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New Paleogene elasmobranch (Chondrichthyes) records from the Gulf Coastal Plain of the United States, including a new species of *Carcharhinus* de Blainville, 1816

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Evaluation of two historical collections of Louisiana vertebrate fossils housed in museum repositories revealed the presence of Paleogene shark and ray taxa that were heretofore unknown from the Gulf Coastal Plain of the USA. These include a new species of *Carcharhinus*, the sharks *Isogomphodon* sp., *Mustelus* sp., and *Xiphodolamia ensis* Leidy, 1877, and the ray *Gymnura* sp. Additionally, the first known lateral tooth of *Eoplinthicus yazooensis* Cappetta & Stringer, 2002 is described, improving our knowledge of the dentition of this extinct mobulid ray. The *Isogomphodon* sp. teeth represent the third fossil record of the genus from North America, whereas a single *Mustelus* sp. tooth is only the second Eocene record of this genus on the continent. One tooth of *X. ensis* provides the first record of the taxon in the Gulf Coastal Plain. The new *Carcharhinus* is distinct from all previously described Paleogene species, and it is the second Bartonian representative of the genus to be identified from deposits of the Eocene Mississippi Embayment. Two late Eocene *Gymnura* sp. teeth are the second Paleogene record of the genus in North America. These fossils improve our knowledge of Paleogene elasmobranch faunas on a local (Louisiana), regional (southeastern USA), and global scale.

KEY WORDS: Eocene, Oligocene, Louisiana, Mississippi Embayment, Galeomorphi, Batomorphi.

Introduction

In Louisiana, USA, Paleogene surface exposures constitute a nearly time-continuous series extending from the Cretaceous-Paleogene boundary to the end of the Oligocene (Fig. 1). In ascending order, the Paleocene units are divided into the Danian Midway Group (Kincaid Formation and Porters Creek Clay) and Selandian/Thanetian Wilcox Group (Naborton, Dolet Hills, Cow Bayou, Converse, Lime Hill, Hall Summit, Marthaville, Pendleton, and Sabinetown formations). The Paleocene-Eocene boundary occurs within the Sabinetown Formation, and although the upper part of the unit is of Ypresian age, the entirety of the formation is placed within the Wilcox Group. The remaining Eocene units are grouped into the Ypresian to upper Bartonian Claiborne Group (Carrizo, Cane River, Sparta, Cook Mountain, Cockfield formations) and Bartonian to Priabonian Jackson Group (Moodys Branch Formation, Yazoo Clay, Danville Landing and Mosley Hill formations). The Oligocene units are divided into the Rupelian Vicksburg Group (Sandel, Rosefield, and Nash Creek formations) and the Chattian Catahoula Formation, which is not placed within a geologic group (Johnston *et al*., 2000).

Although the occurrence of Paleogene elasmobranch teeth in Louisiana has been known since at least the late 19th century (see Hopkins, 1870; Vaughan, 1896; Glenk, 1934; Arata, 1964; Domning, 1969), there has been a paucity of systematic studies on this material. Stringer (1977) appears to have conducted the first systematic evaluation of any Paleogene fish paleofauna in Louisiana, and he reported 17 elasmobranch taxa in association with a diverse teleost otolith assemblage from the Priabonian Yazoo Clay in Caldwell Parish. Breard (1978), Lancaster (1982, 1986), Manning & Standhardt (1986), and McPherson & Manning (1986) subsequently documented the presence of additional shark and ray species from upper Eocene Jackson Group strata in Caldwell, Grant, and La Salle parishes, and some of the species were directly associated with an archaeocete whale skeleton occurring in the Yazoo Clay. Several early Oligocene elasmobranchs were listed by Stringer *et al.* (2001) within their description of otoliths from the type section of the Oligocene Rosefield Formation in Catahoula Parish and, lastly, Cappetta & Stringer (2002) described a new mobulid ray, *Eoplinthicus yazooensis*, based on isolated symphyseal teeth derived from the Yazoo Clay in Caldwell Parish.

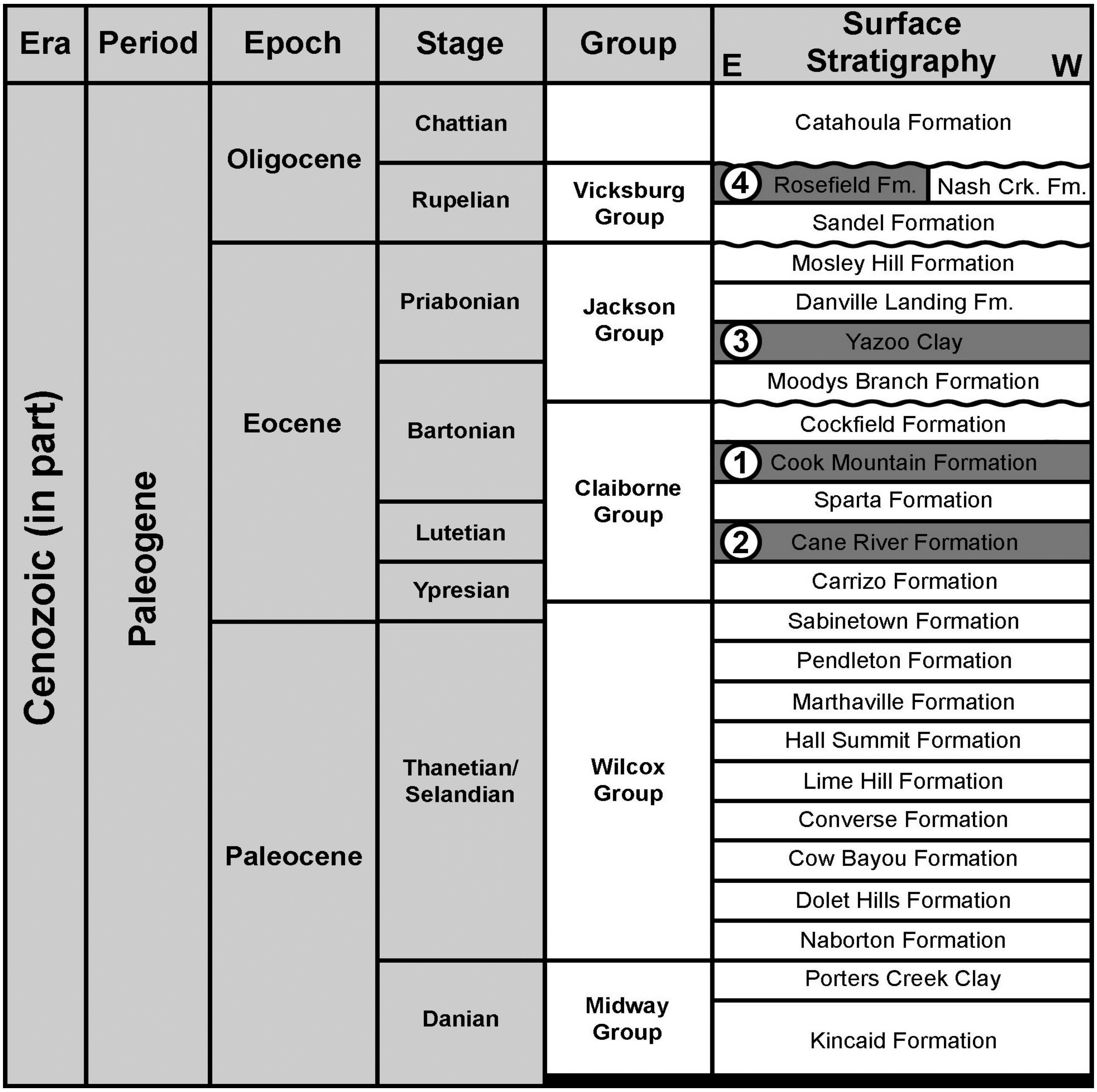

Figure 1. Generalized stratigraphic section for Paleogene strata of Louisiana, USA. Lithostratigraphic units highlighted in dark gray are those formations from which the fossils discussed in this report were derived. Numbers in closed circles correspond to the localities shown in Figure 2, including 1) B.F. Smith quarry, Bossier Parish; 2) Interstate 49 site, Natchitoches Parish; 3) Montgomery Landing, Grant Parish; 4) Rosefield, Catahoula Parish. Modified from Johnston *et al.* (2000).

In December 2020 we examined two large museum collections of Paleogene fossil fish (elasmobranch and teleost) remains from Louisiana, totaling approximately 5000 specimens. Although many of the fossils were previously examined by other researchers, our evaluation resulted in the discovery of several elasmobranch taxa that were previously undocumented from the Paleogene Gulf Coastal Plain record of the USA. The purpose of this report is to describe these noteworthy fossils (n=99) and discuss any taxonomic issues regarding the identified taxa. We also comment on the paleobiological and paleobiogeographical significance of these specimens.

Methods

This report stems from our examination of fossil fish remains from Louisiana that are contained within two large vertebrate paleontology collections. One collection is housed at the Louisiana State University Museum of Natural Science (LSUMG) in Baton Rouge, USA, and the other at McWane Science Center (MSC) in Birmingham, Alabama, USA. The specimens described herein were collected from four distinct Eocene and Oligocene lithostratigraphic units and localities in Louisiana, including the Cook Mountain Formation (B.F. Smith quarry,

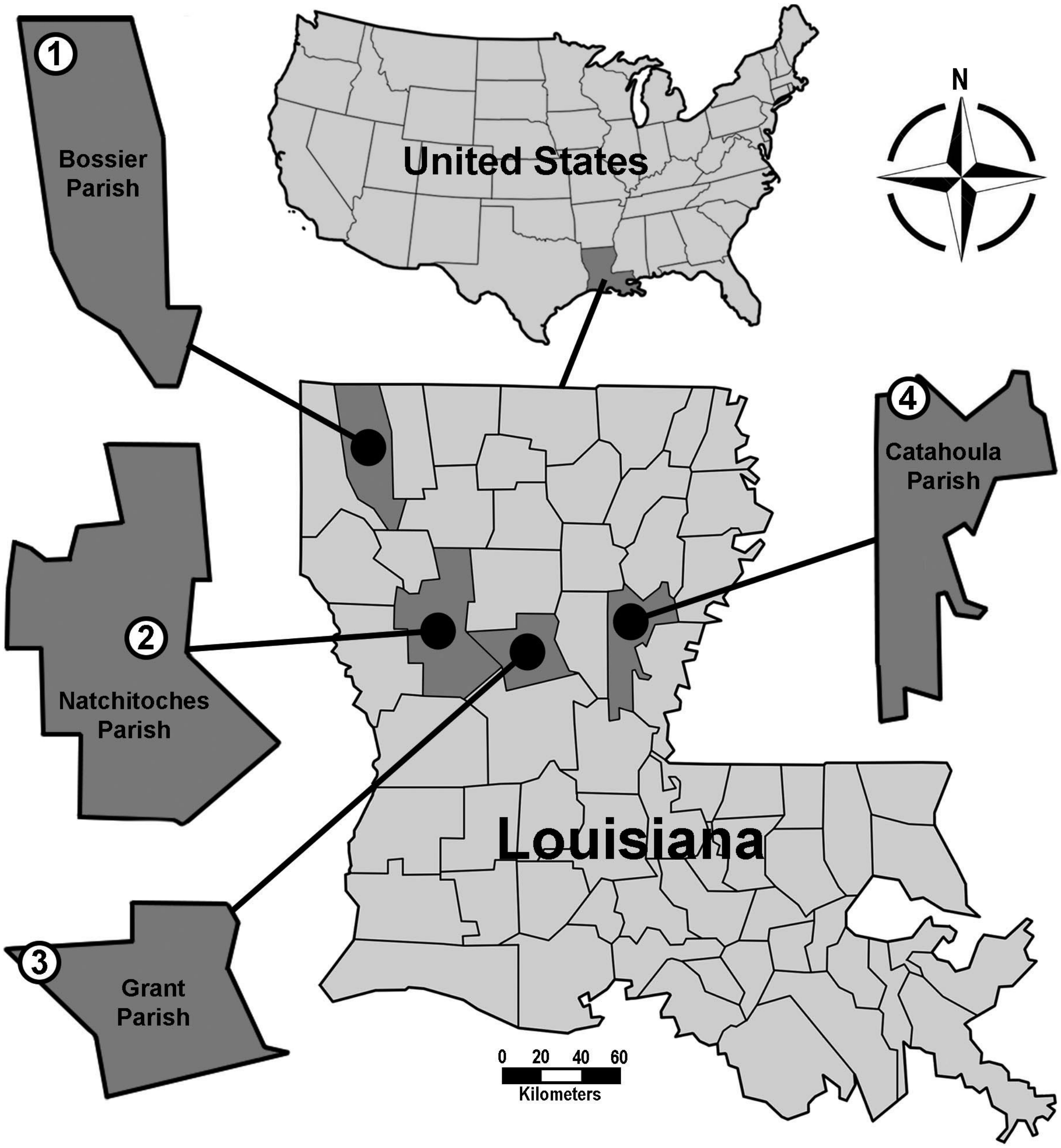

Figure 2. Geographic map showing state outlines of the USA (top) and state outline of Louisiana (bottom). Numbered polygons indicate the parishes and localities discussed in the text, including 1) B.F. Smith quarry, Bossier Parish; 2) Interstate 49 site, Natchitoches Parish; 3) Montgomery Landing, Grant Parish; 4) Rosefield, Catahoula Parish.

Bossier Parish, Fig. 2.1), Cane River Formation (Interstate 49 locality, Natchitoches Parish, Fig. 2.2), Tullos Member of the Yazoo Clay (Montgomery Landing, Grant Parish Fig. 2.3), and Rosefield Formation (Rosefield type locality, Catahoula Parish, Fig. 2.4). Further information regarding these lithostratigraphic units and localities are discussed within the Systematic Paleontology and Discussions sections of this study. As these are historical localities that were discovered prior to the advent of GPS, the geographic location information is based on the Unites States Public Land Survey System of Section, Township and Range. A section represents 2.7 km^2 within an east-west Range unit of 9.7 km and north-south Township unit of 9.7 km.

Specimens larger than 0.5 cm were photographed with a Nikon D80 DSLR camera with Tamron macro lens. Teeth smaller than 0.5 cm were photographed with an AmScope MU1000 camera mounted to an AmScope 3.5x–90x stereo microscope, and 10MB TIFF images were taken using AmScope Toupview software version 3.7. Resulting photographs were rendered and arranged into the present figures using Photoshop CC 2017 software. The higher taxonomic rankings used herein generally follow Nelson *et al.* (2016). Elasmobranch tooth terminology largely follows that of Shimada (2002) and Cappetta (2012), and tooth group terminology follows Siverson (1999).

Systematic Paleontology

Class Chondrichthyes Huxley, 1880
Subclass Euselachii Hay, 1902
Infraclass Elasmobranchii Bonaparte, 1838
Division Selachii Compagno, 1977
Superorder Galeomorphi (*sensu* Nelson *et al.*, 2016)
Order Carcharhiniformes Compagno, 1973
Family Carcharhinidae Jordan & Evermann, 1896
Genus *Carcharhinus* de Blainville, 1816

***Carcharhinus tingae* n. sp.**

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Figures 3.1-3.6, 4.1-4.12

Diagnosis – Upper and lower teeth with a somewhat erect to highly distally inclined cusp (Figs 3.4 and 4.1); post-anterior teeth with elongated distal heel separated from cusp by distinctive notch; distal heel with moderate to strong denticulation; mesial and distal cutting edges nearly completely serrated (not to the cusp apex); mesial serrations largest at the lower part of the cutting edge; serrations weakly compound; denticles of distal heel with serrations on the mesial cutting edge (Figs 3.5b, 3.6b); distinctive angular intersection of crown and root when viewed mesially (I.e., Figs 3.4d, 3.3a, 3.6d, 4.5c, 4.11c).

Etymology – This species is named in honor of Dr Suyin Ding Ting (LSUMG) for her contributions to our knowledge of the fossil record of Louisiana.

Type stratum and age – Reddish-brown ironstone (goethite sensu De Hon *et al*. 2001), upper part of the Cook Mountain Formation, middle Eocene, Bartonian Stage, calcareous nannoplankton Zone NP17 (Fig. 1.1).

Type locality – B.F. Smith quarry, 9.3 km northeast of Plain Dealing, NE ¼, NW ¼, Sec. 29, T. 23 N, R. 12 W, Bossier Parish, Louisiana (Fig. 2.1).

Holotype – LSUMG V-22439 (upper left lateral tooth, Fig. 3.2a-d).

Paratypes – LSUMG V-22422 (upper right latero-posterior tooth, Fig. 3.3a-c), LSUMG V-22436 (lower left anterior tooth, Fig. 3.4a-d), LSUMG V-22437 (upper left anterior tooth, Fig. 3.1a-d), LSUMG V-22438 (lower right lateral tooth, Fig. 3.5a-d), LSUMG V-22451 (lower left latero-posterior tooth, Fig. 3.6a-d).

Additional material examined – LSUMG V-16815 (17 teeth), LSUMG V-22420, LSUMG V-22421, LSUMG V-22423, LSUMG V-22424, LSUMG V-22425, LSUMG V-22426, LSUMG V-22427, LSUMG V-22428, LSUMG V-22429, LSUMG V-22430, LSUMG V-22431, LSUMG V-22432 (Fig. 4.7a-c), LSUMG V-22433, LSUMG V-22434, LSUMG V-22435, LSUMG V-22440, LSUMG V-22441 (Fig. 4.6a-c), LSUMG V-22442 (Fig. 4.8a-c), LSUMG V-22443, LSUMG V-22444 (Fig. 4.2a-c), LSUMG V-22445 (Fig. 4.5a-c), LSUMG V-22446, LSUMG V-22447, LSUMG V-22448, LSUMG V-22449, LSUMG V-22450, LSUMG V-22452, LSUMG V-22453, LSUMG V-22454 (Fig. 4.1a-c), LSUMG V-22455, LSUMG V-22456 (Fig. 4.4a-c), LSUMG V-22457 (Fig. 4.10a-c), LSUMG V-22458, LSUMG V-22459, LSUMG V-22460, LSUMG V-22461, LSUMG V-22462, LSUMG V-22463, LSUMG V-22464, LSUMG V-22465 (9 teeth), LSUMG V-22466, LSUMG V-22467, LSUMG V-22468, LSUMG V-22469, LSUMG V-22470, LSUMG V-22471 (Fig. 4.3a-c), LSUMG V-22472 (Fig. 4.12a-c), LSUMG V-22473, LSUMG V-22474, LSUMG V-22475 (Fig. 4.11a-c), LSUMG V-22476, LSUMG V-22477 (Fig. 4.9a-c), LSUMG V-22478, LSUMG V-22479, LSUMG V-22500, LSUMG V-22501.

Description – Upper and lower anterior teeth have a rather erect cusp. The mesial cutting edge of upper anterior teeth is elongated and concave basally, where the edge extends into a heel-like structure that is poorly differentiated from the rest of the crown (Figs 3.1c, 4.1b). The mesial edge is very coarsely serrated on this structure (Fig. 3.1d), but serrations become finer and are ultimately obsolete at the apex. The upper two-thirds to three-quarters of the mesial edge may be straight (Fig. 4.3a) or slightly convex (Fig. 3.1b). The distal cutting edge is also elongated and very concave basally, where the crown foot extends into an oblique heel (Figs 3.1c, 4.1a, 4.3b). This heel is longer than that of the mesial side, and it also bears coarse serrations. The remainder of the cutting edge is weakly convex, nearly vertical, and bears finer serrations that are ultimately obsolete at the crown apex. The serrations of the mesial and distal edges are weakly compound, although this is not consistent along any particular cutting edge. The mesial and distal cutting edges meet apically to form a relatively low but broadly triangular cusp, which is slightly distally inclined (Figs 3.1c, 4.1b, 4.3a). The root is bilobate, rather thin labio-lingually but high in lingual view. In mesial view the crown and root intersection presents an angular appearance (Fig. 4.1c). Root lobes are rather short but highly diverging, separated by a U-shaped interlobe area, and there is a narrow but long lingual nutritive groove (Figs 3.1b, 4.1a).

On lower anterior teeth, the mesial edge is deeply concave basally (Fig. 3.4b), such that the crown base is extended into a long heel. This edge is finely and regularly serrated nearly to the crown apex (Fig. 3.4d). The distal cutting edge is elongated, finely serrated nearly to the apex, nearly vertical to slightly inclined, and generally straight (Fig. 3.4b). The serrations of both edges are weakly compound, although this is not consistent along any particular cutting edge. The mesial and distal cutting edges meet apically to form a tall and relatively narrow, triangular cusp. This cusp is vertical (Fig. 3.4c) to slightly distally inclined (Fig. 4.9b). A low distal heel extends perpendicularly from the distal cutting edge, and the transition from edge to heel is deeply concave to angular (Figs 3.4a, 4.9a). The heel is evenly serrated, and these have fine serrations on the mesial side (Fig. 3.4b). The root is similar to that of the upper anterior teeth, but the interlobe area is

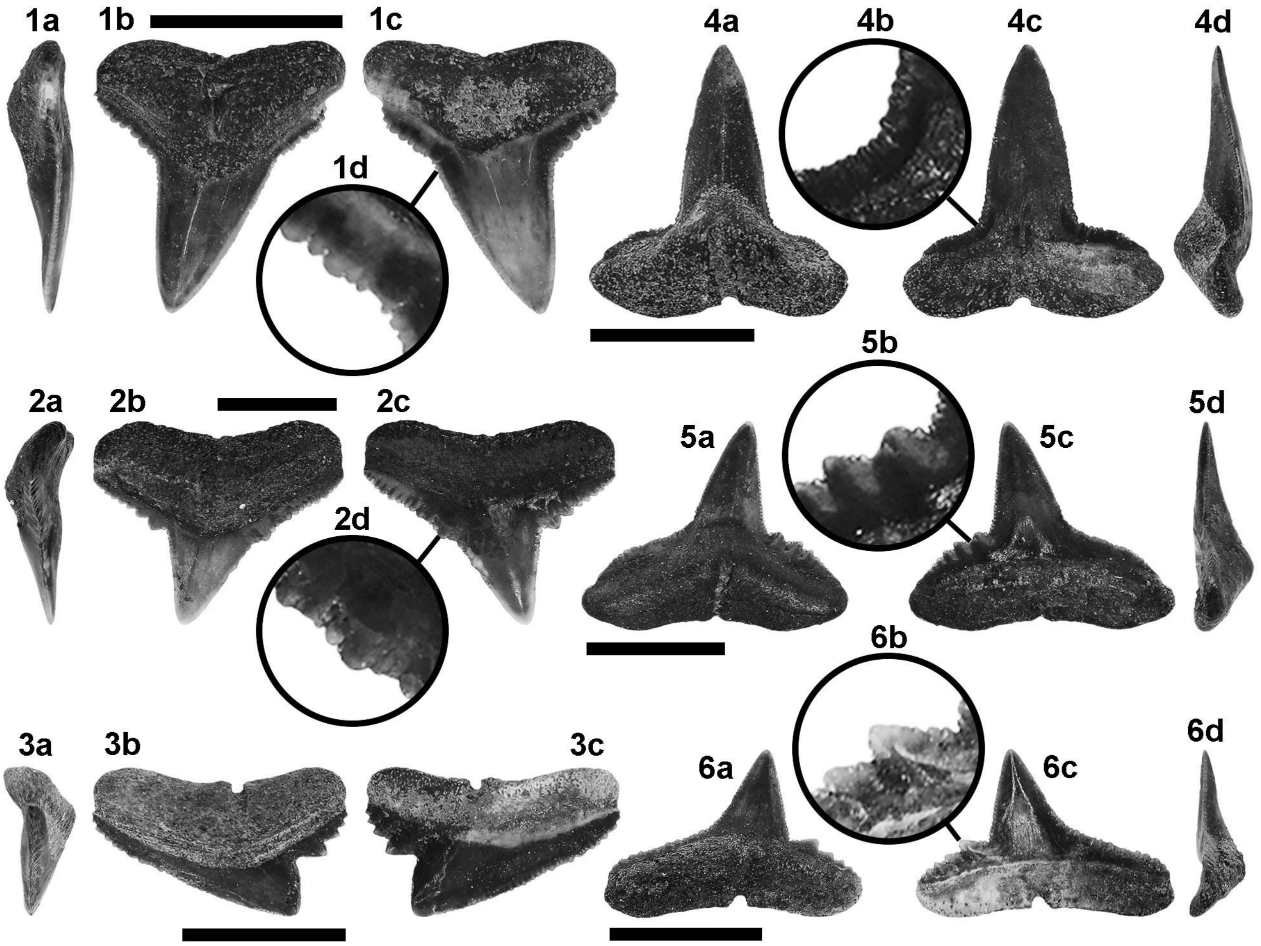

Figure 3.1-6. *Carcharhinus tingae* n. sp. hypodigm. 1a-d) LSUMG V-22437, paratype, upper right anterior tooth in a) mesial, b) lingual, and c) labial views, d) close-up of mesial serrations. 2a-d) LSUMG V-22439, holotype, upper left lateral tooth in a) mesial, b) lingual, and c) labial views, d) close-up of mesial serrations. 3a-c) LSUMG V-22422, paratype, upper right postero-lateral tooth in a) mesial, b) lingual, c) and labial views. 4a-d) LSUMG V-22436, paratype, lower left anterior tooth in a) lingual view, b) close-up of mesial serrations, c) labial view, d) mesial view. 5a-d) LSUMG V-22438, paratype, lower left lateral tooth (reversed for comparison); a) lingual view, b) close-up of distal denticles and serrations, c) labial view, d) mesial view. 6a-d) LSUMG V-22451, paratype, lower left postero-lateral tooth (reversed for comparison); a) lingual view, b) close-up of distal denticles and serrations, c) labial view, d) mesial view. Scale bars = 5 mm.

less concave (Fig. 3.4a).

Upper lateral teeth can be distinguished from the anterior teeth by their more distally inclined cusp, a distinctive notch separates the distal heel from the distal cutting edge, and large denticles occur on the heel (Figs 3.2b, 4.2a, 4.4a, 4.6b). The mesial cutting edge may be weakly sinuous (Fig. 4.6a), relatively straight (Fig. 4.4b), or even slightly convex (Fig. 3.2b). Serrations are largest basally but become obsolete apically. The distal cutting edge is short, finely serrated nearly to the apex, inclined to varying degrees, and ranges from straight to weakly convex. The serrations of both cutting edges are weakly compound, although this is not consistent along any particular cutting edge. The mesial and distal cutting edges meet apically to form a relatively low, broadly triangular cusp that is distally inclined to varying degrees (Fig. 4.4 vs. 4.6). A distal heel extends obliquely from the distal cutting edge, and this transition is marked by a conspicuous notch (Fig. 3.2c). The heel bears up to seven triangular denticles (the largest of which is located at the distal notch) that decrease in size basally. The mesial edge of the denticles is serrated. The root is comparable to that of the anterior teeth, except that root lobes are more elongated, the interlobe area is wider, and lobes are more rounded.

Lower lateral teeth can be distinguished from lower anterior teeth by their lower and distally inclined cusp, and a distal heel is separated from the distal edge by a conspicuous notch. The mesial cutting edge is elongated and strongly concave basally, such that the crown base is extended into a heel-like structure. This edge is finely and regularly serrated nearly to the crown apex. The distal cutting edge is shorter than the mesial edge, finely serrated almost to the apex, may be vertical to weakly inclined, and is generally straight. The serrations on the mesial and distal cutting edge are weakly compound in a manner similar to the anterior teeth. The mesial and distal cutting edges form a moderately high but relatively narrow cusp that is distally inclined to varying degrees (Fig. 4.8b vs 4.10b). The distal heel is oblique, and the transition from the distal cutting edge is marked by a distinct notch and the location of a prominent denticle on the heel (Figs 3.5c, 4.2b). The heel is denticulated in a manner similar that of upper teeth, as they decrease in size basally and bear fine serrae on the mesial edge (Figs 3.5b). The root is comparable to that of the anterior teeth but the root lobes are longer.

Upper and lower posterior teeth are of rather small size, with a very low crown. Upper posterior teeth (Fig. 3.3) have an elongated and weakly convex mesial cutting edge, whereas that of lower posterior teeth is very concave (Fig. 3.6a). The cusp of upper posterior teeth is wide and highly distally inclined, whereas the cusp of lower posterior teeth is somewhat narrower and more erect. The distal heel of both positions is separated from the main cusp by a distinctive notch and the first distal heel denticle (Figs 3.3c, 3.6b, 3.6c). Root lobes are low and sub-rectangular, the interlobe area is shallow and U-shaped, and the lingual nutritive groove is narrow and long (Fig.3.3b, 3.6a).

Remarks – As part of our study, we examined 34 jaws (20 specimens at SC, 14 at MSC) that represent 14 extant species of *Carcharhinus*. These specimens showed that all but the symphyseal files form within one continuous hollow, and the transition from anterior to lateral to posterior files is gradual. Within the upper jaws, the teeth within the anterior-most files, not directly on or adjacent to the symphysis, are roughly symmetrical and slightly smaller in size than teeth within the first few lateral files. These first lateral teeth have a slightly inclined cusp, but teeth become smaller in overall size, lower in overall height, and the cusp becomes more distally inclined towards the commissure. Upper teeth generally have a broader cusp compared to lower teeth.

Based on our evaluation of isolated teeth, the dentition of *Carcharhinus tingae* n. sp. exhibited both monognathic and dignathic heterodonty that is consistent with our observations of the dentitions of extant species. Monognathic heterodonty in the upper and lower jaws is expressed in the form of morphologies that can be referred to as anterior (Figs 3.4, 4.1), lateral (Figs 3.2, 3.5, and posterior (Figs 3.3, 3.6), with the crown becoming wider and the cusp lower and more distally inclined (i.e., more asymmetrical) from the symphysis to the commissure. Also, the distal heel of upper anterior teeth is not clearly separated from the distal cutting edge, whereas on lateral teeth these structures are delineated by a distinctive notch and the location of the first of the heel denticles (i.e., Fig. 4.5a, b). With respect to dignathic heterodonty, the cusp of upper teeth is mesio-distally broader (Fig. 4.4) than that of lower teeth (Fig. 4.8), the mesial cutting edge of lower teeth is much more concave (Fig. 3.5) than on upper teeth (Fig. 3.2), and distal heel denticles are larger and more numerous on upper lateral teeth (Fig. 4.2a) compared to lower laterals (Fig. 4.10a).

An additional tooth morphology differs from those described above by being small in overall size, symmetrical, with a rather high, vertical, narrow and triangular main cusp (Fig. 4.11a). The cusp is flanked by low horizontal shoulders that are nearly perpendicular to the cusp (Fig. 4.11b). In the jaws of extant *Carcharhinus* species that we examined, teeth of this morphology occur within the lower dentition, directly on (symphyseal) or immediately adjacent to (parasymphyseal) the symphysis. In contrast, teeth in equivalent positions in the upper jaw tend to be much larger and have a more broadly triangular cusp.

Teeth of *C. tingae* n. sp. are easily distinguished from those of all other Paleogene *Carharhinus* species by the combination of nearly completely serrated mesial and distal cutting edges, serrations are weakly compound, the distal heel on all lateral teeth is separated from the cusp by a distinctive notch, and denticles of the distal heel are serrated on the mesial edge. We believe that the combination of dental features described above are characteristic of *Carcharhinus* as opposed to one of several somewhat similar, coeval genera. The development of dignathic heterodonty in *C. tingae* n. sp. is in sharp contrast to the dentition of *Galeocerdo* Müller & Henle, 1837, in which isolated upper and lower teeth are difficult to distinguish from one another. Although the teeth of Eocene *Physogaleus* Cappetta, 1980 and *Galeorhinus* de Blainville, 1816 can have a heavily denticulated distal heel, both genera lack nearly completely serrated mesial and distal cutting edges. Eocene *Rhizoprionodon* Whitley, 1929 species lack both a heavily denticulated distal heel and serrated cutting edges. Although the Eocene species *frequens* (Dames, 1883), *gilmorei* (Leriche, 1942), and *marçasi* (Arambourg, 1952) have been assigned to *Carcharhinus*, Underwood & Gunter (2012) consider these teeth more appropriately assigned to *Negaprion* Whitley, 1940 because they lack serrations on the main cusp and the lateral heels are smooth or only weakly serrated.

Carcharinus mancinae Ebersole, Cicimurri & Stringer, 2109 from the Bartonian “upper” Lisbon Formation and Gosport Sand of Alabama is the only other species of *Carcharhinus* that has been identified from the Eocene Mississippi Embayment. Although this species also has weakly compound serrations, the distal heel is not well differentiated from the cusp except for in more posterior files. In contrast, a distinctive notch is present on all post-anterior upper and lower teeth of *C. tingae*. In mesial view, teeth of *C. tingae* n. sp. have an angular appearance due to the juncture of the crown and root, whereas *C. mancinae* teeth are flat. *Carcharinus mancinae* teeth also attain much larger sizes (>1 cm in height) and the serrations are more complex than those of *C. tingae* n. sp. (<1 cm in height). Also, *C. mancinae* has a unique triangular upper anterior tooth morphology that does not appear to be present in the *C. tingae* n. sp. dentition. The *C. tingae* n. sp. morphology does not represent heterodonty within *C. mancinae*, as juvenile specimens of the latter species from the Gosport Sand type section are essentially smaller versions of adult

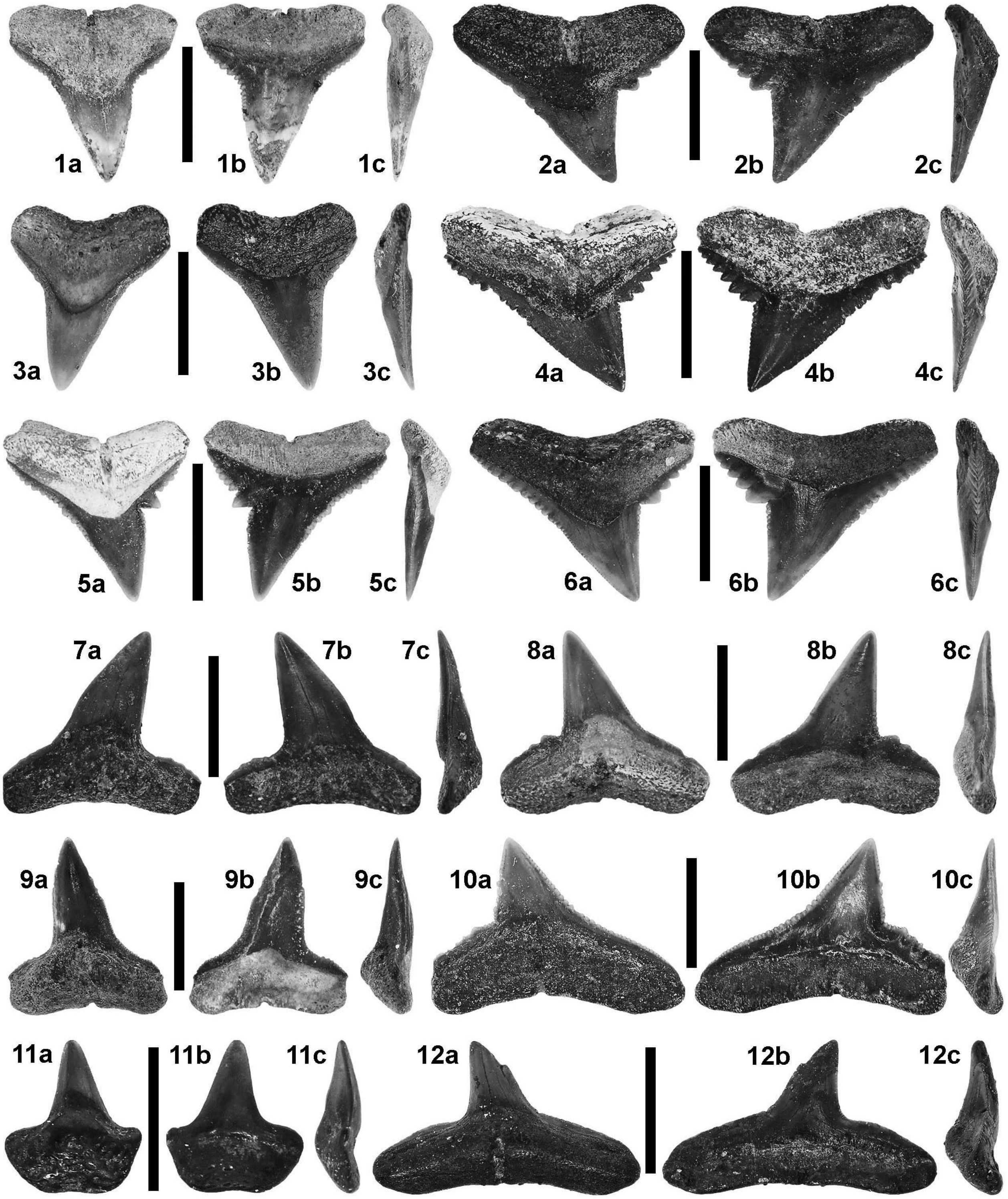

Figure 4.1-12. *Carcharhinus tingae* n. sp. referred specimens. 1a-c) LSUMG V-22454, upper right anterior tooth in a) lingual, b) labial, and c) mesial views. 2a-c) LSUMG V22444, upper right lateral tooth in a) lingual, b) labial, and c) mesial views. 3a-c) LSUMG V-22471, upper left anterior tooth in a) lingual, b) labial, and c) mesial views. 4a-c) LSUMG V-22456, upper right lateral tooth in a) lingual, b) labial, and c) mesial views. 5a-c) LSUMG V-22445, upper right antero-lateral tooth in a) lingual, b) labial, and c) mesial views. 6a-c) LSUMG V-22441, upper right lateral tooth in a) lingual, b) labial, and c) mesial views. 7a-c) LSUMG V-22432, lower right antero-lateral tooth in a) lingual, b) labial, and c) mesial views. 8a-c) LSUMG V-22442, lower left lateral tooth in a) lingual, b) labial, and c) mesial views. 9a-c) LSUMG V-22477, lower left anterior tooth in a) lingual, b) labial, and c) mesial views. 10a-c) LSUMG V-22457, lower left postero-lateral tooth in a) lingual, b) labial, and c) mesial views. 11a-c) LSUMG V-22475, lower symphyseal(?) tooth in a) lingual, b) labial, and c) mesial views. 12a-c) LSUMG V-22472, lower left posterior tooth in a) lingual, b) labial, and c) mesial views. Scale bars = 5 mm.

teeth. Additionally, the Cook Mountain Formation elasmobranch sample we examined lacks the *C. mancina*e morphology.

No other Eocene *Carcharhinus* species have been identified from the United States. However, an additional western hemisphere record of *Carcharhinus* is based on a single upper left tooth from the middle Eocene of Jamaica (Underwood & Gunther, 2012). That specimen differs from upper teeth of *C. tingae* n. sp. by having the largest mesial serrations located at the medial portion of the cutting edge (as opposed to basally), the serrations appear to be simple rather than compound, the distal heel has more denticles, denticles lack serrations on the mesial edges, and the interlobe area is deeply V-shaped instead of shallow and U-shaped. Underwood & Gunter (2012) suggested that the Jamaican tooth was comparable to teeth of *C. balochensis* Adnet, Antoine, Baqri, Crochet, Marivaux, Welcomme & Métais, 2007, but the morphology was more recently considered it to be conspecific with *C. kasserinensis* Adnet, Marivaux, Cappetta, Charruault, Essid, Jiquel, Ammar, Marandat, Marzougui, Merzeraud, Temani, Vianey-Liaud & Tabuce, 2020.

Carcharhinus tingae n. sp. has a sinuous mesial cutting edge, whereas Bartonian *C. kasserinensis* has a more uniformly convex edge, is larger, and the serrations of upper teeth are much coarser. Although the lower teeth of *C. kasserinensis* are poorly known, they appear to differ from those of *C. tingae* n. sp. by having a lower cusp with strongly convex cutting edges, and the mesial and distal ends of the crown are shorter (Adnet *et al*., 2020). The middle-to-late Eocene species *C. underwoodi* Samonds *et al*., 2019 is not known to exhibit dignathic heterodonty (based on the 12 referred specimens and other teeth that were synonymized), which contrasts with our interpretation of the *C. tingae* n. sp. dentition. Additionally, compared to *C. tingae* n. sp. upper teeth, the mesial cutting edge of *C. underwoodi* is straight to only weakly sinuous and its upper portion is not convex, denticles on the distal heel are more numerous, and a notch separating the distal cutting edge from the distal heel is lacking (Samonds *et al*., 2019).

The validity of *Carcharhinus balochensis*, from the late Eocene and early Oligocene of Pakistan, has been questioned. Samonds *et al.* (2019) considered most of the type suite to be conspecific with *Galeocerdo eaglesomei* White, 1955, and the remaining tooth was synonymized with *C. underwoodi*. However, Ebersole *et al.* (2019) considered the dentition of *C. balochensis* to have been similar to *C. mancinae*, and Adnet *et al.* (2020) also maintained usage of *C. balochensis*. The *G. eaglesomei*-like morphology of *C. balochensis* is much larger than teeth of *C. tingae* n. sp. and it lacks a distinctive notch between the distal cutting edge and the distal heel. The *C. balochensis* tooth that Samonds *et al.* (2019) considered synonymous with *C. underwoodi* also lacks a distal notch, and instead the transition from distal cutting edge to distal heel is a rounded corner. Additionally, lower teeth of *C. tingae* n. sp. are taller and the cutting edges less convex than on *C. balochensis* lower teeth (Adnet *et al*., 2007).

Genus *Isogomphodon* Gill, 1862

***Isogomphodon* sp.**
Figures 5.1-5.4

Material examined – MSC 43497.1 (Fig. 5.1a-c), MSC 43497.2 (Fig. 5.4a-c), MSC 43497.3 (Fig. 5.2a-c), MSC 43497.4, MSC 43497.5, MSC 43497.7, MSC 43497.8 (Fig. 5.3a-c), MSC 43497.9.

Stratigraphic occurrence and age – Rosefield Formation (former "Rosefield Marl beds"), lower Oligocene (Rupelian Stage), planktonic foraminiferal Zone P19 (Fig. 1.4).

Locality – "Rosefield Marl beds" type section, 0.2 km east of Rosefield Cemetery, NE ¼, Sec. 31, T. 11 N, R. 5 E, Catahoula Parish, Louisiana (Fig. 2.4).

Description – Upper anterior teeth have a tall, broad-based, sharply pointed main cusp (Fig. 5.2b). The main cusp is labio-lingually thin, with a flat labial face and weakly convex lingual face. In profile view the cusp has a slightly sinuous outline, with the cusp apex curving slightly labially (Fig. 5.2c). The crown enameloid is smooth. The mesial and distal cutting edges are smooth and extend from the crown apex and onto short lateral shoulders at the crown base. The root is bilobate with short, somewhat rectangular, widely diverging lobes. There is a narrow lingual nutritive groove and the interlobe area is shallow and V-shaped (Fig. 5.2a).

The main cusp of lower anterior teeth is very narrow and sharply pointed, with sub-parallel mesial and distal margins that become convex apically (Fig. 5.3b). The labial face is flat to weakly convex, whereas the lingual face is very convex. The crown enameloid is smooth. The cutting edges are smooth and continuous from the apex to the crown foot, where they extend onto short lateral heels. In profile view the crown is slightly lingually curved (Fig. 5.3c). The root is bilobate with rather short, widely diverging, rounded lobes. The interlobe area is V-shaped or U-shaped, and a narrow nutritive groove occurs on the lingual root face (Fig. 5.3a).

Lateral teeth have a narrow, triangular cusp that is sharply pointed (Fig. 5.1). The cusp can be high or low, and erect to slightly distally inclined depending on the file (Fig. 5.1 vs. Fig. 5.4). In profile the cusp is weakly to strongly lingually curving. The labial face is nearly flat to convex, and the lingual face is very convex. Crown enameloid is smooth. The mesial and distal cutting edges are smooth and continuous from the cusp apex to the crown foot, where they extend onto low, elongated lateral heels. The root is bilobate with elongated, widely diverging, sub-rectangular to rounded lobes. The interlobe area is U-shaped and weakly to strongly developed. A narrow lingual nutritive groove is located medially (Figs 5.1a and 5.4a).

Remarks – Although our sample consists of only nine specimens, we identified monognathic and dignathic heterodonty within this *Isogomphodon* species. Upper

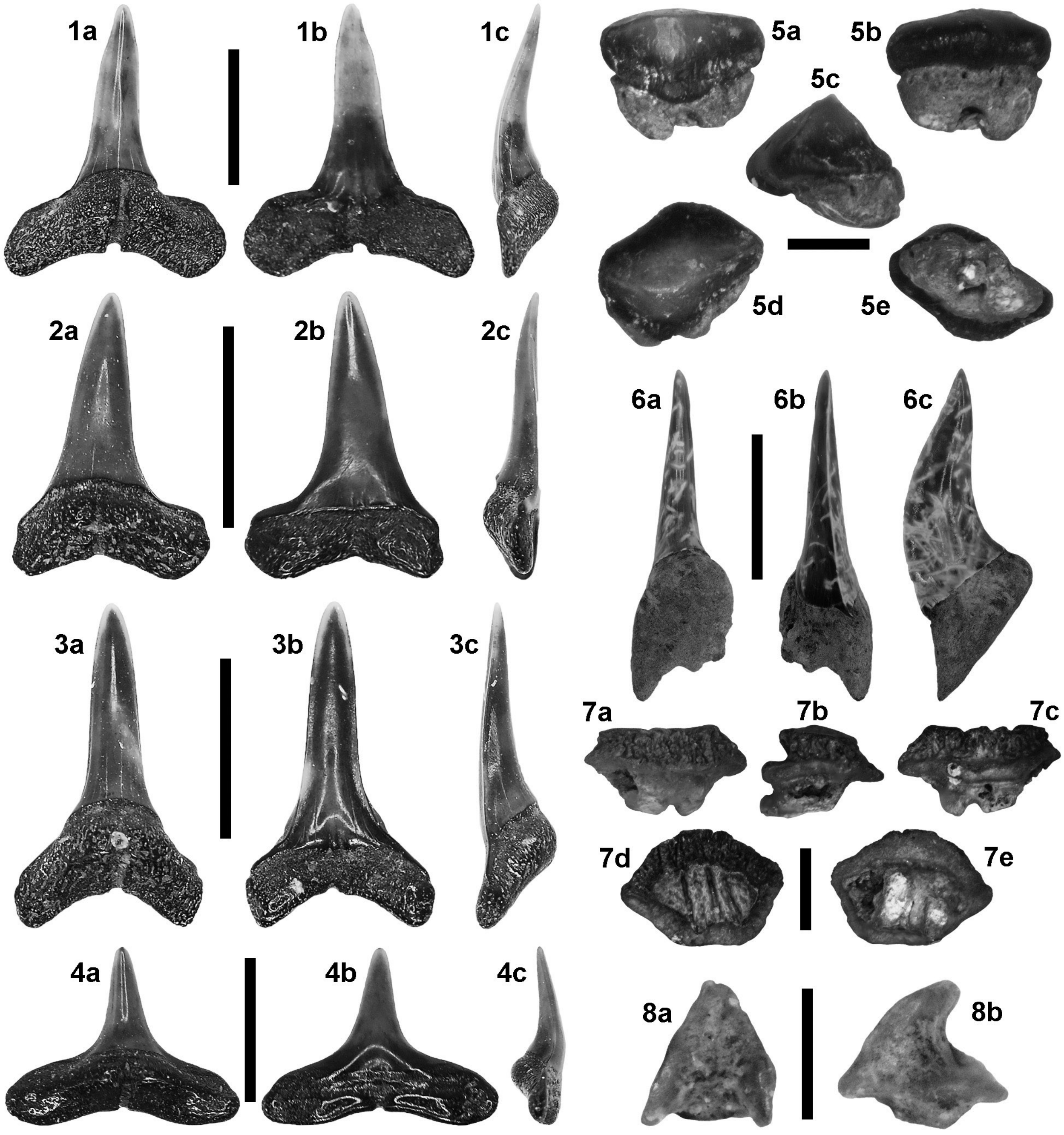

Figure 5.1-8. *Isogomphodon* sp., *Mustelus* sp., *Xiphodolamia ensis*, *Eoplinthicus yazooensis*, and *Gymnura* sp. teeth. 5.1a-c) MSC 43497.1, *Isogomphodon* sp. lower right antero-lateral tooth in a) lingual, b) labial, and c) mesial views, scale bar = 5 mm. 5.2a-c) MSC 43497.3, *Isogomphodon* sp. upper left anterior tooth in a) lingual, b) labial, and c) distal views, scale bar = 5 mm. 5.3a-c) MSC 43497.8, *Isogomphodon* sp. lower anterior tooth in a) lingual, b) labial, and c) distal views, scale bar = 5 mm. 5.4a-c) MSC 43497.2, *Isogomphodon* sp. lateral tooth in a) lingual, b) labial, and c) mesial views, scale bar = 4 mm. 5.5a-e) LSUMG V-22497, *Mustelus* sp. lateral tooth in a) apico-lingual, b) baso-labial, c) distal, d) occlusal, and e) basal views, scale bar = 1 mm. 5.6a-c) MSC 43345, *Xiphodolamia ensis* anterior tooth in a) lingual, b) labial, and c) distal views, scale bar = 1 cm. 5.7a-e) LSUGM V-22499, *Eoplinthicus yazooensis* lateral tooth in a) labial, b) profile, c) lingual, d) occlusal, and e) basal views, scale bar = 2 mm. 5.8a-b) LSUMG V-7613, *Gymnura* sp. tooth in a) labial and b) profile views, scale bar = 1 mm.

anterior teeth (Fig. 5.2) have a labio-lingually thinner but mesio-distally wider crown than lower anterior teeth (Fig. 5.3). The lateral teeth have a narrower crown than the anterior teeth, the lateral shoulders are more elongated and perpendicular to the main cusp, the root lobes are comparatively longer and more widely separated, and the interlobe area is shallower (Figs 5.1, 5.4). There was slight variation in the cusp attitude, ranging from erect to distally inclined, which we interpret to reflect upper (inclined) and lower (erect) lateral files.

Only two Paleogene occurrences of *Isogomphodon* have been previously documented from North America, and both are from the Atlantic Coastal Plain. These include *I. aikenensis* Cicimurri & Knight, 2019 from the upper Eocene (Priabonian) Dry Branch Formation of South Carolina, and *I. acuarias* (Probst, 1879) from the Oligocene Belgrade Formation of North Carolina (Case, 1980; Müller, 1999). The Rosefield Formation specimens differ from *I. aikenensis* by the low, straight heels on the lateral teeth (Cicimurri & Knight, 2019). The Louisiana teeth are similar to those of *I. acuarius*, and the material could be conspecific. However, given the early Oligocene temporal occurrence of the Louisiana taxon, it is possible that it represents a new species when compared to the Eocene (*I. aikenensis*) and Miocene (*I. acuarias*) records documented elsewhere. Compared to the Louisiana Oligocene specimens, teeth of another Mio-Pliocene species, *I. caunellensis* Cappetta, 1970, are larger and the lateral teeth have incomplete cutting edges. Additional specimens will help elucidate the identity and dental composition of the Rosefield Formation *Isogomphodon* species.

Family Triakidae Gray, 1851
Genus *Mustelus* Linck, 1790

***Mustelus* sp.**
Figure 5.5

Material examined – LSUMG V-22497.

Stratigraphic occurrence and age – Yazoo Clay (Tullos Member), upper Eocene (Priabonian) (Fig. 1.3).

Locality – Montgomery Landing, east bank of the Red River, N-S center line of Sec. 20, T. 8 N, R. 5 W, Grant Parish, Louisiana (Fig. 2.3).

Description – The tooth measures 2 mm in mesio-distal width and 1.5 mm in total height. In profile view the crown is low and has a triangular outline (Fig. 5.5c). The labial face is straight apico-basally, and mesio-distally it is only slightly convex. The labial crown foot is very thick and convex, and it protrudes well beyond the root. The enameloid on the labial crown face is generally smooth, but there are numerous longitudinal plications occurring at the crown foot (Fig. 5.5b). In occlusal view the crown is obviously asymmetrical, with the most convex part of the labial margin being located mesially and the convex part of the lingual margin occurring at the distal side (Fig. 5.5d). There is a robust transverse crest connecting the mesial and distal sides of the crown, and it is most convex along an indistinct, distally located cusp. The lingual crown face is mesio-distally convex, particularly at the cusp, and a short and rounded lingual uvula occurs below the cusp. Fine longitudinal ridges occur along the entire width of the lingual face and extend to two-thirds of its height (Fig. 5.5a). The root is rather low, and bilobate. The lobes are sub-triangular in basal outline and separated by a wide but shallow nutritive groove. A large foramen occurs within the groove (Fig. 5.5e), and additional smaller foramina are located immediately below the crown, where the root is slightly constricted.

Remarks – Based on our observations of the dentitions of extant *Mustelus californicus* Gill, 1864 (SC2020.53.10) and *M. canis* (Mitchill, 1815) (SC96.77.8), the crown outline and distal location of the cusp indicates that the LSUMG V-22497 is from a lateral tooth file. Paleogene records of *Mustelus* are extremely uncommon, with the only North American record being that of Parmley & Cicimurri (2003), who reported a single tooth from the Eocene (Bartonian) Clinchfield Formation of central Georgia. Those authors tentatively identified the specimen as *M. vanderhoefti* Herman, 1982, a taxon known from the Eocene of Belgium. An additional Eocene species, *M. whitei* Cappetta, 1976, has been reported from the lower Eocene (Ypresian) London Clay, and an unspeciated specimen was reported the middle Eocene of Antarctica (Englebrecht *et al.* 2017). Specimen LSUMG V-22497 possesses salient features of *Mustelus*, and the single tooth available to us is more similar to *M. vanderhoefti* based on its overall size and development of crown ornamentation. Specimen LSUMG V-22497 differs from *M. whitei* by having a very reduced lingual uvula that is poorly differentiated from the rest of the crown foot (Fig. 5.5e). The extent and robustness of the crown ornamentation, as well as the relatively low root, appear to separate the Louisiana specimen from *Mustelus* sp. teeth from the middle Eocene La Meseta Formation of Antarctica (Englebrecht *et al.* 2017). As the tooth morphology and dental arrangement of *Mustelus* has remained relatively stable since the early Eocene (Adnet & Cappetta, 2008; Englebrecht *et al.* 2017), a larger sample of teeth is needed to more accurately identify the Louisiana species. However, the tooth represents the first fossil occurrence of the genus in the Gulf Coastal Plain, and it provides a rare global Paleogene record of the genus.

Order Lamniformes Berg, 1958
Family Xiphodolamiidae Cappetta, 2012
Genus *Xiphodolamia* Leidy, 1877

***Xiphodolamia ensis* Leidy, 1877**
Figure 5.6

Material examined – MSC 43345.

Stratigraphic occurrence and age – Cane River Formation, middle Eocene (Lutetian) (Fig. 1.2).

Locality – Cane River site (aka I-49 site), 3 km south of Hwy 6 interchange, Sec. 38, T. 8 N, R. 8 W, Natchitoches Parish, Louisiana (Fig. 2.2).

Description – The tooth measures 2.5 cm in total height, of which the crown represents 1.7 cm. In labial view the crown is highly mesio-distally compressed, and the apical portion has a very slight distal bend (Fig.5.6b). In profile view the crown is labio-lingually broad and sinuous (Fig. 5.6c). The lingual crown face is convex, whereas the labial face is developed into a smooth and sharp longitudinal cutting edge (Fig. 5.6a). This edge extends from the cusp apex to the crown base, where it has a slight distal curve and extends onto a very short heel projecting onto the root. The mesial and distal crown faces are weakly convex and the enameloid is smooth. The root is massive and was bilobate (the mesial lobe is damaged), with the distal lobe being very short and basally pointed. The lingual root boss is large and the basal attachment surface is flat and smooth.

Remarks – Although *Xiphodolamia* is considered a member of the order Lamniformes, the familial placement of the taxon is often left unassigned (Adnet *et al.*, 2009; Carlsen & Cuny, 2014). However, Glickman (1964) erected the subfamily Xiphodolamiinae to include the genus, and Cappetta (2012) elevated the ranking to the family Xiphodolamiidae. This ranking was maintained by Nelson *et al.* (2016) and is followed herein. MSC 43345 possesses features that are unique to *Xiphodolamia*, particularly the teardrop-shaped transverse cross section due to the very convex lingual face (Fig. 5.6a) and sharp-edged labial face (Fig. 5.6b). Leidy (1877) originally named the type species, *X. ensis*, based on isolated teeth from the Eocene of New Jersey, and four other Eocene species have been named since that time. However, Cappetta (2006), Adnet *et al.* (2009) and Carlsen & Cuny (2014) have indicated that all but *X. serrata* Adnet *et al.*, 2009 are conspecific with *X. ensis*. Although *X. ensis* was originally described from North America, the taxon was widely distributed, as there are numerous accounts from Eocene strata of Europe and Asia (Paratethys/Tethys), northern Africa (Tethys), and the southern Atlantic Ocean along western Africa (see Moreau *et al.*, 2013).

MSC 43345 is virtually identical to the type specimen of *X. ensis* illustrated by Leidy (1877, pl. 34, figs. 25-27), and it differs from *X. serrata* by having a smooth, rather than serrated, cutting edge. Based on Adnet et al.'s (2009) conclusions regarding the dentition of this shark, MSC 43345 is from an anterior file, but we cannot determine if it represents an upper left or lower right tooth. When compared to Europe and Africa, very few occurrences of *X. ensis* have been reported from North America. Maisch *et al.* (2015) noted several specimens from a lag deposit in New Jersey that were likely reworked from the Shark River Formation. A Shark River Formation source is supported by Case & Borodin (2000), who illustrated a specimen (pl. 1, fig. 7) from this lithostratigraphic unit. Kent (1994) noted that *X. ensis* occurs in the lower Eocene (Ypresian) Nanjemoy Formation of the Cheseapeake Bay region, but the species was not documented from the Potapaco Member of the Nanjemoy Formation of Virginia (Kent, 1999). Case & Borodin (2000) reported ablated teeth from the middle Eocene Castle Hayne Formation of North Carolina. MSC 43345 is the first documented occurrence of *X. ensis* within the Gulf Coastal Plain (Eocene Mississippi Embayment) of the USA.

Division Batomorphi Cappetta, 1980
Order Myliobatiformes Compagno, 1973
Suborder Myliobatoidei Compagno, 1973
Family Myliobatidae Bonaparte, 1835
Subfamily Mobulinae Gill, 1893
Genus *Eoplinthicus* Cappetta & Stringer, 2002

***Eoplinthicus yazooensis* Cappetta & Stringer, 2002**
Figure 5.7

Material examined – LSUGM V-22499.

Stratigraphic occurrence and age – Yazoo Clay (Tullos Member), upper Eocene (Priabonian) (Fig. 1.3).

Locality – Montgomery Landing, east bank of the Red River, N-S center line of Sec. 20, T. 8 N, R. 5 W, Grant Parish, Louisiana. (Fig. 2.3).

Description – The tooth crown measures 5 mm in mesiodistal width, and in occlusal view it is slightly wider than long. In occlusal view the crown is six-sided, with rather straight margins and sharp angles (Fig. 5.7d). The lateral angles are approximately 90° and located medially. The area of the occlusal surface is conspicuously smaller than that of the crown base. The occlusal surface is weakly concave with three deep furrows connecting the labial and lingual margins. In profile (Fig. 5.7b) and labial (Fig. 5.7a) views the crown is rather low. The mesial, distal, and labial crown faces are oblique, sloping away from the occlusal margin. In contrast, the lingual face is inclined so that it slopes toward the labial face. All of the crown margins bear very coarse, irregular longitudinal ridges extending from the apex nearly to the crown foot. The labial crown foot is thick and rounded, and the lingual crown foot forms a lingually directed shelf-like projection (Fig. 5.7c). The crown overhangs the root on all sides, especially labially. The root is low, polyaulocorhize, and subdivided into several lamellae by wide nutritive grooves (Fig. 5.7e).

Remarks – *Eoplinthicus yazooensis* was first described from the Tullos Member of the Yazoo Clay at the Copenhagen locality in Caldwell Parish, LA (Cappetta & Stringer, 2002), and the species was recently reported from the middle Eocene (Bartonian) Gosport Sand of Alabama (Ebersole *et al.*, 2019). Specimen LSUGM V-22499 is characteristic of *Eoplinthicus* by having a relatively low crown with an occlusal outline that is significantly smaller than the basal outline. As the specimen is only twice as wide as it is long, which is much narrower than previously reported specimens, we believe that it represents a lateral file as opposed to a symphyseal file. Only three *E. yazooensis* teeth have been previously reported (see Cappetta & Stringer, 2002; Ebersole *et al.*, 2019), and LSUGM V-22499 represents the first lateral tooth morphology of this species to be described.

The available specimens indicate that the *E. yazooensis* dentition consisted of a symphyseal file and multiple lateral files. The teeth were alternating, with the lateral angles of a tooth fitting into angular recesses formed by the margino-lingual and margino-labial faces of teeth in the preceding/succeeding files. Additionally, the inclined labial crown face abutted tightly against the lingual crown face of the preceding tooth, with the labial crown foot fitting into a transverse lingual furrow and at the same time overlapping a shelf-like ridge at the lingual crown foot. Heavy ornament on the crown faces served as vertically oriented tongue-and-groove joints to tightly interlock teeth.

The features noted above serve to distinguish *Eoplinthicus* from the potentially co-occurring *Burnhamia* Cappetta, 1976 (Ebersole *et al.*, 2019). Although several other late Eocene mobulid genera have been named, these will not be confused with *Eoplinthicus*. However, teeth of some post-Eocene mobulid genera, like *Plinthicus* Cope, 1869, are similar to *Eoplinthicus*. The crown of the Oligo-Pliocene taxon is much higher and labio-lingually thinner, and the occlusal outline is roughly equal to the basal outline when compared to *Eoplinthicus* (Purdy *et al.*, 2001; Cicimurri & Knight, 2009). Additionally, the middle Oligocene taxon *Argoubia arnoldmülleri* Leder, 2015 differs from LSUMG V-7510 by having a convex labial face that is smooth basally, a smooth lingual face, and a large, flat occlusal surface that is denticulated along the lingual margin. Although Stringer *et al.* (2001) listed *Eoplinthicus* as one of the species recovered from the Rosefield Formation (Oligocene, Rupelian), that material is more likely *Plinthicus* or possibly "*Mobula*" *fragilis* (Cappetta, 1970).

Family Gymnuridae Fowler, 1934

Genus *Gymnura* van Hasselt, 1823

***Gymnura* sp.**

Figure 5.8

Material examined – LSUMG V-7613.

Stratigraphic occurrence and age – Yazoo Clay (Tullos Member), upper Eocene (Priabonian) (Fig. 1.3).

Locality – Montgomery Landing, east bank of the Red River, N-S center line of Sec. 20, T. 8 N, R. 5 W, Grant Parish, Louisiana. (Fig. 2.3).

Description – The root of the specimen is not preserved, but the crown measures 1 mm in height and 1 mm in width. In profile and labial views the crown has a triangular outline, although the apex is lingually hooked as seen in profile. The labial face is deeply concave but rather small, framed by lateral crests that occur on distinctive labially directed projections (Fig. 5.8a). The lingual face is very convex mesio-distally but concave apico-basally (Fig. 5.8b). The crown enamleoid is smooth. The crown overhangs the root on all sides, particularly on the labial side.

Remarks – Manning & Standhardt (1986) identified a tooth, LSUMG V-1818, as belonging to a male individual of their "*Dasyatis* sp. B". Although LSUMG V-1818 was not located during our study, comparison of the illustrations provided by Manning & Standhardt (1986: fig. 4-3) to LSUMG V-7613 show that they are conspecific, and both are identified herein as *Gymnura* sp. Teeth of *Gymnura* sp. are easily distinguished from those of male *Dasyatis* spp. by having a very concave labial crown foot when viewed apically. In contrast, *Dasyatis* spp. male teeth have a straight to convex crown foot. Additionally, the transverse crest of male *Dasyatis* spp. teeth divides the crown into roughly equal labial and lingual parts (in profile view), but the labial face of *Gymnura* sp. is not visible in profile. Instead, only the lingual face of *Gymnura* sp. is visible, and the transverse crest is located on the labially projecting mesial and distal sides of the crown.

Specimens LSUMG V-1818 and LSUMG V-7613 may be confused with male teeth of another member of the Gymnuridae, *Jacquhermania duponti* Cappetta, 1982. This latter taxon is known from older Claibornian strata of Alabama (Ebersole *et al.*, 2019), and male anterior teeth differ from those of the Yazoo Clay *Gymnura* sp. by having an erect apex as opposed to being lingually curved. The lateral teeth of *J. duponti* differ from the *Gymnura* sp. teeth by having a less concave labial face, and wider but shorter labially directed crown projections (Cappetta, 1982; Ebersole *et al.*, 2019). Teeth of middle-to-late Eocene *Pachygymnura* Adnet *et al.*, 2020, a taxon tentatively allied with Gymnuridae, lack a deeply convex labial face and labially expanded lateral projections, and the root base is nearly equal in area to that of the crown base.

Although only represented by two teeth, the Yazoo Clay (Priabonian) *Gymnura* sp. teeth appear to differ from Ypresian *G. grootaerti* Herman, 1984 by being larger in overall size, having a less distinctive cusp, and having a labial face that is concave along its entire apico-basal height. Additionally, the two teeth differ from the early Oligocene (Rupelian) *G. hovestadti* Herman, 1984 by having a uniformly convex (as opposed to squared) lingual crown foot, and the labial crown protuberances are shorter. The Yazoo Clay teeth also differ from the only other North American record of *Gymnura* sp., from the late Oligocene (Chattian) of South Carolina (Cicimurri & Knight, 2009), as well as *Gymnura* cf. *altavela* (Linnaeus, 1758) from Germany (Reinecke, 2015), by having a shorter cusp and less concave labial face due to much shorter lateral crown projections. Other *Gymnura* sp. specimens from the Tullos Member of the Yazoo Clay are needed to accurately identify the species. Manning & Standhardt (1986) implied that additional teeth of their *Dasyatis* sp. B had been collected, but we do not know if these represent *Gymnura* sp. or an actual dasyatid ray. The two teeth we have identified are the only representatives of *Gymnura* sp. thus far known from the Eocene Mississippi Embayment. A specimen assigned to *Gymnura* sp. from the middle Eocene (Lutetian) of Alabama (Clayton *et al*., 2013) is more appropriately identified as a male *J. duponti* tooth (Ebersole *et al*., 2019).

Discussion

The discovery of the shark and ray teeth described above came as a surprise to us, given the fact that very few records of the taxa represented are known from Paleogene deposits of North America. Their presence demonstrates that more work remains to be done to adequately document the fossil elasmobranch paleofaunas occurring in Louisiana and within the Gulf Coastal Plain of the USA in general. These new records are important because they improve our knowledge of the paleobiogeographic distributions of the taxa, and they allow us to render further interpretations of the paleoenvironment represented by the fossiliferous strata and the paleoecologies they preserve.

The *Carcharhinus* teeth from the Cook Mountain Formation of Louisiana represent a new species, *C. tingae*, a taxon that is somewhat similar to other Bartonian species occurring in the USA, Jamaica, and the Tethyan/Paratethyan realms. The new species is thus far only known from Louisiana; no evidence of *C. tingae* n. sp. was detected among a sample of roughly 12,000 fish teeth recovered from the Lutetian-Bartonian Lisbon Formation and Bartonian Gosport Sand of southwestern Alabama (Ebersole *et al*., 2019), and it is unknown from elasmobranch paleofaunas of the Moodys Branch Formation (Westgate, 1984; Manning & Standhardt, 1986). The heavily serrated, cuspidate teeth served a cutting-clutching function (*sensu* Cappetta, 2012), and the dentition appears to have been very similar to that of extant requiem sharks like *Carcharhinus dussumieri* (Valenciennes in Müller & Henle, 1841), *C. porosus* (Ranzani, 1840), *C. sealei* (Pietschmann, 1913), *C. sorrah* (Valenciennes in Müller & Henle, 1841), and *C. wheeleri* Garrick, 1982. These sharks are primarily piscivorous but also feed on cephalopods and crustaceans (Cortés, 1999; Last & Stevens, 2009; Voigt & Weber, 2011), and the similarity of the teeth among these species indicates that *C. tingae* n. sp. may have had a comparable diet.

All 87 of the *C. tingae* n. sp. teeth available to us were collected from the same locality, the B.F. Smith quarry in Bossier Parish, LA. Although the geologic exposures at this locality have not been documented in the scientific literature, museum records associated with the specimens (on file at LSUGM) indicate that the exposures at the quarry all belong to the middle Eocene (Bartonian Stage) Cook Mountain Formation. Our correspondence with one of the collectors (Dr A.B. McPherson) revealed that the specimens were derived from a reddish-brown ironstone like those reported by Zumwalt *et al*. (1995) from elsewhere in the state. Based on the invertebrate faunas they examined, Zumwalt *et al*. (1995) concluded that the beds underlying ironstone represented a storm deposit, whereas the overlying bed formed in a marginal marine setting with fluvial influence, and they interpreted an overall deepening-upward trend within the Cook Mountain Formation in northern Louisiana. Within the context of the Cook Mountain Formation, Zumwalt *et al*.'s (1995) study appears to have been focused on the upper three members of the formation, none of which have been formally named. The ironstone noted by Zumwalt *et al*. (1995) appears to be included within the "Middle Sand" member as shown by De Hon *et al*. (2001: fig. 2), and these authors concluded that Cook Mountain Formation ironstones represent estuarine or prodelta environments.

The *C. tingae* n. sp. teeth are stratigraphically younger than the type specimen of the protocetid whale *Natchitochia* Uhen, 1998, which was purportedly recovered from the Milams Member of the Cook Mountain Formation. This lithostratigraphic unit was deposited during the time interval represented by planktonic foraminiferal Zone P13, which is within the lower part of Zone NP17 (Uhen, 1998, Albright *et al*., 2019). Dolin & Dockery (2018) correlated the Cook Mountain Formation (of Texas, Louisiana, and Mississippi) with the "upper" Lisbon Formation of Alabama. Thus, *C. tingae* may be stratigraphically equivalent to *C. mancinae* specimens in the "upper" Lisbon Formation, but stratigraphically separated from (= older than) specimens occurring within the Gosport Sand (Ebersole *et al*., 2019).

Paleogene daggernose sharks (*Isogomphodon* spp.) are known from relatively few localities in North America. The taxon became geographically widely distributed during the Oligo-Miocene, but only a single highly endemic species survives today. The examined specimens were collected during a study conducted by Stringer *et al.* (2001), who recovered both vertebrate and invertebrate fossils from the lower and upper parts of the Rosefield Formation. These authors concluded that the Rosefield Formation was part of a deepening upward sequence, with the lower part accumulating under subtropical conditions within a deep inner-shelf environment (up to 20 m depth), and the upper part representing a central middle-shelf environment up to 50 m deep. Interestingly, the extant species inhabits very nearshore marine, turbid environments, and there is evidence that extinct species preferred a similar habitat (Lessa *et al*., 1999; Cicimurri & Knight, 2019). These conclusions are corroborated by our correspondence with one of the collectors (G.L. Stringer), who indicated that the specimens were recovered from the lower, shallower part of the Rosefield Formation. The *Isogomphodon* dentition is of the tearing type (*sensu* Cappetta, 2012) and used to acquire small bony fishes (Compagno, 1984). Based on the study of the teleost taxa occurring within the Rosefield Formation (Stringer *et al*., 2001), a variety of benthic bony fish could have been food sources for this shark.

Although Paleogene records of *Mustelus* sp. are very uncommon, the genus was widely distributed during the Eocene (Cappetta, 1976; Herman, 1982; Parmley &

Cicimurri, 2003; Englebrecht *et al*., 2017). The Louisiana specimen we identified represents only the second Eocene occurrence of a fossil *Mustelus* in North America and is the first from the Gulf Coastal Plain. As dentitions of extant species are of the crushing type (*sensu* Cappetta, 2012), and the gross morphology of the fossil tooth compares favorably to those of extant species, we presume that the diet of the extinct taxon was similar and consisted largely of crustaceans and other invertebrate species (Cortés, 1999). The lithology of the Tullos Member of the Yazoo Clay varies throughout its vertical thickness, which Manning & Standhardt (1986) concluded represented minor sea level fluctuations. They stated that the deeper water units formed in middle shelf-depth environments between 30 m and 100 m deep, whereas shallower deposits accumulated at inner shelf depths of 20 m to 30 m. These estimates are supported by Fierstine & Stringer (2007), who reported that the lower part of the Tullos Member accumulated within a tropical to subtropical inner shelf-depth environment (<30 m depth), whereas the upper part was deposited within the middle shelf at a depth between 20 m and 100 m. Nolf & Stringer (2003) concluded that their teleost paleofauna represented a subtropical to tropical, middle shelf environment of no more than 50 m depth. These shallow-water interpretations largely correlate to habitat preferences of extant *Mustelus* species (Compagno, 1984). Additionally, present-day species are highly endemic, suggesting it is unlikely that the Louisiana taxon is conspecific with species previously described from outside of North America.

Xiphodolamia ensis was geographically widely distributed during the Eocene (Moreau *et al.,* 2013), but relatively few North American occurrences have been documented. Aside from four records along the Atlantic Coastal Plain of the USA (Leidy, 1877; Kent, 1994; Case & Borodin, 2000; Maisch *et al*., 2015), the single specimen from Louisiana represents the only record from the Gulf Coastal Plain (Eocene Mississippi Embayment) and it extends the paleobiogeographic range of the taxon approximately 1,600 km to the West from the nearest occurrence. The dentition of this extinct shark was highly unusual but of a tearing type (*sensu* Cappetta, 2012), somewhat similar to that of present-day *Isurus* Rafinesque, 1810, which have a diet consisting almost exclusively of pelagic teleosts (Wood *et al*., 2009). Occurrences from elsewhere indicate that *X. ensis* was a pelagic species that inhabited open-ocean, possibly deep-water, environments (Cappetta, 1976; Adnet *et al*., 2009; Eeckhaut & De Schutter, 2009; Diedrich, 2012). Stringer & Breard (1997) and Stringer (2002) have postulated that the Cane River Formation represents an offshore but shallow-water patch reef environment, where water depth was between 20 m and 50 m and climatic conditions were subtropical to tropical.

Eoplinthicus yazooensis and *Gymnura* sp. are the most interesting batoid taxa occurring in the samples we examined. The *Eoplinthicus* tooth represents a previously unknown lateral morphology for this late Eocene species. Although the two species of *Eoplinthicus* that have been described demonstrate a wide paleobiogeographic distribution for the genus (Cappetta & Stringer, 2002; Adnet *et al*., 2015), *E. yazooensis* thus far appears to have been restricted to the Eocene Mississippi Embayment. However, its temporal and geographic range within this region was recently expanded by Ebersole *et al.* (2019), who documented a Bartonian (middle Eocene) occurrence within the Gosport Sand of Alabama. Depending on which horizon within the Tullos Member the *Eoplinthicus* specimens were derived, the unit represents either an inner neritic (<30 m deep) subtropical to tropical environment, or a middle neritic environment with a water depth of approximately 50 m (Manning & Standhardt, 1986; Nolf & Stringer, 2003; Fierstine & Stringer, 2007). Although Cappetta (2012) considered the dentition of *Eoplinthicus* spp. to be a grinding type, the taxon is believed to have been a filter-feeding species based on the lack of heavy wear on the teeth (Cappetta, 2012; Adnet *et al*., 2015).

The fossil record of *Gymnura* spp. in North America is very poorly known. The genus is documented from the Gulf Coastal Plain fossil record for the first time by two teeth occurring in the Priabonian Tullos Member of the Yazoo Clay of Louisiana. Based on the close similarity to the teeth of extant butterfly rays, the extinct species had a clutching dentition (*sensu* Cappetta, 2012) and likely predominantly consumed teleost prey, along with invertebrates like crustaceans and mollusks (*i.e*., Jacobsen *et al*., 2010; Yakota *et al*., 2013; Menon *et al*., 2020). Previous interpretations of the depositional environment of the Tullos Member of the Yazoo Clay differ slightly. Nolf & Stringer (2003) utilized various teleost taxa they identified to determine that their fossiliferous unit represented a subtropical to tropical, normal salinity environment, where water depth was less than 50 m and the sea floor was soft and muddy. Manning & Standhardt (1986) indicated that strata yielding *Gymnura* sp. were deposited in clear water up to 30 m deep, and the substrate was rather coarse-grained.

Conclusions

A new species of *Carcharhinus*, *C. tingae*, was identified from the middle Eocene (Bartonian) Cook Mountain Formation of Bossier Parish, Louisiana. This species may have been endemic within the Bartonian Mississippi Embayment, as it is currently unknown from contemporaneous strata occurring elsewhere within that region. Several teeth of *Isogomphodon* sp. from the Rosefield Formation (Oligocene, Rupelian) in Catahoula Parish represent the first record of the genus in the Mississippi Embayment, and are only the third record of the taxon from North America. A tooth of *Mustelus* sp. from the Tullos Member of the Yazoo Clay (upper Eocene, Priabonian) in Grant Parish is the only known occurrence of the taxon from the Gulf Coastal Plain of the USA, and represents the second Paleogene record in North America. A tooth of *Xiphodolamia ensis* from the middle Eocene (Lutetian) Cane River Formation of Natchitoches Parish is the first record of the taxon in the Mississippi Embayment of the USA and one of the few records of the taxon in North America. A tooth of *Eoplinthicus yazooensis* from the Tullos Member (Yazoo Clay) is only the fourth specimen of this species to be identified and is the first lateral tooth morphology to be described. *Gymnura* sp. is recognized for the first time within Paleogene Gulf Coastal Plain strata based on two teeth from the Tullos Member of the Yazoo Clay. These fossils clearly demonstrate that more work remains to be done to document elasmobranch paleofaunas not just of Louisiana, but within the entirety of the Gulf Coastal Plain of the USA.

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