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Lanternfish otoliths (Myctophidae, Teleostei) from the Miocene of Japan

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Abstract

Lanternfishes (Myctophidae) are one of the most common groups of fishes in the mesopelagic zone of the world ocean, and their otoliths have been dominant in pelagic sediments since at least Miocene times. Many species have a wide geographic distribution, with several being circumglobal. This wide distribution makes myctophid otoliths potentially useful for supraregional stratigraphic purposes. The Sea of Japan and the Northwest Pacific is an important region for investigations into the diversity and evolution of the Myctophidae. Here, we describe a large collection of myctophid otoliths from the late early to early middle Miocene (late Burdigalian to early Langhian) from six localities on western and central Honshu, which were under warm water influence during that time. A total of 22 species are recognized, of which eight are new. In the order in which they are described, the new species are *Bolinichthys higashibesshoensis* **sp. nov.**, *Ceratoscopelus brevis* **sp. nov.**, *Lampadena exima* **sp. nov.**, *Lampanyctus lenticularis* **sp. nov.**, *Lampanyctus tsuyamaensis* **sp. nov.**, *Stenobrachius ohashii* **sp. nov.**, *Diaphus epipedus* **sp. nov.**, and *Diaphus watatsumi* **sp. nov.** At least nine species are also known from coeval sediments outside of Japan, most notably New Zealand and Europe. This distribution reflects the extraordinary geographic spread of myctophid species already in the early Miocene and indicates the potential for their future use for biostratigraphic purposes. The paleoecological and paleobiogeographical implications of the studied myctophid otolith assemblages are discussed. Furthermore, the stratigraphic ranges of the observed species are discussed and compared with data from other regions of the world in an attempt to outline the potential future application of myctophid otoliths for supraregional biostratigraphic purposes.

Keywords

North Pacific, *Diaphus*, biostratigraphy, paleobiogeography, Honshu, new species

1. Introduction

During the late early and middle Miocene, much of Japan was submerged under the seas of the Northwest Pacific (Ogasawara 1994). Large parts of the terrain of Honshu were flooded, and extensive neritic to pelagic sediments were deposited in various basins. Fossil otoliths have been collected from these sediments; and these otoliths have been described by Hatai (1965), Ohe and Araki (1973), Ohe (1977, 1981, 1990), Ohe and Yamaoka (1980), and Takahashi (1976). However, much new material has been collected from locations in western and central Honshu since these studies were conducted, and are particularly rich in lanternfish otoliths. Lanternfishes (Myctophidae) are one of the most common groups of fishes in the mesopelagic zone of the world ocean, and they have been so since at least Miocene times. Their otoliths are dominant in pelagic sediments deposited since then. Many species have a wide geographic distribution, with several of them being circumglobal, making myctophid otoliths potentially useful for supraregional stratigraphic purposes. Japan and the Northwest Pacific represents an important region in the context of myctophid evolution and is characterized today by a rich community of both circumglobal and regional species. Pliocene and Pleistocene myctophid otoliths from Japan have been reviewed by Schwarzhans and Ohe (2019). Here, we review the rich myctophid otolith assemblages from late Burdigalian to early Langhian of western and central Honshu. In our opinion, this otolith assemblage represents an important cornerstone for both future supraregional correlations of fish faunas in a paleobiogeographic sense as well as potential biostratigraphic purposes.

We recognize 22 myctophid species in this collection, of which eight are new to science and five remain in open nomenclature. At least nine species are also known from coeval sediments outside of Japan, most notably New Zealand and Europe, which reflects the extraordinary geographic spread of these species.

2. Geological setting, material, and methods

2.1. Sampling localities

The otoliths were obtained from six localities, of which two are located in the western region of Honshu in Okayama Prefecture (Fig. 1), three are onshore from the Ise Bay in Mie and Gifu Prefectures (Fig. 2A–D), and one borders the Sea of Japan in Toyama Prefecture (Fig. 2E, F). The geographic distribution of these sampling localities from the southwest to the northeast are as follows:

1. - Niimi (Fig. 1A): Road cut on local road near Tesseicho Hattori about 15 km southwest of Niimi Station of the JR Hakubi Line, Niimi City, Okayama Prefecture (PE3102; Fig. 3A). The sampled interval is from the Upper Member (Watanabe and Ishigaki 1986) of the Bihoku Group (Itabashi Formation in Fig. 4; see also Watanabe et al. 1999).
2. - Tsuyama (Fig. 1B): Exposures along the Miya River (Miyagawa) banks directly east of the Mimasaka University complex up to the bridge of the Chugoku Expressway across the Miya River at Numa and the riverbanks 1,500 m north of the bridge at Oda, Tsuyama City, Okayama Prefecture. The sampled section, which consists of 23 levels and was measured in detail by Ujihara (Fig. 3B), belongs to the Takakura Formation of the Katsuta Group (Fig. 4) (see also Watanabe et al. 1999).
3. - Makino River (Fig. 2A): Outcrops along the riverbanks of the Makino River (Makinogawa) 1,200 m southwest of Mashino, Iga City, Mie Prefecture. Levels A 1 and A 2 correspond respectively to locations M1 and M2 in Nishimatsu (2019). The section and sampling intervals have been described in detail by Nishimatsu (2019) and belong to the Makino Formation of the Awa Group (Fig. 4).
4. - Inabacho (Fig. 2C): Outcrops along the riverbanks of the Nagano River (Naganogawa) at Inabacho, Tsu City, Mie Prefecture. The sampled intervals (ML2304, ML2305, and OA1409; Fig. 3C) are from the Katada Formation, Ichishi Group (Oshida et al. 2018; Fig. 4).
5. - Mizunami (Fig. 2B): Small exposure at Okuna about 4 km northeast of Mizunami Station of the JR Chuo Line (Fig. 2B), Mizunami City, Gifu Prefecture, corresponding to location 62 in Itoigawa (1980). The samples were obtained from the basal transgressive Nataki Member of the Oidawara Formation, Mizunami Group (Itoigawa 1980; Kawamura et al. 2011; Fig. 4).
6. - Toyama (Fig. 2E): River floor of the Kubusu River (Kubusugawa) at Kashio (level K 5), Yatsuo machi, Toyama City, Toyama Prefecture; cliff along the Yamada River (Yamadagawa) at Dojima (level H 14), Fuchu machi, Toyama City; and stream beds of a brooklet at Osedani (levels H 20 and H 21), Fuchu machi (Fig. 2E). Levels K 5, H 14, H 20, and H 21 correspond respectively to locations K 5, H 14, H 20, and H 21 in Nishimatsu and Ujihara (2020). The otoliths were obtained from the Kurosedani and Higashibessho formations of the Yatsuo Group (Fig. 4). For a detailed stratigraphic assessment, see Yanagisawa (1999) and Nakajima et al. (2019).

The distribution and abundance of the observed myctophid otoliths are summarized in Table 1.

2.2. Stratigraphy and biostratigraphic correlation

The studied myctophid otoliths stem from formations of late Burdigalian to early Langhian age, all within the planktonic foraminifer zone N8 and spanning the range of the northern Pacific diatom zones 2B to 4A of Yanagisawa and Akiba (1998) (Fig. 4). The stratigraphic correlation is based on Yanagisawa (1999), Nakajima et al. (2019), and Irizuki et al. (2021). With respect to the N7/N8 boundary, we follow the geochronological timescale established by Hoshi et al. (2019) in Japan of approximately 17 Ma (compared to 16.39 Ma in GTS 2020; Gradstein et al. 2020). The studied otoliths were obtained from the following stratigraphic units.

Bihoku Group

The stratigraphy of the Bihoku Group has been studied by, inter alia, Imamura et al. (1953), Itoigawa and Nishikawa (1976), and Ueda (1986). Imamura et al. (1953) subdivided the Bihoku Group in the Miyoshi-Shobara area, Hiroshima Prefecture, into the Lower Sandstone Member and the

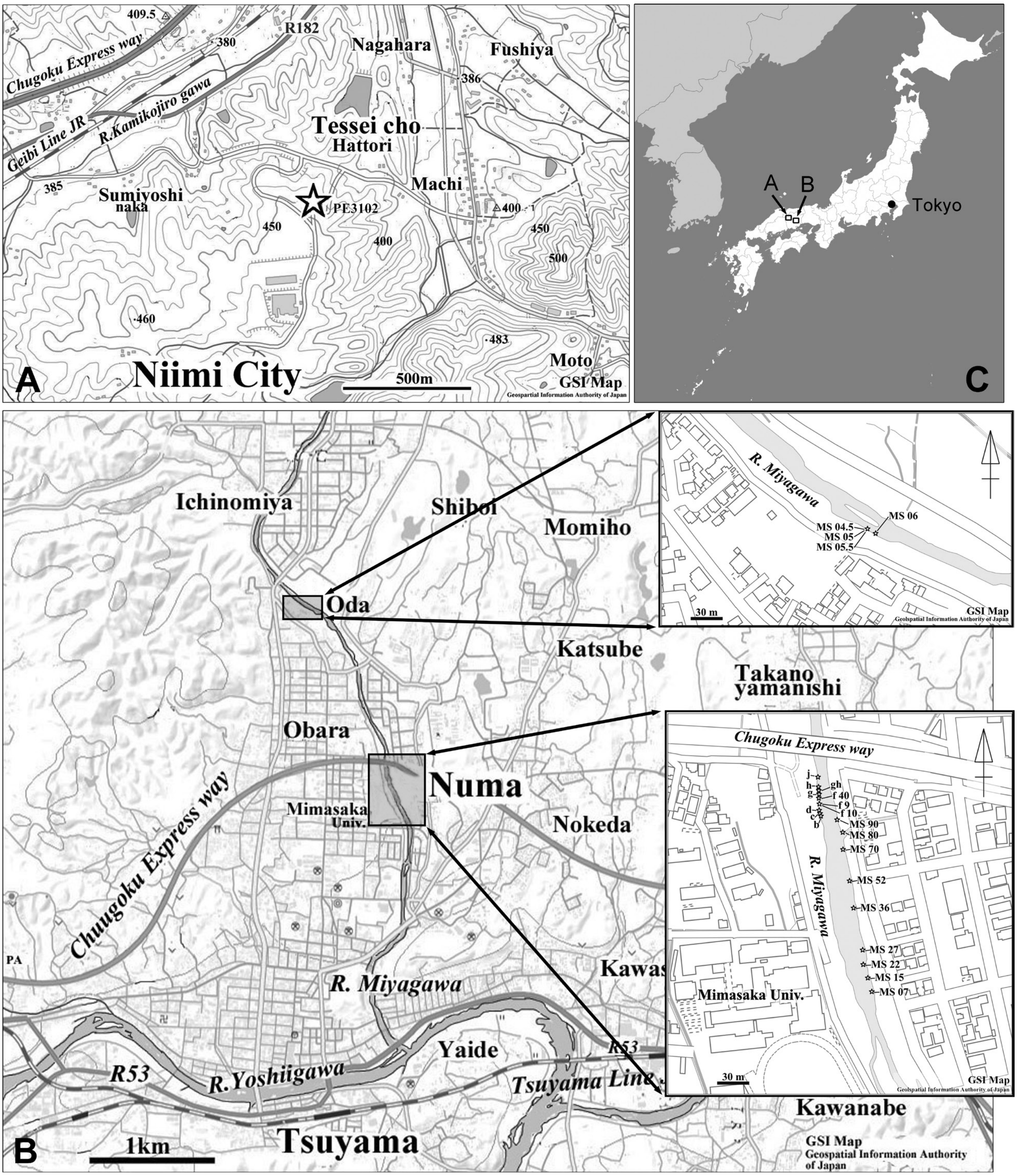

Figure 1. Location map for Niimi City (**A**) and Tsuyama City (**B**) and index map (**C**). Based on the topographic map of the Geospatial Information Authority of Japan, 2021.

Upper Shale Member. Ueda (1986) defined the strata corresponding to the Lower Sandstone Member and the Upper Shale Member in the Shobara area as the Korematsu Formation and the Itabashi Formation, respectively.

Watanabe and Ishigaki (1986) subdivided the Bihoku Group in the western part of Niimi City into the Lower, Middle, and Upper members. The otoliths were collected from the Upper Member. The Upper Member is mainly composed of mudstones and is correlated to the Upper Shale Member of the group in the Miyoshi Shobara area. Watanabe and Ishigaki (1986) suggested a continental slope position for the depositional environment of the member based on the molluscan assemblage. Watanabe et al. (1999) assigned the upper part of the Bihoku Group in the Koyamaichi area, Okayama Prefecture, which presumably correlates with the Upper Member of Watanabe and Ishigaki (1986), to diatom zone NPD3A (upper part) to NPD3B (lower part) of Yanagisawa and Akiba (1998).

Table 1. Distribution of myctophid species in the studied samples from the early to middle Miocene of Japan. Sequence from left to right corresponds to sequence of description of localities from southwest to northeast. Two specimens (*Myctophum* sp. and *Diaphus* sp.1) have been obtained form a location not covered in this study and will be described later by one of us (YT) and hence are not shown in this table.

Localities	**Niimi**	**Tsuyama**	**Makino R.**	**Mizunami**	**Inabacho**	**Toyama**	**Toyama**	**Totals**
Diatome Zones	3A	3A–3B	(3A)	(4A)	(3A)	(2B–3A)	3A–4A	
Planktonic Foraminifer Zones	N8	N8 upper	N8 lower	N8 upper	N8 lower	N8 lower	N8 upper	
Myctophinae								
Diogenichthys aguilerai		1						**1**
Myctophum murbani		20		1				**21**
Protomyctophum ahunga		158					2	**160**
Lampanyctinae								
Bolinichthys higashibesshoensis							2	**2**
Ceratoscopelus brevis		4					2	**6**
Lampadena exima		1						**1**
Lampanyctus lenticularis		33						**33**
Lampanyctus profestus		1						**1**
Lampanyctus tsuyamaensis		18						**18**
Stenobrachius ohashii	4	221				4	5	**234**
Taaningichthys sp.		1						**1**
Diaphinae								
Diaphus angulatus					1		1	**2**
Diaphus epipedus		7					2	**9**
Diaphus metopoclampoides		6		2			4	**12**
Diaphus watatsumi		11						**11**
Diaphus biatlanticus		5		2				**7**
Diaphus cassidiformis				20		60		**80**
Diaphus hataii	4	459	243	931	91	2	14	**1744**
Diaphus sp.2				2				**2**
Gymnoscopelinae								
Notoscopelus kuboensis		36		3	1		2	**42**
Totals	**8**	**982**	**243**	**961**	**93**	**66**	**34**	**2389**

Katsuta Group

The stratigraphy of the Katsuta Group has been studied by, inter alia, Takeyama (1930), Tamura (1957), Kawai (1957), and Taguchi (2002). Kawai (1957) subdivided the Katsuta Group into the Uetsuki, Yoshino, and Takakura formations in ascending order. The otoliths described here were collected from the Takakura Formation.

The Takakura Formation is mainly composed of mudstones in its lower part and alternating sandstones and mudstones in its upper part. Taguchi (2002) inferred that the lower part of this formation was deposited in an environment with a water depth of about 200 m based on the molluscan assemblage. No macrofossils have been found in the upper part of the Takakura Formation, with the exception of plant fragments. Taguchi (2002) assumed that this section was deposited in an environment with a water depth of over 200 m based on lithofacies. Watanabe et al. (1999) correlated the Takakura Formation with the diatom zone NPD3A (upper part) or NPD 3B (lower part) of Yanagisawa and Akiba (1998).

Awa Group

The stratigraphy of the Awa Group has been studied by, inter alia, Araki (1960a), Itoigawa (1961), and Fujiwara et al. (2005). According to Fujiwara et al. (2005), the Awa Group consists of the Higashitanihata, Hiramatsu, and Makino formations in ascending order. The otoliths described here were collected from the Makino Formation.

The Makino Formation is mainly composed of pebbly mudstones and more than 50 m thick (Fujiwara et al. 2005). Molluscs (Itoigawa 1961; Shibata 1978) and elasmobranchs (Nishimatsu 2019) have been described from this formation. Shibata (1978) found co-occurring shallow-water and deep-sea molluscs in the pebbly mudstones of the Makino Formation and assumed that the shallow-water elements were transported into a deep-water environment. Yoshida (1987) correlated the Makino Formation with the planktonic foraminifera zone N8 of Blow (1969), and Fujiwara et al. (2005) concluded that this formation lies within the planktonic foraminifera zones N8–9. Fujiwara et al. (2005) also assigned the Makino Formation to the calcareous nannofossil zone CN3 of Okada and Bukry (1980).

Ichishi Group

The stratigraphy of the Ichishi Group has been studied by, inter alia, Takimoto (1935), Araki (1960b), Shibata (1967), and Yoshida et al. (1995). Shibata (1967) subdivided the Ichishi Group into the Haze, Oi, and Katada formations in ascending order. The otoliths described here were obtained from the Katada Formation.

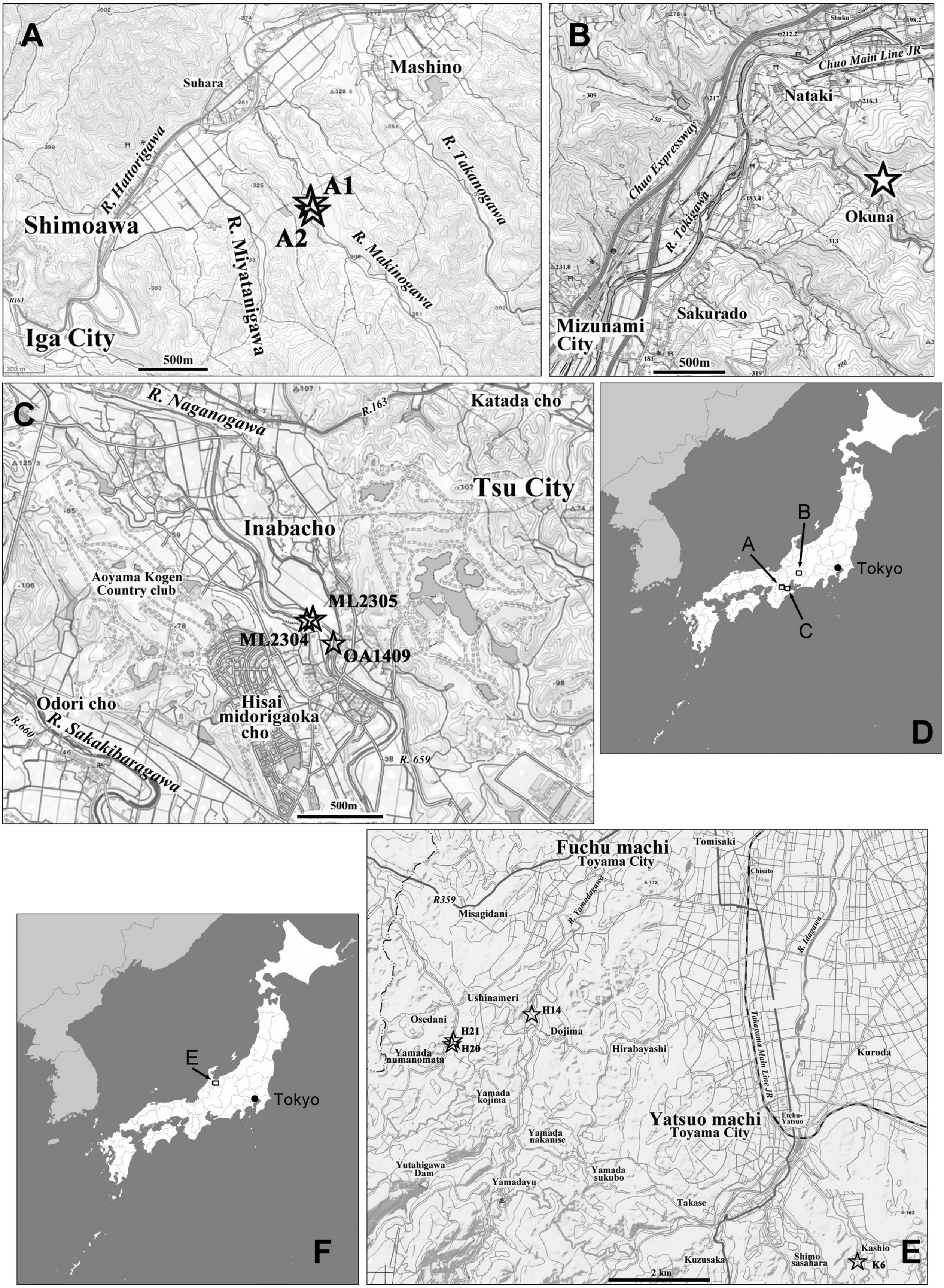

Figure 2. Location map for Makino, Iga City (**A**), Okuna, Mizunami City (**B**), and Inabacho, Tsu City (**C**) with index map (**D**), and Yatsuo machi and Fuchu machi, Toyama City (**E**) with index map (**F**). Based on the topographic map of the Geospatial Information Authority of Japan, 2021.

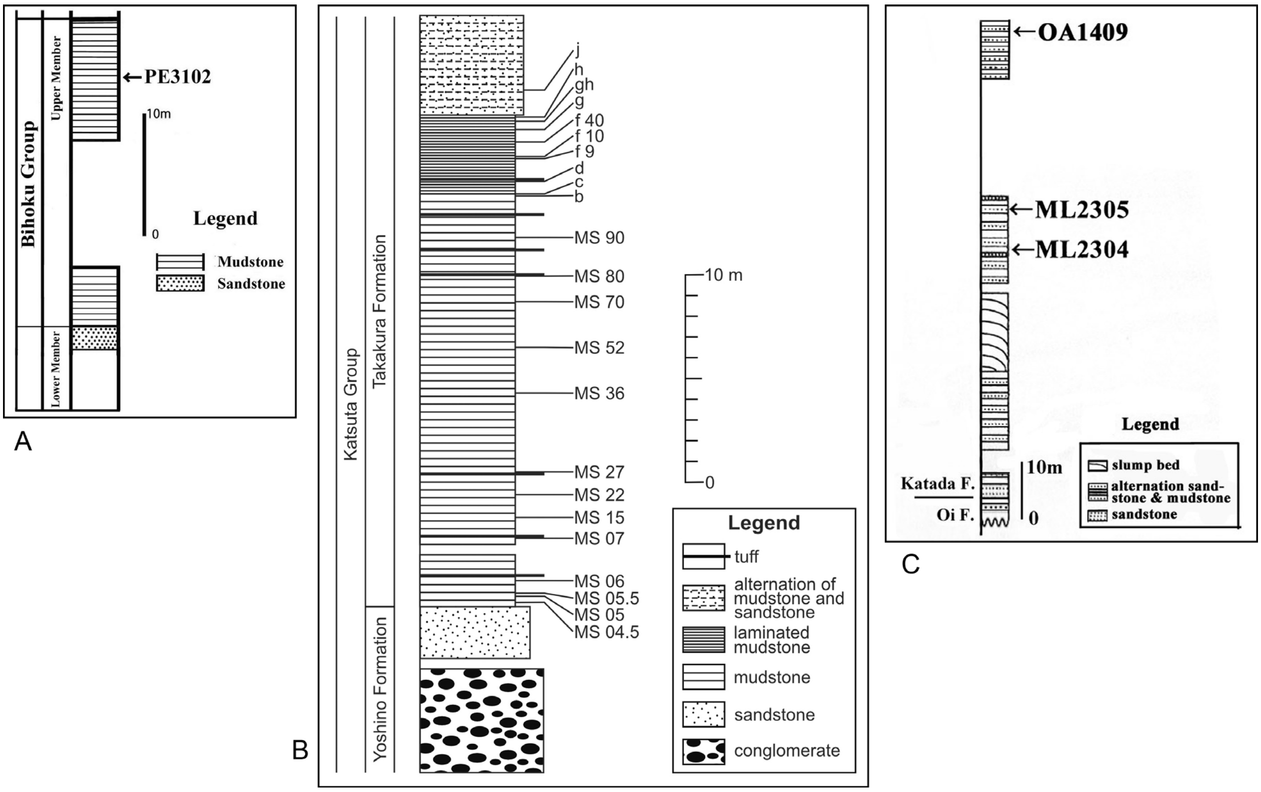

Figure 3. Stratigraphic columns of sampled sections in Niimi City (**A**), Tsuyama City (**B**), and Tsu City (**C**).

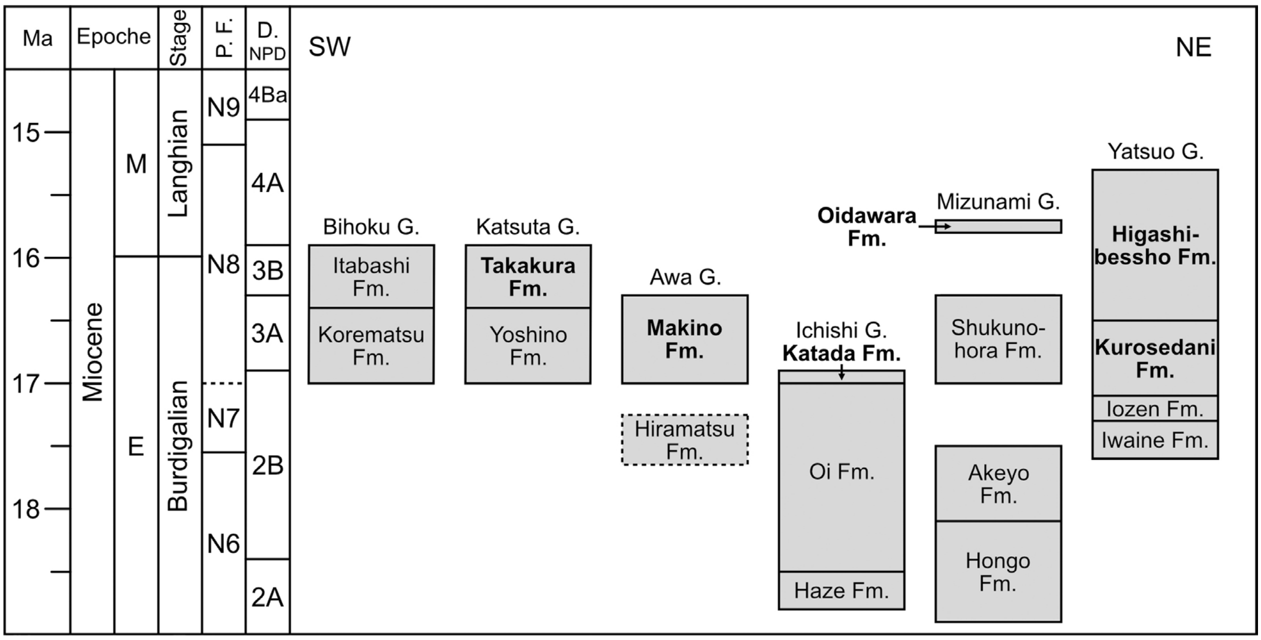

Figure 4. Stratigraphic correlation chart of sampled intervals. The correlation follows the six locations in the described sequence from southwest to northeast. The chronostratigraphy follows the GTS2020 (Gradstein et al. 2020), with the exception of the N7/N8 boundary, which follows Hoshi et al. (2019). The planktonic foraminifer zones (P.F.) are from Blow (1969). The diatom zones (D.NPD) follow Yanagisawa and Akiba (1998). The stratigraphic correlation is based on Yanagisawa (1999), Nakajima et al. (2019), and Irizuki et al. (2021).

The Katada Formation is mainly composed of sandstones and mudstones, with mudstones being predominant at the sampling locality. This formation is approximately 250 m thick (Shibata 1967). Shibata (1970) described the deep-sea molluscan assemblages from the Katada Formation, while Yoshida (1991) and Oshida et al. (2018) assigned the Katada Formation to the planktonic foraminifera zone N8. Hoshi et al. (2019) obtained the U-Pb ages of 17.03±0.11 Ma for the tuff layers in the uppermost part of the Oi Formation which more or less corresponds to the boundary of the planktonic foraminifera zones N7/N8, and 17.09±0.06 Ma for the tuff layer in the upper part of the Katada Formation.

Mizunami Group

The stratigraphic classification of the Mizunami Group was established by Itoigawa (1974) and has since been widely referred to; it was partially revised by Irizuki and Hosoyama (2006). Based on these studies, the Mizunami Group consists of the Toki Lignite Bed and the Hongo, Akeyo, Shukunohora, and Oidawara formations in ascending order (Itoigawa 1974; Irizuki and Hosoyama 2006). The otoliths described here were collected from the Oidawara Formation.

The Oidawara Formation is subdivided into the Nataki Member, from which the otoliths were collected, and the Oidawara Member (Itoigawa 1974). The Nataki Member consists of conglomerates and is only a few meters thick. A variety of fossils, including molluscs (e.g., Itoigawa 1960; Itoigawa et al. 1974; Shibata and Itoigawa 1980), benthic foraminifera (Seto 1992), and fish otoliths (Takahashi 1976), have been described from the Nataki Member. Shibata and Itoigawa (1980) noted that the Nataki Member contains many shallow-water molluscs. In contrast, Seto (1992) inferred that the Nataki Member was deposited in a relatively deep environment based on the analysis of benthic foraminifera. Kawamura et al. (2011) considered the Oidawara Member to represent the diatom zone NPD4A (lower part) of Yanagisawa and Akiba (1988) and concluded that it was deposited during a very short time period from 15.7 to 15.8 Ma.

Yatsuo Group

Many stratigraphic studies have been conducted on the Yatsuo Group since the original work of Makiyama (1930). Hayakawa and Takemura (1987) considered the Yatsuo Group to be composed of the Nirehara, Iwaine, Iozen, Kurosedani, and Higashibessho formations in ascending order. They subdivided the Higashibessho Formation into the Tochiage, Shiotani, Asatani, and Mitani members. The otoliths described here were collected from the Kurosedani Formation and the Tochiage and Shiotani members of the Higashibessho Formation.

The Kurosedani Formation consists of conglomerates alternating with sandstones and mudstones (Hayakawa and Takemura 1987) and is up to approximately 900 m thick (Hayakawa and Takemura 1987). Mudstones form the predominant lithology at the sampling locality. The Higashibessho Formation conformably overlies the Kurosedani Formation (Hayakawa and Takemura 1987) and is approximately 600 m thick (Nakajima et al. 2019). The Tochiage Member is mainly composed of mudstones, while the Shoitani Member is characterized by sandstones.

The Kurosedani and Higashibessho formations are rich in fossils, such as molluscs (e.g., Tsuda 1960; Shimizu et al. 2000; Amano et al. 2004), benthic foraminifera (e.g., Chiji 1954; Hasegawa and Takahashi 1992), ostracods (Ozawa 2016), and elasmobranchs (e.g., Nishimatsu and Ujihara 2019, 2020). The sampling horizons of the Kurosedani and Higashibessho formations seem to have been deposited in a wide range of sublittoral to bathyal depths based on an analyses of benthic foraminifera, molluscs, and ostracods (Hasegawa and Takahashi 1992; Shimizu et al. 2000; Ozawa 2016).

Yanagisawa (1999) placed the Higashibessho Formation in the diatom zones NPD3A–4A of Yanagisawa and Akiba (1988). Tamaki et al. (2006) correlated a reversed polarity interval in the upper part of the Kurosedani Formation to Chrone C5Cn.2r and reversed polarity intervals in the Higashibessho Formation to chrons C5Cn.2r, C5Cn.1r, and C5Br in correlation with the diatom stratigraphy of Yanagisawa (1999). Yoshida et al. (2019) obtained an $^{87}Sr/^{86}Sr$ age of 17.02 ± 0.27 Ma for tusk-shell concretions collected from the upper part of the Kurosedani Formation. Using the U-Pb method, Nakajima et al. (2019) obtained an age of 16.6±0.2 Ma and FT method of 16.4±1.2 Ma for the Yamadanaka Tuff, which is located in the uppermost part of the Kurosedani Formation.

2.3. Methodology and depository

The otoliths were photographed with a Canon EOS 1000D mounted on a Wild M400 photomacroscope; the camera was remotely controlled and the photographs captured from a computer. Individual images of every view of the objects taken at ranges of field of depths were stacked using Heliconsoft's Heliconfocus software. Adjustment of exposure and contrast and retouching were performed in Adobe Photoshop where necessary in order to improve the images without altering any morphological features.

The morphological terminology follows that established by Koken (1884), with amendments by Chaine and Duvergier (1934) and Schwarzhans (1978). The morphometrics were applied as established in Schwarzhans and Aguilera (2013). The abbreviations used are as follows: OL = otolith length, OH = otolith height, OT = otolith thickness, OsL = ostium length, CaL = cauda length, OCL = length of ostial colliculum, and CCL = length of caudal colliculum.

Depository: All type-specimens and figured specimens are deposited in the Senckenberg Museum, Frankfurt am Main, Germany, under the registry SMF PO. 101.112–149.

3. Results

3.1. Systematics

The classification of the Myctophidae follows Martin et al. (2018).

Division Teleostei Müller, 1846
Order Myctophiformes Regan, 1911
Family Myctophidae Gill, 1893
Subfamily Myctophinae Fowler, 1925 (sensu Martin et al., 2018)

Genus *Diogenichthys* Bolin, 1939

Diogenichthys aguilerai Schwarzhans, 2013

Fig. 5A–C, Table 1

2013b *Diogenichthys aguilerai* – Schwarzhans: pl. 2, figs 4–5.
2019 *Diogenichthys aguilerai* Schwarzhans, 2013 – Schwarzhans: fig. 50.12.
2021 *Diogenichthys aguilerai* Schwarzhans, 2013 – Schwarzhans and Nielsen: fig. 7a–d.

Material. A single specimen (SMF PO 101.112) from Miya River at Oda, Tsuyama City, Okayama Prefecture, late Burdigalian, diatom zone 3A–3B, Takakura FM, level MS 04.5.

Discussion. *Diogenichthys aguilerai* is an unspectacular and small high-bodied myctophid otolith with a ratio OL:OH of 0.95–1.05. Its ventral rim is regularly curved and smooth; the dorsal rim is highest slightly behind its middle. Rostrum, excisura, and antirostrum are all small. The inner face is flat, and the outer face is distinctly convex and smooth. The narrow sulcus exhibits a slightly longer ostium than cauda, with the latter being underlain by a very long, anteriorly extended pseudocolliculum.

Diogenichthys aguilerai was apparently widespread during the early Miocene (Aquitanian and Burdigalian) but usually not common, with the exception of a recent find in the late Burdigalian of Chile (Schwarzhans and Nielsen 2021). It was originally described from Angola (Schwarzhans 2013b) but is also known from New Zealand (Schwarzhans 2019) and possibly also from the Caribbean (as *Diogenichthys* sp. in Schwarzhans and Aguilera 2013).

Genus *Myctophum* Rafinesque, 1810

Myctophum murbani (Weinfurter, 1952)

Fig. 5D–L, Table 1

1952 *Scopelus tenuis murbani* – Weinfurter: pl. 2, figs 1, 2.
1976 *Myctophum* sp. – Takahashi: pl. 17, fig. 4.
1994 *Hygophum murbani* (Weinfurter, 1952) – Brzobohatý: pl. 2, figs 10–15.
2013 *Myctophum murbani* (Weinfurter, 1952) – Schwarzhans and Aguilera: pl. 4, figs 5–8 (see there for further synonymies).

Material. 21 specimens: 20 specimens (figured specimens SMF PO 101.113), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 07, MS 15, MS 27, MS 36, MS 52, MS 70, MS 80, d, gh and h, late Burdigalian, diatom zone 3A–3B; 1 specimen, SMF PO 101.114, Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A.

Description. Delicate, moderately large otoliths reaching up to 3.2 mm length (Fig. 5H). OL:OH = 1.15–1.25; OH:OT = 4.0–4.3. Ventral rim well rounded, deep, very regularly curved; dorsal rim much shallower, likewise regularly curved, sometimes with very mild obliquely cut postdorsal section. Rostrum and antirostrum short, of equal length, with very small excisura in between; posterior rim regularly curved. Rostral tip and posterior tip positioned at lower margin of sulcus and distinctly supramedian. All rims delicately crenulated, ventral rim usually more intensely than dorsal rim.

Inner face distinctly convex, smooth, with distinctly supramedian, long, narrow sulcus. OL:SuL = 1.2; OCL:CCL = 1.9–2.5. Dorsal margin of ostium slightly oscillating; cauda slightly bent upwards, with angular upper-posterior termination. Caudal colliculum narrower than ostial colliculum but of equal width when incorporating underlying pseudocolliculum. Dorsal depression shallow, indistinct; ventral furrow indistinct, far from ventral rim of otolith. Outer face flat to slightly convex, less than inner face, with short radial furrows near rims and smooth central portion.

Discussion. *Myctophum murbani* belongs to a group of *Myctophum* species with oval otoliths that usually also show a strong marginal ornamentation. This group contains the extant species *M. lychnobium* Bolin, 1946, *M. obtusirostre* Tåning, 1928, *M. orientale* (Gilbert, 1913), and *M. spinosum* (Steindachner, 1867) (see Ohe 1985 and Schwarzhans and Aguilera 2013 for figures). *Myctophum murbani* is the only fossil representative of this group and differs from all of them in the more gently curving ventral rim (vs. pronounced mid-ventral angle or expansion) and the more regularly curved dorsal rim. In addition, the postdorsal termination of the cauda is less strongly bent upwards and at a less sharp angle than in the extant species. *Myctophum murbani* (Weinfurter, 1952) is a widely distributed tropical to subtropical species that occurred in the late Burdigalian to Langhian in the Caribbean, the Mediterranean, the Paratethys, and now also in Japan. Thus far, no coeval *Myctophum* otoliths are known from the southern hemisphere (i.e., New Zealand or Chile; see Schwarzhans 2019 and Schwarzhans and Nielsen 2021).

Myctophum sp.

Fig. 5M–O

Remarks. An additional, relatively large *Myctophum* species of about 3.5 mm in length is observed in the Ichishi Group and will be described separately by one of us (YT). It is characterized by a regularly rounded outline and a relatively long rostrum.

Genus *Protomyctophum* Fraser-Brunner, 1949

Protomyctophum ahunga Schwarzhans, 2019

Fig. 5P–Z, Table 1

2019 *Protomyctophum ahunga* – Schwarzhans: figs 51.1–5.
2021 *Protomyctophum ahunga* Schwarzhans, 2019 – Schwarzhans and Nielsen: fig. 7i–m.

Material. 160 specimens: 158 specimens (figured specimens SMF PO 101.115), Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 06, MS 07, MS 15, MS 22, MS 27, MS 36, MS 52, MS 70,

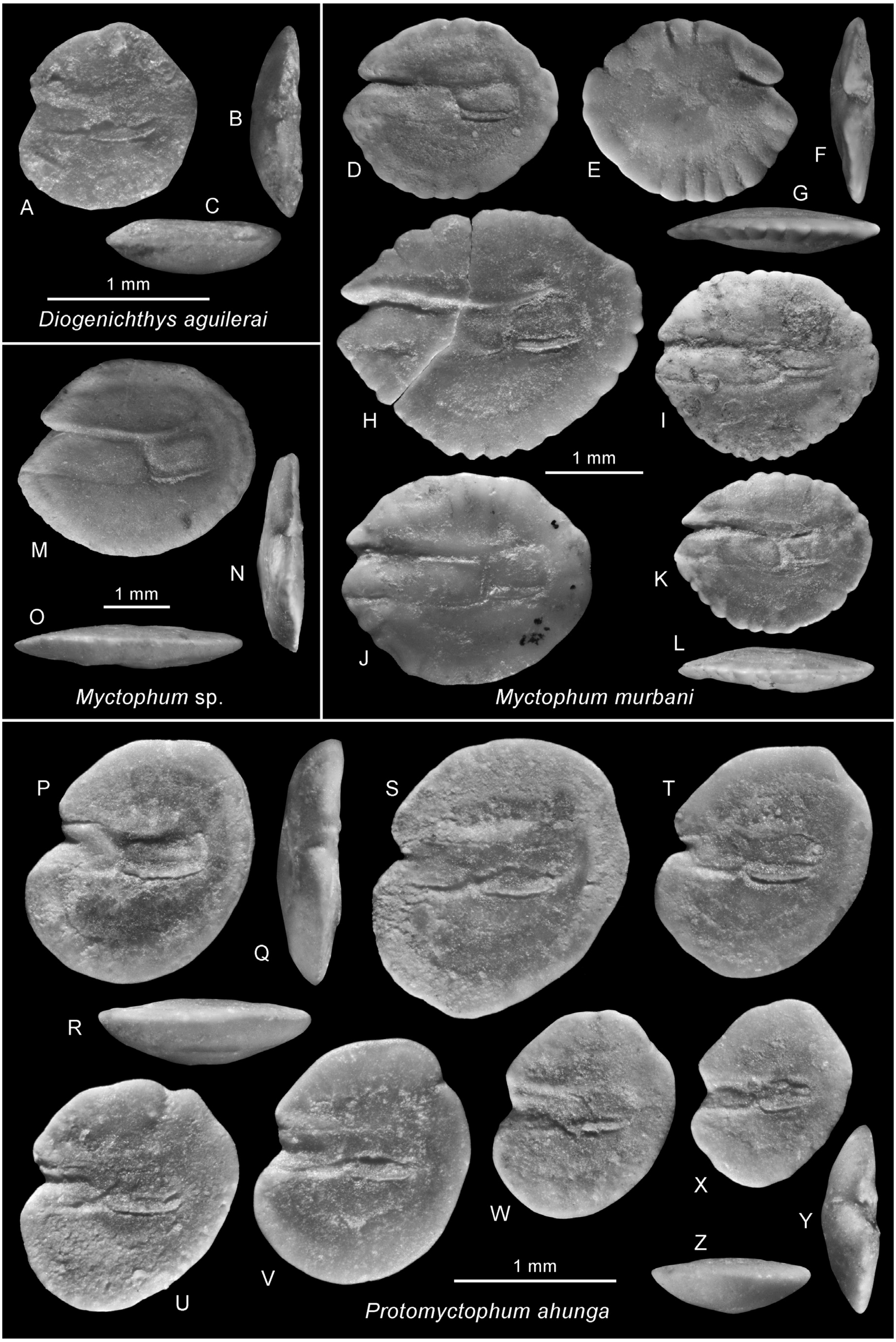

Figure 5. A–C: *Diogenichthys aguilerai* Schwarzhans, 2013, SMF PO 101.112, Tsuyama City, Takakura Formation, level MS 04.5; **D–L:** *Myctophum murbani* (Weinfurter, 1952); **D–I, K–L;** SMF PO 101.113, Tsuyama City, Takakura Formation, levels MS 15, MS 27, MS 52, h, J) SMF PO 101.114 Mizunami City, Oidawara Formation; **M–O:** *Myctophum* sp., col. Tsuchiya, Ichishi Group; **P–Z:** *Protomyctophum ahunga* Schwarzhans, 2019, SMF PO 101.115, Tsuyama City, Takakura Formation, levels MS 15, MS 22, MS 36, h.

MS 80, MS 90, b, d, f9, f10, f40, g, gh, h and j, late Burdigalian, diatom zone 3A–3B; 2 specimens, Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 20, late Burdigalian to early Langhian, diatom zone 3A–4A.

Discussion. For a detailed description, see Schwarzhans (2019) and the subsequent update in Schwarzhans and Nielsen (2021). *Protomyctophum ahunga* is a typical and rather common species in the late Burdigalian of New Zealand and Chile but has not been found in coeval sediments of the Caribbean (Trinidad or Venezuela). Its common occurrence in late Burdigalian to early Langhian sediments of Japan indicates that it may have had an antitropical distribution in the Pacific Ocean during the late early and early middle Miocene.

Subfamily Lampanyctinae Paxton, 1972
Genus *Bolinichthys* Paxton, 1972

Bolinichthys higashibesshoensis sp. nov.

http://zoobank.org/A7B69D07-807A-42AC-AC17-1E9FDBED029D

Fig. 6A–D, Table 1

Etymology. Named after the type formation Higashibessho FM.

Holotype. SMF PO 101.116 (Fig. 6A–D), Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 20, late Burdigalian to early Langhian, diatom zone 3A–4A.

Paratype. One specimen, SMF PO 101.149, same location as holotype, level H 21.

Diagnosis. OL:OH = 1.25. Ventral rim shallow with 4 denticles anteriorly; dorsal rim shallow, smooth. Rostrum inferior, long, rounded, distinctly longer than antirostrum, 18% of OL. OCL:CCL = 1.85. Inner face flat; outer face convex, smooth.

Description. A well preserved and very typical otolith with rounded parallelogram-like outline of 1.8 mm length. OH:OT = 4.0. Ventral rim shallow, anteriorly pronounced and there with 4 broad, rounded denticles; dorsal rim shallow, smooth, with distinct, rounded postdorsal angle at junction with oblique, smooth posterior rim. Rostrum very broad, inferior, with rounded tip, distinctly longer than antirostrum. Antirostrum far dorsally shifted, short, pointed; excisura relatively deep, angular.

Inner face completely flat, with more or less centrally positioned, narrow and relatively shallow sulcus. Ostium nearly twice as long as cauda (OCL:CCL = 1.85). Dorsal margin of ostium straight, oriented slightly upward towards anterior; ventral margin of ostium distinctly concave and curved. Cauda slightly upward oriented; its pseudocolliculum extending forward beyond caudal colliculum. Ventral furrow weak, close to ventral rim of otolith. Dorsal depression large with indistinct boundary except towards sulcus with distinct crista superior. Outer face moderately convex, entirely smooth.

Discussion. *Bolinichthys higashibesshoensis* is a typical species of the genus and cannot be confused with any of the few fossil species of the genus: the late Miocene *B. italicus* (Anfossi & Mosna, 1971) is characterized by a pointed rostrum and the lack of an excisura; *B. kreffti* Schwarzhans, 1986 from the early Pliocene differs in its outline and the more undulating and extended nature of the ventral rim and also shows a straight ostium. Both species have been found in sediments along the Mediterranean, and *B. higashibesshoensis* hence represents the only fossil species from the Pacific. *Bolinichthys higashibesshoensis* resembles extant otoliths of the genus but is more compressed than most of them, with the exceptions of *B. distofax* Johnson, 1975 (Fig. 6E) and *B. supralateralis* (Parr, 1928) (see Brzobohatý and Nolf 2000 for figure), from which it differs in the relatively shorter rostrum, the deeper excisura, and the oscillating ventral margin of the ostium. The latter character is found in certain other extant *Bolinichthys* species, notably *B. indicus* (Nafpaktitis & Nafpaktitis, 1969) and *B. longipes* (Brauer, 1906), from which, however, it differs in the other abovementioned characters.

Genus *Ceratoscopelus* Günther, 1864

Ceratoscopelus brevis sp. nov.

http://zoobank.org/A593637F-5B26-4AA9-98E6-2E45A98C8B85

Fig. 6F–M, Table 1

Etymology. From brevis (Latin) = short, referring to the compressed shape of the otoliths.

Holotype. SMF PO 101.117 (Fig. 6J–M); Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 15, late Burdigalian, diatom zone 3A–3B.

Paratypes. 3 specimens (SMF PO 101.118), same location as holotype, levels MS 07, MS 22, MS 52.

Tentatively assigned specimens. 2 poorly preserved specimens from Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 21 may also represent this species and are tentatively assigned.

Diagnosis. OL:OH = 1.25–1.35. Rostrum moderately long with rounded tip, 18–22% of OL. Dorsal, posterior and ventral rims all continuously curved. OCL:CCL = 1.8–2.5. Outer face with radial furrows close to rims and smooth, slightly bulged central region set off by circular furrow.

Description. Small, delicate otoliths reaching about 2.25 mm in length (holotype 1.8 mm). OH:OT = 3.6–3.8. Dorsal rim gently curving without marked angles, continuously curving into rounded posterior and ventral rims around posterior reaches of otolith. Rostrum massive, broad, moderately long (18–22% of OL), with rounded tip; no or minute antirostrum and excisura. All rims slightly undulating.

Inner face nearly flat, with long, distinctly supramedian, shallow positioned sulcus; OL:SuL = 1.25. Ostium about twice as long as cauda (OCL:CCL = 1.8–2.5), straight and slightly wider. Caudal colliculum oval, underlain by slightly anteriorly shifted pseudocolliculum. Ventral furrow variable in expression and position; dorsal depression narrow, indistinct except towards crista superior. Outer face slightly convex with radial furrows along rims and characteristic smooth central area set off from rest of outer face by distinct circular furrow.

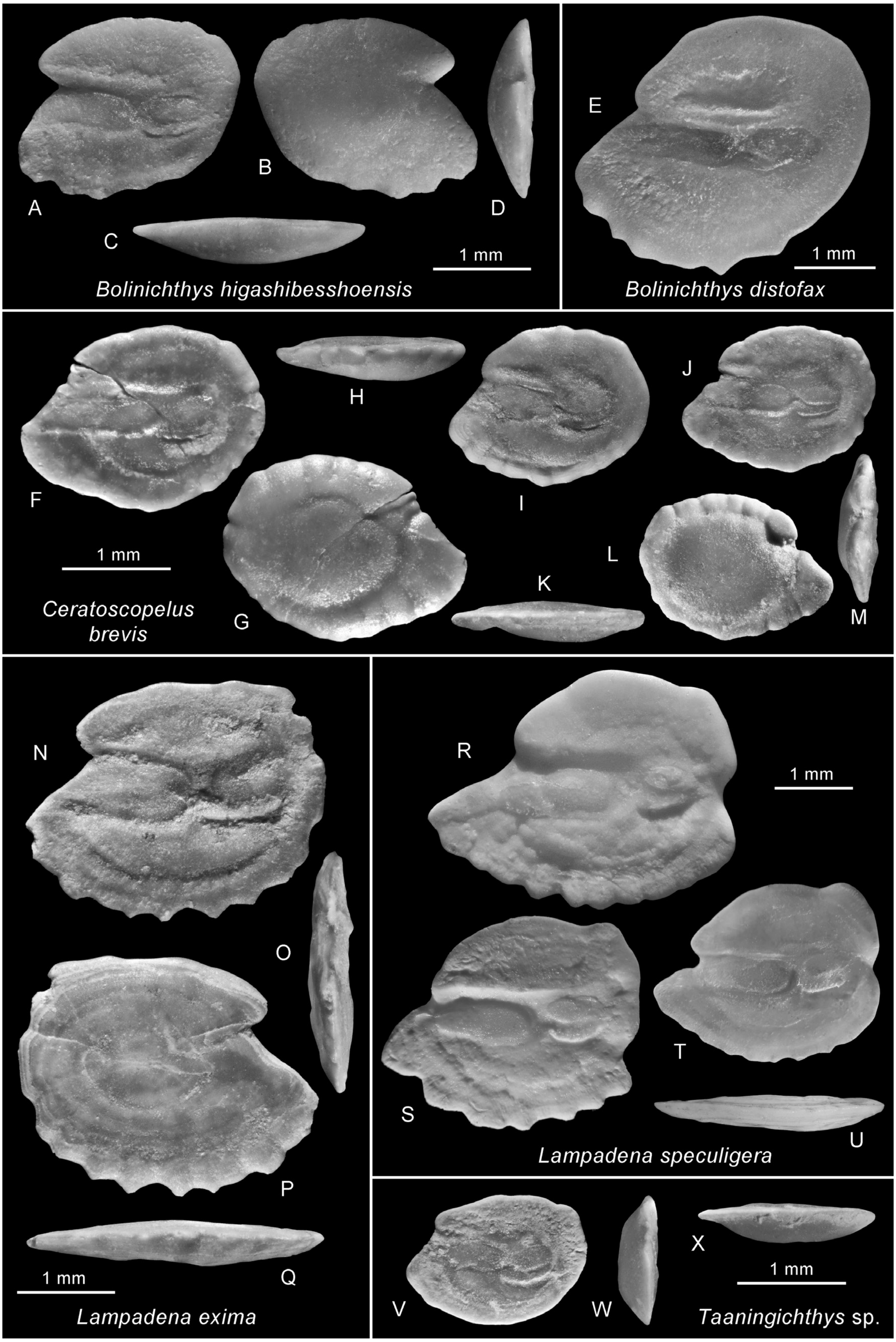

Figure 6. A–D: *Bolinichthys higashibesshoensis* sp. nov., holotype, SMF PO 101.116, Fuchu machi, Toyama City, Higashibessho Formation, level H 20; **E:** *Bolinichthys distofax* Johnson, 1975, coll. Schwarzhans, Recent, Walter Herwig R/V, station 459-71; **F–M:** *Ceratoscopelus brevis* sp. nov., Tsuyama City, Takakura Formation; **J–M:** holotype, SMF PO 101.117, level MS 15; **F–I:** paratypes, SMF PO 101.118, levels MS 7, MS 52; **N–Q:** *Lampadena exima* sp. nov., holotype, SMF PO 101.119, Tsuyama City, Takakura Formation, level MS 36; **R–U:** *Lampadena speculigera* Goode & Bean, 1896, Recent; **R:** coll. Schwarzhans, Walter Herwig R/V, 38°S, 54°W; **S:** MCZ 169474; **T–U:** MCZ 96917; **V–X:** *Taaningichthys* sp., SMF PO 101.120, Tsuyama City, Takakura Formation, level MS 27.

Discussion. Otoliths of *C. brevis* are typical of those of *Ceratoscopelus* otoliths with the flat inner face and the long rostrum paired with minute antirostrum and excisura. *Ceratoscopelus brevis* differs from the three extant species by being more compressed and the regularly curving and undulating rims and characteristic aspect of the outer face. Its proportions are similar to those of the earlier *C. richardsoni* Schwarzhans, 2019 from New Zealand but differ in the very regularly curving posterior rim section of the otolith (vs. presence of a distinct obtuse postdorsal angle). An otolith found *in situ* and described as *C. miocenicus* Bedini, Francalacci & Landini, 1986 from the late Miocene of Italy is even more compressed and shows a pointed rostrum. Otoliths described as *Ceratoscopelus* sp. from the late Burdigalian of Chile (Schwarzhans and Nielsen 2021) differ in the pronounced postdorsal angle at the junction with the posterior rim, the oblique posterior rim, and the lack of any marginal crenulation of the rims. It appears that the Miocene Epoch featured a greater diversity of the genus than that observed today (Linkowski 1997).

Genus *Lampadena* Goode & Bean, 1893

Lampadena exima sp. nov.

http://zoobank.org/890977A5-B6AA-4B35-9D76-D47608468C75

Fig. 6N–Q, Table 1

2012 *Lampadena* sp. – Brzobohatý & Stranik: fig. 7.11.

2015 *Lampadena* aff. *speculigeroides* Brzobohatý & Nolf, 1996 – Lin et al.: fig. 2.21.

Etymology. From eximus (Latin) = excellent, exemplary, referring to the good preservation and clear allocation of the type specimen.

Holotype. SMF PO 101.119 (Fig. 6N–Q); Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 36, late Burdigalian, diatom zone 3A–3B.

Diagnosis (based on holotype and measurements taken from photograph of Lin et al. 2015). OL:OH = 1.25–1.30. Rostrum massive, its length 18–22% of OL. Ventral rim broadly rounded with 6 massive denticles; dorsal rim shallow, nearly straight; posterior rim rounded. Ostium slightly inclined, slightly wider than cauda. OCL:CCL = 1.7–1.8. Caudal pseudocolliculum longer than caudal colliculum, extending forward beyond collum.

Description (based on holotype and measurements taken from photograph of Lin et al. 2015). Thin, delicate otoliths up to 3.5 mm length (holotype 3.1 mm); OH:OT = 5.2. Rostrum broad, massive, relatively long (18–22% of OL); excisura distinct, but not deep; antirostrum short and high on anterior rim. Ventral rim regularly curving, with 6 evenly spaced, massive and robust denticles; dorsal rim shallow, flat, with distinct angle at junction with regularly curved posterior rim. Posterior rim somewhat undulating but without concavity.

Otolith flat, almost not bent along axis, resulting in nearly flat inner and outer faces. Sulcus large, wide, distinctly supramedian, reaching close to posterior rim of otolith; OL:SuL = 1.1–1.2. Ostium longer and wider than cauda, slightly inclined upwards towards anterior, with ostial colliculum opening towards anterior otolith rim. Cauda short, slightly inclined upwards towards posterior. Caudal colliculum small, OCL:CCL = 1.7–1.8. Caudal pseudocolliculum longer than caudal colliculum and extending forward further than caudal colliculum. Ventral furrow distinct, positioned distant from ventral rim; dorsal depression weak, poorly defined and small. Outer face smooth with few faint, very wide radial depressions along ventral rim.

Discussion. *Lampadena exima* more closely resembles the extant *L. speculigera* Goode & Bean, 1896 than the coeval *L. speculigeroides* Brzobohatý & Nolf, 1996 from the Paratethys. It differs from *L. speculigera* (Fig. 6R–U) in the more gently curving outline, particularly the ventral and posterior rims (with the latter not being concave, as is characteristic of *L. speculigera*); the upward inclined ostium (vs. straight); the OCL:CCL relation (1.7–1.8 vs. 2.1–2.3); and the long caudal pseudocolliculum extending forward of the caudal colliculum (vs. similar in length and not forward extended). *Lampadena exima* differs from *L. speculigeroides* in being more compressed (OL:OH = 1.25–1.3 vs. 1.35–1.5), the shallower dorsal rim, the smaller number and more robust nature of the denticles along the ventral rim of the otolith (6 vs. 8 or indistinct undulations), and the relatively wide ostium.

Otoliths of *Lampadena* are among the most diverse in the myctophid genera and are relatively easy to identify. The ease with which they can be identified makes them potentially valuable for biostratigraphic purposes, but unfortunately they are also usually very rare. In any case, it is interesting to note that specimens described by Lin et al. (2015) as *L.* aff. *speculigeroides* from the Tortonian of Italy and by Brzobohatý and Stranik (2012) as *Lampadena* sp. from the Langhian of the Czech Republic seem to represent the same species as our holotype of *L. exima* from the late Burdigalian of Japan. This finding indicates a relatively wide distribution range and a relatively long stratigraphic range.

Genus *Lampanyctus* Bonaparte, 1840

Lampanyctus lenticularis sp. nov.

http://zoobank.org/2B3AE3EF-39C9-4642-B5CE-0CB84A1440AB

Fig. 7A–J, Table 1

Etymology. From lenticularis (Latin) = lens-shaped, referring to the regular outline and small size of the otoliths.

Holoytpe. SMF PO 101.121 (Fig. 7B–D), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level f9, late Burdigalian, diatom zone 3A–3B.

Paratypes. 8 specimens (SMF PO 101.122); same data as holotype, levels f9, g, h, j.

Additional material. 24 specimens; same data as holotype, levels MS 15, MS 36, MS 52, MS 70, d, f9, f40, g, gh, h, j.

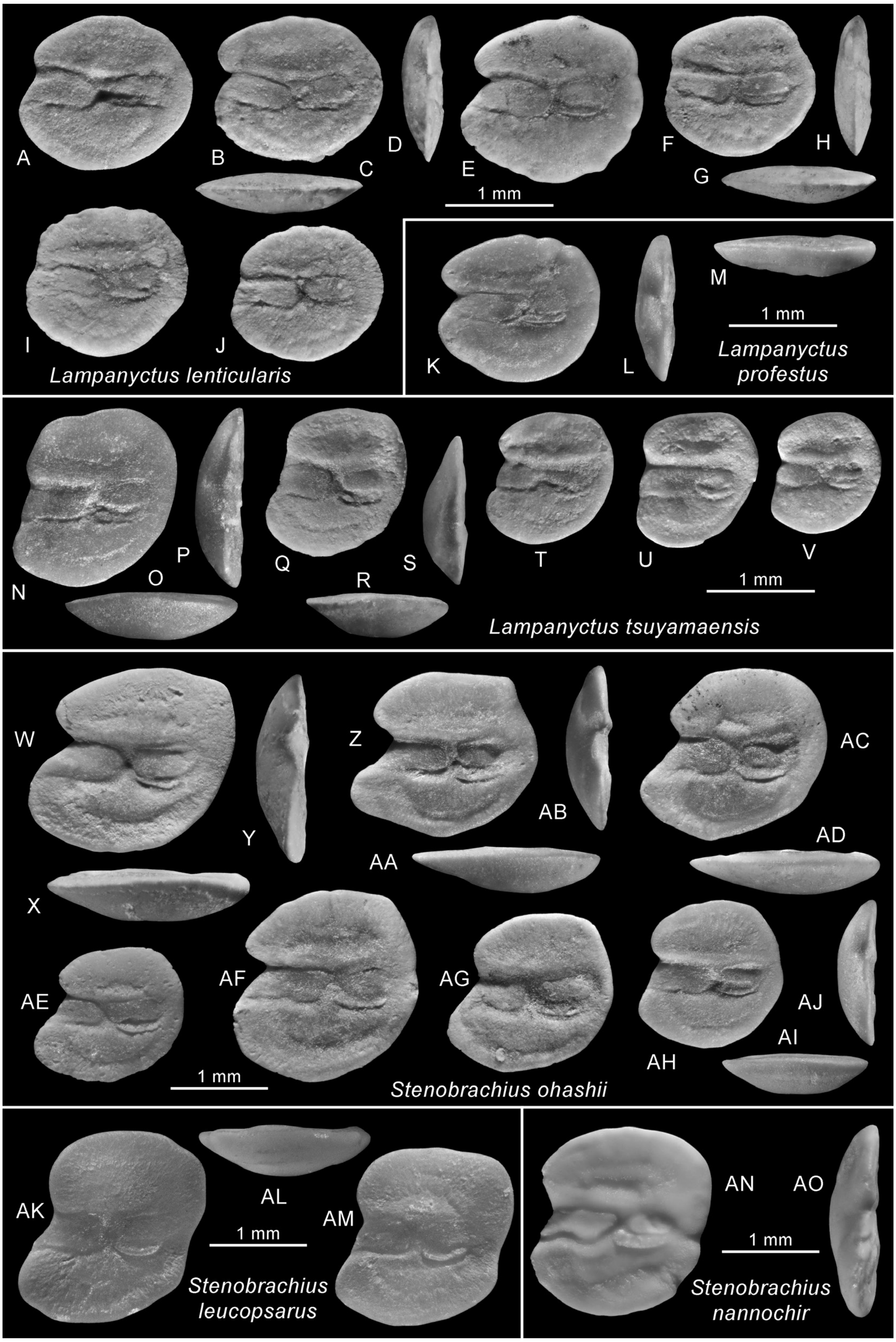

Figure 7. A–J: *Lampanyctus lenticularis* sp. nov., Tsuyama City, Takakura Formation; **B–D:** holotype, SMF PO 101.121, level h; **A, E–J:** paratypes, SMF PO 101.122, levels f, g, h, j; **K–M:** *Lampanyctus profestus* Schwarzhans, 2019, SMF PO 101.123, Tsuyama City, Takakura Formation, level MS 36; **N–V:** *Lampanyctus tsuyamaensis* sp. nov., Tsuyama City, Takakura Formation; **N–P:** holotype, SMF PO 101.124, level MS 15; **Q–V:** paratypes, SMF PO 101.125, levels MS 15, MS 36, MS 90; **W–AJ:** *Stenobrachius ohashii* sp. nov.; **W–Y:** holotype, SMF PO 101.126, Yatsuo machi, Toyama City, Kurosedani Formation, level K 5; **Z–AB, AF–AJ:** paratypes, SMF PO 101.127, Tsuyama City, Takakura Formation, levels MS 15, MS 70; **AC–AD:** paratype, SMF PO 101.128, Niimi City, Bihoku Group; **AE:** paratype, SMF PO 101.129, Fuchu machi, Toyama City, Higashibessho Formation, level H 21; **AK–AM:** *Stenobrachius leucopsarus* (Eigenmann & Eigenmann, 1890), Recent, coll. Schwarzhans, leg. Fitch, off California; **AN–AO:** *Stenobrachius nannochir* (Gilbert, 1890), Recent, NSMT-P.63309, 36°28'N, 141°10'E.

Diagnosis. Small, roundish otoliths; maximal size 1.7 mm; OL:OH = 1.05–1.15. All rims regularly curving without prominent angles. Rostrum short, slightly longer than antirostrum; excisura small. OCL:CCL = 1.3–1.6.

Description. Small, relatively thin and nearly perfectly round otoliths with smooth rims without angles up to about 1.7 mm in length (holotype 1.55 mm). Rostrum short, rounded, only slightly longer than minute antirostrum, 7–15% of OL. Excisura small.

Inner face nearly flat and smooth, with slightly supramedian positioned, relatively narrow, shallow and straight sulcus. Ostium slightly longer and wider than cauda (OCL:CCL = 1.3–1.6). Ostial and caudal colliculi well marked but caudal pseudocolliculum often very narrow and sometimes indistinct. Ventral furrow closely following ventral rim of otolith; dorsal depression wide, but usually indistinct. Outer face slightly more convex than inner face, smooth.

Discussion. The otoliths of most *Lampanyctus* species are small and unspectacular with smooth rims and hence can be easily confused with eroded juvenile otoliths of other myctophids, for instance those of *Diaphus*. It is therefore important to ensure that one is dealing with a sufficient number of well-preserved specimens before attempting a taxonomic classification of *Lampanyctus* otoliths. This is the case here. Even in light of the unspectacular nature of *Lampanyctus* otoliths, those of *L. lenticularis* stand out as particularly poor in traits. *Lampanyctus lenticularis* differs from the coeval *L. profestus* Schwarzhans, 2019 in the regularly rounded dorsal rim (vs. shallow) and the ostial colliculum being relatively little longer than the caudal colliculum (OCL:CCL = 1.3–1.6 vs. 2.0–2.5).

Lampanyctus profestus Schwarzhans, 2019

Fig. 7K–M, Table 1

2019 *Lampanyctus profestus* – Schwarzhans: figs 54.5–9.
2021 *Lampanyctus profestus* Schwarzhans, 2019 – Schwarzhans and Nielsen: fig. 8g.

Material. 1 specimen (SMF PO 101.123); Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 36, late Burdigalian, diatom zone 3A–3B.

Discussion. A single otolith from the Takakura Formation differs from the much more common *L. lenticularis* described above in the shallower, depressed dorsal rim; the much smaller caudal colliculum expressed in the ratio OCL:CCL of 2.35; and a nearly completely flat inner face. The OL:OH (1.1) and OCL:CCL (2.35) ratios are well within the range of diversity observed in the type specimens from the early Miocene of New Zealand (OL:OH = 1.1–1.25; OCL:CCL = 2.0–2.5). The species has recently also been identified from the Burdigalian of Chile (Schwarzhans and Nielsen 2021) and thus, although generally uncommon, appears to represent another myctophid species with an antitropical distribution pattern in the early to middle Miocene of the Pacific Ocean.

Lampanyctus tsuyamaensis sp. nov.

http://zoobank.org/8C5C8DA1-66AA-4B95-971B-4960EE692871

Fig. 7N–V, Table 1

Etymology. Named after Tsuyama City, the type-locality, Okayama Prefecture in western Honshu, Japan.

Holotype. SMF PO 101.124 (Fig. 7N–P), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 15, late Burdigalian, diatom zone 3A–3B.

Paratypes. 6 specimens (SMF PO 101.125); same data as holotype, levels MS 15, MS 36, MS 90.

Additional material. 11 specimens; same data as holotype, levels MS 15, MS 27, MS 36, f40.

Diagnosis. OL:OH = 0.85–0.92. Ventral rim deeply curving, deepest anterior of its middle. Anterior rim slightly inclined, almost straight from broad, inferior rostrum to predorsal angle with minute excisura and antirostrum. Inner face flat, outer face convex, smooth. OCL:CCL = 1.2–1.5.

Description. A small, very high-bodied, robust and thick otolith reaching about 1.5 mm in length (holotype); OH:OT = 3.4–3.7. Ventral rim deeply curving, deepest anterior of its middle, curving backwards into a steeply rounded posterior rim. Dorsal rim relatively shallow and nearly flat with distinct postdorsal angle at junction with posterior rim, somewhat irregular. Anterior rim steeply inclined at 75–85° (with sulcus oriented horizontal), nearly straight from distinct, rounded and inferior rostrum to minute antirostrum and predorsal angle at junction with anterior rim. Excisura minute. All rims smooth.

Inner face completely flat, with long, relatively wide, straight, shallow and slightly supramedian positioned sulcus. Ostial colliculum shallow, slightly longer and distinctly wider than caudal colliculum (OCL:CCL = 1.2–1.5; OCH:CCH = 1.25–1.5). Caudal pseudocolliculum as long as caudal colliculum. Ventral furrow distinct, positioned far from ventral rim of otolith. Dorsal depression wide, occupying almost entire dorsal field, but with indistinct margins. Outer face distinctly convex, smooth.

Discussion. *Lampanyctus tsuyamaensis* resembles *L. popoto* Schwarzhans, 2019 from the early Miocene of New Zealand and *L. latesulcatus* Nolf & Steurbaut, 1983 from the late Miocene of Italy but can be readily distinguished from both species by the more high-bodied shape, which is also expressed in the OL:OH ratio of 0.85–0.92 (vs. 0.95–1.05 and > 1.0, respectively). Another distinctive character is the straight, inclined anterior rim and the asymmetrical ventral rim. The known otoliths of extant species of *Lampanyctus* are usually also less high-bodied, with the exceptions of *L. lepidolychnus* Becker, 1967 and *L. macdonaldi* (Goode & Bean, 1896). Otoliths of *L. lepidolychnus* (see Smale et al. 1995 for figures) differ in the less inclined anterior rim, a more distinct development of a broad excisura, and a more regularly rounded dorsal rim, while those of *L. macdonaldi* are among the very few myctophid otoliths with fused colliculi (note that the specimens of *L. macdonaldi* figured in Smale et al. 1995 are erroneously identified). In contrast, the otoliths of the genus *Nannobrachium* Günther, 1887, which is commonly synonymized with

Lampanyctus, are even more compressed and high-bodied with a near rectangular outline and the sulcus almost reaching the posterior rim of the otolith.

Genus *Stenobrachius* Eigenmann & Eigenmann, 1890

Stenobrachius ohashii sp. nov.

http://zoobank.org/B0C99414-2E14-47BC-8DB0-51176BD45B0D

Fig. 7W–AJ, Table 1

Etymology. Named in honor of Fumitaka Ohashi (Aichi Prefecture, Japan) who collected and donated a large part of the studied otoliths and has undertaken an original thesis on the fossil contents of many of the locations covered in this study.

Holotype. SMF PO 101.126 (Fig. 7W–Y), Kubusu River at Kashio, Toyama City, Toyama Prefecture, Kurosedani FM, level K 5, late Burdigalian, lower part of biozone N8, probably diatom zone 3A.

Paratypes. 6 specimens: 6 specimens: 1 specimen (SMF PO 101.128), near Tesseicho Hattori, Niimi City, Okayama Prefecture, Bihoku Group, late Burdigalian, diatom zone 3A–3B; 4 specimens (SMF PO 101.127), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 15, MS 70, h, late Burdigalian, diatom zone 3A–3B; 1 specimen (SMF PO 101.129), Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 21, late Burdigalian to early Langhian, diatom zone 3A–4A.

Additional material. 227 specimens: 3 specimens, Near Tesseicho Hattori, Niimi City, Okayama Prefecture, Bihoku Group; 217 specimens, Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 04.5, MS 05, MS 05.5, MS 06, MS 15, MS 22, MS 27, MS 36, MS 52, MS 70, MS 80, MS 90, c, d, f9, f10, f40, g, gh, h, j; 3 specimens, Kubusu River at Kashio, Toyama City, Toyama Prefecture, Kurosedani FM, level K 5; 4 specimens, Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 21.

Diagnosis. OL:OH = 1.0–1.15. Rostrum long, massive, with more or less rounded tip, 17–25% of OL. Excisura and antirostrum distinct. Ostium slightly longer than cauda, OCL:CCL = 1.2–1.7. Caudal pseudocolliculum distinct, as long as caudal colliculum or longer. Inner face flat; outer face convex, smooth.

Description. A small, roundish, and moderately thick otolith reaching about 2.1 mm in length (holotype); OH:OT = 3.5–4.0. Ventral rim deeply curving, deepest at or anterior of its middle. Dorsal rim relatively shallow, somewhat irregular with distinct postdorsal angle near junction with posterior rim. Anterior rim with long, massive rostrum with usually rounded tip, 17–25% of OL. Antirostrum distinct, about half the length of rostrum. Excisura deep, usually sharp. Posterior rim variably rounded. All rims smooth.

Inner face completely flat, with moderately long, relatively narrow, straight, shallow and nearly axial positioned sulcus. Ostial colliculum shallow, slightly longer and wider than caudal colliculum (OCL:CCL = 1.2–1.7). Ventral margin of ostial colliculum sometimes flexed anteriorly. Caudal pseudocolliculum distinct, as long as caudal colliculum or anteriorly projecting. Ventral furrow distinct, positioned moderately far from ventral rim of otolith. Dorsal depression wide, occupying almost entire dorsal field, but with indistinct margins. Outer face distinctly convex, smooth.

Discussion. The genus *Stenobrachius* is today known from two species in the North Pacific: *S. leucopsarus* Eigenmann & Eigenmann, 1890 (Fig. 7AK–AM) and *S. nannochir* (Gilbert, 1890) (Fig. 7AN–AO). The fossil *S. ohashii* differs from the otoliths of the extant *S. leucopsarus* in the more regularly rounded ventral and posterior rims, the deeper excisura and sharper antirostrum, and the comparatively longer ostium (OCL:CCL = 1.2–1.7 vs. 1.05–1.3). It differs from the second extant species, *S. nannochir*, in the longer rostrum (vs. rostrum about as long as antirostrum) and the presence of a more or less strongly developed postdorsal angle. *Stenobrachius* otoliths are also quite similar to certain *Lampanyctus* otoliths such as those of the extant *L. lepidolychnus* or the fossil *L. tsuyamaensis* described above. A consistent difference seems to be that the caudal pseudocolliculum is not reduced in length or expression in *Stenobrachius* as it is in most *Lampanyctus* species.

Genus *Taaningichthys* Bolin, 1959

Taaningichthys sp.

Fig. 6V–X, Table 1

Material. 1 specimen (SMF PO 101.120), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 27, late Burdigalian, diatom zone 3A–3B.

Discussion. A single relatively small and slightly eroded otolith of 1.7 mm in length is interpreted as representing an unknown species of the genus *Taaningichthys* and is characterized by a relatively elongate shape (OL:OH = 1.4), a regularly curving ventral rim, a nearly flat dorsal rim, a distinct rostrum and a dorsally shifted posterior tip, and a flat inner face, with a supramedian sulcus with a long ostium and a short cauda (OCL:CCL = 2.0).

Subfamily Diaphinae Paxton, 1972 (sensu Martin et al. 2018)
Genus *Diaphus* Eigenmann & Eigenmann, 1890
Diaphus theta Otolith Group after Schwarzhans (2013a)

Diaphus angulatus Ohe & Araki, 1973

Fig. 8A–F, Table 1

1973 *Diaphus angulatus* – Ohe & Araki: pl. 49, figs 1–2, 20–21.

Material. 2 specimens; 1 specimen (SMF PO 101.130) Nagano River at Inabacho, Tsu City, Mie Prefecture, Katada

FM, level I 2, late Burdigalian, lower part of planktonic foraminifera biozone N8; 1 small, tentatively assigned specimen (SMF PO 101.131), Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 20, late Burdigalian to early Langhian, diatom zone 3A–4A.

Remarks. *Diaphus angulatus* was described based on a single incomplete specimen from the Yakuoji Formation, a partial lateral equivalent of the Katada Formation (see Oshida et al. 2018). Due to the incomplete preservation, *D. angulatus* was considered a doubtful species by Nolf (2013). Now, we have found a second specimen from the Katada FM which perfectly resembles the holotype but again lacks a rostrum (size 4.3+ mm; Fig. 8A–C). A complete smaller specimen of 2.6 mm in length from the Higashibessho FM (Fig. 8D–F) somewhat deviates from the larger specimens in the shape of the posterior rim and is therefore only tentatively assigned to the species. This difference is here considered to reflect an ontogenetic effect. These new finds are here used to revalidate and redefine the species.

Diagnosis (emended). OL:OH = 1.2–1.3. Ventral rim regularly curved with 6 denticles of variable strength. Rostrum long, massive; antirostrum and excisura small. Dorsal rim with prominent postdorsal angle; predorsal portion depressed. Inner face flat. Caudal colliculum shorter and much narrower than ostial colliculum (OCL:CCL = 1.5–1.8; OCH:CCH = 1.6–1.8).

Description (emended). Large, thin otoliths reaching at least 5.5 mm in length (holotype recorded by Ohe and Araki 1973); OH:OT = 4.0 (4.5 in tentatively assigned specimen). Rostrum long, pointed, 20% of OL in tentatively assigned small specimen with completely preserved rostrum (Fig. 8D). Antirostrum distinct, but very short; excisura small. Ventral rim relatively shallow and regularly curved, with 6 denticles of varying strength. Dorsal rim smooth, anteriorly depressed, posteriorly with prominent postdorsal angle positioned above termination of cauda. Posterior rim obliquely cut in large specimens (holotype figured by Ohe and Araki 1973, and Fig. 8A), rounded and without postventral angle in tentatively assigned small specimen of Fig. 8D.

Inner face flat with distinctly supramedian sulcus. Ostial colliculum about twice as long and wide as caudal colliculum; caudal pseudocolliculum long and distinct. Dorsal margin of ostium straight; cauda slightly bent upwards. Ventral furrow distinct, moderately close to ventral rim of otolith; dorsal depression large, rather deep but with indistinct margins except for crista superior towards sulcus. Outer face slightly convex with shallow postcentral umbo, smooth.

Discussion. A typical and rather large otolith-based species of the *Diaphus theta* Otolith Group that resembles the coeval *D. haereticus* (Brzobohatý & Schultz, 1978) but differs in the far more backward positioned postdorsal angle and the much narrower caudal colliculum. In the latter aspect, it resembles *D. audax* Schwarzhans, 2019 from the early Miocene of New Zealand and Chile but again differs in the distinctly further backward positioned postdorsal angle and the complete lack of a postdorsal concavity.

Diaphus epipedus sp. nov.

http://zoobank.org/FEEDFC9A-53E6-468B-B369-53B3BD7ED6B4

Fig. 8G–N, Table 1

Etymology. From epipedos (Greek) = flat, referring to the relatively shallow ventral rim, the main distinguishing character from *D. metopoclampoides*.

Holotype. SMF PO 101.132 (Fig. 8G–I), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 15, late Burdigalian, diatom zone 3A–3B.

Paratypes. 8 specimens; 6 specimens (SMF PO 101.133), same data as holotype, levels MS 15, MS 27, MS 90, j; 2 specimens (SMF PO 101.134), Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 21, late Burdigalian to early Langhian, diatom zone 3A–4A.

Diagnosis. OL:OH = 1.2–1.25. Shape rounded triangular with relatively shallow ventral rim, inferior rostrum and posterior tip and broad mediodorsal bulge. Antirostrum and excisura minute. Ventral rim with 7–9 denticles. Postdorsal rim broadly concave. OCL:CCL = 1.5–1.7.

Description. Otoliths with rounded triangular outline, relatively robust, up to 2.8 mm in length (holotype 2.5 mm); OH:OT = 3.4–3.7. Rostrum far inferior, relatively short and pointed, 10–12% of OL. Antirostrum and excisura minute. Dorsal rim with broad, rounded, pronounced mediodorsal bulge, anteriorly steeply inclined, posteriorly inclined with long depressed or concave section. Ventral rim rather shallow, regularly curved, with 7–9 medium strong denticles. Posterior rim curved, slightly projecting behind termination of cauda, its tip centrally or inframedian.

Inner face relatively flat, only slightly bent in horizontal direction. Sulcus terminating relatively far from posterior rim of otolith, straight, narrow. Ostial colliculum distinctly longer than caudal colliculum (OCL:CCL = 1.5–1.7) but only slightly wider (OCH:CCH = 1.2–1.4). Caudal pseudocolliculum distinct, about as long as caudal colliculum. Ventral furrow indistinct, sometimes not discernable, relatively close to ventral rim of otolith; dorsal depression small, ventrally marked by short crista superior. Outer face moderately convex throughout without distinct umbo, with distinct excisural furrow and few other weak and short radial furrows.

Discussion. *Diaphus epipedus* is an easily recognizable otolith that shares many features, such as the shape of the dorsal rim and the robust appearance without distinct umbo on the outer face, with *D. metopoclampoides* (see below) but differs in the shallow ventral rim, which results in a higher ratio OL:OH of 1.2–1.25 (vs. 1.05–1.1); the relatively long ostium (OCL:CCL = 1.5–1.7 vs. 1.1–1.4); and the narrower sulcus.

Diaphus metopoclampoides Steurbaut, 1983

Fig. 8O–T, Table 1

1983 *Diaphus metopoclampoides* – Steurbaut: pl. 1, figs 22–28.

1984 *Diaphus metopoclampoides* Steurbaut, 1983 – Steurbaut: pl. 7, fig. 23.

2000 *Diaphus metopoclampoides* Steurbaut, 1983 – Brzobohatý & Nolf: pl. 4, figs 7–14.

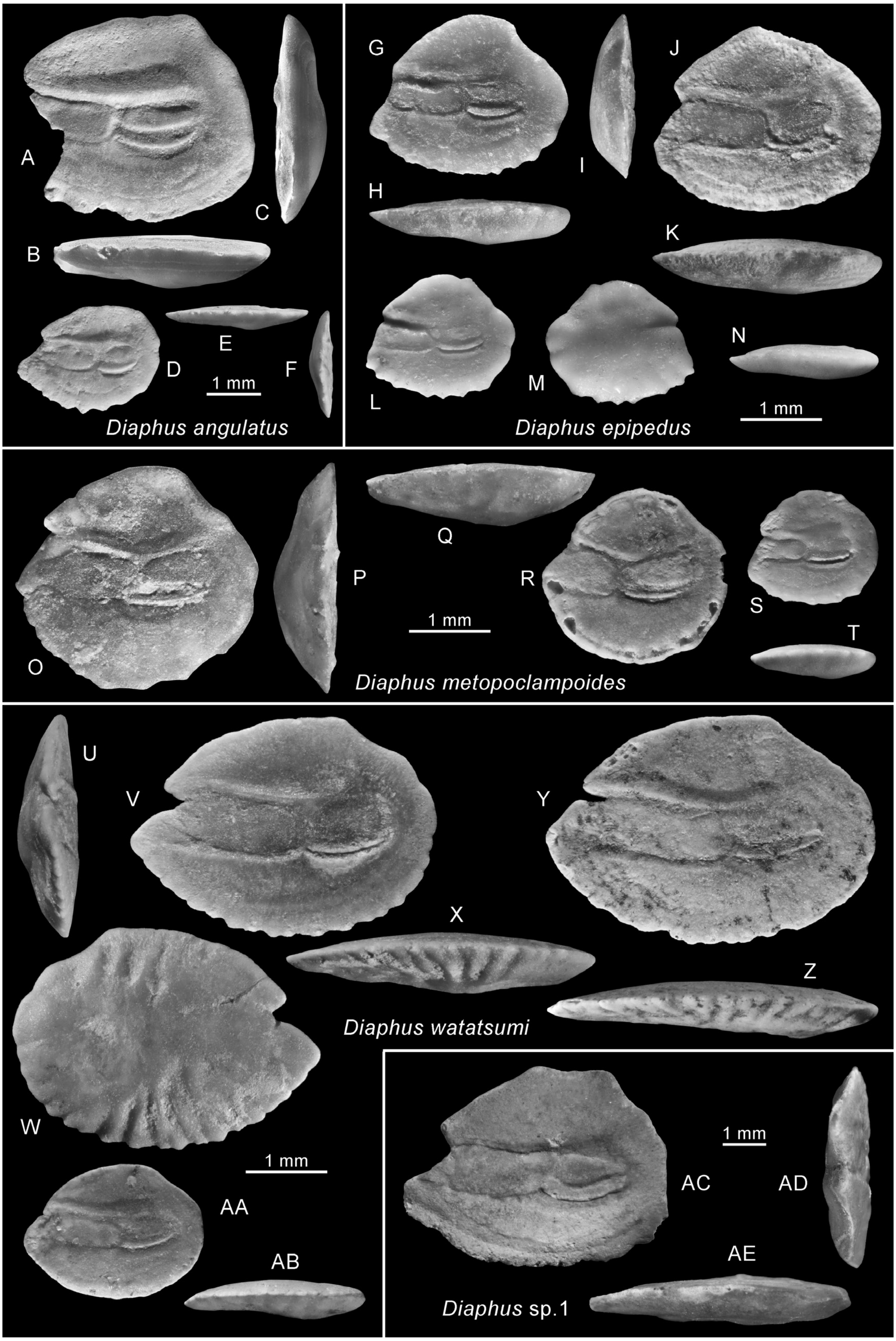

Figure 8. A–F: *Diaphus angulatus* Ohe & Araki, 1973; **A–C:** SMF PO 101.130, Inabacho, Tsu City, Katada Formation, level ML 2305; **D–E:** SMF PO 101.131, Fuchu machi, Toyama City, Higashibessho Formation, level H 20; **G–N:** *Diaphus epipedus* sp. nov.; **G–I:** holotype, SMF PO 101.132, Tsuyama City, Takakura Formation, level MS 15; **K–J:** paratype, SMF PO 101.133, Tsuyama City, Takakura Formation, level MS 15; **L–N:** paratype, SMF PO 101.134, Yatsuo, Toyama City, Higashibessho Formation, level H 21; **O–T:** *Diaphus metopoclampoides* Steurbaut, 1983, SMF PO 101.135, Tsuyama City, Takakura Formation level MS 06, f; **U–AB:** *Diaphus watatsumi* sp. nov., Tsuyama City, Takakura Formation; **U–X:** holotype, SMF PO 101.136, level MS 52; **Y–AB:** paratypes, SMF PO 101.137, levels gh, j; **AC–AE:** *Diaphus* sp.1, col. Tsuchiya, Ichishi Group.

2010 *Diaphus metopoclampoides* Steurbaut, 1983 – Schwarzhans: pl. 15, fig. 7.

Material. 12 specimens; 6 specimens (figured specimens SMF PO 101.135), Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 06, f40, gh, j, late Burdigalian, diatom zone 3A–3B; 2 specimens, Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A; 4 specimens, Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, late Burdigalian to early Langhian, diatom zone 3A–4A.

Discussion. A very characteristic but relatively rare otolith putatively related to *D. epipedus* (see above for distinction) that has thus far only been recorded from the late Burdigalian to Langhian of Europe (stratigraphically younger references in Brzobohatý and Nolf 2000, need verification); however, the records from Japan document a much wider geographical distribution in the northern hemisphere. The systematic positions of both species must be regarded as tentative because they do not clearly align with any of the extant *Diaphus* otolith-based groups.

Diaphus splendidus Otolith Group after Schwarzhans (2013a)

Diaphus watatsumi sp. nov.

http://zoobank.org/211177B6-5D3E-4052-808F-C2DC9D55EB37

Fig. 8U–AB, Table 1

Etymology. Named after Watatsumi, a Shinto spirit of the sea in Japanese.

Holotype. SMF PO 101.136 (Fig. 8U–X), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 52, late Burdigalian, diatom zone 3A–3B.

Paratypes. 3 specimens (SMF PO 101.137), same data as holotype, levels gh, h, j.

Additional material. 7 specimens, same data as holotype, levels MS 15, MS 22, MS 27, MS 36, MS 70, f9, j.

Diagnosis. OL:OH = 1.35–1.45; OH:OT = 3.8–4.5. Dorsal rim with distinct postdorsal angle above central position of cauda, slightly concave postdorsal section and depressed predorsal section. Rostrum moderately long, 16–18% of OL. Ventral rim with 13–15 feeble denticles. Sulcus long, relatively narrow, slightly bent; OCL:CCL = 2.0.

Description. Slender, thin and relatively large otoliths reaching about 4.1 mm in length (holotype 3.8 mm). Rostrum moderately long and pointed; excisura mostly shallow and narrow, antirostrum much shorter than rostrum. Dorsal rim anteriorly depressed, ascending to distinct postdorsal angle positioned relatively forward above center of cauda; postdorsal section inclined, slightly concave. Ventral rim rather shallow and very regularly bent, with 13–15 feeble denticles which erode easily and are rarely completely preserved like in holotype. Posterior rim gently and regularly curved, slightly crenulated.

Inner face slightly bent in horizontal direction, relatively smooth, with long, slightly supramedian and slightly bent, shallow sulcus. Ostium about as wide as cauda but twice as long. Ostial colliculum only slightly wider than caudal colliculum (OCH:CCH = 1.1–1.3). Caudal pseudocolliculum distinct, long, fine. Dorsal margin of ostium slightly oscillating. Ventral furrow very indistinct; dorsal depression large, well marked towards crista superior. Outer face nearly flat except slightly thickened central and postcentral region, with numerous rapidly fading radial furrows on dorsal and ventral fields.

Discussion. *Diaphus watatsumi* is superficially an inconspicuous *Diaphus* otolith but can be relatively easily identified by its proportions and the shape and number of delicate denticles along the ventral rim. It resembles *D. marwicki* (Frost, 1933), a common species in the early and middle Miocene of the southern Pacific in New Zealand and Chile (see Schwarzhans 2019 and Schwarzhans and Nielsen 2021), but differs in the more elongate shape (OL:OH = 1.35–1.45 vs. 1.25–1.35), the thin appearance (OH:OT = 3.8–4.5 vs. 3.5–3.6), the larger number of denticles on the ventral rim (13–15 vs. 10–13), and the anteriorly depressed dorsal rim. *Diaphus watatsumi* resembles even more closely *D. sulcatus* (Bassoli, 1906) from the middle and late Miocene of Europe and the extant *D. splendidus* (Brauer, 1904), which is known since at least the early Pliocene, and is therefore associated with the *Diaphus splendidus* Otolith Group. *Diaphus watatsumi* differs from *D. sulcatus* in the rostrum being much longer than the antirostrum (vs. slightly longer to equal length) and the more depressed and longer predorsal region. It differs from *D. splendidus* in the relatively higher ratio OCL:CCL (2.0 vs. 1.6–1.8) and the higher number of denticles on the ventral rim (13–15 vs. 9–13). *Diaphus watatsumi* also resembles otoliths of the extant *Lobianchia gemellarii* (Cocco, 1838) (see Schwarzhans and Ohe 2019 for figures) but differs in the higher number of denticles along the ventral rim (13–15 vs. 5–9), the more regularly rounded posterior rim and the many radial furrows on the outer face.

Diaphus sp.1

Fig. 8AC–AE

Remarks. An additional relatively large *Diaphus* species of about 6.0 mm in length is observed in the Ichishi Group and will be described separately by one of us (YT). It also belongs to the *Diaphus splendidus* otolith group and is characterized by a relatively long and sharp rostrum, a high postdorsal angle, and the lack of a postdorsal concavity.

Diaphus garmani Otolith Group after Schwarzhans (2013a)

Diaphus biatlanticus (Weiler, 1959)

Fig. 9AD–AG, Table 1

1959 *Nyctophus biatlanticus* – Weiler: figs 9, 10.

2013 *Diaphus biatlanticus* (Weiler, 1959) – Schwarzhans and Aguilera: pl. 11, figs 1–8 (see there for further synonymies).

Material. 7 specimens; 5 specimens (figured specimen SMF PO 101.145), Miya River at Numa, Tsuyama City,

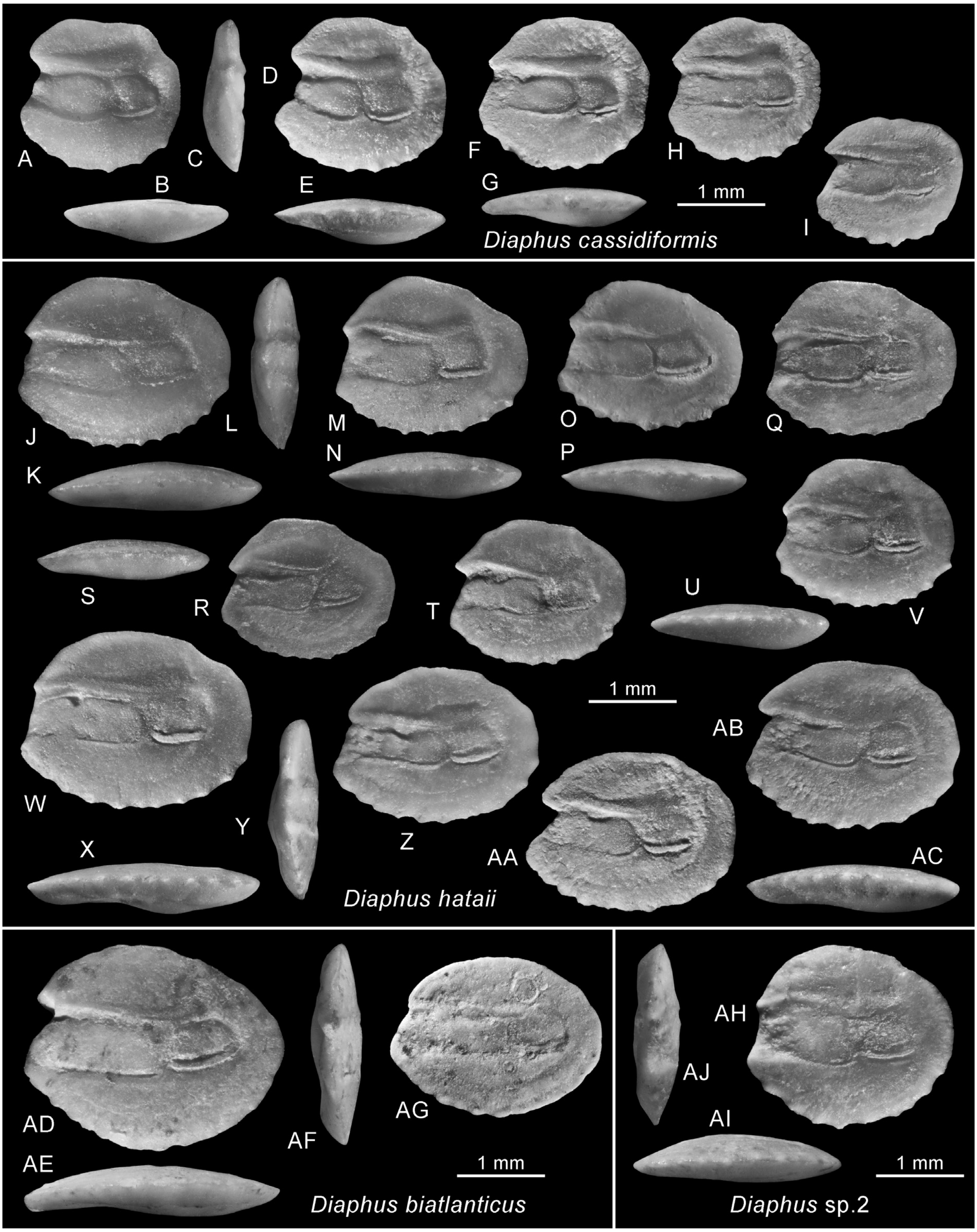

Figure 9. A–I: *Diaphus cassidiformis* (Frost, 1933), SMF PO 101.138, Yatsuo, Toyama City, Kurosedani Formation, level K 5; **J–AC:** *Diaphus hataii* Ohe & Araki, 1973; **J–L:** SMF PO 101.139, Mizunami City, Oidawara Formation; **M–N, Q–V:** SMF PO 101.140, Tsuyama City, Takakura Formation, levels MS 06, MS 07, MS 52, MS 90; **O–P:** SMF PO 101.141, Fuchu machi, Toyama City, Higashibessho Formation, level H 20; **W–AA:** SMF PO 101.142, Makino River, Iga City, Makino Formation, level A 1; **AB–AC:** SMF PO 101.143, Inabacho, Tsu City, Katada Formation, level ML 2305; **AD–AG:** *Diaphus biatlanticus* (Weiler, 1959); **AD–AF:** SMF PO 101.144, Mizunami City, Oidawara Formation; **AG:** SMF PO 101.145, Tsuyama, Takakura Formation, level h; **AH–AJ:** *Diaphus* sp.2, SMF PO 101.146, Mizunami City, Oidawara Formation.

Okayama Prefecture, Takakura FM, levels MS 27, MS 52, h, late Burdigalian, diatom zones 3A–3B; 2 specimens (SMF OP 101.144), Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A.

Discussion. *Diaphus biatlanticus* has thus far only been reported from the early to middle Miocene of tropical America (Trinidad and Venezuela). Its otoliths are characterized by a very regular oval outline, a short rostrum, a short antirostrum and a minute excisura, a relatively long ostium compared to the cauda (OCL:CCL = 2.0–2.4), and a convex inner face combined with a flat to slightly concave outer face. The rare occurrence of the species in the middle Miocene of Japan indicates that it had a much wider geographical distribution than previously believed.

Diaphus cassidiformis **(Frost, 1933)**

Fig. 9A–I, Table 1

1933 *Scopelus cassidiformis* – Frost: figs 17, 18.
1980 *Diaphus cassidiformis* (Frost, 1933) – Schwarzhans: figs 176–177, 597.
1992 *Diaphus* sp. 6 – Radwanska: pl. 4, figs 1–3, textfig. 33.
2013b *Diaphus cassidiformis* (Frost, 1933) – Schwarzhans: pl. 4, figs 4–7.
2019 *Diaphus cassidiformis* (Frost, 1933) – Schwarzhans: figs 58.8–10.

Material. 80 specimens; 20 specimens, Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A; 60 specimens (figured specimens SMF PO 101.138), Kubusu River at Kashio, Toyama City, Toyama Prefecture, Kurosednai FM, level K 5, late Burdigalian, lower part of planktonic foraminifera biozone N8.

Discussion. *Diaphus cassidiformis* is easily recognized by its small, round otoliths. It was widely geographically distributed during the middle Miocene from New Zealand to Gabon (West Africa) and is now also recorded from Japan. It is also here interpreted to be present in the Paratethys based on an ongoing review of the myctophid otoliths originally described by Radwanska (1992). Its occurrence is rather irregular, as it may occur in large numbers at one location and in one formation (e.g., in Japan in the Oidawara and Kurosedani formations), while it may be completely missing from other locations. The reason for this unusual distribution pattern is unknown but most likely has to do with the species' ecological adaptation or with a specific lifestyle (e.g., a pseudoceanic occurrence).

Diaphus hataii **Ohe & Araki, 1973**

Fig. 9J–AC, Table 1

1973 *Diaphus hataii* – Ohe & Araki: pl. 49, figs 3, 4.
1976 *Diaphus* sp. – Takahashi: pl. 17, fig. 5.
1980 *Diaphus hataii* Ohe & Araki, 1973 – Ohe and Yamaoka: figs 7(?) 8–13.
1980 *Diaphus* sp. – Ohe & Yamaoka: fig. 14.
2000 *Diaphus regani* Tåning, 1932 – Brzobohatý & Nolf: pl. 3, figs 15–20.
2013 *Diaphus hataii* Ohe & Araki, 1973 – Schwarzhans and Aguilera, pl. 10, figs 9–16, 17(?) (see there for further synonymies).

Material. 1744 specimens (figured specimens SMF PO 101.139-143): 4 specimens near Tessicho Hattori, Niimi City, Okayama Prefecture, Bihoku Group, late Burdigalian, diatom tone 3A–3B; 459 specimens, Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 04.5, MS 05, MS 05.5, MS 06, MS 07, MS 15, MS 22, MS 27, MS 36, MS 52, MS 70, MS 80, MS 90, b, c, d, f9, f10, f40, g, gh, h, j, early Burdigalian, diatom zone 3A–3B; 243 specimens, Makino River SW of Mashino, Iga City, Mie Prefecture, Makino FM, levels A 1, A 2, late Burdigalian, lower part of planktonic foraminifera biozone N8; 91 specimens, Nagano River at Inabacho, Tsu City, Mie Prefecture, Katada FM, levels I 1, I 2, OA1409, late Burdigalian, lower part of planktonic foraminifera biozone N8; 931 specimens, Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A; 2 specimens, Kubusu River at Kashio, Toyama City, Toyama Prefecture, Kurosedani FM, level K 5, late Burdigalian, lower part of planktonic foraminifera biozone N8; 14 specimens, Yamada River at Dojima and Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, levels H 14, H 20, H 21, late Burdigalian to early Langhian, diatom zone 3A–4A.

Discussion. *Diaphus hataii* is by far the most common myctophid otolith-based species throughout the early and early middle Miocene (late Burdigalian and early Langhian) of Japan, and it represents about 73% of all myctophid otoliths studied here. It is characterized by a short rostrum, which is not or only a fraction longer than the antirostrum; a convex inner face; a ratio OL:OH of 1.20–1.35 (adjusted from Schwarzhans and Aguilera 2013); a ratio OCL:CCL of 1.7–2.0; an oscillating dorsal rim of the ostium; 8–12 fine denticles along the ventral rim (adjusted from Schwarzhans and Aguilera 2013); and a more or less strongly developed predorsal lobe. Schwarzhans and Aguilera (2013) used the latter character as an important means by which to distinguish *D. hataii* from the contemporaneous *D. austriacus* (Koken, 1891), but the newly available material shows a certain degree of variability, as most species show such predorsal lobe (Fig. 9J, M, O, Q, R), while others show a moderately developed predorsal lobe (Fig. 9T, V, W); there are also specimens with a rather regularly curved dorsal rim (Fig. 9Z, AA, AB). We could not recognize sufficient consistency or additional characters that would warrant splitting of *D. hataii* into separate species. However, this also means that the distinction between *D. hataii* and *D. austriacus* becomes less clear. However, the specimens with a regularly curving dorsal rim are also slightly more elongate than the specimens with a distinct predorsal lobe (OL:OH = 1.25–1.35 vs. 1.20–1.25), while specimens of *D. austriacus* do not exhibit a predorsal lobe and are more compressed (OL:OH = 1.1–1.2, rarely to 1.25). In addition, *D. hataii* is thinner than *D. austriacus* (OH:OT = 3.5–4.0 vs. 3.0–3.5) and shows more denticles along the ventral rim of the otolith (8–12 vs. 6–8). We maintain the view that two separate species existed during the late early Miocene (Burdigalian) and middle Miocene (chiefly Langhian), with *D. hataii* being widely distributed in the tropics and the northern hemisphere from Europe through Central America and Japan, while *D. austriacus* appears to have been geographically restricted to Europe and the tropical Atlantic. A further potential vicariant species could be *D. curvatus* Schwarzhans, 1980 in the early and middle Miocene of the South Pacific (New Zealand and Chile; see Biostratigraphic Evaluation chapter).

Diaphus sp. 2

Fig. 9AH–AJ, Table 1

Material. 2 specimens (figured specimen SMF PO 101.146), Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A.

Discussion. Two very compressed, nearly round otoliths differ from the common *D. hataii* in the low index OL:OH of 1.1 and the distinctly widened ostium. The specimens share with *D. hataii* the short rostrum, the number of denticles along the ventral rim (9), and the expanded predorsal lobe. It most likely represents a separate species, but more specimens will have to be obtained before a reliable diagnosis can be established.

Subfamily Gymnoscopelinae Paxton, 1972 (sensu Martin et al. 2018)
Genus *Notoscopelus* Günther, 1864

Notoscopelus kuboensis (Ohe & Araki, 1973)

Fig. 10A–N, Table 1

1973 *Lampanyctus kuboensis* – Ohe & Araki: pl. 49, figs 7–11.
1977 *Lampanyctus* sp. – Takahashi: pl. 25, fig. 4.
1981 *Lampanyctus parvicauda* Parr, 1931 – Ohe: pl. 3, fig. 12.
2019 *Notoscopelus kuboensis* (Ohe & Araki, 1973) – Schwarzhans and Ohe: fig. 13K–M.

Material. 40 specimens (figured specimens SMF PO 101.147-148): 36 specimens, Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 04.5, MS 05, MS 05.5. MS 06, MS 15, MS 22, MS 27, MS 36, MS 70, MS 80, MS 90, f10, f40, gh, h, j, late Burdigalian, diatom zone 3A–3B; 1 specimen, Nagano River at Inabacho, Tsu City, Mie Prefecture, Katada FM, level I 2, late Burdigalian, lower part of planktonic foraminifera biozone N8; 3 specimens Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A; 2 specimens, Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 20, late Burdigalian to early Langhian, diatom zone 3A–4A.

Discussion. *Notoscopelus kuboensis* is a wide-ranging species in the late early and middle Miocene to early Pleistocene of Japan and belongs to the lineage leading to the extant *N. japonicus* (Tanaka, 1908) (see Schwarzhans and Ohe 2019). The new data document a rather large variability of the ratio OL:OH ranging from 1.65 to 1.9, with a single large specimen reaching a ratio of 2.0 (corrected for erosion along the central portion of the ventral rim). This wide range appears to be mostly ontogenetically driven, with specimens up to 3 mm in length having a ratio OL:OH of 1.65–1.7 (Fig. 10J, K, M), those of 3 to 4 mm in length a ratio OL:OH of 1.75–1.85 (Fig. 10E, G, H), and the largest specimens reaching 4.85 mm in length with a ratio OL:OH of 1.9–2.0 (Fig. 10A, B). The specimens described from the Pliocene and early Pleistocene by Schwarzhans and Ohe (2019) are of larger size (4.4–5.0 mm in length) and show a similar ratio of 1.85–1.95. *Notoscopelus kuboensis* differs from the middle Pleistocene *N. praejaponicus* Schwarzhans & Ohe, 2019 and the extant *N. japonicus* (Tanaka, 1908) primarily by the not extended posterior tip of the otolith, the postdorsal angle being positioned further backward on the dorsal rim in comparison to the two other species, and the lack of the distinctive and long postdorsal concavity developed in *N. praejaponicus* and *N. japonicus*.

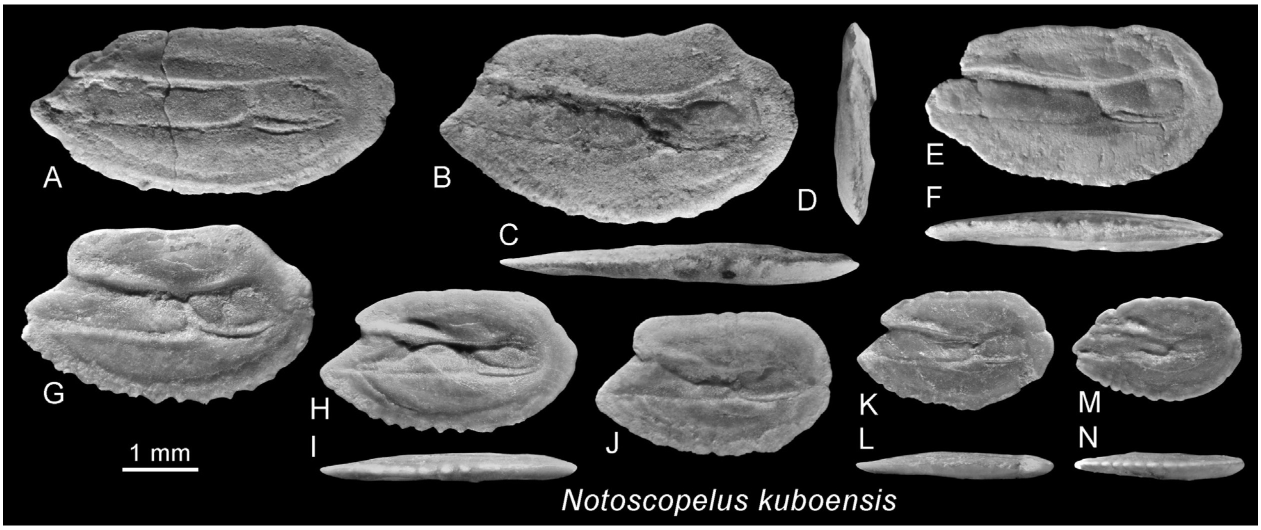

Figure 10. A–N: *Notoscopelus kuboensis* (Ohe & Araki, 1973); **A:** SMF PO 101.147, Inabacho, Tsu City, Katada FM, level ML 2305; **B–N:** SMF PO 101.148, Tsuyama City, Takakura Formation, levels MS 15, MS 36, MS 80, MS 90, j.

3.2. Faunal evaluation

3.2.1. Paleoecology

The late early and middle Miocene was a phase characterized by widespread transgression and submergence of the Japanese Archipelago. A paleogeographic reconstruction of Japan and its vicinity at 16 Ma (base Langhian) by Ogasawara (1994; Fig. 11) shows that large parts of the terrain of the main island, Honshu, were flooded. A broad and mostly deep water strait crossed southern Honshu through the region now occupied by Okayama, Tottori, and Hyogo Prefectures; today's Ise Bay was much wider, occupying terrain across Mie, Aichi, and Gifu Prefectures, and much of the northern area of Honshu and Hokkaido was flooded, with only occasional islands emerging (Fig. 11). Another broad and deep water way existed in the northern part of central Honshu over Toyama and Ishikawa Prefectures. The myctophid otoliths studied here stem from locations in Okayama, Mie, Gifu, and Toyama Prefectures (see Materials and Methods chapter). Some of them were deposited in upper bathyal environments with a shallowing upward tendency such as the Kurosedani and Higashibessho formations in Toyama Prefecture (Nishimatsu and Ujihara 2020). According to Taguchi (2002), the Takakura Formation of Okayama Prefecture was deposited in an upper bathyal to lower shelf environment. In the paleo-Ise Bay, the Makino Formation of Mie Prefecture was deposited on the lower shelf to upper slope at about 200 m water depth (Nishimatsu 2019) and the Katada Formation at Inabacho in Mie Prefecture probably in an upper bathyal position. The rich myctophid association sampled from the basal transgressive Nataki Member of the Oidawara Formation at Okuna, Mizunami City, Gifu Prefecture, was deposited at a relatively shallow shelf environment but with access to the open sea.

Diaphus hataii is a ubiquitous myctophid species in all locations and samples studied and is also the most common species throughout. It dominates the myctophid associations of the Oidawara Formation of Mizunami City, the Makino Formation of Iga City, and the Katada Formation at Inabacho of Tsu City. The paleoenvironment ranges from rather shallow water at Mizunami City to deep shelf and upper slope in Iga and Tsu cities. *Diaphus hataii* is essentially the only myctophid species at Iga, Tsu and Mizunami cities is associated with rare *Diaphus cassidiformis*. Elsewhere, *D. hataii* is also very common in the Higashibessho Formation and the Takakura Formation at Tsuyama City but is associated with a richer myctophid assemblage. Such rich myctophid assemblage is particularly obvious in the Takakura Formation, which commonly yields *Stenobrachius ohashii*, *Protomyctophum ahunga* and less common but still significant, species of *Lampanyctus*, *Myctophum murbani*, and *Notoscopelus kuboensis*. Thus, the Takakura Formation is the most myctophid species-rich location of the entire study. It should be noted, however, that the Takakura Formation has also yielded more myctophid specimens in total than all other locations, with the exception of Mizunami City (just under 1,000 specimens). More significant is the greater myctophid diversity observed in the Takakura Formation of Tsuyama City when compared with the rather uniform assemblage in the Oidawara Formation of Mizunami City.

3.2.2. Paleobiogeography

Lanternfishes of the family Myctophidae belong to the most abundant and widespread high oceanic mesopelagic fishes (Hulley 1981). They have dominated all pelagic otolith communities on a worldwide basis since at least Miocene times, but they probably became already common in the Oligocene (Schwarzhans and Carnevale 2021). Today, myctophid fishes occur in very large swarms offshore in high oceanic regions, where most of them undertake vertical diel migrations; they live at about 1,000 m water depth or more during the day and ascend to near the ocean surface at night together with the oceanic zooplankton on which they feed. These myctophid species are often very widely distributed geographically, with their range often being limited by climate belts and current regimes, and some are indeed circumglobal (Froese and Pauly 2021). Other extant myctophid species live pseudoceanic (sensu Hulley and Lutjeharms 1989) and may have a more disjunctive or regionally restricted distribution pattern. Selected myctophid species are known to have been distributed on a superregional basis during the early Miocene between Chile and New Zealand (Schwarzhans and Nielsen 2021) or in the late Miocene and Pliocene across the Atlantic (Schwarzhans and Aguilera 2013). The late Burdigalian to Langhian time interval is among the best known for pelagic otolith communities on a worldwide basis. Myctophid otoliths are known from the time interval between 17 and 14 Ma from various European Basins, Central America (Caribbean), tropical West Africa, southwest America (Chile), New Zealand, and now also Japan (Fig. 12). With respect to otoliths of a specific environment, it is the first time interval with such widespread occurrence available for analysis and comparison with the extant situation.

Regarding the fauna from the late Burdigalian to early Langhian of Japan described here, the most obvious correlation options in the absence of adequate data from northwestern America are across the equator to the South Pacific (i.e., New Zealand [Schwarzhans 2019] and Chile [Schwarzhans and Nielsen 2021]). Five of the 22 myctophid species identified in the early to middle Miocene of Japan are also known from comparable time intervals from New Zealand, while three are also known from Chile. This is a reasonable correlation, albeit much lower than that between New Zealand and Chile, as 12 of 13 myctophid species identified in Chile are also known from New Zealand. This correlation shows that some exchange took place between the antitropical open ocean environments in the southern and northern Pacific. The

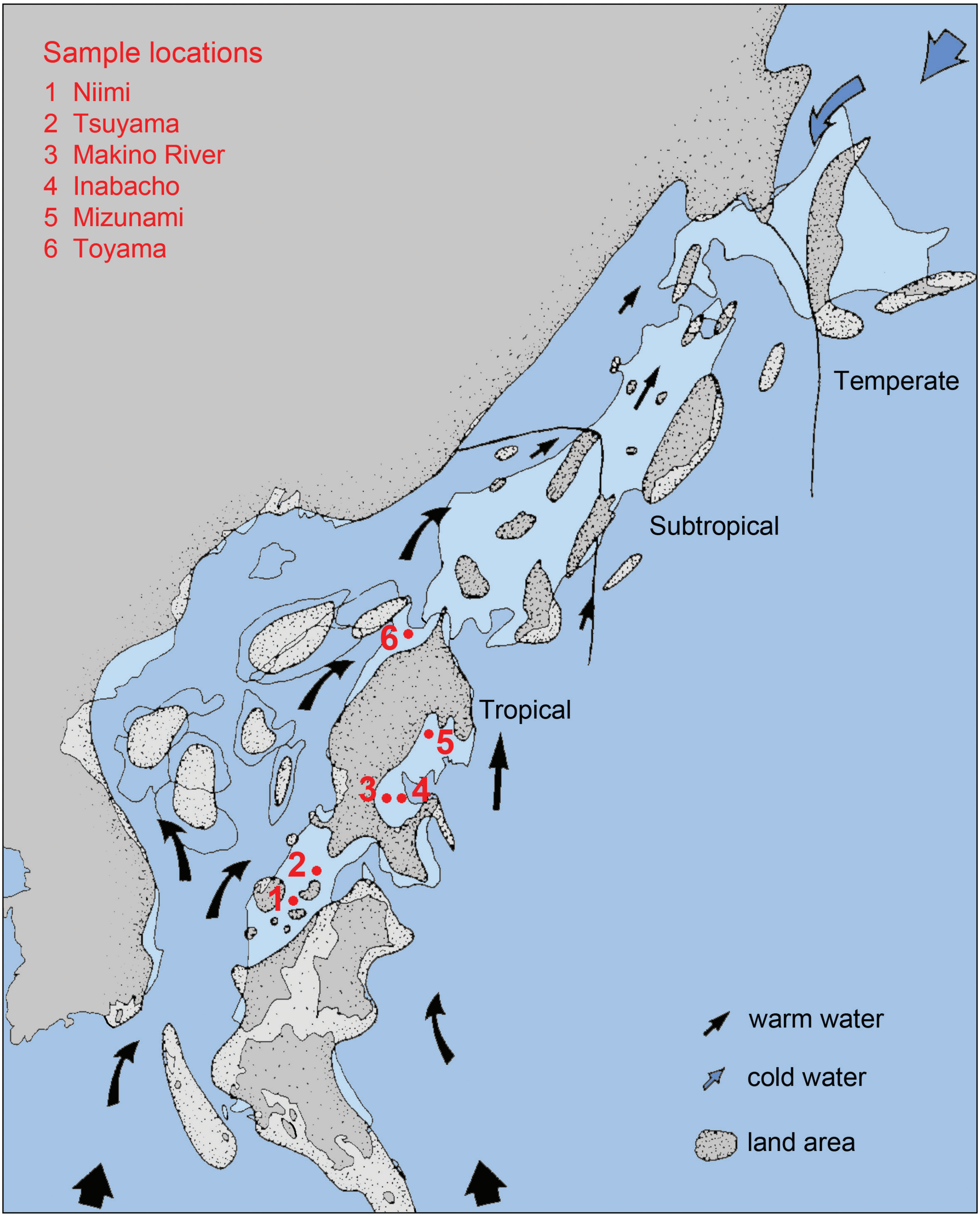

Figure 11. Paleogeographic situation of Japan and sampled locations at about 16 Ma. Based on Ogasawara (1994).

species found in Japan and shared with New Zealand are *Diogenichthys aguilerai*, *Protomyctophum ahunga*, *Lampanyctus profestus*, *Diaphus cassidiformis*, and *Notoscopelus kuboensis* (Fig. 13). Of these, *Diogenichthys aguilerai* and *Diaphus cassidiformis* appear to have been distributed on a global basis at the time, with *D. aguilarai* also known from West Africa and *D. cassidiformis* from West Africa and Europe. There are also myctophid species from the early to middle Miocene of Japan that possibly had a circumglobal distribution in the northern hemisphere. *Myctophum murbani* and *Diaphus hataii*, which are both also known from Europe and Central America, seem to fall into this category. *Diaphus hataii* is of particular interest, as it forms a group of closely related species with

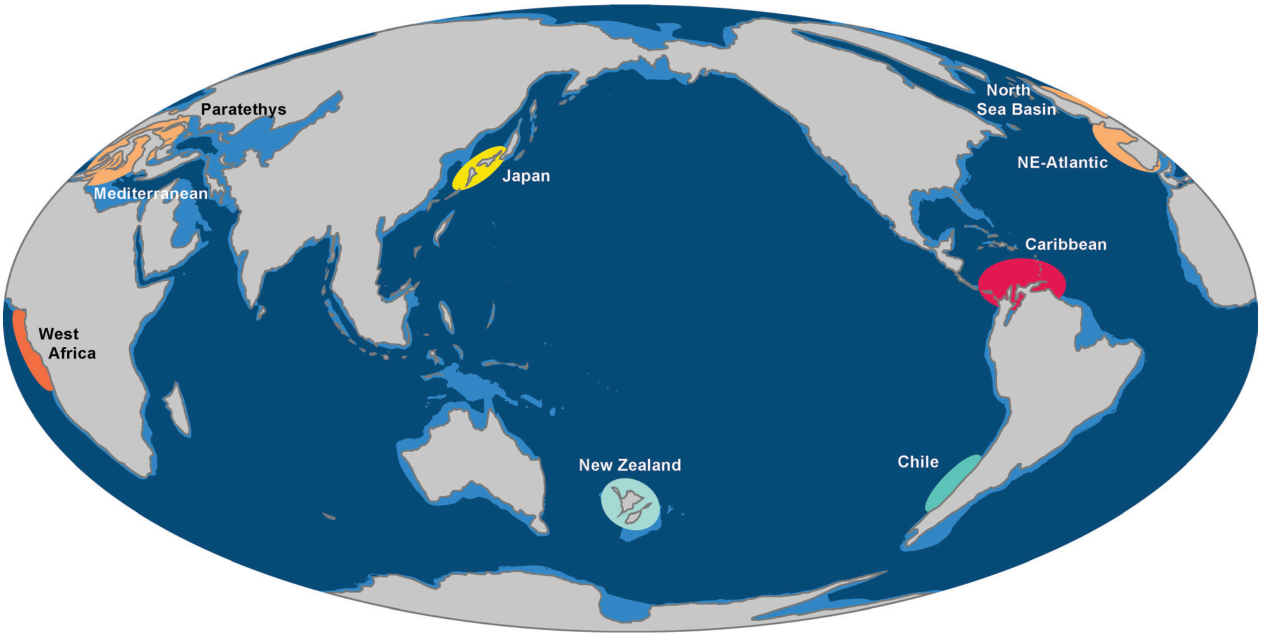

Figure 12. Knowledge base of early to middle Miocene myctophid otoliths based on this work for Japan, Brzobohatý and Nolf (2000, modified) for the Mediterranean, Brzobohatý and Nolf (2000, modified) and ongoing research for Paratethys, Steurbaut (1984, modified) for the northeast Atlantic, Schwarzhans (2010) for the North Sea Basin, Schwarzhans (2013b) for West Africa, Schwarzhans and Aguilera (2013) for the Caribbean, Schwarzhans (2019) for New Zealand, and Schwarzhans and Nielsen (2021) for Chile. Paleogeographic reconstruction based on Blakey (2021).

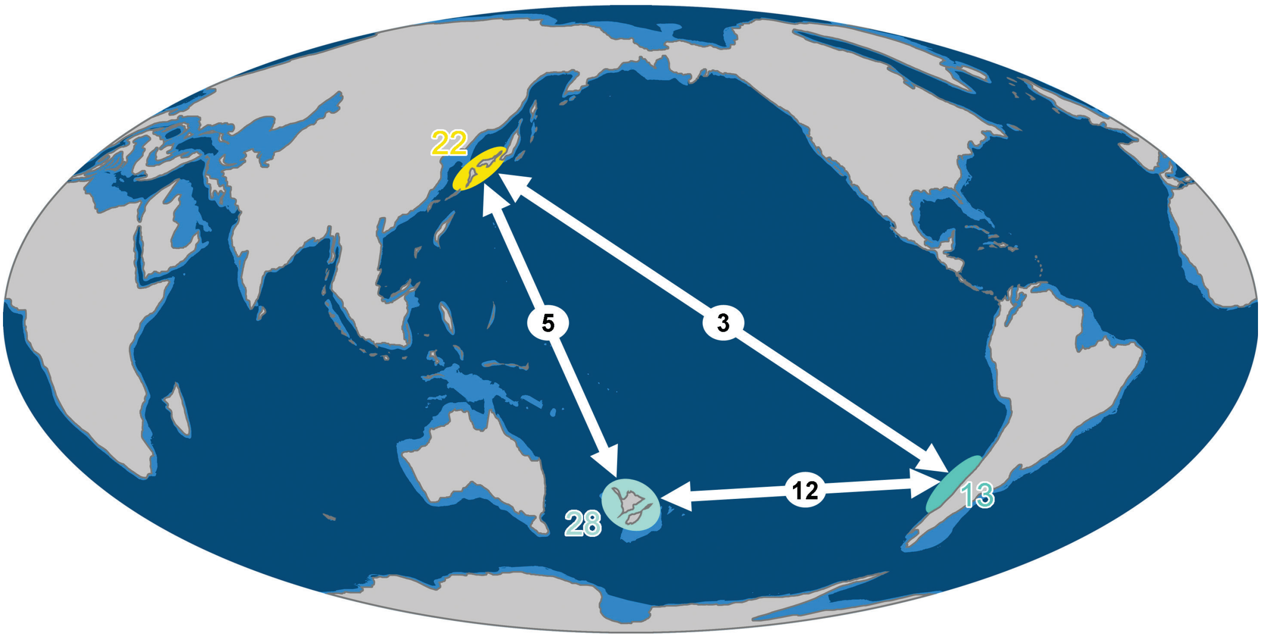

Figure 13. Correlation of myctophid species from the early and middle Miocene across three studied areas around the Pacific based on this work, Schwarzhans (2019), and Schwarzhans and Nielsen (2021). Numbers at regions represent number of myctophid species recognized; number on arrows indicate shared species between regions. Paleogeographic reconstruction based on Blakey (2021).

D. austriacus (Koken, 1891) and *D. curvatus* Schwarzhans, 1980. *Diaphus hataii* appears to have been distributed circumglobally in the northern hemisphere and is known from Japan, the Caribbean, Atlantic Europe, the Western Tethys, and Paratethys (the northern Indian Ocean is inferred, as no data are available as yet) (Fig. 14). *Diaphus austriacus*, however, appears to have been restricted to the Atlantic, including the North Sea Basin, and the Western Tethys and Paratethys (Fig. 14). In these areas it is the dominant species of the group, whereas *D. hataii* is much rarer. In the South Pacific, the group is represented by *D. curvatus* in New Zealand and Chile (Fig. 14). There are no data yet from the South Atlantic or the southern Indian Ocean, and therefore we do not yet know whether *D. curvatus* actually was a circumglobal species in the southern hemisphere.

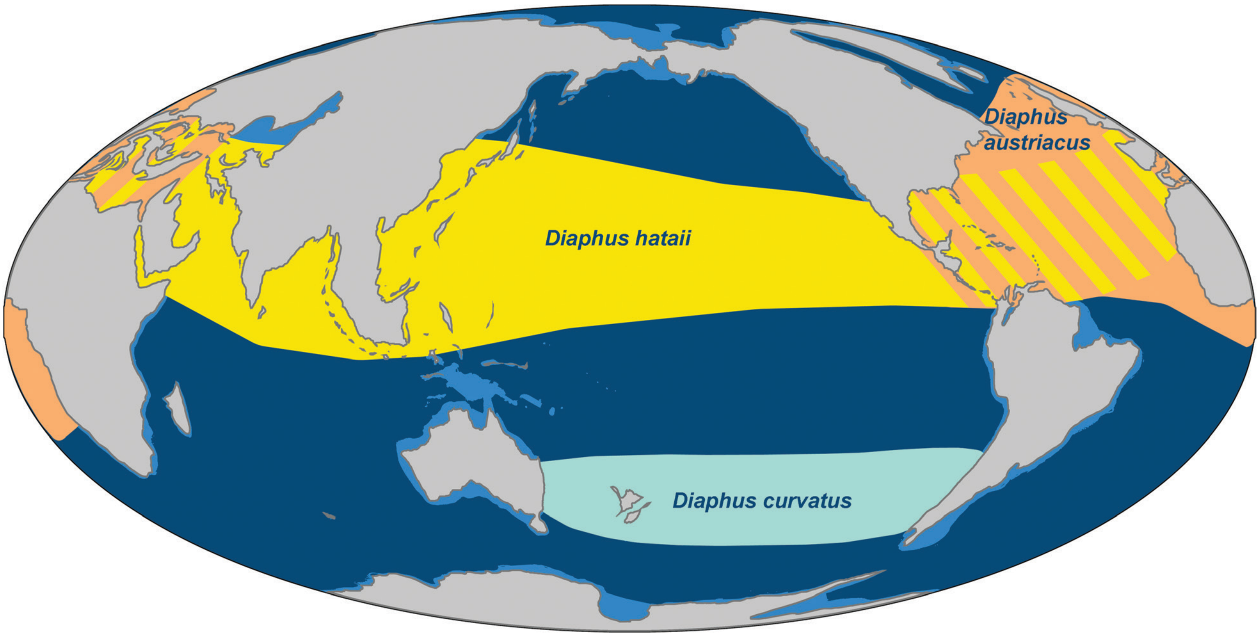

Figure 14. Interpolated biogeographic distribution of the related species *D. hataii*, *D. austriacus*, and *D. curvatus* during the early to middle Miocene. See Fig. 12 for database and paleogeographic reconstructions.

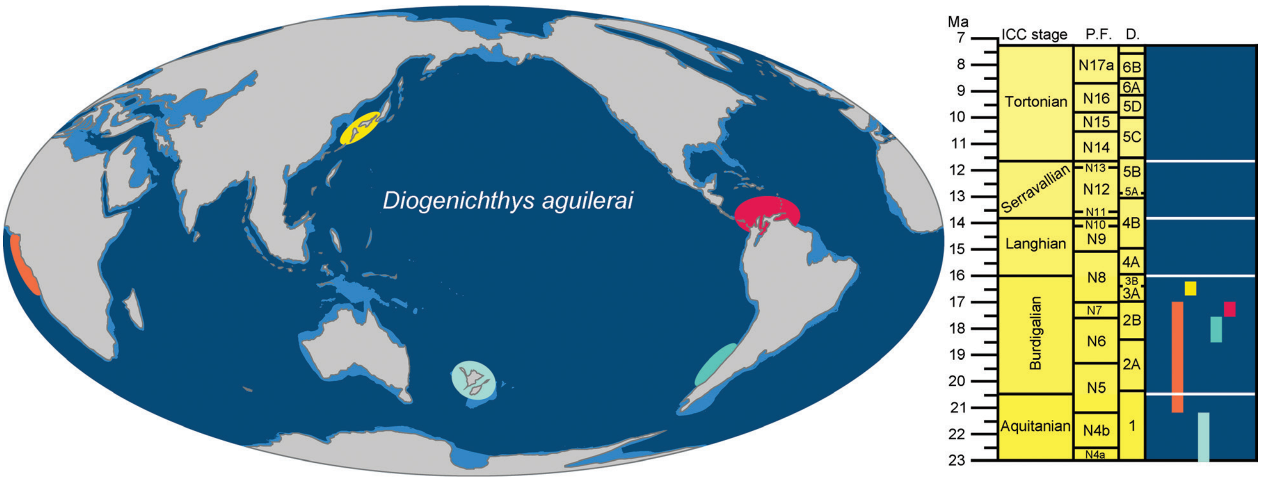

Figure 15. Biostratigraphic and biogeographic distribution of *Diogenichthys aguilerai* Schwarzhans, 2013. See Fig. 12 for database and paleogeographic reconstructions.

3.2.3. The use of myctophid otoliths in biostratigraphy

Myctophid otoliths are easy to recognize as such, although morphological differences between species are often subtle. The fact that they are largely composed of aragonite (like all other teleost otoliths) make them less resistant to diagenesis, leaching, and other syn- and post-depositional effects, but they are also not as easily affected by reworking, as is the case for many more robust constructed microfossils that are used for biostratigraphic purposes. In particular, the delicate denticles along the ventral rim of many myctophid otoliths are easily affected by even brief exposure to erosional abrasion. Therefore, otoliths have the benefit of being mostly autochthonous where preserved (see Carnevale and Schwarzhans 2022). This aspect, in combination with their abundance in pelagic sediments since at least the early Miocene, their diversity, and their often very wide geographical distribution make them potential candidates for biostratigraphic use. Of course, we are currently at the very early stages of using myctophid otoliths for this purpose, but an initial stratigraphic correlation between the Navidad Formation and its equivalents from Chile with the well-known myctophid assemblages of New Zealand has yielded promising results (Schwarzhans and Nielsen 2021). Therefore, in the following, we discuss a number of myctophid otolith-based species observed in the middle Miocene of Japan that appear to have some potential for biostratigraphic purposes in the future.

Diogenichthys aguilerai (Fig. 15) was apparently a very widespread species but, with the exception of the Navidad Formation in Chile (Schwarzhans and Nielsen 2021), has never been found in great quantities. It also

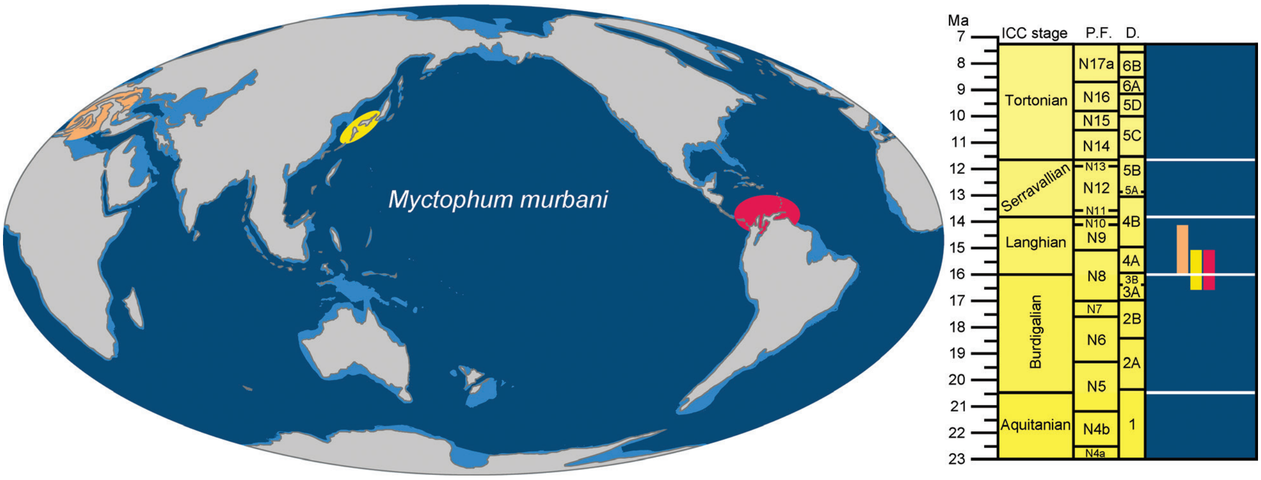

Figure 16. Biostratigraphic and biogeographic distribution of *Myctophum murbani* (Weinfurter, 1952). See Fig. 12 for database and paleogeographic reconstructions.

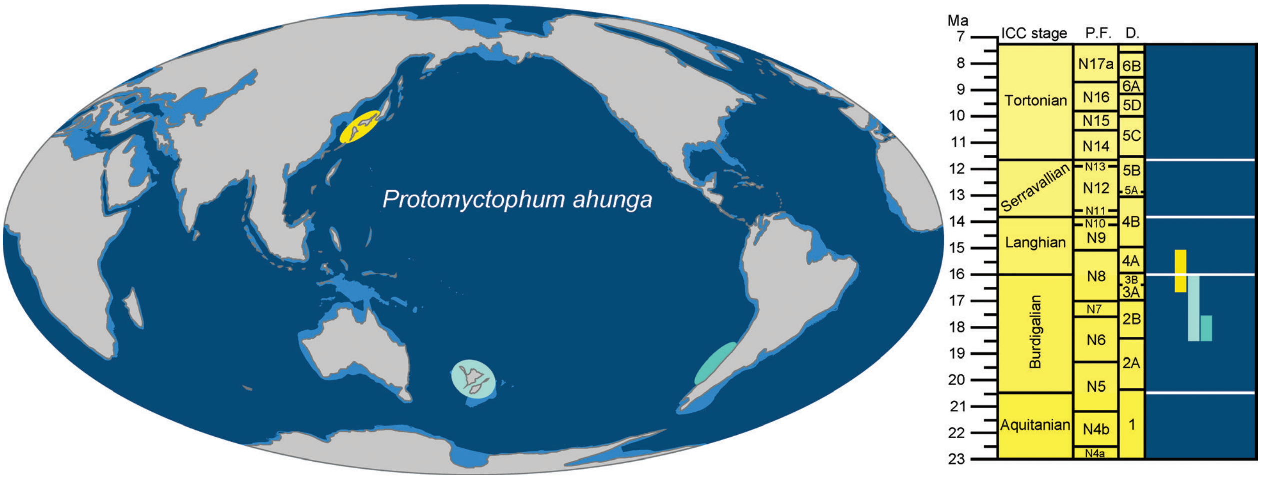

Figure 17. Biostratigraphic and biogeographic distribution of *Protomyctophum ahunga* Schwarzhans, 2019. See Fig. 12 for database and paleogeographic reconstructions.

shows a rather long stratigraphic range from the Aquitanian to the late Burdigalian, with the specimens from Japan described here representing the youngest record. However, *Diogenichthys* otoliths show only a low morphological complexity, and species recognition and distinction by means of otoliths are therefore likely to prove difficult in the future. Therefore, we do not expect *Diogenichthys* otoliths to become prime candidates for biostratigraphic applications despite the seemingly wide geographic distribution that some of the *Diogenichthys* species may exhibit.

In contrast, *Myctophum murbani* (Fig. 16) belongs to a genus the otoliths of which exhibit a relatively larger spectrum of morphological characteristics, which eases their differentiation. Some *Myctophum* species have already been used as stratigraphic indicators (e.g., in tropical America) (Schwarzhans and Aguilera 2013). However, *Myctophum* otoliths are usually not very common, and its fossil species do not seem to be very widely distributed. *Myctophum murbani* may have been more extensively distributed geographically, at least in the northern hemisphere. Furthermore, it has thus far only been positively identified from the late Burdigalian and Langhian, chiefly biozones N8 and N9, and may thus prove to be biostratigraphically useful.

Protomyctophum ahunga (Fig. 17) appears to represent an antitropical transpacific species during the late Burdigalian and Langhian and therefore could prove to be of some regional stratigraphic value.

Ceratoscopelus species are today few, very widely distributed, and common (Froese and Pauly 2021). They would thus seem to be near optimal for superregional stratigraphic purposes. The fossil record in the Miocene, however, has thus far exhibited a much more fractionated distribution pattern as different species are found in different ocean basins, for example tropical West Atlantic (Schwarzhans and Aguilera 2013), the Mediterranean (Bedini et al. 1986), New Zealand (Schwarzhans 2019), and now also Japan with *Ceratoscopelus brevis*. More research will be required to decipher their evolution and to determine their potential for stratigraphic purposes in the Neogene.

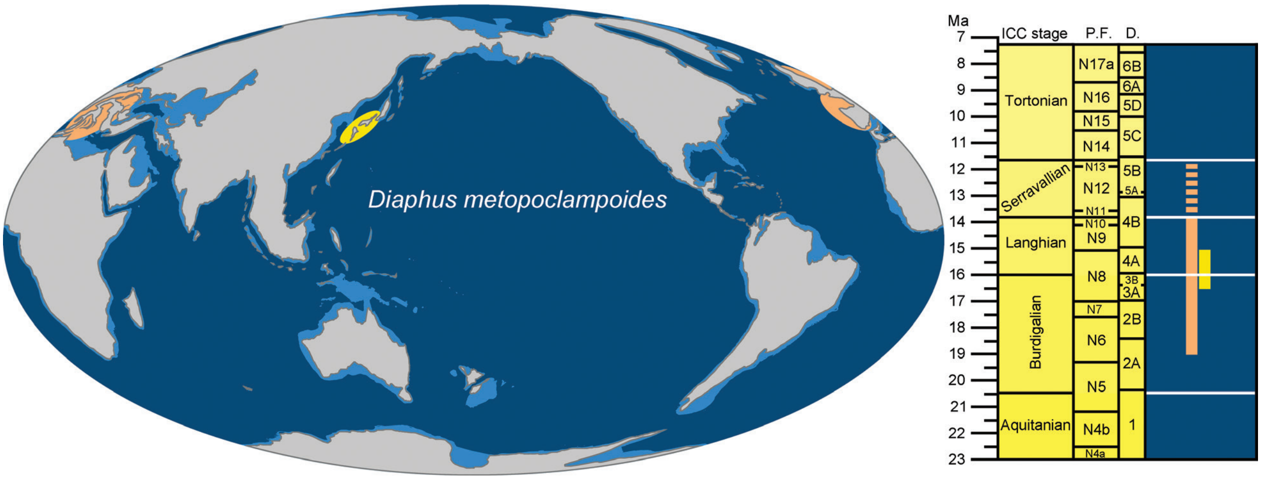

Figure 18. Biostratigraphic and biogeographic distribution of *Diaphus metopoclampoides* Steurbaut, 1983. See Fig. 12 for database and paleogeographic reconstructions.

Otoliths of *Lampadena* are among the most morphologically diverse among the myctophids. They are also often relatively large, which makes identifying them relatively easy and would also make them good candidates for biostratigraphic purposes, as has been demonstrated by Girone and Nolf (2002) with the Pleistocene species *Lampadena ionica* Girone & Nolf, 2002. The here described *L. exima* is known from very few specimens from the late Burdigalian to early Langhian of Japan and the Tortonian of Italy. It also represents an easily recognizable species, but, like so many other species in the genus, it is rare in the fossil record and thus of limited practical value for biostratigraphic purposes.

Lampanyctus otoliths are often difficult to recognize and exhibit little morphological diversity. The Japanese collection described here is the richest in terms of otolith-based *Lampanyctus* species, but mostly lacks potential for comparison with other coeval associations. Future research should evaluate the biostratigraphic potential of *Lampanyctus* otoliths.

Diaphus otoliths are often the most common in Neogene sediments, including the samples described here from Japan, and certainly represent the most taxonomically diverse group. Species are not always easy to distinguish, and identification usually depends on the presence of well-preserved specimens with intact denticles along the ventral rim (which erode easily). Their biostratigraphic usefulness has been postulated several times (e.g., Brzobohatý and Nolf 1995, 2000; Schwarzhans and Aguilera 2013; Schwarzhans 2019; Schwarzhans and Nielsen 2021), and indeed they may represent the prime candidate for such purposes among myctophids. Below, we focus on three species that have been identified in the late Burdigalian to early Langhian of Japan.

Diaphus metopoclampoides (Fig. 18) is one of the most readily recognizable fossil species in the genus *Diaphus*, but its generic allocation is in fact not entirely certain. Brzobohatý and Nolf (2000) stated that it occurred in the Mediterranean from the late Burdigalian until the Messinian. Ongoing research by one of us (WWS), however, has failed to identify this species in the late Miocene (Tortonian and Messinian) of the Mediterranean based on a very large collection. As Brzobohatý and Nolf mentioned, *D. metopoclampoides* bears some resemblance to *Benthosema* otoliths, and it is possible that these researchers mistook late Miocene specimens of *Benthosema taurinense* Carnevale & Schwarzhans, 2022 for *Diaphus metopoclampoides*. If that is true, it would leave a stratigraphic range of the species from the late Burdigalian to Langhian and possibly Serravallian. Furthermore, the species appears to be a temperate to subtropical northern hemisphere species, and its geographic distribution is yet to be investigated. In Japan, *Diaphus epipedus* represents a related coeval species.

Diaphus cassidiformis (Fig. 19) is a small species but is nevertheless relatively easy to recognize by its very compressed shape with an index OL:OH of 1.0–1.1. It was originally described from New Zealand and has subsequently also been identified in West Africa (Schwarzhans 2013b), the Paratethys (following an ongoing review of myctophid otoliths described by Radwanska 1992), and now Japan. Its occurrence is somewhat irregular and disjunctive, which may point to a pseudoceanic rather than high oceanic lifestyle. Thus far, it has not been identified from the Americas. Stratigraphically, it appears to be indicative for the middle Miocene with a confirmed range from the latest Burdigalian (in Japan) through Serravallian (in West Africa). We consider *Diaphus cassidiformis* to be relatively valuable for superregional biostratigraphic correlation.

Diaphus hataii (Fig. 20) was extensively discussed in the previous chapter, which focused on the paleobiogeography of early to middle Miocene myctophids. It is a very common species, particularly in Japan, but is also found in certain basins in Europe and Central America. Its recognition and distinction from other *Diaphus* species, however, are still not well understood and so is its stratigraphic range that seems to be confirmed throughout the Burdigalian and Langhian but could reach into Serravallian or even Tortonian. Tentatively assigned specimens from the early

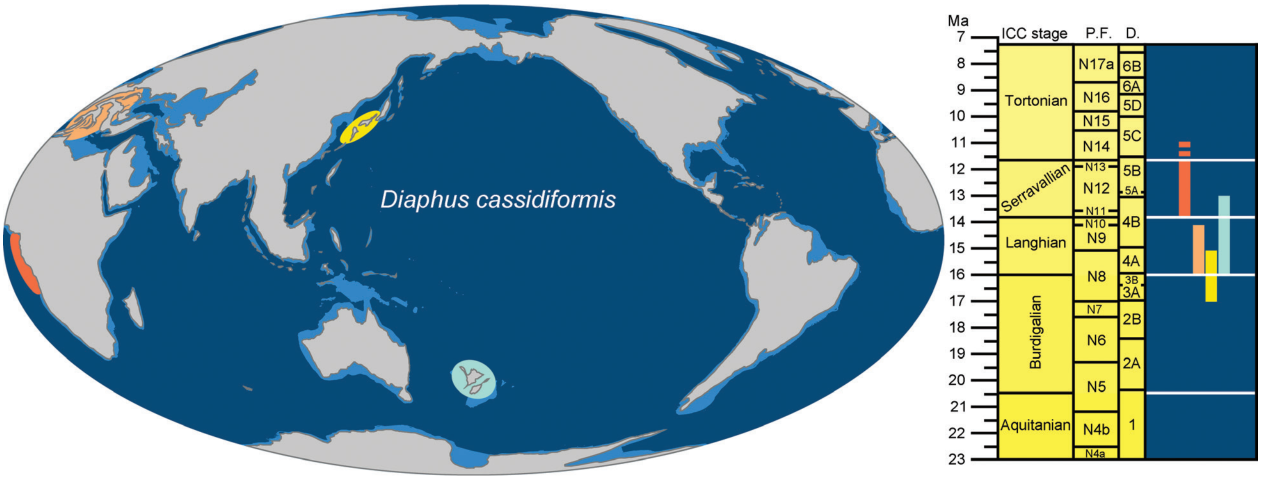

Figure 19. Biostratigraphic and biogeographic distribution of *Diaphus cassidiformis* (Frost, 1933). See Fig. 12 for database and paleogeographic reconstructions.

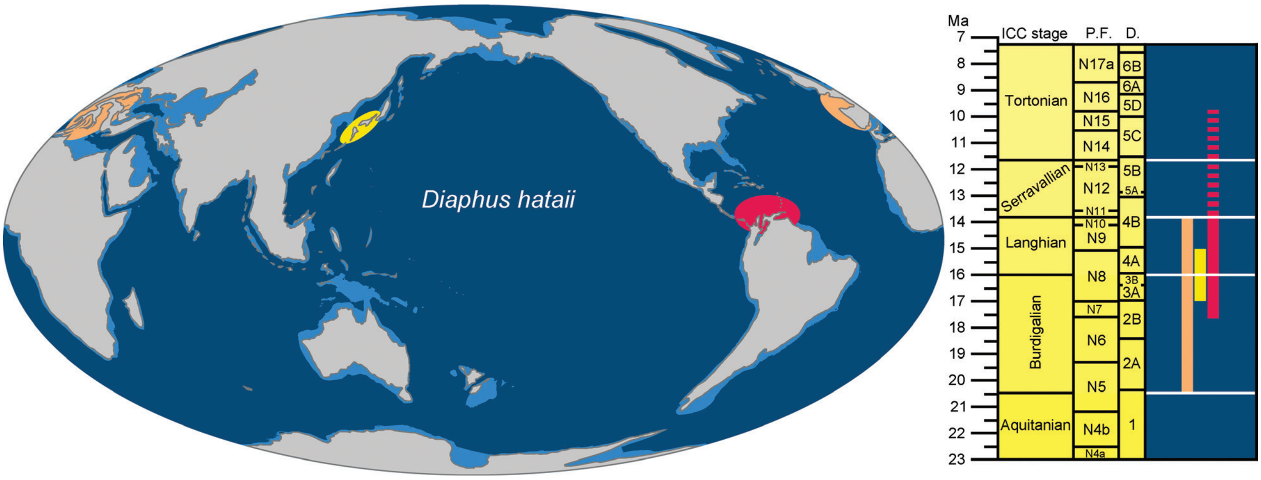

Figure 20. Biostratigraphic and biogeographic distribution of *Diaphus hataii* Ohe & Araki, 1973. See Fig. 12 for database and paleogeographic reconstructions.

Pliocene of Central America in Schwarzhans and Aguilera (2013) likely represent a different species. Nevertheless, despite this species abundance and wide geographic distribution, its practical biostratigraphic value is still problematic and requires further investigation.

4. Conclusions and outlook

The late Burdigalian to early Langhian sediments of western and central Honshu, Japan, have yielded a rich association of myctophid otoliths. This is the first sizeable assemblage so far reported from the Miocene of the North Pacific, with the exception of a study by Ohe and Araki (1973), which, however, was less rich in myctophids. The main results of this study are as follows:

- The myctophid assemblage from the late Burdigalian–early Langhian of Japan fills an important geographic gap and provides initial evidence concerning the composition of mesopelagic fishes at the time from the region.
- A superregional comparison of the early–middle Miocene myctophid assemblage from Japan with faunas from Europe, Central America, and New Zealand indicates that a varied set of shared species existed, which, similarly to the contemporary situation, allows for a direct correlation of mesopelagic fishes from the time across large geographical distances.
- The late early to middle Miocene now harbors the most complete record of fossil myctophids on the globe and indicates the potential of myctophid otoliths with regard to superregional biostratigraphic purposes in the Neogene.

The study of Neogene myctophid otoliths has begun to yield a picture that seems very promising for a variety of future applications, not least the use of these otoliths as an additional tool for superregional biostratigraphy. Otoliths may be less common than planktonic foraminifera or nannoplankton, and they may also be less resistant to destruction by different causes, but they have the advantage of being usually autochthonous due to their vulnerability to erosion. However, much work will be required before a reliable biostratigraphic scheme can be established based on otoliths. Formulating such a scheme will require sampling many more regions of the world and performing detailed stratigraphic sampling. The present study does not really offer much more beyond a glimpse into their potential application. We hope that other researchers will be inspired by the potential of otoliths and thus pay attention to them while conducting their research.

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References

Amano K, Hamuro T, Hamuro M (2004) Latest early-earliest middle Miocene deep-sea molluscs in the Japan Sea borderland: the warm-water Higashibessho fauna in Toyama Prefecture, central Japan. Paleontological Research 8: 29–42. https://doi.org/10.2517/prpsj.8.29

Araki Y (1960a) Tertiary formations of the Awa Basin, Mie Prefecture. Science reports of the Tohoku University, 2nd series, Geology 4: 523–528. [in Japanese]

Araki Y (1960b) Geology, paleontology and sedimentary structures (including Problematica) of the Tertiary formations developed in the environs of Tsu City, Mie Prefecture, Japan. Bulletin of the liberal arts department, Mie University 1, 118 pp.

Bedini E, Francalacci O, Landini W (1986) I pesci fossili del Miocene superiore di Montefiore Conca e Mondaino (Forlì). Memorie del Museo Civico di Storia Naturale di Verona (II serie), sezione Scienze della Terre 3: 1–67.

Blakey R (2020) Deep Time Maps. World Wide Web electronic service. [purchased in March 2021] https://deeptimemaps.com

Blow WH (1969) Late middle Eocene to Recent planktonic foraminiferal biostratigraphy. Proceedings of the First International Conference on Planktonic Microfossils, Geneva 1967, 1: 199–442.

Brzobohatý R (1994) Die Fischotolithen des Badenian von Gainfarn, Niederösterreich (Mittelmiozän, Wiener Becken). Annalen des Naturhistorischen Museums in Wien 96A: 67–93.

Brzobohatý R, Nolf D (1995) *Diaphus* otoliths from the EuropeanOligocene (Myctophidae, Teleostei). Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Sciences de la Terre 65: 257–268.

Brzobohatý R, Nolf D (2000) *Diaphus* otoliths from the European Neogene (Myctophidae, Teleostei). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 70: 185–206.

Brzobohatý R, Stránik Z (2012) Paleogeography of the early Badenian connection between the Vienna Basin and the Carpathian Foredeep. Central European Journal of Geosciences 4: 126–137. https://doi.org/10.2478/s13533-011-0045-z

Chaine J, Duvergier J (1934) Recherches sur les otolithes des poissons. Etude descriptive et comparative de la sagitta des téléostéens. Actes De La Société Linnéenne De Bordeaux 86: 1–254.

Chiji M (1954) On the microbiostratigraphy of the Yatsuo Group in the Yatsuo district of Toyama Prefecture. Journal of the Geological Society of Japan 61: 162–172. [in Japanese] https://doi.org/10.5575/geosoc.61.162

Froese R, Pauly D [Eds] (2020) FishBase. Version 06/2021. http://www.fishbase.se/search.php [accessed September 2021]

Fujiwara Y, Irizuki T, Hayashi H, Tanaka Y, Watanabe M, Shimizu K (2005) Stratigraphy and age of the Miocene Awa Group, eastern Iga City, Mie Prefecture, central Japan. Journal of the Geological Society of Japan 111: 779–791. [in Japanese] https://doi.org/10.5575/geosoc.111.779

Girone A, Nolf D (2002) *Lampadena ionica*, a new teleostean from the Mediterranean Pleistocene. Rivista Italiana di Paleontologia e Stratigrafia 108: 493–500.

Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (2020) Geologic time scale 2020. Elsevier, Amsterdam, 1357 pp. https://doi.org/10.1127/nos/2020/0634

Hasegawa S, Takahashi T (1992) Faunal succession of benthic foraminifera in the upper Yatsuo Group of the Hokuriku district, central Japan: A temporal faunal trend during an early-middle Miocene transgression in Japan. Centenary of Japanese Micropaleontology: 51–66.

Hatai K (1965) Some Pliocene fish otoliths from Japan. Senckenbergiana Lethaea 46: 133–143.

Hayakawa H, Takemura A (1987) The Neogene system in the Yatsuo area, Toyama Prefecture, central Japan. Journal of the Geological Society of Japan 93: 717–732. [in Japanese] https://doi.org/10.5575/geosoc.93.717

Hoshi H, Iwano H, Danhara T, Oshida H, Hayashi H, Kurihara Y, Yanagisawa Y (2019) Age of the N7/N8 (M4/M5) planktonic foraminifera zone boundary: constraints from the zircon geochronology and magnetostratigraphy of early Miocene sediments in Ichishi, Japan. Chemical Geology 530: 1–16. https://doi.org/10.1016/j.chemgeo.2019.119333

Hulley PA (1981) Results of the research cruises of FRV "Walter Herwig" to South America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). Archiv für Fischereiwissenschaft 31: 1–300.

Hulley PA, Lutjeharms JRE (1989) Lanternfishes of the southern Benguela region. Part 3. The pseudoceanic-oceanic interface. Annales of the South African Museum 98: 409–435.

Imamura S, Kojima G, Umegaki Y (1953) Field Excursion Guide: Kamine, Funasa, Miyoshi, Mirasaka, Shobara and Shokozan Areas. Institute of Geology and Mineralogy, Science faculty, Hiroshima University, 59 pp. [In Japanese, original title translated]

Irizuki T, Hosoyama M (2006) The Shukunohora and Oidawara Formations, Mizunami Group: the marine deposit from the tropical shallow-marine to the maximum transgression. In: Geological Society of Japan (Ed.) Regional Geology of Japan, 4, Chubu region. Asakura Publishing, Tokyo, 4, 370–371. [in Japanese, original title translated]

Irizuki T, Yanagisawa Y, Kimura M, Kato K, Hoshi H, Hayashi H, Fujiwara Y, Akai K (2021) Biostratigraphy and correlation of the lower to middle Miocene in the Setouchi Geologic Province of the Kinki District, Southwest Japan. Journal of the Geological Society of Japan 127: 415–429. [in Japanese] https://doi.org/10.5575/geosoc.2021.0002

Itoigawa J (1960) Paleoecological studies of the Miocene Mizunami Group, central Japan. The Journal of Earth Sciences, Nagoya University 8: 246–300.

Itoigawa J (1961) Cenozoic Formation in the Awa Basin, Ayama-gun, Mie Prefecture, Japan. Professor Jiro Makiyama Memorial Volume: 59–66. [in Japanese]

Itoigawa J (1974) Geology of the Mizunami Group. Bulletin of the Mizunami Fossil Museum 1: 9–42. [in Japanese, original title translated]

Itoigawa J (1980) Geology of the Mizunami district, central Japan. Monograph of the Mizunami Fossil Museum 1: 1–50. [and geological map] [in Japanese]

Itoigawa J, Nishikawa I (1976) A few problems on the Miocene Setouchi Series in the northern part of Okayama-Hiroshima Prefecture, southwest Japan. Bulletin of the Mizunami Fossil Museum 3: 127–149. [in Japanese]

Itoigawa J, Shibata H, Nishimoto H (1974) Molluscan fossils from the Mizunami Group. Bulletin of the Mizunami Fossil Museum 1: 43–204. [in Japanese, original title translated]

Kawai M (1957) Geology of the Tsuyama-Tobu District (Quadrangle series, Scale 1:50000). Geological Survey of Japan, Tsukuba. [in Japanese]

Kawamura K, Suto I, Yanagisawa Y (2011) Diatom biostratigraphy of the middle Miocene Oidawara Formation in the Mizunami area, Gifu Prefecture, central Japan. Diatom 27: 17–32. [in Japanese]

Koken E (1884) Über Fisch-Otolithen, insbesondere über diejenigen der norddeutschen Oligocän-Ablagerungen. Zeitschrift Der Deutschen Geologischen Gesellschaft 36: 500–565.

Lin C-H, Girone A, Nolf D (2015) Tortonian fish otoliths from turbiditic deposits in Northern Italy: Taxonomic and stratigraphic significance. Geobios 48: 249–261. https://doi.org/10.1016/j.geobios.2015.03.003

Linkowski TB (1997) Zmienność morfologiczna, systematyka i specjacja grupy *Ceratoscopelus townsendi - C. warmingii* (Osteichthyes: Myctophidae) w świetle badań morfologii i mikrostruktury otolitów. Morski Instytut Rybacki, Gdynia, 198 pp. [in Polish]

Makiyama J (1930) Outline of Tertiary in Ishikawa and Toyama Prefectures. Chikyu (Globe) 14: 161–174. [in Japanese, original title translated]

Martin RP, Olson EE, Girard MG, Smith WL, Davis MP (2018) Light in the darkness: New perspective on lanternfish relationships and classification using genomic and morphological data. Molecular Phylogenetics and Evolution 121: 71–85. https://doi.org/10.1016/j.ympev.2017.12.029

Nakajima T, Iwano H, Danhara T, Yamashita T, Yamagisawa Y, Tanimura Y, Watanabe M, Sawaki T, Nakanishi S, Mitsuishi H, Yamashina O, Imahori S (2019) Revised Cenozoic chronostratigraphy and tectonics in the Yatsuo area, Toyama Prefecture, central Japan. Journal of the Geological Society of Japan 125: 483–516. [in Japanese] https://doi.org/10.5575/geosoc.2019.0005

Nishimatsu K (2019) Deep-sea elasmobranchs from the late early to middle Miocene (Burdigalian-Langhian) Makino Formation (Awa Group), Japan. Journal of Vertebrate Paleontology article 39(2): e1597729. [11 pp] https://doi.org/10.1080/02724634.2019.1597729

Nishimatsu K, Ujihara A (2019) A new deep-sea shark *Scymnodalatias kazenobon* (Squaliformes, Somniosidae) from the Miocene Yatsuo Group in central Japan. Paleontological Research 23: 23–28. https://doi.org/10.2517/2018PR006

Nishimatsu K, Ujihara A (2020) Deep-sea elasmobranch fauna with the first descriptions of genera *Arynchobatis* and *Pseudoraja* from the Miocene Yatsuo Group in Toyama, central Japan. Historical Biology 32: 1120–1142. https://doi.org/10.1080/08912963.2019.1566325

Nolf D (2013) The diversity of fish otoliths, past and present. Royal Belgian Institute of Natural Sciences, Brussels, 222 pp.

Ogasawara K (1994) Neogene paleogeography and marine climate of the Japanese Islands based on shallow-marine molluscs. Palaeogeography, Palaeoclimatology, Palaeoecology 108: 335–351. https://doi.org/10.1016/0031-0182(94)90241-0

Ohe F (1977) Otoliths from the Dainichi Sand and Hosoya tuffaceous Beds of Kakegawa Group (Pliocene), Shizuoka Prefecture, Central Japan. Kaseki no tomo. Bulletin of the Tokai Fossil Society 16: 13–19.

Ohe F (1981) Fish-otoliths from the Dainichi Sand and the Hosoya tuffaceous Members of the Pliocene Kakegawa Group, Shizuoka Prefecture, Central Japan. Bulletin of the Senior High School attached to the Aichi University of Education 8: 125–194.

Ohe F (1985) Marine fish otoliths of Japan. The senior high school attached to the Aichi University of Education, special volume of Bulletin (Earth Science): 1–184.

Ohe F (1990) Faunal change of the Miocene marine fish in Japan. Monograph of the Mizunami Fossil Museum 7: 25–60. [in Japanese with English summary]

Ohe F, Araki Y (1973) Some Miocene fish otoliths from the Yakuoji Formation, Tsu, Mie Prefecture. Science reports of the Tohoku University, second series (Geology) 38: 1–15.

Ohe F, Yamaoka M (1980) Some myctophid and pterothrissid fish otoliths from the Miocene Toyohama and Yamami formations, Chita Peninsula, central Japan. Nagoya Chigoku 38: 1–15.

Okada H, Bukry D (1980) Supplementary modification and introduction of code number to the low-latitude coccolith biostratigraphic zonation (Bukry, 1973;1975). Marine Micropaleontology 5: 321–325. https://doi.org/10.1016/0377-8398(80)90016-X

Oshida H, Hayashi H, Yanagisawa Y, Kurihara Y, Hoshi H (2018) Planktonic foraminiferal and diatom biostratigraphy of the upper part of the Miocene Ichishi Group in Mie Prefecture, central Honshu, Japan. Journal of the Geological Sciety of Japan 124: 919–933. [in Japanese] https://doi.org/10.5575/geosoc.2018.0032

Ozawa H (2016) Early to Middle Miocene ostracods from the Yatsuo Group, central Japan: significance for the Bathyal Fauna between

Japan Sea and Northwest Pacific Ocean during the back-arc spreading. Paleontological Research 20: 121–144. https://doi.org/10.2517/2015PR028

Radwanska U (1992) Fish otoliths from the Middle Miocene (Badenian) deposits of southern Poland. Acta Geologica Polonica 42: 141–328.

Schwarzhans W (1978) Otolith-morphology and its usage for higher systematical units with special reference to the Myctophiformes s.l. Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie 15: 167–185.

Schwarzhans W (1980) Die tertiäre Teleosteer-Fauna Neuseelands, rekonstruiert anhand von Otolithen. Berliner Geowissenschaftliche Abhandlungen, A 26: 1–211.

Schwarzhans W (2010) The otoliths from the Miocene of the North Sea Basin. Backhuys Publishers, Leiden & Margraf Publishers, Weikersheim, 352 pp.

Schwarzhans W (2013a) A comparative morphological study of the Recent otoliths of the genera *Diaphus*, *Idiolychnus* and *Lobianchia* (Myctophidae). Palaeo Ichthyologica 13: 41–82.

Schwarzhans W (2013b) Otoliths from the Miocene of West Africa, primarily from the Mandorové Formation of Gabon. Palaeo Ichthyologica 13: 151–184.

Schwarzhans W (2019) Reconstruction of the fossil marine bony fish fauna (Teleostei) from the Eocene to Pleistocene of New Zealand by means of otoliths. Memorie Della Società Italiana Di Scienze Naturali e Del Museon Di Storia Naturale Di Milano 46: 3–326.

Schwarzhans W, Aguilera OA (2013) Otoliths of the Myctophidae from the Neogene of tropical America. Palaeo Ichthyologica 13: 83–150.

Schwarzhans W, Carnevale G (2021) The rise to dominance of lanternfishes (Teleostei: Myctophidae) in the oceanic ecosystems: a paleontological perspective. Paleobiology 47: 446–463. https://doi.org/10.1017/pab.2021.2

Schwarzhans WW, Nielsen SN (2021) Fish otoliths from the early Miocene of Chile: a window into the evolution of marine bony fishes in the Southeast Pacific. Swiss Journal of Palaeontology 140: e16. [62 pp] https://doi.org/10.1186/s13358-021-00228-w

Schwarzhans W, Ohe F (2019) Lanternfish otoliths (Teleostei, Myctophidae) from the Pliocene and Pleistocene of Japan. Rivista Italiana di Paleontologia e Stratigrafia 125: 355–400.

Seto K (1992) Benthic foraminiferal assemblage from the Mizunami Group. Bulletin of the Mizunami Fossil Museum 19: 165–191. [in Japanese]

Shibata H (1967) Geology of the Miocene Ichishi Group. Journal of the Geological Society of Japan 73: 337–346. [in Japanese] https://doi.org/10.5575/geosoc.73.337

Shibata H (1970) Molluscan faunas of the First Setouchi Series, southwest Japan: Part 1. Fauna of the Ichishi Group. Journal of Earth Sciences, Nagoya University 18: 27–84.

Shibata H (1978) Molluscan paleoecology of the Miocene First Setouchi Series in the eastern part of the Setouchi Geologic Province, Japan. Bulletin of the Mizunami Fossil Museum 5: 23–110.

Shibata H, Itoigawa J (1980) Miocene paleogeography of the Setouchi Province, Japan. Bulletin of the Mizunami Fossil Museum 7: 1–49. [in Japanese]

Shimizu M, Fujii S, Hamuro T (2000) Newly found *Aturia* and molluscan fossil assemblages from Higashibessho Formation, Hokuriku Group, Toyama Prefecture, central Japan. Earth Science (Chikyu Kagaku) 54: 43–48. [in Japanese]

Smale MJ, Watson G, Hecht T (1995) Otolith atlas of South African marine fishes. Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology 1: 1–253. https://doi.org/10.5962/bhl.title.141860

Steurbaut E (1983) Les otolithes de téléostéens de la Formation de Tanaro (Langhian inférieur du Piémont, Italie septentrionale). Geologica et Paleontologica 17: 255–263.

Steurbaut E (1984) Les otolithes de téléostéens de l'Oligo-Miocène d'Aquitaine (Sud-Ouest de la France). Palaeontographica A 186: 1–162.

Taguchi E (2002) Stratigraphy, molluscan fauna and paleoenvironment of the Miocene Katsuta Group in Okayama Prefecture, Southwest Japan. Bulletin of the Mizunami Fossil Museum 29: 95–133.

Takahashi M (1976) Some Miocene fish otoliths from the Mizunami Group, central Japan. Bulletin of the Mizunami Fossil Museum 3: 55–72. [in Japanese]

Takahashi M (1977) Some Pliocene fish otoliths from the Dainichi sands, Kakegawa Group, central Japan. Bulletin of the Mizunami Fossil Museum 4: 97–118. [in Japanese]

Takeyama T (1930) Preliminary report on the geology in the Tsuyama Basin. Globe (Chikyu) 14: 91–101. [in Japanese, original title translated]

Takimoto K (1935) Cenozoic system in the Ichishi-gun area, Mie Prefecture. Globe (Chikyu) 23: 326–338. [in Japanese, original title translated]

Tamaki M, Itoh Y, Watanabe M (2006) Paleomagnetism of the Lower to Middle Miocene Series in the Yatsuo area, eastern part of southwest Japan: clockwise rotation and marine transgression during a short period. Bulletin of the Geological Survey of Japan 57: 73–88. https://doi.org/10.9795/bullgsj.57.73

Tamura M (1957) On the coal bearing tertiary formations in the northern part of Okayama Pref. Memories of the faculty of education Kumamoto University 5: 177–184. [in Japanese]

Tsuda K (1960) Paleo-ecology of the Kurosedani fauna. Journal of the Faculty of Science, Niigata University, Series II 3: 171–203. [in Japanese]

Ueda T (1986) The Miocene Bihoku Group and its molluscan assemblages in the Shobara district, Hiroshima Prefecture, west Japan. Earth Science (Chikyu Kagaku) 40: 437–448. [in Japanese]

Watanabe Y, Ishigaki T (1986) Stratigraphy and sedimentary environment of the Miocene Bihoku Group in the Tojo Area, southwest Japan. Bulletin of the Mizunami Fossil Museum 13: 15–26.

Watanabe M, Miyake M, Nazaki S, Yamamoto Y, Takemura A, Nishimura T (1999) Miocene diatom fossils from the Bihoku Group in Koyamaichi area and the Katsua Group in Tsuyama area, Okayama Prefecture, southwestern Japan. Journal of the Geological Society of Japan 105: 116–121. [in Japanese] https://doi.org/10.5575/geosoc.105.116

Weiler W (1959) Miozäne Fisch-Otolithen aus der Bohrung S. Pablo 1 im Becken von Veracruz in Mexiko. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 109: 147–172.

Weinfurter E (1952) Die Otolithen der Wetzelsdorfer Schichten und des Florianer Tegels (Miozän, Steiermark). Sitzungsberichte der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse I 161: 455–498.

Yanagisawa Y (1999) Diatom biostratigraphy of the lower to middle Miocene sequence in the Yatsuo area, Toyama Prefecture, central

Japan. Bulletin of the Geological Survey of Japan 50: 139–165. [in Japanese]

Yanagisawa Y, Akiba F (1998) Refined Neogene diatom biostratigraphy for the northwest Pacific around Japan, with an introduction of code numbers for selected diatom biohorizons. Journal of the Geological Society of Japan 104: 395–414. https://doi.org/10.5575/geosoc.104.395

Yoshida F (1987) Planktonic foraminifera from the Miocene Awa Group, Mie Prefecture, central Japan. Bulletin of the geological survey of Japan 38: 473–483. [in Japanese]

Yoshida F (1991) Planktonic foraminifera from the Ichishi, Fujiwara and Morozaki Groups in the eastern Setouchi geologic province, central Japan. Bulletin of the Mizunami Fossil Museum 18: 19–32.

Yoshida F, Takahashi Y, Nishioka Y (1995) Geology of the Tsu-Seibu District (Quadrangle series, Scale 1:50000). Geological Survey of Japan, Tsukuba. [in Japanese]

Yoshida H, Asahara Y, Yamamoto K, Katsuta N, Minami M, Metcalfe R (2019) $^{87}Sr/^{86}Sr$ age determination by rapidly formed spherical carbonate concretions. Scientific Reports 9: 1–7. https://doi.org/10.1038/s41598-019-38593-9