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FOSSIL CHIMAEROID REMAINS (CHONDRICHTHYES: HOLOCEPHALI) FROM WILLIAMSBURG COUNTY, SOUTH CAROLINA, USA

David J. Cicimurri

Campbell Geology Museum, Clemson University, Clemson, South Carolina 29634 <dcheech@clemson.edu>

ABSTRACT

Three fossil holocephalian tooth plates have been recovered in Kingstree, Williamsburg County, South Carolina. All of the fossils were collected from a lag deposit containing a temporally mixed vertebrate assemblage. Two specimens, an incomplete left mandibular tooth plate and an incomplete left palatine tooth plate, are *Edaphodon* and compare favorably to *E. mirificus*. The third specimen is an incomplete and highly abraded right mandibular tooth plate from a very young individual that is questionably referred to *Edaphodon*.

The tooth plates were associated with Cretaceous shark and dinosaur teeth, Paleocene shark and crocodilian teeth and turtle bones, and Plio-Pleistocene shark teeth and terrestrial mammal remains. The source of the Cretaceous fossils is arguably from Maastrichtian (late Cretaceous) strata (i.e., Peedee or Steel Creek formations), whereas Paleocene fossils are likely derived from the Danian (lower Paleocene) Rhems Formation. These fossils were probably concentrated together during Plio-Pleistocene sea level highstand, at which time the younger vertebrate material was deposited.

INTRODUCTION

Some of the geologic history of the South Carolina Coastal Plain is preserved as a complex stratigraphic sequence that is far from completely understood. There were many transgressions and regressions of the Atlantic Ocean over the last 75 million years, and sediment composition varies greatly both vertically (time) and laterally (geography). This lithologic variation makes correlation of widely separated areas difficult, especially when units were eroded during marine transgressive/regressive events or terrestrial fluvial processes. The local presence of a particular, generally widely distributed formation is therefore not necessarily predictable. Often, contacts between lithologic units are marked by a conspicuous lag deposit, and in South Carolina fossils of greatly different ages can be found mixed together. One such example is found along the banks of Clapp Creek within the city limits of Kingstree, Williamsburg County, South Carolina (Figure 1). Fossils recovered from a thick lag at the site include a mixture of late Cretaceous, early Paleocene, and Plio-Pleistocene taxa. The Cretaceous component contains a variety of terrestrial (dinosaur) and marine (elasmobranchs) animals, as do the Paleocene (crocodilians, trionychid and chelonioid turtles, elasmobranchs) and Plio-Pleistocene components (equids and proboscideans, elasmobranchs and cetaceans).

Fossils from Clapp Creek came to the attention of Rudy Mancke (then Curator of Natural History at the South Carolina State Museum) in the mid 1980s, and soon thereafter he alerted Bruce Lampright (then of Coastal Carolina University) to the fossil deposits to be found there. Lampright told Aura Baker (former president of the Myrtle Beach Fossil Club) about the deposit and she encouraged club members to collect at the site. Both she and Lampright ultimately contributed significant collections to the SC State Museum.

Some of the fossil species occurring at the Kingstree site have been discussed in the literature (i.e., Briedis and Knight, 1996; Erickson, 1998; Hutchison and Weems, 1998; Knight et al., 2007) and the Baker and Lampright collections are receiving renewed interest by the present author. This collection has proven to be paleontologically significant, as it contained one of the few records of *Schizorhiza stromeri* from North America (Knight et al., 2007), as well as some of the few dinosaur remains (hadrosaurian teeth) from the state (Erickson et al., in press). In a review of the State Museum collection, several more unexpected vertebrate occurrences were noted (currently under study), including the three holocephalian remains that form the basis of this report. The purpose of this paper is to provide a detailed description of the fossils, which represent the first record of *Edaphodon* and only the third, fourth and fifth holocephalian remains reported from the state.

I also discuss the potential ages and stratigraphic provenances of these chimaeroid fossils.

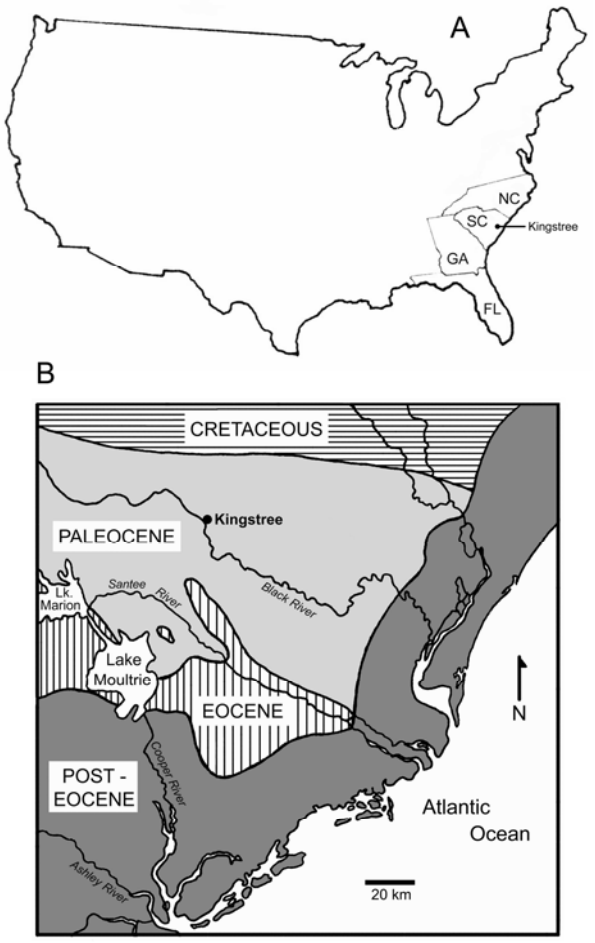

FIGURE 1. A. Outline map of contiguous USA showing some southeastern states. B. View of central South Carolina coastal region showing outcrop belts of coastal plain strata. A modified from Case (1994) and B adapted from Weems and Bybell (1998).

MATERIALS AND METHODS

The three specimens described herein are housed in the South Carolina State Museum (**SC**), and all were collected from Clapp Creek, approx. 75 m downstream from a bridge on Lawrence Street, Kingstree, Williamsburg County, South Carolina. Specimens (or photographs of specimens) from the following institutions have been examined: Academy of Natural Sciences (**ANSP**), Philadelphia, Pennsylvania; New Jersey State Museum (**NJSM**), Trenton, New Jersey; Sternberg Museum of Natural History (**FHSM**), Hays, Kansas; American Museum of Natural History (**AMNH**), New York; and Campbell Geology Museum (**BCGM**), Clemson, South Carolina. Descriptive terminology for tooth plate morphology follows Stahl and Parris (2004). Measurements of the fossils were taken with Marathon digital calipers.

Stahl (1999) included Callorhynchidae, Chimaeridae, and Rhinochimaeridae within Chimaeriformes, placing extinct taxa like *Edaphodon*, *Ischyodus* and others into two subfamilies (Callorhynchinae and Edaphodontinae) within Callorhynchidae (see also Stahl and Chatterjee, 2002; Parmley and Cicimurri, 2005; Takeuchi and Huddleston, 2006; Shin, 2010). However, these taxa are more often placed in the extinct Edaphodontidae (i.e., Ward and Grande, 1991; Nessov and Averianov, 1996; Popov and Beznosov, 2006; Popov and Shapovalov, 2007; Popov, 2008) and this classification is followed here.

SYSTEMATIC PALEONTOLOGY

Elasmobranchii Bonaparte, 1838
Chimaeroidei Patterson, 1965
Edaphodontidae Garman, 1901
Edaphodon Buckland, 1838
Edaphodon sp. cf. *E. mirificus* Leidy, 1856
Figures 2 and 3

Material Examined—SC83.89.19, incomplete left mandibular tooth plate (Figure 2); SC87.158.150, incomplete left palatine tooth plate (Figure 3).

Description—The mandibular tooth plate (SC83.89.19) is missing much of the mesial beak, at least one third of the distal end, and all of the tritor pads. However, the remaining portion is well preserved, with the mesodistal length measuring 67.90 mm and maximum labiolingual width measuring 23.79 mm. The plate is laterally compressed, with the area immediately mesial to the anterior outer tritor forming the beginning of the beak (Figure 2). The left and right mandibular plates articulated along a symphyseal surface, of which only a length of 32.70 mm is preserved (Figure 2A-B). The distal end of the plate appears to diverge at the point immediately distal to the end of the symphyseal surface (Figure 2E-F). The labial face is weakly convex flat dorsally, concave medially, and apparently convex ventrally, with the entire surface finely striated parallel to the plate's length (Figure 2C). As preserved, the ventral aspect of the lingual face (below the middle tritor) is flat and relatively smooth, but it appears that the middle tritor constituted the upper half of the face distal to the beak (Figure 2A-B).

Although no tritoral tissue remains, traces of four tritors are preserved as cancellous-textured and laminar-textured attachment surfaces on the mandibular dentine. The attachment surface of the symphyseal tritor spans the entire length of the labio-ventral face of the tooth plate (Figure 2C-D), and the

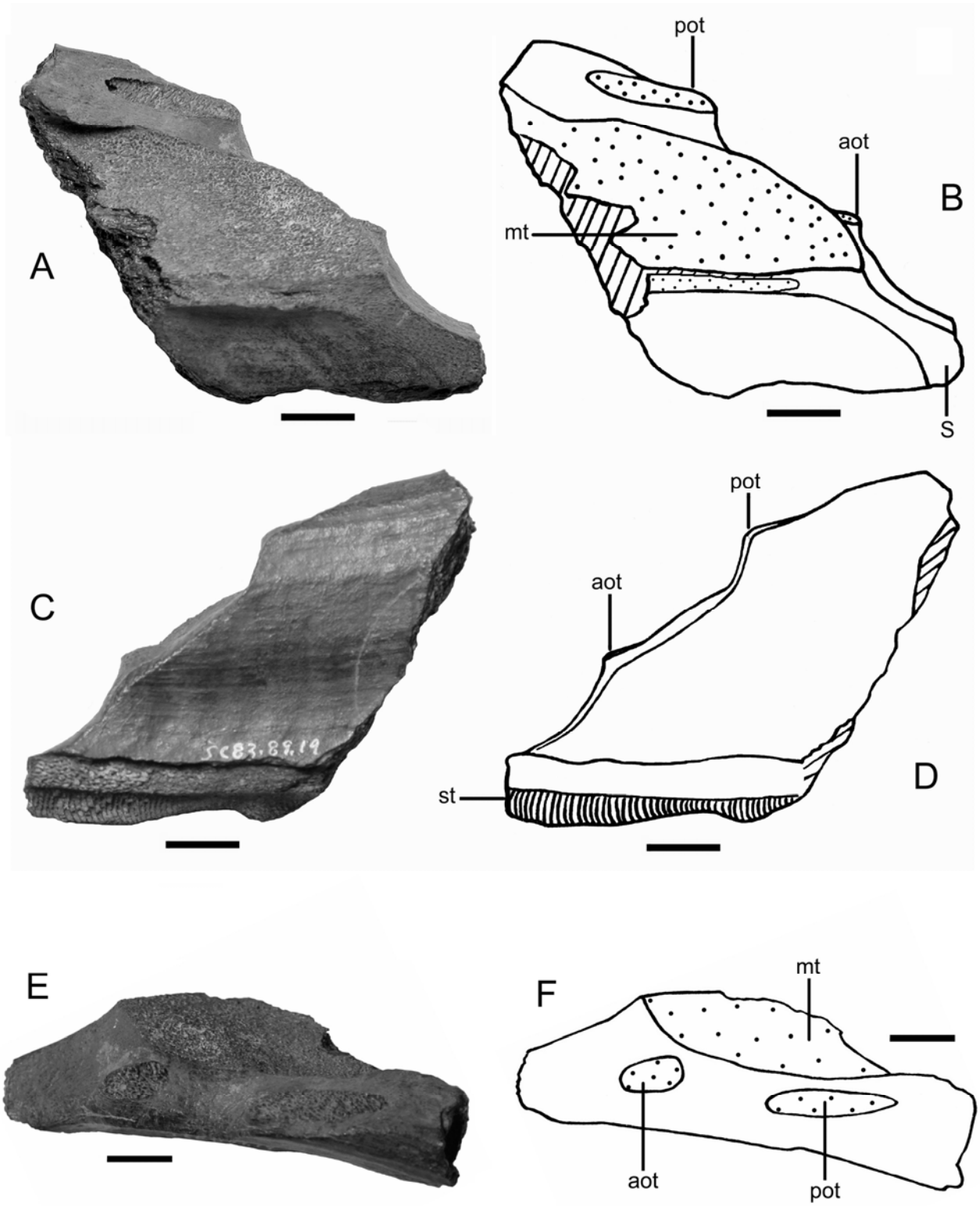

FIGURE 2. SC83.89.19, *Edaphodon* sp. cf. *E. mirificus* left mandibular tooth plate. A-B, specimen (A) and interpretive drawing (B) in lingual view (mesial at right). C-D, specimen (C) and interpretive drawing (D) in labial view. E-F, specimen (E) and interpretive drawing (F) in oral view (mesial at left). In B and D, dotted regions indicate locations of tritors and hatched regions indicate broken surfaces. Abbreviations: aot, anterior outer tritor; mt, middle tritor; pot, posterior outer tritor; S, symphysis; st, symphyseal tritor. Scale bars = 10 mm.

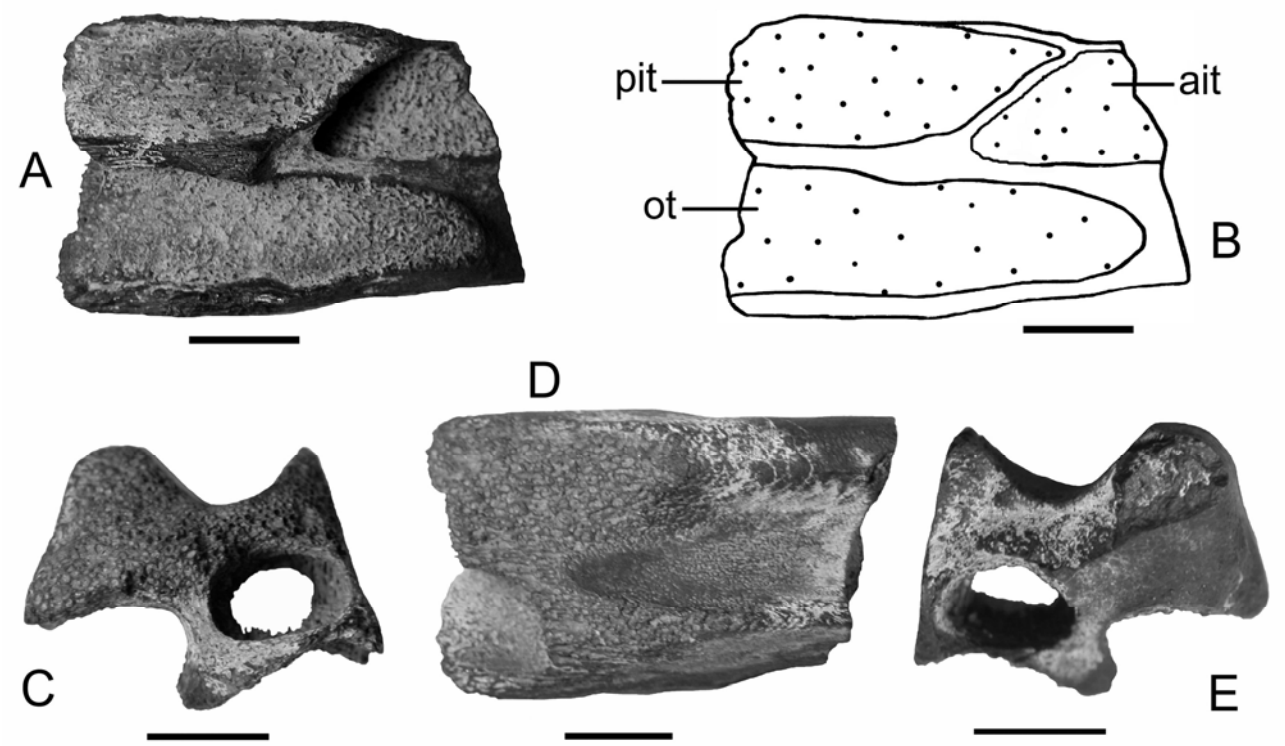

FIGURE 3. SC87.158. 150, *Edaphodon* sp. cf. *E. mirificus* left palatine tooth plate. A-B, specimen (A) and interpretive drawing (B) in oral view (mesial at right, labial at bottom). C, distal view (labial at left). D, aboral view (labial at top). E, mesial view (labial at right). Dotted areas in B indicate locations of tritors. Abbreviations: ait, anterior inner tritor; ot, outer tritor; pit, posterior inner tritor. Scale bars = 10 mm.

dorsal aspect of this surface is cancellous, whereas the ventral aspect bears numerous closely spaced (1 mm apart) vertical laminae. An ovoid anterior outer tritor measured 10.05 mm long x 5.26 mm wide and was situated on a prominence located labially and at the mesial end of the middle tritor (Figure 2B, D, F). The tritor tissue immediately distal to the exposed portion was covered by dentine, but is now preserved as a hollow circular tube located lateral to the middle tritor (separated by as little as 2.5 mm of dentine) and seen at the broken distal surface (29.48 mm from the distal end of the exposed portion of the tritor, 22.90 mm below the dorsal margin). The exposed portion of an ovoid, elongated posterior outer tritor measured 18.89 mm long x 5.91 mm wide. This tritor was situated on a higher prominence on the labial margin, adjacent to the middle tritor (Figure 2B, D, F). Immediately distal to the exposed portion, the tritor tissue was covered by a thin layer of dentine (up to 3 mm thick), but as preserved the location of the tissue is indicated by a hollow circular tube exposed at the broken distal end of the plate. Based on the preserved attachment surface, a very large middle tritor was pointed mesially and separated from the outer tritors by 3 to 4 mm of dentine, and this surface measures 49.26 mm long and 21.43 mm wide (Figure 2B, F). At the distal one quarter of the posterior outer tritor, the dentine overhangs the middle tritor attachment surface (Figure 2A), indicating that the middle tritor pad was covered by dentine in this area (i.e., only the mesial 38.67 mm of the middle tritor pad was exposed in life). In labial view the oral margin of the labial face has a sigmoidal outline due to the prominences (Figure 2C-D).

The palatine plate (SC87.158.150) is incomplete, missing an unknown portion of the mesial end and the entire postoral surface (some of the distal oral surface is also absent). As preserved, the specimen has a rectangular appearance in oral/aboral view (Figure 3A-B, D) and measures 42.18 mm long x 26.27 mm at its widest (the plate is slightly narrower mesially at 22.37 mm). Only 27.36 mm of the symphyseal border is preserved, and this surface is flat and nearly vertical. Although the labial margin is damaged, it appears to flare outward slightly at approximately the middle of the preserved portion. As is the case with the mandibular plate, no tritoral tissue is preserved on the palatine plate, but the attachment surfaces of three tritors occupy nearly the entire oral surface (Figure 3A-B). The attachment surface of the outer tritor is located along the labial margin and measures 37.72 mm long x 10.86 mm at its widest. However, it appears that only the mesial 22.22 mm of tritor was exposed as a triangular pad (dentine is broken away where it would have covered part of the tritor tissue). Attachment

surfaces of the anterior and posterior inner tritors are found along the symphyseal margin. As preserved, 18.25 mm of the anterior tritor was exposed, but at least 21.84 mm of tissue extended into the palatine dentine (only an ovate hollow tube remains above the posterior inner tritor, visible at the broken mesial and distal ends of the plate; Figure 3C, E). The posterior inner tritor was located immediately distal to the exposed anterior inner tritor, and 30.23 mm of the attachment surface is preserved. The outer tritor and anterior inner tritor appear to have been relatively narrow, but because the dentine is incomplete it is unclear if the posterior inner tritor was broader than preserved. In aboral view, unabraded external surfaces are smooth (Figure 3D). A 6.13 mm high x 7.58 mm wide convex ridge is located above the outer tritor and a 5.06 mm high x 5.43 mm wide sharp ridge is located over the anterior outer tritor, and these ridges are separated by a U-shaped furrow (Figure 3C, E).

Remarks—Within Chimaeriformes, only Callorhynchidae and Edaphodontidae have a fossil record in North America, but comparison of the South Carolina material was restricted to Edaphodontidae because Callorhynchidae is only known from egg cases (Hussakof, 1912; Brown, 1946; Obruchev, 1967; Stahl, 1999). Several edaphodontid genera have been reported from Cretaceous deposits of North America, including *Edaphodon*, *Eumylodus*, *Ischyodus*, and *Leptomylus* (i.e., Cope, 1869; Case, 1978; Stahl and Parris, 2004; Cicimurri et al., 2008), but only *Edaphodon* and *Ischyodus* have a Paleocene or younger record (i.e., Cope, 1875; Case, 1996; Hoganson and Erickson, 2005; Parmley and Cicimurri, 2005).

The mandibular plates of *Eumylodus* are unknown, but those of *Edaphodon*, *Ischyodus* and *Leptomylus* are similar in overall morphology. Mandibular plates of *Leptomylus* (ANSP 9440) are very unusual in that outer tritors are lacking and only a very narrow middle tritor is generally developed (see also Hussakof, 1912; Stahl, 1999). Mandibular plates of *Ischyodus* and *Edaphodon* can be difficult to distinguish from one another (Stahl, 1999) if the remains are incomplete, but *Ischyodus* mandibular plates have four or more tritors (i.e., Case, 1978; Ward and Grande, 1991; Popov, 1999a; Hoganson and Erickson, 2005). Although SC83.89.19 is incomplete, there is no indication of large crushing pads other than the anterior and posterior outer and middle tritors. The symphysis of SC83.89.19 is elongated and flat like *Edaphodon* mandibular plates I examined from New Jersey (i.e., NJSM 11362; see also Stahl and Parris, 2004) and Georgia (SC2004.34.1; see also Parmley and Cicimurri, 2005), a feature not observed on mandibular plates of *Ischyodus* or *Leptomylus* that I examined (also Hussakof, 1912; Case, 1978; Ward and Grande, 1991; Stahl, 1999; Hoganson and Erickson, 2005). I conclude that SC 83.89.19 is referable to the genus *Edaphodon*.

Although incomplete, SC87.158.150 (palatine tooth plate) was compared to the palatine plate of *Eumylodus* (FHSM VP-16685), which has four diminutive and widely separated tritors, wide oral region, and lacks a deep longitudinal sulcus on the aboral surface (Cicimurri et al., 2008). The aboral surface of a *Leptomylus densus* palatine plate (ANSP 9441) is relatively flat and smooth, and there are only two narrow and elongated tritors on the oral surface (inner and outer; see also Hussakof, 1912; Stahl, 1999). Palatine plates of *Ischyodus* and *Edaphodon* are morphologically similar, but *Ischyodus* plates bear four large tritors on the oral surface, and there may be accessory tritors along the labial margin (Ward and Grande, 1991; Popov, 1999a; Stahl, 1999; Hoganson and Erickson, 2005). In contrast, *Edaphodon* palatines contain three large tritors (i.e., Stahl and Parris, 2004; Shin, 2010), a fourth is only occasionally present (Ward, 1973), and there are no accessory tritors (Stahl, 1999). SC87.158.150 is incomplete, but there are no indications of tritors other than the anterior and posterior inner tritors and outer tritor. Whereas the aboral surface of *Ischyodus* is generally flat and exhibits a descending lamina, SC87.158.150 and palatine plates of *Edaphodon* exhibit a deep longitudinal sulcus and lack a descending lamina (see Patterson, 1992; Popov, 1999a; Stahl, 1999). These features lead me to assign SC87.158.150 to *Edaphodon*.

The small sample size, incompleteness of the material, and lack of stratigraphic control limits the accuracy of species determination for SC83.89.19 and SC87.158.150. *Edaphodon* has a long temporal distribution (Cretaceous to Pliocene) and was widely distributed geographically (Stahl, 1999). Complete dentitions are known for only a few species (i.e., *E. hesperis*, *Edaphodon mirificus*, *E. sedgwicki*), and many fossil edaphodontids are known only from isolated tooth plates (Stahl, 1999; Duffin, 2001). Tooth plate morphology varies greatly between species, with age (ontogeny; see Hussakof , 1912 and Ward and Grande, 1991), and even within the mouth of a single individual (Stahl and Parris, 2004). This inter- and intra-specific variation adds to the difficulty of identifying the Kingstree *Edaphodon* species.

The post-Cretaceous *Edaphodon* record of the USA very poorly known. However, SC83.89.19 (left mandibular) differs from the Late Eocene *Edaphodon* sp. reported by Parmley and Cicimurri (2005), as well as from lower Paleogene European taxa like *E. leptognathus* (Agassiz, 1843) and *E. bucklandi* (Agassiz, 1843), in that the middle tritor does not appear to have been bifurcated (see also Kemp et al., 1990; Consoli, 2006). The labial face of SC83.89.19 is

convex dorsally and concave ventrally, whereas the incomplete mandibular of *E. eocaenus* (AMNH 7205; see also Cope, 1875) from New Jersey exhibits a more evenly convex labial face.

Considering those *Edaphodon* species reported from US Cretaceous strata, a large number, primarily from Maastrichthian (late Cretaceous) greensands of New Jersey, have been described. Hussakof (1912) synonymized numerous species erected by Cope (1869, 1875) with *E. mirificus* (i.e., *fecundus*, *incrassatus*, *longirostris*), and Stahl (1999) recognized an additional four species: *E. agassizi* (Buckland, 1835), *E. latigerus* (Cope, 1869), *E. sedgwicki* (Agassiz, 1843), and *E. stenobyrus* (Cope, 1875). All of these species occur in Maastrichtian greensands of New Jersey, but unfortunately the stratigraphic position of much of the original material reported by Cope (1869, 1875) is imprecisely known. Although the tooth plates have varied morphologies, the species may someday prove to be conspecific; the possibility of multiple coeval species cannot be ruled out, but this may have been unlikely (see also Popov, 2008) because the great similarities in tooth plate morphologies indicates similar prey preferences, and therefore intra- and interspecific competition for food resources.

Hussakof (1912) synonymized Cope's (1869) *Ischyodus smocki* (see also Fowler, 1911) with the European species *Edaphodon agassizi*, and SC83.89.19 differs from Cope's type mandibular (AMNH 7192) in having a smaller anterior outer tritor, sloping as opposed to horizontal oral margin from this tritor to the posterior outer tritor, and the dorsal margin of the middle tritor is convex, not concave. However, European *E. sedgwicki* occurs in "middle" Cretaceous (Cenomanian and Turonian) strata, and these mandibulars have a narrower but more elongated middle tritor than SC83.89.19, and the posterior outer tritor is also more elongated (see also Patterson, 1992; Duffin and Reynders, 1995; Popov, 2008). In labial view, the type of *E. latigerus* (AMNH 2238) appears very elongated compared to SC83.89.19 due to the much greater length of the anterior prominence (for the anterior outer tritor). In addition, the posterior outer tritor is much more elongated, and the middle tritor is narrower and more elongated than SC83.89.19 (see also Hussakof, 1912; Duffin and Reynders, 1995). Although it is broken, the location of the symphyseal tritor of SC83.89.19 indicates that the tooth plate was not nearly as deep as the type mandibular of *E. stenobyrus* (AMNH 7204). Additionally, the middle tritor of *E. stenobyrus* is much smaller than that of SC83.89.19 (see also Hussakof, 1912; Duffin and Reynders, 1995). Hussakof (1912) synonymized Cope's (1875) *Ischyodus tripartitus* (see also Fowler, 1911) with the European species *E. sedgwicki*. This species has a very elongated beak, a feature not preserved in SC83.89.19. However, both the US and European mandibulars assigned to *E. sedgwicki* bear a median tritor with two or more divisions (Cope, 1875; Hussakof, 1912; Stahl, 1999). In contrast, the middle tritor of SC SC83.89.19 appears to have been large and without division.

The mandible of *E. barberi* Applegate 1970 from the Campanian of Alabama differs significantly from SC83.89.19 in the morphology and locations of the tritors, the labial margin from the beak to the posterior outer tritor is arcuate, and the symphyseal surface is indistinct. The South Carolina specimen also differs from the large mandibular plates of *E. hesperis* (Campanian of Vancouver Is., Canada) in that the anterior and posterior outer tritors are situated more mesially with respect to the middle tritor (see Shin, 2010). With respect to the depth of the mandibular plate, length of the anterior and posterior prominences, location and morphology of the attachment surfaces for the tritor tissues, and the shape of the symphyseal surface, SC83.89.19 is more similar to mandibular plates of *E. mirificus* (see also Fowler, 1911; Hussakof, 1912; Stahl, 1999; Stahl and Parris, 2004) than to the other species mentioned above. In addition, SC87.158.150 is morphologically inseparable from palatine plates of *E. mirificus* that I examined (i.e., ANSP 5481 and 5825, NJSM 11362).

? *Edaphodon*
Figure 4

Material Examined--SC.158.151, incomplete right mandibular tooth plate.

Description—The specimen is the smallest fossil chimaeroid mandibular tooth plate I have encountered. Some of the mesial end and an unknown portion of the distal end are missing, and the tritor tissue is not preserved. The remaining section is highly abraded (post-mortem taphonomic processes). As preserved, the mesodistal length measures only 13.4 mm, with maximum labiolingual width measuring 4.85 mm. The plate is laterally compressed, with the mesial-most area appearing to form the beginning of a beak (Figure 4A, C, D). The labial face is smooth and featureless, and the distal end does not appear to diverge as is does on SC83.89.19. Two tritors form the dorsal aspect of the lingual face, whereas the ventral aspect exhibits a mesially located circular fossa and a more distally located longitudinal furrow below the lower tritor.

As is the case with SC83.89.19, no tritoral tissue is preserved on SC.158.151, but four tritors are indicated by cancellous-textured and laminar-textured surfaces on the mandibular dentine. A symphyseal tritor spans the entire length of the tooth plate (Figure 4A-B) but is best seen linguo-ventrally along the mesial half of the tooth plate as closely spaced (0.5 mm

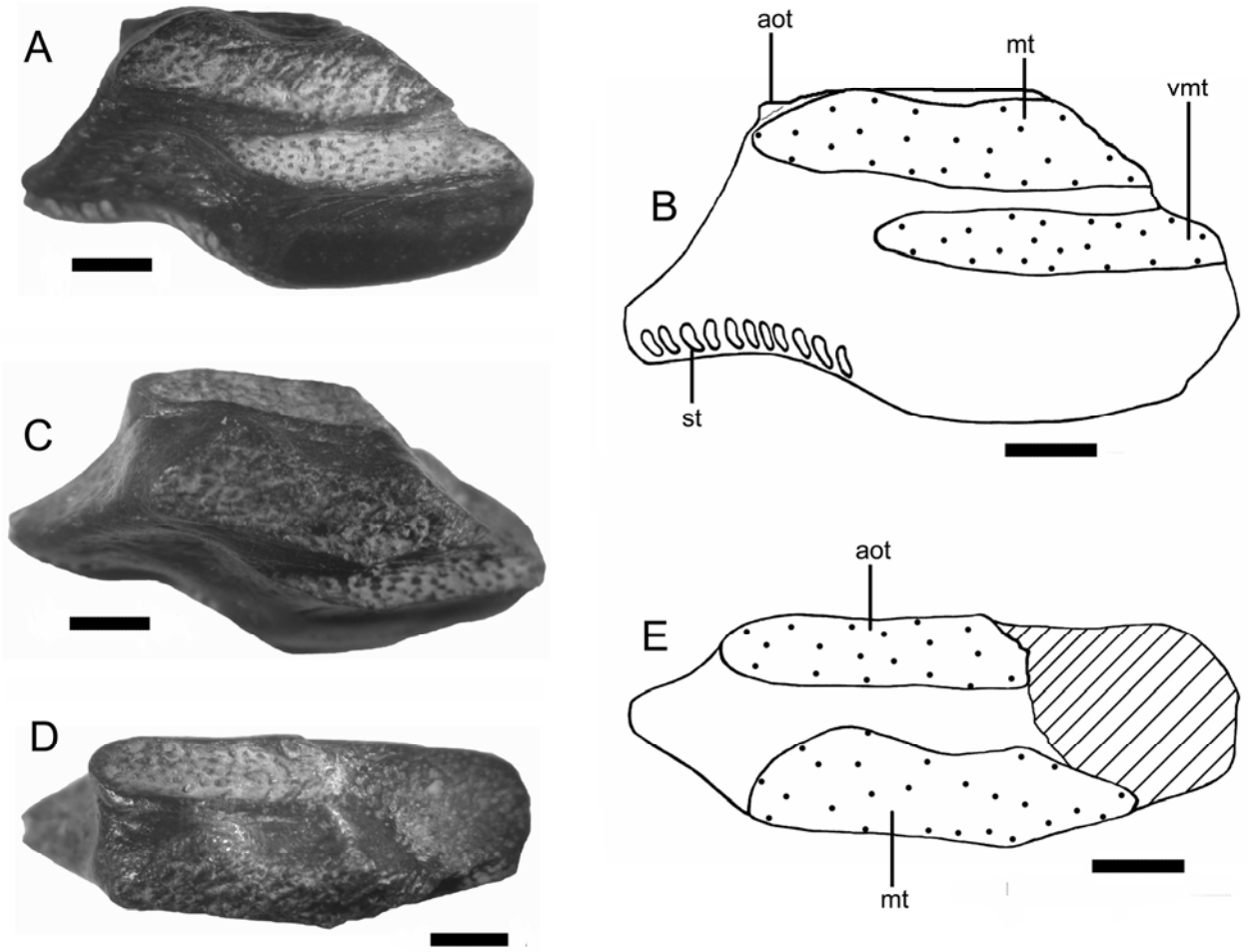

FIGURE 4. SC.158.151, ? *Edaphodon* sp. right mandibular tooth plate. A-B, specimen (A) and interpretive drawing (B) in lingual view (mesial at left). C, oblique lingual view showing anterior outer and middle tritor. D-E, specimen (D) and interpretive drawing (E) in oral view (mesial at left). Abbreviations as in Figure 2, with the addition of vmt, ventral pad of middle tritor. Scale bars = 2 mm.

apart) vertical laminae separated by matrix-filled spaces. As preserved, the surface of an anterior outer tritor measures 6.62 mm long x 1.63 mm wide, but a slight medial constriction indicates that only the mesial half of the tritor tissue functioned as a crushing pad. This tritor is situated on an indistinct prominence located along the labial margin, directly adjacent to and separated from a middle tritor by 1.02 to 1.68 mm of dentine (Figure 4D-E). The surface for the middle tritor is sinuous and extends along the entire dorsal margin of the lingual face, measuring 8.51 mm long x 2.89 mm wide (Figure 4A-B). It is not clear how much of the tritor tissue was exposed in life. An additional tritor is located below the middle tritor and separated from it by only 0.89 mm of dentine (Figure 4A-C). The surface for this lower tritor measures up to 7.99 mm long and 1.32 mm wide, but broken dentine indicates that only the mesial 3.22 mm of tritor tissue was exposed in life.

Remarks—SC.158.151 is highly abraded from post-mortem taphonomic processes, and I have not previously encountered a mandibular plate this small. The laminated symphyseal tritor (Figure 4B) leads me to assign SC.158.151 to Edaphodontidae (see Ward and Grande, 1991). The tritor below the middle tritor (Figure 4A-B) could be interpreted as a posterior inner tritor as seen in *Ischyodus bifurcatus*. The large tritor pad seen on *I. bifurcatus* mandibular tooth plates has been interpreted as being formed from the fusion of the middle tritor with the posterior inner tritor (Case, 1978; and Case and Schwimmer, 1992), and SC.158.151 could therefore represent an ontogenetic stage within the species where the two tritors have not yet fused. However, there is no indication of an anterior inner tritor near the ventral margin as in *I. bifurcatus*, *I. dolloi*, and *Ischyodus rayhaasi* (see Case and Schwimmer, 1992; Stahl, 1999; Hoganson and Erickson, 2005), and no descending lamina is visible, suggesting that the plate is not *Ischyodus*.

This tritor may simply have been exposed as an accessory pad below the middle tritor, and this feature is also seen along the ventral margin of the middle tritor of SC83.89.19 (*Edaphodon*). In Figure 2B, note that there is a small projection of pleromin (not preserved) into the symphyseal surface, and a thin layer of dentine would separate this pleromin from the main body of the middle tritor. A similar thin pleromin body can be seen on mandibular plates of *E. leptognathus* and *E. bucklandi* (see also Kemp et al., 1990), but it is unclear if these pleromin bodies on SC83.89.19 and SC.158.151occurred as an elonageted, functional tritor or were covered by dentine. These do not appear to be equivalent to the inner tritor of *E. mantelli* as identified by Popov (1999b). The apparently large area occupied by the tritoral tissue on SC.158.151 is likely related to the very young age of the individual, as Ward and Grande (1991) noted that the area decreases with age (as tooth plate size increases). An apparent symphysis, that is, the lingual margin extending from the symphyeal tritor to the middle tritor, is slightly concave and somewhat flattened (similar to *Edaphodon*), but it is difficult to ascertain if this latter feature is natural or the result of post-mortem abrasion. Even though SC.158.151 is incomplete and highly abraded, its morphology is more consistent with *Edaphodon* than *Ischyodus*, and this specimen is therefore tentatively attributed to a very young *Edaphodon* sp.

DISCUSSION

Other Chimaeroid Fossils from South Carolina—Unfortunately, of five South Carolina chimaeroid fossils known to us, none are stratigraphically well constrained. The ablated tritor noted by Cicimurri (2007; BCGM 7007) has a rectangular outline in occlusal view, being longer (27.42 mm) than wide (13.64 mm), and I believe that it was located on a palatine tooth plate of *Edaphodon* or *Ischyodus*. The specimen was recovered from a lag deposit at the base of the Peedee Formation (middle Maastrichtian), but Cicimurri (2007) believed that the tritor was reworked from the underlying late Campanian Donoho Creek Formation (Black Creek Group). The only chimaeroid remains previously reported from Black Creek Group deposits were attributed to *Ischyodus bifurcatus* (Robb, 1989), but BCGM 7007 can only be referred to Edaphodontidae indeterminate.

The mandibular tooth plate fragment attributed to *Ischyodus* by Purdy (1998) was collected at St. Stephen, Berkeley County, 30 km SSW of Kingstree. This specimen, ChM PV3899, may have been derived from the upper Paleocene Williamsburg Formation (calcareous nannofossil Zones NP 4 – NP 9), but it was collected as float and its precise stratigraphic position is uncertain; it is not out of the realm of possibility that it originated from the underlying Rhems Formation, which was also exposed at the site. As illustrated by Purdy (1998; Figure 6C), the specimen lacks tritor tissue, but the preserved attachment surface clearly exhibits laminated texture (at the top of the photograph), indicating a laminated tritor. In Edaphodontidae, only symphyseal tritors are laminated (Ward and Grande, 1991), and ChM VP3899 could therefore represent a taxon other than *Ischyodus* (i.e., *Edaphodon*). I have examined this specimen and consider it best to identify it as Edaphodontidae indeterminate because it is too fragmentary for even a generic assignment.

Age of the Kingstree Chimaeroid Fossils and Stratigraphic Provenance—Although SC87.158.150 (palatine tooth plate) and SC83.89.19 (mandibular tooth plate) are incomplete, they may not have been subjected to extensive transport because they are relatively unabraded. As noted earlier, the fossils recovered from the Kingstree lag represent a mixture of Cretaceous, Paleocene, and Pliocene taxa. If SC87.158.150 and SC83.89.19 do represent *Edaphodon mirificus*, Maastrichtian-aged source strata are indicated, as the species is well known from Maastrichtian greensands of New Jersey (i.e., Hussakof, 1912; Stahl and Parris, 2004). This age is supported by the association of *Schizorhiza stromeri* (see Knight et al., 2007), *Rhombodus binkhorsti*, and *Serratolamna serrata*, typically Maastrictian species. The latter two elasmobranch taxa are thus far only known to occur within the Maastrichtian Peedee Formation of South Carolina (DJC unpublished data; see also Case, 1979 for North Carolina records). I conclude that the Cretaceous-aged fossils were derived from strata of Maastrichtian age, and the Peedee Formation has been reported as occurring in the Kingstree area (Weems and Bybell, 1998). The Peedee Formation was deposited in a shallowing upward, outer to inner neritic environment within calcareous nannofossil Zones CC25 and CC26 (69.5-65.6 Ma; see Edwards et al., 2000; Thibault and Gardin, 2006).

The occurrence of dinosaur teeth in the Kingstree lag must also be considered, as dinosaur remains are unknown from the Peedee Formation. Dinosaur and shark teeth are found mixed together in deltaic deposits of the Campanian Black Creek Group in Florence and Darlington counties, 40 to 60 km NNE of Kingstree (Cicimurri, 2007; DJC unpublished data), and it is possible that some of the Kingstree fossils were derived from strata of that age. However, the Maastrichtian Steel Creek Formation, temporally equivalent to the Peedee Formation and representing deltaic deposition (Fallaw and Price, 1995), has been identified in the Turbeville area of Clarendin Cocunty, only 30 km northwest of Kingstree in Clarendon

County (Erickson et al., in press). It is most parsimonious to interpret the mixture of Cretaceous terrestrial and marine taxa in the Kingstree lag as having been derived from a Maastrichtian nearshore marine (deltaic) deposit that contains dinosaur and elasmobranch remains, as opposed to having been derived from a Campanian-aged horizon or being a mixture of Campanian and Maastrichtian fossils.

The Paleocene fossils occurring at Kingstree were reported as being derived from the lower Paleocene (Danian; calcareous nannofossil zone NP 1; possibly as young as NP 3) Rhems Formation (65.5 to 61 Ma; see Weems and Bybell, 1998; Erickson, 1998; Hutchinson and Weems, 1998; Waga et al., in press), and this interpretation is supported by some of the associated batoid fossils (DJC unpublished data). The Rhems Formation is locally exposed in the Kingstree area, and a nearshore marine, possibly deltaic environment is indicated both lithologically and biologically (Erickson, 1998; Sawyer, 1998; Weems and Bybell, 1998; Hutchinson and Weems, 1998).

Although *Edaphodon* is known from Plio-Pleistocene strata of Europe and Australia (Stahl, 1999; Consoli, 2006), no material has been reported from the USA. The Kingstree lag deposit probably accumulated during sea level highstand when a fluvial system emptied into the sea in the Kingstree area. Coastal erosional processes resulted in the mixing of the Cretaceous and Paleocene fossils along with Plio-Pleistocene terrestrial (horse) and marine animals (i.e., whales, sharks and rays).

CONCLUSIONS

The first records of *Edaphodon* from South Carolina consist of an incomplete left mandibular tooth plate, incomplete left palatine tooth plate, and incomplete right mandibular of a very young individual. The morphologies of the former two specimens are most similar to equivalent elements of *E. mirificus* from the Maastrichtian of New Jersey. These chimaeroid fossils were recovered from a lag deposit containing a temporally mixed assortment of fossils, including taxa from the Cretaceous, Paleocene, and Plio-Pleistocene. The Cretaceous fossils are indicative of a Maastrichtian age, and source strata belonged to the Peedee Formation or temporally equivalent Steel Creek Formation. Paleocene fossils indicate a Danian (lower Paleocene) age, and the likely source strata are from the Rhems Formation. These older fossils were probably concentrated together during Plio-Pleistocene sea level high-stand.

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LITERATURE CITED

Aggasiz, L. 1843. Recherches sur les Poissons Fossiles, vol. 3. Neuchâtel et Soleure, Switzerland, 390 pp.

Applegate, S. P. 1970. The vertebrate fauna of the Selma Formation of Alabama. Part 8. The Fishes. Fieldiana Geology Memoirs 3:383-433.

Bonaparte, C. 1838. Selachorum tabula analytica. Nuovi Annali della Scienza Naturali (Blogna) 2:195-214.

Briedis, D., and J. L. Knight. 1996. The Kingstree Fauna: What does it mean? South Carolina Academy of Sciences. 58:76.

Brown, R. W. 1946. Fossil egg capsules of chimaeroid fishes. Journal of Paleontology 20(3):261-266.

Buckland, W. 1835. A notice on the fossil beaks of four extinct species of fishes, referrible to the genus *Chimaera*, which occur in the Oolithic and Cretaceous formations of England. Proceedings of the Geological Society of London 2:205-206.

Buckland, W. 1838. On the discovery of fossil fishes in the Bagshot Sands at Goldworth Hill, 4 miles north of Guilford. Proceedings of the Geological Society of London 2:687-688.

Case, G. R. 1978. *Ischyodus bifurcatus*, a new species of chimaeroid fish from the upper Cretaceous of New Jersey. Geobios 11:21-29.

Case, G. R. 1979. Cretaceous selachians from the Peedee Formation (late Maastrichtian) of

Duplin County, North Carolina. Brimleyana 2:77-89.

Case, G. R. 1996. A new selachian fauna from the lower Hornerstown Formation (early Paleocene/Montian) of Monmouth County, New Jersey. Palaeontographica Abteilung A 242:1-14.

Case, G. R., and D. R. Schwimmer. 1992. Occurrence of the chimaeroid *Ischyodus bifurcatus* Case in the Cusseta Formaiton (Upper Cretaceous, Campanian) of western Georgia and its distribution. Journal of Paleontology 66(2):347-350.

Cicimurri, D. J. 2007. A late Campanian (Cretaceous) selachian assemblage from a classic locality in Florence County, South Carolina. Southeastern Geology 45(2):59-72.

Cicimurri, D. J., D. C. Parris, and M. J. Everhart. 2008. Partial dentition of a chimaeroid fish Chondrichthyes, Holocephali) from the upper Cretaceous Niobrara Chalk of Kansas, USA. Journal of Vertebrate Paleontology 28(1):34-40.

Consoli, C. P. 2006. *Edaphodon kawai*, sp. nov. (Chondrichthyes, Holocephali): A late Cretaceous chimaeroid from the Chatham Islands, Southwest Pacific. Journal of Vertebrate Paleontology 26(4):801-805.

Cope, E. D. 1869. Descriptions of some extinct fishes previously unknown. Proceedings of the Boston Society of Natural History 12:310-317.

Cope, E. D. 1875. The vertebrata of the Cretaceous formations of the West. Report of the United States Geological Survey of the Territories, 2, 303 pp.

Duffin, C. J. 2001. Chimaerid (Holocephali, Chimaeriformes) vomerine toothplate from the upper Cretaceous of Belgium. Palaeontology, 44(6):1179-1188.

Duffin, C. J., and J. P. H. Reynders. 1995. A fossil Chimaeroid from the Gronsveld Member (Late Maastrichthian, Late Cretaceous) of northeast Belgium. Belgian Geological Survey, Special Paper 278:111-156.

Edwards, L. E., Gohn, G. S., Bybell, L. M., Chirico, P. G., Christopher, R. A., Frederiksen, N. O., Prowell, D. C., Self-Trail, J. M., and Weems, R. E. 2000. Supplement to the preliminary stratigraphic database for subsurface sediments of Dorchester County, South Carolina. U.S. Geological Survey Open-File Report 00- 049-B, 44 pp.

Erickson, B .R. 1998. Crocodilians of the Black Mingo Group (Paleocene) of the South Carolina Coastal Plain. Pp. 196-214 in A.E. Sanders (ed.), Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, USA. Transactions of the American Philosophical Society 88(4).

Erickson, B., A. E. Sanders, and J. L. Knight. In press. Cretaceous reptiles and dinosaurs of South Carolina. Proceedings of the Academy of Natural Sciences, Philadelphia.

Fallaw, W. C., and V. Price. 1995. Stratigraphy of the Savannah River Site and vicinity. Southeastern Geology 35(1):21-58.

Fowler, H. W. 1911. A description of the fossil fish remains of the Cretaceous, Eocene and Miocene formations of New Jersey. New Jersey Geological Survey, Bulletin 4, 182 pp.

Garman, S. 1901. Genera and families of the chimaeroids. Proceedings of the new England Zoological Club 2:75-77.

Hoganson, J. W., and J. M. Erickson. 2005. A new species of *Ischyodus* (Chondrichthyes: Holocephali: Callorhynchidae) from upper Maastrichtian shallow marine facies of the Fox Hills and Hell Creek formations, Williston Basin, North Dakota. Palaeontology 48(4):709-721.

Hulbert, R. C., Jr. 2001. The Fossil Vertebrates of Florida. University of Florida Press, Gainesville, 384 pp.

Hussakof, L. 1912. The Cretaceous chimaeroids of North America. Bulletin of the American Museum of Natural History 31:195-288.

Hutchinson, J. H., and R. E. Weems. 1998. Paleocene turtle remains from South Carolina. Pp. 165-195 in A. E. Sanders (ed.), Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, USA. Transactions of the American Philosophical Society 88(4).

Kemp, D., L. Kemp, and D. J Ward. 1990. An Illustrated Guide to the British Middle Eocene Vertebrates. Privately published, London, 59 pp.

Knight, J. K., D. J. Cicimurri, and R. W. Purdy. 2007. New western hemisphere occurrences of *Schizorhiza* Weiler, 1930 and *Eotorpedo* White, 1934 (Chondrichthyes, Batomorphii). Paludicola 6(2):87-93.

Leidy, J. 1856. Notice of the remains of extinct vertebrate animals of New Jersey, collected by Prof. Cook of the State Geological Survey under the direction of Dr. W. Kitchell. Proceedings of the Academy of Natural Sciences of Philadelphia 8:220-221.

Nessov, L. A., and A. O. Averianov. 1996. Early Chimaeriformes of Russia, Ukraine, Kazakhstan and Middle Asia II. Description of New Taxa. Vestnik Sankt-Peterburgskogo Universitita, Series 7, Issue 3(21):3-10 [in Russian].

Obruchev, D. V. 1967. Fossil chimaera egg capsules. International Geology Review 9(4):567–573.

Parmley, D., and D. J. Cicimurri. 2005. First record of a chimaeroid fish from the Eocene of the southeastern United States. Journal of Paleontology 79(6):1219-1221.

Patterson, C. 1965. The phylogeny of the chimaeroids. Philosophical Transactions of the Royal Society of London (B) 249:101-219.

Patterson, C. 1992. Interpretation of the toothplates of chimaeroid fishes. Zoological Journal of the Linnean Society 106:33-61.

Popov, E. V. 1999a. New data on the morphology of dental plates of chimaeroid fishes of the genus *Ischyodus* from the Cretaceous and Paleogene of central Russia and the Volga region. Russian Academy of Sciences, Proceedings of the Zoological Institute 277:67-82 [in Russian with English figure captions].

Popov, E. V. 1999b. On a record of dental plate of the large chimaeroid *Edaphodon mantelli* Buckland, 1835) from the Lower Santonian of the Saratov Province (Holocephali, Edaphodontidae). Transactions of the Scientific Research Geological Institute, new series 1:137-141 [in Russian with English abstract and figure captions].

Popov. E.V. 2008. Revision of the chimaeroid fishes (Holocephali, Chimaeroidei) from the British Cretaceous. Acta Geologica Polonica, 58(2):243-247.

Popov, E. V. and Beznosov, P.A. 2006. Remains of chimaeroid fishes (Holocephali: Chimaeroidei) from the Upper Jurassic deposits of Komi Republic, Russia. Pp. 55-64 in A. Y. Rozanov , A. V. Lopatin, and P. Y. Parkhaev (eds.), Modern Russian paleontology: Classic and newest methods. Russian Academy of Sciences,Paleontological Institute, Moscow [in Russian with English abstract].

Popov, E. V. and Shapovalov, K.M. 2007. New finds of chimaeroid fishes (Holocephali, Chimaeroidei) from the Jurassic of European Russia. Pp. 25-44 in Modern Russian paleontology: Classic and newest methods. Russian Academy of Sciences, Paleontological Institute, Moscow [in Russian with English abstract].

Popov, E. V., and A. A. Yarkov. 2001. A New Giant Species of *Edaphodon* (Holocephali: Edaphodontidae) from the Beryozovaya Beds (Lower Paleocene) of the Volgograd Volga Region. Paleontological Journal 35(2):183-187.

Purdy, R. W. 1998. Chondrichthyan fishes from the Paleocene of South Carolina. Pp. 122-146 in A. E. Sanders (ed.), Paleobiology of the Williamsburg Formation (Black Mingo group; Paleocene) of South Carolina, USA. Transactions of the American Philosophical Society 88(4).

Robb, A. J., III. 1989. The upper Cretaceous (Campanian, Black Creek Formation) fossil fish fauna of Phoebus Landing, Bladen County, North Carolina. Mosasaur 4:75-92.

Sawyer, G. T. 1998. Coprolites from the Black Mingo Group (Paleocene) of South Carolina. Pp. 221-228 in A. E. Sanders (ed.), Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, USA. Transactions of the American Philosophical Society 88(4).

Shin, J.-Y. 2010. A new species of *Edaphodon* (Chondrichthyes: Holocephali) from the upper Cretaceous Haslam Formation, Vancouver Island, British Columbia, Canada. Journal of Vertebrate Paleontology 30(4):1012-1018.

Stahl, B. J. 1999. Chondrichthyes III: Holocephali. In H.-P. Schultze (ed.), Handbook of Paleoichthyology, Volume 4. Friedrich Pfeil, Munich, 164 pp.

Stahl, B. J., and S. Chatterjee. 2002. A Late Cretaceous callorhynchid (Chondrichthyes, Holocephali) from Seymour Island, Antarctica. Journal of Vertebrate Paleontology 22(4):848-850.

Stahl, B. J., and D. C. Parris. 2004. The complete dentition of *Edaphodon mirificus* (Chondrichthyes: Holocephali) from a single individual. Journal of Paleontology 78(2):388-392.

Takeuchi, G. T., and R. W. Huddleston. 2006. A Miocene chimaeroid fin spine from Kern County, California. Bulletin of the Southern California Academy of Science 105(2):85-90.

Thibault, N., and S. Gardin. 2006. Maastrichtian calcareous nannofossil biostratigraphy and paleoecology in the Equatorial Atlantic (Demerara Rise, ODP Leg 207 Hole 1258A). Revue de Micropaléontologie 49:199-214.

Ward, D. J. 1973. The English Paleogene chimaeroid fishes. Proceedings of the Geological Association 84:315-330.

Ward, D. J., and L. Grande. 1991. Chimaeroid fish remains from Seymour Island, Antarctic Peninsula. Antarctic Science 3(3):323-330.

Waga, D. D., A. S. Andreeva-Grigorovich, and N.V. Maslun. In press. Calcareous nannofossil biostratigraphy of the Paleocene sediments of the Odessa Gas Field (NW Black Sea). Geobios.

Weems, R. E., and L. M. Bybell. 1998. Geology of the Black Mingo Group (Paleocene) in the Kingstree and St. Stephen areas of South

Carolina. Pp. 9-27 in A. E. Sanders (ed.), Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, USA. Transactions of the American Philosophical Society 88(4).

Woodward, A. S. 1891. Catalogue of the fossil fishes in the British Museum (Natural History), Part 2. British Museum of Natural History, London, 567 pp.