosport Sand. **Z**. Oral view. **AA**. Basal view. **BB**. Mesial view. **CC**. Distal view. **DD**. Labial view. **EE–II**. MSC 37079, upper median tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **EE**. Oral view. **FF**. Basal view. **GG**. Lingual view. **HH**. Labial view. **II**. Profile view. Labial at the top in oral or basal views of the median teeth. Scale bars = 5 mm.

surfaces on teeth in the first lateral row. MSC 33956 consists of two articulated median teeth, both of which have very convex occlusal surfaces, that we interpret as having formed part of an upper dentition.

ALMNH PV2000.1.45 (Fig. 45) is a beautifully preserved lower dentition consisting of 16 articulated median teeth and 12–13 and 11–12 lateral teeth in two rows on each side (starting at the fourth median tooth). The dentition is virtually flat, except for the anterior-most six median teeth, which curve slightly basally. The anterior half of the dentition is heavily worn through *in vivo* use.

The crown ornamentation occurring on the labial and lingual faces of *Aetomylaeus* teeth, coupled with the sharply pointed labial crown foot that fit into a furrow just above the lingual transverse ridge, and overlapping root lobes, served to strongly articulate individual teeth. These features are likely what contributed to the relatively large sample of dentitions available for study. These same features can be used to easily separate isolated *Aetomylaeus* teeth from those of similar genera occurring within Claibornian strata. The combination of labial pitting and lingual tuberculation contrasts with the fine to coarse vertical wrinkling observed on teeth of *Aetobatus*, *Pseudaetobatus*, and *Leidybatis*, and the occlusal surface lacks the pustulose occlusal ornament seen on *Leidybatis*. *Rhinoptera* differs in having vertical and flat labial and lingual faces that bear vertical wrinkling, and roots are comparatively much lower and do not extend beyond the lingual crown foot. *Aetomylaeus* teeth are most similar to those of *Myliobatis* sp. 2 of the Lisbon Formation and Gosport Sand (see below), but median teeth of the former can be distinguished from the latter in having obtuse, rounded lateral angles, and lateral teeth are diamond-shaped. Additionally, the lingual transverse ridge of *Aetobatus* teeth is generally very thin and sharp, as opposed to thick and rounded as seen on teeth of the other taxa listed above.

The teeth we herein assign to *Aetomylaeus* are, we believe, morphologically identical to those previously assigned to *Myliobatis dixoni*. This conclusion was also reached by Cappetta (2012), who indicated that the species would be more appropriately placed within *Aetomylaeus*. Hovestadt & Hovestadt-Euler (2013) synonymized numerous fossil species of *Myliobatis* with *Pteromylaeus*, a genus placed in synonymy with *Aetomylaeus* based on phylogenetic analyses (Naylor *et al.* 2012; White 2014). Unfortunately, Agassiz (1843) did not include descriptions of the labial or lingual crown ornamentation when naming the *dixoni* morphology, but Woodward (1888) later commented that the crowns exhibited granular and punctate ornamentation. Although he did not mention which sides of the crown bore these types of ornament, Woodward's statement conforms with our observations and those of Cappetta (2012) and Hovestadt & Hovestadt-Euler (2013) regarding the labial and lingual ornamentation on *Aetomylaeus* teeth.

We could not directly compare our Claibornian *Aetomylaeus* with the *dixoni* type specimens, and we cannot therefore know if the labial/lingual crown ornamentation is similar enough to warrant placement of the Alabama taxon into this species. Unfortunately, comparisons of the *Aetomylaeus* teeth occurring within the three Claibornian formations was hampered by the preservation of the material and the limited sample size. The *Aetomylaeus* teeth within the available samples from the Tallahatta and Lisbon formations and Gosport Sand exhibit some degree of variability, with the same variation being observed among the different formations. We did not discern an appreciable difference in overall morphology or labial/lingual crown ornamentation between the various formations, and there is no indication of anything other than intraspecific variation and longevity of a single Claibornian species.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Meridian Sand Member of the Tallahatta Formation and lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at sites ACon-6 and ACov-11, the basal Lisbon Formation at site ACov-11, the "upper" Lisbon Formation at site ACl-3, the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21 and ACl-15. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Genus ***Myliobatis*** Cuvier, 1816

Type species

Raja aquila Linneaus, 1758, Recent.

Myliobatis sp. 1
Fig. 47A–J

Material examined

UNITED STATES OF AMERICA – **Alabama** • 312 isolated teeth; Claiborne Group; MSC 33262, MSC 33293, MSC 33294, MSC 33317, MSC 33319, MSC 33332, MSC 33344, MSC 33345, MSC 33347, MSC 33350, MSC 33351, MSC 33362 (2 specimens), MSC 33363, MSC 33366, MSC 33394, MSC 33396, MSC 33402, MSC 33420, MSC 33471, MSC 33496, MSC 33529, MSC 33536, MSC 33573, MSC 33655, MSC 33672, MSC 33677, MSC 33865, MSC 33878, MSC 33883, MSC 33904, MSC 33913, MSC 33915, MSC 33925, MSC 33928, MSC 35747 (6 specimens), MSC 35748 (4 specimens), MSC 35751 (3 specimens), MSC 38881 (222 specimens), MSC 38937 (7 specimens), MSC 38938 (15 specimens), MSC 38940 (16 specimens), MSC 38941 (5 specimens).

Description

Median teeth wider than long, thick-crowned, six-sided with sharp lateral angles. Labial face weakly concave, slightly lingually inclined, has sharp and labially protruding crown foot. Lingual face weakly convex, slightly lingually inclined, has narrow and angular furrow located immediately above a rounded transverse ridge at crown foot. Labial face bears large and widely spaced vertical ridges that become weaker apically. Secondary ornament of fine anastomosing vertical ridges between large ones. Lingual face similarly ornamented, but more strongly than the labial face. The root is polyaulocorhize, labial face basiolingually directed, lingual margin extends beyond the crown foot. Lateral teeth six-sided and may be symmetrical (1:1 width/length ratio) or wider than long (2:1 ratio). Ornament and root morphology consistent with that observed on median teeth.

Remarks

Teeth of *Myliobatis* sp. 1 occur within the Tallahatta Formation along with several other members of the Myliobatinae, including *Pseudaetobatus*, *Aetomylaeus*, and *Leidybatis*. *Myliobatis* sp. 1 teeth have inclined, concave/convex labial and lingual faces, as opposed to being vertical and straight on *Pseudaetobatus*, and the labial and lingual ridging is coarser than on *Pseudaetobatus*. The occlusal surface of *Myliobatis* sp. 1 lacks the tuberculated enameloid covering of *Leidybatis*. *Aetomylaeus* differs in having a reticulated and tuberculated appearance on the labial and lingual faces, as opposed to being wrinkled. *Rhinoptera* bears weaker labial and lingual wrinkling, the crown faces are vertical and straight, and the root is very low with a vertical labial face and lingual margin that does not extend past the crown foot. Heavily worn teeth of *Myliobatis* sp. 1 can be identified by their heavily crenulated labial crown margin. Although similar in gross morphology, *Myliobatis* sp. 1 differs from the temporally younger *Myliobatis* sp. 2 of the Lisbon Formation and Gosport Sand (see below) in lacking any reticulation but having a highly crenulated labial crown foot.

Several Eocene species of *Myliobatis* have been described, but comments on labial/lingual ornament are usually lacking, and dentitions of extant species can be highly variable (see Hovestadt & Hovestadt-Euler 2013). Without having directly compared our Tallahatta teeth to the type specimens of those Eocene species, we cannot confidently make a more specific determination.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Meridian Sand Member of the Tallahatta Formation and the lower Tallahatta Formation at site ADl-1. Upper Ypresian to lower Lutetian, zones NP12 to NP14.

Myliobatis sp. 2

Figs 47K–T, 48

Myliobatis toliapicus – Clayton *et al.* 2013: fig. 4.g–i.
Ariidae – Maisch *et al.* 2016: fig. 3.1–2.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 287 isolated teeth; Claiborne Group; ANSP 23427, MSC 35007, MSC 35008, MSC 35944 (7 specimens), MSC 35945, MSC 37103, MSC 37152, MSC 37290, MSC 37337 (12 specimens), MSC 37560, MSC 37656, MSC 38640, MSC 38790 (6 specimens), MSC 38795 (5 specimens), MSC 38802 (3 specimens), MSC 38804, MSC 38809 (19 specimens), MSC 38818 (8 specimens), MSC 38828 (101 specimens), MSC 38837, MSC 38841 (20 specimens), MSC 38846 (2 specimens), MSC 38849 (2 specimens), MSC 38855 (3 specimens), MSC 38871 (5 specimens), SC2012.47.220, SC2012.47.221, SC2012.47.222 (3 specimens), SC2012.47.223, SC2012.47.224 (2 specimens), SC2012.47.225 (52 specimens), SC2012.47.226 (10 specimens), SC2012.47.227 specimens), WSU 12, WSU 5004.

Description

Tooth crown on median teeth wider than long, six-sided, has sharp lateral angles. Upper median teeth have convex crown, straight crown foot. Lower teeth relatively flat, have an undulating crown foot (convex medially, straight laterally). Labial face conspicuously overhangs the root, is weakly concave, may be vertical or slightly lingually inclined. Lingual face is correspondingly convex, may be vertical or slightly inclined. Labial crown face bears a network of fine reticulated ridges on the lower part, grading apically into longitudinal ridges that anastomose and become finer towards the occlusal surface. Ornamentation on lingual face similar, but stronger. Shelf-like and rounded basal transverse ridge at the lingual crown foot. Root polyaulocorhize, on unworn teeth it constitutes one-third to one-half the total tooth height. Labial root face oblique; lingual side of root extends past the crown base.

Upper and lower lateral teeth six-sided, nearly equidimensional, have highly irregular occlusal outline. The labial and lingual faces comparable in shape and ornament to median teeth. Root subdivided into three lobes by two nutritive grooves.

Remarks

This species is represented in our sample by two partial dentitions. MSC 35008 (Fig. 48A–F) is the right half of an upper dentition consisting of six incomplete but articulated median teeth, and a single lateral row (articulated with the third through sixth median teeth). Overall, the occlusal surface is convex mesiodistally, and the dentition is convex labiolingually. The two anterior-most median teeth are concave due to their having formed part of the triturating surface.

MSC 35007 (Fig. 48G–L) is a partial lower dentition consisting of five sutured median teeth and a single left lateral tooth between the fourth and fifth medians (the second and third medians had become detached but reconnected with B-76 in ethanol). The sutured median teeth show that the lower dentition was flat mesiodistally and labiolingually. The distal ends of the lateral teeth on both MSC 35007 and

MSC 35008 are ablated and it is not entirely clear if other lateral rows were present. However, the fact the distal ends are angular indicates that there was at least one additional row of lateral teeth.

The heavily wrinkled labial and lingual faces of the crown helps to articulate the teeth tightly together, and in oral view the crowns are heavily sutured. The articulation of individual teeth within the dentition is enhanced by the labial crown foot fitting into a lingual furrow of the preceding tooth, as well as overlap of the labial crown foot with the lingual transverse ridge. The labial face of the root also fits tightly against the sloping lingual face of the preceding tooth.

Myliobatis sp. 2 is easily distinguished from other similar taxa occurring within the Tallahatta/Lisbon contact zone, the Lisbon Formation, and Gosport Sand. The median teeth of Lisbon Formation *Leidybatis* bear an unusual, highly convex area flanked by thinner margins, and the occlusal surface has a thick

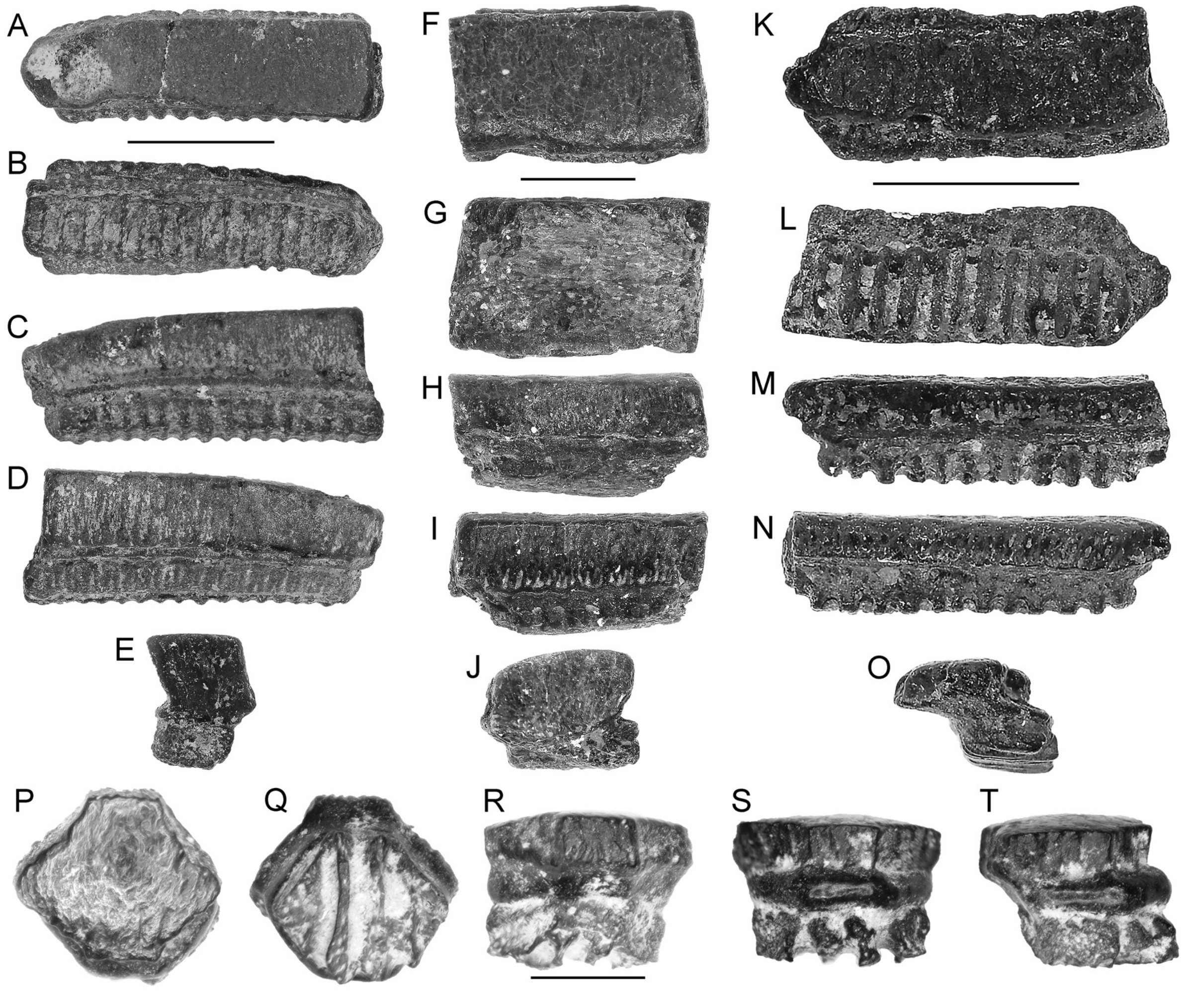


Fig. 47. *Myliobatis* Cuvier, 1816, teeth. **A–J**. *Myliobatis* sp. 1. **A–E**. MSC 38937, median tooth, lower Tallahatta Formation. **A**. Oral view. **B**. Basal view. **C**. Lingual view. **D**. Labial view. **E**. Profile view. **F–J**. MSC 33293, median tooth, lower Tallahatta Formation. **F**. Oral view. **G**. Basal view. **H**. Lingual view. **I**. Labial view. **J**. Profile view. — **K–T**. *Myliobatis* sp. 2. **K–O**. MSC 38640, median tooth, Gosport Sand. **K**. Oral view. **L**. Basal view. **M**. Lingual view. **N**. Labial view. **O**. Profile view. **P–T**. MSC 38849.1, lateral tooth, basal Gosport Sand. **P**. Oral view. **Q**. Basal view. **R**. Labial view. **S**. Lingual view. **T**. Profile view. Labial at top in oral and basal views. Scale bars: A–O = 5 mm; P–T = 2 mm.

and tuberculated enameloid covering, both features that are lacking in *Myliobatis*. Additionally, the root of *Myliobatis* is very high, with an oblique labial face and lamellae that conspicuously extend past the lingual crown foot. This contrasts with the roots of both *Leidybatis* and *Rhinoptera*, which are typically very low compared to crown thickness, the labial faces are vertical, and the lamellae do not extend past the lingual crown foot. The labial and lingual crown faces on the teeth of *Leidybatis*, *Aetobatis*, and *Rhinoptera* bear vertical wrinkling of differing coarseness, whereas the lower part on *Myliobatis* sp. 2 tooth crowns bear reticulated ridges that grade apically into longitudinal ridges. The median teeth of *Aetomylaeus* are similar to *Myliobatis* sp. 2 but can be differentiated by their pitted labial face and beaded appearance on the lingual face. Additionally, the lateral teeth are wider than long

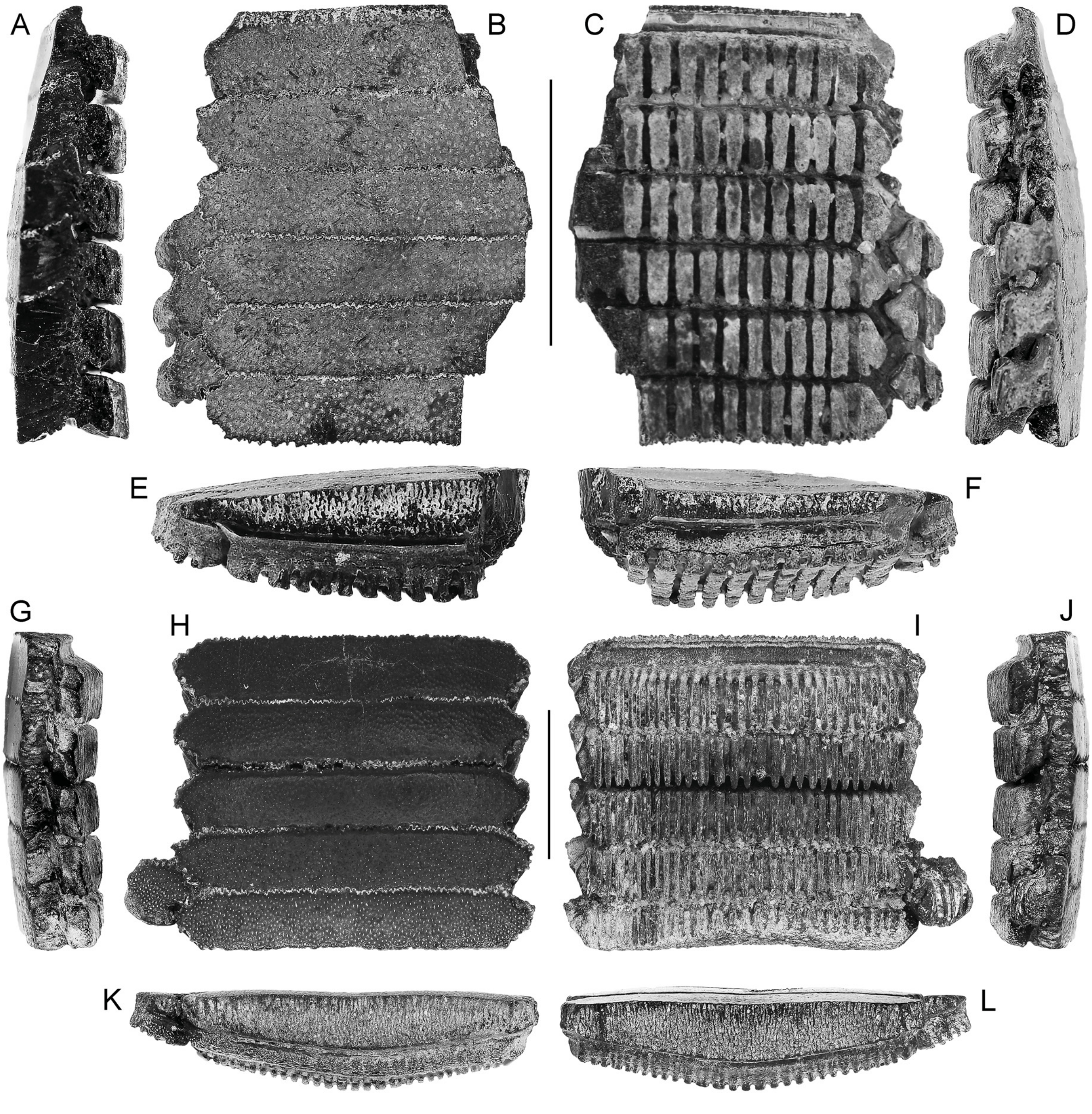


Fig. 48. *Myliobatis* sp. 2, tooth plates. **A–F**. MSC 35008, upper tooth plate, Tallahatta/Lisbon formation contact zone. **A**. Left lateral view. **B**. Oral view. **C**. Basal view. **D**. Right lateral view. **E**. Lingual view. **F**. Labial view. **G–L**. MSC 35007, lower tooth plate, Tallahatta/Lisbon formation contact zone. **G**. Right lateral view. **H**. Oral view. **I**. Basal view. **J**. Left lateral view. **K**. Lingual view. **L**. Labial view. Labial at top in oral, basal, and lateral views. Scale bars = 1 cm.

(nearly diamond-shaped) and not nearly as hexagonal as on *Myliobatis* sp. 2. Lastly, the lateral angles on *Aetomylaeus* teeth are more oblique than on *Myliobatis* sp. 2, and the margins of *Aetobatus* median teeth are straight.

This morphology was identified as *Myliobatis toliapicus* by Clayton *et al.* (2013), but examination of the larger sample of teeth available to us, in addition to the partial dentitions, leads us to believe that the species is similar, if not conspecific, with *M. latidens* as illustrated by Hovestadt & Hovestadt-Euler (2013: pl. 25, figs 12–13). This is based on the labiolingual narrowness of the crown and the highly serrated occlusal outline. However, we refrain from a more specific identification until direct comparisons to the *M. latidens* type material can be made.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at sites ACon-6 and ACov-11, the basal Lisbon Formation at site ACov-11, the “upper” Lisbon Formation at site ACl-3, the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21, ACl-15, and AMo-4. Middle Lutetian to middle Bartonian, zones NP15 to NP17.

Genus ***Pseudaetobatus*** Cappetta, 1986

Type species

Pseudaetobatus casieri Cappetta 1986, Ypresian, Morocco.

Pseudaetobatus belli Cicimurri & Ebersole, 2015

Fig. 49

Pseudaetobatus belli Cicimurri & Ebersole, 2015: 5, figs 4–5.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 225 isolated teeth; Claiborne Group; MSC 33278, MSC 33306, MSC 33311, MSC 33320, MSC 33328, MSC 33338, MSC 33361, MSC 33389, MSC 33412, MSC 33413, MSC 33422, MSC 33430, MSC 33433, MSC 33444, MSC 33449, MSC 33455, MSC 33461, MSC 33475, MSC 33507, MSC 33511, MSC 33520, MSC 33525, MSC 33587, MSC 33643, MSC 33682, MSC 33685, MSC 33688, MSC 33693, MSC 33729, MSC 33858, MSC 33943, MSC 35032, MSC 35048, MSC 35049, MSC 35050, MSC 35051, MSC 35052, MSC 35052, MSC 35053, MSC 35054, MSC 35055, MSC 35056, MSC 35058, MSC 35059, MSC 35060, MSC 35061, MSC 35062, MSC 35063 (13 specimens), MSC 35064, MSC 35065, MSC 35066, MSC 35067, MSC 35068, MSC 35069, MSC 35070, MSC 35071, MSC 35073, MSC 35074, MSC 35075, MSC 35078, MSC 35080, MSC 35081, MSC 35082, MSC 35083 (13 specimens), MSC 35749 (8 specimens), MSC 37058 (90 specimens), MSC 38880 (28 specimens), SC2017.32.1–11 (11 specimens).

Description

Median teeth wide and six-sided. Tooth crown thick with rectangular outline in cross section. Upper median teeth straight to weakly sinuous. Lower median teeth arcuate; distal ends of crown directed lingually (labially convex crown margin). Labial and lingual crown faces ornamented with fine vertical wrinkling. Labial face overhangs the root; has shallow basal transverse groove. Groove articulates with thick and rounded lingual transverse ridge located at the crown base. Tooth root polyaulocorhize; subdivided into thin lamellae by numerous nutritive grooves; root extends well beyond lingual crown base. Two lateral tooth morphologies have been identified. First has six-sided crown that is slightly wider than long, has sharp mesial and distal angles. Second has angular mesial margin but downturned,

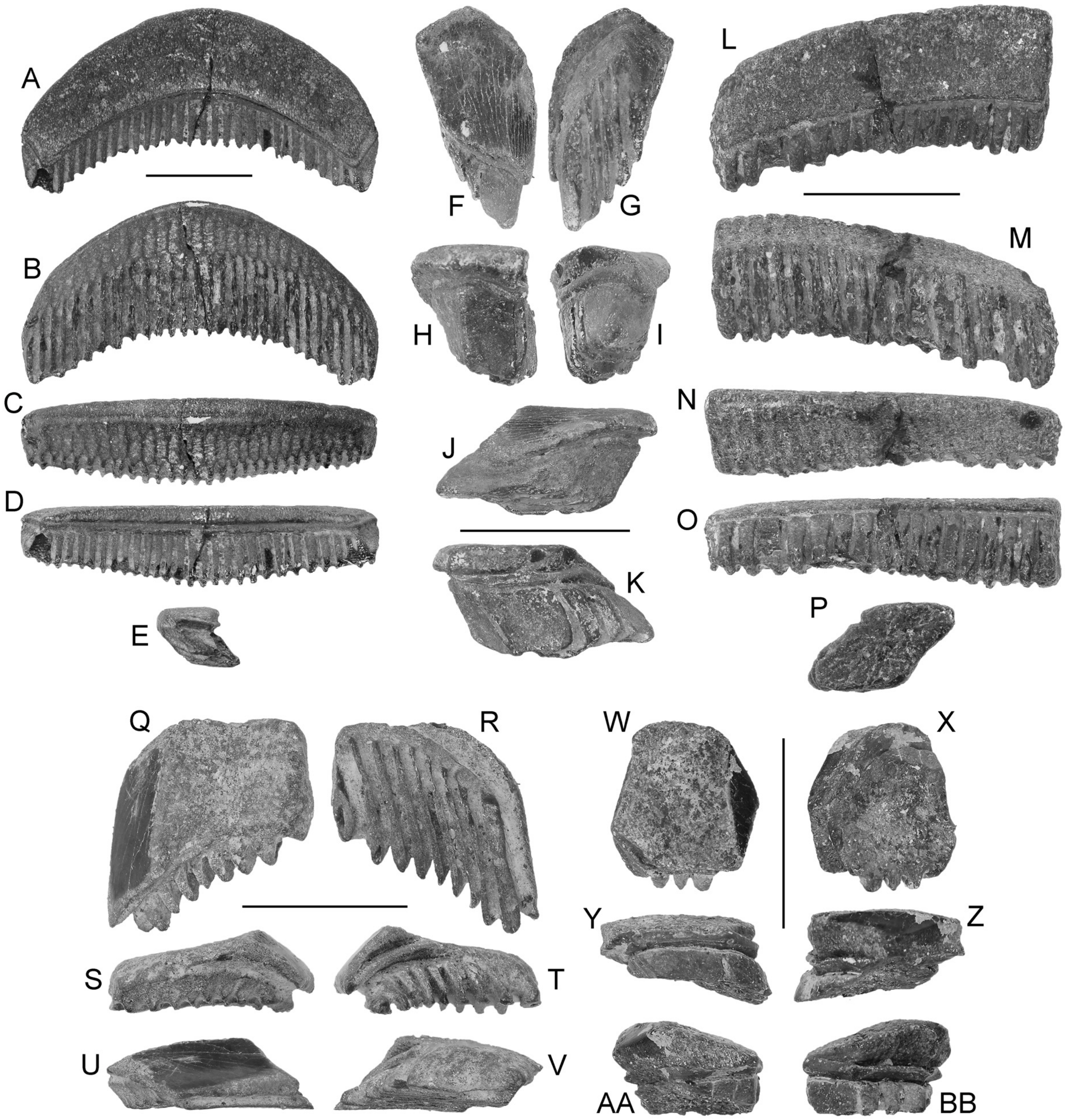


Fig. 49. *Pseudaetobatus belli* Cicimurri & Ebersole, 2015, teeth. **A–E**. MSC 35048, holotype, lower median tooth, lower Tallahatta Formation. **A**. Oral view. **B**. Basal view. **C**. Labial view. **D**. Lingual view. **E**. Profile view. **F–K**. MSC 35054, paratype, lower right distal–most lateral tooth, lower Tallahatta Formation. **F**. Oral view. **G**. Basal view. **H**. Labial view. **I**. Lingual view. **J**. Distal view. **K**. Mesial view. **L–P**. MSC 35058, paratype, upper? median tooth, lower Tallahatta Formation. **L**. Oral view. **M**. Basal view. **N**. Labial view. **O**. Lingual view. **P**. Profile view. **Q–V**. MSC 35059, paratype, upper right distal–most lateral tooth, lower Tallahatta Formation. **Q**. Oral view. **R**. Basal view. **S**. Labial view. **T**. Lingual view. **U**. Distal view. **V**. Mesial view. **W–BB**. MSC 35062, paratype, intermediate lateral tooth, lower Tallahatta Formation. **W**. Oral view. **X**. Basal view. **Y**. Distal view. **Z**. Mesial view. **AA**. Labial view. **BB**. Lingual view. Scale bars = 1 cm.

distally directed and pointed distal margin. Crown ornament and root morphology similar to median teeth.

Remarks

Pseudaetobatus was recently formally recognized in North America by Cicimurri & Ebersole (2015), and two species were identified. *Pseudaetobatus belli* occurs in lower-to-middle Eocene deposits of the Hatchetigbee and Tallahatta formations of Alabama and Mississippi, whereas *P. undulatus* is known only from the upper Eocene Dry Branch Formation of South Carolina (Cicimurri & Knight 2019). Within the Tallahatta Formation, *Pseudaetobatus* occurs with *Aetomylaeus*, *Myliobatis*, and *Rhinoptera*, but median teeth are easily separated from those of *Aetomylaeus* by their weak wrinkling on the labial and lingual faces and thick, rounded lingual transverse ridge. The teeth of *Rhinoptera* lack the very elongated, lingually directed root lobes seen on teeth of *Pseudaetobatus*. *Myliobatis* teeth have concave labial and convex lingual faces, which are lingually inclined, and have coarser vertical wrinkling. Additionally, the lateral-most teeth of *Pseudaetobatus* are distinguished by their downturned, swept-back and pointed distal margin. With respect to this lateral tooth morphology, those interpreted to have been part of a lower dentition are slightly wider than those in the upper dentition.

Pseudaetobatus is not known from the Lisbon Formation, where it seems to have been supplanted by *Aetobatus*. These two genera could theoretically be present in the same deposit, and it would be difficult to distinguish the median teeth of these two taxa. However, there are no lateral teeth in the *Aetobatus* dentition, and the distal ends of median teeth are downturned and swept distally. In contrast, the distal ends of *Pseudaetobatus* median teeth are angular and exhibit an attachment surface for articulation with a lateral tooth.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Meridian Sand Member of the Tallahatta Formation and lower Tallahatta Formation at site ADl-1. Upper Ypresian to lower Lutetian, zones NP12 to NP14.

Subfamily Rhinopterinae Jordan & Evermann, 1896

Genus ***Rhinoptera*** Cuvier, 1829

Type species

Myliobatis marginata Geoffroy St. Hilaire, 1817, Recent.

Rhinoptera sp.

Fig. 50

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1891 isolated teeth; Claiborne Group; ANSP 23423, ANSP 23424, GSA-V705 (2 specimens), MSC 1493 (4 specimens), MSC 199 (12 specimens), MSC 2388 (18 specimens), MSC 2390 (84 specimens), MSC 33272, MSC 33342, MSC 33590, MSC 33844.3, MSC 33844.6, MSC 33957, MSC 35744 (7 specimens), MSC 35746 (3 specimens), MSC 35749 (7 specimens), MSC 37200 (9 specimens), MSC 37396, MSC 37429 (3 specimens), MSC 37465 (5 specimens), MSC 37485 (3 specimens), MSC 37488, MSC 37489, MSC 37534 (3 specimens), MSC 37595, MSC 37601, MSC 37625 (2 specimens), MSC 38403, MSC 38779, MSC 38791 (48 specimens), MSC 38794 (78 specimens), MSC 38800 (13 specimens), MSC 38803 (2 specimens), MSC 38808 (7 specimens), MSC 38812 (8 specimens), MSC 38815 (20 specimens), MSC 38816 (2 specimens), MSC 38816 (2 specimens), MSC 38817 (3 specimens), MSC 38825 (10 specimens), MSC 38827 (14 specimens), MSC 38840 (1164 specimens), MSC 38847 (4 specimens), MSC 38848 (72 specimens), MSC 38852 (3 specimens), MSC 38854 (4 specimens), MSC 38856 (67 specimens), MSC 38870 (9 specimens), MSC 38873 (12 specimens), MSC 38875 (3 specimens), MSC 38884 (6 specimens), MSC 38943 (7 specimens), MSC 38949 (14 specimens), MSC 565, NJSM 24035 (3 specimens), SC2012.47.18 (13 specimens), SC2012.47.19 (29 specimens), SC2012.47.20 (9 specimens), SC2012.47.230 (12 specimens), SC2012.47.231 (65 specimens), SC2012.47.232, SC2012.47.233, SC2012.47.234, SC2012.47.235 (3 specimens), SC2012.47.236 (4 specimens).

Description

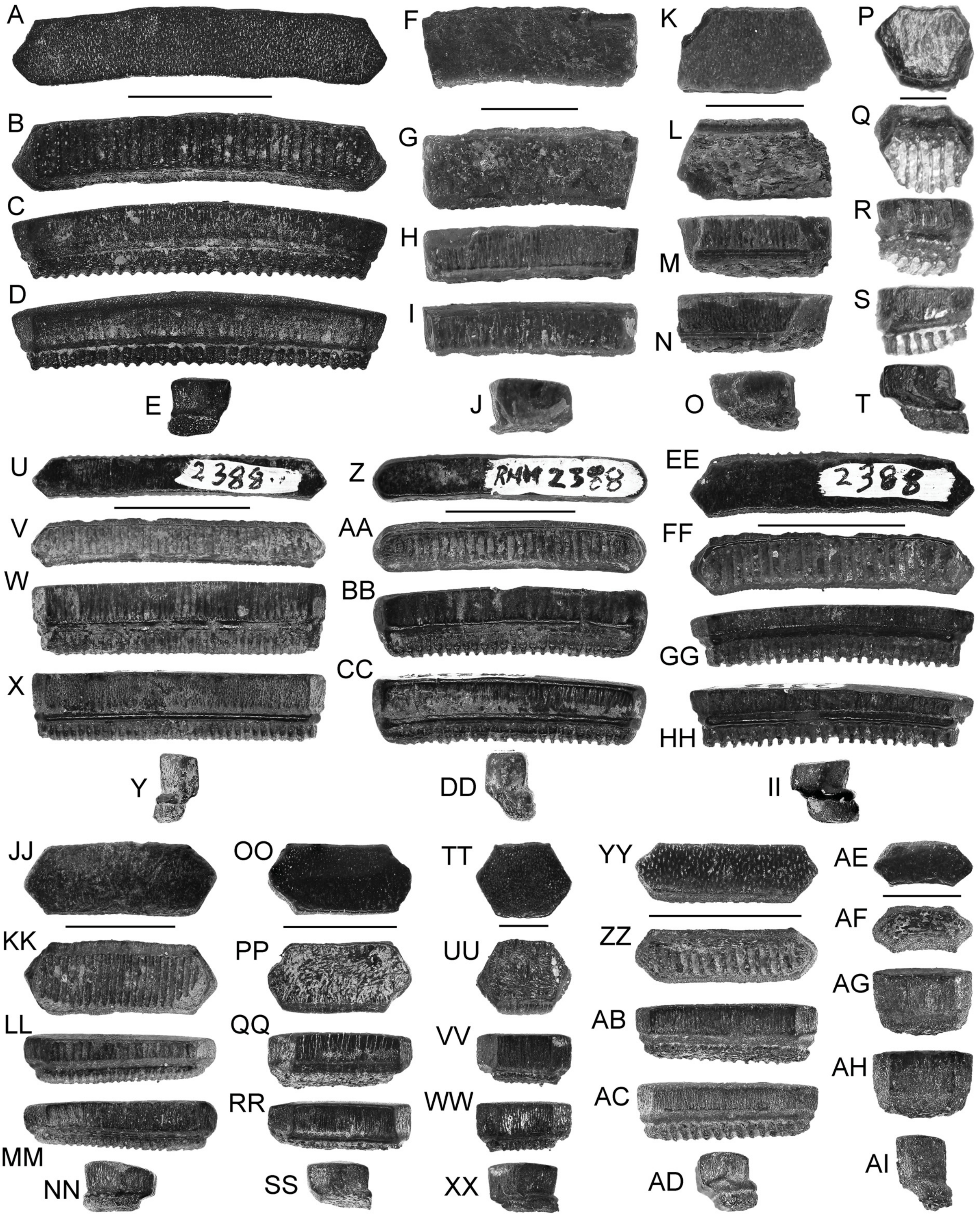
Teeth vary in width, depending on jaw position. Median teeth the widest; lateral teeth become progressively narrower towards the commissure (roughly hexagonal in outline in more distal rows). All teeth six-sided, regardless of position; have sharp lateral angles of approximately 90-degrees. The occlusal surface flat to weakly convex; covered with smooth enameloid. Labial and lingual crown faces vertical and flat. Labial face slightly overhangs the root. Root smooth except for some basal crenulation; more often irregularly spaced vertical wrinkles occur, which are coarsest basally and may terminate before the crown apex. Lingual face always more strongly ornamented than the labial face; ornament varies from fine to coarse vertical wrinkles that bifurcate apically; fine wrinkling of continuous and discontinuous vertical ridges, or beaded texturing in longitudinal rows. Lingual crown foot marked by thick and rounded transverse ridge; ornamentation generally does not intersect with transverse ridge. Root polyaulocorhize, generally very low compared to crown thickness. Labial face usually vertical; root lamellae typically do not pass the lingual crown foot.

Remarks

Rhinoptera occurs in all of the formations within the Claiborne Group, and it was coeval with several taxa with similar crushing dentitions, particularly within the Lisbon Formation. In general, *Rhinoptera* teeth have vertical and straight labial and lingual faces, and the root is low with a vertical labial face and distal lobes that do not extend past the crown foot. In contrast, teeth of *Aetomylaeus* and *Myliobatis* have concave labial and convex lingual faces, the root his high, with an oblique labial root face and distal lobes that extend beyond the crown foot. Additionally, the lingual crown face and the basal transverse ridge form a 90-degree angle, whereas this juncture is less than 90-degrees on *Myliobatis* and *Aetomylaeus*.

Fig. 50 (opposite page)**.** *Rhinoptera* sp., teeth. **A–E**. SC2012.47.233, median tooth, basal Lisbon Formation. **A**. Oral view. **B**. Basal view. **C**. Labial view. **D**. Lingual view. **E**. Profile view. **F–J**. MSC 37389.2, median tooth, lower Tallahatta Formation. **F**. Oral view. **G**. Basal view. **H**. Labial view. **I**. Lingual view. **J**. Profile view. **K–O**. MSC 37389.1, median tooth, lower Tallahatta Formation. **K**. Oral view. **L**. Basal view. **M**. Labial view. **N**. Lingual view. **O**. Profile view. **P–T**. SC2012.47.235, lateral tooth, basal Lisbon Formation. **P**. Oral view. **Q**. Basal view. **R**. Labial view. **S**. Lingual view. **T**. Profile view. **U–Y**. MSC 2388.1, median tooth, Gosport Sand. **U**. Oral view. **V**. Basal view. **W**. Labial view. **X**. Lingual view. **Y**. Profile view. **Z–DD**. MSC 2388.2, median tooth, Gosport Sand. **Z**. Oral view. **AA**. Basal view. **BB**. Labial view. **CC**. Lingual view. **DD**. Profile view. **EE–II**. MSC 2388.3, median tooth, Gosport Sand. **EE**. Oral view. **FF**. Basal view. **GG**. Labial view. **HH**. Lingual view. **II**. Profile view. **JJ–NN**. MSC 38873.2, lateral tooth, Gosport Sand. **JJ**. Oral view. **KK**. Basal view. **LL**. Labial view. **MM**. Lingual view. **NN**. Profile view. **OO–SS**. MSC 38403, lateral tooth, basal Gosport Sand. **OO**. Oral view. **PP**. Basal view. **QQ**. Labial view. **RR**. Lingual view. **SS**. Profile view. **TT–XX**. MSC 37595.1, lateral tooth, basal Gosport Sand. **TT**. Oral view. **UU**. Basal view. **VV**. Labial view. **WW**. Lingual view. **XX**. Profile view. **YY–AD**. MSC 38794.5, lateral tooth, basal Gosport Sand. **YY**. Oral view. **ZZ**. Basal view. **AB**. Labial view. **AC**. Lingual view. **AD**. Profile view. **AE–AI**. MSC 38794.1, lateral tooth, basal Gosport Sand. **AE**. Oral view. **AF**. Basal view. **AG**. Labial view. **AH**. Lingual view. **AI**. Profile view. Labial at top in oral and profile views. Scale bars: A–E, U–SS, YY–AD = 1 cm; F–O, TT–XX, AE–AI = 5 mm; P–T = 2 mm.

Rhinoptera lacks a tuberculated enameloid covering and medial swelling as seen on the median teeth of *Leidybatis*. Teeth of *Aetobatus* and *Pseudaetobatus* have thinner crowns compared to *Rhinoptera*, and the root of the former two taxa have an oblique labial face and the distal lobes extend well beyond the crown foot.



The best sample of Claiborne *Rhinoptera* teeth was derived from the Gosport Sand and they exhibit a high degree of variation. Some of this variation represents monognathic heterodonty, with very wide median teeth being flanked by several rows of lateral teeth that become progressively narrower towards the jaw hinge. Dignathic heterodonty is likely also represented, but this is difficult to discern without the aid of an articulated dentition. Gynandric heterodonty is not known in *Rhinoptera* (Herman *et al.* 2000) and ontogenetic heterodonty does not appear to have been developed, as the smallest teeth in our sample are simply smaller versions of the largest teeth we examined. The teeth we examined from the Tallahatta and Lisbon formations possess the same gross morphology as those from the Gosport Sand, and the types of wrinkling observed also overlaps with what we observed in the Gosport Sand sample. Thus, the evidence available to us at this time suggests that the *Rhinoptera* teeth within all three Claiborne Group formations are conspecific.

Eocene *Rhinoptera* teeth are often not speciated or referred to *R. sherborni* (White 1926; also Arambourg 1952; Hovestadt & Hovestadt-Euler 2013). The gross morphology of the Claiborne Group specimens we examined is comparable to *R. sherborni*, but unfortunately, White (1926) did not comment on the labial or lingual crown faces with respect to the presence or absence of wrinkling on *R. sherborni*. Additionally, the specimens illustrated by White (1926: pl. 10) are all shown in occlusal view and we cannot directly compare them to the Claiborne Group teeth. Although teeth that Arambourg (1952: pl. 32, figs 15–24) identified as *R. sherborni* exhibit wrinkling on the vertical crown faces, the teeth are all worn, and the degree of variation is unknown. This, coupled with the high degree of variability observed in our sample, leads us to refrain from assigning the specimens in our sample to any particular species.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Meridian Sand Member of the Tallahatta Formation and the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at sites ACh-14, ACon-6, and ACov-11, the basal Lisbon Formation at site ACov-11, the "upper" Lisbon Formation at site ACh-8, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACl-15 and ACh-21. Upper Ypresian to middle Bartonian, zones NP12 to NP17.

Subfamily *incertae sedis*

Genus **Meridiania** Case, 1994a

Type species

Meridiania convexa Case, 1994a, early Eocene, Meridian, Mississippi.

***Meridiania* cf. *M. convexa* Case 1994**

Fig. 51

Meridiania convexa Case, 1994a: 124, pl. 13 figs 282–291, pl. 14 figs 292–306.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 4 isolated teeth; Claiborne Group; MSC 38820, MSC 38822 (2 specimens), MSC 38877.

Description

Two morphologies represented in our sample. One represented by a partial tooth that is wider than long; the preserved lateral margin is angular. Crown appears to have had a straight occlusal outline; the highly worn occlusal surface largely consists of dentine with thin outer enameloid layer. Labial crown foot rounded; lingual crown foot has shallow transverse furrow. Root polyaulocorhize; relatively few lamellae separated by wide nutritive grooves.

Second morphology includes teeth with a hexagonal crown. One such tooth worn flat through *in vivo* wear. Occlusal surface formed of dentine surrounded by a layer of enameloid. All have thin and rounded labial margin; transverse furrows are located at the lingual crown foot. All lateral teeth with one-to-two nutritive grooves. Basal attachment surfaces of lobes triangular. The two other teeth with transverse cusp at center of the crown; duller on one specimen due to ablation. Enameloid of ablated specimen is polished and lacks detail. Remaining tooth exhibits discontinuous vertical ridges on the labial and lingual sides of cusp.

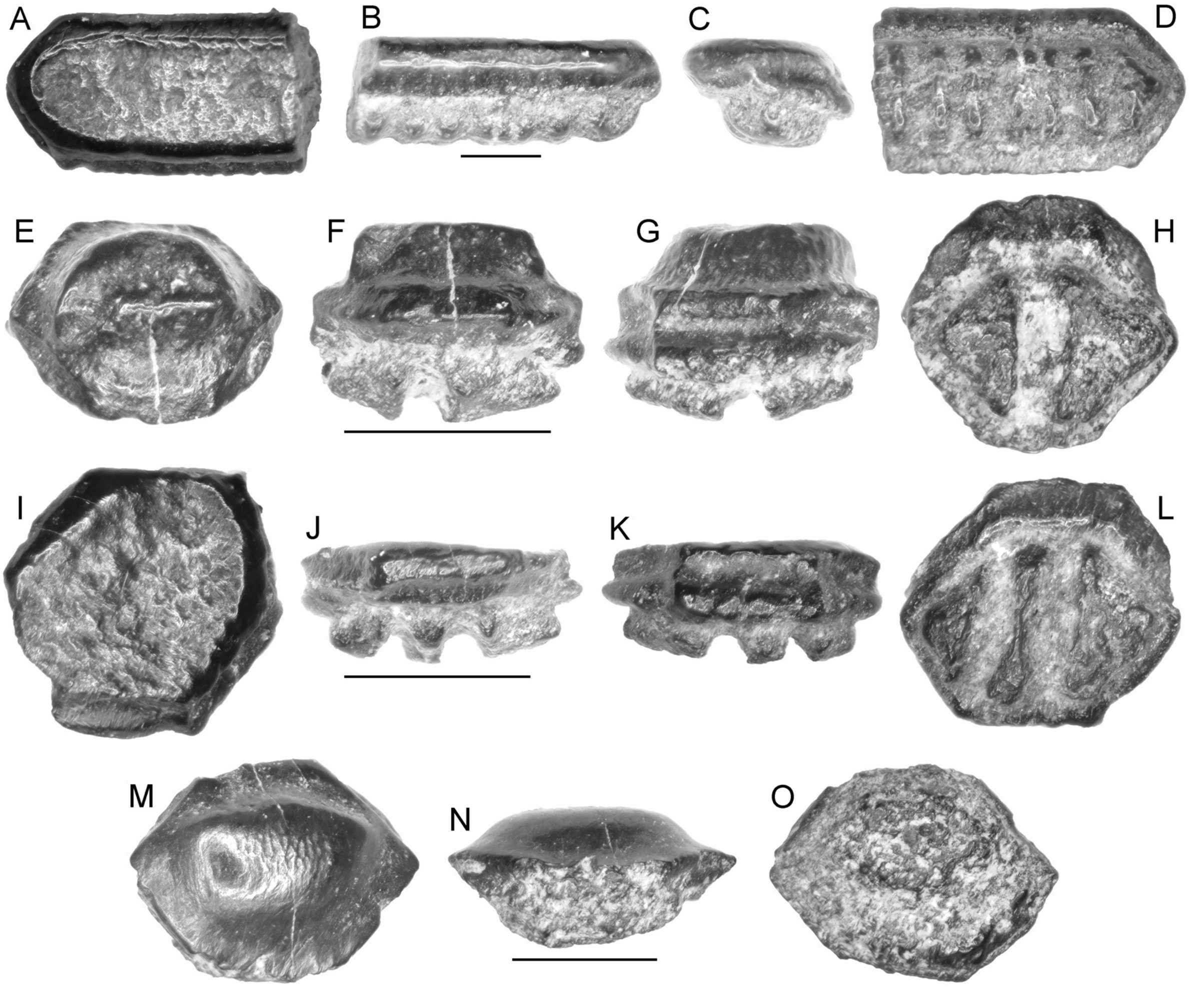


Fig. 51. *Meridiania* cf. *M. convexa* Case 1994, teeth. **A–D**. MSC 38877, median tooth, lower Tallahatta Formation. **A**. Oral view. **B**. Labial view. **C**. Profile view. **D**. Basal view. **E–H**. MSC 38822.2, lateral tooth, Gosport Sand. **E**. Oral view. **F**. Labial view. **G**. Lingual view. **H**. Basal view. **I–L**. MSC 38822.1, lateral tooth, Gosport Sand. **I**. Oral view. **J**. Labial view. **K**. Lingual view. **L**. Basal view. **M–O**. MSC 38820, lateral tooth, basal Gosport Sand. **M**. Oral view. **N**. Lingual view. **O**. Basal view. Labial at top in oral and basal views. Scale bars = 2 mm.

Remarks

The discovery of *Meridiania* in the Tallahatta Formation and Gosport Sand was surprising, considering both occurrences would represent significant range extensions from Zone NP11 strata of the Ypresian Nanjemoy Formation of Virginia (Kent 1999b). In fact, when MSC 38822.1 (Fig. 51–L) was first encountered within the ACl-15 Gosport Sand sample (Zone NP17), our immediate suspicion was that the specimen represented a contaminant. However, the discovery of an additional tooth from the same locality (MSC 38822.2, Fig. 51E–H), as well as a tooth from the Gosport Sand at site ACl-4 (MSC 38820, Fig. 51M–O), spurred us to reconsider this possibility. Closer inspection of these specimens revealed similar preservation to the other myliobatiform teeth within the Gosport samples from both localities.

Unfortunately, only one of the four teeth we examined is preserved well enough for meaningful comparison to *M. convexa*, the only species currently within the genus (i.e., Case 1994a; Kent 1999b; Cicimurri 2010). The three Gosport Sand *Meridiania* specimens we examined are morphologically similar to type specimens of *M. convexa*, which Case (1994a) interpreted as having been part of a dentition similar to that of *Dasyatis*. However, Cicimurri (2010) reevaluated the dentition of *M. convexa* and concluded that the type material represented lateral teeth in a dental battery that was more similar to that of *Rhinoptera*. The broken tooth recovered from the Tallahatta Formation is likely equivalent to the *Meridiania* tooth shown by Cicimurri (2010: 103, fig. 3.1), which was considered to represent a proximal lateral tooth.

The best specimen, MSC 38822.1 (Fig. 51A–D), was compared to a sample of several hundred *M. convexa* lateral teeth from the upper Thanetian Williamsburg Formation of South Carolina (at SC). The only notable differences between the samples is that MSC 38822.1 exhibits a slightly thicker crown margin and the furrows at the lingual crown foot are more concave. However, as Cicimurri (2010) noted, the crowns of *M. convexa* lateral teeth are variable and the slight differences observed on the Gosport Sand specimen cannot be accurately interpreted at this time. Suffice to say, the specimens represent a significant range extension for the genus, from Zone NP11 to Zone NP14 (Tallahatta Formation), with the youngest known record occurring in the Gosport Sand (Zone NP17).

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACl-15. Upper Ypresian and middle Bartonian, zones NP14 and NP17.

Genus ***Leidybatis*** Cappetta, 1986

Type species

Myliobates jugosus Leidy, 1876, Eocene, Burlington County, New Jersey, USA.

Leidybatis jugosus (Leidy, 1876)

Fig. 52

Myliobates jugosus Leidy, 1876, p. 86.

Myliobates jugosus – Leidy 1877: 240, pl. 31, figs 4–5.
Myliobatis cf. *jugosus* – Leriche 1905: 182, pl. 52.
Myliobatis jugosus – Leriche 1942: 26.
Leidybatis jugosus – Cappetta 1986: 189, pl. 4c. — Van den Eeckhaut & De Schutter 2009: 22, figs 5–7.
Leidybatis cf. *jugosus* – Clayton *et al.* 2013: 64, pl. 4a–c.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 71 isolated teeth; Claiborne Group; ALMNH PV1992.28.21, ALMNH PV1992.28.6.3, MMNS VP-5643 (2 specimens), MMNS VP-8189 (6 specimens), MMNS VP-8224 (5 specimens), MSC 35005, MSC 37080, MSC 37081, MSC 37082 (4 specimens), MSC 37083, MSC 37084, MSC 37085, MSC 37086, MSC 37135, MSC 37135, MSC 37249 (2 specimens), MSC 37256, MSC 37257 (3 specimens), MSC 37282, MSC 37291, MSC 37321 (3 specimens), MSC 37681, MSC 38829 (3 specimens), MSC 38876 (2 specimens), MSC 38948, NJSM 24033, SC2012.47.16, SC2012.47.17 (2 specimens), SC2012.47.197 (3 specimens), SC2012.47.198, SC2012.47.199, SC2012.47.200, SC2012.47.201 (2 specimens), SC2012.47.202, SC2012.47.203 (2 specimens), SC2012.47.204, WSU 18, WSU 30, WSU CC 513 (2 specimens), WSU CC 522 (2 specimens), WSU 5009 (3 specimens).

Description

Median teeth very wide and narrow. All median teeth with distinctive swelling on the crown; swelling generally located medially but can be closer to the lateral margin (resulting in an asymmetrical labial/lingual outline). Swelling is in contrast to remainder of crown, which is dorsoventrally very thin. Occlusal surface has thick enameloid covering that is heavily tuberculated on unworn parts of tooth; surface is punctate where enameloid is missing, due to *in vivo* use or taphonomic processes (*in vivo* use is indicated by flat wear facets that on the highly convex portion of the crown of some teeth). Labial crown face overhangs the root; lingual face with thick and rounded transverse ridge at the crown base. Labial and lingual crown faces possess coarse parallel vertical folds that anastomose and become finer apically. Distal ends of crown angular. Root at least as high as thinnest part of crown; is subdivided into thin lamellae by evenly spaced nutritive grooves. Lamellae do not extend lingually past the crown. Lateral teeth are six-sided, nearly symmetrical. Lateral teeth with same tuberculation and wrinkling as observed on median teeth, but root subdivided into only two or three lamellae.

Remarks

Ascribing the teeth described above to a particular species is complicated by the fact that fossil Myliobatidae are often based on a single median tooth, and our knowledge of how the tooth was incorporated into the upper or lower dentition is far from complete. Whole and even partial upper and lower dentitions are more informative, but as Hovestadt & Hovestadt-Euler (2013) have recently shown, there can be a great deal of intraspecific variation within the dentitions of extant species. Several fossil species based on isolated median teeth, including *Myliobatis siculus* Salinas, 1901, *M. pachyrhizodus* Fowler, 1911, *M. tumidens* Woodward, 1889, and *M. jugosus* Leidy, 1876, are very convex, but this phenomenon can largely be attributed to the teeth being from the upper dentition (i.e., see description for *Aetomylaeus* above). Leidy's (1876) taxon, the *jugosus* morphology, has unusually convex median teeth like the ones from the Lisbon Formation we described above. Cappetta (1986) erected the genus *Leidybatis* to include the *jugosus* morphology, as well as his new species, *L. granulosus*. Mendiola (1999) named several species of *Leidybatis*, but Cappetta (2012) considered those species as a *nomina dubia* because they lacked stratigraphic context. Hovestadt & Hovestadt-Euler (2013) indicated that the various tooth morphologies attributed to *Leidybatis* fall within the range they observed in extant species of *Aetomylaeus* and *Myliobatis*, and they considered *L. jugosus* as a *nomen dubium*. However, *Leidybatis* possess labial and lingual ornamentation of parallel vertical folds, which contrasts with the pitting and granulation seen on these areas of *Aetomylaeus* teeth (Leidy 1877; Cappetta 1986; Mendiola 1999; Cappetta 2012; Hovestadt & Hovestadt-Euler 2013). In addition, the labial root face is vertical on *Leidybatis* teeth and root lobes do not extend lingually past the crown base. This contrasts with the roots of *Myliobatis* and *Aetomylaeus*, which have oblique labial faces and the lobes very conspicuously extend past the lingual crown face.

The root characteristics of *Leidybatis* are similar to the condition seen on *Rhinoptera* teeth, and specimens illustrated by Cappetta (1986: fig. 3, 1–8) indicate that *L. granulosus* had lateral teeth of decreasing width like *Rhinoptera*. In support of this is a *Leidybatis* lateral tooth morphology that is comparable to those within more proximal lateral rows of a *Rhinoptera* dentition. SC2012.47.202 (Fig. 52SS–TT) is twice as wide as long and is similar to *Rhinoptera* lateral teeth in our Claiborne sample. We assign this tooth to *Leidybatis* based on the distinctly ornamented occlusal surface and lingual and labial crown ornamentation that is identical to that on the median teeth described above.

We herein support the validity of *Leidybatis* based on our samples of Myliobatinae and Rhinopterinae teeth from the Tallahatta and Lisbon formations. As mentioned above, the labial and lingual vertical wrinkling on *Leidybatis* teeth contrasts with the ornamentation we observed on *Aetomylaeus* teeth from both formations. If one considered the *Leidybatis* morphology aberrant, as do Hovestadt & Hovestadt-Euler (2013), the labial and lingual ornamentation of teeth should still serve as a generic identifier. As an example, we examined a partial *Aetomylaeus* median tooth (MSC 37079, Fig. 46EE–II) that exhibits a convex medial portion but thinner lateral side, similar to *Leidybatis*. The vertical wrinkling seen on *Pseudaetobatus* (Tallahatta Formation) and *Aetobatus* (Lisbon Formation) is much weaker than that of *Leidybatis*, and the root lobes of the former two taxa conspicuously extend lingually past the crown. Lastly, a conspicuous feature of *Leidybatis* teeth is the thick enameloid covering on the crown, which is tuberculated on the occlusal surface. This contrasts with the smooth enameloid occurring on all other Myliobatinae and Rhinopterinae teeth within Clabornian strata.

Within the species of *Leidybatis*, the crowns of *L. granulosus*, *L. rusticus*, and *L. zemensis* appear to be more uniformly convex than *L. jugosus*. MSC 35005 (Fig. 52A–E) is virtually identical to the type specimen illustrated by Leidy (1877: pl. 31, figs 4–5) and Hovestadt & Hovestadt-Euler (2013: pl. 49, fig. 19), and it compares closely with a specimen from the middle Eocene of western Africa shown by Cappetta (1986: pl. 2, fig. 4). Leidy (1877) made no mention of the tuberculated ornamentation we observed on our Claiborne specimens, and he attributed the "dull" surface and thinness of the lateral parts of the crown to *in vivo* usage. The apparent lack of ornament on Leidy's illustrated specimen could be the result of wear or poor representation by the illustrator, but our Claiborne specimens show that the thinness of the sides of the crown reflects the natural morphology of the tooth. Four specimens within

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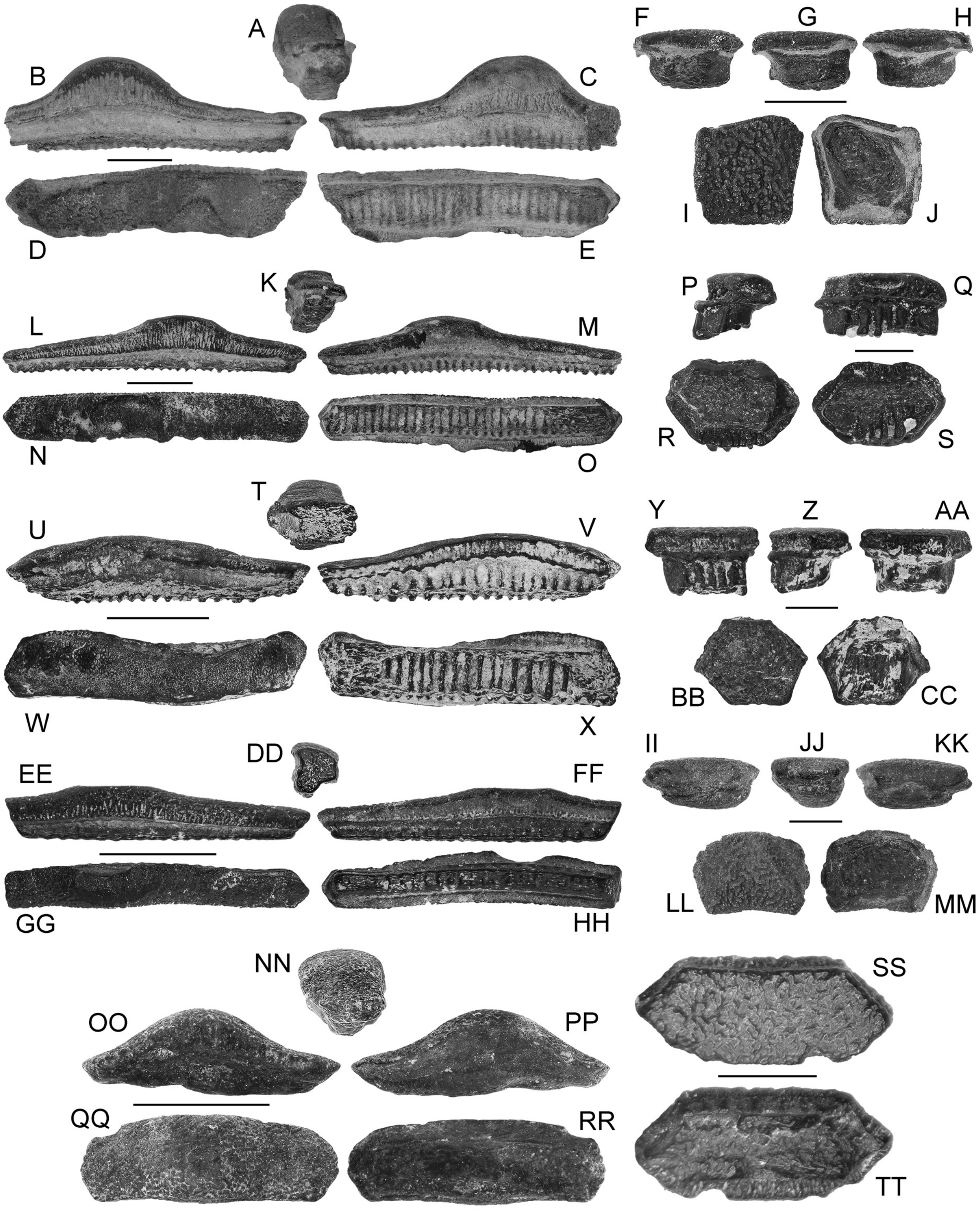
Fig. 52 (opposite page)**.** *Leidybatis jugosus* (Leidy, 1876), teeth. **A–E**. MSC 35005, median tooth, Tallahatta/Lisbon formation contact zone. **A**. Profile view. **B**. Labial view. **C**. Lingual view. **D**. Oral view. **E**. Basal view. **F–J**. MSC 37080, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **F**. Labial view. **G**. Profile view. **H**. Lingual view. **I**. Oral view. **J**. Basal view. **K–O**. MSC 37086, median tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **K**. Profile view. **L**. Labial view. **M**. Lingual view. **N**. Oral view. **O**. Basal view. **P–S**. MSC 37291, lateral tooth, basal Lisbon Formation. **P**. Profile view. **Q**. Lingual view. **R**. Oral view. **S**. Basal view. **T–X**. MSC 37082, median tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **T**. Profile view. **U**. Labial view. **V**. Lingual view. **W**. Oral view. **X**. Basal view. **Y–CC**. MSC 37081, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **Y**. Lingual view. **Z**. Profile view. **AA**. Labial view. **BB**. Oral view. **CC**. Basal view. **DD–HH**. SC2012.47.198, median tooth, basal Lisbon Formation. **DD**. Profile view. **EE**. Labial view. **FF**. Lingual view. **GG**. Oral view. **HH**. Basal view. **II–MM**. MSC 37135, lateral tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **II**. Labial view. **JJ**. Profile view. **KK**. Lingual view. **LL**. Oral view. **MM**. Basal view. **NN–RR**. MSC 37083, median tooth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **NN**. Profile view. **OO**. Labial view. **PP**. Lingual view. **QQ**. Oral view. **RR**. Basal view. **SS–TT**. SC2012.47.202, lateral tooth, basal Lisbon Formation. **SS**. Oral view. **TT**. Basal view. Labial at top in oral and basal views. Scale bars: A–E, K–O, T–X, DD–HH, NN–RR = 1 cm; F–J, P–S, Y–CC, II–MM, SS–TT = 5 mm.

our sample indicate a degree of heterodonty within the median row of *Leidybatis* dentitions. MSC 37082 (Fig. 52T–X) has a broad but very low convexity that is skewed to one side of the tooth. MSC 37086 (Fig. 52K–O) has a more convex swelling that is also offset to one side of the crown, and the shoulders are more elongated than on MSC 37082. MSC 37083 (Fig. 52NN–RR) is a smaller tooth with high, medially located swelling and short shoulders, whereas MSC 35005 (a much larger tooth, Fig. 52A–E) has a very high medial swelling and elongated shoulders. Unfortunately, we lack dentitions and cannot accurately distinguish upper from lower teeth, but we believe the Lisbon sample represents intraspecific



variation within a single species. There is currently no evidence to suggest that the two tooth fragments from the Tallahatta Formation are not conspecific with *L. jugosus*.

Stratigraphic and geographic range in Alabama

Two tooth fragments were collected from the lower Tallahatta Formation at site ADl-1. The remaining sample is from the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, and the basal Lisbon Formation at site ACov-11. Upper Ypresian to middle Lutetian, zones NP14 and NP15.

Subfamily Mobulinae Gill, 1893

Genus ***Burnhamia*** Cappetta, 1976

Type species

Rhinoptera daviesi Woodward, 1889, early Eocene (Ypresian), London Clay, Sheppey, England.

Burnhamia daviesi (Woodward, 1889)

Fig. 53

Rhinoptera daviesi Woodward, 1889: 126, pl. 3, fig. 6.

Burnhamia daviesi – Cappetta 1976: 564.

Material examined

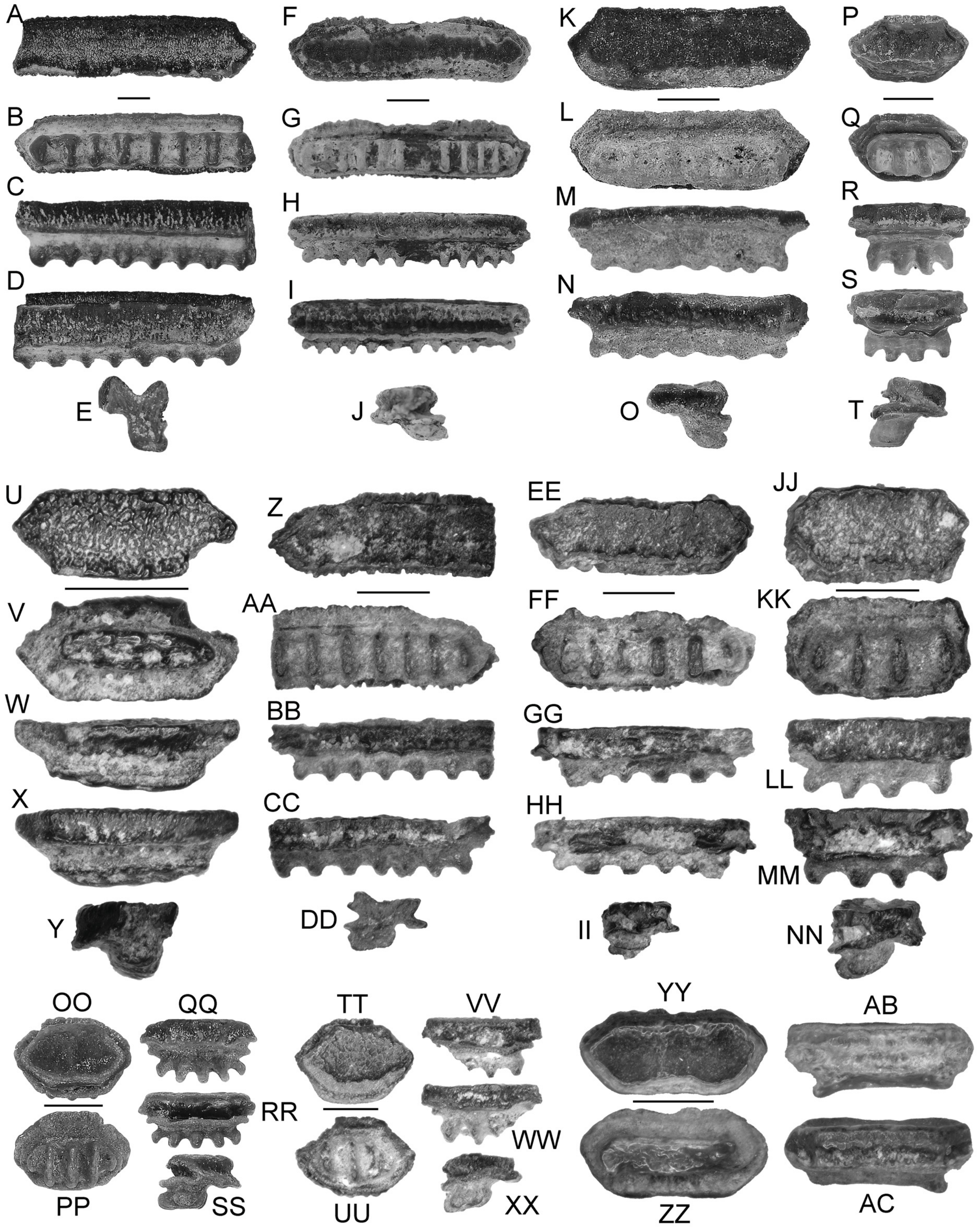
UNITED STATES OF AMERICA – **Alabama** • 12 isolated teeth; Claiborne Group; MSC 38821, MSC 35789, MSC 38823 (4 specimens), MSC 38826, MSC 38878 (5 specimens).

Description

Median teeth very wide and relatively narrow. Lateral teeth two-to-three times wider than long. In oral view, all specimens with six-sided crown with sharp lateral angles. Occlusal surface concave to varying degrees. Concave surface completely surrounded by a conspicuous rim; rim bears fine network of reticulated ridges. Labial crown face vertical; crown foot often developed into a sharp projection.

Fig. 53. *Burnhamia daviesi* (Woodward, 1889), teeth. **A–E**. MSC 38878.2, median tooth, lower Tallahatta Formation. **A**. Oral view. **B**. Basal view. **C**. Labial view. **D**. Lingual view. **E**. Profile view. **F–J**. MSC 38878.1, median tooth, lower Tallahatta Formation. **F**. Oral view. **G**. Basal view. **H**. Labial view. **I**. Lingual view. **J**. Profile view. **K–O**. MSC 38826, median tooth, basal Lisbon Formation. **K**. Oral view. **L**. Basal view. **M**. Labial view. **N**. Lingual view. **O**. Profile view. **P–T**. MSC 38878.3, lateral tooth, lower Tallahatta Formation. **P**. Oral view. **Q**. Basal view. **R**. Labial view. **S**. Lingual view. **T**. Profile view. **U–Y**. MSC 38823.4, lateral tooth, Gosport Sand. **U**. Oral view. **V**. Basal view. **W**. Labial view. **X**. Lingual view. **Y**. Profile view. **Z–DD**. MSC 38823.3, median tooth, Gosport Sand. **Z**. Oral view. **AA**. Basal view. **BB**. Labial view. **CC**. Lingual view. **DD**. Profile view. **EE–II**. MSC 38823.2, lateral tooth, Gosport Sand. **EE**. Oral view. **FF**. Basal view. **GG**. Labial view. **HH**. Lingual view. **II**. Profile view. **JJ–NN**. MSC 38823.1, lateral tooth, Gosport Sand. **JJ**. Oral view. **KK**. Basal view. **LL**. Labial view. **MM**. Lingual view. **NN**. Profile view. **OO–SS**. MSC 38878.4, lateral tooth, lower Tallahatta Formation. **OO**. Oral view. **PP**. Basal view. **QQ**. Labial view. **RR**. Lingual view. **SS**. Profile view. **TT–XX**. MSC 38821, lateral tooth, basal Gosport Sand. **TT**. Oral view. **UU**. Basal view. **VV**. Labial view. **WW**. Lingual view. **XX**. Profile view. **YY–AC**. MSC 35789, lateral tooth, lower Tallahatta Formation. **YY**. Oral view. **ZZ**. Basal view. **AB**. Labial view. **AC**. Lingual view. Labial at top in oral and basal views. Labial at top in oral and basal views. Scale bars = 2 mm.

Lingual face with rounded transverse ridge at the crown foot; has a narrow suprajacent furrow. Often, a second less well-developed transverse ridge is near the crown apex. All crown faces ornamented with fine reticulated ridging and coarser vertical wrinkling. Ornamentation is conspicuous on median teeth; less so on distal lateral teeth. Root polyaulocorhize; relatively few lamellae are separated by wide nutritive grooves and may be one-half or equal to the crown height. Root lamellae may extend slightly past the lingual crown foot.



Remarks

Illustrations of the holotype provided by Woodward (1889), Hovestadt & Hovestadt-Euler (2013), and Underwood *et al.* (2017) showed that the dentition of *Burnhamia daviesi* was similar to that of *Rhinoptera*, consisting of a median row of very wide teeth that is flanked by multiple rows of lateral teeth that decrease in size towards the commissure. Gross tooth morphology and limited crown wear has led to interpretations that *Burnhamia* was a pelagic planktivore related to extant devil rays, and recent phylogenetic analyses placed *Burnhamia* securely within the Mobulidae (Zhelezko & Kozlov 1999; Cappetta 2012; Underwood *et al.* 2017).

Within the Tallahatta Formation, the concave occlusal surface on median and lateral teeth easily distinguish *Burnhamia* from any of the other coeval Myliobatidae, including *Rhinoptera*, *Aetomylaeus*, *Myliobatis* and *Pseudaetobatus*. This singular feature also serves to separate *Burnhamia* from teeth of *Leidybatis*, *Aetobatus*, *Myliobatis*, *Aetomylaeus* and *Rhinoptera* that occur in the Lisbon Formation, as well as teeth of the latter three taxa from the Gosport Sand. However, *Burnhamia* could be confused with *Eoplinthicus yazooensis*, a mobulid taxon that also inhabited the Gosport Sand paleoenvironment (see below). Both genera are exceedingly rare within the sample of several thousand Myliobatidae teeth we examined from the Gosport Sand, but *Burnhamia* can be distinguished by an occlusal surface that is equal to, or only slightly smaller in area than, the crown base, whereas the occlusal surface of *E. yazooensis* is significantly smaller in area than the crown base. Additionally, the labial crown foot is developed into a sharp horizontal or basally directed projection, but the lower half of the labial face of *E. yazooensis* is broadly rounded. In profile, the lateral angles of *Burnhamia* are much more sharply defined than on *E. yazooensis*. Also, the occlusal surface of *Burnhamia* teeth bears a reticulated network of ridges, whereas surfaces of *E. yazooensis* exhibit a series of fine labiolingually oriented striations. The crown of *Burnhamia* has a sharp six-sided outline in occlusal view, whereas the labial margin on *E. yazooensis* is less sharply defined.

Some teeth within the Tallahatta Formation and Gosport Sand samples exhibit a particularly concave occlusal surface surrounded by a very sharp ridge, a condition that is similar to specimens that Underwood *et al.* (2017) identified as possible male teeth within the species. The morphologies of the *Burnhamia* teeth from the Tallahatta Formation and Gosport Sand overlap, and we therefore consider them to be conspecific. The single specimen from the Lisbon Formation is ablated, but it also conforms to teeth recovered from the other two formations.

It has been postulated that *Burnhamia* diverged into two lineages, one where the teeth become progressively smaller and less ornamented over time (i.e., *Burnhamia fetahi*), and a *B. daviesi* lineage that continued until the middle Eocene, giving rise to *Eoplinthicus* (Cappetta 1985; Noubhani & Cappetta 1992; Cappetta & Stringer 2002). However, within our sample, which spans from the Ypresian to middle Bartonian, the *B. daviesi* teeth remain morphologically constant over that time and have stratigraphic overlap with *Eoplinthicus* in the Gosport Sand.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Genus **Eoplinthicus** Cappetta & Stringer, 2002

Type species

Eoplinthicus yazooensis Cappetta & Stringer, 2002, late Eocene (Priabonian), Louisiana, USA.

Eoplinthicus yazooensis Cappetta & Stringer, 2002
Fig. 54

Eoplinthicus yazooensis Cappetta & Stringer, 2002: 51–56, pl. 1.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 isolated tooth; Claiborne Group; ALMNH PV1985.35.65.

Description

A single median tooth is represented in our sample. Tooth is very wide, but labiolingually thin, six-sided. Occlusal surface concave across nearly the entire width; occlusal surface outlined by a sharp, irregular rim. In oral view, crown is conspicuously smaller in area than the crown base. Labial crown face concave, with lower half projecting labially and upper half nearly vertical. Lingual face vertical and straight, slight lingual projection at the crown foot. Very base of lingual crown bears weak transverse ridge immediately above the root. All crown faces with coarse ornamentation of vertical anastomosing and interconnected ridges that become finer apically. Polyaulocorhize root as high as the crown. Labial and lingual faces nearly vertical; 13 narrow lobes are separated by 12 nutritive grooves.

Remarks

When originally described, *Eoplinthicus* was not directly differentiated from *Burnhamia*, possibly because the two genera were not known to co-occur within the Yazoo Clay (Cappetta & Stringer 2002). However, both *Eoplinthicus* and *Burnhamia* were collected from the upper Gosport Sand (see above), and a differential diagnosis is provided here. *Eoplinthicus yazooensis* is now known from three teeth (including two from the Yazoo Clay), all of which can be distinguished from *Burnhamia* by having an

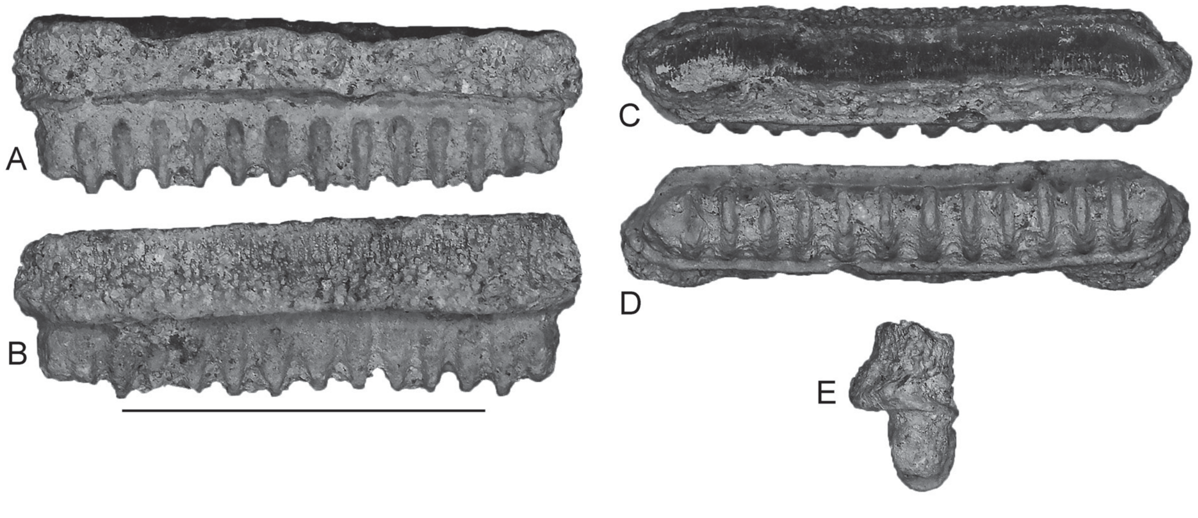


Fig. 54. *Eoplinthicus yazooensis* Cappetta & Stringer, 2002, median tooth. **A**–**E**. ALMNH PV1985.35.65, Gosport Sand. **A**. Lingual view. **B**. Labial view. **C**. Oral view. **D**. Basal view. **E**. Profile view. Labial at top in oral and basal views. Scale bar = 1 cm.

occlusal surface that is significantly smaller in area than the crown base. In contrast, the occlusal surface on *Burnhamia* teeth is equal to, or only slightly smaller in area than, the crown base. Additionally, the lower half of the labial face of *E. yazooensis* is broadly rounded, whereas on *Burnhamia* the labial crown foot is developed into a sharp horizontal or basally directed projection. In profile, the lateral angles of *E. yazooensis* are not as sharply defined as observed on *Burnhamia*. Also, the occlusal surface of *E. yazooensis* bears a series of fine labiolingually oriented striations, as opposed to a somewhat reticulated network of ridges on the oral surface of *Burnhamia* teeth. The labial margin on *E. yazooensis* is less sharply defined than *Burnhamia*, which has a sharp six-sided outline in occlusal view. Cappetta & Stringer (2002) implied that *Eoplinthicus* was a direct descendant of *Burnhamia*, but this theory must be further examined in light of the discovery that these taxa were coeval within the Gosport Sand paleoenvironment.

A second *Eoplinthicus* species, *E. underwoodi* Adnet *et al.* 2012, has been reported from middle-to-upper Eocene strata in Africa. This species differs from *E. yazooensis* in being smaller in size (with six root lamellae) and by having less developed crown ornamentation.

Stratigraphic and geographic range in Alabama

The lone specimen in our sample was collected from the upper Gosport Sand at site ACh-21. Middle Bartonian, Zone NP17.

Batomorphii indet.

Fig. 55

Material examined

UNITED STATES OF AMERICA – **Alabama** • 3 isolated teeth; Claiborne Group; MSC 37675.1–2, SC2012.47.154.

Description

Teeth do not exceed 2 mm in crown height. Upper one-half to two-thirds of crown formed into laterally compressed, vertical to slightly lingually curving cusp. Lower one-third to one-half of crown wider, shelf-like laterally and lingually, with labial crown foot developed into small, divergent projections. Labial projections separated by shallow to deep medial embayment. Lingual crown foot straight or with weakly developed medial notch. Crown with trapezoidal to square outline in oral view, but more triangular in profile. Root located at lingual half of crown, bilobate with wide nutritive groove, extends past the lingual crown foot.

Remarks

The crown on these teeth is distinctive for their tall, laterally compressed cusp, conspicuous, diverging basal labial projections and roughly square oral outline. Although similar to teeth of *Jacquhermania* and the male teeth of "*Dasyatis*" described herein, the three teeth in our sample differ significantly in having a laterally compressed cusp that lacks lateral cutting edges. In addition, male teeth of "*Dasyatis*" bear ornamentation of various types (see above). Although the specimens are morphologically comparable to, and within the size range of, most members of the Torpedinidae, particularly *Torpedo*, the Lisbon specimens differ from all Recent and fossil Torpedinidae, except *Eotorpedo*, in lacking distinctive lateral cutting edges extending from the cusp apex to nearly the crown base (Cappetta 1988; Herman *et al.* 2002).

Eotorpedo White, 1935 can have a cusp similar to the Lisbon specimens described above, as well as labial projections separated by a deep embayment and a notch at the lingual crown foot. A significant difference between the Lisbon specimens and these two species of *Eotorpedo* is the lack of a basal transverse crest on the Alabama teeth. Some specimens identified as *Eotorpedo*, including *Eotorpedo nolfi* Herman, 1974 (Herman 1974: fig. 1, a-c) and *Eotorpedo jaekeli* (Case, 1994) (see Case 1994a) may in fact be *Jacquhermania* (Cappetta 2012; Cappetta & Case 2016). It is possible that the Claibornian specimens described above represent juvenile teeth of *Jacquhermania*, but to our knowledge this morphology has not previously been attributed to this genus. Additional, more complete, specimens are needed to more accurately identify this morphology.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the basal Lisbon Formation at site ACov-11. Lower Lutetian, Zone NP15.

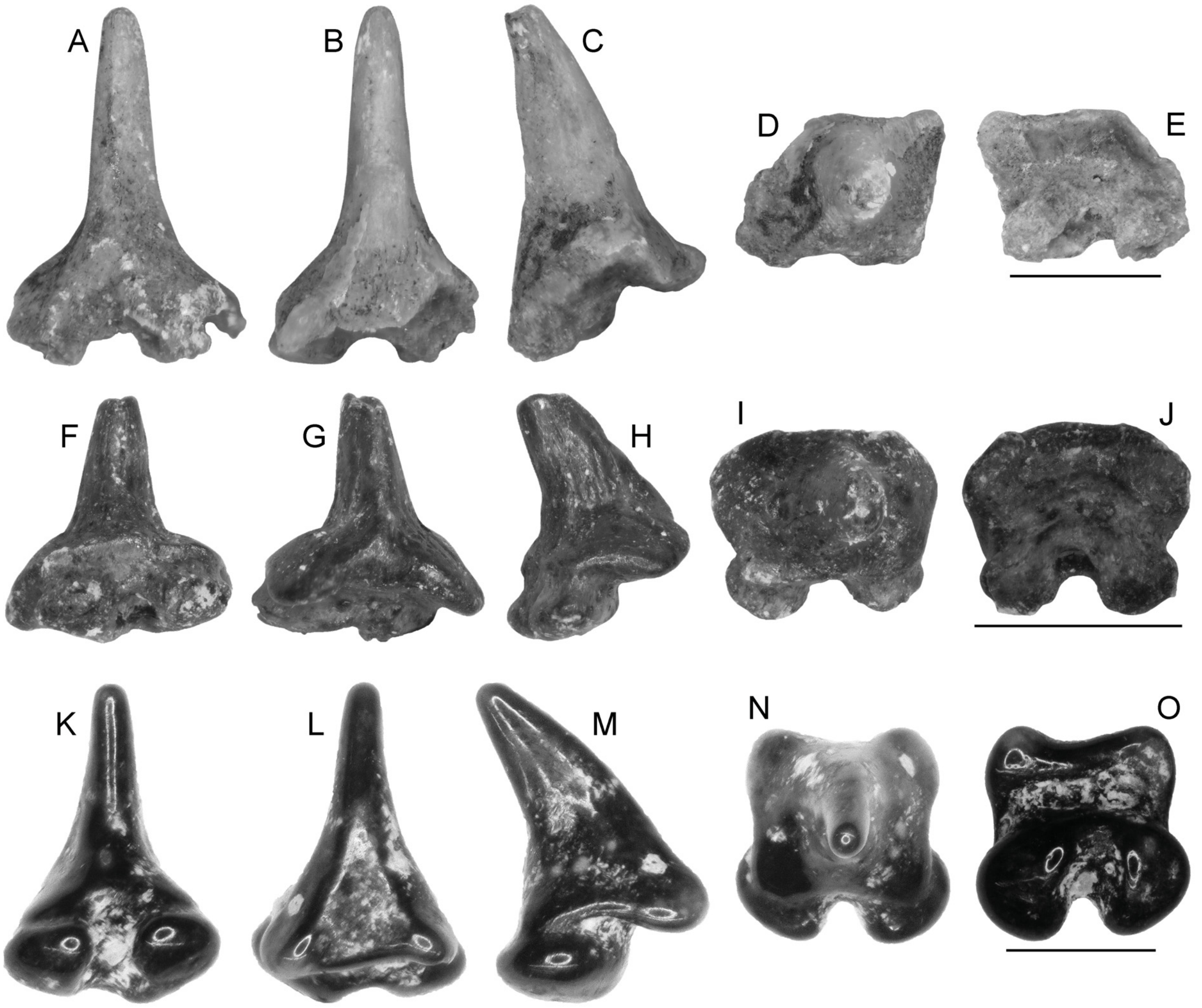


Fig. 55. Batomorphii indet., teeth. **A–E**. MSC 37675.2, basal Lisbon Formation. **A**. Labial view. **B**. Lingual view. **C**. Profile view. **D**. Oral view. **E**. Basal view. **F–J**. MSC 37675.1, basal Lisbon Formation. **F**. Labial view. **G**. Lingual view. **H**. Profile view. **I**. Oral view. **J**. Basal view. **K–O**. SC2012.42.154, basal Lisbon Formation. **K**. Labial view. **L**. Lingual view. **M**. Profile view. **N**. Oral view. **O**. Basal view. Labial at top in oral and basal views. Labial at top in oral and basal views. Scale bars = 1 mm.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii sensu Goodrich, 1930
Infraclass Chondrostei Müller, 1844
Order Acipenseriformes Berg, 1940
Suborder Acipenseriodei Nelson *et al.*, 2016
Family *Incertae sedis*

Genus ***Cylindracanthus*** Leidy, 1856

Type species

Coelorhynchus rectus Agassiz, 1843, Eocene, the United Kingdom.

Cylindracanthus ornatus Leidy, 1856
Fig. 56A–C

Cylindracanthus ornatus Leidy, 1856: 302.

Coelorhynchus ornatus – Cope 1871: 6, pl. 10, fig. 7.
Cylindracanthus rectus – Leriche 1942: pl. 8, fig. 3b.
Cylindracanthus rectus – Casier 1966: p. 174, pl. 22, figs 1–5.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 3 isolated teeth; Claiborne Group; ALMNH PV1992.28.3.2, MMNS VP-8947, SC2012.47.153.

Description

Taxon known only by its rostrum. Rostrum elongated, cylindrical, tapering anteriorly to blunt point; circular cross section measuring up to 20 mm in rostral diameter. Outer surface with strong sub-rounded to flat parallel ridges of varying width along length. Ridges on dorsal surface occasionally intersect or coalesce near anterior end. Two parallel ventral grooves each contain single row of acrodont teeth and/or alveoli; ventral grooves wider than all others on rostrum, do not extend to rostrum tip. One-to-two hollow concavities visible in cross section.

Remarks

Three species of *Cylindracanthus* have been reported from Cretaceous and Eocene deposits in Alabama (see Thurmond & Jones 1981), including *C. acus* Cope, 1870, *C. ornatus* Leidy, 1856, and *C. rectus* (Agassiz, 1843). Leriche (1942) argued that *C. acus* and *C. ornatus* were junior synonyms of *C. rectus*, giving this latter taxon a range that extended from the Late Cretaceous to the Eocene. Parris *et al.* (2001), however, provided convincing evidence that *C. ornatus* was a distinct taxon and could be separated from *C. rectus* and *C. acus* by the presence of two distinct parallel ventral grooves, each containing a single row of acrodont teeth. Parris *et al.* (2001) also noted that the range of *C. ornatus* extended from the Late Cretaceous into the Eocene, whereas *C. acus* and *C. rectus* were confined to the Eocene. Although Parris *et al.* (2001) suggested that all three species should be viewed as valid, they stated that a more extensive review of the genus was necessary. Regarding the Eocene *C. acus* and *C. rectus*, Thurmond & Jones (1981) suggested the two could be differentiated by rostral diameter (*C. acus* up to 7.0 mm; *C. rectus* up to 20 mm) and number of ridges around the rostral circumference (*C. acus* up to 19; *C. rectus* up to 46). Although Thurmond & Jones (1981) mentioned these differences could be related to ontogeny, they concluded that the two taxa were distinct due to the absence of specimens of an intermediate size.

We examined *Cylindracanthus* specimens that were derived from several Cretaceous and Eocene deposits in Alabama, which allowed us to formulate several conclusions regarding the taxonomy of the species in this genus. We view *C. acus* as a junior synonym of *C. rectus* because our sample exhibits a clear size gradient between small and large specimens. Our sample also indicates that the rostral diameter and number of ridges around the circumference are not taxonomically useful characteristics, but instead are related to ontogeny. Furthermore, because the rostra decrease in diameter and ridges often intersect and combine anteriorly, counting the number of ridges on rostrum fragments is problematic because, in cross-section, the distal end of a complete rostrum has fewer ridges than does the proximal end. Of the specimens from Claiborne Group formations, rostra were broadly divided into three groups: 1) those with tooth-bearing ventral grooves; 2) those without tooth-bearing grooves, and; 3) those where the presence of tooth grooves could not be determined due to specimen preservation (i.e., incomplete rostral diameter, matrix-filled grooves). We found that specimens from both groups 1 and 2 can have nearly identical rostral circumferences, suggesting that the presence or absence of teeth is not related to ontogeny. This lends support to the conclusions of Parris *et al.* (2001) that *C. ornatus* (those with teeth) is a distinct species from *C. rectus* (those without teeth) and that these species were coeval during the Eocene. It could be argued that the presence or absence of tooth grooves reflects sexual dimorphism, but all of the Cretaceous specimens we examined have this distinct characteristic. This observation leads us to conclude that the presence or absence of tooth-bearing grooves is a taxonomically viable characteristic that can be used to distinguish the two species. This also indicates that only *C. ornatus* had a range extending back to the Late Cretaceous. Many specimens, including those figured by Maisch *et al.* (2016: 8, fig. 2, 12–14), are not well enough preserved to confidently identify them to species (i.e., specimens ablated, grooves obscured by matrix), and we herein identify them only as *Cylindracanthus* sp.

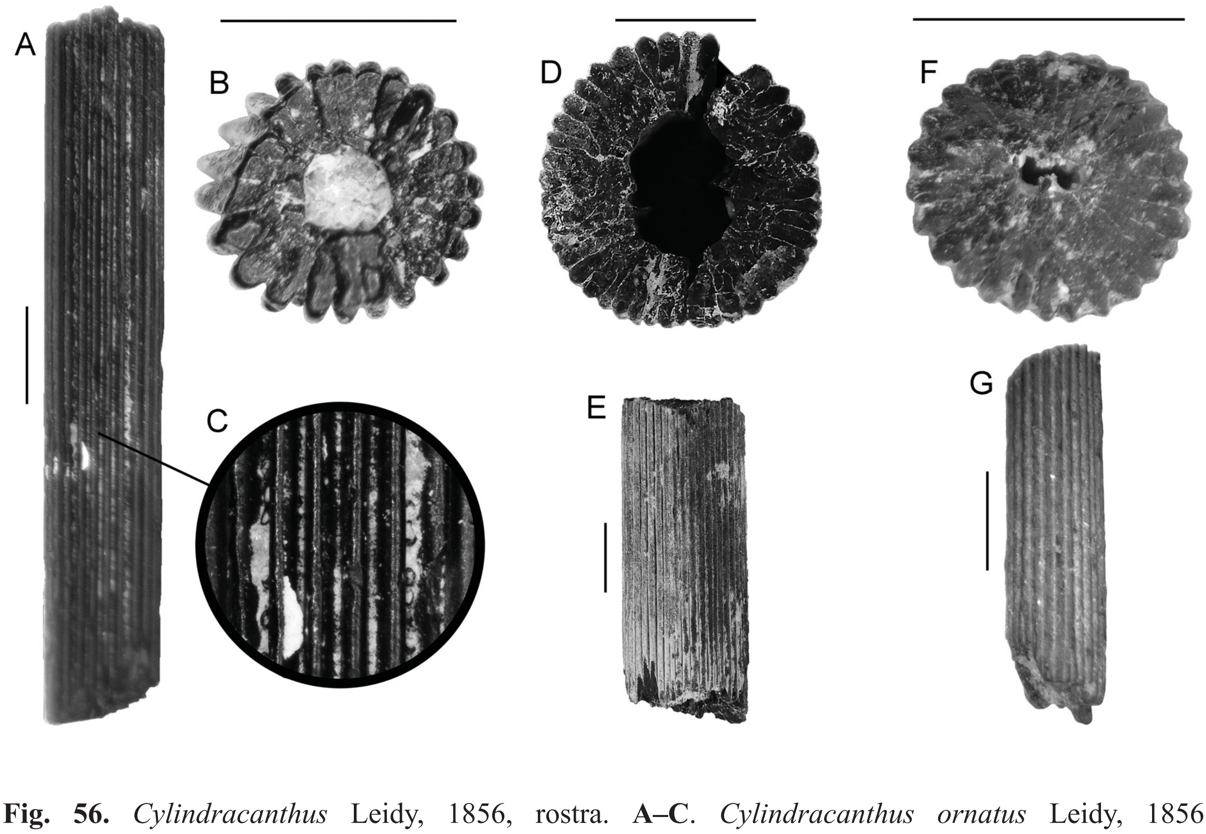


Fig. 56. *Cylindracanthus* Leidy, 1856, rostra. **A**–**C**. *Cylindracanthus ornatus* Leidy, 1856, SC2012.47.153, basal Lisbon Formation. **A**. Ventral view. **B**. Cross–section. **C**. Close–up of denticle rows. — **D**–**G**. *Cylindracanthus rectus* (Agassiz, 1843). **D**–**E**. MSC 38378, “upper” Lisbon Formation. **D**. Cross–section. **E**. Lateral view. **F**–**G**. WSU 5019, basal Lisbon Formation. **F**. Cross–section. **G**. Lateral view. Scale bars: A–C = 2 mm; D–G = 5 mm.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11. Lower Lutetian, zones NP14 and NP15.

Cylindracanthus rectus (Agassiz, 1843)

Fig. 56D–G

Coelorhynchus rectus Agassiz, 1843: 92.
Cylindracanthus acus Cope, 1870: 294.

Cylindracanthus rectus – Fowler 1911: 141, fig. 87.
Cylindracanthus acus – Thurmond & Jones 1981: 107.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 46 isolated teeth; Claiborne Group; ALMNH PV1985.87.41, ALMNH PV1985.87.42, ALMNH PV1985.87.43, ALMNH PV1985.87.44, ALMNH PV1985.87.45, ALMNH PV1985.87.46, ALMNH PV1985.87.47, ALMNH PV1985.87.48, ALMNH PV1985.87.49, ALMNH PV1985.87.50, ALMNH PV1992.28.3.1, ALMNH PV2000.1.43.10 (2 specimens), ALMNH PV2016.3.75, GSA-V718 (3 specimens), MMNS VP-8196 (3 specimens), MMNS VP-8232 (2 specimens), MSC 188.197, MSC 37123.1–2, MSC 37186.1–3, MSC 37445, MSC 38835, MSC 38378, SC2012.47.94 (8 specimens), WSU 5019, WSU 5055 (6 specimens).

Description

Rostra morphologically like *Cylindracanthus ornatus* but lack ventral tooth-bearing grooves.

Remarks

See *Cylindracanthus ornatus* above.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11, the "upper" Lisbon Formation at site ACl-3, and the basal Gosport Sand at site ACl-4. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Unranked Neopterygii Regan, 1923
Order Pycnodontiformes Berg, 1937
Family Pycnodontidae Agassiz, 1835

Genus ***Pycnodus*** Agassiz, 1835

Type species

Pycnodus platessus Agassiz, 1835, early-to-middle Eocene, Italy.

Pycnodus sp.

Fig. 57A–L

Albula sp. – Clayton *et al.* 2013: fig. 6i–j. — Maisch *et al.* 2016: fig. 2, 1–2.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 20 isolated teeth; Claiborne Group; MSC 35773.1–8, MSC 37185, MSC 37912.1–2, MSC 38483.1–6, NJSM 24037, SC2012.47.128, WSU 36, WSU CC 560.

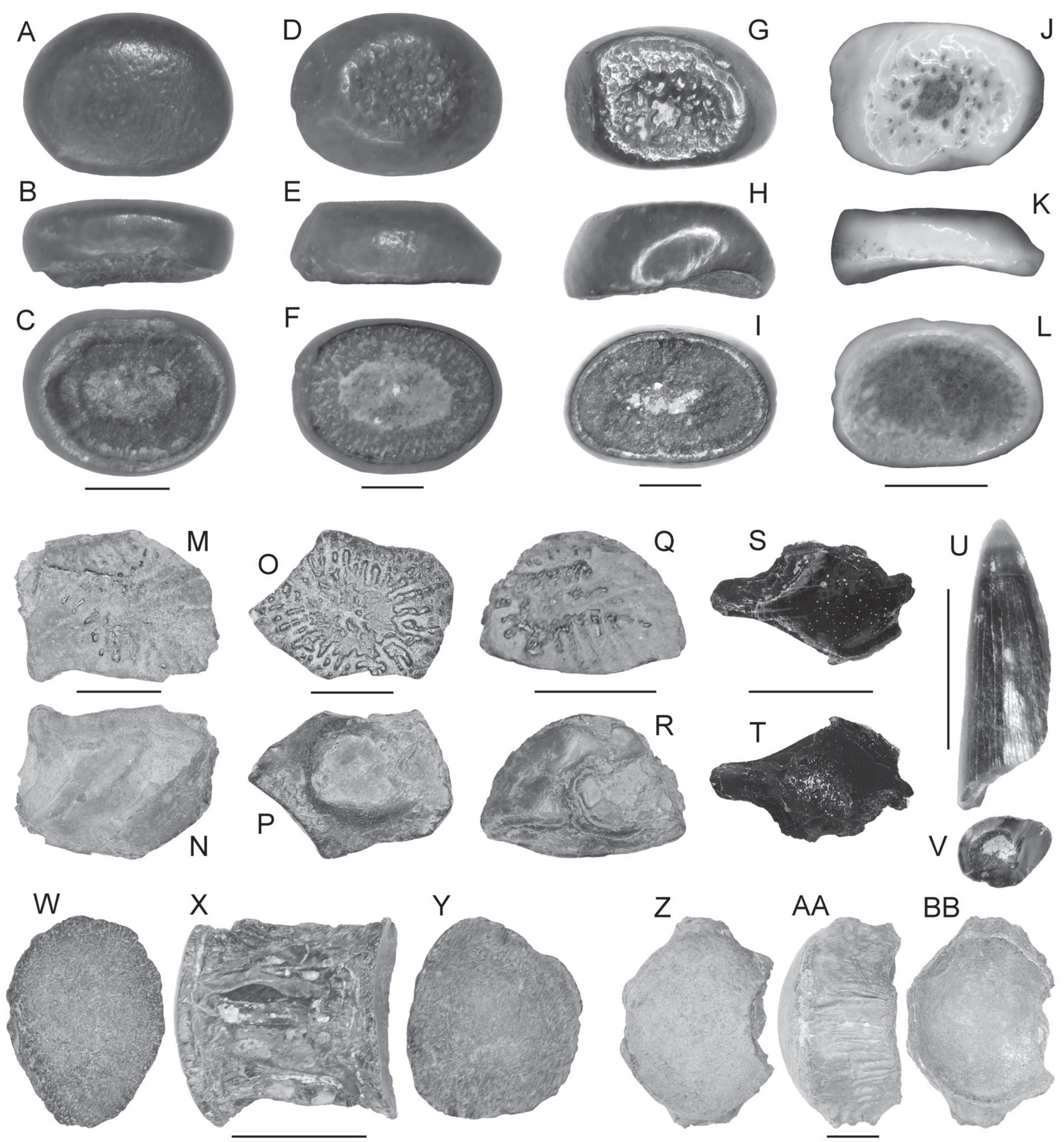


Fig. 57. *Pycnodus* sp., teeth and Lepisosteidae elements. **A–L**. *Pycnodus* sp. **A–C**. MSC 35773.1, tooth, lower Tallahatta Formation. **A**. Oral view. **B**. Profile view. **C**. Aboral view. **D–F**. MSC 35773.2, tooth, lower Tallahatta Formation. **D**. Oral view. **E**. Profile view. **F**. Aboral view. **G–I**. MSC 37185, tooth, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **G**. Oral view. **H**. Profile view. **I**. Aboral view. **J–L**. MSC 37912.1, tooth, basal Lisbon Formation. **J**. Oral view. **K**. Profile view. **L**. Aboral view. — **M–BB**. Lepisosteidae Cuvier, 1825. **M–N**. ALMNH PV1989.4.70, scale, Gosport Sand. **M**. External view. **N**. Internal view. **O–P**. ALMNH PV1989.4.37.2.1, scale, Gosport Sand. **O**. External view. **P**. Internal view. **Q–R**. ALMNH PV1989.4.37.2.2, scale, Gosport Sand. **Q**. External view. **R**. Internal view. **S–T**. MSC 37306, scale, basal Lisbon Formation. **S**. External view. **T**. Internal view. **U–V**. MSC 37473.1, tooth, basal Gosport Sand. **U**. Lateral view. **V**. Basal view. **W–Y**. ALMNH PV1989.2.4, vertebra, Gosport Sand. **W**. Anterior view. **X**. Left lateral view. **Y**. Posterior view. **Z–BB**. ALMNH 1898.4.190, vertebra, Gosport Sand. **Z**. Anterior view. **AA**. Left lateral view. **BB**. Posterior view. Scale bars for A–L = 2 mm. Scale bars: M–T, W–BB = 1 cm; U = 5 mm.

Description

Taxon known in Alabama only from isolated teeth. Teeth measure up to 6.0 mm in greatest diameter. Teeth have an oval outline in occlusal view and have a convex occlusal surface. Teeth may also have a flat medial crown surface. Teeth have a thick enamel covering that is smooth and extends to the base of the crown. There is a large oval basal pulp cavity. The occlusal surface of worn teeth is punctate.

Remarks

Several species of *Pycnodus* have been reported from Paleogene strata, including *P. variabilis* Stromer, 1905b (also Stromer 1910); *P. toliapicus* Agassiz, 1843; and *P. pellei* Priem, 1902. In Alabama the taxon is known only from isolated teeth, and intraspecific variation within the dentitions of this genus is poorly known. This factor, coupled with our small sample size (n = 20), precludes a more precise taxonomic assignment. Clayton *et al.* (2013: fig. 6i–j) illustrated a *Pycnodus* sp. tooth that was incorrectly identified as *Albula* sp. Based on our Claiborne Group sample, teeth of *Pycnodus* sp. can be differentiated from *Albula* in having a more convex occlusal surface, thicker enameloid covering, and large basal pulp cavity. Additionally, worn *Pycnodus* teeth are punctate. Inexplicably, Maisch *et al.* (2016) stated that their specimens of *Albula* sp. were similar to material from Alabama reported by Clayton *et al.* (2013: fig. 6i–j), but the specimen specifically referred to, incorrectly identified as *Albula*, is actually *Pycnodus* sp. Additionally, the tooth shown by Clayton *et al.* (2013) is practically identical to the *Pycnodus* sp. tooth Maisch *et al.* (2016: fig. 2, 1–2) figured in their study.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, and the basal Lisbon Formation at site ACov-11. Upper Ypresian to lower Lutetian, zones NP14 and NP15.

Infraclass Holostei Müller, 1845
Division Ginglymodi Cope, 1871
Order Lepisosteiformes Hay, 1929
Family Lepisosteidae Cuvier, 1825

Gen. et sp. indet.
Fig. 57M–BB

Lepisosteidae – Thurmond & Jones 1981: 84.
Lepisosteus sp. – Clayton *et al.* 2013: 65, fig. 6a. — Maisch *et al.* 2016: 7, fig. 2, 3–4.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 36 isolated teeth; Claiborne Group; ALMNH PV1989.2.4, ALMNH PV1989.4.114.5, ALMNH PV1989.4.118.3, ALMNH PV1989.4.131.2, ALMNH PV1989.4.190, ALMNH PV1989.4.37.1 (4 specimens), ALMNH PV1989.4.37.2 (2 specimens), ALMNH PV1989.4.70, MSC 188.188, MSC 2156, MSC 2404.1–11, MSC 33846, MSC 37306, MSC 37461, MSC 37473.1–3, MSC 37476, MSC 38514.1–2, NJSM 24038, WSU 25.

Description

Teeth, scales, and vertebrae identified in our sample. Teeth average 4.0 mm in overall height, 1.0 mm in greatest width. Teeth cylindrical with apical carinae. Lateral edges of tooth ornamented with low parallel ridges. Ridges strongest basally, fining apically. Crown apex translucent. Lateral edges of tooth base taper apically; lateral edges of crown apex more tapered. Some teeth can have a slight medial bend.

Scales of two morphologies, including large, thickened, with heavy ganoin ornamentation; others small, thin, smooth. Scales generally rhomboidal; thickest medially (up to 0.5 mm); inner surface convex, smooth; lateral edges sharp to rounded. Concentric growth line visible on some specimens.

Vertebrae opisthocoelous, with shallow concave posterior articular surface, slightly convex anterior surface; both surfaces with circular outline. Neural and hemal arches not preserved, but broken spine bases visible.

Remarks

Fossil elements belonging to Lepisosteidae were first reported from the Eocene of Alabama by Thurmond & Jones (1981), and later Clayton *et al.* (2013) and Maisch *et al.* (2016) assigned isolated scales from the Lisbon Formation to *Lepisosteus* sp. Two scale morphologies occur in Clabornian strata, including thin and smooth as well as thin and ornamented. Large, thickened ganoid scales have traditionally been assigned to *Atractosteus*, whereas smaller, thinner, unornamented scales have been identified as *Lepisosteus* (see Wiley 1976; Maisch *et al.* 2016). However, in his study of extant gars, Grande (2010) noted that the degree of ornamentation on the scales of *Atractosteus* varies from heavy to absent. Furthermore, ornamentation is more prevalent on the scales in certain areas on the body (heaviest in the trunk and prepelvic area, for example) and is more prominent on larger (older) individuals (i.e., ontogenetic development, with scale ornamentation in the caudal region being the last to form). Furthermore, Grande (2010) recognized four Eocene genera within the Lepisosteidae, *Atractosteus*, *Cuneatus*, *Lepisosteus*, and *Masillosteus*. Although the scales of *Lepisosteus* lack ganoid ornamentation, it can be present on the scales of *Atractosteus*, *Cuneatus*, and *Masillosteus.* Thus, all four genera can have unornamented scales, depending on the age of the gar and/or location of the scale on the body (Grande 2010), and the presence or absence of ganoin ornamentation on scales is not a taxonomically useful characteristic.

Grande (2010) also demonstrated that centrum length of a vertebra can vary depending on the location in the spinal column, and the morphology of these gar vertebrae overlaps within the various genera. Although size differences can be observed among the vertebrae in our sample, these differences could be attributed to ontogeny. Furthermore, generic identification of isolated gar teeth is also problematical, as Wiley (1976) and Grande (2010) have shown that there is little morphological difference between the various taxa, and gars generally have multiple rows of teeth of varying size. Thus, according to Grande (2010), specific cranial elements or nearly complete articulated gar specimens are needed for generic and specific assignments, since isolated scales, teeth, and vertebrae cannot be confidently identified beyond the familial level.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at site ACh-14, the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Division Teleosteomorpha Arratia *et al.*, 2004
Subdivision Teleostei Müller, 1846
Supercohort Teleocephala de Pinna, 1996
Cohort Elopomorpha Greenwood *et al.*, 1966
Order Elopiformes Sauvage, 1875
Family Phyllodontidae Dartevelle & Casier, 1943

Genus ***Egertonia*** Cocchi, 1864

Type species

Egertonia isodonta Cocchi, 1864, Ypresian, United Kingdom.

Egertonia isodonta Cocchi, 1864
Fig. 58

Egertonia isodonta Cocchi, 1864: 121, pl. 4, figs 1–2.

Triodon sp. – Case 1981: pl. 2, fig. 21.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 128 isolated teeth; Claiborne Group; ALMNH PV1992.28.2, ALMNH PV1993.2.0458 (23 specimens), ALMNH PV2016.4.39, MMNS VP-5646 (3 specimens), MMNS VP-5647, MMNS VP-8227, MSC 33348, MSC 35780.1–34, MSC 37125, MSC 37157, MSC 37323, MSC 37505.1–37, MSC 37651, MSC 37913.1, MSC 38496.1–12, MSC 38562, MSC 38971, NJSM 24040, NJSM 34316, SC2012.47.126 (3 specimens), SC2012.47.127 (2 specimens).

Description

Isolated teeth very low, flat to weakly convex, with circular to sub-hexagonal occlusal outline. A thin concentric ring is present at the tooth base on some specimens. Teeth largely consist of smooth enameloid crowns, with large open basal pulp cavity. Pulp cavity flat to weakly concave. Tooth plates with sub-oval occlusal outline, flat to dome-shaped in profile, consisting of vertically stacked rows of teeth. Largest teeth positioned medially within tooth plate; tooth diameter decreases laterally. Tooth stacking very tight, little interstitial bone.

Remarks

Isolated *Egertonia* teeth could be confused with the sub-circular, peripheral teeth of *Phyllodus*, but they differ by lacking ornamentation and by the presence of a thickened band at the base of most teeth. Although variable, *Egertonia* teeth can also be slightly more dome-shaped than those of *Phyllodus*. *Egertonia* basibrachial tooth plates are morphologically similar to those of *Phyllodus* in that they consist of regular stacks of teeth. However, *Egertonia* tooth plates differ by lacking a medial row of sub-ovate teeth as occurs on the tooth plates of *Phyllodus*. *Egertonia* tooth plates differ from those of *Paralbula* by having unornamented teeth with a lower profile, and by having regular stacks of teeth, as opposed to irregularly overlapping teeth.

Egertonia is currently a monospecific genus, and the isolated teeth and tooth plates in our sample all appear conspecific with the only known species, *Egertonia isodonta*, as described and figured by Cocchi (1864), Casier (1966), Estes (1969), and Weems (1999).

Maisch *et al.* (2016: pl. 2, figs 7–8) described and figured a partial tooth plate (NJSM 24316) that they assigned to *Paralbula marylandica*. Our reexamination of this specimen showed that it instead belongs

Egertonia isodonta, as individual teeth have an evenly convex crown, lack a pulp cavity, and the teeth are evenly stacked in vertical rows in profile view.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

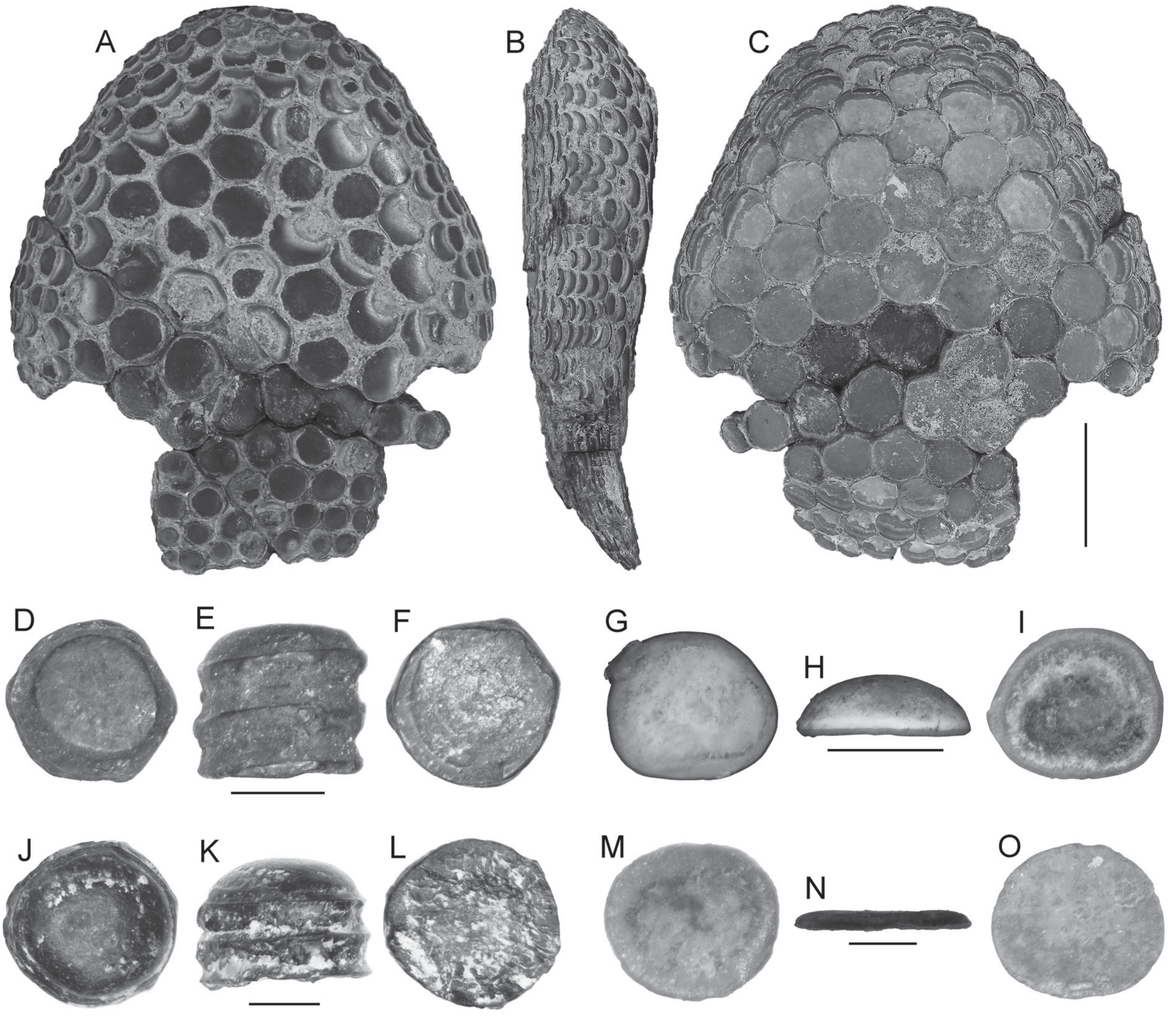


Fig. 58. *Egertonia isodonta* Cocchi, 1864. **A–C**. MSC 33348, tooth plate, lower Tallahatta Formation. **A**. Oral view. **B**. Profile view. **C**. Aboral view. **D–F**. MSC 37651, stack of teeth, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **D**. Oral view. **E**. Lateral view. **F**. Aboral view. **G–I**. MSC 37913.1, tooth, basal Lisbon Formation. **G**. Oral view. **H**. Lateral view. **I**. Aboral view. **J–L**. MSC 37555.1, stack of teeth, basal Gosport Sand. **J**. Oral view. **K**. Lateral view. **L**. Aboral view. **M–O**. MSC 35780.1, tooth, lower Tallahatta Formation. **M**. Oral view. **N**. Lateral view. **O**. Aboral view. Scale bar for A–C = 1 cm. Scale bars for D–O = 2 mm.

Genus ***Paralbula*** Blake, 1940

Type species

Paralbula marylandica Blake, 1940, Thanetian, Maryland, USA.

Paralbula aff. ***P. marylandica*** Blake, 1940

Fig. 59A–O

Paralbula marylandica Blake, 1940: 206, figs 1–2.

Albula sp. – Maisch *et al.* 2016 (partim): fig. 2.7–8 (non 5–6).

Material examined

UNITED STATES OF AMERICA – **Alabama** • 69 isolated teeth; Claiborne Group; MSC 35781.1–17, MSC 37263.1–4, MSC 37911.1–26, MSC 37913.2–4, MSC 38292.1, SC2012.47.124 (10 specimens), WSU 35, WSU CC 561 (5 specimens), WSU CC 563 (2 specimens).

Description

Teeth up to 2.0 mm in diameter, 0.5 mm in crown height. Crown with circular occlusal outline, uniformly convex in profile. Thick cingulum at crown base of some teeth. Crown enameloid extends to tooth base on most specimens, but not on all. Fine granular to wrinkled ornament often on occlusal surface of unworn teeth. Teeth with thickened, flat base; shallow, centrally located, circular pulp cavity.

Remarks

Estes (1969) and Schein *et al.* (2011) recognized three species of *Paralbula* having an Eocene range, including *P. casei* Estes, 1969, *P. marylandica* Blake, 1940, and *P. stromeri* (Weiler, 1929). Although each of these species were described from partial or complete tooth plates, Estes (1969) noted that the teeth of *P. casei* have a much more pronounced granular ornamentation, which is often arranged in lateral ridges that originate at the apex of the crown and extend to the crown base. We have also observed on complete tooth plates from the Paleocene and Cretaceous of Mississippi (MMNS 5367, MMNS 6885, MMNS 8076) that the granular ornamentation and ridges are visible even on worn or abraded teeth. Although the teeth of *P. marylandica* can also have a granular ornamentation, it is often much less apparent than that on *P. casei*, the ornamentation is not organized into radiating ridges, and many of the teeth have smooth enameloid (see Blake 1940; Estes 1969). Similar to *P. marylandica*, the teeth of *P. stromeri* have a smooth crown that lacks ornamentation (see Weiler 1929; Estes 1969). Another species, *Paralbula salvani* (Arambourg 1952), has a similar granular ornamentation to that on the teeth of *P. casei*, but this taxon is known only by the type specimen, which was derived from Paleocene deposits in Morocco (Estes 1969; Schein *et al.* 2011).

The *Paralbula* teeth within our sample have either a smooth crown or exhibit granular ornamentation, indicating that the isolated teeth do not belong to *P. casei* or *P. salvani* but instead represent *P. marylandica* or *P. stromeri*. Although the teeth of the latter two taxa are similar, we tentatively assign the specimens in our sample to *P. marylandica* because this is the only smooth-crowned species that has been described from the Eocene in North America (see Blake 1940; Estes 1969; Weems 1999; Schein *et al.* 2011). *Paralbula stromeri*, on the other hand, appears to have had a limited range that is currently restricted to the upper Eocene of Egypt (Weiler 1929; Estes 1969).

These Claiborne *Paralbula* teeth were differentiated from those of the morphologically similar *Egertonia isodonta* and *Phyllodus toliapicus* by the presence of distinct granular crown ornamentation on some specimens, and a medial pulp cavity on the basal surface. Furthermore, the basibrachial plates of *Paralbula marylandica* consist of teeth that are irregularly stacked (as opposed to columns of regularly stacked teeth on *Egertonia* and *Phyllodus*) and they lack the ovoid median teeth present on the tooth plates of *Phyllodus toliapicus*.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, and the basal Lisbon Formation at site ACov-11. Upper Ypresian to Lutetian, zones NP14 to NP15.

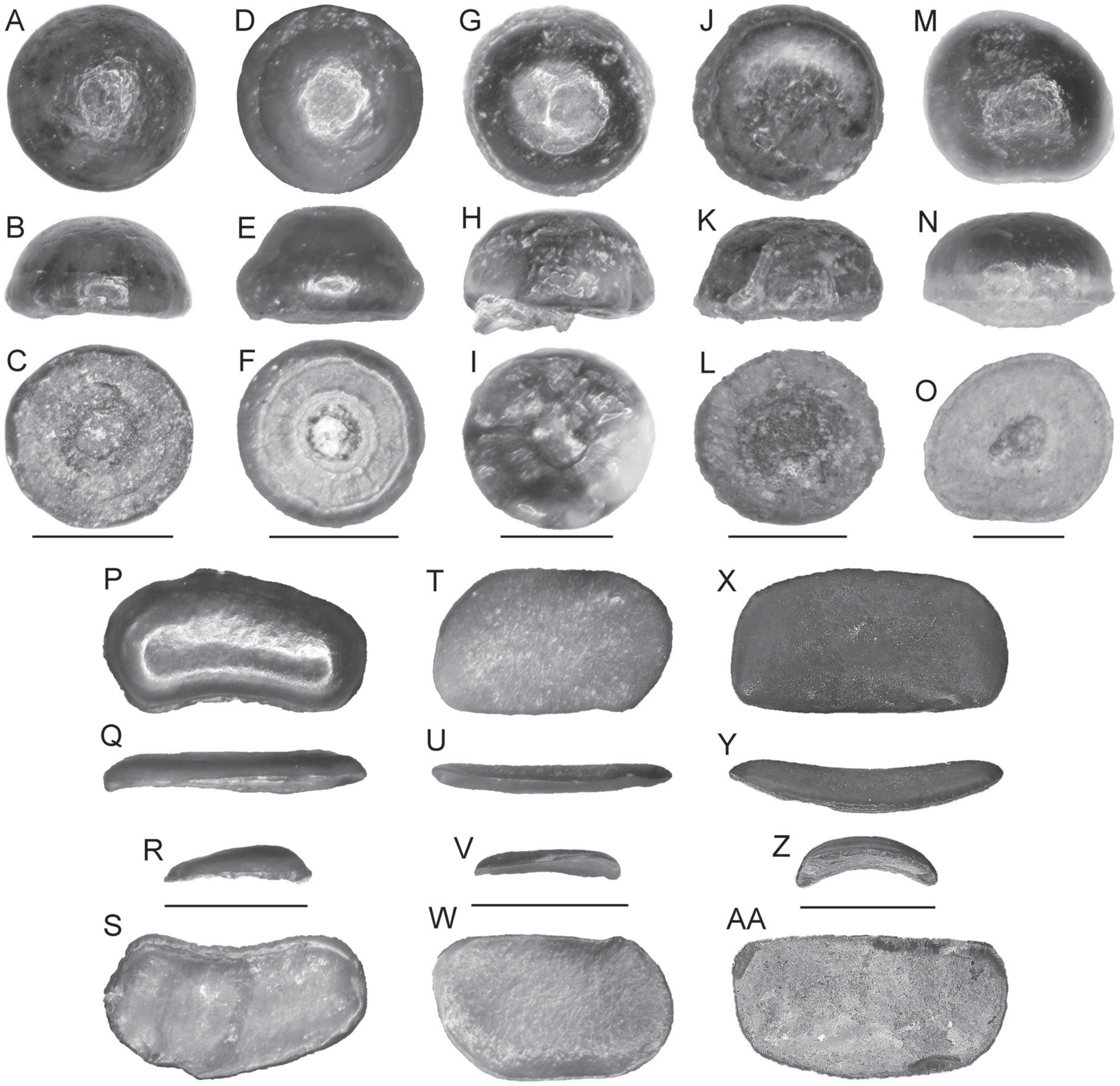


Fig. 59. *Paralbula* aff. *P. marylandica* Blake, 1940 and *Phyllodus toliapicus* Agassiz, 1844, teeth. **A–O**. *Paralbula* aff. *P. marylandica*. **A–C**. MSC 35781.1, lower Tallahatta Formation. **A**. Oral view. **B**. Profile view. **C**. Aboral view. **D–F**. MSC 35781.2, lower Tallahatta Formation. **D**. Oral view. **E**. Profile view. **F**. Aboral view. **G–I**. MSC 37911.2, basal Lisbon Formation. **G**. Oral view. **H**. Profile view. **I**. Aboral view. **J–L**. MSC 37263.2, basal Lisbon Formation. **J**. Oral view. **K**. Profile view. **L**. Aboral view. **M–O**. MSC 37911.3, basal Lisbon Formation. **M**. Oral view. **N**. Profile view. **O**. Aboral view. — **P–AA**. *Phyllodus toliapicus*. **P–S**. MSC 35772.3, lower Tallahatta Formation. **P**. Oral view. **Q**. Labial view. **R**. Profile view. **S**. Aboral view. **T–W**. MSC 35772.2, lower Tallahatta Formation. **T**. Oral view. **U**. Labial view. **V**. Profile view. **W**. Aboral view. **X–AA**. MSC 35772.1, lower Tallahatta Formation. **X**. Oral view. **Y**. Labial view. **Z**. Profile view. **AA**. Aboral view. Scale bars: A–O = 1 mm; P–AA = 5 mm.

Genus ***Phyllodus*** Agassiz, 1843

Type species

Phyllodus toliapicus Agassiz, 1844, Ypresian, United Kingdom.

Phyllodus toliapicus Agassiz, 1844
Fig. 59P–AA

Phyllodus toliapicus Agassiz, 1844: 239, vol. 2, pl. 69a, figs 1–3.

Phyllodus sp. – Thurmond & Jones 1981: 104, fig. 48.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 26 isolated teeth; Claiborne Group; MSC 188.104, MSC 35772.1–8, MSC 37338, MSC 37555.1–2, MSC 37913.5–15, MSC 38292.2–3, WSU 34.

Description

Isolated teeth of two morphologies, sub-oval and sub-circular. Teeth consisting of very low and thin, flat to weakly convex enameloid crown. Sub-rectangular teeth wider than long. Unworn teeth with very fine granular occlusal ornamentation; some worn teeth exhibit smooth medial wear facet. Basal surface is smooth, weakly concave, open. Tooth plates consisting of regularly stacked columns of teeth; teeth in medial row sub-oval, peripheral rows with sub-circular teeth, decreasing in diameter laterally. Teeth tightly packed with little interstitial bone.

Remarks

The basibrachial tooth plates in our sample were differentiated from those of *Paralbula* by the presence of regularly stacked columns of teeth, as opposed to irregularly stacked teeth in *Paralbula*. Complete *Phyllodus* tooth plates can be easily differentiated from those of *Egertonia* by the presence of a medial row of large sub-oval teeth (lacking in the latter genus) and by having teeth with a granular ornament. Partial *Phyllodus* tooth plates in our sample preserving only sub-circular peripheral teeth were differentiated from *Egertonia* by granular occlusal ornamentation and lack of a concentric ring at the tooth base. Isolated sub-circular (peripheral) teeth were identified using the same characteristics, however many had a crown that was too worn to preserve these features. These teeth were conservatively assigned to the Phyllodontidae only.

Because *Phyllodus* is only known from isolated teeth and tooth plates, its taxonomic affinities are somewhat unclear. Because this genus was not listed by Nelson *et al.* (2016), we follow Estes (1969) and Weems (1999) by placing *Phyllodus* within the Phyllodontidae. Historically, numerous species of *Phyllodus* have been named (see Leriche 1942; Casier 1966), but Estes (1969) considered these Cenozoic species to be nominal, suggesting they instead belonged to a single variable species, *Phyllodus toliapicus*. The variability observed within our sample supports this view, and we therefore refer all the teeth to this species.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11, and the basal Gosport Sand at site ACl-4. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Order Albuliformes Greenwood *et al.*, 1966
Family Albulidae Bleeker, 1859
Subfamily Albulinae Fowler, 1958

Genus ***Albula*** Gronow, 1763

Type species

Esox vulpes Linneaus, 1758, Recent.

Albula eppsi White, 1931
Fig. 60A–I

Albula eppsi Frost in White, 1931: 83, figs 137–141.

Albula sp. – Maisch *et al.* 2016 (partim): fig. 2.5–6 (non 7–8).

Material examined

UNITED STATES OF AMERICA – **Alabama** • 33 isolated teeth; Claiborne Group; MSC 37358.1–2, MSC 37541, MSC 37909.1–6, MSC 38445.2–24, NJSM 24039.

Description

Low-crowned teeth, circular occlusal outline; occlusal surface of unworn teeth nearly flat to convex. Crown enameloid thin, smooth, generally not reaching tooth base. Worn teeth flat, with occlusal surface often oblique to tooth height, triturating surface composed of dentine. Lateral tooth edges range from convex to parallel tapering. Tooth base flat; circular basal pulp cavity centrally located.

Remarks

Teeth exhibiting the morphology described above have traditionally been assigned to either *Albula oweni* Owen, 1845 or *Albula eppsi* Frost in White, 1931. White (1931) differentiated these species based on tooth size, with small teeth measuring less than 2.0 mm in diameter being assigned to *A. eppsi* and larger teeth to *A. oweni*. Casier (1966), however, synonymized the two species and suggested that *A. eppsi* represented the juvenile morphology of *A. oweni*. Forey (1973), however, proposed that *A. eppsi* and *A. oweni* were distinct taxa, noting that teeth of an intermediate size between the two were unknown. Weems (1999) came to the same conclusion based on a sample from the lower Eocene Nanjemoy Formation in Virginia, which included two *Albula* tooth plates bearing small teeth, indicating to him a small adult *Albula* morphology coexisted with the larger *Albula oweni*.

Our *Albula* sample includes teeth ranging in diameter from 1.0 mm to nearly 9.0 mm. This size gradient contradicts the observations of Forey (1973), possibly indicating that the varying sizes are related to heterodonty and/or ontogeny within a single species. However, unlike the parasphenoids of extant *Albula vulpes* (Linneaus, 1758), where large medial teeth are flanked by smaller teeth that gradually decrease in size towards the plate margins (see Clothier 1950: fig. 22), teeth on *A. oweni* parasphenoids only slightly decrease in size across the tooth plate (see Owen 1845: pl. 47, fig. 3; Woodward 1893: pl. 17). This suggests that within fossil members of *Albula*, monognathic heterodonty is not the determining factor with regard to tooth size, but is instead related to ontogeny and/or interspecific variation.

Irrespective of size, our *Albula* tooth sample includes two morphologies, including those with lateral sides that taper basally towards the pulp cavity, and those with lateral edges that are straight or weakly convex. Of the teeth that exceeded 5.0 mm in diameter, all have tapered lateral edges and are consistent in size with the type specimens for *A. oweni* as illustrated by Owen (1845: pl. 47, fig. 3) and Casier

(1966: pl. 13, fig. 4). Thus, we assigned all teeth with tapered edges to this taxon. Of the teeth with a diameter of less than 5.0 mm, all have straight and parallel lateral edges, or the edges were biconvex. These teeth appear conspecific to those described as *Albula eppsi* by Weems (1999). This difference in tooth morphology suggests that two species of *Albula* are indeed present within Claiborne strata in Alabama.

Although the teeth in our sample suggest that both *A. eppsi* and *A. oweni* are present, complications exist concerning the use of the name *Albula eppsi*. White (1931) originally named this taxon based on numerous dental elements with teeth, an operculum, and 40 otoliths that were derived from the lower Ypresian London Clay in the UK. The dental elements and teeth were given the name *Albula eppsi* while the otoliths, following the convention of the time regarding otolith-based species, was assigned to *Otolithus* (*Albula*) *eppsi* Frost in White (1931). Several years earlier, Priem (1908) erected the species *Otolithus* (*Trachini*?) *bellevoyei* based on isolated otoliths collected from Thanetian deposits in France. Nolf (2013) recently determined that the *Albula eppsi* otoliths were conspecific with the otolith-based *Albula bellovoyei*, rendering the otoliths of the former a junior synonym of the latter. This creates a taxonomic dilemma for several reasons. First, both White (1931) and Casier (1966) reported two species of *Albula* within the London Clay, *A. oweni* and *A. eppsi*, and their differing dental morphologies support that these are indeed two unique and valid species. The otoliths from the London Clay should therefore belong to one of these two species, rather than represent a third coeval species, *A. bellovoyei*. Thus, if it could be conclusively determined that the otoliths are indeed associated with the *A. eppsi* bony material, all should be referred to *A. bellovoyei*. One the other hand, if it were determined that the otoliths belong to *A. oweni*, *A. bellovoyei* would be designated a junior synonym of *A. oweni* because this latter species

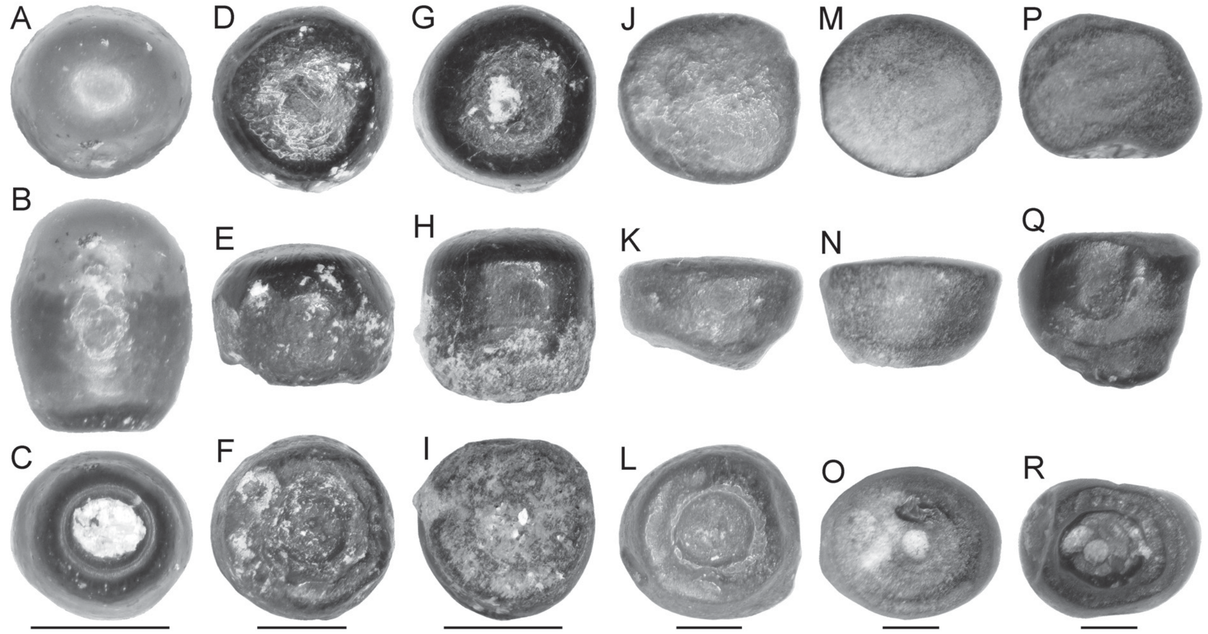


Fig. 60. *Albula eppsi* White, 1931 and *Albula oweni* (Owen, 1845), teeth. **A–I**. *Albula eppsi* **A–C**. MSC 38445.1, lower Tallahatta Formation. **A**. Oral view. **B**. Profile view. **C**. Aboral view. **D–F**. MSC 37909.1, basal Lisbon Formation. **D**. Oral view. **E**. Profile view. **F**. Aboral view. **G–I**. MSC 37541, basal Gosport Sand. **G**. Oral view. **H**. Profile view. **I**. Aboral view. — **J–R**. *Albula oweni*. **J–L**. MSC 38445.1, lower Tallahatta Formation. **J**. Oral view. **K**. Profile view. **L**. Aboral view. **M–O**. MSC 37891, “upper” Lisbon Formation. **M**. Oral view. **N**. Profile view. **O**. Aboral view. **P–R**. MSC 37699, basal Gosport Sand. **P**. Oral view. **Q**. Profile view. **R**. Aboral view. Scale bars = 2 mm.

was named decades earlier, in 1845. Bearing these taxonomic issues in mind, we choose to assign the small Claiborne Group teeth described above to *A. eppsi* as there is currently no definitive link between the teeth described by White (1931) and *A. bellovoyei* otoliths.

Our reexamination of a tooth figured by Maisch *et al.* (2016: fig 2, 5–6) as *Albula* sp. (NJSM 24039) from the Tallahatta/Lisbon contact at site ACh-14 shows it has convex lateral edges, and we identify it as *Albula eppsi.* Furthermore, several specimens identified by Case (1994b: 142, pl. 1, figs 372–375) as *A. eppsi* from the lower Eocene Tuscahoma Sand in Lauderdale County, Mississippi instead belong to *Fisherichthys folmeri* (see Weems 1999; Cicimurri & Knight 2009).

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl–1, the Tallahatta Formation at site AMo–8, the contact of the Tallahatta and Lisbon formations at site ACh-14, the basal Lisbon Formation at site ACov–11, and the basal Gosport Sand at site ACl–4. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Albula oweni (Owen, 1845)

Fig. 60J–R

Pisodus oweni Owen, 1845: 138, atlas p. 13, pl. 47, fig. 3.

Albula oweni – Woodward 1901: 108, pl. 3, figs 3–5.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 25 isolated teeth; Claiborne Group; ALMNH PV1993.2.494 (2 specimens), MSC 35775.1–14, MSC 37166.1–2, MSC 37442, MSC 37699, MSC 37891, MSC 38430, MSC 38445.1, MSC 38491, MSC 38862.

Description

Tooth crown with circular outline in occlusal view; occlusal surface nearly flat to convex. Thin enameloid covering smooth, generally not reaching tooth base; flattened triturating surface of worn teeth composed of dentine. Sides of crown straight or slightly convex, often tapered basally. Tooth base flat with circular, centrally located pulp cavity.

Remarks

The *A. eppsi* teeth in our sample measure less than 5 mm in diameter, whereas teeth of *A. oweni* measure up to 9 mm in diameter. Small teeth with straight or weakly biconvex lateral sides were originally described as *A. eppsi* by White (1931: figs 137–141). In contrast, teeth of *A. oweni* grow to large sizes and have lateral tooth sides that taper basally. The teeth of both *A. eppsi* and *A. oweni* are separable from *Pycnodus* sp. in having a much higher crown covered by only a thin enameloid layer, a small but conspicuous pulp cavity, and worn teeth are not punctate.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at site ACov-11, the “upper” Lisbon Formation at site ACl-3, and the basal Gosport Sand at site ACl-4. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Unranked Osteoglossocephala Arratia, 2010
Cohort Osteoglossomorpha Berg, 1940
Order Osteoglossiformes Berg, 1940
Family Osteoglossidae Bonaparte, 1832

Gen. et sp. indet.
Fig. 61A–H

Material examined

UNITED STATES OF AMERICA – **Alabama** • 16 isolated teeth; Claiborne Group; MSC 35778, MSC 37242, MSC 37307.1–2, MSC 37391, MSC 37515, MSC 37654, MSC 38443, MSC 38444, MSC 38488, MSC 38532, WSU CC 456, WSU CC 488 (3 specimens), WSU CC 555.

Description

Conical teeth up to 1.0 cm in height. Teeth sharply pointed, posteromedially curving, lack carinae. Crown enameloid thin, smooth, not extending to tooth base; apex solid and preserved with different color. Circular basal outline; deep conical pulp cavity. Enameloid often not preserved on lateral edges of the tooth, but almost always preserved at tooth apex.

Remarks

The teeth in our sample fall into two categories, including conical with a wide base, and elongate and cylindrical, with narrow base. The former morphology is similar to those of several Paleogene genera within the Osteoglossidae, including *Brychaetus* Agassiz, 1845, *Phareodus* Leidy, 1873, and *Ridgewoodichthys* Taverne, 2009. These genera are largely differentiated by cranial and dental bones, and difficult to distinguish only from isolated teeth (see Taverne 2009: figs 3, 5). Because our sample consists only of isolated teeth, it is unclear if these two morphologies reflect heterodonty within a single species or represent multiple coeval species. As a result, all are herein assigned only to the Osteoglossidae.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations and basal Lisbon Formation at site ACov-11, the “upper” Lisbon Formation at site ACh-8, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Unranked Clupeocephala Patterson & Rosen, 1977
Cohort Otocephala Johnson & Patterson, 1996
Superorder Otariophysi Rosen & Greenwood, 1970
Series Otophysi Rosen & Greenwood, 1970
Subseries Siluriphysi Fink & Fink, 1996
Order Siluriformes Cuvier, 1817
Suborder Siluroidei Frizzell & Dante, 1965
Superfamily Arioidea Bleeker, 1862
Family Ariidae Berg, 1958

Gen. et sp. indet.
Fig. 61I–Q

Material examined

UNITED STATES OF AMERICA – **Alabama** • 66 isolated teeth; Claiborne Group; ALMNH PV1989.4.105.1, ALMNH PV1989.4.18 (3 specimens), ALMNH PV1989.4.185.2 (2 specimens), ALMNH PV1989.4.84.2 (5 specimens), ALMNH PV1992.28.32 (2 specimens), ALMNH PV2016.4.38,

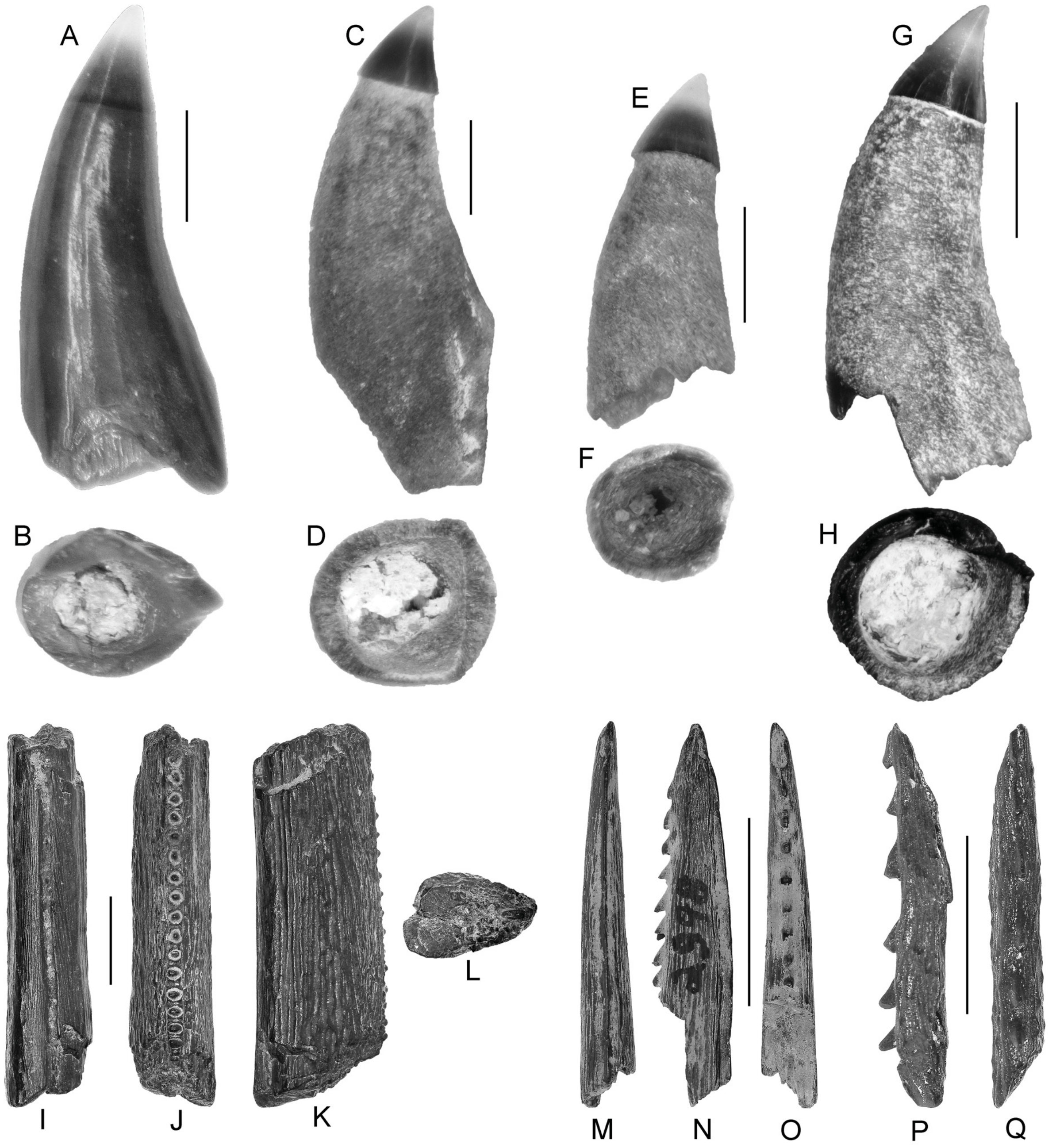


Fig. 61. Osteoglossidae Bonaparte, 1832 and Ariidae Berg, 1958, elements. **A–H**. Osteoglossidae. **A–B**. Tooth, MSC 35778.1, lower Tallahatta Formation. **A**. Lingual view. **B**. Basal view. **C–D**. Tooth, MSC 38444, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **C**. Lateral view. **D**. Basal view. **E–F**. Tooth, MSC 37515, basal Gosport Sand. **E**. Lingual view. **F**. Basal view. **G–H**. Tooth, MSC 37307.1, basal Lisbon Formation. **G**. Lingual view. **H**. Basal view. — **I–Q**. Ariidae. **I–L**. Pectoral spine, MSC 37122, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **I**. Anterior view. **J**. Posterior view. **K**. Lateral view. **L**. Transverse section. **M–O**. Pectoral spine, MSC 2398, Gosport Sand. **M**. Anterior view. **N**. Dorsal view. **O**. Posterior view. **P–Q**. Pectoral spine, MSC 37111, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **P**. Lateral view. **Q**. Posterior view. Scale bars: A–H = 2 mm; I–Q = 1 cm.

MMNS VP-5645, MMNS VP-8225 (2 specimens), MMNS VP-8236, MSC 188.117, MSC 188.275, MSC 2398, MSC 37111, MSC 37122, MSC 37269 (5 specimens), MSC 37297, MSC 37463.1–5, MSC 38513, MSC 38537.1–9, MSC 38561.1 (7 specimens), MSC 38786, MSC 38792, MSC 38793, MSC 38838, MSC 38867 (6 specimens), NJSM 24045, NJSM 24326, WSU 44, WSU CC 461, WSU CC 503.

Description

Fin spines dorsoventrally or mediolaterally compressed (depending on position), tapered distally, weakly convex proximodistally. Some specimens with rounded anterior margin, posterior margin rather flat, with shallow furrow; single row of basally directed denticles emanates from furrow; denticles decrease in size distally. Other specimens with single row of denticles on anterior and posterior edges; anterior margin denticles directed towards the distal tip, those on the posterior edge basally directed. Lateral surfaces bearing numerous irregular sub-parallel to parallel ridges (separated by narrow furrows) extending length of spine.

Remarks

Numerous Paleogene species of sea catfish, particularly *Arius*, have been erected based on isolated fin spines, all of which are based on variations in spine base morphology, ornamentation, and the nature of the anterior and posterior denticulations (Leriche 1922; White 1926). It is unclear if the varied morphologies present in our sample represent the numerous species that have been described, or variation in a more limited number of species. One Gosport specimen resembles spines of *Arius heward-belli* described by White (1926), but it is also similar to material identified by Leriche (1922) as belonging to a juvenile individual of *A. dutemplei*. Compounding this issue, denticles are known to occur on spines of other taxa of sea catfish like *Bagre* sp., and we therefore choose to limit the taxonomic identification of the Claiborne Group specimens to the familial level until more complete material is recovered.

Numerous other teleost fin spines were identified within the Claiborne sample we examined, but these differ from those of the Ariidae in having smooth dorsal and ventral surfaces. The posterior margin on these spines bear a deep V-shaped groove, the anterior and posterior margins lack denticles, and the spine base is yoke-shaped (indicating they are dorsal spines). These spines have been assigned by other researchers to indeterminate percomorph fish (see Weems 1999), but we identify them only as Teleostei.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, the "upper" Lisbon Formation at site ACh-8, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Superorder Acanthopterygii Greenwood *et al.*, 1966
Series Percomorpha Cope, 1871
Subseries Ovalentaria Smith & Near in Wainwright *et al.*, 2012
Order Istiophoriformes Betancur-R *et al.*, 2013
Family Sphyraenidae Berg, 1958

Genus ***Sphyraena*** Walbaum, 1792

Type species

Esox sphyraena Linneaus, 1758, Recent, Mediterranean Sea.

Sphyraena sp.

Fig. 62A–L

Trichiurides oshoshunensis – Arambourg 1952: pl. 35, figs 43–45, 53–56.
Trichiurides sp. – Thurmond & Jones 1981: 106, fig. 50.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 71 isolated teeth; Claiborne Group; ALMNH PV1993.2.496a, ALMNH PVPV 2005.6.436.1, MSC 188.145, MSC 188.60, MSC 2150.1, MSC 2150.3, MSC 2393, MSC 2397, MSC 35779, MSC 37141, MSC 37142, MSC 37162, MSC 37163, MSC 37238, MSC 37286, MSC 37352.1–5, MSC 37434.1–27, MSC 37547, MSC 37590, MSC 38432, MSC 38436.1–2, MSC 38440, MSC 38441, MSC 38505.1–4, MSC 38539.1–3, MSC 38973, MSC 38975, MSC 38978.1–2, MSC 39877, NJSM 24320, NJSM 24321, SC2012.47.99 (2 specimens), WSU CC 550.

Description

Laniary teeth erect, with convex, straight to slightly sinuous posterior; inconspicuous posterior apical barb may be present. Anterior margin sharply carinate, sinuous, smooth. Vertical striations may occur at posterior tooth base. Tooth with teardrop-shaped basal outline; pulp cavity shallow. Dentary teeth lanceolate, very thin labiolingually; sharp, convex, smooth anterior and posterior carinae form sharply pointed apex. Labial and lingual crown faces weakly convex, smooth; crown generally erect but may curve slightly medially. Basal surface may bear shallow pulp cavity.

Remarks

Sphyraena laniary teeth could be confused with the teeth of some trichiurids, particularly *Trichiurus oshosunensis*. However, *Sphyraena* laniary teeth can be differentiated by their nearly straight posterior margin and sinuous anterior margin (as opposed to both margins being sinuous), having a teardrop-shaped basal outline (as opposed to circular), and by their weak to absent posterior barb. Non-laniary *Sphyraena* teeth are similar to *Scomberomorus* and *Palaeocybium*, but they can be separated from the former by their much narrower crown with equally convex labial and lingual faces, and carinae that reach the tooth base. Teeth of *Palaeocybium* can be thicker than those of *Sphyraena*, and the basal pulp cavity is large and deep.

The dentitions of extant *Sphyraena* species exhibit a range of heterodonty (see Berkovitz & Shellis 2016: fig. 4.72), making speciation of isolated fossil teeth difficult. In extant species, large, triangular laniary teeth are located at the anterior margins of the premaxilla and dentary, with those in the upper jaw being somewhat larger than those on the dentary (SC2018.3.1). Lanceolate dentary teeth are comparable in size to those on the palatine, which fit into depressions on the dentary, and the teeth from these jaw elements are much larger than those on the premaxilla. A poorly developed posterior barb has occasionally been observed on premaxillary laniary teeth of extant and Miocene *Sphyraena* specimens (see Nishimoto & Ohe 1982: fig. 4k; Kriwet 2003), and this characteristic was observed on some laniary teeth in our Claiborne sample. The various fossil species have been differentiated based on size and shape of the teeth, and occasionally ornamentation (see Leidy 1877; Casier 1946, 1966; Weems 1999). Several specimens in our sample are approximately the same size as the teeth of *Sphyraena striata* Casier, 1946 and *Sphyraena lugardi* White, 1926 reported elsewhere, but unfortunately enameloid is not preserved on our specimens so they could not be adequately compared to those species. Furthermore, the differential dental characteristics attributed to the various species appears variable but temporally consistent, making specific identifications difficult. Within the Claiborne sample, teeth from the Tallahatta Formation are not morphologically dissimilar to those occurring within the Gosport Sand. As a result, we believe only a single, undetermined species is present within our sample.

Thurmond & Jones (1981: 106, fig. 50) described and figured a tooth from the Tallahatta Formation in Monroe County, AL that they assigned to *Trichiurides* sp. This specimen instead represents a laniary tooth of *Sphyraena* sp.

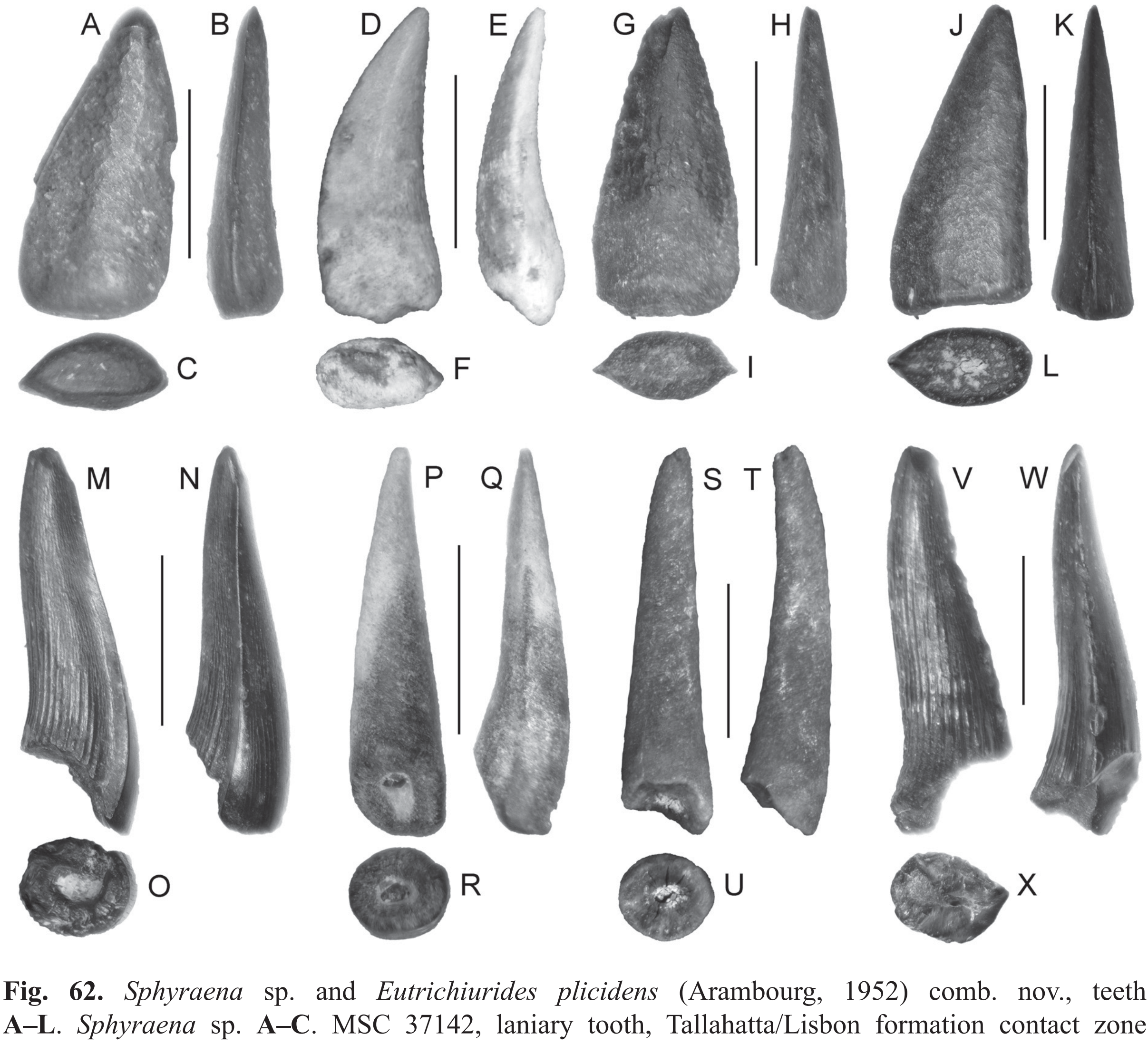


Fig. 62. *Sphyraena* sp. and *Eutrichiurides plicidens* (Arambourg, 1952) comb. nov., teeth. **A–L**. *Sphyraena* sp. **A–C**. MSC 37142, laniary tooth, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **A**. Lingual view. **B**. Anterior view. **C**. Basal view. **D–F**. MSC 35779, lower Tallahatta Formation. **D**. Lingual view. **E**. Carinal view. **F**. Basal view. **G–H**. MSC 37434.1, Gosport Sand. **G**. Lingual view. **H**. Carinal view. **I**. Basal view. **J–L**. MSC 37434.2, laniary tooth, basal Gosport Sand. **J**. Lingual view. **K**. Anterior view. **L**. Basal view. — **M–X**. *Eutrichiurides plicidens* comb. nov. **M–O**. MSC 188.2, Gosport Sand. **M**. Lingual view. **N**. Mesial view. **O**. Basal view. **P–R**. MSC 37908, basal Lisbon Formation. **P**. Lingual view. **Q**. Mesial view. **R**. Basal view. **S–U**. MSC 38482, basal Lisbon Formation. **S**. Lingual view. **T**. Mesial view. **U**. Basal view. **V–X**. MSC 37460, basal Gosport Sand. **V**. Lingual view. **W**. Mesial view. **X**. Basal view. Scale bars: A–C, G–X = 5 mm; D–F = 2 mm.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the Tallahatta Formation at site AMo-8, the contact of the Tallahatta and Lisbon Formations at sites ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at sites ACh-21 and ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Order Scombriformes Bleeker, 1859
Suborder Scombroidei Bleeker, 1859
Family Trichiuridae Rafinesque, 1810
Subfamily Trichiurinae Rafinesque, 1815

Genus ***Eutrichiurides*** Casier, 1944

Type species

Trichiurides delheidi Leriche, 1908, early Oligocene, Belgium.

Eutrichiurides plicidens (Arambourg, 1952) comb. nov.
Fig. 62M–X

Trichiurus (?) *plicidens* Arambourg, 1952: 265, pl. 35, figs 39–42.

Trichiurus sp. – Clayton *et al.* 2013: fig. 6f.
Trichiurides cf. *T. sagittidens* – Maisch *et al.* 2016: fig. 2, 17–18.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 11 isolated teeth; Claiborne Group; MSC 188.2, MSC 37127, MSC 37148, MSC 37153, MSC 37460, MSC 37484, MSC 37908, MSC 38435, MSC 38482, NJSM 24322, WSU 5020.

Description

Largest tooth measuring 1.2 cm in height. Teeth elongated, conical, posteriorly curving. Upper one-third of tooth also with medial bend; some specimens slightly sigmoidal in profile. Anterior and posterior carinae absent. Medial and/or lateral carinae developed; medial carina more pronounced. Posterior face with fine striations extending nearly two-thirds height of the crown; anterior face smooth. Tooth base flat, with wide conical pulp cavity.

Remarks

The teeth in our sample are superficially similar to those of *Trichiurides sagittidens* and *Trichiurus oshosunensis*, but differ from both taxa by having one to two lateral carinae as opposed to anterior and/or posterior carinae. The specimens in our sample appear to be conspecific with Arambourg's (1952) *Trichiurus plicidens*, from the Ypresian of Morocco, as they are slightly sigmoidal, have one-to-two lateral carinae, lack an apical barb, and have striated ornamentation (Arambourg 1952: 265, pl. 35, figs 39–42). Arambourg (1952) tentatively placed this species within *Trichiurus* because of the striations occurring on the tooth crown.

Herein we argue for a new combination for the *plicidens* morphology, placing it within the genus *Eutrichiurides*. This stems from the fact that the *plicidens* morphology has one-to-two lateral carinae (as opposed to anterior or posterior carinae), which is a characteristic of *Eutrichiurides* as seen on the type specimen of *E. winkleri* (Casier 1946: pl. 4, fig. 19b), on White's (1931: fig. 2) figured specimen of *E. orpiensis* (Leriche, 1906), and on specimens illustrated by Casier (1944) when he redescribed *E. delheidi* (Leriche, 1908). Although Gago (1997) observed that apical barbs are present on adult teeth but absent on juvenile teeth of extant *Trichiurus* species, Casier (1944) noted that barbs are completely lacking on teeth of all *Eutrichiurides* (see White 1931: fig. 2; Casier 1944: pl. 1 figs 5–9, 12–18, 1946: pl. 4, fig. 19b; Arambourg 1952: 265, pl. 35, figs 39–42). The combination of having lateral carinae, striations on the tooth crown, and the lack of an apical barb on all the observed specimens suggests these teeth are more closely aligned with *Eutrichiurides*, rather than *Trichiurides* or *Trichiurus*, and serves as the basis for this new combination. An "indeterminate fish tooth" figured by Otero *et al.* (2015: 14, fig. 11) from the Bartonian of Libya may be conspecific with *E. plicidens* comb. nov.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, and the basal Gosport Sand at site ACl-4. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Genus ***Trichiurides*** Winkler, 1874

Type species

Trichiurides sagittidens Winkler, 1874b, Eocene, Belgium.

Trichiurides sagittidens Winkler, 1874

Fig. 63A–I

Trichiurides sagittidens Winkler, 1874b: 31, pl. 2, figs 22–23.

Trichiurus sp. – Thurmond & Jones 1981: 105, fig. 49.
Trichiurides cf. *sagittidens* – Clayton *et al.* 2013: fig. 6e.
Triciurides cf. *T. sagittidens* – Maisch *et al.* 2016: fig. 2, 17–18.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 33 isolated teeth; Claiborne Group; ALMNH PV1989.4.12 (2 specimens), ALMNH PV1989.4.73.2 (4 specimens), ALMNH PV1989.4.102, ALMNH PV1989.4.129, ALMNH PV1989.4.142, ALMNH PV1989.4.151.3, ALMNH PV1993.2.500 (5 specimens), ALMNH PV2005.6.432, ALMNH PV2005.6.433, MMNS VP-8195, MSC 12800, MSC 2159, MSC 2405.1–2, MSC 37356, MSC 37364, MSC 37486, MSC 37520, MSC 38517, MSC 38538, NJSM 24043, WSU 13, WSU 27, WSU CC 547 (2 specimens).

Description

Teeth tall, rather narrow, laterally compressed apically, conical basally. Crown sharply curved distally except for anteriorly directed apical portion. Crown apex with sharp anterior carina; large posterior barb composed of translucent enamel. Tooth base with circular outline; shallow, centrally located pulp cavity.

Remarks

An elongated, distally curved tooth with a laterally compressed apex bearing a large posterior apical barb, and circular basal outline distinguish *Trichiurides sagittidens* from teeth of *Sphyraena* and *Trichiurus*. *Trichiurides sagittidens* teeth lack lateral carinae as seen on *Eutrichiurides plicidens* comb. nov. teeth. The Claiborne specimens in our sample appear to be conspecific with those described and figured by Winkler (1874b: 31, pl. 2, figs 22–23) as *Trichiurides sagittidens*. *Trichiurides* is monospecific and presently only known from laniary teeth. Thurmond & Jones (1981: 105, fig. 49) described and figured a tooth from the Tallahatta Formation in Monroe County, AL as *Trichiurus* sp., but a reexamination of this specimen showed it instead belongs to *Trichiurides sagittidens*.

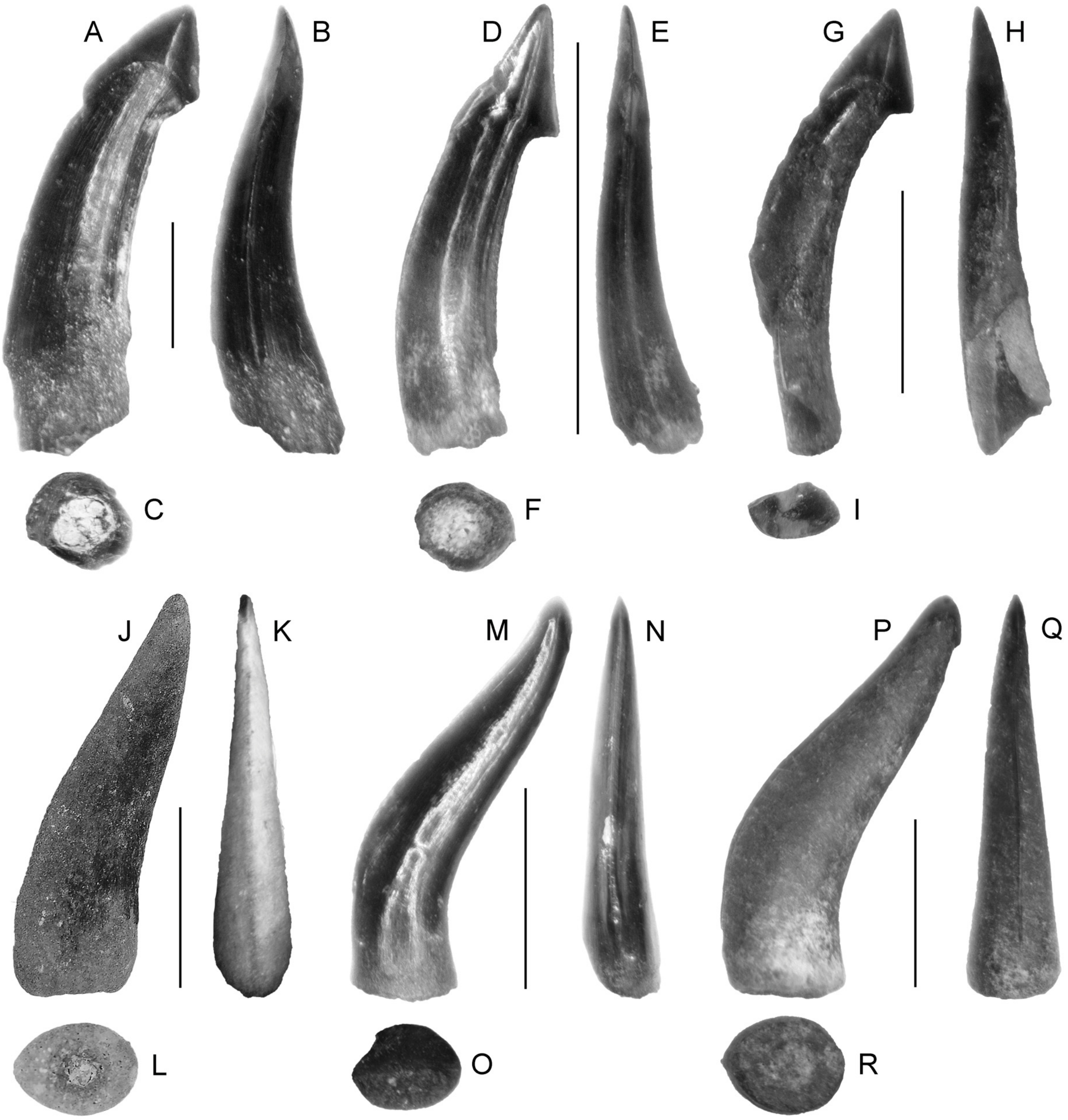


Fig. 63. *Trichiurides sagittidens* Winkler, 1874 and *Trichiurus oshosunensis* White, 1926, teeth. **A–I**. *Trichiurides sagittidens*. **A–C**. MSC 12800, , basal Gosport Sand. **A**. Lingual view. **B**. Anterior view. **C**. Basal view. **D–F**. MSC 2405.1, Gosport Sand. **D**. Lingual view. **E**. Anterior view. **F**. Basal view. **G–I**. MSC 37486, basal Gosport Sand. **G**. Lingual view. **H**. Anterior view. **I**. Basal view. — **J–R**. *Trichiurus oshosunensis*. **J–L**. MSC 38489.1, basal Lisbon Formation. **J**. Profile view. **K**. Anterior view. **L**. Basal view. **M–O**. MSC 37657, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **M**. Profile view. **N**. Anterior view. **O**. Basal view. **P–R**. MSC 37146, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **P**. Profile view. **Q**. Anterior view. **R**. Basal view. Scale bars = 5 mm.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the Tallahatta Formation at site AMo-8, the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21 and ACl-15. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Genus ***Trichiurus*** Linneaus, 1758

Type species

Trichiurus lepturus Linneaus, 1758, Recent, South Carolina, USA.

Trichiurus oshosunensis White, 1926

Fig. 63J–R

Trichiurus oshosunensis White, 1926: 65–66, pl. 16, figs 14–20.

Sphyraena sp. – Maisch *et al.* 2016: 8, fig. 2, 19–22.
Trichiurides oshoshunensis – Arambourg 1952: 264, pl. 35, figs 47–52.
Trichiurides sp. – Thurmond & Jones 1981: 106, fig. 50.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 33 isolated teeth; Claiborne Group; ALMNH PV1985.87.2, ALMNH PV1985.87.3, MSC 37146, MSC 37173.1–2, MSC 37308.1–7, MSC 37657, MSC 37666.1–2, MSC 38437, MSC 38438, MSC 38489.1–7, NJSM 24042, NJSM 24319, SC2012.47.97, SC2012.47.98 (5 specimens), WSU CC 548.

Description

Teeth measuring over 1.0 cm in height. In profile, basal one-third of tooth vertical, but then sharply curved posteriorly; apical portion anteriorly directed. Anterior margin formed into sharp carina, whereas posterior margin uniformly convex. Enameloid generally not preserved, but small apical posterior barb sometimes present. Tooth base with teardrop-shaped outline, shallow pulp cavity may be present.

Remarks

The teeth described above appear to be conspecific with White's (1926) *Trichiurus oshosunensis* from the early-to-middle Eocene of Nigeria. Although similar to the *Sphyraena* laniary teeth we examined, they can be distinguished by being much more sinuous in profile. In contrast, laniary teeth of *Sphyraena* have an oblique, slightly sinuous anterior margin but nearly vertical posterior margin. Arambourg (1952: pl. 35, figs 43–45, 53–56) figured several teeth he assigned to *T. oshosunensis* that better fit our definition of *Sphyraena* sp. in that they have anterior and posterior carinae and are lanceolate in form. Unfortunately, White (1926) only illustrated laniary teeth, and the morphology of other *T. oshosunensis* teeth is uncertain. Until more complete specimens are known, we restrict the usage of *T. oshosunensis* to teeth that match White's (1926) type description.

Trichiurus oshosunensis differs from *Eutrichiurides plicidens* comb. nov. in having a single anterior carina and by lacking posterior crown ornament. It differs from *Trichiurides sagittidens* in being laterally compressed along the entire crown height (not just apically), by having a smaller posterior barb (if present), and by having a teardrop-shaped basal outline (not circular). A laniary tooth identified as *Sphyraena* sp. by Maisch *et al.* (2016) is herein considered to be *T. oshosunensis*. Also, our examination of a specimen that Thurmond & Jones (1981: fig. 50) referred to *Trichiurides* sp. (specimen ALMNH PV2005.6.432) is also referred to *T. oshosunensis*.

Several of the teeth in our sample lack a posterior barb, a feature that Gago (1997) noted as being absent on juveniles of extant *Trichiurus* and could reflect ontogeny as opposed to jaw heterodonty.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, and the basal Lisbon Formation at site ACov-11. Lower Lutetian, zones NP14 and NP15.

Family Scombridae Rafinesque, 1815
Subfamily Scombrinae Rafinesque, 1815
Tribe Scomberomorini Starks, 1910
Tribe Scomberomorini Monsch, 2005

Genus ***Palaeocybium*** Monsch, 2005

Type species

Cybium proosti Storms, 1897, Eocene, Belgium and England.

Palaeocybium proosti (Storms, 1897)
Fig. 64A–I

Cybium proosti Storms, 1897: 242, figs 1–2.

Cybium proosti – Leriche 1905: 79, 150, 192, pl. 10, fig. 2.
Cybium sp. – Case 1981: 2, fig. 17.
Cybium proosti – Case 1986: 6, figs 10–11.
Acanthocybium proosti – Weems 1999: 66, pl. 4.6, fig. g.
Palaeocybium proosti – Monsch 2005: 460.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 6 isolated teeth; Claiborne Group; ALMNH PV1989.4.130, MSC 37423, MSC 38433, MSC 38500.1–2, MSC 37194.4.

Description

Teeth lanceolate, measuring up to 6.15 mm in height. Anterior and posterior carinae sharp, smooth, convex; carinae extend to tooth base, form rounded apex. Labial and lingual faces bi-convex, of equal dimension, smooth. Tooth base slightly thickened, with deep pulp cavity.

Remarks

The specimens in our sample compare well to *Palaeocybium proosti* (Storms, 1897) teeth reported from Europe and North America (see Casier 1946; Kemp *et al.* 1990; Weems 1999). *Palaeocybium proosti* was originally placed within *Cybium*, a genus that is now regarded as a junior synonym of *Scomberomorus* Lacépède, 1802 (see Bannikov 1982; Collette 2003). Weems (1999) placed this morphology within *Acanthocybium* Gill, 1862 based on two partial dentaries from the Nanjemoy Formation in Virginia, suggesting it was a primitive species within the genus. Monsch (2005) later noted that Storms' (1897) type specimen has two rows of teeth on the dentary, an inner and outer, which is a characteristic that

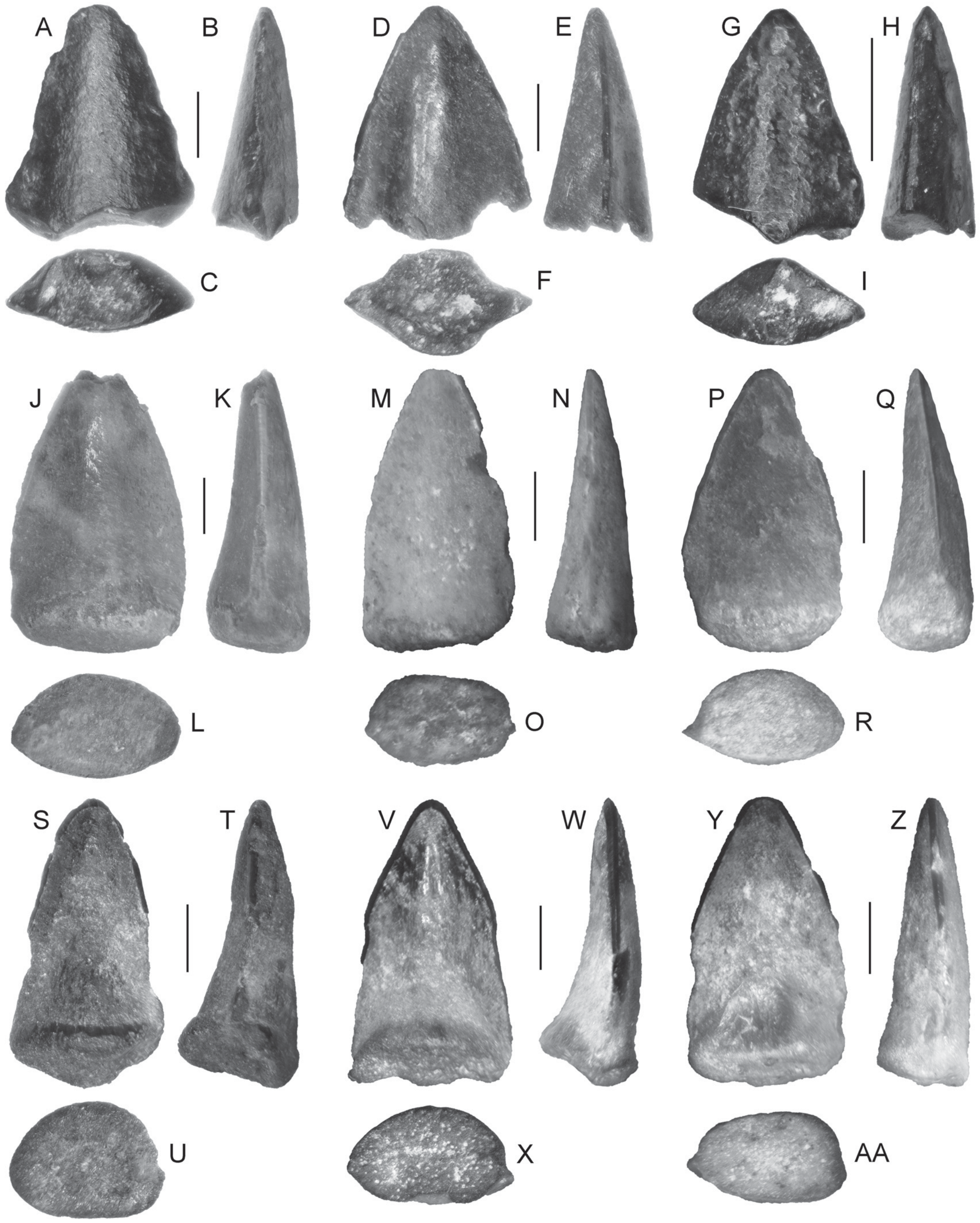


Fig. 64. *Palaeocybium proosti* (Storms, 1897) and *Scomberomorus* Lacépède, 1802, teeth. **A–I**. *Palaeocybium proosti* **A–C**. MSC 37194.4, Tallahatta/Lisbon formation contact zone, courtesy of T. Prescott Atkinson. **A**. Lingual view. **B**. Carinal view. **C**. Basal view. **D–F**. MSC 37423, basal Gosport Sand. **D**. Lingual view. **E**. Carinal view. **F**. Basal view. **G–I**. MSC 38500.2, basal Gosport Sand. **G**. Lingual view. **H**. Carinal view. **I**. Basal view. — **J–R**. *Scomberomorus bleekeri* (Storms, 1892). **J–L**. MSC 37147, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **J**. Lingual view. **K**. Carinal view. **L**. Basal view. **M–O**. MSC 35777.2, basal Gosport Sand. **M**. Lingual view. **N**. Carinal view. **O**. Basal view. **P–R**. MSC 37268.1, basal Lisbon Formation. **P**. Lingual view. **Q**. Carinal view. **R**. Basal view. — **S–AA**. *Scomberomorus stormsi* (Leriche, 1905). **S–U**. MSC 37512.1, basal Gosport Sand. **S**. Lingual view. **T**. Carinal view. **U**. Basal view. **V–X**. MSC 37126, Tallahatta/Lisbon formation contact zone, courtesy of James Lowery. **V**. Lingual view. **W**. Carinal view. **X**. Basal view. **Y–AA**. MSC 38974.1, lower Tallahatta Formation. **Y**. Lingual view. **Z**. Carinal view. **AA**. Basal view. Scale bars = 2 mm.

distinguishes the *proosti* morphology from the dentitions of *Acanthocybium* and *Scomberomorus*. As a result, Monsch (2005) placed the *proosti* species within a new genus, *Palaeocybium*.

Teeth of *Palaeocybium* are conspicuously thicker than morphologically similar teeth of *Sphyraena* (see above), and they have a larger and deeper pulp cavity. The *Palaeocybium* teeth in our sample were differentiated from those of *Scomberomorus* (see below) by having carinae that extend to the base of the teeth, they have a symmetrical basal outline (with carinae visible) and are not basally constricted.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the contact of the Tallahatta and Lisbon formations at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Lower Lutetian to middle Bartonian, zones NP14 to NP17.

Genus **Scomberomorus** Lacépède, 1802

Type species

Scomber regalis Bloch, 1793, Recent.

Scomberomorus bleekeri (Storms, 1892)

Fig. 64J–R

Cybium (*Enchodus*) *bleekeri* Storms, 1892: 3, pl. 1.

Sphyraena sp. – Thurmond & Jones 1981: fig. 103, right.
Scomberomorus bleekeri – Bannikov 1982: 135.
Scomberomorus cf. *stormsi* – Clayton *et al.* 2013: fig. 6d.
Scomberomorus sp. – Maisch *et al.* 2016: 9, fig. 2, 27–33.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 150 isolated teeth; Claiborne Group; ALMNH PV1985.87.4, ALMNH PV1985.87.5, ALMNH PV1992.28.33 (4 specimens), ALMNH PV1993.2.496a (2 specimens), ALMNH PV 2005.6.436.2, MMNS VP-8234 (12 specimens), MSC 34670, MSC 35777.1–5, MSC 37194.1.1–12, MSC 37194.3.1–17, MSC 37292, MSC 37368, MSC 37662.1–3, MSC 37894, MSC 38431.1–2, MSC 38540, MSC 38979, NJSM 24044, NJSM 24323, NJSM 24324, SC2012.47.95, SC2012.47.96 (26 specimens), WSU 24, WSU 5053 (43 specimens), WSU CC 546 (2 specimens).

Description

Teeth measuring less than 6.0 mm high, 4.0 mm wide. Crown medially curved, biconvex; medial face more convex than lateral face; faces with thin layer of smooth enameloid. Crown bicarinate; carinae smooth, sharp, convex, not reaching tooth base. Tooth base thickened medially, D-shaped in basal view.

Remarks

We identified two *Scomberomorus* species in our Claiborne sample, *S. bleekeri* (Storms, 1892) and *S. stormsi* (Leriche, 1905). The teeth of *S. stormsi* (see below) differ by being more elongated and gracile compared to *S. bleekeri* (Kemp *et al.* 1990; Weems 1999), they occasionally bear longitudinal striations on their labial and lingual faces (Casier 1946) and are more ovate in basal outline.

The teeth of *Scomberomorus bleekeri* differ from those of *Palaeocybium* in being asymmetrical in basal view (the carinae divide the crown into a thinner, weakly convex labial face and thicker, very convex lingual face), and by appearing slightly constricted basally due to the carinae stopping short of the tooth base. We consider the *Scomberomorus* material discussed by Clayton *et al.* (2013) and Maisch *et al.* (2016) to represent *S. bleekeri*. Thurmond & Jones (1981: fig. 47) figured three teeth which they assigned to *Sphyraena* sp., but our examination of these teeth revealed that the specimen shown in figure 47 (right) belongs to *S. bleekeri*.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the Tallahatta Formation at site AMo-8, the contact of the Tallahatta and Lisbon formations at sites ACh-7, ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, and the basal Gosport Sand at site ACl-4. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Scomberomorus stormsi (Leriche, 1905)

Fig. 64S–AA

Cybium stormsi Leriche, 1905: 151, pl. 10, fig. 3.

Scomberomorus stormsi – Bannikov 1982: 135.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 12 isolated teeth; Claiborne Group; MSC 37126, MSC 37512.1–2, MSC 38974.1–3, MSC 38977, SC2012.47.248 (5 specimens).

Description

Teeth measuring up to 1.0 cm high, 5.0 mm wide. Crown medially curved, biconvex; medial face more convex than lateral face; faces with thin layer of enameloid; enameloid smooth or finely striated basally. Crown bicarinate; carinae smooth, sharp, not reaching the tooth base; basal half of carinae straight, nearly parallel; tapering to point apically. Basal part of tooth more cylindrical, appears constricted below end of carinae. Tooth base with ovate outline, weak pulp cavity.

Remarks

Scomberomorus stormsi (Leriche, 1905) and *S. bleekeri* (Storms, 1892) are coeval within Eocene strata (Casier 1946, 1966; Weems 1999), but the former can be differentiated from the latter by being more ovate in basal view and being twice as high as wide. The teeth of *S. stormsi* can also exhibit longitudinal striations on the labial and lingual faces. This species can be differentiated from teeth of *Palaeocybium proosti* and *Sphyraena* sp. in having carinae that do not reach the tooth base, a much smaller pulp cavity than *P. proosti*, and a labiolingually thicker crown than *Sphyraena* sp.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations and the basal Lisbon Formation at site ACov-11, and the basal Gosport Sand at site ACl-15. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Subfamily Sardinae Starks, 1910
Tribe Sardini Collette & Chao, 1975

Genus ***Gymnosarda*** Gill, 1862

Type species

Thynnus (*Pelamis*) *unicolor* Rüppell, 1836, Recent, Red Sea.

Gymnosarda sp.
Fig. 65

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 isolated tooth; Claiborne Group; MSC 37271.

Description

Hypural plate roughly triangular in outline, consisting of fused hypurals, parahypural, and urostyle. Dorsal and ventral edges flat, straight, of equal length, wedge-shaped in dorsal and ventral views. Lateral faces flat; hypural sutures worn but visible; posterior margin slightly concave; basal notch nearly closed. Uroneural projecting dorsally from urostyle; face of urostyle ovoid, concave.

Remarks

A diagnostic characteristic of the members of the Scombridae is the fusion of the hypurals and urostyle into a unique hypural plate (Johnson 1986; Monsch 2005). The hypural plate identified in our sample (MSC 37271; Fig. 65) also possesses a fused parahypural and has a basal notch that is nearly closed. According to Monsch (2000, 2005), *Acanthocybium* and the members of the Scomberomorinae have hypural plates with a basal notch that is large and distinct. However, a caudal notch is completely absent on the hypural plates of the members of the Tribe Thunnini Starks, 1910, and nearly absent on those within the Sardini Collette & Chao, 1975. The presence of a reduced notch and fused parhypural on MSC 37271 are characteristic of a single member of Sardini, *Gymnosarda* Gill, 1862 (Monsch 2000, 2005). MSC 37271 is very similar to the hypural plate described on the extant *Gymnosarda unicolor* (Rüppell, 1838) and also very similar to the hypural of the only Eocene member of this genus, *Gymnosarda prisca* Monsch, 2000 (see Monsch

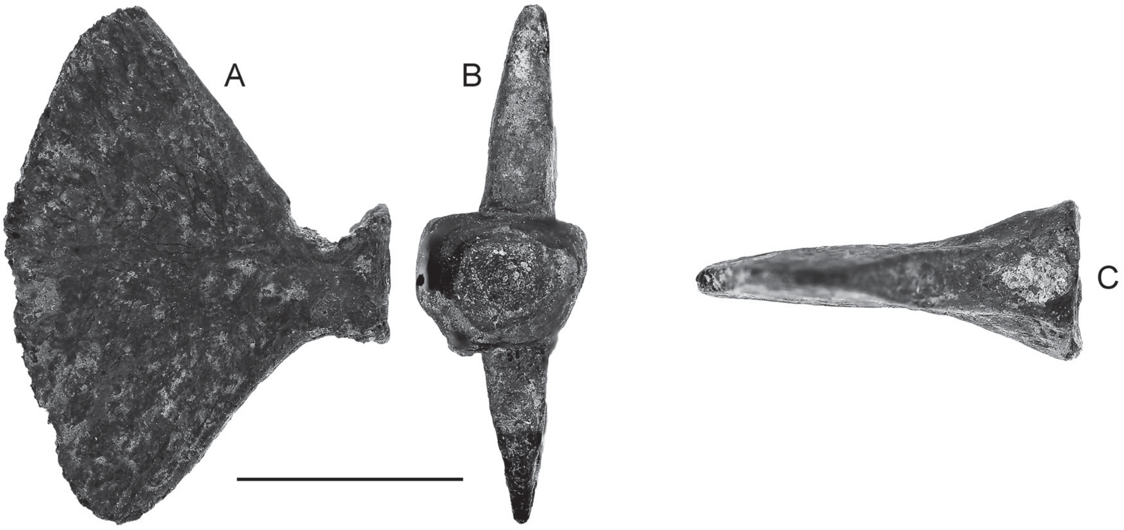


Fig. 65. *Gymnosarda* sp., hypural plate. **A–C**. MSC 37271, basal Lisbon Formation. **A**. Right lateral view. **B**. Anterior view. **C**. Dorsal view. Scale bar = 1 cm.

2000: fig. 1c, 2005: fig. 9c). However, the hypural plate of *G. prisca* has a clear caudal notch, a purported plesiomorphic character within this genus. Monsch (2000) described another Eocene *Gymnosarda* sp. hypural plate that, although damaged along the posterior edge, exhibits a basal notch that appears nearly closed (see fig. 10) and is more elongated dorsoventrally than MSC 37271, suggesting the plates represent two different species. Although MSC 37271 likely represents an undescribed species within *Gymnosarda*, we refrain from erecting one because our sample consist of only a single specimen.

Stratigraphic and geographic range in Alabama

The lone specimen in our sample was collected from the basal Lisbon Formation at site ACov-11. Lower Lutetian, Zone NP15.

Order Acanthuriformes Jordan, 1923
Suborder Sciaenoidei Cuvier, 1828
Family Sciaenidae Cuvier, 1828

Genus ***Fisherichthys*** Weems, 1999

Type species

Fisherichthys folmeri, Weems, 1999, early Eocene, Stafford County, Virginia, USA.

Fisherichthys aff. ***F. folmeri*** Weems, 1999

Fig. 66A–L

Fisherichthys folmeri Weems, 1999: 63, pls 4.7d, 4.8a–b.

Albula eppsi – Case 1994b: 142, pl. 1, figs 372–375.
cf. *Fisherichthys* sp. – Clayton *et al.* 2013: fig. 6k–l.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 6 isolated teeth; Claiborne Group; MSC 38501, SC2012.47.125 (2 specimens), SC2012.47.237, SC2012.47.238, SC2012.47.239.

Description

Small teeth measuring up to 1.5 mm diameter, 1.0 mm crown height. Tooth crown conical in profile, with flat apex. Crown covered by smooth enameloid; apical surface with shallow depression surrounded by small tubercles. Occlusal surface of worn teeth composed of dentine, with a thin outer enameloid layer. Crown base thick, with basal cingulum. Circular basal pulp cavity centrally located.

Remarks

Six specimens in our sample are tentatively assigned to *Fisherichthys folmeri* because they exhibit the features of the type and only known species. The conical profile, apical tubercles, and basal cingulum serve to distinguish teeth of *Fisherichthys* in our sample from the somewhat similar teeth of *Albula*, *Paralbula*, *Pycnodus*, and *Egertonia*.

The occurrence of *Fisherichthys* in Claiborne Group strata, particularly in the Gosport Sand, represents the stratigraphically youngest records for the genus, which was previously not known to occur beyond Zone NP11 of the Ypresian Stage (Case 1994b; Weems 1999; Cicimurri & Knight 2009). Our tentative species identification is due to our small sample size and much younger stratigraphic occurrence.

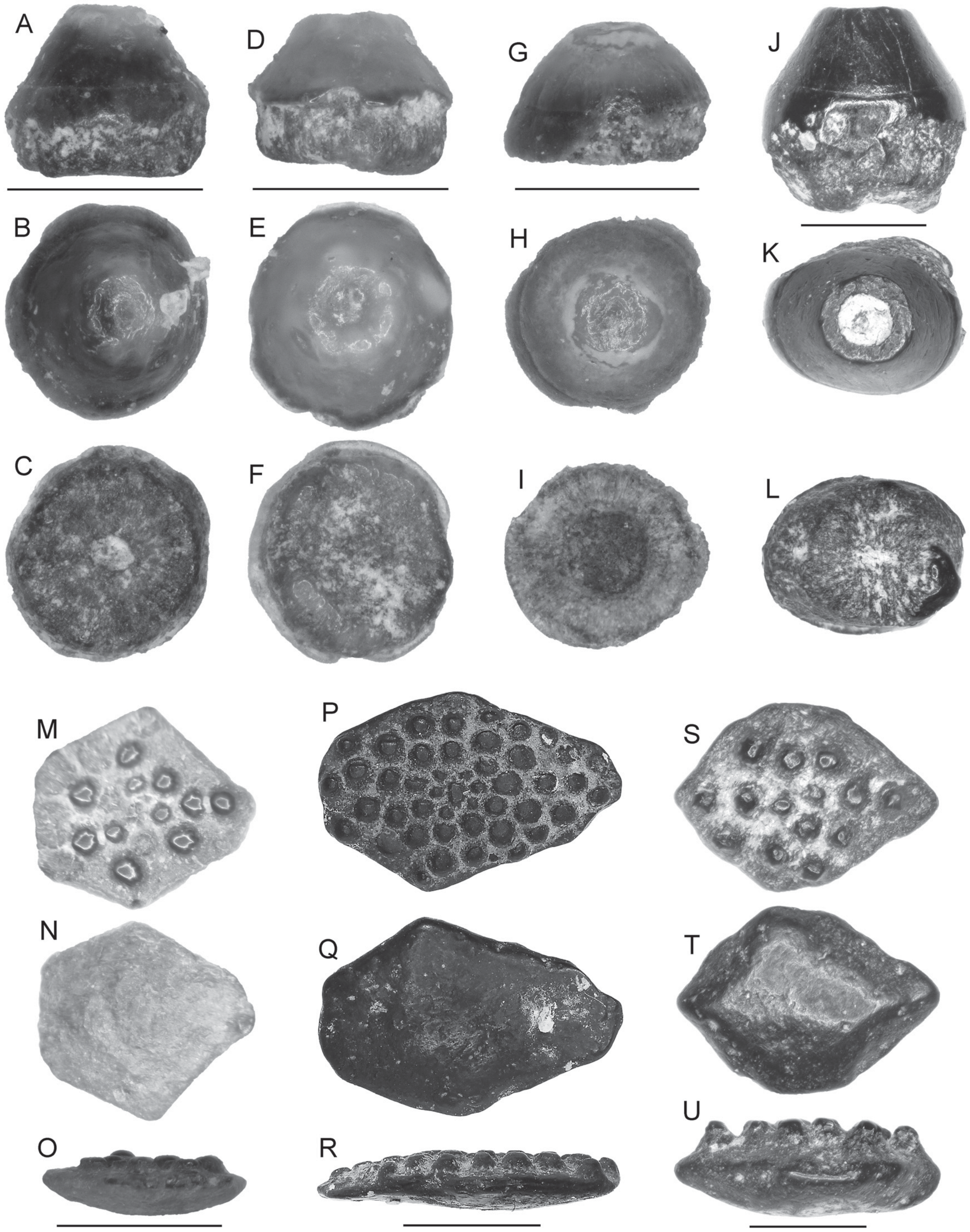


Fig. 66. *Fisherichthys* aff. *F. folmeri* Weems, 1999 and Ostraciidae Rafinesque, 1810, elements. **A–L**. *Fisherichthys* aff. *F. folmeri*. **A–C**. Tooth, SC2012.43.125.1, basal Lisbon Formation. **A**. Profile view. **B**. Oral view. **C**. Aboral view. **D–F**. Tooth, SC2012.43.125.2, basal Lisbon Formation. **D**. Profile view. **E**. Oral view. **F**. Aboral view. **G–I**. Tooth, SC2012.43.125.3, basal Lisbon Formation. **G**. Profile view. **H**. Oral view. **I**. Aboral view. **J–L**. Tooth, MSC 38501, Gosport Sand. **J**. Profile view. **K**. Oral view. **L**. Aboral view. — **M–U**. Ostraciidae. **M–O**. Dermal plate, MSC 35771.1, lower Tallahatta Formation. **M**. External view. **N**. Internal view. **O**. Profile view. **P–R**. Dermal plate, MSC 37121, Tallahatta/Lisbon formation contact zone, courtesy of Bruce Relihan. **P**. External view. **Q**. Internal view. **R**. Profile view. **S–U**. Dermal plate, MSC 37418, basal Gosport Sand. **S**. External view. **T**. Internal view. **U**. Profile view. Scale bars: A–L = 1 mm; M–R = 5 mm; S–U = 2 mm.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the basal Lisbon Formation at site ACov-11 and the basal Gosport Sand at site ACl-4. Lower Lutetian to middle Bartonian, zones NP15 to NP17.

Order Tetraodontiformes Berg, 1940
Suborder Ostracioidea Tyler, 1980
Family Ostraciidae Rafinesque, 1810

Gen. et sp. indet.
Fig. 66M–U

Ostracion sp. – White 1956: 146.
Ostracion meretrix – Case 1981: 2, fig. 22.
Ostracion sp. – Thurmond & Jones 1981: 108.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 12 isolated teeth; Claiborne Group; MMNS VP-8194, MSC 2401, MSC 35771.1–3, MSC 37121, MSC 37136, MSC 37418, NJSM 24046, NJSM 24327, WSU 28, WSU 5005.

Description

Dermal plates generally polygonal, thickest at center but laterally tapered. Outer surface convex, ornamented with concentric pattern of isolated enameloid-covered tubercles surrounding central node. Internal surface smooth, concave.

Remarks

In North America, fossil dermal plates like those described above have been assigned to *Ostracion* Rafinesque, 1815 (see Leriche 1942; White 1956; Stringer 2001). However, as discussed by Winterbottom & Tyler (1983), Tyler & Gregorova (1991), and Weems (1998, 1999), there is a tremendous amount of inter- and intraspecific variation within the dermal armor of ostraciid fish, and even on the body of a single individual. Weems (1998) explained that specimens like those described herein can be assigned to the Ostraciidae because those of Aracanidae, the only other family of boxfishes, are ornamented with a central spine from which radiating lines of tubercles emanate.

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the lower Tallahatta Formation at site ADl-1, the contact of the Tallahatta and Lisbon formations at sites ACh-14 and ACov-11, the basal Lisbon Formation at site ACov-11, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Suborder Balistoidei Rafinesque 1810
Family Balistidae Risso, 1810

Gen. et sp. indet.
Fig. 67

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 isolated tooth; Claiborne Group; MSC 2402.

Description

Teeth anteroposteriorly longer than wide, laterally compressed covered with thick enameloid. Anterior half of tooth wider than posterior half, resulting in pear-shaped occlusal outline. Indistinct cusp located anteriorly, posterior margin slopes towards edge of tooth. Blunt transverse ridge extends across cusp; cusp conspicuously lighter in color than remainder of tooth. Lateral surfaces of crown convex, exhibiting fine growth lines. Basal face rounded.

Remarks

MSC 2402 (Fig. 67) appears to be conspecific with teeth belonging to the Balistidae as described by Tyler (1980) and Tyler & Santini (2002). Tyler & Santini (2002) noted that isolated teeth and jaw fragments have little taxonomic value because the majority of differential characteristics among the described fossil taxa are based on complete specimens, not isolated teeth. The only reported Eocene member of the Balistidae, *Gornylistes prodigiosus* Bannikov & Tyler, 2008, was described from a nearly complete specimen from the middle Eocene of the Caucasus. Although the type description for this specimen mentions the number of teeth in the jaws, the tooth morphologies were not described nor were they illustrated.

The teeth of Balistidae are superficially similar to the pharyngeal teeth of the Eocene fish *Eotrigonodon*. However, teeth of Balistidae teeth differ by having convex lateral edges, as opposed to being mesiodistally compressed with flat lateral edges on the teeth of *Eotrigonodon* (see Ciobanu 2011: figs 5–10). Furthermore, the crown of *Eotrigonodon* teeth has smooth enameloid that lacks transverse growth lines, which are visible on the teeth of Balistidae.

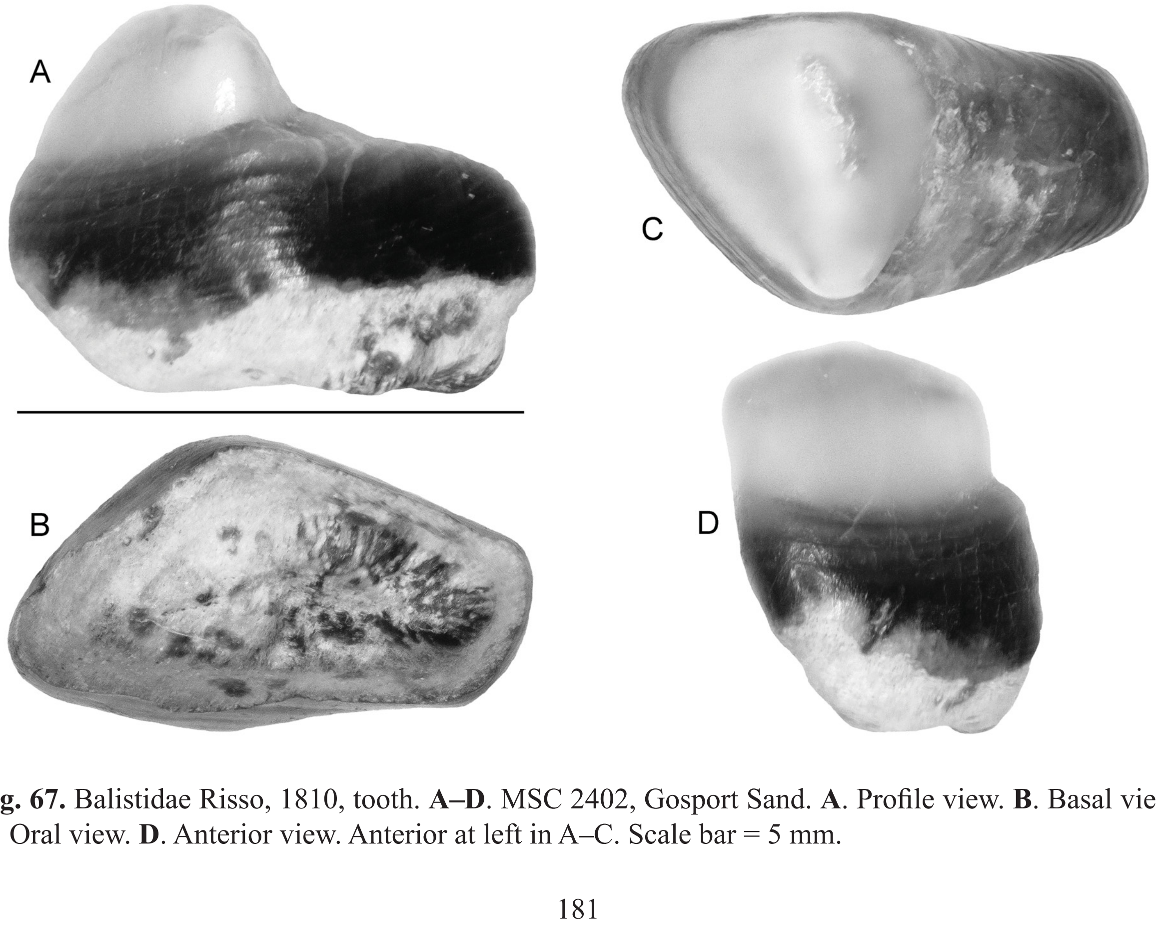


Fig. 67. Balistidae Risso, 1810, tooth. **A–D**. MSC 2402, Gosport Sand. **A**. Profile view. **B**. Basal view. **C**. Oral view. **D**. Anterior view. Anterior at left in A–C. Scale bar = 5 mm.

Stratigraphic and geographic range in Alabama

The lone specimen in our sample was collected from the Gosport Sand at site ACh-21. Middle Bartonian, Zone NP17.

Suborder Tetraodontoidei Nelson *et al.*, 2016
Family Diodontidae Bonaparte, 1838
Genus ***Progymnodon*** Dames, 1883

Type species

Progymnodon hilgendorfi Dames, 1883, middle Eocene, Egypt.

Progymnodon hilgendorfi Dames, 1883
Fig. 68

Progymnodon hilgendorfi Dames, 1883: 148, pl. 3, fig. 13.

Diodon (?*Chilomycterus*) *hilgendorfi* – Weiler 1929: 29, pls 6–7, 9, 13–14.
?*Diodon* sp. – Thurmond & Jones 1981: 108, fig. 51.
Progymnodus cf. *hilgendorfi* – Suraru & Suraru 1987: 128, fig. 1.
Chilomycterus hilgendorfi – Dica 2002: 40, pl. 1, figs 1–2.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 121 isolated teeth; Claiborne Group; MSC 2396, ALMNH PV1993.2.456 (57 specimens), ALMNH PVPV 2005.6.438, MSC 37349.1–2, MSC 37398.1–2, MSC 37435, MSC 37440.1–44, MSC 37443, MSC 37450, MSC 37556, MSC 37602, MSC 37895, MSC 38494.1–5, MSC 38551.1–2, MSC 38842.

Description

Outer margin (the 'beak') composed of numerous stacked rows of very small (less than 1.0 mm) circular to wedge-shaped teeth. Premaxillary margin angular; dentary margin broadly convex. Triturating surface consisting of two stacks of subtriangular teeth; teeth separated from anterior margin by deep gap of bone. Individual teeth consist of thin enameloid crown, weakly convex; medial border (adjacent to tooth on other half of jaw plate) straight; anterior and posterior margins weakly convex, and the teeth have a sub-triangular outline in occlusal view.

Remarks

We identified premaxillary and dentary elements belonging to the Diodontidae based on the size and shape of the triturating teeth, the number of triturating teeth exposed at any one time through *in vivo* usage, and the nature of the anterior beak. Five fossil diodontid genera are considered valid, including *Eodiodon* from the middle and late Eocene, *Progymnodon* from the Paleocene to late Eocene, *Oligodiodon* from the Oligocene and Miocene, *Kyrtogymnodon* from the Pliocene, and *Chilomycterus* and *Diodon* from the Miocene to Recent (see Tavani 1955; Tyler 1980; Weems 1998; Schultz 2006; Ciobanu & Trif 2012). Tyler (1980) and Dica (2002) questioned the validity of *Eodiodon*, with both authors citing that the lone diagnostic characteristic of this genus, the lack of teeth at the biting edge (the "beak"), could be attributed to wear and/or preservation. Diodontid tooth plates have been shown to be highly variable in terms of the shape of isolated triturating teeth and the number of teeth concurrently exposed (see Weems 1998: fig. 6a). Nevertheless, our Claiborne samples were assigned to *Progymnodon* because the triturating teeth are separated from the beak by a bone gap, which is a diagnostic characteristic of this genus (see Ciobanu & Trif 2012). Furthermore, the tooth plates in our sample appear conspecific to those of *Progymnodon hilgendorfi* as described by Dames (1883). Although Dica (2002) synonymized *P. hilgendorfi* with *Chilomycterus*, citing the gap between the beak and the triturating teeth as being characteristic of the latter genus, Ciobanu & Trif (2012) rejected this synonymy, citing the Miocene origins of *Chilomycterus*.

Thurmond & Jones (1981: 108, fig. 51) reported and figured a specimen from the basal Gosport Sand at site ACl-4 in Clarke County, AL that they assigned to "?*Diodon* sp." Our reexamination of this specimen (ALMNH PV 2005.6.438) revealed that it instead belongs to *P. hilgendorfi.*

Stratigraphic and geographic range in Alabama

The specimens in our sample were collected from the basal Gosport Sand at sites ACl-4 and AMo-4, and the Gosport Sand at site ACh-21. Middle Bartonian, Zone NP17.

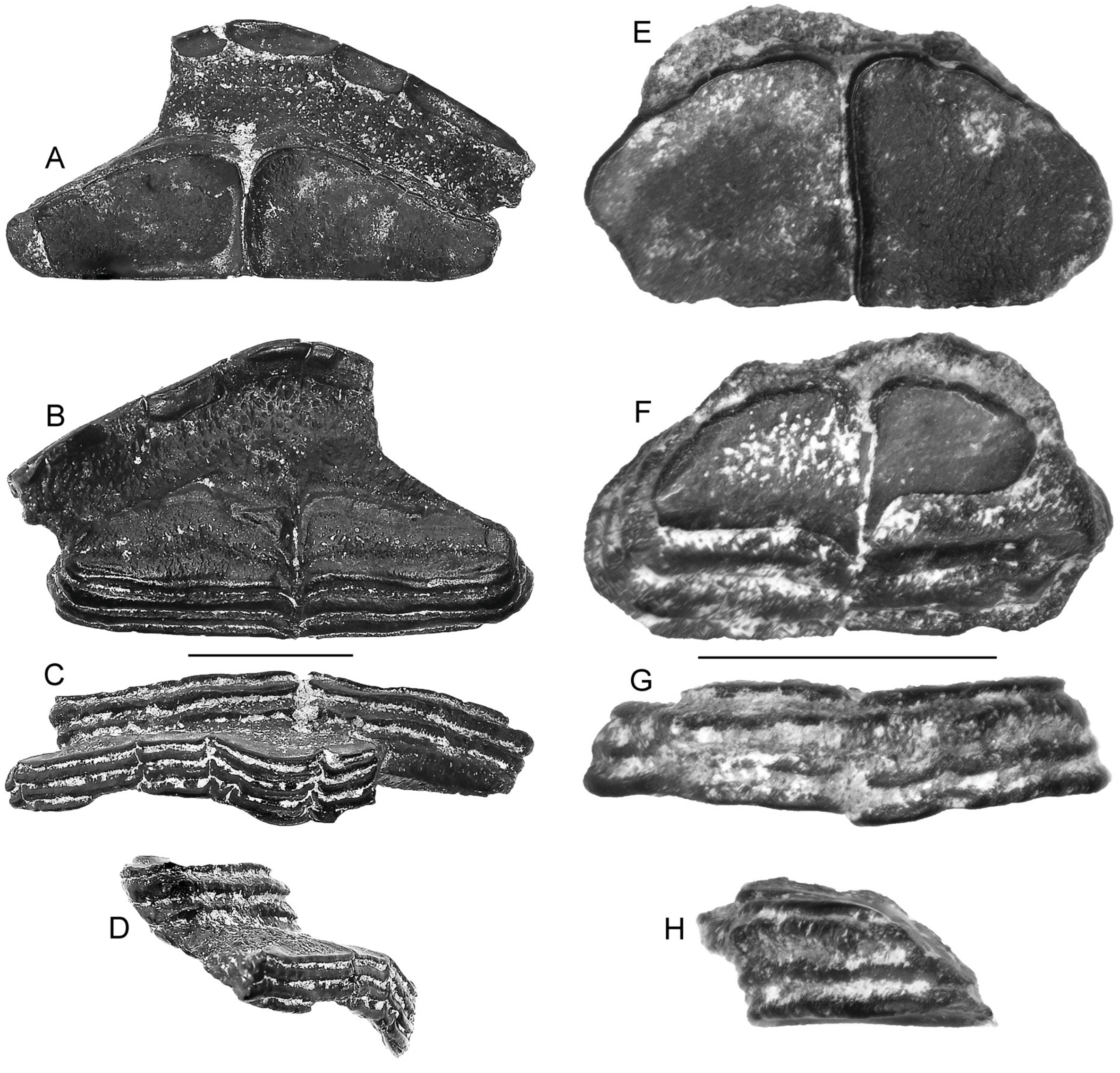


Fig. 68. *Progymnodon hilgendorfi* Dames, 1883, tooth plates. **A–D**. MSC 37450, basal Gosport Sand, upper tooth plate. **A**. Aboral view. **B**. Oral view. **C**. Posterior view. **D**. Profile view. **E–H**. MSC 37398.1, basal Gosport Sand, tooth plate. **E**. Aboral view. **F**. Oral view. **G**. Posterior view. **H**. Profile view. Scale bars: A–D = 1 cm; E–H = 5 mm. Anterior at top in oral and basal views.

Teleostean otoliths from the Claiborne Group of Alabama

Introduction

The vast majority of the fossils utilized for this study represent elements of the skeletal system (over 18 000 elasmobranch specimens, over 2 100 bony fish remains). As detailed previously, these skeletal remains include teeth, vertebrae, scales, rostra, spines, and a variety of other bones, all of which are composed primarily of hydroxyapatite (calcium phosphate). However, the bony fishes are also represented by elements that are not part of the skeletal system. These unique structures, otoliths (aka statoliths, ear stones) are specialized and integral parts of the acoustico-lateralis system of fishes. The otoliths play major roles in equilibrium maintenance, sound perception, angular acceleration, and muscle tone regulation (Stringer 1986). Otoliths are located in the two auditory labyrinths of the teleostean fish, one on each side of the skull, posterior to the brain, and anterior to the first vertebra. The labyrinths have three cavities known as the utriculus, sacculus, and lagena, and each of these cavities contains a single otolith composed of polycrystalline calcium carbonate, primarily in its aragonite form, although there are rare occurrences of vaterite (a polymorph of calcium carbonate). Each of the otoliths is given a name based on the cavity in which they occur: the utriculus contains the lapillus or utriculith; the sacculus contains the sagitta or sacculith; and the lagena contains the asteriscus or lagenalith (Koken 1884; Stinton 1975; Nolf 2013).

Of the three otoliths within each labyrinth, the sagitta is typically the largest and is taxonomically useful in paleontological studies (the lapillus and asteriscus are much smaller and usually not diagnostic). The Ostariophysi is an exception to this generalization, and in this group the sagitta is the smallest and the lapillus and asteriscus are larger. Although the lapillus is typically not used for taxonomic purposes in fossil otolith studies, Ariidae and Sciaenidae are two of the few families in which the lapilli are useful for identifying taxa. However, the sagitta, characterized by a diagnostic sulcus on the inner face, as well as other morphological features like overall shape, margin features, and length/height ratios, are utilized for taxonomy.

Otolith taxonomy

One of the first taxonomic studies of otoliths was conducted by Koken (1884), who was forced to create his own system of nomenclature because of the lack of knowledge of fossil and Recent fish otoliths. Koken (1884) assigned all otoliths to a form genus, *Otolithus.* Then in parentheses, he added the name of the genus, if known, or the family in the genitive plural, followed by the species name. Numerous fossil otoliths from Alabama and Mississippi were originally identified using Koken's (1888) system. As otoliths of Recent fishes became better known, this system was replaced by the more typical binomial nomenclature used in paleontology.

The lack of knowledge of the otoliths of Recent fishes led many otolith researchers in the late 1970s and early 1980s to employ an open generic nomenclature (Nolf 1985; Nolf & Dockery 1990; Schwarzhans 2003; Nolf & Stringer 2003). Although this approach was useful for conveying evolutionary relationships, it had limitations and problems, particularly with regard to compliance with the *International Code of Zoological Nomenclature*. Furthermore, the open generic nomenclature was cumbersome and taxonomic changes were difficult to follow and ascertain. Nolf (2013, and earlier references contained therein) proposed an alternative method of nomenclature that employed collective group names as a genus group name.

This method of nomenclature has been called into question by numerous paleontologists including Janssen (2012), Schwarzhans (2012), Tracey (2014), and Stringer *et al.* (2018). Janssen (2012) noted that a formal genus name must be used in paleontology according to the *International Code of Zoological Nomenclature* article 11.9.3 (ICZN 1999). Schwarzhans (2012) stated that it was not advisable to continue to use the collective generic group in otolith research and strongly recommended that it be discontinued. Tracey (2014) contended that the alternative system of nomenclature proposed by Nolf (2013) did not comply with articles 13.1.1 and 16.1 of the Code (ICZN 1999), and might not qualify as standard scientific names. Tracey (2014) thought Nolf's (2013) system was more appropriately regarded as zoological formulae, according to the Glossary of the Code (ICZN 1999). Furthermore, the current trend with some scientific journals is to not publish otolith studies that employed Nolf's (2013) alternative system of nomenclature, or any type of open generic nomenclature. Many ichthyologists, who often work closely with otolith paleontologists, have opposed any classification except for the traditional binomial system of classification. Each of these major changes in otolith nomenclature has created a plethora of concerns and problems over the years.

Our knowledge of the otoliths of Recent fishes has increased significantly because of specific and detailed taxonomic studies by Nolf (1980, 1995, 2013), Schwarzhans (1993, 1999, 2013a, 2013b), Campana (2004), Lombarte *et al.* (2006), Rossi-Wongtschowski *et al.* (2014), and Lin *et al.* (2016), among others, and it is possible to determine with much greater accuracy if a fossilized otolith is related to an extant form. Therefore, an alternative system of classification is not needed or required. If it cannot be ascertained, after careful analysis and scrutiny, that a fossil otolith cannot be equated to the otolith of a Recent fish, then a fossil genus or species can be assigned. If there is question regarding the generic designation of a fossil otolith, then the recommendations of Janssen (2012) can be employed in which the type genus of the family or subfamily is used followed by a question mark. This indicates that the form might belong to that genus or any other genera (known or as yet unknown) in the family or subfamily. These guidelines are followed in this study.

The otolith taxonomic classification presented herein follows that of Nelson *et al.* (2106), who were greatly influenced by the work of Betancur-R. *et al.* (2013). Ordinal names follow Wiley & Johnson (2010), and family-group names and authors of Recent fishes follow van der Laan *et al.* (2014, 2017, 2018).

Otolith samples

Otoliths were extracted from concentrates of field-collected bulk matrix that was processed in the laboratory. The size of the bulk samples varied widely according to the purposes of the bulk samples. Some small (a few kg) matrix samples were collected for micropaleontological (Foraminifera) analysis, whereas much larger samples were obtained for vertebrate analysis (skeletal remains and otoliths). The largest bulk sample collected for otoliths weighed approximately 681 kg and was obtained from the "upper" Lisbon Formation at site ACh-8 in Choctaw County. All otoliths from the bulk samples that were figured in this study are reposited in the collections at MSC. The non-figured otoliths were retained in the comparative otolith collection of Gary L. Stringer and are referred to as the GLS otolith comparative collection.

Other existing otolith collections housed at MSC, WSU, and GSA were examined. Data associated with the otoliths did not specify how the specimens were collected, but the physical size of most of the otoliths indicates they were obtained from bulk samples. Some of the otoliths are large enough to be seen with the naked eye and could have been surface collected.

When utilizing otolith taxa for paleoenvironmental interpretations, references for bathymetric data for Recent taxa include Ben-Tuvia & McKay (1986), Bohlke & Chaplin (1968, 1993), Chao (2003), Darnell *et al.* (1983), Dennis *et al.* (2004), Hoese & Moore (1998), Johnson & Gill (1998), Kotlyar (1988), McEachran & Fechhelm (1998, 2005), Moore (1993, 2016), Nelson *et al.* (2016), Nielsen *et al.* (1999), Page *et al.* (2013), Poll (1953, 1954, 1959), Smith (1989), Smith & Kanazawa (1977), Snyder & Burgess (2016), and Tavera *et al.* (2012). One of the most useful references for data on the depth ranges of Recent species is *FishBase*, which is edited by Froese & Pauly (2019).

Systematic paleontology

The otolith sample available to us includes 593 specimens. The Lisbon Formation was by far the most prolific, with 565 otoliths. Only one otolith was recovered from the Tallahatta Formation, and 27 were found in the Gosport Sand. We do not believe that large bulk samples would have appreciably increased the number of specimens from the Tallahatta Formation, as it appears that erosion and leaching have destroyed aragonitic remains, including otoliths. This may also be true for the Gosport Sand, as very few otoliths were obtained from bulk samples that yielded thousands of shark and bony fish teeth. Taxonomic analysis of the otoliths revealed 9 orders, 14 families, and 31 unequivocal taxa for the Claiborne Group in Alabama, which are described below.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii sensu Goodrich, 1930
Order Albuliformes Greenwood *et al.*, 1966
Family Albulidae Bleeker, 1849
Subfamily Albulinae Bleeker, 1849

Genus ***Albula*** Scopoli, 1777

Type species

Esox vulpes Linneaus, 1758, Recent.

Albula sp.
Fig. 69A–B

Albula sp. – Stringer 1977: 63–65, pl. 1, fig. 1; 2016: 7, pl. 1: figs e–g, i, k. — Breard & Stringer 1995: 80; 1999: 135. — Stringer *et al.* 2001: 323. — Nolf & Stringer 2003: 4, pl. 1, fig. 2a–b.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 4 otoliths; Claiborne Group; GLS otolith comparative collection (3 specimens), MSC 562.

Description

Sagittae quite large, one specimen exceeding 18 mm in length. Outline sub-elliptical; height/length ratios approximately 50–60%. Margins smooth; anterior margin very short, slightly arched. Dorsal margin almost straight, slopes downward anteriorly and posteriorly. Small, low posterodorsal dome forms highest point on dorsal margin. Posterior margin very short, subtruncate, bluntly pointed. Posteroventral margin short, almost straight, slightly curved inward or outward. Ventral margin very broadly rounded. Anteroventral margin almost straight, forms small, obtuse angle with anterior margin. Inner face conspicuously convex and twisted. Prominent sulcus developed in dorsal and posterior regions. Sulcus very long, extending from anterodorsal margin to posteroventral margin. Sulcus indistinctly divided, with downturned and flexed posterior. Ostium wide, long; length twice that of cauda. Ostium filled with colliculum, only slightly excavated. Ostium opens onto anterodorsal margin. Cauda with anterior sub-horizontal portion and posterior downturned portion. Anterior cauda separated from the cauda by a thickening and roughening of collicular material. Anterior cauda slightly excavated, posterior deeply excavated. Posterior cauda reaches posteroventral margin. Caudal keel present. Crista superior well developed, occurs as broad, raised ridge above cauda. Crista inferior absent. Ventral furrow not developed. The outer face concave, twisted, thin toward anterior, thickest in posterodorsal. Annual rings almost always visible on outer face.

Remarks

The posterior margin is commonly broken on the specimens available to us, but the *Albula* sp. from the Lisbon Formation is very similar to *Albula* sp. known from other Eocene deposits of the Gulf Coast (Stringer 1977; Breard & Stringer 1995, 1999; Nolf & Stringer 2003). The Lisbon *Albula* sp. specimens are large, but late Eocene specimens from the Yazoo Clay in Louisiana are even larger, with some exceeding 25 mm (GLS, pers. observ.).

Stratigraphic and geographic range in Alabama

Specimens were recovered from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Order Anguilliformes Goodrich, 1909
Family Heterenchelyidae Regan, 1912

Genus ***Pythonichthys*** Poey, 1868

Type species

Pythonichthys sanguineus Poey, 1868, Recent, Cuba.

Pythonichthys colei (Müller, 1999)
Fig. 69C–D

Eosolea texana Dante & Frizzell in Frizzell & Dante, 1965: 716, pl. 88, figs 15, 20.

Pythonichthys sp. – Breard & Stringer 1995: 80.
"genus aff. *Panturichthys*" *colei* – Müller 1999: 68, pl. 20, figs 4–5.
"genus *Heterenchelyidarum*" *colei* – Nolf & Stringer 2003: 5, pl. 1, figs 3–8.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 2 otoliths GLS otolith comparative collection (1 specimen), WSU CC 474.4.

Description

Species characterized by small otoliths of 2–3 mm length, height slightly less than length (height/length ratios approximately 85–90%). Shape almost circular to slightly oval. Margins tend to be smooth. Angle along posterodorsal margin. Ventral rim regularly curved. Inner face mainly smooth, convex, with no depressed area or ventral furrow. Sulcus obvious, not deeply impressed. No clear division of ostial and caudal portions of sulcus. Sulcus primarily located medially, extends across approximately 75% of inner face. Ventral margin of sulcus may undulate, especially in posterior portion. Posterior end of sulcus mainly rounded, tapers slightly. No crista superior or crista inferior. Outer face slightly concave, mainly featureless.

Remarks

Pythonichthys colei is quite rare in the Claiborne Group formations, with only two specimens being recovered from the Lisbon Formation. This rare occurrence is not unusual, as Müller (1999) reported only 11 specimens of this species from the approximately 12 000 otoliths from the Tertiary of the US Atlantic Coastal Plain. Although Nolf & Stringer (2003) reported 90 specimens of *P. colei* (as "genus *Heterenchelyidarum*" *colei*) from 5 559 otoliths from the late Eocene Yazoo Clay, the taxon still represented less than 2% of the total assemblage. One unusual occurrence of this species is in the

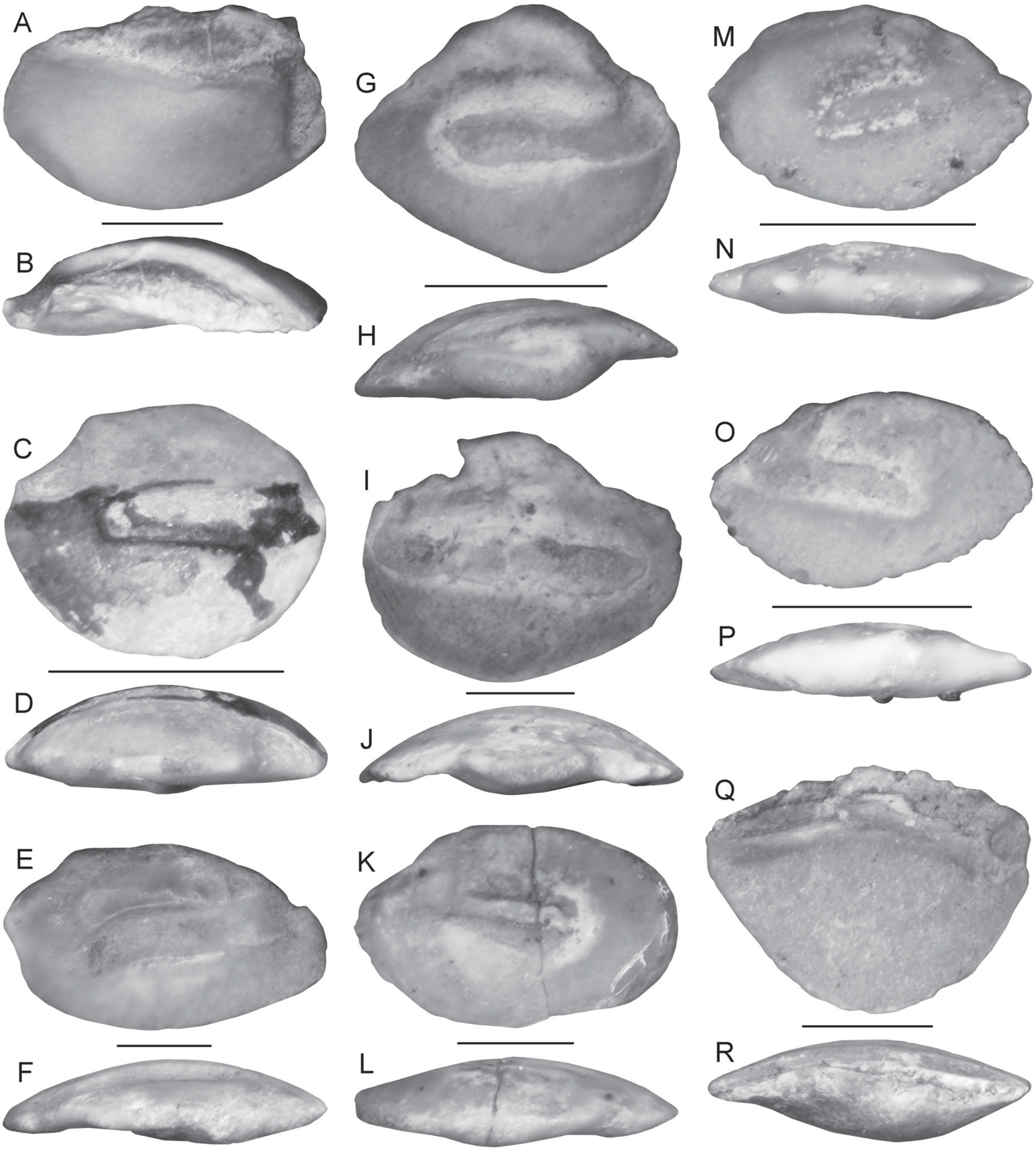


Fig. 69. Claiborne Group, "upper" Lisbon Formation, otoliths. **A–B**. *Albula* sp., MSC 562. **A**. Inner face (right sagitta). **B**. Dorsal view. — **C–D**. *Pythonicthys colei* (Müller, 1999), WSU CC 474. **C**. Inner face (left sagitta). **D**. Dorsal view. — **E–F**. Muraenesocidae Kaup, 1859, indet., MSC 39064. **E**. Inner face (left sagitta). **F**. Dorsal view. — **G–H**. *Ariosoma nonsector* Nolf & Stringer, 2003, MSC 39069. **G**. Inner face (left sagitta). **H**. Dorsal view. — **I–J**. *Paraconger sector* (Koken, 1888), MSC 39052. **I**. Inner face (right sagitta, broken on anterodorsal angle). **J**. Dorsal view. — **K–L**. *Pseudophichthys* sp., MSC 37059.2. **K**. Inner face (right sagitta). **L**. Dorsal view. — **M–N**. *Rhynchoconger* sp., MSC 37059.6. **M**. Inner face (left sagitta). **N**. Dorsal view. — **O–P**. *Gnathophis meridies* (Frizzell & Lamber, 1962), MSC 37059.XX. **O**. Inner face (right sagitta). **P**. Dorsal view. — **Q–R**. *Myripristis* sp., MSC 39047. **Q**. Inner face (right sagitta). **R**. Dorsal view. Scale bars: A–B = 5 mm; C–R = 2 mm.

Clayton Formation (Paleocene) of central Arkansas, where it represents approximately 24% of the total specimens (Stringer & Sloan 2018). This abundance is highly atypical, as, like its fossil counterparts, modern representatives of this family are rare and not well studied (Smith *et al.* 2012).

Stratigraphic and geographic range in Alabama

This species was recovered only from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Family Muraenesocidae Kaup, 1859

Muraenesocidae indet.
Fig. 69E–F

Material examined

UNITED STATES OF AMERICA – **Alabama** • 3 otoliths; GLS otolith comparative collection (2 specimens), MSC 39064.

Description

Shape best described as ovate (sensu Smale *et al.* 1995); height/length ratios approximately 60%. Length ranges from 6.5–7.5 mm. Margins smooth except for dorsal and posterodorsal margins, which may be coarsely lobed or crenulated. Anterior margin short and tapered. Anterodorsal margin slighted inflated, fairly steep, long. Dorsal margin short, irregularly lobed. Posterodorsal margin broadly rounded; posterior margin short, very slightly rounded outwardly, almost vertical. Posteroventral, ventral, anteroventral margins evenly but not deeply rounded. Inner face slightly convex, marked by conspicuous sulcus. Sulcus extending approximately 80% length of inner face; slightly flexed toward the posteroventral margin. Sulcus apparently undivided. Anterior upper margin of sulcus appears upwardly turning near anterodorsal margin. Posterior portion of sulcus more deeply excavated than anterior portion. Posterior end of sulcus rounded. Indications of possible crista superior. No ventral furrow visible. Outer face slightly convex, especially at center. Dorsal portion of outer face more undulating.

Remarks

Unfortunately, all three specimens are eroded, and it was difficult to ascertain detailed morphological features that would have assisted identification beyond the family level. Müller (1999) named *Muraenesox rhomboideus* from the Piney Point Formation of Virginia, which is Claibornian (Lutetian) in age.

Stratigraphic and geographic range in Alabama

This species was recovered only from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Family Congridae Kaup, 1856

Genus ***Ariosoma*** Swainson, 1838

Type species

Ophisoma acuta Swainson, 1838, Recent.

Ariosoma nonsector Nolf & Stringer, 2003
Fig. 69G–H

Otolithus (*Platessae*) *sector* Koken, 1888: 292, pl. 17, figs 5–16.

Ariosoma sp. – Stringer 1979: 102, pl. 1, fig. 4; 1986: 213, pl. 3, fig. 2.

Ariosoma nonsector – Nolf & Stringer 2003: 7, pl. 2, figs 1a–6. — Nolf 2003: 3–4, pl. 1, figs 3–4; 2013: 35–37, pl. 21.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 11 otoliths; GLS otolith comparative collection (10 specimens), MSC 39069.

Description

Species characterized by massive otoliths; height nearly the same as the length, with height/length ratios ranging from 80–86%. Margins typically smooth. Ostial rim slightly concave, most specimens exhibiting some concavity at posterodorsal rim. Posterior margin tends to taper. Ventral rim broadly rounded, marked by distinctive angular central position. Inner face mainly smooth, convex, except for some irregular depressions in upper portion of dorsal area. Sulcus wide, only slightly incised. Sulcus extends from very near anterior margin to posterior (about 85% of sagitta length). Sulcus entirely filled with colliculum, except for dorsal extremity of ostial channel. No clear division of ostial and caudal portions of sulcus. Posterior end of sulcus broadly tapered but showing some widening ventrally. No indications of ventral furrow. Outer face smooth, convex except for area near posterior end, where shallow dorsoventrally oriented depression occurs.

Remarks

This species and *Paraconger sector* (see below) were originally described as one species by Koken (1888), but *Ariosoma nonsector* was separated by Nolf & Stringer (2003). This taxon is known from middle and upper Eocene deposits in Alabama, Louisiana, Mississippi, and Virginia in the USA, and it occurs in lower Oligocene (Rupelian) strata of Alabama, Louisiana, and Mississippi.

Stratigraphic and geographic range in Alabama

Ariosoma nonsector is known only from the "upper" Lisbon Formation at sites ACh-8 and ACl-4. The lack of *A. nonsector* in the Gosport Sand may be related to the very sandy nature of the formation or the lack of extensive bulk sampling. Bartonian, zones NP16 and NP17.

Genus ***Paraconger*** Kanazawa, 1961

Type species

Echelus caudilimbatus Poey, 1867, Recent.

Paraconger sector (Koken, 1888)

Fig. 69I–J

Otolithus (*Platessae*) *sector* Koken, 1888: 292, pl. 17, fig. 14.

Paraconger sector – Nolf 1985: 292, pl. 17, fig. 14; 2003: 4, pl. 1, fig. 2a–b; 2013: 35–37, pl. 24. — Nolf & Stringer 2003: 7, pl. 2, figs 9a–10.

Paraconger americanus – Müller 1999: 70, pl. 20, figs 11–17.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 4 otoliths; GLS otolith comparative collection (3 specimens), MSC 39052.

Description

Species characterized by massive otoliths; height approximately 75% of the length. Margins primarily smooth; anterior margin is rounded. Ostial rim slightly concave, posterodorsal rim displays only very slight concavity. Posterior noticeably tapered, often almost bluntly pointed. Anteroventral rim rounder, shorter than posteroventral rim; posteroventral rim straighter and longer. Very slight angularity along ventral rim, near center. Inner face mainly smooth, convex. Sulcus fairly wide, only slightly incised. Sulcus filled with colliculum; ostial channel present. No clear division of ostial and caudal portions of sulcus. Posterior end of sulcus with some ventral widening. No indication of ventral furrow. Outer face smooth, convex except for area near posterior end, where shallow dorsoventrally oriented depression is located.

Remarks

This species and *Ariosoma nonsector* (see above) were originally described as one species by Koken (1888), but *Paraconger sector* was separated by Nolf & Stringer (2003). *Paraconger sector* is distinguished from *Ariosoma nonsector* by its greater length compared to its height (more elongate) and a narrower sulcus. Like the previous taxon, *P. sector* has a middle-to-late Eocene range in Alabama, Louisiana, Mississippi, and Virginia in the USA, and it also occurs in lower Oligocene (Rupelian) strata of Alabama, Louisiana, and Mississippi.

Stratigraphic and geographic range in Alabama

This taxon is known from the "upper" Lisbon Formation at site ACh-8 and the basal Gosport Sand at site ACl-4. Bartonian, zones NP16 and NP17.

Genus ***Pseudophichthys*** Roule, 1915

Type species

Pseudophichthys latedorsalis Roule, 1915, Recent.

Pseudophichthys sp.

Fig. 69K–L

Otolithus (*Solea*) *glaber* Koken, 1888: 293, pl. 18, fig. 3.

Otolithus (*Solea*) *glaber* – Campbell 1929a: 274–275, pl. 29, fig. 3
"*genus* aff. *Pseudophichthys*" *glaber* – Nolf 1985: 43. — Müller 1999: 82.
Pseudophichthys glaber – Nolf & Stringer 2003: 4, pl. 1, figs 13a–18.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 otolith; MSC 37059.2.

Description

Sagitta with oval to elliptic outline (sensu Smale *et al.* 1995); margins smooth. Height/length ratio equals 56%. Inner face very slightly convex. Sulcus of inner face undivided, slants very slightly in posteroventral direction. Sulcus reaches anterior margin, possibly through shallow ostial channel, extends approximately 75% of length. Anterior and posterior ends of sulcus tapering. Fairly conspicuous depressed area above sulcus.

Remarks

The singular specimen available to us is broken, but the undivided sulcus allows us to identify it as congrid, and other preserved features identify it as *Pseudophichthys*. However, determination to the species level was not possible, although it is very similar to *Pseudophichthys glaber* from the Eocene of Louisiana (Nolf & Stringer 2003).

Stratigraphic and geographic range in Alabama

Only one broken specimen of *Pseudophichthys* sp. was recovered from the "upper" Lisbon Formation at site ACh-7. Bartonian, zones NP16 and NP17.

Genus ***Rhynchoconger*** Jordan & Hubbs, 1925

Type species

Leptocephalus ectenurus Jordan & Richardson, 1909, Recent.

Rhynchoconger sp.

Fig. 69M–N

Hildebrandia sp. – Stringer 1992: 36, fig. 2a. — Müller 1999: 80, pl. 20, figs 28–30.
Rhynchoconger sp. – Nolf & Stringer 2003: 4, pl. 1, figs 12a–b.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 otolith; MSC 37059.6.

Description

Sagitta with elliptical outline; somewhat elongate with a height/length ratio of 48%. Shape noticeably angular, with greatest height slightly anterior to mid-point on dorsal margin. Margins smooth. Anterior tapered but with rounded shape. Posterior also tapered but more pointed. Inner face slightly convex, with distinct undivided sulcus. Sulcus slants slightly in posteroventral direction, covers approximately 60% of inner face. Width of sulcus fairly consistent. Small ostial channel connects ostial portion of sulcus to anterodorsal margin. Ostial channel situated away from anterior margin of sulcus. Well-defined rectangular depressed area above sulcus. No indication of ventral furrow. Outer face slightly convex.

Remarks

Only one specimen, an ablated juvenile sagitta, was attributed to *Rhynchoconger*. However, features of the sulcus and the presence of a depressed area above the cauda are indicative of *Rhynchoconger*. Unfortunately, specific determination was not possible.

Stratigraphic and geographic range in Alabama

The one specimen of *Rhynchoconger* sp. was recovered from the "upper" Lisbon Formation at site ACh-7. Bartonian, zones NP16 and NP17.

Genus ***Gnathophis*** Kaup, 1859

Type species

Myrophis heterognathos Bleeker, 1858, Recent.

Gnathophis meridies (Frizzell & Lamber, 1962)

Fig. 69O–P

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

Paraconger meridies – Nolf 1985: 43.
Gnathophis meridies – Nolf 2013: pl. 22.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 4 otoliths; GLS otolith comparative collection (3 specimens), MSC 37059.

Description

Outline primarily oval with noticeable angularity. Length of sagitta is greater than height; height/length ratios from approximately 60–72%. Margins smooth except for few small lobes on posterodorsal and posteroventral. Anterodorsal margin nearly straight; remaining dorsal and posterodorsal margins rounded. Anteroventral margin only slightly rounded; middle portion of ventral margin almost horizontal. Posteroventral margin rounded. Anterior more tapered than posterior. Prominent sulcus on inner face slants at approximately 45-degrees. Sulcus extends across approximately 75% of inner face. Dorsal and ventral margins of sulcus essentially parallel. Sulcus undivided, no defined ostium and cauda. Ostium does not quite reach anterior margin. Short, fairly wide ostial channel opens onto anterodorsal margin. Posterior of sulcus rounded. No depressed area above sulcus. Crista superior more pronounced than crista inferior. No ventral furrow. Outer face usually convex, thickest at center.

Remarks

Gnathophis meridies is an uncommon component at its type stratum and locality, the lower Eocene Bashi Formation (Wilcox Group) in Meridian, Mississippi. This taxon is also uncommon in the Claiborne Group in Alabama. Species of *Gnathophis* lack a depressed area above the sulcus, a feature that occurs on most congrid otoliths. Although one of the specimens we examined is a juvenile and two specimens are fairly worn, they possess the salient characteristics indicative of *Gnathophis meridies.*

Stratigraphic and geographic range in Alabama

Gnathophis meridies is known only from the "upper" Lisbon Formation at site ACh-7. Bartonian, zones NP16 and NP17.

Congridae indet.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 otolith; GLS otolith comparative collection (1 specimen).

Description

Singular specimen possesses characteristics of Congridae, including fairly prominent, undivided sulcus, and ostial channel. Depressed area above sulcus.

Remarks

The specimen could represent one of the congrids known from the Claiborne Group of Alabama, or it could represent an undescribed congrid. Unfortunately, the poor preservation limits any further study. The Lisbon Formation in Alabama preserves numerous other congrid species.

Stratigraphic and geographic range in Alabama

The specimen of Congridae indet. was found in the "upper" Lisbon Formation at site ACh-7. Bartonian, zones NP16 and NP17.

Order Holocentriformes (sensu Nelson *et al.* 2016)
Family Holocentridae Bonaparte, 1833

Genus ***Myripristis*** Cuvier, 1829

Type species

Myripristis jacobus Cuvier, 1829, Recent.

Myripristis sp.
Fig. 69Q–R

Weileria cajun – Frizzell & Lamber 1961: 20, figs 6, 18–19.
Myripristis creola – Stringer 1977: 88–91, pl. 1, fig. 1; 1986: 215.
Myripristis sp. – Stringer & Breard 1997: 565. — Breard & Stringer 1999: 135.
"genus *Myripristidarum*" *cajun* – Nolf & Stringer 2003: 4, pl. 4, figs 1a–2b.
"*Myripristina*" *cajun* – Nolf 2013: 80, pl. 172.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 2 otoliths; GLS otolith comparative collection (1 specimen), MSC 39047.

Description

Two ablated specimens indicate *Myripristis*. Sagittae distinct in having scutiform shape; greatest length across the dorsal margin. Height/length ratios around 70-75%. Some margins appear coarsely crenulated. Dorsal margin is almost straight; indications of dorsal and posterodorsal domes. Posteroventral margin slants inward, almost straight down to ventral margin. Ventral margin very short, broadly and evenly rounded. Anteroventral margin slants almost straight down from dorsal margin to ventral margin. Inner face slightly convex, marked by conspicuous dorsal sulcus. Sulcus located almost entirely on dorsal margin. Sulcus consists of ostium, anterior cauda, and posterior cauda. Sulcus unevenly excavated, filled with colliculum. Ostium about one-half length of cauda; ostium appears subelliptical in shape. Anterior and posterior cauda areas of approximately equal length. Prominent caudal keel. Anterior part of cauda is filled with colliculum; posterior part of cauda deeply excavated, little colliculum. Outer face irregularly convex, sculptured. Posterior of outer face of many specimens marked by linear pustules merging into incised radial lines.

Remarks

The sulcus of the otoliths, consisting of an ostium and anterior and posterior cauda, is a specialized myripristid feature (Frizzell & Lamber 1961). The *Myripristis* sp. otoliths from the Lisbon Formation in Alabama are very similar to middle and late Eocene otoliths found in Louisiana, Mississippi, and Texas (Stringer 1986, 2016; Breard & Stringer 1995, 1999; Stringer & Breard 1997; Nolf & Stringer 2003).

Stratigraphic and geographic range in Alabama

The two *Myripristis* sp. specimens were recovered from the "upper" Lisbon Formation at site ACh-7. Bartonian, zones NP16 and NP17.

Order Trachichthyiformes (sensu Nelson *et al.* 2016)
Family Diretmidae Gill, 1893

Genus ***Diretmus*** Johnson, 1864

Type species

Diretmus argenteus Johnson, 1864, Recent.

Diretmus*? cf. *D. serratus (Müller, 1999)
Fig. 70A–B

"genus *Caproidarum*" *serratus* Müller, 1999: 130, pl. 29, figs 18–21.

"*Diretmida*" *serrata* – Nolf 2013: 78, pl. 163.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 otolith; MSC 42212.

Description

Sagitta tall (i.e., height twice its length), dorsal and ventral both tapered. Margins appear fairly smooth; evidence of several prominent lobes dorsally. Anterior margin short, nearly vertical, characterized by opening of sulcus. Anterodorsal margin fairly steep, outwardly curved, indications of at least three prominent lobes. Dorsal margin pointed, short. Posterodorsal margin quite steep, incurved. Posterior short, slightly rounded, nearly vertical. Steep posteroventral margin slants from posterior to ventral. Ventral margin short with rounded point. Anteroventral margin steep, relatively straight to slightly outwardly curved. Prominent sulcus extends across nearly 90% of otolith length.

Remarks

Only one ablated sagitta was recovered, but salient characteristics are indicative of to *Diretmus* cf. *D. serratus* (Müller, 1999). The specimen is quite unique in its shape, being uncommonly tall for the otoliths of the Gulf Coast Paleogene (sensu Smale *et al.* 1995). Details of the sulcus are not preserved due to erosion. However, *D. serratus* otoliths from Claibornian strata in Texas indicate that the ostium is very small, and the cauda is approximately four times longer than the ostium. The cauda is fairly wide, and its margins are almost parallel. The posterior of the cauda is rounded. There is a depressed area well above the cauda. The other face is slightly convex and highly sculptured.

Müller (1999) first described this species from the middle Eocene Piney Point Formation (Pamunkey Group) in Hanover County, Virginia. The taxon was originally assigned to the Caproidae, but Nolf (2013) placed it within the Diretmidae. In all known occurrences (Alabama, Texas, Virginia), the species is quite rare within vertebrate assemblages.

Stratigraphic and geographic range in Alabama

Only one specimen of this species was found in the study. It was derived from the "upper" Lisbon Formation at site ACh-7. Bartonian, zones NP16 and NP17.

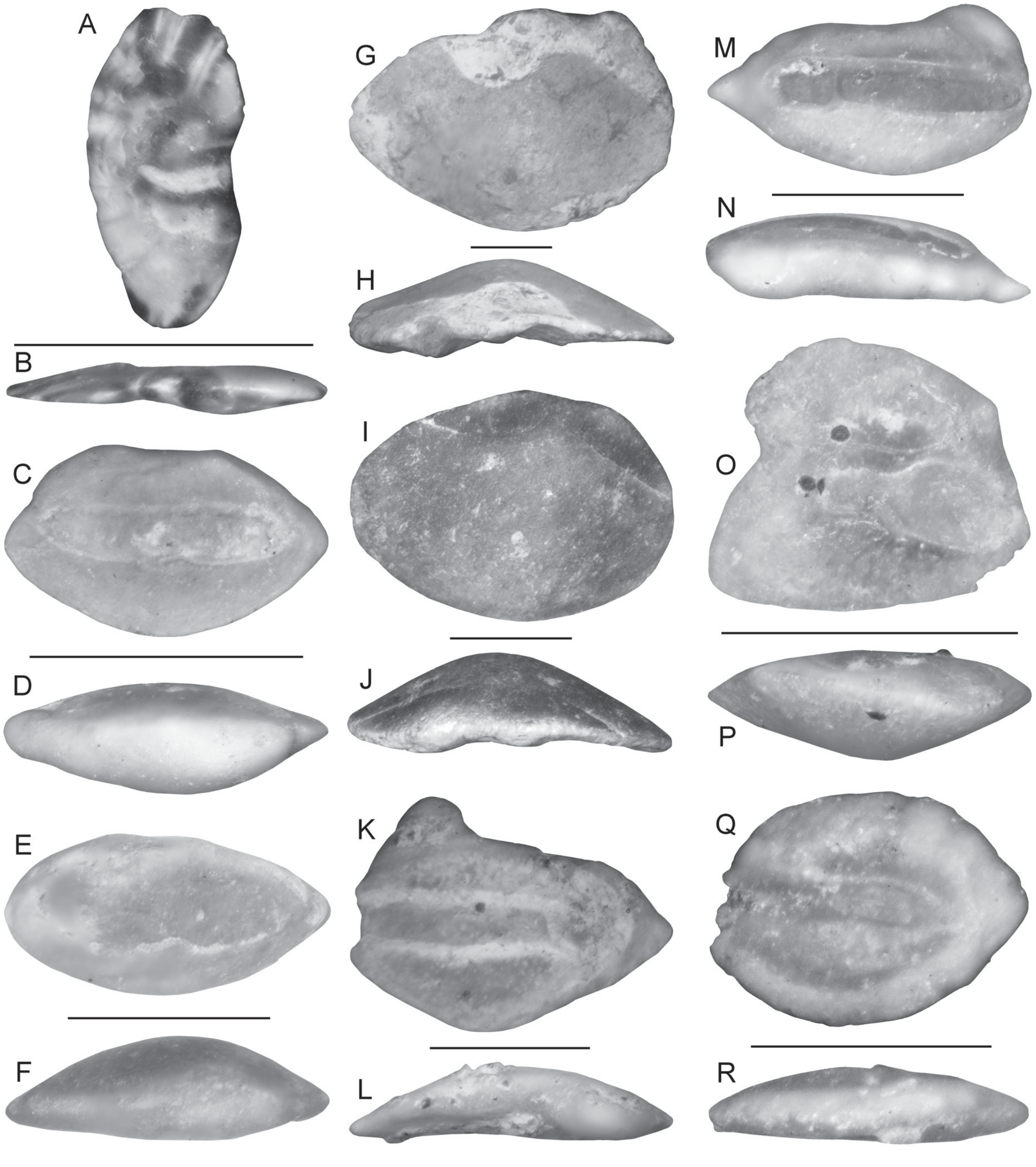


Fig. 70. Claiborne Group, "upper" Lisbon Formation, otoliths. **A–B**. *Diretmus*? cf. *D. serratus* (Müller, 1999), MSC 42212. **A**. Inner face (left sagitta). **B**. Anterior view. — **C–D**. *Preophidion meyeri* (Koken, 1888), MSC 39055. **C**. Inner face (right sagitta). **D**. Dorsal view. — **E–F**. *Preophidion* cf. *P. petropolis* Frizzell & Dante, 1965, MSC 42193. **E**. Inner face (right sagitta). **F**. Dorsal view. — **G–H**. *Signata stenzeli* Frizzell & Dante, 1965, MSC 39051. **G**. Inner face (left sagitta). **H**. Dorsal view. — **I–J**. *Signata nicoli* Frizzell & Dante, 1965, MSC 39046. **I**. Inner face (left sagitta). **J**. Dorsal view. — **K–L**. *Hoplobrotula melrosensis* (Frizzell & Dante, 1965), MSC 37059.3. **K**. Inner face (right sagitta). **L**. Dorsal view. — **M–N**. *Lepophidium? mucronata* (Koken, 1888), MSC 39054. **M**. Inner face (left sagitta). **N**. Dorsal view. — **O–P**. Gobiidae Cuvier, 1816, indet. MSC 39045. **O**. Inner face (left sagitta). **P**. Dorsal view. — **Q–R**. Bothidae Smitt, 1892, indet. MSC 42235. **Q**. Inner face (right sagitta). **R**. Dorsal view. Scale bars: A–P = 2 mm; Q–R = 1 mm.

Order Ophidiiformes (sensu Nelson *et al.* 2016)
Family Ophidiidae Rafinesque, 1810

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

Type species

Preophidion petropolis Frizzell & Dante, 1965, middle Eocene.

Preophidion meyeri (Koken, 1888)
Fig. 70C–D

Otolithus (*Gadidarum*) *meyeri* Koken, 1888: 289–290, pl. 18, figs 8–9.

Otolithus (*Gadidarum*) *meyeri* – Campbell 1929a: 272–273, pl. 29, figs 8–9.
Preophidion meyeri – Frizzell & Dante 1965: 713, 715.
"genus *Lepophidiinorum*" *meyeri* – Nolf 1980: 111, pl. 18, fig. 16; 1985: 66, fig. 51o.
Symmetrosulcus meyeri – Schwarzhans 1981: 75, 78, pl. 20.
"genus *Neobythitinarum*" *meyeri* – Breard & Stringer 1995: 80. — Müller 1999: 126. — Nolf 2003: 5, pl. 1, fig. 9. — Nolf & Stringer 2003: 4–5, pl. 3, figs 3–10.
"*Neobythitina*" *meyeri* – Nolf 2013: 68, pl. 125.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 131 otoliths; MSC 7303.1, MSC 7303.2, MSC 7303.4, MSC 7303.5, MSC 35076.2, MSC 37236.1, MSC 37236, MSC 39055, GLS otolith comparative collection (104 specimens), WSU CC 466.1, WSU CC 466.2, WSU CC 466.3, WSU CC 466.4, WSU CC 467.1, WSU CC 467.2, WSU CC 467.3, WSU CC 467.4, WSU CC 468.1, WSU CC 468.2, WSU CC 468.3, WSU CC 468.4, WSU CC 469.1, WSU CC 469.2, WSU CC 469.3, WSU CC 476.1, WSU CC 476.2, WSU CC 476.3, WSU CC 476.4.

Description

Sagittae biconvex, with oblong to elliptic shape (sensu Smale *et al.* 1995); height/length ratio from approximately 44–53%. Inner face smooth, convex. Adult specimens of small to medium size (rarely exceeding 6 mm). Margins of adult and juvenile specimens smooth. Anterior margin bluntly pointed, anterodorsal margin long, slightly arched. Dorsal margin short, almost horizontal. Posterodorsal margin very slightly arched, longer than anterodorsal margin. Posterior margin thinly pointed. Ventral margin evenly and broadly rounded. Lightly impressed, distinct sulcus located on inner face. Sulcus divided, completely enclosed, marked by incised lines. Ostium is about equal in length to cauda. Sides of ostium nearly parallel. Anterior end of ostium sharply pointed, almost touches anterodorsal margin. Ostium filled with colliculum, not excavated. Slight ventral constriction of ostium near junction (incised line) with cauda. Cauda is approximately same width as ostium. Sides of cauda nearly parallel but for slight ventral constriction near intersection with the ostium. Cauda/ostium intersection marked by thin, slightly inclined, incised line. The cauda filled with colliculum, not excavated. Posterior end of cauda bluntly rounded, separated from posterior margin by distinct, narrow border. Shallow, elongated, irregular depressed area centered above sulcus. Crista superior weakly developed; crista inferior lacking or very weakly developed. Ventral furrow usually absent. Outer face convex, dorsal portion more strongly convex. Outer face strongly sculptured to undulating. Rounded anterodorsal dome visible.

Remarks

This extinct species of cusk-eel was widely distributed and quite abundant within the US Gulf Coast during the Eocene. It has been reported from Alabama, Georgia, Louisiana, Mississippi, and Texas

(Frizzell & Dante 1965; Breard & Stringer 1995; Stringer & Miller 2001; Green & Stringer 2002; Nolf & Stringer 2003; Stringer *et al.* 2013). In Alabama, *P. meyeri* is the only species known from all three of the Claiborne Group formations, and it is the most abundant species we encountered. At one Lisbon Formation site, the species represents almost 50% of the total otolith specimens in the sample.

Stratigraphic and geographic range in Alabama

Specimens were recovered from the lower Tallahatta Formation at site ADl-1, the "upper" Lisbon Formation at site ACh-8, and the Gosport Sand at site ACl-4. Upper Ypresian to middle Bartonian, zones NP14 to NP17.

Preophidion cf. ***P. petropolis*** Frizzell & Dante, 1965

Fig. 70E–F

Preophidion petropolis Dante & Frizzell in Frizzell & Dante, 1965: 713–714, pl. 86, figs 34, 39.

"genus aff. *Sirembo*" *petropolis* – Nolf 1980: 137; 1985: 66.
"genus Sirembinorum" *petropolis* – Müller 1999: 124.
"aff. *Sitrembo*" *petropolis* – Nolf 2013: 66, pl. 128.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 3 otoliths; MSC 7303.3, MSC 35076.1, MSC 39056.

Description

Sagittae oblong to elliptic in shape (sensu Smale *et al.* 1995), biconvex. Sagittae elongated with height/length ratios approximately 55%. Greatest length of adult specimens around 3.5 mm. Margins primarily smooth. Anterior margin bluntly pointed; anterodorsal margin long, arched. Dorsal margin short, slightly arched. Posterodorsal margin very slightly arched, longer than anterodorsal margin. Posterior margin tapered, pointed. Ventral margin evenly and broadly rounded. Inner face smooth, convex, with lightly impressed, distinct sulcus. Sulcus divided, completely enclosed, marked by incised lines. Length of ostium noticeably shorter than cauda. Anterior end of ostium sharply pointed, almost touches anterodorsal margin. Ostium filled with colliculum, not excavated. Slight ventral constriction of ostium near junction (incised line) with cauda. Cauda also slightly wider than ostium. Ventral margin of cauda more rounded than corresponding ventral margin of ostium. Cauda not excavated, filled with colliculum. Posterior end of cauda rounded, somewhat tapered, separated from posterior margin by distinct, narrow border. Cristae lacking or very weakly developed. Ventral furrow usually absent. Outer face convex, with dorsal portion more strongly convex. Outer face undulating to strongly sculptured.

Remarks

The most conspicuous differences between *Preophidion petropolis* and *P. meyeri*, a very abundant taxon in the Alabama Claiborne Group, is the dorsal margin and the intersection of the ostium and cauda. The dorsal margin of *P. petropolis* tends to be more broadly rounded, and the dorsal domes are not as high or prominent. The anterodorsal dome of *P. meyeri* is typically more pronounced, which affects the dorsal outline. The intersection of the cauda and ostium of *P. petropolis* is sharply inclined toward the anterior (approximately 45-degrees) and extends significantly over the posterior of the ostium. In contrast, the intersection on *P. meyeri* is not nearly as inclined (less than half as much as *Preophidion petropolis*).

Frizzell & Dante (1965) noted abundant *P. petropolis* from the Claibornian of Texas, especially at the Stone City Locality, but they did not list the species from Alabama. However, those authors referenced a collection of otoliths from the Gosport Sand at site ACl-4 in Alabama that contained *P. petropolis.* Frizzell & Dante (1965) stated that this species was not found in the Lisbon Formation in Alabama, but we do not know how extensive their collections were. Although we could not corroborate the presence of *P. petropolis* in the Gosport Sand, our sample shows that, while not abundant, this species does occur in the Lisbon Formation in Alabama.

Nolf (1980, 1985, 2013) assigned *P. petropolis* to the ophidiid genus *Sirembo*, and the otoliths of these taxa exhibit some similarities. Our specimens compare well to fossil *Preophidion* as described by Frizzell & Dante (1965), Stinton (1977), Schwarzhans & Bratishko (2011), and Schwarzhans (2012). We retain the specimens within *Preophidion*, but a larger sample size is needed to strengthen our specific identification.

Stratigraphic and geographic range in Alabama

Specimens were recovered from the "upper" Lisbon Formation at sites ACh-8 and ACl-16. Bartonian, zones NP16 and NP17.

Genus ***Signata*** Frizzell & Dante, 1965

Type species

Signata stenzeli Dante & Frizzell in Frizzell & Dante, 1965, middle Eocene.

Signata stenzeli Frizzell & Dante, 1965

Fig. 70G–H

Signata stenzeli Dante & Frizzell in Frizzell & Dante, 1965: 709–710, pl. 88, figs 12, 16–17.

"genus *Ophidiidarum*" *stenzeli* – Nolf 1980: 138, pl. 20, fig. 7.
"*Ophidiida*" *stenzeli* – Nolf 2013: 65, pl. 124.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 6 otoliths; GLS otolith comparative collection (5 specimens), MSC 39051.

Description

Sagittae primarily with ovate shape, height/length ratios tend around 65–70%. Specimens with smooth margins. Anterior margin broadly rounded. Anterodorsal slope fairly straight to slightly incurved, steep. Dorsal margin quite short. Posterodorsal slope slightly outcurved, longer, less inclined than anterodorsal slope. Posterior sharply rounded. Ventral margin broadly and nearly evenly rounded. Smooth inner face strongly convex or inflated near vertical midline, slopes toward margins. Extremely wide, undivided, long sulcus (approximately 95% of otolith length). Very fine incised line marks sulcus. Sulcus extending essentially from anterior margin to very near posterior margin. Very small ostial channel opens on anterior margin (seen on well-preserved specimens). Dorsal margin of sulcus well separated from dorsal margin; ventral margin of sulcus closer to ventral margin. Dorsal margin of sulcus strongly flexed upward near vertical midline of otolith. Ventral margin of sulcus also flexed upward near vertical midline, not as strongly as dorsal margin. Cristae not developed; no depressed area observed. Ventral furrow absent. Outer face shallow, irregularly concave, commonly sculptured with smooth bosses and rugosities, especially in dorsal area.

Remarks

Extensive studies of ophidiid otoliths indicate that *Signata stenzeli* does not correspond to any living species. The genus therefore is fossil-based, representing an extinct form. The genus appears to be most common in the Eocene (Claiborne Group) of the US Gulf Coastal Plain.

Stratigraphic and geographic range in Alabama

Signata stenzeli is known from the "upper" Lisbon Formation at sites ACh-8 and AMo-4. Bartonian, zones NP16 and NP17.

Signata nicoli Frizzell & Dante, 1965

Fig. 70I–J

Signata nicoli Dante & Frizzell in Frizzell & Dante, 1965: 709, pl. 88, figs 3–4, 21, 35.

"genus *Ophidiidarum*" *nicoli* – Nolf 1980: 138, pl. 20, fig. 7.
"*Ophidiida*" *nicoli* – Nolf 2013: 65, pl. 124.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 otolith; MSC 39046.

Description

Sagittae primarily of ovate shape; height/length ratio around 70%. Smooth margins. Anterior margin broadly rounded. Anterodorsal slope shorter and noticeably steeper than posterodorsal slope. Dorsal margin quite short, almost straight. Posterodorsal slope incurved, longer than anterodorsal slope. Posterior sharply rounded. Ventral margin broadly rounded, but posteroventral slope is slightly steeper. Smooth inner face moderately convex or inflated, slopes toward the margins. Extremely wide, undivided, long (approximately 98% of the otolith length) sulcus. Very fine incised line marks sulcus. Sulcus extending essentially from anterior margin to very near posterior margin. Very small ostial channel opens on anterior margin (visible on well-preserved specimens). Dorsal margin of sulcus closer to dorsal margin than ventral margin of sulcus is to ventral margin. Dorsal margin of sulcus noticeably flexed upward anterior to the vertical midline of the otolith. Ventral margin of sulcus slightly curved or sinuous. Cristae not developed; no depressed area observed. Ventral furrow absent. Outer face slightly and irregularly concave, commonly sculptured with smooth bosses and rugosities, especially in dorsal area.

Remarks

The sagitta of *Signata nicoli* is very similar to *S. stenzeli*, but there are some distinct differences. The flexure on the dorsal margin of the sulcus of *S. nicoli* is not nearly as pronounced as on *S. stenzeli*, and the ventral margin of *S. nicoli* has little or no flexure upward. Additionally, the posterodorsal slope on *S. nicoli* is incurved rather than outcurved as on *S. stenzeli.*

Stratigraphic and geographic range in Alabama

The singular specimen was recovered from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Genus ***Hoplobrotula*** Gill, 1863

Type species

Brotula armata Temminck & Schlegel, 1846, Recent.

Hoplobrotula melrosensis (Frizzell & Dante, 1965)

Fig. 70K–L

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

Hoplobrotula melrosensis – Nolf 1980: 103, pl. 20, fig. 6; 1985: 66; 2013: 67, pl. 132.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 otolith; MSC 37059.3.

Description

Sagittae primarily oval in shape but with prominent anterodorsal dome. Height/length ratio is approximately 55%, exclusive of anterodorsal dome. Margins mainly smooth. Anterior margin fairly steep, somewhat rounded. Anterodorsal slope quite steep, depending upon development of anterodorsal dome. Dorsal margin almost straight to slightly inclined toward posterior. Posterodorsal slope gently inclined. Posterior rounded but tapered. Ventral margin broadly rounded, but posteroventral slope slightly steeper. Smooth inner face slightly convex. Sulcus fairly narrow, long (approximately 90% of the otolith's length), clearly divided into ostium and cauda. Sulcus not deeply excavated, edges slightly incised. Sulcus extending essentially from anterior margin to near the posterior margin (distinct space between posterior of sulcus and posterior margin). Dorsal margin of sulcus essentially straight, whereas ventral margin slightly inflated toward ventral in the ostium, constricted at ostium/cauda intersection. Ostium approximately three times longer than cauda. Cauda approximately oval in shape, much smaller in length than ostium. Cristae not developed, no depressed area observed. Ventral furrow weakly developed in anteroventral and mid-ventral. Outer face slightly and irregularly concave.

Remarks

This species is very common in the Claibornian of Texas, especially at the Stone City locality on the Brazos River near Bryan, Texas (Frizzell & Dante 1965) and the Cane River site near Natchitoches, Louisiana (Stringer & Breard 1997; reported as *Hoplobrotula* sp.). An excellent figure of the species is found in Nolf (1980: pl. 20, 6a–6b). The species has been reported as being strongly facies controlled, which may account for its rarity in the Claibornian strata of Alabama. In the original description of this species, Frizzell & Dante (1965) noted that it was common at some levels at the classic middle Eocene (Claiborne Group) Stone City Bluffs on the Brazos River, Burleson County, Texas, USA, but was replaced by an ecological analogue in other levels, typically of varying composition. The complexity of the Stone City Bluffs with cyclic sedimentation, rhythmic alteration of varying grain sizes, and storm deposits has been detailed in Flis *et al.* (2017). Ophidiids are strictly marine (Nelson *et al.* 2016), variations in environmental conditions will affect their distribution. Furthermore, Snyder & Burgess (2016) have pointed out that many of the cusk-eels (ophidiids) are distributed in the marine waters of Florida according to depth preferences. These depth preferences serve to sort out the ophidiids over the continental shelf and the slope edge, which often correspond to different sediment types or facies.

Stratigraphic and geographic range in Alabama

The specimen examined came from the "upper" Lisbon Formation at Locality ACh-7. Bartonian, zones NP16 and NP17.

Genus ***Lepophidium*** Gill, 1895

Type species

Lepophidium profundorum Gill, 1895, Recent.

Lepophidium*? *mucronata (Koken, 1888)

Fig. 70M–N

Otolithus (*Gadidarum*) *mucronatus* Koken, 1888: 290, 292, pl. 17, figs 10–11.

Otolithus (*Gadidarum*) *mucronatus* – Posthumus 1924: 13.
Bauzaia mucronata – Frizzell & Dante 1965: 712–713, pl. 86, figs 43–44.
"genus *Lepophidiinorum*" *mucronatus* – Nolf 1980: 111. — Breard & Stringer 1999: 135. — Müller 1999: 111, pl. 26, figs 14–20. — Nolf 2003: 4, pl. 1, figs 11–13.
"*Lepophidiinus*" *mucronatus* – Nolf 2013: 65, pl. 125.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 9 otoliths; GLS otolith comparative collection (6 specimens), MSC 39054, WSU CC 471.2, WSU CC 471.3.

Description

Sagittae primarily of oval shape, with prominent anterodorsal dome and sharply pointed posterior. Height/length ratios tending to 38–45%. Small, juvenile specimens exhibit very slight lobed margins; larger and adult specimens with smooth margins. Anterior margin fairly evenly rounded. Anterodorsal dome typically becoming more prominent on the larger specimens. Dorsal margin often slightly incurved between dome and posterodorsal slope. Posterodorsal slope straight and gentle. Posterior attenuated into well-developed tip or projection (except for very small specimens). Ventral margin broadly, nearly evenly rounded. Inner face smooth, only very slightly convex. Divided sulcus quite long, filled with colliculum, extending almost entire length of sagitta. Ostium usually about four times longer than cauda, widths approximately equal. Dorsal and ventral margins of ostium straight, parallel. Anterior portion of ostium rounded, almost touches anterior margin. Ostium separated from cauda by straight (sometimes slanted) incised line. Short cauda about same width as ostium, approximately rectangular in shape. Posterior of cauda rounded, almost touches the posterodorsal slope. Distinct crista superior, shallow but distinct, irregularly shaped depressed area above ostium. Ventral furrow absent to poorly developed. Outer face irregularly convex, commonly sculptured.

Remarks

Lepophidium? *mucronata* is known from several Eocene (Claibornian) localities in Texas and Louisiana. The type stratum and locality for the species is the Lisbon Formation at site AMo-4 in Monroe County, Alabama.

Stratigraphic and geographic range in Alabama

This species was recovered from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Lepophidium*? *lamberi Frizzell & Dante, 1965

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

Bauzaia lamberi – Stringer & Breard 1997: 565.
"genus *Lepophidiinorum*" *lamberi* – Müller 1999: 110. — Breard & Stringer 1999: 135.
"*Lepophidiinus*" *lamberi* – Nolf 2013: 65, pl. 125.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 5 otoliths; GLS otolith comparative collection (4 specimens); MSC 37059.9.

Description

Sagittae primarily oval in shape, with prominent anterodorsal dome, pointed posterior; height/length ratio between 60–68%. Adult specimens with smooth margins. Anterior margin short, somewhat truncated. Pronounced anterodorsal dome, nearly vertical, slopes markedly away from plane of inner face. Anterodorsal margin fairly straight, slants towards dorsal margin. Dorsal margin nearly straight. Posterodorsal slope fairly short, truncated by posterior margin. Posterior margin very short, consisting of pointed tip. Ventral margin broadly, nearly evenly, rounded. Inner face smooth, evenly convex. Prominent sulcus divided, quite long, filled with colliculum, extending almost to posterodorsal slope. Ostium approximately three times longer than cauda, not as wide as the cauda. Dorsal and ventral margins of ostium nearly straight, parallel. Anterior portion of ostium appears to open onto anterior margin. Ostium separated from cauda by straight (sometimes slanted), incised line. Cauda short, wider than ostium due to ventral margin of cauda being inflated. Posterior of cauda rounded, located near posterodorsal slope. Low, narrow crista superior extends length of sulcus. Ventral furrow visible on well-preserved specimens, located very near ventral margin. Outer face slightly concave, irregularly sculptured. Coarse to fine bosses often occur on lower half of outer face.

Remarks

This species is known from several Eocene (Claibornian) localities in Texas and Louisiana (Frizzell & Dante 1965; Stringer & Breard 1997), but our specimens represent the first records of the taxon in Alabama.

Stratigraphic and geographic range in Alabama

The four specimens were recovered from the “upper” Lisbon Formation at site ACh-7. Bartonian, zones NP16 and NP17.

Ophidiidae indet.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 11 otoliths; GLS otolith comparative collection (10 specimens), MSC 39042.12.

Description

Several characteristics point to the family Ophidiidae for these specimens. These features include the sulcus, ostium, cauda, and general shape. Unfortunately, the preservation of the specimens prohibits any further, more specific identification.

Remarks

These specimens could belong to an ophidiid species already described from the Claiborne Group of Alabama or could represent a different species. Preservation does not allow this determination.

Stratigraphic and geographic range in Alabama

All of the specimens of Ophidiidae indet. were derived from the “upper” Lisbon Formation at site ACh-7 except for one specimen (MSC 39042.12) which was collected from the Gosport Sand at site AMo-4. Bartonian, zones NP16 and NP17.

Order Gobiiformes (sensu Nelson *et al.* 2016)
Family Gobiidae Cuvier, 1816

Gobiidae indet.
Fig. 70O–P

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 otolith; MSC 39045.

Description

Small otolith measuring 2.1 mm in length, roughly trapezoidal in shape. Inner face primarily smooth (except for depression at dorsal area), convex. Margins smooth, sharp in transversal view. Anterior margin ranging from almost straight to slightly incurved. Anterodorsal unevenly rounded. Dorsal margin only slightly rounded, subparallel with ventral margin. Posterodorsal is characterized by small rounded projection. Posterior incurved. Ventral margin almost straight, horizontal. Well-defined, divided sulcus slants slightly from posterodorsal to anteroventral. Ostium about twice as long and twice as wide as cauda. The ostium oval in shape, much more excavated than cauda. Ostium almost touches anterior margin. Posterior of cauda rounded. Ridge-like crista superior located above sulcus. Prominent, deeply depressed area in dorsal area touches crista superior. Crista inferior is small, ridge-like structure beneath cauda and posterior of ostium. Outer face smooth, convex, thickest at approximately center but thinning towards margins.

Remarks

The oldest known possible gobiid otolith occurred in middle Ypresian strata of India (Nolf *et al.* 2006). Gobiid otoliths are quite rare in all known assemblages until the late Eocene. Nolf & Stringer (2003) noted 57 specimens of gobiids ("genus *Gobiidarum*" *vetustus*) from the upper Eocene Yazoo Clay of Louisiana. We believe that the Lisbon Formation gobiid represents a different species from the Yazoo Clay taxon because of the significant differences between the shape of the otolith sulci, but a larger Lisbon sample is needed to corroborate our observation.

Stratigraphic and geographic range in Alabama

The single gobiid specimen was recovered from the "upper" Lisbon Formation at site ACh-7. Bartonian, zones NP16 and NP17.

Order Pleuronectiformes (sensu Nelson *et al.* 2016)
Family Bothidae Smitt, 1892

Bothidae indet.
Fig. 70Q–R

?"genus *Citharidarum*" *sulcatus* – Nolf & Stringer 2003: 4, pl. 8, figs 10–11b.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 1 otolith; MSC 42235.

Description

Ovate specimen very small, measuring approximately 2.0 mm in length. Inner face flat to very slightly convex. Margins smooth. Anterior margin bluntly rounded, anterodorsal also slightly rounded. Dorsal slightly slanted, almost straight. Posterodorsal tapered but rounded. Ventral margin regularly curved.

Divided sulcus having approximately parallel margins. Sulcus extends from anterior margin about 75% of otolith length. Sulcus may be very slightly inclined toward dorsal. Ostium and cauda difficult to determine but appear to be about equal in length (ostium possibly slightly longer). Width of ostium and cauda also approximately equal. Crista superior located above sulcus. Longitudinal depressed areas occur just above and below sulcus. Poorly defined depressed dorsal area. Ventral furrow appears to be present. Outer face slightly irregular, ranging from almost flat to slightly convex.

Remarks

The Lisbon Formation specimen exhibits some similarity to "genus *Citharidarum*" *hoffmani* from the upper Eocene Yazoo Clay of Louisiana (Nolf & Stringer 2003), but additional material from the Lisbon Formation is needed for more meaningful comparisons.

Stratigraphic and geographic range in Alabama

The one bothid specimen was found in the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Order Perciformes (sensu Nelson *et al.* 2016)
Family Lactariidae Boulenger, 1904

Genus ***Lactarius*** Valenciennes, 1833

Type species

Lactarius delicatulus Valenciennes, 1833 in Cuvier & Valenciennes 1833, Recent.

Lactarius kokeni Frizzell & Dante, 1965
Fig. 71A–B

Brazosiella kokeni Dante & Frizzell in Frizzell & Dante, 1965: 700–701, pl. 87, figs 25, 30, 32–34, 36.

Lactarius kokeni – Nolf 1985: 84; 2013: 101, pl. 252. — Breard & Stringer 1999: 135. — Müller 1999: 151–152, pl. 32, figs 12–16.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 48 otoliths; GLS otolith comparative collection (47 specimens), MSC 39058.

Description

Shape of sagittae primarily elliptical (sensu Smale *et al.* 1995); height/length ratios moderately high at 68–76%. Small, juvenile specimens with finely scalloped margins; larger and adult specimens with smooth margins. Prominent, blunt rostrum with small antirostrum and excisura characterize anterior margin. Anterodorsal slope straight, fairly short. Dorsal margin nearly straight, longer than anterodorsal and posterodorsal slopes. Posterodorsal slope straight and gentle. Posterior broadly rounded on small specimens, narrowly rounded for larger specimens. Ventral margin broadly and unevenly curved. Inner face slightly convex, with prominent sulcus and depressed area above sulcus. Sulcus divided (heterosulcoid type), quite long (about 90% of total otolith length), well excavated. Ostium almost equal in length to cauda, but with markedly greater width. Ostium has elongated subquadrate shape, slants upward slightly. Anterior portion of ostium opens onto anterior margin, small antirostrum present. Cauda, narrower than ostium, has subparallel margins. Posterior of cauda very slightly flexed downward. End

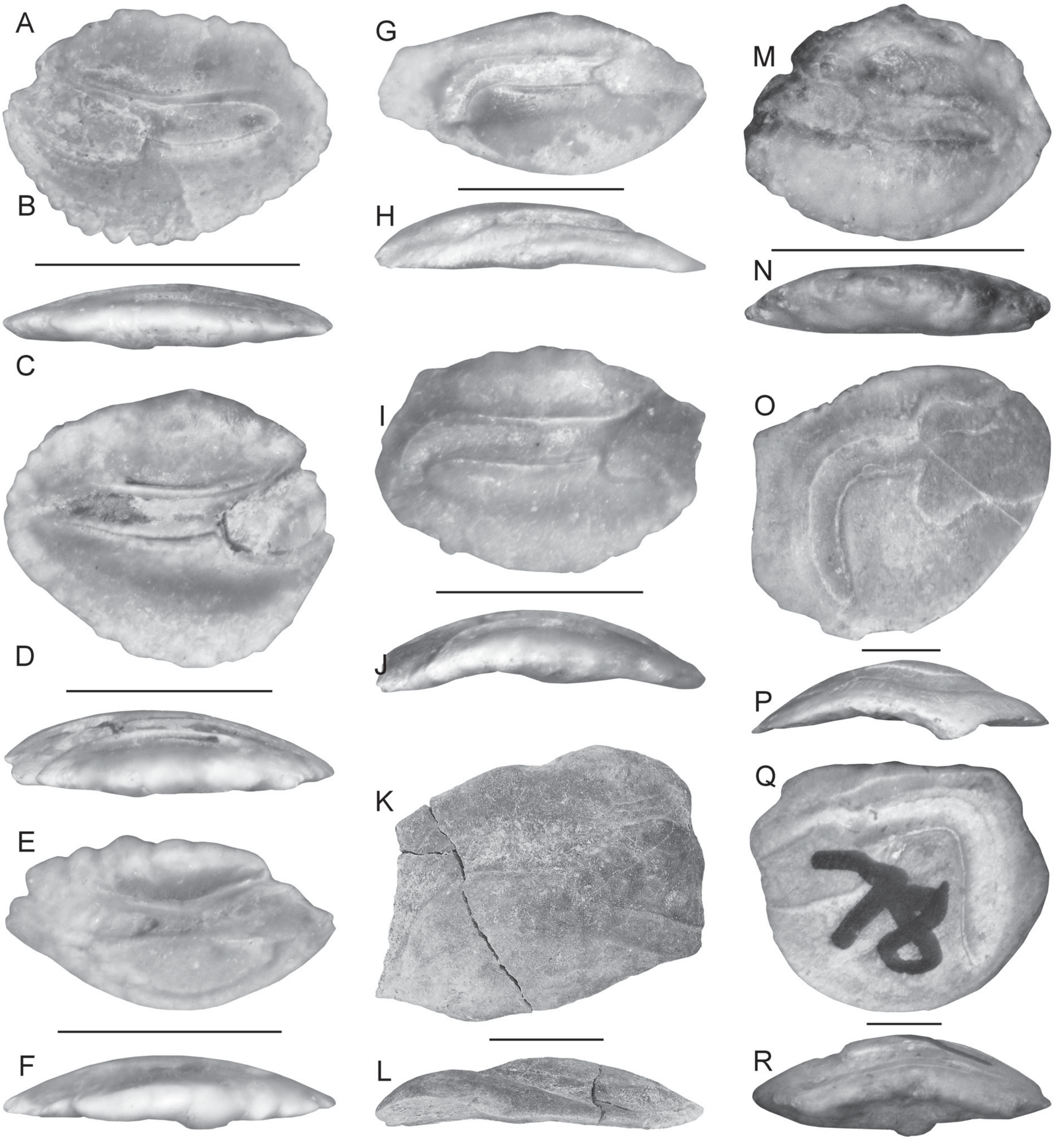


Fig. 71. Claiborne Group, "upper" Lisbon Formation, otoliths. **A–B**. *Lactarius kokeni* Frizzell & Dante, 1965, MSC 39058. **A**. Inner face (right sagitta). **B**. Dorsal view. —**C–D**. *Lactarius amplus* Pomerol, 1973, MSC 39059. **C**. Inner face (left sagitta). **D**. Dorsal view. — **E–F**. *Malacanthus? sulcatus* (Koken, 1888), MSC 39061. **E**. Inner face (left sagitta, cauda worn). **F**. Dorsal view. — **G–H**. *Orthopristis burlesonis* Frizzell & Dante, 1965, MSC 39060. **G**. Inner face (left sagitta). **H**. Dorsal view. — **I–J**. *Haemulon? obliquus* (Müller, 1999), MSC 39062. **I**. Inner face (left sagitta). **J**. Dorsal view. — **K–L**. *Anisotremus*? sp., MSC 42236. **K**. Inner face (right sagitta). **L**. Dorsal view. — **M–N**. Percoidei, indet. 1, MSC 39063. **M**. Inner face (right sagitta). **N**. Dorsal view. — **O–P**. *Sciaena intermedius* (Koken, 1888), MSC 39050. **O**. Inner face (left sagitta). **P**. Dorsal view. — **Q–R**. *Jeftichia copelandi* Frizzell & Dante, 1965, MSC 39053. **Q**. Inner face (right sagitta, worn, especially anterior margin). **R**. Dorsal view. Scale bars: A–J, O–P = 2 mm; K–L, Q–R = 5 mm; M–N = 1 mm.

of cauda rounded, well separated from posterior margin. Distinct crista superior occurs below strongly depressed area, which is located above most of ostium and cauda. Ventral furrow absent or poorly developed. Outer face irregularly and slightly convex, becoming concave near anterior margin.

Remarks

Lactarius kokeni is common in many of the formations of Claibornian age occurring in Texas and Louisiana (Frizzell & Dante 1965; Stringer & Breard 1997; Breard & Stringer 1999). The species has been previously reported from the Lisbon Formation in Monroe and Choctaw counties in Alabama (Frizzell & Dante 1965). Our analysis showed that *L. kokeni* is one of the most common species in the Claiborne Group of Alabama, with 48 identified specimens available to us for study.

Stratigraphic and geographic range in Alabama

Lactarius kokeni specimens were found in the "upper" Lisbon Formation at site ACh-8 and the Gosport Sand at site ACl-4. Bartonian, zones NP16 and NP17.

Lactarius amplus Pomerol, 1973

Fig. 71C–D

Brazosiella moseleyi Dante & Frizzell in Frizzell & Dante, 1965: 701–702, pl. 87, figs 21, 27.

Lactarius amplus Pomerol 1973: 122, fig. 8. — Nolf 1974: 150, pl. 1, fig. 16; 1985: 84; 2013: 101, pl. 252. — Stinton 1978: 181–182, pl. 12, figs 11–16. — Müller 1999: 152–153, pl. 32, figs 6–11.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 34 otoliths; GLS otolith comparative collection (31 specimens), MSC 39059, WSU CC 474.3, WSU CC 475.1.

Description

Sagittae primarily oval in shape (sensu Smale *et al.* 1995); height/length ratios 82–92%. Large specimens tending to somewhat angular on dorsal margins. Small, juvenile specimens exhibit finely crenulated margins; larger and adult specimens generally have smoother margins with some lobes. Anterior margin characterized by fairly prominent, blunt rostrum with a small antirostrum and excisura. Anterodorsal slope fairly steep, varies from almost straight to slightly rounded. Dorsal margin tending to rounded, may also slope toward posterior. Posterodorsal slope tending to fairly steep. Posterior margin short, usually slightly rounded and steep. Ventral margin broadly and mainly evenly curved. Inner face convex, with prominent sulcus and fairly broad, elliptical-shaped, depressed area above sulcus. Sulcus divided (heterosulcoid type), quite long (about 90% of total otolith length), fairly well excavated. Ostium approximately 60% of cauda length, but of greater width. Ostium has elongated subquadrate shape, slants upward slightly. Anterior portion of ostium opens onto anterior margin; small antirostrum is present. Cauda narrower than ostium, margins almost parallel. Posterior of cauda very slightly flexed downward. End of cauda tapering but rounded, well separated from posterior margin. Distinct crista superior located below depressed area, extending across much of ostium and cauda. Ventral furrow generally poorly developed. Outer face irregularly and slightly concave.

Remarks

Nolf was one of the first to recognize that the fossil genus *Brazosiella* was actually the Recent genus *Lactarius* (Nolf 1974, 1980, 1985), and Müller (1999) presented evidence that *Brazosiella moseleyi* should be referred to as *Lactarius amplus*. There has been considerable debate about *Brazosiella mosleyi* since its original description by Frizzell & Dante (1965). The original description of the species was based on a suite of specimens rather than the holotype, which was broken and worn, and many of the specimens in the suite were juveniles. Additionally, the holotype was not figured in the original description. Rather, the paratype was figured showing the inner and outer faces, and the image of the inner face was indistinct. Therefore, it has been difficult to evaluate the validity of the species (Nolf 1985, 2013). A careful study of specimens of *Lactarius* from various middle Eocene sites does seem to indicate that there is another distinct species in addition to *L. kokeni* (see above). Based on Müller's (1999) findings, we utilize the species *L. amplus* in this study. Interestingly *L. amplus* shares many features with the Recent species *L. lactarius* (see Nolf 1985: fig. 63d).

Müller (1999) described *L. amplus* from the middle Eocene Piney Point Formation of Virginia. His description was based on 117 specimens. Like *L. kokeni*, otoliths of *L. amplus* are common in many of the Claiborne formations in Alabama, Louisiana, and Texas (Frizzell & Dante 1965; Stringer & Breard 1997; Breard & Stringer 1999; Müller 1999).

Stratigraphic and geographic range in Alabama

All the specimens of *Lactarius amplus* were found in the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Lactarius sp.

?*Lactarius* sp. – Stringer & Breard 1997: 565.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 2 otoliths; MSC 35076.3, WSU CC 470.3.

Description

These two specimens have numerous salient characteristics of *Lactarius*. These include the shape of the otolith, the type and orientation of the ostium and cauda, the depressed, almost linear area above the crista superior, and a ventral furrow. The specimens may represent *Lactarius amplus*, but their preservation prohibits this determination.

Remarks

These specimens may represent a different species. However, better-preserved, additional adult specimens would be required to make this determination.

Stratigraphic and geographic range in Alabama

The specimens in our sample were found in the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Family Malacanthidae Poey, 1861

Genus ***Malacanthus*** Cuvier, 1829

Type species

Coryphaena plumieri Bloch, 1786, Recent.

Malacanthus*? *sulcatus (Koken, 1888)

Fig. 71E–F

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

"genus *Malacanthidarum*" *sulcatus* – Nolf 2003: 6, pl. 1, figs 14a–b. — Nolf & Stringer 2003: 4, pl. 5, figs 3a–8b.

"*Malacanthida*" *sulcata* – Nolf 2013: 98, pl. 238.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 15 otoliths; GLS otolith comparative collection (14 specimens), MSC 39061.

Description

Sagittae primarily elliptical (sensu Smale *et al.* 1995); height/length ratios range from approximately 49–60%. Dorsal margin with fairly coarse lobes; ventral margin fairly smooth or with much smaller lobes. Anterior margin characterized by usually bluntly tapered rostrum. Anterodorsal slope fairly steep, varies from almost straight to slightly rounded. Dorsal margin tending to rounded and lobed. Posterodorsal slope generally fairly steep; slope sometimes almost straight. Posterior margin short, usually steep, slightly rounded. Ventral margin not very deep, only slightly curved. Inner face convex, with prominent sulcus and irregularly shaped depressed area above sulcus. Sulcus divided (heterosulcoid type), quite long (about 85% of total otolith length), fairly well excavated. Ostium approximately 60% of cauda length, about same width as anterior portion of cauda. Ostium has elliptical shape. Anterior portion of ostium opens onto anterior margin. Anterior portion of cauda about the same width as ostium; width of cauda increases posteriorly. Posterior of cauda noticeably round, very slightly flexed downward. Posterior end of cauda well separated from posterior margin. Ventral furrow generally poorly developed. Outer face only slightly concave.

Remarks

Although fairly numerous at 15 specimens, the species was found at only one Claiborne Group site in Alabama (site ACh-8). The species has been reported (under the name "*Malacanthida*" *sulcata*) from the middle Eocene (Bartonian) Moodys Branch Formation in Mississippi (Nolf 2013). The taxon was found to be fairly common, with 57 specimens (identified as "genus *Malacanthidarum*" *sulcata*), in the upper Eocene Yazoo Clay of Louisiana (Nolf & Stringer 2003). Like the Yazoo Clay specimens, the Claiborne Group *Malacanthus*? *sulcatus* otoliths tended to be fairly small, with the largest being less than 4 mm in length. The otoliths of *Malacanthus*? *sulcatus* compare very well with Recent species of *Malacanthus*, like *M. brevirostris* (see Nolf & Stringer 2003: pl. 5, figs 3–6).

Stratigraphic and geographic range in Alabama

All of the specimens were recovered from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 to NP17.

Family Haemulidae Gill, 1885

Genus ***Orthopristis*** Girard, 1858

Type species

Orthopristis duplex Girard, 1858, Recent.

Orthopristis burlesonis Frizzell & Dante, 1965

Fig. 71G–H

Allomorone burlesonis sp. nov. Dante & Frizzell in Frizzell & Dante, 1965: 703, pl. 87, figs 5, 10, 15.

Orthopristis burlesonensis – Nolf 2013: 102, pl. 252.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 54 otoliths; GLS otolith comparative collection (44 specimens), GSA 157.1, GSA 157.2, GSA 157.3, GSA 157.4, GSA 157.5, GSA 157.6, GSA 157.7, GSA 157.8, MSC 39060, WSU CC 471.1.

Description

Sagittae small to medium-sized (up to 4 mm), elliptical in shape. Dorsal margin very broadly and unevenly arched, small posterodorsal dome. Posterior margin slightly obliquely truncated or slightly incurved. Ventral margin smooth, very broadly and unevenly curved. Anterior margin has fairly prominent rostrum with excisura. Inner face strongly convex, with well-defined heterosulcoid-type sulcus covering at least 75% of length of otolith. Ostium moderately narrow, subquadrate shape, shorter than cauda. Cauda very narrow (about one-half or less than width of ostium). Cauda longer than ostium, has parallel sides, posterior portion bent sharply downward. Crista superior raised along horizontal portion of the sulcus; crista inferior is weakly developed. Shallow area extends along crista superior and upward flexure of ostium. Outer face somewhat concave, generally with irregular surface.

Remarks

This species is known to occur within the middle Eocene Weches and Cook Mountain formations at several localities in Texas, and it has also been reported from Alabama, Louisiana, and Mississippi (Frizzell & Dante 1965; Nolf 2013). The type material of this species was collected from the Lisbon Formation at site AMo-4 in Monroe County, Alabama, where it was reported as common by Frizzell & Dante (1965).

Stratigraphic and geographic range in Alabama

Orthopristis burlesonis specimens were recovered from the "upper" Lisbon Formation at site ACh-8 and the Gosport Sand at site ACl-4. Bartonian, zones NP16 and NP17.

Genus ***Haemulon*** Cuvier, 1829

Type species

Haemulon elegans Cuvier, 1829, Recent.

Haemulon*? *obliquus (Müller, 1999)

Fig. 71I–J

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

"genus *Haemulidarum*" *obliquus* – Nolf & Stringer 2003: 6, pl. 6, figs 1a–2.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 9 otoliths; GLS otolith comparative collection (5 specimens), MSC 39062, WSU CC 470.1, WSU CC 470.2, WSU CC 472.1.

Description

Sagitta generally oval in outline. Margins of smaller specimens sinuate and lobed, slightly lobed on larger specimens. Dorsal margin mainly evenly rounded, no domes, generally more sculptured. Anterior margin usually somewhat tapered, rounded. Posterior margin straighter, not as rounded as anterior margin. Ventral margin more deeply rounded than dorsal margin. Inner face only slightly convex, characterized by distinct sulcus (heterosulcoid-type). Length of ostium less than half the length of cauda; ostium twice the width of cauda. Ventral margin of ostium makes distinct nearly 90-degree upturn at junction with cauda. Dorsal margin makes similar downturn at caudal junction, but angle is less. Dorsal and ventral margins of cauda essentially parallel except for small downturned portion. Downturned portion distinct, short. End of cauda rounded, almost reaches posterior margin. Depressed area somewhat oval, elongated above cauda. Outer face slightly concave.

Remarks

Both Nolf (1985) and Müller (1999) referred this species to the genus *Xenistius.* However, as noted by Nolf & Stringer (2003), the sagittae of *H.? obliquus* do not compare well to the elongated sagittae of extant *Xenistius.* As the generic placement is not certain, the morphology is referred to *Haemulon*, the type genus of the Haemulidae, followed by a question mark as recommended by Janssen (2012).

Stratigraphic and geographic range in Alabama

This species is found in the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Genus ***Anisotremus*?** Gill, 1861

Type species

Sparus virginicus Linnaeus, 1758, Recent.

***Anisotremus*?** sp.

Fig. 71K–L

Anisotremus sp. – Nolf & Stringer 2003: 6, pl. 5, figs 13a–b.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 2 otoliths; GLS otolith comparative collection (1 specimen), MSC MSC 42236.

Description

Specimens quite large; one broken specimen measures approximately 20 mm long, 12 mm wide; more complete specimen 16 mm long. Shape primarily ovate, with posterior having greater width. Height/length ratios around 65%. Margins smooth except for dorsal margin. Anterior margin short, consisting primarily of ostium opening. Anterodorsal margin fairly straight, slants upward. Dorsal margin continues slanting upward, characterized by four sharp crenulations. Posterodorsal margin straight to slightly incurved. Posterior margin short, rounded. Posteroventral margin slightly arched, slants fairly sharply to ventral margin. Ventral margin and posteroventral margin rounded, gently inclined upward to anterior margin. Inner face convex, marked by very large, prominent sulcus. Sulcus (heterosulcoid-type) located slightly more dorsally, extends from anterior margin almost to posteroventral margin (at least 95% of the length). Sulcus unevenly excavated, filled with colliculum. Ostium quite elongated, about same length as cauda. Dorsal and ventral margins of ostium approximately parallel except for very slight arching near cauda. Cauda narrow (about 85% of width of ostium). Horizontal portion of cauda slightly longer than downturned portion. Downturned portion of cauda forms approximately 45-degree angle. Cauda noticeably more excavated than ostium, with downturned portion of cauda being most excavated. Fairly deep, somewhat rectangular depressed area above horizontal portion of cauda. Downturned portion of cauda almost reaches posteroventral margin. Outer face irregularly concave, smoothly sculptured.

Remarks

The Alabama Claibornian otoliths share many morphological features with Recent species of *Anisotremus*, particularly *A. caesius*. The specimens of *Anisotremus*? sp. from the Lisbon Formation of Alabama are similar to the *Anisotremus* sp. described by Nolf & Stringer (2003) from the Eocene of Louisiana, but the Louisiana otoliths have a shorter downturned portion of the cauda.

Stratigraphic and geographic range in Alabama

The two specimens of *Anisotremus*? were recovered from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Suborder Percoidei
Family *incertae sedis*

Percoidei indet. 1
Fig. 71M–N

Material examined

UNITED STATES OF AMERICA – **Alabama** • 5 otoliths; GLS otolith comparative collection (4 specimens), MSC 39063.

Description

Sulcus distinctly divided, clearly heterosulcoid. Wide ostium, much narrower cauda. Cauda is uniform in width, downturned ventrally. Ostium tends to widen ventrally.

Remarks

The five specimens exhibit features of percoids (Suborder Percoidei, Order Perciformes). Perciform otoliths are usually distinctly heterosulcoid, with an ostium that widens ventrally and a much narrower cauda that is usually uniform in its width and bent ventrally. Unfortunately, the specimens could not be identified to a specific perciform family.

Stratigraphic and geographic range in Alabama

All of the specimens assigned to Percoidei indet. 1 were recovered from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Percoidei indet. 2

Material examined

UNITED STATES OF AMERICA – **Alabama** • 4 otoliths; GLS otolith comparative collection.

Description

Sulcus distinctly divided, clearly heterosulcoid. Ostium generally wide, cauda much narrower. Cauda uniform in width, bent ventrally. Ostium tends to widen in ventral direction.

Remarks

The four specimens exhibit features associated with percoids (Suborder Percoidei, Order Perciformes), like a broad ostium that tends to widen in the ventral direction, and a much narrower cauda that is uniform in its width and bent in a ventral direction at the posterior. Unfortunately, the specimens could not be identified to a specific perciform family, but they do appear to have morphological features that distinguish them from Percoidei indet. 1, such as the position of the sulcus on the inner face and slightly different proportions between the length of the ostium and cauda.

Stratigraphic and geographic range in Alabama

All of the specimens assigned to Percoidei indet. 2 were recovered from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Perciformes indet.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 7 otoliths; WSU CC 469.4, WSU CC 472.2, WSU CC 472.3, WSU CC 472.4, WSU CC 474.1, WSU CC 474.2, WSU CC. 475.2.

Description

Sulcus distinctly divided (heterosulcoid), with wider ostium but much narrower cauda. Cauda appears to be of uniform width, bent ventrally. Ostium appears to be widened ventrally.

Remarks

The features described above are characteristic of the Perciformes, but they display very plesiomorphic perciform features. Juvenile specimens could not be assigned to a specific family. Due to their very small size and plesiomorphic nature of the specimens, we cannot determine if they represent species identified above or something different.

Stratigraphic and geographic range in Alabama

All specimens assigned to Perciformes indet. were recovered from the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

Order Acanthuriformes (sensu Nelson *et al.* 2016)
Family Sciaenidae Cuvier, 1829

Genus ***Sciaena*** Linnaeus, 1758

Type species

Sciaena umbra Linnaeus, 1758, Recent.

Sciaena intermedius (Koken, 1888)
Fig. 71O–P

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

Otolithus (*Sciaenidarum*) *intermedius* – Campbell 1929a: 265, pl. 30, figs 2–3.
Corvina intermedia – Frizzell & Dante 1965: 694, pl. 88, figs 9–10, 27, 29–30.
"genus *Sciaenidarum*" *intermedia* – Breard & Stringer 1999: 135.
?"genus aff. *Umbrina*" *livesayi* – Müller 1999: 163, pl. 33, figs 23–30, pl. 34, figs 1–2.
"genus *Sciaenidarum*" *intermedius* – Nolf 2003: 17, pl. 2, figs 12–14.
"*Sciaenida*" *intermedia* – Nolf 2013: 107, pl. 282.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 76 otoliths; GLS otolith comparative collection (65 specimens), MSC 39042.1, MSC 39042.2, MSC 39042.4, MSC 39042.5, MSC 39042.6, MSC 39042.8, MSC 39042.14, MSC 39050, MSC 189, MSC 7302, WSU CC 473.1.

Description

Sagittae with approximately oval to subrectangular outline. Height/length ratios ranging from around 75–90%, typically around 80%. Inner face convex, smooth. Margins smooth except for juveniles, which may be finely sinuate. Dorsal margin slopes gently downward anteriorly and posteriorly from an obtuse central angle. Conspicuous posterodorsal angle. Posterior margin arches inward slightly; ventral margin broadly rounded. Anterior margin very broadly, evenly rounded. Very prominent heterosulcoid-type sulcus. Ostium filled with colliculum, covers about 35% of length of inner face. Anterior of ostium even with anterior margin of sagitta. Dorsal and ventral margins of ostium tend to constrict anteriorly; constriction often more pronounced on smaller (juvenile) specimens. Cauda long and narrow (less than 50% of width of ostium), has horizontal portion and sharply downturned portion. Horizontal portion of cauda about the same length as downturned portion, less excavated (but a variable feature). Downturned portion of cauda more excavated, about same width as horizontal portion. Angle of horizontal and downturned portions approximately 90-degrees. Downturned portion nearly reaches posteroventral margin. End of cauda tapered, still somewhat rounded. Outer face usually slightly concave, sculptured.

Remarks

There has been much debate about the taxonomic position of this species, and our decision to refer to it as *Sciaena intermedius* is defended in the ensuing discussion. The sagittae of *S. intermedius* are similar to those of *Jefitchia copelandi* and *J. claybornensis* (see below), and in fact *S. intermedius* is believed to be closely related to the two *Jefitchia* species. Frizzell & Dante (1965) proposed the fossil genus *Jefitchia*, and John Fitch, then Research Director of the California State Fisheries Laboratory, considered one of the most knowledgeable experts on sciaenid otoliths, confirmed that the genus was distinct from all known Recent sciaenids. In his treatise on modern and fossil Sciaenidae otoliths, Schwarzhans (1993) also considered *Jefitchia* as a valid fossil-based genus, and he accepted the two species proposed by Frizzell & Dante (1965). *Sciaena intermedius* could be considered as a possible species of *Jefitchia*, but it differs significantly from the original description of Frizzell & Dante (1965) and the subsequent description of Schwarzhans (1993) to be placed in this genus. One of the primary differences between the two is in the inflated ostium on *S. intermedius*. Frizzell & Dante (1965) noted the similarity of *S. intermedius* to *J. copelandi*, but they chose to assign the form to *Corvina intermedia.* Schwarzhans (1993) placed *Sciaena intermedius* into synonymy with the fossil-based *Frizzellithus gemma*, but Nolf rejected the fossil-based genus and insisted that *F. gemma* was actually *Aplodinotus gemma* (Nolf 2003, 2013). Furthermore, Nolf did not believe that *S. intermedius* belonged with *Aplodinotus gemma* and that it represented a separate species (Nolf 2003).

Sciaena intermedius bears a striking similarity to the late Eocene-Oligocene sciaenid *Sciaena pseudoradians. Sciaena pseudoradians* was originally described as *Corvina pseudoradians* by Frizzell & Dante (1965). Unfortunately, the holotype was not figured, and the figured paratypes were juvenile otoliths, which were not diagnostic. Nolf (2003) figured a growth series of the taxon and thought that the otoliths of this species seemed to be most closely related to those of *Sciaena*. Thus, the species *S. pseudoradians* was proposed. *Sciaena intermedius* has several major morphological features in common with *S. pseudoradians*, which can be clearly seen in figures 3–6 and 12–14 in plate 2 of Nolf (2013). The outline of the sagittae of the two species, the shape of the ostium, the angle of the downturned portion of the cauda, and the proportion of the horizontal and downturned portions of the cauda appear to indicate a close relationship. The width of the ostium of *S. intermedius* is variable, but it does not reach nearly the width of the ostium in *S. pseudoradians*. However, the width of the ostium of *S. intermedius* is much greater than *Jefitchia copelandi* or *J. claybornensis.* The relationship of *S. intermedius* to *S. pseudoradians* seems to be supported by geometric morphometric analyses reported by Lin (2018: fig. 5). According to his study, *S. intermedius* (reported as "*Sciaenda*" *intermedia*) may be closely related to *S. pseudoradians.* If *S. intermedius* is a transitional form to *S. pseudoradians*, this could explain the difficulty in determining its taxonomic position. It should also be noted that *S. pseudoradians* is primarily an Oligocene taxon, and that Nolf & Stringer (2003) identified the late Eocene form from the Yazoo Clay as *Sciaena* aff. *pseudoradians.* No specimens of *Sciaena pseudoradians* are known from the Claiborne Group.

The sagittae of *Sciaena intermedius* are somewhat similar to *Jefitchia copelandi*, which are also found in the Claiborne Group of Alabama. However, *S. intermedius* is distinguished by its appreciably wider ostium. The downturned portion of the cauda of *J. copelandi* also tends to be 90-degrees or greater measured from horizontal (Nolf 2013: pl. 281), whereas *S. intermedius* is typically less than 90-degrees from horizontal, which is shown well in the three specimens illustrated by Nolf (2013: pl. 282). The type locality for *S. intermedius* (as *Corvina intermedia*) was given as the Lisbon Formation at site AMo-4 in Monroe County, Alabama (Frizzell & Dante 1965), and the species is also known from Louisiana, Mississippi, and Texas.

In his description of Eocene fishes of Alabama, White (1956) discussed a small collection of remains collected by G.F. Harris from the Gosport Sand of Claiborne, Monroe County, Alabama. Harris donated the material, which was composed primarily of shark teeth, to the British Museum in 1892, and a single otolith (P.6827) was included in the remains. White (1956) noted that the otolith belonged to Koken's species *Otolithus* (*Sciaenidarum*) *intermedius* (Koken 1888: table 19, figs 2–3), which is the same as *Corvina intermedia* (Koken) of Frizzell & Dante (1965). However, White (1956) then stated that "Mr. Stinton" informed him that the specimen belonged to *Lutianus.* It is presumed that the "Mr. Stinton" refers to F.C. Stinton, a renowned expert on fossil otoliths, who published extensively on the Eocene otoliths of England. Although the otolith specimen was not examined as part of the present study, the background information provided by White (1956) is nevertheless problematic. If the otolith was correctly identified as *Otolithus* (*Sciaenidarum*) *intermedius*, then it is highly unlikely that Stinton would identify it as *Lutianus* (it should be noted that *Lutianus* is a rejected spelling for *Lutjanus* Bloch, 1790). *Lutjanus* is in Lutjanidae (the snappers), and lutjanid otoliths have little resemblance to Koken's (1888) *Otolithus* (*Sciaenidarum*) *intermedius*. The sciaenid described by Koken has an inflated ostium and a narrow cauda that is downturned at almost 90-degrees, but *Lutjanus* displays none of these characteristics. Therefore, the identification of the Gosport Sand otolith recovered by Harris is unclear based on White's (1956) discussion.

Stratigraphic and geographic range in Alabama

Sciaena intermedius is one of the most abundant taxa in the Claiborne Group of Alabama. It is common in the "upper" Lisbon Formation at site ACh-8 and six specimens were recovered from the Gosport Sand at sites ACl-4 and AMo-4. Bartonian, zones NP16 and NP17.

Genus ***Jefitchia*** Frizzell & Dante, 1965

Type species

Jefitchia copelandi Dante & Frizzell in Frizzell & Dante, 1965, middle Eocene.

Jefitchia copelandi Frizzell & Dante, 1965

Fig. 71Q–R

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

"genus *Sciaenidarum*" aff. *copelandi* – Müller 1999: 161, pl. 33, fig. 22.
"*Sciaenida*" *copelandi* – Nolf 2013: 107, pl. 281.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 21 otoliths; MSC 7299.1, MSC 7299.2, MSC 7299.3, MSC 39042.9, MSC 39042.10, MSC 39042.11, MSC 39042.13, MSC 39053, GLS otolith comparative collection (11 specimens), WSU CC 473.3, WSU CC 473.4.

Description

Sagitta subcircular to subquadrate in outline. Height/length ratios exhibit considerable range related to increasing size. Smaller specimens (less than 2.5 mm) have ratios from around 65–75%; larger specimens (some exceed 12 mm) range from around 80–90%. Inner face convex, smooth. Margins smooth except for fine crenulations on very small juveniles. Dorsal margin nearly straight to somewhat arched. Conspicuous posterodorsal angle. Posterior margin straight to slightly curving inward; ventral margin broadly but unevenly rounded. Anterior margin evenly rounded. Very prominent heterosulcoid-type sulcus. Ostium filled with colliculum, moderately narrow, covers about 35% of length of inner face. Anterior of ostium even with anterior margin of sagitta. Dorsal and ventral margins of ostium essentially parallel anteriorly, but arch outwardly in posterior portion. Posterior margin of ostium nearly vertical. Cauda very long and narrow, has horizontal portion and sharply downturned portion. Horizontal portion of cauda significantly shorter than downturned portion, less excavated. Downturned portion of cauda more excavated, significantly longer, wider. Angle of horizontal and downturned portions around 90-degrees. Downturned portion almost reaches ventral margin. Outer face usually slightly concave, sculptured.

Remarks

Jefitchia copelandi has characteristics in common with *Sciaena intermedius* (see above), but *J. copelandi* is easily distinguished by its narrower ostium, and the dorsal and ventral margins of the ostium are essentially straight and parallel in the anterior portion (Nolf 2013: pl. 281). *Jefitchia copelandi* is also similar to *J. claybornensis* (see below) but differs by the less elongate outline (higher height/length ratios) of *J. copelandi*, as well as by its much longer downturned portion of the cauda, and the angle of the downturned portion of the cauda (90-degrees or more from horizontal). The species appears to have a wide geographical range in the Eocene, as it is known from numerous locations in Alabama, Louisiana, Mississippi, Texas, and Virginia (Frizzell & Dante 1965; Breard & Stringer 1999; Müller 1999).

Stratigraphic and geographic range in Alabama

Sagittae of *J. copelandi* have been recovered from the “upper” Lisbon Formation at site ACh-8 and the Gosport Sand at site AMo-4. Bartonian, zones NP16 and NP17.

Jefitchia claybornensis Frizzell & Dante, 1965
Fig. 72A–D

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

Otolithus (*Sciaenidarum*) *similis* – Koken 1888: 284, pl. 19, figs 10–11.
Jefitchia claybornensis – Frizzell & Dante 1965: 705. — Stringer 1977: 99–101, pl. 1, fig. 15; 1979: 103, pl. 1, fig. 15. — Schwarzhans 1993: 26, figs 5–7. — Breard & Stringer 1995: 80.
“genus *Sciaenidarum*” *claybornensis* – Müller 1999: 161. — Nolf & Stringer 2003: 6, pl. 7, figs 1a–5.
“*Sciaenida*” *claybornensis* – Nolf 2013: 107, pl. 281.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 16 otoliths; GLS otolith comparative collection (12 specimens), MSC 39042.3; MSC 39042.7, MSC 39049, MSC 39057.

Description

Sagittae generally subpyriform to subquadrate in shape. Inner face smooth, convex, thickest at center. Adult specimens quite large, exceeding 15 mm long. Height/length ratios range from approximately 65–82%. Margins smooth on adult specimens, finely crenulate on small specimens. Anterior margin rounded; dorsal margin very gently rounded. Dorsal dome usually present on larger specimens. Posterodorsal dome forms sharp, obtuse angle with posterior margin. Posterior margin somewhat variable, ranging from slightly rounded, straight, to slightly incurved. Ventral margin broadly, unevenly rounded. Very prominent heterosulcoid-type sulcus located on inner face. Ostium fairly narrow (about twice width of cauda), elongated. Ostium filled with colliculum, extends from anterior margin to approximately vertical midline. Anterior sides of ostium approximately parallel, whereas posterior sides slightly arched. Cauda narrow, (one-half width of ostium), with horizontal and downturned portions. Horizontal portion as long or longer than downturned portion. Downturned portion forms obtuse angle. Sides of downturned portion of cauda tend to arch outward slightly. Posterior end of cauda tapered, almost reaches ventral margin. Slightly depressed area located mainly above horizontal portion of cauda. Crista superior developed primarily on horizontal portion of cauda. Ventral furrow usually indistinct. Outer face concave, sculptured, highly undulating.

Remarks

Although *Jefitchia claybornensis* is similar to *J. copelandi* (see above), the otoliths can be distinguished by the more elongate outline (lower height/length ratios) of *J. claybornensis*, as well as the shorter downturned portion of the cauda and the angle of the downturned portion of the cauda (less than 90-degrees from horizontal, especially on larger specimens). A growth series of *J. claybornensis* is shown in Nolf & Stringer (2003: pl. 7, figs 1–5). *Jefitchia claybornensis* also shows some similarity to *Sciaena intermedius* (see above), but this species is easily distinguished by its more inflated ostium. In addition, the downturned portion of the cauda of *S. intermedius* is longer than on *J. claybornensis.*

Koken (1888) originally noted that *Jefitchia claybornensis* was very common at "Clayborne [Claiborne], Alabama." The species is also known from Alabama (Lisbon Formation and Gosport Sand), Louisiana (middle Eocene Moodys Branch Formation, upper Eocene Yazoo Clay), Mississippi (middle Eocene Moodys Branch Formation, upper Eocene Yazoo Clay), and Texas (middle Eocene Weches Formation). Müller (1999: pl. 33, 16–21) described a new species of sciaenid, "genus aff. *Umbrina*" *eanesi*, from the middle Eocene Piney Point Formation of Virginia, but the species is so similar to *J. claybornensis* that it is not possible to distinguish the two. Furthermore, it is believed that "genus aff. *Umbrina*" *eanesi* actually represents variation within *Jefitchia claybornensis.*

Stratigraphic and geographic range in Alabama

This species was recovered from the "upper" Lisbon Formation at site ACh-8, the contact of the Lisbon Formation and Gosport Sand at site AMo-4, and while rare, also from the Gosport Sand at site ACl-4. Bartonian, zones NP16 and NP17.

Genus ***Ekokenia*** Frizzell & Dante, 1965

Type species

Otolithus (*Sciaenidarum*) *eporrectus*, Koken, 1888, Eocene.

Ekokenia eporrecta Frizzell & Dante, 1965

Fig. 72E–F

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

Otolithus (*Sciaenidarum*) *eporrectus* – Posthumus 1924: 27. — Campbell 1929a: 264, pl. 29, figs 16–17.
Ekokenia eporrecta – Frizzell & Dante 1965: 704, pl. 87, figs 11–12, 16; pl. 88, figs 5, 11. — Schwarzhans 1993: 27, fig. 11.
"genus *Sciaenidarum*" *eporrectus* – Breard & Stringer 1999: 135. — Müller 1999: 160, pl. 33, figs 10–15.
"*Sciaenida*" *eporrecta* – Nolf 2013: 107, pl. 281.

Material examined

UNITED STATES OF AMERICA – **Alabama** • 36 otoliths; GLS otolith comparative collection (33 specimens), MSC 7300, MSC 39048, WSU CC 473.1.

Description

Sagittae range from approximately oval (smaller specimens) to elliptical (larger specimens). Inner face fairly smooth, convex. Adult specimens fairly large, exceeding 10 mm in length. Height/length ratios range from approximately 62–74%. Margins irregularly smooth on adult specimens, can be finely crenulate on small specimens. Anterior margin slopes backwards on smaller specimens, nearly vertical on larger specimens. Dorsal margin irregular, dorsal dome usually present. Posterodorsal dome is present on many specimens. Posterior margin straight to slightly incurved. Ventral margin broadly, evenly rounded. Very prominent heterosulcoid-type sulcus occurs on inner face, extending from anterior margin almost to posteroventral margin. Sulcus excavated, posterior slightly flexed downward. Ostium about one-half the length of cauda, twice as wide. Ostium filled with colliculum. Sides of ostium approximately parallel. Cauda narrow (one-half width of ostium), slightly flexed downward at posterior. Posterior of cauda pointed. Very prominent depressed area, nearly rectangular in shape, above sulcus. Crista superior well-developed, forms distinct raised ridge above cauda. Ventral furrow appears absent. Outer face concave; concavity increases with size. Outer face excavated on dorsal half. Irregular undulations common on the larger specimens.

Remarks

Koken (1888) first reported this taxon from Newton, Mississippi, and the formation from which it was found is now known to be the middle Eocene Cook Mountain Formation. The species also occurs in the Cook Mountain Formation of Texas (very common in the Stone City Member) and Louisiana, as well as the middle Eocene Piney Point Formation of Virginia.

Stratigraphic and geographic range in Alabama

This species is common in the "upper" Lisbon Formation at site ACh-8. Bartonian, zones NP16 and NP17.

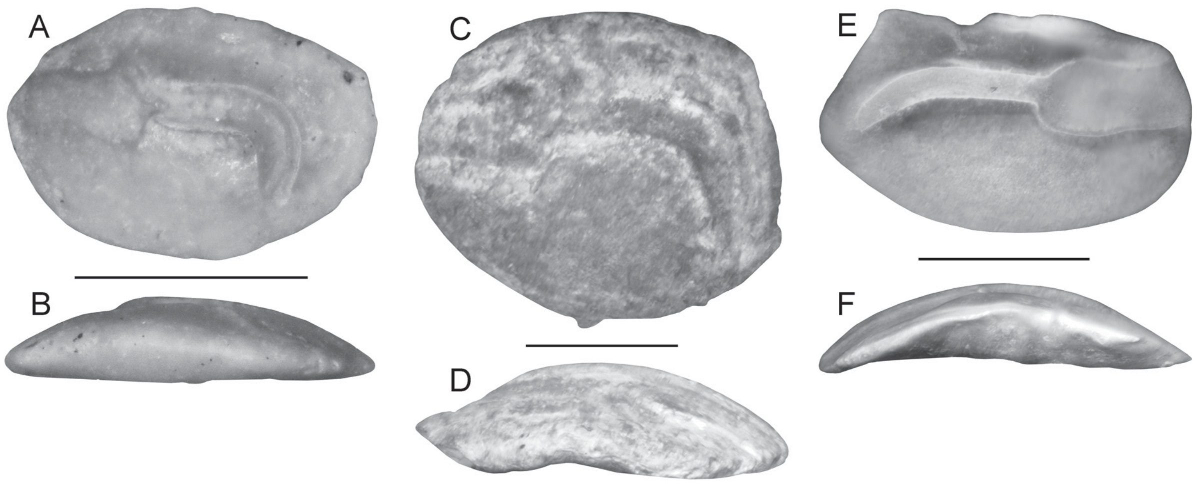


Fig. 72. Claiborne Group, "upper" Lisbon Formation, otoliths. **A–D**. *Jefitchia claybornensis* Frizzell & Dante, 1965. **A–B**. MSC 39057. **A**. Inner face (right sagitta, juvenile). **B**. Dorsal view. **C–D**. MSC 39049. **C**. Inner face (right sagitta). **D**. Dorsal view. — **E–F**. *Ekokenia eporrecta* Frizzell & Dante, 1965, MSC 39048. **E**. Inner face (left sagitta). **F**. Dorsal view. Scale bars: A–D = 2 mm; E–F = 5 mm.

Discussion

We examined a total of 20 338 non-otolith fish specimens during the course of our study, including material from 15 distinct Claiborne Group localities in Alabama. Seventy-five percent of the specimens examined (n = 15 257) are housed at MSC, with the remaining fossils being located within the collections at the ALMNH (n = 1298), ANSP (n = 25), GSA (n = 78), MMNS (n = 652), NJSM (n = 56), SC (n = 1959), and WSU (n = 1041) (see Material and methods for complete institution names). All of these specimens were derived from localities in Alabama, with exposures encompassing nearly the entire stratigraphic extent of the Claiborne Group. Exceptionally large numbers of specimens (5600+) were obtained from three distinct localities, each exposing one or more of the three Claiborne Group formations, including site ADl-1 (Meridian Sand Member of the Tallahatta Formation and lower Tallahatta Formation, n = 5689), site ACov-11 (Tallahatta/Lisbon Formation contact zone and basal Lisbon Formation, n = 6394), and site ACl-4 (basal Gosport Sand, n = 5747). The remaining 2536 specimens were collected from 12 additional Claiborne Group localities in Alabama, all of which are listed in Table 1 and Appendix 2.

Due to the strong sample bias within our otolith sample, with nearly 95% of the specimens being derived from the Lisbon Formation, these remains are excluded from the faunal analysis presented below, as they provided little biostratigraphic data when comparing the three Claiborne Group formations. These specimens are instead described, discussed, and analyzed separately from the osteological remains discussed in this section (see Teleostean otoliths from the Claiborne Group of Alabama below). The sample biases are thought to largely be preservational, as no otoliths were collected from shell-poor units from which an abundance of teeth and bones were recovered. Although the otoliths were obtained through bulk sampling, collecting biases cannot be ruled out.

We strove to minimize these biases in order to maximize the biostratigraphic information contained within our samples. Collecting biases were reduced through the collection of large sample sizes, which helped to better understand the true taxonomic diversity preserved within Claiborne Group strata. Furthermore, nearly equal-sized matrix samples were obtained from each of the three Claiborne Group formations, thus limiting the affect sample size could have relative to taxonomic abundance. We believe that these large sample sizes also allowed us to capture the maximum number of both micro- and macro remains, improving our ability to determine taxonomic diversity. Moreover, samples were obtained from various localities within each formation to help minimize preservation biases. Large, nearly equal-sized, samples (> 5600) were also obtained from one representative site within each formation to help facilitate direct comparisons between the units. Additionally, samples were obtained from lower and upper sections of each formation to help resolve the first and last occurrences, and presence or absence, of taxa within different sections of a formation. Finally, to help minimize identification biases based on previous interpretations, we directly examined all of the specimens included in this study.

Despite our efforts to minimize biases within our sample, they inevitably still had an influence on our dataset. For example, preservation and taphonomic biases strongly favored the recovery of larger and more robust elements (making them more abundant in our sample). Furthermore, tooth replacement rates in sharks differ by growth stage (juvenile individuals tend to replace their teeth at a faster rate than older, more mature, individuals) and by species (Cappetta 2012; Klimley 2013), and the number of teeth in a dentition varies by species, within a species, and can also be influenced by ontogeny (see Compagno 1984). Finally, potentially associated elements belonging to the same individual could not be accounted for (i.e., we could not calculate the minimum number of individuals present in our sample), and therefore had to tabulate each preserved element individually. A combination of these factors had strong influences on determining the relative abundance of particular taxa in our sample, and a note of caution is warranted within discussions of species abundance. However, as these biases are equally present within all three of the Claiborne Group formations, comparing the faunal compositions between the formations allowed us to highlight some potentially informative biostratigraphic trends.

Biostratigraphic and biogeographic trends based on identified genera and species

The 20 338 non-otolith fish specimens in our Claiborne Group sample were identified to the lowest taxonomic ranking possible, and overall numbers of specimens for each taxon were tabulated in a spreadsheet that also included the geologic unit and locality from which the material was derived. The numerical results of this analysis are presented in Appendices 1 and 2. Of the specimens in our sample, a total of 16 031 (78.8%) were identified at least to the family level, and 13 190 specimens were identified at least to the genus level (64.8%). In total, 84 unequivocal non-otolith taxa, 63 genera, and 33 families (with three additional taxa of uncertain familial placement) were identified in our sample. The data in Appendices 1 and 2 were used to identify the biostratigraphic and biogeographic trends discussed below, which are arranged by family and presented systematically.

HETERODONTIDAE. This family is represented only by *Heterodontus*, and a total of seven lateral teeth were identified in our Claiborne sample. The small sample size could reflect the limited occurrence of the taxon within the Claiborne Group formations, but the lack of anterior teeth suggests preservational and/or collecting biases within our sample. All of our *Heterodontus* specimens were obtained through bulk field sampling, and these small teeth can easily be overlooked by surface collecting. The lateral teeth are more numerous within the dentition than anteriors, and they are robust and perhaps more likely to be preserved than the more delicate anterior teeth. As our sample contains specimens from all three Claiborne Group formations, the stratigraphic range of *Heterodontus* in Alabama is now known to extend from the late Ypresian into the Bartonian (Zone NP12 to Zone NP17).

ORECTOLOBIDAE. This family is represented in the Claiborne Group by one taxon, *Orectolobus ziegenhinei*. A total of 180 *O. ziegenhinei* teeth were identified in our sample, all but one of which were recovered from site ACov-11 in Covington County, the type locality for the species. The lone exception was collected from site ACh-14 in Choctaw County (Maisch *et al.* 2014), a locality that exposes the same stratigraphic units as site ACov-11 (the contact of the Tallahatta and Lisbon formations). The absence of *O. ziegenhinei* from all other stratigraphic horizons suggests that this species is stratigraphically confined to the upper half of Zone NP14 and to the lower half of Zone NP15 within the lower Lutetian. According to Cappetta & Case (2016), *O. ziegenhinei* represents the oldest member of the genus.

GINGLYMOSTOMATIDAE. Within our sample this family is represented by two genera and three taxa, including *Ginglymostoma maroccanum*, *Ginglymostoma* sp., and *Nebrius thielensi*. Of the three, *N. thielensi* is the most abundant (n = 170), and this species occurs within all three of the Claiborne Group formations. Far less abundant (n = 8) is *G. maroccanum*, which was only recovered from the Tallahatta Formation. A total of 21 *Ginglymostoma* sp. specimens were recovered from the Gosport Sand. These teeth are too poorly preserved to identify to species, but they differ from *G. maroccanum* in having more lateral cusplets. The apparent absence of *Ginglymostoma* in the Lisbon Formation (the middle of the three Claiborne Group units) is puzzling, but the stratigraphic separation of the Ypresian *G. maroccanum* and Bartonian *Ginglymostoma* sp. lends support that the two *Ginglymostoma* indeed represent different species. The presence of *G. maroccanum* in our Claiborne Group sample represents the first occurrence of this species in North America.

ORECTOLOBIFORMES INDET. A unique tooth, SC2012.47.45, was identified in our Claiborne sample, which appears to belong to a member of the Orectolobiformes. This tooth was collected *in situ* from the basal Lisbon Formation (Lutetian, Zone NP15) at site ACov-11 and resembles the teeth of *Chiloscyllium* and *Delpitoscyllium*. Additional and better preserved specimens are needed to confirm the identification of the taxon represented by this tooth.

Otodontidae. Claibornian members of the Otodontidae are represented by a single genus and two subgenera, *Otodus* (*Carcharocles*) and *Otodus* (*Otodus*). In our sample, teeth assigned to the unserrated *Otodus* (*Otodus*) sp. (n = 9) were recovered only from the lower Tallahatta Formation within zones NP12 to NP14 (upper Ypresian to lowermost Lutetian). Teeth of the serrated *Otodus* (*Carcharocles*) sp. were recovered from stratigraphically higher beds within the Tallahatta Formation, and from within the Lisbon Formation and Gosport Sand (zones NP15 to NP17).

The specimens in our sample appear to corroborate interpretations that these species are part of a continuous lineage beginning with *Cretalamna* in the Cretaceous (see Applegate & Espinosa-Arrubarrena 1996) and culminating with *Otodus* (*Megaselachus*) *megalodon* (Agassiz, 1843) in the Miocene (Glickman 1964; Cappetta 2012). Specifically, the Claiborne Group otodontids seem to document the transition from *Otodus* (*Otodus*) to *Otodus* (*Carcharocles*) through the acquisition of serrations and an increase in overall size. Unserrated *Otodus* (*Otodus*) teeth do not appear in any of our Lisbon Formation or Gosport Sand samples. Cappetta & Case (2016) reported three specimens from site ACov-11 that they claimed were derived from bed 2 of Copeland (1966) at the base of the Lisbon Formation. However, we question the claim made by Cappetta & Case (2016) that the entirety of their Lisbon sample was recovered *in situ* from this bed, as the authors acknowledged that they obtained specimens from avocational collectors, who typically screen from lag deposits along river banks.

Over the past decade the senior author of this study (JAE) has led at least a dozen expeditions to the ACov-11 locality and has observed that Copeland's (1966) bed 2 is only accessible when the water level of the river is extremely low. Although the entirety of this 20 cm thick bed contains vertebrate remains, they are especially concentrated within the lowermost 5.0 cm, a horizon that requires extensive excavation to access and recover samples from, and one where the basal contact is often below the water level. Numerous excavation pits made by avocational collectors have been observed at the site, all of which penetrated beds higher in the Lisbon Formation section, specifically beds three through five of Copeland (1966). Although these higher beds also contain vertebrate remains, teeth and bones are far less abundant than at the base of bed 2. Vertebrate remains at site ACov-11 are commonly obtained by screening gravel bars in the river itself. These specimens, however, lack stratigraphic control, as they may have been derived from any of the fossiliferous beds of the Lisbon Formation or the underlying Tallahatta Formation. These observations suggest that, although many of the teeth described by Cappetta & Case (2016) were derived from bed 2, their sample also contains a mixture of fossils collected from beds higher or lower in the exposed section. It is the higher beds where a majority of the specimens collected by avocational collectors are derived (JAE, pers. observ.).

It is our interpretation that the *Cretalamna* teeth identified by Cappetta & Case (2016) are actually *Otodus* (*Otodus*) and the specimens were likely derived from the Tallahatta Formation, and not within the basal Lisbon Formation as reported. This interpretation is supported by the absence of *Otodus* teeth within our much larger, stratigraphically controlled, basal Lisbon sample from this locality (n = 5121) and is more consistent with our observations of the occurrence of otodontid teeth from all other Claiborne Group localities.

If these observations are correct, it suggests that the acquisition of serrations on otodontid teeth, and thus the transition from *Otodus* (*Otodus*) to *Otodus* (*Carcharocles*), occurred stratigraphically in the upper part of Zone NP14, just below the contact of the Tallahatta and Lisbon formations. This is supported by the absence of *Otodus* (*Carcharocles*) sp. teeth in the Tallahatta Formation (zones NP14 and below), and the apparent absence of the unserrated *Otodus* (*Otodus*) sp. teeth within the Lisbon Formation and from stratigraphically higher units (zones NP15 and above).

MITSUKURINIDAE. This family is represented in our sample by two taxa, *Anomotodon* sp. (n = 6) and *Striatolamia macrota* (n = 2123). Both taxa are present in all three Claiborne Group formations, and *S. macrota* is by far more abundant within these units than *Anomotodon*. In fact, *S. macrota* is the most abundant taxon in our entire Claiborne sample. The *Anomotodon* sp. specimens in our sample represent the first report of this genus in Alabama.

ODONTASPIDIDAE. Eight members of the Odontaspididae are represented in our sample, including *Brachycarcharias atlasi*, *Brachycarcharias lerichei*, *Brachycarcharias twiggsensis*, *Hypotodus verticalis*, *Jaekelotodus robustus*, *Mennerotodus* sp., *Odontaspis winkleri*, and *Tethylamna dunni*. *Brachycarcharias atlasi* (n = 113) occurs in all three Claiborne Group formations, and based on additional samples at MSC, this morphology also occurs in the underlying Thanetian Nanafalia Formation and Ypresian Hatchetigbee Formation. *Brachycarcharias atlasi* teeth appear to be absent from any Danian deposits in Alabama (JAE, pers. observ.), indicating that this species arrived in the Mississippi Embayment of North America in the Thanetian. This species has only been reported from Belgium (Taverne & Nolf 1978), Germany (Von der Hocht 1986), and Morocco (Gheerbrant *et al.* 2017), making the specimens from Alabama the first report of the taxon in North America. *Brachycarcharias lerichei* occurs in all three Claiborne Group formations and is the second most abundant taxon identified in our sample (n = 1370), behind *Striatolamia macrota* (n = 2123). Within other stratigraphic units in Alabama, *B. lerichei* is absent from Danian and Thanetian deposits, with its first appearance in small numbers within the Ypresian Hatchetigbee Formation. Although we identified only 21 specimens belonging to *B. twiggsensis*, this taxon appears confined to the Bartonian Gosport Sand, a lithostratigraphic unit that is temporally slightly older than the *B. twiggsensis* type unit in Georgia (NP19/20), the Dry Branch Formation (see Case 1981). The Gosport Sand specimens represent the first occurrence of *B. twiggsensis* in Alabama.

We identified a number of teeth of *H. verticalis* (n = 121) and *J. robustus* (n = 157) in our sample, and both species were recovered from all three Claiborne Group formations. *Mennerotodus* sp. is represented in our sample by only five teeth and, like *B. twiggsensis*, does not appear until the Bartonian (Gosport Sand). This correlates to the age of the type species for the genus, *Mennerotodus glueckmani* Zhelezko, 1994, from Bartonian deposits in Kazakhstan. This genus has only been reported previously from France (Dutheil *et al.* 2006), Kazakhstan (Zhelezko 1994), and Russia (Malyshkina 2006), and the specimens in our sample represent the first recognized occurrence of *Mennerotodus* in North America. In contrast, *O. winkleri* (n = 5) is absent from our Gosport Sand samples but is present within the Tallahatta and the basal Lisbon formations. This corresponds with the known stratigraphic range of *O. winkleri*, as it occurs in Lutetian deposits elsewhere but is apparently absent in the Bartonian (see Cappetta 2012). *Tethylamna dunni* was originally erected by Cappetta & Case (2016) based on specimens collected from the contact of the Tallahatta and Lisbon formations (zones NP14 and NP15) at site ACov-11. In our sample, additional *T. dunni* specimens (n = 96) were derived from the lower Tallahatta Formation at site ADl-1, the "upper" Lisbon Formation at site ACl-3, the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21. These specimens represent the first of this species to be collected from outside of the type locality (ACov-11) and horizon (Lisbon Formation) and expands the stratigraphic range of *T. dunni* back into upper Ypresian/lower Lutetian of Zone NP14 (i.e., the Tallahatta Formation) and up into the middle Bartonian of Zone NP17 (i.e., the Gosport Sand).

LAMNIDAE. Within the Claiborne Group this family is represented only by *Macorhizodus praecursor*. This species is uncommon in our sample (n = 20), but specimens have been recovered from all three Claiborne Group formations. Additional specimens at MSC indicate that this taxon is more common in Priabonian deposits in the state (such as in the Yazoo Clay).

SCYLIORHINIDAE. The family is represented by two genera in our sample, *Premontreia* and *Stenoscyllium*. The lone *Premontreia* specimen examined is referred to the subgenus *Premontreia* (*Oxyscyllium*) and was collected from the contact of the Tallahatta and Lisbon formations (lower Lutetian) at site ACon-6 (see Maisch *et al.* 2014). A second specimen was referred to *Premontreia* (*Premontreia*) *degremonti* by Cappetta & Case (2016) from the same horizon at site ACov-11. Additional specimens are required to elucidate the presences of one or two species of *Premontreia* within the Tallahatta/Lisbon contact zone, but no *Premontreia* teeth were identified within our "upper" Lisbon Formation or Gosport Sand samples. Members of *Premontreia* have been documented elsewhere from deposits dating as late as the Priabonian (Cappetta 2012).

The *Stenoscyllium* specimens in our sample (n = 3) were all collected from the lower Tallahatta Formation at site ADl-1. These specimens overlap stratigraphically with those collected from the type locality in Morocco, which produced specimens from throughout the Ypresian (Noubhani & Cappetta 1997). *Stenoscyllium* is absent from both our Lisbon Formation and Gosport Sand samples, suggesting that this genus had a very limited Ypresian range. Tentatively referred to *Stenoscyllium* cf. *S. priemi*, the specimens in our sample represent the first occurrence of this genus and species in North America.

TRIAKIDAE. Claibornian representatives of this family include *Pachygaleus* and three species of *Galeorhinus*. *Pachygaleus lefevrei* (n = 9) was recovered from sites that expose the lower Tallahatta Formation (upper Ypresian to lower Lutetian, Zone NP14), the contact of the Tallahatta and Lisbon formations, and the "lower" Lisbon Formation (both Lutetian, zones NP14 and NP15). This species, however, appears absent from any Bartonian deposits in the state and elsewhere (see Cappetta 2012).

Of the three *Galeorhinus* species, *Galeorhinus* aff. *G. duchaussoisi* (n = 10), *Galeorhinus louisi* (n = 2), and *Galeorhinus ypresiensis* (n = 3), only *Galeorhinus* aff. *G. duchaussoisi* occurs in all three Claiborne Group formations. In our sample, *G. louisi* was collected from Zone NP14 deposits within the lower Tallahatta Formation at site ADl-1. This taxon has previously been reported only from the early Ypresian of northern France (Adnet & Cappetta 2008), so the specimens in our sample represent a slight range extension for this species into the late Ypresian and are the first occurrences of this taxon in North America. Teeth of *G. ypresiensis*, on the other hand, were only identified from the Bartonian Gosport Sand at site ACl-15 within Zone NP17. Originally described from Ypresian deposits in Belgium (Casier 1946), this species has since been reported from deposits as young as the Bartonian elsewhere (Leder 2013). The absence of this species from the Tallahatta and Lisbon formations suggests that this taxon arrived relatively late to the Gulf of Mexico. The *G. ypresiensis* specimens in our sample represent the first occurrence of this taxon in Alabama.

HEMIGALEIDAE. The only hemigaleid taxon occurring in the Claiborne Group is *Hemipristis curvatus* (n = 6). This species was identified only from the Bartonian Gosport Sand at site ACh-21 within Zone NP17. *Hemipristis curvatus* seems to first appear in Bartonian deposits elsewhere (see Kruckow & Thies 1990; Mustafa & Zalmout 2002; Parmley & Cicimurri 2003; Chandler *et al.* 2006; Tanaka *et al.* 2006; Adnet *et al.* 2010; Underwood *et al.* 2011; Cappetta 2012), and in Alabama the species is much more common in Priabonian deposits (JAE, pers. observ.).

CARCHARHINIDAE. This family is represented by seven genera (*Carcharhinus*, *Negaprion*, *Rhizoprionodon*, *Scoliodon*, *Abdounia*, *Physogaleus*, *Pseudabdounia* gen. nov.) and 11 species, and is the most diverse family in the Claiborne Group of Alabama. The sole representative of *Carcharhinus* includes a new species, *Carcharhinus mancinae* sp. nov. (n = 103), which is only known from the "upper" Lisbon Formation and Gosport Sand. This range indicates that this species is restricted to the Bartonian (zones NP16 and 17).

Negaprion gilmorei (n = 1519) is the third most abundant taxon identified in our Claibornian sample. Despite this abundance, this species is absent from the Tallahatta Formation (upper Ypresian to lower Lutetian), indicating that it arrived during the middle Lutetian. This seems to correspond with middle Eocene first occurrences documented elsewhere, including the Caribbean (Krukow & Thies 1990), and Georgia (Parmley & Cicimurri 2003), North Carolina (Case 1980), and Virginia (Müller 1999) in the USA.

The single *Rhizoprionodon* species we identified is assigned to *R. ganntourensis* (n = 156). This species occurs within all three Claiborne Group formations, a range that appears to be consistent with its Eocene distribution elsewhere (Cappetta & Traverse 1988; Dutheil 1991; Case *et al.* 1996; Noubhani & Cappetta 1997; Mustafa *et al.* 2005; Paul 2005; Iserbyt & De Schutter 2012). The presence of this species in our sample represents the first confirmation of this taxon in North America.

Scoliodon conecuhensis was first described from the contact of the Tallahatta and Lisbon formations (zones NP14 and NP15) at site ACov-11 (Cappetta & Case 2016). Our sample of 130 specimens indicates this species was present in all three Claiborne Group formations, and our specimens from sites ADl-1, ACh-14, ACh-21, ACl-4, and ACl-15 represent the first occurrences of this taxon from outside of the type locality. These specimens also extend the stratigraphic range of this species into the Ypresian within Zone NP14 (lower Tallahatta Formation) and into the Bartonian within Zone NP17 (Gosport Sand).

Our sample of Claiborne Group *Abdounia* contains three species, including *A. beaugei* (n = 50), *A. enniskilleni* (n = 302), and *A. minutissima* (n = 71). *Abdounia beaugei* and *A. minutissima* were identified from all three Claiborne Group formations, however *A. enniskilleni* is absent from the lower Tallahatta Formation (upper Ypresian to lower Lutetian) and apparently first occurs within the Tallahatta and Lisbon formation contact zone of Lutetian age (the contact of zones NP14 and NP15). The absence of *A. enniskilleni* from Ypresian deposits in our sample is corroborated by reports of its temporal occurrence elsewhere and suggests that the geographic range of this species is limited to the Caribbean and North America (see Westgate 1984; Kruckow & Thies 1990; Müller 1999; Case & Borodin 2000a; 2000b; Parmley & Cicimurri 2003; Robb 2006; Cappetta 2012; Stringer & King 2012). The *A. beaugei* specimens in our sample represent the first occurrence of this taxon in Alabama.

A result of our analysis is that we removed two species from *Abdounia* and placed them within a new genus, *Pseudabdounia* gen. nov. These include *Pseudabdounia claibornensis* gen. et comb. nov. (n = 89) and *P. recticona* gen. et comb. nov. (n = 168). Within our Claibornian sample, *P. recticona* gen. et comb. nov. is absent from the Gosport Sand, whereas *P. claibornensis* gen. et comb. nov. is unknown from the Tallahatta or Lisbon formations. This suggests that *A. recticona* was supplanted by *A. claibornensis* during the middle Bartonian, within Zone NP17.

Two species of *Physogaleus* were identified in our sample, including *P. alabamensis* comb. nov. (n = 507) and *P. secundus* (n = 786). Both species were identified within all three Claiborne Group formations with *P. secundus* having a worldwide distribution (see Cappetta 2012). The *P. alabamensis* comb. nov. morphology is relatively abundant in our Alabama sample, and is also common in the U.K. (D.J. Ward, pers. com.) and is apparently present in both Belgium and India, although the specimens in these latter two occurrences have been misidentified as another taxon (see Van den Eeckhaut & De Schutter 2009: pl. 20, figs 8–11; Pandey *et al.* 2018: fig. 4a–b). Examination of high-resolution images of the *alabamensis* morphology led us to conclude that it is more accurately assigned to *Physogaleus* rather than *Galeocerdo*.

GALEOCERDIDAE. This monogeneric family is represented by two species within the Claiborne sample, *Galeocerdo clarkensis* (n = 86) and *Galeocerdo eaglesomei* (n = 38). *Galeocerdo clarkensis* occurs throughout the Gosport Sand, but the species is absent from the Tallahatta and Lisbon formations.

The type specimens for *G. clarkensis* were derived from upper Eocene (Priabonian) Jackson Group deposits in Clarke County, Alabama (White 1956). The known temporal range of *G. clarkensis* is the Bartonian to Priabonian, and to date this taxon is known with confidence only from Alabama, but the species may occur in Georgia. *Galeocerdo eaglesomei* teeth occur within the contact zone of the Tallahatta and Lisbon formations, and within the Lisbon Formation and Gosport Sand. Interestingly, *Galeocerdo* teeth are absent from the Tallahatta Formation sample, which indicates an lower Lutetian (lower part of Zone NP15) first occurrence of the genus in Alabama.

Galeomorphii indet. A single broken tooth in our sample, SC2012.47.32, differs from all the others in our sample and is reminiscent of a member of the Palaeospinacidae. This tooth was recovered *in situ* from the base of the Lisbon Formation at site ACov-11, placing it within Zone NP15. However, according to Cappetta (2012) and Cappetta & Case (2016), members of the Palaeospinacidae had a range that extended from the early Jurassic to the late Paleocene (Thanetian). Additional and more complete specimens are needed to determine the identity of this tooth.

"Rhinobatidae". One species within this family, "*Rhinobatos*" *bruxelliensis* (n = 68), has been identified from Claiborne Group strata in Alabama. Teeth of this species occur in all three Claiborne Group formations, including 14 specimens from the basal Gosport Sand. These latter specimens indicate a range extension for "*R.*" *bruxelliensis* into the Bartonian (Zone NP17), as prior studies elsewhere reported this taxon from only Ypresian and Lutetian deposits (see Kemp 1982; Bor 1985; Von der Hocht 1986; Ward & Wiest 1990; Averianov & Udovichenko 1993; Kent 1999a; Paul 2005; Tabuce *et al.* 2005; Adnet 2006; Cappetta 2012; Iserbyt & De Schutter 2012).

Pristidae. Rostral spines of three genera were identified within our sample, including *Anoxypristis* sp. (n = 18), *Pristis* sp. (n = 247), and *Propristis schweinfurthi* (n = 10). Spines of *Anoxypristis* sp. and *Pristis* sp. occur in all three Claiborne Group formations, but *Propristis schweinfurthi* was only identified from the Gosport Sand. Additional *P. schweinfurthi* specimens in the collections at MSC were collected from the stratigraphically higher (Priabonian) Yazoo Clay, and the known stratigraphic range for the genus in Alabama extends from the Bartonian to the Priabonian. This temporal range is consistent with occurrences elsewhere in the Atlantic Coastal Plain, where the species occurs in the Tupelo Bay (Bartonian) and Parkers Ferry (Priabonian) formations of South Carolina and the Clinchfield Formation (Bartonian) of Georgia (DJC, unpublished data). The *P. schweinfurthi* specimens in our sample represent the first occurrence of this taxon in Alabama.

Dasyatidae. One dasyatid genus occurs in our Claiborne sample, "*Dasyatis*", and two distinct species have been identified. Sixteen teeth were identified as "*Dasyatis*" *jaekeli*, a species that has been previously reported from early-to-middle Eocene deposits in Belgium (Herman & Van den Eeckhaut 2010), France (Dutheil 1991), Germany (Von der Hocht 1986), Romania (Paul 2005), Togo (Cappetta & Traverse 1988), the United Kingdom (Kemp 1982) and, in the USA, from Alabama (Cappetta & Case 2016) and Mississippi (Case 1994a). The specimens in our sample were collected from the lower Tallahatta Formation and basal Lisbon Formation, representing an upper Ypresian (Zone NP14) to Lutetian (Zone NP15) range for this species in Alabama. We identified eight teeth as "*Dasyatis*" aff. "*D.*" *charlisae*, a species that has been previously reported from middle-to-late Eocene deposits in the Caribbean (Kruckow & Thies 1990) and Pakistan (Case & West 1991), and in the USA from Alabama (Cappetta & Case 2016) and Georgia (Case 1981). The specimens in our sample were derived from the "lower" and "upper" members of the Lisbon Formation, indicating a lower Lutetian to middle Bartonian range for this species in the state (zones NP15 to NP17). An additional eight teeth could not be identified beyond "*Dasyatis*" sp. due to their poor preservation. These specimens were derived from the basal Lisbon Formation (n = 6) and the basal Gosport Sand (n = 2), within zones NP15 and NP17, respectively. Due to the stratigraphic overlap of "*D.*" *charlisae* and "*D.*" *jaekeli* within the Lutetian Zone NP15, it is unclear to which taxon these unspeciated basal Lisbon specimens might belong. However, the specimens from the basal Gosport Sand (Zone NP17) may belong to "*D.*" *charlisae*, as the range of "*D.*" *jaekeli* does not appear to extend into the Bartonian (see Cappetta 2012 and other references cited herein).

Incertae familiae. Three genera in our sample are of uncertain familial placement, *Aturobatis*, *Coupatezia*, and *Hypolophodon*. Two specimens in our sample were identified as belonging to *Aturobatis* aff. *A. aquensis*, a species that has been documented from the middle Lutetian in France (Adnet 2006; Cahuzac *et al.* 2007) and the Priabonian of Morocco (Adnet *et al.* 2010). Cappetta (2012) cited unpublished specimens from the Ypresian of Virginia in the USA, but this report could not be verified from the publication because he did not figure specimens or report their whereabouts. The two specimens in our sample were collected from the basal Lisbon Formation at site ACov-11 (middle Lutetian, Zone NP15) and represent the first confirmed occurrence of the taxon in North America.

The *Coupatezia* sp. teeth in our sample (n = 18) were derived from the lower Tallahatta Formation and the basal Lisbon Formation. The apparent absence of *Coupatezia* from the "upper" member of the Lisbon Formation and the Gosport Sand indicates this species had an upper Ypresian to middle Lutetian (zones NP14 and NP15) range in Alabama.

Hypolophodon teeth, specifically *H. sylvestris* (n = 7), were recovered only from the lower Tallahatta Formation (upper Ypresian, Zone NP 14) at site ADl-1. These teeth represent the first occurrences of this taxon in Alabama.

Gymnuridae. This family is represented in our sample by one taxon, *Jacquhermania duponti*. A total of 28 teeth were identified, and they were derived from the middle Lutetian basal Lisbon Formation (n = 11) and Bartonian Gosport Sand (n = 17). Currently a monospecific genus, *J. duponti* has been previously reported from late Paleocene (Thanetian) to middle Eocene (Lutetian) deposits in Belgium (Herman & Van den Eeckhaut 2010), China (Li 1997), France (Dutheil 1991), Morocco (Arambourg 1952), Nigeria (Cappetta 1972), Tunisia (Arambourg 1952), the United Kingdom (Kemp 1982), and in the USA from Alabama (Cappetta & Case 2016), South Carolina (Case *et al.* 2015), and Virginia (Kent 1999a). The 17 specimens from the Gosport Sand indicate that *J. duponti* persisted into the Bartonian, at least into the middle part of Zone NP17. The species is absent from our Tallahatta Formation sample, suggesting it arrived within the coastal waters of Alabama sometime during the middle Lutetian (Zone NP15).

Myliobatidae. This family is represented in our sample by three known subfamilies, the Myliobatinae, Rhinopterinae, and Mobulinae, and nine genera. The Myliobatinae is represented by five taxa, *Aetobatus* sp. (n = 127), *Aetomylaeus* sp. (n = 392), *Myliobatis* sp. 1 (n = 312), *Myliobatus* sp. 2 (n = 287), and *Pseudaetobatus belli* (n = 225). Teeth belonging to *Aetobatus* sp. were identified from the Tallahatta and Lisbon Formation contact zone, the Lisbon Formation, and Gosport Sand, but were absent from sites exposing Tallahatta Formation proper deposits. In contrast, *P. belli* was found to occur only in the Meridian Sand Member of the Tallahatta Formation, and the lower Tallahatta Formation. This suggests that the ecological niche filled by *P. belli* during the Ypresian was occupied by *Aetobatus* sp. in the lower Lutetian at the top of Zone NP14 and base of Zone NP15. A similar trend was observed with the *Myliobatis* specimens in our sample, as the *Myliobatis* sp. 1 morphology is confined to the Meridian Sand Member and other beds in the lower Tallahatta Formation, whereas the *Myliobatis* sp. 2 morphology was identified from the Tallahatta and Lisbon Formation contact zone, the Lisbon Formation, and Gosport Sand. Because these two morphologies do not appear to co-occur, it suggests the taxon represented by *Myliobatis* sp. 1 was supplanted by the sp. 2 morphology at some point within Zone NP14 in the lower Lutetian. *Aetomylaeus* sp. teeth were the most common member of the Myliobatinae identified in our sample and were confirmed from all three Claiborne Group formations (zones NP12 to NP17).

The Rhinopterinae is represented in our sample by one taxon, *Rhinoptera* sp. A wide range of variation was observed within the *Rhinoptera* sample, and the various morphological variants we encountered were found within each of the Claiborne formations. At this time the evidence suggests a single Clairbornian species, and the number of *Rhinoptera* teeth identified (n = 1891) outnumbered all the members of the Myliobatinae (n = 1424) and Mobulinae (n = 13) combined.

One taxon, *Meridiania* cf. *M. convexa*, is of uncertain subfamilial placement. Nevertheless, *Meridiania* specimens (n = 4) have been confirmed from the lower Tallahatta Formation (n = 1) and the Gosport Sand (n = 3). This taxon, however, is absent from our Lisbon Formation samples, but this could be related to the overall rarity of these teeth in the Claibornian. *Meridiania convexa* teeth have previously been confirmed only from Thanetian and Ypresian deposits in Mississippi (Case 1994a), South Carolina (Cicimurri 2010), and Virginia (Kent 1999a). The specimen from the lower Tallahatta Formation (upper Ypresian, Zone NP14) falls within this stratigraphic range for *M. convexa*. The Gosport Sand specimens indicate that either this species had a range that extended into the Bartonian Zone NP17, or the teeth represent a new Bartonian species of *Meridiania*. Larger samples of specimens will hopefully elucidate the taxonomy of these teeth. Nevertheless, the specimens in our sample represent the first occurrence of *Meridiania* in Alabama, and the Gosport Sand teeth represent a significant temporal range extension for the genus.

An additional myliobatid taxon of uncertain subfamilial placement within our Claiborne sample is *Leidybatis jugosus* (n = 71). This species is known primarily from the Tallahatta/Lisbon Formation contact zone and the basal Lisbon Formation (Lutetian, zones NP14 and NP15), but two specimens were collected from the lower Tallahatta Formation. *Leidybatis jugosus* was absent from our "upper" Lisbon and Gosport Sand samples, indicating a temporal range in the state that extends from the upper Ypresian to the middle Lutetian within zones NP14 and NP15.

The Mobulinae is represented by two taxa, including *Burnhamia daviesi* (n = 12) and *Eoplinthicus yazooensis* (n = 1). Although known from a small number of specimens, *B. daviesi* teeth were identified from all three Claiborne Group formations, giving it a temporal range in the state that extends from the upper Ypresian to the Bartonian (zones NP14 to NP17). The specimens in our sample represent the first occurrences of *B. daviesi* in Alabama. The genus *Eoplinthicus* currently contains two species, *E. yazooensis* and *E. underwoodi*, the latter of which is known only from the Priabonian Gerran Member of the Samlat Formation in Morocco (Adnet *et al.* 2012). *Eoplinthicus yazooensis* was heretofore only known from the Priabonian Yazoo Clay of Louisiana (Cappetta & Stringer 2002), but the singular specimen in our sample, ALMNH PV1985.35.65 (Fig. 54), was collected from the Gosport Sand (Bartonian, Zone NP17) at site ACh-21. Our specimen is significant because it represents the first record of this taxon in Alabama and is the first occurrence of this species from outside of the type locality. In addition, this specimen is the stratigraphically oldest representative of the genus, and the temporal range of the taxon is extended back into the Bartonian, within the middle of Zone NP17.

Batomorphii indet. This family is represented in our sample by three teeth, all of which were collected from the basal Lisbon Formation at site ACov-11 (lower Lutetian, Zone NP15). These teeth are of uncertain generic or specific placement and could only be referred to Batomorphii indet. These teeth appear unique from all the other rays in our sample, but better preserved specimens are needed to determine their identity.

Incertae familiae. One osteichthyan genus in our sample, *Cylindracanthus*, is of uncertain familial placement. Two species of *Cylindracanthus* were identified in Claiborne Group strata, *C. ornatus* (n = 3) and *C. rectus* (n = 46), that were differentiated by the presence or absence of ventral denticle-bearing furrows on the rostrum. However, this distinction could only be made on well preserved specimens exhibiting the complete circumference of the rostrum, and poorly preserved material was identified only as *Cylindracanthus* sp. (n = 72). We identified *C. rectus* rostra from the Tallahatta and Lisbon Formation contact zone, the Lisbon Formation, and Gosport Sand, and the species has also been observed by the senior author (JAE) in the upper Yazoo Clay (Priabonian) in Alabama. Thus, *C. rectus* has a middle Lutetian (at the contact of zones NP14 and NP15) to at least lower Rupelian (Marianna Limestone, NP Zone 21; JAE, pers. observ.) range in Alabama. Definitive *C. ornatus* specimens are much less common in Claiborne Group deposits, being identified only from the basal Lisbon Formation at site ACov-11. This species, however, is known from Upper Cretaceous deposits in Alabama (see Parris *et al.* 2001), and a late Eocene specimen from the state that was originally referred to *C. rectus* by Leriche (1942), also belongs to this taxon. This indicates that *C. ornatus* had an extremely long temporal range, from the Late Cretaceous to the Priabonian, at least into Zone NP18. The paucity of *C. ornatus* specimens in our sample, and its apparent absence from Tallahatta Formation and Gosport Sand samples, could be attributable to the poor preservation of much of our *Cylindracanthus* material, as any of the partial specimens could belong to this species. Although the stratigraphic ranges of both *C. ornatus* and *C. rectus* overlap in the Eocene, the absence of *C. rectus* in the Late Cretaceous (see Thurmond & Jones 1981; Parris *et al.* 2001) lends support to the validity of both species, and that the presence or absence of ventral denticle-bearing furrows on the rostra is a taxonomically viable characteristic and not a result of interspecific variation.

PYCNODONTIDAE. A total of 21 teeth from Claiborne Group deposits were assigned to *Pycnodus* sp. Members of the genus *Pycnodus* have been previously reported from Jurassic to Eocene deposits in Ethiopia (Goodwin *et al.* 1999), France (Laurent 2003), Germany (Münster 1846), India (Rana 1990), Italy (Bannikov & Carnevale 2009), Morocco (Martill *et al.* 2011), Niger (Moody & Suttcliffe 1991), Portugal (Rey 1972), Saudi Arabia (Abbass 1972), Switzerland (Haefeli *et al.* 1965), the United Kingdom (Kemp 1985), and in the USA from Arkansas (Pittman 1984), Mississippi (Case 1994b), and Virginia (Weems 1999). The specimens in our sample were derived from the lower Tallahatta Formation (upper Ypresian to lower Lutetian, Zone NP14), the contact zone of the Tallahatta and Lisbon formations, and the basal Lisbon Formation (all Lutetian Stage, zones NP14 and NP15). These specimens represent the first occurrence of this genus in Alabama, and the apparent absence of teeth from the "upper" member of the Lisbon Formation and the Gosport Sand suggests that *Pycnodus* did not persist into the Bartonian.

LEPISOSTEIDAE. Fossil gars have been reported from Upper Cretaceous (Ciampaglio *et al.* 2013), Eocene (Thurmond & Jones 1981; Clayton *et al.* 2013; Maisch *et al.* 2016), Miocene (Ebersole & Jacquemin 2018), and Pleistocene (Jacquemin *et al.* 2016) deposits in Alabama. Although the teeth, scales and vertebrae in our sample could not be confidently assigned to a genus, Lepisosteidae (n = 36) remains were identified from the contact of the Tallahatta and Lisbon formations, the Lisbon Formation, and the Gosport Sand. No gar fossils were identified within the lower or main body of the Tallahatta Formation, but Ypresian specimens at MSC derived from the underlying Hatchetigbee Formation suggest that the absence may be related to depositional setting, as extant Lepisosteidae primarily inhabit low gradient lentic and lotic freshwater habitats (Page & Burr 2011).

PHYLLODONTIDAE. This extinct family is represented in our sample by three taxa, *Egertonia isodonta* (n = 128), *Paralbula* aff. *P. marylandica* (n = 69) and *Phyllodus toliapicus* (n = 26). According to Estes (1969), Case (1994b), Weems (1999), and Clayton *et al.* (2013), *E. isodonta* has been documented from Paleocene to middle Eocene deposits in Belgium, France, the United Kingdom, and the West Indies, and in the USA from Alabama, Georgia, Mississippi, North Dakota, South Carolina, and Virginia. The specimens in our sample were derived from all three Claiborne Group formations, indicating that *E. isodonta* persisted at least into the Bartonian within the middle of Zone NP17. *Paralbula* aff. *P. marylandica* (n = 69) was only recovered from the lower Tallahatta Formation and "lower" Lisbon Formation in Alabama (upper Ypresian and lower Lutetian, zones NP14 and NP15). *Paralbula* *marylandica* has been previously documented from Upper Cretaceous to lower Eocene deposits in Maryland (Blake 1940), New Jersey (Schein *et al.* 2011), Texas (Westgate 1989), and Virginia (Weems 1999) in the USA, so the "lower" Lisbon Formation specimens in our sample (n = 52) represent a slight Eocene range extension for this species into the lower Lutetian (Zone NP15). Overall, these specimens represent the first occurrence of *Paralbula* aff. *P. marylandica* in Alabama. *Phyllodus toliapicus* seems to have had an extensive temporal and geographic distribution, having been reported from Maastrichtian to middle Eocene deposits in Belgium (Casier 1946), France (Estes 1969), Morocco (Arambourg 1952), the United Kingdom (White 1931), and in the USA from Arkansas (Becker & Chamberlain 2012), Montana (Estes 1969), Mississippi (Case 1994b), New Jersey (Leriche 1942), South Carolina (Weems 1998), Virginia (Weems 1999), and Wyoming (Lillegraven & Eberle 1999). The *P. toliapicus* specimens in our sample were collected from all three Claiborne Group formations, and this material represents the first documented occurrence of this taxon in Alabama. Additionally, three specimens collected from the basal Gosport Sand represent a range extension for this species into the Bartonian (middle of Zone NP17).

ALBULIDAE. Two species of *Albula*, *A. eppsi* (n = 33) and *A. oweni* (n = 25), record the presence of the Albulidae within Claiborne Group strata. The *A. eppsi* teeth were derived from the lower Tallahatta Formation at site ADl-1 (n = 23), the Tallahatta Formation at site AMo-8 (n = 2), the basal Lisbon Formation at site ACov-11 (n = 6), and the basal Gosport Sand at site ACl-4 (n = 1). Prior reports of this species have been limited to lower Eocene deposits in the United Kingdom (White 1931), and Mississippi (Case 1986) and Virginia in the USA (Weems 1999), and a Gosport Sand specimen in our sample represents a slight range extension into the middle Bartonian (within Zone NP17). These *A. eppsi* teeth also represent the first occurrence of the species in Alabama. Teeth of *A. oweni* were recovered from all three Claiborne Group formations. This appears to correspond with the range of *A. oweni* elsewhere, with prior reports from Paleocene to middle Eocene deposits in Belgium (Leriche 1905), Morocco (Arambourg 1952), the United Kingdom (Casier 1966), and in the USA from Arkansas (Becker & Chamberlain 2012), Mississippi (Case 1994b), South Carolina (Weems 1998), and Virginia (Weems 1999).

OSTEOGLOSSIDAE. 16 teeth assigned to the Osteoglossidae demonstrate that members of the family occur within all three Claiborne Group formations. Paleogene members of the Osteoglossidae have been reported previously from Paleocene to Oligocene deposits in Bolivia (Marshall *et al.* 1983), Canada (Li & Wilson 1996), Denmark (Schwarzhans 2003), Kenya (Ducrocq *et al.* 2010), Morocco (Arambourg 1952), Niger (Cappetta 1972), Oman (Thomas *et al.* 1999), Pakistan (Murray & Thewissen 2008), Tanzania (Herendeen & Jacobs 2000), the United Kingdom (Kemp *et al.* 1979), and in the USA from Alabama (Frizzell & Dante 1965), Louisiana (Harlan 1834), Maryland (Weems & Horman 1983), Mississippi (Case 1994b), North Dakota (Crane *et al.* 1990), Texas (Frizzell & Dante 1965), Virginia (Weems 1999), and Wyoming (Divay & Murray 2016).

ARIIDAE. This family is represented in our Claiborne sample by a total of 66 fin spines. According to Nelson *et al.* (2016), the oldest Ariidae spines are known from the Late Cretaceous of South America, and by the Eocene the family was globally distributed. Within our sample, the fin spines were derived from the Tallahatta and Lisbon Formation contact zone, the Lisbon Formation, and the Gosport Sand, but no specimens were recovered from the lower part of the Tallahatta Formation (upper Ypresian, zones NP12 to NP14). However, early Eocene (Ypresian) Ariidae specimens at MSC that were derived from the underlying Hatchetigbee Formation suggest that the absence from the Tallahatta Formation reflects an environmental preference or preservation bias.

SPHYRAENIDAE. Barracuda teeth, *Sphyraena* sp. (n = 71), were recovered from all three Claiborne Group formations. Eocene *Sphyraena* teeth have been reported from India (Rose *et al.* 2006), Italy (Bannikov &

Carnevale 2009), Morocco (Adnet *et al.* 2010), Nigeria (Chavan 1938), Pakistan (Case & West 1991), the United Kingdom (Bone *et al.* 1991), and in the USA from Alabama (Clayton *et al.* 2013; Maisch *et al.* 2016), Arkansas (Palmer 1939), Georgia (Westgate 2001), Louisiana (Lancaster 1986), and Virginia (Weems 1999). Based on mitochondrial DNA from 20 of the 27 species of extant *Sphyraena*, Santini *et al.* (2015) elucidated a late Paleocene origin of the genus and radiation of the modern lineages during the Lutetian (~45 Ma). Numerous nominal Eocene species have been described, and a large Priabonian species in Alabama and South Carolina is represented by fossils at both MSC and SC that are up to three times the size of the specimens in our Claiborne sample (DJC & JAE, pers. observ.).

Trichiuridae. Our Claiborne sample includes three trichiurid genera, each represented by one species. *Eutrichiurides plicidens* comb. nov. teeth (n = 11) (a new combination for teeth formerly placed in *Trichiurus*) were derived from the Tallahatta and Lisbon Formation contact zone and the basal Lisbon Formation at site ACov-11, and the basal Gosport Sand at site ACl-4. Prior reports of this species elsewhere have been limited to the Bartonian of Libya (Otero *et al.* 2015), the Ypresian and Lutetian of Morocco (Arambourg 1952), and the middle Eocene (likely Ypresian or Lutetian) of the Republic of Mali (Radier 1959; Longbottom 1984). The absence of *E. plicidens* comb. nov. from any Ypresian deposits in our sample suggests this species likely arrived in the Mississippi Embayment region of Alabama in the early-to-middle Lutetian, within Zone NP14. The Claibornian *E. plicidens* comb. nov. teeth represent the first occurrence of this taxon in North America.

Trichiurides sagittidens specimens in our sample (n = 33) were collected from all three Claiborne Group formations, reflecting a temporal distribution similar to what has been documented elsewhere. This taxon has been previously reported from late Paleocene through late Eocene deposits in Belgium (Leriche 1905), France (Priem 1908), Morocco (Adnet *et al.* 2010), the United Kingdom (Casier 1966), and in the USA from Alabama (Maisch *et al.* 2016), Georgia (Case & Borodin 2000a), Mississippi (Case 1994b), and Virginia (Weems 1999).

Trichiurus oshosunensis teeth (n = 33) have been recovered from one locality in Alabama, site ACov-ll. This species has only previously been reported from the early-to-middle Eocene Oshosun locality (the type locality) in Nigeria (White 1926), making the Claibornian specimens the first occurrence of the species in North America and from outside of the type locality. Our sample suggests that *T. oshosunensis* is absent from the lower Tallahatta Formation and Gosport Sand in Alabama, but lived within zones NP14 and NP15 of the lower-to-middle Lutetian.

Scombridae. Four scombrid species within three genera are part of Claiborne Group paleofaunas, including *Gymnosarda* sp. (n = 1), *Palaeocybium proosti* (n = 6), *Scomberomorus bleekeri* (n = 150), and *Scomberomorus stormsi* (n = 12). The lone *Gymnosarda* specimen in our sample, MSC 37271, was derived from the basal Lisbon Formation (Lutetian, Zone NP15) at site ACov-11. Prior to this study, Eocene *Gymnosarda* specimens were only known from Ypresian deposits in the United Kingdom (Monsch 2005). Thus, specimen MSC 37271 represents the first Eocene occurrence of this genus in North America and the first report of *Gymnosarda* from any Lutetian deposit.

Teeth of *Palaeocybium proosti* were identified from the Tallahatta and Lisbon Formation contact zone at site ACov-11 (Lutetian, zones NP14 and NP15), the basal Gosport Sand at site ACl-4, and the Gosport Sand at site ACh-21 (both Bartonian, Zone NP17). Although this species has been reported from the late Paleocene in Mississippi (see Case 1994b) and early-to-middle Eocene sites elsewhere (see Priem 1908; Casier 1946; Case 1981; Weems 1999; Monsch 2005), specimens are currently unknown from the Tallahatta Formation (upper Ypresian, lower Lutetian) in Alabama. This absence could be due to the apparent rarity of this species, as only six teeth were identified from our sample of over 20 000 specimens. These teeth represent the first documented occurrence of this taxon in Alabama.

Regarding the occurrence of *Scomberomorus*, *S. bleekeri* (n = 150) was found to be much more abundant in our sample than *S. stormsi* (n = 12), and teeth from both taxa were recovered from all three Claiborne Group formations. This suggests that both species persisted in Alabama at least into the middle Bartonian (within Zone NP17). Although *S. bleekeri* has been previously reported in Alabama (see Clayton *et al.* 2013), the *S. stormsi* specimens are the first record of this taxon in the state.

SCIAENIDAE. This family is represented in our sample by one species, *Fisherichthys* aff. *F. folmeri*, with teeth (n = 6) collected from the basal Lisbon Formation at site ACov-11 and the basal Gosport Sand at site ACl-4. The type species, *Fisherichthys folmeri* Weems, 1999, was reported from the upper Paleocene Williamsburg Formation (Zone NP9a) of South Carolina (Cicimurri & Knight 2009; Cicimurri *et al.* 2016), and it occurs within the lower Eocene Bashi Formation (Zone NP10) of Mississippi (Case 1994b), lower Eocene Nanjemoy Formation (Zone NP11) of Virginia (Weems 1999), and the Lutetian in Alabama (Clayton *et al.* 2013). The six specimens in our sample from ACov-11 confirms the presence of *Fisherichthys* in the Lutetian Zone NP15 as reported by Clayton *et al.* (2013). The single specimen from the basal Gosport Sand represents the stratigraphically youngest representative of this taxon and demonstrates that the genus persisted into the Bartonian (within Zone NP17).

OSTRACIIDAE. All three Claiborne Group formations yielded armor plates (n = 12) of an undetermined member, or members, of the Ostraciidae. Paleocene and Eocene ostraciid fishes have been reported from Belgium (Daimeries 1891), Denmark (Schwarzhans 2003), India (Gayet *et al.* 1984), Italy (Tyler 1975), Morocco (Herman 1972), the United Kingdom (Tyler & Gregorova 1991), and in the USA from Alabama (White 1956), Georgia (Case 1981), Louisiana (Stringer 2001), South Carolina (Weems 1998), Maryland (Leriche 1942), and Virginia (Weems 1999).

BALISTIDAE. A singular specimen representing this family was identified in our sample. Although the identity of this specimen could not be determined beyond the family level, the tooth is significant because it represents the first recognized Eocene occurrence of a member of the Balistidae in North America. This specimen was derived from the Gosport Sand at site ACh-21, but additional material from the overlying Priabonian Yazoo Clay (zones NP18 to NP21) are housed at the ALMNH and MSC. These records suggest that a member, or members, of this family arrived within the Alabama Mississippi Embayment during the Bartonian (within Zone NP17) and persisted in the coastal waters at least until the Priabonian (Zone NP21). This corresponds with the arrival of true fossil Balistidae elsewhere, which have been reported from middle Eocene to Pliocene deposits in Austria (Schultz 2006), Peru (Muizon 1983), Russia (Bannikov & Tyler 2008), Slovakia (Schultz 2004), and Switzerland (Tyler & Santini 2002).

DIODONTIDAE. *Progymnodon hilgendorfi* is the only diodontid taxon we identified from Claiborne Group strata of Alabama. The specimens in our sample were derived from the basal Gosport Sand at sites ACl-4 (n = 118) and AMo-4 (n = 2), and the Gosport Sand proper at site ACh-21 (n = 1). This taxon has been previously reported from Paleocene to late Eocene deposits in Belgium (Casier 1952), Egypt (Tyler 1980), Italy (Bassani 1899), and Romania (Ciobanu & Trif 2012), and in the USA from Alabama (Thurmond & Jones 1981) and South Carolina (Weems 1999). The absence of *P. hilgendorfi* from the Tallahatta and Lisbon formations could indicate that the arrival of the species to the Alabama area of the Mississippi Embayment did not occur until the middle Bartonian (within Zone NP17).

Biostratigraphic trends based on higher taxonomic rankings

Utilizing the 20338 specimens in our sample, we analyzed biostratigraphic trends based on higher taxonomic rankings. In total, 34 families (with three additional taxa of uncertain familial placement) and 19 orders were identified in our sample. The biostratigraphic trends we discerned with respect to higher taxonomic groupings are discussed below.

CHONDRICHTHYES VS OSTEICHTHYES. A large disparity is evident in our sample regarding the total number of Chondrichthyes remains (n = 18,229, 89.5%) versus Osteichthyes (n = 2137, 10.5%). Overall, 19 families of elasmobranchs within eight orders and 13 families of bony fish within 11 orders were identified. Of the 32 families represented, one is extinct (the Otodontidae) but the remaining 31 are extant. Sixty-one unequivocal shark and ray taxa were identified, along with 23 bony fish taxa. The disparity in numbers of specimens between elasmobranchs and bony fish likely reflects taphonomic and preservation biases that strongly favor the preservation of shark teeth, as opposed to the more fragile remains of bony fish. This may be compounded by the larger numbers of elasmobranch teeth that were likely available for fossilization, as more teeth were in the jaws at any one time, each being replaced at constant intervals during the lifetime of an individual.

SELACHII VS BATOMORPHII. Of all 18 219 chondrichthyan remains identified in our sample, 8905 belong to Selachii (sharks), whereas 6710 are attributed to Batomorphii (rays). An additional 2584 specimens were assigned to Chondrichthyes only. Of the 19 chondrichthyan families represented, 13 belong to the Selachii and six to Batomorphii. Furthermore 41 unequivocal shark taxa were identified, as opposed to 21 rays. At the species level, the ratio of unequivocal shark (66%) to ray (34%) taxa is very similar to that documented from the early Paleocene (Danian) by Kriwet & Benton (2004), who estimated a ratio of 70% to 30% in favor of sharks during that period of time. Their findings indicate that preservational and taphonomic biases in our sample had less of an impact on shark and ray remains than on the bony fish, and the diversity ratio within our Claiborne Group sample is likely a good estimation of the percentage of shark versus ray species during the early-to-middle Eocene in Alabama. In contrast, when compared to modern ecosystems, the number of ray species slightly exceeds that of sharks (see Compagno 2005). This suggests that rays diversified tremendously at some point after the time our sample represents (i.e., after the Bartonian).

CARCHARHINIFORMES VS LAMNIFORMES. Regarding numbers of selachian teeth identified, those belonging to Carcharhiniformes (n = 4090) and Lamniformes (n = 4408) were the most abundant within our sample. Five families containing 13 genera were identified within the Carcharhiniformes, and 10 genera within four families of Lamniformes. Twenty species of Carcharhiniformes and 13 species of Lamniformes were identified (see Table 2). These findings indicate that relative abundance and taxonomic diversity within the Claiborne Group slightly favors the Carcharhiniformes.

It has been documented that lamniform diversity was greatly impacted by the K-Pg extinction event, when species richness significantly declined. In the early Paleogene the diversity of Lamniformes was surpassed by the Carcharhiniformes, and the latter group experienced a major radiation during the Eocene (Kriwet & Benton 2004; Adnet *et al.* 2007; Underwood *et al.* 2011; Cappetta 2012; Iserbyt & De Schutter 2012; Brazzi *et al.* 2018; Marrama *et al.* 2018). This increase in carcharhiniform diversity appears to be corroborated by the Claiborne Group fossil specimens and species we identified. In terms of diversity, the number of lamniform taxa occurring within each formation is relatively constant, with 10 or 11 species identified in each of the three Claiborne Group units. Although a nearly equal number of lamniform species can be found in each of the formations, the species represented varies slightly. For example, *Otodus* (*Otodus*) sp. teeth were recovered only in the Tallahatta Formation (upper Ypresian), *Otodus* (*Carcharocles*) sp. suddenly appears within the contact zone of the Tallahatta and Lisbon Formation (Lutetian), and *Brachycharias twiggsensis* and *Mennerotodus* sp. appear for the first time in the Gosport Sand (Bartonian). In contrast, the number of carcharhiniform species appears to increase over time. Eleven species were identified within both the Tallahatta and Lisbon formations, but 14 occur in the Gosport Sand. Although the total number of carcharhiniform species is the same in both the Tallahatta and Lisbon formations, the species compositions vary slightly, with *Galeorhinus louisi* and *Stenoscyllium* cf. *S. priemi* being present only in the Tallahatta Formation (upper Ypresian), *Premontreia* (*Oxyscyllium*) *subulidens* being identified only in the contact zone between the two formations, and

Table 2. Lamniform vs carcharhiniform taxa identified within Claiborne Group units in Alabama. Shaded areas represent the stratigraphic range of taxa within Claiborne Group units. x = taxon confirmed within this unit; ? = taxon not confirmed, but likely occurs in this interval.

Order Lamniformes	**Tallahatta Formation**	**Contact Zone**	**Lisbon Formation**	**Contact Zone**	**Gosport Sand**
Otodus (*Otodus*) sp.	x				
Otodus (*Carcharocles*) sp.		x	x	?	x
Anomotodon sp.	x	x	x	?	x
Striatolamia macrota	x	x	x	x	x
Brachycarcharias atlasi	x	x	x	?	x
Brachycarcharias lerichei	x	x	x	?	x
Brachycarcharias twiggsensis					x
Hypotodus verticalis	x	x	x	?	x
Jaekelotodus robustus	x	x	x	x	x
Mennerotodus sp.					x
Odontaspis winkleri	x	?	x		
Tethylamna dunni	x	x	x	?	x
Macrorhizodus praecursor	x	x	x	x	x
Totals by unit	**10**	**9**	**10**	**3**	**11**

Order Carcharhiniformes	**Tallahatta Formation**	**Contact Zone**	**Lisbon Formation**	**Contact Zone**	**Gosport Sand**
Premontreia (Oxyscyllium) subulidens		x			
Stenoscyllium cf. *S. priemi*	x				
Galeorhinus aff. *G. duchaussoisi*	x	?	x		
Galeorhinus louisi	x				
Galeorhinus ypresiensis					x
Pachygaleus lefeveri	x	x	x		
Hemipristis curvatus					x
Carcharhinus mancinae sp. nov.				x	x
Negaprion gilmorei		x	x	x	x
Rhizoprionodon ganntourensis	x	x	x	?	x
Scoliodon conecuhensis	x	x	x	x	x
Abdounia beaugei	x	x	x	?	x
Abdounia enniskilleni		x	x	?	x
Abdounia minutissima	x	x	x	x	x
Pseudabdounia claibornensis comb. nov.					x
Pseudabdounia recticona comb. nov.	x	x	x	x	
Physogaleus alabamensis	x	x	x	?	x
Physogaleus secundus	x	x	x	?	x
Galeocerdo eaglesomei		x	?	x	x
Galeocerdo clarkensis					x
Totals by unit	**11**	**12**	**11**	**6**	**14**

Abdounia enniskilleni, *Galeocerdo eaglesomei* and *Negaprion gilmorei* appearing for the first time in the contact zone and Lisbon Formation (Lutetian). Within the Gosport Sand (Bartonian) we recorded the first appearance of *Pseudabdounia claibornensis* gen. et comb nov., *Brachycarcharias twiggsensis*, *Carcharhinus mancinae* sp. nov., *Galeocerdo clarkensis*, *Galeorhinus ypresiensis*, and *Hemipristis curvatus*, but we also documented the disappearance of *Pseudabdounia recticona* gen. et comb. nov., *Galeorhinus* aff. *G. duchaussoisi*, and *Pachygaleus lefeveri*. Overall, our Claiborne Group sample indicates that carcharhiniforms were slightly more diverse than the lamniforms during the Ypresian and Lutetian, but as carcharhiniforms continued to diversify into the Bartonian lamniform diversity remained relatively constant.

Analysis of the total numbers of carcharhiniform and lamniform fossils provided some additional information regarding the abundance of these of sharks. Of the 2238 carcharhiniform and lamniform specimens identified from the Tallahatta Formation, 238 (11%) were carcharhiniform and 2000 (89%) were lamniform. Of the 2970 specimens identified from the Lisbon Formation (including the Tallahatta/Lisbon Formation and Lisbon/Gosport Sand contact zones), 1449 (49%) were carcharhiniform and 1521 (51%) were lamniform. Finally, of the 3290 specimens identified from the Gosport Sand, 2385 (72%) were carcharhiniform and 905 (28%) were lamniform. These numbers suggest that the members of the Lamniformes were much more abundant than the Carcharhiniformes by a ratio of almost 9 to 1 in the late Ypresian and early Lutetian, the ratio between the two was nearly 1 to 1 by the middle Lutetian, and by the middle Bartonian the Carcharhiniformes appear to outnumber the Lamniformes by a ratio of 3 to 1. One caveat to these numbers is that tooth replacement rates differ by species (Cappetta 2012; Klimley 2013), but it is certainly not a coincidence that the number of carcharhiniform specimens identified in the Gosport Sand far exceeds that within the other formations, as more carcharhiniform species were identified within this formation. Although these numbers suggest that the carcharhiniforms diversified in the Bartonian, they also suggest a possible increase in the number of carcharhiniform individuals through the three formations. At the same time, the number of lamniform species appears to remain constant throughout the three formations, but their numbers seem to decline through time.

Sample biases aside, these numbers suggest that lamniform populations were dominant in the region into the Ypresian and outnumbered the carcharhiniforms by a ratio of 9 to 1. Within the Lutetian it appears carcharhiniform populations began to increase, and by the middle Bartonian the carcharhiniforms diversified and their populations outnumbered the lamniforms by a ratio of 3 to 1. This trend of carcharhiniform diversification and disparity appears to have continued through to today, as an estimated 270 species of carcharhiniforms are known as opposed to 16 species within the Lamniformes (see Compagno 2005).

Myliobatinae vs Rhinopterinae. Within our Claiborne Group sample, six unequivocal Myliobatinae taxa were identified, including *Aetobatus* sp., *Aetomylaeus* sp., *Leidybatis jugosus*, *Myliobatis* sp. 1, *Myliobatis* sp. 2, and *Pseudaetobatus belli*. In contrast, *Rhinoptera* sp. is the lone representative of the Rhinopterinae. Although the total number of taxa favors the Myliobatinae, the total number of Rhinopterinae teeth (n = 1891) outnumbered the combined sample of Myliobatinae teeth (n = 1414). However, our sample indicates a shift in overall subfamily abundance through time, as only 30 Rhinopterinae teeth (*Rhinoptera*) were identified within the Tallahatta Formation (including the Meridian Sand Member), as opposed to 630 Myliobatinae teeth (*Myliobatis*, *Aetomylaeus*, *Leidybatis*, *Pseudaetobatus*). Within the Lisbon Formation (including the Tallahatta/Lisbon Formation and Lisbon/Gosport Sand contact zones), 205 Rhinopterinae teeth were identified, and 550 teeth were identified as belonging to the Myliobatinae (*Aetomylaeus*, *Myliobatis*, *Aetobatus*, *Leidybatis*). Within the Gosport Sand, 1656 Rhinopterinae teeth were identified, but only 234 for the Myliobatinae (*Myliobatis* sp. 2, *Aetomylaeus*). These numbers indicate species diversity within the Myliobatinae was always greater than in the Rhinopterinae throughout the Claiborne Group, but the relative abundance of Rhinopterinae increases from the late Ypresian into the Lutetian, and by the middle Bartonian *Rhinoptera* sp. overtook the other taxa as the dominant ray taxon in the region. The decline of Myliobatinae diversity and abundance into the middle Bartonian is perhaps explained by a shift in ecology and prey availability, which was not conducive to a larger assortment of Myliobatinae rays.

Order Tetraodontiformes. 134 specimens were assigned to three members of the Tetraodontiformes, including 12 armor plates of Ostraciidae, one tooth of Balistidae, and 121 jaws and teeth of Diodontidae. Ostraciidae elements were identified within all three Claiborne Group formations, but Balistidae and Diodontidae remains were only recovered from the Gosport Sand. This may indicate a slight diversification of the Tetraodontiformes during the middle Bartonian.

Teleostean otoliths from the Claiborne Group of Alabama

As noted previously, the number of skeletal elements within our Alabama Claiborne Group sample greatly exceeded the number of otoliths (non-skeletal elements). Skeletal remains of fishes (sharks, rays, and bony fishes) numbered over 20 000 individual specimens, whereas approximately 600 otoliths were available to us. Of the 20 000+ skeletal elements, only 2137 represented bony fishes. Unfortunately, 1133 of the 2137 bony fish skeletal elements (slightly over 53%) were identifiable only as 'teleost'. Although otoliths do not represent a large portion of our sample, they proved highly significant in gaining a better understanding of the bony fish species occurring within Claiborne Group strata of Alabama.

A comparison of the bony fish species represented by skeletal remains versus species represented by otoliths revealed very little similarity. However, this is not unexpected because there are inherent differences in the two types of preservation, and this phenomenon has been reported in many otolith studies (Nolf 1985; Breard & Stringer 1995; Nolf & Stringer 2003; Nolf 2013). As a generalization, otoliths represent bony fish species that are more numerous and commonly occur in schools. On the other hand, skeletal remains often represent larger, predatory fishes, which are typically less common. In a marine ecosystem, prey fishes would be expected in much greater numbers than the predatory fishes. This scenario is reflected in the otoliths, with predatory fishes like sphyraenids, large scombrids, blochiids, trichiurids, and xiphiids rarely represented as otoliths (primarily) because of their limited abundance in the paleoenvironment. Our analysis of the Alabama Claiborne Group bony fishes represented by skeletal material confirms this observation. Many of the bony fishes based on skeletal elements from the Claiborne in Alabama represent large predatory fishes. We note here that it is possible that *Albula* sp. otoliths we identified could belong to one of the two albulids represented by skeletal remains (i.e., *Albula oweni* or *Albula eppsi*) in our sample. Unfortunately, only four albulid otolith specimens, representing a single species, are known from the Alabama Claibornian.

The most abundant otoliths belong to ophidiids (aka cusk-eels, n = 131). Recent ophidiids are widely distributed in the Atlantic, Indian, and Pacific Oceans and occur throughout a wide bathymetric range (Nelson *et al.* 2016). Although cusk-eels are not as well studied as many other families of bony fishes, research indicates that their primary diet consists of benthic invertebrates, primarily crustaceans (Bohlke & Chaplin 1993; Nielsen *et al.* 1999; Robins & Ray 1999; Nelson *et al.* 2016; Snyder & Burgess 2016). Ophidiids in turn are important food sources for many larger predatory fish. Therefore, the ophidiids would be congruous with our generalization of smaller, abundant prey fishes reflected by otoliths.

Analyzed separately, both the skeletal remains and the otoliths could give indications of the bony fish assemblage of the Claiborne Group of Alabama. However, a much more accurate representation of the bony fish assemblage is achieved by combining the osteological material and the otoliths. Simply stated, analyzing skeletal remains without examining the otoliths produces a more biased interpretation of the bony fish assemblage, and vice versa. The two groups complement one another and analyzing both yields more detail and greater insight into the composition of the bony fish assemblages. The osteological material from the Alabama Claibornian indicates a bony fish assemblage containing approximately 23 taxa. However, coupled with the otolith taxa, the number of Claibornian bony fish exceeds 50 species. Therefore, it is obviously more informative and revealing to analyze both groups.

Unfortunately, this is not always possible. In some cases, bulk samples may contain a far greater number of otolith taxa, whereas skeletal remains are rare. The opposite may also occur where osteological material predominates, and otoliths are rare or missing entirely due to extensive leaching of the aragonitic otoliths. This was illustrated in a study of the upper Eocene Yazoo Clay in Louisiana by Breard & Stringer (1995), which revealed only 12 actinopterygians based on skeletal remains (primarily teeth), but otoliths indicated 44 taxa of bony fishes at the same locality (Nolf & Stringer 2003). We identified 13 taxa of bony fishes based on skeletal remains from the Tallahatta Formation, but otoliths indicate only one species. In this case, the large discrepancy is related to the extensive leaching and weathering of the Tallahatta Formation strata, which effectively destroyed all of the aragonitic otoliths. Within the Lisbon Formation, we identified 21 taxa of bony fishes based on skeletal elements, and 31 taxa are indicated by otoliths. The greater number of taxa from the Lisbon Formation is related at least in part to the preservation of the aragonitic otoliths, and possibly to the availability of more bulk samples.

Bony fish otolith taxa from the Claiborne Group of Alabama include bonefishes (Albulidae), pike congers (Muraenesocidae), conger eels (Congridae), squirrelfishes (Holocentridae), spinyfins (Diretmidae), cusk-eels (Ophidiidae), gobies (Gobiidae), lefteye flounders (Bothidae), false trevallies (Lactariidae), tilefishes (Malacanthidae), grunts (Haemulidae), and drums (croakers) (Sciaenidae). The most diverse families are Ophidiidae and Congridae, with eight and six species, respectively. In terms of relative abundance, Ophidiidae has the greatest number of specimens (166) and constitutes approximately 28% of the total number of otoliths. Although only represented by four taxa, Sciaenidae is represented by 149 specimens, approximately 25% of the total sample size. Likewise, Lactariidae contains three taxa but comprises approximately 14% of the sample (84). Combined, the ophidiids, sciaenids, and lactariids represent approximately 67% of the total number of specimens from the three Claiborne Group formations. Based on the otoliths, the most abundant fishes in the Alabama Claiborne are cusk-eels, drums (croakers), and false trevallies. These determinations are biased toward the Lisbon Formation due to the large percentage of the otoliths recovered from this formation.

In addition to their value in interpreting the taxonomic composition of the bony fish assemblage, otoliths can provide important paleoenvironmental data that augment other lines of paleoecological evidence. For example, analysis of the families represented based on otoliths can provide evidence for freshwater, brackish, or marine paleoenvironments, as well as general climatic and bottom sediment data. As is the case with our taxonomic identifications, the paleoenvironmental data indicated by otoliths are strongly biased toward the Lisbon Formation, as approximately 95% of the specimens were derived from that formation. As shown in Table 3, all 13 bony fish families we identified by otoliths (not including the unknown percoid family) are found in marine environments, and six of these families are restricted to marine waters. Seven of the families can also occur in brackish waters. Five families may be encountered in freshwater, three of these only rarely. Therefore, the families of bony fishes we identified by otoliths are highly indicative of marine conditions. Of the six families confined to marine waters, the Ophidiidae comprises the greatest number of specimens in the Claiborne Group of Alabama. There are lesser indications of brackish conditions, even less evidence of freshwater forms, and there are no exclusively freshwater taxa represented by otoliths.

Examination of the otolith assemblage from the Alabama Claiborne Group revealed the absence of taxa that are indicative of exclusively deep waters (200 m, greater than outer shelf depth). The majority of the taxa we identified by the Claibornian otoliths are presently found in shore waters of the

Table 3. Environmental and climatic preferences of otolith-based taxa identified within Claiborne Group strata in Alabama. Shaded areas = preference ranges. Notes: Albulidae[1] = rarely in freshwater and brackish. Gobiidae[2] = chiefly marine and brackish. Haemulidae[3] = chiefly marine and rarely freshwater.

	Distribution of family			**General climatic ranges**			
Family	**Freshwater**	**Brackish**	**Marine**	**Tropical**	**Subtropical**	**Temperate**	**Arctic**
Albulidae[1]	■	■	■	■			
Heterenchelyidae			■	■			
Muraenesocidae	■	■	■	■			
Congridae			■	■	■	■	
Holocentridae			■	■			
Diretmidae			■	■	■	■	
Ophidiidae			■	■	■	■	
Gobiidae[2]	■	■	■	■	■		
Bothidae			■	■	■		
Lactariidae		■	■	■			
Malacanthidae		■	■	■	■	■	
Haemulidae[3]	■	■	■	■			
Sciaenidae	■	■	■	■	■	■	

continental USA, at or above the continental shelf (less than 200 m) (Page *et al.* 2013, Moore 2016). One exception, Lactariidae, is presently distributed in the Indo-Pacific. However, representatives of this family have long been recognized from the Cenozoic of the USA (Frizzell & Dante 1965; Nolf 1985, 2013; Breard & Stringer 1999), so its occurrence in the Alabama Claiborne Group is not considered anomalous. Therefore, as a general interpretation, the bony fishes represented by otoliths indicate a marine environment no deeper than outer shelf depth, and probably shallower. Furthermore, species of Myctophidae (myctophids) or Macrouridae (macrourids) are absent from our Alabama Claiborne Group sample. Nolf & Brzobohaty (1992) indicated that assemblages lacking or nearly lacking myctophids indicate a neritic environment, with little oceanic influence.

Table 3 also indicates that all the bony fish families represented by otoliths occur in tropical environments, and six of these are restricted to tropical waters. Three of the families in our sample are tropical to subtropical, and five families range from tropical to temperate. This composition is indicative of tropical to (possibly) subtropical conditions, based on the distribution of modern representatives of the families. Additionally, many of the bony fish families indicated by otoliths have representatives that exclusively occur in environments where the bottom is soft or muddy (i.e., sand, silt, clay), and there are no indications of taxa found in rocky environments. Most of the fossil otoliths from the Claibornian of Alabama represent fish expected in normal marine salinity, although a few taxa could tolerate reduced salinities.

Conclusions

This report contains the results of the largest and most comprehensive study of Claiborne Group vertebrates in Alabama, as a combined total of 20931 elasmobranch and bony fish elements were examined among the three Claiborne formations. A number of important conclusions were drawn from our analysis, one being that 115 unequivocal fossil fish taxa were identified from Claiborne Group strata. Amongst the identified taxa, one new species is recognized, *Carcharhinus mancinae* sp. nov. Additionally, we propose the new generic name *Pseudabdounia* gen. nov. for two species formerly referred to *Abdounia*, with new taxonomic combinations including *Pseudabdounia claibornensis* gen. et comb. nov., and *Pseudabdounia recticona* gen. et comb. nov. We propose two additional new taxonomic combinations including *Eutrichiurides plicidens* comb. nov. (formerly *Trichiurus*) and *Physogaleus alabamensis* comb. nov. (formerly *Galeocerdo*).

We report the first North American biogeographic occurrences for 11 taxa, including *Aturobatis* aff. *A. aquensis*, *Brachycarcharias atlasi*, *Eutrichiurides plicidens* comb. nov., *Galeorhinus louisi*, *Ginglymostoma maroccanum*, *Gymnosarda* sp., *Mennerotodus* sp., *Rhizoprionodon ganntourensis*, *Stenoscyllium* cf. *S. priemi*, *Trichiurus oshosunensis*, and a member of the Balistidae. An additional 25 taxa represent first biogeographic occurrences for Alabama, including *Abdounia beaugei*, *Albula eppsi*, *Ariosoma nonsector*, *Anisotremus*? sp., *Anomotodon* sp., *Brachycarcharias twiggsensis*, *Burnhamia daviesi*, *Eoplinthicus yazooensis*, *Galeorhinus ypresiensis*, *Gnathophis meridies*, *Haemulon*? *obliquus*, *Hypolophodon sylvestris*, *Malacanthus*? *sulcatus*, *Meridiania* cf. *M. convexa*, *Palaeocybium proosti*, *Paraconger sector*, *Paralbula* aff. *P. marylandica*, *Phyllodus toliapicus*, *Propristis schweinfurthi*, *Pycnodus* sp., *Pythonichthys colei*, *Scomberomorus stormsi*, *Signata stenzeli*, *Signata nicoli*, and a member of the Gobiidae.

We also documented stratigraphic/temporal range extensions for numerous taxa. Ranges for *Tethylamna dunni* and *Scoliodon conecuhensis*, previously known only from the Lutetian Lisbon Formation, are extended back into the upper Ypresian (Tallahatta Formation) and up into the Bartonian (“upper” Lisbon). Furthermore, the first Bartonian occurrences are reported for *Eoplinthicus yazooensis*, *Jacquhermania duponti*, *Meridiania* cf. *M. convexa*, *Phyllodus toliapicus*, and “*Rhinobatos*” *bruxelliensis*. *Eoplinthicus yazooensis* was previously only documented from the Priabonian Yazoo Clay, but it is now known to occur in the Bartonian Gosport Sand. The occurrence of *Meridiania* in the Gosport Sand represents the youngest known record of the genus, with a significant range extension from Zone NP11 (upper Ypresian) up into Zone NP17. We document a similar range extension for *Fisherichthys* aff. *F. folmeri*, from Zone NP11 to Zone NP17 (middle Bartonian). Additionally, the range of *Galeorhinus louisi* is extended into the late Ypresian, and we report the first Lutetian occurrence of *Gymnosarda*.

Analysis of the Claiborne Group otoliths indicates that deposition of the Lisbon Formation occurred in a tropical marine environment of normal marine salinity. Unfortunately, our sample of otoliths was underrepresented for the Tallahatta Formation and Gosport Sand. However, comparison of the fish paleofaunas, based on osteological remains, of these two units to that of the Lisbon Formation could provide clues as to their depositional environments. Evaluation of the Tallahatta Formation fish assemblage revealed an 82% faunal overlap with the Lisbon Formation, and the Gosport Sand has a faunal overlap of 95%. These similarities, particularly between the Lisbon Formation and Gosport Sand, suggests that fossiliferous strata within all three formations formed under similar environmental conditions.

Despite the sample biases inherent in studies of this nature, the large sample size we examined, derived from three stratigraphically consecutive formations, allowed us to elucidate several biostratigraphic and evolutionary trends. The transition from *Otodus* (*Otodus*) to *Otodus* (*Carcharocles*) (i.e., development of serrated cutting edges) occurred during the early Lutetian, and during the Bartonian Tetraodontiformes diversified, Rhinopterinae became the predominant member of Myliobatidae over Myliobatinae, and carcharhiniform sharks became more diverse and abundant than lamniforms. Studies of the taxa occurring within units that underly Claiborne Group strata, like the Ypresian Hatchetigbee Formation, as well as overlying formations like the Bartonian Moodys Branch Formation and Bartonian to Priabonian Yazoo Clay in Alabama, are currently underway. These will hopefully provide further resolution to the biostratigraphic ranges of many of the taxa described herein and provide additional insights into the evolutionary history of the vertebrate faunas within Eocene marine paleoenvironments.

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Appendix 1 (continued on next four pages)

Number of non-otolith taxa identified to lowest taxonomic ranking within each Claiborne Group unit. Shaded areas represent the stratigraphic range of taxa within Claiborne Group units in Alabama, USA.

Taxon	**Meridian Sand Member**	**lower Tallahatta Fm.**	**Tallahatta Fm.**	**upper Tallahatta Fm.**	**Tallahatta /Lisbon contact**	**“lower” Lisbon Fm.**	**“upper” Lisbon Fm.**	**Lisbon/ Gosport contact**	**lower Gosport Sand**	**Gosport Sand**	**Total**
Chondrichthyes indet.	13	1808	28		3	510			157	85	**2604**
Heterodontus sp.		2				3			1	1	**7**
Orectolobus ziegenhinei					26	154					**180**
Ginglymostoma maroccanum		8									**8**
Ginglymostoma sp.									21		**21**
Nebrius thielensi		30	1		10	106			22	1	**170**
Orectolobidae indet.						1					**1**
Lamniformes indet.		149				96			6	3	**254**
Otodus (*Otodus*) sp.		8		1							**9**
Otodus (*Carcharocles*) sp.					19	1				4	**24**
Anomotodon sp.		2			1	1			1	1	**6**
Striatolamia macrota	29	930			154	267	58	16	468	201	**2123**
Odontaspididae indet.		1			3	2	2		8	67	**83**
Brachycarcharias atlasi	2	59			19	29			4		**113**
Brachycarcharias lerichei	36	711			162	394	3		49	15	**1370**
Brachycarcharias twiggsensis									6	15	**21**
Hypotodus verticalis	7	39			53	19	1		1	1	**121**
Jaekelotodus robustus	5	16			74	41	11	3	2	5	**157**
Mennerotodus sp.										5	**5**
Odontaspis winkleri		3				2					**5**
Tethylamna dunni		1			63	19	6		2	5	**96**

Appendix 1 (continued)

Number of non-otolith taxa identified to lowest taxonomic ranking within each Claiborne Group unit. Shaded areas represent the stratigraphic range of taxa within Claiborne Group units in Alabama, USA.

Taxon	**Meridian Sand Member**	**lower Tallahatta Fm.**	**Tallahatta Fm.**	**upper Tallahatta Fm.**	**Tallahatta /Lisbon contact**	**“lower” Lisbon Fm.**	**“upper” Lisbon Fm.**	**Lisbon/ Gosport contact**	**lower Gosport Sand**	**Gosport Sand**	**Total**
Lamnidae indet.									2		**2**
Macrorhizodus praecursor		1			1		2	1	2	13	**20**
Carcharhiniformes indet.	1					3				2	**6**
Premontreia (*Oxyscyllium*) *subulidens*					1						**1**
Stenoscyllium cf. *S. priemi*		3									**3**
Galeorhinus aff. *G. duchaussoisi*		2	1			4				3	**10**
Galeorhinus louisi			2								**2**
Galeorhinus ypresiensis										3	**3**
Pachygaleus lefeveri		3			1	5					**9**
Hemipristis curvatus										6	**6**
Carcharhinidae indet.						1					**1**
Carcharhinus mancinae sp. nov.								1	101	1	**103**
Negaprion gilmorei					6	18	1	2	1389	104	**1519**
Rhizoprionodon ganntourensis		9	1		3	63			74	5	**156**
Scoliodon conecuhensis		23			4	66		1	30	6	**130**
Abdounia beaugei		13			1	11			3	22	**50**
Abdounia enniskilleni					2	7	5		257	31	**302**
Abdounia minutissima		7	1		3	40		1	2	17	**71**
Abdounia sp.			1		10	2			8	5	**26**
Pseudabdounia claibornensis gen. et comb. nov.									88	1	**89**
Pseudabdounia recticona gen. et comb. nov.		6	1		26	133		2			**168**

Appendix 1 (continued)

Number of non-otolith taxa identified to lowest taxonomic ranking within each Claiborne Group unit. Shaded areas represent the stratigraphic range of taxa within Claiborne Group units in Alabama, USA.

Taxon	**Meridian Sand Member**	**lower Tallahatta Fm.**	**Tallahatta Fm.**	**upper Tallahatta Fm.**	**Tallahatta /Lisbon contact**	**“lower” Lisbon Fm.**	**“upper” Lisbon Fm.**	**Lisbon/ Gosport contact**	**lower Gosport Sand**	**Gosport Sand**	**Total**
Physogaleus alabamensis comb. nov.		31	1		185	232	1		15	17	**507**
Physogaleus secundus		131	1		53	555	1		38	27	**786**
Physogaleus sp.					1	1					**2**
Galeocerdo eaglesomei					4		13	1	2	18	**38**
Galeocerdo clarkensis									83	3	**86**
Galeocerdo sp.									16		**16**
Galeomorphii indet.						1					**1**
Pristidae indet.					4				2	7	**13**
Anoxypristis sp.		1			11	4			2		**18**
Pristis sp.		27			91	27			36	66	**247**
Propristis schweinfurthi									2	8	**10**
Myliobatiformes indet.					1	288	3			60	**352**
“*Dasyatis*” aff. *D. charlisae*						4	4				**8**
“*Dasyatis*” *jaekeli*		3				13					**16**
“*Dasyatis*” sp.						6			2		**8**
Aturobatis aff. *A. aquensis*						2					**2**
Coupatezia sp.		1				17					**18**
Hypolophodon sylvestris		7									**7**
Jacquhermania duponti						11			16	1	**28**
Aetobatis sp.					12	103		1		11	**127**
Aetomylaeus sp.	11	80			12	123	4		153	9	**392**

Appendix 1 (continued)

Number of non-otolith taxa identified to lowest taxonomic ranking within each Claiborne Group unit. Shaded areas represent the stratigraphic range of taxa within Claiborne Group units in Alabama, USA.

Taxon	**Meridian Sand Member**	**lower Tallahatta Fm.**	**Tallahatta Fm.**	**upper Tallahatta Fm.**	**Tallahatta /Lisbon contact**	**“lower” Lisbon Fm.**	**“upper” Lisbon Fm.**	**Lisbon/ Gosport contact**	**lower Gosport Sand**	**Gosport Sand**	**Total**
Myliobatis sp. 1	5	307									**312**
Myliobatis sp. 2					18	207	1		48	13	**287**
Pseudaetobatus belli	15	210									**225**
Rhinoptera sp.	16	14			18	181	1	5	1525	131	**1891**
Meridiania cf. *M. convexa*		1							1	2	**4**
Leidybatus jugosus		2			28	41					**71**
Burnhamia daviesi		6				1			1	4	**12**
Eoplinthicus yazooensis										1	**1**
Batomorphii indet.						4				3	**7**
Myliobatidae indet.		750	4		74	776	1	7	762	212	**2586**
Cylindracanthus ornatus					2	1					**3**
Cylindracanthus rectus					24	16	4		2		**46**
Cylindracanthus sp.		4	4		13	45			6		**72**
Pycnodus sp.		8			2	10					**20**
Lepisostidae indet.					1	2			10	23	**36**
Egertonia isodonta		35			12	7			37	37	**128**
Paralbula aff. *P. marylandica*		17				52					**69**
Phyllodus toliapicus		8				15			3		**26**
Albula eppsi		23	2		1	6			1		**33**
Albula oweni		15			3		1		6		**25**
Albula sp.						3			1		**4**

Appendix 1 (continued)

Number of non-otolith taxa identified to lowest taxonomic ranking within each Claiborne Group unit. Shaded areas represent the stratigraphic range of taxa within Claiborne Group units in Alabama, USA.

Taxon	**Meridian Sand Member**	**lower Tallahatta Fm.**	**Tallahatta Fm.**	**upper Tallahatta Fm.**	**Tallahatta /Lisbon contact**	**“lower” Lisbon Fm.**	**“upper” Lisbon Fm.**	**Lisbon/ Gosport contact**	**lower Gosport Sand**	**Gosport Sand**	**Total**
Osteoglossidae indet.		2			3	8	1		1	1	**16**
Ariidae indet.					11	8	1		34	12	**66**
Sphyraena sp.		1	5		9	10			43	3	**71**
Eutrichiurides plicidens comb nov.					4	4			3		**11**
Trichiurides sagittidens			4		2	4			10	13	**33**
Trichiurus oshosunensis					12	21					**33**
Scombridae indet.					1	1					**2**
Palaeocybium proosti					1				4	1	**6**
Scomberomorus bleekeri		5	3		57	81			4		**150**
Scomberomorus stormsi		3			1	6				2	**12**
Scomberomorus sp.						1					**1**
Gymnosarda sp.						1					**1**
Fisherichthys aff. *F. folmeri*						5			1		**6**
Ostraciidae indet.		3			5	2			1	1	**12**
Balistidae indet.										1	**1**
Progymnodon hilgendorphi									120	1	**121**
Teleostei indet.		17	793		11	162	19	2	93	36	**1133**
Totals	**140**	**5549**	**853**	**2**	**1359**	**5121**	**145**	**43**	**5802**	**1352**	**20366**

Appendix 2 (continued on next four pages)

Number of non-otolith taxa identified to lowest taxonomic ranking from each Claiborne Group locality in Alabama, USA.

Taxon	ADl-1	Amo-8	ACh-7	Ach-14	Acon-6	Acov-1	ACov-11	Ach-8	ACl-3	AWa-2	AMo-4	ACl-4	Ach-21	Acl-14	Acl-15	Total
Chondrichthyes indet.	1821	28	1				512				22	135	2		83	**2604**
Heterodontus sp.	2						3					1	1			**7**
Orectolobus ziegenhinei				1			179									**180**
Ginglymostoma maroccanum	8															**8**
Ginglymostoma sp.												21				**21**
Nebrius thielensi	30	1		1			115					22	1			**170**
Orectolobidae indet.							1									**1**
Lamniformes indet.	149						96					6			3	**254**
Otodus (*Otodus*) sp.	8				1											**9**
Otodus (*Carcharocles*) sp.			1	1	3		15						4			**24**
Anomotodon sp.	2						2					1			1	**6**
Striatolamia macrota	959			2	3	4	412	2	52	1	32	455	161		40	**2123**
Odontaspididae indet.	1						5		1		1	8	65		2	**83**
Brachycarcharias atlasi	61						48					4				**113**
Brachycarcharias lerichei	747				2		551		3			49	8	3	7	**1370**
Brachycarcharias twiggsensis												6	15			**21**
Hypotodus verticalis	46			2			70		1			1	1			**121**
Jaekelotodus robustus	21						115		11		3	2	5			**157**
Mennerotodus sp.													5			**5**
Odontaspis winkleri	3						2									**5**
Tethylamna dunni	1				1		81		5			3	5			**96**
Lamnidae indet.												2				**2**
Macrorhizodus praecursor	1			1			1		2		2		12		1	**20**

Appendix 2 (continued)

Number of non-otolith taxa identified to lowest taxonomic ranking from each Claiborne Group locality in Alabama, USA.

Taxon	**ADl-1**	**Amo-8**	**ACh-7**	**Ach-14**	**Acon-6**	**Acov-1**	**ACov-11**	**Ach-8**	**ACl-3**	**AWa-2**	**AMo-4**	**ACl-4**	**Ach-21**	**Acl-14**	**Acl-15**	**Total**
Carcharhiniformes indet.	1						3						2			**6**
Premontreia (*Oxyscyllium*) *subulidens*					1											**1**
Stenoscyllium cf. *S. priemi*	3															**3**
Galeorhinus aff. *G. duchaussoisi*	2	1					4						3			**10**
Galeorhinus louisi		2														**2**
Galeorhinus ypresiensis															3	**3**
Pachygaleus lefeveri	3			1			5									**9**
Hemipristis curvatus													6			**6**
Carcharhinidae indet.							1									**1**
Carcharhinus mancinae sp. nov.									1		3	98			1	**103**
Negaprion gilmorei				1	1		21		1		9	1382	104			**1519**
Rhizoprionodon ganntourensis	9	1					67					74	5			**156**
Scoliodon conecuhensis	23			1			69				1	30	4		2	**130**
Abdounia beaugei	13						12					3			22	**50**
Abdounia enniskilleni				1	1		7	1	4			257	30		1	**302**
Abdounia minutissima	7	1					43				1	2			17	**71**
Abdounia sp.		1					12					8			5	**26**
Pseudabdounia claibornensis cgen. et omb. nov.												88			1	**89**
Pseudabdounia recticona gen. et comb. nov.	6	1		3	1		155				2					**168**
Physogaleus alabamensis comb. nov.	31	1					442		1			15	14		3	**507**
Physogaleus secundus	131	1		2	2	1	583	1				38	6		21	**786**
Physogaleus sp.				1			1									**2**
Galeocerdo eaglesomei				1	3				13		1	2	18			**38**

Appendix 2 (continued)

Number of non-otolith taxa identified to lowest taxonomic ranking from each Claiborne Group locality in Alabama, USA.

Taxon	**ADl-1**	**Amo-8**	**ACh-7**	**Ach-14**	**Acon-6**	**Acov-1**	**ACov-11**	**Ach-8**	**ACl-3**	**AWa-2**	**AMo-4**	**ACl-4**	**Ach-21**	**Acl-14**	**Acl-15**	**Total**
Galeocerdo clarkensis											3	80	3			**86**
Galeocerdo sp.												16				**16**
Galeomorphii indet.							1									**1**
“*Rhinobatos*” *bruxelliensis*	3						50	1				14				**68**
Pristidae indet.							4					2	7			**13**
Anoxypristis sp.	1						15					2				**18**
Pristis sp.	27			2			116				1	35	66			**247**
Propristis schweinfurthi												2	8			**10**
Myliobatiformes indet.							289	1	2				60			**352**
“*Dasyatis*” aff. *D. charlisae*							4	4								**8**
“*Dasyatis*” *jaekeli*	3						13									**16**
“*Dasyatis*” sp.							6					2				**8**
Aturobatis aff. *A. aquensis*							2									**2**
Coupatezia sp.	1						17									**18**
Hypolophodon sylvestris	7															**7**
Jacquhermania duponti							11					16			1	**28**
Aetobatis sp.				2			113				1		11			**127**
Aetomylaeus sp.	91				1		134		4			153	1		8	**392**
Myliobatis sp. 1	312															**312**
Myliobatis sp. 2					1		224		1		1	48	7		5	**287**
Pseudaetobatus belli	225															**225**
Rhinoptera sp.	30			3	2		194	1			5	1525	109		22	**1891**
Meridiania cf. *M. convexa*	1											1			2	**4**

Appendix 2 (continued)

Number of non-otolith taxa identified to lowest taxonomic ranking from each Claiborne Group locality in Alabama, USA.

Taxon	**ADl-1**	**Amo-8**	**ACh-7**	**Ach-14**	**Acon-6**	**Acov-1**	**ACov-11**	**Ach-8**	**ACl-3**	**AWa-2**	**AMo-4**	**ACl-4**	**Ach-21**	**Acl-14**	**Acl-15**	**Total**
Leidybatus jugosus	2			1			68									**71**
Burnhamia daviesi	6						1					1			4	**12**
Eoplinthicus yazooensis													1			**1**
Batomorphii indet.							4					3				**7**
Myliobatidae indet.	750	4		4	1		845	1			22	762			197	**2586**
Cylindracanthus ornatus							3									**3**
Cylindracanthus rectus							40		4			2				**46**
Cylindracanthus sp.	4	4		3			55					6				**72**
Pycnodus sp.	8			1			11									**20**
Lepisostidae indet.				1			2					10	23			**36**
Egertonia isodonta	35			2			17					37			37	**128**
Paralbula aff. *P. marylandica*	17						52									**69**
Phyllodus toliapicus	8						15					3				**26**
Albula eppsi	23	2		1			6					1				**33**
Albula oweni	15						3		1			6				**25**
Albula sp.							3					1				**4**
Osteoglossidae indet.	2						11	1				1			1	**16**
Ariidae indet.				2			17	1				34	12			**66**
Sphyraena sp.	1	5		2			17					43	2		1	**71**
Eutrichiurides plicidens comb. nov.				1			7					3				**11**
Trichiurides sagittidens		4		1			5					10	12		1	**33**
Trichiurus oshosunensis				2			31									**33**

Appendix 2 (continued)

Number of non-otolith taxa identified to lowest taxonomic ranking from each Claiborne Group locality in Alabama, USA.

Taxon	**ADl-1**	**Amo-8**	**ACh-7**	**Ach-14**	**Acon-6**	**Acov-1**	**ACov-11**	**Ach-8**	**ACl-3**	**AWa-2**	**AMo-4**	**ACl-4**	**Ach-21**	**Acl-14**	**Acl-15**	**Total**
Scombridae indet.							2									**2**
Palaeocybium proosti							1					4	1			**6**
Scomberomorus bleekeri	5	3	1	3			134					4				**150**
Scomberomorus stormsi	3						7								2	**12**
Scomberomorus sp.							1									**1**
Gymnosarda sp.							1									**1**
Fisherichthys aff. *F. folmeri*							5					1				**6**
Ostraciidae indet.	3			1			5					1	1	1		**12**
Balistidae indet.													1			**1**
Progymnodon hilgendorphi											2	118	1			**121**
Teleostei indet.	17	793		1	1		171	19			8	87	33		3	**1133**
Totals	**5689**	**853**	**3**	**52**	**25**	**5**	**6394**	**33**	**107**	**1**	**120**	**5747**	**836**	**4**	**497**	**20366**