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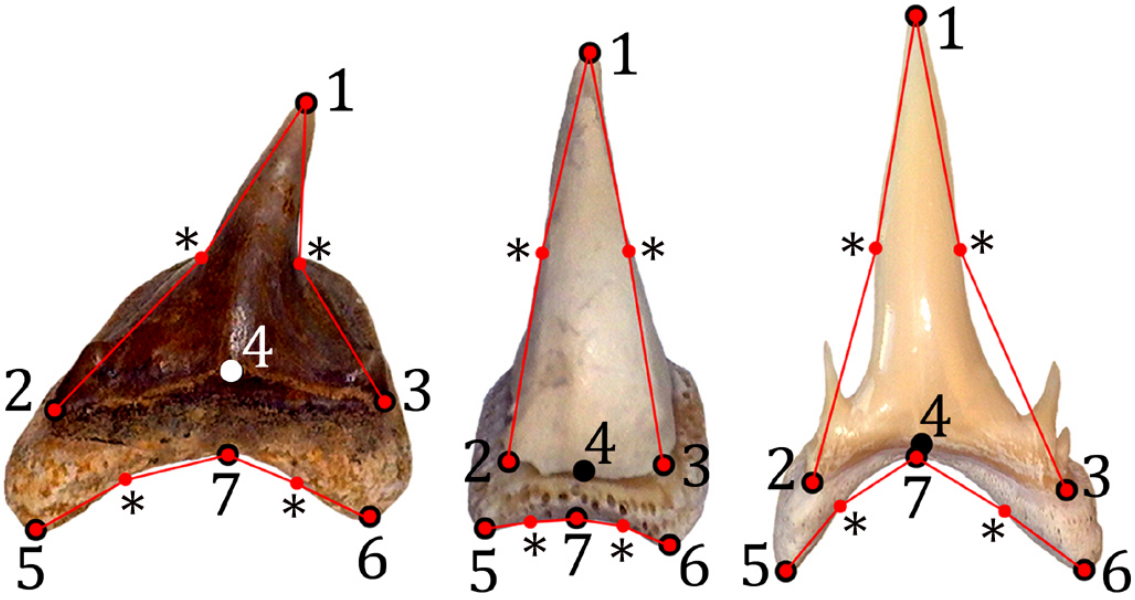

Alexandra M. KRAK and Kenshu SHIMADA (2023). The dentition of the extinct megamouth shark, *Megachasma applegatei* (Lamniformes: Megachasmidae), from southern California, USA, based on geometric morphometrics.

Cover: Landmarks used for morphometric analysis on teeth of (left to right) *Megachasma applegatei*, *Megachasma pelagios*, and *Odontaspis ferox*. See Figure 2 for details.

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The dentition of the extinct megamouth shark, *Megachasma applegatei* (Lamniformes: Megachasmidae), from southern California, USA, based on geometric morphometrics

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Megachasma applegatei is an extinct megamouth shark (Lamniformes: Megachasmidae) commonly found in late Oligocene–early Miocene marine deposits of the western USA, that is known only from isolated teeth exhibiting odontaspidid tooth design. In this study, we investigated the tooth morphometry of the extant megamouth shark (*Megachasma pelagios*) and smalltooth sandtiger (*Odontaspis ferox*: Odontaspididae) to aid in the reconstruction of the dentition of *M. applegatei* based on the tooth morphometry of 207 isolated fossil teeth from the lower Miocene Jewett Sand of southern California. Our landmark-based geometric morphometric analyses show that *M. applegatei* not only possesses a wider morphological range of teeth than *M. pelagios*, but also has morphological variation that can be corresponded to different tooth types in *O. ferox*, forming a unique heterodont dentition typical for macrophagous lamniform sharks known as the 'lamnoid tooth pattern'. Therefore, our study suggests that the dentition of *M. applegatei* could have also exhibited the lamnoid tooth pattern. In order to reconstruct the dentition of *M. applegatei*, specific tooth specimens plotted on the morphospace of *M. applegatei* were selected by identifying teeth of specific tooth types in the corresponding morphospaces of *M. pelagios* and *O. ferox*. However, because the total number of teeth per each dental series cannot be ascertained, we generated three sets of reconstructed dentition for *M. applegatei*. The first set modeled the dentition of *O. ferox*, the second set representing an intermediate form between *O. ferox* and *M. pelagios*, and the third set mimicking the dentition of *M. pelagios*, with the assumption that the true dental pattern for *M. applegatei* lies somewhere between the first and third tooth sets, possibly close to the second set. This study represents the first case of using geometric morphometrics to reconstruct the dentition of an extinct shark.

Keywords: dentition, fossil, lamnoid tooth pattern, *Megachasma*, Megachasmidae, *Odontaspis*

INTRODUCTION

The extant megamouth shark, *Megachasma pelagios* Taylor, Compagno, and Struhsaker (1983) (Megachasmidae: Fig. 1A), is a suspension-feeder belonging to the order Lamniformes that reach up to about 7.1 m in length (Watanabe and Papastamatiou 2019; Fig. 1B). Whereas more than 100 individuals have been documented to date (Watanabe and Papastamatiou 2019), its first discovery in 1976 (teeth of the holotype shown in Fig. 1C, D) represents one of the most spectacular zoological discoveries in the twentieth century (Berra 1997, Compagno 2001). The discovery of extant *M. pelagios* eventually led to the recognition of extinct forms of the megamouth shark, *M. applegatei* Shimada, Welton, and Long (2014) from the late Oligocene–early Miocene of the western USA and *M. alisonae* Shimada and Ward (2016) from the late Eocene of Denmark. In addition, teeth referable to *M. pelagios* have also been reported sporadically from

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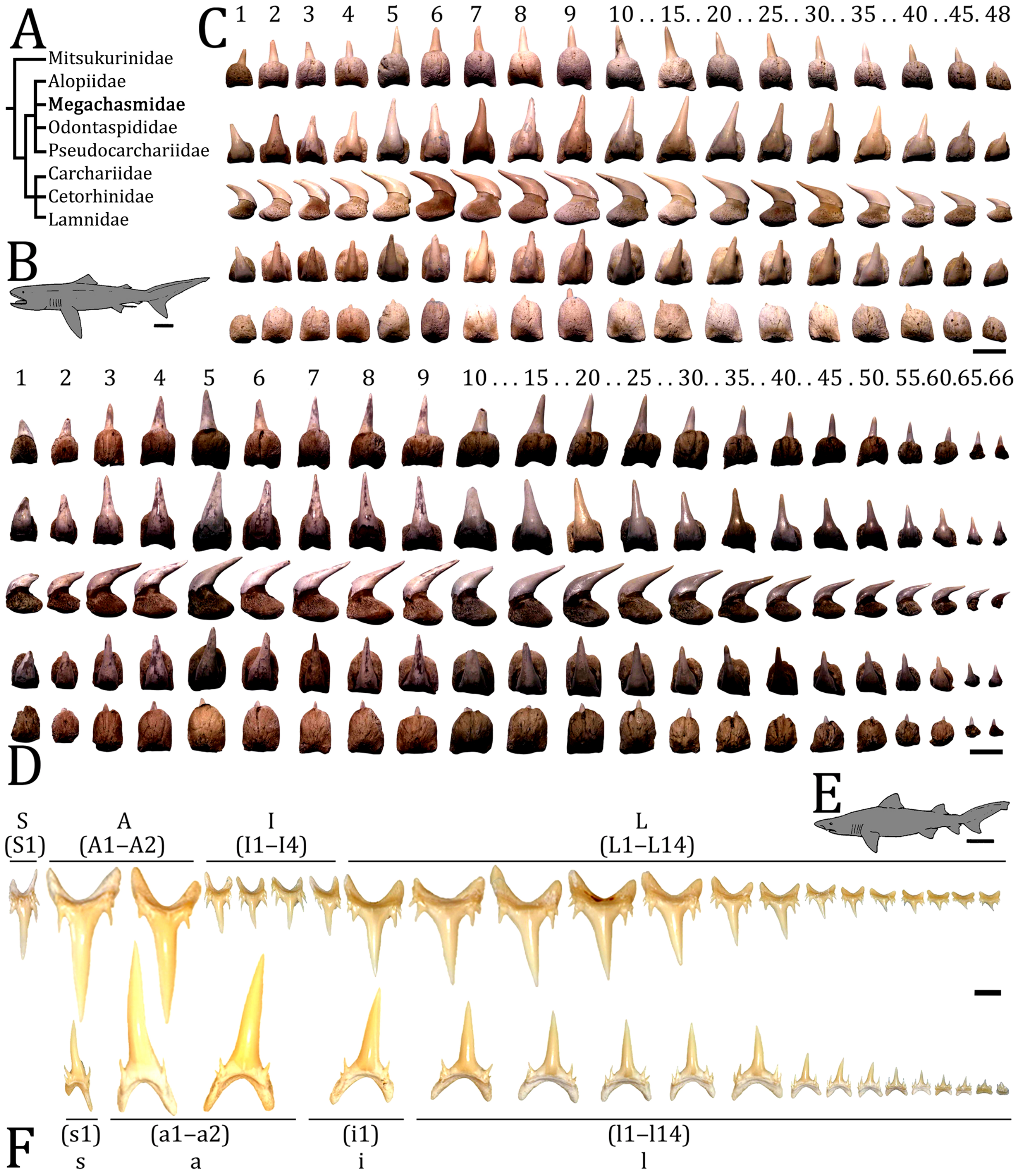

Figure 1. A. Generalized consensus tree of extant lamniform families on the basis of molecular-based phylogenetic studies, highlighting Megachasmidae in bold (see Stone and Shimada 2019, fig. 6, and references therein). **B.** Extant megamouth shark, *Megachasma pelagios* (after Compagno 1984). **C, D.** Right upper (**C**) and right lower (**D**) teeth of extant *M. pelagios* (BPBM 22730, 446 cm TL, male) in (from top row to bottom row) lingual, labial, mesial, apical, and basal views, showing strong tendency towards homodonty. **E.** Extant smalltooth sand tiger, *Odontaspis ferox* (after Compagno 1984). **F.** Left upper and left lower dental series of extant *O. ferox* (BPBM 9335, 297(?) cm TL, male(?)) showing representative 'lamnoid tooth pattern' (A or a = anterior teeth; I or i = intermediate tooth; L or l = lateral tooth; S or s = symphysial tooth). Scale bars: B and E = 50 cm; C, D, F = 5 mm

the Miocene–Pliocene marine deposits of western and eastern North America, western South America, Europe, and Asia (De Schutter and Everaert 2020 and references therein).

Macrophagous lamniform sharks, typified by the piscivorous smalltooth sandtiger (*Odontaspis ferox* (Risso 1810): Odontaspididae; Fig. 1E) among others like the goblin (*Mitsukurina owstoni* Jordan, 1898: Mitsukurinidae), sandtiger (*Carcharias taurus* (Rafinesque 1810): Carchariidae), and white (*Carcharodon carcharias* (Linnaeus 1758): Lamnidae) sharks, possess a unique dental organization called the “lamnoid tooth pattern” (Compagno 1984). This pattern, that is particularly well represented by *O. ferox* (Fig. 1F), refers to a specific heterodonty that consists of four major tooth types in each side of the upper and lower dentitions: symphysial, anterior, intermediate, and lateral teeth (Shimada 2002). Symphyseal teeth are the mesial-most set of teeth within the dentition followed distally by two sets of anterior teeth, up to four intermediate teeth, and fourteen lateral teeth. On the other hand, suspension-feeding (‘microphagous’ or ‘planktivorous’) lamniform sharks, such as the basking shark (*Cetorhinus maximus* (Gunnerus 1765): Cetorhinidae) and megamouth shark, have a homodont dentition consisting of teeth that are small and simple (peg-like) throughout their dentition (Yabumoto et al. 1997, Shimada 2002; Fig. 1C, D). Whereas *M. alisonae* is known only from a single tooth (Shimada and Ward 2016), teeth of another fossil taxon, *M. applegatei*, occur relatively abundantly in the lower Miocene of California, USA (Shimada et al. 2014). The dental morphology of *M. applegatei* is characterized by typically exhibiting a large sharp main cusp along with a pair of lateral cusplets, and it is somewhat reminiscent of teeth of piscivorous lamniform sharks such as those of odontaspidids like *O. ferox* (Shimada et al. 2014, Shimada and Ward, 2016; Fig. 1F). Although the exact phylogenetic position of *Megachasma* remains uncertain (Stone and Shimada 2019), the origin of megachasmids is therefore thought to be rooted in a lamniform with a dentition that exhibited the distinct lamnoid tooth pattern with the odontaspidid tooth design (Shimada et al. 2014). Yet, because the fossil record of *M. applegatei* is limited to isolated teeth, the original organization of teeth in its mouth remains unknown.

In this study, we investigate and characterize the morphometric variation of teeth in a complete dentition of extant *Megachasma pelagios* (Fig. C, D) and *Odontaspis ferox* (Fig. 1F) as well as over 200 isolated teeth of *M. applegatei* collected from the lower Miocene Jewett Sand of southern California. In particular, we examine whether *M. applegatei* could have indeed possessed the lamnoid tooth pattern on the basis of tooth morphometry. We specifically chose *O. ferox* as a comparative taxon, because multiple molecular-based phylogenetic analyses have suggested *Odontaspis* or the family Odontaspididae to be nested within a clade that includes Alopiidae, Pseudocarchariidae, and Megachasmidae (Fig. 1A), where teeth of Alopiidae and Pseudocarchariidae, unlike *Odontaspis* and *M. applegatei*, are more of cutting type typically with no or only a distal cusplet (see Shimada, 2002). Our ultimate goal is to reconstruct the dentition of *M. applegatei* based on geometric morphometric trends observed in *M. pelagios* and *O. ferox*.

MATERIALS AND METHODS

We examined 207 isolated teeth of *Megachasma applegatei* housed in the Natural History Museum of Los Angeles (LACM), California, that included the holotype and paratype specimens described by Shimada et al. (2014). All the fossil teeth came from a single stratigraphic horizon (lower Miocene Jewett Sand) in one general area in southern California (LACM localities 1603, 1626, 1627, 1628, 3351, and 3362). We also examined the dentition of extant *M. pelagios* and *O. ferox* belonging to Bernice P. Bishop Museum (BPBM) in Honolulu, Hawaii, USA. The specimen of *M. pelagios* is the holotype of the species (BPBM 22730, 446 cm TL, male: Taylor et al. 1983) in which its right dentition consists of 47 upper and 42 lower tooth rows (Fig. 1C, D). The specimen of *O. ferox* is BPBM 9335, a head-only specimen from a putative male that measured 297 cm TL (see Jacobs and Shimada 2018), and its right dentition consists of 21 upper tooth rows and 18 lower tooth rows (Fig. 1F). We examined the labial face of the best-preserved functional, or near functional, tooth in each tooth row. For the purpose of this paper, we followed Shimada’s (2002, fig. 8A, B) tooth type identification scheme for the lamnoid tooth pattern as seen in *O. ferox*.

Each tooth specimen was placed on a small white cardboard stage with a millimeter ruler where a piece of rubber putty was used to position the tooth on the cardboard so that the apical, mesial, and distal extremities of the tooth crown in labial view would be on a horizontal plain. It was then photographed under a Dino-Lite Edge Digital Microscope. The exposure on the microscope was altered to optimize the visibility of each tooth photographed. Teeth of the left dentition were not available to photograph for *M. pelagios* and *O. ferox* because they are still preserved in the mouth of the respective preserved

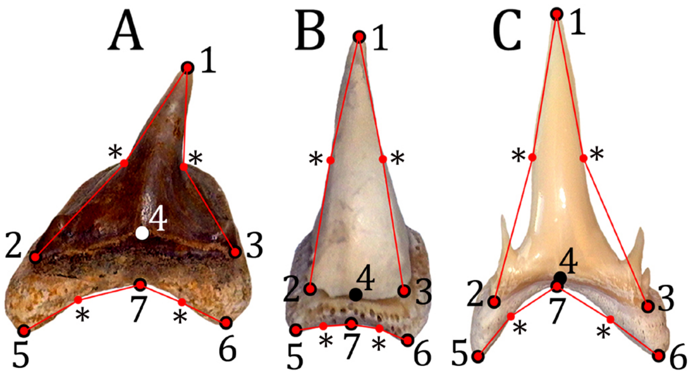

Figure 2. Homologous landmark (numbered black or white circles) and semi-homologous landmark (red circles with asterisk [*] connected by red lines) on tooth samples of *Megachasma applegatei* (**A**), *M. pelagios* (**B**), and *Odontaspis ferox* (**C**) for principal component analysis (not to scale). Seven homologous landmarks: 1, the crown apex, 2 and 3, right- and left-most extremities of the crown; 4, apical-most point around the middle of the crown base; 5 and 6, basal extremity of each of the two root lobes; and 7, apical-most point of the basal root concavity.

specimens; therefore, the photograph of each tooth from the right dentition was copied and horizontally reversed digitally to mimic the tooth from the left dentition. This process was conducted so that teeth from both the right and left sides would be represented in our study. Because whether each tooth of *M. applegatei* comes from an upper or lower dentition is uncertain, every tooth (including *M. pelagios* and *O. ferox*) in this study was photographed in the exact same manner, where the identification between upper and lower teeth of *M. applegatei* was made based on plot distribution of the geometric morphometrics (see below).

All images of the teeth were organized by creating electronic storage files by uploading into the program tpsutil64 (Rohlf 2015), and landmarks were digitized using tpsdig232 (Rohlf 2015) for geometric morphometric analysis. Seven homologous landmarks were placed at the following points on each tooth: the crown apex, right- and left-most extremities of the crown, apical-most point around the middle of the crown base, basal extremity of each of the two root lobes, and apical-most point of the basal root concavity (Fig. 2). In addition, four sets of three-point semi-homologous landmarks were placed on each side of the crown and root, where the middle semi-homologous landmark on each set was an equidistance between the two ends along the curvature of the crown or root (Fig. 2). A millimeter ruler was included in each image to record size. The measure tool in tpsdig232 was also used to eliminate size as a factor upon looking at the different morphology of each tooth. We then performed a principal component analysis (PCA) using MorphoJ 1.06d (Klingenberg 2011) on all the photographed teeth.

A PCA scatter plot diagram was generated for teeth of *Megachasma applegatei*, *M. pelagios*, and *O. ferox* separately, where teeth of *O. ferox* were identified by their tooth types: i.e., symphysial, anterior, intermediate, and lateral teeth. The overall plot distribution pattern of *O. ferox* and that of *M. pelagios* were then compared to the plot distribution of *M. applegatei*. If the range of morphometric variation of *M. applegatei* is found to be larger than that of *M. pelagios*, we assume that *M. applegatei* could have indeed possessed the lamnoid tooth pattern. If so, the approximate position of a specific tooth of *M. applegatei* within the morphospace is then assumed to correspond to the tooth of *O. ferox* situated at a similar region of its morphospace, which would in turn allow the identification of tooth types, resulting in a possible reconstruction of the dentition of *M. applegatei*.

RESULTS

Figure 3A is our scatter plot diagram that shows the morphological variation among the 178 teeth of *Megachasma pelagios* and 78 teeth of *Odontaspis ferox* (all upper and lower as well as right and left teeth combined) as well as 207 isolated teeth of *M. applegatei*. The other three scatter plots (Fig. 3B–D) show the morphometric variation in each of the three species separately. The principal component (PC) 1 shows a percent variation of 62.18%, whereas PC2 has a percent variation of 22.95%. PC3, PC4, and the remaining principal components have negligibly small percent variations (6.02, 3.72, and 5.13%, respectively; Table 1), and they are thus not plotted in this study. It should be noted that the software originally rotated the scatter plots for *M. pelagios* and *M. applegatei* so that the x-axis and y-axis became PC2 and PC1, respectively, contrary to the scatter plots with all three species combined (Fig. 3A) or that with *O. ferox* alone (Fig. 3D). This is simply due to the fact that the software is designed to place the x-axis with the most variation and label it as PC1, where *O. ferox* with the widest morphological variation forced the narrower morphological variations for *M. pelagios* and *M. applegatei* to flip the PC1 and PC2 axes when the three species were combined (Fig. 3A). For the purpose of better comparisons, we rotated the plots and re-labeled the x-axis to PC1 and the y-axis to PC2 for *M. applegatei* (Fig. 3B) and *M. pelagios* (Fig. 3C) to conform to the other two scatter plots (Fig. 3A, D) where they are referred as such consistently below.

PC1 describes the variation in root width. Teeth with a narrower root width had a lower PC score, whereas teeth with a wider root held a higher PC score. PC2 variation is affected by the curvature of the root lobes. A lower PC score was seen when the 'left' lobe of the root was longer than the 'right' as photographed. A higher PC score was

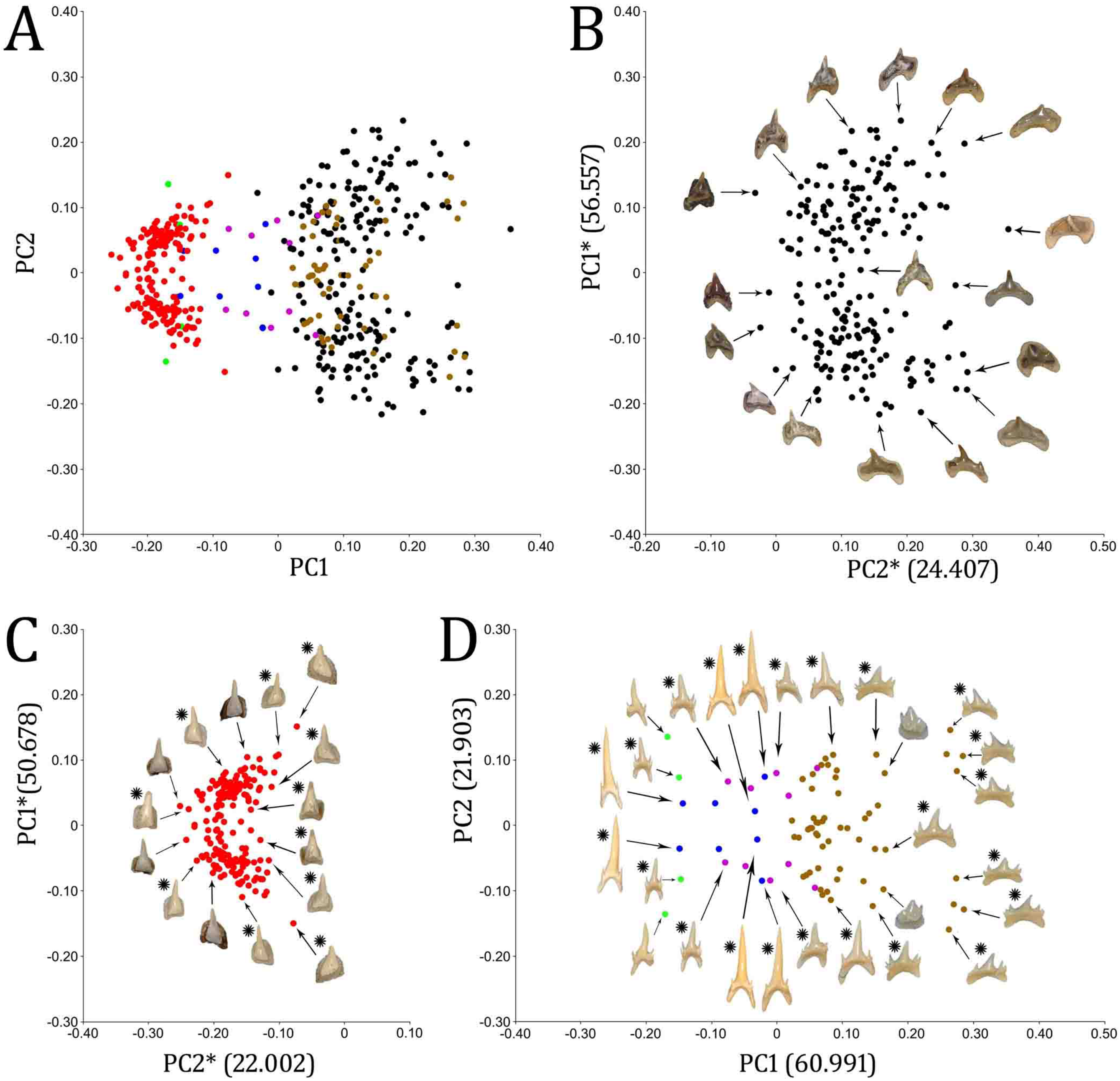

Figure 3. A. Scatter plot diagram showing principal component analysis of 207 teeth of *Megachasma applegatei* (black plots) compared with all 178 teeth of extant *M. pelagios* (red plots), and all 78 teeth of extant *Odontaspis ferox* separated into tooth types using different colors (symphysial teeth = green; anterior teeth = dark blue; intermediate teeth = purple; lateral teeth = brown). **B.** Scatter plot diagram exclusively *of M. applegatei*, showing examples of actual specimens (not to scale) represented by certain plots (illustrated teeth: LACM 9883, 150907, 155340, 155348, 155357, 155373, 155393, 155424, 155434, 155456, 155563, 155622, 155630, 155651, 155653, 155694, and 155700). **C.** Scatter plot diagram exclusively of *M. pelagios*, showing examples of actual specimens (not to scale: see Fig. 1C, D) represented by certain plots. **D.** Scatter plot diagram exclusively of *O. ferox*, showing examples of actual specimens (not to scale: see Fig. 1F) represented by certain plots. Asterisk (*): on axes in B and C = PC1 and PC2 originally labeled inversely by the software (see text for detail); by photograph of teeth in C-D = Upper teeth.

seen when the 'left' lobe of the root was shorter than the 'right' lobe (Fig. 3A). The plot distribution of *Megachasma pelagios* is clearly distinct from that of *M. applegatei* along PC1 without any overlap where the spread of points is wider for *M. applegatei* than *M. pelagios* along both axes (Fig. 3A). On the other hand, the plot distribution of *Odontaspis ferox* overall ranges the extent of the plot distribution of both species of *Megachasma* combined along PC1. Although the plot distribution range of *O. ferox* along PC2 is more similar to that of *M. pelagios* than *M. applegatei* (Fig. 3A), it is noteworthy that the observed morphological variation of teeth in *M. applegatei* (Fig. 3B) is considerably similar to that of *O. ferox* (Fig. 3D) than that of *M. pelagios* (Fig. 3C). For example, for both *M. applegatei* (Fig. 3B) and *O. ferox* (Fig. 3D), teeth with a taller crown and a narrower root are present on the left half of the diagrams, whereas teeth with a shorter crown and a wider root are found on the right half of the diagrams.

In all three species, plots in the upper (above 0 on PC2) and lower (below 0 on PC2) halves of each diagram mirror each other (Fig. 3B–D). In Figure 3C, the plots for the teeth of *Megachasma pelagios* are broadly separated into two morphospace regions. On the upper half of the diagram, teeth from the upper left and lower right side of the jaw are present, whereas on the lower half of the diagram, teeth from the upper right and lower left side of the jaw occur. In the case of *Odontaspis ferox*, teeth from the left side of the jaw lie on the upper half of the diagram, whereas teeth from the right side of the jaw lie on the lower half of the diagram. There is one exception where the left and right teeth are inverted for symphysial teeth in the scatter plot diagram for *O. ferox* (Fig. 3D). Among the plots of *O. ferox*, different tooth types identified in the lamnoid tooth pattern are relatively well separated successively along PC1: symphysial, anterior, and intermediate teeth on the left half and lateral teeth on the right half of the diagram (Fig. 3D).

DISCUSSION

Our analyses (Fig. 3) reveal that: 1) the range of morphometric variation of *M. applegatei* is wider than that of *M. pelagios* (Fig. 3B, C); and 2) the morphological variation present in *M. applegatei* (Fig. 3B) is reminiscent of that in *Odontaspis ferox* (Fig. 3D). These results suggest that the overall morphometric and morphological variations in *M. applegatei* are arguably intermediate between those of *M. pelagios* and *O. ferox*. This interpretation in turn strengthens the assumption that the dentition of *M. applegatei* could have possessed the lamnoid tooth pattern. The fact that teeth with a taller crown and a narrower root are present on the left half of the diagram and teeth with a shorter crown and a wider root are found on the right half in both *M. applegatei* (Fig. 3B) and *O. ferox* (Fig. 3D) indicates that reconstructing the dentition of *M. applegatei* may be possible using *O. ferox* as a template.

One major challenge to reconstruct the dentition of *Megachasma applegatei* is the uncertainty in the total number of teeth in each dental series on each jaw quadrant. For example, the total number of teeth can vary from 19 to 30 teeth on one side of the upper jaw and 17 to 25 teeth on one side of the lower jaw in *Odontaspis ferox*, and from 37 to 56 teeth on one side of the upper jaw and 43 to 74 teeth on one side of the lower jaw in *M. pelagios* (Shimada 2002, Tanaka et al. 2004, Wang et al. 2007, Pollerspöck and Straube 2020). Our morphometric analyses (Fig. 3) show that dental characteristics of *M. applegatei* bear some resemblances to teeth of both *M. pelagios* and *O. ferox*, meaning that it is reasonable to assert that the overall dental organization of *M. applegatei* could have been somewhere between that of the two extant species. Therefore, we chose to reconstruct three sets of upper and lower dentitions for *M. applegatei*. The first set was constructed using *O. ferox* (Fig. 1F) as a model that possesses the lamnoid tooth pattern with much smaller upper and lower tooth counts than *M. pelagios*. The second set was constructed to represent what the dentition of *M. applegatei* would have possibly looked like if it were intermediate between *O. ferox* and *M. pelagios* especially in terms of tooth row counts. The third set was constructed using *M. pelagios* (Fig. 1C, D) as a template that does not exhibit the lamnoid tooth pattern and has much larger upper and lower tooth row counts than *O. ferox*.

In order to reconstruct the first set of dentition, the entire stretch of the plot distribution of *Megachasma applegatei* along PC1 and PC2 (Fig. 3B) was considered to be equivalent to that of *Odontaspis ferox* (Fig. 3D). The approximate position of a specific tooth within the morphospace for *M. applegatei* (Fig. 3B) was then assumed to correspond to the tooth situated at a similar region within the morphospace for *O. ferox* (Fig. 3D). For example, the left side of the scatter plots consisted mostly of mesially located teeth (i.e., symphyseal, anterior, and intermediate) and the right side mostly lateral teeth, whereas the upper half of the scatter plots was generally occupied by lower teeth and the lower half by upper teeth. The plot position correspondences between *M. applegatei* (Fig. 3B) and *O. ferox* (Fig. 3D) suggested the

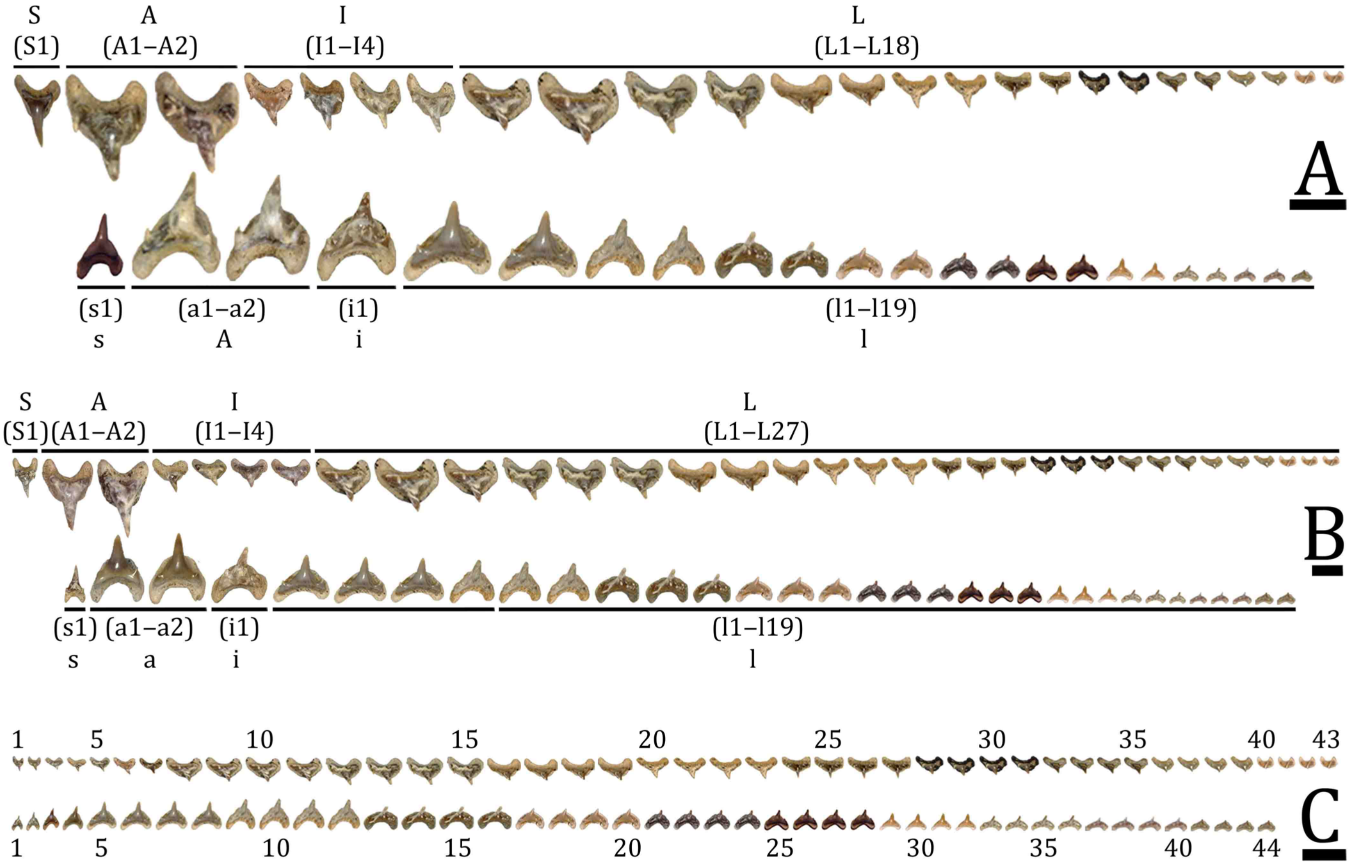

Figure 4. Three reconstructed dentitions of *Megachasma applegatei* under three different assumptions (see text for detail). **A.** Artificial dentition based on *Odontaspis ferox* as a model. **B.** Artificial dentition depicted as intermediate between *O. ferox* and *M. pelagios*. **C.** Artificial dentition based on *M. pelagios* as a model. Scale bar = 5 mm (note: each scale bar applies to each respective dentition consisting of teeth with digitally adjusted sizes [see text]).

following teeth of *M. applegatei* to be suitable representations for each tooth type: LACM 155717 and 122135 as the upper and lower symphysial teeth, respectively; LACM 155385 and 155434 as the two upper anterior teeth; LACM 155422 and 155423 as the two lower anterior teeth; LACM 150911, 155379, 155424, and 155447 as the four upper intermediate teeth; and LACM 155400 as the lower intermediate tooth. For the purpose of this reconstruction, the upper and lower dentitions were assumed to contain 18 and 20 lateral teeth, respectively, based on the typical lateral tooth row counts for *O. ferox* (see Shimada 2002, Pollerspöck and Straube 2020). However, because not all lateral teeth were represented in our samples of *M. applegatei*, the following specific teeth were selected, where some of which were digitally duplicated and edited for appropriate tooth sizes using Adobe Photoshop Elements 2.0 to produce the lamnoid tooth pattern: LACM 155341, 155346, 155351, 155376, 155421, 155425, 155563, 155586, and 155653 for the upper lateral teeth; and LACM 122187, 155392, 155411, 155454, 155458, 155629, 155630, 155681, 155695, and 155719 for the lower lateral teeth. Figure 4A illustrates the outcome of these reconstruction processes using *O. ferox* as a model.

All macrophagous lamniforms universally have two anterior teeth in each dental series along with some possible variability in the number of symphysial and intermediate teeth, but much of the difference in tooth row counts across different species of macrophagous lamniforms generally comes from the variation in the total number of lateral teeth (Shimada 2002). Therefore, the second set of dental reconstruction of *Megachasma applegatei* is generated essentially in the same manner as that for the first set, with a prime exception of having the total number of lateral teeth that would be between *Odontaspis ferox* and *M. pelagios*: i.e., 27 upper lateral teeth and 30 lower lateral teeth. Nevertheless, we also decided to deliberately use different tooth samples of *M. applegatei* for non-lateral teeth to show subtle morphological differences that also occur within each suspected tooth type in the fossil species compared to teeth used for the first set of reconstructed dentition. Based on the plot position correspondences between *M. applegatei* (Fig. 3B) and *O. ferox* (Fig. 3D), the following teeth of *M. applegatei* were considered to be also suitable for each non-lateral teeth: LACM 155401 and 150909 as the upper and lower symphysial teeth, respectively; LACM 155448 and 155459 as the two upper anterior teeth; LACM 155627 and 155723 as the two lower anterior teeth; LACM 155398, 155413, 155437, and 155455 as the four upper intermediate teeth; and LACM 155382 as the single lower intermediate tooth. For the lateral tooth series, the same lateral teeth used for the first set were essentially triplicated by digitally adjusting tooth sizes for the entire dentition to have the lamnoid tooth pattern. Figure 4B illustrates the product of these reconstruction processes that would reflect the dentition that is intermediate between *O. ferox* and *M. pelagios*.

The third set of reconstructed dentition of *Megachasma applegatei* mimics the homodont dentition of *M. pelagios* (Yabumoto et al. 1997, Shimada 2002, fig. 6). The upper and lower dental series in *M. pelagios* may consist of 37–56 teeth and 43–74 teeth, respectively (see above for references). However, because teeth of *M. pelagios* have a bulbous root (Fig. 1C, D) unlike teeth of *M. applegatei*, many of which that are strongly bilobed and mesiodistally wide, the total tooth row count in each dentition of *M. applegatei* was assumed here to be on the smaller end of the aforementioned variation ranges seen in *M. pelagios*. For the dental reconstruction of *M. applegatei*, the entire stretch of the plot distribution of *M. applegatei* along PC1 and PC2 (Fig. 3B) was considered to be equivalent to that of *M. pelagios* (Fig. 3C). The approximate position of a specific tooth within the morphospace for *M. applegatei* (Fig. 3B) was then assumed to correspond to the tooth situated at a similar region within the morphospace for *M. pelagios* (Fig. 3C). For the purpose of this exercise, LACM 155339, 155406, 155413, 155425, 155434, 155447, and 155626 were chosen for the upper dentition, and LACM 155335, 155380, 155432, and 155656 for the lower dentition. These teeth were found to occupy similar corresponding positions in the morphospace of *M. pelagios* marked by teeth situated in the mesial-most region of the respective dentition. For simplicity, the same set of lateral teeth from the previous two sets of dentition were quadrupled to reconstruct the remaining dentition distally by digitally editing the tooth sizes to mimic the tooth pattern seen in *M. pelagios*. Figure 4C shows the result of these reconstruction processes where both upper and lower dentitions consist of 44 teeth.

Because different tooth forms that can be considered to represent different tooth types are recognized in *Megachasma applegatei*, this study strengthens the hypothesis that the dentition of *M. applegatei* likely exhibited the lamnoid tooth pattern. Therefore, the dentition of *M. applegatei* could have been more similar to that of *Odontaspis ferox* (Fig. 1F) than to that of *M. pelagios* (Fig. 1C, D). Hence, we propose that the reconstructed dentition representing the intermediate form between *O. ferox* and *M. pelagios* (Fig. 4B) to be a working hypothesis for the possible dental arrangement of teeth in life for *M. applegatei*, where the discovery of an articulated dentition of the fossil species awaits for its testing.

Geometric morphometrics based on PCA has been recognized as a useful approach for scientific investigations on shark teeth. Most such studies have used PCA by means to identify or separate different species or to examine intraspecific dental variation (e.g., Naylor and Marcus 1994, Nyberg et al. 2006, Whitenack and Gottfried 2010, Marramà and Kriwet 2017, Berio et al. 2020), although some other studies have used PCA to demonstrate changes in morphospace patterns of shark teeth over geologic time (e.g., Belben et al. 2017, Bazzi et al. 2018). By taking advantage of the presence of a modern representative (*Megachasma pelagios*) and the recognition of a possible 'ancestral analog' (*Odontaspis ferox*), we note that, to our knowledge, this study represents the first example of using PCA to reconstruct the dentition of an extinct shark known only from isolated teeth. Although a number of assumptions were necessary and some uncertainties remain (e.g., total tooth counts), our approach is sensible because it is more repeatable than most previous studies that offered reconstructed dentitions of extinct sharks based exclusively on isolated teeth that relied largely on intuition of the investigators (e.g., Applegate and Espinosa-Arrubarrena 1996).

CONCLUSIONS

Megachasma applegatei is an extinct megamouth shark found in the late Oligoene-early Miocene of the western USA. Teeth of *M. applegatei* typically exhibit large sharp main cusps along with a pair of lateral cusplets reminiscent of teeth of piscivorous lamniform sharks such as *Odontaspis ferox* (Shimada and Ward, 2016). Because of this, the origin of megachasmids has been inferred to be rooted from piscivorous lamniform that possibly possessed a dentition with the lamnoid tooth pattern (Shimada et al. 2014).

In this study, we used geometric morphometrics to assess whether *Megachasma applegatei* could have had the lamnoid tooth pattern in its dentition and attempted to reconstruct its dentition based on tooth morphometry. Our results show that 1) the range of morphometric variation of *M. applegatei* is wider than that of *M. pelagios*, and 2) the morphological variation present in *M. applegatei* is reminiscent of that in *Odontaspis. ferox*. These findings suggest that the dentition of *M. applegatei* could have exhibited the lamnoid tooth pattern with different tooth types (i.e., symphysial, anterior, intermediate, and lateral teeth). With this assumption and by utilizing the PCA scatter plots we generated, we constructed three sets of upper and lower dentitions of *M. applegatei* with different plausible tooth arrangements. The first set modeled the dentition of *O. ferox* with the lamnoid tooth pattern, the second set represented what the dentition would have looked like if intermediate between *O. ferox* and *M. pelagios*, and the third set modeled the dentition of *M. pelagios*. We contend that the reconstructed dentition showing an intermediate form between *O. ferox* and *M. pelagios* to be a reasonable inference about the tooth pattern for *M. applegatei* until the discovery of an articulated tooth set of *M. applegatei* in the fossil record.

The use of geometric morphometrics based on PCA to investigate tooth morphology of sharks has gained popularity in recent decades. However, previous studies have used PCA to identify or separate different species, to investigate intraspecific dental variation, or to examine changes in morphospace patterns of shark teeth over geologic time. This present study is significant because our approach is the first example of using PCA to reconstruct the dentition of an extinct shark with the comparison of dental morphospaces of an extant descendent (i.e., *Megachasma pelagios*) and a reasonable 'ancestral analog' (i.e., *Odontaspis. ferox*).

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