# CHONDRICHTHYANS FROM THE TALLAHATTA-LISBON FORMATION CONTACT (MIDDLE EOCENE), SILAS, CHOCTAW COUNTY, ALABAMA

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#### ABSTRACT

In Silas, Alabama, a disconformity with an overlaying lag deposit separates the middle Eocene (Lutetian) Tallahatta and Lisbon Formations along Turkey Creek. This lag deposit consists of blankets and lenses of macrofossil residuum that preserves an unreported assemblage of chondrichthyans represented by at least 13 species. This chondrichthyan assemblage is similar to other contemporaneous nearshore faunas found across North America and elsewhere globally and includes: *Striatolamia acrota* Agassiz, 1843; *Brachycarcharias lerichei* Casier, 1946; *Carcharodon auriculatus* Blainville, 1818; *Otodus obliquus* Agassiz, 1843; *Abdounia recticona* (Winkler, 1873); *Abdounia enniskilleni* (White, 1956); *Galeocerdo eaglesomei* (White, 1955); *Physogaleus secundus* (Winkler, 1874); *Scyliorhinus* sp.; *Rhizoprionodon* sp.; *Pristis* sp.; cf. *Aetomylaeus* sp.; and *Rhinoptera* sp. Additional macrofossils with nearshore affinities occurring in the Turkey Creek lag include bones and teeth from fish, reptiles, and marine mammals as well as mollusc shells. The accumulation and concentration of macrofossils in the Turkey Creek lag are the result of third order eustatic sea level fluctuation prior to late Eocene climatic cooling and global sea level regression associated with the formation of the continental ice sheet on Antarctica. The Turkey Creek assemblage

## INTRODUCTION

For over one hundred and fifty years, numerous published reports indicate that the Alabama Coastal Plain Province preserves an abundant and diverse record of fossil chondrichthyans (Morton, 1834; Tuomey, 1858; Leriche, 1942; White, 1956; Thurmond and Jones, 1981; Westgate, 2001). The majority of this record is derived from rivers and associated creeks in the Alabama Coastal Plain such as the Tombigbee, Black Warrior and Conecuh that erode through nearshore, unconsolidated sediments and provide outcrop exposures. In Alabama, lag deposits that drape contacts between glauconitic clay and arenaceous clay sediments occasionally contain chondrichthyan assemblages (Clayton et al., 2013). Such lag deposits reflect third-order sea level events where fossil accumulations are time-averaged and reflect a few million years of diversity (Case and Schwimmer, 1988; Eaton et al., 1989; Ward and Wiest, 1990; Manning and Dockery, 1992; Rogers and Kidwell, 2000; Burris, 2001; Becker et al., 2006).

Chondrichthyan assemblages from the Alabama Coastal Plain are also noteworthy because sediments range from the late Cretaceous to the Miocene and record evolutionary changes in chondrichthyans that traverse the Cretaceous-Paleogene and Eocene-Oligocene global extinction events (Manning, 2003; Raymond et al., 1988). In general, Alabama Coastal Plain chondrichthyan assemblages carcharhiniforms diversified while lamniforms were significantly reduced as earth's climate transitioned from greenhouse to ice house conditions during the early and middle Cenozoic. This report describes a previously unreported chondrichthyan assemblage from the middle Eocene (Lutetian), Tallahatta-Lisbon Formation contact in Silas, Alabama along Turkey Creek. The Turkey Creek assemblage is dominated by nearshore chondrichthyans concentrated into a lag deposit reflecting a third order sea level fluctuation

event. The Turkey Creek chondrichthyan assemblage is similar to other contemporaneous chondrichthyan assemblages occurring in the Atlantic and Gulf Coastal Plains. Comparison of these regional assemblages provides an opportunity to assess general trends in chondrichthyan evolution leading up to the Eocene–Oligocene mass-extinction event.

**Institutional Abbreviations**—ANSP, Academy of Natural Sciences, Philadelphia.

#### GEOLOGY OF TURKEY CREEK, CHOCTAW COUNTY, SOUTHWESTERN ALABAMA

Alabama's Cenozoic formations crop out in a belt running east-west through the southern portion of the state (Fig. 1). This outcrop belt curves northward along the state's southwestern border and reflects marine inundation of topographically low lying areas in the Mississippi River Valley Region during the Late Cretaceous and Cenozoic (Toulmin and La Moreaux, 1963; Ivany, 1998; Manning, 2003; Savrda et al., 2005; 2010). Eocene sediments in Alabama are represented by the upper Wilcox, Claiborne and Jackson Groups. These groups are divided from oldest to youngest into the Hatchetigbee, Tallahatta and Lisbon, Yazoo Clay, Crystal River and Moody's Branch Formations as well as numerous members, units and beds. Additional details of state-wide, Alabama Coastal Plain Eocene sedimentology, sequence stratigraphy, and regional correlation with neighboring states are available in Bybell and Gibson, (1985); Szabo et al. (1988); Raymond et al. (1988), Manicini and Tew (1994), and Ivany (1998).

Choctaw County, Alabama is located within the southwestern-most Eocene outcrop belt in the state, and is dissected by numerous creeks that flow to the east into the Tombigbee River. The locality described in this report occurs along Turkey Creek, in Silas, Alabama west of County Road 17. Along this section of Turkey Creek, downcutting and headward erosion has exposed outcrops of the upper Tallahatta and lower Lisbon Formations. These two formations are separated along Turkey Creek by a prominent disconformity exposed along the southern bank and near creek level. In the study area, the upper Tallahatta Formation consists primarily of greenish-gray, siliceous, sandy claystone while the lower part of the Lisbon Formation consists of glauconitic, coarse sands with interbedded, silty and glauconitic claystone. The upper Tallahatta Formation achieves a maximum thickness along this section of Turkey Creek of approximately two meters. The maximum thickness of the lower part of the Lisbon Formation along Turkey Creek is about 20 meters however, the thickness of this unit is highly variable due to extensive physical erosion by numerous smaller tributaries. The two formations are separated by a discontinuous, basal lag deposit that consists of blankets and lenses of macrofossil residuum. The macrofossil lag contains original shell material and steinkerns belonging to oysters, pelecypods, and gastropods in addition to bones and teeth from chondrichthyans, fish, reptiles, and marine mammals. Maximum thickness of the Turkey Creek lag is approximately 10-20 centimeters. The contact between the Tallahatta and Lisbon Formation as studied by Mancini and Tew (1994) in Alabama and Mississippi occurs at the sequence boundary between TAGC 3.1 and TAGC 3.2 sea level cycles (Haq et al., 1988; Clayton et al., 2013). We interpret the prominent disconformity between the upper Tallahatta and lower part of the Lisbon Formation, as well as the chondrichthyan lag, along Turkey Creek to represent the boundary between these two sea level cycles as seen in outcrop.

Multiple sources including: planktonic foraminifera (Bandy, 1949); mollusks (Toulmin, 1977); calcareous nannofossil zonation (Siesser, 1983); core hole data (Bybell and Gibson, 1985); geologic mapping (Szabo et al., 1988), and sequence stratigraphy (Mancini and Tew, 1994; Ivany, 1998) indicated that the age of the upper Tallahatta and lower part of the Lisbon Formations belongs to the lower part of the middle Eocene and Lutetian Stage Boundary. This is also consistent with the known ages and stratigraphic occurrences of chondrichthyans recovered from the Turkey Creek field locality and described in this report. The Gosport Sand, which in southwestern Alabama is also known to contain macrofossils including chondrichthyan teeth, occurs in the uppermost Lisbon Formation and has been documented as Bartonian in age by Thurmond and Jones (1981), Mancini and Tew (1994), CoBabe and Allmon (1994), and other sources cited above. Outcrop exposures of the Gosport Sand were not identified along the westernmost extension of Turkey Creek during this study.

#### FIELD AND LABORATORY METHODS

Chondrichthyan fossils described in this report were recovered over three field seasons directly from the lag that separates the upper Tallahatta and lower part of the Lisbon Formations along Turkey Creek. Areas in Turkey Creek, immediately adjacent to the Tallahatta–Lisbon Formation contact, were also collected and represent accumulations of chondrichthyan fossils eroded directly out of the lag and hydrodynamically concentrated nearby in deeper pools. Outcrop sediment and creek accumulations were sieved on site with screens ranging from 10.0-5.0 mm.

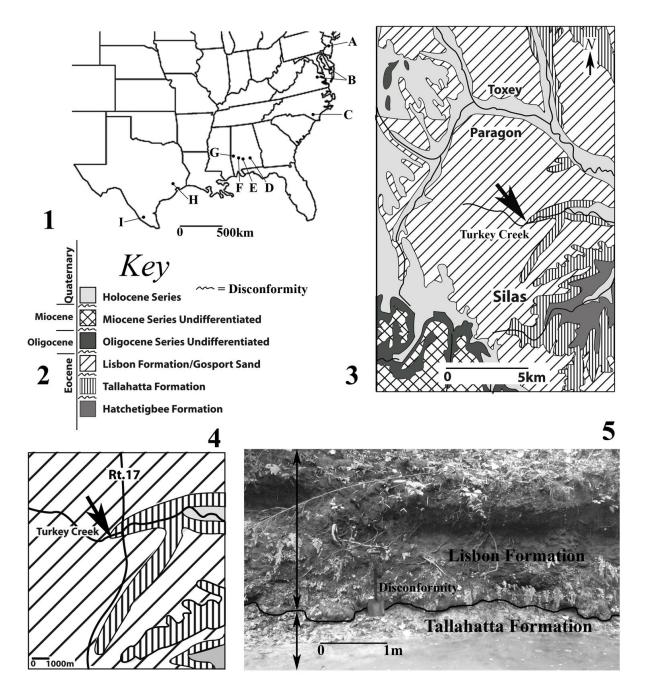


FIGURE 1. Location maps of the Turkey Creek field locality and Tallahatta – Lisbon Formation Contact (middle Eocene), Choctaw County, Silas, Alabama. 1–Middle Eocene Atlantic and Gulf Coastal Plain chondrichthyan localities discussed in this study: A, New Jersey, (Maisch et al., 2013); B, Maryland and Virginia, (Ward and Wiest, 1990; Kent, 1994); C, North Carolina, (Case and Borodin, 2000a); D, southcentral Alabama (Clayton et al., 2013); E, southwestern Alabama (White, 1956); F, southwestern Alabama (Westgate , 2001); G, southwestern Alabama, (this study); H, eastern Texas (Breard and Stringer, 1999); I, western Texas, (Westgate, 1989; 2008). 2 and 3–Stratigraphic column and geologic map of Choctaw County (Eocene) in the southwestern Alabama study area (modified from Osborne et al., 1989). 4–Detailed Geologic Map of the Lisbon–Tallahatta Formation contact along Turkey Creek discussed in text. 5–Outcrop exposure of the lower Tallahatta and upper Lisbon Formations along Turkey Creek, Choctaw County, Silas, Alabama. Note prominent disconformity directly above creek level and 1 meter shovel. Location of the Tallahatta – Lisbon Formation contact (this study) indicated by bold arrows.

Approximately 150 kg of sediment was recovered for laboratory sieve analysis. In the lab, sediment was thoroughly washed through progressively finer meshed screens ranging from 5.0 to 1.0 mm and dried under heat lamps. Teeth were removed using a magnifying glass and imaged directly with an Olympus SZ61 Binocular Microscope attached to an Infinity-2 Digital Camera. Since no new genera or species were identified among the specimens we recovered, abbreviated synonymies are utilized. Chondrichthyan teeth were identified by comparison with well-known regional and international literature including: Thurmond and Jones, 1981, Kent, 1994; 1999a; 1999b; Westgate, 2001; Cappetta, 2012. Reposited chondrichthyan teeth described in this report were selected from an assemblage of over 2000 specimens and are included in the collections of the Academy of Natural Sciences, Philadelphia with the catalogue numbers: ANSP 23404-23428.

#### SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880 Subclass ELASMOBRANCHII Bonaparte, 1838 Cohort EUSELACHII Hay, 1902 Order LAMNIFORMES Berg, 1958 Family ODONTASPIDIDAE Müller and Henle, 1838 Genus STRIATOLAMIA Glickman, 1964 Striatolamia macrota Agassiz, 1843 (Figure 2:1–6)

**Referred Material**—One anterior tooth, one lateral tooth, and one posterior tooth. ANSP 23404–23406.

**Description**—The crown of the anterior tooth is elongated and narrow with a strongly striated lingual face and smooth labial face. Cutting edges are complete and the cusp is sigmoidal in profile. The anterior tooth has a single reduced cusplet on each shoulder. The root of the anterior tooth is holaucorhizous and the mesial root lobe is commonly elongated. On the dorsal edge of the distal root lobe, a rounded protrusion is present. The crown of the lateral tooth is broad and triangular with a striated lingual face. The lateral tooth possesses wide, triangular to shovel-shaped cusplets. The root of the lateral tooth is holaucorhizous. The crown of the posterior tooth is mesio-distally compressed and antero-posteriorly thickened. Lateral cusplets are highly reduced. The root of the posterior tooth is holaucorhizous and the mesial root lobe is thicker and more rounded than the distal root lobe. A lingual protuberance containing a nutritive groove is present on all teeth.

**Discussion**—The teeth of *S. macrota* are very abundant at the Turkey Creek locality. Although these teeth are frequently fragmentary with only the crown remaining, the cutting edges are sharp, indicating minimal transport occurred during reworking and lag formation (e.g., Becker and Chamberlain, 2012). Morphologically, the teeth of S. macrota appear similar to those of Scapanorhychus sp. and Carcharias sp. Research by Cunningham (2000) suggested the tooth variation and morphology of S. macrota is comparable to that seen in the extant sand tiger shark, Carcharias taurus (Rafinesque, 1810). Kent (1994) recognized two Striatolamia species: S. striata (which is defined as having a smaller overall tooth size and longer striations) and S. macrota. Due to the variability seen in the teeth of the modern sand tiger shark, C. taurus, and their similarity to the teeth of S. macrota, we follow Ward and Wiest (1990), who synonymized S. striata with S. macrota, until further ontogenetic information can be ascertained from the teeth of these extinct sharks. The teeth of Sylvestrilamia sp. differ from those belonging to S. macrota because anterior teeth are only weakly sigmoidal and only contain folds in the lower portion of the lingual enamel, and lateral teeth are not as broad and have triangular rather than shovel-shaped cusplets (Cappetta and Nolf, 2005; Cappetta. Additional 2012). confusion identifying S. macrota from Carcharias sp. such as Hypotodus verticalis (Agassiz, 1843) and C. hopei (Ward, 1988) may occur if extensive reworking has occurred during lag formation, and in turn, may eliminate the lingual striations on the teeth of S. macrota (e.g., Gunnell, 2001). S. macrota has a cosmopolitan distribution and has been recovered from Paleocene-Eocene localities including those in: New Jersey (Maisch et al., 2013); Maryland (Ward and Wiest, 1990); Virginia (Cunningham, 2000); North Carolina (Chandler and Timmerman, 1995); South Carolina (Purdy, 1998a); Mexico (Ferrusquia-Villafranca et al., 1999); Texas (Breard and Stringer, 1999; Stidham and Janus, 2008); Georgia (Hulbert et al., 1998; Parmley and Cicimurri, 2003); Alabama (White, 1956; Holman and Case, 1988; Feldmann and Portell, 2007); Mississippi (Case, 1994); Chile (Otero et al., 2012); England (Kemp et al., 1990); France (Adnet, 2006); The Netherlands (Bor, 1985); Belgium (Van den Eeckhaut and De Schutter, 2009) Antarctica (Long, 1992); and Australia (Pledge, 1967). The teeth of S. macrota are morphologically similar to those of the modern sand tiger shark, C. taurus, which is known to inhabit coastal temperate-tropical waters (Compagno et al., 2005). S. macrota may have had similar feeding and habitat preferences.

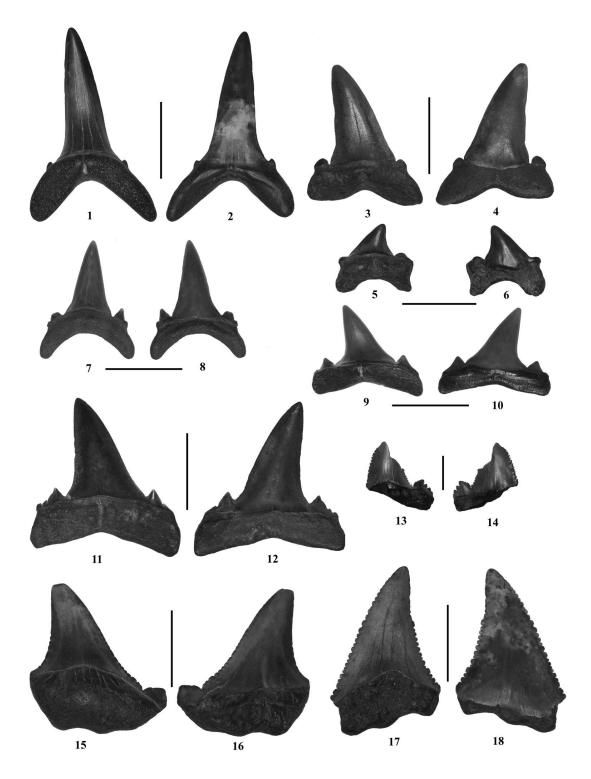


FIGURE 2: Teeth of Lamniforms from the Tallahatta – Lisbon Formation contact, Turkey Creek, Choctaw County, Silas, Alabama. 1–6: *Striatolamia macrota* Agassiz, 1843 (ANSP 23404–23406); 7–12: *Brachycarcharias lerichei* Casier, 1946 (ANSP 23407–23409); 13–18: *Carcharodon auriculatus* Blainville, 1818 (ANSP 23410–23412). Scale bars: 1–18 = 10.0 mm. Orientations: 1, 3, 5, 7, 9, 11, 13, 15, 17 = lingual view; 2, 4, 6, 8, 10, 12, 14, 16, 18 = labial view. Tooth positions: 1, 2, 7, 8 = anterior; 3, 4, 9–12, 15–18= lateral; 5, 6 = posterior.

Genus BRACHYCARCHARIAS Cappetta and Nolf, 2005

Brachycarcharias lerichei (Casier, 1946) (Figure 2:7–12)

**Referred Material**—One anterior tooth and two lateral teeth. ANSP 23407–23409.

**Description**—The crown of the anterior tooth is erect and has complete cutting edges. The lingual surface may contain faint striations however, the labial surface is smooth. Large triangular cusplets are present on the mesial and distal tooth shoulders and may be separated from the main cusp by a notch in the enamel. The root of the anterior tooth is holaucorhizous and contains a faint nutritive groove on the lingual surface. Lateral teeth have broad, triangular crowns with smooth lingual and labial surfaces and are angled distally. Broad, triangular cusps are present on the mesial and distal tooth shoulders and may contain a smaller, needle-like secondary cusplet. The root of lateral teeth is broad, holaucorhizous with the lobes widely separated, and the lingual surface is relatively flat.

**Discussion**—The teeth of *B. lerichei* are frequently recovered from the Turkey Creek locality. These teeth can be differentiated from those of S. macrota and other similar species due to the presence of erect, less sigmoidal cusps and more erect and triangular cusplets. The absence of moderately to strongly striated lingual tooth surfaces and shovelshaped cusplets on lateral teeth of B. lerichei can also aid in identification. Kent (1994) described the overall form of B. lerichei as similar to that of Serratolamna and Lamna. Cappetta and Nolf (2005) erected the genus Brachycarcharias and considered the tooth morphology to represent that of an odontaspid. Purdy and Francis (2007) compared the teeth of B. lerichei to those of the modern porbeagle shark Lamna nasus (Bonnaterre, 1788) and suggested that the B. lerichei morphology may actually belong to Lamna. We follow Cappetta (2012) and assign this species to B. lerichei until further analyses are conducted. The teeth of B. lerichei have been recovered from Eocene localities including those in: Maryland (Ward and Wiest, 1990); North Carolina (Case and Borodin, 2000a); Alabama (Holman and Case, 1988; Feldmann and Portell, 2007; Clayton et al., 2013); Louisiana (Breard and Stringer, 1995); England (Kemp et al., 1990); Belgium (Leriche, 1905; Casier, 1946; Cappetta and Nolf, 2005; Van den Eeckhaut and De Schutter, 2009); Japan (Tanaka et al., 2006); and Uzbekistan (Case et al., 1996). The teeth of B. lerichei resemble those of the modern porbeagle shark, Lamna nasus, which is known to inhabit coastal temperate-cool waters (Compagno et al., 2005).

Brachycarcharias lerichei therefore may have had similar feeding and habitat preferences.

Family LAMNIDAE Müller and Henle, 1838 Genus *CARCHARODON* Smith in Müller and Henle, 1838

> Carcharodon auriculatus Blainville, 1818 (Figure 2: 13–18)

**Referred Material**—One anterior tooth and two lateral teeth. ANSP 23410–23412.

**Description**—The main cusps of the anterior and lateral teeth are robust with convex lingual surfaces, nearly flat labial surfaces, and have coarsely serrated tooth margins. Lateral teeth are angled distally and have a claw-like appearance. Lateral cusplets are present in all tooth positions, are triangular to round in shape, coarsely serrated, and are separated from the main cusp by a distinct notch in the tooth enamel.

**Discussion**—The teeth of *C. auriculatus* are infrequently recovered from the Turkey Creek locality. Due to the large size and presence of serrations on these teeth, they are easily distinguished from all other chondrichthyan species in the Turkey Creek Assemblage. C. angustidens is morphologically similar to C. auriculatus, although overall serration size is smaller and more regular and lateral cusplets are more reduced. C. sokolowi (Jaekel, 1895) has been utilized by some researchers as an intermediate form between C. auriculatus and C. angustidens however, due to varying degrees of ontogenetic heterodonty and general dental morphology seen in the teeth of Carcharodon sp., C. sokolowi has been synonymized with C. auriculatus (e.g., Leriche, 1942; Kent, 1994; Renz, 2002; Adnet, 2006). The late Oligocene-early Miocene chubutensis Ameghino, 1906 *C*. subauriculatus), differs from both C. auriculatus and C. angustidens due to the presence of smaller, regularly spaced serrations and reduced lateral cusplets (Kent, 1994; Purdy et al., 2001; Renz, 2002; Parmley and Cicimurri, 2003). This report intends to document the occurrence of mega-toothed sharks in the middle Eocene of Alabama and does not intend to debate taxonomy. We follow the traditional nomenclature of Applegate and Espinosa-Arrubarrena (1996); Gottfried et al. (1996); Hulbert (2001); and Purdy et al. (2001) and utilize the genus Carcharodon. For additional discussion regarding the taxonomic classification of C. auriculatus and its assignment to Carcharocles or Otodus see Nyberg et al. (2006); Van den Eeckhaut and De Schutter, 2009; Underwood et al. (2011); Ehret et al. (2012); and Cappetta (2012). C. auriculatus has been recovered from Eocene-Oligocene localities including those in: New Jersey (Maisch et al., 2013);

Maryland (Ward and Wiest, 1990); North Carolina (Chandler and Timmerman, 1995); Georgia (Case, 1981; Freile et al., 2001); Alabama (White, 1956; Feldmann and Portell, 2007; Clayton et al., 2013); Mississippi (Dockery and Manning, 1986; Breard, 1991); Louisiana (Breard and Stringer, 1995); Mexico (Ferrusquía-Villafranca et al., 2000); England (Kemp et al., 1990); France (Adnet, 2006); Belgium (Van den Eeckhaut and De Schutter, 2009); Egypt (Underwood et al., 2011); Uzbekistan (Case et al., 1996); Japan (Tanaka et al., 2006); and Australia (Pledge, 1967). *C. auriculatus* has teeth morphologically similar to those of the extant white shark, *C. carcharias*, which is known to be pelagic and inhabit coastal-deep, temperate to tropical waters (Compagno et al., 2005).

Family OTODONTIDAE Glickman, 1964 Genus *OTODUS* Agassiz, 1843 *Otodus obliquus* Agassiz, 1843 (Figure 3:1–2)

**Referred Material**—One anterior tooth. ANSP 23413.

**Description**—The main cusp of the anterior tooth is robust, smooth, and angled distally. The lingual surface is convex and the labial surface is flat. Broad wrinkles are present in the tooth enameloid near the base of the main cusp on the labial surface. A single, well-defined, triangular, and divergent cusplet separated from the main cusp by a distinct notch is present on both the mesial and distal tooth shoulders. A well-defined dental band is present on the lingual surface of the tooth near the base of the main cusp. The root is holaucorhizous with slightly compressed, rounded lobes containing multiple foramina. No nutritive groove is present on the root.

**Discussion**—The teeth of O. obliquus are infrequently recovered from the Turkey Creek locality and are substantially larger and more robust than the teeth of the other chondrichthyan species in the assemblage, excluding C. auriculatus. The presence of multiple foramina throughout the root lobes and more narrow and divergent cusplets on lateral teeth of O. obliquus readily distinguish this species from Cretalamna sp. whereas the lack of serrations distinguishes O. obliquus from C. auriculatus. The teeth of O. obliquus may also appear similar to the teeth of Jaekelotodus trigonalis Jaekel, 1895, however, the taller and broader main cusps, lack of a deep concavity on the labial tooth surface, and lack of secondary or partially serrated primary cusplets in O. obliquus enables these two species to be distinguished from one another. According to Cappetta (2012) Otodus may have arisen from Cretalamna and possibly represents the ancestor of some of the larger and

later Cenozoic lamniforms therefore justifying the use of the genus Otodus for mega-toothed sharks (e.g., Bor et al., 2012; Cappetta, 2012; Ehret et al., 2012). O. obliquus has a cosmopolitan distribution and has been recovered from Paleocene-Eocene localities including those in: New Jersey (Fowler, 1911); Maryland (Ward and Wiest, 1990); North Carolina (Chandler and Timmerman, 1995; Case and Borodin, 2000a); South Carolina (Purdy, 1998a); Arkansas (Becker et al., 2011); England (Kemp et al., 1990); Morocco (Arambourg, 1952); and Australia (Pledge, 1967). O. obliquus has been documented to have an odontaspid dentition however, its more robust tooth morphology resembles that of Lamna, potentially making it similar to modern sand tiger or porbeagle sharks known to inhabit coastal-deep temperate-tropical waters (Applegate and Espinosa-Arrubarrena, 1996; Compagno et al., 2005; Purdy and Francis, 2007).

Order CARCHARHINIFORMES Compagno, 1977 Family CARCHARHINIDAE Jordan and Evermann, 1896

> Genus *ABDOUNIA* Cappetta, 1980 *Abdounia recticona* (Winkler, 1873) (Figure 3:3–6)

**Referred Material**—One anterior tooth and one lateral tooth. ANSP 23414–23415.

**Description**—The crowns of anterior and lateral teeth are smooth with nearly flat labial faces and slightly convex lingual faces. A complete cutting edge is present and up to three coarse, triangular cusplets can be seen on the mesial and distal shoulders of anterior teeth and up to two cusplets can be seen on the lateral tooth. The cusplets are continuous with the main cusp and are not separated by distinct distal and mesial notches on the tooth shoulder. The crown of the lateral tooth is angled distally whereas the crown of the anterior tooth is relatively straight. The root of the anterior tooth is thin, holaucorhizous, transversely extended, and contains a deep nutritive groove while the root base of lateral teeth is slightly thicker. On both anterior and lateral teeth, the basal edge of the labial and lingual root surface is slightly concave.

**Discussion**—The teeth of *Abdounia recticona* are infrequently recovered from the Turkey Creek locality although they are readily identifiable from other chondrichthyan teeth in the assemblage. The presence of erect main cusps, paired, triangular cusplets and the small overall tooth size of *A. recticona*, enable these teeth to be distinguished from those of *Physogaleus* sp., *Galeocerdo* sp., and other similar species. A similar species, *A. beaugei* (Arambourg, 1935), is also known to occur in North America (Kent, 1994).

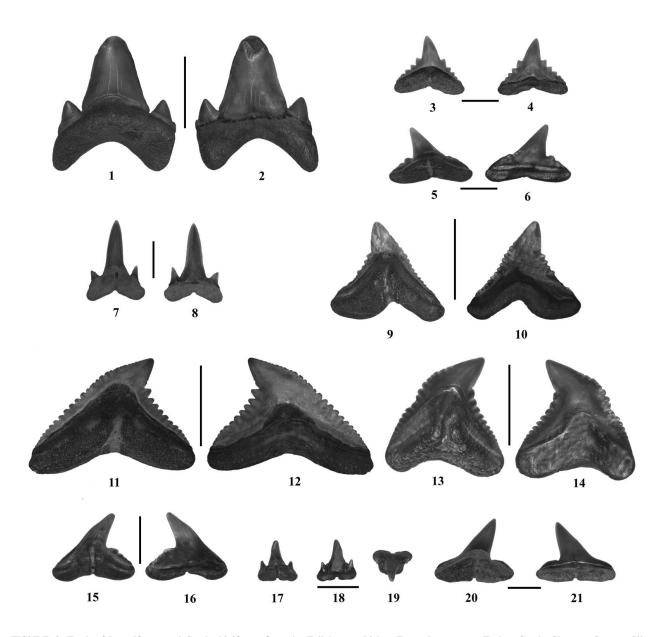


FIGURE 3. Teeth of Lamniforms and Carcharhiniforms from the Tallahatta – Lisbon Formation contact, Turkey Creek, Choctaw County, Silas, Alabama. 1–2: *Otodus obliquus* Agassiz, 1843 (ANSP 23413); 3–6: *Abdounia recticona* (Winkler, 1873) (ANSP 23414–23415); 7–8: *Abdounia enniskilleni* (White, 1956) (ANSP 23416); 9–14: *Galeocerdo eaglesomei* (White, 1955) (ANSP 23417–23419); 15–16: *Physogaleus secundus* (Winkler, 1874) (ANSP 23420); 17–19: *Scyliorhinus* sp. (ANSP 23421); 20–21: *Rhizoprionodon* sp. (ANSP 23422). Scale bars: 1–2; 9–14 = 10.0 mm; 3–8; 15–21= 5.0 mm. Orientations: 1, 3, 5, 7, 9, 11, 13, 15, 17, 20 = lingual view; 2, 4, 6, 8, 10, 12, 14, 16, 18, 21 = labial view; 19 = apical. Tooth positions: 1–4, 7–10, 17–19 = anterior; 5, 6, 11–16, 20, 21= lateral.

However, anterior teeth of *A. beaugei* have two or fewer cusplets, while *A. recticona* has three or more cusplets (Cappetta, 2012). *A. recticona* has a cosmopolitan distribution and has been recovered from Paleocene–Oligocene localities including those in: New Jersey (Maisch et al., 2013); Maryland (Ward and

Wiest, 1990); North Carolina (Chandler and Timmerman, 1995; Case and Borodin, 2000a); Alabama (Feldmann and Portell, 2007; Clayton et al., 2013); Texas (Breard and Stringer, 1999); England (Kemp et al., 1990); France (Adnet, 2006; Adnet and Cappetta, 2008); Belgium (Van den Eeckhaut and De

Schutter, 2009); and Uzbekistan (Case et al., 1996). The teeth of *A. recticona* are morphologically similar to those of modern catsharks, which are known to inhabit coastal temperate-tropical waters (Compagno et al., 2005). *Abdounia reticona* therefore may have had similar feeding and habitat preferences.

Abdounia enniskilleni (White, 1956) (Figure 3:7–8)

**Referred Material**—One anterior tooth. ANSP 23416.

**Description**—The crown of the anterior tooth is erect with a nearly flat labial face, convex and weakly striated lingual face, and contains a complete cutting edge. Single, needle-like, divergent cusplets are present on the mesial and distal tooth shoulders and are continuous with the main cusp enamel. The root of the anterior tooth is thick, holaucorhizous, and contains a deep nutritive groove with central foramina on the lingual surface.

**Discussion**—The teeth of A. enniskilleni are infrequently recovered from the Turkey Creek locality, however they are readily distinguished from the teeth of A. recticona, B. lerichei, and other similar species due to their relatively small size, sharp and erect main cusp with a weakly striated lingual surface, and pair of needle-like and divergent lateral cusplets. The teeth of A. enniskilleni appear very similar to those of A. minutissima (Winkler, 1874) and Scyliorhinus sp. According to Cappetta (2012) the teeth of A. enniskilleni do not have crown enamel overhanging the labial root face and have more developed bilobate roots. Such teeth were initially identified as Scyliorhinus sp. However, the teeth of A. enniskilleni have shorter crown heights and more robust roots with flat, rectilinear basal surfaces. Until further analyses are conducted on the teeth of A. enniskilleni and A. minutissima, we follow Cappetta (2012) and regard them as two different species. A. enniskilleni has been recovered from Eocene localities including those in: North Carolina (Chandler and Timmerman, 1995; Case and Borodin, 2000a); Georgia (Case, 1981; Case and Borodin, 2000b); Alabama (White, 1956; Holman and Case, 1988); Mississippi (Breard, 1991); Louisiana (Manning and Standhardt, 1986; Breard and Stringer, 1995); Arkansas (Westgate, 1984); and Texas (Breard and Stringer, 1999). The teeth of A. enniskilleni are morphologically similar to those of modern catsharks, which are known to inhabit coastal temperate-tropical waters (Westgate, 1984; Compagno et al., 2005). Abdounia enniskilleni therefore may have had similar feeding and habitat preferences.

Genus GALEOCERDO Müller and Henle, 1837 Galeocerdo eaglesomei (White, 1955) (Figure 3: 9–14)

**Referred Material**—One anterior tooth and two lateral teeth. ANSP 23417–23419.

Description—The crowns of anterior and lateral teeth are smooth with flat labial surfaces, slightly convex lingual surfaces, and are coarsely serrated. Compound serrations are not present on any of the Turkey Creek teeth. The cusp is angled distally and the angle becomes more acute further from the symphysis. The distal tooth margins contain a well-developed, serrated shoulder, and are concave whereas the mesial tooth margins are nearly straight in anterior teeth and convex in lateral teeth. Serrations are coarsest near the middle of the crown enamel and become progressively smaller in the apical and basal directions. The roots of anterior and lateral teeth are holaucorhizous and contain a short nutritive groove on the lingual surface. The anterior tooth has a thicker root than those of lateral teeth, although the basal, lingual root surface is slightly concave on roots of both tooth positions. The roots are more exposed on the lingual surface.

**Discussion**—The teeth of *G. eaglesomei* can be readily distinguished from other chondrichthyan teeth in the Turkey Creek assemblage such as Abdounia recticona, Physogaleus secundus, and Rhizoprionodon sp. due to the presence of coarsely serrated tooth margins, relatively thin roots, and a small nutritive groove on the lingual root surface. Previous researchers have described multiple Galeocerdo species based on crown angle, serration size, and root thickness (e.g., Leriche, 1942; White, 1955; Purdy et al., 2001; Cappetta, 2012). G. latidens Agassiz, 1843, is an Eocene species morphologically similar to the lateral teeth of G. eaglesomei although it is defined by having coarse serrations on the distal margin, fine serrations on the mesial margin, a weakly defined distal notch, and a lower overall tooth height and thickness. Manning and Standhardt (1986) synonymized G. clarkensis White, 1956, with G. alabamensis Leriche, 1942, on the basis that G. clarkensis teeth were actually the upper teeth of G. alabamensis. Eocene Galeocerdo sp. with compound serrations on the distal heel which are also referred to as G. alabamensis by Parmley and Cicimurri (2003). G. eaglesomei has been recovered from Eocene localities including those in: North Carolina (Case and Borodin, 2000a); Texas (Westgate, 1989; Breard and Stringer, 1999); Belgium (Van den Eeckhaut and De Schutter, 2009); Nigeria (White,

1955); and Egypt (Strougo et al., 2007; Underwood et al., 2011). The extant tiger shark, *G. cuvier*, is known to inhabit coastal, temperate-tropical waters (Compagno et al., 2005).

Genus *PHYSOGALEUS* Cappetta, 1980 *Physogaleus secundus* (Winkler, 1874) (Figure 3:15–16)

**Referred Material**—One lateral tooth. ANSP 23420.

**Description**—The crown of the lateral tooth is thick, mesio-distally compressed, angled distally, and sigmoidal in profile. The mesial and distal edges of the main cusp are smooth. The base of the mesial cutting edge may contain small serrations and the base of the distal cutting edge that extends onto the tooth shoulder, contains two or more coarse, triangular serrations. The lingual and labial tooth surfaces are convex and the labial surface slightly overhangs the root. The root is holauchorhizous, thick, and contains a large lingual protuberance with a deep nutritive groove. The basal root surface is nearly flat and has a rectilinear appearance.

**Discussion**—The teeth of *P. secundus* are infrequently recovered from the Turkey Creek locality. The presence of a large lingual protuberance, partly serrated crown and distal shoulder enamel, and convex, sigmoidal main cusps enable the teeth of P. secundus to be distinguished from those of morphologically similar Galeocerdo and Abdounia species even though distinct sexual dimorphism has been documented in the teeth of P. secundus. Additionally, the teeth of P. latus (Storms, 1894) have more distally angled cusps, weakly serrated or smooth mesial tooth edges, and thinner roots than the teeth of P. secundus from the Turkey Creek locality. However, current debate exists on the proper classification of *P. secundus*. The genus Physogaleus was erected by Cappetta (1980) who assigned Paleocene and Eocene teeth morphologically similar to G. contortus (Gibbes, 1849) to P. secundus (Winkler, 1874). Purdy et al. (2001) questioned the identity of Physogaleus until the syntypes are found and studied. P. secundus teeth, although larger in size, resemble forms of Paragaleus sp. as identified from the Miocene of North Carolina by Purdy et al. (2001) and have been assigned to the genus Physogaleus by Cappetta (2012). We follow Cappetta (1980; 2012) and assign the Silas teeth to P. secundus until further analyses and revised taxonomic classification occurs. P. secundus has a cosmopolitan distribution and has been recovered from Eocene localities including those in: New Jersey (Maisch et al., 2013); Maryland (Ward and Wiest, 1990); South Carolina (Parmley and Cicimurri, 2003); Alabama (White, 1956; Clayton et al., 2013); Texas (Breard and Stringer, 1999); England (Kemp et al., 1990); Belgium (Van den Eeckhaut and De Schutter, 2009); Morocco (Cappetta, 1980); and Japan (Tanaka et al., 2006). The teeth of *Physogaleus* species are morphologically similar to those of modern sharpnose and weasel sharks, which are known to inhabit coastal temperate-tropical waters (Compagno et al., 2005). *Physogaleus secundus* therefore may have had similar feeding and habitat preferences.

Family SCYLIORHINIDAE Gill, 1862 Genus SCYLIORHINUS Blainville, 1816 Scyliorhinus sp. (Figure 3:17–19)

**Referred Material**—One anterior tooth. ANSP 23421.

Description—The crown of the anterior tooth is erect, thin, and short with a nearly flat labial face, convex lingual face, and a complete cutting edge. Single, needle-like, erect cusplets are present on the mesial and distal tooth shoulders and are continuous with the main cusp enamel. The root of the anterior tooth is thick, holaucorhizous, and contains a deep nutritive groove extending from the labial to lingual face with central foramen on the lingual surface and additional foramina throughout the root. The root base is flat, heart-shaped, and wider on the labial face and no vertical folds or striations are present on the enamel near the root base.

Discussion—The teeth of Scyliorhinus sp. are infrequently recovered from the Turkey Creek locality. These are the smallest chondrichthyan teeth recovered from Turkey Creek and are readily distinguished from other teeth in the assemblage due to their short, thin crowns, and robust root with flat basal surfaces that are roughly heart-shaped in appearance. The teeth of A. enniskilleni are morphologically similar to those of Scyliorhinus sp., however, they are larger in size, have a more erect main cusp with divergent cusplets, and a more well-defined bilobate root structure that is not as thick, or flat on the basal surface as the root of Scyliorhinus sp. Cappetta (2012) identified a tooth similar to those found at the Turkey Creek locality as Premontreia (Oxyscyllium) subulidens while Bor et al. (2012) identified another nearly identical tooth as Pachyscyllium dachiardii (Lawley, 1876). Due to the highly variable morphology seen in Scyliorhinus teeth and scarce occurrence of these teeth at Turkey Creek, we refrain from higher level taxonomic classification. Similar Scyliorhinus sp. have been recovered from Eocene localities including those in: Maryland (Ward and Wiest, 1990); Georgia (Case, 1981); France (Adnet, 2006); and Uzbekistan (Case et al., 1996). The teeth of Scyliorhinus species are morphologically similar to those of modern catsharks, which are known to inhabit coastal temperate-tropical waters (Compagno et al., 2005). *Scyliorhinus* species therefore may have had similar feeding and habitat preferences.

Genus *RHIZOPRIONODON* Whitley, 1929 *Rhizoprionodon* sp. (Figure 3:20–21)

**Referred Material**—One lateral tooth. ANSP 23422.

**Description**—The crown of lateral teeth is short and broad with a complete cutting edge. The cusp is sigmoidal to slightly concave, bent distally and a pronounced, unserrated, distal heel is present. The labial tooth face slightly overhangs the root and displays a convex ridge parallel to the root base while the lingual face is nearly flat. The root is holauchorhizous and rectilinear in appearance and contains a deep nutritive groove.

**Discussion**—The teeth of *Rhizoprionodon* sp. are frequently recovered from the Turkey Creek locality and can be distinguished from those belonging to Sphyrna sp., by the presence of narrower, more sigmoidal main cusps and well-defined distal heels. Rhizoprionodon sp. teeth can also be distinguished from those of Scoliodon sp. by the lack of labial tooth enamel overhanging the root. Recent analyses on teeth from the extant genera: Scoliodon, Loxodon, and Rhizoprionodon have shown dental morphology to be very similar (Springer, 1964; Cappetta, 2012). Additional complications documented in identifying the teeth of Rhizoprionodon sp. include varying degrees of sexual dimorphism and ontogenetic heterodonty. We refrain from lower level taxonomic classification until further studies are conducted on the teeth of Rhizoprionodon sp. Rhizoprionodon has a cosmopolitan distribution and has been recovered from Eocene-recent localities including those in: Delaware (Purdy, 1998b); North Carolina (Case, 1980; Chandler and Timmerman, 1997; Case and Borodin, 2000a as Physogaleus sp.; Purdy et al., 2001); South Carolina (Cicimurri and Knight, 2009); Georgia (Case, 1981); Louisiana (Breard and Stringer, 1995); Florida (Hulbert, 2001); Alabama (Clayton et al., 2013); Texas (Manning, 1990; Stidham and Janus, 2008); Panama (Pimiento et al., 2013); Brazil (Fernandes dos Reis, 2005); Malta (Ward and Bonavia, 2001); Egypt (Case and Cappetta, 1990; Adnet et al., 2011; Underwood et al., 2011); Pakistan (Case and West, 1991; Adnet et al., 2007); and Uzbekistan (Case et al., 1996). Extant Rhizopriondon species are known to inhabit coastal, temperate-tropical waters (Compagno et al., 2005).

Suborder PRISTIOIDEI Cappetta, 1980

Family PRISTIDAE Bonaparte, 1838 Genus *PRISTIS* Linck, 1790 *Pristis* sp. (Figure 4:1–3)

**Referred Material**—One rostral tooth. ANSP 23423.

**Description**—The rostral tooth from the Turkey Creek locality is fragmentary however, the anterior edge of the tooth is rounded and the apex is slightly curved in the posterior direction. The posterior edge of the tooth is nearly flat although a U-shaped groove may be seen on this surface. Lateral grooves are present on the dorsal and basal surface and extend from the tooth base to the tooth apex. The tooth base exposes spongy, cancellous tooth matrix.

**Discussion**—The rostral teeth of *Pristis* sp. are infrequently recovered from the Turkey Creek locality and are usually abraded and fragmentary. Some rostral teeth, thought to belong to juvenile sawfish, may lack a groove along the posterior edge; indicating that ontogenetic heterodonty may be present in Pristis sp. (Purdy et al., 2001). Additionally, many Pristis sp. have been named from isolated rostral teeth leaving their validity in question until further studies are conducted (Cappetta, 2012). Due to the fragmentary nature of the Turkey Creek specimens, we refrain from higher level taxonomic classification. Pristis has a cosmopolitan distribution and has been recovered from Eocene-recent localities including those in: New Jersey (Leidy, 1877; Fowler, 1911; Maisch et al., 2013); Maryland (Ward and Wiest, 1990); North Carolina (Case and Borodin, 2000a; Purdy et al., 2001); South Carolina (Purdy, 1998a; Cicimurri, 2007); Georgia (Case, 1981; Case and Borodin, 2000b); Florida (Olsen, 1964); Alabama (Holman and Case, 1988; Clayton et al., 2013); Mississippi (Breard, 1991; Stringer and Miller, 2001); Louisiana (Manning and Standhardt, 1986; Breard and Stringer, 1995; Stringer et al., 2001); Arkansas (Westgate, 1984); Texas (Westgate, 1989; Breard and Stringer, 1999); England (Kemp et al., 1990); France (Cappetta, 1973); Belgium (Van den Eeckhaut and De Schutter, 2009); Egypt (Case and Cappetta, 1990; Underwood et al., 2011); Uzbekistan (Case et al., 1996); and Antarctica (Kriwet, 2005). The extant sawfish, P. pectinatus is known to inhabit coastal, temperate-tropical waters (Bigelow and Schroeder, 1953).

Superorder BATOMORPHII Cappetta, 1980 Order MYLIOBATIFORMES Compagno, 1973 Family MYLIOBATIDAE Bonaparte, 1838 Genus *AETOMYLAEUS* Garman, 1908 cf. *Aetomylaeus* sp. (Figure 4:7–12)

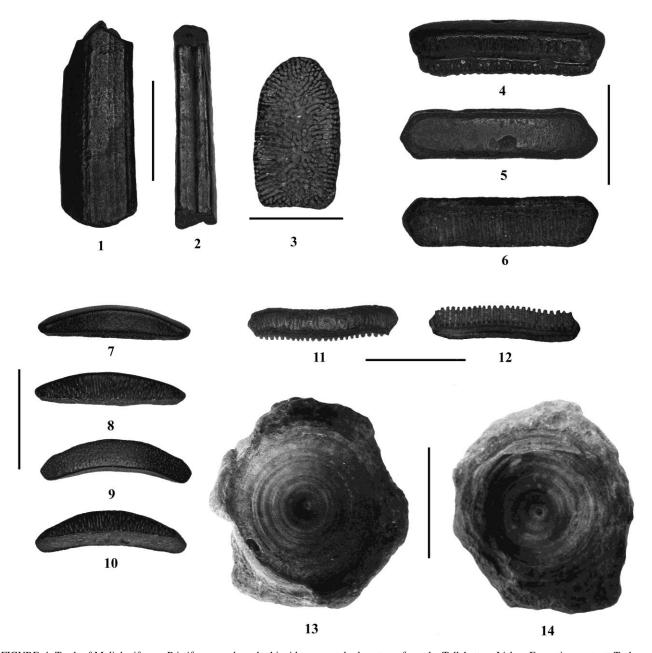


FIGURE 4. Teeth of Myliobatiforms, Pristiforms, and carcharhinoid-type vertebral centrum from the Tallahatta – Lisbon Formation contact, Turkey Creek, Choctaw County, Silas, Alabama. 1–3: *Pristis* sp., (ANSP 23423); 4–6:*Rhinoptera* sp., (ANSP 23424); 7–12: cf. *Aetomylaeus* sp., (ANSP 23425–23427); 13–14: Carcharhinoid-type vertebral centrum (ANSP 23428). Scale bars: 1–2, 4–12 = 10.0 mm; 3 = 5.0 mm; 13–14 = 20.0 mm. Orientations: 1 = ventral view; 2 = posterior tooth side; 3, 6, 10, 12 = basal view; 4, 8 = labial view; 5, 9, 11 = occlusal view; 7 = lingual view; 13–14 = articular surface view.

**Referred Material**—Two median pavement teeth. ANSP 23425–23426.

**Description**—The crowns of the pavement teeth are smooth, arcuate in occlusal view, convex in

labial and lingual view, and broader than they are long. The median tooth from the center of the dental plate has a crown that overhangs the labial face of the root and has angular edges. The median tooth from the posterior region

of the dental plate is more arcuate and has distal tooth edges that are rounded. The root is polyaulacorhizous and contains equidimensional nutritive grooves.

**Discussion**—The median teeth Aetomylaeus sp. are infrequently recovered from Turkey Creek. These teeth can be distinguished from other Silas batoid teeth due to crowns that are not uniform in thickness, and are elongated and arched in occlusal view. The batoids Pteromylaeus sp. Garman, 1913, Myliobatis sp. Cuvier, 1817, Rhinoptera sp. Cuvier, 1829, and Aetobatus sp. Blainville, 1816 bear some resemblance to Aetomylaeus from the Turkey Creek assemblage. However, the median pavement teeth of Pteromylaeus sp. are roughly seven times longer than their width, and upper median teeth retain the hexagonal outline as seen in Myliobatis and Rhinoptera while lower median teeth are gently arched (McEachran and Capapé, 1984; Cappetta, 2012). The median and lateral teeth of Myliobatis sp. have low, uniform crown thicknesses, angular tooth edges, are hexagonal in outline, and are not as broad as those of Aetomylaeus. The teeth of Rhinoptera sp. resemble those of Myliobatis sp. although, they have thick crowns that are uniform in thickness and median teeth that are not distinctly larger than lateral teeth. Aetobatus sp. have pavement teeth that are chevron to gently arched in shape and taper to rounded points as the genus does not contain lateral tooth rows (Bigelow and Schroeder, 1953). Analyses on the spatiotemporal distribution of Aetomylaeus by Cappetta (1987; 2012) suggest the genus has a greater extent than previously documented owing to its confusion with the teeth of Myliobatis sp. and Pteromylaeus sp. Due to the uncertain distribution of Aetomylaeus in the Gulf Coastal plain and the infrequent occurrence in the Silas assemblage, we refrain from definitive genus and species assignment until further studies are conducted on fossil and extant specimens. Aetomylaeus has a cosmopolitan distribution although is currently only documented from Miocene-recent localities including those in: New Jersey (Fowler, 1911 as Myliobatis); Florida (Hulbert, 2001); Cuba (Iturralde-Vinent et al., 1998); France (Cappetta, 1970 as Pteromylaeus); Portugal (Antunes et al., 1999 as Pteromylaeus). Extant Aetomylaeus species are known to inhabit the Red Sea and coastal, temperate-tropical waters of the Pacific and Indian Oceans (Cappetta, 2012).

Family RHINOPTERIDAE Jordan and Evermann, 1896 Genus *RHINOPTERA* Cuvier, 1829 *Rhinoptera* sp. (Figure 4:4–6) **Referred Material**—One median pavement tooth. ANSP 23424.

**Description**—The crown of the pavement tooth has a nearly flat and smooth hexagonal occlusal surface, uniform thickness, and is mesiodistally elongated. The base of the crown overhangs the root on all but the lingual side and contains numerous longitudinal ridges. The root is polyaulacorhizous and contains equidimensional nutritive grooves.

**Discussion**—The pavement teeth of *Rhinoptera* sp. are frequently recovered from the Turkey Creek locality and can be distinguished from other batoid teeth in the Silas assemblage by their nearly flat, hexagonal occlusal surfaces, uniform crown thickness, mesiodistally elongated form, and similarly sized median and lateral teeth (Nishida, 1990; Hulbert, 2001; Purdy et al., 2001; Cappetta, 2012). Median teeth of Rhinoptera have angular edges that correspond with the articular surfaces of adjoining, similarly sized and shaped lateral teeth. The batoids Pteromylaeus Garman, 1913, Aetomylaeus Garman, 1908 and Myliobatis Cuvier, 1817 bear some resemblance to Rhinoptera sp. from the Turkey Creek assemblage. However, according to McEachran and Capapé (1984) the median pavement teeth of *Pteromylaeus* are roughly hexagonal and seven times longer than their width, have lateral teeth that are much smaller than median teeth, and the labial and lingual tooth faces contain numerous pits and grooves. Aetomylaeus has median pavement teeth that are also noticeably longer than the corresponding lateral teeth although, the crowns are centrally thickened, yielding a convex form in addition to a slightly arched appearance in occlusal view. Myliobatis pavement teeth appear very similar to those of Rhinoptera however, they are slightly arched when viewed in labial or lingual view, have thinner crown heights, and have a greater size difference between median and lateral teeth. The highly variable dental morphology of pavement teeth belonging to extant including: genera Myliobatis, Rhinoptera, Aetomylaeus, and Pteromylaeus make the identification of isolated median and lateral pavement teeth extremely difficult (Nishida, 1990; Herman et al., 2000; Cappetta, 2012). The Turkey Creek Rhinoptera sp. pavement teeth resemble those of R. bonasus Mitchill, 1815 and R. sherboni White, 1926 however, we refrain from higher level taxonomic classification until more detailed analyses are conducted on the pavement teeth of fossil and extant Rhinoptera sp. Rhinoptera has a cosmopolitan distribution and has been recovered from Paleocene-recent localities including those in: Delaware (Purdy, 1998b); North Carolina (Case, 1980; Purdy et al., 2001); South Carolina (Purdy, 1998a; Cicimurri and Knight, 2009); Georgia (Case, 1981); Florida (Hulbert, 2001);

Louisiana (Breard and Stringer, 1995); Alabama (Thurmond and Jones, 1981; Feldmann and Portell, 2007; Clayton et al., 2013); Mississippi (Case, 1994); Texas (Westgate, 1989; Breard and Stringer, 1999; Stidham and Janus, 2008); Panama (Gillette, 1984; Pimiento et al., 2013); England (Kemp et al., 1990); France (Cappetta, 1970); Morocco (Arambourg, 1952; Adnet et al., 2010); Nigeria (White, 1926); Germany (Freess, 1992; Gille et al., 2010); Switzerland (Agassiz, 1843); Egypt (Adnet et al., 2011; Underwood et al., 2011); India (Sahni and Mehrotra, 1981); Pakistan (Case and West, 1991); and Uzbekistan (Case et al., 1996). Extant *Rhinoptera* species are known to inhabit coastal, temperate-tropical waters (Rogers et al., 1990; Gilbert and Williams, 2002).

Vertebral Centrum (Figure 4: 13–14)

**Referred Material**—One vertebral centrum. ANSP 23428.

**Description**—The vertebral centrum face is roughly circular in outline, has a concave articulation surface that is 38 mm in diameter, and contains multiple concentric lamella and a centrally-located birthmark. Large foramina for basal cartilage can be seen in dorso-lateral view.

Discussion—In addition to the chondrichthyan teeth, a vertebral centrum was also recovered. Carcharhinoid-type vertebral centra lack paired foramina, are more solid, and lack distinctive septa when compared to lamnoid-type vertebral centra which have many septa and large, paired basidorsal and basiventral foramina (Shimada, 1997; Blanco-Piñón et al., 2005; Becker et al., 2007). The association of isolated chondrichthyan vertebra with a particular genus or species is problematic as demonstrated by the well-known late Cretaceous lamniform, Squalicorax sp. In this species, teeth and associated tooth tissues are that of a lamniform but vertebral centra are more similar to that of a carcharhiniform (e.g., Shimada and Cicimurri, 2005; Becker et al., 2007). In this regard, the Turkey Creek carcharhinoid-type vertebral centrum is no exception and little is known about the skeletal anatomy of Paleogene chondrichthyans in North America.

### DISCUSSION

Composition and Paleoecology of the Turkey Creek Chondrichthyan Assemblage—A list of chondrichthyan genera occurring in the Turkey Creek lag is compiled in Table 1. Also included in this table are middle Eocene Gulf Coastal Plain chondrichthyan assemblages reported by: White (1956); Bread and

Stringer (1999); Westgate (1989, 2008); and Clayton et al. (2013). These five middle Eocene chondrichthyan assemblages occur across 1400 km of the Gulf Coastal Plain. The data in Table 1 indicate that eleven Turkey Creek genera occur in all other assemblages and the most wide-spread genera include: *Striatolamia, Physogaleus, Abdounia, Galeocerdo, Rhinoptera,* and *Pristis*. No chondrichthyans with distinct, deep water and open ocean affinities such as *Isurus* sp., *Alopias* sp., and *Hexanchus* sp. were recovered (Hulbert, 2001; Compagno et al., 2005; Adnet, 2006; Maisch, et al., 2013). However, the availability of deeper ocean water to the south in Alabama and neighboring states is documented by the occurrence of *Carcharodon* (Breard and Stringer, 1995; Manning, 2003).

The genera in Turkey Creek also occur in the middle Eocene of the Atlantic Coastal Plain (Ward and Wiest, 1990; Kent, 1994; Case and Borodin, 2000a; Maisch et al., 2013). These observations suggest that the Turkey Creek chondrichthyans were highly mobile, nektonic predators and scavengers that had broad geographic ranges across the entire middle Eocene shoreline of North America. This geographic distribution continued into the late Eocene in all inundated Gulf and Atlantic Coastal Plains states (Case, 1981; Westgate, 1984; Breard, 1991; Kent, 1994; 1999a; b; Breard and Stringer, 1995; Stidham and Janus, 2008).

The middle Eocene chondrichthyan assemblages in Table 1 derive from glauconitic sand and clay that contains oysters, gastropods and pelecypods diagnostic of coastal environments and consistent with a nearshore or beach facies community. This interpretation is reinforced by the occurrence of reptiles, amphibians and birds with coastal affinities within these chondrichthyan assemblages. Additionally, the shoreline and shallow marine environments of the Gulf Coastal Plain during the middle Eocene were known to have mangrove palm swamps, bays, and lagoons separated by offshore marine sandbar complexes and tidal channels emptying into a nearshore, marine environment (Westgate, 1989; According to Westgate (1989), water temperatures greater than 24 degrees Celsius and higher than normal marine salinity existed as far west as the Rio Grande Embayment along the middle Eocene Gulf Coastal Plain. Middle-late Eocene chondrichthyan species from the Atlantic and Gulf Coastal Plains also compare favorably with those found in Tethyan faunas of Africa, Egypt, Western Europe and elsewhere globally (See discussions in systematic paleontology). Similar marine conditions may have prevailed across the Atlantic and Gulf Coastal Plains throughout the Eocene (Miller et al., 2008) and substantial bay and shoreline habitat loss throughout the Mississippi

TABLE 1. Geographic distribution of middle Eocene chondrichthyan localities in the Gulf Coastal Plain discussed in this report. Notes: Only definitive genus assignments from cited authors are included in Table 1. *Carcharodon* is equivalent to *Carcharocles* as identified by Clayton et al. (2013); *Striatolamia macrota* is equivalent to *Odontaspis macrota* as identified by White (1956).

Order	Conecuh River, near Andalusia, Alabama (Clayton et al., 2013)	Claiborne, Alabama "Red Sands" White (1956)	Little Stave Creek, Jackson, Alabama (Westgate, 2001)	Turkey Creek Silas, Alabama (This Report)	Brazos River, near Bryan, Texas (Breard and Stringer, 1999)	Lake Casa Blanca, near Laredo, Texas (Westgate (1989; 2008)
ORECTOLOBI- FORMES	Nebrius					
LAMNIFORMES	Squatiscyllium Carcharodon Hypotodus			Carcharodon		
				Otodus		
	Striatolamna	Striatolamia Odontaspis	Striatolamia	Striatolamia	Carcharias Striatolamia	Striatolamia
	Brachycarcharias Sylvestrilamia Jaekelotodus	Ouoniuspis		Brachycarcharias		
CARCHARHINI- FORMES	Physogaleus	Physogaleus		Physogaleus	Physogaleus	
	Abdounia Galeocerdo Pachygaleus		Abdounia Galeocerdo	Abdounia Galeocerdo	Abdounia Galeocerdo	Galeocerdo
	70	Galeorhinus Negaprion	Negaprion Hemipristis		Negaprion	
	Rhizoprionodon			Scyliorhinus Rhizoprionodon	Scoliodon	
MYLIOBATI-					Carcharhinus	Carcharhinus
FORMES	Leidybatis					
	Myliobatis Rhinoptera Coupatzia Dasyatis Gymnura Jacquhermania			Rhinoptera	Anoxypristis Myliobatis Rhinoptera	Myliobatis Rhinoptera Dasyatis
RAJIFORMES PRISTOFORMES	Rhinobatos Pristis			Pristis	Rhinobatos Pristis	Rhinobatos Pristis

Embayment across the Eocene/Oligocene Boundary has been documented by Manning (2003).

Chondrichthyan Faunal Turnover and Extinction in the Gulf Coastal Plain: Evidence from Turkey Creek—Faunal assemblages from Gulf Coastal Plain localities such as Turkey Creek provide some general patterns by which chondrichthyan evolution at the genus-level and higher order taxonomy in the Cenozoic can be analyzed. Detailed species level chondrichthyan taxonomy is limited due to well-known and ongoing splitting and lumping problems (e.g.,

Fowler, 1911; Ward, 1988; Hubbell, 1996; Purdy et al., 2001; Hulbert, 2001; Cappetta and Nolf, 2005; Cappetta, 2012). Additional limitations cited by taphonomists include: areas of exposure, differential habitat preferences, and diagenesis (e.g., Brett and Baird, 1986; Kidwell, 1986; Behrensmeyer et al., 2000; Manning, 2003; Labs-Hochstein and MacFadden, 2006). It is also important to note that many Late Cretaceous and Cenozoic chondrichthyan assemblages from the Gulf Coastal Plain and throughout North America, including this report, derive from lag deposits

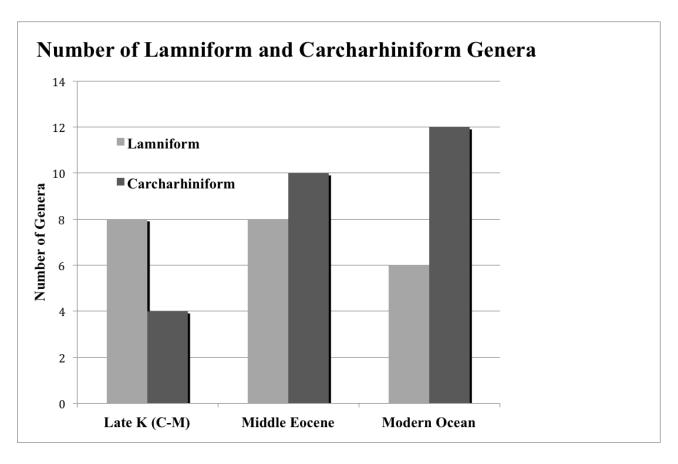


FIGURE 5. Graph displaying the number of lamniform and carcharhiniform genera from the Late Cretaceous (Campanian–Maastrichtian), middle Eocene, and modern Atlantic and Gulf coastal plains of the United States. Sources utilized: Gulf Coastal Plain (White, 1956; Westgate, 1989; 2001; 2008; Manning and Dockery, 1992; Welton and Farish, 1993; Case and Cappetta, 1997; Breard and Stringer, 1999; Clayton et al., 2013; This report). Atlantic Coastal Plain (Ward and Wiest, 1990; Gallagher, 1993; Hartstein et al., 1999; Case and Borodin, 2000a; Chamberlain et al., 2005). Modern Atlantic and Gulf Coastal Plains (Compagno, 1988; Compagno et al., 2005).

(e.g., Manning and Dockery, 1992; Becker et al. 1998; 2006; Breard and Stringer, 1999; Shimada et al., 2006; Clayton et al., 2013; Maisch et al., 2013). The degree of localized reworking during sea level fluctuation may be the products of episodic storm influence, shoreface bathymetry and coastline configuration (Kidwell, 1985; 1986; Morton, 1988; CoBabe and Allmon, 1994; Becker et al., 1996). In this regard, compilations of assemblages, such as those provided in Table 1, are time-averaged, middle Eocene snapshots of diversity trends of chondrichthyan genera across a given region such as the Gulf Coastal Plain (Flessa et al., 1993). Considering these limitations, chondrichthyans from middle Eocene Gulf Coastal plain localities cited and discussed in this report show: 1) an overall decrease in the number of lamniform genera compared to the Late Cretaceous; 2) an overall increase in the number of carcharhiniform genera compared to the Late

Cretaceous; and 3) the appearance large sharks, with large teeth, belonging to the genus *Carcharodon* (See Figure 5).

Reports on county to state-wide Late Cretaceous chondrichthyan assemblages in the Gulf Coastal Plain list numerous lamniform genera. Conversely, only several genera of carcharhiniforms have been reported from these same localities and many well-known Late Cretaceous localities report none (e.g., Manning and Dockery, 1992; Welton and Farish, 1993; Gallagher, 1993; Case and Cappetta, 1997; Hartstein et al., 1999; Chamberlain et al., 2005). By the middle Eocene, many chondrichthyan assemblages like those reported in Table 1, document lamniform diversity loss and contain an almost equal number of lamniform and carcharhiniform genera (e.g., White, 1956; Westgate, 1989; 2001; 2008; Ward and Wiest, 1990; Breard and Stringer, 1999; Case and Borodin, 2000a; Clayton et

al., 2013; This report; Figure 5). This pattern has continued through to the modern Atlantic Ocean and Gulf of Mexico (Compagno, 1988; Compagno et al., 2005).

Over the last two decades, the evolution of Carcharodon in North American and global localities has been intensely studied (e.g., Dockery and Manning, 1986; Uyeno et al., 1989; Kent, 1994; Gottfried et al., 1996; Hubbell, 1996; Applegate and Espinosa-Arrubarrena, 1996; Purdy, 1996; Purdy et al., 2001; Hulbert, 2001; Freile et al., 2001; Gottfried and Fordyce, 2001; Renz. 2002; Nyberg et al., 2006; Ehret et al., 2009; 2012; Cappetta, 2012). Intense debate still exists with regard to Megalodon ancestry and the usage genera, Carcharodon. Carcharocles. Megaselachus, and Otodus. However, the generally accepted evolutionary history links Cretalamna appendiculata in the Late Cretaceous with the intermediate middle Eocene form, Carcharodon auriculatus, seen in the Turkey Creek assemblage and throughout the Atlantic and Gulf coastal plains, to Carcharodon megalodon's last appearance in the Pliocene. A summation of this debate is as follows: 1) Casier (1960) concluded that the mega-tooth line from Carcharodon auriculatus-Carcharodon megalodon was not related to the modern white shark, Carcharodon carcharias (Linnaeus, 1758), and erected the genus Procarcharodon for species with large teeth and fine serrations and the genus Palaeocarcharodon for Paleocene species with smaller teeth and larger serrations. 2) Procarcharodon was challenged by Glickman (1964), who attributed the Eocene-Oligocene teeth of Carcharodon auriculatus and Carcharodon angustidens, containing coarser serrations and larger lateral cusplets, to Otodus obliquus. This superficial grouping resulted in the creation of the genus Megaselachus Glickman (1964) for large teeth with regular serrations and lack of lateral cusplets. However, studies have shown some teeth of Carcharodon sp., including Carcharodon carcharias, to have lateral cusplets in early and later development, making Glickman's classification method unwarranted. Additional work by Purdy et al. (2001), using reconstructed tooth sets of both Otodus and Carcharodon, has documented greater morphological differences between the teeth of these genera than previously assumed. 3) Jordan and Hannibal (1923) created the genus Carcharocles for teeth with large, serrated cusplets. Cappetta (1987) synonymized Procarcharodon and Megaselachus with Carcharocles and 4) Cappetta (2012) further revised mega-toothed shark nomenclature (sensu Zhelezko and Kozlov, 1999) and grouped Carcharocles and Megaselachus with Otodus. Ehret et al. (2012) described an articulated dentition from Peru and erected the species Carcharodon hubbelli for a transitional species between broad-toothed mako sharks (Carcharodon hastalis) and the great white shark (Carcharodon carcharias) and also interpreted the Megalodon lineage as belonging to Otodus. Applegate (1967) and Compagno (1988) documented that serrations have developed several times in sharks and that the loss of lateral cusplets is a general evolutionary trend. This inhibits the use of these characteristics in the construction of phylogenetic scenarios (Purdy et al., 2001). Although controversy exists regarding the exact phylogeny, data indicate that the total body length and tooth size of Carcharodon increased throughout the Cenozoic (e.g., Gottfried et al., 1996; Applegate and Espinosa-Arrubarrena, 1996; Purdy et al., 2001). These evolutionary changes in body and tooth size are thought to reflect middle Cenozoic climatic cooling and predation on larger marine mammals (e.g., Purdy, 1996; Hulbert et al., 1998; Uhen, 1998; 1999; Noriega et al., 2007; Berger, 2007; Weems et al., 2011).

We interpret the composition of the Turkey Creek chondrichthyan assemblage to represent evolutionary changes created by the Cretaceous-Paleogene mass extinction, shallow marine habitat losses and climate cooling. By the middle Eocene, Kriwet and Benton documented the global recovery chondrichthyan communites after the Cretaceous-Paleogene mass extinction event. Their research indicates six widespread lamniform families go extinct along with the genera Scapanorhynchus, Paranomotodon, Archaeolamna, and Squalicorax. These families were replaced by those with similar ecological roles and include the appearance of the Carcharhinidae, Isuridae, and Torpedinidae (Kriwet and Benton, 2004). The Carcharhinidae or requiem sharks are the most abundant genera and commonly occurring teeth in the Turkey Creek assemblage.

Paleoshoreline reconstructions of the Late Cretaceous indicate that a shallow, marine seaway extended hundreds of kilometers inland and covered more than half the state of Alabama (Smith et al., 1994; Kennedy et al., 1998). Late Cretaceous chondrichthyans occurring in Alabama have been found throughout the Atlantic and Gulf Coastal plain states as well as the Western Interior Seaway (e.g., Cappetta and Case, 1975; Gallagher et al., 1986; Case and Schwimmer, 1988; Manning and Dockery, 1992; Welton and Farish, 1993; Hoganson et al., 1996; 1997; Case and Cappetta, 1997; Cicimurri, 1998; Becker et al., 1998; 2006; Hartstein et al., 1999; Hoganson and Murphy, 2002). By the middle Eocene, this shallow marine habitat had been drastically reduced to a small region within the Mississippi Embayment and a marine shelf that fringed the Atlantic and Gulf coastal plains (e.g., Toulmin and La Moreaux, 1963; Ward et al., 1978; Case and

Borodin, 2000a; Bybell and Gibson, 1985; Ward and Wiest, 1990; Mancini and Tew, 1994; Ivany, 1998; Smith et al., 1994; Savrda et al., 2005; 2010; Miller et al., 2008; Maisch et al., 2013). The Turkey Creek chondrichthyans existed as earth's climate transitioned between greenhouse and ice house conditions and experienced carbon dioxide levels more than twice that of the modern times (Norris et al., 2013). Continental glaciation of Antarctica and cooling of the Arctic may have begun in the early Eocene and was responsible for global sea level regression (Pagani et al., 2011; Pearson et al., 2009; Liu et al., 2009). The Alabama Coastal Plain provides an excellent record for studying late Mesozoic and Cenozoic chondrichthyan evolution during substantial sea level lowering and climate changes. Future investigations are necessary to determine how a rapidly warming modern world may again determine the direction of chondrichthyan evolution in local, regional and global populations.

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