PALÆO VERTEBRATA

Preliminary report on the fishes (Chondrichthyes & Teleostei) from the lower Oligocene (Rupelian) Red Bluff Clay at site AMo-9, Monroe County, Alabama, USA

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Abstract: Herein we describe a small but relatively diverse assemblage of fossil fishes derived from the lower Oligocene (Rupelian) Red Bluff Clay at site AMo-9 in Monroe County, Alabama, USA. Identified amongst the remains are 15 unequivocal taxa representing 11 families within five orders, and one additional taxon represents an unknown order and family. Taxa identified include *Eostegostoma* sp., *Otodus* (*Carcharocles*) sp., Mitsukurinidae/Carchariidae indet., *Macrorhizodus praecursor*, *Galeorhinus* sp., *Negaprion gilmorei*, *Physogaleus* sp., "*Sphyrna*" sp., *Galeocerdo* sp., cf. "*Aetobatus*" sp., *Sphyraena* sp., *Xiphiorhynchus kimblalocki*, *Xiphiorhynchus* sp., *Cylindracanthus ornatus*, and *C. rectus*. Several additional fossils could not be identified beyond Lamniformes, Carcharhiniformes, and Teleostei, but they likely belong to one of the identified taxa within this paleofauna. All of the fishes previously reported from the Red Bluff Clay within the entirety of the Gulf Coastal Plain of the USA are otolith-based, and each of the 15 unequivocal taxa reported herein are important new records for this lithostratigraphic unit. In particular, the *Eostegostoma* sp. and *Xiphiorhynchus* spp. specimens represent the first occurrences of these taxa in Alabama. The specimens of *C. ornatus*, *Eostegostoma* sp., and *X. kimblalocki* are stratigraphic and temporal range extensions from the middle and late Eocene into the Rupelian Stage of the Oligocene. Other described taxa may represent transitional forms between those described from the late Eocene and late Oligocene within the region. This study provides a tantalizing preliminary view into faunal transitions that occurred amongst marine fishes across the Eocene/Oligocene boundary within the Gulf Coastal Plain of the USA.

Keywords: Vicksburg Group, Elasmobranchii, Galeomorphi, Batomorphii, Gulf Coastal Plain

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INTRODUCTION

The late Paleogene surficial deposits within the Gulf Coastal Plain of Alabama and Mississippi, USA preserve a nearly complete Oligocene marine sequence (Fig. 1) that can be divided into the lower-to-middle Oligocene Vicksburg Group and an unnamed upper Oligocene group colloquially referred to as the "Chickasawhayan" (Raymond *et al*., 1988; Dockery & Thompson, 2016). In Alabama, the Rupelian Vicksburg Group is comprised of, in ascending order, the Red Bluff Clay, Bumpnose Limestone, Forest Hill Sand, Marianna Limestone, and Byram Formation (which includes the Glendon Limestone, unnamed marl, and Bucatunna Clay members). The overlying Rupelian/Chattian "Chickasawhayan" group is comprised of the Chickasawhay Limestone and Paynes Hammock Sand (Szabo *et al*., 1988).

In Alabama and Mississippi, the lower Oligocene (Rupelian) Red Bluff Clay has long been known for its abundance of both marine macro and micro invertebrate fossils (see Hilgard, 1860; Cooke, 1923; Howe, 1928; Hoppin, 1953; Siesser, 1983; Dockery & Lozouet, 2003). Despite the fossiliferous nature of Red Bluff Clay exposures documented in the region, very few studies have focused on the systematic description of the marine vertebrate remains occurring within this unit. Of these, Frizzell & Lamber (1962) described several congrid otoliths from Red Bluff Clay exposures at the Lone Star Cement Quarry in Washington County, Alabama, and Frizzell & Dante (1965) and Salem (1971) later described additional otoliths from the same unit and locality. Thurmond & Jones (1981, p. 6) reported that the Red Bluff Clay had yielded at least one vertebrate specimen, but this fossil was neither described nor figured and it is unclear whether the authors were referring to something previously reported by Frizzell & Lamber (1962), Frizzell & Dante (1965), or Salem (1971), or to something altogether different. Nolf (1985, 2013) later discussed the same Red Bluff Clay otolith specimens that were originally described by Salem (1971). Although Koken (1888), Campbell (1929), and Manning (2003) each reported otoliths from the Vicksburg Group in Alabama and Mississippi, they did not specify the unit(s) from which the specimens were derived.

Herein we provide the first report of non-otolith-based fish remains from the Red Bluff Clay in the Gulf Coastal Plain of the USA. These fossils were largely derived from the basal-most Red Bluff Clay beds exposed at site AMo-9 in Monroe County, Alabama (Fig. 2). Included herein are detailed descriptions and illustrations of these specimens, and we discuss taxonomic issues associated with the described taxa. Ultimately, the fish taxa we report from the Red Bluff Clay expands our knowledge of the early Oligocene palaeodiversity in the region and lends to our understanding of the fish faunas across the Eocene/Oligocene boundary.

GEOLOGIC SETTING AND AGE

The specimens described herein were largely collected from the lower beds of the Oligocene Red Bluff Clay exposed at site AMo-9 in Monroe County, Alabama, USA (Fig. 2). In southwest Alabama the Red Bluff Clay consists of between 3–18 m of greenish-gray, glauconitic, calcareous clayey marl with selenite crystals, and silty clay with thin beds of sand that is interbedded with a series of indurated yellow glauconitic limestone beds (Copeland & Deboo, 1967; Mancini & Tew, 1990; Raymond *et al*., 1988; Szabo *et al*., 1988; Ellwood *et al*., 2020). The Red Bluff Clay disconformably overlies the blue-gray marine clays of the upper Eocene (Priabonian) Shubuta Marl Member of the Yazoo Clay. In eastern Mississippi and western Alabama the Red Bluff Clay disconformably underlies the Rupelian Forest Hill Sand (Dockery, 1982; Mancini & Tew, 1990), but in central Alabama, including localities like site AMo-9, the Red Bluff Clay is directly overlain by the Rupelian Marianna Limestone (Mancini & Tew, 1990; Ellwood *et al*., 2020). Dockery (1982) and Mancini & Tew (1990) interpreted the Red Bluff Clay as having been deposited in shallow marine, marginal delta bay, and prodelta paleoenvironments.

Bybell (1982) and Siesser (1983) assigned the Red Bluff Clay deposits in Alabama and Mississippi to Zone NP21 based on the absence of the nannoplankton taxa *Dicoaster saipanensis* Bramlette & Riedel, 1954, *Dicoaster barbadiensis* Tan Sin Hok, 1927, and *Reticulofenestra reticulata* (Gartner & Smith, 1967), and the presence of *Coccolithus formosus* (Kamptner, 1963). The last occurrence of *D. saipanensis*, *D. barbadiensis,* and *R. reticulata* fall within zones NP19/20, whereas the last occurrence of *C. formosus* resides within the top of Zone NP21 (Perch-Nielsen, 1985). Furthermore, Mancini (1979) and Mancini & Waters (1986) placed the Red Bluff Clay within the *Pseudohastigerina micra* (Cole, 1927) Planktonic Foraminifera Interval Zone of Stainforth & Lamb (1981) and the P18 Zone of Blow (1979). The stratigraphic overlap of these zonations firmly places the Red Bluff Clay deposits in Alabama and Mississippi within the lower Rupelian Stage of the Oligocene Epoch. The Global Boundary Stratotype Section and Points (GSSP) for the base of the Oligocene is defined at the Massignano Section near Ancona, Italy, and at this site two Eocene genera of planktonic foraminifera, *Hantkenina* and *Cribrohantkenina* (family Hantkeninidae), become extinct and are absent from Rupelian strata (Ogg *et al*., 2016).

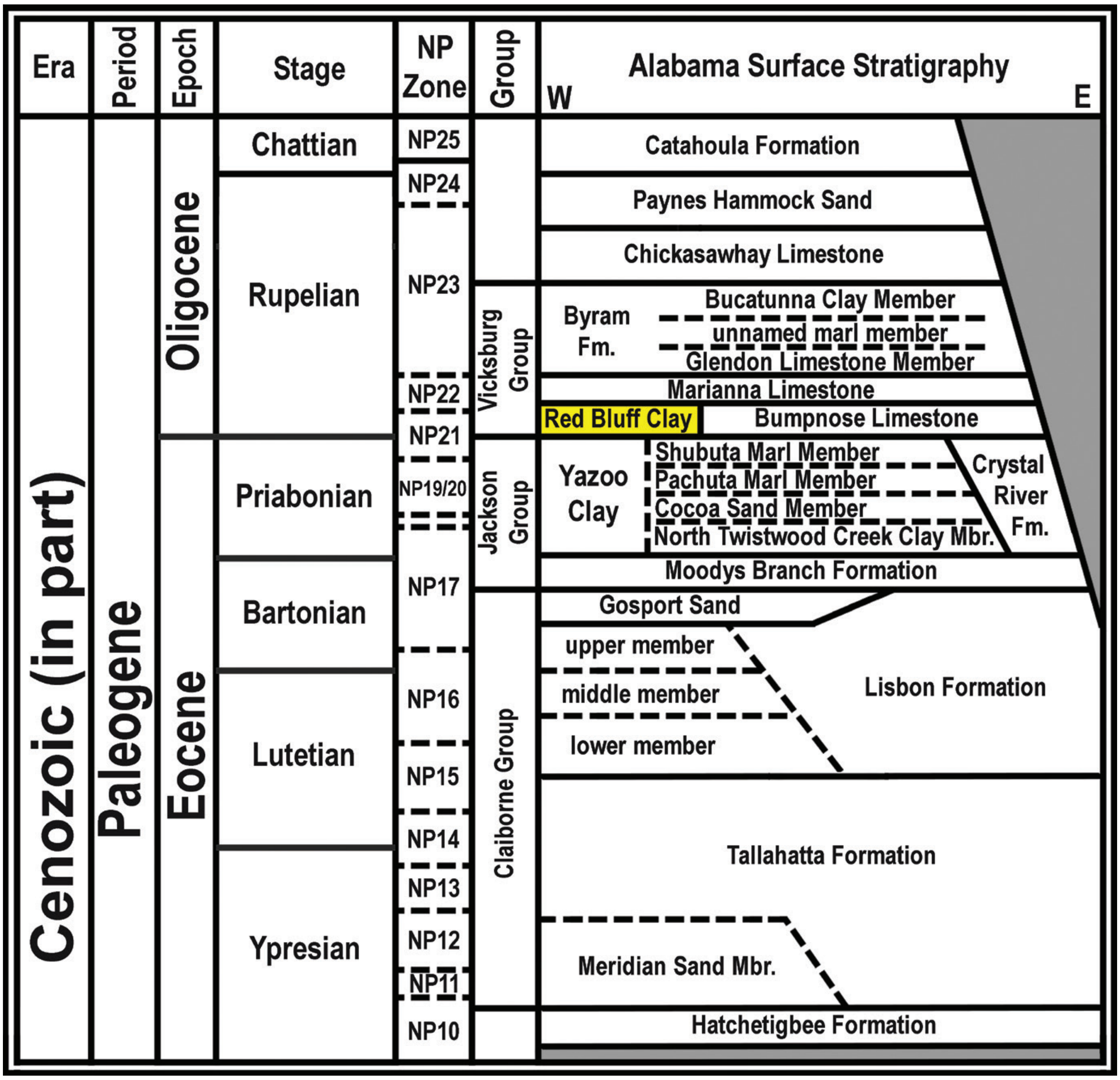

Figure 1. Eocene and Oligocene surface stratigraphy in Alabama and the stratigraphic position of the Red Bluff Clay (highlighted). Gray shaded areas represent unconformities. Stratigraphic column modified from Szabo *et al.* (1988).

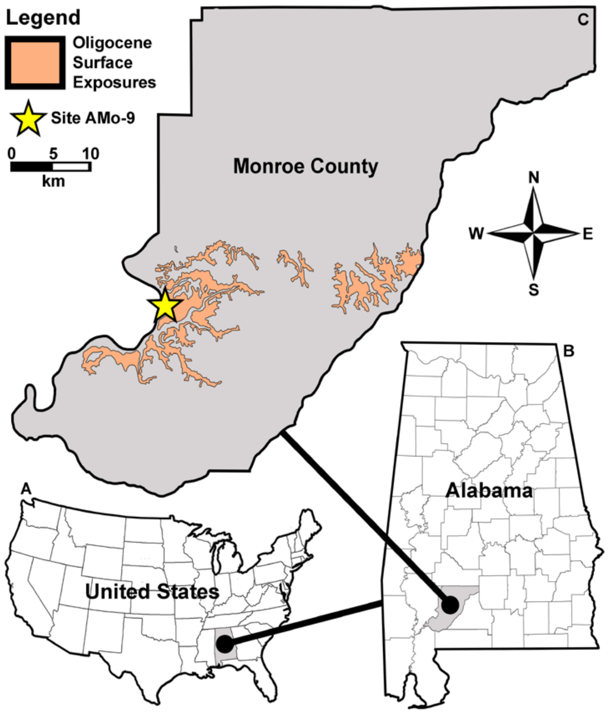

Figure 2. Location of site AMo-9. **A)** Map of the United States showing the location of Alabama. **B)** County map of Alabama showing the location of Monroe County. **C)** Map of Monroe County showing Oligocene surface exposures and the approximate location of site AMo-9.

Ellwood *et al.* (2020) described the stratigraphic section at the study area in detail and documented several Eocene and Oligocene units exposed at this abandoned limestone quarry. In ascending order, these units include the upper Eocene (Priabonian) Pachuta Marl and Shubuta Marl members of the Yazoo Clay, and the Rupelian Red Bluff Clay, Mint Spring Formation, and Marianna Limestone (see Ellwood *et al.*, 2020, fig. 2). At locality AMo-9, the last occurrence of any Hantkeninidae taxon occurs within the upper Shubuta Marl Member of the Yazoo Clay, and the absence of these taxa within the overlying Red Bluff Clay therefore places the Eocene-Oligocene boundary at the contact between these two units (Ellwood *et al.*, 2020).

Ellwood *et al.* (2020) divided the primary exposed Red Bluff Clay section at site AMo-9 into five unconsolidated marl and six interbedded limestone beds (see Ellwood *et al.*, 2020, fig. 2d). All but two of the specimens described herein were derived from the lower Red Bluff Clay beds exposed the at site AMo-9, a stratigraphic interval equivalent to “marl 1” and the directly overlying/underlying indurated beds of Ellwood *et al.* (2020, fig. 2d). As the stratigraphic position of these beds places them just above the Eocene-Oligocene boundary, the fossils described herein represent a lower-most Rupelian marine fauna. The two specimens not derived from the primary section (MSC 49332 and MSC 49333) were collected from a small gully exposure located approximately 300 meters to the southeast. This exposure was confirmed as consisting of Red Bluff Clay because a matrix sample collected from the gully contains conspicuous selenite crystals, a mineral that is present in the Red Bluff Clay exposures at the primary collecting area but is absent from the underlying Shubuta Marl Member of the Yazoo Clay and overlying Marianna Limestone (Szabo *et al.*, 1988). This small gully only exposes a thin section of marl with no adjacent indurated limestone beds, and it is at presently unclear which of the five marl beds this small exposure correlates to within the primary section.

MATERIAL AND METHODS

The specimens described herein were all collected from a locality designated site AMo-9, which is located approximately 10 kilometers southwest of Frisco City near the border of Clarke and Monroe counties in Alabama. (Fig. 2). Site AMo-9 is located on a stretch of private land, and per the wishes of the landowners, the precise locality data is not provided herein in an effort to limit trespassers. However, the details for this McWane Science Center (MSC) designated site number are permanently filed in the archives at MSC in Birmingham, Alabama and available to qualified researchers upon request.

Most of the specimens discussed herein were collected from site AMo-9 by two of the authors (LMS and ADG), but specimen MSC 49756 was discovered and collected by Alabama School of Math and Science (ASMS) student Abigail Richardson and MSC 50129 was discovered and collected by ASMS educator Kristal Webb in July 2023. All but two of the fossils were derived from the lowermost Red Bluff Clay beds, the only unit exposed at the primary collecting area at site AMo-9. The remaining two were collected from a small gully exposure located approximately 300 meters southeast of the primary collecting site. These two specimens (MSC 49332 and MSC 49333) are included within the present study because they were derived from Red Bluff Clay exposures at the locality, and they represent important biostratigraphic and paleobiogeographic records for this region. Due to the indurated nature of the Red Bluff Clay exposures and the low vertebrate density contained within, the bulk sampling of matrix was not conducive at this locality. Rather, most of the specimens were surface collected, with specimen 50032 being recovered from *in situ* matrix surrounding a fossil cetacean that was collected from the site. Specimens were cleaned using manual preparation techniques and broken elements were repaired with commercially available cyanoacrylate. All fossil specimens listed and described herein are permanently accessioned into the collections at MSC.

The fossil specimens described herein were identified through direct comparisons with extant elasmobranch and teleost specimens housed in the collections at MSC and the South Carolina State Museum (SC) in Columbia, USA. In the event no physical specimens were available for a particular taxon, the fossil specimens were compared to those published in the literature (see references cited herein). The taxonomic 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.* (2024), whereas those for orders and families follow van der Laan *et al.* (2014, 2017, 2018). Specimens exceeding 5.0 mm in greatest dimension were photographed with a Nikon D-80 camera with Tamron macro-lens. Specimens smaller than 5.0 mm in greatest dimension were photographed with a Wild Photomakroskop M400 microscope with mounted Canon Eos R50 camera. To account for depth of field, specimens were photographed from several focal lengths and the resulting photographs were stacked and merged in Helicon Focus 8 software. The final plates were produced in Adobe Photoshop v. 22.5.9.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Euselachii Hay, 1902

Infraclass Elasmobranchii Bonaparte, 1838

Division Selachii Cope, 1871

Superorder Galeomorphi (*sensu* Nelson, Grande & Wilson, 2016)

Suborder Orectoloboidei Applegate, 1974

Order Orectolobiformes Applegate, 1974

Superfamily Orectoloboidea Naylor *et al.*, 2012

Family Brachaeluridae Applegate, 1974

Genus *Eostegostoma* Herman, 1977

***Eostegostoma* sp.**

Referred specimen – MSC 50032 (Fig. 3).

Description – The tooth in our sample is small, measuring just under 2 mm in mesiodistal width and 4 mm in apicobasal height. In labial view, the main cusp is tall and triangular and has a slight distal curvature along its height (Fig. 3.1C). The labial and lingual faces of the main cusp are both convex, with the lingual face more so (Fig. 3.1B). A pronounced basally directed labial uvula occurs at the labial crown foot. This structure has a sub-angular basal margin. In profile view, the main cusp is strongly lingually inclined, but it is slightly sinuous due to the weak labially directed curvature near the apex. A smooth cutting edge extends along the mesial and distal sides of the main cusp, but it does not extend to the lateral cusplets. The main cusp is flanked by a pair of rather large lateral cusplets that occur low on the crown (Fig. 3.1A, 1C). The cusplets are blunt and slightly diverging. A single, blunt lateral cusplet occurs distally, whereas there is a second diminutive cusplet at the lateral margin of the mesial cusplet. This secondary cusplet is united to the larger, more medial cusplet (Fig. 3.1D). The root is robust and high lingually but rather low labially. In lingual view, a single nutritive foramen occurs on a pronounced and rounded root protuberance (Fig. 3.1A). In basal view, the root is hemiaulacorhizous and has a heart-shaped basal outline (Fig. 3.1E). The basal attachment surface is deeply concave and an anteriorly located nutritive groove emanates from a large medial nutritive foramen. The root lobes are short, divergent, and have rounded extremities.

Discussion – Specimen MSC 50032 exhibits a tall triangular main cusp, prominent and rounded basal labial uvula, wide and divergent lateral cusplets occurring low on the crown, and hemiaulacorhizous root. This combination of features is characteristic of teeth of members of the Brachaeluridae, two genera of which have been reported from Paleogene strata (Cappetta, 2012). Of the two genera, including *Brachaelurus* and *Eostegostoma*, the gross morphology of MSC 50032 compares most favorably to that of *Eostegostoma*. With respect to the root, it is higher and the root lobes are much more mesiodistally extended on *Brachaelurus* teeth (see Cappetta, 2012, figs. 152 and 153) compared to *Eostegostoma*. Only a single species of *Eostegostoma*, *E. angustum* (Nolf & Taverne in Herman, 1977), has been described, and the taxon is unknown beyond the middle Eocene (Bartonian). If autochthonous, MSC 50032 represents a significant range extension for the genus into the earliest Oligocene. If allochthonous (i.e., reworked from the underlying Yazoo Clay), the specimen represents a less extensive but still significant range extension into the late Eocene (Priabonian). Additional specimens are needed to more precisely determine the identity of the orectolobiform shark represented by MSC 50032.

Order Lamniformes Berg, 1937

Family Otodontidae Glückman, 1964

Genus *Otodus* Agassiz, 1838

Subgenus *Otodus* (*Carcharocles*) (*sensu* Cappetta, 2012)

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

Referred specimen – MSC 49756 (Fig. 4.1).

Description – Specimen MSC 49756 measures 3.1 cm in mesiodistal width and 3 cm in apicobasal height. The tooth has a short, subtriangular, and distally inclined main cusp. In labial and lingual views, the mesial cutting edge is straight at the base, but is convex apically. The distal cutting edge is strongly concave basally, straight medially, and slightly convex apically. The main cusp is flanked by a single pair of broadly triangular lateral cusplets. The cusplets are low, bluntly pointed, divergent, and the mesial cusplet is not well differentiated from the main cusp (Fig. 4.1A). A coarsely serrated cutting edge extends across the main cusp and lateral cusplets. The serrations are even in size across the majority of the cutting edge, but they become finer towards the apex and decrease in size slightly at the base of the main cusp (Fig. 4.1B). The labial face of the main cusp is slightly convex, whereas the lingual face is strongly convex (Fig. 4.1C). The root is robust and has a pronounced lingual root protuberance. No nutritive groove is present, but at least a single nutritive foramen occurs on the lingual face of the root. The crown/root junction is weakly concave labially but very concave lingually. The apicobasal height of the root exceeds the height of the main cusp lingually, but the crown height exceeds the height of the root labially. The root lobes are short, wide, divergent, and have rounded extremities. The interlobe area is wide and U-shaped.

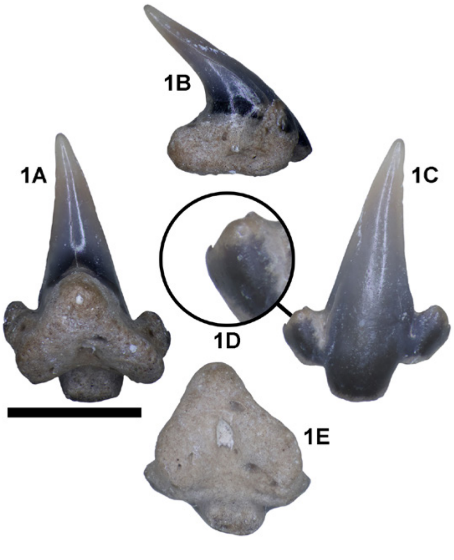

Figure 3. *Eostegostoma* sp. tooth from the Rupelian Red Bluff Clay at site AMo-9. **1A–D.** MSC 50032 in 1A. lingual, 1B. mesial, 1C. labial, and 1E. basal views; 1D. Close-up of the mesial lateral cusplet. Scale bar = 2 mm.

Discussion – Specimen MSC 49756 represents an upper right lateral tooth of a presumed subadult individual. The mesiodistal width of the tooth is slightly greater than its apicobasal height, indicating that this tooth occupied a lateral file located closer to the jaw commissure.

Cappetta (2012) erected the subgenus *Otodus* (*Carcharocles*) for otodontid teeth possessing the combination of serrated cutting edges and distinct lateral cusplets. This subgenus contains many nominal species, and several Eocene and Oligocene taxa are commonly reported in the literature, including *O.* (*C.*) *aksuaticus* (Menner, 1928), *O.* (*C.*) *auriculatus* (de Blainville, 1818), *O.* (*C.*) *sokolovi* (Jaekel, 1895), and *O. (C.) angustidens* (Agassiz, 1835b). The identifying morphological features for these taxa appear to overlap, and it remains to be determined if the nominal taxa represent true individual biological species, heterodonty within fewer species, or are simply a chronospecies. These various species are thought to represent a single lineage that culminated with *Otodus* (*Megaselachus*) *megalodon* (Agassiz, 1835b) (Applegate & Espinosa-Arrubarrena, 1996), although Cappetta (2012) expressed his opinion that several lineages may instead be present. Specimen MSC 49756 differs from the teeth generally referred to *O.* (*C.*) *aksuaticus* by having coarse and evenly serrated cutting edges (as opposed to unevenly serrated), and it differs from *O. (M.) chubutensis* (Ameghino, 1906) teeth by having a single large pair of lateral cusplets that are clearly separated from the mesial and distal cutting edges of the main cusp. It is possible that MSC 49756 belongs to *O.* (*C.*) *sokolovi*, which is a middle Eocene to lower Oligocene species that is thought to be intermediate between *O.* (*C.*) *auriculatus* and *O.* (*C.*) *angustidens*. However, Ebersole *et al.* (2019) expressed their opinion that these three taxa cannot be readily differentiated based on currently published characteristics after their examination of large samples of teeth showed the differential characteristics between these taxa to

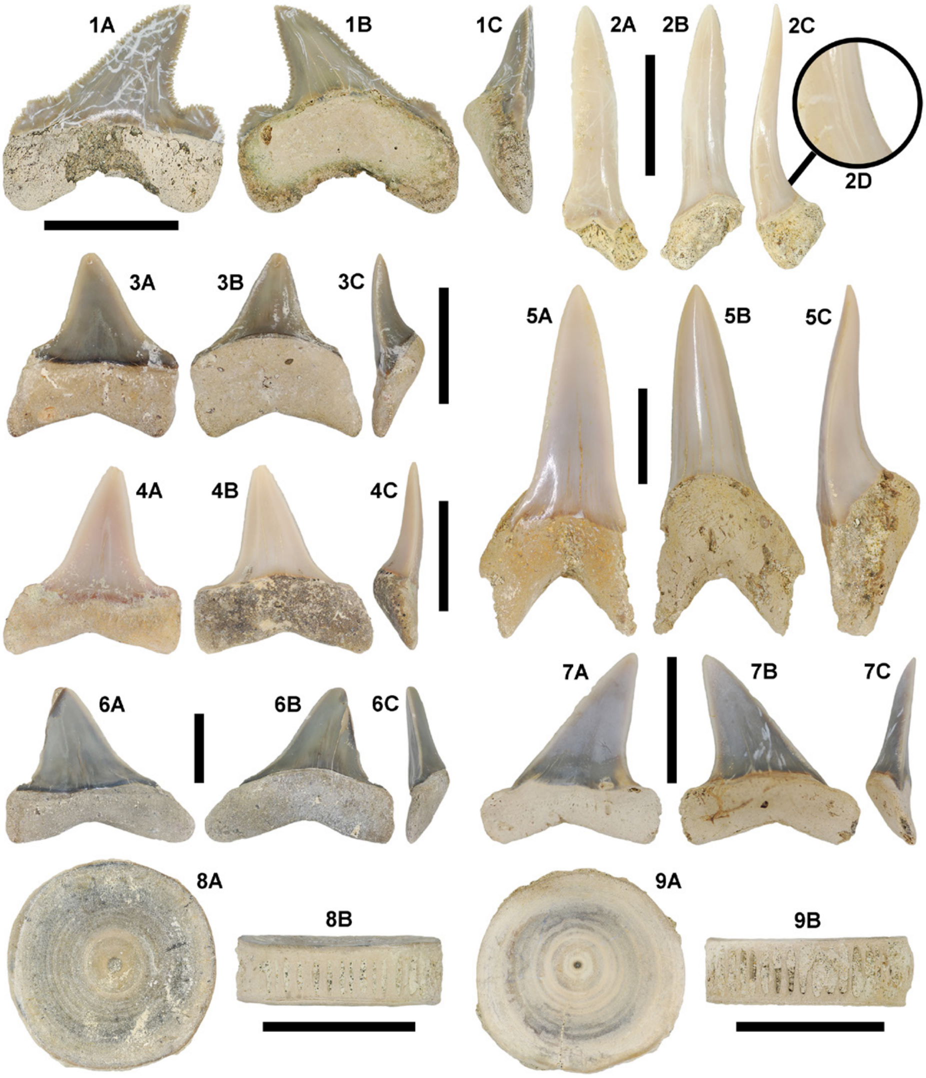

Figure 4. Lamniformes elements from the Rupelian Red Bluff Clay at site AMo-9. **1A–C.** MSC 49756, *Otodus* (*Carcharocles*) sp. upper right lateral tooth in 1A. labial, 1B. lingual, and 1C. mesial views. **2A–D.** MSC 49758, Mitsukurinidae/Carchariidae indet. anterior tooth in 2A. labial, 2B. lingual, and 2C. mesial views, 2D. close-up of lingual crown ornamentation. **3A–C.** MSC 50039, *Macrorhizodus praecursor* lower right posterolateral tooth in 3A. labial, 3B. lingual, and 3C. mesial views. **4A–C.** MSC 49761, *Macrorhizodus praecursor* lower left lateral tooth in 4A. labial, 4B. lingual, and 4C. mesial views. **5A–C.** MSC 50040, *Macrorhizodus praecursor* lower left anterior tooth in 5A. labial, 5B. lingual, and 5C. mesial views. **6A–C.** MSC 50041, *Macrorhizodus praecursor* upper left 1st lateral tooth in 6A. labial, 6B. lingual, and 6C. mesial views. **7A–C.** MSC 50041, *Macrorhizodus praecursor* upper right lateral tooth in 7A. labial, 7B. lingual, and 7C. mesial views. **8A–B.** MSC 49757, Lamniformes indet. vertebra in 8A. articular, and 8B. lateral views. **9A–B.** MSC 50121, Lamniformes indet. vertebra in 9A. articular, and 9B. lateral views. Scale bars for 1–2, 8–9 = 2 cm. Scale bars for 3–7 = 1 cm.

be ambiguous. Specimen MSC 49756 is herein not speciated because the single tooth in our sample cannot shed further light onto the taxonomy of this subgenus.

Family Mitsukurinidae Jordan, 1898 or Carchariidae (*sensu* Stone & Shimada, 2019)

gen et sp. indet.

Referred specimen – MSC 49758 (Fig. 4.2).

Description – MSC 49758 is a broken tooth consisting of the crown and a portion of the root. As preserved, the tooth measures 2.1 cm in apicobasal height and 7 mm in mesiodistal width. In labial and lingual views, the main cusp is very tall and narrow, and it has sinuous mesial and distal margins. The main cusp is slightly constricted near the crown base and is mesiodistally widest near the center of the cusp (Fig. 4.2A). The upper half of the labial crown face is flat, whereas the bottom half is slightly convex. The lingual crown face is strongly convex, and the lower half of which is ornamented with coarse enameloid folds (Fig. 4.2D). In mesial and distal views, the main cusp is slightly sinuous (Fig. 4.2C), and in labial and lingual views, the main cusp has a slight distal inclination (Fig. 4.2B). The root is ablated and no lateral cusplets or root lobes are preserved. However, remnants of a nutritive groove is visible on a lingual root protuberance.

Discussion – The combination of a tall and narrow main cusp with a weakly sigmoidal profile indicates that specimen MSC 49758 is from an anterior jaw file. Unfortunately, the tooth is not well enough preserved to identify it to the generic level. It is morphologically comparable to teeth of Paleogene carchariids and mitsukurinids, the former group including *Striatolamia* and the latter *Anomotodon*, *Mitsukurina*, and *Woellsteinia*. The extent of lingual crown ornamentation on MSC 49758 is similar to the condition observed on Oligocene *Anomotodon cravenensis* Case, 1980 (see pls. 3–4, text fig. 4) and *Woellsteinia oligocaena* Reinecke *et al.*, 2001 (see pls. 26–27), as well as Eocene *Striatolamia*. The anterior teeth of the latter taxon can bear lateral cusplets, whereas teeth of the former two taxa do not. The lack of a preserved root or lateral cusplets on the Alabama tooth does not allow us to confidently assign it to any of the aforementioned genera.

Family Lamnidae Bonaparte, 1835

Genus *Macrorhizodus* Glückman, 1964

Macrorhizodus praecursor (Leriche, 1905)

Referred specimens – n=26; MSC 49755, MSC 49761 (Fig. 4.4), MSC 49765 (20 specimens), MSC 50036 (Fig. 4.7), MSC 50039 (Fig. 4.3), MSC 50040 (Fig. 4.5), MSC 50041 (Fig. 4.6).

Description – Specimen MSC 50041 measures 2.6 cm in mesiodistal width and 2.1 cm in apicobasal height. The tooth has a short, triangular, and distally inclined main cusp. In mesial and distal views, the tooth has a slightly convex mesial cutting edge and a straight distal edge. The labial crown face is slightly convex, whereas the lingual face is strongly convex. The mesial root lobe is mesially extended and has a rounded extremity. The distal root lobe is more angular and has a straight distal edge. The root lobes are divergent and the interlobe area is wide, shallow, and V-shaped. A small nutritive foramen occurs on a low root protuberance.

Specimen MSC 50036 measures approximately 2.1 cm in both mesiodistal width and apicobasal height. This tooth has a tall, broadly triangular, and distally inclined main cusp. The roughly straight mesial margin is oblique to the cusp height, whereas the distal margin is more vertically oriented (Fig. 4.7A). The cutting edges are smooth and continuous along the cusp height, and it extends onto a short distal heel. The cusp apex is weakly biconvex apically. The labial crown face is flat, whereas the lingual face is convex, and there is a slight labial curvature at the apex (Fig. 4.7C). The root is low and has sub-rectangular, strongly divergent root lobes. The root lobes have rather angular extremities, and the interlobe area is shallow, wide, and V-shaped. At least one nutritive foramen occurs on a low root protuberance (Fig. 4.7B).

Specimen MSC 50040 (Fig. 4.5) measures 3.1 cm in apicobasal height and 1.6 cm in mesiodistal width. The tooth has a tall and robust main cusp. In labial and lingual views, the lateral margins of the main cusp are biconvex apically, biconcave basally, but rather straight along most of their length. The mesial and distal cutting edges are smooth and continuous along cusp height, and a short mesial shoulder is evident (Fig. 4.5A). The labial crown face is slightly convex, whereas the lingual face is strongly convex, and the crown is slightly sinuous in profile (Fig. 4.5C). The mesial and distal root lobes are damaged, but the interlobe area is deep and V-shaped. At least two small nutritive foramina occur on a pronounced root protuberance (Fig. 4.5B). The root is higher lingually than it is labially.

Specimen MSC 49761 measures 1.7 cm in mesiodistal width and just over 2 cm in apicobasal height. This tooth has a short and triangular main cusp that exhibits slight distal inclination. The mesial cutting edge is slightly convex along its apical one-half but is concave at the crown base, where a short and oblique mesial shoulder occurs (Fig. 4.4A). The distal cutting edge is nearly straight apically, but evenly convex near the base where it forms a short and more horizontal distal shoulder. The crown has a slight lingual curvature in mesial or distal views (Fig. 4.4C). The root is bilobate with broad and sub-rectangular lobes. The extremity of the mesial root lobe is mesially directed and rounded, whereas the distal root lobe is more angular and has a straight distal edge (Fig. 4.4B). The interlobe area is shallow and V-shaped. At least one small nutritive foramen occurs on a pronounced root protuberance.

Specimen MSC 50039 (Fig. 4.3A) has a mesiodistal width (1.3 cm) that is nearly equal to its apicobasal height (1.4 cm), indicating that it occurred in a tooth file that was located closer to the jaw commissure. In profile view, the labial face is rather flat, but the crown appears to be slightly lingually directed due to the convexity of the of the lingual face (Fig. 4.3C). This tooth is similar to specimen MSC 49761, but the root lobes are more triangular, and the extremities of both root lobes are distally directed (Fig. 4.3B). In addition, the mesial and distal edges of the root lobes are straight.

Discussion – The specimens in our sample document monognathic and dignathic heterodonty, as teeth from both the palatoquadrate and Meckel's cartilage are represented. Based on jaws of extant *Isurus paucus* Guitart-Manday, 1966 and *I. oxyrinchus* Rafinesque, 1810a that we examined (MSC 42606 and SC2020.53.27, respectively) specimen MSC 50041 (Fig.

4.6) is an upper left 1st lateral tooth, which is indicated by the distally inclined cusp and elongated mesial root lobe. Specimen MSC 50036 (Fig. 4.7) is an upper right lateral tooth. Specimen MSC 50040 (Fig. 4.5) is a second lower right anterior tooth based on the presence of a short distal heel on the crown and slightly sigmoidal profile. Specimen MSC 49761 (Fig. 4.4) is a lower left lateral tooth, whereas specimen MSC 50039 (Fig. 4.3) is a lower right posterior tooth as indicated by the high root with distally directed root lobe extremities.

The teeth in our sample are assigned to *Macrorhizodus praecursor* (Leriche, 1905) because they appear to be conspecific with the type specimens figured by Leriche (1906, pl. 16, figs. 8–12) that were derived from the middle Eocene (Lutetian) of Belgium. None of the specimens in our sample possess any semblance of lateral cusplets that appear to be a distinguishing feature of *M. nolfi* Zhelezko in Zhelezko & Kozlov, 1999. The Red Bluff Clay specimens lack crown curvature as occurs on *M. flandricus* (Leriche, 1910) teeth, and the root lobe extremities on the former are more rounded compared to those of the latter.

Leriche (1905) originally named this morphology *Oxyrhina desori praecursor* and suggested it was a stratigraphically older variant of *Oxyrhina desori* Agassiz, 1843. Leriche (1942) later named *Oxyrhina praecursor americana* for teeth derived from the Priabonian Cocoa Sand Member of the Yazoo Clay in Alabama and noted slight morphological differences between these teeth and those of *O. desori praecursor*. Glückman (1964) later assigned these morphologies to a new genus, *Macrorhizodus*, and several subsequent studies viewed both taxa as valid (i.e., Ward & Wiest, 1990; Zhelezko & Kozlov, 1999; Case & Borodin, 2000; Cappetta, 2012). Ebersole *et al.* (2019) reexamined Leriche's (1942) suite of *O. praecursor americana* syntypes and attributed morphological differences to heterodonty and/or intraspecific variation, ultimately concluding that the subspecies was a junior synonym of *Macrorhizodus praecursor*.

Lamniformes indet.

Referred specimens – n=2; MSC 49757 (Fig. 4.8), MSC 50121 (Fig. 4.9).

Description – MSC 49757 and MSC 50121 are vertebral centra that are rostrocaudally thin (9 mm and 10 mm, respectively), have a circular outline in anterior and posterior views, and a greatest diameter of 3.1 cm and 3.3 cm, respectively. The vertebrae are amphicoelous in that they have concave anterior and posterior surfaces. These surfaces have numerous concentric annuli that surround a constricted notochordal canal (Figs. 4.8A and 4.9A). The lateral edges are lined with a dense series of parallel septa that intersect the thick corpus calcareum that lines the articular rims (i.e., Fig. 4.9B). The dorsal and ventral surfaces have a conspicuous pair of cartilage foramina that do not intersect the corpus calcareum.

Discussion – The dense parallel septa that line the lateral edges of the vertebral centra easily differentiate them from those of the Carcharhiniformes (see below), and indicate they belong to a member of the Lamniformes (Kriwet *et al.*, 2014; Frederickson *et al.*, 2015; Romano *et al.*, 2021). Three lamniform sharks have been identified in our Red Bluff Clay fauna, including Mitsukurinidae/Carchariidae indet., *Macrorhizodus praecursor*, and *Otodus* (*Carcharocles*) sp., but we also cannot rule out the possibility that these vertebrae belong to a yet-to-be discovered taxon within the Red Bluff Clay.

Order Carcharhiniformes Compagno, 1973
Family Triakidae Gray, 1851
Genus *Galeorhinus* de Blainville, 1816
Galeorhinus sp.

Referred specimen – MSC 50033 (Fig. 5.1).

Description – MSC 50033 measures approximately 4 mm in mesiodistal width and 2 mm in apicobasal height. The tooth has a low crown with a mesial cutting edge that is relatively straight along its upper one-half but is convex basally. This edge is smooth except for a series of indistinct crenulations along its medial portion (Fig. 5.1A). The main cusp is broadly triangular, short, and strongly distally directed. The distal cutting edge is very short, convex, smooth, and lingually inclined. An elongated distal heel extends obliquely from the main cusp, and these structures are separated by a deep notch. The distal heel is lined with five pronounced denticles that decrease in size distally. The lingual crown face is convex and smooth, whereas the labial crown face is conspicuously concave in profile view (Fig. 5.1C). A distinct enameloid bulge occurs at the labial crown foot that overhangs the root (Fig. 5.1B) and is ornamented with fine enameloid wrinkles across the width of the tooth (Fig. 5.1D). The root is low labially, but high lingually, and a wide and deep nutritive groove occurs on a pronounced lingual root protuberance (Fig. 5.1B). In profile view, the basal face of the root is slightly convex. The root lobes are long, strongly divergent, and rounded. The interlobe area is wide, shallow, and U-shaped.

Discussion – Based on its broad width, low crown height, and strongly distally inclined main cusp, specimen MSC 50033 is a posterolateral tooth. *Galeorhinus* teeth are similar to those of *Pachygaleus* but differ by having a much less convex labial crown base and denticulations that can extend further than one-third up the mesial edge (Cappetta, 2012; Ebersole *et al.*, 2019). A comparison of MSC 50033 to published dentitions of the extant *Galeorhinus galeus* (Linnaeus, 1758) (i.e., Castro, 2011; Ebert & Dando, 2020) revealed that this tooth was likely derived from a lower posterolateral file based on its having a convex mesial edge, short main cusp, and extended distal heel. Several Paleogene *Galeorhinus* species have been reported in the literature, including *G. cuvieri* (Agassiz, 1835c), *G. duchaussoisi* Adnet & Cappetta, 2008, *G. loangoensis* Dartevelle & Casier, 1943, *G. louisi* Adnet & Cappetta, 2008, *G. minutissimus* (Arambourg, 1935), *G. muelleri* (Jaekel, 1898), *G. parvulus* Dartevelle & Casier, 1943, *G. tenuis* Averianov & Udovitshenko, 1993, and *G. ypresiensis* (Casier, 1946). Unfortunately, as far as we can ascertain, very few lower posterolateral teeth of *Galeorhinus* have been described or figured for the various type specimens, making it difficult to speciate MSC 50033 at this time.

Family Carcharhinidae Jordan & Evermann, 1896
Genus *Negaprion* Whitley, 1940
Negaprion gilmorei (Leriche, 1942)

Referred specimens – n=5; MSC 49762 (2 specimens), MSC 50122 (Fig. 5.3), MSC 50123 (Fig. 5.2), MSC 50124 (Fig. 5.4).

Description – Our sample includes two distinct morphologies, including one with a broadly triangular main cusp that is flanked by lateral shoulders (Fig. 5.3). The teeth range in size from 9 mm to 1.4 cm in mesiodistal width and 9 mm to 1 cm in apicobasal height. The main cusp of these teeth is distally directed to varying degrees. The mesial and distal cutting edges are smooth and sharp and intersect apically to form a sharp point. The labial face is flat to weakly convex, whereas the lingual face is convex (Figs. 5.2C and 5.3C). The crown enameloid is smooth. The lateral shoulders occur low on the crown and extend obliquely from the main cusp. These shoulders are separated from the cusp by a shallow notch, and they may be smooth to weakly crenulated (Figs. 5.2A and 5.3A). The root is bilobate with low, elongated, sub-rectangular lobes. There is a conspicuous lingual nutritive groove, and the interlobe area is broadly V-shaped (Figs. 5.2B and 5.3B).

Other teeth have a rather narrow, more vertical main cusp that is flanked by very low lateral shoulders (Fig. 5.4). The main

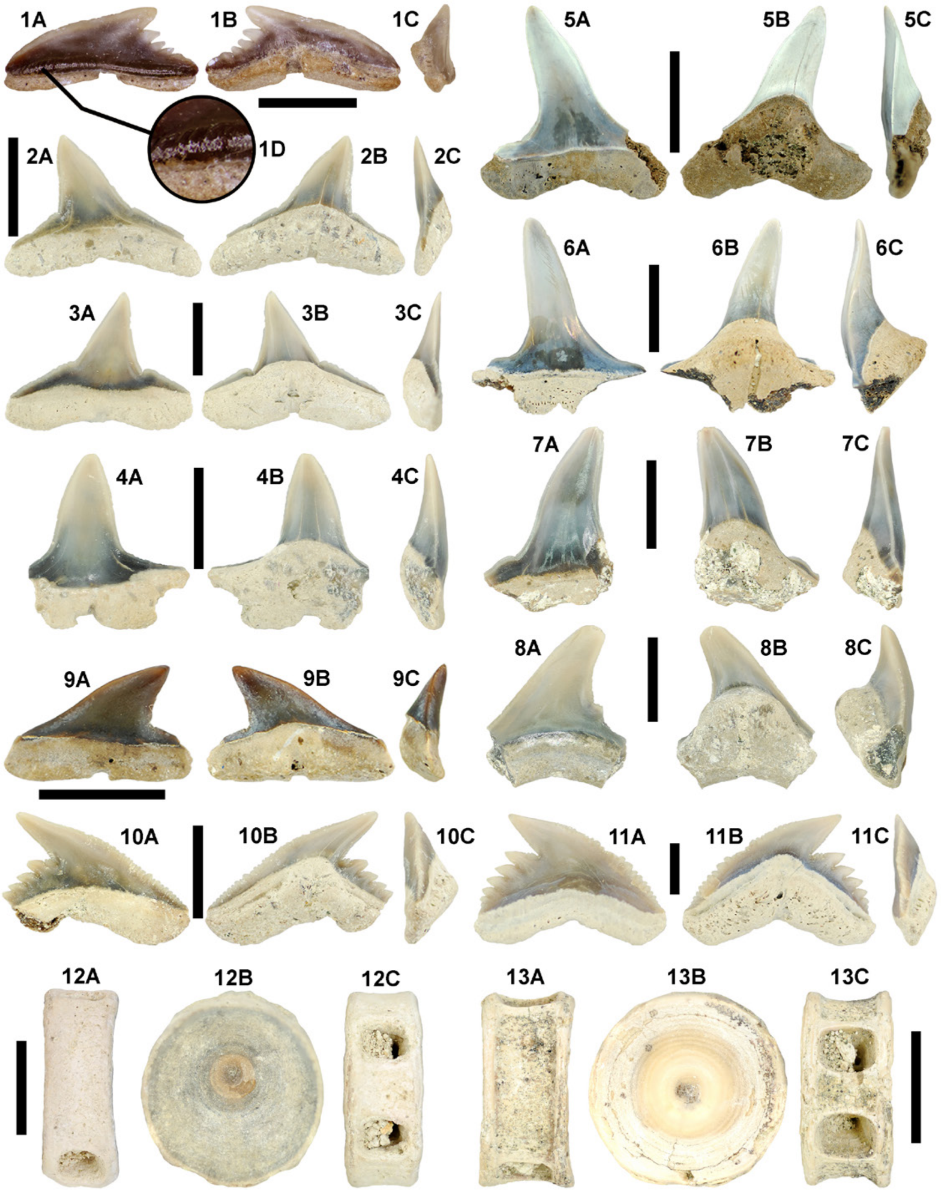

Figure 5. Carcharhiniformes teeth from the Rupelian Red Bluff Clay at site AMo-9. **1A–C.** MSC 50033, *Galeorhinus* sp. tooth in 1A. labial, 1B. lingual, and 1C. mesial view; 1D. close-up of labial crown wrinkling. **2A–C.** MSC 50123, *Negaprion gilmorei* upper left lateral tooth in 2A. labial, 2B. lingual, and 2C. mesial view. **3A–C.** MSC 50122, *Negaprion gilmorei* upper right lateral tooth in 3A. labial, 3B. lingual, and 3C. mesial view. **4A–C.** MSC 50124, *Negaprion gilmorei* lower left lateral tooth in 4A. labial, 4B. lingual, and 4C. mesial view. **5A–C.** MSC 50038, *Physogaleus* sp. anterolateral tooth in 5A. labial, 5B. lingual, and 5C. mesial views. **6A–C.** MSC 50037, *Physogaleus* sp. anterolateral tooth in 6A. labial, 6B. lingual, and 6C. mesial views. **7A–C.** MSC 50042, *Physogaleus* sp. anterolateral tooth in 7A. labial, 7B. lingual, and 7C. mesial views. **8A–C.** MSC 49759, *Physogaleus* sp. lateral tooth in 8A. labial, 8B. lingual, and 8C. mesial views. **9A–C.** MSC 50034, "*Sphyrna*" sp. upper right lateral tooth in 9A. labial, 9B. lingual, and 9C. mesial views. **10A–C.** MSC 49763, *Galeocerdo* sp. tooth in 10A. labial, 10B. lingual, and 10C. mesial views. **11A–C.** MSC 50043, *Galeocerdo* sp. tooth in 11A. labial, 11B. lingual, and 11C. mesial views. **12A–C.** MSC 50125, Carcharhiniformes indet. vertebra in 12A. lateral, 12B. articular, and 12C. dorsal/ventral views. **13A–C.** MSC 50126, Carcharhiniformes indet. vertebra in 13A. lateral, 13B. articular, and 13C. dorsal/ventral views. Scale bars for 1–11 = 5 mm. Scale bars for 12–13 = 1 cm.

cusp is thicker compared to that of the previously described morphology, with a convex labial face and very convex lingual face (Fig. 5.4C). The cutting edges are smooth and sharp along the cusp and transition to the lateral shoulders through a steep slope (Fig. 5.4A). The shoulders are very low and extend well onto the apical surface of the root (Fig. 5.4B). The root is bilobate with a distinct lingual nutritive groove.

Discussion – Our sample demonstrates that monognathic and dignathic heterodonty were developed in this taxon. Upper teeth have a broadly triangular cusp flanked by oblique lateral heels that are separated by a shallow notch (i.e., Fig. 5.3). The cusp of these teeth becomes more distally inclined towards the commissure. Lower teeth have a comparatively narrower main cusp with very low, smooth shoulders that transition from the cusp through a smooth slope (Fig. 5.4).

The teeth in our sample are assigned to *Negaprion gilmorei* because they appear conspecific to the type specimens described and figured by Leriche (1942, pl. 4, fig. 1) that were derived from the Priabonian Cocoa Sand Member of the Yazoo Clay in Choctaw County, Alabama. The Red Bluff Clay specimens differ from the teeth of superficially similar Oligocene *Carcharhinus* species, including *C. elongatus* (Leriche, 1910) and *C. gibbesii* (Woodward, 1899), by having smooth shoulders versus moderately to coarsely serrated shoulders.

Ebersole *et al.* (2019) examined over 1,500 *N. gilmorei* teeth that were collected from various middle Eocene to upper Rupelian strata in Alabama and concluded that all represented the same taxon, and designated multiple taxa as junior synonyms of this species, including *Alopias latidens alabamensis* White, 1956; *Aprinodon greyegertoni* (*sensu* Thurmond & Jones, 1981); *Carcharhinus gilmorei* (*sensu* Müller, 1999); *Carcharhinus greyegertoni* (*sensu* Kruckow & Thies, 1990); *Hypoprion greyegertoni* White, 1956; *Negaprion gibbesi gilmorei* White, 1956; *Sphyrna gilmorei* Leriche, 1942; and *Sphyrna* sp. (*sensu* Cappetta & Case, 2016). The upper lateral teeth in our sample are somewhat similar to teeth herein assigned to *Physogaleus* sp. (see below), but differ by having a shorter main cusp, straight mesial and distal cutting edges, and wider mesial and distal shoulders.

Genus *Physogaleus* Cappetta, 1980

Physogaleus sp.

Referred specimens – n=4; MSC 49759 (Fig. 5.8), MSC 50037 (Fig. 5.6), MSC 50038 (Fig. 5.5), MSC 50042 (Fig. 5.7).

Description – Our sample consists of four broken teeth, the most complete of which is MSC 50038 (Fig. 5.5). This tooth measures 1.2 cm in mesiodistal width and 1.4 cm in apicobasal height. The tooth has a tall and moderately distally inclined main cusp. A smooth cutting edge extends along the entire length of the crown. Apically, the mesial and distal edges are convex, but medially the edges are straight and basally they are concave. On the distal side, the cutting edge extends onto an oblique shoulder. This also appears to have been the case on the mesial side, which is slightly damaged, but the transition from main cusp to shoulder was more gradual compared to the distal side (Fig. 5.5A). The labial crown face is weakly convex, whereas the lingual face is strongly convex (Fig. 5.5C), and enameloid on both faces is smooth. Lingually, the height of the root is nearly equal to the crown height, but labially the root is rather low. The lingual face of the root is damaged medially, but the rather short root lobes are divergent with somewhat rounded extremities, and the interlobe area is shallow and V-shaped (Fig. 5.5B).

Specimens MSC 50037 (Fig. 5.6) and MSC 50042 (Fig. 5.7) consist of a crown with a small portion of preserved root. The crown height on these teeth (measured on the labial face) measures approximately 9 mm and 11 mm, respectively. The crown of both of these specimens is very similar to that MSC 50038, but MSC 50037 is slightly more sinuous in mesial and distal views (Fig. 5.6C). The cutting edges are smooth across the entire crown, and they extend onto short but horizontal heels on the mesial and distal sides (Fig. 5.6A). The root lobes are broken but a robust lingual root boss is bisected by a narrow and deep nutritive groove (Fig. 5.6B). The crown of MSC 50042 has a distally curving main cusp, as the mesial edge is conspicuously convex and the distal edge concave (Fig. 5.7B). The cutting edge is smooth and continuous across the entire preserved crown, and a mesial heel that is delineated from the main cusp by a weak notch (Fig. 5.7A). In mesial view, the crown has a weakly convex labial face and very convex lingual face, and the crown is straight except for slight labial curvature at the apex (Fig. 5.7C). The root of this specimen is not well enough preserved to describe.

MSC 49759 (Fig. 5.8) is missing most of its root but the crown has a labial crown height of approximately 1 cm. The cutting edge on this tooth is smooth and continuous along the preserved portion of the crown, with the mesial edge being straight along its lower one-half but convex apically. The distal cutting edge is strongly and evenly convex and separated from a broken distal heel by a conspicuous notch (Fig. 5.8A). In mesial and distal views, the crown has an evenly convex labial face and concave lingual face, giving the crown an overall lingual bend (Fig. 5.8C). Inconspicuous crenulations are visible along the lower two-thirds of the mesial cutting edge, and a denticle occurs at the origin of the distal heel. Lingually, the height of the root exceeds the crown height. The tooth has a robust lingual root protuberance that is bisected by a nutritive groove, and although the root lobes are not preserved, the interlobe area appears as if it was shallow and U-shaped (Fig. 5.8B).

Discussion – Based on the nature of the tooth profiles, which are either flat or sinuous, we believe that upper (palatoquadrate) and lower (Meckel's cartilage) teeth are represented in the sample. Specimens MSC 50038 (Fig. 5.5) and MSC 50042 (Fig. 5.7) have a flat profile, indicating they were derived from the upper jaw, whereas the sinuous profile of MSC 49759 (Fig. 5.8) and MSC 50037 (Fig. 5.6) suggests they are lower teeth (dignathic heterodonty). Tooth MSC 49759 is more strongly distally curved than MSC 50037, indicating the latter specimen was located further away from the jaw symphysis (monognathic heterodonty).

The three anterolateral teeth (MSC 50037, MSC 50038, MSC 50042) in our sample are ascribed to *Physogaleus* because they have a conspicuously sinuous mesial cutting edge (particularly in mesial view) and robust lingual root protuberance, similar to that seen on *P. contortus* (Gibbes, 1849) (see Cappetta, 2012, fig. 297). These characteristics, along with the lack of serrated cutting edges, serve to differentiate these teeth from the anterior teeth of *Negaprion gilmorei* or the lower teeth of *Carcharhinus* (see Ebersole *et al.*, 2019). The lateral tooth (MSC 49759) is also assigned to *Physogaleus* because it has a robust root and inconspicuous serrations that do not extend onto the apical one-third of the mesial and distal cutting edges. These characteristics were used by Ebersole *et al.* (2019) to separate *Physogaleus* lateral teeth from those of the morphologically similar *Galeocerdo*. The anterolateral teeth in our sample are reminiscent of certain teeth that have been assigned to the Oligocene *Physogaleus maltzani* (Winkler, 1875) (see Reinecke *et al.*, 2005, pl. 42, figs. 7–8) and *P. singularis* (Probst, 1878) (see Haye *et al.*, 2008, pl. 8, fig, 3), and specimen MSC 49759 is similar to lower lateral teeth that have been figured for these taxa (see Reinecke *et al.*, 2005, pl. 44, figs. 8–9; Haye *et al.*, 2008, pl. 7, fig, 12). However, all four teeth in our sample are incomplete and a larger sample of better-preserved specimens is needed to ascertain the identity of this taxon.

Family Sphyrnidae Bonaparte, 1840
Genus *Sphyrna* Rafinesque, 1810b
"*Sphyrna*" sp.

Referred specimen – MSC 50034 (Fig. 5.9).

Description – Specimen MSC 50034 measures 9 mm in mesiodistal width and 5 mm in apicobasal height. Overall, this tooth is broad and has a rather low, distally inclined cusp. The mesial cutting edge on the crown is smooth, elongated, and slightly sinuous along its length, as it is slightly concave basally but convex apically. The distal cutting edge is smooth and only about one-half as long as the mesial edge. It is slightly concave and intersects with the mesial edge at a sharp point, and overall, these structures produce a distally directed cusp. The cusp is separated from a short distal heel by an indistinct notch (Fig. 5.9A). The labial crown face is slightly convex, whereas the lingual face is strongly convex (Fig. 5.9C), and the enameloid is smooth. The root is low and has elongated, sub-rectangular root lobes with rounded extremities. A shallow nutritive groove occurs on an indistinct lingual root protuberance that forms a notch along the otherwise straight basal edge (Fig. 5.9B). One or more nutritive foramina occur medially on the labial root face and within the lingual nutritive groove.

Discussion – Based on our evaluation of a set of Recent *Sphyrna zygaena* jaws (MSC 42600), the specimen described above is a posterolateral tooth. This specimen differs from similar Red Bluff elasmobranch teeth, like *Galeocerdo*, *Negaprion*, *Galeorhinus*, and *Physogaleus*, by having smooth cutting edges that lack any evidence of lateral cusplets, denticulations, or serrations. This tooth varies from other Paleogene genera, like *Scoliodon*, *Loxodon*, and *Rhizoprionodon*, by having a broader main cusp and a conspicuous convexity on the mesial cutting edges that gives the main cusp a distinct mesial "swelling" (see Ebersole *et al.*, 2023).

Of the ten extant sphyrnid taxa, specimen MSC 50034 appears to have affinities with *S. zygaena* (Linnaeus, 1758), as both share teeth having a combination of a broad, triangular main cusp, a distinct "swelling" on the mesial cutting edge, a mesial shoulder that is not distinct from the mesial cutting edge, and smooth cutting edges. Despite these morphological similarities, the assignment of Paleogene sphyrnid teeth to extant species is problematic because molecular divergence estimates provided by Lim *et al.* (2010) indicated that the extant genera *Eusphyra* and *Sphyrna* diverged from common ancestor during the early/middle Miocene, and the Sphyrnidae diverged from *Carcharhinus* during the Ypresian/ Bartonian stages of the early-to-middle Eocene. This data suggests that Paleogene teeth, like the Rupelian MSC 50034, must belong to an unnamed stem genus within the Sphyrnidae lineage, as opposed to *Eusphyra* or *Sphyrna*. As our sample consists of single tooth, and taking into consideration of divergence times for extant taxa, MSC 50034 is herein assigned to "*Sphyrna*" to indicate its likely affinity to extant *Sphyrna* and to denote that this tooth will likely be placed within a different genus once it can be justified by a larger sample size.

The morphological similarity of MSC 50034 to extant *S. zygaena* teeth suggests that this tooth may belong to the Oligocene *S. laevissima* (Cope, 1867), a species that Purdy *et al.* (2001) designated a junior synonym of the former. Reinecke *et al.* (2011) subsequently provided quantitative data that adequately separated *S. laevissima* and *S. zygaena*, and the overall morphology of MSC 50034 is similar to teeth of the *S. laevissima* syntypes as illustrated in Purdy *et al.* (2001, fig. 60) with respect to the smooth cutting edges and broadness and overall morphology of the main cusp. In addition, MSC 50034 looks very similar to a posterior lateral tooth of *S. laevissima* illustrated by Reinicke *et al.* (2011, text fig. 30i–k) by having a convex distal cutting edge (suggesting the two teeth likely were derived from a similar posterolateral tooth file). However, the stratigraphically oldest known *S. laevissima* teeth have been reported from Chattian deposits along the Atlantic Coast of the USA (Müller, 1999; Cicimurri & Knight, 2009; Reinicke *et al.*, 2011). Although specimen MSC 50034 might represent a lower Rupelian occurrence of this taxon, this is difficult to evaluate based on the single tooth in our sample and the tooth is herein not speciated.

Family Galeocerdonidae Poey, 1875
Genus *Galeocerdo* Müller & Henle, 1837
Galeocerdo sp.

Referred specimens – n=2; MSC 49763 (Fig. 5.10), MSC 50043 (Fig. 5.11).

Description – The two specimens in our sample are morphologically similar. Specimen MSC 49763 measures 1.1 cm in mesiodistal width and 1 cm in apicobasal height. Specimen MSC 50043 measures 1.2 cm and 9 mm in the same dimensions. These teeth have a narrow, triangular, and distally directed main cusp. The labial face of the crown is slightly convex, whereas the lingual face is strongly convex. The cutting edges of both specimens are serrated along their entire length, with serrations being larger along the basal one-half, and the cutting edge of MSC 50043 (Fig. 5.11A) is more convex than that of MSC 49763 (Fig. 5.10A). Serrations are somewhat irregular, rounded, vary slightly in height and width, and they are compound (i.e., with additional smaller serrations). The coarsest serrations occur on the lower two-thirds of the mesial cutting edge before becoming finer on the mesial and distal cutting edges of the main cusp and fade towards the apex. In mesial view, the cutting edge is somewhat sinuous along its length (Figs. 5.10C and 5.11C). The distal cutting edges of the main cusp are finely serrated and range from straight to slightly convex. The teeth have a pronounced distal heel that is separated from the distal cutting edge of the main cusp by a deep notch. This heel has numerous large, triangular, and distally directed denticles that decrease in size towards the crown base. The largest, mesial-most denticle has serrations on the basal half of the apical surface. Serrations also occur in smaller numbers on some of the other distal denticles. The root is high lingually, and the crown/root junction is triangular, and a shallow nutritive groove occurs that bears at least one nutritive foramen (Figs. 5.10B and 5.11B). The root lobes are divergent, sub-rectangular, and have rounded extremities. The interlobe area is wide and V-shaped.

Discussion – Türtscher *et al.* (2021) conducted a comprehensive review of 23 nominal fossil and extant species of *Galeocerdo*, and their morphometric analysis supported the occurrence of six valid species, including the Paleogene *G. aduncus* (Agassiz, 1835a), *G. eaglesomei* White, 1955, and *G. clarkensis* White, 1956, Neogene *G. capellini* (Lawley, 1876) and *G. mayumbensis* Dartevelle & Casier, 1943, and the extant *Galeocerdo cuvier* (Péron & Lesueur in Lesueur, 1822). Of these taxa, specimens MSC 49763 and MSC 50043 can be easily separated from the teeth of *G. aduncus* and *G. eaglesomei* by having compound, as opposed to simple, serrations on their cutting edges (Ebersole *et al.*, 2019; Türtscher *et al.*, 2021). Although the Red Bluff Clay *Galeocerdo* teeth have compound serrations like those of *G. clarkensis*, *G. capellini*, *G. cuvier*, and *G. mayumbensis*, they differ from *G. mayumbensis* by having a moderately but evenly convex mesial cutting edge, rather than one that is very convex and even somewhat angular (see Dartevelle & Casier, 1943, pl. 12, figs. 22–30). Additionally, the Red Bluff Clay specimens have a narrower and more elongated main cusp, and larger distal denticles compared to the other taxa (Ebersole *et al.*, 2019; Türtscher *et al.*, 2021). Although these latter characteristics are shared with some species of *Physogaleus*, most species within this latter genus lack distinct serrations (Türtscher *et al.*, 2021). The lone exception to this general rule is the Paleogene to Neogene *P. contortus* (Gibbes, 1849), which has much finer, simple serrations on the cutting edges (Ebersole *et al.*, 2019). Regarding *P. contortus*, specimens MSC 49763 and MSC 50043 differ from the teeth of this taxon by having a less sigmoidal main cusp and cutting edge, a more conspicuous distal notch, and compound serrations.

The Red Bluff Clay specimens have several characteristics in common with the syntypes of *G. clarkensis* (White, 1956, pl. 11, figs 12-14, text fig. 20), a taxon that was originally described from upper Eocene (Priabonian) deposits in Clarke County, Alabama. Although the gracile nature of the main cusp and extremely large distal denticles on the Red Bluff Clay teeth appear to separate them from the *G. clarkensis* syntypes or those described from other middle Eocene deposits in Alabama (Ebersole *et al.*, 2019, fig. 36), we cannot rule out the possibility that these characteristics reflect dental sexual dimorphism or an ontogenetic form of one of the previously described taxa, like *G. aduncus*. Additional specimens are needed in order to make a more precise taxonomic assignment of these teeth.

Carcharhiniformes indet.

Referred specimens – n=42; MSC 49766 (40 specimens), MSC 50125 (Fig. 5.12), MSC 50126 (Fig. 5.13).

Description – Our sample consists of 42 morphologically similar vertebral centra that measure between 0.5 and 2.3 cm in greatest diameter. The specimens are rostrocaudally thin, amphicoelous, and have a circular anterior/posterior outline. The anterior and posterior surfaces exhibit a series of concentric growth annuli that surround a constricted notocordal canal (Figs. 5.12A and 5.13A). The lateral surfaces are smooth and slightly concave, and bands of thick corpus calcareum line the articular rims (Figs. 5.12A and 5.13A). The dorsal and ventral surfaces each possess a pair of sub-rectangular fenestrae that do not reach the corpus calcareum (Figs. 5.12C and 5.13C).

Discussion – These vertebrae differ from those assigned to Lamniformes indet. (see above) by lacking closely spaced, parallel septa on their lateral surfaces. The morphology of these vertebrae is consistent with those that have been associated with various members of the Carcharhiniformes (see Ingle *et al.*, 2018; Morse *et al.*, 2022), and five members of this order have been identified in our Red Bluff Clay fauna, including *Galeocerdo* sp., *Negaprion gilmorei*, *Pachygaleus* sp., *Physogaleus* sp., and "*Sphyrna*" sp. As is the case with the lamniform vertebral centra in our sample (see above), these elements have little taxonomic value and cannot be assigned with confidence to any of these carcharhiniform genera.

Division Batomorphi Cappetta, 1980
Order Myliobatiformes Compagno, 1973
Suborder Myliobatoidei Compagno, 1973
Family Aetobatidae (*sensu* White & Naylor, 2016)
Genus *Aetobatus* de Blainville, 1816
cf. "*Aetobatus*" sp.

Referred specimen – MSC 49753 (Fig. 6.1).

Description – The specimen is a broken symphyseal tooth measuring approximately 1 cm in mesiodistal width. Although an unknown portion of the mesial and distal ends of this tooth are missing, the smooth occlusal surface has straight labial and lingual margins (Fig. 6.1A). The tooth crown is heavily worn through *in vivo* use and the preserved portion is apicobasally thin (Fig. 6.1D). In profile view, the labial face of the root is straight and strongly lingually slanted, and the lingual part of the root extends beyond the crown base (Fig. 6.1E). The lingual crown base is marked by a thick and rounded ridge that extends mesiodistally across the tooth (Fig. 6.1C). The labial, lingual, and basal faces of the root are comprised of an alternating series of parallel lamellae and nutritive grooves (Fig. 6.1B). Labially, the root lamellae are thick, smooth apically but slightly depressed basally (Fig. 6.1D), whereas on the lingual root face the individual lamellae are uniformly convex on their apical surfaces. In labial and lingual views, the root is thickened medially but thins laterally, indicating that this tooth fragment represents a lower symphyseal file.

Discussion – Among the numerous myliobatiform taxa, the teeth of *Aetobatus* and *Pseudaetobatus* are distinct by having a combination of wrinkled labial and lingual crown ornamentation, a thick and rounded lingual transverse ridge, and a lingually projected root (Cicimurri & Ebersole, 2015). These characteristics allow these taxa to be easily identified from other similar taxa, even from partial teeth. These two genera are not known to be coeval in the Gulf Coastal Plain of the USA, as it appears *Pseudaetobatus* (i.e., *P. belli* Cicimurri & Ebersole, 2015) was supplanted by *Aetobatus* at some point within the Ypresian Stage of the lower Eocene (Cicimurri & Ebersole, 2015). However, within the Atlantic Coastal Plain of the USA, the occurrence of *P. undulatus* Cicimurri & Ebersole, 2015 within Priabonian strata in South Carolina demonstrates this genus persisted into the late Eocene. The teeth of *Aetobatus* and *Pseudaetobatus* can be differentiated by the occurrence of angular mesial and distal ends of the symphyseal teeth of the latter, which served as the point of articulation for lateral teeth. In contrast, the dentition of *Aetobatus* consists of a single symphyseal file (see Hovestadt & Hovestadt-Euler, 2013) and therefore the mesial and distal ends of the teeth lack articular facets. However, no unambiguous features have been identified to differentiate these two genera based on medial fragments of symphyseal teeth. The absence of unequivocal middle-to-upper Eocene *Pseudaetobatus* teeth within the Gulf Coastal Plain suggests that specimen MSC 49753 belongs to *Aetobatus*, but the mesial and distal ends are not preserved on this tooth, and we cannot rule out the possibility that it belongs to a Rupelian representative of *Pseudaetobatus*. We therefore choose to be conservative and assign this tooth to cf. "*Aetobatus*". Recent molecular divergence estimates indicate that extant *Aetobatus* diverged from *Myliobatis* at some point during the early-to-middle Miocene (Villalobos-Segura & Underwood, 2020). This in turn suggests that the Paleogene teeth described herein do not belong to *Aetobatus*, but rather represent an undescribed ancestral taxon within the *Aetobatus* lineage. We therefore list "*Aetobatus*" in quotation marks to denote that future studies will likely place MSC 49753 within a different genus within the *Aetobatus* lineage. It should also be noted that extant *Aetobatus* has traditionally been placed within the family Myliobatidae (see Nelson *et al.*, 2016). However, a recent molecular study by White & Naylor (2016) suggested this genus should be placed within its own family, Aetobatidae, which is followed herein.

Order Myliobatiformes indet.

Referred specimens – n=2; MSC 50027 (Fig. 6.3), MSC 50029 (Fig. 6.2).

Description – Our sample consists of two caudal spines (i.e., stings) that differ slightly in overall gross morphology. MSC 50029 (Fig. 6.2) is a fragment of a large caudal spine with only its dorsal surface preserved. The specimen is very wide, measuring nearly 20 mm in greatest width. The enameloid-covered dorsal surface is weakly convex (Fig. 6.2C) and bears a series of at least eight irregularly spaced, parallel longitudinal ridges that are separated by narrow furrows, all extending the length of the preserved portion of the spine (Fig. 6.2A). A single row of minute recurved denticles of various sizes occur along the preserved portions of the lateral edges. The ventral face is ablated and cannot be adequately described (Fig. 6.2B).

Specimen MSC 50027 (Fig. 6.3) is a relatively complete spine measuring approximately 41 mm in preserved length and 6 mm in maximum width. The spine tapers distally and its dorsal surface is covered with shiny enameloid (Fig. 6.3A). The dorsal surface is convex (Fig. 6.3B) and bears a series of alternating ridges and furrows that extend the length of the spine (Fig. 6.3A). The lateral faces of the specimen have single rows of medially located denticles (Fig. 6.3B). These denticles are very closely spaced, very highly distally recurved, and decrease slightly in size near the distal end. The ventral face of the spine lacks enameloid but has a wide dentine ridge that extends medially across the length of the spine (Fig. 6.3C).

Discussion – The lateral denticles of specimen MSC 50027 decrease in size towards the proximal end, where they become obsolete, a feature indicating the specimen represents the proximal end of the spine, closer to where it was covered by connective tissue. Specimen MSC 50029 lacks its proximal and distal ends.

Very few studies have been conducted on the taxonomy of extant ray caudal spines, and therefore the taxonomic utility of these elements is at present unclear. Although Schwartz (2008, 2009) argued that certain ray spines could be identified based on the number of denticles present, complete spines are needed to make this determination. Hovestadt & Hovestadt-Euler (2013) observed that the number of denticles present differs through ontogeny, with older (longer) spines having more denticles than those of juveniles. Further complicating the matter is that several myliobatiform families, like Dasyatidae, Myliobatidae, and Urolophidae, include genera with spines, although not all of the members of this order are known to have them (Schwartz, 2008, 2009; Hovestadt & Hovestadt-Euler, 2013). Regarding those in our Red Bluff Clay sample, the two

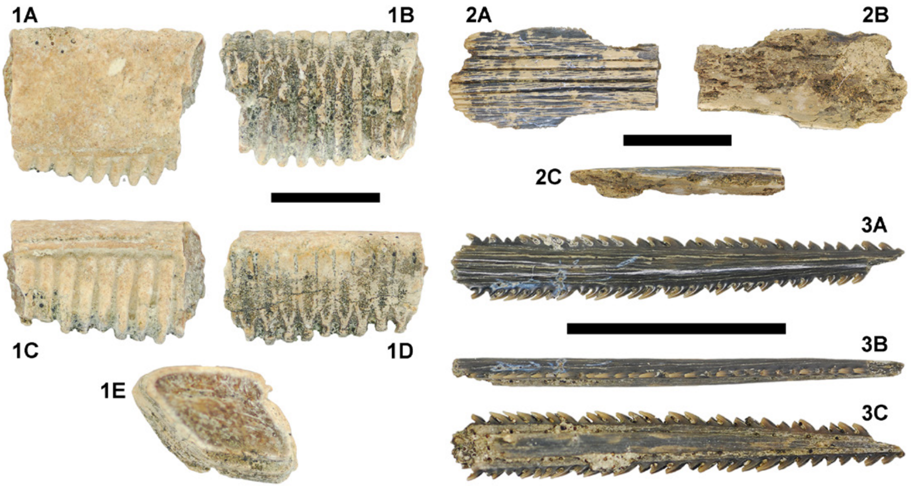

Figure 6. Myliobatiformes elements from the Rupelian Red Bluff Clay at site AMo-9. **1A–E.** MSC 49753, cf. "*Aetobatus*" sp. tooth in 1A. occlusal, 1B. basal, 1C. lingual, 1D. labial, and 1E. profile views. **2A–C.** MSC 50029, Myliobatiformes indet. caudal spine in 2A. dorsal, 2B. ventral, and 2C. right lateral views. **3A–C.** MSC 50027, Myliobatiformes indet. caudal spine in 3A. dorsal, 3B. left lateral view, 3C. ventral view. Scale bar for 1 = 5 mm. Scale bars for 2–3 = 2 cm.

spines are slightly different from each other, with MSC 50029 being over three-times wider than MSC 50027. Furthermore, MSC 50029 has a flat, rather than domed dorsal surface, and it has more than twice the number of dorsal ridges and furrows than MSC 50027. Although we cannot rule out that these morphological differences represent ontogeny within a single taxon, we also cannot rule out the possibility that two different myliobatiform taxa are represented. Due to our current lack of understanding regarding the ontogeny and taxonomic utility of ray caudal spines, these specimens are conservatively assigned to Myliobatiformes indet.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii (*sensu* Goodrich, 1930)
Unranked Neopterygii Regan, 1923
Infraclass Holostei Müller, 1845
Division Teleosteomorpha Arratia *et al.*, 2004
Subdivision Teleostei Müller, 1845
Supercohort Teleocephala de Pinna, 1996
Unranked Clupeocephala Patterson & Rosen, 1977
Cohort Eutelostei Rosen, 1985
Superorder Acanthopterygii Greenwood *et al.*, 1966
Series Percomorpha (*sensu* Nelson *et al.*, 2016)
Subseries Ovalentaria Smith & Near in Wainwright *et al.*, 2012
Order Istiophoriformes Betancur-R *et al.*, 2013
Family Sphyraenidae Rafinesque, 1815
Genus *Sphyraena* Artedi in Röse, 1793
***Sphyraena* sp.**

Referred specimens – n=5; MSC 49754 (Fig. 7.2), MSC 49760 (Fig. 7.1), MSC 50044, MSC 50045 (Fig. 7.3), MSC 50129 (Fig. 7.4).

Description – Two tooth morphologies are represented in our sample, including one with a sinuous profile (Fig. 7.1A). The teeth of this morphology measure between 1.5 and 1.7 cm in apicobasal height and 5 to 6 mm in anteroposterior width. In labial and lingual views, the teeth have a uniformly convex to sinuous anterior edge and a slightly concave to sinuous posterior edge. The anterior margin is formed into a sharp, finely serrated cutting edge that extends the height of the tooth, whereas the posterior margin lacks a cutting edge and is instead convex along its height. The labial crown face is relatively flat and the lingual face weakly convex (Fig. 7.1B), and both faces are ornamented with fine parallel striations that extend nearly to the apex. The teeth have a teardrop-shaped basal outline and shallow basal pulp cavity (Fig. 7.1C).

The second morphology consists of labiolingually thin teeth with a lanceolate labial and lingual outline and biconvex mesial and distal cutting edges (Fig. 7.3A). The labial crown face is relatively flat, whereas the lingual face is weakly convex (Fig. 7.3B) and combined with the sharp cutting edges give the teeth an amygdaliform basal outline (Fig. 7.3C). The cutting edges are smooth and extend to the base of the crown. In profile view, the tooth is widest basally and tapers evenly to the apex. The labial and lingual crown enameloid is smooth on specimen MSC 50045, but the enameloid on MSC 49759 (Fig. 7.3A) is ornamented with fine parallel striations that extend almost the entire height of the tooth before fading at the apex.

A partial right dentary was identified in our sample (MSC 50129, Fig. 7.4). Only the small section of the tooth row is preserved on this specimen, as the ventral, anterior, and posterior portions are missing. As preserved, this dentary fragment measures 4.7 cm in greatest length. In occlusal view, the dentary thickens anteriorly and has a slightly convex labial margin, and slightly concave lingual margin (Fig. 7.4A). The lingual face of the dentary is flat and featureless, whereas the labial face bears a conspicuous anteroposteriorly extending bony ridge (Fig. 7.4B). Four weathered teeth are preserved in the tooth row (Fig. 7.4B-C). These teeth have a lanceolate labial/lingual outline, equally convex labial and lingual faces, a slight lingual bend, and erupt from the dentary at a slight posterior angle. The teeth are tightly packed within the tooth row, and although the alveoli are closely spaced, they are separated from one another by a thin layer of bone.

Discussion – Of the two morphologies in our sample, specimens like those shown in Fig. 7.1 are symphyseal (i.e., laniary) teeth and palatine and/or dentary teeth are of the type shown in Fig. 7.3. Ballen (2021) noted that all species of extant *Sphyraena* have three pairs of symphyseal teeth, including one on the dentary and one each at the premaxillary anterior and premaxillary posterior, and these differ slightly in shape. Based on Ballen's (2021) observations, the robust nature and lack of labiolingual compression on tooth MSC 49754 (Fig. 7.2) indicates that it is likely a dentary symphyseal tooth. In contrast, tooth MSC 49760 (Fig. 7.1) is more gracile, more labiolingually compressed, and has a sigmoidal distal edge, indicating that it is likely an anterior premaxillary symphyseal tooth. Unfortunately, the other palatine and dentary teeth have a more conservative morphology and their location within the jaw cannot be accurately determined.

The Red Bluff Clay *Sphyraena* teeth were compared directly to those of three extant Gulf of Mexico taxa, including *S. barracuda* (Edwards in Catesby, 1771) (MSC 43215, SC2018.3.1), *S. borealis* DeKay, 1842 (MSC 43076), and *S. guachancho* Cuvier, 1829 (MSC 43076). Our examination revealed slight differences between the teeth of these extant taxa, with cutting edges on teeth of the larger *S. barracuda* being conspicuously serrated, whereas the teeth on the smaller *S. borealis and S. guachancho* have smooth carinae. Our Red Bluff Clay sample is small, and the sample of extant specimens was limited, and we cannot determine if the presence (i.e., MSC 49754 and MSC 49760) or absence (i.e., MSC 50044 and MSC 50045) of tooth serrations is taxonomically informative (i.e., two species are represented) or is instead a reflection of ontogeny, where the more mature (longer) fishes develop serrated teeth.

The partial dentary in our sample (MSC 50129) was compared to those of the same three extant *Sphyraena* taxa, as well as to those of extant *Scomberomorus cavalla* (Cuvier, 1829) (MSC 42721), a taxon with morphologically similar teeth. Of these taxa, specimen MSC 50129 compared most favorably to the dentaries of *Sphyraena borealis* and *S. guachancho* by having posteriorly angled teeth, whereas those in *S. barracuda* are more or less erect, and those in *S. cavalla* are angled anteriorly. Furthermore, the larger teeth in the dentary of *S. cavalla* are spaced further apart than they are on MSC 50129, and are separated from one another by smaller, and often unerupted, teeth. These smaller intermediate teeth are absent on MSC 50129, as well as on the three extant *Sphyraena* taxa examined.

In addition, specimen MSC 50129 exhibits a distinct bony ridge along the labial face of the dentary, a characteristic that is present on the dentaries of *Sphyraena borealis* and *S. guachancho*, whereas they are absent on those of *S. barracuda* and *Scomberomorus cavalla*. Finally, the alveoli on specimen MSC 50129 are separated from one another by a thin layer of bone, as seen on the three extant *Sphyraena* specimens examined, whereas the alveoli on *S. cavalla* dentaries generally lack a bony separation and often appear to combine with one another.

Ballen (2021) reviewed the fossil record of *Sphyraena* and listed 28 nominal taxa that are based on isolated teeth (15 taxa), partial dental elements (three taxa), otoliths (two taxa), or partial/nearly complete skeletons (nine taxa), with three of the latter lacking preserved teeth. Ballen (2021) also noted the inadequate descriptions and/or figures originally provided for many of the named species (particularly those named prior to 1960), indicating that fossil representatives of *Sphyraena* need revision. The Red Bluff *Sphyraena* specimens are herein not speciated due to the lack of adequate comparative descriptions for most of the named fossil species.

Family Xiphiidae Swainson, 1839

Genus *Xiphiorhynchus* van Beneden, 1871

Xiphiorhynchus kimblalocki Fierstine & Applegate, 1974

Referred specimen – MSC 49332 (Fig. 8.1).

Description – MSC 49332 is a nearly complete rostrum that measures approximately 180 mm in anteroposterior length and 25 mm in greatest mediolateral width. The dorsal, ventral, and lateral margins of the rostrum are straight, evenly tapered, and converge at an anterior point. The dorsal surface is convex, and the posterior half is ornamented with coarse parallel striations that transition into a fibrous texture anteriorly (Fig. 8.1C). The convex ventral face is covered with a dense patch of minute alveoli that extend onto the lateral edges of the rostrum and almost reach the anterior tip (Fig. 8.1A). The rostrum has an oval cross-section, and although ablated, five nutrient canals are visible, including central, left and right dorsolateral, and left and right ventrolateral (Fig. 8.1B).

Discussion – At least ten species of *Xiphiorhynchus* have been named in the literature, seven of which are known only by the holotype (Fierstine & Stringer, 2007). Of the 10 described taxa, specimen MSC 49332 most closely resembles that of *Xiphiorhynchus kimblalocki*, a species that was originally described from the Priabonian Yazoo Clay in Mississippi (Fierstine & Applegate, 1974), and additional specimens were later reported from the same unit in Louisiana (Fierstein & Stringer, 2007). Specimen MSC 49332 is herein assigned to *X. kimblalocki* because it has an oval cross-section, five internal nutrient canals (including the central, two dorsolateral, and two ventrolateral), and dorsal ornamentation grading from coarse longitudinal striations posteriorly to fibrous anteriorly (Fierstine & Stringer, 2007). This latter characteristic is known in only two taxa, *X. kimblaylocki* and *X. aegyptiacus* Weiler, 1929 (Fierstine & Starnes, 2005), the latter of which has a cross-section that is evenly convex dorsally and rather flat ventrally.

Xiphiorhynchus sp.

Referred specimen – MSC 49333 (Fig. 8.2).

Description – MSC 49333 is represented by the proximal one-third of a rostrum that is missing its anterior tip. It measures 6.8 cm in preserved anteroposterior length and 2.5 cm in mediolateral width. In dorsal or ventral views, the lateral margins are straight and taper anteriorly. The dorsal surface is convex and ornamented with fine striations on the posterior half that transition into a fibrous texture anteriorly. The ventral surface is flat and covered with a dense alveolar patch that extends onto the lateral edges of the rostrum (Fig. 8.2A). The dorsal surface has three shallow grooves that extend anteriorly approximately one-half the length of the preserved portion of the rostrum. One groove is located medially on the dorsal

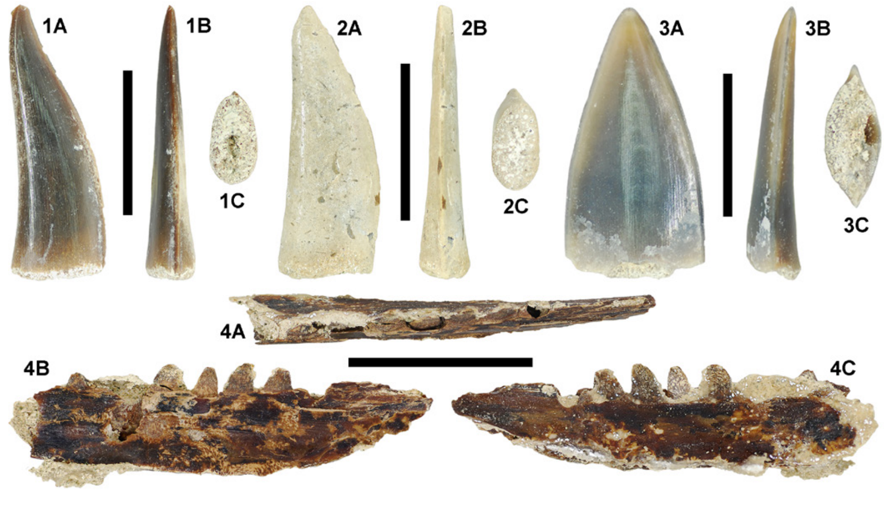

Figure 7. *Sphyraena* sp. elements from the Rupelian Red Bluff Clay at site AMo-9. **1A–C.** MSC 49760, premaxillary symphyseal tooth in 1A. profile, 1B. anterior, and 1C. basal views. **2A–C.** MSC 49754 dentary symphyseal tooth in 2A. profile, 2B. anterior, and 2C. basal views. **3A–C.** MSC 49759, dentary or palatine tooth in 3A. profile, 3B. anterior, and 3C. basal views. **4A–C.** MSC 50129, partial right dentary in 4A. occlusal, 4B. labial, and 4C. lingual views. Scale bars for 1-2 = 1 cm. Scale bar for 3 = 5 mm. Scale bar for 4 = 2 cm.

surface, whereas the other two grooves are located on the lateral edges of the dorsal surface, just above the alveolar patch (Fig. 8.2C). In cross-section, the rostrum is evenly convex dorsally and flat ventrally, and four nutrient canals are visible, including the central, left and right dorsolateral, and right ventrolateral (Fig. 8.2B).

Discussion – Although only partially preserved, MSC 49333 is morphologically similar to a specimen described by Fierstine & Stringer (2007; fig. 3) as *Xiphiorhynchus* sp. that was collected from the Priabonian Yazoo Clay in Louisiana. The dorsal ornamentation on specimen MSC 49333 consists of longitudinal striations that transition into a fibrous texture, a feature present on only two of the ten *Xiphiorhynchus* species recognized by Fierstine & Stringer (2007), including *X. kimblaylocki* and *X. aegyptiacus*. Specimen MSC 49333 has a relatively flat ventral surface but an evenly convex dorsal margin, making it morphology distinct from the biconvex cross section of *X. kimblaylocki* (and specimen MSC 49332) but comparable to *X. aegyptiacus* (Fierstine & Stringer, 2007). Although this feature would indicate that MSC 49333 is *X. aegyptiacus*, the Red Bluff specimen possesses a conspicuous central canal, a characteristic that is purportedly absent from the rostra of this taxon (Fierstine & Stringer, 2007). Specimen MSC 49333 is herein not speciated because of the morphological inconsistencies that we observed between this incomplete specimen and rostra of other species. Nevertheless, specimen MSC 49333 appears to be morphologically distinct from the *X. kimblaylocki* rostrum (MSC 49332) in our sample, indicating that there were two coeval species of *Xiphiorhynchus* inhabiting the Red Bluff Clay paleoenvironment in Alabama.

Order *Incertae sedis*

Family *Incertae sedis*

Genus *Cylindracanthus* Leidy, 1856

***Cylindracanthus ornatus* Leidy, 1856**

Referred specimen – MSC 50028 (Fig. 8.3).

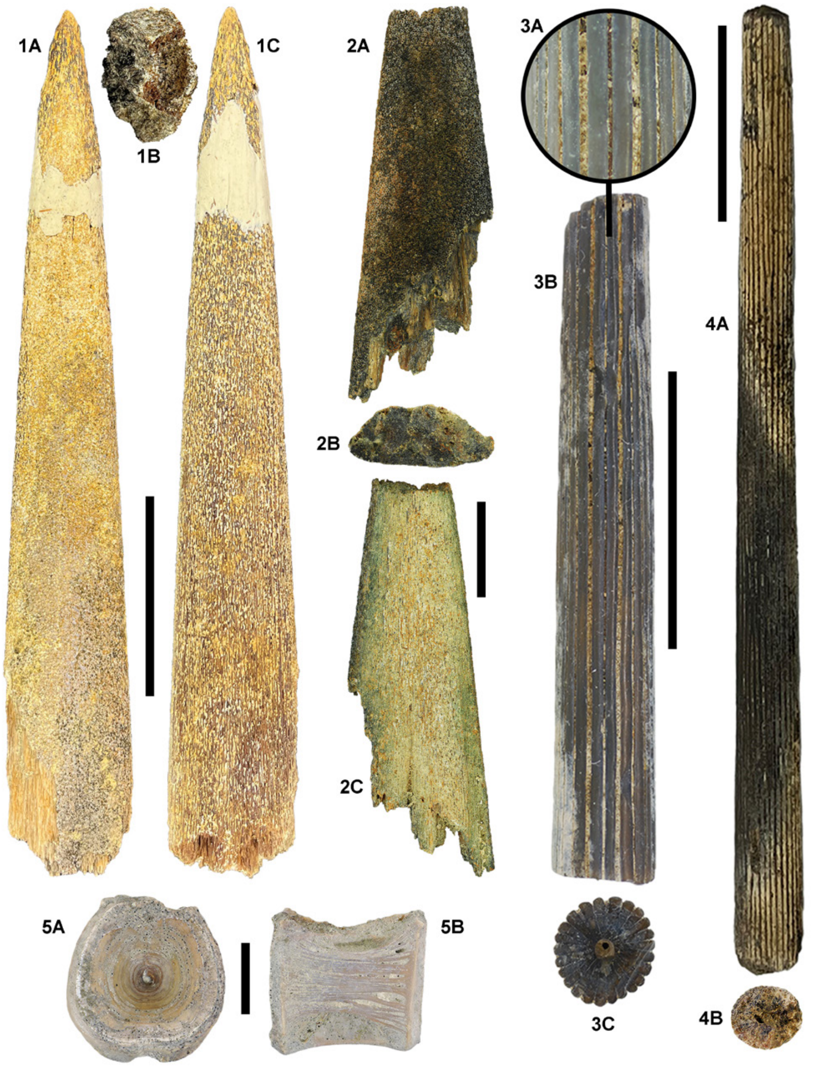

Figure 8. Teleostei elements from the Rupelian Red Bluff Clay at site AMo-9. **1A–C.** MSC 49332, *Xiphiorhynchus kimblalocki* rostrum in 1A. dorsal, 1B. basal, and 1C. ventral views. **2A–C.** MSC 49333, *Xiphiorhynchus* sp. rostrum in 2A. ventral, 2B. basal, and 2C. dorsal views. **3A–C.** MSC 50028, *Cylindracanthus ornatus* rostrum, 3A. Close-up of ventral tooth rows, 3B. ventral view, 3C. cross-section. **4A–B.** MSC 50031, *Cylindracanthus rectus* rostrum in 4A. dorsal view, 4B. cross-section. **5A–B.** MSC 50030, Teleostei indet. vertebra in 5A. articular, and 5B. lateral view. Scale bar for 1 = 5 cm. Scale bars for 3-5 = 2 cm. Scale bar for 5 = 1 cm.

Description – This taxon is represented by an incomplete rostrum. This rostral fragment is elongated, measuring 4.2 cm in preserved anteroposterior length. It is mediolaterally thin and measures 6 mm in greatest width, but the element gradually tapers anteriorly (Fig. 8.3B). The rostrum is cylindrical in cross-section, and a narrow internal canal is visible at the broken anterior end that appears to extend the length of the rostrum. The external surface is ornamented with a series of alternating ridges and furrows that extend the length of the element (Fig. 8.3B). The ridges and furrows are generally parallel, but they occasionally intersect and combine anteriorly. Two wide and parallel furrows occur on the ventral surface, each containing a row of acrodont tooth bases (Fig. 8.3A).

Discussion – Three species of *Cylindracanthus* have been reported in Alabama, including *C. acus* Cope, 1870, *C. ornatus* Leidy, 1856, and *C. rectus* (Agassiz, 1843) (Leriche, 1942; Thurmond & Jones, 1981; Parris *et al.*, 2001; and Ebersole *et al.*, 2019). However, Ebersole *et al.* (2019) concluded that *C. acus* was a junior synonym of *C. rectus*, with the former representing a juvenile morphology of the latter. Although Thurmond & Jones (1981) expressed their opinion that *C. ornatus* and *C. rectus* were conspecific, Parris *et al.* (2001) and Ebersole *et al.* (2019) were able to differentiate the two taxa by the presence (*C. ornatus*) or absence (*C. rectus*) of two rows of acrodont teeth on the ventral surface.

Cylindracanthus ornatus appears to have had a long stratigraphic range in the region, as Parris *et al.* (2001) described a nearly complete specimen from the upper Campanian (Cretaceous) Demopolis Chalk in Alabama. Unpublished specimens in the MSC collection demonstrate that this taxon occurs in the Santonian (Cretaceous) Mooreville Chalk in Alabama, and Ebersole *et al.* (2019) confirmed this taxon within the Lutetian (middle Eocene) Lisbon Formation in the state. Although Leriche (1942) reported a *C. rectus* specimen from the Priabonian (upper Eocene) Cocoa Sand Member of the Yazoo Clay in Choctaw County, Alabama, the specimen he figured (pl. 4, fig. 3) clearly shows two rows of acrodont teeth, leading us to refer the specimen to *C. ornatus*.

The higher taxonomic affinities of *Cylindracanthus* remain unclear. Although studies have viewed *Cylindracanthus* as belonging to an unknown family within the Acipseriformes (see Thurmond & Jones, 1981; Parris *et al.*, 2001; Ebersole *et al.*, 2019), histological work by Grandstaff *et al.* (2017) revealed that *Cylindracanthus* rostra are very different from those of extant billfish, paddlefish, and sturgeons. The histological work also showed that the rostrum of *Cylindracanthus* is comprised of acellular bone, indicating that this fish was a derived teleost (Meunier & Huysseune, 1992; Grandstaff *et al.*, 2017). We herein view *Cylindracanthus* as belonging to an unknown order and family within the Teleostei.

***Cylindracanthus rectus* (Agassiz, 1843)**

Referred specimens – n=2; MSC 50031 (Fig. 8.4), MSC 50127.

Description – Our sample consists of two incomplete rostra that measure 9.6 cm (MSC 50031) and 7.3 cm (MSC 50127) in anteroposterior length. The morphology of these specimens is comparable to that of *C. ornatus* rostra, but they lack rows of acrodont teeth on their ventral surfaces.

Discussion – Ebersole *et al.* (2019) reported the oldest stratigraphic occurrences of *C. rectus* in Alabama as within the middle Eocene Lisbon Formation (Lutetian) and Gosport Sand (Bartonian). Unpublished specimens in the MSC collection show that this taxon to also occurs within the Eocene (Bartonian) Moodys Branch Formation, Priabonian Yazoo Clay, and Oligocene (Rupelian) Marianna Limestone (which overlies the Red Bluff Clay). These records demonstrate that the temporal ranges of *C. ornatus* and *C. rectus* overlapped during the middle Eocene through early Oligocene in Alabama. Only *C. ornatus* is known to occur in Upper Cretaceous deposits in the state (Thurmond & Jones, 1981; Parris *et al.*, 2001; Ebersole *et al.*, 2019), but the Red Bluff Clay fossils demonstrate that both species persisted across the Eocene/Oligocene boundary.

Teleostei indet.

Referred specimens – n=3; MSC 50030 (Fig. 8.5), MSC 50128 (2 specimens).

Description – Our sample consists of three vertebrae of similar morphology, the most complete of which is described herein. This vertebra measures approximately 2.5 cm in both apicobasal height and greatest anterior diameter. The anterior and posterior margins are nearly circular, but a conspicuous medial indention occurs at the ventral margin (Fig. 8.5A). The anterior and posterior faces are strongly concave, have a deep canal passage, and numerous very closely spaced concentric annulae are visible. The neural and hemal spines are not preserved on this specimen, but their broken points of articulation are preserved. In profile the dorsal and ventral margins of the centrum are concave, and the lateral surfaces bear a series of alternating furrows and thick striated ridges (Fig. 8.5B). The dorsal part of the centrum is denoted by a single wide and oval concavity, whereas three such concavities are present on the ventral surface that are separated by robust striated ridges.

Discussion – Vertebrae with biconvex edges represent a common morphology within teleost fishes, and their taxonomic utility is therefore limited. For these reasons, the specimens in our sample are herein assigned to Teleostei indet.

DISCUSSION

The fish sample derived from the Red Bluff Clay of site AMo-9 represents a small but relatively diverse assemblage of lower Rupelian fishes. Identified herein are five orders, 11 families, and 15 unequivocal taxa of fishes, with *Cylindracanthus* potentially belonging to an additional (presently undetermined) order and family. The taxa we identified include *Eostegostoma* sp., *Otodus* (*Carcharocles*) sp., Mitsukurinidae/Carchariidae indet., *Macrorhizodus praecursor*, *Galeorhinus* sp., *Negaprion gilmorei*, *Physogaleus* sp., "*Sphyrna*" sp., *Galeocerdo* sp., cf. "*Aetobatus*" sp., *Sphyraena* sp., *Xiphiorhynchus kimblalocki*, *Xiphiorhynchus* sp., *Cylindracanthus ornatus*, and *C. rectus*. The fossils are the first non-otolith vertebrates to be described from the Red Bluff Clay, and all of the taxa represent first published occurrences for these fishes within this lithostratigraphic unit.

From the evidence at hand, it is our belief that the remains that comprise this fauna have not been reworked and did not originate from a subjacent lithostratigraphic unit. The majority of the specimens are exceptionally preserved and show little post mortem wear, and no sedimentary units aside from the Red Bluff Clay are exposed at the main collecting area at site AMo-9 or at the adjacent gullies from which specimens MSC 49332 and MSC 49333 were derived. In addition, only seven of the 15 taxa (i.e., cf. "*Aetobatus*" sp., *C. ornatus*, *C. rectus*, *M. praecursor*, *N. gilmorei*, *X. kimblaylocki,* and *Xiphiorhynchus* sp.) are known from upper Eocene deposits in this region, whereas the remaining taxa appear unique to Oligocene strata in Alabama and Mississippi (JAE, unpublished data).

The *Eostegostoma* sp. specimen (MSC 50032) described herein represents the first confirmed occurrence of this genus within the Gulf Coastal Plain of North America. Although this genus currently contains only a single species, *E. angustum* (Nolf & Taverne in Herman, 1977), additional specimens are needed to determine if MSC 50032 belongs to this taxon or a heretofore unrecognized species. Nevertheless, this tooth represents the first Oligocene occurrence of *Eostegostoma*, extending its known stratigraphic range from the Bartonian Stage of the middle Eocene into the lower Rupelian (Cappetta, 2012).

A single *Otodus* (*Carcharocles*) sp. tooth (MSC 49756) was identified in our sample. Ebersole *et al.* (2019) confirmed similar *Otodus* (*Carcharocles*) sp. teeth from various middle Eocene units in Alabama, and unpublished specimens in the MSC collection confirm that teeth with a similar morphology also occur within the Marianna Limestone of Alabama, a Rupelian unit that directly overlies the Red Bluff Clay. Interestingly, the MSC collection includes a single *Otodus* tooth (MSC 49567) that was derived from the upper Rupelian Chickasawhay Limestone in Washington County, AL. This tooth has a wide and triangular main cusp and serrated cutting edges like the *Otodus* (*Carcharocles*) sp. tooth described herein, but it also has continuous mesial and distal cutting edges and diminutive lateral cusplets that are offset only by conspicuous indentions along the cutting edges near the crown base. The Chickasawhay Limestone specimen appears to represent an early stratigraphic occurrence of *Otodus* (*Megaselachus*) *chubutensis*, suggesting that the loss of lateral cusplets (i.e., the transition from *Otodus* (*Carcharocles*) to *Otodus* (*Megaselachus*)) may have occurred earlier than the Miocene as other studies have suggested (i.e., Cappetta, 2012; Carrillo-Briceño *et al.*, 2019; Perez *et al.*, 2019; Carrillo-Briceño *et al.*, 2020). Additionally, Ebersole *et al.* (2019) were able to demonstrate that the acquisition of cutting edges within the *Otodus* lineage (i.e., the transition from *Otodus* (*Otodus*) to *Otodus* (*Carcharocles*)) occurred within the Lutetian Stage of the middle Eocene (Zone NP14). The culmination of this data suggests that additional *Otodus* samples from the Red Bluff Clay and underlying and overlying units will not only help elucidate the taxonomy of *Otodus* (*Carcharocles*) teeth within the Gulf Coastal Plain, but also provide precise stratigraphic intervals regarding the morphological transition of these teeth from *Otodus* (*Otodus*) to *Otodus* (*Carcharocles*) to *Otodus* (*Megaselachus*).

A partial tooth in the Red Bluff Clay sample (MSC 49758) appears to belong to a representative of the Mitsukurinidae or Carchariidae. This tooth is not well enough preserved to be assigned to a genus, but the morphology of the main cusp and the lingual ornamentation indicates that it belongs to either *Anomotodon, Mitsukurina*, *Striatolamia*, or *Woellsteinia*. Although additional specimens are needed to determine the generic and specific placement of MSC 49758, this tooth is still significant because it would represent the first occurrence of *Mitsukurina* or *Woellsteinia* within the Gulf Coastal Plain, the first Oligocene occurrence of *Anomotodon* in the region (see Ebersole *et al.*, 2019), or a range extension for *Striatolamia* from the Eocene into the Rupelian (see Cappetta, 2012).

A total of 26 *Macrorhizodus praecursor* teeth were identified in our sample. Ebersole *et al.* (2019) reported the oldest stratigraphic occurrence of this taxon in Alabama within the lower-to-middle Eocene Tallahatta Formation, and unpublished specimens in the MSC collection indicate it persisted into the Marianna Limestone, a Rupelian unit that directly overlies the Red Bluff Clay in the Gulf Coastal Plain. These specimens indicate that *M. praecursor* was one of the few galeomorph species to persist across the Eocene/Oligocene boundary in this region.

A single *Galeorhinus* tooth was identified in our Red Bluff Clay sample (MSC 50033). This tooth could not be speciated, but several *Galeorhinus* species have been confirmed from Eocene deposits in Alabama (see Cappetta & Case, 2016; Ebersole *et al.*, 2019). It is possible that MSC 50033 represents an Oligocene representative of one those Eocene species, but additional specimens are needed to make this determination. Nevertheless, MSC 50033 represents the first occurrence of *Galeorhinus* within the Oligocene of the Gulf Coastal Plain. Although one extant species, *Galeorhinus galeus*, is known from North American waters, the genus has not been reported in the Gulf of Mexico (Parsons, 2006; Castro, 2011).

Six teeth assigned to *Negaprion gilmorei* have been identified in our Red Bluff Clay sample. Ebersole *et al.* (2019) reported the earliest stratigraphic occurrence of this species in Alabama within the Ypresian/Lutetian Tallahatta Formation, and Ebersole *et al.* (2021) confirmed this species within the Rupelian Glendon Limestone Member of the Byram Formation, a unit that overlies the Red Bluff Clay. Unpublished specimens in the MSC collection confirm this species also occurs in the overlying upper Rupelian Chickasawhay Limestone. Along with *M. praecursor*, *N. gilmorei* is one of the few galeomorph species known to occur in both Eocene and Oligocene strata in Alabama. A second species, *Negaprion brevirostris* (Poey, 1868), has been confirmed from Pliocene deposits in Alabama (Ebersole *et al.*, 2017, 2024), and this extant species still resides in the Gulf of Mexico today (Parsons, 2006).

Four teeth in our Red Bluff Clay sample belong to an undetermined species of *Physogaleus*. Ebersole *et al.* (2019) described two species of *Physogaleus*, *P. alabamensis* (Leriche, 1942) and *P. secundus* (Winkler, 1874), from middle Eocene deposits in Alabama, and Ebersole *et al.* (2021) confirmed this genus within the overlying Rupelian Glendon Limestone Member of the Byram Formation in the state. Additional specimens are needed to determine the affinities of the Oligocene occurrences of *Physogaleus* in this region.

A single tooth in our sample (MSC 50034) is referred to "*Sphyrna*" sp. Leriche (1942) erected the taxon *Sphyrna gilmorei* based on two teeth collected from the Priabonian Yazoo Clay in Alabama, and later, Cappetta & Case (2016) referred several Lutetian teeth to *Sphyrna* sp. that were collected from Covington County, Alabama. However, based on a sample of several thousand teeth, Ebersole *et al.* (2019) were able to determine that both of these reported occurrences instead belong to *Negaprion gilmorei*. Ebersole *et al.* (2024) confirmed a single tooth of the extant *Sphyrna mokarran* within Pliocene deposits in Alabama, and three species, including *S.*

tiburo (Linnaeus, 1758), *S. mokarran*, and *S. lewini* (Griffith & Smith, 1834), have an extant range in the Gulf of Mexico (Hoese & Moore, 1998; Parsons, 2006). Specimen MSC 50034 represents the stratigraphically earliest confirmed occurrence of a sphyrnid tooth within the Gulf Coastal Plain of North America and indicates the possible arrival of this family to this region during the Rupelian.

We referred two teeth in our sample (MSC 49763, MSC 50043) to *Galeocerdo* sp. Multiple nominal species of fossil *Galeocerdo* have been reported in Alabama. For example, Tuomey (1858) listed the occurrence of *G. aduncus* Agassiz, 1843 as occurring in "Tertiary" deposits in the state. However, the reported specimen was destroyed by fire near the end of the Civil War (Ebersole & Dean, 2013), so its identity could not be confirmed. Later, Woodward (1889) reported this same species within Eocene deposits in Clarke County, Alabama, but White (1956) later referred several of Woodward's teeth to *G. clarkensis*. Although the identity of the other teeth mentioned by Woodward (1889) remains a mystery, the occurrence of *G. aduncus* elsewhere is generally restricted to the Miocene (see Cappetta, 2012). Woodward (1889) also reported the occurrence of *Galeocerdo contortus* Gibbes, 1849 teeth within Eocene deposits in Clarke County, Alabama, but this species was subsequently referred to the genus *Physogaleus* by Ward & Bonavia (2001). In the same work, Woodward (1889) reported teeth from Eocene deposits in Alabama that he referred to "*Galeocerdo*(?) *minor*." White (1956) reexamined these specimens and assigned them to "?*Physodon secundus*," a taxon that is now recognized as *Physogaleus secundus* (see Cappetta, 1980).

There are several reports of *Galeocerdo latidens* from Alabama, including Tuomey (1858), Westgate (2001), Feldmann & Portell (2007), Clayton *et al.* (2013), and Cappetta & Case (2016). Unfortunately, the specimen reported by Tuomey (1858) was among those destroyed by fire during the Civil War (Ebersole & Dean, 2013). Westgate (2001) reported 13 *G. latidens* teeth from Bartonian deposits in Clarke County but did not figure the specimens. Feldmann & Portell (2007), Clayton *et al.* (2013), and Cappetta & Case (2016) all reported *G. latidens* teeth from the contact of the middle Eocene Tallahatta and Lisbon formations in Covington County. Unfortunately, Feldmann & Portell (2007) also did not figure their specimens, and those reported by Clayton *et al.* (2013) and Cappetta & Case (2016) were reassigned by Ebersole *et al.* (2019) to *Physogaleus*. Ebersole *et al.* (2019) also concluded that *Galeocerdo latidens* should be considered as a *nomen dubium* because the type specimens were published without stratigraphic or locality data (see Agassiz, 1843). Ebersole et al. (2019) considered the *G. latidens* morphology as synonymous with *G. eaglesomei* (White, 1955) (also see Türtsher *et al.*, 2021) and one that would be a considered a junior synonym of this latter taxon if it were valid. Maisch *et al.* (2014) and Ebersole *et al.* (2019) later confirmed the occurrence of *G. eaglesomei* from Lutetian and Bartonian deposits in Alabama, and Ebersole *et al.* (2017, 2024) identified fossil teeth belonging to the extant *Galeocerdo cuvier* (Péron & Lesueur in Lesueur, 1822) from Pliocene deposits in the state. This latter species still occurs in the Gulf of Mexico today (Parsons, 2006).

Although the two Red Bluff Clay teeth in our sample both have compound serrations, they are relatively small, have an evenly convex mesial cutting edge with rather small primary serrations, thus differentiating them from *G. mayumbensis* Dartevelle & Casier, 1943. Although the Red Bluff Clay teeth are not speciated, it is possible they belong to an Oligocene representative of *G. clarkensis*, in turn representing a slight stratigraphic range extension for this species from the Priabonian to the lower Rupelian. Alternatively, if the collection of additional specimens show that the slight morphological differences observed on these teeth sufficiently differentiate them from *G. clarkensis*, it is possible these teeth represent a transitional taxon that occurs between the middle-to-late Eocene *G. clarkensis* and the upper Oligo-Miocene *G. aduncus*. Nevertheless, the Red Bluff Clay specimens represent the first Oligocene records of *Galeocerdo* in Alabama.

Our Red Bluff Clay sample includes a batoid tooth (MSC 49753) and two caudal spines (i.e., stings), the latter of which are referred to Myliobatiformes indet. The gross morphology of the tooth allows placement within the Aetobatidae, and this tooth likely belongs to a heretofore unknown genus within the extant *Aetobatus* lineage. Specimen MSC 49753 represents the first Oligocene occurrence of a member of the Aetobatidae within the Gulf Coastal Plain, although Ebersole *et al.* (2017) reported an unspeciated *Aetobatus* tooth from Pliocene deposits in the Alabama. One member of this family, *Aetobatus narinari* (Euphrasen, 1790), is known to have an extant range in the Gulf of Mexico (Parsons, 2006).

Four *Sphyraena* teeth (MSC 49754, MSC 49760, MSC 50044, MSC 50045) and one dentary fragment (MSC 50129) were identified in our sample. Although there are many ambiguities concerning the taxonomy of fossil *Sphyraena* species (see Ballen, 2021), the occurrence of serrated and unserrated teeth in our sample suggests that at least two distinct taxa are present within the Red Bluff Clay. Multiple authors have reported *Sphyraena* teeth from Eocene deposits in Alabama (see Woodward, 1889; White, 1956; Thurmond & Jones, 1981; Clayton *et al.*, 2013; Maisch *et al.*, 2016), and Ebersole *et al.* (2019) reported this taxon from the overlying Rupelian Glendon Limestone Member of the Byram Formation. Additional unpublished specimens in the MSC collection show the first occurrence of this taxon in Alabama within the Ypresian Hatchetigbee Formation, and additional specimens demonstrate that it occurs within the Priabonian Yazoo Clay and Rupelian Marianna Limestone and Chickasawhay Limestone. Ebersole *et al.* (2024) reported additional *Sphyraena* specimens from Pliocene deposits in Alabama, but it is unclear whether these latter teeth represent the same species as those occurring in Paleogene deposits in the state, or the more likely scenario that they represent fossil occurrences of one of the four taxa inhabiting the present-day Gulf of Mexico (i.e., *S. barracuda*, *S. borealis*, *S. guachancho*, and *S. picudilla*; Hoese & Moore, 1998).

We identified two distinct species of *Xiphiorhynchus* within our Red Bluff Clay sample, including *X. kimblaylocki*, and a morphologically distinct but unidentified species herein referred to *Xiphiorhynchus* sp. The *X. kimblaylocki* rostrum in our sample (MSC 49332) represents a slight range extension for this species from the Priabonian into the lower Rupelian. The second specimen, MSC 49333, is morphologically similar to the Eocene *X. aegyptiacus* (see Fierstein & Stringer, 2007), but slight morphological differences between the rostra of these taxa indicate that MSC 49333 likely belongs to an unrecognized species. Nevertheless, our sample shows that two morphologically distinct, coeval species were present within the Rupelian of Alabama, and both represent new records for the state.

Lastly, two species of *Cylindracanthus*, *C. ornatus* and *C. rectus*, have been identified within our Red Bluff Clay sample. Specimen MSC 50028 represents the first occurrence of *C.*

ornatus within the Oligocene of the Gulf Coastal Plain of the USA, although this species has been reported from various Upper Cretaceous (Parris *et al.*, 2001; Ikejiri *et al.*, 2013) and Eocene (Woodward, 1889; Ebersole *et al.*, 2019) deposits in Alabama. With the confirmation of *C. ornatus* within the Red Bluff Clay in Alabama, the stratigraphic range of this species is extended in the region from the Upper Cretaceous into the Rupelian. Ebersole *et al.* (2019) reported the oldest stratigraphic occurrences of *C. rectus* in Alabama as occurring within the middle Eocene Lisbon Formation (Lutetian) and Gosport Sand (Bartonian). Unpublished specimens in the MSC collection show this taxon also occurs within the Eocene (Bartonian) Moodys Branch Formation, Priabonian Yazoo Clay, and Oligocene (Rupelian) Marianna Limestone, the latter of which overlies the Red Bluff Clay. These records indicate that the stratigraphic ranges of *C. ornatus* and *C. rectus* overlapped from the middle Eocene to early Oligocene in Alabama. Only *C. ornatus* is known to occur in Upper Cretaceous deposits in the state (Thurmond & Jones, 1981; Parris *et al.*, 2001; Ebersole *et al.*, 2019).

CONCLUSIONS

The 15 unequivocal fish taxa identified from the Red Bluff Clay at site AMo-9 in Alabama provides a small glimpse into the diversity of fossil fishes across the Eocene/Oligocene boundary in the Gulf Coastal Plain of North America. Several of the identified taxa, like *Macrorhizodus praecursor*, *Negaprion gilmorei*, *Cylindracanthus rectus*, and *C. ornatus* have been confirmed within middle Eocene deposits in Alabama (see Ebersole *et al.*, 2019), and their occurrence in the Red Bluff Clay (and in some cases, within overlying strata) indicate these species persisted into at least the early Oligocene. Although other identified taxa like *Xiphiorhynchus* spp. represent first occurrences for the state, the confirmation of these taxa within Priabonian deposits in Louisiana and Mississippi (Fierstine & Starnes, 2005; Fierstine & Stringer, 2007) indicate an earlier arrival for these fishes to this region than is indicated by the Red Bluff Clay sample. The confirmation of an *Eostegostoma* sp. tooth in our sample is significant because it represents the first occurrence of this taxon within the Gulf Coastal Plain of North America, and it is also the first Oligocene occurrence of this taxon from anywhere in the world. The absence of this taxon from any Eocene strata in the Gulf Coastal Plain could be the result of a collecting bias but may also suggest an early Oligocene arrival to this region, and perhaps indicates this area served as a final refuge for this shark before its extinction. The identification of a tooth assigned to "*Sphyrna*" sp., combined with the absence of unequivocal sphyrnid teeth from any stratigraphically older deposits in the region, suggests an early Oligocene arrival for this family within the Gulf Coastal Plain. Finally, the occurrence of taxonomically ambiguous taxa like cf. "*Aetobatus*" sp., *Galeocerdo* sp., *Galeorhinus* sp., Mitsukurinidae/Carchariidae indet., *Otodus* (*Carcharocles*) sp., and *Physogaleus* sp. is related to the small (and often incompletely preserved) sample size that did not allow us to accurately determine the taxonomy of these taxa. Alternatively, our inability to further identify these remains suggests that one or more of these taxa represent transitional forms between their Eocene and upper Oligocene counterparts.

Overall, this preliminary study of the fishes from the Red Bluff Clay provides us with our first view of the lowermost Rupelian non-otolith based fishes in the Gulf Coastal Plain of North America. Future collection of additional specimens from the various exposed Red Bluff Clay beds at the AMo-9 locality will undoubtedly increase the number of confirmed taxa within this unit and hopefully will also clarify the taxonomy of many of these fishes. In addition, systematic studies of the fishes with the units that underlie (i.e., the Priabonian Yazoo Clay and its various members) and overlie (the Rupelian Marianna Limestone) the Red Bluff Clay have yet to be undertaken. Only with the completion of these studies will we gain a better understanding of the faunal changes that occurred amongst the various fishes across the Eocene/Oligocene boundary in the Gulf Coastal Plain region.

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