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## An Early Oligocene fish-fauna from Japan reconstructed from otoliths

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### Abstract

The otoliths described in this study from the Late Eocene to Early Oligocene (biozone P18) of the Kishima Formation near Karatsu, Saga Prefecture, represent the earliest record of fossil otoliths from Japan and in fact the entire Northwest Pacific. They were obtained from outcrops along the Shimohirano River. A total of 13 otolith-based teleost taxa are recognized, 11 of which being identifiable to species level and new to science and five new genera. The new otolith-based genera are: *Nishiberyx* n. gen. (Berycidae), *Sagaberyx* n. gen. (Berycoidei family indet.), *Namicauda* n. gen. (Polymixiidae), *Ortugobius* n. gen. (tentatively placed in Gobiidae) and *Cornusolea* n. gen. (Soleidae); the new species are: *Rhynchoconger placidus* n. sp., *Rhynchoconger subtilis* n. sp., *Saurida macilenta* n. sp., *Nishiberyx nishimotoi* n. sp., *Sagaberyx kishimaensis* n. sp., *Namicauda pulvinata* n. sp., *Liza brevirostris* n. sp., *Pontinus? karasawai* n. sp., *Ortugobius cascus* n. sp., *Gymnogobius oligocenicus* n. sp. and *Cornusolea fudoujii* n. sp. The otolith assemblage shows a typical composition of a shallow marine, near shore environment dominated by two species of the Gobioidi. It thus represents one of the earliest rich gobioid otolith-assemblages known to date and gives new insights in the development of this group and the family Gobiidae, one of the most successful fish families in the Recent. *Ortugobius* n. gen. otoliths are characterized by a unique feature, a iugum extending below the entire sulcus, which is not known from extant gobioid otoliths. This character is interpreted to represent an early apomorphy and thus puts *Ortugobius* n. gen. in an only provisionally resolved familial relationship. An unambiguous representative of the family Gobiidae occurs parallel, *Gymnogobius oligocenicus* n. sp. The majority of the otoliths belong to families also represented in Japanese waters of today, with the notable exception of the enigmatic *Sagaberyx* n. gen., which is thought to represent an extinct berycoid of unresolved relationship.

**Key words:** Paleogene, Congridae, Beryciformes, Gobiidae, Soleidae, new species.

### Zusammenfassung

Die hier beschriebenen Otolithen aus dem Ober-Eozän bis Unter-Oligozän (Biozone P18) der Kishima Formation von Karatsu, Saga Prefecture, repräsentieren die ältesten fossilen Otolithen aus Japan und des Nordwest-Pazifiks. Sie wurden aus Aufschlüssen am Ufer des Shimohirano Flusses aufgesammelt. Insgesamt wurden 13 Otolithen-Taxa festgestellt, von denen 11 als neue Arten bestimmt werden konnten sowie 5 neue Gattungen. Die neuen auf Otolithen begründete Gattungen sind: *Nishiberyx* n. gen. (Berycidae), *Sagaberyx* n. gen. (Berycoidei indet.), *Namicauda* n. gen. (Polymixiidae), *Ortugobius* n. gen. (Gobiidae mit Vorbehalt) und *Cornusolea* n. gen. (Soleidae); die neuen Arten sind: *Rhynchoconger placidus* n. sp., *Rhynchoconger subtilis* n. sp., *Saurida macilenta* n. sp., *Nishiberyx nishimotoi* n. sp., *Sagaberyx kishimaensis* n. sp., *Namicauda pulvinata* n. sp., *Liza brevirostris* n. sp., *Pontinus? karasawai* n. sp., *Ortugobius cascus* n. sp., *Gymnogobius oligocenicus* n. sp. und *Cornusolea fudoujii* n. sp. Die Otolithen zeigen eine typische Fischfauna des flachmarinen, küstennahen Bereiches an, die von zwei Arten der Unterordnung Gobioidi dominiert wird. Damit stellt sie die älteste bekannte Gobioidi Otolithen-Gemeinschaft dar und erbringt neue Erkenntnisse zu ihrer Entwicklung und der Familie Gobiidae, eine der erfolgreichsten Fischfamilien in der Gegenwart. Die Otolithen von *Ortugobius* n. gen. sind durch eine spezifische Entwicklung des Iugum gekennzeichnet, das sich unter dem gesamten Sulcus langzieht, wie es von rezenten Gobiiden-Otolithen nicht bekannt ist. Dieses Merkmal wird als eine frühe Apomorphie gewertet, die die eindeutige systematische Zuordnung der Gattung erschwert. Daneben gibt es aber mit *Gymnogobius oligocenicus* n. sp. auch bereits unzweifelhafte Gobiiden. Die Mehrzahl der Otolithen aus der Kishima Formation gehören zu Familien, die auch heute noch in japanischen Gewässern vertreten sind. Eine Ausnahme ist die rätselhafte Gattung *Sagaberyx* n. gen., die möglicherweise eine unbekannte, ausgestorbene Gruppe der Berycoidei repräsentiert.

**Schlüsselwörter.** Paläogen, Congridae, Beryciformes, Gobiidae, Soleidae, neue Arten.

## 1. Introduction

Fossil otoliths have been recorded from Japan since the 1960ies, primarily from Neogene strata, for instance by Hatai (1965), Ohe (1977, 1979, 1981, 1990), Ohe & Araki (1973) and Takahashi (1976, 1977). The otoliths from the Kishima Formation described in the following represent the first record of fossil otoliths from Paleogene strata from the entire Northwest Pacific. They have apparently been transformed from the original aragonitic composition to calcite, which has resulted in very dark, nearly black objects, often with a strong color chagrin, and a certain degree of surface rugosity. Only a certain proportion of the otoliths is therefore well enough preserved for an identification at species level and an even smaller fraction is suitable for photographic documentation. We have therefore figured many specimens as drawings and only the best ones as photographs.

In any case, the otolith assemblage from the Kishima Formation represents a remarkable extension of our knowledge in time and space. It is particularly characterized by an abundance of gobioid otoliths, a fish group, which otherwise has rarely been reported in pre-Miocene rocks. Fossil records in Europe begin with late Oligocene butid otoliths (for example Reichenbacher & Uhlig 2002; Gierl et al. 2013) and a few not specifically identified gobioid otoliths from the early and late Oligocene (Sturbaut 1984; Schwarzahns 1994). A possible early record is a species left in open generic nomenclature and described as “*Gobiida*”

*vetusta* by Nolf & Stringer (2003) from the late Eocene of the USA. Reports from the early and middle Eocene of India by Bajpai & Kapur (2004) show a very plesiomorphic morphological pattern of undefined systematic position within or outside of the Gobioidei proper (see discussion in Gierl et al. 2013).

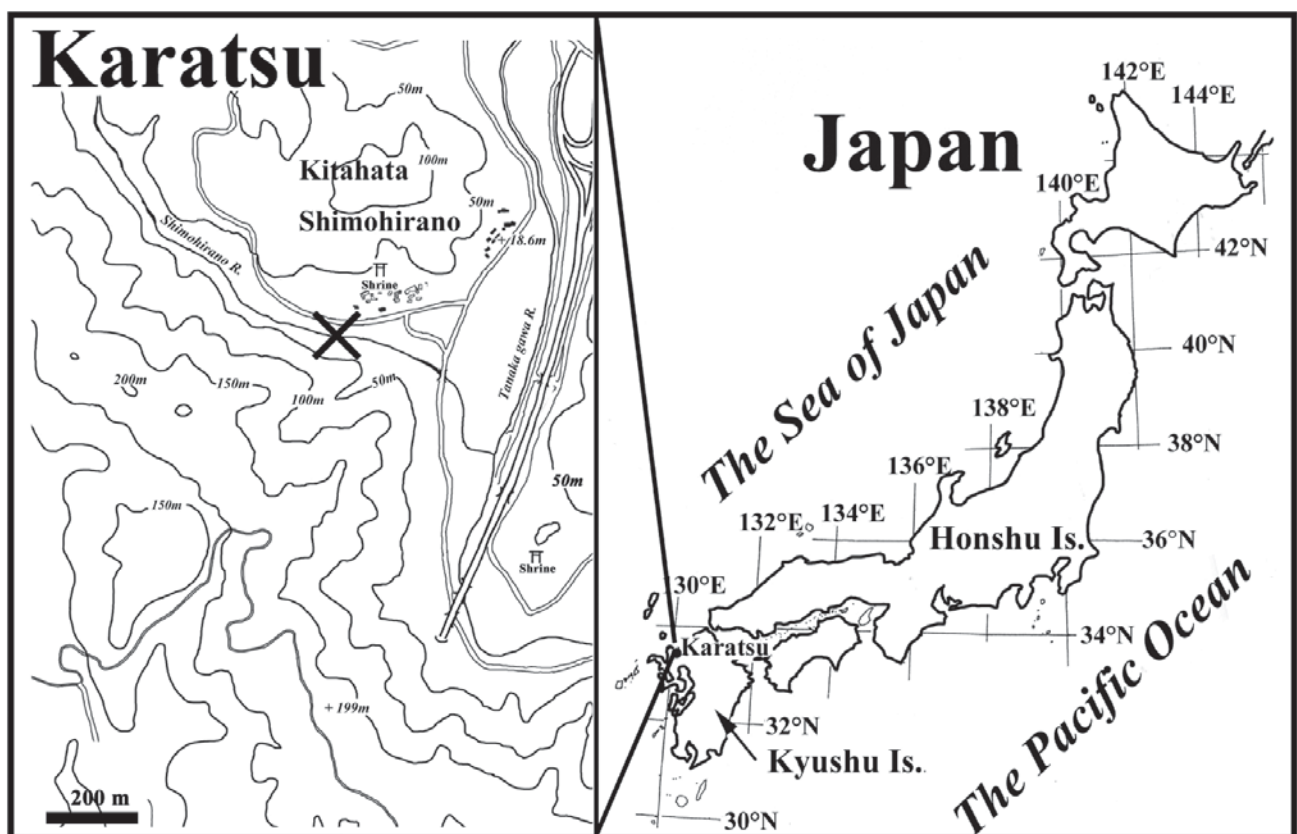
Other common faunal elements from the Kishima Formation refer to congrid eels, beryciforms of a variety of morphologies including an extinct representative of uncertain relationships, a plesiomorphic heterosulcoid otolith interpreted as a scorpaenid and a soleid flatfish. Percoid representatives are very rare (a single unidentifiable carangid record), which is in marked contrast to time equivalent otolith assemblages from Europe or New Zealand (Schwarzahns 1980; Nolf 2013). A total of 13 otolith-based taxa have been identified, 11 of them representing new species, and mostly indicative of a shallow, warm marine environment. We believe that this association shows the potential of fossil fish data yet to be expected in the fossil record of eastern Asia.

## 2. Geological setting, material, and methods

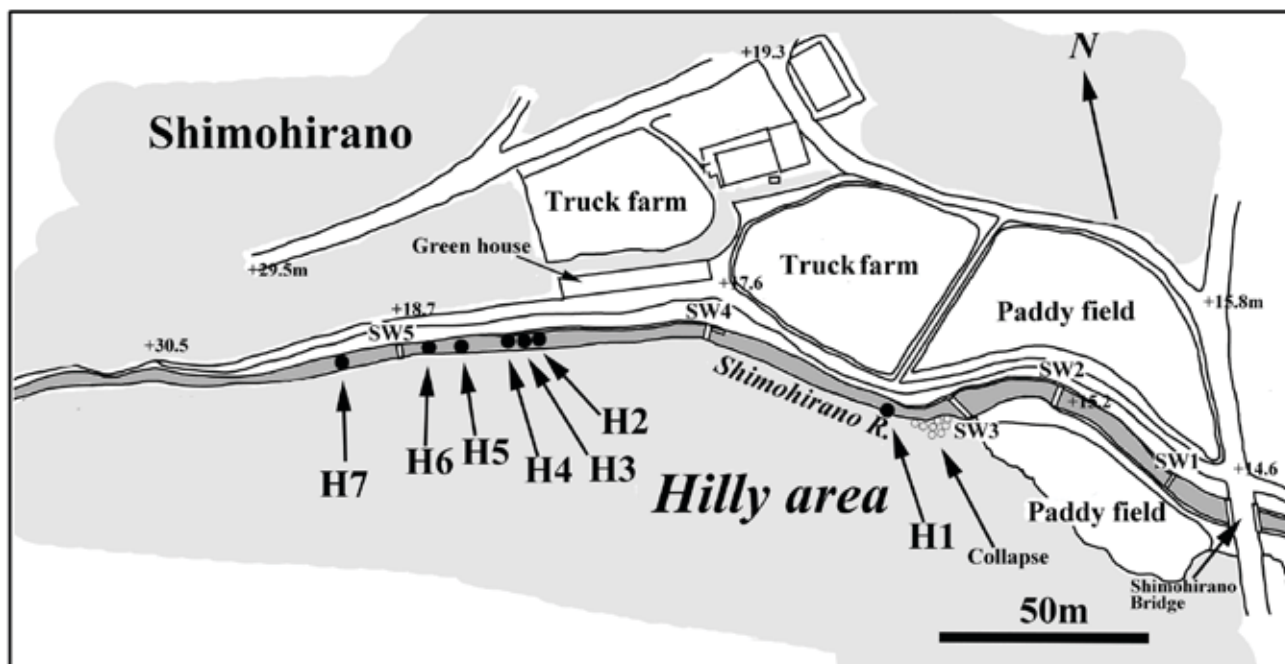
### 2.1 Geological setting

#### 2.1.1 Regional geography

The otoliths were collected in the Shimohirano area of Kitahata, southwest of Karatsu City from out-



Textfigure 1: Location map of Karatsu City, Saga Prefecture; x = area with otolith sampling locations.



**Textfigure 2:** Detailed sketch with otolith sampling locations along the Shimohirano River, Karatsu City.

crops at the riverbed where the Shimohirano River cuts through a low-lying hillside relief at  $33^{\circ}22'50''$  N and  $129^{\circ}55'41''$  E (Loc.11 in Aoki 2008) (Textfigs 1–3). Both river banks are protected by a concrete wall for shore protection. The strata are in nearly horizontal position, though dipping at angle of about two degrees westwards upstream.

### 2.1.2 Otolith sampling locations

Sampling location H1 is 114 m downstream from SW5 (the fifth small concrete weir from the Shimohirano bridge) or 40 m from SW4, and represents the easternmost location. The sediments are composed of a gray coarse-grained sandstone with small nodules, small mollusks such as *Nucula (Ennucula) karatsuensis* Nagao and very few otolith of the gobioid *Ortugobius cascus* n. sp. Location H2 is about 29 m downstream from SW5, and very close to both H3 and H4 locations within 1–2 meters. The otolith bearing rocks from H2 to H4 are composed of the exfoliated sandy mudstone, containing a high proportion of angulated quartz grains, some muscovite and biotite flakes, and minor volcanic glass fragments and pyroxene grains of sizes between 0.1mm and 0.01mm. Locations H5 and H6, are at a distance of 7m and 14m from SW5 respectively. They are the richest with fossils with abundant mollusks and otoliths. Location H7 finally is the only upstream location from SW5 for about 14.4 m. Its black muddy siltstone has yielded only a single otolith specimen of *Ortugobius cascus* n. sp., and small mollusks of *Nucula (Ennucula) karatsuensis* Nagao. Sporadically, these sediments bear ellipsoid nodules of sizes from 1.3 to 2.4 cm containing fossil crabs (*Collinsius simplex* Karasawa).

All horizons sampled for otoliths are gently dipping at an angle of two degrees towards upstream (Aoki 2008). With this angle, the total thickness of beds from location H1 to H7 along a horizontal exposure of 128 m is calculated at 4.5 m total thickness.

### 2.1.3 Stratigraphy

The otoliths studied here were collected from the upper Eocene to lower Oligocene Kishima Formation (Nagao 1972) of the Kishima Group (Matsushita 1949; Nishida et al. 2008) (Textfig. 3)

The total thickness of the Kishima Group is about 1000 meters. The Kishima Group is composed of the Kishima and Karatsu Formations in the Saga Prefecture (Mizuno 1963) (Textfig. 4). The Kishima Formation overlies the upper Eocene Ouchi Group and consists of sandy mudstone, mudstone and sandstone with a thickness of 110–130 m within the Kitahata area of Karatsu City (Nishida et al. 2008). The formation is exposed at the Mizunomotoyama, Yamahiko, Shimohirano and Naribuchi locations (see Nishida et al. 2008) and yields shallow-marine mollusks, decapods, ostracodes, calcareous nanofossils and chondrichthyan teeth (see below). The silty sandstone-beds of the upper part of the Kishima Formation are exposed on both sides of the Yamahiko Fault running more or less along the Shimohirano River valley. The otolith bearing horizons occur along the northeast part of the fault (Nishida et al. 2008). The sediments of the Kishima Formation seem to have been deposited under an inner-shelf to outer-shelf environment as interpreted from mollusks, decapods and ostracods (Inoue 1972; Karasawa 1993; Yamaguchi et al. 2006). The

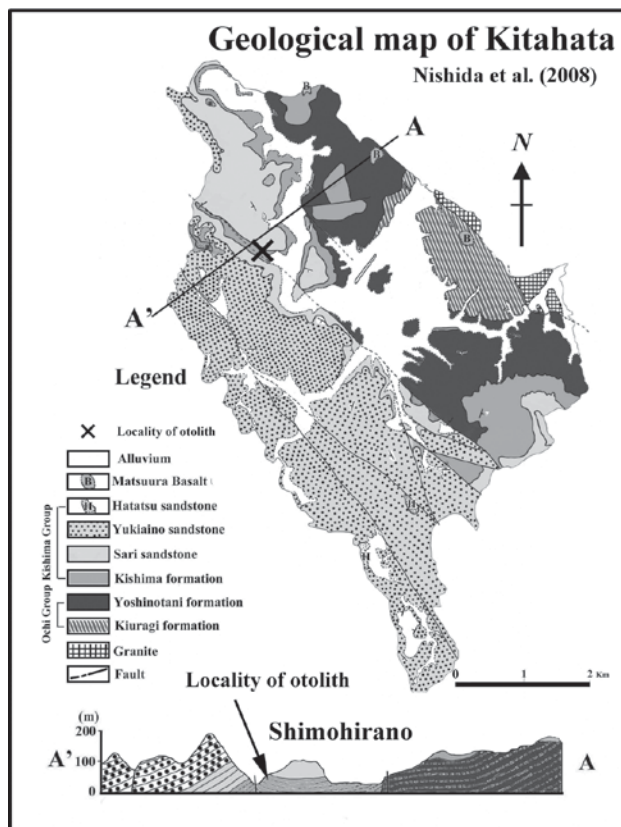


otolith-bearing horizons are in the uppermost part of the Kishima Formation. Okada (1992) showed that the geologic age of the uppermost part of the Kishima Formation is the earliest Early Oligocene (CP16a of Okada and Bukry 1980) on the basis of the calcareous nannofossils. The dating of ostracods from the Kishima Formation of Karatsu (Yamaguchi et al. 2006) corroborate Okada's data. Additionally, Zircon-based fission-track age dating gave an age of  $33.9 \pm 3.3$  Mya (Early Oligocene, planktonic foraminifers biozone P18) from a pyroclastic rock (rhyolitic tuff) obtained from the Sari Sandstone of the Karatsu Formation (Textfig. 4) (Miyachi & Sakai 1991).

#### 2.1.4 Paleontology except fish otoliths

Previously, 27 species of mollusks have been described from these rocks and were considered typical for the Oligocene Kishima Formation (Inoue 1972; Aoki 2008), and were correlated to the "Arita fossil zone (Upper *Pecten sakitoensis* Zone)" of Nagao (1927, 1928a, 1928b).

The sandy mudstone beds are brown in color and bear many mollusks following Inoue (1972) and Aoki (2008): 12 species of pelecypods: *Portlandia* sp., *Acira (Truncacila) nagaoi*, *Nucula (Ennucula) karatsuensis*, *N. (Lamellinucula) mazena*, *Chlamys (Mimachlamys) aff. sakitoensis*, *Crassatellites (Eucrassatella) matsuraensis*, *Venericardia (Ventricardia) yoshidai*, *Fulvia kishimaensis*, *Callista matsuraensis*, *Cyclina compressa*, *Pitar* sp., *Angulus (Tellinids) maximus*; and 15 species in gastropods: *Turitella karatsuensis*,



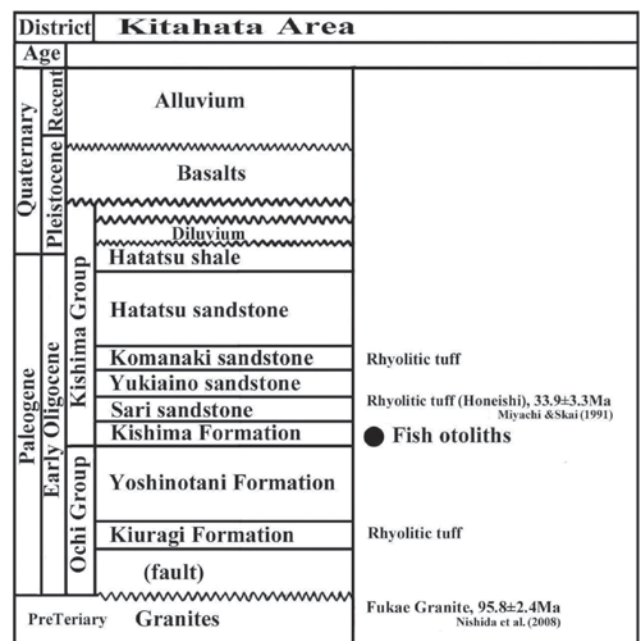
Textfigure 3: Geological map of Kitahata (Nishida et al., 2008).

*Mammilla insignis*, *Ancilla (Turrancilla) matsushitai*, *Gemmula (Hemipleurotoma) kishimaensis*, *Ampullina nagaoi*, *Makiyamaiakurodae*, *M. aritaensis*, *Siphonalia? Nipponiva*, *Antalis ashiyaensis*, *Calypteraea* sp., *Pseudolivia japonica*, *Volutoospina japonica*, *Clathrus submaculosus*, *Eopheurotoma? aff. higoensis*, and *Fulgoraria (Psephaea) sp.*. Later, Ando (2011) added *Limacina conica*, *L. hospes*, *L. karasawai*, *Creseis kishimaensis*. Other fossils recorded include decapods (Karasawa 1993; Karasawa & Fudouji 2000), ostracods (Yamaguchi et al. 2006) and calcareous nanofossils (Okada 1992).

So far, no remains of teleosts had been described, but there are some records of chondrichthyes teeth such as *Isurus hastalis*, *Odontaspis* sp., *Rhinoptera* sp., *Carcharhinus* sp., and *Hexanchus* sp. (Aoki 2008).

#### 2.2 Material and methods

The otolith-material described here was obtained from sediment samples that were collected during several field trips by the second author from a variety of outcrop locations along the Shimohirano River valley as sketched in Textfig. 2. About ten kilogram of rock sample was dug out from exposed beds at each locality. At the laboratory, the rock samples were dried in open air, which was found to be the best method to prepare for further processing by sieving and screening in water. Otoliths were primarily found in the residue of the 0.7 mm mesh and were picked under a stereomicroscope. Additional material (coll. Nishimoto) was collected by the late Hiroyuki Nishimoto and was catalogued at the Mizunami Fossil Museum under the reference MFM 030207.



Textfigure 4: Lithostratigraphic section of the Eocene / Oligocene formations of the Kitahata area based on data of from Okada & Burkry (1980), Nagao (1972), Mizuno (1964) and Nishida et al. (2008).

The otoliths are deposited in the collection of the Mizunami Fossil Museum, under the collection registration MFM 207001 to 207011 (holotypes) and MFM207102 to 207162 (paratypes and non-types). The terminology for the morphological description of the 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 = OCL; cauda length = CCL; sulcus length = SuL. 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.

### 3. Results

#### 3.1 Systematics

Remarks: Fossil skeletons of teleost fishes from the Paleogene are mostly referred to extinct genera (see for instance Bannikov 2010), while Paleogene otoliths are often associated with extant genera. We believe that this apparent discrepancy is mainly due to two effects. Firstly, fish skeletons offer many more characters for diagnoses than otoliths, which makes it easier for paleo-ichthyologists dealing with skeletons to recognize diagnostic differences at higher systematic levels; and, secondly, otolith paleontologists tend to be very conservative when it comes to the genus level mainly to avoid establishment of excessive otolith-based fossil genera or alternatively to avoid usage of open generic nomenclature. In the case of the early Oligocene otoliths from Japan described in the following we have therefore restricted ourselves to establish new fossil otolith-based genera only in those cases, where sufficient distinctive characters are identified for a differential diagnosis and in all other cases extant genus names are used in a broad, *sensu lato* sense, at times associated with a '?' to indicate the tentative nature of the generic assignment. The classification of the systematic part follows Nelson (2006).

Class Osteichthyes Huxley, 1880  
Subclass Actinopterygii Klein, 1885  
Division Teleostei Müller, 1846  
Order Albuliformes Jordan, 1923  
Suborder Albuloidi Jordan, 1923  
Family Pterothrissidae Gill, 1893

Genus *Pterothrissus* Hilgendorf, 1877

*Pterothrissus?* sp.  
Pl. 1, Figs 1, 2

Material. Two poorly preserved, eroded specimens (locations H4 and H6), MFM 207102–207103.

Discussion. Pterothrissid otoliths are widespread, although rarely common, in nearly all otolith bearing strata of Paleogene and late Cretaceous age. The specimens described here from the Early Oligocene of Japan are readily recognized by their very short ostium in combination with a rather elongate shape, a distinctly convex inner face and a flat outer face. They certainly represent an undescribed species and possibly an undescribed genus, but in the light of the poor preservation of the only specimens available we have refrained from such formal action.

Order Anguilliformes Regan, 1909  
Suborder Congroidei Nelson, 1984  
Family Congridae Kaup, 1856

Genus *Rhynchoconger* Jordan & Hubbs, 1925

*Rhynchoconger placidus* n. sp.  
Pl. 1, Figs 3–9; Pl. 7, Figs 1–3

Etymology. From *placidus* (Latin) = calm, gentle, referring to the regular outline of the otolith.

Holotype. MFM 207001 (Pl. 1, Fig. 5, Pl. 7, Fig. 2); Karatsu, coll. Nishimoto; Kishima FM, early Oligocene.

Paratypes. 6 specimens, MFM 207104–207109; Karatsu, coll. Nishimoto and locations H4 and H5; Kishima FM.

Additional material. 6 specimens, Karatsu, locations H4, H5 and H6.

Diagnosis. OL:OH = 1.5–1.65, increasing with size; OH:OT about 2.5. Inner face distinctly convex. Anterior tip rounded, posterior tip pointed, sometimes expanded. Sulcus anteriorly widened with broad ostial channel opening dorsally. Sulcus inclination 5–10°. Dorsal depression distinct; no or feeble ventral furrow close to ventral rim of otolith.

Description. Massive, robust otoliths up to 5.5 mm length (holotype 5.0 mm). Anterior moderately rounded; posterior tip moderately pointed, sometimes somewhat expanded with dorsal concavity as in the holotype. Dorsal rim highest just in front of middle, regularly curved without prominent angles; ventral rim gently curving deepest in front of middle, smooth.

Inner face distinctly convex and rather smooth. Sulcus moderately long, slightly shifted towards anterior and inclined at about 5–10° against horizontal axis of otolith. OL:SuL = 1.6–1.7. Sulcus moderately wide and moderately deep, with somewhat undulating lower margin and rounded posterior tip; anteriorly pointed and terminating at moderate distance from anterior tip of otolith. Ostial channel leading up-

wards at right angle from sulcus at about 1/3 from its anterior tip, shallow, sometimes indistinct, wide, but often fading towards dorsal rim. Dorsal depression small, distinct; ventral furrow absent or faint and close to ventral rim of otolith. Outer face as convex as inner face, smooth.

Discussion. Congroid otoliths are common in many Paleogene and Miocene shallow water sediments of the world. The otoliths described here from Karatsu are recognizable as *Rhynchoconger* by the deep dorsal depression and the moderately deep sulcus with its regular shape, the anterior closure and the presence of a long ostial channel. Similar otoliths of *Rhynchoconger* have been described from the Oligocene of Europe (*R. fallax* (Koken, 1891)), the US Gulf Coast (*R. sanctus* (Frizzell & Lamber, 1962)) and the early Miocene of New Zealand (*R. grantmackiei* (Grenfell, 1984)). *Rhynchoconger fallax* is more compressed (OL:OH = 1.4–1.5 vs 1.5–1.65) and shows an anteriorly reduced ostium terminating further from the anterior tip of the otolith than in *R. placidus*, which is also expressed in the higher ratio OL:SuL (2.0–2.2 vs 1.6–1.7). *Rhynchoconger sanctus* is similar in proportions (OL:OH = 1.5–1.6), but shows a much more strongly inclined sulcus (12–15° vs 5–10°), a higher ratio OL:SuL (1.9–2.0 vs 1.6–1.7) and a flat outer face resulting in a thinner appearance. *Rhynchoconger grantmackiei* finally is similar in proportions and thickness to *R. placidus* but differs in the more triangular shape of the dorsal rim and the nearly horizontally oriented sulcus. Earlier species of the genus such as *R. eocenicus* (Shephard, 1916) (see Nolf 2013) or *R. donzacquensis* (Nolf, 1988) are more compressed and show a very regular dorsal rim. Younger species from the Miocene are either more compressed like *R. pantanelii* (Bassoli & Schubert, 1906) from Europe (see Nolf 2013), or show a triangular dorsal rim and a horizontal sulcus like *R. regularis* (Stinton, 1958) from Australia (see Schwarzhans 1985). We conclude that the genus *Rhynchoconger* had a worldwide occurrence in warm shallow seas already in late Paleogene, much like today, and therewith represents a well established, long ranging phylogenetic lineage within the family.

*Rhynchoconger subtilis* n. sp.  
Pl. 1, Figs 10–14; Pl. 7, Figs 4–6

Etymology. From *subtilis* (Latin) = subtle, slender referring to the slender shape of the otolith.

Holotype. MFM207002 (Pl. 1, Fig. 10, Pl. 7, Fig. 4); Karatsu, location H5; Kishima FM, early Oligocene.

Paratypes. 8 specimens, MFM 207110–207117; Karatsu, coll. Nishimoto and location H5; Kishima FM, early Oligocene.

Additional material. 25 specimens, Karatsu, coll. Nishimoto and locations H4, H5 and H6.

Diagnosis. OL:OH = 1.75–1.8; OH:OT about 2.5. Inner face distinctly convex. Anterior and posterior tips pointed. Sulcus anteriorly widened with narrow ostial channel tapering towards dorsal opening. Sulcus inclination 4–7°. Dorsal depression distinct; no or feeble ventral furrow close to ventral rim of otolith.

Description. Robust otoliths up to 6.65 mm length (holotype). Anterior tip pointed to moderately rounded; posterior tip likewise but somewhat less pointed. Dorsal rim highest just in front of middle, somewhat undulating, with broad, obtuse postdorsal angle; ventral rim gently curving, deepest in front of middle, smooth.

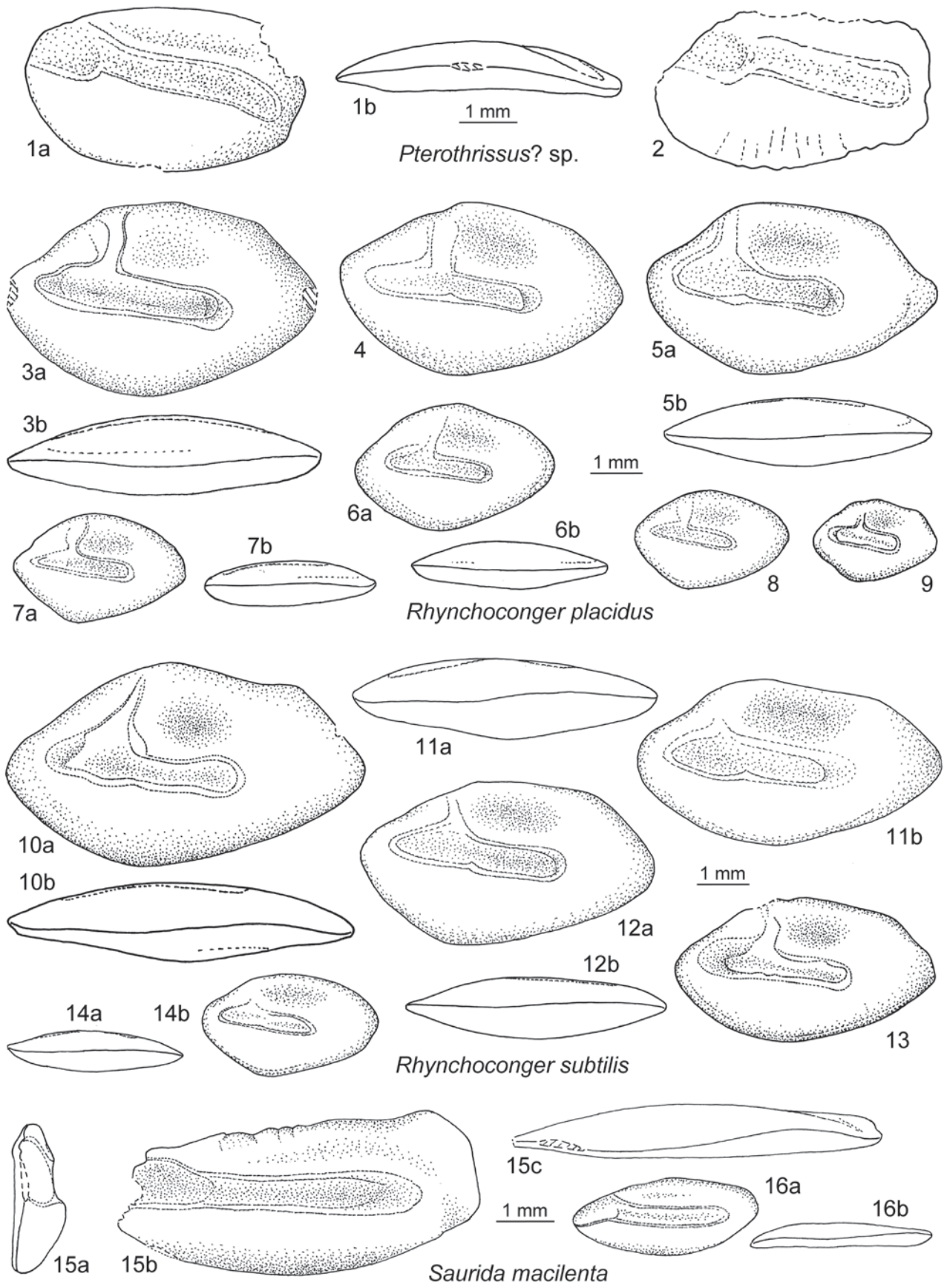
Inner face distinctly convex and rather smooth. Sulcus moderately short, slightly shifted towards anterior and inclined at about 4–7° against horizontal axis of otolith. OL:SuL = 1.6–1.8. Sulcus moderately wide and moderately deep, with somewhat undulating lower margin and rounded posterior tip; anteriorly pointed and terminating at moderate distance from anterior tip of otolith. Colliculum sometimes reduced anteriorly. Ostial channel leading upwards from area at about 1/3 from tip of sulcus, shallow, often indistinct, narrowing, tapering and fading towards dorsal rim. Dorsal depression small, distinct; ventral furrow absent or faint and close to ventral rim of otolith. Outer face slightly less convex than inner face, smooth.

Discussion. *Rhynchoconger subtilis* is distinguished from the co-occurring *R. placidus* (and the other fossil species mentioned above) by the more slender shape resulting in a higher ratio OL:OH (1.75–1.8 vs 1.5–1.65) and the narrow, dorsally tapering ostial channel. Small and poorly preserved specimens, however, are sometimes difficult to differentiate.

Order Aulopiformes Rosen, 1973  
Suborder Synodontoidei Gill, 1872

**Plate 1:** Otoliths from the Kishima Formation: Albuliformes, Anguilliformes, Aulopiformes. **(1,2)** *Pterothrissus?* sp. 1 (reversed): MFM 207102, location H6; 2 (reversed): MFM 207103, location H4. **(3–9)** *Rhynchoconger placidus* n. sp. 5: holotype, MFM 207001, coll. Nishimoto; 3, 4, 6–9: paratypes; 3 (reversed), 4 (reversed), MFM 207104–207105, location H6; 7 (reversed), MFM 207106, location H5; 6 (reversed), 8, MFM 207107–207108, coll. Nishimoto; 9 (reversed), MFM 207109, location H5. **(10–14)** *Rhynchoconger subtilis* n. sp. 10: holotype, MFM 207002, location H5; 11–14: paratypes; 11, MFM 207110, coll. Nishimoto; 12 (reversed), 14, MFM 207111–207112, location H5; 13 (reversed), MFM 207113, location H5. **(15, 16)** *Saurida macilenta* n. sp. 15: holotype, MFM 207003, location H5; 16 (reversed): paratype, MFM 207118, location H4.





Family Synodontidae Gill, 1861  
Genus *Saurida* Cuvier & Valenciennes, 1849

*Saurida macilenta* n. sp.  
Pl. 1, Figs 15, 16; Pl. 7, Fig. 7

Etymology. From *macilentus* (Latin) = skinny, lean, referring to the slender shape of the otolith.

Holotype. MFM 207003 (Pl. 1, Fig. 15, Pl. 7, Fig. 7); Karatsu, location H5; Kishima FM, early Oligocene.

Paratypes. 4 specimens, MFM 207116–20719; Karatsu, locations H4 and H5; Kishima FM, early Oligocene.

Additional material. 6 specimens, Karatsu, locations H4, H5 and H6.

Diagnosis. OL:OH = 2.4+. Otolith thin with flat outer and convex inner face. Dorsal rim flat, anteriorly inclined, with broad, massive postdorsal angle positioned far backwards creating a blunt posterior tip. Cauda straight, widened at tip.

Description. Thin, delicate, relatively large otoliths reaching at least 6.1 mm length (anteriorly damaged holotype). OH:OT = 2.7. Rostrum moderately long and moderately pointed in paratype (Pl. 1, Fig. 6), the only specimen with preserved rostrum. Dorsal rim shallow, anteriorly depressed, inclined towards anterior, slightly undulating, with massive and broad postdorsal angle situated far backwards on dorsal rim close to posterior tip of otolith. Posterior rim dorsally shifted, nearly vertically cut, blunt. Ventral rim shallow, regularly curving, relatively smooth, deepest at about its middle.

Inner face mildly convex, particularly visible in vertical direction. Sulcus wide, long, somewhat deepened, positioned slightly suprmedian and inclined backwards. Ostium and cauda poorly distinguished with short ostium only slightly widened dorsally. Cauda straight, long with rounded and somewhat widened tip. Colliculi poorly marked; caudal colliculum often terminating prior to caudal tip. Dorsal depression narrow, indistinct; ventral field most strongly convex portion of inner face, without ventral furrow. Outer face nearly flat, smooth.

Discussion. Only few specimens are well preserved of this rather rare and delicate otolith. The holotype is a large, diagnostically fully mature specimen, which however lacks the anterior part of the rostrum. All other specimens are smaller and show some sort of erosion. The figured paratype is the most comple-

te specimen of the series, but considerably smaller than the holotype (OL = 3.1 vs 6.1 mm length).

*Saurida macilenta* is recognized as a typical species of the genus characterized by the otolith and sulcus shape, the latter with the straight, long cauda and the narrow ostium and the thin appearance. Fossil *Saurida* otoliths are well known from various Eocene and older deposits, but they become less common in the regions studied during Oligocene and Neogene. *Saurida recta* (Frost, 1933) (see Nolf 2013 for figures) from the European Eocene and *S. germanica* (Weiler, 1942) (see Schwarzhans 2010 for figures) from the European Oligocene and Miocene are probably the most similar in general appearance, but both do not show the massive postdorsal angle and cut posterior rim of *S. macilenta*. *Saurida macilenta* differs further from *S. recta* in being more elongate (OL:OH = 2.4+ vs 2.1–2.2), while *S. germanica* is even more elongate (OL:OH = 2.5–3.0, distinctly increasing with size).

Order Beryciformes Regan, 1909  
Suborder Berycoidei Regan, 1909  
Family Berycidae Lowe, 1839

Genus †*Nishiberyx* n. gen.

Type species: *Nishiberyx nishimotoi* n. sp.

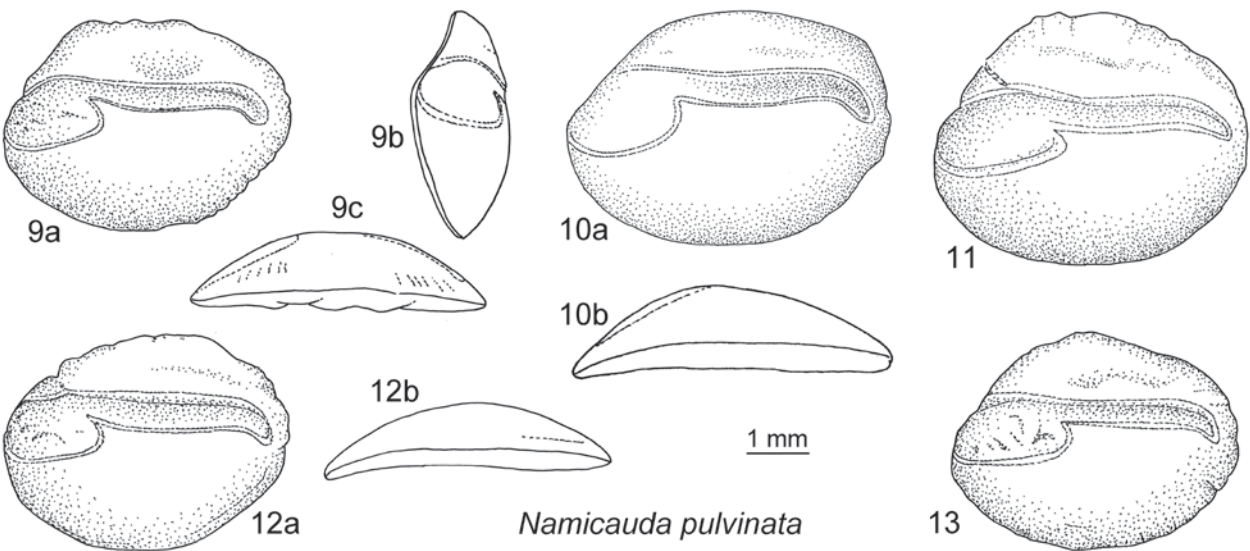
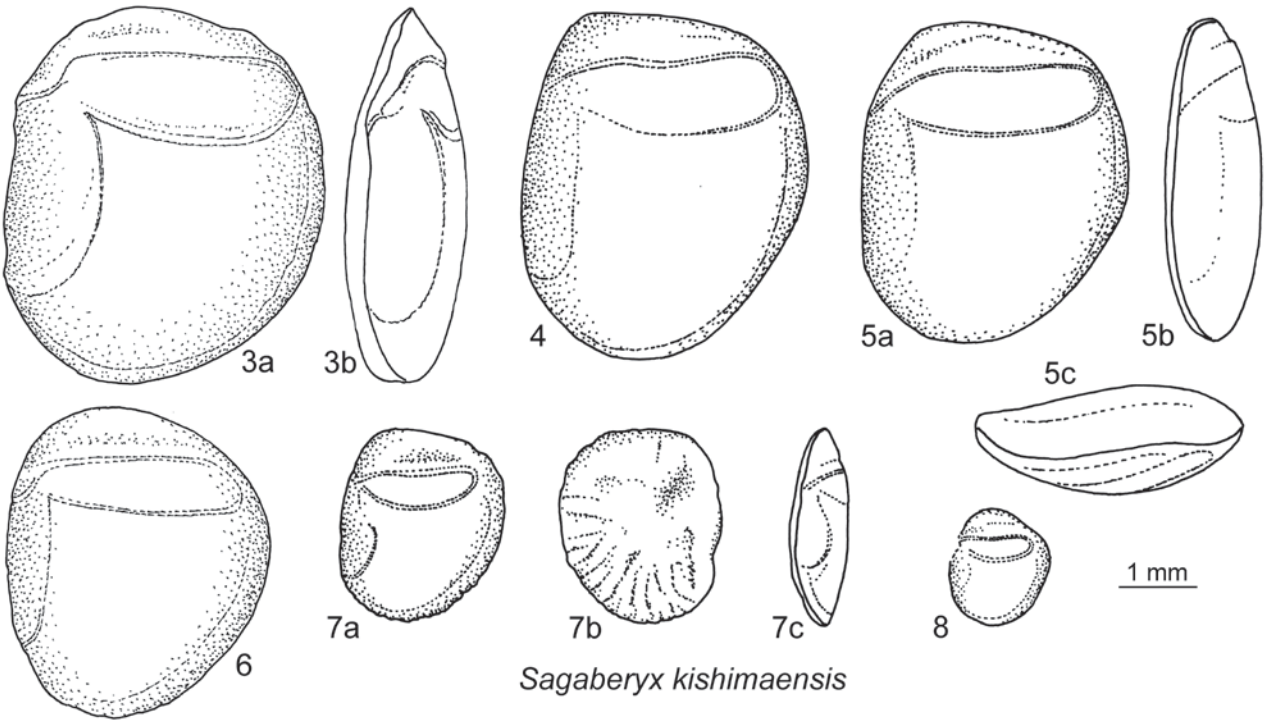
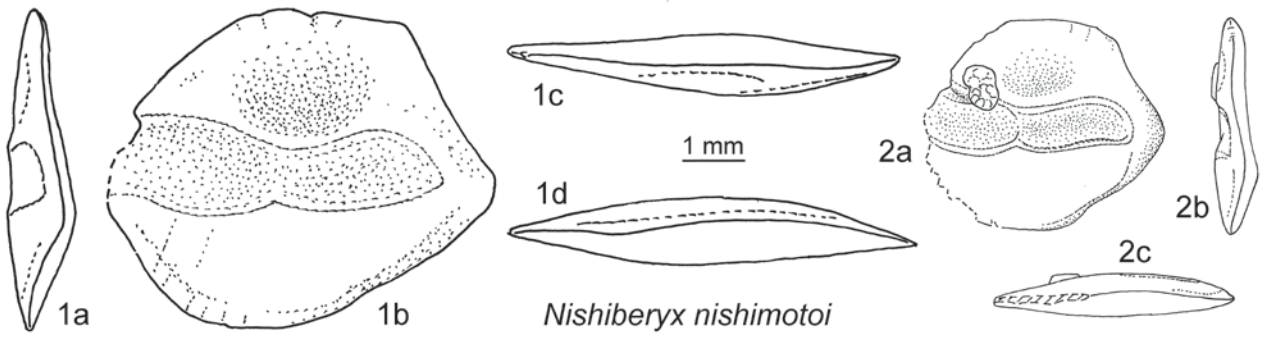
Ethymology. From *nishi* (Japanese) = west, referring to the occurrence in the West of Japan.

Diagnosis. A fossil otolith-based genus of the family Berycidae. Otoliths compressed (OL:OH = 1.2), thin (OH:OT = 5.0), with sharp rims. Anterior tip blunt, broadly rounded, posterior tip pointed, projecting. Inner face nearly flat with centrally positioned sulcus and wide dorsal depression. Ostium and cauda nearly equally long (CaL:OsL = 1.1) and ostium only slightly wider than cauda (OsH:CaH = 1.3) with lower margin of ostium being shallow and nearly flat and dorsal margin expanded. Caudal tip straight, ventrally tapering.

Discussion. *Nishiberyx* resembles otoliths of *Centroberyx*, an extant genus of Berycidae known by otoliths since Late Cretaceous. The main difference of both genera is the shape of the ostium, which is ventrally deepened and dorsally flat in *Centroberyx*, while in *Nishiberyx* it is dorsally more expanded than ventrally with the ventral ostium margin being nearly flat. *Nishiberyx* is yet another example of an extinct otolith-based berycoid genus documenting that while percoids were flourishing after the KT-boundary

**Plate 2:** Otoliths from the Kishima Formation: Beryciformes, Polymixiiformes. (1, 2) *Nishiberyx nishimotoi* n. gen., n. sp. 1 (reversed): holotype, MFM 207004, coll. Nishimoto; 2 paratype, MFM 207122, location H5. (3–8) *Sagaberyx kishimaensis* n. gen., n. sp. 3 (reversed): holotype, MFM 207005, location H5; 4–8: paratypes; 4, 5, MFM 207124–207125 location H5; 6, MFM 207126, coll. Nishimoto; 7, MFM 207127, location H5; 8, MFM 207128, location H3. (9–13) *Namicauda pulvinata* n. gen., n. sp. 9: holotype, MFM 207006, location H5; 10–13: paratypes; 10 (reversed), MFM 207132, location 5; 11, MFM 207133, location H5; 12, MFM 208134, location H5; 13 (reversed), MFM 207135, coll. Nishimoto.





mass-extinction event (Patterson 1993; Friedman 2010; Schwarzhans 2012), the demise of berycoids did not occur suddenly and still showed a distinctly higher diversity and abundance in shallow water Paleogene environments than today.

Species: A single species, *N. nishimotoi*, from the early Oligocene Kishima FM of Kyushu, Japan.

*Nishiberyx nishimotoi* n. sp.  
Pl. 2, Figs 1, 2; Pl. 7, Fig. 8

Etymology. In memory to Hiroyuki Nishimoto (Toki, Japan), who was the first to collect fossil fish remains from the Kishima FM.

Holotype. MFM207004 (Pl. 2, Fig. 1, Pl. 7, Fig. 8); Karatsu, coll. Nishimoto; Kishima FM, early Oligocene.

Paratypes. 2 specimens, MFM 207122–207123; Karatsu, locations H4 and H5; Kishima FM, early Oligocene.

Diagnosis. Same as for genus (monospecific genus).

Description. Compressed, thin otoliths up to at least 6.8 mm length (holotype). Dorsal rim high, with pronounced pre- and postdorsal angles at about 1/3 from anterior and posterior tips. Midsection of dorsal rim nearly straight, horizontal, anterior and posterior sections inclined at 50–60°, posterior section slightly concave. Anterior tip blunt, broadly rounded, thin and slightly damaged in all specimens; posterior tip pointed; both tips located along central axis of otolith. Ventral rim about as deep as dorsal rim, but more regularly curved, without prominent angles. Rims thin and smooth except dorsal rim sometimes slightly crenulated.

Inner face very slightly convex, almost flat. Sulcus positioned along central, horizontal axis. Ostium slightly wider and shorter than cauda, anteriorly opened, ventrally flat, dorsally more expanded at its midsection. Cauda straight, slightly turned upwards towards its tip; caudal tip ventrally tapering and terminating close to posterior tip of otolith. Dorsal depression wide, moderately deep and ventrally well marked by crista superior. Ventral furrow running moderately close to ventral rim of otolith. Outer face very slightly convex and nearly smooth except for few radial furrows on dorsal field.

Family indet.

Genus †*Sagaberyx* n. gen.

Type species: *Sagaberyx kishimaensis* n. sp.

Etymology: Referring to the Saga Prefecture, Kyushu, Japan, the province of the type-location.

Diagnosis: A fossil otolith-based genus of unresolved familial relationship. Otoliths very high-bodied (OL:OH = 0.8–0.9) with deep and regularly curved ventral rim, blunt anterior and posterior rims and shallow dorsal rim. Inner face strongly convex and very smooth, so much that the outline of the sulcus is barely visible. Sulcus far supramedian positioned, with straight, broad cauda running close to dorsal rim and terminating near posterior rim. Ostium short, very shallow, often poorly distinguished from inner face, ventrally much widened along almost entire anterior rim, but dorsally not widened from junction with cauda. Colliculi only marked in cauda. Wide ventral field with faint ventral furrow very close to ventral rim of otolith. Outer face flat.

Discussion: This peculiar otolith with its highly specialized morphology does not resemble much any of the known Recent otoliths. One could even be tempted to consider this otolith to be a lapillus, when rotating it about 90° clockwise, but the presence of an ostium, although not always clearly visible, and the presence of a faint ventral furrow contradict such interpretation. However, we consider the delicate nature of the morphology of the inner face partly owing to the recrystallization of the otoliths which has some coarsening effect on the surface of the otolith. To the best of our knowledge the only reasonably comparable otoliths are found in certain other extinct putative beryciform otoliths such as *Argyroberyx dentatus* (Liebus, 1927), *Beaurya medialis* Schwarzhans, 2010, *Sillaginocentrus alienus* Schwarzhans, 2010 and *Traubiella anagiformis* Schwarzhans, 2010, all from the late Cretaceous of Austria and Germany. We assume that *Sagaberyx* represents an extinct lineage at familial or higher level, which however should not be defined unless fish skeletons with otoliths in situ have been found.

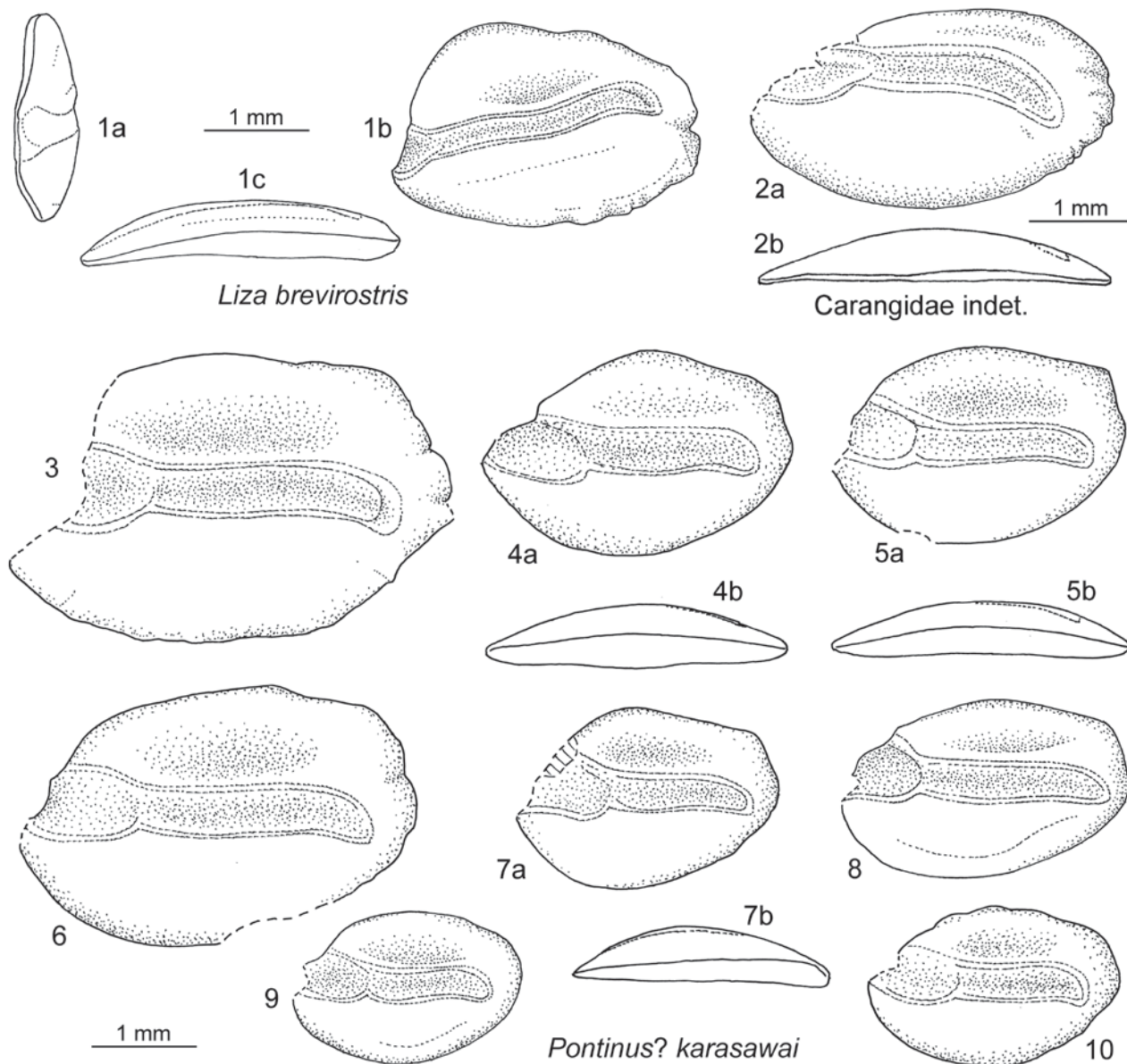
Species: A single species, *S. kishimaensis*, from the early Oligocene Kishima FM of Kyushu, Japan.

*Sagaberyx kishimaensis* n. sp.  
Pl. 2, Figs 3–8; Pl. 7, Figs 9–11

Etymology. Referring to the Kishima Formation from which the otoliths were obtained.

Holotype. MFM 207005 (Pl. 3, Fig. 3, Pl. 7, Fig. 10); Karatsu, location H5; Kishima FM, early Oligocene.

Paratypes. 8 specimens, MFM 207124–207131; Karatsu, coll. Nishimoto and locations H3 and H5; Kishima FM, early Oligocene.



**Plate 3:** Otoliths from the Kishima Formation: Mugiliformes, Perciformes, Scorpaeniformes. **(1)** *Liza brevirostris* n. sp. Holotype, MFM 207007, location H5. **(2)** Carangidae indet., MFM 207142, location H5. **(3–10)** *Pontinus? karasawai* n. sp. 4: holotype, MFM 207008, location H5; 3, 5–10: paratypes; 3 (reversed), 5, 6, MFM 207120, 207136–207137, location H5; 7 (reversed), 10 (reversed), MFM 207138–207139, location H5; 8, MFM 207140, location H5; 9, MFM 207141, location H6.

Additional material. 284 specimens, Karatsu, locations H3, H4, H5 and coll. Nishimoto.

Diagnosis. Same as for genus (monospecific genus).

Description. High-bodied, moderately thick, robust otoliths up to at least 3.65 mm length (holotype). OH:OT about 3.0. Dorsal rim shallow, highest close to anterior tip of otolith, without prominent angles. Anterior and posterior rims nearly vertical, blunt, anterior rim deepest at lower margin of ostium, posterior rim deepest at about its middle. Ventral rim very deep, regularly curved, without angles. All rims smooth, or ventral and posterior rims occasionally finely crenulated.

Inner face distinctly convex, very smooth. Sulcus very shallow with nearly rectangular development of ostium to cauda and with very eccentric position close to dorsal and anterior rims. Its cauda nearly straight, sometimes slightly turned upwards, terminating very close to postdorsal rim. Caudal colliculum sometimes visible. Ostium with very faint, often indiscernible outline along anterior rim of otolith and extending only downwards from junction with cauda. Ostium anteriorly open; no colliculum visible. Dorsal field very narrow, occasionally with very faint narrow depression or edge; ventral field very wide, smooth, with faint ventral furrow close to ventral and post-ventral rims of otolith. Outer face nearly flat, smooth or with few radial furrows on ventral field.



Order Polymixiiformes Patterson, 1964  
Family Polymixiidae Bleeker, 1859

Genus †*Namicauda* n. gen.

Type species: *Namicauda pulvinata* n. sp.

Ethymology: From nami (Japanese) = wave, in combination with the technical term cauda, referring to the oscillating shape of the cauda.

Diagnosis: A fossil otolith-based genus of the family Polymixiidae. Otoliths oval in shape, moderately elongate (OL:OH = 1.2–1.3), a strongly convex inner and flat to slightly concave outer face. Anterior rim regularly rounded including broad, only moderately projecting rostrum. Ostium only ventrally widened, distinctly shorter than cauda (CaL:OsL = 1.45–1.7). Cauda long, narrow, slightly oscillating, with slightly downward bent tip. Ostial and caudal colliculi not separated.

Discussion: *Namicauda* is readily recognized by the shape of the sulcus with the oscillating cauda and the only ventrally widened ostium, and by the continuous colliculum. It resembles otoliths of the extant genus *Polymixia*, but also certain percoids as found in the family Haemulidae. Haemulid otoliths usually have a much more strongly bent caudal tip, a dorsally and ventrally widened ostium and clearly separated ostial and caudal colliculi (see Smale et al. 1995; Lin & Chang 2012; Nolf 2013). Otoliths of *Polymixia* show a similarly shaped cauda and the division of ostial and caudal colliculi is somewhat variable and diffuse and the ostial colliculum is only slightly widened dorsally (see Smale et al. 1995). We consider here the similarity of polymixiid otoliths with certain percoid otoliths to probably be due to functional morphological analogy rather than true homology. Another similar looking otolith in general shape and shape of the sulcus has been described as *Sillaginocentrus alienus* Schwarzhans, 2010 from the Late Cretaceous of Bavaria, Germany, and was interpreted to represent an extinct holocentroid. This otolith-based genus, however, shows a completely flat sulcus at level with the rest of the inner face and therefore we again consider the apparent morphological similarity as non-indicative for a possible relationship. We conclude that *Namicauda* bears the most convincing morphological similarity with extant polymixiid otoliths, but consider its familial allocation as of tentative nature for the time being.

Species: A single species, *N. pulvinata*, from the early Oligocene Kishima FM of Kyushu, Japan.

*Namicauda pulvinata* n. sp.  
Pl. 2, Figs 9–13; Pl. 8, Figs 1, 2

Ethymology. From pulvinata (Latin) = pulvinate, convex, referring to regular convex inner face.

Holotype. MFM 207006 (Pl. 2, Fig. 9, Pl. 8, Fig. 1); Karatsu, location H4; Kishima FM, early Oligocene.

Paratypes. 4 specimens, MFM 207132–207135; Karatsu, coll. Nishimoto and locations H4 and H5; Kishima FM, early Oligocene.

Additional material. 9 specimens, Karatsu, locations H4, H5, H6 and coll. Nishimoto.

Diagnosis. Same as for genus (monospecific genus).

Description. Oval, moderately compressed, otoliths up to at least 5.5 mm length (holotype 4.4 mm). OH:OT = 2.7–3.3. Dorsal rim moderately high to shallow, regularly and gently curving, highest anterior of the middle, slightly undulating. Anterior tip regularly and broadly rounded, with short, blunt, perfectly rounded rostrum and without excisura or antirostrum; posterior tip similarly regularly rounded, but slightly shifted dorsally. Ventral rim much deeper than dorsal rim, very regularly curved, without angles, smooth or very finely crenulated. Rims thin and sharp.

Inner face strongly and very regularly convex. Sulcus distinctly suprmedian, anteriorly shallow, posteriorly slightly deepened. Ostium anteriorly opened, shorter and distinctly wider than cauda, widening almost entirely ventrally; dorsal margin of ostium bending downwards towards opening. Cauda narrow, slightly deepened, oscillating, its tip slightly turned downwards and terminating very close to posterior rim. Dorsal depression indistinct and very narrow, at some distance from dorsal margin of sulcus. No ventral furrow. Outer face flat to slightly concave, with a few vertical furrows and ridges crossing in midsection.

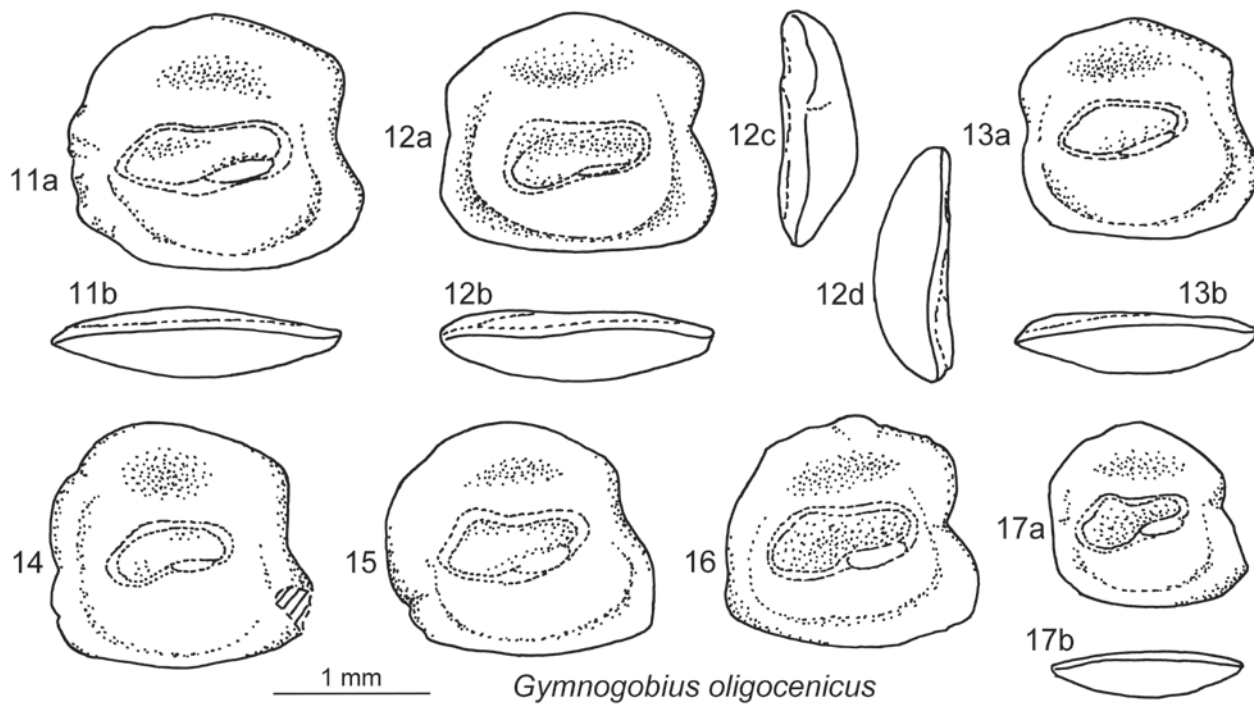
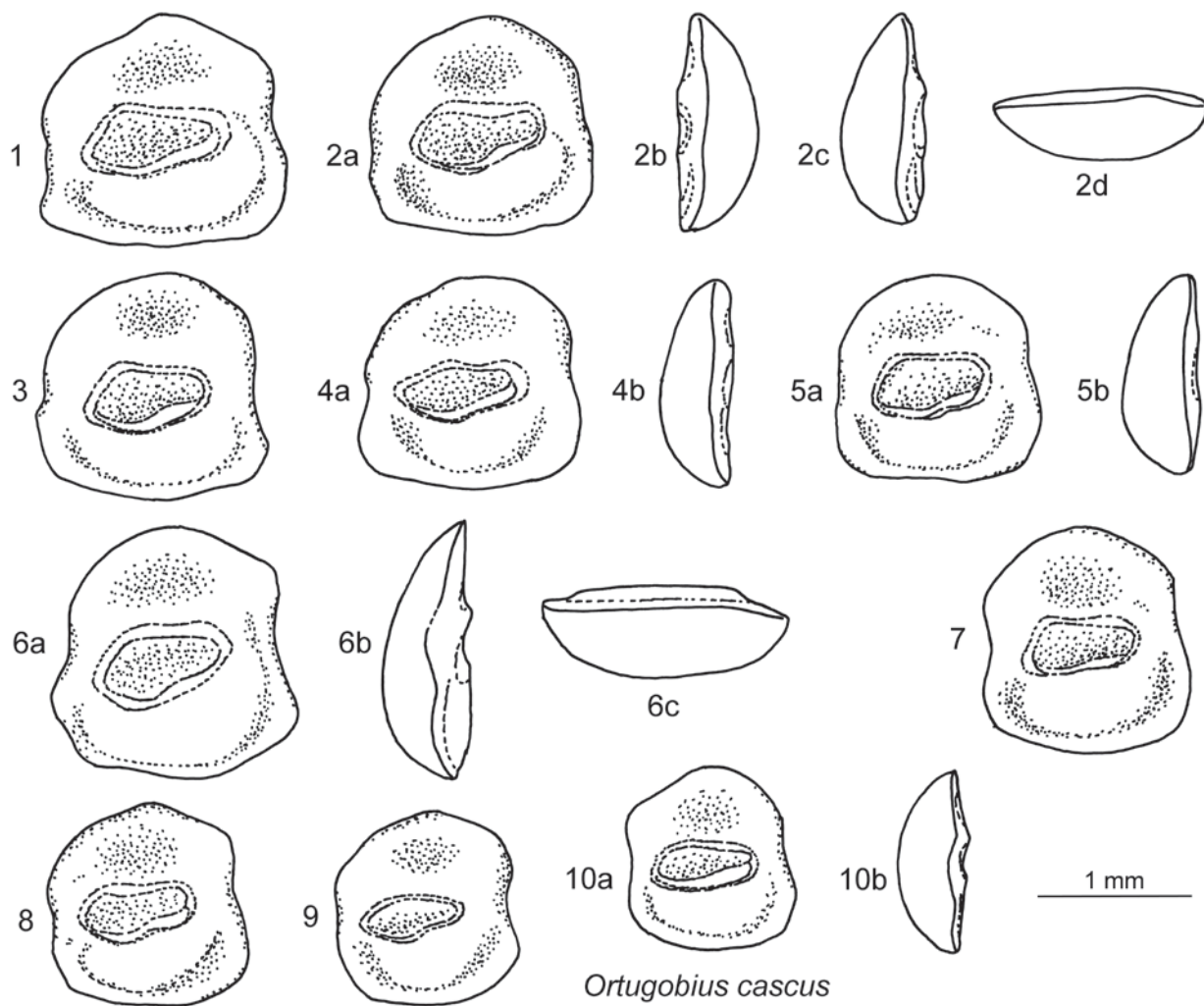
Order Mugiliformes Regan, 1909  
Family Mugilidae Risso, 1827

Genus *Liza* Jordan & Swain, 1884

*Liza brevis* n. sp.  
Pl. 3, Fig. 1; Pl. 8, Fig. 3

Ethymology. From brevis (Latin) = short combined with the technical term for the otolith rostrum, referring to the short rostrum of the species.

**Plate 4:** Otoliths from the Kishima Formation: Gobioidi. **(1–10)** *Ortugobius cascus* n. gen., n. sp. 2 (reversed): holotype, MFM 207009, location H5; 1, 3–10: paratypes; 1 (reversed), 5 (reversed), 6, 8, MFM 207143–207146, location H5; 3 (reversed), 4, 7 (reversed), 9, 10 (reversed), MFM 207147–207151, location H2. **(11–17)** *Gymnogobius oligocenicus* n. sp. 12 (reversed): holotype, MFM 207010, location H2; 11, 13–17: paratypes; 11 (reversed), 13 (reversed), 14, 15 (reversed), MFM 207152–207155, location H5; 16 (reversed), 17, MFM 207156–207157, location H5.



Holotype (and only specimen). MFM 207007 (Pl. 3, Fig. 1, Pl. 8, Fig. 3); Karatsu, location H5; Kishima FM, early Oligocene.

Diagnosis. OL:OH = 1.5. Rostrum very short, inferior. Dorsal rim with strong predorsal lobe. Sulcus strongly inclined anterior-ventrally. Ostium very short. Cauda with typical “wavy” shape; caudal tip only slightly bent downwards.

Description. A single, well preserved otolith of about 3 mm length. OH:OT = 3.7. Dorsal rim with massive, broad predorsal lobe located close to anterior rim; backwards slightly inclined and slightly undulating. Anterior rim steeply inclined downwards to very short, but pointed rostrum. Rostrum much inferior, close to ventral rim. Posterior rim broadly rounded, somewhat undulating. Ventral rim regularly curved, undulating, deepest at its middle.

Inner face markedly convex with narrow, moderately deep sulcus with short, narrow ostium and long cauda; CCL:OCL = 5.5. Sulcus strongly inclined anterior-ventrally at angle of about 20°. Cauda “wavy” with pointed, only slightly bent tip terminating moderately close to posterior rim of otolith. Dorsal depression small, only above central part of cauda; ventral furrow very indistinct, close to ventral rim of otolith. Outer face flat, nearly smooth.

Discussion. This is a typical mugilid otolith recognized by the shape and proportions and orientation of the sulcus. It is a rather compressed mugilid otolith, but also may not represent full grown size. Nevertheless, it is distinguished from other known Recent and fossil otoliths by the broad predorsal lobe, the very short rostrum and ostium and the very inferior position of the rostrum. Similarly compressed otoliths are found in the extant genera *Chelon* Röse, 1793, *Liza* and *Moolgarda* Whitley, 1945, particularly in subadult specimens (see Smale et al. 1995; Rivaton & Bourret 1999; Lombarte et al. 2006; Nolf et al. 2009; Lin & Chang 2012 for figures of representative Recent otoliths). In our view, the combination of a short rostrum and ostium and the broad predorsal lobe is best matched by otoliths of the genus *Liza*. Therefore, we have provisionally associated the species with the extant genus *Liza*, but we are aware that additional data in the future could be interpreted as representing a fossil genus.

Order Scorpaeniformes Garman, 1899  
Suborder Scorpaenoidei Garman, 1899  
Family Scorpaenidae Risso, 1827

Genus *Pontinus* Poey, 1860

*Pontinus?* *karasawai* n. sp.  
Pl. 3, Figs 3–10; Pl. 8, Figs 4–6

Etymology. In honor of Hiroaki Karasawa (Mizuna-

mi) in recognition of his contribution to the paleontology of the Cenozoic formations of Japan.

Holotype. MFM 207008 (Pl. 3, Fig. 4, Pl. 8, Fig. 4); Karatsu, location H5; Kishima FM, early Oligocene.

Paratypes. 7 specimens, MFM 207120, 207136–207141; Karatsu, locations H5 and H6; Kishima FM, early Oligocene.

Additional material. 56 specimens, Karatsu, locations H4, H5, H6 and coll. Nishimoto.

Diagnosis. Moderately elongate, regularly shaped otoliths. OL:OH = 1.5–1.6. Dorsal rim highest mid-dorsally, with broad postdorsal angle. Inner face convex in horizontal and nearly flat in vertical direction. Ostium short; CaL:OsL = 1.8–2.2; cauda nearly straight, with slightly bent, rounded tip. Wide dorsal depression.

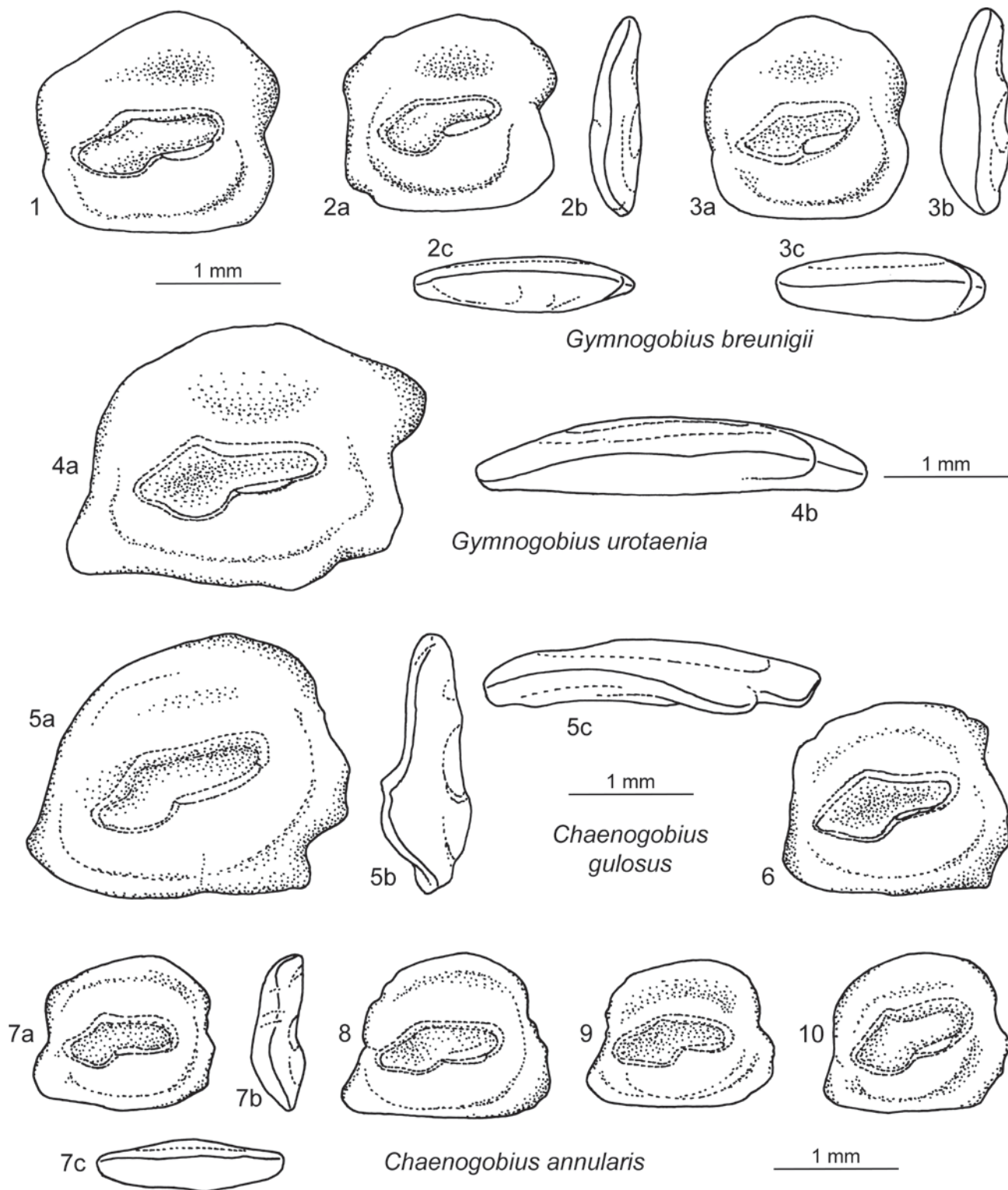
Description. Relatively small, moderately elongate and moderately thin otoliths up to about 4.5 mm length. However, only few specimens are well preserved, and the best one chosen as holotype is 2.9 mm long. Dorsal rim highest at its middle or slightly anterior, with broad, obtuse, rounded post-dorsal angle; ventral rim gently curved, deepest at its middle or slightly anterior. Rims smooth or slightly undulating. Anterior tip rarely well preserved, with angular, broad rostrum; no or minute excisura and antirostrum. Posterior tip massive, broad, somewhat dorsally pronounced.

Inner face slightly convex in horizontal direction, nearly flat in vertical direction. Sulcus long, slightly deepened and slightly suprmedian positioned. Ostium short, moderately wide, ventrally stronger than dorsally. Cauda long, narrow, nearly straight and slightly bent at its distal portion with rounded tip terminating very close to posterior rim of otolith. Colliculi clearly separated. Dorsal depression moderately distinct, large; ventral furrow indistinct or absent, not very close to ventral rim of otolith. Outer face flat, smooth.

Discussion. Scorpaenid otoliths are often rather indistinct due to their plesiomorphic morphologies. They are recognized by the short and small ostium in combination with a nearly straight cauda and an inner face which is only bent in the horizontal direction. We interpret the otoliths described here as representatives of such plesiomorphic scorpaenid morphologies, in this case resembling best those of the genus *Pontinus*. However, the generic allocation must be regarded as tentative due to the generalized appearance of the otoliths.

*Pontinus?* *karasawai* is amongst the most common species at Karatsu, after the two gobioid species (see below) and *Sagaberyx kishimaensis*. It resembles *Scorpaena osterodenensis* Schwarzhan-





**Plate 5:** Recent otoliths for comparison. (1–3) *Gymnogobius breunigii* (Steindachner, 1879). 1: NSMT P.97223, SL 50, Honshu; 2: NSMT P.105434, SL 44, Hokkaido; 3: NSMT P.97223, SL 39, Honshu. (4) *Gymnogobius urotaenia* (Hilgendorf, 1879). NSMT P.91061, SL 85, Hokkaido. (5, 6) *Chaenogobius gulosus* (Sauvage, 1882). 5: NSMT P.110299, SL 93, Sagami Bay; 6: NSMT P.109754, SL 73, Sagami Bay. (7–10) *Chaenogobius annularis* Gill, 1859. 7–9: NSMT P.110013, SL 44–49, Wahae-Jima; 10: BSKU 68803.

2007 from the Middle Eocene of the North Sea Basin but is less elongate (OL:OH = 1.5–1.6 vs 1.8–2.0) and does not show the shallow ventral margin of the ostium that is supposed to be the key diagnostic character for *S. osterodenensis*.

Order Perciformes Bleeker, 1859  
Suborder Percoidei Bleeker, 1859  
Family Carangidae Rafinesque, 1815

Genus indet.

## Carangidae indet.

Pl. 3, Fig. 2; 1 eroded specimen from location H5, MFM 207142.

Suborder Gobioidi Jordan & Evermann, 1896  
Family Gobiidae Cuvier, 1816

Genus *Ortugobius* n. gen.

Type species: *Ortugobius cascus* n. sp.

Etymology: A combination of *ortus* (Latin) = rise, and the name giving genus name *Gobius* referring to the early occurrence of the genus in respect to the known representatives of the family Gobiidae.

Diagnosis: A fossil otolith-based genus of the family Gobiidae with small, compact otoliths rarely exceeding 1 mm in diameter. OL:OH = 0.9–1.05. No or very weak preventral and postdorsal projections. Ventral rim nearly flat, longer than irregularly curved dorsal rim. Inner face flat, outer face markedly convex. Sulcus small, centrally positioned on inner face terminating as far from anterior as from posterior rims of otolith. Sulcus with rounded, poorly developed sole-shape outline with ostial lobe rounded. Iugum missing or narrow and then extending below entire sulcus.

Discussion: *Ortugobius* shows a simple and putatively plesiomorphic otolith morphology characterized by a flat inner face, a rather regular sulcus outline and the lack of prominent projections of the otolith rim. However, it also shows a character not known from any of the extant gobioid fishes so far studied: the iugum extending below the entire sulcus, when present. When Schwarzhan (2014) introduced the term iugum, it was introduced as “sub-caudal iugum” since it was only known then along the ventral margin of the cauda to various extents. The presence of a iugum extending below the entire sulcus in *Ortugobius* thus represents a distinct diagnostically valid character and furthermore, in our opinion, it might be an early autapomorphy that could be interpreted to represent a sistergroup to all extant gobiids. We therefore place *Ortugobius* only tentatively in the family Gobiidae until further data become available, which would allow a more precise allocation.

A large number of similar otoliths have been recorded from the early Oligocene and middle Oligocene of southwest France by Steurbaut (1984) as “genus Gobiidarum” sp. 3 and sp. 4 (Steurbaud 1984: pl. 32, figs 32–37). Steurbaut did not provide for a detailed description, but notes a rather flat inner face. This, in combination with the generally similar outline of the otoliths recorded by him indicates a possible relationship. His drawings, however, indicate presence of a iugum only below the cauda, which would be

typical for a gobiid. Skeletal remains of gobiids have been reported from the early Oligocene of the Upper Rhine Valley in France by Gaudant (1979).

*Ortugobius cascus* n. sp.

Pl. 4, Figs 1–10; Pl. 8, Figs 10–12

Etymology. From *cascus* (Latin) = old, primitive, referring to the early geological occurrence.

Holotype. MFM 207009 (Pl. 4, Fig. 2, Pl. 8, Fig. 11); Karatsu, location H5; Kishima FM, early Oligocene.

Paratypes. 9 specimens, MFM 207143–207151; Karatsu, locations H2 and H5; Kishima FM, early Oligocene.

Additional material. 1987 specimens, Karatsu, locations H1, H2, H4, H5, H6, H7 and coll. Nishimoto.

Diagnosis. Same as for genus (monospecific genus).

Description. Small, compact otoliths of 1.0 to 1.7 mm length (holotype 1.45 mm). OH:OT = 2.5–3.0. Dorsal rim high, gently but somewhat irregularly curving, highest just behind middle, without prominent angles and without postdorsal projection. Anterior and posterior rims nearly vertical, both with slight concavity at level of ostial and caudal tips respectively. Ventral rim flat, nearly straight, with slightly protruding angles with anterior and posterior rims. All rims thick, smooth, slightly undulating.

Inner face nearly completely flat with central portion around sulcus slightly elevated. Sulcus small, centrally positioned, slightly deepened, inclined anterior-ventrally at about 10°, with typical sole-shape but low ostial lobe. Iugum present in about 2/3 of all cases of reasonably preserved specimens, narrow, extending below entire sulcus. Dorsal depression wide, with indistinct borders; ventral furrow distinct, wide, running at some distance from ventral rim of otolith, turning upwards in front and behind sulcus to about level of ostial and caudal tips respectively. Outer face strongly convex, smooth.

Discussion. *Ortugobius cascus* is by far the most common species found at the Karatsu locations, except for location H3, and constitutes with nearly 2000 specimens of 2555 more than 78% of the otolith association.

Genus *Gymnogobius* Gill, 1863

*Gymnogobius oligocenicus* n. sp.

Pl. 4, Figs 11–17; Pl. 8, Figs 7–9

Etymology. Referring to the age of the species (Oligocene).

Holotype. MFM 207010 (Pl. 4, Fig. 12, Pl. 8, Fig. 7); Karatsu, location H2; Kishima FM, early Oligocene.

Paratypes. 7 specimens, MFM 207121, 207152–207157; Karatsu, location H5; Kishima FM, early Oligocene.

Additional material. 74 specimens, Karatsu, locations H1, H2, H4, H5, H6 and coll. Nishimoto.

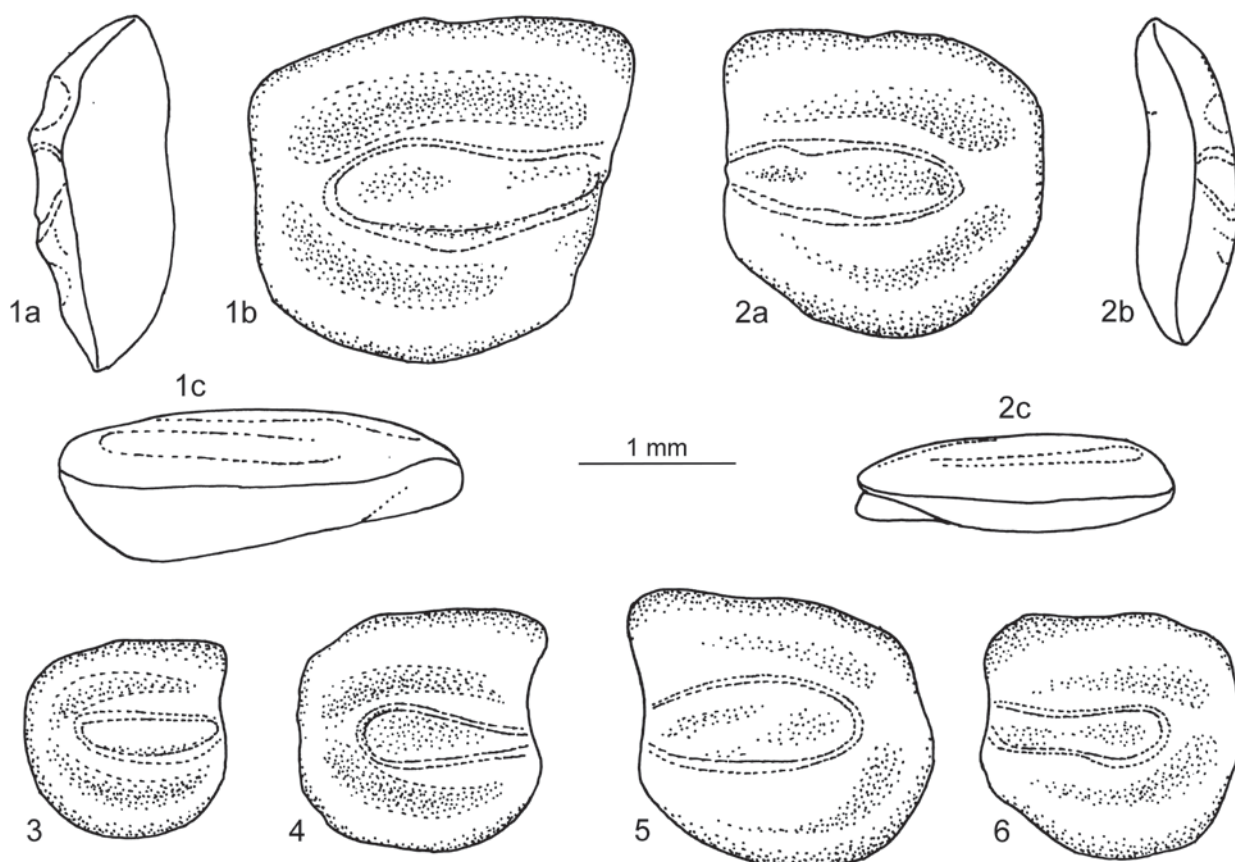
Diagnosis. OL:OH = 1.05–1.15. OH:OT = 3.5–3.7. Postdorsal projection very weak, shorter than the postventral projection. Ventral rim nearly flat. Inner face flat, outer face moderately convex. Sulcus moderately large, centrally positioned on inner face terminating as far from anterior as from posterior rims of otolith. Ostial lobe rounded, poorly developed. Subcaudal iugum well developed and broad below cauda except rear tip.

Description. Small, moderately compact otoliths of 1.0–1.9 mm in length (holotype 1.8 mm). Dorsal rim high, gently, somewhat irregularly curving, highest at about middle, without prominent angles and with very weak postdorsal projection. Anterior and posterior rims nearly vertical both slightly inclined upwards or anterior rim vertical, posterior rim with small con-

cavity at level of caudal tip, anterior rim rarely with concavity at about same level. Ventral rim flat, nearly straight, with slightly protruding projections at angle with anterior and particularly posterior rims. All rims moderately thin, smooth, slightly undulating.

Inner face nearly completely flat. Sulcus moderately large, centrally positioned, slightly deepened, inclined anterior-ventrally at about 10° to 15°, with typical sole-shape and relatively low ostial lobe. Subcaudal iugum well visible in well preserved specimens, broad, located below anterior 2/3 of cauda. Dorsal depression wide, with indistinct borders; ventral furrow distinct, wide, running at some distance from ventral rim of otolith, turning upwards all around tips of sulcus to nearly meet dorsal depression. Outer face moderately convex, smooth or with few radial furrows.

Discussion. *Gymnogobius oligocenicus* is not always easy to be distinguished from the contemporaneous *Ortugobius cascus*, when poorly preserved. When well preserved, however, they are well distinguished by the less compressed shape (OL:OH = 1.05–1.15 vs 0.9–1.05), the thinner appearance (OH:OT = 3.5–3.7 vs 2.5–3.0), the longer sulcus with the distinct sole-shape outline (vs more regular outline) and the short, distinct iugum positioned only



*Cornusolea fudoujii*

Plate 6: Otoliths from the Kishima Formation: Pleuronectiformes. (1–6) *Cornusolea fudoujii* n. gen., n. sp. 2: holotype, MFM 207011, location H5; 1, 3–6: paratypes, MFM 207158–207162, same data as holotype.



below the cauda (vs below entire sulcus). Clearly, *G. oligocenicus* is more advanced morphologically with a more “typical” gobiid sulcus than *Ortugobius cascus*. It is particularly the presence of the subcaudal iugum that characterizes *G. oligocenicus* as a gobiid, since this character so far has only been observed in Gobiidae (though it is not present in all species of the family).

There are few extant goby groups with otoliths that exhibit a postdorsal projection being shorter than the postventral projection. One such group is the *Chasmichthys* group of Birdsong et al. (1998), with a number of genera living in a variety of marine to freshwater habitats along the shores of the temperate northern Pacific. Those of the common extant Japanese genera *Gymnogobius* and *Chaenogobius* show an amazing high degree of similarity. We have figured for comparison otoliths of the Recent *Gymnogobius breunigii* (Steindachner, 1879) (Pl. 5, Figs 1–3), *G. urotaenia* (Hilgendorf, 1879) (Pl. 5, Fig. 4), *Chaenogobius gulosus* (Sauvage, 1882) (Pl. 5, Figs 5, 6) and *C. annularis* Gill, 1859 (Pl. 5, Figs 7–10). We have placed our fossil, early Oligocene otoliths in the genus *Gymnogobius*, since *G. breunigii* shows a very similar otolith outline and morphology of the sulcus.

Order Pleuronectiformes Bleeker, 1859  
Family Soleidae Bonaparte, 1835

Genus *Cornusolea* n. gen.

Type species: *Cornusolea fudoujii* n. sp.

**Etymology:** A combination of *cornus* (Latin) = horn, and the name giving genus name *Solea* referring to the distinct predorsal projection of the outline of the otoliths.

**Diagnosis:** A fossil otolith-based genus of the family Soleidae with moderately small, compact otoliths up to slightly more than 2 mm length. OL:OH = 1.0–1.1. Otoliths nearly round in outline, but with prominent, often sharp predorsal process at junction of dorsal and anterior rims, often underpinned below by broad concavity of anterior rim. Sulcus anteriorly narrowed, posteriorly wide, completely unstructured without indication of ostium and cauda. Circumsulcal depression not connected behind cauda.

**Discussion:** The combination of the round shape with the sharp predorsal projection and the unstructured, drop-shaped sulcus is distinct from all known Recent soleid otoliths as depicted in Schwarzhans

(1999). The lack of a connection of the circumsulcal depression behind the cauda is rated as a plesiomorphic character, while the sulcus morphology and the general appearance of the otolith otherwise is rather apomorphic and typical for soleid otoliths.

*Cornusolea fudoujii* n. sp.  
Pl. 6, Figs 1–6; Pl. 8, Figs 13–15

**Etymology.** In honor of Yasuhiro Fudouji, a local paleontologist at Karatsu.

**Holotype.** MFM 207011 (Pl. 6, Fig. 2, Pl. 7, Fig. 15); Karatsu, location H5; Kishima FM, early Oligocene.

**Paratypes.** 5 specimens, MFM 207158–207162; Karatsu, location H5; Kishima FM, early Oligocene.

**Additional material.** 34 specimens, Karatsu, locations H4, H5, H6 and coll. Nishimoto.

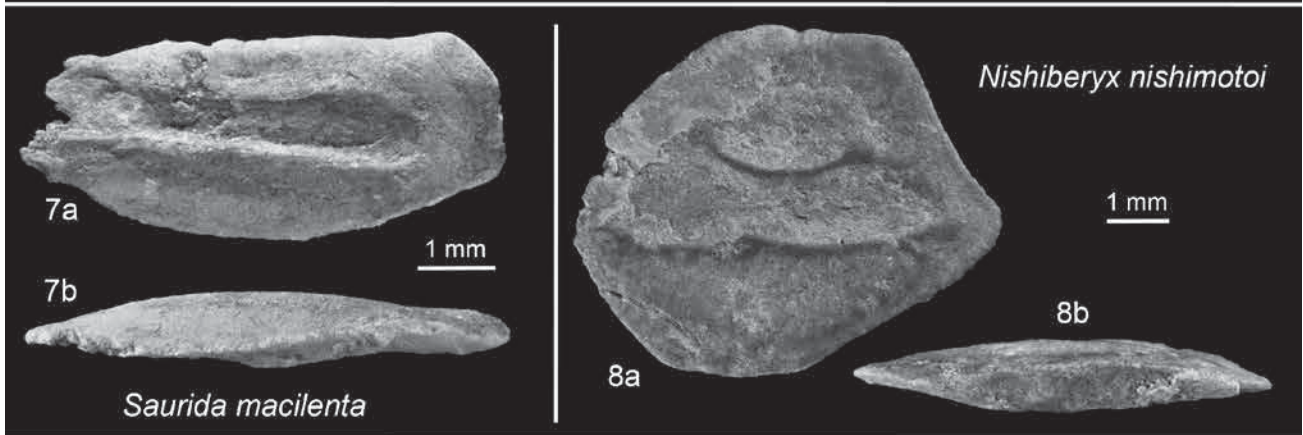
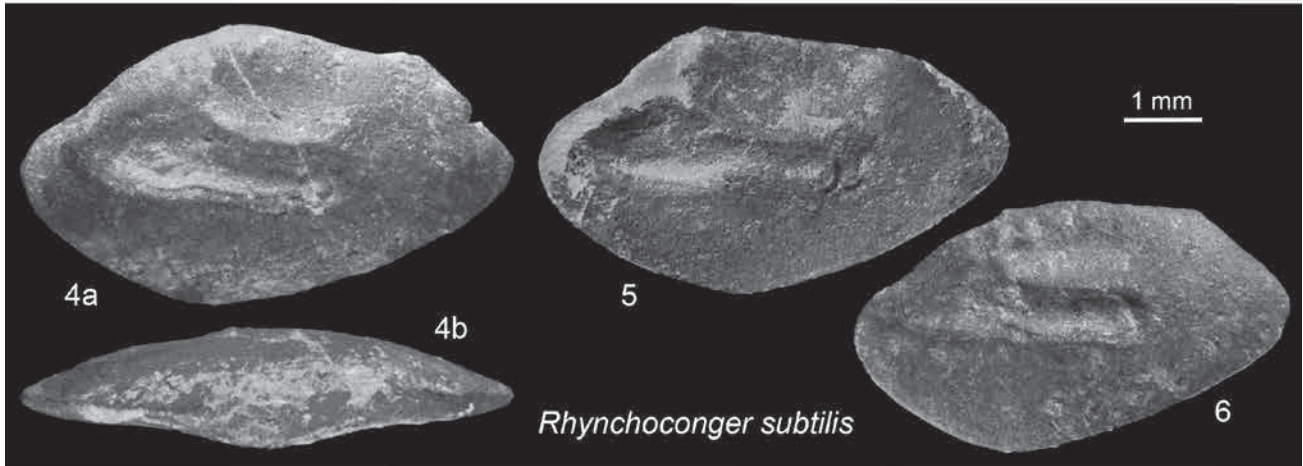
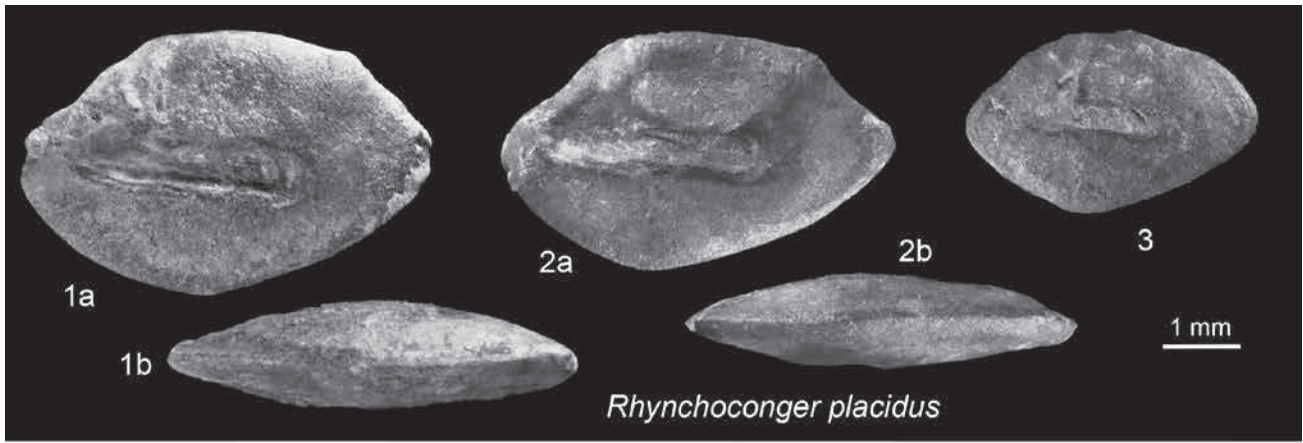
**Diagnosis.** Same as for genus (monospecific genus).

**Description.** Moderately small, robust otoliths up to about 2.5 mm length (holotype 2.05 mm). OH:OT = 2.7–3.0; left otoliths usually somewhat thicker than right otoliths. Outline regularly round except for a mostly sharp horn-like predorsal projection often accompanied by a broad concavity of the anterior rim below; the latter particularly in otoliths of the left side.

Inner face markedly convex, particularly in vertical direction, with central, large, shallow, anteriorly open sulcus. Sulcus with no indication of subdivision in ostium and cauda, anteriorly narrowed, thin, posteriorly widened with rounded tip. Circumsulcal depression broad, with sharp borders, close to sulcus and regularly curved around sulcus, but not jointed behind cauda. Outer face flat and smooth.

**Side dimorphism.** Otoliths of many pleuronectiforms are known for their side dimorphism, which reflects the asymmetry of the fish skulls themselves. However, Schwarzhans (1999) has shown that not all extant pleuronectiforms actually show a discernable degree of side dimorphism in their otoliths. *Cornusolea fudoujii* also is one of the species with a very low degree of side dimorphism, basically restricted to left otoliths usually being slightly thicker than right otoliths and also showing in more often a broad concavity at the anterior rim.

**Plate 7:** Otoliths from the Kishima Formation: photographs 1. (1–3) *Rhynchoconger placidus* n. sp. 2: holotype, MFM 207001, coll. Nishimoto; 1 (reversed), MFM 207104, coll. Nishimoto; 3 (reversed): paratypes, MFM 207107, location H6. (4–6) *Rhynchoconger subtilis* n. sp. 4: holotype, MFM 207002, location H5; 5: paratype, MFM 207110, coll. Nishimoto; 6 (reversed): paratype, MFM 207111, location H5. (7) *Saurida macilenta* n. sp. Holotype, MFM 207003, location H5. (8) *Nishiberyx nishimotoi* n. gen., n. sp. Holotype (reversed), MFM 207004, coll. Nishimoto. (9–11) *Sagaberyx kishimaensis* n. gen., n. sp. 9 (reversed): holotype, MFM 207005, location H5; 10: paratype, MFM 207124, location H5; 11: paratype, MFM 207127, location H5.



### 3.2 Faunal reconstruction

#### 3.2.1 The Kishimia otolith association in context

The Late Eocene / Early Oligocene transition represents a pivotal phase in the Cenozoic geological history characterized by the onset of global cooling triggered by the complete isolation of Antarctica, the establishment of the circum-Antarctic current and the onset of the formation of an Antarctic ice shield (Kennett et al. 1975; Kennett 1977; Liu et al. 2009) and causing a major reorganization of the ocean water bodies (Katz et al. 2011). Our knowledge of fish evolution during this crucial time is rather moderate and patchy, particularly when it comes to shallow marine, near shore clastic environments. The Early Oligocene of the Maykop and Menilite Formations of the Paratethys, which is famous for its rich fauna of articulated fish skeletons was deposited in an anaerobic deep water environment and thus primarily contains epipelagic and mesopelagic fishes (Bannikov 2010; Bienkowska-Wasiluk 2010). Marine otolith-based faunas from the Early Oligocene are also predominantly from deep water (Italy: Nolf & Steurbaut 1987, 2005) or open neritic shelf environments (North Sea Basin: Nolf 1972; Schwarzhans 1977; Central Paratethys: Brzobohaty 1967; US Gulf Coast: Frizzell & Lamber 1962; Nolf 2003). The rich otolith assemblages of New Zealand (Schwarzhans 1980) and Australia (Schwarzhans 1985) have a recording gap over this time interval. Therefore, for the best of our knowledge, only the otolith assemblages from lagoonal and near shore formations in southwestern France (Steurbaut 1984) and the poorly known assemblage from the Mainz Basin in Germany (Koken 1891) are comparable in age and environment to the fauna described here from the Kishima Formation of Karatsu in southwestern Japan. It is therefore no surprise that the Kishima fauna stands out for a number of peculiarities as explained in the following.

#### 3.2.2 The composition of the Kishima otolith association

The otoliths obtained from the Early Oligocene Kishima Formation represent mostly shallow water fishes, such as Congridae, *Saurida*, Gobiidae and Soleidae. Exceptions could be *Pontinus?*, which nowadays is found over the open shelf and the continental slopes, and the enigmatic fossil *Sagaberyx*,

which appears to not have an extant relative. *Ortugobius cascus* is the single most common species making up more than 75% of all otoliths obtained, and all Gobiidae represent 80% of the fauna. The degree of species diversity is low, dominated by a single species (*Ortugobius cascus*) and with only 5 species accounting for 95% of the fauna: *Ortugobius cascus* (78%), *Sagaberyx kishimaensis* (11%), *Gymnogobius oligocenicus* (3%), *Pontinus? krasawai* (2.5%) and *Cornusolea fudoujii* (1.5%).

Only six of the 11 genera recognized in the faunal assemblage of Kishima can be reasonably assigned to extant genera, and they are all still present in the waters around Japan. This indicates a certain degree of stability in the faunal composition since early Oligocene times. However, the high degree of extinct genera, partially of uncertain relationship (*Sagaberyx*), is larger than those of contemporaneous otolith-based faunas as mentioned above, but is in line with the percentage of extinct higher taxa observed in the skeleton-based faunas of the Menilite and Maykop Formations.

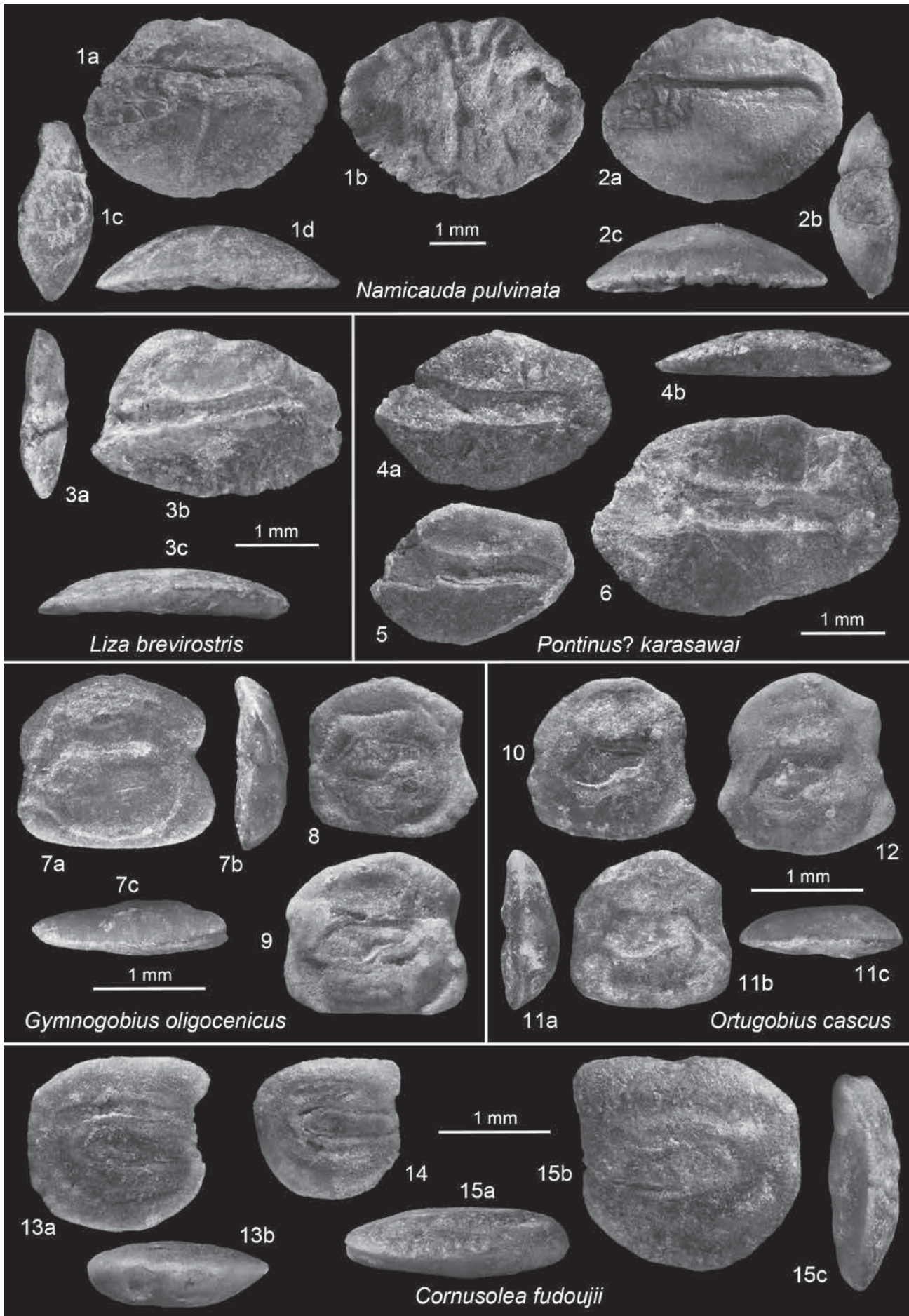
The correlation with time equivalent otolith-based fish faunas from elsewhere is restricted by the large distance gap to most of them, i.e. US Gulf Coast and Europe or even Australia and New Zealand when also considering Late Eocene faunas. It is therefore not surprising that not a single common species could be identified between Kishima and any of the other locations. However, some similarities can be observed on higher systematic levels. *Pterothrissus*, *Rhynchoconger* and *Saurida* represent “old” teleost groups and maintained a wide distribution at that time, and relatives to the species from Kishima are found in many of the other regions mentioned (Nolf 2013). Others are more rarely observed, like *Liza* or *Pontinus*, and *Gymnogobius* is reported for the first time in the fossil record. Its Recent distribution is restricted to northeastern Asia. Apart from these rather unspectacular correlations, there are also three more unusual observations and conclusions that deserve some specific discussion:

(i) The abundance of gobioid otoliths. During Neogene, gobioid otoliths usually represent the dominant group in all warm shallow water and brackish environments studied on a worldwide basis. This is not the case in the Paleogene. During Eocene, small, nowadays extinct ophidiiform fishes appear to have played the role of the later gobioids and are the most abundant in the warm shallow seas for instance in

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**Plate 8:** Otoliths from the Kishima Formation: photographs 2. **(1, 2)** *Namicauda pulvinata* n. gen., n. sp. 1: holotype, MFM 207006, location H5; 2 (reversed): paratype, MFM 207135, coll. Nishimoto. **(3)** *Liza brevirostris* n. sp. Holotype, MFM 207007, location H5. **(4–6)** *Pontinus? karasawai* n. sp. 4: holotype, MFM 207008, location H5; 6: paratype, MFM 207138, location H5; 5 (reversed): paratype, MFM 207137, location H5. **(7–9)** *Gymnogobius oligocenicus* n. sp. 7 (reversed): holotype, MFM 207010, location H2; 8 (reversed): paratype, MFM 207153, location H5; 9: paratype, MFM 207121, coll. Nishimoto. **(10–12)** *Ortugobius cascus* n. gen., n. sp. 11 (reversed): holotype, MFM 207009, location H5; 12: paratype, MFM 207145, location H5; 10 (reversed): paratype, MFM 207147, location H2. **(13–15)** *Cornusolea fudoujii* n. gen., n. sp. 15: holotype, MFM 207011, location H5; 13, 14: paratypes, MFM 207159–207160, same data as holotype.





Europe (Nolf 1985). Comparative rich Paleogene gobioid assemblages in shallow water near shore environments are rare, in fact only three such assemblages are known: two described by Steurbaut (1984) from the early and late Oligocene of southwest France and this one from Japan. Skeletal remains of gobiids have been reported by Gaudant (1979) from the early Oligocene of the Upper Rhine Valley in France. All these occurrences already postdate the regime dominated by small ophidiiforms, but it is premature at this stage to speculate what may have triggered the abundance of gobioids in the respective locations or whether it may be a result of the above mentioned global cooling setting in with the turn of the Eocene to Oligocene. In any case, their otolith morphology is already typical “gobioid” and sometimes even allows correlation with otoliths of extant Gobiidae. This is not the case for the few earlier records from Eocene times, which are more problematical in their systematic position (see extensive discussion in Gierl et al. 2013). However, in the light of the typical gobioid otoliths found in the Early Oligocene it seems likely that the Gobioidae, one of the most successful fish groups in the Recent, should have yet unknown roots deeper in time.

(ii) The near complete absence of percoid otoliths. Percoid otoliths are abundant and diverse in all neritic warm environments sampled since Eocene times. In temperate realms, like in the Oligocene and Neogene of the North Sea Basin, they are much less common, also in shallow, brackish environments, are dominated by gobies. The latter environment is also inferred for the Kishima FM otolith association described here, but nevertheless the near absence of any percoid otoliths is surprising. There is only a single record of a carangid. It is possible that Japan resided at a slightly higher latitude and under the influence of cool currents from the North during Oligocene, as indicated in the paleogeographic atlas of Kazim & Natapov (1998). A warm temperate climate underpinned by such cool current would support the scarcity of percoids.

(iii) The diversity of extinct beryciform and polymixiiform otoliths. Beryciform, in particular berycoid otoliths are common and very diverse in sediments of the Late Cretaceous (Schwarzhan 2010). They are represented by many extinct higher taxa and include a number of otolith morphologies, which are highly specialized and difficult to compare to extant groups, and hence their allocation must be considered as preliminary until otoliths in situ have become available for investigation. Most of these specialized putative beryciform otolith morphologies apparently became extinct prior to the Paleogene, but groups of shallow marine berycoids similar to those persisting until today and which survived across the KT-boundary were not uncommon during Early Paleogene times and showed a broad diversity (Schwarzhan 2012). However, their abundance has already tapered during Oligocene and they have

become rare, except for deep water groups such as *Hoplostethus* and relatives. It is therefore surprising to account for three berycoid and polymixiid taxa in the Kishima Formation, all of which belong to extinct genera and one (*Sagaberyx*) showing a highly specialized morphology of unresolved relationship.

#### 4. Conclusions and outlook

The otolith-based fish fauna from the Early Oligocene of the Kishima Formation in southwest Japan is unique in composition by various aspects: the abundance of gobioids, the scarcity of percoids and the diversity of berycoids and polymixiids. It combines one of the arguably earliest records of fossil gobioids with one of the latest records of highly specialized extinct putative berycoids and polymixiids and therewith represents a faunal community not seen in any other known fossil otolith assemblage. The Kishima otolith assemblage also stands geographically isolated, distant from any comparable other known otolith association in Europe, North America, or from the Late Eocene of Australia and New Zealand. We interpret it as a true representation of a hitherto unknown and unrecorded faunal province of fishes during the terminal Paleogene and regard it as a showcase of what supraregional fossil otolith studies may have to offer of unexpected information. We expect that future studies of fossil otoliths in Japan can produce an important contribution for understanding the evolution of fishes of this rich faunal province. Furthermore, we hope that future supraregional studies of fossil fish otoliths will contribute to a better understanding of biogeographic marine fish provinces in space and time, and finally that it will contribute to a better understanding of the faunal response to major geological events which have affected the marine environment.

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## 5. References

- Ando Y. 2011. Oligocene pteropods (Gastropoda: Thecosomata) from the Kishima Formation, Saga Prefecture, southwest Japan. *Revista Mexicana de Ciencias Geológicas* 28, 245–253.
- Aoki T. 2008. Geology of Kitahata. The Paleogene and fossils. In: Karatsu City, The History of Kitahata, Volume of Nature, Districts and Customs 66–140. (in Japanese)
- Bajpai S, Kapur VV. 2004. Oldest known gobiids from Vastan lignite mine (Early Eocene), Surat District, Gujarat. *Current Science* 87, 433–435.
- Bannikov AF. 2010. Fossil vertebrates of Russia and adjacent countries. Fossil Acanthopterygian fishes (Teleostei, Acanthopterygii). *Geos Moscow*, 244 p. (in Russian)
- Bienkowska-Wasiluk M. 2010. Taphonomy of Oligocene teleost fishes from the Outer Carpathians of Poland. *Acta Geologica Polonica* 60, 479–533.
- Birdsong RS, Murdy EO, Pezold FL. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. *Bulletin of Marine Science* 42, 174–214.
- Brzobohaty R. 1967. Die Fisch-Otolithen aus den Pouzdrany-Schichten. *Acta Musei Moraviae, Scientiae Naturales* 52, 121–168.
- Friedman M. 2010. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proceedings of the Royal Society B* 277, 1675–1683.
- Frizzell DL, Lamber CK. 1962. Distinctive “congruid type” fish otoliths from the Lower Tertiary of the Gulf Coast (Pisces: Anguilliformes). *Proceedings of the California Academy of Science, Series 4* 32, 87–101.
- Gaudant J. 1979. Sur la présence de Gobiidae (Poissons Téléostéens) dans l'Oligocène inférieur de Rouffach (Haut-Rhin). *Sciences Géologiques Bulletin* 32, 131–137.
- Gierl C, Reichenbacher B, Gaudant J, Erpenbeck D, Pharisat A. 2013. An extraordinary gobioid fish fossil from southern France. *Plos One* 8, e64117, 17 p.
- Grenfell HR. 1984. Early Miocene teleost otoliths from Parengarenga Harbour, New Zealand. *New Zealand Journal of Geology and Geophysics* 27, 51–96.
- Hatai K. 1965. Some Pliocene fish otoliths from Japan. *Senckenbergiana Lethaea* 46, 133–143.
- Inoue E. 1972. Lithofacies, fossil assemblage and sedimentary environment of Oligocene Kishima Formation in Karatsu Coal field, Northwest Kyushu, Southwest Japan. *Report of Geological Survey of Japan* 245, 1–72.
- Karasawa H. 1993. Cenozoic decapod Crustacea from Southwest Japan. *Bulletin of the Mizunami Fossil Museum* 20, 1–92.
- Karasawa H, Fudouji Y. 2000. Paleogene decapod Crustacea from the Kishima and Okinoshima Groups, Kyushu, Japan. *Paleontological Research* 4, 239–253.
- Katz ME, Cramer BS, Toggweiler JR, Esmay G, Liu C, Miller KG, Rosenthal Y, Wade BS, Wright JD. 2011. Impact of Antarctic Circumpolar Current development on Late Paleogene ocean structure. *Science* 332, 1076–1079.
- Kazim VG, Natapov LM. (eds.) 1998. The paleogeographic atlas of northern Eurasia. Institute of Tectonics and Lithospheric Plates, Russian Academy of Natural Sciences, Moscow.
- Kennett JP. 1977. Cenozoic evolution of Antarctic glaciation, the Circum-Antarctic Ocean, and their impact on global paleoceanography. *Journal of Geophysical Research* 82, 3843–3860.
- Kennett JP, Houtz RE, Andrews PB, Edwards AR, Gostin VA, Hajos M, Hampton MA, Jenkins DG, Margolis SV, Ovenshine AT, Perch-Nielsen K. 1975. Cenozoic paleoceanography in the southwest Pacific Ocean, Antarctic glaciation and the development of the circum-Antarctic current. *Initial Reports of the Deep Sea Drilling Project* 29, 1155–1169.
- Kobayashi I, Imai I, Matsui K. 1956. “Karatsu”, explanatory text of the geological map of Japan (1/50000). *Geological Survey of Japan, Fukuoka* 59, 69 p.
- Koken E. 1891. Neue Untersuchungen an Tertiären Fischotolithen II. *Zeitschrift der deutschen Geologischen Gesellschaft* 43, 77–170.
- Lin C-H, Chang CW. 2012. Otolith atlas of Taiwan fishes. *NMMBA Atlas series* 12, 415 p.
- Liu Z, Pagani M, Zinniker D, Deconto R, Huber M, Brinkhuis H, Shah SR, Leckie RM, Miyachi M, Sakai H. 1991. Zircon fission-track ages of some pyroclastic rocks from the Tertiary formations in Northwest Kyushu, Japan. *Journal of the Geological Society of Japan* 97, 671–674.
- Lombarte A, Chic O, Parisi-Baradad V, Olivella R, Piera J, Garcia-Ladona E. 2006. A web-based environment for shape analysis of fish otoliths. The AFORO database. *Scientia Marina* 70, 147–152.
- Mizuno A. 1963. Paleogene and early Neogene biochronology of western Japan. *Journal of the Geological Society of Japan* 69, 38–50.
- Nagao T. 1927. Kishima Formation, Paleogene stratigraphy of Kyushu (16). *Journal of Geography, Tokyo Geographical Society* 39, 592–604. (in Japanese)
- Nagao T. 1928a. Paleogene Fossils of the Island of Kyushu, Japan. Part1. *Science Reports of the Tohoku Imperial University* 9, 97–128.
- Nagao T. 1928b. Paleogene Fossils of the Island of Kyushu, Japan. Part2. *Science Reports of the Tohoku Imperial University* 12, 11–140.
- Nelson JS. 2006. *Fishes of the world*. Fourth edition. New Jersey, Hoboken: John Wiley and Sons, 601 p.
- Nishida T, Kawano Y, Aizawa J, Aoki T, Kakubuchi S. 2008. Geology of Kitahata. In: Karatsu City, The History of Kitahata, Volume of Nature, Districts and Customs 33–160. (in Japanese)
- Nolf D. 1972. Sur les otolithes des Sables de Grimmertingen (Oligocène Inférieur de Belgique). *Bulletin de l'Institut Royal des sciences naturelles de Belgique, Sciences de la terre* 48, 1–23.
- Nolf D. 1985. Otolithi Piscium. In: HP Schultze (ed.), *Handbook of Paleichthyology* 10, 1–145
- Nolf D. 1988. Les otolithes de téléostéens éocènes d'Aquitaine et leur intérêt stratigraphique. *Académie Royale de Belgique, Mémoires de la classe des sciences* 19, 1–147
- Nolf D. 2003. Revision of the American otolith-based fish species described by Koken in 1888. *Louisiana Geological Survey, Geological Pamphlet* 12, 1–19
- Nolf D. 2013. The diversity of fish otoliths, past and present. Brussels, Royal Belgian Institute of Natural Sciences CCCLIX + 222 p.
- Nolf D, Steurbaut E. 1987. Description de la première faune ichthyologique exclusivement bathyale du Tertiaire d'Europe: otolithes de l'Oligocène Inférieur du gisement de Pizzocorno, Italie septentrionale. *Bulletin de l'Institut Royal des sciences naturelles de Belgique, Sciences de la terre* 57, 217–230.
- Nolf D, Steurbaut E. 2004. Otolithes de poissons de l'Oligocène Inférieur du bassin Liguro-Piemontais oriental, Italie. *Revista Piemontese Scientias naturales* 25, 21–68.
- Nolf D, de Potter H, Lafond-Grellety J. 2009. Homage to Joseph Chaine and Jean Duvergier. The diversity and variability of fish otoliths. *Palaeo Publishing and Library vzw CIL* + 59 p.
- Ohe F. 1977. Otoliths from the Dainichi Sand and Hosoya tuffaceous Beds of Kakegawa Group (Pliocene), Shizuoka Prefecture, Central Japan. *Kaseki no tomo. Bulletin of the Tokai Fossil Society* 16, 13–19.
- Ohe F. 1979. On the living species of family Pterothrissidae and fossil otoliths from Japanese Miocene deposits. *Kusatsu Chigaku Doukoukai* 5, 23–30.
- Ohe F. 1981. Fish-otoliths from the Dainichi Sand and the Hosoya tuffaceous Members of the Pliocene Kakegawa Group, Shizuoka Prefecture, Central Japan. *Bulletin of the Senior High*



- School attached to the Aichi University of Education 8, 125–194.
- Ohe F. 1990. Faunal change of the Miocene marine fish in Japan. Monograph of the Mizunami Fossil Museum 7, 25–60.
- Ohe F, Araki Y. 1973. Some Miocene fish otoliths from the Yakouji Formation, Tsu, Mie Prefecture. Science reports of the Tohoku University, second series (Geology) 38, 1–15.
- Okada H. 1992. Calcareous nannofossils and biostratigraphy of the Paleogene sequences of northern Kyushu, Japan. The Journal of the Geological Society of Japan 98, 505–528.
- Okada H, Bujery D. 1980. Supplementary modification and introduction of code number to the low-latitude coccolith biostratigraphic Zonation. Marine Micropaleontology 5, 321–325.
- Patterson C. 1993. An overview of the early fossil record of Acanthomorphs. Bulletin of Marine Science 52, 29–59.
- Pearson A. 2009. Global cooling during the Eocene–Oligocene climate transition. Science 323, 1187–1190.
- Reichenbacher B, Uhlig U. 2002. Die Fischfauna der chattischen unteren Cyrenen-Schichten in der Murnauer Mulde (süddeutsche Faltenmolasse). Courier-Forschungsinstitut Senckenberg 237, 175–191.
- Rivaton J, Bourret P. 1999. Les otolithes des poissons de l'Indo-Pacifique. Documents scientifiques et techniques, Institut de recherche pour le développement Nouméa 2, 1–378.
- Schwarzahns W. 1977. Otolithen aus dem Unteroligozän (Tertiär) von Hückelhoven (Kreis Heinsberg, Nordrhein-Westfalen). Decheniana 130, 268–292.
- Schwarzahns W. 1978. Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. Mededelingen Werkgroep Tertiaire en Kwartaire Geologie 15, 167–185.
- Schwarzahns W. 1980. Die tertiäre Teleosteer-Fauna Neuseelands, rekonstruiert anhand von Otolithen. Berliner geowissenschaftliche Abhandlungen, A 26, 1–211. [English translation 1984 in: Report New Zealand Geological Survey 113, 1–269.]
- Schwarzahns W. 1985. Tertiäre Otolithen aus South Australia und Victoria (Australien). Palaeo Ichthyologica 3, 1–60.
- Schwarzahns W. 1994. Die Fisch-Otolithen aus dem Oberoligozän der Niederrheinischen Bucht. Systematik, Palökologie, Paläobiogeographie, Biostratigraphie und Otolithen-Zonierung. Geologisches Jahrbuch, Reihe A 140, 1–248.
- Schwarzahns W. 1999. A comparative morphological treatise of recent and fossil otoliths of the order Pleuronectiformes. Piscium Catalogus. Otolithi Piscium 2, 1–391.
- Schwarzahns W. 2007. The otoliths from the middle Eocene of Osteroden near Bramsche, north-western Germany. Neues Jahrbuch Geologische Paläontologische Abhandlungen 244, 299–369.
- Schwarzahns W. 2010. Otolithen aus den Gerhartsreiter Schichten (Oberkreide: Maastricht) des Gerhartsreiter Grabens (Oberbayern). Palaeo Ichthyologica 4, 1–100.
- Schwarzahns W. 2012. Fish otoliths from the Palaeocene of Bavaria (Kressenberg) and Austria (Kroisbach and Oiching-Graben). Palaeo Ichthyologica 12, 1–88.
- Schwarzahns W. 2014. Otoliths from the middle Miocene (Serravallian) of the Karaman Basin, Turkey. Cainozoic Research 14, 35–69.
- Smale MJ, Watson G, Hecht T. 1995. Otolith atlas of Southern African marine fishes. Ichthyological Monography, J.L.B. Smith Institute of Ichthyology 1, 1–253.
- Steurbaut E. 1984. Les otolithes de téléostéens de l'Oligo-Miocène d'Aquitaine (sud-ouest de la France). Palaeontographica, A 186, 1–162.
- Takahashi M. 1976. Some Miocene fish otoliths from the Mizunami Group, central Japan. Bulletin of the Mizunami Fossil Museum 3, 55–72. (in Japanese)
- Takahashi M. 1977. Some Pliocene fish otoliths from the Dainichi sands, Kakegawa Group, central Japan. Bulletin of the Mizunami Fossil Museum 4, 97–118. (in Japanese)
- Weiler W. 1942. Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. Abhandlungen des Reichsamts für Bodenforschung, Neue Folge 206, 1–140.
- Yamaguchi T, Nagao R, Kamiya T. 2006. Paleogene ostracods from the Kishima Formation, Kishima Group, Saga Prefecture, southwestern Japan. Bulletin of the Mizunami Fossil Museum 33, 87–101.