A TOOTH OF THE EXTINCT LAMNID SHARK, *COSMOPOLITODUS PLANUS* COMB. NOV. (CHONDRICHTHYES: ELASMOBRANCHII) FROM THE MIOCENE OF POHANG CITY, SOUTH KOREA

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Abstract An isolated, upper lateral tooth of the extinct lamnid shark *Cosmopolitodus planus* (Agassiz, 1856), is described from middle Miocene marine deposits (possibly the Duho Formation) in Pohang City, South Korea. This is the first confirmed record of this taxon in the Korean Peninsula. The tooth is less than half the size of a large tooth of this species, suggesting that the tooth comes either from an intermediate or posterior position within the upper jaw, or from a young individual. This report further supports the hypothesis that epipelagic or pelagic sharks were already distributed throughout the entire East Sea in the middle Miocene. It is recommended that the species *planus* should be transferred to the genus *Cosmopolitodus* based on numerous similarities with the type species of this genus, *C. hastalis* (Agassiz, 1838).

Keywords: Neogene, Chondrichthyes, Elasmobranchii, shark tooth, *Cosmopolitodus*, Lamniformes.

INTRODUCTION

Neogene marine rocks exposed in the Pohang Basin in Pohang City, southeastern South Korea, have yielded numerous fossils from both marine and terrestrial organisms (e.g., Kim et al., 2018; Nam et al., 2019). Although the most abundant fossils in these deposits are those of plants (e.g., Jung & Lee, 2009; Jia et al., 2021; Kim et al., 2021), a large number of animal fossils have been recovered and described as well. These fossils include various echinoderms, mollusks, and arthropods (e.g., Seong et al., 2009; Kim & Lee, 2011; Nam et al., 2019), and very occasionally vertebrate remains. The vertebrate fossil remains from these beds have been vastly understudied, partly due to the illegal collecting activities of private fossil collectors and the subsequent destruction of fossil localities. To date only two cetacean fossils, several bony fish skeletons, and two shark teeth have been described from this region (e.g., Choi & Lee, 2017; Kim et al., 2018; Nam et al., 2019; Yun, 2020). The presence of shark fossils in this region has been recognized since the mid-20th century (Takai, 1959) and has occasionally been noted in conference abstracts (e.g., Yun, 2020). However, the vast majority of these elasmobranch fossils are not yet described, and the present whereabouts of many of them is unknown. The only descriptions of these shark fossils to appear in the peer-reviewed literature were published in the past three years and are based on two juvenile teeth of the extinct lamniform *Cosmopolitodus hastalis* (Agassiz, 1838) (Kim et al., 2018; Yun, 2020). In fact, descriptions of any shark fossils from the Korean Peninsula are extremely rare as the only other documented example is that of an isolated tooth of *Carcharodon carcharias* (Linnaeus, 1758) from the Plio-Pleistocene Segwipo Formation in Jeju island (Lee et al., 2014b). Thus, any new descriptions of shark fossils from the Pohang Basin are very significant because little is known about the ichthyodiversity of the East Sea during the Neogene. Furthermore, these shark remains contribute greatly to the reconstruction of the vertebrate body fossil record from the Korean Peninsula, which is poorly known but very important in understanding evolutionary dynamics of vertebrates in East Asia (Choi & Lee, 2017). The present study documents a well-preserved tooth (CNUNHM-F341) of *Cosmopolitodus planus* from the Pohang Basin in Pohang City. This is the first description of a *C. planus* tooth from the Korean Peninsula and represents the first confirmed occurrence of this taxon in the region.

GEOLOGICAL SETTING

Geologic exposures in the Pohang Basin consist of the Neogene non-marine Yangbuk Group and the marine Yeonil Group (Jung & Lee, 2009). The Yangbuk Group is made up mainly by basalts, conglomerates, lignites, sandstones, shales and volcanic tuffs, while the Yeonil Group mainly consists of non-volcanic, clastic marine sediments (e.g., Kim, 2008). The three units that form the Yeonil Group include, in ascending order, the Chunbuk Conglomerate, the Hagjeon Formation, and the Duho Formation (Jung & Lee, 2009; Kim et al., 2021; Fig. 1). The Chunbuk Conglomerate consists of conglomerates and sandstones, while the overlying Hagjeon Formation is composed of grayish white sandstones or mudstones (e.g., Kim, 1999). The uppermost part of the Yeonil Group, the Duho Formation, is composed mainly of yellowish brown to dark gray mudstones (e.g., Jung & Lee, 2009).

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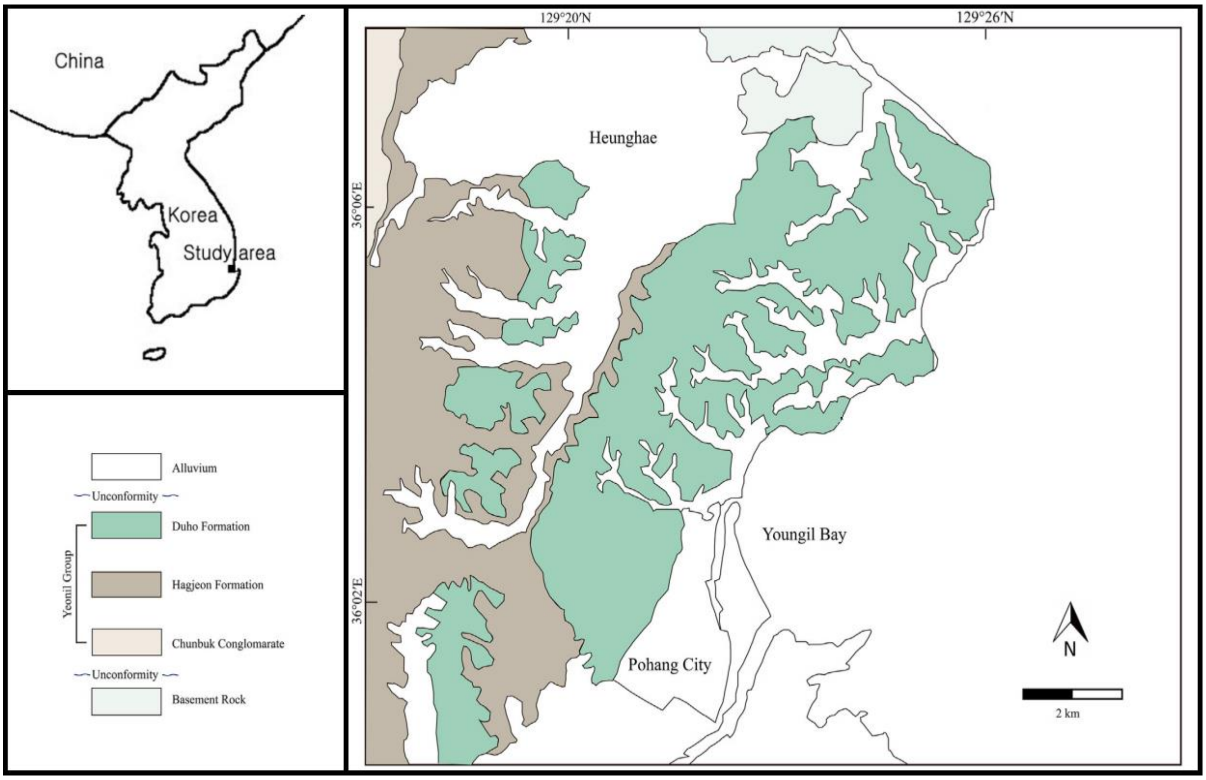

Fig. 1 Geological map of the Pohang Basin. Modified from Jia et al. (2021) and Kim et al. (2021).

The tooth described herein was collected by a now retired professor, Hyesu Yun, who donated the specimen to the Natural History Museum of Chungnam National University (CNUNHM) in 2014. Unfortunately no detailed geological or locality information was provided with the specimen other than that is was derived either from the Hagjeon Formation or the Duho Formation in Pohang City. However, the specimen was likely collected from exposures of the Duho Formation for several reasons. First, the most common Neogene deposits exposed in the northern part of Pohang City belong to the Duho Formation (Nam & Nazarkin, 2018), and the collector himself considers most of the vertebrate fossils in the CNUNHM collection as likely being derived from this formation. Second, all previous records of vertebrate fossils from this region of the basin have been derived from the Duho Formation (e.g., Choi & Lee, 2017). Finally, the matrix associated with the specimen is represented by a yellowish brown mudstone that is consistent with rocks of the Duho Formation (e.g., Kim et al., 2018; Fig. 2). Nevertheless, both the Hagjeon and the Duho formations are middle Miocene in age (Kim et al., 1993; Chun, 2004), indicating that the shark lived in the East Sea during this period.

According to a SHRIMP U-Pb zircon geochronological study by Lee et al. (2014a), the beginning of the sedimentation of the Duho Formation likely occurred between 21.89±1.1 and 21.68±1.2 Ma. Additionally, a K-Ar dating study of the volcanic rocks in the Yeonil Group estimated the age of the group to be about 15 Ma (Lee et al., 1992), and microplankton analyses indicate the Duho Formation as being middle Miocene (Serravallian), respectively approximately and 13 should be separated based on foraminifera, and 14.0-12.0.

Ma using dinoflagellates (Chun, 2004; Nam et al., 2019). Previous studies based on benthic foraminifera and stomatopods have suggested that the depositional environment of the Duho Formation was shallow marine (Kim & Choi, 1977; Yun, 1985). However, more recent studies indicate a hemipelagic, deep-sea accumulation based on the presence of deep-water trace fossils like *Chondrites* and nearly complete fish skeletons, and re-interpreted the aforementioned fossils (e.g., stomatopods) as being transported into deeper waters by turbiditic currents (Kim & Paik, 2013; Kim et al., 2018; Nam et al., 2019).

MATERIAL AND METHODS

The isolated tooth described in this study is catalogued in the collections of the Natural History Museum of Chungnam National University (CNUNHM), and has been given the catalogue number CNUNHM-F341. The specimen is embedded in matrix; given that the museum has no fossil preparation tools, the tooth was not removed from the matrix and only the exposed surface is described here. Photographs were taken using a Samsung SM-G981N camera and cropped using Microsoft PowerPoint 2016 to generate the provided figures. Measurements were taken using the method of Cione et al. (2012), and tooth nomenclature used in this study follows that of Kuga (1985) and Cione et al. (2012). Higher taxonomic rankings follow that of Cappetta (2012) and Nelson et al. (2016).

Fig. 2 Isolated tooth of *Cosmopolitodus planus* with unremoved matrix (CNUNHM-F341), probably from the Duho Formation (Middle Miocene), Pohang City of South Korea.

SYSTEMATIC PALAEONTOLOGY

Clade Chondrichthyes Huxley, 1880
Clade Euselachii Hay, 1902
Clade Elasmobranchii Bonaparte, 1838
Clade Selachii Cope, 1871
Clade Galeomorphi (sensu Nelson et al., 2016)
Clade Lamniformes Garman, 1885
Clade Lamnidae Bonaparte, 1835
Genus † *Cosmopolitodus* Glikman, 1964
† *Cosmopolitodus planus* (Agassiz, 1856) **comb. nov.**

Description: CNUNHM-F341 is a very well preserved fossilized lamnid shark tooth that is still embedded in the matrix (Fig. 2). The exposed labial surface of the tooth is flat and nearly complete, except for some breakage at the base of the mesial crown edge (Fig. 3). The tooth lacks lateral cusplets, but instead has a thick enameloid shoulder where the main cusp meets the root along the distal side (unfortunately this feature is not preserved on the mesial edge). The main cusp is wide and triangular; it measures 17 mm in height, and 15 mm in preserved mesiodistal width (if completely preserved, the estimated mesiodistal width of the main cusp was likely 18 mm). The upper two-thirds of the mesial crown edge is slightly convex, whereas the lower one-third is slightly concave. The distal edge of the crown is nearly straight apically, but strongly concave basally, thereby resulting an overall “hooked” morphology with the apex strongly inclining distally at a 28° angle measured between the midline of the tooth and the crown apex. Both cutting edges are smooth and devoid of any serrations. The preserved length of the mesial crown edge measures 21 mm, but was likely about 25 mm when complete. The distal crown edge length measures 14 mm. The root is large and has rounded mesial and distal root lobes. Both the mesial and the distal roots are extended slightly beyond the crown edges, and the root has a triangular interlobe area. The maximum width and height of the root are 20 mm and 5 mm, respectively.

Remarks: CNUNHM-F341 is assigned to *Cosmopolitodus planus* based on the presence of smooth cutting edges on the crown, nearly flat labial surface, a triangular and wide overall morphology of the crown with an apex that is strongly inclined distally, rounded root lobes, and the absence of lateral cusplets (e.g., Kuga, 1985; Karasawa, 1989; Nazarkin, 2013; Yun, 2020). Although some *Isurus oxyrinchus* (Rafinesque, 1810) teeth bear resemblances to those of *C.planus* in having a relatively flat and distally inclined wide crown, CNUNHM-F341 differs from these by having an apicobasally thick root with rounded lobes (e.g., Kuga, 1985; Boessenecker, 2011; Nazkarin, 2013). CNUNHM-F341 is differentiated from the upper lateral teeth of *Cosmopolitodus hastalis* in being more robust and strongly inclined distally, even compared with the cases with similar profile (e.g., Kim et al., 2018; Yun, 2020). Lastly, the root on CNUNHM-F341 is massive and bears rounded mesial and distal root lobes, and this rounded form strongly differs from narrower and square root lobes on *Cosmopolitodus hastalis* (e.g., Kuga, 1985; Karasawa, 1989; Nazarkin, 2013). Thus, the referral of

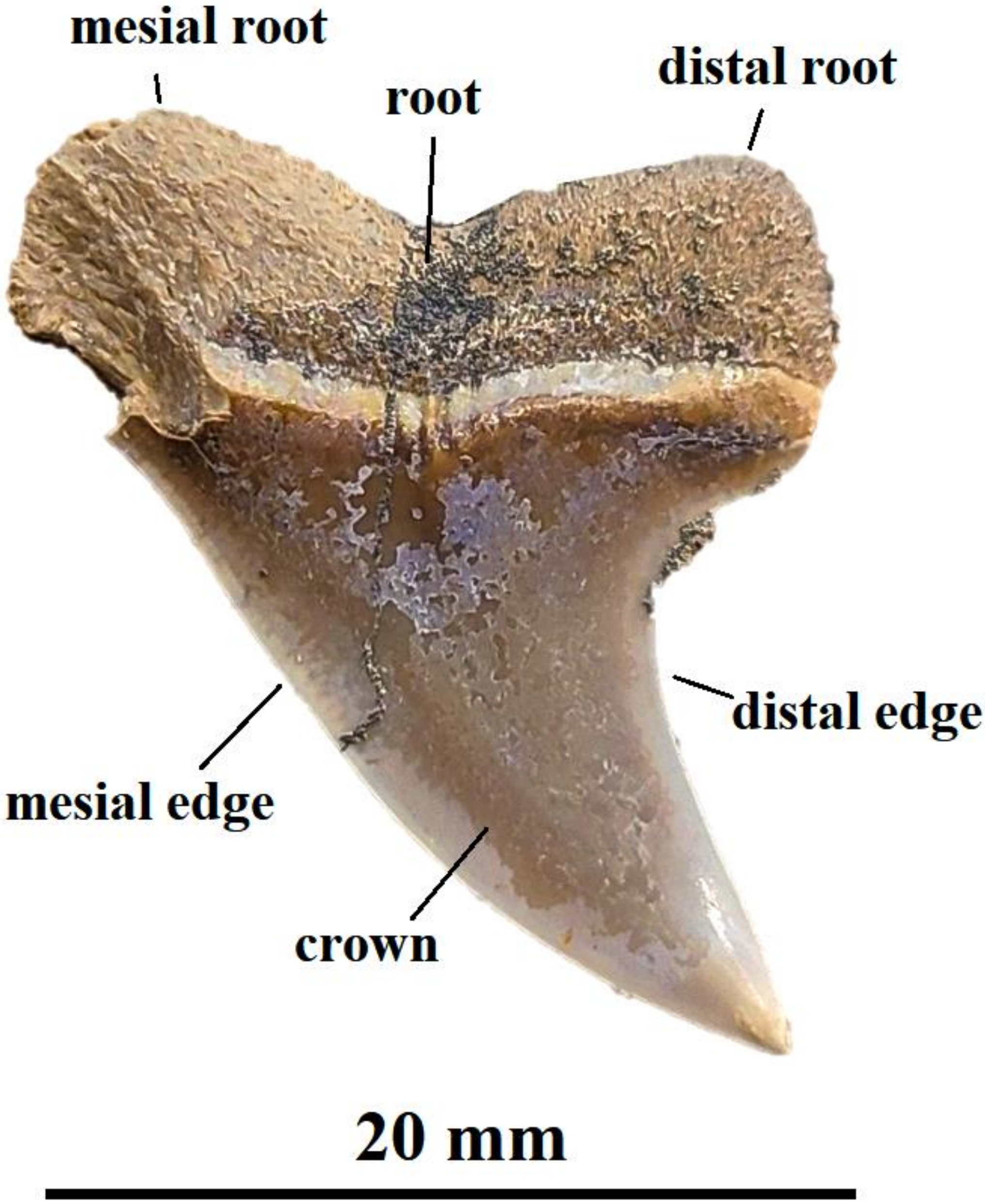

Fig. 3 Detail of CNUNHM-F341, a *Cosmopolitodus planus* tooth, in labial view.

CNUNHM-F341 to *Cosmopolitodus planus* can be confidently justified.

The hooked nature of the main cusp of specimen CNUNHM-F341 suggests it was from the left palatoquadrate of the shark. Furthermore, the height and mesiodistal width of the main cusp, the degree of distal inclination, and the overall size of suggests it is either from an upper intermediate or posterior tooth file, as described upper anterior and larger upper lateral teeth of *C. planus* generally have a mesiodistally wider and taller main cusp (e.g., Nazarkin, 2013). The possibility also exists that the specimen may have been derived from a juvenile individual.

DISCUSSION

Taxonomic note: In this work, *planus* is considered as a species of *Cosmopolitodus*. This taxon was originally erected by Agassiz (1856) as *Oxyrhina plana*, but was later placed within the genus *Isurus* by Jordan (1907). Although the placement of this species within *Isurus* has been followed by nearly all subsequent studies (e.g., Kuga, 1985; Karasawa, 1989; Boessenecker, 2011; Nazarkin, 2013), recent researchers such as Cappetta (2012) have expressed doubt as to whether the *planus* morphology should remain within this genus. Others have suggested the possibility that the *planus* morphology might be synonymous with *Cosmopolitodus hastalis* (Agassiz, 1838) (e.g., Leriche, 1908; Karasawa, 1989), the latter being generally considered as more closely related to white sharks (i.e., *Carcharodon*) as opposed to mako sharks (i.e., *Isurus*) (e.g., Cappetta, 2012; Ebersole et al., 2017; Yun, 2020). While this possible synonymy is not accepted by most recent studies (e.g., Cappetta, 2012; Nazarkin, 2013; Yun, 2020), it nevertheless reflects the striking similarities between these two taxa. Because of the morphological similarities between the teeth of *C. hastalis* and the *planus* morphology, some studies have suggested that the so called "wide-toothed" lamnid sharks (e.g., *C. plicatilis* (Agassiz, 1843), *C. hastalis*) should include "*Isurus*" *planus*, and should be assigned to the genus *Cosmopolitodus* (e.g., Cione et al., 2012; Staig et al., 2015). While the combination "*Cosmopolitodus planus*" has appeared in media such as in an online website (e.g., Bourdon, 2001-2007) or in an abstract (Malyshkina et al., 2021) these are not valid combination nova under the code of ICZN (ICZN, 1999), nor are they peer-reviewed or provide detailed reasons for this recombination. Therefore, this recombination is formally suggested here to reflect the likely close relationship of this taxon with other species of the genus *Cosmopolitodus*. From a morphological perspective, the referral of the *planus* morphology to *Cosmopolitodus* appears justified because the teeth of all members of the genus are united by a set of characteristics that include their often large size, lack of serrations, overall triangular shape of the tooth crown, labiolingually flattened morphology of the tooth, and mesiodistally wider and more distally hooked main cusp in upper files (e.g., Nazarkin, 2013). Additionally, all referred lower teeth of *C. planus* share a mesiodistally narrower and less inclined cusp compared with the upper teeth, and these characters are also present in *C. hastalis* (Kuga, 1985). Lastly, the degree of bifurcation of the root lobes in referred *C. planus* lower teeth closely matches the condition seen in *C. hastalis* (Kuga, 1985). However, the similarities in the lower teeth should be treated as provisional, as *C. planus* is a taxon erected upon upper lateral tooth characters (Agassiz, 1856), and no associated dentition of this species have been reported so far.

Of note, Ehret et al. (2012) classified *Cosmopolitodus* as a junior subjective synonym of *Carcharodon*, as these authors considered the type species of this genus, *C. hastalis*, as ancestral to the modern *Carcharodon carcharias*. However, this classification has not been universally accepted, mainly based on the fact that teeth belonging to both *Cosmopolitodus hastalis* and *Carcharodon carcharias* have been documented from the same deposits, hence the former cannot be a chronospecific ancestor of the latter (e.g., Collareta et al., 2017; Ebersole et al., 2017; Kim et al., 2018; Yun, 2020).

Kent (2018) proposed to include all *Cosmopolitodus* lineages within the genus *Carcharodon* in order to prevent the genus *Carcharodon* being paraphyletic, in which the latter genus was named earlier. However, although it is generally assumed that *Cosmopolitodus* is closely related to *Carcharodon* (e.g., Cappetta, 2012; Cione et al., 2012; Ehret et al., 2012), the idea that the *Carcharodon* lineage with serrated teeth evolved from an unserrated, *Cosmopolitodus* morphotype has never been tested through phylogenetic analyses, and it is thus still uncertain whether the serrated *Carcharodon* morphotype evolved from a narrow, fully serrated ancestor or from a broad crown with unserrated edges (Kent, 2018). Additionally, as already mentioned, *Cosmopolitodus* and *Carcharodon* are coeval and their fossil records start at approximately the same time during the middle Miocene (Ebersole et al., 2017), which may indicate that they share an earlier common ancestor and do not form a single evolutionary lineage (J. Ebersole. pers. comm. to C.-G. Yun, 2020). Thus, *Cosmopolitodus* is here considered both a distinct and a valid genus.

Paleobiological implications: *Cosmopolitodus planus* teeth have been reported from upper Oligocene to middle Miocene deposits of Australia, and middle to upper Miocene deposits of California (USA), Mexico, the Sakhalin Island (Russia), and Japan (e.g., Kuga, 1985; Yabumoto & Uyeno, 1994; Nazkarin, 2013). These records suggest that *Cosmopolitodus planus* was a widely distributed taxon throughout the Pacific Ocean in the Neogene Epoch.

Yun (2020) reconstructed a preliminary assemblage of the fossil sharks in the Duho Formation in South Korea based on the peer reviewed literature and conference abstracts, and found that teeth possibly belonging to *Cosmopolitodus planus* had been excavated from this unit. Additionally, Malyshkina et al. (2021) referred some shark teeth from the Duho Formation to this taxon in a conference abstract. Although these reports suggest that other *Cosmopolitodus planus* specimens/fossils have possibly been excavated from the formation, these specimens were not formally described or figured, and some of them reside in a private collection (Yang, 2013). Thus, the recognition of CNUNHM-F341 as *Cosmopolitodus planus* represents the first confirmed occurrence of this taxon from the Korean Peninsula. Additionally, outside of Japan, CNUNHM-F341 represents the second record of *Cosmopolitodus planus* in Northeast Asia, with the only other specimen being derived from Sakhalin Island in Russia (Nazkarin, 2013). Based on comparisons with known Neogene shark assemblages from Japan and a preliminary list of shark fossils from the Duho Formation, Yun (2020) hypothesized that epipelagic or pelagic sharks were already distributed throughout the East Sea during the middle Miocene when this sea was at the early stage of development.

Kim et al. (2018) and Yun (2020) reported teeth of *Cosmopolitodus hastalis* from the Duho Formation that are rather small for the species, suggesting that they were derived from young individuals. The small size of CNUNHM-F341 suggests it, too, may be from a juvenile individual, which would make all the recognized lamnid fossils in the region representing young individuals. Collareta et al. (2017) suggested that, like their extant counterparts such as juvenile *Carcharodon carcharias*, young individuals of extinct lamnids like *Cosmopolitodus* mainly lived and foraged in shallow marine environments. Based on this suggestion as well as on the inferred depositional model of the Duho Formation, Kim et al. (2018) considered their young specimen of *Cosmopolitodus hastalis* to represent a tooth transported into deep-sea by turbiditic currents. However, because even a small amount of transport by waves could extensively damage a shark tooth (Jovanović et al., 2019), such idea of a turbiditic transport may contrast with the relatively well-preserved nature of CNUNHM-F341. Furthermore,extant juvenile lamnids like *Carcharodon carcharias* have been reported at depths of 1000 m (Bruce & Bradford, 2008) as they occasionally forage on bottom-dwelling fish or batoids (Grainger et al., 2020).This suggests an alternative explanatory model for the occurrence of these teeth: they may have belonged to specimens that dwelled in open oceanic environments or considerably deeper waters. However, as long as the majority of the elasmobranch assemblage from the Duho Formation remains undescribed, at this time very little can be confidently said about which model of occurrences of shark teeth is more plausible. Hopefully, continued fieldwork on the Duho Formation will reveal additional fossils that can potentially explain this unresolved problem.

Modern *Carcharodon carcharias*, including juveniles, forage on a variety of vertebrates including pelagic, benthopelagic, benthic fishes, and occasionally even on other sharks and on marine mammals (e.g., Grainger et al., 2020), and it is expected that the diet spectrum of the different *Cosmopolitodus* species was largely similar (e.g., Bianucci et al., 2010; Collareta et al., 2017). Numerous bony fish fossils, both described and undescribed, have been recovered from the Duho Formation since several decades and attributed to a variety of different clades (Choi & Lee, 2017; Kim et al., 2018; Nam et al., 2019). Additionally, rostra of kentriodontid and platanistid dolphins were described from the Duho Formation (Lim, 2005; Lee et al., 2012),while some important cetacean fossils from the same formation remain undescribed (Choi & Lee, 2017). Therefore, it is reasonable to assume that the two recognized species of *Cosmopolitodus* from the Duho Formation fauna, *C. hastalis* and *C. planus*, likely foraged on all these animals.

CONCLUSIONS

An isolated lamnid shark tooth, possibly from the Duho Formation (middle Miocene) of South Korea, is described and identified as an upper lateral tooth of *Cosmopolitodus planus* (Agassiz, 1856) comb. nov. This referral was based on the presence of a distally hooked main cusp and rounded root lobes, and these features link this tooth with *Cosmopolitodus planus* comb. nov., but distinguish it from other taxa with similar tooth morphology such as *Cosmopolitodus hastalis*. While the species *planus* was generally considered as a member of the genus *Isurus*, this taxon should be considered as a species of *Cosmopolitodus* based on many shared features (e.g., large size, labiolingually flat but mesiodistally wide triangular crown) with the type species of this genus, *C. hastalis*.

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