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The occurrence of early Pleistocene marine fish remains from the Gulf Coast of Mobile County, Alabama, USA

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Abstract

We examined 91 specimens recovered as beach wash on the shores of Dauphin Island and the nearby Sand/Pelican Island Complex located in the northern Gulf of Mexico in Mobile County, Alabama, USA. A total of 12 unequivocal taxa were identified within our sample, including *Carcharias taurus*, *Carcharodon carcharias*, *Cosmopolitodus hastalis*, *Carcharhinus leucas*, *Carcharhinus* sp. cf. *C. longimanus*, *Carcharhinus obscurus*, *Carcharhinus* sp. cf. *C. plumbeus*, *Negaprion brevirostris*, *Galeocerdo cuvier*, *Hemipristis serra*, *Aetobatus* sp., and Diodontidae. Although not collected *in situ*, the preservation of the teeth, the biostratigraphic ranges of the taxa, and local stratigraphy suggests these fossils were derived from the shallow lower Pleistocene, Biloxi Formation and may be as young as Calabrian in age. Two extinct taxa in our sample, *C. hastalis* and *H. serra*, are among the stratigraphically youngest occurrences for each species. A comparison to extant representatives suggests this fossil assemblage preferred a warm, shallow, near-shore habitat with a water depth of 100 m or less. These fossils represent the first Quaternary marine vertebrates reported from Alabama.

Keywords: Chondrichthyes, Osteichthyes, North America, Dauphin Island, Sand/Pelican Island Complex, Gulf of Mexico.

1. Introduction

The marine record of fossil fishes in Alabama is among the most diverse and stratigraphically extensive in the United States. Fossil sharks and other marine fishes have been described in Alabama from strata ranging from the Paleozoic to the Cenozoic, with published reports of taxa from the Carboniferous (CIAMPAGALIO et al. 2011), Late Cretaceous (IKEJIRI et al. 2013; CIAMPAGALIO et al. 2013; CICIMURRI & EBERSOLE 2014), Paleocene (EHRET & EBERSOLE 2014; CICIMURRI & EBERSOLE 2015a), Eocene (CLAYTON et al. 2013; CICIMURRI & EBERSOLE 2015b; MAISCH et al. 2014, 2016; CAPPETTA & CASE 2016), and Oligocene (WHETSTONE & MARTIN 1978). Absent from this fossil record, however, are any reports of marine vertebrates from Pliocene or Pleistocene strata in Alabama. Although the Pleistocene vertebrate record has been thoroughly documented in the state, these reports have been limited to terrestrial and fluvial species (see EBERSOLE & EBERSOLE 2011; JACQUEMIN et al. 2016).

The purpose of this study is to report and describe the first early Pleistocene marine fish remains from Alabama. Reported herein are 91 specimens collected as beach wash on the Gulf of Mexico barrier islands, Dauphin Island and nearby Sand Island and Pelican Island (now referred to as the Sand/Pelican Island Complex), located in southern Mobile County, Alabama, USA. Although verbal reports have surfaced regarding the occurrence of fossil shark teeth on Dauphin Island beaches (D. EHRET, pers. comm. 2015), these reports have heretofore gone unverified. Herein, we also comment on the age of these fossils, provide discussions on their potential lithostratigraphic units of origin, and discuss the possible geological processes that led to them being deposited on the beaches.

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2. Material and methods

The 91 specimens examined as part of this study were collected by ROBERT DIXON of the DISL, predominately on the western beaches of Dauphin Island, Alabama, USA. A few additional specimens were collected by R. DIXON on the nearby beaches of Sand/Pelican Island Complex, located just southeast of the eastern end of Dauphin Island. Species identifications and tooth positions within

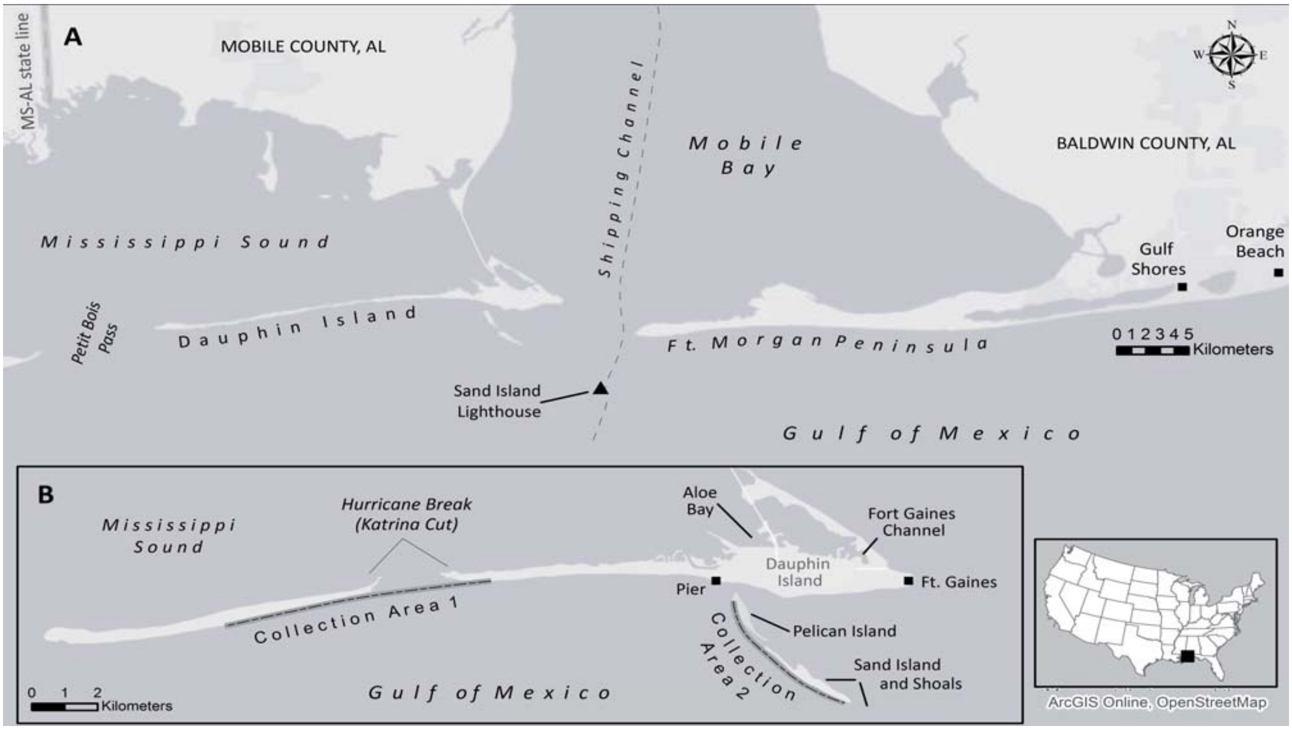


Fig. 1. Study area for this paper. **(A)** The southernmost part of the mainland of coastal Alabama. **(B)** A detailed view of Dauphin Island, including areas of fossil collection.

the mouth were determined primarily by direct comparison to isolated teeth and articulated jaws of Recent species housed at McWane Science Center, Birmingham, Alabama, USA and the South Carolina State Museum, Columbia, USA. The higher taxonomic rankings presented herein follow that of Nelson (2016), and any deviations from this source are discussed within the text. Within the *Systematic Paleontology* section, extinct genera and species are highlighted by the symbol "†". The geographic and stratigraphic ranges are not all inclusive and are instead intended to provide a broad scope of the range of each taxon. Although cited ranges were derived from peer reviewed studies, identifications of the taxa reported herein were not personally confirmed as part of the current study.

All examined specimens were photographed with a Nikon D80 camera with Tamron macro lens and all photographs were rendered in Adobe Photoshop CC 2015.5 software as part of the production of the presented figures. All specimens are accessioned in the collections at the DISL located on Dauphin Island, Alabama, USA.

The specimens examined in this study were predominately collected on the western beaches on Dauphin Island, Alabama, USA, but a few were collected from the beaches of the adjacent Sand/Pelican Island Complex (Fig. 1). These specimens were collected over the course of a 25-year period and were generally recovered after storm events (R. Dixon, pers. comm. 2015). Dauphin Island is a 23-km-long microtidal barrier island located approximately 8.0 km offshore from the mainland edge of southwestern Alabama in Mobile County. Dauphin Island is situated between Mississippi Sound to the north and the Gulf of Mexico to the south. Immediately northeast of the island is Mobile Bay, the ebb-tidal delta of which separates Dauphin Island and Fort Morgan Peninsula, located 4.3 km (3.0 mi) to the east. Just to the southeast of Dauphin Island, siliciclastic sediments have formed two small islands, Pelican Island and Sand Island, which have recently joined to form the Sand/Pelican Island Complex (Froede 2008). The Sand/Pelican Island Complex has slowly moved in a northwesterly direction and is now merged with the southeastern shore of Dauphin Island.

The surface geology and sediment of Dauphin Island is chiefly Holocene beach sand and sand dunes, and the eastern end of the island has a Pleistocene core of Citronelle Formation (Hummell & Parker 1995; Hummell 1996; Hummell & Smith 1996; Morton 2007), an iron-stained silty-clay paleosol (Fig. 2). This Citronelle core, however, is not present on the western side of the island. The source of the Holocene barrier island sand is mainly from westward long-shore currents traveling from the Florida panhandle, across Fort Morgan Peninsula (Douglass &

Haubner 1992). Sand and silt from Mobile Bay also contribute to Dauphin Island, the Sand/Pelican Island Complex, and the associated shoals (Douglass & Haubner 1992; Morton 2007). Some of the beaches on Dauphin Island also contain dredged material from underwater berms. Dredged sand from within the Mobile Ship Channel was used in 1987 to create an underwater berm on the ebb-tidal delta shield (Douglass & Haubner 1992); this sand later migrated to Sand Island shoal complex (Douglass & Haubner 1992; Hands 1991). Sand dredged in 1980 from Fort Gaines Channel was deposited along the shoreline in front of Fort Gaines (Douglass & Haubner 1992) and was also eroded by the same westerly currents that have been moving sediments to the Sand/Pelican Island Complex. In 1991, as part of beach restoration efforts at the request of the Dauphin Island Park and Beach Board, Mobil Exploration and Producing U.S., Inc. dredged a section of Aloe Bay and transported an estimated 14,000 cubic meters of the material to the public beach area of the fishing pier on the eastern end of the island (Douglass & Haubner 1992). Over time, this material has been carried westerly along the shore with the normal currents (Douglass & Haubner 1992), and storm wave action (Morton 2007) may have also contributed to erosion and deposition of this material. As reported by Mobil, the average shell content of the dredged material was 5% (Douglass & Haubner 1992). The first engineered beach nourishment project in this area took place in Spring of 2016, utilizing material that was mined 7.2 km (4.5 mi) south of the eastern end of the island (S. Douglass, pers. comm. 2016).

The specimens examined in this study were collected from two areas, the Gulf side of western Dauphin Island along a hurricane break (Fig. 1B), and on the beaches of the Sand/Pelican Island Complex (Fig. 1B). The specimens we examined were found as beach wash and not collected *in situ*, and their precise stratigraphic origin is therefore not known. However, all specimens, except for one, are fossilized, indicating they were derived from pre-Holocene strata. The fossilized specimens are all blackish-blue and brown in color, suggesting a similar method of preservation and place of origin. The lone exception, DISL 2015.1.15 (Fig. 3), is whitish in color and not as dense as the other specimens, suggesting it may be Recent in origin. Nevertheless, the discovery of fossilized marine vertebrate remains on the beaches of Dauphin Island and adjacent Gulf Shores and Orange Beach, AL is extremely uncommon (JAE and SME, personal observation), and no occurrences of such remains have been previously documented in the literature.

Although they were not collected *in situ*, these fossils were likely derived from the shallow subsurface pre-Holocene units of Dauphin Island and/or the pre-Holocene sediment dredged from nearby areas (Fig 2). Cores taken from Mississippi Sound and Dauphin Island show Pleistocene (Cronin 2001; Hummel 1996; McBride et al. 1991) facies below the present Holocene material. The pre-Holocene units include shoal to eolian sands of the Gulfport Formation (Otvos 2001), the alluvial Prairie Formation, and the underlying Biloxi Formation (Hummel 1996; Otvos 1972, 1991, 1997). The sand of the Gulfport Formation sometimes overlies the Prairie Formation, and sometimes the Biloxi, but has not been well identified (or understood) in the immediate Dauphin Island area. The Biloxi Formation is a compositionally fossiliferous, gray, or greenish-gray, to brown sand and clayey sand that was interpreted by Otvos (2001) as representing estuarine to open-shelf environments with transgressive and regressive cycles. Samples from USGS-Belle Fontaine No. 1 Core indicate an age as old as late Pleistocene based on the ostracode assemblage (Cronin 2001), and calcareous nannofossils suggest an age as old as the Calabrian (Gohn et al. 2001). Similarly, in a Mississippi Sound core (core S-2, drillhole #25; Otvos 1981), large forms of the calcareous nannofossils *Gephyrocapsa oceanica* and *Gephyrocapsa caribbeanica* were identified in the Biloxi Formation and interpreted as being as old as early Calabrian by Cita et al. (2012). Interpretation of depth to Biloxi and other pre-Holocene units on and around Dauphin Island varies with the subsurface lithology samples (Hummell 1996), and ranges from 70 feet deep to at or near the surface (e.g., Otvos DI-2, Gsa 1007, Otvos DI-9 of P'-P" in Hummell 1996).

It is plausible that some of the fossils collected on western Dauphin Island may have originated from material reworked by heavy storm and wave action. Examples of the intensity of reworking include island breaks (Fig. 1B) as wide as 2.4 km and even larger areas undergoing washovers and deep scouring from high velocity flow during Hurricanes Frederick (1979), Georges (1998), Ivan (2004), and Katrina (2005) (Morton 2007). These events of severe erosion and overwash deposits may have allowed erosion and deposition of material from older underlying units onto the current beach. If the fossil specimens indeed originated from lower Dauphin Island strata, storm reworking may be one possible mechanism of displacement. An example of a recent break on Dauphin Island was formed by Hurricane Katrina in 2005. Known locally as the "Katrina Cut", the hurricane incised a shallow, several meter-wide break through the western end of Dauphin Island. Over the succeeding five years, continued ebb and flow erosion had widened this gap to nearly 2.4 km, making the far western side of the island inaccessible to beachgoers. Most of the specimens examined in this study were collected along the edges of the "Katrina Cut" (Fig. 1B), suggesting their origin might be the result of the aforementioned mechanism.

It is also possible that some of the specimens, especially those collected on the Sand/Pelican Island Complex, were derived from dredged sediment from either the

Mobile Bay Shipping Channel or Fort Gaines Channel, which was carried by currents to the Sand/Pelican Island Complex. Dredged material from Aloe Bay (Douglass & Hauber 1992), may also account for fossils found west of the pier. Strong tropical storms passing over or through the Dauphin Island area, depending on surge and wind intensity, can naturally dredge large quantities of sand and other material and transport it to varying depths and distances, thus providing another possible mechanism of transport of the fossils.

3. Systematic paleontology

Chondrichthyes Huxley, 1880
(Cartilaginous fishes, rays, and sharks)
Not figured

Referred material: DISL 2015.1.58; DISL 2015.1.63; DISL 2015.1.67; DISL 2015.1.70; DISL 2015.1.71; DISL 2015.1.91.

Remarks: Of the 91 specimens in our sample, 54 (59%) could be identified to at least the generic level. Due to abrasion and/or breakage, 31 (34%) of the teeth in our sample could only be identified to the ordinal or familial level, and the six specimens listed above were referable to Chondrichthyes only.

Euselachii Hay, 1902

Elasmobranchii Bonaparte, 1838b

Selachii Cope, 1871

Galeomorphii Compagno, 1973

Odontaspididae Müller & Henle, 1839

Carcharias Rafinesque, 1810

Carcharias taurus Rafinesque, 1810
(Sand Tiger Shark)
Pl. 1, Figs. 3–5

Referred material: DISL 2015.1.36, upper left lateral tooth; DISL 2015.1.37, upper right lateral tooth; DISL 2015.1.38, lower right lateral tooth; DISL 2015.1.46, lower left anterior tooth; DISL 2015.1.47, lower right lateral tooth; DISL 2015.1.48, lower lateral tooth; DISL 2015.1.51, upper left anterior tooth; DISL 2015.1.72, lower lateral tooth.

Description: *Carcharias taurus* teeth have long and slender crowns with a sharply pointed apex. Anterior teeth sigmoidal in profile view, lingual crown face highly convex, labial face largely flat. Weak longitudinal folds present on the lingual face of some teeth but are completely absent on others. Short medial ridge present at the labial crown base of some teeth. Mesial and distal cutting edges generally do not reach the base of the crown on anterior teeth. Teeth have one to two pairs of small, sharp, rounded lateral cusplets that angle medially. Roots strongly holaulacorhizous with thin rounded root lobes. Roots on anterior teeth generally have a slender V-shape interlobe area; this area is wider on lateral teeth. Lower teeth generally erect in all tooth positions; lateral teeth in upper files have a slight distal inclination, except for those in the third upper anterior files, which incline mesially.

Remarks: Recent literature suggests that the fossil record of *Carcharias taurus* extends back at least to the Miocene (i.e. Apolin et al. 2004; Portell et al. 2008; Cione et al. 2011; Reinecke et al. 2011), giving the species a stratigraphic range that overlaps with an extinct member of the genus, *Carcharias acutissima* Agassiz 1843 (see Cappetta 2012). According to Antunes & Balbino (2003), the teeth of *C. acutissima* can be separated from those of *C. taurus* by the presence of faint striations on the lingual crown base that, at times, extend nearly halfway up the crown. Cappetta (1970), however, noted that these striations are much more evident on juvenile teeth and can be indistinct on adult specimens. Furthermore, Cappetta (2012) observed that many Pliocene teeth assigned to *C. acutissima* are nearly indistinguishable from those belonging to extant *C. taurus* specimens, suggesting that many of the reported occurrences of *C. taurus* may actually belong to the extinct *C. acutissima*. Although this may apply to the Alabama specimens examined in this study, all show no evidence of striations on any of the specimens, regardless of size. As a result, all are here assigned to *C. taurus.*

On occasion, the members of *Carcharias* have been referred to the genus *Eugomphodus* (i.e. Yang & Ishihara 2002; Parsons 2006; Iglésias 2013), a name generally considered a junior synonym of *Carcharias* (Iczn 1987). Parsons (2006) reported that extant *C. taurus* populations have been declining in the Gulf of Mexico, however, this taxon can still be observed in shallow near-shore environments at depths between 1.0 and 191 m.

An additional 21 teeth in our sample (DISL 15.1.35, DISL 15.1.50, DISL 15.1.59, DISL 15.1.61, DISL 15.1.62, DISL 15.1.64, DISL 15.1.65, DISL 15.1.68, DISL 15.1.73, DISL 15.1.77, DISL 15.1.79, DISL 15.1.80, DISL 15.1.81, DISL 15.1.82, DISL 15.1.83, DISL 15.1.85, DISL 15.1.86, DISL 15.1.87, DISL 15.1.88, DISL 15.1.89, and DISL 15.1.90) are conservatively referred to the Odontaspididae. Although their state of preservation precludes further identification, these teeth likely belong to *C. taurus* because the only other odontaspid known to reside in the Gulf of Mexico today, *Odontaspis noronhai* (Maul, 1955), is extremely uncommon and inhabits waters ranging from 600 to 1000 meters in depth (Parsons 2006).

Lamnidae Müller & Henle, 1838

Carcharodon Smith in Müller & Henle, 1838

Carcharodon carcharias (Linnaeus, 1758)
(Great White Shark)
Pl. 1, Fig. 7

Referred material: DISL 2015.1.1, upper anterior tooth; DISL 2015.1.2, first upper left anterior tooth; DISL 2015.1.3, lower lateral tooth.

Description: Teeth of *Carcharodon carcharias* are large, triangular, labiolingually compressed, and nearly symmetrical. Upper files mesiodistally wider than lower files.

Medium to coarse irregular serrations present on both mesial and distal cutting edges. Evidence of serrations is visible even on abraded specimens. Labial face is flat: lingual face is slightly convex but flat medially. Base of the crown is broad; no dental band present. Upper lateral files display a slight distal inclination. Both upper and lower posterior teeth with slightly sloping shoulders at the crown base. Roots holaulacorhizous with angular root lobes. Roots on lower teeth have a deeper interlobe area.

Remarks: According to Cappetta (2012), teeth that can be definitively assigned to the genus *Carcharodon* extend back as far as the early Pliocene, with widespread reports from Africa, Europe, Japan, North America, and South America. In North America, Pliocene and Pleistocene reports have been limited to California (Jordan 1907; Jordan & Hannibal 1923; Fitch 1964, 1968, 1970; Fitch & Reimer 1967; Long 1993); North and South Carolina (Leriche 1942); and Florida (Scudder et al. 1995; Morgan & Portell 1996). Teeth of *Carcharodon carcharias* can be differentiated from those of a stratigraphically older species, *C. hubbelli*, in being more evenly serrated and by having serrations that are more complex (Ehret et al. 2012).

Today, *Carcharodon carcharias* has a global distribution with populations concentrated in the northeastern Pacific Ocean and off the coasts of Australia, New Zealand, and South Africa (Jorgensen et al. 2010). Although *C. carcharias* has a contemporary range in the Gulf of Mexico, it is considered rare, with sightings limited to the winter months between January and April. This species has been observed close to shore at the surfline, and although it has been tracked at depths of over 1,200 m (Last & Stevens 1994), tagging studies of juvenile *C. carcharias* individuals off the coast of California have shown it spends upwards of 99% of its time in water depths of 50 m or less (Weng et al. 2007). In the Gulf of Mexico, this taxon has been recorded in water temperatures that range between 18.7 to 21.6˚ C (Parsons 2006).

†*Cosmopolitodus* Glikman, 1964

†*Cosmopolitodus hastalis* (Agassiz, 1843)
(Extinct mako shark)
Pl. 1, Fig. 8

Referred material: DISL 2015.1.28, upper left anterior tooth; DISL 2015.1.29, upper? tooth; DISL 2015.1.30, lower tooth; DISL 2015.1.31, upper tooth.

Description: Teeth of *Cosmopolitodus hastalis* are large, triangular, and labiolingually compressed. Labial and lingual crown faces smooth. Labial crown face is flat, lingual face is slightly convex. Crown sometimes overhangs the root labially with a medial or distal bulge. Cutting edges are distinct. Root is high and holaulacorhizous. Root lobes are elongated and more angular in upper files. Lingual protuberance present on the root, generally with a foramen. Teeth similar in overall morphology to *Carcharodon carcharias*, but lack serrations on the cutting edges. Lower teeth symmetrical in labial view, and straight in profile. Upper teeth grade from erect in anterior positions to distally inclined in lateral and posterior files. Lower teeth are labiolingually thicker and narrower mesiodistally.

Remarks: Recent studies have placed teeth with this morphology within one of three genera – *Carcharodon* (i.e. Ehret et al. 2012), *Cosmopolitodus* (i.e. Cappetta 2012), or *Isurus* (i.e. Applegate & Espinosa-Arrubarrena 1996) – with assignment generally depending on one's point of view on its evolutionary relationship to *Carcharodon carcharias* (see aforementioned references for competing hypotheses). Agassiz (1843) originally assigned teeth with this morphology to *Oxyrhina hastalis;* however, within this same publication he also named *Oxyrhina xiphodon*, a species with very similar teeth but differing from *hastalis* in having a wider tooth crown. Leriche (1926) questioned whether the *xiphodon* morphology represented a separate species, suggesting these wider-crowned teeth were an ontogenetic variant of the *hastalis* morphology (with the tooth crowns getting wider as the animal gets older). Purdy et al. (2001), however, suggested that *Isurus xiphodon* should be considered a valid species, arguing that ontogenetic heterodonty was nearly absent in the dentitions of *Isurus hastalis.* Whitenack & Gottfried (2010) later utilized morphometrics to test whether the *hastalis* and *xiphodon* morphologies were conspecific, and their results suggested both should be considered separate and valid species. Ehret et al. (2012), however, considered the two tooth morphologies identified by Whitenack & Gottfried (2010), wide-crowned and narrow-crowned, to be a result of ontogenetic and/or gynandric heterodonty within the same species, and assigned both to *Carcharodon hastalis.*

Ward & Bonavia (2001) brought to light additional taxonomic issues with these teeth, as they considered Agassiz's (1843) *Oxyrhina xiphodon* to be a *nomen dubium* because the stratigraphic information published with the type specimens was incorrect. Recognizing the instability of the *xiphodon* name, Cione et al. (2012) suggested the usage of *Isurus plicatilis* (Agassiz, 1843) for teeth with the wide-crowned morphology because not only was the name valid and available, but the type specimens described by Agassiz (1843) have long been considered conspecific with *O. xiphodon*. With regard to the validity of two separate species, both Colloreta et al. (2017) and Landini et al. (2017) agreed with the conclusions of Purdy et al. (2001), Whitenack & Gottfried (2010), and Cione et al. (2012), but suggested a new combination for teeth with the wide-crowned "*xiphodon*" morphology, *Cosmopolitodus plicatilis* (Agassiz, 1843).

Our analysis of five sets of jaws from extant *Isurus*, including *I. paucus* and *I. oxyrinchus*, did not elucidate the correct interpretation of these teeth. We observed that the adult teeth of *I. oxyrinchus* are more gracile than those of adult *I. paucus*, but also that juvenile teeth of both species are more gracile than their adult counterparts. From a biological perspective, we find it problematic to assign these teeth to *Carcharodon*, as teeth belonging to both *Carcharodon carcharias* and the "*xiphodon*" morphology have been recovered from the same stratigraphic deposits at numerous localities in both North and South America (González-Rodríguez et al. 2013; Iturralde-Vinent et al. 1996; Purdy et al. 2001; Scudder et al. 1995). This suggests that the "*xiphodon*"/*hastalis* morphologies and *C. carcharias* do not belong to the same chrono-specific line and should likely be placed within separate genera. Furthermore, within nearly all recent reports of the "*xiphodon*" morphology, teeth with the *hastalis* morphology have also been documented from the same deposits (Purdy et al 2001; Whitenack & Gottfried 2010; Ehret et al. 2012; Colloreta et al. 2017; Landini et al. 2017). This makes it more likely that the two morphologies are conspecific as opposed to the less-likely event of two similar shark species occupying the same ecological niche (with the morphological differences likely being a result of various types of heterodonty; i.e. ontogenetic, dignathic, and/or gynandric). Although future studies may conclude the two morphologies do indeed represent distinct species, we take a more conservative approach and view the two as conspecific. Nevertheless, all of the teeth in our sample represent those of the wide-crowned "*xiphodon*" morphology. Here we choose to utilize the name *Cosmopolitodus hastalis*, not to suggest its taxonomic relationship to any of the other lamnids or odontasipids, but simply as it is the name most commonly applied in the recent literature to teeth with this morphology (Cappetta 2012; Nelson et al. 2016; Colloreta et al. 2017; Landini et al. 2017).

Cappetta (2012) reported that *Cosmopolitodus hastalis* had a stratigraphic range that extended from the early Miocene to the late Pliocene. However, *C. hastalis* teeth reported by Scudder et al. (1995) from the Leisey Shell Pits in Florida suggest this taxon may have survived into the Calabrian of the Pleistocene. One specimen in our sample, DSIL 15.1.4, has the general characteristics of *C. hastalis* as it has a triangular crown and lacks serrations on its mesial and distal blades. However, due to its abraded and broken condition, it is conservatively assigned to Lamnidae only.

Carcharhiniformes Compagno, 1984

Carcharhinidae Jordan & Evermann, 1896

Carcharhinus De Blainville, 1816

Carcharhinus leucas (Valenciennes in Müller & Henle, 1839) (Bull Shark)
Pl. 1, Fig. 6

Referred material: DISL 2015.1.5, upper anterior tooth; DISL 2015.1.6, upper right anterior tooth; DISL 2015.1.14, upper left lateral tooth; DISL 2015.1.20, upper left lateral tooth; DISL 2015.1.33, upper anterior tooth; DISL 2015.1.16, upper anterior? tooth.

Description: Upper teeth of *Carcharhinus leucas* are labiolingually compressed. Labial crown face flat, lingual crown face slightly concave. Both crown faces smooth. Anterior teeth erect, lateral teeth display a slight distal inclination. Mesial and distal cutting edges serrated. Serrations are generally largest medially, but decrease in size towards the crown base and fade towards the crown apex. Root holaulacorhizous with shallow interlobe area. Weak nutritive groove may or may not be present on the lingual face of the root. Strong dignathic heterodonty present, as upper and lower tooth morphologies vary greatly. Crowns mesiodistally wider in upper teeth. Contact between the crown base and root creates a distinct V-shape dental band on the lingual surface of upper teeth.

Remarks: Four species of *Carcharhinus* have been identified in our sample, *Carcharhinus leucas*, *Carcharhinus* sp. cf. *C. longimanus*, *Carcharhinus obscurus*, and *Carcharhinus* sp. cf. *C. plumbeus*. The upper teeth assigned here to *C. leucas* were differentiated from these other *Carcharhinus* species by the following: 1) the mesial and distal serrations are less coarse than those on *C. longimanus* and more coarse than those of *C. plumbeus*; 2) the distal inclination of the mesial blade is more than that on *C. longimanus*, but less than that on *C. obscurus*; 3) has a mesial edge that is less convex than that on *C. obscurus*; and 4) the average mesiodistal width is twice that of the teeth of *C. plumbeus*. One specimen in our sample, DISL 15.1.33, has the general characteristics of an upper anterior tooth of *C. leucas*, but due to its heavily abraded condition, it is conservatively assigned to *Carcharhinus* sp. cf. *C. leucas*.

The stratigraphic record of *Carcharhinus leucas* extends back to the Miocene, and fossils of this age have been reported from the Amazon (Lundberg et al. 2001), Egypt (Cook et al. 2014), India (Sahni & Mehrotra 1981), Panama (Pimiento et al. 2013), Peru (Apolín et al. 2004), and Portugal (Antunes & Balbino 2004; Antunes et al. 1999). In North America, fossil representatives of this taxon have been reported from localities in California (González-Barba & Thies 2000), Florida (Webb & Tessmann 1968; Scudder et al. 1995; Morgan & Portell 1996), Georgia (Hulbert & Pratt 1998), and North Carolina (Purdy et al. 2001). Modern *C. leucas* populations have a cosmopolitan distribution, inhabit warm tropical and sub-tropical waters worldwide, and occasionally can be found in freshwater (Séret 2003). *C. leucas* has a range throughout the Gulf of Mexico today (Parsons 2006) and has been observed in coastal areas at depths between 1 and 152 m (Sommer et al. 1996).

Carcharhinus longimanus (Poey, 1861)
(Oceanic Whitetip Shark)
Pl. 1, Fig. 9

Referred material: DISL 2015.1.16, upper right anterior tooth; DISL 2015.1.21, upper left lateral tooth.

Description: Two upper teeth in our sample are here identified as belonging to *Carcharhinus* sp. cf. *C. longimanus*. These teeth are morphologically similar to those of *C. leucas* and *C. obscurus*, but differ in having coarser medial serrations and a more erect mesial blade. The specific identification of these teeth, however, is here only tentative as a tremendous amount of individual variation exists among the members of this genus.

Remarks: Like *C. leucas*, fossil reports of *C. longimanus* suggest its temporal range extends back to the Miocene (i.e. Antunes 1963; Sahni & Mehrotra 1981; Müller 1999; Laurito & Valerio 2008; Aguilera et al. 2011; Sharma & Patnaik 2014). In North America, the fossil record of this taxon is known from two reports, noting its occurrences in the Neogene of North Carolina and Virginia (Müller 1999) and the Pliocene of South Carolina (Cicimurri & Knight 2009). Although *C. longimanus* is known to have a distribution in the Gulf of Mexico today, it is an oceanic species that is rarely observed near shore (Parsons 2006). *C. longimanus* is known to swim at depths of up to 150 m, but is most often observed at or near the water surface (Compagno 1984).

Carcharhinus sp. cf. *C. obscurus* (LeSueur, 1818)
(Dusky Shark)
Pl. 1, Fig. 10

Referred material: DISL 2015.1.23, upper left lateral tooth; DISL 2015.1.25, upper right lateral tooth; DISL 2015.1.26, upper left lateral tooth; DISL 2015.1.27, upper right lateral tooth; DISL 2015.1.52, upper left lateral tooth.

Description: The teeth identified herein as *Carcharhinus obscurus* are morphologically similar to those of *C. leucas* and *C. longimanus*. These teeth differ, however, by having a more distally inclined mesial blade than the aforementioned taxa, and by having less coarse serrations than *C. longimanus*.

One specimen in our sample, DISL 2015.1.52, possesses the general morphology of *C. obscurus*, however, due to abrasion, no serrations are preserved. Thus, this specimen is only tentatively assigned to this taxon.

Remarks: Extant *C. obscurus*, like the other *Carcharhinus* taxa reported here, likely diverged from a common ancestor in the Miocene, and fossil representatives have been reported from various localities in Chile (Suárez et al. 2002), Costa Rica (Laurito 2004), Cuba (Iturralde-Vinent et al. 1996; MacPhee et al. 2003), Egypt (Cook et al. 2014), the Grenadine Islands (Portell et al. 2008), Portugal (Antunes et al. 1999), Japan (Ishiwara 1921; Goto 1972), North America (Purdy et al. 2001), Panama (Pimiento et al. 2013), and Venezuela (Sánchez-Villagra et al. 2000). Extant representatives have a similar cosmopolitan distribution (see Voigt & Weber 2011) and, despite declining populations, are known to have a range in the northern Gulf of Mexico today (Parsons 2006). *C. obscurus* is reported to inhabit both nearshore and deep waters, at depths between 1.0 and 400 m (Voigt & Weber 2011).

Carcharhinus sp. cf. *C. plumbeus* (Nardo, 1827)
(Sandbar Shark)
Pl. 1, Fig. 11

Referred material: DISL 2015.1.56, upper left lateral tooth; DISP 2015.1.66, upper right lateral tooth; DISP 2015.1.75, upper left lateral tooth; DISP 2015.1.84, upper right lateral tooth.

Description: Upper teeth belonging to *Carcharinus plumbeus* have the general form attributed to members of the genus, but differ from the other *Carcharinus* species in our assemblage by having much finer serrations and a smaller mesiodistal width (< 1.0 cm). Although the four teeth in our sample possess these morphological characteristics, we could not rule out that they might belong to a juvenile representative of one of the other three described taxa. Thus, these specimens are only tentatively assigned to this species.

Remarks: *C. plumbeus* is a fourth species of *Carcharhinus* in our sample that appears to have origins in the Miocene (see Caretto 1972; Antunes et al. 1999). Living representatives have a range in the Gulf of Mexico today, but populations have been reported to be declining (Parsons 2006). This taxon has a global distribution (see Voigt & Weber 2011) and generally inhabits coastal areas at depths between 1.0 and 200 m (Parsons 2006).

Carcharhinus sp. (Requiem sharks)
Pl. 1, Figs. 12–13

Referred material: DISL 2015.1.32, upper right lateral tooth; DISL 2015.1.34, upper right lateral tooth; DISL 2015.1.42, lower lateral tooth; DISL 2015.1.55, upper left lateral tooth; DISL 2015.1.69, upper right lateral tooth.

Description: Both upper and lower teeth of *Carcharhinus* sp. have been identified in our sample. Although many of these specimens possess the general upper tooth morphology of *Carcharhinus*, we could not assign them to a species due to their incomplete and/ or abraded preservation. In some cases, the serrations are worn and not preserved, and in others, the crowns are incomplete, both preventing species-level identifications. Although a few are well preserved, the lower teeth of *Carcharhinus* were difficult to speciate because the lower dentitions of the various species are similar and the specimens in our sample are abraded. These teeth differ from those in the upper files by being distinctly T-shaped, with mesial and distal crown edges that slope to form distinct shoulders. These teeth also have thinner root lobes than those on upper teeth.

Remarks: Despite our inability to speciate these teeth, it is our belief that they likely belong to one of the four *Carcharhinus* taxa described above. Parsons (2006) recognized 14 species of *Carcharhinus* in the Gulf of Mexico today, all but three of which prefer to inhabit shallow near-shore waters.

An additional seven specimens in our sample (DISL 15.1.41, DISL 15.1.43, DISL 15.1.44, DISL 15.1.45, DISL 15.1.54, DISL 15.1.74, and DISL 15.1.76) are conservatively referred to the Carcharinidae. All appear to represent teeth from the lower dentition, however their state of preservation precludes any refined identification. Another tooth in our sample, DISL 15.1.53, is represented by a partial tooth root, likely from the upper dentition. Due to its fragmentary condition, this specimen is here referred only to the Carchariniformes.

Negaprion Whitley, 1940

Negaprion brevirostris (Poey, 1868) (Lemon Shark)
Pl. 1, Fig. 14

Referred material: DISL 2015.1.49, upper tooth; DISL 2015.1.57, lower tooth; DISL 2015.1.78, lower tooth.

Description: *Negaprion brevirostris* teeth display little monognathic heterodonty, making it difficult to assign them to tooth groups. Teeth T-shaped, especially in lower files. Cusps high and triangular. Labial and lingual crown faces smooth. Labial crown face flat; lingual face slightly convex. Crown shoulders extend almost to the lateral edges of the root lobes. Roots holaulacorhizous and laterally extended. Strong nutritive groove on lingual face of root. Crown shoulders weakly serrated in upper lateral files; main cusp not serrated. Heals on lower teeth generally not serrated. Root slightly thicker on anterior teeth. Cusps slightly narrower and thicker in lower files. Crowns on lower teeth have a slight lingual bend.

Remarks: Although the teeth in our sample clearly belong to the genus *Negaprion*, their specific assignment is less clear. Fossil representatives of this genus, reported mainly from Eocene and Miocene deposits, have been referred to *Negaprion eurybathodon* (Blake, 1862) (see Purdy et al. 2001; Visaggi & Godfrey 2010), thought to be the ancestor of the extant taxon from the Americas, *Negaprion brevirostris* (Poey, 1868). Unfortunately, the morphological characteristics that have been used to separate the teeth of these two taxa are ambiguous, leading some authors to suggest that the two species are conspecific (Purdy et al. 2001; Pimiento et al. 2013). However, as part of their genetic study on the two extant members of the genus, *Negaprion brevirostris* and *N. acutidens* (Rüppell, 1837), Schultz et al. (2008) estimated that the two species diverged approximately 10 Ma and became genetically isolated roughly by 3.5 Ma. Citing the fossil record, Schultz et al. (2008) further suggested that *Negaprion eurybathodon* was likely the cosmopolitan ancestor of the two extant species. This data suggests both *N. eurybathodon* and *N. brevirostris* should be considered valid taxa, but the use of *N. eurybathodon* should a restricted to fossils dating from deposits older than 10 Ma (upper Miocene), the estimated time of divergence of the extant species. Late Miocene through Pleistocene representatives from the Americas should therefore be assigned to *N. brevirostris*, as this is after the time of divergence and within the temporal range of extant populations. Furthermore, the data presented by Schultz et al. (2008) indicated that the two extant species became geographically and genetically separated roughly 3.5 Ma by the emergence of the Isthmus of Panama (Schultz et al. 2008), thus leading to their differences in tooth morphology. Although we are aware of the inherent issues surrounding molecular clocks, the genetic data presented by Schultz et al. (2008) provides sufficient evidence for us to confidently assign the teeth in our sample to *N. brevirostris.*

Extant populations of *N. brevirostris* reside on the continental shelf of the Gulf of Mexico and are common residents in mangrove swamps (Parsons 2006). *N. brevirostris* is a shallow-water taxon that on occasion swims to the open ocean, but typically prefers water depths of 1 to 92 m (Compagno 1984).

Galeocerdidae Herman et al., 2010

Galeocerdo Müller & Henle, 1837

Galeocerdo cuvier (Péron & Lesueur in Lesueur, 1822)
(Tiger Shark)
Pl. 1, Figs. 15–16

Referred material: DISL 2015.1.12, lateral tooth; DISL 2015.1.13, anterior tooth; DISL 2015.1.15, lateral tooth; DISL 2015.1.17, anterior tooth; DISL 2015.1.18 anterior? tooth; DISL 2015.1.19, anterior tooth; DISL 2015.1.22, lateral tooth; DISL 2015.1.24, lateral tooth.

Description: *Galeocerdo cuvier* teeth are distinct by having a strong distal hook and pronounced distal notch. Strong distal heel present. Lingual face strongly convex, labial face with slight convexity. Mesial and distal cutting edges serrated with compound serration pattern. Mesial serrations are largest medially but decrease in size apically. Serrations on distal heel increase in size from the distal edge to the distal notch and are the largest serrations on the tooth. Serrations on the distal cutting edge are fine, of consistent size, and fade toward the apex. The distal notch has a complex serration pattern, and the mesial edge of the largest distal serration is lined with minute serrations. Nutritive groove may or may not be present on lingual face of the root. Upper and lower teeth difficult to distinguish. Lateral teeth mesiodistally wider than tall. Roots holaulacorhizous with angular lobes.

Remarks: Cappetta (2012) recognized five species of fossil *Galeocerdo*, three of which, *G. aduncus* Agassiz, 1843, *G. cuvier*, and *G. mayumbensis* Dartevelle & Casier, 1943, have been described from Neogene deposits. The *Galeocerdo* teeth in our sample differ from those of *G. aduncus* by being larger in size (with those of *G. aduncus* generally not exceeding 2.0 cm in mesiodistal width), having a more convex mesial cutting edge, and by having compound serrations on both the mesial and distal cutting edges (those on *G. aduncus* are generally restricted to the distal cutting edges). The teeth in our sample are differentiated from those of *G. mayumbensis* in being lower crowned, having a more convex mesial cutting edge, a more conspicuous notch at the juncture between the distal cutting edge and distal heel, the distal heel is more convex, and cutting edges are more complexly serrated (see Dartevelle & Casier 1943). These features are more consistent with teeth we examined in the jaws of the extant species, *Galeocerdo cuvier.* Fossil reports of this taxon are widespread, but North American accounts have been limited to California (Applegate 1978), Florida (Webb & Tessman 1968; Scudder et al. 1995), Georgia (Hulbert & Pratt 1998), North Carolina (Cappetta 1987), South Carolina (Cicimurri & Knight 2009), and Virginia (Müller 1999). Today this taxon is found throughout the Gulf of Mexico (Parsons 2006) and occurs on or adjacent to continental shelves in tropical to temperate seas, generally between depths of 1 to 140 m (Smith 1997).

This species has been referred in some recent studies by the incorrect spelling "*G. cuvieri*" (i.e., Parsons 2006; Mondal et al. 2009). However, the code of the International Commission on Zoological Nomenclature requires the original spelling of the specific name to be retained, in this case, *Squalus cuvier* Péron & Lesueur in Lesueur, 1822. Although Cappetta (2012) and Nelson et al. (2016) place *Galeocerdo* within the family Carcharhinidae, recent mitochondrial DNA studies show *Galeocerdo cuvier* to be an outgroup from the otherwise monophyletic Carcharhinidae (see López et al. 2006; Naylor et al. 2012). We support recent placement of the species in the family Galeocerdidae (Herman et al. 2010; Naylor et al. 2012).

Hemigaleidae Hasse, 1879

Hemipristis Agassiz, 1843

†*Hemipristis serra* Agassiz, 1843 (Snaggletooth Shark)
Pl. 1, Fig. 17

Referred material: DISL 2015.1.7, upper left lateral tooth; DISL 2015.1.8, upper right lateral tooth; DISL 2015.1.9, upper left lateral tooth; DISL 2015.1.10, upper right lateral tooth.

Description: *Hemipristis serra* had a dentition with strong disjunct heterodonty, but only upper teeth were identified within our sample. Crowns on upper teeth are triangular with a distinct distal hook. Crowns bend lingually. Mesial cutting edge is sinuous and bears large serrations perpendicular to cutting edge, which curve upward to the apex. Serrations do not reach apex. Distal cutting edge concave, with larger, less numerous serrations than on mesial side. Mesial and distal serrations increase in size toward the apex. Root high with deep nutritive groove on lingual face. Root holaulacorhizous with asymmetrical lobes. Mesial lobe flat and angular, distal lobe rounded. Roots with V-shaped interlobe area.

Remarks: This extinct species had a cosmopolitan distribution and a long temporal range that extended from the Oligocene to the Pleistocene. Generally common in Miocene and Pliocene deposits around the globe, teeth belonging to *H. serra* are often abundant at sites with depositional settings representing warm neritic environments (Cappetta 2012). Pleistocene occurrences are rare and have been reported only from Indonesia (Hooijer 1954), Mexico (Dickerson & Kew 1917), California (Jordan & Hannibal 1923), and Florida (Scudder et al. 1995). No extant members of the Hemigaleidae are known to have ranges in the Gulf of Mexico today (see Parsons 2006), and the only living member of the genus, *Hemipristis elongata* (Klunzinger, 1871), has a range that is limited to the Indo-West Pacific region (Scudder et al. 1995). This Recent taxon prefers

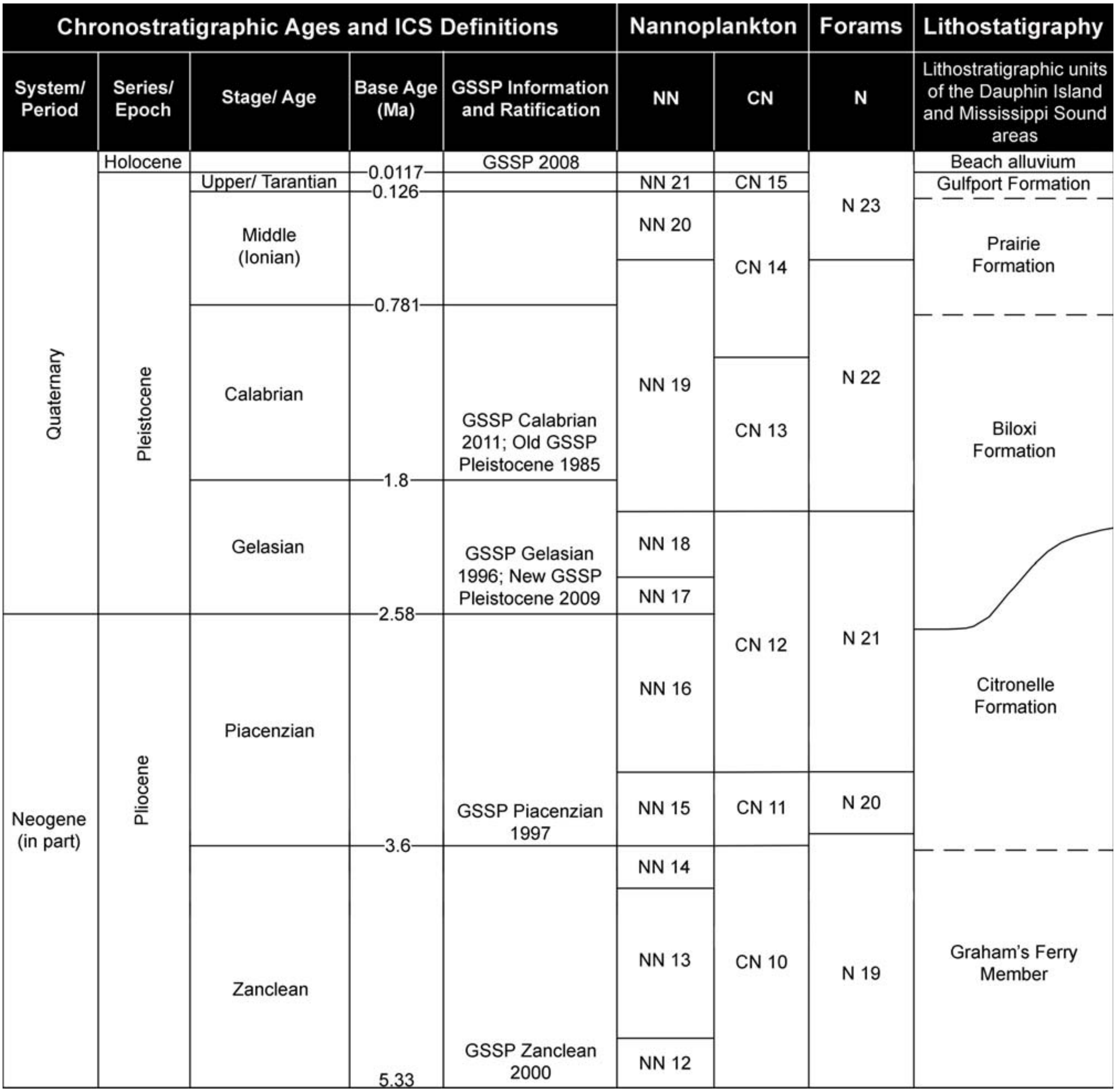


Fig. 2. Stratigraphy of the Dauphin Island and Mississippi Sound areas. GSSP, Global Boundary Stratotype Section and Point. Ma, millions of years ago. N, foraminiferan zone of Blow (1969). NN, Neogene calcareous nannofossil zonations of Martini (1971). CN, calcareous nannofossil zonations of Okada & Bukry (1980). Coccoliths Neogene Lithostratigraphic ages based in part on nannoplankton from Belle Fontaine core (Gohn et al. 2001) and Mississippi Sound core S-2, drillhole #25 (Otvos 1981, 2001) and estimated stratigraphic position.

tropical waters and inhabits depths of between 1 to 130 m (Last & Stevens 1994).

Batomorphi Cappetta, 1980

Myliobatiformes Compagno, 1973

Suborder Myliobatoidei Compagno, 1973

Myliobatidae Bonaparte, 1838a

Aetobatus De Blainville, 1816

Aetobatus sp. (Eagle ray)
Pl. 1, Fig. 18

Referred material: DISL 2015.1.40, upper medial tooth.

Description: *Aetobatus* tooth plates consist of a single medial file. In oral view, crown of lower teeth anteriorly convex, whereas upper tooth crowns straight to sinuous, with slight distal curvature at lateral edges. Crown also antero-posteriorly wider in medial region. Labial and lingual crown faces bear fine vertical ridges and grooves. Root polyaulocorhizous, lingually extended. Nutrititve grooves faint at labial face of root, deep basally, and extend onto dorsal surface of root. Root higher than crown in medial region of upper teeth.

Remarks: Cappetta (2012) recognized three species of *Aetobatus* in the fossil record – *A. arcuatus* (Agassiz, 1843); *A. cappettai* Antunes & Balbino, 2006; and *A. irregularis* (Agassiz, 1843) – with an overall stratigraphic range that extended back to the Eocene. Due to the amount of individual variation within the tooth plates of extant *Aetobatus* species, Hovestadt & Hovestadt-Euler (2013) questioned whether any of the fossil members of the genus can truly be speciated based on isolated teeth. Combined with the incomplete preservation of the tooth in our sample, this specimen is here only assigned to the generic level. This tooth, however, does not differ appreciably from those belonging to the extant *A. narinari* (Euphrasen, 1790), the Spotted Eagle Ray, which is the only member of the genus known to have a range in the Gulf of Mexico today. This is a near shore taxon with a water depth preference of 1 to 80 m (Parsons 2006).

Osteichthyes Huxley, 1880

Actinopterygii Klein, 1885

Holostei Müller, 1846

Teleosteomorpha Arratia et al., 2004

Teleostei Müller, 1846

Teleocephala de Pinna, 1996

Clupeocephala Patterson & Rosen, 1977

Otocephala Johnson & Patterson, 1996

Acanthopterygii Greenwood et al., 1966

Percomorpha Rosen, 1973

Ovalentaria Smith and Near in Wainwright et al., 2012

Tetradontiformes Berg, 1940

Tetradontoidei Nelson et al., 2016

Diodontidae Bonaparte, 1835
(Porcupinefishes and burrfishes)
Pl. 1, Fig. 19

Referred material: DISL 2015.1.11, dentary consisting of fused lower tooth plate and beak.

Description: In oral view, anterior edge of the beak is rounded (as opposed to pointed on the premaxilla). Dentary consists of two fused plates and two stacks of lamellar trituration plates. Anterior edge composed of small, individual teeth tightly packed into a row. Anterior tooth row separated from trituration plates by a shallow gap of bone. Two large trituration plates located in the dorso-medial region of the dentary. Trituration plates sub-triangular or heart-shaped in dorsal and ventral views and tightly fused along their midline. In lateral view, the numerous trituration plates are tightly stacked. In oral view, only the dorso-posterior edge of each plate is exposed. The ventral surface of trituration plates is smooth; oral surface exhibits slight ornamentation and irregular wear.

Remarks: Neogene diodontid toothplates from North America have commonly been assigned to the genera *Diodon* or *Chilomycterus*. Tyler (1980) and Purdy et al. (2001), however, discussed how the skulls and dentitions of these two genera are not taxonomically useful and that the two can only be reliably differentiated by their dermal spines. Because only a single dentary is preserved in our sample, it is herein only conservatively assigned to Diodontidae only.

The fossil record of the diodontids extends at least back to the Late Cretaceous (see Gallo et al. 2009). Of extant representatives, McEachran & Fechhelm (2005) recognized three species of *Diodon* (*D. eydouzii*, *D. holocanthus*, and *D. hystrix*) and four species of *Chilomycterus* (*C. antennatus*, *C. antillarum*, *C. reticulatus*, and *C. schoepfi*) that have ranges within the Gulf of Mexico today. Of these, only one is considered pelagic (*D. eydouzii*; Kuiter & Tonozuka 2001), while all the others prefer shallow reef habitats or coastal waters no deeper than 100 m (Robins & Ray 1986; Lieske & Myers 1994; Smith 1997; McEachran & Fechhelm 2005).

4. Discussion

Most of the 91 specimens described in this study were found washed up on the beach on the western end of Dauphin Island in south Alabama (with a few others collected from the adjacent Sand/Pelican Island Complex). Among these specimens, 12 unequivocal taxa representing six families, eight genera, and nine species were identified. Of these 12 unequivocal taxa, two are extinct (*Hemipristis serra* and *Cosmopolitodus hastalis*), eight are extant and still have ranges in the Gulf of Mexico today (*Carcharias taurus*, *Carcharodon carcharias*, *Carcharhinus leucas*, *Carcharhinus* sp. cf. *C. longimanus*, *Carcharhinus obscurus*, *Carcharhinus* sp. cf. *C. plumbeus*, *Negaprion brevirostris*, and *Galeocerdo cuvier*) and two (*Aetobatus* sp. and Diodontidae) could not be speciated, but each have representatives that currently reside in the Gulf of Mexico. With the exception of the described *Aetobatus* sp. and Diodontidae specimens, the remaining unequivocal taxa each represent first fossil records for Alabama.

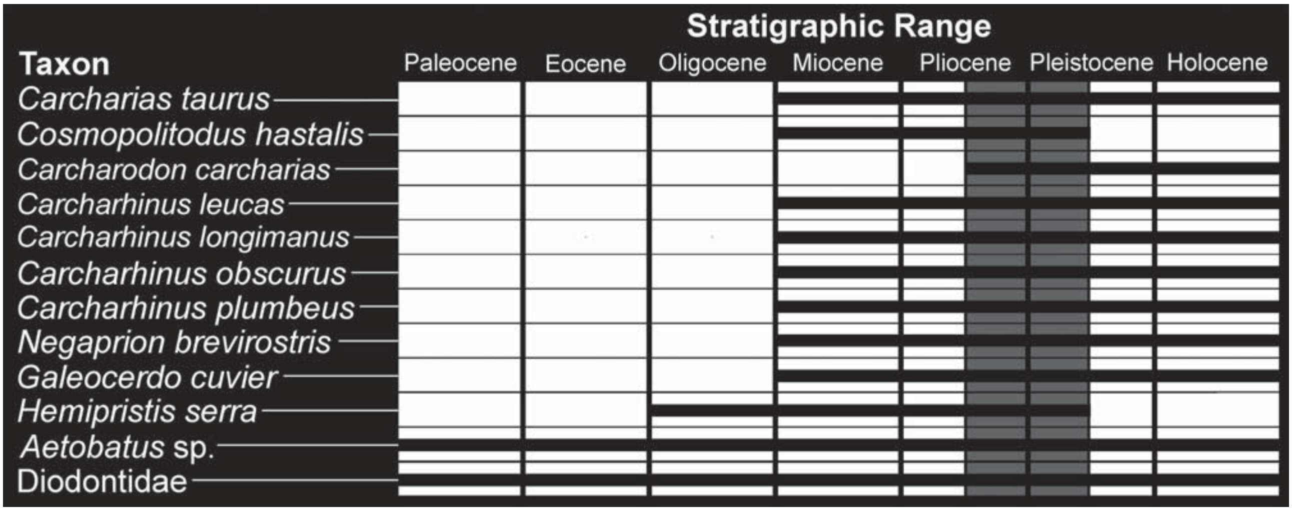
As noted previously, the specimens examined in this study were not recovered *in situ* but likely eroded from subsurface pre-Holocene units present at or around Dauphin Island and Sand/Pelican Island Complex and subsequently re-deposited on the surface. Three pre-Holocene lithologic units have been identified within the vicinity of these islands, including the upper Pliocene to lower Pleistocene (upper Piacenzian to Gelasian) Citronelle Formation, the lower Pleistocene (Gelasian to Calabrian) Biloxi Formation, and the middle Pleistocene (Ionian) Prairie Formation (Fig. 2). Of these three formations, circumstantial evidence suggests the fish remains in our sample were likely derived from the Biloxi Formation.

Previous analyses of microfossils from Biloxi Formation cores suggest a temporal age for this unit that ranges from the Gelasian to Calabrian of the early Pleistocene (Cita et al. 2012; Otvos 1981; Fig. 2). The possibility that the teeth in our sample could be as young as the early Pleistocene is supported by an analysis of the published stratigraphic distributions for the taxa identified (Table 1). The temporal ranges presented were compiled through a search of the peer-reviewed literature for localities that reported the occurrence of any of the unequivocal taxa identified within our sample. Recent literature was examined on a global scale (see references cited herein), and with the recent 2008 ratification of the Pliocene/Pleistocene boundary from 1.8 to 2.6 Ma (Gibbard & Head 2010; see Fig. 2), the geology of any locality reporting a late Pliocene age was reexamined to determine the amended age for the reported assemblage.

The results of this analysis (see Table 1) suggest that nearly all the taxa we identified were present, or even originated, in the Miocene. The lone exception in our sample is the occurrence of *Carcharodon carcharias*. Although occurrences of *Carcharodon* have been reported from the Miocene (i.e., Visaggi & Godfrey 2010; Cione et al. 2011; Sharma & Patnaik 2014), Cappetta (2012) suggests that any reports of pre-Pliocene *C. carcharias* should be treated with skepticism because they likely represent an ancestral form of the modern taxon. This was supported by Ehret et al. (2012), who proposed the origin of *C. carcharias* to have occurred within the middle Pliocene, possibly around 4.0 Ma (D. J. Ehret, pers. comm. 2016). This in turn suggests the Dauphin Island assemblage can be no older than middle Pliocene in age.

Our sample also includes two extinct taxa, *Cosmopolitodus hastalis* and *Hemipristis serra*. Although recent studies suggest these two species became extinct at the end of the Pliocene, Scudder et al. (1995) documented the recovery of *C. hastalis* and *H. serra* teeth from the lower Pleistocene component of the Belmont Formation at the Leisley Shell Pits in Hillsboro County, Florida. Utilizing several lines of evidence, Morgan &

Table 1. Published stratigraphic ranges for fossil taxa represented in the Dauphin Island assemblage. Shaded area represents the range of stratigraphic overlap of all recovered taxa.



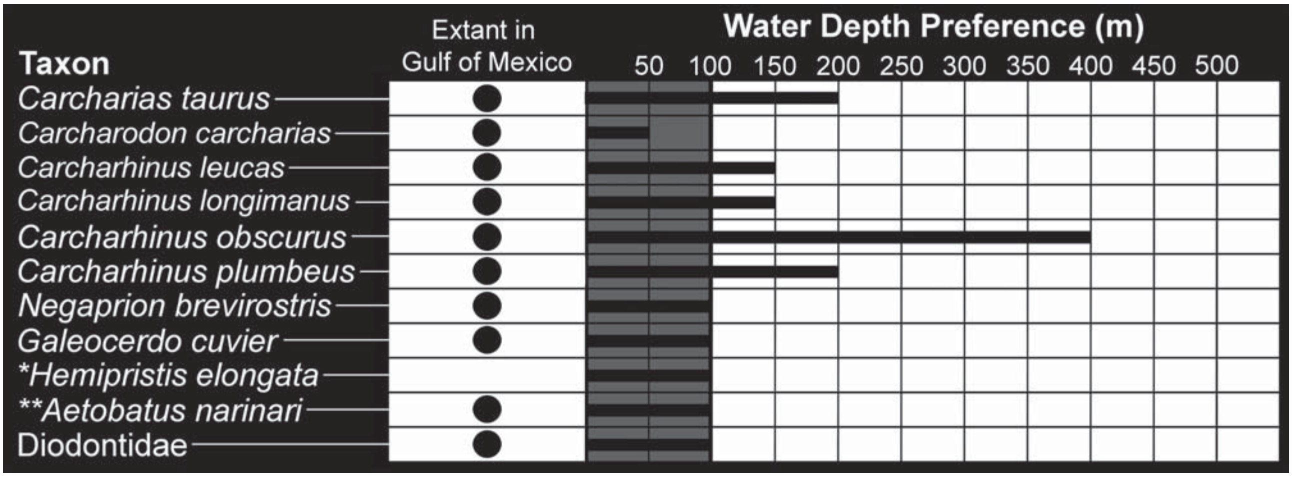
Hulbert (1995) elucidated an estimated age range of 1.07 to 1.55 ma (Calabrian) for the Pleistocene exposures at the site. Although an unconformity exists at the locality where the Pleistocene strata directly overlie those of Miocene age, Scudder et al. (1995) proposed that, due to their pristine condition, the teeth had not been reworked and were indeed early Pleistocene in age. These teeth represent the youngest occurrences of both *C. hastalis* and *H. serra* in the fossil record, indicating that populations of these taxa survived in the Gulf of Mexico at least into the Calabrian. Furthermore, when combined with the occurrence of *Carcharodon carcharias* in our sample, the presence of *C. hastalis* and *H. serra* suggest a bracketed age for our assemblage that ranges from the middle Pliocene to early Pleistocene (see Table 1). Because *C. hastalis* and *H. serra* are two taxa that are not known to persist into the middle Pleistocene, this makes it unlikely that the teeth in our sample were derived from the Ionian Prairie Formation.

Although the eastern end of Dauphin Island is known to have a Citronelle Formation core, this formation is absent within the western part island (Hummell & Parker 1995; Hummell 1996; Hummell & Smith 1996; Morton 2007), the location where most of the teeth in our sample were collected. The absence of the Citronelle Formation at the main area of collection leads us to believe the specimens were derived from shallow underlying deposits of the Biloxi Formation. The Biloxi Formation depositional setting was interpreted by Otvos (2001) to be an estuarine to open-shelf environment (Otvos 2001). Similarly, the recovered fossil assemblage consists of species that today prefer warm, shallow, near-shore habitats with a water depth of 100 m or less (see Table 2 and references cited herein). Although we cannot definitively rule out that these specimens could have come from the Citronelle Formation, the aforementioned lines of circumstantial evidence lead us to believe they were more than likely derived from the lower Pleistocene Biloxi Formation and may be as young as Calabrian in age.

5. Conclusions

A total of 12 unequivocal fish taxa were identified within our sample of Dauphin Island fossils: *Carcharias taurus*, *Carcharodon carcharias*, *Cosmopolitodus hastalis*, *Carcharhinus leucas*, *Carcharhinus* sp. cf. *C. longimanus*, *Carcharhinus obscurus*, *Carcharhinus* sp. cf. *C. plumbeus*, *Negaprion brevirostris*, *Galeocerdo cuvier*, *Hemipristis serra*, *Aetobatus* sp., and Diodontidae. Although these specimens were not collected *in situ*, circumstantial evidence suggests these specimens originated from the lower Pleistocene (Gelasian to Calabrian) Biloxi Formation. If this stratigraphic context is correct, the 91 specimens described herein represent the first Quaternary marine vertebrates of any kind reported from Alabama, and aside from the remains of *Aetobatus* sp., and Diodontidae, the first fossil occurrences in the state for each of the remaining unequivocal taxa. Two extinct taxa, *Cosmopolitodus hastalis* and *Hemipristis serra*, were identified within our sample. In conjunction with the specimens reported by Scudder et al. (1995) from the Leisley Shell Pits in Hillsboro County, Florida, the Dauphin Island *C. hastalis* and *H. serra* specimens are likely among the youngest stratigraphic occurrences of each of these species. When compared to modern representatives, the rep-

Table 2. Water depth preferences for extant taxa represented in the Dauphin Island fossil assemblage. **Hemipristis elongata* is used as a modern analogue for *Hemipristis serra*. ***Aetobatus narinari*, an extant member of the genus known to reside in the Gulf of Mexico today, is used in place of the unspeciated *Aetobatus* sp. Shaded area represents the overlap of depth preferences for the assemblage.



Taxon	Extant in Gulf of Mexico
Carcharias taurus	●
Carcharodon carcharias	●
Carcharhinus leucas	●
Carcharhinus longimanus	●
Carcharhinus obscurus	●
Carcharhinus plumbeus	●
Negaprion brevirostris	●
Galeocerdo cuvier	●
**Hemipristis elongata*	
***Aetobatus narinari*	●
Diodontidae	●

resented fossil taxa likely preferred a warm, shallow, nearshore habitat with a water depth of 100 m or less.

Although these specimens were all found as beach wash, it is plausible that they were derived from the shallow subsurface pre-Holocene units present at, or around, Dauphin Island and subsequently re-deposited on shore through beach restoration projects and/or storm wash. This latter hypothesis is supported by the fact that a large majority of the teeth were collected adjacent to the "Katrina Cut", a hurricane-induced break that once divided the western side of Dauphin Island into two parts. This break undoubtedly incised into the shallow subsurface pre-Holocene deposits that make up the island (likely the Biloxi Formation), with ebb and flow tides more than likely uncovering and redepositing the specimens onshore.

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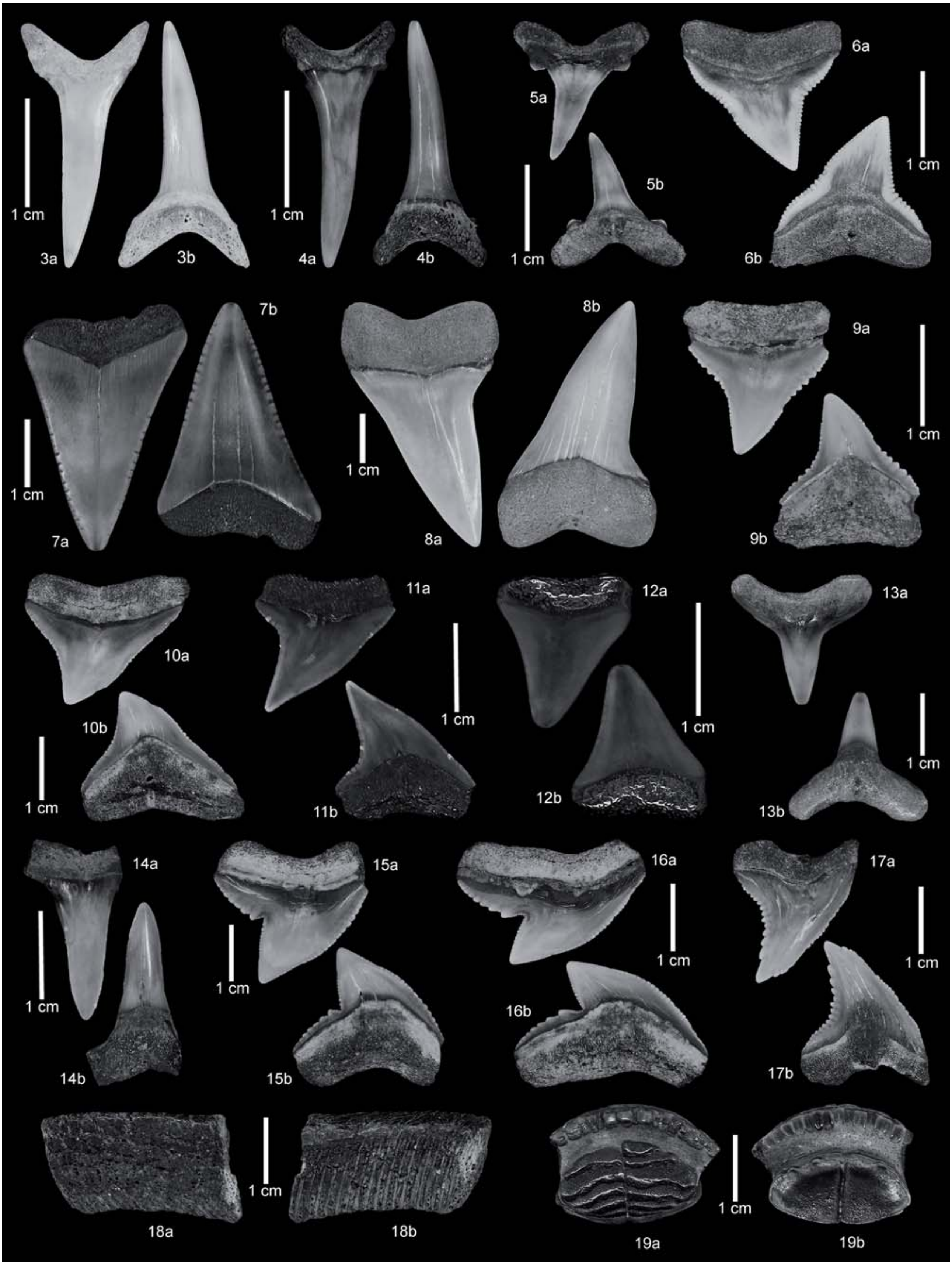
Plate 1

(3) *Carcharias taurus*, DISL 15.1.51, upper left anterior tooth; **a**: labial view; **b**: lingual view.
(4) *C. taurus*, DISL 15.1.46, upper left anterior tooth; **a**: labial view; **b**: lingual view.
(5) *C. taurus*, DISL 15.1.37, upper right lateral tooth; **a**: labial view; **b**: lingual view.
(6) *Carcharhinus leucas*, DISL 15.1.14, upper left lateral tooth; **a**: labial view; **b**: lingual view.
(7) *Carcharodon carcharias*, DISL 15.1.2, first upper left anterior tooth; **a**: labial view; **b**: lingual view.
(8) *Cosmopolitodus hastalis*, DISL 15.1.28, upper left anterior tooth; **a**: labial view; **b**: lingual view.
(9) *Carcharinus* sp. cf. *C. longimanus*, DISL 15.1.16, upper right anterior tooth; **a**: labial view; **b**: lingual view.
(10) *Carcharinus obscurus*, DISL 15.1.25, upper right lateral tooth; **a**: labial view; **b**: lingual view.
(11) *Carcharinus* sp. cf. *C. plumbeus*, DISL 15.1.84, upper right lateral tooth; **a**: labial view; **b**: lingual view.
(12) *Carcharinus* sp., DISL 15.1.34, upper right lateral tooth; **a**: labial view; **b**: lingual view.
(13) *Carcharinus* sp., DISL 15.1.42, lower lateral tooth; **a**: labial view; **b**: lingual view.
(14) *Negaprion brevirostris*, DISL 15.1.49, upper tooth; **a**: labial view; **b**: lingual view.
(15) *Galeocerdo cuvier*, DISL 15.1.19, anterior tooth; **a**: labial view; **b**: lingual view.
(16) *G. cuvier*, DISL 15.1.12, lateral tooth; **a**: labial view; **b**: lingual view.
(17) *Hemipristis serra*, DISL 15.1.10, upper right lateral tooth; **a**: labial view; **b**: lingual view.
(18) *Aetobatus* sp., DISL 15.1.40, upper medial tooth; **a**: oral view; **b**: basal view.
(19) Diodontidae, DISL 15.1.11, fused lower tooth plate with beak; **a**: oral view; **b**: ventral view.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