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A NEW FOSSIL MEGAMOUTH SHARK (LAMNIFORMES, MEGACHASMAIDAE) 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–Aquitanian) 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 odontaspidid 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 megamashid 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 CHONDRICTHYES 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 APPLIGATEI, 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.: Cocke, 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
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, 155514–155569, 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 “Lamminiformes incertae sedis” by Phillips et al., 1976:149, fig. 5A–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, Oregon; E, Jumppoff Joe (LACM locality 4318; early Miocene Nye Mudstone), Lincoln County, Oregon.

Etyymology—The species name, applegatei, is in honor of the late Shelton P. Applegate, who initially recognized the unique character of these small multicuspate 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
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 lingually 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. 4B1) 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 lingually, 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 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 (Carcharhiniformes: Scyliorhinidae) or false cat sharks (Carcharhiniformes: Pseudotriakidae).
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 Lammiformes 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 Lammiformes 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 pseudocarcharid.

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 (CW) 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(7)69 teeth in each side of the upper jaw and lower jaw, respectively, and possesses a dentition with a mononogathic 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; Kajjura 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 odontaspidids (Odontaspis sp.) 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 odontaspidids 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. 4B) 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 odontaspidid-like.

**DISCUSSION**

**Taxonomy of Cenozoic Megachasms**

An extinct Cenozoic carcharhiniform taxon, Megascyliorhinus (Parasqualurus) 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 megachasms 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, 2003; as Hexanchus pointed out by Cappetta, 2012), Zanclean 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
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 Belgian 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–earliest Miocene deposits of the western United States described here is older than all other reported Cenozoic fossil megachasms that are here referred to *M. cf. M. pelagios* ('... cf. M. 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 megachasms (*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. 4B1). 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 specious, known only from two or three species: *M. pelagios*, *M. applegatei*, sp. nov., and a dubious *M. comanchensis*. As it currently stands, establishment of a new genus does not add any particular scientific merit and would potentially create an 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 isolated 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.,...
The estimated 8.1 m TL for *M. applegatei* indicates that the relationship between the TL and maximum TH is considerably larger than the largest known extant *M. pelagios* (ca. 5.5 m TL; Compagno, 2001). However, it should be noted that the fossil taxon (LACM 122197) is an exceptionally large tooth, an outlier, among all the teeth in the type series (Appendix 1; Fig. 4B1), as well as other referred specimens described here. Thus, typical adult individuals of *M. applegatei*, sp. nov., could be 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. 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., Whitewack 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 macrozooplanktonic 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 silstones 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 nektonic 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 (Aquitanian) 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 (Aquitanian) 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 nektobenthic feeder in both deep and shallow water habitats, possibly similar to the feeding ecology of extant *M. pelagios*.

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A new fossil megamouth shark (Lamniformes, Megachasmidae) from the Oligocene–Miocene of the western United States

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APPENDIX 1. Dental measurements (in millimeters) and other dental characteristics taken from holotype (asterisk) and paratype specimens of *Megachasma applegatei* sp. nov. (number in parentheses indicates estimated value). **Abbreviations** (see also Fig. 6A): CH, crown height; CT, crown thickness; CW, crown width; G, nutritive groove dominant; nDC, number of distal cusplets (number in quote marks indicates poorly-developed lateral cusplet represented by minute rise of cutting edge); nMC, number of mesial lateral cusplets (number in quote marks indicates poorly-developed lateral cusplet represented by minute rise of cutting edge); P, nutritive pore(s) dominant; RL, root length; TH, total tooth height; TT, total tooth thickness; TW, total tooth width (i.e., equivalent to ‘root width’ [RW]).

| Specimen   | TH  | TW  | TT  | CH  | CW  | CT  | RL  | nMC | nDC | P/G |
|------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| LACM 122130 | 9.6 | 8.4 | 5.6 | 7.6 | 6.5 | 3.4 | 6.3 | 0   | 0   | P   |
| LACM 122132 | 5.8 | 5.3 | 3.3 | 5.0 | 4.5 | 2.5 | 4.3 | ‘1’ | ‘1’ | G   |
| LACM 122133 | 10.1| 8.7 | 5.6 | 7.3 | 7.4 | 2.8 | 8.3 | 1   | 1   | G   |
| LACM 122134 | 8.2 | 9.4 | 5.3 | 6.6 | 7.1 | 2.4 | 6.0 | 1   | ‘1’ | G   |
| LACM 122135 | 8.3 | 7.2 | 4.2 | 6.5 | 5.9 | 2.6 | 5.1 | 1   | 1   | G   |
| LACM 122136 | 6.0 | 6.1 | 3.8 | 4.5 | 5.1 | 2.0 | 5.0 | 1   | 1   | G   |
| LACM 122137 | 8.5 | 7.8 | 4.0 | 6.9 | 6.6 | 2.6 | 5.3 | ‘1’ | 1   | G   |
| LACM 122138 | 5.6 | 3.7 | 2.3 | 3.3 | 3.3 | 1.0 | 4.3 | 1   | 1   | G   |
| LACM 122139 | 9.6 | 7.6 | 4.6 | 5.9 | 6.0 | 2.7 | 6.6 | 0   | 0   | G   |
| LACM 122140 | 4.8 | 5.6 | 3.1 | 3.6 | 4.6 | 1.7 | 4.5 | 1   | 1   | G   |
| LACM 122141 | 7.1 | 7.1 | 4.3 | 5.3 | 6.5 | 2.5 | 5.5 | 1   | ?   | G   |
| LACM 122142 | 9.0 | 8.2 | 5.0 | 7.3 | 6.8 | 2.9 | 6.2 | ‘2’ | ‘2’ | G   |
| LACM 122143 | (5.5)| 7.0 | 3.4 | (4.3)| 6.2 | 1.7 | 3.6 | ‘2’ | 1   | G   |
| LACM 122145 | 5.7 | 4.7 | 3.1 | 4.7 | 4.3 | 1.9 | 3.9 | 1   | 1   | P   |
| LACM 122146 | 7.9 | 7.8 | 3.9 | 6.0 | 7.1 | 2.3 | 5.3 | 1   | 1   | G   |
| LACM 122147 | 6.3 | 5.8 | 3.4 | 4.5 | 3.3 | 1.7 | 4.5 | 1   | 1   | G   |
| LACM 122148       | 5.7  | 4.6  | 3.4  | 4.3  | 4.0  | 1.9  | 4.5  | 1   | 1   | P   |
|-------------------|------|------|------|------|------|------|------|-----|-----|-----|
| LACM 122149       | 6.5  | 7.1  | 4.2  | 4.3  | 5.1  | 2.1  | 5.1  | 1   | 1   | G   |
| LACM 122150       | 7.6  | 6.6  | 4.6  | 6.0  | 5.2  | 2.3  | 5.6  | 1   | 1   | G   |
| LACM 122151       | 5.1  | 6.3  | 3.5  | 3.7  | 5.4  | 1.3  | 4.5  | ‘1’ | 1   | P   |
| LACM 122153       | 3.4  | 4.1  | 2.1  | 2.5  | 3.4  | 0.9  | 2.5  | 1   | 1   | P   |
| LACM 122154       | (5.8)| 6.9  | 3.8  | (3.9)| 5.6  | 1.7  | 4.3  | 1   | 1   | P   |
| LACM 122155       | 5.5  | 6.0  | 3.5  | 3.5  | 5.4  | 1.9  | 4.7  | 1   | 1   | P   |
| LACM 122156       | 7.0  | 4.7  | 3.8  | 3.4  | 4.0  | 1.6  | 6.0  | 1   | 1   | G   |
| LACM 122157       | 5.6  | 4.3  | 2.5  | 4.4  | 3.9  | 1.7  | 3.8  | 1   | 1   | P   |
| LACM 122158       | 7.7  | 7.6  | 3.9  | 5.8  | 5.7  | 1.9  | 5.5  | 1   | 1   | G   |
| LACM 122159       | 6.6  | 6.5  | 3.7  | 5.0  | 6.2  | 2.0  | 5.0  | 1   | 1   | P   |
| LACM 122160       | 5.1  | 4.9  | 3.1  | 3.8  | 3.2  | 1.9  | 5.0  | ‘1’ | ‘1’ | G   |
| LACM 122161       | 4.7  | 4.6  | 3.0  | 3.6  | 4.1  | 1.7  | 4.3  | 1   | 1   | G   |
| LACM 122162       | (6.0)| 8.9  | 3.5  | 4.5  | 5.7  | 1.1  | 5.5  | 0   | 0   | G   |
| LACM 122163       | 3.5  | 3.9  | 2.3  | 2.6  | 3.2  | 0.9  | 3.4  | 1   | 1   | G   |
| LACM 122164       | 4.6  | 4.4  | 3.1  | 3.8  | 3.7  | 1.6  | 3.1  | 0   | 0   | P   |
| LACM 122165       | 5.8  | 4.7  | 3.0  | 4.6  | 4.4  | 1.4  | 4.2  | 0   | 1   | P   |
| LACM 122166       | 5.3  | 6.7  | 3.1  | 4.1  | 5.6  | 1.8  | 4.8  | 1   | 1   | G   |
| LACM 122167       | 6.2  | 5.6  | 3.9  | 5.1  | 4.7  | 1.5  | 4.7  | 0   | 1   | G(+P)|
| LACM 122168       | 8.2  | 6.6  | 4.5  | 6.4  | 5.5  | 2.0  | 5.9  | 1   | 1   | G   |
| LACM 122169       | 7.0  | 6.7  | 3.8  | 5.1  | 5.8  | 1.9  | 5.0  | 1   | 1   | P   |
| LACM 122170       | 6.8  | 7.3  | 3.8  | 5.2  | 5.6  | 2.4  | 5.1  | 1   | 0   | G   |
| LACM 122171       | 5.8  | 5.4  | 3.4  | 4.5  | 4.6  | 1.7  | 4.4  | 1   | 1   | G   |
| LACM 122172 | 6.5  | (6.9) | 3.9  | 5.0  | 5.5  | 2.1  | 4.8  | 1    | 1    | P    |
| LACM 122173 | 5.9  | 6.7   | 3.8  | 3.2  | 5.4  | 1.7  | 5.6  | 1    | 0    | G    |
| LACM 122174 | 7.8  | 6.6   | 3.9  | 6.0  | 5.8  | 1.9  | 5.6  | 1    | 1    | G    |
| LACM 122175 | 5.0  | 4.3   | 2.6  | 3.4  | 3.7  | 1.2  | 4.3  | 1    | 1    | G    |
| LACM 122176 | 7.0  | 5.5   | 4.1  | 5.3  | 4.4  | 2.0  | 5.1  | 1    | 1    | G    |
| LACM 122177 | 5.6  | 5.5   | 3.4  | 3.8  | 4.6  | 1.2  | 4.8  | 1    | 1    | G    |
| LACM 122178 | 5.5  | 7.9   | 3.4  | 4.3  | 6.9  | 1.9  | 3.6  | 1    | 1    | P    |
| LACM 122179 | 5.0  | 7.3   | 3.1  | 4.0  | 6.1  | 2.1  | 3.6  | 1    | ‘2’  | P    |
| LACM 122181 | (3.6)| 3.3   | 2.3  | (2.8)| 3.1  | 1.0  | 2.8  | 1    | 1    | G    |
| LACM 122182 | 5.4  | 4.7   | 3.3  | 4.2  | 3.8  | 1.8  | 4.5  | ‘1’  | 0    | G    |
| LACM 122183 | 5.2  | 6.9   | 2.9  | 4.5  | 6.3  | 1.7  | 3.5  | 1    | 1    | P    |
| LACM 122184 | 6.1  | 6.0   | 3.7  | 4.8  | 5.0  | 1.8  | 4.3  | ‘1’  | 0    | G    |
| LACM 122186 | 7.4  | 7.0   | 4.2  | 5.5  | 5.7  | 2.0  | 6.0  | ‘1’  | 0    | G    |
| LACM 122187 | 7.4  | 7.0   | 4.5  | 5.4  | 6.0  | 1.9  | 6.5  | 1    | 1?   | G    |
| LACM 122189 | 6.4  | 5.2   | 3.4  | 5.1  | 4.5  | 2.0  | 4.5  | 1    | 1    | P    |
| LACM 122190*| 8.6  | 8.3   | 4.3  | 7.0  | 6.6  | 2.2  | 6.1  | 1    | 1    | G    |
| LACM 122191 | 6.8  | 6.2   | 3.9  | 4.7  | 5.4  | 2.0  | 5.1  | 0    | 1    | G    |
| LACM 122192 | 6.0  | 7.3   | 3.1  | 4.9  | 6.6  | 2.0  | 4.0  | 1    | ‘1’  | P    |
| LACM 122193 | 7.3  | 7.4   | 4.6  | 5.4  | 5.8  | 1.8  | 7.3  | ‘1’  | 1    | G    |
| LACM 122194 | (5.5)| 5.2   | 4.8  | (4.4)| 4.8  | 1.5  | 5.2  | 1    | 1    | G    |
| LACM 122195 | 8.2  | 7.5   | 4.8  | 5.9  | 5.5  | 2.2  | 5.9  | 1    | ‘1’  | G    |
| LACM 122196 | 6.7  | 9.3   | 4.3  | 5.1  | 8.2  | 2.0  | 5.5  | 1    | 1    | G    |
| LACM 122197 | 14.7 | 10.2  | 9.2  | 12.9 | 8.0  | 3.2  | 8.3  | 0    | 0    | P    |
| LACM 122198 | (11.6) | (8.2) | 8.2 | 8.5 | 6.7 | 3.0 | (8.6) | 1 | 1 | G |
|------------|--------|--------|-----|-----|-----|-----|-------|---|---|---|
| LACM 122199| 6.1    | 7.0    | 3.7 | 4.8 | 5.0 | 1.8 | 3.8   | ‘1’| 0 | P |
| LACM 122200| 5.4    | 6.4    | 6.6 | 4.5 | 5.9 | 1.7 | 3.3   | 1 | 1 | G(+P) |
| LACM 122201| 5.3    | 7.3    | 3.1 | 3.8 | 5.6 | 1.5 | 4.2   | ‘1’| ‘1’| G(+P) |
| LACM 122202| 6.0    | 5.0    | 4.1 | 3.2 | 4.5 | 1.7 | 4.5   | 1 | 0 | G |

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A new fossil megamouth shark (Lamniformes, Megachasmidae) from the Oligocene–Miocene of the western United States

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APPENDIX 2. Dental measurements (all in millimeters) taken from extant *Megachasma pelagios* taken from illustrations in published literature (number in parentheses indicates estimated value). **Abbreviations** (see also Fig. 6A): CH, crown height; CW, crown width; RL, root length; RW, root width.

| Specimen          | CH  | CW  | RL  | RW  | Source                                      |
|-------------------|-----|-----|-----|-----|---------------------------------------------|
| BPBM 22730        | 9.0 | 4.0 | 6.6 | 5.8 | Taylor et al. (1983:fig. 8A, C)             |
| LACM 43745-1      | 5.0 | 7.7 | 7.0 | 5.5 | Herman et al. (1993:pls. 45, 48 [top ‘a’]) |
| LACM 43745-1      | 9.5 | 7.0 | 9.0 |     | Herman et al. (1993:pls. 45, 48 [top ‘l’]) |
| LACM 43745-1      | 7.0 | 4.5 | 5.6 | 5.5 | Herman et al. (1993:pls. 45, 48 [top ‘p’]) |
| LACM 43745-1      | 12.0| 5.5 | 9.1 | 7.5 | Herman et al. (1993:pls. 45, 48 [bottom ‘a’]) |
| LACM 43745-1      | 8.0 | 5.2 | 8.0 | 7.2 | Herman et al. (1993:pls. 45, 48 [bottom ‘l’]) |
| LACM 43745-1      | 7.0 | 6.2 | 5.8 | 9.4 | Herman et al. (1993:pls. 45, 48 [bottom ‘p’]) |
| Fukuoka specimen  | 3.7 | 1.8 | 2.3 | 2.5 | Yabumoto et al. (1997:fig. 3A)              |
| Fukuoka specimen  | 5.1 | 2.6 | 3.5 | 3.6 | Yabumoto et al. (1997:fig. 3B)              |
| Fukuoka specimen  | 5.8 | 3.5 | 3.9 | 4.3 | Yabumoto et al. (1997:fig. 3C)              |
| Fukuoka specimen  | 5.4 | 3.3 | 3.3 | 4.2 | Yabumoto et al. (1997:fig. 3D)              |
| Fukuoka specimen  | 4.3 | 3.2 | 3.0 | 3.7 | Yabumoto et al. (1997:fig. 3E)              |
| Fukuoka specimen  | 3.1 | 2.7 | 2.7 | 3.2 | Yabumoto et al. (1997:fig. 3F)              |
| Fukuoka specimen  | 5.5 | 2.7 | 3.6 | 3.3 | Yabumoto et al. (1997:fig. 5A)              |
| Fukuoka specimen  | 9.4 | 4.0 | 6.5 | 5.6 | Yabumoto et al. (1997:fig. 5B)              |
| Fukuoka specimen  | 8.6 | 5.0 | 6.0 | 6.8 | Yabumoto et al. (1997:fig. 5C)              |
|                |   |   |   |                       |
|----------------|---|---|---|-----------------------|
| Fukuoka specimen | 7.0 | 4.1 | 5.1 | 5.0 Yabumoto et al. (1997:fig. 5D) |
| Fukuoka specimen | 5.8 | 3.6 | 3.9 | 5.1 Yabumoto et al. (1997:fig. 5E) |
| Fukuoka specimen | 4.9 | 3.3 | 3.5 | 4.1 Yabumoto et al. (1997:fig. 5F) |
| MZB 12906.LLIPI.1 | 1.7 | 1.0 | 1.2 | 1.3 De Schutter (2009:pl. 11A–D) |
| MZB 12906.LLIPI.2 | 1.6 | 1.0 | 1.1 | 1.2 De Schutter (2009:pl. 11E–H) |
| MZB 12906.LLIPI.3 | 1.7 | 1.0 | 1.1 | 1.2 De Schutter (2009:pl. 11I–L) |
| LACM 43745-1    | (8.0) | 6.8 | 7.1 | 6.8 De Schutter (2009:pl. 11M–R) |