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FIRST DEEP-SEA SHARK FOSSIL TEETH FROM THE MIOCENE OF SOUTH KOREA

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First Deep-Sea Shark Fossil Teeth from the Miocene of South Korea. Chan-gyu Yun. — Important vertebrate fossil remains were collected in the Pohang Basin in South Korea for many decades, but only few have been described up to now. Here, three deep-sea shark teeth are described, which most likely derived from the Duho Formation (middle Miocene) near Pohang City, South Korea. One of the teeth is identified as belonging to the genus *Mitsukurina*, while the others are assignable to *Dalatias*. None of these taxa were previously reported from the Korean Peninsula. The occurrences of these deep-water fishes in the Pohang Basin support the hypotheses that the Duho Formation was deposited in a deep-sea environment, and sharks, even including benthopelagic forms were already widely distributed throughout the East Sea when this sea was still developing.

Key words: Pohang Basin, Miocene, Korean Peninsula, East Sea, shark fossil.

Introduction

Although our knowledge about Neogene deep-water elasmobranchs has been increased significantly by several new and important discoveries made in the last decades (e. g., Adnet et al., 2008; Carrillo-Briceño et al., 2019), their fossil record still is very poor compared to other extensively described elasmobranch remains from shallower paleoenvironments. The majority of currently known records are from a few sites in restricted areas (Adnet et al., 2008). Thus, little is known about the evolution and ecology of deep-water sharks during the Neogene period (e. g., Takakuwa, 2006; Adnet et al., 2008; Kriwet and Klug, 2009; Underwood and Schlögl, 2013; Suzuki, 2015; Nishimatsu, 2019; Nishimatsu and Ujihara, 2019), and it is unquestionable that any new fossil records, especially those from sites where deep-marine elasmobranch remains previously unrecognized will significantly contribute to our knowledge on these understudied, yet very important fishes.

Various important marine fishes were found in Miocene deposits of the Pohang Basin in South Korea, but only very few records have been reported so far despite their high importance in understanding evolutionary dynamics of marine organisms in East Asia (e. g., Choi and Lee, 2017; Nam and Nazarkin, 2018; Nam et al., 2019). Within the fossil ichthyofauna of the Pohang Basin, chondrichthyans represent one of the most poorly understood groups and so far, only two juvenile teeth of a single pelagic lamnid shark, *Cosmopolitodus hastalis* have been described (Kim et al., 2018; Yun, 2020). In fact, the record of fossil shark teeth from the Korean Peninsula has received very scant attention over the years as the only other work on this subject is a short note by Lee et al. (2014 b) about a *Carcharodon carcharias* tooth crown from the Plio-Pleistocene Segwipo Formation that is located on Jeju Island. Up to date, the vast majority of Neogene fossil remains of elasmobranchs in Northeast Asia are from Japan (e. g., Kim et al., 2018), with a few exceptions from deposits on Sakhalin Island of Russia (Nazarkin, 2013, 2014; Nazarkin and Malyskhina, 2012). Consequently, additional material from the Pohang Basin of South Korea

is crucial for understanding early dispersal patterns of marine fishes in the East Sea (Sea of Japan) when this sea was in early stages of development and expansion (Pavlyutkin et al., 2016; Yun, 2020).

The purpose of this study is to report for the first time three deep-marine elasmobranch teeth from the Pohang Basin, probably from the middle Miocene Duho Formation. They are identified as *Mitsukurina* cf. *M. lineata*, *Dalatias licha* and *Dalatias* cf. *D. licha*. These fossils are important because they represent the first fossil record of these taxa from the Korean Peninsula contributing to our knowledge about the fossil record of deep-sea sharks, which are generally rare all around the world (Takakuwa, 2006).

Geological setting

The fossils described here were recovered from the marine Yeonil Group of the Pohang Basin, which is composed of three formations termed Chunbuk Conglomerate, Hageon Formation, and Duho Formation in ascending order (Jung and Lee, 2009). Only scant information about the locality and horizon for the specimens described here is available, which indicates that they either come from the Hageon or Duho formations of the Yeonil Group. However, the teeth are embedded within brownish dark grey mudstones (figs 1, 2, 3) that are similar to rocks commonly found in the Duho Formation (Nam et al., 2019). Additionally, the teeth are well preserved in three-dimensions and show only minor breakage, and these preservational features match the interpreted low-energy, deep-water depositional environment with relatively complete fossils of the Duho Formation rather than the high-energy depositional environment with severely disarticulated fossils of the Hageon Formation (Seong et al., 2009; Nam et al., 2019). Furthermore, all recognized vertebrate fossil records from the Pohang Basin are interpreted to be from the Duho Formation (Choi and Lee, 2017). Finally, the taxa recognized in this study have bathydemersal or benthopelagic distributions (Cappetta, 2012) that agree with the assumed deep-marine depositional environment of the Duho Formation rather than the shallow marine depositional environment of the Hageon Formation (Kim and Paik, 2013). Therefore, these fossils are best interpreted to be from the Duho Formation. The Duho Formation is up to 250 m thick (Jung and Lee, 2009; Yun, 2020) and has produced a variety of fossils such as plants, invertebrates, microfossils, and vertebrate fossils like cetaceans and marine fishes (Choi and Lee, 2017; Kim et al., 2018). A SHRIMP U-Pb Zircon geochronological study suggests an age of about 21.89 ± 1.1 Ma and 21.68 ± 1.2 Ma for the beginning of the sedimentation of the formation (Lee et al., 2014 a), and the microplankton analysis dates the beds of the formation to 13.4 Ma or 14–12 Ma (Chun, 2004; Nam et al., 2019). A K-Ar dating study estimated an age about 15 Ma for the volcanic rocks of the Yeonil Group (Lee et al., 1992). Thus, it can be said the Duho Formation is middle Miocene in age.

Material and methods

The specimens described here are housed in the Natural History Museum of Chungnam National University (CNUNHM). No permission was given to remove the teeth from the matrix and there is no appropriate preparation tool at the museum. Thus, only the exposed parts could be studied here except for CNUNHM-F268 in which the breakage of the distal root lobe allowed observation of the lingual part of this tooth as well. Dental nomenclature and the systematics used in this work follow those of Cappetta (2012), Suzuki (2015) and Welton (2016). Tooth measurements are taken following the methods described by Cione et al. (2012) and Welton (2016) and photographs were obtained with Samsung SM-G981N and SM-G977N cameras. Taxonomic identifications are based on literature review. Of note, when this manuscript was in peer review, the author received notice that another research group is underway of describing elasmobranchii assemblage of the Duho Formation, which may potentially include the taxa described here but using different specimens, and have been presented in abstract form (Malyskina et al., 2021). This work was performed independently, and the author declares that he has no competing interests.

Systematic Paleontology

Clade Lamniformes Berg, 1937

Clade Mitsukurinidae Jordan, 1898

Genus *Mitsukurina* Jordan, 1898

Mitsukurina* cf. *M. lineata (Probst, 1879)

Referred material. One upper lateral tooth CNUNHM-F268 (fig. 1).

Description. The maximum height of the tooth is 16 mm. The cusp of the crown is slightly asymmetrical in that the apex is slightly inclined distally, indicating that it is either from a lateral position of the right palatoquadrate or the left meckelian cartilage. The cusp is nearly straight in lateral view but the apex is slightly curved lingually. The mesial cutting edge is 13 mm, whereas the distal cutting edge is 12 mm long. Both edges are smooth. There is a very small cusplet on the disto-basal part of the crown. On the lingual surface, vertical striations are well developed and closely arranged to each other. The crown height is 12 mm, and the basal crown width is 8 mm. There is no axial nutritive groove on the lingual surface

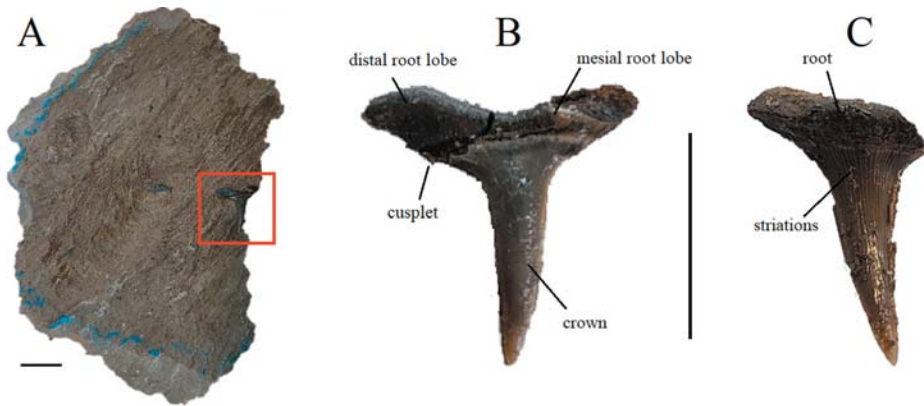


Fig. 1. Tooth of *Mitsukurina* cf. *M. lineata*, CNUNHM-F268: A — photograph of the specimen; B — enlarged photograph of the labial surface of the tooth; C — enlarged photograph of the lingual part of the tooth. Left scale bar, for A, equals 20 mm. Right scale bar, for B and C, equals 10 mm.

of the root but this may represent a taphonomic artifact. The distal root lobe is well preserved, but there is a crack in the portion where it meets the crown, and the labial part of the mesial root lobe is broken off. Both lobes are elongated and rounded at their basal margins. They are well separated, forming an angle about 125° . The maximum height of the root is 3 mm.

Remarks. The combination of well-separated root lobes, presence of the very small cusplet, a densely striated lingual surface of the cusp, and the slender, elongated morphology of the crown suggests that CNUNHM-F268 is a tooth assignable to *Mitsukurina*, and separates the specimen easily from other mitsukurinid or odontaspimid taxa with similar tooth morphologies (see e. g., Kocsis, 2007; Cappetta, 2012; Carrillo-Briceño et al., 2020). Currently, *Mitsukurina lineata* is the only recognized species within this genus in the Miocene and considered as the most likely candidate for CNUNHM-F268. However, CNUNHM-F268 lacks an axial groove on the lingual side of the root, which is typically present in *Mitsukurina* teeth (Cappetta, 2012), although it is certainly possible that this is merely a taphonomic artifact. Therefore, a more tentative approach of referring this specimen as *Mitsukurina* cf. *M. lineata* is used in this work.

Clade Squaliformes Goodrich, 1909

Clade Dalatiidae Gray, 1851

Genus *Dalatias* Rafinesque, 1810

Dalatias licha (Bonnaterre, 1788)

Referred material. One lower lateral tooth CNUNHM-F279 (fig. 2).

Description. CNUNHM-F279 represents a lower lateral tooth that is lacking the distal root lobe. The maximum height of the tooth, as preserved, is 12.73 mm. The crown height is 7.4 mm. The main cusp is nearly vertically directed, and both mesial and distal edges are strongly serrated. The serrations are apically directed. A faint notch separates the cusp from the distal heel, and the apical margin of the heel forms a low-elevated cusplet, which is serrated. The length of the heel is 1.85 mm, and the height of the distal cusplet is 5.6 mm. Overall, the labial surface of the crown is flat and its maximum width is 7.5 mm. Not much can be ascertained about the basal part of the specimen as the root is not complete, but it is certain that a long and bi-lobed apron is present in the tooth and there is a button-shaped foramen between them.

Remarks. The specimen bears a flat, triangular cusp with serrated edges and a button-shaped foramen positioned between mesial and distal aprons, supporting its assignment to Dalatiidae (e. g., Cappetta, 2012; Suzuki, 2015; Welton, 2016). CNUNHM-F279 possesses a main cusp that is wide and directed nearly vertical, and both cutting edges are serrated and the serrations are apically hooked. These features closely match the condition that can be observed

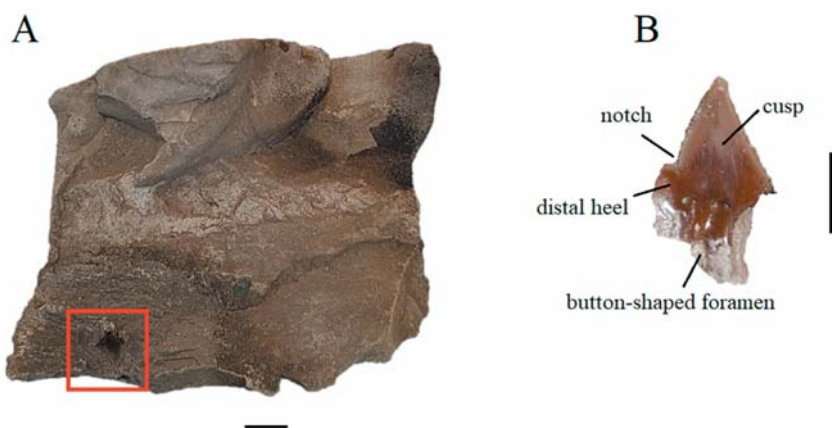


Fig. 2. Tooth of *Dalatias licha*, CNUNHM-F279: **A** — photograph of the specimen; **B** — enlarged photograph of the labial surface of the tooth. Left scale bar, for **A**, equals 10 mm. Right scale bar, for **B**, equals 5 mm.

in typical *Dalatias* lower teeth (e. g., Cappetta, 2012; Carrillo-Briceño et al., 2015, 2016, 2020). Lastly, this specimen possesses a button-shaped foramen surrounded by mesial and distal aprons, which is a character that is present especially in species of *Dalatias* and *Isistius* according to Pollerspöck and Straube (2018). CNUNHM-F279 can be easily distinguished from the lower teeth of *Isistius* by its much larger size, distinctively developed serrations and the presence of the distal heel (Cappetta, 2012; Suzuki, 2015; Pollerspöck and Straube, 2018). Thus, this specimen is referred to a genus *Dalatias*. *Dalatias* teeth from Neogene deposits are morphologically identical to those of the modern *Dalatias licha*, and thus referable to this species (Keyes, 1984; Cappetta, 2012; Carrillo-Briceño et al., 2016). Thus, CNUNHM-F279 is assigned to this species as well.

Dalatias cf. *D. licha* (Bonnaterre, 1788)

Referred material. One lower lateral tooth CNUNHM-F392 (fig. 3).

Description: CNUNHM-F392 is a nearly complete lower lateral tooth that is only missing a labial part of a mesial root lobe that is broken off, and an apex of the cusp embed within a matrix. The exposed height of the crown is about 4.06 mm. The cusp is sub-vertical, although the axis is slightly inclined distally. Both cutting edges are serrated, but it is not certain whether the serrations are directed upwards as they are extremely small having about 5–6 serrations per mm in the mesial edge. Small serrations are present on the distal heel as well. The crown width is 6.64 mm at its basis, and the length of the heel is 1.47 mm. The root is high, and both mesial and distal edges are nearly straight. The maximum height of the root is 7.72 mm and the width is 7.13 mm. The part where the “button hole” in dalatiid lower teeth would be is filled with matrix, but it is likely that it is similarly shaped as in other *Dalatias* teeth as both mesial and distal aprons surrounding it are not different from other examples of this genus (e. g., Cappetta, 2012: Fig. 112 D). Having a relatively low profile of the cusp and a transversely wide, tongue-shaped nature of the mesial apron, it is possible that this tooth comes from a more lateral position teeth within the lower jaw.

Remarks. For the same reason as CNUNHM-F279, CNUNHM-F392 is assignable to Dalatiidae. The specimen probably shares a button-shaped foramen with *Dalatias* and *Isistius* but distinguishable from the latter in having a distal heel (Pollerspöck and Straube, 2018). Therefore, referral to *Dalatias* is very plausible. However, CNUNHM-F392 differs from lower teeth of both Neogene and modern specimens of *Dalatias licha* in having minute serrations along the main cusp’s cutting edges. While it is possible that this is merely due to a preservational artifact or an individual variation, the impossibility of removal of the tooth from the matrix makes it impossible to verify this assignment. Thus, a more tentative approach of referring this specimen as *Dalatias* cf. *D. licha* is used here.

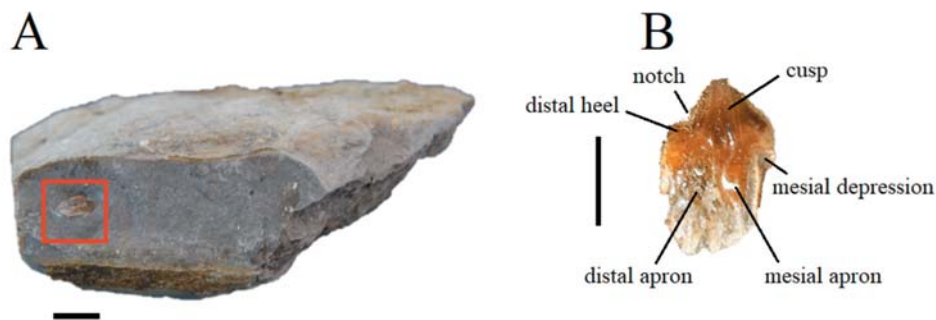


Fig. 3. Tooth of *Dalatias* cf. *D. licha*, CNUNHM-F392: A — photograph of the specimen; B — enlarged photograph of the labial surface of the tooth. Left scale bar, for A, equals 10 mm. Right scale bar, for B, equals 5 mm.

Discussion

Paleoecological and Paleoenvironmental implications. The fossil *Dalatias* species from the Miocene is considered to be same species as the modern *Dalatias licha* (Cappetta, 2012; Carrillo-Briceño et al., 2016). Additionally, only minor differences are present between teeth of Neogene *Mitsukurina lineata* and modern *Mitsukurina owstoni* (Cappetta, 2012; Carrillo-Briceño et al., 2020). This suggests largely similar feeding habits or ecological niches of these two Neogene sharks as for their modern representatives. Therefore, paleoecological and paleoenvironmental interpretations are made for *Dalatias licha* and *Mitsukurina* cf. *M. lineata* of the Duho Formation fauna, based on ecology of modern counterparts.

While individuals of modern *Mitsukurina* species may enter neritic areas occasionally (Yano et al., 2007; Cappetta, 2012; Carrillo-Briceño et al., 2020), they are usually considered deep-sea benthopelagic sharks inhabiting continental slopes, insular slopes, the sea floor, or mid-waters with depths ranging from 270 m to at least 1300 m (e. g., Duffy, 1997; Duffy et al., 2004; Yano et al., 2007; Cappetta, 2012; Cappetta et al., 2016; Nakaya et al., 2016; Carrillo-Briceño et al., 2016, 2020), but occurring in depths ranging from 0 to 200 m is certainly an unusual case. *Dalatias licha* is another benthopelagic shark that prefers habitats near the continental slope or sea floor (e. g., Mannering and Hiller, 2008; Cappetta, 2012; Carrillo-Briceño et al., 2016; Finucci et al., 2018), and is most commonly found at depths of 200–1800 m (e. g., Roberts et al., 2015; Carrillo-Briceño et al., 2016, 2020; Finucci et al., 2018). Additionally, this taxon is the most benthic member of Dalatiidae (Cappetta, 2012) and even bioluminescent (Mallefet et al., 2021).

While earlier studies on benthic foraminifera and stomatopods suggested that the Duho Formation was deposited under shallow marine conditions on a continental shelf (Kim and Choi, 1977; Yun, 1985), more recent studies have suggested a deep-sea accumulation model possibly of up to 500–2000 m depositional depth based on the occurrences of fossils such as *Chondrites* and *Vinciguerria* (Jung and Lee, 2009; Seong et al., 2009; Kim and Paik, 2013; Nam and Nazarkin, 2018; Nam et al., 2019). The tooth crowns of the specimens described in this work are relatively well-preserved, suggesting that these were also deposited in a low-energy, deep-water environment and the possibility that these represent the ones transported from the shallow marine environment by turbiditic currents is unlikely as such processes would severely damage the tooth (Seong et al., 2009; Jovanović et al., 2019). Thus, the presence of *Mitsukurina* cf. *M. lineata* and *Dalatias* spp. in the Duho Formation fauna is considered as another paleontological evidence supporting a deep-sea accumulation model of the formation. This is also consistent with previous studies that considered these taxa as positive evidence of deep-marine paleoenvironments (e. g., Cappetta, 2012; Carrillo-Briceño et al., 2016, 2020).

It is recognized that mesopelagic or other deep-water bony fishes occupy significant portions in diet of modern representatives of *Mitsukurina* and *Dalatias* (e. g., Duffy, 1997; Ergüden et al., 2017). Various bony fish fossils including *Pleuronichthys*, *Vinciguerria* and

Zaprora previously were reported from the Duho Formation and these are assumed to be mesopelagic or benthic fishes (Ko and Nam, 2016; Nam and Nazarkin, 2018; Nam et al., 2019). Therefore, it is reasonable to assume that *Mitsukurina* cf. *M. lineata* and *Dalati*s spp. in the Duho Formation fauna may have preyed on these fishes, possibly near the sea floor (fig. 4).

Paleobiogeographical implications. So far, fossil of *Dalati*s and *Mitsukurina* in Northeast Asia have been reported only from Japan (e. g., Takakuwa, 2006; Cappetta, 2012) and therefore CNUNHM-F268, 279 and 392 represent the first records of these taxa in the Korean Peninsula as well as the whole Northeast Asia outside the Japanese archipelago. Therefore, these fossils extend the known paleobiogeographical ranges of *Mitsukurina* and *Dalati*s in the Neogene significantly, and their implications on the development and changes that occurred in the Neogene ichthyofauna of the East Sea are discussed here.

The East Sea started to form in the early Miocene by separation of the northern and southern Japanese archipelagos (e. g., Ko and Nam, 2016). The Duho Formation was deposited during the early stages of development and expansion of the East Sea in the middle Miocene (Pavlyutkin et al., 2016; Yun, 2020). Yun (2020) reconstructed a preliminary assemblage of fossil sharks of the Duho Formation and found it to be largely similar to those of contemporaneous Japanese marine deposits. Based on this observation, Yun (2020) hypothesized that sharks were already distributed throughout the East Sea during the middle Miocene when this area of the western Pacific was still in its early stage of formation. However, this was only based on epipelagic and pelagic taxa. According to a survey of Takakuwa (2006), fossils of *Dalati*s and *Mitsukurina* occur in middle Miocene sediments in the center of the Japanese archipelago as well. Thus, *Dalati*s and *Mitsukurina* fossils from the Duho Formation confirm that even benthopelagic sharks were also widely distributed throughout the East Sea already during the middle Miocene. This wide distribution of sharks with different lifestyles may be a result of invasion of warm oceanic currents into the East Sea during the Early Miocene to middle Miocene (Yun, 2020).

Takakuwa (2006) suggested that the outline of the recent deep-sea shark fauna of the Northwest Pacific might already have been established in the Miocene, based on similarities in generic compositions of Japanese fossil and modern records. However, at present there are no records of *Mitsukurina* and *Dalati*s in the modern-day East Sea (Soto and Mincarone, 2001; Duffy et al., 2007; Yano et al., 2007; Finucci et al., 2018), and this and the fossil records from South Korea and Japan rather suggest that complex faunal changes occurred between the Miocene and Holocene in this part of the western Pacific. However, this is only based on two taxa at the moment and due to scarcity of deep-water shark fossils globally (Takakuwa, 2006; Adnet et al., 2008), much remains unresolved. Therefore, this interpretation should be considered preliminary and additional fossil remains of deep-marine elasmobranchs during this period are crucial for testing these hypotheses.

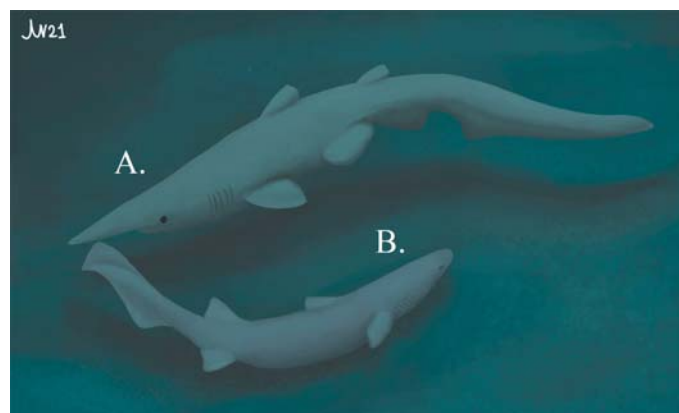


Fig. 4. Life reconstruction of deep-water sharks lived in the East sea of middle Miocene: **A** — *Mitsukurina* cf. *M. lineata*; **B** — *Dalati*s licha. Artwork by Jun-Hyeok Jang.

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