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First Marine Fossil Otoliths (Teleostei) from East Africa (Tanzania) †

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Abstract: Otoliths are common in the fossil record and can provide important insight into the evolution and spatial and stratigraphic distribution of fishes, but have remained understudied in many areas of the world. Here, we describe the first marine otolith assemblage from East Africa. The material is from Tanzania Drilling Project cores of late Eocene to early Oligocene age, spanning the Eocene-Oligocene transition (EOT). The assemblage consists of 10 identifiable species of which 5 are new, and 4 remain in open nomenclature. The new species are as follows: *Protanago africanus*, *Bregmaceros tanzaniensis*, *Ortugobius pandeanus*, "*Serranus*" *plasmaticus*, and *Acanthocepola signanoae*. The association of shallow and deep-water taxa along with the dominance of the family Cepolidae, which has not been observed in either the extant or fossil record, makes the faunal composition unusual. However, when taxon occurrences are correlated with stable isotope records from the same cores and compared with previous studies, it is clear the otoliths reflect the sea-level fall known to occur during the EOT, with deeper dwelling taxa in the late Eocene and taxa preferring shallower, which are more shelf-like environments in the early Oligocene.

Keywords: Eocene-Oligocene transition; Tanzania; East Africa; bony fish; otoliths; new species; sea-level

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1. Introduction

Otoliths of bony fishes (Teleostei) are common in the fossil record wherever aragonite is preserved in the sediment. Despite nearly 150 years of fossil otolith research, many regions of the world have remained significantly under-explored for otoliths. Only Europe, North and Central America, and New Zealand have experienced substantial efforts in this field (Figure 1). Although some taxa are known from West and North Africa, to date, no fossil otoliths have been described from East Africa, with the exception of a single discovery of an in situ otolith within a cichlid in Miocene freshwater deposits of central Kenya [1]. Here, we describe the first fossil otoliths from marine deposits across the Eocene-Oligocene transition (EOT) from two drill sites in coastal Tanzania, part of the Tanzania Drilling Project (e.g., [2,3]). The collection is small, consisting of 44 specimens of which 34 are identifiable—representing 10 species, which nevertheless represents an important first data point for the region (Figure 1).

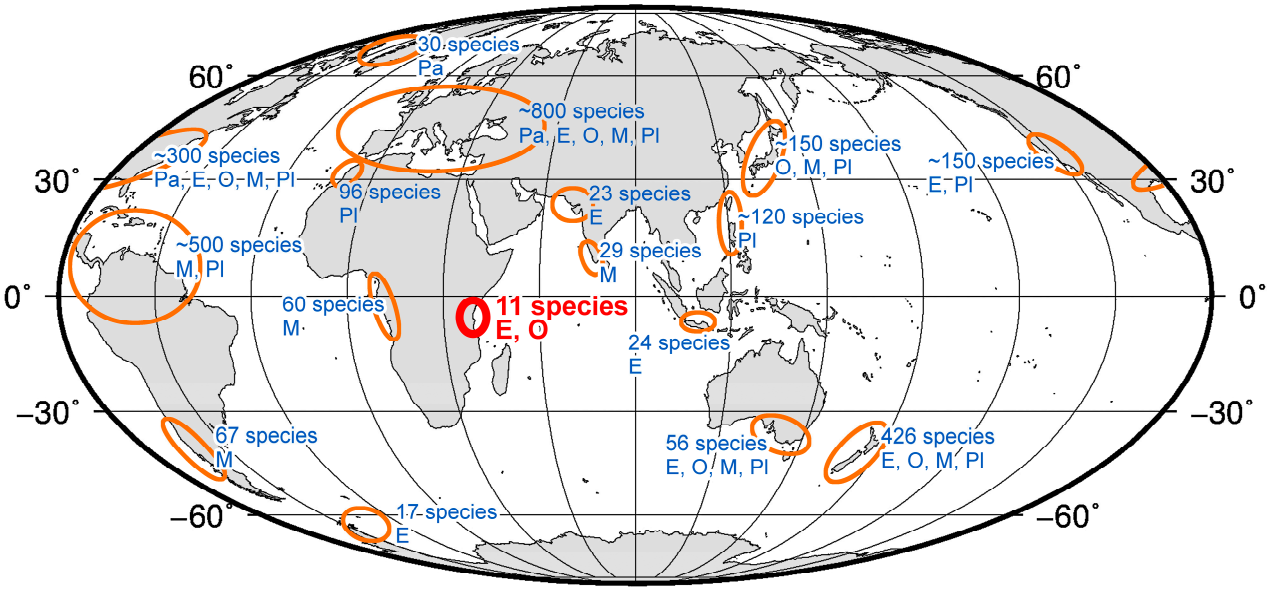


Figure 1. The global fossil otolith record showing approximate numbers of validly described species in different geographic regions. Data compiled from available literature. Abbreviations: Pa = Paleocene; E = Eocene; O = Oligocene; M = Miocene; Pl = Pliocene.

The EOT is an important interval in Earth's climatic history occurring between approximately 34.44–33.65 Ma. It represents the transition from 'greenhouse' to 'icehouse' and is associated with the onset of Antarctic glaciation, widespread oceanographic changes, and taxonomic overturning [4–6]. Oxygen isotope data show a multi-stepped increase in values linked to both global cooling and sea-level fall due to the formation of continental ice, estimated to be up to 70 m [6,7]. In addition, ocean nutrient supply and productivity are also thought to have increased around the EOT [8,9] all of which would have strongly impacted shallow marine environments, as well as the open ocean. Rapid changes in the plankton composition at the EOT have long been observed in several biota, for instance, in the coccolithophorids [10]. However, the impact on macrofauna, such as fish, is less clear. Molecular clock data for Goby fishes (Acanthomorpha: Percomorpha: Gobiiformes) suggest that they may have had a large radiation around the EOT [11]. The freshwater cyprinids also diversified around this time interval and expanded into Europe [12]. Our otolith record, therefore, represents not only a first regional record but also contributes to understanding the complex response of fish to this major climatic event.

Regional Geology and Locations

Paleogene sediments are found along the coastal region of southern Tanzania between the regions of Kilwa and Lindi [2]. The sediments are a series of claystones, marls, and interbedded debris-flow limestones, deposited in hemi-pelagic marine environments. The Paleogene sediments belong to the Kilwa Group, which is divided into four formations: the Nangurukuru (Upper Cretaceous), Kivinje (Paleocene to lower Eocene), Masoko (middle Eocene), and Pande (upper Eocene to lower Oligocene), which accumulated during a time of subsidence in the region. The Pande formation was drilled by the Tanzania Drilling Project (TDP) in 2004 and 2005 and successfully recovered at 3 sites—TDP 11, 12, and 17. Specimens in this study are from TDP sites 11 and 17 (Figure 2; TDP 17—UTM 37L; 560,539 8984483; TDP 11—UTM 37L; 560,250 8983211); the two sites are positioned north and south of the town of Stakishari and less than 2 km apart.

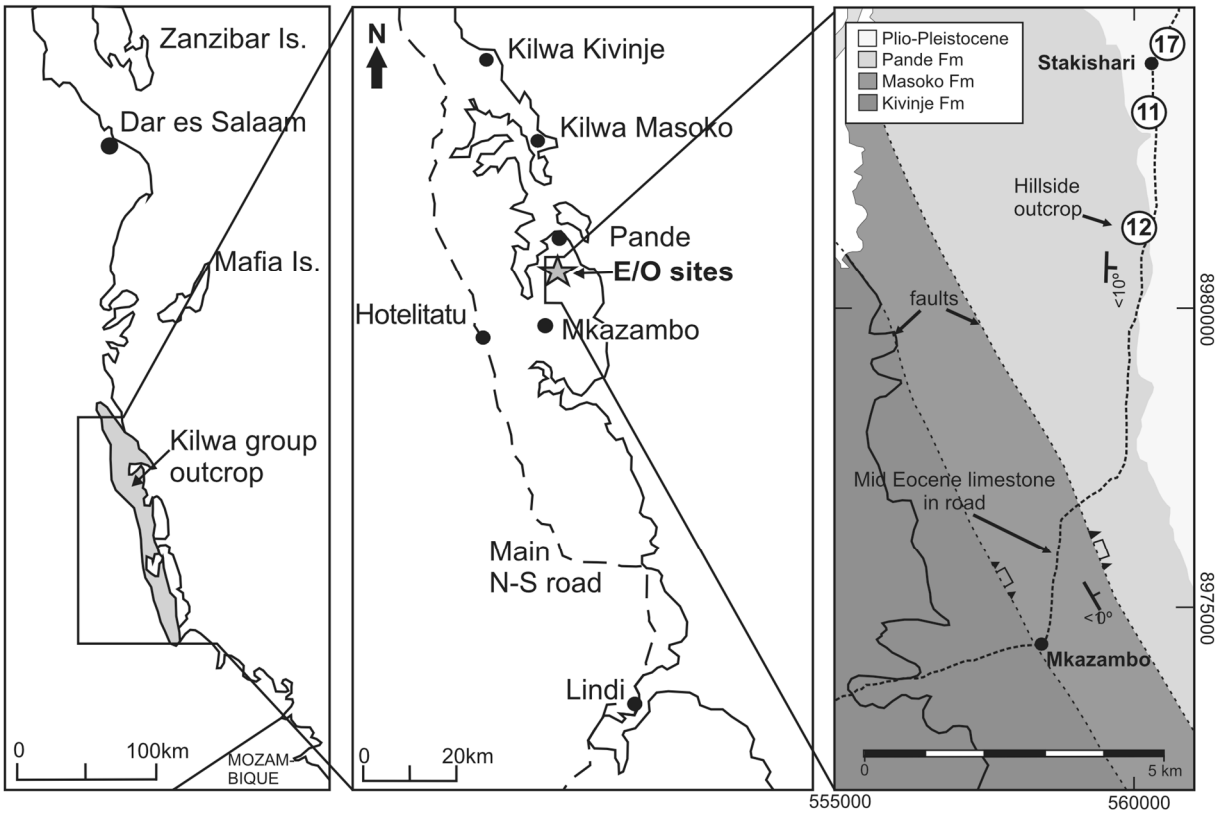


Figure 2. Location map with geological overlay. Numbers in circles refer to TDP Sites. The otoliths studied herein originated from sites TDP 11 and 17. Modified after [2].

The sediments comprise dark greenish-grey clays, and are known for their exceptional preservation of foraminifera and nannofossils including preservation of aragonite (e.g., [3,13,14]). Interbedded limestone deposits contain larger foraminifera and are thought to be the result of penecontemporaneous debris flows from the nearby shelf. The site was estimated to be approximately 50 km from the palaeo-coast [2], and deposited at a depth of 300–500 m based on preliminary studies of smaller benthic foraminifera. However, this is difficult to estimate accurately. Small-sized, larger foraminifera are also found within the clays alongside byozoa, dasycladacae, molluscs, echinoderm fragments, and otoliths. The exceptional preservation and apparent complete recovery of the Eocene-Oligocene transition has led to extensive biostratigraphic, biodiversity, and geochemical studies [3,15–19].

2. Materials and Methods

The otoliths studied here are housed within the vertebrate paleontology collection of the Natural History of Denmark (NHMD), specimen numbers are given with systematic descriptions.

We use the residues previously prepared for the work of [3,15] and subsequently studied by [17]. These consist of half-round core sections approximately 5–10 cm in length which have been washed through a 63 micron sieve and dried in a low temperature over. To obtain otoliths the samples were dry-sieved through a 350-micron sieve, and picked under a stereo microscope. The depth conversion of supplemental information in ref. [3] was used to convert to depth and correlate between the cores.

Photographs of the otoliths were captured with a Canon EOS 1000D (Tokyo, Japan) that was mounted on a Wild M400 photomacroscope (Heerbrugg, Switzerland) and remotely controlled from a computer. Individual pictures of every view of the objects taken at ranges

of field of depths were stacked using Helicon Soft's Helicon Focus software (Kharkiv, Ukraine). When necessary, retouching and adjustment of exposure and contrast were performed in Adobe Photoshop (San José, CA, USA) to improve the images without altering any morphological features.

The morphological terminology follows that of [20] with amendments by [21] and [22]. The abbreviations used are OL = otolith length; OH = otolith height; OT = otolith thickness; OsL = ostium length; CaL = cauda length; OCL = length of ostial colliculum; and CCL = length of caudal colliculum; SuL = sulcus length.

3. Systematic Paleontology

The classification of the taxa follows the phylogenetic classification of Actinopterygii (ray-finned fishes) of [23]. The only exception from their classification is that we keep the Antigoniidae as a separate family from Caproidae. Species that cannot be attributed to a defined genus are shown in the type genus of the respective family with quotation marks. Taxon authorities that are not discussed in the text are not shown in references. These can be found in [23] for higher classification group names, ref. [24] for family group names, and [25] for genera and species group names.

Division Teleostei Müller, 1848 [23]
Order Anguilliformes Regan, 1909 [23]
Family Congridae Kaup, 1856 [24]
Genus *Protanago* Schwarzhans, Stringer & Takeuchi, 2024 [26]
Protanago africanus n. sp. (Figure 3A–C)

Holotype: NHMD 1811334 (Figure 3A–C), Early Oligocene, Pande Formation, TDP 11, core 19 (76.1 m).

Etymology: Named after Africa.

Diagnosis: OL:OH = 1.15. Dorsal rim with rounded middorsal expansion. Ventral rim deep, deepest anterior of middle. OL:SuL = 1.3. Dorsal margin of sulcus straight; ostial channel narrow, vertical.

Description: A single otolith of 2.75 mm in length. OL:OH = 1.15; OH:OT = 3.6. Dorsal rim moderately high, with rounded middorsal expansion and small concavity in front and behind. Dorsal rim slightly undulating. Ventral rim deeply curved, deepest anterior of middle, smooth. Anterior rim broadly rounded; posterior tip rounded, much narrower than anterior tip, slightly supramedian positioned.

Inner face distinctly convex, smooth, with supramedian positioned, shallow, moderately long sulcus; OL:SuL = 1.3. Dorsal margin of sulcus straight, ventral margin with small incursion marking distinction of ostium and cauda, anteriorly broadly deepened. Cauda ventrally deepened at beginning, with dorsally tapering termination. Uniform colliculum filling entire sulcus except for short, narrow, vertical ostial channel near anterior tip of sulcus. Dorsal depression indistinct; no ventral furrow. Outer face flat, smooth.

Discussion: The fossil otolith-based genus *Protanago* currently comprises six species, all known from the Eocene of North America and one [*P. nonsector* (Nolf & Stringer, 2003)] [27] in addition to the Eocene of Europe [26]. *Protanago africanus* thus represents the first record outside of the known area of distribution. It shows similar otolith proportions as *P. nonsector* (see [26] for figures) but a lower dorsal rim and a more asymmetrical otolith shape because of the broad anterior tip and the slightly tapering posterior tip. The sulcus is longer in *P. africanum* than in *P. nonsector* (OL:SuL = 1.3 vs. 1.4–1.45) and the dorsal margin of the sulcus is straight (vs. slightly convex).

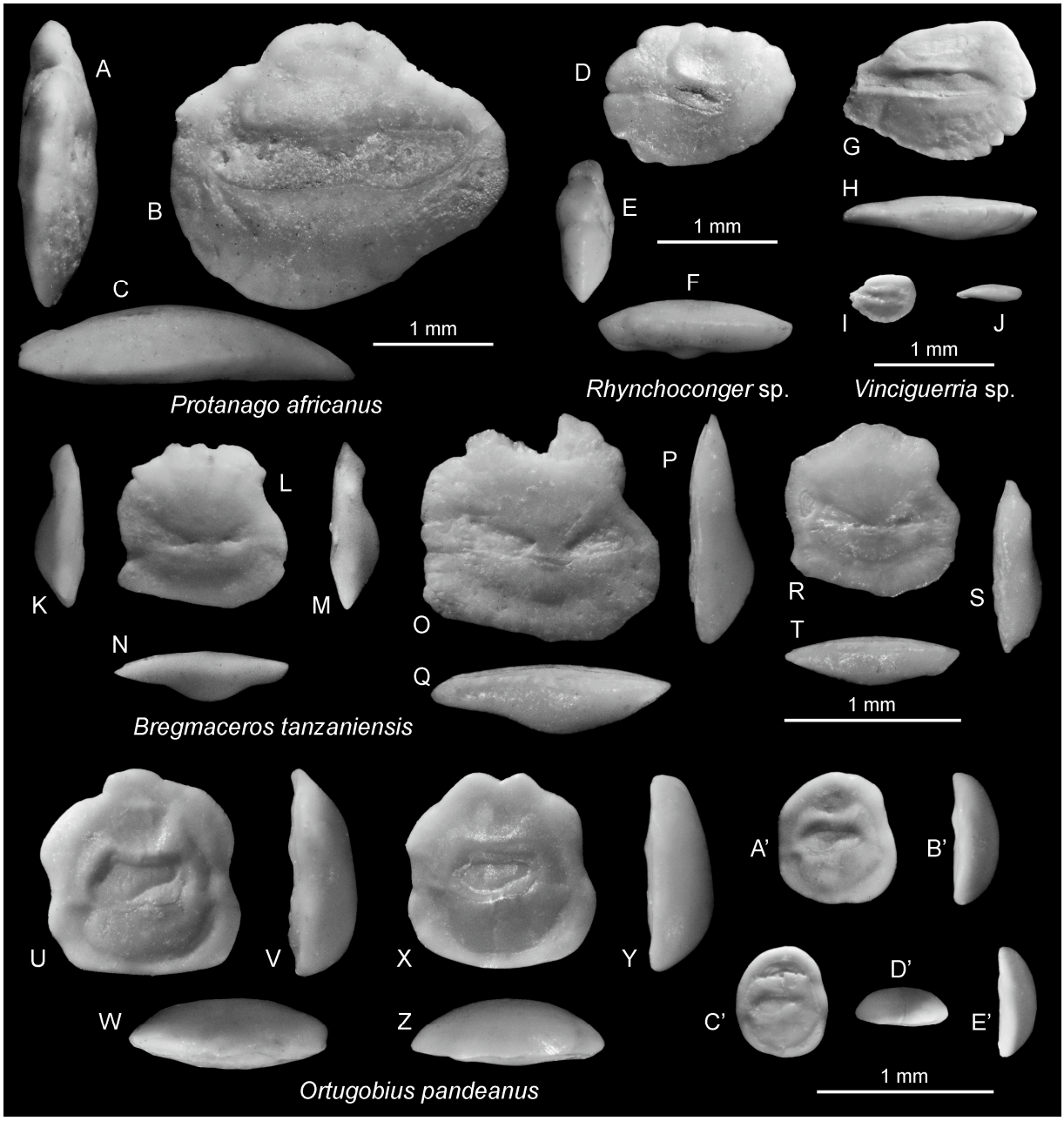


Figure 3. (**A**–**C**) *Protanago africanus* n. sp.; holotype, NHMD 1811334, Early Oligocene, Pande Formation, TDP 11, core 19 (76.1 m); (**D**–**F**) *Rhynchoconger* sp. NHMD 1811335, Early Oligocene, Pande Formation, TDP 17, core 34 (97.9 m); (**G**–**J**) *Vinciguerria* sp. NHMD 1811338 and NHMD 1811339, early Oligocene, Pande Formation, TDP 11, core 27 (93.2 m) (mirror imaged); (**K**–**T**) *Bregmaceros tanzaniensis* n. sp.; R–T holotype, NHMD 1811341, late Eocene, Pande Formation, TDP 17, core 37 (118.9 m); (**K**–**P**) paratypes, early Oligocene, Pande Formation, (**K**–**N**) NHMD 1811365, TDP 11, core 10 (51.28 m) (mirror imaged); (**O**–**Q**) NHMD 1811364, TDP 17, core 31 (90.9 m); (**U**–**E′**) *Ortugobius pandeanus* n. sp. early Oligocene, Pande Formation; (**U**–**W**) holotype, NHMD 1811342, TDP 11, core 10 (51.28 m); (**X**–**E′**) paratypes, (**X**–**Z**) NHMD 1811344, TDP 11, core 26 (93.14 m) (mirror imaged), (**A′**,**B′**) NHMD 1811343, same data as holotype (mirror imaged), (**C′**–**E′**) NHMD 1811345, TDP 11, core 27 (94.55 m) (mirror imaged).

Genus *Rhynchoconger* Jordan & Hubbs, 1925 [25]

Rhynchoconger sp. (Figure 3D–F)

Material: In total, 1 juvenile specimen, NHMD 1811335, Early Oligocene, Pande Formation, TDP 17, core 34 (97.9 m).

Discussion: The single small otolith of 1.55 mm in length exhibits all hallmarks of a juvenile morphology typical for this genus such as the rounded and crenulated outline and the lens-like appearance in lateral view. The distinct though small dorsal depression characterizes it as a representative of the genus *Rhynchoconger*. The very short sulcus and cauda do not align with any known Paleogene *Rhynchoconger* species and this indicates that the specimen may represent an undescribed species.

Order Stomiiformes Regan, 1909 [23]
Family Phosichthyidae Weitzman, 1974 [24]
Genus *Vinciguerria* Jordan & Evermann, 1896 [25]
Vinciguerria sp. (Figure 3G–J)

Material: In total, 5 specimens; 2 specimens, late Eocene, Pande Formation: TDP 17, core 37 NHMD 1811336 (118.9 m) and core 41 NHMD 1811337 (131.5 m); 3 specimens, early Oligocene: TDP 11, core 27, 2 specimens NHMD 1811338-1811339 (93.2 m) and 1 specimen NHMD 1811340 (94.55 m).

Discussion: Most specimens available are small, less than 0.7 mm in length, and a single one of 1.6 mm in length with a broken rostrum (Figure 3G,H). The only complete specimen available (Figure 3I,J) is 0.55 mm in length and shows a rather short rostrum, which, however, could represent an ontogenetic effect. *Vinciguerria* otoliths are known from several species since the late Oligocene; and a single specimen has been recorded from the late Eocene of the Aquitaine Basin: *V. biarritzensis* (Šulc, 1932) [28]. The largest specimen of Figure 3G,H differs from *V. biarritzensis* in the more slender, albeit incomplete rostral region and the dorsal rim being inclined towards anterior. It likely represents an undescribed species but the available specimens are insufficient for a reliable diagnosis.

Order Gadiformes Goodrich, 1909 [23]
Family Bregmacerotidae Gill, 1872 [24]
Genus *Bregmaceros* Thompson, 1840 [25]
Bregmaceros tanzaniensis n. sp. (Figure 3K–T)

Holotype: NHMD 1811341 (Figure 3R–T), late Eocene, Pande Formation, TDP 17, core 37 (118.9 m).

Paratypes: In total, 2 specimens, early Oligocene, Pande Formation; 1 specimen NHMD 1811364, TDP 17, core 31 (90.9 m), 1 specimen 10 NHMD 1811365, TDP 11, core (51.28 m).

Etymology: Named after the country Tanzania.

Diagnosis: OL:OH = 0.98–1.02. Dorsal rim with broad dorsal lobe; anterior rim vertical. Sulcus position axial. Colliculi small, caudal colliculum smaller than ostial colliculum; CCL:OCL = 1.25–1.55. Outer face with pronounced infra-central umbo.

Description: Moderately thick otoliths with delicate rims reaching a size of about 1.3 mm in length (holotype 0.9 mm). OH:OT = 3.3–3.5. Otolith shape is characterized by being about as long as high, with a nearly vertical anterior margin, moderately strong preventral lobe, and broad, backward-inclined dorsal lobe. Ventral rim shallow, anteriorly straight, inclined until small, obtuse midventral angle or rounded denticle, thereafter broadly rounded. Dorsal rim anteriorly inclined; steep concavity behind dorsal lobe (damaged in largest specimen, Figure 3O). Posterior rim is broadly rounded below postdorsal concavity. Rims smooth or slightly undulating.

Inner face slightly convex with an axially positioned, narrow concave, fairly evenly curved sulcus. Colliculi small, ostial colliculum longer than caudal colliculum (OCL:CCL = 1.25–1.55), slightly distinctly deepened. Collum relatively wide, with small ventral pseudocolliculum and no bulge of inner face below collum. No discernible dorsal

depression; ventral field with broad, indistinct furrow below central part of sulcus at considerable distance from ventral rim of otolith. Inner face relatively smooth without prominent radial furrows. Outer face with distinct, broad umbo below centre of otolith.

Discussion: *Bregmaceros tanzaniensis* exhibits a rather modern morphology that occurs first in the middle to late Eocene. Several otolith-based *Bregmaceros* species have been described from late Eocene or early Oligocene formations from North America, Europe, and New Zealand resembling *B. tanzaniensis*. *Bregmaceros moersi* Schwarzhans, Stringer & Takeuchi, 2024 [26] from the late Eocene of the U.S. Gulf Coast differs in the relatively narrow and long colliculi and the less pronounced umbo on the outer face from *B. tanzaniensis*. *Bregmaceros minimus* (Frost, 1934) [29] from the Bartonian of England and *B. brihandensis* Nolf, 1988 [30] from the Priabonian of the Aquitaine Basin are characterized by much more evenly shaped otoliths with vertical dorsal lobes. *Bregmaceros brihandensis* further differs from *B. tanzaniensis* in the dorsal lobe being relatively narrow and *B. minimus* in the inclined anterior rim and the strong marginal crenulation. *Bregmaceros antiquus* Schwarzhans, 1980 [31] from the late Eocene of New Zealand differs from *B. tanzaniensis* in the more compressed shape (OL:OH = 0.88–0.94 vs. 0.98–1.02); the broader dorsal lobe and the shallower ventral rim.

Remarks: Four small *Bregmaceros* specimens < 0.05 mm in length have been found in addition to the three-type specimens of *B. tanzaniensis* that show no useful diagnostic features and therefore cannot be identified at the species level. These stem from the early Oligocene of TDP 11, cores 24 (86.98 m), 25 (91.6 m) and 27 (93.2 m) (NHMD 1811380-1811382).

Order Gobiiformes Günther, 1880 [23]

Family Gobiidae Cuvier, 1816 [24]

Genus *Ortugobius* Schwarzhans, Ohe & Ando, 2017 [32]

Ortugobius pandeanus n. sp. (Figure 3U–E′)

Holotype: NHMD 1811342 (Figure 3U–W), early Oligocene, Pande Formation, TDP 11, core 10 (51.28 m).

Paratypes: In total, 4 specimens, early Oligocene, Pande Formation; 1 specimen NHMD1811343, same data as holotype, 1 specimen NHMD 1811344, TDP 11, core 26 (93.14 m), 1 specimen NHMD 1811345, TDP 11, core 27 (93.2 m), 1 specimen NHMD 1811346, TDP 11, core 27 (94.55 m).

Etymology: Named after the Pande Formation.

Diagnosis: OL:OH = 0.85–0.95. Anterior and posterior rims without prominent projections. Inner face flat. Sulcus small (OL:SuL = 2.0–2.3), with low ostial lobe, moderately inclined (6–15°). Subcaudal iugum continuous below sulcus but widened below cauda. Outer face convex.

Description: Small, compact otoliths up to 1.05 mm in length (holotype). OL:OH = 0.85–0.95, increasing with size; OH:OT = 3.0. Dorsal rim high, regularly curved in specimens < 0.7 mm in length (Figure 3A′,C′), irregularly undulating in larger specimens (Figure 3U,X), highest at about middle, without prominent angles, and without postdorsal projection. Anterior rim nearly vertical, posterior rim slightly inclined dorsally, both with slight concavity at level of ostial and caudal tips, respectively. Ventral rim slightly bent, smooth, with rounded angles with anterior and posterior rims.

Inner face flat. Sulcus small, centrally positioned, slightly deepened, inclined anteriorventrally at about 6° to 15°, with rounded sole-shape and low ostial lobe. Iugum extending below entire sulcus in most specimens but widened and somewhat separated below cauda, or, in some specimens, only below cauda. Dorsal depression small, cup-shaped; ventral furrow distinct, wide, running at some distance from ventral rim of otolith, turning up-

wards in front and behind sulcus and reaching to dorsal depression. Outer face strongly convex, smooth.

Discussion: The otolith-based genus *Ortugobius* was described from the lowermost Oligocene of Japan [32] and was then understood as a Gobioidei with unknown relationships. We now consider *Ortugobius* as a pan-Gobiidae following [33]. Similar otoliths have been described from the early Oligocene of the Aquitaine Basin in France (as "genus *Gobiidarum*" sp. 3 and sp. 4 in [34]), and the Oligocene of northern Italy [35]. *Ortugobius pandeanus* differs from the only described congener, *O. cascus* Schwarzhans, Ohe & Ando, 2017 [32] in the small, cup-shaped dorsal depression, the ventral furrow being connected upwards to the dorsal depression and the wider subcaudal iugum. As for the specimens from the Aquitaine Basin, it is not clear from [34] drawings whether they contain a subcaudal iugum or not.

Order Perciformes Bleeker, 1859 [23]
Family Serranidae Swainson, 1839 [24]
Genus indet.
"*Serranus*" *plasmaticus* n. sp. (Figure 4B–E)

Holotype: NHMD 1811347 (Figure 4B,C), early Oligocene, Pande Formation, TDP 17, core 35 (101.4 m).

Paratypes: In total, 2 specimens, early Oligocene, Pande Formation; 1 specimen NHMD 1811348, TDP 11, core 16 (70.18 m), 1 specimen NHMD 1811349, TDP 11, core 22 (82.25 m).

Etymology: From plasmatikos (Greek) = notional, virtual, referring to the difficult-to-relate features of the otoliths.

Diagnosis: OL:OH = 1.7–1.8. Rostrum and posterior tip of otolith equally pointed. Sulcus short (OL:SuL = 1.3–1.35); ostium and cauda equally long (CaL:OsL = 1.0–1.05). Cauda moderately flexed across posterior half. No ventral furrow.

Description: Small, elongate otoliths with fusiform shape reaching 2.4 mm in length (holotype); OL:OH = 1.7–1.8; OH:OT = 2.6–3.0. Dorsal and ventral rims regularly curved, most expanded at respective middle, without prominent angles; dorsal rim irregularly undulating, ventral rim finely crenulated. Rostrum and posterior tip of otolith about equally pointed and symmetrically positioned along horizontal axis of otolith. Rostrum 20% of OL. Excisura and antirostrum minute.

Inner face markedly convex with slightly supramedian positioned, slightly deepened and short heterosulcoid sulcus. Ostium and cauda about equally long. Ostium nearly twice as wide as cauda, spatulate, dorsally, and ventrally equally widened at collum. Cauda gently flexed along its posterior half, terminating far from posterior tip of otolith. Dorsal depression small, only above anterior half of cauda; no ventral furrow. Outer face flat to concave, smooth.

Discussion: The combination of a short, rather regularly bent cauda and fusiform otolith shape without any prominent angles does not correlate to known extant or fossil serranid otoliths. The otolith morphology is sufficiently mature to exclude that it represents a juvenile pattern. However, the otolith pattern of "*Serranus*" *plasmaticus* is not sufficiently distinct to warrant establishment of a fossil otolith-based genus.

Order Acanthuriformes Jordan, 1923 [23]
Family Antigoniidae Jordan & Evermann, 1898 [24]
Genus *Antigonia* Lowe, 1843 [25]
Antigonia sp. (Figure 4A)

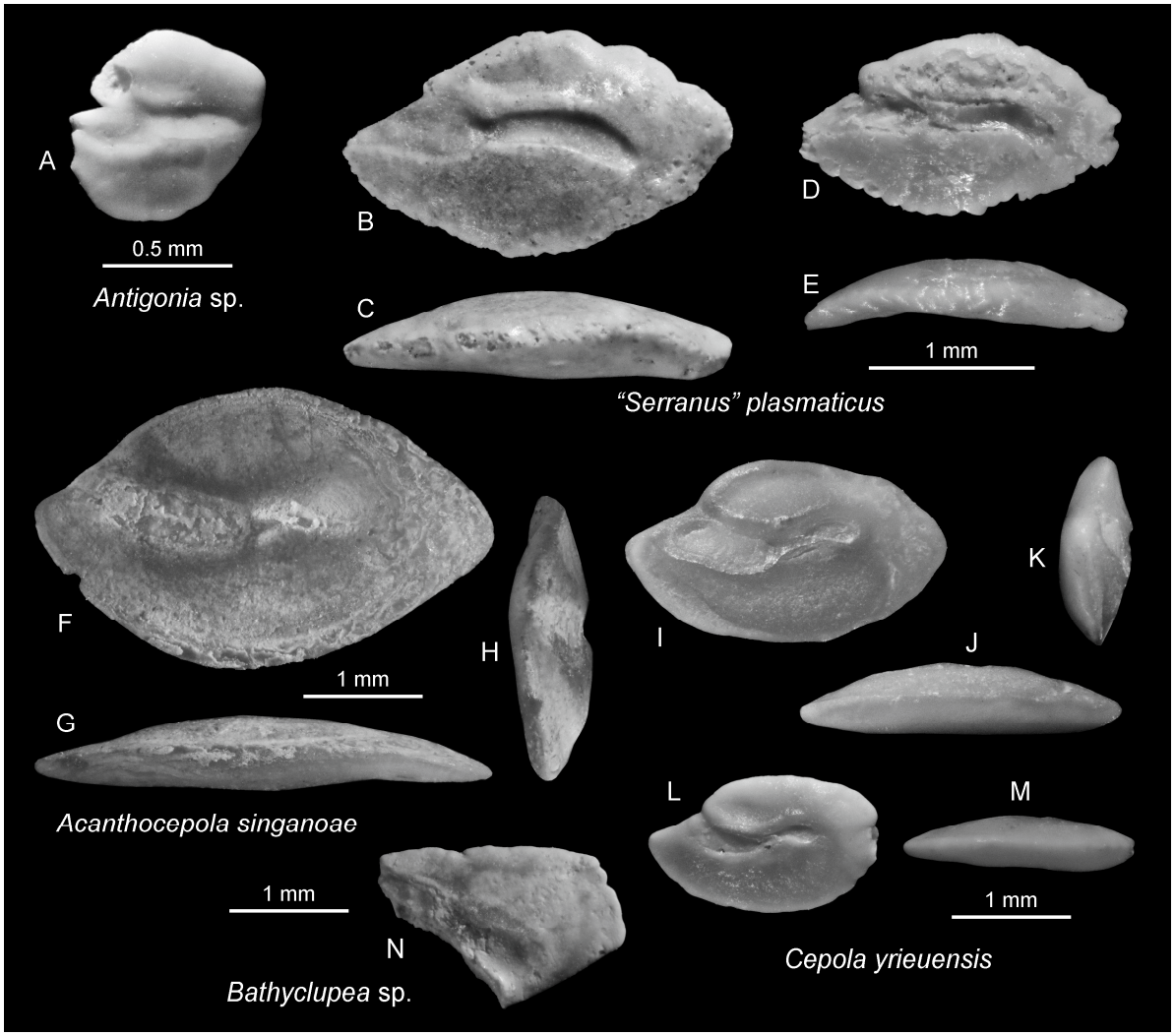


Figure 4. (**A**) *Antigonia* sp. NHMD 1811350, early Oligocene, Pande Formation, TDP 11, core 10 (51.28 m); (**B**–**E**) "*Serranus*" *plasmaticus* n. sp.; (**B**,**C**) holotype, NHMD 1811347, early Oligocene, Pande Formation, TDP 17, core 35 (101.4 m) (mirror imaged); (**D**,**E**) paratype, NHMD 1811348, TDP 11, core 16 (70.18 m); (**F**–**H**) *Acanthocepola singanoae* n. sp.; holotype, NHMD 1811352, early Oligocene, Pande Formation, TDP 17, core 31 (80.9 m) (mirror imaged); (**I**–**M**) *Cepola yrieuensis* Steurbaut, 1984 [34], early Oligocene, Pande Formation; I–K NHMD 1811360, TDP 17, core 33 (95.9 m); (**L**,**M**) NHMD 1811361, TDP 17, core 34 (99.81 m) (mirror imaged); (**N**) *Bathyclupea* sp. NHMD 1811363, early Oligocene, Pande Formation, TDP 11, core 10 (51.28 m) (mirror imaged).

Material: In total, 1 specimen NHMD 1811350, early Oligocene, Pande Formation, TDP 11, core 10 (51.28 m).

Discussion: A small, somewhat damaged otolith of 0.8 mm in length represents an unidentifiable juvenile otolith of the genus *Antigonia*. *Antigonia* otoliths are commonly recorded in Paleogene sediments (see e.g., [26]).

Family Cepolidae Rafinesque, 1810 [24]

Genus Acanthocepola Bleeker, 1874 [25]

Acanthocepola singanoae n. sp. (Figure 4F–H)

Holotype: NHMD 1811352 (Figure 4F–H), early Oligocene, Pande Formation, TDP 17, core 31 (80.9 m).

Etymology: Named after Joyce Singano, prominent Tanzanian micropalaeontologist and key collaborator on the Tanzania Drilling Project.

Diagnosis: OL:OH = 1.6. OH:OT = 3.8. Otolith-shaped diamond-like with equally pointed rostrum and posterior tip. Dorsal and ventral rims smooth. Sulcus s-shaped; ostial colliculum much longer than caudal colliculum (OCL:CCL = 2.8).

Description: Moderately large, diamond-shaped, thin otolith of 3.9 mm in length. Dorsal rim high, its pre- and postdorsal sections only slightly bent, inclined upwards at about 40° to broadly rounded middorsal expansion. Ventral rim mirror-image of dorsal rim. Rostrum and posterior tip equally pointed and symmetrical along horizontal axis of otolith. No antirostrum or excisura. All rims sharp and smooth. Inner face slightly convex, smooth, with shallow, supramedian, s-shaped sulcus. Ostium much longer than cauda (OsL:CaL = 1.7; OCL:CCL = 2.8), and distinctly wider. Ostial colliculum not opening to anterior rim of otolith. Pseudocolliculum below collum short. Dorsal depression indistinct; ventral furrow weak, close and parallel to ventral rim of otolith. Outer face flat, smooth.

Discussion: *Acanthocepola singanoae* resembles extant otolith of *Acanthocepola* species in shape and general appearance (see [36] for extant otoliths) but differs in the regularly shaped, high dorsal rim. The species represents the first fossil record of the genus.

Genus *Cepola* Linnaeus, 1764 [25]

Cepola yrieuensis Steurbaut, 1984 [34] (Figure 4I–M)

1984 *Cepola yrieuensis*—Steurbaut: pl. 29, figs 13–17.

Material: In total, 7 specimens. Pande Formation; 6 specimens early Oligocene, NHMD 1811356–1811361, TDP 11, core 16 (70.18 m), core 19 (76.1 m), core 22 (82.25 m), TDP 17, core 31 (80.9 m), core 33 (95.9 m), core 34 (99,81 m); 1 specimen late Eocene, NHMD 1811362, TDP 17, core 36 (116 m).

Discussion: The specimens from Tanzania resemble in shape and smooth outline the specimens described from coeval strata from the Aquitaine Basin [34] and mentioned as a distinctive character of a distinct angle at the ventral margin of the collum. This feature is not apparent in the Tanzanian specimens, but we would consider this as an expression of intraspecific variability.

Teleostei incertae sedis

Family Bathyclupeidae Gill, 1896 [24]

Genus *Bathyclupea* Alcock, 1891 [25]

Bathyclupea sp. (Figure 4N)

Material: In total, 1 specimen NHMD 1811363, early Oligocene, Pande Formation, TDP 11, core 10 (51.28 m).

Discussion: Despite the rather small fragment, this specimen is clearly recognizable as a *Bathyclupea* because of the boxed posterior rim and the steeply inclined, straight sulcus.

4. Discussion

4.1. Faunal Evaluation

Although the faunal association obtained from TDP 11 and 17 from Tanzania is rather small, observations can be made as to its composition. The most common faunal elements are Cepolidae (eight specimens), followed by Bregmacerotidae (seven specimens), Gobiidae (five specimens), and Phosichthyidae (five specimens) (Figure 5). Each of these faunal components represents a distinct ecology and distribution. Cepolids are demersal fishes living on the shelf, particularly on the lower shelf region and sometimes also in the upper bathyal zone [37]. We know of no environment extant or fossil where cepolids represent the dominant faunal fish component. It is therefore difficult to interpret the nature of their abundance in the late Eocene to early Oligocene of Tanzania. Bregmacerotids are mesopelagic to epipelagic fishes in the warm seas. Their distribution in the fossil

otolith-based record is very uneven and where they occur they are typically indicative of a deepwater environment or an open shelf environment (e.g., [38]). Interestingly, the most common mesopelagic fish family, the Myctophidae, is not present in the studied samples. This is even more surprising since another meso to bathypelagic family, the Phosichthyidae with the genus *Vinciguerria*, represents another common element. Finally, the Gobiidae as a family rarely occur below 100 m of water depth (e.g., [33]). Gobies are demersal fishes that can be used to interpret paleobathymetric conditions. We, therefore, conclude that these four most common groups of fishes in the Eocene to Oligocene of the TDP Sites are not typically expected to form an autochthonous assemblage. However, when put into the context of being a changing assemblage through a major climatic event the assemblage is much more consistent in terms of environment.

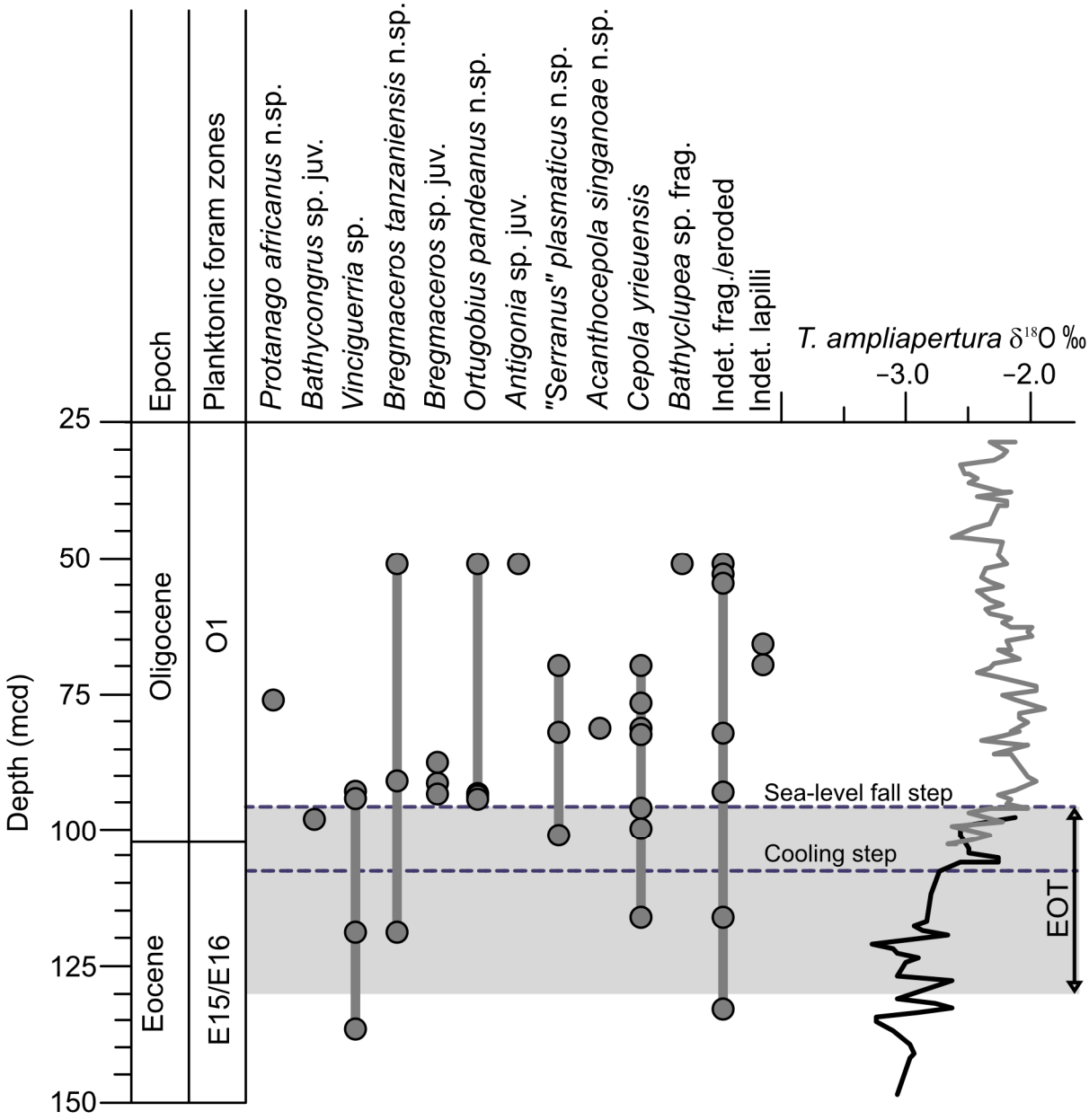


Figure 5. Range chart showing distribution of otolith taxa through the Tanzanian Eocene-Oligocene transition (EOT), plotted next to the planktonic foraminifera stable isotope record of [3] from the same succession. The EOT is indicated by the grey bar. Planktonic formainifera zones after [39].

4.2. Correlation with Events of the EOT

Sites TDP 11 and 17 from where the otoliths originate are well known as one of the most intensively studied and best records of the EOT globally. This allows for a detailed correlation between climate events and otolith occurrence when plotted against the stable isotope record [3] (Figure 5). The Tanzanian oxygen isotope record shows a two-stepped decrease in values across the transition, the first is largely attributed to temperature decrease (approximately 2–3 °C in Tanzania) at approximately 106.4 m and the second to sea-level fall associated with the growth of continental ice on Antarctica at 96.64 m [7]. Our otolith findings are remarkably consistent with the isotopic work, namely that the deepest living fish group of the genus *Vinciguerria* of the Phosichthyidae occurs only in the deep section between 93.2 and 131.5 m. Conversely, the shallow water indicating Gobiidae occur only above the sea level fall, i.e., above 94.55 m. This finding is additionally interesting given the radiation of Gobiidae indicated to occur around the EOT [11,33], although our small sample set precludes any broader implications.

The Cepolidae occurs first at 116 m but becomes a dominant faunal component only in the higher section above 82.25 m. The same is true for the Bregmacerotidae, which except for a single occurrence at 119.2 m are only found above 93.2 m. This indicates perhaps that *Bregmaceros tanzaniensis* was an epipelagic fish. Overall, the vertical distribution of the otoliths in the EOT succession of TDP Sites 11 and 17 shows a good correlation with the changes in the paleo-water depth across this interval. Shallow and deep-water fishes do mostly not occur in the same assemblage, except for a short intermediate interval between approximately 93 to 95 m in the early Oligocene just above the bathymetric shift in the sequence (Figure 5).

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Abbreviations

The following abbreviations are used in this manuscript:

NHMD	Natural History Museum Denmark
TDP	Tanzania Drilling Project
OL	Otolith length
OH	Otolith height
OT	Otolith thickness
OsL	Ostium length
CaL	Cauda length
OCL	Length of ostial colliculum
CCL	Length of caudal colliculum
SuL	Sulcus length

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