LATE CRETACEOUS ELASMOBRANCHS FROM THE EUTAW FORMATION AT LUXAPALILA CREEK, LOWNDES COUNTY, MISSISSIPPI

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ABSTRACT

A diverse vertebrate assemblage was recovered from the Eutaw Formation along a stretch of Luxapalila Creek in Lowndes County, Mississippi. The assemblage is dominated by elasmobranchs but also includes osteichthyans (seven species), archosaurs (one crocodilian, two dinosaurs), and turtles (trionychid and chelonioid). Twenty one elasmobranch taxa were identified (14 selachians and seven batoids), including new species *Meristodonoides multiplicatus*, *Lonchidion cristatum*, and *Cantioscyllium grandis*. Our sample also enabled us to expand the known range of variation for some other poorly diagnosed species. The elasmobranch assemblage consists predominantly of species with presumed benthic habits (14), including the orectolobiform sharks and sclerorhynchid rays, whereas the seven lamniform sharks represent pelagic species. We believe that the sharks and rays inhabited a warm-water, nearshore marine environment.

Introduction

Upper Cretaceous strata of the Eutaw Group are exposed in northeastern Mississippi (figure 1) as part of an outcrop belt that extends from west-central Georgia, through central Alabama, and into western Tennessee (see Mancini & Soens, 1994). The Eutaw Group of eastern Mississippi includes the McShan Formation and overlying Eutaw Formation, and the Eutaw Formation is further subdivided into the Eutaw and overlying Tombigbee Sand members (figure 2). The Tombigbee Sand Member was deposited during a marine transgression that began in the late Santonian and continued into the early Campanian (Mancini & Soens, 1994; Kennedy *et al.*, 1997).

Numerous site visits were made to an exposure of the Eutaw Formation exposed along the south bank of Luxapalila Creek in Lowndes County, Mississippi (figures 1 & 3). Field work at the site consisted of measuring the exposed vertical section, documenting the lithological variation within beds, and bulk sampling fossiliferous matrix. The bulk sampling yielded a highly diverse vertebrate assemblage, and the purpose of this report is to provide a detailed analysis of the elasmobranch species that were discovered. In addition, we revise taxonomic nomenclature for several tooth morphologies, discuss the paleobiogeographic distribution of species, comment on the paleobiology of species, and reconstruct the paleoecology at the time of deposition of the fossil deposit based on lithology and species content.

Previous work on Eutaw Formation Fossil Vertebrates

A wide variety of fossil vertebrates are found throughout the Eutaw Formation outcrop belt. Leidy (1873) described and illustrated (*i.e.*, pl. 28) a number of specimens that were collected by William Spillman from "Cretaceous sandstone near Columbus, Mississippi." The fossils were in fact recovered from the Tombigbee Sand Member, probably from Plymouth Bluff, in Lowndes County (Russel, 1986; Manning, 1994). Leidy (1873) identified several fish from Spillman's collection, including the teleosts *Pycnodus faba* (= *Anomoeodus phaseolus*; see also Leidy, 1872; Kriwet, 2002) and *Hadrodus priscus*, and the elasmobranchs *Ptychodus mortoni*, *Galeocerdo falcatus* (= a mixture of *Squalicorax* sp. aff. *S. yangaensis* and *S.* sp. cf. *kaupi* as identified herein), *Oxyrhina extenta* (= *Cretoxyrhina mantelli*), *Lamna* sp. (= *Scapanorhynchus texanus*), and the chimaeroid *Eumylodus laqueatus*. Fish species associated with a mammal tooth recovered from the Tombigbee Sand Member at Vinton Bluff (Tombigbee River) in Clay County, Mississippi, were identified as *Hybodus* sp., *Squalicorax* sp., *Cretalamna* sp., *Striatolamia* sp., *Ptychodus* cf. *P. mortoni*, cf. *Dasyatis* sp., *Raja* sp., *Ginglymostoma* sp., *Otodus* sp., *Ischyrhiza* sp., and *Rhincodo*n sp. (see Emry *et al.*, 1981). The pycnodont *Anomoeodus* was also reported by Emry *et al.* (1981), and Hooks *et al.* (1999) documented *Phacodus punctatus* from the Tombigbee Sand Member in both Mississippi (Clay County) and Alabama (Dallas County).

Numerous fish taxa have been reported from the Eutaw Formation of Alabama, and Meyer (1974) was the first to conduct a study of the fossil elasmobranchs. Whetstone and Collins (1982) identified a small ichthyofauna they collected in Montgomery County, including the elasmobranchs *Hybodus* sp., *Ptychotrygon* sp., *Scapanorhynchus* sp., *Cretalamna* sp., *Odontaspis* sp., *Squalicorax* sp., and bony fish *Belonostomus* sp. and *Enchodus* sp. Lamb *et al.* (1991) later updated the Montgomery County fish assemblage and listed *Cretoxyrhina mantelli*, *Cretalamna appendiculata*, *Ptychodus mortoni*, *Scapanorhynchus texanus*, and *Squalicorax kaupi*, along with bony fish *Bananogmius*, *Enchodus*, *Pachyrhizodus*, and *Xiphactinus*. The large coelacanth *Megalocoelocanthus dobiei* also occurs in the Eutaw Formation (Schwimmer *et al.*, 1994). More recently, Ciampaglio *et al.* (2013) reported a variety of fossil fish from Greene County, but this assemblage could consist of a mixture of material from the Eutaw Formation and overlying Mooreville Chalk Formation.

Reptilian remains from the Eutaw Formation include a partial hadrosaurine dinosaur collected along the Tombigbee River near Columbus, Mississippi (Kaye & Russel, 1973). Lamb *et al.* (1991) also documented a number of reptiles, including a toxochelyid turtle, a plesiosaur, two crocodylians, three mosasaurs (*Tylosaurus* was identified by Kiernan [2002]), and dinosaurs. Schwimmer and others (1985) reported the occurrence of two pterosaur bones from the Eutaw Formation of Chatahoochee County, Georgia. Birds also inhabited the region

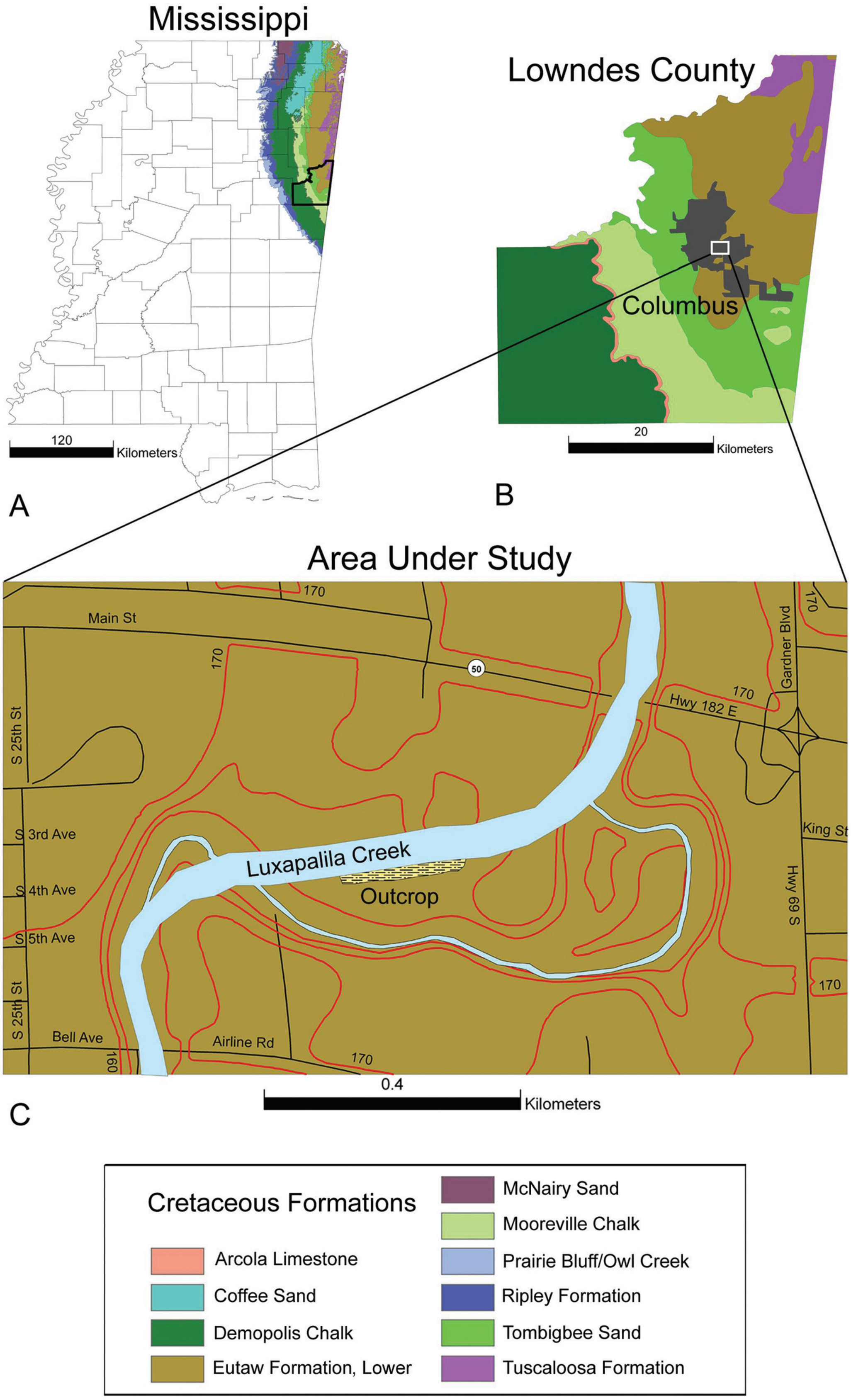

Figure 1. Geographic and stratigraphic occurrence of Eutaw Formation elasmobranchs recovered during our study. A) County map of Mississippi showing regional late Cretaceous geology. B) Plan view of Lowndes County showing local geology. C) Enlarged view of area highlighted in B showing the portion of Luxapalila Creek from which fossils were collected. Figure by C.N. Ciampaglio.

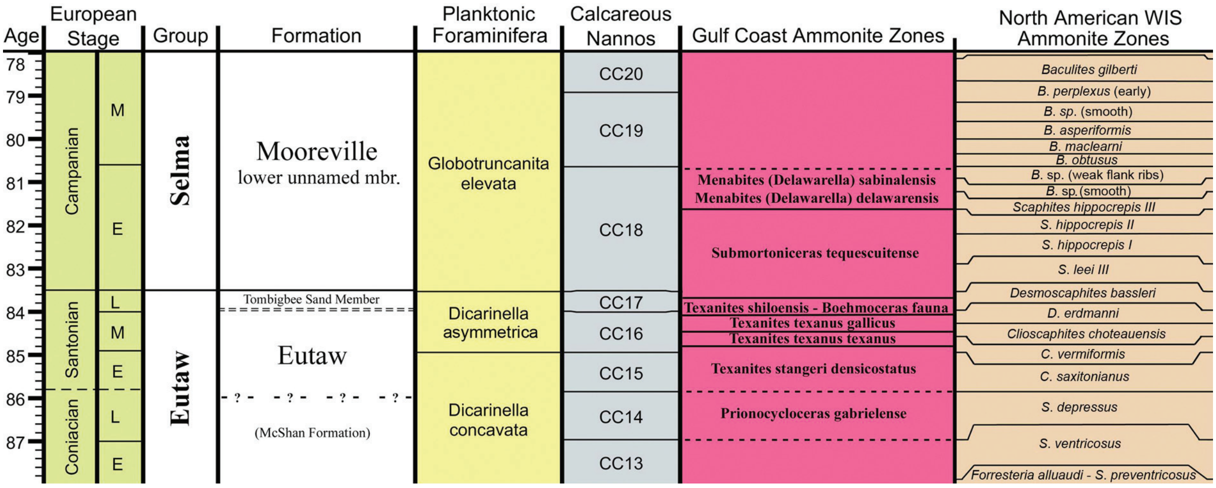

Figure 2. Lithostratigraphic, chronostratigraphic, and biostratigraphic chart for Coniacian to Campanian strata in northeastern Mississippi. Figure by C.N. Ciampaglio.

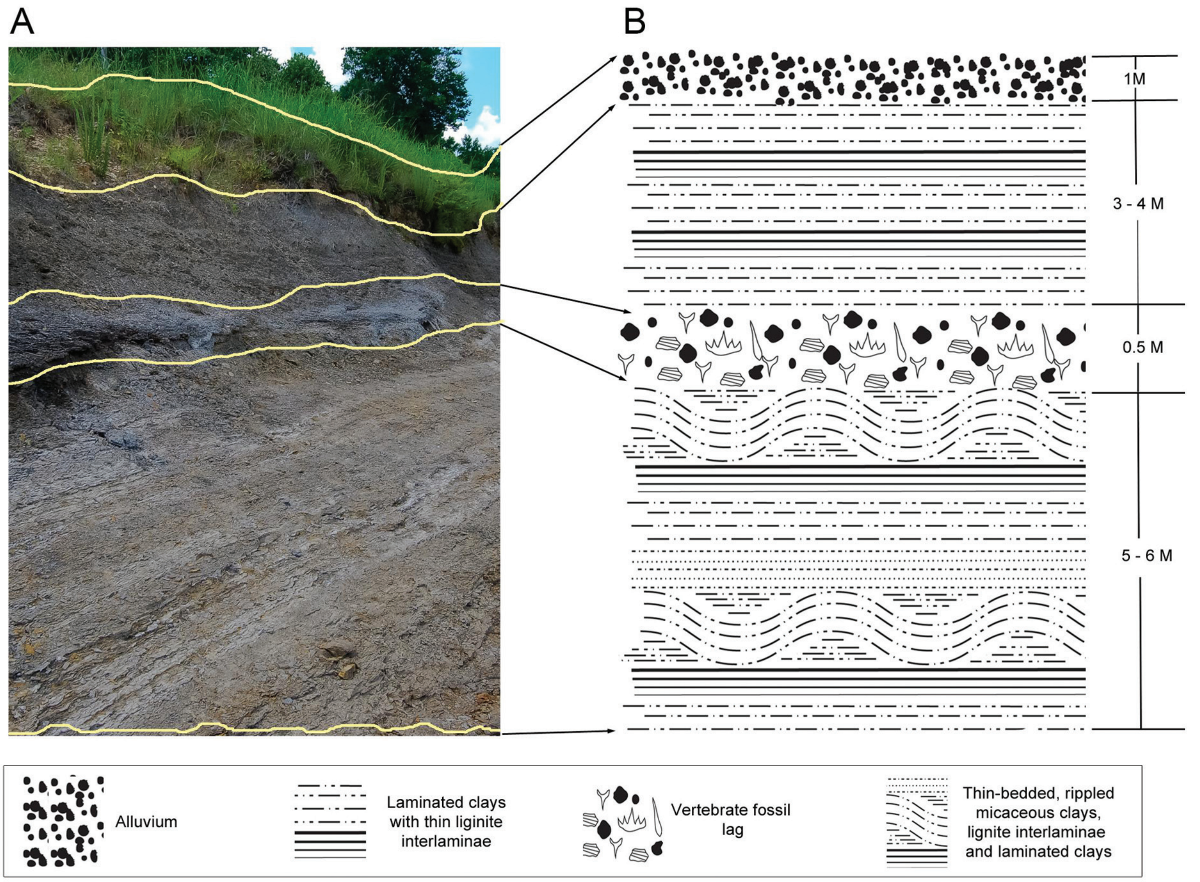

Figure 3. Stratigraphic occurrence of fossils recovered during our study. A) Photograph showing exposure of Eutaw Member strata along south bank of Luxapalila Creek. Solid yellow lines indicate boundaries between beds. B) Simplified stratigraphic column for exposure seen in A (legend shown along bottom). Figure by C.N. Ciampaglio.

of Eutaw Formation deposition, as numerous feathers have been collected from estuarine deposits of the Ingersoll Shale in Russell County, Alabama (Knight & Bingham, 2007; Bingham *et al.*, 2008).

Geology and Geologic Setting

The locality discussed herein occurs along low banks on the south side of Luxapalila Creek in Columbus, Lowndes County, Mississippi (figure 1). An approximately 1.3 km exposure of predominantly clay and sandy clay beds of the Eutaw Formation were exposed. Within the exposed section, a clastic macrofossil-bearing layer (referred to herein as the "Lux lag") ranging in thickness from 21 cm to 87 cm is bounded above and below by thinly laminated clays with lignite interlaminae (see figure 3). In a few places, variably bedded sands exhibiting occasional *Ophiomorpha* trace fossils were observed. These strata are traditionally associated with the lower Eutaw Formation.

The Lux lag is coarse, glauconitic, fossil-rich, fining upwards, and contains a relatively dense concentration of whole and fragmented bones, teeth, coprolites, macroinvertebrate skeletal debris (now completely leached but represented by phosphatic steinkerns), silicified and lignitized wood, pebbles and other rock clasts, medium to coarse quartz sand (many grains are spherical), occasional rose quartz and garnet grains, as well as muscovite and biotite mica. The larger bones, bone fragments, pebbles, and other clasts (teeth) are typically found in the lower part of the Lux lag, whereas the upper part contains a greater abundance of the smaller clast types, mostly fish teeth, scales, denticles, spines, and very small rounded pebbles. The vertebrate fossil content of the Lux lag consists of a mixture of various terrestrial, brackish water, and fully marine taxa. Bone, teeth, and coprolites show variable amounts of wear and breakage.

The Lux lag is located between ripple laminated clay and thinly bedded clay facies that have consistently been associated with the Eutaw Member in Mississippi (Stephenson & Monroe, 1940; Kaye, 1955) and Alabama (Wahl, 1966; Soens, 1984; Puckett, 1997). Stratigraphically, the Lux lag occurs more than three meters below massive-bedded, fine-grained and fossiliferous sands of the Tombigbee Sand Member. A major disconformity between the Eutaw and Tombigbee Sand members is thought to represent the first transgressive surface within the Upper Zuni A Gulf Coast-3.0 (UZAGC) depositional cycle of Mancini *et al.* (1995). This Gulf Coast cycle correlates to the third order cycles 3.4 and 3.5 within UZA-3 of Haq *et al.* (1988). Mancini *et al.* (1995) defined the transgressive surface of UZAGC-3.0 as the boundary between low stand systems tract deposits of the Eutaw Member and transgressive systems tract deposits of the supradjacent Tombigbee Sand Member. A fossil-rich lag occurring at the base of the Tombigbee Sand is similar in faunal composition to the Lux lag.

The UZAGC-3.0 transgressive surface and associated lag at the base of the Tombigbee Sand Member have been studied in Greene County, Alabama by Becker *et al.* (1998), who provided a model for transgressive lag accumulation. In their model, fine sediment was winnowed from pre-existing clast-bearing, fossiliferous beds (of the lower Eutaw Formation) by the descending wave base during a net marine regression late in a low stand systems tract. However, we envision a different scenario for the formation of the Lux lag. Although the possibility of time-averaged reworking cannot be ruled out, the condition of the fossils (teeth are not rounded and polished) and the overall species content indicate that the Lux lag accumulated within a somewhat turbid shallow marine, nearshore environment. The Lux lag may represent a condensed zone within the third-order cycle Upper Zuni A 3.4 (see Haq *et al.*, 1988).

Age of Deposits

Biostratigraphic and radiometric work on Eutaw Formation deposits within the Tombigbee River valley in east-central Mississippi has yielded relative ages of upper Santonian and lower Campanian. These studies include biozonal measurements taken by Dowsett (1989), Mancini & Soens (1994) and Puckett (2005) at several sites along the Tombigbee River, including the type locality of the Tombigbee Sand at Plymouth Bluff. Kennedy & Cobban (1991) and Kennedy *et al.* (1997) analyzed a suite of ammonite species collected from different stratigraphic levels within the Tombigbee Sand Member at Plymouth Bluff (Columbus Lock and Dam) and other sites along the river. Russel (1986) examined planktonic foraminifera and nannoplankton from the Tombigbee Sand Member at Plymouth Bluff. Emry *et al.* (1981) considered their Mississippi vertebrate fauna to be of late Santonian age, but further to the east Lamb *et al.* (1991) and Becker *et al.* (1998) found that latest Santonian and early Campanian species of ammonites occur with vertebrate fossils, indicating that the Santonian/Campanian boundary is contained within the basal Tombigbee Sand lag in that area. Obradovich *et al.* (1993) obtained an absolute age of 84.09 ±0.4 Ma from sanidine crystals collected in bentonite beds within the lower part of the Tombigbee Sand Member south of Aberdeen, 15 miles north and along strike of Plymouth Bluff and the Luxapalila Creek. The International Commission on Stratigraphy (ICS, 2012) placed the Santonian-Campanian boundary at 83.5+/- 0.7 Ma, and the Lux lag would be latest Santonian based on its stratigraphic position 3 m below the Tombigbee Sand. If the Lux lag represents the Upper Zuni A 3.4 condensed zone, the absolute age is closer to 83.75 Ma based on the dating results of Haq *et al.* (1988).

Institutional Abbreviations

The fossils from the Luxapalila Creek site that we examined and photographed are housed at:

MMNS, Mississippi Museum of Nature and Science, Jackson;
SC, South Carolina State Museum, Columbia.

Additional fossils are located at:

Wright State University, Celina, Ohio.

Methods

Vertebrate fossils were recovered from the site through surface collecting and bulk sampling. Bulk matrix samples were processed in the laboratory, with sediment being disaggregated in 5 gallon buckets of water and then gently screened with USA Standard Testing Sieves down to 0.25 mm (# 60 screen). The remaining concentrates were examined under a microscope. Specimens under 1 cm in greatest dimension were mounted to 1 mm - head insect pins with carbowax, and all specimens were photographed using a Nikon D7000 camera with an inverted Nikkor 28 mm fixed lens.

Numerous publications discussing dignathic, ontogenetic, and gynandric heterodonty within extant elasmobranch species include, among others, Feduccia & Slaughter (1974), Gruber & Compagno, (1981), Powlik (1995), Kajiura & Tricas (1996), Shimada (2002, 2005), Summers *et al.* (2004), Purdy & Francis (2007), and Gutteridge & Bennett (2014). All could serve as a guide when attempting to interpret heterodonty within fossil elasmobranch species. The results of previous studies on Eutaw Formation elasmobranch teeth by Meyer (1974) and Case *et al.* (2001), notably morphological variation and taxonomic assignments, had a particular bearing on the present report.

Systematic Paleontology

Hybodontoidea
Hybodontidae Owen, 1846
Meristodonoides Underwood & Cumbaa, 2010
Meristodonoides multiplicatus n. sp.

Figures 4 & 5

Holotype – MMNS 5603, lateral tooth crown.

Paratypes – MMNS 5310.1, complete lateral tooth; MMNS 3264.1, large tooth cusp; SC2012.48.8, incomplete anterior tooth crown; SC2012.48.9, anterolateral tooth crown.

Etymology – Species name alludes to the numerous longitudinal ridges occurring on the labial (and particularly) lingual crown faces.

Additional material examined – MMNS 3264.2, large tooth cusp; MMNS 3264.3, 6 main cusps and 1 incomplete crown; MMNS 3264.4, anterolateral tooth crown; MMNS 5310.2, crown; MMNS 5310.3, six tooth cusps; SC2012.48.10, anterolateral tooth crown; SC2012.48.11, 11 incomplete tooth crowns; SC2012.48.12, crown main cusp; SC2012.48.13, incomplete miniscule crown; SC2012.48.14, 3 incomplete miniscule crowns; SC2012.48.15, 109 main cusps; MMNS 5474.1, fin spine fragment; MMNS 5474.2, two fin spine fragments; MMNS 5599, fin spine fragment; MMNS 5600, fin spine fragment.

Remarks – Interpreting tooth morphology and potential heterodonty within our sample was difficult because of the incompleteness of the material. Of the 143 specimens, only one is complete (MMNS 5310.1), five are crowns preserving at least part of the mesial and distal shoulders, 17 are crowns preserving either the mesial or distal shoulder, and 120 consist of only the main cusp of the tooth crown. However, our sample exhibits some variation with regard to cusp shape, lateral cusplet development, and crown ornamentation. We identified anterior and lateral tooth positions using Maisey's (1983) reconstruction of the *Egertonodus basanus* (see Maisey, 1987) dentition as a guide. Presumed anterior teeth have a tall and vertical or slightly distally oriented main cusp

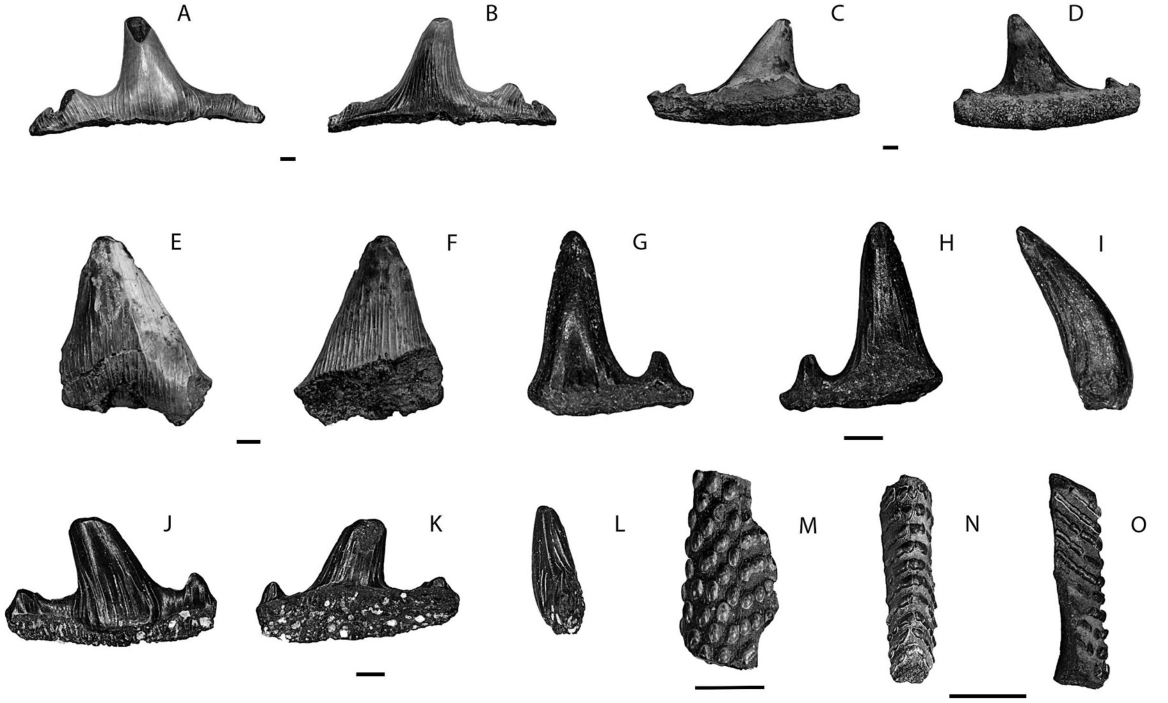

Figure 4. Hybodont shark teeth, *Meristodonoides multiplicatus* n. sp., from the Eutaw Formation at Luxapalila Creek, Mississippi. A-B, holotype, MMNS 5603, in A) labial, B) lingual views. C-D, paratype, MMNS5301.1, in C) labial, D) lingual views. E-F, paratype, MMNS 3264.1, in E) labial, F) lingual views. G-I, paratype, SC2012.48.8. G), labial, H) lingual, I) profile views. J-L, paratype, SC2012.48.9, in J) labial, K) lingual, L) mesial views. M-O, dorsal fin spine fragments. MMNS 5599 in M) lateral view. MMNS 5474.1 in N) anterior, O) lateral views. Labial is at right in I, at left in L. Scale bars = 1 mm. Photographs by K.E. Runyon.

and apparently a single pair of lateral cusplets of rather equal height. Lateral teeth have a lower and more obviously distally inclined main cusp, a wider crown base, and two pairs of lateral cusplets. The holotype, MMNS 5603, shows that the first pair of lateral cusplets is larger than the second, and interestingly that the mesial cusplets are poorly differentiated from the crown shoulder (figure 4A-B). In contrast, the first mesial and distal cusplet on MMNS 5310.1, a complete tooth and paratype, are of equal size, with only a vestigial second mesial cusplet (this area is damaged on the distal side; see figure 4C-D). Two teeth, MMNS 5310.2 and SC 2012.48.10, exhibit an intermediate morphology between our proposed anterior and posterior jaw positions. Both specimens have a single pair of lateral cusplets, but the main cusp is distally inclined as in the holotype (figure 5A-B & G-H). The potential significance of this is uncertain, but could indicate that anterior teeth furthest from the symphysis have sharply inclined cusps or lateral teeth closer to the symphysis had only a single pair of lateral cusplets. Both MMNS 5310.2 and SC 2012.48.10 are smaller than MMNS 5603, and they could represent a younger growth stage where lateral teeth have only a single pair of lateral cusplets (see additional discussion on ontogenetic heterodonty below).

The labial and lingual crown faces of all of the teeth bear longitudinal ridges, with those on the lingual face being noticeably more robust than those on the labial face. Whereas the labial ridges are generally restricted to the lower one third of the main cusp (but may extend to one half the cusp height, particularly at the side of the cusp), lingual ridges extend one half to four fifths or more of the cusp height. Ridges on the lateral cusplets on both sides extend to the apex or nearly so.

In general, the main cusps are conical to subconical and have a highly convex labial crown foot. Several specimens, those greater than 8 mm in height, have a more broadly triangular cusp (in labial view) with flatter labial crown foot. This is particularly true for two specimens, MMNS 3264.1 and MMNS 3264.2, the dimen-

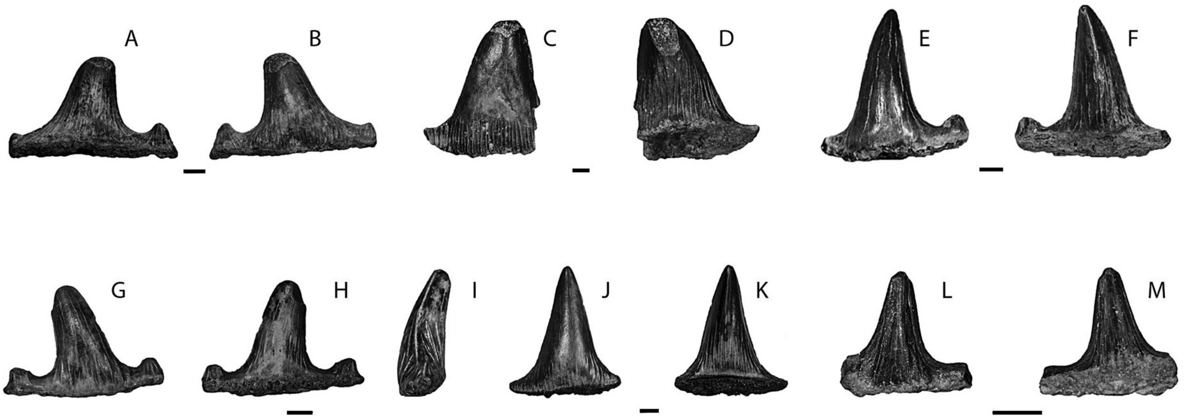

Figure 5. Hybodont shark teeth, *Meristodonoides multiplicatus* n. sp. from the Eutaw Formation at Luxapalila Creek, Mississippi. A-B, MMNS 5301.2 in A) lingual, B) labial views. C-D, MMNS 3264.2 in C) labial, D) lingual views. E-F, MMNS 3264.4 in E) labial, F) lingual views. G-I, SC2012.48.10 in G) labial, H) lingual, I) mesial views. J-K, SC2012.48.12 in J) labial, K) lingual views. L-M, SC2012.48.13 in L) labial, M) lingual views. Scale bars = 1 mm. Photographs by K.E. Runyon.

sions of which are approximately 11 mm in height and 8 to 9 mm width (see figures 4E-F & 5C-D). These crowns are labio-lingually flattened, with concave baso-medial surfaces on the labial and lingual faces. The nature of the lateral cusplets is unknown, but labial and lingual ornamentation is consistent with what was observed on more conical specimens.

Although the possibility that these variations in morphology represent more than one species cannot be ruled out, we believe that our sample represents heterodonty within a single species. Maisey (1983) noted that cusplet morphology and number within *E. basanus* varied, as did the development of labial and lingual ornamentation. Maisey's (1983) reconstructed *E. basanus* dentition, based on a specimen in which the teeth are preserved *in situ* on the jaws, shows monognathic heterodonty (p. 49, fig. 20), with main cusps of anterior teeth being more erect than on lateral teeth, and cusp height decreasing but distal inclination increasing posteriorly. Dignathic heterodonty is also indicated by the comparatively smaller size and narrower main cusp of upper teeth. Monognathic (and possibly dignathic) heterodonty within *M. multiplicatus* is comparable to *E. basanus*, but our sample of isolated teeth also appears to reflect ontogenetic heterodonty within *M. multiplicatus*. As tooth size increases, so do the number of labial and lingual longitudinal ridges, and the main cusp becomes less conical and more broadly triangular (*i.e.*, main cusps become wider into adulthood). Additionally, cusplets may not have formed until the teeth were at least 6 mm in height, as four teeth in our sample, 2.5 mm to 4.5 mm in height, are apparently devoid of cusplets (at least on the side preserved) and instead have an elongated shoulder bearing a straight cutting edge (see figure 5, L-M).

Underwood & Cumbaa (2010) recently erected *Meristodonoides* to include hybodont tooth morphologies like the ones described above. In the process they also synonymized with the new genus several species that had been assigned to *Hybodus*, including post-Coniacian *H. montanensis* (Case, 1978) and *H. novojerseyensis* (Case & Cappetta, 2004). Two morphotypes occurring together in Campanian strata of the Western Interior Seaway were identified as separate species based on tooth size, development of lateral cusplets, and formation of crown ornamentation. These morphologies were originally identified as *Hybodus montanensis* and *H. wyomingensis* by Case (1978, 1987a), but Rees (1999) has since suggested that the morphologies represented ontogenetic heterodonty within the *montanensis* species. This species has been assigned to *Meristodonoides* by Underwood & Cumbaa (2010). The Eutaw teeth differ from the *montanensis* and *wyomingensis* morphologies in that the crown ornamentation is much more extensive, reaching up to one half the crown height on the labial face and up to four fifths the height on the lingual face, and anterior teeth of *montanensis* apparently lack lateral cusplets (present on Eutaw anterior teeth except for specimens less than 5 mm in height). Teeth of Campanian-Maastrichtian *M. novojerseyensis* are nearly devoid of ornamentation at the center of the labial face, the ridges on the lingual face are shorter, and lateral cusplets, of which there are up to two pairs, appear to be taller than on the Eutaw teeth (see Case & Cappetta, 2004).

It is difficult to put into perspective the specimens that Meyer (1974) collected during his study. He identified *Hybodus* sp. aff. *H. bulteri* from Santonian and Campanian strata of the Mississippi Embayment, including the Eutaw Formation in eastern Mississippi. All of his specimens are incomplete and the morphology of the lateral shoulders is unknown. Differences in crown ornamentation could be related to heterodonty or be indicative of more than one species. However, the specimens Meyer (1974) illustrated (fig. 7) appear to be within the range of variation we observed in our sample. Bourdon *et al.* (2011) tentatively identified three different hybodont genera within their Santonian sample from New Mexico. Their discussion regarding teeth that they referred to *M. montanensis* was limited to specimens preserving the main cusp and at least one lateral shoulder, and it appears that all of these specimens were rather small (less than 9 mm in crown width). Although the New Mexico specimens are similar to teeth of equivalent size in our sample in that they lack pronounced cusplets, they differ in having labial and lingual crown ridges that are less than one half lingual cusp height, as opposed to half or more on the Mississippi sample.

Several of the dorsal fin spine fragments in our sample preserve enough ornamentation to allow us to conclude that they are conspecific with the specimen illustrated by Case *et al.* (2001: pl. 1, figs.5-7) from the Eutaw Formation of Georgia. The spine ornamentation, consisting of a series of oblique enameloid ridges that transition postero-apically into enameloid-covered tubercles, leads us to associate the morphology with *Meristodonoides* rather than *Lonchidion*, which apparently has ornamentation consisting of multiple ridges running parallel to spine length (*i.e.*, Estes, 1964; Duffin, 1985; see figure 7A-B). It should be noted here that the fin spines attributed to *M. montanensis* and *H. wyomingensis* by Case (1978, 1987a, respectively) are very similar to each other and compare favorably with spines attributed to *Lonchidion*.

Lonchidiidae Herman, 1977
Lonchidion Estes, 1964
Lonchidion cristatum n. sp.

Figure 6

Holotype – SC2012.48.71, tooth crown.

Paratypes – SC2012.48.72, tooth crown; SC2012.48.74, incomplete tooth crown; SC2012.48.75, tooth crown.

Additional material examined – MMNS 5477, tooth crown; SC2012.48.73, 2 tooth crowns; SC2012.48.76, 2 tooth crowns; SC2012.48.77, 2 ablated teeth.

Etymology – The species name alludes to the crests (ridges) occurring at various locations on the tooth crown.

Diagnosis – The teeth measure up to 4 mm in width. All specimens have a robust transverse crest extending the width of the crown, a small crest on the labial protuberance, and a short vertical medial crest on the lingual face. The root is unknown.

Description – Two morphotypes are included in the sample, the first of which has a greatly expanded labial crown face and resulting sub-triangular outline in occlusal view, and a labial protuberance that is not well differentiated from the labial margin (see figure 6A-H). The occlusal surface is convex with a blunt central apex, and the crown appears arched in labial view. There is no indication of accessory cusplets along the transverse crest, but nodes may occur on the labial and/or lingual side of this crest. The labial protuberance bears a bifurcated ridge.

The second morphotype, of which four specimens are available, consists of a wide (reconstructed width approximately 4 mm), labio-lingually narrow crown that is straight in both occlusal and labial views (figure 6I-P). The labial protuberance is clearly differentiated from the labial face, and it bears a simple crest. The transverse crest divides the occlusal surface into nearly equal labial and lingual parts, and there is no evidence of a medial cusp or accessory cusplets.

Remarks – Although the morphotypes are quite different from each other we consider them to be conspecific based on the nature of the transverse crest, the presence of a crest on the labial protuberance, and a medial longitudinal crest on the lingual face. We believe

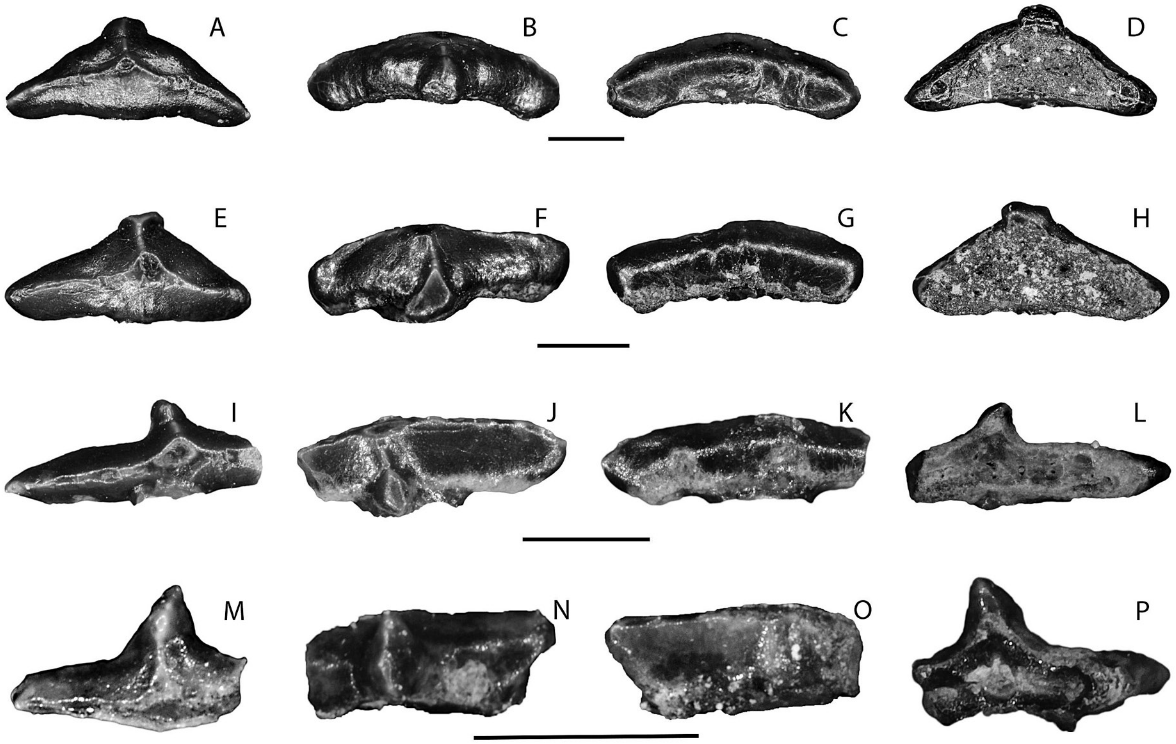

Figure 6. Hybodont shark teeth, *Lonchidion cristatum* n.sp., from the Eutaw Formation at Luxapalila Creek, Mississippi. A-D, holotype, SC2012.48.71, in A) occlusal, B) labial, C) lingual, D) basal views. E-H, paratype, SC2012.48.72, in E) occlusal, F) labial, G) lingual, H) basal views. I-L, paratype, SC2012.48.74, in I) occlusal, J) labial, K) lingual, L) basal views. M-P, paratype, SC2012.48.75, M) occlusal, N) labial, O) lingual, P) basal views. Labial at top in occlusal and basal views. Scale bars = 1 mm. Photographs by K.E. Runyon.

the morphologies represent monognathic heterodonty within a single individual, with the holotype morphology (*i.e.*, figure 6A) being located in anterior jaw positions, whereas the other morphology occupying more lateral and/or posterior positions (*i.e.*, figure 6I; see also Duffin, 1985: fig. 12).

The generic assignment of Cretaceous teeth of similar morphology has changed over the years, having gone full circle from *Lonchidion* (*i.e.*, Estes, 1964) to *Lissodus* (*i.e.*, Cappetta & Case, 1975a; Duffin, 1985) and back to *Lonchidion* (Rees & Underwood, 2002). Meyer (1974) collected several teeth from the Eutaw Formation that he tentatively identified as *Lonchidion breve*. Meyer (1974) based his identifications on the work of Patterson (1966), who erected several subspecies of *L. breve* from the early Cretaceous of England. Duffin (1985) later elevated these morphologies to species status, but none of these satisfactorily compares with *L. cristatum* n. sp. Crowns of *L. breve* are smaller in overall size and lack crests on the labial protuberance and lingual face, as well as accessory ornamentation as seen on our holotype. *Lonchidion crenulatum* and *L. pustulatum* are more similar to *L. cristatum* n. sp. in overall morphology, but they are smaller in overall size, lack a lingual vertical crest, and have crenulated transverse crests and accessory cusplets and/or vertical striations. Three other North American species, Albian *L. anitae*, Campanian *L. griffisi*, and Maastrichtian *L. selachos* bear multiple cusplets (see Estes, 1964; Thurmond, 1971; Case, 1987a). Campanian *L. babulskii* is wider than *L. cristatum* n. sp., lacks the robust transverse crest, and is devoid of other ornamentation except for an occasional, non-bifurcated crest on the labial protuberance (see Cappetta & Case, 1975a). Cenomanian *L. weltoni* is smaller in overall size than *L. cristatum* n. sp. but generally bears a much larger medial cusp that may be striated (Duffin, 1985).

Hybodontidae or Lonchidiidae

Figure 7A-M

Material examined – MMNS 3265, cephalic spine crown; MMNS 5482, cephalic spine crown; MMNS 5496, incomplete cephalic spine; MMNS 5598, incomplete cephalic sine crown; MMNS 5604, incomplete cephalic spine and unassociated cephalic spine crown; MMNS 5606, cephalic spine crown apex; MMNS 5607, cephalic spine base; MMNS 5622, three incomplete cephalic spines; MMNS 5623, 13 incomplete cephalic spines;

Remarks – Hybodont cephalic spines occur as paired elements, and there may be one or two pairs on the head, depending on species. Cephalic spines are known to have been located just above and behind the orbit, over the lateral otic process, and in the region of the parietal fossa (see Maisey, 1982). Two distinctive morphologies are represented in our sample, one of which is symmetrical and consists of a base bearing a posteriorly curving crown at the anterior end, posteriorly directed lateral wings and a posterior, dorsally directed projection. These spines are similar to those illustrated by Bermúdez-Rochas (2009: fig. 4, 2a-3b), but the exact morphology of the anterior crown projection of the Eutaw specimens is unknown because it is not preserved. Smaller spines grouped into this category lack lateral projections, but it is unclear if these represent the second of two sets of paired spines, or if these specimens represent a juvenile growth stage.

The second spine morphology, much larger in size, is quite unlike the one previously described. The larger spines emanate from the anterior end of a thickened, reniform base. The crown is laterally compressed, sharply curved posteriorly and slightly retrorse, inclined away from the middle of the head, and occupies at least half of the dorsal surface of the base. Ornamentation consists of fine discontinuous ridges on lateral, posterior, and medial surfaces. The crown apex is smooth and pointed, with a sharp carina extending onto the dorsal surface of a large posterior barb (figure 7D-F). Following Maisey (1982), it is possible to determine from which side of the head a spine was located, even for specimens consisting of just the base or just the crown. For spine bases, the medial lobe indicates the part of the spine closer to the sagittal midline of the head (*i.e.*, the lobe being on the right indicates that the spine was on the left side of the head; see figure 7J). The crowns curve slightly medially, and lateral ornamentation is more robust and obliquely intersects an inconspicuous anterior carina (figure 7F, H, L).

The taxonomic utility of isolated cephalic spines may be limited, as morphologies similar to figures 7C & G have been attributed to *Meristodonoides novojerseyensis* (Case & Cappetta, 2004), *Hybodus* (Maisey, 1982, 1983), *Lonchidion* (Maisey, 1982; Duffin, 1985) and even Triassic *Asteracanthus* (Rieppel, 1981).

Neoselachii(?) Compagno, 1977
Ptychodontidae Jaekel, 1898
Ptychodus mortoni Agassiz, 1839

Figure 7N-P

Material examined – MMNS 3778, two teeth; MMNS 4527, two teeth; MMNS 5114, lateral tooth; MMNS 5309, lateral tooth; MMNS 5541, two teeth; MMNS 5523, six crown fragments.

Remarks – This tooth conforms to *P. mortoni* in having a robust conical cusp bearing radiating ridges that emanate from the apex and become finer and highly branching towards the crown base. The crowns of anterior-most teeth are symmetrical and have no clearly differentiated cusp, but cusps of lateral teeth are conspicuous from the marginal area and offset distally (*i.e.*, figure 7N-O).

Heterodontiformes Berg, 1940 (in part)
Heterodontidae Gray, 1851
Heterodontus Blainville, 1816
Heterodontus sp. aff. *H. rugosus* (Agassiz, 1839)

Figure 8A

Material examined – SC2012.48.34, crown fragment

Remarks – SC2012.48.34 is a portion of a large lateral tooth from an adult individual. There is a transverse edge that divides the crown into labial and lingual faces, with the labial face bearing a vermiculate pattern and the lingual face having a reticulated pattern. This ornamentation is similar to Campanian *H. rugosus*, but our identification is tentative due to the sample available to us. Meyer (1974) recovered teeth of *Heterodontus* from the Eutaw Forma-

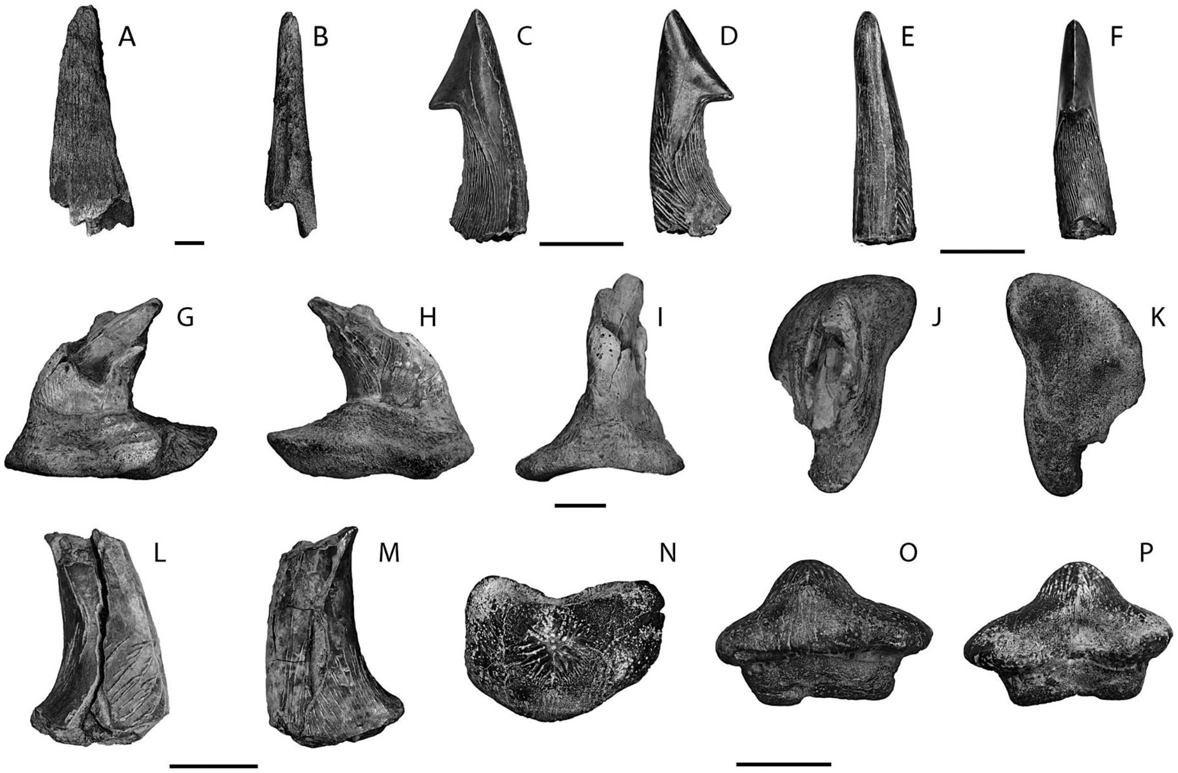

Figure 7. Hybodont spines and *Ptychodus* tooth from the Eutaw Formation at Luxapalila Creek, Mississippi. A-B, *Lonchidion*? sp. dorsal fin spine, MMNS 6376, in A) left lateral, B) posterior views. C-F, hybodont cephalic spine, MMNS 5496, in C) left lateral, D) right lateral, E) anterior, F) posterior views. G-K, hybodont cephalic spine, MMNS 5606, in G) left lateral, H) right lateral, I) anterior, J) apical, K) basal views. L-M, hybodont cephalic spine, MMNS 5598, in L) right lateral, M) left lateral views. N-P, *Ptychodus mortoni*, MMNS 5309, in N) occlusal, O) labial, P) lingual views. Anterior at top in J-K. Labial at bottom in N. Scale bars = 1 mm. Photographs by K.E. Runyon.

tion of western Alabama, but it is difficult at this time to determine if that material is conspecific with SC2012.48.34.

Orectolobiformes Compagno, 1973
Hemicylliidae Gill, 1862
Chiloscyllium Müller & Henle, 1837
Chiloscyllium sp.

Figure 8B-H

Material examined – SC2012.48.78, anterior tooth; SC2012.48.79, lateral tooth; SC2012.48.80, 3 incomplete teeth.

Remarks – These teeth might be confused with *Cantioscyllium grandis* n. sp., but they are distinguished by their much smaller overall size (1.5 mm or less in width), single pair of lateral cusplets, and lack of labial crown ornamentation. Meyer (1974) identified specimens from the Tombigbee Sand Member as *C. greeni*, but our sample is not sufficient to make a more specific determination.

Ginglymostomatidae Gill, 1862
Cantioscyllium Woodward, 1889
Cantioscyllium grandis new species

Figure 8I-P & 9

Holotype – SC2012.48.82, lateral tooth.

Paratypes – SC2012.48.81, anterior tooth; SC2012.48.83, lateral tooth; SC2012.48.84, lateral tooth.

Additional material examined – MMNS 5127.1, tooth; MMNS 5127.2, tooth; MMNS 5479, five teeth; SC2012.48.85, lateral tooth; SC2012.48.86, anterior? tooth; SC2012.48. 87, 21 teeth; SC2012.48.88, tiny anterior tooth; SC2012.48.89, 3 tiny teeth; SC2012.48.117, lateral tooth.

Remarks – Our specimens are conspecific with *Cantioscyllium saginatus* erected by Meyer (1974), the holotype of which was collected from the Tombigbee Sand Member. The Santonian *saginatus* morphology differs from *Cantioscyllium decipiens* in its larger overall size,

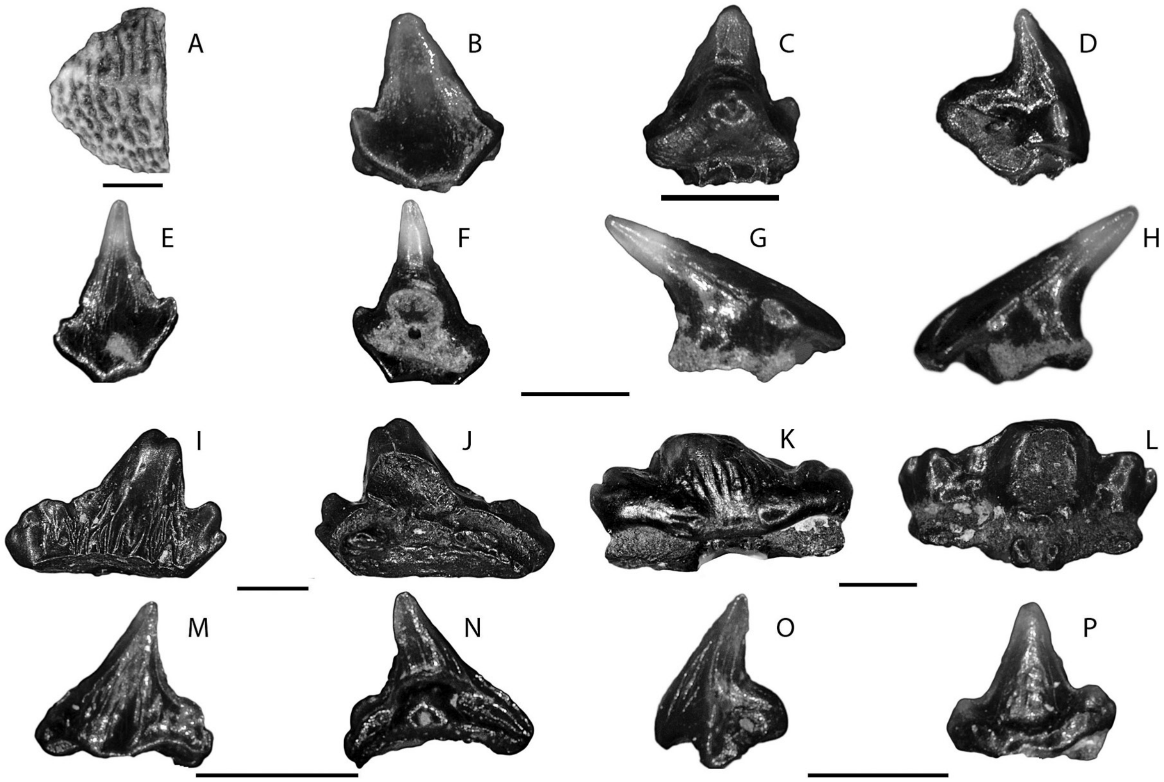

Figure 8. Fossil shark teeth from the Eutaw Formation at Luxapalila Creek, Mississippi. A) *Heterodontus* sp. aff. *H. rugosus* lateral tooth, SC2012.48.34, in occlusal view. B-D, *Chiloscyllium* sp, SC2012.48.87, in B) labial, C) lingual, D) distal views. E-H, *Chiloscyllium* sp., SC2012.48.79, in E) labial, F) lingual, G) mesial, H) distal views. I-J, *Cantioscyllium grandis* n. sp., SC 2012.48.85, in I) labial, J) lingual views. K-L, *C. grandis* n. sp., SC2012.48.117, in K) labial, L) lingual views. M-O, *C. grandis* n. sp., SC2012.48.88, in M), labial, N) lingual, O) distal views. P) *C. grandis* n. sp., MMNS 5127.2, in labial view. Labial at bottom in A. Scale bars = 1 mm. Photographs by K.E. Runyon.

more numerous pairs of lateral cusplets, and less pronounced labial ornamentation (see Cappetta, 1973). Unfortunately, the *saginatus* name is a nomen nudum because Meyer's work was never published. More than two decades after Meyer's work, *C. saginatus* was synonymized with *C. meyeri*, a morphology that occurs in Campanian and Maastrichtian strata (Case & Cappetta, 1997; Cappetta & Case, 1999; also Cicimurri, 2007). However, the *C. meyeri* morphology, as identified by Case & Cappetta (1997) and Cicimurri (2007), differs from the Santonian specimens in being smaller (smaller than *C. decipiens*), meso-distally narrower, and bearing fewer pairs of lateral cusplets. We therefore conclude that the Santonian morphology is not conspecific with *C. meyeri*. Teeth identified as *Cantioscyllium decipiens* from Santonian strata of New Mexico (Williamson *et al.*, 1989; Bourdon *et al.*, 2011) and as *Chiloscyllium* sp. from the Santonian of Georgia (Case *et al.*, 2001) appear to be conspecific with our Eutaw specimens.

The largest teeth in our sample are more than 5 mm in width, and all bear robust sinuous and bifurcating labial ridges extending from just above the crown foot to slightly below the apical margins. Some teeth also bear lingual rugosities near the lateral cusplets. Monognathic heterodonty is evident in our sample, with anterior and lateral positions being identified. Anterior teeth are symmetrical, whereas lateral teeth have a distally inclined cusp and a more elongated mesial side, and generally two pairs of lateral cusplets (second pair vestigial). One specimen appears to have had a third mesial cusplet. An ontogenetic series may be represented by SC2012.48.88, MMNS 5217.2, and SC2012.48.82, wherein as tooth size increased, so did crown robustness, formation of lateral cusplets, and development of ornamentation (see figures 8M-P & 9A-C, respectively).

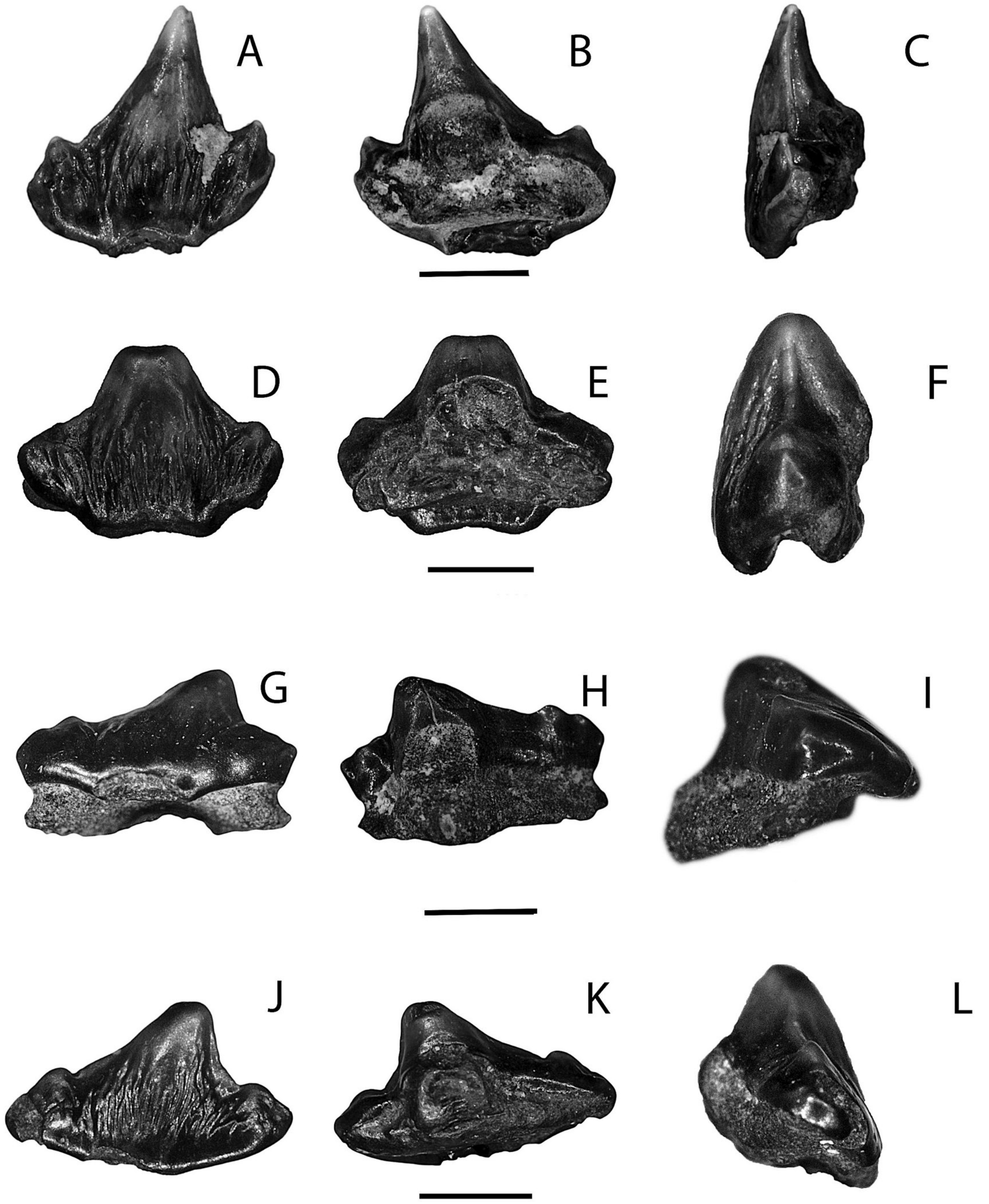

Figure 9. Orectolobiform shark teeth, *Cantioscyllium grandis* n.sp., from the Eutaw Formation at Luxapalila Creek, Mississippi. A-C, holotype, SC2012.48.82, in A) labial, B) lingual, C) distal views. D-F, paratype, SC2012.48.81, in D) labial, E) lingual, F) mesial views. G-I, paratype, SC2012.48.83, in G) labial, H), lingual, I) mesial views. J-L, paratype, SC2012.48.84, in J), labial, K) lingual, L) mesial views. Scale bars = 1 mm. Photographs by K.E. Runyon.

Family incertae cedis
Columbusia Case *et al*., 2001
Columbusia fragilis Case *et al*., 2001

Figure 10

Material examined – MMNS 5484, one tooth; MMNS 5126.1, two teeth; 5126.2, tooth; 5126.3, tooth; SC2012.48.61, juvenile tooth; SC2012.48.62, anterior tooth; SC2012.48.63, anterolateral tooth; SC2012.48.64, anterolateral tooth; SC2012.48.65, lateral tooth; SC2012.48.66, 33 teeth; SC2012.48.67, 6 incomplete teeth; SC2012.48.68, 38 incomplete teeth; SC2012.48.69, 4 incomplete teeth; SC2012.48.70, large tooth.

Remarks – We are able to emend the original diagnosis for this species (Case *et al*., 2001) based on the teeth in our sample. The cusp is conical, with very convex labial and lingual faces, and on all but two specimens it is erect and not distally inclined (and then only very slightly). Twelve specimens bear a short longitudinal ridge on the labial face (*i.e.*, figure 10M), but the remaining teeth lack this feature. Of the twelve teeth with the ridge, all but one is 1mm or less in width, whereas the reconstructed width of the remaining specimen is 2 mm. The significance of this ridge, if any, is unknown.

Lateral shoulders are well separated from the cusp, and these may be short with a very convex cutting edge, or elongated with a rather straight edge. In occlusal view, the shoulders may extend straight out from the cusp base or their distal ends may be curved lingually. In labial view, the shoulders may be perpendicular to the cusp or extend obliquely from the cusp (figures 10A & Q, respectively). The former feature, combined with a high cusp and elongated basal protuberance, produces a cruciform labial outline. The cutting edge is sharp on the lateral shoulders and onto the lower half of the cusp, but it becomes indistinct or absent altogether near the cusp apex (compare figures 10C & F).

The root is low, sub-triangular in basal view, and may have a flat or concave basal attachment surface. The root may be holaulocorhizous or hemiaulocorhizous. Teeth with hemiaulocorhizous roots have a large central basal foramen located more to the lingual side, and there is a small foramen at the vertical face of the lingual root margin. On teeth with holaulocorhizous roots, a deep groove extends to the lingual root margin, but the labial portion of the groove is very shallow. In general, a single small foramen is located at each side of a medial bulge on the dorsal surface of the lingual root projection (sometimes two), as well other tiny scattered foramina.

We consider some of the variation in tooth crown morphology to represent monognathic heterodonty, with crowns of presumed anterior teeth having short and cusp-like lateral shoulders (*i.e.*, figure 10A), whereas lateral teeth have more elongated and less convex shoulders (figure 10J). The root also becomes wider in more

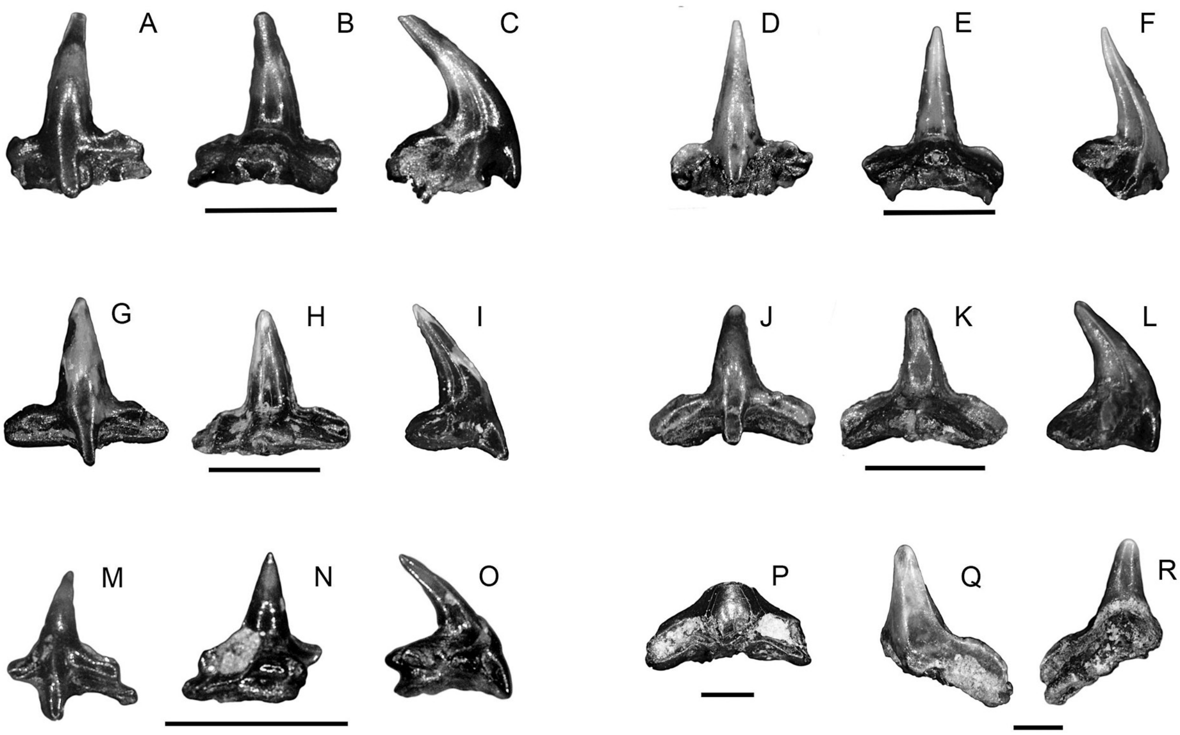

Figure 10. Orectolobiform shark teeth, *Columbusia fragilis*, from the Eutaw Formation at Luxapalila Creek, Mississippi. A-C, SC2012.48.82 in A) labial, B) lingual, C) profile views. D-E, SC2012.48.63 in D) labial, E) linlgual, F) profile views. G-I, SC2012.48.64 in G) labial, H) lingual, I) distal view. J-L, SC2012.48.65 in J) labial, K) lingual, L) profile views. M-O, SC 2012.48.61 in M) labial, N) lingual, O), profile views. P) SC2012.48.70 in labial view. Q-R, MMNS 5126.2 in Q) labial, R) lingual views. Scale bars = 1 mm. Photographs by K.E. Runyon.

lateral positions, and although the cusp remains rather erect (some distal inclination was observed) it becomes lower. Ontogenetic heterodonty is also apparent, with the tiniest teeth (0.5 mm in width or less) being gracile and having a very narrow cusp, very narrow and elongate labial basal protuberance, and sharper labial longitudinal ridge that is bifurcated. As tooth size increases, the cusp becomes broader and the cutting edge more restricted to the cusp base and lateral shoulders, and the basal protuberance becomes shorter and wider (compare figures 10M & P).

Cappetta (2012) has allied *Columbusia* with sclerorhynchid rays based on the superficial similarity of the tooth root to some species within Sclerorhynchiformes. However, *Columbusia fragilis* is very similar to *Cretorectolobus*, an orectolobiform shark, in its overall morphology, and both genera have roots that may be holaulocorhizous or hemiaulocorhizous (Case, 1978; Siverson, 1995; Underwood & Cumbaa, 2010). We add *Columbusia* to an undetermined orectolobiform family that also includes *Cretorectolobus* (see also Siverson, 1995; Underwood & Cumbaa, 2010). *Columbusia fragilis* differs from *Cretorectolobus* in having a narrower, very conical and nearly always erect (not distally inclined) cusp, the labial basal protuberance is narrower and much more elongated, the cutting edge, although smooth and sharp across the lateral shoulders and onto the base of the cusp, may not be well developed apically, there is no lingual enameloid-covered uvula, and there are fewer foraminae on the dorsal surface of the lingual root projection.

Lamniformes Berg, 1958
Anacoracidae Casier, 1947
Squalicorax Whitley, 1939
Squalicorax sp. aff. *S. yangaensis* (Darteville & Casier, 1943)

Figure 11A-H

Material examined – MMNS 3501.1, 39 teeth; MMNS 4711.1, 33 teeth; MMNS 4711.2, small tooth; SC2012.48.1, anterior tooth; SC2012.48.2 anterolateral tooth; SC2012.48.3, lateral tooth; SC2012.48.4, 50 teeth; SC2012.48.6, 55 incomplete teeth.

Remarks – The mesial edge is most convex medially, and the serrations in this region are also the largest and often compound. The crowns appear to be constricted at the base of the cusp due to a notch between the distal edge and distal heel, and a concavity near the base of the mesial edge (particularly in figure 11E-F). The convexity of the mesial edge lessens towards the commissure. The distal edge varies from convex to straight.

Multiple jaw positions are represented in our sample, including anterior, lateral, and posterior files. Anterior-most teeth have a rather vertical cusp that has a convex mesial edge and shorter but equally convex distal edge. Teeth in more lateral positions have broader and more distally directed cusps, a more elongated distal heel, and the mesial notch is less conspicuous. Posterior teeth have a low and highly distally directed cusp. Pronounced in vivo wear was observed on two teeth, where the upper half of the cusp was broken and the exposed surface subsequently worn smooth (the teeth are in otherwise pristine condition).

Although of similar size to *Squalicorax kaupi*, our Eutaw sample differs from that species in that there is a distinctive constriction near the base of the crown. This feature is consistent with two species reported from the upper Cretaceous of Africa, *S. yangaensis* (Campanian; see Darteville & Casier, 1943) and *S. bassanii* (Maastrichtian, see Gemmellaro, 1920). Some of the teeth are reminiscent of *S. bassanii* in having simple serrations of consistent size. However, most specimens are more like *S. yangaensis* and exhibit very large, compound serrations on the most convex part of the mesial edge, and we therefore assign our sample to this latter species.

At least some of the Tombigbee Sand specimens that Meyer (1974) identified as *S. kaupi* are conspecific with our *S.* sp. aff. *S. yangaensis*. The assignment of identical Eutaw Formation teeth to *S. falcatus* by Case *et al.* (2001) may have followed Leidy (1873), who identified specimens from Mississippi as *Galeocerdo* (= *Squalicorax*) *falcatus*. *Squalicorax yangaensis* has been reported from New Mexico, an area that was situated at the southwestern portion of the Western Interior Seaway during the Santonian (Williamson *et al.*, 1989; Wolberg & Bellis, 1989; Bourdon *et al.*, 2011).

Squalicorax sp. cf. *S. kaupi* Agassiz, 1843

Figure 11I-L

Material examined – MMNS 3501.2, incomplete tooth; SC2012.48.6, incomplete tooth.

Remarks – The two teeth in our sample lack the distal heel and much of the root. The preserved crowns differ from *S.* sp. aff. *S. yangaensis* in that there is no concavity near the base of the mesial edge, and the simple serrations are smaller, more uniform in size, and mesially curving. In these respects the two teeth are similar to those identified as *S. kaupi* from Campanian strata of the US Western Interior and Gulf and Atlantic Coastal plains (*i.e.*, Cappetta & Case, 1975a; Case, 1987a; Lauginiger & Hartstein, 1983; Manning & Dockery, 1992). Bourdon *et al.* (2011) identified similar teeth from the Santonian of New Mexico as *S. lindstromi* and suggested that this species name (following Einarsson *et al.*, 2010) be applied to North American Santonian to Maastrichtian teeth previously identified as *S. kaupi*. A detailed comparison of the North American material to *S. lindstromi* remains to be undertaken, and Davis (1890) himself did not provide a direct comparison to *S. kaupi*, stating only that "Whilst recognizing the possibility that many of the specimens now supposed to represent separate species may ultimately be proved to have been associated in the same jaws, it may be advantageous to consider them as distinct until material shall be acquired which will render their determination certain." Leidy's (1873) sample of teeth from the Eutaw Formation of Mississippi, which he identified as *Galeocerdo* (= *Squalicorax*) *falcatus*, contains a mixture of *S.* sp. aff. *S. yangaensis* and *S.* sp. cf. *S. kaupi*.

Scindcorax Bourdon *et al.*, 2011
? *Scindcorax* sp.

Figure 11M-N

Material examined – SC2012.48.7, anterior tooth.

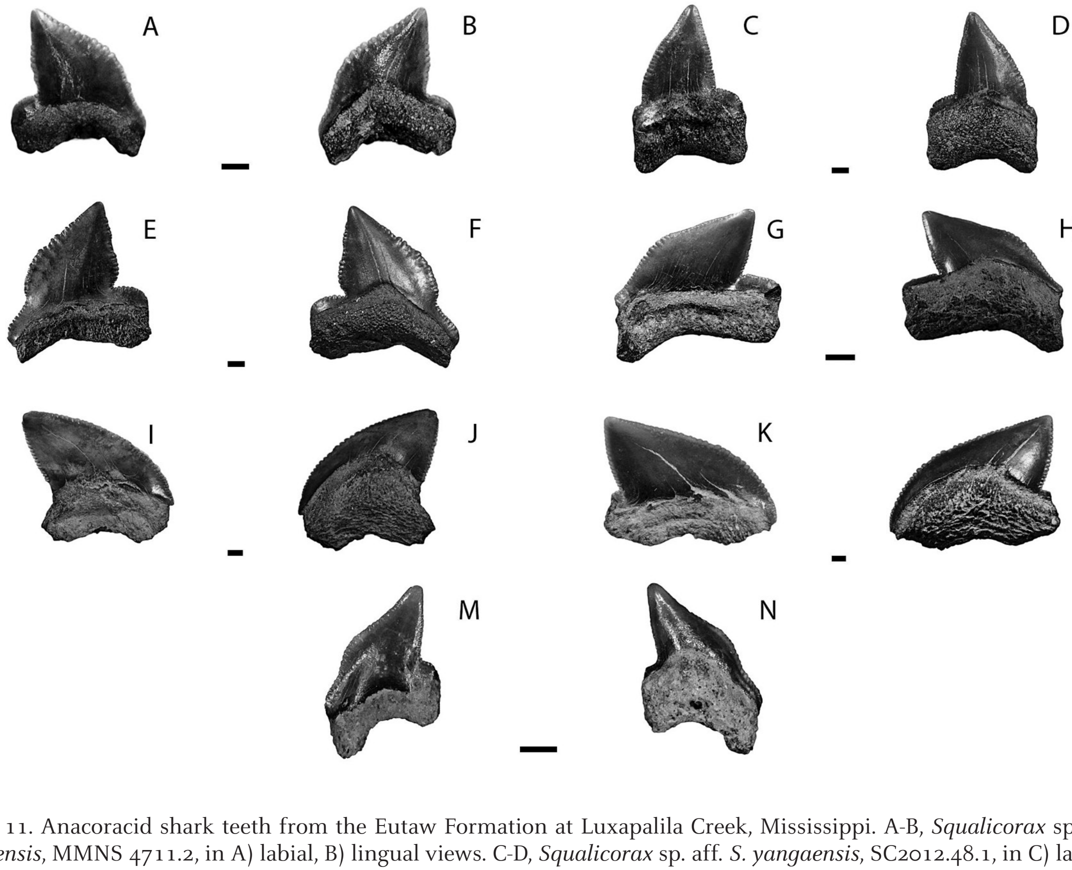

Figure 11. Anacoracid shark teeth from the Eutaw Formation at Luxapalila Creek, Mississippi. A-B, *Squalicorax* sp. aff. *S. yangaensis*, MMNS 4711.2, in A) labial, B) lingual views. C-D, *Squalicorax* sp. aff. *S. yangaensis*, SC2012.48.1, in C) labial, D) lingual views. E-F, *Squalicorax* sp. aff. *S. yangaensis,* SC2012.48.3 in E) labial, F) lingual views. G-H, *Squalicorax* sp. aff. *S. yangaensis*, SC2012.48.2, in G) labial, H) lingual views. I-J, *Squalicorax* sp. aff. S. *kaupi*, MMNS 3501, in I) labial, J) lingual views. K-L, *Squalicorax* sp. aff. *S. kaupi*, SC2012.48.6, in K) labial, L) lingual views. M-N, ?*Scindcorax* sp., SC2012.48.7, in M) labial, N) lingual views. Scale bars = 1 mm. Photographs by K.E. Runyon.

Remarks – SC2012.48.7 is morphologically similar to material Bourdon *et al.* (2011) identified as a new anacoracid taxon, *Scindcorax*. It is the smallest anacoracid tooth in our sample, measuring slightly over 3 mm in width and 4 mm in total height, and more gracile in its appearance than the next smallest anacoracid tooth in our sample, which measures 5 mm in width and height (see figure 11A-B). This latter tooth is regarded as representing a young growth stage of *S.* sp. aff. *S. yangaensis*, and it is entirely possible that SC2012.48.7 belonged to an even younger individual, rather than a distinctly diminutive anacoracid species. The possibility that this morphology represents ontogenetic variation within *Squalicorax* sp. cf. *S. yangaensis* was not discussed by Bourdon *et al.* (2011) when naming *Scindcorax*.

Mitsukurinidae Jordan, 1898
Scapanorhynchus Woodward, 1889
Scapanorhynchus texanus (Roemer, 1849)

Figure 12

Material examined – MMNS 5485; incomplete pathological lateral tooth; MMNS 5517.1, large lateral tooth; MMNS 5517.2, 7 large lateral teeth; MMNS 5525.1, anterior tooth; MMNS 5525.2, 79 small lateral teeth; MMNS 5614, 64 teeth; MMNS 5615, 40 small anterior teeth; MMNS 5616.1, symphyseal tooth; MMNS 5616.2, 6 symphyseal teeth; MMNS 5617, 32 small to medium teeth; MMNS 5620, latero-posterior tooth; MMNS 5624, 4 distal lateral teeth; MMNS 5625, 2 posterior teeth; MMNS 5626, posterior tooth; MMNS 5629, 4 lateral and posterior teeth; MMNS 5630, 5 symphyseal teeth; MMNS 5631, symphyseal tooth; SC2012.48.16, anterior tooth; SC2012.48.17, 3 large lateral teeth; SC2012.48.18, 14 incomplete teeth; SC2012.48.19, 230 teeth; SC2012.48.20, 177 tooth crowns; SC2012.48.21, anterior tooth; SC2012.48.22, anterolateral tooth; SC2012.48.23, lateral tooth; SC2012.48.24, 13 symphyseal teeth; SC2012.48.25, 4 posterior teeth; SC2012.48.26, lateral tooth; SC2012.48.27, anterolateral tooth; SC2012.48.28, anterolateral tooth; SC2012.48.29, lateral tooth; SC2012.48.37, two pathologic teeth; SC2012.48.96, anterior tooth, SC2012.48.114, tiny anterior tooth; SC2012.48.115, tiny lateral tooth; SC2012.48.116, 6 tiny teeth.

Remarks – Monognathic, dignathic, and ontogenetic heterodonty are evident in our sample. Symphyseal, anterior, lateral and posterior jaw positions can be distinguished, and lower teeth appear to be more symmetrical than upper teeth (which are more distally inclined than lowers). The various tooth morphologies have been described in detail by Meyer (1974) and Cappetta & Case (1975a), but in brief the teeth that we consider to have been on or just lateral to the symphysis have a tall and very narrow sigmoidal crown that lacks lateral cusplets, and laterally compressed root with poorly differentiated, asymmetrical lobes (figure 12A-B). Other teeth, which may have been just to the side of the symphysis (= parasymphyseal) are not as laterally compressed, have a single pair of minute to moderately developed lateral cusplets, and more elongated root lobes. One specimen of this type has a tiny distal cusplet, but there is an elongated mesial enameloid shoulder extending onto the root lobe. Anterior teeth are distinguished by their high, narrow, sigmoidal crowns and elongated, diverging root lobes. At least in the first anterior tooth, the crown lacks lateral cusplets (*i.e.*, figure 12C-D), but more laterally situated anterior teeth have shorter root lobes that are highly divergent, and one pair of lateral cusplets is conspicuous (figure 12S-T). Teeth in lateral positions have a much broader and labio-lingually thinner crown that is often distally inclined, and lateral cusplets are broadly triangular with sharp cutting edges (figure 12M-N). The roots of lateral teeth are short and sub-rectangular, and the mesial lobe may be slightly more elongated. Posterior teeth have a low and highly distally curved crown and large triangular lateral cusplets.

We believe that Meyer's (1974) interpretation of ontogenetic heterodonty in *S. texanus* is correct. On anterior teeth, the number of lingual longitudinal ridges increases with tooth size, and lateral cusplets decrease in size or are absent altogether. It is our observation that anterior teeth of less than 10 mm in crown height have rather tall needle-like cusplets (figure 12O-P), whereas relatively few of the 120+ anterior teeth 12 mm or greater in height show any indication of lateral cusplets (figure 12E-F). Our sample also indicates that as lateral teeth increase in size, the crown becomes wider, the lateral cusplets become lower and broader, and the lingual crown ornamentation becomes re-

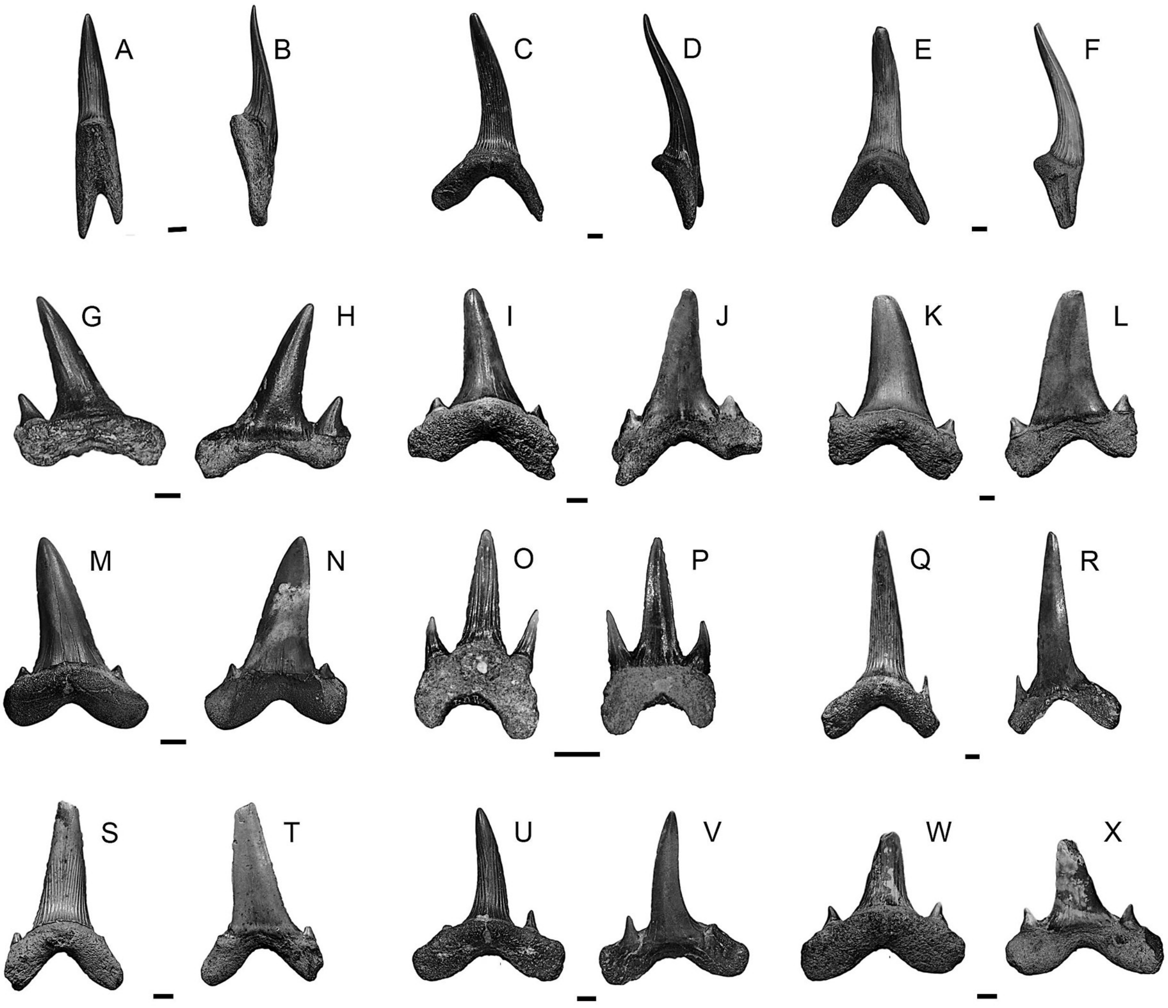

Figure 12. Mitsukurinid shark teeth, *Scapanorhynchus texanus*, from the Eutaw Formation at Luxapalila Creek, Mississippi. A-B, symphyseal tooth, MMNS 5616.1, in A) lingual, B) profile views. C-D, SC2012.48.16 in C) lingual, D) profile views. E-F, MMNS 5525.1 in E) lingual and F) profile views. G-H, SC2012.48.29 in G) lingual, H) labial views. I-J, SC2012.48.23 in I) lingual, J) labial views. K-L, SC2012.48.26 in K) lingual, L) labial views. M-N, MMNS 5517.1 in M) lingual, N) labial views. O-P, SC2012.48.114 in O) lingual, P) labial views. Q-R, SC2012.48.21 in Q) lingual, R) labial views. S-T, SC2012.48.96 in S) lingual, T) labial views. U-V, SC2012.48.27 in U) lingual, V) labial views. W-X, SC2012.48.28 in W) lingual, X) labial views. Scale bars = 1 mm. Photographs by K.E. Runyon.

duced to absent (compare figure 12G-H with 12M-N, figure 12I-J with 12K-L). Another possible variation is that anterior and lateral teeth 10 mm or less in crown height often bear plications at the labial crown foot. The smallest teeth in our sample, 5 mm or less in tooth height, are similar to those identified as *Microdontaspis tenuis* by Case *et al.* (2001). We believe that these smaller teeth represent very young *Scapanorhynchus* sharks, and an ontogenetic progression is apparent in our sample, wherein as tooth size increases, the labial ridges become restricted to the lateral cusplets and only lateral margins of the main cusp, and eventually they are absent altogether on the largest teeth. The functional significance of the labial ridges, if any, is unknown, and more than half of the anterior and lateral teeth of at least 10 mm in crown height lack the feature. Plications were observed on posterior teeth of all sizes.

Our identification of the teeth in this sample as *S. texanus* is based on our observation of Campanian specimens from North Carolina and New Jersey, as well as samples of *S. raphiodon* from South Dakota and Wyoming. Although many of the teeth in our sample fall within the size range for *S. raphiodon*, the number of lingual longitudinal ridges is greater and anterior teeth generally lack lateral cusplets. In addition, the largest teeth in our sample, all lateral teeth, measure up to 39 mm in total height and are more robust than equivalent teeth of *S. raphiodon*. The material identified as *S. raphiodon* by Case *et al.* (2001) from the Eutaw Formation of Georgia is conspecific with our Eutaw sample.

Cretoxyrhinidae Glickman, 1958
Cretoxyrhina Glickman, 1958
Cretoxyrhina mantelli (Agassiz, 1843)

Figure 13A-B

Material examined – MMNS 4863, lateral tooth.

Remarks – MMNS 4863 is indistinguishable from *C. mantelli* teeth reported from Coniacian through lower Campanian strata elsewhere (*i.e.*, Applegate, 1970; Shimada, 1997), and this tooth represents the largest of the lamniform sharks known thus far from the Eutaw Formation. Apart from large size, the tooth can be distinguished from those of other non-anacoracid lamniform sharks in being broadly triangular, with smooth enameloid lateral shoulders as opposed to cusplets, and lack of crown ornamentation.

Otodontidae Glickman, 1958
Cretalamna Glickman, 1958
Cretalamna appendiculata (Agassiz, 1843)

Figure 13C-H

Material examined – MMNS 5086, 11 teeth; SC2012.48.90, anterior tooth; SC2012.48.91, lateral tooth; SC2012.48.92, posterior tooth; SC2012.48.93, 12 teeth; SC2012.48.94, 7 incomplete teeth.

Remarks – Anterior (figure 13C), lateral (figure 13E), and posterior (figure 13G) jaw positions are represented in our sample. Anterior teeth are symmetrical with elongated and rounded lobes, but towards the commissure the teeth become wider, the main cusp lower and distally curving, lateral cusplets broader, and root lobes short and rectangular. Crowns lack ornamentation.

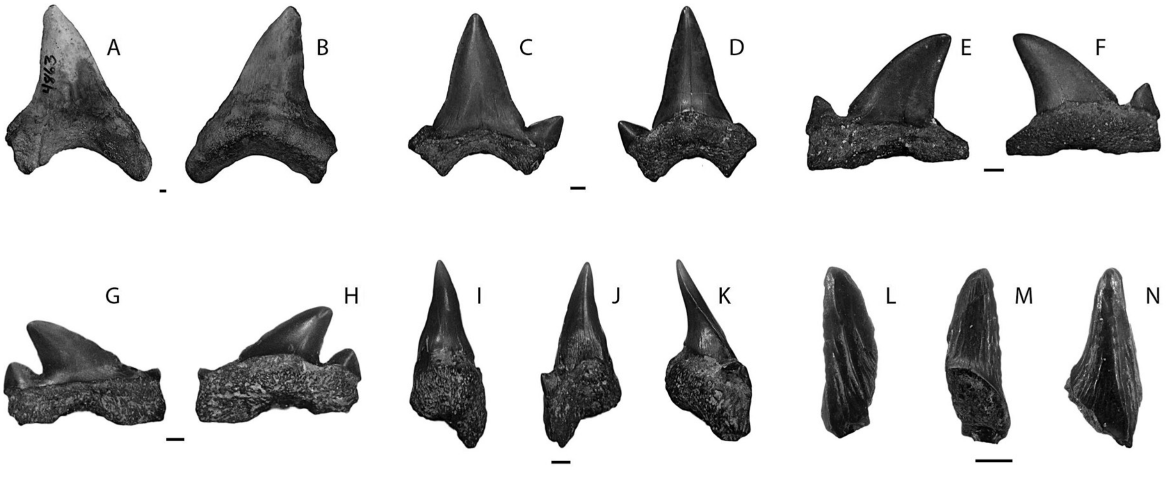

Figure 13. Lamniform shark teeth from the Eutaw Formation at Luxapalila Creek, Mississippi. A-B, *Cretoxyrhina mantelli,* MMNS 4863 in A) labial, B) lingual views. C-D, *Cretalamna appendiculata* anterior tooth, SC2012.48.90, in C) labial, D) lingual views. E-F, *C. appendiculata* lateral tooth, SC2012.48.91, in E) labial, F) lingual views. G-H, *C. appendiculata* posterior tooth, SC2012.48.92, in G) labial, H) lingual views. I-K, *Protolamna borodini*, SC2012.48.38, in I) labial, J) lingual, K) mesial views. L-N, *P. borodini*, SC2012.48.39, in L) labial, M) lingual, N) profile views. Scale bars = 1 mm. Photographs by K.E. Runyon.

Eoptolamnidae Kriwet *et al*., 2008
Protolamna Cappetta, 1980
Protolamna borodini (Cappetta & Case, 1975a)

Figure 13I-N

Material examined – MMNS 5282, incomplete tooth; SC2012.48.38, incomplete tooth; SC2012.48.39, main cusp.

Remarks – These small teeth are distinguished by a narrow but labio-lingually thick main cusp, single pair of lateral cusplets that are situated slightly labial to the main cusp, and crown ornamentation consisting of longitudinal ridges. Crown ornamentation is variable, as SC 2012.48.38 (figure 13I-K) has fine ridges on the lower half of the labial face, but the lingual face is virtually smooth. In contrast, SC 2012.48.39 (figure 13L-N) has coarse labial ridges that extend more than halfway up the face, and the lingual face is also plicated. The conspicuous lingual root boss is not bisected by a groove, and the two root lobes are closely spaced.

This species was originally attributed to *Plicatolamna* (Cappetta & Case, 1975a) and later transferred to *Cretodus* (*i.e.*, Case & Schwimmer, 1988; Case *et al.*, 2001). More recently, Case & Cappetta (2004) referred the species to *Protolamna*, and Kriwet *et al.* (2008) removed the genus from Cretoxyrhinidae and placed it within Eoptolamnidae. Based on comparisons with other species occurring in Texas (*i.e.*, Cappetta & Case, 1999), the laterally compressed nature of the *borodini* morphology indicates that assignment to *Protolamna* is appropriate, and this generic name is applied herein.

Batoidea
Sclerorhynchiformes Kriwet, 2004
Ptychotrygonidae Kriwet and others, 2009
Ptychotrygon Jaekel, 1894
Ptychotrygon chattahoochieensis Case *et al*., 2001

Figure 14

Material examined – MMNS 5130, tooth; SC2012.48.51, tooth; SC2012.48.52, tooth; SC2012.48.53, tooth; SC2012.48.54, juvenile tooth; SC2012.48.55, posterior? tooth; SC2012.48.56, 21 teeth.

Remarks – *Ptychotrygon chattahoochieensis* was erected based on a single tooth, but the overall morphology of the type specimen is consistent with the teeth in our sample, and we consider them to be conspecific. We also believe that the morphology is conspecific with Meyer's (1974) *P. triangularis eutawensis*, but because his work was never published that name is invalid, and we utilize *P. chattahoochieensis*. It should be noted that this morphology is not the same as *Ptychotrygon eutawensis* erected by Case *et al.* (2001), which is morphologically similar to some teeth we identified as *Texatrygon* (see below).

Teeth of *P. chattahoochieensis* are smaller and have different crown ornamentation than Turonian *P. triangularis* (see Cappetta, 1973). Nearly all of the teeth in our sample are cuspidate and have a transverse crest dividing the crown into a larger labial face and smaller lingual face. The labial face bears at least one other transverse crest, and the region of the labial protuberance generally bears another short transverse ridge or irregular nodes. Ontogenetic heterodonty is not evident, as teeth 1 mm or less in width are comparable in shape and discrete features to the largest teeth in the sample, which measure up to 3 mm in width. Monognathic heterodonty is difficult to interpret, but variations in cusp height could reflect anterior (higher cusp) vs. lateral (lower cusp) positions. SC 2012.48.55 is unique in having a flat crown with reniform occlusal outline, two nearly equally robust transverse ridges, and cingulum around nearly the entire crown margin (figure 14Q-T). This particular tooth could represent a posterior jaw position. We believe that the two teeth tentatively identified as *P. triangularis* by Case *et al.* (2001) are actually ontogenetic variants of *P. chattahoochiensis*.

Ptychotrygon rugosum (Case *et al*., 2001)

Figure 15

Material examined – MMNS 3500, tooth; MMNS 3761.1, tooth; MMNS 3761.2, incomplete tooth; MMNS 3781.1, tooth; MMNS 3781.2, tooth; MMNS 4883, two teeth; MMNS 5081.1, tooth; MMNS 5081.2, tooth; MMNS 5610, tooth; SC2012.48.30, two incomplete tooth crowns.

Remarks – This morphology was originally assigned to *Erguitaia* by Case *et al.* (2001; p. 95, pl. 5, figs. 100-104), but the type specimen

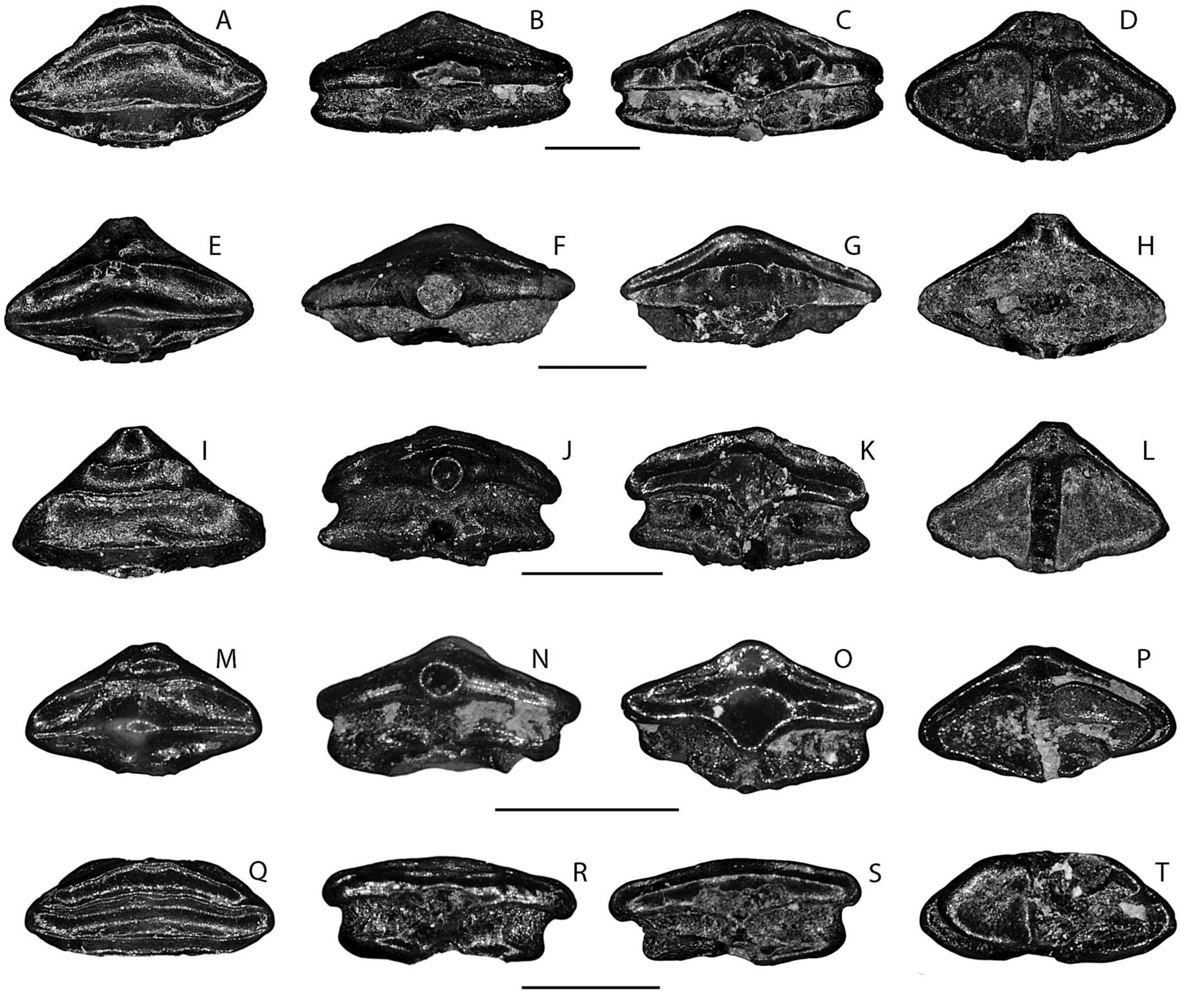

Figure 14. *Ptychotrygon chattahoochiensis* teeth from the Eutaw Formation at Luxapalila Creek, Mississippi. A-D, SC 2012.48.51 in A) occlusal, B) labial, C) lingual, D) basal views. E-F, SC2012.48.52 in E) occlusal, F) labial, G) lingual, H) basal views. I-L, SC2012.48.53 in I) occlusal, J) labial, K) lingual, L) basal views. M-P, SC2012.48.54 in M) occlusal, N) labial, O) lingual, P) basal views. Q-T, SC2012.48.55 in Q) occlusal, R) labial, S) lingual, T) basal views. Labial at top in occlusal and basal views. Scale bars = 1 mm. Photographs by K.E. Runyon.

is very heavily ornamented and has a massive, poorly differentiated labial protuberance, features that are inconsistent with *Erguitaia*. Only the type specimen was available to Case *et al.* (2001), but our larger sample size allows us to provide a more detailed morphological analysis of this species. In general, the thick crown is slightly wider than long, sub-trapezoidal in occlusal outline, and has a flat to weakly convex occlusal surface bearing four to six equally robust transverse ridges. A labial crown protuberance, half as wide as the entire crown, is blunt and greatly overhangs the root.

Tooth crowns measure up to 8 mm in width, 6 mm in length, and 3 mm in height. A thin transverse ridge divides the crown into a very narrow lingual face and much more expansive labial face. The labial face bears four to five shorter but equally robust transverse ridges, whereas the lingual face bears very fine discontinuous and anastomosing ridges that are perpendicular to crown width. The labial ridges are parallel and may be straight or crescentic (curved towards the labial margin), and may also be interconnected by finer perpendicular ridges. The massive labial protuberance has a squared appearance. There is a shallow medial fossa at the lingual crown foot. The root is unusual in being high, bisected by a deep nutritive groove, and having rather small basal attachment surfaces when compared to other sclerorhynchid teeth in our sample.

Cappetta (2006, 2012), without supporting argument, recently placed the morphology within *Ptychotrygon*. We concur with this assignment and note that, although atypical, the

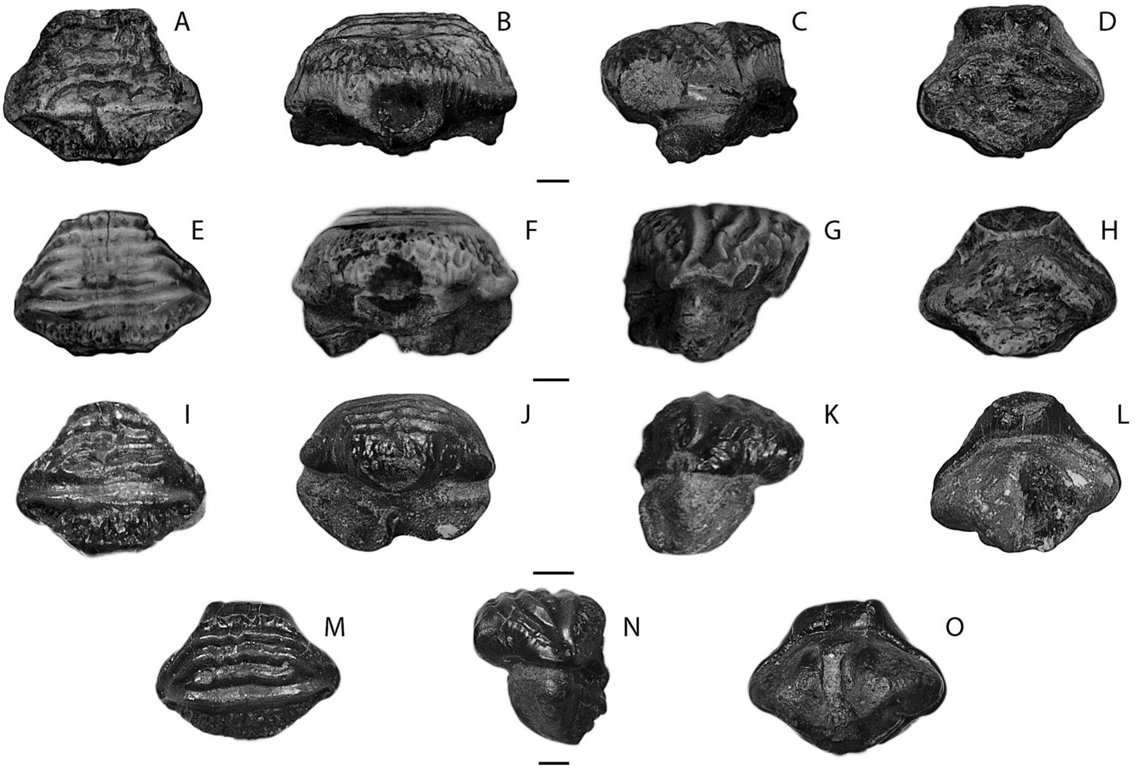

Figure 15. *Ptychotrygon rugosum* teeth from the Eutaw Formation at Luxapalila Creek, Mississippi. A-D, MMNS 3761.1 in A) occlusal, B) labial, C) profile, D) basal views. E-F, MMNS 5081.1 in E) occlusal, F) labial, G) profile, H) basal views. I-L, MMNS 3781.1 in I) occlusal, J) labial, K) profile, L) basal views. M-O, MMNS 5610 in M) occlusal, N) profile, O) basal views. Labial at top in occlusal and basal views, at left in C & N, at right in G & K. Scale bars = 1 mm. Photographs by K.E. Runyon.

morphology is more consistent with *Ptychotrygon*, particularly to species like *P. triangularis* (see Cappetta, 1973). We amend the spelling of the species name to reflect the gender of the generic name according to Article 34.2 of the International Code of Zoological Nomenclature (ICZN). *Ptychotygon rugosum* differs from all other species within the genus in its very large size and rather flat but expansive occlusal surface, having five to six labial transverse ridges in combination with longitudinal ridges on vertical surfaces, and massive, squared labial protuberance that greatly overhangs the root. The crown of this species could easily be confused with small *Ptychodus* (particularly *P. decurrens*), and it is remarkably similar to the extant rhinobatoid, *Rhina ancylostoma*. In fact, wear patterns observed on *P. rugosum* are comparable to those on *R. ancylostoma* teeth, and it is possible that *P. rugosum* occupied a similar trophic niche, crushing shelled invertebrates like small clams, snails, and crustaceans.

Texatrygon Cappetta & Case, 1999
Texatrygon benningensis (Case *et al*., 2001)

Figure 16

Material examined – MMNS 4754, tooth; MMNS 5128.1, six teeth; MMNS 5128.2, symphyseal? tooth; MMNS 5480, tooth; MMNS 5481, 3 teeth; SC2012.48.57, tooth; SC2012.48.58, tooth; SC2012.48.59, tootn; SC2012.48.60, 17 teeth.

Remarks – This morphology was also originally assigned to *Erguitaia* by Case *et al.* (2001: 94-95, pl.4, figs. 90-94). However, the crown of the *benningensis* morphology is inconsistent with the two currently recognized species, *E. misrensis* (Cappetta, 1991) and *E. arganiae* (see Arambourg, 1952) from the Maastrichtian of Africa, in that the crown is strongly cuspidate as opposed to nearly flat, and the labial protuberance is broadly united to the labial margin as opposed to sharply separated (in occlusal view). The *benningensis* morphology is clearly more similar to various species of *Ptychotrygon* that have been identified from North America (*i.e.*, McNulty & Slaughter, 1972; Cappetta,

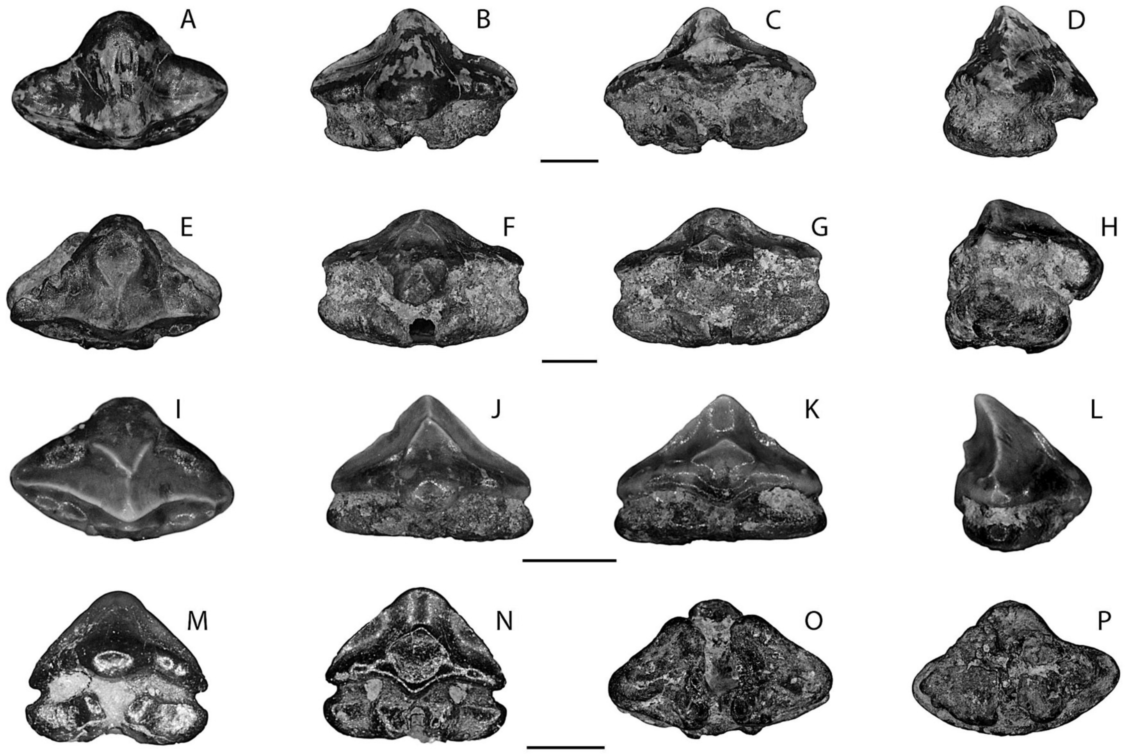

Figure 16. *Texatrygon benningensis* teeth from the Eutaw Formation at Luxapalila Creek, Mississippi. A-D & P, SC2012.48.57 in A) occlusal, B) labial, C) lingual, D) profile, P) basal views. E-H & O, SC2012.48.58 in E) occlusal, F) labial, G) lingual, H) profile, O) basal views. I-L, SC2012.48.59 in I) occlusal, J) labial, K) lingual, L) profile views. M-N, MMNS 5128.2 in M) labial, N) lingual views. Labial at top in occlusal and basal views, at right in profile views. Scale bars = 1 mm. Photographs by K.E. Runyon.

1975; Case, 1987a), and Cappetta (2006, 2012) has assigned the species to this genus. However, Cappetta & Case (1999) proposed the generic name *Texatrygon* to identify high-cusped teeth that lack labial transverse ridges and may be smooth or only weakly ornamented labially. The Eutaw specimens bear medial labial ornamentation consisting of a chevron-shaped ridge, sometimes with intermediate branching ridges (see figures 16A, E, I), but their overall morphology and development of enameloid rugosities is consistent with *Texatrygon*, and we therefore utilize this name for the *benningensis* tooth morphology. Crowns of *T. benningensis* are more consistently ornamented than those of three species currently assigned to *Texatrygon*, including *T. hooveri* (see McNulty & Slaughter, 1972), *T. greybullensis* (see Case, 1987a), and *T. copei* (Cappetta & Case, 1999). The species *T. stouti* from the Santonian of New Mexico (Bourdon *et al.*, 2011) appears to be the same as *T. benningensis*, and if so *T. stouti* is a junior subjective synonym of *T. benningensis*.

We interpret variations in crown morphology to represent monognathic and ontogenetic heterodonty. Teeth that may have been closer to the jaw symphysis are of nearly equal width and height (figure 16M-N), whereas those in more lateral positions are obviously wider than high (figure 16I-K). Overall tooth size ranges from 1.5 to 5 mm in width, and teeth within the lower range are simply smaller versions of teeth within the higher range. Wear patterns on crowns cusps (apices are often worn down to reveal internal dentine) indicate that teeth were used for clutching shelled prey.

Sclerorhynchidae Cappetta, 1974
Ischyrhiza Leidy, 1856
Ischyrhiza mira Leidy, 1856

Figure 17A-Q

Material examined – MMNS 3787, rostral spine; MMNS 5489.1, incomplete rostral spine; MMNS 5489.2, 2 incomplete rostral spines; MMNS 5125, 6 rostral spines; MMNS 5478 rostral spine; SC2012.48.31, 3 incomplete rostral spines; SC2012.48.32, incopmplete rostral spine; SC2012.48.35, tooth; SC2012.48.36, 2 teeth; SC2012.48.45, rostral? denticle; SC2012.48.46, rostral denticle; SC2012.48.47, rostral spine; SC2012.48.48, 3 rostral? denticles; SC2012.48.49, 16 rostral spines.

Remarks – Slaughter & Steiner (1968) considered rostral spine root histology to be taxonomically significant, and suggested that *Ischyrhiza mira* was derived from *I. schneideri*. Meyer (1974) compared the rostral spine histology of Campanian *I. mira*, Coniacian *I. schneideri*, and Santonian material from the Tombigbee Sand Member that he identified as *I.* sp. cf. *I mira*. He stated that the histology and overall spine size of the Santonian sample was intermediate between the Coniacian and Campanian samples, corroborating Slaughter & Steiner's (1968) hypothesis. The validity of identifying *Ischyrhiza* species based on spine histology has yet to be rigorously tested, and although the spines and teeth in our sample are smaller than the maximum size of equivalent remains of Campanian *I. mira* that we examined (from New Jersey, North Carolina, and South Carolina), the morphologies are comparable. It may simply be that we have only recovered remains of younger individuals thus far. The material that Meyer (1974) identified as *Ptychotrygon palaeformis* is herein considered to represent teeth of *I. mira* (see figure 17A-D for an example).

A number of denticles and very small spines with ornamented crowns have also been collected during our study. The denticles and spines have a crown that is posteriorly inclined, with a flat and smooth anterior surface, and convex posterior surface that bears several robust longitudinal ridges that may reach the crown apex. The identification of these remains has been confusing, and the spines are morphologically consistent with material identified as *I. georgiensis* by Case *et al.* (2001), *Ischyrhiza* sp. by Meyer (1974), and *Ptychotrygon eutawensis* by Bourdon *et al.* (2011). Meyer (1974) reportedly did not find his *Ischyrhiza* sp. spines directly associated with larger spines that he tentatively identified as *I. mira*, and it is possible that Case *et al.* (2001) are correct in that the spines represent a distinct and possibly diminutive species of *Ischyriza* (and similarly *I. avonicola*; see Estes, 1964). Assignment of the spines to species within Ptychotrygonidae (*i.e.*, Case, 1987a; Bourdon *et al.*, 2011) is controversial because it remains to be conclusively shown (through articulated cranial remains) that any species within the family possessed rostral spines (see Cappetta, 1987; Underwood, 2006).

As noted above, the general crown morphologies of denticles and tiny spines are identical. Denticles have a short crown, and the base is rather flat, circular in dorsal view, with a flat basal surface and lateral projections emanating from the margin (figure 17P-Q). Spines have a more elongated crown and the peduncle is cylindrical below the crown but basally expanding into two diverging protuberances (figure 17J-L). Denticles of intermediate morphology are shown in figure 17M-O. It must be noted here that the posterior crown base of some larger *I. mira* rostral spines in our sample bear numerous short longitudinal ridges that are oblique to crown length (see figure 17F; also noted by Meyer, 1974), and this feature can also be seen on Campanian *I. mira* spines. We associate the highly ornamented denticles and tiny rostral spines with *I. mira*, following Meyer's (1974) interpretation for *I. schneideri*. Denticles like SC 2012.48.45 (figure 17P-Q) may have been located on dorsal and/or ventral surfaces of rostra, whereas spines like SC 2012.48.47 (figure 17J-L) could represent juvenile individuals or a more proximal portion of an adult rostrum (also Cicimurri, 2007).

Borodinopristis Case, 1987b
Borodinopristis ackermani Case *et al.*, 2001

Figure 17R-Y

Material examined – MMNS 5476, rostral spine; SC2012.48.41, rostral spine; SC2012.48.42, rostral spine; SC2012.48.43, incomplete rostral spine; SC2012.48.44, 5 incomplete rostral spines.

Remarks – These diminutive rostral spines (less than 6 mm in total spine length) are similar to those of *Onchopristis* in that they bear several posterior barbs (see Dunkle, 1948; McNulty & Slaughter, 1962; Williamson *et al.*, 1993). However, the Eutaw spines differ in that an arcuate enameloid 'collar' is associated with each barb. Meyer (1974) was the first to document these unique spines, from both Eutaw Formation and Coffe Sand (Campanian) strata of Mississippi, but he tentatively referred to the material as *Sclerorhynchus* sp. 2 (see p.109-110, fig. 29C). The morphology was later identified as a new genus, *Borodinopris-*

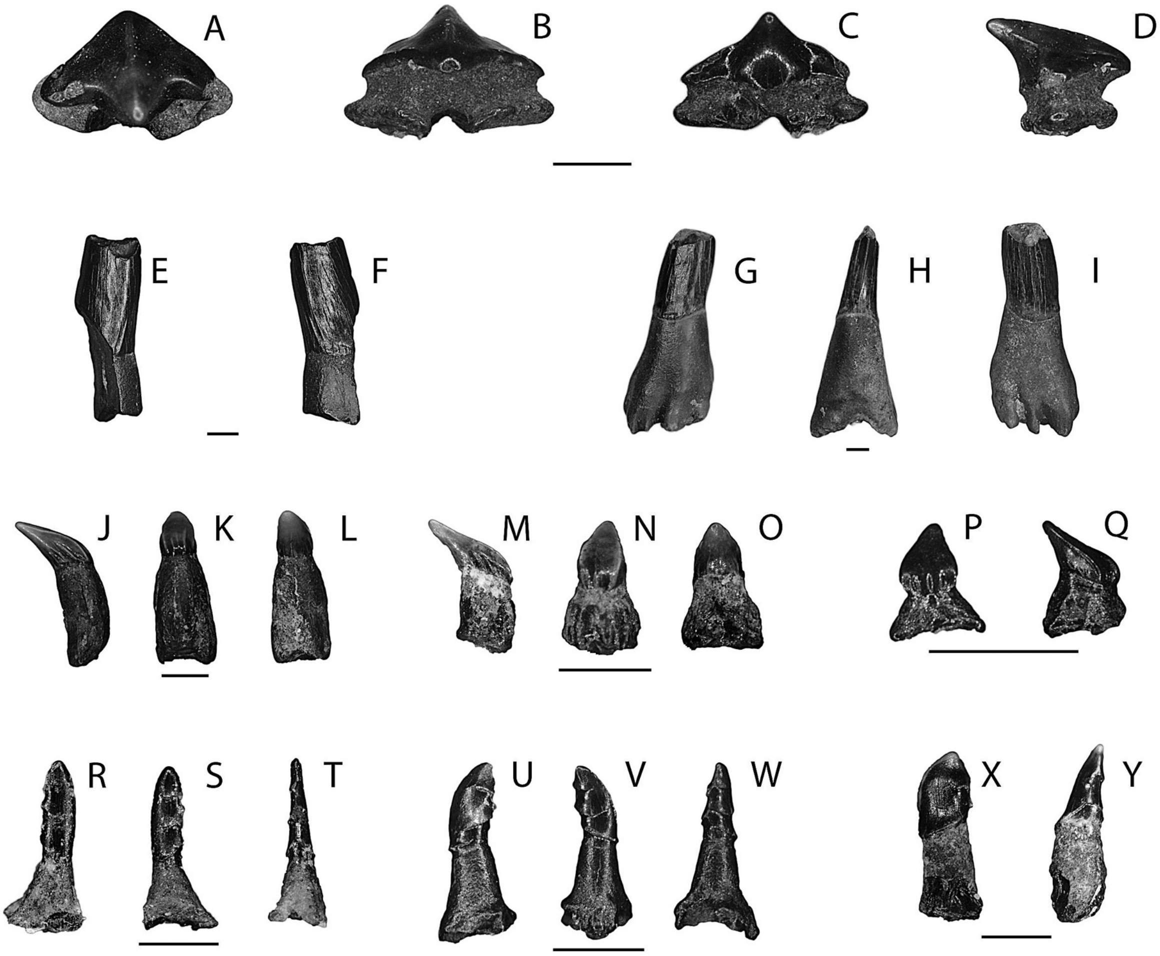

Figure 17. Sclerorhynchid ray teeth and rostral spines from the Eutaw Formation at Luxapalila Creek, Mississippi. A-Q, *Ischyrhiza* sp. cf. *I. mira*. A-D, tooth, SC2012.48.35, in A) occlusal, B) labial, C) lingual, D) profile views. E-F, rostral spine, SC 2012.48.32, in E) dorsal, F) ventral views. G-I, rostral spine, MMNS 5489.1 in G) dorsal, H) posterior, I) ventral views. J-L, rostral spine, SC2012.48.47, in J) profile, K) anterior, L) posterior views. M-O, rostral denticle, SC2012.48.46, in M) profile, N) anterior, O) posterior views. P-Q, rostral denticle, SC2012.48.45, in P) anterior, Q) posterior views. R-Y, *Borodinopristis ackermani* rostral spines. R-T, SC2012.48.41 in R) dorsal, S) ventral, T) posterior views. U-W, SC2012.48.42, in U) ventral, V) dorsal, W) posterior views. X-Y, SC2012.48.43, in X) dorsal, Y) posterior views. Scale bars = 1 mm. Photographs by K.E. Runyon.

tis, by Case (1987b), and three species, *B. ackermani* (Eutaw Formation; Case et al., 2001), *B. schwimmeri* (Campanian of the Gulf and Atlantic coastal plains; Case, 1987b; Cicimurri, 2007), and *B. shannoni* (Campanian of the Atlantic Coastal Plain; Case and others, 2012), have been described.

Borodinopristis ackermani and *B. schwimmeri* were originally distinguished based on tooth crown morphology (Case *et al.*, 2001), but no comments were made on the taxonomic utility of the rostral spines. Teeth of *B. shannoni* have yet to be described and illustrated (Case and others, 2012). We have not recovered any teeth, but close inspection of our rostral spines shows that they are identical to those of *B. ackermani* illustrated by Case *et al.* (2001; pl. 2, figs. 28-31). Ultimately, *Borodinopristis* rostral spines are useful for species determination. In posterior view, the dorsal and ventral collars of *B. ackermani* are asymmetrical, with the dorsal part of the collar being more basal (closer to the peduncle) than the ventral part, and forming a zig-zag pattern with the posterior carina (see figures 17T, W, Y). In contrast, collars of *B. schwimmeri* are much more symmetrical in posterior view and meet as a straight posterior carina. Rostral spines of *B. shannoni* may have an intermediate morphology, with the posterior barbs and carinae being less asymmetrical than on *B. ackermani*, but not as symmetrical as on *B. schwimmeri*. Additionally, the collars of *B. shannoni* may be incompletely or irregularly formed (Case and others, 2012).

Rajiformes Berg, 1940
Rhinobatidae Müller & Henle, 1838

Not illustrated

Material examined – SC2012.48.40, tooth crown.

Remarks – SC2012.48.40 is a very poorly preserved tooth that is missing the root, and a large portion of the crown is damaged. The specimen is morphologically consistent with guitarfish teeth, particularly *Rhinobatos*, but more precise identification cannot be made based on the available sample.

Myliobatiformes Compagno, 1973
Myliobatidae Bonaparte, 1838
Brachyrhizodus Romer, 1942
Brachyrhizodus ellipsis (Case *et al.*, 2001)

Figures 18 & 19

Material examined – MMNS 4525, seven teeth; MMNS 5084, five teeth; MMNS 5487, one tooth; MMNS 5529, two teeth; SC2012.48.96, rhomboidal tooth; SC2012.48.97, 40 rhomboidal teeth; SC2012.48.98, circular tooth; SC2012.48.99, 26 circular to ovate teeth; SC2012.48.100, sub-hexagonal tooth;

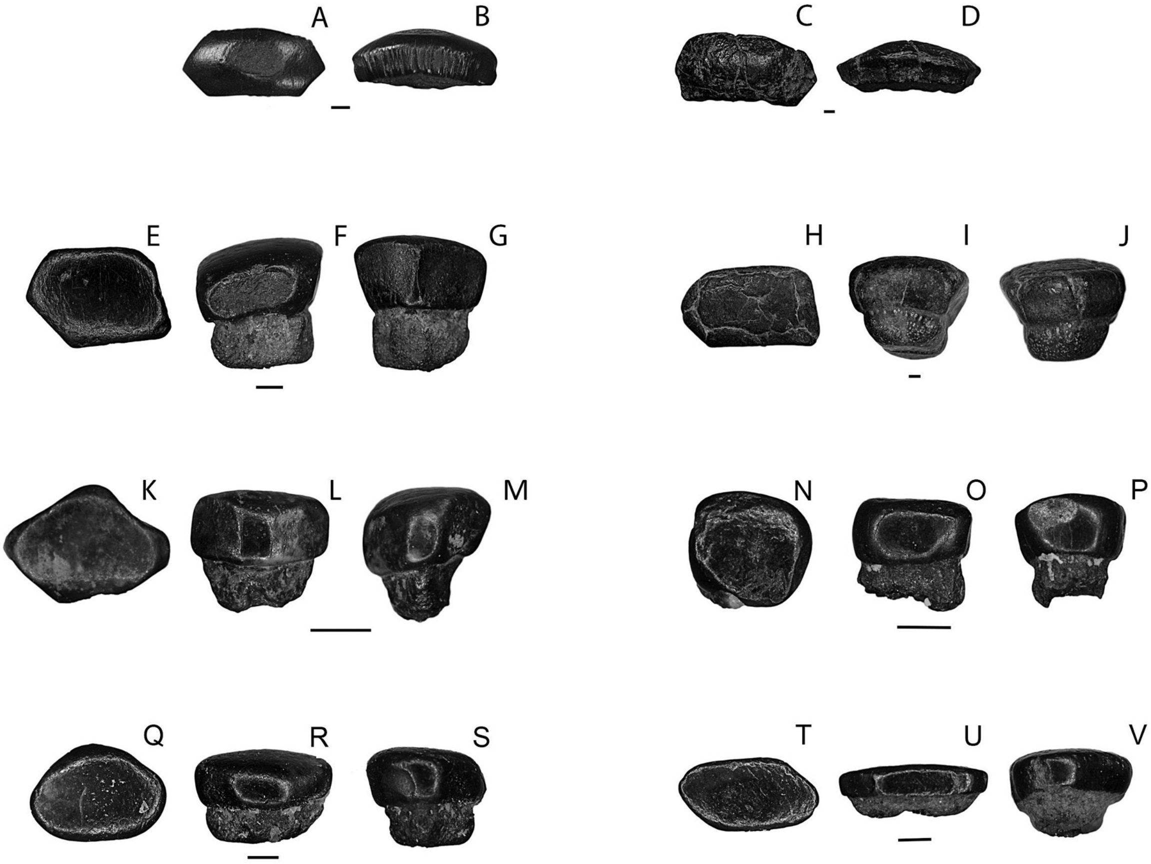

Figure 18. *Brachyrhizodus ellipsis* teeth from the Eutaw Formation at Luxapalila Creek, Mississippi, and *B. wichitaensis* teeth from Campanian strata of New Jersey and South Carolina. A-B, *Brachyrhizodus ellipsis* tooth, MMNS 5987, in A) occlusal, B) labial views. C-D, *B. wichitaensis*, SC uncurated, Coachman Formation of Darlington County, SC. C) occlusal, D) labial views. E-G, *B. ellipsis* tooth, SC2012.48.104 in E) occlusal, F) mesial, G) distal view. H-J, *B. wichitaensis* tooth, SC uncurated, Wenonah Formation of Monmouth County, NJ. H) occlusal, I) mesial, J) distal views. K-M, *B. ellipsis* tooth, SC2012.48.96, in K) occlusal, L) labial, M) profile views. N-P, *B. ellipsis* tooth, SC2012.48.98, in N) occlusal, O) labial, P) profile views. Q-S, *B. ellipsis* tooth, SC2012.48.100, in Q) occlusal, R) labial, S) profile views. T-V, *B. ellipsis* tooth, SC2012.48.101, in T) occlusal, U) labial, V) profile views. Labial at right in P, S, & V. Scale bars = 1 mm. Photographs by K.E. Runyon.

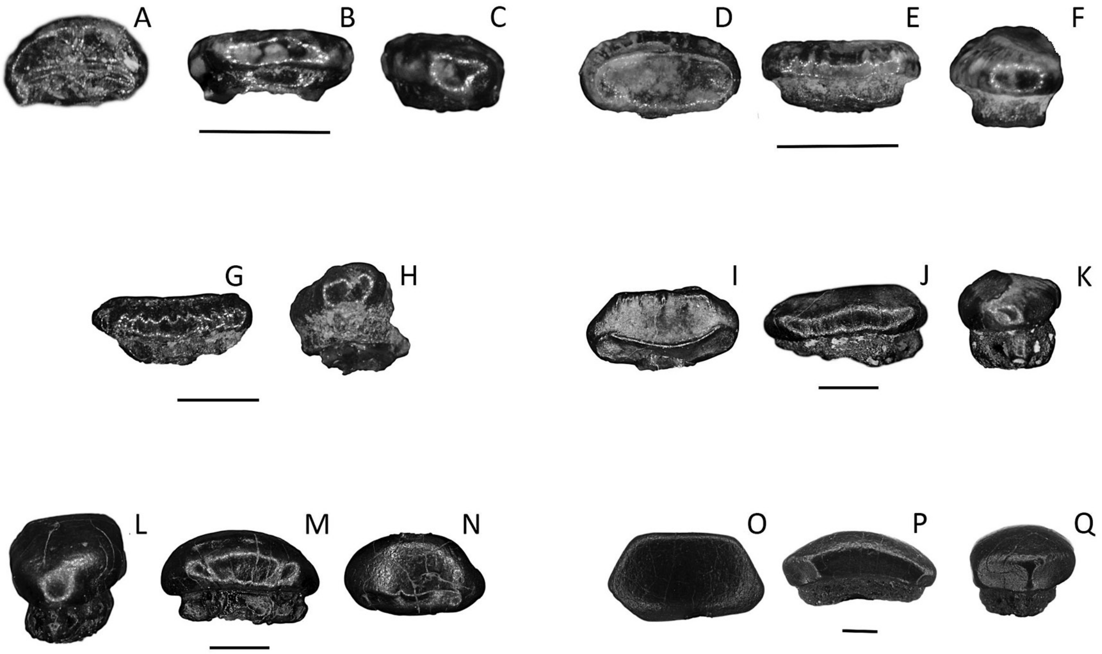

Figure 19. *Brachyrhizodus ellipsis* teeth from the Eutaw Formation at Luxapalila Creek, Mississippi. A-C, juvenile tooth, SC 2012.48.105, in A) occlusal, B) labial, C) profile views. D-F, juvenile tooth, SC2012.48.106, in D) occlusal, E) labial, F) profile views. G-H, juvenile tooth, SC2012.48.107, in G) labial, H) profile views. I-K, uvenile tooth, SC2012.48.108, in I) occlusal, J) labial, K) profile views. L-N, sub-adult tooth, SC2012.48.109, in L) profile, M? labial, N) occlusal views. O-Q, adult tooth, SC 2012.48.110, in O) occlusal, P) labial, Q) profile views. Labial at top in A & D, bottom in I, N, O. Scale bars = 1 mm. Photographs by K.E. Runyon.

SC2012.48.101, ovate tooth; SC2012.48.102, 10 ovate and sub-hexagonal teeth; SC2012.48.103, 4 six-sided teeth; SC2012.48.104, six-sided tooth; SC2012.48.105, reniform tooth 1; SC2012.48.106, reniform tooth 2; SC2012.48.107, reniform tooth 3; SC2012.48.108, reniform tooth 4; SC2012.48.109, reniform tooth 5; SC2012.48.110, small six-sided tooth; SC2012.48.111, medium six-sided tooth; SC2012.48.112, large six-sided tooth; SC2012.48.113, 22 reniform teeth.

Remarks – The morphologies that we attribute to this taxon are varied, but we consider them to be conspecific for reasons that are outlined below. Meyer (1974) utilized teeth from the Eutaw Formation of Mississippi as representative specimens of his *Parahypolophus mcnultii* (sic), a generic name change for teeth previously assigned to ?*Hypolophus mcnultyi* by Thurmond (1971). Shortly thereafter, Cappetta & Case (1975b) erected *Pseudohypolophus* for the *mcnultyi* morphology. *Pseudohypolophus ellipsis* was named by Case *et al.* (2001) based on a single specimen from the Eutaw Formation of Alabama, and the only two characteristics that they used to distinguish their holotype from *P. mcnultyi* was in being "considerably larger" and more elliptical as opposed to rhomboidal. However, in addition to not having a statistically significant sample to properly diagnose a new species, Case *et al.* (2001) apparently overstated the size of their type specimen (see Bourdon *et al.*, 2011:43). Teeth of *P. mcnultyi* are variable and may have ovate, sub-hexagonal (wider than long, six-sided but with rounded corners) or rhomboidal crowns. Therefore, the claim that *P. ellipsis* has a more elliptical as opposed to rhomboidal crown is also erroneous. Everhart *et al.* (2003) assigned teeth classically identified as *Pseudohypolophus mcnultyi* to *Brachyrhizodus* (*B. mcnultyi*), but this classification scheme was not discussed in detail until several years later. Manning (2006) argued that the *mcnultyi* morphology should be assigned to *Brachyrhizodus* because *mcnultyi* and *B. whichitaensis* have orthodont histology, and *mcnultyi* occasionally has a polyaulocorhizous root (Johnson & Lucas, 2002), a condition seen more consistently in *Brachyrhizodus whichitaensis*. This argument has apparently not been widely accepted.

All of the specimens in our sample have crowns covered with a layer of enameloid, and on every specimen where it is preserved, the root is holaulocorhizous. The larger teeth in our sample, which measure up to nearly 1 cm in width, have a thick crown that is conspicuously six-sided, and unworn teeth exhibit a convex occlusal surface (figure 18A-B). Labial and lingual faces are roughly vertical and generally smooth, but some specimens exhibit coarse wrinkling. The sharp edges and corners, and flat labial and lingual faces, indicate that the teeth were tightly packed within the dentition. Except for the fact that roots are holaulocorhizous, these teeth are virtually identical to Campanian *Brachyrhizodus whichitaensis* (see also Cappetta & Case, 1975a; Lauginiger & Hartstein, 1983; Robb, 1989). As examples, compare the tooth of *B. whichitaensis* from the Campanian of South Carolina (figure 18C-D) to *B. ellipsis* shown in figure 19O-Q, as well as the tooth of *B. whichitaensis* from the Campanian of New Jersey (figure 18H-J) to *B. ellipsis* in figure 18E-G.

Many teeth in our sample are similar to the type of *P. ellipsis* and to *P. mycnultyi* (see figure 18N-V; also Thurmond, 1971; Cappetta & Case, 1975b; Cicimurri, 2000), and still others have a rhomboidal outline similar to *Rhombodus levis* (*i.e.*, figure 18K-M; see also Cappetta & Case, 1975a; Robb, 1989). These teeth have rounded corners and edges, and only portions of vertical surfaces are flat, indicating less contact between teeth and therefore a less rigid dentition. The most unusual teeth in our sample are the smallest specimens, which measure less than 2 mm in width (figure 19A-K). These teeth have a reniform occlusal outline and distinctive crescent-shaped transverse crest and nodes on the occlusal surface, features that are reminiscent of the single known specimen of *Enantiobatis tarrantensis* from the Cenomanian of Texas (Cappetta & Case, 1999).

We interpret these varied morphologies as representing ontogenetic and monognathic (and possibly dignathic) heterodonty within a single species, rather than two, three, or four distinct species. The six-sided *B. whichitaensis*-type teeth may have occurred close to or even on the jaw symphysis, whereas the ovate to rhomboidal *Pseudohypolophus*- and *Rhombodus*-type morphologies may have occupied more lateral and posterior positions. If this association is correct, the holotype of *P. ellipsis* described Case *et al.* (2001) could represent a lateral jaw position. The tiny *Enantiobatis*-like morphology is considered to be a juvenile growth stage, and we envision an ontogenetic series where the crown size, thickness, and convexity of the occlusal surface increased, the labial margin became straighter, crown margins became sharper and more angular, and the transverse crest was reduced and eventually lost as an individual grew. Figure 19 shows a hypothetical growth series, with A-K representing progressively larger juvenile teeth, L-M a sub-adult stage, and O-Q an adult.

We also propose assigning all of these morphologies to *Brachyrhizodus* rather than *Pseudohypolophus* because our presumed adult teeth (from more medial jaw positions) very closely resemble Campanian *B. whichitaensis*. The fact that the roots of our Late Santonian teeth are holaulocorhizous rather than polyaulocorhizous is attributed to the evolutionary stage of the genus, where a single blood vessel was sufficient to nourish the tooth. The larger teeth of *B. whichitaensis* may have required more blood while developing, and it should be noted that lateral teeth of this species can be holaulocorhizous. Although the term '*ellipsis*' does not accurately reflect the range of morphology within the species, it is retained herein.

Discussion

Santonian elasmobranch records from North America are sparse, but unsurprisingly the assemblage we collected compares quite well to Eutaw Formation assemblages documented by Meyer (1974) and Case *et al.* (2001). Many of the species we identified also inhabited the southern portion of the Western Interior Seaway, particularly in the area of present-day New Mexico (Point Lookout Sandstone; see Williamson *et al.*, 1989; Bourdon *et al.*, 2011), and to a lesser extent in Kansas (Niobrara Formation; see Shimada & Felitz, 2006). It is also interesting to note that the Eutaw Formation assemblage bears similarities to Campanian elasmobranch assemblages documented from the Gulf Coastal Plain (*i.e.*, Meyer, 1974; Case & Schwimmer, 1988; Manning & Dockery, 1992).

Deposits of the Eutaw Formation preserve a deepening-upward (transgressive) sequence, with rippled sandstones and interbeds of parallel laminated sandstone and claystone (bimodal) within the Eutaw Member, indicating tidally influenced nearshore deposits, possibly a delta, prograding beach, or river mouth (see Whetstone & Collins, 1982). Massive, bioturbated and glauconitic beds with crustacean burrows suggest offshore marine shelf, and thin to massive, moderately bioturbated, calcareous beds at the top of the Tombigbee Sand represent lower energy and more offshore marine environments. The overlying Mooreville Chalk consists of shelf mudstones (Soens, 1984; Russel, 1986; Mancini & Soens, 1994). Stratigraphically, the fossil-bearing unit we sampled has been mapped as part of the Eutaw Member, and it occurs within the section representing tidally influenced nearshore marine deposits. Paleontologically, the deposit contains a mixture of terrestrial, brackish, and normal marine taxa.

Additional vertebrate fossils associated with the elasmobranch material include osteichthyan remains, which consist primarily of teeth but also skull bones, vertebrae, and scales. Taxa include *Lepisosteus* sp., *Enchodus* sp. cf. *E. petrosus*, *Xiphactinus* sp. cf. *X. vetus*, indeterminate plethodid jaw fragments, *Megalocoelocanthus* sp., *Anomoeodus* sp. cf. *A. latidens*, cf. *Hadrodus priscus*, and a lungfish (currently under study by G. Phillips). Archosaurs are represented by teeth of two dinosaurs, a theropod and a hadrosaur, and teeth and osteoderms of a crocodilian. Shell fragments of unidentified trionychid and chelonioid turtles are uncommon.

Invertebrate fossils are poorly represented in our sample and consist mostly of fragments of black, phosphatic steinkerns. Some pieces of decapod crustacean carapace and chelipeds appear to represent the pagurid *Pagurus convexus* and the callianassid *Callianassa* sp. One or two species of gastropod (including a possible turritellid) and one pelecypod are also present. Ablated echinoderm plates were recovered, as were several cephalopod tentacle hooklets. Fossil wood is relatively common and consists of both lignitized fragments and silicified pieces. Several amber grains 1 mm or less in size were also recovered.

Conclusions

Twenty one elasmobranch species were recovered from a highly fossiliferous deposit within the Eutaw Member of the Eutaw Formation exposed along Luxapalila Creek in Lowndes County, Mississippi. These include *Meristodonoides multiplicatus* n. sp., *Lonchidion cristatum* n. sp., and *Cantioscyllium grandis* n. sp. Three additional species have been reassigned to genera other than those originally named, including *Ptychotrygon rugosum* (formerly *Ergruitaia*), *Texatrygon benningensis* (formerly *Erguitaia* and *Ptychotrygon*), and *Brachyrhizodus ellipsis* (formerly *Pseudohypolophus*). The elasmobranchs are associated with bony fish, turtle, crocodilian, dinosaur, and crustacean remains, and these fossils, along with wood fragments and amber grains, indicate deposition occurred close to a forested shoreline in less than 30 m water depth.

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