ニシン科魚類を中心とした日本産魚類の耳石の形態に関する基礎的および応用的研究

博士学位論文

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（2021 年 3 月）

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［課程博士・論文博士共通］

博士学位論文内容要旨
Abstract

専　攻 Major	応用生命科学専攻	氏　名 Name	三井　翔太
論文題目 Title	ニシン科魚類を中心とした日本産魚類の 耳石の形態に関する基礎的および応用的研究		

耳石は魚類の内耳に存在する平衡器官で、主に $CaCO_3$ から構成されている。耳石は胃内容物や化石として得られる事から、耳石に基づく種同定法が必要とされてきた。しかし、種の識別形質が明らかにされた分類群はごく僅かである。そこで本研究では、識別形質に関する知見の少ない分類群を対象とした日本産魚類の耳石による種同定法の確立と、その応用を目的とした。第 1 章では耳石形態学の基礎的研究として、ニシン科魚類の耳石の外部形態比較を行った。第 2 章では、耳石形態学の応用的研究として、耳石化石の同定と化石魚類相の復元、そして化石群集に基づく古環境推定を行った。

第 1 章では、ウルメイワシおよびマイワシについて，体成長に伴う耳石の形態変化について記載すると共に、ニシン・ウルメイワシ・ミズン・ヒラ・コノシロ・リュウキュウドロクイ・ドロクイ・カタボシイワシ・オグロイワシ・サッパ・マイワシ・キビナゴの 12 種の耳石の形態学的記載および種間比較に基づく種の識別形質の探索を行った。その結果、ウルメイワシ・マイワシの 2 種では体長約 100 mm を境に全形が楕円形から長楕円形に漸移する事、OL:OH（耳石長：耳石高）および AL:RL（上部嘴状突起長：嘴状突起長）の成長変化パターンが種間で異なる事が明らかとなった。さらに、幼魚を除いた種間比較を行った結果、OL:OH、AL:RL、全形、背部・腹部・後部周縁の形態、crista superior の隆起の 7 形質において種間に差異が確認され、これらの形質に基づく種の識別が可能である事が示された。以上の結果を総括し、耳石の形態に基づく種までの検索表を作成した。

第 2 章では、神奈川県三浦市南下浦町鹿穴台に位置する第四系更新統チバニアン階・宮田層鹿穴凝灰質砂部層の露頭より得られた 1,675 点の魚類化石（耳石を主体とし、ごく少数の骨と板鰓類の歯化石を含む）について、1）第 1 章で作成した検索表、既往の文献および現生耳石標本との比較に基づく同定、2）化石群集に基づく本層堆積時の化石魚類相の復元と古環境の推定を行った。その結果、1）では第 1 章の検索表を用いてニシン、マイワシの耳石化石が同定されたのをはじめ、スケトウダラやハダカイワシなど、少なくとも 62 分類群の化石が見出された。また、2）において、本部層の化石魚類相は、温帯性および暖水性魚類が優占し、少数の寒帯・亜寒帯、冷温帯性および暖温帯性魚類が含まれる寒・暖混合群集であったことが示唆された。さらに、産出した標本数および種数に基づき、黒潮・親潮が波及する温帯海域の、水深約 100–200 m の大陸棚という古環境が推定された。

今後、ニシン科以外の分類群を含む日本及びその周辺海域に分布する魚類の耳石の外部形態比較を進めることで、化石や胃内容物の正確な種同定が可能となり、日本における海産魚類相の成立過程や、鯨類などの海産大型動物の食性の解明など幅広い研究分野への応用が可能になると期待される。

目次

緒言

耳石は，硬骨魚類の内耳にある生態鉱物で，炭酸カルシウム（CaCO3）が主成分である。耳石は扁平石 sagitta，礫石 lapillus，星状石 asteriscus の 3 種類が，それぞれ内耳の小嚢，通嚢，壷に存在している（Nolf, 2013）。礫石が発達するナマズ目や星状石が発達するコイ目魚類を除けば，一般的に条鰭類では扁平石が最も大きいため，耳石の研究では主に扁平石が用いられてきた（Ohe, 1985）。

耳石は，炭酸カルシウムから構成されているために丈夫で，捕食者の消化管内で消化を受け難く，胃内容物として耳石だけが残留している場合が多い。そのため，魚食性魚類や鯨類など高次捕食者の食性解明を目的とした胃内容物調査において，胃から抽出された耳石に基づく種同定が行われてきた（Yamazaki *et al*., 2008; 三井ほか, 2014）。また，魚類の死後に軟組織が分解されても，耳石だけが堆積物中に埋没して保存されることが多く，しばしば堆積物中において高密度に含まれる。そのため，古生物学分野においては，地層から産出した耳石化石を同定し，過去の魚類相や古環境を復元する研究が広く行われてきた（例えば Schwarzhans, 2019a; 大江ほか, 2020 など）。さらに，同様な理由で耳石は考古遺跡においても保存される場合があることから，貝塚から出土した耳石に基づく種同定も行われている（Lin et al., 2013; 大江ほか, 2014）。これらの成果は，ひいては海洋における食物網の解明や高次捕食者の保全および資源管理，化石魚類相や古環境の変遷および現在の魚類相・環境の成立過程の復元，有史時代における人類の食生活や漁労の復元に繋がる。このような研究において，耳石に基づく正確な種同定を行うには，個体差や成長変化といった種内での形態差を把握したうえで，各種の耳石における種の識別形質を明らかにする必要がある。

耳石の形態に基づいた種同定を行う際には，これまでは各研究機関が所蔵する比較標本コレクションや，多くの分類群の耳石が記載された文献が用いられてきた（Smale et al., 1995; Campana, 2004; Furlani et al., 2004; Svetocheva　et al., 2007; Ye et al., 2007; Lin and Chang, 2012; Nolf, 2013 など）。日本産魚類についても，Ohe（1985），飯塚・片山（2008）が多くの分類群の耳石を網羅的に記載している。しかし，これらの文献において，詳細な種間比較が行われ，種

の識別点まで言及されている分類群はごく僅かである。その一方で，目や科などの上位分類群を対象に，耳石の形態に基づく種までの検索表を付した研究例も存在するが（たとえばタラ科（Frost, 1981），ニベ科（Schwarzhans, 1993），カレイ目（Schwarzhans, 1999），ハダカイワシ科のうちハダカイワシ属など 3 属（Schwarzhans, 2013），ホタルジャコ科ヒメスミクイウオ属（Schwarzhans and Prokofiev, 2017），ウナギ目のうち 4 科（Schwarzhans, 2019b），チゴダラ科（Schwarzhans, 2019c），Trachiniformes（Schwarzhans, 2019d）），多くの分類群においては耳石上の標徴形質は未だ明らかでない。

それにも関わらず，特に古生物学的研究において，明らかに誤同定であると思われる耳石の記載がしばしば見受けられる。たとえば Hatai (1965)が報告した“ドンコ *Odontobutis obscula*”や高橋（1976）が報告した“アイアナゴ属 *Uroconger* sp.”の耳石化石について，大江（1990）はそれぞれチゴダラ属 *Physiculus* sp.，ギンアナゴ属 *Gnathophis* sp.の誤同定であることを指摘している。また，*Nibea pacifica* や *Gobius notoensis* のように，現生種をはじめとする他種との比較が不十分なまま耳石化石に基づいて記載された化石種も多い（Hatai, 1965; Aoki, 1967, 1968, 1971, Aoki and Baba, 1980）。このように，耳石による種同定の正確さを欠く理由としては，各分類群における種の標徴形質や，種内における形態変異についての知見の不足が大きな要因であると思われる。

また，一般的に，消化や摩耗による外部形態の損傷が著しい耳石は「同定不能」として扱われ，結果の解析には用いられないことが多い（Aoki, 1968; 三井ほか, 2014）。そのため，食性調査や化石魚類相の研究の結果は常に耳石の保存状態によるバイアスを受けており，そのことがデータ解析や考察に影響を及ぼしている可能性がある。古環境や古生物地理，進化学的な知見を蓄積する上で，これら誤同定の可能性がある耳石化石の再同定は必要不可欠である。

そこで本研究では，耳石の形態に関する基礎的および応用的研究として、1）識別形質に関する知見の少ない分類群の耳石の種同定法の確立，2）耳石の種同定の応用的研究として、耳石化石の同定とその結果に基づく化石魚類相の復元および古環境の推定を行った。

まず、第 1 章では、日本産のニシン科魚類を用いた耳石の形態記載および種間での形態比較

を行った。ニシン科魚類（Clupeidae）は条鰭綱ニシン目（Actinopterygii; Clupeiformes）に属し，日本近海からは 11 属 19 種が報告されている（青沼・柳下, 2013; Hata and Motomura, 2019a, b）。ニシン科魚類は鯨類等の捕食者の餌生物として重要であり，日本近海で行われた小型ハクジラ類の胃内容物調査において，ニシン科魚類の耳石が発見されているほか（Miyazaki et al., 1991; Shirakihara et al., 2008; Yamazaki et al., 2008），古生物学および考古学的研究においてもニシン科の耳石が発見されている（Aoki, 1968; 大江ほか, 2016; 大江ほか, 2020）。以上の事から，ニシン科魚類は，耳石の形態に基づいた種判別方法の確立が求められている分類群であるといえる。本章では，ニシン科魚類 12 種の耳石の形態記載（ウルメイワシ、マイワシの 2 種については，体成長に伴う耳石の形態変化の検討も行った）および種間での形態比較を行い，各種の標徴形質を見出し，種までの検索表の作成を試みた。

第 2 章では，第 1 章の応用研究として，第 1 章で示した検索表を用いた耳石化石（神奈川県三浦半島の更新統・宮田累層より産出）の同定，および共産した魚類耳石を含む魚類化石群集の数量解析に基づく古環境の推定と古生物地理学的意義に関する考察を行った。

Chapter 1. Comparative otolith morphology and species identification of clupeids from Japan

Introduction

Otoliths are biominerals composed primarily of calcium carbonate layered within a proteinaceous matrix that are found in the inner ears of teleost fishes (Lin and Chang, 2012). Each inner ear usually contains three kinds of otoliths, namely the sagitta, lapillus, and asteriscus. These structures work as static organs and are responsible for the sense of balance, gravity, acceleration and the perception of sound. Fish otoliths show various degrees of species-specific morphology and may constitute a taxonomic tool for species identification (e.g. Lin and Chang, 2012). Also, because they are highly calcified and acellular (Campana, 1999), their degradation after the death of the fish takes considerably longer than bones and soft tissues. For that reason, otoliths are often found in the stomach contents of piscivorous predators such as whales and dolphins even after all other body parts have been digested (e.g. Yamazaki et al., 2008; Mitsui et al., 2014). Otoliths are also frequently found as fossils in ancient geological strata (e.g. Aguilera et al., 2014; Schwarzhans, 2019a), in sea bottom sediments (e.g. Lin et al. 2017, 2018), and in archaeological sites (e.g. Lin et al., 2013; Ohe et al., 2016). Thus, otoliths can be an important source of information regarding the paleo-environment, taphonomy, and feeding habits of ancient civilizations as well as on the ecology of marine fish predators.

The above scientific fields benefit greatly from the existence of systematic descriptions of otolith morphology (e.g. Campana, 2004; Furlani et al., 2007; Lin and Chang, 2012) or comparison with otolith reference collections deposited in research institutions. Ohe (1985) and Iizuka and Katayama (2008) provided a comprehensive description of the otolith morphology of fishes from Japanese waters. Diagnostic features for species identification based on otolith morphology have been described for Gadidae (Frost, 1981), Sciaenidae (Schwarzhans, 1993), Pleuronectiformes (Schwarzhans, 1999), Myctophidae (Schwarzhans, 2013), genus *Scombrops* (Schwarzhans and Prokofiev, 2017), four families of Anguilliformes (Schwarzhans, 2019b), Moridae (Schwarzhans, 2019c) and Trachinoidei (Schwarzhans, 2019d) among others, but are still unavailable for the majority of teleost taxa.

One of these groups is the clupeids (Clupeiformes, Actenopterygii). The clupeids are common pelagic species in marine, estuarine, and in some cases even freshwater environments around the world

(Nelson et al., 2016). Eleven genera and 19 species have been recorded from Japanese waters (Aonuma and Yagishita, 2013; Hata and Motomura, 2019a, b). Clupeid fishes are an important food item for many marine predators and their otoliths are often found in the stomach of whales (Miyazaki et al., 1991; Shirakihara et al., 2008). Fossil otoliths resembling those of extant clupeids have been retrieved in relatively good condition from Quaternary strata in Japan (Aoki, 1968, 1971; Ohe et al., 2020). In addition, an otolith of *Ilisha elongata* was recovered from the shell midden at Saga City, Saga Prefecture, Japan (Ohe et al., 2016). Some studies have dealt with clupeid otolith morphology (Ohe, 1985; Iizuka and Katayama, 2008; Lin and Chang, 2012) but there are still insufficient diagnostic features for species identification. The objective of this study was to develop a species identification guide for clupeid fishes from Japan based on otolith morphology. For this aim, we compared the amount of intra- and interspecific variation in the otolith morphology using 12 species from Japanese waters.

Materials and Methods

Fish and otolith collection. The following species were examined: *Clupea pallasii*, *Etrumeus micropus*, *Herklotsichthys quadrimaculatus*, *Ilisha elongata*, *Konosirus punctatus*, *Nematalosa come*, *Nematalosa japonica*, *Sardinella aurita*, *Sardinella melanura*, *Sardinella zunasi*, *Sardinops melanostictus* and *Spratelloides gracilis*. Classification, scientific and standard Japanese names followed Aonuma and Yagishita (2013) for all species except *E. micropus* and *S. aurita* for which we followed the nomenclature of Randall and DiBattista (2012) and Stern et al. (2017), respectively. All fishes except *H. quadrimaculatus* and *S. zunasi* were collected from fish markets. Specimens of *S. zunasi* from Tokyo Bay were caught by hook and line and were anesthetized and subsequently killed in ice-water. Specimens of *H. quadrimaculatus* from Ogasawara Islands were caught by cast net and also anesthetized and then killed in ice-water. Fish were identified, measured (standard length, SL, to the nearest 0.1 mm), photographed for archival purposes, and the sagittal otoliths were extracted. Otoliths were rinsed with 70 % ethanol and then air dried. All analyzes were performed using only the right otoliths of each fish. Otoliths shown in the figures were photographed using a scanning electric microscope (SEM; Miniscope TM4000 Plus, Hitachi High-Technologies). The number of individuals, the SL and the location of the capture sites are shown in Table 1-1. The type otoliths shown in the figures were deposited in the Kanagawa Prefectural Museum of Natural History (KPMNH), Japan, with the registration code KPM-NI. All other otolith specimens were stored either in the KPMNH or the Laboratory of Population Biology, Tokyo University of Marine Science and Technology (TUMSAT), Japan. Photographs of the fishes were deposited in the Image Database of Fishes of KPMNH, with the registration code KPM-NR.

Morphological description and measurements. The specimens collected for this study comprised adults from all species and adults and young from *E. micropus* and *S. melanostictus*. Hence, the description of the two latter species includes information on the ontogenetic changes in otolith morphology. Morphological terminology and locations of measurements were adapted from Ohe (1985), Secor et al. (1992) and Lin and Chang (2012) (Figs. 1-1a–c). The following features were noted: otolith shape and particularities of the antirostrum, rostrum, excisura, margins of otoliths, sulcus, ostial and caudal collicula, crista superior and inferior, dorsal and ventral areas. Otolith length (OL), otolith height (OH), rostrum length (RL), and antirostrum length (AL) were measured following Ohe (1985) and Secor et al. (1992) to the nearest 0.01 mm on images captured with a digital microscope (VHX-900, KEYENCE, Japan) using the attached measuring software (3D High Dynamic Range plus play software ver. 1.0, KEYENCE, Japan). The OL:OH and AL:RL ratios were calculated as indices of otolith slenderness and excisura depth, respectively. Otolith slenderness based on the OL:OH ratio was classified as "elliptical" ($1.5 < \mathrm{OL:OH} < 2.0$) and "oblong" ($\mathrm{OL:OH} > 2.0$) after Iizuka and Katayama (2008). The relative growth of OL, OH, OL:OH ratio, AL, RL and AL:RL ratio to SL was tentatively described by regression analysis. The existence of inflection points was tested by multiline fitting and Akaike's information criterion (AIC) (Akaike, 1973).

Results

Genus *Clupea* Linnaeus, 1758

Clupea pallasii Valenciennes 1847

(Standard Japanese name: Nishin) (Figs. 1-2a, 3a, Table 1-2)

Description. Otolith ovate and oblong; OL:OH ratio 2.10–2.43 (mean 2.23) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and pointed. Excisura shallow; AL:RL ratio 0.15–0.28 (mean 0.22) (Table 1-2). Dorsal margin approximately straight and poorly crenulated. Ventral margin approximately straight and crenulated. Postrostrum with an excisura minor (Fig. 1-2a, indicated by an arrowhead). Sulcus ostio-caudal and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with a crest-like ridge and poor development in the ratio of 7:3 (Fig. 1-3a). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *C. pallasii* can be distinguished from those of all species examined in this study in the presence of excisura minor and the ostio-caudal sulcus (Figs. 1-2a–2l). Additionally, it is also distinguished from the otoliths of *I. elongata*, *N. come*, *S. melanura*, *S. zunasi* and *S. gracilis* by their oblong shape (Figs. 1-2a, 2d, 2f, 2i, 2j, 2l)..

Genus *Etrumeus* Bleeker, 1853

Etrumeus micropus (Temminck and Schlegel, 1846)

(Standard Japanese name: Urumeiwashi) (Figs. 1-2b, 3b, 4a–c, 5, Table 1-2)

Description. Otolith ovate and oblong; OL:OH ratio 1.87–2.38 (mean 2.19) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum extremely short. Rostrum protruding and pointed. Excisura extremely shallow; AL:RL ratio 0.03–0.25 (mean 0.14) (Table 1-2). Dorsal margin curved dorsally and smooth. Ventral margin straight and serrated. Postrostrum curved posteriorly and smooth, and angled at the postero-dorsal region. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with a ridge-like, absence of any development, and poor development in the ratio of 4:4:2 (Fig. 1-3b). Crista inferior with a crest-like ridge. Dorsal and ventral areas slightly depressed.

Ontogenetic changes. Unlike in adults, the otoliths of small *E. micropus* individuals (smaller than 100 mm SL) are elliptic in shape and the ventral and dorsal margins of the rostrum are round and almost straight, respectively (compare Figs. 1-4a–c). Thus, with growth, the otoliths change from elliptic to oblong in shape and there is an inversion in shape of the ventral and dorsal margins. The OL and OH of *E. micropus* increased proportionally with body size (Fig. 1-5a, 5b) but their ratio becomes asymptotic near the SL of 143 mm (Fig. 1-5c; equations and AIC value are indicated by the figures). The RL increases with body size whereas AL and the AL:RL ratio become asymptotic near the SL of 168 mm (Fig. 1-5d–f; equations and AIC values are indicated by the figures).

Interspecific comparison. Otoliths of *E. micropus* smaller than 100 mm SL were omitted considering abovementioned ontogenetic changes (Table 1-2). Otoliths of *E. micropus* can be distinguished from those of *I. elongata*, *N. come*, *S. melanura*, *S. zunasi* and *S. gracilis* by their oblong shape (Figs. 1-2b, 2d, 2f, 2i, 2j, 2l). In comparison to *C. pallasii*, *H. quadrimaculatus*, *K. punctatus*, *N. japonica*, *S. aurita* and *S. melanostictus*, otoliths of *E. micropus* can be distinguished by their combination of a low AL:RL ratio (below 0.25; Table 1-2), a smooth, curved dorsal margin, a smooth postrostrum without an excisura minor, and an ostial sulcus (Figs. 1-2a–c, 2e, 2g, 2h, 2k).

Genus *Herklotsichthys* Whitley, 1951

Herklotsichthys quadrimaculatus (Rüppell, 1837)

(Standard Japanese name: Mizun) (Figs. 1-2c, 3c, Table 1-2)

Description. Otolith ovate and oblong; OL:OH ratio 1.93–2.30 (mean 2.12) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and blunt. Excisura relatively deep; AL:RL ratio 0.31–0.57 (mean 0.46) (Table 1-2). Dorsal margin smooth and slightly curved at the anterior region. Ventral margin straight and indented; denticles relatively sharp. Postrostrum smooth and angled at the postero-ventral region. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with poor development, a crest-like ridge, and poor development in the ratio of 3:4:3 (Fig. 1-3c). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *H. quadrimaculatus* can be distinguished from those of *I. elongata*, *N. come*, *S. melanura*, *S. zunasi* and *S. gracilis* by their oblong shape (Figs. 1-2c, 2d, 2f, 2i, 2j, 2l). In comparison to *C. pallasii*, *E. micropus*, *K. punctatus*, *N. japonica*, *S. aurita* and *S. melanostictus*, the otoliths of *H. quadrimaculatus* can be distinguished by their combination of an AL:RL ratio ranging 0.31 to 0.57 (Table 1-2), a dorsal margin without a projection, a straight and indented ventral margin, a postrostrum without an excisura minor, and an ostial sulcus (Figs. 1-2a–c, 2e, 2g, 2h, 2k).

Genus *Ilisha* Richardson, 1846

Ilisha elongata (Bennett, 1830)

(Standard Japanese name: Hira) (Figs. 1-2d, 3d, Table 1-2)

Description. Otolith pentagonal and elliptic; OL:OH ratio 1.57–1.86 (mean 1.72) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and sharply pointed. Excisura shallow; AL:RL ratio 0.16–0.48 (mean 0.28) (Table 1-2). Dorsal margin straight and nearly smooth, and angled at the base of the antirostrum. Ventral margin strongly curved and crenulated. Postrostrum straight and smooth, and angled at the postero-dorsal and -ventral regions. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with marked development, a crest-like ridge, the absence of any development, and marked development in the ratio of 2.5:3.5:1:3 (Fig. 1-3d). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *I. elongata* can be distinguished from those of all species examined in this study by their elliptic and pentagonal shape (Figs. 1-2a–l).

Genus *Konosirus* Jordan and Snyder, 1900

Konosirus punctatus (Temminck and Schlegel, 1846)

(Standard Japanese name: Konoshiro) (Figs. 1-2e, 3e, 6a, 6b, Table 1-2)

Description. Otolith ovate and oblong; OL:OH ratio 2.06–2.48 (mean 2.28) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and pointed. Excisura relatively deep; AL:RL ratio 0.30–0.55 (mean 0.46) (Table 1-2). Dorsal margin straight and smooth (Fig. 1-2e, 6a) or sometimes slightly notched (Figs. 6b). Ventral margin straight and crenulated. Postrostrum curved and angled at the postero-dorsal region. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with marked development, a crest-like ridge, and marked development in the ratio of 4.5:4:1.5 (Fig. 1-3e). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *K. punctatus* can be distinguished from those of *I. elongata*, *N.*

come, *S. melanura*, *S. zunasi* and *S. gracilis* by their oblong shape (Figs. 1-2d–f, 2i, 2j, 2l). In comparison to *C. pallasii*, *E. micropus*, *H. quadrimaculatus*, *N. japonica* and *S. melanostictus*, the otoliths of *K. punctatus* can be distinguished by their combination of an AL:RL ratio ranging 0.30 to 0.55, a dorsal margin without a projection, a straight and crenulated ventral margin, a postrostrum without an excisura minor, and an ostial sulcus (Figs. 1-2a–c, 2e, 2g, 2k). The otoliths of *K. punctatus* are very similar to those of *S. aurita* (Figs. 1-2e, 2h). The former species has otoliths with a relatively larger AL:RL ratio (0.30–0.55 (mean±standard deviation (SD): 0.46±0.06) vs. 0.33–0.48 (0.40±0.05)) than the latter, but their ranges overlap widely (Table 1-2).

Genus *Nematalosa* Regan, 1917

Nematalosa come (Richardson, 1846)

(Standard Japanese name: Ryukyudorokui) (Figs. 1-2f, 3f, Table 1-2)

Description. Otolith ovate and elliptic; OL:OH ratio 1.80–2.07 (mean 1.92) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and pointed. Excisura relatively deep; AL:RL ratio 0.53–0.62 (mean 0.57) (Table 1-2). Dorsal margin nearly smooth. Ventral margin curved and uneven. Postrostrum curved and angled at the postero-dorsal and -ventral regions. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with poor development, a crest-like ridge, and poor development in the ratio of 3:5:2 (Fig. 1-3f). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *N. come* can be distinguished from those of *C. pallasii*, *E. micropus*, *H. quadrimaculatus*, *K. punctatus*, *N. japonica*, *S. aurita* and *S. melanostictus* by their elliptic shape (Figs. 1-2a–c, 2e–h, 2k). In comparison to *I. elongata*, *S. melanura*, *S. zunasi* and *S. gracilis*, the otoliths of *N. come* can be distinguished by their combination of an ovate shape, an AL:RL ratio ranging 0.53 to 0.62, and a curved and uneven ventral margin (Figs. 1-2d, 2f, 2i, 2j, 2l, Table 1-2).

Nematalosa japonica Regan, 1917

(Standard Japanese name: Dorokui) (Figs. 1-2g, 3g, Table 1-2)

Description. Otolith ovate and oblong; OL:OH ratio 2.00–2.37 (mean 2.18) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and pointed. Excisura relatively deep; AL:RL ratio 0.50–0.54 (mean 0.52) (Table 1-2). Dorsal margin with a shallow notch and its anterior region slightly curved. Ventral margin curved and uneven. Postrostrum curved and angled at the postero-dorsal region. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with poor development, a crest-like ridge, and poor development in the ratio of 4:4:2 (Fig. 1-3g). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *N. japonica* can be distinguished from those of *I. elongata*, *N. come*, *S. melanura*, *S. zunasi* and *S. gracilis* by their oblong shape (Figs. 1-2d, 2f, 2g, 2i, 2j, 2l). In comparison to *C. pallasii*, *E. micropus*, *H. quadrimaculatus*, *K. punctatus*, *S. aurita* and *S. melanostictus*, the otoliths of *N. japonica* can be distinguished by their combination of an AL:RL ratio ranging 0.50 to 0.54, a dorsal margin without a projection, a curved and uneven ventral margin, a postrostrum without an excisura minor, and an ostial sulcus (Figs. 1-2a–c, 2e, 2g, 2h, 2k, Table 1-2).

Genus *Sardinella* Valenciennes, 1847

Sardinella aurita Valenciennes, 1847

(Standard Japanese name: Kataboshiiwashi) (Figs. 1-2h, 3h, 6c, 6d, Table 1-2)

Description. Otolith ovate and oblong; OL:OH ratio 2.15–2.75 (mean 2.38) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and pointed. Excisura relatively deep; AL:RL ratio 0.33–0.48 (mean 0.40) (Table 1-2). Dorsal margin slightly notched (Fig. 1-2h, 6c) or sometimes straight (Fig. 1-6d). Ventral margin straight and crenulated. Postrostrum curved and angled at the postero-dorsal and -ventral regions. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with poor development, a crest-like ridge, and poor development in the ratio of 3:5:2 (Fig. 1-3h). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *S. aurita* can be distinguished from those of *I. elongata*, *N. come*, *S. melanura*, *S. zunasi* and *S. gracilis* by their oblong shape (Figs. 1-2d, 2f, 2h, 2i, 2j, 2l). In comparison to *C. pallasii*, *E. micropus*, *H. quadrimaculatus*, *N. japonica* and *S. melanostictus*, the otoliths of *S. aurita* can be distinguished by their combination of an AL:RL ratio ranging 0.33 to 0.48, a straight or slightly curved dorsal margin without a projection, a crenulated ventral margin, a postrostrum without an excisura minor, and an ostial sulcus (Figs. 1-2a–c, 2g, 2h, 2k). The otoliths of *S. aurita* are very similar to those of *K. punctatus* (Figs. 1-2e, 2h). The former species has otoliths with a relatively lower AL:RL ratio than the latter (0.33–0.48 (0.40±0.05) vs. 0.30–0.55 (0.46±0.06)), but their ranges overlap widely (Table 1-2).

Sardinella melanura (Cuvier, 1829)

(Standard Japanese name: Oguroiwashi) (Figs. 1-2i, 3i, Table 1-2)

Description. Otolith ovate and elliptic; OL:OH ratio 1.73–2.08 (mean 1.89) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and pointed. Excisura shallow; AL:RL ratio 0.16–0.42 (mean 0.31) (Table 1-2). Dorsal margin straight and poorly crenulated. Ventral margin straight and serrated. Postrostrum slightly curved and angled at the postero-ventral region. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with marked development, ridge-like, and poor development in the ratio of 2:6:2 (Fig. 1-3i). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *S. melanura* can be distinguished from those of *C. pallasii*, *E. micropus*, *H. quadrimaculatus*, *K. punctatus*, *N. japonica*, *S. aurita* and *S. melanostictus* by their elliptic shape (Figs. 1-2a–c, 2e–i, 2k). In comparison to *I. elongata*, *N. come*, *S. zunasi* and *S. gracilis*, the otoliths of *S. melanura* can be distinguished by their combination of an ovate shape, an AL:RL ratio ranging 0.16 to 0.42, a serrated ventral margin, and a crista superior with a ridge-like area (Figs. 1-2d, 2f, 2i, 2j, 2l, Table 1-2).

Sardinella zunasi (Bleeker, 1854)

(Standard Japanese name: Sappa) (Figs. 1-2j, 3j, Table 1-2)

Description. Otolith ovate and elliptic; OL:OH ratio 1.68–2.03 (mean 1.84) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and blunt. Excisura relatively deep; AL:RL ratio 0.21–0.51 (mean 0.37) (Table 1-2). Dorsal margin straight and nearly smooth. Ventral margin straight and indented; denticles blunt. Postrostrum curved and angled at postero-dorsal and -ventral regions. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with poor development, a crest-like ridge, and poor development in the ratio of 3:5:2 (Fig. 1-3j). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *S. zunasi* can be distinguished from those of *C. pallasii*, *E. micropus*, *H. quadrimaculatus*, *K. punctatus*, *N. japonica*, *S. aurita* and *S. melanostictus* by their elliptic shape (Figs. 1-2a–c, 2e, 2g, 2h, 2j, 2k). In comparison to *I. elongata*, *N. come*, *S.melanura* and *S. gracilis*, the otoliths of *S. zunasi* can be distinguished by their combination of an ovate shape, an AL:RL ratio ranging 0.21 to 0.51, an indented ventral margin, blunt dentitions, and a crista superior showing an area with a crest-like ridge (Figs. 1-2d, 2f, 2i, 2j, 2l, Table 1-2).

Genus *Sardinops* Hubbs, 1929

Sardinops melanostictus (Temminck and Schlegel, 1846)

(Standard Japanese name: Maiwashi) (Figs. 1-2k, 3k, 4d–f, 7, Table 1-2)

Description. Otolith ovate and oblong; OL:OH ratio 2.12–2.91 (mean 2.46) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed. Rostrum protruding and pointed. Excisura shallow; AL:RL ratio 0.15–0.36 (mean 0.25) (Table 1-2). Dorsal margin nearly straight with a projection at the center (Fig. 1-2k, indicated by an arrowhead). Ventral margin straight and serrated. Postrostrum strongly curved and angled at the postero-dorsal and -ventral regions. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with poor development, a crest-like ridge, and poor development in the ratio of 2:5:3 (Fig. 1-3k). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Ontogenetic changes. The otoliths of small *S. melanostictus* have a ridge on the anterior region of the crista superior and no dorsal projection (Fig. 1-4d). With growth, particularly above 100 mm SL, the ridge on the anterior region of the crista superior becomes inconspicuous and a projection appears in the center of the dorsal margin (Figs. 1-4e, 4f). Values of OL, OH, AR, AL, and their ratios are lower in small individuals and increase with body growth, but without an asymptote (Figs. 1-7a–f).

Interspecific comparison. Otoliths of *S. melanostictus* smaller than 100 mm SL were omitted considering the abovementioned ontogenetic changes (Table 1-2). Otoliths of this species can be easily distinguished from those of all species examined in this study by their nearly straight dorsal margin with a projection (Figs. 1-2a–2l). In addition, it can be distinguished from the otoliths of *I. elongata*, *N. come*, *S. melanura*, *S. zunasi* and *S. gracilis* by their oblong shape (Figs. 1-2d, 2f, 2i–l). In comparison to *C. pallasii*, *E. micropus*, *H. quadrimaculatus*, *N. japonica* and *S. aurita*, the otoliths of *S. melanostictus* can be also distinguished by their combination of an AL:RL ratio ranging 0.15 to 0.36, a straight and serrated ventral margin, a smooth postrostrum without an excisura minor, and an ostial sulcus (Figs. 1-2a–c, 2e, 2g, 2h, 2k, Table 1-2).

Genus *Spratelloides* Bleeker, 1851

Spratelloides gracilis (Temminck and Schlegel, 1846)

(Standard Japanese name: Kibinago) (Figs. 1-2l, 3l, Table 1-2)

Description. Otolith spindle and elliptic; OL:OH ratio 1.68–1.98 (mean 1.88) (Table 1-2). Inner face slightly convex. Outer face slightly concave. Antirostrum short and pointed or indistinct. Rostrum protruding and pointed. Excisura shallow or indistinct; AL:RL ratio 0–0.41 (mean 0.15) (Table 1-2). Dorsal margin curved and smooth. Ventral margin strongly curved, smooth and poorly serrated at the anterior and posterior regions, respectively. Posterior margin curved and smooth. Sulcus ostial and funnel-like. Ostial colliculum deeper than caudal colliculum. Crista superior showing areas with ridge-like, absence of any development, and poor development in the ratio of 6:2:2 (Fig. 1-3l). Crista inferior with a crest-like ridge. Dorsal area depressed. Ventral area slightly depressed.

Interspecific comparison. Otoliths of *S. gracilis* can be distinguished from those of all species examined in this study by their elliptic and spindle shape (Figs. 1-2a–l).

Discussion

Examination of the morphological features on the otoliths of 12 clupeids in Japan revealed a mixture of agreement and disagreement with current taxonomical classifications. Otoliths of *I. elongata* and *S. gracilis* are pentagonal or spindle-shaped while those of the other species are ovate (Figs. 1-2a–2l). These results support recent phylogenetic analysis by Egan et al. (2018) suggesting that genera *Ilisha* and *Spratelloides* should be classified into Pristigasteridae (sister to Engraulidae) and Spratelloidinae (sister to all other Clupeoidei examined in Egan et al. (2018)), respectively. On the other hand, there were several instances of convergent and divergent morphology, rendering it impossible to prepare a simple, straightforward flow-chart following the currently accepted taxonomic classification or one that is based on one single morphological feature of the otoliths. For example, in the genus *Sardinella*, one species (*S. aurita*, Fig. 1-2h) has an oblong otolith with crenulated ventral margin whereas the other two species have elliptical otoliths with the ventral margin either indented (*S. zunasi*, Fig. 1-2j) or serrated (*S. melanura*, Fig. 1-2i), characteristics which in turn are found also in other genera. In contrast, *K. punctatus* and *S. aurita*, which belong to different genera, have otoliths with similar marginal structures (Figs. 1-2e, 2h). Moreover, there was always an inherent degree of individual variation in otolith morphology, which is most clearly evidenced in the great overlap and absence of clear-cut values from morphological measurements (e.g. OL:OH and AL:RL ratios). Nevertheless, this guide and a simplified version provided for quick reference (Fig. 1-8) make possible to identify clupeid otoliths by comparing and matching the morphological features of the specimens with the key features described in this study.

A word of caution is necessary in that the current otolith-based taxonomic key applies only to specimens in the size ranges shown in Table 1-2, together with the summary of morphological features. Utilization for otoliths from younger fish is precluded by the marked ontogenetic changes in otolith morphology, as we showed for two species (*E. micropus* and *S. melanostictus*). These changes were especially evident in the outline shape and in the OL:OH and AL:AR ratios, particularly in the former species. Ontogenetic changes in otolith morphology are caused by changes in the direction of accretion growth which may be initiated by physiological, environmental or ecological factors (Katayama, 2018). The discontinuous changes in OL:OH and AL:RL ratios in *E. micropus* (Figs. 1-5c, 5d, 5f), for instance, might indicate a progressively slowdown in the growth of the antirostrum. Changes in the OL:OH ratio with body growth have been shown also in *I. elongata*, *K. punctatus*, *S. zunasi* and *S. gracilis* (Iizuka and Katayama, 2008) and other taxa such as in sciaenids from Rio de la Plata (Waessle et al., 2003). The

OL:OH ratio has been historically utilized as a diagnostic feature and may constitute a valuable tool for species identification (e.g. Schwarzhans, 2013), but, as the results of this study indicate, proper consideration of the ontogenetic changes is required. It is also necessary to consider thoroughly the degree of integrity of the otoliths during examination. Clupeid otoliths in relatively good condition have been retrieved from the alimentary tract of predators, fossiliferous strata, or shell middens and have been successfully used for species identification (e.g. Aoki, 1968, 1971; Miyazaki et al., 1991; Shirakihara et al., 2008; Ohe et al., 2016; Schwarzhans, 2019a). However, external features of the otoliths are prone to be abraded chemically or physically under digestion in the stomach of predators or taphonomic processes (Nolf, 1985; Wijnsma et al., 1999). Needless to say, eroded otoliths should be inspected only based on undamaged, remaining diagnostic features.

In resume, description of the diagnostic features of fish otoliths has the potential to provide new insights on fisheries ecology including the feeding habits of endangered animals. In fact, otolith analysis has contributed valuable information on the life history of whales and dolphins (e.g. Nemoto, 1959; Miyazaki et al., 1991) and commercial marine resources such as Pacific bluefin tuna *Thunnus orientalis* (Shimose et al., 2013) and flying squid *Ommastrephes bartramii* (Watanabe et al., 2004). It should also contribute to our understanding on the paleo-environment, -ecology, -biogeography, and evolution of fishes based on fossil otoliths and on ancient fisheries by studying otolith remains from archaeological sites. The information provided in this study is the first systematic approach concerning the otoliths of Japanese clupeids. Future studies should examine the remaining clupeid species not included in this study (e.g. *Amblygaster leiogaster*, *Amblygaster sirm*, *Dussumieria elopsoides*, *Sardinella alcyone*, *Sardinella electra*, *Spratelloides atrofasciatus* and *Spratelloides delicatulus*; Aonuma and Yagishita, 2013; Hata and Motomura, 2019a, b) and fully scrutinize the ontogenetic changes in the otolith of all species. Due consideration should be paid also to the usefulness of other morphometrical methods (e.g. Tuset et al., 2016; He et al., 2018).

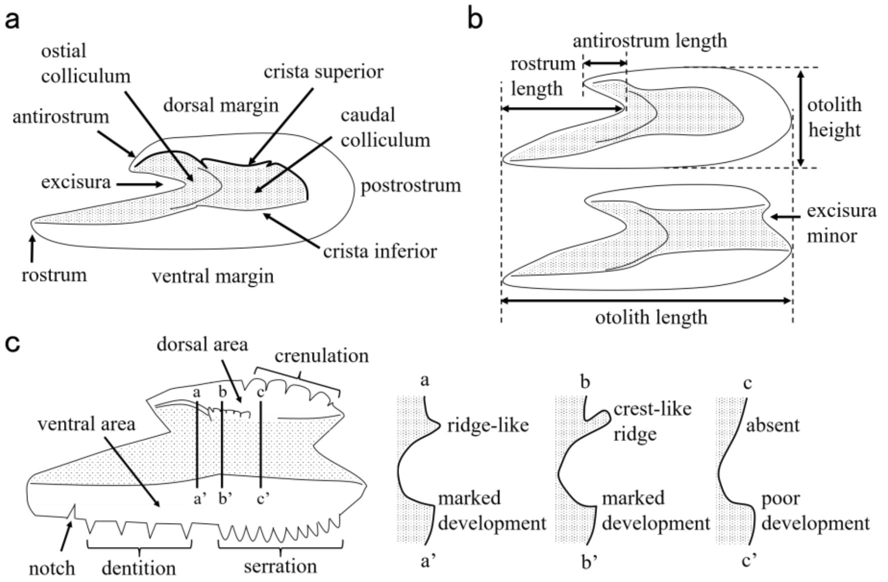

Fig. 1-1 Morphological terminology (**a**), locations of measurements in otoliths (**b**) with an ostial sulcus (above) and with an ostio-caudal sulcus and excisura minor (below), and definitions of surface structures of the otoliths (**c**).

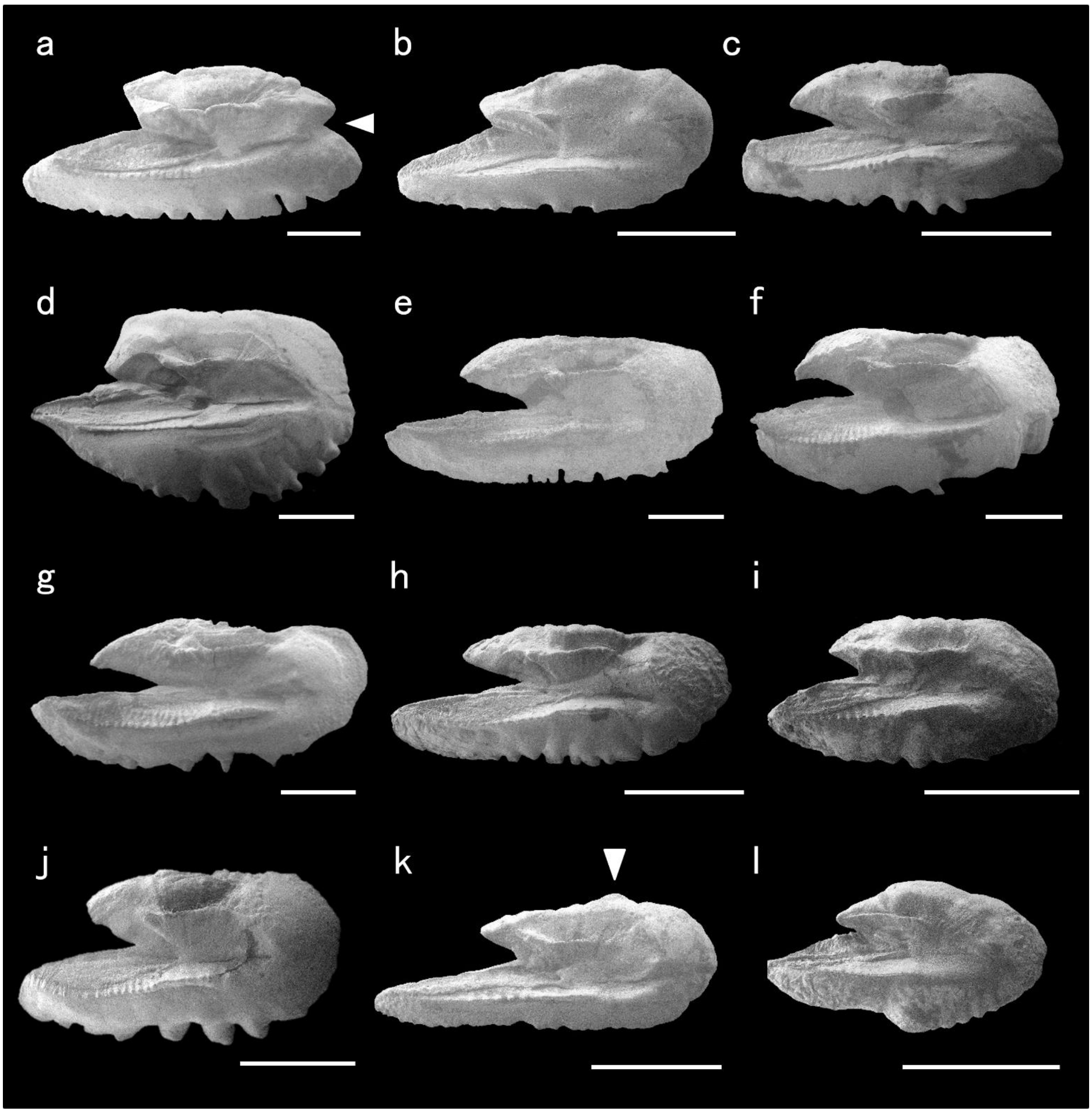

Fig. 1-2. Otoliths of clupeid fishes from Japan examined in this study (right sagitta; codes indicate accession number in the collection of the Kanagawa Prefectural Museum of Natural History). *Clupea pallasii*, KPM-NI 35544, 275.7 mm SL, 5.14 mm OL (**a**); *Etrumeus micropus*, KPM-NI 35514, 140.6 mm SL, 2.91 mm OL (**b**); *Herklotsichthys quadrimaculatus*, KPM-NI 35542, 90.7 mm SL, 2.64 mm OL (**c**); *Ilisha elongata*, KPM-NI 49972, 224.3 mm SL, 5.26 mm OL (**d**); *Konosirus punctatus*, KPM-NI 35546, 221.7 mm SL, 5.21 mm OL (**e**); *Nematalosa come*, KPM-NI 35550, 195.9 mm SL, 4.55 mm OL (**f**); *Nematalosa japonica*, KPM-NI 35549, 184.9 mm SL, 5.16 mm OL (**g**); *Sardinella aurita*, KPM-NI 35534, 141.3 mm SL, 3.12 mm OL (**h**); *Sardinella melanura*, KPM-NI 35536, 75.8 mm SL, 1.99 mm OL (**i**); *Sardinella zunasi*, KPM-NI 35538, 120.8 mm SL, 3.07 mm OL (**j**); *Sardinops melanostictus*, KPM-NI 35529, 130.7 mm SL, 2.74 mm OL (**k**); *Spratelloides gracilis*, KPM-NI 35520, 82.6 mm SL, 1.88 mm OL (**l**). Scale bars below otolith images represent 1 mm. Arrowheads indicate an excisura minor and a projection in otoliths of *C. pallasii* and *S. melanostictus*, respectively.

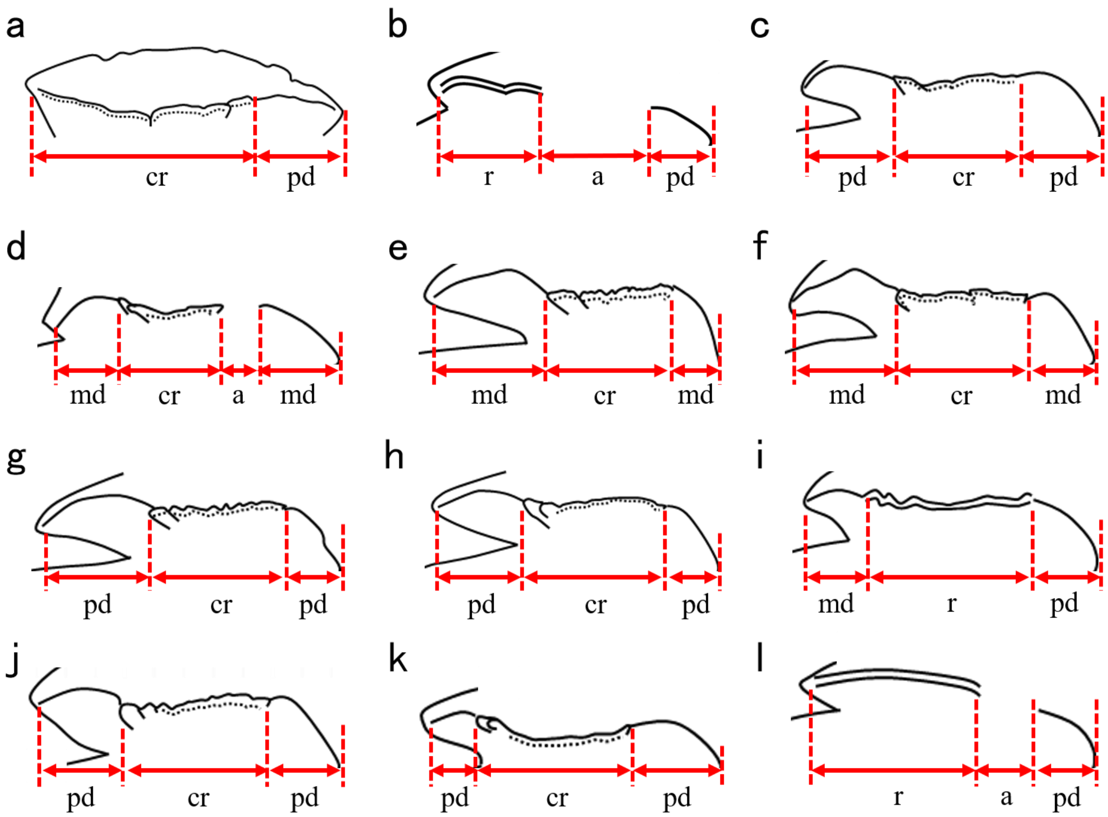

Fig. 1-3. Morphological features of the crista superior in *Clupea pallasii* (**a**), *Etrumeus micropus* (**b**), *Herklotsichthys quadrimaculatus* (**c**), *Ilisha elongata* (**d**), *Konosirus punctatus* (**e**), *Nematalosa come* (**f**), *Nematalosa japonica* (**g**), *Sardinella aurita* (**h**), *Sardinella melanura* (**i**), *Sardinella zunasi* (**j**), *Sardinops melanostictus* (**k**), *Spratelloides gracilis* (**l**). Letters indicate morphological features as follows: r: ridge-like, a: absence of development, pd: poor development, cr: crest-like ridge, md: marked development.

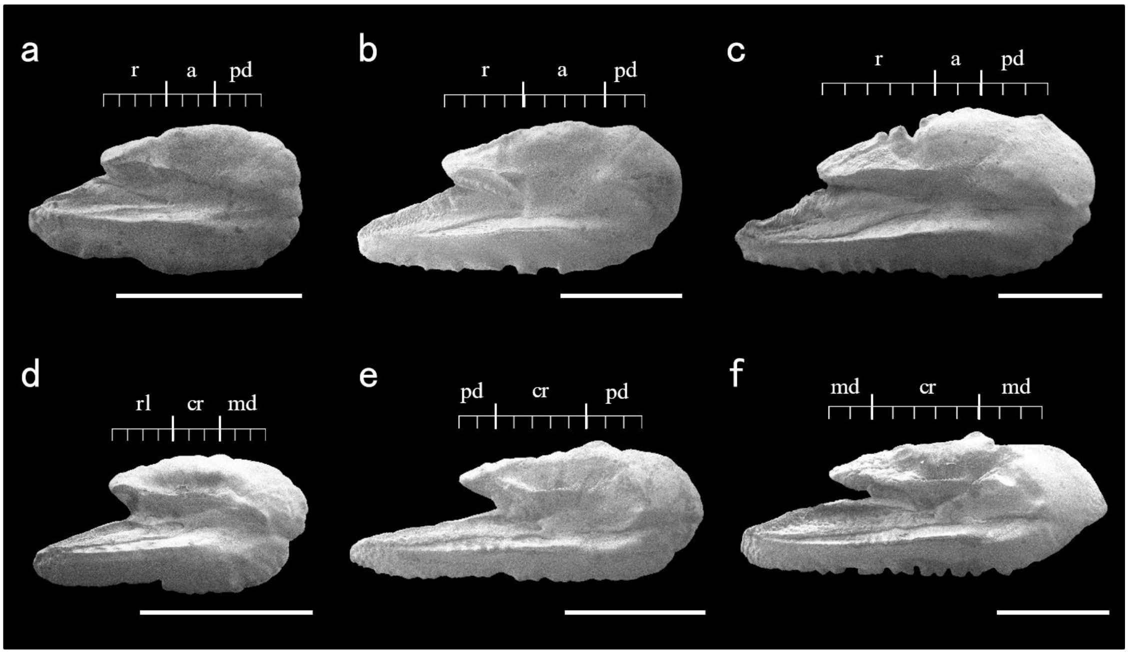

Fig. 1-4. Changes in otolith (right sagitta) morphology with growth in *Etrumeus micropus* (**a–c**) and *Sardinops melanostictus* (**d–f**) (codes indicate accession number in the collection of the Kanagawa Prefectural Museum of Natural History). **a** KPM-NI 35517, 64.6 mm SL, 1.61 mm OL; **b** KPM-NI 35514, 140.6 mm SL, 2.91 mm OL; **c** KPM-NI 35525, 197.3 mm SL, 3.82 mm OL; **d** KPM-NI 35531, 83.5 mm OL, 1.76 mm OL; **e** KPM-NI 35529, 130.7 mm SL, 2.74 mm OL; **f** KPM-NI 35530, 171.7 mm SL, 3.53 mm OL. Scales above the otoliths indicate the length of the crista superior with 10 reference units and letters indicate morphological features as follows: r: ridge, a: absence of any development, pd: poor development, cr: crest-like ridge, md: marked development. Scale bars below the otoliths represent 1 mm.

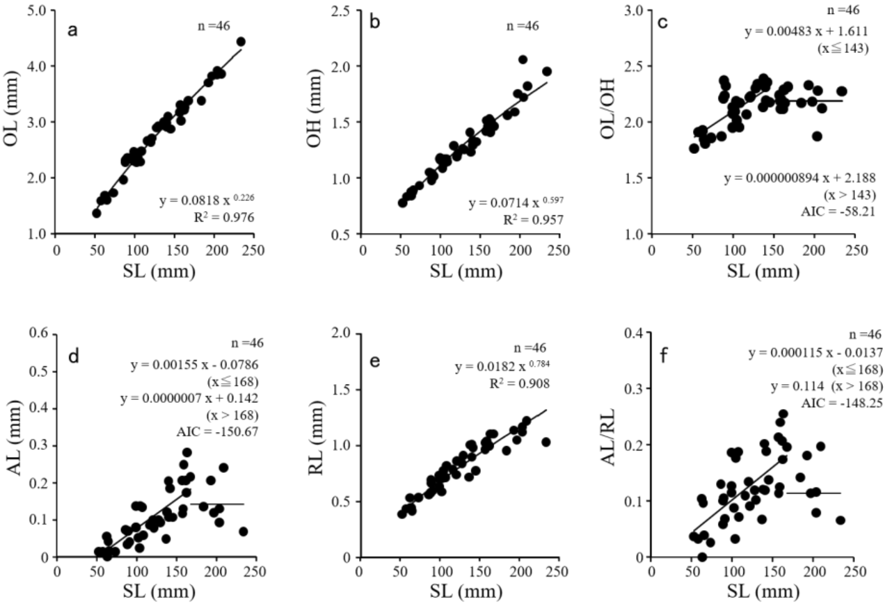

Fig. 1-5. Relationships between standard length and otolith length, otolith height, antirostrum length, and rostrum length and their ratios in *Etrumeus micropus*.

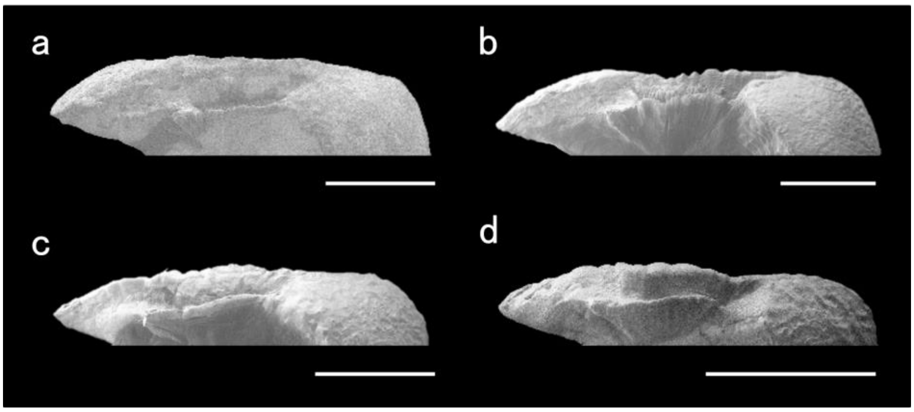

Fig.1-6. Intraspecific morphological variation in the shape of the dorsal margin in *Konosirus punctatus* and *Sardinella aurita* (codes indicate accession number in the collection of the Kanagawa Prefectural Museum of Natural History). a, b: *Konosirus punctatus* with a dorsal margin straight (KPM-NI 35546, 221.7 mm SL, 5.21 mm OL) or notched and curved at the anterior region (KPM-NI 35547, 231.3 mm SL, 5.46 mm OL), respectively; c, d: *Sardinella aurita* with a dorsal margin straight (KPM-NI 53585, 200.2 mm SL, 4.49 mm OL) or notched and curved at the anterior region (KPM-NI 35534, 141.3 mm SL, 3.12 mm OL), respectively. Scale bars below otolith images represent 1 mm.

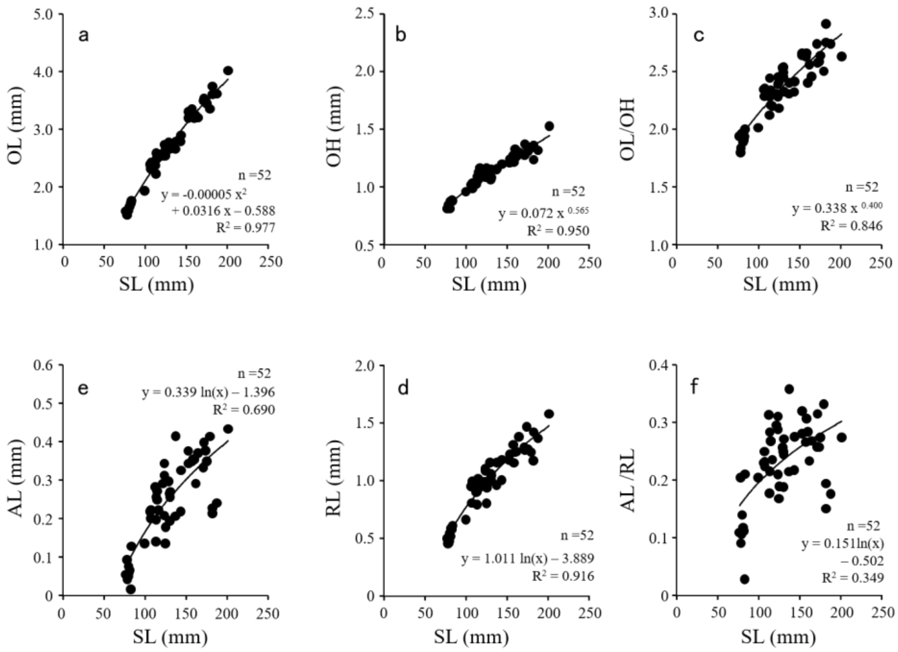

Fig. 1-7. Relationships between standard length and otolith length, otolith height, antirostrum length, rostrum length and their ratios in *Sardinops melanostictus*.

	Species	OL:OH	AL:RL	Otolith shape	Ventral margin	Excisura minor	Dorsal margin	Crista superior
a	*Clupea pallasii*	2.10–2.43 (2.23±0.12)	0.15–0.28 (0.22±0.04)	ovate	straight, crenulated	present	straight	cr : pd = 7 : 3
b	*Etrumeus micropus*	1.87–2.38 (2.19±0.12)	0.03–0.25 (0.14±0.06)	ovate	straight, serrated	absent	round	r : a : pd = 4 : 4 : 2
c	*Herklotsichthys quadrimaculatus*	1.93–2.30 (2.12±0.09)	0.31–0.57 (0.46±0.06)	ovate	straight, indented	absent	straight	pd : cr : pd = 3 : 4 : 3
d	*Ilisha elongata*	1.57–1.86 (1.72±0.10)	0.16–0.48 (0.28±0.08)	pentagonal	curved, crenulated	absent	straight	md : cr : a : d = 2.5 : 3.5: 1 : 3
e	*Konosirus punctatus*	2.06–2.48 (2.28±0.12)	0.30–0.55 (0.46±0.06)	ovate	straight, crenulated	absent	straight or notched	md : cr : md = 4.5 : 4 : 1.5
f	*Nematalosa come*	1.80–2.07 (1.92±0.09)	0.53–0.62 (0.57±0.04)	ovate	curved, uneven	absent	straight	md : cr : md = 3 : 5 : 2
g	*Nematalosa japonica*	2.00–2.37 (2.18±0.18)	0.50–0.54 (0.52±0.02)	ovate	curved, uneven	absent	concave	pd : cr : pd = 4 : 4 : 2
h	*Sardinella aurita*	2.15–2.75 (2.38±0.16)	0.33–0.48 (0.40±0.05)	ovate	straight, crenulated	absent	notched or straight	pd : cr : pd = 3 : 5 : 2
i	*Sardinella melanura*	1.73–2.08 (1.89±0.07)	0.16–0.42 (0.31±0.07)	ovate	straight, serrated	absent	straight	md : r : pd = 2 : 6 : 2
j	*Sardinella zunasi*	1.68–2.03 (1.84±0.09)	0.21–0.51 (0.37±0.08)	ovate	straight, indented	absent	straight	pd : cr : pd = 3 : 5 : 2
k	*Sardinops melanostictus*	2.12–2.91 (2.46±0.18)	0.15–0.36 (0.25±0.05)	ovate	straight, serrated	absent	1 projection	pd : cr : pd = 2 : 5 : 3
l	*Spratelloides gracilis*	1.68–1.98 (1.88±0.07)	0–0.41 (0.15±0.09)	spindle	strongly curved	absent	round	r : a : pd = 6 : 2 : 2

Fig. 1-8. Descriptive keys for the otoliths of 12 clupeid species from Japan. "n" indicates the number of the otoliths analyzed. Letters indicate morphological features as follows: OL: otolith length; OH: otolith height; AL: antirostrum length; RL: rostrum length, r: ridge, a: absence of any development, pd: poor development, cr: crest-like ridge, md: marked development.

Table 1-1. Standard length (SL), location of capture, and number of fishes (n) used in this study.

Species	SL (mm)	Location of capture	n
Clupea pallasii	194.7–290.7	Off Hokkaido	2
		Off Aomori	7
Etrumeus micropus	52.7–234.0	Sagami Bay, off Kanagawa	43
		Kagoshima Bay, off Kagoshima	3
Herklotsichthys quadrimaculatus	90.0–130.6	Nago Bay, off Okinawa	25
		Chichijima, Ogasawara Islands	29
Ilisha elongata	164.9–456.5	Ariake Sea, off Nagasaki	12
Konosirus punctatus	157.8–253.6	Sagami Bay, off Kanagawa	12
Nematalosa come	186.4–222.8	Nakagusuku Bay, off Okinawa	6
Nematalosa japonica	161.1–184.9	Nakagusuku Bay, off Okinawa	4
Sardinella aurita	108.0–236.1	Sagami Bay, off Kanagawa	16
		Kagoshima Bay, off Kagoshima	2
Sardinella melanura	57.0–86.6	Kadogawa Bay, off Miyazaki	20
Sardinella zunasi	69.4–126.2	Tokyo Bay, off Tokyo	9
		Sagami Bay, off Kanagawa	7
Sardinops melanostictus	76.9–201.4	Sagami Bay, off Kanagawa	52
Spratelloides gracilis	52.3–92.9	Sagami Bay, off Kanagawa	23

Table 1-2. Results of measurements on the otoliths of 12 Clupeid species from Japan.

Species	n	Otolith length (OL, range, mm)	Otolith height (OH, range, mm)	Antirostrum length (AL, range, mm)	Rostrum length (RL, range, mm)	OL:OH (mean ± S.D.)	AL:RL (mean ± S.D.)
Clupea pallasii	9	4.36–5.25	1.84–2.38	0.28–0.49	1.54–1.90	2.10–2.43 (2.23±0.12)	0.15–0.28 (0.22±0.04)
Etrumeus micropus	31	2.27–4.43	1.09–2.06	0.02–0.28	0.58–1.22	1.87–2.38 (2.19±0.12)	0.03–0.25 (0.14±0.06)
Herklotsichthys quadrimaculatus	54	2.43–3.14	1.18–1.45	0.25–0.54	0.65–1.04	1.93–2.30 (2.12±0.09)	0.31–0.57 (0.46±0.06)
Ilisha elongata	12	3.88–8.14	2.36–4.54	0.23–0.67	1.04–2.43	1.57–1.86 (1.72±0.10)	0.16–0.48 (0.28±0.08)
Konosirus punctatus	12	4.16–5.75	1.88–2.54	0.51–1.31	1.40–2.57	2.06–2.48 (2.28±0.12)	0.30–0.55 (0.46±0.06)
Nematalosa come	6	4.21–5.32	2.35–2.72	0.72–1.06	1.37–1.87	1.80–2.07 (1.92±0.09)	0.53–0.62 (0.57±0.04)
Nematalosa japonica	4	4.16–5.16	1.93–2.25	0.76–1.06	1.51–1.96	2.00–2.37 (2.18±0.18)	0.50–0.54 (0.52±0.02)
Sardinella aurita	18	2.53–4.66	1.14–1.94	0.31–0.85	0.89–1.76	2.15–2.75 (2.38±0.16)	0.33–0.48 (0.40±0.05)
Sardinella melanura	20	1.40–2.17	0.81–1.11	0.10–0.27	0.46–0.81	1.73–2.08 (1.89±0.07)	0.16–0.42 (0.31±0.07)
Sardinella zunasi	16	1.98–3.31	1.09–1.64	0.17–0.50	0.65–1.12	1.68–2.03 (1.84±0.09)	0.21–0.51 (0.37±0.08)
Sardinops melanostictus	42	2.23–4.01	0.99–1.53	0.14–0.43	0.79–1.58	2.12–2.91 (2.46±0.18)	0.15–0.36 (0.25±0.05)
Spratelloides gracilis	23	1.34–2.11	0.74–1.09	0–0.15	0.29–0.63	1.68–1.98 (1.88±0.07)	0–0.41 (0.15±0.09)

Chapter 2. Fossil fish otoliths from the Chibanian Miyata Formation, Kanagawa Prefecture, Japan, with comments on the paleoenvironment

Introduction

On the coast of southern Kanto, where the confluence of the warm Kuroshio and cold Oyashio Currents takes place, the fish fauna is characterized by a rich species diversity (e.g. Senou et al., 2006; Kohno, 2011). However, the historical processes shaping such a rich marine fish fauna are still unclear. Fossil records of fishes can provide paleontological evidence as to how modern fish fauna have established. Correct identification based on well-preserved body fossils allows us to address detailed evolutionary, paleobiogeographical and paleoenvironmental questions (Yabumoto, 2019), but the localities yielding such material are limited in Japan. On the other hand, partial fish remains are often abundant in fossiliferous beds (Takahashi, 2000). Teleostean otoliths and chondrichthyan teeth, for example, have been used in paleobiogeographical or paleoenvironmental studies (e.g., Kawase and Nishimatsu, 2016; Schwarzhans and Ohe, 2019).

The Kanto Plateau was mostly covered by the Paleo-Tokyo Bay during the transgressive periods of the Middle-Late Pleistocene (about 0.5–0.1 Ma; Sugai et al., 2013). Teleostean otoliths (Aoki, 1968, 1971; Aoki and Baba, 1980; Takahashi and Fukuda, 1991) and chondrichthyan teeth (Uyeno and Matsushima, 1979; Goto et al., 1984; Naruse et al., 1994; Tanaka, 1997; Taru and Matsushima, 1998; Fujii et al., 2010) were reported from the Pleistocene strata of this area, but related paleontological data is still fragmentary.

Recently, one of the authors (SM) collected fossil fish otoliths and teeth from the Sha’ana Tuffaceous Sand Member, Miyata Formation (Middle Pleistocene: Chibanian), in the southwesternmost region of the Paleo-Tokyo Bay (Kikuchi, 1980). Fish remains from this formation are not uncommon. However, only one taxon, namely *Odontaspis* sp., has been described from the Tsukuihama Sandy Gravel Member (Taru and Matsushima, 1998). In spite of their significance in understanding the regional paleoichthyofauna, no fossil records from the Sha’ana Tuffaceous Sand Member have ever been described.

The objective of this study is therefore to reconstruct the paleoichthyofauna from fossil fish otoliths and teeth and interpret the associated paleoenvironment of the Miyata Formation, and to reveal the formative processes of marine ichthyofauna in southern Kanto.

Geological setting

The Miyata Formation was firstly described by Aoki (1925) and further investigated by subsequent geologists (Okumura et al., 1977; Kanie and Ohkoshi, 1981; Kasama and Shioi, 2019). Okumura et al. (1977) subdivided this formation into five members according to its lithology: the Sugaruya Sand Member, the Tsukuihama Sandy Gravel Member, the Koenbo Sand Member, the Sha'ana Tuffaceous Sand Member, and the Itchoda Sand Member in the ascending order (Fig. 2-1). Recently, Kasama and Shioi (2019) recognized four units (A–D in Fig. 2-1) in this formation with angular unconformity. Our fossil material was collected from the Sha'ana Tuffaceous Sand Member.

The estimated age of the Sha'ana Tuffaceous Sand Member varies with different approaches. By using Electron Spin Resonance, Toyota and Okumura (2000) estimated an age of 0.325±0.40 Ma, while results of calcareous nannofossils indicated 1.22–0.44 Ma (small *Gephyrocapsa* Zone or *Pseudoemiliania lacunosa* Zone of Gartner, 1977; Yamaguchi et al., 1983) and 1.02–0.46 Ma (CN14a Subzone of Okada and Bukry, 1980; Kanie et al., 2000). More recently, Kasama and Shioi (2019) estimated Ft and U-Pb ages of 0.41±0.07 Ma by using zircon minerals of the Funakubo Tuff (Fn in Fig. 2-1) which is intercalated in the unit C. However, the correlation of unit C is yet to be explored.

Fossil molluscs (Okumura et al., 1979, 2005), brachiopods (Kuramochi and Katsuzawa, 1999), barnacles (Kanie et al., 2000) and ophiuroids (Okanishi et al., 2019) have been collected and studied.

Material and methods

Locality, lithology, and preservation. The sampling site was an exposure in Sha'ana-dai, Kamimiyada, Minami-Shitaura Town, Miura City, Kanagawa Prefecture, Japan (Fig. 2-2, see also Fig. 1 in Okanishi et al., 2019). Sediments were generally semi-consolidated, poorly-sorted, and contained pumice, scoria, and pebbles (diameter < 14 mm), which corresponded to the lithology of the Sha'ana Tuffaceous Sand Member (Okumura et al., 1977).

The lithology of the exposure (section) was examined in detail by subdividing into 11 levels with intervals of 10 cm each (SH01–SH11), and 80 g of sediments were analyzed for their mud contents (after Kitazaki and Majima, 2003). The result allowed us to recognize two horizons in the exposure: the upper sandy mud (SH01–SH07) and the lower muddy sand (SH08–SH11) horizons (Fig. 2-3).

An articulated shell of Mizuhopecten tokyoensis was buried in SH02 in life position. Additional articulated shells of *Cyclocardia ferruginea*, *Acira mirabilis*, *Jupitaria* (*Saccella*) *gordonis*, *Nuculana yokoyamai*, and *Macoma carcarea* were found in SH01–SH07, and shells of *C. ferruginea*, *N. yokoyamai*, and *Anomia chinensis* were found in SH08–SH11. Large, disarticulated shells of *M. tokyoensis* were accumulated in SH09–SH10. Gastropods (*Homalopoma amussitatum*, *Niveotectura pallida*, and *Puncturella nobilis*, etc.), brachiopods, foraminifers, and fragments of polyplacophores, gorgonaceans, decapods, barnacles, bryozoans and echinoids were abundant in all levels. The majority of fossils thus showed allochthonous preservation.

About five kg of sediments from each of the 11 levels were collected from Nov. 21, 2018 to March 13, 2019. An additional sample (about 40 kg) from SH03–SH06 (unlocalized; collected from Aug. 2, 2009 to Nov. 29, 2017) was also used. Sediments were boiled after weighing dry weight, wet sieved using a mesh size of 0.5 mm, and then air-dried. Fish remains were picked from this residue. Examined materials were deposited in the paleovertebral collection (with registration code KPM-NNV) in the Kanagawa Prefectural Museum of Natural History (KPMNH).

Sampling, preparation, and measurement. Fossils were measured to the nearest 0.1 mm on digital images captured with a digital microscope (VHX-900, KEYENCE, Japan) using the measuring software (VHX-900 3D High Dynamic Range plus play software ver. 1.0, KEYENCE, Japan). "+" was attached after measurements if the specimen was incomplete and/or broken during processing. Fossils shown in the figures were mostly photographed using the digital microscope but a scanning electron microscope (SEM; Miniscope TM4000 Plus, Hitachi High-Technologies) was occasionally used if higher resolution was necessary. Otoliths of extant species for comparison were photographed by SEM and measured to the nearest 0.1 mm.

Paleoenvironmental analysis. We applied the paleobathymetric method of Nolf and Brzobohaty (1994) with a modification to estimate the water depth of the fish assemblages deposited. In this method, vertical bathymetric distribution of the fish taxa in each fossil assemblage is estimated by their recent analogues. Number of potential presences (expressed as the number of species and specimens) for each 50 m depth interval is calculated and expressed as a percentage of the total number of species and specimens. Paleobathymetry was separately analyzed using all taxa and only the benthic/benthopelagic (B/B) taxa, because the latter are often a better indicator of the water depth (Lin et al., 2016, 2017).

For paleoclimatic estimation, we compared the richness and abundance of our fossil materials with those of the extant fishes which are classified into various climatic zone categories: arctic/subarctic (AS), cold temperate (CT), temperate (TP), warm temperate (WT), temperate–tropical (TT), and tropical–subtropical (TS). We finally removed the TS category in the analysis since no remains of fishes related to this zone were recovered. Richness and abundance are expressed as percentage of the total number of species and specimens involved in the analysis.

Results

Systematic paleontology. A total of 1,675 fish remains were collected of which 1,389 were identified to at least 62 taxa belonging to 20 orders and 31 families (Table 2-1). Classification of fishes followed Nelson et al. (2016). Scientific names of the species followed Nakabo (2013a), Amaoka (2016), Last et al (2016), and Schwarzhans and Prokofiev (2017) except for the class Actinopterygii which followed Schwarzhans et al. (2020). The abbreviation “cf.” was used for incomplete specimens, and “aff.” was used when specific identity could not be reached unequivocally. All fossil otoliths are sagittae, and the reference collection is deposited in KPMNH with the registration code KPM-NI, Natural History Museum and Institute, Chiba with the registration code CBM-ZF, and Kagoshima University Museum with the registration code KAUM-I.

Important taxa are briefly described below and other taxa are described in Appendix A. Morphological terminologies of otoliths followed Schwarzhans (1999), Lin and Chang (2012), Schwarzhans (2013), and Nolf (2013), and those of chondrichthyan teeth followed Cappetta (2012). Measurements of specific characters were taken following Nolf (2013) and Schwarzhans (2013, 2014). Abbreviations are as follows: OL: otolith length, OH: otolith height, AL: antirostrum length, RL:

rostrum length, CL: colliculum length, OCL: ostial colliculum length, CCL: caudal colliculum length, OsL: ostium length, CaL: caudal length.

Class Chondrichthys Huxley, 1880

Order Carchariniformes Campagno, 1977

Family Triakidae Gray, 1851

Genus *Hypogaleus* Smith, 1957

*Hypogaleu*s cf. *hyugaensis* (Miyoshi, 1939)

(Standard Japanese name: None) (Fig. 2-4a, 4a')

Material. KPM-NNV 924: n=1, jaw tooth, 4.84 + mm Labial crown height, 5.58 + mm Lingual crown height, 4.59 + mm Maximum crown width, bulk sample (Fig. 2-4a, 4a').

Description. The tooth crown has a sigmoidal shaped primary cusp and two distal cusplets. The mesial cusplet is absent. The cutting edges of the primary cusp are smooth. The length of the distal cutting edge of the primary cusp is approximately 3.14 times as long as the length of mesial one. The labial face is approximately flat. The lingual face is convex. The ornamentation on the surface of the tooth crown is absent. The root is not preserved.

Remarks. The tooth is comparable to those of *H. hyugaensis* in the following characters: a sigmoidal primary cusp, having at least two distal cusplets, the length of the mesial cutting edge is three times as long as the mesial one (Herman et al., 1991). However, the specimen is lacking the root.

Order Squaliformes Goodrich, 1909

Family Squalidae Bonaparte, 1834

Genus *Squalus* Linnaeus, 1758

Squalus sp.

(Standard Japanese name: None) (Fig. 2-4b, 4b')

Material. n=1. KPM-NNV 1500: jaw tooth, 1.39 mm Labial crown height, 1.90 + mm Maximum crown width, SH06 (Fig. 2-4b, 4b').

Description. The tooth has a short, distally inclining cusp and a distal heel. The mesial cutting edge of the cusp is smooth, slightly sigmoidal. The distal cutting edge of the cusp is smooth, straight. The crown base has an apron on the labial face. The crown base of the lingual face and the root is not preserved.

Remarks. The tooth is comparable to those of genus *Squalus* in the following characters: a short, distally inclining cusp, presence of a distal heel and an apron (Cappetta, 2012). However, the species identification based on the teeth is difficult because of the interspecific similarity of the shape of the teeth (Suzuki, 2007). Therefore, we refrained from our identification to the species.

Order Rajiformes Berg, 1940

Family Rajidae Bonaparte, 1831

Rajidae indet.

(Standard Japanese name: None) (Fig. 2-4c, 4c')

Material. KPM-NNV 925: jaw teeth, 1.70 mm Tooth crown height, 1.55 mm Tooth crown width, bulk sample (Fig. 4c, 4c').

Description. The tooth crown is approximately oval shaped in the occlusal view, and has a slender, long cusp. The labial face is convex. The lingual face is concave. The lingual and labial visors are convex. The surface of cusp is smooth. The root is short, bilobed, but it is abraded.

Remarks. The tooth is comparable to those of the male of genus *Bathyraja* in the following characters: an oval shaped tooth crown in the occlusal view, presence of a slender, long cusp, a bilobed root (Herman et al., 1996: pls. 5–8). However, we refrained from our conclusive identification because the root is abraded, and the morphological comparison with the other genus is still insufficient.

Order Pristiformes Compagno, 1973

Family Rhynchobatidae Garman, 1913

Genus *Rhynchobatus* Müller and Henle, 1837

Rhynchobatus sp.

(Standard Japanese name: None) (Fig. 2-4d, 4d')

Material. n=1. KPM-NNV 967: jaw teeth, 0.96 mm Tooth crown height, 1.78 mm Tooth crown width, SH06 (Fig. 2-4d, 4d').

Description. The tooth crown is spindle shape in the occlusal view. The crown has a transverse crest dividing the crown into the convex labial face and the slightly convex lingual face. The lingual face has a centro-lingual uvula. The root is not preserved.

Remarks. The tooth is comparable to those of *R. djiddensis* (Forsskål, 1775) and *R. luebberti* (Ehrenbaum, 1914) in the following characters: a spindle shaped tooth crown in the occlusal view, and presence of a centro-lingual uvula (Herman et al., 1997: pls. 15–18). However, we refrained from our identification to the species because the root is not preserved.

Class Actinopterygii *sensu* Goodrich, 1930

Order Anguilliformes Berg, 1943

Family Congridae Kaup, 1856

Genus *Conger* Oken, 1817

Conger myriaster (Brevoort, 1856)

(Standard Japanese name: Maanago) (Fig. 2-4e)

Material. n=1. KPM-NNV 1501: right sagitta, 2.66 mm OL, 1.32 mm OH, OL:OH = 2.01, SH01 (Fig. 2-4e).

Description. The otolith shape is oblong. The inner face is slightly convex and the outer face is slightly concave. The anterior rim is rounded and smooth, but has a notch at the opening of the ostial channel. The dorsal and ventral margins are smooth and slightly curved. The posterior rim is smooth and rounded. The sulcus is para-ostial, horizontal and has an ostial channel. The colliculum fills the sulcus. The cristae are well developed, but are abraded. The dorsal and ventral areas are not depressed, but are abraded.

Remarks. The otolith is most similar to those of *C. myriaster* in an oblong otolith shape, the OL:OH ratio (2.3 in a recent specimen) and a para-ostial sulcus (Ohe, 1985: p. 40).

Genus *Gnathophis* Kaup, 1859

Gnathophis sp.

(Standard Japanese name: None) (Fig. 2-4f, 4h)

Material. n=2. KPM-NNV 900: left sagitta, 3.45 mm OL, 2.34 mm OH, OL:OH = 1.47, bulk sample; KPM-NNV 1502: right sagitta, 1.45 mm OL, 0.93 mm OH, OL:OH = 1.56, SH05 (Fig. 2-4f, 4h). Recent material: *G. heterognathos*, n=2. KPM-NI 46384: 303.7 mm TL, 5.39 mm OL, 3.89 mm OH, OL:OH = 1.39 (left sagitta), Suruga Bay; KPM-NI 52535: 58.7 mm TL, 1.67 mm OL, 1.17 mm OH, OL:OH = 1.43 (right sagitta), Sagami Bay (Fig. 2-4g, 4i).

Description. The otolith shape is rhomboidal. Both the inner and outer faces are convex. The antirostrum is not protruding. The excisura is extremely shallow. The rims are smooth, or poorly crenulated. The sulcus is ostial, straight, and runs along the longitudinal axis of the otolith. A colliculum fills the sulcus. The cristae are well-developed. The dorsal and ventral areas are not depressed.

Remarks. The otoliths are most comparable to those of *Gnathophis heterognathos* (Bleeker, 1858) and *G. xenica* (Matsubara and Ochiai, 1951) in the rhomboidal outline, smooth or slightly crenulated margins and straight sulcus (Fig. 4g, 4i); Schwarzhans, 2019b: pl. 4, fig. 15). The otolith of the remaining Japanese species, *G. ginanago* (Asano, 1958) is more slender and spindle shaped (Schwarzhans, 2019b: pl. 4, fig. 4).

Order Clupeiformes Bleeker, 1859

Family Engraulidae Gill, 1861

Genus *Engraulis* Cuvier, 1816

Engraulis japonica Temminck and Schlegel, 1846

(Standard Japanese name: Katakuchiiwashi) (Fig. 2-4j)

Material. n=1. KPM-NNV 895: left sagitta, 2.67 mm OL, 1.10 mm OH, OL:OH = 2.43, bulk sample (Fig. 2-4j).

Description. The otolith is slender spindle shaped. The inner face is slightly convex and the outer face is slightly concave. The antirostrum is short and pointed. The rostrum is protruding and pointed. The excisura is shallow; the AL:RL ratio is 0.12. The dorsal rim is smooth and slightly curved. The ventral rim is slightly curved and indented. The posterior rim is pointed. The sulcus is ostial, straight and its shape is funnel-like. The ostial colliculum is deeper than caudal colliculum. The cristae are ridge-like. The dorsal and ventral areas are slightly depressed.

Remarks. The otolith is most similar to those of *E. japonica* in its slender, spindle shape, an indented ventral margin and a funnel-like shaped sulcus (Ohe, 1985: p. 36; Lin and Chang, 2012: p. 35–36, pls. 3, 71).

Order Clupeiformes Bleeker, 1859

Family Clupeidae Cuvier, 1817

Genus *Clupea* Linnaeus, 1758

Clupea pallasii Valenciennes, 1847

(Standard Japanese name: Nishin) (Fig. 2-4k, 4l)

Material. n=2. KPM-NNV 894: left sagitta, 4.00 mm OL, 1.68 mm OH, OL:OH = 2.38, bulk sample; KPM-NNV 1503: right sagitta, 1.82 mm OL, 1.00 mm OH, OL:OH = 1.82, SH09 (Fig. 2-4k, 4l). Recent material: *C. pallasii*, n=1. KPM-NI 53290, 55.5 mm SL, 2.96 mm OL, 1.64 mm OH, OL:OH = 1.80 (right sagitta), Hokkaido (Fig. 2-4m).

Description. The shape of the otolith is slender, ovate. The inner face is slightly convex and the outer face is slightly concave. The antirostrum is short but pointed (blunt in a smaller one (Fig. 2-4l). The rostrum is protruding and its tip is pointed. The excisura is shallow; the AL:RL ratio is 0.13–0.22. The dorsal rim is approximately straight. The ventral rim is poorly crenulated; and it is approximately straight in the larger specimen (Fig. 2-4k), but slightly convex in the smaller one (Fig. 2-4l). The specimens have a weak notch on the posterior rim. The sulcus is ostio-caudal (ostial in a smaller one, Fig. 2-4l), straight, and its shape is funnel-like. The ostial colliculum is deeper than the caudal colliculum. The crista superior with a crest-like ridge and the crista inferior is well-developed. The dorsal area is depressed whereas the ventral area is not.

Remarks. The large specimen is most similar to those of *C. pallasii* in the following characters: a slender to ovate outline, the OL:OH ratio exceeding 2.0, a notch on the posterior rim, a ostio-caudal sulcus, and a crista superior which is ridge-like (Mitsui, 2020: figs. 2a, 3a, ESM fig. 2). The ventral rim of recent *C. pallasii* is finely crenulated (Mitsui et al., 2020: figs. 2a, 3a, ESM fig. 2), but it is abraded in the fossil specimen (Fig. 2-4k). Likewise, the small specimen is also similar to the small otoliths of *C. pallasii*; it has an ovate shape with similar OL:OH ratio (1.80 in a recent material), a shallow excisura (AL:RL = 0.17 in a recent material), a convex ventral rim, and a crista superior with a crest-like ridge (Fig. 2-4m).

Genus *Sardinops* Hubbs, 1929

Sardinops melanostictus (Temminck and Schlegel, 1846)

(Standard Japanese name: Maiwashi) (Fig. 2-4n)

Material. n=1. KPM-NNV 1504: left sagitta, 2.27 mm OL, 1.01 mm OH, OL:OH = 2.25, SH07 (Fig. 2-4n).

Description. The otolith shape is slender, ovate. The inner face is slightly convex and the outer face is slightly concave. The antirostrum is short and pointed. The excisura is shallow; the AL:RL ratio is 0.21. The rostrum is protruding and pointed. The dorsal rim has a projection behind the midpoint of the dorsal rim. The ventral rim is approximately straight and serrated. The posterior rim is pointed, smooth. The sulcus is ostial, funnel-like shaped. The ostial colliculum is deeper than the caudal colliculum. The crista superior shows an area with a crest-like ridge. The crista inferior is ridge-like. The dorsal and ventral areas are depressed.

Remarks. The otolith is most similar to those of *S. melanostictus* in the following characters: a slender and ovate otolith shape, the OL:OH ratio is over 2.0, the AL:RL ratio is below 0.3, a projection on the dorsal rim, a straight and serrated ventral rim, and a crista superior with a crest-like ridge (Mitsui et al., 2020: figs. 2k, 3k, 4d–f, ESM fig. 2).

Order Argentiniformes Johnson and Paterson, 1996

Family Argentinidae Bonaparte, 1838

Genus *Glossanodon* Guichenot, 1867

Glossanodon semifasciatus (Kishinouye, 1904)

(Standard Japanese name: Nigisu) (Fig. 2-4o)

Material. n=1. KPM-NNV 1505: right sagitta, 4.17 mm OL, 2.69 mm OH, OL:OH = 1.55, SH05 (Fig. 2-4o).

Description. The otolith shape is approximately pentagonal. The inner face is flat and the outer face is slightly convex. The antirostrum and excisura are indistinct. The rostrum is sharply pointed; the OL:RL ratio is 3.50. The dorsal rim is straight and crenulated. The ventral rim is strongly curved and poorly serrated. The posterior rim is slightly curved. The sulcus is ostial, narrow funnel shaped. The ostial colliculum is deeper than the caudal colliculum. The cristae are ridge-like. The dorsal area is slightly depressed. The ventral area is flat.

Remarks. The otolith is most similar to those of *G. semifasciatus* in the following characters: a pentagonal otolith shape, an ostial and narrow funnel-like shaped sulcus and the OL:RL ratio (3.1–3.4 in the recent specimens; Ohe, 1985: p. 45). *Argentina kagoshimae* Jordan and Snyder, 1902 has the similar otoliths, but the OL:RL ratio is larger (2.4–2.7; Ohe, 1985: p. 45).

Order Osmeriformes Nelson, 2006

Family Osmeridae Regan, 1913

Osmeridae indet.

(Standard Japanese name: None) (Fig. 2-4p)

Material. n=1. KPM-NNV 336: n=1, left sagitta, 1.99 + mm OL, 1.63 mm OH, bulk sample (Fig. 2-4p).

Description. The otolith shape is discoidal, but the rostrum is broken. The inner face is flat and the outer face is convex. The dorsal and posterior rims are strongly curved and roughly crenulated. The ventral rim is strongly curved and smooth. The sulcus is ostial, funnel shaped; the caudal end of the sulcus extends to near the posterior rim. The ostial colliculum is slightly deeper than the caudal colliculum. The dorsal and ventral areas are flat.

Remarks. The otolith is comparable to those of *Hypomesus japonicus* (Brevoort, 1856) and of *Mallotus villosus* (Müller, 1776) in a discoidal shape of the otolith excluding the rostrum, and a straight, funnel shaped sulcus which extends to near the posterior rim (Ohe, 1985: p. 47). However, we refrained from our identification to the genus since the specimen is not preserved entirely.

Order Stomiiformes Regan, 1909

Family Sternoptychidae Gill, 1863

Genus *Valenciennellus* Jordan and Evermann, 1896

Valenciennellus tripunctulatus (Esmark, 1871)

(Standard Japanese name: Hoshieso) (Fig. 2-5a)

Material. n=1. KPM-NNV 902: right sagitta, 0.83 mm OL, 0.98 mm OH, OL:OH is 0.85, bulk sample (Fig. 2-5a).

Description. The otolith is tall, oval shape. The inner face is flat and the outer face is convex. The antirostrum and rostrum are short, blunt. The excisura is extremely shallow; the AL:RL ratio is 0.18. The dorsal rim is curved and smooth, but has a shallow notch at the antero-dorsal region. The ventral rim is smooth and strongly curved. The posterior rim is slightly curved. The sulcus is ostial, funnel shaped. The ostium is widely opening anteriorly. The cauda is straight with a constriction. The ostial colliculum is deeper than the caudal colliculum. The crista superior is well developed, but is ridge-like at the central region of the sulcus. The crista inferior is well developed. The dorsal area is depressed and the ventral area is flat.

Remarks. The otolith is most similar to those of *V. tripunctulatus* in the following characters: a tall and oval otolith shape, the short and blunt antirostrum and rostrum, and a funnel shaped sulcus with a constriction at the caudal region (Lombarte et al., 2006: Fish ID 9045–11960, n=9, in the AFORO Database).

Order Myctophiformes Regan, 1911

Family Myctophidae Gill, 1893

Genus *Benthosema* Goode and Bean, 1896

Benthosema suborbitale (Gilbert, 1913)

(Standard Japanese name: Sokohadaka) (Fig. 2-5b)

Material. n=1. KPM-NNV 881: right sagitta, 1.42 mm OL, 1.18 mm OH, OL:OH = 1.20, bulk sample (Fig. 2-5b).

Description. The otolith is nearly discoidal in shape. The inner face is flat, and the outer face is slightly convex. The antirostrum is extremely short and blunt. The rostrum is protruding and pointed. The excisura is extremely shallow; the AL:RL ratio is 0.06. The dorsal rim is slightly curved and crenulated, and the posterodorsal angle is pointed. The dorsal rim is curved, and it has a denticle each on the antero- and posteroventral region. The posterior rim is curved and smooth. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 1.20. The collicular crest is below the caudal colliculum. The cristae are well-developed. The dorsal and ventral areas are flat.

Remarks. The otolith is most similar to those of *B. suborbitale* in the nearly discoidal otolith shape, an extremely short antirostrum and a curved ventral rim with two denticles (Campana, 2004: p. 97; Schwarzhans and Aguilera, 2013: figs. 15, 16).

Genus *Ceratoscopelus* Günther, 1864

Ceratoscopelus warmingii (Lütken, 1892)

(Standard Japanese name: Gokouhadaka) (Fig. 2-5c)

Material. n=1. KPM-NNV 917: left sagitta, 2.09 mm OL, 1.23 mm OH, OL:OH = 1.70, bulk sample (Fig. 2-5c).

Description. The otolith is slender, sesame seed-like shaped. The inner face is flat, and the outer face is slightly convex. The antirostrum and excisura are indistinct. The rostrum is protruding and pointed. The dorsal rim is slightly curved and poorly crenulated. The ventral rim is curved and crenulated. The dorsal and ventral angles are distinct and blunt. The posterior rim is nearly vertical and crenulated. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 1.83. The collicular crest is below the caudal colliculum. The cristae are poorly developed.

Remarks. The otolith is most similar to those of *C. warmingii* in the slender, sesame seed-like shaped otolith and the shape of sulcus with a collicular crest (Ohizumi et al., 2001: p. 628, pls. 3–5).

? *Ceratoscopelus* sp.

(Standard Japanese name: None) (Fig. 2-5d)

Material. n=1. KPM-NNV 1512: right sagitta, 1.32 mm OL, 0.83 mm OH, OL:OH = 1.32, SH06 (Fig. 2-5d).

Description. The otolith is sesame-seed shaped. The inner face is flat and the outer face is slightly convex. The antirostrum is extremely short and blunt. The excisura is extremely shallow. The rostrum is protruding and its tip is pointed. The dorsal and ventral margins are smoothly curved and poorly crenulated. At least two dentitions are at the center of the ventral margin. The posterior margin is rounded and smooth. The sulcus is ostial, and slightly bending upward, but our specimen is abraded on the whole. The ostial and caudal collicula are present. The cristae are well-developed, but they are also abraded. The dorsal and ventral areas are approximately flat.

Remarks. The otolith is most similar to those of the juveniles of *Ceratoscopelus warmingii* (Lütken, 1892) and *C. townsendi* (Eigenmann and Eigenmann, 1889) in the shape, but present fossil material is different in having the dentitions on the ventral margin (Lombarte et al., 2006: Fish ID 11221, n=1 in the AFORO Database; Lowry, 2011: p. 39, 40).

Genus *Diaphus* Eigenmann and Eigenmann, 1890

Diaphus aliciae Fowler, 1934

(Standard Japanese name: Niramihadaka) (Fig. 2-5e)

Material. n=1. KPM-NNV 921: right sagitta, 1.80 mm OL, 1.46 mm OH, OL:OH = 1.23, bulk sample (Fig. 2-5e).

Description. The otolith is approximately discoidal shape. The inner face is flat, and the outer face is slightly convex. The antirostrum is extremely short and pointed. The rostrum is protruding and pointed. The excisura is extremely shallow; the AL:RL ratio is 0.07. The dorsal rim is curved and smooth, and slightly recessed behind the postero-dorsal angle. The ventral rim is curved with five denticles. The posterior rim is nearly vertical and straight, smooth. The sulcus is ostial and bending up dorsally. The OCL:CCL ratio is 1.16. The collicular crest is below the caudal colliculum. The cristae are well-developed. The dorsal and ventral areas are flat.

Remarks. The otolith is most similar to those of *D. aliciae* in the nearly discoidal otolith shape, an extremely short antirostrum, a blunt postero-dorsal angle, a recessed postero-dorsal region of the dorsal rim, and a ventral rim with a denticle (Schwarzhans, 2013: p. 50, pl. 2, figs. 1–5, table 1). The OL:OH and OCL:CCL ratios of our fossil material are slightly higher than that of recent *D. aliciae* specimens (ranging 1.1–1.2; Schwarzhans, 2013: p. 50). This could represent individual variation. The otolith of *D. theta* is also similar to our fossil material in the otolith shape and the OCL:CCL ratio which is ranging 1.0–1.2, but it is different in a larger antirostrum and a curved posterior rim (Schwarzhans, 2013: p. 52, pl. 4, figs. 3–6, table 1).

Diaphus luetkeni (Brauer, 1904)

(Standard Japanese name: Gantenhadaka) (Fig. 2-5f)

Material. n=1. KPM-NI 1510: right sagitta, 1.33 mm OL, 1.04 mm OH, OL:OH = 1.28, SH03 (Fig. 2-5f).

Description. The otolith is sesame seed-like shaped. The inner face is flat, and the outer face is slightly convex. The antirostrum and excisura are indistinct. The rostrum is protruding and pointed. The dorsal rim is pointed at the midpoint, and poorly crenulated. The ventral rim is curved with a denticle at the midpoint. The posterior rim is curved and smooth. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 1.35. The collicular crest is below the caudal colliculum. The cristae are well-developed. The dorsal and ventral areas are flat.

Remarks. The otolith is most similar to those of *D. luetkeni* in the sesame seed-like shape, the OL:OH and OCL:CCL ratios (ranging 1.3–1.4 and 1.3–1.5 in the recent otoliths, respectively) and a pointed dorsal rim (Schwarzhans, 2013: p. 56, pl. 6, figs. 1–4, table 1). The otolith of this species has usually 5–7 denticles on the ventral rim (Schwarzhans, 2013: p. 56, table 1), however, the dentitions are not preserved in our fossil material, possibly caused by abrasion (Fig. 2-5f).

Diaphus watasei Jordan and Starks, 1904

(Standard Japanese name: Hadakaiwashi) (Fig. 2-5g)

Material. n=1. KPM-NNV 889: right sagitta, 1.89 mm OL, 1.43 mm OH, OL:OH = 1.32, bulk sample (Fig. 2-5g).

Description. The otolith is approximately oval in shape. The inner face is flat, and the outer face is slightly convex. The antirostrum is short and pointed. The rostrum is protruding and pointed. The excisura is shallow; the AL:RL ratio is 0.52. The dorsal rim is slightly expanded and crenulated at the antero-dorsal region, and slightly recessed behind the postero-dorsal angle. The ventral rim is curved and bears many denticles. The posterior rim is nearly vertical and crenulated. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 1.74. The collicular crest is below the caudal colliculum. The cristae are well-developed. The dorsal and ventral areas are flat.

Remarks. The otolith is most similar to those of *D. watasei* in the nearly oval shape, the OL:OH ratio (ranging 1.3–1.4 in the recent otoliths), an expanding antero-dorsal region of dorsal rim, a distinct postero-dorsal angle, a recessed postero-dorsal region of dorsal rim, and the many denticles along the ventral rim (Schwarzhans, 2013: p. 64, pl. 9, figs. 9, 10, table 1).

Genus *Diogenichthys* Bolin, 1939

Diogenichthys atlanticus (Tåning, 1928)

(Standard Japanese name: Itahadaka) (Fig. 2-5h, 5h')

Material. n=1. KPM-NNV 1507: left sagitta, 1.03 mm OL, 1.02 mm OH, OL:OH = 1.01, SH06 (Fig. 2-5h, h').

Description. The otolith is discoidal shaped. The inner face is flat, and the outer face is convex. The antirostrum is short and blunt. The rostrum is protruding and blunt. The excisura is shallow; the AL:RL ratio is 0.15. The rims are curved and smooth. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 1.48. The collicular crest is below the caudal colliculum. The cristae are poorly-developed. The dorsal and ventral areas are slightly depressed.

Remarks. The otolith is most similar to those of *D. atlanticus* in the discoidal otolith shape, a convex outer face, the blunt antirostrum and rostrum, and the smooth rims (Schwarzhans and Aguilera, 2013: pl. 1, figs. 19, 20). The small sized otoliths of Stenobrachius leucopsarus (Eigenmann and Eigenmann, 1890) are also similar to our fossil material, but the outer face of the otoliths of *S. leucopsarus* is less convex (Lowry, 2011: p. 41).

Genus *Electrona* Goode and Bean, 1896

Electrona risso (Cocco, 1829)

(Standard Japanese name: Darumahadaka) (Fig. 2-5i)

Material. n=1. KPM-NNV 1506: right sagitta, 1.37 mm OL, 1.41 mm OH, OL:OH = 0.97, bulk sample (Fig. 2-5i).

Description. The otolith is tall, nearly discoidal shape. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum and rostrum is short and blunt, the tip of rostrum is slightly forward of the tip of antirostrum. The AL:RL ratio is 0.58. The antero-dorsal region of dorsal rim is slightly expanded, and the postero-dorsal region of dorsal rim is slightly recessed behind the postero-dorsal angle. The ventral rim is strongly curved and smooth. The posterior rim is nearly vertical and smooth. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 0.77. The collicular crest is below the caudal colliculum. The cristae are well-developed. The dorsal area is slightly depressed whereas the ventral area is not.

Remarks. The otolith is most similar to those of *E. risso* in the tall, discoidal otolith shape, the shapes of dorsal and ventral rims, and the OCL:CCL ratio (Campana, 2004: p. 106; Furlani et al., 2007: p. 45; Lin and Chang, 2012: p. 53, pls. 10, 78). The otolith of genus *Hygophum* is also similar to our fossil material, but the ostial colliculum is longer than the caudal colliculum, and the OCL:CCL ratio is over 1.0 (Schwarzhans and Aguilera, 2013: p. 98–100, pl. 2, figs. 4–9, 11, 14).

Genus *Hygophum* Bolin, 1939

Hygophum sp.

(Standard Japanese name: None) (Fig. 2-5j)

Material. n=1. KPM-NNV 1508: right sagitta, 1.90 mm OL, 1.73 mm OH, OL:OH = 1.10, bulk sample (Fig. 2-5j).

Description. The otolith is discoidal shaped. The inner face is flat, and the outer face is slightly convex. The antirostrum and rostrum is short and pointed, the tip of rostrum is slightly forward of the tip of antirostrum. The AL:RL ratio is 0.68. The antero-dorsal region of dorsal rim is slightly expanded, and the postero-dorsal region of dorsal rim is slightly recessed behind the postero-dorsal angle. The ventral rim is curved and smooth. The posterior rim is curved and smooth. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 2.27. The collicular crest is below the caudal colliculum. The cristae are well-developed. The dorsal area is slightly depressed whereas the ventral area is not.

Remarks. The otolith is most similar to those of species of the genus *Hygophum* in the discoidal otolith shape, the shapes of the rims and the OCL:CCL ratio which is over 2.0 (Ohizumi et al., 2001: p. 631, pls. 36–39; Schwarzhans and Aguilera, 2013: p. 98–100, pl. 2, figs. 4–9, 11, 14). However, the otoliths of recent Japanese species (*H. proximum* Becker, 1965 and *H. reinhardti* (Lütken, 1892)) are very similar and poorly distinguishable (Ohizumi et al., 2001).

Genus *Lampadena* Goode and Bean, 1893

Lampadena sp.

(Standard Japanese name: None) (Fig. 2-5k)

Material. n=1. KPM-NNV 1513: left sagitta, 4.16 mm OL, 2.70 mm OH, OL:OH = 1.54, SH09 (Fig. 2-5k).

Description. The otolith is approximately spindle-like in shape. The inner face is flat, and the outer face is slightly convex. The antirostrum is short, but pointed. The rostrum is protruding, and its tip is pointed. The excisura is shallow; the AL:RL ratio is 0.18. The antero-dorsal region of dorsal rim is expanded, and the postero-dorsal region of dorsal rim is slightly recessed behind the postero-dorsal angle. The ventral and posterior rims are curved and crenulated. The sulcus is ostial and straight. The OCL:CCL ratio is 2.28. The collicular crest is below the caudal colliculum. The cristae are abraded. The dorsal and ventral areas are flat, but they are abraded.

Remarks. The otolith is similar to those of the species of the genus *Lampadena* in the shallow excisura, the shape of the dorsal rim, the flat inner face and slightly convex outer face, and the shape of the sulcus with a collicular crest (Ohizumi et al., 2001: p. 631–632, pls. 41, 42; Girone and Nolf, 2002: pl. 1; Schwarzhans and Aguilera, 2013: p. 109, pl. 5). However, we refrained from our identification to the species level, because the features on the inner face were abraded.

Genus *Lampanyctus* Bonaparte, 1840

Lampanyctus tuneri (Fowler, 1934)

(Standard Japanese name: Katahadaka) (Fig. 2-5l)

Material. n=1. KPM-NNV 886: left sagitta, 0.86 mm OL, 0.81 mm OH, OL:OH = 1.06 bulk sample (Fig. 2-5l). Recent material: *L. tuneri*, n=1. CBM-ZF 5379, 51.5 mm SL, 1.12 mm OL, 1.04 mm OH, OL:OH = 1.08 (right sagitta), Sagami Bay (Fig. 2-5m).

Description. The shape of the otolith is discoid. The inner face is flat and the outer face is convex. The antirostrum and rostrum are blunt, and both are similar in size with their tips extending equally. The excisura is deep and wide. The dorsal rim is approximately straight and smooth, and the ventral and posterior rims are convex and smooth. The sulcus is ostial and slightly bending upward. The OCL:CCL ratio is 1.94. The dorsal and ventral areas are flat.

Remarks. The otolith is most similar to those of *L. tuneri* in the discoidal otolith shape, the antirostrum and rostrum which are blunt and similar in size with their tips extending equally, and the approximately straight dorsal rim (the recent material is slightly eroded under the immersion storage) (Fig. 2-5m).

Genus *Myctophum* Rafinesque, 1810

Myctophum asperum Richardson, 1845

(Standard Japanese name: Arahadaka) (Fig. 2-5n)

Material. n=1. KPM-NNV 908: left sagitta, 1.99 mm OL, 1.30 mm OH, OL:OH = 1.53, bulk sample (Fig. 2-5n).

Description. The otolith is approximately pentagonal in shape. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum and rostrum are short and pointed, the tip of the rostrum is forward of the tip of the antirostrum. The AL:RL ratio is 0.33. The dorsal rim is nearly straight and crenulated, and the postero-dorsal region of dorsal rim is straight, and not recessed behind the postero-dorsal angle. The ventral rim is curved and poorly crenulated. The posterior rim is pointed. The sulcus is ostial and bending up dorsally. The OCL:CCL ratio is 2.44. The collicular crest is below the caudal colliculum. The crista superior is well-developed, and the crista inferior is poorly-developed. The dorsal and ventral areas are flat.

Remarks. The otolith is most similar to those of M. asperum in the approximately pentagonal otolith shape and an ostial colliculum which is much longer than the caudal colliculum (Ohizumi et al., 2001: p. 633, pls. 54–56; Schwarzhans and Aguilera, 2013: pl. 3, figs. 10, 11).

Genus *Notoscopelus* Günther, 1864

Notoscopelus resplendens (Richardson, 1845)

(Standard Japanese name: Isaribihadaka) (Fig. 2-5o)

Material. n=1. KPM-NNV 1509: right sagitta, 1.51 mm OL, 0.96 mm OH, OL:OH = 1.58, bulk sample (Fig. 2-5o).

Description. The otolith is oval in shape. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum is extremely short and blunt, but indistinct. The rostrum is protruding and pointed. The excisura is indistinct; the AL:RL ratio is 0.03. The dorsal rim is nearly straight. The ventral rim is curved and poorly crenulated. The posterior rim is slightly curved and roughly crenulated. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 2.20. The collicular crest is indistinct. The cristae are well-developed. The dorsal and ventral areas are not depressed.

Remarks. The otolith is most similar to those of *N. resplendens* in the oval otolith shape, the OL:OH ratio (about 1.5–1.56 in the recent specimens) an indistinct antirostrum and excisura, and an ostial colliculum which is much longer than the caudal colliculum (Giaretta et al., 2017: p. 270, pl. 19).

Genus *Stenobrachius* Eigenmann and Eigenmann, 1890

Stenobrachius leucopsarus (Eigenmann and Eigenmann, 1890)

(Standard Japanese name: Kohirehadaka) (Fig. 2-5p)

Material. n=1. KPM-NNV 890: left sagitta, 1.52 mm OL, 1.67 mm OH, OL:OH = 0.91, bulk sample (Fig. 2-5p).

Description. The otolith is high-bodied in shape. The inner face is flat, and the outer face is convex. The antirostrum is extremely short and blunt. The rostrum is protruding and its tip is blunt. The excisura is shallow; the AL:RL ratio is 0.25. The dorsal and posterior rims are slightly curved and smooth. The ventral rim is strongly curved and smooth. The sulcus is ostial and slightly bending up dorsally. The OCL:CCL ratio is 1.53. The collicular crest is below the caudal colliculum. The cristae are poorly-developed. The dorsal area is slightly depressed, and the ventral area is flat.

Remarks. The otolith is most similar to those of *S. leucopsarus* in the high-bodied otolith shape, the OL:OH ratio which is nearly 1.0, the blunt and short antirostrum and rostrum, a shallow excisura and smooth rims (Ohizumi et al., 2001: p. 635–636, pls. 73, 74).

Genus Taaningichthys Bolin, 1959

Taaningichthys minimus (Tåning, 1928)

(Standard Japanese name: Kurohadaka) (Fig. 2-5q)

Material. n=1. KPM-NNV 1511: right sagitta, 1.27 mm OL, 0.90 mm OH, OL:OH = 1.41, SH10 (Fig. 2-5q)

Description. The otolith is oval in shape. The inner face is flat, and the outer face is slightly convex. The antirostrum is short and blunt. The rostrum is protruding and its tip is blunt. The excisura is shallow; the AL:RL ratio is 0.04. The dorsal rim is nearly straight and smooth, and the postero-dorsal angle is distinct but blunt. The ventral and posterior rims are curved and smooth. The sulcus is ostial and inclined. The OCL:CCL ratio is 1.56. The collicular crest is indistinct. The cristae are well-developed. The dorsal and ventral areas are flat.

Remarks. The otolith is most similar to those of *T. minimus* in the oval otolith shape, a short and blunt antirostrum, a nearly straight dorsal rim, the curved ventral and posterior rims, and an inclined sulcus (Campana, 2004: p. 124).

Myctophidae indet.

(Standard Japanese name: None) (Fig. 2-5r)

Materials. n=1. KPM-NNV 1514: right sagitta, 1.25 mm OL, 0.85 mm OH, OL:OH = 1.48, SH09 (Fig. 2-5r).

Description. The otolith is sesame seed-like in shape. The inner face is flat, and the outer face is slightly convex. The antirostrum is extremely short and blunt. The rostrum is protruding, and its tip is pointed. The excisura is extremely shallow; the AL:RL ratio is 0.01. The dorsal and ventral rims are curved and poorly crenulated. The posterior rim is curved and smooth. The sulcus is ostial and straight. The OCL:CCL ratio is 1.86. The collicular crest is indistinct. The cristae are well-developed. The dorsal and ventral areas are flat.

Remarks. The otolith was most similar to those of Myctophidae in the sulcus shape (Nolf, 2013: fig. 3). However, we refrained from our identification to the genus level, because the specimen was too small.

Order Gadiformes Goodrich, 1909

Family Macrouridae Bonaparte, 1831

Genus *Abyssicola* Goode and Bean, 1896

Abyssicola macrochir (Günther, 1877)

(Standard Japanese name: Tenagadara) (Fig. 2-6a, 6a')

Material. n=1. KPM-NNV 1515: right sagitta, 3.28 mm OL, 2.22 mm OH, OL:OH = 1.48, SH06 (Fig. 2-6a, a'). Recent material: *A. macrochir*, n=1. KPM-NI 53284: 119.2 mm TL, 4.86 mm OL, 3.27 mm OH, OL:OH = 1.49 (right sagitta), Suruga Bay (Fig. 2-6b).

Description. The otolith is approximately rhomboidal in shape. The inner face is slightly convex; the outer face is convex and lobulated. The antirostrum and the excisura are indistinct. The rostrum is pointed. The dorsal rim is crenulated; it is markedly protruding upward, making the highest point approximately above the collum. The ventral rim is also crenulated and slightly curved. The posterior rim is blunt. The sulcus is ostio-pseudocaudal, very slightly bending upward. The collicula are homomorph; the OCL:CCL ratio is 0.87. The collum is oval. The cristae are well-developed; the crista inferior is curving ventrally below the collum. The dorsal area is slightly depressed. The ventral area is approximately flat.

Remarks. The otolith is most similar to those of *A. macrochir* in the following characters: an approximately rhomboidal otolith shape, a protruding dorsal rim, homomorph collicula, similar

OCL:CCL ratio (0.85 in a recent material) and a crista inferior which is curving below the collum (Fig. 2-6b). The otoliths of Coelorinchus kishinouyei Jordan and Snyder, 1900 are also similar to our fossil, however, the crista inferior is recessed below the collum (Lin and Chang, 2012: p. 57, pls. 12, 80).

Genus *Ventrifossa* Gilbert and Hubbs, 1920

Ventrifossa sp.

(Standard Japanese name: None) (Fig. 2-6c)

Material. n=1. KPM-NNV 928: left sagitta, 1.73 mm OL, 1.15 mm OH, OL;OH = 1.51, bulk sample (Fig. 2-6c).

Description. The otolith is rhomboidal shape. The inner face is flat. The outer face is convex and roughly lobulated. The antirostrum and excisura are indistinct. The rostrum is blunt. The dorsal rim is protruding at the antero-dorsal region. The ventral rim is slightly curved. The posterior rim is pointed, and its tip is above the sulcus. The sulcus is pseudo-ostiocaudal and straight. The ostial and caudal colliculum is oblong shape, but the posterior region of the caudal colliculum is broken. The cristae are abraded. The dorsal and ventral areas are flat.

Remarks. The otolith is comparable to those of genus *Ventrifossa* in the rhomboidal otolith shape, the shapes of the rims and a straight sulcus (Lin and Chang, 2012: p. 58, pls. 12, 80). However, we refrained from our identification to the species because the specimen is small, and more or less abraded.

Macrouridae indet.

(Standard Japanese name: None) (Fig. 2-6d)

Material. n=1. KPM-NNV 1516: left sagitta, 1.69 mm OL, 1.08 mm OH, OL:OH = 1.57, bulk sample (Fig. 2-6d).

Description. The otolith is approximately spindle-like in shape. The inner face is flat, and the outer face is slightly concave. The antirostrum and excisura are indistinct. The rostrum is pointed. The dorsal rim is curved and crenulated. The ventral rim is slightly curved and nearly smooth. The posterior rim is pointed, and its tip is below the sulcus. The sulcus is pseudo-ostiocaudal and bending up dorsally. The collicula are teardrop-like shaped; the OCL:CCL ratio is 1.21. The cristae are poorly developed. The dorsal area is slightly depressed, and the ventral area is flat.

Remarks. The otolith is similar to those of *Coryphaenoides* in the nearly spindle-like otolith shape and the shape of sulcus and collicula (Lin and Chang, 2012: p. 57, pls. 12, 80), however, we refrained from an identification to genus because it is too small.

Family Moridae Moreau, 1881

Genus *Guttigadus* Taki, 1953

Guttigadus nana (Taki, 1953)

(Standard Japanese name: Himedara) (Fig. 2-6e, 6e')

Material. n=1. KPM-NNV 566: right sagitta, 1.96 mm OL, 1.13 mm OH, OL:OH = 1.72, bulk sample (Fig. 2-6e, e'). Recent material: *G. nana*, n=3. KAUM-I. 75041, 75043, 75230: 30.7–57.6 mm SL, 1.50–2.18 mm OL, 1.02–1.34 mm OH, OL:OH = 1.37–1.63 (right sagittae), East China Sea (Fig. 2-6f, 6f').

Description. The otolith is approximately L-shaped. The inner face is slightly convex. The outer face is concave at the vertical midline of the otolith, and the posterior from the midline is strongly convex, and the papillary umbo is dorsally protruding at the anterior from the midline. The anterior rim is pointed. The dorsal and ventral rims are slightly curved, and their posterior tips are coordinate. The posterior rim is slightly curved. The sulcus is caudal, horizontal and straight. The ostial colliculum is oval shaped. The caudal colliculum is keel-like shaped, and extending to the posterior tip of the otolith. The OCL:CCL and CCL:OL ratios are 0.38 and 0.66, respectively. The cristae are well-developed.

Remarks. The otolith is most similar to those of *G. nana* in the approximately L-shaped otolith, the papillary umbo on the outer face, and the keel-like shaped caudal colliculum which is extending to the posterior tip of the otolith, although the recent materials are more or less eroded under the immersion storage (Fig. 6f, 6f').

The morphological features of our fossil material are entirely similar to those of this species in the literature, but the specimen shown in the literature is larger, and its papillary umbo is lower (Schwarzhans, 2019c: pl. 2, fig. 7). Note that Schwarzhans (2019c) has placed this species in the genus

Pseudophycis in his taxonomic revision on the morids. We tentatively followed the older taxonomy in Meléndez and Markle (1997), though, since the taxonomic revision of Schwarzhans (2019c) was based only on otolith morphology.

Genus *Physiculus* Kaup, 1858

Physiculus sp.

(Standard Japanese name: None) (Fig. 2-6g, 6g')

Material. n=1. KPM-NNV 897: right sagitta, 4.04 mm OL, 1.26 mm OH, OL:OH = 3.21, bulk sample (Fig. 2-6g, g').

Description. The otolith is slender, spindle-like in shape. The inner face is flat. The outer face has an umbo at the anterior region, and has a keel which is developing downward at the postero-ventral region. The anterior rim is pointed. The dorsal rim is slightly curved, and its length is two-thirds of the otolith length. The ventral rim is nearly straight, and its length is nine-tenths of the otolith length. The posterior rim is strongly recessed. The sulcus is caudal. The ostial colliculum is oblong in shape. The caudal colliculum is forming a keel which is extending to the posterior end of the otolith. The CCL:OCL ratio is 2.55. The cristae are well-developed. The dorsal area is flat, and the ventral area is slightly depressed.

Remarks. The otolith is most similar to those of *Physiculus* in the spindle-like otolith shape, the OL:OH ratio (2.8–4.0 in the recent species), the flat inner face, the outer face with an umbo, the CCL:OCL ratio (1.7–2.5 in the recent species), an oblong ostial colliculum and a keel-like caudal colliculum (Schwarzhans, 2019c: p. 362–364, pl. 4, figs. 6–20). The fossil material is most similar to the otolith of *P. japonicus* Hilgendorf, 1879 in the shapes of the sulcus, collicula and a keel on the postero-ventral region of the outer face (Lin and Chang, 2012: p. 59, pls. 12, 80; Schwarzhans, 2019c: pl. 4, fig. 12), however, we refrained from our identification to the species because the morphological information of the otoliths of the other Japanese species is insufficient.

Family Gadidae Rafinesque, 1810

Genus *Theragra* Lucas in Jordan and Evermann, 1898

Theragra chalcogramma (Pallas, 1814)

(Standard Japanese name: Suketoudara) (Fig. 2-6h, 6h')

Material. n=1. KPM-NNV 899: left sagitta, 4.16 mm OL, 1.84 mm OH, OL:OH = 2.26, bulk sample (Fig. 2-6h, 6h').

Description. The shape of the otolith is slender, spindle-type. The inner face is slightly convex, and the outer face is slightly concave, lobulated. The ventral lobulations on the outer face is not extending to the midline of the otolith. The anterior rim is blunt. The dorsal and ventral rims are slightly convex and crenulated. A postero-dorsal angle is near the posterior tip of the otolith. The posterior rim is pointed. The sulcus is ostio-pseudocaudal, horizontal and straight. The collicula are approximately homomorph, and the OsL:CL ratio is 0.86. The collum is approximately situated at the midpoint of the otolith. The cristae are well-developed. The dorsal area is approximately flat. The ventral area is not depressed.

Remarks. The otolith is most similar to those of *T. chalcogramma* in the following characters: a slender otolith shape (OH is approximately 44 % in OL), a concave outer face, a ventral lobulations which is not extending to the midline of the outer face (Frost, 1981: p. 56, fig. 2; Matta and Kimura, 2012: figs. 17–19). The specimen is also similar to the otoliths of *Eleginus gracilis* (Tilesius, 1810) in the slender otolith shape, however, the postero-dorsal angle is situated anteriorly in E. gracilis (Frost, 1981: fig. 4; Harvey et al., 2000: p. 15).

Order Trachichthyiformes Moore, 1993

Family Trachichthyidae Bleeker, 1859

Genus *Hoplostethus* Cuvier, 1829

Hoplostethus sp.

(Standard Japanese name: None) (Fig. 2-6i)

Material. n=1. KPM-NNV 1517: right sagitta, 5.15 mm OL, 3.46 mm OH, OL:OH = 1.49, SH08 (Fig. 2-6i).

Description. The otolith is rhomboidal in shape. The inner face is flat, and the outer face is slightly convex. The antirostrum and excisura are indistinct. The rostrum is protruding and blunt. The dorsal rim is nearly trapezoidal, and roughly crenulated. The ventral rim is curved and smooth. The posterior rim is pointed. The sulcus is ostial and markedly bending up dorsally, its shape is tadpole-like. The cristae are well-developed and the dorsal and ventral areas are flat, but they are abraded.

Remarks. The otolith is most similar to those of genus *H. japonicus* in the rhomboidal otolith shape and the shape of sulcus (Ohe, 1985: p. 70; Lin and Chang, 2012: p. 74, pl. 18). However, we refrained from an identification to the species since the inner face and rims of the fossil material are more or less abraded.

Order Kurtiformes Jordan, 1963

Family Apogonidae Günther, 1859

Apogonidae indet.

(Standard Japanese name: None) (Fig. 2-6j)

Material. n=1. KPM-NNV 1519(190313-1-8): left sagitta, 3.41 mm OL, 2.39 mm OH, OL:OH = 1.43, SH01 (Fig. 2-6j).

Description. The otolith is oval shape. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum and the excisura are indistinct. The rostrum is protruding, and its tip is blunt. The dorsal rim is slightly curved, and its outline is nearly trapezoidal in shape. The ventral rim is curved and smooth. The posterior rim is slightly curved and smooth. The sulcus is ostial and slightly bending up dorsally. The ostial colliculum is wider and slightly deeper than the caudal colliculum. The cristae are well-developed. The dorsal area is slightly depressed whereas the ventral area is not.

Remarks. The otolith is comparable to those of the apogonids in the shape of the otolith and sulcus (Ohe, 1985: p. 79–80; Lin and Chang, 2012: p. 111–114, pls. 38, 39, 98, 99). However, we refrained from a specific identification since the marginal structures are abraded.

Order Gobiiformes Günther, 1880

Family Oxudercidae Günther, 1861

Genus *Amblychaeturichthys* Bleeker, 1874

Amblychaeturichthys sciistius (Bleeker, 1853)

(Standard Japanese name: Komochijako) (Fig. 2-6k, 6k’, 6l)

Material. n=2. KPM-NNV 892: left sagitta, 2.30 mm OL, 2.03 mm OH, OL:OH = 1.13, bulk sample; KPM-NNV 1527: right sagitta, 1.26 mm OL, 1.34 mm OH, OL:OH = 0.94, bulk sample (Fig. 2-6k, 6k', 6l). Recent material: *A. sciistius*, n=1. KPM-NI 53287: 21.8 mm SL, 1.28 mm OL, 1.25 mm OH, OL:OH = 1.02 (right sagitta), Tokyo Bay (Fig. 2-6m).

Description. The shape of the otolith is sliced bread-like in the larger specimen (Fig. 2-6k, 6k'), but it is discoidal in the smaller one (Fig. 2-6l). The inner face is flat and the outer face is convex. The anterior rim is slightly curved and crenulated in the larger specimen (Fig. 2-6k, 6k'), but protruding and roughly crenulated in the smaller one (Fig. 2-6l). The dorsal rim is slightly curved and crenulated in the larger specimen (Fig. 2-6k, 6k'), but the curve is strong and roughly crenulated in the smaller one (Fig. 2-6l). The ventral rim is straight and smooth in the larger specimen (Fig. 2-6k, 6k'), while it is curved and slightly crenulated in the smaller one (Fig. 2-6l). The posterior rim is protruding posteriorly in the postero-dorsal region and angled in the postero-ventral region in the larger specimen (Fig. 2-6k, k'), but it is slightly curved posteriorly and having a weak notch at the center in the smaller one (Fig. 2-6l). The sulcus is mesial, sole-like shaped. The colliculum fills the sulcus; the CL:OL ratios are 0.42 in the larger specimen (Fig. 2-6k) and 0.47 in the smaller one (Fig. 2-6l). The cristae are ridge-like and a subcaudal iugum is present below the caudal region of the sulcus. The dorsal and ventral areas are flat.

Remarks. The larger otolith is most similar to those of *A. sciistius* in the sliced bread-like otolith shape, strongly protruding postero-dorsal region of the posterior rim, and mesial, sole-like shaped sulcus (Ohe, 1985: p. 133). The smaller otolith is also similar to those of the juveniles of *A. sciistius* in the following characters: discoidal outline, roughly crenulated margins, protruding anterior rim, slightly curved posterior rim, sole-like shaped sulcus and the OL:OH and CL:OL ratios (1.02 and 0.47, respectively, in a recent specimen) (Fig. 2-6m).

Amblychaeturichthys hexanema (Bleeker, 1853)

(Standard Japanese name: Akahaze) (Fig. 2-7a, 7a')

Material. n=1. KPM-NNV 1528: right sagitta, 1.89 mm OL, 1.38 mm OH, OL:OH = 1.37, SH04 (Fig. 2-7a, 7a').

Description. The otolith is slender and sliced bread-like in shape. The inner and outer faces are slightly convex. The anterior and dorsal rims are smooth and slightly curved. The antero-dorsal and -ventral regions of the rims are angular. The postero-dorsal region of the rim is markedly protruding, and its tip is blunt and smooth. The postero-ventral region of the rim is slightly curved. The posterior rim has a notch at the midpoint. The sulcus is mesial, and sole-like in shape. The colliculum fills the sulcus; the CL:OL ratio is 0.46. The cristae are poorly-developed and a subcaudal iugum is present below the caudal region of the sulcus. The dorsal and ventral areas are not depressed.

Remarks. The otolith is most similar to those of *A. hexanema* in the slender, sliced bread-like otolith shape and sole-like shaped sulcus (Ohe, 1985: p. 132).

Genus *Gymnogobius* Gill, 1863

Gymnogobius aff. *heptacanthus* (Hilgendorf, 1879)

(Standard Japanese name: None) (Fig. 2-7b, 7b')

Material. n=1. KPM-NNV 1534: right sagitta, 0.96 mm OL, 0.89 mm OH, OL:OH = 0.93, SH02 (Fig. 2-7b, 7b'). Recent material: *G. heptacanthus*, n=3. KPM-NI 53567: 29.9 mm SL, 0.79 mm OL, 0.92 mm OH, OL:OH = 0.86 (left sagitta), Tokyo Bay; KPM-NI 53568, 53569: 30.3–34.8 mm SL, 0.87–1.01 mm OL, 0.99–1.10 mm OH, OL:OH = 0.88–0.92 (right sagittae), Tokyo Bay (Fig. 2-7c). *Redigobius bikolanus* (Maeda, Saeki and Satoh, 1927), n=3. KPM-NI 53283, 53564, 53565, 19.8–23.6 mm SL, 0.80 mm OL, 0.77–0.97 mm OH, OL:OH = 0.82–0.85 (right sagittae), Kanagawa Prefecture (Fig. 2-7d).

Description. The otolith shape is approximately tall pyriform. The inner face is flat; the outer face is convex and smooth. The anterior rim is approximately straight, slightly crenulated. The dorsal rim is curved and smooth. The ventral rim is slightly curved and smooth. The posterior rim is approximately smooth, but it has an extremely shallow notch at the midpoint. The sulcus is mesial, sole-like shaped. The colliculum fills the sulcus; the CL:OL ratio is 0.42. The cristae are ridge-like and a subcaudal iugum is present below the caudal region of the sulcus. The dorsal are is slightly depressed. The ventral area is flat.

Remarks. The otolith is comparable to those of *G. heptacanthus* in the tall otolith shape, an approximately straight posterior rim which has an extremely shallow notch and a mesial, sole-like shaped sulcus (Fig. 2-7c), however, the CL:OL ratio is smaller (CL:OL ratio is 0.58 in the recent specimens) (Fig. 2-7c). In addition, the otoliths of *R. bikolanus* are also similar to our fossil material in the tall otolith shape and approximately smooth margins, however, it is different in the slightly concave inner face and the slender ostium (Fig. 2-7d).

Genus *Pterogobius* Gill, 1863

Pterogobius zacalles Jordan and Snyder, 1901

(Standard Japanese name: Ryuguhaze) (Fig. 2-7e, 7e')

Material. n=1. KPM-NNV 1529: left sagitta, 2.15 mm OL, 1.82 mm OH, OL:OH = 1.18, SH08 (Fig. 2-7e, e'). Recent material: *P. zacalles*, n=1. KPM-NI 53285: 119.2 mm SL, 2.96 mm OL, 2.41 mm OH, OL:OH = 1.23 (right sagitta), Tokyo Bay (Fig. 2-7f, 7f').

Description. The otolith shape is parallelogram. The inner face is convex and the outer face is concave. The anterior rim is approximately straight. The antero-ventral region of the rim is angled, slightly protruding anteriorly. The dorsal rim is approximately horizontal, poorly crenulated. The ventral rim is horizontal, straight. The postero-dorsal and -ventral regions of the rims are angled and protruding posteriorly; both are similar in size with their tips extending parallel. The posterior rim has a notch at the midpoint. The sulcus is mesial and golf club-like in shape; the ostial region of the sulcus is widening ventrally. The colliculum fills the sulcus; the CL:OL ratio is 0.54. The cristae are ridge-like but the subcaudal iugum is absent. The dorsal area is slightly depressed. The ventral area is flat.

Remarks. The otolith is most similar to those of *P. zacalles* in the following characters: a parallelogram otolith shape, the OL:OH ratio (1.23 in a recent material), the protruding postero-dorsal and -ventral regions of the rim, a notch at the midpoint of the posterior rim, ventrally widening ostial region of the sulcus (Fig. 2-7f, 7f').

Gobiiformes indet. 1

(Standard Japanese name: None) (Fig. 2-7g, 7g')

Material. n=1. KPM-NNV 887: right sagitta, 1.92 mm OL, 1.78 mm OH, OL:OH = 1.08, bulk sample (Fig. 2-7g, 7g').

Description. The otolith is approximately discoidal in shape. The inner face is flat, and the outer face is convex and lobulated. The antero-dorsal region of the rim is protruding. The antero-ventral region of the rim is angular. The anterior rim is slightly curved below a notch which is located at the midpoint. The dorsal rim is slightly curved, and roughly crenulated. The ventral rim is nearly straight and smooth. The postero-dorsal angle is indistinct. The postero-ventral region of the rim is angular. The posterior rim is nearly vertical and crenulated. The sulcus is mesial, and sole-like in shape. The colliculum fills the sulcus; the CL:OL ratio is 0.44. The cristae are well-developed and a subcaudal iugum is present below the caudal region of the sulcus. The dorsal and ventral areas are flat.

Remarks. The otolith is similar to those of *Amblychaeturichthys sciistius* in the crenulated rims, and a sole-like shaped sulcus (Fig. 2-6k, 6k'), however, it is different in the discoidal otolith shape. The otoliths of juvenile *A. sciistius* shows discoidal shape, but its size is much smaller than that of this fossil material, and the ventral rim of this material is nearly straight (Figs. 2-6m, 7g, 7g').

Gobiiformes indet. 2

(Standard Japanese name: None) (Fig. 2-7h, 7h')

Material. n=1. KPM-NNV 1531: left sagitta, 1.73 mm OL, 1.71 mm OH, OL:OH = 1.01, bulk sample (Fig. 2-7h, 7h').

Description. The otolith is discoidal shape. The inner face is flat, and the outer face is convex and lobulated. The anterior rim is slightly curved and crenulated. The dorsal and ventral rims are slightly curved and roughly crenulated. The postero-ventral region of the rim is protruding, and the postero-dorsal region angle is blunt. The posterior rim has a notch at the midpoint. The sulcus is mesial and sole-like in shape. The colliculum fills the sulcus; the CL:OL ratio is 0.45. The cristae are well-developed and a subcaudal iugum is present below the caudal region of the sulcus. The dorsal and ventral areas are flat.

Remarks. The otolith is very similar to those of Gobiiformes indet. 1 in the discoidal otolith shape, the crenulated rims, a sole-like shaped sulcus and the OL:OH and CL:OL ratios (Fig. 2-7g, g'), however, its postero-ventral region is more prominent than that of Gobiiformes indet. 1. The morphological differences between the otoliths of Gobiiformes indet. 1 and 2 may represent intraspecific variation, but we tentatively described them separately. The shape of this fossil otolith is also similar to those of juveniles of *A. sciistius* (Fig. 2-6m), but it is much larger in size as well as Gobiiformes indet. 1.

Gobiiformes indet. 3

(Standard Japanese name: None) (Fig. 2-7i, 7i')

Material. n=1. KPM-NNV 1532: 1.91 mm OL, 2.00 mm OH, OL:OH = 0.95, bulk sample (Fig. 2-7i, 7i').

Description. The otolith is tall, sliced bread-like in shape. The inner face is flat, and the outer face is convex and lobulated. The anterior rim is nearly vertical and roughly crenulated. The antero-ventral region of the rim is angular. The dorsal rim is curved and roughly crenulated. The ventral rim is nearly straight and smooth. The postero-dorsal angle and the postero-ventral region of the rim are slightly protruding, and the posterior rim has a notch at the midpoint. The sulcus is mesial and sole-like in shape. The colliculum fills the sulcus; the CL:OL ratio is 0.44. The cristae are well-developed and a subcaudal iugum is present below the caudal region of the sulcus. The dorsal and ventral areas are flat.

Remarks. The otolith is similar to those of Gobiiformes indet. 1 in the crenulated rims, a sole-like shaped sulcus and the CL:OL ratio (Fig. 2-7g, 7g'), however, the otolith is taller and the OL:OH ratio is lower.

Gobiiformes indet. 4

(Standard Japanese name: None) (Fig. 2-7j, 7j')

Material. n=1. KPM-NNV 1533: right sagitta, 2.27 mm OL, 2.33 mm OH, OL:OH = 0.97, SH07 (Fig. 2-7j, 7j').

Description. The otolith is sliced bread-like in shape. The inner face is flat, and the outer face is convex and smooth. The antero-dorsal region of the rim is protruding. The anterior rim has a notch at the midpoint. The antero- and postero-ventral regions of the rims are angled. The ventral rim is nearly straight and smooth. The postero-dorsal angle is blunt, and the posterior rim is nearly vertical and roughly crenulated. The sulcus is mesial, and sole-like in shape. The colliculum fills the sulcus; the CL:OL ratio is 0.50. The cristae are ridge-like but the subcaudal iugum is absent. The dorsal area is slightly depressed, and the ventral area is flat.

Remarks. The otolith is similar to those of *A. sciistius* in the sliced bread-like otolith shape, a convex and smooth outer face and the sole-like shaped sulcus , however, the shape of the otolith is taller, and the OL:OH ratio is lower (1.18 in the recent specimens) (Ohe, 1985: p. 133). More fossil and extant specimens are required for species identification.

Gobiiformes indet. 5

(Standard Japanese name: None) (Fig. 2-7k, 7k')

Material. n=1. KPM-NNV 936: left sagitta, 1.55 mm OL, 1.68 mm OH, OL:OH = 0.92, bulk sample (Fig. 2-7k, 7k').

Description. The otolith is approximately pentagonal in shape. The inner face is flat, and the outer face is convex and roughly lobulated in the dorsal region. The antero- dorsal and -ventral regions of the rims are angled, and the tip of antero-dorsal region of the rim is slightly forward. The dorsal rim is pointed and smooth. The ventral rim is straight and smooth. The postero-dorsal angle is distinct, and the postero-ventral region of the rim is curved. The anterior and posterior rims have a shallow notch at the midpoint. The sulcus is mesial, and sole-like in shape. The colliculum fills the sulcus; the CL:OL ratio is 0.48. The cristae are well-developed and a subcaudal iugum is present below the caudal region of the sulcus. The dorsal and ventral areas are flat.

Remarks. The otolith is comparable to those of Gobiiformes in the sole-like shaped sulcus (e.g. Schwarzhans, 2014: fig. 2), however, more fossil and extant specimens are required for species identification.

Gobiiformes indet. 6

(Standard Japanese name: None) (Fig. 2-8a, 8a')

Material. n=1. KPM-NNV 1535: right sagitta, 2.96 mm OL, 2.71 mm OH, OL:OH = 1.09 (Fig. 2-8a, 8a').

Description. The otolith is sliced bread-like in shape. The inner face is slightly convex. The outer face is slightly concave, and roughly lobulated. The anterior rim is nearly straight and crenulated. The antero-dorsal region of the rim is slightly curved, and the antero-ventral region of the rim is distinctly angled. The dorsal rim is curved and nearly smooth. The ventral rim is straight and smooth. The postero-dorsal angle and the postero-ventral region of the rim are protruding, and both are similar in size with their tips extending parallel. The posterior rim has a notch at the midpoint. The sulcus is mesial and sole-like in shape. The colliculum fills the sulcus; the CL:OL ratio is 0.44. The cristae are ridge-like but the subcaudal iugum is absent. The dorsal and ventral areas are flat.

Remarks. The otolith is comparable to those of Gobiiformes in the sole-like shaped sulcus (e.g. Schwarzhans, 2014: fig. 2), however, more fossil and extant specimens are required for species identification.

Order Carangiformes Jordan, 1923

Family Carangidae Rafinesque, 1815

Genus *Trachurus* Rafinesque, 1810

Trachurus japonicus (Temminck and Schlegel, 1844)

(Standard Japanese name: Maaji) (Fig. 2-8b)

Material. n=1. KPM-NNV 898: left sagitta, 3.50 mm OL, 2.13 mm OH, OL:OH = 1.64, bulk sample (Fig. 2-8b).

Description. The otolith is spindle-like in shape. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum is extremely short and pointed. The rostrum is protruding and pointed. The excisura is extremely shallow; the AL:RL ratio is 0.02. The dorsal rim is slightly curved and crenulated, and the postero-dorsal angle is distinct but blunt. The ventral rim is curved and poorly crenulated. The posterior rim is pointed. The sulcus is ostial, its shape is straight and funnel-like, and flexed ventrally at the posterior end. The colliculum fills the sulcus. The cristae are well-developed. The dorsal area is slightly depressed whereas the ventral area is not.

Remarks. The otolith is most similar to those of *T. japonicus* in the spindle-like otolith shape, the OL:OH ratio which is below 2.0, and the shape of sulcus (Ohe, 1985: p. 83; Lin and Chang, 2012: p.

123, pls. 34, 102). The otoliths of genus *Decapterus* is also similar to the fossil material, however, they are more slender and the OL:OH ratio is over 2.0 (Ohe, 1985: p. 82–84; Lin and Chang, 2012: p. 120–121, pls. 33, 101).

Order Pleuronectiformes Bleeker, 1859

Family Paralichthyidae Chabanaud, 1937

Genus *Paralichthys* Girard, 1858

Paralichthys sp.

(Standard Japanese name: None) (Fig. 2-8c)

Material. n=1. KPM-NNV 1536: left sagitta, 2.44 mm OL, 1.39 mm OH, OL:OH = 1.75, SH07 (Fig. 2-8c).

Description. The otolith is slender, spindle in shape. The inner face is convex, and the outer face is slightly concave. The antirostrum and the excisura are indistinct. The rostrum is protruding and pointed. The dorsal rim is curved and roughly crenulated. The ventral rim is curved and smooth. The posterior rim is pointed. The sulcus is ostial, straight and funnel-like in shape. The ostium is longer than cauda; the OsL:CaL ratio is 1.83. The colliculum fills the sulcus. The cristae are ridge-like. The circumsulcal depression is slightly depressed.

Remarks. The otolith is comparable to those of genus *Paralichthys* in the straight and funnel-like shaped sulcus, and the long ostium (Schwarzhans, 1999: p. 114–124, figs. 185–208). However, the otoliths of Japanese extant species *P. olivaceus* (Temminck and Schlegel, 1846) are oval or nearly pentagonal in shape (Ohe, 1985: p. 164; Schwarzhans, 1999: p. 122, figs. 205, 206). Furthermore morphological comparison with the otoliths of the other extant paralichthyid fishes is required.

Genus *Tarphops* Thompson, 1914

Tarphops sp.

(Standard Japanese name: None) (Fig. 2-8d)

Material. n=1. KPM-NNV 923: left sagitta, 1.48 mm OL, 1.34 mm OH, OL:OH = 1.10, bulk sample (Fig. 2-8d).

Description. The otolith is approximately square in shape. The inner face is convex, and the outer face is concave. The anterior rim is slightly curved, and has a shallow notch above the sulcus. The dorsal rim is approximately straight, and has a shallow notch at the midpoint. The ventral rim is strongly curved and smooth. The posterior rim is nearly straight and poorly crenulated. The sulcus is ostial and straight. The CL:OL ratio is 0.72. The cristae are ridge-like. The circumsulcal depression is flat.

Remarks. The otolith is similar to those of *T. oligolepis* (Bleeker, 1859) in the approximately square otolith shape, the OL:OH ratio (1.0–1.05 in the recent specimens) and the ostial, straight sulcus (Schwarzhans, 1999: p. 134–135, figs. 240–242), however, we need the morphological comparison with the otoliths of the other congeneric species *T. elegans* Amaoka, 1969.

Bothidae Rafinesque, 1810

Genus *Crossorhombus* Regan, 1920

Crossorhombus kanekonis (Tanaka, 1918)

(Standard Japanese name: Kanekodarumagarei) (Fig. 2-8e)

Material. n=1. KPM-NNV 1537: right sagitta, 1.93 mm OL, 1.37 mm OH, OL:OH = 1.41, SH09 (Fig. 2-8e).

Description. The otolith is oval in shape. The inner face is slightly convex, and the outer face is slightly concave. The anterior and ventral rims are curved and smooth. The dorsal rim is slightly curved, poorly and roughly crenulated. The posterior rim is pointed. The sulcus is ostial and straight. The OCL:CCL ratio is 1.75. The cristae are ridge-like. The circumsulcal depression is flat.

Remarks. The otolith is most similar to those of *C. kanekonis* in the oval otolith shape, the OL:OH and OCL:CCL ratios (1.35–1.4 and 1.8 in the recent specimens) (Schwarzhans, 1999: p. 204, figs. 474, 475).

Family Pleuronectidae Cuvier, 1816

Genus *Limanda* Gottsche, 1835

Limanda punctatissima (Steindachner, 1879)

(Standard Japanese name: Sunagarei) (Fig. 2-8f)

Material. n=1. KPM-NNV 1539(190313-7-19): left sagitta, 2.41 mm OL, 1.90 mm OH, OL:OH = 1.27, SH07 (Fig. 2-8f). Recent material: *L. punctatissima*, n=3. KPM-NI 52542, 53570, 53571: 184.2–226.5 mm SL, 4.37–4.50 mm OL, 3.20–3.72 mm OH, OL:OH = 1.21–1.37 (left sagittae), Hokkaido (Fig. 2-8g).

Description. The otolith is approximately semicircular. The inner face is nearly flat and the outer face is slightly concave. The anterior rim is curved, and has a shallow notch; the antero-dorsal region of the rim is angled and slightly protruding. The dorsal rim is approximately straight. The ventral and posterior rims are curved. The sulcus is mesial and straight, the neck is indistinct. The collicula are oblong, depressed; the OCL:CCL ratio is 1.80. The cristae are well developed. The circumsulcal depression is slightly depressed.

Remarks. The otolith is most similar to those of *L. punctatissima* in the following characters: an approximately semicircular otolith shape, the OL:OH ratio (1.21–1.37 in the recent specimens), an angled antero-dorsal region of the rim, a mesial sulcus, the concave and the oblong collicula (the OCL:CCL ratio is 1.70–1.90 in the recent specimens) (Fig. 2-8g).

Genus *Pseudopleuronectes* Bleeker, 1862

Pseudopleuronectes herzensteini (Jordan and Snyder, 1901)

(Standard Japanese name: Magarei) (Fig. 2-8h)

Material. n=1. KPM-NNV 1538: left sagitta, 3.58 mm OL, 2.30 mm OH, OL:OH = 1.56, SH03 (Fig. 2-8h). Recent material: *P. herzensteini*, n=1. KPM-NI 52536: 210.6 mm SL, 5.42 mm OL, 3.53 mm OH, OL:OH = 1.54 (left sagitta), Hokkaido (Fig. 2-8i).

Description. The otolith is approximately "D" shape. The inner face is slightly convex, and the outer face is slightly concave. The anterior rim is protruding and strongly curved, and the antero-dorsal region of the rim is curved. The dorsal rim is straight and smooth, and the postero-dorsal angle is pointed. The ventral rim is curved, its anterior region is smooth but its posterior region is crenulated. The posterior rim is slightly curved and crenulated. The sulcus is ostial and straight, and the neck is indistinct. The collicula are oblong and depressed; the OCL:CCL ratio is 1.82. The cristae are well-developed. The circumsulcal depression is slightly depressed.

Remarks. The otolith is most similar to those of *P. herzensteini* in the approximately “D” shaped otolith, the OL:OH and OCL:CCL ratios (1.54 and 1.83 in the recent specimen), and the straight sulcus without neck (Fig. 8(I)). The otolith of *P. yokohamae* (Günther, 1877) is also similar to our fossil material, however, its shape is more slender, the OL:OH ratio is 1.65–1.80 (Schwarzhans, 1999: p. 238, figs. 581, 582).

Order Trachiniformes Rafinesque, 1810

Family Pinguipedidae Günther, 1860

Pinguipedidae indet.

(Standard Japanese name: None) (Fig. 2-8j)

Material. n=1. KPM-NNV 927: left sagitta, 4.66 mm OL, 1.66 mm OH, OL:OH = 2.80, bulk sample (Fig. 2-8j).

Description. The otolith is slender and spindle-like in shape. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum is distinct but it is not protruding, and the excisura is indistinct. The rostrum is protruding and pointed. The dorsal rim is nearly straight, and gradually declined from the postero-dorsal angle to the posterior tip of the otolith. The ventral rim is nearly straight. The posterior tip of the otolith is pointed. The sulcus is ostial and funnel-like in shape, and its posterior end is flexing ventrally. The colliculum fills the sulcus. The cristae are well-developed. The dorsal area is slightly depressed whereas the ventral area is not, but they are abraded.

Remarks. The otolith is comparable to those of pinguipedid fishes in the slender, spindle shaped otolith with a distinct postero-dorsal angle, and the shape of sulcus (e.g. Lin and Chang, 2012: p. 188–189, pls. 54, 122). However, we refrained from identification to the genus or species level since the preservation of the specimen is poor.

Family Ammodytidae Bonaparte, 1832

Genus *Ammodytes* Linnaeus, 1758

Ammodytes sp.

(Standard Japanese name: None) (Fig. 2-8k)

Material. n=1. KPM-NNV 1525: right sagitta, 2.51 mm OL, 1.15 mm OH, OL:OH = 2.25, bulk sample (Fig. 2-8k). Recent material: *A. japonicus* Duncker and Mohr, 1939, n=3. KPM-NI 52540, 53580, 53582: 161.2–164.4 mm SL, 2.85–3.23 mm OL, 1.27–1.45 mm OH, OL:OH = 2.17–2.29 (right sagittae), Hokkaido (Fig. 2-8l).

Description. The otolith is slender, sesame seed-like shaped. The inner face is convex and the outer face is slightly concave. The anterior rim is sharply pointed. The antero-dorsal and -ventral regions are straight, poorly crenulated. The dorsal and ventral margins are slightly curved and smooth. The posterior rim is smooth and markedly protruding. The sulcus is ostial, narrow, and funnel-like. The ostial colliculum is slightly deeper than the caudal colliculum. The caudal colliculum fills the cauda. The cristae are ridge-like. The dorsal area is slightly depressed whereas the ventral area is not.

Remarks. The otolith is comparable to those of *A. japonicus* in the following characters: a slender, sesame seed-like otolith shape, the OL:OH ratio (2.17–2.29 in a recent specimen), a narrow and a funnel-like shaped sulcus (Fig. 2-8l). However, the otoliths of the three congeneric species, *A. japonicus*, *A. hexapterus* Pallas, 1814 and *A. heian* Orr, Wildes and Kai, 2015, distributed in the Western North Pacific are difficult to distinguish (Muto and Yamada, 2019). Therefore this specimen was classified only up to the genus level.

Order Perciformes Bleeker, 1863

Family Acropomatidae Gill, 1893

Genus *Parascombrops* Alcock, 1889

Parascombrops ohei Schwarzhans and Prokofiev, 2017

(Standard Japanese name: None) (Fig. 2-8m)

Material. n=1. KPM-NNV 1518: right sagitta, 3.94 mm OL, 1.97 mm OH, OL:OH = 2.00, SH04 (Fig. 2-8m).

Description. The shape of the otolith is oblong. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum is short and pointed. The rostrum is protruding and its tip is pointed. The excisura is shallow; the AL:RL ratio is 0.13. The dorsal rim is slightly curved and poorly crenulated. The ventral rim is curved and poorly crenulated, its bottom is located at about 1/3 of the otolith length.

The posterior rim is slightly curved and poorly crenulated. The sulcus is ostial, straight and oar-like in shape; the neck is distinctly constricted at the ventral side. The OsL:CaL ratio is 1.01. The collicula fill the sulcus. The cristae are well-developed. The dorsal and ventral areas are flat.

Remarks. The otolith is most similar to those of *P. ohei* in the oblong otolith shape, the OL:OH ratio (1.9–2.1 (mean value is 2.0) in the recent specimens) and the oar-like shaped sulcus (Schwarzhans and Prokofiev, 2017: p. 41–43, fig. 14S–U, table 7).

Family Cepolidae Rafinesque, 1810

Genus *Cepola* Linnaeus, 1764

Cepola schlegeli Bleeker, 1854

(Standard Japanese name: Sumitsukiakatachi) (Fig. 2-8n)

Material. n=1. KPM-NNV 1521: left sagitta, 2.68 mm OL, 1.46 mm OH, OL:OH = 1.84, SH07 (Fig. 2-8n).

Description. The otolith is slender, approximately spindle-like in shape. The inner and outer faces are convex. The antirostrum and the excisura are indistinct. The rostrum is protruding, and its tip is pointed. The antero-dorsal region of the rim is angular. The dorsal rim is straight and smooth, and the postero-dorsal angle is blunt and weak. The ventral rim is straight and smooth, and the antero- and postero-ventral regions of the rims are curved. The posterior rim is strongly curved and smooth. The sulcus is ostial and its shape is glasses-like; the neck is strongly constricted. The ostium is longer than cauda; the OsL:CaL ratio is 2.43. The cristae are ridge-like. The dorsal and ventral areas are not depressed.

Remarks. The otolith is most similar to those of *C. schlegeli* in the approximately spindle-like otolith shape, the OL:OH ratio (1.9 in the recent specimen) and the glasses-like shaped sulcus (Ohe, 1985: p. 86).

Order Scorpaeniformes Bloch, 1789

Family Scorpaenidae Risso, 1826

Genus *Sebastiscus* Jordan and Starks, 1904

Sebastiscus marmoratus (Cuvier, 1829)

(Standard Japanese name: Kasago) (Fig. 2-8o)

Material. KPM-NNV 882: left sagitta, 3.30 mm OL, 1.73 mm OH, OL:OH = 1.91, bulk sample (Fig. 2-8o).

Description. The otolith is slender and spindle in shape. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum is poorly protruding, and its tip is blunt. The rostrum is protruding, and its tip is pointed. The excisura is extremely shallow; the AL:RL ratio is 0.05. The dorsal and ventral rims are curved and poorly crenulated. The posterior rim is strongly curved. The sulcus is ostial, funnel-like in shape and its posterior end is flexing ventrally, but the neck is indistinct. The collicula fill the sulcus. The crista superior is ridge-like, and the crista inferior is well-developed. The dorsal area is slightly depressed whereas the ventral area is not.

Remarks. The otolith is most similar to those of *S. marmoratus* in the slender, spindle-like in shape, with an extremely shallow excisura, and a nearly straight, funnel shaped sulcus (Ohe, 1985: p. 154).

Family Triglidae Risso, 1826

Genus *Lepidotrigla* Günther, 1860

Lepidotrigla sp.

(Standard Japanese name: None) (Fig. 2-9a)

Material. n=1. KPM-NNV 906: right sagitta, 3.37 mm OL, 2.61 mm OH, OL:OH = 1.29, bulk sample (Fig. 2-9a).

Description. The otolith is approximately spindle-like in shape. The inner face is convex, and the outer face is concave. The antirostrum is poorly protruding, and its tip is blunt. The rostrum is short, and its tip is blunt. The excisura is wide but it is extremely shallow; the AL:RL ratio is 0.23. The dorsal rim is strongly curved and angular at the midpoint. The ventral rim is slightly curved and with an angle at the midpoint, and the postero-ventral region of the rim is distinctly angular. The posterior rim is vertical. The sulcus is ostial, and sigmoidal shaped. The ostium is wider than the cauda. The colliculum is indistinct. The crista superior is crest-like, but it is poorly-developed above the ostium. The crista inferior is ridge-like, but it is poorly-developed below the ostium. The dorsal area is depressed whereas the ventral area is not.

Remarks. The otolith is similar to those of *L. guntheri* and *L. japonica* in the approximately spindle-like otolith shape with the angles at the dorsal and ventral rims, and a sigmoidal shaped sulcus (Lin and Chang, 2012: p. 90, pls. 23, 91), however, we need more morphological comparison with the recent materials.

Family Platycephalidae Gill, 1872

Platycephalidae indet.

(Standard Japanese name: None) (Fig. 2-9b)

Material. n=1. KPM-NNV 919: left sagitta, 1.82 + mm OL, 0.72 mm OH, OL:OH is incalculable, bulk sample (Fig. 2-9b).

Description. The otolith is slender, spindle-like in shape, but the tip of rostrum is broken. The inner face is convex, and the outer face is slightly concave. The antirostrum and the excisura are indistinct. The dorsal rim is curved and smooth. The ventral rim is slightly curved and smooth. The posterior rim is tapering and its tip is sharply pointed. The sulcus is ostial and straight, its shape is funnel-like. The ostial colliculum is slightly deeper than the caudal colliculum. The cristae are ridge-like. The dorsal area is depressed whereas the ventral area is not.

Remarks. The otolith is comparable to those of platycephalid fishes in the slender, nearly spindle otolith shape, a sharply pointed posterior tip of the otolith, and a straight, funnel-like shaped sulcus (Lin and Chang, 2012: p. 93–95, pls. 24, 25, 92, 93), however, we refrained from an identification to the genus or species level since its rostrum is broken.

Family Cottidae Bonaparte, 1831

Genus *Triglops* Reinhardt, 1830

Triglops sp.

(Standard Japanese name: None) (Fig. 2-9c)

Material. n=1. KPM-NNV 1523: right sagitta, 2.17 mm OL, 1.15 mm OH, OL:OH = 1.89, SH07 (Fig. 2-9c). Recent material: T. jordani (Jordan and Starks, 1904), n=1. KPM-NI 23525: 177.1 mm SL, 3.27 mm OL, 1.81 mm OH, OL:OH = 1.81 (right sagitta), off Akita (Fig. 2-9d).

Description. The otolith is spindle shaped. The inner face is convex and the outer face is slightly concave. The antirostrum is blunt and not protruding anteriorly. The rostrum is protruding anteriorly and pointed at the tip. The dorsal margin is curved and roughly crenulated. The ventral margin is smooth, slightly curved. The posterior rim is pointed. The sulcus is ostial and straight. The ostial colliculum is deeper than the caudal one. The crista superior is poorly-developed. The crista inferior is ridge-like. The dorsal and ventral areas are not depressed.

Remarks. The otolith is most similar to those of *T. jordani* and *T. pingelii* in the spindle otolith shape, the blunt antirostrum which is not protruding anteriorly, the deeper ostial colliculum, the poorly developed crista superior and the ridge-liked crista inferior (Fig. 2-9d; Lombarte et al., 2006: Fish ID 10040, n=1, in the AFORO Database).

Order Spariformes Bleeker, 1876

Family Sillaginidae Richardson, 1846

Genus *Sillago* Cuvier, 1817

Sillago japonica Temminck and Schlegel, 1843

(Standard Japanese name: Shirogisu) (Fig. 2-9e)

Material. KPM-NNV 905: right sagitta, 3.72 mm OL, 2.27 mm OH, OL:OH = 1.64, bulk sample (Fig. 2-9e).

Description. The otolith is spindle-like in shape. The inner face is convex, and the outer face is slightly concave. The antirostrum and the excisura are indistinct. The rostrum is pointed. The dorsal and ventral rims are curved and poorly crenulated. The posterior rim is pointed. The sulcus is ostio-pseudocaudal and straight. The neck of the sulcus is distinct at the ventral side, and the ventral rim of cauda has a notch at the midpoint. The colliculum fills the sulcus. The cristae are ridge-like. The dorsal and ventral areas are not depressed.

Remarks. The otolith is most similar to those of *S. japonica* in the spindle-like otolith shape, the OL:OH ratio (1.5–1.68 in the recent specimens), and the shape of sulcus (Ohe, 1985: p. 118; Lin and Chang, 2012: p. 115–116, pls. 32, 100).

Family Sparidae Rafinesque, 1810

Genus *Pagrus* Cuvier, 1816

Pagrus major (Temminck and Schlegel, 1843)

(Standard Japanese name: Madai) (Fig. 2-9f)

Material. KPM-NNV 1520: right sagitta, 3.42 mm OL, 2.52 mm OH, OL:OH = 1.36, SH04 (Fig. 2-9f).

Description. The otolith is approximately spindle-like in shape. The inner face is slightly convex, and the outer face is slightly concave. The antirostrum is blunt, but it is poorly protruding. The rostrum is protruding and its tip is pointed. The excisura is wide but extremely shallow; the AL:RL ratio is 0.02. The dorsal rim is slightly curved and roughly crenulated, and the posterodorsal angle is distinct. The ventral rim is curved and crenulated, and angular at the midpoint. The posterior rim is slightly curved and crenulated. The sulcus is ostial and tadpole-like in shape, and its posterior end is flexing ventrally. The neck of the sulcus is distinct. The ostial colliculum is slightly deeper than the caudal colliculum. The cristae are well-developed. The dorsal area is depressed whereas the ventral area is not.

Remarks. The otolith is most similar to those of *P. major* in the spindle otolith shape, the crenulated rims and the shape of sulcus (Watanabe et al., 2004: "*Pagrus major*" in the CD-ROM software "A guide for otoliths of fishes off Japan").

Paleoenvironmental analysis. The bathymetric distribution and climatic zone categories based on the marine fish distribution of recent analogues are shown in Table 2-2. Both number of taxa (richness) and number of specimens (abundance) were higher in the sandy mud assemblage (samples SH01-SH07 and bulk) than in the muddy sand assemblage (samples SH08-SH11) (Table 2-1). However, variations in the indices for both assemblages were very similar either in "all taxa" or "benthic/benthopelagic (B/B) taxa" analyses in the paleobathymetric analyses (Fig. 2-10). In "all taxa" analysis, richness and abundance in both assemblages were highest in the uppermost 0–100 m interval, decreased around 200 m, and increased again at depths around 400 m. The richness then gradually decreased below 400 m, while the abundance maintained a moderate level until 1500 m. A different pattern could be seen in the analysis of "B/B taxa". Both indices for richness and abundance were also highest in the uppermost interval and then decreased, first drastically and then gradually at further depths.

Paleoclimate analysis on both assemblages revealed similar patterns with two peaks in the percentages of richness and abundance in TP taxa and TT taxa. In comparison, richness and abundance of other taxa were negligible (Fig. 2-11).

Discussion

The present study provides the first record of 62 fish taxa from the Sha'ana Tuffaceous Sand Member, of which 31 extant species are newly recorded from the Chibanian of Kanto region, although *Trachurus japonicus* and *Sillago japonica* were previously recovered from the Kioroshi Formation (Takahashi and Fukuda, 1991) (we tentatively excluded the Aoki's taxa from the fossil records as mentioned below). Our assemblage from this member complements the scant fossil record for the Kanto region during this age that includes only 8 studies (Aoki, 1968, 1971; Uyeno and Matsushima, 1979; Aoki and Baba, 1980; Goto et al., 1984; Takahashi and Fukuda, 1991; Naruse et al., 1994; Tanaka, 1997; Taru and Matsushima, 1998; Fujii et al, 2010; Aida et al., 2016). Here we note another remarkable fossil record of *Theragra chalcogramma*: it was previously recorded from the Pleistocene from Chiba Prefecture in the Kanto region (Aoki, 1971) and from Ishikawa, Akita, and Aomori Prefectures in northern Japan (Ohe and Watanabe, 2018). Therefore the specimens found in this study represent the southwesternmost fossil record for this species in Japan and suggest the past occurrence of this boreal fish (Endo, 2009) off the coast of temperate Kanto.

Bathymetric analysis indicates that both sandy mud and muddy sand assemblages were likely under similar sedimentary environment. In "all taxa" analyses, richness and abundance of both assemblages showed higher values at depths of <200 m and >400 m, suggesting possible paleo-water depths (Fig. 2-10). However, the increase of indices at depths >400 m is mainly due to the otoliths of mesopelagic myctophids. The myctophids are characterized by their diel vertical migration and can be found in both epipelagic and mesopelagic zones (Table 2-1). Moreover, otoliths of myctophids are also commonly recovered from the sediments of shallow sea bottoms (< 200 m), not only strictly confined to the sediments of the deep sea (e.g., Schwarzhans, 2013; Lin et al., 2016, 2017). On the other hand, the high values for richness and abundance in the analysis of "benthic/benthopelagic taxa (B/B)" strongly suggest a very shallow paleobathymetry (Fig. 2-10). Despite the occurrence of otoliths of *Abyssicola macrochir* (recent species found at depths of 158–830 m) and *Parascombrops ohei* (175–200 m) in the sandy mud assemblage indicate a slightly deeper paleoenvironment, their bathymetric range does not exclude waters <200 m. Therefore, the whole fauna was likely deposited at depths shallower than 200 m.

Fossil invertebrates from Sha'ana-dai generally show an accumulative and allochthonous preservation, suggesting the possibility of post-mortem transportation, concentration, and time-averaging of remains during taphonomic processes (Nojo and Suzuki, 1999). Okumura et al. (1979) recognized that the molluscan assemblage from the Kamimiyada Tuffaceous Sand Member (geologically identical to the Sha'ana Tuffaceous Sand Member) was composed of dwellers from both intertidal zone and continental shelf, and suggested the shells from intertidal zones might have drifted to the deeper continental shelf. In Sha'ana-dai, we also found a mixture of many intertidal mollusks, e.g., *Homalopoma amussitatum*, and bivalves with articulated shells from deeper continental shelf (recent species found at depths of 50–200 m; Okutani, 2017). Similarly, the remains of very shallow water fishes dwelling at depths <100 m could have drifted from their habitats to deeper zones, or could have been transported through predators down slope (Lin et al., 2016), resulting in allochthonous preservation. This could be the case, for example, of the otoliths of *Amblychaeturichthys sciistius*, *Pterogobius zacalles*, and *Limanda punctatissima* in our assemblages (Table 2-1, 2). According to the lithology of the section, the recognized semiconsolidated sandy mud and muddy sand are generally deposited on the outer continental shelf at depths below 70 m (Saito, 1989). Consequently, Sha'ana Tuffaceous Sand Member exposed in Sha'ana-dai is likely deposited in the outer continental shelf at depths of 100–200 m.

The composition of paleoichthyofauna in Sha'ana-dai consisted of diverse climate-related taxa (AS, CT, TP and TT taxa, Fig. 2-11). This could be derived from the geographical and oceanographical factors in the Paleo-Tokyo Bay during the Chibanian. Temperate (TP) and tropical–temperate (TT) taxa dominated the assemblages. TP species, except *Guttigadus nana*, *Crossorhombus kanekonis*, and *Parascombrops ohei*, all occur in the present fish fauna in the region (Senou et al., 2006). However, the recent distribution of TT taxa includes the warm Kuroshio Current in Japanese waters (Nakabo, 2013a), which strongly suggests that the warm water current inflow in the Kanto area persists since the Chibanian. On the other hand, the relatively rare, but perhaps more significant arctic/subarctic (AS, e.g. *Clupea pallasii* and *Theragra chalcogramma*) and cold temperate (CT, e.g. *Pseudopleuronectes herzensteini*) taxa suggest the presence of cold water current(s). The articulated extant bivalves co-occurring in the assemblages are temperate species (e.g. *Cyclocardia ferrungia*, *Acira mirabilis*, and *Nuculana yokoyamai*), but extant boreal molluscs (e.g. *H. amussitatum*, *Puncturella nobilis*, and *Macoma calcarea*) and tropical–temperate planktonic mollusks (e.g. *Clio pyramidata*) were also abundant. It is known that the warm Kuroshio Current extended to the latitude of about 35° N for at least 3 Ma (Gallagher et al., 2015), and the subarctic front between the cold Oyashio and warm Kuroshio Currents fluctuated north- and southward at the coast of southeastern Japan during the Chibanian (Suganuma et al., 2018). Kanie and Ohkoshi (1981) considered that the sedimentary basin of the Kamimiyada Tuffaceous Sand Member (equivalent of Sha'ana Tuffaceous Sand Member) is opening towards the east. The Paleo-Tokyo Bay is considered to be widely opened to the southeast (Sugai et al., 2013), and hence the warm and cold water currents could project into the inner bay (Kaneko et al., 2018). Therefore, the paleoclimate zone for Sha'ana-dai can be considered as temperate, and it was located at a place where the influence of both warm Kuroshio and cold Oyashio currents was significant.

In conclusion, based on fish assemblages, the paleoenvironment of Sha'ana-dai during the deposition period of the Sha'ana Tuffaceous Sand Member is interpreted as a continental shelf environment with depths of 100–200 m. The location of deposition was within the temperate zone where both cold Oyashio and warm Kuroshio Currents existed. This interpretation on the paleoenvironment agrees with those drawn from studies on molluscan (Okumura et al., 1977, 1979, 2005) and brachiopod assemblages (Kuramochi and Katsuzawa, 1999).

The study opens an exciting new perspective for understanding the content of the paleo ichthyofauna in the temperate region where warm and cold currents met during the Chibanian. Paleo-biogeographical insights based on the associated fish fauna from the region would provide a more comprehensive view on how fish communities have changed since the Pleistocene. Many fossil otoliths collected from the Pleistocene strata in the Kanto region were described in Aoki (1968, 1971) and Aoki and Baba (1980). However, taxonomy and/or identification in these publications are problematical since comparison to extant fish otoliths was incomplete. Our ongoing studies include a review of previous materials with an updated version of modern systematics (Aoki, 1968, 1971; Aoki and Baba, 1980; Takahashi and Fukuda, 1991) and exploring unstudied otoliths from museum collections (e.g. the Chibanian Naganuma Formation, the type horizon of Aoki's taxa, stored at KPMNH). Moreover, knowledge on the related stratigraphy and geological age of the members belonging to the Miyata Formation remains scarce (Kasama and Shioi, 2019), hindering the horizontal correlation of the local fauna to those from other regions. In doing so, we expect to understand better the past spatiotemporal dynamics of the fish fauna during the Chibanian in the Western Pacific, particularly in Japan.

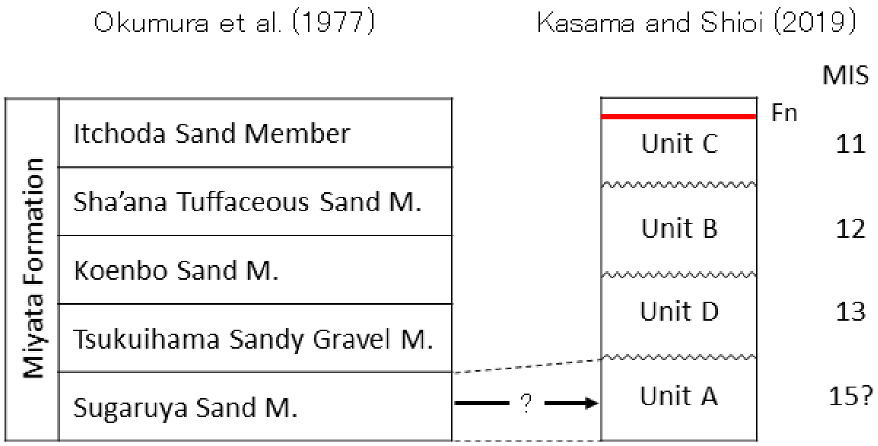

Fig. 2-1. Stratigraphy of the Miyata Formation after Okumura et al. (1977) and Kasama and Shioi (2019). Fn: Funakubo Tuff. MIS: marine isotope stage.

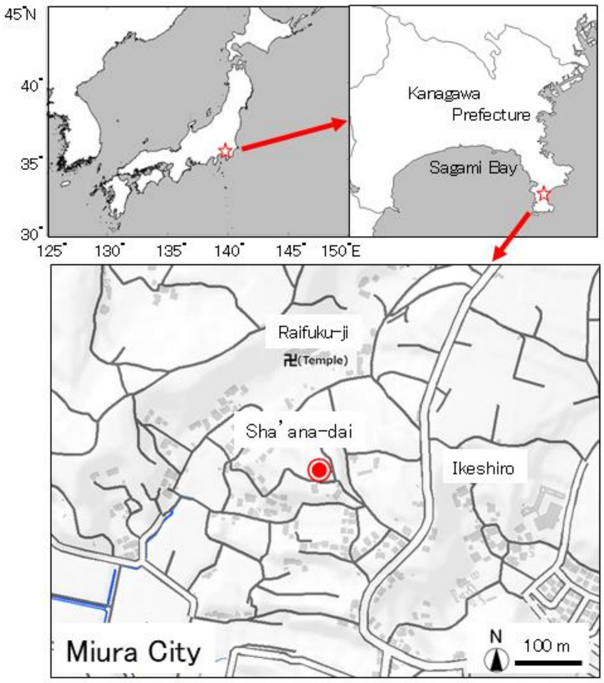

Fig. 2-2. Position of sampling locality. Topographic maps by the Geological Survey Institute (URL: https://www. gsi.go.jp/kihonjohochousa/multilingual.html, accessed 25.10.2019).

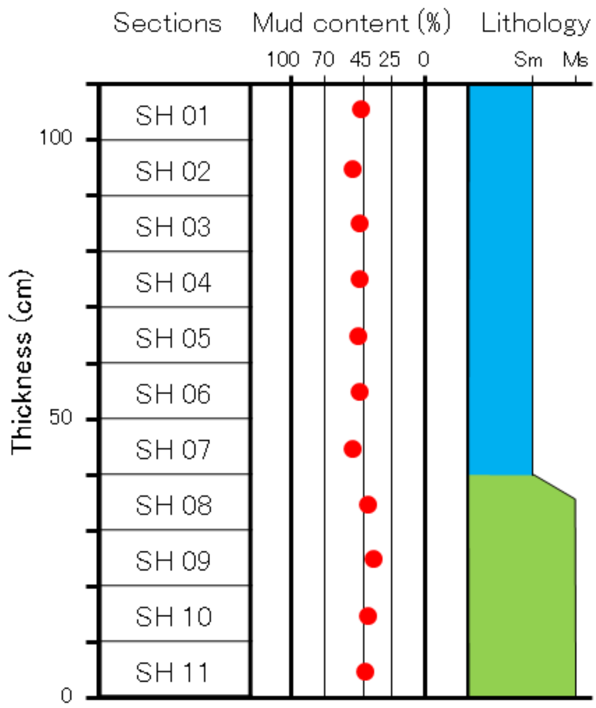

Fig. 2-3. Columnar section of the Sha'ana Tuffaceous Sand Member exposed at Sha'ana-dai. Sm: sandy mud; Ms: muddy sand. Criteria of mud content followed Kitazaki and Majima (2003).

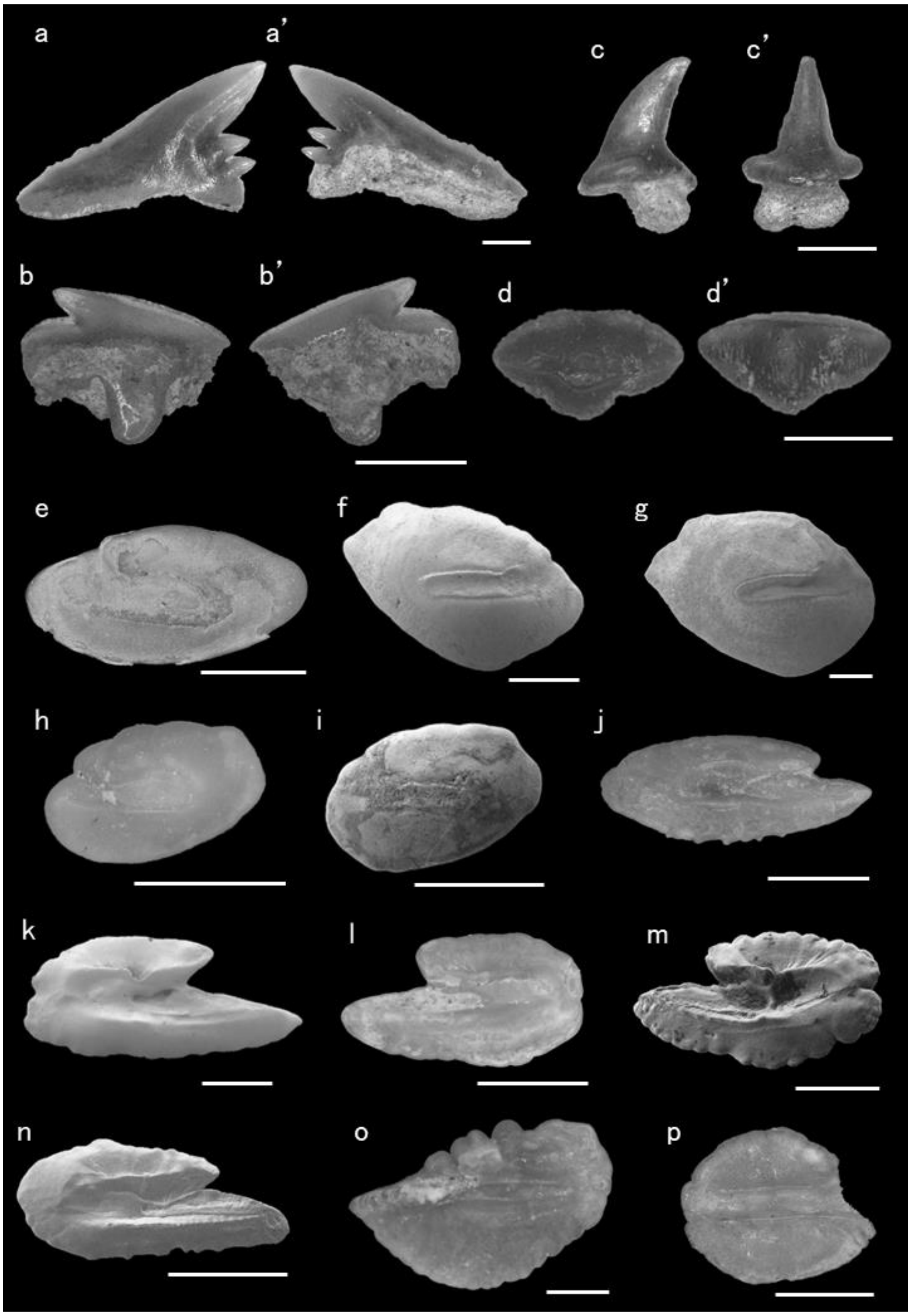

Fig. 2-4. Fish remains from Sha’ana-dai. Pictures of otoliths are inner views unless otherwise indicated. Registration codes of fossil materials are described in “Systematic description”. a, a’: *Hypogaleus* cf. *hyugaensis*. a: labial view, a’: lingual view. b, b’: *Squalus* sp. b: labial view, b’: lingual view. c, c’: Rajidae indet. c: lateral view, c’: frontal view. d, d’: *Rhynchobatus* sp. d: occlusal view, d’: lingual view. e: *Conger myriaster*. f, h: *Gnathophis* sp. g, i: *Gnathophis heterognathos*, recent materials. g: left sagitta. KPM-NI 46384, 303.7 mm TL, Suruga Bay. i: right sagitta. KPM-NI 52535, 58.7 mm TL, Sagami Bay. j: *Engraulis japonica*. k–m: *Clupea pallasii*. m: a recent material, right sagitta. KPM-NI 53290, 55.5 mm SL, Hokkaido. n: *Sardinops melanostictus*. o: *Glossanodon semifasciatus*. p: Osmeridae indet. Scale bars represent 1 mm (0.5 mm in l, m).

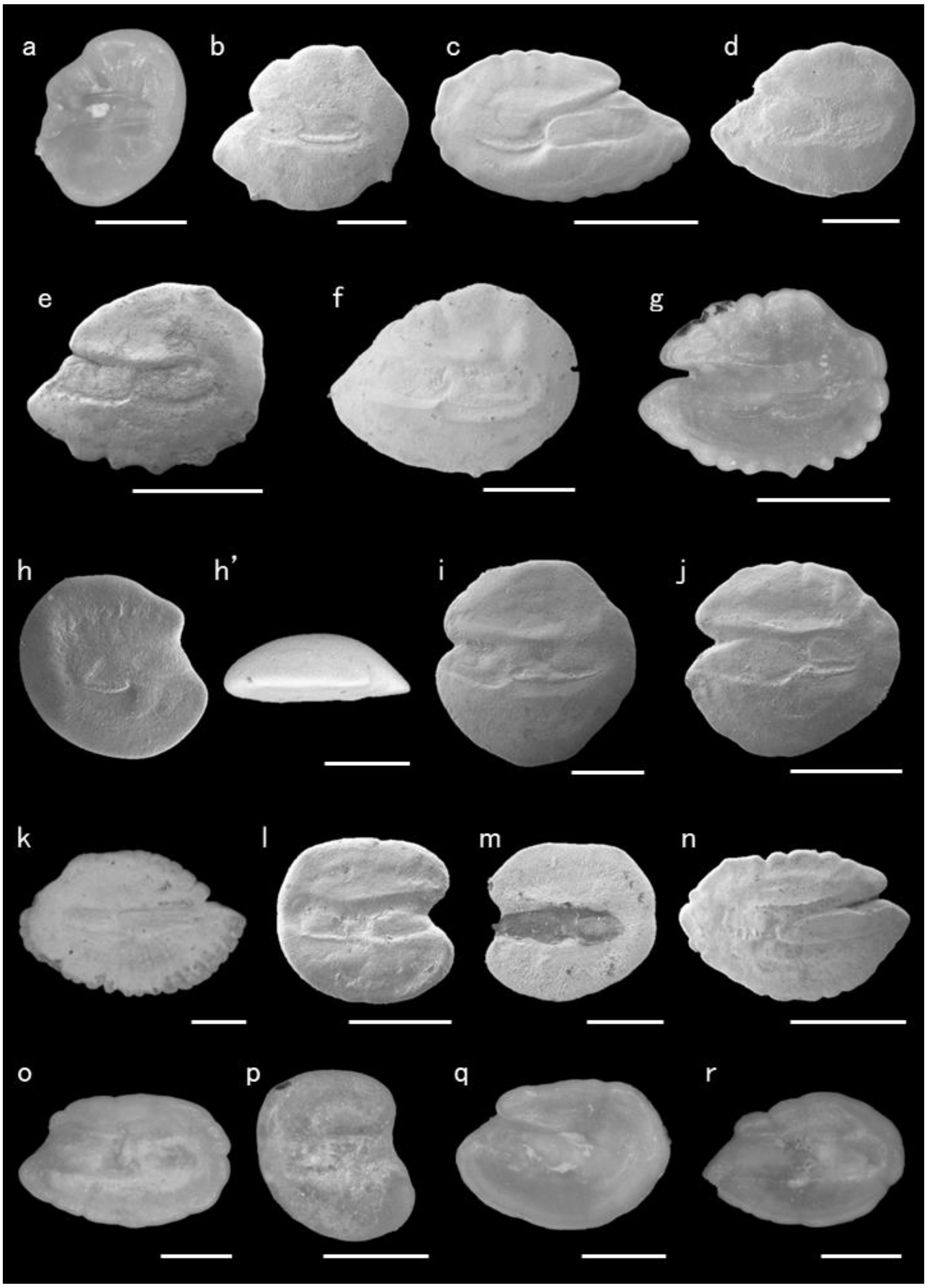

Fig. 2-5. Fish remains from Sha’ana-dai. Pictures of otoliths are inner views unless otherwise indicated. Registration codes of fossil materials are described in “Systematic description”. a: *Valenciennellus tripunctulatus*. b: *Benthosema suborbitale*. c: *Ceratoscopelus warmingii*. d: *Ceratoscopelus* sp. e: *Diaphus aliciae*. f: *Diaphus luetkeni*. g: *Diaphus watasei*. h, h’: *Diogenichthys atlanticus*. h: inner view, h’: dorsal view. i: *Electrona risso*. j: *Hygophum* sp. K. *Lampadena* sp. l, m: *Lampanyctus tuneri*. m: a recent specimen, right sagitta. CBM-ZF 5379, 51.5 mm SL, Sagami Bay. n: Myctophum asperum. o: *Notoscopelus resplendens*. p: *Stenobrachius leucopsarus*. q: *Taaningichthys minimus*. r: Myctophidae indet. Scale bars represent 0.5 mm (1 mm in c, e, g, j, n, p).

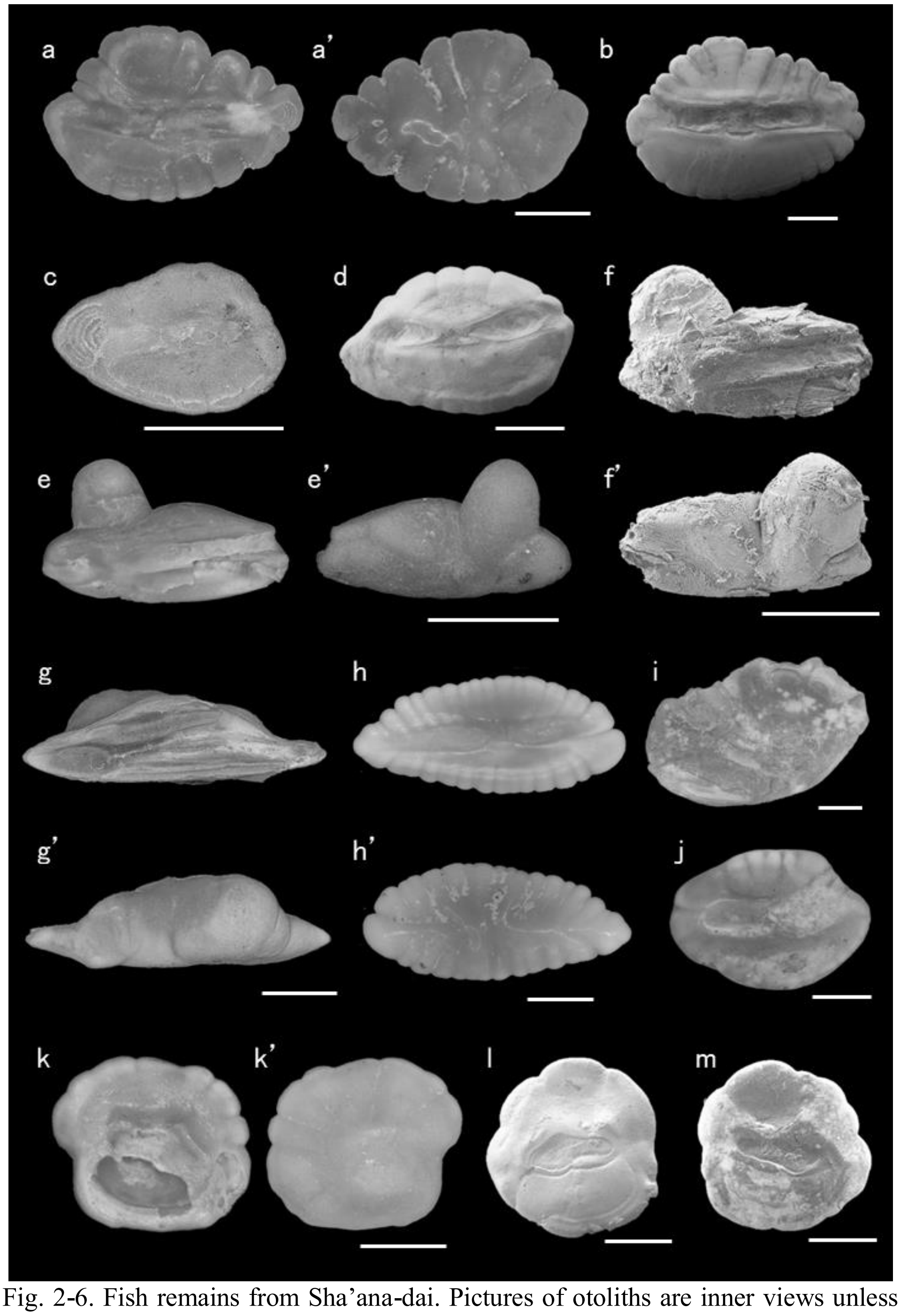

Fig. 2-6. Fish remains from Sha'ana-dai. Pictures of otoliths are inner views unless otherwise indicated. Registration codes of fossil materials are described in "Systematic description". a–b. *Abyssicola macrochir*. a: inner view, a': outer view. b: a recent material, right sagitta, KPM-NI 53284, right sagitta, 119.2 mm TL, Suruga Bay. c: *Ventrifossa* sp. d: Macrouridae indet. e–f': *Guttigadus nana*. e: inner view, e': outer view. f, f': a recent material, right sagitta. KAUM-I. 75043, 57.6 mm SL, East China Sea. f: inner view, f': outer view. g, g': *Physiculus* sp. h, h': *Theragra chalcogramma*. i: *Hoplostethus* sp. j: Apogonidae indet. k–m: *Amblychaeturichthys sciistius*. k: inner view, k': outer view. m: a recent specimen, right sagitta, KPM-NI 53287, 21.8 mm SL, Tokyo Bay. Scale bars represent 1 mm (0.5 mm in d, l, m).

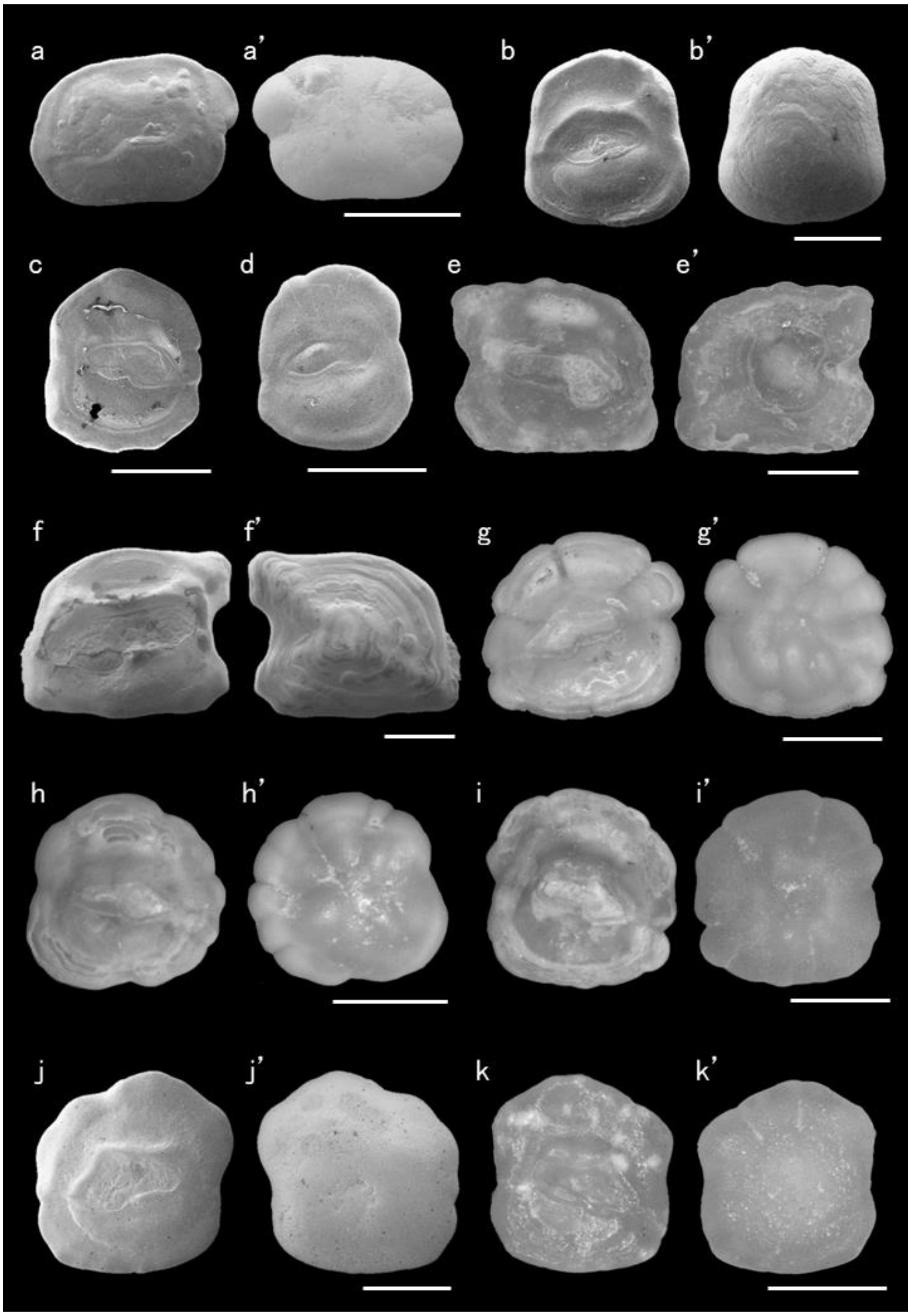

Fig. 2-7. Fish remains from Sha'ana-dai. Pictures of otoliths are inner views unless otherwise indicated. Registration codes of fossil materials are described in "Systematic description". a, a': *Amblychaeturichthys hexanema*. b, b': *Gymnogobius* aff. *heptacanthus*. b: inner view, b': outer view. c: *G. heptacanthus*, a recent material, left sagitta. KPM-NI 53567, 29.9 mm SL, Tokyo Bay. d: *Redigobius bikolanus*, a recent material, right sagitta. KPM-NI 53565, 19.8 mm SL, Kanagawa. e–f': *Pterogobius zacalles*. e: inner view, e': outer view. f, f': a recent specimen, right sagitta, KPM-NI 53285, 119.2 mm SL, Tokyo Bay. f: inner view, f': outer view. g, g': Gobiiformes indet. 1. g: inner view, g': outer view. h, h': Gobiiformes indet. 2. h: inner view, h': outer view. i, i': Gobiiformes indet. 3. i: inner view, i': outer view. j, j': Gobiiformes indet. 4. j: inner view, j': outer view. k, k': Gobiiformes indet. 5. k: inner view, k': outer view. Scale bars represent 1 mm (0.5 mm in b–d).

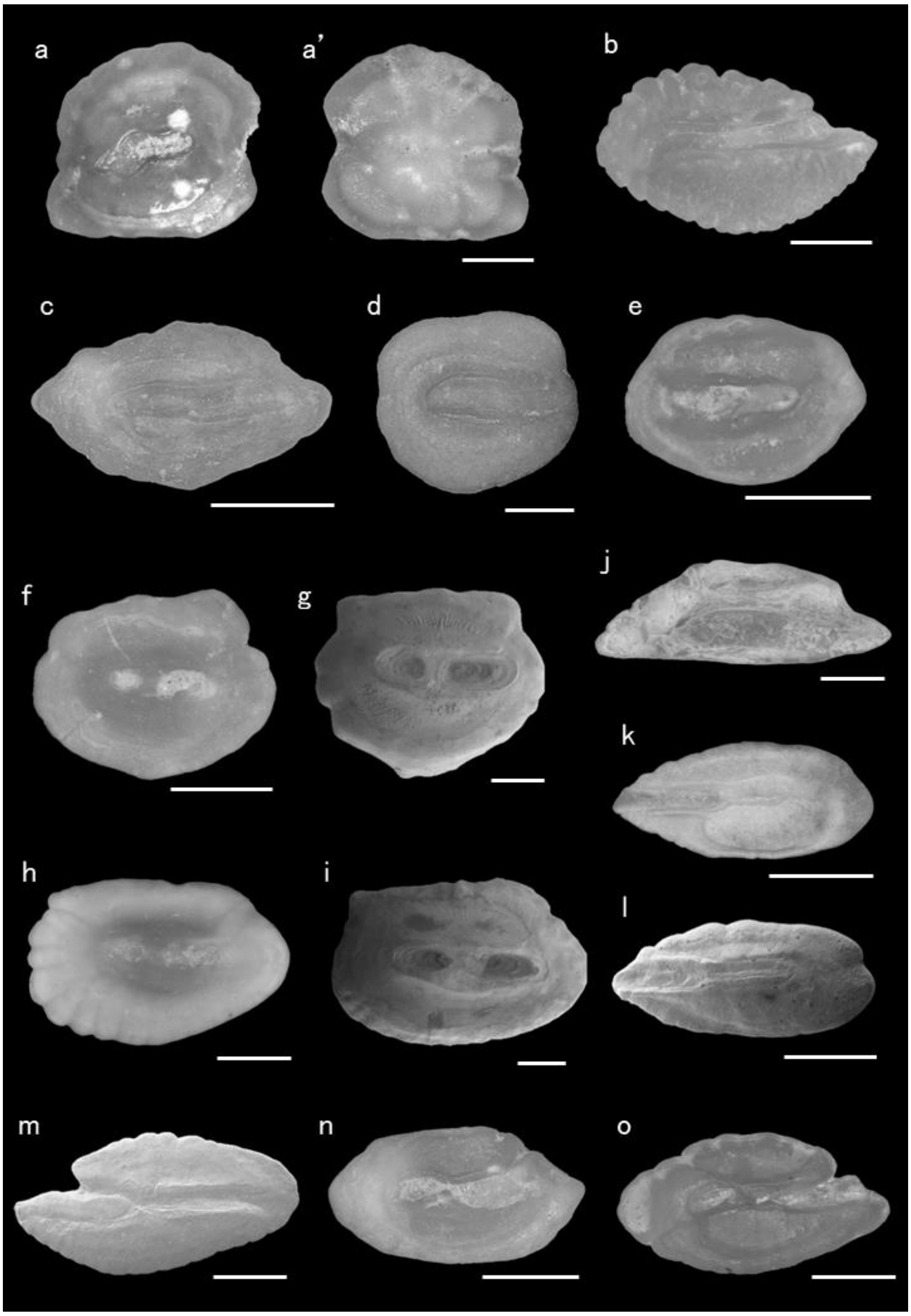

Fig. 2-8. Fish remains from Sha'ana-dai. Pictures of otoliths are inner views unless otherwise indicated. Registration codes of fossil materials are described in "Systematic description". a, a': Gobiiformes indet. 6. a: inner view, a': outer view. b: *Trachurus japonicus*. c: *Paralichthys* sp. d: *Tarphops* sp. e: *Crossorhombus kanekonis*. f, g: *Limanda punctatissima*. g: a recent specimen, left sagitta. KPM-NI 52542, 226.5 mm SL, Hokkaido. h, i: *Pseudopleuronectes herzensteini*. i: a recent specimen, left sagitta. KPM-NI 52536, 210.6 mm SL, Hokkaido. j: Pinguipedidae indet. k: *Ammodytes* sp. l: *Ammodytes japonicus*, a recent specimen, right sagitta. KPM-NI 52540, 161.2 mm SL, Hokkaido. m: *Parascombrops ohei*. n: *Cepola schlegeli*. o: *Sebastiscus marmoratus*. Scale bars represent 1 mm (0.5 mm in d).

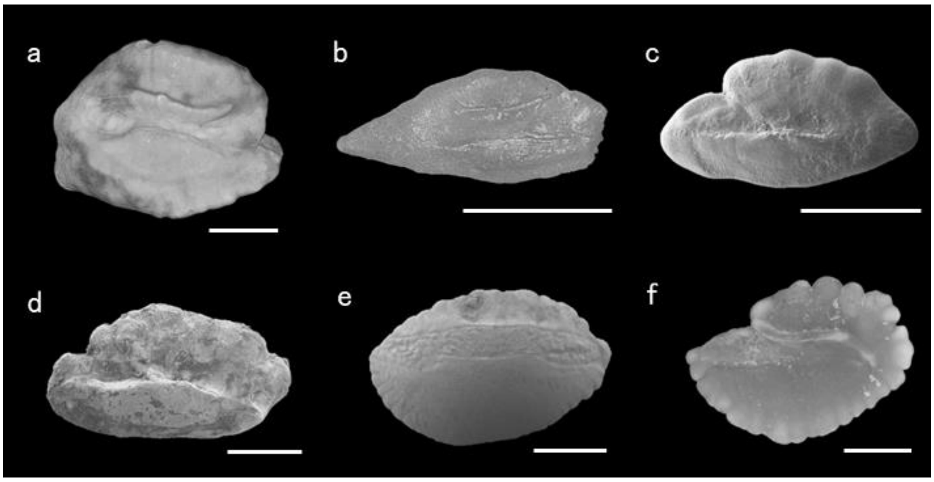

Fig. 2-9. Fish remains from Sha'ana-dai. Pictures of otoliths are inner views unless otherwise indicated. Registration codes of fossil materials are described in "Systematic description". a: *Lepidotrigla* sp. b: Platycephalidae indet. c: *Triglops* sp. d: *Triglops jordani*. a recent specimen, right sagitta. KPM-NI 23525, 177.1 mm SL, off Akita. e: *Sillago japonica*. f: *Pagrus major*. Scale bars represent 1 mm.

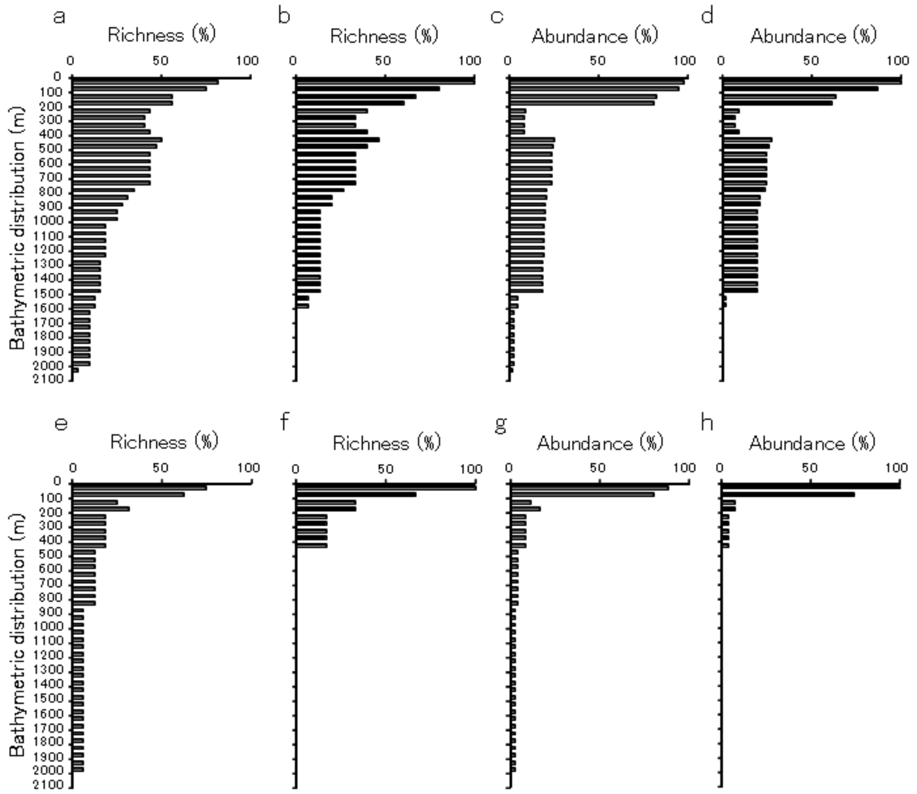

Fig. 2-10. Paleobathymetric analyses. a, b: richness of all species in the sandy mud assemblage (a) and the muddy sand assemblage (b). c, d: abundances of all taxa in the sandy mud assemblage (c) and the muddy sand assemblage (d). e, f: richness in of the benthic/benthopelagic (B/B) taxa in the sandy assemblage (e) and the muddy sand assemblage (f). g, h: abundances of the B/B taxa in the sandy mud assemblage (g) and the muddy sand assemblage (h).

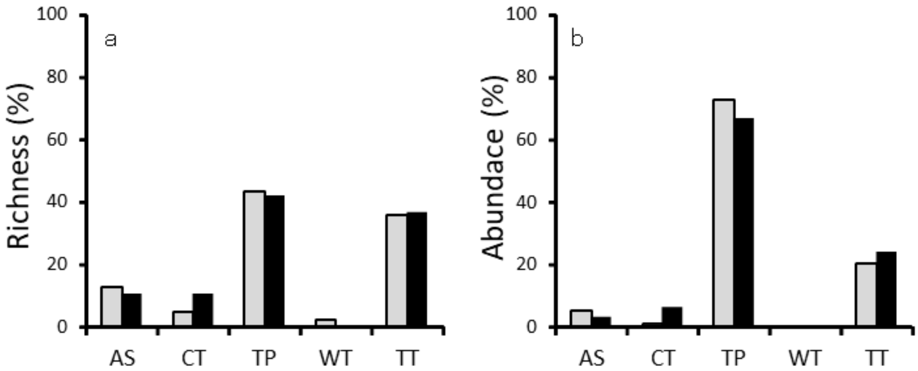

Fig. 2-11. Paleoclimatic analyses. Richness (a) and abundance (b) of the species in both assemblages. Shaded bars indicate the indices of the sandy mud assemblage, and solid bars indicate the indices of the muddy sand assemblage. AS: arctic/subarctic. CT: cold-temperate. TP: temperate. WT: warm-temperate. TT: tropical–temperate.

Table 2-1. Fish remains from each horizon.

Lithology	Sandy mud									Muddy sand					Total
Horizon	SH01	SH02	SH03	SH04	SH05	SH06	SH07	Bulk samlple	Total	SH08	SH09	SH10	SH11	Total	
Hypogaleus cf. *hyugaensis*								1	1					0	1
Squalus sp.						1			1	1				1	2
Rajidae indet.								1	1			1		1	2
Rhynchobatus sp.						1			1					0	1
Conger myriaster	1								1					0	1
Gnathophis sp.		5	1	1	6	3	3	45	64	3	4	2	2	11	75
Englauris japonica	7	18	11	12	10	18	18	109	203	5	9	4	7	25	228
Clupea pallasii								1	1		1			1	2
Sardinops melanostictus		1		1			1	2	5	2		1		3	8
Glossanodon semifasciatus					1		1	1	3	1				1	4
Osmeridae, indet.						1		1	2					0	2
Valenciennellus tripunctulatus								1	1					0	1
Benthosema suborbitale						1		1	2	1		1		2	4
Ceratoscopelus warmingii	1	2	1	4	3	3	1	38	53	5	3	2	4	14	67
? *Ceratoscopelus* sp.			4	1				8	13	1	3		2	6	19
Diaphus aliciae		1	1	2		1	1	1	7	1				1	8
Diaphus luetkeni			2						2		1			1	3
Diaphus watasei	1		1	1				1	4					0	4
Diogenichthys atlanticus						1			1					0	1
Electrona risso								1	1					0	1
Hygophum sp.	1	2		2			1	7	13	1			1	2	15
Lampadena sp.						1		1	2		1			1	3
Lampanyctus turneri								5	5		1	1		2	7
Myctophum asperum						1	2	4	7					0	7
Notoscopelus resplendens								2	2					0	2
Stenobrachius leucopsarus								1	1					0	1
Taaningichthys minimus				1				1	2				1	1	3
Myctophidae, indet.									0		1			1	1
Poorly preserved myctophids				1	4	1		4	10	1				1	11
Abyssicola macrochir						1			1					0	1
Ventrifossa sp.				1				1	2					0	2
Macrouridae, indet.								1	1					0	1
Guttigadus nana			1			1	1	1	4					0	4
Physiculus sp.	1		2	3	2	1		11	20	1	3	1	2	7	27
Theragra chalcogramma								2	2					0	2
Hoplostethus sp.									0	1				1	1
Apogonidae indet.	1								1					0	1
Amblychaeturichthys sciistius	5	4	5	2	3	4	10	3	36	3	5	7	2	17	53
Amblychaeturichthys hexanema				1					1					0	1
Gymnogobius aff. *heptacanthus*		1	1					1	3					0	3
Pterogobius zacalles		1						2	3	3	1	1		5	8
Gobiiformes indet. 1			5	5		4	1	17	32	3	9	4	11	27	59
Gobiiformes indet. 2			3	2		5	3	21	34	1	1	1	6	9	43
Gobiiformes indet. 3			1	1		4	2	13	21	7	3	1	11	22	43
Gobiiformes indet. 4							1		1					0	1
Gobiiformes indet. 5								3	3					0	3
Gobiiformes indet. 6								1	1	2				2	3
Poorly preserved gobiids	24	29	18	20	27	27	22	311	478	15	10	15	25	65	543
Trachurus japonicus	1	2	3	1		2	1	19	29	1	2		1	4	33
Paralichthys sp.							1	1	2					0	2
Tarphops sp.								1	1					0	1
Limanda punctatissima		1					1		2					0	2
Pseudopleuronectes herzensteini			1					1	2		1			1	3
Crossorhombus kanekonis								3	3	1	1			2	5
Pinguipedidae, indet.								1	1					0	1
Ammodytes sp.	1	2	1	1	1	1	2	11	20	1	1	2		4	24
Parascombrops ohei		1		1				1	3					0	3
Cepola schlegeli							1		1					0	1
Sebastiscus marmoratus								1	1					0	1
Lepidotrigla sp.				1				3	4					0	4
Platycephalidae, indet.								1	1					0	1
Triglops sp.	1	1	3	1	3	1	3	8	21	1	1			2	23
Sillago japonica					1			1	2					0	2
Pagrus major		1		1					2				1	1	3
Unidentified shark teeth						1			1					0	1
Unidentified teleostean otoliths	2	13	12	9	4	10	14	91	155	7	9	1	4	21	176
Unidentified teleostean teeth								4	4				1	1	5
Unidentified teleostean bones	4	9	5	3	2	24	11	22	80	11	3	3	7	24	104
Total	51	94	82	79	67	118	102	793	1386	79	74	48	88	289	1675

Table 2-2. Vertical and horizontal distributions of extant fishes. References as below: 1, 2. Nakabo (2013a, b). 3. Schwarzhans and Prokofiev (2017). 4. Ishikawa and Senou (2010). 5. Yamada et al. (2007). 6. Coad and Reist (2004). 7. Hata and Motomura (2011). 8. Yang et al. (1996). 9. Ohizumi et al. (2001).

Species	Vertical distribution (m)	Reference	Horizontal distribution	Reference
Benthic/benthopelagic				
Conger myriaster	0-100	1	temperate	2
Gnathophis sp.			temparate	2
Glossanodon semifasciatus	70-430	1	temparate	2
Guttigadus nana	0-94	1	temparate	2
Ventrifossa sp.			temparate	2
Abyssicola macrochir	158-830	1	temparate	2
Theragra chalcogramma	0-2000	1	arctic/subarctic	2
Amblychaeturichthys sciistius	20-60	1	temperate	2
Amblychaeturichthys hexanema	30-125	5	temparate	2
Pterogobius zacalles	3-45	1	cold temparate	2
Tarphops sp.			temparate	2
Pseudopleuronectes herzenstein	0-100	1	cold temparate	2
Limanda punctatissima	0-30	1	arctic/subarctic	2
Crossorhombus kanekonis	0-30	1	temperate	2
Parascombrops ohei	175-200	3	temparate	3
Cepola schlegeli	about 100	1	temparate	2
Sebastiscus marmoratus	2-43	1	warm temparate	2
Triglops sp.			arctic/subarctic	2
Sillago japonica	3-70	4	temparate	2
Pagrus major	30-200	1	temparate	2
Pelagic/mesopelagic				
Englauris japonica	27-170	5	temparate	2
Clupea pallasii	0-475	6	arctic/subarctic	2
Sardinops melanostictus	0-50	7	temparate	2
Valenciennellus tripunctulatus	100-1000	8	tropical-temperate	2
Benthosema suborbitale	0-125 (n), 375-800 (d)	1	tropical-temperate	2
Ceratoscopelus warmingii	0-200 (n), 425-1500 (d)	1	tropical-temperate	2
Diaphus watasei	0-100 (n), 100-2005 (d)	9	tropical-temperate	2
Diaphus aliciae	0-1594	1	tropical-temperate	2
Diaphus luetkeni	40-325 (n), 375-750 (d)	1	tropical-temperate	2
Diogenichthys atlanticus	10-1050 (n), 400-1250 (d)	1	tropical-temperate	2
Electrona risso	90-700 (n), 200-750 (d)	1	tropical-temperate	2
Hygophum sp.			tropical-temperate	2
Lampadena sp.			tropical-temperate	2
Lampanyctus turneri	0-212	1	tropical-temperate	2
Myctophum asperum	0-125 (n), 425-750 (d)	1	tropical-temperate	2, 9
Notoscopelus resplendens	0-800 (n), 25-2000 (d)	1	tropical-temperate	2, 9
Stenobrachius leucopsarus	0-30 (n), 200-1000 (d)	1	arctic/subarctic	9
Taaningichthys minimus	0-600 (n), 0-875 (d)	1	tropical-temperate	2
Trachurus japonicus			temparate	2

総合考察

第 1 章では，耳石の外部形態に基づく種判別形質の探索を目的として，日本産ニシン科魚類 12 種（ニシン，ウルメイワシ，ヒラ，ミズン，コノシロ，リュウキュウドロクイ，ドロクイ，カタボシイワシ，オグロイワシ，サッパ，マイワシ，キビナゴ）の耳石の外部形態比較を行うとともに，ウルメイワシとマイワシの 2 種について成長に伴う耳石の形態変化を検証した。その結果，1）全形，OL:OH，AL:RL，背部周縁，腹部周縁および後部周縁の形状，crista superior の隆起の 7 形質に基づき各種の識別が可能であること，2）ウルメイワシとマイワシの 2 種において，体成長に伴う OL:OH および AL:RL の変化パターンが異なる事が明らかとなった。さらに，これらの結果に基づき，日本産ニシン科魚類 12 種の耳石の種同定のための検索表を作成した。

第 2 章では，1 章で作成した検索表の応用的研究として，神奈川県三浦市南下浦町鹿穴台の第四系チバニアン階・宮田層の一露頭から産出したニシン科魚類の耳石化石の同定を行った。さらに, 文献や現生標本との比較に基づき, 共産した耳石化石（および少数の板鰓類の歯化石）の同定をも行い，宮田層堆積当時の化石魚類相および古環境の復元を行った。その結果，1）第 1 章で作成した検索表を用いることによりニシンおよびマイワシの 2 種のニシン科魚類が同定され，その他の耳石化石についても文献や現生標本との比較を行った結果，少なくとも 62 タクサが識別された。さらに，2）本層の化石魚類相は温帯性・暖水性魚類が優占し，少数の寒帯・亜寒帯性および冷温帯性魚類を含む寒・暖混合群種であったこと，3）本層堆積当時の鹿穴台は親潮・黒潮の両方が波及する温帯海域の，水深約 100–200 m の大陸棚であったことが示唆された。

今後進めていくべき研究課題としては，まず，ニシン科魚類を含む日本産魚類の耳石の形態学的研究および検索表の作成が挙げられる。第 1 章で述べたように，今回扱う事ができなかったホシヤマトミズン *Amblygaster sirm* などを含む日本産ニシン科魚類全種の耳石の形態比較を行い，胃内容物や化石として得られる可能性のある各種の耳石の標徴形質を明らかにする必要がある。さらに，ニシン科以外の他の分類群についても，本研究と同様な種内・種間での形態

学的な比較を行い，各種の標徴形質の探索を行う必要がある。例えば，日本産ハゼ目魚類の耳石については，一部の種について図示・記載が行われているが（Ohe, 1985; 飯塚・片山, 2008），多くの分類群（科・属）では種間での形態比較が不十分である。そのため，化石として本目魚類の耳石はよく産出するものの，多くの場合は目あるいは科レベルの同定に留められており（高橋, 1976, 1977; 大江, 1989; 宮田ほか, 2018 など), かつて記載された化石種はいずれも現生種との分類学的な比較検討が必要とされている（第 2 章の Discussion を参照）。そのため，本目魚類の耳石の種間形態比較は急務であるといえよう。それに加えて, 第 1 章で示したように，耳石に基づく種同定には，体成長に伴う形態変化を考慮する必要がある。将来的には，本研究で示した検索表の対象を日本産魚類全種に広げ，さらに体成長に伴う形態変化をも網羅する必要があると考えられる。

このような形態学的な基礎研究を行う事により，古生物学においては，耳石化石の現生種との比較が可能となり，種同定，そして絶滅種であるか否かの判断が従来よりも正確となると考えられる。将来的には，関東地方をはじめ各地より産出する耳石化石群集の同定や分類学的な検討が進展し，各時代における日本近海における化石魚類相や古生物地理，そしてその変遷の解明がなされ, 現世の海産魚類相や分布様式, 種内の地域個体群の成立過程への理解が深まり，ひいては海洋生物の種多様性保全に貢献できると期待される。

さらに，将来的な課題の一つとして，今回扱わなかった胃内容物や考古遺跡から出土した耳石についても，検索表の実用性を検証する必要がある。現在，著者らは相模湾沿岸に漂着した鯨類の胃内容物調査を進めており，ニシン科魚類の耳石を多数得ている（鷲見ほか, 未発表）ほか，相模湾の海底堆積物からもニシン科魚類をはじめとする多くの分類群の耳石を得ている（三井, 未発表）。今後，このような広範な分野において検索表が利用されることで，例えば新たな形質の探索の必要性など，改良すべき点も明らかになると考えられる。

謝辞

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