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The first Cenozoic record of a fossil megamouth shark (Lamniformes, Megachasmidae) from Asia

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Abstract. The megamouth shark (Lamniformes, Megachasmidae) is one of four extant planktivorous elasmobranch lineages, but its fossil record is quite limited. In the present study, we report a new discovery of a rare megachasmid shark fossil from the late Miocene–early Pleistocene interval of Okinawa Island, Japan. To date, this specimen represents the only reliable record of a megachasmid fossil from Asia.

Key words: Cenozoic, lamniform shark, *Megachasma*, megamouth shark, Okinawa, Pacific distribution

Introduction

The megamouth shark, *Megachasma pelagios* (Lamniformes, Megachasmidae), is a large elasmobranch, which was first discovered off Hawaii in 1978 (Taylor *et al*., 1983). On the basis of its large body size (up to *ca*. 5.5 m) and unique morphology, the discovery of this species is considered to be one of the ichthyological highlights of the 20th century (Berra, 1997; Nakaya, 2010).

Together with the basking shark, the whale shark, and mobulid rays, the megamouth shark is the fourth planktivorous elasmobranch lineage (Taylor *et al*., 1983). The fossil records of planktivorous elasmobranchs are important for clarifying the processes whereby elasmobranchs have filled the ecological niche for giant plankton feeders (Friedman *et al.*, 2010). However, the fossil record of these three planktivorous sharks is limited, partly because of their small tooth size (generally <5 mm in height). Recent summaries of the megamouth shark fossil record suggest that this genus is reported from only approximately 10 localities, including North America, South America, and Europe (De Schutter, 2009; Cappetta, 2012; Shimada *et al*., 2014b). To the best of our knowledge, the Asian record of the megamouth shark was documented only in an unpublished doctoral dissertation by Kuga (1985). The description was based on a single piece of material housed in a private collection, and the specimen is not accessible at present.

The present study reports a new discovery of a megamouth shark fossil from a Neogene or lower Quaternary deposit on Okinawa Island, Japan. The specimen is noteworthy because, to date, it is the only verifiable fossil record of a megamouth shark from Asia.

Locality and geological setting

The specimen was collected on a beach along the west coast of the southern region of Okinawa Island (Figure 1), where the lithology consists of the Shimajiri Group, the Chinen Formation, and the Ryukyu Group (Iryu *et al.*, 2006). The specimen was *ex situ*, but it almost certainly came from the Shimajiri Group or the Chinen Formation, which is broadly exposed in the area. The rocks of the two stratigraphic units in the area mainly consist of muddy very fine-grained sandstone, thereby suggesting that it was deposited in an outer shelf or deeper environment. The Shimajiri Group is known to include a large number of elasmobranch remains, some of which (*Megaselachus megalodon*, *Parotodus benedini*, and *Cosmopolitodus hastalis*) were described previously (Uyeno and Oshiro, 1982). The geologic ages of the Shimajiri Group and the Chinen Formation are estimated to be Miocene to lower Pleistocene on the basis of the planktonic foraminiferal and calcareous nannofossil assemblages (Tanaka and Ujiié, 1984; Imai *et al.*, 2013).

Systematic paleontology

Cohort Euselachii Hay, 1902

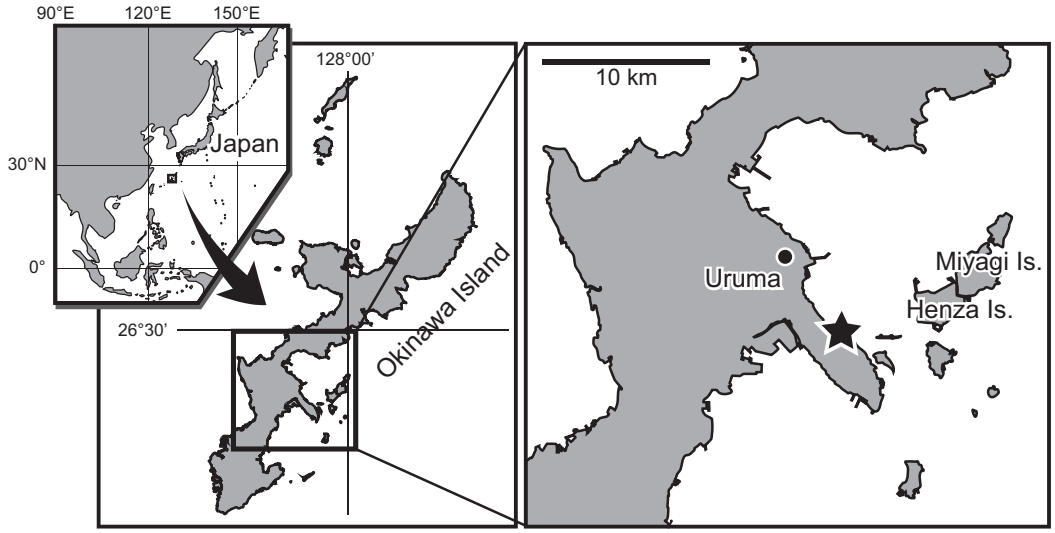

Figure 1. Map of Okinawa Island showing the location of the fossil megachasmid specimen.

Subcohort Neoselachii Compagno, 1977
Order Lamniformes Berg, 1958
Family Megachasmidae Taylor, Compagno, and Struhsaker, 1983
Genus *Megachasma* Taylor, Compagno, and Struhsaker, 1983
Megachasma cf. *pelagios* Taylor, Compagno, and Struhsaker, 1983

Figure 2

Material and method.—One isolated tooth, NMNS-PV 22659, housed in the National Museum of Nature and Science, Tsukuba, Japan. Dental terminology follows Cappetta (2012), and morphological measurements follow Shimada *et al*. (2014b).

Description.—The specimen measures 10.8 mm in total tooth height, 10.4 mm in total tooth width, 9.1 mm in crown height, 8.9 mm in crown width, 2.7 mm in crown thickness, and 8.4 mm in root length. The central cusp is short and strongly flexed lingually. The central cusp is distally inclined, suggesting that the specimen is an upper left or lower right lateral tooth. The labial and lingual surfaces of the central cusp are smooth and strongly convex from side to side. The lingual crown surface is more convex than the labial surface. The basal portion of the central cusp is mesio-distally extended. Cutting edges along lateral sides of the crown are unclear, possibly due to surface erosion after fossilization. There is no lateral cusplet, but very weak projections are present at both lateral sides of the crown. The root is thick and has short lobes. The lingual protuberance is strong, and a single nutrient groove is developed

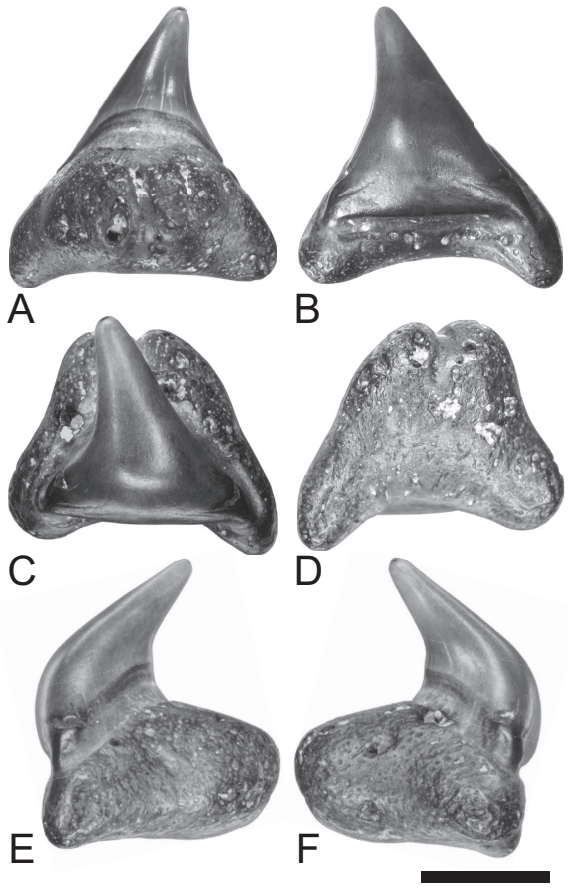

Figure 2. Tooth of fossil megachasmid shark (NMNS-PV 22659) from Okinawa, Japan. Lingual (A), labial (B), apical (C), basal (D), mesial (E), and distal (F) views. Scale = 5 mm.

at the center of the lingual surface. The tooth neck located between the crown and the root is narrow and completely encircles the tooth.

Discussion

The morphology of the specimen suggests that it belongs to the genus *Megachasma*. The specimen can be distinguished from other lamniform genera by its small tooth size, strongly lingually flexed central cusp, and a massive root with a strong lingual protrusion (Cappetta, 2012).

There is much debate on the classification of megamouth shark fossils. De Schutter (2009) tentatively divided the Cenozoic megamouth sharks into two morphological groups: (1) "*Megachasma* sp.," characterized by the general presence of lateral cusplets and long, well separated root lobes, including early Miocene specimens from California and early Miocene?–early Pliocene? specimens from Belgium; and (2) "*M*. cf. *pelagios*," characterized by a general absence of lateral cusplets and poorly separated short root lobes, including late Miocene–early Pliocene specimens from Chile, eastern USA (Florida and North Carolina), and Greece.

Shimada *et al*. (2014b) subsequently erected a new species, *Megachasma applegatei*, based on numerous isolated teeth, including 67 type specimens, collected from Oligocene–early Miocene deposits in western USA (California and Oregon). The authors accepted De Schutter's two morphological groups (i.e., "*Megachasma* sp." and "*M*. cf. *pelagios*") and suggested that "*Megachasma* sp." should be assigned to *M*. *applegatei*. However, the taxonomic status of "*M*. cf. *pelagios*" of De Schutter (2009) was not stated by Shimada *et al*. (2014b), in part because De Schutter's (2009) specimens were based on a private collection with tenuous chronostratigraphy. In the present study, we follow the division into these two morphological groups and identify NMNS-PV 22659 as belonging to "*M*. cf. *M*. *pelagios*" because it lacks lateral cusplets and displays a weakly bilobate root.

It remains unclear whether the fossil "*M*. cf. *pelagios*" is the same species as the extant *M*. *pelagios*. The morphological resemblance between the fossil "*M*. cf. *pelagios*" and *M*. *pelagios* indicates their close relationship (De Schutter, 2009). However, it should be noted that the crown slenderness of NMNS-PV 22659 (crown height/crown width = 1.02) fell outside the range of the extant *M*. *pelagios* (total range, 1.1–2.4; interquartile range, 1.5–2.0; Yabumoto *et al*., 1997; Shimada *et al*., 2014b). Future discussion on the taxonomic status of "*M*. cf. *pelagios*" should be based on larger sample sizes, but this is beyond the scope of the present study.

Fossil megamouth sharks also include one Mesozoic species, *Megachasma comanchensis* (Shimada, 2007). This species was erected for four isolated teeth obtained from a mid-Cretaceous (Cenomanian) deposit in Colorado, USA (Shimada, 2007). Later, Shimada *et al*. (2014a) suggested that this species may not belong to the family Megachasmidae but to the family 'Odontaspidae', so its taxonomic position is still unsettled. This species is distinguishable from NMNS-PV 22659 in having a well developed nutrient groove and wide and flattened basal attachment surfaces of the tooth root (Shimada, 2007).

Kuga (1985) described a single isolated tooth found from the Tomioka Formation (Pliocene) of Fukushima Prefecture, Japan, and identified this fossil as *Megachasma* cf. *pelagios*. However, the description was based on a specimen in a private collection, and the specimen is not accessible at present. The non-Asian occurrences of Cenozoic megamouth shark fossils were summarized by Cappetta (2012) and Shimada *et al*. (2014b) as follows: Chattian of California, USA (Phillips *et al*., 1976); late Chattian–Aquitanian of California and Oregon, USA (Shimada *et al*., 2014b); Aquitanian of Mexico (González-Barba and Thies, 2000); Miocene of Oregon (Taylor *et al*., 1983); upper Miocene of Chile (Cappetta, 2012); Tortonian of Greece (Keupp and Bellas, 2002); Zanclean of North Carolina, USA (Purdy *et al*., 2001); lower Miocene?–lower Pliocene? of Belgium (De Schutter, 2009); and Neogene of Florida, USA (De Schutter, 2009). The extant megamouth shark is known to have a global distribution in tropical to temperate seas (Compagno, 2002; Nakaya, 2010). Similar to the extant species, the worldwide occurrences of the fossil megamouth shark may reflect its circumglobal distribution.

In addition to the megamouth shark, the large planktivorous basking shark (*Cetorhinus*) lived around Japan during the Cenozoic. A tooth of the basking shark was reported from Miocene deposits (Karasawa, 1989), and many gill rakers were discovered in several localities of Oligocene–Pleistocene rocks in Japan (Kikuchi and Takaoka, 1979; Uyeno *et al*., 1983, 1984; Nakagawa and Yasuno, 1985; Tomita and Oji, 2010). On the basis of current knowledge, only three shark and one batoid lineages are recognized as having acquired a planktivorous lifestyle during elasmobranch life history. The present discovery of a fossil megamouth shark from Japan confirms that at least two of these four planktivorous elasmobranch lineages were represented in the western North Pacific during the Neogene or the early Pleistocene.

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