Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 125(2): 355-400. **July 2019**

LANTERNFISH OTOLITHS (TELEOSTEI, MYCTOPHIDAE) FROM THE PLIOCENE AND PLEISTOCENE OF JAPAN

WERNER SCHWARZHANS[1] & FUMIO OHE[2]

[1]Ahrensburger Weg 103, D-22359 Hamburg; Natural History Museum of Denmark, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen. E-mail: wwschwarz@aol.com
[2]Nara National Research Institute for Cultural Properties, Nara 630-8577, Japan. E-mail: fumi-ohe-fish@rio.odn.ne.jp

To cite this article: Schwarzhans W. & Ohe F. (2019) - Lanternfish otoliths (Teleostei, Myctophidae) from the Pliocene and Pleistocene of Japan. *Riv. It. Paleontol. Strat.*, 125(2): 355-400.

Keywords: Japan; late Neogene; Myctophidae; otoliths; Kakegawa; Okinawa; Shikoku; Fiji.

Abstract. Myctophid otoliths are the most common fossil otoliths to be found in Neogene deep water sediments below approximately 200 m depositional depth. The southeastern part of Japan is particularly rich in such locations. Here we describe myctophid otoliths from late Pliocene to early Pleistocene locations on Okinawa, Shikoku and central Honshu and review previous publications. These faunas represent the tropical to subtropical faunal zone, which was established as the "Kakegawa Fauna" based on molluscs. A total of 37 species are recognized by means of otoliths in the family Myctophidae and one in the family Neoscopelidae. Two species are recorded in open nomenclature, 23 as persistent extant species and 12 extinct species, thereof 7 new. The new species are: *Diaphus caurus, Diaphus endoi, Diaphus kakegawaensis, Diaphus nafpaktitisi, Diaphus noboriensis, Symbolophorus moriguchii* and *Notoscopelus praejaponicus*. Two very large myctophid otoliths (>8 mm length) from the putative Piacenzian of Fiji are also described, one being a new species - *Diaphus grebneffi* - representing the largest by far otolith associated with the So-group of species in the genus so far known.

The myctophid otolith assemblage is characterized by an abundance of large specimens (>5 mm length) which certainly derived from fully adult fishes and represents the biggest association of its kind described so far from the fossil record of the northern Pacific. Its composition is interpreted for stratigraphic and environmental purposes. The occurrence of a few, rare species with links to coeval finds in the Caribbean exemplify the potential of myctophid otoliths for supraregional biostratigraphic purposes. The comparison of the fossil assemblage with the distribution in the Recent supports the concept of a warm "Kakegawa Fauna" as established by molluscs and at the same time documents that certain tropical species reached further north during the late Pliocene than they do today.

Introduction

Mesopelagic fishes constitute the largest biomass of any vertebrate group in any of the world's environments (Irigoien et al. 2014). The dominant taxa in mesopelagic fishes are lanternfishes (Myctophidae) and bristlemouths (*Cyclothone* spp., family Gonostomatidae). Fishes of the family Myctophidae are widely distributed in the midwaters of all major oceans. With nearly 250 currently recognized species, the Myctophidae represent the family inhabiting open oceans with the most species. Sediments dredged from the sea bottom were found to be dominated by myctophid otoliths below a water depth of 200 m (Schwarzhans 2013a). Similar observations have been made in the fossil record where myctophid otoliths dominate all pelagic sediments of Neogene times (Schwarzhans & Aguilera 2013). The earliest unambiguous myctophid records are from the late Paleocene (Schwarzhans 1985). During Eocene and Oligocene they form regular faunal elements in many intermediate and deepwater deposits (Nolf & Steurbaut 1988, 1990, 2004), but it is only during the Miocene that they increased to the degree of abundance foreshadowing the dominance

Received: February 17, 2019; accepted: April 16, 2019

in todays oceans. An acceleration of diversity and increased growth has been observed beginning with the times of the biogenic bloom during late Miocene and Pliocene (Schwarzhans & Aguilera 2013).

Japan occupies an important location in respect to the ocean currents of the NW Pacific. It is under the influence of the Kuroshio warm water current that splices off from the North Equatorial Current (NEC) off Luzon and flows northwards along the east coast of Taiwan, along the 200 m shelf break line in the East China Sea west of the Ryukyu Island Chain and along the Pacific shore of southern Japan up to central Honshu north of Tokyo before turning eastwards as the Kuroshio Extension into the open Pacific (Qiu 2001). It is met by the counter-directional Oyashio cold water current flowing southwards along the Kuriles Island Chain and off the Pacific coast of Hokkaido (Qiu 2001). The Kuroshio and Oyashio currents meet off the coasts between Choshi and Kinkazan, resulting in a rich fish fauna of that area (Masuda et al. 1984). The Kuroshio warm water current is essential for the thriving of many fish species of the rich tropical West Pacific fauna of the Philippines, and of the evolution of warm water endemic fishes off the Ryukyus and southern Japan. This is also reflected in the highly diverse myctophid fauna found in Japanese waters (Kawaguchi & Shimizu 1978).

The purpose of our study is to describe and evaluate the rich myctophid otolith-based fauna obtained from three areas within the early late Pliocene to early Pleistocene “Kakegawa Fauna” (Matsubara 2004) ranging from about 3.58 to 1.4 Ma and representing the early geological equivalent of todays southern Japanese bioprovince under the influence of the Kuroshio Current. The otoliths were obtained from the Shinzato Formation (3.1-2.3 Ma) of Okinawa (and few otoliths from the upper Yonabaru Formation, 3.58-3.1 Ma; and Chinen Formation, 1.9-1.6 Ma), from the Nobori Formation (3.35-3.1 Ma) of the Shikoku Island, and from the Dainichi Formation (2.3-1.9 Ma) and an interval in the Hijikata Formation (1.6-1.4 Ma) of the Kakegawa area, Shizuoka Prefecture, central Honshu. It is a rich collection of more than 2500 myctophid otolith specimens spanning the time interval of late Pliocene to early Pleistocene. It represents an important cornerstone for the long-term target of developing a superregional biostratigraphic correlation scheme based on myctophid otoliths.

The otoliths of the Dainichi Formation and of the Hosoya Tuffaceous Member have been subject of a monograph by Ohe (1981, as Fosoya tuffaceous member) and those of the Hijikata Formation by Ohe (1983). The myctophid otoliths described by Ohe (1981 and 1983) are being reviewed in this study. Previous studies of otoliths from the Dainichi Formation by Ohe (1977) and Takahashi (1977) include few myctophid otoliths and are revised from their respective documentations. Aoki (1971) and Aoki & Baba (1980) described otoliths from the middle to late Pleistocene from northwestern central Honshu, Boso and Miura Peninsulas, which have not been subject to review. In two instances their documentations allowed revision: the extant *Ceratoscopelus warmingii* as senior synonym of *Otolithus (Myctophidarum) makutaensis* Aoki, 1971 and the extant *Diaphus theta* as senior synonym of *Diaphus quadratus* Aoki & Baba 1980. Their proclivity must be criticized of having introduced many new species for such young geological otoliths seemingly without adequate knowledge of extant species. Ohe et al. (1997) described a few otoliths from the late Pleistocene Ryukyu limestone sequence of Okinawa containing a few myctophid otoliths, which as far as can be identified all represent extant species.

LOCATIONS AND GEOLOGICAL SETTING

The otoliths investigated and described for this study originated from several locations in three distinct regions of southern Japan. From South to North they are: Okinawa, Kochi on Shikoku and Kakegawa on central Honshu (Fig. 1). The sampled sediments are of late Pliocene to early Pleistocene age spanning the time interval from early Piacenzian to early Calabrian and represent the faunal province of the tropical to subtropical “Kakegawa Fauna” (Nakamura et al. 1999; Tsuchi 2002).

The Pliocene-Pleistocene biostratigraphic framework in Japan is based primarily on planktonic foraminifer zones (Ikebe et al. 1981; Ujiie 1985, 1994) and nannoplankton zones (Tanaka & Ujiie 1984). We follow the most widely used planktonic foraminifer zonation. Two planktonic foraminifer biozonation schemes are generally used. Blow (1969) defined the biozone N21 by the first appearance date (FAD) of *Globorotalia tosaensis* and the biozone N22 by the FAD of *Globorotalia trun-*

Fig. 1 - Location plate showing the three regions from which Pliocene-Pleistocene otoliths were collected.

catulinoides. The biozone N20 is not recognized in Japan and therefore N21 follows directly on N19. The chronological age for the FAD of *G. tosaensis* was noted as 3.35 Ma and that of *G. truncatulinoides* as 1.93 Ma by Wade et al. (2011). The FAD of *G. truncatulinoides* was found to be diachronous in the SW-Pacific where it occurs earlier by 0.5 Ma (Dowsett 1988).

The biozonation of Berggren (1973) as emended by Berggren et al. (1995) is more detailed in the interval of interest and nowadays is more widely used. It does not make use of the FAD's of *G. tosaensis* or *G. truncatulinoides* but instead relies on a set of last appearance dates (LAD). The relevant planktonic foraminifer zones of that scheme for the studied intervals are the following: PL3 defined as the biostratigraphic interval between the LAD of *Globorotalia margaritae* (base) and the LAD of *Sphaeroidinellopsis seminulina* (top); PL4 defined as a short biostratigraphic interval from the LAD of *Sphaeroidinellopsis seminulina* (base) to the LAD of *Dentoglobigerina altispira* (top); PL5 defined as the biostratigraphic interval between the LAD of *Dentoglobigerina altispira* (base) and the LAD of *Globorotalia miocenica* (top); PL6 defined as the biostratigraphic interval from the LAD of *Globorotalia miocenica* (base) to the LAD of *Globigerinoides fistulosus* (top); PT1a defined as the biostratigraphic interval between the LAD of *Globigerinoides fistulosus* (base) and the LAD of *Globorotalia tosaensis* (top). Berggren's (1973) zones PL4-6 would correspond to Blow's (1969) zone N21.

However, there are certain complications when correlating the changing definitions of the biozones and associated geochronological calibrations. Wade et al. (2011) reviewed the Cenozoic tropical planktonic foraminiferal biostratigraphy and calibrated 187 events with a geochronological time scale. They listed rather strongly departing time intervals for the biozones PL3 through PL6 between the Atlantic (Berggren's type scheme) and the Pacific (see also Chunlian et al. 2012). Following their assessment the Pacific LAD of *Sphaeroidinellopsis seminulina* would be 3.59 Ma (vs 3.16 Ma in the Atlantic) and of *Dentoglobigerina altispira* 3.47 Ma (vs 3.13 Ma in the Atlantic), i.e., prior to the FAD of *Globorotalia tosaensis* at 3.35 Ma. This assessment is obviously in conflict with observations made by Ujiie (1985) in Okinawa who found *G. tosaensis* and *D. altispira* overlapping for a certain interval and Takayanagi & Saito (1962) at Nobori on Shikoku who described all three species co-occurring (see also discussion below of Nobori location). We have therefore decided for the purpose of this work to remain with Berggren's et al. (1995) original definition and timing.

Okinawa (Fig. 2): The majority of otoliths from this area were obtained from the mudstones and siltstones of the Shinzato Formation (FM), the youngest formation in the Shimajiri Group (Ujiie & Kaneko 2006). The Shinzato FM comprises the planktonic foraminifer zone PL5 (after the LAD of *Dentoglobigerina altispira*) and thus the late Piacenzian to early Gelasian. Few specimens were obtained from the upper Yonabaru FM (PL3, early Piacenzian) and the Chinen FM (PT1a, early Calabrian). The Shinzato and Yonabaru FMs represent the upper Shimajiri Group and are characterized by clastic dominated sediments deposited at a water depth of 250 to 1000 m (Noda 1977; Nakagawa et al. 2001; Imai et al. 2013). The Chinen FM represents the basal unit of the overlying Ryukyu Group of middle to late Pleistocene age. The contact to the underlying Shinzato FM forms a widespread unconformity and is characterized by a drastic change in sedimentation from a clastic dominated "mud sea" to a carbonatic dominated "coral sea" (Imai et al. 2013).

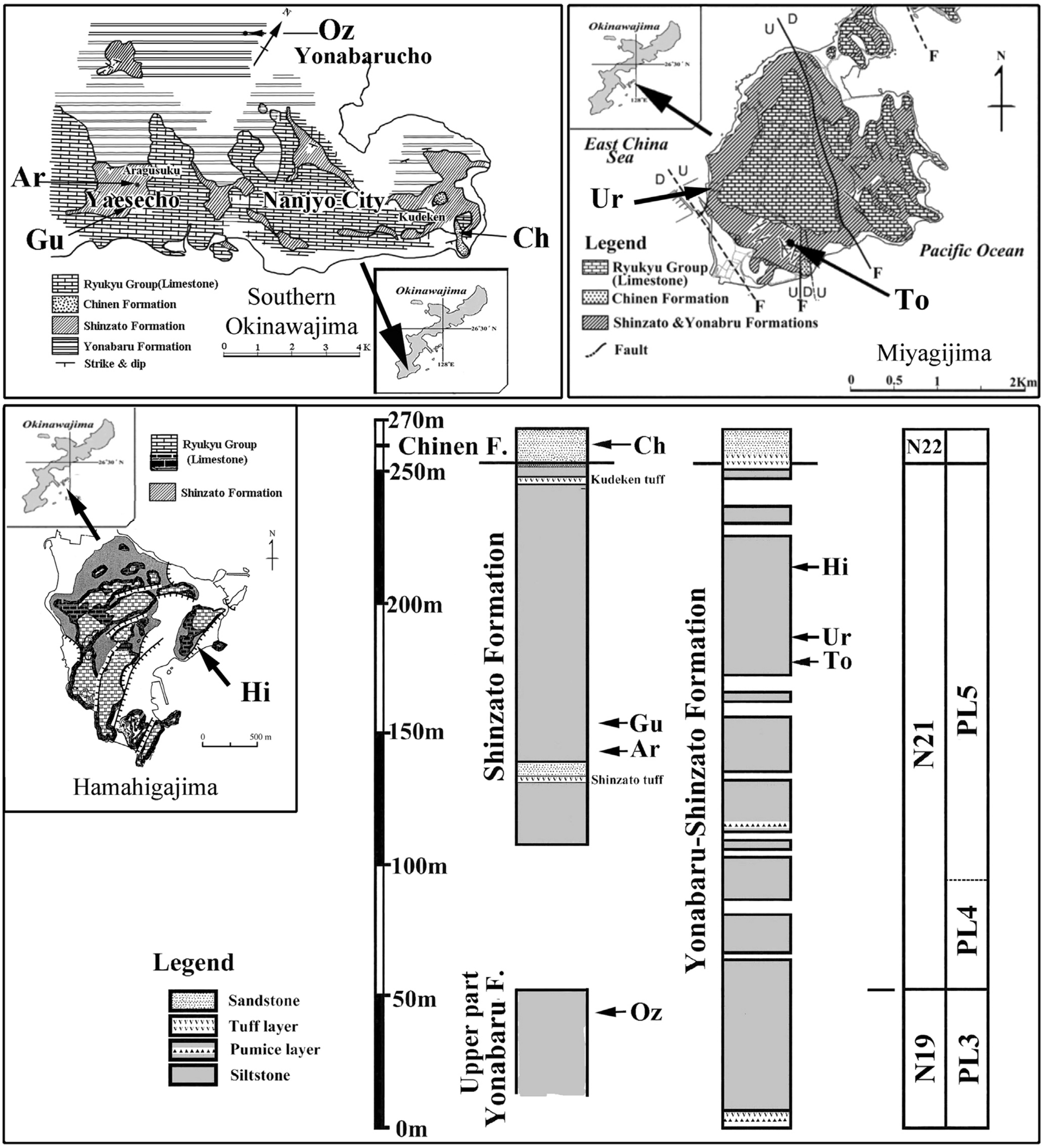


Fig. 2 - Okinawa region location plate. Map of southern Okinawajima from Tsuchi (1975), map of Hamahigajima from Oshimizu & Iryu (2002), map from Miyagijima from Hanagata (2004) Left stratigraphic column refers to southern Okinawajima after Ibaraki (1979) and Noda (1980); right stratigraphic column refers to Hamahigajima and Miyagijima after Oshimizu & Iryu (2002) and Hanagata (2004). Abbreviations used for localities are: Ar = Aragusku, Ch = Chinen, Gu = Gushichan, Hi = Higa , Oz = Ozatofurugen, To = Tobaru, Ur = Uruma.

The Chinen FM is essentially composed of calcareous sandstones while the younger Ryukyu Group formations grade from platform carbonates to reefal environments (Ujiie & Kaneko 2006). Gallagher et al. (2015) explained the change in sedimentation along the Pacific side of the Ryukyu chain as an expression of the paleo-Kuroshio Current switching from a course east of the Ryukyus to a course in the back-arc of the islands. They assumed the Kuroshio Current having been in place and flowing northwards to near todays extend by c. 5 Ma. The Chinen FM is interpreted to have been deposited at 100 to 300 m water depth (Sato et al. 2004; Imai et al. 2013).

The stratigraphy of the section is primarily based planktonic foraminifers (Ibaraki & Tsuchi 1975; Ujiie 1985; Hanagata 2004), nannoplankton (Tanaka & Ujiie 1984; Nakamura et al. 1999; Sato et al. 2004; Imai et al. 2016) and mollusks (Noda 1977, 1980, 1988, 1991, 2002). The age of the interface of the Shinzato FM and the overlying Chinen FM has been confined to 1.97 Ma in a paleomagnetism analysis by Komatsubara et al. (2005). Two fish species have been described from the Shinzato FM based on articulated skeletons: *Niphon macrocephalus* Kon & Yoshino, 1997a, a Serranidae, and *Cookeolus spinolacrymatus* Kon & Yoshino, 1997b, a Priacanthidae. The regional stratigraphic details are from Noda (1980) for Okinawa-jima, Hanagata (2004) for Miyagi-jima and Oshimizu & Iryu (2002) for Hamahiga-jima.

Sampled locations are on the southern area of Okinawa-jima, on Miyagi-jima and on Hamahiga-jima:

Chinen FM:

Chinen (Ch), Nanjyo City, Okinawa: 26°10'10"N, 127°49'27"E

Shinzato FM:

Aragusku (Ar), Yaesecho Shimajirigun, Okinawa: 26°8'08"N, 127°44'28"E

Gushichan (Gu), Yaesecho, Shimajirigun, Okinawa: 26°7'26"N, 127°44'29"E

Tobaru (To), Uruma City, Miyagi-jima: 26°21'31"N, 127°58'48"E

Uruma (Ur), Uruma City, Miyagi-jima, western coast cliff, collected by S. Kiel.

Higa (Hi), Hamahiga-jima, eastern cliff, collected by S. Kiel.

Upper Yonabaru FM:

Ozatofurugen (Oz), Nanjyo City, Okinawa: 26°11'18"N, 127°44'55"E

Shikoku (Fig. 3): All otoliths from Shikoku were collected from the Nobori FM of the Tonohama Group at Nobori, Kochi Prefecture. The Nobori FM is exposed in a rather restricted area in the vicinity of Cape Muroto near the SE tip of Shikoku, mainly in the clay pit for the cement plant Hane-sangyosha Co. Ltd. (HANESAN) and its vicinity. It is about 140 m thick, the lower half of it only known from the subsurface as evidenced from a core drilling near the type location (Kurihara 1968; Katto et al. 1980). The Nobori FM rests on basement and starts with a coarse conglomeratic to sandy facies only known from the subsurface (Kurihara 1968; Iwai et al. 2006). The main part of the formation from which the otoliths have been obtained is composed of deep marine, homogenous, massive bluish-gray silt- and mudstones and considered to be deposited in an upper slope environment (Kurihara 1968). The presence of abundant otoliths of the macrourid *Cetonurus naboriensis* (Aoki & Baba, 1984) (see Ohe 2011) in our assessment indicates a depositional water depth in the range of 800 to 1000 m, possible shallowing towards the uppermost section to 400 m, as exposed at the NW outcrop section. The top contact of the Nobori FM is usually disconformable to the overlying Ropponmatsu and Anani FMs.

The age of the Nobori FM has long been a matter of dispute since its definition by Katto et al. (1953) and maping by Katto et al. (1960). It was first considered to be late Miocene based on planktonic foraminifera (Takayanagi & Saito 1962) or early Pliocene based on mollusca (Kurihara 1968). The assessment of Takayanagi & Sato was based on the occurrence of *Globigerina nepenthes* in the Nobori FM, a species that became extinct in the late Miocene, but subsequently was considered a different species (Uchio 1967). Uchio (1967) also questioned the identification of *Sphaeroidinellopsis seminulina* by Takayanagi & Sato (1962). Matsubara (2004) summarizes the twisted biostratigraphic history of the Nobori FM and concluded it would be of late early to early late Pliocene age, i.e., nannoplankton biozones CN11b and CN12a, or NN16 respectively (Nishida 1971, 1979). The exposed upper Nobori section from which the otoliths have been obtained would represent nannoplankton zone CN12a or the lower part of the planktonic foraminifer zone N21 respectively. The Nobori location is also the type locality of *Globorotalia tosaensis* which according to Wade et al. (2011) has a FAD of 3.35 Ma. The co-occurrence of *S. seminulina* and *Dentoglobigerina altispira* indicate an age not younger than 3.16 Ma, but is in conflict with the Pacific LAD's of the two species as given by Wade et al. (2011).

The Nobori FM has been extensively studied for a variety of fossils, including mollusks (e.g., Aoki 1966; Katto & Masuda 1993; Matsubara 2004; Mimoto & Nakao 2004), foraminifera (Takayanagi & Saito 1962; Uchio 1967; Kurihara 1968), calcar-

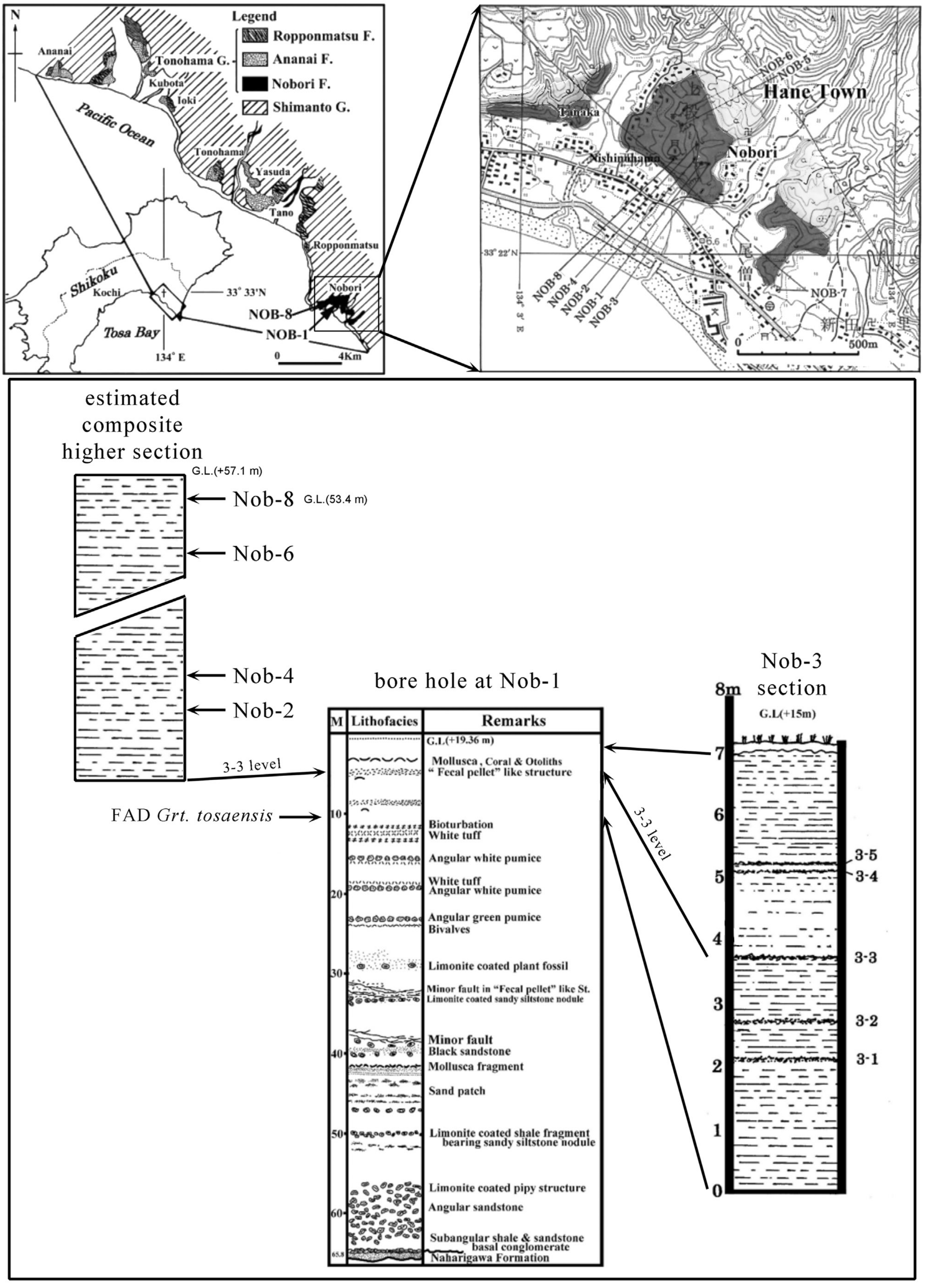


Fig. 3 - Shikoku region location plate. Regional map on left side from Iwai et al. (2006), detail map on right side after Takayanagi & Saito (1962). Composite litho-section on left composed from field data, litho-sections of borehole Nob-1 and of Nob-3 from Katto et al. (1980).

eous nannoplankton (Nishida 1971, 1979; Takayama 1980), radiolarians (Sugiyama et al. 1992) and diatoms (Koizumi & Ujiie 1976). Katto (1960) recorded teeth of *Carcharodon megalodon* (now *Otodus* (*Carcharocles*) *megalodon* after Capetta 2012).

Sampled locations are:

NOB-1, Nobori, Hane, Muroto City: 33°22'24"N, 134°3'20"E, +19.36 m above SL

NOB-2, Nobori, Hane, Muroto City: 33°22'32"N, 134°3'17"E, +22.1 m above SL

NOB-3, Nobori, Hane, Muroto City: 33°22'24"N, 134°3'21"E, +16.8 m above SL (now obscured)

NOB-4, Nobori, Hane, Muroto City: 33°22'27"N, 134°3'18"E, +23.6m above SL

NOB-6, Nobori, Hane, Muroto City: 33°22'22"N, 134°3'18"E, +33.4 m above SL

NOB-8, Nobori, Hane, Muroto City: 33°22'25"N, 134°3'15"E, +53.4 m above SL

Kakegawa (Fig. 4): The late Pliocene and Pleistocene outcrops of the Kakegawa Group in the Kakegawa district represent classical locations in Japan for the late Cenozoic and lent their name to the "Kakegawa Fauna", which characterizes a warm, tropical to subtropical fauna along the Pacific shores of southern Japan as the precursor of the Kuroshio fauna of today (Tsuchi 1955; Masuda et al. 1998; Matsubara 2004). The otoliths studied here have been obtained from the Dainichi FM of Gelasian age and the Hijikata FM of early Calabrian age. They have previously been subject of studies by Ohe (1981, 1983) and the myctophid otoliths are here reviewed. The Dainichi FM consists of a transgressive sand sequence on a narrow shelf and the sampled locations have been deposited on the outer shelf at about 100 to 200 m. Mollusca were first recorded from Dainichi by Yokoyama (1923). The Hijikata mudstone sequence more or less conformably overlays the Dainichi FM and was probably deposited at 50 to 100 m water depth. The paleo-water depth assessments are based on correlation with the environmental characterization of molluscan assemblages by Nobuhara (1992, 1993). The Hosoya Tuffaceous Member is intercalated in the Dainichi FM near the interface of both formations. The total thickness of the Kakegawa sequence can reach 3000 m (Satoguchi & Nagahashi 2012; Sakai & Masuda 1995). The Dainichi and Hijikata sequence reach a thickness of 600+ m (Oda 1978).

The Kakegawa sedimentary sequence contains about 80 intercalated tuffaceous beds, which have been used for direct age determinations with the fission-track method and resulted in a refined tephrostratigraphy (Nishimura 1977; Shibata et al. 1984; Mizuno et al. 1987; Satoguchi et al. 1996; Shiba et al. 2007, 2010; Satoguchi & Nagahashi 2012). This has led to a well constrained chronostratigraphic framework in combination with planktonic foraminifera (Oda 1978; Ibaraki 1985, 1986), nannoplankton (Kameo 1998) and paleomagnetic studies (Yoshida & Niitsuma 1976; Ishida et al. 1980). The Dainichi FM was deposited during the early Pleistocene Gelasian between 2.3 and 1.9 Ma below the FAD of *Globorotalia truncatulinoides*, i.e., during the upper part of planktonic foraminifera zone N21 corresponding to PL6 (Ibaraki 1986; Shiba et al. 2007; Wade et al. 2011) and below the Olduvai Chrone (Yoshida & Niitsuma 1976; Ishida et al. 1980). The Hosoya Tuffaceous Member was age dated at 1.9 Ma by fission-track (Shiba et al. 2007). The overlaying siltstones of the Hijikata FM are of Calabrian age from 1.9 to 1.0 Ma (Shiba et al. 2007). According to Kameo (1998) the Hijikata FM lies within nannoplankton zone CN13 / NN19 respectively. The locations sampled for otoliths are stratigraphically positioned above the Haruoka = Soga ash layer within the parasequence PH4 according to Shiba et al. (2007) with a range of 1.7 to 1.5 Ma and above the *Pulleniatina* dextral coiling datum of 1.6 Ma (Ibaraki 1986). Satoguchi & Nagahashi (2012) show Iriyamase at about 1.4 Ma. In consequence we estimate an age range of 1.6 to 1.4 Ma for the sampled interval. Note that the stratigraphic range of the Hijikata FM differs from Ibaraki (1986) to the currently used scheme of Shiba et al. (2000) and also the Harinouchi sequence below the Dainichi FM in Ibaraki has been renamed and subdivided in the Kamiuchida and Higashiyokoji FMs by Shiba et al. (2000) (Fig. 4).

Sampled locations are:

Hijikata FM:

Iriyamase (St1-1), Kakegawa City: 10 m south of St1-2

Iriyamase (St1-2), Kakegawa City: 34°43'49"N, 138°1'10"E, +82.4 m

Iriyamase (St1-3), Kakegawa City: 34°43'49"N, 138°1'10"E, +82.4 m

Hosoya Tuffaceous Member:

Fosoya (Fo; local variant of name), Kakegawa City: 34°47'34"N, 137°58'3"E, +57.9 m

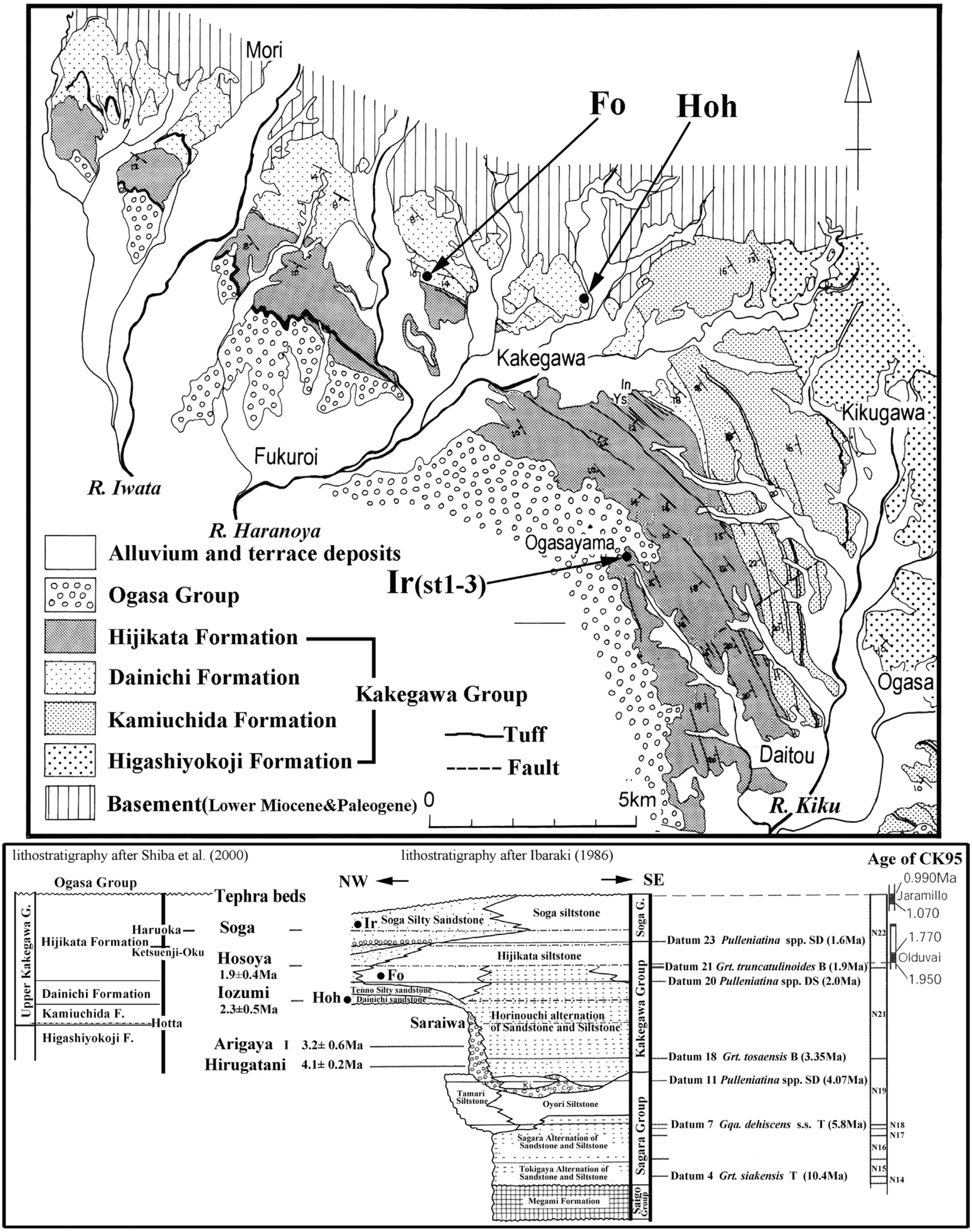


Fig. 4 - Kakegawa region location plate. Map from Shiba et al. (2000). Lithostratigraphy after Shiba et al. (2000) (left) and Ibaraki (1986) (center). Age dating of tephra beds after Nishimura (1977), Shibata et al. (1984) and Mizuno et al. (1987). Planktonic foraminifer dates after Ibaraki (1986) adjusted from Wade et al. (2011). Paleomagnetic stratigraphy after Yoshida & Niitsuma (1976) and Ishida et al. (1980). Abbreviations used for localities are: Fo = Fosoya, Ir = Iriyamase, Hoh = Hongohigashi.

Dainichi FM:

Hongohigashi (Hoh), Kakegawa City: 34°48'18"N, 137°57'51.10"E, +61.5 m

Honohashi, Kakegawa City: 34°47'15."N, 138°0'32"E, +34.0 m (otoliths studied in Ohe 1981).

In addition to the otoliths from southern Japan, two large and well-preserved otoliths from putative Piacenzian strata of Fiji are here included because they represent the far southern region of a putative late Pliocene West Pacific bioprovince. These otoliths were obtained from excavations near the township of Weila, southeastern Viti Levu, by Andrew Grebneff and were found by the senior author upon a visit at the Geological Institute of the University of Otago in Dunedin, New Zealand. The label indicated a stratigraphic level at planktonic foraminifera biozone N22, but a review of holoplanktic gastropods by Janssen & Grebneff (2012) concluded a Piacenzian age and correlated the fauna with the Japanese Takanabe Member of the Miyazaki Group (SW Japan), planktonic foraminifera zone N21 (Piacenzian). For further details of location and geology see Janssen & Grebneff (2012).

Material and methods

The otolith-material described here was collected by the junior author at Okinawa, Nobori and Kakegawa and by M. Moriguchi (Naha) from Okinawa-jima and Miyagi-jima between 1981 and 2004. All type specimens and figured otoliths from this collection are deposited in the collection of the Senckenberg Museum und Forschungsinstitut in Frankfurt/Main, Germany (SMF PO). Further specimens collected by S. Kiel (Stockholm) from Miyagi-jima and Hamahiga-jima are deposited at the Swedish Museum of Natural History (NRM-PZ). The specimens from Fiji are deposited at the Geology Museum of the Otago University in Dunedin, New Zealand (OU).

The terminology for the morphological description of the sagittal otoliths follows Koken (1891), Weiler (1942) and Schwarzhans (1978). The following abbreviations are used in morphometric measurements: otolith length = OL; otolith height = OH; otolith thickness = OT; ostium length = OsL; ostial colliculum length = OCL; cauda length = CaL; caudal colliculum length = CCL; sulcus length = SuL. Other abbreviations used: FM = formation.

All otoliths are shown as if from the right side in order to facilitate easier comparison. Left otoliths are mirror imaged and annotated accordingly in the figure captions.

Systematic paleontology

The classification of the systematic part follows Nelson et al. (2016). The allocation of genera in subfamilies follows Martin et al. (2018). The arrangement of species within the specious genus *Diaphus* follows the grouping proposed by Schwarzhans (2013b) based on otoliths.

A good and wide knowledge of extant otoliths of the Myctophidae is mandatory for a proper identification of fossil otoliths from such young strata. Fortunately, the situation is very good in the collections of Ohe and Schwarzhans and many Recent and fossil Neogene otoliths have been figured and described in recent literature (for example Ohe 1985; Brzobohaty & Nolf 1996, 2000; Girone & Nolf 2002; Lombarte et al. 2006; Schwarzhans 2103a, 2013b, 2013c; Schwarzhans & Aguilera 2013; Nolf 2013). Extant otoliths are therefore only figured in cases where pertinent new information can be added. We have figured representatives of all identified species in the fossil record and included discussions about their recognition and distribution, but detailed descriptions are only provided for new species or in cases where pertinent new information can be added.

Order **Myctophiformes** Regan, 1911
Family Neoscopelidae Parr, 1928
Genus *Neoscopelus* Johnson, 1863

Neoscopelus microchir Matsubara, 1943

Fig. 5 A-C

Material: 1 specimen SMF PO 91993, Tobaru, Okinawa, Shinzato FM, Piacenzian.

Discussion. Otoliths of *Neoscopelus microchir* differ from the co-occurring *N. macrolepidotus* Johnson, 1863 in the long ostium, which is about as long as the cauda (vs distinctly shorter than the cauda at about 50%) and the relatively long dorsal rim, which is anteriorly not or only slightly inclined (see Rivaton & Bourret 1999; Nolf 2013). This is the first fossil record of the species.

Family Myctophidae Gill, 1893
Subfamily Myctophinae Fowler, 1925
Genus *Benthosema* Goode & Bean, 1896

Benthosema fibulatum (Gilbert & Cramer, 1897)

Fig. 5 P-Q

1997 *Benthosema fibulatum* (Gilbert & Cramer, 1897) - Ohe, Kawai & Kawase: pl. 1, fig. 6.

1997 *Diaphus lucidus* (Goode & Bean, 1896) - Ohe, Kawai & Kawase: pl. 1, fig. 3.

Material: 17 specimens Okinawa, Shinzato FM, Piacenzian: 15 specimens NRM-PZ 16735, Uruma, 2 specimens NRM-PZ 16736, Higa.

Discussion. *Benthosema fibulatum* is the largest growing species of the genus up to about 10 cm SL and also has the largest otoliths to about 5.2 mm length. The fossil otolith specimens from Okinawa reach sizes of up to 3.5 mm length, which is still larger than those of the related *B. pterotum*. Other than the larger size, *B. fibulatum* otoliths differ from *B. pterotum* primarily in the continuous dentition along the ventral rim, which however is mostly eroded in the specimens from Okinawa, and the thinner appearance. Further specimens are recorded from the Pleistocene Ryukyu Limestone of Okinawa by Ohe et al. (1997).

Benthosema fibulatum is a tropical species of the Indian Ocean between 18°N and 20°S and in the western and central Pacific between 21°N and 10°S (Froese & Pauly 2018). In Japan it is known from an isolated population off the Mie coast between 33° and 34°N (Masuda et al. 1984).The occurrence in the Piacenzian and late Pleistocene to early Holocene of Okinawa indicates a more northerly distribution in the past (except for the extant occurrence off Mie).

Benthosema pterotum (Alcock, 1890)

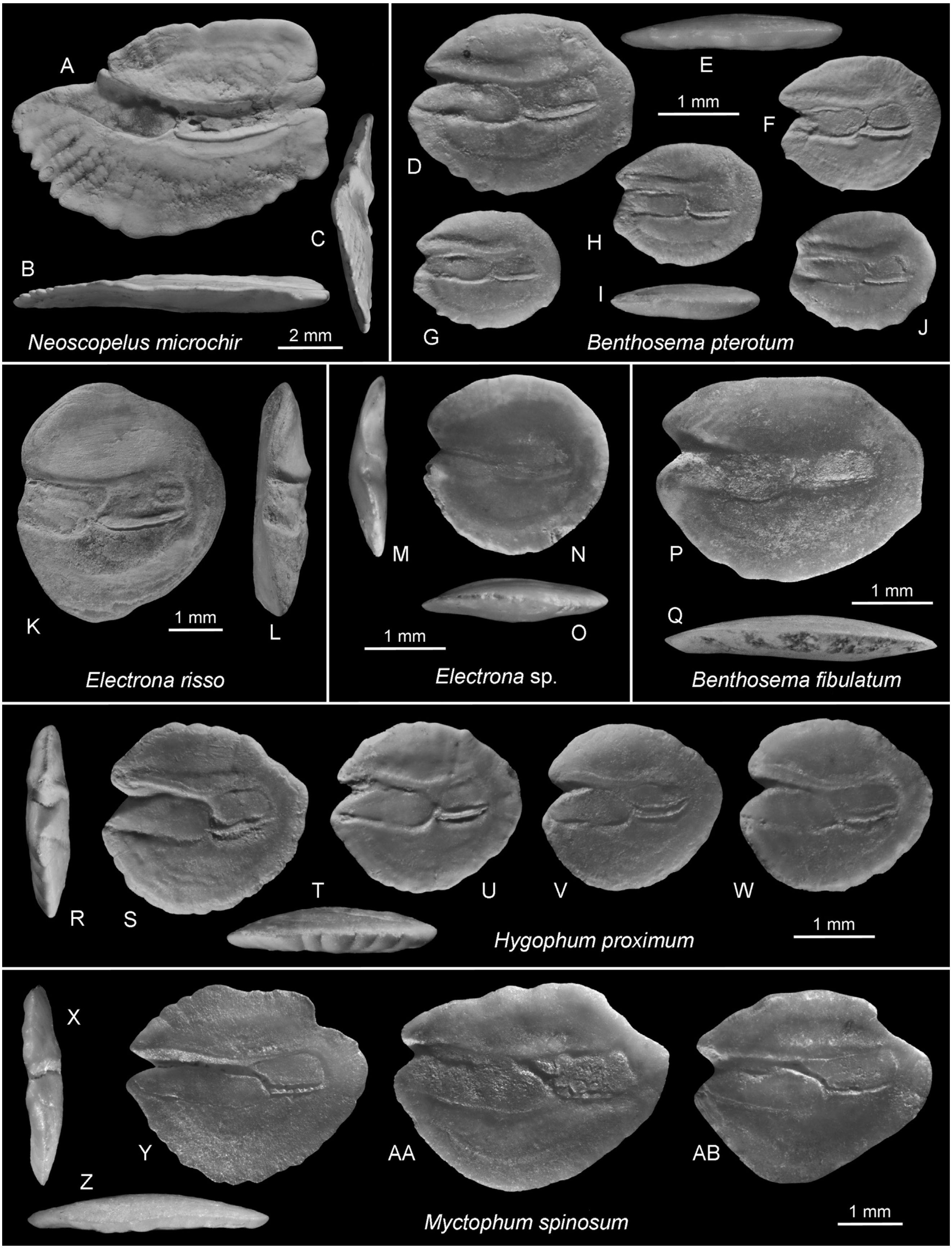
Fig. 5 D-J

Material: 1734 specimens: 68 specimens Okinawa: 1 specimen Ozatofurugen, upper Yonabaru FM, early Piacenzian, 67 specimens Shinzato FM, Piacenzian: 1 specimen Gushichan, (figured specimen SMF PO 91994), 7 specimens Uruma, 59 specimens Higa; 1666 specimens, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 1562 specimens Nob-1 (figured specimens SMF PO 91995), 102 specimens Nob 3+4, 2 specimens Nob-8 (figured specimen SMF PO 91996).

Discussion. Otoliths of *Benthosema pterotum* are elongate oval and characterized by a strong denticle on the rear portion of the ventral rim and one to three small denticles at the anterior section of the ventral rim while the remainder of the ventral rim is entirely smooth. Generally, the gap of denticles at the middle section of the ventral rim is typical for *Benthosema* otoliths.

Benthosema pterotum is widely distributed in the Indian Ocean and West Pacific (Froese & Pauly 2018). In the East Pacific it is replaced by the closely related *B. panamense* (Tåning, 1932). Both species are known for residing in the oxygen minimum zones during daytime to escape predators. Gjøsæter (1984) calculated *Benthosema pterotum* to be extremely abundant in the anoxic zone of the Arabian Sea during daytime. There is no comparable oxygen minimum zone in southern Japan nowadays. Considering the similarity of the putative ecology during the time of the "Kakegawa Fauna" it appears likely that the situation has been similar during Pliocene and Pleistocene. However, Sassa et al. (2014) found that the pseudoceanic *B. pterotum* is very common in the East China Sea at relatively shallow water depth over the lower shelf (50-100 m). They postulated that this unusual occurrence may be related to diming effects caused by turbidite offload that would allow the fishes to reside in comparative shallower water. They also found that *B. pterotum* is more tolerant to lower salinities than most other myctophids. We found that otoliths of *B. pterotum* are rare in all Plio-Pleistocene locations studied except the upper Nobori FM, where they are so common in some levels that they constitute more than half of the total of mytophid otoliths studied here. The upper Nobori FM was deposited in 400 to 1000 m water depth, which would be the depth interval where an oxygen minimum zone could be expected. Whatever the cause for the striking abundance of *Benthosema pterotum* in the upper Nobori FM might be, it was certainly an effect not mirrored in any of the other locations studied.

Fig. 5 - A-C) *Neoscopelus microchir* Matsubara, 1943, SMF PO 91993, reversed, A - inner face, B - ventral view, C - anterior view; D-J) *Benthosema pterotum* (Alcock, 1890), D-E, G-I SMF PO 91995 (reversed), F SMF PO 91994, J SMF PO 91996 (reversed), D, F, G, H, J - inner faces, E, I - ventral views; K-L) *Electrona risso* (Cocco, 1829), SMF PO 91997, K - inner face, L - anterior view; M-O) *Electrona* sp., SMF PO 91998 (reversed), M - anterior view, N - inner face, O - ventral view; P-Q) *Benthosema fibulatum* (Gilbert & Cramer, 1897), NRM-PZ 16736, P - inner face, Q - ventral view; R-W) *Hygophum proximum* Becker, 1965, R-U SMF PO 91999 (R-T reversed), V-W SMF PO 101000, S, U-W - inner faces, R - anterior view, T ventral view; X-AB) *Myctophum spinosum* (Steindachner, 1867), SMF PO 101001 (reversed), Y, AA, AB - inner faces, X - anterior view, Z - ventral view.


A
B
C
Neoscopelus microchir
2 mm
D
E
1 mm
F
H
G
I
J
Benthosema pterotum
K
L
1 mm
Electrona risso
M
N
O
1 mm
Electrona sp.
P
1 mm
Q
Benthosema fibulatum
R
S
T
U
V
W
1 mm
Hygophum proximum
X
Y
Z
AA
AB
1 mm
Myctophum spinosum

Genus *Electrona* Goode & Bean, 1896

Electrona risso (Cocco, 1829)

Fig. 5 K-L

1983 *Diogenichthys* cf. *D. laternatum* (Garman, 1899) - Ohe: pl. 4, fig. 2.

Material: 2 specimens Okinawa, Shinzato FM, Piacenzian: 1 specimen Gushichan, 1 specimen Tobaru (figured specimen SMF PO 91997).

Discussion. Otoliths of *Electrona risso* are easily recognized by there high bodied shape, the specific course of the dorsal rim, which is strongly expanded anteriorly and depressed posteriorly, the ostium and cauda being of nearly equal length and the excisural furrow cutting through the ostial colliculum. *Electrona risso* is a widespread species throughout the three world oceans and is well known in the fossil record since early Pliocene. Its distribution is limited by the 10°C and 15°C isotherms at 200 m water depth and a high productivity greater than 50 g carbon per square meter per year (Hulley 1986). It is missing from the tropical East Pacific, the northern Indian Ocean and off West Africa between 5°S and 13°S. This makes *E. risso* an effective counter indicator of the presence of oxygen minimum zones. In Japan, it has first been observed by Kubota & Uyeno (1972) in the Suruga Bay and off Tohoku (i.e., the Kuroshio - Oyashio transition zone). However, Masuda et al. (1984) listed the records as *Electrona* sp. arguing that they could represent a distinct species.

Electrona sp.

Fig. 5 M-O

?1981 *Hygophum* cf. *H. macrochir* (Günther, 1864) - Ohe: pl. 3, fig. 7.
?1981 *Hygophum* cf. *H. hygomi* (Lütken, 1892) - Ohe: pl. 3, fig. 8.
1981 *Hygophum* cf. *H. benoiti* (Cocco, 1838) - Ohe: pl. 3, fig. 9.

Material: 1 specimen, Fosoya, Kakegawa, Hosoya Tuffaceous Member, Dainichi FM, Gelasian (figured specimen SMF PO 91998).

Discussion. A few more otoliths of this unidentified species have been described from Kakegawa by Ohe (1981). They resemble otoliths of *Electrona risso* in the deep ventral rim, the ostium and cauda being of almost equal length and the excisural furrow cutting through the ostial colliculum. They differ from *E. risso* in the gently curved, much shallower dorsal rim and the smaller maximal size of about 2.5 mm length (vs 5 mm). Except for *E. risso*, the genus *Electrona* is confined to the subantarctic and southern temperate waters. The finds from the Pleistocene of Japan indicate the presence of another *Electrona* species in the northern Pacific in the past.

Genus *Hygophum* Bolin, 1939

Hygophum proximum Becker, 1965

Fig. 5 R-W

Material: 25 specimens: 12 specimens, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 11 specimens Nob-1 (figured specimens SMF PO 91999), 1 specimen Nob3+4; 13 specimens, Hongohigashi, Kakegawa, Dainichi FM, Gelasian (figured specimens SMF PO 101000).

Discussion. Otoliths of the genus *Hygophum* are difficult to distinguish from each other. Those of *H. proximum* are characterized by regularly rounded rims and an index OL:OH of 1.0 or larger (see Schwarzhans & Aguilera 2013 for figure). *Hygophum proximum* is widespread in the tropical and subtropical waters of the Indian and Pacific oceans. In Japan it is known from the Kii Peninsula southward, which is north of the Nobori locations but south of the Kakegawa locations.

Genus *Myctophum* Rafinesque, 1810

Myctophum spinosum (Steindachner, 1867)

Fig. 5 X-AB

1981 (Myctophidarum) gen. et sp. indet. - Ohe: pl. 3, fig. 6.
1983 *Myctophum orientale* (Gilbert, 1913) - Ohe: pl. 6, figs. 9-12.

Material: 13 specimens: 8 specimens, Hongohigashi, Kakegawa, Dainichi FM, Gelasian (figured specimens SMF PO 101001); 5 specimens, Iriyamase, Kakegawa, Hijikata FM, early Calabrian.

Discussion. Otoliths of *Myctophum spinosum* belong to the group of *Myctophum* otoliths characterized by a sharp bend at the middle of the deep ventral rim and a broad concavity at the postdorsal rim, which include *M. asperum* Richardson, 1845, *M. brachygnathum* (Bleeker, 1856), *M. orientale* (Gilbert, 1913) and *M. spinosum*, which all occur along the Pacific shores of Japan. Otoliths of *M. spinosum* resemble those of *M. asperum* differing primarily in the more compressed shape (OL:OH = 1.1-1.2 vs 1.3-1.4) (see Schwarzhans & Aguilera 2013 for figures). Otoliths of *M. brachygnathum* are more compressed than those of *M. spinosum* (1.0-1.05 vs 1.1-1.2) and those of *M. orientale* are more elongate, like *M. asperum*, and both species differ additionally in a less pronounced postdorsal concavity.

Genus *Symbolophorus* Bolin & Wisner, 1959

Symbolophorus californiensis (Eigenmann & Eigenmann, 1898)

Fig. 6 A-C

1981 *Symbolophorus evermanni* (Gilbert, 1905) - Ohe: pl. 2, fig. 10.
1983 *Symbolophorus evermanni* (Gilbert, 1905) - Ohe: pl. 3, fig. 4.

Material: 4 specimens: 2 specimens, Hongohigashi, Kakegawa, Dainichi FM, Gelasian; 2 specimens, Iriyamase, Kakegawa, Hijikata FM, early Calabrian (figured specimens SMF PO 101002).

Discussion: *Symbolophorus californiensis* belongs to the *Symbolophorus rufinus* otolith group of Schwarzhans & Aguilera (2013) characterized by an almost flat inner face, a high dorsal rim, a very regularly curved ventral rim and a short cauda. In this group of four species, *S. californiensis* is characterized by a strongly developed postdorsal angle which is located far backwards, close to the joint of the dorsal rim with the posterior rim and positioned posterior of the caudal tip, and by the lack of a postdorsal depression. The posterior rim is often nearly vertically cut, like in the figured specimens, which leaves only a very narrow space between the caudal tip and the posterior rim of the otolith.

Symbolophorus californiensis is a typical myctophid species of the transition region between the subarctic and subtropical water mass of the northern Pacific occurring off Japan and North America (Sassa 2009). In Japan it is one of the dominant mesopelagic fishes in the transition region between the Oyashio and Kuroshio fronts off the Pacific coasts from Choshi to Kinkazan. Its occurrence in the early-middle Pleistocene is confined to the northernmost locations of the Kakegawa region, which probably indicates vicinity to the paleo-transition region.

Symbolophorus evermanni (Gilbert, 1905)

Fig. 6 D-G

1981 *Symbolophorus* sp. A type - Ohe: pl. 2, fig. 11.

Material: 46 specimens: 5 specimens, Tobaru, Okinawa, Shinzato FM, late Piacenzian; 5 specimens, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 1 specimen Nob-1, 3 specimens Nob-6 (figured specimens SMF PO 101003), 1 specimen Nob-8; 36 specimens, Hongohigashi, Kakegawa, Dainichi FM, Gelasian (figured specimens SMF PO 101004).

Discussion. *Symbolophorus evermanni* also belongs to the *Symbolophorus rufinus* otolith group like the preceding *S. californiensis*, from which it is readily distinguished by the more anteriorly positioned postdorsal angle above the central part of the cauda, the well developed and deep postdorsal concavity and the more expanded posterior rim, which leaves ample space between the caudal tip and the posterior rim of the otolith.

Symbolophorus evermanni is the subtropical to tropical counterpart of *S. californiensis* and is widely distributed in the Pacific and Indian Ocean. In Japan it is found in the waters of the Kuroshio Current and occasionally north to off Tohoku. Its relatively common occurrence in all three locations studied indicates influence of subtropical water. However, its lack in the Hijikata FM of the Kakegawa region may indicate a shift to cooler conditions in that region after the deposition of the Dainichi FM.

Symbolophorus moriguchii n. sp.

Fig. 6 H-M

Etymology: Named in honor of Mitsuru Moriguchi, Naha, Okinawa, who has collected most of the otolith material from Okinawa.

Holotype: SMF PO 101005 (Fig. 6 H-I); Tobaru, Miyagi Jima, Okinawa, Shinzato FM, Piacenzian, planktonic foraminifer zone N21 (PL"5-6"), 3.35-2.3 Ma.

Paratypes: 7 specimens: 5 specimens SMF PO 101006 (Fig. 6 J-L), same data as holotype; 2 specimens, SMF PO 101007 (Fig. 6 M), Hongohigashi, Kakegawa, Dainichi FM, Gelasian.

Further specimens: 20 specimens: 18 specimens same data as holotype; 1 specimen Nobori, Nob-1, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian; 1 specimen, Hongohigashi, Kakegawa, Dainichi FM, Gelasian.

Diagnosis: OL:OH = 1.35-1.4. Dorsal rim anteriorly depressed, posteriorly raising to broad mediodorsal region and rounded postdorsal angle. Small postdorsal concavity. Posterior rim broadly rounded with few broad crenulations. Ventral rim more strongly bent at middle section. Cauda short; OCL:CCL = 2.5-3.0.

Description. Moderately elongate and thin otoliths up to about 5.5 mm length (holotype 5.35 mm). OH:OT = 5.5. Dorsal rim anteriorly depressed, gently raising to broad mid-dorsal region followed by obtuse postdorsal angle located above rear part of cauda; short, moderately deep postdorsal concavity following postdorsal angle; dorsal rim smooth or somewhat undulating. Ventral rim regu-

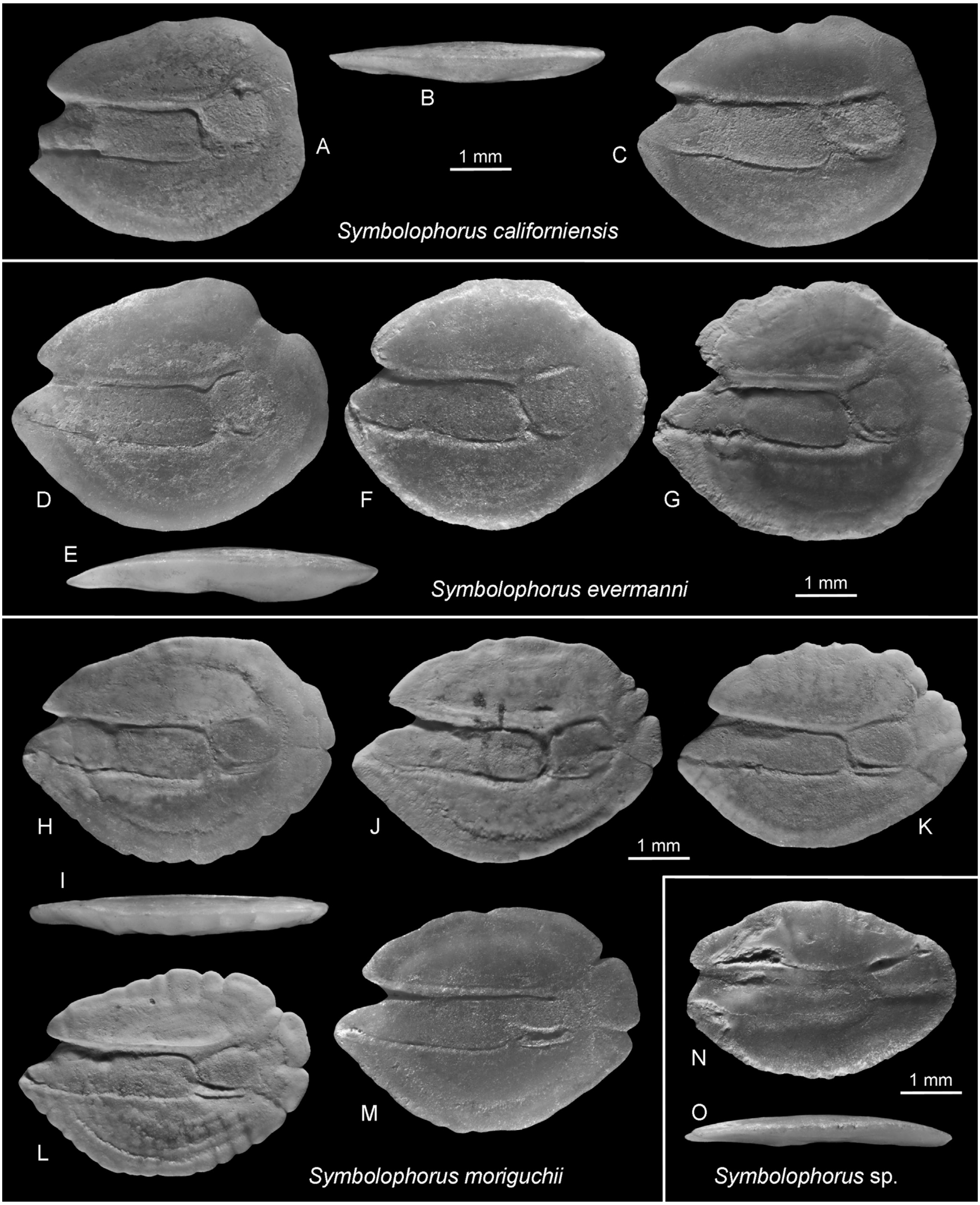


Fig. 6 - A-C) *Symbolophorus californiensis* (Eigenmann & Eigenmann, 1898), SMF PO 101002 (A-B reversed), A, C - inner faces, B - ventral view; D-G) *Symbolophorus evermanni* (Gilbert, 1905), D-F SMF PO 101003 (D-E reversed), G SMF PO 101004, D, F, G - inner faces, E - ventral view; H-M) *Symbolophorus moriguchii* n.sp. H-I - holotype, SMF PO 101005 (reversed), J-L - paratypes, SMF PO 101006 (K-L reversed), M paratype, SMF PO 101007, H, J-M - inner faces, I - ventral view; N-O) *Symbolophorus* sp., SMF PO 101008 (reversed), N - inner face, O - ventral view.

larly curved, smooth or slightly crenulated, deepest at its middle and slightly more strongly bent at middle section. Rostrum slightly superior, longer than antirostrum, with moderately pointed tip, 10-15% of OL. Excisura sharp, moderately deep. Posterior rim broadly rounded, with two to three broad crenulations.

Inner face nearly perfectly flat with axial to slightly supramedian sulcus. Ostium long, narrow, slightly bent upwards. Cauda short, slightly bent upwards, with box-shaped termination at some distance from posterior rim of otolith. Caudal pseudocolliculum small, straight, weakly developed, shorter than caudal colliculum. OCL:CCL = 2.5-3.0. Dorsal depression wide, with indistinct margins and weak crista superior towards sulcus. Ventral furrow distinct, running at moderate distance from ventral rim of otolith. Outer face flat smooth or with few radial furrows near its margins.

Discussion. The flat inner face and the short cauda characterize *Symbolophorus moriguchii* as a member of the *Symbolophorus rufinus* otolith group. With a range of the index OL:OH of 1.35-1.4 it is intermediate between the more compact otoliths of the *Symbolophorus rufinus* group (OL:OH = 1.2-1.35) and the more elongate otoliths of the *Symbolophorus boops* group (OL:OH = 1.4-1.55). The relatively deeply curved ventral rim with its middle section bent stronger than the anterior and posterior sections also reminds of the otoliths of the *Symbolophorus boops* group. The high index OL:OH and the shape of the ventral rim distinguish *S. moriguchii* from the other members of the *Symbolophorus rufinus* group. From *S. californiensis* it further differs in the presence of a postdorsal concavity and from *S. evermanni* in the anteriorly depressed dorsal rim and the thinner appearance (OH:OT = 5.5. vs 3.5-4.0).

Symbolophorus moriguchii has the same distribution pattern as *S. evermanni* in the locations studied. We assume that it represents an extinct warm water species of the northeastern Pacific that is phylogenetically closer to the dichotomy of the two main groups in the genus than the other species of the *Symbolophorus rufinus* group.

Symbolophorus sp.

Fig. 6 N-O

Material: 2 specimens, Hongohigashi, Kakegawa, Dainichi FM, Gelasian (figured specimen SMF PO 101008).

Discussion. Two eroded specimens belong to the *Symbolophorus boops* group. They are characterized by an elongate outline (OL:OH = 1.5), a regularly curved, shallow dorsal rim, a short rostrum not longer than the antirostrum and a very long sulcus with its cauda terminating close to the posterior tip of the otolith.

Subfamily Lampanyctinae Paxton, 1972

Genus *Ceratoscopelus* Günther, 1864

Ceratoscopelus townsendi (Eigenmann & Eigenmann, 1889)

Fig. 7 A-H

1981 *Ceratoscopelus* sp. - Ohe: pl. 3, fig. 10.
1981 *Ceratoscopelus townsendi* (Eigenmann & Eigenmann, 1889) - Ohe: pl. 3, fig. 11.
1983 *Ceratoscopelus townsendi* (Eigenmann & Eigenmann, 1889) - Ohe: pl. 7, fig. 4.
1983 *Ceratoscopelus* sp. - Ohe: pl. 7, fig. 5.

Material: 198 specimens: 7 specimens Okinawa, Shinzato FM, Piacenzian: 4 specimens Tobaru (figured specimen SMF PO 101009), 1 specimen Uruma, 2 specimens Higa; 61 specimens, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 54 specimens Nob-1 (figured specimens SMF PO 101010), 7 specimens Nob-3+4 (figured specimens SMF PO 101011); 130 specimens, Hongohigashi, Kakegawa, Dainichi FM, Gelasian (figured specimens SMF PO 101012).

Discussion. Otoliths of *Ceratoscopelus* are easily recognizable by the combination of a long and massive rostrum, the elongate shape with a very shallow curved ventral rim and the completely flat inner face. Distinction of the three extant species is less clear by means of otoliths, particularly when it comes to distinction of the two widespread tropical to subtropical species *C. townsendi* and *C. warmingii* (Lütken, 1892). In recent literature (e.g., Shinohara et al. 2009) only *C. warmingii* is recorded from off Japan and earlier records of *C. townsendi* (e.g., Mead & Taylor 1953) have been revised to *C. warmingii.* Otoliths of *C. warmingii* are variable in OL:OH proportions and crenulation of the otolith rims (see Linkowski 1997), but they never seem to have such a strongly developed postdorsal angle at the joint with the posterior rim, as *C. townsendi* does. We therefore follow Ohe (1981) in regarding the fossil *Ceratoscopelus* otoliths known so far from Japan as *C. townsendi.* Aoki (1971), however figured otoliths as *Otolithus* (*Myctophidarum*) *makutaensis* Aoki, 1971 from the late Pleistocene of the Boso Peninsula in Japan that show all typical characters of the extant *C. warmingii* and are here allocated to the Recent species.

Linkowski (1997) undertook an extensive morphological study of *C. warmingii* from all its distribution areas except Japan and found multiple subtle differences in more than 20 different geographical populations. He also studied otoliths and found considerable differences in various populations as well, but according to his work they did not always match with the populations defined by body luminescence patterns. However, Linkowski's work also indicates that the variations of otoliths in the various populations of *C. warmingii* can be larger than the distinction of some of them compared to *C. townsendi*. His assumption was that *C. townsendi* evolved in the Pacific from *C. maderensis* (Lowe, 1839) of the North Atlantic after separation of both oceans following the rise of the Isthmus of Panama during early Pliocene as a peripheral Pacific population. Following his conclusions, *C. warmingii* would have developed subsequently from the *C. townsendi* stock and would then have spread westward to the Indian and Atlantic oceans. Consequently, the Pacific stocks would be the oldest. A find of otoliths in the late Miocene of Gabon, tropical West Africa, identified as *C. warmingii* (Schwarzhans 2013c), however, contradicts Linkowski's assumption, and would rather suggest an Atlantic origin and a subsequent spread eastwards. The finding of *Ceratoscopelus townsendi* otoliths in the late Pliocene and early Pleistocene of Japan and of *C. warmingii* in the late Pleistocene of Japan (Aoki 1971 and unpublished data by F. Ohe) would be consistent with these assumptions, with the caveat however that the differentiation of *C. warmingii* and *C. townsendi* by means of otoliths is not conclusively assessed.

Otoliths of *Ceratoscopelus maderensis* are known from the Mediterranean since early Pliocene (Schwarzhans 1986, Nolf & Cappetta 1989). The late Miocene of Italy has yielded yet another extinct *Ceratoscopelus* species, *C. miocenicus* Bedini, Francalacci & Landini, 1986, known from articulated skeletons with otoliths in situ. Their otoliths show a distinctly shorter rostrum, indicating that the highly diagnostic look of extant *Ceratoscopelus* otoliths is a relatively late achievement.

Genus *Lampadena* Goode & Bean, 1893

Lampadena scapha Schwarzhans & Aguilera, 2013

Fig. 7 I-K

Material: 4 specimens: 1 specimen OU 41327b, excavation in Weila (A. Grebneff location 224), Nausori, SE Viti Levu, Fiji, Nakosi FM, presumably Piacenzian; 3 fragmented specimens from the Shinzato FM, Piacenzian of Okinawa: 1 from Tobaru, 2 investigated at the Mizunami Fossil Museum, Japan.

Description. *Lampadena scapha* was established on a holotype of 5.5 mm length from the Piacenzian of Panama and a smaller, less well preserved specimen from the late Tortonian of Panama. The find of a large specimen of 10.3 mm length in Fiji and fragments of other large specimens in Okinawa now offers the opportunity to refine the original description. The large specimen from Fiji is nearly complete except a small part broken along the anterior-dorsal rim that gives the erroneous indication of a concavity.

Thin, large, elongate otolith; OL:OH = 1.45-1.7, decreasing with size; OH:OT = 5.0-6.0. Dorsal rim moderately high, somewhat irregularly formed with depression above rear part of cauda (increasing in intensity and depth with size). Ventral rim very regularly and deeply curved, deepest at its middle or slightly in front, slightly undulating. Rostrum distinctly supramedian, moderately pointed, long, with broadly rounded ventral margin and nearly horizontal dorsal margin. Excisura short or absent; antirostrum short, high, or negligible. Posterior rim rounded, somewhat undulating, its tip distinctly supramedian at about level of rostrum resulting in a nearly symmetrical shape of otolith and particularly dorsal rim.

Inner face almost flat, very slightly bent, with long, wide, slightly bent sulcus. Ostium about twice as long as cauda and distinctly wider; OCL:CCL = 1.7-2.0; OCH:CCH = 1.65-1.8 (corrected from Schwarzhans & Aguilera 2013); OCH:CCH including pseudocolliculum = 1.1-1.2. Ostium slightly upward directed towards anterior; cauda slightly upward directed towards posterior, reaching close to indentation of posterior dorsal rim, with rounded tip. Ostial colliculum anterior-dorsally reduced in large specimen; caudal colliculum variably strongly reduced posterior-dorsally. The caudal pseudocolliculum is long and distinct. Dorsal depression wide, indistinct; ventral furrow variably distinct, moderately far from ventral rim of otolith. Outer face flat, with few short radial furrows particularly along ventral rim, otherwise smooth.

Discussion. The large specimen from Fiji shows a few differences to the holotype of about half the size: it is less elongate (OL:OH = 1.45 vs 1.7), shows a distinctly deeper postdorsal incision and a distinct, albeit short excisura. We consider these small differences as expression of a late ontogenetic development.

Schwarzhans & Aguilera (2013) compared *L. scapha* with the extant *L. luminosa* (Garman, 1899) and *L. atlantica* Maul, 1969 (see Girone & Nolf 2002 for figures). The additional specimens now available indicate that the relationship is probably closer with *L. atlantica* and *L. urophaos* Paxton, 1963, two species which have been considered as subspecies in the past and may have derived from a common ancestor. It is possible that *L. scapha* represents this common ancestor. *Lampadena scapha* differs from *L. urophaos* in being less thin (OH:OT 5-6 vs 8) and slightly bent (vs flat), the anteriorly expanded dorsal rim (vs depressed) and the relatively shorter ostial colliculum expressed in a lower index OCL:CCL (1.7-2.0 vs 2.0-2.3). More similar in all these aspects are the otoliths of *L. atlantica*, which differ from *L. scapha* in the more intensely denticulate or crenulated ventral rim, the narrower ostial colliculum (OCH:CCH = 1.3-1.45 vs 1.65-1.8), the posteriorly more reduced caudal colliculum and the distinct denticle at the postdorsal angle just before the postdorsal depression. Anyhow, this means that the fossil *L. scapha* is morphologically closer to *L. atlantica* than *L. urophaos* which also indicates that the otolith morphology of *L. urophaos* is more advanced. The wide geographical distribution of *L. scapha* during the Piacenzian in the Caribbean, NW Pacific (Japan) and SW Pacific (Fiji) is consistent with an interpretation of it representing the common ancestor of the two extant species.

Genus *Lampanyctus* Bonaparte, 1840

Lampanyctus alatus Goode & Bean, 1896

Fig. 7 L-N

Material: 4 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 3 specimens Nob-1, 1 specimen Nob-6 (figured specimen SMF PO 101013).

Discussion. Otoliths of the many extant *Lampanyctus* species are very diverse but all share a flat inner face and smooth rims. The latter can easily lead to misidentifications of eroded specimens in the fossil record as *Lampanyctus* otoliths, for instance of the genus *Diaphus*. In any case, verified fossil *Lampanyctus* otoliths have been rarely described, which contrasts with the abundance in the modern record in the oceans. On the other hand *L. carpaticus* (Brzobohaty, 1965) is very abundant in the uppermost Early Miocene (Karpatian) of the Central Paratethys (Brzobohaty et al. 2003).

Otoliths of *Lampanyctus alatus* are moderately compressed (OL:OH = 1.1) with a shallow dorsal and a deep, anteriorly pronounced ventral rim, and a short cauda (OCL:CCL < 2.0) (see Smale et al. 1995 for figures). *Lampanyctus alatus* is widely distributed in the warm waters of the Pacific, Indian and Atlantic oceans and in Japan occurs from off Tohoku to the Ryukyu Islands (Masuda et al. 1984).

Lampanyctus festivus Tåning, 1928

Fig. 7 O-Q

1983 *Stenobrachius leucopsarus* (Eigenmann & Eigenmann, 1890) - Ohe: pl. 6, figs. 13-14.

Material: 2 specimens Iriyamase, Kakegawa, Hijikata FM, early Calabrian (figured specimen SMF PO 101014).

Discussion. Otoliths of *Lampanyctus festivus* are amongst the most compressed found in the genus, except for the species usually placed in *Nannobrachium* Günther, 1887. It is further characterized by the strong antirostrum, which is as long or longer than the broadly rounded rostrum (see Smale et al. 1995 for figures). The long antirostrum could be mistaken as the rostrum and the otolith be rotated by 180°. It would then look similar to *Stenobrachius* otoliths with a strong rostrum. However, dorsal depression, ventral furrow, presence of a small caudal pseudocolliculum and orientation of upward bent cauda indicate an orientation as figured here.

Lampanyctus festivus is widely distributed in the temperate waters of the oceans of both hemispheres and in Japan is recorded from off Tohoku (Masuda et al. 1984). It is another indicator for the cooling of the sea in the Kakegawa area during the Hijikata FM.

Lampanyctus nobilis Tåning, 1928

Fig. 7 R-V

1981 *Diogenichthys* sp. - Ohe: pl. 2, fig. 13.

Material: 79 specimens: 4 specimens, Ozatofurugen, Okinawa, upper Yonabaru FM, early Piacenzian (figured specimen SMF PO 101015); 50 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 46 specimens Nob-1 (figured specimens SMF PO 101016), 4 specimens Nob-3+4; 25 specimens Hongohigashi, Kakegawa, Dainichi FM, Gelasian (figured specimens SMF PO 101017).

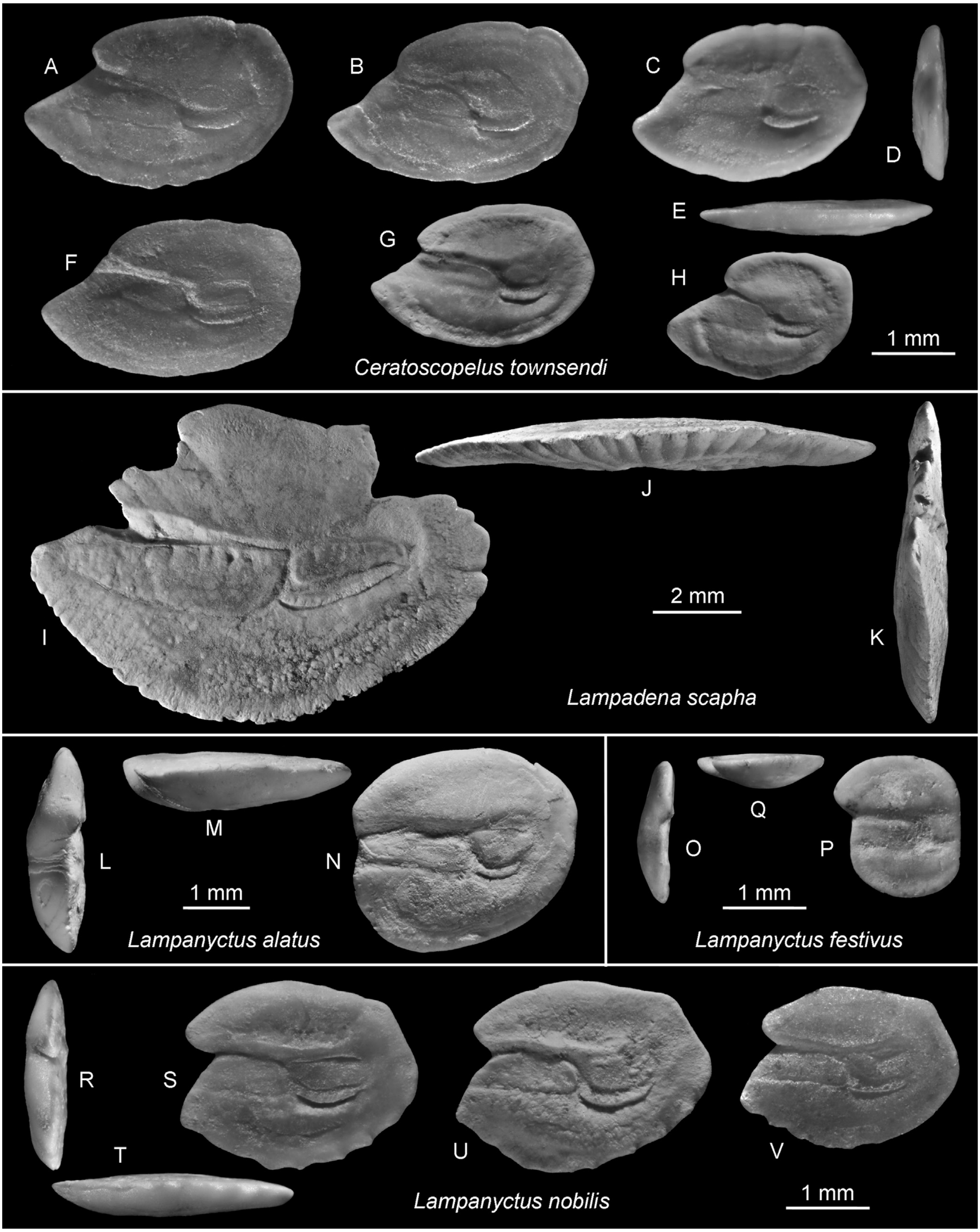


Fig. 7 - A-H) *Ceratoscopelus townsendi* (Eigenmann & Eigenmann, 1889), A, B, F SMF PO 101012 (reversed), D-E SMF PO 101010, G SMF PO 101011, H SMF PO 101009 (reversed), A-C, F-H - inner faces, D - anterior view, E - ventral view; I-K) *Lampadena scapha* Schwarzhans & Aguilera, 2013, OU 41327b (reversed), I - inner face, J - ventral view, K - anterior view; L-N) *Lampanyctus alatus* Goode & Bean, 1896, SMF PO 101013, L - anterior view, M - ventral view, N - inner face; O-Q) *Lampanyctus festivus* Tåning, 1928, SMF PO 101014, O - anterior view, P - inner face, Q - ventral view; R-V) *Lampanyctus nobilis* Tåning, 1928, R-T SMF PO 101016 (reversed), U SMF PO 101015 (reversed), V SMF PO 101017, R - anterior view, T - ventral view, S-V - inner faces.

Discussion. Otoliths of *Lampanyctus nobilis* belong to a group of more elongate forms (OL:OH = 1.25-1.4) and is widely distributed in all tropical seas. So far a single fossil record has been described from the early Pliocene of Venezuela (Schwarzhans & Aguilera 2013).

Subfamily Diaphinae Paxton, 1972
Genus *Diaphus* Eigenmann & Eigenmann, 1890

Remarks. The otoliths of the many species of *Diaphus* are not always easy to distinguish and often depend on relatively subtle characters. For a reliable species identification, it therefore requires well preserved otoliths of a size considered to be diagnostically mature. Identification of eroded or small *Diaphus* otoliths is still possible in many instances when associated with well preserved large specimens of a given species. Still, many eroded or small fossil *Diaphus* otoliths can not be specifically identified and they are omitted from the following section. Literature references based on not clearly identifiable *Diaphus* otoliths are omitted as well.

Diaphus termophilus otolith group

Diaphus termophilus Tåning, 1928

Fig. 8 A-C

Material: 1 specimen SMF PO 101017, Fosoya, Kakegawa, Hosoya Tuffaceous Member, Hijikata FM, Gelasian.

Discussion. A single specimen from the middle Pleistocene is being associated with *Diaphus termophilus* based on the following characters: OL:OH = 1.2 (range in Recent specimens 1.15-1.3); rostrum massive, 18% of OL; antirostrum and excisura small; postdorsal angle strong, pointed, placed above rear part of cauda; postdorsal rim not depressed; narrow and relatively short ostium (OCL:CCL = 1.5, range 1.4-1.6 in Recent specimens) (see Schwarzhans 2013b).

Diaphus termophilus is primarily a subtropical oceanic species with a disjunctive distribution pattern in the northern Atlantic between 10°N to 37°N and the western Pacific in the Tasman Sea and the south-east Asian Sea between 8°N and 7°S (Hulley 1984). The singular find in the early Pleistocene of Japan indicates that the species may have been more widely distributed in the past.

Diaphus theta otolith group

Diaphus caurus n. sp.

Fig. 8 D-F

1983 *Diaphus* cf. *D. hudsoni* Zurbrigg & Scott, 1976 - Ohe: pl. 5, fig. 1.

Etymology: From caurus (Latin) = northwest, referring to the occurrence of this species in the northwestern Pacific.

Holotype: SMF PO 101018 (Fig. 8 D-F); Iriyamase, Kakegawa, Hijikata FM, early Calabrian, planktonic foraminifer zone N22, 1.9-1.6 Ma.

Paratypes: 3 specimens, SMF PO 101019, same data as holotype.

Diagnosis: OL:OH = 1.15. OH:OT = 3.0-3.5. Dorsal rim anteriorly inclined, posteriorly with sharp postdorsal angle located above middle of cauda, followed by mild postdorsal concavity. Rostrum about twice as long as antirostrum. Ventral rim with 6-7 delicate denticles. Cauda nearly as long as ostium and narrower; OCL:CCL = 1.3.

Description. Compact, thick and small otoliths up to 1.9 mm length (holotype). OH:OT = 3.0-3.5, decreasing with size. Dorsal rim anteriorly inclined downwards, posteriorly with prominent and sharp postdorsal angle located slightly behind middle of dorsal rim and above middle part of cauda. Postdorsal angle followed by steep, slightly concave postdorsal rim. Ventral rim gently and regularly curving with 6 to 7 delicate, mostly sharp denticles. Rostrum moderately long (20% of OL) and about twice as long as antirostrum, both pointed and excisura sharp. Posterior rim gently and regularly rounded.

Inner face flat with slightly supramedian sulcus. Ostium slightly longer and wider than cauda. OsL:CaL = 1.3; OsH:CaH = 1.1. Ostium slightly widened anteriorly. Caudal termination box-shaped, at moderate distance from posterior rim of otolith. Caudal pseudocolliculum strong, relatively wide and slightly longer than caudal colliculum. Caudal colliculum shorter and narrower than ostial colliculum. OCL:CCL = 1.3; OCH:CCH = 1.45; OCH:CCHP = 1.0. Dorsal depression large, with indistinct margins and weak crista superior towards sulcus. Ventral furrow distinct, running about halfway between ventral margin of sulcus and ventral rim of otolith. Outer face distinctly convex, smooth.

Discussion. *Diaphus caurus* combines a number of characters found in the various otolith subgroups of the *Diaphus theta* otolith group (see Schwarzhans 2013b for figures of Recent otoliths). The compressed shape with the low index OL:OH of less than 1.2 resembles otoliths of the *Diaphus fulgens* otolith subgroup. The shape of the dorsal rim resembles otoliths of the *Diaphus holti* otolith subgroup and the thickness those of the *Diaphus anderseni* otolith subgroup. *Diaphus caurus* differs from otoliths of the *Diaphus fulgens* otolith subgroup in the expression of the dorsal rim with the prominent postdorsal angle and the following depression (vs regularly rounded) and the thickness (OH:OT = 3.0-3.5 vs 3.5-4.0). From *D. anderseni* it differs also in the expression of the dorsal rim, the relatively wide ostium and in the long rostrum. From otoliths of the *Diaphus holti* subgroup it differs in the compressed outline (OL:OH = 1.15 vs 1.2-1.4) and the relatively short and wide ostial colliculum. We therefore consider *D. caurus* to represent an extinct member of the *Diaphus holti* otolith subgroup, and here it resembles most *Diaphus holti* Tåning, 1918 from the temperate North Atlantic and Southern Oceans, *D. hudsoni* Zurbrigg & Scott, 1976 and *D. meadi* Nafpaktitis, 1978, both species of the temperate Southern Oceans. *Diaphus caurus* may represent an extinct northern Pacific off-spring derived from that clade.

Aoki & Baba (1980) described *Diaphus quadratus* Aoki & Baba, 1980 from the middle Pleistocene of the Nojima FM near Yokohama, which in fact represents a junior synonym of *Diaphus theta* Eigenmann & Eigenmann, 1890. *Diaphus theta* is a typical subarctic to temperate species of the northern Pacific distributed from California to northern Japan southwards to the Kashimanada Sea into the Oyashio / Kuroshio transition zone. The Nojima FM is slightly younger than the Hijikata FM and about 1° further North and West. This was apparently enough in the middle Pleistocene of Japan to switch from a warm water fauna with some temperate influence to a temperate water fauna.

Diaphus grebneffi n. sp.

Fig. 8 Q-S

Etymology: In memoriam of Andrew Grebneff (Dunedin, New Zealand), who collected the unique and quite exceptional holotype from Fiji.

Holotype: OU 41327a (Fig. 8 Q-S); excavation in Weila (A. Grebneff location 224), Nausori, SE Viti Levu, Fiji, Nakosi FM, presumably Piacenzian (see Janssen & Grebneff 2012).

Diagnosis: Very large size of 8.5 mm length. OL:OH = 1.4. OH:OT = 3.5. Dorsal rim anteriorly inclined, with small middorsal depression in front of broad postdorsal angle. Rostrum short, no clearly developed excisura and antirostrum. Ventral rim with 12 robust denticles. OCL:CCL = 1.6; OCH:CCH = 1.2. Ostial colliculum dorsally and anteriorly significantly reduced, not opening to otolith rim.

Description. The unique holotype a robust, oval elongate and very large otolith of 8.5 mm length. Dorsal rim anteriorly and posteriorly depressed, inclined at 40-45°; small middorsal depression; strong, broad postdorsal angle located above central part of cauda, no postdorsal concavity. Rostrum moderately long; no distinct excisura or antirostrum developed. Posterior rim rounded with tip at level with rostral tip. Ventral rim broadly and regularly curved, about as deep as dorsal rim high, with 12 robust denticles (slightly eroded and denticle number 4 broken).

Inner face only slightly bent in horizontal direction, nearly flat in vertical direction. Sulcus with median position, relatively narrow and short leaving much space behind caudal tip; OL:SuL = 1.25. Ostium about 50% longer than cauda but distinctly narrower (OH:CH = 0.75), but ostial colliculum slightly wider than caudal colliculum (OCH:CCH = 1.2; OCH:CCH including pseudocolliculum = 0.8). Ostial colliculum dorsally and anteriorly reduced, not meeting anterior rim of otolith; caudal colliculum straight, posteriorly and postdorsally reduced. Dorsal rim of ostium slightly oscillating; dorsal rim of cauda turned upward (not mirrored in shape of caudal colliculum). Caudal pseudocolliculum long and distinct. Dorsal depression wide, relatively deep, with distinct crista superior towards sulcus. Ventral furrow distinct, moderately distant from ventral rim of otolith and parallel. Outer face flat except for well developed postcentral umbo; smooth except few short radial furrows ventrally.

Discussion. This otolith shows all the hallmarks of otoliths from the *Diaphus theta* otolith group (more or less equivalent to the So-group of Kawaguchi & Shimizu (1978) as defined by the head photophore pattern): almost flat, slightly bent inner face; distinct postcentral umbo on the outer face; narrow sulcus; distinct postdorsal angle; no postdorsal concavity; predorsal rim not expanded. Similar otoliths are also found in the *Diaphus termophilus* and the *Diaphus signatus* otolith groups. However, none of the extant or fossil species accounted in these groups reach the size of *D. grebneffi* by a big margin. The largest otolith specimens seen from these groups are those of *D. subtilis* Nafpaktitis, 1968 with 5.7 mm length from a specimen of 90 mm SL. The largest growing extant species in these group is *D. theta* Eigenmann & Eigenmann, 1890, which may reach 110 mm SL (Froese & Pauly

2018). The largest known extant *Diaphus* otoliths stem from *D. whitleyi* Fowler, 1934 (8.4 mm OL at 170 mm SL), *D. watasei* Jordan & Starks, 1904 (8.6 mm OL at 170 mm SL), *D. mascarensis* Becker, 1990 (8.5 mm OL at 143 mm SL) and *D. adenomus* Gilbert, 1905 (10.5 mm OL at 200 mm SL) (data from Schwarzhans 2013b and unpublished data). Thus, the size of the fish must have been in the range of 145 to 170 mm SL, from which the holotype of *D. grebneffi* originated. This is at least a third bigger than any specimen of any extant species of the *Diaphus theta* otolith group, which includes *D. grebneffi,* or otoliths of the related *D. termophilus* or *D. signatus* otolith groups.

Apart from its shear size, *D. grebneffi* also differs from the otoliths of other species of the mentioned groups in the presence of the middorsal depression and the anteriorly reduced sulcus opening without antirostrum and excisura and an anteriorly reduced ostial colliculum. It is also more slender than the otoliths of most other species in the *Diaphus theta* group with an index OL:OH of 1.4, except *D. rafinesquii* (Cocco, 1838), which however has a distinctly longer rostrum.

Diaphus kuroshio Kawaguchi & Nafpaktitis, 1978

Fig. 8 G-K

1983 *Diaphus kuroshio* Kawaguchi & Nafpaktitis, 1978 - Ohe: pl. 2, fig. 8.
1997 *Diaphus kuroshio* Kawaguchi & Nafpaktitis, 1978 - Ohe, Kawai & Kawase: pl. 1, fig. 4.

Material: 11 specimens: 1 specimen Hongohigashi, Kakegawa, Dainichi FM, Gelasian; 10 specimens Iriyamase, Kakegawa, Hijikata FM, early Calabrian (figured specimen SMF PO 101020).

Description. More specimens have become available from Recent fishes of *Diaphus kuroshio* than the one figured in Schwarzhans (2013b) warranting a refined description. Moderately thick and elongate otoliths up to about 5.0 mm length. OL:OH = 1.25-1.3; OH:OT = 3.0-3.3. Dorsal rim anteriorly depressed, inclined downwards in a straight line without predorsal angle, posteriorly with broad postdorsal angle located above middle part of cauda. Postdorsal rim downward inclined in straight or slightly convex line, not concave. Ventral rim gently and regularly curving with 7 to 9 rather strong denticles. Rostrum moderately long, 14-17% of OL. Antirostrum and excisura short, small. Posterior rim gently and regularly rounded.

Inner face slightly bent along horizontal axis, flat along vertical axis. Sulcus moderately narrow, straight, its cauda slightly bent upwards. Cauda termination box-shaped, relatively close to posterior rim of otolith; OL:SuL = 1.15-1.2. Ostium slightly longer than cauda; OsL:CaL = 1.4-1.6. Ostium with straight dorsal margin. Caudal pseudocolliculum strong, relatively wide and slightly longer than caudal colliculum. Caudal colliculum shorter and narrower than ostial colliculum. OCL:CCL = 1.6-2.0; OCH:CCH = 1.05-1.15; OCH:CCHP = 0.75-0.8. Dorsal depression large, with distinct lower margin (crista superior) towards sulcus. Ventral furrow distinct, running at moderate distance from ventral rim of otolith. Outer face distinctly convex, with postcentral umbo but also thickened in anterior region; smooth or with few radial furrows.

Discussion. Otoliths of *D. kuroshio* are very similar to those of *D. rafinesquii* (Cocco, 1838) from the subtropical and temperate northern Atlantic. The differences are subtle: *Diaphus kuroshio* is less elongate (OL:OH = 1.25-1.3 vs 1.35-1.4), has a broader convex outer face while in *D. rafinesquii* the anterior region is thinner than at the postcentral umbo, the dorsal rim is straight and inclined in *D. kuroshio* (vs with a broad predorsal bulge), the postdorsal angle is located above the middle of the cauda (vs above rear part of cauda), the sulcus is longer in respect to the otolith length (OL:SuL = 1.15-1.2 vs 1.25-1.3) and the postdorsal rim is straight to slightly convex (vs slightly concave).

Diaphus kuroshio is only known from the Kuroshio Current and the Kuroshio extension in the northwestern Pacific chiefly off Japan and obviously dates back in the area to the early Pleistocene. Two extant specimens of *Diaphus kuroshio* are shown for comparison (Fig. G-J). In the Kuroshio extension it might overlap with specimens described by Wisner (1976) as *Diaphus rafinesquii* species complex in the northern Pacific. No otoliths are known from these specimens. For comparison with *D. mollis* see below.

Similar fossil otolith-based species are *Diaphus crassus* Schwarzhans, 1978 from the early Pliocene of the northern subtropical to tropical Atlantic and *Diaphus ecuadorensis* Schwarzhans & Aguilera, 2013 from the late Miocene of the tropical eastern Pacific. *Diaphus kuroshio* differs from *D. crassus* in being slightly more elongate (OL:OH = 1.25-1.3 vs 1.15-1.25), the longer rostrum (14-17% of OL vs

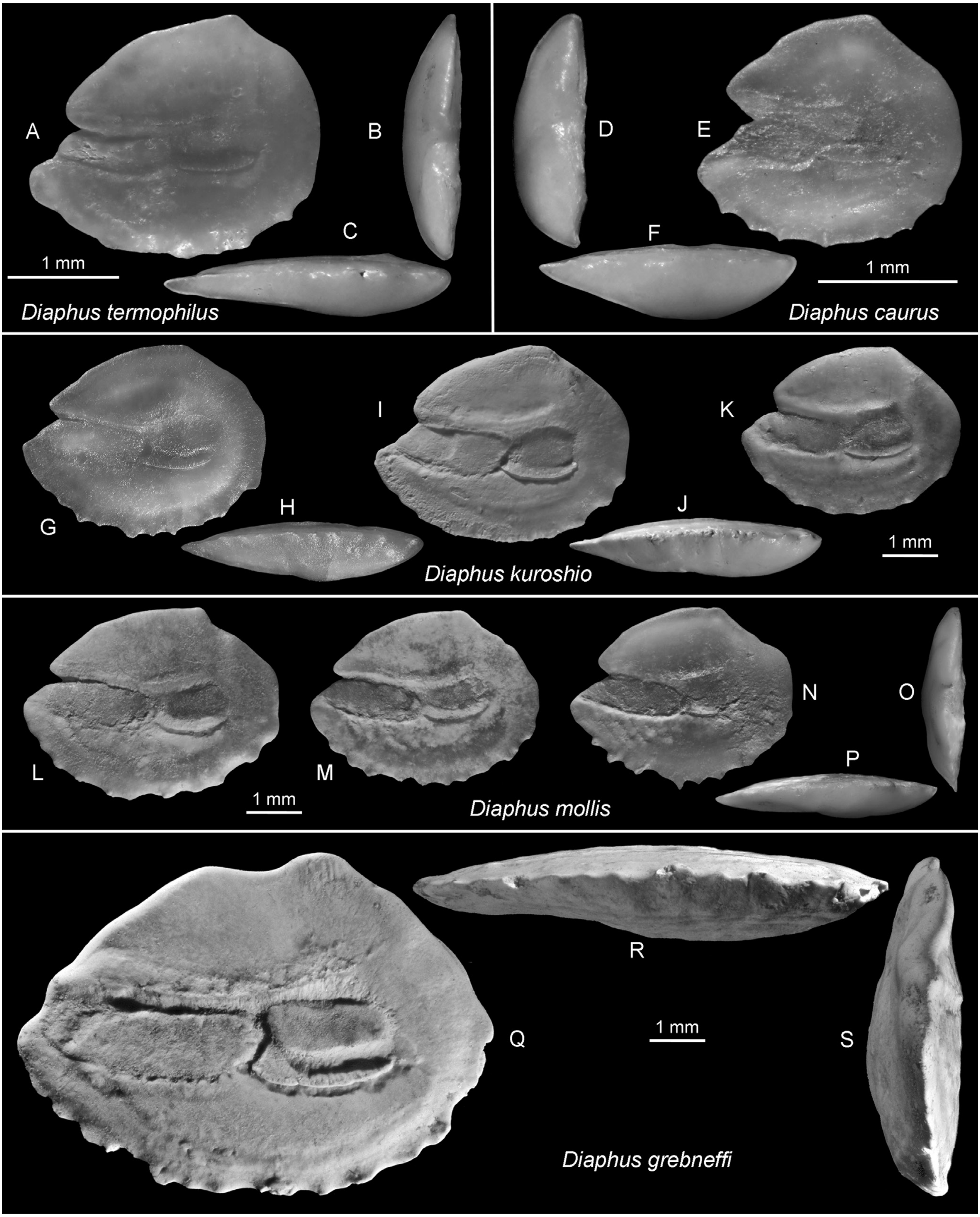


Fig. 8 - A-C) *Diaphus termophilus* Tåning, 1928, SMF PO 101017, A - inner face, B - anterior view, C - ventral view; D-F) *Diaphus caurus* n.sp., holotype, SMF PO 101018, D - anterior view, E - inner face, F - ventral view; G-K) *Diaphus kuroshio* Kawaguchi & Nafpaktitis, 1978, G-H Recent, coll. Ohe (OPC 800902) SL 72 mm, Suruga Bay, I-J Recent, NSMT-P 48297, SL 63 mm, 36°27'N-141°24'E, K SMF PO 101020, G, I, K - inner face, H, J - ventral view; L-P) *Diaphus mollis* Tåning, 1928, L, N-P SMF PO 101022, M SMF PO 101021 (reversed), L-N - inner faces, O - anterior view, P - ventral view; Q-S) *Diaphus grebneffi* n.sp., holotype, OU 41327a, Q - inner face, R - ventral view, S - anterior view.

10-13%), the anteriorly depressed dorsal rim and the higher number of denticles on the ventral rim (9-10 vs 6-8). From *D. ecuadorensis* it differs in being more thickset (OH:OT = 3.0-3.3 vs 4.5), the anteriorly depressed dorsal rim (vs regularly curved) and the somewhat wider ostium and sulcus. *Diaphus kuroshio* occurs first in the early Pleistocene of Kakegawa, but has also been recorded from the late Pleistocene to Holocene of Kikaijima of the Amami Islands (northern Ryukyu Island Chain) by Ohe et al. (1997), which is close to the southern limit of the distribution of the species nowadays (Kawaguchi & Nafpaktitis 1978).

Diaphus mollis Tåning, 1928

Fig. 8 L-P

Material: 18 specimens: 17 specimens Okinawa, Shinzato FM, Piacenzian: 3 specimens Gushichan (figured specimen SMF PO 101021), 14 specimens Tobaru (figured specimens SMF PO 101022); 1 specimen Nob-1, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian.

Discussion. Otoliths of *Diaphus mollis* differ from those of *D. kuroshio* in being thinner (OH:OT = 4.0-4.3 vs 3.0-3.5) and showing a long and concave postdorsal rim (vs straight or slightly convex). The latter is also the main difference to other similar extant species such as *D. aliciae* Fowler, 1934 and *D. parri* Tåning, 1932 (see Schwarzhans 2013b). *Diaphus mollis* is widely distributed in the tropical and subtropical waters of all three oceans. In Japan it has been recorded off the Ryukyu Islands and Ogasawara (Masuda et al. 1984). In the fossil record it is common in the Piacenzian of Okinawa, but lacking from the early Pleistocene of Kakegawa.

Diaphus richardsoni Tåning, 1932

Fig. 9 A-D

Material: 2 specimens Tobaru, Okinawa, Shinzato FM, Piacenzian (figured specimens SMF PO 101023).

Discussion. Otoliths of *Diaphus richardsoni* are characterized by their thin appearance (OH:OT = 4.5-5.5), the relatively flat inner face with a rather narrow sulcus, the regularly rounded, anteriorly slightly expanded dorsal rim with a straight, inclined postdorsal section, 11-14 irregular denticles on the ventral rim and an index OCL:CCL of about 2.0. It is usually related to *D. brachycephalus*, but differs in a number of aspects, such as the more elongate shape (OL:OH = 1.3-1.4 vs 1.1), the straight postdorsal section (vs distinctly concave), the high index OCL:CCL of 1.9-2.1 (vs 1.2-1.4) and more denticles on the ventral rim (11-14 vs 8-10) (see Schwarzhans 2013b).

Diaphus richardsoni is a tropical to subtropical oceanic species of the Indio-West Pacific. In Japan it is known from a single species washed ashore in the Suruga Bay (Masuda et al. 1984).

Diaphus splendidus otolith group

Diaphus endoi n. sp.

Fig. 9 G-O

Etymology: Named in honor of Hiromitsu Endo, Kochi, for his many contributions to the knowledge of Japanese fishes.

Holotype: SMF PO 101024 (Fig. 9 G-I), Tobaru, Miyagi Jima, Okinawa, Shinzato FM, Piacenzian, planktonic foraminifer zone N21 (PL"5-6"), 3.35-2.3 Ma.

Paratypes: 5 specimens: 4 specimens SMF PO 101025 (Fig. 9 J-L, N-O), same data as holotype; 1 specimen NRM-PZ 16737 (Fig. 9 M), Higa.

Further specimens: 235 specimens: 232 specimens same data as holotype, 3 specimens Higa.

Diagnosis: OL:OH = 1.3-1.4. OH:OT = 5.5. Dorsal field high; dorsal rim anteriorly broadly rounded, posteriorly with prominent postdorsal angle, followed by deep, angular postdorsal concavity and reduced, bluntly rounded posterior rim. Rostrum short, 10-15% of OL, but distinctly longer than antirostrum. Ventral rim with 9-12 irregular denticles. Ostium with slightly lobate dorsal margin; ostial colliculum dorsally reduced; OCL:CCL = 1.8-2.1.

Description. Thin, moderately elongate and large otoliths reaching up to 6.0 mm length (holotype 5.7 mm). Dorsal rim anteriorly steeply downward inclined in front of broadly rounded section; posteriorly highly elevated, with prominent, nearly orthogonal angle, followed by deep angular postdorsal concavity. Posterior rim reduced in specimens of more than 4.5 mm length, bluntly rounded. Ventral rim shallow, regularly curving with 9 to 12 very irregular denticles or lobes, distinct denticle projecting at joint of ventral with posterior rim. Rostrum short, 10-15% of OL, but distinctly longer than sharp and pointed antirostrum (length rostrum to antirostrum 1.2-1.5); excisura variable, usually shallow but sometimes deep and sharp (Fig. 9 L).

Inner face very slightly bent along horizontal axis, flat along vertical axis. Sulcus narrow, straight, its cauda slightly bent upwards. Cauda termination box-shaped, relatively close to posterior rim of otolith; OL:SuL = 1.1-1.15. Ostium distinctly longer than cauda, slightly narrowing towards opening and with slightly lobate dorsal rim; OsL:CaL = 1.5-1.8. Ostial colliculum dorsally reduced leaving broad area with excisural furrow. Caudal pseudocolliculum strong but narrow and slightly longer than caudal colliculum. Caudal colliculum distinctly shorter but not much narrower than ostial colliculum. OCL:CCL = 1.8-2.1; OCH:CCH = 1.0-1.15; OCH:CCHP = 0.85-0.95. Dorsal field very wide, voluminous, with indistinct dorsal depression only marked by fine, long crista superior towards sulcus. Ventral furrow broad, indistinct, running at moderate distance from ventral rim of otolith. Outer face flat, with few radial furrows.

Discussion. *Diaphus endoi* resembles otoliths of several large growing Recent species such as *D. coeruleus* (Klunzinger, 1871), *D. gigas* Gilbert, 1913, *D. rivatoni* Bourret, 1985 and *D. watasei* Jordan & Starks, 1904. It differs from otoliths of *D. coeruleus* in the more compressed shape (OL:OH = 1.3-1.4 vs 1.6) and the high dorsal rim with its broadly rounded anterior-dorsal section (vs depressed). From the single known otolith of *D. rivatoni* figured in Rivaton & Bourret (1999) it differs in the higher dorsal field, the narrow ostium and dorsally reduced ostial colliculum expressed best in the index OCH:CCHP (0.85-0.95 vs 1.1) and the slightly lobate dorsal margin of the ostium (vs straight). The closest resemblance is with otoliths of *D. gigas* and *D. watasei*. *Diaphus endoi* differs from otoliths of *D. watasei* in the lesser number of denticles on the ventral rim (9-12 vs 12-15), the more bluntly cut posterior rim (vs slightly expanded and rounded) and the very high dorsal field (see Fig. 9 T-V). From *D. gigas* it differs in the nearly flat inner face (vs markedly convex), the lower number of denticles along the ventral rim (9-12 vs 15-17) and the distinctly shorter rostrum (length rostrum to antirostrum 1.2-1.5 vs 1.7-2.3) (see Fig. 9 P-S). *Diaphus gigas* is a species of the transition zone between the Oyashio and Kuroshio Currents while the other three extant species and also *D. endoi* represent tropical to subtropical species.

Diaphus endoi probably belongs to the same lineage as *D. coeruleus* and *D. watasei* (see also Nafpaktitis 1978). *Diaphus endoi* also resembles the fossil *D. depressifrons* Schwarzhans & Aguilera, 2013 from the late Miocene and early Pliocene of the Caribbean but differs in the higher dorsal field, the lower index OL:OH (1.3-1.4 vs 1.4-1.5), the much deeper postdorsal depression and the lack of a denticle at the postdorsal angle.

Diaphus endoi is by far the most common myctophid species in the Shinzato FM of Okinawa and so far appears to be restricted to it. Few specimens from the younger Chinen FM of Okinawa and the Hijikata FM of Kakegawa resemble *D. endoi* but differ in certain other aspects and are therefore placed provisionally in *D.* aff. *endoi* (see below) until more specimens have become available for a more reliable identification.

***Diaphus* aff. *endoi* n. sp.**

Fig. 9 E-F

1983 *Diaphus gigas* Gilbert, 1913 - Ohe: pl. 4, fig. 1.

Material: 6 specimens: 2 specimens SMF PO 101026, Chinen, Okinawa, Chinen FM, early Calabrian; 4 specimens SMF PO 101027 (Fig. 9 E-F), Iriyamase, Kakegawa, Hijikata FM, early Calabrian.

Discussion. Four smaller specimens from the early Pleistocene Hijikata FM of Kakegawa and two from the coeval Chinen FM of Okinawa (all 4.0-4.5 mm length) resemble the typical specimens of *D. endoi* from the Shinzato FM of Okinawa but differ in certain aspects and therefore may represent a different species which can not be defined with the currently available material. They are slightly more elongate than specimens from the Shinzato FM of similar sizes (OL:OH = 1.35-1.45 vs 1.3-1.4) which is expressed in the less highly developed dorsal field and the more rounded posterior rim (vs bluntly rounded). Also, they tend to have a longer rostrum (14-18% OL vs 10-15% OL) which is also distinctly longer than the antirostrum (60-85% of rostrum length vs 30-55%). The number of denticles on the ventral rim (9-10) tends to be at the lower margin of the range observed in *Diaphus endoi*. However, a sufficient number of well-preserved, larger specimens in the range of 5 to 6 mm length is required to evaluate ontogenetic effects and for a reliable identification of the early Pleistocene specimens.

***Diaphus kakegawaensis* n. sp.**

Fig. 10 L-S

1981 *Benthosema* cf. *B. fibulatum* Gilbert & Cramer, 1897 - Ohe: pl. 2, fig. 12.

Etymology: Named after the region Kakegawa with several locations from which this species was collected and also in reference to the “Kakegawa Fauna” (after Nobuhara 1993).

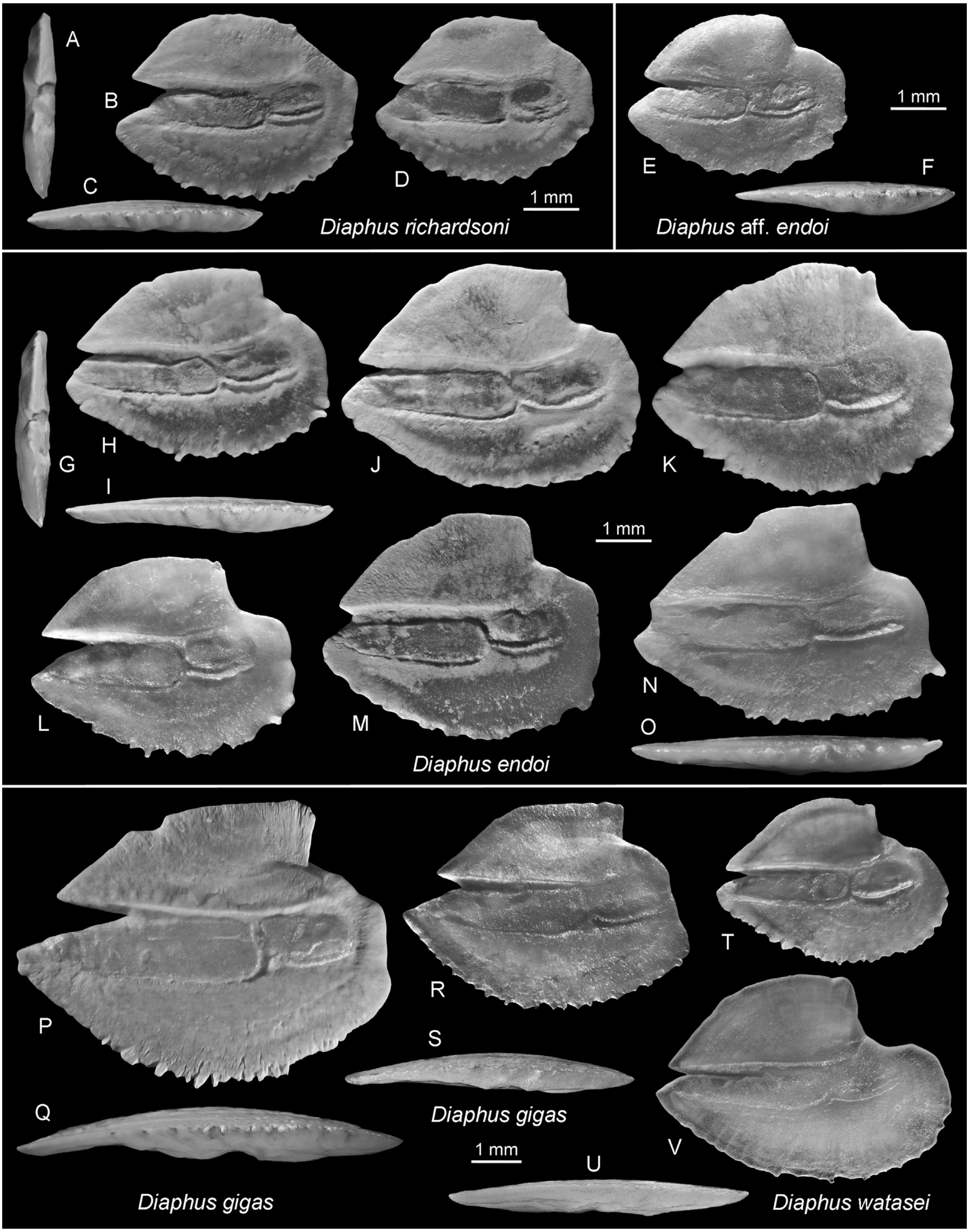


Fig. 9 - A-D) *Diaphus richardsoni* Tåning, 1932, SMF PO 101023, A - anterior view, B, D, - inner faces, C - ventral view; E-F) *Diaphus* aff. *endoi* n.sp., SMF PO 101027, E - inner face, F - ventral view; G-O) *Diaphus endoi* n.sp., G-I - holotype, SMF PO 101024, J-L, N-O - paratypes, SMF PO 101025 (K, L reversed), M - paratype, NRM-PZ 16737 (reversed), G - anterior view, H, J-N - inner faces, I, O - ventral view; P-S) *Diaphus gigas* Gilbert, 1913, Recent, P-Q NSMT-P 48231, SL 134 mm, off Tohoku, R-T coll. Ohe, OPC 811026, Suruga Bay, P, R - inner faces, Q, S - ventral views; T-V) *Diaphus watasei* Jordan & Starks, 1904, Recent, T coll. Ohe (OPC 691011), Suruga Bay, U-V - coll. Schwarzhans, Mimase fish market, T, V - inner faces, U - ventral view.

Holotype: SMF PO 101028 (Fig. 10 L-N), Hongohigashi, Kakegawa, Dainichi FM, Gelasian, planktonic foraminifer zone N21 (PL6), 2.3-2.0 Ma.

Paratypes: 5 specimens, SMF PO 101029 (Fig. 10 O-S), same data as holotype.

Further specimens: 70 specimens, same data as holotype.

Diagnosis: OL:OH = 1.2-1.35. OH:OT = 4.2-4.8. Dorsal rim anteriorly expanded, posteriorly without prominent postdorsal angle or concavity but strongly reduced posterior rim. Rostrum about as long as antirostrum or slightly longer. Ventral rim deeply curved, with 7-10 irregular denticles. Ostial colliculum dorsally reduced; OCL:CCL = 2.2-3.0.

Description. Thin, moderately compressed and large otoliths reaching up to 6.0 mm length (holotype 5.6 mm). Dorsal rim anteriorly expanded, without postdorsal angle or depression, regularly curved or undulating with three distinct lobes. Posterior rim reduced in specimens of more than 4.0 mm length (Fig. 10 L-Q), rounded in smaller specimens (Fig. 10 R-S)). Ventral rim deeply and regularly curving with 7 to 10 irregular denticles or lobes, distinct denticle projecting at joint of ventral with posterior rim. Rostrum very variable in length depending on depth of excisura, 10-20% of OL, as long as antirostrum or slightly longer, both rostrum and antirostrum about equally sharp and high; excisura variable, deep and sharp or rather shallow.

Inner face slightly bent along horizontal axis, flat along vertical axis. Sulcus moderately wide, straight, its cauda slightly bent upwards. Cauda termination box-shaped, relatively close to posterior rim of otolith; OL:SuL = 1.1-1.2. Ostium distinctly longer than cauda, slightly narrowing towards opening and with slightly lobate dorsal rim; OsL:CaL = 1.8-2.3. Ostial colliculum dorsally reduced leaving broad area with excisural furrow. Caudal pseudocolliculum weak, narrow, about as long as caudal colliculum. Caudal colliculum distinctly shorter but not much narrower than ostial colliculum. OCL:CCL = 2.2-3.0; OCH:CCH = 1.05-1.2; OCH:CCHP = 0.85-0.95. Dorsal field wide, with indistinct dorsal depression only marked along crista superior towards sulcus. Ventral furrow distinct, running at moderate distance from ventral rim of otolith. Outer face flat but with very weak postcentral umbo, with few radial furrows.

Ontogeny. *Diaphus kakegawaensis* shows a rather strong degree of intraspecific variability and ontogenetic changes that may complicate recognition. The expression of the dorsal rim varies from nearly smooth with a very indistinct postdorsal depression to irregularly undulating, sometimes with up to three prominent lobes and no postdorsal depression. Usually, smaller specimens show a more regularly curved dorsal rim than larger ones. Other variable characters are the index OL:OH varying between 1.2 and 1.35, the degree of the reduction of the posterior rim, which is also expressed in the variation of the index OL:OH and relative length of the caudal colliculum expressed in the variation of the index OCL:CCL. These three variable characters seem to interact and also seem to have some degree of an ontogenetic component. Many large *Diaphus* otoliths are known for the reduction of the posterior rim (see Schwarzhans 2013b), while smaller specimens of the same species may have a regular posterior rim. This is also the case in *D. kakegawaensis*: the large specimens of more than 4.0 mm length generally show an advanced reduction of the posterior rim and therewith tend to be more compressed and also tend to have a shorter caudal colliculum. The transition to a reduced posterior rim takes place in a range between 4.3 and 4.6 mm length (compare Figs. 10 P and 10 R). It goes in hand with the beginning of an undulation of the dorsal rim.

Discussion. *Diaphus kakegawaensis* is easily recognized by the lack of a postdorsal angle or depression, the reduced postdorsal rim, the dorsally reduced ostial colliculum and rostrum and antirostrum being very similar in expression and length. These characteristics distinguish *D. kakegawaensis* from otoliths of all Recent species of the *Diaphus coeruleus* otolith subgroup as well as *D. endoi* described above. A similar development of the postdorsal rim with no or a small concavity is only found in *D. lucidus* (see below), which however has a distinctly longer rostrum than antirostrum and a more expanded but shorter dorsal field. *Diaphus kakegawaensis* is confined to the Dainichi FM of early Pleistocene (Gelasian) age and possibly indicates slightly cooler conditions than assumed for the more southerly Shikoku and Okinawa locations.

Diaphus lucidus (Goode & Bean, 1896)

Fig. 10 G-K

Material: 55 specimens: 53 specimens Tobaru, Okinawa, Shinzato FM, Piacenzian (figured specimens SMF PO 101030); 2 specimens Nob-6, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian.

Discussion. Otoliths of *Diaphus lucidus* are amongst the most high bodied in the *Diaphus coeruleus* otolith subgroup with an index OL:OH of 1.15-1.3. Other typical aspects are the deep excisura leading to a long and sharp rostrum and slightly shorter antirostrum and the reduced posterior rim in specimens of 4.0-6.0 mm length leaving room for no or only a very indistinct and small postdorsal concavity.

Diaphus lucidus is known from the tropical to subtropical waters of the Atlantic, western Indian Ocean and the western and central Pacific. In the western Pacific it is known northwards to off Luzon and Taiwan, but is not recorded from Japanese waters. Its common occurrence in the Shinzato FM of Okinawa probably indicates warmer climate at that location compared to Shikoku (few specimens in the Nobori FM) and the Kakegawa area (absent from the Dainichi FM).

Diaphus nafpaktitisi n. sp.

Fig. 10 A-C

Etymology: Named in honor of Basil Nafpaktitis, formerly LACM (Los Angeles) in recognition of his outstanding contribution to the knowledge of *Diaphus* species.

Holotype: SMF PO 101031 (Fig. 10 A-C), Nob-1, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian, planktonic foraminifer zone N21.

Paratypes: 6 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 4 specimens SMF PO 101032, Nob-6, 2 specimens SMF PO 101033, Nob-8.

Diagnosis: OL:OH = 1.35-1.45. OH:OT = 5.0-6.0. Dorsal rim anteriorly depressed, posteriorly with distinct postdorsal angle located above middle to rear part of cauda, followed by a shallow and short postdorsal concavity and a reduced, broadly rounded posterior rim. Rostrum short, 8-15% of OL, distinctly longer than weak antirostrum; excisura shallow. Ventral rim with 7-10 irregular denticles and lobes. Ostium with straight dorsal margin; ostial colliculum not reduced dorsally. Caudal colliculum much shorter than ostial colliculum and narrowed; OCL:CCL = 1.8-2.2; OCH:CCH = 1.4-1.5.

Description. Thin, moderately elongate and large otoliths reaching up to 6.5 mm length (holotype 5.8 mm). Dorsal rim anteriorly depressed or slightly rounded, postdorsal angle distinct, located above central to rear part of cauda, followed by short, steeply inclined, slightly concave section. Posterior rim reduced, rounded. Ventral rim shallow, regularly curving with up to 7-10 irregular denticles or lobes. Rostrum short, pointed, 8-15% of OL, distinctly longer than minute antirostrum; excisura shallow.

Inner face flat. Sulcus moderately wide, straight, its cauda slightly bent upwards. Cauda termination box-shaped, relatively close to posterior rim of otolith; OL:SuL = 1.1-1.15. Ostium distinctly longer than cauda, with straight dorsal rim; OsL:CaL = 1.7-2.1. Ostial colliculum not dorsally reduced. Caudal pseudocolliculum narrow, longer than caudal colliculum. Caudal colliculum distinctly shorter and much narrower than ostial colliculum. OCL:CCL = 1.8-2.2; OCH:CCH = 1.4-1.5; OCH:CCHP = 0.9-1.1. Dorsal field moderately wide and long, with indistinct dorsal depression only marked long crista superior towards sulcus. Ventral furrow distinct, running at moderate distance from ventral rim of otolith. Outer face flat, with some long radial furrows ventrally.

Discussion. *Diaphus nafpaktitisi* is a relatively rare species from the early late Pliocene of southern Japan. It resembles *D. endoi* but differs in the more shallow dorsal rim with the backward positioned postdorsal angle, the short postdorsal concavity and the narrow caudal colliculum resulting in a very high index OCH:CCH of 1.5 (vs 1.0-1.15). Other subtler differences are the straight upper margin of the ostium (vs slightly lobate) and the not dorsally reduced ostial colliculum (vs reduced). It differs from *D. lucidus* and *D. kakegawaensis* in the more elongate shape (OL:OH = 1.35-1.45 vs 1.15-1.35) and the narrow caudal colliculum (OCH:CCH = 1.5 vs 1.0-1.2). From *D. lucidus* it is further distinguished by the shallow excisura and from *D. kakegawaensis* additionally by the completely flat inner face and the anteriorly depressed dorsal rim (vs expanded and rounded). From *D. coeruleus* it differs in being less elongate (OL:OH = 1.35-1.45 vs 1.5-1.6), the higher dorsal field and the longer rostrum. The depressed predorsal rim and the very small antirostrum and excisura also resemble *D. depressifrons* Schwarzhans & Aguilera, 2013 from the late Miocene and early Pliocene of the Caribbean. *Diaphus nafpaktitisi* differs however in lacking the denticle at the postdorsal angle, the strongly reduced height of the caudal colliculum (OCH:CCH = 1.5 vs 1.1-1.3 and OCH:CCHP = 1.0-1.1 vs 0.85-0.95 respectively) and the deepest point of the ventral rim being at the middle vs being shifted backwards.

Diaphus splendidus (Brauer, 1904)

Fig. 10 D-F

1983 *Diaphus* aff. *D. coeruleus* (Klunzinger, 1871) - Ohe: pl. 2, fig. 7, pl. 3, fig. 1.
1983 *Diaphus sagamiensis* Gilbert, 1913 - Ohe: pl. 3, fig. 2.

Material: 5 specimens Iriyamase, Kakegawa, Hijikata FM, early Calabrian (figured specimens SMF PO 101034).

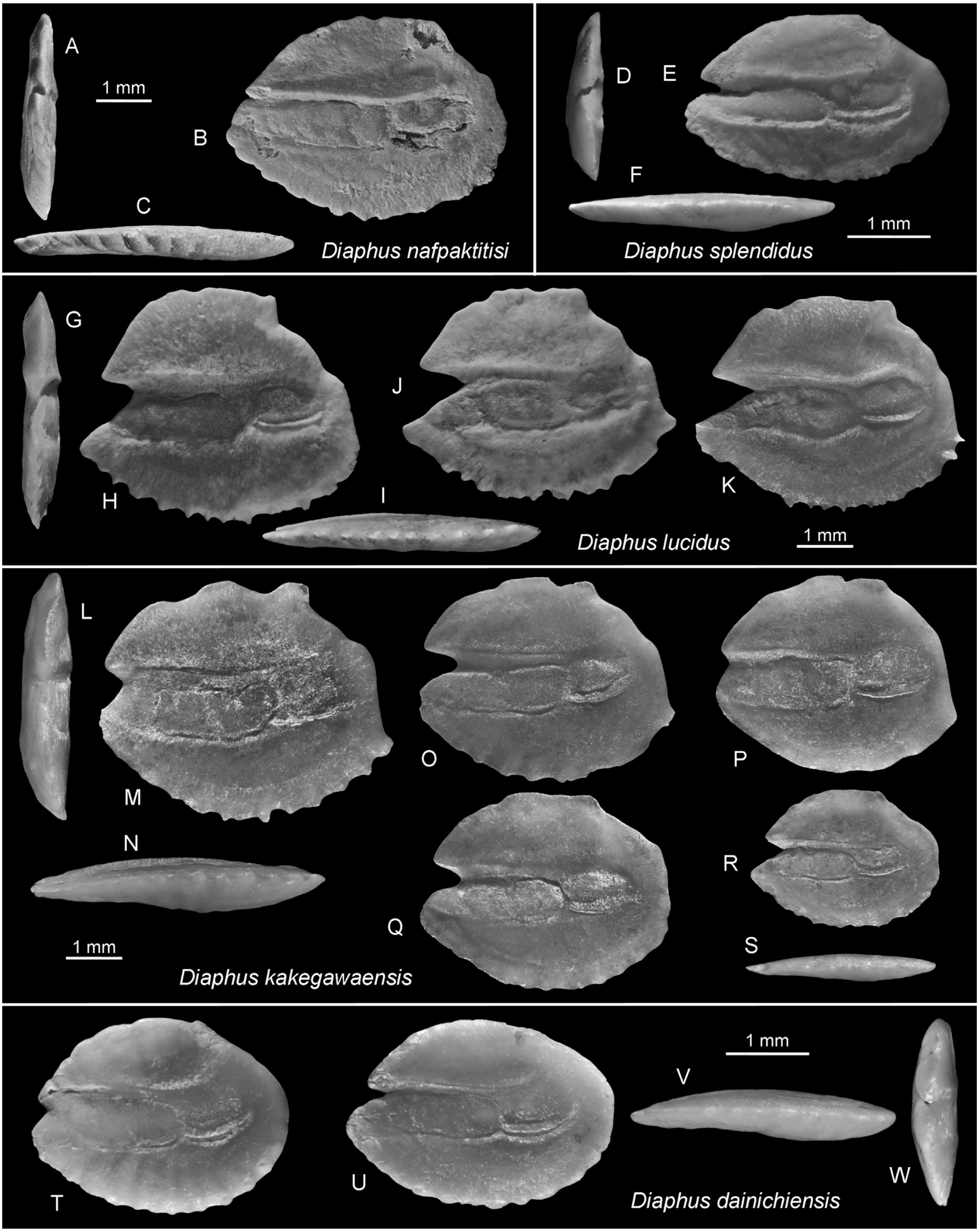


Fig. 10 - A-C) *Diaphus nafpaktitisi* n.sp., holotype, SMF PO 101031 (reversed), A - anterior view, B - inner face, C - ventral view; D-F) *Diaphus splendidus* (Brauer, 1904), SMF PO 101034, D - anterior view, E - inner face, F - ventral view; G-K) *Diaphus lucidus* (Goode & Bean, 1896), SMF PO 101030 (K reversed), G anterior view, H, J, - K inner faces, I - ventral view; L-S) *Diaphus kakegawaensis* n.sp., L-N - holotype, SMF PO 101028, O-S - paratypes, SMF PO 101029 (reversed), L - anterior view, M, O-R - inner faces, N, S - ventral views; T-W) *Diaphus dainichiensis* Ohe, 1981, SMF PO 101035 (U-W reversed), T-U - inner faces, V - ventral view, W - anterior view.

Discussion. Otoliths of *D. splendidus* are relatively inconspicuous, rather elongate with an index OL:OH of 1.4-1.55, no pronounced postdorsal angle or concavity and reaching sizes to about 5.0 mm length (see Schwarzhans 2013b for figures). They have been regularly recorded in the fossil record since at least late Miocene times, but possibly as early as Serravallian (Brzobohaty & Nolf 2000). In the Recent, *Diaphus splendidus* is a widely distributed oceanic species in the tropical and subtropical waters of all three oceans except for the eastern Pacific. In Japan it is only known from the Tsushima Current in the Sea of Japan (Masuda et al. 1984).

Diaphus garmani otolith group

Diaphus dainichiensis Ohe, 1981

Fig. 10 T-W

1977 *Myctophum* sp. - Ohe: fig. 4
1981 *Diaphus dainichiensis* - Ohe: pl. 2, fig. 6.
1983 *Diaphus latus* Gilbert, 1913 - Ohe: pl. 5, figs. 10-13.
1983 *Diaphus* sp. - Ohe: pl. 5, figs. 14-15.
1983 *Myctophum nitidulum* Garman, 1899 - Ohe: pl. 5, fig. 16, pl. 6, fig. 1.
1983 *Lampadena* sp. - Ohe: pl. 6, fig. 3.

Material: 127 specimens: 4 specimens Okinawa, Higa, Shinzato FM, Piacenzian; 123 specimens: from Kakegawa: 47 specimens Hongohigashi, Dainichi FM, Gelasian (figured specimens SMF PO 101035); 76 specimens Iriyamase, Hijikata FM, early Calabrian.

Discussion. *Diaphus dainichiensis* is an inconspicuous and relatively small otolith with oval outline reaching sizes of about 3.5 mm length. Its inconspicuous appearance, high variability and various erosional effects have led specimens of this common species to be regarded as several different representatives (see Ohe 1983). *Diaphus dainichiensis* is characterized by an index OL:OH of 1.3-1.35, a regularly curved dorsal rim, which is anteriorly slightly expanded and posteriorly shows only a very weak postdorsal angle and depression. The ventral rim bears 9 to 10 small lobes rather than denticles. It is characterized as a member of the *Diaphus garmani* otolith group by the mildly convex inner face and the distinctly lobate upper margin of the ostium. *Diaphus dainichiensis* appears to be restricted to the early to middle Pleistocene of the Kakegawa area.

Diaphus adenomus otolith group

Diaphus coatsi Schwarzhans & Aguilera, 2013

Fig. 11 A-B

Material: 3 specimens, Okinawa, Shinzato FM, Piacenzian: 1 specimen NRM-PZ 16738, Higa; 2 specimens coll. Moriguchi, Tobaru.

Discussion. The large figured otolith of 8.7 mm length closely resembles the type specimens described from the Piacenzian of the Caribbean coast of Panama, and two additional specimens from the collection of Moriguchi are also tentatively assigned to the species. They share the diagnostic characters (values of type-specimens in brackets) such as OL:OH = 1.45 (1.4-1.5), OCL:CCL = 1.9 (1.7-2.0), the feeble rostrum and very feeble antirostrum and excisura, the much expanded anterior-dorsal rim, the broad depressed postdorsal rim, the deeply curved ventral rim, the anteriorly narrowing ostium and the sulcus being anteriorly and posteriorly slightly bent upwards. Denticles along the ventral rim are not or incompletely preserved due to slight marginal erosion. It is similar to otoliths of the extant *D. adenomus* Gilbert, 1905 and may represent its ancestor. Otoliths of *D. coatsi* differ from those of *D. adenomus* in the anteriorly narrowed ostium, the longer ostium (OCL:CCL = 1.7-2.0 vs 1.4-1.6) and the very weekly developed or absent excisura. The occurrence of *D. coatsi* in the Piacenzian of Japan indicates that this species like the extant species too had a wide geographic distribution. So far, it has only been found in the Piacenzian and may bear stratigraphic value.

Diaphus fragilis otolith group

Diaphus chrysorhynchus Gilbert & Cramer, 1897

Fig. 11 C-H

1997 *Diaphus problematicus* Parr, 1928 - Ohe, Kawai & Kawase: pl. 1, fig. 2.

Material: 42 specimens: 2 specimens Ozatofurugen, Okinawa, upper Yonabaru FM, early Piacenzian (figured specimen SMF PO 101036); 23 specimens Tobaru, Okinawa, Shinzato FM, Piacenzian (figured specimen SMF PO 101037); 17 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 10 specimens Nob-1 (figured specimen SMF PO 101038), 7 specimens Nob-3+4.

Discussion. Otoliths of *Diaphus chrysorhynchus, D. fragilis* Tåning, 1928 and *D. thiollierei* Fowler, 1934 are all very similar (see Schwarzhans 2013b for figures). *D. chrysorhynchus* differs from *D. fragilis*

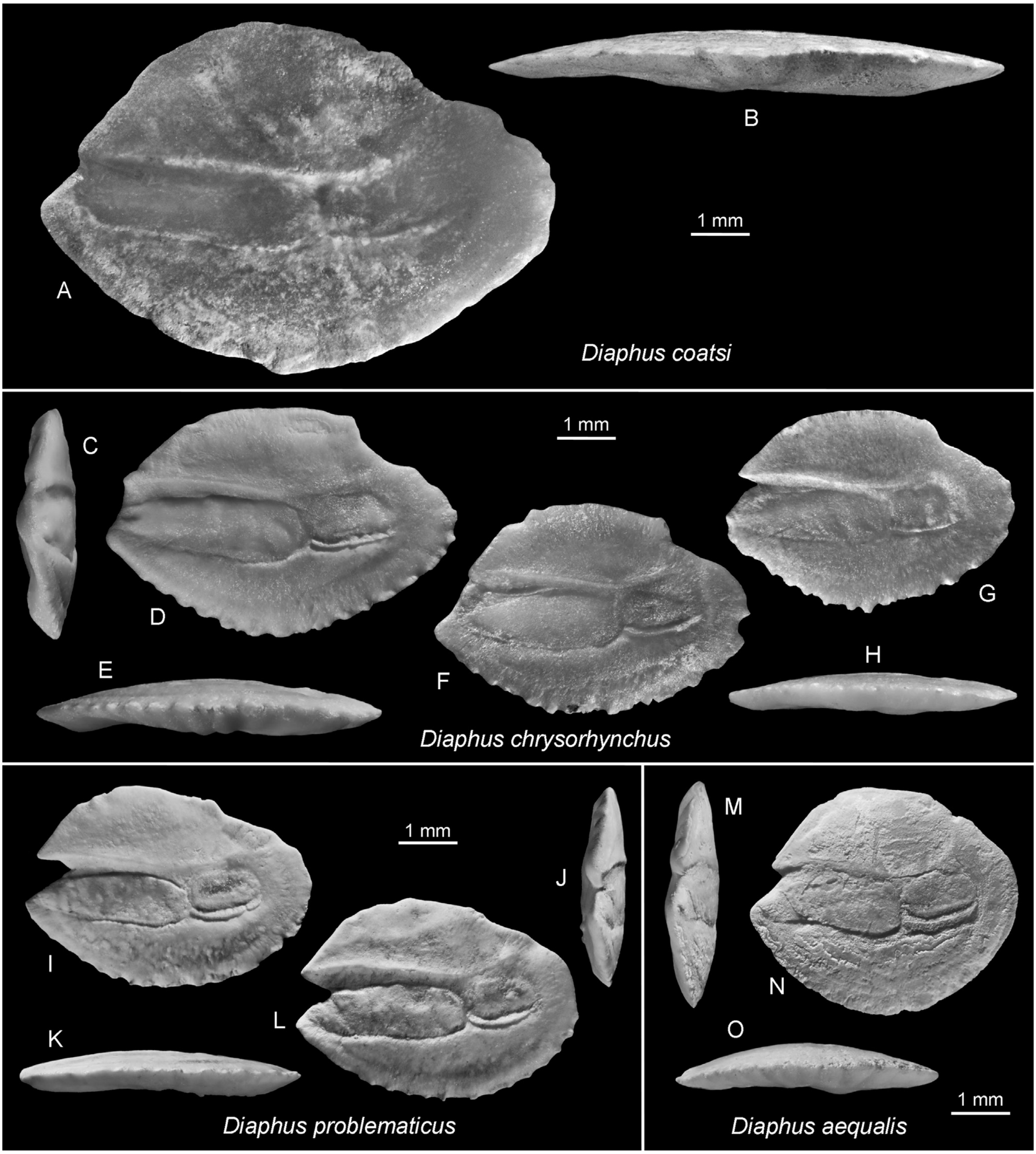


Fig. 11 - A-B) *Diaphus coatsi* Schwarzhans & Aguilera, 2013, NRM-PZ 16738, A - inner face, B - ventral view; C-H) *Diaphus chrysorhynchus* Gilbert & Cramer, 1897, C-E SMF PO 101036 (reversed), F SMF PO 101038, G-H SMF PO 101037 (reversed), C - anterior view, D, F, G - inner faces, E, H - ventral views; I-L) *Diaphus problematicus* Parr, 1928, SMF PO 101039 (I reversed), I, L - inner faces, J - anterior view, K - ventral view; M-O) *Diaphus aequalis* Schwarzhans & Aguilera, 2013, SMF PO 101040, M - anterior view, N - inner face, O - ventral view.

in being slightly more elongate (OL:OH = 1.5-1.6 vs 1.3-1.4) and from *D. thiollierei* in the more pronounced predorsal expansion. *Diaphus chrysorhynchus* (including *D. sagamiensis* Gilbert, 1913 considered as junior synonym following Paxton 1979) is a tropical and subtropical species of the western Pacific and off Hawaii. In Japan it is commonly caught off the shores washed by the Kuroshio Current. In the fossil record of Japan it is not uncommon in Okinawa and Shikoku, but missing from Kakegawa.

Diaphus problematicus Parr, 1928

Fig. 11 I-L

Material: 112 specimens: 77 specimens Tobaru, Okinawa, Shinzato FM, Piacenzian (figured specimens SMF PO 101039); 19 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 13 specimens Nob-1, 4 specimens Nob-3+4, 2 specimens Nob-6; 16 specimens Hongohigashi, Kakegawa, Dainichi FM, Gelasian.

Discussion. Otoliths of *Diaphus problematicus* are similar to those of *D. chrysorhynchus, D. fragilis* and *D. thiollierei* and differ only in two subtle characters, i.e., the less bent inner face and the narrower ostium (see Schwarzhans 2013b for figures). *Diaphus problematicus* is widely distributed in tropical waters of all three oceans with extensions into higher latitudes in western boundary currents. In Japan it is known only from off Okinawa and Ogasawara Islands (Masuda et al. 1984). Its abundance in the fossil record of Okinawa is consistent with the Recent occurrence, but during Plio-Pleistocene it apparently migrated further northwards in Japan and is also found in Shikoku and the Kakegawa region.

Diaphus effulgens otolith group

Diaphus aequalis Schwarzhans & Aguilera, 2013

Fig. 11 M-O

2013 *Diaphus aequalis* - Schwarzhans & Aguilera: pl. 13, figs. 13-25.

Material: 1 specimen SMF PO 101040, Tobaru, Okinawa, Shinzato FM, Piacenzian.

Discussion. *Diaphus aequalis* is easily recognized by its almost perfectly round outline (OL:OH = 1.15-1.25) with a regularly curved dorsal rim without prominent angles and no postdorsal depression, the rostrum being about as long as the antirostrum or very slightly longer and its convex inner face and relatively thick appearance (OH:OT = 3.5-4.0). It is common in the tropical West Atlantic during late Miocene to late Pliocene, but also seems to be present in the early Pliocene of the Mediterranean (see Schwarzhans & Aguilera 2013). It is also found in the late Pliocene of the tropical western Pacific of the Philippines (Van Hinsbergh & Helwerda 2019) and Okinawa.

Diaphus noboriensis n. sp.

Fig. 12 A-K

1977 *Diaphus* sp. - Takahashi: pl. 25, fig. 3.
1981 *Diaphus elucens* (Brauer, 1904) - Ohe: pl. 2, fig. 2.
1981 *Diaphus* sp. A - Ohe: pl. 2, fig. 3.

Etymology: Named after the type strata, Nobori FM, from which most specimens of this species were obtained.

Holotype: SMF PO 101041 (Fig. 12 B-D), Nob-1, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian, planktonic foraminifer zone N21 (PL5), 3.35-3.0 Ma.

Paratypes: 7 specimens: 4 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 2 specimens SMF PO 101042, same data as holotype, 1 specimen SMF PO 101043, Nob-2, 1 specimen SMF PO 101044, Nob-6; 3 specimens Okinawa, Shinzato FM, Piacenzian: 1 specimen SMF PO 101045, Aragusku, 1 specimen SMF PO 101046, Tobaru, 1 specimen NRM-PZ 16739, Higa.

Further specimens: 33 specimens: 5 specimens Okinawa, Tobaru, Shinzato FM, Piacenzian; 17 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 12 specimens Nob-1, 1 specimen Nob-3+4, 4 specimens Nob-6; 11 specimens Hongohigashi, Kakegawa, Dainichi FM, Gelasian.

Tentatively assigned specimens: 1 specimen SMF PO 101047 (Fig. 12 A), Tobaru, Okinawa, Shinzato FM, Piacenzian.

Diagnosis: OL:OH = 1.25-1.4. OH:OT = 4.8-5.5. Dorsal rim broadly expanded along anterior half, deeply depressed and concave along posterior half. Rostrum moderately long, 13-20% of OL, distinctly longer than sharp antirostrum. Excisura deep and wide. Ventral rim with 17-21 irregular denticles or lobes extending onto posterior rim. Ostium very wide; OCH:CCH = 1.5-1.6.

Description. Thin, moderately elongate and very large otoliths reaching up to 7.7 mm length (holotype 6.5 mm). Dorsal rim broadly expanded along its anterior half and irregularly undulating; posterior half deeply depressed and concave, usually with distinct postdorsal angle. Posterior rim not reduced, rounded, often with denticles. Ventral rim deep, regularly curving with 17 to 21 irregular denticles or lobes of varying intensity; 1 to 3 denticles extending onto posterior rim. Rostrum moderately long, sharp, massive, 13-20% of OL, distinctly longer than sharp and pointed antirostrum; excisura very variable, often wide and deep but sometimes very small and indistinct.

Inner face distinctly convex. Sulcus very wide, its dorsal margin almost straight except slightly upward bend at caudal tip, its ventral margin convex, deepest at rear portion of ostium. Cauda termination rounded, close to posterior rim of otolith; OL:SuL = 1.1. Ostium distinctly longer and wider than cauda, slightly narrowing towards opening from ventral margin and with straight or slightly lobate dorsal rim; OsL:CaL = 2.0-2.3. Ostial colliculum anterior-dorsally slightly reduced. Caudal pseudocolliculum strong but narrow and slightly longer than caudal colliculum. Ostial colliculum very wide and much longer than caudal colliculum. OCL:C-

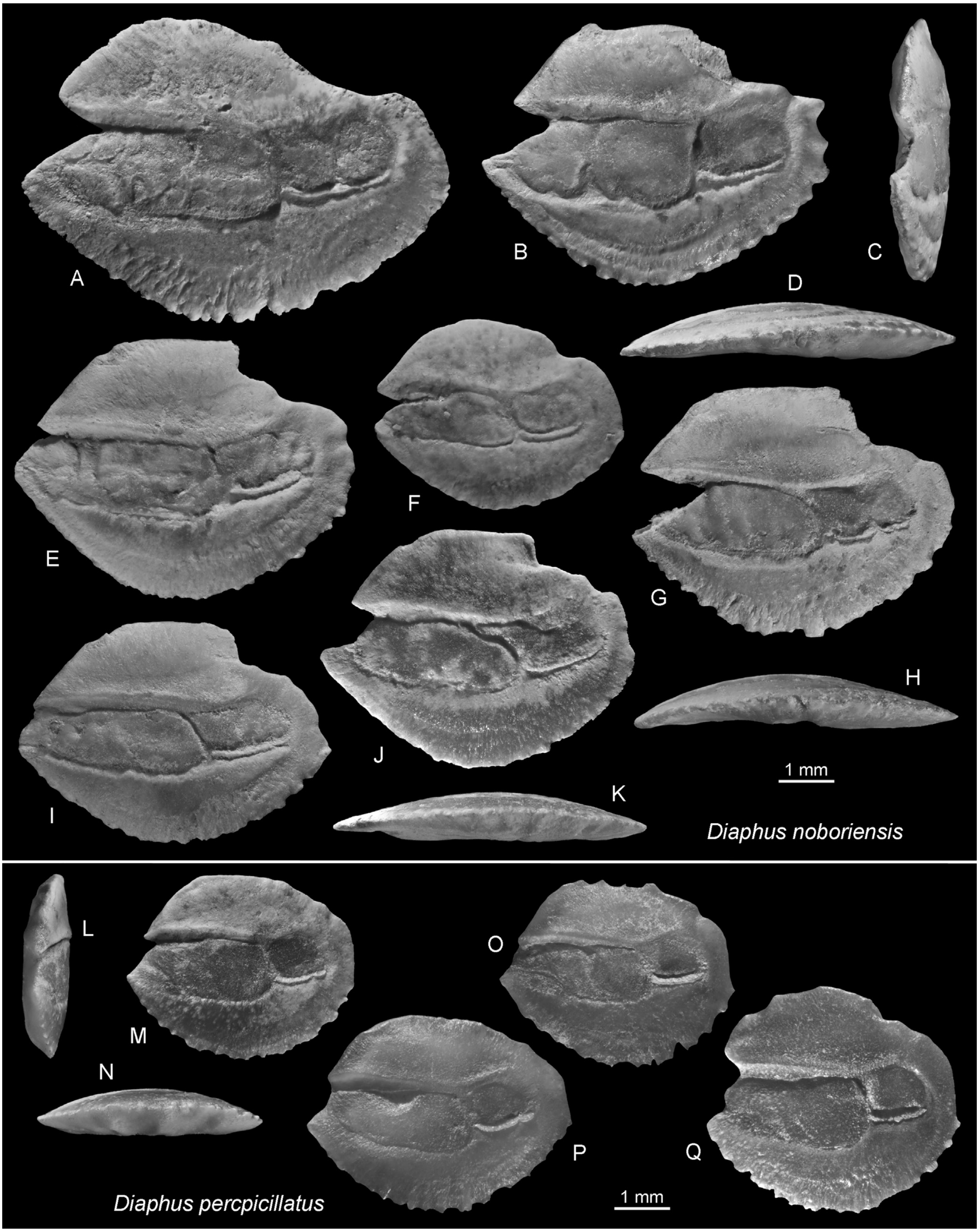


Fig. 12 - A-K) *Diaphus noboriensis* n.sp., B-D - holotype, SMF PO 101041, A - tentatively assigned specimen, SMF PO 101047, E - paratype, SMF PO 101044 (reversed), F - paratype, SMF PO 101046, G-H - paratype, SMF PO 101043, I - paratype, SMF PO 101042 (reversed), J-K - paratype NRM-PZ 16739 (reversed), A, B, E-G, I-J - inner faces, C - anterior view, D, H, K - ventral views; L-Q) *Diaphus perspicillatus* (Ogilby, 1898), L-O SMF PO 101048, Q NRM-PZ 16740 (reversed), L - anterior view, M, P-Q - inner faces, N - ventral view.

CL = 2.2-2.4; OCH:CCH = 1.5-1.6; OCH:CCHP = 1.2-1.3. Both colliculi can be vertically divided into two parts in very large specimens. Dorsal field short, moderately wide, with indistinct dorsal depression only marked by crista superior towards sulcus. Ventral furrow broad, distinct, running across middle of ventral field. Outer face flat, with few vertical furrows across central part.

Discussion. *Diaphus noboriensis* is one of the largest otoliths known of the genus and therefore also supposedly one of the largest fish species. The largest specimen of 7.7 mm length from Okinawa, however, is only tentatively assigned to this species. It differs in a relatively high index OL:OH of 1.4 and a not as much widened ostium (Fig. 12 A). Otherwise, *Diaphus noboriensis* is easily recognized by the very wide and large ostium, the eye-catching shape of the dorsal rim, the many denticles on the ventral rim extending onto the posterior rim, the deep ventral rim and several other more subtle characters described above. The compressed shape with the deep ventral rim and the shape of the dorsal rim resembles otoliths of *Diaphus effulgens* (Goode & Bean, 1896) and *D. ostenfeldi* Tåning, 1932, but *D. noboriensis* is more elongate (OL:OH = 1.3-1.4 vs 1.1-1.2) and shows a longer and extremely wide ostium (OCL:CCL = 2.2-2.4 vs 1.8-1.9 and OCH:CCHP = 1.2-1.3 vs 0.9-1.1). *Diaphus noboriensis* also resembles otoliths of the *Diaphus fragilis* otolith group such as *D. mascarensis* Becker, 1990, or *D. adenomus* Gilbert, 1905 sole species of the *Diaphus adenomus* otolith group (see Schwarzhans 2013b for figures). With otoliths of these species, *D. noboriensis* shares the more elongate shape, but differs in the deeper ventral rim and the voluminous ostium. We consider *D. noboriensis* to represent an extinct clade either within the *Diaphus effulgens* otolith group or an extinct group related to it.

Diaphus perspicillatus otolith group

Diaphus perspicillatus (Ogilby, 1898)

Fig. 12 L-Q

1983 *Symbolophorus* sp. B - Ohe: pl. 3, fig. 3.

Material: 93 specimens: 91 specimens, Okinawa, Shinzato FM, Piacenzian: 3 specimens Gushichan, 83 specimens Tobaru (figured specimens SMF PO 101048), 4 specimens Higa (figured specimen NRM-PZ 16740); 1 specimen Nob-1, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian; 1 specimen Hongohigashi, Kakegawa, Dainichi FM, Gelasian.

Discussion. Otoliths of *D. perspicillatus* are readily recognized by the combination of a nearly oval outline with a short rostrum and weak antirostrum and excisura, a distinctly convex inner face and a very wide ostium and ostial colliculum, the latter comparable only to *D. noboriensis*. *Diaphus perspicillatus* is widely distributed in the tropical and subtropical waters of all three oceans except for the eastern Pacific. In Japan, it is found in waters washed by the Kuroshio Current.

Genus *Lobianchia* Gatti, 1903

Lobianchia dofleini (Zugmayer, 1911)

Fig. 13 A-B

Material: 7 specimens: 1 specimen Nob-1, Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian; 6 specimens Iriyamase, Kakegawa, Hijikata FM, early Calabrian (figured specimens SMF PO 101049).

Discussion. Otoliths of *Lobianchia dofleini* are well known in the fossil record since latest Miocene in the Mediterranean and late Pliocene in the tropical West Atlantic (Schwarzhans & Aguilera 2013). In the Recent, *Lobianchia dofleini* is primarily a species of temperate to subtropical seas except for a more continuous distribution off the west African shores. It is circumglobal in the Southern Ocean and common in the North Atlantic and Mediterranean, but missing from the northern Pacific. The record from the late Pliocene and middle Pleistocene of Japan indicates an even wider geographic distribution in the past.

Lobianchia gemellarii (Cocco, 1838)

Fig. 13 C-J

1997 *Lobianchia gemellarii* (Cocco, 1838 - Ohe, Kawai & Kawase: pl. 1, fig. 5.

Material: 143 specimens: 2 specimens Ozatofurugen, Okinawa, upper Yonabaru FM, early Piacenzian (figured specimen SMF PO 101050); 111 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 48 specimens Nob-1 (figured specimens SMF PO 101051), 9 specimens Nob-3+4, 68 specimens Nob-6; 16 specimens Hongohigashi, Kakegawa, Dainichi FM, Gelasian (figured specimen SMF PO 101052).

Discussion. Otoliths of *L. gemellarii* are similar to many otoliths found in the genus *Diaphus*, for instance in the *Diaphus splendidus* otolith group (see discussion in Schwarzhans 2013b). The best character to distinguish otoliths of *L. gemellarii* from

Diaphus otoliths is probably the concentration of the denticles at the middle of the ventral rim. The anterior third of the ventral rim is usually smooth and the posterior third may have just few denticles.

In the Recent, *L. gemellarii* mostly reaches sizes of up to 60 mm SL (up to 4 mm OL), but large specimens of 85 to 100 mm SL (up to 6.5 mm OL) are also known from the slope water of New England, northwestern Atlantic and elsewhere as expatriates (Hulley, 1984). These large specimens yielded otoliths, which differ ontogenetically from the regular sized ones in the more forward positioned postdorsal angle followed by a mild concavity (see Schwarzhans 2013b). The many otoliths obtained from the Nobori FM are also all relatively large (5.2-6.2 mm long) and correspond perfectly with the extant specimens from New England. They may indicate a dominance of expatriate specimens of *L. gemellarii* in the late Pliocene of Okinawa.

Lobianchia gemellarii is found high oceanic in tropical and subtropical waters of all three oceans. In Japan it is found common from Okinawa to Tohoku. Their common occurrence in the Nobori FM thus is not unexpected, but the large size of most specimens is surprising.

Subfamily Gymnoscopelinae Paxton, 1972

Genus *Notoscopelus* Günther, 1864

Notoscopelus kuboensis (Ohe & Araki, 1973)

Fig. 13 K-M

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.

Material: 15 specimens: 2 specimens Okinawa, Shinzato FM, Piacenzian: 1 specimen Tobaru, 1 specimen Higa; 5 specimens Nobori, Kochi Prefecture, Shikoku, upper Nobori FM, Piacenzian: 3 specimens Nob-1, 2 specimens Nob-6 (figured specimen SMF PO 101053); 8 specimens Hongohigashi, Kakegawa, Dainichi FM, Gelasian (figured specimens SMF PO 101054).

Discussion. *Notoscopelus kuboensis* are slender otoliths with an index OL:OH of 1.85 to 1.95 and a rounded, not expanded posterior rim sometimes accentuated by a small postdorsal concavity. *Notoscopelus kuboensis* has first been described from the late early Miocene of Japan. We are unable to identify any significant differences between the Miocene and the Pliocene specimens studied here, which results in an unusual long duration of the species in the order of 15 myr.

Notoscopelus praejaponicus n. sp.

Fig. 13 N-R

1983 *Lampanyctus parvicauda* Parr, 1931 - Ohe: pl. 4, fig. 3.

Etymology: Named after its relationships to the extant *Notoscopelus japonicus* (Tanaka, 1908).

Holotype: SMF PO 101055 (Fig. 13 N-P), Iriyamase, Kakegawa, Hijikata FM, early Calabrian, planktonic foraminifer zone N22, 1.9-1.6 Ma.

Paratypes: 6 specimens: 5 specimens SMF PO 101056, same data as holotype; 1 specimen SMF PO 101057. Chinen, Okinawa, Chinen FM, early Calabrian.

Diagnosis: OL:OH = 2.0-2.1. Dorsal rim very shallow, with long and broad postdorsal concavity. Posterior rim only slightly expanded. Rostrum moderately long, 12-17% of OL. Ventral rim shallow, with 10-12 irregular and small denticles or lobes. Ostium narrow, much longer than cauda; OCL:CCL = 2.5-2.7. Cauda terminating at moderate distance from posterior tip of otolith; OL:SuL = 1.15.

Description. Very elongate, thin and relatively large otoliths reaching sizes of up to 6.0 mm length (holotype 5.7 mm). OH:OT = 4.5-5.0. Dorsal rim shallow, regularly curved, sometimes with obtuse postdorsal angle above middle part of cauda and with broad, moderately deep postdorsal concavity. Posterior rim slightly expanded with rounded tip at junction with depressed postdorsal rim at level of upper margin of cauda. Ventral rim shallow, slightly deeper than dorsal rim and more regularly curved, with 10 to 12 small irregular denticles or lobes. Rostrum moderately long, variably sharp, 12-17% of OL; antirostrum and excisura small.

Inner face flat. Sulcus narrow, slightly supramedian, with straight dorsal and slightly curved ventral margins. Cauda termination rounded, moderately close to posterior rim of otolith; OL:SuL = 1.15. Ostium distinctly longer than cauda but not wider; OsL:CaL = 2.8-3.0. Joint of ostial and caudal colliculi distinctly inclined. Caudal pseudocolliculum indistinct, narrow and shorter than caudal colliculum. Ostial colliculum much longer than caudal colliculum. OCL:CCL = 2.5-2.7; OCH:CCH = 1.2-1.3; OCH:CCHP = 1.0-1.1. Dorsal field narrow, with indistinct dorsal depression only marked by crista superior towards sulcus. Ventral furrow broad, distinct, running at some distance from ventral rim of otolith. Outer face flat, smooth or with few short furrows.

Discussion. *Notoscopelus praejaponicus* clearly belongs to the clade that includes the earlier *N. kuboensis* and leads to the Recent *N. japonicus*. It differs from the earlier *N. kuboensis* in the more slender shape (OL:OH = 2.0-2.1 vs 1.85-1.95) the slightly

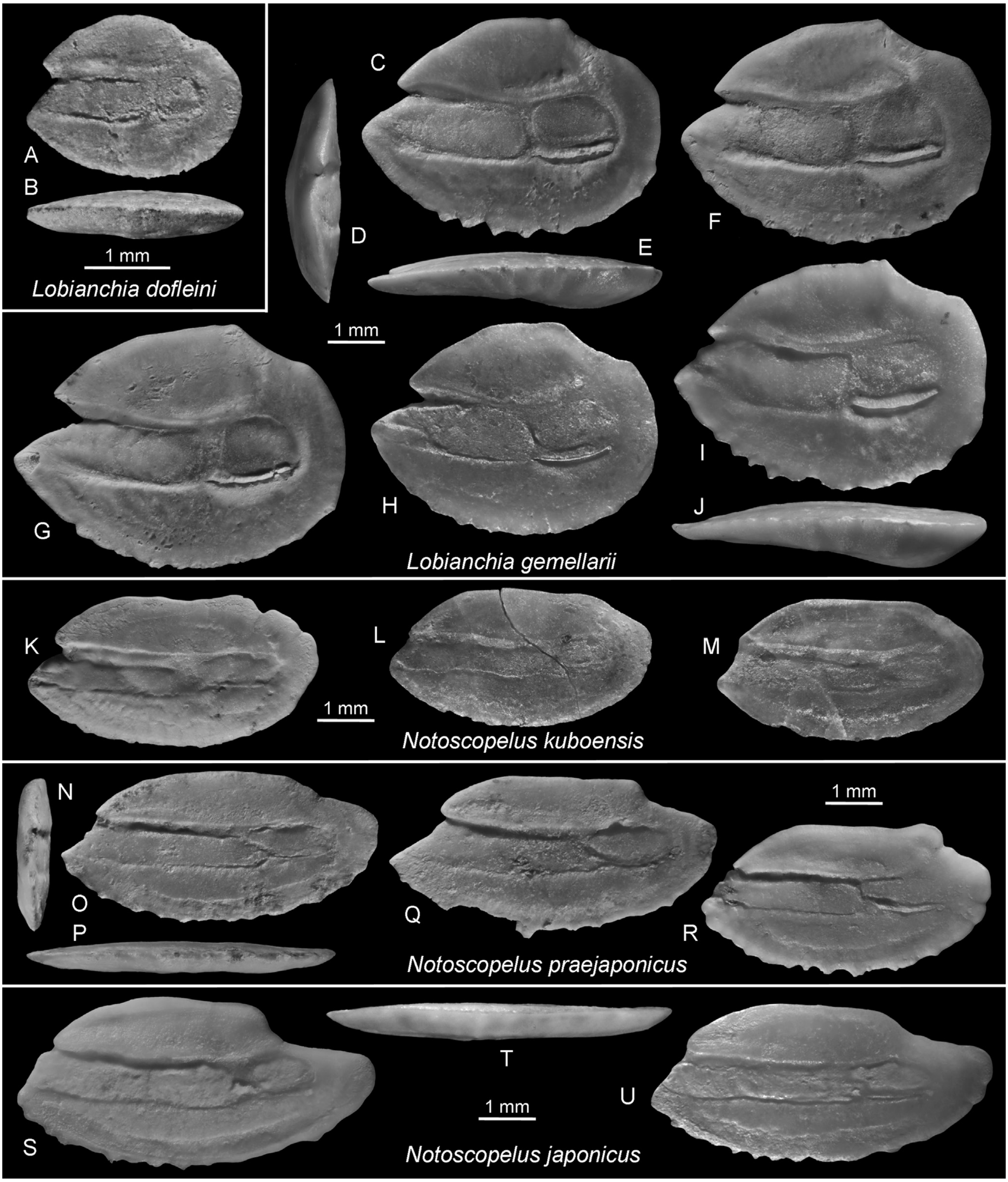


Fig. 13 - A-B) *Lobianchia dofleini* (Zugmayer, 1911), SMF PO 101049 (reversed), A - inner face, B - ventral view; C-J) *Lobianchia gemellarii* (Cocco, 1838), C-G SMF PO 101051, H SMF PO 101052 (reversed), I-J SMF PO 101050 (reversed), C, F-I - inner faces, D - anterior view, E, J - ventral views; K-M) *Notoscopelus kuboensis* (Ohe & Araki, 1973), K SMF PO 101053 (reversed), L-M SMF PO 101054 (L reversed), all views inner faces; N-R) *Notoscopelus praejaponicus* n.sp., N-P - holotype, SMF PO 101055, Q - paratype, SMF PO 101056, R - paratype SMF PO 101057 (reversed), N - anterior view, O, Q, R - inner faces, P - ventral view; S-U) *Notoscopelus japonicus* (Tanaka, 1908), Recent, S-T NSMT-P 63306, TL 131 mm, 36°27'N-141°09'E, U NSMT-P 92385, TL 137 mm, off Tohoku, S, U - inner faces, T - ventral view.

expanded posterior tip and the depressed postdorsal rim. From the Recent *N. japonicus* (Fig. 13 S-U) it differs in the sharper and longer rostrum (vs blunt, reduced and 12-17% of OL vs 10%), the less expanded posterior rim (vs long and pointed) best expressed in the index OL:SuL (1.15 vs 1.2-1.25) and the shorter postdorsal concavity. Thus, *N. praejaponicus* shows an intermediate morphology between the long-lived *N. kuboensis* and the extant *N. japonicus* during middle Pleistocene. It is therefore of stratigraphic significance in Japan.

Notoscopelus japonicus is endemic to the transitional region of the western North Pacific (Masuda et al. 1984) and known from off Japan from southern Hokkaido to Shikoku and the Ogasawara Islands. It is probable that *N. praejaponicus* likewise was endemic to Japan, which also occurred in transitional temperature environments while *N. kuboensis* so far is only known from warmer environments.

FAUNAL ANALYSIS

The tectonically active Pacific margin of Japan has brought up late Cenozoic deepwater sediments which are now exposed in multiple locations of several regions. The late Pliocene to early Pleistocene deep water sediments sampled for this study from Okinawa, Shikoku and central Honshu have yielded a diverse and exceptionally rich association of large, adult, and mostly well-preserved myctophid otoliths (Tab. 1) along many other teleost otoliths which are not subject of this study.

About one third of all living myctophid taxa belong to the genus *Diaphus*. Davis et al. (2014) and Martin et al. (2018) have identified the *Diaphus*-clade as diversifying at an accelerated rate. This observation is confirmed in the fossil record of the Neogene, particularly since late Miocene, where *Diaphus* is by far the most common and most specious of all myctophid genera. In this study dealing with late Pliocene and early Pleistocene otoliths from southern Japan, otoliths of the genus *Diaphus* constitute nearly half of all identified myctophid species (17 *Diaphus* species in a total of 36 myctophid species). Their accelerated diversification rate is supported by the fact that *Diaphus* is the only genus in myctophids of the studied time interval with any significant amount of fossil taxa (8 in 17 species), while the remainder of myctophid genera just contain an additional 4 fossil species. The Lyellian percentage is about 60% in the Piacenzian and nearly 80% in the Gelasian and early Calabrian.

Biostratigraphy with myctophid otoliths (Fig. 14)

Due to their abundance and diversity, particularly in the late Neogene (see above), and their often wide geographical distribution myctophid otoliths bear a considerable potential as an additional tool for supraregional biostratigraphic correlation (Schwarzhans & Aguilera 2013). The rich myctophid association studied here is well positioned to serve as a cornerstone for this purpose and for the tropical to subtropical NW Pacific of the time interval. This is aided by the good and detailed chronstratigraphic constraint of most of the strata and locations that were sampled (see chapter locations and geological setting). However, one must bear in mind that the stratigraphical distribution of many of the species is still incompletely known and that only few reasonably verified evolutionary lineages exist to date.

Nevertheless, it is tentatively possible to specify certain characteristic and relatively common species for certain time intervals and to identify potential biostratigraphic events. *Diaphus noboriensis* is an easily recognizable species occurring in the Piacenzian and Gelasian in all three areas studied. *Diaphus kakegawaensis* likewise is an easily recognizable species, but is known only from the Gelasian Dainichi FM of the Kakegawa region. Time equivalent sediments of Okinawa or Shikoku have not been available for study. Therefore, it is uncertain at present if this narrow distribution range in space and time would be biased by lagerstätten effects. Another highly diagnostic first occurrence in the sequence is *Diaphus kuroshio* in the Dainichi FM (Gelasian), which is also known from Calabrian of the Hijikata FM and the late Ionian to Holocene Wan FM of the northern Ryukyu Islands (Ohe et al. 1997). However, distinction from the similar *D. mollis*, which occurs earlier stratigraphically already in the Piacenzian is only reliable in the presence of well-preserved specimens. There are two potential lineages that could prove to be useful for biostratigraphic applications: *Diaphus nafpaktitisi* a rare species in the

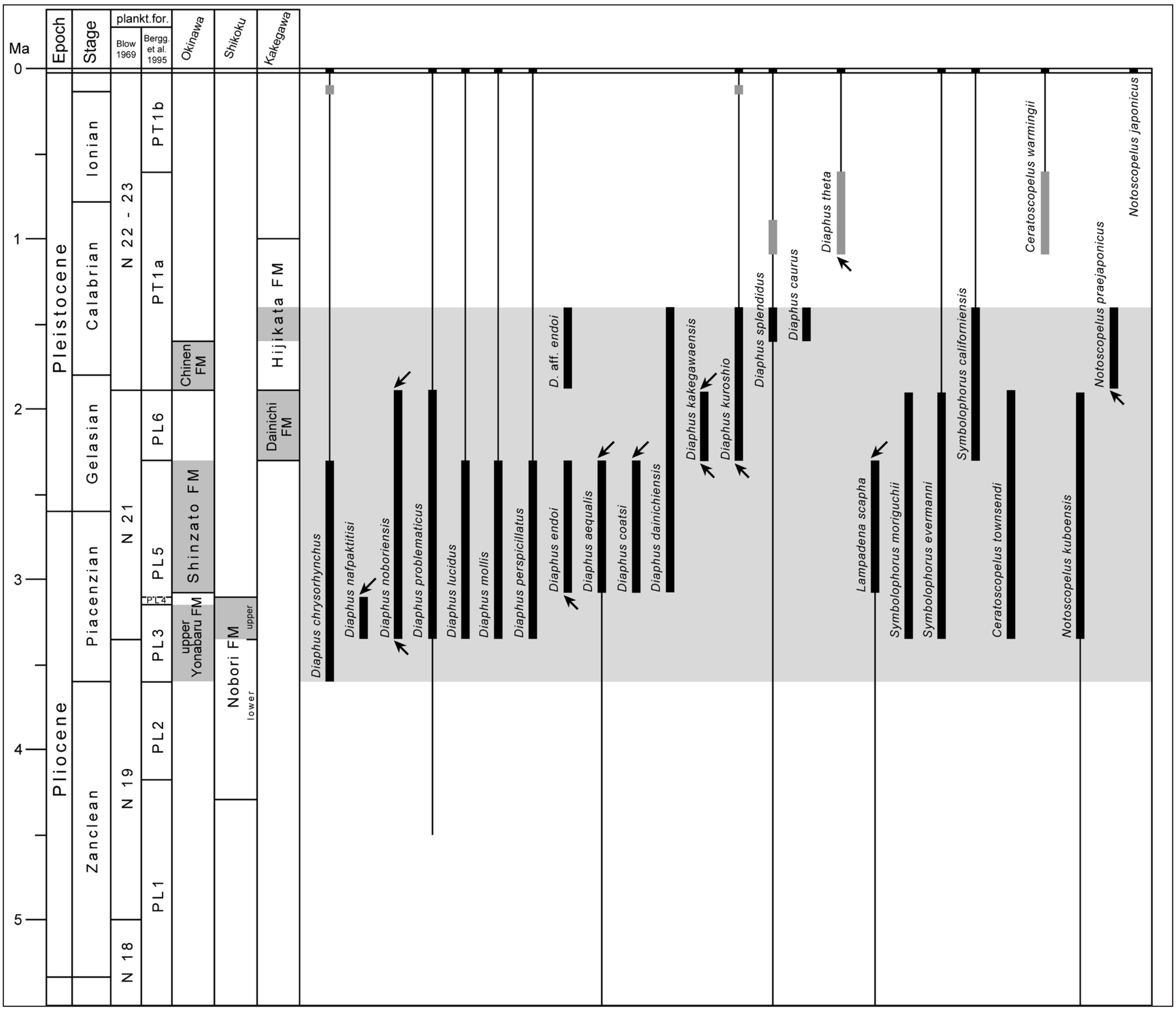


Fig. 14 - Stratigraphic range chart of selected myctophid species from the Pliocene and Pleistocene of Japan. Broad black bars indicate stratigraphic ranges based on material studied here, broad dark grey bars indicate range extensions from reviewed literature from Japan and thin lines indicate ghost ranges inferred from extant occurrence or older fossil occurrence. Arrows indicate events of potential stratigraphic significance.

early Piacenzian that may be ancestral to *Diaphus endoi* in the Shinzato FM (middle Piacenzian to early Gelasian, PL5). However, the upper stratigraphic range of *D. endoi* is unclear. Few and smaller specimens from the early Calabrian of the Chinen FM of Okinawa and the Hijikata FM of Kakegawa may represent the same species or an ascendant of it and is denoted as *Diaphus* aff. *endoi*. The other lineage, which is even more clearly defined is that leading to the extant endemic NW Pacific species *Notoscopelus japonicus*. The lineage starts with the long ranging *N. kuboensis* characterized by a rounded, not prolonged posterior rim, which is known from middle Miocene till Gelasian. It is replaced in early Calabrian by *N. praejaponicus* which is characterized by a prolonged posterior tip with a concave postdorsal portion usually accompanied by a distinct angle or denticle just in front. The extant species, *N. japonicus*, is characterized by a much more prolonged and sharper posterior tip, a longer postdorsal concavity and a reduced rostrum length. It is not clear at present, where the transition from *N. praejaponicus* to *N. japonicus* takes place in time. Finally, the late Calabrian / early Ionian witnesses the advent of *Diaphus theta* (originally described as *Diaphus quadratus* Aoki & Baba, 1980). However, *Diaphus theta* represents a cool water Oyashio Current immigrant from the NE Pacific and may not be expected in the subtropical waters of the Kuroshio Current at any time.

There are also a few, mostly rare species occurring in the Shinzato FM (middle Piacenzian to early Gelasian) of Okinawa that relate to coeval occurrence in the tropical Atlantic (Schwarzhans & Aguilera 2013). These are *Diaphus aequalis, Diaphus coatsi* and *Lampadena scapha*. All three species have originally been described from the late Neogene of the Caribbean. Their occurrence in the West Pacific shows that certain myctophid species of the past were just as widely distributed as today and thus demonstrates their potential for supraregional biostratigraphic purposes. *Diaphus coatsi* is known from exactly the same time interval from the Caribbean and from off Okinawa. *Diaphus aequalis* is known from the Messinian to Piacenzian in the tropical West Atlantic, Zanclean of the Mediterranean (Schwarzhans & Aguilera 2013) and now also from the Piacenzian of the tropical West Pacific. In addition to the specimen from Okinawa it has also recently been reported from the Piacenzian of the Philippines (van Hinsbergh & Helwerda 2019). The otoliths of *Lampadena* are amongst the largest and most diverse in myctophids. They also seem to have undergone a rapid diversification during the Neogene, but unfortunately their otoliths are rare. Their biostratigraphic potential is highlighted by the recognition of *Lampadena ionica* Girone & Nolf, 2002 from the early and middle Pleistocene of the Mediterranean. *Lampadena scapha* has been described from two specimens from the Neogene of the Caribbean, the holotype from the Piacenzian and a paratype from the late Tortonian (Schwarzhans & Aguilera 2013). The occurrence of *L. scapha* in the Piacenzian of Fiji and Okinawa thus is from the late stratigraphic range of the species. Its occurrence in the tropical Atlantic and West Pacific is also of interest in consideration of its two putative phylogenetic successors, the extant *L. urophaos* in the Pacific and *L. atlanticus* in the Atlantic (originally understood as a subspecies of *L. urophaos*).

Our results clearly document the biostratigraphic potential of myctophid otoliths, but it would be too early to formulate otolith based biozones at this stage. However, we recognize a number of occurrences and disappearances of myctophid species in southern Japan that may ultimately be of stratigraphic significance. These potential events are marked with arrows in figure 14.

Myctophid otoliths as indicators for paleo-temperatures and paleo-currents (Fig. 15)

The Pacific shores of Japan are under the influence of two counteractive currents that have created the exceptional wealth and diversity of the marine fauna of Japan (Masuda et al. 1984). These are the warm, subtropical Kuroshio Current from the south originating from the North Equatorial Pacific Current off the northern Philippines and flowing East of Taiwan and West of the Ryukyu Island Chain before turning eastward to follow the Pacific shores and slopes of southern Japan, and the cold water Oyashio Current originating from the counter clockwise North Pacific Subarctic Gyre and flowing southward along the east coasts of the Kuriles Island Chain and northern Japan (Qui 2001). They meet between about 35°N where the Kuroshio Current turns eastwards into the open North Pacific to form the Kuroshio extension and 40°N where the North Pacific Subarctic Current leaves the NE Asian shores (Fig. 15). The transition zone in between along the Pacific shores of Tohoku are particularly rich in fish resources (Masuda et al. 1984). Gallagher et al. (2015) reconstructed the late Neogene history of the Kuroshio Current based on the analysis of fossil evidence of molluscs, foraminifers, diatoms, ostracods and nannoplankton and assumed that it was in place and reaching near its present-day position by Piacenzian times at about 3 Ma. However, during the late Pliocene the Kuroshio Current was flowing along the east coast of the Ryukyu Island Chain and only switched west of it during middle Pleistocene (Gallagher et al. 2015). This switch brought about a drastic change in sedimentation from a mud-dominated sea to a carbonate and reef environment along the Ryukyus (Imai et al. 2013).

The study of Gallagher et al. (2015) has summarized the results of decades of detailed faunal evaluations of late Cenozoic fossils studied from locations along the Pacific shores of Japan. The warm tropical to subtropical mollusc assemblage of late Pliocene age was coined the "Kakegawa Fauna" by Otuka (1939) (see also Tsuchi 1986 and Ozawa et al. 1995). Its counterpart is the mild to cool temperate "Omma-Manganij Fauna" of central and northern Honshu (Tsuchi 1986, Ozawa et al. 1995) and further to the north in Hokkaido the subboreal "Tatsunokuchi Fauna" (Ozawa et al. 1995). In late Pleistocene / Holocene the "Kakegawa Fauna" gave way

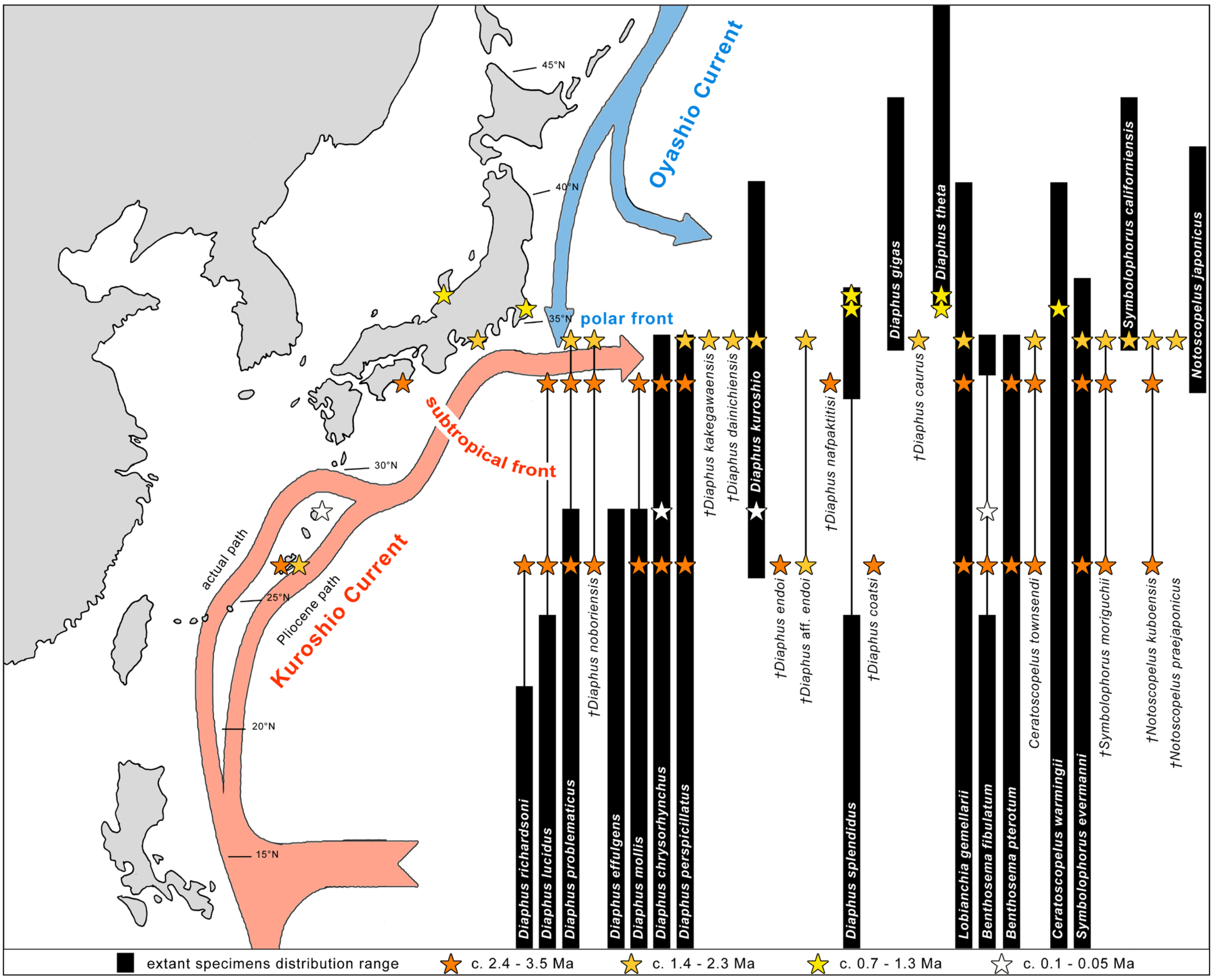


Fig. 15 - Geographic and temperature range chart of extant and fossil myctophids along the Pacific shores of Japan and position of Kuroshio and Oyashio Currents. Currents from Qui (2001) with Pliocene path of Kuroshio Current after Gallagher et al. (2015).

to the extant "Kuroshio Fauna" and the "Manganji and Tatsunokuchi Faunas" to the "Oyashio Fauna" while the "Omma Fauna" would be the equivalent of the transitional fauna between the Kuroshio and Oyashio Currents (see Ozawa et al. 1995).

The otoliths studied here all stem from locations within the "Kakegawa" faunal zone of southern Japan. Our findings of their composition are consistent with those made by molluscs with only minor modifications. The myctophid assemblages of Okinawa and Shikoku are more similar to each other than to that of Kakegawa indicating that the transition between a tropical / subtropical zone to a warm temperate zone, the core of the "Kakegawa Fauna" would be located slightly further northwards than interpreted from molluscs (Ozawa et al. 1995). A drastic faunal change occurred further north between Kakegawa and Boso and Miura Peninsulas (see above), with the latter showing the first definitive occurrence of cool water *Diaphus theta* in Japan. However, this change may in fact represent a combination of a temperature and a stratigraphic effect since the Boso and Miura locations studied in Aoki (1971) and Aoki & Baba (1980) are younger than any of the strata from which otoliths were obtained for our study. In the classification defined for molluscs, the Boso and Miura otolith assemblages should represent the "Omma Fauna". Few otoliths studied from the Calabrian of the Kanazawa area on the western coast of Japan, the type location of the "Omma Fauna" (Kitamura & Kondo 1990, Ogasawara 1996), have also yielded specimens of *Diaphus theta* and additionally of *Diaphus splendidus*.

A graphic analysis of the geographic distribution ranges of certain myctophid species during the late Neogene shows that some tropical to subtrop-

	Okinawa								Nobori, Kochi, Shikoku						Kakegawa				
	3.58-3.1 Ma	3.1-2.3 Ma					1.9-1.6 Ma		3.35-3.1 Ma						2.3-1.95 Ma	1.95-1.9 Ma	1.6-1.4 Ma		
	upper Yonabaru FM - PL3	Shinzato FM, 200-500 m - N21 (PL5)					Chinen FM - N22		upper Nobori FM, lower section 800-1000 m			upper Nobori FM, uppermost section 400-800 m			Dainichi FM N21 (PL6)	upper Dainichi (Fosoya tuff)	Hijikata FM 50-100m - N22 (PT1 part)		
	Ozatofurugen (Oz)	Aragusku (Ar)	Gushichan (Gu)	Tobaru (To)	Uruma (Ur)	Higa (Hi)	Chinen (Ch)	**total**	NOB-1	NOB-3+4	NOB-2	NOB-6	NOB-8	**total**	Hongohigashi (Hoh)	Fosoya (Fo)	Iriyamase (Ir)	**total**	**grand total**
Diaphus																			
aequalis Schwarzhans & Aguilera, 2013				1				**1**											**1**
caurus n.sp.																	4	**4**	**4**
chrysorhynchus Gilbert & Cramer, 1897	2			23				**25**	10	7				**17**					**42**
coatsi Schwarzhans & Aguilera, 2013				2		1		**3**											**3**
dainichiensis Ohe, 1981						4		**4**							47		76	**123**	**127**
endoi n.sp.				237		4		**241**											**241**
aff. *endoi* n.sp.							2	**2**									4	**4**	**6**
kakegawaensis n.sp.															76			**76**	**76**
kuroshio Kawaguchi & Nafpaktitis, 1978															1		10	**11**	**11**
lucidus (Goode & Bean, 1896)				53				**53**				2		**2**					**55**
mollis Taaning, 1928			3	14				**17**	1					**1**					**18**
nafpaktitisi n.sp.									1			4	2	**7**					**7**
noboriensis n.sp.		1		6		1		**8**	15	1	1	5		**22**	11			**11**	**41**
perspicillatus (Ogilby, 1898)			4	83		4		**91**	1					**1**	1			**1**	**93**
problematicus Parr, 1928				77				**77**	13	4		2		**19**	16			**16**	**112**
richardsoni Taaning, 1932				2				**2**											**2**
splendidus (Brauer, 1904)																	5	**5**	**5**
termophilus Taaning, 1928																1		**1**	**1**
Lobianchia																			
dofleini (Zugmayer, 1911)									1					**1**			6	**6**	**7**
gemellarii (Cocco, 1838)	2							**2**	48	9		68		**125**	16			**16**	**143**
Benthosema																			
fibulatum (Gilbert & Cramer, 1897)					15	2		**17**											**17**
pterotum (Alcock, 1890)	1		1		7	59		**68**	1562	102			2	**1666**					**1734**
Ceratoscopelus																			
townsendi (Eigenmann & Eigenmann, 1889)				4	1	2		**7**	54	7				**61**	130			**130**	**198**
Electrona																			
risso (Cocco, 1829)			1	1				**2**											**2**
sp.																1		**1**	**1**
Myctophum																			
spinosum (Steindachner, 1867)															8		5	**13**	**13**
Hygophum																			
proximum Becker, 1965									11	1				**12**	13			**13**	**25**
Symbolophorus																			
californiensis (Eigenmann & Eigenmann, 1889)															2		2	**4**	**4**
evermanni (Gilbert, 1905)				5				**5**	1			3	1	**5**	36			**36**	**46**
moriguchii n.sp.				24				**24**	1					**1**	3			**3**	**28**
sp.															2			**2**	**2**
Lampadena																			
scapha Schwarzhans & Aguilera, 2013				1				**1**											**1**
Lampanyctus																			
alatus Goode & Bean, 1896									3			1		**4**					**4**
festivus Taaning, 1928																	2	**2**	**2**
nobilis Taaning, 1928	4							**4**	46	4				**50**	25			**25**	**79**
Notoscopelus																			
kuboensis (Ohe & Araki, 1973)				1		1		**2**	3			2		**5**	8			**8**	**15**
praejaponicus n.sp.							1	**1**									6	**6**	**7**
Neoscopelus																			
microchir Matsubara, 1943				1				**1**											**1**
Sum	**9**	**1**	**9**	**535**	**23**	**78**	**3**	**658**	**1771**	**135**	**1**	**87**	**5**	**1999**	**395**	**2**	**120**	**517**	**3174**

Tab. 1 - Distribution of identified myctophid and neoscopelid otolith-based species in the Pliocene and Pleistocene of the studied Japanese locations.

ical species were reaching further northwards along the Pacific shores of Japan than today, e.g., *Diaphus richardsoni, D. lucidus, D. problematicus* and *D. mollis* (Fig. 15). The ancestral species of *Notoscopelus japonicus,* i.e., *N. praejaponicus* and *N. kuboensis*, maintained a more southerly and warmer distribution pattern than the extant species. *Benthosema fibulatum* appears to have had a more continuous distribution pattern along the Pacific shores of southern Japan than the disjunctive occurrence of today. A typical species of the Kuroshio Current and the transitional zone of today, *Diaphus kuroshio*, appears to have had a stable distribution pattern since its first occurrence in the Gelasian. The first occurrences of the cool water species *Symbolophorus californiensis* in the early Pleistocene and *Diaphus theta* in the middle to late Pleistocene are congruent with their southernmost occurrences today.

The myctophid assemblage from the late Pliocene of Okinawa and Shikoku appears to show a good relationship with a coeval association having been described from the Philippines (van Hinsbergh & Helwerda 2019), which would be expected. Two isolated otoliths from Fiji included in this study represent a species also known from Okinawa (*Lampadena scapha*) and a second one exclusive to Fiji (*Diaphus grebneffi*). These finds are a first indication of the presence of a wider tropical to subtropical western Pacific bioprovince during late Pliocene, however with some localized species patterns.

CONCLUSIONS AND OUTLOOK

The exceptionally rich and diverse myctophid otolith associations recovered from the late Pliocene and early Pleistocene of southern Japan (Tab. 1) represents an important cornerstone for unraveling of the history of this important mesopelagic family in the Pacific Ocean. The key conclusions are:

1. The abundance of many large otoliths and the recognition of several extinct species in the late Pliocene of Japan confirm the accelerated phylogenetic diversification of myctophids since the late Miocene / Pliocene biogenic bloom, particularly in the genus *Diaphus*.
2. The richness and diversity of the studied myctophid otolith associations indicate the potential for biostratigraphic applications of the group.
3. The, albeit rare, occurrence of coeval species first identified in the Caribbean demonstrate the potential of myctophid otoliths for supraregional biostratigraphic purposes.
4. The late Pliocene / Pleistocene otolith associations from Okinawa, Shikoku and central Honshu represent a tropical to subtropical fauna equivalent to the "Kakegawa Fauna" established on molluscs, which is the precursor of todays "Kuroshio Fauna".

We regard the myctophid otolith association studied here from the Plio-Pleistocene of southern Japan as a first step to map the evolution of the past fish fauna of the Northern Pacific by means of otoliths. We are certain that there will be many more locations prospective for otolith research along the circum-Pacific realms and we hope that our colleagues will be encouraged to undertake such investigations in the future. For instance in Japan the cooler northerly locations of the same time interval promise interesting results and comparison with the association described here when it comes to the Myctophidae. It must be emphasized though that any study of late Neogene otoliths must be based on an adequate command of otoliths of the relevant extant fishes, like it is the case for this study, in order to avoid the risk of establishing ill-defined so-called fossil species or of remaining in a scheme of open nomenclature, which would both prevent meaningful correlations and applications.

Acknowledgements: We wish to thank Mitsuru Moriguchi (Okinawa University, Naha) and Steffen Kiel (NRM, Stockholm) for providing many otoliths from various locations of the Okinawa Islands. We are very thankful to Masaki Umemoto (Tokai Fossil Society, Nagoya) and Takashi Ito (Shizuoka) for donating many otoliths from the Kakegawa Group, mainly Dainichi FM. Itsuro Oshiro (Naha, Okinawa) kindly guided the junior author to locations on Okinawa which are prospective for otoliths. Yukitoshi Tsukuda (president of HANESAN, Hane, Muroto, Kochi Prefecture) and his father Yukimori Tsukuda generously granted access to the junior author for collecting otoliths in their clay pit. Much help was received from colleagues in stratigraphic issues and making literature and figures available for usage in this article: Masahiro Shiba (Museum of Natural Environment History, Shizuoka) helped in respect to the stratigraphy of the upper Kakegawa Group; Satoshi Hanagata (Akita Prefectural Office) allowed usage of figures from his publications about the stratigraphy of Miyagijima; Yasuo Kondo (Geological department of Kochi University) supported with advice to the stratigraphy of the Tonohama Group; Kenji Mimoto (Kochi City) helped with geological information about the Nobori FM; Masako Ibaraki (Emeritus of the Geoscience Institut Shizuoka) advised in respect to planktonic foraminifers stratigraphy. Ewan Fordyce (Otago University, Dunedin, New Zealand) made otolith specimens available from the late Pliocene of Fiji from the heritage of Andrew Grebneff. Hiroaki Karasawa (Mizunami Fossil Museum) is thanked for showing their collection of Okinawa otoliths to us. Finally, the senior author wishes to thank many ichthyological colleagues from marine biology institutions for providing Recent myctophid otoliths or allowing access to extract otoliths from museum voucher specimens, e.g., Hiromitsu Endo (BSKU, Kochi), Gento Shinohara (NSMT, Tsukuba, Tokyo), John Paxton (AMS, Sydney), Karsten Hartel (MCZ, Cambridge Ms.), David Catania (CAS, San Francisco), Rick Feeney (LACM, Los Angeles), Jeffrey Williams (USNM, Washington) Peter Møller and Jørgen Nielsen (ZMUC, Copenhagen) and Philippe Béarez (MNHN, Paris). Finally, we would very much thank the reviewers for their constructive review of the manuscript.

REFERENCES

Aoki N. (1966) - Molluscan fossils from the Nobori Formation, Shikoku, Japan. *Trans. Proc. Palaeont. Soc. Japan, N.S.*, 62: 251-259.

Aoki N. (1971) - Some Pleistocene fish-otoliths from the Boso and Miura Peninsulas (second report). *Sci. Rep. Tokyo Kyoiku Daigaku, C*, 104: 11-34.

Aoki N. & Baba K. (1980) - Some Pleistocene fish-otoliths from the Boso and Miura Peninsulas (third report). *Ann. Rep. Inst. Geosci. Univ. Tsukuba*, 6: 55-61.

Aoki N. & Baba K. (1984) - Additions to the molluscan fossils from the Nobori Formation, Shikoku. *Ann. Rep. Inst. Geosci. Univ. Tsukuba,* 10: 73-79.

Bedini E., Francalacci P. & Landini W. (1986) - I pesci fossili del Miocene superiore di Montefiore conca e Mondaino (Forlì). *Mem. Mus. Civ. St. Nat. Verona, Sez. Sci. Terra*, 3: 1-67.

Berggren W.A. (1973) - The Pliocene time scale: Calibration of planktonic foraminiferal and calcareous nannoplankton zones. *Nature*, 243: 391-397.

Berggren W.A., Kent D.V., Swisher C.C. & Aubry M.-P. (1995) - A revised Cenozoic geochronology and chronostratigraphy. *SEPM Sp. Publ.*, 54: 129-212.

Blow W.H. (1969) - Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. In: Bronnimann P. & Renz H.H. (Eds) - *Proc. First Internat. Conf. Planktonic Microfossils (Geneva, 1967)*, Leiden, E. J. Brill, 1: 199-421.

Brzobohaty R. & Nolf D. (1996) - Otolithes des myctophidés (poissons téléostéens) des terraines tertiares d'Europe: révision des genres *Benthosema, Hygophum, Lampadena, Notoscopelus* et *Symbolophorus*. *Bull. Inst. roy. Sci. natur. Belg., Sci. de la Terre*, 66: 151-176.

Brzobohaty R. & Nolf D. (2000) - *Diaphus* otoliths from the European Neogene (Myctophidae, Teleostei). *Bull. Inst. roy. Sci. natur. Belg., Sci. de la Terre*, 70: 185-206.

Brzobohaty R., Reichenbacher B. & Gregorova R. (2003) - Teleostei (otoliths, skeletons with otoliths *in situ*) from the Karpatian of the Central Paratethys. In: Brzobohaty R., Cicha I., Kovac M. & Rögl F. (Eds) - The Karpatian, a Lower Miocene stage of the Central Paratethys. Masaryk University, Brno: 265-279.

Cappetta H. (2012) - Chondrichthyes; Mesozoic and Cenozoic Elasmobranchii: teeth. Handbook of Paleoichthyology, 3E, Verlag Dr. Friedrich Pfeil, München, 512 pp.

Chunlian L., Yi H., Jie W., Guoquan Q., Tingting Y., Lianze X. & Suqing Z. (2012) - Miocene-Pliocene planktonic foraminiferal biostratigraphy of the Pearl River Mouth Basin, northern South China Sea. *J. Palaeogeography*, 1: 43-56.

Davis M.P., Holcroft N.I., Wiley E.O., Sparks J.S. & Smith W.L. (2014) - Species-specific bioluminescence facilitates speciation in the deep sea. *Mar. Biol.*, 161: 1139-1148.

Dowsett H.J. (1988) - Diachrony of late Neogene microfossils in the southwest Pacific Ocean: Application of the graphic correlation method. *Paleoceanography*, 3: 209-222.

Froese R. & Pauly D. (Eds) (2018) - FishBase. World Wide Web electronic publication. www.fishbase.org, version (10/2018).

Gallagher S.J., Kitamura A., Iryu Y., Koizumi I. & Hoiles P.W. (2015) - The Pliocene to recent history of the Kuroshio and Tsushima Currents: a multi-proxy approach. *Prog. Earth Planet. Sci.*, 2: 17: 1-23.

Girone A. & Nolf D. (2002) - *Lampadena ionica*: a new teleost from the Mediterranean Pleistocene. *Riv. It. Paleontol. Strat.*, 108: 493-500.

Gjøsaeter J. (1984) - Mesopelagic fish, a large potential resource in the Arabian Sea. *Deep Sea Res. A. Oceanogr. Res. Pap.*, 31: 1019-1035.

Hanagata S. (2004) - Pliocene-Pleistocene planktonic foraminiferal biostratigraphy in the Miyagijima and adjacent islands, off Katsuren Peninsula, east of Okinawa-jima, Japan. *Bull. Mizunami Fossil Mus.*, 31: 37-48 [in Japanese with English abstract].

Hulley P.A. (1984) - Myctophidae. In: Whitehead P.J.P., Bauchot M.-L., Hureau J.-C., Nielsen J. and Tortonese E. (Eds) - Fishes of the north-eastern Atlantic and the Mediterranean. UNESCO, Paris. 1: 429-483.

Ibaraki M. (1985) - Neogene planktonic foraminiferal biostratigraphy of the Kakegawa area on the Pacific coast of central Japan. *Rep. Fac. Sci., Shizuoka Univ.*, 20: 39-173 [in Japanese].

Ibaraki M. (1986) - Planktonic foraminiferal datum levels recognized in the Neogene sequence of the Kakegawa area, and their relationship with the lithostratigraphy. *Jour. Geol. Soc. Japan*, 92: 119-134 [in Japanese with English abstract].

Ibaraki M. & Tsuchi R. (1975) - Planktonic foraminifera from the upper part of the Neogene Shimajiri Group and the Chinen sand, the Okinawa Island. *Rep. Fac. Sci., Shizuoka Univ.*, 10: 129-143 [in Japanese].

Ikebe N., Chiji M. & Huang T.Y. (1981) - Important datum-planes of the western Pacific Neogene. *Bull. Osaka Mus. Nat. Hist.*, 34: 79-86.

Imai R., Sato T. & Iryu Y. (2013) - Chronological and palaeoceanographic constraints of Miocene to Pliocene 'mud sea' in the Ryukyu Islands (southwestern Japan) based on calcareous nannofossil assemblages. *Island Arc*, 22: 522-537.

Imai R., Sato T. & Iryu Y. (2016) - Calcareous nannofossil assemblages of the upper Miocene to Pliocene Shimajiri Group on Okinawa-jima, Ryukyu Islands, southwestern Japan. *Jour. Asian Earth Sci.*, 135: 16-24.

Irigoien X., Klevjer T.A., Røstad A., Martinez U., Boyra G., Acuña J.L., Bode A., Echevarria F., Gonzales-Gordillo J.I., Hernandez-Leon S., Agusti S., Aksnes D.L., Duarte C.M. & Kaartvedt S. (2014) - Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Communications*, 5: 3271: 1-10.

Ishida A., Makinouchi T., Nishimura A., Takemura K., Danhara T., Nishiyama K. & Hayashida A. (1980) - Middle Pleistocene of Kakegawa district, central Japan. *Quat. Res. Japan,* 19: 133-134 [In Japanese with English abstract].

Iwai M., Kondo Y., Kikuchi N. & Oda M. (2006) - Overview of stratigraphy and paleontology of Pliocene Tonohama Group, Kochi Prefecture, southwest Japan. *J. Geol. Soc. Japan*, 112 Supplement: 27-40 [in Japanese].

Janssen A.W. & Grebneff A. (2012) - Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 22. Further pelagic gastropods from Viti Levu, Fiji Archipelago. *Basteria*, 76: 15-30.

Kameo K. (1998) - Upper Neogene and Quaternary stratigraphy in the Kakegawa district based on the calcareous nannofossil datum planes. *J. Geol. Soc. Japan*, 104: 672-686 [in Japanese with English abstract].

Katto J. (1960) - Report of geological investigation. In: Report of fundamental investigation for establishment of the Ashizuri-Muoto Natinal Park. Muroto Section. Kochi Prefectural Government: 1-20 [in Japanese].

Katto J., Kojima J., Sawamura T. & Suyari K. (1960) - Geological and mineral resources map (1:200000) of Kochi Prefecture. Explanatory text, Kochi Prefecture, 129 pp. [in Japanese].

Katto J. & Masuda K. (1993) - Mollusks of the Tonohama Group. The explanatory booklet for special exhibition, Sakawa Geology Museum and Institute, 1: 1-52 [in Japanese].

Katto J., Nakamura J. & Takayanagi Y. (1953) - Stratigraphical and paleontological studies of the Tonohama Group, Kochi Prefecture, Japan. *Res. Rep. Kochi Univ., Nat. Sci.*, 2 (32): 1-15 [in Japanese].

Katto J., Takayanagi Y., Masuda K., Taira A. & Okamura M. (1980) - Reevaluation project of the Tonohama Group - a preliminary report. In: Taira A. & Tashiro M. (Eds) - Geology and Paleontology of the Shimanto Belt - Selected Papers in Honor of Prof. J. Katto, Kochi Branch, Rin-ya Kosai Kai, Kochi: 27-36 [in Japanese with English abstract].

Kawaguchi K. & Nafpaktitis B.G. (1978) - A new lanternfish, *Diaphus kuroshio* (Family Myctophidae), from the Kuroshio waters off Japan. *Japan. J. Ichthyol.*, 25: 89-91.

Kawaguchi K. & Shimizu H. (1978) - Taxonomy and distribution of the lanternfishes, genus *Diaphus* (Pisces, Myctophidae) in the western Pacific, eastern Indian Ocean and the southeast Asian seas. *Bull. Ocean Research Inst. Univ. Tokyo*, 10: 1-145.

Kitamura A. & Kondo Y. (1990) - Cyclic changes of sediments and molluscan associations caused by glacio-eustatic sea-level changes during the early Pleistocene - a case study of the middle part of the Omma Formation at the type locality. *J. Geol. Soc. Japan*, 96(1): 19-36.

Kobuta T. & Uyeno T. (1972) - On the occurrence of the lanternfish *Electrona rissoi* in Japan. *Japan. J. Ichthyol.*, 19: 125-128.

Koizumi I. & Ujiie H. (1976) - On the age of the Nobori Formation, Shikoku, southwest Japan - particularly based on diatoms. *Mem. Nat. Sci. Mus., Tokyo,* 9: 61-70.

Koken E. (1891) - Neue Untersuchungen an tertiären Fisch-Otolithen II. *Z. deut. geol. Ges.*, 43: 77-170.

Komatsubara J., Sato T., Nakagawa H., Matsumoto R., Iryu Y., Matsuda H., Omura A., Odawara K. & Takeuchi R. (2005) - Paleomagnetism of the upper part of the Shinzato Formation (Shimajiri Group) and the Chinen Formation, southern Ikonawa-jima, southwestern Japan. *J. Sed. Soc. Japan*, 61: 5-13 [in Japanese with English abstract].

Kon T. & Yoshino T. (1997a) - *Niphon macrocephalus* sp. nov., a late Pliocene serranid fish from Okinawa, Japan. *Ichthyol. Res.*, 44: 35-42.

Kon T. & Yoshino T. (1997b) - *Cookeolus spinolacrymatus* sp. nov., a late Pliocene priacanthid fish from Okinawa, Japan. *Ichtyhol. Res.*, 44: 347-356.

Kurihara K. (1968) - Notes on the benthonic foraminifera of the Tonohama Group, Shikoku, Japan. *Trans. Proc. Palaeont. Soc. Japan. N.S.,* 70: 267-283.

Linkowski T.B. (1997) - Morphological variation, systematics and speciation of the *Ceratoscopelus townsendi - C. warmingii* complex (Osteichthyes: Myctophidae) based on the studies on the morphology and microstructure of otoliths. Morski Instytut Rybacki, Gdynia, 197 pp. [in Polish with English summary].

Lombarte A., Chic O., Parisi-Baradad V., Olivella R., Piera J. & Garcia-Ladona E. (2006) - A web-based environment from shape analysis of fish otoliths. The AFORO database. *Scientia Marina*, 70: 147-152. www.isis.cmima.csic.es/aforo/index.jsp, version 11/22/2018.

Martin R.P., Olson E.E., Girard M.G., Smith W.L. & Davis M.P. (2018) - Light in the darkness: New perspective on lanternfish relationships and classification using genomic and morphological data. *Mol. Phylogenet. Evol.*, 121: 71-85.

Masuda H., Amaoka K., Araga C., Uyeno T. & Yoshino T. (1984) - The fishes of the Japanese Archipelago. Tokai University Press, 437 pp.

Masuda F., Ozawa T., Tanaka T. & Tomida S. (1998) - Pliocene to Early Pleistocene warm water molluscan fauna from the Kakegawa Group, central Japan. *Nagoya Univ. Furukawa Mus.*, Spec. Rep., 7: 205p.

Matsubara T. (2004) - Catalogue of the Pliocene Mollusca from the Tônohama Group in Kôchi Prefecture, Shikoku, Japan, in the museum of nature and human activities, Hyogo (Takao Sendô collection). *Nat. Hum. Activ.*, 8: 49-95.

Mead G.W. & Taylor F.H.C. (1953) - A collection of oceanic fishes from off northeastern Japan. *J. Fish. Res. Bd. Can.*, 10: 560-582.

Mimoto K. & Nakao K. (2004) - Holoplanktonic gastropods from the Pliocene Tonohama Group in Kochi Prefecture, Japan. *Tokushima Pref. Mus.*, 14: 15-25.

Mizuno K., Sugiyama Y. & Shimokawa K. (1987) - Tephorostratigraphy of the Sagara Group and the lower part of the Kakegawa Grop in the Omaezaki area, Shizuoka Prefecture. *Bull. Geol. Surv. Japan.*, 38(12): 785-808 [in Japanese].

Nafpaktitis B.G. (1978) - Systematics and distribution of lanternfishes of the genera *Lobianchia* and *Diaphus* (Myctophidae) in the Indian Ocean. *Nat. Hist. Mus. Los Angeles County Sci. Bull.*, 30: 1-92.

Nakagawa H., Matsuda H., Sato T., Hiratsuka M. & Oda T. (2001) - Preliminary study on sedimentary facies and depositional age of the Chinen Formation in the southern part of Okinawa Island. *J. Sedimentol. Soc. Japan*, 53: 99-101 [in Japanese].

Nakamura Y., Kameo K., Asahara Y. & Ozawa T. (1999) - Stratigraphy and geologic age of the Neogene Shimajiri Group in Kumejima Island, Ryukyu Islands, southwestern Japan. *J. Geol. Soc. Japan*, 105(11): 757-770.

Nelson J.S., Grande T.C. & Wilson M.V.H. (2016) - Fishes of the world. 5th ed. Hoboken, John Wiley and Sons.

Nishida S. (1971) - Nannofossils from Japan IV. Calcareous nannoplankton fossils from the Tonohama Group, Shikoku, southwest Japan. *Trans. Proc. Palaeont. Soc. Japan, N.S.*, 83: 143-161.

Nishida S. (1979) - Restudies of calcareous nannoplankton biostratigraphy of the Tonohama Group, Shikoku, Japan. *Bull. Nara Univ. Educ.*, 28: 97- 110.

Nishimura S. (1977) - Re-examination of age determination of tephra layers by fission track method. *Rep. Kansai Region, Geol. Soc. Japan*, 8 [in Japanese].

Nobuhara T. (1992) - Bathyal molluscan assemblages in the Plio-Plistocene in the Kakegawa area, Shizuoka Prefecture, central Japana; their relationships with water masses. *Bull. Mizunami Fossil Mus.*, 19: 515-528.

Nobuhara T. (1993) - The relationship between bathymetric depth and climate change and its effect on molluscan faunas of the Kakegawa Group, central Japan. *Trans. Proc. Palaeont. Soc. Japan, N.S.,* 170: 159-185.

Noda H. (1977) - Stratigraphic relationship between the Shinzato and Chinen Formations and its geological significance in southern Okinawa-jima, Okinawa Prefecture, southwest Japan. In: Kizaki K. (Ed.) - Geological Studies of the Ryukyu Islands, 2: 55-60, Ryukyu University, Okinawa (in Japanese with English abstract).

Noda H. (1980) - Molluscan fossils from the Ryukyu Islands, southwest Japan. *Sci. Rep. Inst. Geosci. Univ. Tsukuba, Sec. B Geol. Sci.*, 1: 1-95.

Noda H. (1988) - Molluscan fossils from the Ryukyu Islands, southwest Japan. Part 2, Gastropoda and Pelicypoda from the Shinzato Formation in the middle part of Okinawa-jima. *Sci. Rep. Inst. Geosci. Univ. Tsukuba, Sec. B Geol. Sci.*, 9: 29-85.

Noda H. (1991) - Molluscan fossils from the Ryukyu Islands, southwest Japan. Part 3, Gastropoda and Pelicypoda from the Yonabaru Formation in the southwestern part of Okinawa-jima. *Sci. Rep. Inst. Geosci. Univ. Tsukuba, Sec. B Geol. Sci.*, 12: 1-63.

Noda H. (2002) - Molluscan fossils from the Ryukyu Islands, southwest Japan. Part 4, Gastropoda and Pelicypoda from the Nakoshi Formation in the Motobu Peninsula part of Okinawa-jima. *Sci. Rep. Inst. Geosci. Univ. Tsukuba, Sec. B Geol. Sci.*, 23: 53-116.

Nolf D. (2013) - The Diversity of Fish Otoliths, Past and Present. Royal Belgian Institute of Natural Sciences, Brussels, 222 pp.

Nolf D. & Cappetta H. (1988) - Otolithes des poissons Pliocènes du Sud-Est de la France. *Bull. Inst. Roy. Sci. Natur. Belg.,* 58: 209-271.

Nolf D. & Steurbaut E. (1988) - Description de la première faune ichthyologique exclusivement bathyale du Tertiare d'Europe: otolithes de l'Oligocène Inférieur du gisement de Pizzocorno, Italie septentrionale. *Bull. Inst. Roy. Sci. Natur. Belg.,* 57: 217-230.

Nolf D. & Steurbaut E. (1990) - Découverte de poissons bathyaux d'âge Oligocène inférieur à Pizzocorno, près de Voghera. *Quad. Sci. Natur. Civ. Mus. Voghera*, 10: 15-31.

Nolf D. & Steurbaut E. (2004) - Otolithes de poissons de l'Oligocène inférieur du bassin liguro-piemontese oriental, Italie. *Riv. Piem. St. Nat.*, 25: 21-68.

Oda M. (1978) - Planktonic foraminiferal biostratigraphy of the late Cenozoic sedimentary sequence, central Honshu, Japan. *Tohoku Univ. Sci. Rep. 2nd ser. (Geol.),* 48: 1-72.

Ogasawara K. (1996) - Paleobiogeographic significance of the Omma - Manganji Fauna. *HGI Report (University of Tsukuba, Institute of Geoscience)*, 5: 245-262 [in Japanese with English abstract].

Ohe F. (1977) - Otoliths from Dainichi Sand and Hosoya tuffaceous beds of Kakegawa Group (Pliocene), Shizuoka Prefecture, Central Japan. *Kaseki no Tomo (Pub. Tokai Foss. Soc.)*, 16: 13-19.

Ohe F. (1981) - Fish-otoliths from the Dainichi sand and the Fosoya tuffaceous members of the Pliocene Kakegawa Group, Shizuoka Prefecture, central Japan. *Bull. Senior Highschool, Aichi Univ.*, 8: 125-194 [in Japanese with English abstract].

Ohe F. (1983) - On the otoliths of deep water fishes from Pliocene Hijikata mud formation exposed in the southern part of Kakegawa City, Shizuoka Prefecture, central Japan. *Bull. Senior Highschool, Aichi Univ.*, 10: 1-54.

Ohe F. (1985) - Marine fish-otoliths of Japan. *Bull. Senior Highschool, Aichi Univ.*, spec. vol., 184 pp.

Ohe F. (2011) - Macrourid *Cetonurus* species "Nobori dangohige" in new Japanese name, in the Nobori Formation of Tonohama Group, and its spatial-temporal distribution. *Paleontol. Soc. Japan*, 169th meeting: 37 [in Japanese].

Ohe F. & Araki Y. (1973) - Some Miocene fish otoliths from the Yakuoji Formation, Tsu, Mie Prefecture. *Tohoku Univ. Sci. Rep. 2nd ser. (Geol.),* 6 (Hatai Memorial Volume): 407-413.

Ohe F., Kawai H. & Kawase M. (1997) - Fish-otoliths from the Pleistocene Wan Formation, Ryukyu Group, Kikajima, Kagoshima Prefecture. *Kaseki no Tomo (Pub. Tokai Foss. Soc.)*, 44: 27-32.

Oshimizu T. & Iryu Y. (2002) - Stratigraphy of the Chinen Formation and the Ryukyu Group on islands off Katsuren Peninsula, Okinawa-jima, Ryukyu Islands, Japan. *Jour. Geol. Soc. Japan*, 108: 318-335 [in Japanese with English abstract].

Otuka Y (1939) - Tertiary crustal deformations in Japan with short remarks of Tertiary paleogeography. *Jubilee Pub. Commem. Prof. Yabe's 60th Birthday*: 481-519.

Ozawa T., Inoue K., Tomida S., Tanaka T. & Nobuhara T. (1995) - An outline of the Neogene warm-water molluscan faunas in Japan. *Palaeont. Soc. Japan*, 58: 20-27 [in Japanese with English abstract].

Qui B. (2001) - Kuroshio and Oyashio Currents. In: Steele J.H., Thorpe S.A., Turekian K.K. (Eds) - Encyclopedia of ocean sciences. Academic Press, London: 1413-1425.

Rivaton J. & Bourret P. (1999) - Les otolithes des poissons de l'Indo- Pacifique. *Documents scientifiques et techniques, Institut de recherche pour le dévelopment, Nouméa,* 2: 1-378.

Sakai T. & Masuda F. (1995) - Sequence stratigraphy of the Plio-Pleistocene Kakegawa Group, Shizuoka, Japan. *Mem. Geol. Soc. Japan*, 45: 154-169.

Sassa C. (2009) - Feeding ecology of *Symbolophorus californiensis* larvae (Teleostei: Myctophidae) in the southern transition region of the western North Pacific. *J. Mar. Biol. Ass. U.K.*, 90: 1249-1256.

Sassa C., Takahashi M. & Tsukamoto Y. (2014) - Distribution, hatch-date, growth, and mortality of larval *Benthosema pterotum* (Pisces: Myctophidae) in the shelf region of the East China Sea. *Jour. Marine Biol. Ass. U.K.*, 95: 161-174.

Sato T., Nakagawa H., Komatsubara J., Matsumoto R., Iryu Y., Matsuda H., Omura A., Odawara K. & Takeuchi R. (2004) - Geological age of the Chinen Formation in southern Okinawa-jima based on calcareous microfossils. *Jour. Geol. Soc. Japan*, 110: 38-50 [in Japanese with English abstract].

Satoguchi Y. & Nagahashi Y. (2012) - Tephrostratigraphy of the Pliocene to middle Pleistocene series in Honshu and Kyushu islands, Japan. *Island Arc*, 21: 149-169.

Satoguchi Y., Yoshikawa S., Sasao E. & Nagahashi Y. (1996) - Volcanic ash layers of the upper Kakegawa Group in the Shizuoka Prefecture, Japan and the correlation with volcanic ash layers in other areas. *Earth Science (Chikyu Kagaku)*, 50: 483-500 [in Japanese].

Schwarzhans W. (1978) - Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. *Meded. Werkgr. Tert. Kwart. Geol*, 15: 167-185.

Schwarzhans W. (1985) - Tertiäre Otolithen aus South Australia und Victoria (Australien). *Palaeo Ichthyologica*, 3: 1-60.

Schwarzhans W. (1986) - Die Otolithen des Unter-Pliozän von Le Puget, S-Frankreich. *Senckenbergiana lethaea*, 67: 219-273.

Schwarzhans W. (2013a) - Otoliths from dredges in the Gulf of Guinea and off the Azores - an actuo-paleontological case study. *Palaeo Ichthyologica*, 13: 7-40.

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

Schwarzhans W. (2013c) - Otoliths from the Miocene of West Africa, primarily from the Mondorové Frmation of Gabon. *Palaeo Ichthyologica*, 13: 151-184.

Schwarzhans W. & Aguilera O. (2013) - Otoliths of the Myctophidae from the Neogene of tropical America. *Palaeo Ichthyologica*, 13: 83-150.

Shiba M., Watanabe K., Yokoyama K., Sasaki A., Udo F. & Ogata C. (2000) - Volcanic ash beds of the upper Kakegawa Group. *Sci. Rep. Mus. Tokai Univ.*, 2: 53-108 [in Japanese with English abstrac].

Shiba M., Yokoyama K., Akao R., Kase T., Sanada R., Shibata S., Nakamoto T. & Miyamoto A. (2007) - Sequence stratigraphy and biostratigraphic horizon in the upper Kakegawa Group. *Jubilee Publ. Commem. Prof. Kamei's 80th Birthday*: 219-230 [in Japanese].

Shiba M., Oishi T., Takahara H., Yokoyama K., Sakamoto K., Hasegawa Y., Murakami C. & Udo F. (2010) - Volcanic ash beds of the lower of the Kakegawa Group. *Sci. Rep. Mus. Tokai Univ.*, 10: 17-50 [in Japanese with English abstract].

Shibata K., Nishimura S. & Chinzei K. (1984) - Radiometric dating related to Pacific Neogene planktonic datum planes. In: Ikebe N. & Tsuchi R. (Eds) - Pacific Neogene datum planes - contributions to biostratigraphy and chronology. Univ. Tokyo Press., Tokyo: 85-89.

Shinohara G., Narimatsu Y., Hattori T., Ito M., Takata Y. & Matsuura K. (2009) - Annotated checklist of deep-sea fishes from the Pacific coast off Tohoku District, Japan. In: Fujita T. (Ed.) - Deep-sea fauna and pollutants off Pacific coast of northern Japan. *Nation. Mus. Nature Sci. Monogr.*, 39: 683-735.

Sugiyama K., Nobuhara T. & Inoue K. (1992) - Preliminary report on Pliocene radiolarians from the Nobori Formation, Tonohama Group, Shikoku, Southwest Japan. *J. Earth Planet. Sci. Nagoya Univ.*, 39: 1-30.

Takahashi M. (1977) - Some Pliocene fish otoliths from the Dainichi sands, Kakegawa group, central Japan. *Bull. Mizunami Fossil Mus.*, 4: 97-118 [in Japanese with English abstract].

Takayama T. (1980) - Geological age of the Nobori Formation, Shikoku, Japan; calcareous nannofosil evidence. *Prof. Kanno Mem.*: 365-372.

Takayanagi Y. & Saito T. (1962) - Planktonic foraminifera from the Nobori Formation, Shikoku, Japan. *Sci. Rep. Tohoku Univ. Sendai*, 2nd Ser. (Geol.), spec. vol. 5: 67-106.

Tanaka Y. & Ujiie H. (1984) - A standard late Cenozoic microbiostratigraphy in southern Okinawa-jima, Japan. Part 1. Calcareous nannoplankton zones and their correlation to the planktonic foraminiferal zones. *Bull. Nat. Sci. Mus. Tokyo, Ser. C*, 10: 141-168.

Tsuchi R. (1955) - The Paleoecological significance of the Later Pliocene molluscan fauna from the Kakegawa district, the Pacific coasts of central Japan. *Rep Liberal Arts Fac., Shizuoka Univ.* (*Nat. Sci.*), 8: 45-59.

Tsuchi R. (1975) - Geology of southern Okinawa Island, with reference to the formation of the Yamashita-cho cave. *J. Anthrop. Soc. Nippon*, 82: 131-136.

Tsuchi R. (1986) - Late Cenozoic molluscan faunas and their development in southwestern Japan. In: Kotaka I. (Ed.) - Japanese Cenozoic molluscs - their origin and migration. *Palaeont. Soc. Japan, spec. pap.*, 29: 33-45.

Tsuchi R. (2002) - Neogene evolution of surface marine climate in the Pacific and noted on related events. *Rev. Mex. Cienc. Geol.*, 19(3): 260-270.

Uchio T. (1967) - Is the geologic age of the Nobori Formation, Shikoku, Japan, Miocene or Pliocene? *Trans. Proc. Palaeontol. Soc. Japan*, *N.S.*, 67: 114-124.

Ujiie H. (1985) - A standard late Cenozoic microbiostratigraphy in southern Okinawa-jima, Japan. Part 2. Details on the occurrence of planktonic foraminifera with some taxonomic annotations. *Bull. Nat. Sci. Mus. Tokyo, Ser. C*, 11: 104-136.

Ujiie H. (1994) - Early Pleistocene birth of the Okinawa Trough and Ryukyu Island Arc at the northwestern margin of the Pacific: evidence from late Cenozoic planktonic foraminiferal zonation. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 108: 457-474.

Ujiie H. & Kaneko N. (2006) - Geology of the Naha and Okinawashi-Nambu districts. *Quadrangle Series 1:50,000*, *Geological Survey of Japan, AIST*: 1-48 [in Japanese with English abstract: 46-48].

Van Hinsbergh V. & Helwerda R. (2019) - Fish otoliths from the Cabarruyan Piacenzian-Gelasian fauna found in the Philippines. *Zootaxa*, 4563 (3): 401-443.

Wade B.S., Pearson P.N., Berggren W.A. & Pälike H. (2011) - Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth-Sci. Rev.*, 104: 111-142.

Weiler W. (1942) - Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. *Abh. Reichsamt Bodenforsch., NF,* 206: 140 pp.

Yokoyama M. (1923) - Tertiary mollusca from Dainichi in Tôtômi. *J. College of Science, Tokyo Imperial Univ.*, 45, art. 2: 1-18 [in Japanese].

Yoshida T. & Nitsuma N. (1976) - Magnetostratigraphy in the Kakegawa district. In: Tsuchi R. (Ed.) - 1st CPNA Guidebook Exc. 3, Kakegawa District: 54-59.