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NOTE

REVISED TAXONOMY, AGE, AND GEOGRAPHIC RANGE OF THE LARGE LAMNIFORM SHARK *CRETODUS SEMIPLICATUS*

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Sharks are well-known from Upper Cretaceous marine strata of the eastern Gulf of Mexico Coastal Plain (e.g., Applegate, 1970; Case and Schwimmer, 1988; Case and Schwimmer, 1992; Schwimmer et al., 1997; Case et al., 2001). This note adds the presence of *Cretodus semiplicatus* from two Santonian deposits in Georgia and Alabama. The occurrences reported here are noteworthy for the following reasons: the teeth are from a substantially larger selachian taxon than any so far reported in the Late Cretaceous of the eastern Gulf Coastal Plain; the specimens comprise a significant age extension of this species, as all previous reports are from Cenomanian–Turonian strata; and, finally, these rare teeth bear on the taxonomic status of *C. crassidens*, which is considered here a junior synonym of *C. semiplicatus*.

SYSTEMATIC PALEONTOLOGY

Institutional Abbreviations—**ALMNH**, Alabama Museum of Natural History, the University of Alabama; **AUMP**, Auburn University Museum of Paleontology; **CSUK**, Columbus State University Cretaceous Collections.

Order LAMNIFORMES Berg, 1958
Family CRETOXYRHINIDAE Glikman, 1958
Genus *CRETODUS* Sokolov, 1965

CRETODUS SEMIPLICATUS (Münster *in* Agassiz, 1843)
(Fig. 1A–H)

Otodus semiplicatus Agassiz (ex Münster), 1843:272, pl. 36, fig. 32.
Otodus sulcatus Geinitz, 1843:5; pl. 4, fig. 2.
Otodus semiplicatus Reuss, 1845:5, pl. 3, figs. 20, 21.
Otodus sulcatus Reuss, 1846:100; pl. 21, fig. 41; Geinitz, 1850:5, pl. 4, fig. 2.
Oxyrhina crassidens Dixon, 1850:357, pl. 31, fig. 13.
Otodus Gervais, 1852; pl. 76, fig. 11.
Otodus sulcatus Fischer, 1856:141, pl. 2, fig. 41.
Otodus michoni Coquand, 1860:98.
Otodus semiplicatus Sauvage, 1872:26, pl. 16, figs. 25, 26.
Otodus sulcatus Sauvage, 1872:29, pl. 17, figs. 60–69.
Otodus cf. *semiplicatus* Stoliczka, 1873:67, pl. 12, fig. 24.
Oxyrhina sp. Stoliczka, 1873:68, pl. 12, fig. 34.
Otodus divaricatus Leidy, 1873:305, pl. 18, figs. 26–28.
Otodus semiplicatus Geinitz, 1875:294, pl. 65, figs. 4, 5; Fritsch, 1878: 7, fig. 10; Woodward, 1888:292.
Otodus crassus, Woodward, 1888:292.
Lamna sulcata Woodward, 1889:398–399; Woodward, 1894:197.
Lamna semiplicata Woodward, 1894:197, pl. 6, figs. 3, 4.
Scyliorhynchus rugosus Williston, 1900:245, pl. 24, fig. 5.
Lamna sulcata Williston, 1900:248, pl. 24, figs. 1, 1b.
Otodus semiplicatus Leriche, 1902:114–115, pl. 3, fig. 48.
Otodus sulcatus Leriche, 1902:115–116, pl. 3, fig. 47; Hay, 1903:397, pl. 26, figs. 3, 4.
Otosus semiplicatus Leriche, 1906:62.
Oxyrhina crassidens Woodward, 1911:205–206, pl. 44, figs. 1, 2.
Lamna semiplicata Woodward, 1911:208, pl. 44, figs. 10, 11.
Lamna sulcata Woodward, 1911:208, pl. 44, figs. 12, 13.
Lamna semiplicata Leriche, 1929:248–249; Dalenkivicius, 1935, pl. 5, figs. 110–111; Leriche, 1936:380, pl. 26, figs. 1–4; Cappetta, 1973:506–507, pl. 1, figs. 7, 7′.
Leptostyrax semiplicatus, Meyer, 1974:270–276, fig. 81.
Leptostyrax crassidens Meyer, 1974:276–280, fig. 83.
Plicatolamna semiplicata Herman, 1975:197–199, pl. 8, fig. 1.
Plicatolamna crassidens Herman, 1975:200–201, pl. 8, fig. 2.
Leptostyrax crassidens Martin and Stewart, 1977:973–974.
Plicatolamna semiplicata Cappetta, 1980:97, pl. 7, fig. 3.
Cretodus semiplicatus Wolberg, 1985a:4, figs. 3a–g; Wolberg, 1985b: 10, figs. 3.10–3.21.
Cretodus crassidens Cappetta, 1987:98; Welton and Farish, 1993:98–99.
Cretodus semiplicatus Welton and Farish, 1993:100; Williamson et al., 1993:453–454, figs. 5.6–5.11.
Cretodus crassidens Shimada, 1997:145.

Emended Diagnosis—Large, robust, high-crowned lamnoid shark teeth with vertical or near-vertical crowns in the anterior and anterolateral series; largest known teeth reach 66 mm total height. Most teeth with paired, stout, strongly divergent, triangular lateral cusplets, forming a continuous labial cutting surface with the main cusp; cusplets may have single notches on lateral edges. Crowns slightly sigmoid in profile, with smooth enameloid distally. Crown bases and dental bands with numerous, evenly-spaced, well-demarcated, short vertical grooves on labial aspect of all teeth, reaching no more than 20% of crown height. Two to five deep vertical plications also present on the labial face of larger teeth, with the longest and deepest groove medial, reaching midway up the cusp. Lingual face with similar vertical grooves at the crown and dental band, reaching 20–40% of crown height; lingual grooves more extensive and better-demarcated in smaller teeth (i.e., less than 4.0 cm). Holaulacorhizous roots very robust, with prominent lingual shelves on all teeth, and with nutritive groove indistinct. Roots U-shaped, deeply forked and laterally narrow, especially in the lower jaw.

Distribution—Africa: Angola; Asia: Lebanon, India; Europe: Belgium, France, England, Germany, Lithuania; North America: Arizona, New Mexico, Texas, Kansas, South Dakota, Alabama, Georgia.

Revised Stratigraphic Range—Upper Cretaceous: Cenomanian–Santonian.

Referred Material—CSUK-82-23-1, from the Eutaw formation (Santonian), east bank of Upatoi Creek at the crossing of US Route 27/280, Chattahoochee County (Fort Benning), Georgia. The specimen was in situ a few centimeters below the outcrop surface in the approximate middle of the formation, 2.0 m below a bioherm of *Ostrea cretacea*, which is a molluskan index species for the upper portion of the Eutaw formation (Reinhardt and Donovan, 1986). Locally, the Eutaw formation is well constrained (Reinhardt et al., 1994) between the early Santonian Stage and the base of the Campanian. ALMNH PV2000.2 and AUMP 2752 are both from the Tombigbee Sand Member, Eutaw formation (Santonian), Catoma Creek, Montgomery County, Alabama. The outcrop at this locality includes the contact between the lower Mooreville formation (lower Campanian) and the underlying Tombigbee Sand Member (Santonian to basal Campanian: Smith, 1989). The teeth come from a horizon slightly below this contact: therefore, their age is late Santonian-lowermost Campanian.

Description—Tooth positions below are hypothetical and based on typical modern lamnoid sharks, notably *Lamna nasus*. CSUK-82-23-1

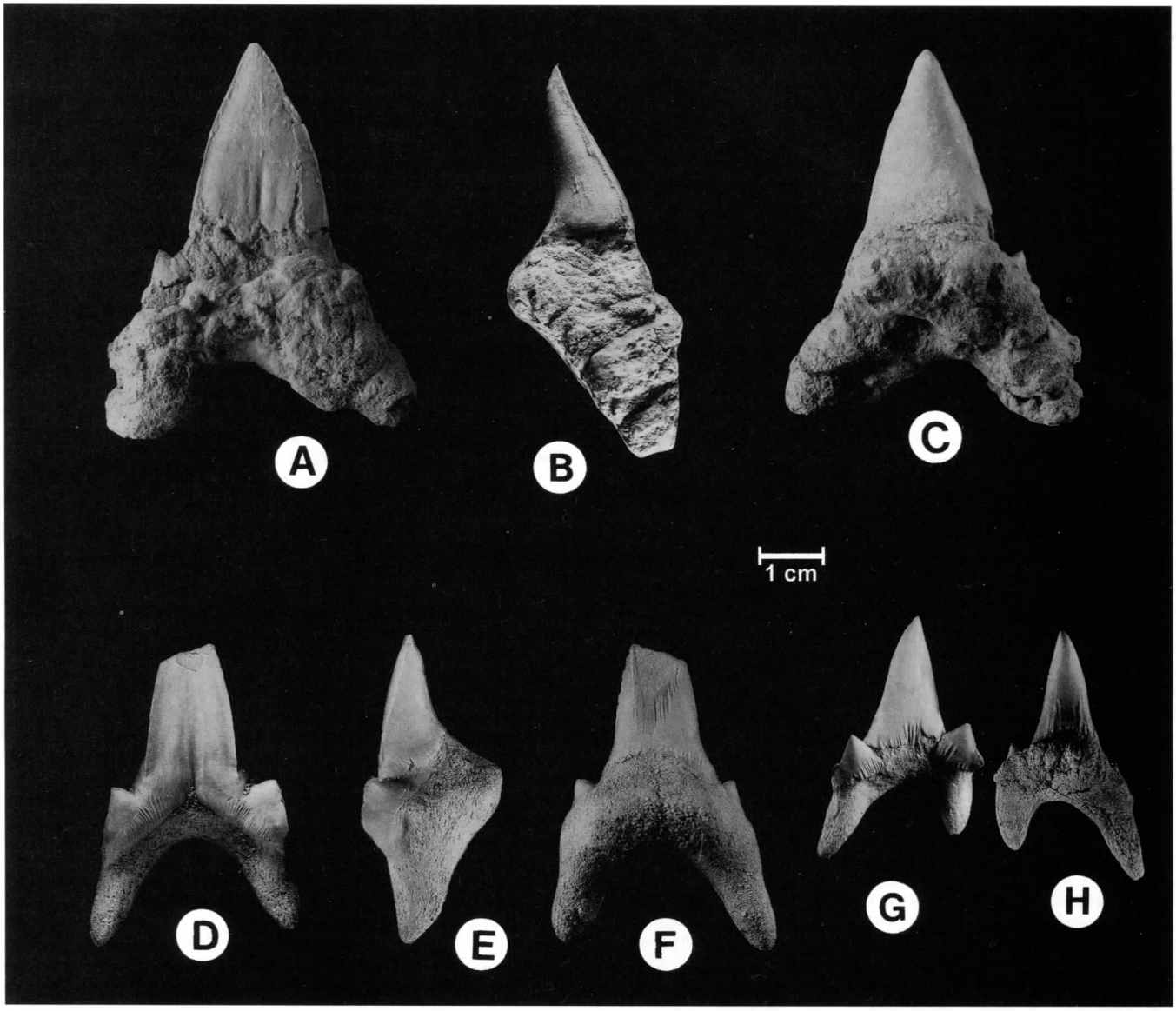

FIGURE 1. Teeth of *Cretodus semiplicatus* from the eastern Gulf Coastal Plain. All specimens × 1.0. **A–C**, large, upper anterior tooth CSUK-82-23-1, Eutaw formation, Fort Benning, Georgia, labial, lateral, and lingual views, showing post-exposure ablation at the crown base and root due to crystal growth: total height 59 mm, maximum width of root as preserved 45 mm; **D–F**, large, lower anterior tooth ALMNH PV2000.2, Tombigbee Sand Member, Eutaw formation, Montgomery County, Alabama, labial, lateral and lingual views; **G-H**, smaller, lower left lateral tooth AUMP-2752, same locality as **D-F**, labial and lingual views.

(Fig. 1A–C) is a large tooth with a relatively divergent root and a laterally broad, vertical cusp. The labial face of the cusp bears three deep vertical furrows, reaching mid-height, with the medial furrow especially deep. One lateral cusplet is preserved, containing a secondary notch and showing remnants of a continuous enameloid surface between lateral and main cusps. The total preserved height of this tooth is 59 mm, and the width across the roots is 45 mm. The tooth is considerably ablated, leading to loss of some characteristics of the species. Based on the vertical, wide cusp and relatively wide root, this is probably an upper anterior tooth.

ALMNH PV2000.2 (Fig. 1D–F) is also a large tooth (total height as preserved 48 mm, width of root 33 mm), with a deeply forked, narrow root and a narrow, vertical cusp. Restoring the broken tip yields an estimated total tooth height of ~54 mm. The symmetrical root and narrow, vertical cusp suggest this is a lower anterior tooth. Numerous short, deep vertical striations are evident on the labial face, extending uniformly across the lateral cusplets and central cusp, reaching less than 20% of the crown height. A single, deep, medial plication and two additional indistinct plications are also present on either side of the labial surface, extending from the base of the crown to 40% of the cusp height. Very short striations are evident at the base of the crown on the labial surface, barely extending above the root. An indistinct nutritive groove is present, which appears to be relatively prominent in Figure 1F because the root is cracked.

AUMP 2752 (Fig. 1G, H) is a smaller tooth (total height 35 mm, width across root 19 mm), with a deeply forked, narrow, asymmetrical root and a slightly inclined, narrow cusp. Based on the crown inclination and the assumption that the longer side of the root is medial, this is a lower, left, lateral tooth. The lateral cusplets are laterally wide, with well-defined notches. Vertical striations are present on both sides of the central cusp and lateral cusplets, reaching approximately 20% of the central cusp height labially, and nearly 50% the crown height lingually.

Discussion—Because these are the youngest *Cretodus semiplicatus* reported, even considering nearby occurrences in the central Gulf of Mexico (Meyer, 1974; Welton and Farish, 1993), it is important to first comment that these teeth were not likely redeposited from older strata. This is evident from the nearly perfect preservation of lateral cusplets and the sharp edges of cutting surfaces in all specimens. The ablation

of the specimen in Figure 1A–C is due to post-exposure gypsum crystal growth on the outcrop surface, which is common with fossils at this site.

The taxonomy of *Cretodus semiplicatus* has a long and tortuous history, as the synonymy (see above) shows. The relationship between *Cretodus semiplicatus* (Agassiz, 1843) and *C. crassidens* (Dixon, 1850) has most recently been evaluated by Cappetta (1973, 1987), Meyer (1974), Williamson et al. (1993) and Welton and Farish (1993). Cappetta (1973) considered them to be conspecific, commenting that the typically large *C.* (*Oxyrhina*) *crassidens* specimens could be "a morphological variation" (Cappetta, 1973:506) of (*Lamna*) *semiplicata*. Subsequent authors, including Cappetta himself, did not follow this suggestion and separated *Cretodus crassidens* and *C. semiplicatus* (e.g., Cappetta, 1987; Williamson et al., 1993; Welton and Farish, 1993). Cappetta (1987) and Welton and Farish (1993) differentiated the two species by the larger, more robust tooth size, shorter lingual striations on the crown base, and reduction of the lateral cusplets of the "typical" *C. crassidens* morphology. Meyer (1974) recognized similar differential criteria for *C. crassidens* (which he assigned to the genus *Leptostyrax*), emphasizing that (*Leptostyrax*) *crassidens* had the "tendency for poor expression of the lateral cusplets on larger teeth." These putative diagnostic characters are noteworthy in light of the following observations.

Although only three teeth are reported here, they provide evidence that *C. semiplicatus* and *C. crassidens* are synonymous. All three show combinations of characters previously considered diagnostic for each of the species. Two of the specimens (Fig. 1A–F) are among the larger reported for the genus and clearly conform in most other respects with the morphology traditionally attributed to *C. crassidens* (e.g., Meyer, 1974; Cappetta, 1987, and Welton and Farish, 1993). They are notably larger (by approximately 2 times) than any teeth attributed to *C. semiplicatus*. However, they each have well-developed lateral cusplets, *contra* the diagnosis of *C. crassidens* in Meyer, 1974 and Cappetta, 1987. The smaller tooth (Fig. 1G, H), while still within the size range typically attributed to *C. crassidens*, features striations on the lingual side reaching nearly halfway up the central cusp, a characteristic previously attributed only to the *C. semiplicatus* morphology (Meyer, 1974; Welton and Farish, 1993).

It has also been assumed by some previous workers that *Cretodus semiplicatus* and *C. crassidens* could be referred to specific and different paleohabitats. Shimada (1997) observed that *C. crassidens* was characteristically found in nearshore deposits in Kansas, and that its occurrence there might be environmentally controlled. C. M. Cicimurri (2000, DRS, pers. comm.) made similar observations in South Dakota, where he attributed smaller *C. semiplicatus* teeth to offshore deposits and larger *C. crassidens* teeth to nearshore deposits. An opposite contention was presented by Williamson et al. (1993), who stated that in Arizona, *C. semiplicatus* "is most common in nearshore deposits . . . and is rare in deep-marine deposits." The recognition here that *Cretodus semiplicatus* and *C. crassidens* are conspecific may explain these apparent anomalies.

It is noteworthy that the last surviving species of the genus, *Cretodus borodini*, was first reported from the Campanian of New Jersey on the Atlantic Coastal Plain (Cappetta and Case, 1975), and that it also occurs in Campanian strata in Alabama and Georgia (Case and Schwimmer, 1988), North Carolina (Robb, 1989) and Delaware (Lauginiger and Hartstein, 1983). This post-Coniacian persistence of *Cretodus* only on the Atlantic and eastern Gulf Coastal Plains is consistent with the genus' apparent disappearance at this time from the Western Interior Seaway and the western side of the Gulf of Mexico.

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