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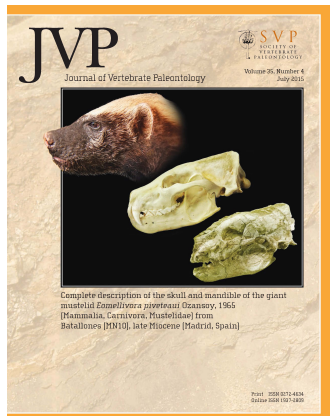
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A new clade of putative plankton-feeding sharks from the Upper Cretaceous of Russia and the United States

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A NEW CLADE OF PUTATIVE PLANKTON-FEEDING SHARKS FROM THE UPPER CRETACEOUS OF RUSSIA AND THE UNITED STATES

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ABSTRACT—*Eorhincodon casei* from Russia and *Megachasma comanchensis* from the United States are two Cretaceous taxa initially described as putative planktivorous elasmobranchs, but the type specimens of these two taxa were subsequently reinterpreted to represent taphonomically abraded teeth of an odontaspimid, *Johnlongia* Siverson (Lamniformes: Odontaspidae). Here, we redescribe the type materials of '*E. casei*' and '*M. comanchensis*' and describe additional specimens of these species from other Late Cretaceous localities in Russia and the United States. These specimens demonstrate that (1) the two fossil taxa are valid species; (2) they warrant the establishment of a new genus of presumed planktivorous sharks, *Pseudomegachasma*, gen. nov., to accommodate the two species; and (3) the new genus is sister to *Johnlongia* and together constitute a new subfamily Johnlonginae, subfam. nov., tentatively placed in the family Odontaspidae sensu stricto. This taxonomic placement indicates that the putative planktivorous clade was derived from a presumed piscivorous form (*Johnlongia*), with an implication that *Pseudomegachasma*, gen. nov., evolved a plankton-eating habit independent of the four known planktivorous elasmobranch clades (Rhincodontidae, Megachasmidae, Cetorhinidae, and Mobulidae). It also indicates that planktivorous diets evolved independently at least three times in the order Lamniformes (i.e., Megachasmidae, Cetorhinidae, and Odontaspidae), and more significantly, *Pseudomegachasma*, gen. nov., would represent the oldest known plankton-feeding elasmobranch in the fossil record. The present fossil record suggests that *Pseudomegachasma*, gen. nov., evolved in a relatively shallow-water environment in Russia in the early Cenomanian or earlier and subsequently migrated to the North American Western Interior Seaway by the mid-Cenomanian.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Megachasma pelagios Taylor, Compagno, and Struhsaker, 1983 ('megamouth shark'; Lamniformes: Megachasmidae), is a large (up to ca. 5.5 m total length [TL]) planktivorous shark (Compagno, 2001). Since the discovery of the extant *M. pelagios*, megachasmid teeth have been known from the Cenozoic fossil record (Cappetta, 2012), although the origin of megachasmids was suggested to have been rooted sometime in the Mesozoic (Shirai, 1996; Martin et al., 2002). Subsequently, Shimada (2007) reported a fossil shark from the Cretaceous of Colorado, U.S.A., which he attributed to a new megachasmid, *M. comanchensis* Shimada, 2007. However, because of the stratigraphic gap of fossil megachasmids between the mid-Cenomanian and late Paleogene, some workers expressed their skepticism of this claim (e.g., De Schutter, 2009; Maisey, 2012). Recently, Cappetta (2012:201, 252) explicitly dismissed Shimada's (2007) proposition by

suggesting that the type specimens of *M. comanchensis*, along with allegedly the oldest whale shark, *Eorhincodon casei* Nessov, 1999, from the early Cenomanian of Russia, represent "rolled [= taphonomically abraded] teeth" of the odontaspimid shark *Johnlongia* Siverson, 1996.

Here, we redescribe '*Eorhincodon casei*' and '*Megachasma comanchensis*' by reexamining previously described materials, including their type specimens, as well as examining newly collected specimens from Upper Cretaceous deposits in Russia (Fig. 1) and the United States to demonstrate that the two fossil taxa are valid species. However, we introduce a new genus to accommodate the two species (and replace the junior homonym *Eorhincodon*) with an interpretation that this megachasmid-like taxon does not have a direct phylogenetic link to Megachasmidae, represented by the single genus *Megachasma*. Rather, we consider the new taxon to represent a separate putative planktivorous shark clade that followed an earlier evolutionary pathway, convergent on the later evolution of the Megachasmidae. We also erect a new subfamily to accommodate the planktivorous clade along with its proposed sister taxon, *Johnlongia*.

*Corresponding author.

Institutional Abbreviations—**CNIGRM**—Chernyshev’s Central Museum of Geological Exploration, St. Petersburg, Russia; **FHSM**, Fort Hays State University, Sternberg Museum of Natural History, Hays, Kansas, U.S.A.; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; **SSU**, Saratov State University, Saratov, Russia; **ZIN PC**, paleontological collection, Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia.

SYSTEMATIC PALEONTOLOGY

Order LAMNIFORMES Berg, 1958

Family ODONTASPIDIDAE Müller and Henle, 1839

Subfamily JOHNLONGINAE, subfam. nov.

Type Genus—*Johnlongia* Siverson, 1996.

Included Genera—*Johnlongia* Siverson, 1996 (Fig. 2), and *Pseudomegachasma*, gen. nov. (Figs. 3, 4).

Etymology—Named for the genus *Johnlongia* that typifies this group.

Diagnosis—Lamnoids possessing anterior teeth with strongly lingually curved cusp; extremely tall lingual protuberance of root; exceptionally prominent nutritive groove that deeply bisects root; and one or more enlarged, lateral root foramina immediately lingual to mesial and distal extremities of tooth neck.

Remarks—*Johnlongia* and *Pseudomegachasma*, gen. nov., differ significantly from all other described *Odontaspis*-like genera by (1) their *Megachasma*-like anterior teeth (particularly evident in *Pseudomegachasma*, gen. nov.) with an extremely large lingual root protuberance; (2) the lack of one or both lateral cusplets in some large anterior teeth (presumably from adult individuals) of species in both genera (Siverson 1996:pl. 5, fig. 1; Fig. 4Y); and (3) the greatly enlarged lateral foramina on the lingual side of the root (Figs. 2K, 3AB) even in commissural teeth (Siverson 1996:pl. 5, fig. 14). Although *Cenocarcharias* Cappetta and Case, 1999, exhibits similar foramina (Cappetta, 2012:fig. 184E), they are not as large as those on most teeth of *Johnlongia* and *Pseudomegachasma*, gen. nov. The unique dental features of *Johnlongia* and *Pseudomegachasma*, gen. nov., warrant taxonomic distinction and justify the establishment of a new suprageneric taxon. The decision to establish a new subfamily rather than a new family was influenced by the lack of more complete remains (e.g., associated teeth and/or skeletal remains).

The family Odontaspidae sensu lato traditionally comprises two extant genera, *Carcharias* Rafinesque, 1810, and *Odontaspis* Agassiz, 1838 (e.g., Compagno, 1984), that are often collectively referred to as ‘sandtiger sharks.’ However, recent morphological (Compagno, 1990; Shimada, 2005) and molecular (Martin et al., 2002; Heinicke et al., 2009; Vélez-Zuazo and Agnarsson, 2011; Naylor et al., 2012) studies have suggested that ‘Odontaspidae’ is likely non-monophyletic; thus, the genera *Carcharias* and *Odontaspis* may be better assigned to two separate families, the Carchariidae Müller and Henle, 1838, and Odontaspidae sensu stricto, respectively. There are also numerous tooth-based fossil taxa classified into Odontaspidae sensu lato (e.g., Cappetta, 2012, recognizes 16 extinct odontaspidae genera), but given the difficulties in deciphering even the phylogeny of extant lamniforms where whole specimens and molecular samples are at hand, it is probably naive to assume that teeth of all Cretaceous ‘sandtiger sharks’ are referable to this single family in a strict sense. It is quite possible that many of the early ‘sandtiger’ forms, including *Johnlongia* and *Pseudomegachasma*, gen. nov., are related rather distantly to the Carchariidae and/or Odontaspidae sensu stricto. We tentatively assign Johnlonginae, subfam. nov., to the Odontaspidae sensu stricto rather than to the Carchariidae based on the comparatively tall and upright main cusp in distally situated teeth of *Johnlongia* (e.g., Siverson 1996: pl. 5, figs. 14, 15; for dentition of extant *Carcharias* and

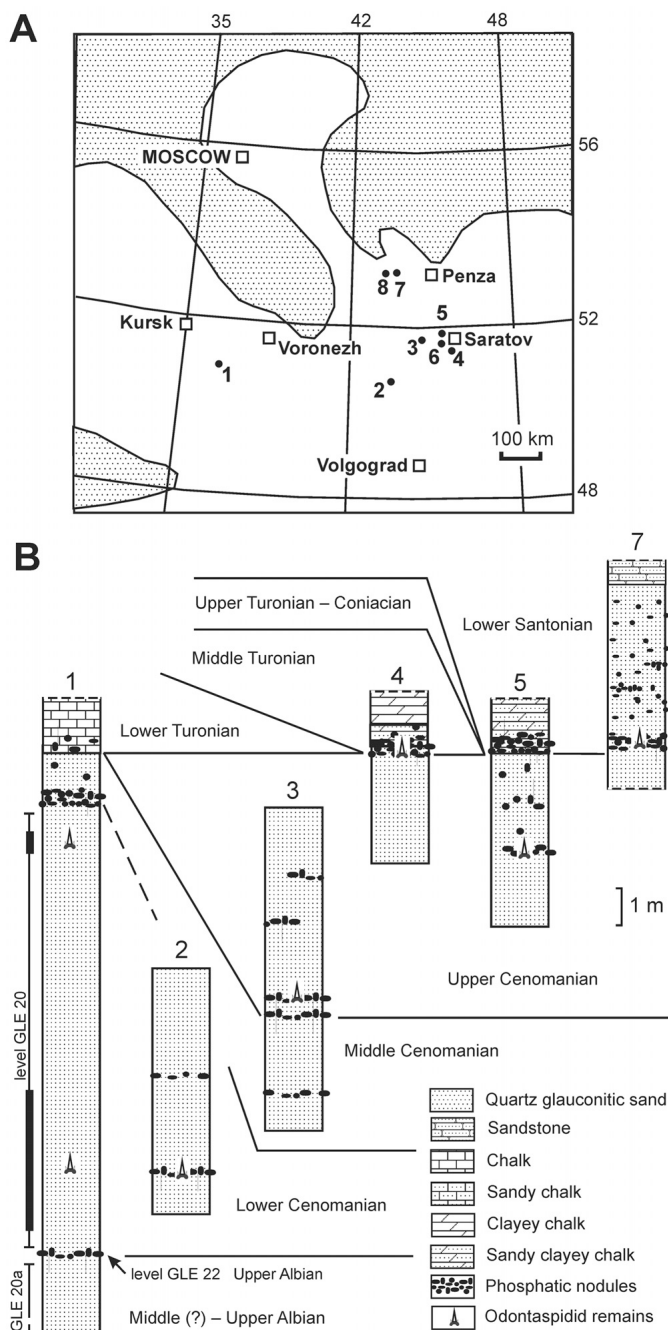


FIGURE 1. Geographic and stratigraphic positions of ‘odontaspid’ shark remains from Russia described in this paper. **A**, Cenomanian paleogeographic map (after Sobolevskaya, 1951) showing land masses (dotted area) and sea (white space) with discussed fossil localities (1, Lebedinskij quarry locality; 2, Melovatka-5 locality; 3, Bezobrazovka-1 locality; 4, Bagaevka locality; 5, Saratov-1 locality; 6, Saratov-2 locality; 7, Kikino locality; 8, Mochaleika locality; see Supplementary Data Appendix S1 for detailed stratigraphic information); **B**, stratigraphic sections at selected localities indicating odontaspid-bearing horizons (Fig. 1 A).

Odontaspis, see Compagno, 1984:217, 220, 221) and the large relative size of the lateral cusplets in teeth from young individuals of this extinct genus (e.g., Siverson, 1996:pl. 5, fig. 4; note that lateral cusplets are highly reduced or absent in very young free-swimming extant *Carcharias*; see Bass et al., 1975). In extant *Carcharias*, distally located teeth typically have a very low,

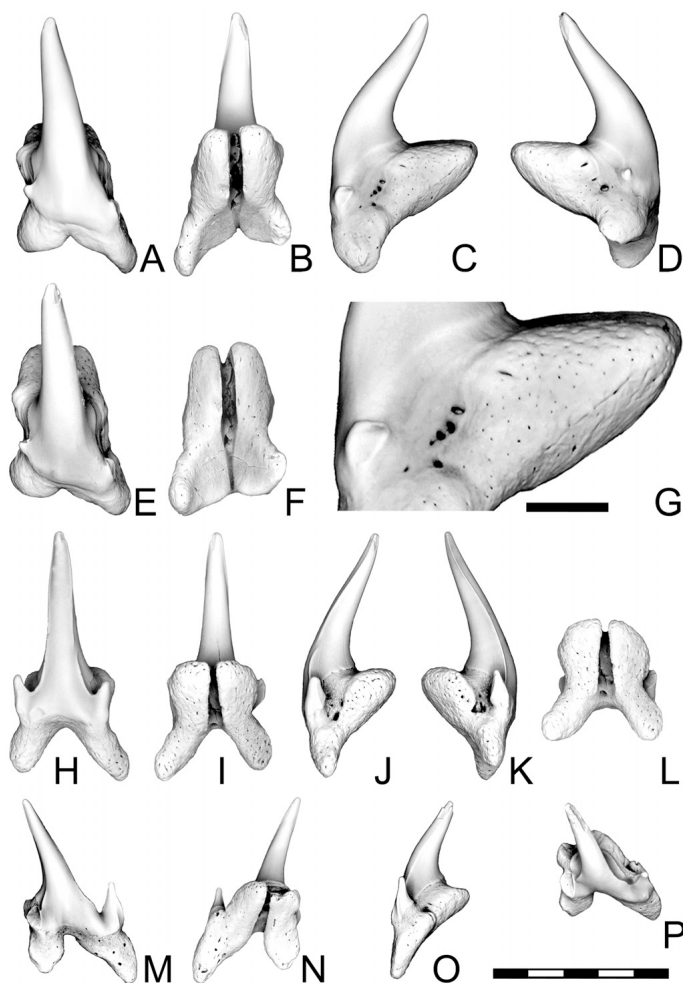


FIGURE 2. Teeth of *Johnlongia allocotodon* Siverson, 1996, from upper Cenomanian Melovatka Formation in Saratov Province (5° in Fig. 1), Russia. A–G, SSU 155/93 in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views plus close-up view of prominent lateral root foramina on mesial root surface (G; cf. Fig. 2C); H–L, SSU 155/94 in labial (H), lingual (I), mesial (J), distal (K), and basal (L) views; M–P, SSU 155/95 (distal cusplet broken) in labial (M), lingual (N), mesial (O), and apical (P) views. Scale bars equal 5 mm (A–P except for G) and 1 mm (G).

mesiodistally elongated crown and are densely spaced to collectively form a pavement-like surface (e.g., Cunningham, 2000:pl. 10, fig. 1). There is no indication that *Johnlongia* and *Pseudomegachasma*, gen. nov., had crushing-type teeth. In the absence of associated skeletal and dental remains, we take a conservative approach by not establishing a new taxon above subfamily level for *Johnlongia* and *Pseudomegachasma*, gen. nov.

Genus *PSEUDOMEGACHASMA*, gen. nov.

Type Species and Type Locality—*Eorhincodon casei* Nessov, 1999, from Polpino Formation (lower Cenomanian) of Lebedinskij quarry, Belgorod Province, Russia (see below for detail; '1' in Fig. 1).

Other Included Species—*Megachasma comanchensis* Shimada, 2007, from basal Greenhorn Limestone (middle Cenomanian) in southeastern Colorado, U.S.A. (see Shimada et al., 2006; Gallardo et al., 2013) (see below for detail).

Etymology—Named for its superficial resemblance to the megamouth shark in tooth morphology: *pseudo* (Greek 'pseudes') = false; *Megachasma* = genus name of megamouth shark.

Diagnosis—Small lamnoid teeth (known specimens no more than 9 mm in total tooth height) consisting of tall crown (erect or inclined), well-marked tooth neck on lingual side, and massive root, along with the following combination of characters; crown with sharply pointed apex and sprawling base; crown apex strongly directed lingually, giving hook-like appearance, but crown apex may be flexed occlusally; mesial and distal cutting edges on crown weak and blunt, and may be absent from crown base to mid-portion of crown; crown surfaces smooth; lingual crown face strongly convex and labial face moderately convex; basal margin of crown gently convex or concave on labial face and broadly and deeply concave on lingual face; labiolingual length and mesiodistal length at crown base about equal; short sharp or blunt lateral cusplet, or mesiodistally oriented low heel, may be present at mesial and distal extremities, or on one side, of crown base; root massive and apicobasally short, with deep nutritive groove that bisects pronounced lingual protuberance and may possess one or more prominent nutritive pores near center of groove; apical face of lingual protuberance flat or weakly convex; one or more lateral root foramina immediately lingual to mesial and distal extremities of tooth neck; and labio-mesial corner of root labially pointing and labiodistal corner less pointy than labiomesial corner.

Remarks—The genus name *Eorhincodon* was preoccupied by another shark taxon erected by Li (1995) in a separate paleontological context. Li's (1995) specimen of *Eorhincodon* is now interpreted to be a carcharhiniform tooth (Cappetta, 2006:303, 2012:299), but the genus name remains unavailable. Thus, a new genus name (*Pseudomegachasma*, gen. nov.) is needed to accommodate Nessov's (1999) '*E. casei*' and Shimada's (2007) '*M. comanchensis*'.

PSEUDOMEGACHASMA CASEI (Nessov, 1999), comb. nov. (Fig. 3)

Rhincodontidae: Nessov, Mertinene, Golovneva, Potapova, Sablin, Abramov, Bugaenko, Nalbandyan, and Nazarkin, 1988:126, fig. 1.10.

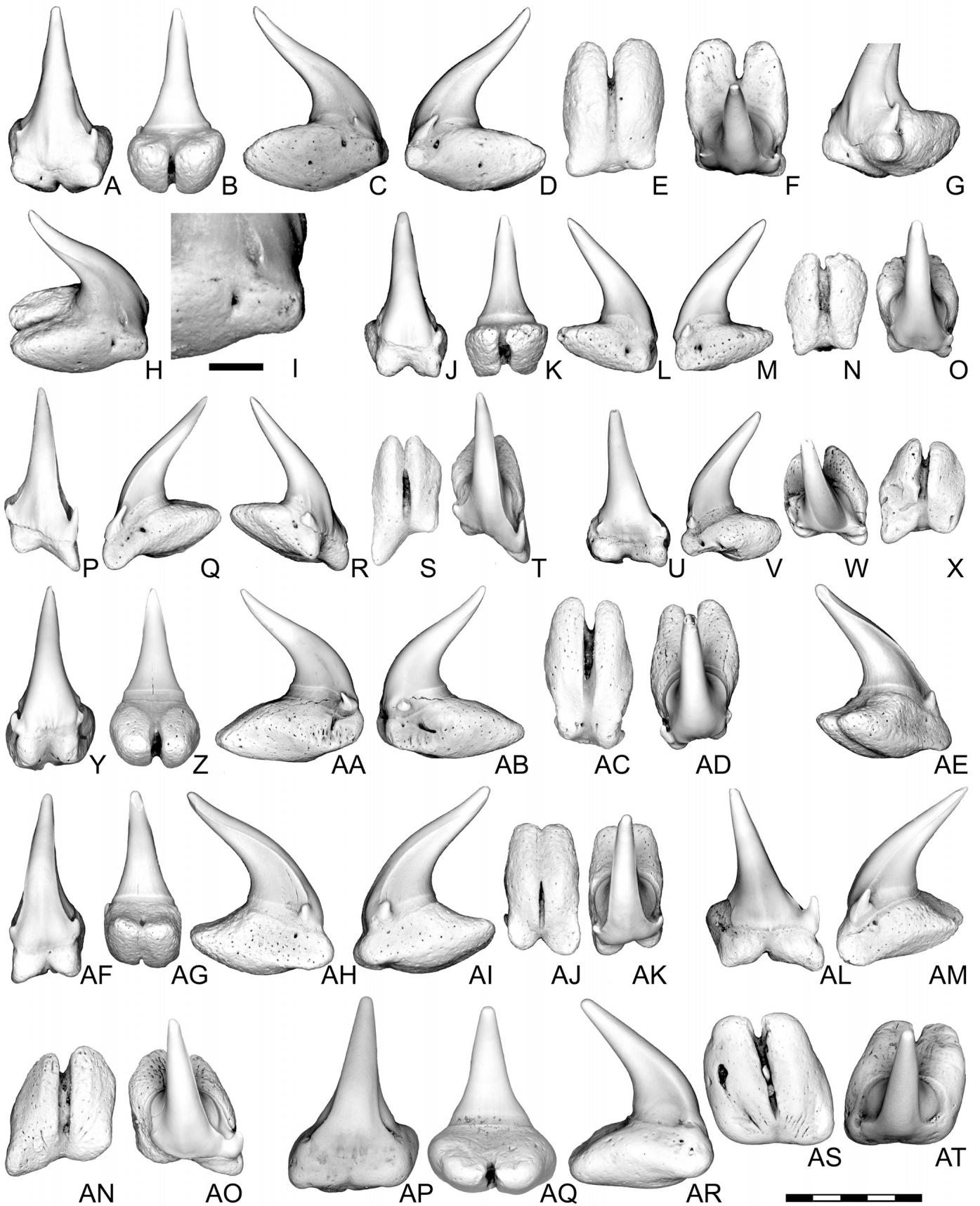
Eorhincodon casei: Nessov, 1997:pl. 1, fig. 14a, b (nomen nudum).

Eorhincodon casei, sp. nov.: Nessov, 1999:101, figs. a–c (original description).

Type Specimen—CNIGRM 10/12292 (holotype), tooth (Fig. 3A–I; erroneously referred to as '30/12292' under an old institutional acronym 'TSNIGM' in Nessov, 1999).

Referred Specimens—ZIN PC15/30, tooth (Fig. 3J–O); PC16/30, tooth (Fig. 3P–T); PC17/30, tooth; PC18/30, tooth; PC19/30, tooth; PC20/30, tooth; SSU 155/80, tooth (Fig. 3U–X); 155/81, tooth; 155/82, tooth; 155/83, tooth; 155/84, tooth (Fig. 3Y–AD); 155/85, tooth; 155/86, tooth (Fig. 3AE–AK); 155/87, tooth (Fig. 3AL–AO); 155/88, tooth; 155/89, tooth (Fig. 3AP–AT); 155/90, tooth; 155/91, tooth (this study).

Ages and Localities—'Level GLE 20' (Nessov, 1999) within Polpino Formation (early Cenomanian), Lebedinskij quarry, Gubkin town, Belgorod Province, Russia, for type specimen and ZIN PC15/30–PC20/30 ('1' in Fig. 1); lower member (early Cenomanian) of Melovatka Formation, 'Melovatka-5' locality, Volgograd Province, Russia, for SSU 155/80–155/85 ('2' in Fig. 1); upper member (late Cenomanian) of Melovatka Formation, 'Bezobrazovka-1' locality, Kalininsk District, Saratov Province, Russia, for SSU 155/87 ('3' in Fig. 1); basal horizon (middle Turonian but specimen likely reworked from Cenomanian) of Bannovka Formation, 'Bagaevka' locality, Bagaevka, Saratov



District, Saratov Province, Russia for SSU 155/89 ('4' in Fig. 1); upper member (late Cenomanian) of Melovatka Formation, 'Saratov-1' locality, Saratov District, Saratov Province, Russia, for SSU 155/86 ('5' in Fig. 1); upper member (late Cenomanian) of Melovatka Formation, 'Saratov-2' locality, Saratov District, Saratov Province, Russia, for SSU 155/88 ('6' in Fig. 1); basal horizon (early Santonian but specimen likely reworked from Cenomanian) of Kirsanov Formation, 'Kikino' locality, Kamenka District, Penza Province, Russia, for SSU 155/90 ('7' in Fig. 1); basal horizon (early Santonian but specimen likely reworked from Cenomanian) of Kirsanov Formation, 'Mochaleika' locality, Kamenka District, Penza Province, Russia, for SSU 155/91 ('8' in Fig. 1).

Diagnosis—As for the genus *Pseudomegachasma*, gen. nov., with following combination of characters, including distinguishing characters from *P. comanchensis*, comb. nov. (see below): weak mesial and distal cutting edges on crown more prominent than in *P. comanchensis*, comb. nov.; smooth labial crown face at crown base more convex than in *P. comanchensis*, comb. nov., and shows low, blunt longitudinal rise at center of crown base; and lateral cusplets generally present and sharply pointed.

Description—Specimens of *Pseudomegachasma*, comb. nov., from Russia are represented by 19 teeth from eight different localities, of which the largest number of specimens (seven teeth including the holotype) comes from the type locality (Supplementary Data, Appendix S2). Whereas most specimens come from either early Cenomanian or late Cenomanian deposits, three teeth come from post-Cenomanian (middle Turonian and early Santonian) deposits. However, those three teeth show signs of taphonomically induced rounding and are interpreted to represent reworked fossils from underlying Cenomanian rocks.

All teeth are small; the tallest tooth is SSU 155/89, measuring 8.1 mm in total tooth height and the crown height is 7.6 mm. The crown is apicobasally high (generally about twice the crown width). The average crown height is 5.8 mm (range: 4.4–7.6 mm) and average crown width is 2.6 mm (range: 2.0–3.7 mm) (n = 19; Supplementary Data, Appendix S2). The crown base is moderately broad mesiodistally and narrows rapidly just above the base, developing apically into a sharp, narrow cusp. The lateral extensions of the crown base generally come with one pair of lateral cusplets that varies from narrow, needle-like, lingually recurved forms to blunt, conical forms, although at least five teeth (and possibly as many as nine teeth) in the sample lack the distal lateral cusplet and one tooth lacks the mesial lateral cusplet (Supplementary Data, Appendix S2). Where a lateral cusplet is absent, the crown base forms a short rounded shoulder extending basally onto the root. Where lateral cusplets are present, they may be either symmetrical or asymmetrical. Individual cusplets are apicobasally short, and although they are usually distinct, lateral cusplets are not well separated from the base of the main cusp. Smooth mesial and distal cutting edges of the main cusp are usually present that extend across the apex and basally,

usually terminating at a point where the crown base flares into lateral cusplets, but cutting edges are usually not developed on mesial and distal sides of lateral cusplets. The main cusp is strongly flexed lingually and its apex is straight or very slightly recurved labially. The labial crown face is smooth and moderately convex, and the crown base is gently curved and lacks a basal ledge or groove. The lingual crown face is smooth and strongly convex. The tooth neck is well developed on the lingual face immediately basal to the shoulders of the crown, but it does not extend to the crown base on the labial side. The crowns are symmetrical to strongly asymmetrical with varying degrees of distal inclination of the main cusp.

The root is proportionally massive in relation to the crown, although crown length is always greater than root length. The average root length is 4.2 mm (range: 2.9–6.0 mm), and the average root width is 3.1 mm (range: 2.0–5.5 mm) (n = 19; Supplementary Data, Appendix S2). Only two specimens (SSU 155/88 and 155/90) have a root width that exceeds its root length (Supplementary Data, Appendix S2). Roots are bilobate, but each lobe is usually exceptionally short. The mesial and distal root lobes are of nearly equal length in teeth with an erect main cusp, whereas the mesial root lobe is longer than the distal root lobe in teeth with a greater inclination of the main cusp. The lingual root face is developed into a massive protuberance that also constitutes the basal surface of the root. The basal surface is rounded to flat and is generally bisected by a deep nutritive groove that may be variable in width from a wide prominent groove to a slit-like narrow groove. The bisection may extend as much as one-fourth of the way into the root labially from the tip of the lingual protuberance. Whereas many minute, scattered foramina are present throughout the root surface, one to a few prominent lateral root foramina are generally present immediately lingual to mesial and distal lateral cusplets or shoulders of the crown on both mesial and distal surfaces of the root (Fig. 3I).

Remarks—Nessov (1999) erected '*Eorhincodon casei*' based primarily on 38 isolated teeth from the lower Cenomanian. Most of the 38 teeth came from the lower part (0.5–3.5 m from the bottom) of 'Level GLE 20,' but at least one tooth came from the uppermost part of 'Level GLE 20' that is 6–7 m above the basal phosphatic layer of the Polpino Formation and 2–3 m below the overlying middle Turonian deposit (indicated by thickened portions of 'Level GLE 20' in Fig. 1B). Nessov (1999:101) also reported an additional tooth of '*E. casei*' from the Cenomanian of Volgograd Province. The whereabouts of all teeth described by Nessov (1999) are unknown except the holotype, and they are considered to be lost.

Nessov (1999) also documented four large complete and three fragmentary isolated vertebrae from Belgorod Province which he attributed to his '*Eorhincodon casei*.' He noted (p. 101) that the four complete vertebrae, one of which measured more than 9 cm in diameter, came from the lower Cenomanian (level GLE-20), whereas the three fragmentary vertebrae came from the

← FIGURE 3. Teeth of *Pseudomegachasma casei*, comb. nov. (Nessov, 1999), from Upper Cretaceous of Russia. **A–I**, CNIGRM 10/12292 (holotype) from lower Cenomanian Polpino Formation in Belgorod Province ('1' in Fig. 1) in labial (**A**), lingual (**B**), mesial (**C**), distal (**D**), basal (**E**), apical (**F**), and oblique (**G, H**) views plus close-up view of lateral root foramina on mesial root surface (**I**; cf. Fig. 3H); **J–O**, ZIN PC15/30 from lower Cenomanian Polpino Formation in Belgorod Province ('1' in Fig. 1) in labial (**J**), lingual (**K**), mesial (**L**), distal (**M**), basal (**N**), and apical (**O**) views; **P–T**, ZIN PC16/30 from lower Cenomanian Polpino Formation in Belgorod Province ('1' in Fig. 1) in labial (**P**), mesial (**Q**), distal (**R**), basal (**S**), and apical (**T**) views; **U–X**, SSU 155/80 from lower Cenomanian Melovatka Formation in Volgograd Province ('2' in Fig. 1) in labial (**U**), mesial (**V**), apical (**W**), and basal (**X**) views; **Y–AD**, SSU 155/84 from lower Cenomanian Melovatka Formation in Volgograd Province ('2' in Fig. 1) in labial (**Y**), lingual (**Z**), mesial (**AA**), distal (**AB**), basal (**AC**), and apical (**AD**) views; **AE–AK**, SSU 155/86 from upper Cenomanian Melovatka Formation in Saratov Province ('5' in Fig. 1) in oblique (**AE**), labial (**AF**), lingual (**AG**), mesial (**AH**), distal (**AI**), basal (**AJ**), and apical (**AK**) views; **AL–AO**, SSU 155/87 from upper Cenomanian Melovatka Formation in Saratov Province ('3' in Fig. 1) in labial (**AL**), mesial (**AM**), basal (**AN**), and apical (**AO**) views; **AP–AT**, SSU 155/89 from the middle Turonian Bannovka Formation (reworked from Cenomanian) in Saratov Province ('4' in Fig. 1) in labial (**AP**), lingual (**AQ**), mesial (**AR**), basal (**AS**), and apical (**AT**) views. Scale bars equal 5 mm (**A–AT** except for **I**) and 1 mm (**I**).

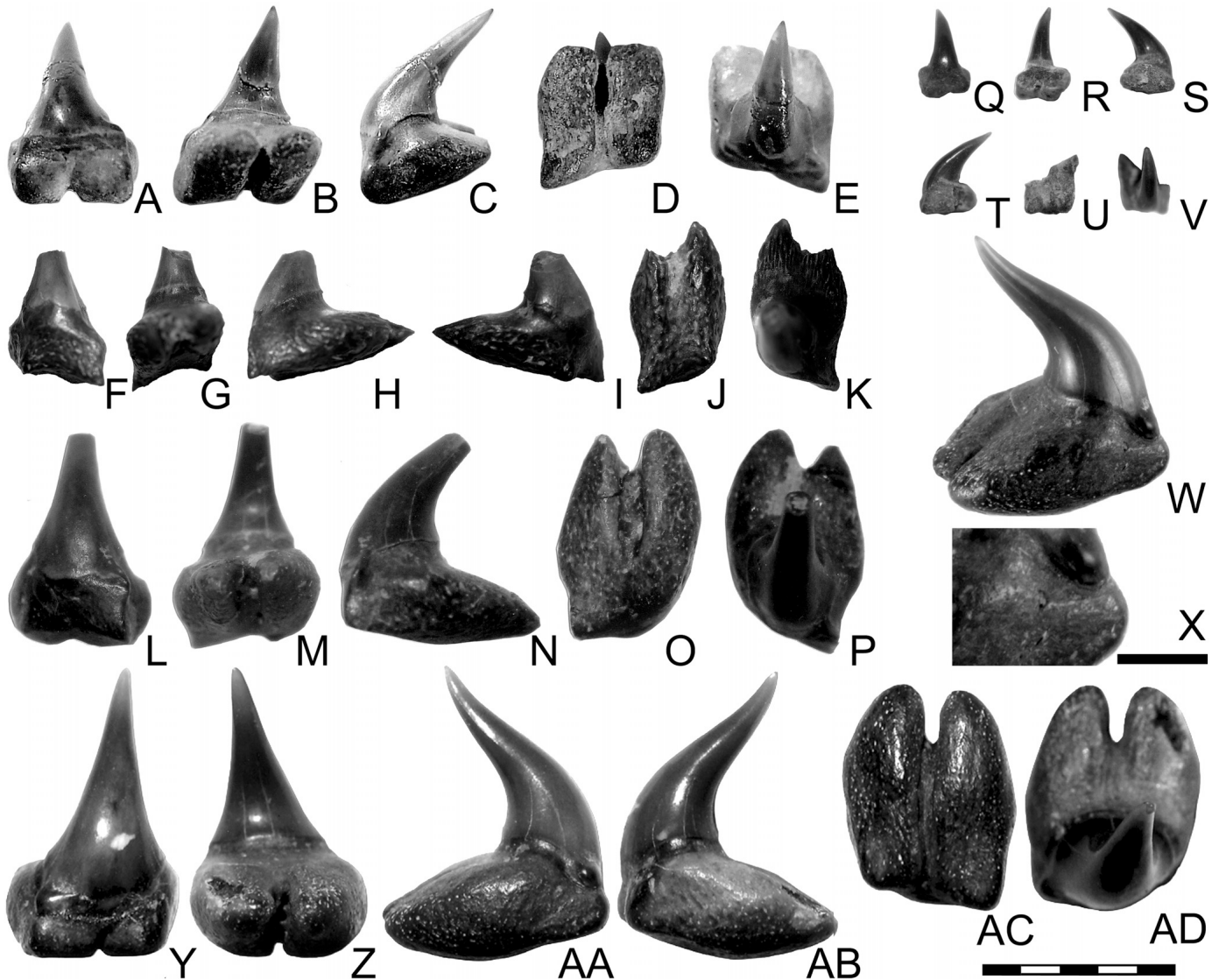


FIGURE 4. Teeth of *Pseudomegachasma comanchensis*, comb. nov. (Shimada, 2007), from Upper Cretaceous of the United States. **A–H**, FHSM VP-15095 (holotype) from basal Lincoln Limestone (late middle–early late Cenomanian) of Greenhorn Limestone in Colorado (see Shimada, 2007) in labial (**A**), lingual (**B**), mesial (**C**), basal (**D**), and apical (**E**) views; **F–K**, FHSM VP-15176 (paratype) from basal Lincoln Limestone (late middle–early late Cenomanian) of Greenhorn Limestone in Colorado (see Shimada, 2007) in labial (**F**), lingual (**G**), mesial (**H**), distal (**I**), basal (**J**), and apical (**K**) views; **L–P**, FHSM VP-17628 from basal Lincoln Limestone (late middle–early late Cenomanian) of Greenhorn Limestone in Colorado (see Gallardo et al., 2013) in labial (**L**), lingual (**M**), mesial (**N**), basal (**O**), and apical (**P**) views; **Q–V**, FHSM VP-17629 from basal Lincoln Limestone (late middle–early late Cenomanian) of Greenhorn Limestone in Colorado (see Gallardo et al., 2013) in labial (**Q**), lingual (**R**), mesial (**S**), distal (**T**), basal (**U**), and apical (**V**) views; **W–AD**, NMMNH P-67453 from Bouldin Flags Member of Eagle Ford Formation in Texas in oblique (**W**), labial (**Y**), lingual (**Z**), mesial (**AA**), distal (**AB**), basal (**AC**), and apical (**AD**) views plus close-up view of lateral root foramen on mesial root surface (**X**; cf. Fig. 4W). Scale bars equal 5 mm (**A–AD** except **X**) and 1 mm (**X**).

upper Albian. Like most tooth specimens, the whereabouts of all Nessov's (1999) vertebral specimens are unknown, and they are considered to be lost.

PSEUDOMEGACHASMA COMANCHENSIS (Shimada, 2007), comb. nov.
(Fig. 4)

cf. *Johnlongia* sp.: Shimada, Schumacher, Parkin, and Palermo, 2006:13, fig. 9.8.

Megachasma comanchensis: Shimada, 2007:513–514, fig. 1 (original description).

Megachasma comanchensis Shimada, 2007: Cumbaa, Shimada, and Cook, 2010: table 1, fig. 4G.

Megachasma comanchensis Shimada, 2007: Gallardo, Shimada, and Schumacher, 2013:fig. 3K, L.

Type Specimens—FHSM VP-15095 (holotype), tooth (Fig. 4A–E); VP-15176 (paratype), tooth (Fig. 4F–K) (as described by Shimada, 2007).

Referred Specimens—FHSM VP-15177, two tooth fragments (Shimada, 2007); VP-17628, tooth (Fig. 4L–P); VP-17629, tooth (Gallardo et al., 2013; Fig. 4Q–V); NMMNH P-67453, tooth (this study; Fig. 4W–AD).

Ages and Localities—Lincoln Limestone Member (middle Cenomanian) of Greenhorn Limestone, 'Tobe locality' (Shimada et al., 2006) and 'Table Mesa locality' (Gallardo et al., 2013), southeastern Colorado, U.S.A.; Bouldin Member (late

Cenomanian or possibly early Turonian; Kennedy, 1988) of Eagle Ford Formation, Austin, Texas, U.S.A. (this paper).

Diagnosis—As for the genus *Pseudomegachasma*, with the following combination of characters, including distinguishing characters from *P. casei*, comb. nov. (see above): weak mesial and distal cutting edges on crown even less prominent than *P. casei*, comb. nov., and may even be absent at mid-portion of crown giving circular outline in transverse section; smooth labial crown face at crown base flatter than *P. casei*, comb. nov.; and lateral cusplets generally absent, and if present, less prominent and less sharply pointed than in *P. casei*, comb. nov.

Description—Specimens of *Pseudomegachasma comanchensis*, comb. nov., from the United States include five complete or nearly complete teeth from three different localities (note: two fragmentary teeth listed in Shimada, 2007, are not included here). Four teeth are from two mid-Cenomanian localities in southeastern Colorado, including the holotype and paratype (Shimada, 2007; Gallardo et al., 2013). An additional, previously undescribed specimen (NMMNH P-67453) comes from the Bouldin Flags Member (upper Cenomanian or possibly lower Turonian) of the Eagle Ford Formation of Texas (NMMNH locality 8855; Fig. 4W–AD) and represents the geologically youngest specimen of *P. comanchensis*, comb. nov. It also represents the largest and most complete specimen of the species.

All five teeth are small, where the tallest tooth (NMMNH P-67453) measures 8.6 mm in total tooth height and 7.6 mm in crown height. The crown is apicobasally high (generally about twice crown width); the average crown height is 4.0 mm (range: 2.0–7.6 mm) and average crown width 3.4 mm (range: 0.7–4.3 mm) ($n = 5$; Supplementary Data, Appendix S2). The crown base is moderately broad mesiodistally and narrows rapidly just above the base, developing apically into a sharp, narrow cusp. The lateral extensions of the crown base generally come with no definite lateral cusplets but instead short rounded shoulders extend basally onto the root, although the labiomesial corner of the crown base in NMMNH P-67453 shows a low blunt tubercle that likely represents a vestigial lateral cusplet (e.g., Fig. 4Y). Based on specimens that preserve the cusp apex, smooth mesial and distal cutting edges of main cusp are usually present but they are restricted to its apical one-third. The main cusp is strongly curved lingually where its apex is straight or is very slightly recurved labially. The labial crown face is smooth and moderately convex, and the crown base is gently curved and lacks a basal ledge or groove. The lingual crown face is smooth and strongly convex. The tooth neck is well developed on the lingual face particularly immediately basal to the crown shoulders, and it extends faintly to the crown base on the labial side. The crowns are symmetrical to moderately asymmetrical with varying degrees of distal inclination of the main cusp.

The root is proportionally massive in relation to the crown where the crown length is equal to or greater than the root length. The average root length is 3.5 mm (range: 2.0–6.5 mm) and the average root width is 2.5 mm (range: 1.3–5.2 mm); root length always exceeds root width ($n = 5$; Supplementary Data, Appendix S2). Roots are bilobate, but each lobe is exceptionally short, especially the distal one. The lingual root face is developed into a massive protuberance that also constitutes the basal surface of the root. The basal surface is rounded to flat and is bisected by a deep nutritive groove that may vary in width and may show one or two large foramina within it. The bisection extends about one-fifth to one-fourth of the way into the root labially from the tip of the lingual protuberance. Whereas many minute scattered foramina are present throughout the root surface, one lateral root foramen is generally present immediately lingual to mesial and distal shoulders of the crown on both mesial and distal root surfaces (e.g., Fig. 4X).

DISCUSSION

Teeth of *Pseudomegachasma casei*, comb. nov., and *P. comanchensis*, comb. nov., are strikingly similar to each other (Figs. 3, 4) and are thus interpreted to be congeneric where both species are considered taxonomically distinct. We reject Cappetta's (2012) proposition that *P. comanchensis*, comb. nov., and *P. casei*, comb. nov., represent abraded and reshaped teeth of *Johnlongia* for the following two reasons. First, the holotype and many other specimens of *P. casei*, comb. nov., as well as NMMNH P-67453 from Texas and at least one additional specimen of *P. comanchensis*, comb. nov., from Colorado (Fig. 4Q–V) preserve a delicate cusp apex and root surface with no signs of major pre- or post-depositional sedimentary abrasion. The interpretation of taphonomic alteration in this instance is inconsistent with laboratory simulations and observations of other in situ instances of sedimentary abrasion on elasmobranch teeth (Irmis and Elliott, 2006; Becker and Chamberlain, 2012; Boesenecker et al., 2014). We also note that a number of specimens of the Oligocene–Miocene megachasmid (*Megachasma applegatei* Shimada, Welton, and Long, 2014), including its holotype, show slight taphonomic modification from sedimentary abrasion (Shimada et al., 2014: figs. 3–5). The 'rounding effect' due to sedimentary abrasion is expressed as slight erosion throughout different features of each of those teeth (i.e., crown apex, lateral cusplets, and root lobes all alike), not just confined to root lobes, and is consistent with similar observations of overall mild abrasive wear by Pyenson et al. (2009). Second, *Johnlongia* teeth have not been recovered from the Lebedinskij quarry and Melovatka-5 localities ('1' and '2' in Fig. 1 and Supplementary Data, Appendix S2) where *P. casei*, comb. nov., is represented by multiple specimens. In addition, the possibility of such megachasmid-like teeth representing teeth of *Johnlongia* from different tooth positions can be dismissed given that such a tooth form (i.e., lobeless root) is not known from localities with reasonably large sample sizes of *Johnlongia* (e.g., Siverson, 1996; Cappetta, 2012). Therefore, we consider *Pseudomegachasma*, gen. nov., to be a valid taxon, and not congeneric with *Johnlongia*.

The separation between *Johnlongia* and *Pseudomegachasma*, gen. nov., is further substantiated on the basis of quantitative analysis using dental variables, such as crown height (CH), crown width (CW), root length (RL), and root width (RW) (Fig. 5A). Figure 5B shows the relationships between CH/CW ratios and RL/RW ratios among *J. allocotodon* ($n = 8$), *P. casei*, comb. nov. ($n = 19$), and *P. comanchensis*, comb. nov. ($n = 5$). Whereas the plots of *P. comanchensis*, comb. nov., completely overlap with those of *P. casei*, comb. nov., for both ratios, they are noticeably different from plots of *J. allocotodon*, although there is partial overlap in data. Figure 5D and E are box plots showing the difference in each type of ratio. They indicate that the two species of *Pseudomegachasma*, gen. nov. tend to have slender crowns with narrower roots (i.e., likely due to reduced lateral cusplets) relative to the teeth of *Johnlongia*. It should be noted that the two species of *Pseudomegachasma*, gen. nov., can be separated from each other on the basis of CH/RL ratios (Fig. 5C, F). Teeth of *P. comanchensis*, comb. nov., tend to have a prominent root (primarily due to their robust lingual root protuberance) relative to the crown compared to teeth of *P. casei*, comb. nov., which are quantitatively more similar to teeth of *Johnlongia* despite the reduced root lobes in *P. casei*, comb. nov. In summary, the two genera, *Johnlongia* and *Pseudomegachasma*, gen. nov., are distinguishable morphologically and quantitatively (Fig. 5D, E). Likewise, our analysis shows that *P. casei*, comb. nov., and *P. comanchensis*, comb. nov., are not only noticeably different on a morphological basis (see descriptions above) but also on a quantitative basis (Fig. 5F).

Nessov (1999) described *Pseudomegachasma casei*, comb. nov., under his new genus *Eorhincodon*, meaning 'the first whale

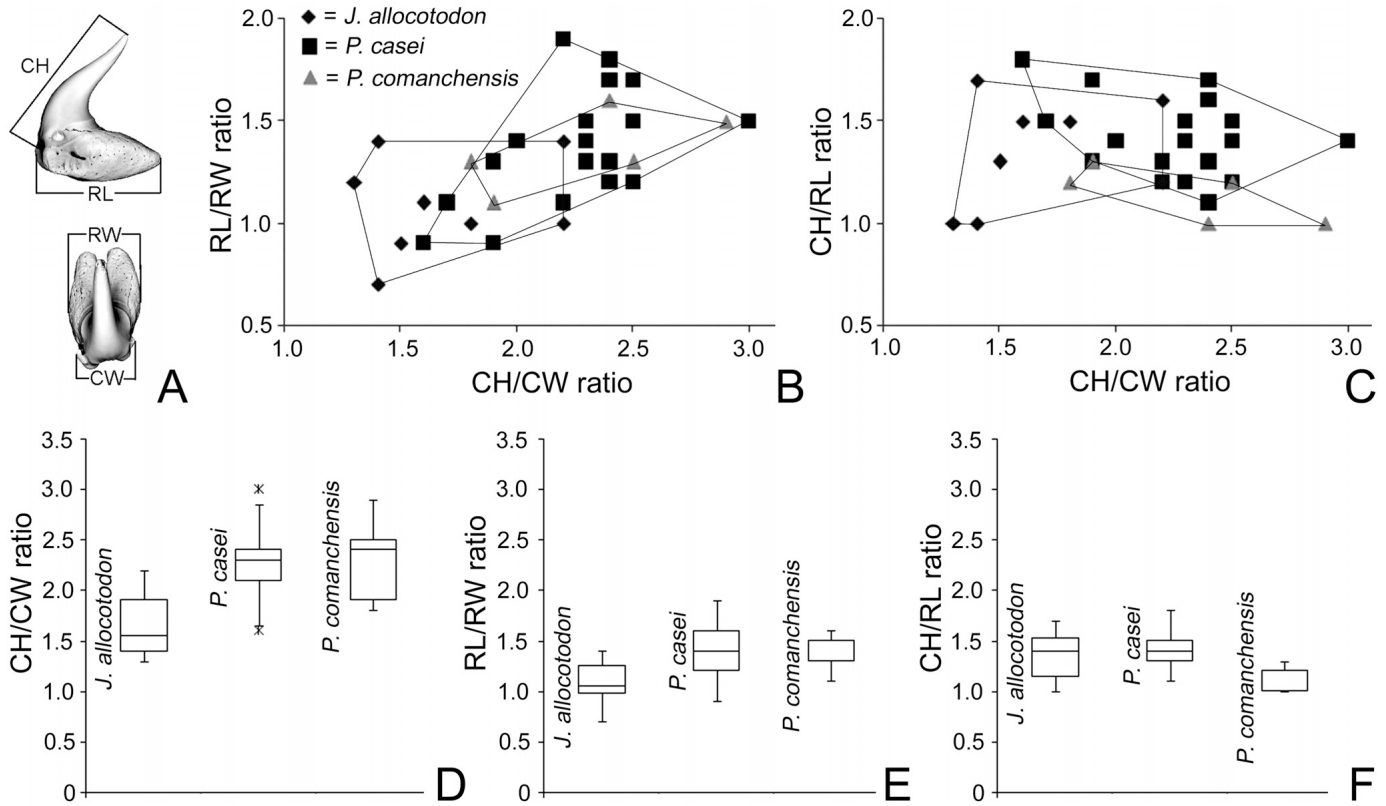


FIGURE 5. Dental measurements and comparisons among teeth of *Johnlongia allocotodon* from Russia ($n = 8$), teeth of *Pseudomegachasma casei*, comb. nov., from Russia ($n = 19$), and teeth of *P. comanchensis*, comb. nov., from the United States ($n = 5$). **A**, measured variables using specimen SSU 155/84 as an example (top, profile view; bottom, apical view; see Supplementary Data Appendix S2 for measurements of each tooth); **B**, scatter plots comparing CH/CW ratios and RL/RW ratios among the three taxa; **C**, scatter plots comparing CH/CW ratios and CH/RL ratios among the three taxa; **D–F**, box plot representations of CH/CW ratios (**D**), RL/RW ratios (**E**), and CH/RL ratios (**F**) of the three taxa (box, interquartile range, i.e., central 50% data; horizontal line in box, mean value; vertical whiskers, total range of data); asterisks, maximum and minimum outliers. **Abbreviations:** **CH**, crown height; **CW**, crown width; **RL**, root length; **RW**, root width.

shark,' because he interpreted the taxon as a putative planktivorous shark within the whale shark family Rhincodontidae (Orectolobiformes). Nesson's (1999) proposition that his new taxon represented a planktivore is reasonable, because teeth of all four known planktivorous elasmobranchs (Rhincodontidae, Megachasmidae, Cetorhinidae, and Mobulidae) display a trend toward secondary homodonty as a result of reduced tooth sizes, simplified conical to hook-like main cusp with vestigial or no lateral cusplets, and reduced root lobes often making the root bulbous (e.g., see Cappetta, 2012). Whereas *P. comanchensis*, comb. nov., has also been proposed to be a planktivorous shark (Shimada, 2007), Nesson's (1999) *Eorhincodon*, however, cannot be placed in the whale shark clade because teeth of the genus more closely resemble those of *Megachasma pelagios* (e.g., see Yabumoto et al., 1997) than any known rhincodontids (note a pronounced overhang of the labial crown base and constriction at the tooth neck in rhincodontid teeth, unlike *M. pelagios*; e.g., Herman et al., 1992:pl. 27; Cappetta, 2012:fig. 165). We consider *Pseudomegachasma*, gen. nov., to have no direct phylogenetic affinity with Rhincodontidae on this basis.

Teeth of *Pseudomegachasma*, gen. nov., are reminiscent of those of *Megachasma pelagios* in exhibiting a hook-like crown, well-defined tooth neck on the lingual face, and a lobeless root. Moreover, the morphological variability seen in teeth of *P. casei*, comb. nov., and *P. comanchensis*, comb. nov. (e.g., Figs. 3, 4), indicates that, like *M. pelagios*, the dentition of both species of *Pseudomegachasma*, gen. nov., can be interpreted to exhibit a weak monognathic heterodonty. However, *Pseudomegachasma*,

gen. nov., is distinguished from *M. pelagios* by an exceptionally prominent nutritive groove and the presence of lateral root foramina, much like a Cretaceous, putative odontaspidae, *Johnlongia* (Shimada, 2007; cf. Fig. 2 vs. Figs. 3, 4). Despite the resemblance between *Pseudomegachasma*, gen. nov., and *M. pelagios*, the similarity is here interpreted to be superficial (i.e., convergence; see further discussion below) because the recently described Oligocene–Miocene megachasmid from the western United States, *M. applegatei*, is now considered to be the sister taxon to *M. pelagios* that diverged no later than the earliest late Miocene (Shimada et al., 2014). In addition, there is a 70-Ma gap between *Pseudomegachasma*, gen. nov. (mid-Late Cretaceous), and *Megachasma* (late Paleogene; Shimada et al., 2014) that has no fossil record of shark teeth with the megachasmid tooth pattern.

Teeth of *Pseudomegachasma*, gen. nov., and *Johnlongia* are similar in possessing a well-defined tooth neck on the lingual face and an enormous lingual protuberance of the root marked by an exceptionally deep nutritive groove (Cappetta, 2012; this study). The close morphological resemblance between the two taxa is exemplified by the fact that Cappetta (2012) considered 'Megachasma comanchensis' and 'Eorhincodon casei' to be taphonomically altered *Johnlongia*. Whereas *Johnlongia* has been placed in the family Odontaspidae (Siverson, 1996; Cappetta, 2012), possibly incorrectly in a strict sense (see above for discussion of the family), the close resemblance between *Pseudomegachasma*, gen. nov., and *Johnlongia* is considered here as evidence that these two

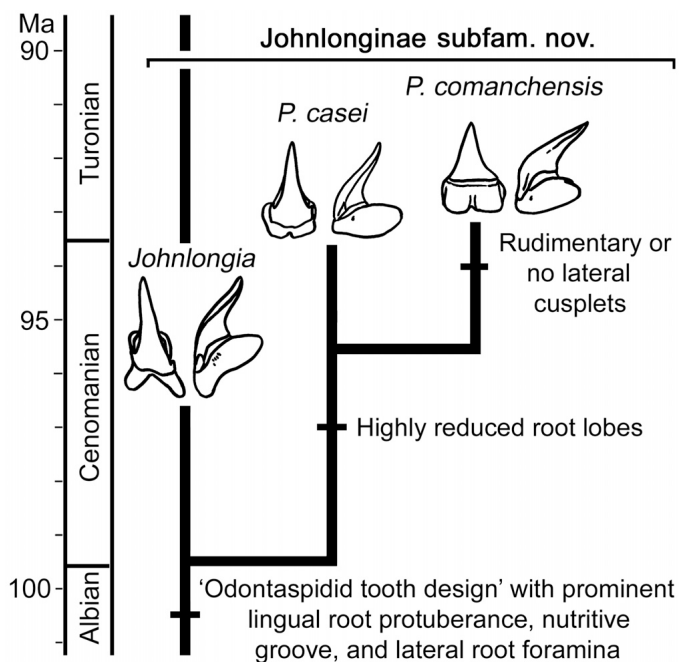


FIGURE 6. Stratigraphic ranges of the two species of *Pseudomegachasma* and their phylogenetic relationships with *Johnlongia* within the proposed new subfamily Johnlonginae, subfam. nov. Sources of illustrated teeth (left, labial view; right, profile view; not to scale): *Johnlongia* (SSU 155/93 in this study; cf. Fig. 2 A, C); *P. casei*, comb. nov. (CNIGRM 10/12292 in this study; cf. Fig. 3A, D); and *P. comanchensis*, comb. nov. (Shimada, 2007:fig. 1B, C; see also Fig. 4A, E in this study).

genera shared an immediate common ancestry that forms the basis of Johnlonginae, subfam. nov. (see above; Fig. 6). This *Pseudomegachasma*-*Johnlongia* sister relationship concomitantly implies that *Pseudomegachasma*, gen. nov., also belongs to the Odontaspidae. This taxonomic placement is significant because it makes *Pseudomegachasma*, gen. nov., an odontaspidid that putatively evolved a plankton-feeding adaptation independent of the four known planktivorous elasmobranch clades (i.e., Rhincodontidae, Megachasmidae, Cetorhinidae, and Mobulidae). It also indicates that plankton-feeding evolved at least three times independently in Lamniformes (i.e., Megachasmidae, Cetorhinidae, and Odontaspidae), and more significantly, *Pseudomegachasma*, gen. nov., would represent the oldest known planktivorous elasmobranch in the fossil record (Fig. 7; see below for further discussion).

Evidence at hand suggests that the extant *Megachasma pelagios* shares an immediate common ancestry with the Oligocene–Miocene *M. applegatei* that is characterized by a crown with a large, narrow main cusp, well-developed lateral cusplets, and a strongly bilobed root with a prominent lingual protuberance (Shimada et al., 2014). The fossil record shows that Odontaspidae sensu lato emerged by 130 Ma (Hauterivian; Cappetta, 2012), and *Johnlongia* was in existence by 105 Ma (early late Albian Toolebuc Formation in Queensland, Australia; M.S., personal observation of specimen housed in Kronosaurus Korner Museum, Richmond, Queensland). The *Johnlongia*-*Pseudomegachasma* sister relationship is intriguing because it suggests that *Pseudomegachasma*, gen. nov., with the planktivorous tooth pattern was also derived from the piscivorous tooth pattern as seen in *Johnlongia* through reduction in root lobes, reduction or loss of lateral cusplets, and morphological simplification of the main cusp. Thus, one can argue for the convergence of the planktivorous tooth pattern between *M. pelagios* and *Pseudomegachasma*, gen. nov., in

which the planktivorous tooth pattern evolved from the piscivorous tooth pattern independently in a parallel manner in the two lamniform clades, Megachasmidae and Odontaspidae, albeit at different times (Cretaceous vs. Miocene) (Fig. 7). It should be noted that our notion of ‘planktivory’ here is a robust one, as demonstrated by the fact that certain extant ‘planktivorous elasmobranchs’ (e.g., Rhincodontidae) can also feed on sizable nektonic organisms, such as bony fishes and squid (Compagno, 2001). In fact, it is quite possible that *Pseudomegachasma*, gen. nov., could have been a facultative planktivore where it could have still fed on small nektonic fishes. The crown apex of some teeth of the taxon (e.g., Fig. 3J, P) shows slight wear that appears to support this idea.

Shirai (1996:fig. 4) hypothesized that the megachasmid lineage emerged during the Mesozoic despite the lack of corroborating fossil evidence, but subsequent molecular studies have placed the estimated origination time for the megachasmid clade in the 104–90 Ma range, supporting its Mesozoic origin (Martin et al., 2002:fig. 5; Heinicke et al., 2009:fig. 2, table 1, which also lists the total range of ‘confidence/credibility interval’ of 139–73 Ma based on the most inclusive data set). Hence, Shimada et al.’s (2014) proposition that their Oligocene–Miocene *Megachasma applegatei* represents the oldest known species of *Megachasma* appears to be incongruent with the molecular-based origination time estimates for Megachasmidae. However, we here offer a possible explanation for the perceived discrepancy. Based on the fact that teeth of *M. applegatei* are reminiscent of odontaspidid teeth (Shimada et al., 2014), it is likely that the ancestor of megachasmids possessed teeth much like typical odontaspidid teeth. Whereas the oldest odontaspidid sharks are known from the Hauterivian, there are many known mid-Cretaceous species attributed to the family ‘Odontaspidae’ (Cappetta, 2012). Because Megachasmidae appears to have close phylogenetic affinity with Odontaspidae sensu stricto (and Pseudocarchariidae) based on molecular data (Naylor et al., 2012), one possibility is that the megachasmid ancestor (and the pseudocarchariid ancestor) with no direct phylogenetic ties to Johnlonginae, subfam. nov., may be nested unrecognized within these mid-Cretaceous taxa with the ‘odontaspidid tooth pattern.’ In other words, where geologically younger *M. applegatei* is more odontaspidid-like (i.e., ‘more archaic’) than *Pseudomegachasma*, gen. nov., there is nothing to presuppose that the ‘molecularly defined Megachasmidae’ in deep time must, or ought to, have had the ‘megachasmid tooth pattern.’ As Maisey et al. (2004:45) stated, “the absence of apomorphic characters in teeth [i.e., the lack of the ‘megachasmid tooth pattern’ in this case], rather than the absence of teeth themselves [i.e., the lack of undisputed megachasmid teeth in the Cretaceous], may prevent us from recognizing a taxon’s presence [i.e., Megachasmidae] in the fossil record and lead us to underestimate its first occurrence [i.e., mid-Cenozoic].” Therefore, we contend that the ‘megachasmid tooth pattern’ present in *Pseudomegachasma*, gen. nov., has no direct phylogenetic attribution to the megachasmid clade.

Both *Pseudomegachasma casei*, comb. nov., and *P. comanchensis*, comb. nov., are highly derived forms in achieving a planktivorous tooth pattern (Fig. 7). However, *P. casei*, comb. nov., is slightly more Plesiomorphic than *P. comanchensis*, comb. nov., because the former generally possesses prominent lateral cusplets, unlike the latter. The Plesiomorphic morphology of *P. casei*, comb. nov., is consistent with the fact that the earliest material of *P. casei*, comb. nov., occurs in rocks slightly older (early Cenomanian) than rocks that yield the earliest specimens of *P. comanchensis*, comb. nov. (late middle Cenomanian). The fossil record at present indicates that *Johnlongia* gave rise initially to *P. casei*, comb. nov., at least by the early Cenomanian, and then *P. casei*, comb. nov. gave rise to *P. comanchensis*, comb. nov., at least by the late middle Cenomanian (Fig. 6).

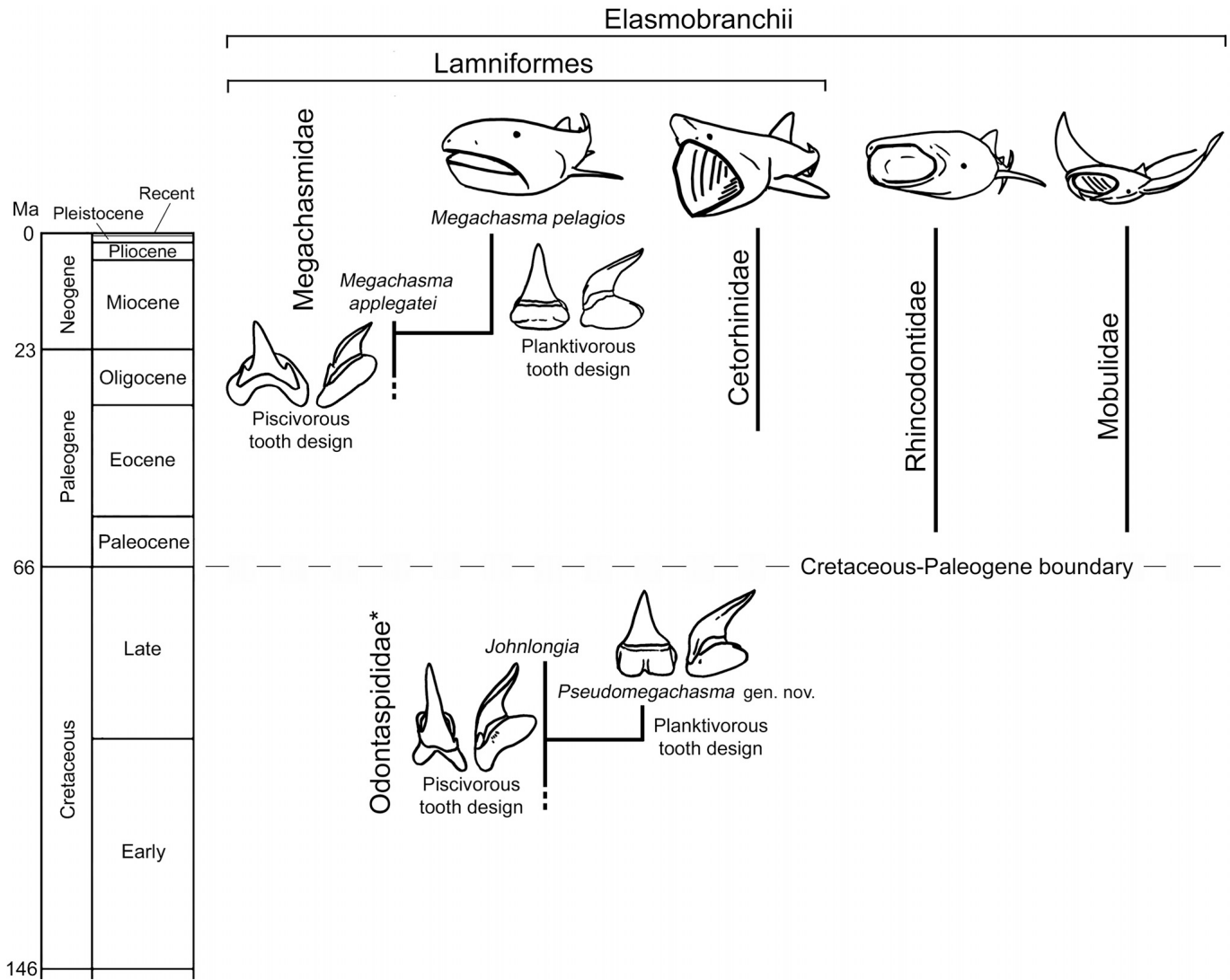


FIGURE 7. Stratigraphic distributions of elasmobranch families that contain planktivorous forms and highlighting *Johnlongia* and *Pseudomegachasma*, gen. nov., as well as *Megachasma applegatei* and *M. pelagios* to show parallel evolution and convergence of ‘megachasmid tooth pattern’ from ‘odontaspidid tooth pattern’ in each clade (*, excludes other odontaspidid taxa outside of this particular clade, i.e., Johnlonginae, subfam. nov.; stratigraphic data based on Friedman et al., 2010:fig. 3; Cappetta, 2012; Shimada et al., 2014). Sources of illustrated teeth (left, labial view; right, profile view; not to scale): *Johnlongia* (SSU 155/93 in this study; cf. Fig. 2 A, C); *Pseudomegachasma*, gen. nov. (Shimada, 2007:fig. 1B, C; see also Fig. 4A, E in this study); *Megachasma applegatei* (Shimada et al., 2014:fig. 3B, C); and *M. pelagios* (Taylor et al., 1983:fig. 8A, C).

Pseudomegachasma, gen. nov., is so far represented at 11 Late Cretaceous localities, eight in Russia and three in the United States (Supplementary Data, Appendix S2). Their geographic distribution shows that they are all restricted to the mid-latitude zone of the Northern Hemisphere (between 30°N and 55°N). More intriguingly, all the North American and Russian localities are located well into respective epicontinental seas, the sea-covered Russian Plate and the Western Interior Seaway (Sobolevskaya, 1951; Kauffman and Caldwell, 1993). These epicontinental seas were still relatively shallow in the early and middle Cenomanian, respectively (e.g., Haq et al., 1987), with highly productive ecosystems (e.g., Shimada et al., 2006; Kholodov et al., 2007). The fossil record suggests that *Pseudomegachasma*, gen. nov., and more specifically *P. casei*, comb. nov., evolved in the early Cenomanian in a shallow-water environment in Russia. Whereas the estimated water-depth range in the Russian region is 100–150 m during the late Albian (Baraboshkin and Nikul’shin, 2006), it is estimated to be no more than

50 m at least in parts of the Volga River Basin during the early Cenomanian, and the shallow-water condition (e.g., 70–80 m; no more than 200 m) continued through the end of the late Cenomanian (Zozyrev, 2006). *Pseudomegachasma*, gen. nov., eventually migrated to North America, likely following the warm, westward circum-global ocean currents through the Tethys Seaway and Atlantic Ocean (e.g., see Jacobs et al., 2005). It is noteworthy that at least some teeth of *P. casei*, comb. nov., found, or presumably derived, from Cenomanian deposits (e.g., SSU 155/91; Fig. 3AP–AT) are somewhat reminiscent of teeth of *P. comanchensis*, comb. nov., in exhibiting more rounded cutting edges and less prominent lateral cusplets relative to teeth of *P. casei*, comb. nov., from the early Cenomanian deposits. This observation suggests that the evolution of ‘comanchensis-grade’ morphology appears to have begun in Russia within the clade of *P. casei*, comb. nov.

Pseudomegachasma, gen. nov., represents a putative planktivorous elasmobranch based solely on dental morphology. There

are some other elasmobranch taxa that exhibit tooth morphologies indicative of planktivorous diet (see above for dental characterizations of planktivorous elasmobranchs). Suggested examples include *Archaeomanta* Herman, 1979, from the Paleogene, *Cretomanta* Case, Tokaryk, and Baird, 1990, from the Upper Cretaceous, *Nanocetorhinus* Underwood and Schlögl, 2013, from the Miocene, and *Pseudocetorhinus* Duffin, 1998, from the Upper Triassic (see Cappetta, 2012, and Underwood and Schlögl, 2013, for illustrations of their teeth; note that Ginter, 2008, described ‘filter-feeding sharks’ from the Devonian, but his notion of ‘filter-feeding’ is quite different from planktivory because he stated that those sharks possibly used their delicate multicuspid teeth like “sieve, preventing minute organisms from escaping from the buccal cavity before swallowing” [p. 147]). However, whereas *Pseudocetorhinus* may not be a planktivore because many of its teeth are actually broad mesiodistally with little resemblance to teeth of extant planktivorous elasmobranchs (e.g., see Cappetta, 2012:fig. 320), the exact systematic positions of these tooth-based taxa are uncertain (Adnet et al., 2012; Cappetta, 2012; Underwood and Schlögl, 2013). We contend *Pseudomegachasma*, gen. nov., to be the oldest planktivorous elasmobranch clade in the fossil record with the assumption that *Pseudocetorhinus* is likely not a planktivore (see above) and the fact that the only other possible planktivorous elasmobranch in the pre-Cenozoic fossil record is *Cretomanta*, with an oldest known occurrence from the mid-Cenomanian (e.g., Shimada et al., 2006; Underwood and Cumbaa, 2010). Nevertheless, the presence of other possible planktivorous taxa indicates that the evolutionary history of plankton-feeding elasmobranchs may have been more complex than our current understanding suggests.

One may wonder as to why the fossil record of *Pseudomegachasma*, gen. nov., is limited, but its scarcity is not necessarily surprising given that it took over two decades for the discovery of the first example of *Johnlongia* outside of North America (Cappetta, 2012:201) and, more remarkably, over 130 years to recover the first specimen of *Johnlongia* from the well-studied Niobrara Chalk of Kansas (Shimada et al., 2004; Shimada and Fielitz, 2006). The preferred habitat of *Pseudomegachasma*, gen. nov., appears to have been quite specific (middle of epicontinental seas), and it was geologically relatively short-lived (Cenomanian–?Turonian). The absence of definite early Turonian records of *Pseudomegachasma*, gen. nov., is possibly related to the extreme rarity or absence of preserved shallow-water deposits of this age (e.g., see Smith et al., 2001). Whereas it is possible that specimens of *Pseudomegachasma*, gen. nov., may have been overlooked or misidentified in existing paleontological collections, it is likewise reasonable to assert that the genus was a rare component of marine communities during the Cretaceous.

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