

Additions to the Pliocene fish assemblage (Chondrichthyes; Osteichthyes) from Dauphin Island, Alabama, USA

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Abstract

Several thousand fossils recovered from dredge deposits occurring on Dauphin Island, Alabama, USA include teeth, otoliths, spines and other skeletal remains of chondrichthyan and osteichthyan fishes. Fifty-two unequivocal fish taxa have been identified from these remains, and the assemblage represents the most diverse Pliocene fish fauna recovered from the northern Gulf Coastal Plain of the USA. The species composition of the paleofauna indicates that the fishes inhabited a subtropical estuarine environment with nearby marine influence. This paleoenvironmental scenario is similar to that of present-day Mobile Bay, indicating that the Early Pliocene shoreline of Alabama was located several kilometers south of its present location. Additionally, the species occurring in the Gulf of Mexico at that time, with few exceptions, still inhabit these waters.

keywords: Graham Ferry Formation, Zanclean, Gulf Coastal Plain, fossil, elasmobranch, Teleostei

Introduction

Neogene marine fish fossils remain poorly documented from within the Gulf Coastal Plain of the USA, and the only published accounts of such remains include those of Ebersole et al. (2017) and Stringer et al. (2020, 2023). Those fossils were derived from offshore sands that were subsequently dredged and deposited on Dauphin Island (Mobile County, Alabama, USA) as part of beach nourishment efforts in 2016 (Stringer et al. 2020, 2023). Ebersole et al. (2017) identified a diodontid tooth plate and 11 chondrichthyan taxa from these dredged deposits, including teeth from the extinct sharks *Cosmopolitodus hastalis* (Agassiz, 1838) and *Hemipristis serra* Agassiz, 1835. Ebersole et al. (2017) believed these remains to be of Early Pleistocene age, but subsequent investigations by Stringer et al. (2020, 2023) posited that the fossils are instead Pliocene in origin based on additional data collected from the site.

Stringer et al. (2020) reported 250 fossil otoliths collected from the east end of Dauphin Island that represented 22 osteichthyan taxa. From a much larger sample of 3,840 otoliths, Stringer et al. (2023) identified 12 additional bony fish taxa from the same site. Each of the taxa reported by Ebersole et al. (2017) and Stringer et al. (2020, 2023) represented new Neogene occurrences within the northern Gulf Coastal Plain strata of the USA.

Herein we report an additional 13 unequivocal taxa from skeletal remains (i.e., teeth, spines, and bony elements) that were derived from the dredged deposits on Dauphin Island. The combined list of species reported from the Dauphin Island Pliocene sediments now includes 52 unequivocal chondrichthyan and osteichthyan taxa. This assemblage offers a unique glimpse into the paleobiodiversity and paleoenvironment of coastal Alabama during the Pliocene, as well as on the paleobiogeography of the various species identified.

Geographical & geological settings

The specimens described herein were derived from dredged sands that were deposited as part of beach renourishment efforts in two locations on Dauphin Island, Mobile County, USA (Fig. 1). The first collection site is at the east end beach on the island and was designated by Stringer et al. (2020) as site AMb-2. The second site, Pelican Island (known colloquially as “Pelican Peninsula” because it is now a southern extension of Dauphin Island), is designated herein as site AMb-3. Nearly all of the sand that comprises site AMb-2 was dredged from an offshore borrow area located approximately 8 km south of the site, in the Gulf of Mexico (Forrest-Vandera et al. 2011, Stringer et al. 2020). In 2016, approximately 275,000 cubic meters of sand was dredged from the borrow area and deposited in several locations on site AMb-3, and subsequently pumped onto site AMb-2 (Steve Jones, pers. comm. 2023). Stringer et al. (2020) were able to determine an Early Pliocene (Zanclean) age for the dredged sands on site AMb-2 based on 1) the occurrence of the extinct chondrichthyan taxa *Cosmopolitodus hastalis* (Agassiz, 1843) and *Hemipristis serra* (Agassiz, 1835) (both of which have a Miocene to Early Pleistocene range; see Cappetta 2012, Ebersole et al. 2017), and 2) the absence of the extinct bivalve *Rangia johnsoni* (Dall, 1892) within the shell hash at the site. In the Gulf Coastal Plain of the USA, the last occurrence of *R. johnsoni* marks the Miocene-Pliocene boundary, a stratigraphic relationship that has been well-defined in southeastern Mississippi, USA by Starnes & Berry (2017) and Stewart & Starnes (2017). Stringer et al. (2020, 2023) suggested the fossils from site AMb-2 were likely derived from an offshore lag of the Graham Ferry Formation, which is the only Pliocene lithostratigraphic unit currently recognized at the surface or shallow subsurface of Alabama and Mississippi (Starnes & Berry 2017, Stewart & Starnes 2017, GSA 2018, Stringer et al. 2020). However, because the fossil specimens collected from sites AMb-2 and AMb-3 were derived from dredged sands and not found *in situ*, Stringer et al. (2020, 2023) suggested they were either derived directly from the Graham Ferry Formation or an offshore age-equivalent deposit. Whereas the base of the Graham Ferry Formation is well-defined by the absence of *R. johnsoni* (and its presence in the underlying Pascagoula Formation), Stewart & Starnes (2017) noted that the top of the unit had been truncated by a series of Pleistocene stream and coastal terraces. Although a majority of the Graham Ferry Formation resides within the Zanclean, it is currently unclear how much, if any, of the top of the unit extends into the Piacenzian (Stringer et al. 2023).

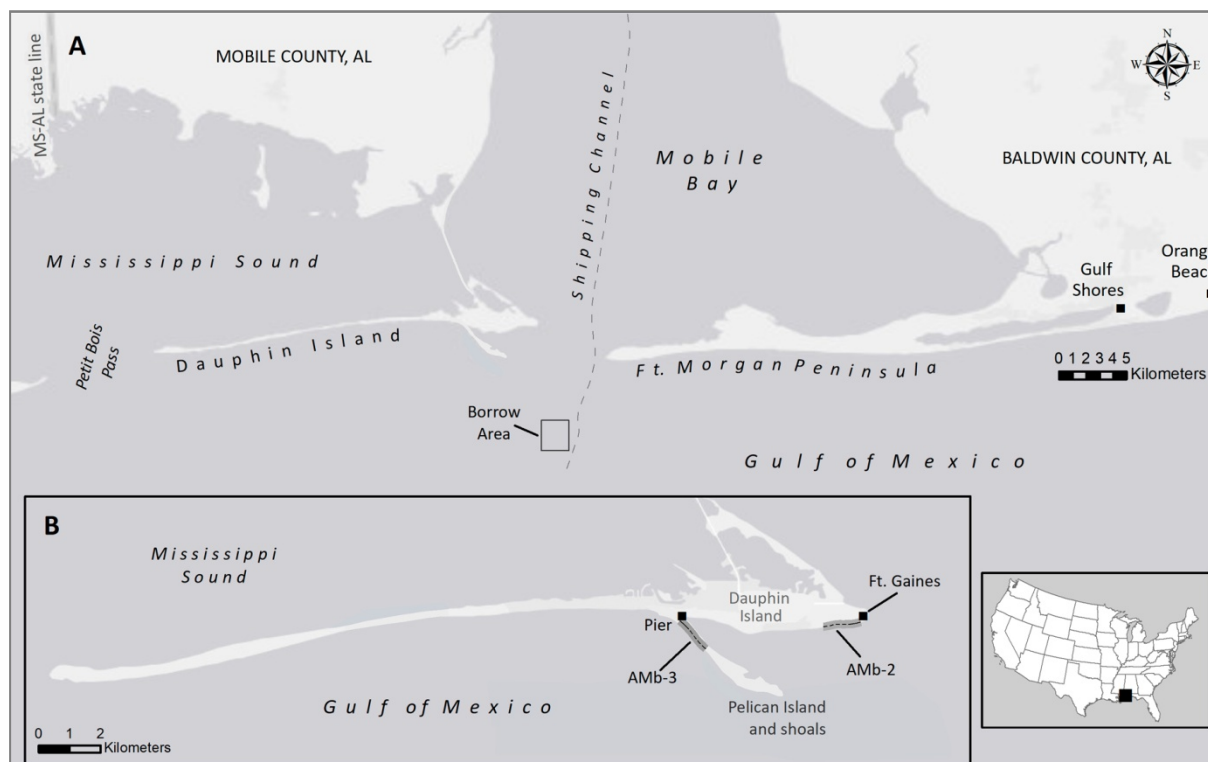


fig. 1. Location of sites AMb-2 and AMb-3 on Dauphin Island, Mobile County, USA. A) Approximate location of Dauphin Island and the borrow area in the Gulf of Mexico, USA. B) Close-up of Dauphin Island showing the locations of sites AMb-2 and AMb-3.

Material & methods

All of the specimens described herein were surface collected from sites AMb-2 and AMb-3 or were picked directly from bulk matrix samples collected from both sites. Surface specimens were collected either by the senior author (JAE) or numerous residents of Mobile County (see Acknowledgements) and subsequently donated to McWane Science Center (MSC) in Birmingham, AL, for inclusion in this study. Approximately 23 kg of screened shell hash was collected by the senior author (JAE) between the years 2018 and 2023. To collect this shell hash, beach sand was screened through a 0.5 mm mesh, and the resulting concentrate was picked under magnification in the laboratory at MSC. Skeletal remains recovered from sites AMb-2 and AMb-3 were identified through direct comparisons with extant comparative specimens housed in the collections at MSC and the South Carolina State Museum (SC) in Columbia, USA. In the event no comparative material was available for a specific taxon, fossil specimens were compared to those published in the literature (see references cited herein). The classification scheme utilized herein generally follows that of Nelson et al. (2016), but any deviation from this work is noted and explained. Taxonomic authorities for genera and species follow Fricke et al. (2021), whereas those for orders and families follow van der Laan et al. (2014, 2017, 2018). Specimens were photographed with a Nikon D-80 camera with Tamron macro-lens. To account for depth of field, specimens were photographed from several focal lengths and the resulting photographs were merged in Adobe Photoshop v. 22.5.9 utilizing the software's auto-align and auto-blend functions. All fossil specimens listed and described herein are permanently accessioned into the collections at MSC.

Institutional abbreviations

MSC McWane Science Center, Birmingham, Alabama, USA
 SC South Carolina State Museum, Columbia, USA

Systematic relationships of the taxa treated below

class	CHONDRICHTHYES Huxley, 1880
subclass	Euselachii Hay, 1902
infraclass	Elasmobranchii Bonaparte, 1838
division	Selachii Cope, 1871
superorder	Galeomorphi (<i>sensu</i> Nelson et al., 2016)
order	Lamniformes Garman, 1885
family	Lamnidae Bonaparte, 1835
genus	<i>Isurus</i> Rafinesque, 1810
species	<i>Isurus paucus</i> Guitart Manday, 1966
order	Carcharhiniformes Compagno, 1973
family	Carcharhinidae Jordan & Evermann, 1896
genus	<i>Carcharhinus</i> Blainville, 1816
species	<i>Carcharhinus acronotus</i> (Poey, 1860)
species	<i>Carcharhinus brachyurus</i> (Günther, 1870)
species	<i>Carcharhinus limbatus</i> (Valenciennes, 1839)
genus	<i>Rhizoprionodon</i> Whitley, 1929
species	<i>Rhizoprionodon</i> cf. <i>terraenovae</i> (Richardson, 1836)
order	Carcharhiniformes Compagno, 1973
family	Sphyrnidae Bonaparte, 1840
genus	<i>Sphyrna</i> Rafinesque, 1810
species	<i>Sphyrna mokarran</i> (Rüppell, 1837)
division	Batomorphi Cappetta, 1980
order	Myliobatiformes Compagno, 1973
species	Myliobatiformes indet.
family	Myliobatidae Bonaparte, 1835
subfamily	Rhinopterinae Jordan & Evermann, 1896
genus	<i>Rhinoptera</i> Cuvier, 1829
species	<i>Rhinoptera</i> aff. <i>bonusus</i> (Mitchill, 1815)
class	OSTEICHTHYES Huxley, 1880
subclass	Actinopterygii (<i>sensu</i> Goodrich, 1930)
unranked	Neopterygii Regan, 1923
division	Teleostomorpha Arratia et al., 2004
subdivision	Teleostei Müller, 1845
supercohort	Teleocephala de Pinna, 1996
unranked	Cluieocephala Patterson & Rosen, 1977

cohort	Otocephala (<i>sensu</i> Nelson et al. 2016)
superorder	Ostariophysii (<i>sensu</i> Nelson et al. 2016)
series	Otophysi (<i>sensu</i> Fink & Fink, 1981)
subseries	Siluriphysi Fink & Fink, 1996
order	Siluriformes Cuvier, 1816
suborder	Siluroidei (<i>sensu</i> Nelson et al. 2016)
superfamily	Arioidea (<i>sensu</i> Nelson et al. 2016)
family	Ariidae Bleeker, 1858
subfamily	Ariinae Bleeker, 1858
genus	<i>Ariopsis</i> Gill, 1861
species	<i>Ariopsis felis</i> (Linnaeus, 1766)
cohort	Euteleostei Rosen, 1985
superorder	Acanthopterygii Greenwood et al., 1966
series	Percomorpha (<i>sensu</i> Nelson et al., 2016)
subseries	Ovalentaria Smith and Near, 2012
order	Istiophoriformes Betancur-R et al., 2013
family	Sphyraenidae Rafinesque, 1815
genus	<i>Sphyraena</i> Artedi, 1793
species	<i>Sphyraena</i> sp.
order	Scombriformes Rafinesque, 1810b
suborder	Scombroidei Bleeker, 1859
family	Trichiuridae Rafinesque, 1810
subfamily	Trichiurinae Rafinesque, 1810
genus	<i>Trichiurus</i> Linnaeus, 1758
species	<i>Trichiurus lepturus</i> Linnaeus, 1758
order	Scombriformes Rafinesque, 1810
suborder	Scombroidei Bleeker, 1859
family	Scombridae Rafinesque, 1815
subfamily	Scombrinae Rafinesque, 1815
genus	<i>Scomberomorus</i> Lacépède, 1801
species	<i>Scomberomorus</i> sp.
order	Spariformes (<i>sensu</i> Nelson et al., 2016)
family	Sparidae Rafinesque, 1818
genus	<i>Archosargus</i> Gill, 1865
species	<i>Archosargus</i> aff. <i>probatocephalus</i> (Walbaum, 1792)
order	Tetraodontiformes Berg, 1940
suborder	Balistoidei Rafinesque, 1810
family	Balistidae Rafinesque, 1810
species	Balistidae indet.

Systematic paleontology

***Isurus paucus* Guitart Manday, 1966**

material examined

N = 1: MSC 43077 | Fig. 2A-C

description

The specimen is an upper left lateral tooth that has a low, broadly triangular, and distally inclined main cusp. The labial and lingual crown faces are convex, but the lingual face is significantly more rounded. In labial or lingual views, the mesial cutting edge is slightly sinuous but overall moderately convex. The distal cutting edge is straight but curves sharply basally to a short, oblique shoulder. The cutting edges are smooth and continuous along the entire crown. The enameloid is smooth and devoid of ornamentation. The root lobes are divergent and angular, and the interlobe area is shallow and U-shaped. A faint lingual nutritive groove is visible under magnification, and two nutritive foramina occur on a low lingual root protuberance.

remarks

Specimen MSC 43077 was compared to teeth within several sets of extant *Isurus* jaws at SC and MSC. Of six jaws available to us, four were *I. oxyrinchus* Rafinesque, 1810a (MSC 42608, SC86.186.2, SC2020.53.11, SC2020.53.15) and two *I. paucus* (SC2020.53.22, SC2020.53.24). Although the total lengths of the individual sharks are unknown, the jaws are of variable sizes that reflect ontogeny. Based on these extant specimens, the fossil tooth is from a lateral position, as the crown is rather broad, the apex is distally directed, and the root lobes are short and widely diverging. Additionally, MSC 43077 represents an upper lateral file, as crowns from the equivalent lower files of *Isurus* are narrower and erect. In terms of

specific morphological features, those of MSC 43077 are most consistent with upper lateral teeth of *I. paucus*, as all have a broad-based crown with convex mesial cutting edge, and apex that appears distally curving. In contrast, upper lateral teeth of *I. oxyrinchus* are comparatively narrower, the mesial edge is much straighter, and the cusp apex is not distally curved. Tooth MSC 43077 is superficially similar to upper lateral teeth of *Carcharhinus brachyurus* (Günther, 1870) but is quite easily distinguished by its smooth (versus serrated) cutting edges (see below).

***Carcharhinus acronotus* (Poey, 1860)**

material examined

N = 1: MSC 44439 | Fig. 2D-F

description

The tooth is from an upper right lateral tooth file. The specimen has a short and triangular main cusp that is distally inclined, with the lingual crown face being strongly convex and the labial face virtually flat. The distal cutting edge on the main cusp is straight, whereas the mesial cutting edge is slightly convex. The tooth exhibits mesial and distal heels, with the distal heel being convex and separated from the remainder of the cutting edge by a distinct distal notch. The mesial heel is convex, albeit less so than the distal heel, and is not well delineated from the mesial cutting edge. Instead, the mesial heel and mesial cutting edge are separated by an indistinct depression. The cutting edge is continuous across crown width, and the serrations are coarsest basally but become finer towards the apex. The root is higher on the lingual face and has a triangular upper margin. The root lobes are rounded and divergent, and the interlobe area is shallow and V-shaped. A shallow nutritive groove is located on the lingual root face and forms a distinct basal notch.

remarks

The tooth in our sample compares very well to those in the upper right posterolateral files of an extant *Carcharhinus acronotus* dentition we examined (SC96.77.7). The specimen can be distinguished from upper lateral teeth of other extant *Carcharhinus* species from the northern Gulf of Mexico, USA by having a combination of evenly and finely serrated cutting edges (versus very coarse, or coarse basally but fining apically), a poorly differentiated mesial heel (versus uniformly convex mesial edge), and a finely serrated distal heel (versus denticulated or coarsely serrated) that is separated from the distal cutting edge by a distinct distal notch (as opposed to being contiguous with highly concave transition to the distal cutting edge).

***Carcharhinus brachyurus* (Günther, 1870)**

material examined

N = 2: MSC 42713, MSC 43084 | Fig. 2G-L

description

MSC 42713 has a tall and triangular crown. The crown has a strongly convex lingual face and a weakly convex labial face. In labial or lingual views, the mesial cutting edge is evenly convex, whereas the distal cutting edge is slightly concave. Together, these cutting edges result in the crown apex having a distinctive distal hook. The crown has a flat distal heel that intersects the main cusp at almost a 110° angle, and a thin and elongated mesial shoulder is not well delineated from the remainder of the mesial cutting edge. The cutting edges are distinctly serrated, with the coarsest serrations occurring medially on both sides of the crown. In mesial or distal views, the crown apex has a conspicuous labial curvature and the mesial and distal cutting edges are uniquely concave. The root is higher on the lingual face and has an evenly convex upper margin. The root lobes are rounded and strongly divergent. A robust lingual root protuberance is bisected by a deep nutritive groove that forms a basal notch.

MSC 43084 exhibits a mesiodistally narrow, triangular cusp. The lingual face is strongly convex, whereas the labial face is relatively flat. In labial or lingual views, the mesial cutting edge is distinctly convex except for a concave portion at the base. The distal cutting edge is more sinuous than the mesial edge, as it is concave at the base and convex towards the apex. The crown has elongated mesial and distal shoulders that thin towards the mesial and distal edges. The crown enameloid is smooth and the tooth has continuous cutting edges that are uniformly serrated and extend to the crown base. The root lobes are rounded and extremely divergent, and the distal root lobe is longer than the mesial lobe. A prominent lingual root protuberance is bisected by a deep nutritive groove that forms a distinct basal notch. The interlobe area is shallow and V-shaped.

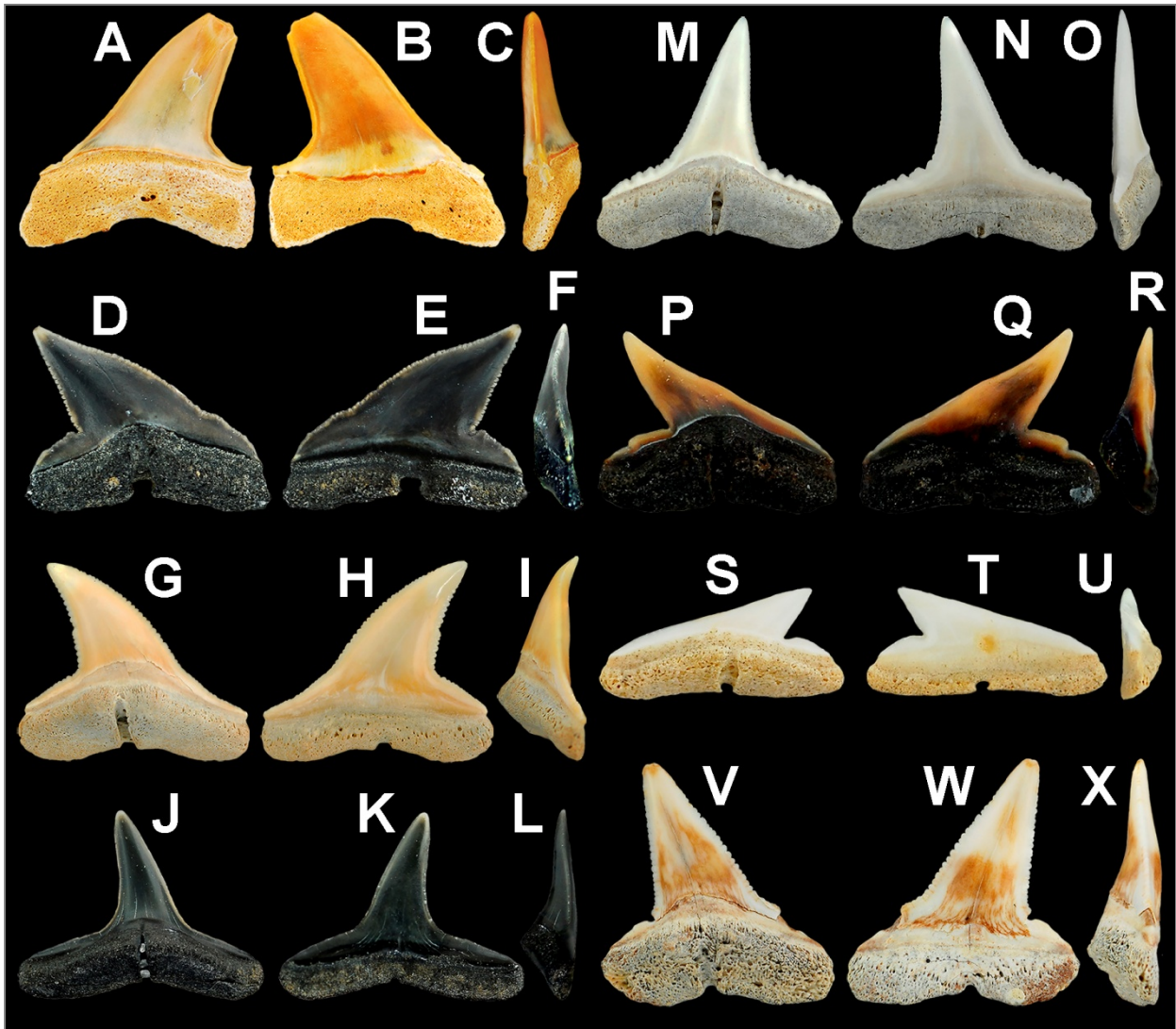


fig. 2. Pliocene galeomorph teeth from Dauphin Island, Mobile County, Alabama, USA. A-C) MSC 43077, *Isurus paucus* upper left lateral tooth in A) lingual, B) labial, and C) mesial views. D-F) MSC 44439, *Carcharhinus acronotus* upper right lateral tooth in D) lingual, E) labial, and F) mesial views. G-I) MSC 43084, *Carcharhinus brachyurus* upper right lateral tooth in G) lingual, H) labial, and I) mesial views. J-L) MSC 42713, *Carcharhinus brachyurus* lower left lateral tooth in J) lingual, K) labial, and L) mesial views. M-O) MSC 43083.1, *Carcharhinus limbatus* upper left lateral tooth in M) lingual, N) labial, and O) mesial views. P-R) MSC 43491.1, *Rhizoprionodon cf. terraenovae* upper right lateral tooth in P) lingual, Q) labial, and R) mesial views. S-U) MSC 43491.2, *Rhizoprionodon cf. terraenovae* upper left posterior tooth in S) lingual, T) labial, and U) mesial views. V-X) MSC 49241, *Sphyrna mokarran* lower left anterolateral tooth in V) lingual, W) labial, and X) mesial views. Scale bars for A-C, G-O, V-X = 5.0 mm; D-F, P-R = 3.0 mm; S-U = 2.0 mm.

remarks

The two specimens are comparable to teeth within the jaws of extant *Carcharhinus brachyurus* that we examined (MSC 42607, SC2020.53.9). MSC 242713 is an upper right lateral tooth, and the distinct labially bent apex of the fossil suggests the tooth was likely located in a file from the medial region of the jaw. The labiolingually thick crown base, labially bent apex, and strong distal hook of the main cusp (as opposed to distally inclined) distinguishes this tooth from the upper teeth of the other *Carcharhinus* species currently known to inhabit the Gulf of Mexico (see Voigt & Weber 2011). These same characteristics distinguish this tooth from the morphologically similar tooth of *Sphyrna mokarran* (Rüppell, 1837) in our sample (see below). *Carcharhinus brachyurus* lower teeth can be separated from those of the other *Carcharhinus* species by having a combination of a rather narrow main cusp that is distally curving (i.e., more evenly convex mesial edge and concave distal edge), finely serrated cutting edges along the lateral heels and extending to the cusp apex (as opposed to coarsely serrated heels, or smooth cutting edges along some portion of the main cusp), and lateral shoulders that are contiguous with the main cusp via a concave margin (versus differentiated by mesial and/or distal notches).

***Carcharhinus limbatus* (Valenciennes in Müller & Henle, 1839)**material examined

N = 20: MSC 42714, MSC 42814, MSC 43079, MSC 43081, MSC 43086.1-3, MSC 43093.1-3, MSC 44443, MSC 44452, MSC 44771, MSC 44762.1-2, MSC 46568, MSC 47072, MSC 47074, MSC 49232, MSC 49245 | Fig. 2M-O

description

Our sample consists of upper teeth. The teeth are characterized by their tall and triangular crown. The crown may be erect or have a very slight distal inclination. The lingual crown face is convex, whereas the labial face is essentially flat. In labial and lingual views, the mesial cutting edge of the crown varies from straight to slightly convex, whereas the distal cutting edge varies from straight to slightly concave. The main cusp is flanked by mesial and distal shoulders that have cutting edges ranging from straight to slightly convex. The intersection of the mesial shoulder and mesial edge of the main cusp is somewhat angular, but distally the transition varies from angular to convex; the cutting edges lack mesial and distal notches. The cutting edges are serrated, with the largest serrations occurring on the mesial and distal heels and smallest ones located on the cusp. Serrations on the heels are weakly compound. The root is higher on the lingual face and has an apical margin that is convex just below the main cusp. The root lobes are rounded and strongly divergent, and the interlobe area is shallow and generally U-shaped. The lingual face of the root is bisected by a deep nutritive groove that forms a distal notch on some teeth.

remarks

The teeth described above compare favorably to those occurring in the palatoquadrate (upper jaw) of extant *Carcharhinus limbatus* jaws that we examined (MSC 42621, SC96.77.1, SC2020.53.24). Our fossil sample includes anterior and lateral teeth, with those from anterior positions being nearly symmetrical and those from lateral positions having a distally directed apex. Based on the extant jaws that we examined, the upper teeth of the fossil taxon become progressively lower and more strongly distally inclined towards the commissure. Teeth of *C. limbatus* differ from those of the other *Carcharhinus* species in the present-day Gulf of Mexico by having a combination of a tall, triangular, and erect main cusp, clearly delineated mesial and distal shoulders, and the largest serrations occur on the shoulders.

***Rhizoprionodon cf. terraenovae* (Richardson, 1836)**material examined

N = 40: MSC 42707.1-7, MSC 42708, MSC 42709, MSC 42710, MSC 43480.1-3, MSC 43491.1-4, MSC 47070, MSC 49233.1-3, MSC 49247.1-8, MSC 49248.1-9, MSC 49249, MSC 49251, MSC 49256 | Fig. 2P-U

description

The teeth have a triangular and distally inclined main cusp. The lingual face of the crown is convex, whereas the labial face is essentially flat. In labial or lingual views, the mesial cutting edge ranges from slightly sinuous to straight to slightly convex. The distal cutting edge is shorter and convex. A distinct distal heel is separated from the distal cutting edge by a conspicuous notch. The cutting edge on the distal heel can have a rounded, triangular, or bifurcated appearance. A mesial shoulder is not delineated from the mesial cutting edge of the main cusp, but it can be short to elongated. The cutting edges on individual teeth can be smooth, irregular, or serrated, or have varying combinations of all three. The root lobes are rounded and divergent. An interlobe area is either absent or is extremely shallow and V-shaped or U-shaped. The lingual root protuberance is bisected by a deep nutritive groove that forms a conspicuous distal notch on nearly all teeth.

remarks

The teeth in our sample were compared to those in the jaws of several species of extant *Rhizoprionodon* jaws in the MSC and SC collections (see Ebersole et al. 2023 for a complete listing). Based on that comparison we conclude that the isolated teeth from Dauphin Island represent upper and lower anterior and lateral teeth. Ebersole et al. (2023) recently detailed significant morphological dental variation within a large sample of male and female *R. terraenovae* from the northern Gulf of Mexico that reflects monognathic, dignathic, ontogenetic, and gynandric heterodonty.

With respect to monognathic heterodonty, the main cusp of teeth is lower and more distally inclined, and the mesial shoulder is more elongated the closer a tooth is located to the commissure. Additionally, the cusp apex is upturned on teeth in anterior files but not on those from lateral and posterior files. The lower teeth are similar in morphology to those in the upper files but have a shorter and narrower main cusp with a more conspicuous upturned apex (dignathic heterodonty). Ontogenetic heterodonty is reflected in the overall tooth size, presence or absence of serrations, and the shape of the distal heel.

These phenomena were also observed in our fossil sample. Due to the large amount of heterodonty observed in extant *R. terraenovae*, Ebersole et al. (2023) expressed doubt that isolated teeth from the seven extant *Rhizoprionodon* species could be sufficiently differentiated from each other, and we herein follow their suggestion by tentatively assigning our fossil teeth to *R. terraenovae*, as this is the only species with an extant range in the northern Gulf of Mexico (Parsons, 2006). A second species, *R. porosus* (Poey, 1861), occurs further south in the Gulf of Mexico, and we cannot conclusively rule out the possibility that our sample includes a Pliocene occurrence of this species from the north part of the basin.

***Sphyrna mokarran* (Rüppell, 1837)**

material examined

N = 1: MSC 49241 | Fig. 2V-X

description

MSC 49241 exhibits a tall, triangular crown having a distally inclined main cusp. Both the labial and lingual crown faces are convex, but more so lingually, and in mesial or distal views the crown has a slightly sigmoidal profile. The mesial cutting edge is weakly convex and has a slight outward swelling at the medial portion, whereas the distal cutting edge is somewhat shorter and straight. There is a rounded distal heel that is separated from the distal cutting edge by a conspicuous notch. Only a portion of the mesial shoulder is preserved, and it intersects with the main cusp at an approximately 160° angle. The mesial and distal cutting edges bear serrations that are generally of equal size and shape, but they are finer towards the cusp apex. Serrations are not obvious on the distal heel and mesial shoulder. The crown enameloid is smooth. The root lobes are divergent and rounded. The tooth has a flat labial root face that is bisected by a deep nutritive groove. The root is higher lingually and has a V-shaped upper margin. A basal notch is present and the interlobe area is shallow and V-shaped.

remarks

MSC 49241 was compared to a set of extant *Sphyrna mokarran* jaws at SC (SC2000.120.2), and the apicobasal height of the tooth versus mesiodistal width of the root, coupled with the distal inclination of the main cusp, indicates that this tooth is either from a lower anterolateral file or a proximal lateral file. The mesial cutting edge on *S. mokarran* upper teeth have a pronounced medial convexity, and the cusp apex is more distally inclined. Of the galeomorph shark teeth in our sample, specimen MSC 49241 could be confused with the upper teeth of *Carcharhinus acronotus* and *C. brachyurus*. However, MSC 49241 differs from the former by having a main cusp that is taller, less distally inclined, and has straighter mesial and distal edges. MSC 49241 differs from the latter by having coarser serrations, a slight outward swelling on the mesial cutting edge, and a main cusp that is distally inclined as opposed to distally hooked.

***Rhinoptera* aff. *bonasus* (Mitchill, 1815)**

material examined

N = 2: MSC 42074, MSC 43078 | Fig. 3A-C

description

In occlusal view, the crowns are six-sided and wider than long, with a width/length (W/L) ratio of 3:1. The lateral angles are sharp but the mesial and distal-most points are more labially located so that the outline is not symmetrical. The labial crown margin is slightly convex, but the lingual margin is slightly concave. In profile view the crown overhangs the root labially, but the root does not extend beyond the lingual crown foot. In labial or lingual views, the occlusal surface is slightly convex. The labial crown base is marked by a distinct furrow that extends the width of the tooth, whereas a conspicuous labial ridge marks the transition from crown to root. Although the crowns of both teeth are worn, the remaining portion of the labial and lingual faces are ornamented with thick, often interconnected, vertical ridges. The root is low with nearly vertical labial and lingual faces. It is polyaulocorhize, comprised of an alternating series of approximately 14 lamellae separated by nutritive grooves.

remarks

Three ray genera with an extant range in the Gulf of Mexico have teeth that articulate into dental pavements, including *Aetobatus*, *Myliobatis*, and *Rhinoptera* (Parsons 2006). All of these taxa have dentitions that include a symphyseal file comprised of teeth with W/L ratios of 4:1 or longer. *Myliobatis* and *Rhinoptera* dentitions include two or more lateral tooth files, whereas these teeth are absent in the dentition of *Aetobatus* (which consist of a single upper and lower symphyseal files). Although dentitions of *Myliobatis* and *Rhinoptera* include distal lateral teeth having W/L ratios of approximately 1:1, *Rhinoptera* is the only

one to have proximal lateral files consisting of teeth with W/L ratios of approximately 3:1. These intermediate lateral files are situated between the symphyseal and distal lateral files. Because they have a W/L ratio of 3:1, the two fossil teeth in our sample are identified as proximal lateral teeth of *Rhinoptera*. Our conclusion is confirmed by two extant *Rhinoptera bonasus* dentitions that we examined (MSC 42598, SC88.120.1) that exhibit teeth having similar W/L ratios. Additionally, the lateral crown angles of these teeth are sharp and the mesial and distal-most points are slightly offset. Lastly, in labial/lingual view the mesial side of the crown is higher than on the distal side, a characteristic of *Rhinoptera* lateral teeth we have examined from other fossil sites (i.e., Ebersole et al. 2019).

Two *Rhinoptera* species occur in the Gulf of Mexico – *R. bonasus* and *R. brasiliensis* Müller, 1836. Unfortunately, it is currently unclear if these two taxa can be accurately differentiated by their isolated teeth. Therefore, the two fossil teeth in our sample are tentatively assigned to *Rhinoptera* aff. *R. bonasus* based on the geographic occurrences of the two extant species. Whereas *R. bonasus* is extremely common in the northern Gulf of Mexico (Parsons 2006), *R. brasiliensis* is considered very rare and has only recently been confirmed in this region (Palacios-Barreto et al. 2017).

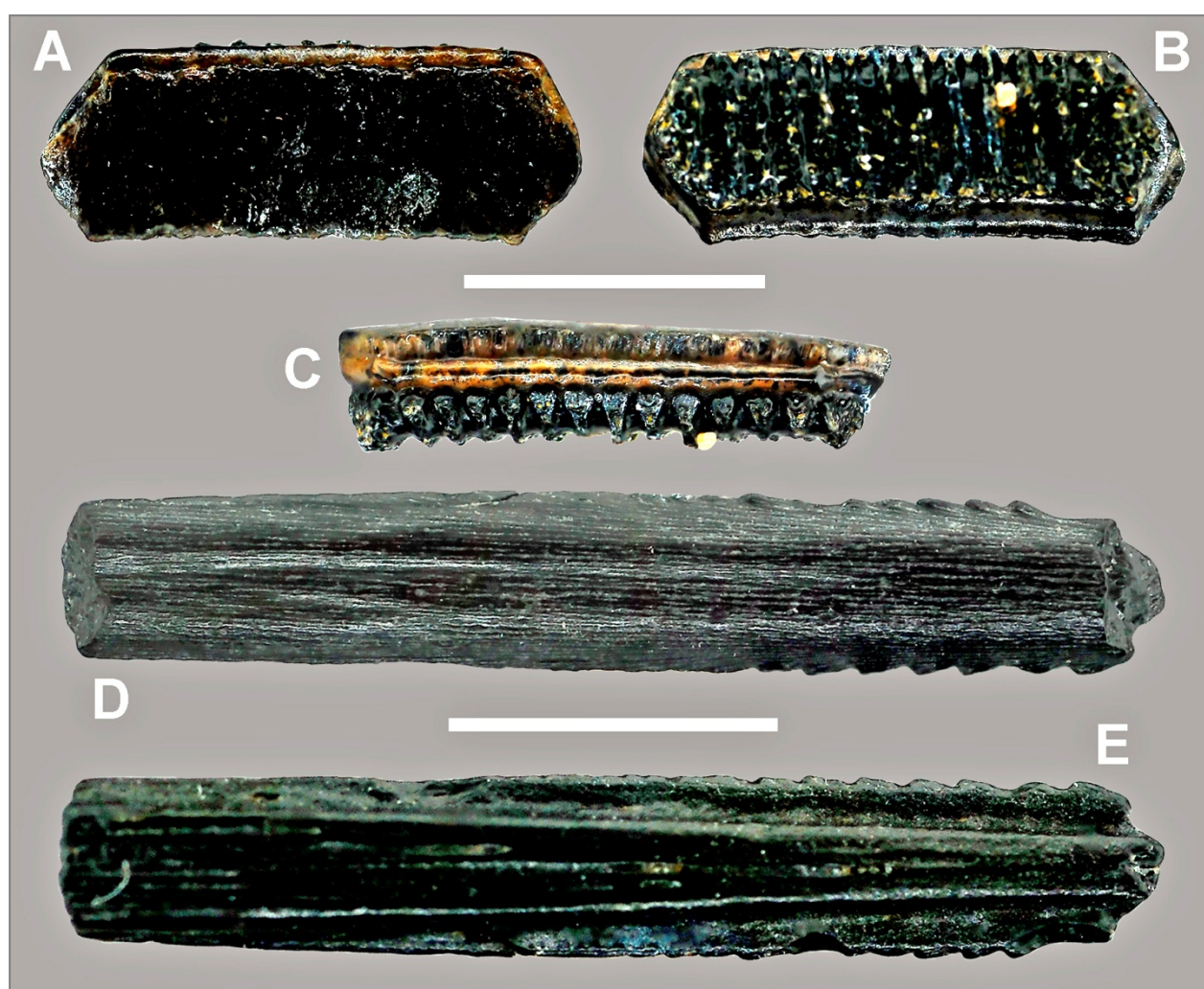


fig. 3. Pliocene batoid elements from Dauphin Island, Mobile County, Alabama, USA. A-C) MSC 43078, *Rhinoptera* aff. *R. bonasus* proximal lateral tooth in A) occlusal, B) basal, and C) lingual views. D-E) MSC 42703, Myliobatiformes indet. caudal spine (sting) in D) dorsal and E) ventral views. Scale bars = 5.0 mm.

Myliobatiformes indet.material examined

N = 2: MSC 42703.1, MSC 42703.2 | Fig. 3D-E

description

Both specimens are caudal spines (aka stings). The specimens are incomplete but similar in overall morphology. The spines are anteroposteriorly elongated, laterally narrow, and dorso-ventrally thin. In dorsal view, the lateral margins are sub-parallel but taper slightly distally. The dorsal surface is convex and covered by enameloid that is ornamented with faint longitudinal striations. The ventral surface is characterized by a smooth ridge that extends the length of the spine and narrows towards the posterior end. Although worn on both specimens, the lateral edges of the spines are lined with a single row of anteriorly recurved denticles that do not extend to the proximal end. The transverse cross-section of the spines is roughly oval.

remarks

Schwartz (2008, 2009) argued that isolated caudal spines of extant rays could be assigned to a genus based on the number of denticles occurring along the lateral margins. However, Hovestadt & Hovestadt-Euler (2013) demonstrated that differences in the number of these lateral denticles is influenced by ontogeny, with older spines having more denticles compared to those of juveniles. We concur with Hovestadt & Hovestadt-Euler (2013) regarding the limited taxonomic utility of isolated ray caudal spines. Several extant families of rays in the present-day Gulf of Mexico possess caudal spines, including Aetobatidae, Dasyatidae, Myliobatidae, and Urolophidae (see Parsons 2006). The spines in our sample could belong to any of the regional taxa within these families, and we therefore conservatively assign them to Myliobatiformes indet.

***Ariopsis felis* (Linnaeus, 1766)**material examined

N = 1: MSC 43479 | Fig. 4A

description

MSC 43479 is a neurocranium fragment that measures approximately 1 cm in greatest dimension as preserved. The bone is dorsoventrally thin, and its dorsal surface is ornamented with a series of tightly packed pits and tuberculations that combine to form a pattern of radiating ridges and furrows. The ventral surface is irregular and unornamented.

remarks

This neurocranium fragment was compared to the skull of an extant *Ariopsis felis* specimen in the MSC collection (MSC 49116). Although the extant specimen exhibits ornamentation on the frontal, pterotic, and supraoccipital, ornamentation is absent from the ethmoid cornu, lateral ethmoid, and supraethmoid. The distinctive ornamentation on the fossil specimen appears to be consistent with that on the frontal of MSC 49116, indicating the fossil bone was likely derived from this region of the neurocranium. Stringer et al. (2020) identified *A. felis* from site AMb-2 based on otoliths, and this taxon is thus far the only one within the Dauphin Island fish assemblage that is represented by both otoliths and skeletal material.

***Sphyaena* sp.**material examined

N = 4: MSC 42706, MSC 49236, MSC 49263, MSC 49264 | Fig. 4B-C

description

The isolated teeth are very thin labiolingually, and in labial or lingual views the crown has a symmetrical lanceolate outline. The labial and lingual crown faces are slightly convex, but the base of the lingual face is somewhat more rounded. In anterior and posterior views, the tooth is nearly vertical with only a slight medial curvature. The teeth have sharp anterior and posterior carinae that converge apically to form a sharp point. The enameloid is ablated on the basal half of several teeth in our sample, exposing the inner dentine core. Enameloid forms the anterior and posterior carinae, and these cutting edges are unserrated. The basal outline is sub-oval with anterior and posterior points.

remarks

The *Sphyaena* teeth in our sample are morphologically similar to those of *Scomberomorus* but were differentiated by being more labiolingually compressed and having much less medial curvature. Four extant *Sphyaena* species are native to the Gulf of Mexico, including *S. barracuda* (Edwards in Catesby, 1771), *S. borealis* DeKay, 1842, *S. guachancho* Cuvier, 1829, and *S. picudilla* Poey, 1860 (Hoese & Moore 1998). The teeth in our sample are small and unserrated and could belong to the smaller species *S. borealis*, *S. guachancho*, or *S. picudilla*. In contrast, teeth of the large-bodied *S. barracuda* are serrated. Although the fossil teeth compared favorably with the dentary teeth from an extant *S. guachancho* specimen in the MSC collection (MSC 43076), we could not compare them directly to specimens of the other small taxa, nor could we rule out that serrations are absent on juvenile *S. barracuda* teeth (ontogeny). We therefore refrain from speciating the fossil teeth in our sample.

***Trichiurus lepturus* Linnaeus, 1758**material examined

N = 1: MSC 46489 | Fig. 4D-E

Description

MSC 46489, a lanian tooth, has convex labial and lingual crown faces. In labial or lingual views, the tooth has a convex anterior margin, whereas the distal margin is concave on the lower two-thirds of the tooth and the upper one-third is characterized by a distinct apical barb. The tooth is tapered anteriorly, and the apex is slightly anteriorly directed. The crown enameloid is only preserved on the upper one-third of the tooth, in the region of the apical barb, whereas dentine is exposed on the basal two-thirds. A sharp and smooth anterior cutting edge extends along most of the tooth height. A smooth posterior cutting edge is confined to the triangular apical barb, whereas the remainder of the posterior margin is evenly convex. In mesial or distal views, the tooth has a slight medial bend. In basal view, the tooth has a teardrop-shaped outline.

remarks

Although extant Trichiuridae is relatively diverse (Froese & Pauly 2023), only one member of this family, *T. lepturus*, occurs in the Gulf of Mexico (Hoese & Moore 1998). Our fossil tooth was compared to an extant *T. lepturus* specimen in the MSC collection (MSC 42592). MSC 46489 is tall, somewhat sinuous in profile, and bears a distinctive postero-apical barb, features that are consistent with lanian teeth of the extant species. Lanian teeth of *T. lepturus* occur at the anterior-most portion of premaxilla and the anterior half of the dentary. Specimen MSC 46489 is identified as a lower lanian tooth because it is not as posteriorly recurved as equivalent teeth in the premaxilla, and the lingual bend further indicates it is from the right dentary.

***Scomberomorus* sp.**material examined

N = 1: MSC 49257 | Fig. 4F-H

Description

The single tooth has a lanceolate outline in labial or lingual views. The anterior and posterior margins are convex and bear sharp carinae that converge at a pointed apex. The labial and lingual faces of the crown are strongly convex (particularly at the lingual base), and the tooth is thickest basally. In mesial or distal views, the tooth has a convex labial margin and a concave lingual margin, resulting in a distinctive medial curvature. The base of the tooth is damaged, but the cutting edges extend to the base of the preserved portion of the tooth. The tooth has a sub-circular basal outline with sharp anterior and posterior points.

remarks

The gross morphology of MSC 49257 is similar to teeth occurring in the premaxilla and dentary of extant *Scomberomorus cavalla* (Cuvier, 1829) specimens that we examined (MSC 42721, SC2018.3.14, SC2018.3.19). Unfortunately, the premaxillary and maxillary teeth of *S. cavalla* are similar, and we could not determine the jaw location of the fossil tooth. Although MSC 49257 is similar to the fossil *Sphyaena* sp. teeth in our sample, it differs from the latter by having more convex labial and lingual crown faces, a labiolingually thicker crown base, a much stronger medial curvature, and a sub-circular basal outline with sharp anterior and posterior points. In addition to *S. cavalla*, *S. maculatus* (Mitchill, 1815) and *S. regalis* (Bloch, 1793) have also been reported in the Gulf of Mexico (Hoese & Moore 1998). The teeth of the three

taxa are morphologically similar and we were unable to accurately assign the fossil specimen to one of them.

***Archosargus* aff. *probatocephalus* (Walbaum, 1792)**

material examined

N = 1: MSC 42704.1 | Fig. 4I-K

description

In labial or lingual views, this tooth is distinctively spade-shaped, with a crown that is mesiodistally wider than the tooth base. The mesial and distal edges of the cusp are convex. In profile view, the tooth base is labiolingually wider than the crown. The crown has a virtually straight lingual face, whereas the labial face is evenly convex, and the crown has an overall slight lingual curvature. The labial tooth base is wide but the lingual side is narrow and medially expanded, resulting in a sub-triangular basal outline. In labial or lingual view, the mesial side of the crown apex is higher than the distal side, resulting in a slanted chisel-like cutting edge. The enameloid is smooth, black in color, and ends abruptly at the tooth base. The tooth has a hollow crown that lacks a dentine core.

remarks

Of the two species of extant *Archosargus* inhabiting the Gulf of Mexico, *A. probatocephalus* (Walbaum, 1792) and *A. rhomboidalis* (Linnaeus, 1758), MSC 42704.1 is morphologically indistinguishable from teeth of extant *A. probatocephalus* specimens in the MSC collection (MSC 42584, MSC 42744, MSC 43484). These extant specimens show that the fossil tooth is an incisiform that was from the anterior of the premaxilla or dentary. The fossil specimen is nearly identical to those in extant *A. probatocephalus* that range from 38-50 cm in total length, but no extant *A. rhomboidalis* specimens were available to us and we cannot rule out the possibility that the fossil tooth belongs to a large representative of this latter taxon (which has a maximum length of 33 cm; Froese & Pauly, 2023). Specimen MSC 42704.1 is only tentatively assigned to *A. probatocephalus* based on its similarity to this extant species and our lack of comparative *A. rhomboidalis* material.

Balistidae indet.

material examined

N = 1: MSC 44770 | Fig. 4L-M

description

Specimen MSC 44770 is split in half and only the mesial side of the tooth is preserved. In profile view, the tooth is apicobasally elongated and has a slightly but evenly convex labial margin. The apex of the tooth is cuspidate, with the cusp located on the labial half of the tooth. The cusp is blunt, rounded, and slightly angled lingually. In profile view, the occlusal margin on the lingual half of the tooth is convex and strongly slanted lingually. In occlusal view, it is apparent that the cusp is positioned on the antero-mesial side of the crown. The mesial face of the tooth is convex and has smooth enameloid. Interestingly, the enameloid of the cusp exhibits a lighter greenish-gray color compared to the enameloid covering the remainder of the crown. Unfortunately, the morphology of the distal half of the tooth and tooth base is not preserved and therefore cannot be described.

remarks

MSC 44770 was compared to teeth of two extant balistid taxa in the MSC collection, including *Balistes capriscus* Gmelin, 1789 (MSC 49123) and *Canthidermis maculata* (Bloch, 1786) (MSC 43705, MSC 49305). The fossil tooth compares very well to the incisiform teeth of both of these extant taxa, and the extant material shows that the fossil specimen originated from the premaxilla or dentary. However, Hoese & Moore (1998) reported at least 15 members of the Balistidae that currently inhabit the Gulf of Mexico, and we lacked the comparative material necessary to determine the generic affiliation of the fossil tooth. Because it is unclear to us if extant taxa can be readily differentiated by their incisiform teeth, specimen MSC 44770 is conservatively assigned to Balistidae indet.

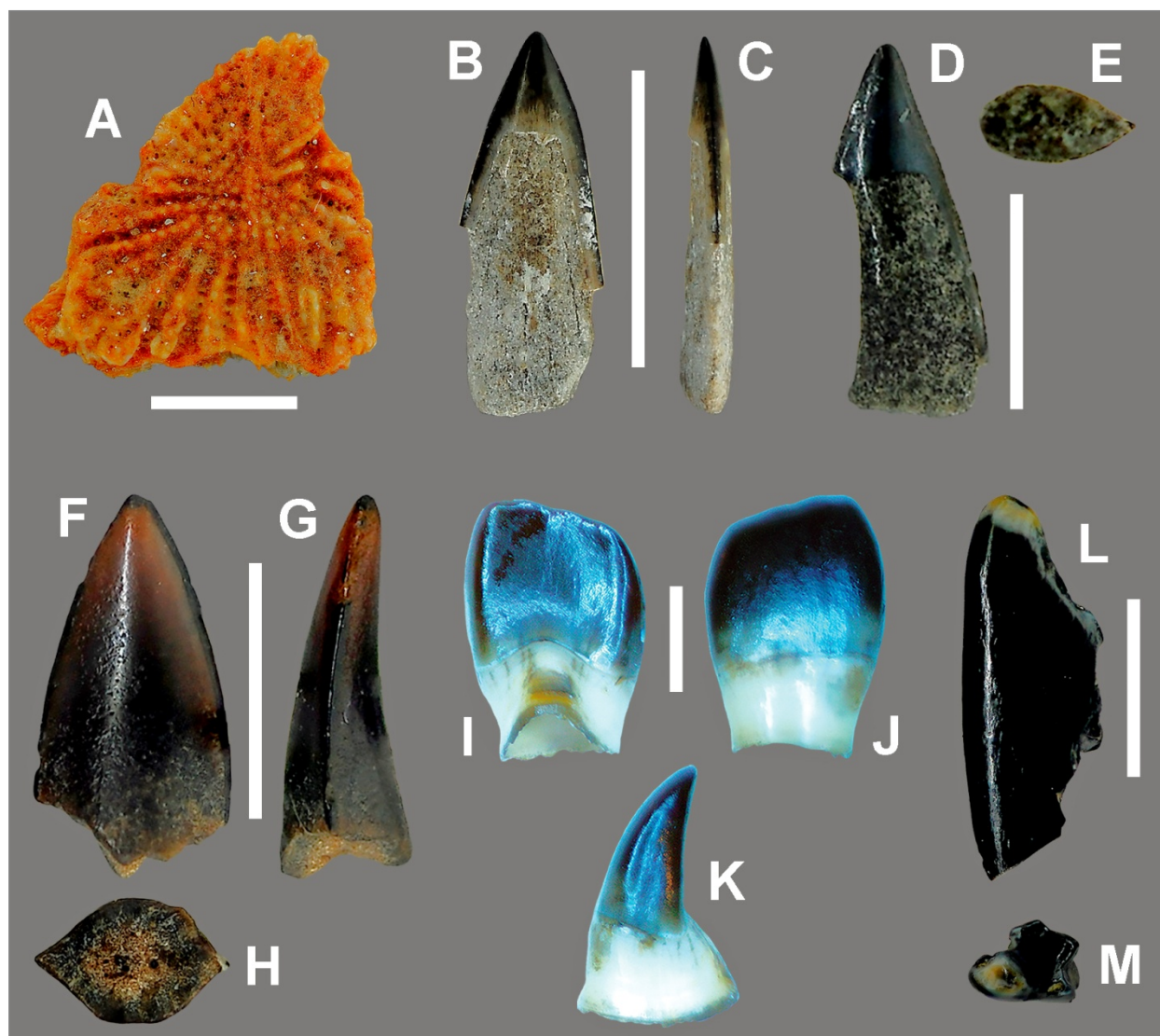


fig. 4. Pliocene teleost elements from Dauphin Island, Mobile County, Alabama, USA. A) MSC 43479, *Ariopsis felis* frontal fragment in dorsal view. B-C) MSC 42706, *Sphyræna* sp. tooth in B) lingual and C) carinal views. D-E) MSC 43489, *Trichiurus lepturus* right laniary tooth in D) lingual and E) basal views. F-H) MSC 49257, *Scomberomorus* sp. tooth in F) lingual, G) carinal, and H) basal views. I-K) MSC 42704.1, *Archosargus* aff. *probatocephalus* incisiform tooth in I) lingual, J) labial, and K) mesial views. L-M) MSC 44770, Balistidae indet. incisiform tooth in L) profile and M) occlusal views. Scale bars for A-C, F-H, L-M = 5.0 mm; D-E, I-K = 2.0 mm.

Discussion

The Pliocene fish assemblage from Dauphin Island, AL, USA

The Pliocene fish assemblage from Dauphin Island in Mobile County, AL, USA has now been documented in four studies, including Ebersole et al. (2017), Stringer et al. (2020, 2023), and the present work. Of the numerous taxa identified in these studies (see Table 1), only one species, *Ariopsis felis*, is known by both otoliths and skeletal remains (Stringer et al. 2020, this report). This lack of taxonomic overlap between otolith and skeletal remains highlights an interesting phenomenon in the fossil record. Several studies have suggested that the otoliths in an assemblage generally represent bony fish species that are more numerous and occur in schools, whereas the osteological remains belong to the less common, albeit larger predatory fishes (Nolf 1985, Breard & Stringer 1995, Nolf & Stringer 2003, Nolf 2013, and Ebersole et al. 2019). These studies have suggested that a primary way otoliths become part of the fossil record is through their excretion by piscivorous organisms. Thus, when we combine the fossil taxa based on both otoliths and osteological remains, a more complete understanding of the Pliocene bony fish assemblage from sites AMb-2 and AMb-3 on Dauphin Island is obtained.

The Pliocene fish assemblage derived from sites AMb-2 and AMb-3 on Dauphin Island is currently comprised of 19 orders, 26 families, and 52 unequivocal taxa (Table 1). The majority of the taxa in this

assemblage (49 of 52; 94%) have living representatives in the Gulf of Mexico today. Only two extinct taxa occur, *Cosmopolitodus hastalis* and *Hemipristis serra*, which were first identified by Ebersole et al. (2017), and the Dauphin Island specimens may be the youngest recorded specimens of these taxa from the Gulf Coastal Plain of the USA. To our knowledge, the only other northern or eastern Gulf of Mexico records of these taxa are those reported from the Leisey Shell pits in Hillsborough County, FL (Scudder et al. 1995). The shark teeth reported by Scudder et al. (1995) were associated with a Pleistocene mammal fauna, but the fossil horizon disconformably overlies strata of Miocene age and the possibility of reworking from the older deposit cannot be decisively discounted.

Stringer et al. (2023) reported six otoliths of *Cynoscion regalis* (Bloch & Schneider, 1801), a taxon that is currently restricted to the Atlantic Coast of the USA (see Froese & Pauly 2023). Occurrences of this taxon in the Gulf of Mexico are considered exotic, and Stringer et al. (2023) postulated that the presence of *C. regalis* in the Dauphin Island assemblage may be a result of Florida being non-emergent, or only partly emergent, during the Pliocene, which would have allowed fish to more easily traverse the waters between the Atlantic and Gulf coasts. A second exotic taxon in our sample is *Isurus paucus*, as regional records of this species are known from the extreme southern Gulf of Mexico off of Florida (Parsons 2006). The occurrence of this largely Atlantic Coast taxon in the Dauphin Island assemblage is also likely a result of a submerged Florida during the Pliocene. Although teeth of *Carcharias taurus* are relatively common among the elasmobranch remains found at sites AMb-2 and AMb-3 (JAE, pers. observation, 2023), the species may also be considered somewhat exotic within the present-day Gulf of Mexico. Although multiple sources cite the occurrence of *C. taurus* in the Gulf of Mexico (see Hoese & Moore 1998, Parsons 2006, Froese & Pauly 2023), records of this taxon along the Gulf and Atlantic coasts of the USA are steadily decreasing due to anthropogenic reasons, like commercial overfishing and non-point source pollution (Carlson et al. 2009).

Extensive collecting of additional otoliths from site AMb-2 helped refine the specific identifications of three taxa originally reported by Stringer et al. (2020), including *Larimus* sp., *Paralichthys* sp., and *Porichthys* sp. These additional otoliths allowed Stringer et al. (2023) to refine the identifications to *Larimus fasciatus*, *Paralichthys albigutta*, and *Porichthys plectrodon*, respectively. Ebersole et al. (2017) reported numerous lower teeth of *Carcharhinus* sp. and suggested that these could represent any of the species confirmed in the Dauphin Island assemblage by their more diagnostic upper teeth (currently seven), or other species currently known to inhabit the Gulf of Mexico (see Parsons 2006). Several fossil taxa from Dauphin Island remain to be speciated due to the limited material available, including *Aetobatus* sp., *Otophidium* sp., *Peprilus* sp., *Rhynchoconger* sp., *Sphyaena* sp., and *Syacium* sp. (Ebersole et al. 2017, Stringer et al. 2020, 2023).

Some otoliths and skeletal remains could not be identified beyond the family level. For example, Stringer et al. (2020) reported otoliths that, due to poor preservation, could not be identified beyond Sciaenidae indet. or Ophidiidae indet. These otoliths may belong to one of the sciaenid taxa (seven) or ophidiid taxa (five) occurring in the Dauphin Island assemblage (see Stringer et al. 2020, 2023, Table 1), but we cannot rule out the possibility that the fossils represent some other member(s) of these families that currently live in the Gulf of Mexico (see Hoese & Moore 1998). Ebersole et al. (2017) identified a single fossil tooth plate of Diodontidae from Dauphin Island, and herein we document a partial incisiform tooth belonging to a member of the Balistidae. Although these remains could not be identified beyond the familial level, both more than likely belong to members of their respective families that have an extant range in the Gulf of Mexico.

Herein we report ray caudal spines that were not identified beyond Myliobatiformes. As discussed earlier, these spines could belong to either of the ray taxa confirmed from Dauphin Island by teeth (i.e., *Aetobatus* sp. or *Rhinoptera* aff. *R. bonasus*), or to any of the other members of the Aetobatidae, Dasyatidae, Myliobatidae, and Urolophidae that have been reported from the Gulf of Mexico (see Hoese & Moore 1998, Parsons 2006). Additional collecting from the Pliocene deposits at sites AMb-2 and AMb-3 may further elucidate the specific identities of some or all of these taxa.

Paleoenvironmental considerations

Based on their analysis of nearly 4,000 otoliths collected from site AMb-2, Stringer et al. (2023) believed that the dredged deposits represent a shallow, soft bottom estuarine paleoenvironment with possible oligohaline creeks (i.e., those with a salinity between 0.5 and 5 ppt). Based on the abundance of otoliths of juvenile *Micropogonias undulatus* (Linnaeus, 1766), Stringer et al. (2023) suggested the area was a primary nursery area for this bony fish, and that an open estuary with a shallow (i.e., less than 20 m) marine (neritic) coastal area was in close proximity, with little deep-water influence. Stringer et al. (2023) also suggested a subtropical paleoclimate during the Early Pliocene (Zanclean).

An analysis of the taxa identified from skeletal remains appears to corroborate the interpretations provided by Stringer et al. (2023). Table 2 includes the 18 extant taxa that were identified to species by skeletal remains from Dauphin Island. When the ecological records of these taxa are examined, all 18 (100%) species occur in marine habitats. Of these, 22% (4 of 18) are exclusively marine, 72% (13 of 18) are found

table 1. Comprehensive listing of Pliocene fish taxa identified from Dauphin Island based on otoliths and osteological remains. Status in GOM (Gulf of Mexico) data derived from Hoesé & Moore (1998).

Identified Taxa			Reported in				status in GOM
Order	Family	Taxon	Ebersole et al. 2017	Stringer et al. 2020	Stringer et al. 2023	this study	
Lamniformes	Carchariidae	<i>Carcharias taurus</i>	X				Present
Lamniformes	Lamnidae	<i>Carcharodon carcharias</i>	X				Present
Lamniformes	Lamnidae	<i>Cosmopolitodus hastalis</i>	X				Extinct
Lamniformes	Lamnidae	<i>Isurus paucus</i>				X	Present
Carcharhiniformes	Hemigaleidae	<i>Hemipristis serra</i>	X				Extinct
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus acronotus</i>				X	Present
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus brachyurus</i>				X	Present
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus leucas</i>	X				Present
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus limbatus</i>				X	Present
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus longimanus</i>	X				Present
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus cf. obscurus</i>	X				Present
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus cf. plumbeus</i>	X				Present
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus sp.</i>	X				Present
Carcharhiniformes	Carcharhinidae	<i>Negaprion brevirostris</i>	X				Present
Carcharhiniformes	Carcharhinidae	<i>Rhizoprionodon cf. terraenovae</i>				X	Present
Carcharhiniformes	Galeoceridae	<i>Galeocerdo cuvier</i>	X				Present
Carcharhiniformes	Sphyrnidae	<i>Sphyrna mokarran</i>				X	Present
Myliobatiformes	Aetobatidae	<i>Aetobatus sp.</i>	X				Present
Myliobatiformes	Myliobatidae	<i>Rhinoptera aff. bonasus</i>				X	Present
Myliobatiformes	Incertae sedis	Myliobatiformes indet.				X	Present
Anguilliformes	Congridae	<i>Ariosoma balearicum</i>			X		Present
Anguilliformes	Congridae	<i>Rhynchoconger sp.</i>			X		Present
Clupeiformes	Engraulidae	<i>Anchoa hepsetus</i>		X			Present
Clupeiformes	Engraulidae	<i>Anchoa mitchilli</i>		X			Present
Siluriformes	Ariidae	<i>Ariopsis felis</i>		X		X	Present
Siluriformes	Ariidae	<i>Bagre marinus</i>			X		Present
Gadiformes	Gadidae	<i>Urophycis regia</i>		X			Present
Ophidiiformes	Ophidiidae	<i>Lepophidium jeannae</i>			X		Present
Ophidiiformes	Ophidiidae	<i>Ophidion cf. marginatum</i>		X			Present
Ophidiiformes	Ophidiidae	<i>Ophidion grayi</i>			X		Present
Ophidiiformes	Ophidiidae	<i>Ophidion josephi</i>			X		Present
Ophidiiformes	Ophidiidae	<i>Otophidium sp.</i>		X			Present
Ophidiiformes	Ophidiidae	Ophidiidae indet.		X			Present
Batrachoidiformes	Batrachoididae	<i>Porichthys cf. plectrodon</i>			X		Present
Batrachoidiformes	Batrachoididae	<i>Porichthys sp.</i>		X			Present
Istiophoriformes	Sphyrnaeidae	<i>Sphyrna sp.</i>				X	Present
Pleuronectiformes	Paralichthyidae	<i>Citharichthys macrops</i>		X			Present
Pleuronectiformes	Paralichthyidae	<i>Paralichthys albigutta</i>			X		Present
Pleuronectiformes	Paralichthyidae	<i>Paralichthys sp.</i>		X			Present
Pleuronectiformes	Paralichthyidae	<i>Syacium sp.</i>		X			Present
Pleuronectiformes	Cynoglossidae	<i>Symphurus cf. plagiusa</i>			X		Present
Scombriformes	Stromateidae	<i>Peprilus sp.</i>		X			Present
Scombriformes	Trichiuridae	<i>Trichiurus lepturus</i>				X	Present
Perciformes	Malacanthidae	<i>Lopholatilus chamaeleonticeps</i>		X			Present
Perciformes	Haemulidae	<i>Orthopristis chrysoptera</i>		X			Present
Trachiniformes	Uranoscopidae	<i>Astroscopus ygraecum</i>			X		Present
Scorpaeniformes	Triglidae	<i>Prionotus aff. carolinus</i>		X			Present
Acanthuriformes	Sciaenidae	<i>Cynoscion arenarius</i>		X			Present
Acanthuriformes	Sciaenidae	<i>Cynoscion nebulosus</i>			X		Present
Acanthuriformes	Sciaenidae	<i>Cynoscion regalis</i>			X		Exotic
Acanthuriformes	Sciaenidae	<i>Larimus fasciatus</i>			X		Present
Acanthuriformes	Sciaenidae	<i>Larimus? sp.</i>		X			Present
Acanthuriformes	Sciaenidae	<i>Leiostomus xanthurus</i>		X			Present
Acanthuriformes	Sciaenidae	<i>Menticirrhus cf. americanus</i>		X			Present
Acanthuriformes	Sciaenidae	<i>Micropogonias undulatus</i>		X			Present
Acanthuriformes	Sciaenidae	Sciaenidae indet.		X			Present
Spariformes	Sparidae	<i>Archosargus aff.</i>				X	Present
Tetraodontiformes	Balistidae	Balistidae indet.				X	Present
Tetraodontiformes	Diodontidae	Diodontidae indet.	X				Present

table 2. Pliocene fish species identified from Dauphin Island by osteological remains and the ecological and climatic preferences of their extant representatives. Ecological and climatic data derived from Froese & Pauly (2023).

Taxon	Ecology	Climate
<i>Archosargus aff. probatocephalus</i>	Marine; brackish	Subtropical
<i>Ariopsis felis</i>	Marine; brackish	Subtropical
<i>Carcharhinus acronotus</i>	Marine	Subtropical
<i>Carcharhinus brachyurus</i>	Marine; brackish	Subtropical
<i>Carcharhinus leucas</i>	Marine; freshwater; brackish	Subtropical
<i>Carcharhinus limbatus</i>	Marine; brackish	Subtropical
<i>Carcharhinus longimanus</i>	Marine	Subtropical
<i>Carcharhinus cf. obscurus</i>	Marine; brackish	Subtropical
<i>Carcharhinus cf. plumbeus</i>	Marine; brackish	Subtropical
<i>Carcharias taurus</i>	Marine	Subtropical
<i>Carcharodon carcharias</i>	Marine; brackish	Subtropical
<i>Galeocerdo cuvier</i>	Marine; brackish	Subtropical
<i>Isurus paucus</i>	Marine	Subtropical
<i>Negaprion brevirostris</i>	Marine; brackish	Subtropical
<i>Rhinoptera aff. bonasus</i>	Marine; brackish	Tropical
<i>Rhizoprionodon cf. terraenovae</i>	Marine; brackish	Subtropical
<i>Sphyrna mokarran</i>	Marine; brackish	Subtropical
<i>Trichiurus lepturus</i>	Marine; brackish	Subtropical

in marine and brackish habitats, and one species (0.06%), *Carcharhinus leucas* (Valenciennes in Müller & Henle, 1839), is known to inhabit marine, brackish, and freshwater ecosystems. In addition, when the climatic preferences of these taxa are examined, 94% (17 of 18) prefer subtropical climates and only one species (0.06%), *Rhinoptera bonasus*, is regarded as a tropical taxon. Together, these data provide evidence for a subtropical climate in the region during the Zanclean, with both marine and brackish paleoenvironments influencing the area.

Interestingly, the paleoenvironment interpreted by Stringer et al. (2023) for the borrow area closely mimics that of Mobile Bay in Alabama, a body of water that is located directly north-northeast of Dauphin Island (Fig. 1). The aerial extent of Mobile Bay is approximately 1000 km², ranging in depth from 3 to 15 m, and is deepest at the mouth near Dauphin Island (O'Neil & Metee 1982, Valentine et al. 2004). The marine waters of Mobile Bay receive a large freshwater discharge from a watershed that is regarded as the sixth largest in the continental USA, and fourth largest in terms of freshwater discharge (MBNEP 2002, Valentine et al. 2004). The amount of freshwater discharge into Mobile Bay results in fluctuating salinity that ranges from 0-24 ppt in the upper bay and 0-36 in the lower bay (Schroder 1978, Berrell 2002, Park et al. 2007, Valentine et al. 2004). The amount of sediment discharge is extensive (4.85 million metric tons annually; Ryan 1969, MBNEP 2002, Valentine et al. 2004) and forms vast offshore sediment plumes that are readily apparent on aerial imagery. The freshwater and sediment output into Mobile Bay results in nutrient-rich oligohaline habitats that contain a remarkable diversity of marine, brackish, and freshwater organisms (Valentine et al. 2004). The borrow area for which the sediments of sites AMb-2 and AMb-3 were derived is located approximately 8 km south of Dauphin Island (Fig. 1), an area within the Gulf of Mexico that is south of the nutrient-rich sediment plumes, contains almost exclusively marine taxa, and has more stable annual mean salinity of approximately 32-34 ppt (Dzwonkowi et al. 2018). The current environment at the borrow area is quite different from its Pliocene counterpart as interpreted by Stringer et al. (2023), indicating that the south Alabama shoreline was likely much closer to the borrow area during the Zanclean than it is today (i.e., ~8 km south of its current location). This would account for the lower salinity and more nearshore paleoenvironment determined by Stringer et al. (2023).

Conclusions

The dredged sands occurring at sites AMb-2 and AMb-3 on Dauphin Island have yielded a diverse array of fossil fish taxa based on otoliths and skeletal material (i.e., bones, spines, and teeth). When the taxa identified herein are combined with records previously provided by Ebersole et al. (2017) and Stringer et al. (2020, 2023), a total of 52 unequivocal fish taxa (Table 1) within 19 orders and 26 families are recognized from the Pliocene deposits at Dauphin Island. Two exotic taxa, *Cynoscion regalis* and *Isurus paucus* were identified in the assemblage, as well as teeth of the extinct sharks *Cosmopolitodus hastalis* and *Hemipristis*

serra (Ebersole et al. 2017, Stringer et al. 2020). These latter two taxa allowed Stringer et al. (2020, 2023) to provide a bracketed Lower Pliocene (Zanclean) age for the dredged deposits at Dauphin Island. Stringer et al. (2023) interpreted the paleoenvironment of the offshore dredged area to represent a subtropical shallow, near shore, estuarine environment with nearby marine influence, and possibly oligohaline creeks with a salinity between 0.5 and 5 ppt. This paleoenvironmental interpretation closely mimics that of present-day Mobile Bay, suggesting the shoreline in Alabama was located several kilometers south of its present location during the Zanclean.

Acknowledgements

We thank the numerous individuals who collected and donated fossil specimens from Dauphin Island for inclusion in this study. These individuals include Destiny Buchanan, Henry Carr, Connie Chieh, Carissa Clay, Christopher Davis, Jr., McKenzie Dimson, Rebecca Domangue, Chloe Dykes, Gabriel Gurt, Erin Harney, Shannon Harney, Elyjah Houston, Brantley Howard, John Hoyle, Bryan Huerta-Beltrán, Drew Gentry, Greg Graeber, Greta Graeber, Jane Graeber, Lela Graeber, Mendel Graeber, Owen Graeber, Dinali Jayasena, Grace Jones, Tuyako Khristoforova, Nandu Kondamuru, Alexa Lopez, Zoi Moon, Grace Morin, Sophie Neno, Meagan Nix, Natalie Ortell, Emily Seubert, James Starnes, Kaeli Stevens, and Connie Unich. We also thank the reviewers, Nicholae Trif and Alberto Collareta, and handling editor, Stefan Koerber, for their helpful feedback that improved an earlier version of this study.

References

- Agassiz, L. (1835): Recherches sur les poissons fossiles. Tome IV (livr. 4). Neuchatel: Imprimerie de Petitpierre
- Agassiz, L. (1838): Recherches sur les poissons fossils. Tome III (livr. 11, Nov.1838). Neuchâtel: Petitpierre et Prince (text) and H. Nicolet (plates)
- Agassiz, L. (1843): Recherches sur les poissons fossils. Tome III (livr. 15&16, Mar.1843). Neuchâtel: Jent and Gassmann, Soleure (text) and H. Nicolet (plates)
- Arratia, G., R.A. Scasso & W. Kiessling (2004): Late Jurassic fishes from Longing Gap, Antarctic Peninsula. *Journal of Vertebrate Paleontology* 24 (1): 41-55
- Berg, L.S. (1940): Classification of fishes, both recent and fossil. *Travaux de l'Institut Zoologique de l'Academie des Sciences de l'URSS* 5 (2): 85-517
- Berrell, T.A. (2002): Variability in bottom-up enrichment in Mobile Bay and its effects on growth rates of *Rangia cuneata* [thesis]. Mobile, AL: University of South Alabama.
- Betancur-R. R., R. Broughton, E. Wiley, K. Carpenter, J. López, C. Li, N. Holcroft, D. Arcila, M. Sanciangco, J. Cureton II, F. Zhang, T. Buser, M. Campbell, J. Ballesteros, A. Roa-Varon, S. Willis, W. Borden, T. Rowley, P. Reneau, D. Hough, G. Lu, T. Grande, G. Arratia & G. Ortí (2013): The Tree of Life and a New Classification of Bony Fishes. *PLOS Currents: Tree of Life*. Online version, accessed 01.May.2023. [\[link\]](#)
- Blainville, H.M.D. de. (1816): Prodrome d'une nouvelle distribution systématique du règne animal. *Bulletin des Sciences, par la Société Philomatique de Paris* 8: 105-124
- Bleeker, P. (1858): De visschen van den Indischen Archipel. Beschreven en toegelicht. Siluri. *Acta Societatis Regiae Scientiarum Indo-Neerlandicae* 4: 1-370
- Bleeker, P. (1859): Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. *Acta Societatis Regiae Scientiarum Indo-Neerlandicae* [Verhandelingen der Natuurkundige Vereeniging in Nederlandsch Indië] 6: 1-276
- Bloch, M.E. (1786): *Naturgeschichte der ausländischen Fische*. Berlin
- Bloch, M.E. (1793): *Naturgeschichte der ausländischen Fische*. Berlin
- Bloch, M.E. & J.G. Schneider (1801): M.E. Blochii, *Systema Ichthyologiae iconibus cx illustratum*. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider, Saxo. Berolini. Sumtibus Austoris Impressum et Bibliopolio Sanderiano Commissum
- Bonaparte, C.L. (1835): *Prodromus systematis ichthyologiae*. *Nuovi Annali delle Scienze naturali Bologna* (Ser. 1) 2 (4): 181-196, 272-277
- Bonaparte, C.L. (1838): *Selachorum tabula analytica*. *Nuovi Annali della Science Naturali Bologna* 1 (2): 195-214
- Bonaparte, C.L. (1840): *Iconografia della fauna italica per le quattro classi degli animali vertebrati*. Tomo III. Pesci. Roma. Fasc. 27-29, puntata 136-154
- Breard, S. & G. Stringer (1995): Paleoenvironment of a diverse marine vertebrate fauna from the Yazoo Clay (Late Eocene) at Copenhagen, Caldwell Parish, Louisiana. *Gulf Coast Association of Geological Societies Transactions* 45: 77-85
- Cappetta, H. (1980): Les Sélaciens du Crétacé supérieur du Liban. II. Batoïdes. *Palaeontographica Abt. A* 168 (5-6): 149-229
- Cappetta, H. (2012): Chondrichthyes Mesozoic and Cenozoic Elasmobranchii: Teeth. *In*: Schultze, H.P. (ed.): *Handbook of Paleoichthyology*, Volume 3E (pp. 1–512). München: Gustav Fischer Verlag

- Carlson, J.K., C.T. McCandless, E. Cortés, R.D. Grubbs, K.I. Andrews, M.A. Macneil & J.A. Musick (2009): An update on the status of the Sand Tiger Shark, *Carcharias taurus* in the northwest Atlantic Ocean. NOAA Technical Memorandum NMFS-SEFSC-585: 1-24
- Catesby, M. (1771): The natural history of Carolina, Florida and the Bahama Islands: containing the figures of birds, beasts, fishes, serpents, insects, and plants : particularly, the forest-trees, shrubs, and other plants, not hitherto described, or very incorrectly figured by authors : together with their descriptions in English and French : to which, are added observations on the air, soil, and waters : with remarks upon agriculture, grain, pulse, roots, &c. : to the whole, is prefixed a new and correct map of the countries. London
- Compagno, L.J.V. (1973): Interrelationships of living elasmobranchs. Zoological Journal of the Linnean Society 53 (Supplement 1): 15-61
- Cope, E.D. (1871): Observations on the systematic relations of the fishes. The American Naturalist 5: 579-593
- Cuvier, G. (1816): Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides, Tome II. Paris: Deterville
- Cuvier, G. (1829): Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition 2. v. 2. Paris: Deterville
- Dall, W.H. (1892): Contributions to the Tertiary fauna of Florida with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. 2. Streptodont and other gastropods, concluded. Transactions of the Wagner Free Institute of Science, Philadelphia 3 (2): 201-473
- DeKay, J.E. (1842): Zoology of New-York, or the New-York fauna; comprising detailed descriptions of all the animals hitherto observed within the state of New-York, with brief notices of those occasionally found near its borders, and accompanied by appropriate illustrations. Part IV. Fishes. Albany: W. & A. White & J. Visscher
- Dzwonkowi, B., S. Fournier, J.T. Reager, S. Milroy, K. Park, A.M. Shiller, A.T. Greer, I. Soto, S.L. Dykstra & V. Sanial (2018): Tracking sea surface salinity and dissolved oxygen on a river-influenced, seasonally stratified shelf, Mississippi Bight, northern Gulf of Mexico. Continental Shelf Research 169 (1): 25-33
- Ebersole, J.A., D.J. Cicimurri & G.L. Stringer (2019): Taxonomy and biostratigraphy of the elasmobranchs and bony fishes (Chondrichthyes and Osteichthyes) of the lower-to-middle Eocene (Ypresian to Bartonian) Claiborne Group in Alabama, USA, including an analysis of otoliths. European Journal of Taxonomy 585: 1-274
- Ebersole, J.A., S.M. Ebersole & D.J. Cicimurri (2017): The occurrence of early Pleistocene marine fish remains from the Gulf Coast of Mobile County, Alabama, USA. Palaeodiversity 10 (1): 97-115
- Ebersole, J.A., A.T. Kelosky, B.L. Huerta-Beltrán, D.J. Cicimurri & J.M. Drymon (2023): Observations on heterodonty within the dentition of the Atlantic Sharpnose Shark, *Rhizoprionodon terraenovae* (Richardson, 1836) from the north-central Gulf of Mexico, USA, with implications on the fossil record. PeerJ 11: e15142
- Fink, S.V. & W.L. Fink (1981): Interrelationships of the ostariophysan fishes (Teleostei). Zoological Journal of the Linnean Society 72 (4): 297-353
- Fink, S.V. & W.L. Fink (1996): Chapter 11: Interrelationships of the ostariophysan fishes (Teleostei). In: Stiassny, M.L.J., L.R. Parenti & G.D. Johnson (eds): Interrelationships of Fishes (pp. 209-249). San Diego: Elsevier, Inc.
- Forrest-Vandera, B.M., M. Larenas & J.A. Andrews (2011): Dauphin Island coastline restoration and search investigation (prepared for Town of Dauphin Island, Alabama). Boca Raton (Florida): Coastal Planning & Engineering, Inc.
- Fricke, R., W.N. Eschmeyer & R. Van der Laan (eds.) (2021): Eschmeyer's Catalog of Fishes: Genera, Species, References. Online version, accessed 01.May.2023. www.researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp
- Froese, R. & D. Pauly (2023): FishBase, version (02/2021). Online version, accessed 01.May.2023. www.fishbase.org
- Garman, S. (1885): *Chlamydoselachus anguineus* Garm. - A living species of Cladodont shark. Bulletin of the Museum of Comparative Zoology at Harvard College 12 (1): 1-35
- Gill, T.N. (1861): Catalogue of the fishes of the eastern coast of North America, from Greenland to Georgia. Proceedings of the Academy of Natural Sciences of Philadelphia 13: 1-63
- Gill, T.N. (1865): Synopsis of the fishes of the Gulf of St. Lawrence and Bay of Fundy. Canadian Naturalist 2: 244-266
- Gmelin, J.F. (1789): Caroli a Linné ... Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species; cum characteribus, differentiis, synonymis, locis. Editio decimo tertia, aucta, reformata. 3 vols. in 9 parts. Lipsiae, 1788-93 1 (3): 1033-1516
- Goodrich, E.S. (1930): Studies on the structure & development of vertebrates. London: MacMillan
- Greenwood, P.H., D.E. Rosen, S.H. Weitzman & G.S. Myers (1966): Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131 (4): 341-455
- GSA (Geological Survey of Alabama) (2018): Assessment of groundwater resources in Alabama, 2010–16. Alabama Geological Survey Bulletin 186: 1-426
- Guitart Manday, D.J. (1966): Nuevo nombre para una especie de tiburón del género *Isurus* (Elasmobranchii: Isuridae) de aguas Cubanas. Poeyana, Series A, Instituto de Biología 15: 1-9
- Günther, A. (1870): Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegasidae, and of the Lophobranchii, Plectognathi, Dipnoi, Ganiodei, Chondropterygii, Cuclostomata, Leptocardi, in the British Museum. London: British Museum
- Hay, O.P. (1902): Bibliography and catalogue of the fossil vertebrata of North America. Bulletin of the United States Geological Survey 179: 1-868
- Hoese, H.D. & R.H. Moore (1998): Fishes of the Gulf of Mexico, second edition. College Station: Texas A&M University Press
- Hovestadt D.C. & M. Hovestadt-Euler (2013): Generic assessment and reallocation of Cenozoic Myliobatinae based on new information of tooth, tooth plate and caudal spine morphology of extant taxa. Palaeontos 24: 1-66

- Huxley, T.H. (1880): On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880: 649-662
- Jordan, D.S. & B.W. Evermann (1896): The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. Bulletin of the United States National Museum 47: 1-1240
- Lacepède, B.G.E. de (1801): Histoire naturelle des poissons. Paris: Plassan
- Linnaeus, C. (1758): Systema Naturae, Ed. X. (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata). Holmiae: Laurentii Salvii
- Linnaeus, C. (1766): Systema naturae sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 12th ed. v. 1 (pt 1). Holmiae: Laurentii Salvii
- MBNEP (Mobile Bay National Estuary Program) (2002): Comprehensive conservation and management plan, Volume I—a call to action. Mobile, AL: Mobile Bay National Estuary Program. Online version, <http://www.mobilebaynep.com/news/Documents/Characterization%20Reports/CCMP%20Final%20Volume%201.pdf>
- Mitchill, S.L. (1815): The fishes of New-York, described and arranged. Transactions of the Literary and Philosophical Society of New-York 1 (5): 355-492
- Müller, J. (1836): Vergleichende Anatomie der Myxinoiden, der Cyclostomen mit durchbohrtem Gaumen. Erster Theil. Osteologie und Myologie. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1834: 65-340
- Müller, J. (1845): Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. Archiv für Naturgeschichte 11 (1): 91-141
- Müller, J. & F.G.J. Henle (1839): Systematische Beschreibung der Plagiostomen. Veit und Comp., Berlin: 27-102
- Nelson, J.S., T.C. Grande & M.V.H. Wilson (2016): Fishes of the World, 5th edition. New York: John Wiley & Sons
- Nolf, D. (1985): Otolithi Piscium. In: Schultze, H.P. (ed.): Handbook of Paleoichthyology, Volume 10 (pp. 1-145). Stuttgart: Gustav Fischer Verlag
- Nolf, D. (2013): The diversity of fish otoliths, past and present. Brussels, Belgium: Operational Directorate “Earth and History of Life” of the Royal Belgian Institute of Natural Sciences
- Nolf, D. & G. Stringer (2003): Late Eocene (Priabonian) fish otoliths from the Yazoo Clay at Copenhagen, Louisiana. Louisiana Geological Survey Geological Pamphlet 13: 1-23
- O’Neil, P.E. & M.F. Mettee (1982): Alabama coastal region ecological characterization. Volume 2. A synthesis of environmental data. FWS/QBS- 82/42. Washington, DC: US Fish and Wildlife Service, Office of Biological Services
- Palacios-Barreto, P., V.P. Cruz, F. Foresti, B.D. Rangel, M. Uribe-Alcocer & P. Diaz-Jaimes (2017): Molecular evidence supporting the expansion of the geographical distribution of the Brazilian cownose ray *Rhinoptera brasiliensis* (Myliobatiformes: Rhinopteridae) in the western Atlantic. Zootaxa 4341 (4): 593-600
- Park, K., C.-K. Kim & W.W. Schroeder (2007): Temporal variability in summertime bottom hypoxia in shallow areas of Mobile Bay, Alabama. Estuaries and Coasts 30: 54-65
- Parsons, G.R. (2006): Sharks, skates, and rays of the Gulf of Mexico. Jackson: University Press of Mississippi
- Patterson, C. & D.E. Rosen (1977): Review of the ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158: 83-172
- Pinna, M.C.C. de (1996): Teleostean monophyly. In M.L.J. Stiassny, L.R. Parenti & G.D. Johnson (eds.): Interrelationships of Fishes (pp. 147-162). San Diego: Academic Press
- Poey, F. (1860): Memorias sobre la historia natural de la Isla de Cuba, acompañadas de sumarios Latinos y extractos en Francés. Tomo 2. La Habana
- Poey, F. (1861): Memorias sobre la historia natural de la Isla de Cuba, acompañadas de sumarios Latinos y extractos en Francés. Tomo 2. La Habana
- Rafinesque, C.S. (1810a): Caratteri di alcuni nuovi generi e nuove specie di animali e pinate della Sicilia, con varie osservazioni sopra i medesimi, lère partie. Palermo: Per le stampe di Sanfilippo
- Rafinesque, C.S. (1810b): Indice d’ittologia siciliana; ossia, catalogo metodico dei nomi latini, italiani, e siciliani dei pesci, che si rinvencono in Sicilia disposti secondo un metodo naturale e seguito da un’appendice che contiene la descrizione de alcuni nuovi pesci siciliani. Messina: Presso Giovanni del Nobolo
- Rafinesque, C.S. (1815): Analyse de la nature, ou tableau de l’univers et des corps organises, Palermo: Per le stampe di Sanfilippo
- Rafinesque, C.S. (1818): Description of three new genera of fluviatile fish, *Pomoxis*, *Sarchirus* and *Exoglossum*. Journal of the Academy of Natural Sciences, Philadelphia 1 (2): 417-422
- Regan, C.T. (1923): The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. Proceedings of the Zoological Society of London 1923 (1-2): 445-461
- Richardson, J. (1836): The Fish. In Fauna Boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under the command of Sir John Franklin, Part 3) pp. 1-327). London: R.N.J. Bentley
- Röse, A.F. (1793): Petri Artedi Angermannia-Sueci synonymia nominum piscium fere omnium. Ichthyologiae pars IV, editio II. Grypeswaldiae
- Rosen, D.E. (1985): An essay on euteleostean classification. American Museum Novitates 2827: 1-57
- Rüppell, W.P.E.S. (1835-38): Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des Rothen Meeres. Frankfurt am Main: Siegmund Schmerber
- Ryan, J.J. (1969): A sedimentologic study of Mobile Bay, Alabama [dissertation]. Tallahassee, Florida: Department of Geology, Sedimentological Research Laboratory Contribution 30. Florida State University

- Schroeder, W.W. (1978): Riverine influence on estuaries: a case study. 347-364. *In*: Wiley, M.L. (ed.): Estuarine interactions. New York: Academic Press.
- Schwartz, F.J. (2008): A survey of tail spine characteristics of stingray species (order Myliobatiformes) frequenting the eastern Pacific Ocean from the international dateline to the Americas. *Journal of the North Carolina Academy of Science* 124 (3): 72-81
- Schwartz, F.J. (2009): Ways to identify stingrays of the world possessing or lacking serrated stinging tail spines. *Journal of the North Carolina Academy of Science* 125 (3): 107-109
- Scudder, S.J., E.H. Simons & G.S. Morgan (1995): Chondrichthyes and Osteichthyes from the early Pleistocene Leisey Shell Pit local fauna, Hillsborough County, Florida. *Bulletin of the Florida Museum of Natural History* 37 (1, 8): 251-272
- Starks, E. C. (1910): The osteology and mutual relationships of the fishes belonging to the family Scombridae. *Journal of Morphology* 21: 77-99
- Starnes, J.E. & R.T. Berry (2017): Geologic map of the Ramsey Springs Quadrangle Stone and George counties. Mississippi Department of Environmental Quality – Office of Geology, Open-File Report OF-281
- Stewart, L. & J.E. Starnes (2017): Geologic map of Jackson County. Mississippi Department of Environmental Quality – Office of Geology, Open-File Report OF-285
- Stringer, G.L., J.A. Ebersole, J.E. Starnes & S.M. Ebersole (2020): First Pliocene otolith assemblage from the Gulf Coastal Plain, Dauphin Island, Mobile County, Alabama, USA. *Historical Biology* 33 (10): 2147-2170
- Stringer, G.L., J.A. Ebersole, J.E. Starnes & S.M. Ebersole (2023): Additions to the early Pliocene fish otolith assemblage from site AMb-2 on Dauphin Island, Alabama, USA, and their taxonomic and paleoecologic implications. *Paleoichthys* 7: 1-29
- Valentine, J.F., K.L. Keck, Jr., M.R. Dardeau & H. Burch. 2004. Chapter 4: Ecosystem-based management of Mobile Bay, Alabama. 71-92. *In*: Day, J.W. & A. Yáñez-Arancibia (eds.): Gulf of Mexico Origin, Waters, and Biota. Volume 4, ecosystem-based management. College Station: Texas A&M University Press.
- van der Laan, R., W. Eschmeyer & R. Fricke (2014): Family-group names of Recent fishes. *Zootaxa* 3882 (2): 1-230
- van der Laan, R., W. Eschmeyer & R. Fricke (2017): Addenda to family-group names of Recent fishes. *Zootaxa* 3882 (2): 1-230
- van der Laan, R., W. Eschmeyer & R. Fricke (2018): Addenda to family-group names of Recent fishes. *Zootaxa* 3882 (2): 1-230
- Voigt, M. & Weber, D. (2011): Field guide for sharks of the genus *Carcharhinus*. München: Verlag Dr. Friedrich Pfeil
- Wainwright, P.C., W.L. Smith, S.A. Price, K.L. Tang, J.S. Sparks, L.A. Ferry, K.L. Kuhn, R.I. Eytan & T.J. Near (2012): The evolution of pharyngognath: a phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. *Systematic Biology* 61 (6): 1001-1027
- Walbaum, J.J. (1792): Petri Arredi sueci genera piscium. In quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Redactis speciebus 242 ad genera 52. *Ichthyologiae pars III. Grypeswaldiae: Ant. Ferdin. Rose*
- Whitley, G.P. (1929): Additions to the check-list of the fishes of New South Wales. No. 2. *Australian Zoologist* 5 (4): 353-357

Ebersole, J.E., D.J. Cicimurri & S.M. Ebersole (2024): Additions to the Pliocene fish assemblage (Chondrichthyes; Osteichthyes) from Dauphin Island, Alabama, USA. *Paleoichthys* 8: 1-20

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support & grant

Since 2003 PecesCriellos is a long-term project supported by the [German Ichthyological Society](https://www.gfi.de/) (Gfi).

This project, including PALEOICHTHYS, would not have been possible without Gfi's granting.

