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To cite this article: Tatiana P. Malyskina, Gi-Soo Nam & Seung H. Kwon (2022) Basking shark remains (Lamniformes, Cetorhinidae) from the Miocene of South Korea, Journal of Vertebrate Paleontology, 41:5, e2037625, DOI: [10.1080/02724634.2021.2037625](https://doi.org/10.1080/02724634.2021.2037625)

To link to this article: <https://doi.org/10.1080/02724634.2021.2037625>

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SHORT COMMUNICATION

BASKING SHARK REMAINS (LAMNIFORMES, CETORHINIDAE) FROM THE MIOCENE OF SOUTH KOREA

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

Citation for this article: Malyshkina, T. P., G.-S. Nam, and S. H. Kwon. 2022. Basking shark remains (Lamniformes, Cetorhinidae) from the Miocene of South Korea. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2021.2037625

Recent basking sharks (Cetorhinidae) are plankton-feeders, filtering huge volumes of water through their gills (Compagno et al., 2005). In the fossil state, they are represented by teeth, gill rakers, scales, vertebrae, and partial skeletons (Hovestadt and Hovestadt-Euler, 2012). The family Cetorhinidae includes three genera: the extinct genera *Keasius* Welton, 2013a (middle Eocene to middle Miocene), *Caucasochasma* Prokofiev & Sytchevskaya, 2018 (Oligocene, Rupelian), and the extant *Cetorhinus* Blainville, 1816 (Miocene to Recent). To date, four species have been described in the genus *Keasius*: *K. parvus* (Leriche, 1908) (upper Rupelian (Oligocene) Boom Clay of Belgium), *K. septemtrionalis* Reinecke, Von Der Hocht and Dufraing, 2015, *K. rhenanus* Reinecke, Von Der Hocht and Dufraing, 2015 (Oligocene and lower Miocene of Germany), *K. taylori* Welton, 2013a (upper Eocene of Oregon, USA). *Keasius* (until 2013 attributed to *Cetorhinus*) occurs in the middle Eocene of Antarctic (Cione and Reguero, 1998) and West Siberian Basin (Malyshkina, 2006), middle-upper Eocene of Sakhalin (Nazarkin, 2014) and Kamchatka (Nazarkin and Malyshkina, 2020), in the Oligocene to the upper middle Miocene of Europe (Leriche, 1910; Reinecke et al., 2001, 2015; Hovestadt and Hovestadt-Euler, 2012; Kovalchuk and Barkaszi, 2021) and North America (Jordan and Hannibal, 1923; Cappetta, 2012; Welton, 2013a).

Caucasochasma is a monospecific genus; the species *C. zherikhini* is found exclusively in the Rupelian of the North Caucasus (Prokofiev and Sytchevskaya, 2018).

The recent genus *Cetorhinus* is represented by one extant species, *C. maximus* (Gunnerus, 1765), which has a circumglobal range, both in oceans and in seas, including the north-west Pacific (Rigby et al., 2021). In the fossil record this genus known from the Miocene of Europe, Japan, Sakhalin and North America (Leriche, 1908; Uyeno and Matsushima, 1974; Uyeno et al., 1983; Van Der Bruggen, 2005; Welton, 2013b, 2014, 2015; Nazarkin, 2014). Several nominal extinct species of *Cetorhinus* have been described from the Oligocene–Pliocene of Europe but are recognized as synonyms of *C. maximus* or nomina dubia (Cappetta, 2006). Two species are described in the U.S.A.: *C. huddlestoni* Welton, 2014

(middle Miocene of California) and *C. piersoni* Welton, 2015 (lower Miocene of Oregon).

Cetorhinus huddlestoni was described from isolated teeth and vertebrae and *C. piersoni* is based only on teeth. The gill rakers were not described for either species. These species have only been recorded from their type localities.

In the middle Miocene sediments of the Duho Formation in the Pohang area of South Korea, a single cetorhinid tooth was found, which we have attributed to *Cetorhinus huddlestoni*. In the same deposit, *Cetorhinus* gill rakers have been found, which differ from previously described cetorhinids. Since the gill rakers have a unique set of features and are found in the same sediments, we attribute them to the same species. Thus, this article describes for the first time the gill rakers of *C. huddlestoni* together with the tooth.

LOCALITY, MATERIAL, AND METHODS

The Duho Formation (Fig. 1) is 150–200 m in thickness. It consists of mudstone, siltstone, shale, and sandstone (Yun, 1986; Yoon, 1992). The sediments have been formed in open ocean, deep-water conditions (Sohn et al., 2001). The mudstone yields abundant fossil plants, nannoplankton, dinocysts, foraminifers, mollusks, ophiuroid, osteichthyans, and sharks (Kim et al., 1982, 2018; Chun, 2004; Lim, 2005; Nam and Nazarkin, 2018; Malyshkina et al., 2021; Yun, 2021), and is dated as middle Miocene (Lee et al., 1992; Bak et al., 1996), or about 15 Ma (Lee et al., 1992).

All the specimens are deposited in the Gongju National University of Education, Gongju, South Korea (GNUE) with collection numbers GNUE32901, GNUE32902, GNUE32903, GNUE32914, GNUE32916 (gill rakers) and GNUE32915 (oral tooth mold).

The dental and gill raker nomenclature and measurements are based on Welton (2013a).

Anatomical Abbreviations—**B**, base; **Ba**, basal angle; **Beb**, basal edge of base; **Bh**, height of the raker base; **Bi**, bight; **Bis**, bight shape; **Bh**, base height; **Bw**, base weight; **Bl**, base length; **Cfb**, curvature of the filament base; **Deb**, distal edge of the base; **Dpb**, distal protuberance of base; **F**, filament; **For**, foramina; **Mp**, medial process; **Mpl**, length of the medial process; **Tme**, total mesial edge; tooth, **P**: **CH**, crown height; **CW**, crown weight; **RH**, root height; **RW(TW)**, root weight (total weight); **TH**, total height.

*Corresponding author.

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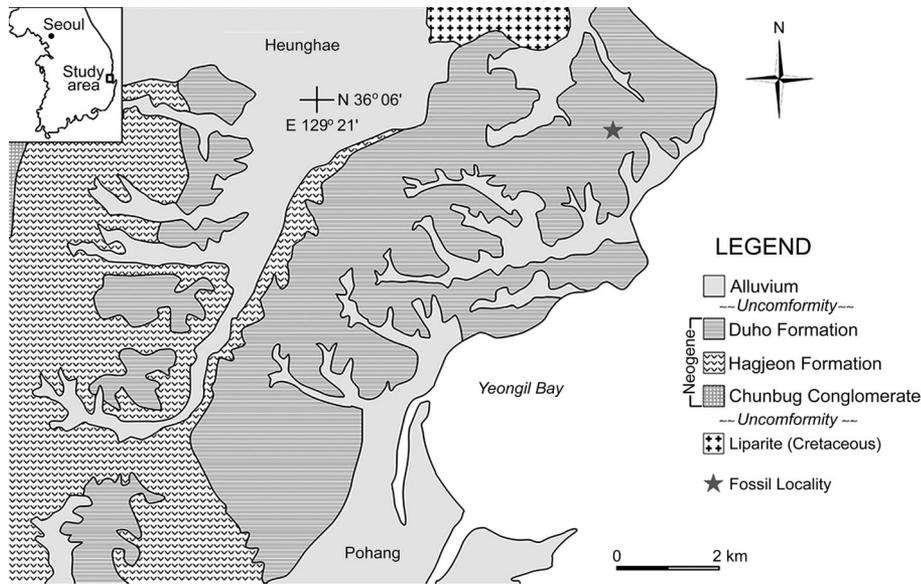


FIGURE 1. Sketch map of South Korea showing geology of Pohang area and position of the fossil locality.

SYSTEMATIC PALEONTOLOGY

Order LAMNIFORMES Berg, 1958
 Family CETORHINIDAE Gill, 1861
 Genus *CETORHINUS* Blainville, 1816

Differential Diagnosis—Established on gill rakers, dentition, and vertebrae, see Welton, 2013a.

† *CETORHINUS HUDDLESTONI* Welton, 2014
 (Fig. 2)

Cetorhinus cf. maximus Welton, 2013b:6, fig. 6.
Cetorhinus huddlestoni Welton, 2014:32 (original description).

Description

Tooth—The specimen GNUE32915 (Fig. 2A) is the well-preserved mold of the labial surface of the tooth 6.9 mm in height. The crown is narrow and rather slender for cetorhinid tooth, 4.0 mm in height and 2.6 mm in width, slightly crescent-shaped, with rounded tip. The additional cusplets are not present, probably as result of erosion. The crown-root junction is almost straight. The root, 2.9 mm in height and 3.9 mm in width, is bilobed. The arch of the root is wide, shallow, U-shaped. The nutritive groove forms a notch in the center of the arch. The root lobes are short, narrow, the mesial lobe is rounded, the distal one is more acuminate. The root lateral edges are subparallel. There are numerous large foramina on the labial root surface, mainly in the root center and on both lobes.

Gill Rakers—We follow the nomenclature of Welton (2013a: fig. 11). For measurements see Table S1.

GNUE32901 (Fig. 2C, H). F is weakly curved near the base, upper inclines mesially. Beb is of medium length, slightly rounded. Dpb is not prominent; the Deb is short, vertical. Mp has medium length and triangle shape with straight distal edge and slightly rounded mesial edge. Tme is slightly rounded. Amp is sharp. Ba is subangular, sharp. Bi is subangular, U-shaped, intermediate.

GNUE32902 (Fig. 2D, I). F is strongly curved near base, vertical in the middle part and inclines distally in the upper part. Beb of the base is short, straight. Dpb is not prominent, Deb is high, vertical. Mp has medium length and triangle shape with straight edges. Amp is sharp. Tme is straight. Ba is subangular, sharp. Bi is subangular, U-shaped, long and narrow.

GNUE32903 (Fig. 2E, J). F is weakly curved in the lower part then inclined mesially. Beb is slightly rounded, of medium length. Dpb is not prominent. Mp is of medium length, triangular with straight edges. Amp is sharp. Ba is subangular, sharp. Tme is straight. Bi is subangular, U-shaped, quite long and narrow.

GNUE32914 (Fig. 2F, L, M). F is broken in the middle part and moderately to strongly curved near base. Beb is short, straight. Dpb is slightly prominent. Mp is triangular, of medium length, with almost straight edges. Amp is sharp. Tme is near straight. Ba is subangular, sharp. Bi is subangular, U-shaped, long and narrow.

GNUE32916 (Fig. 2G, K). F is broken in the lower part. Beb is rounded, of medium length. Dpb is slightly prominent. Mp is of medium to long length, triangular with straight edges. Tme is straight. Ba is subangular and sharp. Bi is subangular, U-shaped, long and narrow.

DISCUSSION

Teeth

The features distinguishing *Cetorhinus* teeth from those of *Keasius* are: their larger size, narrow high crowns with a single apex, lateral edges of the teeth are often parallel or subparallel (Welton, 2013a). On the basis of these characters, the tooth GNUE32915 described here is referred to *Cetorhinus*. It differs from teeth of *C. maximus* in its slender shape with subparallel crown edges, passing into the root edges, and clearly defined root branches. From *C. piersoni* GNUE32915, it differs in being larger, slender in shape with subparallel lateral edges of the crown and root, and having a taller and more slender root. GNUE32915 fully consistent with teeth of *C. huddlestoni* illustrated by Welton (2014). According to the TH/TW ratio (Welton, 2015:fig. 11) the tooth GNUE32915 with a TH/TW

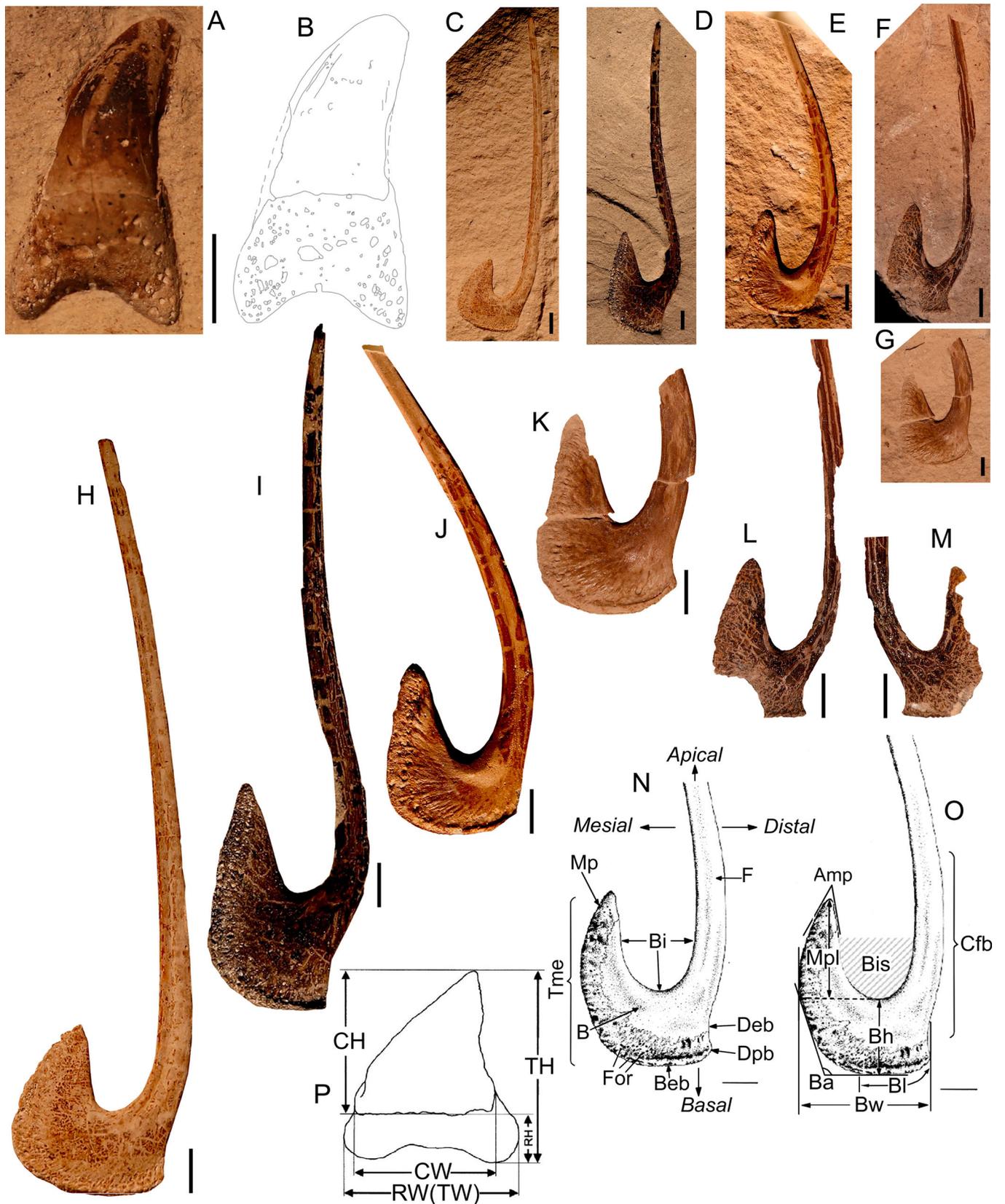


FIGURE 2. **A–M**, *Cetorhinus huddlestoni* from the middle Miocene of Duho Formation, Pohang area, South Korea. **A**, GNUE32915, imprint of tooth labial side; **B**, drawing of the GNUE329015; **C–G**, the gill rakers on the matrix; **H–M**, gill rakers cutting by PhotoShop ordered presumably from distal to medial positions on the branchial arch; **C** and **H**, gill raker GNUE32901; **D** and **I**, gill raker GNUE32902; **E** and **J**, imprint of gill raker GNUE32903; **F**, **L**, and **M**, gill raker GNUE32914; **L**, part, **M**, counterpart of the lower part; **G** and **K**, gill raker GNUE32916. **N**, *Cetorhinus maximus* gill raker structure and descriptive terminology, adapted from Welton (2013a); **O**, measurements of gill raker on example *C. maximus*, adapted from Welton (2013a); **P**, measurements of tooth on example *C. maximus*, from Welton (2013a). Scale bars equal 2 mm.

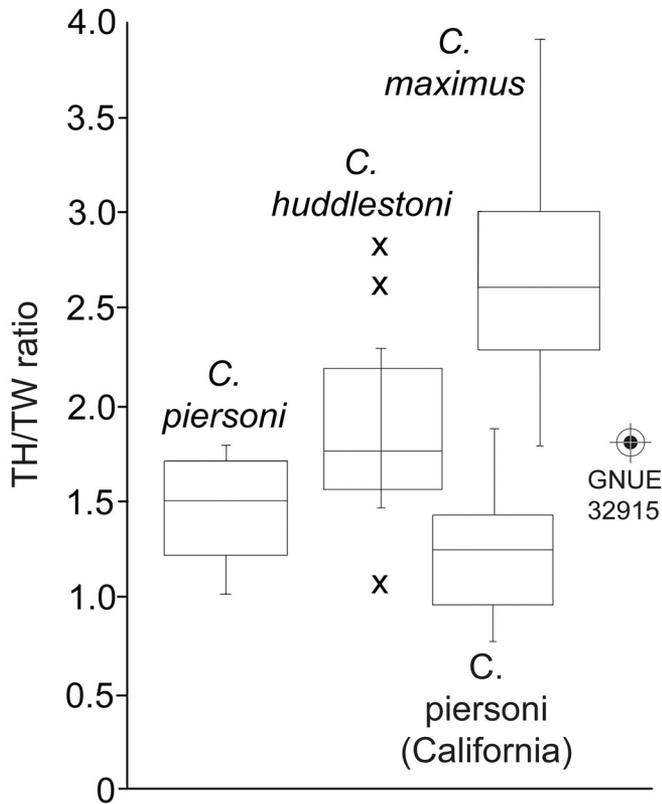


Figure 3. Comparison of teeth of all known *Cetorhinus* species redrawn from Welton (2015, Fig. 11D) and added by GNUE32915 from Duho Fm. Box-and-whisker plots of TH/RW ratios for *C. maximus* (n=52), *C. huddlestoni* (n=23), *C. piersoni* (n=23), teeth referred to *C. piersoni* (California) (n=22), GNUE32915.

ratio of 1.8 lies statistically in the sample of *C. huddlestoni* and does not correspond to other species of *Cetorhinus* (Fig. 3).

Gill rakers

Kovalchuk and Barkashi (2021) claim that gill rakers are of low diagnostic value of because of their intraspecific variability. In our opinion, the gill rakers are species-specific, but when diagnosing it is necessary to take into account their position on the branchial arch, as one does with teeth around a shark's jaw. Based on the rows of gill rakers (Hovestadt and Hovestadt-Euler, 2012; Welton, 2013a), it can be concluded that from the periphery to the central part of the arch in both *Keasius* and *Cetorhinus*, the raker base becomes narrower and lower, the bight is narrower and deeper, the medial process is longer and directed distally. Comparing the gill rakers from Duho Fm with other taxa (see below), we considered the position of the rakers on the gill arch, based on the reported gill raker variability of *K. parvus* (Reinecke et al., 2001:pl. 36, 38; 2015:fig. 16; Hovestadt and Hovestadt-Euler, 2012:fig. 10), *K. septentrionalis* (Reinecke et al., 2015:fig. 11), and *C. maximus* (Hovestadt and Hovestadt-Euler, 2012:fig. 9; Welton, 2013a). The suggested order from the periphery to the center of the branchial arch is shown in Figure 2, from H to M, respectively. It should be noted that because of the limited number of works describing complete rows of gill rakers, the problem of the specific diagnostic of the cetorhinids requires further research.

Welton (2013a) identified several features that distinguish the gill rakers of *Cetorhinus* from those of *Keasius*: a longer medial process, a broadly rounded sub-triangular bight, and a narrow zone of attachment. These characteristics make it possible to classify the gill rakers from Duho Fm as *Cetorhinus*.

One of the most obvious differences between the gill rakers from Duho and *C. maximus* is sub-angular and acute basal angle (70–80°) in Duho specimens, and obtuse or right, often rounded in the gill rakers of *C. maximus*. The distal protuberance is well developed in all gill rakers of *C. maximus* and is not prominent in the Duho specimens. Hovestadt and Hovestadt-Euler (2012:fig. 9) described the rows of the *C. maximus* gill rakers of the Recent juvenile male, pre-adult female and adult female. One of the principal differences between the gill rakers from Duho and those of *C. maximus* is the subangular and sharp basal angle and less prominent distal protuberance. In addition, from the rakers of Recent young male *C. maximus* (Hovestadt and Hovestadt-Euler 2012:fig. 9a–h) the rakers from Duho differ in more robust medial process and a more distinct basal angle and straight mesial edge of the bight. From the gill rakers of adult females the rakers from Duho differ in possessing a straight mesial edge of the bight (Hovestadt and Hovestadt-Euler 2012:fig. 9i–l) and shorter medial process (Hovestadt and Hovestadt-Euler 2012:fig. 9p–u). The same differences may be observed with gill rakers of two types of Recent *C. maximus* (Siccardi, 1961). The gill rakers of *C. cf. maximus* from Pliocene of Belgium (Van der Bruggen, 2005) are very similar to those of a Recent adult male of *C. maximus* (Welton, 2013a). From both the descriptions in Siccardi (1961) and Van der Bruggen (2005), the Duho gill rakers differ by having a straight mesial edge of the bight, straight mesial edge of the medial process, basal edge of the base and acute basal angle. The gill raker described by Uyeno and Matsushima (1974) from lower Pleistocene of Hokkaido, clearly differs from the Duho specimens by the wide rounded bight. The gill raker from the lower Miocene of the Netherlands (Everaert et al., 2019) differs from Duho specimens by the rounded edges of bight, convex mesial edge of the base and directed distally medial process. The gill raker from middle-upper Miocene of Sakhalin Island (Nazarkin, 2014:fig.1c) in comparison with samples from Duho formation has a very high and narrow base, narrow bight with convex mesial edge, and rounded mesial edge of the base.

The gill rakers from Duho Fm differ from the rakers of *Caucasochasma* (Prokofiev and Sychevskaya, 2018:fig. 3); the latter have a narrower and more angular shape, a more prominent distal protuberance and concave mesial edge of the gill base.

Thus, the Duho Fm gill raker design does not correspond to any described fossil or Recent species. The presence of the *Cetorhinus huddlestoni* tooth in the Duho Formation makes it most likely that they belong to the same species. This is because there has never been more than one *Cetorhinus* species recorded in any one deposit; the same situation is observed in most other genera of large sharks.

Until now, *C. huddlestoni* was known exclusively from the middle Miocene deposits of California, which is geographically located at about the same latitude as the Duho Fm in South Korea, but on the east coast of the North Pacific. Data on modern *C. maximus* indicates that these sharks make long-distance migrations, visiting the East (Japan) Sea. Obviously, the ability to migrate is inherited by *C. maximus* from the previous species, and this behavior can be characteristic of other extinct filter-feeding sharks.

CONCLUSION

New basking shark specimens from the middle Miocene Duho Formation, Pohang, South Korea, made it possible for the first time to supplement the description of the fossil species of

basking shark *Cetorhinus huddlestoni* with information on the morphology of its gill rakers, as well as significantly expand the geographic range of this species and speculate on its ability to make long-distance migrations.

ACKNOWLEDGMENTS

We thank D. J. Ward for lengthy discussions that enhanced the quality of this paper and helping to improve the English, and M. V. Nazarkin for help in preparing the article. Editors J. Harris, C. Underwood, A. López-Arbarelo and reviewers made constructive suggestions for improvement of the manuscript. The study was funded by RFBR and National Research Foundation of Korea: research project no. 19-54-51001 under the framework of international cooperation program managed by the National Research Foundation of Korea (2019K2A9A1A0609922511), as well as State task of the IGG UB RAS no. AAAA-A18-118052590025-8.

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Submitted August 18, 2021; revisions received August 18 and September 8, 2021; accepted January 7, 2022.

Handling Editor: Charles Underwood.