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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
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10 INTRODUCTION

11 The megatoothed sharks (Family Otodontidae) are well known in the marine fossil record 12 of the Paleocene through Pliocene. These large, macro-predatory sharks are cosmopolitan in their 13 distributions, and they are present in the fossil records of Asia, Africa, Europe, and North and 14 South America (Cappetta, 2012). Beginning with Otodus obliquus (Agassiz, 1838) in the 15 Paleocene and including the largest shark that ever lived, Carcharocles megalodon (Agassiz, 16 1835), otodontids are arguably the most well known of all fossil chondrichthyans. While C. 17 *megalodon* is probably the most abundant and widely recognized species, other species of 18 Otodus and Carcharocles are less often reported in the literature, which may have had a negative 19 affect on the distribution and abundance of these species (Cappetta, 2012). This discrepancy 20 might be related to a sampling bias, the familiarity of C. megalodon compared with other 21 megatoothed species, or it might actually reflect the dispersal patterns of these other otodontid 22 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

30 The collections of the Alabama Museum of Natural History (ALMNH) in Tuscaloosa, the 31 Geological Survey of Alabama (GSA) in Tuscaloosa, and McWane Science Center (MSC/RMM) 32 in Birmingham were examined for specimens of otodontid sharks from Alabama. All three 33 collections contained specimens that are previously unreported in the literature. In these 34 collections, most specimens of C. auriculatus were correctly identified, however many of the 35 Otodus specimens were incorrectly assigned to either Carcharias or Lamna. These 36 misidentifications are likely the reason that *Otodus* has not been accurately reported from the 37 state previously.

38 Five O. obliguus specimens were identified in the collections of the Geological Survey of 39 Alabama (GSA) (Table 1). These specimens were collected in the late 1800's and early 1900's, 40 with all being unidentified or misidentified. Specimens of Carcharocles auriculatus located in 41 the ALMNH and MSC collections were collected over the last century from Choctaw, Clarke, 42 Covington, Washington, and Wilcox counties (Fig. 1, Table 1). All C. auriculatus specimens 43 were collected in Early to Middle Eocene deposits (mainly Lutetian and Bartonian) of 44 southwestern Alabama and all specimens examined in this study were found by surface collection 45 methods over the past 100+ years.

46 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

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54 the Pine Barren and McBryde Limestone members) is the basal unit in the Midway Group, a 55 group that also includes, in ascending order, the Porters Creek (with the Matthews Landing Marl 56 Member) and Naheola (with the Oak Hill and Coal Bluff Marl members) formations. The 57 Midway Group is conformably overlain by the Paleocene/Eocene Wilcox Group. The Paleocene 58 units within the Wilcox Group include, in ascending order, the Nanafalia Formation (with the 59 Gravel Creek Sand Member, an informal unit referred locally as the "Ostrea thirsae beds," and 60 the Grampian Hills Member), and the Tuscahoma Sand (which includes the Greggs Landing Marl 61 and the Bells Landing Marl members).

62 The uppermost unit of the Wilcox Group is the Early Eocene (Ypresian) Hatchetigbee 63 Formation, which contains the Bashi Marl Member at its base. The Wilcox Group is 64 disconformably overlain by the lithostratigraphic units within the Claiborne and Jackson groups. 65 The Claiborne Group consists of, in ascending order, the Tallahatta and Lisbon (with informal 66 "lower," "middle," and "upper" members) formations, and the Gosport Sand. The Jackson Group 67 includes the Moodys Branch and Crystal River formations and the Yazoo Clay. The Yazoo Clay 68 in Alabama is further subdivided into the following chronologic members: the North Twistwood 69 Creek, Cocoa Sand, Pachuta Marl, and Shubuta (Fig. 2).

OVOTEMATIC DALEONTOLOCY
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

78 Referred Specimens

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

80 Occurrence

81 Wilcox County, Alabama

82 Description

83 Otodus obliquus teeth were identified using the following characteristics: triangular cusp, 84 lacking serrations on cutting edges; labial face is moderately convex and does not overhang the 85 root; lingual face is smooth and convex; a well developed v-shaped chevron on the lingual face; a 86 pair of triangular cusplets that lack serrations; and a highly developed lingual protuberance of the 87 root (Cappetta, 2012). Five O. obliquus specimens were identified in the historical collections 88 housed at the Geological Survey of Alabama (GSA). GSA CZ 5051 (Fig. 3A) is part of the 89 Schowalter Collection and was collected prior to 1889. Unfortunately the precise locality and 90 formation of origin for GSA CZ 5051 is unknown as the specimen is only accompanied by a label 91 marked "Tertiary, Wilcox," presumably referring to the Cenozoic strata in Wilcox County, 92 Alabama. Of the Cenozoic units within this county, exposures can be found of all five Paleocene 93 formations, which make up the Midway Group (Clayton, Porters Creek, and Naheola formations)

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.

102 GSA CZ 5050 (Fig. 3B) represents a right posterolateral tooth that is accompanied with a 103 label inscribed "Sucarnoochee, Clarence Jones' Place." The term "Sucarnoochee" refers to the 104 Sucarnoochee beds, a historical and informal unit that was described as being between the 105 Paleocene Clayton and the Naheola formations. "Clarence Jones' Place" refers to a historic 106 locality located near Camden in Wilcox County that is known for its fine exposures of the 107 Matthews Landing Marl, which is the upper member of the Porters Creek Formation (Smith and 108 Johnson, 1887). This member falls within the *Morozovella angulata* planktonic foraminiferal 109 zone, placing it within the early Thanetian (Mancini and Tew, 1988). The tooth is fairly worn, 110 and it is missing the distal cusplet as well as portions of the root. The main crown is 22.6 mm 111 high and 16.0 mm wide and it does display a prominent v-shaped chevron, making the 112 identification possible.

113 GSA CZ 5052 (Fig. 3C) was found in the GSA collections with a label inscribed 114 "Naheola, Matthews Landing, Alabama River", referring to the Naheola Formation and the 115 historic locality Matthews Landing which is located along the Alabama River in Wilcox County. 116 The listed formation, however, is likely an error as this locality represents the type section for the 117 Matthews Landing Marl Member, which is the uppermost unit of the Porters Creek Formation. 118 This member underlies the Naheola Formation, but in historical usage, the Matthews Landing 119 Marl was incorrectly thought to be a member of the Naheola Formation (see Keroher et al., 120 1966). Therefore, the specimen can be referred to the very latest Danian or earliest Selandian. 121 GSA CZ 5052 represents an anterior tooth, based on the symmetry of the main cusp. The tooth 122 displays well-developed cusplets, a v-shaped chevron, smooth cutting edges, and a pronounced 123 lingual protuberance of the root. The apex of the crown is chipped, but the remaining portion 124 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.

132 The final O. obliquus specimen found in collections is GSA CZ 5054 (Fig. 3E). The label 133 associated with this specimen states: "State Collection Midway Group". Although the exact 134 locality for this specimen is unknown, the label indicates that it was discovered within the strata 135 of the Midway Group. This lower to middle Paleocene group includes the Clayton, Porters Creek, 136 and Naheola formations, meaning the tooth is either latest Danian or Selandian. This specimen is 137 highly worn, missing the apex of the crown, cusplets, and most of the root. However, it does 138 preserve the v-shaped chevron, which is diagnostic for the Otodontidae. The remaining portion of 139 the crown is 18.4 mm in height and 19.1 mm wide.

140 Remarks

141 The taxonomic assignment of the Otodontidae is a contentious subject that has been 142 debated for over a century (Agassiz, 1843; Jordan and Hannibal, 1923; Glikman, 1964; Cappetta, 143 1987, 2012; Applegate and Espinosa-Arrubarrena, 1996; Zhelezko and Kozlov, 1999; Purdy et 144 al., 2001; Nyberg et al., 2006; Pimiento et al., 2010, 2013; Ehret et al., 2009, 2012). Original 145 descriptions by Agassiz (1843) placed the megatoothed sharks within the Lamnidae, however 146 they have since been reclassified as the Otodontidae by Glikman (1964) to recognize their 147 distinct evolutionary history. Since being formally described in the 1840s, the taxonomy of the 148 otodontids has undergone a multitude of changes reflecting reinterpretations of their relationships 149 by a host of researchers (see references above). It is beyond the scope of this study to address the 150 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 151 152 contrast with Glikman (1964) and Cappetta (2012), who both referred species with large lateral 153 cusplets to *Otodus*, and those with small or no cusplets to the genus *Megaselachus*. Cappetta 154 (2012) revised the taxonomy further, by separating the genus *Otodus* into three subgenera based 155 on the presence, absence, or size of serrations and cusplets as well as differences in root 156 morphology. Furthermore, Zhelezko and Kozlov (1999) separated many of the Otodus and 157 Carcharocles species into subspecies (e.g., Otodus obliguus mugodzharicus and Otodus 158 poseidoni poseidoni) based on specimens from Kazakhstan. These constructions only further 159 complicate the taxonomy of the Otodontids and do little to elucidate the relationships of the 160 megatoothed sharks. We also argue that, under a biological species concept, it is not possible to 161 recognize subgenera and subspecies in the fossil record. Therefore, we reject these confusing and 162 somewhat subjective designations. Otodontids do likely represent a chronospecific sequence, 163 with individual species derived from a pattern of development that replaces one species with 164 another sequentially through geologic time by incremental morphological and genetic changes 165 (Applegate and Espinosa-Arrubarrena, 1996; Cappetta, 2012). This mechanism results in a 166 descendant that is much different from its original ancestor, however when looking at smaller 167 time intervals, species distinctions are much more difficult to discern. In the absence of a 168 phylogenetic or a more thorough morphometric analysis, and until further work is conducted and 169 published, we refer the unserrated form to *Otodus obliguus* and serrated forms to the genus 170 Carcharocles.

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- Genus *Carcharocles* Jordan and Hannibal, 1923 *Carcharocles auriculatus* Blainville, 1818 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

186

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

187 Description

188 Characters used to identify *C. auriculatus* in this study include: a large, triangular crown 189 with the presence of lateral, serrated cusplets; serrated cutting edges that are fairly coarse and 190 irregular; presence of a v-shaped chevron on the lingual surface of the crown; and developed 191 lingual protuberance on the root. Remains of *Carcharocles auriculatus* are much more prevalent 192 in Alabama than those of *Otodus obliquus*. This difference is likely related to the fact that 193 Middle-Late Eocene deposits are much more expansive in Alabama than are sediments of the 194 Paleocene and Early Eocene.

195 In the ALMNH collections, 30 specimens of C. auriculatus were identified (Fig. 4A, E-G, 196 Table 1). These teeth were collected from Choctaw, Clarke, Covington, Washington, and Wilcox 197 counties in Alabama. Most of the teeth in the ALMNH collections were found in the Yazoo Clay 198 of the Jackson Group and are Priabonian in age. Outcrops of the Yazoo Clay are prevalent 199 throughout the western portion of Alabama and are well known for their marine fossils including 200 early cetaceans such as Basilosaurus, Zygorhiza, and Cynthiacetus (Uhen, 2013). One specimen 201 each of C. auriculatus was collected in the Lisbon Formation and the Gosport Sand, which are 202 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.

209 One specimen in the collections at MSC (MSC 34423; Fig. 3F) bears resemblance to the 210 Late Paleocene – Early Eocene Otodus aksuaticus (Menner, 1928). Here, we define O. 211 aksuaticus as specimens that exhibit triangular lateral cusplets; a triangular cusp; coarse 212 serrations that fine towards the apex of the cusp; a v-shaped chevron; and a strong lingual 213 protuberance of the root. This species is considered to be part of the chronospecies sequence 214 between O. obliquus and C. auriculatus (Zhelezko and Kozlov, 1999) as it exhibits a transition 215 from the unserrated O. obliquus to the serrated C. auriculatus, by means of coarse, irregular 216 serrations that do not continue to the apex of the crown. This pattern of serration acquisition is 217 very similar to that seen in the transition from Carcharodon hastalis to Carcharodon carcharias 218 via Carchardon hubbelli, with coarser serrations at the base of the crown, fining towards the apex 219 (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. 227 Two other specimens in the ALMNH collections, ALMNH 1992.28.44.1 and ALMNH 228 1992.28.44.2 (Fig. 3G-H), we also refer to C. auriculatus, however they demonstrate more coarse 229 serrations that fine towards the apex as seen in the earlier O. aksuaticus. The specimens are also 230 Lutetian in age, having been collected at the boundary between the Lisbon and Tallahatta 231 formations in Covington County, Alabama. Both teeth have broken apices and average 1.2 232 serrations per mm on their cutting edges. Although we assign all three of the aforementioned 233 teeth to *C. auriculatus*, based on their similar morphology, we think there is a good potential for 234 also finding O. aksuaticus in Alabama.

One partial vertebral centrum, MSC 20968 (Fig. 4H), recovered from the Point A Dam 235 236 locality in Covington County, is also referred to C. auriculatus. The partial specimen 237 (representing approximately one half of the centrum) is approximately 11.2 cm in diameter and 238 3.9 cm in thickness. The centrum is typically lamniform in appearance, laterally compressed with 239 concave articular surfaces and radiating calcified lamellae within the intermedialia. Only one pit 240 is preserved for the insertion of either the neural or haemal arch, however the centrum is 241 fragmentary and it cannot be deduced as whether or not it is dorsal or ventral. We are confident in 242 referring this specimen to C. auriculatus because of its lamniform appearance, age, and large 243 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) 244 245 reported a 6th vertebral centrum diameter of 30 mm for a recent *Odontaspis ferox* specimen with a 246 total body length of 297 cm, which is significantly smaller than our fossil specimen.

247 DISCUSSION

248 Surprisingly, the presence of otodontid sharks in Alabama has not been extensively 249 reported in the literature. Agassiz (1843) noted the presence of *Otodus crassa* in Alabama, 250 although he provided no additional details. Leriche (1926) synonymized O. crassa with 251 *Carcharodon hastalis*, which is probably correct for some of the specimens figured in Agassiz 252 (1843). However, the Miocene C. hastalis has not been reported from Alabama and at least one 253 of the specimens figured in Agassiz (1843) appears to be O. obliquus. As a result, it stands to 254 reason that Agassiz (1843) might have been the first researcher to identify O. obliguus from 255 Alabama. A few years later, Gibbes (1848) described the presence of *Otodus crassus* within the 256 Cretaceous of Alabama. Describing what appears to be Carcharocles auriculatus, Gibbes, like 257 many researchers at the time, mistakenly referred the Eocene deposits in the state to the Upper 258 Cretaceous (Ebersole and Dean, 2013). Since that time, however, no other *Otodus* teeth are 259 known to have been reported in Alabama. As discussed above, many of the *Otodus* teeth in the 260 GSA collections were misidentified as *Odontaspis*, *Lamna*, or *Carcharias*, which could have 261 confounded the situation. Furthermore, outcrops of the Midway and Wilcox groups are not 262 widely exposed in Alabama, making it difficult to find Paleocene and Early Eocene fossils. 263 Another large *O. obliguus* specimen was observed by one of the authors in the collection of a 264 private collector; unfortunately this specimen could not be secured for the ALMNH collections at 265 the present time (D. Ehret, pers. observ.). Otodus specimens have also been found in nearby 266 states including the Williamsburg Formation of South Carolina (Purdy, 1998) and the Tuscahoma 267 Formation of Mississippi (Case, 1994). These discoveries leads us to propose that Otodus teeth 268 might be more prevalent in Alabama than previously thought if the proper aged outcrops are 269 targeted for collecting.

270 *Carcharocles auriculatus* is the megatoothed species that is more commonly found in271 Alabama. Its predominance is likely a result of the comparably numerous outcrops of the Eocene

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.

294 CONCLUSIONS

295 The fossil record of otodontid sharks in Alabama has gone largely unreported in the 296 literature. Reviews of the collections at the Alabama Museum of Natural History, McWane 297 Science Center, and the Geological Survey of Alabama have yielded late Paleocene through 298 Eccene otodontids including O. obliquus and C. auriculatus from the state. This study represents 299 the first reliable report of *Otodus* from Alabama, with specimens identified from multiple 300 localities. Otodus obliguus was identified in the collections at the Geological Survey of Alabama, 301 most of which were collected prior to 1910. Based on observations of amateur collections, we 302 think that the presence of *O. obliquus* is likely more common than what the few specimens in 303 museum collections suggest. C. auriculatus is the most common otodontid shark recovered in 304 Alabama, typically recovered from Lutetian-Ypresian outcrops in southwestern Alabama. While 305 large specimens are not as common as they were 50-100 years ago, teeth assigned to this taxon 306 are still recovered with some regularity. We also refute Thurmond and Jones' (1981) report of C. 307 angustidens from the state. This specimen was most likely C. auriculatus, however, its status is 308 unknown until the tooth can be rediscovered. C. chubutensis and C. megalodon are currently not 309 known from Alabama, but with increased collection in the southern Cenozoic deposits in the 310 state, specimens might be recovered.

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317 **REFERENCES**

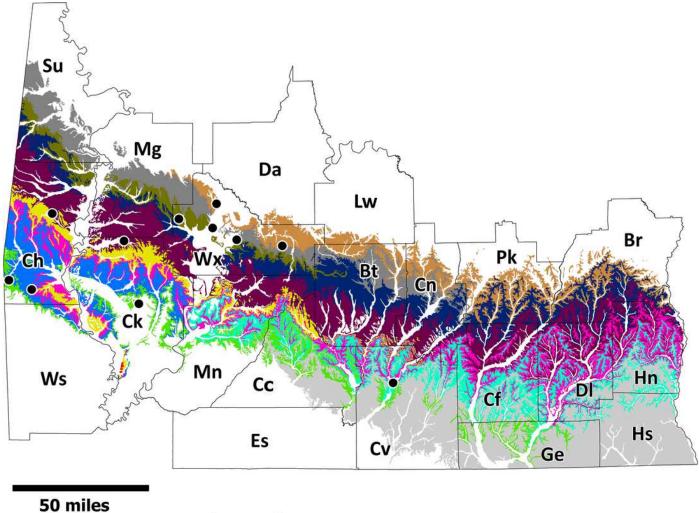
- Agassiz LJR. 1833-1844. *Recherches sur les poisons fossils*. Text (5 vols; I. xlix + 188 pp., II xii
 + 310 + 366 pp., III viii + 390 pp., IV XVI + 296 pp., V xii + 122 + 160 pp.) and Atlas.
 Neuchâtel, Imprimerie de Petitpierre.
- Applegate SP, Espinosa-Arrubarrena L. 1996. The fossil history of *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.
- 326 Bieler R, Dockery III DT. 2007. Recognition of the Paleocene gastropods "Solariella"
- 327 *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, 1512.
- 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.
- 341 Ebersole JA, Dean LS. 2013. The history of Late Cretaceous vertebrate research in Alabama.
 342 *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*
- 345 *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.
- Glikman LS. 1964. *Sharks of the Paleogene and their stratigraphic significance*. Moscow: Nakua
 Press, Moscow. [In Russian]
- 358 Hansen BB, Cuny G, Rasmussen BW, Shimada K, Jacobs P, Heilman-Clausen C. 2013.
- 359 Associated skeletal and dental remains of a fossil odontaspid shark (Elasmobranchii:

- Lamniformes) from the Middle Eocene Lillebælt Clay Formation in Denmark. *Bulletin of the 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.
- Jordan DS, Hannibal H. 1923. Fossil sharks and rays of the Pacific Slope of North America.
 Bulletin of the Southern California Academy of Sciences 22:27-63.
- Keroher GC et al., 1966. Lexicon of geologic names of the United States for 1936-1960. U.S. *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
 Naturelle de Belgique 32:367-472.
- Mancini EA, Tew BH. 1988. Paleocene sequence Stratigraphy of southwestern Alabama. *Gulf Coast Association of Geological Societies Transactions* 38:453-460.
- Mancini EA, Tew BH. 1991. Relationships of Paleogene state and planktonic foraminiferal zone
 boundaries to lithostratigraphic and allostratigraphic contacts in the eastern Gulf Coastal
 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]
- Nolf D, Dockery III DT. 1993. Fish otoliths from the Matthews Landing Marl Member (Porters
 Creek Formation), Paleocene of Alabama. *Mississippi Geology* 14(2):24-39.
- Nyberg KG, Ciampaglio CN, Wray GA. 2006. Tracing the ancestry of the great white shark,
 Carcharodon carcharias, using morphometric analyses of fossil teeth. *Journal of Vertebrate Paleontology* 26:806-814.
- Pimiento C, Ehret DJ, MacFadden BJ, Hubbell G. 2010. Ancient nursery area for the extinct
 giant shark Megalodon from the Miocene of Panama. PLoS One 5(5): e10552.
- Pimiento C, Gonzalez-Barba G, Hendy AJW, Jaramillo C, MacFadden BJ, Montes C, Suarez SC,
 Shippritt M. 2013. Early Miocene chondrichthyans from the Culebra Formation, Panama: A
 window into marine vertebrate faunas before closure of the Central American Seaway. *Journal of South American Earth Sciences* 42: 159-170.
- Purdy R. 1998. Chondrichthyan fishes from the Paleocene of South Carolina. In: Sanders AE, ed. *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
- 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
 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 of403 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.
- 408 White EI. 1956. The Eocene fishes of Alabama. *Bulletins of American Paleontology*, 36 (156):
 409 123-150.
- 410 Zhelezko V, Kozlov V. 1999. Elasmobranchii and Paleogene biostratigraphy of Transurals and
- 411 Central Asia. *Materials on stratigraphy palaeontology of the Urals*, Vol. 3. Russian Academy
- 412 of Sciences, Urals Branch, Uralian Regional Interdepartment Stratigraphical Commission,
- 413 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).











Eocene-Oligocene

Residuum

Eocene

- Jackson Group undifferentiated
 - Gosport Sand and Lisbon undiff.

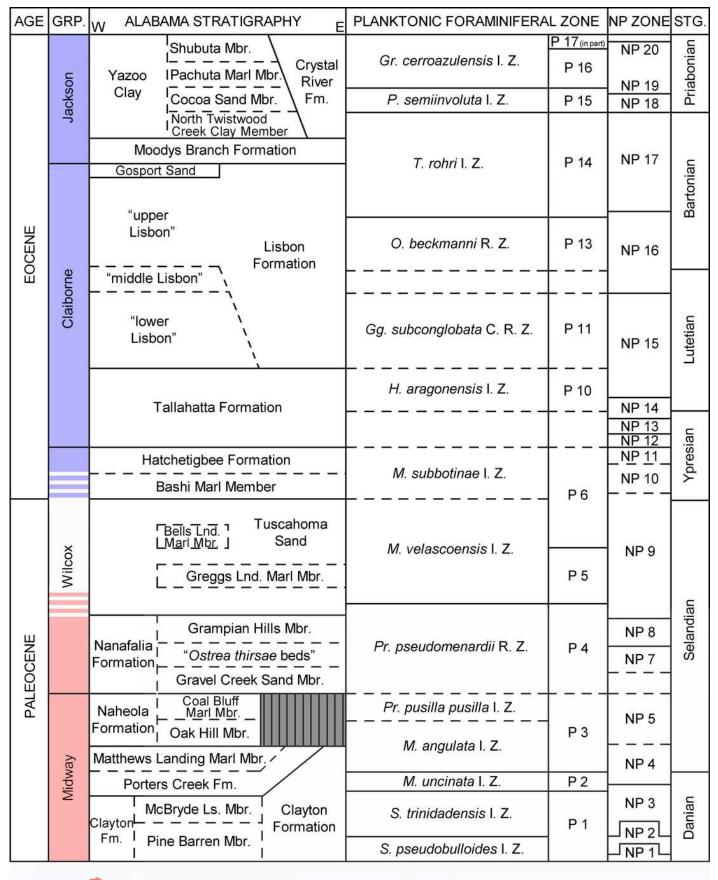
Lisbon Formation

Tallahatta Formation

Hatchetigbee Formation

Paleocene and Eocene Stratigraphy of Alabama

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



Range of Otodus obliquus in Alabama

Range of *Carcharocles* auriculatus in Alabama

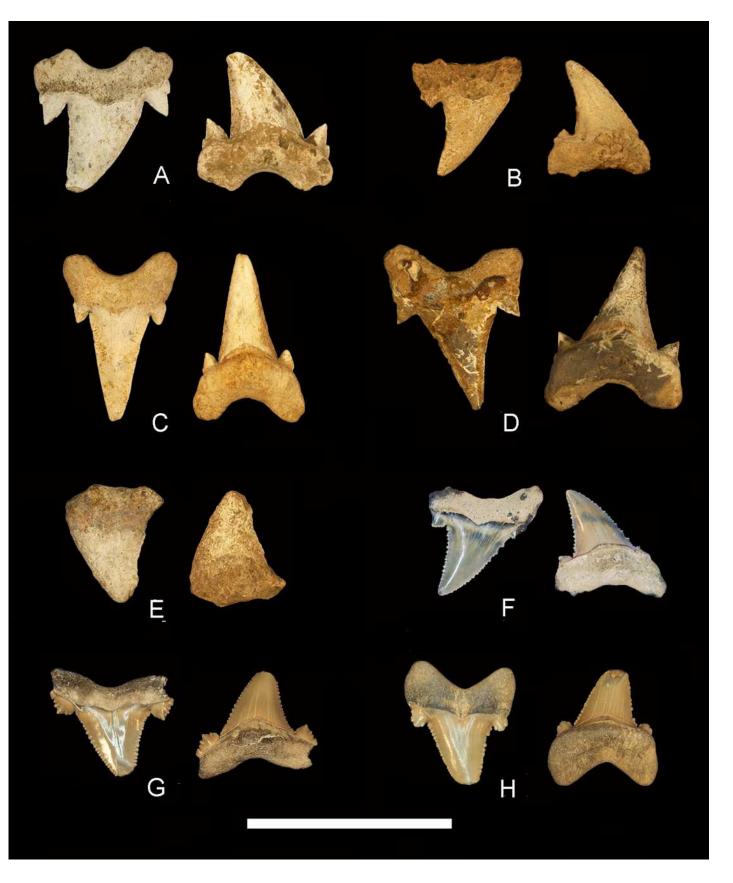
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Otodus obliquus and Carcharocles auriculatus teeth from Alabama

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.

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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.

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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 Lutetian/Bartonian	Choctaw	AL	Shell Creek
ALMNH 1985.72.33	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1985.72.43.3	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1985.72.55.2	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	Unknown
ALMNH 1985.72.62.3	Carcharocles	auriculatus	Unknown	Unknown	Unknown	AL	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 n	Unknown	AL	Unknown
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 n	Choctaw	AL	Unknown
ALMNH 2000.1.16.1	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia n	Choctaw	AL	Unknown
ALMNH 2000.1.27.1	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Choctaw	AL	Unknown
ALMNH 2000.1.29.1	Carcharocles	auriculatus	Yazoo Clay	Bartonian/Priabonia	Choctaw	AL	
ALMNH 2000.1.33.1	Carcharocles	auriculatus	Pachuta Marl Member	n Priabonian	Washington	AL	Unknown Bashi
ALMNH 2000.1.53	Carcharocles	auriculatus	Yazoo	Bartonian/Priabonia n	Choctaw	AL	Unknown
ALMNH 2000.1.57	Carcharocles	auriculatus	Yazoo	Bartonian/Priabonia	Choctaw	AL	Unknown
ALMNH 2000.1.59	Carcharocles	auriculatus	Yazoo	Bartonian/Priabonia	Choctaw	AL	
ALMNH 2005.6.259	Carcharocles	auriculatus	Yazoo Clay	n Bartonian/Priabonia	Choctaw	AL	Unknown
ALMNH 2005.6.279	Carcharocles	auriculatus	Yazoo Clay	n Bartonian/Priabonia	Clarke	AL	Unknown 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	AL	Unknown Ducieis Dlasff
ALMNH 2005.6.408.1	Carcharocles	auriculatus	Unknown	Unknown	Wilcox	AL	Prairie Bluff
ALMNH 2010.5.3	Carcharocles	auriculatus	Unknown Motthews Londing Morl	Unknown	Unknown Wilcox	AL AL	Unknown Camden
GSA 5050	Otodus	obliquus	Matthews Landing Marl Member	Selandian			
GSA 5051	Otodus	obliquus	Unknown	Unknown	Wilcox	AL	Unknown
GSA 5052	Otodus	obliquus	Matthews Landing Marl Member	Selandian	Wilcox	AL	Matthews Landing
GSA 5053	Otodus	obliquus	Porters Creek Formation	Danian	Wilcox	AL	Graveyard Hill No. 4
GSA 5054	Otodus	obliquus	Midway Group	Danian/Selandian	Unknown	AL	Unknown
MSC 20969	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20970	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20971	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	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	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20983	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	Point-A Dam
MSC 20984	Carcharocles	auriculatus	Lisbon-Tallahatta Contact	Lutetian	Covington	AL	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
MSC 34422	Carcharocles	auriculatus	Yazoo Clay - Pachuta Marl Mbr.	Priabonian	Washington	AL	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