SELACHIANS FROM THE UPPER CRETACEOUS (SANTONIAN) HOSTA TONGUE OF THE POINT LOOKOUT SANDSTONE, CENTRAL NEW MEXICO

JIM BOURDON[1], KEITH WRIGHT[2], SPENCER G. LUCAS[2], JUSTIN A. SPIELMANN[2] AND RANDY PENCE[2]

[1] 33 Nordica Dr., Croton-on-Hudson, NY 10520, email: jim_bourdon@elasmo.com;
[2] New Mexico Museum of Natural History and Science, 1801 Mountain Rd. NW, Albuquerque, NM 87104-1375

Abstract—In Bernalillo County, central New Mexico, a thin sandstone bed in the upper part of the Hosta Tongue of the Point Lookout Sandstone (Upper Cretaceous, Santonian) yields a diverse assemblage of selachian and other vertebrate fossils. The selachian teeth are assigned to the following taxa: ?*Egertonodus* sp., *Meristodonoides* sp. cf. *M. montanensis*, *Planohybodus* sp., *Lonchidion* sp., *Ptychodus mortoni*, *Parasquatina* sp., *Cantioscyllium decipiens*, *Chiloscyllium* sp., *Cederstroemia ziaensis* new species, *Columbusia* sp. cf. *C. fragilis*, *Scindocorax novimexicanus* new genus and species, *Squalicorax* sp. cf. *S. lindstromi*, *S.* sp. aff. *S. yangaensis*, *Cretoxyrhina mantelli*, *Scapanorhynchus puercoensis* new species, *S.* sp. cf. *S. tenuis*, *S.* sp. cf. *S. texanus*, "*Carcharias*" sp., *Eostriatolamia* sp., *Pueblocarcharias kawaikensis* new genus and species, *Cretalamna* sp., *Ptychotrygon eutawensis*, *Texatrygon stouti* new species, *Ischyrhiza* sp. aff. *I. mira*, cf. *Onchosaurus* sp., *Sclerorhynchus* sp., *Rhinobatos* sp., *Proplatyrhina* sp. aff. *P. renae*, *Myledaphus* sp. and "*Pseudohypolophus*" *ellipsis*. In addition to the selachians, the Hosta Tongue assemblage includes fossils of teleost fish, turtles, plesiosaurs, mosasaurs, crocodiles, and dinosaurs. Teeth of *Scapanorhynchus* dominate the selachian assemblage (~51%), followed by sclerorhynchids (teeth and rostral spines, ~22%) and rhinobatoids (~16%); the other selachians are minor components.

INTRODUCTION

In 1858, Jules Marcou (p. 33, pl. 1, figs. 4-4a) proposed the first scientific name for a vertebrate fossil from New Mexico, an isolated tooth of the Late Cretaceous selachian *Ptychodus whipplei* (Lucas, 2006). Since then, a diverse assortment of Late Cretaceous selachian fossils has been collected from New Mexico (see reviews by Hunt and Lucas, 1993 and Williams, 2006). One of the most significant Late Cretaceous selachian localities in New Mexico was discovered by one of us (RP) in 1981 in the Santonian Hosta Tongue of the Point Lookout Sandstone at a locality in Bernalillo County (Fig. 1). Pence et al. (1986), Lucas et al. (1988) and Williamson et al. (1989) presented preliminary reports on the selachian and non-selachian vertebrate fossils from this locality. Here we present a comprehensive study of the selachian assemblage from the Hosta Tongue at this locality. In this article, NMMNH refers to the New Mexico Museum of Natural History and Science, Albuquerque.

GEOLOGICAL CONTEXT

The fossil site is NMMNH locality 297, which is in the SE¼, sec. 9, T11N, R02W, along the western side of the Rio Puerco about 35 km NNW of metropolitan Albuquerque (Fig. 1). Hunt (1936, pl. 19) published the most recent detailed geological mapping (at a scale of 1:63,360) of the area around this site and identified the stratigraphic unit at the locality as the "Hosta Sandstone Member of the Mesaverde Formation." In current lithostratigraphic terminology, this is the Hosta Tongue of the Point Lookout Sandstone (e.g., Molenaar, 1983).

Lucas et al. (1988, fig. 7) published a measured stratigraphic section at NMMNH locality 297, and they identified the Mulatto Tongue of the Mancos Shale as being overlain by the (ascending order) Dalton Sandstone Member of the Crevasse Canyon Formation (it yields selachian and other vertebrate fossils that were the subject of a preliminary report by Johnson and Lucas, 2003), the coal-bearing Gibson Coal Member of the Crevasse Canyon Formation, and the Hosta Tongue of the Point Lookout Sandstone. The coal beds in the Gibson Coal Member can be correlated to those in measured section 245 of Hunt (1936, pl. 33).

We remeasured the section from the uppermost lignitic strata of the Gibson Coal Member to the faulted out local top of the Hosta Tongue, and we found that locally the Hosta Tongue is ~45 m thick, and the fossil horizon is ~6.5 m below the local top, so it is stratigraphically high in the Hosta Tongue (Fig. 2).

AGE OF NMMNH LOCALITY 297

The age of the Hosta Tongue of the Point Lookout Sandstone is well constrained as Santonian by stratigraphically-bracketing ammonoid assemblages (e.g., Molenaar, 1983). However, few ammonoid data have been published from the Hosta Tongue in New Mexico to determine a more precise age within the Santonian. At NMMNH locality 297, no ammonoids are known to determine the precise age of the vertebrate fossil assemblage. However, farther to the northeast along the Rio Puerco drainage, NMMNH locality 6936 is stratigraphically low in the Hosta Tongue, and provided an assemblage of well-preserved ammonites and other molluscs that will be described elsewhere in collaboration with Paul Sealey. The collection includes the ammonoids *Placenticeras syrtale* (Morton), *Baculites* cf. *B. codyensis* Reeside, *Eutrephoceras alcesense* Reeside and the inoceramid *Cordiceramus gilberti* (White). *Placenticeras syrtale* has a long stratigraphic range, with published records in the lower Santonian (Scott et al., 1986), upper Santonian to lower Campanian (Kennedy et al., 2001) and lower Santonian to lower Campanian (Kennedy and Cobban, 1991b, 1993). *Baculites codyensis* ranges from the middle Coniacian to the middle Santonian (Kennedy and Cobban, 1991a). *Cordiceramus gilberti* has been reported in the upper Santonian (Walaszczyk and Cobban, 2006), but it has also been reported from the uppermost Coniacian to lower Santonian (Kauffman, 1977).

Varriale (2003) reported *Clioscaphites saxitonianus* (McLearn) and *Cladoceramus undulatoplicatus* (Roemer) from the Hosta-Dalton sandstones in the Galisteo region in Santa Fe County. These two taxa indicate an early Santonian age. Also, the lower part of the Satan Tongue near Cuba, Sandoval County, is middle Santonian in age and overlies the El Vado Sandstone Member, which is stratigraphically lower than the Hosta (Sealey and Lucas, 2011). Nearby, at Cabezon, the uppermost part of the Satan Tongue is upper Santonian or lowermost Campanian. Molenaar (1983) noted the occurrence of *Texanites texanus* (Roemer) in the Hosta Tongue in the southern San Juan Basin and considered it middle Santonian because it indicates the zone of *Clioscaphites vermiformis* (Meek and Hayden). Therefore, we consider the Hosta Tongue of the Point Lookout Sandstone at NMMNH locality 297 to be
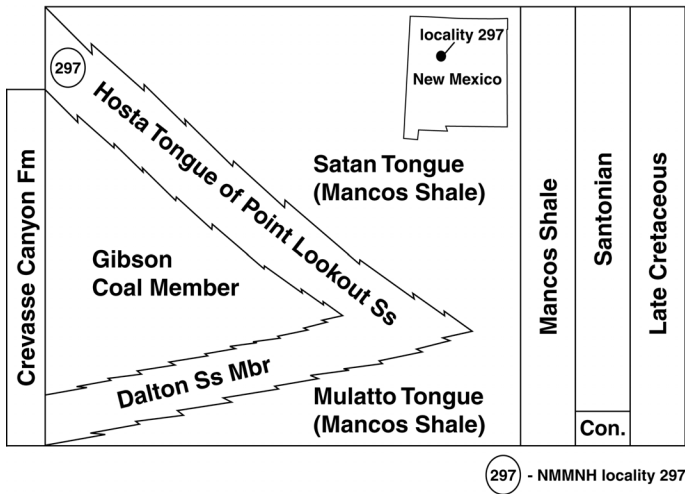
FIGURE 1. Map and generalized lithostratigraphy showing geographic location and stratigraphic position of NMMNH locality 297.

early to middle Santonian in age. A more precise age can only be determined through the discovery of ammonoid (particularly scaphitid) fossils near the vertebrate fossil assemblage.

FOSSIL ASSEMBLAGE

Fossil vertebrates at NMMNH locality 297 occur as isolated teeth and bones within a ~0.5 cm-thick interval of medium to coarse quartzose sandstone. Lucas et al. (1988) documented the non-selachian vertebrate fossils and identified turtles (shell fragments of Trionychidae and Baenidae?), mosasaurs (cf. *Platecarpus* sp.), plesiosaurs (Elasmosauridae), crocodilians, and dinosaurs (teeth of dromaeosaurids, tyrannosaurids and hadrosaurids).

Some of these fossils represent freshwater or terrestrial animals, and indicate that the vertebrate fossil assemblage from locality 297 contains an allochthonous mixture of marine and nonmarine taxa. In general, the paleoenvironment of Hosta deposition was a paralic setting in which sand accumulated along the shoreline of the Western Interior Seaway (e.g., Molenaar, 1983). Thus, paleoenvironments ranged from fluvio-deltaic to offshore sandbar. The paleoenvironment at locality 297 was likely that of a "beach" in which freshwater and marine fossils were mixed. However, a more precise assessment of the depositional environment of locality 297 awaits additional study.

MATERIALS AND METHODS

The vertebrate fossils from NMMNH locality 297 were collected by both surface picking and screenwashing. The specimens documented by Lucas et al. (1988) and Williamson et al. (1989) were largely derived by surface collecting an acre-sized area of the Hosta Tongue; a small percentage (approximately 5%) resulted from the screenwashing of bulk samples.

For this new study, approximately 80 kg of bulk matrix was removed from the bonebed, which we interpret as a basal channel lag. The material was dried at 110° C for 12 to 24 hours, soaked in water for several hours and then sieved wet. The sieves employed were: 3/8", #4 (4.75 mm), #10 (2 mm) and #30 (0.6 mm), and specimens were then picked and sorted. Any matrix material captured in the larger three sieves was dried again and the process repeated. Some matrix needed to be processed several times, and this repetition was necessary to remove persistent matrix adhering to fossils. Due to the fractured nature of the fossils, larger specimens from the matrix were removed and glued back together prior to processing. Specimens requiring additional cleaning were cleaned manually with water or acetic acid; those less subject to damage were treated to varying durations of ultrasonic cleaning (Haier HU3805).
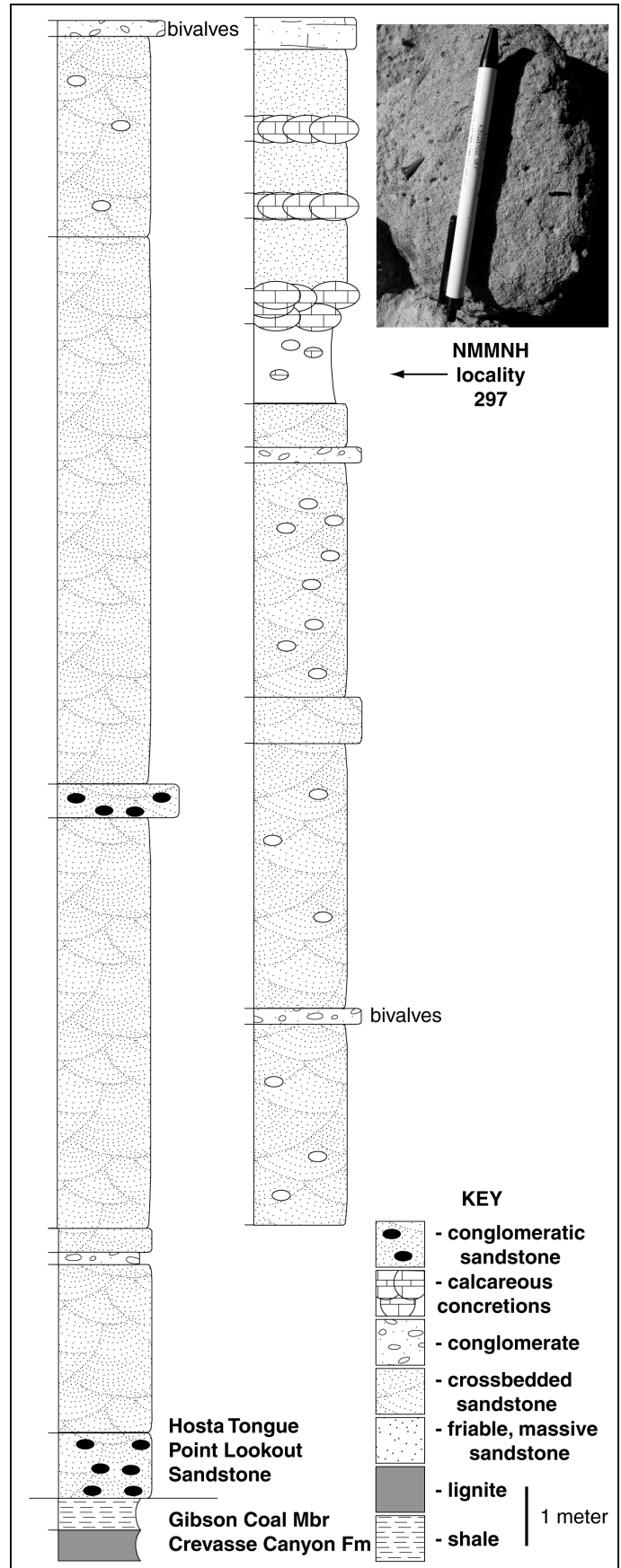

FIGURE 2. Measured stratigraphic section at NMMNH locality 297 with inset photograph that shows occurrence of selachian teeth at the locality.
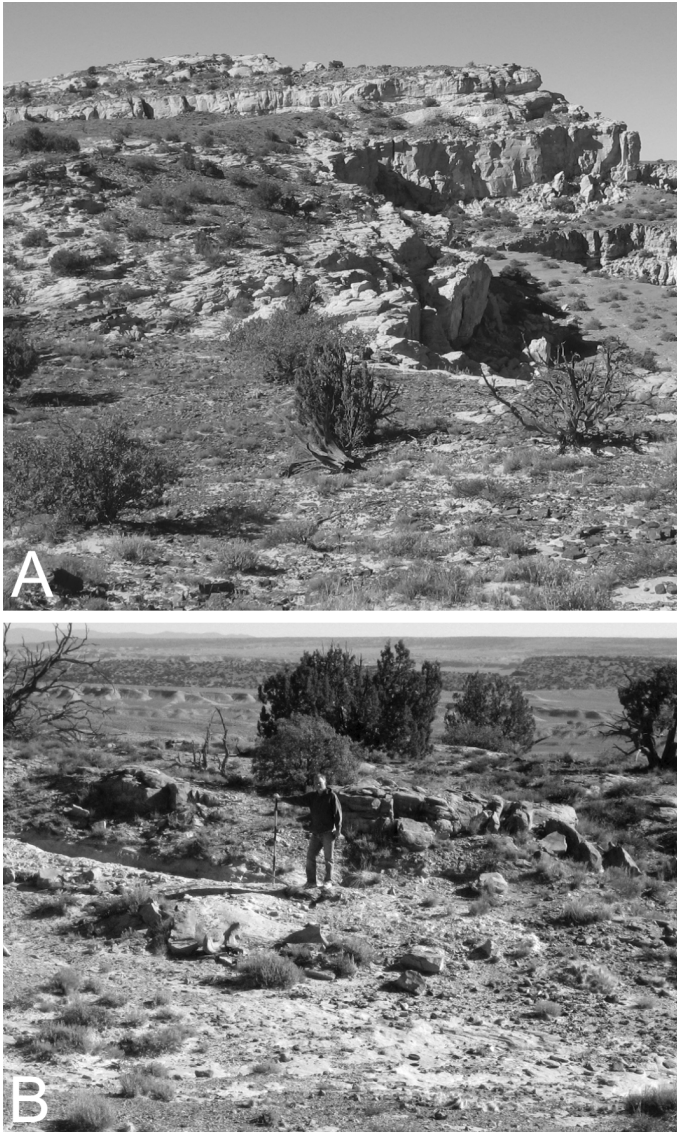
FIGURE 3. **A**, Overview of outcrops near NMMNH locality 297, showing cliff- and bench-forming Hosta Tongue of Point Lookout Sandstone. **B**, NMMNH locality 297; Randy Pence is standing on the fossiliferous sandstone bed.

Relevant specimens were then imaged, usually from four or five perspectives, using a digital scanner (HP5300c and HP4570c) at 600, 1200 or 2400 dpi optical resolution, depending on specimen size. The resulting images were then processed, with background removed, brightness adjusted, contrast enhanced, and object rotated to orient perspectives similarly between specimens.

The 8933 specimens were collected under a BLM permit and are housed under catalog numbers NMMNH P-60682-P-61185, P-61427-P-61453, P-61462-P-61465 and P-61483-P-61566 and P-61921. The 529 specimen images created for this study are archived on CD by the NMMNH for future reference.

TERMINOLOGY

Tooth terminology largely follows Cappetta (1987), and positional nomenclature, Siverson (1999). Certain terms will be employed that are ambiguous (used differently by various authors) or more tightly defined. They include:

A0: Extant odontaspidid and mitsukurinid lamniforms have three upper and four lower anterior teeth; the fourth is often a reduced version, and the mesial-most of the group. As the mesial-most lower anterior, Cunningham (2000) referred to this tooth position as a lower first anterior (LA1). An unfortunate consequence of this numbering is that subsequent lower anteriors (A2-A4) are numbered differently than their corresponding uppers (A1-A3).

As referred to here, when a fourth tooth is present in the lower anterior hollow, it will be referred to as position A0, permitting the remaining upper and lower positions to share similar numbers (A1-A3). This A0 position is not intended to replace parasymphyseal tooth-positions, which are a distinct group (one or more) of teeth with coalesced lobes, found (when present) at the leading margin of the anterior hollow. Underwood and Cumbaa (2010, pl. 5, fig. 18) included as a parasymphyseal, a *Roulletia canadensis* sp. nov specimen that would be referred to as an A0 in our paper. Shimada (2002, p. 53) included as symphyseals, *Carcharias*, *Odontaspis* and *Mitsukurina* positions that are included as A0s here.

Characteristic vs. Propensity: Every selachian tooth in reasonable condition can be described as including a certain group of characteristics. Tooth-based taxonomic determinations largely rely on the presence (or absence) of various morphological features of the root and crown; however, some of these features may be subject to positional, ontogenetic, sexual or individual variations. Descriptions that are overly broad by including all the possible variations can result in "lumping," while more tightly-defined descriptions may result in "splitting." When used here, "propensity" will refer to a characteristic that is usually but not necessarily always displayed.

Dentition-design: As used here, this will refer to a characteristic set that includes: positional tooth-design, tooth count, functionality and heterodontic variabilities. Recent lamniform teeth may be largely identified on the basis of tooth-design; however, within the carcharhiniforms, particularly *Carcharhinus*, tooth-design alone can be ambiguous and requires positional examples and tooth counts. The diversity of lamniform taxa during the Late Cretaceous often requires dentition-design to be considered.

Design-envelope: This term is primarily used to indicate that known positional design and heterodonty (individual, ontogenetic, sexual and regional) was considered when assessing a specimen. Design-envelope is not a known, rather an objective; a means of including (lumping) or separating (splitting) specimens sharing a tooth-design. In this paper, two design-envelopes are included as *Scindocorax novimexicanus* n. sp. and *S.* aff. *S. novimexicanus*. Only additional study can resolve if these two tooth-designs represent different taxa or express variations of a single species.

File vs. row: File refers to a labiolingual series and row to a mesiodistal series of teeth.

Meso- and distolaterals: Siverson (1999) referred to teeth from the lateroposterior hollow as lateroposteriors. For descriptive purposes it is useful to view them as two groups: mesolaterals, mesially-positioned lateroposteriors that are consistent between individuals, and distolaterals, those reduced, distally-positioned teeth that vary in count between individuals. At this time, the mesolateral count is subjective; there is often no means of distinguishing a definitive breakpoint between the two groupings.

Tooth-design: When referring to a specific tooth, tooth-design is the characteristic-set displayed by that specimen. When applied to a group of teeth from a particular species, this term refers to a propensity-set; the characteristics that are usually displayed, but may sometimes vary, due to positional, ontogenetic, sexual and individual heterodonty. A positional tooth-design would be a propensity-set but more tightly constrained as it refers only to characteristics or propensities associated with a particular tooth position within the dentition.

SYSTEMATICS

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Order HYBODONTIFORMES Maisey, 1987

Remarks: Zangerl (1981, p. 56) erected the superfamily Hybodontoidea within the order Euselachii. Maisey (1987, p. 4) placed the hybodontids (with an emended diagnosis) in plesion Hybodontiformes in the subclass Elasmobranchii; Maisey (1989, p 11) continued to refer to plesion Hybodontiformes, and, in a cladogram of phylogenetic relationships, did not include ptychodontids within Hybodontiformes. Cappetta (1987, p. 30, 37) included the hybodontids in the superfamily Hybodontoidea, simply as a member of the cohort Euselachii; subsequently, Cappetta and Case (1999, p. 8) included the hybodontids in Hybodontiformes. Shimada et al. (2009, p. 336) included the superfamily Hybodontoidea in the order Hybodontiformes Maisey, 1987; while Underwood and Cumbaa (2010, p. 906), in reporting hybodontid teeth from Saskatchewan, reported the superfamily as Hybodontoidea Owen, 1846 *sensu* Zangerl, 1981 and the order as Hybodontiformes Maisey, 1989.

Family HYBODONTIDAE Owen, 1846
Genus *Egertonodus* Maisey, 1987

Type species: *Hybodus basanus* Egerton, 1845, Lower Cretaceous of southern England.

Remarks: Maisey (1987) erected this genus based on cranial elements. Rees and Underwood (2008) provided details on tooth-design, noting a strong cutting edge, flattened labial cusp face, multiple slender lateral cusplets and moderate ornamentation (weak folds of the lower crown face); they went on to describe *Egertonodus duffini*. In that paper, the authors limited the distribution of the genus to the Bathonian to the Barremian or Aptian of England.

?*Egertonodus* sp.
Fig. 4A

Referred specimen: NMMNH P-60809; a single, moderately-sized (16 mm wide), severely fractured tooth with a complete root.

Description: Large central cusp well separated from two lateral cusplets by a low shoulder; cutting edge complete; labial cusp face less convex than the lingual. Labially, the crown has short and weak basal folds; lingually, the folds are more pronounced, extending higher (over half the height of the primary cusp). The medial-most cusplet on the shoulders is significantly larger than the more lateral. The root is porous, lacking distinct foramina; viewed basally, there is a distinct transverse labial depression.

Discussion: This specimen was not fully cleaned to insure that the highly fractured cusplets would remain intact. The cusp is less conical, folds are weaker and cusplets more gracile than *Meristodonoides* or *Hybodus*. The shoulders are much lower and the cusp-to-cusplet spacing is greater than those of *Planohybodus*.

If interpreted correctly, the presence of these teeth in the Santonian of New Mexico represents a significant range expansion for this genus – chronologic, longitudinal and latitudinal.

Genus *Meristodonoides* Underwood and Cumbaa, 2010

Type species: *Hybodus rajkovichi* Case, 2001 from the Late Cretaceous (Cenomanian) of Minnesota, USA.

Remarks: This genus is diagnosed by: a single rounded symmetrical cusp with striae and weak but complete cutting edge; cusplets lacking or small and detached from the cusp and a low root, usually well-vascularized. Species previously attributed to *Hybodus* Agassiz, 1837 and now assigned to this new genus also include: *Hybodus butleri*

Thurmond, 1971, *Hybodus montanensis* Case, 1978 and *Hybodus novojerseyensis* Case and Cappetta, 2004.

Williamson et al. (1989, p. 241) reported 81 teeth from NMMNH locality 297; NMMNH P-4007 (n = 79), P-4027 (n = 1) and P-4028 (n = 1). These teeth were all referred to *Hybodus* cf. *H. butleri*, as were spine fragments (NMMNH P-4017). Our new bulk-sampling study yielded 93 (mostly fragmentary) specimens. The tooth counts below are limited to specimens with a primary cusp and at least one shoulder.

ptera*Meristodonoides* sp. cf. *M. montanensis* (Case, 1978)**
Fig. 4B-F

Referred specimens: NMMNH P-60812-P-60818, P-60820, P-60824; 37 teeth, all small (6.5 – 8.5 mm wide) and lacking roots.

Description: Anterior positions with taller, rather erect cusps and low, smooth shoulders; distally, the primary cusp becomes shorter and more inclined and the distal shoulder develops a small, rather oblique cusplet(s). Lingually, the crown face has short basal folds, often limited to the lateral margins of the main cusp and sometimes extending to 30-40% of the cusp height. Folds may be broad, low and widely spaced; often the shoulders show no folds. Labially, folds tend to be shorter and weaker than their lingual counterparts.

Discussion: Thurmond (1971, p. 212-215, text-fig. 3) designated a holotype for *H. butleri* from the Aptian-Albian of Texas lacking lateral cusplets, which he deemed an anterior tooth and designated more lateral teeth as paratypes (his text-fig. 4). Although not smooth, the cutting edges of the shoulders lack clearly defined cusplets. He described the striae (folds) of the anterior teeth as reaching halfway up the cusp; in lateral teeth, they may reach the apex. The Hosta Tongue specimens have a much smoother cutting edge on the shoulders with fewer, weaker and shorter folds, bearing a cusplet(s) in distal tooth-positions and appear to have a taller main cusp relative to crown width.

Case (1978 p. 180-82) designated a tooth lacking lateral cusplets, which he deemed a lower lateral, as the holotype (his pl. 2.1) of *Hybodus montanensis*, a Campanian specimen. "Antero-lateral" teeth with two cusplets on each shoulder were designated as paratypes (his text-fig. 2). Anteriorly positioned teeth from the Hosta Tongue assemblage compare very well with Case's holotype, but no teeth well represent the tooth-design reflected by his paratype (see below).

Based on similarities of some Hosta Tongue specimens with the *Meristodonoides montanensis* holotype, the specimens referred here appear to be closely aligned with *M. montanensis*.

ptera*Meristodonoides* sp. aff. *M. montanensis* Case, 1978**
Fig. 4G

Referred specimens: NMMNH P-60821-P-60822; two small (approximately 5 mm wide) teeth, each lacking a root.

Discussion: Two poorly-preserved teeth may be within the range of variation of *Meristodonoides montanensis*. The first (Fig. 4G) is an anterior tooth with an acute distal cusplet, thick cusp and weak but elongate (running half the height of the cusp) folds. The second (not figured), a lateral tooth, bears mesial and distal cusplets and strong folds. The smaller size of these teeth may reflect ontogenetic variation.

Genus *Planohybodus* Rees and Underwood, 2008

Type species: *Planohybodus peterboroughensis* Rees and Underwood, 2008 from the Callovian, Middle Jurassic of Peterborough, southern England.

Remarks: Teeth of this genus are *Meristodonoides*-like; however, they tend to be larger, the labial crown-face flatter, cusp wider and more compressed, cutting edge better developed, higher shoulders bear cusplets, usually multiple and slender and a root with a basal face well-excavated labially. The known distribution, as reported by Rees and Underwood (2008), is the Middle (possibly Early) Jurassic to Early Cretaceous (Berriasian–Barremian) of Western Europe. Two tooth-de-
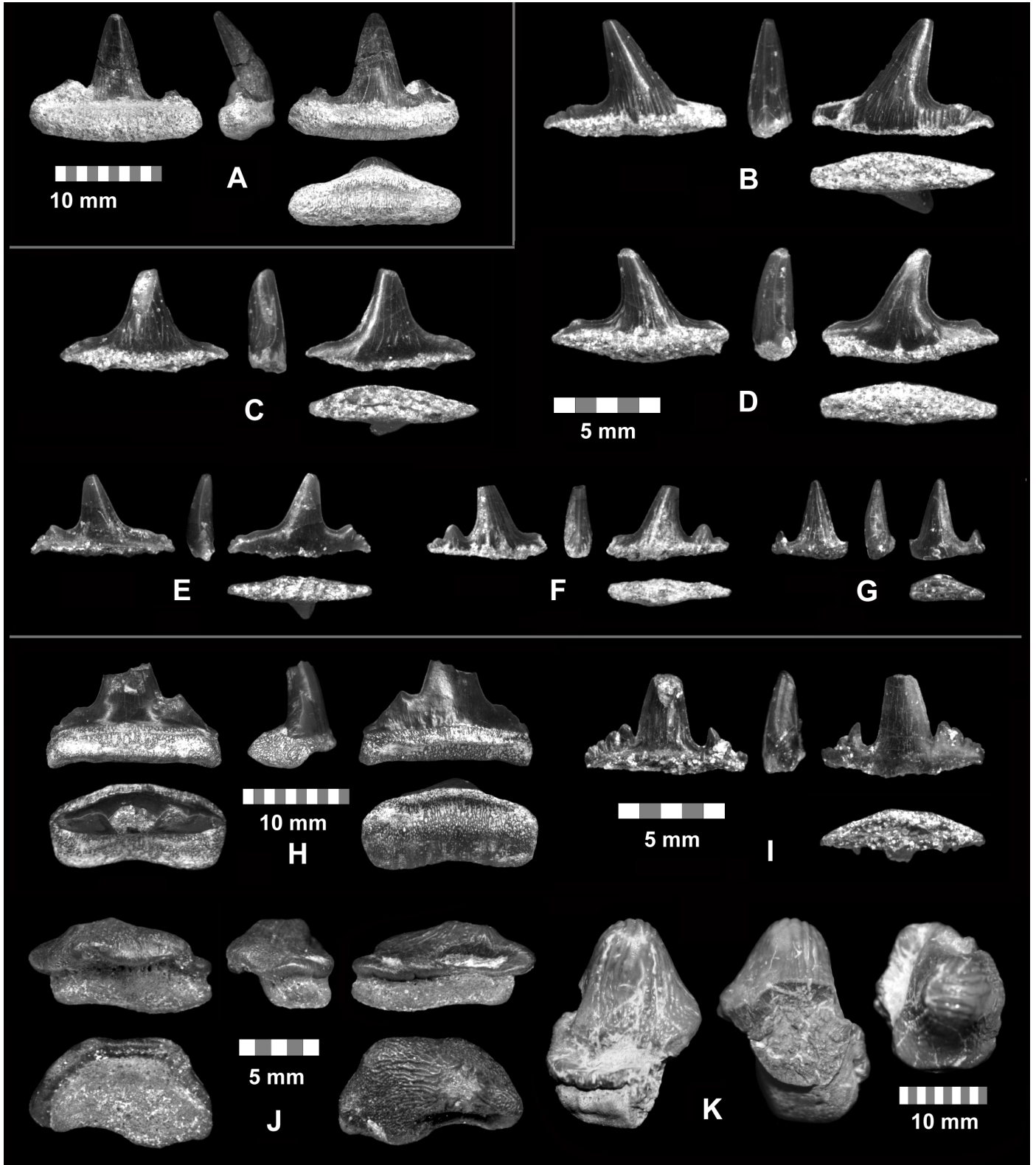
FIGURE 4. Hybodontids and ptychodontids, all presented (left-right) lingual, lateral, labial and basal/occlusal views; some specimens digitally mirrored for comparative purposes. **A**, ?*Egertonodus* sp., NMMNH P-60809, 10 mm scale bar. **B-F**, *Meristodonoides* sp. cf. *M. montanensis*, all specimens similarly scaled, 5 mm scale bar, **B**, NMMNH P-60814, **C**, NMMNH P-60812 (mirrored), **D**, NMMNH P-60818, **E**, NMMNH P-60813 (mirrored), **F**, NMMNH P-60820 (mirrored). **G**, *Meristodonoides ?montanensis*, NMMNH P-60821. **H**, *Planohybodus* sp., NMMNH P-60810, 10 mm scale bar. **I**, *Planohybodus* sp., NMMNH P-60811, 5 mm scale bar. **J**, *Ptychodus mortoni*, NMMNH P-61494, distolateral, 5 mm scale bar. **K**, *Ptychodus* sp. NMMNH P-28943, distolateral, 10 mm scale bar.

signs are reported together herein as they likely represent positional and ontogenetic variations of a single species.

Planohybodus sp.
Fig. 4H-I

Referred specimens: NMMNH P-60810, P-60811, P-60819; two damaged teeth and a shoulder fragment.

Description: NMMNH P-60810: a moderately large (16.5 mm wide) tooth with a complete root and damaged cusp. This specimen appears to have been an anteriorly-positioned tooth with a wide high cusp and mesiodistally-compressed crown. The shoulders are very high with a cuspidate (broad and triangular) mesial edge and a weakly raised and irregular distal edge. The labial crown face has numerous weak and short basal folds, barely reaching the height of the shoulders. The lingual face has fainter basal folds, less numerous and shorter than the labial. The neck is broad, growing more so laterally. The root is porous, lacking distinct foramina.

NMMNH P-60811: a small (7.5 mm wide) rootless tooth with damaged cusp. Tall and wide main cusp, well demarked from cuspidate shoulders. The labial crown face has short, faint, basal folds appearing nearly smooth; the lingual folds are weak to strong, extending half the height (or more) of the main cusp. The shoulders are high and strongly separated from the cusp with multiple, medially-curved cusplets (n = 5 in examples) forming high on the shoulder.

Discussion: NMMNH P-60810 significantly differs from *Meristodonoides* and *Egertonodus* by its high shoulders. NMMNH P-60811 differs from *Meristodonoides* by its broad flattened cusp, weak ornamentation, high shoulders, and numerous cusplets; and *Egertonodus* by the high shoulders and numerous cusplets; and from palaeospinacids, by the separation of the cusplets that do not extend to the base of the crown.

The presence of this genus in the Santonian of New Mexico greatly expands the chronological and spatial range of the genus.

Family LONCHIDIIDAE Herman, 1977
Genus *Lonchidion* Estes, 1964

Type species: *Lonchidion selachos* Estes, 1964, from the Maastrichtian Lance Formation, Late Cretaceous of eastern Wyoming, USA.

Remarks: In describing *Lissodus weltoni* (Cenomanian, Oregon, US), Duffin (1985) synonymized *Lonchidion* with *Lissodus* Brough, 1935; Cappetta (1987, p. 34-36) also included *Lonchidion* as a junior synonym and would continue to view it as such (Cappetta and Case, 1999). In their review of *Lissodus*, Rees and Underwood (2002) followed Antunes et al. (1990) by recognizing *Lonchidion* as a distinct genus – an interpretation followed here.

Lonchidion sp.
Fig. 5A

Referred specimen: NMMNH P-60825; single small (2 mm wide) tooth with complete root.

Description: Viewed labially, the coronal-root boundary is mesiodistally "pinched" relative to the width of the crown and root. The crown is slightly higher and wider than the root, and the shoulders reflect no lateral cusplets. Viewed laterally, the specimen is labiolingually compressed, and occlusally the labial protuberance of the crown is narrowly triangular. There is no visible evidence of folds on either face of the crown. The lingual face of the root has four relatively large foramina, giving the root face a ridged appearance. Below a weak lingual protuberance, the root is concave and bears a large foramen; smaller foramina are present laterally.

Discussion: *Lonchidion* has a long and widespread record in North America. *Lonchidion humblei* Murry, 1981 was described from the Late Triassic (Carnian) of Texas and subsequently reported from New Mexico (Heckert and Lucas, 2002) and, possibly, Virginia (Rees and Underwood, 2002). Multiple taxa have been erected from the Late Cretaceous of the US:

- *L. babulskii* Cappetta and Case, 1975a – Campanian-Maastrichtian of the Atlantic and Gulf coasts (Lauginger and Hartstein, 1983; Case and Schwimmer, 1988; Manning and Dockery, 1992; Cappetta and Case, 1997);
- *L. griffisi* (Case, 1987) – Campanian of Wyoming;
- *L. selachos* Estes, 1964 – Maastrichtian of Wyoming and Campanian of Texas (Welton and Farish, 1993); and
- *L. weltoni* (Duffin, 1985) – Cenomanian of Oregon.

Meyer (1974) identified Cenomanian-Campanian Gulf Coast teeth as *Lonchidion* aff. *L. breve* Patterson, 1966 based on the lack of ornamentation, a non-cuspidate transverse crest, and the labial protuberance. Despite the excellent preservation, a single Hosta specimen (likely an anterior) does not permit assignment below the genus level.

Subcohort NEOSELACHII Compagno, 1977
Order PTYCHODONTIFORMES Hamm, 2008

Remarks: Cappetta (1987, p. 30, 37) included the ptychodontids in the superfamily Hybodontoidea; however, Maisey (1989, p. 37) excluded ptychodontids from the Hybodontiformes. Cappetta and Case (1999, p. 9) included ptychodontids as hybodontiforms, but Shimada (2006, p. 165) deemed the ordinal assignment for ptychodontids as incertae sedis. In a comprehensive and detailed Masters thesis regarding ptychodontids, Hamm (2008) proposed the new order Ptychodontiformes ("nested within the Super Order Galeomorpha"). Shimada et al (2009, p. 336) assigned the ptychodontids to the superfamily Hybodontoidea, order Hybodontiformes Maisey, 1987, and provided detailed background (p. 337) on the evolving thought on the family's placement. Shimada et al. (2010, p. 249) simply noted: "enigmatic ptychodontid sharks (Elasmobranchii: Hybodontiformes?)." Underwood and Cumbaa (2010, p. 910), in reporting ptychodontid teeth from Saskatchewan, reported the order as Incertae Sedis. Based on the arguments provided in Hamm (2008), we have included *Ptychodus* within his proposed order.

Family PTYCHODONTIDAE Jaekel, 1898
Genus *Ptychodus* Agassiz, 1835

Type species: *Ptychodus mammillaris* Agassiz, 1839 from the Late Cretaceous of Europe.

Ptychodus mortoni Agassiz, 1839
Fig. 4J

Referred specimens: NMMNH P-61494 and P-61515; a distolateral (12 mm wide) tooth and a crown fragment.

Description: The distolateral (Fig. 4J) has a low, globular asymmetrical crown, with a broad, mesially-positioned and worn cusp. The upper portion of the cusp bears multiple apico-basal vermiculated ridges that bifurcate and intertwine basally and extend to the margins of the crown. In profile, the lower labial crown face extends well beyond the root. The root is high, lacks a nutritive groove and is perforated below the crown with numerous foramina.

Discussion: Bulk sampling yielded two additional specimens. Williamson et al. (1989, p. 241) attributed nine teeth from NMMNH locality 297 to *Ptychodus* cf. *P. mortoni*; NMMNH P-4008 (n = 8) and NMMNH P-4029 (n = 1). Williamson et al. (1989), referring to Meyer (1974), noted these specimens might reflect a transitional form between *P. anonymous* Williston, 1900 and *P. mortoni*. The new specimen combined with the earlier specimens better supports the assignment to *P. mortoni*.

Ptychodus sp.

Fig. 4K

Referred specimen: NMMNH P-28943; a single (approximately 2 cm high) damaged tooth.

Description: The cusp is high and from an occlusal perspective, circular; it merges obtusely but abruptly with the lower crown. Five complete broad transverse ridges are present on the upper cusp becoming punctuated midway down the cusp. Ornamentation of the lower crown face is a series of concentric rings made up of punctuated ridges.

Discussion: The specimen's extensive damage precludes assignment to a tooth position or a particular species; however, there are two possibilities. *Ptychodus whipplei* Marcou, 1858 has not been reported from sediments younger than the Coniacian; however there are features of the crown (high circular cusp) that are similar to that taxon. Based on the damaged condition of this tooth, it may represent a specimen reworked into the Hosta Tongue; however, the damage does not appear to be transportational in nature. Hamm (2010) reassigned Late Coniacian-Santonian teeth, previously reported as *Ptychodus anonymous* Williston 1900, to *P. rugosus* Dixon, 1850 and limited the former to Middle Cenomanian-Middle Turonian. This Hosta Tongue specimen shares characteristics with *P. rugosus* medial positions and falls within the chronorange of that taxon.

Order SQUATINIFORMES Buen, 1926
Family ?SQUATINIDAE Bonaparte, 1838

Remarks: In a recent study of squatiniform skeletal material and isolated teeth from the Anglo-Paris Basin, Guinot et al. (in press) documented various, somewhat similar, tooth-designs from the Late Cretaceous of Western Europe. They argued that certain Cretaceous *Squatina* Linnaeus, 1758 taxa should be included in the subgenus *Cretascyllium* Müller and Diedrich, 1991. Using over 500 specimens spanning the Early Santonian through Late Campanian, they more clearly defined positional variations of "*Squatina* (*Cretascyllium*)" *hassei* Leriche, 1929 and concluded that reports of this species from North America may represent an orectolobiform taxon with a convergent crown-design.

A second Late Cretaceous fossil genus, *Parasquatina* Herman, 1982, was recognized and tentatively assigned to Squatinidae; this tooth design combines features of the *Squatina* crown-design with a root that displays both squatiniform and orectolobiform characteristics. *Parasquatina* teeth were much less common in their study, and there was no Cretaceous skeletal material to provide collaborative detail. The Hosta Tongue specimens compare much better with *Parasquatina*, as included in Guinot et al. (in press), than those of *Squatina* (*Squatina*), "*S.* (*Cretascyllium*)" or most of those typically referred to as *Squatina hassei* sensu Cappetta and Case (1975a; pl. 1, figs.17-21) in North American literature.

Genus *Parasquatina* Herman, 1982

Type species: *Parasquatina cappettai* Herman, 1982; Maastrichtian, Late Cretaceous, Hemmoor, northwestern Germany.

?*Parasquatina* sp.
Fig. 5B-D

Referred specimens: NMMNH P-60803-P-60807; five very small (1.6 - 2.4 mm wide) complete teeth.

Description: The crown has a narrow cusp with a well-defined apron (labial), extending beyond and slightly overhanging the root with a rounded basal margin; the labial and lingual crown faces are smooth, lacking vertical ornamentation; the shoulders are laterally elongate, smooth and extending to, but not reaching, the lateral margins of the root; the mesial edge is obliquely concave, the distal more acutely defined, creating a moderate distal heel; the cutting edge is complete. In lateral view, the cusp is lingually directed with a slight labial recurvature in some specimens; the lingual protuberance is somewhat high and elongate.

The hemiaulacorhizous root is broad, somewhat low, concave labially and flatter lingually with a strong lingual protuberance; the lobes are weakly rounded and well-defined, somewhat parallel mesially and more splayed distally; the lobes form a V-shape with a lingually positioned foramen that opens on the lower lingual face of the root. Small margino-lingual foramina below the crown could not be observed; however, a single margino-lingual foramen is positioned midway up the root, on each side of the protuberance. Anterior teeth have taller, more erect cusps and higher roots, with a concavity between the lobes; distally, the teeth become more elongate, the cusp lower, more lingually inclined and the root flatter.

Discussion: Late Cretaceous angelshark-type teeth from North America have been most typically attributed to *Squatina* "*hassei*;" this is particularly true along the East and Gulf coasts: Case and Schwimmer (1988), Robb (1989), Hartstein et al. (1999), Case et al. (2001) and Becker et al. (2006). However, more than one tooth-design has been reported (none corresponding with *S. hassei* as documented in Guinot et al., in press). Meyer (1974, p. 166-168) included *S. hassei*? from the Santonian-Early Maastrichtian of Mississippi; the figured specimens represent at least two species, including *Squatina* "*hassei*". Williamson et al. (1989, fig. 3f-g; NMMNP P-4005) reported as *Squatina* sp. (Santonian, New Mexico), a *Cederstroemia* tooth. Welton and Farish (1993, p. 77) included *S. hassei* in the Campanian and Maastrichtian of Texas; however, the figured teeth differ from *Squatina* "*hassei*" by their broad crown and labial ornamentation (vertical ridges); these may represent *Parasquatina*. Becker et al. (2004, fig. 4 a-d) figured a tooth from the Maastrichtian of South Dakota having an elongate, mesiodistally compressed apron and a low root (orectolobiform-like design).

The Hosta Tongue teeth are most easily differentiated from *Cederstroemia*, *Columbusia* and *Cretorectolobus* by the length and shape of the apron, which is shorter, less compressed and more rounded; as in *Squatina* (*Squatina*), "*S.* (*Cretascyllium*)" and *Parasquatina*. They also lack the flat basal root face of "*Squatina* (*Cretascyllium*)" and are more similar to the tooth-design included as *Parasquatina*. *Parasquatina cappettai* (Maastrichtian, Germany) and "*P. justinensis*" Guinot et al., in press (Middle Turonian, France) both have smooth, but broadly triangular crowns – unlike the Hosta Tongue examples. "*Parasquatina jarvisi*" Guinot et al., in press (Late Santonian, United Kingdom) is of similar age and crown design, but bears vertical ornamentation of the labial crown face. Therefore, the New Mexico teeth may represent juvenile examples of the unnamed tooth-design, commonly referred to as *Squatina* "*hassei*" in North America, which may be a squatinid or orectolobid. However, they compare better with the described *Parasquatina* tooth-design, which was tentatively included as a squatinid by Guinot et al. (in press).

Order ORECTOLOBIFORMES Compagno, 1973

Remarks: Cappetta (1987, p. 71) attributed this order to Applegate, 1972; however, he went on to note in the bibliography (p. 183) that the name wasn't published by Applegate until 1974. Therefore, Compagno's (1973) introduction of the name has priority.

Family GINGLYMOSTOMATIDAE Gill, 1862

Remarks: Compagno (2001, p. 188) noted that Gill (1862, p. 406) assigned these sharks to the family Ginglymostomatoidae; it was Gill (1872, p. 24) who named the family Ginglymostomatidae.

Genus *Cantioscyllium* Woodward, 1889

Type species: *Cantioscyllium decipiens* Woodward, 1889, Late Cretaceous (Cenomanian), Kent, England.

Cantioscyllium sp. aff. *C. decipiens* Woodward, 1889
Fig. 5E-I

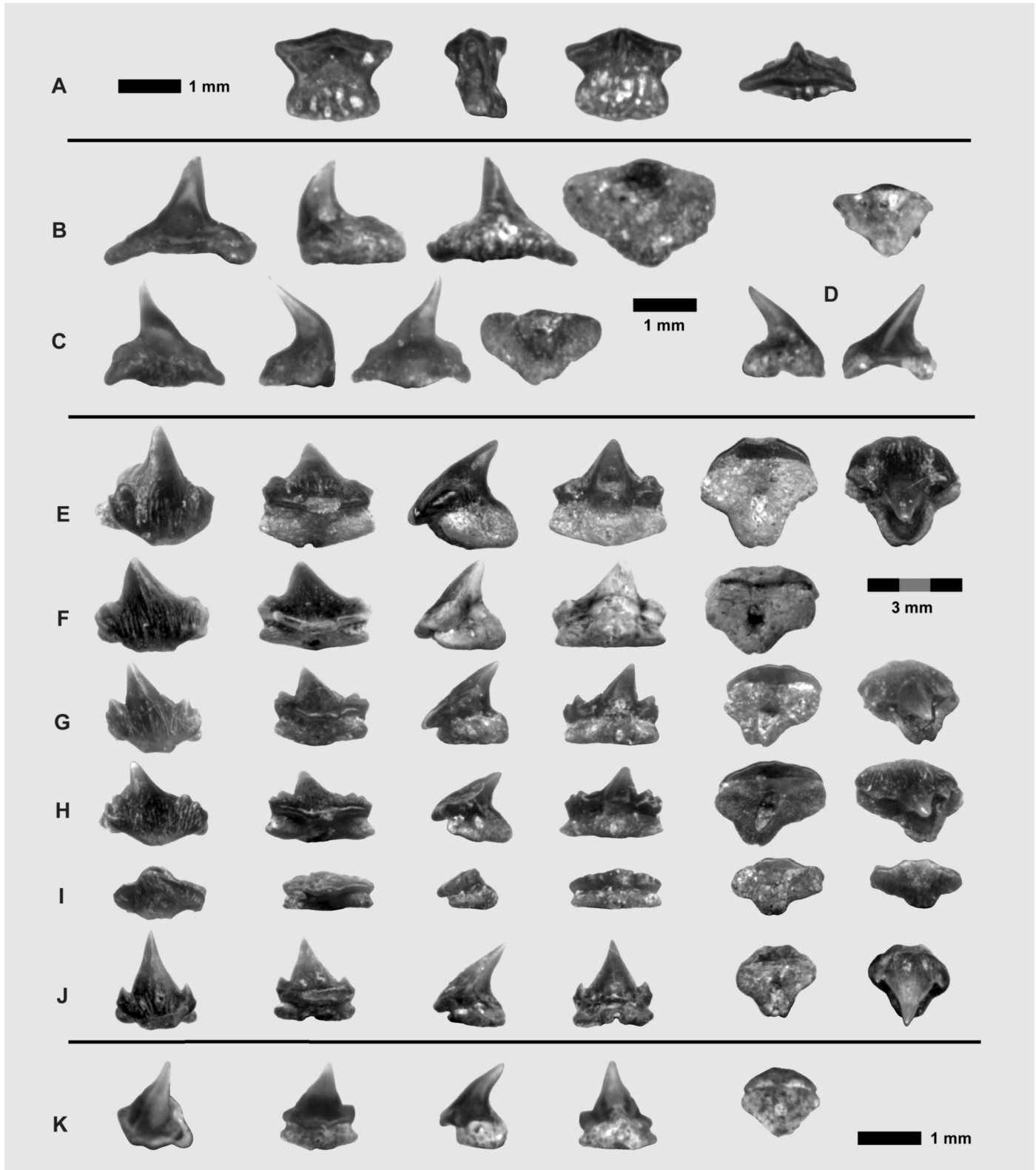**Referred specimens:** NMMNH P-60826, P-60828-P-60837;

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FIGURE 5. Various families, grouped specimens similarly scaled as noted (L-R = Left to right). **A**, *Lonchidion* sp. anterior, NMMNH P-60825, L-R: lingual, lateral, labial and occlusal. **B-D**, ?*Parasquatina* sp., L-R: labial, lateral, lingual and basal, **B**, anterolateral, NMMNH P-60807, **C**, lateral, NMMNH P-60804, **D**, lateral, NMMNH P-60805. **E-I**, *Cantioscyllium* sp. aff. *C. decipiens* positional examples; L-R: cuspal, labial, lateral, lingual, basal and occlusal, **E**, anterior, NMMNH P-60828, **F**, lateral, NMMNH P-60830, **G**, lateral, NMMNH P-60832, **H**, lateral, NMMNH P-60829, **I**, posterior, NMMNH P-60834. **J**, *Cantioscyllium* sp., NMMNH P-60827, L-R: cuspal, labial, lateral, lingual, basal and occlusal. **K**, *Chiloscyllium* sp., NMMNH P-60808, L-R cuspal, labial, lateral, lingual and basal.

321 small (3-4 mm wide) teeth.

Description: Teeth small, following the nurseshark-design: a low, robust, lingually-inclined cusp, with a wide, thick, often bifid, lower labial margin (apron) extending well beyond the V-shaped root. The lateral margins have one to three low, rounded cusplets on oblique shoulders. The labial crown face bears strong apico-basal enameloid folds. The root has a large, lingually-positioned, central pore that opens on the lingual face of the root and a margino-lingual foramen on the external face of each lobe. The dentition is clutching in design with gradational monognathic heterodonty. Anterior teeth are mesiodistally compressed with more upright crowns when contrasted with the lower, mesiodistally expanded, lateral and posterior positions.

Discussion: In North America, the *Cantioscyllium* tooth morphology was initially referred to *C. decipiens* (Turonian, South Dakota; Cappetta, 1973); however, Meyer (1974, p. 174-83) recognized two *Cantioscyllium* tooth-designs from the Late Cretaceous of the Gulf Coastal Plain, *C. decipiens* (Cenomanian-Coniacian; p. 175-78, fig. 56) and a second, which he proposed as *C. "saginatus"* (Santonian-Maastrichtian; p.178-82, fig. 57). In contrast (p. 181-82), *C. "saginatus"* was larger, more likely to have two pairs of cusplets, and less pronounced labial face folds, "which are segmental rather than more or less continuous, intercalcating rather than bifurcating and anastomosing." *C. decipiens* was subsequently reported from multiple Late Cretaceous North American marine faunas (Cenomanian-Maastrichtian), including: Maryland (Hartstein et al., 1999); Mississippi (Manning and Dockery 1992); New Mexico (Williamson et al., 1989); and Texas (Welton and Farish, 1993).

Case and Cappetta (1997, p. 136, pl. 6, figs. 5-7) described *Cantioscyllium meyeri* from the Maastrichtian of Texas; compared to *C. decipiens*, the teeth were described as smaller, less folded with fewer cusplets and the laterals not as broad. Cappetta and Case (1999, p. 29, pl. 17, figs. 1-5) expanded *C. meyeri* to include Texas Campanian specimens; referred Meyer's (1974 unpub.) *C. "saginatus"* figured specimens (fig. 57; despite the much different text descriptions) to *C. meyeri*; reported as *C.* aff. *decipiens*, Turonian-Coniacian specimens (including Cappetta's 1973 specimens); and used *Cantioscyllium* sp. for Late Cenomanian teeth from Texas as well as some of Meyer's (1974, fig. 56a-b) *C. decipiens* examples.

The Hosta *Cantioscyllium* teeth, as included here, compare best with Meyer's *C. "saginatus"* description (*nomen nudum*) and not with the description of *C. meyeri* (s.s. Case and Cappetta 1997); therefore, they have been simply identified as *C.* sp. aff. *C. decipiens* (not *sensu* Cappetta and Case, 1999).

Cantioscyllium sp.
Fig. 5J

Referred specimen: NMMNH P-60827; singular very small (2.7 mm high) tooth.

Description: Follows the *Cantioscyllium decipiens* tooth-design, with the exception of the angular cusp and cusplets, the latter represented by a single triangular one on each shoulder.

Discussion: This small tooth appears unique with its singular angular cusplets; however, it may simply represent a near symphyseal position from a juvenile *Cantioscyllium* sp. aff. *C. decipiens*. Case and Cappetta (1997, p. 136, figs. 5-7) erected *Cantioscyllium meyeri* for small *Cantioscyllium* teeth from the Maastrichtian of Texas. They noted that compared with Herman's (1977, pl. 6) *C. decipiens* specimen suite, the teeth were smaller, the laterals less laterally expanded, the marginal cusplets less numerous and there is a reduced number of labial folds; they did not report finding *C. decipiens*. This Hosta Tongue specimen differs from *C. meyeri* by its well-defined lateral cusplets and the strength of the ornamentation.

Family HEMISCYLLIIDAE Gill, 1862
Genus *Chiloscyllium* Müller and Henle, 1837

Type species: *Scyllium plagiosum* Bennett, 1830, Recent.

Chiloscyllium sp.
Fig. 5K

Referred specimen: NMMNH P-60808; single, very small (1.3 mm high) tooth.

Description: Broad, smooth, triangular cusp, which is baso-apically elongate and relatively erect; the crown includes a single low cusplet on each side. Viewed laterally, the crown is thick, narrowing apically and lingually directed; a weak transverse carina is present. The lower labial face is broad, extending well beyond and overhanging the root (apron bifid in this specimen). Viewed basally, the root is triangular (broader labially) and concave; splayed lobes are separated by a strong, incomplete groove (hemiaulacorhizous); the central foramen opens labially and the external face of the lingual protuberance shows a small foramen.

Family incertae sedis
Genus *Cederstroemia* Siverson, 1995

Type species: *Cederstroemia triangulata* Siverson, 1995, Judith River Fm., Late Cretaceous (Campanian), Blaine Co., Montana, USA.

Diagnosis: Summarizing Siverson (1995), *Cederstroemia* teeth may be characterized by their small but robust teeth (as tall as wide in anterior positions), short cusp, oblique shoulders, lack of cusplets, well-developed apron (labial), uvula (lingual) flattened medially, and thick root (hol- or hemiaulacorhizous). Although small in a general sense, these are large when compared with other Mesozoic orectolobiformes.

Cederstroemia ziaensis, new species
Fig. 6A-E

Holotype: NMMNH P-61439.

Referred specimens: NMMNH P-60798-P-60802, P-61438-P-61439; eight small (5.0 – 7.5 mm wide) teeth, many with worn cusps or other damage.

Type Locality and Age: NMNNH locality 297, Bernalillo County, New Mexico; Hosta Tongue Member of the Point Lookout Sandstone, Santonian.

Etymology: Named in honor of the Zia people; their tribal lands are to the northeast of the type locality.

Diagnosis: *Cederstroemia* teeth differentiated from other species by a unique combination of characteristics: a subtriangular basal profile, hemiaulacorhizous root and a shoulder smoothly merging with the cusp.

Description: The holotype (Fig. 6B) has a triangular cusp, weakly inclined distally, that extends basally, forming a long, mesiodistally-compressed apron that extends to the bottom of the labial root face. The shoulders are long, smooth, merge obtusely with the cusp and extend downward to the lateral margins of the root; a complete, smooth, cutting edge is present. The labial crown-face bulges above the root, but only the apron extends beyond it. Viewed laterally, the cusp is thick, lingually directed, and extends to or just beyond the lingual margin of the root. Viewed occlusally, the tooth is asymmetrical (distal portion more elongated), the apron extends well beyond the root, the shoulders are labiolingually compressed and the crown positioned labially on the root. The root is weakly arched, moderately high, positioned lingual to the crown and the protuberance notched. Viewed basally, the root is subtriangular and mesiodistally elongated; the lobes are well splayed and lack a complete nutritive groove; a central foramen is present, positioned labial to the coalesced lobes.

In general, the cusp is thick, triangular and lingually directed with an elongated apron positioned labially beyond and extending to the base of the root. Viewed labially, the cusp is erect to distally-inclined and merges gently and obliquely with the shoulders that are high, smooth (no cusplets) and bear a strong, complete cutting edge. Viewed basally, the root is subtriangular with a notched lingual protuberance and straight labial margin. The lobes are V-shaped with a central pore that corre-
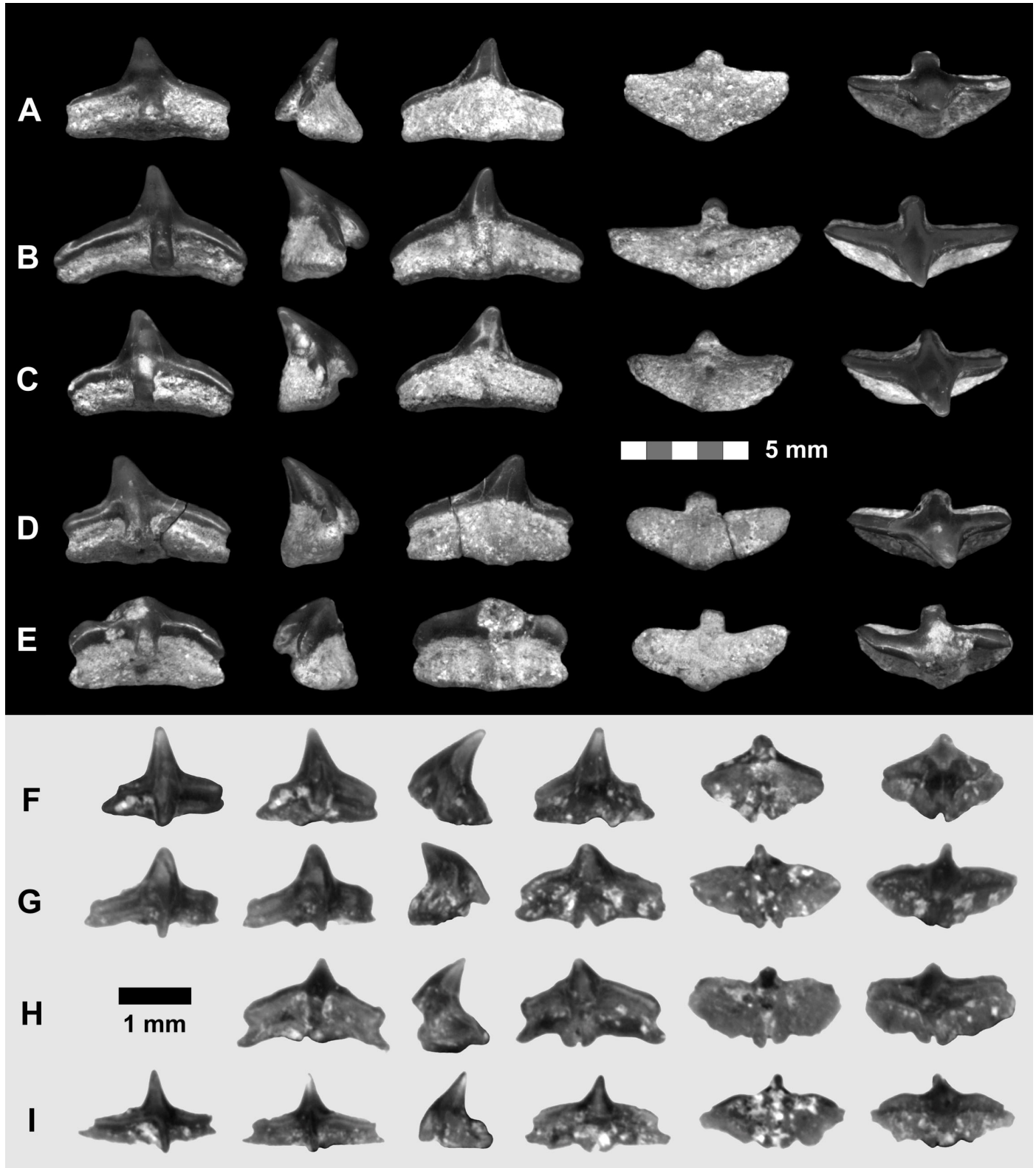
FIGURE 6. Orectolobiformes incertae sedis, from left to right, labial, lateral, lingual, basal and apical perspectives, grouped specimens similarly scaled. **A-E**, *Cederstroemia ziaensis* nov. sp. positional examples (anteriors not represented), 5 mm scale bar, **A**, NMMNH P-60798, **B**, NMMNH P-61439 (holotype), **C**, NMMNH P-61438, **D**, NMMNH P-60800, **E**, NMMNH P-60799. **F-I**, *Columbusia* sp. cf. *C. fragilis*, positional examples arranged mesiodistally, laterolabial perspective included to left for three specimens, 1 mm scale bar, **F**, NMMNH P-60796, **G**, NMMNH P-60795, **H**, NMMNH P-60797 (damaged apron) and **I**, NMMNH P-60794.

sponds with a lingual foramen visible on some specimens (hemiaulacorhizous); in no specimen is the nutritive groove open (holaulacorhizous).

Discussion: The Hosta Tongue specimens appear to only include lateral positions; there are no tall, symmetrical, mesiodistally compressed specimens that correspond with the anterior teeth as illustrated by Siverson (1995, figs. 1-2). The holotype (Fig. 6B) is a distally positioned lateral, and the other specimens are more mesially positioned.

These Santonian specimens differ from the Campanian taxa described by Siverson by including elements of each. The subtriangular profiles of these teeth correspond with *Cederstroemia triangulata* Siverson, 1995 (fig. 1, Montana) rather than the subrectangular shape of *C. nilisi* Siverson, 1995 (fig. 2, Sweden). The hemiaulacorhizous roots of all specimens are a characteristic of *C. nilisi*, but not *C. triangulata*. The cusp and mesial shoulders of lateral positions merge much more smoothly in these teeth than those of *C. triangualta* or *C. nilisi*.

Williamson et al. (1989, fig. 3f-g) reported this tooth-design from New Mexico as *Squatina* sp.; Siverson (1995, p. 975) referred their illustrated specimen to *Cederstroemia*.

Genus *Columbusia* Case et al., 2001

Type species: *Columbusia fragilis* Case et al., 2001, Eutaw Formation, Late Cretaceous (Early-Middle Santonian), Chattahoochee Co., Georgia, USA.

Remarks: Case et al. (2001) included this genus in the family Orectolobidae. We will take a more conservative approach and limit the assignment to the ordinal level only. Meyer (1974, p. 192) included similar teeth from the Santonian of Mississippi and Alabama as *Squatirhina* cf. *S. lonzeensis* Casier, 1947. Welton and Farish (1993, p. 84. fig. 1a-d) included a similar tooth-design from the Turonian of Texas as *Cretorectolobus* sp.

Columbusia sp. cf. *C. fragilis* Case et al., 2001
Fig. 6F-I

Referred specimens: NMMNH P-60794-P-60797; four very small (1.7 – 2.2 mm wide) orectolobiform teeth.

Description: In general, the cusp is thick labiolingually but narrow mesiodistally, erect and lingually directed, broadest at the level of the shoulders. The apron is elongate, reaching the base of the root, narrowing basally and projecting well forward of the labial margin of the root. The shoulders obliquely merge with the cusp; they are high and elongate with a smooth cutting edge (no cusplets) and asymmetrical in length and height (shorter and lower distally). Relative to the crown, the root is lower and wider. Viewed basally, the tooth has a wing-like appearance; both sides of the labial margins are convex with a mid-point apex. The lingual margin is more strongly convex with the apex more medially positioned. The root is broadly concave labially; lingually the root is flat with a narrow but strong nutritive groove (holaulacorhizous). There is a margino-lingual depression resulting in a distinct protuberance of the lobes adjacent to the nutritive groove. Positionally, anterior teeth tend to have conical, more robust cusps and less broad but more concave roots; posteriorly, the cusps are narrower (mesiodistally compressed) and the roots more elongate and flatter.

Discussion: These teeth are reminiscent of, but different than, described species of both *Cederstroemia* and *Cretorectolobus* (as emended by Siverson, 1995, p. 978); *Cederstroemia* has much higher roots and *Cretorectolobus*, cuspidate shoulders and a hemiaulacorhizous root. *Columbusia* can be differentiated from *Parasquatina* by the apron, which is shorter, thicker and more rounded on the latter. In *Ischyrhiza*, there is no elongate apron, only a broad thick visor.

The Hosta Tongue teeth do compare well with the specimens illustrated by Case et al. (2001, pl. 2, figs. 32-36) from the Santonian of Georgia. NMMNH P-60794 (Fig. 6I) is comparable with their holotype (pl. 2, figs. 32-34) and NMMNH P-60797 (Fig. 6H) with the paratype (pl. 2, figs. 35-36).

Order LAMNIFORMES Berg, 1958
Family ANACORACIDAE Casier, 1947

Remarks: The genus *Squalicorax* Whitley, 1939, has historically been used to encompass taxa with a wide range of tooth morphologies. Additional genera were erected by Glikman and Shvazhaite (1971), but these were poorly defined and not considered valid by Cappetta (1987, p. 109-110). Despite recognizing the presence of several distinct morphological groups, the conservative use of *Squalicorax* was continued by Siverson et al. (2007) when describing the Albian taxa *S. pawpawensis* and *S. priscoserratus*. Shimada (2008) followed similar conservative usage when describing *S. microserratodon* (Coniacian-Santonian, Kansas).

Based on a number of shared characteristics, Underwood and Cumbaa (2010) reintroduced *Palaeoanacorax* and included *P. microserratodon*, *P. pawpawensis*, *P. primulus* (Müller and Diedrich, 1991), *P. priscoserratus* and *P. volgensis* Glikman, in Glikman and Shvazhaite, 1971, and suggested that the genus *Eoanacorax* Glikman and Shvazhaite, 1971, was also likely to be valid. *Palaeoanacorax* certainly appears to be a valid genus, but the species (beyond *P. volgensis*) that should be included will be debated; Siverson et al. (2007) described differences between *S. pawpawensis* and *S. priscoserratus* that appear to be above the species level.

In addition to teeth commonly attributed to *Squalicorax kaupi* Agassiz, 1843, or *S. falcatus* Agassiz, 1843, the current study recognizes teeth from the Hosta Tongue that share morphological features with species previously considered to be referable to both *Palaeoanacorax* and *Eoanacorax*, but differ from both in possessing serrated teeth forming a tearing dentition with well-defined monognathic heterodonty.

Genus *Scindocorax*, new genus

Etymology: Named for its tearing dentition: *scindo* (Latin) – tear and *corax* (Latin) – raven (Agassiz's original genus name).

Type species: *Scindocorax novimexicanus*, new genus and species.

Distribution: Santonian of central New Mexico.

Diagnosis: Genus characterized by small teeth with a broad neck, smooth triangular cusp and distal heel possessing a cutting edge that may be partially or completely serrate. The dentition displays well-defined monognathic heterodonty with teeth of anterior positions having mesiodistally-compressed cusps. The root is notched, lacks a nutritive groove, bears one or more weak lingual foramina and numerous labial foramina below the crown, which bulges medially over the root. Anterior teeth possess a narrow cusp and high-lobed root. In lateral teeth the cusp is broader and more distally inclined; the lobes are high but more obtusely splayed. Lateral and most anterior positions have a distal heel meeting the cusp either acutely or obtusely. Two tooth forms, gracile and robust, are described here and are currently interpreted as representing the same species; the designated holotype and paratypes are of the gracile variety. These differ, with the teeth of the gracile form having narrower cusps and thinner overall than the robust form.

Included species: Only the type species.

Remarks: There are two forms of *Scindocorax* n. gen. teeth present in the fauna; a common gracile variation (Form 1) and a less common, more robust design (Form 2). They will be described separately. Eighty-four specimens were deemed to belong to this new genus of which the better examples (n = 41) were cleaned and imaged; only these imaged specimens are included below.

Scindocorax novimexicanus, new species
Figs. 7-8

Holotype: NMMNH P-60858 (Fig. 8D), lateroposterior tooth.

Paratypes: NMMNH P-60840 (Fig. 8B), lateroposterior tooth and NMMNH P-60842 (Fig. 7C), anterior tooth.

Referred specimens: NMMNH P-60838-P-60858, P-60860-P-60873; 33 teeth in fair to good condition, ranging from 3.0 to 6.7 mm in height and 2.2 to 5.7 mm in width.

Type Locality: Hosta Tongue, Point Lookout Sandstone; Rio Puerco, Bernalillo County, New Mexico.

Age: Santonian.

Etymology: Named for the state of New Mexico.

Diagnosis: Same as for the genus.

Description: The holotype (Fig. 8D) is a lateral tooth with a well-preserved root measuring (H x W) 5.0 x 5.5 mm. The cusp has a distally-directed subtriangular cusp with an un-notched distal heel. The distal edge is slightly concave, and the convex mesial edge terminates at the mesial margin of the root. The cutting edge is serrate, but serrations do not extend to the apex; those on the lower portion of the mesial edge are larger than those on the distal edge. The crown faces are smooth, the neck is broad and the lower labial face extends beyond the root. In lateral profile, the tooth is straight, the lingual face convex, the labial flat, and the root is not offset relative to the labial cusp face. The root is somewhat high and labiolingually compressed with a weak protuberance and small central foramen. The lobes are splayed and well-defined, with the mesial lobe more elongated and the distal more erect. On the labial root face, foramina are present just below the crown and extend onto the lobes.

One paratype (Fig. 8B), a lateral measuring (H x W) 5.6 x 5.9 mm, has a distally directed triangular cusp with a well-defined (notched) distal heel and a nearly straight mesial edge terminating medial to the root. The cutting edge is serrate (homogeneous and small), although serrations extend only 80% up the cusp (possibly as a result of wear) and are slightly enlarged midway up the mesial edge. The labial and lingual crown faces are smooth with a moderately broad neck. The lower labial face extends beyond the root medially. In lateral profile, the cusp is straight with a slightly labially-directed tip and not particularly thick; the lingual face is convex and the labial flat; the root lobes are labially offset relative to the cusp face. The root is high but labiolingually compressed with a weak protuberance and lacks a nutritive groove. The lobes are splayed, well-defined and angular with the mesial much more elongated and the distal much more erect. Although not directly observable, the margin of the basal labial crown face has depressions normally associated with foramina.

A second paratype (Fig. 7C), measuring (H x W) 6.7 x 3.2 mm, is an anterior with a high, inclined, subtriangular cusp, lacking a distinct distal heel and including a complete and serrate cutting edge with small homogeneous serrations extending to the tip. The cusp is distally directed with a convex mesial and concave distal margin. In cross-section, the lingual face is strongly convex and the labial, nearly flat. The labial and lingual crown faces are smooth, the neck moderately broad and the lower labial face extends beyond the root medially. In lateral profile, the tooth is slightly lingually curved with a somewhat short and stout cusp and relatively thick root. The root has a moderate lingual protuberance with one or two foramina. The lobes are long and acutely splayed with the mesial longer than the more upright distal. Basally, the root is mesiodistally compressed and labiolingually somewhat thick with a longer mesial lobe, a characteristic associated with a lamniform LA2. Foramina could not be observed.

All teeth have a smooth subtriangular cusp that is not particularly thick with a convex lingual and relatively flat labial contour. The serrate cutting edge appears to extend 80-90% up the cusp; serrations are generally small and homogeneous (Fig. 8B); mesial serrations may be inflated or ragged (Fig. 7E) and possibly compound (NMMNH P-60845, not illustrated). The neck is smooth and quite broad; the lower labial crown face extends beyond the root. The root lacks a nutritive groove, may bear foramina on the lingual face, and when visible, a series of foramina extend from lobe to lobe below the crown.

Anterior teeth are characterized by a narrow cusp, which may or may not include a distal heel. In more mesial positions, the teeth lack a

distal heel and the cusp is slightly inclined; more distal anteriors have a cusp that is more inclined and that meets the heel obtusely. The root is labiolingually thick and mesiodistally compressed; the lobes are rather erect and poorly splayed. In one specimen (Fig. 7C), the lobes are particularly long, but it is unknown if this is the normal condition for un-damaged roots beyond that tooth position. There is a propensity for the mesial lobe to be longer and the distal more erect.

Lateral teeth are characterized by a broader, more inclined cusp, a distinct distal heel and a root that is labiolingually compressed and mesiodistally elongate. In mesolateral positions, the lobes are high and obtusely splayed; the mesial lobe is longer and the distal more erect. In distolaterals, the lobes are lower and much more splayed. The distal inclination of the cusp makes the mesial edge more convex and sometimes angular, in which case the upper and lower mesial edges may become slightly concave.

Discussion: The significant differences of cusp broadness and lobe shape, between the anterior and lateral positions, indicate disjunct monognathic heterodonty. The variations in the width and shape of cusps in various positions suggest weak to moderate dignathic heterodonty may be present. Tooth counts are likely in the range of 12 or more files per quadrant. The thick cusps, distally curved in both uppers and lowers, likely indicate a tearing functionality. No marked ontogenetic heterodonty appears to be present, but variations in cusp width suggest sexual dimorphism may be present.

If species such as *Squalicorax lindstromi* (Davis, 1890), *S. hartwellii* (Cope, 1872) and *S. yangaensis* Dartevelle and Casier, 1943 are correctly referred to *Squalicorax*, each of those taxa represent variations of a cutting dentition (*sensu* Cappetta, 1987, p. 15, text fig. 22d) and display gradational monognathic heterodonty very different from that shown by the teeth of *Scindocorax novimexicanus*. The study-set was then compared with other small anacoracid teeth reported from North America. *S. microserratodon* teeth (Coniacian-Santonian, Kansas) have low broad crowns, highly splayed roots and a narrow neck (Shimada 2008, p. 1191, fig. 3), clearly different from the above description. *S. priscoserratus* teeth (Albian, Texas) have a narrow neck and well-splayed lobes (Siverson et al., 2007, p. 941-42, text fig. 3); again, a very different tooth-design. *S. pawpawensis* teeth (Albian, Texas) have a broad neck (Siverson et al., 2007, p. 945-48, pl. 1, text fig. 2a); however, the more triangular cusp is much broader and lobes shorter in anterior positions; in lateral positions, the lobes are more splayed. *S. volgensis* teeth (Cenomanian of Russia) described and figured by Siverson (1996, p. 845, figs. 1-12) and Underwood and Cumbaa (2010, p. 932-35, fig. 5) are more similar to the tooth design of *Scindocorax novimexicanus* than other *Squalicorax* species. However, the Hosta Tongue material has higher and narrower anterior cusps and higher roots with much more elongate lobes. This study set's tooth-design is different than others previously reported for anacoracid sharks, as is the functionality of the dentition-design.

Scindocorax sp. aff. *S. novimexicanus*
Fig. 9

Referred specimens: NMMNH P-60888-P-60895; eight teeth in fair to good condition, ranging from 2.5 to 5.0 mm in height and 2.6 to 4.2 mm in width.

Description: These are small, serrate anacoracid teeth with stout subtriangular cusps that are narrower in anterior positions; the heel is short and high. The roots of anteriors and mesolaterals are high-lobed with central foramina and a series of labial foramina running from lobe to lobe. The neck is broad and the lower labial cusp face extends beyond the root.

One specimen (NMMNH P-60891, Fig. 9B), measuring (H x W) 4.9 x 3.6 mm, has been interpreted to be a distally positioned anterior. The cusp is stout, narrow, subtriangular and distally inclined; it joins the heel obtusely. The serrate cutting edge extends well up the cusp, but feeding wear precludes an assessment of the full extent (likely 80% or more). Serrations are small and homogeneous. The mesial edge is broadly
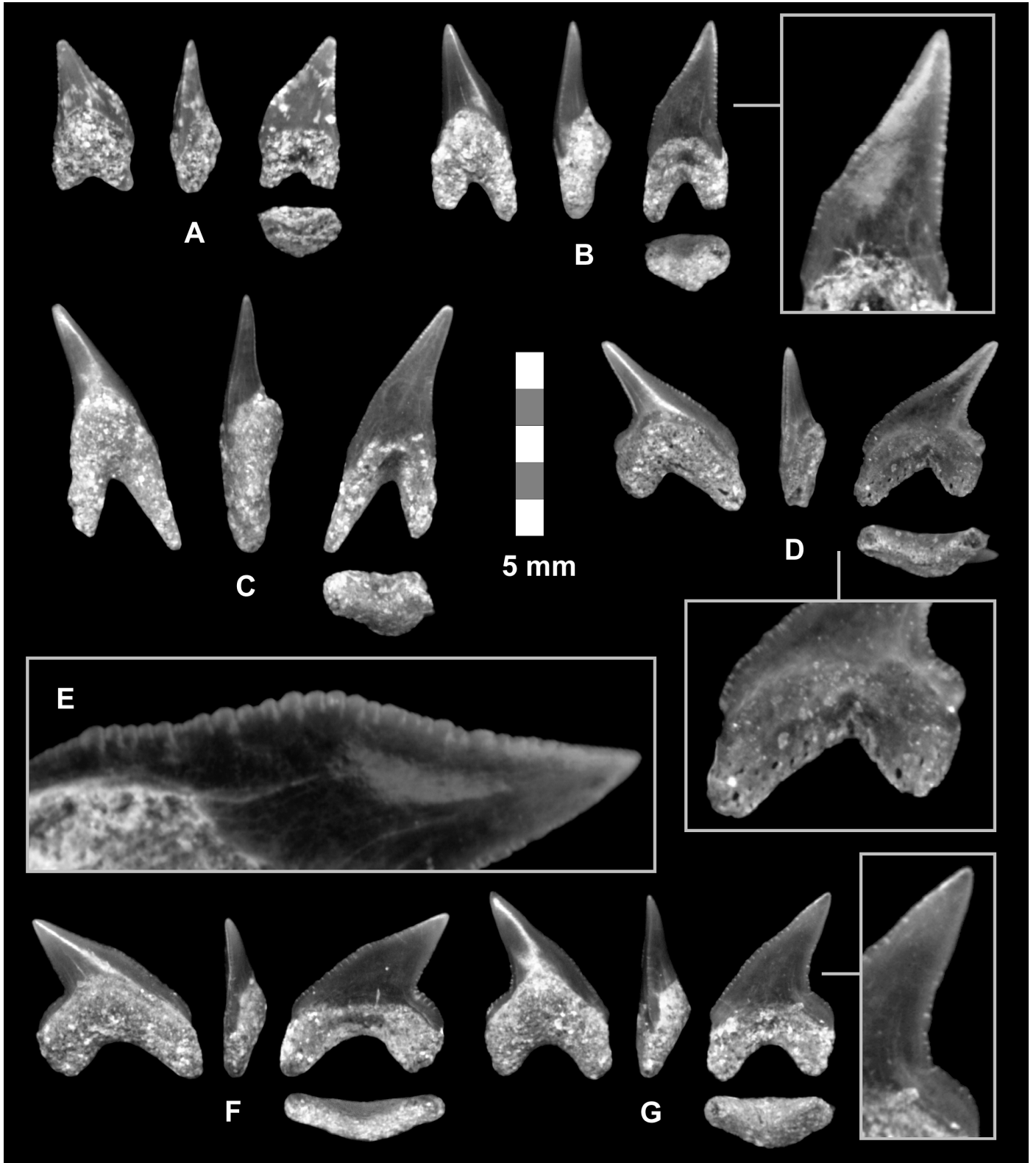
FIGURE 7. *Scindocorax novimexicanus* gen. et sp. nov., positional examples (4-perspective: lingual, lateral, labial and basal); all specimens similarly scaled, 5 mm scale bar. **A**, NMMNH P-60861, upper. **B**, NMMNH P-60849, anterior with 2x cusp enlargement. **C**, NMMNH P-60842.m (paratype), anterior. **D**, NMMNH P-60848, anterior, with 2x enlargement. **E**, NMMNH P-60866, lateral, 2x mesial cutting edge enlargement. **F**, NMMNH P-60846, lateral. **G**, NMMNH P-60843.m, anterior, 2x enlargement.
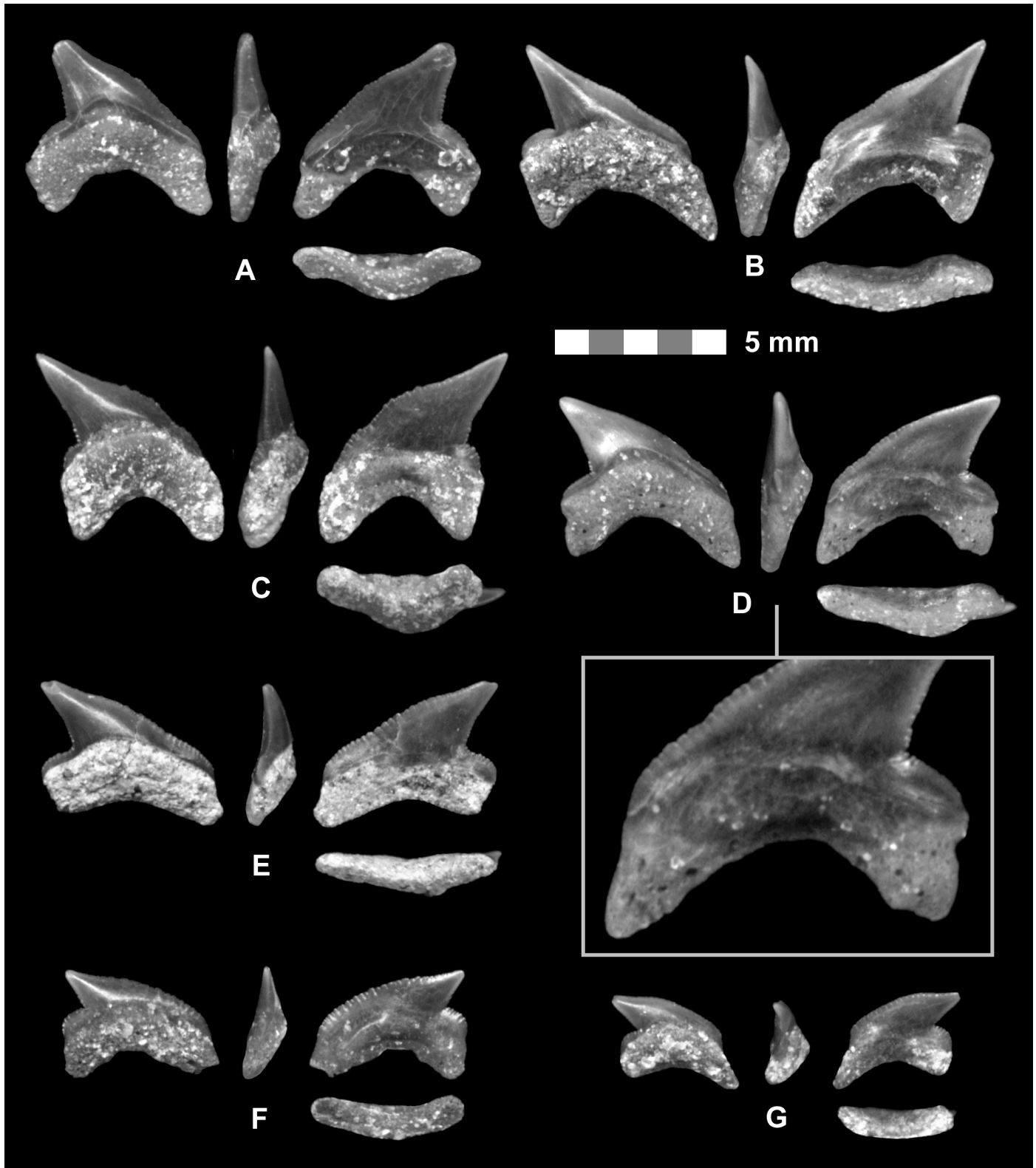
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FIGURE 8. *Scindocorax novimexicanus* gen. et sp. nov., lateral examples (4-perspective: lingual, lateral, labial and basal); all specimens similarly scaled, 5 mm scale bar. **A**, NMMNH P-60855.m, lateral. **B**, NMMNH P-60840 (paratype), lateral. **C**, NMMNH P-60841.m, lateral. **D**, NMMNH P-60858.m (holotype), lateral with 2x root enlargement. **E**, NMMNH P-60845.m, lateral. **F**, NMMNH P-60850.m, lateral. **G**, NMMNH P-60854, lateral.

convex and the distal straight. In cross-section, both faces would be convex, much more so with the lingual. The neck is broad and smooth; the lower labial face is V-shaped and extends over the root medially. Viewed laterally, the cusp is thick and lingually curved; the root is not labially offset. The root is high but not particularly thick, the protuberance fairly weak and a single central foramen is present. On the labial root face a series of foramina extends from lobe to lobe between the crown and the lower margin of the root. The lobes are long, relatively narrow and acutely splayed; the mesial is longer and the distal more erect. From a basal perspective, the shape is that of a lamniform third anterior tooth.

A second specimen (NMMNH P-60893, Fig. 9E), measuring (H x W) 4.2 x 3.3 mm, is a mesolateral from an anterior position. The cusp is broadly subtriangular, thick, distally inclined and meets the heel at nearly a right angle. The cutting edge has small homogeneous serrations that are observable 85% up the mesial edge. The distal edge is weakly concave; the mesial is convex projecting forward of the crown-root contact. In cross-section, the lingual face would be strongly convex and the labial weakly. The neck is broad; the lower labial face margin is weakly concave and projects over the root. Viewed laterally, the cusp is thick and straight; the root is not labially offset. The root is high with a moderate protuberance and a single salient central foramen. On the labial root face, foramina extend from lobe to lobe between the crown and the lower margin of the root. The lobes are high, wide and acutely splayed; the mesial is longer, and the distal more erect, with a medially-inclined distal margin.

Another specimen (NMMNH P-60890, Fig. 9D), measuring (H x W) 4.5 x 4.2 mm, is a lateroposterior. The cusp is thick, subtriangular and distally inclined with a convex mesial and concave distal edge; it joins the heel at an obtuse angle. The cutting edge is complete through the undamaged portion of the cusp (80-90%); the serrations appear to be slightly larger and less homogeneous (ragged) than the above specimens. In cross-section, the lingual face would be strongly convex and the labial less so. The neck is broad; the lower labial face margin is weakly concave and the labial bulge prominent. Viewed laterally, the cusp is thick and straight, the root is labially offset relative to the cutting edge but not to the labial face due to the strong labial overhang. The root is high with a moderate protuberance and two or three small central foramina. On the labial root face, foramina extend from lobe to lobe between the crown and the lower margin of the root. The lobes are moderately high, wide and obtusely splayed; the mesial is longer but both are similarly erect based on the lateral margins.

In general, the crown is thick and the cusp distally directed and subtriangular – narrow in anteriors and broad in lateroposteriors. Both cusp faces are convex, much more so with the lingual. A short heel is present in all but anteriormost positions, usually meeting the distal edge at an obtuse angle except in more distal positions where it is acute. The cutting edge is serrate; the serrations are small and homogeneous anteriorly, becoming slightly larger and more ragged posteriorly (Fig. 9F). The neck is broad and the lower labial margin concave, extending beyond the root face. The root is high with a moderate protuberance. One or more central foramina are present on the lingual root face; the labial face has a series of foramina extending from lobe to lobe between the crown and basal root margin. Foramina can sometimes be observed basal to the neck (Fig. 9A). The roots are high and mesiodistally compressed anteriorly, gradually becoming shorter and more elongated distally.

Discussion: Within the *Scindocorax novimexicanus* n. gen., n. sp. general tooth-design there are two morphologically different forms referred to here as *S. novimexicanus* and *S.* sp. aff *S. novimexicanus* that may represent distinct taxa or be from a single species with considerable dental variation. There are several features that favor two distinct taxa being present. Teeth of *S. novimexicanus* are much more gracile overall than those of *S.* sp. aff. *S. novimexicanus* and show rather different coronal wear with teeth of *S. novimexicanus* tending to have worn serrations, whereas *S.* sp. aff. *S. novimexicanus* teeth have much more severe apical damage, presumably as a result of different feeding strategies. The root durability also differs between forms; *S. novimexicanus* teeth had

the tendency to fragment or disintegrate during ultrasonic cleaning, whereas those of *S.* sp. aff. *S. novimexicanus* withstood longer sessions with little damage, possibly as a result of different degrees of root porosity (see Siverson et al., 2007). There is also a difference in labial foramina placement; when visible, *S. novimexicanus* teeth appear to have the foramina higher on the root than in *S.* sp. aff. *S. novimexicanus*, although the inability to fully clean the specimens may be misleading. In addition, *S. novimexicanus* teeth outnumber those of *S.* sp. aff. *S. novimexicanus* by four to one. The differences between the two forms are unlikely to be due to ontogenetic or dignathic heterodonty as there is no consistent size difference and both forms contain teeth from a wide range of jaw positions. Gynandric heterodonty could explain many of the observed differences; the Recent taxon *Alopias supercilious* (Lowe, 1840) demonstrates that sexual dimorphism of the teeth may sometimes be significant (JB, pers. obs.). The difference in specimen counts between forms could be explained by seasonal dimorphism (Kajiura and Tricas, 1996) as seen in the Recent Atlantic Stingray, *Dasyatis sabina* (Lesueur, 1824). Based on the results from a single fauna, there is no definitive answer as to the presence of one or two species; additional observations from multiple faunas are required.

Genus *Squalicorax* Whitley, 1939

Type species: *Corax pristodontus* Agassiz, 1843, from the Maastrichtian of The Netherlands.

Diagnosis: Teeth with a smooth triangular cusp, complete serrate cutting edge and usually, a distal heel. The root is often high, notched, lacks a nutritive groove, bears one or more weak lingual medial pores and numerous labial foramina below the crown, which tends to bulge above the root.

Remarks: Williamson et al. (1989, p. 239) reported 225 *Squalicorax* teeth (NMMNH P-4014, P-4036, P-4039) from NMMNH location 297 and attributed all to *S. kaupi* (Agassiz, 1843). A review of this original material (KW) revealed that 188 specimens were in sufficiently good condition to be tentatively attributed to various *Squalicorax* species as noted below.

Squalicorax sp. cf. *S. lindstromi* (Davis, 1890)
Fig. 10A-F

Referred specimens: NMMNH P-60884-P-60887, P-61447-P-61453; 11 medium-sized teeth (9 – 20 mm wide); 78 specimens from the Williamson et al. (1989) specimen groups (NMMNH P-4014, P-4036, P-4039) also conform to this tooth-design.

Description: Tooth with a serrate, triangular cusp that is distally directed, distal heel and high bilobate root. The mesial edge is convex, and its lower margin may be nearly straight. The distal edge is straight to weakly convex above the heel, which it joins obtusely in anterior positions becoming more acute distally; there is no distinct notch. Serrations are small and homogeneous, the neck is broad and the lower labial crown face bulges over the root. The root lacks a nutritive groove, and the labial root face includes multiple foramina below the crown.

Discussion: Einarsson et al. (2010) reintroduced a long-overlooked taxon, *Squalicorax lindstromi*, for a tooth-design commonly attributed to *Squalicorax kaupi*, which is here regarded as one species within a suite of similar taxa that have typically been lumped under a single name. The Hosta Tongue determination is partially based upon a comparison with a larger study-set of this tooth-design from Mississippi (Santonian, Mississippi Museum of Natural Science, JB unpublished). The Mississippi specimens compare very well with the Davis (1890, p. 412-13, pl. XLII, figs. 3-11) description and specimen suite. The Hosta Tongue teeth differ from the Mississippi specimens by having less-homogeneous serrations. Williamson et al. (1989, p. 239, figs. 2f, g) included these teeth as *S. kaupi*. This identification revision is not intended to be applicable to all North American *Squalicorax* specimens attributed to *S. kaupi*, which can only be done by a direct review of relevant material.
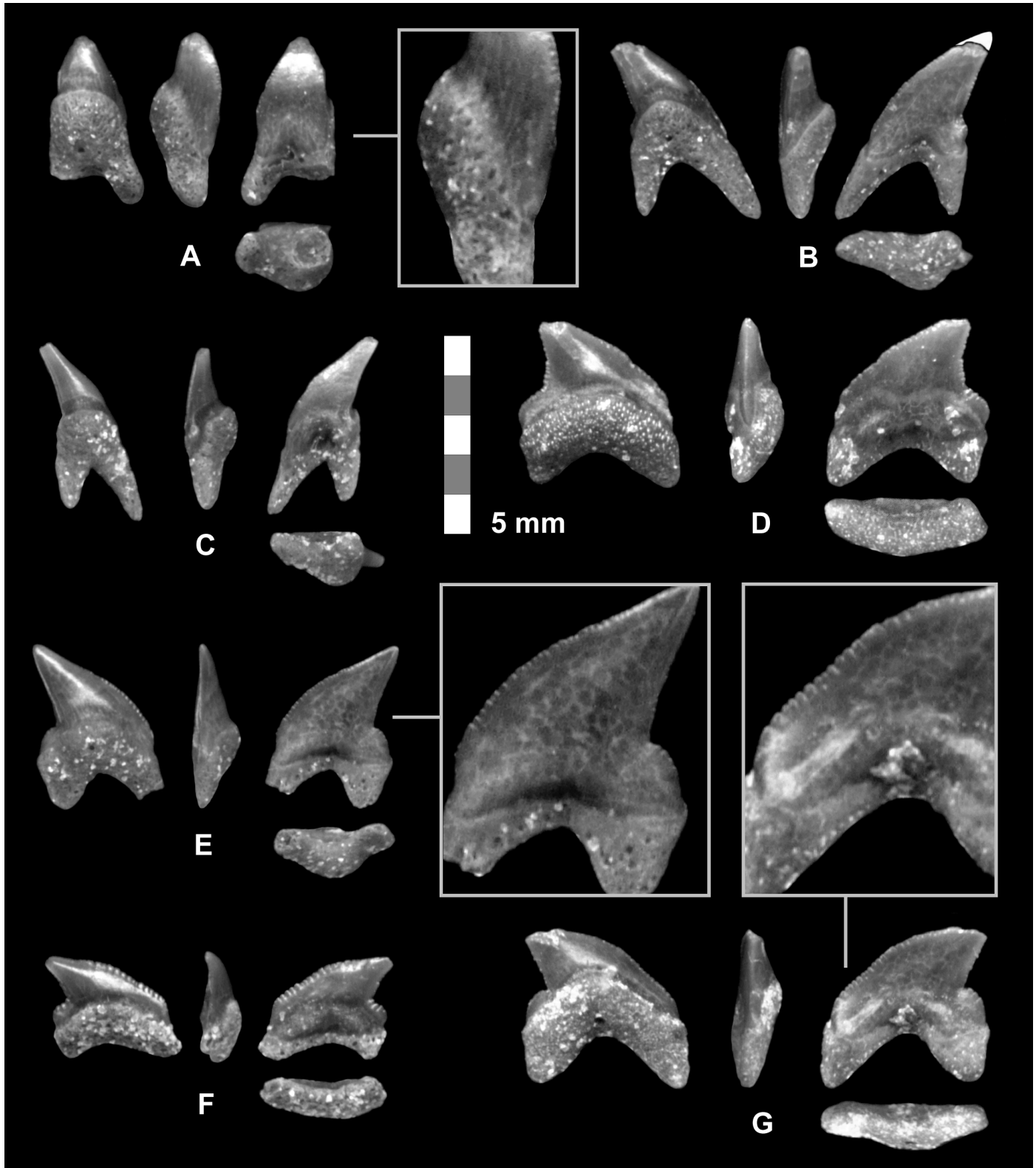
FIGURE 9. *Scindocorax* sp. aff. *S. novimexicanus* gen. et sp. nov., lateral examples (4-perspective: lingual, lateral, labial and basal); all specimens similarly scaled, 5 mm scale bar. **A**, NMMNH P-60895, anterior, with 2x enlargement. **B**, NMMNH P-60891, anterior. **C**, NMMNH P-60892, anterior. **D**, NMMNH P-60890.m, lateral. **E**, NMMNH P-60893, anterolateral with 2x enlargement. **F**, NMMNH P-60889, lateral. **G**, NMMNH P-60888.m, lateral, with 2x enlargement.

Squalicorax sp. aff. *S. yangaensis* (Dartevelle and Casier, 1943)
Figs. 10G-H, 11A-G

Referred specimens: NMMNH P-60875-P-60882, P-61440-P-61447; 15 medium-sized teeth (8 – 20 mm wide); 110 specimens from the Williamson et al. (1989) specimen groups (NMMNH P-4014, P-4036, P-4039) correspond with this tooth-design.

Description: *Squalicorax* teeth characterized by a concave lower part of the mesial cutting edge, which leads into a strongly convex mid-section, inflated mesial serrations, which are often complex with secondary serrations, and an elongated relatively straight distal heel usually forming an acute to near acute angle with the distal cutting edge. The root is high and bilobate, the distal lobe elongated and the labial face punctured by multiple foramina just below the crown

Discussion: The concave margin of the lower mesial edge and the inflated serrations of the middle mesial edge separate these teeth from other contemporary (Santonian-Campanian) *Squalicorax* teeth. Meyer (1974, p. 305-06) included this tooth-design as *Squalicorax* sp. aff. *S. kaupi*, however, these teeth compare better with *Squalicorax yangaensis* Dartevelle and Casier (1943, p. 96-97, pl. 1. fig 14-29) from the Upper Cretaceous of the Congo. Lacking a large sample from the Hosta Tongue, and relying solely on the Congo paper, contrasting the two is limited to generalized differences. In the New Mexico specimens, the lower mesial edge appears slightly longer and more erect than in its African counterparts. In addition, the mid-mesial serrations appear less inflated and the distal heel more elongate. These teeth differ from their Santonian (Tombigbee Sand) counterparts from Mississippi (JB unpublished) and Campanian examples from the U.S. East Coast (JB, pers. obs.) by having a longer distal heel. Wolberg and Bellis (1989) noted *S. yangaensis* in the Late Cretaceous of New Mexico, and Schwimmer (2007) suggested its presence in the southeastern U.S. In addition, these Hosta Tongue teeth differ from *Squalicorax bassanii* (Gemmellaro, 1920, p. 182-186, pl. 2, figs. 4-19) illustrations, which show a much more inflated mesial edge (projecting to the mesial root margin), much more defined lower mesial heel and less differentiated root lobes.

Family CRETOXYRHINIDAE Glikman, 1958
Genus *Cretoxyrhina* Glikman, 1958

Type species: *Oxyrhina mantelli* Agassiz, 1843 from the Late Cretaceous of England.

Cretoxyrhina mantelli (Agassiz, 1843)
Fig. 11H-I

Referred specimens: NMMNH P-61050, P-61429; two teeth, 11 and 20 mm in height.

Description: The larger specimen (Fig. 11H) has a broadly based and moderately high triangular crown that is distally inclined. The cutting edge is smooth and complete and a broad neck is present. The root lobes are obtusely splayed with rounded tips and possess a distinct lingual protuberance. There is no nutritive groove, but two small lingual foramina are present. The second specimen (Fig. 11I) has a narrower crown and more acutely splayed lobes; the mesial lobe is longer and more labiolingually compressed than the distal.

Discussion: The larger specimen is an upper lateral, and the smaller is likely to be from the third non-symphyseal file; the latter interpreted as a juvenile third anterior following Siverson (1999) or an intermediate (*sensu* Shimada, 1997b). Presumed pelagic shark material is very scarce in this assemblage.

Family EOPTOLAMNIDAE Kriwet et al., 2008

Referred specimens: NMMNH P-61036, P-61039-P-61044, P-61045-P-61049, P-61072-P-61096; 43 eoptolaminid teeth, displaying characteristics of both *Protolamna* Cappetta, 1980 and *Leptostyrax* Williston, 1900 were present in the sample. This material is currently

under study by Bourdon and Kriwet for publication elsewhere.

Family MITSUKURINIDAE Jordan, 1898
Genus *Scapanorhynchus* Woodward, 1889

Type species: *Rhinognathus lewisii* Davis, 1887, Late Santonian, Late Cretaceous, Sahel Alma, Lebanon.

Remarks: North American teeth of this genus were first depicted by Morton (1834, p. 31, pl. 11, fig. 2 and possibly 3 and 11) as *Lamna contortidens* Agassiz, 1833, but the location/horizon (likely Cretaceous of Alabama) and tooth characteristics were not fully documented. Morton (1835, p. 276, pl. XI) noted that Mantell had showed his 1834 figures to Agassiz, who identified one (pl. XI.11) as *Lamna acuminata* Agassiz, 1833 and two others (pl. XI.2, 3) as *Lamna plicata* Agassiz, 1833. Agassiz (1843) would go on to erect *Lamna raphiodon* based on a group of isolated anterior cusps from the Chalk of Lewes (Sussex, England), but included no stratigraphic detail. In 1849, Roemer (p. 52, pl. 1 fig. 7) erected *Lamna texana* (Late Cretaceous, Texas) and Gibbes (1849, pl. 26, fig. 119) reported *Lamna contortidens* (Late Cretaceous of New Mexico) for this general tooth-design. Unfortunately, these early American reports were based on the first anterior tooth position, which is the most ambiguous (least diagnostic) within the genus. Woodward (1889) erected *Scapanorhynchus* and designated *Rhinognathus lewisii* Davis, 1887, which is known from whole skeletons from the Santonian of Lebanon, as the type species. Williston (1900, p. 40) synonymized all reported American material with *Scapanorhynchus raphiodon*.

Woodward (1911, pl. 44, figs. 15, 17) and Herman (1977, pl. 7, figs. 1a-i) reported their interpretation of the *Scapanorhynchus raphiodon* tooth morphology using better-preserved specimens. Based on short basal labial folds, Meyer (1974, p. 227-230) separated NA *Scapanorhynchus* teeth into *S.* ?*raphiodon* (Coniacian and older) and *S.* ?*texanus* (Santonian and younger). Cappetta and Case (1975a) documented multiple positions of *S. texanus* from the Late Cretaceous of New Jersey. When describing *Scapanorhynchus perssoni* Siverson (1992, p. 542) noted, "I compare the teeth of *S. perssoni* sp. nov. with those figured by Herman (1977) as *S. raphiodon*, hoping that his specimens belong to the same species as the poorly preserved teeth figured by Agassiz." Cappetta and Case (1999), when reporting on selachians from the Late Cretaceous of Texas, included: *S.* aff. *S. praeraphiodon* Sokolov, 1978 (Cenomanian), *S.* cf. *S. raphiodon* (Turonian - Coniacian) and *S. texanus* (Campanian). Recent American reports tend to have *Scapanorhynchus* teeth separated chronologically into one of two species, *S. raphiodon* or *S. texanus*, with a preference for applying *S. raphiodon* to Santonian records (Williamson et al., 1989; Case et al., 2001). Glikman (1980, p. 119) proposed the genus *Raphiodus* for teeth attributed to *S. texanus*, to acknowledge their difference from *Scapanorhynchus lewisii*; Cappetta (1987, p. 92) rejected this notion.

Siverson (pers. commun. to JB, 2007) believes that *S. raphiodon* should be deemed a *nomen dubium*. Herman's specimen suite was used as the comparative basis for European *S. raphiodon* teeth. There is also no intention to project these observations beyond this fauna; Hamm and Shimada (2002) discussed a partial tooth set that they identified as *S. raphiodon*, but this morphology is not present in the Hosta Tongue assemblage.

Referred specimens: NMMNH P-60896-P-61005, P-61007-P-61020, P-61023-P-61030, P-61032, P-61034, P-61430-P-61437, P-61563, P-61556, P-61559-61562; more than 3500 teeth, ranging from 3 to 49 mm in height, have been catalogued as likely *Scapanorhynchus*; 3100 of these are small teeth embedded in matrix and show little more than a folded lingual cusp face. These teeth likely represent *Scapanorhynchus puercoensis* n. sp., but only specimens cleaned of matrix have been included as such. Because more than one species is interpreted as present in the fauna, certain damaged and ambiguous specimens have not been included.
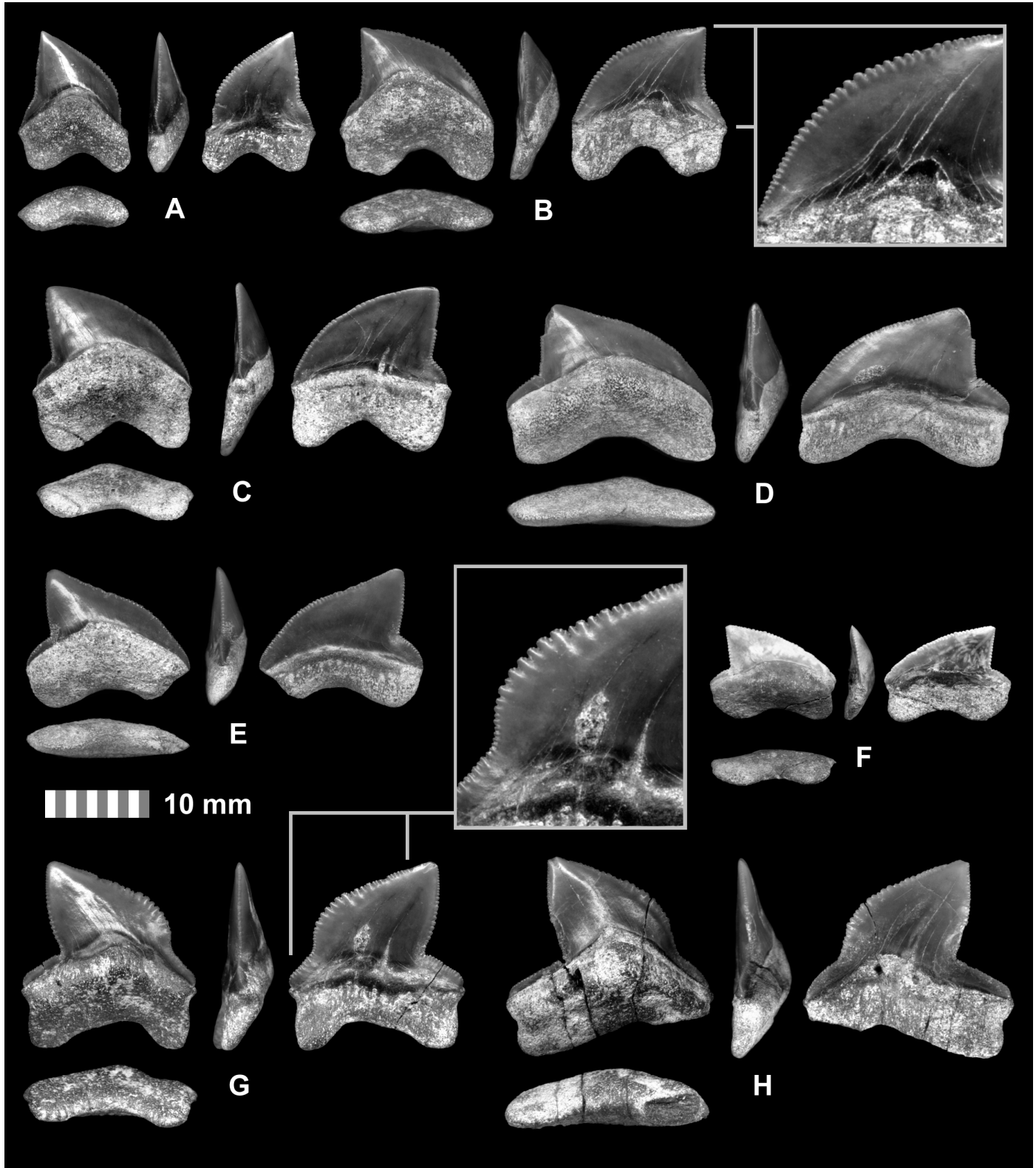
FIGURE 10. *Squalicorax* spp., all specimens similarly scaled and presented (left-right) lingual, lateral, labial and basal (below), scale bar 10 mm. **A-F**, *Squalicorax* sp. cf. *S. lindstromi* positional examples, **A**, NMMNH P-61448, **B**, NMMNH P-61449 with 2x cutting edge enlargement, **C**, NMMNH P-61452, **D**, NMMNH P-61447, **E**, NMMNH P-60884, **F**, NMMNH P-60885. **G-H**, *Squalicorax* sp. aff. *S. yangaensis* positional examples, **G**, NMMNH P-61446, with 2x enlargement of compound serrations and **H**, NMMNH P-60875.

***Scapanorhynchus puercoensis*, new species**
Figs. 12-14

Holotype: NMMNH P-60918 (Fig. 12E).

Paratypes: NMMNH P- 60965 (Fig, 13D), P-60990 (Fig. 13M).

Referred specimens: NMMNH P-60915-P-60918, P-60920-P-60923, P-60926, P-60928- P-60929, P-60931- P-60932, P-60934, P-60956-P-60999, P-60941, P-60016- P-60018, P-60020, P-61023, P-61025-P-60029, P-61034; 137 teeth prepared and 69 imaged for descriptive purposes, ranging in height from 3 to 14 mm.

Type Locality and age: NMMNH locality 297, Bernalillo County, New Mexico; Hosta Tongue Member of the Point Lookout Sandstone, Santonian

Etymology: Named for the nearby Rio Puerco.

Diagnosis: Small *Scapanorhynchus* teeth with the following features: (1) a strongly folded lingual cusp face in both anteriors and laterals; (2) a smooth labial cusp face, often bearing short parallel basal folds; (3) a single cusplet in anterior files with the laterals bearing a pair, the second highly reduced; the cusplets of the upper lateral files are not divergent, the mesial is upright to apically directed, the distal is more inclined towards the commissure; (4) a moderately broad neck; (5) a moderate lingual protuberance with a nutritive groove; and (6) lobes are long, narrow and splayed to give the basal margin a V-shape.

Description: The type specimen (NMMNH P-60918, Fig. 12E) measures 10.0 mm high by 7.5 mm wide and is an upper third anterior tooth. The cusp is subtriangular with a broad base, narrowing apically and mesially curved. Each shoulder bears a short, triangular (slightly enlarged at the base), upright cusplet that is lingually inclined; the mesial shoulder is distinctly elongate. The lingual cusp face is convex and bears 17 folds that extend three quarters up the face and tend to curve laterally; the neck is moderately broad. The labial face is weakly convex and smooth, lacking short basal folds; the basal crown margin is concave and projects beyond the root medially. The cutting edge is complete, extending to the cusplet. In profile, the crown is weakly sigmoidal with a labially-curved apex. A moderate lingual protuberance bears a nutritive groove. Root lobes are divergent and well formed, but somewhat narrow, the mesial being longer and less erect than the distal. Basally, the mesial lobe is elongate, and the distal shows a lingual curvature of the lobe tip.

One paratype (NMMNH P-60965, Fig. 13D), measures 8.1 mm high by 6.9 mm wide and is an upper mesolateral. The cusp is narrowly subtriangular with a broad base and distally inclined; the cutting edge is complete, extending to the cusplets. Each shoulder bears two cusplets, an elongate primary and a reduced lateral; the mesial primary is erect, and the distal primary is inclined, similar to the main cusp. The lingual cusp face is convex and bears 14 folds, and the medial extends 60% up the face; the neck is moderately broad. The labial face is nearly flat and smooth, lacking short basal folds; the basal crown margin is weakly concave and does not bulge over the root. In profile, the crown is slightly sigmoidal with a labially curved tip. The root is bilobate and thick, and the lingual protuberance bears a nutritive groove. Root lobes are somewhat high and broadly V-shaped, the mesial longer than the distal.

Paratype NMMNH P- 60990 (Fig. 13M) measures 8.2 mm high by 6.7 mm wide and is interpreted as a lower left mesolateral and described as from the left-hand quadrant. The cusp is subtriangular with a broad base; it is nearly erect with a mesial recurvature of the distal edge. The cutting edge is complete, extending to the cusplets. Each shoulder bears two moderately divergent cusplets, an elongate primary and a reduced lateral. The lingual cusp face is convex, bears approximately 12 folds and the medial extends 60% up the face; the neck is moderately broad. The labial face is nearly flat, smooth and lacks short basal folds; the basal crown margin is concave and extends over the root medially. In profile, the crown is somewhat sigmoidal and slightly lingually directed. The root is bilobate and thick; the lingual protuberance bears a nutritive groove. Root lobes are moderately high and V-shaped, the mesial longer than the distal.

All teeth are small (up to 1.4 cm high) and have a lingual face that is folded but not densely (approximately 12-18 on anteriors); these folds extend about 80% on anteriors and 65% on lateroposteriors up the cusp face. The labial face is smooth on anteriors, but nearly 50% of the lateroposteriors show very short basal folds. All positions have cusplets except those interpreted as parasymphyseal, LA0 (may or may not) and LA1 (single example without). The neck is medium wide and shows no evidence of ridges. The protuberance is rather prominent, particularly in the anteriors, and bears a nutritive groove. The lobes are long, rather narrow and splayed to form a V-shaped basal margin.

Anterior teeth (Fig. 12) have tall, erect to slightly inclined cusps and a slender to subtriangular cusplet (positionally and ontogenetically dependent, see A2 and A3 variations: Fig. 12C -E, and Fig. 12K-L) on each side; (one specimen had two cusplets). Viewed laterally, the LA0 is lingually directed, the A1 sigmoidal, the upper A2 and A3 rather straight with a labially curved tip and the lower A2 and A3 lingually curved. The root is labiolingually thicker anteriorly and mesiodistally elongate posteriorly. In the second and third positions, the mesial lobe is longer than the distal, more so in the third. Roots are thicker and the lobes longer in lower teeth.

In most lateroposterior positions (Figs. 13A, C-O), the cusps are elongate and subtriangular; the primary cusplet is large and erect and the secondary greatly reduced; the mesial lobe is longer and narrower than the distal. In upper laterals, the cusp is distally inclined with a cutting edge that extends to the cusplets. In profile, the cusp is straight with a slight labial curvature of the tip. In lower files, the cusps are more erect, the cutting edge stops before the cusplet, and the mesial cusplets tend to be erect, whereas the distals are more inclined.

Small teeth (Figs. 12F-H) interpreted as intermediates (sensu Siverson, 1999) are similar to the anteriors and mesolaterals but differentiated by their low crown (relative to root size) and a root that is labiolingually expanded and mesiodistally compressed with a broad, flat basal face. Very small, mesiodistally-compressed teeth of this taxon with coalesced roots, which are very high relative to crown, have been deemed parasymphyseals (Fig. 12A). The lingual face is folded, there are no cusplets and the root is labiolingually compressed.

As interpreted, anterior teeth number three uppers and four lowers. Insufficient lateroposteriors in good condition were available to establish tooth counts for these hollows. At least six or seven upper mesolaterals are present as are four, but probably more, distolaterals. Heterodonty is disjunct monognathic and dignathic; and ontogenetic variation within the selected material is largely limited to cusplet shape. Functionality can best be described as tearing-clutching, in the fashion of the Recent *Odontaspis ferox* (Risso, 1810); however, Cappetta (1987, p. 16, fig. 22b) refers to this as simply a tearing-type.

Discussion: Several aspects of these teeth require more detailed comment:

Artificial tooth set: Although it is not possible to determine the actual dentition design of *Scapanorhynchus puercoensis*, n. sp., from the prepared material, positional examples present do permit speculation on a tooth set reconstruction. Two significantly reduced tooth-designs are present: one (Fig. 12I) with well-differentiated lobes and a lingual curvature, was interpreted as a lower anterior, and the second (Fig. 12A), with very high and coalesced lobes and a labially recurved tip, an upper parasymphyseal. Placement of a single specimen as an upper parasymphyseal should not be interpreted as limiting parasymphyseal teeth to the upper jaw or that only a single file was present; it only indicates that the particular specimen was likely an upper parasymphyseal. Teeth were grouped on the basis of crown and root morphology and arranged. The general dentition-design of *S. texanus* (JB, unpublished) and that of *Mitsukurina owstoni* (Shimada, 2005; JB, pers. obs.) were used during final tooth set reconstruction (Fig. 14). Once relative placement was established, positional examples could then be re-scaled to harmonize root size and cusp width. Interestingly, the final product appears closer to that of *S. lewisii* than that of *S. texanus* or
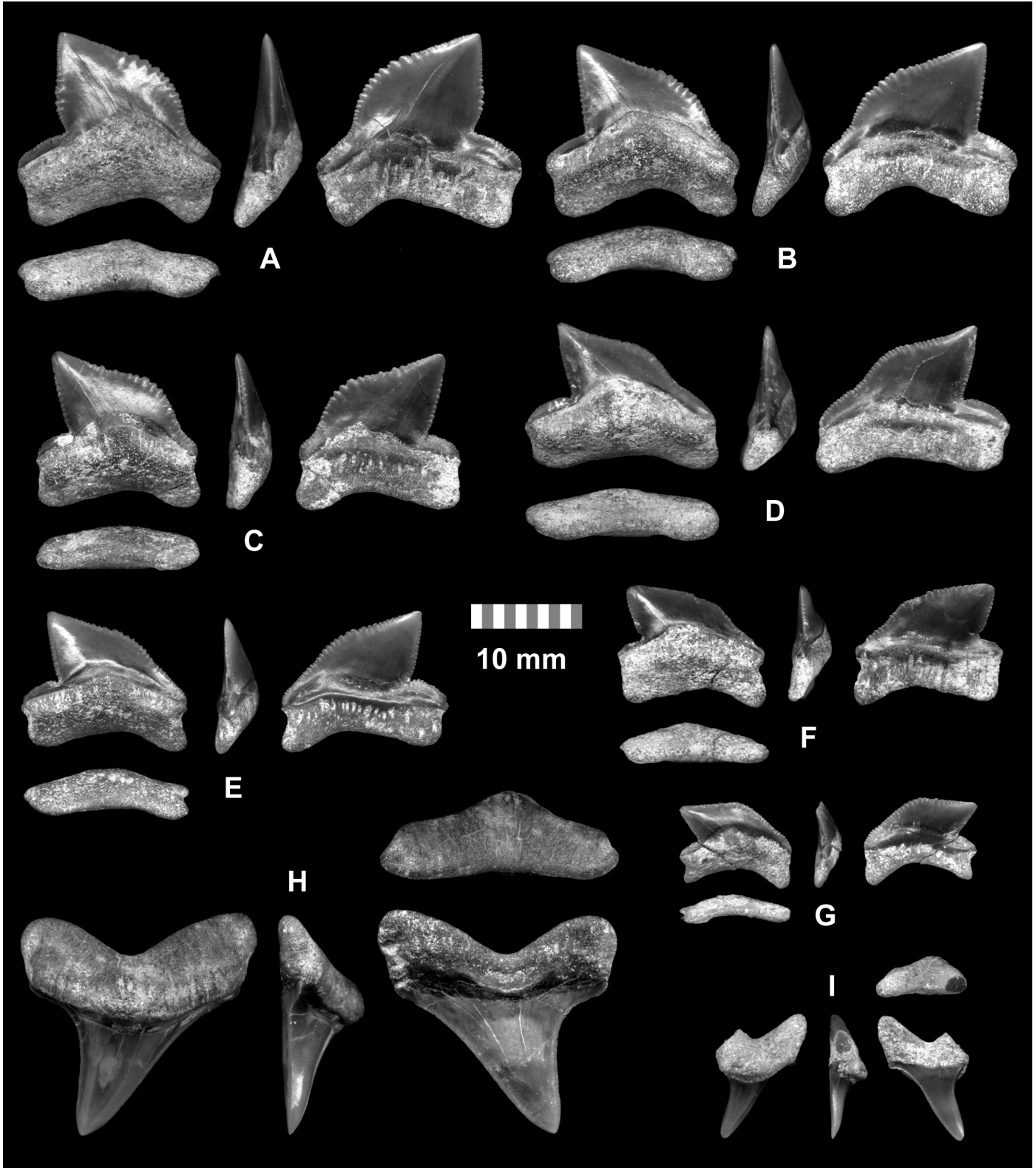
FIGURE 11. *Squalicorax* and *Cretoxyrhina* teeth, all specimens similarly scaled and presented (left-right) lingual, lateral, labial and basal (below or above), scale bar 10 mm. **A-G**, *Squalicorax* cf. *S. yangaensis* positional examples, **A**, NMMNH P-61443.m, **B**, NMMNH P-61442, **C**, NMMNH P-60876, **D**, NMMNH P-61445.m, **E**, NMMNH P-61440, **F**, NMMNH P-60877.m, **G**, NMMNH P-60879. **H-I**, *Cretoxyrhina mantelli* examples, **H**, NMMNH P-61429.m and **I**, NMMNH P-61050.
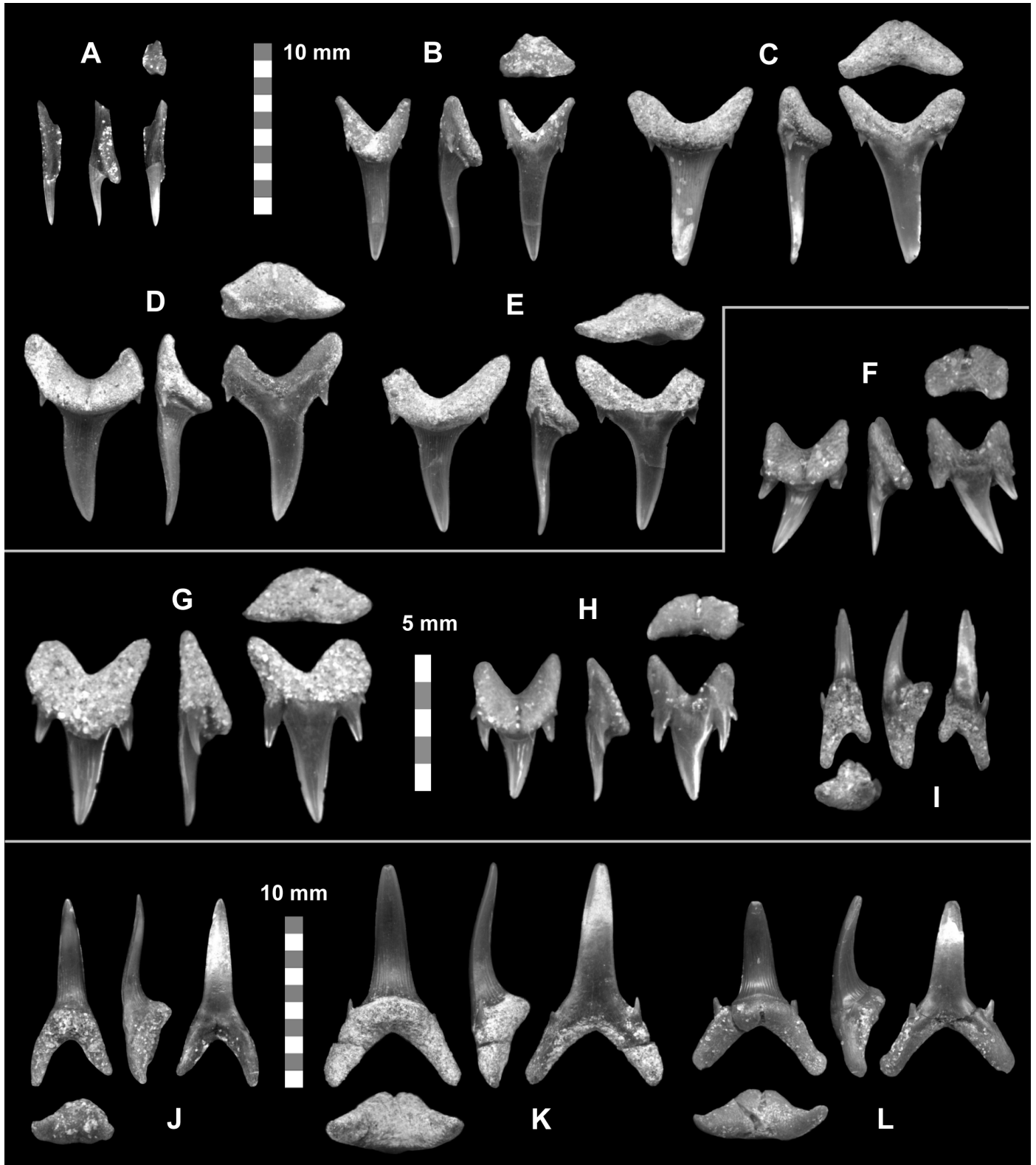
FIGURE 12. *Scapanorhynchus puercoensis* n. sp., four perspectives (lingual, lateral, labial and/or basal), specimens similarly-scaled within groups. **A-E**, Upper anterior teeth, 10 mm scale bar, **A**, NMMNH P-60934, parasymphyseal, **B**, NMMNH P-60929.m, A1, **C**, NMMNH P-60928, UA2, **D**, NMMNH P-60920.m, UA3, **E**, NMMNH P-60918, UA3 (holotype). **F-H**, Intermediate teeth, 5 mm scale bar, **F**, NMMNH P-61023, **G**, NMMNH P-61027, **H**, NMMNH P-61029. **I**, NMMNH P-61026, LA0, 5 mm scale bar. **J-L**, Lower anterior teeth, 10 mm scale bar, **J**, NMMNH P-60926, LA1, **K**, NMMNH P-60915.m, LA2 and **L**, NMMNH P-60932.m, LA3.
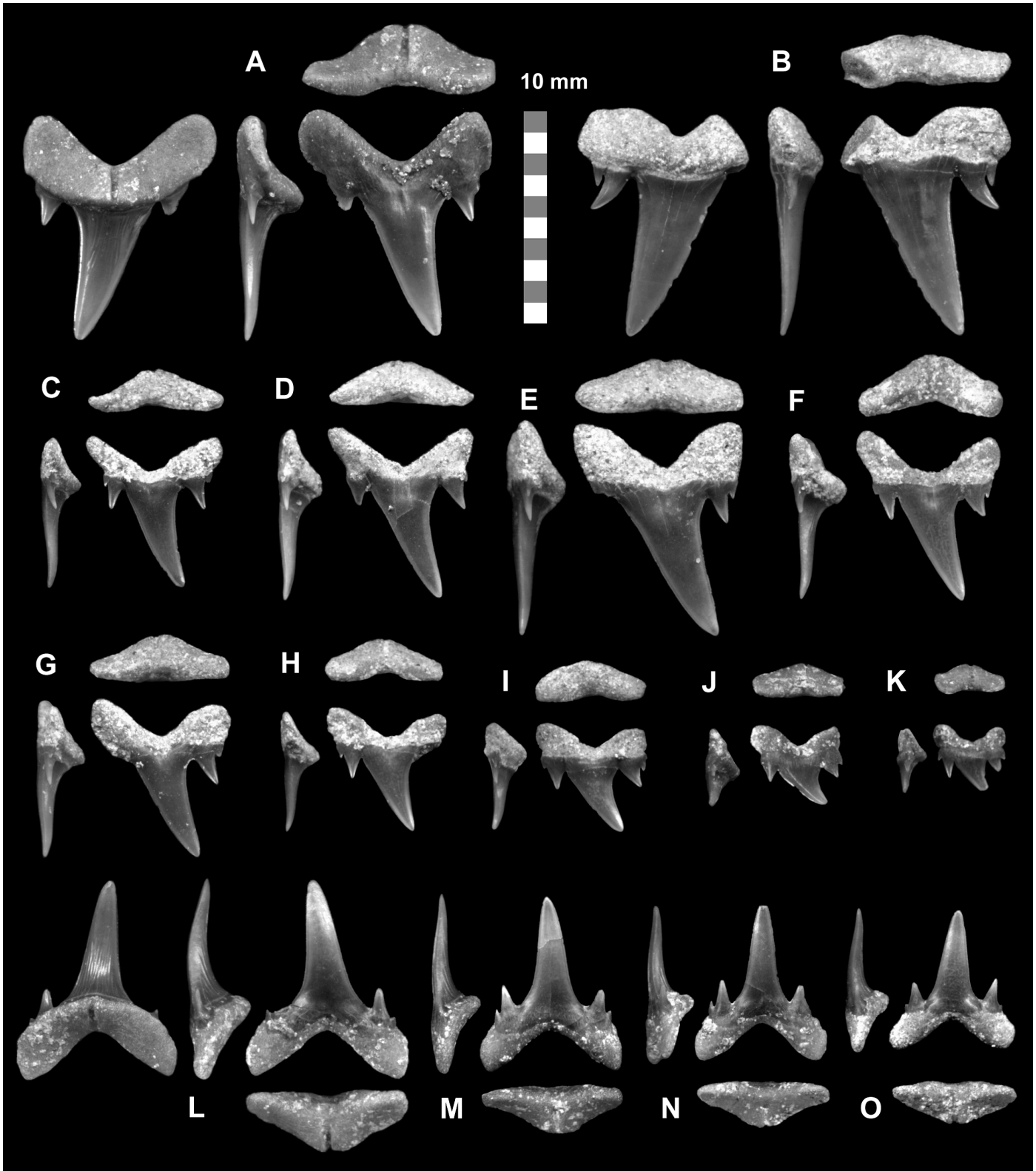
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FIGURE 13. *Scapanorhynchus* spp., lateroposterior teeth, perspectives noted from left to right, all specimens similarly scaled, 10 mm scale bar. **A-B**, mesolateral comparison, 4-perspective (labial, lateral, lingual and basal), **A**, NMMNH P-60985.m, *S. puercoensis* n. sp. upper and **B** NMMNH P-61024, *S.* sp. cf. *S. texanus* upper. **C-K**, *S. puercoensis* n. sp. upper lateroposterior examples, 3-perspective, oriented as upper LH files from front to rear, **C**, NMMNH P-60968.m, **D**, NMMNH P-60965.m (paratype), **E**, NMMNH P-60988.m, **F**, NMMNH P-60957.m, **G**, NMMNH P-60976, **H**, NMMNH P-60992, **I**, NMMNH P-60994, **J**, NMMNH P-60982.m and **K**, NMMNH P-60999.m. **L-O**, *S. puercoensis* lower lateroposterior examples, 3 or 4-perspective, **L**, NMMNH P-60970, **M**, NMMNH P-60990 (paratype), **N**, NMMNH P-60979 and **O**, NMMNH P-60991.
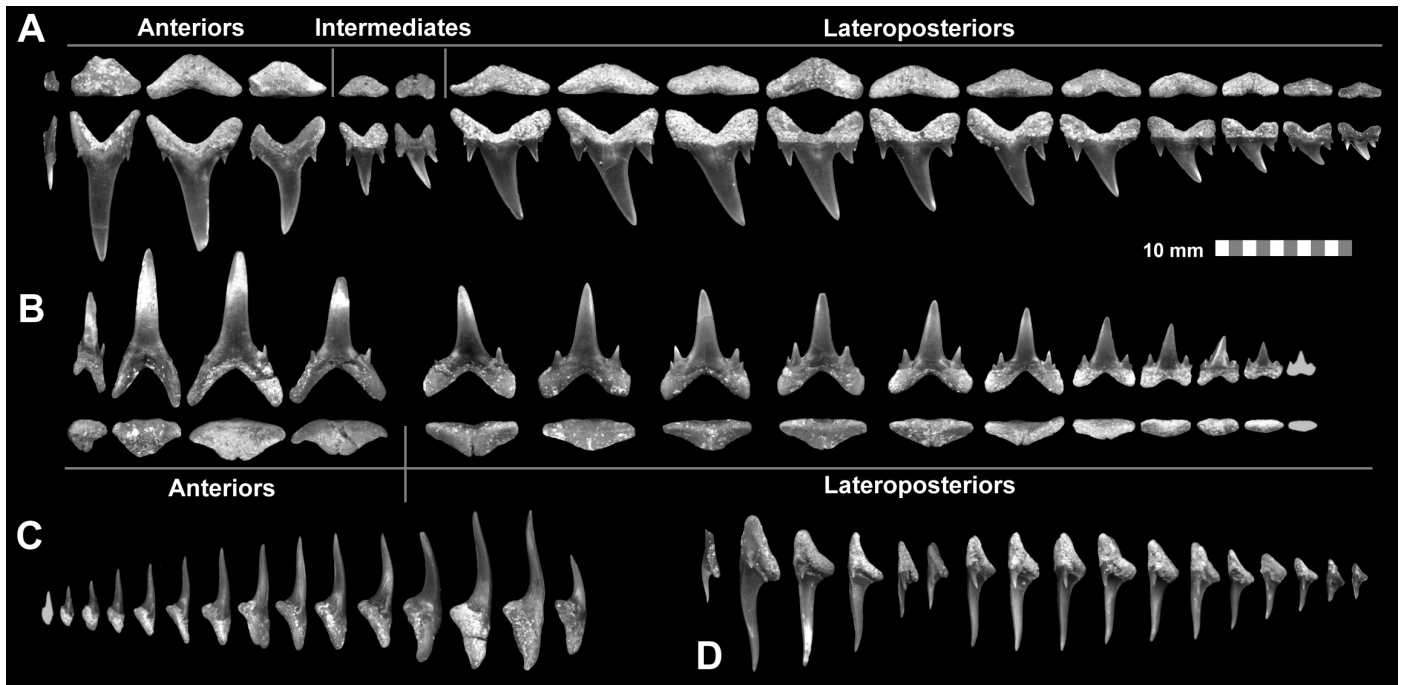
FIGURE 14. *Scapanorhynchus puercoensis* n. sp., hypothetical tooth set reconstruction, re-scaling employed (see Appendix 1), 10 mm scale bar. **A**, Teeth positioned as upper left-hand files, labial and basal perspectives. **B**, Teeth positioned as lower left-hand files, labial and basal perspectives. **C**, Lower files, positioned from right to left, lateral perspective. **D**, Upper files, positioned from left to right, lateral perspective.

M. owstoni. The specimens and their metrics, used in this reconstruction, are summarized in Appendix 1

Body size: Shimada and Seigel (2005) proposed a set of algorithms to estimate mitsukurinid body lengths based on crown height. One author (JB) tested these on two extant tooth sets and found them to be relatively predictive. Although cusp height often is variable among individuals, there may be a reasonable correlation within *M. owstoni*, detailed in Appendix 1. Applying these algorithms to *S. puercoensis*, n. sp., the artificial tooth set would represent a 70-75 cm long shark. With that said, the teeth from the anterior hollows (particularly the lower) were proportionately much different from those seen in the extant taxon, suggesting a different hollow-design. Based on different habitats (shallow versus deep water) this algorithm may apply better to *S. lewisii* than *S. puercoensis*, n. sp. or other fossil members of the family.

Ontogenetic stage: Teeth included as *S. puercoensis* n. sp. represent a small size range (anteriors 9.0-14.0 mm in height); although there is no continuity of development represented, those larger anterior teeth (20-23.5 mm) included as *Scapanorhynchus ? puercoensis* (Fig. 15A-C) display very similar characteristics (i.e., the V-shaped roots of NMMNH P-61431). It is our hypothesis that *S. puercoensis* n. sp. represents juvenile teeth, likely in their nursery area, and those included as *S. ?puercoensis* n. sp. are adult examples.

Comparisons: The tooth and positional designs are most similar to that erected by Davis (1887), and more fully described by Cappetta (1980a), for *Scapanorhynchus lewisii*. The Hosta Tongue teeth differ from those of *S. lewisii* on the basis of tooth-design. In *S. lewisii* (BM(NH) P-4769), the: (1) anterior teeth have more elongate cusplets; (2) upper third anterior, although mesially recurved, lacks an elongate mesial shoulder; (3) upper laterals have a single cusplet on each shoulder lacking the small accessory (secondary) cusplets; and (4) there are more lateroposterior positions - Cappetta (p. 105) observed 11 upper laterals, 9 upper posteriors, 11 lower laterals and 11 lower posteriors; this far exceeds the tooth positions identified in the Hosta Tongue specimens (upper 7+4, lower 6+4, see Appendix 1).

The teeth of the extant taxa, *Mitsukurina owstoni* Jordan, 1898, when compared with *S. puercoensis* n. sp., are more gracile with nar-

rower cusps and root lobes, lack well-defined lateral cusplets, and have lower lateroposterior teeth that are more lingually directed. In the three Recent (Taiwan) *M. owstoni* comparative tooth sets used in this study, lateroposterior files ranged from 13 to 16 uppers and 12 to 14 lowers; however, this largely appeared to have been the result of different numbers of posterior files.

Scapanorhynchus texanus teeth differ in several specific ways: (1) first and second anterior teeth rarely have cusplets; (2) the lack of intermediate teeth (*sensu* Siverson, 1999); (3) lower, broader and more rounded lobes in lateroposterior teeth; and (4) the smallest example of *S. texanus* (Fig. 13B) and the largest example of *S. puercoensis* n. sp. (Fig. 13A) are different in cusp shape and more importantly root design.

Teeth of *Scapanorhynchus raphiodon* (Agassiz, 1844; *sensu* Hamm and Shimada, 2002; Late Coniacian, Kansas) have the high splayed lobes of *S. puercoensis* n. sp., but crowns are more robust and they lack cusplets in anterior positions. In *Scapanorhynchus raphiodon* (*sensu* Herman 1977, p. 175-180, pl. 1a-i; Turonian, France) the: (1) lateral teeth have moderately broad roots and a high, U-shaped notch between lobes; (2) first anterior teeth (pl. 1a) lack cusplets; and (3) figured upper A3 (pl. 1e) has the elongated mesial shoulder seen in *S. puercoensis* n. sp., but it has two cusplets on the distal shoulder, the medial more elongate.

Scapanorhynchus ?puercoensis
Figs. 15A-E, 17B

Referred specimens: NMMNH P-60936, P-60947-P-60949, P-61005, P-61431; six teeth reaching 23.5 mm in height. An additional four teeth are likely attributable to this tooth design: NMMNH P-61001, P-61011, P-61013 and P-61020.

Description: Anterior teeth with a tall, erect, narrowly triangular cusp and a singular slender cusplet on each shoulder. The lingual face bears 13-17 well-developed folds that extend 60% up the cusp (in one instance, Fig. 15A, a fold branches apically). The enameloid of the labial face is completely smooth, lacking basal folds. The neck is medium in width, and two examples appear to be weakly ridged. The cutting edge is complete, extending across the cusplets, which are slender. Visible por-
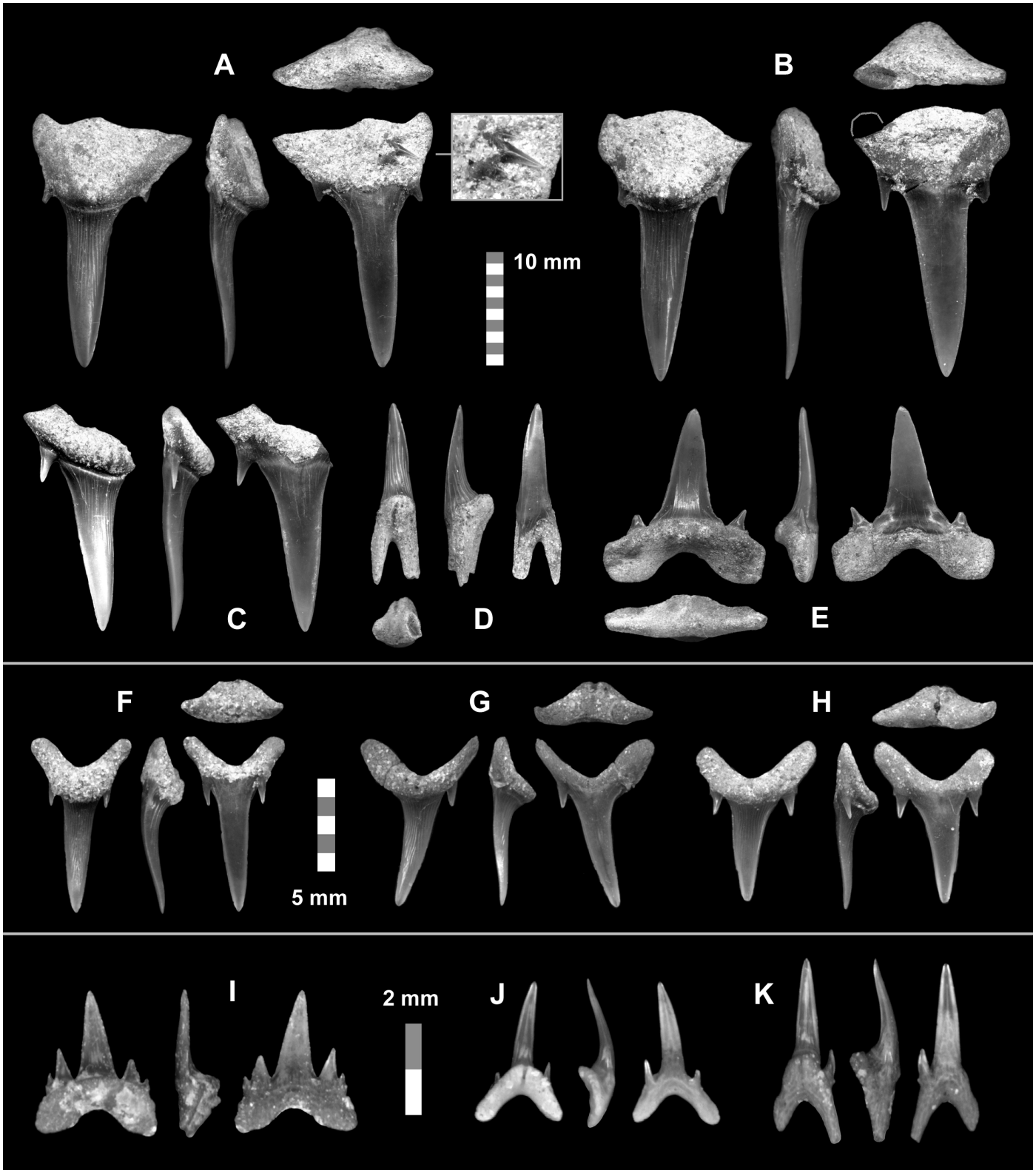
FIGURE 15. *Scapanorhynchus* specimens, all specimens similarly scaled within groups. **A-E**, *Scapanorhynchus* ?*puercoensis* n. sp., 4-perspective, 10 mm scale bar, **A**, NMMNH P-60949, anterior, intermediate in matrix, 2x enlargement, **B**, NMMNH P-60948, upper anterior, **C**, NMMNH P-60947, anterior, **D**, NMMNH P-60936, lower A0 and **E**, NMMNH P-61005, lower mesolateral. **F-H**, *Scapanorhynchus* sp. cf. *S. tenuis*, 4-perspective, 5 mm scale bar, **F**, NMMNH P-60930, anterior, **G**, NMMNH P-60927, uA?2 and **H**, NMMNH P-61019.m, UA3. **I-K**, *S.* sp. cf. *S. tenuis*, 3-perspective, 2 mm scale bar, **I**, NMMNH P-61015, lateroposterior (matrix adhering to lingual root face), **J**, NMMNH P-60924, LA and **K**, NMMNH P-60925, A1.

tions of the root suggest long, well-defined lobes; the lingual protuberance is not particularly strong and has a short nutritive groove. From a lateral perspective, the cusps are relatively thin (labiolingually) and the profile either weakly sigmoidal (Figs. 15A, C) or straight with a labially curved tip (Fig. 15B).

Represented by a single upper lateroposterior (Fig. 17B), the cusp is subtriangular with a single cusplet on each shoulder. The lingual face bears faint folds, and the labial is smooth without basal folds. The neck is smooth and of medium width; the cutting edge extends to the cusplet. In profile, the cusp is straight with a very slight labial curvature of the tip. The root is high and angular with a V-shaped basal profile; the protuberance is moderate and the nutritive groove distinct; the lobes are splayed with rectilinear tips.

The single lower lateroposterior (Fig. 15E) has a nearly erect triangular cusp and a single cusplet on each shoulder. The lingual cusp face includes 14 folds that extend 40% up the cusp; the labial face is smooth without basal folds and displays a mild basal bulge. The cutting edge extends to each cusplet, and, in profile, there is a slight lingual curvature of the cusp. The root is high, but not thick, and the protuberance moderate with a weak (eroded?) nutritive groove. The lobes are not well splayed, and the basal margin is U-shaped medially.

Discussion: Due to the perceived rarity of these teeth in the Hosta Tongue, combined with the fractured nature of many specimens, it was deemed prudent to incompletely prepare the teeth and retain some matrix on the specimens for the sake of stability, rather than further compromise the anterior teeth. Three anterior positions are represented in the group (Fig.15A-C); all three appear as greatly enlarged examples of *S. puercoensis* n. sp. anterior teeth, including the single cusplet on each shoulder. The lateroposteriors represent teeth that were not compatible with the *Scapanorhynchus texanus* specimens and displayed characteristics (primarily root shape) seen in specimens attributed to *S. puercoensis* n. sp.

There are few other examples of *Scapanorhynchus* teeth that include well-developed cusplets in anterior positions. In *Scapanorhynchus perssoni* Siverson, 1992, the cusp is thicker (labiolingually), the cusplets longer, and the lingual folds much more numerous (45-60) and extending farther up the cusp (75%); the lateroposterior cusplets of *S. perssoni* are somewhat similar but more robust.

Scapanorhynchus sp. cf. *S. tenuis* (Case et al., 2001)
Fig. 15F-K

Referred specimens: NMMNH P-60924, P-60925, P-60927, P-60930, P-61015, P-61019, P-61030; seven specimens, anterior teeth from 3.0 to 9.5 mm in height.

Description: Small teeth with a folded lingual and smooth labial cusp face; the cutting edge extends to the lateral cusplets; the neck is moderately broad and smooth. In anterior teeth, the cusp is narrow and elongate; the primary cusplets are long and narrow, and the secondary may be short or represented by a basal bulge on the lateral margins. Lingual folds become stronger, longer and more numerous as size increases; a 3 mm anterior (e.g. Fig. 15J-K) may have three or four weak folds extending a third up the cusp face, whereas a larger specimen (e.g., Fig. 15F) has 14 stronger folds extending three-quarters up the face. In profile, the cusp is thick basally; depending on jaw, either erect and weakly sigmoidal (upper) or lingually curved (lower). The lingual protuberance is moderately deep and notched; the lobes are long and narrow, becoming more obtusely splayed distally. The single lateroposterior example (Fig. 15I) has a cusp that is shorter and subtriangular, the cusplets triangular and more numerous (2 or 3) and the lower labial crown face has short basal folds. In profile, the cusp is erect and labio-lingually compressed.

Discussion: Of the Hosta Tongue teeth, the *Scapanorhynchus* sp. cf. *S. tenuis* tooth-design is most similar to the much more numerous teeth included as *S. puercoensis* n. sp. Seven teeth, otherwise similar to

S. puercoensis n. sp., could not be seamlessly placed within that tooth set (Fig. 14) and were subsequently excluded from that grouping on the basis of several differences: (1) cusplets of anterior teeth, particularly the uppers, more elongate; (2) an anterior (Fig. 15G, ?UA2) could not be placed within that tooth set; (3) the mesial shoulder of a specimen interpreted as a UA3 (Fig. 15H) is much shorter than the *S. puercoensis* n. sp. morphology (Fig. 12D,E); and (4) the single lateroposterior (Fig. 15I) has longer, more triangular cusplets.

These excluded teeth correspond with the morphology (as depicted in pl. 4, figs. 69-70, 73-74, 83-89) included by Case et al. (2001) in *Microdontaspis tenuis*; the original diagnosis was limited to, "Extremely small teeth anterior, lateral and posterior of an early sandshark." Based on the scaling provided in that paper, their Santonian specimens from the Eutaw Formation of Georgia were somewhat smaller, ranging in height from 1 to 5 mm. However, a re-examination of type material revealed errors in the enlargement factors reported in that paper and the incorrect labeling of some paratype figures. Fortunately, the holotype (Columbus State University; CSUK 97-2-8, figs. 85-87) was correctly labeled; the specimen (?LA2) measures approximately 4.2 mm in height and shows 4 or 5 folds extending nearly 50% up the lingual face. One paratype (?UA2, CSUK 97-2-9; figs. 73-74) measures nearly 7 mm and has 9-10 folds extending 60% up the face. Another paratype (CSUK 97-2-77, 3 mm in height) does not compare well with the specimen illustrated for it (figs. 69-70); the actual specimen represented in those figures (UA3) does not have a unique identifier but measures 7 mm in height and has approximately 11 folds extending 60% up the lingual cusp face.

No specimens reported from Georgia correspond with the tooth-design included here as *S. puercoensis* n. sp. Case et al. (2001) provided no rationale for considering these teeth odontaspidids; based on the similarities of *S. puercoensis* n. sp. with *S. lewisii* and "*Microdontaspis*" *tenuis* with *S. puercoensis* n. sp., the species has been moved to *Scapanorhynchus* as a mitsukurinid.

Scapanorhynchus sp. cf. *S. texanus* Roemer, 1849
Figs. 16, 17A, C-O

Referred specimens: NMMNH P-60940, P-60942-P-60946, P-60950-P-60955, P-61000, P-61002-P-61004, P-61007-P-61010, P-61012, P-61014, P-61024, P-61032, P-61430, P-61432-P-61437, P-61560, P-61556; 41 teeth up to 4.9 cm in height.

Description: In anterior teeth (Fig. 16) the lingual face is folded (3/4 up cusp, 12-20/cusp), the neck is usually not ridged (present in 3 of 14 anterior specimens) and the labial face is smooth and lacking basal folds. Cusplets are limited to the A3 position where they are singular and highly reduced; the cutting edge terminates at the base of the cusp. In profile, lower anteriors (A0-A3) are lingually directed (less so distally), and upper anteriors (A1-A3) are sigmoidal with a labial curved tip (becoming less pronounced distally). Roots are bilobate with a well-developed protuberance and nutritive groove; lobes are narrow and less splayed distally. Viewed basally, the A1 root is thick and triangular; in subsequent positions, the mesial lobe becomes more elongated and the protuberance less pronounced. No specimens were found to suggest that parasymphyseal or intermediate teeth were present.

In upper lateroposteriors (Fig. 17A, C-O), the cusp is distally inclined (in mL1-4, 78-80 degrees) and the lingual face usually smooth but may bear folds (running 40-65% up the cusp) in more mesial positions. The labial face is smooth (no basal folds in studied material) with a weak labial bulge. The cusplets are subtriangular, may be singular or include a reduced secondary; the mesial cusplet is usually erect and the distal posteriorly inclined. The neck is moderately wide, and one specimen (Fig. 17A) displays a ridged neck. The cutting edge of the cusp is complete, terminating at the cusplet. In profile, the cusp is straight with a slight labial curvature of the tip. The root is high but compressed with a weak protuberance, nutritive groove and U-shaped basal margin (medially).
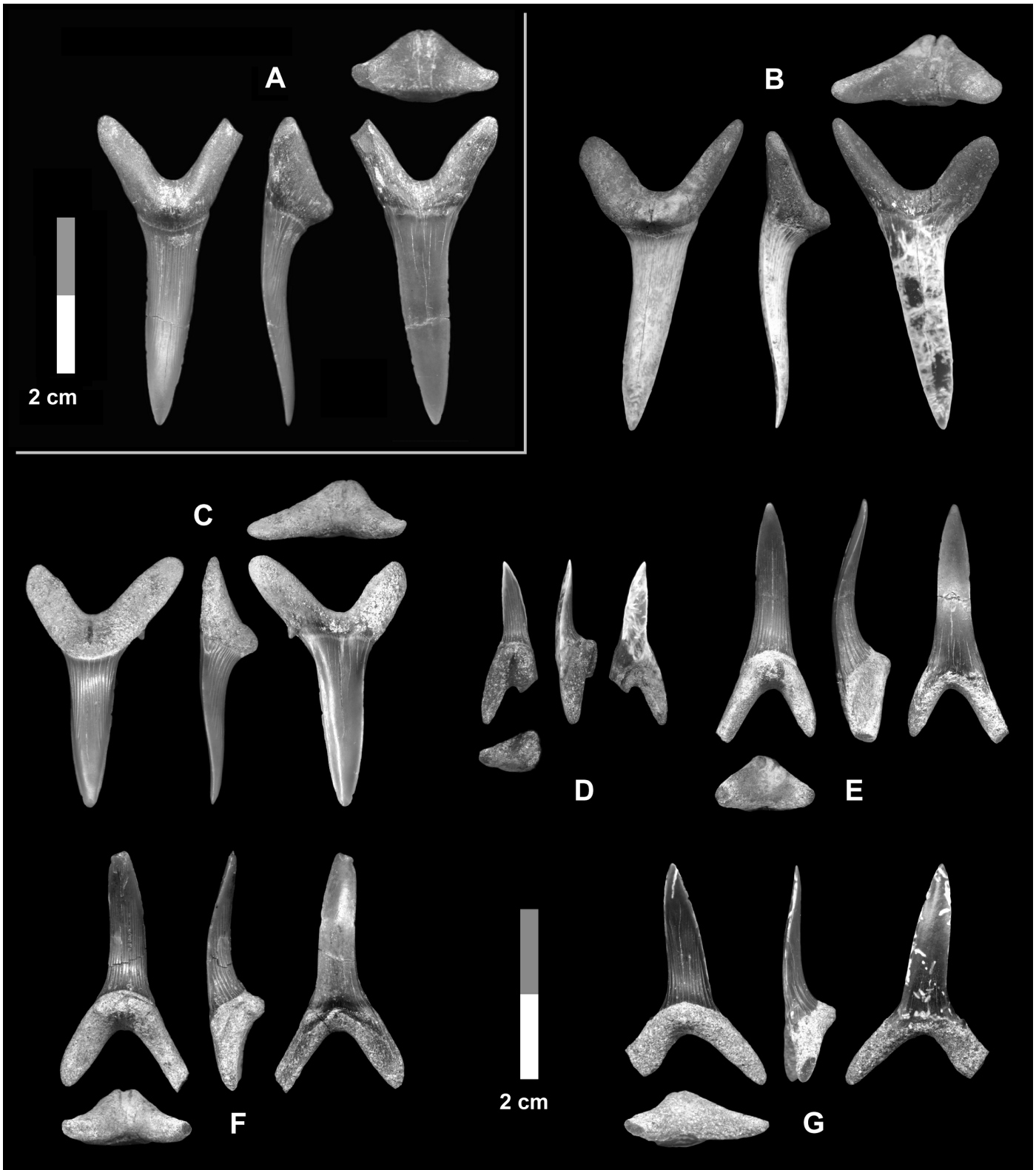
FIGURE 16. *Scapanorhynchus* sp. cf . *S. texanus*, anterior teeth, 4 perspectives (lingual, lateral, labial and basal), 2 cm scale bar. **A**, NMMNH P-61437.m, UA1, 0.92x relative to other specimens (mirrored). **B-G**, all specimens similarly scaled, **B**, NMMNH P-60951.m, UA2 (mirrored), **C**, NMMNH P-60943, UA3, **D**, NMMNH P-60944, LA0, **E**, NMMNH P-60955.m, LA1 (mirrored), **F**, NMMNH P-60953, LA2 and **G**, NMMNH P-60952, LA3.

Lower lateroposteriors are poorly represented, but the cusp is erect in mesolateral positions, and the lingual face may be smooth or folded with a medium-sized neck. The labial face is smooth, although one specimen (Fig. 17N) shows basal folds on the cusplets, and includes a moderate basal bulge. Cusplets are divergent and singular (or may have a second represented by a bulge at the lateral base). In profile, the cusp has a slight lingual curvature, although one specimen has a labially curved tip. The root has a moderate protuberance, nutritive groove and relatively low, obtusely splayed lobes.

The dentition displays disjunct monognathic and dignathic heterodonty; there are too few specimens to speculate on ontogenetic or sexual variations. The study-set included three upper and four lower anterior tooth positions without evidence of parasymphyseal (included by Cappetta and Case, 1975a, pl. II, fig. 7) or intermediate (*sensu* Siverson, 1999) teeth. Recognized upper lateroposterior positions include seven mesolaterals and four distolaterals; the actual number of files could not be determined. Functionality is deemed to have been cutting-clutching.

Discussion: As noted above and documented by Meyer (1974), it is difficult to interpret *Scapanorhynchus* teeth solely on the basis of tooth-design – positional, ontogenetic, sexual, and individual variations lead to a design-envelope so large that most *Scapanorhynchus* teeth could be viewed as belonging to one species. Meyer deemed the presence of short lower labial folds a particularly relevant characteristic in his interpretation of the genus in North America and concluded that those generally having folds might best be deemed *S.* ?*texanus* and those faunas in which they generally lack folds, *S.* ?*raphiodon*. In the Hosta Tongue fauna, most teeth lack basal folds, but two groups of teeth are still present, one with a *S. texanus*-like dentition design and a second with distinctly different anterior teeth. As with ridges on the neck, the short basal folds of the lower labial crown face appear to be an evolutionary trend within the genus and not a diagnostic characteristic of a particular species.

Excluding the propensities for a ridged neck and lower labial folds, the Hosta Tongue teeth described here agree well with *S. texanus* (*sensu* Cappetta and Case, 1975a), with anterior teeth being nearly identical. Lateral teeth show some differences in that the Campanian examples from Mississippi (JB, unpublished) include: a cusp that appears to be slightly more erect and broader in similarly-sized teeth; the distal cusp edge straighter; and cusplets that are more clearly differentiated as primary and secondary.

Using Herman (1977, pl. VII, fig. 1a-i) as a representation of *S. raphiodon* tooth morphologies, his upper A1 (fig. 1a) and upper A2 (fig. 1b) are very close to positional designs in the Hosta Tongue fauna (although interpreted differently here); however, his "upper uA4" (fig. 1c) and lower anterolateral (fig. 1e) are not present. In addition, not included in his plate were positions such as the upper A2 and upper A3, found here. Arguably, the Cenomanian teeth from Belgium might share a common lineage with *Scapanorhynchus texanus*, but there are some significant positional differences. *S. raphiodon* (*sensu* Hamm and Shimada, 2002; Late Coniacian, Kansas) significantly differs from the Hosta Tongue *S.* sp. cf. *S. texanus* teeth by its higher, more angularly splayed root lobes, particularly the lateroposteriors, and a more triangular cusp.

Family "ODONTASPIDIDAE" Müller and Henle, 1839

Remarks: In the 1970s (e.g., Meyer, 1974 and Cappetta and Case, 1975a, b), *Odontaspis* Agassiz, 1838 was the preferred generic name used for Late Cretaceous odontaspidid-like teeth in North America. Glikman (1980) erected *Eostriatolamia* for a Cretaceous odontaspidid from the Russian platform. This genus was synonymized with *Synodontaspis* White, 1931 when Cappetta (1987, p. 86-91) separated certain fossil odontaspidids s.l. into *Odontaspis* and *Synodontaspis*. Shortly after, ICZN (1987) opinion 1459 ruled in favor of *Carcharias* Rafinesque, 1810 for the large-toothed sandtigers, a judgment adopted for their fossil counterparts.

Glikman and Averianov (1998) argued that their morphometric studies showed that *Eostriatolamia* was a long-lived and widely distributed genus and, based on tooth counts, it was distinct from Recent taxa. In so doing, they expressed the opinion that certain North American taxa, including *Carcharias amonensis* (Cappetta and Case, 1975b), *Carcharias samhammeri* (Cappetta and Case, 1975a) and *Carcharias holmsdelensis* (Cappetta and Case, 1975a) might be attributable to this genus. Underwood and Cumbaa (2010, p. 916) added *E. tenuiplicatus* (Cappetta and Case, 1975b) to this list.

Underwood and Cumbaa (2010, p. 916), citing Human et al.'s (2006) molecular phylogenetic studies that argued the Recent taxa included in the Odontaspididae (*Carcharias* and *Odontaspis*) may represent more than one family, concluded that the two lineages should be grouped separately within the Late Cretaceous as *Carcharias taurus* group *sensu lato* and ?*Odontaspis ferox* group *sensu lato*. Grouping the genera as such presupposes that only two families were present, both with living members of that lineage. Few Late Cretaceous odontaspidids have been documented beyond general tooth-design, and proposed tooth sets have not been tested. This paper will follow the conservative course, grouping all as odontaspidids but acknowledging the likelihood that two or more families are represented by these teeth.

A revisionary study by Cappetta and Nolf (2005) of Paleogene odontaspidids of Europe concluded that multiple genera had been included within *Carcharias* s .l. This conclusion is likely applicable to the Late Cretaceous, where multiple odontaspidid lineages were probably present as well.

Genus *Carcharias* Rafinesque, 1810

Type species: *Carcharias taurus* Rafinesque, 1810, Recent.
Remarks: Because this assemblage includes teeth that may represent a different genus from that including *C. taurus*, this material has only been provisionally included in *Carcharias*.

"*Carcharias*" sp.
Fig. 18A-J

Referred specimens: NMMNH P-61033, P-61053-P-61061, P-61557-P-61558; 12 teeth reaching 2.3 cm in height.
Description: Anterior teeth with a tall, erect, triangular cusp that is constricted basally. The crown is completely smooth; the lingual cusp face is strongly, and the labial weakly convex; the lower labial crown margin is strongly concave. Each shoulder has a single, small, triangular cusplet; the cutting edge of the cusp terminates at the cusplet. The neck is smooth, and medium to broad in width. In profile, uppers are weakly sigmoidal; lowers are thicker and gently curved lingually. The root is thick with a strong protuberance and long nutritive groove. The lobes are thick, moderately long, splayed (acute to obtuse depending on position) and have rounded tips. One specimen (Fig. 18J) has faint basal folds on the lingual crown face and is included in the figure as ?*Carcharias* sp.

Compared with anteriors, the lateroposterior teeth have a thinner crown, a cusp that is more broadly triangular, a straighter basal labial margin with a weak bulge and a second very small cusplet present laterally. The uppers are inclined, more so distally; in profile, they are straight or labially curved. The lowers have a relatively broad, erect cusp and in profile may be straight to lingually curved.

Discussion: The lack of sufficient specimens precludes establishment of an anterior tooth formula. The nutritive groove and general positional tooth form is characteristic of a large-toothed sandtiger; however, these teeth do not compare well with other taxa described from the Late Cretaceous of North America. There are some similarities with *Carcharias* (aka *Eostriatolamia*) *amonensis*, known from a small smooth-crowned tooth from the Cenomanian of Texas and Kansas (Welton and Farish, 1993; Cappetta and Case, 1999; Everhart et al., 2005; Shimada and Martin, 2008); however, the cusplets, cusp inclination and cusp width all differ.
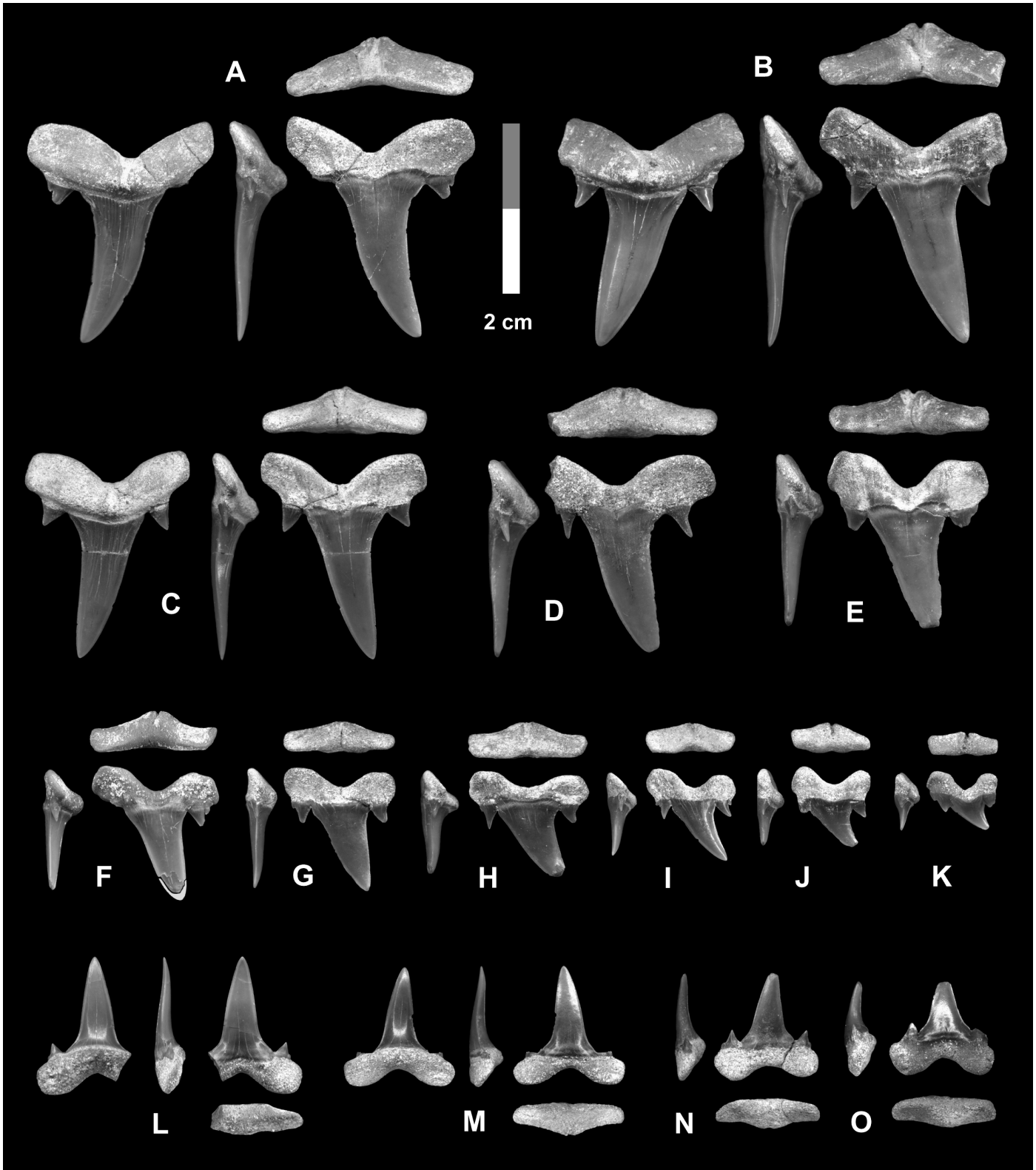
28

FIGURE 17. *Scapanorhynchus* spp. lateroposterior positional examples, 3 or 4 perspectives (lingual, lateral, labial and basal), 2 cm scale bar. **A-B**, Comparative examples - mesolaterals (four perspectives), **A**, NMMNH P-61009, *Scapanorhynchus* sp. cf. *S. texanus*, mL?2 and **B**, NMMNH P-61431.m, *Scapanorhynchus* ?*puercoensis* n. sp., mL?2. **C-K**, *S.* sp. cf. *S. texanus*, upper lateroposteriors presented from front to rear (three or four perspectives), **C**, NMMNH P-61430.m, mL1, **D**, NMMNH P-61008, mL?3, **E**, NMMNH P-61432, **F**, NMMNH P-61560, **G**, NMMNH P-61434, **H**, NMMNH P-61433, **I**, NMMNH P-61007.m, **J**, NMMNH P-61003.m and **K**, NMMNH P-61014.m. **L-O**, *S.* sp. cf. *S. texanus*, lower lateroposterior examples (3 or 4 perspectives), **L**, NMMNH P-61556.m, **M**, NMMNH P-61010, **N**, NMMNH P-61012.m and **O**, NMMNH P-61032.

Campanian odontaspidids s.l. from North America include: *Odontaspis hardingi* Cappetta and Case, 1975a, which has higher and narrower lobes, a lingual cusp face bearing strong folds and a lower labial bulge that is stronger; *Eostriatolamia holmdelensis* (Cappetta and Case, 1975a), which has a folded lingual cusp face, stronger (albeit weak) labial bulge and more gracile cusplets; and *Carcharias samhammeri* (Cappetta and Case, 1975a), which has the most similar teeth, but differs on the basis of a lower root with a more angular mesial end.

These teeth appear to represent a new and undescribed taxon or a chrono-variation of *C. samhammeri*. The available material, however, does not lend itself to properly describe the species. Teeth in good condition are from ambiguous positions (first and second anteriors) or represent a younger individual that can best be differentiated on a direct comparative basis from those of the common small *Scapanorhynchus* in the fauna. Larger, wide-crowned lateroposteriors are all significantly damaged and would make poor representative examples of the species.

Genus *Eostriatolamia* Glikman, 1980

Type species: *Lamna venusta* Leriche, 1929, from the Campanian of France.

?*Eostriatolamia* sp.
Fig. 18K-M

Referred specimens: NMMNH P-61006, P-61021, P-61031, P-61462-P-61463; five teeth reaching 1.8 cm in height.

Description: Only lateral positions are represented. The cusp is subtriangular, narrow apically and flaring basally; the mesial edge is straight to weakly concave and the distal more strongly concave basally. Lower teeth have a slight distal inclination, and upper teeth are strongly inclined. The lingual face is smooth with the exception of one specimen (NMNH P-61021, Fig. 18M), which possesses folds reaching halfway up the cusp; the neck is moderately broad. The labial face is smooth, but bears short basal folds; the basal margin is concave, nearly V-shaped medially and extends beyond the root face. The cutting edge of the main cusp terminates at the cusplet. Each shoulder has a short, triangular cusplet that may be accompanied by a second, much reduced one; the distal cusplet is apically directed, not inclined; the labial face has a medial crest. In profile, the lower crown is relatively thick and the upper thin; the lingual face is convex and the labial flat to slightly convex. The root is thick and bilobate, has a moderated protuberance and a distinct nutritive groove. The lobes are splayed but somewhat high, forming a V-shaped basal margin

Discussion: These teeth differ from the *Scapanorhynchus* in the fauna by their thicker root with a V-shaped basal margin, the orientation of the distal cusplet and morphometric relationship between height/width ratio and cusp inclination. They can be distinguished from "*Carcharias*" by their narrower cusp, concave mesial margin, the presence of short folds on the lower labial crown face and the higher, less obtusely splayed, lobes. The short triangular cusplets are very different from the slender elongate morphology of both *Odontaspis* and *Pueblocarcharias* n. gen. The cusp and cusplet shape, crown ornamentation, and root morphology are all in agreement with *Eostriatolamia* lateroposterior design, but the lack of anterior positions precludes positive assignment to a particular species or the genus.

Genus *Pueblocarcharias*, new genus

Type Species: *Pueblocarcharias kawaikensis*, new genus, new species.

Included Species: Only the type species.

Etymology: Named in honor of the native Pueblo cultures of northwestern New Mexico; Pueblo and the Greek *carcharias* (shark).

Diagnosis: Lamniform teeth with narrow triangular cusp, multiple long narrower accessory cusplets and short compound basal folds of the labial crown face – forming a cutting-grasping dentition displaying gradational (probably disjunct) monognathic and dignathic heterodonty.

Distribution: Santonian of New Mexico.

Pueblocarcharias kawaikensis, new species
Fig. 19A-H

Holotype: NMMNH P-61063 (Fig. 19A).

Paratypes: NMMNH P-61062 (Fig. 19C) and NMMNH P-61069 (Fig. 19F).

Referred specimens: NMMNH P-61062-P-61071; 10 teeth ranging in height from 4.0 to 10.8 mm.

Type Locality and age: Bernalillo County, New Mexico; Hosta Tongue Member of the Point Lookout Sandstone; Santonian; NMNNH locality 297.

Etymology: Named in honor of the Kawaik people of nearby Laguna Pueblo.

Diagnosis: Same as for the genus.

Description: The holotype (Fig. 19A) measures 9.2 mm high by 7.7 mm wide and is interpreted as an upper anterior; the cusp is narrowly triangular with straight margins and is distally inclined (80-degrees). The lingual cusp face is convex, thickest basally and flatter apically with completely smooth enameloid; the labial face is weakly convex and characterized by highly distinct short folds of the lower crown face (bourrelet) that often branch basally. The neck is moderately broad and smooth, and the basal labial crown face weakly extends beyond the root. The cusp's cutting edge is smooth, well developed and appears to terminate prior to the cusplets, with which the cusp joins acutely. The bases of two slender non-divergent cusplets are present on each shoulder. In lateral profile, the cusp is straight with a weak labial curvature of the apex. The root is well developed with a distinct nutritive groove and small foramen. Lobes are well defined and broadly splayed (weakly U-shaped) and spatulate with rounded tips; the lingual protuberance would be best described as moderate. The mesial lobe is longer than the distal.

One paratype (NMMNH P-61062, Fig. 18C) measures 9.0 mm high by 8.9 mm wide and is interpreted as an upper mesolateral; the cusp is narrow with a convex mesial and concave distal margin; it is distally inclined (61-degrees). The lingual cusp face is convex with smooth enameloid; the labial face is slightly convex and characterized by short basal folds that may branch basally. The neck is broad and smooth; the basal labial crown face is straight and barely projects beyond the root. The cutting edge is smooth, well developed, and terminating before the cusplets where the cusp joins acutely. The mesial shoulder bears three narrow cusplets, the medial strongly elongate; the cusplets are oriented on the same plane as the cusp. The distal shoulder shows evidence that at least two cusplets had been present. In lateral profile, the cusp is straight with a labial curvature of the cusp tip. The root is eroded, but does not appear to have been particularly thick; evidence of a nutritive groove is present, but additional detail has been lost. Lobes are well defined and splayed (weakly V-shaped) with rounded tips; root lobes are rather equal-sized.

Another paratype (NMMNH P-61069, Fig. 18F), measuring 6.8 mm in width (cusp damaged), is interpreted as a lower mesolateral; the cusp is relatively erect (likely 85-degrees) and subtriangular, with basal margins that are concave. The lingual cusp face is strongly convex with smooth enameloid; the labial face is less convex and characterized by short basal folds, which may branch basally. The neck appears to be relatively broad; the basal labial crown face is slightly concave and weakly projects beyond the root. The cutting edge is smooth, terminating on the lower cusp margin; the cusp joins the cusplets acutely. The shoulders bear two narrow, apically-directed cusplets. The root is thick, with a relatively strong nutritive groove. Lobes are well defined and splayed with rounded tips; the mesial lobe thicker and slightly longer than the distal.

In upper lateral teeth, the crowns are progressively more inclined, with a convex mesial and concave distal cusp edge. The medial-most primary cusplet is significantly longer than the secondary and apically
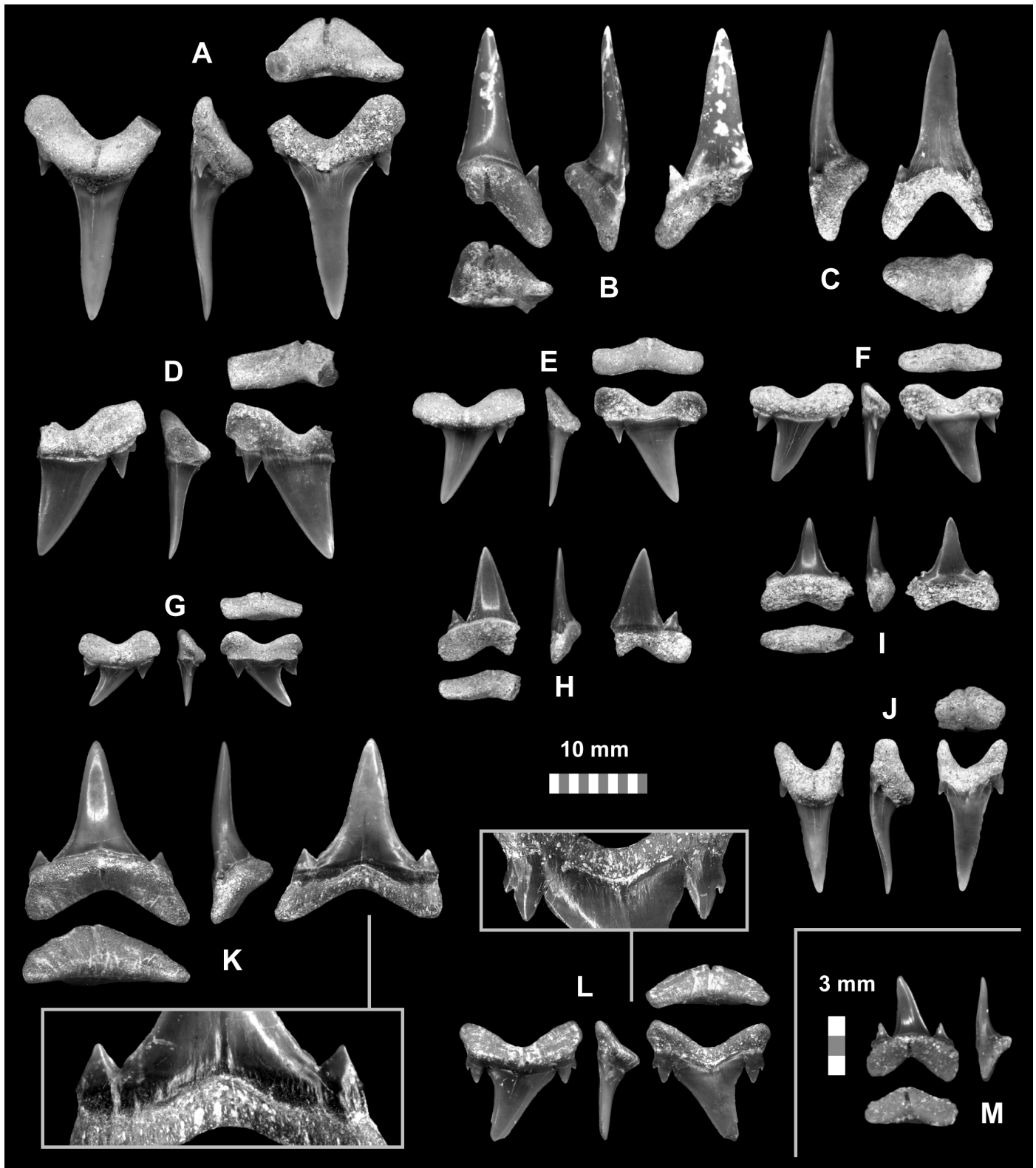
FIGURE 18. "*Carcharias*" and ?*Eostriatolamia*, tooth examples, three or four-perspectives noted from left to right (lingual, lateral, labial and basal), all grouped specimens similarly scaled (10 mm scale bar). **A-I**, "*Carcharias*" sp., positional examples, **A-C**, anteriors, **A**, NMMNH P-61059, **B**, NMMNH P-61060 and **C**, NMMNH P-61056, **D-I**, laterals, **D**, NMMNH P-61055.m, **E**, NMMNH P-61557.m, **F**, NMMNH P-61558, **G**, NMMNH P-61057, **H**, NMMNH P-61054 and **I**, NMMNH P-61033. **J**, NMMNH P-61058, ?"*Carcharias*" sp., upper first anterior. **K-M**, ?*Eostriatolamia* sp., **K**, NMMNH P-61462, lower anterolateral with 2x enlargement, **L**, NMMNH P-61463, upper lateral with 2x enlargement and **M**, NMMNH P-61021, lower lateral, 2x enlargement, 3 mm scale bar.

directed; a very small third cusplet may be present. Root lobes are more splayed (V-shaped) than those of the anterior. In lateral profile, the cusp is straight with a weak labial curvature of the tip; the crown at the level of the protuberance is more labiolingually compressed than seen in the anterior.

Lower lateral teeth are positionally much more erect than their upper counterparts. The lower labial crown face bulge is better developed, but still weak, and is more concave apicobasally. Laterally, the lowers are erect, but lack the labial curvature of the apex. Basally, the root is thicker than that of the upper laterals.

Discussion: Despite the inability to hypothesize a complete tooth arrangement or dental formula due to the few available specimens, the tooth design is rather distinct with its smooth lingual crown face, slender elongated cusplets, complexly folded labial bourrelet and well-developed nutritive groove; these are a set of characteristics not reported from other Late Cretaceous species.

Odontaspis Agassiz, 1838, teeth include some of these features, but the scythe-like upper laterals and lower laterals lacking a definitive labial bulge argue against assignment to that genus. The Late Cetaceous taxon of the Western North Atlantic, *Odontaspis aculeatus* (Cappetta and Case, 1975a), lacks the highly folded bourrelet and distally inclined cusplets seen in the Hosta teeth.

Carcharias Rafinesque, 1810, teeth have not been described with either the slender cusplets or complex bourrelet. *Carcharias samhammeri* (Cappetta and Case, 1975a), from the Late Cretaceous of the Western Atlantic and Gulf coasts, has a broad smooth cusp with little lower labial bulge; however, the cusplets are low and triangular, and the basal labial margin concave rather than straight as seen in *Pueblocarcharias kawaikensis* laterals.

Cenocarcharias Cappetta and Case, 1999 was erected for teeth initially described as *Odontaspis tenuiplicatus* Cappetta and Case,1975b and later included as *Carcharias* (e.g. Welton and Farish, 1993, p. 90); Underwood and Cumbaa (2010) reassigned this species to *Eostriatolamia*. *Cenocarcharias tenuiplicatus* teeth differ from *Pueblocarcharias kawaikensis* by the more substantial basal ornamentation of the labial crown face and the triangular cusplets.

The closest described tooth morphology is that of *Palaeohypotodus* Glikman, 1964, a widely reported Paleogene genus that has an ornamented lower labial crown face and two or more lateral cusplets on each side. However, when compared with *Pueblocarcharias kawaikensis*, *Palaeohypotodus rutoti* (Winkler, 1874) teeth have broader, more triangular and more splayed cusplets; a more concave basal labial crown margin; and higher, more U-shaped lobes. At times, the basal labial margin may be highly folded, sometimes appearing as denticles. Cappetta (1987, p. 88) reported the genus in the Paleocene of Europe and North Africa; and Ward and Wiest (1990) and Purdy (1998) documented it from the Paleocene of the Western North Atlantic. There are no reports of the genus from the Late Cretaceous.

Previous studies of Santonian faunas (e.g., Meyer, 1974; Williamson et al., 1989; Case et al., 2001) made no mention of this tooth-design. *Pueblocarcharias* n. gen. has therefore been erected to account for this new set of tooth characteristics and assigned to the odontaspidids s.l.

Family OTODONTIDAE Glikman, 1958
Genus *Cretalamna* Glikman, 1958

Type species: *Otodus appendiculatus* Agassiz, 1843, from the Turonian of England.

Remarks: As available specimens are limited to positions diagnostic of the genus only, no specific determination could be made. Despite the fact that teeth of this genus are typically referred to the species *Cretalamna appendiculata*, a number of separate species are probably present.

Cretalamna sp.
Fig. 19I

Referred specimens: NMMNH P-61051-P-61052, P-61427-P-61428; six teeth ranging in height from 1 to 1.5 cm.

Description: Specimens limited to upper and lower lateroposterior positions; short teeth with a triangular to subtriangular cusp, and one low, broad, triangular cusplet on each shoulder. The upper tooth has a straight mesial edge and a weakly concave distal edge; the lowers have a weakly concave mesial and more concave distal margin. The crown face is smooth, lacking any ornamentation; the neck is moderately broad; the lower labial crown face is relatively even, with the root and its margin weakly concave. The cutting edges of the cusp and cusplets are complete but do not join. The labial cusp face is weakly and the lingual strongly convex; in profile, teeth interpreted as lowers are lingually curved, and the uppers are relatively straight.

The root is high and bilobate with a moderate protuberance and no nutritive groove. The lobes are obtusely splayed, the basal margin is concave and they may be strikingly high and U-shaped medially.

Superorder BATOMORPHII Cappetta, 1980b
Order SCLERORHYNCHIFORMES Kriwet, 2004
Suborder SCLERORHYNCHOIDEI Cappetta, 1980b

Remarks: There is a lack of consensus on the ordinal assignment of Mesozoic "sawfishes." Cappetta (1987) included them within the rajiforms. Kriwet (2004) proposed a separate order, Sclerorhynchiformes, but Underwood (2006) preferred including them within the rajiforms.

A discussion of this topic requires terminology to refer to the enlarged denticles emanating from the lateral margins of the rostrum (teeth, rostral teeth, rostral denticles or rostral spines). Meyer (1974) referred to these as "rostral spines," and Kriwet (2004, p. 63) followed Herman et al. (1997) and used "rostral spine." This terminology will be used here. Although somewhat redundant, the term oral teeth will be employed (when needed) to avoid ambiguity.

Family PTYCHOTRIGONIDAE Kriwet et al., 2009

Remarks: Kriwet et al. (2009, p. 333) erected this family within Sclerorhynchiformes for the *Ptychotrygon* tooth morphology, designating it the type for the family. Cappetta (1987, p. 156) and Cappetta and Case (1999, p. 39) included *Ptychotrygon* as a rajiform, family uncertain. Underwood (2006, p. 226) questioned the sclerorhynchoid affinity of this taxon, noting they "do not appear to have possessed rostral teeth...and these taxa may represent additional, separately evolving, clades."

Only *Ptychotrygon* was included in this new family, despite the similarities among *Ptychotrygon* and genera such as *Texatrygon* Cappetta and Case, 1999 and *Kiestus* Cappetta and Case, 1999, both of which had formerly been included in *Ptychotrygon*. Based on the compliance of the *Texatrygon* tooth design with ptychotrygonid diagnostic characteristics, it has been included within the Ptychotrigonidae.

Genus *Ptychotrygon* Jaekel, 1894

Type species: *Ptychodus triangularis* Reuss, 1845, Turonian, Late Cretaceous (Turonian), Bohemia, Czech Republic.

Remarks: In North America, there have been a number of different perspectives when it comes to oral teeth of this genus. The extreme interpretations for the Gulf/southern Western Interior Seaway include Welton and Farish (1993, p. 147-51), who recognized five species, with *P. triangularis* spanning the Cenomanian-Maastrichtian. Cappetta and Case (1999, p. 47) appeared to view the general *P. triangularis* morphology in Texas as more of a chronocline: *P. slaughteri* Cappetta and Case, 1975b (Cenomanian), *P. blainensis* Case, 1978 (Turonian) and *P. triangularis* (Turonian-Coniacian). Manning (2006) considered there to be a single species, *P. triangularis*, with variable and broadly changing tooth morphology over time. Williamson et al. (1989, p. 241) attributed their 96 Hosta Tongue specimens to *Ptychotrygon triangularis*.
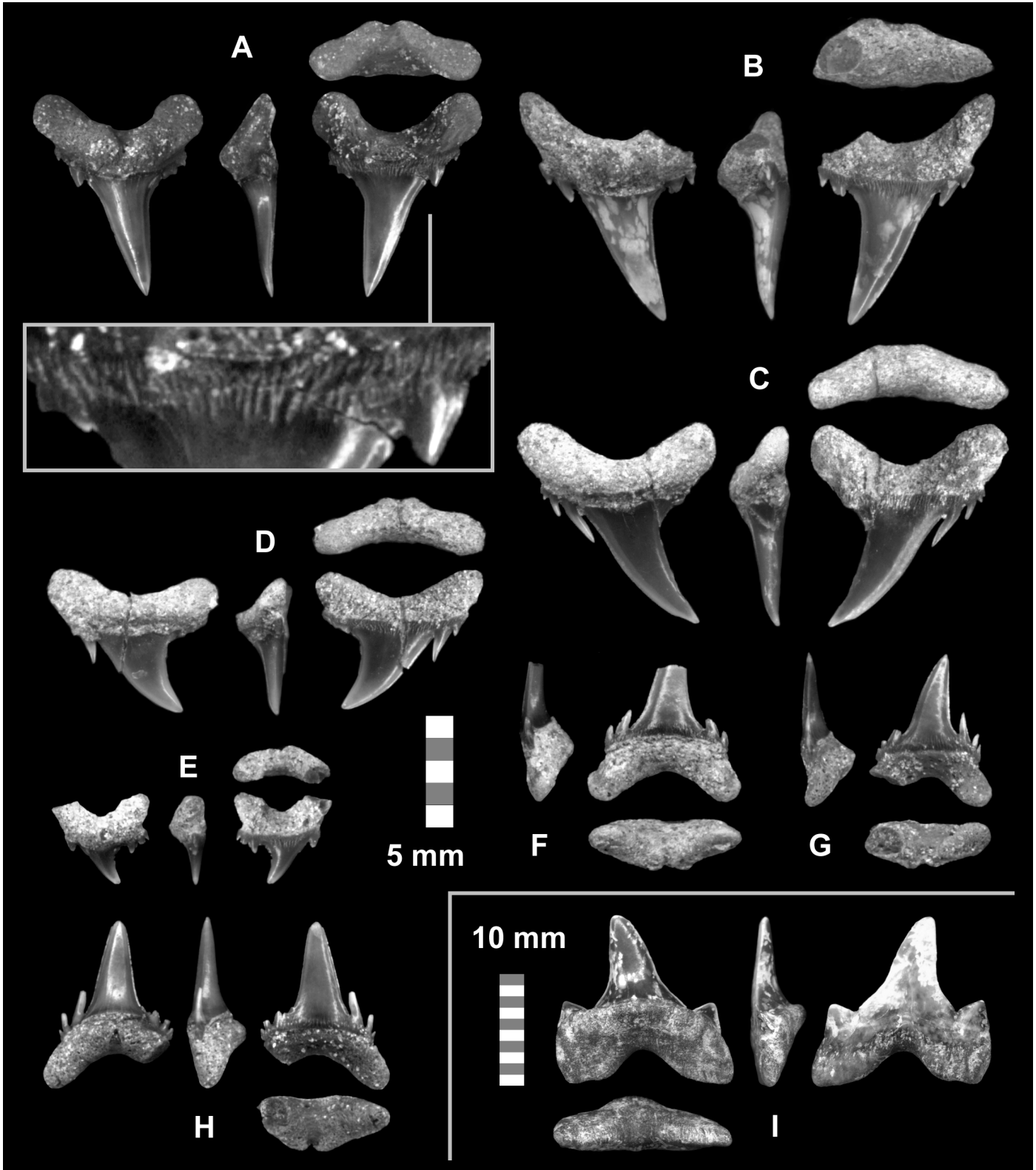
FIGURE 19. *Pueblocarcharias* and *Cretalamna* examples, three or four perspectives noted from left to right (lingual, lateral, labial and basal), all grouped specimens similarly scaled. **A-H**, *Pueblocarcharias kawaikensis* gen. et sp. nov., 5 mm scale bar, **A**, NMMNH P-61063 (holotype), upper anterior, enlargement of lower labial crown face ornamentation, **B**, NMMNH P-61067, upper anterior, **C-E**, upper lateroposteriors, **C**, NMMNH P-61062 (paratype), **D**, NMMNH P-61064 and **E**, NMMNH P-61065, **F-H**, lower lateroposteriors, **F**, NMMNH P-61069 (paratype), **G**, NMMNH P-61068 and **H**, NMMNH P-61071. **I**, NMMNH P-61428, *Cretalamna* sp., lower lateroposterior.

Ptychotrygon eutawensis Case et al., 2001
Fig. 20A-F

Referred specimens: NMMNH P-61156-P-61173, P-61176; 1364 oral teeth, ranging from 1.5 to 4.0 mm in width.

Description, oral tooth: Teeth best characterized by their small size, sub-triangular occlusal shape and dual transverse ridges. The primary ridge forms a transverse crest, the secondary is half way down the labial face and may be accompanied by a third over the visor (the enameloid is otherwise smooth). All teeth have cusps worn to various degrees, and actual cusp height is uncertain. The visor is thick and extends well beyond the root; the uvula is thick but short and strongly indented above (giving the appearance of an additional lingual transverse crest when viewed laterally). The root is relatively low and bears a strong but narrow groove with a distinct central pore; the root and crown widths are very similar. The lobes are triangular and include a margino-lateral foramen. Anterior positions are higher-crowned with more inflated roots and are more mesiodistally compressed; the secondary ridge is irregular and may be apically curved medially; below the secondary ridge are irregular ridges that may be apically directed. Lateral teeth become lower-crowned and mesiodistally expanded; the secondary ridge is relatively straight, and a tertiary labial ridge may be present as well.

Discussion: *Ptychotrygon* teeth have been largely differentiated on the basis of transverse ridge pattern and crown ornamentation as expressed in anterior and anterolateral file positions; more lateral positions often lack distinct ornamentation. Using the more anterior positions as a comparative basis: *P. triangularis* has a transverse ridge pattern similar to *P. eutawensis*, however, the lower labial crown face bears baso-apical ridges, often complex, which may meander or branch (Turonian-Coniacian, Europe and North America); *P. ledouxi* Cappetta, 1973 is *P. triangularis*-like but described as smaller with a lower crown and less apparent medial ridge (Turonian, South Dakota); *P. gueveli* Cappetta 2004 has a less well-defined secondary transverse ridge and highly ornate lingual and lower labial, crown face (Late Turonian, France); *P. blainensis* Case, 1978 has an incomplete secondary ridge permitting the depression labial to the primary ridge to extend onto the visor. The labial crown face below the transverse crest may bear weak ornamentation. In profile, the visor is elongate and apico-basally compressed (Campanian, Montana and Texas); *P. vermiculata* Cappetta, 1975 has two or three transverse ridges; the secondary is complete and bends towards the visor. The lower labial face is smooth or weakly ridged, and below the transverse crest, there may be weak ornamentation (Campanian, New Jersey to Texas); and *P. cuspidata* Cappetta and Case, 1975a lacks a secondary transverse ridge; the cusp is relatively high and the labial face is smooth but features some weak ornamentation below the transverse ridge (Campanian, NC; Maastrichtian, New Jersey).

?*Ptychotrygon eutawensis* (Case et al., 2001)
Fig. 20G-Q

Referred specimens: NMMNH P-61118-P-61130, P-61541; 37 rostral spines.

Description, rostral spines: Spines are small (1.5- 3.0 mm long) with a tall, conical peduncle (neck) above a splayed (varying degrees), weakly differentiated root. The cusp is much reduced, posteriorly directed and dorsoventrally compressed. The basal margin of the anterior face bears multiple ridges, two of which are long and extend apically, creating a lateral/transverse carina; on some specimens, a second set of ridges (medial to the lateral) extends to the apex (Figs. 20H-I, K). The anterior face is flat to weakly convex, often with a short medial ridge; there is no posterior carina or basal rim. Short ridges may be present posterior to the transverse carina (Fig. 20L). Viewed anteriorly, the spines incline to one direction, assumed to be ventral. Positionally, the peduncle becomes shorter and roots more splayed (wider) posteriorly.

Remarks: There is no general consensus on the presence of rostral spines in this taxon, but there are few reports (Case, 1987; Kriwet,

1999b; Manning, 2006). Cappetta (pers. commun. to JB, 2009) remains unconvinced these are *Ptychotrygon* and believes they are associated with a taxon with very small teeth that have yet to be reported.

There appears to be a correlation between the *Ptychotrygon* tooth and the rostral spine morphology included here (JB pers. obs.). As a single species appears to be present in this fauna, this hypothesis is extended to the specific level.

Genus *Texatrygon* Cappetta and Case, 1999

Type species: *Ptychotrygon hooveri* McNulty and Slaughter, 1972, Late Cretaceous (Late Turonian), Texas, USA.

Texatrygon stouti, new species
Fig. 21A-F

Holotype: NMMNH P-61142 (Fig. 21D).
Paratypes: NMMNH P-61142 (Fig. 21C), NMMNH P-61144 (Fig. 21A).
Referred specimens: NMMNH P-61141-P-61150; 12 medium-sized (3.2- 4.9 mm wide) oral teeth.
Type Locality and age: NMMNH locality 297, Bernalillo County, New Mexico; Hosta Tongue Member of the Point Lookout Sandstone, Santonian.
Etymology: Named in honor of the artist William Stout for his contributions to paleontologic illustration.
Diagnosis: Teeth characterized by a stout, pyramid-shaped crown lacking ornamentation, with a low, broad, cone-like cusp, complete transverse carina and robust visor. The roots are high with inflated lobes and a broad nutritive grove and central pore.
Description: The holotype (NMMNH P-61142, Fig. 21D), likely a lateral, was selected on the basis of root condition, although the cusp is well worn. The tooth is 4.9 mm wide, 3.4 mm deep and the height, 2.4 mm, probably was originally close to 2.8 mm. It has a stout crown, low pyramidal in form and bluntly cuspidate. The enameloid is smooth and lacks distinct ornamentation. The cusp is broadly cone-like, differentiated from the shoulders by a weak depression that extends to the labial and lingual margins; viewed apically, the crown is sub-rhombic with concave margins and a thick and strong visor. A broad, low medial ridge extends partially down the labial cusp face. A transverse crest (carina) is present, reaching the lateral margins of the crown. The uvula is thick but not strongly extended and is depressed at the lingual margin of the cusp. In profile, the lingual crown face is abbreviated and acutely inclined; in contrast, the labial face is long, very thick and obtusely inclined, projecting well beyond the labial face of the root. The root is approximately as high as the crown with inflated lobes that extend slightly beyond the crown lingually. Viewed basally, the groove is deep and wide, particularly around the central foramina. The lobes are subtriangular, with a weakly convex labial margin and concave lingual margin, forming a margino-lingual notch.

One paratype (NMMNH P-61142, Fig. 21C), an anterolateral, is 4.2 mm wide, 3.0 mm deep and 2.7 mm high. As in the holotype, the crown is stout, low pyramidal in form and bluntly cuspidate; the enameloid is smooth and lacks distinct ornamentation. A low, irregular medial ridge extends partially down the labial cusp face, and the transverse crest extends along unworn portions of the cusp to the lateral margins of the crown. Viewed apically, the crown is sub-rhombic with more strongly concave margins differentiating the cusp from the shoulder. Other elements of the holotype design are present in this specimen.

Another paratype (NMMNH P-61144, Fig. 21A) is likely an anterior and measures: 3.2 mm wide, 2.7 mm deep and 2.4 mm high. Unlike the other two described teeth, the tooth is mesiodistally compressed; the shoulders are shorter, and, in occlusal view, the visor-shoulder angle much more salient and the visor more prominent and angular. The cusp shows little wear, and the transverse crest appears to be complete. Unlike the other two specimens, from a basal perspective the nutritive groove is relatively narrow and the lobes are much more asymmetrical.
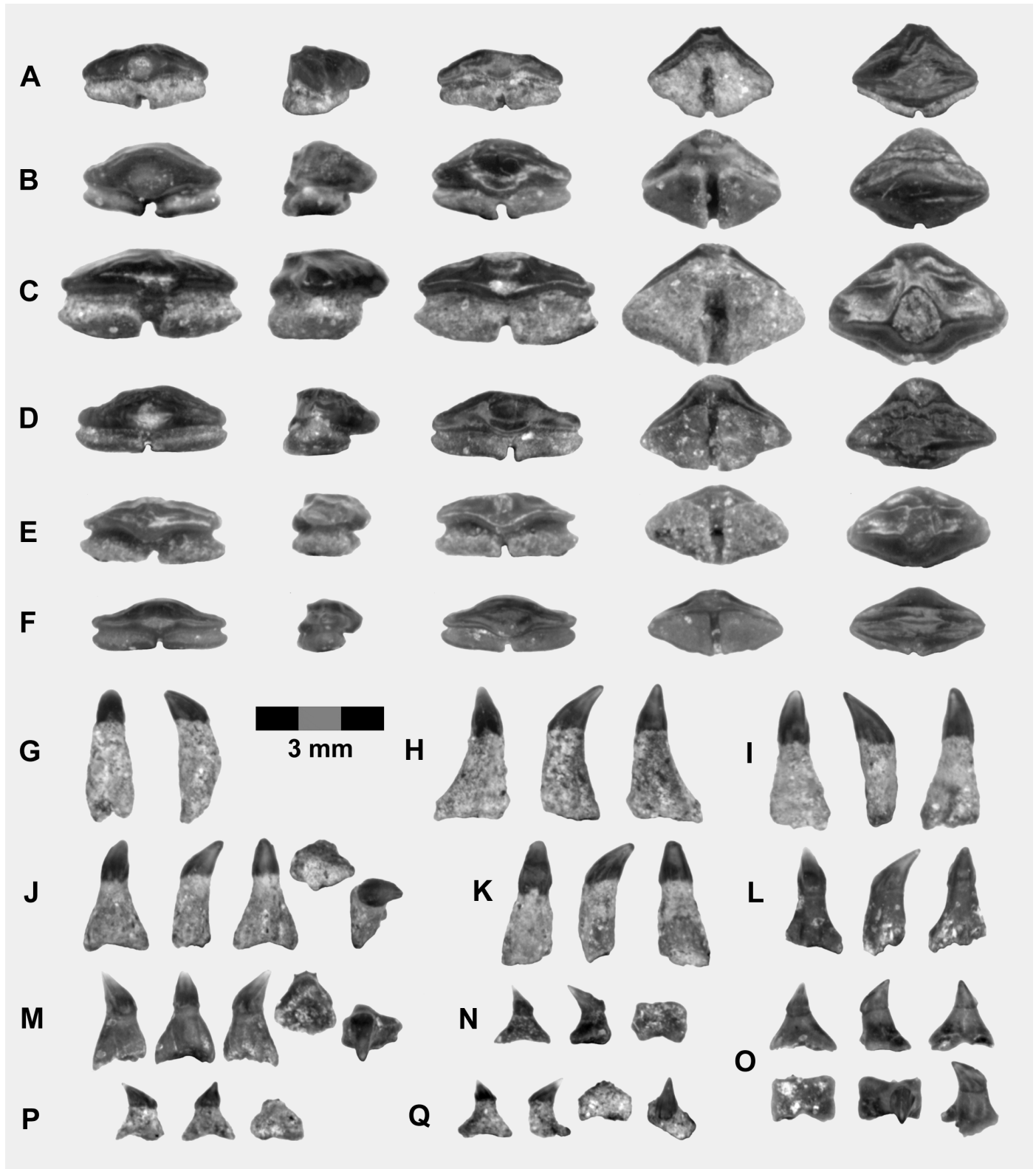
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FIGURE 20. *Ptychotrygon eutawensis*, all specimens similarly scaled, 3 mm scale bar. **A-F**, Oral teeth presented left to right, labial, lateral, lingual, basal, occlusal, **A**, NMMNH P-61161, **B**, NMMNH P-61163, **C**, NMMNH P-61164, **D**, NMMNH P-61169, **E**, NMMNH P-61173 and **F**, NMMNH P-61165. **G-O**, ?*Ptychotrygon eutawensis* n. sp., rostral spines, 2-6 perspectives presented, presented left to right. anterior, lateral, posterior, basal, apical, **G**, NMMNH P-61128, **H**, NMMNH P-61127, **I**, NMMNH P-61120, **J**, NMMNH P-61121, **K**, NMMNH P-61119, **L**, NMMNH P-61129, **M**, NMMNH P-61122, **N**, NMMNH P-61124 and **O**, NMMNH P-61118, with posterio-dorsal aspect.

The general form of the other specimens largely complies with the holotype's description. Variations are mostly positional in nature; anterior teeth are more mesiodistally compressed with higher cusps; distally, the teeth have lower crowns, become more mesiodistally elongated and labiolingually compressed. Some specimens have very low, broad, short and faint ridges – usually no more than an undulation of the surface, low on the labial or lingual face. One specimen requires additional comment – NMMNH P-61166 (Fig. 21I) is likely a juvenile, but is described separately below as the roots are very low.

Discussion: Specimens are similar to those included by Cappetta and Case (1999, p. 41, pls. 26.11, 27.1-5) when they erected *Texatrygon*, but differ in that *Texatrygon hooveri* has a labiolingually narrower shoulder, strong short folds of the lower labial crown face and a more inclined visor; Cappetta and Case included this as a Turonian-Coniacian taxon. *Texatrygon copei* Cappetta and Case, 1999 (reported as Early Campanian) has a lingual face that is much less inclined (labially), a uvula that is more basally directed and a crown with strong labiomarginal projections.

Texatrygon sp. aff. *T. stouti*
Fig. 21I

Referred specimens: NMMNH P-61166; a single small (2.5 mm wide) tooth.

Description: A lateroposterior tooth with a high dome-shaped cusp, broadly rising shoulders and a transverse carina extending to the lateral margins of the crown. The visor is short and broad and the enameloid is smooth except for numerous short ridges on the visor. The uvula is short with a strong depression above it. The root is low, and has a complete nutritive groove and central pore; the lobes are triangular, each bearing two margino-lingual foramina.

Discussion: This specimen compares with one of the Welton and Farish (1993, p. 148, figs. 2-3) examples of *Ptychotrygon hooveri*, but lacks the labial ornamentation. It has been interpreted to represent a juvenile *Texatrygon stouti* n. sp.

?*Texatrygon stouti*
Fig. 21G-H

Referred specimens: NMMNH P-61136-P-61137; two rostral spines, 2.5 and 4 mm in length.

Description: ?*Ptychotrygon*-like rostral spine (see above) with a medium height cusp and short peduncle. The roots are similar to those included as ?*Ptychotrygon eutawensis*, but the crown has a strong basal rim that projects beyond the peduncle. The cusp is lingually directed, mesiodistally compressed, and has an anterior, but no lateral carina. The basal margin of the crown has weak bulges that do not extend up the face in ridge-like fashion.

Discussion: There are currently no reports of rostral spines being present in this genus. The crown of these spines shares characteristics with both ?*Ptychotrygon eutawensis* and those often referred to as *Ischyrhiza avonicola* Estes, 1964, but they are distinct from each. Because all of the sclerorhynchid oral teeth in this fauna, except for *Texatrygon*, have known or associated rostral spines, it appears likely that these rostral spines belong with the *Texatrygon* teeth. This hypothesis needs to be validated with similar spines in other faunas.

Family SCLERORHYNCHIDAE Cappetta, 1974
Genus *Ischyrhiza* Leidy, 1856

Type species: *Ischyrhiza mira* Leidy, 1856, Late Cretaceous, USA, locality information not provided.

Ischyrhiza sp. aff. *I. mira* Leidy, 1856
Oral teeth: Fig. 22A-F

Referred specimens: NMMNH P-61100-P-61117; 54 small (1.5 -2.6 mm wide) oral teeth representing multiple positions. Williamson et al. (1989, p. 241, fig. 3.l-m) reported a single oral tooth (NMMNH P-4031) as *Ischyrhiza mira* that corresponds with these specimens.

Description: Cuspidate, lingually-directed crown with low broad shoulders; the subtriangular, lower labial crown face (visor) extends well beyond the root; a uvula (lingual) is present and generally lacks a circular depression above it. A transverse cutting edge is present, extending down the cusp and onto the shoulder; the cusp bears a medial carina, sometimes extending to the edge of the visor. The shoulders may be smooth or bear short apico-basal ridges extending from the visor; otherwise, the enameloid is smooth. The root is high, broader than the crown, with a deep nutritive groove that may be wide or narrow; each lobe has a margino-lingual foramen, which may be accompanied by a notch of the root face. When viewed basally, the lobes are triangular in shape, the groove broadens near the anterior margin of the crown and there is a distinct central foramen. Positionally, the cusp can be rather long; less inclined mesially and quite low in posteriolaterals; the roots broaden in more distal positions.

There are extremes of similarly-sized teeth that correspond with this description. In the first (Fig. 22A-B), the shoulders are smooth, the main cusp broader and the medial ridge well developed on the visor. In the second (Fig. 22E-F), there are short ridges extending apically from the margin of the visor; the cusp is narrower and the medial ridge more accentuated apically. Remaining specimens were deemed ambiguous (Fig. 22C-D).

Discussion: Although these are smaller and more gracile than typical *Ischyrhiza mira* teeth, as seen in the Campanian (e.g., Welton and Farish 1993, p. 141; Cappetta and Case, 1975a), these could represent juvenile teeth with a poorly published record. *I. mira* teeth are reported as having a smooth crown; the basal ornamentation seen in some of these teeth may merely be an ontogenetic variation of the typical tooth-design, sexual dimorphism or reflect two species with otherwise similar tooth-designs. Cappetta (pers. commun. to JB, 2009) found these two forms very similar and likely represented individual or "gynandric heterodonty with male teeth more ornamented than females ones." A lack of detail in the published record does not permit a better determination for these teeth.

Ischyrhiza sp. aff. *I. mira* Leidy, 1856
Rostral spines: Fig. 22G-K

Referred specimens, large: NMMNH P-61151-P-61154; three complete (1-2 cm long) and 10 damaged rostral spines. Sixty-eight additional broken or fragmentary rostral spines (NMMNH P-61155) have not been considered but appear to largely reflect an *Ischyrhiza mira* design. Williamson et al. (1989, p. 241, fig 3.n-o) reported 202 *Ischyrhiza mira* "rostral teeth."

Referred specimens, small: NMMNH P-61131-P-61133; six (1.5-3.0 mm) rostral spines.

Description, large: The cap is rather erect in anterior positions and more inclined and shorter caudally; the anterior margin is straight and the posterior, convex; it is dorsoventrally compressed, bears a complete posterior carina and smooth enameloid; there is flaring of the cap where it meets the peduncle, and, when viewed anteriorly, the cap is directed ventrally. The peduncle is massive in larger specimens, expanding basally; depressions along the basal lateral face create a finger-like appearance, and there is a strong antero-posterior basal depression.

Description, small: Cap broad at the base, becoming more dorsoventrally compressed apically; caudally inclined; and usually shorter than the peduncle. The enameloid is smooth, and there is an anterior carina, a weak lateral rim, and a small lateral ridge may be present low on the cap. The peduncle is broad, with the roots flaring out dorsoventrally, creating a broad basal depression.

Discussion: Meyer (1974, p. 83-85, 90-93) discusses the problems associated with attributing rostral spines to *Ischyrhiza avonicola* outside the type area; they may only represent positional variations of
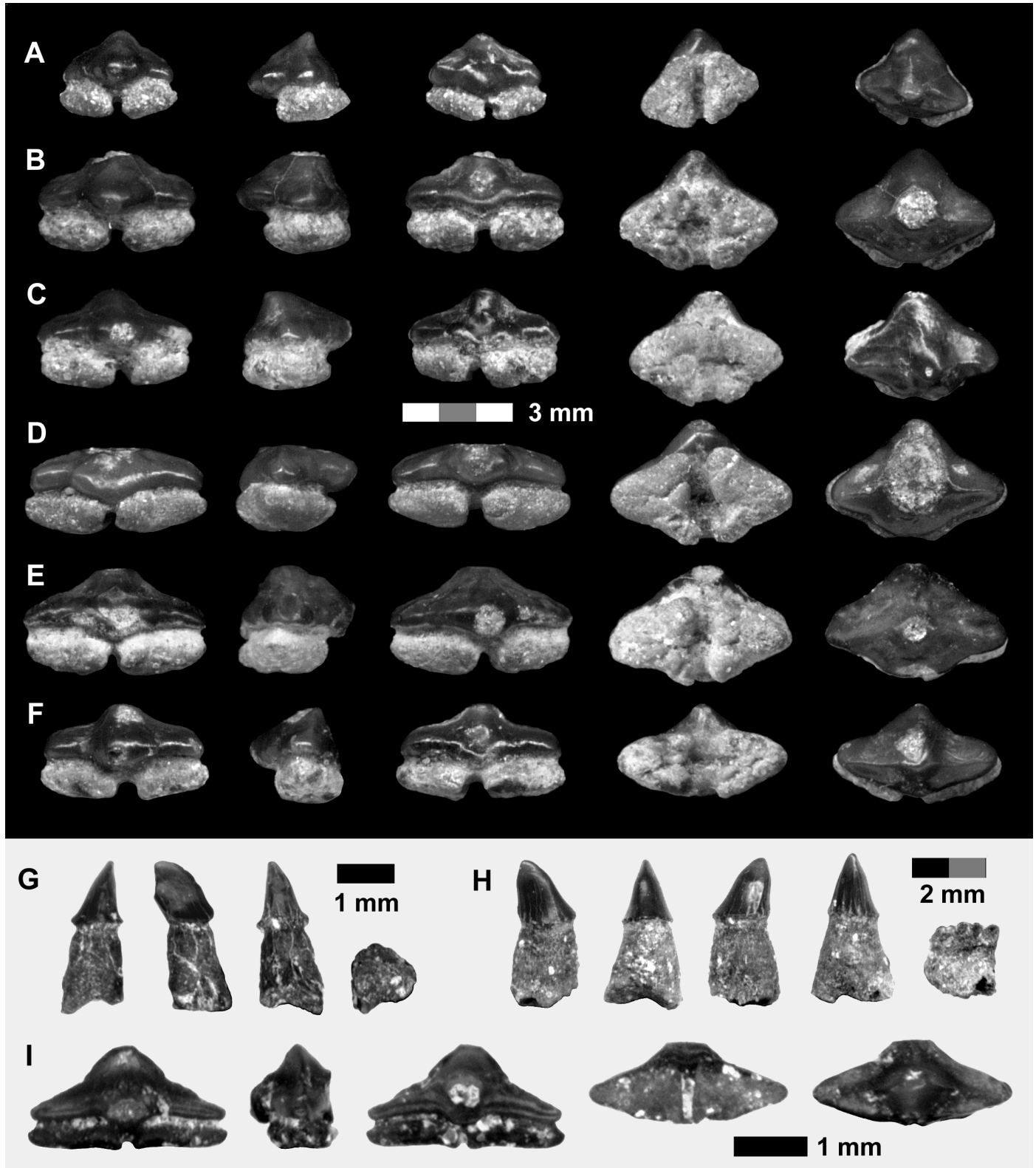
FIGURE 21. *Texatrygon stouti* n. gen., n. sp, teeth and rostral spines. **A-F**, Oral teeth all specimens similarly scaled and presented (left-right) labial, lateral, lingual, basal and occlusal views, scale bar 3 mm, **A**, NMMNH P-61144 (paratype), **B**, NMMNH P-61146, **C**, NMMNH P-61142 (paratype), **D**, NMMNH P-61147 (holotype), **E**, NMMNH P-61148 and **F**, NMMNH P-61149. **G-H**, ?*Texatrygon stouti* gen. and sp. nov., rostral spines, specimens individually scaled, **G**, NMMNH P-61136, anterior, dorsal, posterior and basal views, 1 mm scale bar and **H**, NMMNH P-61137, ventral, anterior, dorsal, posterior and basal aspects, 2 mm scale bar. **I**, ?*Texatrygon stouti* nov. gen., nov. sp, NMMNH P-61166, oral tooth, same views, 1 mm scale bar.

the contemporary *Ischyrhiza* taxon in a given fauna. He concluded that Santonian rostral spines from the Tombigbee Sand of Mississippi appeared transitional between *Ischyrhiza schneideri* Slaughter and Steiner, 1968 and referred them to *Ischyrhiza* sp. aff. *I. mira*. These forms are included together here but described separately (large and small) to avoid commingling characteristics.

Genus *Onchosaurus* Gervais, 1852

Type species: *Onchosaurus radicalis* Gervais, 1852, Senonian, Late Cretaceous, Paris Basin, France.

cf. *Onchosaurus* sp.
Fig. 23A

Referred specimens: NMMNH P-4013, P-4033-P-4035; four fragmentary rostral spines.

Remarks: Williamson et al. (1989, p. 241, fig. 4g-j) tentatively identified four fragmentary rostral spines as cf. *Onchosaurus*. The bulk-sampled material included no rostral spines that might be assigned to this genus. We re-examined the original NMMNH specimens and reaffirmed the conclusions of Williamson et al. (1989), based on the large size, baso-apically furrowed lobes, sub-parallel basal profile and lack of a pulp cavity. Without a cap, the identification cannot be further refined. Lehman (1989) reported as *Onchosaurus pharo* (Dames, 1887) capless fragments from the Middle Campanian of Texas.

?*Onchosaurus* sp.
Fig. 23B-D

Referred specimens: NMMNH P-61097-P-61099; three small (2.5 - 4.2 mm high) oral teeth.

Description: The crown is robust, strongly cuspidate, lingually directed and mesiodistally compressed; the enameloid is smooth and lacks ornamentation. The apron is thick and projects well beyond the labial root face; there is a slight basal inclination to its labial margin. The uvula is short, thick and bears a central concavity. The shoulders are low and thick; their length is dependent on tooth position (Fig. 23C very short and Fig. 23D moderate). A transverse carina runs from shoulder to shoulder, and is stronger apically; the labial crown face shows no distinct medial ridge. Viewed occlusally, the cusp (apron-apex) is elongate, teardrop in shape and broadly convex. Shoulders project almost perpendicularly from the cusp; the crown is narrower than the root. Viewed labially, the shoulders join the cusp at a low position.

The root is high and inflated, extending well beyond the basal margin of the crown laterally and lingually; the basal face is convex. Viewed basally, there is a deep and narrow nutritive groove with a central pore positioned lingually. The lobes are subtriangular – broader distally; the nutritive groove does not open labially. Marginolingual foramina are not clearly visible.

Discussion: A single tooth of this morphology, if found with similarly-sized *Ischyrhiza* specimens, could easily be interpreted as a near symphyseal position (mesiodistally compressed) of that taxon, in which the teeth are mesiodistally elongate. However, these Hosta Tongue teeth show multiple positions, and *Ischyrhiza* teeth from this fauna are significantly smaller.

Compared with *Onchopristis dunklei* McNulty and Slaughter, 1962 teeth, as illustrated by Cappetta and Case (1999, pl. 23, figs. 9-10, pl. 24, figs. 1-9), the Hosta Tongue teeth have a less-developed apron, lower shoulders, a higher, more inflated root and a narrower, more parallel nutritive groove. There are also some similarities with *Pucapristis branisi* Schaeffer, 1963, as depicted by Cappetta (1987, p. 154-55, text fig. 132c-h). However, in that species the cusp is lower with a medial ridge and weak ornamentation, the apron thicker, the shoulders less well differentiated and the nutritive groove broadly opens labially. Other

sclerorhynchid oral tooth morphologies, such as *Borodinopristis*, *Ganopristis* and *Sclerorhynchus*, have smaller teeth with lower crowns that bear multiple baso-apical ridges.

Cappetta (pers. commun. to JB, 2009) noted that he had seen this tooth-design in North African sediments that yielded *Onchosaurus* rostral spines. Because *Onchosaurus* rostral spines were reported by Williamson et al. (1989, p. 241) as present in the Hosta Tongue, it is very possible these are the corresponding oral teeth.

Genus *Sclerorhynchus* Woodard, 1889

Type species: *Sclerorhynchus atavus* Woodward, 1889, Late Cretaceous (Late Santonian), Sahel Alma, Lebanon.

Sclerorhynchus sp.
Fig. 23E-F

Referred specimens: NMMNH P-61134-P-61135; two rostral spines, 5.5 and 11.5 mm in length.

Description: The rostral spines have a dorsoventrally compressed crown (cap) that thickens basally. The anterior edge is gently convex; the posterior is concave apically and basally, but convex in the midsection. The cap lacks baso-apical folds, and the posterior carina terminates well above the peduncle. The lower cap has a weak basal rim extending posteriorly that may (Fig. 23F) begin to rise and extend towards the base of the posterior carina. The peduncles are damaged, but if complete, were likely shorter than the crown.

Discussion: Slaughter and Steiner (1968) identified Turonian through Campanian *Sclerorhynchus* rostral spines as *Sclerorhynchus atavus*. Case and Cappetta (1997) and Cappetta and Case (1999) described additional taxa based on morphological differences of oral tooth crowns and rostral spine caps. Rostral spine changes may be viewed as either a gradual change in the shape of the posterior margin from a weak bulge (Turonian) to a strongly hooked barb (Maastrichtian), or the presence of two taxa, one with a weak posterior bulge and the other with a more barbed posterior margin.

Cappetta and Case (1999, p. 38) preferred the latter; their Turonian-Coniacian rostral spines included: *Sclerorhynchus priscus* Cappetta and Case, 1999, which has a weak bulge of the posterior margin and a cap that might be smooth, but often folded; and *Sclerorhynchus* sp. 2 Cappetta and Case, 1999, which has a posterior edge with a lower more defined (?pre-barb) bulge. Cappetta and Case (1999) obtained no Santonian material from Texas and differentiated *S. priscus* from *S. atavus* (Santonian, Lebanon) on the basis of oral tooth design and a cap that is only smooth in the latter. From the Campanian and Maastrichtian, respectively, they included: *Sclerorhynchus fanninensis* Cappetta and Case, 1999 with a smooth cap and strong posterior bulge; and *Sclerorhynchus pettersi* Case and Cappetta 1997, with a folded basal cap and hooked barb; the latter is also present in the Bluffport Marl (Late Campanian) of Mississippi (JB pers. obs.).

Lacking oral teeth and complete rostral spines, identification has been restricted to the genus level only.

Order RAJIFORMES, Berg, 1940
Family RHINOBATIDAE Müller and Henle, 1838
Genus "*Rhinobatos*" Linck, 1790

Remarks: Recent *Rhinobatos* are represented by five subgenera and 34 species (Compagno, 1999) sharing a similar tooth-design; attempting to differentiate the various species based on isolated teeth would be an extremely difficult to near impossible task. In the fossil record, it is highly unlikely that isolated teeth can be interpreted more clearly; in those instances where sexual dimorphism is not the cause, differing morphologies more likely represent different genera rather than distinct species.

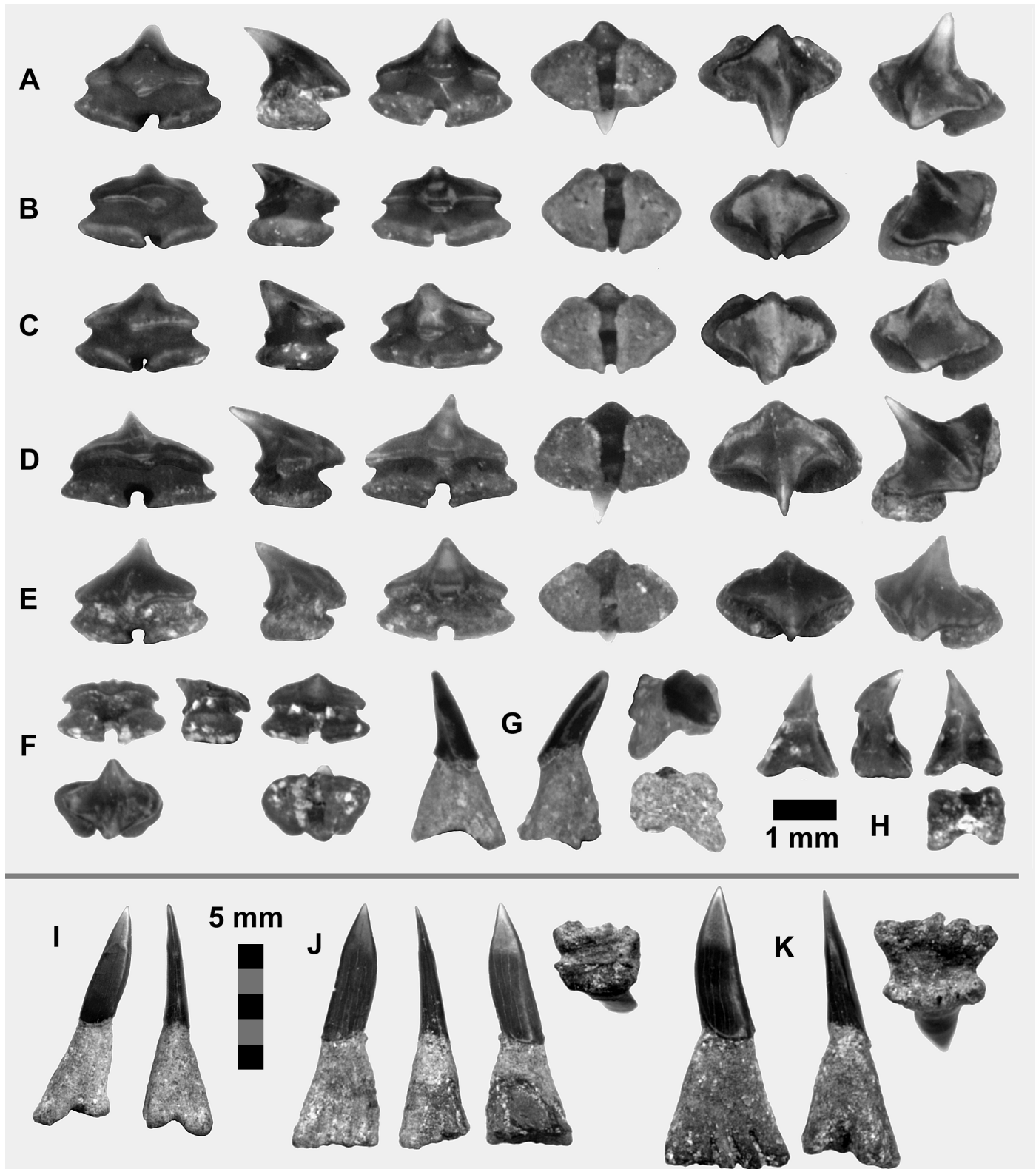**Type species:** *Rhinobatos rhinobatos* Linnaeus, 1758, Recent.

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FIGURE 22. *Ischyrhiza* sp. aff. *I. mira*, teeth and rostral spines. **A-F**, Oral teeth all specimens similarly scaled and presented (left-right) labial, lateral, lingual, basal and occlusal views, scale bar 1 mm, **A**, NMMNH P-61103, **B**, NMMNH P-61106, **C**, NMMNH P-61104, **D**, NMMNH P-61105, **E**, NMMNH P-61110 and **F**, NMMNH P-61102. **G-H**, Rostral spines, specimens similarly scaled, 1 mm scale bar, **G**, NMMNH P-61132, anterior, dorsal, cuspal and basal views and **H**, NMMNH P-61131, anterior, ventral, posterior and basal views. **I-K**, Rostral spines, specimens similarly scaled, 5 mm scale bar, **I**, NMMNH P-61151, dorsal and anterior views, **J**, NMMNH P-61152, ventral, posterior, dorsal and basal views and **K**, NMMNH P-61153, dorsal, posterior and basal views.
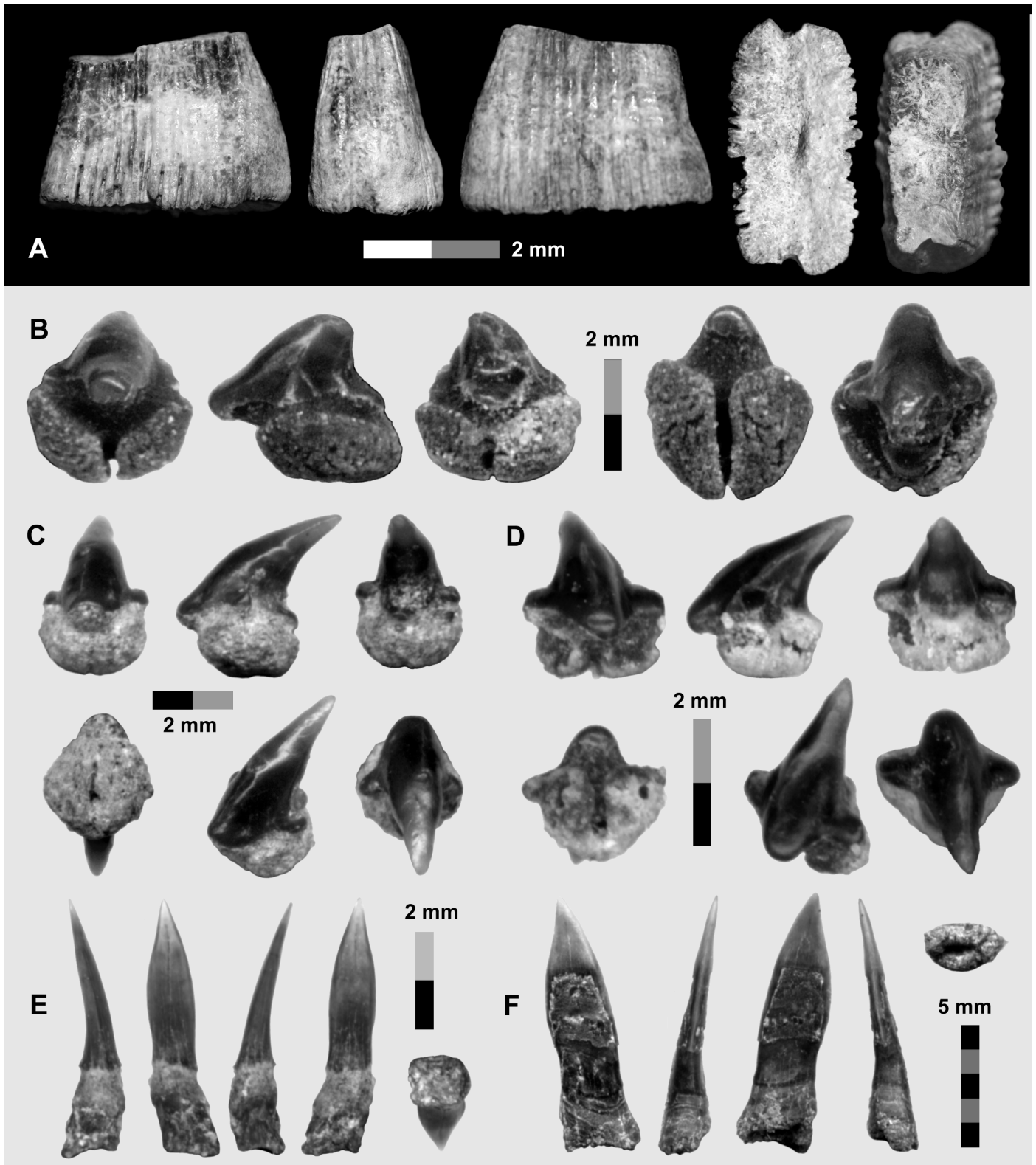
FIGURE 23. *Onchosaurus* sp. and *Sclerorhynchus* sp., specimens individually scaled. **A**, cf. *Onchosaurus* sp. (NMMNH P-4013) rostral spine, ventral, posterior, dorsal, basal and occlusal views, 2 cm scale bar. **B-D**, ?*Onchosaurus* sp., oral teeth presented with labial, lateral, lingual, basal and occlusal views, 2 mm scale bar, **B**, NMMNH P-61099, (damaged cusp and shoulder), **C**, NMMNH P-61098; added latero-labial view and **D**, NMMNH P-61097, added latero-labial view (occlusal view prior to cleaning). **E-F**, *Sclerorhynchus* sp. rostral spines, individually scaled, **E**, NMMNH P-61135, anterior, ventral, posterior, dorsal and basal views, 2 mm scale and **F**, NMMNH P-61134, dorsal, anterior, ventral, posterior and basal views, 5 mm scale bar.

"*Rhinobatos*" sp.
Fig. 24A-B

Referred specimens: NMMNH P-60725-P-60726, P-61464-P-61465; 10 very small (1 mm range) teeth.

Description: Globular crown with smooth enameloid; rounded labial face (visor) that extends well beyond root; long thick lingual uvula and shorter lateral uvulae. Laterally the crown faces rise to form a transverse carina. The root is high, wider than the crown and lingually displaced. The nutritive groove is wide and deep, broadening labially; the central pore is large. The lobes are triangular, narrowing lingually, and there is a strong margino-lingual notch accompanied by a rather large foramen.

Discussion: The accompanying description compares well with the *Rhinobatos* tooth-design provided by Cappetta (1987, p. 137); any attempt to further refine the determination would be highly speculative, particularly with the wear of the occlusal surface.

The Hosta Tongue specimens are casually similar to *Rhinobatos casieri* Herman, 1977 (Santonian, Belgium), also reported by Cappetta and Case (1975a) from the Campanian of New Jersey. However, it seems unlikely that the Belgian taxon from higher latitudes of the Eastern Atlantic was also present in the lower latitudes and warmer waters of the WIS. Of the 35 guitarfish reported on FishBase (2010), only one species, *Rhinobatos percellens* (Walbaum, 1792), is known from both sides of an ocean (central Atlantic), and in that case at similar latitudes.

Cappetta and Case (1999, p. 31-33, pls. 18, 19) erected three new Late Cretaceous guitarfish taxa and included *Rhinobatos* sp. from Texas, none of which compare well with "*Rhinobatos*" sp. When viewed occlusally, the lingual margin of the crown is smooth in the Hosta Tongue specimens while weakly scalloped in *Rhinobatos lobatus*, *R. ladonianensis* and *R. kiestensis*. Viewed labially, "*Rhinobatos*" sp. lacks evidence of a cuspidate crown as displayed by their *R. kiestensis* and *Rhinobatos* sp.

Cappetta (1973, p. 509-510, pl. 2) described ?*Rhinobatos incertus* and reported *Rhinobatos* sp. from the Turonian of South Dakota. The Hosta Tongue teeth lack the high cusp present in the former and are much more similar to the *Rhinobatos* sp. description. Everhart (2007) suggested these two forms represent sexual dimorphism within a single taxon; Herman et al. (1997, p. 122, pls. 27, 28) noted this heterodonty to be present in the Recent *Rhinobatos rhinobatos* (Linnaeus, 1758), but only as a low cusp.

Family HYPSOBATIDAE Cappetta, 1992
Genus *Protoplatyrhina* Case, 1978

Type species: *Protoplatyrhina renae* Case, 1978, Judith River Formation, Late Cretaceous (Campanian), Montana, USA.

Protoplatyrhina sp. aff. *P. renae* Case, 1978
Fig. 24C-H

Referred specimens: NMMNH P-60689-P-60724; 36 small teeth (1.5 – 3.0 mm wide) were prepared and imaged for descriptive purposes. Many (100+) additional specimens were collected, some as small as 1.0 mm; the bulk (n = 638) were encased in matrix and weren't prepared in order to properly differentiate them from similarly-sized *Pseudohypolophus* teeth.

Description: The crown is smooth, somewhat globular in larger teeth and rhombic in smaller teeth; about equal in height with the root. Viewed occlusally, the labial margin is smoothly curved and the lingual more rectilinear; the root is not broader than the crown. Viewed laterally, the labial crown face extends beyond and slightly overhangs the root face (very short broad visor); the root extends beyond the lingual crown face (short and broad uvula).

The root is bilobate with a deep and sometimes broad nutritive groove; the labial portion of the root is broader than the lingual; a large central pore is present and extends into each lobe (paracentral). Lobes are sub-equal in size (particularly in larger teeth) and sub-triangular in shape; there is a large margino-lingual foramen separating the broader labial and narrower lingual portions of each lobe. The labial lobe face bears two or more coronally-positioned foramina.

Moving from the center to the side of the jaw, the crown becomes lower relative to the root height; teeth become more elongate (labio-lingually compressed); root lobes become more asymmetrical (larger mesial lobe), and for a particular position, the mesial root height is greater than the distal. Coronal offset is not as severe as seen in *Pseudohypolophus*.

Discussion: Case (1978, p. 193, pl. 5, figs. 4-6; text figs. 14-15) noted that a canal of *Protoplatyrhina* extended from the central pore to the margino-lingual foramen; this was only observed in a single, 1-mm-class Hosta Tongue specimen (NMMNH P-61504). The Santonian-Maastrichtian specimens as figured by Case (1978), Welton and Farish (1993, p. 133, figs. 1-2), Case and Cappetta (1997, p. 147, pl.11, fig. 3) and Case et al. (2001, p. 93, pl. 1, fig. 12) all tend to resemble the Hosta Tongue material. The teeth lack a uvula as strong as suggested by Cappetta (1987, p.142-43, text fig. 120a-c), however, it is better developed than that illustrated for *Protoplatyrhina hopii* by Williamson et al. (1993, fig. 9.11-9.15) from the Toreva Formation (Turonian) of Arizona.

Family incertae sedis
Genus *Myledaphus* Cope, 1876

Type species: *Myledaphus bipartitus* Cope, 1876, Judith River Formation, Late Cretaceous (Campanian), Montana, USA.

Myledaphus sp.
Fig. 25A-C

Referred specimens: NMMNH P-60682, P-60685-P-60688; five teeth ranging in width from 3.7 to 6.7 mm

Diagnosis: *Myledaphus bipartitus* tooth-design but with a smooth crown.

Description: The largest example (NMMNH P-60682, Fig. 25A) has a smooth crown with a sharply hexagonal profile; the occlusal surface is worn but lacks evidence of ornamentation (apico-basal ridges). The crown extends beyond the root in all directions and lacks a uvula. The root is high, particularly between the nutritive groove and crown (neck); the upper root has numerous small foramina on the labial face and elongate foramina extending onto each lobe of the lingual face. There are central and paracentral foramina in the deep nutritive groove.

In general, the crown is smooth, angular and not inflated as seen in "*Pseudohypolophus*" *ellipsis*; it is rhombic or hexagonal in shape and mesiodistally elongate. In lateral positions, the crown is offset relative to the nutritive groove. Viewed laterally, the crown, when unworn, is likely as high as the root; the non-lobe portion of the root is high and may be constricted; there is no distinct uvula; the labial crown face extends beyond the root. Viewed basally, the root is large with triangular or pentangular lobes. The nutritive groove is complete and deep with central and paracentral foramina. Labially, numerous small foramina are positioned just below the crown; the lingual root face has fewer foramina, but may be baso-apically elongate.

Discussion: The few specimens available provide an incomplete sample of ontogenetic and positional variations, making it difficult to interpret dentition-design. Occlusally, all fall into the design-envelope as provided by the articulated file series depicted in Neuman and Brinkman (2005, p. 170, fig. 9.2.a). The high root neck differentiates them from *Pseudohypolophus*, but compares very well with those included by Cappetta (1987, p.141, fig. 119a-d) in *Myledaphus bipartitus*. Lacking the characteristic apico-basal ridges, this tooth-design likely represents a new species; however, the condition and limited number of specimens preclude a proper description.

Genus *Pseudohypolophus* Cappetta and Case, 1975b

Type species: *Hypolophus* ?*mcnultyi* Thurmond, 1971, Late Cretaceous (Cenomanian), Texas, USA.
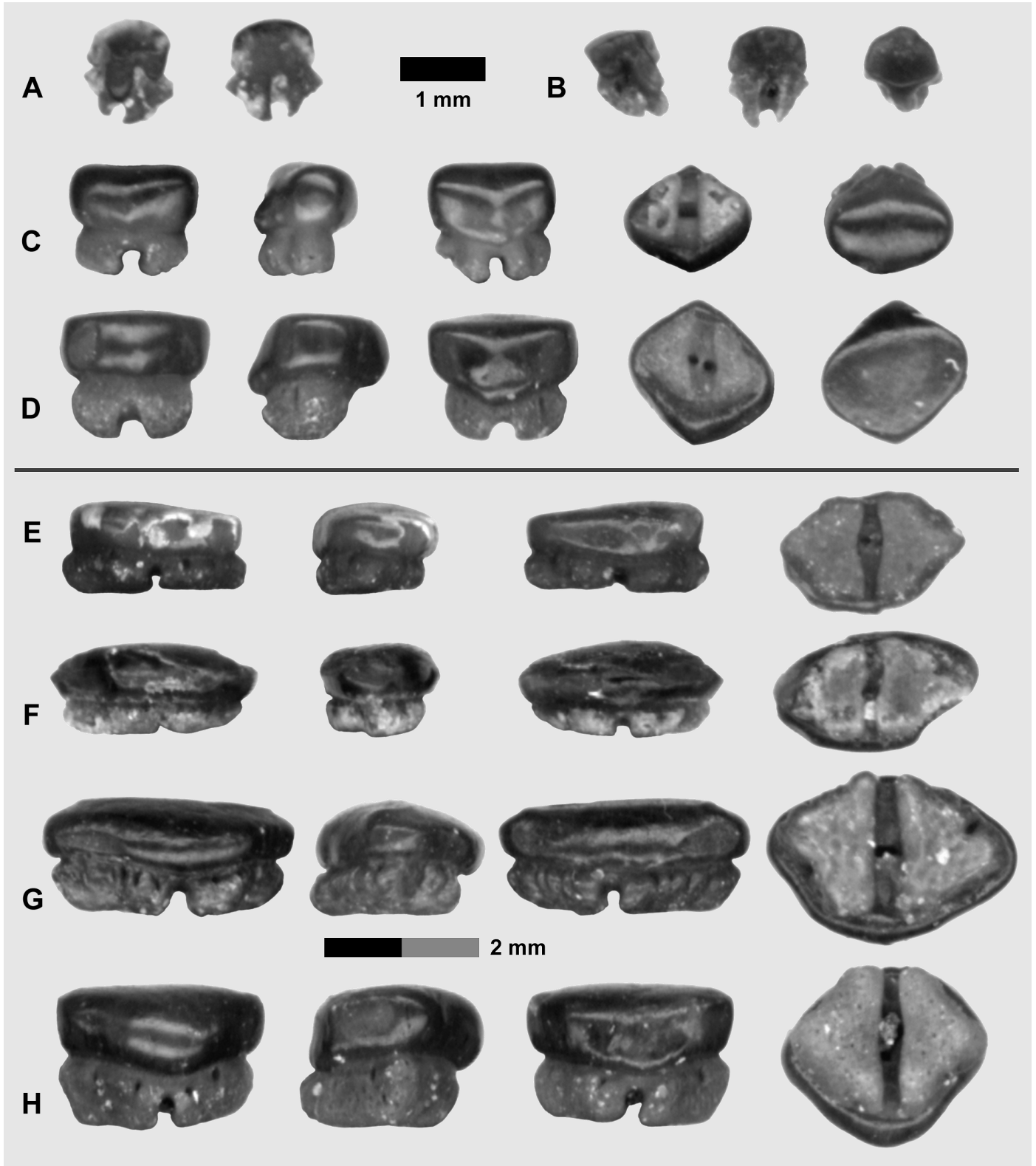
FIGURE 24. Specimen examples, perspectives noted from left to right, all specimens similarly scaled within groups. **A-B**, "*Rhinobatos*" sp., 1 mm scale bar, **A**, NMMNH P-60725, laterolingual and basal perspectives and **B**, NMMNH P-60726, laterolingual, basal and occlusal perspectives. **C-H**, *Protoplatyrhina* sp. aff. *P. renae*, **C-D**, labial, lateral, lingual, basal and occlusal perspectives, 1 mm scale bar, **C**, NMMNH P-60704 and **D**, NMMNH P-60707, **E-H**, labial, lateral, lingual and basal perspectives, 2 mm scale bar (9% reduction relative to above), **E**, NMMNH P-60712, **F**, NMMNH P-60702, **G**, NMMNH P-60700 and **H**, NMMNH P-60699 (mirrored).
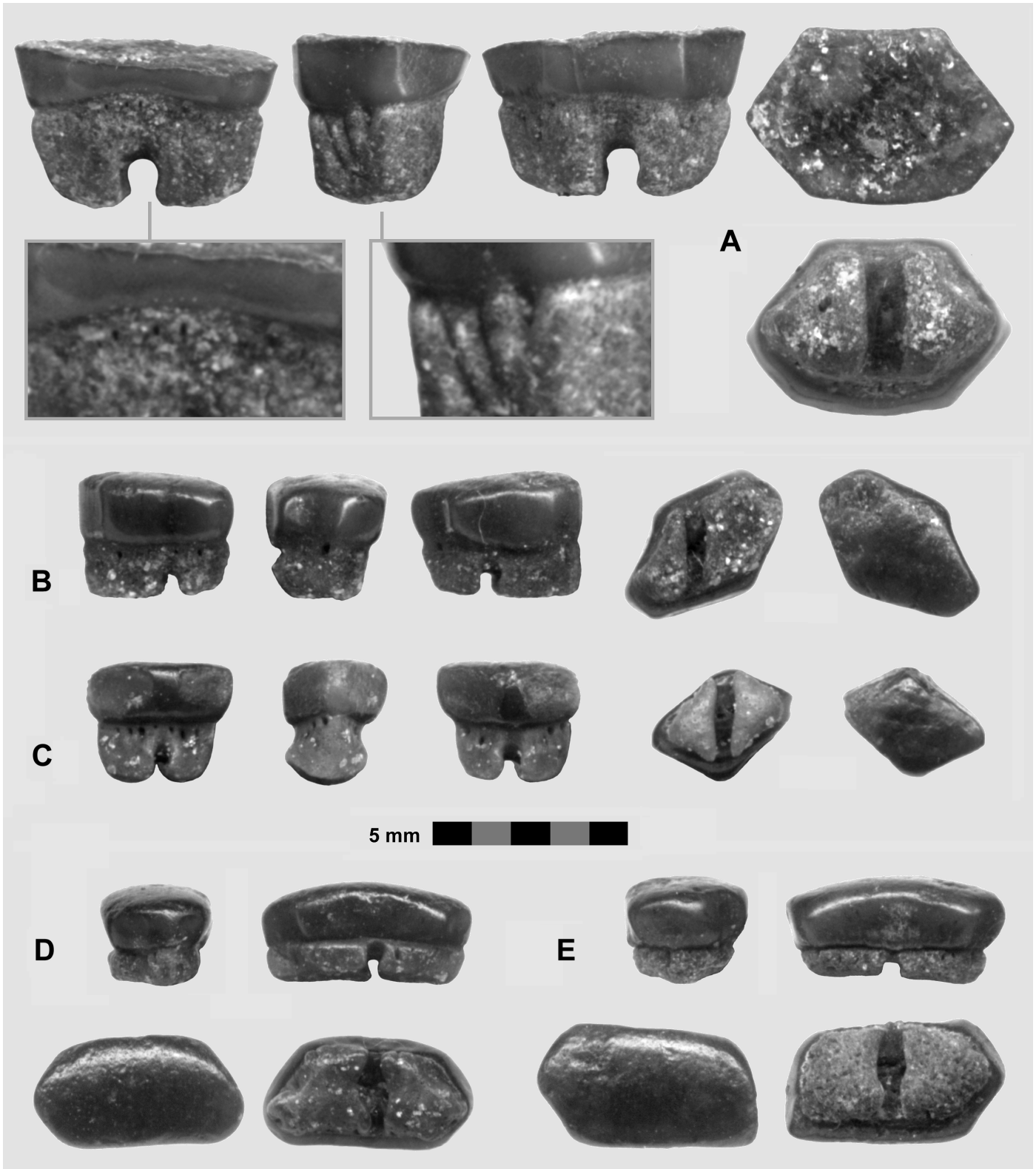
FIGURE 25. *Myledaphus* and "*Pseudohypolophus*" specimen examples, perspectives noted from left to right, all specimens similarly scaled (5 mm scale bar). **A-C**, *Myledaphus* sp., labial, lateral, lingual, occlusal and basal perspectives, **A**, NMMNH P-60682, anterior, 2x enlargements of foramina, **B**, NMMNH P-60686, distolateral and **C**, NMMNH P-60685, lateral. **D-E**, "*Pseudohypolophus*" *ellipsis* anterior variations, lateral, lingual, occlusal and basal perspectives, **D**, NMMNH P-60744 and **E**, NMMNH P-60766.

Remarks: *Pseudohypolophus mcnultyi* refers to a tooth morphology that has been broadly reported from the Aptian to Cenomanian of Texas (McNulty, 1964; Thurmond, 1971; Meyer, 1974; Cappetta and Case, 1975b; Welton and Farish, 1993). Meyer (1974, p. 156-57, text fig. 48) expanded the range to the Santonian and Campanian of the Mississippi Embayment and included teeth with inflated crowns. Cappetta and Case (1975b) erected *Pseudohypolophus* and attributed *mcnultyi*-like teeth from the Cenomanian of Texas to this new genus. Case et al. (2001, p. 92, pl. 2, figs. 37-42) erected *Pseudohypolophus ellipsis* for a specimen with an inflated crown from the Santonian of Georgia. As the dentition-design of *P. ellipsis* differs from that of *P. mcnultyi*, as discussed below, the Hosta Tongue specimens will be assigned to "*Pseudohypolophus*" to indicate the possibility that the genus may be a "wastebasket" for overly-generalized tooth morphology.

"*Pseudohypolophus*" *ellipsis* Case et al., 2001
Figs. 25D-E, 26A-N

Referred specimens: NMMNH P-60683-P-60684, P-60727-P-60789; 65 small (1.5 – 5.7 mm wide) teeth were prepared and imaged for descriptive purposes. Although not fully cleaned, specimens over 3 mm in width (NMMNH P-60790-P-60793, n = 338) all appeared to be attributable to this taxon. Smaller specimens not removed from matrix (n = 638) included both *Pseudohypolophus* and *Protoplatyrhina* morphologies and could not be differentiated without preparation.

Description: Crown is inflated, pentagonal or hexagonal in shape and mesiodistally elongated with rounded margins; in smaller examples, the median teeth may be more circular or rhombic. In lateral positions, the crown is offset relative to the nutritive groove. Viewed laterally, the crown is higher than the root, there is no distinct uvula and the labial crown face extends beyond the root.

The root is low, but large, with pentagonal or triangular lobes. The nutritive groove is complete and moderately deep with central and paracentral foramina; a weak secondary groove (Fig. 26D, G) may be present in some median file(s). Labially, numerous small foramina are positioned just below the crown; the lingual root face has fewer foramina high on the root. The external root face may have a weak laterolingual notch that often includes a small foramen.

Discussion: The holotype of this species (Columbus State University, CSUK97-2-13) was re-examined and found to be half the size (4.7 mm, rather than "approximately 1 cm in its overall width") as described and figured by Case et al. (2001). This smaller size is within the range present in the Hosta specimens.

Although not noted by Case et al. (2001) when describing these teeth, an important characteristic is the orientation of the crown relative to the nutritive groove (coronal offset). In medial teeth (Fig. 26A, B) the crown axis is perpendicular to the groove; distally, the crowns become progressively more offset until the ?penultimate position (Fig. 26M), which is rotated nearly 40-degrees relative to the nutritive groove. This continuous arch is different than Thurmond's (1971, p. 221) original *P. mcnultyi* description, which stated: "Roots slightly smaller than crown, not offset in hexagonal teeth but offset in rhombic specimens." – a more angular row arrangement. In "*Pseudohypolophus*" *ellipsis*, only the smallest teeth (juvenile) might be referred to as rhombic, and those are medially-positioned, and display little coronal offset. As the Hosta teeth differ from the original description, and its tooth-design is more similar to the *P. ellipsis* form, they have been attributed to this species.

Compared with *Protoplatyrhina* sp. aff. *P. renae*, similarly-sized teeth of the latter tend to have: a short broad uvula; more distinct marginolingual foramen; lower, more lingually positioned root; more angular less elongate crown; and less coronal offset.

DERMAL ELEMENTS

Various dermal elements (denticles, scutes, tubercles, etc.) are common in the sample from NMMNH locality 297. As too little is known to assign these items to a particular taxon, they were omitted from the systematics discussion, but they have been included separately to document their presence and provide a relative abundance for comparative purposes with other assemblages.

Form 1 (Fig. 27A-C)

Referred specimens: NMMNH P-61516-P-61517, P-61522, P-61540.

Remarks: The most common morphology (n = 215) is a rajiform-like denticle characterized by a long, narrow, distally-inclined cusp and a raised base that is thin, dense and has a concave base. Depending on body location, the denticle may be elongate or round. Due to their high abundance, these are likely associated with one of the more common batoids in the fauna – *Ischyrhiza*, *Ptychotrygon* or *Pseudohypolophus*.

Form 2 (Fig. 27D-G)

Referred specimens: NMMNH P-61524-P-61526, P-61528, P-61539.

Remarks: Numerous items (n = 122) with low circular crowns are present; the bases may be low or very massive. Small examples may appear to be teleost pharyngeal fragments; however, the very deep base and somewhat angular shape are more characteristic of a dermal plate.

Form 3 (Fig. 27H-K)

Referred specimens: NMMNH P-61520, P-61530-P-61531, P-61536, P-61538.

Remarks: This morphology (n = 18) is highly distinctive with its low, broad, flat and smooth crown; the low dense root has a concave basal face.

Form 4 (Fig. 28A-C)

Referred specimens: NMMNH P-61519, P-61532, P-61534.

Remarks: Three varying designs have been grouped on the basis of the ridged, lower anterior crown face. Baso-apical articulation of one specimen (Fig. 28B) differentiates it from the other examples.

Form 5 (Fig. 28D-F)

Referred specimens: NMMNH P-61521, P-61527, P-61537.

Remarks: This grouping (n = 3) includes denticles with a circular base and laterally compressed, basically smooth crown positioned somewhat high above the base. Other than the smooth crown, this morphology is quite similar to those included as Form 4.

Form 6 (Fig. 28G)

Referred specimens: NMMNH P-61529.

Remarks: This morphology, represented by a single specimen, is quite distinct with its low stellate crown.

Form 7 (Fig. 28H-I)

Referred specimens: NMMNH P-61533, P-61535.

Remarks: These two denticles have a delicate stellate base with a highly cuspidate crown and could possibly represent positional variations of a rostral spine.

Form 8 (Fig. 28J-K)

Referred specimens: NMMNH P-61518, P-61523.

Remarks: These two items may represent more than one taxon. They are grouped on the basis of the lateral ridges and relative size.

HOSTA TONGUE ASSEMBLAGE

Nearly 9000 specimens were picked from the processed material, a total that would have been higher if all teleost vertebral examples were retained (only 1100+ included). This bias against selecting and cleaning all vertebrae makes their inclusion in relative abundance statistics mis-
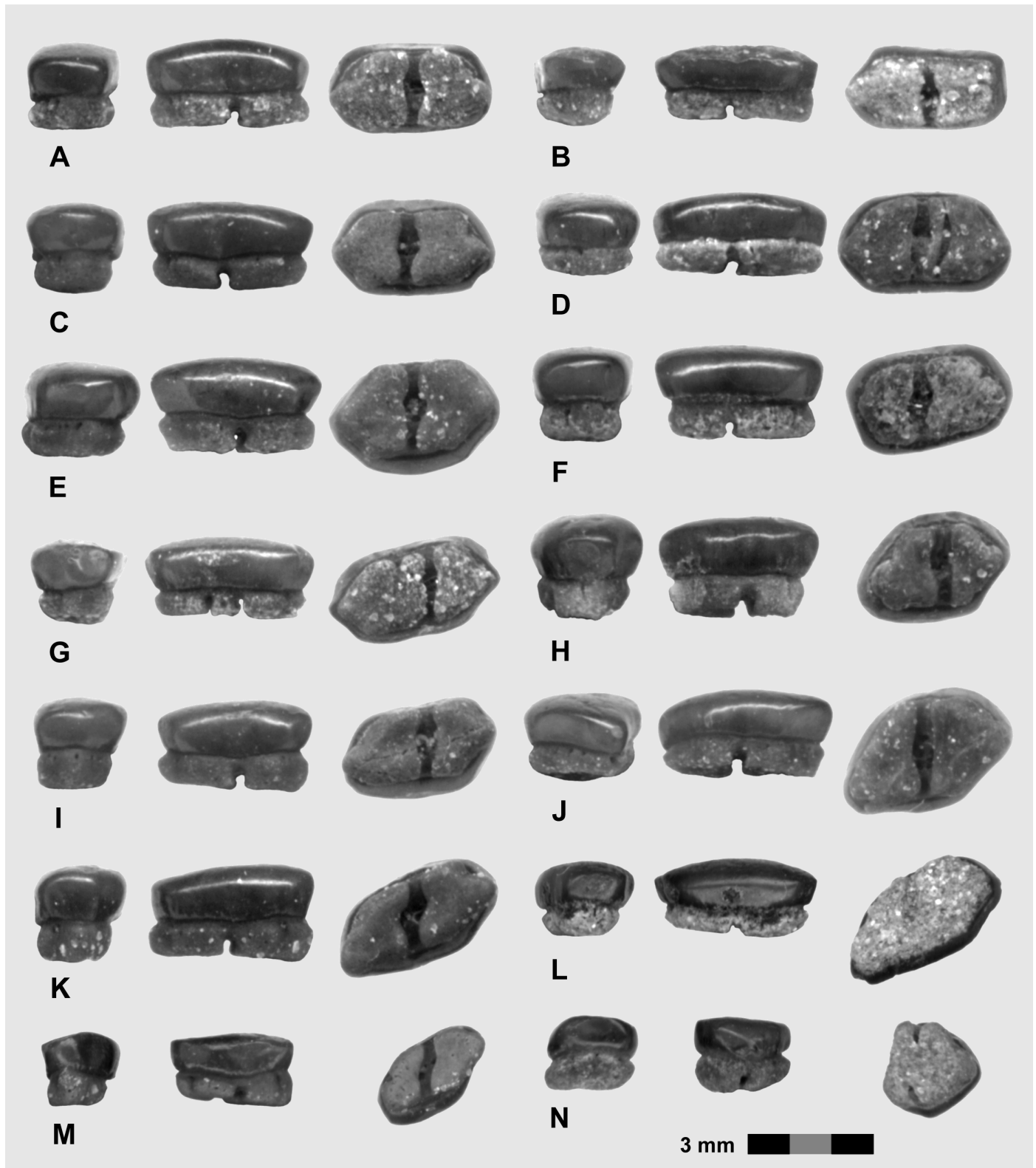
FIGURE 26. "*Pseudohypolophus*" *ellipsis* positional variations, perspectives (left to right) lateral, lingual and basal, all specimens similarly scaled (3 mm scale bar), mirrored specimens with '.m' suffix. **A**, NMMNH P-60775. **B**, NMMNH P-60773. **C**, NMMNH P-60727. **D**, NMMNH P-60743.m (second groove). **E**, NMMNH P-60785. **F**, NMMNH P-60770.m. **G**, NMMNH P-60772.m (second groove). **H**, NMMNH P-60740. **I**, NMMNH P-60781. **J**, NMMNH P-60777.m. **K**, NMMNH P-60764. **L**, NMMNH P-60754.m. **M**, NMMNHP-60760.m. **N**, NMMNH P-60731, terminolateral.
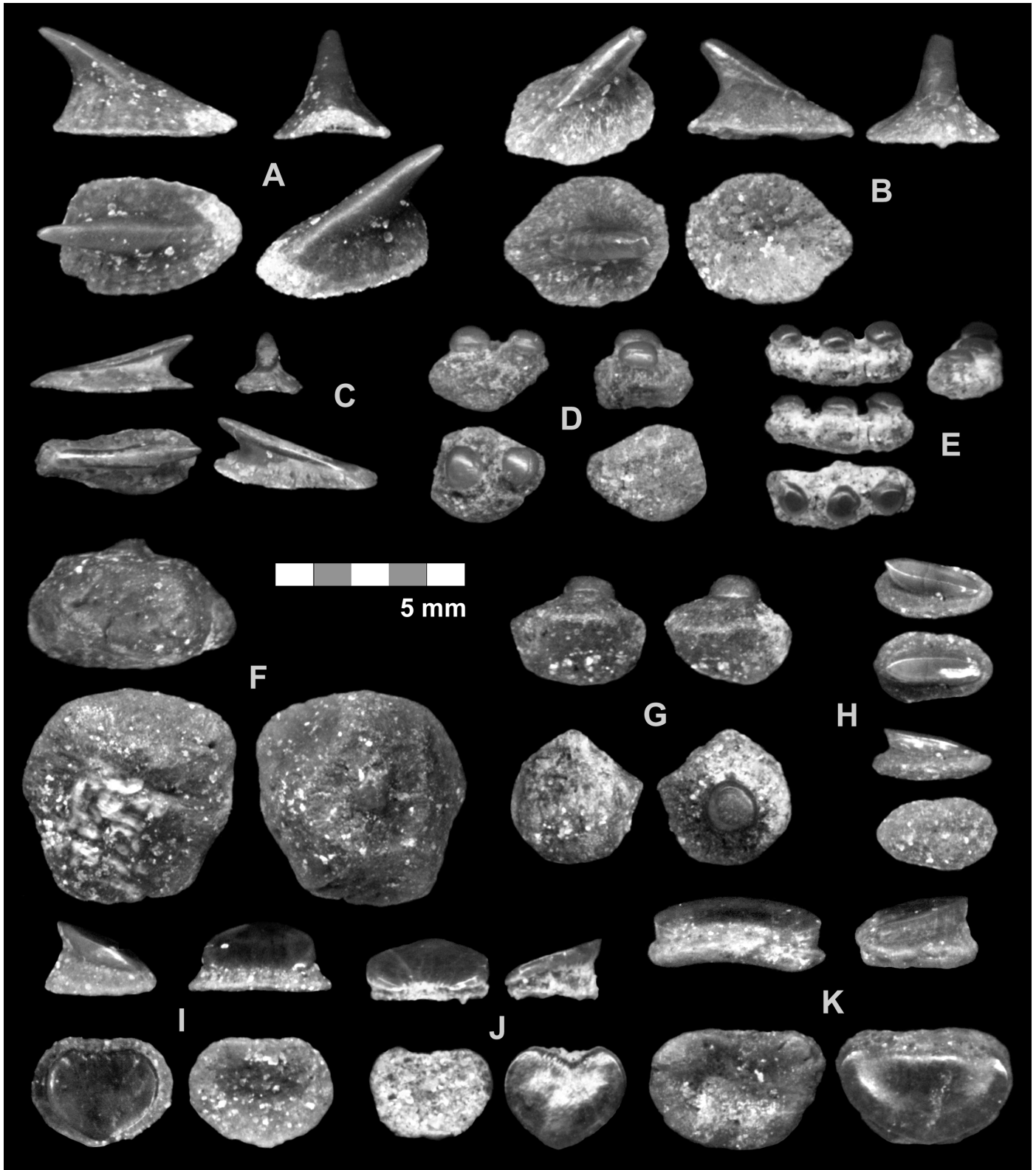
FIGURE 27. Dermal elements (denticles/scutes), all specimens similarly scaled, 5 mm scale bar. **A-C**, Form 1, **A**, NMMNH P-61516, 4 perspectives, **B**, NMMNH P-61522, 5 perspectives and **C**, NMMNH P-61517, 4 perspectives. **D-G**, Form 2, **D**, NMMNH P-61528, 4 perspectives, **E**, NMMNH P-61526, 4 perspectives, **F**, NMMNH P-61524, 3 perspectives and **G**, NMMNH P-61525, 4 perspectives. **H-K**, Form 3, **H**, NMMNH P-61536, 4 perspectives, **I**, NMMNH P-61520, 4 perspectives, **J**, NMMNH P-61530, 4 perspectives and **K**, NMMNH P-61531, 4 perspectives.
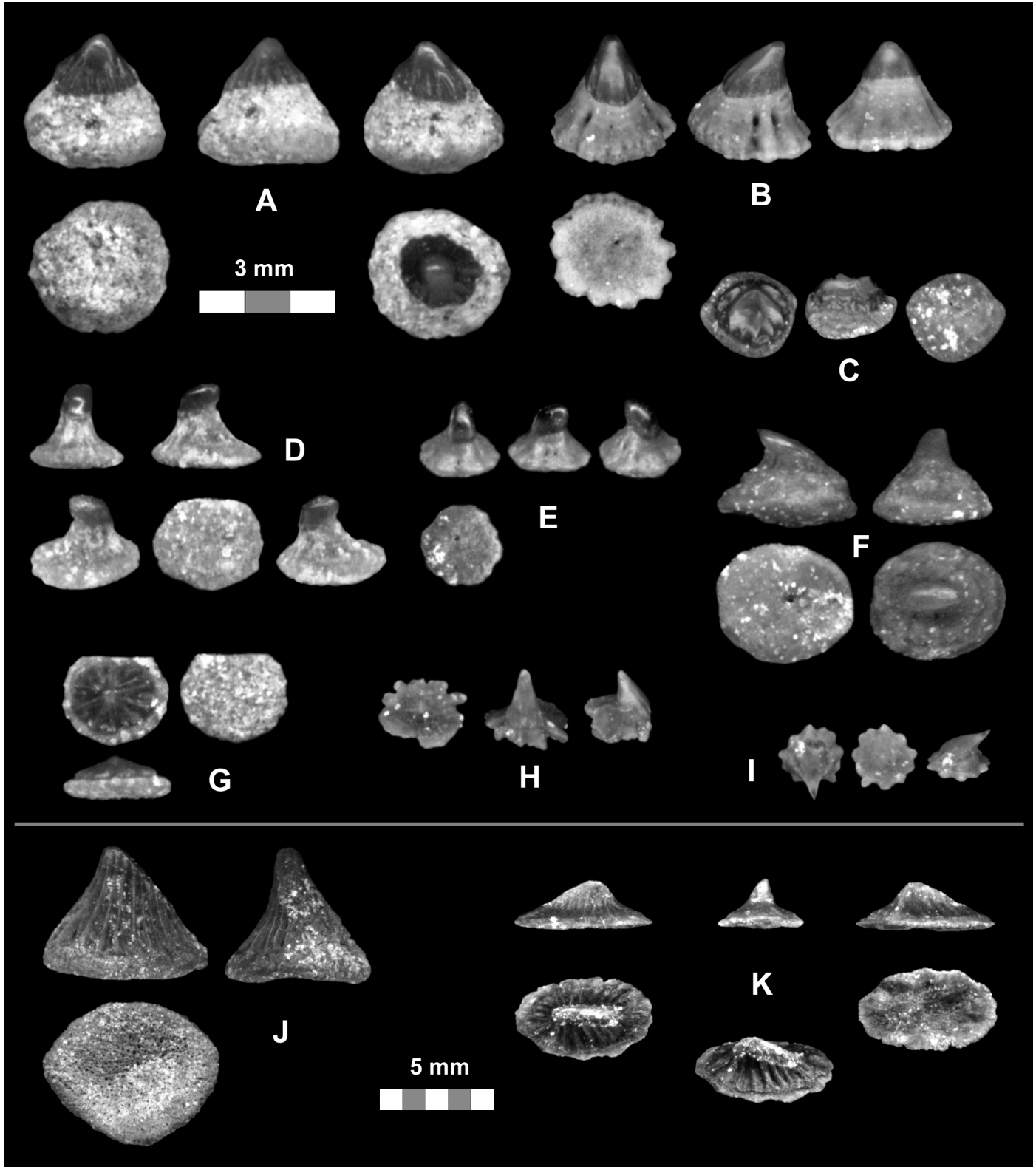
FIGURE 28. Dermal elements (denticles/scutes). **A-I**, all specimens similarly scaled, 5 mm scale bar, **A-C**, Form 4, **A**, NMMNH P-61519, 5 perspectives, **B**, NMMNH P-61534, 4 perspectives and **C**, NMMNH P-61532, 3 perspectives. **D-F**, Form 5, **D**, NMMNH P-61521, 5 perspectives, **E**, NMMNH P-61537, 4 perspectives and **F**, NMMNH P-61527, 4 perspectives. **G**, Form 6, NMMNH P-61529, 3 perspectives. **H-I**, Form 7, **H**, NMMNH P-61535, 3 perspectives and **I**, NMMNH P-61533, 3 perspectives. **J-L**, Form 8, similarly scaled, 5 mm scale bar, **J**, NMMNH P-61523, 3 perspectives and **K**, NMMNH P-61518, 6 perspectives.

leading, so they have been ignored. Very small (<1 mm) teleost teeth are under represented as well, due to a similar bias as noted with the vertebrae – only about 375 were included in the specimen count. The teleost component includes two gar scales (?*Atractosteus* sp. or *Lepisosteus* sp., NMMNH P-61498 and P-61497); however, other than *Anomoedus* sp. (NMMNH P-61183), *Enchodus* sp. (NMMNH P-61181) and a possible *Pachyrhizodus leptopsis* Cope, 1874 (NMMNH P-61183), most teeth lack diagnostic characteristics, and the vertebrae are less identifiable. Several reptile and dinosaur specimens were present but have little statistical significance. Lucas et al. (1988) discussed this topic and identified marine and terrestrial components: Trionychidae, ?Baenidae, Elasmosauriidae, Mosasauriidae, Crocodylia, Dromaeosauridae, Tyrannosauridae and Hadrosauridae.

From the selachian material (n = 6974), over half were mitsukurinid teeth (n = 3516, 50.4%), mostly *Scapanorhynchus puercoensis* n. sp. (Fig. 29). Various sclerorhynchoid teeth and rostral spines (n = 1568, 22.5%) were the next most abundant group, followed by the rhinobatoids (n = 1082, 15.5%). Minor components included: orectoloboids (n = 335, 4.8%; mostly *Cantioscyllium*); anacoracids (n = 132, 1.9%); hybodontoids (94, 1.4%) and other selachians (n = 247, 3.5%; mostly undetermined posteriors and eoptolamnids).

As noted above, the depositional environment of NMMNH locality 297 can be broadly identified as a beach, but further detailed analysis is needed to provide a more precise characterization. We note that the terrestrial taxa (dromaeosaur and hadrosaur) and freshwater turtle shell fragments suggest a riverine component to the assemblage. Also, the very high number of small *Scapanorhynchus* teeth suggests the site may have been near a nursery area.

Documented Santonian marine assemblages in North America are largely limited to those of Kansas, New Mexico and the Mississippi Embayment; the former being much different from the others. The Kansas chalk represents low energy, somewhat deep, off shore waters yielding a low diversity of well-preserved, sometimes articulated, material. In contrast, Mississippi Embayment and New Mexico assemblages reflect higher energy nearshore waters – reported diversity is much greater but limited to disarticulated specimens. Comparing and contrasting Santonian marine assemblages is subject to biases that must be acknowledged but cannot be resolved at this time: 1) Collecting, the Kansas Smoky Hill specimens were largely found by surface collecting chalk exposures; most micro-material was derived from the detailed processing of specimen matrices. The Mississippi Embayment collecting methods were not well-documented, but suggested that bulk sampling was often employed and sometimes processed to the sub-millimeter level. Early New Mexico reports were based on careful surface collecting of a large area while this paper relied on the bulk sampling and processing to the sub-millimeter level; 2) Relative abundance, Smoky Hill Chalk papers and Case et al. (2001) lack specifics that would permit refined judgments on relative abundance; and 3) Identifications, significant differences in identifications and/or the design-envelope for a given taxon permits only loose comparisons (generic level or broader). Although no conclusive comparisons can be drawn among these assemblages, there are similarities and differences worthy of note.

Smoky Hill Chalk – Santonian of Kansas, USA

The Smoky Hill Chalk of the Western Interior Seaway provides an extraordinary record of Late Cretaceous (Late Coniacian to Early Campanian) marine vertebrates including articulated teleosts, sharks and reptiles; as well as the remains of pterosaurs and toothed birds. Shimada and Fielitz (2006) summarized published reports (1868-2005) of fossil fishes collected from the Smoky Hill Chalk and included at least 15 elasmobranch taxa. Most of the original reports, however, provide no detail as to the locality or stratigraphic level in the chalk from which the specimens were recovered.

Everhart (2011) placed the Coniacian/Santonian boundary of the Smoky Hill Chalk between Hattin's (1982) Marker Units 6 and 7 and the Santonian/Campanian at approximately Marker Unit 18. Everhart (2011) noted that the selachian taxa currently known from the Santonian portion are: *Ptychodus mortoni*, *Squalicorax* "falcatus," *Squalicorax* "kaupi," *Pseudocorax laevis* (Leriche, 1906), *Cretoxyrhina mantelli*, *Cretalamna appendiculata* and *Rhinobatos* sp. Beeson and Shimada (2004) noted the presence of *Squalicorax volgensis* in Smoky Hill material deemed to be Santonian in origin; these specimens were never fully described.

In the Hosta Tongue *Pseudocorax* teeth have not been found and those of *Cretalamna* sp., *Cretoxyrhina mantelli* and *Ptychodus mortoni* are relatively scarce. Despite the low specimen count, the small surface area (Williamson et al., 1989) and limited bulk sampling (this paper) does not support a hypothesis that these sharks were any less common in New Mexico than Kansas

In broad terms, two *Squalicorax* species are present in each but they aren't necessarily comparable because of the wastebasket-nature of the specific names used for Smoky Hill Chalk anacoracids. It can be said that the Hosta Tongue teeth do not compare well with two Kansas forms, *S.* "falcatus" (= *Galeocerdo hartwellii* Cope, 1872) and *S.* "kaupi" (= *Galeocerdo crassidens*, Cope, 1872; both figured in Hussakof, 1908, fig. 6) and represented by associated tooth sets that have yet to be described. A full review of Kansas anacoracid material is required to determine if taxa from the Upper and Lower Chalk represent distinct species, and if so, whether those from the Upper Chalk are comparable with those from the Hosta Tongue.

Eutaw Formation – Santonian of Georgia, USA

Reports on selachians from the Eutaw Formation (Santonian) of the Gulf Coast were provided by Meyer (1974, Mississippi and Alabama) and Case et al. (2001, Georgia). A full direct review of their study material was not attempted, but the published observations were compared with those from New Mexico.

Eutaw Formation hybodontid teeth were attributed to *Hybodus* and *Lonchidion*/*Lissodus*; in the Hosta Tongue, these morphologies were included as *Meristodonoides* and *Lonchidion*, and were more diverse with the presence of ?*Egertonodus* and *Planohybodus*. *Ptychodus mortoni* was the sole ptychodontid species present in each fauna. Meyer (1974, p. 169) noted the presence of *Heterodontus* in the Eutaw Formation; angelshark-like teeth from the Eutaw were identified as *Squatina hassei* while the Hosta Tongue teeth were referred to ?*Parasquatina*. Orectolobiforms were relatively similar – *Cantioscyllium*, *Chiloscyllium* and *Squatirhina*/*Columbusia*; however, the Hosta Tongue included *Cederstroemia* and the Columbus State University collection included two unpublished specimens of the *Ginglymostoma* tooth-design (JB pers. obs.).

Larger anacoracid teeth were similar but identified differently; the New Mexico material was deemed to represent both *Squalicorax* sp. cf. *S. lindstromi* and *S.* sp. aff. *S. yangaensis*. Similar Eutaw Formation teeth were interpreted as *S.* sp. aff. *S. kaupi* by Meyer or *S. falcatus* by Case et al. The Hosta Tongue also included *Scindocorax novimexicanus* n. sp., a morphology not reported from the Gulf Coast.

Meyer (p. 317-321) reported *Anomotodon* sp. aff. *A. angustidens* (Reuss, 1845) from the Eutaw, a morphology not included by Case et al. or from the Hosta Tongue; this thresher-shark-like tooth-design is now referred to *Paranomotodon* Herman in Cappetta and Case 1975a. Both formations yield *Cretoxyrhina mantelli* teeth, but Meyer (1974, p. 252) included them as the subspecies *C. m. extenta* Leidy, 1873. Eoptolamnid teeth are less common in the Santonian. Meyer (1974) included none; Case et al. (2001, p. 91) reported *Cretodus borodini* Cappetta and Case, 1975a from Georgia; and Schwimmer et al. (2002) included *Cretodus semiplicatus* (Münster in Agassiz, 1843) in the Santonian of Georgia and Alabama. Neither of these species were present in New Mexico material; however, a previously undescribed taxon is present and will be described elsewhere.
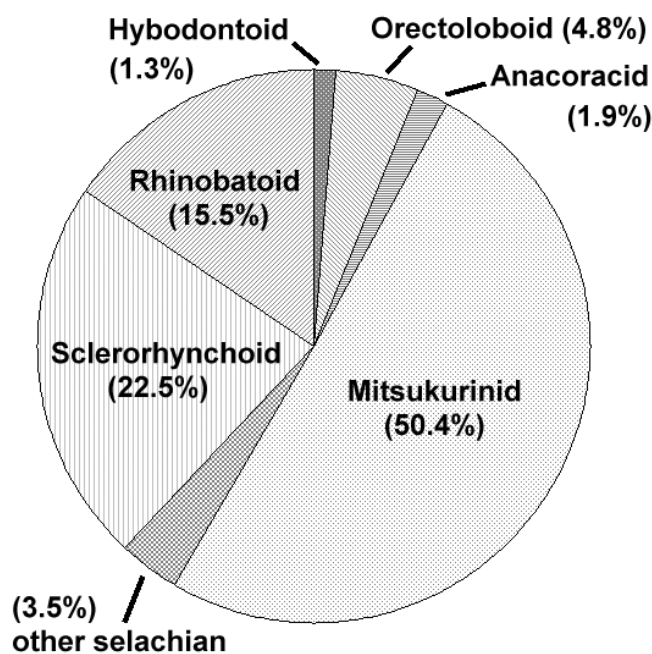
FIGURE 29. Relative abundances of selachian teeth from NMMNH locality 297.

Case et al. included large *Scapanorhynchus* teeth as *S. raphiodon*, while Meyer and this paper identify the design as *S. ?texanus and S.* sp. cf. *S. texanus*, respectively. Described from New Mexico is *S. puercoensis* n. sp., a tooth-design not reported from the Eutaw Formation. Case et al. (p. 90-91) erected *Microdontaspis tenuis* for small teeth interpreted by them as sandtigers; this morphology was included in New Mexico as *Scapanorhynchus* sp. cf. *S. tenuis*.

Least clear in both formations are the odontaspidids. The small *Microdontaspis* teeth of Case et al. were reassigned here to *Scapanorhynchus*; Meyer's *Odontaspis* sp. aff. *O. tenuis* (Davis, 1890) teeth appear to be odontaspidid although the actual genus is unclear based on the figures and description. The Hosta Tongue assemblage includes smooth-crowned *Carcharias*-like teeth, folded specimens displaying *Eostriatolamia* propensities and a unique design described as

Pueblocarcharias. All three reports included *Cretalamna*, but only Meyer (1974, p. 325-327) included scyliorhinid (type 2) teeth.

Both formations have somewhat similar batoid components, particularly the rhinobatoids. Each included the form referred to by Meyer (1974, p. 149) as "*Parahypolophus mcnultii*" or by Case et al. (2001, p. 92) as *Pseudohypolophus ellipsis*. Meyer did not report *Protoplatyrhina* and Case did not include *Rhinobatos* – both identified in New Mexico. Only the Hosta Tongue yielded teeth of the *Myledaphus* design.

The ptychotrigonids are similar but different; each formation included *Ptychotrygon eutawensis* Case et al., 2001, although Meyer (1974, p. 118) reported it as *P. triangularis eutawensis* (*nomen nudum*). The Hosta Tongue alone included *Texatrygon*, although Meyer (1974, p. 124-25) included a form as *Ptychotrygon* sp. aff. *P. hooveri*, which Case et al. (2001, p. 94-95) described as *Erguitaia benningensis*, family uncertain. Case et al. (2001, p. 95-96) also described *Ptychotrygon chattahoocheensis* from the Eutaw Formation. Both faunas included small rostral spines; Meyer included as *Ischyrhiza* sp., Case et al. (2001) as *Ptychotrygon* sp. or the newly described *Ischyrhiza georgiensis* and the New Mexico examples as ?*Ptychotrygon eutawensis* or ?*Texatrygon stouti*. More striking are the differences within the sclerorhynchids. Both faunas include *Sclerorhynchus* and *Ischyrhiza*, but in the case of the Hosta Tongue, the *Ischyrhiza* oral teeth are inordinately small. Both Eutaw Formation papers included *Borodinopristis*, however, there is no evidence of the taxon in the Santonian of New Mexico. In contrast, *Onchosaurus* rostral spines were reported by Williamson et al. (1989) from the Hosta Tongue and not from contemporary sediments in Georgia or Mississippi.

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APPENDIX 1 – TOOTH SET DEVELOPMENT AND METRICS

Scapanorhynchus puercoensis n. sp. teeth were cleaned and, if condition permitted, imaged. Images were then oriented and digitally mirrored to appear as from the lower left hand quadrant. The (imaged) specimens were then sorted by general tooth-design: crown shape, cusp inclination, root thickness and lobe design; they were then attributed to upper and lower jaws based on crown and root characteristics.

POSITIONAL NOMENCLATURE

Three different positional reference schemes are included in the chart: a simple one-up numbering within the quadrant (**File**), the nomenclature used in this paper (**Pos**), and that used in Shimada and Seigel (2005) for *Mitsukurina owstoni* (**sPos**), which was interpreted on the basis of corresponding tooth-designs. Some tooth positions present in *Scapanorhynchus puercoensis* n. sp. were not present in Shimada and Seigel's *M. owstoni* illustration (fig. 2).

DOCUMENTED METRICS

Teeth were similarly oriented with the marginal crown-root contacts on a similar plane (AB) by digital rotation of the image. Tooth width (**Tooth wid.**) was deemed to be the widest horizontal distance between perpendicular lines at the margins of the oriented root; tooth height (**Tooth hgt.**) was the perpendicular distance between the lowest point of the root and a line placed parallel to AB at the level of the apex. Measurements were derived by converting the digital distances in pixels to millimeters. Crown width was considered the distance between the two marginal contact points of AB; crown height (as included in the **Crown h/w** factor) is the perpendicular distance between AB and the cusp's apex (C). Crown inclination (**Crown inclin.**) was derived from the mid-point of AB to C.
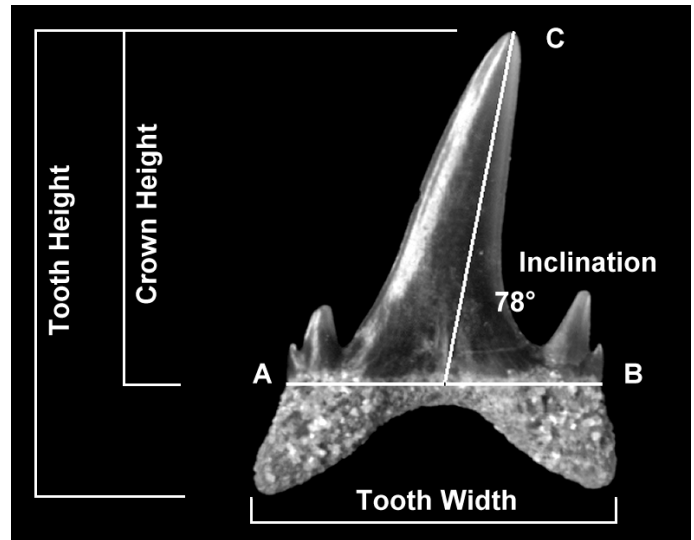
Shimada and Seigel's mitsukurinid total length (TL) equations were based on crown height without a clear definition of tooth orientation or the basal position of the measurement. The crown height (**Crown hgt.**) measurement, as included in Table 1, represents an oriented tooth (as defined above) and blends crown height (as defined above) with the perpendicular height of the medial root-crown contact to the apex.

POSITIONAL ARRANGEMENT

Anteriors were positioned using general lamniform anterior propensities. In upper laterals, the first was positioned by virtue of a labiolingually compressed mesial lobe; the second chosen for its elongated mesial lobe; the third and fourth are highly subjective and the order may be misinterpreted; remaining mesolaterals and distolaterals could be arranged using a combination of height/width and crown inclination. Lower laterals were similarly arranged but metrics (height/width) were relied on, starting in the mLP4 position. Intermediates were placed based on cusp shape and inclination. The specimen referred to herein as a parasymphyseal was placed in the upper jaw on the basis of lateral profile; arguably, this tooth-design could be deemed an upper A0.

SPECIMEN RESCALING

Insufficient specimens were available to provide a full group of teeth from similarly-sized individuals. The most common lateral sizes were used as a proposed baseline for tooth size. Lateroposterior images were then rescaled to harmonize root size and basal cusp width between adjacent files. The anterior groups were then similarly rescaled then harmonized as a group with the lateroposteriors. The average rescaling was 92%, but the most relevant files (anteriors and mesolaterals 1-5) were 96%. The embedded scale bar in the tooth set image (Fig. 28) was adjusted accordingly. Image rescaling factors are included under the table title **Adj. factor**.

Explanation of measurement protocols using NMMNH P-60986 as an example.

TOTAL LENGTH ESTIMATION

Shimada and Seigel (2005) tendered a series of positional equations for *Mitsukurina owstoni* teeth to estimated body size (TL) based on crown height; the authors suggested that they should be tested with mitsukurinid fossil material. The proposed *Scapanorhynchus puercoensis* n. sp. tooth set appeared to represent an opportunity to apply and evaluate that proposal. The tooth orientation was not specified; the measurement was defined as, "the maximum vertical enameloid height on the labial side" of the functional row. Although this definition appears definitive, applying it to isolated teeth creates ambiguities in both orientation and longest vertical distance; therefore, the previous clarification for the crown height (in mm) as included herein. Before applying their equations, actual crown height was adjusted by the Adjustment factor (**Adj. factor**) and included as **Adj. hgt**. The resulting body length results are included under **Shimada TL**.

Because *Mitsukurina owstoni* lateroposterior tooth counts vary between individuals and the greatest difference is attributable to posterior-most positions (distolaterals), only the anterior files and the first five lateroposteriors (mesolaterals) were used for the estimation. Using the equations, TL estimations would be: uAnt = 69, umLP = 80, lAnt = 56 and lmLP = 72 cm -- average 70 cm. The mesolaterals yield relatively similar results (average 76 cm). The anteriors, however, appear to be significantly different. Not only do they yield a different estimation of TL (average 63 cm), but individual tooth positions within each hollow vary more greatly: 54 to 82 in the upper and 40 to 80 cm in the lower.

There was no underlying expectation that results would be consistent as these represent different genera, most strongly expressed in the anterior hollow designs; these comparative metrics serve as collateral evidence of that difference. Incorrect rescaling assumptions in this paper may account for some of the greater variations seen in the upper mesolaterals. The overall consistency of mesolateral TL calculations (72 to 80 cm) suggests there may be an underlying correlation in lateroposterior hollow designs and that the average (76 cm) may be a reasonable estimation of total length.

TABLE 1. *Scapanorhynchus puercoensis* n. sp. metrics and calculations.

Cat. No. NMMNH	Jaw	File	Pos	Tooth (mm) wid.	Tooth (mm) hgt.	Crown hgt. (mm)	Crown h/w factor	Crown Inclin.	Adj. factor	Adj'd hgt. (mm)	Shimada sPos	Shimada TL (cm)
P-60934	upr	1	ps	1.5	7.5	3.6	3.83	91	0.90	3.2		
P-60929.m	upr	2	A1	4.4	9.6	7.1	2.16	91	1.11	7.8	S	53
P-60928	upr	3	A2	7.4	10.7	7.8	1.46	85	0.92	7.2	A1	72
P-60920.m	upr	4	A3	7.1	11.0	8.0	1.28	90	0.75	6.0	A2	82
P-61029	upr	5	I1	3.6	5.4	3.7	1.35	88	0.95	3.5	I1	
P-61023	upr	6	I2	2.5	4.0	2.7	1.14	72	1.15	3.1	l2	
P-60968.m	upr	7	mL1	6.5	7.2	5.2	1.03	78	1.10	5.7	L1	92
P-60965.m	upr	8	mL2	6.9	8.1	5.9	1.06	75	1.03	6.1	L2	73
P-60988.m	upr	9	mL3	8.0	10.2	7.2	1.03	73	0.82	5.9	L3	73
P-60957.m	upr	10	mL4	6.9	8.0	5.5	0.99	76	1.00	5.5	L4	87
P-60969	upr	11	mL5	7.4	8.4	6.0	0.94	76	0.86	5.1	L5	76
P-60976	upr	12	mL6	6.6	7.5	5.3	0.93	73	0.92	4.9	L6	83
P-60992.m	upr	13	mL7	5.7	5.8	4.1	0.86	75	1.00	4.1	L7	72
P-60994	upr	14	dL1	5.2	5.2	3.6	0.74	70	0.92	3.3	L8	71
P-60981.m	upr	15	dL2	5.8	5.6	3.6	0.70	68	0.69	2.5	L9	92
P-60982.m	upr	16	dL3	4.3	3.8	2.4	0.69	65	0.81	2.0	L10	119
P-61018	upr	17	dL4	3.3	2.9	1.8	0.66	67	0.96	1.7	L11	143
Average all uppers									**0.935**			
Average ant + 5/mLP									**0.963**			**74.7**
P-61026	lwr	1	A0	2.0	6.0	3.9	2.84	89	1.20	4.7	a1	80
P-60926	lwr	2	A1	4.9	11.0	7.7	2.23	89	1.01	7.8	a2	60
P-60915.m	lwr	3	A2	8.2	13.3	9.7	1.73	87	0.84	8.1	i1	45
P-60932.m	lwr	4	A3	7.8	10.6	7.3	1.43	88	0.86	6.3	l1	40
P-60970.m	lwr	5	mL1	7.6	9.3	6.9	1.12	96	0.85	5.9	l2	75
P-60967.m	lwr	6	mL2	6.5	8.1	6.1	1.23	90	1.00	6.1	l3	64
P-60990	lwr	7	mL3	6.8	8.4	6.1	1.11	93	0.94	5.7	l4	74
P-60979	lwr	8	mL4	6.4	7.6	5.5	1.08	89	0.98	5.4	l5	74
P-60991	lwr	9	mL5	6.1	6.7	4.9	1.05	88	1.00	4.9	l6	76
P-60959	lwr	10	mL6	7.3	8.2	5.9	0.99	87	0.76	4.5	l7	103
P-60973	lwr	11	dL1	5.8	6.6	4.9	0.98	87	0.76	3.7	l8	109
P-60996.m	lwr	12	dL2	4.4	5.3	3.9	0.95	84	0.86	3.3	l9	178
P-60997.m	lwr	13	dL3	3.6	4.2	2.9	0.89	83	0.85	2.4	110	204
P-60998	lwr	14	dL4	3.6	3.5	2.5	0.77	90	0.81	2.0	111	222
Average all lowers									**0.909**			
Average ant + 5/mLP									**0.964**			**64.3**
Average all upr & lwr									**0.922**			
Upr-lwr ant + 5/mLP									**0.963**			**69.5**