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RESEARCH ARTICLE

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Otoliths of the Gobiidae from the Neogene of tropical America

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Abstract

Otoliths are common and diverse in the Neogene of tropical America. Following previous studies of Neogene tropical American otoliths of the lanternfishes (Myctophidae), marine catfishes (Ariidae), croakers (Sciaenidae), and cusk-eels (Ophidiiformes), we describe here the otoliths of the gobies (Gobiidae). The Gobiidae represent the richest marine fish family, with more than 2000 species worldwide and about 250 in America. In the fossil record too they are the species richest family in the Neogene of tropical America. We have investigated otoliths sampled from Ecuador, Pacific and Atlantic Panama, Atlantic Costa Rica, Dominican Republic, Venezuela, and Trinidad, ranging in age from late Early Miocene (late Burdigalian) to late Early Pleistocene (Calabrian). Most of the studied material originates from the collection expeditions of the Panama Paleontology Project (PPP). Our study represents the first comprehensive record of fossil gobies from America, and we recognize 107 species, of which 51 are new to science, 35 are in open nomenclature, and 19 represent species that also live in the region today. Previously, only two fossil otolith-based goby species have been described from the Neogene of tropical America. The dominant gobies in the fossil record of the region are from the Gobiosomatini, particularly of genera living over soft bottoms or in deeper water such as *Bollmannia*, *Microgobius*, *Antilligobius*, and *Palatogobius*. Another purpose of our study is to provide a first comprehensive account of otoliths of the extant Gobiidae of America, which we consider necessary for an adequate identification and interpretation of the Neogene otoliths. We studied otoliths of 130 extant American gobiid species and figured 106 of them for comparison. We also present a morphological analysis and characterization of the extant otoliths as a basis for the identification of fossil otoliths. Problems that commonly arise with the identification of fossil otoliths and specifically of fossil goby otoliths are addressed and discussed. A comparison of the history of the Gobiidae in tropical America reveals a high percentage of shared species between the Pacific and the Atlantic basins during the Late Miocene (Tortonian and Messinian) from at least 11 to 6 Ma. A recording gap on the Pacific side across the Pliocene allows a comparison again only in the late Early Pleistocene (Calabrian, 1.8 to 0.78 Ma), which shows a complete lack of shared species. These observations support the effective closure of the former Central American Seaway and emersion of the Isthmus of Panama in the intervening time. Groups that today only exist in the East Pacific were also identified in the Miocene and Pliocene of the West Atlantic, and there is also at least one instance of a genus now restricted to the West Atlantic having occurred in the East Pacific as late as the Pleistocene. The evolution of gobies in tropical America and the implications thereof are extensively discussed. Furthermore, observations of fossil gobies in the region are discussed in respect to paleoenvironmental indications and paleobiogeographic aspects.

Keywords Tropical America, Neogene, Gobiidae, Gobiosomatini, Otoliths, New genera and species

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Introduction

The otoliths described here were either collected during several field trips of the Panama Paleontological Project of the Smithsonian Tropical Research Institute in Panama from 1986 to 2008 or come from collections made by associates of the Natural History Museum of Basel, Switzerland. Regionally, collections were made on the Pacific side of Central America in Ecuador and Panama and on the Atlantic side in Costa Rica, Panama, Venezuela, Dominican Republic, and Trinidad and span the time interval from the late Early Miocene (Burdigalian) to the late Early Pleistocene (Calabrian). Also reviewed are relevant otoliths from the Early Miocene from the eastern Amazon Pirabas Formation of Brazil described by Aguilera et al. (2014).

This study is part of a project describing and evaluating Neogene otoliths from tropical America that was initiated by the authors in 2012. It soon became clear that the amount of data and diversity was too much and the requirement to establish a sufficient extant otolith database relevant for the region too complex to be handled in a single monograph. It was therefore decided to split the work into more manageable sections featuring specific systematic entities of teleosts that would be published in individual articles. So far the following articles have been published: Myctophidae with 61 species (Schwarzhans & Aguilera, 2012), Ariidae with 10 species (Aguilera et al., 2013, 2020), Sciaenidae with 85 species (Aguilera et al., 2016), and Ophidiiformes with 43 species (Schwarzhans & Aguilera, 2016). Together with 20 additional otolith-based species described from the Early Miocene of Brazil by Aguilera et al. (2014), 219 otolith-based species are so far recognized from the Neogene of tropical America.

Here, we describe the fossil otoliths of the family Gobiidae, comprising 107 species, of which 51 are new, 19 extant (also known as fossils), and 35 in open nomenclature, making it the most diverse complex to be covered in this project and bringing the total count to 324 species. The entire assemblage of gobiid otoliths contains 3200 specimens, of which 2916 are identifiable to genus level and 2615 to species level. All otoliths stem from marine or marginal marine environments, and therefore no otoliths have been found of freshwater gobioids, i.e., of the family Eleotridae or *Sicydium* of the *Stenogobius* lineage of the gobiid subfamily Oxudercinae. One additional volume is envisaged to cover the remainder, which primarily includes families represented by relatively few taxa in the Neogene of tropical America.

The Gobiidae are also a highly diverse and species-rich group in America today, with about 250 species currently recognized as valid (Tornabene et al., 2016; van Tassell, 2011). Little is known so far about the otoliths of this large family, and therefore the first task was to establish a comparative database for the fossil goby otoliths. Although this task was greatly supported by many institutions and scientists in America and worldwide (see Acknowledgements), the recovery of otoliths from museum voucher specimens always encounters one major obstacle: most museum fishes have been fixed in formalin for some time. Formalin is destructive to otoliths, and even after transfer of the fish specimens to alcohol, small amounts of formalin may remain in the brain capsule and continue their destructive work, albeit at a much slower pace. The best chance for finding well-preserved otoliths in museum specimens is generally to be expected in relatively freshly caught specimens (ideally 10 years or less; there is a high risk that the otoliths of specimens older than 20 years have been destroyed) or old specimens caught before the use of formalin, provided that they have not been re-fixed in formalin at a later stage. Furthermore, small otoliths in small fish dissolve faster than compact otoliths in larger fish; and there are many small fishes in the Gobiidae.

For this study, we retrieved otoliths from extant fishes representing 48 of the currently recognized 58 gobiid genera occurring in American waters. Those not represented are mostly from small, often rare fishes, for which we were not able to identify specimens with preserved otoliths. We successfully extracted otoliths from 130 extant American goby species, which is slightly more than 50%. In a first step, we identified the fossil otoliths to the genus level of the predominant genera in the record. As expected, these were mostly fishes living in environments with good potential for sedimentation and hence fossilization of otoliths, i.e., fishes living on muddy to sandy substrate in marine environments such as those of the genera *Bollmannia*, *Microgobius*, *Antilligobius*, and *Palatogobius*. In a second step, we tried to cover as many extant species of these genera as possible to provide a solid basis for the identification of the fossil otoliths and recognize extant species occurring in the fossil record. Extant otoliths of certain rich coral-associated small gobies (for instance, of the genera *Gobiosoma*, *Elacatinus*, or *Tigrigobius*) are poorly represented mainly for the reasons explained above. These otoliths are also rather uncommon in the fossil record and in the younger section (Pliocene and Pleistocene) could often not be identified to species level.

Since extant goby otoliths from America have rarely been figured so far, we figure all relevant extant goby otoliths (of 106 species) here alongside the fossil ones. In addition to the documentation, a morphological analysis and character definition is provided before the descriptive part, with the aim of guiding higher-level allocations of the studied otoliths and explaining the value of certain characters for the identification and description.

Regional geology and localities

The otoliths described here were obtained from a variety of Neogene formations from various localities in tropical America, the stratigraphic information of which is briefly summarized below. Figure 1 summarizes the local formations in their regional stratigraphic frame, highlighting the intervals from which otoliths have been obtained for this study. The stratigraphical and geochronological time scale, stage names, and biozones for the Neogene are employed from Gradstein et al. (2020). The description of the formations from which the otoliths were sampled is organized from west in the Pacific to east in the Atlantic and from early to late ages. At the bottom of each brief description of a formation, the sample localities from which the otoliths have been obtained are listed. Geological maps on which the sample localities are marked accompany the descriptions. The geological maps are taken from published resources, and the coloration of stratigraphic units on each map has been maintained.

Ecuador (Fig. 2)

The Angostura FM (Stainforth, 1948) is of Late Miocene, Tortonian (NN10–11) age, and is found in the western Borbón Basin, northwestern coast of Ecuador. It includes middle neritic and shallow outer neritic facies exposed along the Río Santiago and Punta Verde, respectively. It consists of muddy, fine-grained sandstones with mollusk shells dispersed in the matrix (Baldock, 1982; Cantalamessa et al., 2007). The supposed paleoenvironment is shore-face to inner-shelf; however, based on the fossil chondrichthyan fauna,

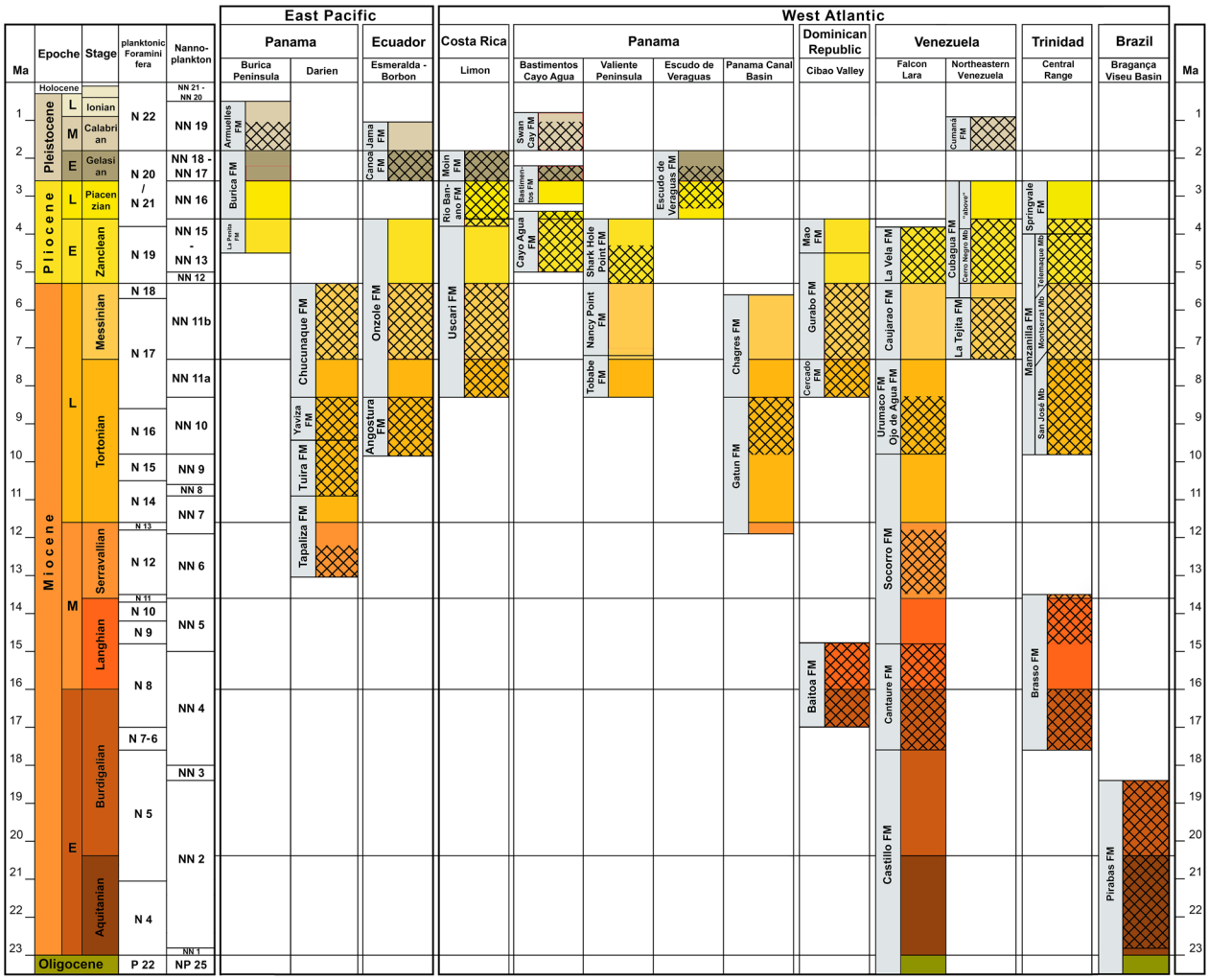


Fig. 1 Stratigraphic correlation chart depicting stratigraphic positions of otoliths obtained and described herein (hatched). Stratigraphic correlation is based on referenced literature

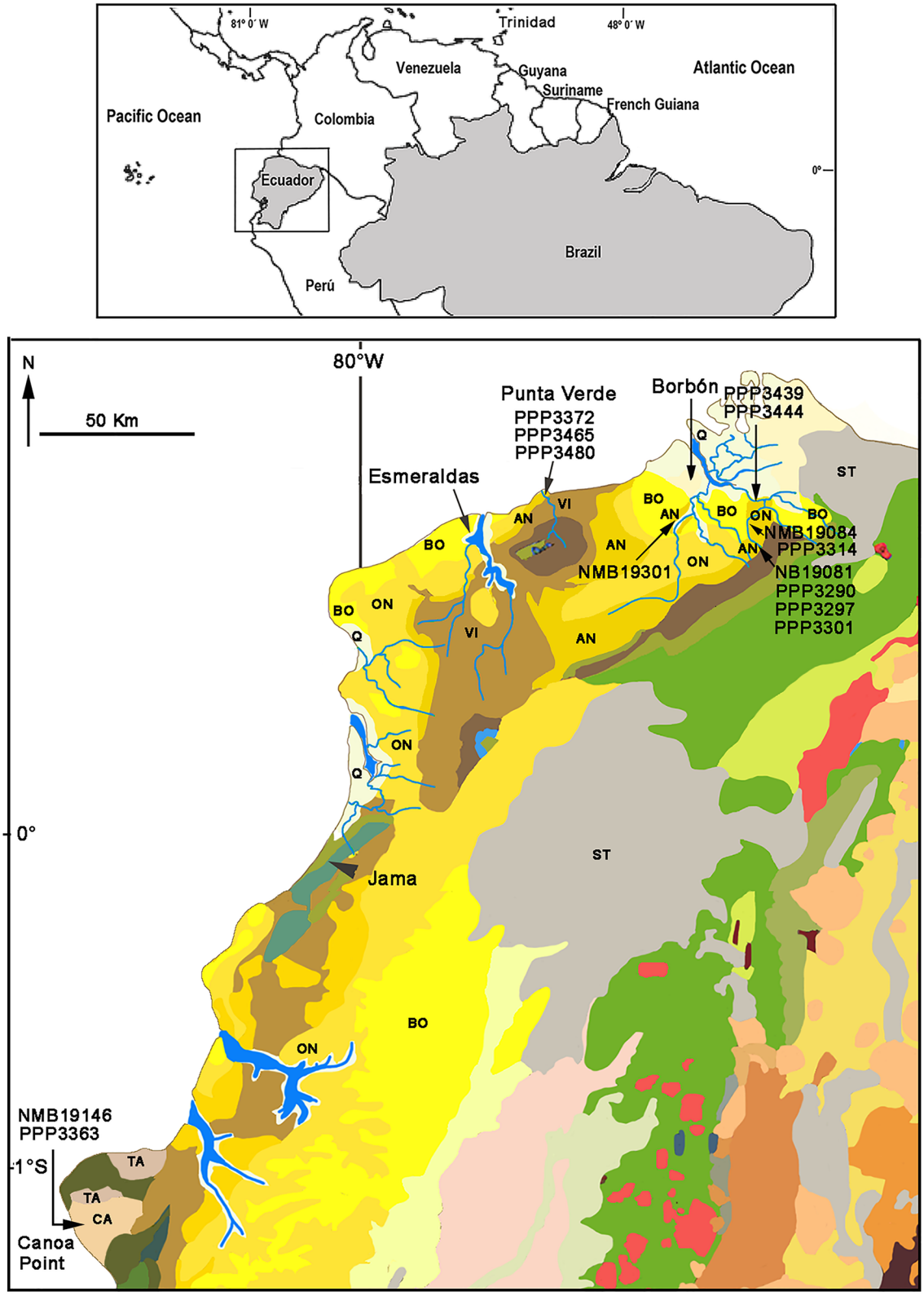


Fig. 2 Location plate of Ecuador, based on the geological map of Ecuador (Baldock, 1982). Formation abbreviations: Q, Quaternary; ST, San Tadeo FM (Pleistocene); TA, Tablazo FM (Pleistocene); CA, Canoa FM (Pleistocene); BO, Borbon/Upper Onzole FM (Pliocene); ON, (lower) Onzole FM (Upper Miocene, Messinian); AN, Angostura FM (Upper Miocene, Tortonian); VI, Viche FM (Middle Miocene)

Carrillo-Briceño et al. (2014) suggested that an upper bathyal paleoenvironment was present within a short distance from the coast, which is supported by the occurrence of lanternfish otoliths (Schwarzhans & Aguilera, 2013), albeit cusk-eels and brotulas with a preference to shallow water (Schwarzhans & Aguilera, 2016), croakers (Aguilera et al., 2016), and gobies (this study) prevailed—sample localities**:** NMB 19081, NMB 19301, PPP 3290, PPP 3297, PPP 3301, PPP 3369, PPP 3372, PPP 3439, PPP 3444, PPP 3465, PPP 3480.

The Onzole FM ranged from the Late Miocene to the Early Pliocene (Carnevale et al., 2011). Whittaker (1988) subdivided the Onzole FM into two main units (informally named lower Onzole and upper Onzole FM) separated by a regionally extensive angular unconformity of Late Miocene to Early Pliocene age. These outcrops are situated near Punta Gorda and Esmeraldas and are composed mainly of fine-grained muddy turbidites, having regular vertical sequences of sedimentary structures associated with fining upward sequences and bioturbation restricted mostly to the tops of the beds. The remainder of the beds consists of volcanic ash, mud, and glauconitic silts and turbidites. Vertical sequential analyses of stratigraphic sections for the most part show no pronounced trends in bed thickness or grain size. Facies relations, paleontological data, and regional geologic settings suggest sediment accumulation on an inner trench slope in a basin situated ocean-ward of the Pliocene trench–slope break (Aalto & Miller, 1999). This interpretation is consistent with abundant records of lanternfishes (Schwarzhans & Aguilera, 2013) and scarcity of goby otoliths. The otoliths described here were all obtained from the lower Onzole FM of Late Miocene (Messinian) age—sample localities: NMB 19084, PPP 3314.

The Canoa FM has extensive outcrops along the sea cliff south of Manta in Manabí Province (Landini et al., 2001, 2002), and its age has been given as Early Pleistocene (Di Celma et al., 2005; Landini et al., 2001, 2002). The lithology of the Canoa FM consists mainly of sandstone and sandy mudstone, divided into two sections (Pilsbry & Olsson, 1941). The lower Canoa FM, exposed on the sea cliff south of Punta Canoa, is a 36 m thick, cyclothemic succession of bluish, chiefly fine-grained strata that rest unconformably on Miocene rocks of the Tosagua FM. The upper Canoa FM consists of 38-m-thick shore face and inner-shelf deposits, and represent shallow-water deposits (Di Celma et al., 2005). The records of croaker (Aguilera et al., 2016) and cusk-eel otoliths (Schwarzhans & Aguilera, 2016) suggest a neritic paleoenvironment—sample localities: NMB 19146, PPP 3363.

Panama, Pacific side (Fig. 3)

The Tapaliza FM (Schuchert, 1935; Esso Exploration and Production Panama, 1971) from the Tapaliza River in Darien consists of foraminiferal mudstone and siltstone containing abundant mollusk-rich horizons and minor 0–20 cm thick volcanic sandstone units, often with prominent calcareous 5–10 cm concretions (Coates et al., 2004). The age is estimated as upper Middle Miocene (nannoplankton zone NN6–7) (Coates et al., 2004)—sample localities: PPP 1152, PPP 1538.

The Tuira FM (Terrey, 1926) from the Chucunaque-Tuira basin consists of thin and regularly bedded alternations of blue-gray greywacke and arkosic sandstone with dark green to black silty claystone and siltstone. Abundant fossils are of plant debris and scattered small mollusks, particularly pectinids and nuculanids. Many units have pervasive bioturbation or thalassinoid burrow systems. Pebble breccia, shell beds, and stringers of rip-up clasts may occur occasionally. The lower part of the Tuira FM cannot be assigned to a calcareous nannofossil biozone, but represents the planktonic foraminiferal zone N15. Its upper part belongs to subzone NN9b and partly zone NN10 and zone N16, ranging from 11.2 to 9.4 Ma (Coates et al., 2004). The otoliths have been collected from the upper part. Otoliths of the Gobiidae are common and suggest varying inner platform paleoenvironments a short distance from the coast—sample localities: PPP 1132, PPP 1134, PPP 1137, PPP 1139, PPP 1142, PPP 1154, PPP 1163, PPP 1164, PPP 1593, PPP 1603, PPP 1606, PPP 1627, PPP 1997.

The Yaviza FM (Coates et al., 2004) is named after the township of Yaviza, the termination point of the Pan-American highway from the north and the beginning of the so-called Darien Gap. The formation consists of clayey and silty, shelly sandstone and blue-gray, volcaniclastics. Whole arcids, *Pecten*, turretellids, and other mollusks are abundant. Shelly hard beds are common, especially with *Turritella*, *Anadara*, and oysters. Many units are pervasively bioturbated, with shell-filled burrows, with occasional ahermatypic corals and common, often large, concretions (Coates et al., 2004). The age is estimated to be Late Miocene, nannofossil zone NN10 between 9.4 and 8.6 Ma (Coates et al., 2004). Many otoliths were obtained from this formation, which is particularly rich in gobies—sample localities: PPP 1145, PPP 1149, PPP 1171, PPP 1528, PPP 1553, PPP 1565, PPP 1566, PPP 1570, PPP 1607, PPP 1609, PPP 1620.

The Chucunaque FM (Shelton, 1952) from the Tuquesa River in Darien consists of gray weathering,

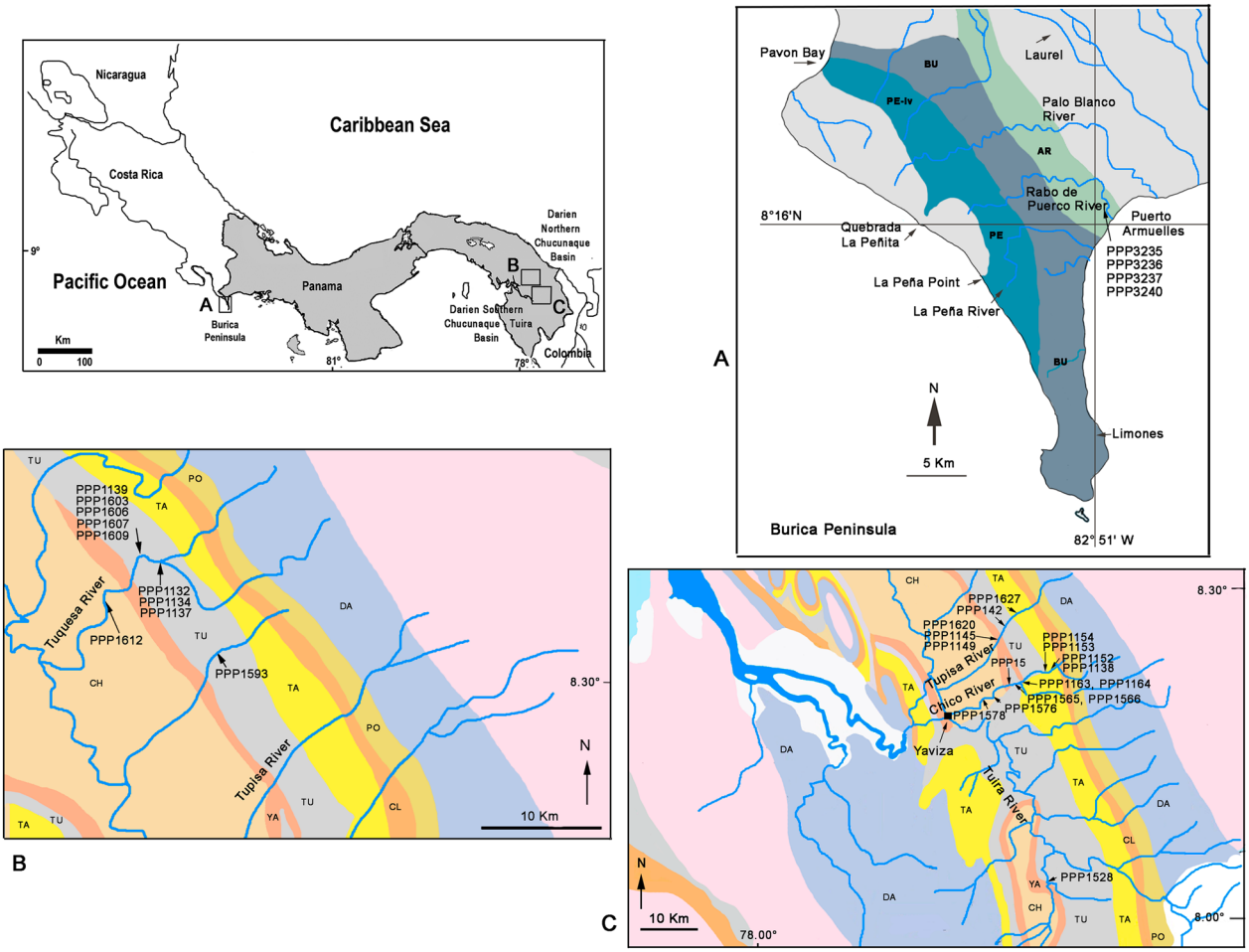


Fig. 3 Location plate of Pacific Panama, Burica Peninsula (**A**) and Darien Province (**B**, **C**), based on the geological maps of Coates et al., (1992, 2004). Formation abbreviations Burica Peninsula **A** AR, Armuelles FM (Pleistocene, Calabrian); BU, Burica FM (Upper Pliocene–Lower Pleistocene); PE, Peñita FM (Lower Pliocene). Formation abbreviations Darien **B**, **C** CH, Chucunaque FM (Upper Miocene, Messinian); YA, Yaviza FM (Upper Miocene, upper Tortonian); TU, Tuira FM (Upper Miocene, lower Tortonian); TA, Tapaliza FM (Middle Miocene, Serravallian); CL, Clarita FM (Middle Miocene, Langhian); PO, Porcona FM (Oligocene); DA, Darien FM (Eocene–Oligocene)

greenish-blue to black, blocky to massive, silty claystone and siltstone, with minor thin horizons and stringers of volcanic sandstone. Calcareous concretions are common. Calcified thalassinoid burrows are typical. The age is estimated to be the latest Miocene (Messinian) at about 7.1 (possibly from 8.6) to 5.6 Ma (NN11a/NN11b to NN11/NN12 zonal boundaries) (Coates et al., 2004). Few otoliths have been obtained from this formation, including Sciaenidae (Aguilera et al., 2016) and gobies, thus suggesting a shallow-water environment—sample localities: PPP 1576, PPP 1578, PPP 1612.

The Armuelles FM (Terry, 1941) is of Early Pleistocene or younger and consists of a pebbly conglomerate, unconsolidated greenish-blue siltstone and litharenite in the lower part. The formation overlays the deep marine Burica FM of Late Pliocene age, thereby showing a shallowing upward sedimentary succession. The upper part contains gray-blue, clayey siltstone and fine litharenite predominate, with sporadic bedded coarse sand. A marker bed near the top consists of large boulders, richly encrusted with oysters, corals, and cheilostome bryozoans, immediately below which is a biostrome consisting of the bivalve *Pinna* (Coates et al., 1992). Few otoliths have been obtained from the lower part of the section—sample localities: PPP 3235, PPP 3236, PPP 3237, PPP 3240.

Panama, Atlantic side (Fig. 4)

The Gatun FM (Howe, 1907) was first described from Gatun in the course of the construction of the Panama Canal between Mount Hope and Sabanita at the northern end of the Canal. The formation is divided into three members (Woodring, 1957). The section of the lower member is exposed along the trans-isthmian highway about 12 km east of Colón City, from Sabanita to Cativa.

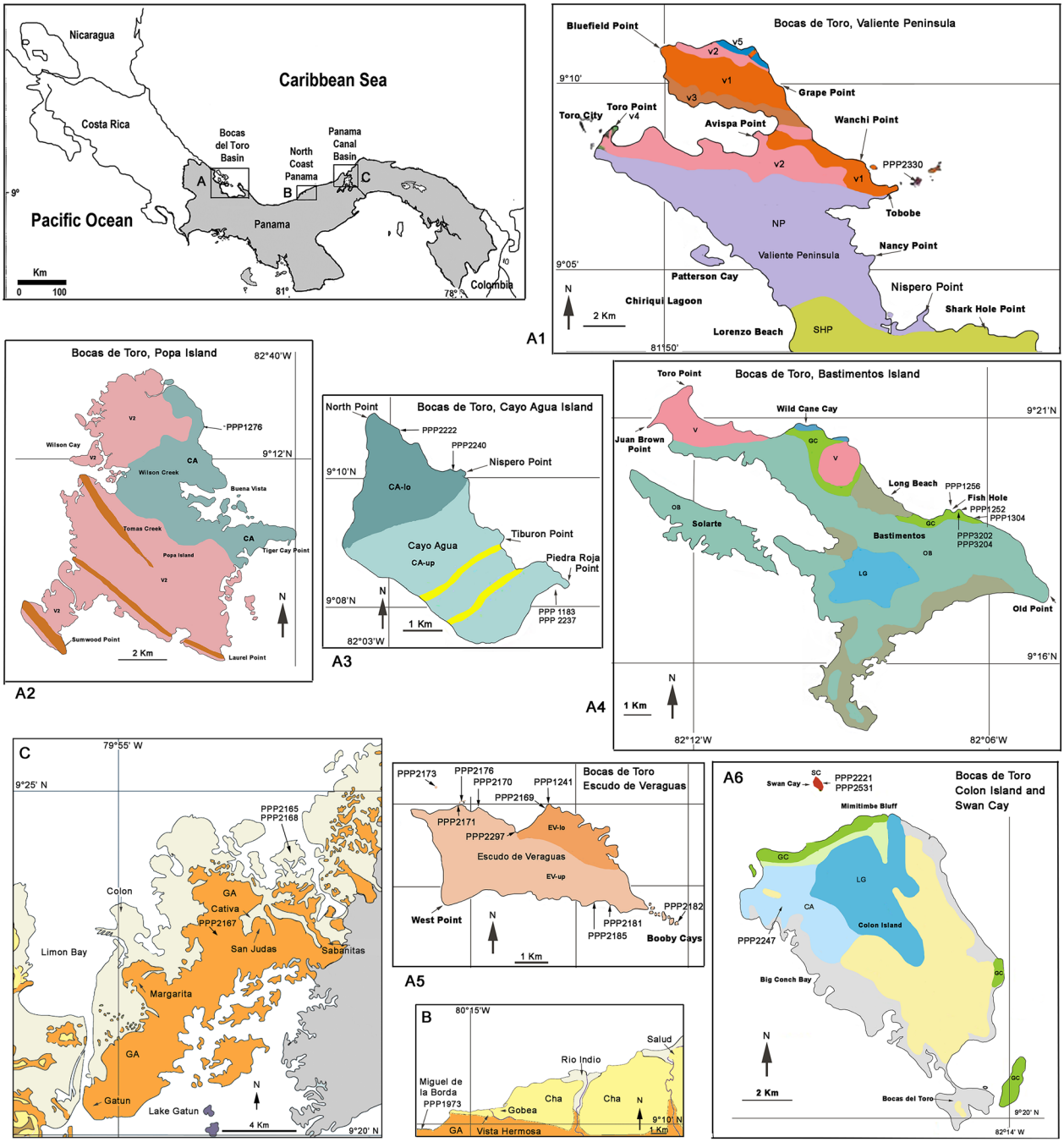


Fig. 4 Location plate of Atlantic Panama, Bocas del Toro Basin (**A**), north coast of Panama (**B**) and Canal Basin (**C**), based on the geological maps of Coates et al., (1992, 2005). Formation abbreviations Bocas del Toro Basin (**A**): Valiente Peninsula **A1** SHP, Shark Hole Point FM (Lower Pliocene); NP, Nancy Point FM (Upper Miocene, Messinian); V1–V5 Valiente FM volcanics. Popa Island **A2** CA, Cayo Agua FM (Pliocene); V2, Valiente FM volcanics. Cayo Agua Island **A3** CA-up, upper Cayo Agua FM (Lower Pliocene, upper Zanclean); CA-lo, lower Cayo Agua FM (Lower Pliocene, lower Zanclean). Bastimentos Island **A4** GC, Ground Creek Unit of Bastimentos FM (lower Pleistocene, Gelasian); LG, La Gruta Unit of Bastimentos FM (lower Pleistocene, Gelasian); OB, Old Bank Unit of Bastimentos FM (lower Pleistocene, Gelasian); V, volcanics. Escudo de Veraguas (A5): EV-up, upper Escudo de Veraguas FM (lower Pleistocene, Gelasian); EV-lo, lower Escudo de Veraguas FM (upper Pliocene, Piacenzian). Colon Island and Swan Cay (A6): GC, Ground Creek Unit of Bastimentos FM (Pleistocene); LG, La Gruta Unit of Bastimentos FM (Pleistocene); OB, Old Bank Unit of Bastimentos FM (Pleistocene); SC, Swan Cay FM (Pleistocene, Calabrian). Formations abbreviations Panama north coast (**B**) and Canal Basin (**C**): Cha, Chagres FM (Upper Miocene); GA, Gatun FM (Upper Miocene, Tortonian)

This member consists of burrowed, concretionary, gray-green, tuffaceous, silty litharenite. The section of the middle member is located in the region between Cativa and Gatun and consists of massive, borrow-mottled, silty, tuffaceous, and occasionally calcareous litharenite, ashy siltstone, and thin conglomerate with abundant mollusks, echinoid fragments, and wood. The section of the upper part, of Late Miocene, middle Tortonian age (NN10), is exposed about 2–3 km north of Gatun and to the west of the Panama Canal. This section has yielded the otoliths described herein and is characterized by clayey, biocalcarenite, tuffaceous siltstone and fine silty litharenite that is burrow-mottled, and among others contained fishbones of porcupine fishes (Aguilera et al., 2017), otoliths of marine catfishes (Aguilera et al., 2020), croakers (Aguilera et al., 2016), lanternfishes (Schwarzhans & Aguilera, 2013), cusk-eels (Schwarzhans & Aguilera, 2016), and gobies. The sediment is also rich in scattered mollusks (Coates et al., 1992) and is assumed to have been deposited at a paleo-depth of between 15 and 40 m (Aguilera & Rodrigues de Aguilera, 1999; Collins et al., 1999). The total thickness of the Gatun Formation, recorded in a borehole near Colón City, is about 500 m (Woodring, 1957)—sample localities: PPP 1973, PPP 2165, PPP 2166, PPP 2167, PPP 2168.

The Shark Hole Point FM (Coates et al., 1992) is of Early Pliocene (NN12–15) age. The type section is located in a sequence of about 205 m thickness from the Butchuqua to Bruno Bluff, Atlantic Panama. It consists of micaceous, clayey siltstone apparently pervasively bioturbated, with scattered mollusks and abundant large scaphopods. Rare thin, coarse sand and cross-bedded laminated silt horizons also occur, and the upper part is distinguished by numerous regular concretionary horizons. At Bruno Bluff the formation consists of medium to massive-bedded, dark-gray siltstone with a tight clayey matrix, and frequent small vertical ichnofossils (Coates et al., 1992, 1999). Previous research in fossil fish included Aguilera and Rodrigues de Aguilera (1999) and Schwarzhans and Aguilera (2013, 2016)—sample localities: PPP2217, PPP 2218, PPP 2219.

The Cayo Agua FM (Coates et al., 1992) is of Early to Late Pliocene, Zanclean to Piacenzian age (NN13–16), and is found on the Cayo Agua Island about 6 km to the west of Toro Point, Valiente Peninsula, Atlantic Panama. The formation is well exposed along the east coast and consists lithologically of pervasively bioturbated, muddy, silty sandstone with common horizons of abundant thick-shelled mollusks, ahermatypic corals, and wood fragments. Occasional horizons of pebble conglomerate and coarse-grained volcaniclastic sandstone are common in the middle part of the formation. A distinctive marker bed of corals occurs near the top of the formation and is well exposed at Tiburón Point and the unnamed point to the south. The corals appear to be mostly free-living, hermatypic, grass flat corals, as well as ahermatypic species, associated with benthic foraminifera, ostracods, and teleostean fish. A depositional water depth of 30–50 m is assumed (Aguilera & Rodrigues de Aguilera, 1999; Collins et al., 1999). However, bathypelagic lanternfishes were described by Schwarzhans and Aguilera (2013) as well as cusk-eels and brotulas (Schwarzhans & Aguilera, 2016), indicating some open sea influence. The age of the Cayo Agua FM is dated at the base, ~ 5.0–3.5 Ma, and at the top, 3.7–3.4 Ma (Coates et al., 1992). Otoliths were collected from the lower and middle part of the section below the limestone marker—sample localities: lower part: PPP 1276, PPP 2222, PPP 2240; middle part: PPP 1188.

The Escudo de Veraguas FM (Coates et al., 1992) ranges in age from Late Pliocene, Piacenzian, to Early Pleistocene, Gelasian (NN16–18). It is known only from the island of the same name that lies 27 km east of Nancy Point, Atlantic Panama. The lower section of this formation (3.5 Ma) is found along the coast on the east side of the V-shaped embayment situated in the central part of the north coast, about 1 km east of Long Bay Point. It is more indurated with common and densely packed cemented ichnofossils, scattered ahermatypic corals through the middle part as well as variably abundant mollusks, and at the top a coral biostrome dominated by *Stylophora* and sand dollars. The paleo-depth based on ahermatypic species, benthic foraminifera, ostracods, and teleostean fish was estimated to be between 100 and 150 m (Aguilera & Rodrigues de Aguilera, 1999; Collins et al., 1999). Mesopelagic lanternfishes were described by Schwarzhans and Aguilera (2013); however, a shallow-water croaker (Aguilera et al., 216) was also recorded. The upper section of the formation (1.8 Ma) lies along the west coast for about 1 km south of Long Bay Point and consists of gray-blue, pervasively bioturbated clayey siltstone and silty claystone, with frequent concretions, and scattered shelly hash, often with scattered whole and diverse mollusks and small, cornute, ahermatypic corals (Coates et al., 1992). The top and bottom units were deposited in an inner neritic environment, but the middle part of the lower succession, from which most of the otoliths were collected, has abundant benthic foraminifera, indicating deposition in outer neritic to upper bathyal waters (Collins, 1993). Goby otoliths are rare in this part of the section but relatively common in the upper section, deposited in shallower water—sample localities: Piacenzian: PPP 1241, PPP 2169, PPP 2181, PPP 2182; Gelasian: PPP 2170, PPP 2171, PPP 2173, PPP 2176, PPP 2297.

The Bastimentos FM (Coates et al., 1992) is of Early Pleistocene, Gelasian age (NN16–18), and its stratotype is located on Bastimentos Island, Atlantic Panama. It consists of reef deposits sitting directly on the Miocene basalt of the Valiente Formation, which are well exposed on Wild Cane Key and along the coast for 2 km to the east, with reef limestone extensively re-crystallized with many coral colonies. A particularly well-preserved example of the La Gruta reef, packed with large and diverse coral colonies, is exposed at the base of the cliffs in three small bays at Fish Hole, at the southern end of Long Beach. More than 50% of the species in the coral assemblage are extinct (Coates et al., 2005). Otoliths were obtained from the Ground Creek Unit adjacent to the reef complex and showed a mixture of reef-associated fishes (gobies) and open marine species (Myctophidae; Schwarzhans & Aguilera, 2013)—sample localities: PPP 1252, PPP 1256, PPP 1304, PPP 2247, PPP 2249, PPP 2250, PPP 3202, PPP 3204.

The Swan Cay FM (Coates et al., 1992) is of Early Pleistocene age (NN19, N22) and is named for the small island that lies 1.7 km off the northern coast of Colon Island, Atlantic Panama. The stratotype runs from north (youngest) to south (oldest) across Swan Cay. The formation has three components. The lower 15 m are exposed on the southerly low hill of the island and consist of silty sandstone and shelly calcarenitic siltstone, with coral rubble and red algal fragments and balls. The middle 4 m consist of calcarenitic clayey siltstone, with dense, fine shell-hash horizons and abundant large coral colonies in the lower part. The upper 60 m of the formation consist of massively thick-bedded, pale tan-white limestone. The uppermost 30 m include a 4 m thick coral bed with large *Montastraea* colonies, other corals, and mollusks. The lower 30 m contains silty calcarenite with common red algae and large foraminifera, shell hash, and micromollusks. Cave deposits, about 5 m above the base of the calcarenite, consist of silty, shelly, volcaniclastic sandstone, mixed with abundant volcanic cobbles and boulders, and calcareous reef rubble containing an abundant and diverse molluskan assemblage (Coates et al., 2005). Based on ahermatypic species, benthic foraminifera, ostracods, and teleostean fish, a range of depths is indicated, containing reworked fore-reef debris deposited at about 100 m (Aguilera & Rodrigues de Aguilera, 1999; Collins et al., 1999). Abundant large and freshly preserved globigerinid planktonic foraminifera combined with paleomagnetic data strongly suggest that the deposit is Early Pleistocene (0.78–1.77 Ma). Previous research of fossil otoliths recorded lanternfish otoliths (Schwarzhans & Aguilera, 2013), pearlfishes, cusk-eels, and brotulas (Schwarzhans & Aguilera, 2016), which represent open marine influence. Here we describe reef-associated goby otoliths representing a near-reef assemblage—sample localities: PPP 2221, PPP 2531.

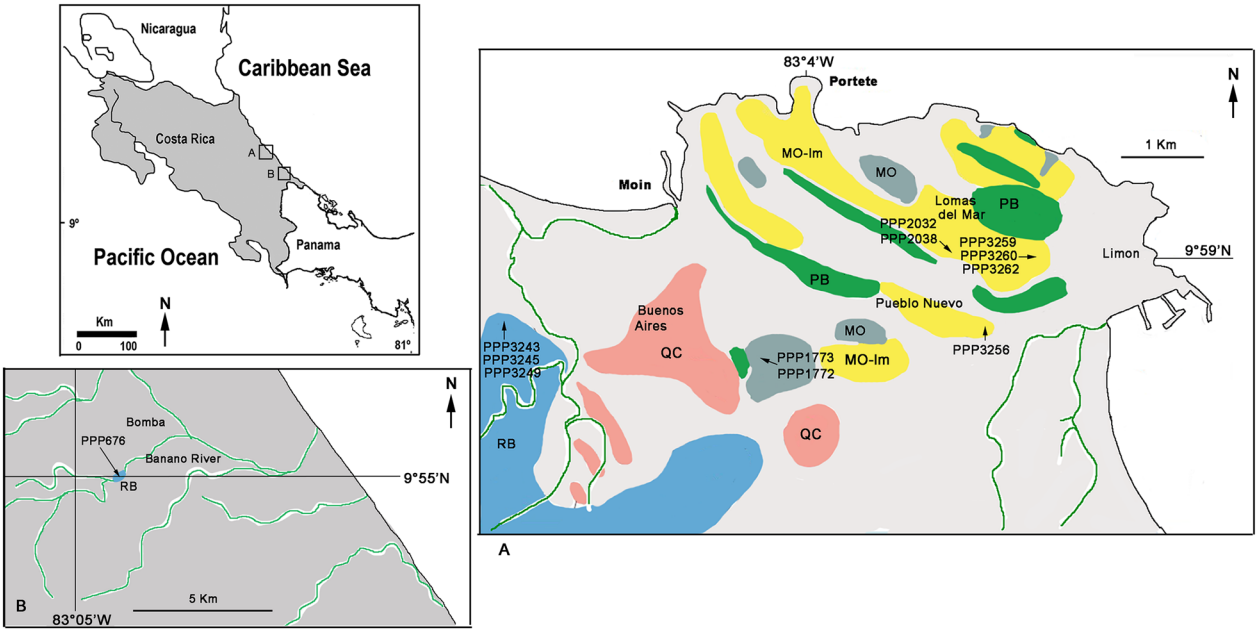


Fig. 5 Location plate of Atlantic Costa Rica, Limón province, based on the geological maps of Coates et al. (1992) and McNeill et al. (2000). MO, Moin FM mudstone member (Pleistocene, Gelasian); MO-lm, Moin FM limestone member (Pleistocene, Gelasian); PB, Pueblo Nuevo Sand Member (upper Pliocene, Piacenzian); RB, Río Banano FM (Pliocene, Piacenzian–Zanclean); US (not shown), Uscari FM (upper Miocene)

Costa Rica, Atlantic side (Fig. 5)

The Uscari FM consists of blue-gray to greenish-gray claystones and siltstones, including intercalations of fine-grained sandstones, calcilutites, and lenses of conglomeratic material (Laurito, 1996). The Alto Guayacán outcrop is characterized by clayey strata and siltstone intercalations that vary to clay, with strong bioturbation (Laurito, 1996) and diverse fish otoliths with an age range between the Early Miocene and the Early Pliocene. The fish assemblage suggests an upper mesopelagic paleoenvironment close to the platform edge under oceanic influence. Only a few goby otoliths have been obtained from an interval of Late Miocene age—sample locality: PPP 3270.

The Río Banano FM was described by Taylor (1975), and Cassell (1986) established the type section west of the railroad bridge at Bomba on the Banano River, 14 km south-southwest of Limón. The oldest unit of the Río Banano FM, from which the otoliths were obtained, correlates biostratigraphically to the late Early to Late Pliocene, although it may be older in the southern Limón Basin. The formation is ~ 750 m thick and consists of burrow-mottled, blue-gray siltstone and volcanic litharenite with frequent shell-rich lenses and scattered mollusk hash. Mollusks, sand dollars, and callianassid burrows are common and indicate a shallow-water paleoenvironment in agreement with the records of shallow water-inhabiting fishes such croakers (Aguilera et al., 2016) and gobies—sample localities: PPP 676, PPP 1732, PPP 3243. PPP 3245, PPP 3249.

The Moin FM (Cassell, 1986; Cassell & Sem Grupta, 1989; Coates et al., 1992) of Late Pliocene to Early Pleistocene age (3.0 to 1.9–1.6 Ma) is located near the mouth of the Moin River, about 6 km west of Limón in Costa Rica, and includes two members: the Empalme Mb and the Lomas del Mar Mb. The Lomas del Mar Mb, where the otoliths come from, is composed of blue-gray, clayey siltstone and calcarenite that flank beds immediately adjacent to reef patches. Sediments are packed with small, diverse mollusks, including vermetids, small solitary and oculinid ahermatypic corals, bryozoans, serpulids, and large echinoid spines (Coates, 1999)—sample localities: PPP 1772, PPP 1773, PPP 1776, PPP 2032, PPP 2038, PPP 3256, PPP 3259, PPP 3260, PPP 3262.

Dominican Republic (Fig. 6)

The Baitoa FM (Cooke, 1920) is of late Burdigalian age (N8, NN4–5) and is composed of silts interbedded with conglomerates (Saunders et al., 1986)—sample locality: NMB 17290.

The Cercado FM (Cooke, 1920) of Late Miocene, late Tortonian age (NN11a) is found in several river bank sections of the Cibao Valley, Dominican Republic. It is composed of calcareous silts that are occasionally separated by thin, sandy conglomerates in a shallow, near-shore environment in the west (Río Cana) and gradually deepening eastward (Río Gurabo and Río Mao) (Saunders et al., 1986). Previous research of fossil otoliths included lanternfishes (Schwarzhans & Aguilera, 2013), pearlfishes and brotulas (Schwarzhans & Aguilera, 2016), croakers (Aguilera et al., 2016), and marine catfish (Aguilera et al., 2020)—sample localities: NMB 15903, NMB 15912, NMB 16915, NMB 16916, NMB 16918, NMB 16923, NMB 16837, NMB 17003.

The Gurabo Formation (Maury, 1919, 1931) of Late Miocene, Messinian age (NN11b) to Early Pliocene, Zanclean age (NN12–13) is also exposed in the Cibao Valley, Dominican Republic. It consists of calcareous silt and fine sandy silt, rich in branches and heads of corals and in mollusks (Saunders et al., 1986). Previous research in fossil fish included Nolf and Stringer (1992), who interpreted the fish assemblage as coming from a shallow neritic paleoenvironment at depths of less than 50 m. The reviewed myctophid otoliths are all from the basal member of the Gurabo FM from the NN11b biozone (Schwarzhans & Aguilera, 2013). Further otolith records include croakers (Aguilera et al., 2016), cusk-eels, pearlfishes, and brotulas (Schwarzhans & Aguilera, 2016)—sample locality: NMB 15864.

Venezuela (Fig. 7)

The Cantaure FM (Hunter & Bartok, 1974) is of late Early Miocene, late Burdigalian to early Langhian age (NN4–5, N7–8). The age at the base is about 16.5 Ma (Griffiths et al., 2012). Outcrops of the formation are found west of Casa Cantaure and are composed of silty shales interbedded with thin algal limestones and shell beds (Hunter & Bartok, 1974). There is an unexposed unit of Cantaure FM that is 48 m thick and was accessed by a local artisan well. The section consists mainly of silty to medium sandstone, intercalated with massive mudstone. A diverse otolith-based fossil fish fauna has been described (Aguilera et al., 2016, 2020; Nolf & Aguilera, 1998; Schwarzhans & Aguilera, 2013). The teleostean assemblage together with the elasmobranch fauna (Carrillo-Briceño et al., 2016) are indicative of a tropical-marine, clear-water near-shore neritic environment of normal marine salinity, probably in an insular inner-middle shelf environment—sample localities: PPP 2539, PPP 2543, PPP 2545, PPP 2546.

The Socorro FM (El Saladillo section) (Gamero & Díaz De Gamero, 1963) is characterized by an interval of micro-fossiliferous gray shales with intercalations of hard and compact limestones. Sandstones are fine-grained and friable, forming thin layers. The marls are gypsum and fossiliferous. The age is assigned to the late

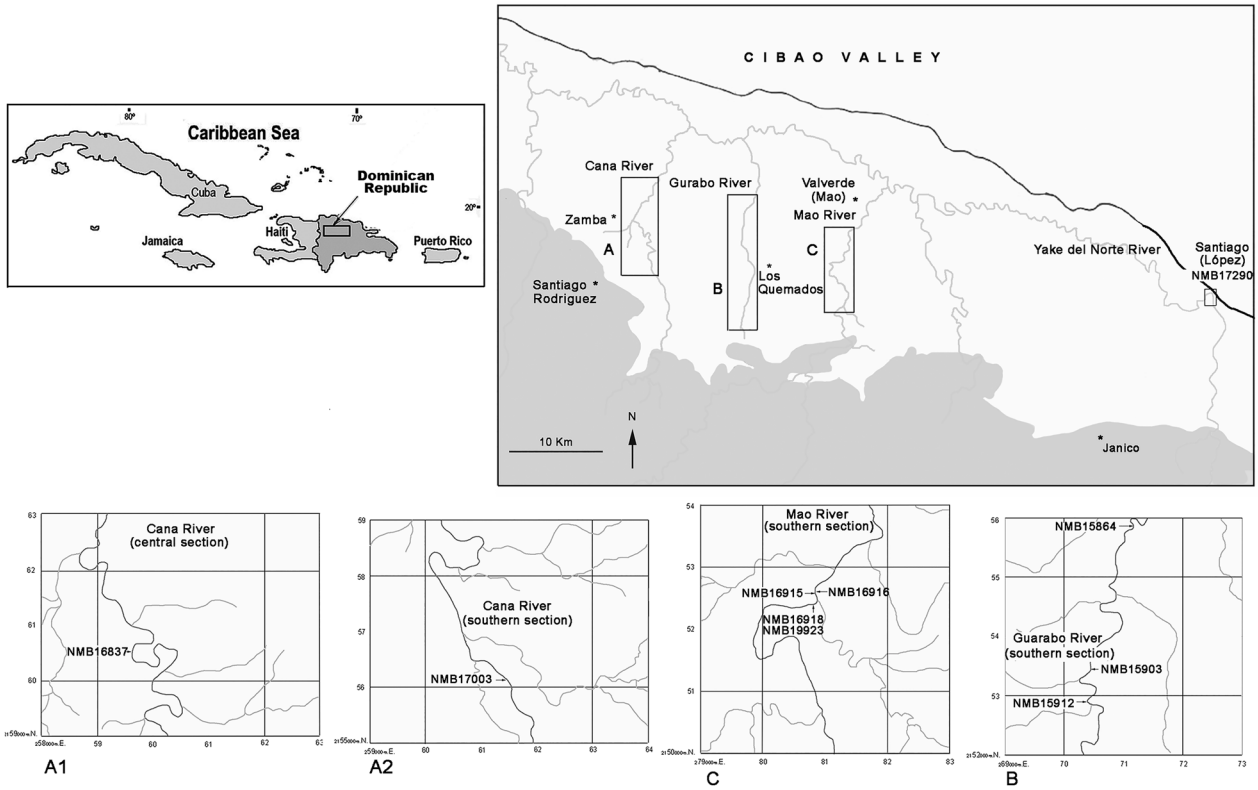


Fig. 6 Location plate of the Dominican Republic, based on Saunders et al. (1986)

Langhian–early Tortonian (15–10 Ma) based on planktonic foraminifera and palynomorph findings (Díaz De Gamero, 1989; Lorente, 1986)—sample localities: PPP 2642, PPP 2644.

Ojo de Agua FM is characterized by micaceous sandstones intercalated with clays, conglomerates, and sandy to nodular fossiliferous limestones containing predominantly mollusks. The facies correspond to shallow and brackish marine paleoenvironments near the coast. The age is considered to be Late Miocene (Gonzales De Juana et al., 1980)—sample locality: NMB 15730.

La Tejita FM consists of a basal conglomerate, with quartz and rich igneous pebbles, with a matrix of calcareous sandstone with *Crassostrea virginica* Gmelin (Macsotay et al., 2009). The lower part, where the otoliths were collected, consists of an alternating sequence of gray sandy siltstones with an abundance of *Thallasinoides* sp. and ochre calcareous sandstones with abundant gastropods (Padron et al., 1993). According to Macsotay et al. (2009) and Padron et al. (1993), the age of La Tejita Formation is Late Miocene. Previous research of fossil croaker otoliths (Aguilera et al., 2016) suggests a shallow-water paleoenvironment—sample locality: PPP 3087.

La Vela FM (Chiguaje Mb) (Hodson, 1926) was deposited at a shallow to middle neritic depth and is characterized by a lithology of cross-bedded sandstones, sandy siltstones, and blue-gray shales with occasional marine limestone horizons. The basal unit is uppermost Miocene in age, but most of the section is of Early Pliocene age (*Globorotalia margaritae* zone = zones N18–19 and M14–PL2) (Smith et al., 2010)—sample localities: PPP 2532, PPP 2647.

The Cubagua FM (Dalton, 1912) is found in the northeastern part of Venezuela. The Cerro Negro Mb, from which many of the otoliths described here were obtained, is exposed on Cubagua Island and the westernmost part of the Araya Peninsula. The Cerro Negro Mb consists of a 2-m-thick basal sandy marl, which is highly fossiliferous with *Ostrea haitiensis* and *O. crassissima*, followed by thin intercalations of sandy lime, fossiliferous marl, and limestone marl. The age of the Cubagua FM at the Cerro Negro Mb is Early Pliocene, Zanclean (NN13–15), and strata occasionally sampled above the Cerro Negro Mb are considered to be of late Early and Late Pliocene age. The exceptional fish assemblage of the Cerro Negro Mb (teleostean otolith and elasmobranch tooth) indicate deep water (epipelagic, mesopelagic, and benthopelagic),

with some influx from shallow-water (neritic) taxa where an oceanic paleo-upwelling system influenced the shallow tropical water (Aguilera & Rodrigues de Aguilera, 2001; Aguilera et al., 2016, 2020; Schwarzhans & Aguilera, 2013)—sample localities: Cerro Negro Mb: PPP 2549, PPP 2554, PPP 2555, PPP 2556, PPP 2557, PPP 2563, PPP 3055, PPP 3057, PPP 3066, PPP 3093; above Cerro Negro Mb: PPP 2568, PPP 2570, PPP 2571, PPP 2572, 2653.

The Cumaná FM (Rivero, 1956; Léxico Estratigráfico de Venezuela, 1997) is of late Early Pleistocene age and crops out in Cerro Caigüire in Cumaná City. It consists mainly of shellfish beds and bryozoans with remains of corals, micritic, light-colored limestone, mudstones, and light-gray clays interbedded with light-gray to bluish-gray silts, with abundant fragments of echinoderms, bivalves and other mollusks, and fossiliferous calcarenite, calcareous and quartz sandstone, gray and fine-grained to very fine, olive siltstones. Previous results from croaker otoliths (Aguilera et al., 2016) suggest a shallow tropical paleoenvironment—sample locality: PPP 3038.

Trinidad (Fig. 8)

The Brasso FM (Renz, 1942) is of late Early to early Middle Miocene, late Burdigalian to late Langhian age (NN4–5, N7–11) and has been described from Central Trinidad. It consists of massive, gray to gray-brown claystones and sandy claystones. Planktonic and benthonic foraminifera indicate a paleo-depth of approximately 60 m (middle neritic) to 470 m (deep upper bathyal) (Wilson, 2003, 2005). Previous research of fossil fish otolith includes Nolf (1976) and Schwarzhans and Aguilera (2013, 2016)—sample localities: lower Brasso FM: KR 6666; upper Brasso FM: Cb. 1852, KR 7546, KR 7573, KR 9244 (Fig. 8).

The Tamana FM is of early Tortonian age (N14, NN7–8) and comprises massive, white to yellow, granular to

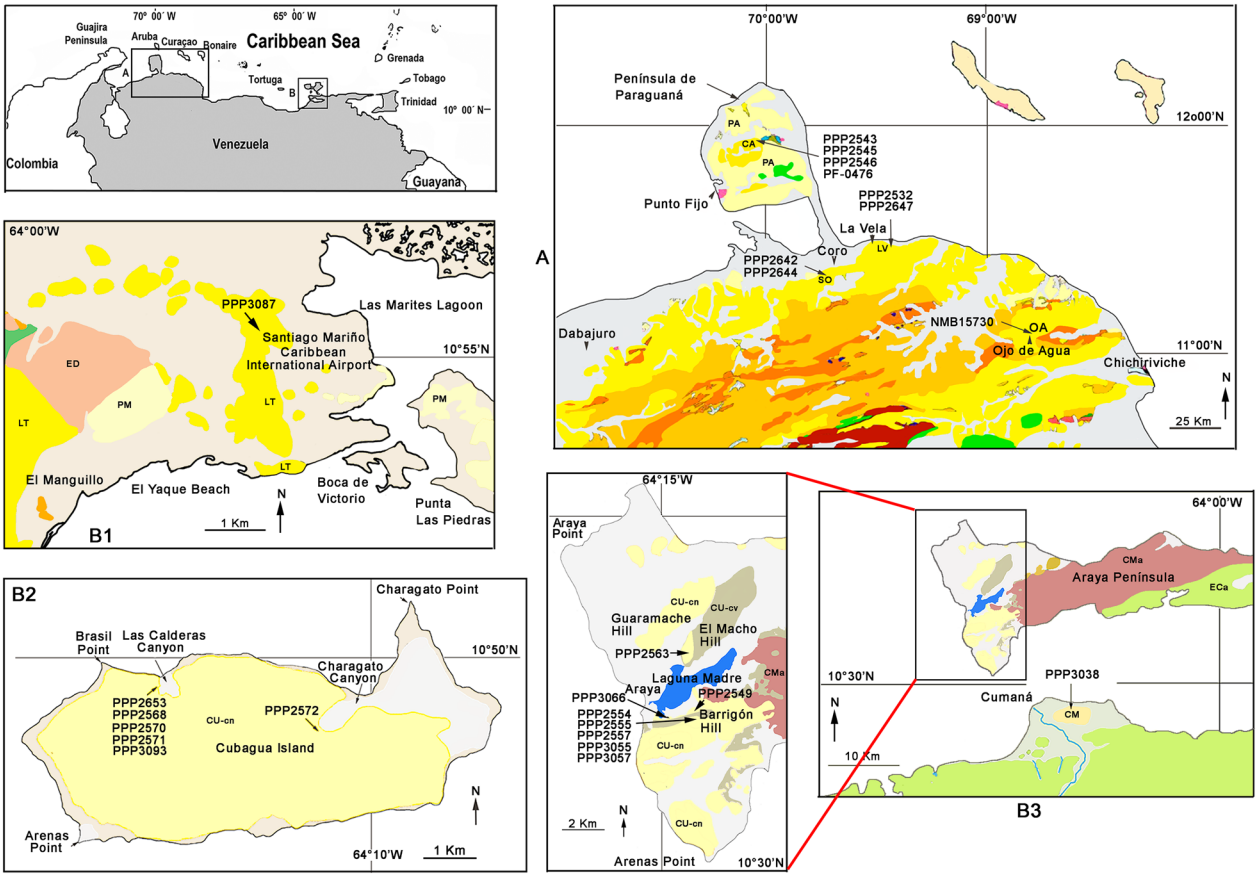


Fig. 7 Location plate of Venezuela, based on geological maps of Padron et al. (1993) and Albert-Villanueva et al. (2017). Falcón (**A**): PA, Paraguaná FM (Pliocene); CA, Cantaure FM (Lower Miocene, Burdigalian); LV, La Vela FM (Lower Pliocene, Zanclean); SC, Socorro FM (Middle Miocene, Serravallian); OA, Ojo de Agua FM (Middle Miocene) [LV, OA and SC not distinguished by color on map]. Margarita Island (**B1**): PM, El Manglillo FM (Pleistocene); LT, La Tejita Mb, Cubagua FM (Upper Miocene, Messinian); ED, El Dátil FM (Eocene). Cubagua Island (**B2**) and Araya Peninsula (**B3**): CM, Cumaná FM (Pleistocene, Calabrian); CU-cn, Cubagua FM, Cerro Negro Mb (Lower Pliocene, Zanclean); CU-cv, Cubagua FM, Cerro Verde Mb (Upper Miocene, Messinian); ECa, Eocene; CMa, metamorphic basement

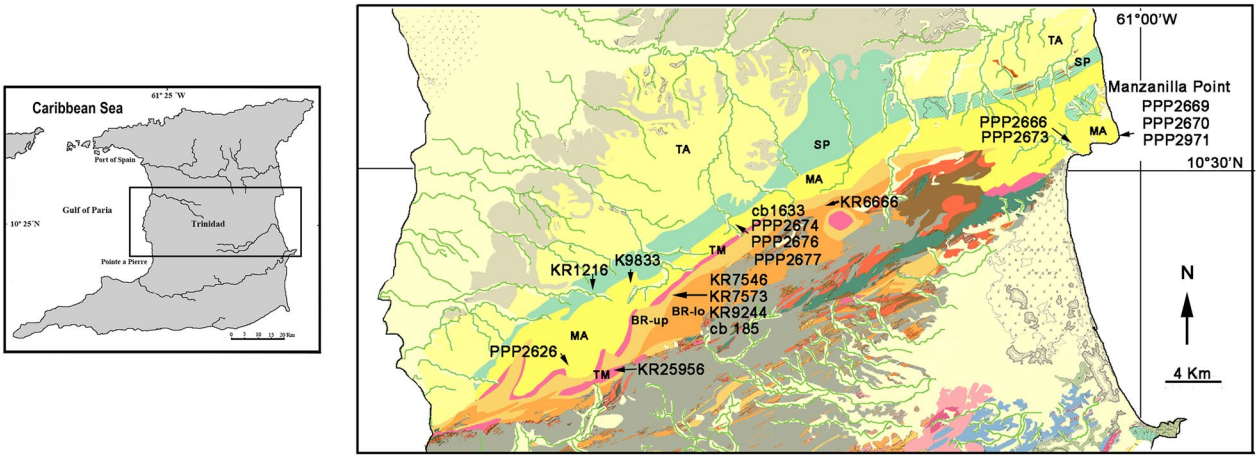


Fig. 8 Location plate of Trinidad, based on geological maps of Kugler (1959): TA, Talparo FM (Lower to Upper Pliocene); SP, Springvale FM (Lower Pliocene, Zanclean); MA, Manzanilla FM (Upper Miocene to Lower Pliocene, Tortonian to lower Zanclean); TM, Tamana FM (Upper Miocene, Tortonian); BR-up, upper Brasso FM (Middle Miocene, Langhian); BR-lo, lower Brasso FM (Lower Miocene, Burdigalian)

crystalline limestones with intercalated sands and clays. The fauna is dominated by benthic foraminifera and coral algae (Donovan, 1994)—sample locality: KR 25956.

The Manzanilla FM (Wall & Sawkins, 1860) ranges from Late Miocene to Early Pliocene in age and is located in the northern Trinidad Basin. It includes three members: the Telemaque, Montserrat, and San José Mbs. The San José Mb is the oldest, of late Tortonian age, comprising dark-gray to black, calcareous silts that have been bioturbated. A rich fauna of foraminifera and small mollusks indicates an open marine, inner sublittoral environment of deposition (Donovan, 1994). The Montserrat Mb overlies the San José Mb and is associated with a delta-front environment (Huggins, 2012). The Telemaque Mb is the youngest, primarily Early Pliocene in age, and is considered to be delta-plain related (Huggins, 2012). Previous research in fossil fish otolith includes Nolf (1976) and Schwarzhans and Aguilera (2013, 2016)—sample localities: San José Mb (Tortonian): Cb. 1633, PPP 2669, PPP 2670, PPP 2671, PPP 2674, PPP 2676; Montserrat Mb (Messinian): PPP 2666, PPP 2673, PPP 2677; Telemaque Mb (Zanclean): KR 9833.

The Springvale FM (Guppy, 1910) is of Early to Late Pliocene age and is composed of sandstones with intercalated mudstones (Kugler, 1956). The Springvale FM contains three members according to Donovan (1994), the oldest being the Gransaull Clay Mb, composed of silt and sand. The middle one is the Savaneta Glauconitic Sandstone Member and the youngest the Chickland Clay Mb. The goby otoliths described here were obtained from the Chickland Mb, which is shallow marine, coastal sands with oyster beds—sample locality: Chickland Clay Mb: KR 1216.

Brazil

The Pirabas FM (Maury, 1925) has been assigned controversially to Early to Middle Miocene ages (Gomes et al., 2023) and contains distinct and diverse facies (Aguilera et al., 2022, 2023). Otoliths have been described by Aguilera et al. (2014) and originated from an interval at the base of the sequence that apparently is not exposed any longer at the sea shore. We include here only a review of the gobiid otoliths and otherwise refer to Aguilera et al. (2014).

Material and methods

The studied material was collected during various expeditions from the outcrop localities shown on the geological maps. The outcrops were visited by field parties in Costa Rica, the Dominican Republic, the Canal Basin in Panama, Trinidad and Venezuela. Localities in the Bocas del Toro Archipelago were visited from sea going ships. Outcrops in the Darien province of Panama and in Ecuador mostly occur on high banks of small rivers and creeks. Here, sample localities were accessed from canoes. Some specimens were picked from the surfaces along the stratigraphic sequences. Generally, however, 15 kg of bulk sample of each sampling locality denoted by PPP numbers were collected and transferred to the laboratory of the Smithsonian Tropical Institute at Panama. There, the samples were processed and sieved with water using screens of 2 mm, 1 mm, and 0.5 mm mesh sizes. The picking of specimens was performed using a stereomicroscope. All specimens are deposited in the paleontological collection of NMB following the agreement of the PPP project coordination.

Otoliths were photographed using a Canon EOS mounted on the phototube of a Wild M400 photomacroscope. Photographs were taken at different focus levels remotely controlled from a computer to ensure clarity in the depth of field. The individual photographs from each focus level were merged using the Helicon Focus software of Helicon Soft (Charkiv, Ukraine). The continuously focused images were digitally processed with Adobe Photoshop to enhance contrast or balance or retouch small inconsistences, where necessary and without altering the otolith morphology in any manner. During the photographic process, the central portion of the inner and outer faces of the otoliths was carefully positioned to be level in order to avoid any distortion that would occur in strongly bent specimens. The same principle was applied for lateral views, in which the otoliths were oriented in an upright position along either the horizontal or the vertical axis for dorsal and posterior views, respectively. The most effective method of achieving the desired orientation was to fix the otoliths in plasticine during photographing. Light was used from two sources perpendicular to each other and perpendicular to the orientation of the sulcus. One light source was employed at a low angle of incidence to increase contrast; the other was applied at a steeper angle and lower intensity to slightly lighten the shadow effects of the intense and low-angle-oriented first light source.

All of the figured specimens illustrate otoliths from the right side of the fish; left otoliths are mirror imaged. Inner faces and often also dorsal and posterior views are routinely depicted and are considered self-explanatory.

In the systematics, the morphological terminology of the sagittal otoliths (otolith hereinafter) adheres to the work of Koken (1884) with revisions from Chaine and Duvergier (1936) and Schwarzhans (1978). The specific terminology of gobioid otoliths follows Schwarzhans (2014). The measurements used in the taxonomic descriptions were achieved using a camera lucida mounted on the microscope or from photographs obtained from the photomacroscope.

Abbreviations used: general abbreviations: FM = Formation, Mb = Member, MCO = Miocene Climate Optimum, MMCT = Middle Miocene Climate Transition, LOW = Late Oligocene Warming.

Fish and otolith terminology: SL = standard length in fishes, OL = otolith length, OH = otolith height, OT = otolith thickness, SuL = sulcus length.

Collections: NMB Naturhistorisches Museum Basel, Basel, Switzerland, where NMB denotes field localities and NMB P stands for the paleontological collection; KR refers to samples of Karl Rohr and Cb. of C.J. Campbell. PPP = Panama Paleontology Project of the Smithsonian Tropical Research Institute at Panama City, Republic of Panama.

Institutions: AMNH = American Museum of Natural History, New York, U.S.A.; BMNH = Natural History Museum (formerly British Museum of Natural History), London, Great Britain; CAS = California Academy of Science (including formerly SU = Stanford University), San Francisco, California, U.S.A.; FSBC = Florida Fish and Wildlife Conservation Commission (formerly Florida State Board of Conservation), St. Petersburg, Florida, U.S.A.; LACM = Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A.; MNHN = Muséum National d'Histoire Naturelle, Paris, France; SMF = Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; TCWC = Texas A&M University, Texas Cooperative Wildlife Collection, College Station, Texas, U.S.A.; USNM = National Museum of Natural History (formerly United States National Museum), Washington D.C., U.S.A.; ZMUC = Københavns Universitet Zoologisk Museum, Copenhagen, Denmark.

Gobioid otolith characterization

General aspects

Gobioid otoliths are easily recognized as such by their compact, nearly rectangular outline and the centrally or slightly forward positioned undivided sulcus with a single colliculum typically described in shape as resembling the sole of a shoe ("sole-shaped"). When attempting to identify isolated gobioid otoliths at genus or species level, however, one must deal with certain obstacles.

The first and probably the most intriguing obstacle is the difference in sizes. Gobioids include some of the smallest fishes known to date, with just over 8 mm of standard length (SL) for maturity, while the largest reach sizes of about 450 mm SL. In America today, *Paedovaricus imswe* is apparently mature at 8 mm SL and reaches a maximum of 13.5 mm SL (Tornabene et al., 2016). Conversely, certain species of *Akko* reach 90 mm SL (van Tassell & Baldwin, 2004), species of *Bollmannia* 100 mm SL (van Tassell et al., 2012), species of *Gobionellus* 185 mm SL (Froese & Pauly, 2023), and species of *Gobioides* 450 mm SL (Froese & Pauly, 2023). The largest species have an elongated trunk, while the head size of species of *Gobioides*, for example, is not much bigger than that of *Bollmannia*. The difficulty that arises from these differences in size is that otoliths of small species are difficult to distinguish from otoliths of small, juvenile specimens of large species (see, for example, discussion of *Rhinogobiops nicholsii* below). Nolf (1985) expressed the view that otoliths of small gobiid species therefore remain largely unrecognized in the record of isolated fossil otoliths. Recent studies of extant gobiid otoliths by Gut et al. (2020) and Reichenbacher et al. (2023), however, have revealed that in many instances otoliths of small gobiid

species can indeed be distinguished from otoliths of juveniles of large species with the help of a detailed morphological analysis. Nevertheless, we have left many small otoliths below 1 mm in length unidentified here because of prevailing uncertainties.

Another complexity in the identification of fossil goby otoliths is the fact that the level of possible morphological diversity in such a large group with a highly specific overall otolith appearance is limited, depending on often rather subtle features, and therefore homoplasies occur commonly. It is not possible in all instances to distinguish otoliths of closely related species. Nominal fossil otolith-based species could therefore in certain cases represent more than a single "biological" species. Moreover, the allocation to genera, both extant and fossil, suffers from this complexity. Because of the subtlety of many features that must be analyzed, good preservation is required to be certain that pertinent traits are genuine (see discussion of "subcaudal iugum" below). Finally, a good understanding of inter- and intraspecific variability and ontogenetic morphological changes is required to facilitate a reasonable species identification of fossil otoliths in general and in the case of gobiids in particular. These complexities have contributed to a relatively large percentage of goby otoliths from tropical America not being identifiable to species level (18.5%). In fact, many small or slightly eroded fossil American goby otoliths are only allocated to a particular species because they have been found alongside well-preserved specimens of the species in question, thus allowing the identification of the less preferential preserved ones. Otherwise, and with a more rigid identification practice, the number of otoliths not identified to the species level would be much higher. We have not followed such practice primarily to facilitate more realistic statistical means, which would be required for environmental, biogeographic, or stratigraphic evaluations.

Because of these complexities one meets when attempting to identify fossil gobioid otoliths, Nolf (2013) considered gobiid otolith paleontology as being in a chaotic state (p.118) and suggested abstaining from descriptions of new fossil otolith-based gobiid species, at least in the genus *Gobius*, until extant gobiid otoliths are better known (than they were in 2013). We agree with Nolf's statement for the time in which it was made; since then, however, several studies of extant goby otoliths, or studies including such, have greatly increased our knowledge and led to a better morphological character analysis (e.g., Gut et al., 2020; Lombarte et al., 2014; Reichenbacher et al., 2023; Schwarzhans et al., 2020a, 2020b; Zarei et al., 2023). In situ finds in the European Neogene have provided important cases for the calibration of isolated goby otoliths (e.g., Gierl & Reichenbacher, 2015; Reichenbacher & Bannikov, 2021, 2022; Schwarzhans et al., 2017a, 2017b). No fossil otoliths in situ are yet known from the Americas.

Morphological analysis and character definition for American goby otoliths

The discussion below of the variations and value of morphological traits in goby otoliths follows a sequence of observations recommended to be undertaken when attempting to identify fossil goby otoliths from the Neogene of tropical America (Additional file 1: Table S1). The terminology of goby otoliths and the morphometric measurements used here follow those established by Schwarzhans (2014) and are depicted in Fig. 9.

Otolith size (is important): American goby otoliths can generally be classified by size into four groups: those larger than 3 mm OL, between 2 and 3 mm OL, between 1 and 2 mm OL, and smaller than 1 mm OL. Otoliths of relatively few species reach sizes of more than 2 mm OL: in the genera (in the sequence of description) *Bollmannia*, *Akko*, *Parrella*, *†Magnogobius*, *Rhinogobiops*, *Bathygobius*, *Ctenogobius*, *Gobioides*, *Gobionellus*, *Gillichthys*, and *Quietula*. Otoliths larger than 3 mm OL are only found in *Bollmannia*, *†Magnogobius*, *Gobioides*, *Gobionellus*, and *Gillichthys*. Otoliths of species of the genera reaching sizes between 1 and 2 mm OL are numerous, e.g., *Antilligobius*, *Palatogobius*, *Microgobius*,

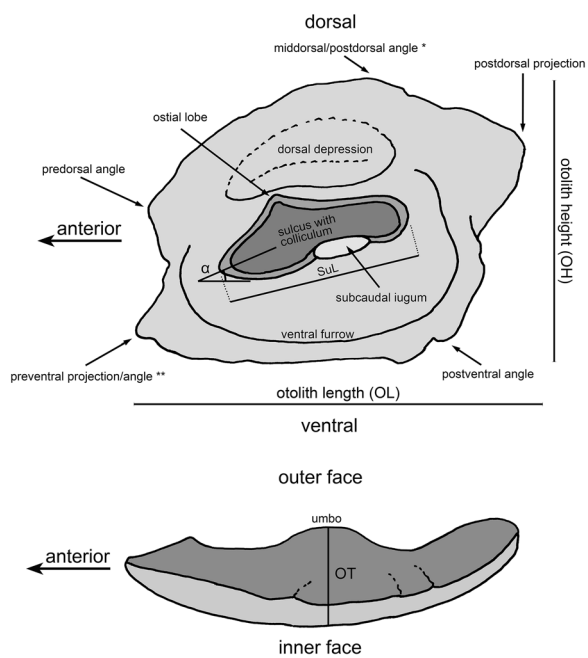


Fig. 9 Morphological terminology of gobioid otoliths after Schwarzhans (2014). Middorsal/postdorsal* depending on position along dorsal rim; preventral projection/angle** depending on strength of feature; α sulcus inclination angle

and genera of the *Barbulifer* and *Nes* subgroups. They usually offer sufficient diverse features to distinguish them from otoliths of potential juveniles of the larger category. The most problematic are otoliths smaller than 1.2 mm to 1 mm OL, because here the distinction between otoliths of small species that do not reach larger sizes and those of juveniles from larger species is particularly difficult. Reliable characteristics for differentiation are often few and subtle, and it is no surprise that in this category we classified a large proportion of otoliths as indeterminable. The otoliths of species of the following genera do not reach sizes larger than 1 mm OL or at most 1.2 mm OL: *Gobiosoma* and *Elacatinus* subgroups, *Lythrypnus*, *Clevelandia*, *Eucyclogobius*, *Lepidogobius*, *Typhlogobius*, and supposedly most extant genera from tropical America of which otoliths remain unknown and which are generally very small fishes.

Subcaudal iugum (Fig. 10): Presence or absence of the subcaudal iugum is a highly diagnostic feature, but unfortunately it is also easily affected by erosion. Hence, the determination of absence of the subcaudal iugum should only be made on very well-preserved otoliths. Rarely is the status of the subcaudal iugum of such a nature that its presence or absence varies within a taxonomic entity. In the case of the American goby otoliths, a broad and usually distinctive and long subcaudal iugum is present in *Bollmannia*, *†Brassoichthys*, *Akko*, *†Cubaguanichthys*, *Parrella*, *†Proparrella*, *Antilligobius*, *Palatogobius*, *†Magnogobius*, and *Microgobius*, i.e., all genera of the *Microgobius* group of the Gobiosomatini. The subcaudal iugum is broad and distinct in *Bollmannia* and relatively slender and thin but still distinct in *†Magnogobius*, with all other mentioned genera somewhere between these two extreme morphotypes. In some species of the genus *Microgobius*, the subcaudal iugum extends around the posterior rim of the cauda into which it ingresses, thereby reducing the size of the colliculum in that area. This is a clearly derived feature observed primarily in otoliths of juvenile *Microgobius* specimens but is also maintained in adult specimens of certain species. Generally, the subcaudal iugum is developed in taxa of the *Microgobius* group from a very small size (about 0.6 mm to 1 mm OL) onward.

A subcaudal iugum is generally absent in otoliths of the species and genera of the *Gobiosoma* group of the Gobiosomatini, although rarely a small indication can be visible, indicating that the absence of the subcaudal iugum is probably a derived character in the *Gobiosoma* group. Thus, presence or absence of the subcaudal iugum (and size) is the most reliable trait to distinguish the otoliths of the two main groups of American gobies in the tribe Gobiosomatini. Other taxonomic units of American gobies lacking a subcaudal iugum are *Lythrypnus*, *Bathygobius*, *Ctenogobius* except for the *Ctenogobius sagittula* plexus, *Gobioides*, most *Gobionellus* species, *Gnatholepis*, and all genera of the *Gymnogobius* group. In *Gobionellus* only *G. microdon* has a rather large and long subcaudal iugum below the entire caudal section. Most species of the *Coryphopterus* group have no subcaudal iugum, but some show a faint, small and narrow subcaudal iugum just below the anterior part of the cauda where the ventral sulcus margin exhibits a slight concavity. A similar kind of subcaudal iugum is present in *Ctenogobius sagittula*.

Sulcus shape, size, orientation and depth (Fig. 10): Morphological details of the sulcus are generally considered to provide the most important and diverse features for otolith taxonomy, and this is also the case for American gobies. As already pointed out, goby otoliths are characterized by the sole-shaped, closed sulcus positioned on the center or slightly forward on the inner face. Morphological differences, however, are often subtle in nature and may show some variation. The sulcus bears a single colliculum, which is usually well defined and closely follows the outline of the sulcus. In descriptions, we generally refer to the sulcus and only specifically mention the colliculum when significant differences exist between the outline of the sulcus and the colliculum. For measurements we have used the sulcus length (SuL) for consistency even though in some instances a colliculum length could be measured more exactly.

Gobiosomatini generally have otoliths with a sulcus that shows a low-to-moderate ostial lobe and a straight cauda without ventral concavity. *Bollmannia* and *Microgobius* are typical representatives of this pattern. In *Bollmannia*, the sulcus inclination angle is mostly 10–15°, rarely up to 20°, and in *Microgobius* mostly 15–20°, rarely up to 25°. The ostial lobe is more strongly developed in *Microgobius* than in *Bollmannia*. The ostial lobe is low, as is the sulcus inclination angle (4–12°), in *†Brassoichthys*, *Antilligobius*, and *Palatogobius*. *Palatogobius* is one of the few gobiid genera in which the sulcus is sometimes nearly horizontal. The sulcus is relatively short (OL:SuL = 1.8 or more often > 2.0) in species of *Akko*, *Antilligobius*, and *Palatogobius* (except 1.6 in the fossil *Akko lobatus* n. sp.). Otoliths of *†Magnogobius* have a much expanded, rounded ostial lobe and a wide sulcus. The sulci of *†Magnogobius* and certain species of *Microgobius* are also among the longest to be found in American goby otoliths with an OL:SuL ratio < 1.5. Otoliths of *†Proparrella* and some species of *Microgobius* are remarkable for a narrow cauda.

In the *Gobiosoma* group, the ostial lobe is usually very low (*Aruma*, *Barbulifer*, *Enypnias*) or completely reduced, resulting in a nearly oval sulcus outline (*Elacatinus*, *Ginsburgellus*, *Risor*, *Tigrigobius*). The other genera

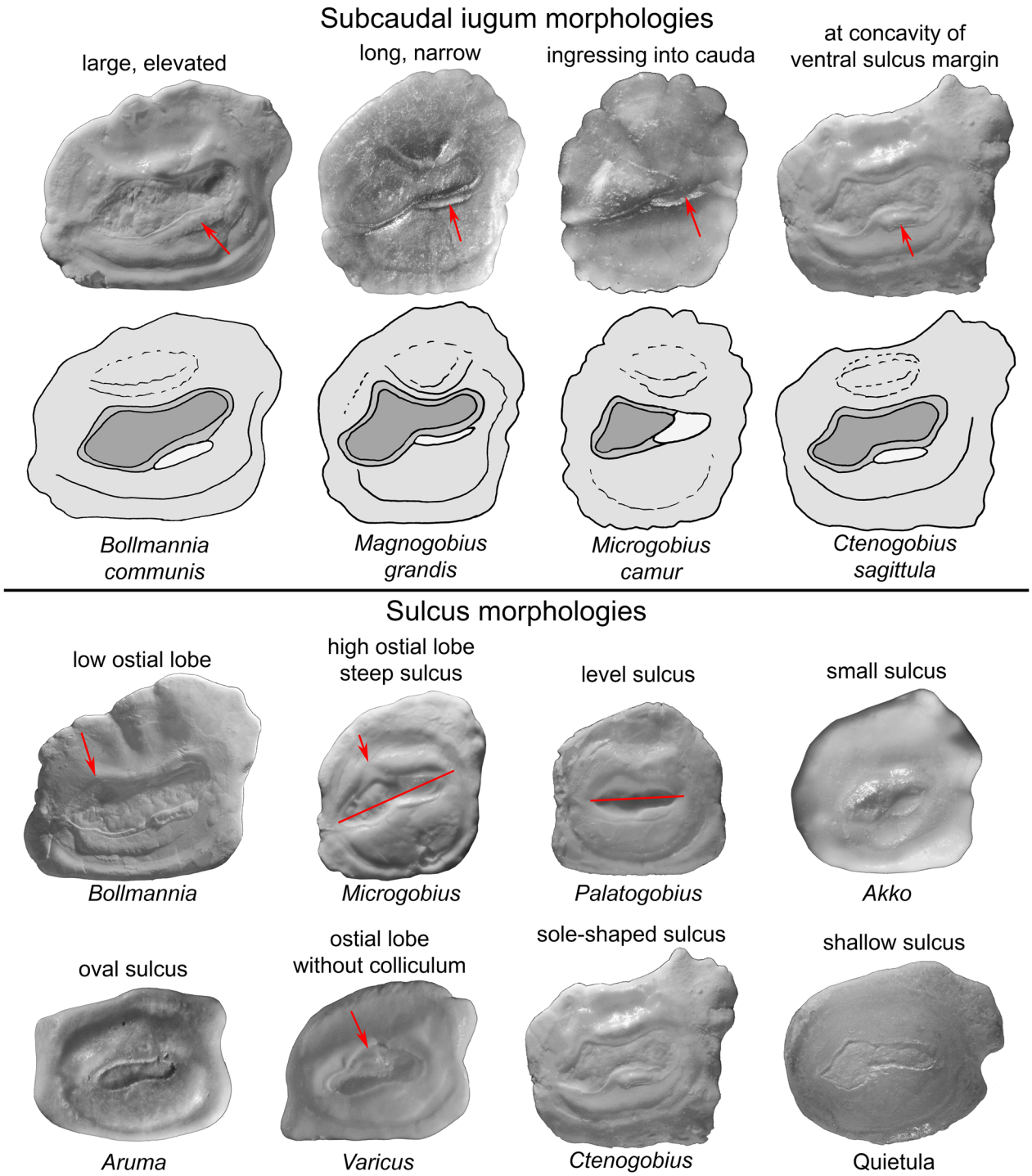


Fig. 10 Examples of variations in the expression of the subcaudal iugum (upper row) and sulcus morphology (lower row) in otoliths of American gobies. Red arrows point at denoted traits; red lines indicate sulcus axis

(of the *Nes* and *Gobiosoma* subgroups) are somewhat intermediate in the expression of the ostial lobe. Some species of *Varicus* are remarkable for an elongated ostial lobe that is not or not entirely filled with the colliculum. In most Gobiosomatini, the sulcus is moderately deep, but in the genera *Chriolepis*, *Eleotrica*, and *Gobulus*, it is distinctly deeper.

In *Lythrypnus* and *Priolepis*, the only two genera of the *Priolepis* lineage now occurring in tropical America, the sulcus is almost oval in shape without an ostial lobe and very slightly inclined (5–10°). The sulcus is also relatively shallow and short (OL:SuL > 2.0).

The otoliths of the genera in the *Lophogobius* lineage and *Bathygobius* of the *Glossogobius* lineage show a sulcus shape that is often regarded as typical gobiid, i.e., sole-shaped, with a distinct ostial lobe. The sulcus inclination angle (10–20°), sulcus size (OL:SuL = 1.5–2), and the moderate depth of the sulcus are all inconspicuous. Another, more diagnostically valid feature is the slight concavity of the ventral sulcus margin along the anterior part of the cauda, which adds to the semblance of a sole-shape.

The two marine oxudercine lineages represented in tropical America show relatively few distinctive sulcus features. The ostial lobe is mostly low, but in some genera (*Ctenogobius*, *Gobionellus*, *Gnatholepis*, *Evermannia*, *Gillichthys*, and *Quietula*) expanded ostial lobes are also observed. The sulcus inclination angle is generally low, 5–15° and exclusively less than 10° in *Gobionellus*, *Clevelandia*, and *Typhlogobius*. American genera of the *Acanthogobius* lineage are remarkable for a generally small sulcus (OL:SuL > 1.8, usually > 2.0). Some of its genera show a remarkably shallow sulcus (*Clevelandia*, *Ilypnus*, *Quietula*, and *Typhlogobius*).

Otolith proportions (ratio OL:OH) (Fig. 11): Gobiid otoliths are mostly rather compressed in outline. The otoliths of the genera occurring in tropical America can be grouped into three categories according to the ratio OL:OH: otoliths that are higher than long, i.e., have a ratio OL:OH < 1.0; those with a roughly rectangular outline (OL:OH between 1.0 and 1.25); and those with a more elongate shape (OL:OH > 1.25). Gierl et al. (2022) used overall otolith shape as an important trait for their integration of otolith morphology in a total-evidence approach for the phylogenetic analysis of the Gobioidei. Among other terms, they used "high-rectangular", "quadratic", and "long-rectangular" as descriptors that, although circumscriptive without giving ratios, probably correspond in part to the OL:OH categories proposed here. Schwarzhans et al. (2020a, 2020b), introduced a second otolith length measurement, OL2, that is taken along the central horizontal otolith axis. OL2 was introduced to accommodate the strong preventral and postdorsal projections seen in many taxa of the *Gobius* lineage, particularly those that have the tendency to distort the traditional OL measurement. These morphological tendencies, however, do not play a major role in the case of American goby otoliths (see below), and we have therefore refrained from using OL2 measurements here.

Many genera and even species straddle the line between an OL:OH ratio < 1.0 and > 1.0 or an OL:OH ratio < 1.25 and > 1.25, but there are a sufficient number of genera in which this relationship has considerable value for diagnosis and distinction. Genera with otoliths distinctly shorter than high (OL:OH < 1.0) are *Antilligobius*, *†Magnogobius*, *Microgobius*, *Nes*, *Garmannia*, *Risor*, *Tigrigobius*, and *Lepidogobius* (and probably *Lethops*, judging from Fitch, 1968). *Risor*, *Tigrigobius*, and *Lepidogobius* have the most compressed of these, often with OL:OH ratios of 0.9 or even 0.8. Particularly slender otoliths with an OL:OH ratio > 1.25 are rare in America: *†Cubaguanichthys*, *Aruma*, *Barbulifer*, *Psilotris*, *Eleotrica*, and *Gobulus*. The species-rich genera *Bollmannia*, *Chriolepis*, and *Bathygobius* contain otoliths with OL:OH ratios mostly exceeding 1.1 and in some species 1.25.

Specific features of the otolith rims (Fig. 11): Typical features along the rims of goby otoliths are a preventral projection, a postdorsal projection, which in combination can result in a parallelogram-like otolith outline, flatness or curvature of the ventral rim, other detailed features of the dorsal rim, and incision of the posterior and anterior rims near the respective termination levels of the sulcus. In the case of the American goby otoliths, the preventral and postdorsal are generally rather weak, and incisions of the anterior and posterior rims are likewise weak or absent; hence, the latter are not reflected here, and no OL2 measurements are taken (see above).

As stated above, the postdorsal projection is generally weak or absent in American goby otoliths. They are strongest in *Gobulus*, *Eleotrica*, some species of *Varicus*, and the genera of the *Lophogobius* lineage. A rather unusual feature, however, is a cut or recessed postdorsal region, which is a diagnostic feature particularly in *Bathygobius* but is also seen less prominently in genera of the *Priolepis* lineage, and less prominent still in *Gymneleotris*, *Garmannia*, and *Lepidogobius*.

Like the postdorsal projection, the preventral projection is also usually not strongly developed in American goby otoliths. The preventral projection is strongest, in *Cubaguanichthys*, *Psilotris*, *Lythrypnus*, *Priolepis*, *Bathygobius*, the American genera of the *Lophogobius* lineage, and in some species of *Bollmannia* and *Gobiosoma*. In *Cubaguanichthys*, *Bathygobius*, *Lythrypnus*, and *Priolepis*, a relatively strong preventral projection is combined with an absent or negative postdorsal projection, which results in a highly characteristic otolith shape. Rounded or negative preventral angles are commonly observed, for instance in *Akko*, *Parrella*, *†Magnogobius*, *Microgobius*, *Gobulus*, *Risor*, *Gobioides*, and several American genera of the *Acanthogobius* lineage.

The ventral rim of goby otoliths is nearly flat and horizontal in the vast majority of cases. Curved, even mildly

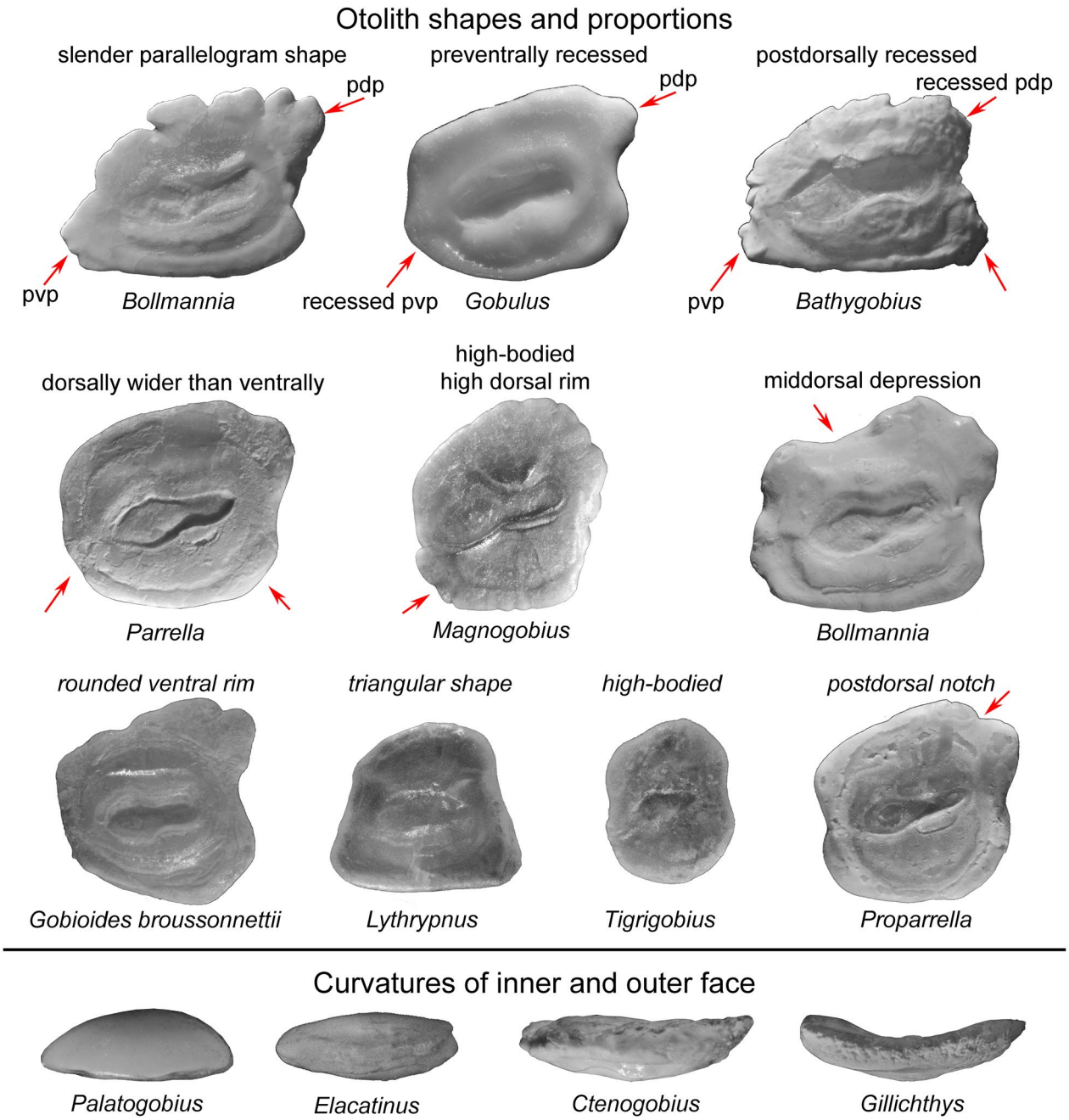


Fig. 11 Examples of variations in otolith shape (upper row) and curvatures depicted in dorsal views (lower row) in otoliths of American gobies. Red arrows point at specific traits; pdp postdorsal projection; pvp, preventral projection

curved, ventral rims are rare and therefore may occasionally be of diagnostic value. This feature is particularly well developed in certain genera of the *Gobiosoma* group such as *Psilotris*, *Gobulus*, *Gymneleotris*, *Ginsburgellus*, *Risor*, and *Tigrigobius*. With the exception of *Gobulus*, this feature seems to occur mainly in relatively small otoliths and could therefore represent a connected feature. The strongest curvature of the ventral rim is observed in *Gobioides broussonnetii*.

The dorsal rim possesses the largest degree of morphological diversity of all marginal features, but it is mostly useful at the species level and only rarely for the differentiation of genera. The height of the predorsal angle, the position and strength of the middorsal section, and

peculiarities of the postdorsal rim are features that can be used to distinguish morphotypes. *†Proparrella* is characterized by a conspicuous postdorsal notch between the middorsal angle and the weak postdorsal projection. This feature is specific to *†Proparella*, and only a few genera in the *Stenogobius* lineage show a similar, but always less prominent, development. A middorsal depression is observed in some species of the genera *Bollmannia* and *Ctenogobius*.

Dorsal depression and ventral furrow (Fig. 12): The dorsal depression and ventral furrow are usually features that do not show much morphological variation, but this is not the case here. The ventral furrow in goby otoliths often follows more or less closely the ventral rim of the otolith and turns up anteriorly along the anterior rim of the otolith and posteriorly along the posterior rim of the otolith. The upturned anterior and posterior portions may fade upward from where they reach the level of the anterior and posterior tips of the sulcus or continue further upward to meet the anterior and posterior terminations of the dorsal depression. In most goby otoliths, the ventral furrow is quite distinct but usually not widened. In the gobiid otoliths studied from tropical America, however, two additional and presumably apomorphic character states occur. One feature is a half-moon-shaped ventral furrow on the ventral field that runs rather distant from the ventral rim of the otolith and not parallel to it. This character state is typical for the otoliths of *Akko*, *Elacatinus*, *Ginsburgellus*, *Risor*, *Tigrigobius*, *Lythrypnus*, *Priolepis*, *Gobioides*, *Gillichthys*, and *Typhlogobius*. Some genera have very wide ventral furrows (*Gillichthys*) and others narrow ones that together with the connected narrow dorsal depression resembles a furrow all around the otoliths (*Quietula*). Otoliths of the *Priolepis* lineage and some genera in the Gobiosomatini (e.g., *Aruma, Chriolepis, Gobulus*) usually show a bulged portion of the inner face between the ventral furrow and the ventral margin of the sulcus. An unusual status of the ventral furrow is observed in species of *Ctenogobius, Gobionellus*, and *Gnatholepis*. In otoliths of fully mature specimens of these three genera the ventral furrow does not curve upward anteriorly and posteriorly as is usual in gobiid otoliths, but opens to the anterior-ventral and posterior-ventral rims, respectively. The state of the connection of the ventral furrow with the dorsal depression around varies from widely separated (e.g., *Bollmannia, Bathygobius, Gobionellus, Gnatholpis*), sometimes anteriorly terminating at the ventral margin of the ostium (*Magnogobius*) to well and continuously connected (e.g., *Aruma, Priolepis* lineage, *Gillichthys* clade).

The dorsal depression is often poorly delimitated in gobiid otoliths, particularly its dorsal rim. There are taxa known from other regions in which the dorsal depression opens to the dorsal rim of the otolith (Carolin et al., 2022; Schwarzhans et al., 2022), but we have not seen such morphologies in tropical America. The most aberrant form in tropical America is a cup-shaped dorsal depression with relatively sharp lower margin (crista superior) that closely approaches the sulcus, while the dorsal depression is usually widely separated from the dorsal margin of the sulcus. This cup-shaped dorsal depression is observed in *†Magnogobius* and in *Ctenogobius sagittula*. There are also taxa in the American *Acanthogobius* lineage with a rather smooth inner face with a shallow sulcus and a very shallow, almost absent dorsal depression. This character state is observed in otoliths of the genera *Clevelandia*, *Evermannia*, and *Quietula*. Both character states, the cup-shaped dorsal depression and the shallowing, are considered apomorphic features.

Curvature of inner and outer faces (Fig. 11): Otoliths are three-dimensional objects even though the details of the inner face offer most of the diagnostic features. The outer face, in contrast, offers few features other than sometimes radial furrows on its dorsal part or an umbo somewhat ventral of the otolith center. These features can in most cases be adequately shown in lateral views, and figures depicting the outer face are therefore rarely included here. Lateral views, which for gobioid otoliths are preferable to dorsal and posterior views in order to depict curvatures of the postdorsal projection (if present), are used to show the curvature of the inner and outer faces and their relation. We classify four different combinations: a flat inner and convex (often strongly convex) outer face, biconvex inner and outer faces, a convex inner and flat outer face, and a convex inner and concave outer face. The least common of these combinations is the convex inner and concave outer face, which is observed in large specimens of the genera *Bathygobius*, *Evorthodus*, *Gobioides*, *Gobionellus*, *Gillichthys*, and *Quietula*. Smaller specimens of these genera often have a flat outer face. The other extreme combination, that of a flat inner and convex outer face, is a common feature in Gobiosomatini and the *Priolepis* lineage and also occurs in some genera of the *Acanthogobius* lineage (*Eucyclogobius*, *Lepidogobius*, *Typhlogobius*).

Characterization of otolith groups of American gobiids

The purpose of the morphological analysis and description of valuable diagnostic features of gobiid otoliths (see above) is to provide guidance for the recognition of systematic groups or genera of American gobiids by means of otoliths. The pertinent features in the systematic context are listed in Additional file 1: Table S1, visualized in Figs. 13 and 14, and summarized in brief below.

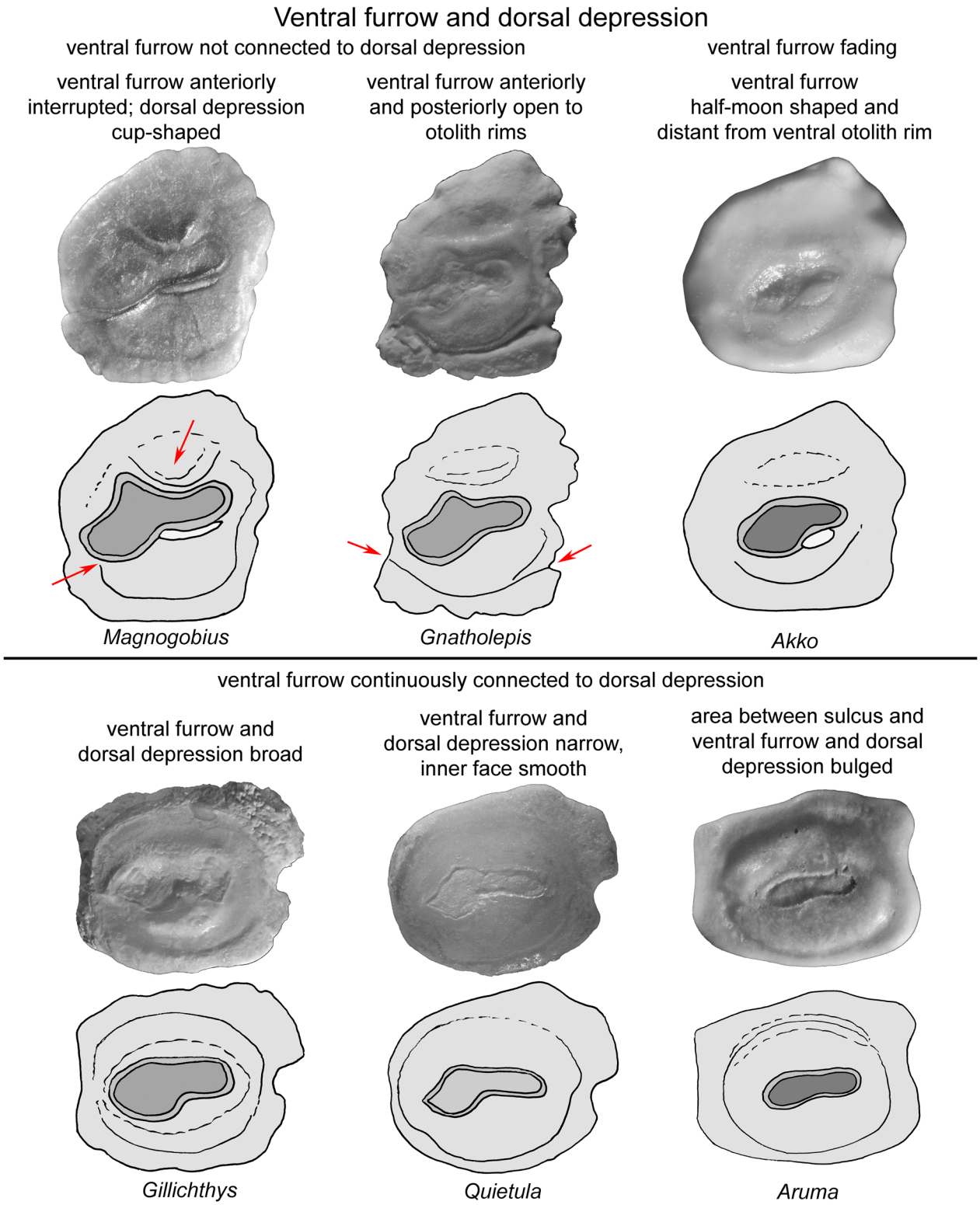


Fig. 12 Examples of variations in the expression of the ventral furrow and the dorsal depression in otoliths of American gobies. Upper row depicts patterns with ventral furrow not continuously connected to dorsal depression; lower row depicts patterns with ventral furrow continuously connected with dorsal depression. Red arrows point at specific traits

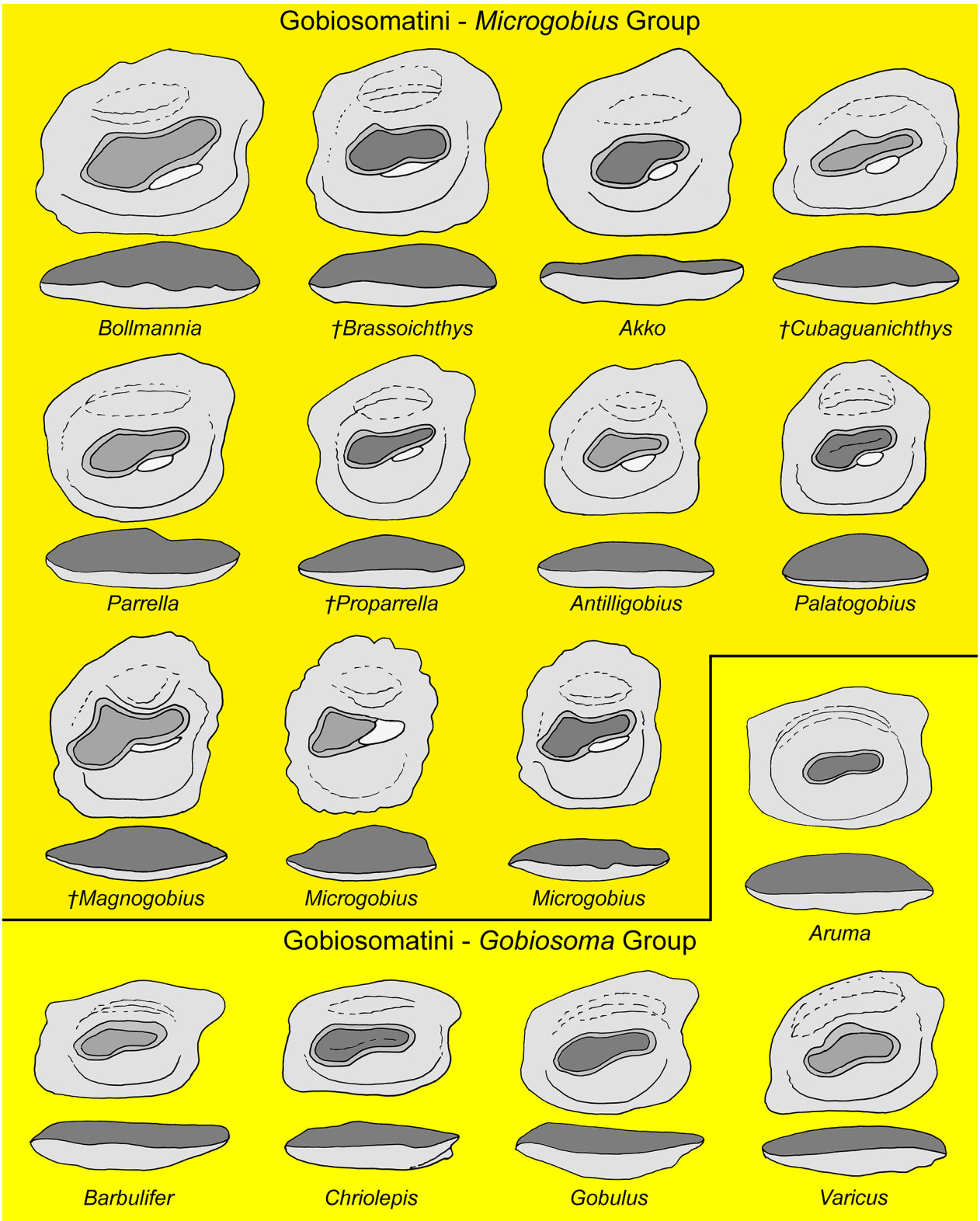


Fig. 13 Schematic drawings of representative otoliths of the Gobiosomatini (1) for a quick-look identification. Background colors indicate systematic position: dark yellow *Microgobius* Group; light yellow *Gobiosoma* Group. Note: different species in each genus may depart from the pattern shown

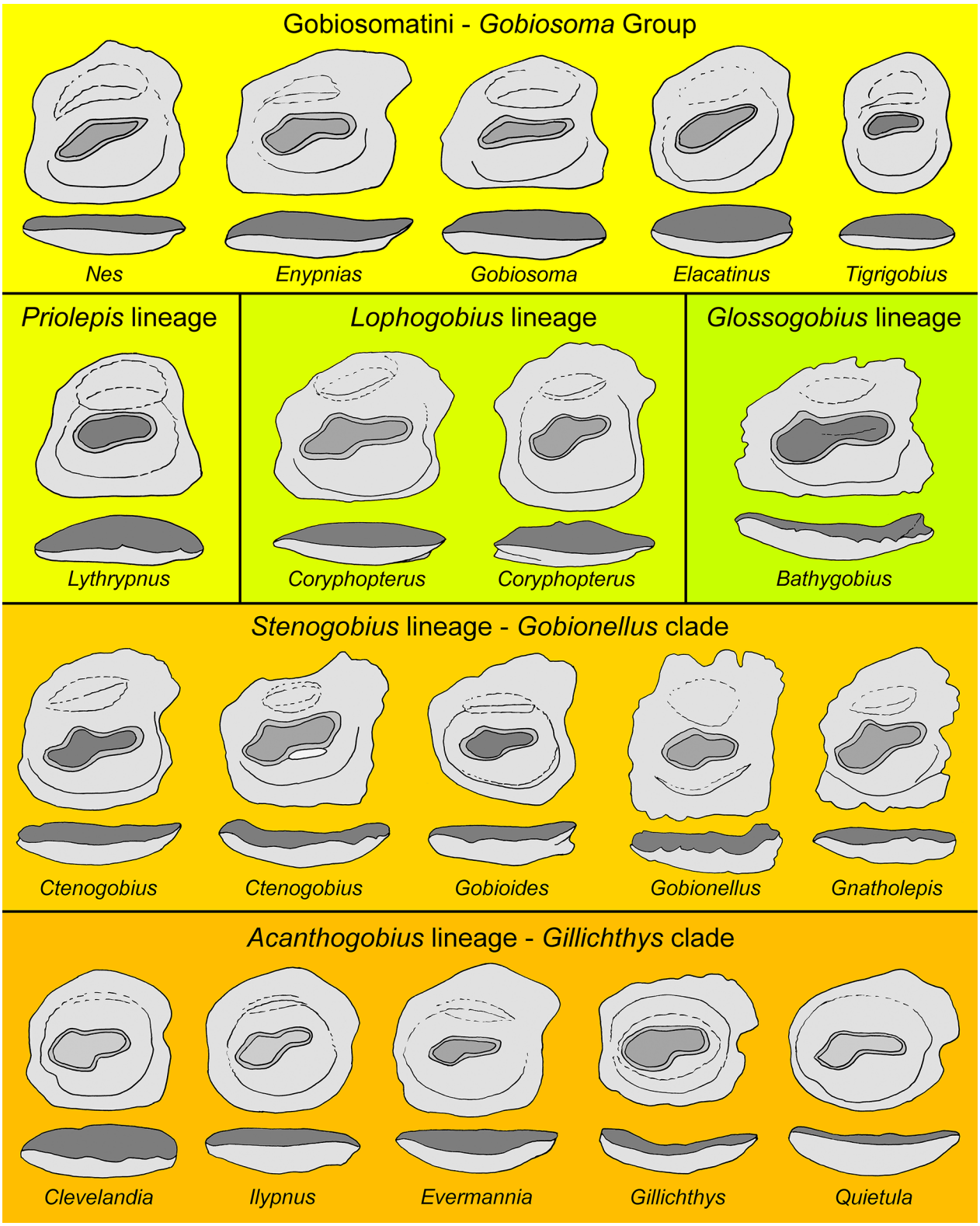


Fig. 14 Schematic drawings of representative otoliths of the Gobiosomatini (2), other American Gobiinae and Oxudercinae clades for a quick-look identification. Background colors indicate systematic position: light yellow, *Gobiosoma* Group; green-yellow, *Priolepis* lineage; light green, *Lophogobius* lineage; dark green, *Glossogobius* lineage; light orange, *Stenogobius* lineage; dark orange, *Acanthogobius* lineage. Note: different species in each genus may depart from the pattern shown

The otoliths of the Gobiosomatini are by far the most common in the fossil gobiid record in tropical America. The otoliths of the *Microgobius* group are easily recognized by their large and often wide subcaudal iugum. Outside of the *Microgobius* group, only *Gobionellus microdon* was found in the region bearing a comparable sized subcaudal iugum. Other typical characteristics of otoliths of the *Microgobius* group are a straight cauda, a low-to-moderate ostial lobe (except *†Magnogobius* and *Microgobius*), and a distinctly less curved (flat) inner than outer face (convex), except *Akko* and *Parrella*. Otoliths of the *Bollmannia* and *Akko* subgroups are distinctly longer than high (OL:OH > 1.1). Those of the *Bollmannia* subgroup have a nearly flat inner face and a distinctly convex outer face, while in genera of the *Akko* subgroup, the outer face is either flat or only as convex as the distinctly bent inner face (except *†Proparrella*). Otoliths of the genus *Akko* differ from other members in this group in the short sulcus, the rounded preventral tip, and the half-moon-shaped ventral furrow. Otoliths of the *Antilligobius* and *Microgobius* subgroups are distinctly more compressed than those of the *Bollmannia* and *Akko* subgroups, i.e., OL:OH < 1.1, mostly < 1.0. Otoliths of the *Antilligobius* subgroup are further characterized by a low inclination angle of the sulcus. Otoliths of the *Microgobius* subgroup show a number of highly apomorphic features such as the expanded ostial lobe, the cup-shaped dorsal depression (*†Magnogobius*), or the expanded subcaudal iugum occupying space in the posterior part of the cauda (some species of *Microgobius*).

Otoliths of the other group of the Gobiosomatini, the *Gobiosoma* group, are generally smaller than those of the *Microgobius* group, which is a reflection of the smaller size of the fishes, and lack a subcaudal iugum. The sulcus is often small and nearly oval in shape, with only a weak or no ostial lobe. All these characteristics are interpreted as representing a reduced morphological state that in combination with their small size makes identification of members of this group often difficult or ambiguous. Otoliths of the genera *Barbulifer*, *Enypnias*, and *Varicus* have a distinct postdorsal projection and the latter two also a preventral projection. These are features found in many unrelated clades within gobioids and thus additionally complicate the recognition of otoliths of these genera. The *Gobiosoma* group contains many genera that have been aligned in various subgroups or informal clades by authors (e.g., Rüber et al., 2003; Tornabene et al., 2016, 2022). The various published groupings and content and the alignment adopted here are extensively discussed in the section following the title "*Gobiosoma* Group sensu Tornabene et al., 2016 " within the "Systematic paleontology".

Otoliths of the *Priolepis* lineage share the reduced sulcus morphology with those of the *Gobiosoma* group. They are further characterized by a negative postdorsal region and the portion of the inner face between the ventral furrow and the ventral margin of the sulcus being elevated.

The otoliths of the *Lophogobius* lineage best reflect the typical goby pattern of all gobiids living in the seas around America with a sole-shaped sulcus and distinct preventral and postdorsal projections. They are distinguished from other gobiid otoliths in tropical America by the inner face being more strongly convex than the outer face and the absence of a subcaudal iugum (except a small subcaudal iugum in the concave section of the anterior part of the cauda in a few *Coryphopterus* species). With very few exceptions, the ratio OL:OH is distinctly larger than 1.0.

The otoliths of *Bathygobius* represent the only genus of the *Glossogobius* lineage present in America. Their otoliths are similar in many respects to those of the *Lophogobius* lineage, but can be relatively easily distinguished by the negative postdorsal angle. Moreover, the sulcus is relatively large, wide, and deep, with the ratio OL:SuL mostly < 1.5, rarely up to 1.7, and typically a broad concavity at the junction of ostium and cauda without a subcaudal iugum.

The Oxudercinae are represented by two different clades in the seas of America: the *Stenogobius* lineage and the *Acanthogobius* lineage. The otoliths of the *Stenogobius* lineage are high-bodied, usually higher than long (OL:OH < 1.0) even though they also show a (small) postdorsal projection. They are often relatively thin, with a convex inner and a concave outer face. Otoliths of adult specimens of some of the genera of the *Stenogobius* lineage show an unusual development of the ventral furrow, which does not curve upward anteriorly and posteriorly but instead opens to the anterior-ventral and posterior-ventral rims of the otolith.

The otoliths of the *Acanthogobius* lineage found in America are today restricted to the central Eastern Pacific but in the past apparently also occurred in the Atlantic. These otoliths lack a subcaudal iugum and often have relatively small sulci. They show a diverse otolith morphology but a number of derived, presumably apomorphic characteristics that facilitates a relatively easy recognition of some of the genera. The most easily recognizable pattern is the combination of a shallow, often small sulcus and a shallow dorsal depression, best seen in *Clevelandia*, *Evermannia*, *Ilypnus*, and *Quietula*. *Gillichthys* and *Typhlogobius* are characterized by a half-moon-shaped ventral furrow. Otoliths of *Gillichthys* and *Quietula* have a convex inner and concave outer face.

Systematic paleontology

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii sensu Goodrich, 1930

Division Teleostei Müller, 1846

Order Gobiiformes Günther, 1880 (sensu Thacker, 2009**)**

Suborder Gobioidei Jordan & Evermann, 1896

The systematics of the Gobioidei follows Agorreta et al. (2013). The complete list of identified fossil gobioid otoliths of this study is summarized in Additional file 2: Table S2.

Family Gobiidae Cuvier, 1816

Subfamily Gobiinae Cuvier, 1816

Tribe Gobiosomatini Birdsong, 1975

***Microgobius* Group sensu Tornabene et al.,** 2016

Otoliths of the fishes in the *Microgobius* Group are distinguished from those of the *Gobiosoma* Group by the presence of an, often large, subcaudal iugum.

Bollmannia clade

Discussion In this informal clade, we combine *Bollmannia* and the fossil otolith-based genus *Brassoichthys* n. gen. that share a specific otolith morphology characterized by an otolith shape that is longer than high, or as long as high, and that show a relatively flat inner face with a relatively large, somewhat deepened sulcus and a large subcaudal iugum.

Genus *Bollmannia* Jordan, 1890

Discussion Fricke et al. (2023) list 11 valid extant *Bollmannia* species, four in the West Atlantic, seven in the East Pacific. Otoliths are available from all species except *B. gomezi* Acero, 1981, from the Pacific coast of southern Colombia. We distinguish four groups (otolith plexus) within the genus based on certain otolith patterns:

The *Bollmannia boqueronensis* otolith plexus containing the extant *B. boqueronensis* Evermann & Marsh, 1899 (Fig. 15a), from the West Atlantic; and *B. marginalis* Ginsburg, 1939 (Fig. 15k), and *B. ocellata* Gilbert, 1892 (Fig. 15l–m), from the East Pacific. The otoliths of this plexus are characterized by a relatively high predorsal angle and a compressed shape (OL:OH = 1.0–1.1).

The *Bollmannia chlamydes* otolith plexus containing the extant *B. chlamydes* Jordan, 1890 (Fig. 17a–b), and *B. umbrosa* Ginsburg, 1939 (Fig. 19f), from the East Pacific; and *B. communis* Ginsburg, 1942 (Fig. 17e), and *B. litura* Ginsburg, 1935 (Fig. 17k–l), from the West Atlantic. The otoliths of this plexus differ from the foregoing one in being more elongate (OL:OH = 1.1–1.3) and often showing a distinctly depressed predorsal angle.

The *Bollmannia stigmatura* otolith plexus containing the extant *B. macropoma* Gilbert, 1892 (Fig. 20o), and *B. stigmatura* Gilbert, 1892 (Fig. 20p), from the East Pacific. Acero (1981) considered *B. gomezi* as being related to *B. macropoma* and *B. stigmatura*, and this species may therefore belong to the same plexus, but its otoliths are not known. The otoliths of the *B. stigmatura* plexus resemble those of the *B. chlamydes* plexus in proportions (OL:OH = 1.1–1.2) but show a remarkable broad middorsal concavity.

The *Bollmannia eigenmannorum* otolith plexus containing the extant *B. eigenmannorum* (Garman, 1896) (Fig. 21e) from the West Atlantic. These otoliths differ from all the others in the nearly rectangular outline and the rather short and narrow sulcus (OL:SuL > 1.9 vs < 1.9 in other *Bollmannia* species).

There is no comprehensive phylogenetic evaluation of *Bollmannia* species. Van Tassell et al. (2012), however, reviewed the Atlantic species of the genus. They found that *B. eigenmannorum* was the most distinct of the Atlantic species and commented that Ginsburg considered separating it into its own subgenus. In the review of Van Tassell et al. (2012), *B. communis* and *B. litura* were considered closely related (in agreement with comments they mentioned from Ginsburg). In fact, the otoliths of both species are so similar that they may not be distinguishable. Ginsburg (1939) considered *B. marginalis* from the Pacific to be most closely related to the Atlantic *B. litura*, while we have *B. marginalis* in the *B. boqueronensis* plexus. Ginsburg (1939) also compared *B. chlamydes*, *B. macropoma*, and *B. umbrosa*. Acero (1981) related *B. macropoma*, *B. stigmatura*, and *B. gomezi*. The otolith plexus grouping is consistent with results from the review of Van Tassell et al. (2012) and Acero (1981) and also appears to be mostly consistent with comments by Ginsburg (1939) commented in Van Tassell et al. (2012).

***Bollmannia boqueronensis* otolith plexus**

***Bollmannia boqueronensis* Evermann & Marsh, 1899**

Figure 15a–h

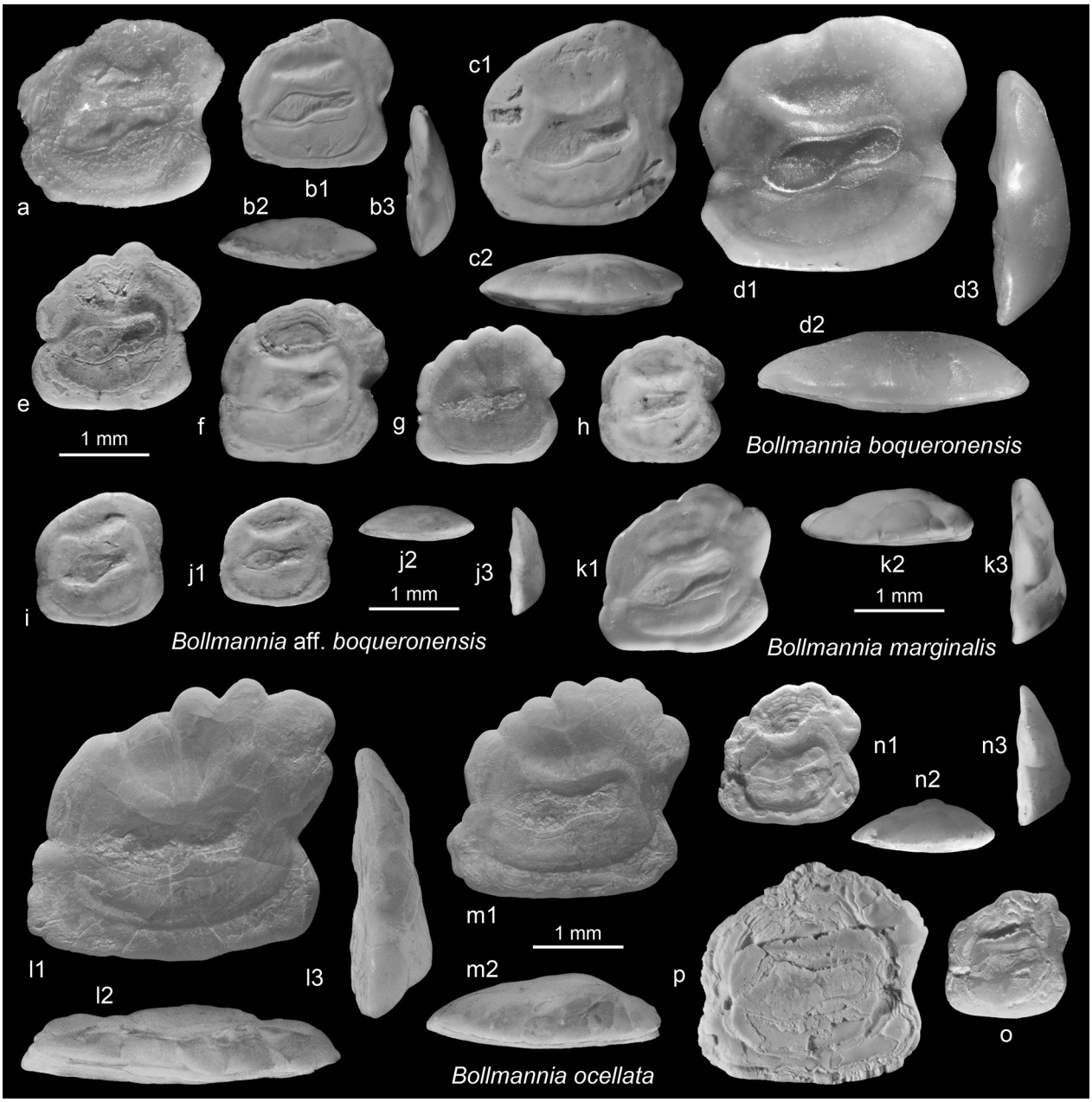


Fig. 15 **a**–**h** *Bollmannia boqueronensis* Evermann & Marsh, 1899; **a** extant, MNHN 1989–0786, Brazil; **b** extant, USNM 438752, Dominica, SL31; **c, f, h** Escudo de Veraguas FM, Atlantic Panama, PPP 2170, NMB P15471; **d** Escudo de Veraguas FM, Atlantic Panama, PPP 2182, NMB P15472; **e** Cubagua FM, Venezuela, PPP 2571, NMB P15473; **g** Cubagua FM, Venezuela, PPP 2556, NMB P15474. **i**–**j** *Bollmannia* aff. *boqueronensis* Evermann & Marsh, 1899, Cayo Agua FM, Atlantic Panama, PPP 1188, NMB P15475. **k** *Bollmannia marginalis* Ginsburg, 1939, extant, USNM 116367, Ecuador, SL39. **l**–**p** *Bollmannia ocellata* Gilbert, 1892; **l**–**m** extant, LACM coll Fitch, SE of Guyanas; **n** Armuelles FM, Pacific Panama, PPP 3236, NMB P15476; **o** Armuelles FM, Pacific Panama, PPP 3235, NMB P15478; **p** Chucunaque FM, Darien, Panama, PPP 1578, NMB P15477

Material (fossil specimens) 92 specimens: Zanclean (49 specimens): Atlantic Panama, Cayo Agua FM, 2 specimens PPP 1276; Venezuela, Cubagua FM, 2 specimens PPP 2554; 3 specimens PPP 2555; 1 specimen PPP 2556 (figured specimen NMB P15474); 1 specimen PPP 2557; 21 specimens PPP 2568; 19 specimens PPP 2571 (figured specimen NMB P15473). Piacenzian (3 specimens): Atlantic Panama, Escudo de Veraguas FM, 2 specimens PPP 2181; 1 specimen PPP 2182 (figured specimen NMB P15472). Gelasian (40 specimens): Atlantic Panama, Escudo de Veraguas FM, 7 specimens PPP 2170 (figured specimens NMB P15471); Bastimentos FM, Ground

Creek Unit, 12 specimens PPP 1252; 1 specimen PPP 1304; Atlantic Costa Rica, Moin FM, 4 specimens PPP 1773; 1 specimen PPP 2038; 5 specimens PPP 3259. Calabrian: Atlantic Panama, Swan Cay FM, 4 specimens PPP 2221; Venezuela, Cumaná FM, 6 specimens PPP 3038.

Description Otolith size up to 3 mm in length. OL:OH = 1.0–1.08; OH:OT = 2.9–3.3. Otolith shape nearly rectangular, predorsal angle high, broadly rounded, postdorsal angle higher than predorsal angle, postdorsal projection blunt, only slightly longer than postventral angle, not bent outward. Ventral rim straight, horizontal. Anterior and posterior rims nearly vertical; preventral angle blunt, nearly orthogonal; posterior rim with distinct indentation at its middle. All rims smooth, dorsal and anterior rims slightly undulating, weakly crenulated in small specimens (Fig. 15e–h).

Inner face flat in vertical direction and slightly bent in horizontal direction. Sulcus sole-shaped with low ostial lobe, deepened, inclined at 10–15°. OL:SuL = 1.7–1.9. Subcaudal iugum large, broad. Dorsal depression wide, relatively deep and close to sulcus with distinct crista superior. Ventral furrow distinct, moderately close to ventral rim of otolith. Outer face distinctly convex, strongest inframedian, relatively smooth with few faint furrows on dorsal field.

Discussion Bollmannia boqueronensis has been an inconspicuous and apparently widely distributed species in the tropical Atlantic since at least Early Pliocene. For comparison with coeval species, see below. Extant specimens of *B. boqueronensis* were collected over sandy and muddy bottoms and flat areas adjacent to coral reefs at 8.4–73 m throughout the Caribbean and the eastern Gulf of Mexico (Van Tassell et al., 2012).

Bollmannia aff. *boqueronensis* Evermann & Marsh, 1899

Figure 15i–j

Material 13 specimens: Zanclean: Atlantic Panama, Cayo Agua FM, 7 specimens PPP 1276; upper Cayo Agua FM, 6 specimens PPP 1188 (figured specimens NMB P15475).

Discussion A few specimens from the Pliocene of the Atlantic side of Panama differ from the typical *B. boqueronensis* in the completely smooth outline and could possibly represent a different species. However, all specimens available are smaller than 1.5 mm in length, likely represent juveniles and thus do not qualify for a proper identification.

Bollmannia ocellata Gilbert, 1892

Figure 15l–p

Material (fossil specimens) 9 specimens: Messinian (*Bollmannia* cf. *ocellata*): Pacific Panama, Chucunaque FM, 1 specimen PPP 1576, 1 specimen PPP 1578 (figured specimen NMB P15477). Calabrian: Pacific Panama, Armueles FM, 6 specimens PPP 3235 (figured specimen NMB P15478); 1 specimen PPP 3236 (figured specimen NMB P15476).

Discussion Otoliths of *B. ocellata* resemble those of *B. boqueronensis* described above but differ in a few subtle characters: a more strongly and regularly crenulated dorsal rim, the slightly projecting preventral angle and the caudal tip being slightly bent upward, a feature commonly observed in a number of *Bollmannia* species. The otoliths of *B. ocellata* also resemble those of *B. marginalis* (Fig. 15k), but differ in the more intense crenulation of the dorsal rim and the slightly upward bent caudal tip.

The two figured specimens from the Calabrian of Armuelles (Fig. 15n–o) are well preserved but small (OL = 1.5 mm), probably from juveniles. The single large specimen from the Messinian of Darien (Fig. 15p) is rather poorly preserved and therefore only tentatively allocated.

Bollmannia ocellata today is found from the Gulf of California to Ecuador at depths of 10–120 m on muddy bottoms (Froese & Pauly, 2023).

Bollmannia nubila Schwarzhans, 2010

Figure 16a–b

2010 *Bollmannia nubila*—Schwarzhans: pl. 101, Fig. 1.
2014 Gobiidae, genera and species indet. 1—Aguilera et al.: Fig. 12/5–7.
Material 9 specimens: holotype (refigured from Schwarzhans, 2010) from the Langhian of Dingden, northern Germany, North Sea Basin (SMF PO 83052). Aquitanian to Burdigalian: Brazil, Pirabas FM, 8 specimens (1 specimen refigured from Aguilera et al., 2014 as Gobiidae indet.) (MPEG-1820-V).

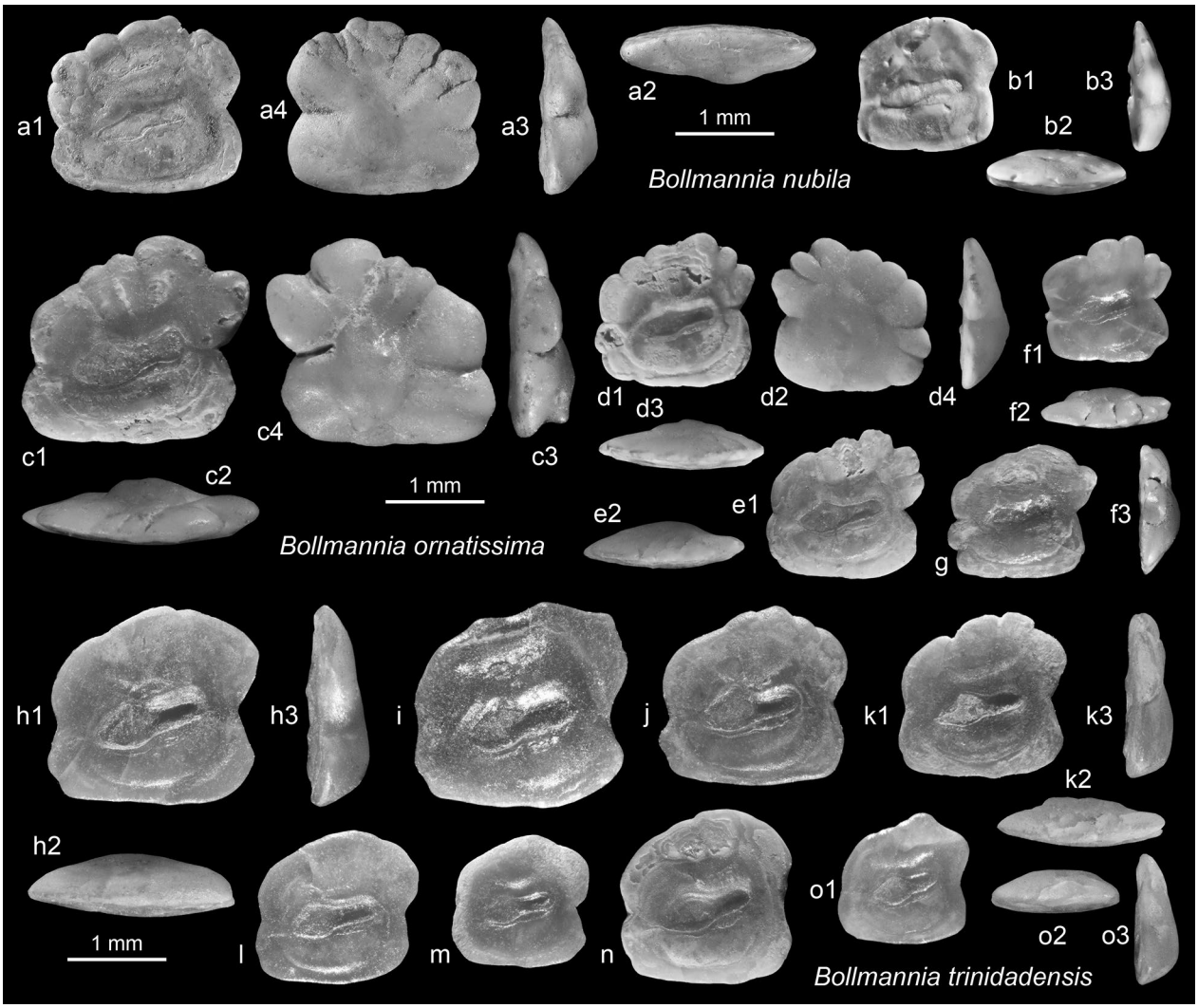


Fig. 16 **a–b** *Bollmannia nubila* Schwarzhans, 2010; a refigured holotype from Schwarzhans (2010), Reinbekian (Langhian), Dingden, Northern Germany, SMF PO 83052; **b** refigured from Aguilera et al., (2014; as Gobiidae indet.1), Pirabas FM, Brazil, Pará, MPEG-1820-V. **c–f** *Bollmannia ornatissima* n. sp.; **c** holotype, NMB P15479, Yaviza FM, Darien, Panama, PPP 1609; **d–f** paratypes, **d** Tuira FM, Darien, Panama, PPP 1137, NMB P15480 (plus 15481-82 not figured); **e** Yaviza FM, Darien, Panama, PPP 1566, NMB P15483; **f–g** Manzanilla FM, Trinidad, PPP 2666, NMB P15484-85. **h–o** *Bollmannia trinidadensis* n. sp.; **h** holotype, NMB P681, Brasso FM, Trinidad, KR 6666; **i–o** paratypes; **i**, **j**, **l**, **m** Brasso FM, Trinidad, KR 6666, NMB P15486-89; **k, o** upper Brasso FM, Trinidad, KR 9244, NMB P15490-91; **n** Cantaure FM, Venezuela, PPP 2546, NMB P15492

Description Otolith size up to 2 mm in length. OL:OH = 1.05–1.1; OH:OT = 3.0–3.2. Otolith shape nearly rectangular, predorsal angle high, nearly as high as postdorsal angle, postdorsal projection blunt, not longer than postventral angle, not bent outward. Ventral rim straight, horizontal, smooth. Anterior and posterior rims nearly vertical; preventral angle blunt, nearly orthogonal; posterior rim with broad, shallow indentation at its middle. All rims smooth, dorsal rim occasionally crenulated.

Inner face nearly flat. Sulcus sole-shaped but very narrow with low ostial lobe, slightly deepened, inclined at 10–15°. OL:SuL = 1.65–1.85. Subcaudal iugum long, relatively narrow. Dorsal depression wide, indistinct. Ventral furrow distinct, close to ventral rim of otolith. Outer face distinctly convex, strongest inframedian, relatively smooth with few short furrows on dorsal field.

Discussion Bollmannia nubila is the earliest record of the genus and now known from two rather extreme geographic positions: the unique type from the North Sea Basin and the now-assigned referred specimens from Brazil. *Bollmannia nubila* is readily distinguished from its congeners by the very narrow sulcus, the relatively narrow subcaudal iugum, and the high predorsal angle.

It resembles *B. eigenmannorum*. It is therefore possible that *B. nubila* is positioned relatively closely to the origin of the genus and thus combines characteristics of the *B. boqueronensis* plexus and the *B. eigenmannorum* plexus.

***Bollmannia ornatissima* n. sp.**

Figure 16c–g

Holotype NMB P15479 (Fig. 16c), Tortonian (NN 10), Yaviza FM, Panama, Darien, Río Tuquesa, PPP 1609.

Paratypes 6 specimens: Tortonian: Tuira FM, 3 specimens PPP 1137 (NMB P15480-82); Yaviza FM, 1 specimen PPP 1566 (NMB P15483). Messinian: Trinidad, Manzanilla FM, 2 specimens PPP 2666 (NMB P15484-85).

Referred material 5 specimens: Tortonian: Panama, 2 specimens same data as holotype; Yaviza FM, 1 specimen PPP 1566. Messinian: Trinidad, Manzanilla FM, 2 specimens PPP 2666.

Etymology Superlative of ornatus (Latin) = ornamented, referring to the strongly crenulated dorsal rim.

Diagnosis OL:OH = 1.0–1.1. Maximal size 2.35 mm (holotype). Predorsal rim high; postdorsal region distinctly higher. Dorsal rim strongly crenulated, with radial furrows extending on inner and outer faces. Sulcus narrow. Subcaudal iugum long, narrow.

Description Otolith size up to 2.35 mm in length (holotype). OH:OT = 3.0–3.2. Otolith shape rectangular with elevated postdorsal region, predorsal angle high, rounded, distinctly lower than postdorsal angle, postdorsal projection blunt, slightly longer than postventral angle, not bent outward. Ventral rim straight, horizontal, smooth or slightly undulating. Anterior and posterior rims nearly vertical; preventral angle blunt; posterior rim with distinct, mostly sharp indentation at its middle. All rims slightly undulating to strongly crenulated, particularly dorsal rim.

Inner face nearly flat in vertical direction, slightly bent in horizontal direction. Sulcus sole-shaped, narrow with low ostial lobe, slightly deepened, inclined at 10–15°. OL:SuL = 1.8–1.9 (rarely 2.1, Fig. 16f). Subcaudal iugum long, relatively narrow. Dorsal depression wide, relatively short and moderately indistinct, with some radial furrows ingressing from the marginal crenulation, close to central portion of sulcus. Ventral furrow distinct, relatively close to ventral rim of otolith. Outer face distinctly convex, strongest inframedian, with several strong radial furrows related to marginal crenulation.

Discussion *Bollmannia ornatissima* is a relatively uncommon species in the Late Miocene of Pacific Panama (Darien) but has also been found in time-equivalent strata of Trinidad. The specimens from Trinidad (Fig. 16f–g) differ from the Panamanian ones in the relatively short sulcus (OL:SuL = 1.9–2.1 vs 1.8–1.9), but we do not consider this difference as warranting separation on species level, particularly since the few Trinidadian specimens are also relatively small (OL = 1.3 mm and 1.45 mm in length).

Bollmannia ornatissima is best recognized by its intense marginal crenulation, particularly the dorsal rim, and the relatively narrow subcaudal iugum. It resembles *B. nubila* in the latter trait and the narrow sulcus but shows a much more pronounced postdorsal region. *Bollmannia ornatissima* differs from other species in the plexus such as *B. marginalis* and *B. ocellata* in the stronger crenulation of the dorsal rim, the narrower sulcus, and the narrower subcaudal iugum.

***Bollmannia trinidadensis* n. sp.**

Figure 16h–o

Holotype NMB P681 (Fig. 16h), Burdigalian (N 7, NN 4), Brasso FM, Trinidad, Tamanaquito River, KR 6666.

Paratypes 7 specimens: Burdigalian (N 7): Trinidad, Brasso FM, 4 specimens same data as holotype (NMB P15486-89). Burdigalian (N 8): Venezuela, Cantaure FM, 1 specimen PPP 2546 (NMB P15492). Langhian: Trinidad, upper Brasso FM (N 10-12), 2 specimens KR 9244 (NMB P15490-91).

Referred material 390 specimens: Burdigalian: Trinidad, Brasso FM, 82 specimens same data as holotype; Venezuela, Cantaure FM, 16 specimens PPP 2543; 43 specimens PPP 2545; 235 specimens PPP 2546; 3 specimens PPP 2539. Langhian: Trinidad, upper Brasso FM, 11 specimens KR 9244.

Etymology After Trinidad, the country of origin of the holotype.

Diagnosis OL:OH = 1.0–1.05. Maximal size 2.2 mm. Predorsal rim high; postdorsal region somewhat higher. Dorsal rim smooth to slightly undulating or crenulated. Sulcus wide, relatively deep. Subcaudal iugum long, narrow.

Description Otolith size up to 2.2 mm in length (holotype 2.1 mm). OH:OT = 3.0–3.2. Otolith shape nearly rectangular with moderately elevated postdorsal region, predorsal angle high, rounded, slightly lower than postdorsal angle, postdorsal projection blunt, not or slightly longer than postventral angle, not bent outward. Ventral rim straight, horizontal, smooth. Anterior and posterior rims nearly vertical; preventral angle blunt; posterior rim with distinct, broad indentation at its middle. All rims smooth, dorsal rim undulating to mildly crenulated.

Inner face nearly flat in vertical direction, slightly bent in horizontal direction. Sulcus sole-shaped, broad but with low ostial lobe, distinctly deepened, inclined at 12–17°. OL:SuL = 1.75–1.85. Subcaudal iugum long, relatively narrow. Dorsal depression wide, relatively long, distinct, moderately close to sulcus with broad crista superior. Ventral furrow distinct, moderately close to ventral rim of otolith. Outer face distinctly convex, strongest inframedian, more or less smooth.

Discussion Bollmannia trinidadensis is best recognized by its wide and rather deep sulcus in combination with a relatively narrow subcaudal iugum and a very weak marginal ornamentation. It is a common species in the late Burdigalian of Trinidad (Fig. 16h–m, o) and the Cantaure Formation (Langhian) of Venezuela (Fig. 16o).

Bollmannia chlamydes **otolith plexus**

Bollmannia chlamydes **Jordan, 1890**

Figure 17a–d

Material (fossil specimens) 11 specimens: Calabrian: Pacific Panama, Armuelles FM, 2 specimens PPP 3235 (figured specimens NMB P15493–94), 9 specimens PPP 3236.

Description Otolith size up to 4.2 mm in length. OL:OH = 1.15–1.4, increasing with size; OH:OT = 2.9–3.5, decreasing with size. Predorsal angle low, often depressed, postdorsal angle expanded, postdorsal projection blunt, only slightly longer than postventral angle, not or very slightly bent outward. Ventral rim straight, horizontal. Anterior rim inclined, with projecting preventral angle; posterior rim nearly vertical, with broad, wide indentation at its middle. All rims smooth, except dorsal rim undulating and increasingly intense crenulated in large specimens (Fig. 17b).

Inner face flat in vertical direction and slightly bent in horizontal direction. Sulcus sole-shaped with low ostial lobe, moderately deepened, inclined at 15–18°. Caudal tip rounded, slightly bent upward. OL:SuL = 1.65–1.95. Subcaudal iugum long, relatively narrow. Dorsal depression wide, relatively deep and close to sulcus with distinct crista superior. Ventral furrow distinct, relatively distant from ventral rim of otolith. Outer face moderately to distinctly convex, decreasingly convex with size, strongest inframedian, relatively smooth with few furrows on dorsal field.

Discussion Only relatively small specimens are found in the Calabrian of Pacific Panama, which are here attributed to *B. chlamydes* (Fig. 17c–d). They differ from the large extant ones (Fig. 17a–b) in the lower ratio OL:OH (1.15–1.2 vs 1.25–1.4) and in being thicker (OH:OT < 3.1 vs > 3.2). We contribute these differences to allometric growth. Today, *B. chlamydes* is reported from Pacific Colombia to northern Peru over muddy bottoms at depths of 10–120 m (Froese & Pauly, 2023).

Bollmannia communis **Ginsburg, 1942**

Figure 17e–j

1992 Gobiidae sp. 2—Nolf & Stringer: pl. 17, Fig. 13.

Material (fossil specimens) 48 specimens: Messinian: 1 specimen Dominican Republic, Gurabo FM, NMB 15864 (NMB P407); Zanclean, Atlantic Panama: 35 specimens; 2 specimens Shark Hole FM, PPP 2217; 25 specimens Cayo Agua FM, 24 specimens PPP 1276 (NMB P15496), 1 specimen PPP 2222; 8 specimens Cubagua FM, 5 specimens PPP 2570, 3 specimens PPP 2571 (NMB P15498); 1 specimen Piacenzian, Atlantic Costa Rica, Rio Banano FM, PPP 3245 (NMB P15495); 11 specimens Gelasian: 7 specimens Atlantic Panama, Bastimentos FM, Ground Creek Unit, 5 specimens PPP 1256, 2 specimens PPP 3204; 4 specimens, Atlantic Costa Rica, Moin FM, 1 specimen PPP 1776 (NMB P15497), 2 specimens PPP 2032, 1 specimen PPP 2038.

Discussion Otoliths of *B. communis* are similar to those of *B. chlamydes* (see above) from the East Pacific and those of the West Atlantic *B. litura* (Fig. 17k–l). They differ from *B. chlamydes* in the less projecting preventral angle, the higher predorsal angle, the often slightly projecting postdorsal angle and in the generally less strongly developed ornamentation of the dorsal rim. Furthermore, otoliths of *B. communis* remain thicker at large sizes compared to *B. chlamydes* (OH:OT = 2.75–3.0 vs 3.2–3.5 at sizes > 2.8 mm in length). We were unable to identify a reliable morphological difference between the otoliths of *B. communis* and *B. litura*.

Extant specimens of *B. communis* were collected on mud bottoms at depths of 18–77 m (Van Tassell et al.,

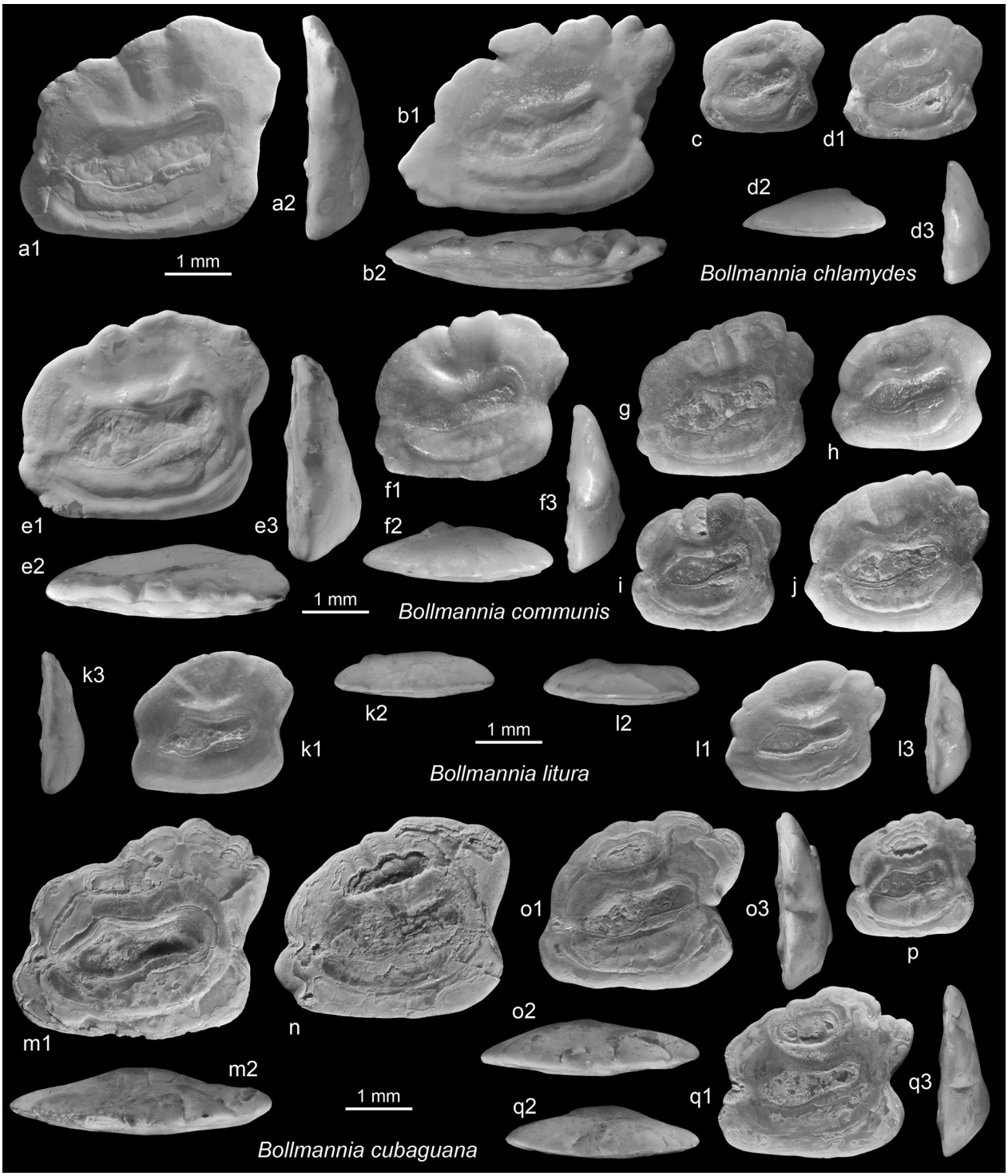


Fig. 17 **a**–**d** *Bollmannia chlamydes* Jordan, 1890; **a** extant, MNHN coll. Bearez #8040; **b** extant, USNM 322592, 08°56′N 79°30′W, 10-12 m; **c**–**d** Armuelles FM, Pacific Panama, PPP 3235, NMB P15493-94. **e**–**j** *Bollmannia communis* Ginsburg, 1942; **e** extant, CAS 6712, 26°41′N 96°56′W, Gulf of Mexico; **f** Río Banano FM, Atlantic Costa Rica, PPP 3245, NMB P15495; **g** Cayo Agua FM, Atlantic Panama, PPP 1276, NMB P15496; **h** Limón, Atlantic Costa Rica, PPP 1776, NMB P15497; **i**–**j** Cubagua FM, Venezuela, PPP 2571, NMB P15498. **k**–**l** *Bollmannia litura* Ginsburg, 1935, extant, AMNH 253411, 09°00′ 81°59′W, Bocas del Toro, SL 35 and 43 mm. **m**–**q** *Bollmannia cubaguana* n. sp.; **m** holotype, NMB P15499, Cubagua FM, Venezuela, PPP 2568; **n**–**q** paratypes, Cubagua FM, Venezuela; **n** PPP 2568, NMB P15500; **o**–**q** PPP 2571, NMB P15502-04

2012). They were primarily taken from the Gulf of Mexico and off Puerto Rico and French Guiana (Van Tassell et al., 2012). *Bollmannia litura* was taken at depths of 12.8–71 m over mud and mixed-mud bottoms in the western Caribbean (Van Tassell et al., 2012).

***Bollmannia cubaguana* n. sp.**

Figure 17m–q

Holotype NMB P15499 (Fig. 17m), Zanclean, Cubagua FM above Cerro Negro Member, Venezuela, Isla Cubagua, PPP 2568.

Paratypes 11 specimens: Zanclean, Cubagua FM above Cerro Negro Member, Venezuela, Isla Cubagua, 2 specimens PPP 2568 (NMB P15500-01), 6 specimens PPP 2571 (NMB P15502-04), 3 specimens PPP 2572 (NMB P15508-10).

Etymology After the Cubagua Formation, the type formation.

Diagnosis OL:OH = 1.1–1.15. Maximal size 3.9 mm (holotype). Predorsal rim slanted; postdorsal region slightly elevated. Dorsal rim irregularly undulating or crenulated. Preventral angle slightly projecting. Sulcus wide; OL:SuL = 1.85–1.95. Subcaudal iugum long, moderately wide.

Description Otolith size up to 4.0 mm in length (holotype 3.9 mm). OH:OT = 3.1–3.3. Predorsal angle low, often depressed, postdorsal angle expanded, postdorsal projection blunt, only slightly longer than postventral angle, not bent outward. Ventral rim straight, horizontal. Anterior rim inclined, with slightly projecting preventral angle; posterior rim nearly vertical, with broad, wide and rather deep indentation at its middle. All rims smooth, except dorsal rim irregularly undulating or crenulated.

Inner face almost entirely flat. Sulcus sole-shaped with low ostial lobe, moderately deepened, inclined at 12–15°. Caudal tip rounded, slightly bent upward. OL:SuL = 1.85–1.95. Subcaudal iugum long, moderately wide. Dorsal depression wide, indistinct and close to sulcus with distinct crista superior. Ventral furrow distinct, moderately distant from ventral rim of otolith. Outer face moderately to distinctly convex, strongest inframedian, relatively smooth with few furrows on dorsal field.

Discussion Bollmannia cubaguana is very similar to *B. chlamydes* differing only in few subtle characters, primarily in being less elongate in specimens larger than 3 mm in length (OL:OH 1.1–1.15 vs 1.25–1.4) and the less strongly inclined sulcus (12–15° vs 15–18°). Presumably, *B. cubaguana* represents an extinct geminate species in the West Atlantic to the extant East Pacific *B. chlamydes*. The largest specimen (holotype) of *B. cubaguana* shows a slightly middorsal concavity, similar to but much less strongly developed as in otoliths of the *B. stigmatura* plexus (see below).

***Bollmannia gatunensis* Schubert,** 1908

Figure 18a–n

1908 *Otolithus* (*Gobius*) *gatunensis*—Schubert: Fig. 7.

1908 *Otolithus* (*Gobius*) *vicinalis* Koken, 1891—Schubert: Fig. 6.

1976 Gobiidae—Nolf: pl. 9, Fig. 7.

Material 188 specimens, Tortonian: 2 specimens Trinidad, Tamana FM, KR 25956 (NMB P541 and P511); 15 specimens Ecuador, Angostura FM, 3 specimens PPP 3290, 2 specimens PPP 3297 (NMB P15511), 5 specimens PPP 3301 (NMB P15512), 2 specimens PPP 3369, 1 specimen PPP 3372, 2 specimens PPP 3465; 54 specimens Pacific Panama, Darien, Tuira FM, 7 specimens PPP 1132 (figured specimen NMB P15522), 14 specimens PPP 1137, 1 specimen PPP 1139 (NMB P15520), 4 specimens, PPP 1593, 2 specimens 1142, 4 specimens PPP 1627, 21 specimens PPP 1163, 1 specimen PPP 1164; 57 specimens Pacific Panama, Darien, Yaviza FM, 5 specimens PPP 1607, 5 specimens PPP 1609, 3 specimens PPP 1528, 3 specimens PPP 1145, 12 specimens PPP 1620, 6 specimens PPP 1149 (figured specimen NMB P15521), 9 specimens PPP 1171, 1 specimen PPP 1565, 13 specimens PPP 1566 (figured specimen NMB P15519); 47 specimens Atlantic Panama, Gatun FM, 1 specimen PPP 1973, 5 specimens PPP 2165 (NMB P15514), 1 specimens PPP 2166 (NMB P15513), 28 specimens PPP 2167 (figured specimens NMB P15515-16), 12 specimens PPP 2168 (figured specimen NMB P15517). 13 specimens Messinian: Chucunaque FM, Pacific Panama, Darien, PPP 1612 (figured specimen NMB P15518),

Description Otolith size up to 3.1 mm in length. OL:OH = 1.02–1.12; OH:OT = 3.1–3.4. Predorsal angle relatively high, postdorsal angle expanded, postdorsal projection rounded, projecting beyond postventral angle, slightly bent outward. Ventral rim straight, horizontal. Anterior rim nearly vertical, with nearly orthogonal

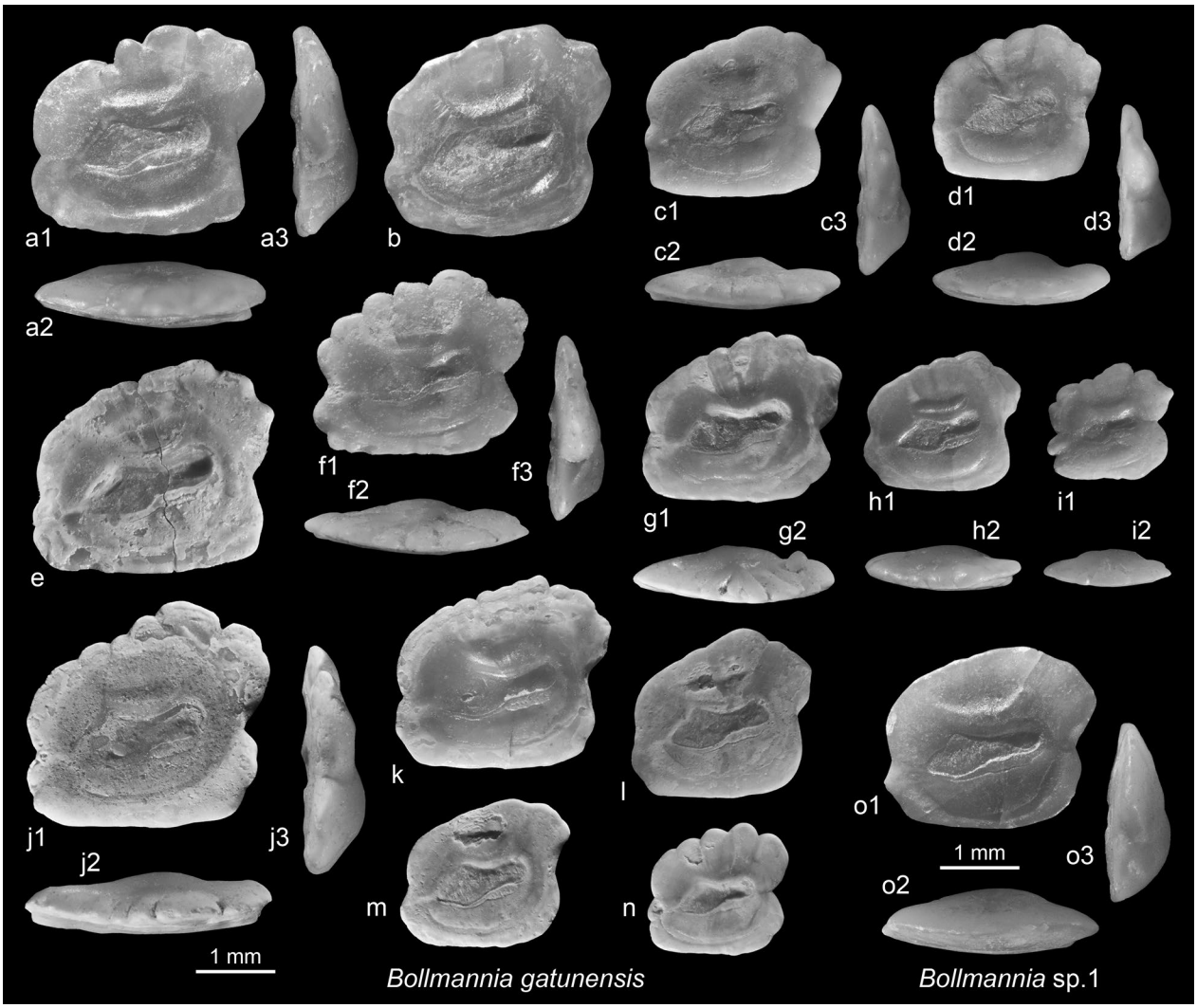


Fig. 18 **a**–**n** *Bollmannia gatunensis* (Schubert, 1908); **a**–**b** Tamana FM, Trinidad, KR 25956, **a** NMB P541, **b** NMB P511; **c**–**d** Angostura FM, Ecuador, **c** PPP 3297, NMB P15511, **d** PPP 3301, NMB P15512; **e**–**i** Gatun FM, Atlantic Panama, **e** PPP 2166, NMB P15513, **f** PPP 2165, NMB P15514, **g**–**h** PPP 2167, NMB P15515-16, **i** PPP 2168, NMB P15517; **j**, **l**, **n** Tuira FM, Darien, Panama, **j** PPP 1612, NMB P15518, **l** PPP 1139, NMB P15520, **n** PPP 1132, NMB P15522; **k**, **m** Yaviza FM, Darien, Panama, **k** PPP 1566, NMB P15519, **m** PPP 1149, NMB P15521. **o** *Bollmannia* sp.1, Cercado FM, Dominican Republic, NMB 15912, NMB P396

preventral angle; posterior rim slightly inclined, with broad and rather deep indentation at its middle. Ventral rim smooth, dorsal rim irregularly undulating or crenulated.

Inner face flat in vertical direction and slightly bent in horizontal direction. Sulcus sole-shaped with moderate ostial lobe, moderately deepened, inclined at 10–15°. Caudal tip rounded, slightly bent upward. OL:SuL = 1.65–1.85. Subcaudal iugum long, moderately wide. Dorsal depression wide, distinct and close to sulcus with distinct crista superior. Ventral furrow distinct, relatively distant from ventral rim of otolith. Outer face moderately to distinctly convex, strongest inframedian, with radial furrows on dorsal field.

Discussion Bollmannia gatunensis is a common species during the Tortonian from Ecuador in the East Pacific to Trinidad in the West Atlantic. *Bollmannia gatunensis* is very similar to *B. communis* but tends to be thinner (OH:OT = 3.1–3.4 vs 2.75–3.0) and shows a more

strongly ornamented dorsal rim and more distinct post-dorsal projection. No doubt, both species are closely related.

***Bollmannia propensa* n. sp.**

Figure 19a–e

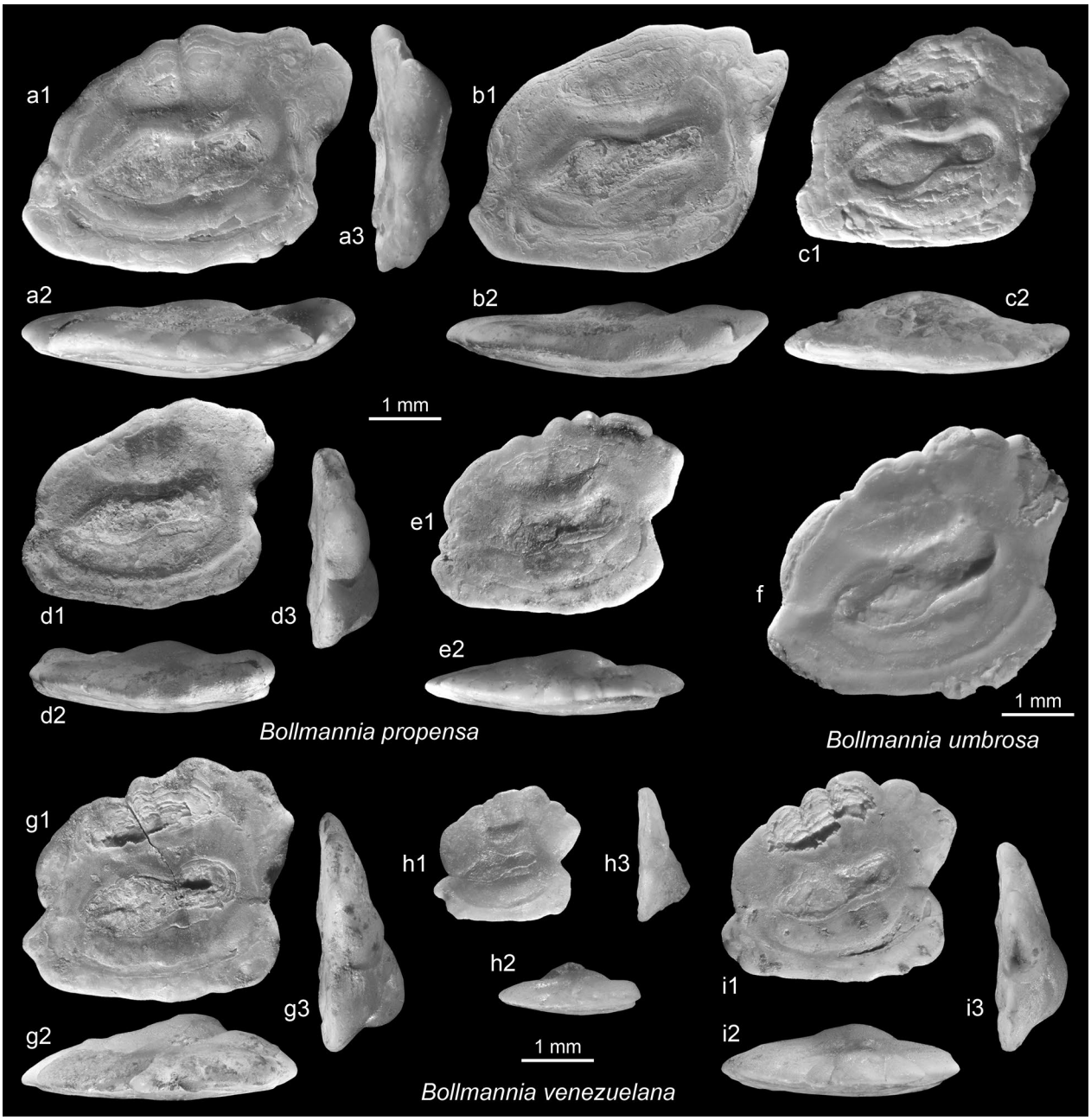


Fig. 19 **a–e** *Bollmannia propensa* n. sp.; **a** holotype, NMB P15523, Onzole FM, Ecuador, PPP 3314; **b–e** paratypes; **b** Angostura FM, Ecudor, PPP 3480, NMB P15526; **c** Yaviza FM, Darien, Panama, PPP 1620, NMB P15527; **d** Angostura FM, Ecuador, PPP 3465, NMB 15528; **e** Onzole FM, Ecuador, PPP 3314, NMB P15524-25 (15525 not figured). **f** *Bollmannia umbrosa* Ginsburg, 1939, extant, LACM 32544–1, Costa Rica, Punta Urita, SL 76 mm. **g–i** *Bollmannia venezuelana* n. sp.; **g** holotype, NMB P15529, Ojo de Agua FM, Venezuela, NMB 15730; **h–i** paratypes; **h** Brasso FM, Trinidad, KR 7546, NMB P540; **i** Ojo de Agua FM, Venezuela, NMB 15730, NMB P15530-31

Holotype NMB P15523 (Fig. 19a), Messinian, Onzole FM, Ecuador, PPP 3314.

Paratypes 5 specimens: 1 specimen Tortonian, Pacific Panama, Darien, Yaviza FM PPP 1620 (NMB P15527); 2 specimens Tortonian, Ecuador, Angostura FM, 1 specimen PPP 3480 (NMB P15526), 1 specimen PPP 3465 (NMB P15528; 2 specimens same data as holotype (NMB P15524-25).

Referred specimens 18 specimens: 3 specimens Tortonian, Pacific Panama, Yaviza FM, 1 specimen PPP 1620, 2 specimens PPP 1566; 3 specimens Tortonian, Ecuador, Angostura FM, 1 specimen PPP 3439, 2 specimens PPP 3465; 3 specimens Messinian, Ecuador, Onzole FM PPP 3314; 9 specimens Messinian, Pacific Panama, Darien, Chucunaque FM, 6 specimens PPP 1576, 3 specimens PPP 1578.

Etymology From propensus (Latin) = inclined, skewed, referring to the parallelogram-like shape of the otolith.

Diagnosis OL:OH = 1.2–1.3. Maximal size 4.6 mm (holotype). Predorsal rim rounded or depressed; postdorsal region slightly elevated. Preventral projection and postdorsal projection strong giving otolith a parallelogram-like shape. Dorsal rim irregularly undulating or slightly crenulated. Sulcus large; OL:SuL = 1.65–1.85. Subcaudal iugum long, wide.

Description Otolith size up to 4.6 mm in length (holotype). OH:OT = 3.1–3.4 (one specimen of Fig. 19d OH:OT = 2.7). Predorsal angle low, slanted or depressed, postdorsal angle slightly expanded. Postdorsal projection projecting well beyond postventral angle, slightly bent outward; preventral angle distinctly projecting; both resulting in parallelogram-like otolith shape. Ventral rim straight, horizontal. Anterior rim inclined, posterior rim inclined, with variable, broad and shallow or no indentation at its middle. Ventral rim smooth, dorsal rim irregularly undulating or slightly crenulated.

Inner face flat in vertical direction and distinctly bent in horizontal direction. Sulcus sole-shaped with moderate ostial lobe and narrow cauda, moderately deepened, inclined at 12–15°. Caudal tip rounded, slightly bent upward. OL:SuL = 1.65–1.85. Subcaudal iugum long, wide. Dorsal depression wide, rather indistinct and close to sulcus with moderately developed crista superior. Ventral furrow distinct, relatively distant from ventral rim of otolith. Outer face nearly flat with moderate subcentral umbo (only one specimen with strongly convex outer face—Fig. 19d), few radial furrows on dorsal field close to otolith margin.

Discussion Bollmannia propensa is easily recognized by its parallelogram-like shape, thin appearance and distinctly bent inner face in horizontal direction. It appears to be restricted to the late Miocene of the East Pacific. It resembles most the extant *B. umbrosa* (Fig. 19f) but differs in the more slender shape (OL:OH = 1.2–1.3 vs 1.1–1.15) and the distinctly expanded postdorsal projection.

***Bollmannia venezuelana* n. sp.**

Figure 19g–i

1976 Gobiidae—Nolf: pl. 9, Fig. 6.

Holotype NMB P15529 (Fig. 19g), Tortonian, Ojo de Agua FM, Venezuela, NMB 15730.

Paratypes 4 specimens: 2 specimens Langhian, Trinidad, Brasso FM, 1 specimen KR 7546 (NMB P540), 1 specimen KR 7573 (NMB P692); 2 specimens same data as holotype (NMB P15530-31).

Referred specimens 5 specimens same data as holotype.

Etymology After Venezuela, the country of origin of the holotype.

Diagnosis OL:OH = 1.07–1.12. Maximal size 3.8 mm (holotype). Predorsal angle high, rounded; postdorsal region elevated, distinctly and irregularly ornamented. Preventral angle slightly projecting; postdorsal projection slightly extending beyond postventral angle. Sulcus wide; OL:SuL = 1.7–1.8. Subcaudal iugum long, wide. Outer face with narrow but strongly projecting umbo close to ventral rim of otolith.

Description Otolith size up to 3.8 mm in length (holotype). OH:OT = 2.6–3.0. Predorsal angle low, rounded, postdorsal angle expanded. Postdorsal projection projecting slightly beyond postventral angle, not bent outward; preventral angle slightly projecting. Ventral rim straight, horizontal. Anterior and posterior rims slightly inclined, posterior rim with relatively deep indentation at its middle. Ventral rim smooth, dorsal rim broadly and irregularly crenulated.

Inner face nearly flat. Sulcus sole-shaped with moderate ostial lobe, moderately deepened, inclined at 14–20°. Caudal tip rounded, slightly bent upward. OL:SuL = 1.7–1.8. Subcaudal iugum moderately long and wide. Dorsal depression wide, rather indistinct and close to sulcus with moderately developed crista superior. Ventral furrow distinct, relatively distant from ventral rim of otolith. Outer face with narrow, strongly projecting, subcentral

umbo close to ventral rim of otolith, few radial furrows on dorsal field close to otolith margin.

Discussion Bollmannia venezuelana is relatively inconspicuous in appearance and differs from fossil and extant congeners only in subtle characteristics. It is distinctly more compressed than *B. propensa* with less projecting preventral and postdorsal projections. *Bollmannia venezuelana* most closely resembles the extant *B. umbrosa* from the East Pacific but differs in the higher predorsal angle (vs depressed) and the distinct subcentral umbo on the outer face, a trait that is not seen in a similar expression in any of the other known *Bollmannia* species. *Bollmannia venezuelana* differs from *B. gatunensis* in the less prominent postdorsal projection and the more strongly inclined sulcus (14–20° vs 10–15°).

***Bollmannia* sp. 1**

Figure 18o

Material 2 specimens, Dominican Republic, Tortonian, Cercado FM, 1 specimen NMB 15912 (NMB P396), 1 specimen NMB 16837 (NMB P410).

Discussion Two moderately large specimens (the figured one is 2.65 mm in length) differ from the otherwise similar *B. gatunensis* in the robust appearance and completely smooth rims without crenulation. It is possible that these specimens still fall within the variability of *B. gatunensis*, but because they too are found only in the north Dominican Basin it is also possible that they represent yet another species. More specimens from that region must be awaited before a reliable identification can be made.

***Bollmannia stigmatura* otolith plexus**

***Bollmannia baldwinae* n. sp.**

Figure 20a–m

Holotype NMB P15537 (Fig. 20g), Tortonian, Yaviza FM, Pacific Panama, Darien, PPP 1609.

Paratypes 12 specimens: 4 specimens late Burdigalian, Venezuela, Cantaure FM, 1 specimen PPP 2545 (NMB P15533), 2 specimens PPP 2546 (NMB P15534-35), 1 specimen PPP 2539 (NMB P15536); 2 specimens Langhian, Trinidad, Brasso FM, Cb. 1852 (NMB P676 and NMB P15532); 3 specimens same data as holotype, 1 specimen PPP 1607 (NMB P15538), 2 specimens PPP 1620 (NMB P15539-40); 1 specimen Tortonian, Trinidad, Manzanilla FM, PPP 2666 (NMB P15543); 2 specimens Messinian, Venezuela, Isla Margarita, La Tejita FM, PPP 3087 (NMB P15541-42).

Referred specimens 88 specimens: 24 specimens late Burdigalian, Venezuela, Cantaure FM, 6 specimens PPP 2545, 18 specimens PPP 2546; 2 specimens Langhian, Trinidad, Brasso FM, Cb. 1852; 12 specimens Langhian, Venezuela, Socorro FM, 4 specimens PPP 2642, 8 specimens PPP 2644; 2 specimens Langhian, Pacific Panama, Darien, Tapaliza FM, 1 specimen PPP 1152, 1 specimen PPP 1538; 4 specimens Tortonian, Pacific Panama, Darien, Tuira FM, 1 specimen PPP 1134, 1 specimen PPP 1139, 2 specimens PPP 1627; 36 specimens Tortonian, Pacific Panama, Darien, Yaviza FM, 8 specimens PPP 1607, 1 specimen PPP 1528, 2 specimens PPP 1145, 11 specimens PPP 1620, 3 specimens PPP 1149, 8 specimens PPP 1171, 1 specimen PPP 1565, 2 specimens PPP 1566; 5 specimens Tortonian, Trinidad, Manzanilla FM, PPP 2666; 3 specimens Messinian, Venezuela, Isla Margarita, La Tejita FM, PPP 3087.

Etymology Named in honor of Carole Baldwin (USNM, Washington D.C.) in recognition of her many contributions to the understanding of gobies from America.

Diagnosis OL:OH = 1.05–1.12. Maximal size 2.6 mm. Dorsal rim with distinctive middorsal indentation. Predorsal angle high, postdorsal region elevated, preventral angle orthogonal; postdorsal projection slightly extending beyond postventral angle. Sulcus wide, deep; OL:SuL = 1.6–1.8. Subcaudal iugum short, wide. Sulcus inclination 8–16°.

Description Otolith size up to 2.6 mm in length (holotype 2.4 mm). OH:OT = 3.0–3.3. Dorsal rim with distinct,

(See figure on next page.)

Fig. 20 **a**–**m** *Bollmannia baldwinae* n. sp.; **g** holotype, NMB P15537, Yaviza FM, Darien, Panama, PPP 1609; **b**–**m** paratypes, **a**–**b** Brasso FM, Langhian, Trinidad, Cb. 1852, **a** NMB P676, **b** NMB P15532; **c** Cantaure FM, El Hatillo-1, Venezuela, PPP 2545, NMB P15533; **d**, **f** Cantaure FM, Casa Cantaure, Venezuela, PPP 2546, NMB P15534-35; **e** Cantaure FM, San José de Cocodite, Venezuela, PPP 2539, NMB P15536; **h**–**j** Yaviza FM, Darien, Panama, **h** PPP 1607, NMB P15538, **i**–**j** PPP 1620, NMB P15539-40; **k**–**l** Tejita FM, Isla Margarita, Venezuela, PPP 3087, NMB P15541-42; **m** Manzanilla FM, Trinidad, PPP 2666, NMB P15543. **n** *Bollmannia* sp. 2, Bastimentos FM, Ground Creek Unit, Bastimentos, PPP 1256, NMB P15544. **o** *Bollmannia macropoma* Gilbert, 1892, extant, CAS 44137, Cost Rica, Golfo de Nicoya, SL 86 mm. **p** *Bollmannia stigmatura* Gilbert, 1892, extant, USNM 116364, Pacific Columbia, Puerto Utria. **q** *Bollmannia* sp. 3, Socorro FM, Paraguaná, Venezuela, PPP 2642, NMB P15545

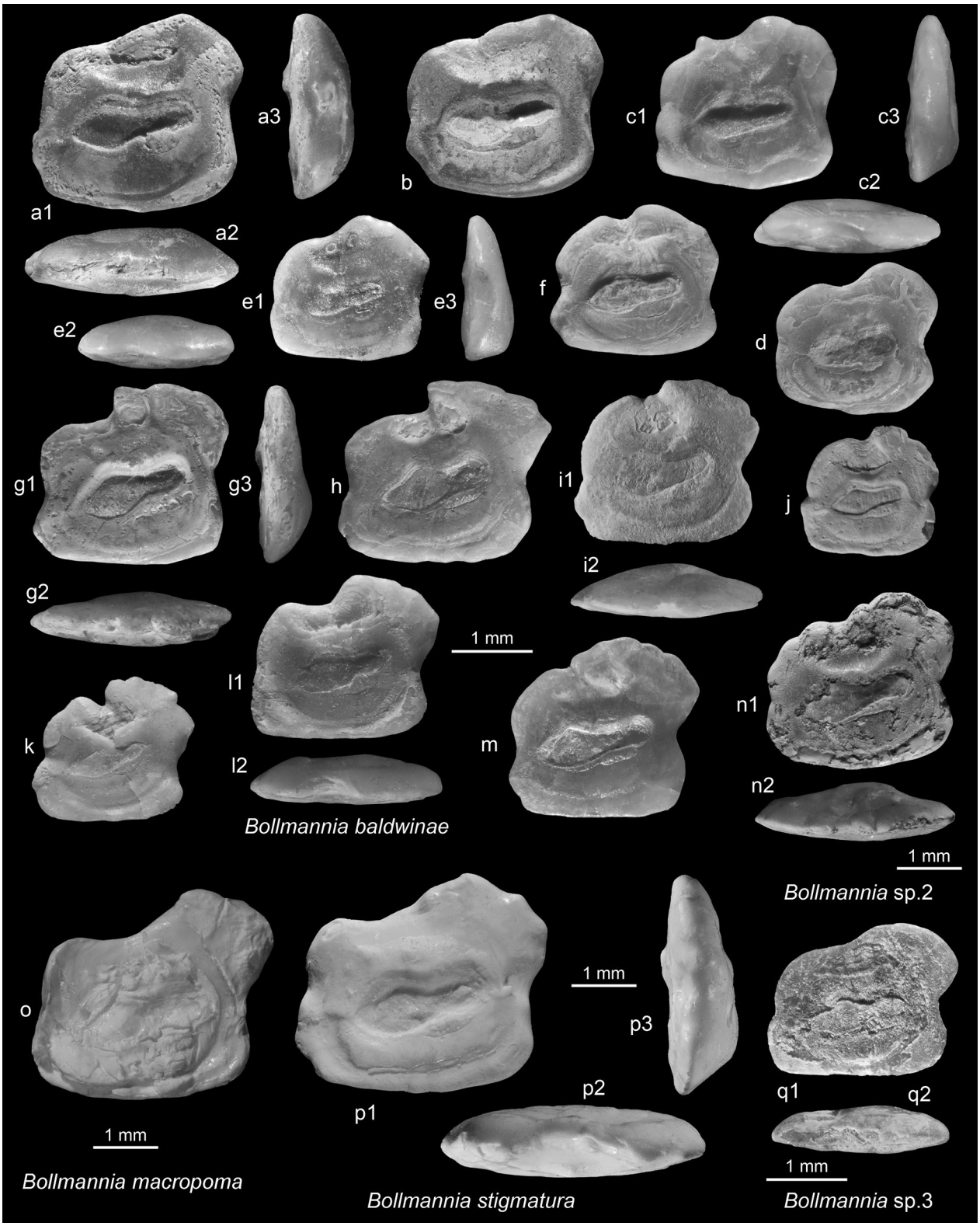


Fig. 20 (See legend on previous page.)

somewhat variable but mostly sharp and deep middorsal indentation in front of postdorsal expansion. Predorsal angle high, rounded, postdorsal region expanded, often with steep anterior border. Postdorsal projection projecting slightly beyond postventral angle, not bent outward; preventral angle orthogonal. Ventral rim straight to slightly curved, horizontal. Anterior rim nearly vertical, posterior rim slightly inclined, with relatively broad indentation at its middle. Ventral rim smooth, dorsal rim smooth or irregularly undulating.

Inner face nearly flat. Sulcus sole-shaped with moderate ostial lobe, deep, inclined at 8–16°. Caudal tip rounded. OL:SuL = 1.6–1.8. Subcaudal iugum short, wide to almost as wide as long in cases. Dorsal depression wide, deep and mostly distinct, open to dorsal rim of otolith and close to sulcus with well-developed crista superior. Ventral furrow distinct, relatively close to ventral rim of otolith. Outer face broadly convex, smooth.

Discussion Bollmannia baldwinae is readily distinguished from its fossil congeners by the distinct middorsal indentation. The middorsal indentation varies somewhat in expression and strength from broadly concave to nearly orthogonally incised and usually increases in strength with size. *Bollmannia baldwinae* is distinguished from the extant congeners of the plexus *B. macropoma* (Fig. 20o) and *B. stigmatura* (Fig. 20p) in being more compressed (OL:OH = 1.05–1.12 vs 1.15–1.2) and showing a broader, more pronounced postdorsal region. The short and wide subcaudal iugum is also characteristic of *B. baldwinae*. *Bollmannia baldwinae* is a widely distributed species in the East Pacific and West Atlantic with a long duration range from the late Burdigalian to the Messinian over about 11 to 12 mya. The species is regarded as the earliest record in the *Bollmannia stigmatura* otolith plexus because of its conspicuous middorsal indentation.

Bollmannia sp. 2

Figure 20n

Material 1 specimen Gelasian, Atlantic Panama, Bastimentos FM, Ground Creek Unit, PPP 1256 (NMB P15544).

Discussion A single, rather poorly preserved otolith from the early Pleistocene of Bastimentos Island, Atlantic Panama, of 2.8 mm in length shows a mild middorsal indentation. This could either represent a somewhat unusual variation of a known extant Atlantic species such as *B. communis* or indicate that species of the *Bollmannia stigmatura* otolith plexus which nowadays is restricted to the East Pacific also existed in the West Atlantic until the Gelasian.

Bollmannia sp. 3

Figure 20q

Material 3 specimens: 1 specimen Langhian, Venezuela, Socorro FM, PPP 2642 (NMB P15545); 2 specimens Messinian, Pacific Panama, Darien, Chucunaque FM, 1 specimen PPP 1576, 1 specimen PPP 1578.

Discussion Three poorly preserved, slender otoliths with a broad middorsal concavity could possible represent another species of the *Bollmannia stigmatura* otolith plexus.

Bollmannia eigenmannorum otolith plexus

Bollmannia angosturae n. sp.

Figure 21a–d

Holotype NMB P15529 (Fig. 21a), Tortonian, Angostura FM, Ecuador, PPP 3465.

Paratypes 3 specimens: 2 specimens Tortonian, Atlantic Panama, Gatun FM, PPP 2167 (NMB P15548-49); 1 specimen Messinian, Onzole FM, Ecuador, NMB 19084 (NMB P15547).

Etymology After the type formation, the Angostura FM of Tortonian age in Ecuador.

Diagnosis OL:OH = 1.05–1.15. Maximal size 2.25 mm (holotype). Otolith shape nearly rectangular with rounded dorsal rim. Predorsal angle high, postdorsal region not significantly elevated, preventral angle not projecting, postdorsal projection not extending beyond postventral angle. Sulcus narrow, small, with very low ostial lobe; OL:SuL = 1.9–2.2. Subcaudal iugum long, relatively narrow. Sulcus inclination angle 7–12°.

Description Otolith size up to 2.25 mm in length (holotype). OH:OT = 2.7–2.9. Dorsal rim relatively low, regularly curved, with high, rounded predorsal angle and rounded postdorsal angle. Postdorsal projection blunt, not projecting beyond postventral angle, not bent outward; preventral angle orthogonal or rounded. Ventral rim straight, horizontal. Anterior and posterior rims nearly vertical, posterior rim with relatively weak indentation at its middle. All rims smooth, dorsal rim slightly undulating.

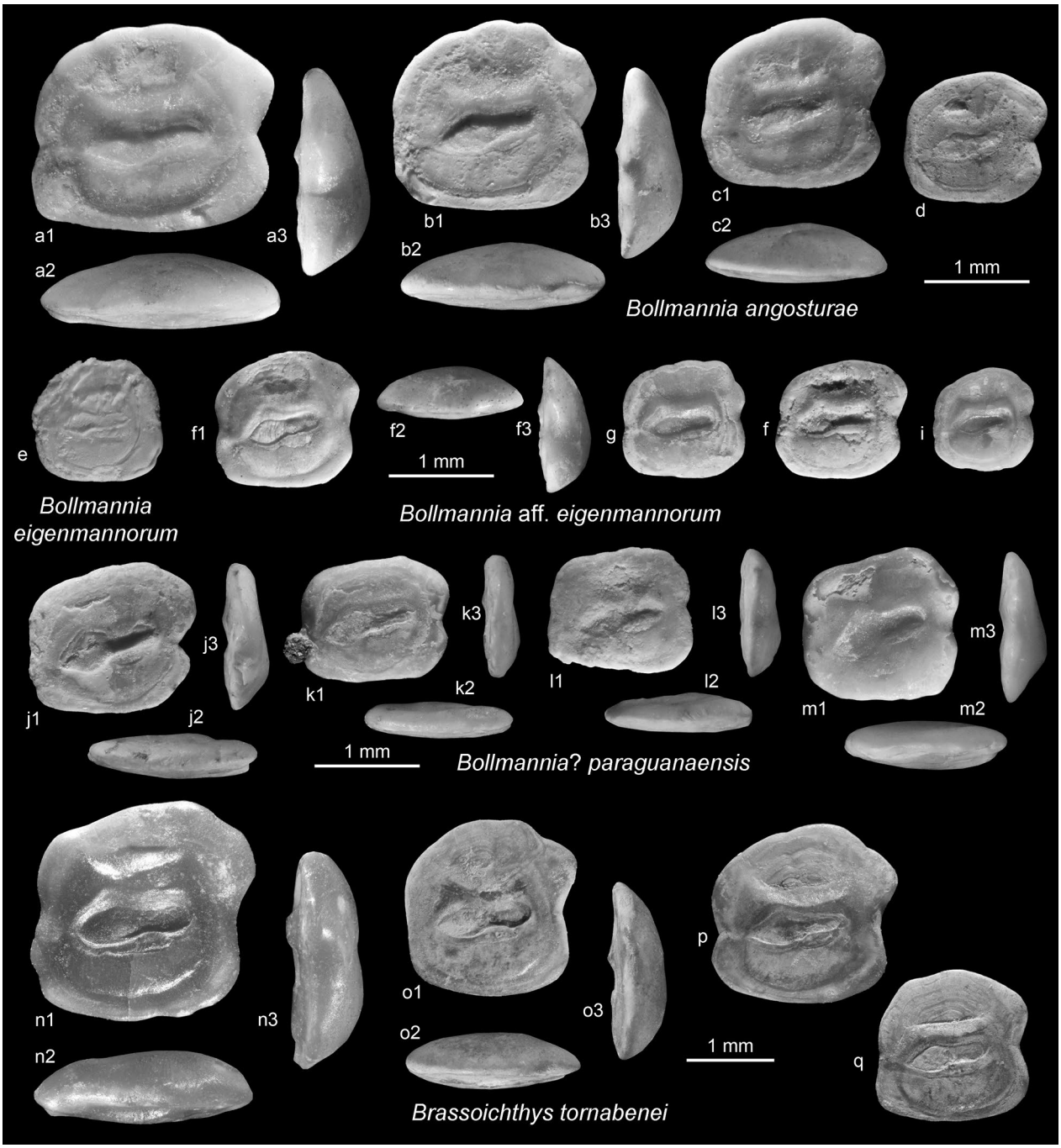


Fig. 21 **a**–**d** *Bollmannia angosturae* n. sp.; **a** holotype, NMB P15546, Angostura FM, Ecuador, PPP 3465; **b**–**d** paratypes; **b** Onzole FM, Ecuador, NMB 19084, NMB P15547; **c**–**d** Gatun FM, San Judas Tadeo, Panama, PPP 2167, NMB P15548-49. **e** *Bollmannia eigenmannorum* (Garman, 1896), extant, USNM 442038, Bonaire, SL 26 mm. **f–i** *Bollmannia* aff. *eigenmannorum* (Garman, 1986), Uscari FM, Limón, Costa Rica, PPP 3270, NMB P15550 (6 specimens). **j**–**m** *Bollmannia*? *paraguanaensis* n. sp.; **j**–**l** Cantaure FM, El Hatillo-1, Venezuela, PPP 2545, **j** holotype, NMB P15551, **k**, **l** paratypes, NMB P15552-53; **m** paratype, Tuira FM, Darien, Panama, PPP 1593, NMB P15554. **n**–**q** *Brassoichthys tornabenei* n. gen., n. sp., Brasso FM, Trinidad, Cb. 1852; **n** holotype, NMB P15555; **o–q** paratypes, NMB P680

Inner face nearly flat. Sulcus sole-shaped, narrow, small, with low ostial lobe, moderately deep, inclined at 7–12°. Caudal tip rounded. OL:SuL = 1.9–2.2. Subcaudal iugum long, narrow, often relatively weak. Dorsal depression wide, deep and distinct, open to dorsal rim of otolith and moderately close to sulcus with well-developed crista superior. Ventral furrow distinct, gently curved and clipping preventral and postventral tips of otolith. Outer face broadly convex, smooth.

Discussion Bollmannia angosturae is similar to the extant *B. eigenmannorum* (Fig. 21e) sharing the small and narrow and only slightly inclined sulcus and the weak preventral and postdorsal projections. It differs from the extant West Atlantic species in being more elongate (OL:OH = 1.05–1.15 vs 1.0–1.05) and the relatively weak subcaudal iugum.

***Bollmannia* aff. *eigenmannorum* (Garman, 1886)**

Figure 21f–i

Material 6 specimens Tortonian, Atlantic Costa Rica, Uscari FM, PPP 3270 (NMB P15550).

Discussion Six small specimens (< 1.4 mm in length) from the Uscari Formation of Costa Rica resemble the single known otolith of the extant *B. eigenmannorum* (Fig. 21e). However, the extant specimen is affected by formalin, and does not reveal all pertinent characteristics for comparison with the fossil otoliths. The allocation is therefore provisional. Extant specimens of *B. eigenmannorum* have been taken over muddy bottoms at depths of 36.5–170 m from the Florida Keys, throughout the Gulf of Mexico to Venezuela (Van Tassell et al., 2012).

***Bollmannia? paraguanaensis* n. sp.**

Figure 21j–m

Holotype NMB P15551 (Fig. 21j), late Burdigalian, Cantaure FM, Venezuela, PPP 2545.

Paratypes 3 specimens: 2 specimens same data as holotype (NMB P15552-53); 1 specimen Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1593 (NMB P15554).

Referred specimens 1 specimen late Burdigalian, Cantaure FM, Venezuela, PPP 2546.

Etymology After the Paraguaná Peninsula, Venezuela, where the type location is situated.

Diagnosis OL:OH = 1.02–1.15. Maximal size 1.55 mm (holotype). Otolith shape nearly rectangular with rounded predorsal, preventral, postdorsal and postventral angles. Otolith thin (OH:OT = 3.3–3.5). Sulcus long, with wide ostium and narrow cauda; OL:SuL = 1.55–1.65. Subcaudal iugum long, relatively narrow. Sulcus inclination angle 15–22°.

Description Otolith size up to 1.55 mm in length (holotype). Dorsal rim relatively low, nearly straight, slightly ascending towards posterior. Postdorsal projection blunt, not projecting beyond postventral angle, not bent outward; preventral angle orthogonal. Ventral rim straight, horizontal. Anterior and posterior rims nearly vertical, posterior rim with weak indentation at its middle. All rims smooth.

Inner face nearly flat. Sulcus sole-shaped, deep, inclined at 15–22°; ostium wide, with moderate ostial lobe, cauda narrow, straight. OL:SuL = 1.55–1.65. Subcaudal iugum long, narrow, often relatively weak. Dorsal depression indistinct, with weak crista superior. Ventral furrow distinct, gently curved and clipping preventral and postventral tips of otolith. Outer face nearly flat, smooth.

Discussion Bollmannia? *paraguanaensis* is only tentatively placed in the genus *Bollmannia*, primarily because of the long subcaudal iugum, which, however, is often rather poorly developed/visible. It differs from typical *Bollmannia* otoliths in the thin appearance caused by the nearly flat outer face and the relatively long sulcus. The single late Miocene specimen from Darien is more compressed than the ones from the early Miocene Cantaure Formation (OL:OH = 1.02 vs 1.07–1.15) indicating that potentially two separate species could be involved.

Genus *Brassoichthys* n. gen.

Type species Brassoichthys tornabenei n. sp.

Etymology Named after the type formation, the Brasso Formation of Trinidad.

Diagnosis A fossil otolith-based genus of the Gobiosomatini, *Microgobius* Group, *Bollmannia* clade with the following combination of characters. Otoliths nearly quadratic in outline with rounded dorsal rim and slightly expanded postdorsal projection; OL:OH = 0.98–1.03. Inner face flat; outer face mildly convex, smooth. Sulcus relatively large and wide but with low ostial lobe; OL:SuL = 1.7–1.85; sulcus inclination angle 7–10°. Subcaudal iugum moderately large. Dorsal depression deep; ventral furrow distinct, gently curving.

Discussion Brassoichthys is an easily recognizable otolith pattern that occupies a morphological position between the *Bollmannia* type and the *Microgobius* type pattern. The nearly equal OL:OH ratio of around 1.0 matches this intermediate position, with *Bollmannia* otoliths being more slender and those of *Microgobius* more compressed and high-bodied. The sulcus shape and expression of the subcaudal iugum matches those of both clades; the low sulcus inclination angle is to the lower end of the range found in the putatively related taxa.

Species A single species, *B. tornabenei*, from the early middle Miocene, Langhian, Brasso FM of Trinidad.

***Brassoichthys tornabenei* n. sp.**

Figure 21n–q

Holotype NMB P15555 (Fig. 21j), Langhian, Brasso FM, Trinidad, Cb. 1852.

Paratypes 5 specimens same data as holotype NMB P680.

Etymology Named in honor of Luke Tornabene (Seattle, Washington State) in recognition of his many contributions to the understanding of gobies from America.

Diagnosis See diagnosis of genus (monospecific genus).

Description Otolith size up to 2.45 mm in length (holotype); OL:OH = 0.98–1.03; OH:OT = 3.0–3.2. Otoliths nearly quadratic in outline with rounded dorsal rim and slightly expanded, blunt postdorsal projection. Ventral rim slightly curved, horizontal. Anterior and posterior rims nearly vertical, posterior rim with moderate indentation at its middle. All rims smooth or slightly undulating.

Inner face flat. Sulcus relatively large and wide but with low ostial lobe; OL:SuL = 1.7–1.85; sulcus inclination angle 7–10°. Subcaudal iugum moderately large, often relatively weak. Dorsal depression deep, wide, dorsally open to dorsal rim of otolith, well-marked to sulcus by distinct crista superior. Ventral furrow distinct, gently curving, moderately distant from ventral rim of otolith. Outer face mildly convex, smooth.

***Akko* clade**

Discussion The genus *Akko* was reviewed by Van Tassell and Baldwin (2004) and was deemed to contain three species: *Akko dionaea* Birdsong & Robbins, 1995, from the Atlantic off northern Brazil; *A brevis* (Günther, 1896) in the Pacific from El Salvador to Peru; and *A. rossi* Van Tassell & Baldwin, 2004, based on a single specimen from off El Salvador. *Akko* is characterized by a number of autapomorphic characters and its relationships have long been enigmatic. Van Tassell and Baldwin (2004) placed *Akko* in the *Microgobius* group of the Gobiosomatini and compared it to *Bollmannia* and *Parrella*. This placement is apparently supported by molecular phylogenetic analysis shown by Tornabene and Van Tassell (2014) and Tornabene et al. (2016). In the latter article and Tornabene et al. (2022), *Akko* is shown in a clade further containing *Parrella* and *Microgobius.* Based on otoliths we consider *Akko* and *Parrella* to constitute a separate clade, closely related, however, to a clade combining all *Microgobius* species.

Fishes of the genus *Akko* have a secretive lifestyle in burrows or covered in mud in the substrate at depth down to about 20 m (Froese & Pauly, 2023). The reduced eye size may be indicative of living in muddy environments or being hidden in the substrate (Birdsong & Robins, 1995) Their large, caninoid teeth suggest that they could be ambush hunters.

Otoliths are available from two of the three extant species of *Akko*, namely *A. dionaea* (Fig. 22b–c) and *A. brevis* (Fig. 22a), and of two of the five species of *Parrrella*, namely *P. ginsburgi* Wade, 1946 (Fig. 22h) and *P. lucretiae* (Eigenmann & Eigenmann, 1888) (Fig. 22n–o) both from the East Pacific. In addition, we place two new fossil otolith-based genera in this clade, namely *Cubaguanichthys* n. gen. and *Proparrella* n. gen. The otoliths of these genera are characterized by being slightly longer than or equally long as high, showing a recessed preventral angle (except in *Cubaguanichthys*, where it is projecting), lack or weak indentation of the posterior rim which is nearly vertical, a sole-shaped sulcus with low ostial lobe, and a distinct subcaudal iugum (sulcus reduced in size in

(See figure on next page.)

Fig. 22 **a** *Akko brevis* (Günther, 1864), extant, USNM 368666, 13°41′N 90°00′W, 13 m. **b**–**c** *Akko dionaea* Birdsong & Robins, 1995, extant, paratypes, USNM 329525, Brazil, 02°32′N 49°57′W, SL 80 and 83 mm. **d–e** *Akko canoa* n. sp.; **d** holotype, NMB P15556, Canoa FM, Ecuador, PPP 3363; **e** paratype, Canoa FM, Ecuador, NMB 19146, NMB P15557. **f** *Akko lobata* n. sp., holotype, NMB P15558, Yaviza FM, Darien, Panama, PPP 1566. **g** *Cubaguanichthys lanceolatus* n. gen., n. sp., holotype, NMB P15559, Cubagua FM, Venezuela, PPP 2568. **h**–**i** *Parrella ginsburgi* Wade, 1946; **h** extant, CAS ex SU 46827, Costa Rica, Gulf of Nicoya; **i** Armuelles FM, Pacific Panama, PPP 3236, NMB P 15560. **j** *Parrella* sp., Swan Cay FM, Swan Cay, Atlantic Panama, PPP 2221, NMB P15561. **k**–**m** *Parrella lucida* n. sp.; **k** holotype, NMB P690, Manzanilla FM, Trinidad, K 9833; **l**–**m** paratypes, **l** Shark Hole FM, Valiente Peninsula, Panama, PPP 2217, NMB P15562, **m** Cubagua FM, Venezuela, PPP 2653, NMB P15563. **n**–**o** *Parrella lucretiae* (Eigenmann & Eigenmann, 1888), extant, USNM 322734, 08°06′N 80°31′W

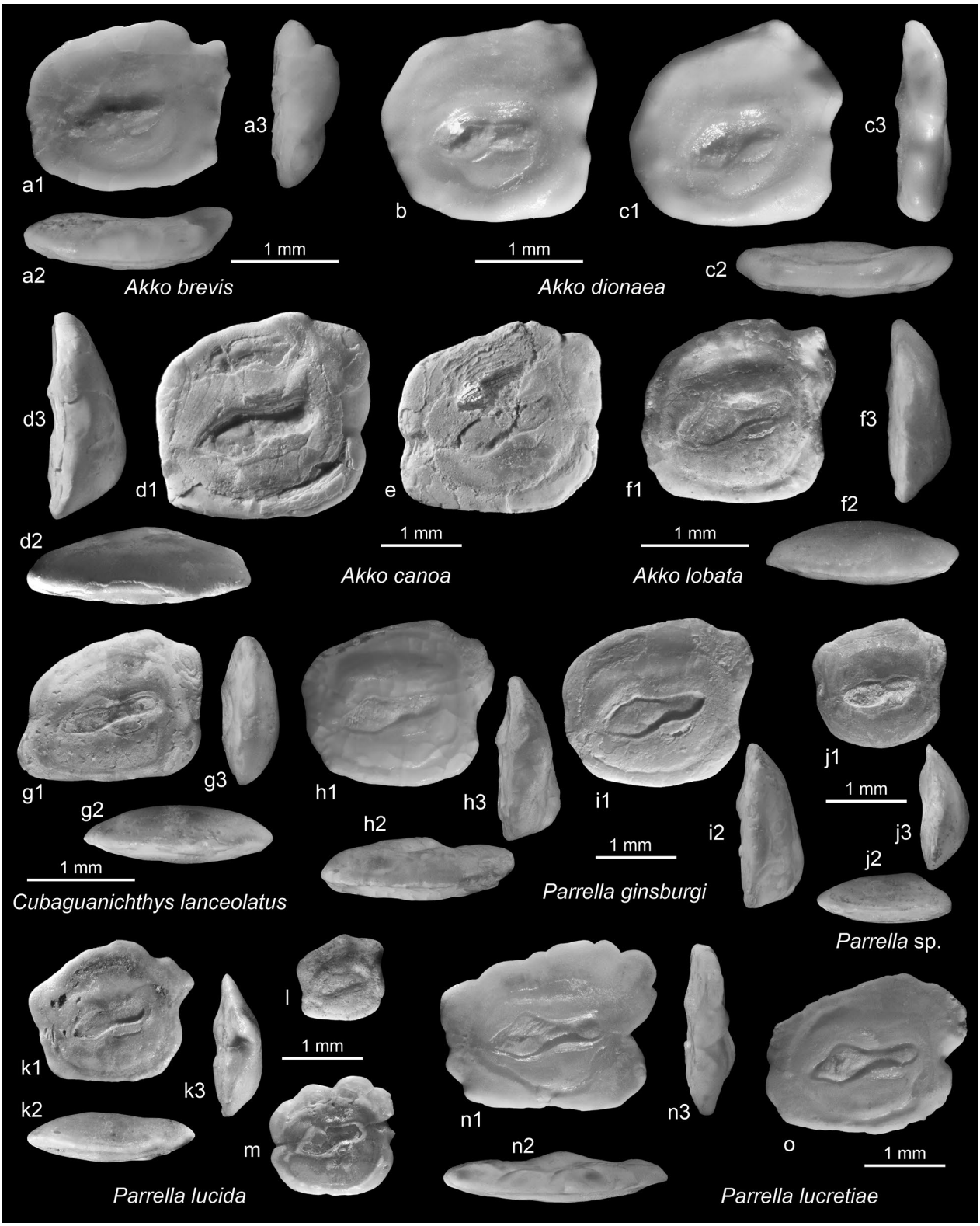


Fig. 22 (See legend on previous page.)

Akko). Otoliths of the proposed *Antilligobius* and *Microgobius* clades are higher than long.

Genus *Akko* Birdsong & Robins, 1995

***Akko canoa* n. sp.**

Figure 22d–e

Holotype NMB P15556 (Fig. 22d), Gelasian, Canoa FM, Ecuador, PPP 3363.

Paratypes 1 specimen, Gelasian, Canoa FM, Ecuador, NMB 19146 (NMB P15557).

Etymology After the type formation, the Canoa FM of Gelasian age in Ecuador.

Diagnosis OL:OH = 1.04–1.08. Maximal size 2.6 mm (holotype). Otolith shape nearly rectangular with postdorsal rim slightly elevated. Predorsal angle high, preventral angle orthogonal; posterior rim nearly vertical, without indentation and no marked postdorsal projection. Sulcus narrow, moderately small, with very low ostial lobe; OL:SuL = 1.8–1.9. Subcaudal iugum short, wide. Sulcus inclination angle 16–22°.

Description Otolith size up to 2.6 mm in length (holotype). OH:OT = 2.7. Dorsal rim relatively low, smooth, nearly straight, slightly ascending towards posterior. Predorsal angle high, rounded, no distinct postdorsal projection; preventral and postventral angles orthogonal. Ventral rim straight, horizontal. Anterior and posterior rims nearly vertical, posterior rim without marked indentation at its middle. All rims smooth.

Inner face flat in vertical direction, slightly bent in horizontal direction. Sulcus sole-shaped, moderately deep, narrow, inclined at 16–22°; low ostial lobe, cauda with rounded tip slightly bent upward. OL:SuL = 1.8–1.9. Subcaudal iugum short, wide. Dorsal depression indistinct, with indiscernible crista superior. Ventral furrow distinct, half-moon shaped and regularly curved at moderate distance from ventral rim of otolith. Outer face broadly convex, smooth.

Discussion Akko canoa resembles the otoliths of the two known species in shape and sulcus organization but differs in being thicker (OH:OT = 2.7 vs 3.0–3.6), the larger sulcus (OL:SuL = 1.8–1.9 vs 2.0–2.2) and the less strongly bent inner face which in the two extant species studied shows a distinct outward bent posterior region of the otolith. *Akko canoa* shows that a further species of the genus existed in the East Pacific other than the extant species.

***Akko lobata* n. sp.**

Figure 22f

Holotype NMB P15558 (Fig. 22f), Tortonian, Yaviza FM, Pacific Panama, Darien, PPP 1566.

Etymology From lobatus (Latin) = lobed, referring to the continuously curved anterior and dorsal rims.

Diagnosis OL:OH = 1.03. Size 1.75 mm (holotype). Anterior and dorsal rim continuously curved. Posterior rim nearly vertical, with weak and broad indentation. Sulcus narrow, moderately large, with moderate ostial lobe; OL:SuL = 1.6. Subcaudal iugum short, wide. Sulcus inclination angle 18°.

Description Otolith size up to 2.6 mm in length (holotype). OH:OT = 2.8. High-bodied otolith; anterior and dorsal rim continuously curved, postdorsal rim slightly elevated and with small indentation in front of postdorsal tip. Preventral angle rounded orthogonal; posterior rim nearly vertical, with weak and broad indentation and weak, blunt postdorsal projection. Ventral rim straight, horizontal. All rims smooth, dorsal rim slightly undulating.

Inner face nearly flat. Sulcus sole-shaped, moderately deep, long, inclined at 18°; moderate ostial lobe, cauda with rounded tip. OL:SuL = 1.6. Subcaudal iugum short, wide. Dorsal depression distinct, with poorly defined crista superior. Ventral furrow distinct, regularly curved close to ventral rim of otolith. Outer face broadly convex, smooth.

Discussion Akko lobata represents what one might envisage as a plesiomorphic otolith morphology for the genus where the sulcus is still relatively large, the ventral furrow close to the ventral rim of the otolith and the inner face is nearly flat. This character status is also observed in otoliths of *Bollmannia* and *Microgobius*.

Genus *Cubaguanichthys* n. gen.

Type species Cubaguanichthys lanceolatus n. sp.

Etymology Named after the type formation, the Cubagua Formation of Venezuela.

Diagnosis A fossil otolith-based genus of the Gobiosomatini, *Microgobius* Group, *Akko* clade with the following

combination of characters. Ventral rim straight, horizontal and posterior rim straight, vertical forming orthogonal angle; dorsal rim regularly curved, anteriorly depressed; preventral projection pointed, distinct; OL:OH = 1.2. Outer face convex, smooth. Sulcus long, narrow, with very low ostial lobe; OL:SuL = 1.8; sulcus inclination angle 16°. Subcaudal iugum short, wide, oval shaped. Ventral furrow distinct, close to ventral rim of otolith.

Discussion Cubaguanichthys has a highly distinctive otolith pattern that resembles otoliths of *Akko* in the straight, vertical posterior rim without indentation, the sulcus with a very low ostial lobe, and the wide, short subcaudal iugum. It differs in the more slender shape, the projecting preventral angle, and the long and narrow sulcus. The allocation of *Cubaguanichthys* to the *Microgobius* group and *Akko* clade of the Gobiosomatini therefore remains tentative. It also seems possible that *Cubaguanichthys* represents an exotic faunal element in the tropical West Atlantic of the Late Pliocene that had emigrated from another region, but we know of no gobiid otolith morphology from outside of the American taxa that would show any significant similarity.

Species A single species, *C. lanceolatus*, from the Early Pliocene, Zanclean, Cubagua FM, above Cerro Negro Member, of Venezuela.

***Cubaguanichthys lanceolatus* n. sp.**

Figure 22g

Holotype NMB P15559 (Fig. 22g), Zanclean, Cubagua FM, above Cerro Negro member, Venezuela, PPP 2568.

Etymology From lanceolatus (Latin) = lanceolate, referring to the pointed preventral angle.

Diagnosis See diagnosis of genus (monospecific genus).

Description Otolith size 1.7 mm in length; OL:OH = 1.2; OH:OT = 2.5. Ventral rim straight, horizontal and posterior rim straight, vertical forming orthogonal angle. Dorsal rim regularly curved, anteriorly depressed, highest posteriorly at moderately developed postdorsal angle; no postdorsal projection. Preventral projection pointed, distinct; posterior rim without indentation. All rims smooth, slight concavity on dorsal rim behind obtuse postdorsal angle.

Inner face slightly bent. Sulcus relatively long, very narrow, shallow, with very low ostial lobe; OL:SuL = 1.8; sulcus inclination angle 16°. Subcaudal iugum short, wide, nearly oval in shape. Dorsal depression indistinct. Ventral furrow distinct, close to ventral rim of otolith. Outer face distinctly convex, more than inner face, smooth.

***Genus Parrella* Ginsburg, 1938**

***Parrella ginsburgi* Wade, 1946**

Figure 22h–i

Material (fossil specimen) 1 specimen, Calabrian, Pacific Panama, Armuelles FM, PPP 323 (NMB P15560).

Discussion The single fossil specimen from the late Early Pleistocene perfectly matches the otoliths of the extant specimens of this species (Fig. 22h) that occurs in the same region. Typical is the recessed, rounded preventral angle, the high and projecting predorsal angle, the small concavity of the dorsal rim behind its highest point at the postdorsal angle, the shallow, even sulcus and the short but wide subcaudal iugum. Today, *P. ginsburgi* is found from the Gulf of California to Panama in nearshore, soft bottom habitats at depths at 1–10 m.

***Parrella lucida* n. sp.**

Figure 22k–m

Holotype NMB P690 (Fig. 22k), Zanclean, Manzanilla FM, Telemaque Member, Trinidad, K 9833.

Paratypes 3 specimens Zanclean: 2 specimens Shark Hole FM, Atlantic Panama, Valiente Peninsula, PPP 2217 (NMB P15562); 1 specimen, Cubagua FM above Cerro Negro Member, Venezuela, PPP 2653 (NMB P15563).

Etymology From lucidus (Latin) = clear, referring to the clear allocation of the holotype to the genus *Parrella*.

Diagnosis (holotype) OL:OH = 1.15. Maximal size 2.05 mm (holotype). Otolith shape dorsally expanded with predorsal angle and postdorsal projection projecting strongest. Sulcus narrow, short, with low ostial lobe; OL:SuL = 2.1. Subcaudal iugum moderately long and wide. Sulcus inclination angle 20°.

Description (holotype) Otolith size up to 2.05 mm in length (holotype). OH:OT = 2.9. Predorsal angle high, rather sharp and distinctly projecting; postdorsal projection also sharp and projecting resulting in longest axis of otolith shifted way above sulcus. Dorsal rim regularly curved, highest shortly behind its middle, undulating. Preventral and postventral angles rounded, recessed. Anterior rim straight, downward inclined; posterior rim

straight, downward inclined, with slight concavity below pointed postdorsal projection. Ventral rim straight, horizontal.

Inner face slightly convex. Sulcus sole-shaped, moderately deep, narrow, inclined at 20°; low ostial lobe, cauda with rounded tip. OL:SuL = 2.1. Subcaudal iugum moderately long, wide. Dorsal depression broad, indistinct. Ventral furrow distinct, regularly curved, relatively close to ventral rim of otolith. Outer face broadly convex, slightly more than inner face, smooth.

Remarks The paratypes associated with this species are distinctly smaller and show less clear characteristics than the holotype, which we consider an ontogenetic effect. However, with more specimens being recovered it could also appear that they represent juveniles of another species.

Discussion Parrella lucida differs from the known extant congeners in the otolith shape with the projecting predorsal and postdorsal regions and the relatively narrow sulcus. Today, a single species occurs in the West Atlantic, *P. macropteryx* Ginsburg, 1939, of which otoliths are not known.

Genus *Proparrella* n. gen.

Type species Proparrella darienensis n. sp.

Etymology Combination of pro (Latin) for before and the genus name *Parrella*, indicating its presumed plesiomorphic position as compared to *Parrella*.

Diagnosis A fossil otolith-based genus of the Gobiosomatini, *Microgobius* Group, *Akko* clade with the following combination of characters. Small otoliths to about 2 mm in length and nearly quadratic otolith shape with slightly elevated postdorsal region; OL:OH = 1.0–1.1. Postdorsal rim with conspicuous narrow concavity behind postdorsal angle and before blunt, short postdorsal projection. Sulcus long, narrow, with low ostial lobe and long, narrow, straight, sometimes tapering cauda; OL:SuL very variable, ranging from 1.5 to 2.2; sulcus inclination angle 12–18°. Subcaudal iugum moderately long, relatively narrow. Dorsal depression shifted dorsally with straight lower margin and broad crista superior. Ventral furrow distinct, close to ventral rim of otolith.

Discussion Proparrella is best recognized by the characteristic shape of the postdorsal region with the narrow concavity in front of a short, blunt postdorsal projection and the, at first perhaps, inconspicuous shape of the cauda. *Proparrella* resembles otoliths of *Akko* as well as *Parrella* and is therefore considered to represent a fossil genus related to these taxa. It differs from *Akko* in the shape of the cauda, the broad crista superior, and the relatively long sulcus (except a few tentatively assigned specimens; see below), which it shares with the most plesiomorphic species in that genus, *Akko lobata*. *Proparrella* differs from *Parrella* in being more compressed and in the shape of the dorsal rim and the broad crista superior. It appears plausible that *Proparrella* represented an extinct branch as a sister taxon to *Akko*.

Species At least two species: the widespread *Proparrella darienensis* n. sp., known from the Tortonian to Zanclean and distributed from Ecuador to Trinidad; and *P. pusilla* n. sp., known from the Tortonian and Messinian of Panama.

***Proparrella darienensis* n. sp.**

Figure 23a–m

Holotype NMB P15565 (Fig. 23a), Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1154.

Paratypes 12 specimens: 9 specimens Tortonian: 3 specimens Angostura FM, Ecuador, 1 specimen PPP 3297 (NMB P15572), 2 specimens NMB 19301 (NMB P15576-77); 1 specimen Tuira FM, Pacific Panama, Darien, PPP 1163 (NMB P15569); 2 specimens Yaviza FM, Pacific Panama, Darien, PPP 1566 (NMB P15567-68); 3 specimens Gatun FM, Atlantic Panama, PPP 2168 (NMB P15573-75). 3 specimens Zanclean: 1 specimen Cubagua FM, above Cerro Negro Member, Venezuela, PPP 2568 (NMB P15566); 2 specimens Cayo Agua FM, Atlantic Panama, PPP 1276 (NMB P15570-71).

Referred specimens 198 specimens: 183 specimens Tortonian: 11 specimens Angostura FM, Ecuador, 4 specimens PPP 3297, 6 specimens PPP 3301, 1 specimen PPP 3465; 15 specimens Tuira FM, Pacific Panama, Darien, 6 specimens PPP 1139, 1 specimen PPP 1593, 1 specimen PPP 1627, 4 specimens PPP 1163, 3 specimens PPP 1164; 64 specimens Yaviza FM, Pacific Panama, Darien, 6 specimens PPP 1607, 1 specimen PPP 1609, 2 specimens PPP 1528, 1 specimen PPP 1145, 3 specimens PPP 1620, 36 specimens PPP 1171, 4 specimens PPP 1565, 11 specimens PPP 1566; 93 specimens Gatun FM, Atlantic Panama, PPP 2168. 6 specimens Messinian: 1 specimen Chucunaque FM, Pacific Panama, Darien, PPP 1578; 3 specimens Manzanilla FM, Montserrat Member, Trinidad, PPP 2666; 2 specimens, La Tejita FM, Venezuela, Isla Margarita, PPP 3087. 9 specimens Zanclean, Cubagua

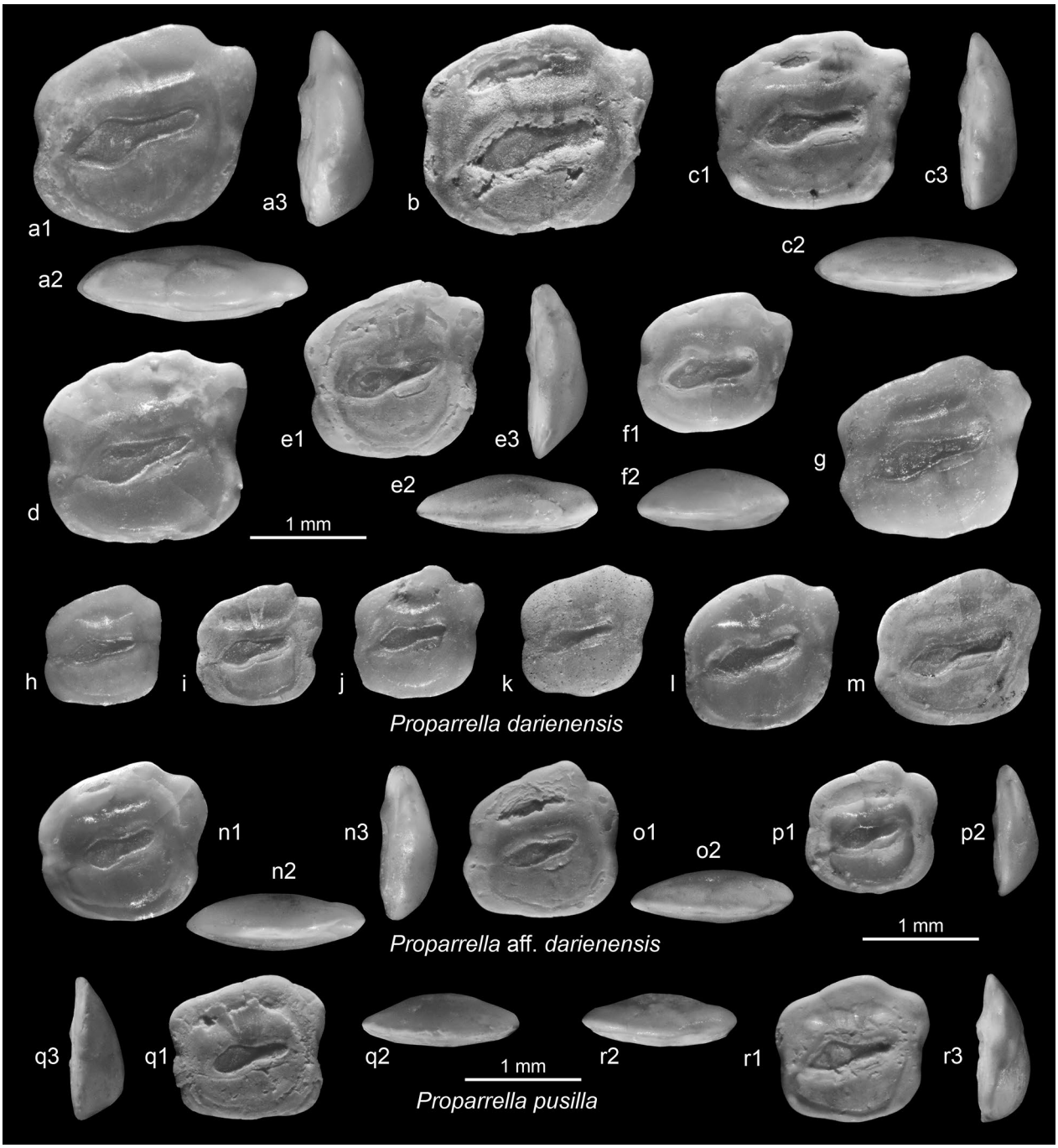


Fig. 23 **a**–**m** *Proparrella* n. gen. *darienensis* n. sp.; **a** holotype, NMB P15565, Tuira FM, Darien, Panama, PPP 1154; **b**–**m** paratypes, **b** Cubagua FM, Venezuela, PPP 2568, NMB P15566, **c**–**d** Yaviza FM, Darien, Panama, PPP 1566, NMB P15567-68, **e** Tuira FM, Darien, Panama, PPP 1163, NMB P15569, **f**, **k** Cayo Agua FM, Atlantic Panama, PPP 1276, NMB P15570-71, **g** Angostura FM, Ecuador, PPP 3297, NMB P15572, **h**, **j**, **l** Gatun FM, Atlantic Panama, PPP 2168, NMB P15573-75, **i**, **m** Angostura FM, Ecuador, NMB 19301, NMB P15576-77. **n**–**p** *Proparrella* aff. *darienensis* n. gen., n. sp.; Cubagua FM, Venezuela, PPP 2568, NMB P15583-85. **q**–**r** *Proparrella pusilla* n. gen., n. sp.; **r** holotype, NMB P15578, Gatun FM, Atlantic Panama, PPP 2168; **q** paratype, Chucunaque FM, Darien, Panama, PPP 1576, NMB P15582

FM, above Cerro Negro Member, Venezuela, 3 specimens PPP 2568, 6 specimens PPP 2571.

Etymology After Darien, Province in Panama, from which the holotype originates and which has yielded so many fossil gobiid otoliths.

Diagnosis OL:OH = 1.04–1.1. Maximal size 2.0 mm. Otolith shape nearly quadratic with postdorsal region slightly elevated. Postdorsal rim with conspicuous narrow concavity behind postdorsal angle and before blunt, short postdorsal projection. Sulcus long, narrow, with low ostial lobe and long, narrow, straight, sometimes tapering cauda; OL:SuL = 1.5–1.75; sulcus inclination angle 12–18°. Subcaudal iugum moderately long, relatively narrow. Dorsal depression shifted dorsally, with straight lower margin and broad crista superior. Ventral furrow distinct, close to ventral rim of otolith.

Description Otolith size up to 2.0 mm in length (holotype 1.9 mm). OH:OT = 2.4–2.9. Dorsal rim anteriorly straight, ascending from high predorsal angle to slightly elevated postdorsal angle, followed by narrow, distinct postdorsal concavity just before narrow, blunt, short postdorsal projection. Preventral and postventral angles rounded, nearly orthogonal. Ventral rim straight to slightly bent, horizontal. Anterior and posterior rims nearly vertical or slightly inclined downward, posterior rim without or with shallow and broad indentation at its middle. All rims smooth.

Inner face slightly convex. Sulcus sole-shaped, relatively deep, inclined at 12–18°; ostium relatively wide but with moderate ostial lobe; cauda long, narrow, straight, sometimes with tapering tip. OL:SuL = 1.5–1.75. Subcaudal iugum moderately long, relatively narrow. Dorsal depression long, shifted dorsally, with straight lower margin and broad crista superior. Ventral furrow distinct, regularly curved and relatively close to ventral rim of otolith. Outer face broadly convex, smooth.

Discussion Proparrella darienensis is a common, widespread and relatively small species of the Late Miocene and Early Pliocene that is best recognized by the specific shape of the dorsal rim, the overall quadratic shape and the shape of the cauda.

***Proparrella* aff. *darienensis* n. sp.**

Figure 23n–p

Material 4 specimens Zanclean, Cubagua FM, above Cerro Negro Member, Venezuela, PPP 2568 (figured specimens NMB P15583-85).

Discussion A few specimens from the Zanclean of the Cubagua FM in Venezuela differ from the typical *P. darienensis* specimens in the relatively short sulcus (OL:SuL = 2.0–2.2 vs 1.5–1.75) which may indicate the presence of a further species of *Proparrella*. However, the few specimens are only 1.1 to 1.4 mm in length and therefore do not warrant a clear definition.

***Proparrella pusilla* n. sp.**

Figure 23q–r

Holotype NMB P15578 (Fig. 23r), Tortonian, Gatun FM, Atlantic Panama, PPP 2168.

Paratypes 4 specimens: 3 specimens same data as holotype (NMB P15579-81); 1 specimen, Messinian, Chucunaque FM, Pacific Panama, Darien, PPP 1576 (NMB P15582).

Referred specimens 5 specimens Messinian, Chucunaque FM, Pacific Panama, Darien, 2 specimens PPP 1576, 3 specimens PPP 1578.

Etymology From pusillus (Latin) = teeny, small, referring to the small size of the specimens of this species.

Diagnosis OL:OH = 1.03–1.08. Maximal size 1.4 mm. Otolith shape nearly quadratic with similarly high and projecting predorsal angle and postdorsal projection. Dorsal rim relatively low with weak concavity behind postdorsal angle. Sulcus long, narrow, with low ostial lobe and long, narrow, straight cauda; OL:SuL = 1.75–2.0; sulcus inclination angle 12–14°. Subcaudal iugum moderately long, narrow. Dorsal depression indistinct. Ventral furrow distinct, close to ventral rim of otolith.

Description Otolith size up to 1.4 mm in length (holotype). OH:OT = 2.7–2.9. Dorsal rim anteriorly straight, posteriorly slightly concave, with broadly rounded, nearly centrally positioned postdorsal angle. Predorsal angle projecting, high, at about the level and strength of postdorsal projection resulting in nearly symmetrical otolith outline. Preventral and postventral angles rounded, slightly recessed. Ventral rim straight, horizontal. Anterior and posterior rims nearly straight, slightly inclined downward. All rims smooth.

Inner face nearly flat. Sulcus sole-shaped, relatively deep, inclined at 12–14°; ostium moderately wide with moderate ostial lobe; cauda long, narrow, straight. OL:SuL = 1.75–2.0. Subcaudal iugum moderately long, narrow, sometimes rather indistinct. Dorsal depression shallow, indistinct. Ventral furrow distinct, regularly curved and relatively close to ventral rim of otolith. Outer face broadly convex, smooth.

Discussion Despite of its small size, the otoliths of *P. pusilla* are relatively constant in expression and are therefore believed to represent a small species rather than juvenile specimens. The highly distinctive otolith outline and the relatively short sulcus distinguish it from its parallel occurring congener, *P. darienensis*.

Antilligobius clade

Discussion The genera *Antilligobius* and *Palatogobius* represent a clade of mesophotic gobies in the tropical West Atlantic generally occurring at depths of about 100 m to 300 m (Tornabene & Baldwin, 2017; Tornabene et al., 2016). They are shown as the sister group to genera here combined in the *Akko* and *Microgobius* clades of Tornabene et al. (2016) or the *Bollmannia* clade (Tornabene et al., 2022). *Antilligobius* is monospecific with *A. nikkiae* Van Tassell & Colin, 2012 (Fig. 24a–b), and *Palatogobius* contains three species, two of which are small, and otoliths are known from the largest, *P. grandoculus* Greenfield, 2002 (Fig. 25a).

The otoliths of the two genera share certain features that, despite their generally small size, mostly distinguish them well from juveniles of other gobiid taxa of the region. These features are the high-bodied shape with an OL:OH ratio of about 1.0 or less, a low sulcus inclination angle of 12° or less (mostly < 10°), and the stretch from the preventral to the postventral angle being longer than from the high-positioned predorsal angle to the postdorsal tip (no distinct postdorsal projection developed). This morphological pattern is reasonably similar to otoliths of the *Akko* and *Microgobius* clades and thus supports the phylogenetic analysis of Tornabene et al. (2016).

Genus *Antilligobius* Van Tassell & Tornabene, 2012

Antilligobius nikkiae Van Tassell & Colin, 2012

Figure 24a–i

Material (fossil specimens) 137 specimens: 1 specimen late Zanclean, upper Cayo Agua FM, Atlantic Panama, PPP 1188 (NMB P15592); 9 specimens Piacenzian, Escudo de Veraguas FM, Atlantic Panama: 6 specimens PPP 1241, 3 specimens PPP 2169. 97 specimens Gelasian: 36 specimens Escudo de Veraguas FM, Atlantic Panama, 34 specimens PPP 2170 (figured specimens NMB P15587-89), 1 specimen PPP 2173, 1 specimen PPP 2297; 47 specimens Bastimentos FM, Ground Creek Unit, Atlantic Panama, 18 specimens PPP 1252, 12 specimens PPP 1256 (figured specimen NMB P15586), 27 specimens PPP 3204 (figured specimen NMB P15591); 4 specimens Moin FM, Atlantic Costa Rica, PPP 2032. 30 specimens Calabrian, Swan Cay FM, Atlantic Panama, 24 specimens PPP 2221 (figured specimen NMB P15590), 6 specimens PPP 2531.

Description Otolith size up to 1.6 mm in length; OL:OH = 0.92–1.02; OH:OT = 3.2–3.7. Otolith shape high-bodied with predorsal angle positioned high and at same level as postdorsal tip; preventral and postventral angles well developed and longest horizontal section of otolith between them. Dorsal rim distinctly curved, sometimes irregularly undulating or highest at broad postdorsal angle. Ventral rim straight, horizontal. Anterior and posterior rims steep, dorsally inclined, with weak and broad central concavities. All rims smooth.

Inner face flat with region above ventral furrow and below dorsal depression slightly bulged. Sulcus small, narrow, relatively deep, with low ostial lobe; sulcus inclination angle 6–12°; OL:SuL = 1.9–2.1. Subcaudal iugum moderately long, wide. Dorsal depression large, wide, somewhat variably expressed. Ventral furrow distinct, regularly curved, relatively close to ventral rim of otolith. Outer face variably convex, smooth.

Discussion Antilligobius nikkiae is a common species in many of the deeper water sediments in the western Caribbean from Late Pliocene through Pleistocene. Today, *Antilligobius nikkiae* occurs hovering above the substrate in small schools at depth of about 100 to 200 m in the Caribbean (Tornabene et al., 2016).

Antilligobius collinsae n. sp.

Figure 24j–s

Holotype NMB P15593 (Fig. 24j), Piacenzian, Escudo de Veraguas FM, Atlantic Panama, PPP 1241.

Paratypes 9 specimens: 2 specimens Tortonian: 1 specimen Angostura FM, Ecuador, 1 specimen PPP 3301 (NMB P15602); 1 specimen Tuira FM, Pacific Panama, Darien, PPP 1132 (NMB P15594). 1 specimen Messinian, Chucunaque FM, Pacific Panama, Darien, PPP 1578 (NMB P15599). 1 specimen Zanclean, Cubagua FM, Cerro Negro Member, Venezuela, PPP 3055 (NMB P15601). 1 specimen, Gelasian, upper Escudo de Veraguas FM, Atlantic Panama, PPP 2170 (NMB P15600). 4 specimens Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 3202 (NMB P15595-98).

Referred specimens 141 specimens: 34 specimens Tortonian: 10 specimens Tuira FM, Pacific Panama, Darien, 3 specimens PPP 1132, 6 specimens PPP 1134, 1 specimen PPP 1164; 8 specimens Yaviza FM, Pacific Panama,

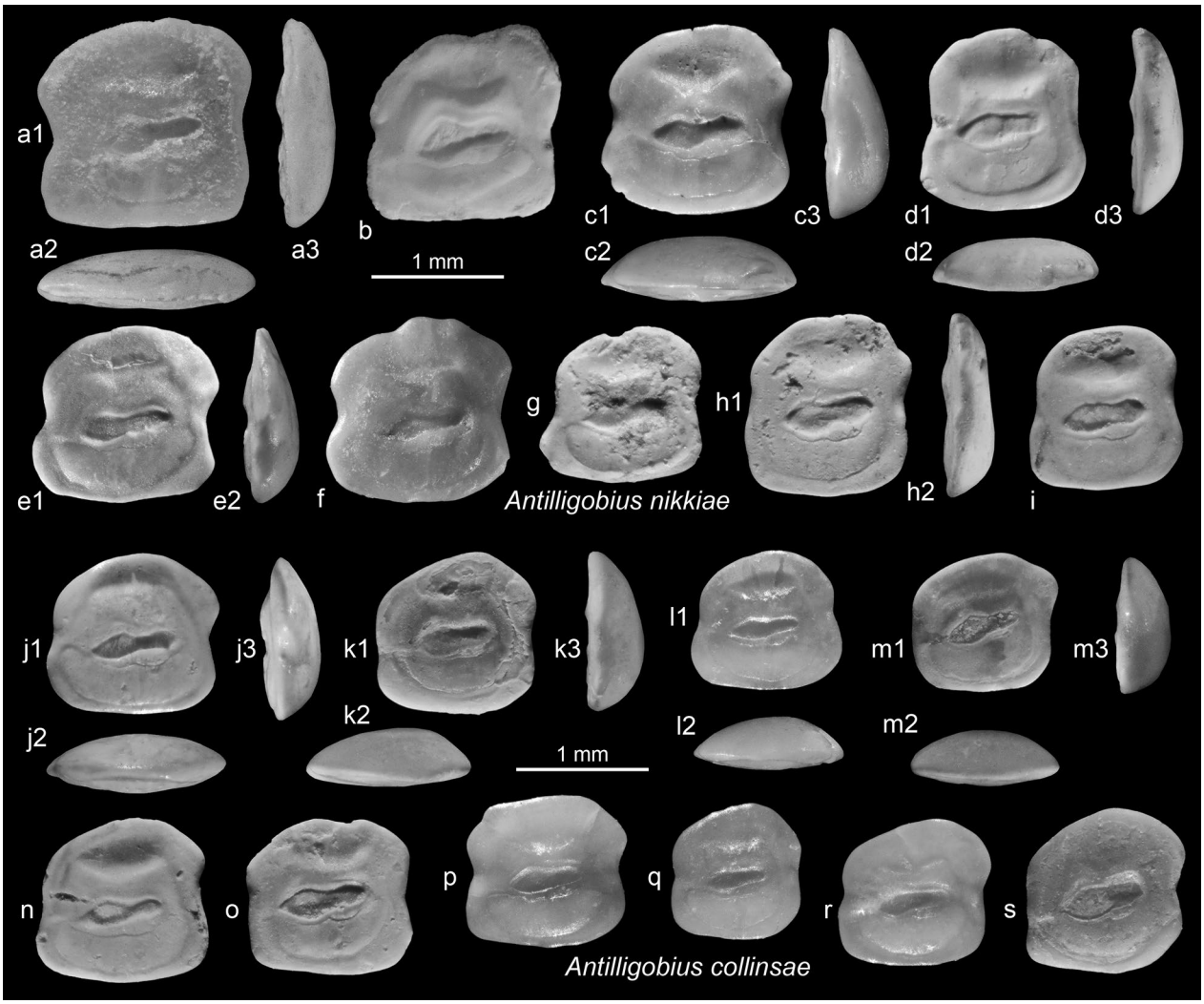


Fig. 24 **a**–**i** *Antilligobius nikkiae* Van Tassell & Colin, 2012; **a** extant, USNM 406127, Curacao, 78–133 m; **b** extant, USNM 442802, Sint Eustatius, SL 31 mm; **c** Bastimentos FM, Ground Creek Unit, Isla Bastimentos, Panama, PPP 1256, NMB P15586; **d**, **h**, **i** Escudo de Veraguas FM, Atlantic Panama, PPP 2170, NMB P15587-89; **e** Swan Cay FM, Atlantic Panama, PPP 2221, NMB P 15590; **f** Bastimentos FM, Ground Creek Unit, Isla Bastimentos, Panama, PPP 3204, NMB P15591; **g** Cayo Agua FM, Atlantic Panama, PPP 1188, NMB P15592. **j**–**s** *Antilligobius collinsae* n. sp.; **j** holotype, NMB P15593, Escudo de Veraguas FM, Atlantic Panama, PPP 1241; **k**–**s** paratypes; **k** Tuira FM, Darien, Panama, PPP 1132, NMB P15594; **l**, **p**–**r** Bastimentos FM, Ground Creek Unit, Bocas del Toro, Panama, PPP 3202, NMB P15595-98; **m** Chucunaque FM, Darien, Panama, PPP 1578, NMB P15599; **n** upper Escudo de Veraguas FM, Atlantic Panama, PPP 2170, NMB P15600; **o** Cubagua FM, Venezuela, PPP 3055, NMB P15601; **s** Angostura FM, Ecuador, PPP 3301, NMB P15602

Darien, PPP 1566; 16 specimens Gatun FM, Atlantic Panama, PPP 2167. 5 specimens Messinian, Chucunaque FM, Pacific Panama, Darien, PPP 1578. 6 specimens Zanclean: 3 specimens Cubagua FM, Venezuela, 1 specimen PPP 2556, 2 specimens PPP 3055; 3 specimens Springvale FM, Trinidad, KR 1216. 8 specimens Piacenzian, Escudo de Veraguas FM, Atlantic Panama, PPP 1241. 88 specimens Gelasian: 15 specimens, Gelasian, upper Escudo de Veraguas FM, Atlantic Panama, PPP 2170; 52 specimens Bastimentos FM, Ground Creek Unit, Atlantic Panama, 40 specimens PPP 3202, 3 specimens PPP 1256, 9 specimens PPP 3204; 21 specimens Moin FM, Atlantic Costa Rica, 4 specimens PPP 2032, 4 specimens PPP 2038, 7 specimens PPP 3259, 2 specimens PPP 3260, 4 specimens PPP 3262.

Etymology Named in honor of Laurel Collins (Florida International University) in recognition of her important contribution to the understanding of the geology and paleontology of the Isthmus of Panama.

Diagnosis OL:OH = 1.05–1.1; OH:OT = 2.65–2.8. Maximal size 1.3 mm. Otolith shape nearly quadratic with

predorsal angle positioned high and at same level as postdorsal tip. Sulcus short, narrow, with very low ostial lobe; OL:SuL = 1.85–2.05; sulcus inclination angle 6–12°. Subcaudal iugum moderately long, relatively narrow. Dorsal depression indistinct, small. Ventral furrow distinct, regularly curving, close to ventral rim of otolith.

Description Otolith size up to 1.3 mm in length (holotype 1.25 mm); Otolith shape high-bodied with predorsal angle positioned high and at same level as postdorsal tip; preventral and postventral angles well developed. Dorsal rim variably curved or relatively flat, with variable postdorsal tip, smooth. Ventral rim straight, horizontal. Anterior and posterior rims steep, without or with weak and broad central concavities. All rims smooth.

Inner face flat with region above ventral furrow and below dorsal depression slightly bulged. Sulcus small, narrow, relatively deep, with very low ostial lobe; sulcus inclination angle 6–12°; OL:SuL = 1.85–2.05. Subcaudal iugum moderately long, relatively narrow. Dorsal depression indistinct, mostly small. Ventral furrow distinct, regularly curved, relatively close to ventral rim of otolith. Outer face variably convex, smooth.

Discussion Antilligobius collinsae differs in only few subtle characters from the extant *A. nikkiae*, i.e., the slightly less compressed appearance (OL:OH 1.05–1.1 vs 0.92–1.02) and in being thicker (OH:OT = 2.65–2.8 vs 3.2–3.7). *Antilligobius collinsae* appears to represent a plesiomorphic counterpart to the extant species and occurs earlier in the stratigraphy in the Tortonian (Late Miocene) but shows a considerable stratigraphic overlap with *A. nikkiae* over the Piacenzian and Gelasian.

Genus *Palatogobius* Greenfield, 2002

Palatogobius grandoculus Greenfield, 2002

Figure 25a–g

Material (fossil specimens) 28 specimens: 19 specimens Zanclean, Cubagua FM, Venezuela: 4 specimens PPP 2554, 9 specimens PPP 3055 (figured specimen NMB P15608), 6 specimens PPP 3057 (figured specimens NMB P15603-04). 9 specimens Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama: 7 specimens PPP 1252 (figured specimen NMB P15607), 2 specimens PPP 3204 (NMB P15605-06).

Description Otolith size up to 1.3 mm in length; OL:OH = 0.92–1.0; OH:OT = 2.8–3.2. Otolith shape high-bodied with relatively regularly curved dorsal rim without prominent predorsal or postdorsal angles, highest at its middle. Ventral rim straight, horizontal. Preventral and postventral angles distinct, longest section of otolith between them. Anterior and posterior rims steep, dorsally inclined. All rims smooth.

Inner face flat with region above ventral furrow and below dorsal depression slightly bulged. Sulcus small, narrow, relatively deep, with very low ostial lobe; sulcus inclination angle 2–7°; OL:SuL = 2.1–2.6. Subcaudal iugum moderately long, relatively narrow. Dorsal depression large, wide, somewhat variably expressed. Ventral furrow distinct, regularly curved, moderately close to ventral rim of otolith. Outer face convex, smooth.

Discussion The otoliths of *Palatogobius grandoculus* are quite similar to those of *Antilligobius nikkiae*, differing in the more regularly curved dorsal rim without marked angles, the even smaller sulcus (OL:SuL = 2.1–2.6 vs 1.9–2.1) and the less inclined sulcus (2–7° vs 6–12°). The species occurs regularly but never very common since the Early Pliocene in deeper water sediments of Venezuela and Atlantic Panama. Today, *Palatogobius grandoculus* occurs hovering above the substrate in small schools at depth of about 220 to 280 m in the Caribbean (Tornabene et al., 2016).

Palatogobius magnus n. sp.

Figure 25h

Holotype NMB P15609 (Fig. 25h), Zanclean, Cayo Agua FM, Atlantic Panama, PPP 2240.

(See figure on next page.)

Fig. 25 **a**–**g** *Palatogobius grandoculus* Greenfield, 2002; **a** extant, USNM 438754, 15°34′N 61°28′W, 194 m; **b**–**c** Cubagua FM, Venezuela, PPP 3057, NMB P15603-04; **d**, **e** Bastimentos FM, Ground Creek Unit, Bocas del Toro, Panama, PPP 3204, NMB P15605-06; **f** Cubagua FM, Venezuela, PPP 3055, NMB P15608; **g** Bastimentos FM, Ground Creek Unit, Bastimentos Island, Panama, PPP 1252, NMB P15607. **h** *Palatogobius magnus* n. sp., holotype (h1 SEM picture), Cayo Agua FM, Atlantic Panama, PPP 2240, NMB P15609. **i**–**k** *Palatogobius pacificus* n. sp., Armuelles FM, Pacific Panama; **k** holotype, NMB P15610, PPP 3240, **i**–**j** paratypes, PPP 3237, NMB P15611-12. **l**–**q** *Palatogobius vantasselli* n. sp., Manzanilla FM, Trinidad, PPP 2666; **l** holotype, NMB P15613; **m**–**q** paratypes, NMB P15614-18. **r**–**u** *Palatogobius* sp.1, Cubagua FM, Venezuela, PPP 2571, NMB P15619-22. **v** *Palatogobius* sp.2, Tuira FM, Darien, Panama, PPP 1137, NMB P15623

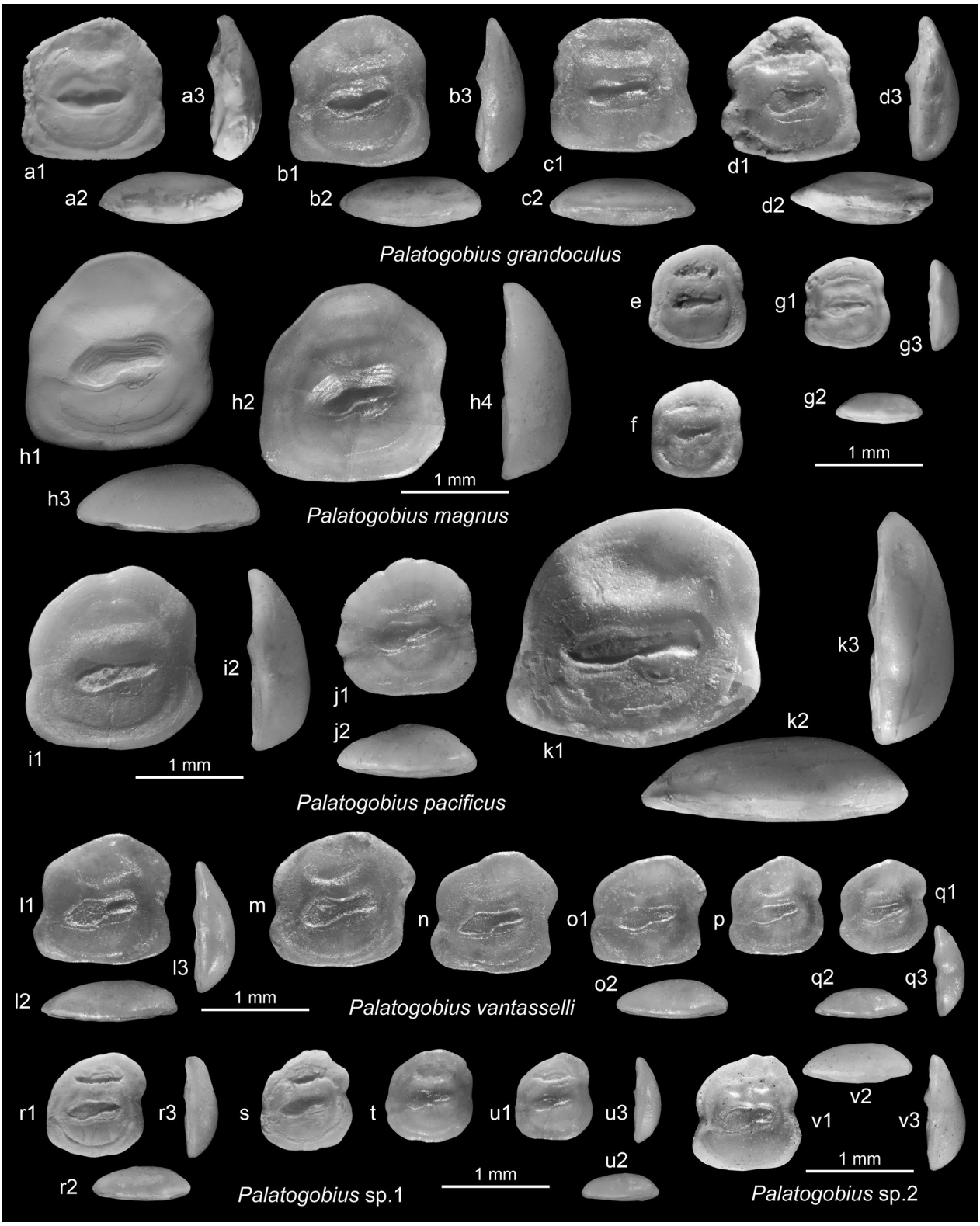


Fig. 25 (See legend on previous page.)

Etymology From magnus (Latin) = large, referring to the large size of the otolith.

Diagnosis Otolith size 1.7 mm in length. OL:OH = 0.92; OH:OT = 3.0. Otolith shape high-bodied with relatively regularly curved dorsal rim, highest at its middle. Inner face completely flat. Sulcus deep, short, relatively wide, with very low ostial lobe; OL:SuL = 2.0; sulcus inclination angle 11°. Subcaudal iugum moderately long, relatively narrow. Dorsal depression wide, with indistinct margins. Ventral furrow distinct, regularly curving, relatively distant from ventral rim of otolith.

Description Otolith size 1.7 mm in length. Otolith shape high-bodied with relatively regularly curved dorsal rim; dorsal rim highest at its middle, with rounded postdorsal tip and high, very gently rounded predorsal angle. Anterior and posterior rims near vertical; posterior rim with very wide and shallow concavity. Ventral rim straight, horizontal. Preventral angle well-developed, postventral angle broadly rounded. All rims smooth.

Inner face completely flat. Sulcus small, wide, deep, with very low ostial lobe; sulcus inclination angle 11°; OL:SuL = 2.0. Subcaudal iugum moderately long, well-developed and relatively wide. Dorsal depression large, wide, with indistinct margins, reaching close to sulcus. Ventral furrow distinct, regularly curved, relatively distant from ventral rim of otolith. Outer face evenly convex, smooth.

Discussion Palatogobius magnus is remarkable for its size, which immediately puts it apart from the extant *P. grandoculus* and the other two species, of which otoliths are not known, but which are distinctly smaller even than *P. grandoculus*. The otolith and sulcus shape, however, characterize the single, very well preserved holotype unequivocally in the genus *Palatogobius*.

***Palatogobius pacificus* n. sp.**

Figure 25i–k

Holotype NMB P15610 (Fig. 25k), Calabrian, Armuelles FM, Pacific Panama, PPP 3240.

Paratypes 2 specimens, Calabrian, Armuelles FM, Pacific Panama, PPP 3237 (NMB P15611-12).

Referred specimen 1 specimen same data as holotype.

Etymology Referring to the occurrence in the Pacific Ocean.

Diagnosis Otolith size up to 2.35 mm in length (holotype). OL:OH = 0.95–1.05; OH:OT = 2.6–3.0. Otolith shape high-bodied with regularly curved dorsal rim, highest at its middle. Inner face completely flat. Sulcus deep, short, narrow, with very low ostial lobe; OL:SuL = 1.85–2.05; sulcus inclination angle 5–10°. Subcaudal iugum short, very wide. Dorsal depression wide, with indistinct margins. Ventral furrow distinct, regularly curving, relatively close to ventral rim of otolith.

Description Otolith size up to 2.35 mm in length (holotype). Otolith shape high-bodied with regularly curved dorsal rim without prominent angles; dorsal rim highest at its middle or slightly behind. Anterior rim slightly inclined, posterior rim near vertical, with wide, indistinct concavity. Ventral rim straight or slightly bent, horizontal. Preventral angle well-developed, postventral angle rounded. All rims smooth.

Inner face completely flat. Sulcus small, narrow, deep, with very low ostial lobe; sulcus inclination angle 5–10°; OL:SuL = 1.85–2.05. Subcaudal iugum moderately long, well-developed and very wide. Dorsal depression large, wide, with indistinct margins, not reaching close to sulcus. Ventral furrow distinct, regularly curved, relatively close to ventral rim of otolith. Outer face evenly convex, smooth.

Discussion Palatogobius pacificus represents the only species of the genus in the East Pacific while all extant species are strictly West Atlantic. It is also the largest species in the genus, larger even than *P. magnus* from the Early Pliocene of the Atlantic side of Panama. *Palatogobius pacificus* differs from *P. magnus* in the more regularly curved dorsal rim, and the narrower sulcus. Both species likely represented geminate species on either side of the Isthmus of Panama.

***Platogobius vantasselli* n. sp.**

Figure 25l–q

Holotype NMB P15613 (Fig. 25l), Messinian, Manzanilla FM, Montserrat Member, Trinidad, PPP 2666.

Paratypes 5 specimens same data as holotype (NMB P15614-18).

Referred specimen 51 specimens: 1 specimen Tortonian: Manzanilla FM, San José Member, Trinidad, PPP 2669. 50 specimens Messinian: 45 specimens same data as holotype; 5 specimens Manzanilla FM, Montserrat Member, Trinidad, PPP 2677.

Etymology Named in honor of James Van Tassell (New York) in recognition of his many contributions to the understanding of gobies from America.

Diagnosis Otolith size up to 1.32 mm in length. OL:OH = 0.95–1.05; OH:OT = 2.8–3.2. Otolith shape high-bodied with regularly curved dorsal rim, highest near its middle and symmetrically developed predorsal angle and short postdorsal projection. Inner face completely flat. Sulcus deep, short, narrow, with low ostial lobe; OL:SuL = 1.9–2.0; sulcus inclination angle 10–15°. Subcaudal iugum long, narrow. Dorsal depression small, with distinct margins, not reaching close to sulcus. Ventral furrow distinct, close to ventral rim of otolith.

Description Otolith size up to 1.32 mm in length (holotype 1.28 mm). Otolith shape high-bodied with regularly curved dorsal rim highest near its middle. Predorsal angle and postdorsal projection similarly developed and nearly symmetrical. Anterior rim slightly inclined, posterior rim near vertical, both with wide, shallow central concavity. Ventral rim straight, horizontal. Preventral angle well-developed, sometimes projecting, postventral angle less pronounced. All rims smooth.

Inner face completely flat. Sulcus small, moderately narrow, deep, with low ostial lobe; sulcus inclination angle 10–15°; OL:SuL = 1.9–2.0. Subcaudal iugum long, narrow. Dorsal depression relatively small, cup-shaped, not reaching close to sulcus. Ventral furrow distinct, regularly curved, relatively close to ventral rim of otolith. Outer face evenly convex, smooth.

Discussion Palatogobius vantasselli differs from its later congeners in the more pronounced predorsal angle and postdorsal projection, the mild concavities at the anterior and posterior margins, the steeper sulcus inclination angle (10–15° vs 2–11°) and the relatively narrow subcaudal iugum. These features are all considered plesiomorphic for the genus and would thus indicate that *P. vantasselli* might be positioned near the base of the *Antilligobius* clade.

Palatogobius sp. 1

Figure 25r–u

Material 65 specimens Zanclean, Cubagua FM, Venezuela, 5 specimens PPP 2556, 3 specimens PPP 2563, 4 specimens PPP 3057, 31 specimens PPP 2568, 22 specimens PPP 2571 (figured specimens NMB P15619-22).

Discussion The Cubagua FM of Venezuela has yielded a number of small gobiid otoliths not exceeding 0.9 mm in length that appear to represent a species of *Palatogobius*. In the light the Early Pliocene age and the fact that otoliths of two very small extant *Palatogobius* living in the Caribbean are not known, these otoliths are here referred to in open nomenclature.

Palatogobius sp. 2

Figure 25v

Material 1 specimen Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1137 (NMB P15623).

Discussion A single small (1 mm long), high-bodied otolith (OL:OH = 0.94) from the Tortonian of Darien may possibly represent another species of *Palatogobius* similar to *P. vantasselli* but because of its small size and singular occurrence we refrain from description.

Microgobius clade

Discussion In this informal clade we combine *Microgobius* and the fossil otolith-based genus *Magnogobius* n. gen. that share a specific otolith morphology characterized by an otolith shape which is higher than long, the inner face being more or less strongly bent in the horizontal direction, and a large sulcus, often with a distinct ostial lobe and with a large subcaudal iugum.

Genus *Magnogobius* n. gen.

Type species Magnogobius grandis n. sp.

Etymology Combination of magnus (Latin) for large and the genus name *Gobius*, indicating the large size of the otoliths that infers also a large size of the fishes from which they originated, and also as antagonism to the name of the putatively related genus *Microgobius*.

Diagnosis A fossil otolith-based genus of the Gobiosomatini, *Microgobius* Group, *Microgobius* clade with the following combination of characters. Large otoliths to about 3.3 mm in length and high-bodied with an elevated postdorsal region and a broad predorsal angle and postdorsal projection; OL:OH = 0.83–0.97. Sulcus large, with a wide ostium and a pronounced ostial lobe; cauda long, narrow, straight, slightly deepened; OL:SuL = 1.3–1.5; sulcus inclination angle 12–20°. Subcaudal iugum very long, distinct, narrow. Dorsal depression small, only above central part of sulcus. Ventral furrow distinct, anteriorly not extending beyond ostium.

Discussion Magnogobius is recognized by its large size in combination with a high-bodied shape, the large sulcus with a distinct ostial lobe, the narrow, long, and distinct subcaudal iugum, and the small dorsal depression. The otolith size and the expression of the ostial lobe and the subcaudal iugum are the main features distinguishing *Magnogobius* from the otoliths of the putatively related *Microgobius*. Otoliths are known from all other large-growing extant American gobioid genera, and none of them resemble *Magnogobius* in any significant way. It cannot, however, be entirely ruled out that *Magnogobius* is of an exotic origin in the Miocene and Pliocene of the West Atlantic and that the genus is related to one outside of America. For instance, otoliths of the West African *Porogobius schlegeli* (Günther, 1861) somewhat resemble *Magnogobius* in the distinct and long subcaudal iugum and the distinct ostial lobe, but they have a massive postdorsal projection and a concave outer face not matched in *Magnogobius* otoliths. We therefore interpret *Magnogobius* as representing an extinct genus of the Gobiosomatini, *Microgobius* group, and possibly related to the genus *Microgobius*.

Species Two species: *Magnogobius costaricensis* n. sp. from the Tortonian of Panama, Darien to the Piacenzian of Atlantic Costa Rica and Panama, and *Magnogobius grandis* n. sp. from the Tortonian of Panama, Darien and the Tortonian to Gelasian of the Dominican Republic, Atlantic Costa Rica and Panama.

***Magnogobius costaricensis* n. sp.**

Figure 26a–g

Holotype NMB P15624 (Fig. 26a), Piacenzian, Río Banano FM, Atlantic Costa Rica, PPP 1732.

Paratypes 7 specimens: 5 specimens Piacenzian, Río Banano FM, Atlantic Costa Rica; 1 specimen PPP 676 (NMB P15629); 4 specimens same data as holotype (NMB P15625-28). 1 specimen late Zanclean, upper Cayo Agua FM, Atlantic Panama, PPP 1188 (NMB P15630). 1 specimen Tortonian, Yaviza FM, Pacific Panama, Darien, PPP 1609 (NMB P15631).

Referred specimen 6 specimens: 1 specimen Tortonian, Yaviza FM, Pacific Panama, Darien, PPP 1609. 1 specimen Zanclean, upper Cayo Agua FM, Atlantic Panama, PPP 1188. 5 specimens Piacenzian: 4 specimens Río Banano FM, Atlantic Costa Rica, PPP 1732.

Etymology Referring to Costa Rica where the holotype was found.

Diagnosis Otolith size up to 2.25 mm in length. OL:OH = 0.9–0.97. Otolith shape high-bodied; dorsal rim irregularly curved, with pronounced postdorsal angle and slight postdorsal projection; predorsal angle slightly projecting. Inner face slightly convex. Sulcus long, moderately wide, with distinct ostial lobe and deepened cauda; OL:SuL = 1.35–1.5; sulcus inclination angle 12–17°. Subcaudal iugum long, narrow. Dorsal depression small, oval, only above central part of sulcus.

Description Otolith size up to 2.25 mm in length (holotype). OH:OT = 3.0–3.3. Otolith shape high-bodied with irregularly curved dorsal rim highest at its postdorsal angle. Predorsal angle rounded, often slightly projecting; postdorsal projection blunt or rounded, slightly projecting. Anterior and posterior rims vertical to slightly inclined towards ventral; posterior rim with or without shallow central concavity. Ventral rim straight to slightly bent, horizontal. Preventral angle recessed, postventral angle rounded. All rims smooth except dorsal rim often irregularly undulating.

Inner face slightly convex, particularly in horizontal direction. Sulcus long, moderately wide, with distinct ostial lobe; cauda straight, with rounded tip, slightly upward bent and slightly deepened; sulcus inclination angle 12–17°; OL:SuL = 1.35–1.5. Subcaudal iugum long, narrow, distinct. Dorsal depression small, oval, only above central part of sulcus. Ventral furrow distinct, moderately close to ventral rim of otolith, anteriorly terminating at tip of ostium. Outer face evenly convex, relatively smooth.

(See figure on next page.)

Fig. 26 **a**–**g** *Magnogobius costaricensis* n. gen., n. sp.; **a** holotype, NMB P15624, Río Banano FM, Limón, Costa Rica, PPP 1732; **b**–**g** paratypes; **b** Río Banano FM, Limón, Costa Rica, PPP 676, NMB P15629; **c**, **f**, **g** Río Banano FM, Limón, Costa Rica, PPP 1732, NMB P15625-28; **d** Cayo Agua FM, Bocas del Toro, Panama, PPP 1188, NMB P15630; **e** Yaviza FM, Darien, Panama, PPP 1609, NMB P15631. **h**–**o** *Magnogobius grandis* n. gen., n. sp.; **h** holotype, NMB P386, Cercado FM, Dominican Republic, NMB 16915; **i**–**o** paratypes; **i**, **l** Cercado FM, Dominican Republic, NMB 16918, **i** NMB P386, **l** NMB P15632; **j** Cayo Agua FM, Bocas del Toro, Panama, PPP 2222, NMB P15633; **k** Cercado FM, Dominican Republic, NMB 16916, NMB P403; **m** Río Banano FM, Limón, Costa Rica, PPP 1732, NMB P15636; **n** Cayo Agua FM, Bocas del Toro, Panama, PPP 1188, NMB P15637; **o** Tuira FM, Darien, Panama, PPP 1163, NMB P15638

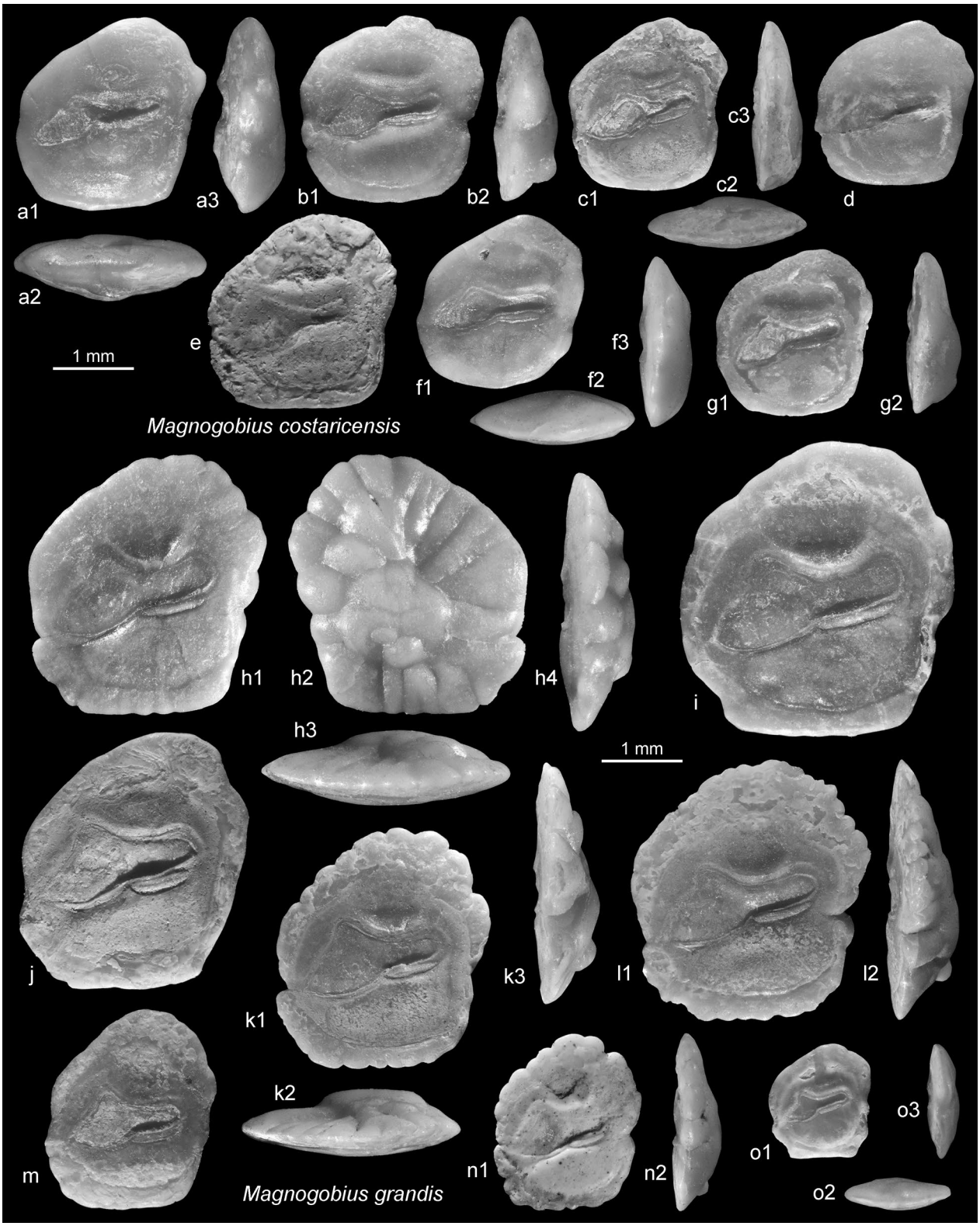


Fig. 26 (See legend on previous page.)

Discussion Magnogobius costaricensis does not grow to the large sizes observed in *M. grandis* n. sp. and further differs in the narrower sulcus, the less strongly developed ostial lobe and the oval dorsal depression. Both species occur parallel in space and time.

***Magnogobius grandis* n. sp.**

Figure 26h–o

1992 Gobiidae sp. 1—Nolf & Stringer: pl. 17, Fig. 12.

Holotype NMB P386 (Fig. 26h), Tortonian, Cercado FM, Dominican Republic, NMB 16915.

Paratypes 11 specimens: 8 specimens Tortonian: 7 specimens Cercado FM, Dominican Republic; 2 specimens NMB 16918 (NMB P15632); 2 specimens, NMB 16916 (NMB P403); 1 specimen NMB 16923 (NMB P405); 2 specimens NMB 15903 (NMB P389); 1 specimen Tuira FM, Pacific Panama, Darien, PPP 1163 (NMB P15638). 2 specimen Zanclean, Cayo Agua FM, Atlantic Panama, 1 specimen PPP 2222 (NMB P15633), 1 specimen PPP 1188 (NMB P 15637). 1 specimen Piacenzian, Río Banano FM, Atlantic Costa Rica, PPP 1732 (NMB P15636).

Referred specimen 22 specimens: 6 specimens Tortonian: 3 specimens Tuira FM, Pacific Panama, Darien, 1 specimen PPP 1627, 1 specimen PPP 1154, 1 specimen PPP 1164; 2 specimens Cercado FM, Dominican Republic, NMB 16923. 12 specimens Zanclean, Atlantic Panama: 1 specimen Shark Hole FM, PPP 2219; 11 specimens Cayo Agua FM, 6 specimens PPP 1276, 5 specimens, PPP 1188. 3 specimens Piacenzian, Río Banano FM, Atlantic Costa Rica, 1 specimen PPP 676, 2 specimens PPP 1732. 1 specimen Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 1252.

Etymology From grandis (Latin) large, referring to the large size of the otoliths.

Diagnosis Otolith size up to 3.3 mm in length. OL:OH = 0.83–0.92. Otolith shape high-bodied; dorsal rim regularly curved, crenulated, with rounded postdorsal angle and slight postdorsal projection; predorsal angle slightly projecting. Inner face slightly convex. Sulcus long, wide, with strong ostial lobe and deepened cauda; OL:SuL = 1.35–1.5; sulcus inclination angle 15–20°. Subcaudal iugum long, narrow, distinct. Dorsal depression small, cup-shaped, only above central part of sulcus and close to sulcus.

Description Otolith size up to 3.3 mm in length (holotype 2.9 mm). OH:OT = 3.4–3.7. Otolith shape high-bodied with regularly curved dorsal rim highest at its postdorsal angle and usually crenulated. Predorsal angle rounded, often slightly projecting; postdorsal projection blunt or rounded, slightly projecting. Anterior and posterior rims vertical to slightly inclined towards ventral; posterior rim usually straight. Ventral rim straight to slightly bent, horizontal. Preventral angle recessed, postventral angle rounded. All rims crenulated to various extents.

Inner face slightly convex, particularly in horizontal direction. Sulcus long, wide, with strong, often sharp ostial lobe; cauda straight, with rounded tip, slightly upward bent and slightly deepened; sulcus inclination angle 15–20°; OL:SuL = 1.35–1.5. Subcaudal iugum long, narrow, distinct. Dorsal depression small, cup-shaped, only above central part of sulcus; separated from sulcus only by narrow crista superior. Ventral furrow distinct, moderately close to ventral rim of otolith, anteriorly terminating below tip of ostium. Outer face convex, intensely ornamented.

Discussion Magnogobius grandis differs from *M. costaricensis* in the larger size the otoliths can attain, the larger sulcus with the more strongly developed ostial lobe, the more evenly curved and crenulated dorsal rim, the strongly ornamented outer face and the more steeply inclined sulcus (15–20° vs 12–17°). Both species occur parallel in a number of locations.

Genus *Microgobius* Poey, 1876

Discussion Fricke et al. (2023) list 15 valid extant *Microgobius* species, six in the West Atlantic and nine in the East Pacific. Otoliths are available from all Atlantic species and from the majority of Pacific species except for *Microgobius cyclolepis* Gilbert, 1890, *M. emblematicus* Jordan & Gilbert, 1882, *M. miraflorensis* Gilbert & Starks, 1904, and *M. urraca* Tornabene, van Tassell & Robertson, 2012. We distinguish four groups (otolith plexus) within the genus based on certain otolith patterns:

The *Microgobius gulosus* otolith plexus containing the extant *M. gulosus* (Girard, 1858) (Fig. 27a) and *M. microlepis* Longley & Hildebrand, 1940 (Fig. 27i), from the West Atlantic; and *M. tabogensis* Meek & Hildebrand, 1928 (Fig. 27c–d), from the East Pacific. The otoliths of this plexus are characterized by the lowest height (OL:OH = 0.86–0.97) and an almost rectangular outline.

The *Microgobius carri* otolith plexus containing the extant *M. carri* Fowler, 1945 (Fig. 28a), *M. meeki* Evermann & Marsh, 1899 (Fig. 28i), *M. signatus* Poey, 1876 (Fig. 28d), and *M. thalassinus* Jordan & Gilbert, 1883 (Fig. 29h–i), from the West Atlantic; and *M. brevispinis*

Ginsburg, 1939 (drawing of otolith provided by D. Nolf), and *M. crocatus* Birdsong, 1968 (Fig. 28j–l), from the East Pacific. The otoliths of this plexus are distinctly more high-bodied than those of the *Microgobius gulosus* plexus (OL:OH = 0.77–0.88 vs 0.86–0.97) and are usually associated with a highly curved dorsal rim.

The *Microgobius erectus* otolith plexus containing the extant *M. curtus* Ginsburg, 1939 (Fig. 30m), and *M. erectus* Ginsburg, 1938 (Fig. 30n), from the East Pacific. The otoliths of this plexus are characterized by a similarly high-bodied shape as the *Microgobius carri* plexus but are distinguished by the longest axis of the otolith being shifted dorsally to the predorsal angle and postdorsal projection. This shift of the axis is primarily caused by the anterior rim being inclined ventrally, while in other *Microgobius* otoliths the anterior rim is either vertical or inclined towards dorsal.

The *Microgobius camur* otolith plexus is exclusively composed of fossil otolith-based species, with four species from the West Atlantic and one specimen in open nomenclature from the East Pacific. Since otoliths are known from all West Atlantic *Microgobius* species but not from all East Pacific species, it is possible that this plexus is represented today only in the East Pacific.

The composition of the *Microgobius* otoliths in these four otolith plexuses is only meant to be for comparison purposes and does not imply in any way possible phylogenetic relationships within the genus. In his review of the genus, Birdsong (1981) commented on an unpublished study by Ginsburg that was to define seven subgenera. Birdsong himself, however, stated that he has "come to many tentative conclusions, but only one seems worth mentioning: I don't know how they are related to each other." In a study about the speciation in Gobiosomatini that also included molecular phylogenetic data, Rüber et al. (2003) presented a cladogram containing six *Microgobius* species plus one *Microgobius* sp. Their phylogenetic association of the six species of *Microgobius* partly coincides with the otolith plexus grouping and partly does not.

Extant *Microgobius* species occur mostly in shallow, near-shore waters, although a few have been caught at a depth to 30 m, such as *M. erectus* and *M. cyclolepis* (Birdsong, 1981). Some species typically occur in mangrove environments, such as *M. meeki*, *M. curtus*, *M. crocatus*, and *M. tabogensis* (Birdsong, 1981). Certain species tolerate varying salinity levels and are commonly found in estuarine environments, such as *M. gulosus* and *M. miraflorensis*, and burrowing also appears to be not uncommon in the species of this genus, as, for instance, in *M. carri*, *M. microlepis*, and *M. gulosus* (Birdsong, 1981).

Microgobius gulosus otolith plexus

Microgobius gulosus (Girard, 1858)

Figure 27a–b

Material 2 specimens late Zanclean, upper Cayo Agua FM, Atlantic Panama, PPP 1188 (NMB P15639).

Discussion Microgobius gulosus has the most compressed otoliths known so far from extant species in the genus, with an OL:OH ratio of 0.95–0.97, caused primarily by the rather low dorsal rim, and a relatively small sulcus (OL:SuL = 1.65–1.85). Two well-preserved specimens from the Late Pliocene of Atlantic Panama are reported south of the southernmost extant occurrence, which according to Froese and Pauly (2023) is the Yucatan Peninsula of Mexico. *Microgobius gulosus* is known to commonly live in burrows (Birdsong, 1981).

Microgobius cantaurensis n. sp.

Figure 27e–h

1998 Gobiidae indet.—Nolf & Aguilera: pl. 15, Fig. 9–11.

Holotype NMB P15641 (Fig. 27f), Burdigalian, Cantaure FM, Venezuela, PPP 2539.

Paratypes 6 specimens: 2 specimens Burdigalian, same data as holotype (NMB P15642-43). 4 specimens Tortonian: 1 specimen Gatun FM, Atlantic Panama, PPP 2165

(See figure on next page.)

Fig. 27 **a**–**b** *Microgobius gulosus* (Girard, 1858); **a** extant, CAS ex SU 5507, Galveston Bay; **b** Cayo Agua FM, Bocas del Toro, Panama, PPP 1188, NMB P15639. **c**–**d** *Microgobius tabogensis* Meek & Hildebrand, 1928, extant, USNM 367369, El Salvador, 13°10′N 88°28′W, SL 35 and 36 mm. **e**–**h** *Microgobius cantaurensis* n. sp.; **f** holotype, NMB P15641, Cantaure FM, Paraguaná, Venezuela, PPP 2539; **e**, **g**–**h** paratypes; **e** Gatun FM, Colon, Panama, PPP 2165, NMB P15647; **g** Cantaure FM, Paraguaná, Venezuela, PPP 2539, NMB P15642; **h** Tuira FM, Darien, Panama, PPP 1606, NMB P15644. **i**–**l** *Microgobius microlepis* Longley & Hildebrand, 1940; **i** extant, FSBC 34988, 27°844N 80°44W, SL 31 mm; **j**–**l** Cumaná FM, Venezuela, PPP 3038, NMB P15648-50. **m**–**s** *Microgobius verecundus* n. sp.; **n** holotype, NMB P15651, Tuira FM, Darien, Panama, PPP 1163; **m**, **o**–**s** paratypes; **m**, **p**, **q** Angostura FM, Ecuador, PPP 3301, NMB P15652-54; **o**, **r**, **s** Tuira FM, Darien, Panama, PPP 1163, NMB P15655-57

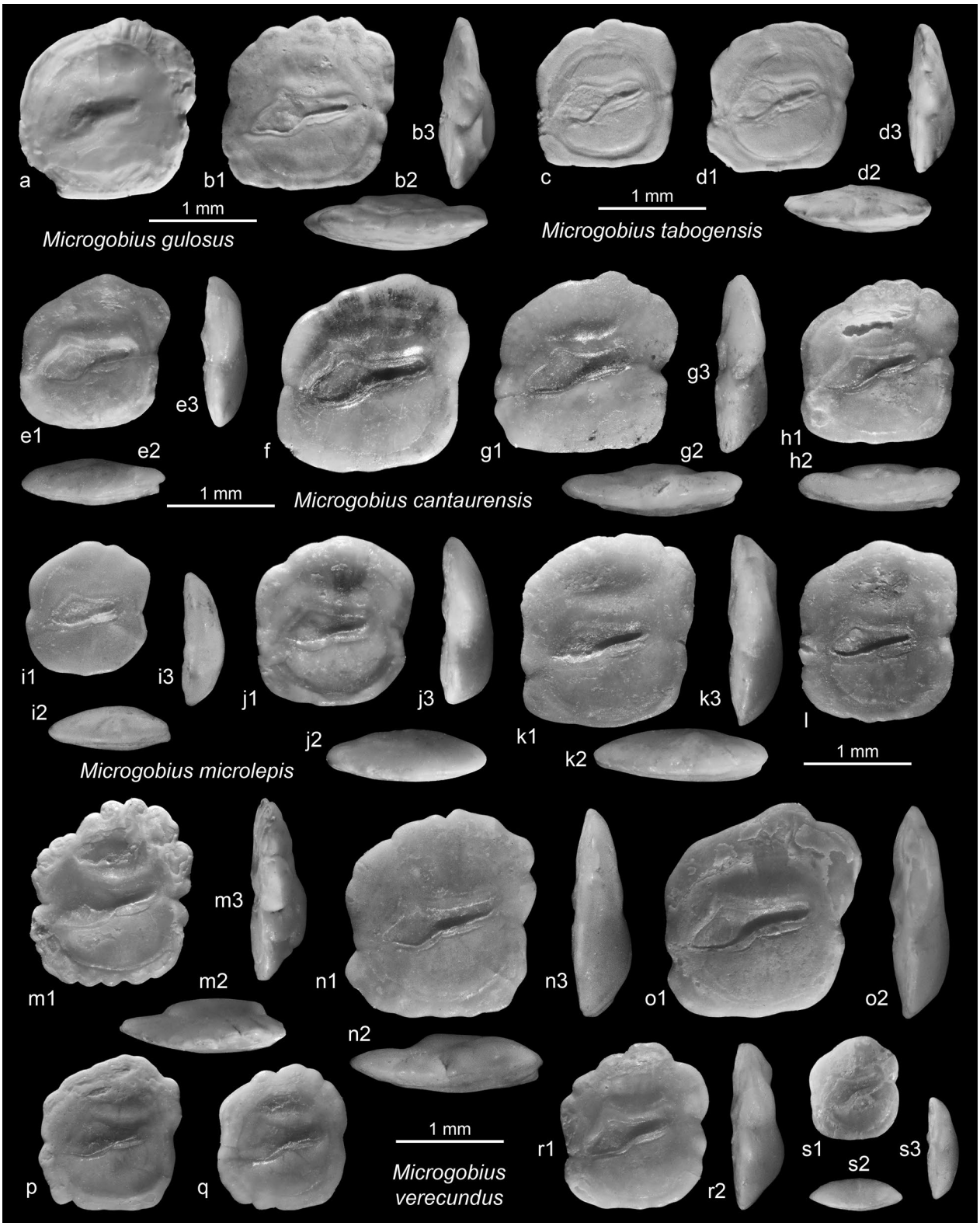


Fig. 27 (See legend on previous page.)

(NMB P15647); 3 specimens Tuira FM, Pacific Panama, Darien, PPP 1606 (NMB P15644-46).

Referred specimen 17 specimens Tortonian, Gatun FM, Atlantic Panama, 3 specimens PPP 2165, 2 specimens PPP 2167, 12 specimens PPP 2168.

Etymology Referring to the Cantaure FM of Venezuela, the type formation.

Diagnosis Otolith size up to 1.7 mm in length. OL:OH = 0.95–0.97. Otolith shape nearly rectangular; dorsal rim irregularly curved, low, with pronounced postdorsal projection. Inner face slightly convex. Sulcus long, moderately wide, with distinct ostial lobe and deepened cauda; OL:SuL = 1.4–1.55; sulcus inclination angle 12–15°. Subcaudal iugum long, narrow. Ventral furrow very close and parallel to ventral rim of otolith.

Description Otolith size up to 1.7 mm in length (holotype). OH:OT = 3.4–3.5. Otolith shape nearly rectangular with irregularly curved and undulating dorsal rim highest at its postdorsal angle. Predorsal angle rounded; postdorsal projection rounded, slightly projecting. Anterior rim near vertical, posterior rim slightly inclined towards ventral; posterior rim with weak central concavity. Ventral rim straight to slightly bent, horizontal. Preventral angle orthogonal, postventral angle orthogonal, rounded. All rims smooth except dorsal rim.

Inner face slightly convex, particularly in horizontal direction. Sulcus long, moderately wide, with distinct ostial lobe; cauda straight, with rounded tip, slightly deepened; sulcus inclination angle 12–15°; OL:SuL = 1.4–1.55. Subcaudal iugum long, narrow. Dorsal depression small, usually indistinct. Ventral furrow distinct, very close and parallel to ventral rim of otolith. Outer face evenly convex or with slight ventral umbo, relatively smooth.

Discussion Microgobius cantaurensis closely resembles the extant and Late Pliocene *M. gulosus* particularly in otolith shape and proportions. It differs from *M. gulosus* in the much larger sulcus (OL:SuL = 1.4–1.55 vs 1.65–1.85) and the more strongly developed postdorsal projection.

Microgobius microlepis Longley & Hildebrand, 1940

Figure 27i–l

Material 31 specimens Calabrian, Cumaná FM, Venezuela, PPP 3038 (figured specimens PPP15648-50).

Discussion Otoliths of *M. microlepis* are recognized by their nearly rectangular shape characterized by near vertical anterior and posterior rims and a relatively shallow and gently curved dorsal rim (OL:OH = 0.85–0.92). It is further characterized by a relatively short sulcus with tapering cauda and triangular ostial lobe, while the ventral sulcus margin is nearly straight. These relatively characteristic otoliths have only been found in the Pleistocene, Calabrian of Venezuela, which is south of the present distribution of the species in the Gulf of Mexico and the western Caribbean along the coasts Yucatan and Belize.

Microgobius verecundus n. sp.

Figure 27m–s

Holotype NMB P15651 (Fig. 27n), Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1163.

Paratypes 7 specimens Tortonian: 4 specimens same data as holotype (NMB P15655-58); 3 specimens Angostura FM, Ecuador, PPP 3301 (NMB P15652-54).

Referred specimen 112 specimens: 111 specimens Tortonian: 19 specimens Angostura FM, Ecuador, 7 specimens PPP 3297, 12 specimens PPP 3301; 33 specimens Tuira FM, Pacific Panama, Darien, 2 specimens PPP 1132, 11 specimens PPP 1134, 7 specimens PPP 1137, 2 specimens PPP 1606, 5 specimens PPP 1997, 3 specimens PPP 1142, 1 specimen PPP 1154, 1 specimen PPP 1163, 1 specimen PPP 1164; 31 specimens Yaviza FM, Pacific Panama, Darien, 3 specimens PPP 1607, 9 specimens PPP 1609, 3 specimens PPP 1528, 4 specimens PPP 1171, 5 specimens PPP 1570, 2 specimens PPP 1565, 5 specimens PPP 1566; 13 specimens Gatun FM, Atlantic Panama, PPP 2168; 13 specimens Manzanilla FM, San José Member, Trinidad, 1 specimen PPP 2669, 1 specimen PPP 2670, 10 specimens PPP 2671, 1 specimen PPP 2676. 3 specimens Messinian, Chucunaque FM, Pacific Panama, Darien, PPP 1576, 2 specimens PPP 1612.

Etymology From verecundus (Latin) = modest, referring to the unspectacular morphology of the otoliths of this species.

Diagnosis Otolith size up to 1.8 mm in length. OL:OH = 0.86–0.9. Otolith shape nearly rectangular; dorsal rim irregularly curved, with weak postdorsal projection. Sulcus long, relatively narrow, with relatively low ostial lobe and deepened cauda; OL:SuL = 1.55–1.75; sulcus inclination angle 15–20°. Subcaudal iugum

moderately long, narrow. Ventral furrow very close to ventral rim of otolith, relatively regularly curved.

Description Otolith size up to 1.8 mm in length (holotype 1.75 mm). OH:OT = 3.5–3.8. Otolith shape nearly rectangular with irregularly curved, slanting dorsal rim highest at its postdorsal angle. Predorsal angle rounded; postdorsal projection rounded, slightly projecting. Anterior rim near vertical, posterior rim slightly inclined towards ventral; posterior rim with weak central concavity. Ventral rim straight, horizontal. Preventral and postventral angles rounded. All rims irregularly undulating or, rarely, crenulated (Fig. 27m).

Inner face flat in vertical direction and slightly bent in horizontal direction. Sulcus long, relatively narrow, with relatively low ostial lobe; cauda straight, with rounded or tapering tip, slightly deepened; sulcus inclination angle 15–20°; OL:SuL = 1.55–1.75. Subcaudal iugum moderately long, not reaching posterior tip of cauda, narrow. Dorsal depression small to moderate in size, with indistinct margins. Ventral furrow distinct, very close to ventral rim of otolith and relatively regularly curved. Outer face with slight ventral umbo, moderately ornamented.

Discussion Microgobius verecundus is an inconspicuous species that is more compressed than *M. cantaurensis* (OL:OH = 0.86–0.9 vs 0.95–0.97) and is distinguished from *M. microlepis* by the larger size of the sulcus (OL:SuL = 1.55–1.75 vs 1.8–1.9) and its different shape. It is a common and widespread species during the Tortonian from Ecuador to Trinidad.

Microgobius carri otolith plexus

Microgobius carri Fowler, 1945

Figure 28a–c

Material 6 specimens Gelasian, Moin FM, Atlantic Costa Rica, PPP 1773 (figured specimens NMB P15659-60).

Discussion The otoliths of *M. carri* are moderately compressed (OL:OH = 0.85–0.87) and characterized by an inclined predorsal rim and pronounced, high postdorsal angle. Anterior and posterior rims are almost vertical. Another typical feature is the long sulcus (OL:SuL = 1.35–1.45), with a wide ostium and rounded ostial lobe, and a sulcus inclination angle of 15–20°. Today, *M. carri* occurs in moderately deep water (6 to 21 m) in the vicinity of coral reefs (Birdsong, 1981). The only identified fossil occurrence in the Early Pleistocene of Costa Rica is consistent with the extant distribution pattern.

Microgobius chocorum n. sp.

Figure 28e–h

Holotype NMB P15661 (Fig. 28e), Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1163.

Paratypes 6 specimens Tortonian: 5 specimens Pacific Panama, Darien: 4 specimens Tuira FM, 2 specimens PPP 1593 (NMB P15662-63), 1 specimen PPP 1154 (NMB P 15664), 1 specimen PPP 1137 (NMB P15666); 1 specimen Yaviza FM, PPP 1565 (NMB P15667); 1 specimen Manzanilla FM, San José Member, Trinidad, PPP 2674 (NMB P15665).

Referred specimen 10 specimens Tortonian: 7 specimens Tuira FM, Pacific Panama, Darien, 1 specimen PPP 1137, 6 specimens PPP 1163; 3 specimens Gatun FM, Atlantic Panama, PPP 2165.

Etymology Named after the Chocó Indians living in the Chocó Province in Darien, Panama.

Diagnosis Otolith size up to 1.4 mm in length. OL:OH = 0.75–0.8. Otolith shape high-bodied; dorsal rim high, with weak postdorsal projection. Sulcus moderately long and wide, with relatively broad ostial lobe; OL:SuL = 1.45–1.65; sulcus inclination angle 16–18°. Subcaudal iugum long, narrow. Ventral furrow moderately close to ventral rim of otolith, regularly curved.

Description Otolith size up to 1.4 mm in length (holotype 1.35 mm). OH:OT = 3.5–4.3. Otolith shape high-bodied, with high dorsal rim and prominent middorsal angle. Predorsal angle rounded; postdorsal region rounded, not projecting. Anterior and posterior rims near vertical; posterior rim with weak central concavity. Ventral rim slightly curved, horizontal. Preventral and postventral angles rounded. All rims smooth, dorsal rims sometimes undulating or crenulated (Fig. 28f).

Inner face flat in vertical direction and slightly bent in horizontal direction. Sulcus moderately long and wide, with broad ostial lobe; cauda straight, with rounded tip, not particularly deepened; sulcus inclination angle 16–18°; OL:SuL = 1.45–1.65. Subcaudal iugum long, narrow, may expand over posterior tip of cauda in juvenile specimens (Fig. 28h). Dorsal depression moderate in size, with indistinct margins. Ventral furrow distinct, moderately close to ventral rim of otolith and regularly curved. Outer face with slight ventral umbo, smooth.

Discussion Microgobius chocorum resembles the extant *M. carri* and *M. crocatus*. It differs from *M. carri* in the

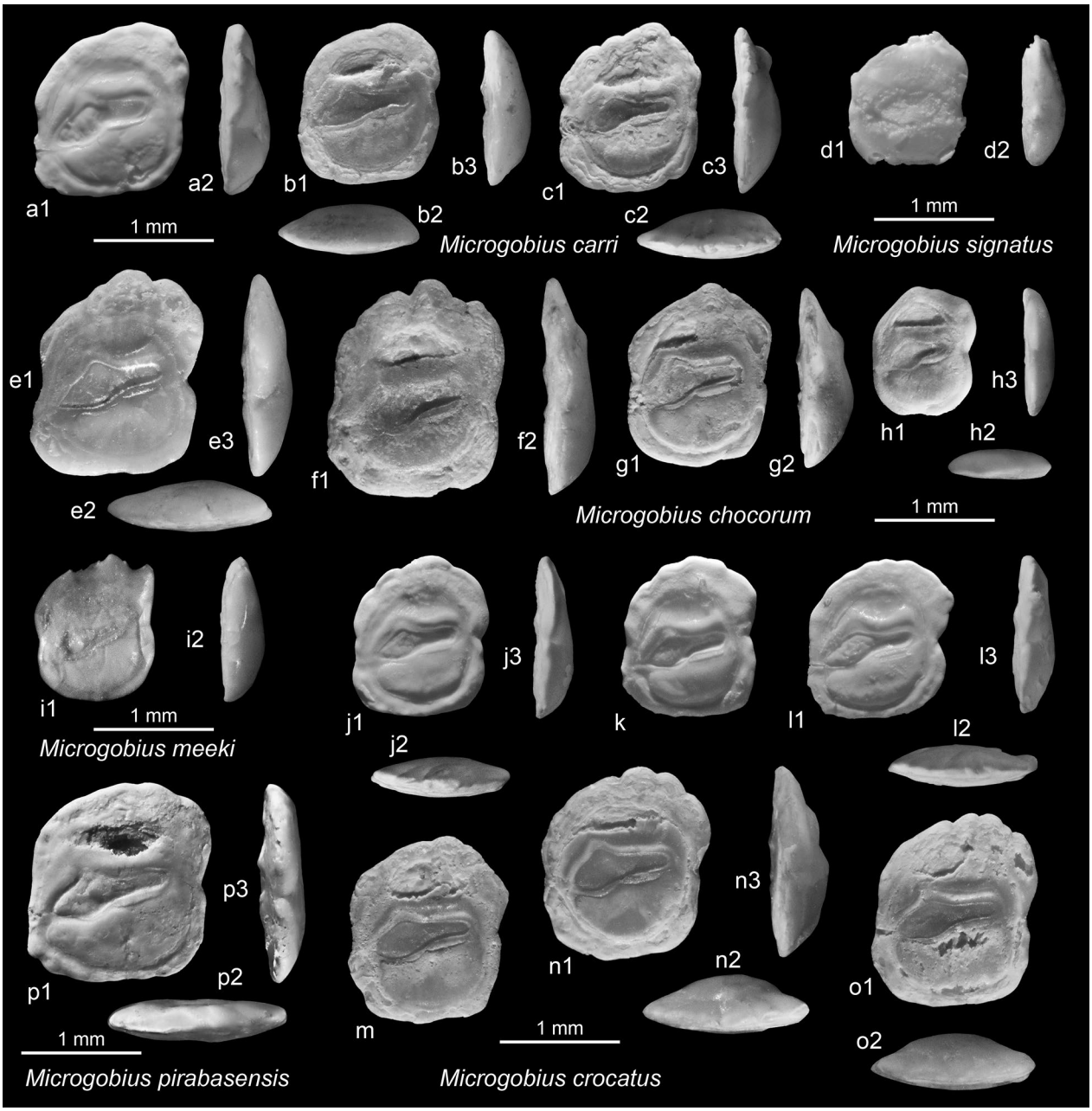


Fig. 28 **a–c** *Microgobius carri* Fowler, 1945; **a** extant, USNM 413298, 11°09′N 60°50′W; **b**–**c** Moin FM, Limón, Costa Rica, PPP 1773, NMB P15659-60. **d** *Microgobius signatus* Poey, 1876, extant, USNM 413432, 12°08′N 68°58′W. **e**–**h** *Microgobius chocorum* n. sp.; **e** holotype, NMB P15661, Tuira FM, Darien, Panama, PPP 1163; **f**–**h** paratypes; **f** Tuira FM, Darien, Panama, PPP 1593, NMB P15662 (plus 15663 not figured); **g** Tuira FM, Darien, Panama, PPP 1154, NMB P15664; Springvale FM, Trinidad, KR-1216, NMB P15665. **i** *Microgobius meeki* Evermann & Marsh, 1899, extant, USNM 389979, Atlantic Panama, Bocas, SL 24 mm. **j**–**o** *Microgobius crocatus* Birdsong, 1968; **j**–**l** extant, USNM 367361, 13°10′N 88°28′W; **m**–**o** Tuira FM, Darien, Panama, PPP 1137, NMB P15668-70. **p** *Microgobius pirabasensis* n. sp., holotype, MPEG-1947-V (refigured from Aguilera et al., 2014, Fig. 12/10), Pirabas FM, Brazil

more high-bodied shape (OL:OH = 0.75–0.8 vs 0.85–0.87) and from *M. crocatus* in the distinct middorsal angle (vs regularly curved) and in being more compressed (OL:OH = 0.75–0.8 vs 0.83–0.88). Otoliths of the extant *M. meeki* (Fig. 28i) and *M. signatus* (Fig. 28d) are similarly compressed, as far as can be judged from the available, somewhat formalin-eroded specimens. Otoliths of *M. meeki* differ from *M. chocorum* in the high postdorsal angle and the steeply inclined sulcus (25° vs 16–18°) and those of *M. signatus* in the small sulcus

(OL:SuL = 1.8 vs 1.45–1.65) and the low sulcus inclination angle (about 10° vs 16–18°).

***Microgobius crocatus* Birdsong, 1968**

Figure 28j–o

Material 20 specimens Tortonian, Pacific Panama, Darien: 17 specimens Tuira FM, PPP 1137 (figured specimens NMB P15668-70); 3 specimens Yaviza FM, 1 specimen PPP 1609, 2 specimens PPP 1528.

Discussion The otoliths of *M. crocatus* are relatively unremarkable and are best recognized by the regularly curved, high, and evenly crenulated or undulating dorsal rim that distinguishes them from otoliths of *M. carri* and *M. chocorum*. *Microgobius crocatus* occurs today in mangrove environments in the tropical East Pacific (Birsdong, 1981). Its fossil occurrence is rare, concentrated in a single location in the Tortonian of Darien, Río Tuquesa (PPP 1137), which has been described as "clayey siltstone and bioclastic and lithic sandstone, rich in bivalves, especially *Pecten*" (Coates et al., 2004). *Pecten* clams are not specific or even common in mangrove environments, and the cause for the singular abundance of *M. crocatus* in that location is therefore unknown. Moreover, *M. crocatus* represents the earliest extant goby species identified by otoliths in tropical America.

***Microgobius cumana* n. sp.**

Figure 29a–g

Holotype NMB P15671 (Fig. 29b), Calabrian, Cumaná FM, Venezuela, PPP 3038.

Paratypes 7 specimens same data as holotype (NMB P15672-78).

Referred specimen 43 specimens same data as holotype.

Etymology Named after the type formation, the Cumaná FM.

Diagnosis Otolith size up to 1.9 mm in length. OL:OH = 0.79–0.93. Otolith shape high-bodied; dorsal rim high, with angular, high predorsal angle, obtuse middorsal angle and short but angular to pointed postdorsal projection. Sulcus relatively short and narrow, with low ostial lobe and tapering caudal tip; OL:SuL = 1.7–1.8; sulcus inclination angle 13–17°. Subcaudal iugum long, narrow. Ventral furrow close to ventral rim of otolith, regularly curved.

Description Otolith size up to 1.9 mm in length (holotype 1.4 mm). OL:OH = 0.79–0.93, mostly 0.79–0.87, but largest specimen 0.93 (Fig. 29a); OH:OT = 3.4–4.0. Otolith shape high-bodied. Dorsal rim with high, angular to slightly rounded predorsal angle, obtuse middorsal angle and short but angular or pointed postdorsal projection. Anterior rim vertical, with broad, shallow concavity at level of ostium; posterior rim vertical to slightly inclined and broadly concave. Ventral rim flat to slightly curved, horizontal. Preventral angle orthogonal, postventral angle rounded. All rims smooth, except dorsal rim intensely lobed in largest specimen (Fig. 29a).

Inner face flat in vertical direction and slightly bent in horizontal direction. Sulcus moderately long and wide, with broad ostial lobe; cauda straight, with rounded tip, not particularly deepened; sulcus inclination angle 13–17°; OL:SuL = 1.7–1.8. Subcaudal iugum long, narrow, may expand over posterior tip of cauda in juvenile specimens (Fig. 28h). Dorsal depression moderate in size, with indistinct margins. Ventral furrow distinct, moderately close to ventral rim of otolith and regularly curved. Outer face with slight ventral umbo, smooth.

Discussion Microgobius cumana is recognized by the high-bodied otolith with its characteristic shape of the dorsal rim, the relatively short sulcus (OL:SuL = 1.7–1.8), the low ostial lobe and tapering caudal tip. In the latter two characters it resembles otoliths of *M. microlepis* with which it occurs parallel at the same location, but differs in the specific shape of the dorsal rim and the more compressed appearance (OL:OH = 0.79–0.87, rarely 0.93 vs 0.85–0.92) and the more steeply inclined sulcus (13–17° vs 9–11°). *Microgobius cumana* also resembles the otoliths of extant *M. thalassinus* (Fig. 29h–i) from the West Atlantic and *M. brevispinis* (according to drawings provided by D. Nolf) from the East Pacific, but differs in the specific shape of the dorsal rim and the broadly concave posterior rim (vs vertical).

***Microgobius ecuadorensis* n. sp.**

Figure 29j–q

Holotype NMB P15679 (Fig. 29l), Tortonian, Angostura FM, Ecuador, NMB 19301.

Paratypes 7 specimens Tortonian, Angostura FM, Ecuador: 1 specimen PPP 3369 (NMB P15680), 2 specimens PPP 3444 (NMB P15681-82), 4 specimens PPP 3301 (NMB P15683-86).

Referred specimen 95 specimens Tortonian: 94 specimens Angostura FM, Ecuador: 3 specimens NMB 19301, 28

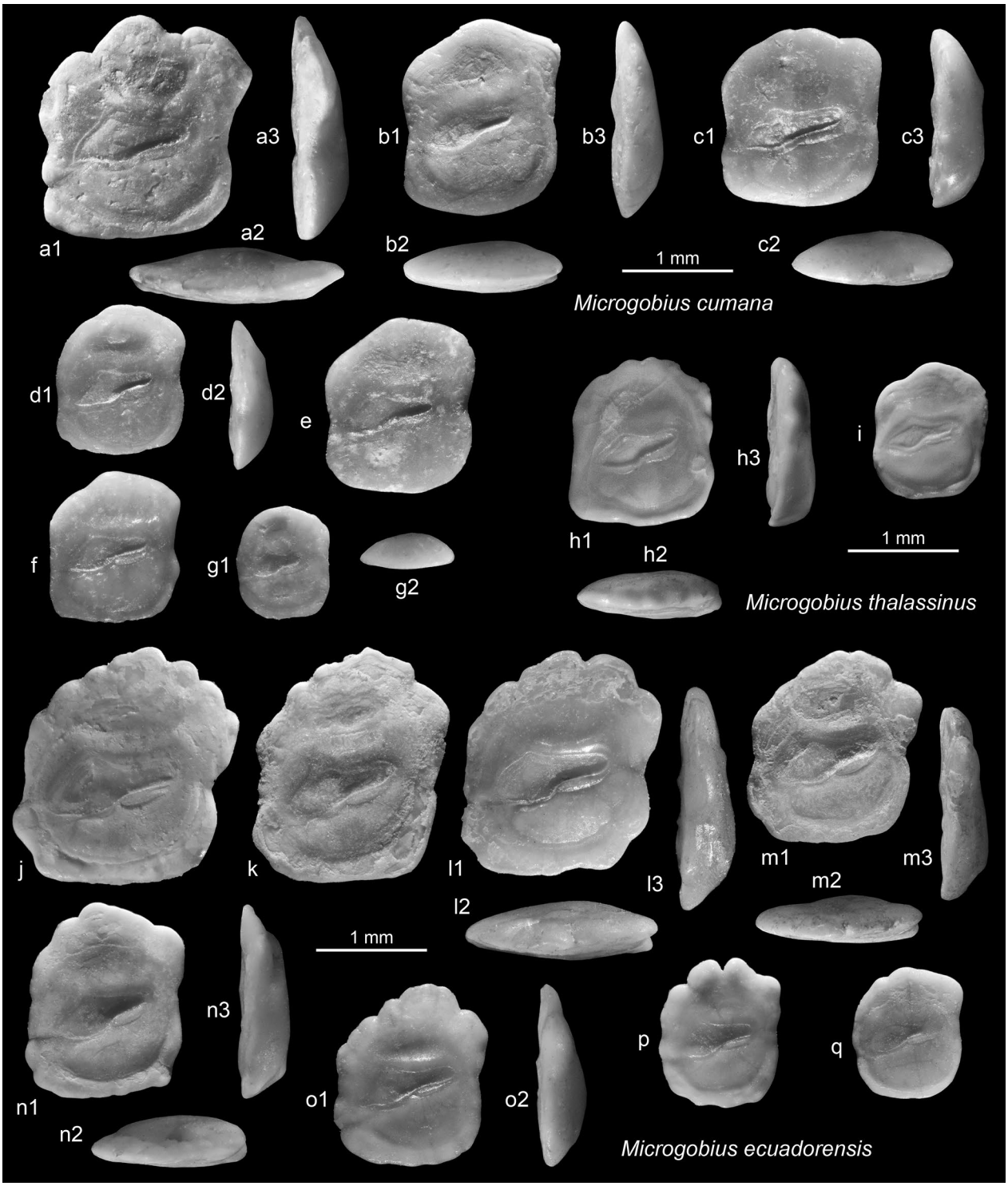


Fig. 29 **a–g** *Microgobius cumana* n. sp., Cumaná FM, Venezuela, PPP 3038; **b** holotype, NMB P15671; **a**, **c**–**g** paratypes, NMB P15672-77. **h**–**i** *Microgobius thalassinus* (Jordan & Gilbert, 1883), extant, USNM 429824, 38°53′N 76°32′W. **j**–**q** *Microgobius ecuadorensis* n. sp.; **l** holotype, NMB P15679, Angostura FM, Ecuador, NMB 19301; **j**–**k**, **m**–**q** paratypes; **j** Angostura FM, Ecuador, PPP 3369, NMB P15680; **k**, **m** Angostura FM, Ecuador, PPP 3444, NMB P15681-82; **n**–**q** Angostura FM, Ecuador, PPP 3301, NMB P15683-86

specimens PPP 3297, 51 specimens PPP 3301, 10 specimens PPP 3369, 3 specimens PPP 3372, 1 specimen PPP 3444; 1 specimen Tuira FM, Pacific Panama, Darien, PPP 1132.

Etymology Named after Ecuador, the country from which the type specimens originate.

Diagnosis Otolith size up to 2.0 mm in length. OL:OH = 0.78–0.9. Otolith shape high-bodied; dorsal rim high, regularly crenulated, with rounded, obtuse middorsal angle and short rounded postdorsal projection. Sulcus moderately large and wide, with broad ostial lobe and rounded caudal tip; OL:SuL = 1.5–1.7; sulcus inclination angle 15–20°. Subcaudal iugum long, moderately wide. Ventral furrow distant from ventral rim of otolith, regularly curved.

Description Otolith size up to 2.0 mm in length (holotype 1.75 mm). OH:OT = 3.9–4.2. Otolith shape high-bodied. Dorsal rim high, regularly crenulated, with broadly rounded predorsal angle, obtuse to rounded middorsal angle and short broadly rounded postdorsal projection. Anterior rim near vertical or slightly inclined towards dorsal; posterior rim vertical to slightly inclined and with indistinct central concavity. Ventral rim flat to slightly curved, horizontal. Preventral angle orthogonal, postventral angle rounded. All rims slightly undulating and dorsal rim regularly crenulated.

Inner face flat in vertical direction and slightly bent in horizontal direction. Sulcus moderately long and wide, with broad ostial lobe; cauda straight, with rounded tip, slightly deepened; sulcus inclination angle 15–20°; OL:SuL = 1.5–1.7. Subcaudal iugum long, moderately wide, may expand over posterior tip of cauda in juvenile specimens (Fig. 29q). Dorsal depression moderate in size, with indistinct margins. Ventral furrow distinct, distant ventral rim of otolith and regularly curved. Outer face with slight ventral umbo, slightly ornamented.

Discussion Microgobius ecuadorensis is characterized by its broadly crenulated dorsal rim, which distinguishes it from most of its congeners except for *M. crocatus* and *M. verecundus*. It differs from *M. crocatus* in the higher and less regularly curved dorsal rim and the shorter sulcus (OL:SuL = 1.5–1.7 vs 1.4–1.55). *Microgobius ecuadorensis* differs from the parallel occurring *M. verecundus* in being mostly more compressed (OL:OH = 0.78–0.9 vs 0.86–0.9) and thinner (OH:OT = 3.9–4.2 vs 3.5–3.8) and the usually more regularly developed crenulation of the dorsal rim.

***Microgobius pirabasensis* n. sp.**

Figure 28p

2014Gobiidae, Genera and species indet. 3—Aguilera et al.: Fig. 12/10.

Holotype MPEG-1947-V (Fig. 28p), Aquitanian to Burdigalian, Pirabas FM, Brazil.

Etymology Named after the type formation, the Pirabas FM.

Diagnosis Otolith size 1.45 mm in length. OL:OH = 0.88. Otolith shape nearly rectangular; dorsal rim shallow, nearly flat and horizontal. Sulcus moderately long and narrow, with relatively low ostial lobe; OL:SuL = 1.45; sulcus inclination angle 16°. Subcaudal iugum long, narrow. Ventral furrow close to ventral rim of otolith.

Description Otolith size 1.45 mm in length (holotype). OH:OT = 4.4. Otolith shape nearly rectangular, with low, nearly flat and horizontal dorsal rim and high, rounded predorsal angle and orthogonal postdorsal projection. Anterior and posterior rims near vertical; posterior rim with very weak central concavity. Ventral rim slightly relatively straight, horizontal. Preventral and postventral angles rounded orthogonal. All rims slightly undulating.

Inner face almost flat in vertical direction and slightly bent in horizontal direction. Sulcus moderately long and narrow, with relatively low and broad ostial lobe; cauda straight, with rounded tip, not particularly deepened; sulcus inclination angle 16°; OL:SuL = 1.45. Subcaudal iugum long, narrow. Dorsal depression not discernable. Ventral furrow distinct, parallel and close to ventral rim of otolith. Outer face relatively flat and smooth.

Discussion Microgobius pirabasensis is recognized by its nearly flat, horizontal dorsal rim resulting in an almost perfect compressed rectangular otolith shape. Other characteristical features like the low ostial lobe and the ventral furrow running close and parallel to the ventral rim of the otolith are considered plesiomorphic.

***Microgobius robertsoni* n. sp.**

Figure 30a–g

2014Gobiidae, Genera and species indet. 2—Aguilera et al.: Fig. 12/8–12/9.

Holotype NMB P15687 (Fig. 30b), Burdigalian, Cantaure FM, Venezuela, PPP 2539.

Paratypes 12 specimens: 8 specimens Burdigalian, Cantaure FM, Venezuela: 5 specimens same data as holotype (NMB P15688-92), 3 specimens PPP 2545 (NMB P15693-95). 3 specimens Burdigalian, Balboa FM, Dominican Republic, NMB 17290 (NMB P400). 1 specimen Aquitanian to Burdigalian, Pirabas FM, Brazil (MPEG-1946-V).

Referred specimen 238 specimens: 233 specimens Burdigalian, Cantaure FM, Venezuela: 87 specimens same data as holotype, 4 specimens PPP 2543, 135 specimens PPP 2545, 10 specimens PPP 2546. 1 specimen Burdigalian, Brasso FM, Trinidad KR 6666. 1 specimen Aquitanian to Burdigalian, Pirabas FM, Brazil.

Etymology Named in honor of Ross Robertson (Panama City, Republic of Panama) for his contribution to the knowledge of the fishes of the tropical East Pacific.

Diagnosis Otolith size up to 1.8 mm in length. OL:OH = 0.83–0.88. Otolith shape high-bodied; dorsal rim high, relatively smooth, with rounded, obtuse postdorsal angle and short rounded postdorsal projection. Anterior rim ventrally expanded below ostium. Sulcus moderately large and wide, with broad ostial lobe and rounded caudal tip; OL:SuL = 1.4–1.5; sulcus inclination angle 15–22°. Subcaudal iugum moderately long, narrow. Ventral furrow close to ventral rim of otolith, regularly curved.

Description Otolith size up to 1.8 mm in length (holotype). OH:OT = 3.6–3.9. Otolith shape high-bodied. Dorsal rim high, regularly curved, with broadly rounded predorsal angle and broadly rounded middorsal angle, and short broadly rounded postdorsal projection. Anterior rim slightly inclined towards dorsal, with bulge or rounded projection ventral of ostial tip in specimens larger than 1.5 mm in length (Fig. 30a, b, g); posterior rim vertical to slightly inclined and with indistinct central concavity. Ventral rim flat to slightly curved, horizontal. Preventral angle recessed below bulge of anterior rim, postventral angle rounded. All rims smooth to slightly undulating.

Inner face nearly flat in vertical direction and slightly bent in horizontal direction. Sulcus moderately large and wide, with broad ostial lobe; cauda straight, with rounded tip, slightly deepened; sulcus inclination angle 15–22°; OL:SuL = 1.4–1.5. Subcaudal iugum moderately long, narrow. Dorsal depression small, with indistinct margins. Ventral furrow distinct, close ventral rim of otolith and regularly curved. Outer face nearly flat or with slight ventral umbo, smooth.

Discussion Microgobius robertsoni is characterized by the rather smooth otolith rims and, in larger otoliths longer than 1.5 mm, the bulge at the anterior rim below the ostium. These are also the characters distinguishing *M. robertsoni* from *M. ecuadorensis*. *Microgobius robertsoni* differs from the parallel occurring *M. cantaurensis* in the more compressed shape (OL:OH = 0.83–0.88 vs 0.95–0.97) and steeper inclined sulcus (15–22° vs 12–15°), and from *M. verecundus* in the larger sulcus (OL:SuL 1.4–1.5 vs 1.55–1.75).

***Microgobius rohri* n. sp.**

Figure 30h–l

Holotype NMB P15696 (Fig. 30h), Burdigalian, Brasso FM, Trinidad, KR-6666.

Paratypes 5 specimens same data as holotype (NMB P15697-701).

Referred specimen 45 specimens same data as holotype.

Etymology Named in memory of Karl Rohr, who has conducted important field reconnaissance work in Trinidad including the collecting of the otoliths of *Microgobius rohri*.

Diagnosis Otolith size up to 1.6 mm in length. OL:OH = 0.83–0.9. Otolith shape high-bodied; dorsal rim high, relatively smooth, with rounded and broadly

(See figure on next page.)

Fig. 30 **a**–**g** *Microgobius robertsoni* n. sp.; **b** holotype, NMB P15687, Cantaure FM, Paraguaná, Venezuela, PPP 2539; **a**, **c**–**g** paratypes; **a**, **g** same data as holotype, NMB P15688-89; **c**–**f** Cantaure FM, Paraguaná, Venezuela, PPP 2545, NMB P15693-95; **e** MPEG-1946-V (refigured from Aguilera et al., 2014, Fig. 12/9), Pirabas FM, Brazil. **h**–**l** *Microgobius rohri* n. sp., Brasso FM, Trinidad, KR-6666; **h** holotype, NMB P15696; **i–l** paratypes, NMB P15697-15700. **m** *Microgobius curtus* Ginsburg, 1939, extant, USNM 293571, 08°26′N 78°06′W.**n** *Microgobius erectus* Ginsburg, 1938, extant, USNM 322733, Pacific Panama, 07°25′N 80°11′W, SL 55 mm. **o**–**t** *Microgobius pezoldi* n. sp.; **p** holotype, NMB P15702, Chucunaque FM, Darien, Panama, PPP 1578; **o**, **q**–**t** paratypes; **o** Angostura FM, Ecuador, NMB 19301, NMB P15703; **q** Tuira FM, Darien, Panama, PPP 1132, NMB P15704; **r** Manzanilla FM, Trinidad, PPP 2674, NMB P15705; **s**–**t** Manzanilla FM, Trinidad, PPP 2671, NMB P15706-07

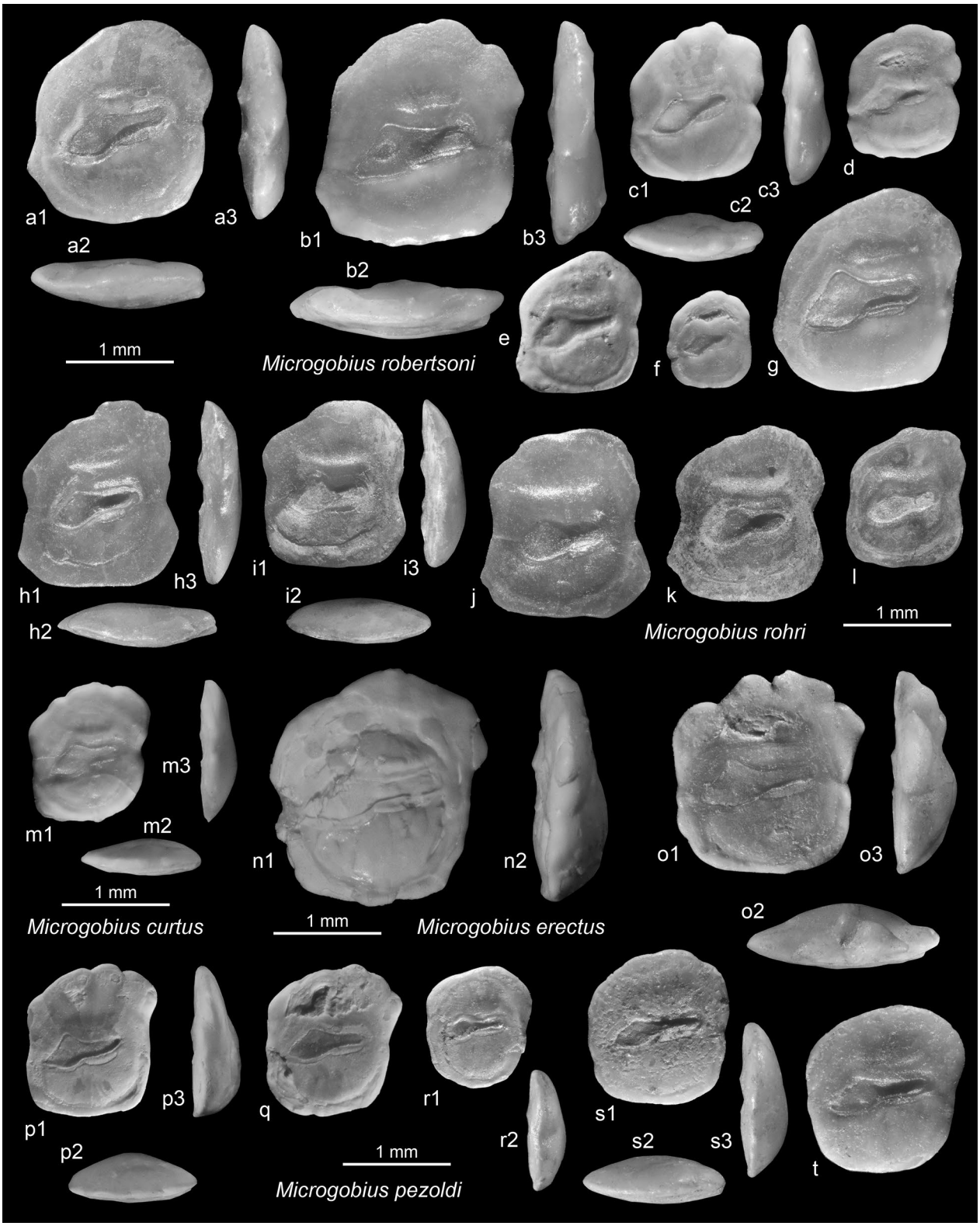


Fig. 30 (See legend on previous page.)

expanded postdorsal angle and short blunt postdorsal projection. Preventral and postventral angles projecting. Sulcus small, wide, with rounded ostial lobe and rounded caudal tip; OL:SuL = 1.7–1.9; sulcus inclination angle 8–12°. Subcaudal iugum short, narrow. Ventral furrow distant from ventral rim of otolith, regularly curved. Outer face nearly flat.

Description Otolith size up to 1.6 mm in length (holotype 1.5 mm). OH:OT = 3.9–4.4. Otolith shape high-bodied. Dorsal rim high, with rounded predorsal angle and rounded, broadly expanded postdorsal angle and short blunt postdorsal projection. Anterior and posterior rims slightly inclined towards dorsal, and with mild central concavities. Ventral rim flat to slightly curved, horizontal. Preventral and postventral angles protruding resulting distance between them clearly marking longest axis. All rims smooth or slightly and irregularly undulating.

Inner face nearly flat in vertical direction and slightly bent in horizontal direction. Sulcus small and wide, with rounded ostial lobe; cauda straight, with rounded tip, slightly deepened; sulcus inclination angle 8–12°; OL:SuL = 1.7–1.9. Subcaudal iugum short, not reaching caudal tip, narrow. Dorsal depression broad, with distinct ventral margin and broad crista superior. Ventral furrow distinct, relatively distant from ventral rim of otolith and regularly curved. Outer face nearly flat, smooth.

Discussion Microgobius rohri is easily distinguished from its congeners by the protruding preventral and postventral angles, the small sulcus and its low inclination angle. It likely represents an extinct lineage and could alternatively be placed in a separate genus.

Microgobius sp.1

Figure 31x

Material 2 specimens Calabrian, Armuelles FM, Pacific Panama, PPP 3236 (NMB P15738).

Discussion Two large and rather well-preserved otoliths from the upper Lower Pleistocene Armuelles FM of Pacific Panama resemble the Early Miocene *Microgobius robertsoni* in the presence of a bulge on the anterior rim just below the ostial tip. They differ, however, in the short subcaudal iugum terminating far from the posterior tip of the cauda and the short sulcus (OL:OH = 1.75 vs 1.4–1.5). This find indicates that this specific otolith morphology may be present in extant *Microgobius* species in the tropical East Pacific.

Microgobius erectus otolith plexus

Microgobius pezoldi n. sp.

Figure 30o–t

Holotype NMB P15702 (Fig. 30p), Messinian, Chucunaque FM, Pacific Panama, Darien, PPP 1578.

Paratypes 7 specimens Tortonian: 1 specimen Angostura FM, Ecuador NMB 19301 (NMB P15703); 3 specimens Tuira FM, Pacific Panama, Darien, 1 specimen PPP 1132 (NMB P15704), 2 specimens PPP 1163 (NMB P 15708–09); 3 specimens Manzanilla FM, San José Member, Trinidad, 1 specimens PPP 2674 (NMB P15705), 2 specimens PPP 2671 (NMB P 15706–07).

Referred specimen 19 specimens: 16 specimens Tortonian: 3 specimens Angostura FM, Ecuador, 2 specimens NMB 19301, 1 specimen NMB 19081; 7 specimens Tuira FM, Pacific Panama, Darien, 1 specimen PPP 1137, 3 specimens PPP 1139, 1 specimen PPP 1593, 2 specimens PPP 1164; 1 specimens Yaviza FM, Pacific Panama, Darien, PPP 1171; 5 specimens Manzanilla FM, San José Member, 1 specimen PPP 2669, 1 specimen PPP 2670, 2 specimens PPP 2671, 1 specimen PPP 2676. 2 specimens Messinian, Chucunaque FM, Pacific Panama, Darien, PPP 1576. 1 specimen Piacenzian, Río Banano FM, Atlantic Costa Rica, PPP 1732.

Etymology Named in honor of Frank Pezold (Corpus Christi, Texas), in recognition of his distribution to the knowledge of extant gobies from tropical America.

Diagnosis Otolith size up to 1.75 mm in length. OL:OH = 0.85–0.93. Otolith shape high-bodied; dorsal rim shallow, broadly crenulated; predorsal angle protruding and on same level as slightly protruding postdorsal projection. Preventral and postventral angles rounded orthogonal. Sulcus long, narrow, with low ostial lobe and rounded caudal tip; OL:SuL = 1.45–1.65; sulcus inclination angle 11–15°. Subcaudal iugum long, moderately narrow. Ventral furrow parallel and close to ventral rim of otolith.

Description Otolith size up to 1.75 mm in length (holotype 1.2 mm). OH:OT = 3.0–3.2. Otolith shape high-bodied. Dorsal rim shallow, nearly flat, without prominent postdorsal angle, smooth or broadly crenulated; predorsal angle high, distinct, slightly protruding at same level as slightly protruding postdorsal projection. Longest horizontal axis of otolith shifted dorsally to predorsal angle–postdorsal projection level. Anterior and posterior

rims slightly inclined towards ventral, straight, without marked concavities. Ventral rim flat to slightly curved, horizontal. Preventral and postventral angles recessed, rounded. All rims smooth except dorsal rim.

Inner face nearly flat in vertical direction and slightly bent in horizontal direction. Sulcus long, narrow, with low ostial lobe; cauda straight, with rounded tip, slightly deepened; sulcus inclination angle 11–15°; OL:SuL = 1.45–1.65. Subcaudal iugum long, moderately narrow. Dorsal depression indistinct. Ventral furrow distinct, relatively close and parallel to ventral rim of otolith. Outer face distinctly convex, with inframedian umbo, relatively smooth.

Discussion Microgobius pezoldi is a typical member of the *M. erectus* plexus, which is characterized by the slightly protruding predorsal angle and postdorsal projection, resulting in a dorsal shift of the longest axis of the otolith. It resembles *M. curtus* (Fig. 30m) but tends to be less compressed (OL:OH = 0.85–0.93 vs 0.84). It is also similar to the extant *M. erectus* but has a more pronounced ostial lobe. The shape of the postdorsal projection distinguishes it from both extant congeners. *Microgobius pezoldi* is a widely distributed species from the Tortonian of Ecuador to Trinidad and the Piacenzian of Costa Rica but is nowhere common.

Microgobius camur otolith plexus

Microgobius aphioides n. sp.

Figure 31a–e

Holotype NMB P15710 (Fig. 31a), Zanclean, Cubagua FM, Venezuela, PPP 2549.

Paratypes 5 specimens Zanclean, Cubagua FM, Venezuela, 1 specimen PPP 2568 (NMB P15711), 2 specimens PPP 3057 (NMB P15712-13), 1 specimen PPP 3066 (NMB P15714), 1 specimen PPP 2549 (NMB P15715).

Referred specimen 71 specimens Zanclean: 54 specimens Cubagua FM, Venezuela, 5 specimens PPP 2549, 1 specimen PPP 2556, 6 specimens PPP 2557, 8 specimens PPP 3055, 7 specimens PPP 3057, 16 specimens PPP 2568, 4 specimens PPP 2570, 7 specimens PPP 2571; 7 specimens Cayo Agua FM, Atlantic Panama, PPP 1188; 9 specimens Springvale FM, Trinidad, KR-1216; 1 specimen La Vela FM, Venezuela, PPP 2532.

Etymology Named after the resemblance to otoliths of the northeastern Atlantic and Mediterranean genus *Aphia*.

Diagnosis Otolith size up to 1.25 mm in length. OL:OH = 0.8–0.85. Otolith shape high-bodied; dorsal rim elevated; predorsal angle and postdorsal projection rounded, not protruding. Preventral angle orthogonal, postventral angle rounded. Sulcus short, narrow, with broad, rounded ostial lobe and cauda posteriorly reduced by ingressing subcaudal iugum; OL:SuL = 1.7–2.0; sulcus inclination angle 13–18°. Subcaudal iugum long, wide, turning around caudal tip. Ventral furrow moderately close to ventral rim of otolith, regularly curved.

Description Otolith size up to 1.25 mm in length (holotype 1.0 mm). OH:OT = 3.2–3.5. Otolith shape high-bodied. Dorsal rim high, often with obtuse, rounded middorsal angle; predorsal angle high, broadly rounded, not protruding, postdorsal projection rounded or blunt, not protruding. Anterior and posterior rims near vertical and relatively straight. Ventral rim flat to slightly curved, horizontal. Preventral angle orthogonal, postventral angle rounded. All rims smooth.

Inner face completely flat. Sulcus small, short, narrow, with broad, rounded to triangular ostial lobe; cauda straight, short, with rounded or tapering tip; sulcus inclination angle 13–18°; OL:SuL = 1.7–2.0. Subcaudal iugum long, wide, turning upward posteriorly and then ingressing into posterior tip of cauda to various extends. Dorsal depression indistinct. Ventral furrow distinct, moderately close to ventral rim of otolith and regularly curved. Outer face evenly convex, smooth.

Discussion The otoliths of *Microgobius aphioides* are smaller than most *Microgobius* otoliths and could be confused with otoliths of juveniles of other species. The characteristic ingression of the subcaudal iugum into the rear part of the cauda is rarely observed in otoliths of juveniles of other species, but the shape of the sulcus with its low, rounded to triangular ostial lobe and the relatively wide subcaudal iugum distinguish *M. aphioides* from such otoliths of juveniles. The smooth otolith rims and nearly vertical anterior and posterior rims distinguish *M. aphioides* from other species in the *Microgobius camur* plexus. The ingression of the subcaudal iugum into the rear part of the cauda is stronger in *M. aphioides* than in *M. glaber*, resulting in a shorter sulcus (OL:SuL = 1.7–2.0 vs 1.5–1.6). *Microgobius aphioides* differs from *M. camur* in the relatively narrow ostium and the smooth otolith rims. Most similar morphologically are the otoliths of the small species *M. praeglaber*, which, however, is distinguished by its eccentrically forward-positioned sulcus and the curved ventral rim.

***Microgobius camur* n. sp.**

Figure 31f–k

Holotype NMB P15716 (Fig. 31f), Gelasian, Escudo de Veraguas FM, Atlantic Panama, PPP 2171.

Paratypes 5 specimens: 1 specimen Zanclean, Cayo Agua FM, Atlantic Panama, PPP 1275 (NMB P15720). 1 specimen Piacenzian, Escudo de Veraguas FM, Atlantic Panama, PPP 1241 (NMB P15718). 2 specimens Gelasian: 1 specimen Escudo de Veraguas FM, Atlantic Panama, PPP 2170 (NMB P15717); 1 specimen Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 1252 (NMB P15719). 1 specimen Calabrian, Swan Cay FM, Atlantic Panama, PPP 2221 (NMB P15721).

Referred specimen 8 specimens: 2 specimens Piacenzian: 1 specimen Río Banano FM, Atlantic Costa Rica, PPP 3243; 1 specimen Escudo de Veraguas FM, Atlantic Panama, PPP 1241. 1 specimen Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 1252. 5 specimens Calabrian: 1 specimen Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 2249; 4 specimens Swan Cay FM, Atlantic Panama, PPP 2221.

Etymology From camur (Latin) = hooked, curved, referring to the hooked shape of the subcaudal iugum.

Diagnosis Otolith size up to 1.65 mm in length. OL:OH = 0.76–0.83. Otolith shape high-bodied; dorsal rim elevated, regularly crenulated; predorsal angle and postdorsal projection not protruding. Preventral and postventral angles rounded. Sulcus short, wide, with high, triangular ostial lobe and cauda posteriorly shortened by ingressing subcaudal iugum; OL:SuL = 1.65–2.05; sulcus inclination angle 15–20°. Subcaudal iugum long, wide, hook-like extended into rear part of cauda. Ventral furrow close and parallel to ventral rim of otolith, regularly curved.

Description Otolith size up to 1.65 mm in length (holotype). OH:OT = 3.3–4.0, decreasing with size. Otolith shape high-bodied. Dorsal rim high, rounded or with rounded middorsal angle; predorsal angle indistinct, postdorsal projection blunt, not protruding. Anterior rim nearly vertical, posterior rim slightly inclined toward ventral and straight. Ventral rim flat to slightly curved, horizontal. Preventral and postventral angles rounded. All rims more or less strongly crenulated or undulating.

Inner face completely flat. Sulcus short, wide, particularly broad, triangular ostial lobe widened; cauda short, with rounded or tapering tip; sulcus inclination angle 15–20°; OL:SuL very variable, depending on degree of ingression of subcaudal iugum, 1.65–2.05. Subcaudal iugum long, wide, usually ingressing into posterior portion of cauda to various extends: ranging from very strong and considerably shortening cauda (Fig. 31f, g, j) to moderately strong ingressing (Fig. 31i, k), however, almost not ingressing in rare cases (Fig. 31h). Dorsal depression indistinct, wide. Ventral furrow mostly distinct, close and parallel to ventral rim of otolith and regularly curved. Outer face evenly convex, variably ornamented.

Discussion Microgobius camur is the largest species in this otolith plexus and readily recognized by the combination of the intense crenulation or undulation of its rims, particularly the dorsal rim, the high triangular ostial lobe resulting in a wide sulcus and the large subcaudal iugum, which often very strongly ingresses into the rear part of the cauda thereby considerably shortening the length of the sulcus.

***Microgobius glaber* n. sp.**

Figure 31l–p

Holotype NMB P15722 (Fig. 31l), Messinian, Manzanilla FM, Montserrat Member, Trinidad, PPP 2666.

Paratypes 9 specimens: 6 specimens Messinian, same data as holotype (NMB P15723-28). 3 specimens Tortonian, Cercado FM, Dominican Republic, NMB 17003 (NMB P392).

(See figure on next page.)

Fig. 31 **a–e** *Microgobius aphioides* n. sp., Cubagua FM, Venezuela; **a** holotype, NMB P15710, PPP 2549; **b**–**e** paratypes; **b** PPP 2568, NMB P15711; **c** PPP 3057, NMB P15712; **d** PPP 3066, NMB P15714; **e** PPP 2549, NMB P15715. **f**–**k** *Microgobius camur* n. sp.; **f** holotype, NMB P15716, Escudo de Veraguas FM, Bocas del Toro, Panama, PPP 2171; **g**–**k** paratypes; **g** Escudo de Veraguas FM, Bocas del Toro, Panama, PPP 2170, NMB P15717; **h** Escudo de Veraguas FM, Bocas del Toro, Panama, PPP 1241, NMB P15718; **i** Bastimentos FM, Ground Creek Unit, Bastimentos Island, Panama, PPP 1252, NMB P15719; **j** Cayo Agua FM, Atlantic Panama, PPP 1276, NMB P15720; **k** Swan Cay FM, Atlantic Panama, PPP 2221, NMB P15721. **l**–**p** *Microgobius glaber* n. sp.; **l** holotype, NMB P15722, Manzanilla FM, Trinidad, PPP 2666; **m**–**p** paratypes; **m**–**o** Cercado FM, Dominican Republic, NMB 17003, NMB P392; **p** Manzanilla FM, Trinidad, PPP 2666, NMB P15723. **q**–**v** *Microgobius praeglaber* n. sp.; **q** holotype, NMB P15729, upper Brasso FM, Trinidad, KR-9244; **r**–**v** paratypes; **r**–**t** upper Brasso FM, Trinidad, KR-9244, NMB P15730-32; **u**–**v** Gatun FM, Colon, Panama, PPP 2167, NMB P15734-35. **w** *Microgobius* sp.2, Armuelles FM, Pacific Panama, PPP 3236, NMB P15737. **x** *Microgobius* sp.1, Armuelles FM, Pacific Panama, PPP 3235, NMB P15738

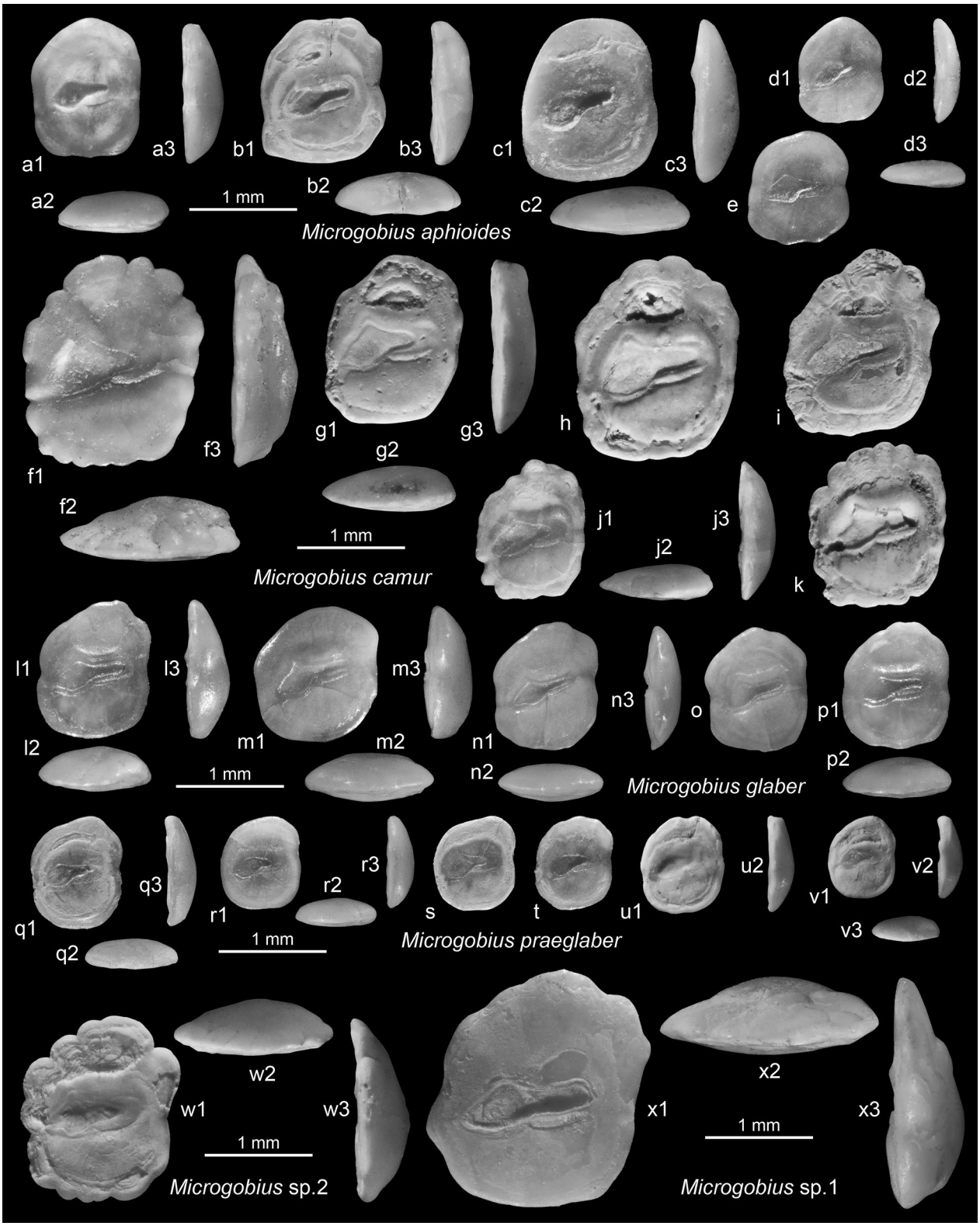


Fig. 31 (See legend on previous page.)

Referred specimen 50 specimens: 31 specimens Tortonian: 2 specimens Tuira FM, Pacific Panama, Darien, PPP 1134; 7 specimens Yaviza FM, Pacific Panama, Darien, PPP 1528; 10 specimens Gatun FM, Atlantic Panama, 2 specimens PPP 2165, 8 specimens PPP 2168; 5 specimens Manzanilla FM, San José Member, Trinidad, 1 specimen PPP 2671, 1 specimen PPP 2674, 3 specimens PPP 2676; 7 specimens Cercado FM, Dominican Republic, NMB 17003. 19 specimens Messinian, same data as holotype.

Etymology From glaber (Latin) = smooth, referring to the smooth outline and surface of these otoliths.

Diagnosis Otolith size up to 1.15 mm in length. OL:OH = 0.83–0.9. Otolith shape high-bodied; dorsal rim elevated, with rounded postdorsal angle; predorsal angle and postdorsal projection not protruding. Preventral and postventral angles rounded. Sulcus long, narrow, with moderately wide, angular ostial lobe and very narrow cauda; OL:SuL = 1.5–1.6; sulcus inclination angle 13–23°. Subcaudal iugum long, narrow, slightly bent around rear part of cauda and ingressing cauda from ventral. Ventral furrow close and parallel to ventral rim of otolith, regularly curved. Inner and outer faces smoothened.

Description Otolith size up to 1.15 mm in length (holotype 1.05 mm). OH:OT = 2.9–3.4. Otolith shape high-bodied. Dorsal rim high, rounded or with rounded postdorsal angle; predorsal angle broadly rounded, postdorsal projection blunt, not protruding. Anterior and posterior rims nearly vertical, nearly straight. Ventral rim slightly curved, horizontal. Preventral and postventral angles rounded. All rims smooth.

Inner face flat in vertical direction and slightly bent in horizontal direction. Sulcus long, narrow, with moderately wide, angular ostial lobe and very narrow cauda, with tapering tip; sulcus inclination angle very variable, 13–23°; OL:SuL = 1.5–1.6. Subcaudal iugum long, narrow, seemingly ingressing cauda ventrally, extending as narrow feature around caudal tip and sometimes also extending anteriorly below ostium. Dorsal depression wide, with distinct crista superior towards sulcus. Ventral furrow distinct, close and parallel to ventral rim of otolith and regularly curved. Outer face evenly convex, smooth.

Discussion Microgobius glaber differs from the other species in the *Microgobius camur* plexus in the combination of the smooth rims and inner and outer faces and the unusually narrow cauda.

***Microgobius praeglaber* n. sp.**

Figure 31q–v

Holotype NMB P15729 (Fig. 31q), Langhian to Serravallian, upper Brasso FM, Trinidad, KR-9244.

Paratypes 7 specimens: 4 specimens Langhian to Serravallian, same data as holotype (NMB P15730-33). 3 specimens Tortonian, Gatun FM, Atlantic Panama, PPP 2167 (NMB P15734-36).

Referred specimen 6 specimens Langhian to Serravallian, same data as holotype.

Etymology A combination of prae (Latin) = before, earlier and the species-name glaber of *Microgobius glaber* indicating its possible relationship to that species and its earlier occurrence.

Diagnosis Otolith size up to 0.85 mm in length. OL:OH = 0.79–0.83. Otolith shape high-bodied; dorsal rim elevated, with rounded postdorsal angle. Anterior rim slightly curved; posterior rim vertical, straight. Ventral rim curved. Sulcus short, anteriorly widened, posteriorly tapering, eccentrically forward positioned; OL:SuL = 2.0–2.2; sulcus inclination angle 12–16°. Subcaudal iugum long, wide, ingressing into rear part of cauda. Ventral furrow close and parallel to ventral rim of otolith, regularly curved.

Description Otolith size up to 0.85 mm in length (holotype). OH:OT = 3.3–4.0. Otolith shape high-bodied. Dorsal rim high, rounded or with rounded postdorsal angle; predorsal angle indistinct, postdorsal projection indistinct. Anterior rim slightly curved, posterior rim nearly vertical, straight. Ventral rim distinctly curved. Preventral and postventral angles broadly rounded. All rims smooth.

Inner face completely flat. Sulcus short, droplet-shaped, eccentrically positioned towards anterior, with rounded, widened anterior tip and rounded ostial lobe, and short cauda, with tapering, often pointed tip; sulcus inclination angle 12–16°; OL:SuL = 2.0–2.2. Subcaudal iugum long, wide, broadly extending around caudal tip and ingressing into cauda from ventral and posterior. Dorsal depression distinct. Ventral furrow distinct, close and parallel to ventral rim of otolith and regularly curved. Outer face evenly convex, smooth.

Discussion Microgobius praeglaber is characterized by small otoliths that at first sight could be taken as stemming from juvenile specimens of some other gobiid species. It does, however, show a number of unique features that exclude such explanation, including the droplet-shaped forward-positioned sulcus and the massive

ingression of the wide subcaudal iugum into the cauda. We therefore postulate that *M. praeglaber* and *M. aphioides* represented small, possibly hemipelagic gobies similar to the extant *Aphia minuta*.

Microgobius sp. 2

Figure 31w

Material 1 specimen Calabrian, Armuelles FM, Pacific Panama, PPP 3236 (NMB P15737).

Discussion A single, 1.45 mm long and relatively well-preserved specimen from the middle Pleistocene of Pacific Panama is characterized by a regularly crenulated otolith rim, a small and narrow sulcus with a very low ostial lobe and a massive subcaudal iugum ingressing into the cauda from ventral and posterior. The ratio OL:OH is 0.85; the ratio OL:SuL = 2.2. There is a good chance that this otolith belongs to one of the four extant *Microgobius* species from the East Pacific from which otoliths are not yet known. This would also mean that the *Microgobius camur* otolith plexus, which apparently is extinct in the West Atlantic could have survived in the East Pacific.

Gobiosoma Group sensu Tornabene et al., 2016

Otoliths of the fishes in the *Gobiosoma* group are distinguished from those of the *Microgobius* group by the absence of a subcaudal iugum. The *Gobiosoma* group contains a large number of often very small species. Small otoliths in small fishes are more easily destroyed during exposure to formalin than larger otoliths, and therefore the coverage of extant otoliths of the genera and species in the *Gobiosoma* group is less comprehensive than in the *Microgobius* group. Otoliths are known from 16 of the 27 genera currently recognized in the *Gobiosoma* group. Otoliths are not known from the genera *Aboma*, *Birdsongichthys*, *Carrigobius*, *Cryptopsilotris*, *Evermannichthys*, *Ophiogobius*, *Paedovaricus*, *Pariah*, *Pinnichthys*, *Robinsichthys*, and *Vomerogobius*. These are mostly small, monotypic genera, many of them living in specific reef environments that offer little chance for the fossilization of otoliths.

Rüber et al. (2003) and Tornabene et al., (2016, 2022) have undertaken extensive phylogenetic analyses of the *Gobiosoma* group. Tornabene et al. (2016) recognized two subgroups, the *Barbulifer* and the *Nes* subgroups. Tornabene et al. (2022) recognized an additional subgroup, the *Robinsichthys* subgroup. Rüber et al. (2003) did not formulate subgroups but instead recognized nine clades in the Gobiosomatini, two in the *Microgobius* group (the *Bollmannia* and the *Microgobius* clades) and seven in the *Gobiosoma* group (the *Nes*, *Aboma*, *Barbulifer*, *Gobiosoma*, *Risor*, *Tigrigobius*, and *Elacatinus* clades). The phylogenies of the three publications are generally congruent but differ somewhat in details.

With some variations, we have followed here the grouping in clades by Rüber et al. (2003), primarily because it is easier to relate to the otolith findings. We are aware that certain clades or subgroups are not represented by otoliths for the reasons mentioned above, i.e., the *Aboma* clade of Rüber et al. (2003) and the *Robinsichthys* subgroup of Tornabene et al. (2022). Only the *Barbulifer* and *Nes* clades of Rüber et al. (2003) are comprehensively represented. Most other clades or subgroups are represented by a limited number of taxa. This means that species recognition in the fossil record is hampered, except for the *Barbulifer* and *Nes* clades and a few other characteristic genera, and therefore many otoliths must remain in open nomenclature for the time being.

Barbulifer clade sensu Rüber et al., 2003

Genus *Aruma* Ginsburg, 1933

Aruma atlantica n. sp.

Figure 32c–g

Holotype NMB P15739 (Fig. 32c), Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 1256.

Paratypes 7 specimens: 2 specimens Piacenzian, Escudo de Veraguas FM, Atlantic Panama, PPP 1241 (NMB P15745-46). 5 specimens Calabrian, Swan Cay FM, Atlantic Panama, PPP 2221 (NMB P15740-44).

Referred specimen 7 specimens Gelasian: 4 specimens Escudo de Veraguas FM, Atlantic Panama, PPP 2170; 3 specimens Bastimentos FM, Ground Creek Unit, Atlantic Panama, 1 specimen PPP 3202, 2 specimens PPP 1256.

Etymology Named after its occurrence in the West Atlantic.

Diagnosis Otolith size up to 1.65 mm in length. OL:OH = 1.25–1.3. Otolith shape nearly rectangular with orthogonal predorsal, preventral and postventral angles and not protruding postdorsal projection. Dorsal rim highest at obtuse postdorsal angle; ventral rim straight to slightly bent, horizontal. Sulcus small, without ostial lobe; OL:SuL = 2.15–2.55; sulcus inclination angle 10–15°. No

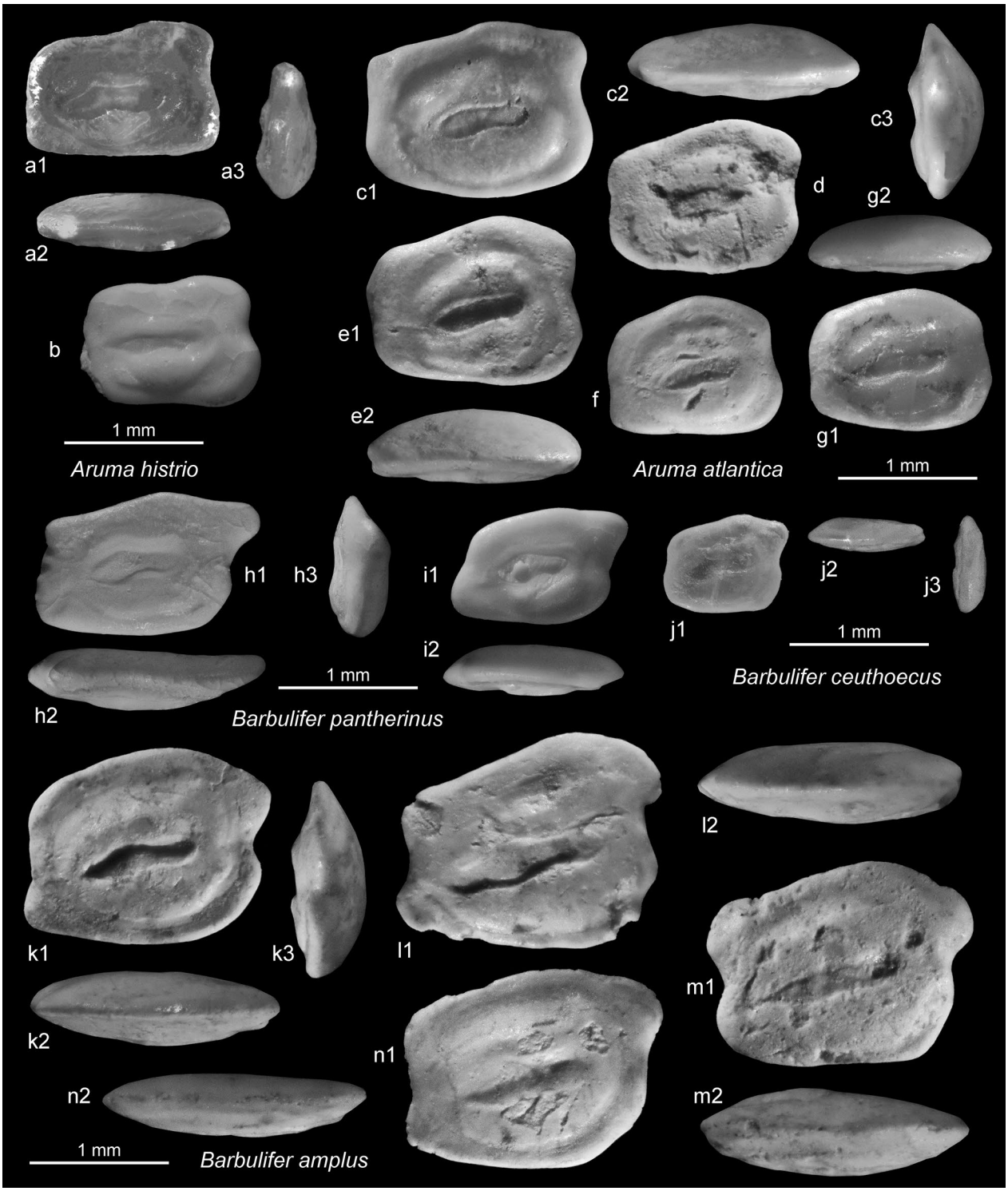


Fig. 32 **a**–**b** *Aruma histrio* (Jordan, 1884), extant; **a** LACM coll. Fitch; **b** USNM 322575, Gulf of California, SL 46 mm. **c**–**g** *Aruma atlantica* n. sp.; **c** holotype, NMB P15739, Bastimentos FM, Ground Creek Unit, Isla Bastimentos, Panama, PPP 1256; **d**–**e**, **g** paratypes; **d**–**e**, **g** Swan Cay FM, Atlantic Panama, PPP 2221, NMB P15740-42; **f** Escudo de Veraguas FM, Bocas del Toro, Panama, PPP 1241, NMB P15745. **h**–**i** *Barbulifer pantherinus* (Pellegrin, 1901), extant; **h** CAS 17711, Baja California, San Francisquito Bay, SL 35 mm; **i** USNM 322588, 28°45'N 112°59'W, 12 m tidepool. **j** *Barbulifer ceuthoecus* (Jordan & Gilbert, 1884), extant, USNM 413638, Bahamas, SL 19 mm. **k**–**n** *Barbulifer amplus* n. sp., Swan Cay FM, Atlantic Panama, PPP 2531; **m** holotype, NMB P15747; **k**–**l**, **n** paratypes, NMB P15748-50

subcaudal iugum. Dorsal depression connected to ventral furrow forming continuous circumsulcal furrow.

Description Otolith size up to 1.65 mm in length (holotype). OH:OT = 2.3–2.6. Otolith shape nearly rectangular. Dorsal rim low, anteriorly straight and slightly inclined, with broad, obtuse postdorsal angle as highest point, and short, not protruding postdorsal projection. Predorsal and preventral angles nearly orthogonal and anterior rim almost vertical. Postventral angle rounded orthogonal and as strongly developed as postdorsal projection; posterior rim near vertical, with moderate concavity at about level of caudal tip. Ventral rim flat or slightly curved, horizontal to slightly inclined. All rims smooth.

Inner face flat but area around sulcus somewhat bulged. Sulcus small, somewhat deepened, evenly wide, without ostial lobe, and rounded caudal tip; sulcus inclination angle 10–15°; OL:SuL = 2.15–2.55. No subcaudal iugum. Dorsal depression distinct, narrow, curved, close to dorsal rim of otolith, continuously connected around sulcus with distinct ventral furrow. Resulting circumsulcal furrow almost oval, clipping otolith angles. Outer face evenly and relatively strongly convex, smooth.

Discussion The genus *Aruma* today is known from a single species, *Aruma histrio* (Jordan, 1844) (Fig. 32a–b), a secretive species inhabiting rocky crevices and tide pools in the Gulf of California (Robertson & Allen, 2015). Its otoliths are characterized by the elongate rectangular outline and the small sulcus without clear differentiation of ostium and cauda and no ostial lobe. *Aruma* otoliths differ from those of the other genus in the clade, *Barbulifer*, in the absence of a protruding postdorsal projection. It is of interest to note that, from the Late Pliocene to the late Early Pleistocene, a presumably vicariant species existed in the tropical West Atlantic. *Aruma atlantica* differs from otoliths of the Pacific *A. histrio* in the shorter sulcus (OL:SuL = 2.15–2.55 vs 1.8–2.0) and the obtuse postdorsal angle (vs flat dorsal rim). *Aruma atlantica* seems also to have grown to larger sizes than its extant counterpart in the East Pacific. *Aruma atlantica* has been found in only a few localities, which may indicate a specific environmental adaptation. Of particular interest is its relatively common occurrence in the Swan Cay FM in locality PPP 2221, which represents a carbonatic sand layer in a cavity in a fossil reef bioherm.

Genus *Barbulifer* Eigenmann & Eigenmann, 1888

***Barbulifer amplus* n. sp.**

Figure 32k–n

Holotype NMB P15747 (Fig. 32m), Calabrian, Swan Cay FM, Atlantic Panama, PPP 2531.

Paratypes 4 specimens same data as holotype (NMB P15748-51).

Referred specimen 9 specimens: 2 specimens Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 3202. 7 specimens Calabrian, Swan Cay FM, Atlantic Panama, 1 specimen PPP 2221, 6 specimens same data as holotype.

Etymology From amplus (Latin) = great, wide, referring to the comparatively large size of the otoliths.

Diagnosis Otolith size up to 1.9 mm in length. OL:OH = 1.25–1.35. Otolith shape parallelogram-like to slightly trapezoidal. Dorsal rim highest at obtuse, rounded postdorsal angle; predorsal angle distinct; postdorsal projection distinctly protruding; ventral rim straight to slightly bent, horizontal. Sulcus long, with very low ostial lobe; OL:SuL = 1.85–2.05; sulcus inclination angle 13–15°. No subcaudal iugum. Dorsal depression anteriorly connected to ventral furrow.

Description Otolith size up to 1.9 mm in length (holotype). OH:OT = 2.5–3.1. Otolith shape parallelogram-like or sometimes trapezoidal (Fig. 32m). Dorsal rim low, anteriorly straight and slightly inclined, with broadly rounded postdorsal angle as highest point. Predorsal angle distinct, sometimes protruding (Fig. 32m, n), postdorsal projection more or less strongly protruding. Preventral angle orthogonal or protruding, postventral angle broadly rounded. Anterior rim short, vertical or slightly inclined, with distinct central concavity; posterior rim slightly inclined toward ventral, with moderate concavity at level above caudal tip. Ventral rim flat or slightly curved, horizontal. All rims smooth.

Inner face moderately convex in both directions. Sulcus long, somewhat deepened, with very low ostial lobe, and rounded caudal tip; sulcus inclination angle 13–15°; OL:SuL = 1.85–2.05. No subcaudal iugum. Dorsal depression distinct, narrow, curved, close to dorsal rim of otolith, anteriorly connected around sulcus with distinct ventral furrow. Ventral furrow distinct, regularly curved, clipping preventral angle. Outer face evenly convex, about as strong as inner face, smooth.

Discussion Barbulifer amplus has relatively large otoliths for the genus indicating fish sizes in the range of 30 mm SL or more. The only extant *Barbulifer* species reaching that size is *B. pantherinus* (Pellegrin, 1901) (Fig. 32h–i) from the Gulf of California. Its otoliths have a more pronounced

postdorsal projection and a small sulcus. Today, *Barbulifer* has five species, two in the East Pacific, two in the Caribbean, and one off central Brazil. The two extant Caribbean *Barbulifer* species, *B. antennatus* Böhlke & Robins, 1968, and *B. ceuthoecus* (Jordan & Gilbert, 1884), seem not to achieve sizes larger than 20 mm SL for *B. antennatus* (see Froese & Pauly, 2023) and 30 mm SL for *B. ceuthoecus* (see Robertson & Allen, 2015). Otoliths of *B. ceuthoecus* (Fig. 32j) do resemble *B. amplus* in otolith shape but have a larger sulcus (OL:SuL = 1.65 vs 1.85–2.05). *Barbulifer amplus* has been found in the same environment as *Aruma atlantica*, primarily in the sand layer in a cavity in a fossil reef bioherm of the Swan Cay FM at Swan Cay (PPP 2221 and 2531), and differs in the longer sulcus (OL:SuL = 1.85–2.05 vs 2.15–2.55) and the protruding postdorsal projection.

Nes clade sensu Rüber et al.,2003 ≅ Nes subgroup sensu Tornabene et al., 2016

The *Nes* clade or *Nes* subgroup is a diverse unit with several genera and many species. Otoliths are only known from a fraction of those, i.e., *Chriolepis semisquamata* (Rutter, 1904 (Fig. 33a–b), *Chriolepis zebra* Ginsburg, 1938 (Fig. 33c), *Psilotris laurae* van Tassell, Tornabene & Baldwin, 2016 (Fig. 33d), *Eleotrica cableae* Ginsburg, 1993 (Fig. 34a–b), *Gobulus crescentalis* (Gilbert, 1892) (Fig. 34c), *Gymneleotris seminuda* (Günther, 1864) (Fig. 34d), *Nes longus* (Nichols, 1914) (Fig. 34e), *Varicus decorum* van Tassell, Baldwin & Tornabene, 2016 (Fig. 35a), *Varicus veliguttatus* van Tassell, Baldwin & Gilmore, 2016 (Fig. 35b) and *Varicus cephalocellatus* Gilmore, van Tassell & Baldwin, 2016 (Fig. 35c). This hampers considerably the identification of fossil otoliths in this group except for those genera with few species (*Nes, Gobulus*), specimens from outside the extant distribution range (*Varicus*) or species in the Miocene (*Chriolepis*) considering that almost all Miocene goby specimens found in tropical America have been shown to represent extinct species.

Genus *Chriolepis* Gilbert, 1892

The genus *Chriolepis* currently comprises 10 recognized species (Fricke et al., 2023), thereof 8 in the East Pacific and 2 in the West Atlantic. Otoliths are known from two East Pacific species—*C. semisquamata* (Fig. 33a–b) and *C. zebra* (Fig. 33c). Otoliths are not known from any of the 4 species of the related genus *Pinnichthys* and only one species of 7 of the genus *Psilotris*, *P. laurae* (Fig. 33d). Species of *Chriolepis* are mostly taken from sand and rubble bottoms in shallow water, but some species like *C. fisheri* Herre, 1942 or *C. vespa* Hastings & Bortone, 1981 are caught at depths down to about 200 m (Froese & Pauly, 2023). The same is true for some species of *Pinnichthys* and *Psilotris* caught at depths of 70 to 150 m (Tornabene et al., 2016), e.g., *Psilotris laurae*.

Chriolepis altus n. sp.

Figure 33e–f

Holotype NMB P15752 (Fig. 33e), Tortonian, Yaviza FM, Pacific Panama, Darien, PPP 1145.

Paratypes 2 specimens Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1137 (NMB P15753-54).

Etymology From altus (Latin) = high, referring to the comparatively compressed shape of the otoliths.

Diagnosis Otolith size up to 1.15 mm in length. OL:OH = 1.05–1.1. Otolith shape rectangular to parallelogram-like. Postdorsal projection distinctly protruding; ventral rim straight, horizontal. Sulcus long, with very low ostial lobe; OL:SuL = 1.7–1.85; sulcus inclination angle 14–16°. No subcaudal iugum. Ventral furrow close to ventral rim of otolith.

Description Otolith size up to 1.15 mm in length (holotype 1.1 mm). OH:OT = 2.5–2.8. Otolith shape rectangular to parallelogram-like. Dorsal rim anteriorly depressed, with broadly rounded, shallow postdorsal angle. Predorsal angle distinct, not protruding, postdorsal projection pointed, slightly protruding. Preventral angle orthogonal, not protruding, postventral angle rounded. Anterior rim slightly inclined, with weak or without central concavity; posterior rim slightly inclined toward ventral, with

(See figure on next page.)

Fig. 33 **a**–**b** *Chriolepis semisquamata* (Rutter, 1904), extant, USNM 322622, 27°57′N 111°22′W. **c** *Chriolepis zebra* Ginsburg, 1938, extant, USNM 322602, Gulf of California, SL 26 mm. **d** *Psilotris laurae* van Tassell, Tornabene & Baldwin, 2016, extant, USNM 442092, Bonaire, 12°05′N 68°17′W, 134-165 m, SL 28 mm. **e**–**f** *Chriolepis altus* n. sp.; **e** holotype, NMB P15752, Yaviza FM, Darien, Panama, PPP 1145; **f** paratype, Tuira FM, Darien, Panama, PPP 1137, NMB P15753. **g** *Chriolepis* sp.1, Bastimentos FM, Ground Creek Unit, Bocas del Toro, Panama, PPP 3202, NMB P15755. **h**–**k** *Chriolepis balboa* n. sp.; **h** holotype, NMB P15756, Angostura FM, Ecuador, PPP 3301; **i**–**k** paratypes, Gatun FM, Colon, Panama, PPP 2168, NMB P15757-59. **l** *Chriolepis* sp.2, Cumaná FM, Venezuela, PPP 3038, NMB P15761. **m**–**n** *Chriolepis* sp.3, Moin FM, Limón, Costa Rica, PPP 3259, NMB P15762-63. **o** *Chriolepis* sp.4, Río Banano FM, Limón, Costa Rica, PPP 3249, NMB P15764. **p**–**q** *Chriolepis* sp.5, Cubagua FM, Venezuela; **p** PPP 2557, NMB P15765; **q** PPP 3057, NMB P15766

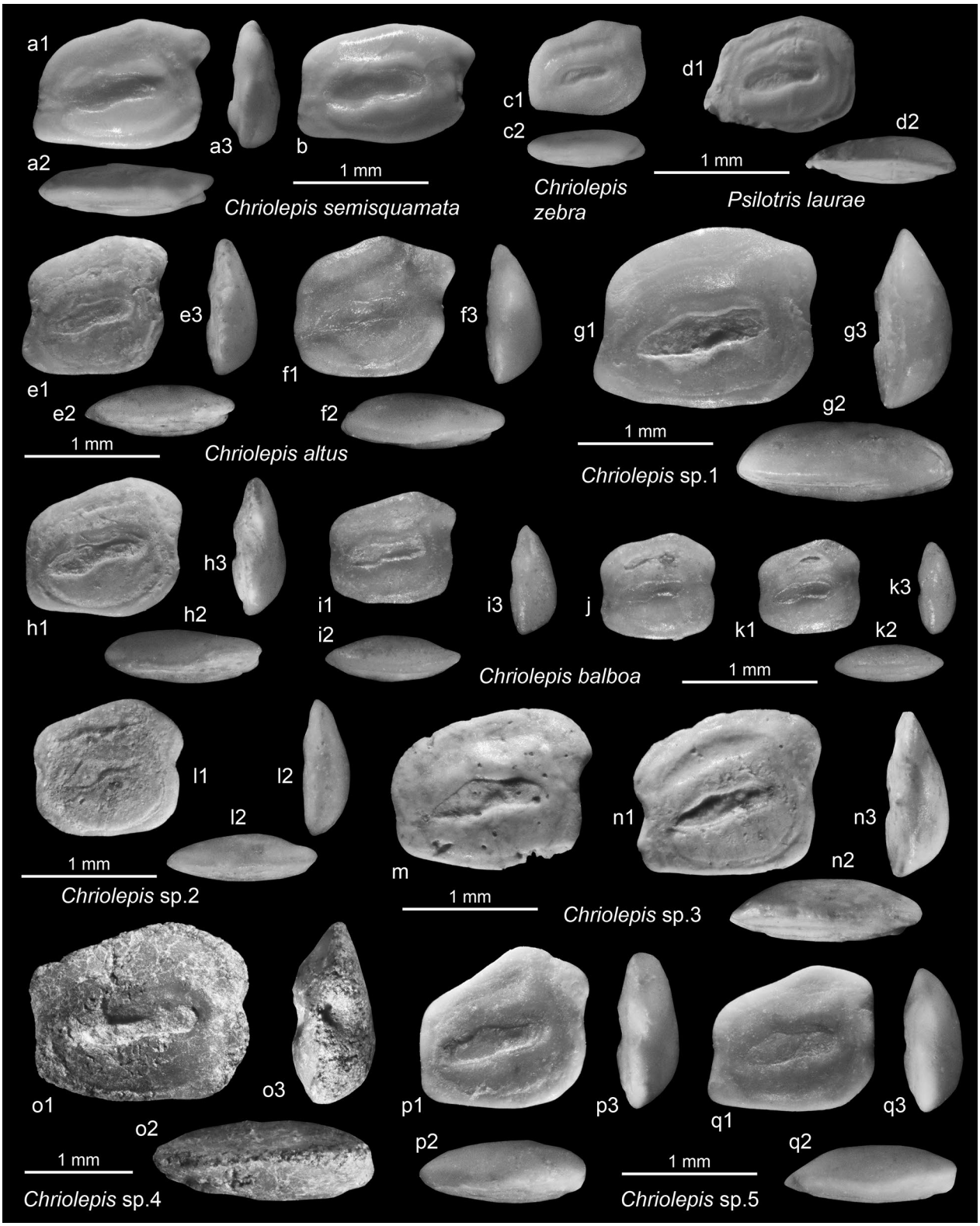


Fig. 33 (See legend on previous page.)

moderate concavity at level above caudal tip. Ventral rim flat, horizontal. All rims smooth.

Inner face moderately convex in both directions; area around sulcus slightly bulged. Sulcus moderately long, slightly deepened, with very low ostial lobe, and rounded caudal tip; sulcus inclination angle 14–16°; OL:SuL = 1.7–1.85. No subcaudal iugum. Dorsal depression indistinct; ventral furrow distinct, close and parallel to ventral rim of otolith. Outer face evenly convex, slightly stronger than inner face, smooth.

Discussion Chriolepis altus is recognized by its relatively compressed shape and the relatively large sulcus. The available otoliths of the few extant species show a great variety in sulcus size and development of the preventral angle and the postdorsal projection. A typical feature is also the bulging of the inner face around the sulcus which is often supported by the ventral furrow being connected around the sulcus to the dorsal depression.

***Chriolepis balboa* n. sp.**

Figure 33h–k

Holotype NMB P15756 (Fig. 33h), Tortonian, Angostura FM, Ecuador, PPP 3301.

Paratypes 4 specimens Tortonian: 1 specimen Tuira FM, Pacific Panama, Darien, PPP 1163 (NMB P15760); 3 specimens Gatun FM, Atlantic Panama, PPP 2168 (NMB P15757-59).

Referred specimens 2 specimens Tortonian, Gatun FM, Atlantic Panama, PPP 2168.

Etymology Named after Vasco Núñez de Balboa, the first to name the Pacific Ocean after having crossed the Isthmus of Panama.

Diagnosis Otolith size up to 1.15 mm in length. OL:OH = 1.1. Otolith shape nearly rectangular but with depressed predorsal section. Postdorsal projection slightly protruding; ventral rim straight, horizontal. Sulcus long, with very low ostial lobe; OL:SuL = 1.55–1.7; sulcus inclination angle 8–14°. No subcaudal iugum. Ventral furrow close to ventral rim of otolith, regularly curved.

Description Otolith size up to 1.15 mm in length (holotype). OH:OT = 2.4–2.6. Otolith shape nearly rectangular with orthogonal preventral and postventral angles but somewhat depressed predorsal region and obtuse predorsal angle. Postdorsal projection rounded, slightly protruding. Anterior rim nearly vertical; posterior rim slightly inclined toward ventral, with weak concavity at level above caudal tip. Ventral rim flat, horizontal. All rims smooth.

Inner face moderately convex in both directions; area around sulcus slightly bulged. Sulcus long, slightly deepened, with very low ostial lobe, and rounded caudal tip; sulcus inclination angle 8–14°; OL:SuL = 1.55–1.7. No subcaudal iugum. Dorsal depression indistinct; ventral furrow distinct, close to ventral rim of otolith and regularly curved. Outer face evenly convex, slightly stronger than inner face, smooth.

Discussion Chriolepis balboa is a typical otolith of the genus *Chriolepis* but with an unusually long sulcus.

***Chriolepis* sp. 1**

Figure 33g

Material 3 specimens Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 3202 (NMB P15755).

Discussion Unusually large otoliths for the genus *Chriolepis* up to 1.65 mm in length with a rounded dorsal rim, a short preventral projection, a weak postdorsal projection (OL:OH = 1.25) and a relatively long sulcus (OL:SuL = 1.7).

***Chriolepis* sp. 2**

Figure 33l

Material 1 specimen Calabrian, Cumaná FM, Venezuela, PPP 3038 (NMB P15761).

Discussion A rather compressed, nearly rectangular otolith with a high positioned predorsal angle and a weak postdorsal projection. The sulcus is short and shows moderate ostial lobe. OL:OH = 1.1; OL:SuL = 2.0.

***Chriolepis* sp. 3**

Figure 33m–n

Material 3 specimens Gelasian, Moin FM, Atlantic Costa Rica, 1 specimen PPP 1773, 2 specimens PPP 3259 (NMB P15762-63).

Discussion Relatively compact otoliths with weak preventral and postdorsal projections. Characteristic is the straight, inclined dorsal rim, which is anteriorly

depressed, and the long sulcus oriented parallel to the dorsal rim. OL:OH = 1.1–1.2; OL:SuL = 1.7–1.75.

Chriolepis sp. 4

Figure 33o

Material 1 specimen Piacenzian, Río Banano FM, Atlantic Costa Rica, PPP 3249 (NMB P15764).

Discussion The single, relatively large otolith of 2 mm in length is remarkable for its thick appearance (OH:OT = 2.2), the rather large, wide and somewhat deepened sulcus (OL:SuL = 1.65) and the relatively slender shape (OL:OH = 1.25) with a rounded postdorsal projection.

Chriolepis sp. 5

Figure 33p–q

Material 9 specimens Zanclean, Cubagua FM, Venezuela, 1 specimen PPP 2549, 1 specimen PPP 2555, 2 specimens PPP 2556, 1 specimen PPP 2557 (NMB P15765), 2 specimens PPP 2563, 2 specimens PPP 3057 (NMB P15766).

Discussion This is a rather characteristic species with a highly elevated postdorsal region and a strongly depressed predorsal angle and with a steeply inclined predorsal rim (25–33°). Anterior and posterior rims are nearly vertical and the postdorsal projection is very week. OL:OH = 1.05–1.15; OL:SuL = 1.7–1.8; sulcus inclination angle = 13°. These otoliths may represent an undescribed species but because of their low stratigraphic age and the lack of knowledge of West Atlantic *Chriolepis, Pinnichthys* and *Psilotris* species we have refrained from a formal action.

Genus *Gobulus* Ginsburg, 1933

The genus *Gobulus* contains four extant species, three in the East Pacific and one in the West Atlantic. Otoliths are only known from the East Pacific *G. crescentalis* (Gilbert, 1892) (Fig. 34c). For further comparison, otoliths are also shown of the three monotypic genera *Eleotrica* Ginsburg, 1933—*E. cableae* Ginsburg, 1933 (Fig. 34a–b)—*Gymneleotris* Bleeker, 1874—*G. seminuda* (Günther, 1864) (Fig. 34d)—and *Nes* Ginsburg, 1933—*N. longus* (Nichols, 1914) (Fig. 34e).

The otoliths of *Gobulus* and *Eleotrica* are recognized by their relatively elongate shape with a distinct postdorsal projection (OL:OH = 1.2–1.35), the inner face being markedly bent in the horizontal direction, and the sulcus being relatively large, distinctly deepened and with a low ostial lob and relatively wide cauda (OL:SuL = 1.7–1.85); the sulcus inclination angle is relatively low at 5–15°. The otoliths of *Gymneleotris* differ in being more compact without a pronounced postdorsal projection and with a small sulcus (OL:SuL = 2.2). The otoliths of *Nes* finally differ in being more high-bodied (OL:OH about 0.95) and showing a narrow and rather steeply inclined sulcus (> 20°).

Eleotrica is endemic to the Galapagos Islands where it inhabits shallow sand-rubble adjacent to rocky reefs (Robertson & Allen, 2015). *Gobulus* and *Gymneleotris* occur over sand, on rocks and cobbles at depths down to 20 m (Robertson & Allen, 2015). *Nes* lives in association with shrimps in burrows in silty substratum (Böhlke & Robins, 1968).

Gobulus limonensis n. sp.

Figure 34f–g

Holotype NMB P15767 (Fig. 34f), Gelasian, Moin FM, Atlantic Costa Rica, PPP 1773.

Paratype 1 specimen Gelasian, Moin FM, Atlantic Costa Rica, PPP 1772 (NMB P15768).

Etymology Named after the province Limón, Costa Rica, where the specimens were collected.

Diagnosis Otolith size up to 2.5 mm in length. OL:OH = 1.2–1.25. Otolith moderately elongate but with depressed predorsal section. Postdorsal projection and postventral angle equally protruding with broad concavity of posterior rim in between; ventral rim curved, horizontal. Sulcus moderately long, wide, with very low ostial lobe; OL:SuL = 1.85–1.95; sulcus inclination angle 5–6°. No subcaudal iugum. Ventral furrow regularly curved.

Description Otolith size up to 2.5 mm in length (holotype). OH:OT = 2.8–3.2. Otolith moderately elongate; dorsal rim shallow, predorsal section depressed, regularly declining towards low predorsal angle; postdorsal angle highest point, broadly rounded. Postdorsal projection distinct, moderately protruding, about as strongly as projecting postventral angle; posterior rim with broad, distinct concavity between postdorsal and postventral projections. Anterior rim short, nearly vertical. Ventral rim curved, horizontal. All rims smooth.

Inner face moderately convex in both directions; area around sulcus slightly bulged. Sulcus relatively short but wide, deepened, with very low ostial lobe, and cauda about equally wide as ostium; sulcus inclination angle 5–6°; OL:SuL = 1.85–1.95. No subcaudal iugum. Dorsal

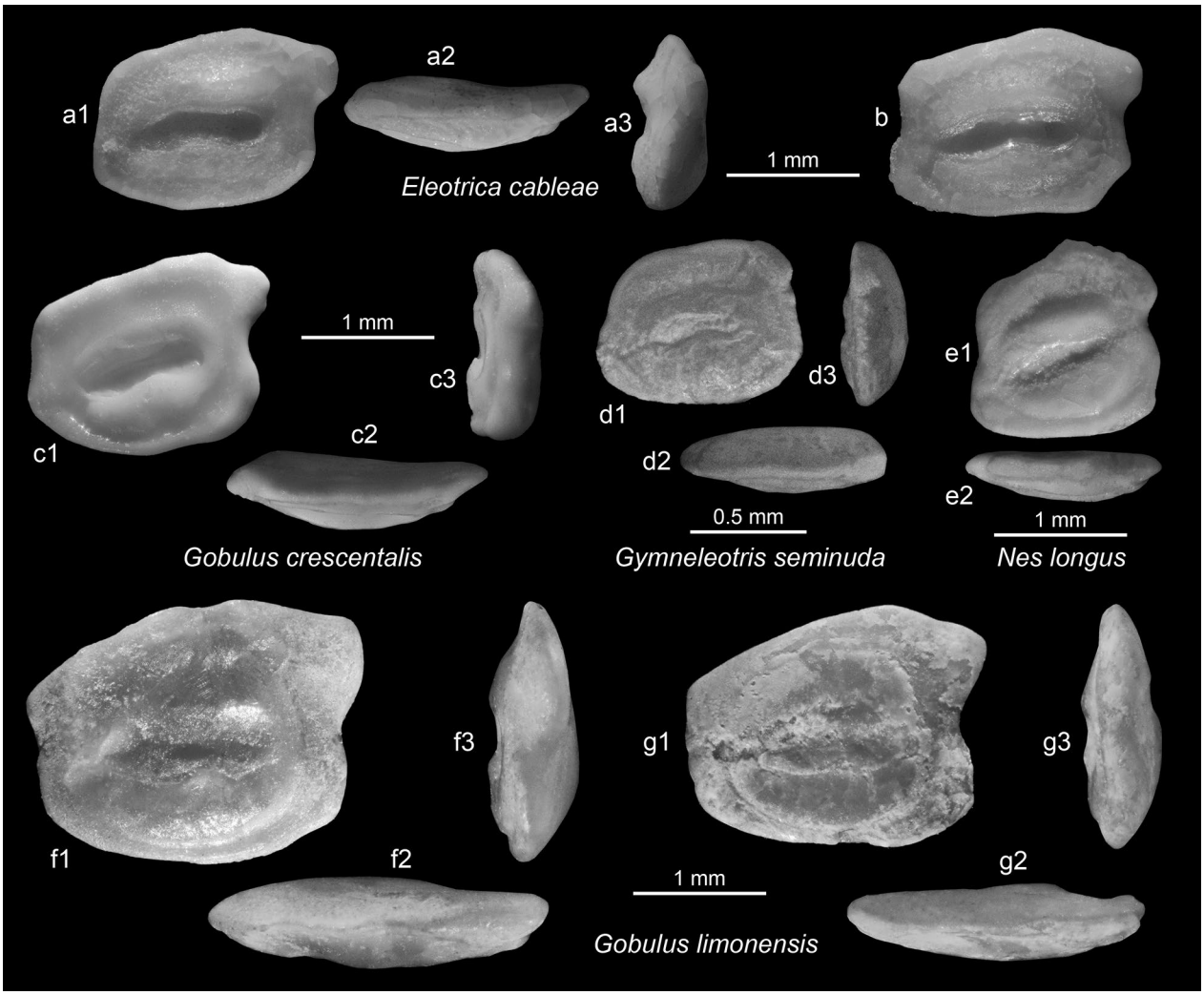


Fig. 34 **a**–**b** *Eleotrica cableae* Ginsburg, 1933, extant, CAS 31203, Galapagos, Santa Cruz. **c** *Gobulus crescentalis* (Gilbert, 1892), extant, USNM 214508, Baja California, lagoon, SL 61 mm. **d** *Gymneleotris seminuda* (Günther, 1864), extant, LACM coll. Fitch, det. B. Walker, Gulf of California. **e** *Nes longus* (Nichols, 1914), extant, USNM 321016, Belize, between Carry Bow and Twin Cays. **f–g** *Gobulus limonensis* n. sp. Moin FM, Limón, Costa Rica; **f** holotype, NMB P15767, PPP 1773; **g** paratype, PPP 1772, NMB P15768

depression indistinct, joint to distinct ventral furrow around sulcus; ventral furrow half-moon shaped, close to ventral rim of otolith only at central part. Outer face nearly flat, smooth.

Discussion Otoliths of *Gobulus limonensis* are exceptionally large for otoliths of the *Nes* clade or the genus *Gobulus*. An otolith of the extant *G. crescentalis* of 61 mm SL, which is the largest recorded specimen of the species (Robertson & Allen, 2015) and represents the largest extant species of the genus, is 1.8 mm in length. The fishes from which the fossil *G. limonensis* otoliths are described may have surpassed 80 mm SL. In a redescription of the only extant Atlantic species, *Gobulus myersi* Ginsburg, 1939, Hastings (1983) found no specimen larger than 29.3 mm SL among all known specimens. The size correlation therefore rules out *G. limonensis* being synonymous with the extant *G. myersi*, even though no otoliths are known from the latter.

Genus *Varicus* Robins & Böhlke, 1961

Varicus is a genus inhabiting deep-shelf environments in the tropical West Atlantic mostly at depths of 100 m to 300 m, where they are usually benthic and solitary (Tornabene et al., 2016). In a recent article, Fuentes et al. (2023) described two new deep-water species of *Varicus*, bringing the count to 12 species. Otoliths are known from only three of those: *Varicus decorum* (Fig. 35a), *V. veliguttatus* (Fig. 35b), and *V. cephalocellatus* (Fig. 35c). The otoliths

show a parallelogram-like shape, as is also typical for many Atlanto-Mediterranean goby otoliths, with a relatively short sulcus. The expression of the ostial lobe appears to be highly variable and could represent an important characteristic for differentiation of species in this genus.

***Varicus pliocenicus* n. sp.**

Figure 35d–f

Holotype NMB P15769 (Fig. 35d), Zanclean, Cubagua FM, Venezuela, PPP 2568.

Paratypes 2 specimens same data as holotype (NMB P15770-71).

Referred specimen 1 specimen Zanclean, Cubagua FM, Venezuela, PPP 3093.

Etymology Named after the occurrence of the species in the (early) Pliocene.

Diagnosis Otolith size up to 1.9 mm in length. OL:OH = 1.2–1.3. Otolith shape parallelogram-like with pronounced preventral angle and expanded postdorsal projection. Dorsal rim regularly curved. Sulcus moderately long, relatively narrow, with pointed ostial tip and

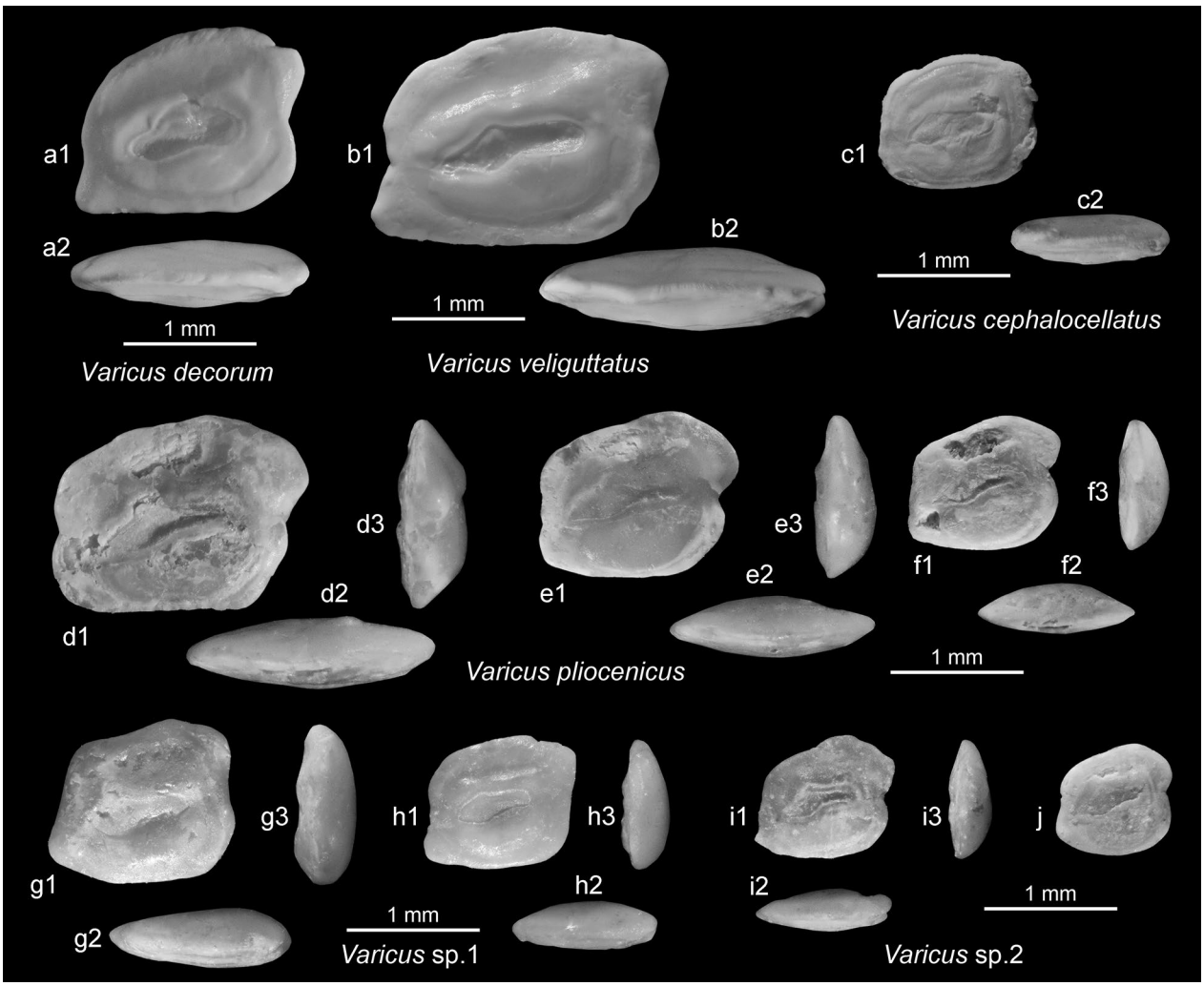


Fig. 35 **a** *Varicus decorum* van Tassell, Baldwin & Tornabene, 2016, extant, USNM 442131, 12°05′N 68°17′W, 163 m. **b** *Varicus veliguttatus* van Tassell, Baldwin & Gilmore, 2016, extant, USNM 442770, 17°27′N 62°59′W, 240 m. **c** *Varicus cephalocellatus* Gilmore, van Tassell & Baldwin, 2016, extant, USNM 442058, Bonaire, 12°05′N 68°17′W, 84-226 m, SL 28 mm. **d**–**f** *Varicus pliocenicus* n. sp., Cubagua FM, Venezuela, PPP 2568; **d** holotype, NMB P15769; **e**–**f** paratypes, NMB P15770-71. **g**–**h** *Varicus* sp.1, Cumaná FM, Venezuela, PPP 3038, NMB P15772-73. **i**–**j** *Varicus* sp.2, Cubagua FM, Venezuela; **i** PPP 3057, NMB P15774; **j** PPP 3055, NMB P15775

tapering caudal tip; ostial lobe rounded with colliculum not extending into lobe; OL:SuL = 1.75–1.9; sulcus inclination angle 12–15°. No subcaudal iugum. Ventral furrow regularly curved.

Description Otolith size up to 1.9 mm in length (holotype). OH:OT = 2.7–2.9. Otolith parallelogram-like in shape with pronounced preventral angle, broad and expanded postdorsal projection and obtuse, rounded predorsal and postventral angles. Dorsal rim regularly curved with broad, rounded postdorsal angle. Anterior rim short, nearly vertical to slightly inclined towards dorsal. Posterior rim slightly inclined towards ventral, with narrow concavity at level of tip of cauda. Ventral rim straight, horizontal. All rims smooth.

Inner face moderately convex in both directions. Sulcus moderately long, narrow, slightly deepened, its ostial tip pointed, caudal tip tapering, narrow; ostial lobe low with rounded expansion without extension of colliculum; sulcus inclination angle 12–15°; OL:SuL = 1.75–1.9. No subcaudal iugum. Dorsal depression indistinct; ventral furrow regularly curved, closest to ventral rim of otolith at central part. Outer face convex, usually more strongly than inner face, smooth.

Discussion Varicus pliocenicus is characterized by the parallelogram-like shape that resembles the extant *V. veliguttatus*; the unusual expansion of the ostial lobe without extension of the colliculum, a feature also seen in a slightly different form in the extant *V. decorum*; and the pointed ostial tip and tapering, narrow caudal tip of the sulcus. *Varicus pliocenicus* is thus a well-defined and easily recognized otolith of this genus. None of the 12 extant *Varicus* species are known from off Venezuela, but three are known off Curacao: *V. decorum*, *V. lacerta*, and *V. veliguttatus*. Otoliths of *V. decorum* (Fig. 35a) resemble *V. pliocenicus* in the unusual development of the ostial lobe but otherwise show little similarity. Otoliths of *V. veliguttatus* resemble *V. pliocenicus* in otolith proportions and the pointed ostial tip of the sulcus, but differ in the rounded caudal tip, the lack of the expansion of the ostial lobe, and the less strongly developed postdorsal projection. Otoliths of *V. lacerta* are not known.

Varicus sp. 1

Figure 35g–h

Material 3 specimens Calabrian, Cumaná FM, Venezuela, PPP 3038 (figured specimens NMB P15772-73).

Discussion These are relatively small and compressed specimens with a small and simple-shaped sulcus that resemble in habitus the extant *V. cephalocellatus* (Fig. 35c).

Varicus sp. 2

Figure 35i–j

Material 2 specimens Zanclean, Cubagua FM, Venezuela, 1 specimen PPP 3057 (NMB P15774), 1 specimen PPP 3055 (NMB P15775).
Discussion Like *Varicus* sp. 1 mentioned above these are compressed otoliths but with a relatively long and structured sulcus.

Gobiosoma clade sensu Rüber et al., 2003

The *Gobiosoma* clade in the composition of Rüber et al. (2003) is here understood to contain the genera *Enypnias*, *Garmannia*, and *Gobiosoma*. A recent phylogenetic study by Tornabene and van Tassell (2014) suggests that *Enypnias* is nested within *Gobiosoma* and hence would be a synonym. The position and extent of *Garmannia* also appears to vary, and Rüber et al. (2003) show the genus as non-monophyletic in their cladogram. We have retained all three nominal genera because of the differing otolith pattern with that of the nominal genus *Enypnias* probably representing the most plesiomorphic one with its parallelogram-like otolith shape (Fig. 36a–d). The otoliths of the genera *Gobiosoma* (Fig. 36g–o) and *Garmannia* (Fig. 36f) are more compressed in shape with a typically depressed predorsal angle and a "simplified" sulcus pattern. The otolith of *Gobiosoma chiquita* (Jenkins & Evermann, 1889) (Fig. 36g) occupies a morphologically intermediate pattern.

The three genera contain among them 19 extant species. Otoliths are only known from a few of them: *Enypnias aceras* Ginsburg, 1939 (Fig. 36a), *Enypnias seminudus* (Günther, 1861) (Fig. 36b–d), *Garmannia schultzi* Ginsburg, 1944 (Fig. 36f), *Gobiosoma chiquita* (Jenkins & Evermann, 1889) (Fig. 36g), *Gobiosoma bosc* (Lacepède, 1800) (Fig. 36h–k), and *Gobiosoma robustum* Ginsburg 1933 (Fig. 36m–o). In consequence, we have refrained from specific identifications of any of the fossil otoliths attributed to these genera except for one highly characteristic case from the Late Miocene. Another hindering aspect in identifying isolated otoliths of this clade is their small size, which causes them to be easily confused with otoliths of juveniles of larger gobies. It is likely that further unrecognized *Gobiosoma* otoliths are contained among the many unidentifiable small goby otoliths.

The fishes of the genera *Gobiosoma* and *Enypnias* occur mostly in shallow near-shore environments, for instance in mangrove and tide pools or rocky environments. Several species inhabit freshwater and brackish waters or are euryhaline.

Genus Garmannia Jordan & Evermann, 1895

***Garmannia* sp.**

Figure 36e

Material 1 specimen Zanclean, Springvale FM, Trinidad, KR-1216 (NMB P15776).
Discussion A single, very small otolith of 0.55 mm in length closely resembles that of the extant *G. schultzi* (Fig. 36f) and is therefore tentatively placed in the genus *Garmannia*.

Genus *Gobiosoma* Girard, 1858

***Gobiosoma emberae* n. sp.**

Figure 36l

Holotype NMB P15777 (Fig. 36l), Messinian, Chucunaque FM, Pacific Panama, Darien, PPP 1612.

Etymology Named after the indigenous Indian tribe Embera inhabiting the Darien province of Panama.

Diagnosis Otolith size 0.9 mm in length. OL:OH = 0.95. Otolith shape more or less rectangular with pronounced predorsal, preventral and postventral angles and angular postdorsal projection. Anterior, posterior and predorsal rims slightly concave. Sulcus long, relatively narrow, deepened, without ostial lobe; OL:SuL = 1.55; sulcus inclination angle 20°. No subcaudal iugum. Ventral furrow regularly curved.

Description A small otolith of 0.9 mm in length (holotype). OH:OT = 2.8. Otolith more or less rectangular. Dorsal rim shallow, with nearly orthogonal, high positioned predorsal angle, slightly concave ascending predorsal rim, obtuse but distinct postdorsal angle and angular, not protruding postdorsal projection. Ventral rim nearly flat, horizontal, with orthogonal preventral angle and rounded postventral angle. Anterior rim vertical, broadly concave; posterior rim vertical, very slightly concave. All rims smooth.

Inner face moderately convex in both directions; area around sulcus markedly bulged. Sulcus long, relatively narrow, distinctly deepened, its ostial tip more pointed than caudal tip; no ostial lobe discernable; sulcus inclination angle 20°; OL:SuL = 1.55. No subcaudal iugum. Dorsal depression marked, long and narrow, with wide crista superior toward sulcus, connected to evenly curving ventral furrow around sulcus. Outer face convex, smooth.

Discussion Despite its small size, *G. emberae* is well characterized by its shape, particularly the sharply angled, high predorsal angle and the concave predorsal and anterior rims. These characters and the long sulcus set *G. emberae* apart from coeval otoliths and the known extant *Gobiosoma* otoliths.

***Gobiosoma* sp. 1**

Figure 36p–q

Material 3 specimens Zanclean, Cubagua FM, Venezuela, PPP 3057 (figured specimens NMB P15778-79).

Discussion These otoliths are in many ways similar to *G. emberae* from the Tortonian but differ in the posterior rim being inclined toward dorsal, the more rounded angles and the ventral furrow running further away from the ventral rim of the otolith. It also resembles the extant *G. robustum* (Fig. 36m–o), but is thicker and has a shorter sulcus with a lower, almost flat ostial lobe.

***Gobiosoma* sp. 2**

Figure 36r

(See figure on next page.)

Fig. 36 **a** *Enypnias aceras* Ginsburg, 1939, extant, BMNH 1975.4.25.11-12, Panama canal, Miraflores. **b**–**d** *Enypnias seminudus* (Günther, 1861), extant, USNM 407784, 13°22'N 87°52'W. **e** *Garmannia* sp., Springvale FM, Trinidad, KR-1216, NMB P15776. **f** *Garmannia schultzi* Ginsburg, 1944, extant, USNM 121550, Venezuela, Lago Maracaibo. **g** *Gobiosoma chiquita* (Jenkyns & Evermann, 1889), extant, LACM coll Fitch, Gulf of California. **h**–**k** *Gobiosoma bosc* (Lacepède, 1800), extant; **h**, **k** TCWC-20131.04 Texas, Oso Bay SL 36, 54 mm; **i** LACM coll Fitch, Rappahonnock; **j** USNM 420904, 28°41'N 96°13'W. **l** *Gobiosoma emberae* n. sp., holotype, NMB P15777, Tuira FM, Darien, Panama, PPP 1612. **m**–**o** *Gobiosoma robustum* Ginsburg, 1933, extant; **m, o** TCWC 20141.03, off Texas, SL 23,5 and 25,5 mm; **n** CAS 36379, Florida, Sanibel Island. **p**–**q** *Gobiosoma* sp.1, Cubagua FM, Venezuela, PPP 3057, NMB P15778-79. **r** *Gobiosoma* sp.2, Tuira FM, Darien, PPP 1593, NMB P15780. **s** *Gobiosoma* sp.3, Swan Cay FM, Atlantic Panama, PPP 2221, NMB P15781. **t**–**v** *Gobiosoma* sp.4, Cumaná FM, Venezuela, PPP 3038, NMB P15782-84. **w** *Gobiosoma* sp.5, Moin FM, Limón, Costa Rica, PPP 2038, NMB P15785

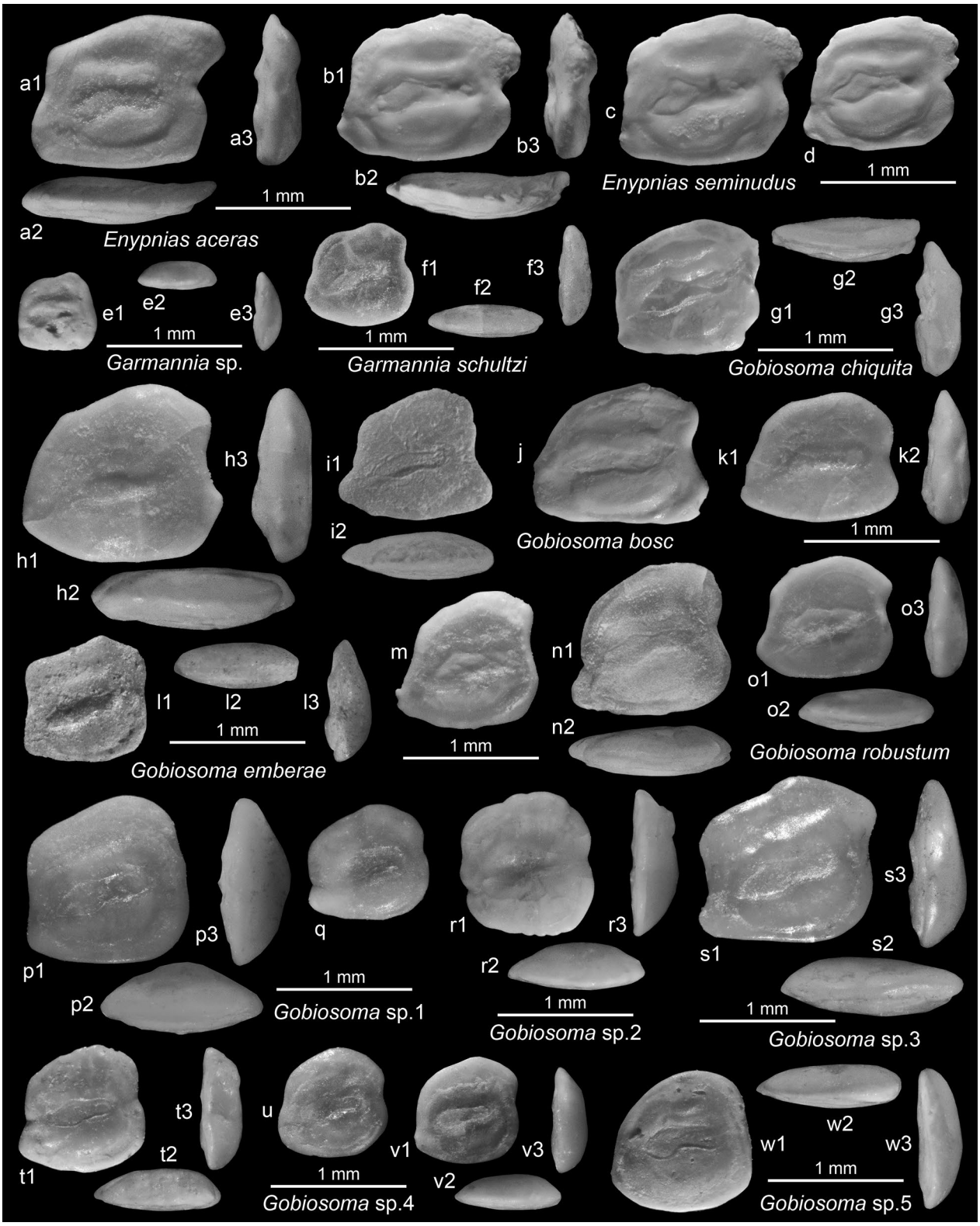


Fig. 36 (See legend on previous page.)

Material 1 specimen Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1593 (NMB P15780).

Discussion A relatively high-bodied otolith (OL:OH = 0.93) that also resembles otoliths of *Elacatinus* (see below).

***Gobiosoma* sp. 3**

Figure 36s

Material 1 specimen Calabrian, Swan Cay FM, Atlantic Panama, PPP 2221 (NMB P15781).

Discussion A relatively large otolith for a *Gobiosoma* species of 1.3 mm length. It resembles *G. emberae* in shape but has a sharper preventral projection and a more forward positioned postdorsal angle. This otolith likely pertains to an extant species that may have derived from such a Late Miocene form like *G. emberae*.

***Gobiosoma* sp. 4**

Figure 36t–v

Material 20 specimens Calabrian, Cumaná FM, Venezuela, PPP 3038 (figured specimens NMB P15782-84).

Discussion These otoliths resemble *Gobiosoma* sp. 1 from the Zanclean of Venezuela and differ mainly in the more rounded dorsal rim and in being thinner.

***Gobiosoma* sp. 5**

Figure 36w

Material 1 specimen Gelasian, Moin FM, Atlantic Costa Rica, PPP 2038 (NMB P15785).

Discussion The single, slightly eroded otolith resembles otoliths of the extant *G. robustum* but is remarkable for its rounded triangular shape with the relatively small dorsal field on the inner face.

***Elacatinus* clade, including *Tigrigobius* and *Risor* clades of Rüber et al.,** 2003

This clade contains many small fishes of the genera *Elacatinus* Jordan, 1904, *Evermannichthys* Metzelaar, 1919, *Ginsburgellus* Böhlke & Robins, 1968, *Ophiogobius* Gill, 1863, *Pariah* Böhlke, 1969, *Risor* Ginsburg, 1933, and *Tigrigobius* Fowler, 1931. Many of the species in this clade are known for specific environmental adaptations usually in rock reef settings (Böhlke & Robins, 1968; Rüber et al., 2003; Tyler & Böhlke, 1972). *Risor* and *Evermannichthys* as well as several species of *Elacatinus* are sponge dwellers. *Ginsburgellus* and *Tigrigobius multifasciatus* live under sea urchins in shallow water. Many species of *Elacatinus* are known as cleaner gobies. Other species of *Elacatinus* and most species of *Tigrigobius* live secretively in reef caves and various reef environments. It is clear from these environmental adaptations that the prospect for preservation of otoliths in the fossil record is relatively low. In addition, as with the otoliths of the fishes of the *Gobiosoma* clade, the identification of isolated otoliths of this clade is hindered by their small size making them easily confused with otoliths of juveniles of larger gobies.

The aforementioned genera of this clade contain nearly 50 valid species according to Fricke et al. (2023): 24 species in *Elacatinus*, 16 in *Tigrigobius*, five in *Evermannichthys*, and one each in *Risor*, *Ginsburgellus*, *Ophiogobius*, and *Pariah*. Otoliths are known from only a few of these taxa: *Elacatinus chancei* (Beebe & Hollister, 1933) (Fig. 37a–b), *E. horstii* (Metzelaar, 1922) (Fig. 37c–d), *E. lori* Colin, 2002 (Fig. 37e), *E. oceanops* Jordan, 1904 (Fig. 37f), *E. puncticulatus* (Ginsburg, 1938) (Fig. 37g), *E. xanthipora* (Böhlke & Robins, 1968) (Fig. 37h), *Ginsburgellus novemlineatus* (Fowler, 1950) (Fig. 38a), *Risor ruber* (Rosén, 1911) (Fig. 38c), and *Tigrigobius macrodon* (Beebe & Tee Van, 1928) (Fig. 38d). Because of this low coverage, the fossil otoliths described here have been left in open nomenclature, except for one otolith that can be attributed to an extant species (*Ginsburgellus novemlineatus*).

Genus *Elacatinus* Jordan, 1904

***Elacatinus* sp. 1**

Figure 37i–j

Material 4 specimens: 1 specimen Zanclean, Cubagua FM, Venezuela, PPP 2568; 2 specimens Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 2247 (figured specimen NMB P15787); 1 specimen Calabrian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 2250 (NMB P15786).

Discussion These otoliths are characterized by their high-bodied appearance (OL:OH = 0.88–0.93), the strong postdorsal angle and the relatively large sulcus without ostial lobe. They resemble otoliths of the extant species *E. chancei* (Fig. 37a–b) and *E. lori* (Fig. 37e, formalin-eroded specimen).

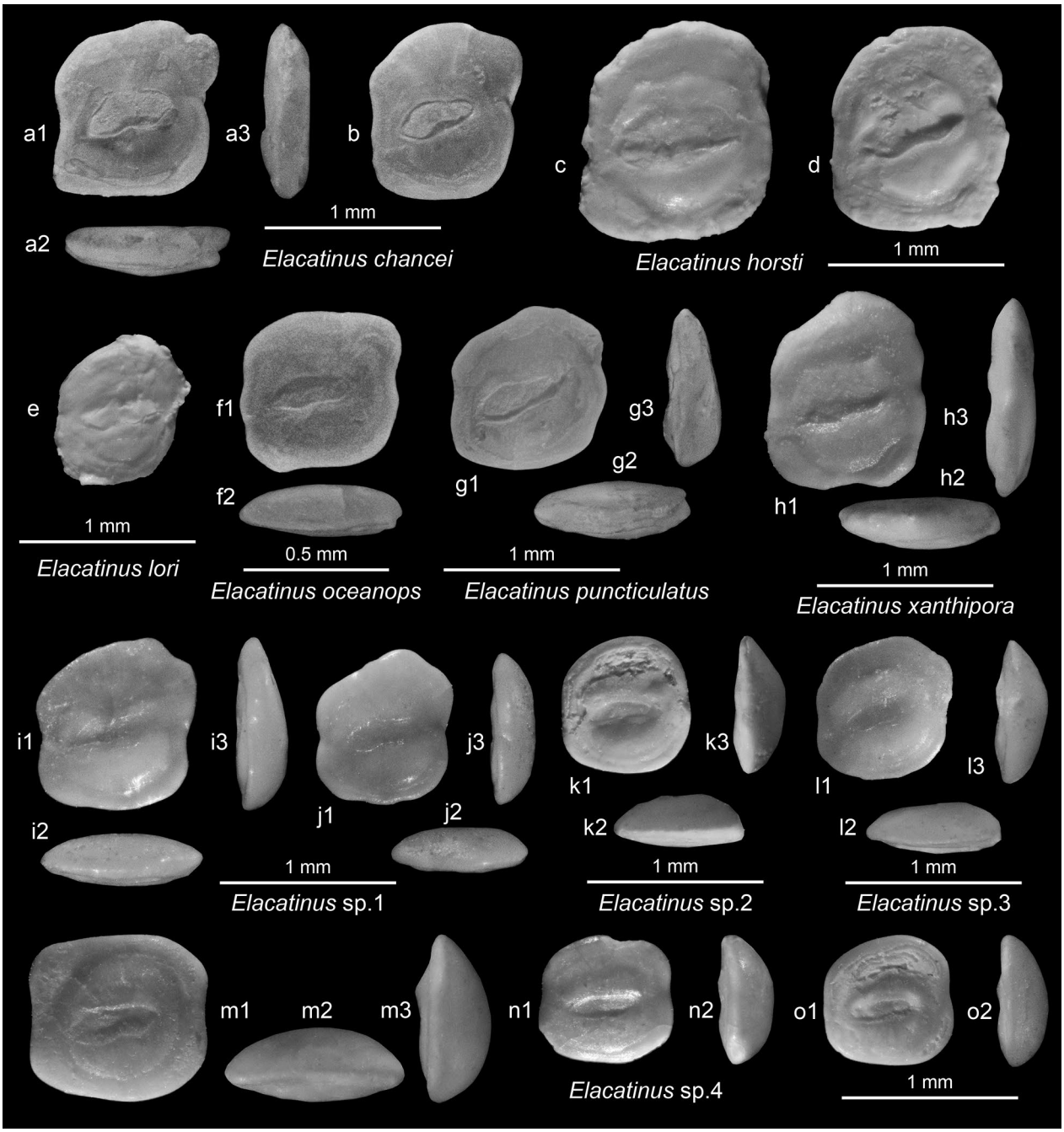


Fig. 37 **a**–**b** *Elacatinus chancei* (Beebe & Hollister, 1933), extant, USNM 441849, Sint Eustatius, SL 27 and 28 mm. **c**–**d** *Elacatinus horsti* (Metzelaar, 1922), extant; **c** USNM 413792, Curacao, SL 40 mm; **d** USNM 413817, Curacao. **e** *Elacatinus lori* Colin, 2002, extant, USNM 442111, Bonaire, SL 28 mm. **f** *Elacatinus oceanops* Jordan, 1904, extant, LACM coll. Fitch. **g** *Elacatinus puncticulatus* (Ginsburg, 1938), extant, LACM coll. Fitch. **h** *Elacatinus xanthipora* (Böhlke & Robins, 1968), extant, USNM 415068, Belize, 16°46′N 88°07′W, SL 31 mm. **i**–**j** *Elacatinus* sp.1, Bastimentos FM, Ground Creek Unit, Bocas del Toro, Panama,; **i** PPP 2250, NMB P15786; **j** PPP 2247, NMB P15787. **k** *Elacatinus* sp.2, Shark Hole FM, Valiente Peninsula, Panama, PPP 2218, NMB P15788. **l** *Elacatinus* sp.3, Cubagua FM, Venezuela, PPP 2549, NMB P15789. **m**–**o** *Elacatinus* sp.4, Cubagua FM, Venezuela; **m**, PPP 2557, NMB P15790; **n** PPP 3057, NMB P15791; **o** PPP 3055, NMB P15792

***Elacatinus* sp. 2**

Figure 37k

Material 1 specimen Zanclean, Shark Hole FM, Atlantic Panama, PPP 2218 (NMB P15788).

Discussion The single, small specimen of 0.7 mm length is remarkable for its rather evenly rounded shape, which could be an indication for a juvenile specimen, and the very small kidney-shaped sulcus (OL:SuL = 2.3).

***Elacatinus* sp. 3**

Figure 37l

Material 1 specimen Zanclean, Cubagua FM, Venezuela, PPP 2549 (NMB P15789).

Discussion This small otolith resembles *Elacatinus* sp. 2 but has an even smaller sulcus (OL:SuL = 2.65) which is also somewhat forward positioned. It further differs in the more strongly inclined sulcus (22° vs 10°). It thus resembles the extant *E. puncticulatus* (Fig. 37g) which, however, has a distinctly larger sulcus.

***Elacatinus* sp. 4**

Figure 37m–o

Material 3 specimens Zanclean, Cubagua FM, Venezuela, 1 specimen PPP 2557 (NMB P15790), 1 specimen PPP 3057 (NMB P15791), 1 specimen PPP 3055 (NMB P15792).

Discussion These are relatively distinctive otoliths characterized by a nearly quadrate shape (OL:OH = 1.0–1.05), and only slightly inclined oval sulcus (7–10°) and the dorsal depression and ventral furrow joint to a nearly circular furrow surrounding the sulcus. The area between the circular furrow and the sulcus is bulged. *Elacatinus* sp. 4 is very similar to the extant *E. oceanops* (Fig. 37f) and could possibly represent the same or a closely related species.

Genus *Ginsburgellus* Böhlke & Robins, 1968

***Ginsburgellus novemlineatus* (Fowler, 1950)**

Figure 38a–b

Material 1 specimen late Zanclean, upper Cayo Agua FM, Atlantic Panama, PPP 1188 (NMB P15793).

Discussion The single fossil specimen perfectly matches the available extant specimen although the latter is slightly eroded (Fig. 38a), but is slightly larger. Characteristic features are the rounded orthogonal preventral and postventral angles, the rounded middorsal angle, the otolith proportion (OL:OH = 1.0 in the extant specimen vs 1.03 in the fossil) and the small, oval sulcus which is only slightly inclined (7°).

Genus *Tigrigobius* Fowler, 1931

***Tigrigobius* sp. 1**

Figure 38e

Material 1 specimen Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1132 (NMB P15794).

Discussion Only two extant specimens have been available from the many species in the genus: *T. macrodon* (Fig. 38d) and *T. saucrus* (Robins, 1960) kindly made available as photograph by Chien-Hsiang Lin. Both are characterized by a high-bodied shape (OL:OH < 1.0), a rounded ventral rim and a very small, oval sulcus. An otolith of *Risor ruber* (Fig. 38c) is figured for further comparison. The single fossil otolith from the Tortonian shows the same small, oval sulcus and a reasonable comparison of the otolith shape to interpret it as an early representative of *Tigrigobius*. It is, however, too poorly preserved for any further identification.

***Tigrigobius* sp. 2**

Figure 38f–h

Material 4 specimens Calabrian, Cumaná FM, Venezuela, PPP 3038 (figured specimens NMB P15795-97).

Discussion These otoliths show a high oval shape with a small kidney-shaped sulcus that reminds of *Tigrigobius*. However, their notable variability hinders a further identification.

***Priolepis* lineage sensu Agorreta et al., 2013**

Otoliths of the *Priolepis* lineage are characterized by a mostly shallow kidney-shaped sulcus, not the usual gobiid sole-shape outline, and a ventral furrow close to the sulcus and joined to a similarly furrow-like dorsal depression, with the area between the circumsulcal furrow and the sulcus being somewhat elevated. Fossil otoliths have rarely been observed (Schwarzhans et al., 2020a, 2020b).

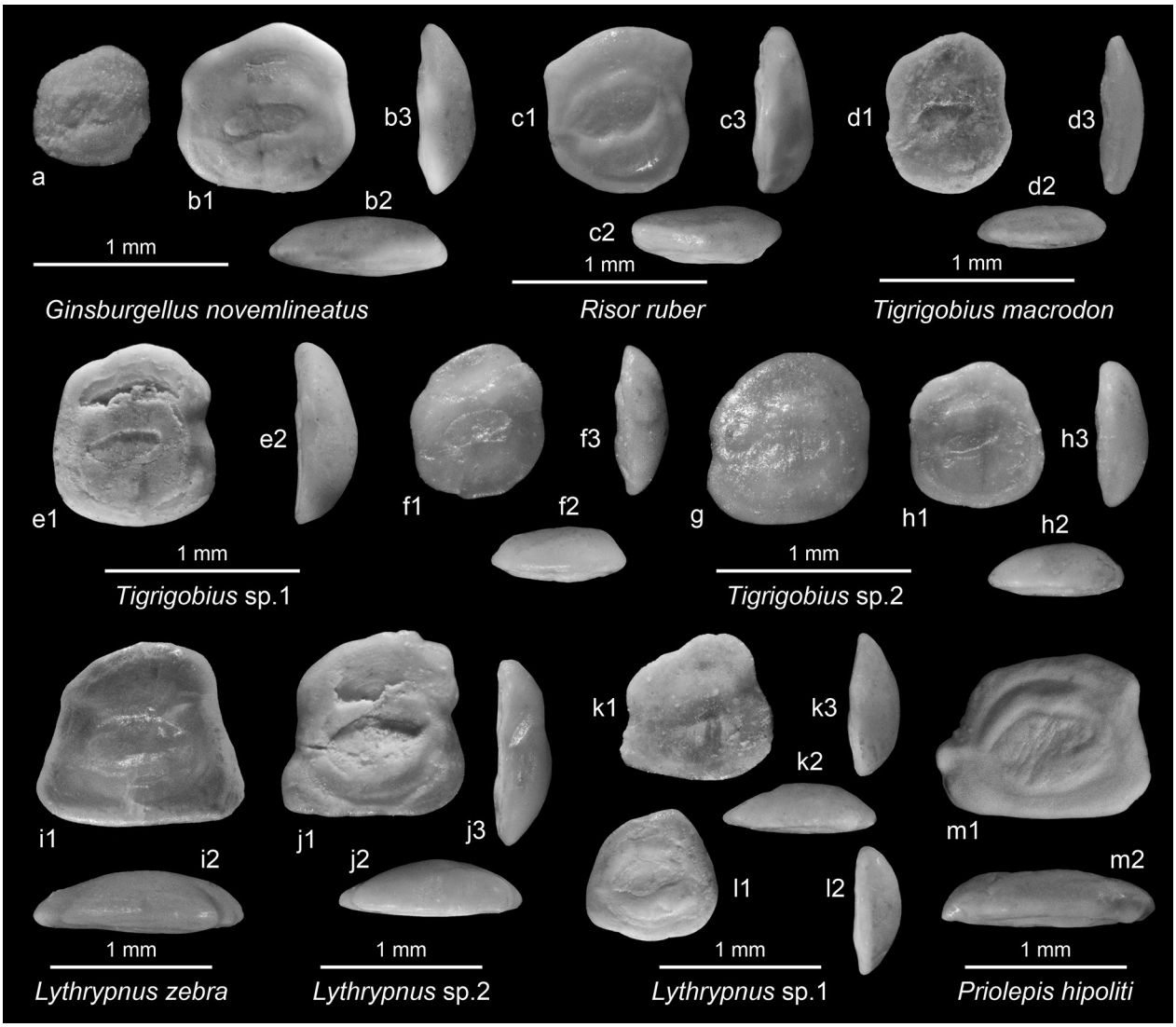


Fig. 38 **a**–**b** *Ginsburgellus novemlineatus* (Fowler, 1950); **a** extant, USNM 413975, Curacao; **b** Cayo Agua FM, Bocas del Toro, Panama, PPP 1188, NMB P15793. **c** *Risor ruber* (Rosén, 1911), extant, LACM 45694–1, Venezuela, 10°57′N 63°49′W, rocky pool 2 m, SL 21 mm. **d** *Tigrigobius macrodon* (Beebe & Tee Van, 1928), extant, LACM coll. Fitch. **e** *Tigrigobius* sp.1, Tuira FM, Darien, Panama, PPP 1132, NMB P15794. **f**–**h** *Tigrigobius* sp.2, Cumaná FM, Venezuela, PPP 3038, NMB P15795-97. **i** *Lythrypnus zebra* (Gilbert, 1890), extant, coll. Schwarzhans leg. Fitch, of California. **j** *Lythrypnus* sp.2, Swan Cay FM, Atlantic Panama, PPP 2221, NMB P15798. **k**–**l** *Lythrypnus* sp.1; **k** Cubagua FM, Venezuela, PPP 2549, NMB P15799; **l** Swan Cay FM, Atlantic Panama, PPP 2221, NMB P15800. **m** *Priolepis hipoliti* (Metzelaar, 1922), extant, USNM 413835, Curacao, SL 27 mm

Most extant taxa occur in the Indo-West Pacific, but the genus *Lythrypnus* Jordan & Evermann, 1896, is endemic to the Americas, and the genus *Priolepis* Valenciennes, 1837, is also represented by one species in the West Atlantic, *P. hipoliti* (Metzelaar, 1922) (Fig. 38m). Otoliths are only known from a single species of the 20 recognized extant *Lythrypnus* species (Fricke et al., 2023), *Lythrypnus zebra* (Gilbert, 1890) (Fig. 38i). *Lythrypnus* species inhabit rocky bottoms and reefs and hence are rare in the fossil record of tropical America. Because of the poor knowledge of extant species, the fossil ones can only be generically assigned.

Genus *Lythrypnus* Jordan & Evermann, 1896

***Lythrypnus* sp. 1**

Figure 38k–l

Material 2 specimens: 1 specimen Zanclean, Cubagua FM, Venezuela, PPP 2549 (NMB P15799). 1 specimen Calabrian, Swan Cay FM, Atlantic Panama, PPP 2221 (NMB P15800).

Discussion Two slightly eroded small otoliths (0.95 and 0.8 mm long) could possibly represent specimens pertaining to *Lythrypnus*. Particularly the specimen from Swan Cay (Fig. 38l) bears the typical characters of the *Priolepis* lineage.

Lythrypnus sp. 2

Figure 38j

Material 1 specimen Calabrian, Swan Cay FM, Atlantic Panama, PPP 2221 (NMB P15798).

Discussion This otolith is very similar to the East Pacific *Lythrypnus zebra* (Fig. 38i). It is also interesting that it was found in a closely reef-associated setting, i.e., in a fossil reef cave sediment.

Lophogobius lineage sensu Agorreta et al., 2013

Otoliths of the *Lophogobius* lineage are relatively inconspicuous and show a typical goby otolith pattern with a sole-shaped sulcus, a usually pronounced predorsal angle, and a protruding postdorsal projection. A subcaudal iugum is sometimes present but often indistinct. Three genera are represented in America: *Coryphopterus* Gill, 1863, *Lophogobius* Gill, 1862, and *Rhinogobiops* Hubbs, 1926. The coverage of otoliths from extant species is good and allows a reliable identification of fossil otoliths in most cases. Otoliths are known from 10 of the 14 extant *Coryphopterus* species: *Coryphopterus dicrus* Böhlke & Robins, 1960 (Fig. 39a), *C. curasub* Baldwin & Robertson, 2015 (Fig. 39b), *C. glaucofraenum* Gill, 1863 (Fig. 39c–d), *C. thrix* Böhlke & Robins, 1960 (Fig. 39e), *C. urospilus* Ginsburg, 1938 (the only East Pacific species in the genus) (Fig. 39f), *C. venezuelae* Cervigón, 1966 (Fig. 39g–h), *C. eidolon* Böhlke & Robins, 1960 (Fig. 39i), *C. tortugae* (Jordan, 1904) (Fig. 39j), *C. lipernes* Böhlke & Robins, 1962 (Fig. 40a), and *C. personatus* (Jordan & Thompson, 1905) (Fig. 40c–d). *Lophogobius* contains two species, *L. cristulatus* Ginsburg, 1939, in the East Pacific and *L. cyprinoides* (Pallas, 1770) (Fig. 40i–n) in the West Atlantic. *Rhinogobiops* is monospecific with *R. nicholsi* (Bean, 1882) (Fig. 40o–p) in the East Pacific. *Rhinogobiops nicholsii* is a large-growing species (up to 150 mm TL according to Froese & Pauly, 2023), and the two otoliths figured from a large adult specimen (OL = 2.75 mm; Fig. 40o) and a small juvenile specimen (OL = 1.15 mm; Fig. 40p) show a significant degree of allometric growth. The still relatively large size of the otolith from the juvenile specimen exemplifies the problem that can arise when identifying small goby otoliths in the range of about 1 mm in length.

Genus *Coryphopterus* Gill, 1863

Coryphopterus contains two rather distinct otolith morphotypes, one where the otolith proportions (OL:OH) are equal or larger than 1.0 which contains most of the species, and one containing *C. lipernes* and *C. personatus* which are characterized by high-bodied otoliths with a ratio OL:OH < 1.0 and broadly concave anterior and posterior rims. In a phylogenetic assessment of the Atlantic species of the genus *Coryphopterus* by Baldwin et al. (2009) *C. lipernes* and *C. personatus* are shown in a discrete clade together with *C. hyalinus* of which otoliths are not known. Baldwin et al. (2009) also showed *C. dicrus, C. glaucofraenum, C. tortugae* and *C. venezuelae* in one clade and *C. thrix* and *C. eidolon* somewhat separated from both. *Coryphopterus alloides* and *C. kuna* were regarded as the most basal taxa in the phylogeny of *Coryphopterus.* Unfortunately, otoliths of these two species are unknown. *Coryphopterus* species occur mostly in shallow water over sand and reef rubble, and some species are reef associated.

Coryphopterus cuevae n. sp.

Figure 39m

Holotype NMB P15803 (Fig. 39m), Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1137.

(See figure on next page.)

Fig. 39 **a** *Coryphopterus dicrus* Böhlke & Robins, 1960, extant, USNM 413296, 11°09′N 60°50′W, 5-9 m. **b** *Coryphopterus curasub* Baldwin & Robertson, 2015, extant, USNM 442134, Bonaire SL 31 mm. **c**–**d** *Coryphopterus glaucofraenum* Gill, 1863, extant, USNM 388062, 17°21′N 63°15′W, 15-18 m. **e** *Coryphopterus thrix* Böhlke & Robins, 1960, extant, USNM 413803, Curacao. **f** *Coryphopterus urospilus* Ginsburg, 1938, extant, coll. Schwarzhans leg. Fitch, Baja California. **g**–**h** *Coryphopterus venezuelae* Cervigón, 1966, extant; **g** USNM 413044, S Caicos; **h** USNM 413804, Curacao. **i** *Coryphopterus eidolon* Böhlke & Robins, 1960, USNM 397696, 17°30′N 63°13′W. **j**–**l** *Coryphopterus tortugae* (Jordan, 1904); **j** extant, USNM 411902, 21°29′N 71°31′W; **k**–**l** Cumaná FM, Venezuela, PPP 3038, NMB P15801-02. **m** *Coryphopterus cuevae* n. sp., holotype, NMB P15803, Tuira FM, Darien, Panama, PPP 1137. **n**–**q** *Coryphopterus rodriguezi* n. sp., Tuira FM, Darien, Panama; **n** holotype, NMB P15804, PPP 1612; **o**–**q** paratypes; **o**–**p** PPP 1612, NMB P15805-06; **q** PPP 1137, NMB P15807. **r**–**t** *Coryphopterus xenosus* n. sp.; **r** holotype, NMB P15808, Cubagua FM, Venezuela, PPP 2556; **s**–**t** paratypes; **s** Cubagua FM, Venezuela, PPP 2556, NMB P15809; **t** Manzanilla FM, Trinidad, PPP 2673, NMB P15810

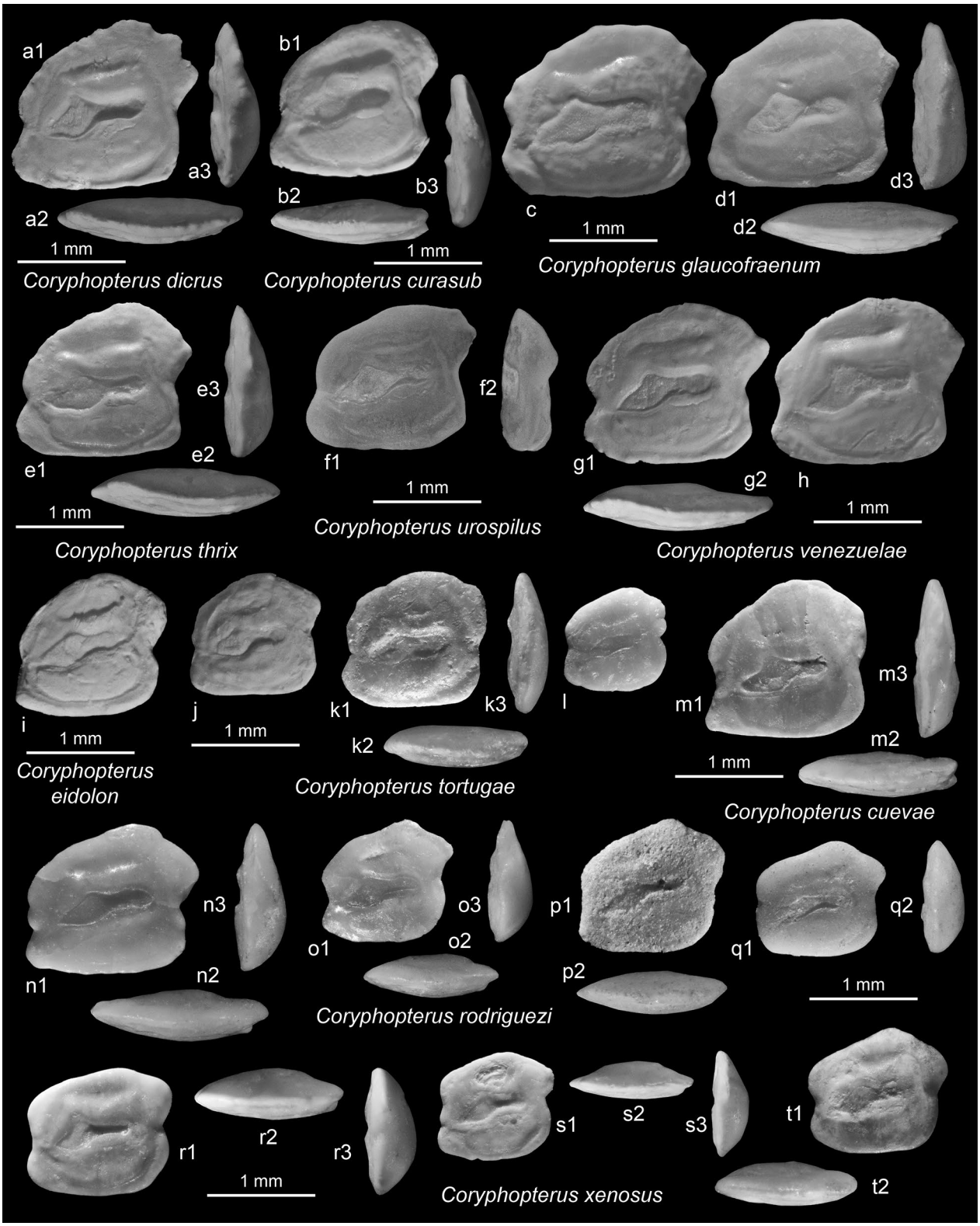


Fig. 39 (See legend on previous page.)

Etymology Named after the Cueva, indigenous Indians living in Panama.

Diagnosis Otolith size 1.5 mm in length. OL:OH = 1.0. Otolith with and regularly curved dorsal rim. Preventral projection pointed; postdorsal projection rounded, slightly protruding. Sulcus relatively short and narrow, with strong ostial lobe and narrow cauda; OL:SuL = 1.8; sulcus inclination angle 13°. No subcaudal iugum. Ventral furrow regularly curved.

Description Otolith size 1.5 mm in length (unique holotype). OH:OT = 3.6. Otolith with high and regularly curved dorsal rim; predorsal angle rounded, relatively low; postdorsal projection broadly rounded, slightly protruding. Anterior rim slightly inclined towards dorsal, with prominent and pointed preventral projection and broad concavity at level of ostial tip. Posterior rim slightly inclined towards ventral, with broad, shallow concavity at level of tip of cauda and rounded orthogonal postventral angle. Ventral rim straight, horizontal. All rims smooth, except dorsal rim slightly undulating.

Inner face moderately convex in both directions. Sulcus relatively short, narrow, slightly deepened, its ostial and caudal tips tapering; ostial lobe strong, as much expanded as sulcus height; sulcus inclination angle 13°; OL:SuL = 1.8. No subcaudal iugum. Dorsal depression indistinct, several weak but long radial furrows ingressing dorsal field from dorsal rim of otolith; ventral furrow regularly curved, closest to ventral rim of otolith at central part. Outer face slightly convex, smooth.

Discussion *Coryphopterus cuevae* is easily recognized by its high and regularly curved dorsal rim resulting in a relatively low ratio OL:OH of about 1.0 and the strong ostial lobe. With the latter it resembles such otoliths as from the extant *C. dicrus* (Fig. 39a), *C. glaucofraenum* (Fig. 39c–d) or *C. venezuelae* (Fig. 39g–h) but is further distinguished by the less strongly protruding postdorsal projection.

***Coryphopterus rodriguezi* n. sp.**

Figure 39n–q

Holotype NMB P15804 (Fig. 39n), Messinian, Chucunaque FM, Pacific Panama, Darien, PPP 1612.

Paratypes 3 specimens: 2 specimens Messinian: same data as holotype (NMB P15805-06). 1 specimen Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1137 (NMB P15807).

Referred specimens 3 specimens: 2 specimens Messinian same data as holotype, PPP 1612. 1 specimen Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1137.

Etymology Named in honor of Felix Rodriguez (Panama City, Republic of Panama) for his support during field trips and laboratory work.

Diagnosis Otolith size up to 1.6 mm in length. OL:OH = 1.1–1.15. Otolith rectangular to parallelogram-shaped. Preventral projection blunt, short; postdorsal projection relatively sharp, moderately protruding. Sulcus relatively short and narrow, with low ostial lobe and narrow cauda; OL:SuL = 1.7–1.8; sulcus inclination angle 10–17°. No subcaudal iugum. Ventral furrow relatively indistinct, regularly curved.

Description Otolith size up to 1.6 mm in length (holotype). OH:OT = 2.8–3.0. Otolith rectangular to parallelogram-shaped; dorsal rim anteriorly depressed and its predorsal part straight, downward inclined; postdorsal angle obtuse, angular; predorsal angle rounded, relatively low; postdorsal projection relatively sharp, somewhat protruding. Anterior rim slightly inclined towards dorsal, with short, blunt preventral projection, straight or with weak concavity at level of ostial tip. Posterior rim slightly inclined towards ventral, with broad, relatively distinct concavity at level of tip of cauda. Ventral rim straight, horizontal, with rounded orthogonal postventral angle. All rims smooth or slightly undulating.

Inner face moderately convex in vertical direction and distinctly bent in horizontal direction. Sulcus relatively short, narrow, slightly deepened, its ostial and caudal tips tapering; ostial lobe low; sulcus inclination angle 10–17°; OL:SuL = 1.7–1.8. No subcaudal iugum. Dorsal depression relatively distinct, narrow, with broad crista inferior towards sulcus; ventral furrow relatively indistinct, close and parallel to ventral rim of otolith. Outer face slightly convex, smooth.

Discussion Because of the low ostial lobe, otoliths of *C. rodriguezi* resemble those of the extant species *C, eidolon* (Fig. 39i) or *C. thrix* (Fig. 39e) but differ in the relatively low dorsal rim and the blunt preventral projection. Also the angular postdorsal angle and the relatively straight inclined predorsal rim distinguish *C. rodriguezi* from the two extant species. From *C. eidolon* it further differs in the more slender shape (OL:OH = 1.1–1.15 vs 1.05).

***Coryphopterus tortugae* (Jordan, 1904)**

Figure 39j–l

Material 8 specimens Calabrian, Cumaná FM, Venezuela, PPP 3038 (figured specimens NMB P15801-02).

Discussion The specimens retrieved from the Calabrian of the Cumaná FM (Fig. 39k–l) match well its extant counterpart (Fig. 39j) in otolith proportions and the low sulcus inclination angle (11–12°). Smaller specimens differ in a relatively small and less structured sulcus (Fig. 39l). Today, *C. tortugae* does not seem to occur so far south in the Caribbean at the coast of Venezuela.

***Coryphopterus xenosus* n. sp.**

Figure 39r–t

Holotype NMB P15808 (Fig. 39r), Zanclean, Cubagua FM, Venezuela, PPP 2556.

Paratypes 2 specimens: 1 specimen same data as holotype (NMB P15809); 1 specimen Messinian, Manzanilla FM, Montserrat Member, Trinidad, PPP 2673 (NMB P15810).

Referred specimens 1 specimen Zanclean, Cubagua FM, Venezuela, PPP 25565.

Etymology From xenos (Greek) = foreign, referring to the unusual pattern of the otolith.

Diagnosis Otolith size up to 1.35 mm in length. OL:OH = 1.15. Otolith skewed rectangular with relatively high predorsal angle and slightly protruding postdorsal projection. Preventral projection blunt, short. Sulcus short and narrow, with moderately developed low ostial lobe and narrow cauda; OL:SuL = 1.9; sulcus inclination angle 12–14°. No subcaudal iugum. Ventral furrow distinct, regularly curved.

Description Otolith size up to 1.35 mm in length (holotype). OH:OT = 2.5–2.8. Otolith skewed rectangular; dorsal with straight, downward inclined predorsal part, shallow postdorsal angle and high, distinct, rounded predorsal angle; postdorsal projection rounded, slightly protruding beyond broadly rounded postventral angle. Anterior rim nearly vertical, with weak concavity at level of ostial tip. Posterior rim slightly inclined towards ventral, with weak concavity at level of tip of cauda. Ventral rim straight, horizontal, with rounded slightly protruding preventral projection. All rims smooth.

Inner face slightly convex. Sulcus relatively short, narrow, distinctly deepened, its ostial and caudal tips tapering; ostial lobe moderately developed; sulcus inclination angle 12–14°; OL:SuL = 1.9. No subcaudal iugum but sometimes weak indications (Fig. 39s, t) similar to certain extant otoliths of the genus. Dorsal depression relatively distinct, narrow, short, with broad crista inferior towards sulcus; ventral furrow distinct, close and to ventral rim of otolith. Outer face distinctly convex, much stronger than inner face, smooth.

Discussion Coryphopterus xenosus differs from the otoliths of the known extant species in the more rectangular otolith shape and the relatively thick habitus of the otolith. Also untypical is the high positioned predorsal angle. It is possible that this species rather represents an extinct genus but we would consider such allocation premature at the moment considering the limited knowledge of fossil *Coryphopterus* today.

***Coryphopterus lipernes* Böhlke & Robins, 1962**

Figure 40a–b

Material 1 specimen Zanclean, Springvale FM, Trinidad, KR-1216 (NMB P15811).

Discussion Coryphopterus lipernes and *C. personatus* belong to the high-bodied otolith morphotype found in the genus, which is further characterized by high positioned predorsal angle and thus is easily distinguished from the known otoliths of the other extant *Coryphopterus* species. The otoliths of *C. lipernes* are slightly less high-bodied than those of *C. personatus* (OL:OH = 0.9–0.95 vs 0.85–0.9) and show a narrower sulcus. The only available extant specimen of *C. lipernes* (Fig. 40a) is somewhat eroded by formalin but nevertheless allows a reliable correlation with the fossil specimen (Fig. 40b).

***Coryphopterus* sp.**

Figure 40e–f

Material 8 specimens Gelasian, Bastimentos FM, Ground Creek Unit, Atlantic Panama, PPP 3202 (figured specimens NMB P15812-13).

Discussion These rather eroded specimens are characterized by a relatively high-bodied otolith shape (OL:OH = 1.05), a relatively flat inner face and strongly

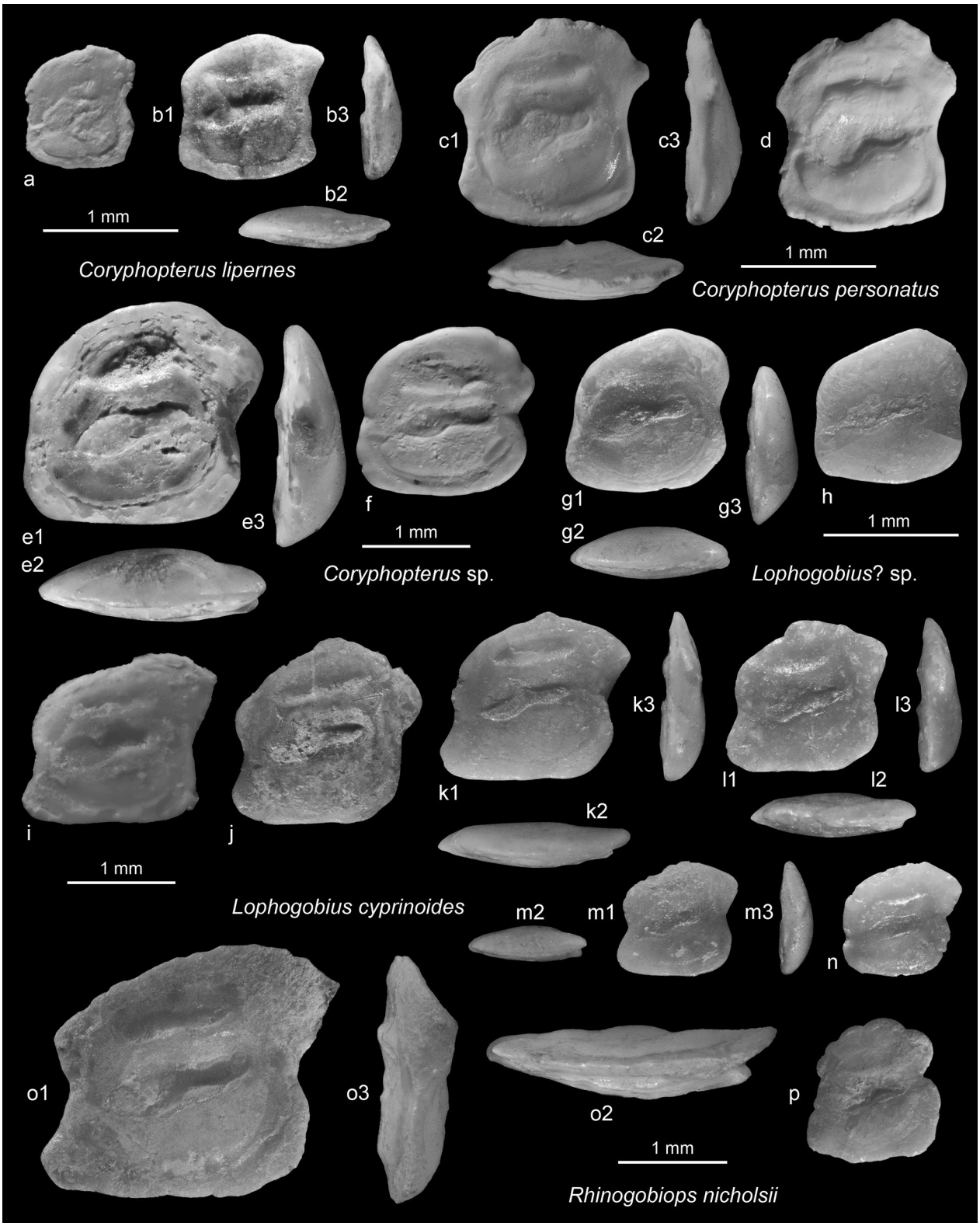


Fig. 40 **a**–**b** *Coryphopterus lipernes* Böhlke & Robins, 1962; **a** extant, USNM 438844, Dominica SL 16,5 mm; **b** Springvale FM, Trinidad, KR-1216, NMB P15811. **c**–**d** *Coryphopterus personatus* (Jordan & Thompson, 1905), extant, USNM 330053, Bermuda. **e**–**f** *Coryphopterus* sp., Bastimentos FM, Bocas del Toro, Panama, PPP 3202, NMB P15812-13. **g**–**h** *Lophogobius*? sp., Baitoa FM, Dominican Republic, NMB 17290, NMB P15849 (ex P400, two specimens). **i**–**n** *Lophogobius cyprinoides* (Pallas, 1770); **i** extant, USNM 414424, 12°08′N 68°58′W, mangrove; **j**–**l**, **n** Cumaná FM, Venezuela, PPP 3038, NMB P15814-17; **m** Cubagua FM, Venezuela, PPP 2549, NMB P15818. **o**–**p** *Rhinogobiops nicholsi* (Bean, 1882); extant, California, LACM coll. Fitch

convex outer face and a broadly rounded predorsal angle. They resemble otoliths of *C. eidolon* (Fig. 39i) but could also represent a species of which otoliths are not yet known.

Genus *Lophogobius* Gill, 1862

***Lophogobius cyprinoides* (Pallas, 1770)**

Figure 40i–n

Material 11 specimens: 3 specimens Zanclean, Cubagua FM, Venezuela, 1 specimen PPP 2549 (NMB P15818), 2 specimens PPP 2556. 8 specimens Calabrian, Cumaná FM, Venzuela, PPP 3038 (figured specimens NMB P15814-17).

Discussion Otoliths of *Lophogobius cyptinoides* show pronounced preventral and postdorsal projections and do not differ significantly from certain species in the genus *Coryphopterus* such as *C. thrix* (Fig. 39e) or *C. urospilus* (Fig. 39f). *Lophogobius* otoliths tend to have a smaller sulcus and lower ostial lobe than species of *Coryphopterus* with the exception of *C. curasub* (Fig. 39b). The fossil specimens (Fig. 40j–n) appear to have a higher postdorsal rim than the figured extant specimen (Fig. 40i). However, the only available extant specimen has a slightly damaged dorsal rim because of formalin erosional effects and therefore this could be a misleading impression.

***Lophogobius* ? sp.**

Figure 40g–h

Material 2 specimens, late Burdigalian, Baitoa FM, Dominican Republic, NMB 17290 (NMB P15849).
Discussion The two small and eroded specimens likely represent a species of either the genus *Lophogobius* to which it is tentatively associated, or another genus of the *Lophogobius* lineage.

***Glossogobius* lineage sensu Agorreta et al., 2013**

Genus *Bathygobius* Bleeker, 1878

Agorreta et al. (2013) placed *Bathygobius* in a distinct clade within their *Glossogobius* lineage. The otoliths of *Bathygobius*, however, are quite distinct from those of *Glossogobius*, for example characterized by the lack or weak development of a postdorsal projection; the protruding postventral angle; a large, wide, and deep sulcus with a broad concavity at the ventral sulcus margin at the ostial–caudal joint; a widened, rounded tip of the cauda; and the lack of a subcaudal iugum. This is a unique combination of features that makes the recognition of *Bathygobius* otoliths relatively easy.
Bathygobius is a widely distributed goby genus throughout the tropics and subtropics inhabiting sheltered and exposed shallow rocky and sandy shorelines, reefs, mangroves, seagrass beds, and brackish/estuarine environments (Rodriguez-Rey et al., 2018). All these environments are unfavorable for the fossilization of otoliths, and it is therefore not surprising that so far no confirmed fossil otolith records of the genus exist. According to Rodriguez-Rey et al. (2018), *Bathygobius* currently contains 29 recognized species, seven in the West Atlantic, three in the East Atlantic (one thereof, *B. soporator*, shared with the West Atlantic), and four in the East Pacific. For comparison, we figure here otoliths of the following extant species: *Bathygobius andrei* (Sauvage, 1880) (Fig. 41a–b) and *B. ramosus* Ginsburg, 1947 (Fig. 41i), from the East Pacific; *B. antilliensis* Tornabene, Baldwin & Pezold, 2010 (Fig. 41d), *B. geminatus* Tornabene, Baldwin & Pezold, 2010 (Fig. 41f), *B. lacertus* (Poey, 1860) (Fig. 41g), *B. mystacium* Ginsburg, 1947 (Fig. 41h), and *B. soporator* (Valenciennes, 1837) (Fig. 41j) from the West Atlantic; and *B. casamancus* (Rochebrune, 1880) (Fig. 41e) from the East Atlantic.

The overall otolith pattern is similar to the characterization above, but certain differences exist in the expression of features or proportions. Some species show a more pronounced albeit rounded postdorsal projection, which, however, never expands further than the postventral projection (*C. andrei*, *C. casamancus*, *C. lacertus*); other species are characterized by a more compressed otolith shape and a high, expanded postdorsal angle (*C. geminatus*, *C. mystacium*).

***Bathygobius andrei* (Sauvage, 1880)**

Figure 41a–c

Material 1 specimen, Calabrian, Armuelles FM, Pacific Panama, PPP 3235 (NMB P15819).

Discussion The single, slightly eroded otolith from the Armuelles FM (Fig. 41c) resembles extant otoliths of *C. andrei* well but show a postdorsal projection that protrudes as much as the postventral projection, i.e., more strongly than observed in the two extant specimens (Fig. 41a–b). We consider these small differences to reflect a degree of variability.

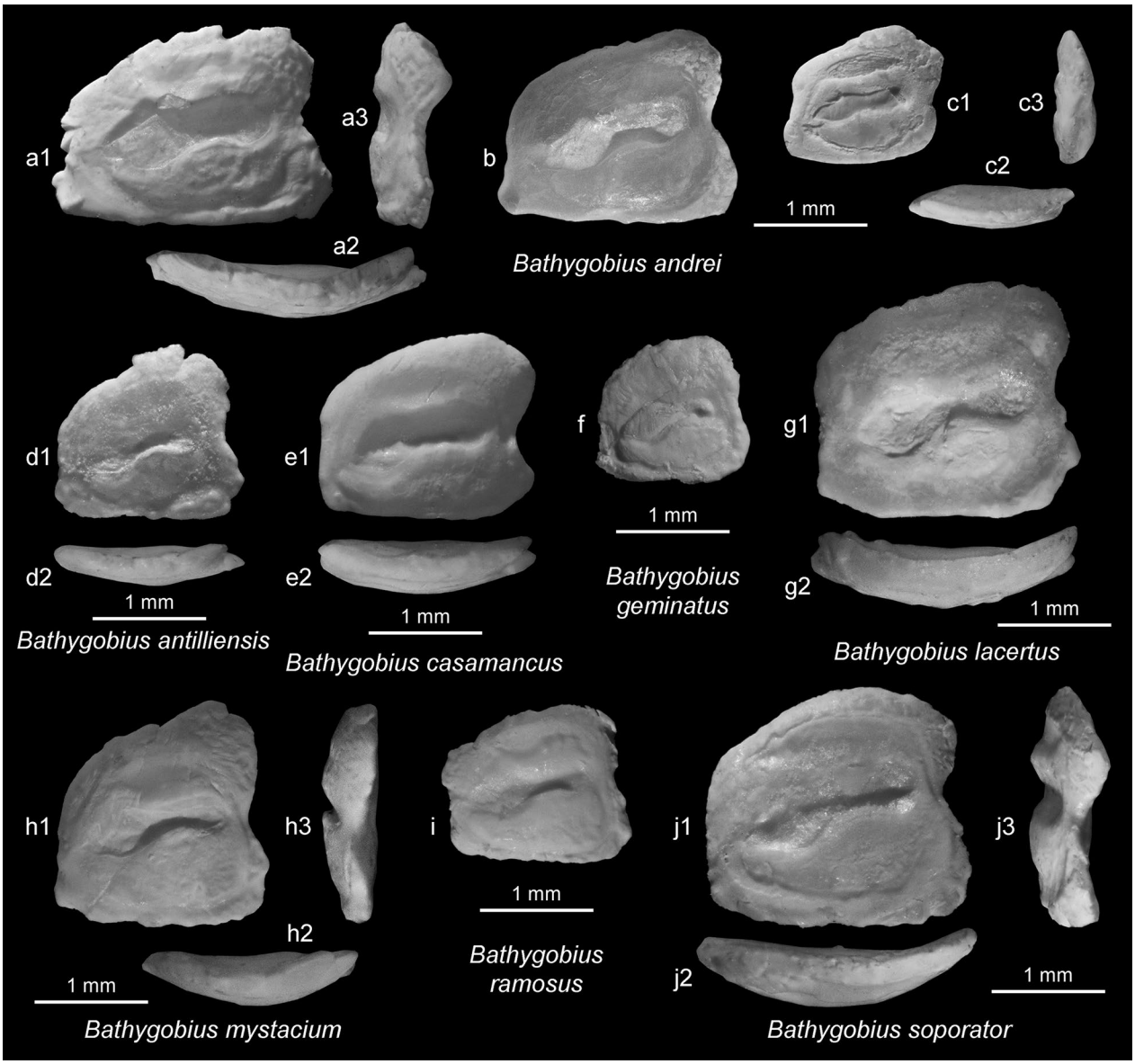


Fig. 41 **a**–**c** *Bathygobius andrei* (Sauvage, 1880); **a**–**b** extant, MNHN 2003–0986, Ecuador; **c** Armuelles FM, Burica, Pacific Panama, PPP 3235, NMB P15819. **d** *Bathygobius antilliensis* Tornabene, Baldwin & Pezold, 2010, extant, USNM 406086, Curacao, 12°10′N 68°51′W, SL 46 mm. **e** *Bathygobius casamancus* (Rochebrune, 1880), extant, BMNH 1977.3.21.159–163, Ghana, Matrukui Point. **f** *Bathygobius geminatus* Tornabene, Baldwin & Pezold, 2010, extant, USNM 398110, Florida, 24°12′N 80°11′W, SL 36 mm. **g** *Bathygobius lacertus* (Poey, 1860), extant, USNM 406155, Curacao, SL 72 mm. **h** *Bathygobius mystacium* Ginsburg, 1947, extant, USNM 442055, Bonaire, 12°06′N 68°17′W, SL 50 mm. **i** *Bathygobius ramosus* Ginsburg, 1947, extant, USNM 407796, El Salvador, SL 39 mm. **j** *Bathygobius soporator* (Valenciennes, 1837), extant, USNM 416447, Bahamas, SL 63 mm

Subfamily Oxudercinae Günther, 1861

***Stenogobius* lineage sensu Agorreta et al.,** 2013

***Gobioides/Gobionellus* clade sensu Pezold,** 2004

It is difficult to identify otolith features or patterns that would define the otoliths of the genera in the *Gobioides*/*Gobionellus* clade. Their otoliths tend to be high-bodied, with an OL:OH usually < 1.0, but exceptions exist (e.g., *Ctenogobius sagittula*). The otoliths are usually quite thin, with a convex inner and concave to flat outer face. The sulcus shows the typical gobioid sole-shaped outline in some genera, such as *Ctenogobius*, but is more reduced in most others. A subcaudal iugum is mostly not developed, but exceptions exist with a rather wide and long subcaudal iugum (e.g., *Ctenogobius sagittula* and *Gobionellus microdon*). Otoliths of adult specimens

of some species of *Gobionellus* and *Gnatholepis* show an unusual development of the ventral furrow, which does not curve upward anteriorly and posteriorly but instead opens to the anterior-ventral and posterior-ventral rims of the otolith.

Ctenogobius Gill, 1858

The genus *Ctenogobius* was redefined by Pezold (2004) and reviewed by Pezold (2022), where 15 species were recognized, two of which in the East Pacific, 12 in the West Atlantic, and one in the East Atlantic. We figure otoliths of the following extant species: *Ctenogobius boleosma* (Jordan & Gilbert, 1882) (Fig. 42a–c), *C. fasciatus* Gill, 1858 (Fig, 42f–g), *C. shufeldti* (Jordan & Eigenmann, 1887) (Fig. 42i–j), *C. smaragdus* (Valenciennes, 1837) (Fig. 42k–m), and *C. stigmaticus* (Poey, 1860) (Fig. 42p) from the West Atlantic; and *C. manglicola* (Jordan & Starks, 1895) (Fig. 42h) and *C. sagittula* (Günther, 1862) (Fig. 43a–c) from the East Pacific. For further comparison, otoliths are figured from the extant *Evorthodus lyricus* (Girard, 1858) (Fig. 42v–x), *E. minutus* Meek & Hildebrand, 1928 (Fig. 42y), *Gobioides peruanus* (Steindachner, 1880) (Fig. 43f), and *G. broussonnetii* Lacepède, 1800 (Fig. 43g). For the genera *Gobionellus* and *Gnatholepis*, see below.

Otoliths of the genus *Ctenogobius* show considerable variation, but are mostly compressed, usually higher than long (OL:OH ≤ 1.0), with a sole-shaped sulcus. The details of the otolith outline, particularly the dorsal rim, vary from one species to another, but the otoliths usually show a moderate or regressed postdorsal projection. The otoliths of one species, however, differ considerably from those known of other species. *Ctenogobius sagittula* has more elongate otoliths (OL:OH = 1.05–1.15), a massively developed postdorsal projection that expands toward dorsally and posteriorly with a flat to slightly concave middorsal section and the presence of a distinct subcaudal iugum. The species also keys out first in the identification key published by Pezold (2022), who confirmed in a personal message (2023) that *C. sagittula* is the most divergent species in the genus. Otoliths of *Evorthodus* have a reduced sulcus morphology. Those of *Gobioides* also show a somewhat simplified sulcus morphology, a nearly horizontal sulcus, and a distinct circumsulcal furrow composed of the ventral furrow and the furrow-like dorsal depression.

Species of *Ctenogobius* inhabit shallow sand and mud bottoms in bays and estuaries, often in tidal or mangrove environments. Many species are euryhaline and enter brackish water; some inhabit fresh and brackish water (Pezold, 2004, 2022). Most species of *Ctenogobius* are facultative air-breathing (Froese & Pauly, 2023).

Ctenogobius aff. *boleosoma* (Jordan & Gilbert, 1882)

Figure 42d–e

Material 2 specimens Gelasian, Moin FM, Atlantic Costa Rica, PPP 1772 (NMB P15820-21).

Discussion Two otoliths found in the Moin FM of Costa Rica resemble extant otoliths of *C. boleosoma* (Fig. 42a–c) but differ slightly in showing a deepened sulcus (vs shallow). They also do not show the widened pre- and postdorsal margins of the otolith, which appears to be typical for some *Ctenogobius* species. Therefore, and because of the inconspicuous overall appearance the fossil otoliths are only tentatively assigned to *C. boleosoma*.

Ctenogobius smaragdus (Valenciennes, 1837)

Figure 42k–o

Material 13 specimens Gelasian, Moin FM, Atlantic Costa Rica, PPP 3256 (figured specimens NMB P15822-23).

Discussion The fossil otoliths (Fig. 42n–o) placed here in *C. smaragdus* are smaller than the extant ones (Fig. 42k–m) studied. However, they show a very similar otolith shape, the ventral furrow closely approaching the anterior and posterior rims and a deepened sulcus with a well-developed ostial lobe and a rounded caudal tip, which we consider to be typical for the species.

(See figure on next page.)

Fig. 42 **a**–**c** *Ctenogobius boleosoma* (Jordan & Gilbert, 1882), extant, TCWC 18306.13, Texas, Brazoria, SL 25, 27 and 29 mm. **d**–**e** *Ctenogobius* aff. *boleosoma* (Jordan & Gilbert, 1882), Moin FM, Limón, Costa Rica, PPP 1772, NMB P15820-21. **f**–**g** *Ctenogobius fasciatus* Gill, 1858, extant; **f** CAS 18574, 09°07′N 77°57′W, Panama, San Blas, Mosquito Bay; **g** TCWC 20534.10 Trinidad and Tobago, SL 24 mm. **h** *Ctenogobius manglicola* (Jordan & Starks, 1895), extant, USNM 407631, 13°16′N 87°44′W. **i**–**j** *Ctenogobius shufeldti* (Jordan & Eigenmann, 1887), extant, BMNH 1985.6.30.37–39, Baia de Sepetiba, Brazil. **k**–**o** *Ctenogobius smaragdus* (Valenciennes, 1837); **k**–**m** extant, USNM 371772, 23°02′N 80°03′W, mangrove swamp; **n**–**o** Moin FM, Limón, Costa Rica, PPP 3256, NMB P15822-23. **p** *Ctenogobius stigmaticus* (Poey, 1860), extant, USNM 357714, Rio de Janeiro, SL 50 mm. **q**–**t** *Ctenogobius* sp.1, Springvale FM, Trinidad, KR-1216, NMB P15824-27. **u** *Ctenogobius* sp.2, Moin FM, Limón, Costa Rica, PPP 1772, NMB P15828. **v**–**x** *Evorthodus lyricus* (Girard, 1858), extant, BMNH 1980.9.22.48-51, Florida, Sebastian Inlet. **y** *Evorthodus minutus* Meek & Hildebrand, 1928, extant, USNM 408804, 13°13′N 87°31′W

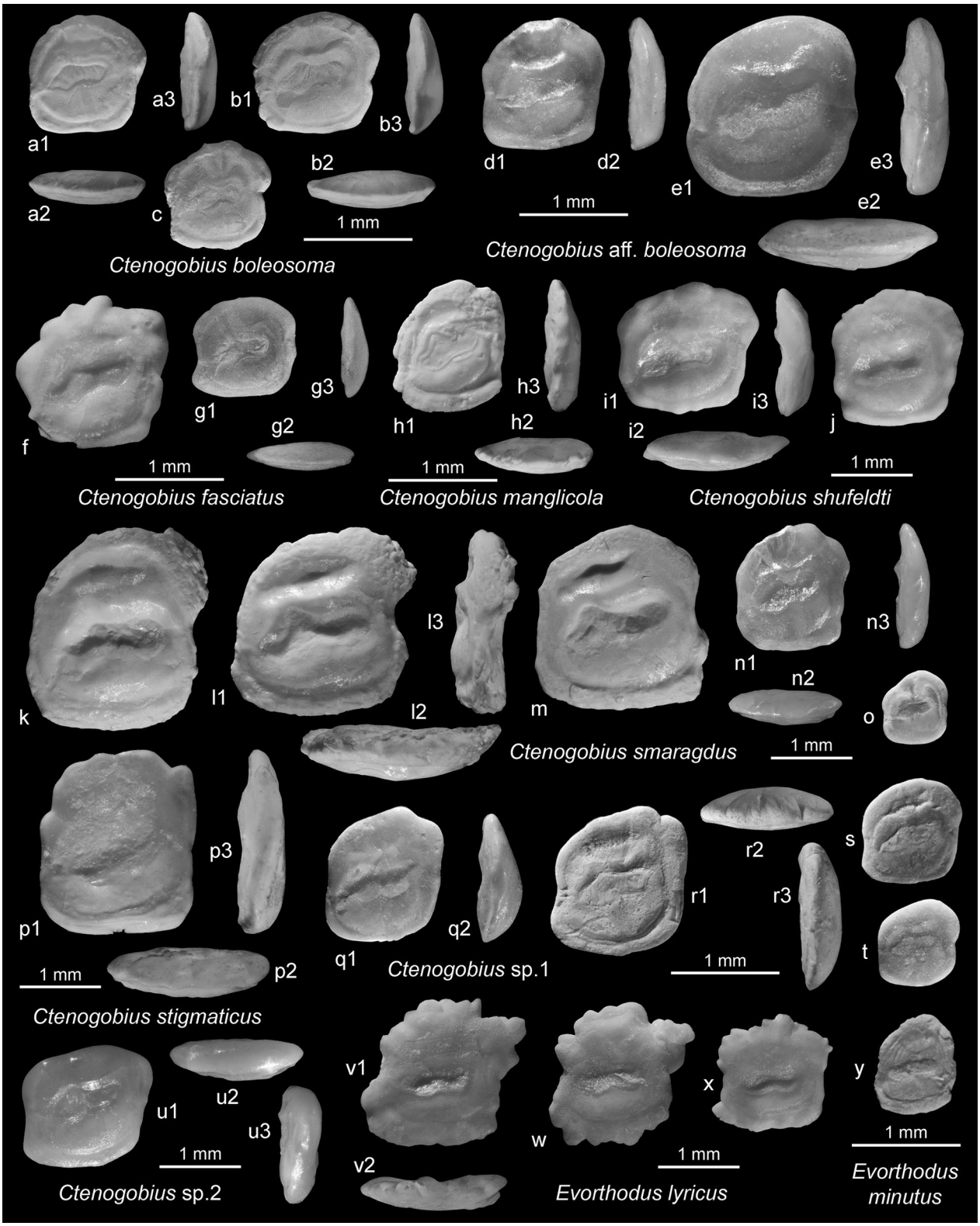


Fig. 42 (See legend on previous page.)

***Ctenogobius* sp. 1**

Figure 42q–t

Material 38 specimens Zanclean: 34 specimens Springvale FM, Trinidad, KR-1216 (figured specimens NMB P15824-27); 4 specimens Cayo Agua FM, Atlantic Panama, PPP 1276.

Discussion These are otoliths characterized by a high-bodied shape (OL:OH = 0.83–0.9) and the straight, slightly inclined posterior rim, and a distinct ventral furrow curving around the cauda to near the narrow dorsal depression. These otoliths resemble the extant *C. stigmaticus* (Fig. 42p) except for the development of the ventral furrow. We have refrained from a species description because of the relatively small size of the otoliths, the presence of only a few well-preserved specimens in the otherwise large assemblage, and the limited knowledge of otoliths of extant *Ctenogobius* species.

***Ctenogobius* sp. 2**

Figure 42u

Material 1 specimen Gelasian, Moin FM, Atlantic Costa Rica, PPP 1772 (NMB P15828).

Discussion The single, somewhat eroded otolith is remarkable for its depressed, shallow dorsal rim. Otherwise it shows the expanded pre- and postdorsal projections which are typical for several extant species of the genus like *C. boleosoma* (Fig. 42a–c), *C. fasciatus* (Fig. 42f–g) and *C. shufeldti* (Fig. 42i–j).

***Ctenogobius darienensis* n. sp.**

Figure 43d–e

Holotype NMB P15829 (Fig. 43d), Tortonian, Yaviza FM, Pacific Panama, Darien, PPP 1607.

Paratypes 2 specimens Tortonian, Tuira FM, Pacific Panama, Darien, 1 specimen PPP 1554 (NMB P15830), 1 specimen PPP 1171 (NMB P15831).

Etymology Named after the province Darien of Panama where the otoliths of this species have been found.

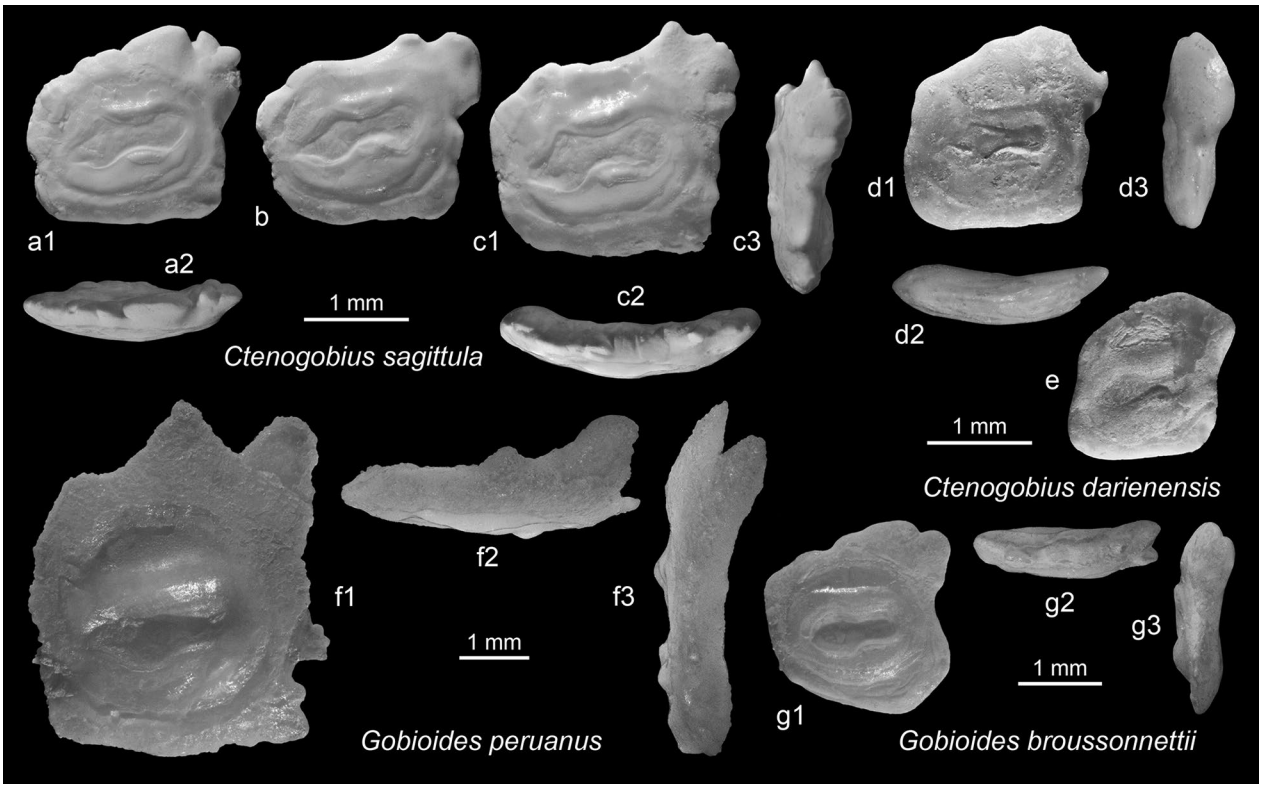


Fig. 43 **a**–**c** *Ctenogobius sagittula* (Günther, 1862), extant, USNM 367341, 13°22′N 87°52′W. **d**–**e** *Ctenogobius darienensis* n. sp.; **d** holotype, NMB P15829, Yaviza FM, Darien, Panama, PPP 1607; **e** paratype, Tuira FM, Darien, Panama, PPP 1554, NMB P15830. **f** *Gobioides peruanus* (Steindachner, 1880), extant, LACM coll. Fitch, Costa Rica, Pacific. **g** *Gobioides broussonnetii* Lacepède, 1800, extant, SMF 15399, off Guyana

Diagnosis Otolith size up to 1.95 mm in length. OL:OH = 0.95. Otolith ventrally box-shaped and dorsally with strongly expanded postdorsal region. Preventral and postventral angles orthogonal; postdorsal projection broad, protruding. Sulcus relatively short, with moderate ostial lobe, narrowed at ostial-caudal joint and rounded caudal tip; OL:SuL = 1.9–2.0; sulcus inclination angle 6–10°. Small subcaudal iugum located within ventral collum-like ingression. Ventral furrow distinct, regularly curved and relatively distant from ventral rim of otolith.

Description Otolith size up to 1.95 mm in length (holotype). OH:OT = 3.7. Otolith high-bodied with rectangular, box-shaped ventral part and high expanded postdorsal part; dorsal rim with relatively high, rounded predorsal angle, ascending to massive postdorsal region; postdorsal projection broad, high, distinctly protruding. Anterior rim slightly inclined towards dorsal, straight. Posterior rim slightly inclined towards ventral, with weak concavity below postdorsal projection. Ventral rim perfectly straight and horizontal, with orthogonal pre- and postventral angles. All rims smooth or slightly undulating.

Inner face distinctly bent in horizontal direction. Sulcus relatively short, relatively shallow, sole-shaped with moderate ostial lobe, its ostial tip tapering; sulcus margins at ostial-caudal joint broadly but not strongly ingressing, thereby narrowing sulcus; cauda slightly widened and with rounded tip; sulcus inclination angle 6–10°; OL:SuL = 1.9–2.0. Small subcaudal iugum in ventral ingression of sulcus margin at collum (ventral ingression of sulcus margin). Dorsal depression relatively indistinct; ventral furrow distinct, relatively distant from ventral rim of otolith, anteriorly approaching anterior rim of otolith, posteriorly curving behind cauda. Outer face slightly concave, smooth.

Discussion *Ctenogobius darienensis* closely resembles otoliths of the extant *C. sagittula* (Fig. 43a–c) in the specific development of the postdorsal region, the very specific shape of the sulcus and even the expression of the ventral furrow. The main differences are the more compressed shape (OL:OH = 0.95 vs 1.05–1.15), the straight predorsal rim (vs middorsal concavity), the non-protruding rounded predorsal angle and the smaller subcaudal iugum. *Ctenogobius darienensis* looks like one might envisage the special features of *C. sagittula* have developed from more plesiomorphic otolith morphologies.

Genus *Gobionellus* Girard, 1858

The genus *Gobionellus* contains seven recognized species according to Froese and Pauly (2023): three in the East Pacific, three West Atlantic, and one in the East Atlantic. Otoliths are known from *Gobionellus liolepis* (Meek & Hildebrand, 1928) (Fig. 44a–b), *G. dague* (Eigenmann, 1918) (Fig. 44e), and *G. microdon* (Gilbert, 1892) (Fig. 44g) from the East Pacific; *G. oceanicus* (Pallas, 1770) (Fig. 44d) from the West Atlantic; and *G. occidentalis* (Boulenger, 1909) from the East Atlantic. Otoliths are not known from the two remaining West Atlantic species, i.e., *G. munizi* Vergara, 1978, endemic to Cuba, and *G. stomatus* Starks, 1913, endemic to Brazil.

The otoliths of *Gobionellus* are characterized by a high-bodied shape (OL:OH = 0.8–1.0) with a much-expanded postdorsal region, a commonly strongly sculptured dorsal rim, a relatively short and somewhat simplified sole-shaped sulcus (OL:SuL = 1.8–2.2) with a low inclination angle (3–10°), and the ventral furrow running relatively distant from the ventral rim of the otolith and commonly opening to the anterior-ventral and posterior-ventral rims of the otolith. The otoliths are usually thin with a concave to flat outer face. A subcaudal iugum is usually not present, except in *G. microdon*, where it is large and well developed.

Specimens of *Gobionellus* are collected in shallow estuarine, tide pool, and mangrove environments (Pezold, 2004).

Gobionellus sp.

Figure 44f

(See figure on next page.)

Fig. 44 **a**–**b** *Gobionellus liolepis* (Meek & Hildebrand, 1928), extant; **a** USNM 367354, 13°09′N 87°59′W, 16-18 m; **b** LACM 44426–1, Costa Rica, Punta Morales, SL 118 mm. **c** *Gobionellus occidentalis* (Boulenger, 1909), extant, BMNH 1989.1.6.31–33, Nigeria, Port Harcourt. **d** *Gobionellus oceanicus* (Pallas, 1770), extant, USNM 265066, 13°14′N 59°33′W. **e** *Gobionellus dague* (Eigenmann, 1918), extant, USNM 257680, 01°36′N 77°02′W. **f** *Gobionellus* sp., Cubagua FM, Venezuela, PPP 3093, NMB P15832. **g** *Gobionellus microdon* (Gilbert, 1892), extant, USNM 318278, 08°06′N 80°31′W, SL 91 mm. **h**–**j** *Gnatholepis thompsoni* Jordan, 1904, extant; **h** BMNH 1979.1.5.168–174, Ascension Island; **i**–**j** USNM 414225, 21°29′N 71°30′W. **k**–**q** *Gnatholepis gunae* n. sp.; **k** holotype, NMB P15833, Gatun FM, Colon, Panama, PPP 2168; **l**–**q** paratypes; **l**–**o** Gatun FM, Colon, Panama, PPP 2168, NMB P15834-37; **p**–**q** Tuira FM, Darien, Panama, PPP 1137, NMB P15838-39

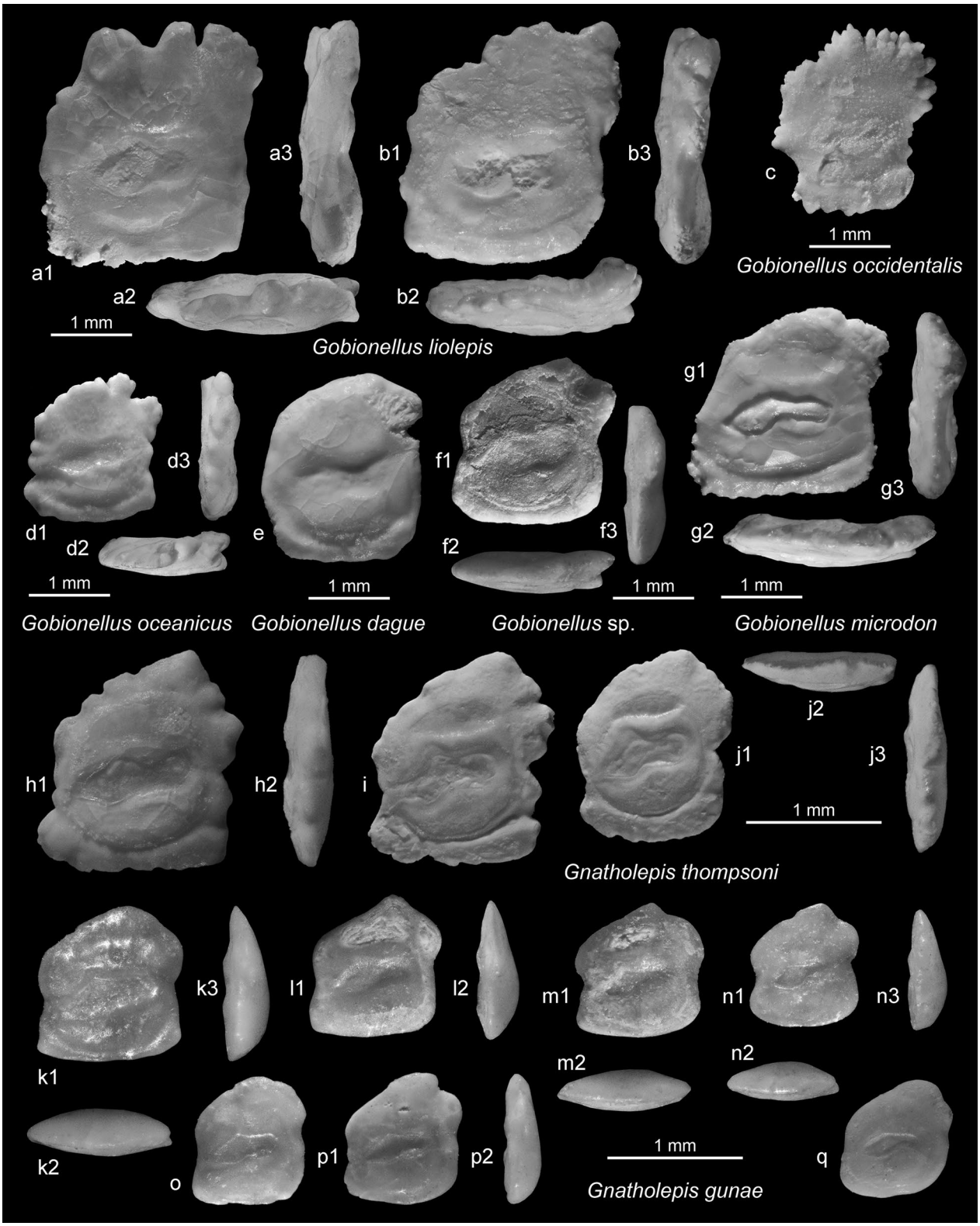


Fig. 44 (See legend on previous page.)

Material 5 specimens Zanclean, Cubagua FM, Venezuela, 4 specimens, Cerro Negro Member, PPP 3093 (figured specimen NMB P15832), 1 specimen, level above Cubagua FM, Venezuela, PPP 2653.

Discussion Rather eroded specimens the best of which is figured (Fig. 44f). It bears the main features found in the genus in respect to otolith shape and proportions and also the specific shape of the ventral furrow but differs from the known extant species in the large sulcus (OL:OH = 1.7). It probably represents a fossil species close to *G. oceanicus* (Fig. 44d) but more and better preserved specimens are required for a reliable definition.

Genus *Gnatholepis* Bleeker, 1874

Gnatholepis is a genus predominantly distributed in the Indo-West Pacific. Only one of 10 recognized extant species (Froese & Pauly, 2023) lives in the West Atlantic and a few areas of the East Atlantic: *Gnatholepis thompsoni* Jordan, 1904. Otoliths are figured of *G. thompsoni* from the West Atlantic (Fig. 44i–j) and from Ascension Island in the central Atlantic (Fig. 44h). The otoliths of *G. thompsoni* do not show any significant morphological difference in the two regions. The otoliths of *G. thompsoni* are characterized by a high-bodied shape (OL:OH = 0.8–0.88) underpinned by a strongly elevated postdorsal region and the unusual development of the ventral furrow that opens anteriorly and posteriorly to the ventral parts of the anterior and posterior rims. This latter feature appears to be fully developed only in specimens from a certain size onward (about 1.2 mm in length; compare Fig. 44i, j).

***Gnatholepis gunae* n. sp.**

Figure 44k–k

Holotype NMB P15833 (Fig. 44k), Tortonian, Gatun FM, Atlantic Panama, PPP 2168.

Paratypes 6 specimens Tortonian: 4 specimens same data as holotype (NMB P15834-37); 2 specimens Tuira FM, Pacific Panama, Darien, PPP 1137 (NMB P15838-39).

Referred specimens 12 specimens Tortonian: 2 specimens Tuira FM, Pacific Panama, Darien, PPP 1137; 1 specimen Yaviza FM, Pacific Panama, Darien, PPP 1553; 9 specimens same data as holotype.

Etymology Named after the Guna, the indigenous Indians inhabiting the region of the type location.

Diagnosis Otolith size up to 1.05 mm in length. OL:OH = 0.85–0.92. Otolith high-bodied, with expanded, angular middorsal angle. Preventral angle pointed, postventral angle orthogonal; postdorsal projection rounded, slightly protruding. Sulcus large, with moderate ostial lobe; OL:SuL = 1.65–1.8; sulcus inclination angle 9–14°. No subcaudal iugum. Ventral furrow distinct, regularly curved in specimens below 1 mm in length; anteriorly and posteriorly open in larger specimens.

Description Otolith size up to 1.05 mm in length (holotype). OH:OT = 3.3. Otolith high-bodied; dorsal rim high, with angular, relatively high predorsal angle, per- and postdorsal rims ascending to elevated to relatively sharp middorsal angle in straight lines; postdorsal projection broad, high, slightly protruding. Anterior rim slightly inclined towards dorsal, with weak concavity at level of ostium. Posterior rim inclined towards ventral, with weak concavity below postdorsal projection. Ventral rim straight to slightly bent and horizontal, with sharp preventral and orthogonal postventral angles. All rims smooth.

Inner face only bent in horizontal direction. Sulcus wide, relatively large, slightly deepened, sole-shaped with moderate ostial lobe, its ostial tip tapering; sulcus margins at ostial-caudal joint broadly but not strongly ingressing, thereby narrowing sulcus; cauda with rounded tip; sulcus inclination angle 9–14°; OL:SuL = 1.65–1.8. No subcaudal iugum. Dorsal depression wide, with indistinct margins; ventral furrow distinct, relatively close to ventral rim of otolith, anteriorly and posteriorly opening to ventral portions of anterior and posterior rims in large specimens (Fig. 44k), curving upward behind cauda in smaller specimens (Fig. 44l–q). Outer face slightly convex, smooth.

Discussion Otoliths of *G. gunae* are smaller than those of the extant *G. thompsoni*, but the development of the ventral furrow touching the anterior and posterior rims in morphologically mature specimens indicates that specimens larger than 1 mm in length are mature, and hence *G. gunae* is indeed a relatively small species. *Gnatholepis gunae* resembles the extant *G. thompsoni* in many aspects but differs in the smaller size, the lower OL:OH ratio (0.85–0.92 vs 0.8–0.88), and the smooth otolith rims. The occurrence of *G. gunae* in the Tortonian of tropical America confirms the long presence of this genus in the region.

Acanthogobius lineage sensu Agorreta et al., 2013

Gillichthys clade

A number of oxudercine genera are distributed along the Pacific coast of Central and Northern America that seem to form a distinct clade within the *Acanthogobius* lineage of the gobioid phylogeny as depicted in Agorreta et al. (2013). The American genera are here informally combined in a clade named for the genus *Gillichthys*. This *Gillichthys* clade contains the genera *Clevelandia* Eigenmann & Eigenmann, 1888, *Eucyclogobius* Gill, 1862, *Evermannia* Jordan, 1895, *Gillichthys* Cooper, 1864, *Ilypnus* Jordan & Evermann, 1896, *Lepidogobus* Gill, 1859, *Lethops* Hubbs, 1926, *Quietula* Jordan & Evermann, 1895, and *Typhlogobius* Steindachner, 1879. Many of these genera are monospecific; others contain only few species. Otoliths are shown from all genera except *Lethops*, for which reference is made to Welton (2015; as Gobiidae indet.): *Clevelandia ios* (Jordan & Gilbert, 1882) (Fig. 45a–b), *Eucyclogobius newberryi* (Girard, 1856) (Fig. 45e–h), *Evermannia* sp. [possibly *E. longipinnis* (Steindachner, 1879)] (Fig. 45i), *Evermannia erici* Bussing, 1983 (Fig. 45j), *Evermannia panamensis* Gilbert & Starks, 1904 (Fig. 45k–l), *Evermannia zosterura* (Jordan & Gilbert, 1882) (Fig. 45m), *Gillichthys mirabilis* Cooper, 1864 (Fig. 46a–c), *Gillichthys seta* (Ginsburg, 1938) (Fig. 46d), *Lepidogobius lepidus* (Girard, 1858) (Fig. 46f), *Typhlogobius californiensis* Steindachner, 1879 (Fig. 46g), *Ilypnus gilberti* (Eigenmann & Eigenmann, 1889) (Fig. 46h–i), *Quietula ycauda* (Jenkins & Evermann, 1889) (Fig. 46k), and *Quietula guamasiae* (Jenkins & Evermann, 1889) (Fig. 46m–n).

The otoliths in this group fall into two more or less well-defined morphological groups. One morphotype is characterized by a convex, relatively smooth inner face, a shallow sulcus, which is usually somewhat morphologically reduced in various ways, and a narrow ventral furrow that curves around the sulcus and joins up with a narrow, furrow-like dorsal depression. This highly distinctive morphological group combines the genera *Clevelandia*, *Evermannia*, *Gillichthys*, *Ilypnus*, and *Quietula*. The second morphotype bears less recognizable features. Its otoliths are usually high-bodied, with a flat inner face, a broad ventral furrow connected to a relatively broad dorsal depression, and a morphologically reduced sulcus of variable size. This morphological group contains the genera *Eucyclogobius*, *Lepidogobius*, *Lethops*, and perhaps *Typhlogobius*. None of the taxa in this clade shows a subcaudal iugum.

Most of the fishes in the *Gillichthys* clade inhabit shallow coastal to estuarine environments. *Gillichthys mirabilis* is well known for its facultative air-breathing (Graham & Wegner, 2010; Todd & Ebeling, 1966), and species of *Quietula* may also possess this ability (Todd & Ebeling, 1966). *Typhlogobius* is a blind goby living secretively under rocks, in holes in rocks, and in kelp beds in shallow water (Froese & Pauly, 2023). *Lethops* also has reduced eyes and lives under rocks and in kelp canopies (Froese & Pauly, 2023). Other species of the *Gillichthys* clade inhabit coastal waters, mudflats, and lagoons, and some occur in brackish water and estuaries.

Genus *Clevelandia* Eigenmann & Eigenmann, 1888

Clevelandia? sp.

Figure 45c–d

Material 2 specimens Zanclean, Springvale FM, Trinidad, KR-1216 (NMB P15840-41).

Discussion These two specimens from the Early Pliocene of Trinidad resemble otoliths of the extant *Clevelandia ios* (Fig. 45a–b) in the shape of the shallow sulcus, the smooth inner face, and the course of the thin ventral furrow, which tapers anteriorly below the ostium and curves posteriorly upward behind the cauda to connect to the shallow and vague dorsal depression. The otoliths differ from those of *Clevelandia ios* in being more compressed (OL:OH = 0.85–0.9 vs 0.95–1.0) and showing an elevated dorsal rim. It is, however, also possible that these otoliths represent juvenile forms of a species of which otoliths have not yet been found. The allocation to *Clevelandia* is therefore tentative until more specimens have been found. *Clevelandia ios* is the only known species of the genus; it is an euryhaline species inhabiting estuaries, lagoons, and tidal environments on sand and mud bottoms from British Columbia to Baja California (Froese & Pauly, 2023).

Genus *Evermannia* Jordan, 1895

Evermannia chiriquiensis n. sp.

Figure 45n

Holotype NMB P15842 (Fig. 45n), upper Zanclean, upper Cayo Agua FM, Atlantic Panama, PPP 1188.

Etymology Named after the Laguna de Chiriqui located in the back of the Cayo Agua Island, the type locality.

Diagnosis Otolith size 1.65 mm in length. OL:OH = 1.0. Otolith high-bodied, with strongly expanded postdorsal region. Preventral angle orthogonal, postventral angle

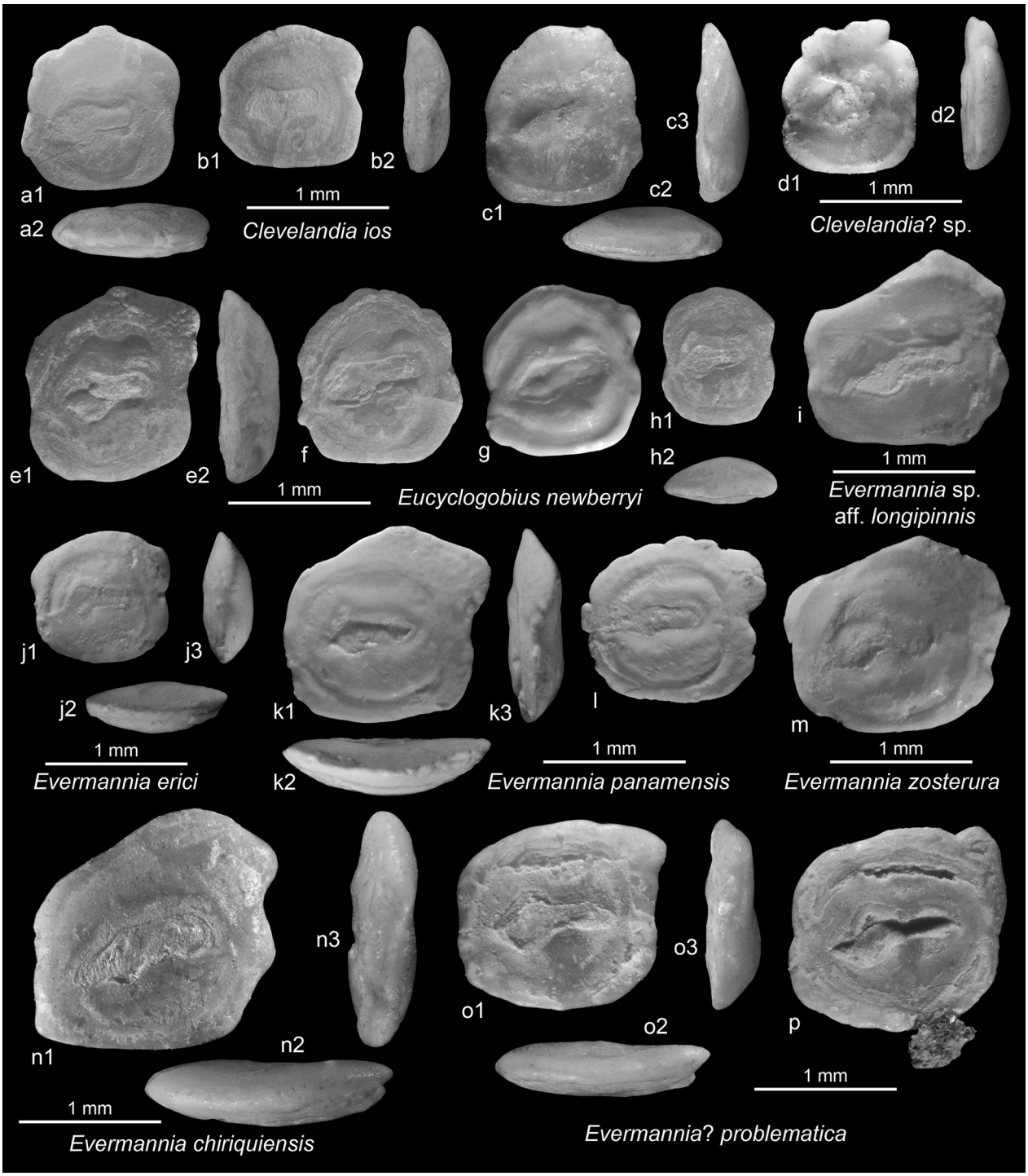


Fig. 45 **a**–**b** *Clevelandia ios* (Jordan & Gilbert, 1882), extant, LACM 57151–1, California, Ballona lagoon, SL 30–36 mm. **c**–**d** *Clevelandia*? sp., Springvale FM, Trinidad, KR-1216, NMB P15840-41. **e**–**h** *Eucyclogobius newberryi* (Girard, 1856), extant; **e**–**f**, **h** LACM coll. Fitch; **g** LACM-58239 Santa Barbara, San Antonio Creek. **i** *Evermannia* sp. / aff. *longipinnis* (Steindachner, 1879), extant, CAS 18421, 31°20′N 113°38′W, 0-3ft. **j** *Evermannia erici* Bussing, 1983, extant, paratype, USNM 254313, Pacific Costa Rica, Tamarindo, SL 22 mm. **k–l** *Evermannia panamensis* Gilbert & Starks, 1904, extant, USNM 367346, 13°13′N 87°31′W, mangroves with pools. **m** *Evermannia zosterura* (Jordan & Gilbert, 1882), extant, BMNH 95.5.27.132-135, Mazatlan. **n** *Evermannia chiriquiensis* n. sp., holotype, NMB P15842, Cayo Agua FM, Bocas del Toro, Panama, PPP 1188. **o**–**p** *Evermannia*? *problematica* n. sp., Cantaure FM, Paraguaná, Venezuela, PPP 2545; **o** holotype, NMB P15843 **p** paratype, NMB P15844

recessed; postdorsal projection angular, not protruding beyond middle part of posterior rim. Sulcus large, shallow, with nivellated ostial lobe and broad indentation of ventral sulcus margin at collum; OL:SuL = 1.65; sulcus inclination angle 20°. No subcaudal iugum. Ventral furrow narrow, curving around sulcus to join narrow, furrow-like dorsal depression.

Description Otolith size 1.65 mm in length (holotype). OH:OT = 3.6. Otolith high-bodied; dorsal rim high, with broad, strongly expanded postdorsal region, slightly depressed rounded predorsal angle, and straight, relatively steeply inclined predorsal rim; postdorsal projection angular, slightly protruding but not beyond tip of posterior rim. Anterior rim nearly vertical, straight. Posterior rim with concavity below postdorsal projection followed towards ventral by distinct bulge. Ventral rim straight, horizontal, with orthogonal preventral angle and deeply recessed postventral angle. All rims smooth.

Inner face convex, particularly bent in horizontal direction, relatively smooth. Sulcus moderately wide, shallow, sole-shaped with low, rounded ostial lobe, its ostial tip tapering; sulcus margins at ostial-caudal joint broadly ingressing ventrally; cauda with rounded tip; sulcus inclination angle 20°; OL:SuL = 1.65. No subcaudal iugum. Dorsal depression very narrow, close to dorsal rim of otolith, relatively indistinct; ventral furrow narrow, relatively close to ventral rim of otolith, turning around sulcus and joining up to dorsal depression. Outer face slightly concave, smooth.

Discussion Evermannia chiriquiensis is based on a single, well-preserved, and large otolith that matches extant otoliths of *Evermannia* in many diagnostic features, i.e., the shape of the sulcus with the low ostial lobe and the ventral indentation, the sulcus being shallow, the shape of the posterior rim, the convex and smooth inner face, and the pattern of the ventral furrow joining up with the narrow, furrow-like dorsal depression. Otoliths are known of three of the four extant species of *Evermannia*, plus a species identified as *Evermannia* sp. that originates from near the type location of *E. longipinnis* and may represent that species (Fig. 45i). The otoliths of the extant species of *Evermannia* show a variety of diagnostic features. Thus, the shape of the dorsal rim of *E. chiriquiensis* resembles the shape in *E.* sp. (Fig. 45i) and *E. zosterura* (Fig. 45m) but is more strongly expanded. The specific shape of the posterior rim most resembles that of *Evermannia* sp. The sulcus shape resembles that of *E. erici* (Fig. 45j) and *E. zosterura*, while that of *Evermannia* sp. shows a rounded ostial lobe, and the sulcus of *E. panamensis* (Fig. 45k–l) is very small. *Evermannia chiriquiensis* differs from the otoliths of all extant species in the strongly inclined sulcus (20° vs ≤ 15°).

***Evermannia? problematica* n. sp.**

Figure 45o–p

Holotype NMB P15843 (Fig. 45o), Burdigalian, Cantaure FM, Venezuela, PPP 2545.

Paratypes 2 specimens same data as holotype (NMB P15844-45).

Referred specimen 1 tentatively assigned specimen, Tortonian, Tuira FM, Pacific Panama, Darien, PPP 1154.

Etymology From problematicus (Latin) = problematical, owing to tentative nature of the generic assignment of the species.

Diagnosis Otolith size up to 1.5 mm in length. OL:OH = 1.05–1.1. Otolith shape nearly quadratic, with flat dorsal rim and pointed, short postdorsal projection. Preventral angle orthogonal, high. Sulcus large, moderately shallow, with rhombic ostium; OL:SuL = 1.7–1.8; sulcus inclination angle 8–12°. No subcaudal iugum. Ventral furrow narrow, curving around sulcus to join narrow dorsal depression.

Description Otolith size up to 1.5 mm in length (holotype 1.45 mm). OH:OT = 3.4. Otolith nearly quadratic in shape with flat dorsal rim; postdorsal projection narrow, pointed, slightly protruding. Anterior and posterior rims nearly vertical, straight, without concavities. Ventral rim slightly bent, horizontal, with rounded preventral and postventral angles. All rims slightly undulating.

Inner face slightly convex. Sulcus relatively large and wide, moderately shallow, ostium diamond-shaped with angular ostial lobe and angular ventral expansion and angular tip; cauda with rounded tip; sulcus inclination angle 8–12°; OL:SuL = 1.7–1.8. No subcaudal iugum. Dorsal depression narrow, close to dorsal rim of otolith, relatively indistinct; ventral furrow narrow, relatively close to ventral rim of otolith, turning around sulcus and joining up to dorsal depression. Outer face flat, smooth.

Discussion Evermannia? *problematica* resembles in outline the smooth otolith shape found in the extant *E. erici* (Fig. 45j) and *E. panamensis* (Fig. 45k–l). The sulcus shape is similar to that of the otolith of *Evermannia* sp. (Fig. 45i) from the northern Gulf of California. However, we are not entirely certain whether this species really

represents the genus *Evermannia* or possibly an extinct lineage in the *Gillichthys* clade.

Genus *Gillichthys* Cooper, 1864

***Gillichthys caribbaeus* n. sp.**

Figure 46e

Holotype NMB P15846 (Fig. 46e), Tortonian, Manzanilla FM, San José Member, Trinidad, PPP 2670.
Etymology Named after the occurrence of this species in the Caribbean while the genus today is strictly East Pacific.

Diagnosis Otolith size 1.65 mm in length. OL:OH = 1.15. Otolith oval, with regularly curved dorsal rim and expanded postdorsal region. Preventral and postventral angles rounded, recessed; postdorsal projection broad, rounded, protruding. Sulcus large, wide, shallow, with low ostial lobe; OL:SuL = 1.8; sulcus inclination angle 15°. No subcaudal iugum. Ventral furrow narrow, distant from ventral rim of otolith, curving around sulcus to join narrow, furrow-like dorsal depression.

Description Otolith size 1.65 mm in length (holotype). OH:OT = 3.5. Otolith with a generally rounded, more or less oval shape. Dorsal rim high, regularly curved, broadly expanded postdorsal region, slightly depressed rounded and slightly protruding predorsal angle; postdorsal projection broad, rounded, protruding. Anterior rim slightly curved, slightly inclined toward ventral, without concavity. Posterior rim with mild concavity below postdorsal projection followed towards ventral by slight bulge. Ventral rim straight, horizontal, with broadly rounded and recessed preventral and postventral angles. All rims relatively sharp in lateral view, slightly undulating.

Inner face convex, particularly bent in horizontal direction, relatively smooth but area outside of central field defined by circular ventral furrow and dorsal depression somewhat undulating. Sulcus large, wide, shallow, sole-shaped with low, rounded ostial lobe, its ostial tip rounded; cauda with rounded tip; sulcus inclination angle 15°; OL:SuL = 1.8. No subcaudal iugum. Dorsal depression narrow, close to sulcus and distant from dorsal rim of otolith, relatively distinct but not deep; ventral furrow narrow, relatively close to sulcus and distant from ventral rim of otolith, turning around sulcus posteriorly and joining up to dorsal depression; curvature anteriorly interrupted by tip of sulcus. Outer face slightly concave, relatively smooth.

Discussion The single, superbly preserved but thin and fragile otolith bears all the typical hallmarks of otoliths of the extant *Gillichthys mirabilis* (Fig. 46a–b), including the general shape of the otolith and the sulcus and the pattern of the ventral furrow and its connection to the dorsal depression, which is distant from the dorsal rim of the otolith. *Gillichthys caribbaeus* differs from *G. mirabilis* in being slightly more compressed (OL:OH = 1.15 vs 1.2–1.25), the relatively large sulcus (OL:SuL = 1.8 vs 2.0–2.2), and the ventral furrow running more distant from the ventral rim of the otolith. Clearly, *G. caribbaeus* represents an extinct species of the lineage that today is strictly East Pacific but was in the Atlantic during the Late Miocene. In fact the otolith suggests that *G. caribbaeus* is more closely related to *G. mirabilis* than the latter is to the second extant species, *G. seta* (Fig. 46d). Most of the fishes in the *Gillichthys* clade inhabit shallow coastal to estuarine environments. *Gillichthys mirabilis* inhabits shallow coastal environments such as mudflats and bays and is well known for its facultative air-breathing (Todd & Ebeling, 1966).

Genus *Ilypnus* Jordan & Evermann, 1896

***Ilypnus arayanensis* n. sp.**

Figure 46j

Holotype NMB P15847 (Fig. 46j), Zanclean, Cubagua FM, Venezuela, PPP 3055.

Etymology Named after the type locality on the Araya Peninsula in Venezuela.

Diagnosis Otolith size 1.15 mm in length. OL:OH = 1.05. Otolith rectangular with rounded angles. Postdorsal

(See figure on next page.)

Fig. 46 **a**–**c** *Gillichthys mirabilis* Cooper, 1864, extant; **a**, **c** LACM coll. Fitch; **b** LACM 57250-3, California, Marina del Rey, SL 108 mm. **d** *Gillichthys seta* (Ginsburg, 1938), extant, LACM coll. Fitch, LTF 701207-2, Gulf of California. **e** *Gillichthys caribbaeus* n. sp., holotype, NMB P15846, Manzanilla FM, Trinidad, PPP 2670. **f** *Lepidogobius lepidus* (Girard, 1858), extant, coll. Schwarzhans leg. Fitch. **g** *Typhlogobius californiensis* Steindachner, 1879, extant, coll. Schwarzhans leg. Fitch. **h**–**i** *Ilypnus gilberti* (Eigenmann & Eigenmann, 1889), extant, LACM coll. Fitch. **j** *Ilypnus arayanensis* n. sp., holotype, NMB P15847, Cubagua FM, Venezuela, PPP 3055. **k** *Quietula ycauda* (Jenkins & Evermann, 1889), extant, LACM coll. Fitch. **m**–**n** *Quietula guamasiae* (Jenkins & Evermann, 1889), extant, LACM 680204-1, coll. Fitch, Cabo Tepopa, Sonora, SL 52 and 70 mm. **o**–**p** *Quietula rueberi* n. sp., Manzanilla FM, Trinidad, Cb.1633; **o** holotype, NMB P15848; **p** paratype, NMB P678

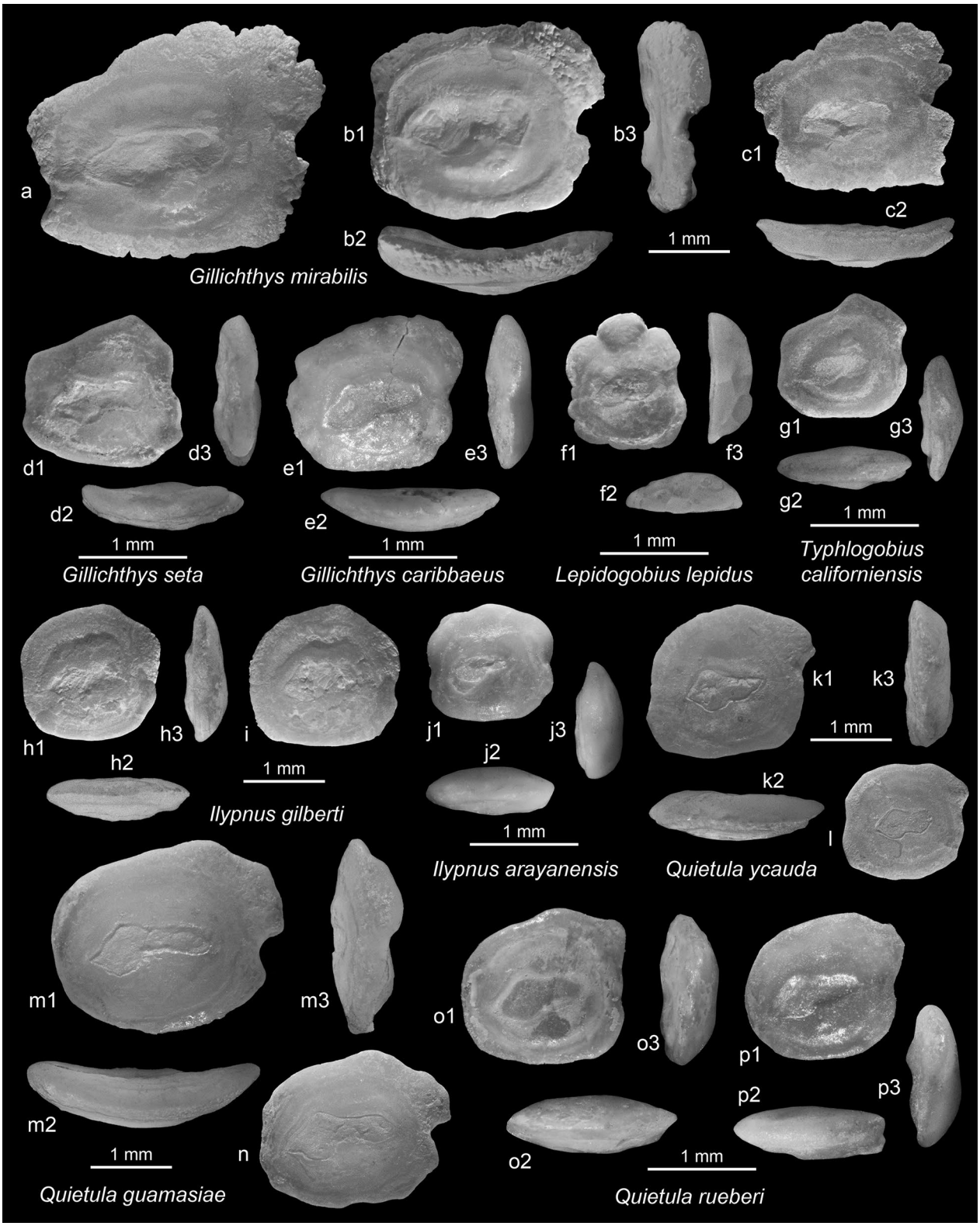


Fig. 46 (See legend on previous page.)

projection broad, rounded, not protruding. Sulcus small, shallow, slightly forward positioned, with rounded, widened ostium and short, narrow cauda; OL:SuL = 2.5; sulcus inclination angle 12°. No subcaudal iugum. Ventral furrow narrow, close to ventral rim of otolith, curving around sulcus to join narrow dorsal depression.

Description Otolith size 1.15 mm in length (holotype). OH:OT = 2.5. Otolith rectangular with regularly rounded predorsal, postdorsal, preventral and postventral angles. Dorsal rim shallow, with weak, broad, rounded middorsal angle. Postdorsal projection broad, rounded, not protruding. Anterior rim straight, vertical, without concavity. Posterior rim with very small concavity at its middle. Ventral rim slightly curved, horizontal, with broadly rounded preventral angle and rounded, recessed postventral angle. All rims thick in lateral view, slightly undulating.

Inner face convex, smooth. Sulcus small, shallow, droplet-shaped with rounded ostium and narrow, short cauda; sulcus inclination angle 12°; OL:SuL = 2.5. No subcaudal iugum. Dorsal depression narrow, shallow, positioned across middle of dorsal field; ventral furrow narrow, relatively close to ventral rim of otolith, turning around sulcus anteriorly and posteriorly and joining up to dorsal depression. Outer face about as convex as inner face, smooth.

Discussion Ilypnus arayanensis resembles the extant *I. gilberti* (Fig. 46h–i) in otolith shape, the small, shallow sulcus, the smooth inner face, and the narrow ventral furrow close to the ventral rim of the otolith and joined to the dorsal depression. It differs primarily from the extant species in the lower dorsal rim and the slightly eccentrically forward-positioned sulcus. Otoliths of the second extant species of the genus, *Ilypnus luculentus* (Ginsburg, 1938) from the Gulf of California, are not known. *Ilypnus gilberti* is found on mudflats and shallow bays, and males are known to guard the eggs (Froese & Pauly, 2023).

Genus *Quietula* Jordan & Evermann, 1895

***Quietula rueberi* n. sp.**

Figure 46o–p

Holotype NMB P15848 (Fig. 46o), Tortonian, Manzanilla FM, San José Member, Trinidad, Cb. 1633.

Paratype 1 specimen same data as holotype (NMB P678).

Etymology Named in honor of Lukas Rüber (Bern, Switzerland) for his contributions to the knowledge of Gobiosomatini fishes.

Diagnosis Otolith size up to 1.5 mm in length. OL:OH = 1.05. Otolith oval in shape with pronounced but short postdorsal projection. Sulcus large, moderately shallow, with rounded ostium; OL:SuL = 1.8–1.9; sulcus inclination angle 15–18°. No subcaudal iugum. Ventral furrow narrow, curving around sulcus to join narrow dorsal depression.

Description Otolith size up to 1.5 mm in length (holotype). OH:OT = 2.7–2.8. Otolith oval in shape; predorsal, preventral and postventral angles all broadly rounded; postdorsal projection pronounced, angular, not or slightly protruding. Anterior rim broadly curved, convex; posterior rim nearly vertical, straight. Ventral rim slightly bent, horizontal. All rims smooth.

Inner face distinctly convex, smooth. Sulcus tadpole-shaped, relatively large and wide, moderately shallow, ostium rounded, with gently curving ostial lobe and rounded tip, ventrally expanded; cauda short, with rounded tip; sulcus inclination angle 15–18°; OL:SuL = 1.8–1.9. No subcaudal iugum. Dorsal depression narrow, close to dorsal rim of otolith, relatively indistinct; ventral furrow narrow, relatively close to ventral rim of otolith, regularly curved, turning around sulcus and joining up to dorsal depression. Outer face convex like inner face, smooth.

Discussion Quietula rueberi is a typical species of the genus *Quietula* and resembles the extant *Q. ycauda* (Fig. 46k–l) in otolith and sulcus shape and proportions but differs in the slightly longer sulcus (OL:SuL = 1.8–1.9 vs 2.2) and in being thicker (OH:OT = 2.7–2.8 vs 3.2), which is caused by the convex outer face (vs flat). The second extant *Quietula* species, *Q. guamasiae* (Fig. 46m–n), has more slender otoliths than *Q. rueberi* (OL:OH = 1.2–1.25 vs 1.05), and the sulcus shows a longer cauda. Extant species of *Quietula* are found on mudflats of lagoons and river mouths along the Pacific coast from California to Mexico (Froese & Pauly, 2023). They are known for their facultative air-breathing (Todd & Ebeling, 1966) and for the males guarding the eggs. *Quietula rueberi* is yet another species and representative of another genus in the *Gillichthys* clade that apparently has occurred in the Caribbean in the geologic past.

Remarks

Weiler (1959) described three species of goby otoliths from the Middle Miocene of the well San Pablo 2 from the province Veracruz, Atlantic Mexico: *Lepidogobius gatunensis* (Schubert, 1909) and two new species, *Gobius atlanticus* Weiler, 1959, and *Gobius*? *gracilis* Weiler, 1959. Unfortunately, the specimens are not available for review,

and their whereabouts are not known. Weiler's descriptions and documentation do not allow an interpretation of these finds and nominal species.

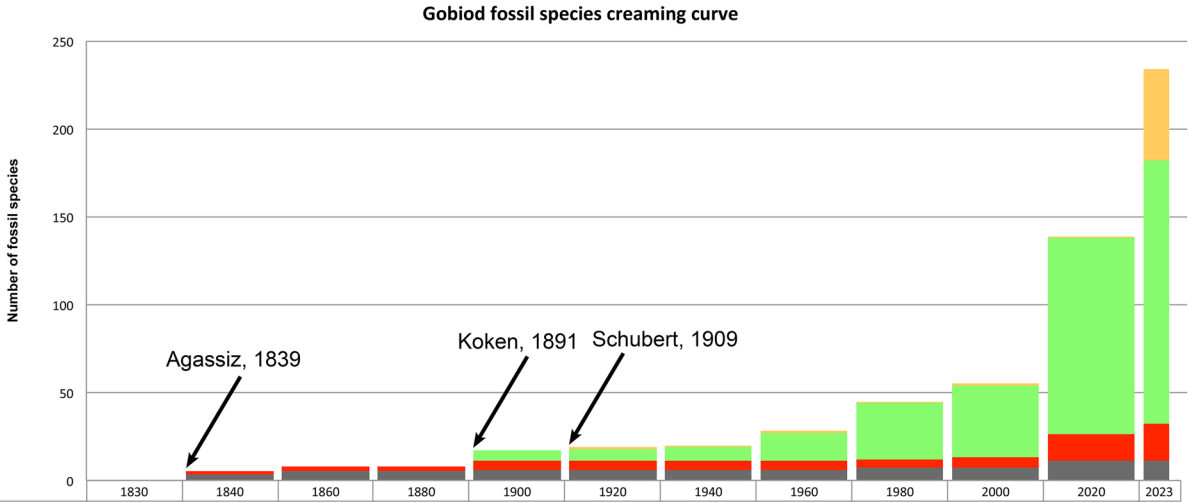
Fossil gobioid knowledge base: a brief historical review

The family Gobiidae (including Oxudercinae) contains more than 2000 extant species and thus represents the largest marine fish family according to FishBase (Froese & Pauly, 2023). The count is actually in a dynamic stage, because multiple changes occur through revisions and descriptions of new species year after year. Other families in the Gobioidei add probably less than 500 species to the count.

In contrast to this impressive diversity, the fossil record of gobies has been trailing behind considerably but has recently gained some momentum in the description of both skeleton-based and otolith-based taxa, and, pleasingly, the number of otoliths found in situ is also continually rising. The following is a brief review of the historical record of fossil gobioids, in terms of both cumulative additions over time and a breakdown of the current status in respect to the geological time frame.

The first fossil gobioid skeletons were described by Agassiz (1839) (Fig. 47), even though most of those finds were not recognized as gobioid fishes at the time. Many of the fossil skeleton-based gobies were originally thought to represent cottoids or percoids of some sort before they were later recognized as gobioids (e.g., Reichenbacher et al., 2013; Gierl & Reichenbacher, 2018). The first to describe fossil gobiid otoliths was Koken (1891) (Fig. 47), the founder of fossil otolith research. The first fossil goby otolith from tropical America, from what is now *Bollmannia gatunensis*, was described by Schubert (1909) (Fig. 47). Schubert described otoliths that were collected during the ill-fated first attempt to construct a Panama Canal to connect the Atlantic and Pacific oceans. Interestingly, it was never difficult to recognize fossil goby otoliths, unlike the skeletal data, which were often initially not recognized as gobioids.

The record of fossil gobioids nevertheless remained low for many decades both for skeletal and otolith records (Fig. 47). Possible reasons for that low level of recognition of fossil goby species were a combination of inadequate knowledge of extant comparative material and difficulties in defining valuable diagnostic features. This taxonomic uncertainty has led to fossil goby remains having been recorded in open nomenclature. As late as 2013, Nolf suggested abstaining from descriptions of new fossil otolith-based gobiid species, at least in the genus *Gobius*, until extant gobiid otoliths are known better, which was



	1830	1840	1860	1880	1900	1920	1940	1960	1980	2000	2020	2023
Neogene tropical American goby otoliths						1	1	1	1	1	1	52
otolith based species					6	7	8	16	32	41	112	150
articulated skeletons with otoliths in situ		2	3	3	5	5	5	5	5	6	15	21
articulated skeletons		3	5	5	6	6	6	6	7	7	11	11

Fig. 47 Fossil gobioid creaming curve showing cumulative description of fossil taxa from articulated skeletons (black), articulated skeletons with otoliths in situ (red), otolith-based species (green) and otolith-based species from America. The records reflect fossil gobioid species currently accepted as valid. Otolith-based species are compiled from Nolf (1985, 2013) and own evaluation for articles after 2012; skeletal records compiled from Gierl and Reichenbacher (2015, 2017), Bannikov and Carnevale (2016), Schwarzhans et al., (2017a, 2017b), Reichenbacher et al., (2017, 2020, 2023), Bradić-Milinović et al. (2019), and Reichenbacher and Bannikov (2021, 2022). Extant species also recorded as fossils and species in open nomenclature are not included. The first description of a fossil gobioid skeleton (Agassiz, 1939), the first fossil gobioid otolith (Koken, 1891), and the first fossil gobioid otolith from America (Schubert, 1908) are annotated

a sensible assessment of the situation at the time. The situation has changed since then with the application of modern anatomical knowledge and analytical methods for characterizing otoliths found in situ from fossil articulated gobioid skeletons (e.g., Reichenbacher et al., 2007, 2013; Schwarzhans et al., 2017a, 2017b; Gierl & Reichenbacher, 2018; Bradic-Milinovic et al., 2019; Reichenbacher & Bannikov, 2021, 2022). Likewise, comprehensive studies of extant gobioid otoliths were undertaken to facilitate the identification of fossil otolith-based species (Gut et al., 2020; Lombarte et al., 2018; Reichenbacher et al., 2023; Schwarzhans, 2014; Schwarzhans et al., 2020a, 2020b; Zarei et al., 2023; and this study). As a result, the number of fossil gobioid species has significantly increased since 2014 both for skeletal-based data and otoliths. The number of fossil gobioid species now stands at a minimum of 42 skeleton-based and 202 otolith-based species, 51 of which are described here from the Neogene of tropical America, highlighting the importance of its fauna. The cumulative creaming curve depicted in Fig. 47 shows that the recognition and description of fossil gobioids has entered a dynamic stage. The recognition of many more fossil gobioid taxa has to be expected, since creaming curves principally follow a sigmoidal course, and this recognition should occur before the creaming curve enters an asymptotic terrain of maturation.

Abundance and composition of goby otoliths in the Neogene of tropical America

The gobies living today in tropical America inhabit a great diversity of environments ranging from tidal, lagoonal, and fresh and brackish water environments to rocky shore and reefs (see also next chapter) and environments with soft bottoms away from reefs and into deeper water to depths of about 300 m (Additional file 2: Table S2). The fossilization potential and preservation potential for otoliths varies considerably across these environmental settings. Naturally, taxa adapted to abrasive environments like rocky shores or certain tidal settings are underrepresented in the fossil record and may only occur as rare "by-catch" if their otoliths have been transferred into a sedimentary environment by lateral transport of some kind. Taxa inhabiting terrain over sedimentary environments will dominate the fossil record. Most samples thus originate from environments where fine pelitic sediments (clay, silt, sand) has been deposited below wave base. These boundary conditions favor the recovery of otoliths of fishes living on or over soft bottoms and in deep water. In the case of American fossil gobies, it is thus not surprising that otoliths of the genera *Bollmannia*, *Microgobius*, *Antilligobius*, and *Palatogobius* and the related fossil *Proparella* are the most abundant (Tab. 2). These are all genera living over soft bottoms and/or in deep water. Otoliths of all other genera are rare and often found under specific circumstances only. Such specific circumstances include, for instance, vicinity to reefs or coastal mudflats. Some locations, however, such as the Cubagua FM, show a mixture of deep- and, rarely, shallow-water components, indicating lateral transport of shallow-water faunal elements into deeper water either by currents or by predator activities.

Gobies as environmental indicators in the Neogene of tropical America

Since gobies often show specific environmental adaptations, their fossil otolith records can also be used as environmental indicators if sufficient correlation of the fossil taxa is possible with extant ones. As stated above and shown in Fig. 48, the many gobiid genera occurring in tropical America inhabit a great diversity of environments. Even though their otolith abundance is governed by sedimentation and certain preservation aspects, a number of observations can be made in respect to the linking of gobiid otolith occurrences and specific sedimentary environments.

Darien environmental setting (Late Miocene)

Many different locations have been sampled during six Darien expeditions of the Smithsonian Tropical Reserach Institute under the Panama Paleontological Project during the years 1990–1996 (Coates et al., 2004). Otoliths were mainly found in the Tortonian Tuira and Yaviza formations and to a lesser extent in the Messinian Chucunaque Formation. The Tuira FM is considered to be of early Tortonian age (nannoplankton zone NN9b) and the Yaviza FM of nannoplankton zone N10 (Coates et al., 2004). The Darien Basin today opens to the Pacific Ocean but during the time of the Late Miocene sedimentation represented a continuous marine connection via the Atrato Basin in Colombia between the tropical East Pacific and West Atlantic. The composition of the fauna in the predominantly shallow marine deposits sampled during these expeditions is therefore of particular help in understanding differences in micro-environments that may have existed along the pathway. The goby association recovered from 25 sample localities and levels is rich, with a total of 28 species.

Detailed published results of the sampled localities and levels are available (Coates et al., 2004, supplement) and facilitate an assessment of variations in the goby distribution. In the following assessment, we have focused on samples that have yielded 19 or more goby otolith specimens: PPP 1132, PPP 1134, PPP 1137, PPP 1149, PPP 1163, PPP 1171, PPP 1528, PPP 1565, PPP 1566, PPP 1607, PPP 1609, PPP 1612 and PPP 1620. Several species are widespread in the goby otolith assemblage of the Tuira and Yaviza formations but with some change in abundance, for instance *Bollmannia gatunensis*, *B.*

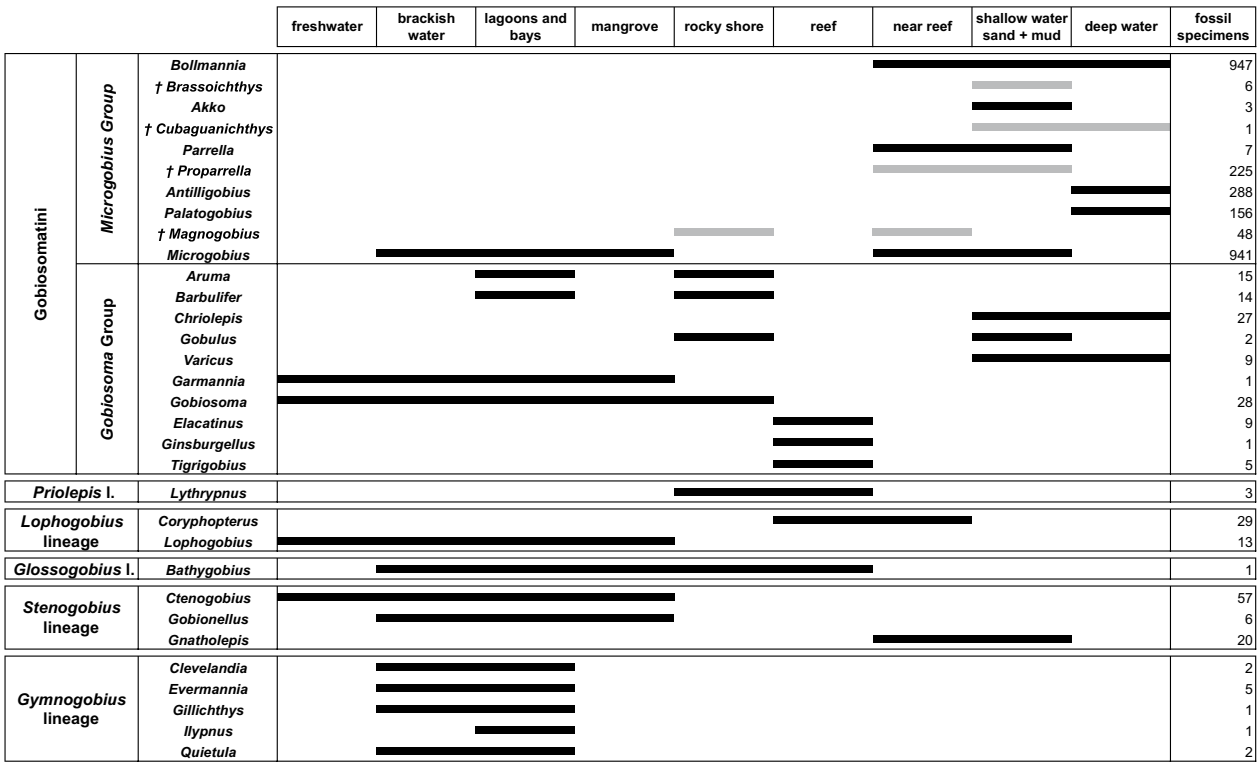


Fig. 48 Environmental habitats of American goby genera. Extant genera compiled from cited literature; fossil taxa (grey) deduced from sedimentological and environmental data of cited literature

baldwinae, *Proparrella darienensis*, and *Microgobius verecundus*. Other species are too rare or too randomly distributed to be of any obvious micro-environmental significance. In the following, we discuss those findings that seem to show some relation to specific environments described from the expedition logs (Coates et al., 2014, supplement).

Samples PPP 1171, 1565, and 1566 of the Yaviza FM were described by Coates et al. (2004) as silty sandstone, often packed with mollusks, especially *Turritella*, *Anadara*, and oysters with abundant shell hash and a horizon of extremely abundant large *Melongena*. The abundant shell hash indicates a shallow marine setting, possibly shallow subtidal or intertidal. *Melongena* is a marine gastropod that lives in the tropical intertidal in muddy areas and in mangrove areas. It is not known whether any of the three otolith-rich samples stem from the *Melongena* horizon, but in any case the sediments appear to have been deposited under shallow, near-shore environmental conditions. The gobiid assemblage contains many of the generally common and widely distributed species but is particularly rich in *Proparrella darienensis*. Locality PPP 1566 is the type and only location of *Akko lobatus*.

Sample PPP 1528 of the Yaviza FM originates from a silty to clayey sandstone interval, which is pervasively bioturbated and with snails encrusted with *Septastrea* (an extinct ahermatypic scleractinian coral), barnacles, and vermetids (Coates et al., 2004, supplement). This interval is underlain and overlain by hard beds. The sedimentary environment thus seems to be deposited in shallow water, possibly intertidal, with a relatively low sedimentation rate enabling encrusting biota to settle. This sample is remarkable for the small species *Microgobius glaber* and the abundance of small, unidentifiable *Microgobius* otoliths that probably came from juvenile fishes.

Pervasively bioturbated silty to clayey sandstones, sometimes with intercalated hard beds, prevail in many of the localities and levels with common otoliths. Mollusk content is variable, and arthropod burrows are often observed. The goby associations vary somewhat from one sample to another. Samples PPP 1132 and 1134 of the Tuira FM, for instance, are relatively rich in *Antilligobius collinsae* and lack specimens of *Proparrella darienensis*, which may indicate a deeper sublittoral environment. Sample PPP 1163 of the Tuira FM is remarkable for the abundance of *Microgobius chocorum* and *Bollmannia*

gatunensis and the occurrence of *Proparrella darienensis*. This interval has been described by Coates et al. (2004) as pervasively bioturbated, volcanic, silty sandstone with arthropod burrows and many small diverse mollusks. Like samples PPP 1132 and 1134, therefore, sample PPP 1163 may be interpreted as a slightly deeper and sheltered environment. The diversity of small mollusks, however, indicates an environment also allowing for a higher diversity of fishes, and this seems to be expressed by the differences in the composition of the goby association.

A sample with a rather unusual association of gobies is PPP 1137 from the Tuira FM. The sample is remarkable for the occurrence of the extant species *Microgobius crocatus*. *Microgobius crocatus* today inhabits mangrove environments, but the description of Coates et al. (2004) for this sample–i.e., clayey siltstone and bioclastic and lithic sandstone rich in bivalves, especially *Pecten*–does not suggest a mangrove environment. The sample is also the only one outside of Gatun (see below) to contain *Gnatholepis gunae* and is rich in *Bollmannia gatunensis*. *Proparrella darienensis* is absent.

Sample PPP 1612 that is from the Chucunaque FM is described as massive silty sandstone with extensive bioturbation. This sample is remarkable for the occurrence of *Coryphopterus rodriguezi*.

Samples PPP 1149 and 1620 of the Yaviza FM have been described by Coates et al. (2014) as a highly diverse fossil-rich clayey, silty, and shelly sandstone. This rich diversity in shells and other biota is not mirrored in goby otoliths, however, with the exceptions of the occurrence of *Bollmannia propensa*, which is the dominant *Bollmannia* species in the Messinian sediments studied (Chucunaque FM and Onzole FM of Ecuador).

In summary, we observe certain environmental differentiation in the composition of goby associations in Tortonian sediments of the Darien Basin but perhaps less than one might have expected. Many species are too widely or too sparsely distributed for a reasonable analysis. A few interdependencies, however, appear to be observable (Fig. 49):

- *Proparrella darienensis* and *Antilligobius collinsae* appear to be almost mutually exclusive. *Proparrella darienensis* occurs in intertidal to subtidal environments and is common overall but rare to absent in deeper zones or in environments of low biotic diversity. *Antilligobius collinsae* was perhaps not the deep-dwelling species like its extant counterpart *A. nikkiae* but was probably already adapted to slightly deeper and sheltered environments.
- *Microgobius glaber* and common unidentifiable *Microgobius* otoliths of putative juvenile fishes are characteristic of intertidal environments with a relatively low sedimentation rate.
- An unresolved but nevertheless interesting occurrence is that of *Microgobius crocatus*, a persisting extant species co-occurring with *Gnatholepis gunae*.

Angostura, Gatun, Manzanilla, and Cercado formations (Late Miocene)

Counterparts to the Darien Basin Tortonian localities have been studied from the Angostura FM (Ecuador), Gatun FM (Atlantic Panama), Manzanilla FM, San José Member (Trinidad), and Cercado FM (Dominican Republic). The sampled localities are fewer than in Darien and environmentally less diverse, but some samples have been rich in goby otoliths.

The samples PPP 3397, 3301, and 3369 of the Angostura FM have yielded only six species, all of which except *Microgobius ecuadorensis* have also been observed in Darien: *Bollmannia gatunensis*, *Proparrella darienensis*, *Antilligobius collinsae* (rare), *Microgobius verecundus*, and *Chriolepis balboa* (rare). The Angostura FM is composed of muddy, fine-grained sandstones with abundant mollusk shells considered to be deposited in shore-face to inner-shelf environments (Carrillo-Briceño et al., 2014). No details are available for the samples studied here, but the association corresponds well to the shallow-water environments sampled in the Darien Basin.

The Gatun FM on the Atlantic side of Panama has yielded two samples (PPP 2167 and 2168) rich in goby otoliths. The samples stem from a temporary construction excavation and have not been placed in any of the sections published by Collins and Coates (1999). The general environmental setting, however, has been described as shallow marine not deeper than about 20 m. Nevertheless, the two samples show a distinctly different composition except for the ubiquitous *Bollmannia gatunensis*. For instance, sample PPP 2167 contains *Antilligobius collinsae* but lacks *Proparrella darienensis*, while it is the other way round for PPP 2168. In regard to small *Microgobius* species, PPP 2167 contains *M. praeglaber*, a species otherwise known from the Middle Miocene Brasso FM of Trinidad but not from the Tortonian, while *M. glaber* is represented in PPP 2168. This discrepancy could indicate a stratigraphic separation of the two samples. Sample PPP 2168 further contains *Microgobius verecundus*, *Chriolepis balboa*, and, notably, *Gnatholepis gunae*. The latter species is common in this sample and otherwise has only been found in PPP 1137 and a single specimen in PPP 1553 both from the Darien Basin. The extant *Gnatholepis thompsoni*, which lives in the West Atlantic, inhabits open sand, rock, and rubble areas. It "feeds on organisms and organic material by taking sand into its mouth and expelling it through the gill openings, filtering

out its food in the process" (Froese & Pauly, 2023). It is not clear how the habit and environmental occurrence of the extant species may relate to the fossil *G. gunae*.

Relatively few goby otoliths have been found in the localities on Trinidad pertaining to the Manzanilla FM, San José Member, which have nevertheless yielded seven species. The most common species are *Microgobius verecundus* and *M. pezoldi*. Interestingly, these samples have also yielded two of the rare species of the *Gillichthys* clade in the West Atlantic: *Gillichthys caribbaeus* in sample PPP 2670 and *Quietula rueberi* in sample Cb. 1633. Considering that both genera are known for their estuarine and mudflat living habitat and of being facultative air-breathing, we would assume that comparable environments must have been available near these sample localities. Notably, neither *Bollmannia* nor any of the deep-water gobies are represented.

The sampled localities from the Cercado FM of the Dominican Republic are lean in otoliths and have yielded only three goby species. One of the species is *Magnogobius grandis*, which occurs regularly in several samples but has rarely been found elsewhere. The sediments of the localities where the species was found were described as "silt extremely rich in mollusks and a conglomeratic layer with mollusks in a silt matrix" (Saunders et al., 1986), which suggests a shallow, high-energy environment. Sample NMB 17003 contains only a few specimens of *Microgobius glaber* and is described as a small lens rich in *Tellina* and other small mollusks intercalated between beds of calcareous sponges, coral heads, and pebbles, indicating a shallow near-reef environment with a low sedimentation rate (Saunders et al., 1986). This occurrence is consistent with the occurrence of the species in sample PPP 1528 in the Darien Basin. Notably, neither *Bollmannia* nor any of the deep-water gobies are represented.

Microgobius glaber is also regularly found in the Manzanilla FM of Trinidad, relatively rarely in the San José Member, but is very common in PPP 2666 in the Messinian Montserrat Member together with the dominant *Palatogobius vantasselli*. The Montserrat Member is described as glauconitic sandstone (Kugler, 1956), which would support the affinity of *M. glaber* to shallow marine environments with slow accommodation rates. *Bollmannia* otoliths are relatively rare and are represented by *B. ornatissima* and *B. baldwinae*.

The conclusions regarding certain environmentally indicative species in the Darien Basin are confirmed in these areas as well, and the following additional observations are made (Fig. 49):

- Members of the *Gillichthys* clade are generally rare, but when occurring (*Gillichthys* and *Quietula*) they seem to have inhabited a similar mudflat-related shallow-water environment in the Late Miocene of the West Atlantic as they do today in the East Pacific.
- *Magnogobius grandis* is primarily found in shallow-water environments above wave base, as indicated by an association with conglomeratic components in the sediment.
- *Bollmannia* otoliths, which form one of the most dominant gobiid elements throughout the tropical

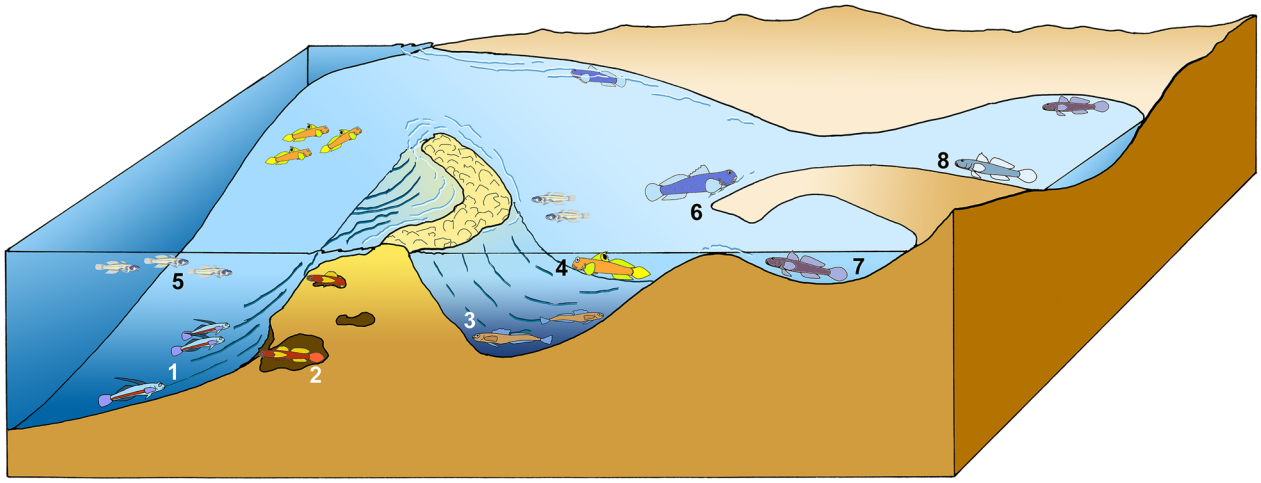


Fig. 49 Late Miocene/Pliocene life reconstruction of characteristic goby species in their habitat as interpreted in this study. Body shape is based on extant relatives. Legend: 1 *Antilligobius collinsae*; 2 *Aruma atlantica*; 3 *Palatogobius vantasselli*; 4 *Bollmannia gatunensis*; 5 *Microgobius aphioides*; 6 *Magnogobius grandis*; 7 *Quietula rueberi*; 8 *Gillichthys caribbaeus*. Environments depicted are (species in brackets): reef with crevasses and caves (2); deep forereef (1); deep backreef with lower oxygenation (3); moderately deep water (4); pelagic (5); nearshore with wave action (6); sheltered nearshore and mudflats (7 and 8)

American Neogene, are rare or absent in shallow environments above wave base or on mudflats.

- Another highly facies-dependent species appears to be *Gnatholepis gunae*, but this species cannot be clearly related at present.
- *Palatogobius vantasselli* is typical for the Montserrat Glauconite Sandstone Member of Trinidad. Glauconite forms under marine conditions at low sedimentary accumulation rates and is commonly associated with low-oxygen conditions. Thus, *Palatogobius vantasselli* may have adapted to reduced oxygen levels in its demersal habitat.

Cubagua Formation (Early Pliocene)

Otoliths were collected from different intervals in the Cubagua FM, one being the Cerro Negro Member and the other informally named "above Cerro Negro Member" (see Schwarzhans & Aguilera, 2013). The sediments of the Cerro Negro Member have been deposited in a deep-water, upwelling-influenced environment (Aguilera & Rodriguez de Aguilera, 2001) and are rich in otoliths of mesopelagic Myctophidae (Schwarzhans & Aguilera, 2013). Gobiid otoliths are generally rare in this interval, and many of them have probably been laterally transported into deep water either by currents or by predator activities. Such an allochthonous origin would explain the surprisingly diverse goby assemblage of 16 species. Only a few species have a slightly increased abundance, namely *Palatogobius grandoculus*, *Palatogobius* sp.1, and *Microgobius aphioides*. The two *Palatogobius* species are deep-water species, but, interestingly, another iconic deep-water goby, *Antilligobius*, is relatively rare in the Cubagua FM. We suspect the small *Microgobius aphioides* was probably a pelagic species similar to today's *Aphia*, since it occurred in unrelated environments in shallow and deep water during the Zanclean and Piacenzian.

The interval above the Cerro Negro Member, in contrast, is relatively lean in Myctophidae (Schwarzhans & Aguilera, 2013) but contains a significant number of gobiid specimens. This change in faunal composition may indicate a shallowing upward trend in the sedimentation regime of the Cubagua FM. This interval, however, contains only 11 species, but some of them are quite common, such as *Bollmannia boqueronensis*, *B. cubaguana*, *Proparrella darienensis*, *Palatogobius* sp.1, and *Microgobius aphioides.* The occurrence of *Bollmannia* and *Palatogobius* indicates that the water may still have been relatively deep, at least for gobies, but not as deep as during the deposition of the Cerro Negro Member. This is also the latest stratigraphical record for *Proparrella darienensis*, and it could be that the species migrated into slightly deeper water from its origins in the Late Miocene.

Deep-water gobies in the Neogene of tropical America

Several extant American gobiids inhabit water depths between 100 m and about 300 m. These groups are generally considered deep-water gobies. They comprise the genera *Bollmannia*, *Antilligobius*, *Palatogobius*, *Varicus*, some species of *Chriolepis* and *Psilotris*, and the genera *Birdsongichthys* and *Robinsichthys*, of which otoliths are not known (Tornabene et al., 2022). *Antilligobius*, *Palatogobius*, and *Varicus* exclusively inhabit deep water, whereas species of *Bollmannia* have a variable and generally wide depth range. Otoliths of *Bollmannia*, *Antilligobius*, and *Palatogobius* are common in the fossil record of tropical America, those of *Varicus* relatively rare. Because of the relatively wide depth range, *Bollmannia* otoliths cannot be taken as indicators for deep water, but they do not or rarely occur in shallow coastal environments such as lagoons, bays, mangrove environments, or environments above the wave base and can be seen as counter indicators for such settings. The occurrence of otoliths of the genera *Antilligobius*, *Palatogobius* and *Varicus* are generally considered to indicate deeper water. In the case of the Late Miocene *Antilligobius collinsae*, however, a more shallow-water habitat is probably to be considered (see above). Interestingly, otoliths of *Antilligobius* and *Palatogobius* rarely occur together, and if so, one of them is more common than the other. In comparing the occurrence of the two extant deep-water species *Antilligobius nikkiae* and *Palatogobius grandoculus*, there does not appear to be a trend of depth segregation between the two, and it is more likely that different environmental preferences are at work that are presently not well understood in the fossil record.

Antilligobius nikkiae is common in the Piacenzian Escudo de Veraguas FM, the Gelasian Bastimentos FM, and the Calabrian Swan Cay FM, all on the Atlantic side of Panama. *Antilligobius collinsae* is more irregular in the Piacenzian and Gelasian and occurs in some locations of the Escudo de Veraguas FM, presumably shallower samples of the Bastimentos FM, and in the Moin FM of Atlantic Costa Rica. A further indicator of open ocean and hence deep-water influence is the abundance of myctophid otoliths. These are moderately common in some samples of the Escudo de Veraguas FM, abundant in sample PPP 1256 of the Bastimentos FM, and moderately common in sample PPP 2221 of the Swan Cay FM. These samples coincide with an abundance of *Antilligobius* otoliths. The distribution of *Palatogobius* otoliths is more patchy, and the taxonomy is more diverse. *Palatogobius grandoculus* is relatively common in the Cubagua FM,

Cerro Negro Member, and occurs in a few samples of the Bastimentos FM. *Palatogobius vantasselli* is restricted in its distribution to the Montserrat Glauconite Sandstone Member of the Manzanilla FM of Trinidad, where it is the dominant gobiid species. This occurrence may indicate a preference of the species for environments with a lower sedimentation rate and a lower oxygenation level. The unique *Palatogobius magnus* is only known from the Cayo Agua FM of Atlantic Panama, and *P. pacificus* is remarkable for its occurrence in the Armuelles FM (Calabrian) of Pacific Panama. The Armuelles FM forms the shallower overlying unit above the deep marine Burica FM.

Near-reef localities (Limón, Bastimentos Island and Swan Cay)

Otoliths of typical reef-associated gobies such as those of the genera *Elacatinus*, *Tigrigobius*, *Lythrypnus*, or *Coryphopterus* are rare in the fossil record of tropical America and difficult to identify. Otoliths of *Coryphopterus* are the most common among them, but their distribution is too patchy to be of use as an environmental indicator.

Of more interest, however, are certain other genera usually associated with rocky bottoms and reef rubble: *Aruma*, *Barbulifer*, and *Gobulus*. *Aruma* is a monotypic genus in the East Pacific, and the other two are also more species-rich today in the East Pacific. We have good evidence for all of them, however, in the Piacenzian, Gelasian, and Calabrian of the West Atlantic. The fossil *Aruma atlantica* occurs in the Escudo de Veraguas FM, the Bastimentos FM, and the Swan Cay FM in Atlantic Panama, all formations that have deep-water characteristics with variable contents of myctophids and species of *Antilligobius* and *Palatogobius*. *Barbulifer amplus* has been found in the Ground Creek and Swan Cay formations. The question may be asked whether such occurrences do not contradict the deep-water environment indicated by myctophid and deep-water goby otoliths. In fact, the samples from the Ground Creek Formation of Bastimentos Island are adjacent to and interfingering with adjacent hermatypic reefs and are located in a fore-reef setting (Coates et al., 2005). This facies association may explain the seemingly contradictory co-occurrence of deep-water gobies and rocky bottom and reef-associated gobies. The situation is similar for the Swan Cay FM at Swan Cay, where reef rubble sediments occur in front of a reef. Sample PPP 2221 stems from cave sediment at the foot of a fore-reef complex (Coates et al., 2005; Collins & Coates, 1999). Here again, a mixture of deep-water and reef/rubble-associated gobies is plausible. *Gobulus limonensis* occurs in samples of the Moin FM in the Limón province of Costa Rica that are also adjacent to a reef body (see Fig. 4) and was taken from samples collected from an interval between a volcanic, tuffaceous sandstone and calcarenite below and a *Porites* coral thicket above (Collins & Coates, 1999). The two relevant locations PPP 1772 and 1773 were apparently further away from a deep-water environment and hence no deep-water indicators were found.

Were any mudflat environments sampled?

A certain number of extant tropical and subtropical American gobies are typical for mudflats in lagoons, estuaries, or other sheltered shallow-water to intertidal environments. Several of those, such as *Gillichthys*, *Quietula*, and *Ctenogobius*, are known for their facultative air-breathing, which is an advantage in such environments. We believe that sediments from such environments would be relatively lean in otoliths, with very few fish taxa represented. We know of no samples that have yielded otoliths for this study that would qualify to represent such facies. Species of the *Gillichthys* clade, which are typical for such environments, are today restricted to the East Pacific. *Ctenogobius* species are widely distributed both in the East Pacific and in the West Atlantic.

The otoliths of these groups are rarely encountered in the fossil record of tropical America. The earliest otoliths of *Ctenogobius* belong to the rare *C. darienensis* from the Yaviza FM (Tortonian) of the Darien Basin. In fact, *Ctenogobius* otoliths are relatively common in only two distinct samples: KR 1216 from the Early Pliocene Springvale FM of Trinidad and PPP 3256 from the Gelasian Moin FM of Costa Rica. Sample KR 1216 stems from the Chickland Clay Mb of the Springvale FM and was taken from the top of an oyster bed according to the NMB field log. *Ctenogobius* sp. is the most common gobiid species in the sample, which may indeed represent the closest environment to mudflats sampled in the entire study. The only other common species in that sample is *Microgobius aphioides*, a species occurring in a variety of unrelated environments, which we consider to be an indication that the species probably lived pelagically like today's *Aphia*.

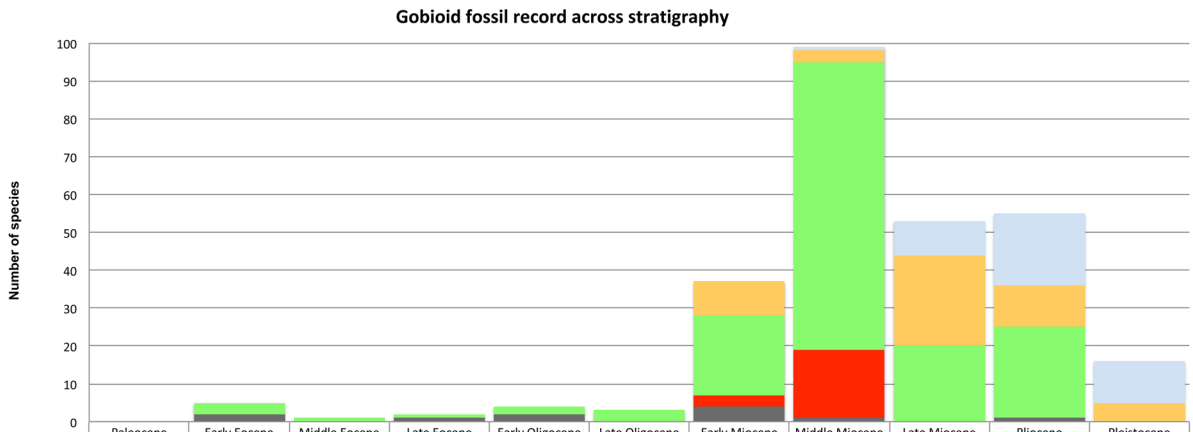
Otoliths of the *Gillichthys* clade are not common at any location or in any sample, but a number of species are recognized in the fossil record of the West Atlantic. This indicates that the clade originally had an amphiamerican distribution and that its current geographical restriction to the East Pacific is a secondary endemic effect. The latest occurrence in the West Atlantic is *Evermannia chiriquiensis* in the late Zanclean of the upper Cayo Agua FM in Panama. It is not known what led to the demise of the group in the West Atlantic, but it seems to coincide with an extinction event observed with other biota (O'Dea & Jackson, 2009).

Goby evolution in the Neogene of tropical America

General aspects of the evolution of gobioid fishes

The Gobioidei have a rich (Fig. 47) but relatively short fossil record. The earliest confirmed fossil records of any kind of gobioid fossil remains date back to the early Eocene (Fig. 50). These early records contain one skeletal record and four otolith records from Eocene times (Fig. 51). The earliest gobioid skeletal record *Carlomonnius quasigobius* Bannikov & Carnevale, 2015, is from the late Ypresian. It was described as showing a "unique combination of features that cannot be confidently accommodated within a familial category and is therefore interpreted as *incertae sedis* within Gobioidei" (Bannikov & Carnevale, 2015). The authors discussed the unusual combination of plesiomorphic and derived characters that sets *Carlomonnius* clearly apart from any members of extant families.

Few otolith-based gobioid species have been described from the Eocene. Two of them stem from the early Eocene (Ypresian) of India (Bajpai & Kapur, 2004; Nolf et al., 2006) and possibly represent the oldest record. Nolf et al. (2006) regard one of the species, "genus Gobiidarum" *vastani* Bajpai & Kapur, 2004, as probably representing a true goby while the second, "genus? Gobiidarum" *nolfi* (Bajpai & Kapur, 2004), was tentatively interpreted as a plesiomorph sister taxon of the other known gobiid taxa. "Genus Gobiidarum" *vetustus* was described by Nolf and Stringer (2003) from the late Eocene (Priabonian) of Louisiana, US. The otoliths of this species show the typical sole-shaped sulcus and a ridge-like feature in the ventral portion of the cauda that could be interpreted as a subcaudal iugum. Specimens made available for review by G. Stringer (Monroe, Louisiana) to WS show that this feature is located inside the cauda as part of the slightly elevated caudal colliculum and not part of the crista inferior as would be the case for a subcaudal iugum. Furthermore, the specimens show a ventral furrow that is bent upward and inward posteriorly to meet the tip of the cauda, which is a feature not observed in gobioid otoliths but in many trachinoid ones (Schwarzhans, 2019a, 2019b). In particular, the fossil genus *Waitakia* of the family Hemercoetidae exhibits such a pattern (Schwarzhans, 2019a). Recently, Lin and Nolf (2022) described *Waitakia beelzebub* from the Lutetian of Virginia, US. We now interpret *Gobius*? *vetustus* to possibly also represent a hemerocoetid rather than a gobioid. There is one further group of teleosts with a similar otolith pattern, the Hoplichthyidae (see Nolf, 2013, for figures). They too have a sole-shaped sulcus and a roughly rectangular otolith outline; however, they also show a ventral furrow that posteriorly curves upward and inward to meet the tip of the cauda, just as in Hemerocoetidae. We thus conclude that while gobioid otoliths are generally easy to recognize, certain care must be taken to avoid confusion with hemerocoetid and hoplichthyid otoliths, and the shape of the ventral furrow may eventually qualify as the best distinguishing characteristic.



	Paleocene	Early Eocene	Middle Eocene	Late Eocene	Early Oligocene	Late Oligocene	Early Miocene	Middle Miocene	Late Miocene	Pliocene	Pleistocene
Extant species								1	9	19	11
Neogene tropical American goby otoliths							9	3	24	11	5
otolith based species		3	1	1	2	3	21	76	20	24	
articulated skeletons with otoliths in situ							3	18			
articulated skeletons		2		1	2		4	1		1	

Fig. 50 Gobioid fossil record across stratigraphy. The records reflect fossil gobioid species currently accepted as valid and extant species also recorded as fossils. Otolith-based species are compiled from Nolf (1985, 2013) and own evaluation for articles after 2012; skeletal records compiled from Gierl and Reichenbacher (2015, 2017), Bannikov and Carnevale (2016), Schwarzhans et al., (2017a, 2017b), Reichenbacher et al., (2017, 2020, 2023), Bradić-Milinović et al. (2019), and Reichenbacher and Bannikov (2021, 2022)

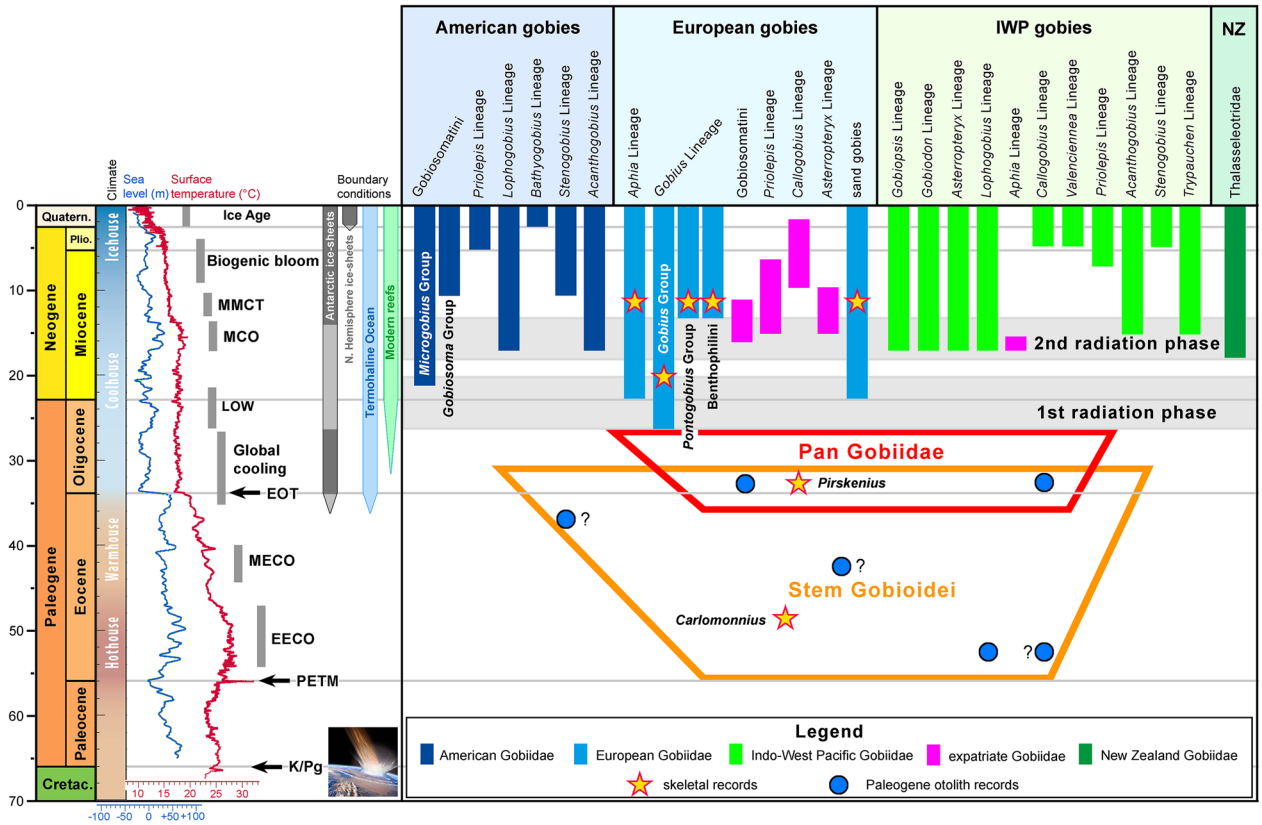


Fig. 51 Summary chart of gobioid evolution in context with changes of Earth's geosphere. Abbreviations: K/Pg, Cretaceous–Paleogene boundary event (Chicxulub meteor impact); PETM, Paleocene–Eocene Thermal Maximum; EECO, Early Eocene Climate Optimum; MECO, Middle Eocene Climate Optimum; EOT, Eocene–Oligocene Transition; LOW, Late Oligocene Warming; MCO, Miocene Climate Optimum; MMCT, Middle Miocene Climate Transition. Gobioid data compiled from same sources as is Fig. 50, plus NZ (New Zealand) from Schwarzhans (2019a) and IWP (Indi-West Pacific) from Carolin et al. (2021) and ongoing research

There is one further otolith morphology observed in Eocene otoliths that has been associated with the Gobioidei, the family Odontobutidae in this case. Genus? *Odontobutidarum triangularis* was described by Schwarzhans (2007) from the Lutetian of Germany. A similar species was described as "genus Batrachoididarum" *trapezoidalis* Nolf, 1998, from the Lutetian of Belgium and as Gobioidei? indet. by Nolf et al. (2006) from the Ypresian of India. Schwarzhans (2007) compared *Odontobutis*? *triangularis* with the otoliths of the extant *Micropercops swinhonis* (Günther, 1873), a southeast Asian freshwater odontobutid. All these otoliths are characterized by an expanded ventral rim projecting anteriorly and posteriorly, a reduced dorsal field, and a sulcus that appears to be opening to or closely approaching the anterior rim. Recent otoliths of extant Rhyacichthyidae (Gierl et al., 2022) show a comparable pattern, and it therefore appears plausible that these otoliths indeed represent some kind of stem gobioid. The only comfortably assigned fossil odontobutid otolith, however, is *Micropercops pomahaka* Schwarzhans, Lee & Gard, 2017, from the late Oligocene of New Zealand. We consider the European and Indian otoliths as requiring confirmation.

In conclusion, we consider only skeleton-based *Carlomonnius quasigobius* and the otolith-based *Gobius*? *vastani* as reliable Eocene gobioid records (Fig. 50). All other records either require confirmation by more detailed investigation and comparison or may be considered to represent non-gobioids. Figure 49 shows a low speciation level of the Gobioidei throughout the Eocene and Oligocene. At least for the Eocene, this low level is considered to be a true evolutionary signal, since Eocene strata have been prospected for otoliths in many areas of the world (Lin & Nolf, 2022; Nolf, 2013; Schwarzhans, 2019a).

The situation changes in the early Oligocene, however. In skeletal records, *Pirskenius* Obrhelová, 1961, has been described from Rupelian freshwater deposits of the Czech Republic. Because of the unusual count of seven branchiostegal rays (five in Gobiidae and six in all other extant families), *Pirskenius* has remained an enigmatic record placed in its own family, Pirskeniidae, or in Eleotridae (Přikryl, 2014). Recently, a detailed phylogenetical

analysis placed the Pirskeniidae as the stem-group of Gobiidae plus Thalasseleotridae (Reichenbacher et al., 2020). Otoliths have been found in shallow-water, near-shore environments of the early Oligocene of southwest France (Steurbaut, 1984) and Japan (Schwarzhans et al., 2017a, 2017b). The Japanese otoliths have been placed in a fossil genus, *Ortugobius* Schwarzhans et al., 2017a, 2017b, of uncertain relationship within the Gobioidei but likely near the Gobiidae and in the recent genus *Gymnogobius* Gill, 1863, which, however, requires confirmation. The specimens from France were recorded as "genus Gobiidarum" sp. 3 and 4 by Steurbaut (1984) and according to his drawings are similar in morphology and size to the Japanese ones. Here, we consider these otoliths to represent a group of "Pan-Gobiidae" of uncertain relationships (Fig. 51). Interestingly, gobioid otoliths occur in very few Oligocene localities, like these pan-gobiid otoliths, but where they are found, they represent by far the most dominant group in terms of specimens. The knowledge of Oligocene otoliths, however, is still relatively punctual and may therefore show a species underrepresentation in Fig. 50. However, the Oligocene is the first time in geological history that gobioid otoliths are really common in selected environments, and this indicates a change in the evolution dynamics of the group. This burst of abundance, albeit of a local nature, coincides with a global cooling period and the demise of a group that could be seen as competitors to gobies on the shallow, sand-dominated shelf, the Ophidiiformes (Schwarzhans et al., ms). During the Eocene, an abundance of small, shallow-water ophidiiforms existed and were common and diverse, but they came to a rather sudden termination in the early Oligocene (Schwarzhans et al., ms).

The late Oligocene–Early Miocene interval shows the first records of gobiids that can be attributed to extant groups and in some cases even genera, for instance the record of the genus *Gobius* from the Early Miocene based on articulated skeletons (Reichenbacher et al., 2017). The otolith record is more diverse and richer, and it corroborates the observations made with skeletons and particularly gains momentum during the Early Miocene (Fig. 50). In Europe, which has the rocks most intensively studied for otoliths, Early Miocene otolith records already contain all three extant Atlantic-Mediterranean gobiid lineages (Fig. 50): the *Aphia* and the *Gobius* lineages and the sand gobies (Schwarzhans, 2010; Schwarzhans et al., 2021). In tropical America, the Gobiosomatini have been present since the Early Miocene, with the *Microgobius* group (Fig. 51) containing representatives of the *Bollmannia* and *Microgobius* clades. It seems that during the phase from the late Oligocene to the Early Miocene, a major radiation took place in gobiids (Fig. 51) that may have formed the nucleus in the major shallow- and warm-water regions of the world for the subsequent diversification of gobies. However, this postulated 1st radiation phase is as yet poorly constrained, primarily because of the limited data of that time interval in many regions of the world.

Continuous records of strata investigated for otoliths in America and the Indo-West Pacific region, however, begin only with the late Burdigalian. During the time span from late Burdigalian to Tortonian, another major phase of radiation appears to have taken place. This 2nd radiation phase is better constrained than the postulated 1st one (see above), and it is remarkable for its regional content (Fig. 51). There are three main regional areas of the world shelf communities where gobies are thriving today: tropical America in the tropical East Pacific and the West Atlantic; Europe and West Africa, forming the Atlantic-Mediterranean goby center; and the Indo-West Pacific, the region with the largest diversity in the Gobiidae. Interestingly, most of the extant lineages occur in the respective regions during this time interval, which appears to be largely congruent with the Miocene Climate Optimum (MCO). It appears as if the lineages radiated in their regions of origin during the time without much interaction between the regions. An exception is Europe, which is probably due to a late phase of Tethyan connectivity prior to the abandonment that occurred during the Middle Miocene Climate Transition (MMCT) (Bialik et al., 2019; Sun et al., 2021) (Fig. 51). Gobiid otoliths show a dramatic increase of taxa during the Miocene, particularly in the Middle Miocene (Fig. 50). This Middle Miocene increase appears to be a combination of a real speciation phase and a predominance of strata studied from the various European basins that at that time were exceptionally diverse and variable. This setting favored an accelerated endemic evolution in some parts of Europe, e.g., the Paratethys (now Ponto-Caspian basin) during the Middle Miocene (Bratishko et al., 2023; Schwarzhans et al., 2020a, 2020b). We regard the suspicious decline of the species diversity depicted in Fig. 50 for the Late Miocene and Pliocene to be the result of fewer suitable sediments for gobies having been studied in fewer regions and therefore to be misleading.

Timing and events in the evolution of tropical American gobies

No goby otoliths (or skeletons) are known from the intensely collected Paleogene rocks of North America, except for the problematic record of *Gobius*? *vetustus* from the late Eocene of Louisiana (see above). Furthermore, Müller (1999) did not record any gobiid otolith from the Neogene of the Atlantic coastal plains of the US. The abundance of gobiid otoliths in the Neogene

sediments of tropical America thus represents a stark contrast.

The fossil otolith record in tropical America commences with an assemblage described from the Early Miocene (late Aquitanian or early Burdigalian) of the Pirabas FM near today's Amazon river mouth in Brazil (Aguilera et al., 2014). Gobiid otoliths are relatively rare in this assemblage and are represented by species of the Gobiosomatini of the genera *Bollmannia* and *Microgobius*, as here reviewed (Fig. 52). One of the species, *Bollmannia nubila*, represents a rare case of cross-Atlantic distribution and was originally described from the North Sea Basin in Europe (Schwarzhans, 2010).

Initially, relatively few genera were added to the list of occurrences during the Middle Miocene (Fig. 52). Gobiid otoliths started to become much more abundant in the late Burdigalian to Langhian interval, for instance in the Brasso FM of Trinidad and the Cantaure FM of Venezuela. This gobiid otolith abundance, however, is carried by only a few species. New occurrences are rare but document the first appearances of other endemic American gobies such as *Coryphopterus* of the *Lophogobius* lineage or *Evermannia* of the *Gillichthys* clade of the *Acanthogobius* lineage (Fig. 52). Apparently, the increase of abundance in gobiids predated the increase of diversification (Fig. 53). This increase of abundance also coincides with a brief global warming phase, the Miocene Climate Optimum (MCO) (Fig. 53). Unfortunately, there is as yet a recording gap for the later part of the Middle Miocene, the Serravallian.

A boost in goby diversification is manifested with the beginning of the Late Miocene Tortonian at about 11 Ma (Fig. 53). Many genera of the Gobiosomatini are recorded for the first time from this time interval, including the first deep-water gobies of the genera *Antilligobius* and *Palatogobius* (Fig. 52). More genera of other endemic American gobies are also first recorded from the Tortonian such as *Ctenogobius* of the *Gobionellus* clade of the *Stenogobius* lineage and *Gillichthys* and *Quietula* of the *Gillichthys* clade of the *Acanthogobius* lineage (Fig. 52). Another genus first recorded from the Tortonian is *Gnatholepis* of the *Gobionellus* clade (Fig. 52). Such an early occurrence of *Gnatholepis* (*G. gunae*) is perhaps surprising, since it may be considered a genus of Indo-West Pacific origin, where it contains most extant species, while in America there is only one extant species: *Gnatholepis thompsoni* (Froese & Pauly, 2023). We interpret the relatively sudden increase in gobiid diversity in the early Tortonian as the expression of a major speciation phase of gobies in America. This initial increase of diversity is not obviously connected to a global climate shift other than the terminal phase of the Middle Miocene Climate Transition (MMCT) toward a cooler climate (Fig. 53). It is also not known what role, if any, the MMCT may have actually played for the goby evolution in tropical America due to the lack of fossil otolith data from the Serravallian.

Two further boosts in the speciation of American gobies are recognized in the Early Pliocene (Zanclean) and the Early Pleistocene (Gelasian) (Fig. 53). Many extant American goby genera are recorded for the first time from the Early Pliocene (Fig. 52). The otoliths of most of these new records are morphologically close or identical to extant species, and it is therefore possible that their true origin would be earlier, maybe also in the Late Miocene. In any case, with the onset of the Early Pliocene, the tropical American goby fauna more or less reached today's diversity level, assuming of course that certain environments are underrepresented in the fossil record because of the effects of selective taphocenosis in the fossil record (see above). The Early Pliocene increase of diversification in American gobies also coincides with the phase of the Biogenic Bloom in the oceans (Fig. 53), but it is not known how much this could have influenced the evolution of gobies. The youngest speciation phase at the Pliocene–Pleistocene interface slightly postdates the final closure of the Panamanian seaway and the rise of the Isthmus of Panama between 3.2 and 2.76 Ma (Coates & Stallard, 2012; Coates et al., 1996; O'Dea et al., 2016). This speciation phase may have been influenced by the establishment of the ice-house climate regime, the latitudinal restriction of the world's tropical belt, and a reorganization of the environmental setting in tropical America.

The late Neogene is also the time of certain extinction phases, the first during the Messinian (terminal Miocene) and two further ones, one at the Zanclean–Piacenzian interphase (Late Pliocene) and one during the Early Pleistocene (Calabrian). These potential extinction phases are biased, however, and possibly overrated in the otolith record, because many apparent otolith-based species from Pliocene and Pleistocene sediments have remained in open nomenclature due to the lack of comparative extant otoliths in certain genera. Many of these records in open nomenclature are thought to represent extant species of which otoliths are not yet known. Once attributable, they will dilute the number of species extinctions. The Messinian marks the last occurrence dates of many of the common Late Miocene species in the genera *Bollmannia* and *Microgobius*. This extinction phase also marks the highest level of last occurrences in the goby record (Fig. 53), even though it does not indicate a major faunal shift, as no lineage seems to have become extinct or disappeared from either the East Pacific or Caribbean basins.

The following goby extinction phase in the Caribbean at the Zanclean–Piacenzian interphase is well

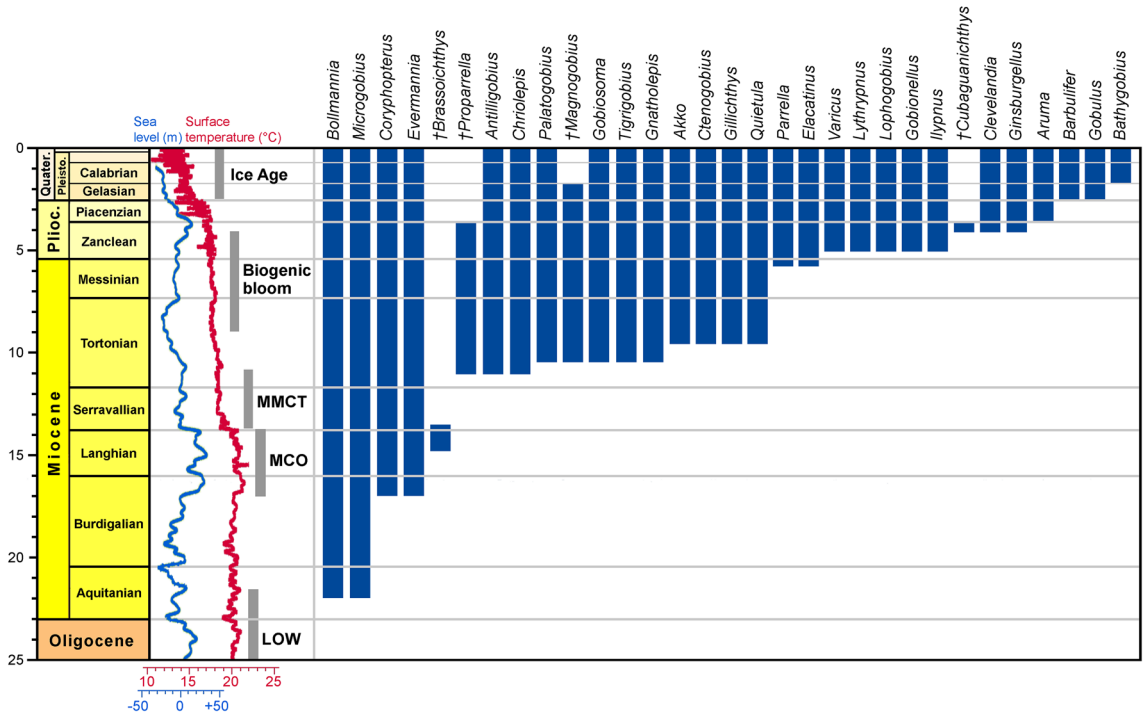


Fig. 52 First occurrences and ranges of gobiid genera observed in the fossil otolith-based record of tropical America. Ghost ranges not differentiated. Abbreviations: LOW, Late Oligocene Warming; MCO, Miocene Climate Optimum; MMCT, Middle Miocene Climate Transition

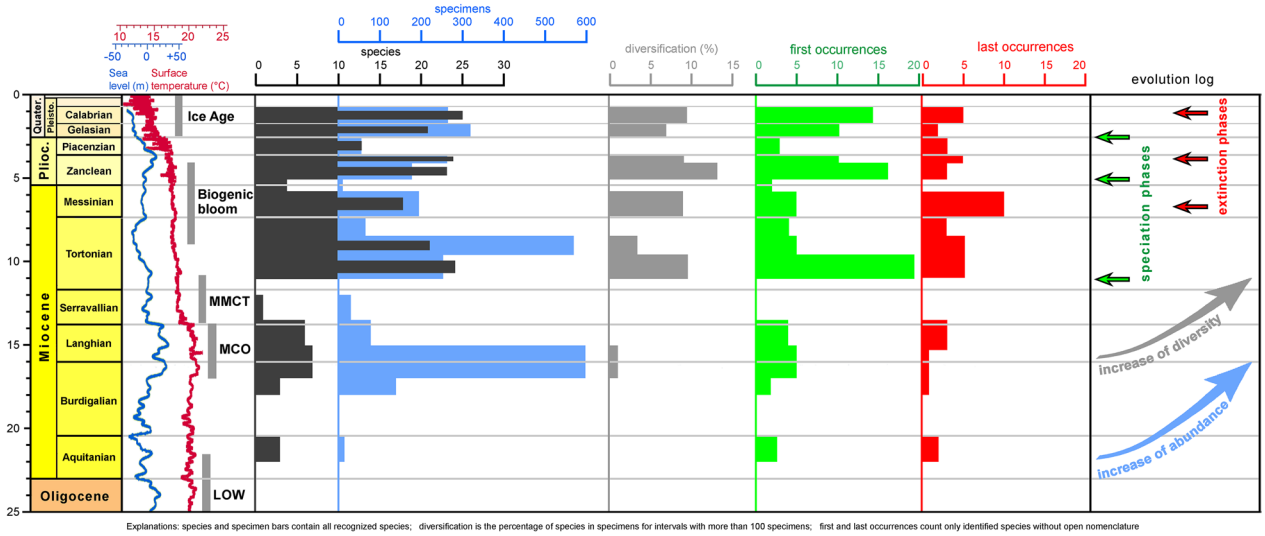


Fig. 53 Summary chart depicting American gobiid evolution trends based on the fossil otolith record. Stratigraphic units clustered to allow for Columns are from left to right: black number of species observed per stratigraphic unit; blue number of specimens observed per stratigraphic unit; grey diversification (number of species in percent of number of specimens) for stratigraphic units with more than 100 specimens; green number of first species occurrences per stratigraphic unit; red number of last species occurrences per stratigraphic unit; evolution log summarizing phases in gobiid evolution as here interpreted

documented independently in several different biota and coincides with effects observed in bryozoans (Martino et al., 2018; O'Dea & Jackson, 2009), the family Pectinidae of lamellibranchiates (Smith & Jackson, 2009), gastropods (Todd et al., 2001), and corals of both free-living and colonizing taxa (Budd, 2000; Budd et al., 2011; Klaus

et al., 2011a, 2011b). O'Dea and Jackson (2009) correlated the decrease of bryozoans in the Caribbean with the closure of the seaway across the Isthmus of Panama, the decline in upwelling, and as a result the collapse in planktonic productivity (O'Dea et al., 2007). They explained the extinction event of bryozoans between 3 and 1 Ma as being related to increasing oligotrophy in the Caribbean Sea. O'Dea and Jackson (2009) also noted a lagging of bryozoan extinction in relation to patterns observed with other biota, and they explained that extinct species increasingly "failed to become more robust when the new environmental conditions arose." In gobies, the fossil genus *Proparrella*, which had previously been a common and widely distributed genus since the Tortonian throughout tropical America, became extinct (Fig. 51). A relatively diverse albeit rare assemblage of taxa of the *Gillichthys* clade (*Acanthogobius* lineage) disappeared from the Caribbean at the Zanclean–Piacenzian interface. Today, these genera are only known from the East Pacific. Certain small species of the *Microgobius camur* otolith plexus (*M. aphioides* and *M. glaber*) became extinct at the same time. These small species occurred relatively facies-independently, and we interpret this distribution as potentially indicating a pelagic way of life similar to today's *Aphia minuta*. Another genus today only known from the East Pacific, *Aruma*, remained well represented in near-reef environments in the Caribbean through the Late Pliocene and Early Pleistocene. A recording gap in fossil otoliths from the East Pacific at the time prohibits any assessment of goby evolution in that ocean basin.

A third, less prominent extinction phase seems to have occurred near the end of the Early Pleistocene (Fig. 53). Only a few species are recorded in the Gelasian (2.58–1.81 Ma) or Calabrian (1.81–0.78 Ma) for the last time. Among them are the fossil genus *Magnogobius* (Fig. 52); the genus *Aruma* in the Caribbean, which today is only recorded from the East Pacific; the genus *Palatogobius* in the East Pacific, which today is only known from the tropical West Atlantic; and two large species of the genera *Barbulifer* and *Gobulus* in the Caribbean, genera which today are more diverse in the East Pacific. The habitat of these taxa differed from each other. *Magnogobius* appears to have been adapted to near-shore environments at or above wave base. *Palatogobius* is a deep-water goby. The fossil Caribbean species of *Aruma*, *Barbulifer*, and *Gobulus* occurred in near-reef settings. It seems likely that the extinction of these reef-associated gobies at the end of the Early Pleistocene is connected to a change of coral environments in the Caribbean. Budd et al. (2011) noted that the transition from the Late Pliocene *Stylophora*-dominated reefs to the *Acropora*-dominated reefs of the Late Pleistocene may have occurred during the (poorly represented) time window between 1.2 and 0.5 Ma. They concluded that "Late Pliocene reefs typically consisted of patch reefs and low-relief thickets, while late Pleistocene reefs formed well-developed reef crests with steep forereef slopes and backreef lagoons." Another drastic change occurred during the Late Pliocene–Pleistocene interval: the demise of free-living corals in the Caribbean (Klaus et al., 2011a, 2011b).

Tip dating with fossils compared to molecular clock dating

The diversity of the Gobiosomatini has attracted molecular-based phylogenetic analyses in recent studies, e.g., Rüber et al. (2003) and Tornabene et al., (2016, 2022). These studies also included dating of lineages and dichotomies by applying molecular clock calculations. The abundant finds of fossil goby otoliths in Neogene sediments of tropical America now allows comparison of some of the molecular clock origination times with fossil tip dates. Most importantly, the tip dates should always be somewhat younger than the molecular clock dates because of the uncertainties afflicting the fossil record. Such uncertainties may be related to the discontinuous or simply lacking fossil record, preservation issues, lack of soft anatomical data, difficulties in recognizing early stages of a lineage, or the presence of fossil lineages of uncertain relationships. Fossil data therefore have the tendency to indicate younger lineage-origination dates than molecular clock dating. However, maximum age levels are set where the fossil record only shows pan or stem representatives for the systematic unit in question. In the case of Gobiidae, such a maximum limit should be set no earlier than the base of the Lower Oligocene at about 34 Ma (Fig. 51). In contrast, when tip dates indicate an older date than molecular clock dates, then the phylogenetic modeling and the identification of the fossils should be checked for possible errors.

In the aforementioned phylogenetic studies, a range for the origination of the Gobiosomatini is shown in the respective phylogenies between 40 Ma (Tornabene et al., 2016) and 34 Ma (Rüber et al., 2003; Tornabene et al., 2022). Both origination times are slightly earlier than would be expected from the fossil record but certainly within tolerance. The timing of the individual lineages/genera is shown mostly between 5 and 15 Ma and that of larger clusters between 10 and 25 Ma in all three phylogenetic analyses. These ranges are consistent with the fossil data and thus confirm the phylogenetic modeling. The available fossil data of American gobies indicate that the Gobiosomatini were firmly established at about 22 Ma and that even individual clades within the *Microgobius* group at that time can be recognized, i.e., the *Bollmannia* and the *Microgobius* clades (Fig. 52). These occurrences indicates that the origination of the Gobiosomatini can be expected during the Late Oligocene, i.e., 27–23 Ma.

Representatives of the *Lophogobius* lineage (*Coryphopterus*) and the *Acanthogobius* lineage (*Evermannia*) are identified in the fossil record from about 17 Ma (Fig. 52), indicating that they may have a similar origination time in America as the Gobiosomatini. All major lineages are firmly established since 10 Ma (Fig. 52), and many of them may have originated earlier during Early to Middle Miocene times.

The origination and evolution of the deep-water Gobiosomatini clades have been the particular focus of the studies by Tornabene et al., (2016, 2022). Since two of these genera (*Antilligobius* and *Palatogobius*) also commonly occur in the fossil record along with several other genera of the *Microgobius* group, these form an interesting test case to compare molecular phylogenetic assessments with the fossil record. The result of the correlation shows a striking degree of congruence (Fig. 54). The earliest records of the deep-water genera *Antilligobius*, *Palatogobius*, and *Varicus* fit well in the time frame modeled from molecular analyses (Fig. 54). In the case of *Antilligobius* and *Palatogobius*, the fossil record is more diverse and richer than the extant one. Interestingly, the first *Antilligobius* species, *A. collinsae*, appears to have inhabited shallower waters than the extant *A. nikkiae*. The same appears to be true for *Palatogobius*, with its earliest record, *P. vantasselli*, apparently having occurred in relatively shallow water. The other fossil species from the Late Pliocene and Pleistocene, *P. magnus* and *P. pacificus*, have been found in deep-water sediments. *Palatogobius pacificus* is the only member in this group that has been found in the East Pacific. The stratigraphic ranges of other genera in the *Microgobius* group are also consistent with the timing of the molecular clock, e.g., the genera *Akko*, *Bollmannia*, *Microgobius*, and *Parrella*. Moreover, the common extinct genera *Brassoichthys*, *Magnogobius*, and *Proparrella* are well nested in the *Microgobius* group (Fig. 54).

Paleobiogeographical evaluation

Gobies are predominantly demersal fishes and do not move over large distances in their adulthood. Furthermore, during their larval stages, many species apparently stay over the continental shelves close to their settling area and do not seem to be present in the oceanic pelagic plankton (e.g., Sponaugle & Cowen, 1994; Victor, 2007). As a result, the Gobiidae are usually confined to specific regions, and large oceanic basins act as barriers to their distribution. Marine goby communities are concentrated in three major regions of the world, the Americas, the Atlantic-Mediterranean region, and the Indo-West Pacific, each of which harbors diverse and yet distinct goby stocks. There must have been a phase in the history of goby evolution when geographic spread was enhanced, i.e., during the late Paleogene (see above), giving rise to

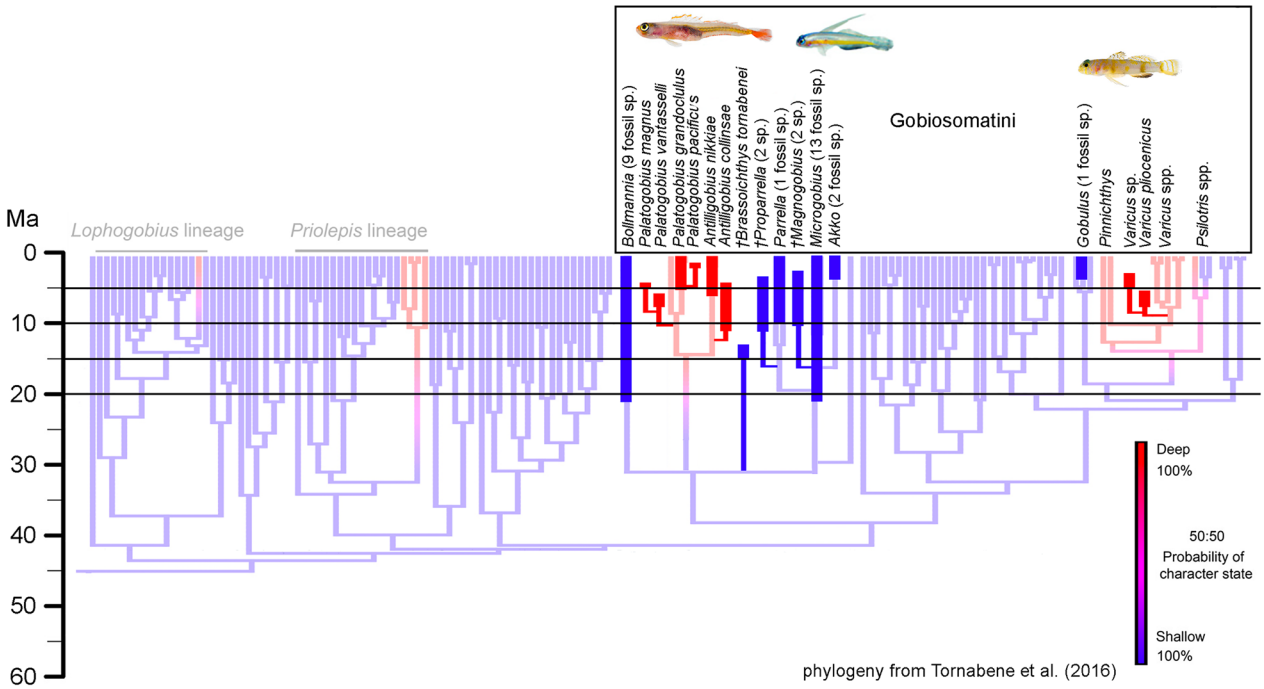


Fig. 54 Occurrences of certain gobiosomatine genera and species in the context of the phylogeny of the Gobiosomatini as presented in Tornabene et al. (2016)

the current bioprovinces, but the mechanisms for such a spreading phase are not yet understood.

The pronounced regionalism and immense speciation speed or endemic evolution force of gobies and their preference for shallow-water environments makes them ideal candidates to study migration patterns and the connectivity of marine habitats even under ephemeral and shallow-water conditions.

Exchange across the Panama Strait

A particularly interesting aspect is the extent and range of fish species present on both sides of today's Isthmus of Panama. The distribution of fossil gobies in tropical America in space and time can help to evaluate the faunal exchange between the East Pacific and the West Atlantic and when it may have terminated due to the separation of both ocean basins. Unfortunately, the only time interval that allows for a conclusive evaluation of fossil fish faunas between the East Pacific and the West Atlantic is the Late Miocene, especially the Tortonian and with some limitation the Messinian. Pacific faunas are known from Ecuador and the Darien Basin in Panama and Atlantic faunas from Gatun on the Atlantic side of Panama, Trinidad, and the Dominican Republic. Seventeen of a total of 27 gobiid species are distributed on both sides of Middle America, corresponding to 63% of Late Miocene gobiids (Fig. 55). The Messinian samples obtained from Ecuador and Darien in the Pacific realms and the Dominican Republic, Trinidad, and Venezuela on the Atlantic side are sparse and show little consistency. Many of the goby species found in the Messinian are also known in the Tortonian, however, and in combining the sparse Messinian data with the richer Tortonian data, the number of shared species between the East Pacific and the West Atlantic is significant at about 75% (Fig. 55). It may be concluded from this that up to at least 6 Ma there was a continuous faunal exchange between the East Pacific and the Atlantic, probably lasting until about 4 Ma. The entire region from Ecuador in the west to Trinidad in the east may be considered a single bioprovince for gobies, similar to the assessment depicted for other fish groups in Schwarzhans & Aguilera (2013) and Aguilera et al. (2016).

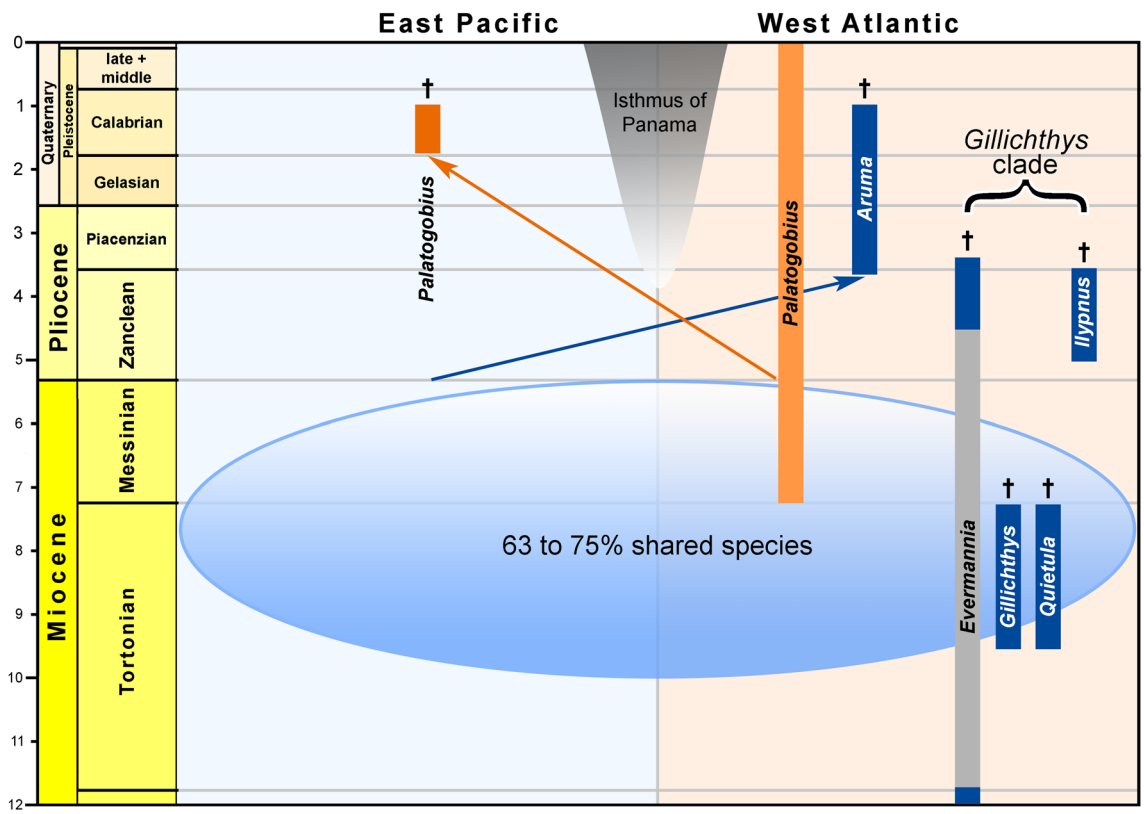


Fig. 55 The role of the Panamanian Seaway and its closure for the exchange of goby lineages. During Tortonian and Messinian between 63 and 75% of species were shared between the East Pacific and the West Atlantic. Clades of putative East Pacific origin (blue) persisted in the West Atlantic well up until the Zanclean–Piacenzian interface and in the case of *Aruma* into the Calabrian. *Palatogobius* of supposed West Atlantic origin (orange) occurred also in the Calabrian of the East Pacific

The possible extent of an East Pacific–West Atlantic connectivity during the Pliocene cannot be evaluated by means of fossil otolith assemblages because of the lack of adequate data from the East Pacific. Studies of planktonic foraminifera and coccolithophores indicate that faunal exchange was still possible well into the Pliocene until about 3.5 to 2.7 Ma (O'Dea et al., 2016). Studies of gastropods indicate that faunal exchange between both seas may have still been active into Late Pliocene and possibly even Early Pleistocene times (Beu, 2019).

The only stratigraphic interval after the Tortonian exhibiting a reasonably comparable representation of otolith abundances in the East Pacific and the West Atlantic is from the late Early Pleistocene Calabrian from the Burica Peninsula, Pacific Panama, and various locations on the Atlantic side of Panama and Venezuela. These assemblages do not show a single shared gobiid species. We therefore conclude that any faunal exchange of the fish fauna between the East Pacific and the West Atlantic had effectively terminated before the Calabrian, i.e., before about 1.8 Ma.

However, a number of lineages that today are only represented in the East Pacific were also present in the West Atlantic and persisted for a while until they became extinct well after the presumed closure of the Panamanian Seaway. Representatives of such lineages in the West Atlantic during Zanclean to Piacenzian are taxa of the *Gillichthys* clade (*Acanthogobius* lineage), and the genus *Aruma* of the *Gobiosoma* Group until the Calabrian (Fig. 55; see also chapter "Timing and events in the evolution of tropical American gobies" above). The *Gillichthys* clade appears to have been present in the West Atlantic since at least Tortonian times and possibly since Langhian (*Evermannia*? *problematica*) and became extinct in the West Atlantic at the Zanclean–Piacenzian interface (Fig. 55). *Aruma* is only known from a fossil species (*A. atlantica*) in the West Atlantic from Piacenzian to Calabrian while today it is known from a single species (*A. histrio*) from the Gulf of California. Judging from the current distribution pattern, both groups, the *Gillichthys* clade and the genus *Aruma* are considered to be of East Pacific origin that expanded into the West Atlantic before the Panamanian Seaway closed. Conversely, the deep-water genus *Palatogobius*, which today is only known from the West Atlantic apparently was also distributed in the East Pacific during Calabrian (Fig. 55; see also chapter "Timing and events in the evolution of tropical American gobies" above). *Palatogobius* is well represented in the West Atlantic since at least Messinian (Fig. 55) and possibly late Tortonian. We therefore assume that the genus expanded from a West Atlantic root into the East Pacific before the closure of the Panamanian Seaway became effective.

Impatriates and expatriates

Gobiid speciation occurred primarily regionally in three main regions of the oceans (America, Atlantic-Mediterranean, and Indo-West Pacific) after an initial spreading phase that presumably took place during the late Eocene and/or early Oligocene (see above). After the establishment of the three regional evolutionary centers, faunal exchange in respect to gobiids was minimal. A certain amount of faunal interaction still took place along the former Tethyan Seaway between southeastern European basins and the Indian Ocean for a while during the final days of shallow-water connection (Carolin et al., 2022; Schwarzhans et al., 2020a, 2020b).

Today, a few gobiid genera (*Gobioides* and *Gobionellus*) and one species (*Gnatholepis thompsoni*) are known from both sides of the Atlantic. This clearly shows that faunal exchange of gobies across the Atlantic is limited. The case of *Gnatholepis thompsoni* is of interest, as it has been shown to have a prolonged larval stage (Sponaugle & Cowen, 1994). The authors suggest that a flexible and prolonged larval duration may enhance dispersal to or colonization of wider biogeographic regions. Interestingly, the West Atlantic *Gnatholepis thompsoni* also occurs near several East Atlantic oceanic islands (Froese & Pauly, 2023). The species is one of only two gobies inhabiting the remote Ascension and St. Helena Islands, the other being an endemic species of the genus *Priolepis*. However, *Gnatholepis* shows the highest degree of diversity today in the Indo-West Pacific (nine species according to Froese & Pauly, 2023). Surprisingly, though, *Gnatholepis gunae* is an otolith-based species known from the Late Miocene (Tortonian) of Panama, on the Pacific and Atlantic side. This species does not seem to be directly related to the extant *G. thompsoni* but indicates that an increased dispersal ability could have been a virtue of the species in this genus since the Late Miocene.

Other gobiid genera present in America today but with a center of diversity in the Indo-West Pacific are *Priolepis* and *Oxyurichthys*. Neither genera is recorded in the fossil record of tropical America. The species-rich genus *Bathygobius* is today distributed circumglobally in reef-related tropical regions. It is about equally diverse in tropical America and the Indo-West Pacific. The morphological pattern of *Bathygobius* otoliths is well defined (see above), but its fossil record is extremely sparse. A single specimen of the extant *B. andrei* has been found in the Calabrian of Pacific Panama. Another single possible *Bathygobius* specimen has been described from the Serravallian of the Paratethys in Ukraine from a

near-reef environment (Schwarzhans et al., 2022). Thus, faunal exchange of gobies between America and the Indo-West Pacific must have also been rare and probably dates some time back in geological history because of the established diversity of species. A phylogenetic analysis of American *Bathygobius* species by Rodriguez-Rey et al. (2018) revealed the presence of species sister pairs on either side of tropical America caused by the emersion of the Isthmus of Panama and the separation of the American *Bathygobius* clades from the Indo-West Pacific ones at about 15 to 20 Ma. One could indeed imagine that a land connection around the North Pacific during a warm climate phase, such as the Miocene Climate Optimum (MCO) that occurred between 17 and 14 Ma, could have facilitated a (limited) faunal exchange of warm-water coastal fishes across the North Pacific. Another enigmatic distribution pattern that could be explained similarly has, for instance, been observed in Dinematichthyidae, where the Indo-West Pacific genus *Alionematichthys* is represented with one species, *A. minyomma* (Sedor & Cohen, 1987), in the Caribbean (Møller & Schwarzhans, 2008).

The fossil otolith-based record of gobies in tropical America does not contain any clear indication of impatriates, with the possible exception of *Gnatholepis gunae* (see above). The few otolith morphologies that cannot be directly related to extant gobiid genera in America are plausibly explained as extinct lineages within the Gobiosomatini, *Microgobius* group. It is of course always possible that their systematic position could be revised, particularly if articulated skeletons with otoliths in situ are found, but with our current understanding there is no reason to assume any of them represents an impatriate. Expatriate American fishes in the fossil record of Europe are known from a few groups, such as *Cynoscion* of Sciaenidae (see Schwarzhans, 2010) or *Verilus* of Acropomatidae (see Schwarzhans & Prokofiev, 2017; Agiadi et al., 2018; Schwarzhans, 2023). In gobies, expatriate American species in Europe are also rare, the most notable being *Bollmannia nubila*, which was originally described from the Langhian of the North Sea Basin by Schwarzhans (2010) and is now identified from the Aquitanian to Burdigalian of Brazil. Recently, Schwarzhans et al. (2022) described two otolith-based taxa from a near-reef environment in the Serravallian of western Ukraine that have been placed in a fossil genus (*Parenypnias* Schwarzhans, Klots & Kovalchuk, 2022) that has tentatively been interpreted to be of Gobiosomatini relationships. Considering the uniqueness of the environment from which the Ukrainian otoliths have been retrieved, such a relationship across the Atlantic to typical near-reef American gobiosomatine clades appears plausible. All in all, however, the Neogene otolith-based goby assemblages show a strong regional American composition with little evidence of exchange with other gobioid bioprovinces.

Conclusions and outlook

The rich otolith resources from the Neogene of tropical America have revealed that the American gobies, and in particular the Gobiosomatini, have a long history in the region and have represented a diverse and fast-evolving group since at least the Late Miocene (approximately 11 Ma). Here we identified otoliths representing 107 species of the family Gobiidae, of which 51 are new, 19 are extant that are also known as fossils, and 35 are in open nomenclature. The main results of our study are as follows:

1) We document as much as possible extant American gobiid otoliths and establish characteristics to distinguish their great taxonomic diversity by means of morphological analysis of their otoliths. We regard this approach as mandatory as basis for an integrated identification and evaluation of fossil otoliths, particularly for otoliths from Neogene strata.
2) Gobiids of the tribe Gobiosomatini are the most diverse today and also dominate the fossil otolith record in tropical America. The most common groups are from fishes living over soft bottoms or in deep water, which enhances fossilization and preservation, e.g., of the genera *Bollmannia*, *Microgobius*, *Antilligobius*, and *Palatogobius*. Groups adapted to abrasive environments like rocky shores or inhabiting environments unfavorable for otolith preservation such as reefs or mudflats are underrepresented.
3) The origination of the American goby association dates back to at least 22 Ma and probably not beyond 27 Ma. It exhibits a rapid pace of diversification, of which at least three phases can be identified in the Late Miocene (beginning of the Tortonian), the Early Pliocene (Zanclean), and the Early Pleistocene (Gelasian).
4) We also identify three phases of increased extinction in the evolution of American gobies that followed the diversification phases in the latest Miocene (Messinian), the Early to Late Pliocene interface (Piacenzian), and the late Early Pleistocene (Calabrian). The Piacenzian extinction phase seems to reflect environmental changes that occurred in the Caribbean after the final closure of the Central American Seaway. The Calabrian extinction phase seems to have been related to the change of the coral reef-building structure in the Caribbean.
5) Congruent with observations made in the other major biogeographic goby provinces (Atlantic-Mediterranean, Indo-West Pacific), the evolution of the gobies in America stayed mainly confined to the American continent with very little exchange with other regions. Exotic species are few, most notably

Gnatholepis gunae in the Tortonian of Pacific and Atlantic Panama.

6) Goby clades now restricted to the East Pacific such as the *Gillichthys* clade are identified in the West Atlantic, where they became extinct at the Early to Late Pliocene interface. Conversely, a species of the genus *Palatogobius* that today is only known from the West Atlantic has been found in the East Pacific as late as Early Pleistocene (Calabrian).
7) Because of the intimate ecological dependencies of many gobiid fishes, their fossil otoliths can be used as environmental indicators. Examples discussed here are from the Darien Basin and deep-water and near-reef settings.
8) Gobies can also be useful in determining the connectivity of basins, because they can make use of short-lived shallow-water connections or connections under variable and changing salinity conditions. Because of their enormous speciation power and tendency to react with endemic evolution in a short time, they are also ideally positioned to signal the separation of basins. For example, the faunal exchange between the East Pacific and West Atlantic is evident from goby otoliths throughout the Late Miocene but terminated at the latest in the Early Pleistocene.

We believe that despite the increase of knowledge from the reconnaissance of fossil gobiid otoliths in America that we present, several areas remain that offer important subjects for future research. First, a more continuous coverage in the Neogene of the East Pacific could be attempted. In particular, there is a complete lack of Pliocene gobiid otolith collections from this region. If such data were found, they could help to contribute substantially to the timing of the marine connectivity between the East Pacific and the West Atlantic. Another field of future research would be to close the recording gap in the earlier history of the tropical West Atlantic goby fauna ranging from the late Eocene to the late Early Miocene. A particularly promising area appears to be the prospection for sediments along the Mexican Gulf coast in the US and Mexico. The origination of the Gobiidae in America is still obscure and poorly understood. Finally, we hope that eventually fossil gobiid skeletons can also be found with otoliths in situ, since calibration of isolated otoliths is so important.

We furthermore believe that our study can contribute to a better understanding and interpretation of fossil goby otoliths in America in the future. We hope that our study will motivate fellow researchers to search for more fossil otoliths in the region and beyond.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-023-00302-5.

Additional file 1: Table S1. Character matrix of American goby otoliths.

Additional file 2: Table S2. Condensed gobiid otolith-based species in tropical America clustered for formations and regions. Unidentifiable specimens shown in grey. Blue denotes East Pacific locations; orange denotes West Atlantic locations.

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Author contributions

WS: conceptualization, identifications and descriptions, photography and drawings. OA: material acquisition, identifications, drawings and proofing.

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Availability of data and materials

All materials studied, described and figured in this manuscript has been registered and deposited in public institutional scientific collections. All other data are contained in the text.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

The authors give their consent for the publication of identifiable details to be published in the above Journal and Article. No further consents applicable.

Competing interests

The authors declare that there are no competing interests.

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