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A NEW FOSSIL MEGAMOUTH SHARK (LAMNIFORMES, MEGACHASMIDAE) FROM THE OLIGOCENE–MIOCENE OF THE WESTERN UNITED STATES

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ABSTRACT—The extant megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), is a large filter-feeding fish. We here describe a new species of *Megachasma*, *M. applegatei*, sp. nov., a putative sister species of the extant *M. pelagios*, based on isolated teeth from late Oligocene–early Miocene (late Chattian–Aquitainian) marine deposits in California and Oregon, U.S.A. Although showing a megachasmid tooth design, teeth of *M. applegatei*, sp. nov., exhibit a wide morphological range and are reminiscent to those of odontaspimid sharks with strong heterodonty. *Megachasma applegatei*, sp. nov., could have commonly measured approximately 6 m in total length and likely had a wide range of diet, possibly including small fishes and planktonic invertebrates. The fossil record indicates that either *M. applegatei*, sp. nov., was broadly adapted to a wide bathymetric tolerance or was a nektopelagic feeder over both deep and shallow water habitats.

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

INTRODUCTION

The megamouth shark, *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983 (Lamniformes: Megachasmidae), is a large (up to ca. 5.5 m) filter-feeding elasmobranch that was first discovered in 1976, and was so enigmatic that it was classified in a new genus and family. Since the discovery of the extant *M. pelagios*, fossil megachasmids have been reported sporadically from several Neogene marine deposits of North America, South America, and Europe (Purdy et al., 2001; De Schutter, 2009; Cappetta, 2012). Even though these forms have been documented in the literature, their identifications have remained as *Megachasma* sp. at best, including fossil teeth from the upper Oligocene and lower Miocene of the western United States (Lavenberg and Seigel, 1985; Compagno, 1990; Lavenberg, 1991; Stewart, 1991; Long, 1994).

In this paper, we formally describe the fossil megachasmid from the late Oligocene–early Miocene marine deposits of California and Oregon (Figs. 1, 2). Teeth of the fossil form are sufficiently different from those of the extant *Megachasma pelagios*, and the fossil taxon is thus described as a new species. We also discuss the taxonomy of fossil megachasmids in the Cenozoic fossil record and the paleoecology of the new fossil taxon.

Institutional Abbreviations—LACM, Natural History Museum of Los Angeles County, Los Angeles, California; UCMP, Museum of Paleontology, University of California at Berkeley, Berkeley, California.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838

Cohort EUSELACHII Hay, 1902
Subcohort NEOSELACHII Compagno, 1977
Order LAMNIFORMES Berg, 1958
Family MEGACHASMIDAE Taylor, Compagno,
and Struhsaker, 1983
Genus *MEGACHASMA* Taylor, Compagno, and Struhsaker,
1983
MEGACHASMA APPLEGATEI, sp. nov.
(Figs. 3–5)

Lamniformes incertae sedis: Phillips, Welton, and Welton, 1976:149, fig. 5.4a–c.

Miocene megachasmid: Stewart, 1991:34–35.

Undescribed California megachasmid(?): Compagno, 1990:358, fig. 2j–l.

Megachasma sp.: Long, 1994:75.

Megachasma sp.: Cöcke, 2002:111.

Megachasmidae, gen. et sp. indet.: Shimada, 2007:512, fig. 2g.

Megachasma sp.: De Schutter, 2009:fig. 6, pl. 8a–k, pl. 9a–k.

Diagnosis—Megachasmid differing from all known species of *Megachasma* by having teeth with apicobasally shorter crowns that have strong lingual cusp inclination and commonly with one pair of lateral cusplets, and with massive bilobate roots with robust lingual protuberance.

Holotype—LACM 122190, complete tooth (Fig. 3A–G).

Type Locality and Horizon—LACM locality 1626, Pyramid Hill Sand Quarry in southeastern San Joaquin Valley (Fig. 1A; detailed locality information is on file at LACM). The fossil-bearing horizon is in the ‘grit zone’ at the base of the Pyramid Hill Sand Member of the Jewett Sand (Mitchell and Tedford, 1973:fig. 1; Fig. 2). The grit zone unconformably overlies the non-marine Walker Formation and represents the oldest marine strata exposed at Pyramid Hill (Addicott, 1970:12; Mitchell and Tedford, 1973:fig. 4; Barnes, 1979; Olson, 1988). Mollusks from the grit

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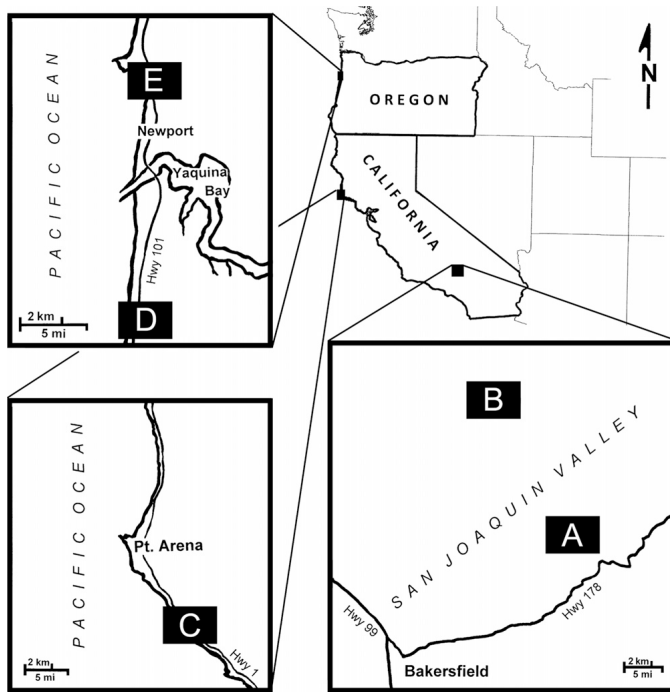


FIGURE 1. Map of western United States showing approximate location of each fossil megachasmid locality discussed in this paper. **A**, Pyramid Hill (LACM localities 1603, 1626, 1627, and 1628; early Miocene Jewett Sand), Kern County, California; **B**, Horse Canyon (LACM localities 3351 and 3362; early Miocene Jewett Sand), Kern County, California; **C**, Skooner Gulch (UCMP locality V-75135; latest Oligocene Skooner Gulch Formation), Mendocino County, California; **D**, Ona Beach State Park (LACM locality 4290; late Oligocene Yaquina Formation), Lincoln County, Oregon; **E**, Jumpoff Joe (LACM locality 4318; early Miocene Nye Mudstone), Lincoln County, Oregon.

zone are indicative of the early Miocene ‘Vaqueros Stage’ of the provincial Californian molluscan chronology (Addicott, 1970:33, 1972:9), and is coeval with the latest Juanian or Pillarian provincial Pacific northwest molluscan stages of Addicott (1976:96, fig. 1; 1981). Pectens from the grit zone have yielded strontium isotope dates suggesting an age of 23 ± 1 Ma (Olson, 1988:192). Foraminiferans from the Jewett Sand and Freeman Silt near the eastern edge of the valley are indicative of Saucesian age, but westward in the subsurface, in deeper-water-facies equivalents of the Jewett-Freeman rocks, the Zemorrian-Saucesian boundary occurs within the lower part of this sequence (Bartow and McDougall, 1984; Olson, 1988). Mitchell and Tedford (1973:217) correlate the grit zone with the Arikareean North American Land Mammal Age. According to Berggren (1972:202, fig. 4), the lower Saucesian Stage is correlative with planktonic foraminifer zone N4 (Fig. 2). These biostratigraphical zones correspond to the earliest Aquitanian (Fig. 2).

Paratypes—LACM 122130, 122132–122143, 122145–122151, 122153–122179, 122181–122184, 122186, 122187, and 122189–122202, 66 teeth (one tooth under each catalog number; Fig. 4) from LACM locality 1626.

Other Referred Specimens—The following referred non-type specimens of *Megachasma applegatei*, sp. nov., are listed according to their geographic occurrence (detailed locality data are on file at respective institutions).

Pyramid Hill Sand Member (early Miocene; Saucesian; Aquitanian) of the Jewett Sand, California (Fig. 1A, B): LACM 9882 (mentioned in Shimada, 2007:512), 122122–122129, and

155364–155369, 15 teeth from LACM locality 1603, Pyramid Hill, Kern County; LACM 9881 (mentioned in Shimada, 2007:512), 9883 (mentioned in Shimada, 2007:512), 10353, 155371–155373, 155514–155659, 155682–155685, 155688, 155690–155698, 155700, 155702–155709, 155711–155724, and 155725 (histological thin section; Fig. 3H), 190 teeth from LACM locality 1626, Pyramid Hill; LACM 122205 (mentioned in Shimada, 2007:512), 155333, and 155335–155356, 24 teeth from LACM locality 1627, Pyramid Hill; LACM 10333 (mentioned in Shimada, 2007:512, fig. 2G), 155357, and 155359–155362, six teeth from LACM locality 1628, Pyramid Hill; LACM 122203 (mentioned in Shimada, 2007:512), 150901–150912, and 155376–155431, 98 teeth from LACM locality 3351, Horse Canyon, Kern County; LACM 155680 and 155681, two teeth from LACM locality 3362, Horse Canyon.

Skooner Gulch Formation (latest Oligocene; late Zemorrian; late Chattian) of California (Phillips et al., 1976; Fig. 1C): UCMP 114537, one tooth from UCMP locality V-75135, Skooner Gulch, Mendocino County (Fig. 5A; described as “Lamniformes incertae sedis” by Phillips et al., 1976:149, fig. 5.4a–c).

Upper member of the Yaquina Formation (late Oligocene; late Zemorrian; late Chattian) of Oregon (Harrison and Eaton, 1920; Goodwin, 1973; Fig. 1D): LACM 122120 and 122121, two teeth from LACM locality 4290, Ona Beach State Park, Lincoln County (Fig. 5B, C).

Nye Mudstone (early Miocene; Saucesian; Aquitanian) of Oregon (Schenck, 1927; Armentrout, 1981; Fig. 1E): LACM 122113–122119, seven teeth from LACM locality 4318, Jumpoff Joe, Lincoln County (Fig. 5D, E).

Etymology—The species name, *applegatei*, is in honor of the late Shelton P. Applegate, who initially recognized the unique character of these small multicusped teeth from Pyramid Hill about 15 years prior to the discovery of the Recent megamouth shark (see ‘Remarks’ below).

Description—Teeth small, average total tooth height 6.6 mm (range: 3.4–14.7 mm; $n = 67$), average total tooth width 6.4 mm (range: 3.3–10.2 mm; $n = 67$), and average total tooth thickness 3.9 mm (range: 2.1–9.2 mm; $n = 67$); ca. 63% (42 teeth) of type series ($n = 67$) with tooth height that exceeds tooth width (Appendix 1, Supplemental Data); osteodont tooth histology (sensu Radinsky, 1961) with root and entire crown filled with osteodentine surrounded by thin layer of pallial dentine and thick external enameloid coating based on thin section (Fig. 3H).

Crown apicobasally short, average crown height 5.0 mm (range: 2.5–12.9 mm; $n = 67$), average crown width 5.3 mm (range: 3.3–8.2 mm; $n = 67$), and average crown thickness 1.9 mm (range: 0.9–3.4 mm; $n = 67$); ca. 36% (24 teeth) of type series ($n = 67$) with crown height that exceeds crown width (Appendix 1); crown base mesiodistally broad and narrows rapidly just above base, developing apically into sharp, narrow cusp; lateral extensions of crown base with strongly rounded shoulders extending outward onto each root lobe; lateral cusplets variable in presence and number (Appendix 1, Supplemental Data) as well as in height and development; when present, individual cusplets always apicobasally short but morphology varies from narrow, needle-like and lingually recurved, broad and somewhat blade-like, to subordinate incipient bumps on crown shoulders, and sometimes situated on mesial and distal cutting edges of main cusp; one lateral cusplet on both sides of main cusp present in ca. 75% (50 teeth; Fig. 3I) of type series, usually well separated from base of main cusp, in which lateral cusplets either symmetrical or asymmetrical and variably developed on mesial and distal shoulders (note: poorly developed mesial lateral cusplet is accompanied by a few notches along mesial cutting edge, giving a serration-like appearance; Fig. 3N); only one lateral cusplet present in 15% (10 teeth) of type series, in which lacking distal one (seven teeth; Fig. 3K) more common than lacking mesial one (three teeth; Fig. 3J); lateral cusplets completely absent in ca. 7.5% (five teeth; Fig. 3M) of type series, whereas

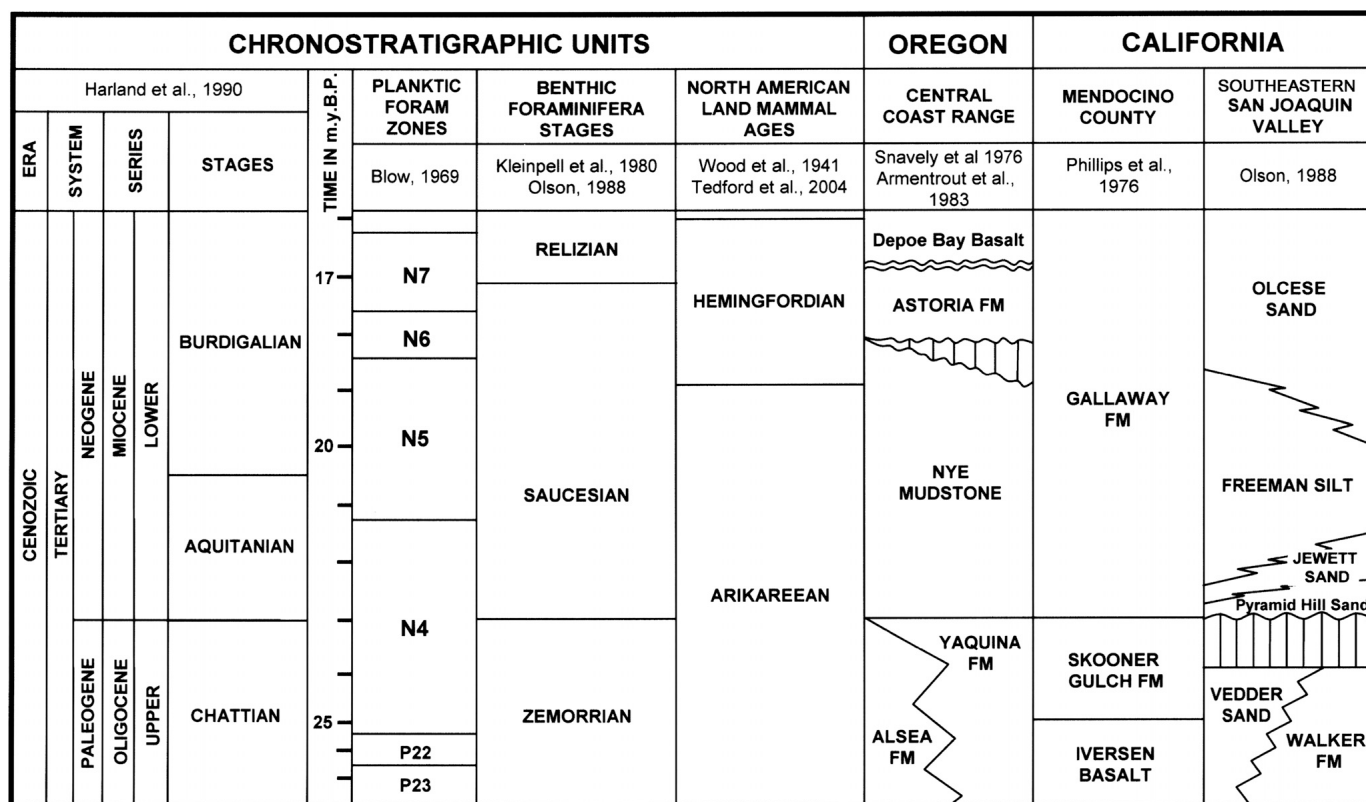


FIGURE 2. Correlation chart of late Oligocene and early Miocene stratigraphic sections in Oregon and California, U.S.A., with west coast North American provincial and global chronostratigraphic units (modified from Phillips et al., 1976; Armentrout et al., 1983; Olson, 1988).

two blunt, poorly developed lateral cusplets present on one side or both sides of cusp in ca. 5.5% (three teeth; Fig. 3L) of type series; smooth mesial and distal cutting edges of main cusp always present but variably developed, extending across apex and basally, usually terminating at point where crown foot flares into lateral shoulders; cutting edges usually developed on mesial and distal sides of lateral cusplets, but are frequently absent from side adjacent to main cusp or from rounded lateral cusplets, and rarely continuous from cusp apex to the lateral cusplets; main cusp strongly flexed linguallly and rarely parallels lingual attachment surface of root; cusp apex very slightly recurved, giving cusp sinuous profile in mesial and distal views; cusp apex strongly recurved (e.g., in largest tooth in type series, LACM 122197; Fig. 4BI) or without recurvature; labial crown face strongly convex; crown foot gently curved, lacks basal ledge or groove, and lacks ornamentation (e.g., striations); lingual crown face strongly convex and smooth, lacking ornamentation; tooth neck well defined and completely encircles crown foot, both labially and linguallly, and particularly well developed immediately basal to shoulders of crown on lingual face; crowns symmetrical to strongly asymmetrical with varying degrees of distal inclination of main cusp; decreasing crown height with corresponding increase in distal cusp inclination relative to higher crowned teeth with little or no distal inclination.

Root proportionally massive in relation to crown, generally dwarfing crown, with average root length of 5.0 mm (range: 2.5–8.6 mm; $n = 67$) and average root width (= tooth width) of 6.4 mm (range: 3.3–10.2 mm; $n = 67$) (Appendix 1, Supplemental Data); ca. 6% (four teeth) of type series ($n = 67$) with root length that exceeds root width (Appendix 1, Supplemental Data); roots strongly bilobate; mesial and distal root lobes closely spaced in teeth with erect main cusps and more widely spaced in

teeth with greater inclination of main cusp; lingual root face developed into massive protuberance that almost parallels lingual surface of main cusp; lingual attachment surface rounded to flat; mesial and distal root lobes rounded to tabular and basal profile below crown foot may be gently rounded, strongly arched, or almost angular; nutritive groove absent or variably developed, ranging from weak and short (Fig. 3Q) to deep and long (Fig. 3R) on lingual attachment surface; nutritive pits absent (or not apparent) where well-developed nutritive groove is present (ca. 66%, or 44 teeth, of type series; Fig. 3R) or variably present on root without nutritive groove (ca. 30%, or 20 teeth, of type series; Fig. 3O) or within nutritive groove (ca 4%, or three teeth, of type series; Fig. 3P) (Appendix 1); minute scattered foramina present on labial root face immediately below crown foot (Fig. 3G).

Remarks—A diverse fauna of early Miocene marine and terrestrial vertebrates occurs in the ‘grit zone’ or lower 3 m of the Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill, Kern County, California (Jordan and Hannibal, 1923; Kellogg, 1932; Savage and Barnes, 1972; Mitchell and Tedford, 1973; Barnes, 1979; Welton, 1979, 1981). Applegate in Mitchell and Tedford (1973:268–269) provided a list of sharks and rays represented by fossil teeth from LACM locality 1626, the Pyramid Hill Sand Quarry. Approximately 30 species of sharks and rays were listed, including reference to a new genus and species of a shark thought to belong either to the cat sharks (Carcharhiniiformes: Scyliorhinidae) or false cat sharks (Carcharhiniiformes: Pseudotriakidae). In many features, including overall proportions, external morphology, inferred heterodonty, and especially osteodont tooth histology, teeth of the alleged new taxon are most similar to those of Lamniformes (sensu Compagno, 1977) among living sharks, and in addition to their large size, lack most diagnostic dental characters of scyliorhinids, pseudotriakids, or

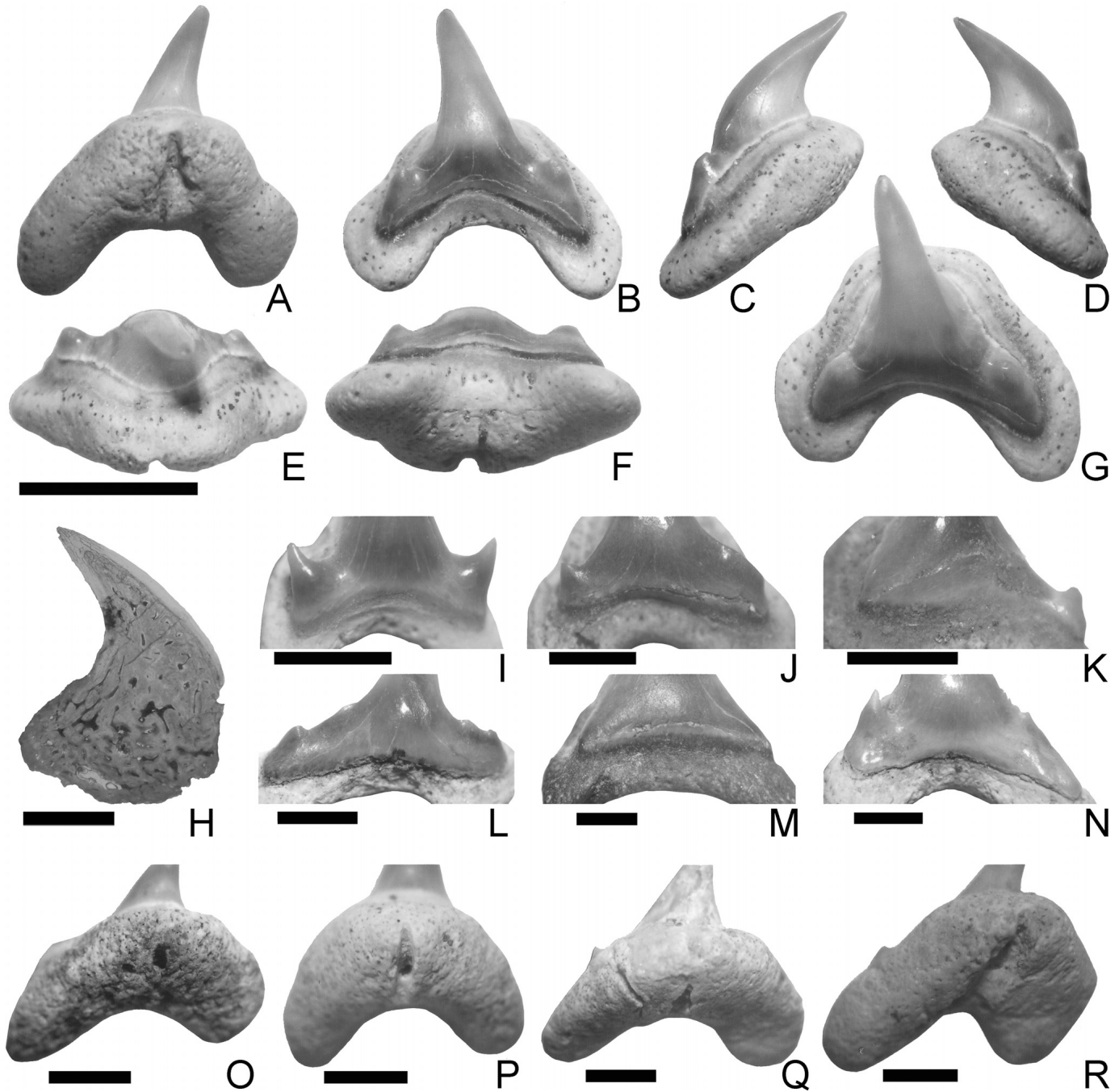


FIGURE 3. Holotype (A–G) of *Megachasma applegatei*, sp. nov., and selected specimens showing notable features (H–R). A, LACM 122190, holotype in lingual view; B, LACM 122190, holotype in labial view; C, LACM 122190, holotype in mesial view; D, LACM 122190, holotype in distal view; E, LACM 122190, holotype in apical view; F, LACM 122190, holotype in basal view; G, LACM 122190, holotype in apicolabial view; H, LACM 155725, longitudinal histological section of tooth (lingual to the left) showing osteodentine core; I, LACM 122157, part of paratype in labial view showing one pair of prominent lateral cusplets; J, LACM 122191, part of paratype in labial view showing cusplet only on distal side; K, LACM 122202, part of paratype in labial view showing cusplet only on mesial side; L, LACM 122179, part of paratype in labial view showing two pairs of lateral cusplets; M, LACM 122130, part of paratype in labial view showing no lateral cusplets; N, LACM 122137, part of paratype in labial view showing prominent distal cusplet and poorly developed mesial lateral cusplet accompanying a few notches, giving serration-like appearance along mesial cutting edge; O, LACM 122151, part of paratype in lingual view showing nutritive pores on root; P, LACM 122167, part of paratype in lingual view showing nutritive pore in nutritive groove of root; Q, LACM 122170, part of paratype in lingual view showing nutritive pore and nutritive groove separate on root; R, LACM 122173, part of paratype in lingual view showing prominent nutritive groove on root. A–G, scale bar equals 5 mm; H–R, all scale bars equal 2 mm.

Carcharhiniformes in general. This same taxon was later reported by Phillips et al. (1976:149, fig. 5.4a–c) from the late Oligocene Skooner Gulch Formation, near Point Arena, California, and referred to Lamniformes incertae sedis. Subsequently, after the first extant *Megachasma pelagios* was discovered, it became apparent that those unidentified fossil shark teeth from California and Oregon belonged to a fossil megachasmid, but still no formal species description was made even though many workers noted the existence of the fossil megachasmid (Lavenberg and Seigel, 1985; Compagno, 1990; Lavenberg, 1991; Stewart, 1991; Long, 1994; Berra, 1997; Cöcke, 2002:111). It is here interpreted that all of the aforementioned specimens of Lamniformes incertae sedis, the Pyramid Hill ‘cat shark,’ and a fossil taxon based on unofficial accounts represent a single species of megachasmid shark described here as *M. applegatei*, sp. nov. It should be noted that Lucas et al. (1997:6) reported the occurrence of an “undetermined genus and species of megachasmid (LACM 140707)” from the early Miocene Vaqueros Formation in southern California; however, our examination of the specimen (one tooth) indicates that it is not a megachasmid, but a pseudocarchariid.

The genus *Megachasma* is previously known from two species: extant *M. pelagios* and Cretaceous *M. comanchensis*. Whereas the validity of *M. comanchensis* has been questioned (De Schutter, 2009; Cappetta, 2012; Maisey, 2012), the Cretaceous species is readily distinguishable from *M. applegatei*, sp. nov., by the lack of lateral cusplets, an extremely prominent lingual protuberance with a well-developed nutritive groove, and wide and flattened basal attachment surfaces on either side of the nutritive groove with essentially no root lobes (see Shimada, 2007). On the other hand, although root lobes are also short in *M. pelagios*, a number of teeth of *M. applegatei*, sp. nov., closely resemble those of *M. pelagios*. Thus, an attempt was made to quantitatively differentiate the two species. Figure 6B shows crown height (CH) to crown width (CH) ratios plotted against the root length (RL) to root width (RW) ratios in *M. pelagios* and *M. applegatei*, sp. nov. Whereas the type series represents the samples for *M. applegatei*, sp. nov. ($n = 67$; Appendix 1), the dental measurements of *M. pelagios* are taken from published illustrations (Appendix 2, Supplemental Data). Because the extant samples ($n = 23$) consist of teeth from two adult males (including the holotype by Taylor et al., 1983; Herman et al., 1993; De Schutter, 2009), an adult female (Yabumoto et al., 1997), and a juvenile (De Schutter, 2009) represented by a reasonably wide range of tooth positions, the data set is considered to reasonably capture the range of tooth variation present in the extant species. The bivariate scatter plots (Fig. 6B) show that whereas the difference between the two species in RH/RW ratios is not so wide, a substantial difference in CH/CW ratios between the two species is detected. The data indicate that *M. pelagios* tends to have more slender crowns compared with *M. applegatei*, sp. nov., which has crowns with more or less equal height and width. The difference in CH/CW ratios between the two species is even more evident using box plots (Fig. 6C), in which the two interquartile ranges are completely separated from one another, and only small portions of teeth have comparable CH/CW ratios between the two species (i.e., overlapping ‘vertical whiskers’). Thus, *M. applegatei*, sp. nov., is considered to be a distinct megachasmid species, and it is regarded as a sister species of *M. pelagios*.

The extant *Megachasma pelagios* has 42–56 teeth and 43(?)–69 teeth in each side of the upper jaw and lower jaw, respectively, and possesses a dentition with a monognathic gradient close to a homodont condition in both jaws (see Shimada, 2002). The exact total number of teeth as well as the pattern of the dentition of *M. applegatei*, sp. nov., are uncertain, and its dental reconstruction is beyond the scope of this study. Accurately reconstructing the original dentition of any given shark taxon on the basis of isolated teeth represented likely by multiple individuals is often difficult. This is because, in elasmobranchs, heterodonty

is commonly present (e.g., Shimada, 2002), and besides pathological or abnormally formed teeth (e.g., Gudger, 1937), a wide range of tooth variations (individual, ontogenetic, sexual, and/or geographic) is known to occur in different taxa (e.g., Taniuchi, 1970; Reif, 1976; Kajiura and Tricas, 1996; Lucifora et al., 2003). Nevertheless, a considerable range of variation seen in teeth of *M. applegatei*, sp. nov. (even within the type series alone; Fig. 4), suggests that the dentition of the fossil shark must have exhibited strong heterodonty.

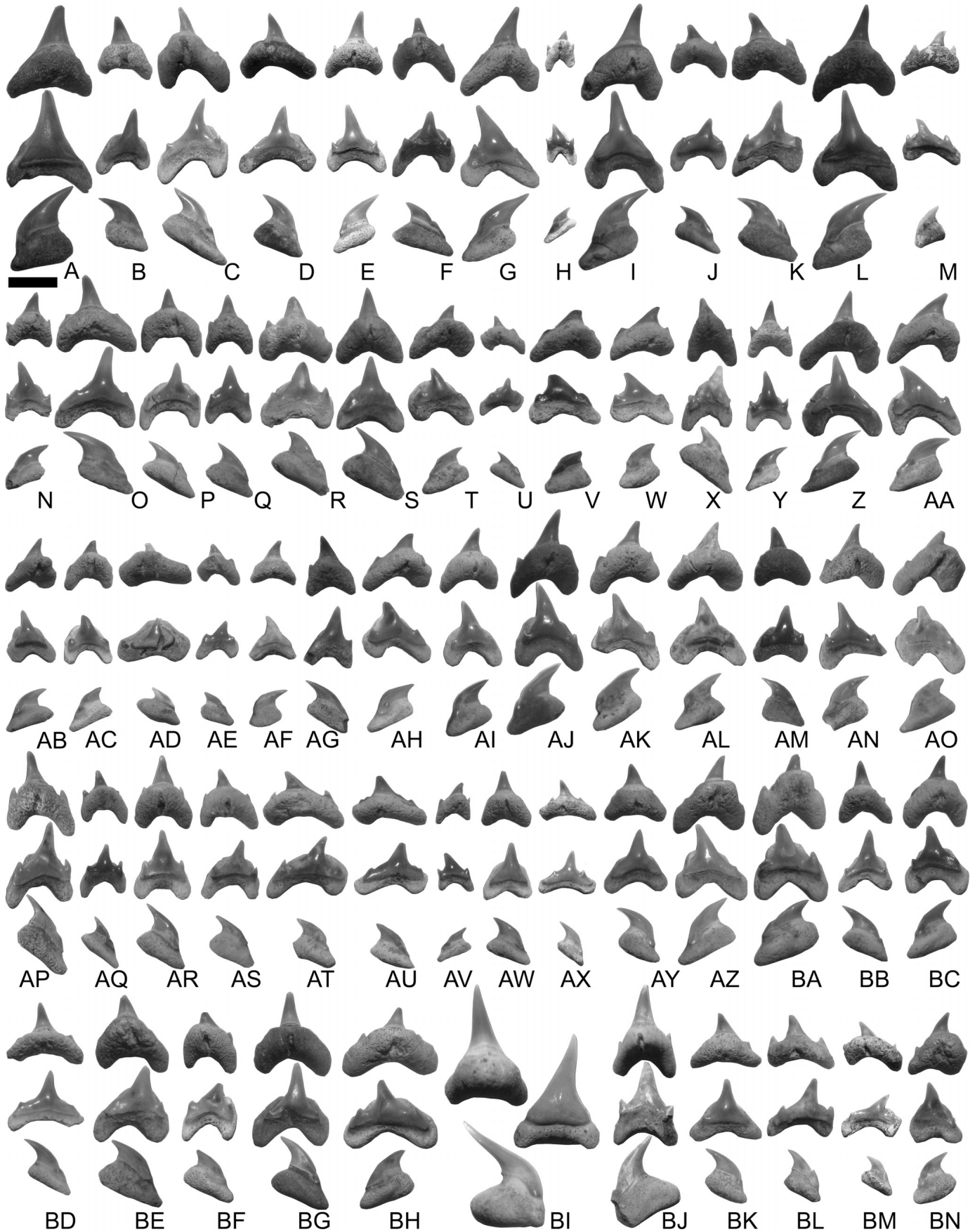
Teeth of *M. applegatei*, sp. nov., are reminiscent of teeth of odontaspids (*Odontaspis* spp.) by commonly possessing a crown with one large main cusp and one or more pairs of slender lateral cusplets and strongly bilobate root with a distinct nutritive groove on its lingual protuberance (e.g., Compagno, 2001:figs. 55, 56; Cappetta, 2012:figs. 12B, 192A). As representatives of macrophagous lamniforms, extant odontaspids possess a typical ‘lamnoid tooth pattern’ characterized by uniquely differentiated teeth that can be categorized into different tooth types (Compagno, 1984; Long and Waggoner, 1996; Shimada, 2002). Decisive tooth type assignments are difficult based solely on isolated teeth, but some teeth are large and have slender erect main cusps (e.g., Fig. 4BJ) that can be attributed to ‘anterior teeth,’ whereas some are small and have broad-based main cusps with strong distal inclinations (e.g., Fig. 4U) that can be referred to some of the distal-most ‘lateral teeth’ (sensu Shimada, 2002). The vast majority of the rest of the teeth fall in between the two extremities, including the holotype (Fig. 3A–G), and the range of morphological variation seen in teeth of *M. applegatei*, sp. nov., is wide enough to hypothesize that the dentition of the fossil species was odontaspid-like.

DISCUSSION

Taxonomy of Cenozoic Megachasmids

An extinct Cenozoic carcharhiniform taxon, *Megascyliorhinus* Cappetta and Ward, 1977, was once considered to be a megachasmid (Compagno, 1990), but it has been removed from Megachasmidae because the taxon exhibits orthodont tooth histology (Cione, 1986; Cappetta, 2012). Although megachasmids may also occur in the middle Eocene (Naylor et al., 1997:fig. 10), the Cenozoic fossil record of *Megachasma* summarized by Cappetta (2012) includes the Chattian of California (Phillips et al., 1976), Aquitanian of Mexico (Gonzalez-Barba and Thies, 2000), ‘Miocene’ of Oregon (Taylor et al., 1983), ‘Upper Miocene’ of Chile (Cappetta, 2012:fig. 231; see also Cöcke, 2002:110), Tortonian of Greece (Keupp and Bellas, 2002, as *Hexanchus* pointed out by Cappetta, 2012), Zanchlean of North Carolina (Purdy et al., 2001), U.S.A., and early Miocene(?)–early Pliocene(?) of Belgium (De Schutter, 2009). In addition, based on unpublished accounts, De Schutter (2009) noted the occurrence of megachasmid teeth from the Neogene of northeast Florida, U.S.A., that are reminiscent of teeth from Chile and North Carolina, and a possible Langhian occurrence of a megachasmid tooth from Mexico.

Based on comparisons among megachasmid teeth from various Cenozoic fossil localities, De Schutter (2009) classified them into two broad categories: (1) a category he referred to ‘*Megachasma* sp.’ exemplified by materials from California and Belgium; and (2) the other to ‘*Megachasma* cf. *pelagios*,’ typified by teeth from North Carolina, Florida, Chile, and Greece. De Schutter’s (2009) sample size from each locality was small (e.g., $n = 1$ for the Greece occurrence). Additionally, whether or not his samples are an adequate representation of the entire megachasmid assemblage at each locality is uncertain, especially because his material included “commercially acquired specimens” (p. 181) that may have involved collecting bias. Nevertheless, we agree with De Schutter’s (2009) observation on the existence of two broad megachasmid categories by noting that the former is characterized by the common occurrence of lateral cusplets and



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the latter by the lack of lateral cusplets similar to the extant *M. pelagios*, in which lateral cusplets are rare. The former type is here assigned to *M. applegatei*, sp. nov., provisionally including the Belgium materials, in which their perceived differences from the California materials (De Schutter, 2009:table 2) are not sufficient to designate them to a separate species due to small sample size ($n = 13$) and to the fact that they reside in private collections. On the other hand, the latter type should be referred to as *M. cf. M. pelagios*, if not *M. pelagios*.

Unfortunately, De Schutter's (2009) Belgium materials come from a deposit with a poor chronostratigraphic constraint, giving a range of early Miocene(?) to early Pliocene at best. Therefore, the exact youngest occurrence for *Megachasma applegatei*, sp. nov., cannot be ascertained, but *M. applegatei*, sp. nov., from the late Oligocene–early Miocene deposits of the western United States described here is older than all other reported Cenozoic fossil megachasmids that are here referred to *M. cf. M. pelagios* (= '*M. cf. pelagios*' of De Schutter, 2009). The fact that the form assignable to *M. pelagios* (e.g., *M. cf. M. pelagios*) is present in late Miocene deposits suggests that the evolution of the modern-grade megachasmids (*M. pelagios* and *M. cf. M. pelagios*) took place no later than the earliest late Miocene.

Cappetta (2012:252) noted that megachasmid teeth from the Oligocene of Oregon and lower Miocene of California (i.e., described as *Megachasma applegatei*, sp. nov., here) represent "a new genus, probably an ancestor of *Megachasma*" because they are much smaller relative to other known Neogene–Recent megachasmid teeth and commonly possess lateral cusplets. Although we agree that those North American Oligo–Miocene forms are morphologically archaic, we do not agree that the taxon merits an assignment to a new genus for three reasons. First, the morphological and size ranges of *M. applegatei*, sp. nov., and extant *M. pelagios* overlap (e.g., Fig. 6B). This is particularly true for the largest tooth in the type series (LACM 122197), which is practically indistinguishable from teeth of extant *M. pelagios* shape-wise (Fig. 4BI). Second, the close morphological resemblance between *M. pelagios* (including *M. cf. M. pelagios*) and *M. applegatei*, sp. nov., with no other known Cenozoic megachasmid taxon indicates that the two taxa should be considered as sister species. If so, there is no reason to designate the *M. applegatei*, sp. nov., to a different genus. Third, the family Megachasmidae is not speciose, known only from two or three species: *M. pelagios*, *M. applegatei*, sp. nov., and a debatable *M. comanchensis*. As it currently stands, establishment of a new genus does not add any particular scientific merit and would potentially create inadvertent misstep for a small sample of isolated fossil megachasmid teeth that cannot be decisively identified as *M. pelagios* or *M. applegatei*, sp. nov. (e.g., note the morphometrically overlapping zone in Fig. 6B). For these reasons, we retain the species *M. applegatei*, sp. nov., under the genus *Megachasma*.

Paleoecology of *Megachasma applegatei*

Accurately inferring the body size of *Megachasma applegatei*, sp. nov., is difficult because the species is represented only by iso-

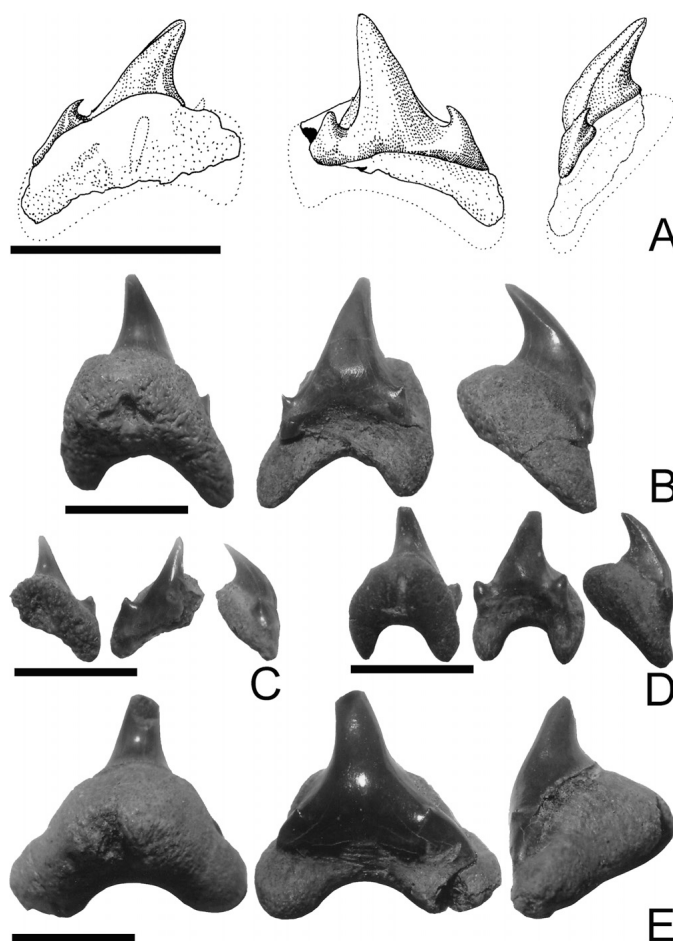


FIGURE 5. Examples of *Megachasma applegatei*, sp. nov., from Skooner Gulch Formation (late Oligocene), Yaquina Formation (late Oligocene), and Nye Mudstone (early Miocene) of western United States (from left to right, lingual, labial, and mesial views, respectively). **A**, UCMP 114537 from Skooner Gulch Formation of California (modified from Phillips et al., 1976:fig. 5.4a–c); **B**, LACM 122120 from Yaquina Formation of Oregon; **C**, LACM 122121 from Yaquina Formation of Oregon; **D**, LACM 122119 from Nye Mudstone of Oregon; **E**, LACM 122118, from Nye Mudstone of Oregon. All scale bars equal 5 mm.

lated teeth. There are a number of ambiguities, such as the uncertainty in their original tooth positions as well as in the body structure and pattern of dentition, including the relationship between the body size and tooth size. Nevertheless, as a proxy to estimate the body length of *M. applegatei*, sp. nov., one can use an extant female *M. pelagios* that had a total body length (TL) of 471 cm and a maximum tooth height (TH) of 8.5 mm (Yabumoto et al.,

← FIGURE 4. Entire paratype series of *Megachasma applegatei*, sp. nov. (from top to bottom, lingual, labial, and mesial views, respectively; note that order of illustrated teeth is simply based on order of catalog numbers and does not reflect sequence of tooth positions). **A**, LACM 122130; **B**, LACM 122132; **C**, LACM 122133; **D**, LACM 122134; **E**, LACM 122135; **F**, LACM 122136; **G**, LACM 122137; **H**, LACM 122138; **I**, LACM 122139; **J**, LACM 122140; **K**, LACM 122141; **L**, LACM 122142; **M**, LACM 122143; **N**, LACM 122145; **O**, LACM 122146; **P**, LACM 122147; **Q**, LACM 122148; **R**, LACM 122149; **S**, LACM 122150; **T**, LACM 122151; **U**, LACM 122153; **V**, LACM 122154; **W**, LACM 122155; **X**, LACM 122156; **Y**, LACM 122157; **Z**, LACM 122158; **AA**, LACM 122159; **AB**, LACM 122160; **AC**, LACM 122161; **AD**, LACM 122162; **AE**, LACM 122163; **AF**, LACM 122164; **AG**, LACM 122165; **AH**, LACM 122166; **AI**, LACM 122167; **AJ**, LACM 122168; **AK**, LACM 122169; **AL**, LACM 122170; **AM**, LACM 122171; **AN**, LACM 122172; **AO**, LACM 122173; **AP**, LACM 122174; **AQ**, LACM 122175; **AR**, LACM 122176; **AS**, LACM 122177; **AT**, LACM 122178; **AU**, LACM 122179; **AV**, LACM 122181; **AW**, LACM 122182; **AX**, LACM 122183; **AY**, LACM 122184; **AZ**, LACM 122186; **BA**, LACM 122187; **BB**, LACM 122189; **BC**, LACM 122191; **BD**, LACM 122192; **BE**, LACM 122193; **BF**, LACM 122194; **BG**, LACM 122195; **BH**, LACM 122196; **BI**, LACM 122197; **BJ**, LACM 122198; **BK**, LACM 122199; **BL**, LACM 122200; **BM**, LACM 122201; **BN**, LACM 122202. Scale bar equals 5 mm.

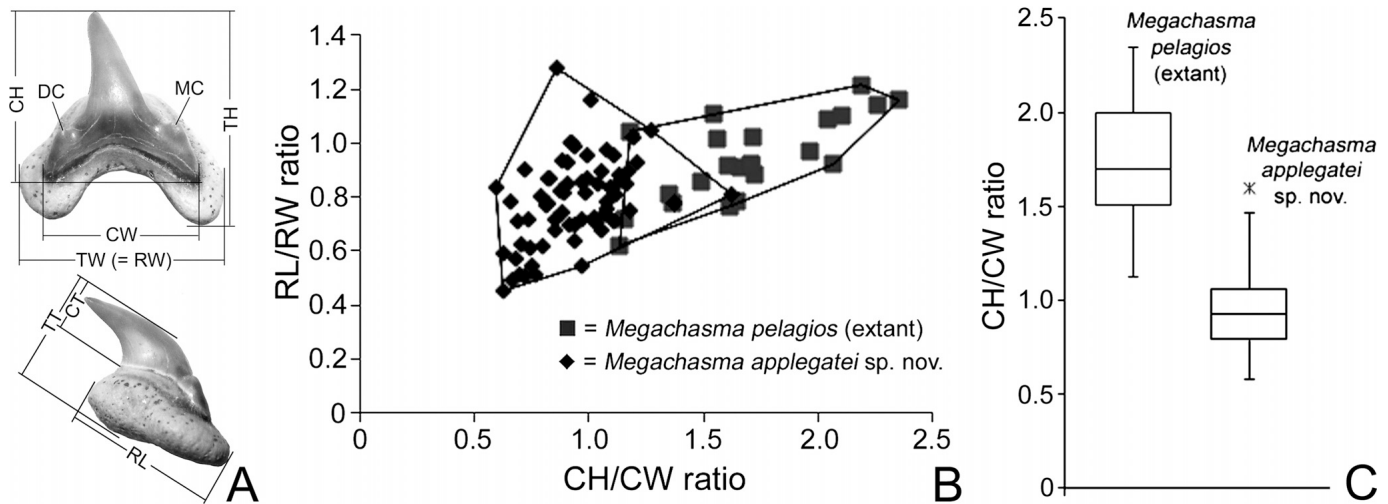


FIGURE 6. Dental measurements (A) and comparisons between teeth of extant *Megachasma pelagios* and teeth of *M. applegatei*, sp. nov. (B, C). A, measured variables using holotype of *M. applegatei*, sp. nov., as an example (top, labial view; bottom, distal view; cf. Fig. 3A–G); B, scatter plots between CH/CW ratios and RL/RW ratios comparing extant *M. pelagios* ($n = 23$) and *M. applegatei*, sp. nov. ($n = 67$) (original data in Appendices 1 and 2); C, box plot representation of CH/CW ratios between extant *M. pelagios* and *M. applegatei*, sp. nov. (box, interquartile range, i.e., central 50% of data; horizontal line in box, mean value; vertical whiskers, total range of data; asterisk, outlier). **Abbreviations:** CH, crown height; CT, crown thickness; CW, crown width; DC, distal lateral cusplet; MC, mesial lateral cusplet; RL, root length; RW, root width; TH, total tooth height; TT, total tooth thickness; TW, total tooth width.

1997). The tallest tooth in the type series of *M. applegatei*, sp. nov. (14.7 mm; LACM 122197; Appendix 1, Supplemental Data; Fig. 4BI), is 1.73 times greater than the tallest tooth of *M. pelagios*. This proportion would yield an estimated TL of about 8.1 m for the fossil individual if the tallest tooth of *M. applegatei*, sp. nov., is assumed to be the tallest tooth in its original dentition, and if *M. applegatei*, sp. nov., is assumed to have had a similar relationship between the TL and maximum TH as the *M. pelagios* individual. The estimated 8.1 m TL for *M. applegatei*, sp. nov., is clearly larger than the largest known extant *M. pelagios* (ca. 5.5 m TL; Compagno, 2001). However, it should be noted that the fossil tooth (LACM 122197) is an exceptionally large tooth, an outlier, among all the teeth in the type series (Appendix 1; Fig. 4BI) as well as other referred specimens described here. Thus, typical adult individuals of *M. applegatei*, sp. nov., could have been smaller. The average TH of the type series consisting of various tooth positions is 6.6 mm ($n = 67$), and it would yield an estimated TL of 3.7 m. Hence, *M. applegatei*, sp. nov., could have commonly measured somewhere between 3.7 and 8.1 m TL, perhaps close to the median of these two values, ca. 6 m TL. If so, large individuals of *M. applegatei*, sp. nov., were comparable in body size to those of extant *M. pelagios*. In addition, it is also noteworthy that teeth of the ‘early *M. pelagios*’ (= *M. cf. M. pelagios*) from the late Miocene–early Pliocene range up to 20 mm TH (De Schutter, 2009:table 2), indicating that those large fossil teeth likely came from gigantic individuals that could have measured up to ca. 11 m TL.

The extant *Megachasma pelagios* employs filter feeding using its gill rakers primarily on epipelagic–mesopelagic euphausiid shrimp but also on copepods and sea jellies (Compagno, 2001). Although *M. applegatei*, sp. nov., is a megachasmid, teeth of the fossil taxon are archaic in that they are odontaspidid-like (see above). Although extant odontaspidids (*Odontaspis* spp.) feed primarily on smaller teleosts, elasmobranchs, and cephalopods (Compagno, 2001; Fergusson et al., 2008), tooth morphology alone does not conclusively indicate the diet of the shark (e.g., Whitenack and Motta, 2010) nor its filter-feeding behavior. However, the mosaic of megachasmid–odontaspidid characters

present in *M. applegatei*, sp. nov., may imply that the fossil taxon had a wider range of diet than the extant *M. pelagios* by possibly feeding on small fishes as well as macro-zooplanktonic invertebrates.

The extant *Megachasma pelagios* ranges from tropical equatorial waters to temperate zones north and south of the equator (Compagno, 2001), but the marine realm of *M. applegatei*, sp. nov., in western North America was much more tropical than at present (Hall, 2002). The extant *M. pelagios* migrates vertically between shallow waters at night and deeper waters (at least 165 m) during the days in oceans as deep as 4600 m (Lavenberg, 1991; Nelson et al., 1997). Teeth of *M. applegatei*, sp. nov., occur in inner to middle shelf transgressive (deepening water) marine sands of the Jewett Sand at Pyramid Hill, and upper bathyal siltstones of the Freeman Silt at Horse Canyon in Kern County, California (Olson, 1988; Figs. 3, 4), in bathyal to abyssal deposits of the Skooner Gulch Formation in northern California (Phillips et al., 1976; Fig. 5A), in shallow, inner shelf deltaic sands of the upper member of the Yaquina Formation, Oregon (Goodwin, 1973; Fig. 5B, C), and bathyal sediments of the Nye Mudstone, Oregon (Heacock, 1952; Welton, 1979; Fig. 5D, E). Therefore, *M. applegatei*, sp. nov., occurs in rock units consisting of both deep and shallow coastal water sediments, indicating that either the fossil shark was broadly adapted to a wide bathymetric tolerance or was a nektopelagic feeder over both deep and shallow water habitats similar to the extant *M. pelagios*.

CONCLUSION

Megachasma applegatei, sp. nov., is a new megachasmid shark based on isolated teeth from Oligo-Miocene marine deposits in the western United States, including the Pyramid Hill Sand Member (Aquitian) of the Jewett Sand in California, the Skooner Gulch Formation (late Chattian) of California, the Yaquina Formation (late Chattian) of Oregon, and the Nye Mudstone (Aquitian) of Oregon. The fossil taxon is interpreted to be phylogenetically sister to the extant *M. pelagios*. *Megachasma applegatei*, sp. nov., clearly exhibits megachasmid tooth design,

but its teeth show wide morphological variations and are reminiscent to those of odontaspidid sharks, indicating that the fossil taxon likely had a dentition with strong heterodonty. Comparisons with extant *M. pelagios* suggest that *M. applegatei*, sp. nov., could have commonly measured somewhere between 3.7 and 8.1 m TL, possibly about 6 m TL, in life. The mosaic of megachasmid-odontaspidid characters present in *M. applegatei*, sp. nov., may imply that the fossil taxon had a wide range of diet, possibly including small fishes and planktonic invertebrates. Because *M. applegatei*, sp. nov., occurs in both deep and shallow water deposits, either the fossil shark was broadly adapted to a wide bathymetric tolerance or was a nektopelagic feeder in both deep and shallow water habitats, possibly similar to the feeding ecology of extant *M. pelagios*.

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LITERATURE CITED

- Addicott, W. O. 1970. Miocene Gastropods and Biostratigraphy of the Kern River Area, California. United States Geological Survey Professional Paper 642, 174 pp.
- Addicott, W. O. 1972. Provincial middle and late Tertiary molluscan stages, Temblor Range, California; pp. 1–26 in E. H. Stinemeyer (ed.), Proceedings of the Pacific Coast Miocene Biostratigraphic Symposium, Society of Economic Paleontologists and Mineralogists, 47th Annual Pacific Section Convention, Bakersfield, California, March 9–10, 1972.
- Addicott, W. O. 1976. Molluscan Paleontology of the Lower Miocene Clallam Formation, Northwestern Washington. United States Geological Survey Professional Paper 976, 44 pp.
- Addicott, W. O. 1981. Significance of pectinids in Tertiary biochronology of the Pacific Northwest; pp. 17–37 in J. M. Armentrout (ed.), Pacific Northwest Cenozoic Biostratigraphy. Geological Society of America Special Paper 184.
- Armentrout, J. M. 1981. Correlation and ages of Cenozoic chronostratigraphic units in Oregon and Washington; pp. 137–148 in J. M. Armentrout (ed.), Pacific Northwest Cenozoic Biostratigraphy. Geological Society of America Special Paper 184.
- Armentrout, J. M., D. A. Hull, and J. D. Beaulieu. 1983. Correlation of Cenozoic Stratigraphic Units of Western Oregon and Washington. State of Oregon, Department of Geology and Mineral Industries, Oil and Gas Investigation Number 7.
- Barnes, L. G. 1979. Fossil enaliarctine pinnipeds (Mammalia: Otariidae) from Pyramid Hill, Kern County, California. Natural History Museum of Los Angeles County, Contributions in Science 318:1–41.
- Bartow, J. A., and K. McDougall. 1984. Tertiary Stratigraphy of the Southeastern San Joaquin Valley, California. Contributions to Stratigraphy, United States Geological Survey Bulletin 1529-J, 41 pp.
- Berg, L. S. 1958. System der Rezenten und Fossilen Fischartigen und Fische. Hochschulbücher für Biologie, Berlin, 310 pp.
- Berggren, W. A. 1972. A Cenozoic time scale—some implications for regional geology and paleobiogeography. *Lethaia* 5:195–215.
- Berra, T. M. 1997. Some 20th century fish discoveries. *Environmental Biology of Fishes* 50:1–12.
- Blow, W. H. 1969. Late middle Eocene to Recent planktonic foraminiferal biostratigraphy; pp. 199–422 in P. Bronnimann and H. H. Renz (eds.), Proceedings of the First International Conference on Planktonic Microfossils, Geneva, 1967, Leiden, E. J. Brill, Volume 1.
- Bonaparte, C. L. 1838. *Selachorum tabula analytica*. *Nuovi Annali della Scienze Naturali*, Bologna 1(2):195–214.
- Cappetta, H. 2006. Elasmobranchii post-Triadici (index generum et specierum); in W. Riegraf (ed.), *Fossilium Catalogus I, Animalia*, 142. Backhuys Publish, Leiden, 472 pp.
- Cappetta, H. 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: teeth; in H.-P. Schultze (ed.), *Handbook of Paleozoichthyology*, Volume 3E. Verlag Dr. Friedrich Pfeil, Munich, 512 pp.
- Cappetta, H., and D. J. Ward. 1977. A new Eocene shark from the London Clay of Essex. *Palaeontology* 20:195–202.
- Cione, A. L. 1986. A new *Megascyliorhinus* (Chondrichthyes, Galeomorphii) from the middle Tertiary of Patagonia. *Journal of Vertebrate Paleontology* 6:105–122.
- Cöcke, J. 2002. *Fossil Shark Teeth of the World: A Collector's Guide*. Lamna Books, Torrance, California, 150 pp.
- Compagno, L. J. V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* 17:303–322.
- Compagno, L. J. V. 1984. FAO species catalogue. Volume 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Food and Agriculture Organization Fisheries Synopsis 125(4):1–655.
- Compagno, L. J. V. 1990. Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding habits. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service 90:357–379.
- Compagno, L. J. V. 2001. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Volume 2: bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). Food and Agriculture Organization Species Catalogue for Fishery Purposes 1(2):1–269.
- Davis, M. P., and C. Fielitz. 2010. Estimating divergence times of lizard-fishes and their allies (Euteleostei: Aulopiformes) and the timing of deep-sea adaptations. *Molecular Phylogenetics and Evolution* 57:1194–1208.
- De Schutter, P. 2009. The presence of *Megachasma* (Chondrichthyes: Lamniformes) in the Neogene of Belgium, first occurrence in Europe. *Geologica Belgica* 12:179–203.
- Fergusson, I. K., K. J. Graham, and L. J. V. Compagno. 2008. Distribution, abundance and biology of the smalltooth sandtiger shark *Odontaspis ferox* (Risso, 1810) (Lamniformes: Odontaspidae). *Environmental Biology of Fishes* 81:207–228.
- Gonzalez-Barba, G., and D. Thies. 2000. Asociaciones faunísticas de condriactos en el Cenozoico de la Península de Baja California, Mexico. *Profil* 18:1–4.
- Goodwin, C. J. 1973. Stratigraphy and sedimentation of the Yaquina Formation, Lincoln County, Oregon. M.S. thesis, Oregon State University, Corvallis, Oregon, 121 pp.
- Gudger, E. W. 1937. Abnormal dentition in sharks, Selachii. *Bulletin of the American Museum of Natural History* 72:249–280.
- Hall, C. A., Jr. 2002. Nearshore Marine Paleoclimatic Regions, Increasing Zoogeographic Provinciality, Molluscan Extinctions, and Paleoshorelines, California: Late Oligocene (27 Ma) to Late Pliocene (2.5 Ma). Geological Society of America Special Paper 357, 489 pp.
- Harland, W. B., R. L. Armstrong, A. V. Cox, L. E. Craig, A. G. Smith, and D. G. Smith. 1990. *A Geologic Time Scale 1989*. Cambridge University Press, Cambridge, U.K., 263 pp.
- Harrison and Eaton. 1920. Report on investigation of oil and gas possibilities of western Oregon. Oregon Bureau of Mines and Geology, Mineral Resources of Oregon 3(1):3–37.
- Hay, O. P. 1902. Bibliography and Catalogue of the Fossil Vertebrata of North America. *Bulletin of the United States Geological Survey* 179, 868 pp.
- Heacock, R. L. 1952. Stratigraphy and foraminifers of the upper part of the Nye Formation, Yaquina Bay, Oregon. M.S. thesis, Oregon State University, Corvallis, Oregon, 47 pp.
- Herman, J., M. Hovestadt-Euler, and D. C. Hovestadt. 1993. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supra-specific taxa of Chondrichthyan fishes: part A. Selachii. No. 1b: Order: Hexanchiformes—Family: Chlamydoselachidae. 5: Order: Heterodontiformes—Family: Heterodontidae. 6: Order:

- Lamniformes—Families: Cetorhinidae, Megachasmidae. Addendum 1 to 3: Order Squaliformes. Addendum 1 to 4: Order: Orectolobiformes. General Glossary. Summary Part A. Bulletin de L'Institut Royal des Sciences Naturelles de Belgique, Biologie 63:185–256.
- Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological Society of London 43:649–661.
- Jordan, D. S., and H. Hannibal. 1923. Fossil sharks and rays of the Pacific slope of North America. Bulletin of the Southern Californian Academy of Science 22:27–68.
- Kajiura, S. M., and T. C. Tricas. 1996. Seasonal dynamics of dental sexual dimorphism in the Atlantic stingray *Dasyatis sabina*. Journal of Experimental Biology 199:2297–2306.
- Kellogg, R. 1932. A Miocene long-beaked porpoise from California. Smithsonian Miscellaneous Collections 87(2):1–11, pls. 1–4.
- Keupp, H., and S. Bellas. 2002. Miozan-Fossilien aus NW-Kreta. III. Die Beckenfazies. Fossilien 19:34–40.
- Kleinpell, R. M., G. Hornaday, A. D. Warren, and A. Tipton. 1980. The Miocene stratigraphy of California revisited. American Association of Petroleum Geologists Studies in Geology 11:1–182.
- Lavenberg, R. J. 1991. Megamania: the continuing saga of megamouth sharks. Terra 30(1):30–33, 36–39.
- Lavenberg, R. J., and J. A. Seigel. 1985. The Pacific's megamystery—megamouth. Terra 23(4):29–31.
- Long, D. J. 1994. Historical biogeography of sharks from the eastern North Pacific Ocean. Ph.D. dissertation, Department of Integrative Biology, University of California, Berkeley, California, 371 pp.
- Long, D. J., and B. M. Waggoner. 1996. Evolutionary relationships of the white shark: a phylogeny of lamniform sharks based on dental morphology; pp. 37–47 in A. P. Klimley and D. Ainley (eds.), Great White Sharks: The Biology of *Carcharodon carcharias*. Academic Press, San Diego, California.
- Lucas, S. G., D. P. Whistler, and H. M. Wagner. 1997. Giant entelodont (Mammalia, Artiodactyla) from the early Miocene of southern California. Contributions in Science, Los Angeles County Museum 466:1–9.
- Lucifora, L. O., A. L. Cione, R. C. Menni, and A. H. Escalante. 2003. Tooth row counts, vicariance, and the distribution of the sand tiger shark *Carcharias taurus*. Ecography 26:567–572.
- Maisey, J. G. 2012. What is an 'elasmobranch'? The impact of palaeontology in understanding elasmobranch phylogeny and evolution. Journal of Fish Biology 80:918–951.
- Mitchell, E. D., and R. H. Tedford. 1973. The Enaliarctinae. A new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. Bulletin of the American Museum of Natural History 151:201–284.
- Naylor, G. J. P., A. P. Martin, E. G. Mattison, and W. M. Brown. 1997. Interrelationships of lamniform sharks: testing phylogenetic hypotheses with sequence data; pp. 199–218 in T. D. Kocher and C. A. Stepien (eds.), Molecular Systematics of Fishes. Academic Press, San Diego, California.
- Nelson, D. R., J. N. McKibben, W. R. Strong, C. G. Lowe, J. A. Sinneros, D. M. Schroeder, and R. J. Lavenberg. 1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. Environmental Biology of Fishes 49:389–399.
- Olson, H. C. 1988. Oligocene-middle Miocene depositional systems north of Bakersfield, California: eastern basin equivalents of the Temblor Formation; pp. 189–205 in S. A. Graham (ed.), Studies of the Geology of the San Joaquin Basin. Pacific Section, Society of Economic Paleontologists and Mineralogists, Volume 60.
- Phillips, F. J., B. J. Welton, and J. Welton. 1976. Paleontologic studies of the middle Tertiary Skooner Gulch and Gallaway formations at Point Arena, California; pp. 137–157 in A. E. Fritsche, H. T. Best, and W. W. Wornardt (eds.), The Neogene Symposium. Annual Meeting, Pacific Section, Society of Economic Paleontologists and Mineralogists, San Francisco, California, April 1976.
- Purdy, R. W., V. P. Schneider, S. P. Applegate, J. H. McLellan, R. L. Meyer, and B. H. Slaughter. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. Smithsonian Contributions to Paleobiology 90:71–202.
- Radinsky, L. 1961. Tooth histology as a taxonomic criterion for cartilaginous fishes. Journal of Morphology 109:73–92.
- Reif, W. E. 1976. Morphogenesis, pattern formation and function of the dentition of *Heterodontus* (Selachii). Zoomorphologie 83:1–47.
- Savage, D. E., and L. G. Barnes. 1972. Miocene vertebrate geochronology of the west coast of North America; pp. 125–145 in The Proceedings of the Pacific Coast Miocene Biostratigraphic Symposium. Society of Economic Paleontologists and Mineralogists, Pacific Section, 47th Annual Convention, Bakersfield, California, 9–10 March 1972.
- Schenck, H. G. 1927. Marine Oligocene of Oregon. University of California Publications in Geological Sciences 16:449–460.
- Shimada, K. 2002. Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). Journal of Morphology 251:38–72.
- Shimada, K. 2007. Mesozoic origin for megamouth shark (Lamniformes: Megachasmidae). Journal of Vertebrate Paleontology 27:512–516.
- Smith, A. 1828. Descriptions of new or imperfectly known objects of the animal kingdom, found in the south of Africa. South African Commercial Advertiser 3(145):2.
- Snavely, P. D., N. S. MacLeod, and H. C. Wagner. 1976. Geologic map of the Yaquina and Toledo quadrangles, Lincoln County, Oregon. United States Geological Survey Miscellaneous Investigation Series, Maps I 866, I 867, and I 868.
- Stewart, J. D. 1991. Fossil teeth fill in part of the story. Terra 30(1):34–35.
- Taniuchi, T. 1970. Variation in the teeth of the sand shark, *Odontaspis taurus* (Rafinesque) taken from the East China Sea. Japanese Journal of Ichthyology 17:37–44.
- Taylor, L. R., L. J. V. Compagno, and P. J. Struhsaker. 1983. Megamouth—a new species, genus, and family of lamnoid shark (*Megachasma pelagios*, Family Megachasmidae) from the Hawaiian Islands. Proceedings of the California Academy of Science 43:87–110.
- Tedford, R. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia-Villafranca, R. M. Hunt Jr., J. E. Storer, C. C. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikarean through Hemphillian interval (late Oligocene through early Pliocene) epochs; pp. 169–231 in M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.
- Welton, B. J. 1979. Late Cretaceous and Cenozoic Squalomorphii of the Northwest Pacific Ocean. Ph.D. dissertation, University of California, Berkeley, California, 553 pp.
- Welton, B. J. 1981. A new species of *Oxynotus* Rafinesque 1810 (Chondrichthyes: Squalidae) from the Early Miocene (Saucesian) Jewett Sand, Kern County, California, U.S.A. Tertiary Research 3:141–152.
- Whitenack, L. B., and P. J. Motta. 2010. Performance of shark teeth during puncture and draw: implications for the mechanics of cutting. Biological Journal of the Linnean Society 100:271–286.
- Wood, H. E., II, R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. Geological Society of America Bulletin 52:1–48.
- Yabumoto, Y., M. Goto, and T. Uyeno. 1997. Dentition of a female megamouth, *Megachasma pelagios*, collected from Hakata Bay, Japan; pp. 63–75 in K. Yano, J. F. Morrissey, Y. Yabumoto, and K. Nakaya (eds.), Biology of Megamouth Shark. Tokai University Press, Tokyo.

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