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NEW WESTERN HEMISPHERE OCCURRENCES OF *SCHIZORHIZA* WEILER, 1930 AND *EOTORPEDO* WHITE, 1934 (CHONDRICHTHYES, BATOMORPHII)

James L. Knight[1], David J. Cicimurri[2], and Robert W. Purdy[3],

[1]South Carolina State Museum, P.O. Box 100107, Columbia, South Carolina 29202 U.S.A.,
jim.knight@museum.state.sc.us,
[2]Bob Campbell Geology Museum, 103 Garden Trail, Clemson, South Carolina 29634 U.S.A., dcheech@clemson.edu,
[3]Department of Paleobiology, National Museum of Natural History, P. O. Box 37012, NHB, MRC121
Washington, District of Columbia 20013 U.S.A., purdyr@si.edu

ABSTRACT

A single rostral spine of *Schizorhiza stromeri* Weiler, 1930 was collected from a temporally mixed vertebrate assemblage recovered from Williamsburg County, South Carolina. Although well known from Upper Cretaceous strata of Africa, the South Carolina *Schizorhiza* occurrence represents one of the few records of the taxon from North America. In addition, our specimen is the northern-most Western Hemisphere occurrence, originating from approximately the same latitude as previous accounts from the Tethyan region of northern Africa.

Eight teeth referable to *Eotorpedo hilgendorfi* (Jaekel, 1904) have thus far been recovered from Berkeley County, South Carolina. These specimens are important because they constitute the only evidence of *Eotorpedo* White, 1934 in the Western Hemisphere. *Eotorpedo hilgendorfi* could have reached South Carolina by following ocean currents from the Tethyan region down the western coast of Africa, across the Atlantic Ocean to the Caribbean, and northward to North America.

INTRODUCTION

The majority of eastern United States Coastal Plain formations are of marine origin, and some of these units have proven to be rich sources of both late Mesozoic and early Cenozoic chondrichthyan remains (i.e., Lawrence and Hall, 1987; Robb, 1989; Kent, 1999; Purdy et al., 2001). Recent investigations of some of the marine units in South Carolina's Coastal Plain have shown interesting results, with the promise of future opportunities to collect little-understood (or completely unstudied) faunas from different late Mesozoic and Cenozoic time periods.

One location, within the city limits of Kingstree, Williamsburg County, South Carolina, has produced a mixed vertebrate assemblage containing Cretaceous, Paleogene, and Neogene fossils (Breidis and Knight, 1996; Purdy, 1998). Among the fossils recovered from Kingstree were the first South Carolina dinosaur remains, which were intermixed with broken teeth of Pleistocene horses and mastodonts. Several taxa found within this fauna, including *Schizorhiza stromeri* Weiler, 1930, may be temporally constrained and thus provide significant data for understanding the paleofaunas of South Carolina, North America, and the Western Hemisphere in general.

A second site, in an active limestone quarry near Jamestown, Berkeley County, South Carolina, has yielded an unexpectedly diverse vertebrate assemblage that is dominated by elasmobranchs. *Eotorpedo hilgendorfi* (Jaekel, 1904) is only one of the many important new records for the state, and the composition of the Jamestown selachian assemblage indicates a lower Eocene age for the deposit.

The purpose of this report is to illustrate the new material, especially *Eotorpedo hilgendorfi*, and provide a discussion of the paleobiology and paleogeographic distributions of *Schizorhiza* and *Eotorpedo*. The specimens discussed in this report are housed in the collections of the South Carolina State Museum (**SC**), Columbia, and the Bob Campbell Geology Museum (**BCGM**), Clemson, South Carolina.

METHODS

At the Kingstree site, members of the Myrtle Beach Fossil Club used 6 mm mesh sieves to screen wash matrix from the banks of a small creek feeding into the Black River. The fossiliferous deposit at the

Jamestown site is overlain by a thick section of limestone and is not exposed. However, some material is brought to the surface from a water-filled portion of the quarry as drag-lines remove the limestone from under 14+ m of water. JLK and DJC recovered matrix from spoil piles for processing in the laboratory. The matrix was disaggregated in water and gently screen washed, with the finest sieve size being 0.25 mm. The remaining concentrate was dried and sorted under a binocular microscope.

SYSTEMATIC PALEONTOLOGY

Order Sclerorhynchiformes Kriwet 2004
Family Sclerorhynchidae Cappetta 1974
Subfamily Schizorhizinae Kirkland and Aguillón-Martinez 2002
Schizorhiza Weiler 1930
Schizorhiza stromeri Weiler 1930
Figure 1, A-B

Material—SC 87.158.103, an isolated rostral spine, Kingstree faunal assemblage, Williamsburg County, South Carolina (79°49'43" W lat., 33°40'16" N long.).

Description——specimen highly ablated and incomplete, preserved length measures 10.1 mm; enameloid-covered crown much shorter than peduncle; crown dorsoventrally compressed, with smooth cutting edges, asymmetrical diamond-shaped outline (anterior edge longer than posterior edge); base of crown narrows significantly where it joins peduncle; peduncle bilobate, with widely diverging and dorsoventrally flattened dorsal and ventral lobes (one lobe broken from just below base of crown); base of more complete lobe fluted.

Remarks—*Schizorhiza* is chiefly known from isolated rostral spines and two species, *S. stromeri* (Weiler, 1930) and *S. weileri* (Serra, 1933), have been described. Cappetta (1987) considers the genus to be monospecific, with *S. weileri* being a junior synonym of *S. stromeri*. Although primarily known from rocks of Maastrichtian age (Cappetta, 1987), *Schizorhiza* has been recovered from latest Campanian strata (Kirkland and Aguillón-Martinez, 2002). The genus is well documented in Africa, having been reported from Angola, Egypt, Libya, Morocco, Niger, Nigeria, Tunisia, and Zaire, (Weiler, 1930; Serra, 1933; Darteville and Casier, 1943; Arambourg, 1952; Cappetta, 1987, 1991). In the Middle East *Schizorhiza* has been identified in Iraq and Syria (Cappetta, 1987; Bardet et al., 2000). Previous reports of *Schizorhiza* from the Western Hemisphere are very limited, with isolated reports from Mexico (Kirkland and Aguillón-Martinez, 2002; Gonzalez-Barba et al., 2004), Bolivia (Cappetta, 1975), and Texas and Arkansas (Dunkle, 1948; Welton and Farish, 1993; Becker et al., 2006), U.S.A.

Most sclerorhynchid rays, like *Schizorhiza*, were similar to Recent sawsharks and sawfish in that they possessed an elongated, spined rostrum (Slaughter and Springer, 1968; Tricas et al., 1997; Compagno and Last, 1999; Kirkland and Aguillón-Martinez, 2002; Becker et al., 2003; Kriwet, 2004). Whereas rostral spines of extant sawfish are set in deep alveoli and are not regularly replaced (Miller, 1974), rostral spines of *Schizorhiza* and sawsharks attach to the lateral margins of the rostrum and are replaced throughout life (Slaughter and Springer, 1968; Kirkland and Aguillón-Martinez, 2002; Kriwet, 2004). Rostral spines of *Schizorhiza* appear to be unique among sclerorhynchids in their manner of replacement and arrangement on the rostrum. Kirkland and Aguillón-Martinez (2002) have shown that new rostral spines form between the widely flaring lobes of the peduncle of the preceding spine (p. 20, fig. 5, p. 21, fig. 7), and spines were very closely packed on the rostrum (p. 21, fig. 6, p. 22, fig. 9). Because the rostral spines formed a continuous serrated edge, Kirkland and Aguillón-Martinez (2002) hypothesized that, rather than probing the substrate for prey, *Schizorhiza* was an open water predator that used its rostrum to slash at prey.

Order Torpediniformes Buen 1926
Family Torpedinidae Bonaparte 1838
Eotorpedo White 1934
Eotorpedo hilgendorfi (Jaekel 1904)
Figure 2, A-I

Material—BCGM 6894 - BCGM 6897, BCGM 7026, SC 2006.16.1 - SC 2006.16.3, isolated teeth from Martin Marietta Aggregates quarry near Jamestown, Berkeley County, South Carolina (79° 40' 14" W lat., 33° 19' 43" N long.).

Description—teeth with characteristic four-lobed appearance in occlusal view; flat-based crown dominated by tall, conical cusp; cusp strongly curved lingually; lower part of labial face bifurcates into widely diverging, basally curving lobes; wide medial notch at lingual crown base; root apico-basally thin, extends lingually past margin of crown, with large, centrally located basal foramen.

Remarks——Four species of *Eotorpedo* are currently recognized. *Eotorpedo zennaroi* Cappetta 1988, from the lower Paleocene of Morocco, differs from *E. hilgendorfi* (upper Paleocene to lower Eocene) in having a laterally compressed cusp with distinct labio-lingual cutting edges, and a conspicuous transverse labial ridge (Cappetta, 1988). *Eotorpedo jaekeli* White 1934, from the upper Paleocene of Nigeria, is similar to *E. zennaroi* in having a laterally compressed cusp with a labiolingually oriented cutting edge. Teeth of *E. jaekeli* differ from *E. hilgendorfi* in having much smaller labial crown lobes, and the lingual root notch is narrower (White, 1934). *Eotorpedo nolfi* Herman 1974, from the lower Eocene of Belgium, is based on a single tooth. The specimen was distinguished primarily on the basis of its small size (estimated less than 3 mm in total height), although it also appears to lack lingual crown lobes as seen in *E. hilgendorfi* (Herman, 1974).

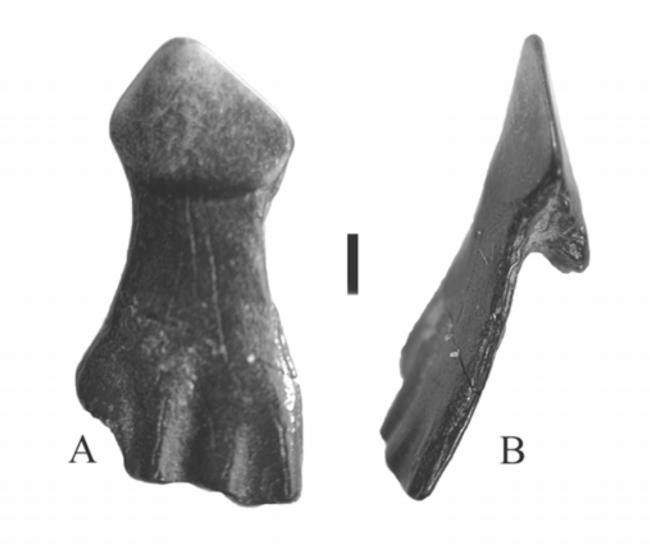

FIGURE 1-- *Schizorhiza stromeri* Weiler, 1930, rostral spine, SC 87.158.103. **A**, dorsal or ventral view (anterior at right); **B**, anterior view (slightly oblique). Scale bar = 1 mm.

The cusp of BCGM 7026, the largest tooth available for study (measuring 6 mm in height as preserved), is meso-distally compressed and has indistinct lateral cutting edges (Fig. 2, H-I). Cusps of the remaining specimens (the cusp is missing from BCGM 6894) have a more circular cross section and bear smooth lateral cutting edges. The cusps of most of the specimens are slightly distally inclined, and we regard the weak morphological variation seen in Figure 2 as representing heterodonty within a single species. The high-cusped teeth of *Eotorpedo hilgendorfi* combined to form an effective clutching dentition (see Cappetta, 1987) used for capturing fish and/or crustaceans. Compared to extant torpediniform rays, *Eotorpedo* was a large fish. Based on tooth size, Jaekel (1904) estimated that *Eotorpedo hilgendorfi* reached a total body length of two to three meters.

Previous reports of *E. hilgendorfi* are from northern and western Africa, including Cabinda, Cameroon, Morocco, Niger, Nigeria, and Tunisia (Jaekel, 1904; Dartevelle and Casier, 1943; Arambourg, 1952; Cappetta, 1972, 1988), and the taxon has been identified in Saudi Arabia (Madden et al., 1995; Whybrow and Clemens, 1999). *Eotorpedo* is deemed to be a relatively rare component of the Jamestown elasmobranch assemblage because only eight teeth have thus far been recovered from the hundreds of kilograms of matrix processed.

DISCUSSION

Although the Kingstree fossils represent temporally mixed assemblages, it is relatively easy to identify the Cretaceous, Paleocene, and Pleistocene taxa. The oldest lithostratigraphic unit in the Kingstree area is the Maastrichtian Peedee Formation (Weems and Bybell, 1998), and we believe the Cretaceous material (including SC 87.158.103) was locally reworked from this unit. Our conclusion is supported by other associated elasmobranch fossils, especially *Rhombodus binkhorsti*, a taxon apparently restricted to the Maastrichtian (Welton and Farish, 1993; Noubhani and Cappetta, 1994). Unfortunately, our investigations into the Peedee Formation have not yielded additional *Schizorhiza* material, and the taxon was not reported from the deposit in North Carolina (Case, 1979). *Schizorhiza* is virtually unknown from post-Cretaceous deposits, and Kirkland and Aguillón-Martinez (2002) hypothesized that Paleocene records in Mexico represent specimens reworked from underlying Cretaceous strata. The Kingstree fossils provide another example of how vertebrate remains, particularly elasmobranch teeth, can survive in relatively good condition despite being reworked (possibly several times) into younger deposits.

The occurrence of *Schizorhiza* (SC 87.158.103) in the Kingstree faunal assemblage is important because the taxon was previously unknown from the Cretaceous record of South Carolina, and the lone rostral spine represents one of the rare occurrences from the Western Hemisphere. Additionally, the South Carolina *Schizorhiza* is the northern-most record in the Western Hemisphere, occurring at approximately the same latitude as previous reports from the Tethyan region of Africa and the Middle East (i.e., Arambourg, 1952; Bardet et al., 2000). A mode of dispersal for *Schizorhiza* may have been similar to that proposed by Hooks et al. (1999) for the Cretaceous pycnodont fish, *Phacodus*. *Schizorhiza* could have travelled along continental shelves, following clockwise circulation patterns in the Atlantic Ocean. Africa and South America were closer together during the Maastrichtian (Smith et al., 1994), and a short open-ocean crossing would have been possible, especially if *Schizorhiza* were a pelagic predator as suggested by Kirkland and Aguillón-Martinez (2002).

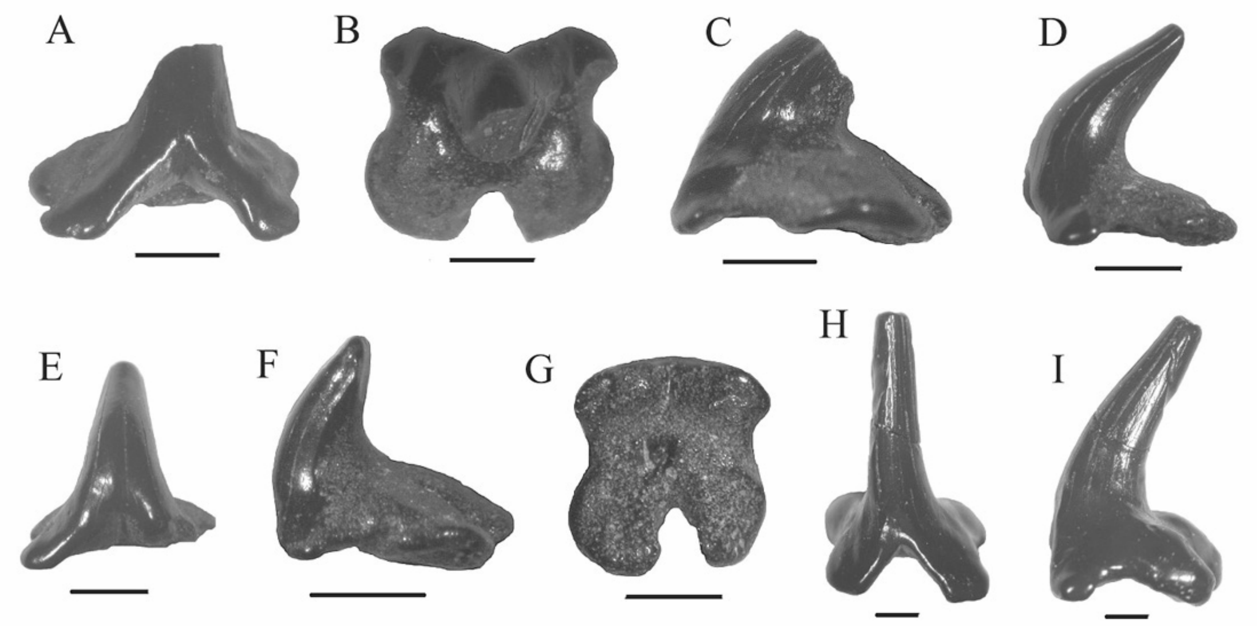

FIGURE 2. Teeth of *Eotorpedo hilgendorfi* (Jaekel, 1904). **A**, BCGM 6895, labial view; **B**, same, occlusal view; **C**, same, lateral view; **D**, BCGM 6896, lateral view (horizontally rotated 180°); **E**, same, labial view; **F**, BCGM 6897, mesial view; **G**, same, basal view; **H**, BCGM 7026, labial view; **I**, same, lateral view. Labial is left in lateral views, top in occlusal and basal views. Scale bar = 1 mm.

As we await the outcome of nannofossil analyses, the precise stratigraphic position and age of the Jamestown *Eotorpedo* specimens remains in question. The unit underlies middle Eocene limestone of the Moultrie Member, Santee Limestone, and we believe the fossils to be of Ypresian age because of the association of *Meridiania convexa*, a batomorph taxon previously reported from only two other locations, both of which are in the United States. In Mississippi, *Meridiania* occurs in lowermost Eocene strata of the Bashi Formation, which is assigned to the base of calcareous nannofossil zone NP 10 (Case, 1994; Harrington, 2003) and was deposited approximately 54.9 Ma (Berggren et al., 1995). In Virginia, *Meridiania* occurs in younger deposits of the basal part of Bed B of the Potapco Member, Nanjemoy Formation (Kent, 1999; Weems and Grimsley, 1999), which has been assigned to zone NP 11 (Gibson and Bybell, 1991). This zone represents an interval of time of only 800,000 years, from 53.6 to 52.8 Ma (Berggren et al., 1995).

The South Carolina *Eotorpedo* teeth represent the only definitive record of the genus from the Western Hemisphere. Specimens from Mississippi identified as *E. jaekeli* by Case (1994, pl. 12) lack distinctive labial longitudinal cutting edges, as well as the characteristic quadri-lobate appearance of *Eotorpedo* (especially in basal view). We believe those teeth actually represent a more cosmopolitan taxon, *Heterotorpedo*. As is the case with *Schizorhiza*, South Carolina *Eotorpedo hilgendorfi* occur at about the same latitude as material collected from the Tethyan region of Africa and Asia (i.e. Cappetta, 1972, 1988; Whybrow and Clemens, 1999). The Jamestown elasmobranch assemblage indicates a relatively shallow, warm-water, normal salinity environment.

An early Eocene age for the South Carolina *Eotorpedo* supports the data of Berggren and Hollister (1974), who suggested that various foraminiferan families occur in the fossil record earlier in the Tethyan region than in the Americas. *Eotorpedo* has its origins in the Tethyan region of northern Africa, with the earliest species, *E. zennaroi*, occurring in the lower Paleocene of Morocco. The genus spread into coastal waters of western Africa by the upper Paleocene (*E. hilgendorfi*), and by the lower Eocene extended its range northward into Europe (*E. nolfi*), eastward to Saudi Arabia (*E. hilgendorfi*), and westward to the United States (*E. hilgendorfi*). Berggren and Hollister (1974) reported that circulation patterns in the Eocene Atlantic Ocean flowed from the Tethys Sea down and around the west coast of Africa, across the Atlantic into the Caribbean, where a gyre sent warm water up the east coast of North America (see also Haq, 1984). This model shows how the radiation of marine organisms from the Tethyan region across the Atlantic Ocean to the Americas was possible. Furthermore, it explains the occurrence of organisms with Tethyan origins like foraminifera (Berggren and Hollister, 1974), decapod crustaceans (Feldmann et al., 1998), and selachians (i.e., *Eotorpedo*) in the Atlantic Coastal Plain of the Americas.

Exactly how *Eotorpedo* is related to other genera within Torpediniformes is unknown and may not be resolved without the aid of skeletal material. Jaekel (1904) allied *Eotorpedo* with Torpediniformes because of the dental similarities with extant torpedinid rays, especially *Torpedo*. Subsequent authors have followed this taxonomic arrangement, with a more refined placement within Torpedinidae (White, 1935; Arambourg, 1952; Herman, 1974; Cappetta, 1987). In his comprehensive review of Torpediniformes, Cappetta (1988) retained *Eotorpedo* within Torpedinidae, although he noted that the teeth of the earliest species, *E. zennaroi* (Early Paleocene), were already highly derived. Cappetta (1988) also stated that *Narcine* (Narcinidae), a taxon with its earliest occurrence in the Upper Eocene, is the ancestral taxon of Recent Torpediniformes, including *Torpedo*.

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