### A peer-reviewed version of this preprint was published in PeerJ on 14 October 2014.

<u>View the peer-reviewed version</u> (peerj.com/articles/625), which is the preferred citable publication unless you specifically need to cite this preprint.

Ehret DJ, Ebersole J. 2014. Occurrence of the megatoothed sharks (Lamniformes: Otodontidae) in Alabama, USA. PeerJ 2:e625 <a href="https://doi.org/10.7717/peerj.625">https://doi.org/10.7717/peerj.625</a>

# Occurrence of the Megatoothed sharks (Lamniformes:Otodontidae) in Alabama, USA

The Otodontidae include some of the largest sharks to ever live in the world's oceans (i.e. *Carcharocles megalodon*). Here we report on Paleocene and Eocene occurrences of *Otodus obliquus* and *Carcharocles auriculatus* from Alabama, USA. Teeth of *Otodus* are rarely encountered in the Gulf Coastal Plain and this report is one of the first records for Alabama. *Carcharocles auriculatus* is more common in the Eocene deposits of Alabama, but its occurrence has been largely overlooked in the literature. We also refute the occurrence of the Oligocene *Carcharocles angustidens* in the state. Raised awareness and increased collecting of under-sampled geologic formations in Alabama will likely increase sample sizes of *O. obliquus* and *C. auriculatus* and also might unearth other otodontids, such as *C. megalodon* and *C. chubutensis*.

- 1 Occurrence of the Megatoothed sharks (Lamniformes:Otodontidae) in Alabama, USA
- 2 Authors: Ehret, Dana J.<sup>1</sup> and Ebersole, Jun<sup>2</sup>
- <sup>1</sup>Alabama Museum of Natural History, PO Box 870340, Tuscaloosa, Alabama 35487-0340
- 4 Email: djehret@ua.edu
- 5 <sup>2</sup>McWane Science Center, 200 19<sup>th</sup> Street North, Birmingham, Alabama 35203
- 6 Email: jebersole@mcwane.org
- 7 Corresponding Author: Ehret, Dana J.
- 8 Alabama Museum of Natural History, PO Box 870340, Tuscaloosa, Alabama 35487-0340
- 9 Email: djehret@ua.edu

#### INTRODUCTION

The megatoothed sharks (Family Otodontidae) are well known in the marine fossil record of the Paleocene through Pliocene. These large, macro-predatory sharks are cosmopolitan in their distributions, and they are present in the fossil records of Asia, Africa, Europe, and North and South America (Cappetta, 2012). Beginning with *Otodus obliquus* (Agassiz, 1838) in the Paleocene and including the largest shark that ever lived, *Carcharocles megalodon* (Agassiz, 1835), otodontids are arguably the most well known of all fossil chondrichthyans. While *C. megalodon* is probably the most abundant and widely recognized species, other species of *Otodus* and *Carcharocles* are less often reported in the literature, which may have had a negative affect on the distribution and abundance of these species (Cappetta, 2012). This discrepancy might be related to a sampling bias, the familiarity of *C. megalodon* compared with other megatoothed species, or it might actually reflect the dispersal patterns of these other otodontid species.

Previous reports of otodontids from Alabama have varied in accurate identifications, including references to *C. auriculatus*, *C. angustidens* (Agassiz, 1835), *Otodus crassa* (Agassiz, 1843), and *O. crassus* (Gibbes, 1848) (Thurmond and Jones, 1981). Although middle Eocene outcrops are fairly prevalent in Alabama, studies of the otodontids have largely been overlooked in the state. Here we present and discuss records of *O. obliquus* and *C. auriculatus* (Blainville, 1818) in the Paleocene and Eocene of Alabama, respectively.

#### **MATERIAL AND METHODS**

The collections of the Alabama Museum of Natural History (ALMNH) in Tuscaloosa, the Geological Survey of Alabama (GSA) in Tuscaloosa, and McWane Science Center (MSC/RMM) in Birmingham were examined for specimens of otodontid sharks from Alabama. All three collections contained specimens that are previously unreported in the literature. In these collections, most specimens of *C. auriculatus* were correctly identified, however many of the *Otodus* specimens were incorrectly assigned to either *Carcharias* or *Lamna*. These misidentifications are likely the reason that *Otodus* has not been accurately reported from the state previously.

Five *O. obliquus* specimens were identified in the collections of the Geological Survey of Alabama (GSA) (Table 1). These specimens were collected in the late 1800's and early 1900's, with all being unidentified or misidentified. Specimens of *Carcharocles auriculatus* located in the ALMNH and MSC collections were collected over the last century from Choctaw, Clarke, Covington, Washington, and Wilcox counties (Fig. 1, Table 1). All *C. auriculatus* specimens were collected in Early to Middle Eocene deposits (mainly Lutetian and Bartonian) of southwestern Alabama and all specimens examined in this study were found by surface collection methods over the past 100+ years.

#### **Geologic Setting**

In Alabama, *Otodus obliquus* and *Carcharocles auriculatus* specimens have been collected from lithostratigraphic units ranging from the early Paleocene to Middle Eocene including the Midway, Sabine, Claiborne, Jackson groups (Figs. 1 and 2, Table 1). The Paleocene and Eocene formations in the state make up a nearly time-continuous series that ranges from the K/Pg contact to the Eocene/Oligocene contact (Raymond, 1988). A small unconformity exists between the upper-most Cretaceous units in the state, the Prairie Bluff Chalk and Providence Sand, and the lower-most Paleocene Clayton Formation. The Clayton Formation (which includes

the Pine Barren and McBryde Limestone members) is the basal unit in the Midway Group, a group that also includes, in ascending order, the Porters Creek (with the Matthews Landing Marl Member) and Naheola (with the Oak Hill and Coal Bluff Marl members) formations. The Midway Group is conformably overlain by the Paleocene/Eocene Wilcox Group. The Paleocene units within the Wilcox Group include, in ascending order, the Nanafalia Formation (with the Gravel Creek Sand Member, an informal unit referred locally as the "Ostrea thirsae beds," and the Grampian Hills Member), and the Tuscahoma Sand (which includes the Greggs Landing Marl and the Bells Landing Marl members).

The uppermost unit of the Wilcox Group is the Early Eocene (Ypresian) Hatchetigbee Formation, which contains the Bashi Marl Member at its base. The Wilcox Group is disconformably overlain by the lithostratigraphic units within the Claiborne and Jackson groups. The Claiborne Group consists of, in ascending order, the Tallahatta and Lisbon (with informal "lower," "middle," and "upper" members) formations, and the Gosport Sand. The Jackson Group includes the Moodys Branch and Crystal River formations and the Yazoo Clay. The Yazoo Clay in Alabama is further subdivided into the following chronologic members: the North Twistwood Creek, Cocoa Sand, Pachuta Marl, and Shubuta (Fig. 2).

#### SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880 Subclass Elasmobranchii Bonaparte, 1838 Order Lamniformes Berg, 1958 Family Otodontidae Glikman, 1964 Genus *Otodus* Agassiz, 1838 *Otodus obliquus* Agassiz, 1838 Figure 3A-D, Table 1

#### **Referred Specimens**

GSA CZ 5050, GSA CZ 5051, GSA CZ 5052, GSA CZ 5053, GSA CZ 5054

#### Occurrence

Wilcox County, Alabama

#### **Description**

Otodus obliquus teeth were identified using the following characteristics: triangular cusp, lacking serrations on cutting edges; labial face is moderately convex and does not overhang the root; lingual face is smooth and convex; a well developed v-shaped chevron on the lingual face; a pair of triangular cusplets that lack serrations; and a highly developed lingual protuberance of the root (Cappetta, 2012). Five O. obliquus specimens were identified in the historical collections housed at the Geological Survey of Alabama (GSA). GSA CZ 5051 (Fig. 3A) is part of the Schowalter Collection and was collected prior to 1889. Unfortunately the precise locality and formation of origin for GSA CZ 5051 is unknown as the specimen is only accompanied by a label marked "Tertiary, Wilcox," presumably referring to the Cenozoic strata in Wilcox County, Alabama. Of the Cenozoic units within this county, exposures can be found of all five Paleocene formations, which make up the Midway Group (Clayton, Porters Creek, and Naheola formations) and Wilcox Group (Nanafalia Formation and Tuscahoma Sand) in Alabama. Wilcox County also

has exposures of the Ypresian Hatchetigbee Formation, also part of the Wilcox Group (Fig. 1). Based on the surface exposures of these formations, we argue this specimen is either Selandian (Naheola Formation) or Thanetian (Tuscahoma Sand) in age. The tooth is a nearly complete posterolateral that exhibits large triangular cusplets, with a secondary pair also present. GSA CZ 5051 also exhibits a v-shaped chevron on its lingual surface, and smooth cutting edges on the main cusp. Although the tip is broken, the measured main crown height is 25.5 mm, while its width is 17.9 mm.

GSA CZ 5050 (Fig. 3B) represents a right posterolateral tooth that is accompanied with a label inscribed "Sucarnoochee, Clarence Jones' Place." The term "Sucarnoochee" refers to the Sucarnoochee beds, a historical and informal unit that was described as being between the Paleocene Clayton and the Naheola formations. "Clarence Jones' Place" refers to a historic locality located near Camden in Wilcox County that is known for its fine exposures of the Matthews Landing Marl, which is the upper member of the Porters Creek Formation (Smith and Johnson, 1887). This member falls within the *Morozovella angulata* planktonic foraminiferal zone, placing it within the early Thanetian (Mancini and Tew, 1988). The tooth is fairly worn, and it is missing the distal cusplet as well as portions of the root. The main crown is 22.6 mm high and 16.0 mm wide and it does display a prominent v-shaped chevron, making the identification possible.

GSA CZ 5052 (Fig. 3C) was found in the GSA collections with a label inscribed "Naheola, Matthews Landing, Alabama River", referring to the Naheola Formation and the historic locality Matthews Landing which is located along the Alabama River in Wilcox County. The listed formation, however, is likely an error as this locality represents the type section for the Matthews Landing Marl Member, which is the uppermost unit of the Porters Creek Formation. This member underlies the Naheola Formation, but in historical usage, the Matthews Landing Marl was incorrectly thought to be a member of the Naheola Formation (see Keroher et al., 1966). Therefore, the specimen can be referred to the very latest Danian or earliest Selandian. GSA CZ 5052 represents an anterior tooth, based on the symmetry of the main cusp. The tooth displays well-developed cusplets, a v-shaped chevron, smooth cutting edges, and a pronounced lingual protuberance of the root. The apex of the crown is chipped, but the remaining portion measures 29.8 mm in height and is 14.3 mm wide.

GSA CZ 5053 (Fig. 3D) is listed as coming from "Grave Yard Hill No. 4" in Wilcox County. Graveyard Hill is another important historic locality in eastern Wilcox County that contains a fossil zone located at the top of the Porters Creek Formation, making the specimen latest Danian or earliest Selandian (Toulmin, 1977). The specimen represents an anterior or first posterolateral tooth, with a crown height of 31.0 mm and a crown width of 18.8 mm. GSA CZ 5053 is worn, likely from being exposed for a long period of time, but exhibits a pronounced lingual protuberance, v-shaped chevron, and has well developed cusplets.

The final *O. obliquus* specimen found in collections is GSA CZ 5054 (Fig. 3E). The label associated with this specimen states: "State Collection Midway Group". Although the exact locality for this specimen is unknown, the label indicates that it was discovered within the strata of the Midway Group. This lower to middle Paleocene group includes the Clayton, Porters Creek, and Naheola formations, meaning the tooth is either latest Danian or Selandian. This specimen is highly worn, missing the apex of the crown, cusplets, and most of the root. However, it does preserve the v-shaped chevron, which is diagnostic for the Otodontidae. The remaining portion of the crown is 18.4 mm in height and 19.1 mm wide.

#### Remarks

140

141

142

143

144

145

146

147

148

149

150

151152

153

154

155

156

157

158

159

160

161

162

163

164

165

166

167

168

169

170

The taxonomic assignment of the Otodontidae is a contentious subject that has been debated for over a century (Agassiz, 1843; Jordan and Hannibal, 1923; Glikman, 1964; Cappetta, 1987, 2012; Applegate and Espinosa-Arrubarrena, 1996; Zhelezko and Kozlov, 1999; Purdy et al., 2001; Nyberg et al., 2006; Pimiento et al., 2010, 2013; Ehret et al., 2009, 2012). Original descriptions by Agassiz (1843) placed the megatoothed sharks within the Lamnidae, however they have since been reclassified as the Otodontidae by Glikman (1964) to recognize their distinct evolutionary history. Since being formally described in the 1840s, the taxonomy of the otodontids has undergone a multitude of changes reflecting reinterpretations of their relationships by a host of researchers (see references above). It is beyond the scope of this study to address the taxonomic stability of the otodontid sharks, however we recognize the genera Otodus and Carcharocles for the lineage ending with Carcharocles megalodon. This arrangement stands in contrast with Glikman (1964) and Cappetta (2012), who both referred species with large lateral cusplets to *Otodus*, and those with small or no cusplets to the genus *Megaselachus*. Cappetta (2012) revised the taxonomy further, by separating the genus *Otodus* into three subgenera based on the presence, absence, or size of serrations and cusplets as well as differences in root morphology. Furthermore, Zhelezko and Kozlov (1999) separated many of the Otodus and Carcharocles species into subspecies (e.g., Otodus obliquus mugodzharicus and Otodus poseidoni poseidoni) based on specimens from Kazakhstan. These constructions only further complicate the taxonomy of the Otodontids and do little to elucidate the relationships of the megatoothed sharks. We also argue that, under a biological species concept, it is not possible to recognize subgenera and subspecies in the fossil record. Therefore, we reject these confusing and somewhat subjective designations. Otodontids do likely represent a chronospecific sequence, with individual species derived from a pattern of development that replaces one species with another sequentially through geologic time by incremental morphological and genetic changes (Applegate and Espinosa-Arrubarrena, 1996; Cappetta, 2012). This mechanism results in a descendant that is much different from its original ancestor, however when looking at smaller time intervals, species distinctions are much more difficult to discern. In the absence of a phylogenetic or a more thorough morphometric analysis, and until further work is conducted and published, we refer the unserrated form to Otodus obliquus and serrated forms to the genus Carcharocles.

171 Genus Carcharocles Jordan and Hannibal, 1923
 172 Carcharocles auriculatus Blainville, 1818
 173 Figures 3F-H, 4A-G, Table 1

174 Referred Specimens: ALMNH 1985.30.2, ALMNH 1985.35.2, ALMNH 1985.72.28.5,
 175 ALMNH 1985.72.33, ALMNH 1985.72.43.3, ALMNH 1985.72.55.2, ALMNH 1985.72.62.3,

176 ALMNH 1985.72.83, ALMNH 1985.72.84, ALMNH 1985.72.88, ALMNH 1988.1.9, ALMNH

177 1988.29.1, ALMNH 1989.4.50.1, ALMNH 1992.28.44.1, ALMNH 1992.28.44.2, ALMNH

178 2000.1.4.1, ALMNH 2000.1.16.1, ALMNH 2000.1.27.1, ALMNH 2000.1.29.1, ALMNH

179 2000.1.33.1, ALMNH 2000.1.53, ALMNH 2000.1.57, ALMNH 2000.1.59, ALMNH 2005.6.259,

180 ALMNH 2005.6.279, ALMNH 2005.6.294, ALMNH 2005.6.334.6, ALMNH 2005.6.407,

181 ALMNH 2005.6.408.1, ALMNH 2010.5.3, MSC 20968, MSC 20969, MSC 20970, MSC 20971,

182 MSC 20972, MSC 20973, MSC 20974, MSC 20975, MSC 20976, MSC 20977, MSC 20978,

- 183 MSC 20979, MSC 20980, MSC 20981, MSC 20982, MSC 20983, MSC 20984, MSC 20985,
- 184 MSC 34422, MSC 34423, RMM 2370, RMM 2371

#### 185 Occurrence

Choctaw, Clarke, Covington, Washington, and Wilcox counties, Alabama

#### **Description**

Characters used to identify *C. auriculatus* in this study include: a large, triangular crown with the presence of lateral, serrated cusplets; serrated cutting edges that are fairly coarse and irregular; presence of a v-shaped chevron on the lingual surface of the crown; and developed lingual protuberance on the root. Remains of *Carcharocles auriculatus* are much more prevalent in Alabama than those of *Otodus obliquus*. This difference is likely related to the fact that Middle-Late Eocene deposits are much more expansive in Alabama than are sediments of the Paleocene and Early Eocene.

In the ALMNH collections, 30 specimens of *C. auriculatus* were identified (Fig. 4A, E-G, Table 1). These teeth were collected from Choctaw, Clarke, Covington, Washington, and Wilcox counties in Alabama. Most of the teeth in the ALMNH collections were found in the Yazoo Clay of the Jackson Group and are Priabonian in age. Outcrops of the Yazoo Clay are prevalent throughout the western portion of Alabama and are well known for their marine fossils including early cetaceans such as *Basilosaurus*, *Zygorhiza*, and *Cynthiacetus* (Uhen, 2013). One specimen each of *C. auriculatus* was collected in the Lisbon Formation and the Gosport Sand, which are Lutetian and Bartonian in age, respectively.

Twenty-two *C. auriculatus* specimens were identified in the MSC collections. (Fig. 4B-D, H, Table 1). A majority (17) of these teeth were collected from a single locality called Point A Dam in Covington County. Outcrops at this locality represent the boundary of the Tallahatta and Lisbon formations (middle Lutetian; Clayton et al., 2013). The remaining specimens were recovered from the Bartonian Gosport Sand in Choctaw County and the Priabonian Pachuta Marl Member of the Yazoo Clay of Washington County.

One specimen in the collections at MSC (MSC 34423; Fig. 3F) bears resemblance to the Late Paleocene – Early Eocene *Otodus aksuaticus* (Menner, 1928). Here, we define *O. aksuaticus* as specimens that exhibit triangular lateral cusplets; a triangular cusp; coarse serrations that fine towards the apex of the cusp; a v-shaped chevron; and a strong lingual protuberance of the root. This species is considered to be part of the chronospecies sequence between *O. obliquus* and *C. auriculatus* (Zhelezko and Kozlov, 1999) as it exhibits a transition from the unserrated *O. obliquus* to the serrated *C. auriculatus*, by means of coarse, irregular serrations that do not continue to the apex of the crown. This pattern of serration acquisition is very similar to that seen in the transition from *Carcharodon hastalis* to *Carcharodon carcharias* via *Carchardon hubbelli*, with coarser serrations at the base of the crown, fining towards the apex (Ehret et al., 2012).

MSC 34423 is here referred to *C. auriculatus* as it was discovered in sediments located at the Middle Eocene (Lutetian) boundary between the Lisbon and Tallahatta formations in Choctaw County. This specimen does exhibit coarse serrations that fine towards the apex of the cusp and might be close to *O. aksuaticus*, but we refer it here to *C. auriculatus* based on its Lutetian age. MSC 34423 represents a lateral tooth with a crown height of 18.8 mm and a crown width of 14.5 mm. The tooth has an average of 1.2 serrations per mm on both anterior and distal cutting edges.

Two other specimens in the ALMNH collections, ALMNH 1992.28.44.1 and ALMNH 1992.28.44.2 (Fig. 3G-H), we also refer to *C. auriculatus*, however they demonstrate more coarse serrations that fine towards the apex as seen in the earlier *O. aksuaticus*. The specimens are also Lutetian in age, having been collected at the boundary between the Lisbon and Tallahatta formations in Covington County, Alabama. Both teeth have broken apices and average 1.2 serrations per mm on their cutting edges. Although we assign all three of the aforementioned teeth to *C. auriculatus*, based on their similar morphology, we think there is a good potential for also finding *O. aksuaticus* in Alabama.

One partial vertebral centrum, MSC 20968 (Fig. 4H), recovered from the Point A Dam locality in Covington County, is also referred to *C. auriculatus*. The partial specimen (representing approximately one half of the centrum) is approximately 11.2 cm in diameter and 3.9 cm in thickness. The centrum is typically lamniform in appearance, laterally compressed with concave articular surfaces and radiating calcified lamellae within the intermedialia. Only one pit is preserved for the insertion of either the neural or haemal arch, however the centrum is fragmentary and it cannot be deduced as whether or not it is dorsal or ventral. We are confident in referring this specimen to *C. auriculatus* because of its lamniform appearance, age, and large size. Other lamniform taxa recovered from the Point A Dam locality are primarily odontaspids (Clayton et al., 2013), which would not have centra this large. For example, Hansen et al. (2013) reported a 6<sup>th</sup> vertebral centrum diameter of 30 mm for a recent *Odontaspis ferox* specimen with a total body length of 297 cm, which is significantly smaller than our fossil specimen.

#### **DISCUSSION**

Surprisingly, the presence of otodontid sharks in Alabama has not been extensively reported in the literature. Agassiz (1843) noted the presence of *Otodus crassa* in Alabama, although he provided no additional details. Leriche (1926) synonymized O. crassa with Carcharodon hastalis, which is probably correct for some of the specimens figured in Agassiz (1843). However, the Miocene C. hastalis has not been reported from Alabama and at least one of the specimens figured in Agassiz (1843) appears to be O. obliquus. As a result, it stands to reason that Agassiz (1843) might have been the first researcher to identify O. obliquus from Alabama. A few years later, Gibbes (1848) described the presence of *Otodus crassus* within the Cretaceous of Alabama. Describing what appears to be Carcharocles auriculatus, Gibbes, like many researchers at the time, mistakenly referred the Eocene deposits in the state to the Upper Cretaceous (Ebersole and Dean, 2013). Since that time, however, no other *Otodus* teeth are known to have been reported in Alabama. As discussed above, many of the *Otodus* teeth in the GSA collections were misidentified as *Odontaspis*, *Lamna*, or *Carcharias*, which could have confounded the situation. Furthermore, outcrops of the Midway and Wilcox groups are not widely exposed in Alabama, making it difficult to find Paleocene and Early Eocene fossils. Another large O. obliquus specimen was observed by one of the authors in the collection of a private collector; unfortunately this specimen could not be secured for the ALMNH collections at the present time (D. Ehret, pers. observ.). Otodus specimens have also been found in nearby states including the Williamsburg Formation of South Carolina (Purdy, 1998) and the Tuscahoma Formation of Mississippi (Case, 1994). These discoveries leads us to propose that *Otodus* teeth might be more prevalent in Alabama than previously thought if the proper aged outcrops are targeted for collecting.

Carcharocles auriculatus is the megatoothed species that is more commonly found in Alabama. Its predominance is likely a result of the comparably numerous outcrops of the Eocene

295

296

297

298

299

300

301

302

303

304

305

306

307

308

309

310

311

312

313

314

272 Tallahatta and Lisbon formations and the Yazoo Clay. The large size of the teeth is also likely a 273 factor in their discovery and collection. The closely related Carcharocles angustidens was 274 reported from Alabama by White (1956) and Thurmond and Jones (1981). The specimens 275 discussed in White (1956) that are housed in the British Museum (NHM London) are referred to 276 the Jackson Group and, based on specimens discussed and figured here, are most likely C. 277 auriculatus. Thurmond and Jones (1981) figured a specimen (Fig. 22, pg. 56) referred to C. 278 angustidens as a line drawing, which was reported as being part of the former Birmingham 279 Southern College collections and collected from an unknown locality. Unfortunately the 280 whereabouts of this specimen are unknown, and the poor quality of the figure does not allow for 281 an accurate identification. C. angustidens is a species of otodontid recorded from the Oligocene 282 that exhibits a larger overall tooth size, smaller cusplets, and finer serrations than C. auriculatus. 283 Because there are relatively few Oligocene outcrops in Alabama and the relatively high 284 prevalence of Eocene outcrops, we are confident that all records of Carcharocles in Alabama 285 thus far represent C. auriculatus. Furthermore, prospecting Oligocene sediments in Alabama by 286 both authors has only yielded small to microscopic chondrichthyan teeth of Carcharhiniformes, 287 Ginglymostomatidae, and Myliobatidae. No occurrences of Carcharocles chubutensis or 288 Carcharocles megalodon have been accurately reported from Alabama, likely a result of the 289 historic lack of systematic collecting in the Mio-Pliocene formations in the state. However more 290 concentrated collecting efforts in southern Alabama where Oligocene-Pleistocene deposits are 291 more concentrated may yield new specimens. Additionally, the use of historic collections (e.g., 292 the Geological Survey of Alabama collections) can be a valuable resource in identifying 293 overlooked or misidentified specimens.

#### CONCLUSIONS

The fossil record of otodontid sharks in Alabama has gone largely unreported in the literature. Reviews of the collections at the Alabama Museum of Natural History, McWane Science Center, and the Geological Survey of Alabama have yielded late Paleocene through Eocene otodontids including O. obliquus and C. auriculatus from the state. This study represents the first reliable report of *Otodus* from Alabama, with specimens identified from multiple localities. Otodus obliquus was identified in the collections at the Geological Survey of Alabama, most of which were collected prior to 1910. Based on observations of amateur collections, we think that the presence of O. obliquus is likely more common than what the few specimens in museum collections suggest. C. auriculatus is the most common otodontid shark recovered in Alabama, typically recovered from Lutetian-Ypresian outcrops in southwestern Alabama. While large specimens are not as common as they were 50-100 years ago, teeth assigned to this taxon are still recovered with some regularity. We also refute Thurmond and Jones' (1981) report of C. angustidens from the state. This specimen was most likely C. auriculatus, however, its status is unknown until the tooth can be rediscovered. C. chubutensis and C. megalodon are currently not known from Alabama, but with increased collection in the southern Cenozoic deposits in the state, specimens might be recovered.

#### **Acknowledgements**

Many thanks to Sandy Ebersole, Geological Survey of Alabama, for access to the fossil collections and help compiling the geologic data for Figure 1. The authors would also like to thank Dave Cicimurri, South Carolina Museum of Natural History, and Chuck Ciampaglio,

336

337

- Wright State University, for useful discussions on otodontid records. We would also like to thank
- 316 the reviewers of this manuscript.

#### REFERENCES

317

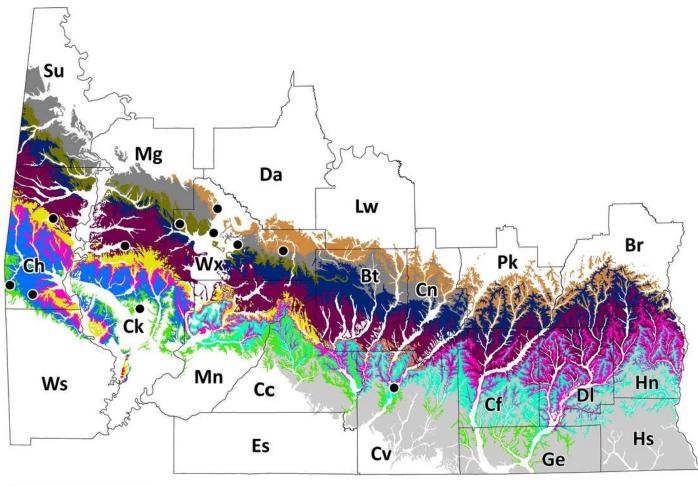
- 318 Agassiz LJR. 1833-1844. Recherches sur les poisons fossils. Text (5 vols; I. xlix + 188 pp., II xii
- 319 + 310 + 366 pp., III viii + 390 pp., IV XVI + 296 pp., V xii + 122 + 160 pp.) and Atlas.
- Neuchâtel, Imprimerie de Petitpierre.
- 321 Applegate SP, Espinosa-Arrubarrena L. 1996. The fossil history of *Carcharodon* and its possible
- ancestor, *Cretolamna*: a study in tooth identification. In: Klimley A, Ainley D, eds. *Great*
- White Sharks: the Biology of Carcharodon carcharias. San Diego: Academic Press, 19-36.
- Berg S. 1958. System der rezenten und fossilen Fischgartigen und Fische. Berlin: Deutsche
   Verlag Wissenschaften.
- Bieler R, Dockery III DT. 2007. Recognition of the Paleocene gastropods "Solariella"
- *alabamensis* (Aldrich, 1886) as a member of lower heterobranchs (Mathildidae), with
- description of *Toulminella* n. gen. *Paläontologische Zeitschrift* 81(3):283-290.
- Blainville HMD de. 1818. Prodrome d'une distribution systematique du regne animal. *Bulletin* des Sciences pars la Société Philomathique de Paris 8:105-124.
- Bonaparte CL. 1838. Selachorum tabula analytica. *Nuovi Annali della Science Naturali, Bologna* 2:195-214.
- Cappetta H. 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. In: Schultze HP, ed. *Handbook of Paleoichthyology Volume 3B*. New York: Verlag Dr. Gustav Fischer, 1-193.
  - Cappetta H. 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Schultze HP, ed. *Handbook of Paleoichthyology Volume 3E*. Munich: Verlag Dr. Gustav Fischer, 1-512.
- Clayton AA, Ciampagalio CN, Cicimurri, DJ. 2013. An inquiry into the stratigraphic occurrence of a Claibornian (Eocene) vertebrate fauna from Covington County, Alabama. *Bulletin of the Alabama Museum of Natural History* 31(2):60-73.
- Ebersole JA, Dean LS. 2013. The history of Late Cretaceous vertebrate research in Alabama.
   Bulletin of the Alabama Museum of Natural History 31(1):3-45.
- Ehret DJ, Hubbell G, MacFadden BJ. 2009. Exceptional preservation of the white shark
   *Carcharodon* (Lamniformes, Lamnidae) from the early Pliocene of Peru. *Journal of Vertebrate Paleontology* 29(1):1-13.
- Ehret DJ, MacFadden BJ, Jones DS, DeVries TJ, Foster DA, Salas-Gismondi R. 2012. Origin of
   the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the upper
   Neogene Pisco Formation of Peru. *Palaeontology* 55(6):1139-1153.
- Garner J, Bowles E. 1939. The *Venericardia planicosta* Group in the Gulf Province. Geological
   Survey Professional Paper 189–F:143-215.
- Geological Survey of Alabama. 2006. Geologic map of Alabama Digital Version 1.0. Alabama
   Geological Survey Special Map 220A. Geological Survey of Alabama, Tuscaloosa, Alabama
   [adapted from Szabo, et al., 1988].
- Gibbes RW. 1848. Monograph of the fossil Squalidae of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 7:191-206.
- 356 Glikman LS. 1964. *Sharks of the Paleogene and their stratigraphic significance*. Moscow: Nakua 357 Press, Moscow. [In Russian]
- 358 Hansen BB, Cuny G, Rasmussen BW, Shimada K, Jacobs P, Heilman-Clausen C. 2013.
- Associated skeletal and dental remains of a fossil odontaspid shark (Elasmobranchii:

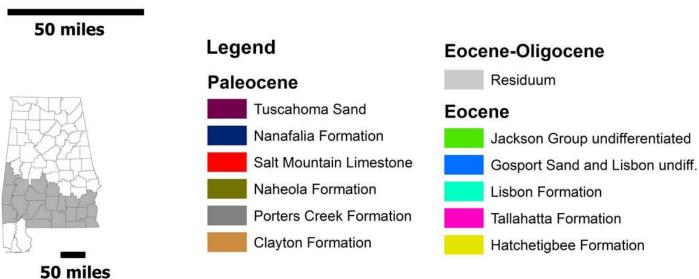
- 360 Lamniformes) from the Middle Eocene Lillebælt Clay Formation in Denmark. Bulletin of the 361 Geological Society of Denmark 61:37-46.
- 362 Huxley TH. 1880. A manual of the anatomy of vertebrated animals, D. New York: Appleton.
- 363 Johnson CW. 1932. Truman Hemingway Aldrich. *The Nautilis* 46(1):34-35.
- 364 Jordan DS, Hannibal H. 1923. Fossil sharks and rays of the Pacific Slope of North America.
- 365 Bulletin of the Southern California Academy of Sciences 22:27-63.
- 366 Keroher GC et al., 1966. Lexicon of geologic names of the United States for 1936-1960. U.S. 367 Geological Survey Bulletin 1200, 3 parts, 4,341 p.
- Leriche M. 1926. Les poisons Néogènes de la Belgique. Mémoires de Museé Royal du d'Histoire 368 369 Naturelle de Belgique 32:367-472.
- 370 Mancini EA, Tew BH. 1988. Paleocene sequence Stratigraphy of southwestern Alabama. Gulf 371 Coast Association of Geological Societies Transactions 38:453-460.
- 372 Mancini EA, Tew BH. 1991. Relationships of Paleogene state and planktonic foraminiferal zone 373 boundaries to lithostratigraphic and allostratigraphic contacts in the eastern Gulf Coastal 374 Plain. Journal of Foraminiferal Research 21(1):48-66.
- 375 Menner VV. 1928. The Palaeogene sharks of Mangyschlak, Emba and from the east of Oural. 376 Bulletin de la Société des Naturalistes de Moscou Section, Géologique 6(3-4): 291-338. [In 377 **Russian**]
- 378 Nolf D, Dockery III DT. 1993. Fish otoliths from the Matthews Landing Marl Member (Porters 379 Creek Formation), Paleocene of Alabama. *Mississippi Geology* 14(2):24-39.
- 380 Nyberg KG, Ciampaglio CN, Wray GA. 2006. Tracing the ancestry of the great white shark, 381 Carcharodon carcharias, using morphometric analyses of fossil teeth. Journal of Vertebrate 382 Paleontology 26:806-814.
- 383 Pimiento C, Ehret DJ, MacFadden BJ, Hubbell G. 2010. Ancient nursery area for the extinct 384 giant shark Megalodon from the Miocene of Panama. PLoS One 5(5): e10552.
- 385 Pimiento C, Gonzalez-Barba G, Hendy AJW, Jaramillo C, MacFadden BJ, Montes C, Suarez SC, 386 Shippritt M. 2013. Early Miocene chondrichthyans from the Culebra Formation, Panama: A 387 window into marine vertebrate faunas before closure of the Central American Seaway.
- 388 Journal of South American Earth Sciences 42: 159-170.
- Purdy R. 1998. Chondrichthyan fishes from the Paleocene of South Carolina. In: Sanders AE, ed. 389 390
- Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South 391
- Carolina, U.S.A. Transactions of the American Philosophical Society Vol. 88, Pt. 4:122-146.
- 392 Purdy R, Schneider VP, Applegate SP, McLellan JH, Meyer RL, Slaughter BH. 2001. The
- 393 Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. In: Ray
- 394 CE, Bohaska DJ, eds. Geology and Paleontology of the Lee Creek Mine, North Carolina, III.
- 395 Smithsonian Contributions to Paleobiology no. 90: 71-202.
- 396 Raymond DE, Osborne WE, Copeland CW, Neathery TL. 1988. Alabama Stratigraphy. 397 Geological Survey of Alabama Circular 140. 97 pp.
- Smith EA, Johnson LC. 1887. Tertiary and Cretaceous strata of the Tuscaloosa, Tombigbee, and 398 399 Alabama Rivers. Bulletin of the United States Geological Survey 43:1-189.
- 400 Szabo MW, Osborne WE, Copeland CW, Jr., Neathery TL. 1988. Geologic map of Alabama 401 (1:250,000): Alabama Geological Survey Special Map 220, Tuscaloosa.

- 402 Thurmond JT, Jones DE. 1981. Fossil vertebrates of Alabama. Tuscaloosa: University of 403 Alabama Press. 404 Toulmin LD. 1977. Stratigraphic Distribution of Paleocene and Eocene Fossils in the Eastern 405 Gulf Coast Region, Volume I. Geological Survey of Alabama Monograph 13, 602 pp. 406 Uhen MD. 2013. A review of North American Basilosauridae. Alabama Museum of Natural 407 *History Bulletin* 31 (2): 1–45. White EI. 1956. The Eocene fishes of Alabama. Bulletins of American Paleontology, 36 (156): 408 409 123-150. 410 Zhelezko V, Kozlov V. 1999. Elasmobranchii and Paleogene biostratigraphy of Transurals and
- Zhelezko V, Kozlov V. 1999. Elasmobranchii and Paleogene biostratigraphy of Transurals and
   Central Asia. *Materials on stratigraphy palaeontology of the Urals*, Vol. 3. Russian Academy
   of Sciences, Urals Branch, Uralian Regional Interdepartment Stratigraphical Commission,
   Yekaterinburg, 324 pp.

Geologic map of Paleocene and Eocene strata in Alabama

Map showing Paleocene and Eocene strata in Alabama and known collecting localities for Otodontid specimens. County abbreviations: Br, Barbour; Bt, Butler; Cc, Conecuh; Cf, Coffee; Ch, Choctaw; Ck, Clarke; Cn, Crenshaw; Cv, Covington; Da, Dallas; Dl, Dale; Es, Escambia; Ge, Greene; Hn, Henry; Hs, Houston; Lw, Lowndes; Mg, Marengo; Mn, Monroe; Pk, Pike; Su, Sumter; Ws, Washington, and Wx, Wilcox. Compiled using Geological Survey of Alabama digital geology data (GSA, 2006).

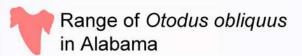


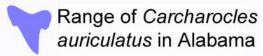


Paleocene and Eocene Stratigraphy of Alabama

Stratigraphic chart showing the age of Paleocene and Eocene formations of Alabama. Modified from Mancini and Tew (1991).

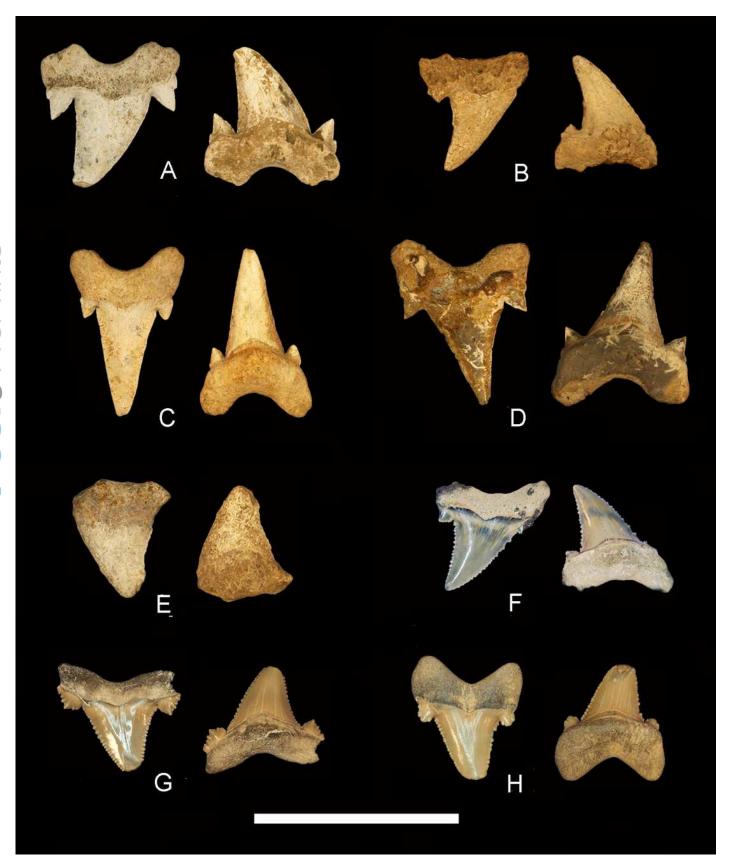
AGE	GRP.	W ALABAMA STRATIGRAPHY E	PLANKTONIC FORAMINIFERA	L ZONE	NP ZONE	STG.	
EOCENE	Jackson	Shubuta Mbr. Crystal Yazoo IPachuta Marl Mbr. River	Gr. cerroazulensis I. Z.		NP 20 NP 19	Priabonian	
		Clay Cocoa Sand Mbr. Fm.	P. semiinvoluta I. Z.	P 15	NP 18	F.	
	Claiborne	North Twistwood Creek Clay Member  Moodys Branch Formation Gosport Sand	Moodys Branch Formation		NP 17	Bartonian	
		"upper Lisbon" Lisbon	sbon"  Lisbon  O. beckmanni R. Z.		NP 16	<u>в</u>	
		"lower \ Lisbon"	Gg. subconglobata C. R. Z.	P 11	NP 15	Lutetian	
		Tallahatta Formation	H. aragonensis I. Z. — — — — — — — —	P 10	NP 14		
		Hatchetigbee Formation Bashi Marl Member	M. subbotinae I. Z.	P6	NP 13 NP 12 NP 11 NP 10	Ypresian	
PALEOCENE	Wilcox	「Bells Lnd.」 Tuscahoma LMarl Mbr. 」 Sand	M. velascoensis I. Z.	, F0	NP 9	Selandian	
		Greggs Lnd. Marl Mbr.		P 5			
		Grampian Hills Mbr.		P 4	NP 8		
		Nanafalia "Ostrea thirsae beds" Gravel Creek Sand Mbr.	Pr. pseudomenardii R. Z.		NP 7		
	Midway	Naheola Coal Bluff Naheola Marl Mbr. Formation Oak Hill Mbr.  Matthews Landing Marl Mbr.	Pr. pusilla pusilla I. Z.  M. angulata I. Z.	gulata I. Z. P3 NI		1	
		Porters Creek Fm.	M. uncinata I. Z.	P2	NP 4		
		McBryde Ls. Mbr. Clayton Clayton Formation Fm. Pine Barren Mbr.	S. trinidadensis I. Z.		NP3	Danian	
		I I I I I I I I I I I I I I I I I I I	S. pseudobulloides I. Z.		VP 1℃	14	





Otodus obliquus and Carcharocles auriculatus teeth from Alabama

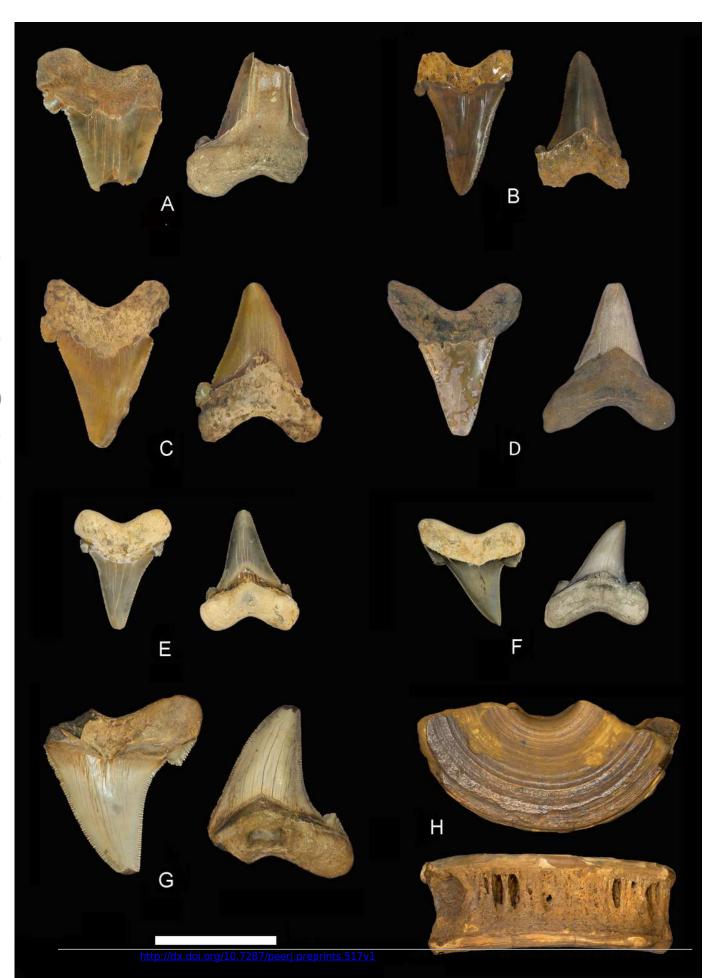
Otodus obliquus specimens from Alabama. Labial view on left, lingual view on right. A) GSA CZ 5051, Unknown formation; B) GSA CZ 5050, Matthews Landing Marl Mbr.; C) GSA CZ 5052, Matthews Landing Marl Mbr.; D) GSA CZ 5053, Porters Creek Fm. E) GSA CZ 5054, Midway Group; Carcharocles auriculatus specimens, labial view on left, lingual view on right. F) MSC 34423, Lisbon-Tallahatta fms.; F) ALMNH 1992.28.44.1, Lisbon-Tallahatta fms.; G) ALMNH 1992.28.44.2, Lisbon-Tallahatta fms. Scale Bar = 5 cm.



Carcharocles auriculatus teeth from Alabama

Carcharocles auriculatus specimens from Alabama. Labial view on left, lingual view on right.

A) ALMNH 1988.29.1, Hatchetigbee Fm.; B) MSC 20970, Lisbon-Tallahatta Fms.; C) MSC 20973, Lisbon-Tallahatta Fms.; D) RMM 2371, Gosport Sand; E) ALMNH 2000.1.29.1, Yazoo Clay; F) ALMNH 2000.1.33.1, Yazoo Clay; G) ALMNH 2005.6.294, Unknown formation; H) MSC 20968, Lisbon-Tallahatta Fm. Scale Bar = 5 cm.



### Table 1(on next page)

Otodus and Carcharocles specimens in museum collections from Alabama

Otodus and Carcharocles specimens from the Alabama Museum of Natural History (ALMNH), Geological Survey of Alabama (GSA), and McWane Science Center collections (MSC/RMM).

Catalog/Accession Number	Genus	Species	Formation/Unit	Stage	County	State	Locality
ALMNH 1985.30.2	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1985.35.2	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1985.72.28.5	Carcharocles	auriculatus	Hatchetigbee or Lisbon Fm.	Ypresian or	Choctaw	AL	Shell Creek
				Lutetian/Bartonian			
ALMNH 1985.72.33	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1985.72.43.3 ALMNH 1985.72.55.2	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL AL	Unknown
ALMNH 1985.72.62.3	Carcharocles Carcharocles	auriculatus auriculatus	Unknown Unknown	Unknown Unknown	Unknown Unknown	AL	Unknown Unknown
ALMNH 1985.72.83	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1985.72.84	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1985.72.88	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1988.1.9	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Unknown	AL	Unknown
				n			
ALMNH 1988.29.1	Carcharocles	auriculatus	Gosport Sand	Bartonian	Choctaw	AL	Puss Cuss Creek
ALMNH 1989.4.50.1	Carcharocles	auriculatus	Lisbon Fm.	Lutetian/Bartonian	Choctaw	AL	Butler
ALMNH 1992.28.44.1	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
ALMNH 1992.28.44.2	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
ALMNH 2000.1.4.1	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Choctaw	AL	Unknown
ALMNH 2000.1.16.1	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Choctaw	AL	Ulikilowii
ALWINI 2000.1.10.1	Carcharocies	auriculaius	1 azoo Ciay	n	Choctaw	AL	Unknown
ALMNH 2000.1.27.1	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Choctaw	AL	Cintile wii
			_	n			Unknown
ALMNH 2000.1.29.1	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Choctaw	AL	
				n			Unknown
ALMNH 2000.1.33.1	Carcharocles	auriculatus	Pachuta Marl Member	Priabonian	Washington	AL	Bashi
ALMNH 2000.1.53	Carcharocles	auriculatus	Yazoo	Bartonian/Priabonia	Choctaw	AL	
ALABHI 2000 1 57	0 1 1		37	n n	CI.	4.7	Unknown
ALMNH 2000.1.57	Carcharocles	auriculatus	Yazoo	Bartonian/Priabonia n	Choctaw	AL	Unknown
ALMNH 2000.1.59	Carcharocles	auriculatus	Yazoo	Bartonian/Priabonia	Choctaw	AL	Clikilowii
74271111 2000.1.37	Curcharocies	dancadas	14200	n	Chociaw	, iL	Unknown
ALMNH 2005.6.259	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Choctaw	AL	
			_	n			Unknown
ALMNH 2005.6.279	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Clarke	AL	Grove Hill
				n			
ALMNH 2005.6.294	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 2005.6.334.6	Carcharocles	auriculatus	Tallahatta Fm.	Ypresian/Lutetian	Wilcox	AL	Prairie Bluff
ALMNH 2005.6.407	Carcharocles	auriculatus	Unknown	Unknown Unknown	Unknown Wilcox	AL	Unknown
ALMNH 2005.6.408.1 ALMNH 2010.5.3	Carcharocles Carcharocles	auriculatus auriculatus	Unknown Unknown	Unknown	Unknown	AL AL	Prairie Bluff Unknown
GSA 5050	Otodus	obliquus	Matthews Landing Marl	Selandian	Wilcox	AL	Camden
35.13050	Olouis	Obliquis	Member	Joinnan .	Wilcon	1.2	Cumacii
GSA 5051	Otodus	obliquus	Unknown	Unknown	Wilcox	AL	Unknown
GSA 5052	Otodus	obliquus	Matthews Landing Marl	Selandian	Wilcox	AL	Matthews
			Member				Landing
GSA 5053	Otodus	obliquus	Porters Creek Formation	Danian	Wilcox	AL	Graveyard Hill
991 5951			161	P 1 10 1 11	** 1		No. 4
GSA 5054	Otodus	obliquus	Midway Group	Danian/Selandian	Unknown	AL	Unknown
MSC 20969 MSC 20970	Carcharocles Carcharocles	auriculatus auriculatus	Lisbon-Tallahatta Contact Lisbon-Tallahatta Contact	Lutetian Lutetian	Covington Covington	AL AL	Point-A Dam Point-A Dam
MSC 20970 MSC 20971	Carcharocles	auriculatus	Lisbon-Tallahatta Contact Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam Point-A Dam
MSC 20972	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20973	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20974	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20975	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20976	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20977	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20978	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20979	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20980	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20981	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20982 MSC 20983	Carcharocles	auriculatus auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20983 MSC 20984	Carcharocles Carcharocles	auriculatus auriculatus	Lisbon-Tallahatta Contact Lisbon-Tallahatta Contact	Lutetian Lutetian	Covington Covington	AL AL	Point-A Dam Point-A Dam
MSC 20985	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 29068	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
	Carcharocles	auriculatus	Yazoo Clay - Pachuta Marl	Priabonian		AL	
MSC 34422			Mbr.		Washington	l -	Unknown
MSC 34423	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Choctaw	AL	Silas
RMM 2370	Carcharocles	auriculatus	Gosport Sand	Bartonian	Choctaw	AL	Puss Cuss Creek
RMM 2371	Carcharocles	auriculatus	Gosport Sand	Bartonian	Choctaw	AL	Puss Cuss Creek