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Middle Campanian Euselachian Diversity of the Southern Region of the Atlantic Coastal Plain of North America

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Abstract: A euselachian assemblage from the middle Campanian Bladen Formation, located near Elizabethtown, Bladen County, North Carolina, USA, is described. The assemblage consists of 18 species from 17 genera, at least 14 families, and seven orders, and introduces the new taxon *Cantioscyllium clementsi* sp. nov. The recovered *Squatina*, *Plicatoscyllium*, and six lamniform species had large cosmopolitan distributions, whereas the new ginglymostomatid species and remaining hybodontid and batoid taxa were likely endemic to the waters of North America.
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INTRODUCTION

Deposits along the Atlantic and Gulf coastal plains of North America are a rich source of Late Cretaceous euselachian fossil dentitions (e.g., Cappetta and Case 1975; Lauginiger 1984; Case and Schwimmer 1988; Case 1991; Becker et al. 1998; Cicimurri 2007; Case et al. 2017). The Bladen Formation of North Carolina has produced a relatively diverse shark and ray fauna. This formation represents a delta-shelf system (Sohl and Owens 1991) and is middle Campanian in age based on palynological analysis (Prowell et al. 2003). Previously, Crane (2011) reported numerous species belonging to at least 17 euselachian genera, and Case et al. (2012) described the rostral spines of the sclerorhynchid sawfish *Borodinopristis shannoni* from this formation. The *Borodinopristis* material was part of a larger euselachian assemblage that was collected at that time (Case et al. 2012). Herein, we provide an updated taxonomic assessment of the previously described taxa and present additional euselachian species recovered from the Bladen Formation.

METHODS AND MATERIALS

As reported in Case et al. (2012), a large number of additional euselachian specimens were collected along with the *Borodinopristis shannoni* rostral spines. They (p. 592) noted the fossil remains were "recovered near Elizabethtown, Bladen County, NC, USA, from a landfill (garbage) pit now filled and located at 34° 36.458' N, 78° 36.490' W." The specimens, housed in the collections of the University of Alberta Laboratory for Vertebrate Palaeontology (UALVP), were recovered via handpicking and bulk sampling using a U.S. Standard Sieve Series No. 30 (530 microns/0.0234 in opening). Smaller specimens were imaged using either a Hitachi S-2500 or FEI Quanta 650 FEG scanning electron microscope, whereas larger specimens were coated with ammonium chloride and digitally imaged using a Canon EOS Rebel T6 50mm compact-macro lens camera. Taxonomy and dental terminology within this paper largely follow that of Cappetta (2012).

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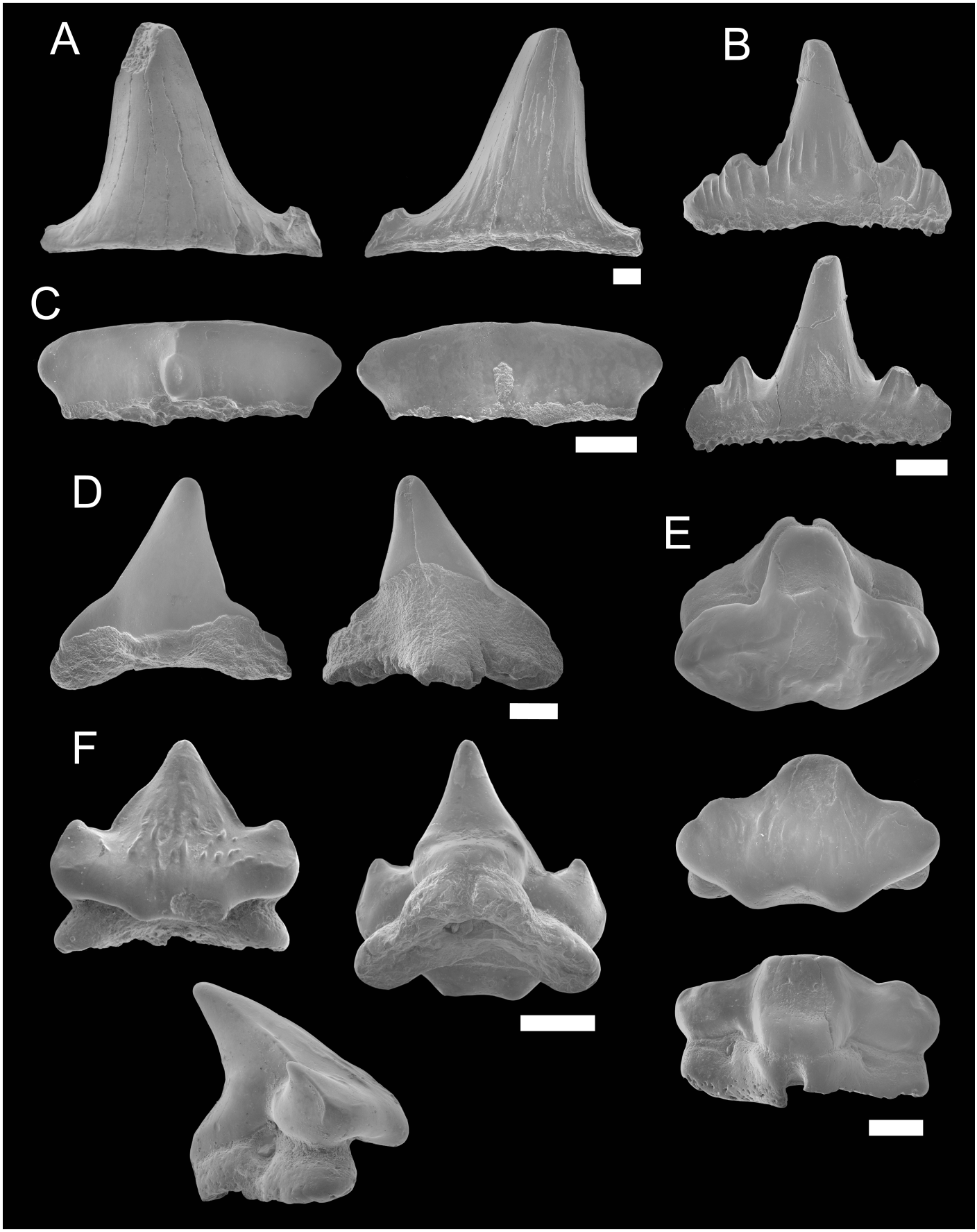
SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Order HYBODONTIFORMES Maisey, 1989
Family HYBONTIDAE Owen, 1845
Genus *Meristodonoides* Underwood and Cumbaa, 2010
Meristodonoides novojerseyensis (Case and Cappetta, 2004)
Figure 1A

Referred Material: UALVP 58755, incomplete tooth; UALVP 58756 five additional incomplete teeth.

Description: The crown consists of a tall and relatively broad median cusp. The labial crown face is convex and bears short enameloid folding along the base. The lingual crown face is also convex but possesses long enameloid


A
B
C
D
E
F

folding that extends approximately three-fourths the crown height. The faces are separated by a weak cutting edge. The lateral cusplets are more or less missing, except for an incipient cusplet positioned medially to the median cusp. The entire root is missing.

Remarks: This species was originally described as *Hybodus novojerseyensis* from material recovered from the early Maastrichtian of New Jersey (Case and Cappetta 2004). Underwood and Cumbaa (2010) subsequently reassigned this species to *Meristodonoides* based on morphological characters including the single well developed median cusp, lateral cusplets that are either absent or small, lack of a labial boss, and a root that is low and highly vascularized. This species has also been reported from the late Campanian of Delaware (Lauginiger 1984, as *Hybodus* sp.) and Mississippi (Manning and Dockery 1992).

Meristodonoides sp.
Figure 1B

Referred Material: UALVP 58757, incomplete tooth.

Description: The crown consists of a tall and relatively narrow median cusp that is flanked by two pairs of small lateral cusplets. Both labial and lingual faces are strongly convex and separated by a distinct cutting edge. Robust enameloid folding extends from the crown base to approximately half the height of the median cusp and to the apex on the lateral cusplets. The entire root is missing.

Remarks: This species is easily distinguished from *Meristodonoides novojerseyensis* by its relatively narrow median cusp, strong enameloid folding that extends higher on the labial crown face, well-developed lateral cusplets, and an overall smaller size. The fragmented tooth described by Crane (2011), also from the Bladen Formation, has similar median cusp morphology.

Genus *Lonchidion* Estes, 1964
Lonchidion babulskii Cappetta and Case, 1975
Figure 1C

Referred Material: UALVP 58758, incomplete tooth; UALVP 58759, three additional incomplete teeth.

Description: The crown is mesodistally elongated and labiolingually compressed. Both labial and lingual crown faces are smooth and separated by a well-developed transverse ridge. A distinct labial protuberance is present on the labial crown face. The crown is narrowed at the crown-root border and the root is missing.

Remarks: This species is well documented along the Atlantic and Gulf coastal plains. This species was first described from the early Maastrichtian of New Jersey (Cappetta and Case 1975) and subsequently reported from the early–middle Santonian of Georgia (Case et al. 2001), the late Campanian of Delaware (Lauginiger and Hartstein 1983), Mississippi (Manning and Dockery 1992), and South Carolina (Cicimurri 2007), and late Maastrichtian of Texas (Case and Cappetta 1997). The tooth described as *Lonchidion selachos* Estes, 1964 by Crane (2011) from the Bladen Formation lacks incipient lateral cusplets and appears more similar to that of *L. babulskii*. Likewise, the tooth figured by Schubert et al. (2017) as *L. selachos* from the middle Campanian of Texas more closely resembles that of *L. babulskii*.

Division NEOSELACHII Compagno, 1977
Superorder SQUALOMORPHII Compagno, 1973
Order SQUATINIFORMES de Buen, 1926
Family SQUATINIDAE Bonaparte, 1838
Genus *Squatina* Dumeril, 1806
Squatina sp.
Figure 1D

Referred Material: UALVP 58760, incomplete tooth.

Description: The crown has a median cusp that is slightly distally inclined with a rounded apex and relatively wide base. The labial and lingual crown faces are smooth and separated by a weak cutting edge. The heels are relatively short and oblique. The base of the labial crown has a well-developed and rounded apron that is slightly damaged. The lingual crown face has a lingual protuberance. The root is damaged but is relatively triangular basally and has a large central foramen.

Remarks: The overall morphology of this specimen is similar to that of teeth reported from a number North

←Opposite Page

Figure 1. Hybodontiform, squaliform, and orectolobiform teeth recovered from the middle Campanian Bladen Formation of North Carolina. A, *Meristodonoides novojerseyensis*, UALVP 58755 (incomplete tooth); B, *Meristodonoides* sp., UALVP 85757 (incomplete tooth); C, *Lonchidion babulskii*, UALVP 58758 (incomplete tooth); D, *Squatina* sp., UALVP 58760 (incomplete tooth); E, *Plicatoscyllium globidens*, UALVP 58761 (complete lateral tooth); F, *Cantioscyllium clementsi* sp. nov., UALVP 587625 (holotype, complete lateral tooth). Views: labial (left) and lingual (right) for A, C, and D; labial (top) and lingual (bottom) for B; occlusal (top), labial (center), and lingual (bottom) for E; labial (left), lingual (right), and profile (bottom) for F. Scale bars = 1 mm.

American deposits as *Squatina hassei* Leriche, 1926 (e.g., Cappetta and Case 1975; Case et al. 2001; Becker et al. 2004, 2006). Recently, Siversson et al. (2016:259) questioned the validity of *S. hassei* noting that the species "cannot be placed with certainty in either of the two subgenera of *Squatina* and is here regarded as a prime example of a nomen dubium." As such, we conservatively leave this species in open nomenclature. The *Squatina* tooth figured by Crane (2011), also from the Bladen Formation, is likely conspecific to the tooth described herein.

Superorder GALEOMORPHII Compagno, 1973
Order ORECTOLOBIFORMES Applegate, 1972
Family GINGLYMOSTOMATIDAE Gill, 1862
Genus *Plicatoscyllium* Case and Cappetta, 1997
Plicatoscyllium globidens Cappetta and Case, 1975
Figure 1E

Referred Material: UALVP 58761, complete lateral tooth.

Description: The low crown is relatively broad. The lingual directed median cusp has a blunt apex and is flanked by a pair of poorly developed and rounded lateral cusplets. The labial face contains weak enameloid folding that is limited to the basal half of the crown. The wide apron overhangs the labial root face and has a concave basal edge. The smooth lingual face has a well-developed medio-lingual protuberance. The root lobes are V-shaped and a large central foramen is present.

Remarks: *Plicatoscyllium globidens* was first reported from the lower Maastrichtian of New Jersey (Cappetta and Case 1975, as *Ginglymostoma globidens*). The species has been subsequently reported from Campanian-Maastrichtian deposits of Georgia (e.g., Case and Schwimmer 1988) and Mississippi (e.g., Case 1991). Vullo (2005) conservatively identified two poorly preserved teeth as *P.* cf. *P. globidens* from the Campanian of France. Given that the vagility of extant orectolobiforms varies considerably (Musick et al. 2004) it is not improbable that this species frequented water on both sides of the Atlantic.

Genus *Cantioscyllium* Woodward, 1889
Cantioscyllium clementsi sp. nov.
Figure 1F

Holotype: UALVP 58762, complete tooth of indeterminate jaw position.

Diagnosis: Teeth that contain a median cusp with irregular enameloid folding labially and a pair of well-developed lateral cusplets.

Type Locality and Horizon: Bladen Formation near Elizabethtown, Bladen County, North Carolina, USA.

Etymology: Named after Don Clements for his work on the geology of North Carolina.

Description: The crown contains a lingually directed median cusp with a sharp apex. The slightly convex labial crown face bears irregular enameloid folding that is largely limited to the basal half of the cusp. The apron overhangs the labial root face and has a basal edge that is slightly concave. The strongly convex lingual face is smooth and possesses a well-developed lingual protuberance. A pair of relatively well-developed lateral cusplets flanks the median cusp. The root lobes are V-shaped and a large central foramen and margin-lingual foramina are present.

Remarks: *Cantioscyllium clementsi* sp. nov. bears some resemblance to that of the Eocene species *Protoginglymostoma ypresiensis* (Casier, 1946). Both species have a similar median cusp and overall root morphology; however, the former has weaker enameloid folding, a narrower apron, and a single pair of lateral cusplets with a sharper apex. Cappetta (2012) questioned the validity of *Protoginglymostoma*, recognizing only *P. ypresiensis*, and suggesting that Campanian-Maastrichtian species *P. bighornensis* (Case, 1987) and *P. estesi* (Herman, 1977) were closer to those of *Cantioscyllium*.

The overall morphology of UALVP 58762 is similar to the teeth of *Cantioscyllium decipiens* Woodward, 1889, originally described from the Cenomanian of Kent, England, and *C. meyeri* Case and Cappetta, 1997, first reported from the late Maastrichtian of Texas. Case and Cappetta (1997) noted that the teeth of the latter species are smaller in size with fewer lateral cusplets. UALVP 58762 can be distinguished from other *Cantioscyllium* spp. by having a more developed pair of lateral cusplets and a labial crown face with weaker and somewhat irregular enameloid folding than the elongated ridges observed in other species. A tooth described as *Ginglymostoma globidens* by Crane (2011), also from the Bladen Formation, has morphology similar to that of *C. clementsi* sp. nov., and is likely conspecific. A tooth identified as *Cantioscyllium* sp. by Bourdon et al. (2011, fig. 5J) from the Santonian of New Mexico may also be conspecific with the species described herein.

Order LAMNIFORMES Berg, 1937
Family MITSUKURINIDAE Jordan, 1898
Genus *Scapanorhynchus* Woodward, 1889
Scapanorhynchus texanus (Roemer, 1849)
Figure 2A and B

Referred Material: UALVP 58763, complete anterior tooth; UALVP 58764, complete lateral tooth; UALVP 58765, numerous additional fragmented cusps.

Description: The anterior tooth crown contains a tall median cusp. The labial crown is flat and more or less

smooth. The lingual crown is convex and contains distinct enameloid folds that extend from the crown base to approximately two-thirds the height of the cusp. The cutting edge is well developed and sigmoid in profile view. The root has a prominent lingual protuberance that contains a well-developed nutrient groove. The mesial root lobe is more elongated and narrower than the distal lobe. The root lobes are separated by a deep basal concavity.

The median cusp of the lateral tooth is distally inclined and more labiolingually compressed than that of the anterior tooth. A distinct cutting edge separates the very slightly convex labial face from the convex lingual face. Both faces are smooth. Two pairs of lateral cusplets flank the median cusp. The more laterally positioned pair is more or less incipient. The weak lingual protuberance bears a nutrient groove. The root lobes are relatively wide and separated by a distinct basal concavity.

Remarks: *Scapanorhynchus texanus* has been reported from Campanian–Maastrichtian deposits of the Western Interior Seaway (e.g., Welton and Farish 1993; Case 1987) and the Atlantic (e.g., Cappetta and Case 1975; Case 1979; Lauginiger 1984) and Gulf (e.g., Dockery and Jennings 1988; Becker et al. 2008) coastal plains of North America. Crane (2011) previously reported this species from the Bladen Formation.

Family OTODONTIDAE Glikman, 1964
Genus *Cretalamna* Glikman, 1958
Cretalamna sp.
Figure 2C

Referred Material: UALVP 58766, largely complete lateral tooth.

Description: The crown contains a distally inclined median cusp with a sharp apex. The labial crown face is flat, whereas the lingual face is convex. Both faces are smooth and separated by a distinct cutting edge. A pair of low triangular lateral cusplets flanks the median cusp. A narrow lingual band is present. The slightly eroded root has a weak lingual protuberance that lacks a distinct nutrient groove. The root lobes are relatively broad and separated by a shallow basal concavity.

Remarks: With the exception of having a more narrowed median cusp, the overall morphology of this specimen bears some similarity to lateral teeth reported as *Cretolamna appendiculata lata* by Cappetta and Case (1975) from the late Campanian/early Maastrichtian of New Jersey. Crane (2011) previously described this species and subspecies from the Bladen Formation. A recent detailed re-evaluation of *Cretalamna appendiculata* type revealed multiple species (Siverson et al. 2015). In that study, Siverson et al. (2015) noted that the New Jersey teeth have a morphology somewhat akin to that of *C. sarcoportheta*. It was also noted that "pristine root preservation" is important in the diagnosis of *Cretalamna* to species level (Siverson et al. 2015:352). Given the poor preservation of the root of UALVP 58766, we conservatively assign the specimen described herein as *Cretalamna* sp.

Family ARCHAEOLAMNIDAE Underwood and Cumbaa, 2010
Genus *Archaeolamna* Siverson, 1992
Archaeolamna kopingensis (Davis, 1890)
Figure 2D

Referred Material: UALVP 58767, largely complete anterior tooth; UALVP 58768, one additional complete lateral tooth.

Description: The crown contains a tall median cusp that is slightly distally inclined. The labial crown face is more or less flat, whereas the lingual crown face is convex. Both faces are smooth and separated by a distinct cutting edge. Flanking the median cusp is a pair of relatively tall, narrow, and slightly divergent lateral cusplets. A narrow lingual band is present. The root is somewhat eroded but has a well-developed lingual protuberance and elongated root lobes that are separated by a deep basal concavity.

Remarks: *Archaeolamna* has a wide palaeobiogeographical range and has been reported from Albian–Maastrichtian deposits in Europe (e.g., Siverson 1992; Biddle 1993; Vullo et al. 2007) and Australia (e.g., Siverson 1996, 1997). North American reports include the Western Interior Seaway (e.g., Beavan and Russell 1999; Shimada and Martin 2008; Cook et al. 2008; Underwood and Cumbaa 2010). Given its rather large temporal range and subtle differences in tooth morphology, teeth reported as *Archaeolamna kopingensis* from various deposits likely represent multiple closely related taxa (Cumbaa et al. 2006; Underwood and Cumbaa 2010; Cook et al. 2008). Siverson (1992) recognized two subspecies, *A. kopingensis kopingensis* from the Campanian of Sweden and *A. kopingensis judithensis* from the Campanian of Montana. The latter has a broader, shorter, and more labiolingually compressed crown and a root that is more robust with shorter root lobes and a lower situated lingual protuberance (Siverson 1992). It was also noted that teeth described by Cappetta and Case (1975, as *Plicatolamna arcuata*), from the early Maastrichtian of New Jersey, have "a dental morphology roughly intermediate between the two subspecies." (Siverson 1992:534). The specimen described herein largely conforms to this intermediate morphology. As such, we conservatively refrain from assigning UALVP 58767 and 58768 to a subspecies.

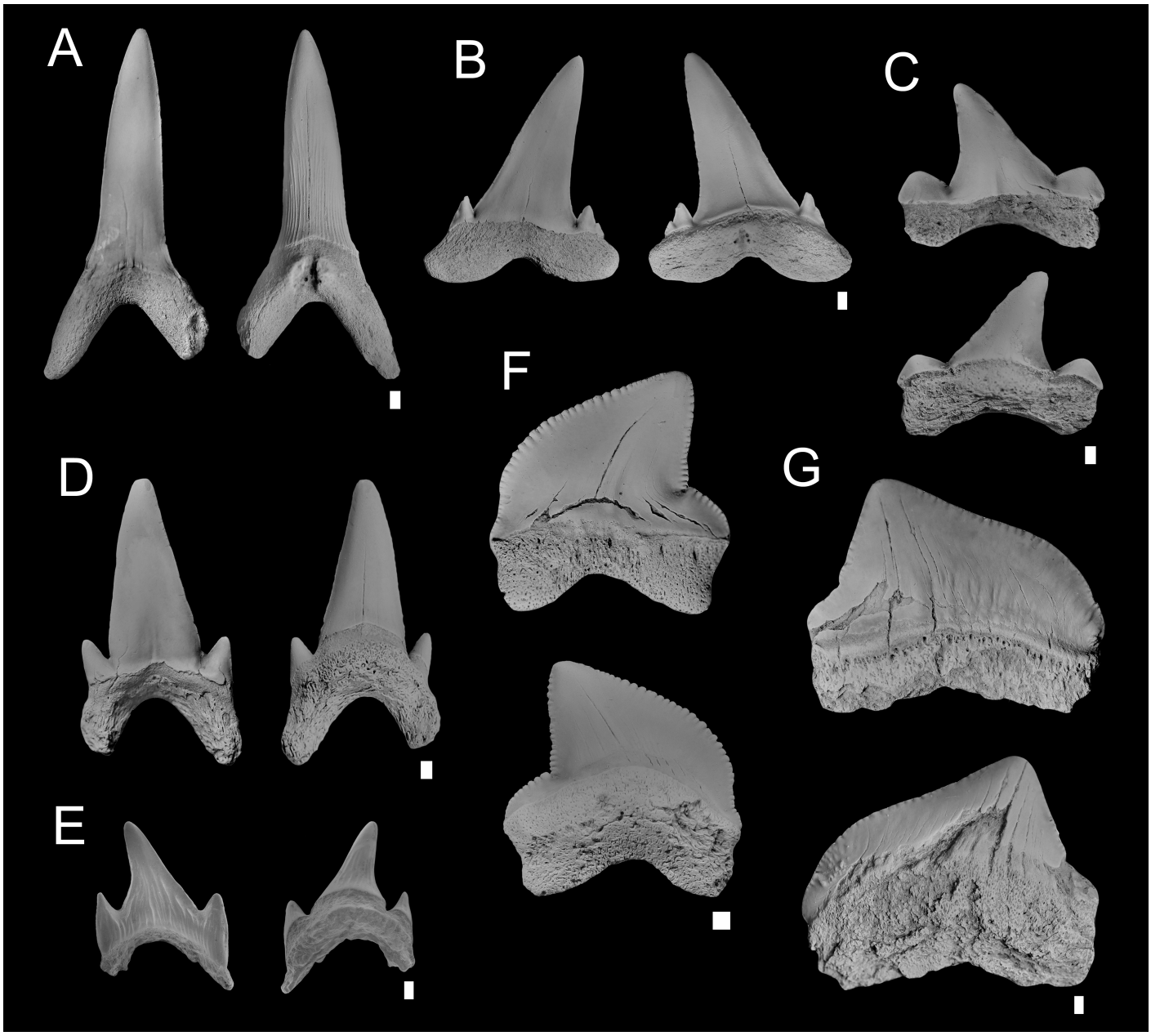


Figure 2. Lamniform teeth recovered from the middle Campanian Bladen Formation of North Carolina. A, *Scapanorhynchus texanus*, UALVP 58763 (complete anterior tooth); B, *Scapanorhynchus texanus*, UALVP 58765 (complete lateral tooth); C, *Cretalamna* sp., UALVP 58766 (largely complete lateral tooth); D, *Archaeolamna kopingensis*, UALVP 58767 (largely complete anterior tooth); E, *Protolamna borodini*, UALVP 58769 (incomplete lateral tooth); F, *Squalicorax kaupi*, UALVP 58770 (complete lateral tooth); G. *Squalicorax* cf. *S. pristodontus*, UALVP 58772 (incomplete lateral tooth). Views: labial (left) and lingual (right) for A, B, D, and E; C, labial (top) and lingual (bottom) for C, F, and G. Scale bars = 1 mm.

Family EOPTOLAMNIDAE Kriwet, Klug, Canudo and Cuenca-Bescos, 2008
Genus *Protolamna* Cappetta, 1980a
Protolamna borodini (Cappetta and Case, 1975)
Figure 2E

Referred Material: UALVP 58769, incomplete lateral tooth.

Description: The lateral tooth crown contains a tall median cusp that is slightly distally inclined. The labial crown face is flat, whereas the lingual face is convex. Both faces contain distinct enameloid folds that extend from the crown base to approximately two-thirds the height of the cusp. A pair of well-developed lateral cusplets also contains folding on the lingual surface. A distinct cutting edge is present. The heavily eroded root has a prominent lingual

protuberance and a deep basal concavity that separates the rather narrow root lobes.

Remarks: *Protolamna borodini* was originally described by Cappetta and Case (1975) as *Plicatolamna borodini* from the early Maastrichtian of New Jersey. Subsequently, this species has been reported from Campanian–Maastrichtian deposits of the Atlantic coastal plain of North America (e.g., Case 1979; Case and Schwimmer 1988) and Campanian deposits of Europe (e.g., Siverson 1992; Vullo 2005).

Family ANACORACIDAE Casier, 1947
Genus *Squalicorax* Whitley, 1939
Squalicorax kaupi (Agassiz, 1843)
Figure 2F

Referred Material: UALVP 58770, largely complete lateral tooth; UALVP 58771, six additional incomplete teeth.

Description: The crown contains a median cusp that is broad and distally inclined. The labial and lingual crown faces are smooth and convex. The basal half of the mesial cutting edge is strongly convex, whereas the apical half is more or less straight. The distal cutting edge is straight and vertically oriented. Both edges bear simple but coarse serrations that decrease in size towards the base and apex of the crown. The rather low distal heel is obliquely directed and contains serrations that decrease in size toward the base. A distinct lingual band is present. The weak lingual protuberance lacks a nutrient groove and the asymmetrical root lobes are separated by a deep basal concavity. The labial and lingual root faces contain numerous foramina of varying size.

Remarks: This cosmopolitan species has been described from numerous Coniacian–Maastrichtian deposits on both sides of the Atlantic (see Cappetta 2012). In North America, *Squalicorax kaupi* has been reported from the Western Interior Seaway (e.g., Welton and Farish 1993; Cappetta and Case 1999; Shimada and Cicimurri 2006) and the Atlantic (e.g., Cappetta and Case 1975; Case et al. 2001, 2017) and Gulf (e.g., Becker et al. 2006) coastal plains. Crane (2011) previously reported *S. kaupi* from the Bladen Formation. The low heel and obtuse angle formed with that of the distal cutting edge distinguishes the specimen from *S. lindstromi* (see Bourdon et al. 2011).

Squalicorax cf. *S. pristodontus* (Agassiz, 1843)
Figure 2G

Referred Material: UALVP 58772, incomplete lateral tooth.

Description: The crown contains a broad median cusp that is distally inclined. The labial crown face is smooth and more-or-less flat. The lingual crown face is smooth, convex, and markedly damaged. The mesial cutting edge is sigmoid, whereas the distal cutting edge is straight and obliquely directed. Both cutting edges bear serrations; however, they have been considerably eroded on this specimen. The distal heel is weakly differentiated from the distal cutting edge. The root is heavily damaged.

Remarks: Similar to *Squalicorax kaupi*, *S. pristodontus* had a wide paleobiogeographical range, being reported from Campanian–Maastrichtian deposits of Europe, Africa, and South America (see Cappetta 2012). North American reports include the Western Interior Seaway (e.g., Welton and Farish 1993; Case and Cappetta 1997; Shimada and Cicimurri 2006) and the Atlantic and Gulf coastal plains (e.g., Cappetta and Case 1975; Case et al. 2017; Harrell et al. 2016). The tooth of *S. pristodontis* described by Crane (2011) from the Bladen Formation is less damaged than that described here.

Superorder BATOMORPHII Cappetta, 1980b
Order RAJIFORMES Berg, 1937
Rhinobatoidei incertae familiae
Genus *Pseudohypolophus* Cappetta and Case, 1975
Pseudohypolophus ellipsis Case, Schwimmer, Borodin and Leggett, 2001
Figure 3A

Referred Material: UALVP 58773, complete tooth; UALVP 58774, 23 additional complete and incomplete teeth.

Description: The crown is weakly hexagonal in occlusal view. The occlusal, labial, and lingual faces are slightly convex, whereas the margino-labial and margino-lingual faces are slightly concave. The root is centrally located under the crown and bears a distinct nutrient groove separating the root lobes.

Remarks: *Pseudohypolophus ellipsis* was first described by Case et al. (2001) for teeth recovered from the early to middle Santonian of Georgia, and later reported from the Western Interior Seaway by Bourdon et al. 2011 as "*Pseudohypolophus*" *ellipsis*. Case et al. (2001) noted that the teeth of this species differed from those of *P. mcnultyi* by having a less rhomboidal occlusal surface.

Order SCLERORHYNCHIFORMES Kriwet, 2004
Family SCLERORHYNCHIDAE Cappetta, 1974
Genus *Ischyrhiza* Leidy, 1856
Ischyrhiza mira Leidy, 1856
Figure 3B and C

Referred Material: UALVP 58775, largely complete rostral spine; UALVP 58776, incomplete oral tooth; UALVP 58777, six additional incomplete oral teeth.

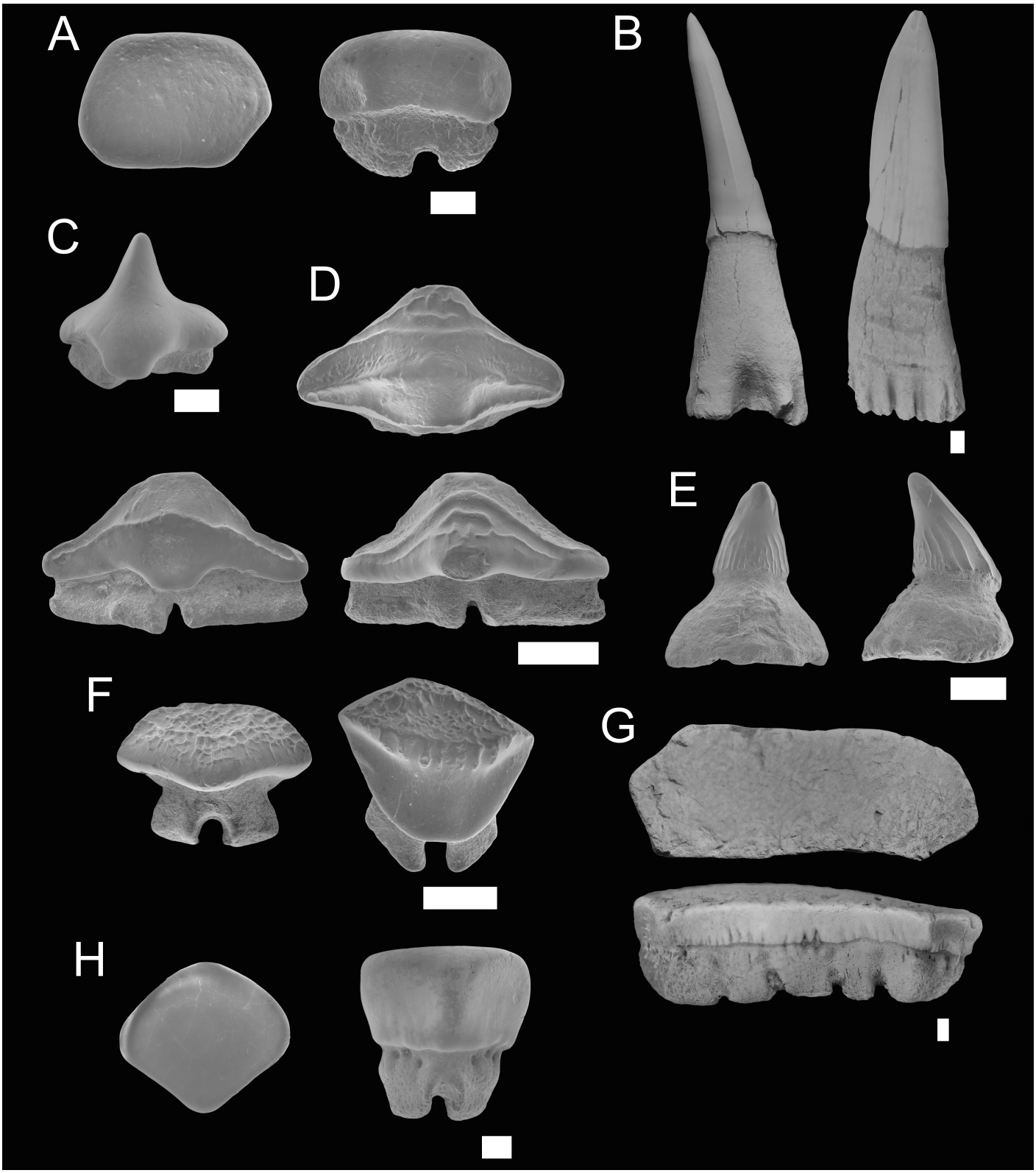


Figure 3. Batoid teeth recovered from the middle Campanian Bladen Formation of North Carolina. A, *Pseudohypolophus ellipsis*, UALVP 58773 (complete tooth); B, *Ischyrhiza mira*, UALVP 58775 (largely complete rostral spine); C, *Ischyrhiza mira*, UALVP 58776 (incomplete tooth); D, *Ptychotrygon vermiculata*, UALVP 58778 (complete tooth); E, Sclerorhynchidae indeterminate, UALVP 58780 (complete rostral spine); F, *Dasyatis* cf. *D. commercensis*, UALVP 58781 (complete tooth); G, *Brachyrhizodus wichitaensis*, UALVP 58782 (complete lateral tooth); H, *Rhombodus laevis*, UALVP 58784 (complete tooth). Views: occlusal (left) and labial (right) for A and H; anterior (left) and dorsal (right) for B; labial for C; occlusal (top), labial (left), and lingual (right) for D; posterior (left) and dorsal (right) for E; labial (left) and lingual (right) for F; occlusal (top) and labial (bottom) for G. Scale bars = 1 mm. Scale bars = 1 mm.

Description: The crown (= cap) of the rostal spine is dorsoventrally compressed and slightly bent ventrally. The anterior margin is slightly convex, whereas the posterior margin is more or less straight. A distinct cutting edge runs continuously along the crown margins. The root (= peduncle) is approximately equal in length to the crown. The basal region of the root is expanded dorsoventrally and anteroposteriorly and forms two short lobes that are divided by a groove.

The oral tooth has a crown with a narrow, lingually directed median cusp that is flanked by convex heels. The smooth labial crown face is slightly convex and forms a relatively broad apron with a rounded edge. The smooth lingual crown face is convex and forms a distinct uvula. The root is partially damaged. A well-developed nutrient groove separates the root lobes and contains a large central foramen. Large margino-lingual foramina are also present.

Remarks: *Ischyrhiza mira* has been reported from numerous Turonian–Maastrichtian deposits of the Western Interior Seaway (e.g., Williamson et al. 1993; Welton and Farish 1993; Case and Cappetta 1997; Beavan and Russell 1999; Becker et al. 2004; Schubert et al. 2017) and the Atlantic (e.g., Cappetta and Case 1975; Case and Schwimmer 1988, Case et al. 2017) and Gulf Coastal plains (e.g., Case 1991; Becker et al. 2006) of North America. Given its exceptionally long chronological range, identifying fossil material as representing a single species of *I. mira* is somewhat suspect. A more complete oral tooth of this taxon from the Bladen Formation was described by Crane (2011).

Family PTYCHOTRYGONIDAE Kriwet, Nunn, and Klug, 2009
Genus *Ptychotrygon* Jaekel, 1894
Ptychotrygon vermiculata Cappetta, 1975
Figure 3D

Referred Material: UALVP 58778, complete tooth; UALVP 58779, 36 additional complete and incomplete teeth.

Description: This tooth contains a dome-shaped cusp that is situated lingually on the crown. A transverse crest separates the labial crown face from the lingual face. The labial face has two distinct transverse ridges that run parallel to the labial crown edge. The well-developed labial visor and apron slightly overhang the labial face of the root. The lingual crown face has a single transverse ridge and distinct median lingual uvula with a relatively deep central depression. The mesodistally expanded root has two large lobes that are separated by a nutrient groove.

Remarks: There are numerous *Ptychotrygon* spp. reported from Albian–Maastrichtian deposits on both sides of the Atlantic (see Cappetta 2012; Case et al. 2017). The overall morphology UALVP 58778 including the number of transverse ridges, is similar to that of *Ptychotrygon vermiculata*, originally described from the early Maastrichtian of New Jersey (Cappetta 1975). This species has been recovered from Campanian–Maastrichtian deposits along the Atlantic and Gulf coastal plains (e.g., Case and Schwimmer 1988; Case 1991, 1995) and the Western Interior Seaway (Case and Cappetta 1997; Becker et al. 2004, 2006). It should be noted that some authors state that *P. triangularis* and *P. texana* may be synonymous with *P. vermiculata* (e.g., Case and Schwimmer 1988, Case and Cappetta 1997), which would considerably increase the temporal range of this species. The tooth figured by Crane (2011), also from the Bladen Formation, is likely conspecific to the tooth described herein.

Sclerorhynchidae indeterminate
Figure 3E

Referred Material: UALVP 58780, complete rostral spine.

Description: Rostral spine (= tooth) with a relatively short crown that is more or less conical and posteriorly directed. The anterior face is slightly less convex than the remainder of the crown. Multiple enameloid folds are present along the base of the crown with some extending close to the apex. The root is constricted below the crown but greatly expands basally in all directions. It lacks any orientation and has a flat basal face.

Remarks: The systematics of sclerorhynchids is problematic (Bourdon et al. 2011; Kirkland et al. 2013) and the identification of rostral spines to species level is difficult. The overall contour of UALVP 58780 does share some similarities with rostral spines identified as *Ptychotrygon* (e.g., ?*Ptychotrygon eutawensis* by Bourdon et al. 2011) and *Ischyrhiza* (e.g., *Ischyrhiza* cf. *I. avonicola* by Schubert et al. 2017). Kirkland et al. (2013) suggested that *Ischyrhiza avonicola* should be reassigned to *Texatrygon*. The conical morphology of the crown, unique enameloid orientation, and flat basal face of the root separates UALVP 58780 from other described sclerorhynchid material; in fact, this specimen may be an enlarged dermal denticle rather than a rostral spine. With such uncertainty, we conservatively leave this specimen as Sclerorhynchidae indeterminate.

Order MYLIOBATIFORMES Campagno, 1973
Family DASYATIDAE Jordan, 1888
Genus *Dasyatis* Rafinesque, 1810
Dasyatis cf. *D. commercensis* (Case and Cappetta, 1997)
Figure 3F

Referred Material: UALVP 58781, complete tooth.

Description: This tooth has a large crown. The labial face is slightly concave and has a broad visor bearing strong alveolate enameloid ornamentation. The smooth concave lingual crown face is divided by a weak median lingual ridge and has a distinct visor. A transverse crest divides the crown faces. The lobes of the lingually positioned root are divided by a deep nutrient groove.

Remarks: The overall morphology of UALVP 58781 largely conforms to that of *Dasyatis commercensis* originally described by Case and Cappetta (1997) from the late Maastrichtian of Texas and subsequently reported from the Maastrichtian of North Carolina (Case et al. 2017) and Arkansas (Becker et al. 2006). However, this specimen has an alveolar ornamentation somewhat reminiscent of the extant *D. margarita* (Günther, 1870), rather than a more pit-like enameloid. A tooth described as *Dasyatis* sp. by Crane (2011) from the Bladen Formation does not appear to bear any enameloid ornamentation and may represent a distinct species.

Family MYLIOBATIDAE Bonaparte, 1838
Genus *Brachyrhizodus* Romer, 1942
Brachyrhizodus wichitaensis Romer, 1942
Figure 3G

Referred Material: UALVP 58782, complete lateral tooth; UALVP 58783, one additional complete lateral tooth.

Description: The mesodistally elongated crown is hexagonal in occlusal view. All crown faces are more or less flat and smooth. The root contains five root lobelets that are separated from each other by distinct grooves.

Remarks: This species has been reported from Campanian–Maastrichtian deposits of the Western Interior Seaway (e.g., Welton and Farish 1993; Schubert et al. 2017) and the Atlantic and Gulf coastal plains (e.g., Cappetta and Case 1975; Case and Schwimmer 1988; Becker et al. 1998). Antunes and Cappetta (2002) reported a single lateral tooth from a late Campanian–Maastrichtian deposit of Angola. Crane (2011) previously reported this species from the Bladen Formation.

Family RHOMBODONTIDAE Cappetta, 1987
Genus *Rhombodus* Dames, 1881
Rhombodus laevis Cappetta and Case, 1975
Figure 3H

Referred Material: UALVP 58784, complete tooth; UALVP 58785, three additional complete teeth.

Description: The crown is rhombic in occlusal view. The occlusal surface is smooth and more or less flat. The margino-labial face is very slightly concave and smooth. The margino-lingual faces are slightly convex and smooth. A weak lingual bulge is present. The root lobes are divided by a well-developed nutrient groove bearing a distinct central foramen. Multiple small foramina are present labially, just below the crown-root border.

Remarks: Cappetta and Case (1975) originally described this species from teeth recovered from the early Maastrichtian of New Jersey. Subsequently, *Rhombodus laevis* has been recovered from the Maastrichtian of the Western Interior Seaway (e.g., Becker et al. 2004; Schubert et al. 2017) and the Atlantic coastal plain (e.g., Case and Schwimmer 1988). This species is unique compared to other *Rhombodus* spp. in having a smooth crown; this distinction may suggest it belongs to a different genus (Cappetta 2012). We conservatively assign UALVP 58784 and UALVP 58785 to *R. laevis* until a detailed review of this species is completed. A tooth from the Bladen Formation identified as *Rhombodus binkhorsti* by Crane (2011) lacks distinct enameloid folding along the margino-labial and margino-lingual faces and is likely *Rhombodus laevis*.

DISCUSSION

The middle Campanian Bladen Formation euselachian assemblage described herein consists of 18 species in 17 genera, at least 14 families, and seven orders. Previously, Crane (2011) reported 20 species from this formation, of which five taxa (*Galeorhinus* sp., *Rhinobatos casieri*, *Protoplatyrhina* sp., *Ischyrhiza avonicola*, and *Schizorhiza* sp.) were not recovered in the collection described herein. It should be noted that Crane (2011) did not figure these taxa. The morphology of the rostral spine assigned to *Borodinopristis schwimmeri* by Crane (2011) appears to be more similar to that of *B. shannoni* (see Case et al. 2012). An additional six species (*Meristodonoides novojerseyensis*, *Plicatoscyllium globidens*, *Archaeolamna kopingensis*, *Protolamna borodini*, *Pseudohypolophus ellipsis,* and *Dasyatis* cf. *D. commercensis*), not previously reported, can be added to the euselachian faunal composition associated with the Bladen Formation.

Of the reported species, *Scapanorhynchus texanus*, *Archaeolamna kopingensis*, *Squalicorax kaupi*, and *S. pristodontus* are well documented outside of North America. The species identified as *Protolamna borodini* and *Cretalamna* sp. herein, were also likely cosmopolitan. As noted above, the taxonomic uncertainty of *Squatina hassei* and the poor preservation of the recovered specimens of *Plicatoscyllium*

globidens from Europe make it difficult to determine whether or not these species had large palaeobiogeographical ranges. The remaining taxa in the Bladen Formation assemblage appear to be limited to North American deposits.

Schubert et al. (2017) described a similar-aged assemblage from the Aguja Formation of West Texas. This assemblage includes a number of species also recovered from the Bladen Formation. Both contain the species *Squalicorax kaupi*, *Scapanorhynchus texanus*, *Ischyrhiza mira*, *Rhombodus laevis*, and *Brachyrhizodus wichitaensis*. Teeth identified as *Meristodon* sp., *Lonchidion selachos*, *Squatina* sp., and *Cretalamna* cf. *C. sarcoportheta* from the Texas assemblage may be conspecific with taxa reported as *Meristodonoides novojerseyensis*, *Lonchidion babulskii*, *Squatina* sp., and *Cretalamna* sp. described herein. Moreover, *Rhinobatos casieri*, *Protoplatyrhina* sp., and *Ischyrhiza avonicola* reported from the Texas assemblage were also reported by Crane (2011) from the Bladen Formation. Schubert et al. (2017) reported 11 additional taxa (*Cantioscyllium* aff. *C. meyeri*, *Chiloscyllium* aff. *C. greeni*, *Columbusia* sp., *Serratolamna* cf. *S. caraibaea*, *Squalicorax* aff. *S. yangaensis*, *Squalicorax* aff. *S. lindstromi*, *Ptychotrygon* sp., *P. agujaensis*, *Ptychotrygon* aff. *P. cuspidate*, *P. triangularis*, *Texatrygon* cf. *T. copei* and *Igdabatis indicus*) that are absent from the Bladen Formation assemblage. It should be noted that the teeth identified as *Ptychotrygon triangularis* may be conspecific with *P. vermiculata*, as the former is considered to be a *nomen nudum* (Cappetta 2006).

In addition to *Cantioscyllium clementsi* sp. nov., the Bladen Formation assemblage has six taxa (*Plicatoscyllium globidens*, *Archaeolamna kopingensis*, *Protolamna borodini*, *Squalicorax* cf. *S. pristodontus*, *Pseudohypolophus ellipsis*, and *Dasyatis* cf. *D. commercensis*) that are not present in the Texas assemblage but have been recovered from other deposits within the Western Interior Seaway. The absence of *Archaeolamna kopingensis* from the Aguja Formation is not unexpected, as this species likely had an antitropical distribution (Cook et al. 2011).

Comparing the Bladen Formation assemblage with the late Campanian assemblage reported by Cicimurri (2007) from the Donoho Creek Formation of South Carolina, we are able to document regional changes in faunal composition over a relatively short period of time. Both assemblages share nine species (*Lonchidion babulskii*, *Squalicorax kaupi*, *S. pristodontus*, *Archaeolamna kopingensis*, *Cretodus borodini* (presumably *Protolamna borodini*), *Ischyrhiza mira*, *Rhombodus laevis*, *Brachyrhizodus wichitaensis*, and *Ptychotrygon vermiculata*). Unfortunately, the teeth of these species reported from the Donoho Creek Formation were not figured. Teeth identified as *Hybodus* sp., *Squatina hassei*, and *Cretalamna appendiculata* from the Donoho Creek assemblage may be conspecific with *Meristodonoides novojerseyensis*, *Meristodonoides* sp., *Squatina* sp., and *Cretalamna* sp. from the Bladen Formation assemblage, but no images were provided in Cicimurri (2007) which would have facilitated comparison. Cicimurri (2007) reported an addition 10 species (*Heterodontus* aff. *H. granti*, *Cantioscyllium meyeri*, *Chiloscyllium* sp., *Pararhincodon* sp., *Carcharias holmdelensis*, *C. samhammeri*, *Rhinobatis casier*, *Pseudohypolophus mcnultyi*, *Borodinopristis schwimmeri*, and *Ischyrhiza avonicola*) that were not recovered from the Bladen Formation assemblage. The absence of *Heterodontus granti*, *Carcharias samhammeri*, and *C. holmdelensis* is not surprising, as the earliest appearance of these species is in the late Campanian (e.g., Cicimurri 2007). Conversely, the Bladen Formation assemblage has four species (*Plicatoscyllium globidens*, *Scapanorhynchus texanus*, *Pseudohypolophus ellipsis*, and *Dasyatis* cf. *D. commercensis*), in addition to *Cantioscyllium clementsi* sp. nov. and the indeterminate sclerorhynchid that were not reported from the Donoho Creek Formation.

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