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Brief report

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The oldest fossil record of the megamouth shark from the late Eocene of Denmark and comments on the enigmatic megachasmid origin

KENSHU SHIMADA and DAVID J. WARD

The megamouth shark (Lamniformes: Megachasmidae) has sporadic occurrences both in the present-day oceans and in the fossil record. In this paper, we describe a new megachasmid, *Megachasma alisonae* sp. nov., on the basis of a morphologically distinct tooth collected from the Pyt Member of the late Eocene Søvind Marl Formation at Moesgård Strand in Denmark, that represents the geologically oldest known *Megachasma*. The tooth likely came from an individual that measured somewhere between 1.3 and 3.5 m long, and its morphology and chipped cusp tips suggest that it possibly fed on macro-zooplankton and small fishes that had hard skeletal components. Its occurrence in the mid-Priabonian Pyt Member at least suggests that the shark inhabited a relatively deep, open marine environment about 36 Ma ago. This Eocene specimen is significant because it illustrates the dental condition of early megachasmids, which is distinctively odontaspidid-like morphologically.

Introduction

Reaching up to about 5.5 m in length, one of the most spectacular zoological discoveries in the twentieth century was the suspension-feeding megamouth shark, *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983 (Lamniformes: Megachasmidae) (Berra 1997; Compagno 2001). The discovery of the extant form prompted the recognition of megachasmids in the late Cenozoic fossil record (e.g., Lavenberg and Seigel 1985; Compagno 1990), and morphological (Shirai 1996) and molecular (Martin et al. 2002) studies suggested the Mesozoic (Cretaceous) origin for the megachasmid lineage. This Mesozoic-origin hypothesis appeared to have been supported by the discovery of "*M.*" *comanchensis* (Shimada, 2007) from the Late Cretaceous (mid-Cenomanian) of Colorado, USA, that closely resembled the extant *M. pelagios* (Shimada 2007), followed by an additional molecular study that gave the estimated origination time for the megachasmid clade also in the Late Cretaceous (Heinicke et al. 2009). However, while some workers expressed their skepticism on the identity of "*M. comanchensis*" because of a 70-Ma gap to the next megachasmid fossil record (De Schutter 2009; Maisey 2012; Cappetta 2012), the description of *M. applegatei* Shimada, Welton, and Long, 2014, from late Oligocene–early Miocene marine deposits in the western USA led to the conclusion that *M. applegatei* is sister to *M. pelagios* (Shimada et al. 2014). A paradox that emerged from the description of *M. applegatei* was that teeth of "*M.*" *comanchensis* were more similar to teeth of the extant *M. pelagios* than to those of the Oligocene–Miocene *M. applegatei*. However, the matter was later resolved by newly recognized dental similarities between "*M.*" *comanchensis* and a Cretaceous odontaspidid shark genus *Johnlongia* and placing "*M.*" *comanchensis* into a new genus *Pseudomegachasma* with an interpretation that the resemblance between *P. comanchensis* and *M. pelagios* is a result of convergent evolution (Shimada et al. 2015).

Prior to this note, the geologically oldest known fossil record of megachasmids was represented by teeth of *Megachasma applegatei* from the late Chattian (late Oligocene; ca. 23 Ma) of the western USA (Shimada et al. 2014, 2015). In literature, however, Naylor et al. (1997: fig. 10) noted a possible Eocene occurrence, but it has remained formally undescribed. The purpose of this present paper is to verify the Eocene record by describing the material that was the very basis for Naylor et al.'s (1997: fig. 10) note—i.e., an unequivocal megachasmid tooth from the upper Eocene Søvind Marl in Denmark (Fig. 1). This Eocene record is significant not only because it pushes back the megachasmid fossil record by about 13 Ma, but also because it represents a new species and provides new insights into the origin and evolution of the genus *Megachasma* and family Megachasmidae.

Institutional abbreviations.—LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; NHMUK, The Natural History Museum, London, UK.

Other abbreviations.—CH, crown height; CT, crown thickness; CW, crown width; RL, root length; RW, root width; TH, total tooth height; TL, total body length; TT, total tooth thickness; TW, total tooth width (for dental measurements, see Shimada et al. 2014: fig. 6A).

Geological setting, material and methods

In the area where the Eocene megachasmid tooth occurred, the Søvind Marl, that underlies the Oligocene Viborg Formation, consists of three stratigraphic members: in ascending order, the Pyt Member, Moesgård Member, and Kysing Member (Thomsen et al. 2012; Fig. 1). Whereas the Søvind Marl represents a bathyal deposit with almost pure pelagic facies

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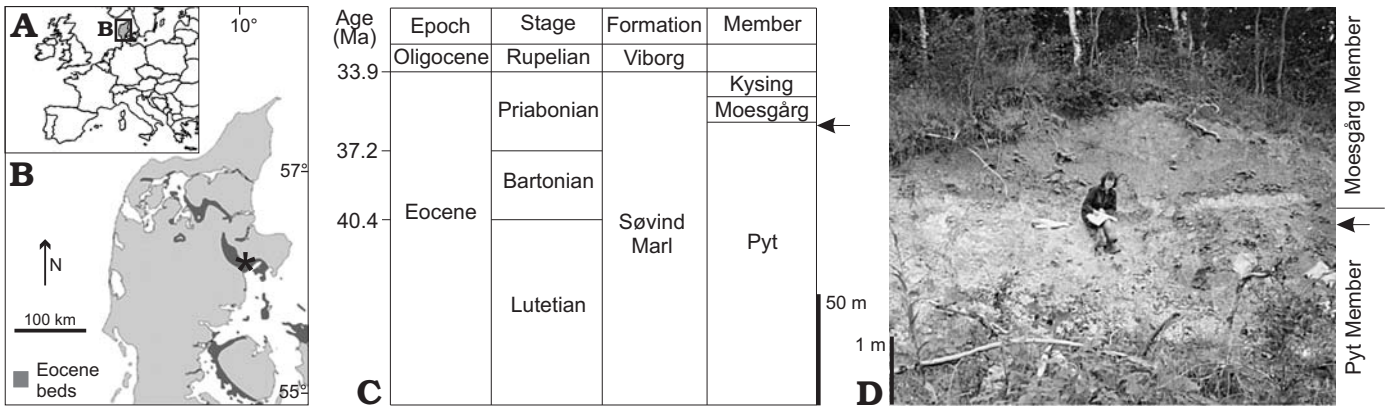


Fig. 1. **A**. Location of the studied area in Europe. **B**. Geological map (modified from Schwarzhans 2007: fig. 1) showing distribution of Eocene beds and location of the Eocene megachasmid locality (asterisk) in Moesgård Strand, Denmark. **C**. Generalized stratigraphy of the upper Paleogene marine deposits in Denmark (based on Thomsen et al. 2012). **D**. Photograph of the locality taken in 1988 by DJW with Alison Ward as a scale. The arrow in C, D points to bulk-sampled horizon that yielded the Eocene megachasmid tooth.

formed at an open marine environment (Heilmann-Clausen and Van Simaeys 2005), specifically, the tooth of *Megachasma* come from the upper part of the Pyt Member where it is characterized by soft, whitish, intensely glauconitic marl. This horizon is abundant in dinoflagellate cysts as well as planktonic and benthic foraminifera, and their taxonomic composition and abundance correspond to the biozone NP19-20 that is mid-Priabonian in age, about 36 Ma (Heilmann-Clausen and Van Simaeys 2005; Thomsen et al. 2012; King 2016).

A 1600 kg bulk sample of sediment was collected in 1988 from the upper-most 50 cm of the Pyt Member. The sediment sample was screened to 500 microns in an automatic sediment washing machine (see Ward 1981).

Systematic palaeontology

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

Type species: *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983; Recent, near Oahu, Hawaii, USA.

Megachasma alisonae sp. nov.

Fig. 2A.

Etymology: In honor of Alison Ward (Fig. 1D), who assisted DJW with the field work and sediment sorting that led to the discovery of the specimen described here.

Holotype: NHMUK PV P73711 (thus far only known specimen of this species). A nearly complete tooth (either upper right or lower left lateral tooth based on distal cusp inclination and asymmetrical root; Fig. 2A, B).

Type locality: A sea cliff along Moesgård Strand in Denmark; coordinates: 56º04’53” N, 010º15’07” E (Fig. 1A, B).

Type horizon: Pyt Member of the late Eocene Søvind Marl Formation.

Diagnosis.—Dental morphology similar to *Megachasma applegatei* by possessing apicobasally shorter crown with strong lingual cusp inclination, one pair of lateral cusplets, and massive bilobate root (Shimada et al. 2014: 281) but distinctly differing from it by exhibiting much smaller lingual protuberance, more labially situated and relatively larger lateral cusplets, and more widely spaced root lobes.

Description.—Small tooth with TH of 4.0 mm, TW of 4.5 mm, and TT of 1.8 mm. Crown apicobasally short with CH of 2.1 mm, CW of 4.1 mm, and CT of 1.2 mm; crown base mesiodistally broad and narrows rapidly just above base, developing apically into sharp, narrow cusp; lateral extensions of crown base with rounded shoulders extending shortly onto each root lobe on labial face; pair of prominent lateral cusplets present and situated slightly labially compared to position of main cusp; height of lateral cusplets about half of main cusp, but mesial cusplet slightly larger and taller than distal one; minute heel-like rise along mesial margin of mesial lateral cusplet present; each cusplet triangular and lingually recurved, well separated from main cusp; smooth mesial and distal cutting edges present along main cusp and lateral cusplets, but absent between main cusp and each lateral cusplet; main cusp flexed lingually; labial crown face overall weakly convex; crown foot gently concave, lacking basal ledge, groove, or ornamentation (e.g., striations); lingual crown face strongly convex and smooth, lacking ornamentation; tooth neck encircles crown foot and particularly well developed immediately basal to both mesial and distal sides of main cusp on lingual face; crown slightly asymmetrical with weak distal inclination of main cusp. Root proportionally massive in relation to crown, dwarfing crown, with RL of 3.2 mm and RW (= TW) of 4.5 mm; root strongly bilobate; mesial and distal root lobes widely spaced; lingual root face gently rounded with robust protuberance basal to main cusp; mesial and distal root lobes rounded and connected with gently arched basal concavity; shallow, weak nutritive

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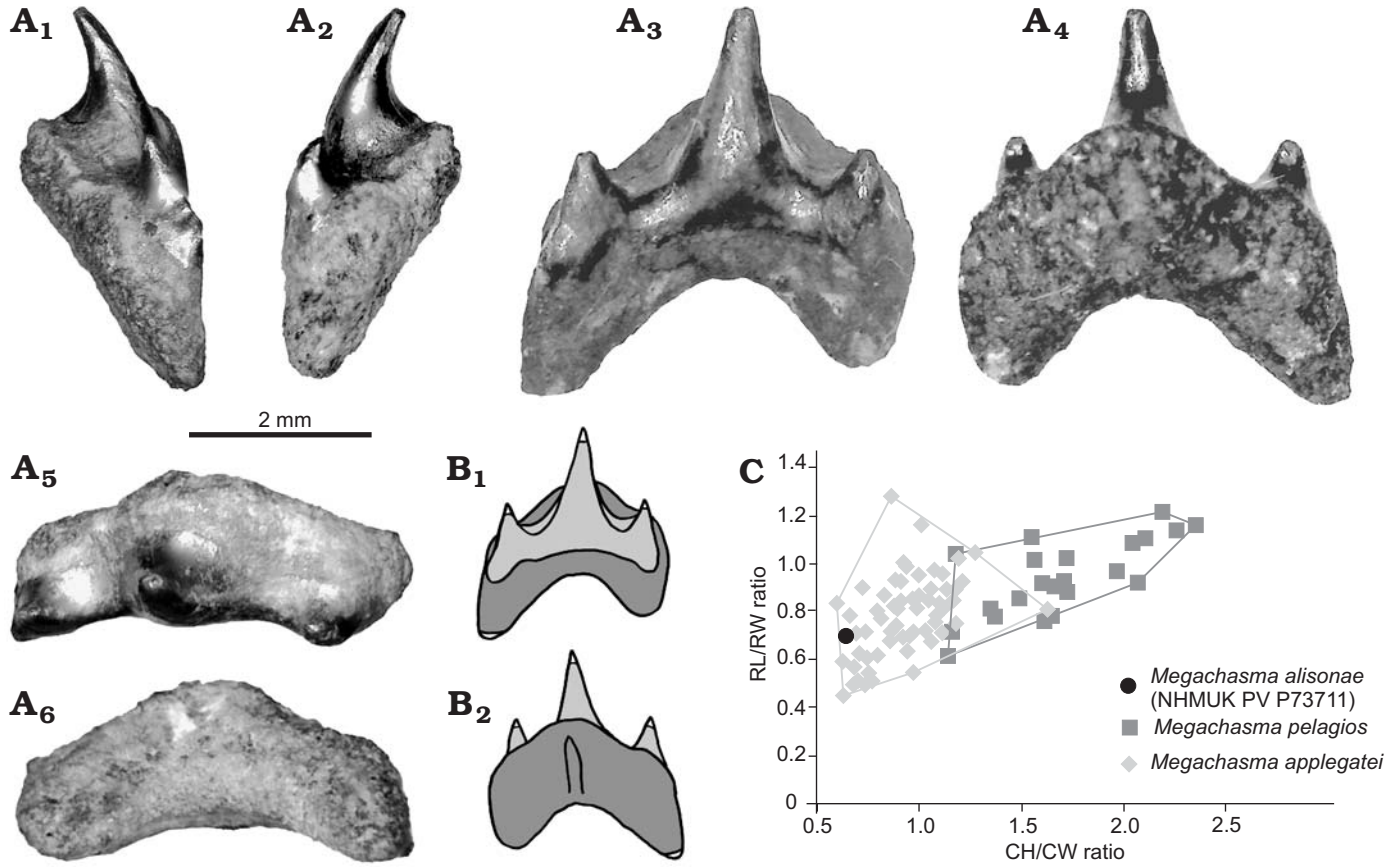


Fig. 2. Tooth of megamouth shark *Megachasma alisonae* sp. nov. (NHMUK PV P73711) from the Pyt Member (mid-Priabonian) of the upper Eocene Søvind Marl Formation of Moesgård Strand, Denmark. **A**. Photograph in labial (A_1), lingual (A_2), basal (A_3), distal (A_4), mesial (A_5), and apical (A_6) views. **B**. Line drawing showing crown (light gray) and root (dark gray) as well as missing portions (white). **C**. Scatter plots between CH/CW ratios and RL/RW ratios comparing NHMUK PV P73711 with extant *M. pelagios* (n = 23) and type series of *M. applegatei* from Aquitanian (early Miocene) of California, USA (n = 67) (after Shimada et al. 2014: fig. 6B). Abbreviations: CH, crown height; CW, crown width; RL, root length; RW, root width.

groove present on lingual root face that continues to basal root concavity.

Remarks.—The genus *Megachasma* is now known from three species: *M. pelagios*, *M. applegatei*, and *M. alisonae* sp. nov. Figure 2C shows Shimada et al.'s (2014: fig. 6B) graph plotting CH-to-CW ratios against RL-to-RW ratios. Whereas the difference between *M. pelagios* and *M. applegatei* in RH/RW ratio is relatively small, the graph reveals that *M. pelagios* tends to have more slender crowns compared to *M. applegatei* that has crowns with similar height and width. If NHMUK PV P73711 with a RL/RW ratio of 0.71 and a CH/CW ratio of 0.66 is plotted (Fig. 2C), it clearly falls in the range of *M. applegatei*. As its diagnosis suggests (see above), *M. alisonae* sp. nov. indeed bears characteristics of *M. applegatei*, likely suggesting their close phylogenetic affinity. However, the observed morphological differences in the robustness of the lingual protuberance, the position and size of lateral cusplets, and the spacing between the two root lobes are large between the two species and justify NHMUK PV P73711 to be considered a separate species from *M. applegatei* (and *M. pelagios*), hence the decision to erect a new species, *M. alisonae* sp. nov.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Paleoecology.—Body size of organisms, predators and prey alike, is an important biological attribute in ecology and evolution because it influences various physiological demands and trophic interactions (e.g., Cohen et al. 1993). However, accurately inferring the body size of fossil sharks are often difficult on the basis of isolated teeth. The case for NHMUK PV P73711 is no exception to this situation because not only its exact tooth position is uncertain, the pattern of dentition and body form, including the relationship between the body size and tooth size, of the Eocene taxon are unknown in the first place. However, if *Megachasma alisonae* sp. nov. is assumed to have had a similar relationship between the TL and sizes of teeth as extant *M. pelagios*, a rough estimation of its TL is possible. One extant adult *M. pelagios* has a TL of 471 cm and a maximum TW of 6.1 mm (Yabumoto et al. 1997). The TW of NHMUK PV P73711 is 4.5 mm, meaning that it is 73.8% of the widest tooth of that extant individual (note: we use TW that generally has a smaller difference from tooth position to tooth position in the mouth compared to TH or CH; cf. Shimada et al. 2014). This proportion would yield an estimated TL of about 347 cm for the Eocene *Megachasma*. However, because NHMUK PV

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P73711 is a lateral tooth that was most certainly not the largest tooth in its mouth, the fossil individual was likely much smaller than 347 cm TL. Whereas the maximum TW in the extant *M. pelagios* occurs in the lower dentition relatively close to the jaw symphysis, the minimum TW among lateral teeth found close to the distal end of the upper dentition measures 2.3 mm, that is 37.7% of its maximum TW. If this percentage is applied to the 347-cm-TL estimate for the Eocene shark based on the maximum TW of the extant *M. pelagios*, NHMUK PV P73711 would have measured about 131 cm TL. Therefore, this particular individual of *M. alisonae* sp. nov. probably measured somewhere between 1.3 and 3.5 m TL. Given that the smallest known extant *M. pelagios* individuals are about 2 m TL (Compagno 2001; Castillo-Géniz et al. 2012), this estimation is not unreasonable.

The extant *Megachasma pelagios* uses its gill rakers to filter-feed primarily on epipelagic–mesopelagic euphausiid shrimp, although reported stomach contents also include sea jellies and copepods (Compagno 2001). Therefore, whereas tooth morphology alone does not conclusively indicate sharks' diet (e.g., Whitenack and Motta 2010), the use of teeth for prey capturing is likely limited for the extant *M. pelagios*. On the other hand, teeth of *M. applegatei* are odontaspidid-like (Shimada et al. 2014), and because extant odontaspidids (*Odontaspis* spp.) feed primarily on small bony fishes, shrimp, and squid (Compagno 2001), *M. applegatei* possibly had a broader range of diet than the extant *M. pelagios*, spanning from macro-zooplankton to small fishes (Shimada et al. 2014). With more prominent lateral cusplets and less robust lingual root protuberance than those in typical *M. applegatei*, NHMUK PV P73711 is even more odontaspidid-like. Superficially, NHMUK PV P73711 particularly resembles small distally-located teeth of odontaspidids (e.g., see Compagno 2001: figs. 55, 56), but it clearly differs from them by having a large gap between the main cusp and each lateral cusplet to the extent that its lingual root protuberance is visible even in labial view at each gap (Fig. 2A_3, B_1). It is also noteworthy that, whereas most fossil shark teeth collected from the Pyt Member locality using the same method (see above) are superbly well-preserved with practically no taphonomic damage (DJW, personal observation), the apex of its main cusp and lateral cusplets in NHMUK PV P73711 shows chisel fractures. Such damage quite possibly indicates that the tooth came in contact with something hard, such as skeletal components of small fishes or sizable zooplankton, where similar damage is commonly seen in extant odontaspidids (KS and DJW, personal observation).

The extant *Megachasma pelagios* vertically migrates between deeper waters (at least 165 m) during the day and shallow waters at night (e.g., Nelson et al. 1997). The fossil record of *M. applegatei* from the Oligocene–Miocene of the western USA comes from a wide range of rock types consisting of both deep and shallow coastal water deposits. Therefore, *M. applegatei* is thought to have had either a broad bathymetric tolerance or was a nektopelagic feeder over both shallow and deep water environments similar to the extant *M. pelagios*. The discovery of NHMUK PV P73711 from the upper part of the Søvind Marl is intriguing because the faunal composition of foraminiferan taxa as well as sedimentological evidence indicate that the deposit formed at a well-oxygenated, cool-water, fully marine environment that had upper bathyal depths possibly ranging 200–600 m (Thomsen et al. 2012). Although the vertebrate fauna remains undescribed, other co-occurring shark taxa include *Heptranchias*, *Hexanchus*, *Notorynchus*, *Orthechinorhinus*, *Squalus*, *Paraetmopterus*, and *Mitsukurina* (DJW, unpublished data), supporting the nannofossil-based interpretation that the upper Pty Member formed in a deep-water environment. This deposition at upper bathyal depths at least indicates that *Megachasma alisonae* sp. nov. inhabited in an open marine environment although whether it exhibited the vertical migration behavior or it preferred deep waters cannot be ascertained.

Paleobiogeographical and evolutionary remarks.—The living *Megachasma pelagios* inhabits tropical to temperate waters north and south of the equator (Compagno 2001), whereas *M. applegatei* that lived during the Oligocene–Miocene in the western USA at least lived in a much more tropical environment than the present-day climate (Shimada et al. 2014). Fig. 3 summarizes all documented fossil megachasmid remains plotted on the late Eocene paleogeographic map that is sufficiently close to the overall present-day continental configuration. The plots are based on information compiled by Cappetta (2012) and Shimada et al. (2014) as well as two newer reports by Spadini and Manganelli (2015) and Tomita and Yokoyama (2015). For the purpose of this paleogeographic analysis, fossil megachasmid teeth with prominent lateral cusplets (i.e., *M. alisonae* sp. nov., *M. applegatei*, or *M.* cf. *M. applegatei*) are referred to as "*applegatei*-grade" *Megachasma*, whereas all other fossil megachasmid teeth with no or rudimentary lateral cusplets (i.e., *M. pelagios* or *M.* cf. *M. pelagios*) are referred to as "*pelagios*-grade" *Megachasma*—i.e., the two broad categories recognized by De Schutter (2009) and Shimada et al. (2014). Taxonomic identifications of the material from the Aquitanian of Mexico (Fig. 3: locality 6, plotted as "*applegatei*-grade") and the Neogene of Florida (Fig. 3: locality 9, plotted as "*pelagios*-grade") are inferred from its Aquitarian occurrence along western North America and information noted by De Schutter (2009), respectively, because those materials have never been illustrated. De Schutter (2009) also noted a possible Langhian (mid-Miocene) occurrence of a megachasmid tooth from Mexico without any illustration or referred specimen, but it is not plotted in Fig. 3 because its exact taxonomic identity is uncertain.

The fossil record of *Megachasma* is undoubtedly incomplete, and thus, the distributional pattern of fossil megachasmids shown in Fig. 3 should be interpreted with caution. Nevertheless, the discovery of *M. alisonae* sp. nov. from the Priabonian (Eocene) of Denmark (Fig. 3) now alludes to the possibility that the *Megachasma* origin may be rooted somewhere in Europe, perhaps the North Sea or Arctic Ocean. However, the Chattian (Oligocene) occurrence from the western USA clearly indicates that the "*applegatei*-grade" *Megachasma* dispersed into the Pacific if not globally, while

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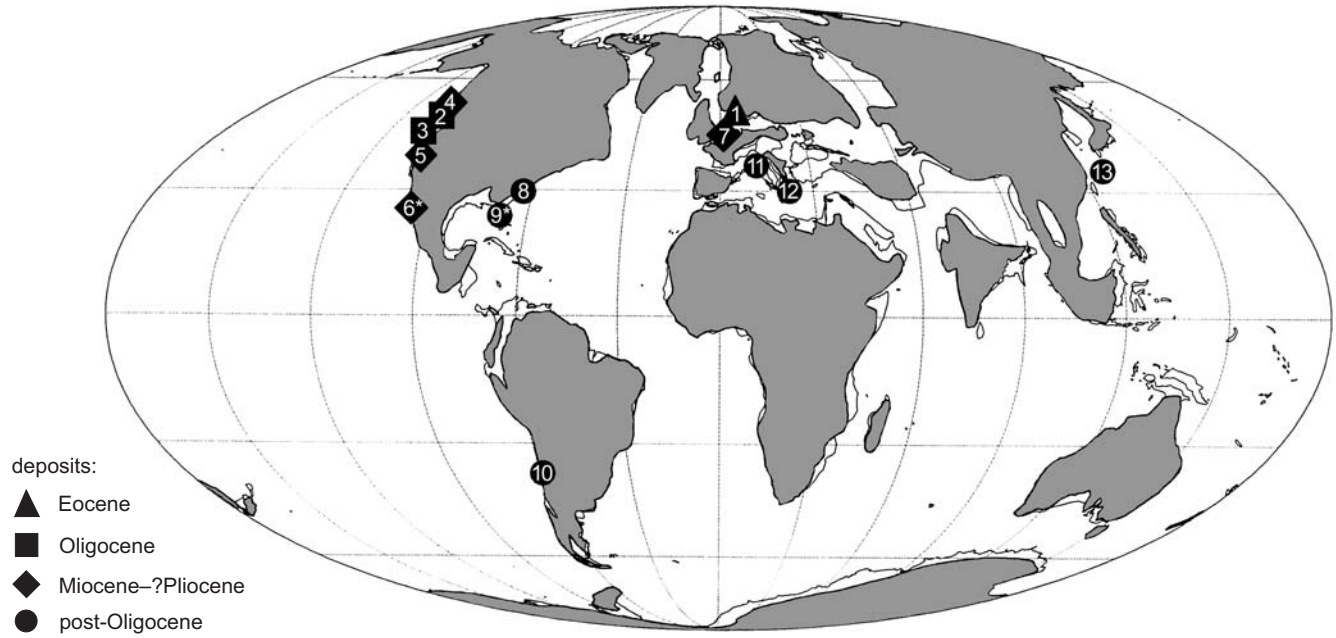


Fig. 3. Priabonian (late Eocene) paleogeographic map (after Smith et al. 1994: 29) showing the fossil record of "*applegatei*-grade" *Megachasma* (i.e., *M. alisonae* sp. nov., *M. applegatei*, or *M.* cf. *M. applegatei*) from Eocene, Oligocene, and Miocene–?Pliocene deposits as well as "*pelagios*-grade" *Megachasma* (i.e., *M. pelagios* or *M.* cf. *M. pelagios*) from post-Oligocene deposits. Asterisk indicates inferred taxonomic identification (see text). Localities: 1, Priabonian of Denmark (this study); 2, Chattian of Oregon, USA; 3, Chattian of California, USA; 4, Aquitanian of Oregon, USA; 5, Aquitanian of California, USA (Shimada et al. 2014); 6, Aquitanian of Mexico (Gonzalez-Barba and Thies 2000); 7, "early Miocene (?)"–"early Pliocene (?)" of Belgium (De Schutter 2009); 8, Zanclean of North Carolina, USA (Purdy et al. 2001); 9, "Neogene" of Florida, USA (De Schutter 2009); 10, "Upper Miocene" of Chile (Cappetta 2012); 11, Tortonian of Greece (Keupp and Bellas 2002; De Schutter 2009; Cappetta 2012); 12, Zanclean of Italy (Spadini and Manganelli 2015); 13, "late Miocene"–"early Pleistocene" of Okinawa, Japan (Tomita and Yokoyama 2015).

it likely persisted into as recent as early Pliocene in Europe (Belgium; unless, it locally became extinct in Oligocene and re-migrated back to Europe from the Pacific later). The fossil record of "*pelagios*-grade" *Megachasma* is suggestive of its global distribution by the Pliocene, if not earlier in the late Miocene. Whereas "*applegatei*-grade" *Megachasma* has not been recorded from the Southern Hemisphere unlike "*pelagios*-grade" *Megachasma*, megachasmid fossils are conspicuously absent in the equatorial zone, but rather clustered in mid-latitudinal temperate regions. Whether this perceived geographic distribution is biological or sampling issue cannot be ascertained at the present time.

Shimada et al. (2014) determined that *Megachasma pelagios* and *M. applegatei* are sister species, and that the evolution of the "modern-grade megachasmids" (i.e., equivalent to the "*pelagios*-grade" *Megachasma* here) took place no later than in the earliest late Miocene. The exact geologically youngest occurrence of the "*applegatei*-grade" *Megachasma* remains uncertain in which it could have existed as recent as the early Pliocene (Shimada et al. 2014, based on data by De Schutter 2009). On the other hand, the geologically oldest "*pelagios*-grade" *Megachasma* with a well-constrained stratigraphic control is the Tortonian record from Greece (Keupp and Bellas 2002; De Schutter 2009; Cappetta 2012; Fig. 3). At present, there is no fossil locality where both *M. applegatei* and *M. pelagios* are reported to have co-occurred. However, it is worth pointing out that the morphology of the type series of *M. applegatei* quantitatively overlaps *M. pelagios* (Fig. 2C) and thus the diagnosis for *M. applegatei* is set rather robust to accommodate its wide morphological range. In fact, Shimada et al. (2014) noted that at least one tooth, the largest specimen, in the type series (LACM 122197; Shimada et al. 2014: fig. 4BI) is practically indistinguishable from teeth of the extant *M. pelagios*, and thus, it is possible that LACM 122197 may actually belong to a "*pelagios*-grade" *Megachasma*. If this is indeed the case, not only it would represent the geologically oldest record and the first Pacific record along North America for the "*pelagios*-grade" *Megachasma*, but it would also suggest (i) that the "*applegatei*-grade" and "*pelagios*-grade" *Megachasma* contemporaneously inhabited at least during the Aquitanian, and (ii) that the divergence of "*pelagios*-grade" *Megachasma* from *M. applegatei* took place during the earliest Miocene at the latest.

Despite lacking direct fossil evidence, multiple molecular studies have placed the estimated origination time for the megachasmid clade in the Late Cretaceous about 104–90 Ma (Martin et al. 2002: fig. 5; Heinicke et al. 2009). Shimada et al. (2015) offered an explanation for the absence of Cretaceous–early Paleogene megachasmid record by considering that the rate of molecular evolution possibly did not coincide with the rate of changes in tooth morphology, and that megachasmids could have indeed been in existence during the time interval but have remained undetected due to tooth designs unconventional for megachasmids. In this regard, NHMUK PV P73711 is particularly important because its morphology further supports the hypothesis that *Megachasma* must have

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been derived from a lamniform clade with an "odontaspidid tooth design" that may, or may not, have direct phylogenetic affinity to the family Odontaspididae (Shimada et al. 2015). As noted above, *M. alisonae* sp. nov. has more prominent lateral cusplets and a less robust lingual root protuberance than those in Oligocene–Miocene *M. applegatei* (cf. Shimada et al. 2014), making the tooth even more odontaspidid-like, and such an odontaspidid tooth design is considered primitive for *Megachasma*. Therefore, NHMUK PV P73711 has offered critical morphological characteristics needed for the quest to search for even older megachasmids in the geologic record. Whereas more specimens from the Priabonian are needed to evaluate the range of morphological variation within *M. alisonae* sp. nov., the occurrence of NHMUK PV P73711 in the Pyt Member also suggests that deep-water marine deposits are the types of rocks that may yield pre-Priabonian megachasmids with small odontaspidid-like teeth. One likely factor that has eluded the discovery of early megachasmids is the fact that rock exposures containing deep-sea elasmobranch faunas are far rarer than outcrops with shallow, nearshore faunas (e.g., Adnet et al. 2008), combined with the fact that very few attempts have been made to screen large volumes of sediment needed to obtain fossil remains as small as, or smaller than, NHMUK PV P73711. Faunal investigations that specifically target small fossil remains in deep-sea deposits may be the key to future discoveries of early megachasmids, possibly even extending back to the Late Cretaceous as suggested by molecular data.

Conclusions

NHMUK PV P73711 is a tooth of *Megachasma alisonae* sp. nov. collected from the upper part of the upper Eocene Søvind Marl at Moesgård Strand in Denmark. The size of the tooth suggests that it possibly came from an individual that measured somewhere between 1.3 and 3.5 m TL, and its morphology and chipped cusp apices suggest that *M. alisonae* sp. nov. likely fed on macro-zooplankton and small fishes with hard skeletal elements. Its occurrence from the mid-Priabonian Pyt Member at least suggests that the shark lived in a relatively deep (200–600 m?), open marine environment about 36 Ma, and pushes back the geologic record of the genus by about 13 Ma. Although the time span of 13 Ma may appear insignificant for the Earth's long geologic history, it is substantial for the 65-Ma-history of the Cenozoic, and more importantly, *M. alisonae* sp. nov. offers the morphological state of early megachasmids necessary to hunt for geologically even older forms. Teeth of the early forms of *Megachasma* were likely small and odontaspidid-like, and as Shimada et al. (2015) suggested, the megachasmid origin may ultimately be traced back to a clade of Cretaceous taxa with the odontaspidid tooth design that may, or may not necessarily, belong to Odontaspididae taxonomically.

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