Swiss Journal of Palaeontology

RESEARCH ARTICLE

Fish otoliths from the early Miocene of Chile: a window into the evolution of marine bony fishes in the Southeast Pacific

Werner W. Schwarzhans[1,2]* and Sven N. Nielsen[3]

Abstract

Few fossil fish otolith associations have been described from the Pacific side of the Americas and, except for a single species (*Steindachneria svennielseni*), none have been described from Pacific South America south of the Central American tropical region. Here, we describe a rich otolith assemblage obtained from fifteen early Miocene outcrop locations along the Chilean coast from about 33°S to about 45°S. More than 2,000 specimens were studied resulting in the recognition of 67 species, with 27 being new to science. This assemblage represents an important new data point distant from any previously known otolith-based fish fauna, with the nearest coeval associations being from the Caribbean Province in Venezuela, which lies about 5000 km to the north, and New Zealand, which is about 9000 km to the west. The fauna represents a mixture of offshore and shallow water fishes and is rich in myctophids, paralichthyids (*Citharichthys*), ophidiids (*Lepophidium*), steindachneriids, and macrourids. Typical tropical American fishes are nearly completely absent, with the exception of *Steindachneria* and certain anguilliforms. The mesopelagic faunal component, chiefly Myctophidae, shows a striking resemblance to the well-known coeval fish fauna from New Zealand, and both are interpreted as representing an early South Pacific mesopelagic bioprovince. The strong correlation with the mesopelagic otolith-based fish fauna from New Zealand constricts the time interval of the sampled sediments to the middle Burdigalian (approximately 17.5 to 18.5 Ma). All otoliths obtained from the early Miocene of Chile relate to extant fish groups of the area and few exotic components not currently present in the East Pacific. The sole exception is a morpho-type described as *Navidadichthys* which has an unresolved relationship, possibly with the Prototroctidae, a family that is today endemic to the freshwater and nearshore marine environments of Australia and New Zealand. The new taxa are in the sequence of taxonomic description: *Pterothrissus transpacificus* n. sp., *Pythonichthys panulus* n. sp., *Chiloconger chilensis* n. sp., *Gnathophis quinzoi* n.sp., *Rhynchoconger chiloensis* n. sp., *Navidadichthys mirus* n. gen. et n. sp., *Maurolicus brevirostris* n. sp., *Polyipnus bandeli* n. sp., *Lampanyctus ipunensis* n. sp., *Physiculus pichi* n. sp., *Coelorinchus fidelis* n. sp., *Coelorinchus rapelanus* n. sp., *Nezumia epuge* n. sp., *Paracarapus chilensis* n. gen. et n. sp., *Lepophidium chonorum* n. sp., *Lepophidium mapucheorum* n. sp., *Sirembola supersa* n. sp., *Spectrunculus sparsus* n. sp., *Pseudonus humilis* n. sp., *Capromimus undulatus* n. sp., *Agonopsis cume* n. sp., *Cottunculus primaevus* n. sp., *Kuhlia orientalis* n. sp., *Citharichthys parvisulcus* n. sp., *Citharichthys vergens* n. sp., *Achirus australis* n. sp., *Achirus chungkuz* n. sp.

Keywords: Teleost otoliths, Burdigalian, Chile, Myctophidae, South America, New species

Introduction

Fossil otoliths are an important resource when attempting to reconstruct past teleost faunas. In many areas, such as New Zealand (Schwarzhans, 2019a, 2019b, 2019c), they represent nearly the only evidence concerning the evolution of bony fishes of the region. The same

---

is true for Chile, where, until now, Miocene bony fishes have been, with one exception, only reported based on skeletal remains from freshwater deposits (see Arratia, 2015 and references therein). Here, we describe a rich association of early Miocene fish otoliths from Chile, which, barring a single species previously described by Nolf (2002), represents the first record of its kind from the southeastern Pacific south of Ecuador. We investigated more than 2000 otolith specimens from the early Miocene of Chile resulting in the recognition of a total of 67 otolith-based fish species, of which 27 are new species and 22 remain in open nomenclature. The early Miocene otolith assemblages from Chile represent an important correlation point with the extraordinary rich and stratigraphically and ecologically diverse otolith-based fish fauna from New Zealand to the west (e.g., Grenfell, 1984; Schwarzhans, 1980, 2019a) and the tropical American otolith associations to the north, knowledge of which has expanded in recent years (e.g., Aguilera et al., 2016; Nolf, 1976; Nolf & Aguilera, 1998; Nolf & Stringer, 1992; Schwarzhans & Aguilera, 2013, 2016).

The otoliths were obtained from coastal sediment outcrops of four geological units (Navidad, Ranquil, and Lacui formations and Ipún beds) between 33°53′S and 44°35′S, thus spanning roughly 1200 km of north–south distance. Several of the locations are remote and difficult to access and many outcrops are restricted in areal size due to intense humid vegetation. Having been positioned along an active continental margin since long before Miocene times (see Oliveros et al., 2020; Encinas et al., 2021, and literature cited therein), the sedimentary environments are typified by narrow shelves and steep slopes; the latter characteristics are thought to be responsible for the contained fossil associations, which are often characterized by a mixture of shallow and deep-water faunal elements enhanced by down slope transportation or re-sedimentation (see below). The narrow shelf and adjacent open ocean/slope environment has been noted in the otolith assemblages of several studies in the Caribbean and Central/South American areas (Stringer, 1998; Nolf & Stringer, 1992, Aguilera & Rodrigues de Aguilera 2001).

Geological setting

The lower Miocene deposits of the Navidad Formation and its southern equivalents are among the most intensively studied in Chile. The Navidad Formation was briefly described from coastal bluffs and named by Charles Darwin (1846) during his voyage on HMS Beagle. He also collected several fossils from this formation and from the Chonos Archipelago, among others, which were described by G.B. Sowerby I. in that same work (see Griffin & Nielsen, 2008). Since that time, other geological units with similar faunas have been described; the Navidad Formation, being the most intensely studied, has come to serve as a regional lower Miocene reference unit in Chile. Geological units further south that have been shown to correlate with the Navidad Formation are the Ranquil Formation on the Arauco Peninsula just south of Concepción, the Lacui Formation of Chiloé Island, and the Ipún beds of the Chonos Archipelago. All these units share macrofaunal composition (Kiel & Nielsen, 2010; Philippi, 1887; Villafaña et al., 2019) and geological history (Encinas et al., 2018), and all, with the exception of the Ipún beds, also share the same biostratigraphic age (Finger, 2013), microfaunal composition (Finger, 2013; Finger et al., 2007), and strontium isotope age (Nielsen & Glodny, 2009). The Ipún beds have not yet been investigated for such data. Sediments of shallow-water origin were re-deposited at greater depth, occurring intercalated with deep-water sediments (Encinas et al., 2008, 2018; Finger et al., 2007). The otoliths described here were mostly obtained from the same localities as those reported in previous studies dealing with mollusks and foraminifera (e.g., Finger, 2013; Kiel & Nielsen, 2010; Nielsen & Glodny, 2009).

Navidad formation

There is a longstanding and complex debate over the stratigraphic age and depositional environment of the Navidad Formation. The expanded concept of the unit further inland and away from the type-region (Tavera, 1979) was later revised, and the name is now restricted to the coastal area (Encinas et al., 2006). While it was initially considered to be of Miocene age (Möricke, 1896), there was debate of the exact timing ranging from lower to uppermost Miocene due to misidentified planktonic foraminifera in some of those works (e.g., Ibaraki, 1992; Finger et al., 2007; see Finger, 2013). The current consensus, which is based on revised foraminifera biostratigraphy (Finger, 2013) and strontium isotope stratigraphy (Nielsen & Glodny, 2009; Gutierrez et al., 2013), is that it represents an Aquitanian to Burdigalian age. The numerical Ar/Ar-dating by Encinas (2006 cited by Gutierrez et al., 2013) is consistent with this conclusion. A single data point that led Gutierrez et al. (2013) to propose a middle Miocene age for a supposed "upper unit" needs verification. No faunal change of the foraminifera can be observed between their "units", and strontium ages from the "upper unit" agree with a lower Miocene age (locality PTA [see below], Nielsen & Glodny, 2009). The depositional environment of the Navidad Formation has originally been interpreted as representing relatively shallow water, mostly based on assessments of the mollusk fauna and sedimentary structures (Darwin 1846, Cecioni, 1978, 1980), but following the reassessment by Finger et al.

(2007) is now interpreted as representing rather deep water, with shallow-water sediments and biotic contents re-deposited at greater depth. While microfossils generally show mixed-depth assemblages at any given locality (Finger, 2013; Finger et al., 2007), localities with shallow- and deep-water mollusk associations can be clearly distinguished (Finger et al., 2007; Nielsen et al., 2004; Nielsen, 2005a). Localities interpreted to have been deposited in shallow water contain a subtropical fauna (Darwin 1846, Nielsen & Frassinetti, 2007a; Nielsen & Glodny, 2009).

Otolith-bearing localities and acronyms: RAP, blocks predominantly of brown sandstone fallen from the bluffs north of the Rapel River (Nielsen et al., 2004); PPP, grey fine sandstone from the intertidal platform at Punta Perro with mostly deep-water fauna (Nielsen & DeVries, 2002; Nielsen, 2005a); PPN, yellowish sandstone south of Punta Perro with the typical shallow-water Navidad macrofauna (Nielsen & Frassinetti, 2007b); PPS, a lens of coarse light-grey sandstone south of Punta Perro yielding common small brachiopods and the coral *Sphenotrochus* (Cairns, 2003); PTA, grey mudstone at Punta Alta with a peculiar deep-water fauna (Frassinetti & Covacevich, 1982); and MAT, greenish sandstone about 1 km north of Matanzas (Nielsen et al., 2004).

Ranquil formation

The Ranquil Formation was first described by Tavera (1942) and later formalized by García (1968), who attributed it to the Miocene based on its faunas of mollusks and foraminifera. It has been less intensely studied than the Navidad Formation, but foraminifera biostratigraphy (Finger, 2013), strontium isotope stratigraphy (Nielsen & Glodny, 2009), and mollusk fauna (Kiel & Nielsen, 2010) confirm it being equivalent to the Navidad Formation. At its type area near Ranquil, brown sandstones with abundant glauconite in some beds and grey mudstone are overlain by a thick, coarse-grained, light-grey sandstone (Pérez-Barría & Nielsen, 2020), forming deep dike injections going down from the base of the sandstone into the underlying deposits. This sandstone has been interpreted as being a result of a possible mega-tsunami backflow (Le Roux et al., 2008).

Otolith-bearing localities: FRM, light grey mudstone at Punta el Fraile on the north coast of Arauco (Nielsen et al., 2004, 2009; Nielsen, 2005b); RQS, coarse light-grey sandstone with reworked siltstone blocks at Punta Huenteguapi north of Ranquil (Le Roux et al., 2008; Nielsen, 2013), with the few recovered otoliths likely having come from those blocks; LEB, greenish sandstone from just north of Lebu (Groves & Nielsen, 2003; Nielsen et al., 2004).

Lacui formation

Deposits of the Lacui Formation are mostly known from Chiloé Island. Fossil-bearing deposits from that area were first mentioned by Darwin (1846) and later by Philippi (1887, 1897). Valenzuela (1982) proposed the name Lacui Formation for the sedimentary unit known from the Lacui Peninsula at the northwestern tip of Chiloé and described in some detail by Antinao et al. (2000) and Arenas and Duhart (2003). Here, we use the term Lacui Formation in the broad sense, which also includes the informal Cucao beds occurring south of Cucao, along the west coast of Chiloé (see Quiroz et al., 2004).

Otolith-bearing localities: CHO, grey sandstones on the southern side of Punta Chocoy, opposite Chiloé (Finger, 2013); CUC, mostly grey sandstone on the intertidal platform and fallen blocks from coastal bluffs south of Cucao (Nielsen et al., 2009).

Ipún beds

Fossiliferous sedimentary rocks from the Chonos Archipelago (Ipún, Lemo, and Stokes islands) have been known since Darwin (1846). Nielsen and Encinas (2014) provided a general description of the sequence, which mostly consists of sandstones, and interpreted the depositional environment as having deepened considerably through time from its base on Stokes Island to the highest parts on Ipún Island. The name Ipún beds was informally used by Encinas et al. (2018), who analyzed that unit in a broader geological context. Frassinetti (2001, 2004) described the mollusk fauna, which contains several warm-water taxa (Nielsen & Ampuero, 2020; Nielsen & Frassinetti, 2007b; Nielsen & Glodny, 2009; Rojas & Nielsen, 2020) and is generally similar to the units described above (Kiel & Nielsen, 2010).

Otolith-bearing localities: LEM01, fine sandstone with abundant solitary corals and shell debris just below a hardground on the northern side of Lemo; IPN14, brown sandstone on the northern coast of Ipún, about 200 m east of locality IPN13 of Nielsen and Encinas (2014); IPN16, brown to black sandstone, northern part of the east coast of Ipún (locality 5 of Frassinetti, 2004); IPN18, sandstone, just south of the previous locality (locality 4 of Frassinetti, 2004).

Geological unit	Locality	GPS coordinates
Navidad Formation	RAP	33°53′20″S/71°49′34″W
	PPP	33°54′15″S/71°50′13″W
	PPN	33°54′23″S/71°50′18″W
	PPS	33°54′39″S/71°50′38″W
	PTA	33°56′23″S/71°51′04″W
	MAT	33°56′55″S/71°51′59″W

Geological unit	Locality	GPS coordinates
Ranquil Formation	FRM	37°12′13″S/73°29′27″W
	RQS	37°30′19″S/73°35′23″W
	LEB	37°35′39″S/73°38′16″W
Lacui Formation	CHO	41°44′43″S/73°50′36″W
	CUC	42°42′28″S/74°08′10″W
Ipún beds	LEM01	44°38′36″S/74°42′39″W
	IPN14 (GPS for IPN13)	44°32′46″S/74°46′44″W
	IPN16	44°33′13″S/74°44′06″W
	IPN18	44°35′15″S/74°42′48″W

Materials and methods

The collected samples are all bulk samples, but they vary sigificantly in size (~0.5–50 kg) depending on outcrop size and visible macrofossil contents. Sediment samples were treated 24 h with 10% hydrogen peroxide, washed and sieved (mesh sizes 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm), dried, and hand-picked under a stereomicroscope.

All otoliths were studied with a reflected-light microscope. Photographs were taken remotely controlled from a computer with a Canon EOS 1000 mounted on the phototube of a Wild M400 photomacroscope at regular field-of-depth levels for each view. The individual photographs of each view were stacked using Helicon Soft's Helicon Focus software. The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast, or balance exposition, or retouch small inconsistencies, such as sand grains, incrustations, or pigmentation spots, insofar as doing so without altering the otolith morphology was possible. Particular care was taken to photograph inner and outer otolith faces with the central portion of the faces positioned at level to avoid the distortions that can otherwise occur in strongly bent specimens (for an explanation, see fig. 3.9 in Lombarte & Tuset, 2015).

The morphological terminology of sagittal otoliths (hereafter, "otolith") follows Koken (1884), with amendments by Chaine and Duvergier (1934) and Schwarzhans (1978). Measurements were taken either with the help of a camera lucida mounted on the microscope or from photographs obtained from the photomacroscope. The following abbreviations are used for expressing ratios: OL = otolith length, OH = otolith height, OT = otolith thickness, CaL = cauda length, CaH = cauda height, CCL = length of caudal colliculum, OsL = ostium length, OsH = ostium height, OCL = length of ostial colliculum, OCH = height of ostial colliculum, CCH = height of caudal colliculum, SuL = sulcus length, SuH = sulcus height, and SCL = length of colliculum in case of lack of differentiation of ostial and caudal colliculi.

Types and other materials are deposited in the following institutions: SGO.PV—Vertebrate Paleontology Collection, Museo Nacional de Historia Natural, Santiago, Chile; additional material is also deposited in the Paleontology Collection, Universidad Austral de Chile, Valdivia, Chile.

Systematic section

The higher classification of teleosts is in flux due to molecular gene analyses having become commonplace in phylogenetic studies. This increasingly dynamic state has led to challenges to many of the traditional arrangements in the higher classification of fishes, most notably in Percomorphi and Perciformes (e.g., Wiley & Johnson, 2010; Betancur et al., 2013, 2017; Chen et al., 2014; Miya & Nishida 2014, and most recently Hughes et al., 2018). In the following accounts, we follow Nelson et al. (2016), but, in the sequence of description, we follow an arrangement consistent with that of Nelson (2006), that is, Ophidiiformes after Gadiformes, Scorpaeniformes before Perciformes, and Gobiiformes and Pleuronectiformes at the end (Figs. 1, 2).

Order Albuliformes

Family Pterothrissidae

Genus *Pterothrissus* Hilgendorf, 1877

Pterothrissus transpacificus n. sp.
(Fig. 3a, b).

Holotype: Fig. 3b, SGO.PV.1593, Navidad Formation, north of Rio Rapel (RAP).

Paratypes: 2 specimens, SGO.PV.1594, same data as holotype.

Name: Named after the occurrence of the species across the Pacific Ocean from its nearest relatives in Japan and New Zealand.

Diagnosis: Rounded rectangular outline with shallow dorsal rim and pronounced postdorsal angle. OL:OH = 1.5–1.65. Sulcus distinctly supramedian, slightly inclined at angle of 8 to 10°. CaL:OsL = 1.2–1.25. Inner face distinctly convex; outer face less convex than inner face.

Description: Moderately sized, probably not fully mature otoliths up to 3.5 mm length (holotype) with a rounded rectangular outline. OL:OH = 1.5–1.65; OH:OT = 2.8–3.0. Dorsal rim shallow, horizontal, with obtuse mediodorsal hump and expanded postdorsal projection; ventral rim regularly curved, deepest anterior
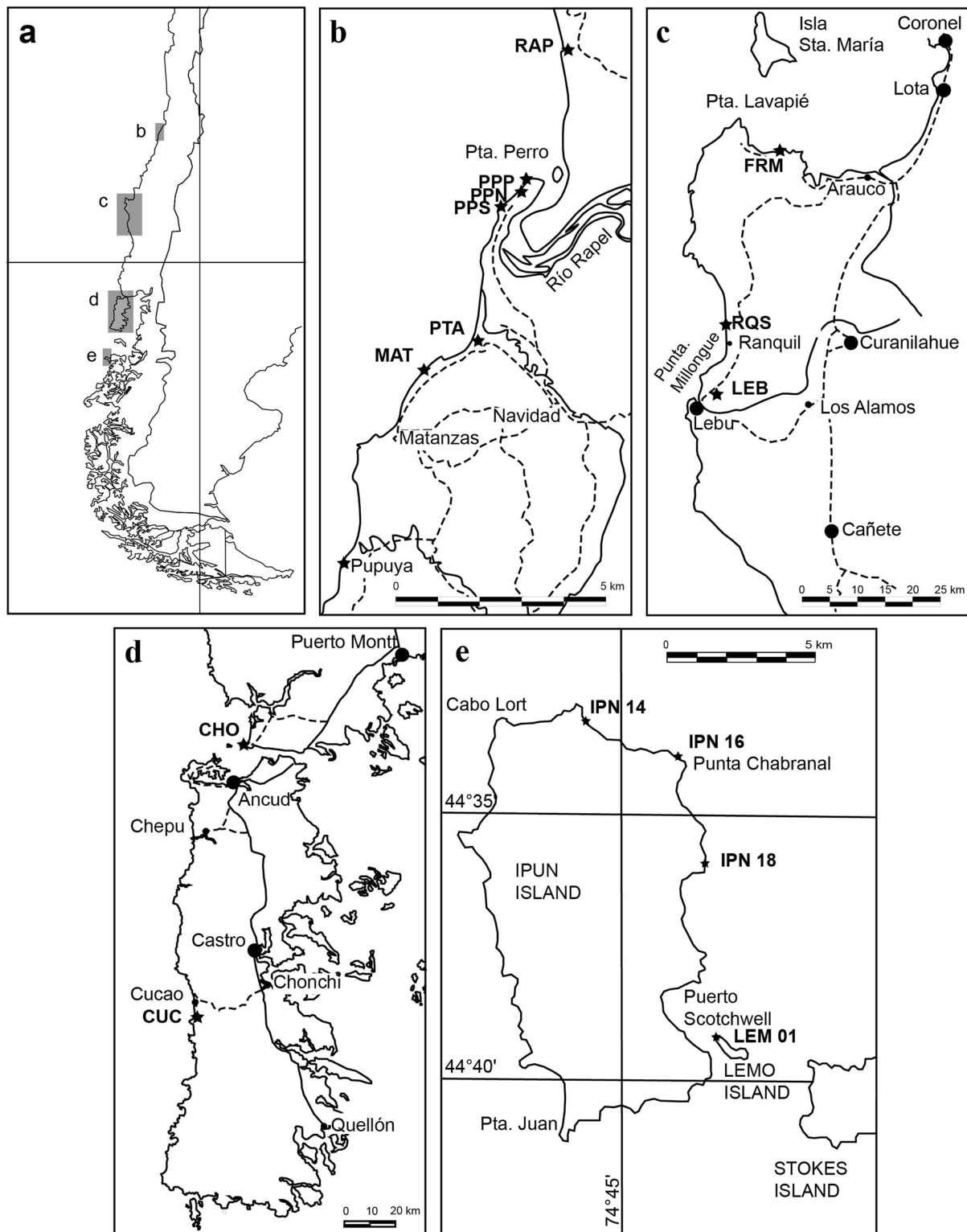
Fig. 1 Location plate; **a** General map of southern South America south of 28°S; shaded areas mark inserted detail maps; **b** map for Navidad Formation localities; **c** map for Ranquil Formation localities; **d** map for Lacui Formation localities; **e** map for Ipún beds localities
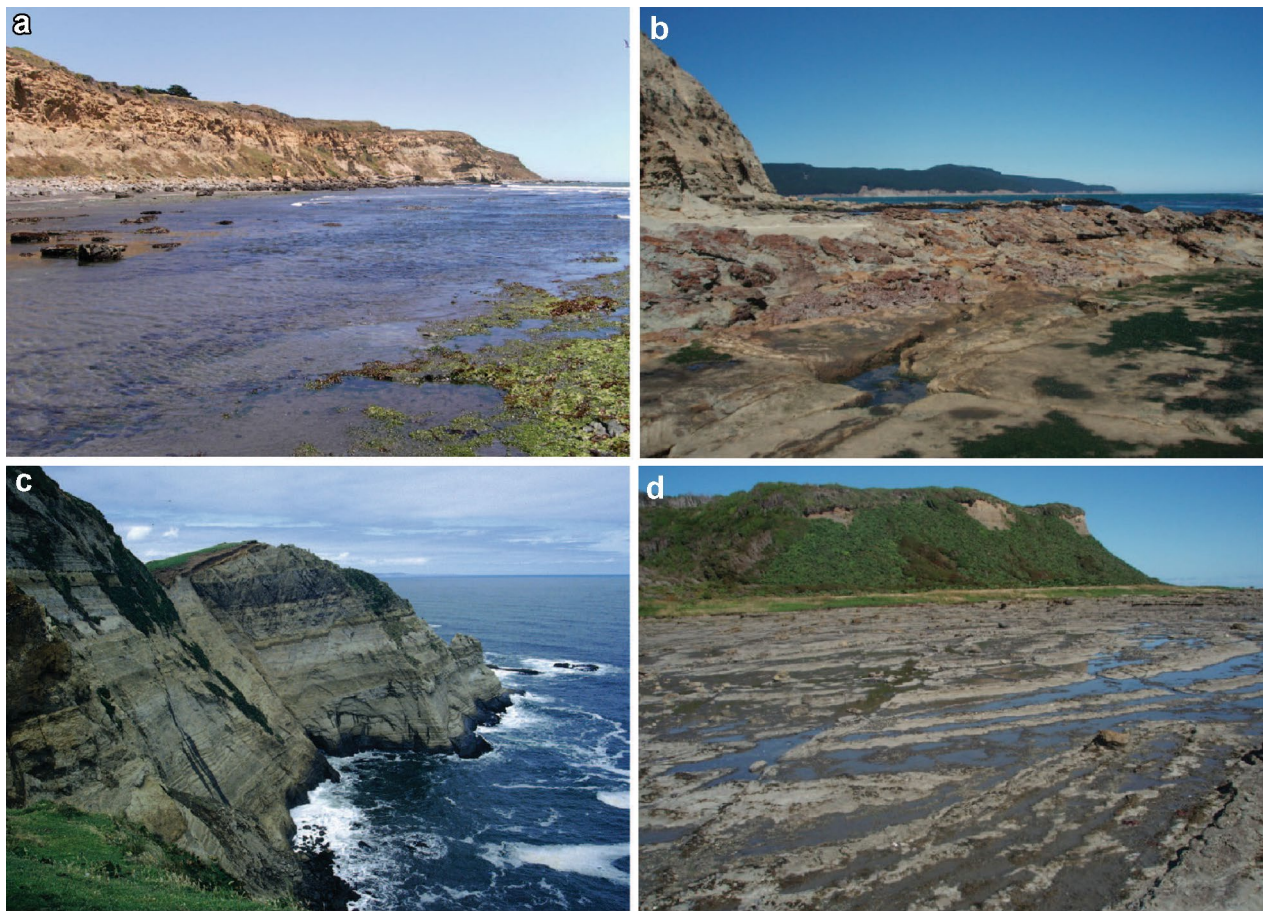
Fig. 2 Selected photographs of outcrops; **a** Navidad Formation, Punta Perro, intertidal platform of locality PPP, and locality PPN in the back slightly higher in the bluff; **b** Ranquil Formation, intercalation of brown and green (glauconitic) sandstone at locality RQS, bluff in the back at Caleta Millongue; **c** Lacui Formation forming bluffs south of Cucao, locality CUC is the intertidal platform below high tide water level; **d** Ipún beds on Ipún Island at Punta Juan

of its middle; anterior and posterior rims blunt, ventrally rounded and continuous with ventral rim, dorsally pronounced.

Inner face distinctly convex with long, distinctly supramedian, slightly inclined sulcus (8–10°). Ostium shorter and wider than cauda, indistinctly opening anteriorly and dorsally. CaL:OsL = 1.2–1.25; OsH:CaH = 1.7–2.2. Cauda terminating at considerable distance from posterior rim of otolith. Dorsal depression broad, distinct. Ventral field wide, smooth except many faint radial furrows and no ventral furrow parallel to ventral rim of otolith. Outer face nearly flat or at least much less convex than inner face, nearly smooth or poorly ornamented.

Discussion: The genus *Pterothrissus* is restricted presently to two species on the deep shelf off Japan and West Africa (the latter now placed in a genus of its own: *Nemoossis* Hidaka et al., 2017), with this distribution clearly representing a secondary relict endemism. The Pterothrissidae are an early teleost family known since late Early Cretaceous (Schwarzhans, 2018) and showed a wide, nearly cosmopolitan distribution during the Paleogene and early Neogene (Schwarzhans, 2019a). *Pterothrissus transpacificus* is the first fossil record of the genus and family in the Neogene of the eastern Pacific. It differs from its congeners known from the Paleogene and Miocene of Japan, Australia, New Zealand, and Europe in the shallow dorsal rim with its broad central hump, the relatively smooth surface and the outer face being flat and the inner face being distinctly more convex.
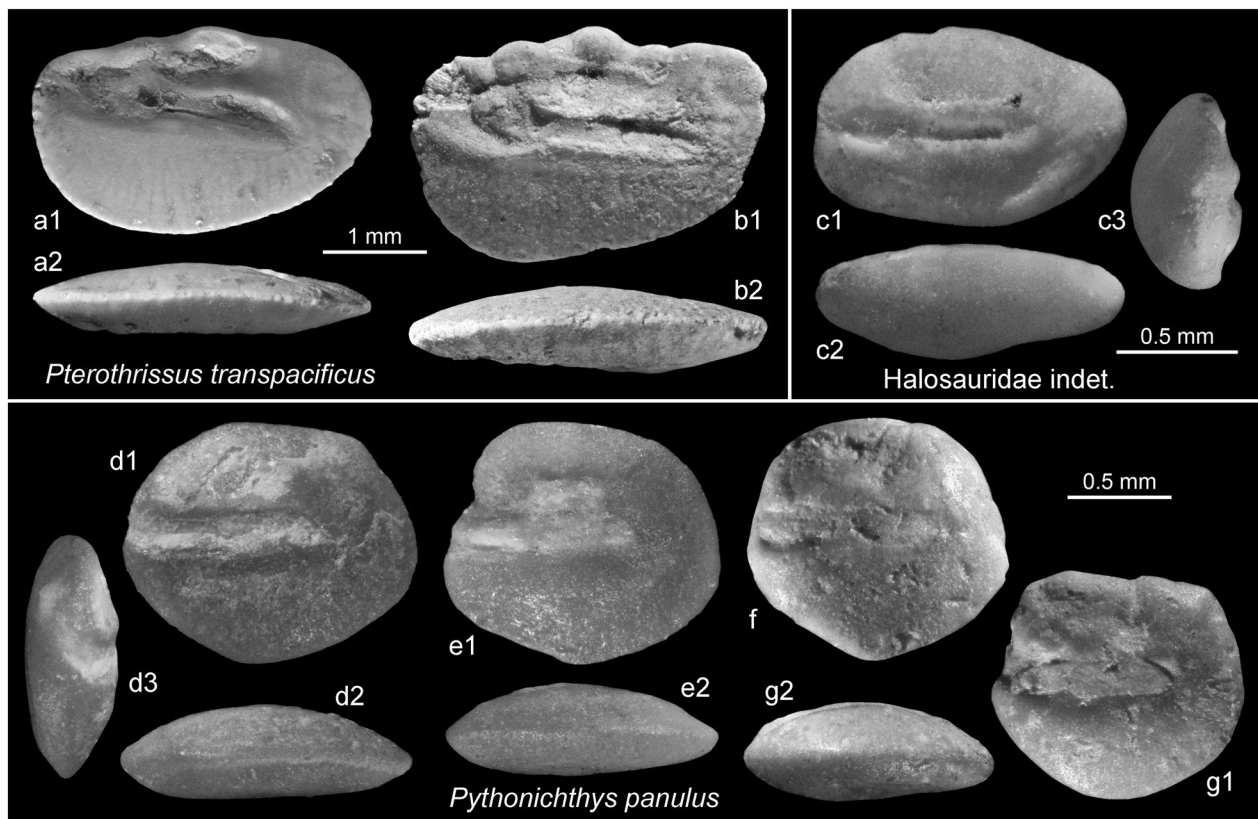
Fig. 3 *Pterothrissus transpacificus* n. sp. RAP (reversed); **a** paratype, SGO.PV.1593; **b** holotype, SGO.PV.1594. **c** Halosauridae indet., PPP, SGO.PV.1595. *Pythonichthys panulus* n. sp.; **d** holotype (reversed), CUC, SGO.PV.1596; **e)** paratype, CUC, SGO.PV.1597; **f**, **g** paratypes (g reversed), LEB, SGO.PV.1598

Order Nothacanthiformes

Family Halosauridae

Genus indet

Halosauridae indet
(Fig. 3c).

Material: 1 specimen, SGO.PV.1595, Navidad Formation, Punta Perro (PPP).

Discussion: A single, well-preserved robust small otolith of about 1.3 mm length. OL:OH = 1.55; OH:OT = 1.85. The relatively flat inner face shows a centrally positioned, narrow, somewhat deepened sulcus, with the ostium slightly wider but shorter than the cauda and nearly opening to the anterior rim of the otolith. The dorsal depression is distinct and deepened towards the ridge-like crista superior. A broad and deep ventral furrow is also well developed. The outer face is strongly convex giving the otolith a robust appearance and smooth. This otolith appears to represent a halosaurid (see Nolf, 2013 for figures) of unresolved affinities until more and larger specimens have been found.

Order Anguilliformes

Suborder Anguilloidei

Family Heterenchelyidae

Genus *Pythonichthys* Poey, 1868

***Pythonichthys panulus* n. sp.**
(Fig. 3d–g).

Holotype: Fig. 3d, SGO.PV.1596, Lacui Formation, Chiloé (CUC).

Paratypes: 16 specimens; 9 specimens, same data as holotype, SGO.PV.1597, 6 specimens Ranquil Formation from Lebu (LEB), SGO.PV.1598, and 1 specimen Navidad Formation from Punta Perro (PPN), SGO.PV.1721.

Name: From panulus (Latin) = small bread, bread roll, as an allegory to the appearance of these small otoliths.

Diagnosis: Small, round, compact otoliths with strongly convex inner face and nearly flat outer face. OL:OH = 1.05–1.2; OH:OT = 2.4–2.8. Ventral rim regularly curved; dorsal rim with slightly flattened central portion. Sulcus narrow, anteriorly open, terminating distant from posterior rim. Colliculi smooth, shallow, undivided. OL:SuL = 1.4–1.5.

Description: Small, almost circular, compact otoliths up to 1.4 mm in length (holotype). All rims regularly curved; dorsal rim commonly with slightly flattened central portion of varying extend. All rims sharp with dorsal rim sometimes thickened at central portion, smooth.

   Inner face strongly convex and smooth with feeble dorsal depression and no ventral furrow. Sulcus narrow, short, slightly supramedian, anteriorly open but without incision of anterior rim, shallow, filled with an undivided colliculum. Colliculum sometimes with indication of equally long ostium and cauda and not anteriorly open. Outer face smooth and flat or slightly convex.

Discussion: Heterenchelyid otoliths exhibit few characters for diagnosis, which, therefore, largely depends on subtle ratios of the otolith outline and the thickness and proportions of the sulcus. Likewise, distinction of the otoliths of the two known genera (*Panturichthys* and *Pythonichthys*) is only tentatively defined, with those of the genus *Pythonichthys* usually being somewhat thinner than those of *Panturichthys*. Today, heterenchelyids are geographically restricted to the tropical shores of both Americas, West Africa, and the Mediterranean. In the fossil record, a much wider distribution pattern as has been noted by Schwarzhans (2019a) and is evident with one species recently having been described from time-equivalent strata of New Zealand—*Panturichthys grenfelli* Schwarzhans, 2019a, 2019b, 2019c. *Pythonichthys panulus* differs from the New Zealandian species in being more compressed (OL:OH = 1.05–1.2 vs 1.2–1.3) and having a narrower and shorter sulcus (OL:SuL = 1.4–1.5 vs 1.3–1.4). In addition, a single otolith, *Pythonichthys* sp., was described by Schwarzhans (2019a) from the Altonian (= Burdigalian) of New Zealand; this otolith is more elongate (OL:OH = 1.55) and rather thin with a very short sulcus (OL:SuL = 1.8).

Suborder Congroidei

Family Congridae

Genus *Chiloconger* Myers & Wade, 1941

***Chiloconger chilensis* n. sp.**
(Fig. 4a, b).

Holotype: Fig. 4b, SGO.PV.1599, Navidad Formation, Matanzas (MAT).

Paratypes: 2 specimens, SGO.PV.1600; Navidad Formation from Punta Perro (PPS).

Name: Referring to Chile.

Diagnosis: Compressed otoliths with distinct predorsal lobe. OL:OH = 1.3–1.45. Inner face distinctly convex, smooth. Sulcus short, its cauda slightly bent and its ostium with vertical ostial channel. OL:SuL = 1.55–1.7. Sulcus inclination angle 2–5°. No distinct dorsal depression; ventral furrow distinct, close to ventral rim of otolith.

Description: Deeply bodied, compressed otoliths with distinct predorsal lobe and regularly curved ventral rim up to 6.6 mm length (holotype 3.25 mm). OL:OH = 1.3–1.45; OH:OT = 2.5–2.8. Dorsal rim with slightly concave section between predorsal lobe and low postdorsal angle. Anterior rim broadly rounded, posterior rim rounded, less broadly than anterior rim. All rims smooth.

   Inner face strongly convex, smooth, with slightly supramedian positioned, mildly inclined, short sulcus. Ostium short, not much widened, anteriorly fading, with broad, vertically directed ostial channel meeting the anterior-dorsal rim just before predorsal lobe. Ostium slightly deepened or shallow, not clearly separated from cauda with undivided colliculum. Cauda slightly bent with broadly rounded posterior termination. Dorsal depression very weak and indistinct; ventral field smooth except for long ventral furrow close to ventral rim of otolith. Outer face slightly convex to flat in large specimens, sometimes with mild umbo, smooth.

Discussion: *Chiloconger* is known from two extant species—*C. dentatus* (Garman, 1899) from the tropical eastern Atlantic and *C. philippinensis* Smith & Karmo*v*skaya, 2003 from the Philippines (for figures of the otoliths of both species see Schwarzhans, 2019b), and one tentatively assigned fossil otolith-based species—*C.? yazooensis* (Nolf & Stringer 2003) from the late Eocene of the US Gulf Coast. Bathymyrine otoliths are characterized by the distinct predorsal lobe and most genera also by the shape of the sulcus (see Schwarzhans, 2019b). Within Bathymyrinae, the otoliths of *Chiloconger* are recognized by a relatively simple and short cauda when compared to the other genera of the subfamily, which has been interpreted by Schwarzhans (2019b) as a plesiomorphic character state in the group. *Chiloconger chilensis* differs from *C.? yazooensis* in the slightly bent caudal tip (vs straight), the more pronounced postdorsal angle, and the presence of a ventral furrow (vs absent). Of the two extant species
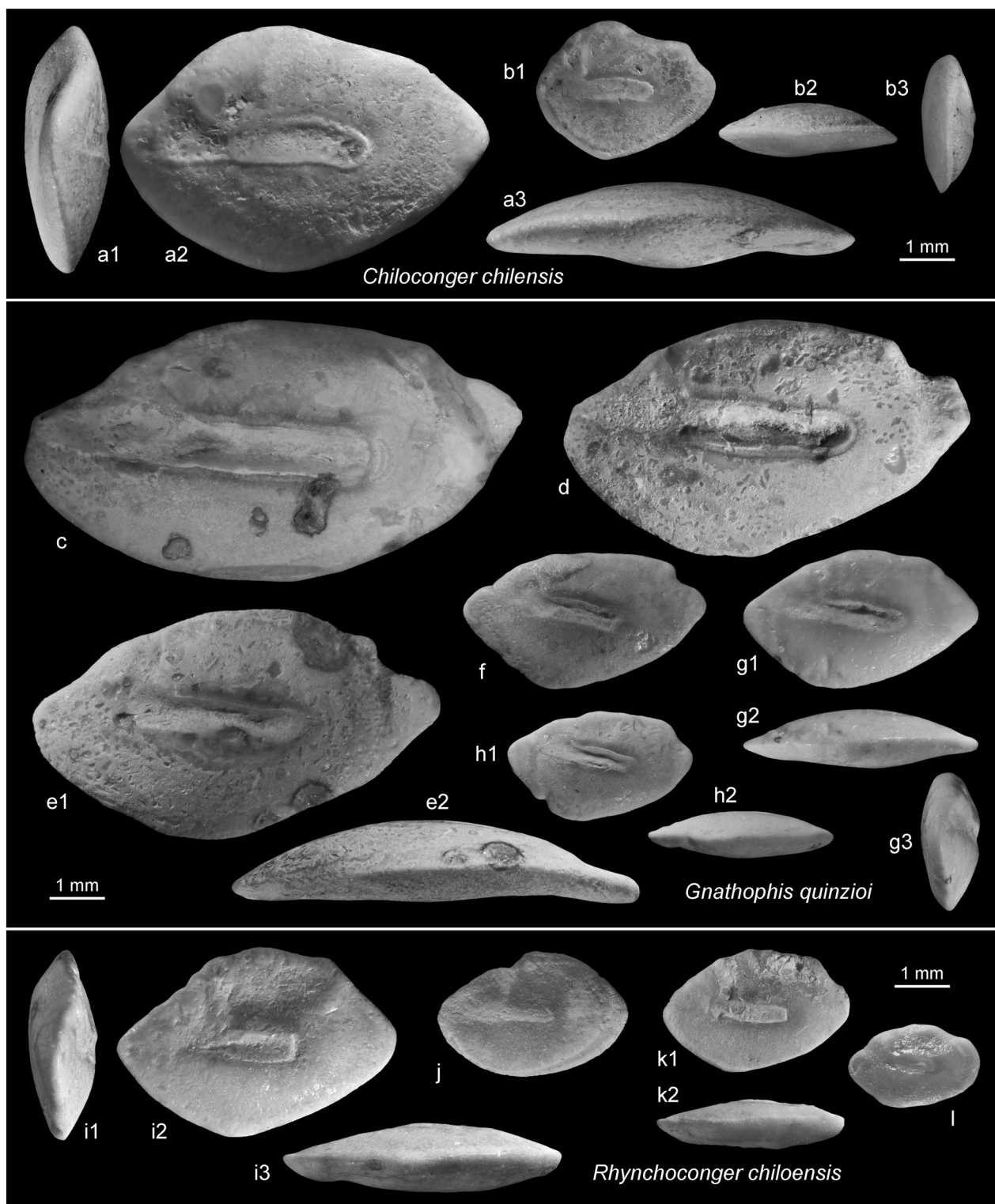
Fig. 4 *Chiloconger chilensis* n. sp. (reversed); **a** paratype, PPS, SGO.PV.1599; **b** holotype, MAT, SGO.PV.1600. *Gnathophis quinzioi* n. sp. PPS; **c, d, f–h** paratypes (c reversed), SGO.PV.1601; **e** holotype, SGO.PV.1602. *Rhynchoconger chiloensis* n. sp.; **i** holotype, PPS, SGO.PV.1603; **j** paratype, MAT, SGO. PV.1604; **k, l** paratypes, CUC (l reversed), SGO.PV.1605

those of *C. dentatus* are the most similar differing also in the straight cauda and the inner face being convex to the same degree as the outer face (vs inner face strongly convex and outer face flat to slightly convex).

Genus *Gnathophis* Kaup, 1859

Gnathophis quinzioi n. sp.
(Fig. 4c–g).

Holotype: Fig. 4e, SGO.PV.1601, Navidad Formation, Punta Perro (PPS).

Paratypes: 22 specimens, SGO.PV.1602; same data as holotype.

Further material: 29 specimens Navidad Formation: 3 specimens, Rio Rapel (RAP), 2 specimens, Punta Perro (PPP), 19 specimens, Punta Perro (PPN), 1 specimen, Punta Alta (PTA), 4 specimens, Matanzas (MAT).

Name: Named in honor of paleontologist and regional geologist Luis Arturo Quinzio Sinn (Universidad de Concepción) for introducing the junior author to Chilean paleontology.

Diagnosis: Elongate otoliths with pointed and supramedian positioned anterior and posterior tips and distinct postdorsal angle. OL:OH = 1.7–1.9, increasing with size. Inner face distinctly convex; outer face slightly convex to slightly concave. Sulcus with wavy ventral margin, its ostium reaching close to anterior-dorsal rim of otolith with short vertical ostial channel. OL:SuL = 1.5–1.9. Sulcus inclination angle 6–10°. No distinct dorsal depression; no distinct ventral furrow.

Description: Relatively slender and thin otoliths reaching up to 9 mm length (holotype 7.4 mm). OL:OH = 1.7–1.9, increasing with size; OH:OT = 2.3–2.8, decreasing with size. Anterior and posterior tips distinctly supramedian positioned, relatively sharp, posterior tip set off dorsally by slight concavity from postdorsal angle. Dorsal rim shallow, anteriorly often depressed, middorsally broadly rounded or flat and with distinct postdorsal angle. Ventral rim regularly curving, deepest anterior of its middle. All rims smooth.

Inner face distinctly convex, relatively smooth, with supramedian positioned, moderately short and distinctly inclined sulcus. Ventral sulcus margin wavy as defined in Schwarzhans (2019b). Ostium short, not widened, anteriorly fading, and reaching close to anterior-dorsal rim of otolith, with broad-based, tapering, short vertically directed ostial channel. Cauda somewhat deepened, with straight dorsal and wavy ventral margin; its tip rounded and slightly dorsally pronounced. Dorsal depression very weak or absent; ventral field smooth, much wider than dorsal field, without ventral furrow. Outer face slightly convex in small specimens becoming flat or slightly concave in large specimens, smooth.

Discussion: This is a typical species of the genus *Gnathophis* characterized by shape and inclination of the sulcus, the short ostial channel, and the absence of a dorsal depression. *Gnathophis quinzioi* resembles most *G. ornatus* (Frost, 1928) from the late Oligocene and early Miocene of New Zealand and probably represents a vicariant species. It differs from *G. ornatus* in the generally more elongate shape (OL:OH = 1.7–1.9 vs 1.55–1.75) and the more pointed anterior and posterior tips, particularly with the short concave section of the dorsal rim between postdorsal angle and posterior tip. *Gnathophis quinzioi* is a common species in the northern locations in the Navidad Formation but has not been found in the Ranquil and Lacui formations, which are located to the south.

Genus *Rhynchoconger* Jordan & Hubbs, 1925

Rhynchoconger chiloensis n. sp.
(Fig. 4i–l).

Holotype: Fig. 4i, SGO.PV.1603, Navidad Formation, Punta Perro (PPS).

Paratypes: 16 specimens: 2 specimens SGO.PV.1722, same data as holotype; 2 specimens SGO.PV.1723, Punta Perro (PPP); 1 specimen SGO.PV.1604, Matanzas (MAT); 1 specimen SGO.PV.1724, Ranquil Formation, Lebu (LEB); 10 specimens SGO.PV.1605, Lacui Formation, Chiloé (CUC).

Name: Named after Chiloé, where this species is the most common congrid in the early Miocene.

Diagnosis: Rhombical otoliths with centrally positioned pointed anterior and posterior tips. OL:OH = 1.5–1.55. Inner and outer faces moderately convex. Sulcus short, positioned at center of inner face, with distinct, long vertical ostial channel. OL:SuL = 2.2–2.4. Sulcus inclination

angle 0–4°. Broad and distinct dorsal depression; faint ventral furrow close to ventral rim of otolith.

Description: Relatively compressed otoliths of nearly rhomboid outline reaching up to 5 mm length (holotype). OL:OH = 1.5–155; OH:OT = 2.4–2.8. Anterior and posterior tips pointed, positioned on central otolith axis. Dorsal rim high, with more or less rounded, closely positioned pre- and postdorsal angles. Ventral rim regularly curving, deepest at rounded angle anterior of its middle. All rims smooth except middorsal section sometimes slightly undulating.

  Inner face moderately convex, with centrally positioned, short, may or may not be slightly inclined sulcus terminating far from anterior and posterior tips of otolith. Ostium short, not widened, anteriorly much reduced and fading, with distinct and long vertically directed ostial channel. Cauda short, straight with well-defined colliculum with blunt termination. Dorsal depression broad, distinct; ventral furrow feeble, close to ventral rim of otolith. Outer face moderately convex to the same degree as inner face, smooth.

Discussion: *Rhynchoconger chiloensis* is remarkable for its short sulcus which terminates far from the anterior tip of the otolith. In this respect, it resembles *R. nitens* (Jordan & Bollman, 1890), the only extant species of the genus in the tropical East Pacific, while all other extant and fossil *Rhynchoconger* species and *Macrocephenchelys brevirostris* (Chen & Wang, 1967) from the West Pacific show a comparatively longer sulcus reaching further to the anterior rim of the otolith (see Schwarzhans, 2019b for otolith figures). *Rhynchoconger chiloensis* differs from *R. nitens* in being slightly more compressed (OL:OH = 1.5–1.55 vs 1.65), showing a slightly longer sulcus (OL:SuL = 2.2–2.4 vs 2.5–2.6) and the presence of pre- and postdorsal angles (vs a single middorsal angle). We interpret the two species to belong to a lineage within *Rhynchoconger* separated from other congeners already by early Miocene.

Order Clupeiformes

Family Prystigasteridae

Genus *Opisthopterus* Gill, 1861

***Opisthopterus* sp.**
(Fig. 5a).

Material: A single, broken and poorly preserved specimen of about 3.7 mm length from the Navidad Formation of Punta Perro (PPP), SGO.PV.1606.

Discussion: *Opisthopterus* is a widespread genus in the Pacific, with the center of diversity in the tropical East Pacific (Whitehead, 1985). This is only the third fossil otolith record of the family, after *Neopisthopterus* sp. and *Pellona* sp. recorded from the early Miocene of Venezuela by Nolf and Aguilera (1998), and the first fossil occurrence of the genus.

Family Clupeidae

Genus indet

Clupeidae indet
(Fig. 5b).

Material and discussion: A total of 20 otolith fragments of one or more unidentifiable clupeid species have been found in the Navidad Formation (SGO.PV.1607) from Rio Rapel, Punta Perro and Matanzas and in the Lacui Formation of Punta Chocoi and Cucao.

Order Galaxiiformes

Family Prototroctidae?

Genus *Navidadichthys* n. gen.

Type species: *Navidadichthys mirus* n. sp., by original designation and monotypy.

Name: Named after the Navidad Formation.

Diagnosis: A fossil otolith-based genus, presumably of the family Prototroctidae with the following combination of characters: Small otoliths up to 2.8 mm length with subtriangular outline with a shallow ventral rim and a high, forward inclined dorsal rim with expanded broad predorsal lobe. OL:OH = 1.05–1.25. Anterior tip blunt; posterior tip distinctly inferior, pointed. Inner face distinctly convex; outer face flat to concave. Sulcus supramedian, long, anteriorly open, with slightly widened, short ostium and narrow, long cauda with bent tip terminating close to posterior-dorsal rim. CaL:OsL = 1.5–1.6; OsH:CaH = 1.3–1.5.

Discussion: Otoliths are known from all teleost families and most genera occurring along the shores of Chile and the tropical East Pacific, and none of them show any convincing similarity with this enigmatic morphological pattern. Extensive research into published otolith literature and unpublished extant otoliths available to one of the authors has revealed but one possible candidate as a potential relative, namely *Prototroctes maraena* Günther,
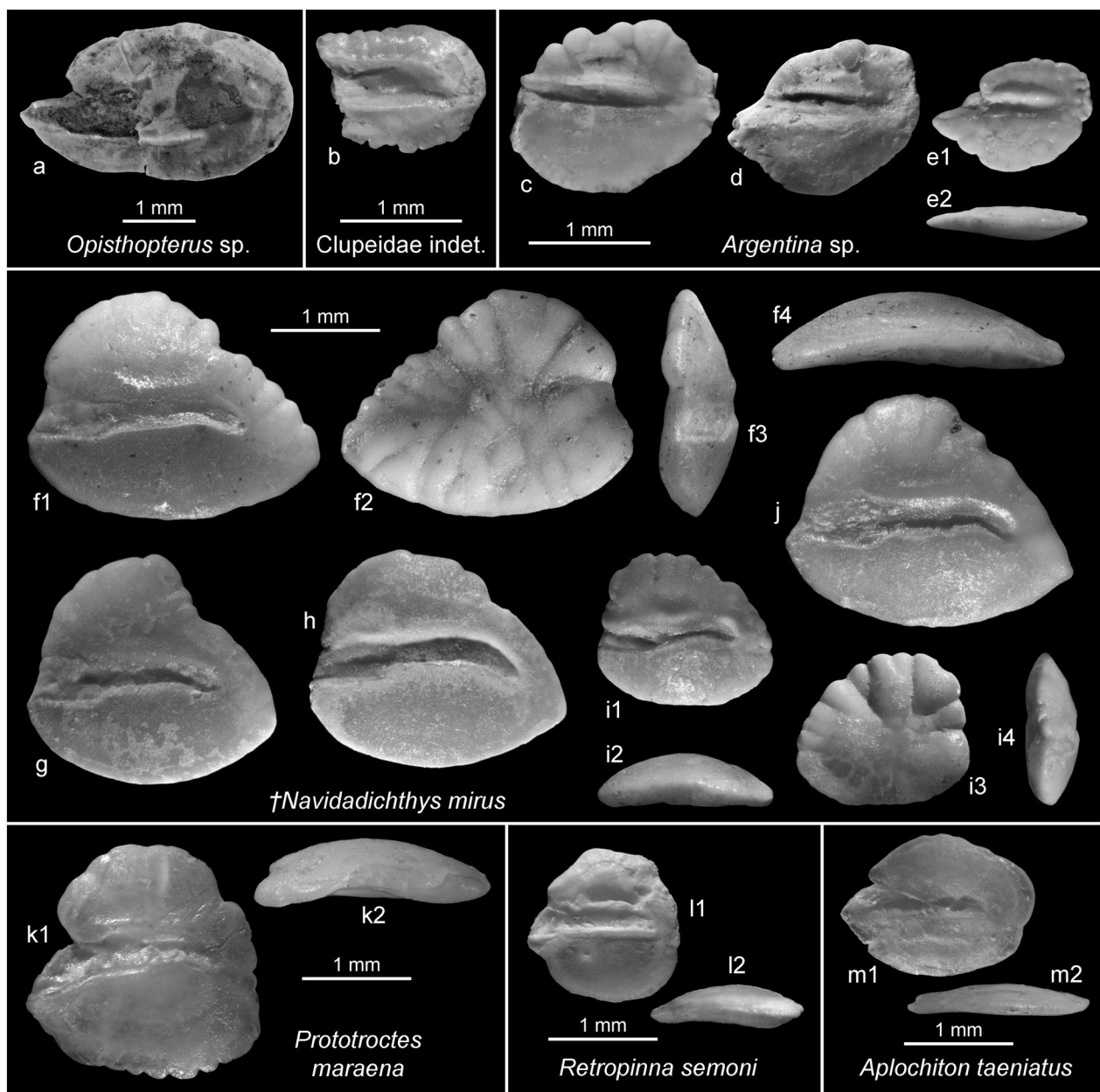
Fig. 5 a *Opisthopterus* sp.; PPP (reversed, digitally merged broken specimen), SGO.PV.1606. **b** Clupeidae indet., RAP, SGO.VP.1607. **c–e** *Argentina* sp., reversed; **c, d** CUC; SGO.PV.1608; **e** RAP, SGO.PV.1609. **f–j** *Navidadichthys mirus* n. gen., n. sp.; **f** holotype (reversed), PPN, SGO.PV.1610; **g** paratype, MAT, SGO.PV.1611; **h–j** paratypes (j reversed), PPN, SGO.PV.1612. **k** *Prototroctes maraena* Günther, 1864, Recent, New South Wales, Australia, coll. Schwarzhans, leg. AMS. **i** *Retropinna semoni* (Weber, 1895), Recent, South Australia, coll. Schwarzhans, leg. SAMA. **m** *Aplochiton taeniatus* Jenyns, 1842, Recent, southern Chile, coll. Schwarzhans, leg. N. Colin

1864 (Fig. 5k), an amphidromous fish from temperate southern Australia. The family Prototroctidae further contains the possibly extinct *P. oxyrhynchus* Günther, 1870 from New Zealand and two fossil otolith-based species from the early Miocene of New Zealand—*P. vertex* Schwarzhans, 2012 and *P. modestus* Schwarzhans, 2012 (both in Schwarzhans et al., 2012). *Navidadichthys* n.

gen. shares with *Prototroctes* the high and expanded dorsal rim, the sulcus with an only mildly widened, anteriorly open sulcus, and the narrow, distally bent cauda terminating close to the posterior rim of the otolith. Otoliths of the related Retropinnidae with anadromous and potamodromous species in southern Australia and New Zealand are also similar but lack the distinct bent

of the caudal tip (e.g., *Retropinna semoni* (Weber, 1895), Fig. 5l). Otoliths of the more distantly related Galaxiidae, which exhibit a similar lifestyle, also feature a generally similar sulcus organization but usually with a shorter and straight cauda and a more regular triangular outline. Today, galaxiids occur primarily in Australia and New Zealand, but a few species can be found in South Africa and South America. We have here figured for comparison an otolith of the endemic Pacific South American genus *Aplochiton*—that is *Aplochiton taeniatus* Jenyns, 1842 (Fig. 5m)—which, however, differs in the very short and straight cauda, which is shorter than the ostium. *Navidadichthys* differs from all extant galaxiiform otoliths in the combination of the relatively shallow ventral rim, the much expanded and forward positioned predorsal lobe, and the long cauda with the distinctly bent tip. We interpret *Navidadichthys* as representing a separate lineage of South American galaxiiforms that is now extinct and that may be most closely related to the Prototroctidae of temperate Australia and New Zealand.

Navidadichthys mirus n. sp.
(Fig. 5f–j).

Holotype: Fig. 5f, SGO.PV.1610, Navidad Formation, Punta Perro (PPN).

Paratypes: 20 specimens: 19 specimens SGO.PV.1612, same data as holotype; 1 specimen SGO.PV.1611, Matanzas (MAT).

Further material: 29 specimens Navidad Formation: 8 specimens, Rio Rapel (RAP), 5 specimens, Punta Perro (PPP), 3 specimens, Punta Perro (PPN), 6 specimens, Punta Perro (PPS), 7 specimens, Matanzas (MAT).

Name: From mirus (Latin) = amazing, remarkable, referring to the unexpected occurrence of this otolith morphology in South America.

Diagnosis: See diagnosis of genus (monospecific genus).

Description: Small otoliths up to 2.8 mm length (holotype). OH:OT = 1.05–1.25; OH:OT about 3.0. Outline subtriangular, with massive predorsal lobe and relatively regularly curved ventral rim. Section of dorsal rim behind predorsal lobe depressed or even concave. Anterior rim blunt, nearly vertical, with short, blunt, very inferior rostrum. Posterior tip much more pronounced, relatively sharp, likewise very inferior like rostrum, below level of tip of cauda. Inclination angle of anterior rim 70–80°, of posterior rim 45–55°. Dorsal rim irregularly and variably crenulated; ventral rim smooth.

Inner face strongly convex with long and narrow sulcus positioned near central axis of otolith. Sulcus anteriorly open with relatively short ostium. Ostium relatively narrow ventrally more widened than dorsally, often with clearly defined colliculum. Cauda longer, narrower, somewhat deepened, usually with less clearly defined colliculum, distinctly bent at its tip and terminating close to posterior-dorsal otolith rim. CaL:OsL = 1.5–1.6; OsH:CaH = 1.3–1.5. Inclination angle of bent caudal Sect. 30–35°. Dorsal depression small, only above anterior, horizontal part of cauda, Some short, often feeble radial furrows ingressing onto inner face from dorsal crenulation. Ventral field wide, smooth, with faint ventral furrow very close to ventral rim of otolith. Outer face slightly concave, with radial furrows of variable intensity particularly on dorsal half.

Distribution: *Navidadichthys mirus* is a relatively common species in the northern locations of the Navidad Formation but it is missing from the Ranquil and Lacui formations in the south.

Order Argentiniformes

Family Argentinidae

Argentina Linnaeus, 1758

Argentina sp.
(Fig. 5c–e).

Material: 6 specimens: 3 specimens, SGO.PV.1609, Navidad Formation, Rio Rapel (RAP); 3 specimens, SGO.PV.1608, Lacui Formation, Chiloé (CUC).

Discussion: All *Argentina* specimens are either small, juvenile (Fig. 5e) or incomplete (Fig. 5c, d), and thus, do not warrant an unambiguous identification to species level. It must be noted, however, that *Argentina subfrigida* Schwarzhans, 1980 has commonly been recorded from the late Oligocene and early Miocene of New Zealand and it is possible that the specimens from the early Miocene of Chile represent the same or a closely related species.

Order Stomiiformes

Family Gonostomatidae

Genus *Margrethia* Jespersen & Tåning, 1919
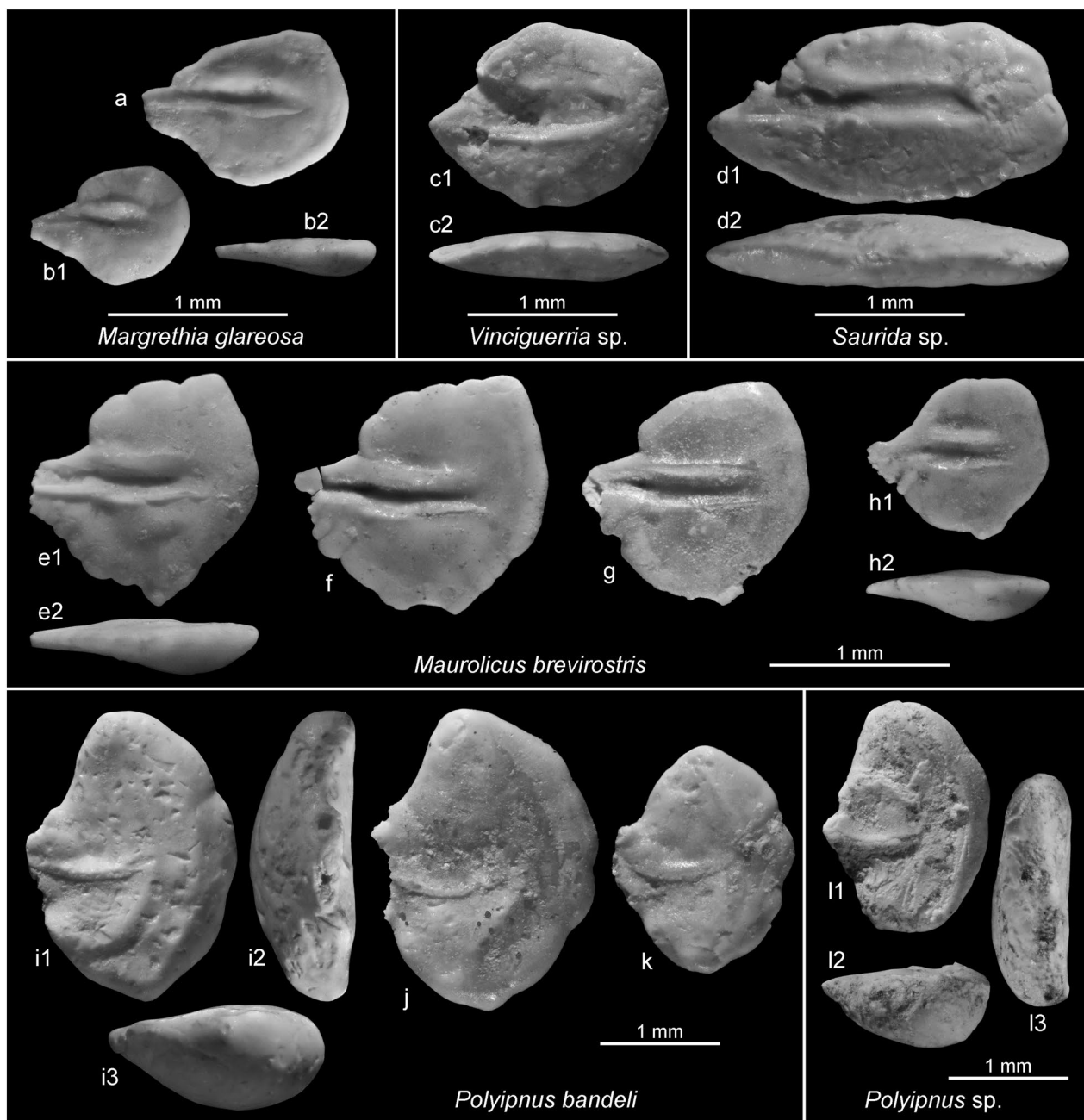
Fig. 6 **a**, **b** Margrethia glareosa (Schwarzhans, 1980); **a** MAT, SGO.PV.1613; **b** RAP, SGO.PV.1614. **c** *Vinciguerria* sp., CHO (reversed), SGO.PV.1615. **d** *Saurida* sp., PPS (reversed), SGO.PV.1616. **e–h** *Maurolicus brevirostris* n. sp., RAP; **e** holotype (reversed), SGO.PV.1617; **f–h** paratypes (f, g reversed), SGO. PV.1618. *Polyipnus bandeli* n. sp.; **i** holotype (reversed), PPS, SGO.PV.1619; **j**, **k** paratypes (k reversed), PPN, SGO.PV.1620. **l** *Polyipnus* sp., PPP (reversed), SGO.PV.1621

Margrethia glareosa (Schwarzhans, 1980)
(Fig. 6a, b).
1980—*Polymetme glareosus*—Schwarzhans: Fig. 55.
2019a—*Margrethia glareosa* (Schwarzhans, 1980)—Schwarzhans: Fig. 45.1–4.

Material: 2 specimens, Navidad Formation: 1 specimen, SGO.PV.1614, Rio Papel (RAP); 1 specimen, SGO.PV.1613, Matanzas (MAT).

Discussion: *Margrethia glareosa* is a relatively rare species in the late Burdigalian of New Zealand characterized

as a gonostomatid by the sag of the central portion of the lower margin of the cauda. Other diagnostic characters are the narrow ostium, distinct postdorsal expansion and anterior-ventral concavity underpinning a moderately long rostrum. For a detailed description see Schwarzhans (2019a).

Family Phosichthyidae

Genus *Vinciguerria* Jordan & Evermann, 1896

Vinciguerria? sp.
(Fig. 6c).

Material: 2 specimens: 1 specimen SGO.PV.1725, Navidad Formation, Punta Perro (PPP); 1 specimen SGO.PV.1615, Lacui Formation, Punta Chocoi (CHO).

Description: Based on the two small otoliths, the length does not seem to exceed 1.6 mm in length. OL:OH = 1.25; OH:OT = 3.7. Dorsal rim somewhat expanded anteriorly, regularly declining posteriorly; ventral rim deeply curving, irregularly undulating. Anterior tip with pointed but rather short rostrum and minute antirostrum; posterior tip broadly rounded, dorsally shifted. Rostrum length about 20% of OL.

Inner face relatively flat with slightly supramedian sulcus. Ostium anteriorly slightly widening, open, slightly deepened, distinctly longer than short cauda. Cauda tapering with rounded tip, terminating moderately far from posterior rim of otolith. OL:SuL = 1.2; OsL:CaL = 1.7. No distinct dorsal depression; no ventral furrow.

Discussion: These otoliths are characterized by a short rostrum compared to its congeners and because of that is only tentatively allocated with *Vinciguerria*. Nolf and Brzobohaty (2002) described a similar species with a relatively short rostrum from the late Burdigalian of France as *Vinciguerria brevis* Nolf & Brzobohaty, 2002.

Family Sternoptychidae

Genus *Maurolicus* Cocco, 1838

Maurolicus brevirostris n. sp.
(Fig. 6e–h).

Holotype: Fig. 6e, SGO.PV.1617, Navidad Formation, Rio Rapel (RAP).

Paratypes: 6 specimens SGO.PV.1618, same data as holotype.

Further material: 34 specimens, same data as holotype.

Name: Combination of brevis (Latin) = short and rostris (Latin) referring to the diagnostic short rostrum of the species.

Diagnosis: High bodied, compressed otoliths; OL:OH = 1.0–1.1. Ostium and rostrum short. Rostrum 22–27% of OL. Cauda with sag of ventral margin just behind collum.

Description: Small, high bodied, delicate, and fragile otoliths up to about 1.5 mm length (holotype with incomplete rostrum, 1.3 mm). OL:OH = 1.0–1.1; OH:OT = 3.3–4.0. Rostrum very fragile and rarely completely preserved, comparatively short (22–27% of OL), broad without underlying concavity of anteroventral rim of otolith, slightly supramedian positioned. Antirostrum above right-angled excisura, broad, blunt. Dorsal rim ascending from antirostrum to much expanded postdorsal angle in more or less straight line. Posterior rim blunt, nearly vertical, broadly rounded at level of sulcus, ventrally curving continuously into ventral rim. Ventral rim very deep, with variably expressed central spine positioned anterior of vertical line through postdorsal angle; anterior section of ventral rim straight below rostrum, slightly bulged before reaching the ventral spine. Dorsal and ventral rim broadly undulating or crenulated, anterior section of ventral rim more intensely and finely crenulated; posterior rim mostly smooth.

Inner face nearly flat, with slightly supramedian, slightly deepened narrow sulcus. Ostium short, narrow, joining cauda at collum below excisura. Cauda longer, straight but with slight ventral sag at its beginning behind collum, with fading tip terminating at some distance from posterior rim of otolith. OL:SuL = 1.2–1.25; CaL:OsL = 1.5–1.8. Dorsal depression wide, ventrally marked by distinct crista superior. Ventral furrow very faint or absent, running far from ventral rim of otolith. Short radial furrows extending onto inner face, particularly anterior-ventrally. Outer face mildly convex with broad postcentral umbo, rather smooth with few short radial furrows.

Discussion: *Maurolicus brevirostris* differs from the time-equivalent *M. aegrotus* Schwarzhans, 1980 from New Zealand in the short rostrum (22–27% of OL vs 33–38% of OL) without underlying concavity of the anterior-ventral rim (vs present), which is also expressed in the lower index OL:OH of 1.0–1.1 (vs 1.1–1.15). Both species likely represent allopatric vicariant species across the southern Pacific without direct relationship to extant species. Extant fishes of the genus *Maurolicus* have undergone significant taxonomic changes over the last decades. Grey (1964) collapsed 13 previously described nominal species into the single cosmopolitan *Maurolicus muelleri* (Gmelin, 1789), because she could not identify clear distinguishing morphological

characters. In a review of the genus *Maurolicus*, Parin & Kobylianski (1996) resurrected six of the previously recognized species and described nine additional new species, thus reaching a total of 15 valid species showing distinct geographical regionalization. Recently, Rees et al. (2020) criticized the morphological definitions of Parin & Koblylianski and suggested only four valid species synonymizing several of the species established by them based on molecular analyses (with five additional nominal species not having been available for molecular analysis). The fossil finds are still too insufficient to allow for an in-depth analysis, but the presence of two morphologically clearly distinct species on either side of the southern Pacific during the early Miocene indicates that some degree of regionalization may have occurred in the geological past. It is also remarkable that *M. brevirostris* is only known from a single location in Chile, where, however, it occurs in relatively large numbers.

Genus *Polyipnus* Günther, 1887

Polyipnus bandeli n. sp.
(Fig. 6i–k).

Holotype: Fig. 6i, SGO.PV.1619, Navidad Formation, Punta Perro (PPS).

Paratypes: 5 specimens, Navidad Formation, Punta Perro: 3 specimens (PPP) SGO.PV.1726, 2 specimens (PPN) SGO.PV.1620.

Name: Named in honor of paleontologist Klaus Bandel (Universität Hamburg), doctoral committee chair and mentor of the junior author who casually put him on a path to work on and in Chile.

Diagnosis: High bodied, "half-moon shaped", compressed otoliths; OL:OH not measurable (fragile rostrum not preserved in any specimen). Dorsal and ventral rims nearly symmetrical; posterior rim regularly curved, broadly undulating. Antirostrum very weak or not developed. Dorsal rim of cauda fading; cauda terminating far from posterior rim of otolith. Posterior furrow running far from posterior rim.

Description: Otoliths very high. massive, posteriorly thickened, "half-moon shaped", reaching about 2.5 mm in height (holotype 2.4 mm). OL:OH not measurable (fragile rostrum not preserved in any specimen), otolith length measured from concavity above antirostrum to OH = 0.6–0.7; OH:OT = 2.8. Dorsal rim very high with prominent mediodorsal projection; predorsal rim steeply declining, straight or slightly concave, and smooth.

Ventral symmetrical to dorsal rim with prominent midventral projection and steeply ascending, nearly straight preventral rim. Posterior rim very regularly curving, broadly undulating. Rostrum broken on all recovered specimens; no or very feeble antirostrum.

Inner face flat with sulcus positioned along horizontal axis. Ostium missing (positioned on broken-off rostrum); cauda short, about as short as section behind cauda to posterior rim, wide, dorsally fading. Caudal colliculum marked only by ridge-like ventral margin. Furrow leading from concavity behind antirostrum diagonally to cauda. Furrow running parallel to posterior rim touching caudal tip at midsection, ridge situated further towards posterior rim. Outer face smooth, strongly convex posteriorly, becoming very thin anteriorly towards broken rostrum.

Discussion: *Polyipnus bandeli* differs from *P. plebeius* Grenfell, 1984 from the early Miocene of New Zealand in the anterior-ventral rim being straight as compared to distinctly bulged, the lack of a distinct antirostrum, a shorter cauda terminating further from the posterior rim of the otolith, and consequently the posterior furrow running further away from the posterior rim.

Polyipnus sp.
(Fig. 6l).

Material: 5 specimens SGO.PV.1621, Navidad Formation, Punta Perro (PPP).

Discussion: In addition to *P. bandeli* a second species seems to occur in the Navidad Formation of Chile characterized by an even more compressed shape and a very wide cauda. However, the available otoliths are too poorly preserved for a species definition.

Order Aulopiformes
### Family Synodontidae
Genus *Saurida* Valenciennes, 1849
Saurida sp.
(Fig. 6d).

Material: 4 specimens Navidad Formation: 1 specimen SGO.PV.1727, Punta Perro (PPP); 2 specimens SGO.PV.1616, Punta Perro (PPS); 1 specimen SGO.VP.1728, Punta Alta (PTA).

Discussion: These are typical specimens of the genus *Saurida*. However, they are very small and mostly poorly preserved, which prohibits specific identification.
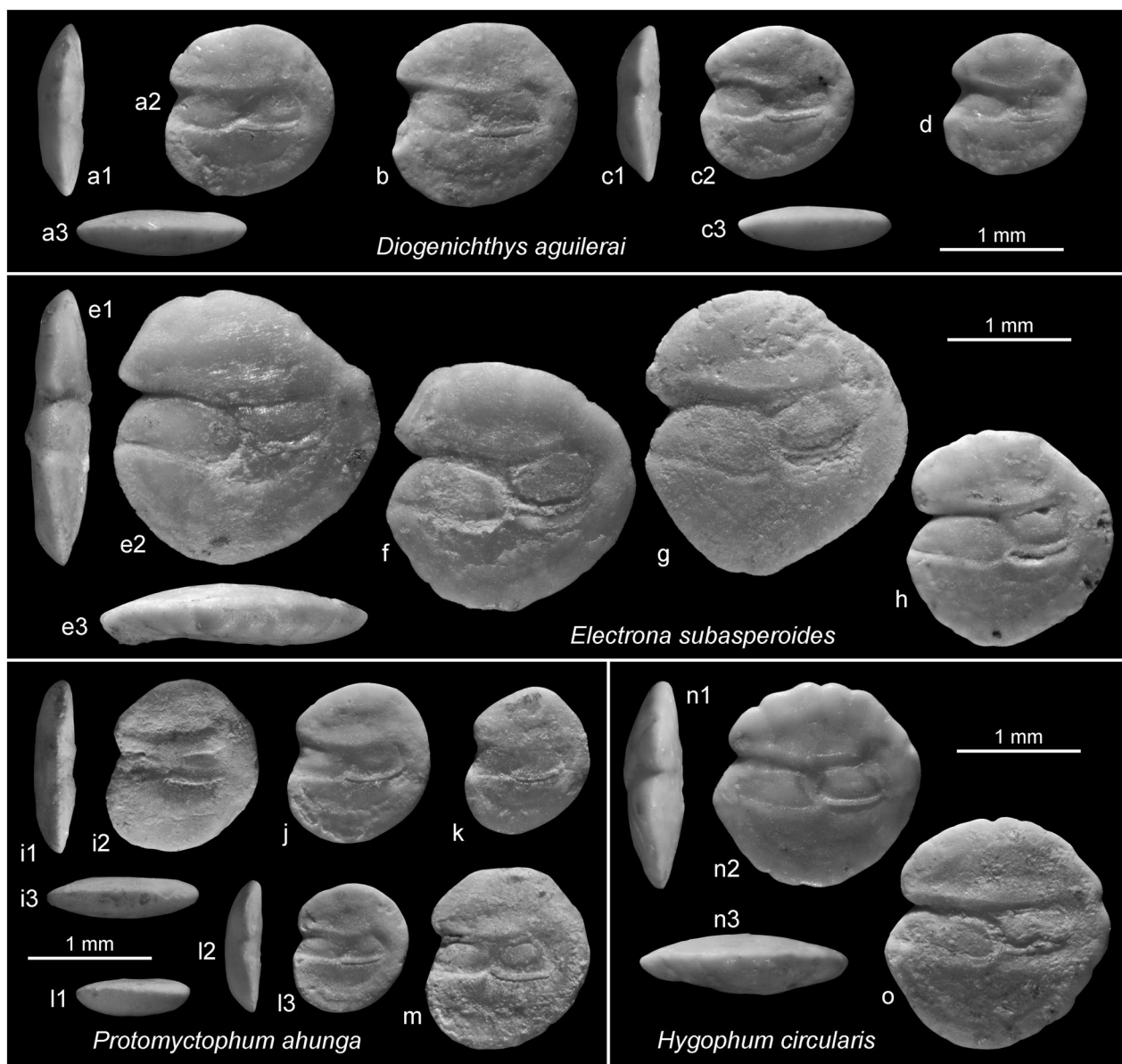
Fig. 7 a–d *Diogenichthys aguilerai* Schwarzhans, 2013, PPN (a, b reversed), SGO.PV.1622. **e–h** *Electrona subasperoides* Schwarzhans, 2019, PPP (g reversed), SGO.PV.1623. **i–m** *Protomyctophum ahunga* Schwarzhans, 2019, PPP (k reversed), SGO.PV.1624. **n–o** *Hygophum circularis* (Frost, 1924); **n** PPN, SGO.PV.1625; **o** FRM, SGO.PV.1626

Order Myctophiformes

Family Myctophidae

Subfamily Myctophinae

Genus *Diogenichthys* Bolin, 1939

***Diogenichthys aguilerai* Schwarzhans, 2013**
(Fig. 7a–d).

?2013—*Diogenichthys* sp.—Schwarzhans & Aguilera: pl. 2, fig. 3.
2013c—*Diogenichthys aguilerai*—Schwarzhans: pl. 2, figs. 4–5.
2019a—*Diogenichthys aguilerai*—Schwarzhans, 2013—Schwarzhans: fig. 50.12.

Material: 110 specimens: 96 specimens Navidad Formation: 3 specimens, Rio Rapel (RAP); 7 specimens, Punta Perro (PPP); 66 specimens (figured specimens SGO.PV.1622), Punta Perro (PPN); 6 specimens, Punta Perro

(PPS); 1 specimen, Punta Alta (PTA); 13 specimens, Matanzas (MAT); 5 specimens Ranquil Formation: 3 specimens, Ranquil (RQS); 2 specimens, Punta El Fraile (FRM); 2 specimens, Lacui Formation, Cucao (CUC); 7 specimens Ipún beds, Ipún Island: 3 specimens, IPN 14; 4 specimens, IPN 16.

Discussion: *Diogenichthys aguilerai* was originally described from the Burdigalian of Angola by Schwarzhans (2013c) and later also from the late Oligocene to early Miocene of New Zealand (Schwarzhans, 2019a) based on a relatively limited number of specimens. It may also be present in the Burdigalian of Trinidad if a record described by Schwarzhans and Aguilera (2013) as *Diogenichthys* sp. could be verified by more specimens. It has now been identified as the third most common myctophid in the early Miocene of Chile. It is an inconspicuous myctophid species rarely exceeding 1 mm in length (the largest specimen, found in New Zealand, is 1.9 mm long) with a nearly perfectly round outline interrupted only by a wide and moderately deep excisura. Ostium and cauda are of nearly equal length and height. The cauda shows a long and relatively straight ventral pseudocolliculum. The ventral furrow runs parallel to the ventral otolith rim at some distance from it. The large number of specimens now available from Chile show relatively little variation and confirm that the specimens from Angola and New Zealand fall well within the variability spectrum. Furthermore, the records from Chile indicate that *D. aguilerai* was likely a widely distributed, potentially cosmopolitan myctophid species during the latest Oligocene and early Miocene of the southern hemisphere.

Genus *Electrona* Goode & Bean, 1896

Electrona subasperoides Schwarzhans, 2019
(Fig. 7e–h).
2019a—*Electrona subasperoides*—Schwarzhans: fig. 50.3–8.

Material: 63 specimens, Navidad Formation, Punta Perro: 61 specimens SGO.PV.1623, PPP; 2 specimens SGO.PV.1729, PPS.

Discussion: *Electrona subasperoides* is a fairly common myctophid species during the late Oligocene and early Miocene of New Zealand and now also commonly recorded from the Navidad Formation of Chile. It is easily recognized by the high bodied appearance with a ratio OL:OH of 0.87–0.97, the anteriorly expanded and posteriorly depressed dorsal rim and the wide ostium with the sinuate ventral margin.

Genus *Hygophum* Bolin, 1939

Hygophum circularis (Frost, 1924)
(Fig. 7n–o).
1924—*Scopelus circularis*—Frost: fig. 2.
1933—*Scopelus circularis* Frost, 1924—Frost: figs. 11–12.
1980—*Hygophum* aff. *circularis* (Frost, 1924)—Schwarzhans: fig. 110.
2019a—*Hygophum* aff. *circularis* (Frost, 1924)—Schwarzhans: fig. 50.9–11.

Material: 2 specimens: 1 specimen SGO.PV.1625, Navidad Formation, Punta Perro (PPN); 1 specimen SGO.PV.1626, Ranquil Formation, Punta El Fraile (FRM).

Discussion: *Hygophum circularis* differs from *Electrona subasperoides* in the more regularly curved dorsal rim, the slightly less high bodied shape (OL:OH = 0.97–1.05 vs 0.87–0.97) and the narrower ostium with a more regularly formed ventral margin. It has previously been described from the late Burdigalian to early Langhian of New Zealand.

Genus *Protomyctophum* Fraser-Brunner, 1949

Protomyctophum ahunga Schwarzhans, 2019
(Fig. 7i–m).
1980—*Diogenichthys* sp.—Schwarzhans: Fig. 100.
2019a—*Protomyctophum ahunga*—Schwarzhans: Fig. 51.1–5.

Material: 21 specimens: 19 specimens Navidad Formation: 1 specimen SGO.PV.1730, Rio Rapel (RAP); 18 specimens SGO.PV.1624, Punta Perro (PPP); 2 specimens SGO.PV.1731, Lacui Formation, Cucao (CUC).

Discussion: *Protomyctophum ahunga* is recognized by the very high bodied shape (OL:OH = 0.83–0.93, mostly < 0.9), the deep ventral rim with its deepest point distinctly in front of its midpoint and ostium and cauda being of almost equal length. *Protomyctophum ahunga* has been described from the late Burdigalian (Altonian) of New Zealand and is relatively common in the early Miocene of Chile, again showing a trans-southern Pacific distribution pattern of mesopelagic, oceanic fishes during the early Miocene.

Subfamily Lampanyctinae

Genus *Ceratoscopelus* Günther, 1864

Ceratoscopelus sp.
(Fig. 8a, b).
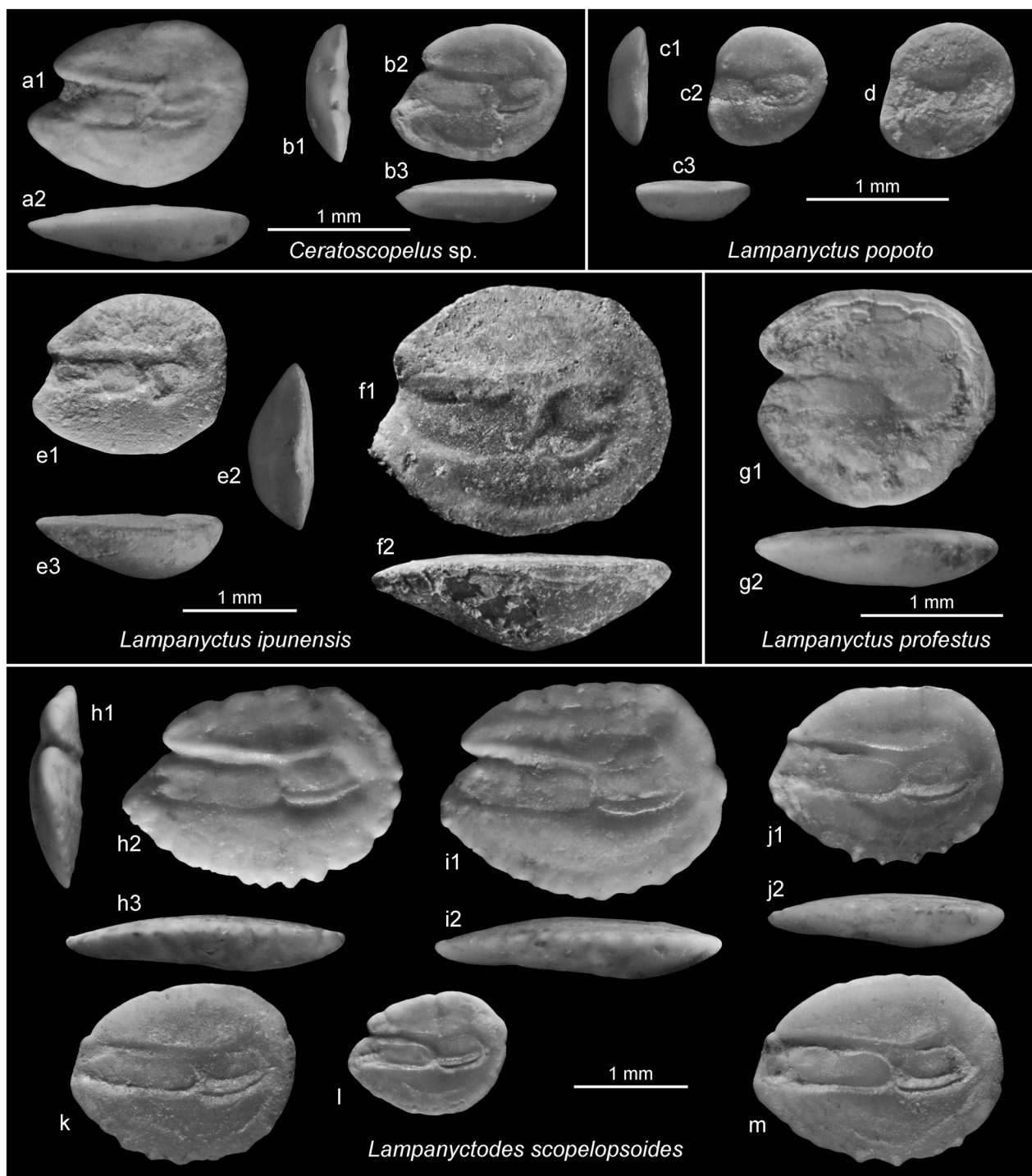
Fig. 8 a, **b** *Ceratoscopelus* sp.; **a** FRM, SGO.PV.1627; **b** CUC (reversed), SGO.PV.1628. **c–d** *Lampanyctus popoto* Schwarzhans, 2019, PPP (d reversed), SGO.PV.1629. **e–f** *Lampanyctus ipunensis* n. sp.; **e** holotype, IPN 16 (reversed), SGO.PV.1630; **f** paratype, CD807, Altonian, Parengarenga Harbour north shore, New Zealand North Island. **g** *Lampanyctus profestus* Schwarzhans, 2019, PPP (reversed), SGO.PV.1631. **h–m** *Lampanyctodes scopelopsoides* Schwarzhans, 1980; **h** PPN (reversed), SGO.PV.1632; **i** PPS, SGO.PV.1633; **j, k, m** RAP (j, k reversed), SGO.PV.1634; **l** PPP, SGO.PV.1635

Material: 6 juvenile specimens: 3 specimens SGO. PV.1627, Ranquil Formation, Punta El Fraile (FRM); 3 specimens, SGO.PV.1628, Lacui Formation, Cucao (CUC).

Discussion: A number of small but rather well preserved specimens up to about 1.5 mm length represent a species of the genus *Ceratoscopelus* characterized by a completely flat inner face, a moderately elongate shape (OL:OH = 1.3), a strongly projecting but robust rostrum (rostrum length 17–20% of OL) with a moderately deep excisura, a shallow ventral rim and a marked postdorsal angle positioned close to the posterior tip of the otolith. These are all characters typical for extant *Ceratoscopelus* otoliths, which, however, are usually more elongate with a longer rostrum. So far, two otolith-based *Ceratoscopelus* species have been described from the early to early middle Miocene—*C. richardsoni* Schwarzhans, 2019 from New Zealand and *C. priscus* Schwarzhans & Aguilera, 2013 from Venezuela. *Ceratoscopelus richardsoni* has a similarly long rostrum but a more middorsally pronounced dorsal rim and no excisura. *Ceratoscopelus priscus* is slender, but with an even shorter rostrum (< 15% of OL) and shows a slight twist of the inner face along the horizontal axis. Therefore, we assume that the specimens from the early Miocene of Chile likely represent yet another *Ceratoscopelus* species, but the small size of the available specimens (extant otoliths reach well over 2.5 to 3 mm in length) indicate juvenile stages probably not yet having all pertinent diagnostic characters developed and, therefore, not warranting formal diagnosis.

Genus *Lampanyctus* Bonaparte, 1840

Lampanyctus ipunensis n. sp.
(Fig. 8e, f).
2019a—*Diaphus* sp. 2—Schwarzhans: fig. 56.9.

Holotype: Fig. 8e, SGO.PV.1630, Ipún beds, Ipún Island (IPN 16).

Paratype: 1 specimen CD807, New Zealand, Northland, Parengarenga Harbour (N02/f7608) Altonian (late Burdigalian), refigured from Schwarzhans (2019a).

Name: Named after the type location Ipún Island.

Diagnosis: Massive, oval otoliths with small rostrum and minute excisura and antirostrum. OL:OH = 1.2; OH:OT = 2.4–2.6. Inner face completely flat; outer face distinctly convex with strong, nearly central umbo. Sulcus with short cauda and caudal pseudocolliculum; OCL:CCL = 1.85–2.1. All rims smooth without prominent angles.

Description: Relatively small, massive otoliths up to 2.7 mm length. Dorsal and ventral rims regularly and moderately deeply curving without prominent angles or denticles. Posterior rim regularly rounded. Rostrum slightly inferior, 9–14% of OL; excisura and antirostrum very small. All rims smooth.

Inner face nearly completely flat with moderately wide sulcus positioned along central axis, anteriorly open, posteriorly closing at moderate distance from posterior rim of otolith. Sulcus with straight upper margin, its ostium distinctly longer than cauda (OCL:CCL = 1.85–2.1). Caudal pseudocolliculum very short and strongly curved, only below anterior aprt of caudal colliculum. Dorsal depression very large, occupying nearly entire dorsal field, underlain by distinct crista superior. Ventral field with ventral furrow running at some distance from ventral rim of otolith. Outer face strongly convex, with distinct, nearly conical central to slightly postcentral umbo, smooth.

Discussion: A single specimen was described by Schwarzhans (2019a) as *Diaphus* sp. from the early Miocene of New Zealand and was assumed to represent an eroded specimen from an unknown *Diaphus* species. A newly recognized specimen from the early Miocene of Chile now reveals that the lack of denticles along the ventral rim of the otolith is not a result of erosion and that it, therefore, represents a species of *Lampanyctus*. Otoliths of *Lampanyctus* differ from *Diaphus* in the completely flat inner face, the lack of denticles along the ventral rim, and the indistinct caudal pseudocolliculum. *Lampanyctus ipunensis* is readily recognized by the very thick appearance with a strongly convex, nearly conical smooth outer face and the very short and strongly bent caudal pseudocolliculum.

Lampanyctus popoto Schwarzhans, 2019
(Fig. 8c, d).
2019a—*Lampanyctus popoto*—Schwarzhans: fig. 54.1–4.

Material: 6 specimens: 4 specimens Navidad Formation: 3 specimens SGO.PV.1629, Punta Perro (PPP); 1 specimen SGO.PV.1732, Punta Perro (PPN); 1 specimen SGO. VP.1733, Lacui Formation, Cucao (CUC); 1 specimen SGO-PV.1734, Ipún beds, Ipún Island (IPN 14).

Discussion: *Lampanyctus popoto* are comrpessed, small, relatively thick and robust otoliths. They differ from the coeval *Diogenichthys aguilerai* in the thicker appearance (OH:OT = 3.0 vs 3.5–3.8), the completely flat inner face, and the absence of a distinct excisura. From
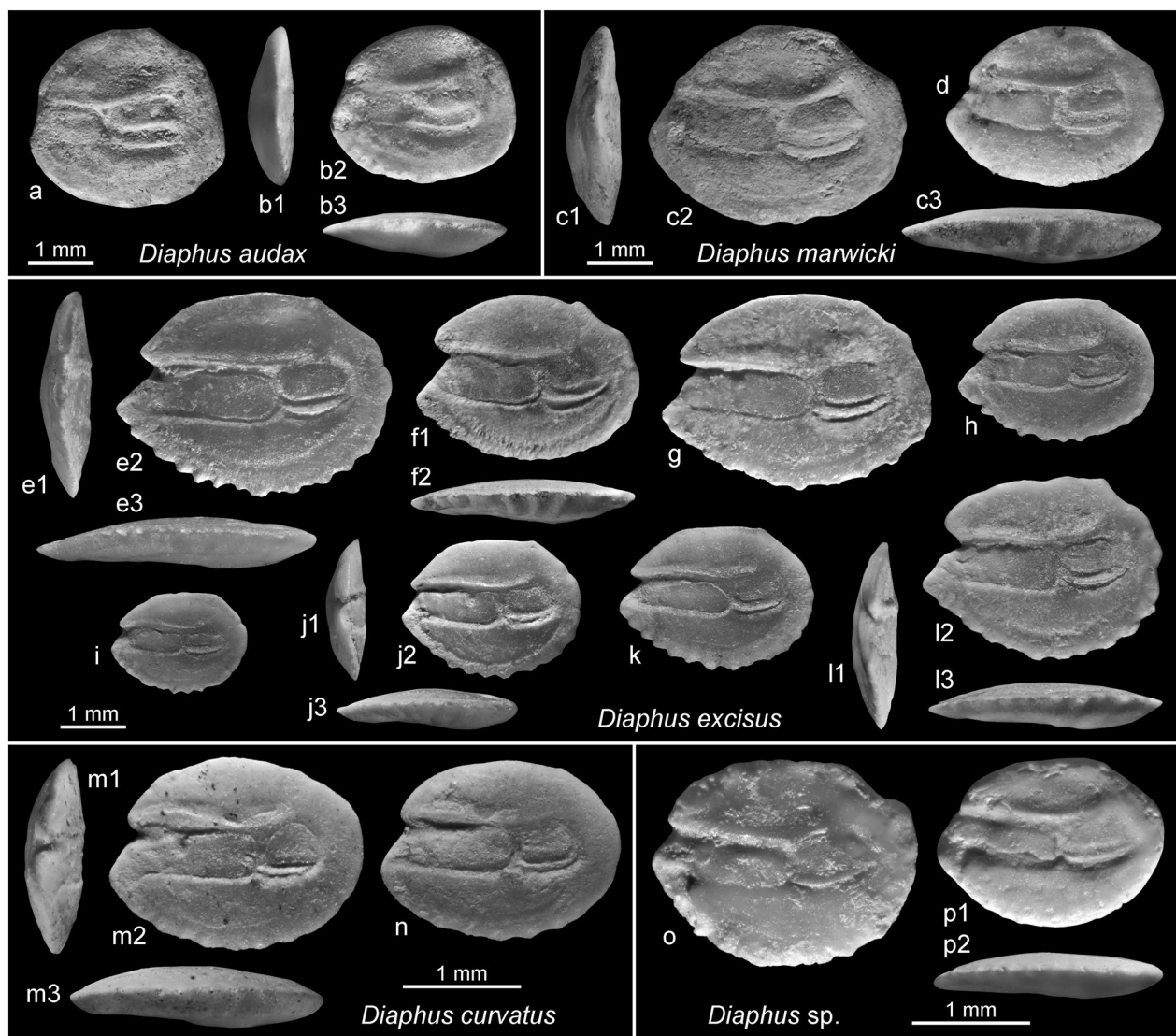
Fig. 9 a, b *Diaphus audax* Schwarzhans, 2019, PPP (reversed), SGO.PV.1636. **c, d** *Diaphus marwicki* (Frost, 1933); **c** PTA (reversed), SGO.PV.1637; **s** PPP, SGO.PV.1638. **e–l** *Diaphus excisus* (Frost, 1933); **e** MAT, SGO.PV.1639; **f** FRM, SGO.PV.1640; **g** PPN, SGO.PV.1641; **h, i, k**RAP, SGO.PV.1642; **j** PPP, SGO.PV.1643; **l** PPS (reversed), SGO.PV.1644. **m, n** *Diaphus curvatus* Schwarzhans, 1980, PTA, SGO.PV.1645. **o, p** *Diaphus* sp.; **o** PPN, SGO.PV.1646; **p** MAT, SGO.PV.1647

Protomyctophum ahunga they differ in the more robust appearance (OH:OT = 3.0 vs 3.6–4.2) and the less compressed shape expressed in the otolith proportions (OL:OH = 0.95–1.05 vs 0.83–0.93). *Lampanyctus popoto* has been described from the early Miocene (Otaian and Altonian) of New Zealand and thus represents another myctophid distributed across the southern Pacific from New Zealand to Chile.

Lampanyctus profestus Schwarzhans, 2019

(Fig. 8g).
2019a—*Lampanyctus profestus*—Schwarzhans: Fig. 54.5–9.

Material: 3 specimens: 2 specimens Navidad Formation: 1 specimen SGO.VP.1735, Rio Rapel (RAP); 1 specimen SGO.PV.1631, Punta Perro (PPP); 1 specimen SGO.VP.1736, Lacui Formation, Cucao (CUC).

Discussion: *Lampanyctus profestus* represents a different morphotype of otoliths in this large genus characterized by a thinner appearance, a low dorsal rim compared to the deep ventral rim, and a rostrum and antirostrum of

equal length. Like the forgoing species it has first been described from the early Miocene (Otaian and Altonian) of New Zealand and is now also recorded from the early Miocene of Chile.

Subfamily Gymnoscopelinae

Genus *Lampanyctodes* Fraser-Brunner, 1949

Lampanyctodes scopelopsoides (Schwarzhans, 1980)
(Fig. 8h–m).
1980—?*Notoscopelus scopelopsoides*—Schwarzhans: figs. 198–200.
1980—*Lampanyctodes serratus* (Stinton, 1957)—Schwarzhans: figs. 185–186.
2019a—*Lampanyctodes scopelopsoides* (Schwarzhans, 1980)—Schwarzhans: Figs. 61.11–17.

Material: 210 specimens: 191 specimens Navidad Formation: 67 specimens (figured specimens SGO.PV.1634), Rio Rapel (RAP); 108 specimens (figured specimens SGO.PV.1635), Punta Perro (PPP); 8 specimens SGO. PV.1632, Punta Perro (PPN); 4 specimens SGO.PV.1633, Punta Perro (PPS); 2 specimens SGO.PV.1737, Punta Alta (PTA); 4 specimens SGO.PV.1738, Ranquil Formation, Ranquil (RQS); 10 specimens SGO.PV.1739, Lacui Formation, Cucao (CUC); 7 specimens Ipún beds, Ipún Island; 1 specimen SGO.PV.1740, IPN 14; 6 specimens SGO.PV.1741, IPN 16.

Discussion: *Lampanyctodes* today is monospecific with *L. hectoris* (Günther, 1876) occurring circum-global over the deep continental shelf and slope of the southern continents in the temperate oceans. *Lampanyctodes scopelopsoides* represents the earliest fossil record of the genus and is common during the early Miocene to early middle Miocene of New Zealand. During the early Miocene of Chile, it represents the second most common species.

Subfamily Diaphinae

Genus *Diaphus* Eigenmann & Eigenmann, 1890

Diaphus theta Otolith Group after Schwarzhans (2013b)

Diaphus audax Schwarzhans, 2019
(Fig. 9a, b).
2019a—*Diaphus audax*—Schwarzhans: Figs. 55.1–7.

Material: 5 specimens: 3 specimens SGO.PV.1636, Navidad Formation, Punta Perro (PPP); 1 specimen SGO.

PV.1742, Lacui Formation, Cucao (CUC); 1 specimen Ipún beds SGO.PV.1743, Ipún Island (IPN 18).

Discussion: All five specimens from Chile are somewhat eroded and hence do not have the denticles of the ventral margin preserved. Nevertheless, *Diaphus audax* is still reliably identified based on the unique combination of a compressed shape with a relatively flat inner face and distinctly convex outer face, the high dorsal rim without postdorsal concavity, the sulcus with ostium and cauda being of almost equal length, and the caudal colliculum being extremely narrow. *Diaphus audax* was originally described from the late Oligocene and early Miocene (Waitakian to Altonian) of New Zealand.

Diaphus marwicki (Frost, 1933)
(Fig. 9c, d).
1933—*Scoeplus marwicki*—Frost: figs. 1–4.
2019a—*Diaphus marwicki* (Frost, 1933)—Schwarzhans: Figs. 55.8–14 (see there for further synonymy references).

Material: 8 specimens: 7 specimens Navidad Formation: 4 specimens SGO.PV.1638, Punta Perro (PPP); 3 specimens SGO.PV.1637, Punta Alta (PTA); 1 specimen Ipún beds, SGO.VP.1744, Lemo Island (LEM 01).

Discussion: Like with *D. audax* above, no specimen is available of *D. marwicki* from the early Miocene of Chile with preserved denticles on the ventral margin. However, details of the outline, and proportions of otolith and sulcus are characteristic for this common species in the early and middle Miocene of New Zealand (see Schwarzhans, 2019a for a detailed description).

Diaphus splendidus Otolith Group after Schwarzhans (2013b)

Diaphus excisus (Frost, 1933)
(Fig. 9e–l).
1933—*Scopelus excisus*—Frost: figs. 7–8.
2019a—*Diaphus excisus* (Frost, 1933)—Schwarzhans: Figs. 57.4–10 (see there for further synonymy references).

Material: 488 specimens: 455 specimens Navidad Formation: 24 specimens SGO.PV.1642, Rio Rapel (RAP); 349 specimens (figured specimens SGO.PV.1643), Punta Perro (PPP); 22 specimens SGO.PV.1641, Punta Perro (PPN); 10 specimens SGO.PV.1644, Punta Perro (PPS); 38 specimens, Punta Alta (PTA); 12 specimens SGO. PV.1639, Matanzas (MAT); 8 specimens SGO.PV.1640, Ranquil Formation, Punta El Fraile (FRM); 24 specimens,

Lacui Formation, Cucao (CUC); 1 specimen, Ipún beds, Ipún Island (IPN 14).

Description: Relatively elongate and thin otoliths up to 4.25 mm length (in Chile, 4.5 mm in New Zealand); OL:OH = 1.25–1.35; OH:OT = 3.6–4.1. Dorsal rim very regularly curved and smooth, with weak postdorsal angle, sometimes developed as small denticle, positioned above center of cauda. Postdorsal rim behind postdorsal angle rounded in small specimens, flat or very slightly concave in large specimens. Posterior rim broadly curved, slightly irregularly undulating. Ventral rim regularly curved, relatively shallow, with 9 delicate denticles in specimens smaller than 2.5 mm length (Fig. 9i) and 10 to 11 denticles in larger specimens. Rostrum pointed, relatively short but about twice as long as antirostrum; rostrum length 10–15% SL; excisura distinct, sharp, not very deep.

Inner face slightly convex with slightly supramedian, long, terminating at moderate distance from posterior rim of otolith. Ostium more than twice as long as cauda and slightly wider, its dorsal margin nearly straight. OCL:CCL = 2.0–2.2; OCH:CCH = 1.3–1.5. Dorsal depression long, narrow, with well-developed crista superior towards sulcus; ventral furrow distinct, moderately far from ventral rim of otolith. Outer face nearly flat, slightly concave anteriorly and slightly convex in broad postcentral umbo, smooth with few short radial furrows ventrally.

Discussion: *Diaphus excisus* is a long-ranging but rather poorly defined species in the early to late Miocene of New Zealand. It represents the most common otolith-based species in the early Miocene of Chile and is about 10 times more abundant than in New Zealand. Therefore, the description of Schwarzhans (2019a) is here emended based on specimens from Chile. All morphological details and morphometrics of the Chilean specimens fall well within the range observed for New Zealand specimens (see Schwarzhans, 2019a). *Diaphus excisus* is yet another case of temperate to subtropical southern hemisphere early Miocene myctophid species occurring on either side of the South Pacific. In tropical America (Mexico, Trinidad, and Venezuela), it is replaced by *D. biatlanticus* (Weiler, 1959), which differs in its entirely regularly curved dorsal rim without angles or concavities, a more convex inner face, and a shorter rostrum (see Schwarzhans & Aguilera, 2013).

Diaphus garmani Otolith Group after Schwarzhans (2013b)
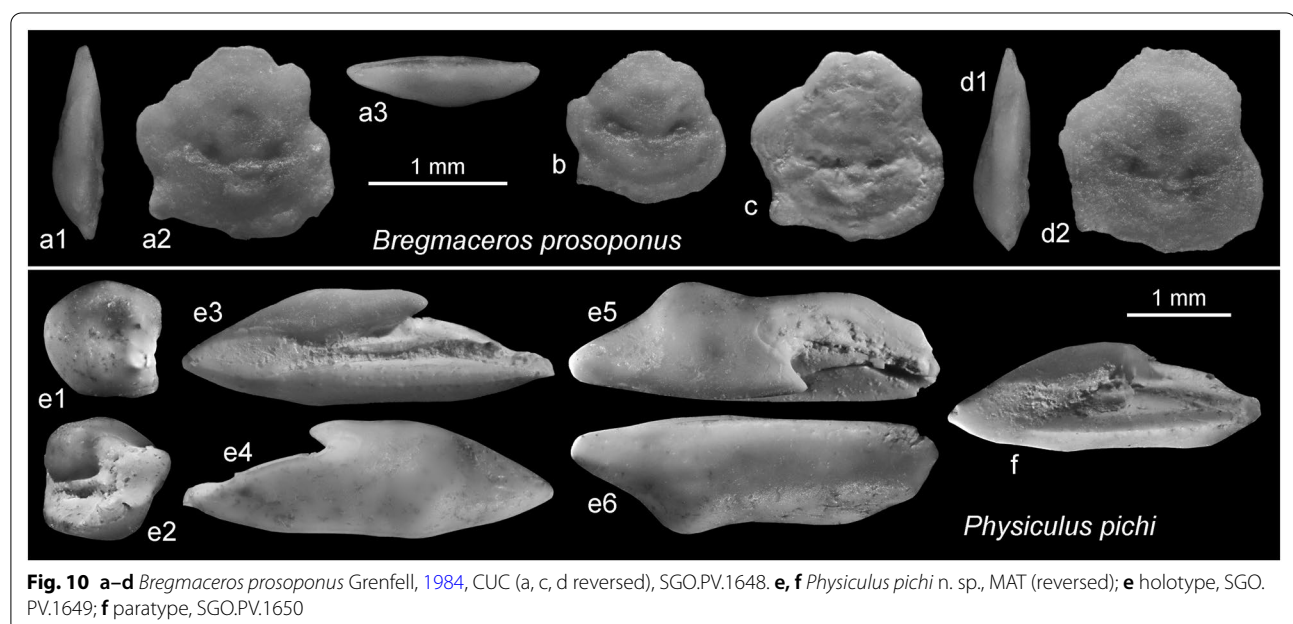
Diaphus curvatus Schwarzhans, 1980

(Fig. 9m, n).
1980—*Diaphus curvatus*—Schwarzhans: Figs. 163–165.
1984—*Diaphus* sp.—Grenfell: Fig. 39.
2019a—*Diaphus curvatus* Schwarzhans, 1980—Schwarzhans: Figs. 59.1–5.

Material: 4 specimens Navidad Formation: 2 specimens SGO.PV.1745, Rio Rapel (RAP); 2 specimens SGO.PV.1645, Punta Alta (PTA).

Fig. 10 a–d *Bregmaceros prosoponus* Grenfell, 1984, CUC (a, c, d reversed), SGO.PV.1648. **e, f** *Physiculus pichi* n. sp., MAT (reversed); **e** holotype, SGO.PV.1649; **f** paratype, SGO.PV.1650

Discussion: *Diaphus curvatus* is recognized by its regular oval outline, the strongly convex inner face, and the low number of denticles along the ventral rim (6–8). It is the most common myctophid in the early Miocene (Waitakian to Atonian) of the temperate southern New Zealand bioprovince. In Chile, in contrast, it is rare.

Unidentified Diaphus otolith group

Diaphus **sp.**
(Fig. 9o, p).

Material: 3 specimens Navidad Formation: 1 specimen SGO.PV.1746, Rio Rapel (RAP); 1 specimen SGO.PV.1646, Punta Perro (PPN); 1 specimen SGO.PV.1647, Matanzas (MAT).

Discussion: Three poorly preserved, eroded specimens of moderate size (1.9–2.2 mm length) represent yet a further species of *Diaphus*. The otoliths are characterized by a relatively narrow ostium, a somewhat bent, concave-up sulcus, a relatively deep ventral rim and shallow dorsal rim with distinct postdorsal depression, and a thin appearance. Denticles along the ventral rim are not preserved but probably were more than eight. These otoliths most likely represent an undescribed species and one that is not known from New Zealand. Its sulcus and outline somewhat resemble otoliths of the extant *D. bertelseni* Nafpaktitis, 1966 from the Atalntic Ocean that according to the assessment of extant *Diaphus* otoliths represents an otolith group of its own (Schwarzhans, 2013b).

Order Gadiformes

Family Bregmacerotidae

Genus *Bregmaceros* Thompson, 1840

Bregmaceros prosoponus **Grenfell,** 1984
(Fig. 10a–d).
1984*Diaphus—Bregmaceros   prosoponus*—Grenfell: Figs. 47–50, 150–153.
2019a—*Bregmaceros   prosoponus* Grenfell, 1984—Schwarzhans: Figs. 65.12–15.

Material: 34 specimens Lacui Formation, Cucao (CUC), figured specimens SGO.PV.1648.

Discussion: *Bregmaceros prosoponus* is characterized by an OL:OH ratio of 1.0–1.05, a relatively broad and not very high dorsal lobe, some marginal crenulation or undulation, and relatively rounded median anterior and ventral posterior rims. This species was originally described from the early Miocene (Otaian to Altonian) of the warm-water province of the North Island of New Zealand and has rarely been identified elsewhere in New Zealand. In the cooler water provinces of New Zealand, it is replaced by *B. minutus* (Stinton, 1958; see Schwarzhans, 2019a). It has often been observed that *Bregmaceros* otoliths occur common in one location but may be very rare or absent in other time-equivalent locations of the same region (Schwarzhans, 2008, 2013c), the reason for which is not yet understood. The same situation is now observed in the early Miocene of Chile, where *B. prosoponus* is common in one location (Cucao) and completely absent in any of the other locations. *Bregmaceros*, the single genus of the family, today contains 14 described species recognized as valid (Froese & Pauly 2020) and several undescribed ones (personal communication by Ho and Endo, 2019), some of which are widely distributed in certain ocean basins or almost cosmopolitan, while others are relatively restricted in their geographic distribution. *Bregmaceros prosoponus* appears to have been a warm-water southern Pacific species.

Family Moridae

Genus *Physiculus* Kaup, 1858

Physiculus pichi **n. sp.**
(Fig. 10 e, f).

Holotype: Fig. 10e, SGO.PV.1649, Navidad Formation, Matanzas (MAT).

Paratype: 1 specimen SGO.PV.1650, same data as holotype.

Name: From pichi (Mapudungun) = small, slender, referring to the small size and the slender shape of the otolith.

Diagnosis: Slender, fusiform otoliths; OL:OH = 2.9–3.2. OH:OT = 1.0. Anterior tip of otolith sharply pointed. Dorsal rim regularly curved, anteriorly depressed. Ostium short; CCL:OCL = 2.0–2.3. Crista superior about half as long as crista inferior. Ridge-like caudal colliculum mildly arcuate posteriorly.

Description: Elongate, fusiform otoliths, about as thick as high, with nearly flat inner face, up to 3.6 mm long (holotype). Dorsal rim gently curving, reaching to about middle of cauda, low, anteriorly depressed, without predorsal lobe. Ventral rim very shallow, very weakly bent anteriorly and nearly straight at middle section, and very slightly bent in posterior section. Anterior tip tapering, sharply pointed. Posterior tip with three projections: middle projection bearing ridge-like caudal colliculum longest; crista inferior slightly shorter and joined to middle projection; crista superior about half the length of crista inferior, with acute tip.

   Inner face almost completely flat, only very faintly bent along horizontal axis. Ostium shallow, short, with oval colliculum; CCL:OCL $=2.0–2.3$; CaH:OsH $=1.1$; OCL:OCH $=3.5$; OL:OsL $=3.0–3.1$. Cauda deep, widening posteriorly and widely opened posterior-dorsally. Caudal colliculum forming highly elevated, thin central ridge, anteriorly joined to ostial colliculum, posteriorly slightly arcuate. Ventral field extremely narrow, shallow, set-off from outer face by distinct edge. Dorsal field narrow, but not as narrow as ventral field, and very short, with rounded edge towards not overlapping outer face. Posterior dorsal portion of inner face incorporating posterior dorsal part of outer face due to deeply excavated cauda. Outer face strongly convex in vertical direction, smooth, with broad umbo opposite of ostial-caudal collicular joint, slightly overlapping onto inner face along ventral margin.

Discussion: Morids live benthopelagic on the continental slope at depths characterized by optimal sound transmission and low noise levels. Their otoliths exhibit a unique morphology (Fitch & Barker, 1972; Karrer, 1971; Schmidt, 1968; Schwarzhans, 2019c) that has been shown to be linked to a unique pattern of the macula acustica, both being considered to represent a highly specialized adaptation to improved hearing (Deng et al., 2011). *Physiculus* is the most species-rich genus today with 42 currently recognized species and most of them confined within rather limited geographic distribution ranges. Well-preserved otoliths are rarely found in the fossil record because of their delicate ridge-like caudal colliculum and the posterior tips. The holotype thus represents one of those rare finds. The paratype was originally well preserved, too, but unfortunately lost its posterior tip of the crista inferior during sample processing. *Physiculus pichi* differs from the time-equivalent *P. beui* Schwarzhans, 2019 from New Zealand (Otaian to Altonian) in the more slender and thinner appearance (OL:OH $=2.9–3.2$ vs $2.5–3.0$ and OH:OT $=1.0$ vs $0.9–1.0$), the regularly curved and anteriorly compressed dorsal rim (vs anteriorly with small lobe) and the longer ostium

(CCL:OCL $=2.0–2.3$ vs $2.7–3.0$ and OL:OsL $=3.0–3.1$ vs $3.5–4.0$).

Family Steindachneriidae

Genus *Steindachneria* Goode & Bean, 1896

Remarks: The genus *Steindachneria* is monospecific today with *S. argentea* Goode & Bean, 1896, which chiefly occurs along the upper continental slopes at water depths of 400 to 500 m (Cohen et al., 1990) in the Gulf of Mexico and along the Caribbean coast of South America. In an article dedicated to the fossil record and paleogeography of *Steindachneria*, Nolf (2002) has shown that the genus was more species-rich in the geological past (early Miocene) and distributed across a much larger region that included the Pacific side of North and South America and the Mediterranean. An articulated fossil skeleton from the late Oligocene of Poland was described as *Parasteindachneria oligocenica* by Swidnicki (1990; see Kotlarczyk et al., 2006). Recently, Gregorova (2008) has confirmed the presence of steindachneriid skeletal remains in the late Oligocene from the Czech Republic and described them as *Steindachneria* sp.

   The phylogenetic position of the Steindachneriidae has been subject to much discussion and alternative placing within the Gadiformes; in older studies, the Steindachneriidae were often considered to constitute a subfamily of the Merlucciidae (Cohen et al., 1990) or an independent family of uncertain relationships (see discussion in Fahay, 1989). More recently, Roa-Varon & Orti (2009) regarded the Steindachneriidae as the sister-family of the Macruronidae and both together as the sister-group to the Macrouridae and Bathygadidae (but without Trachyrincidae) based on molecular data. The relationship between Steindachneridae and Macruronidae appears plausible in respect to their otolith morphology.
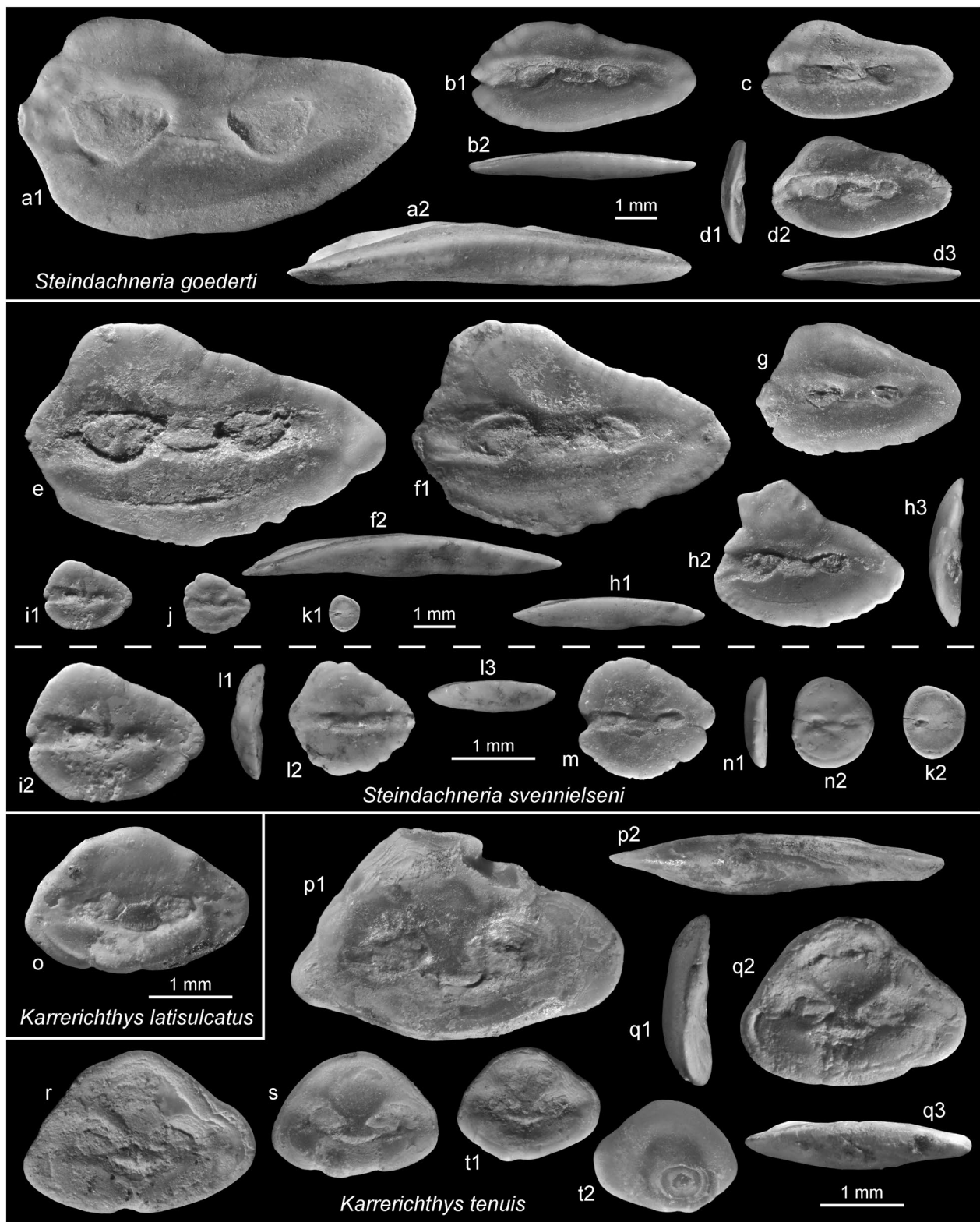
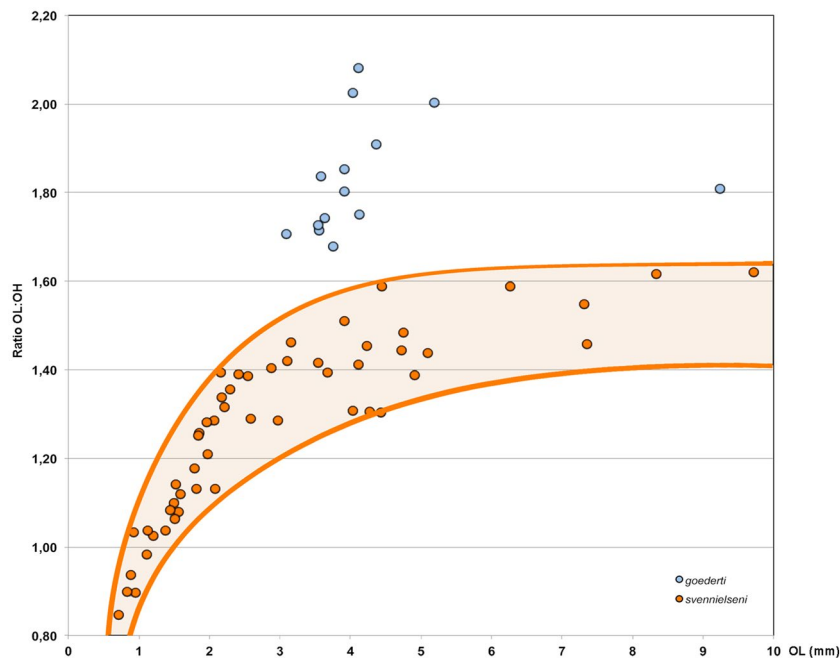### *Steindachneria goederti* Nolf, 2002
(Figs. 11 a–d, 12).
2002—*Steindachneria goederti*—Nolf: pl. 1, figs. 6–8.

Material: 25 specimens: 8 specimens Navidad Formation: 7 specimens SGO.PV.1652, Rio Rapel (RAP); 1 specimen SGO.PV.1651, Punta Perro (PPS); 17 specimens Lacui Formation: 2 specimens SGO.PV.1653, Punta Chocoi (CHO); 15 specimens SGO.PV.1654, Cucao (CUC).

Discussion: *Steindachneria goederti* is relatively slender when compared to the coeval *S. svennielseni* Nolf, 2002

Fig. 11 **a–d** *Steindachneria goederti* Nolf, 2002; **a** PPS (reserved), SGO.PV.1651; **b** RAP, SGO.PV.1652; **c** CHO (reversed), SGO.PV.1653; **d** CUC, SGO. PV.1654. **e–n** *Steindachneria svennielseni* Nolf, 2002; **e, f, h** PPN (e reversed), SGO.PV.1655; **g, i, k, m** CUC (g, m reversed), SGO.PV.1656; **j, l, n** RAP, SGO.PV.1657. **o** *Karrerichthys latisulcatus* (Frost, 1933), IPN 16 (reversed), SGO.PV.1658. **p–t** *Karrerichthys tenuis* (Stinton, 1957), PPP (r, t reversed), SGO. PV.1659

Fig. 12 Cross plot of otolith length vs ratio otolith length: otolith height of the species *Steindachneria goederti* and *S. svennielseni*

(OL:OH = 1.7–2.1 vs < 1.65), which is mostly due to the relatively low predorsal lobe, and further differs in the ventral furrow running distinctly closer to the ventral rim of the otolith than is the case in *S. svennielseni.* Nolf (2002) described *S. goederti* from the lower Miocene of the Astoria Formation of Washington State, USA, but did not mention it from the Navidad Formation of Chile, which was at that time considered to be probably of late Miocene (Tortonian?) age. The early to middle Miocene (late Burdigalian to early Langhian) fauna from the Cantaure Formation of Venezuela represents the only comparable collection from tropical America. Nolf and Aguilera (1998) described otoliths of a *Steindachneria* sp. from the Cantaure Formation, which is here interpreted as most likely representing *S. svennielseni.* Based on the limited data at hand, it appears that *S. goederti* possibly represented an antitropical species at the eastern Pacific of North and South America.

Steindachneria svennielseni Nolf, 2002
(Figs. 11e–n, 12).
?1998—*Steindachneria* sp.—Nolf & Aguilera: pl. 6, figs. 7–9.
2002—*Steindachneria svennielseni*—Nolf: pl. 1, figs. 9–12.
?2002—*Steindachneria* sp. ind.—Nolf: pl. 1, figs. 13–14.

Material: 104 specimens: 47 specimens Navidad Formation: 26 specimens (figured specimens SGO.PV.1657), Rio Rapel (RAP); 4 specimens SGO.PV.1747, Punta Perro (PPP); 10 specimens SGO.PV.1655, Punta Perro (PPN); 2 specimens SGO.PV.1748, Punta Perro (PPS); 2 specimens SGO.PV.1749, Punta Alta (PTA); 3 specimens SGO.PV.1750, Matanzas (MAT); 1 specimen SGO.PV.1751, Ranquil Formation, Punta El Fraile (FRM); 56 specimens Lacui Formation: 11 specimens SGO.PV.1752, Punta Chocoi (CHO); 45 specimens (figured specimens SGO.PV.1656), Cucao (CUC).

Ontogeny: The large number of otoliths of *S. svennielseni* now available from the early Miocene of Chile has revealed an extraordinary degree of allometric ontogenetic changes of a magnitude not observed in otoliths of any other species known thus far. Otoliths ranging from 4 mm in length to the largest known specimen of 9.7 mm in length exhibit the typical steindachneriid morphology with a pronounced, anteriorly positioned predorsal lobe and an OL:OH ratio between 1.4 and 1.65 (Figs. 11e–h, 12). The smallest specimens, which are just under 1 mm in length, differ fundamentally in exhibiting a strongly compressed, high oval otolith shape with blunt posterior tip and a high dorsal rim without distinct predorsal lobe (Fig. 11k, n) and a ventral furrow close to the ventral rim of the otolith. Their OL:OH ratios range from
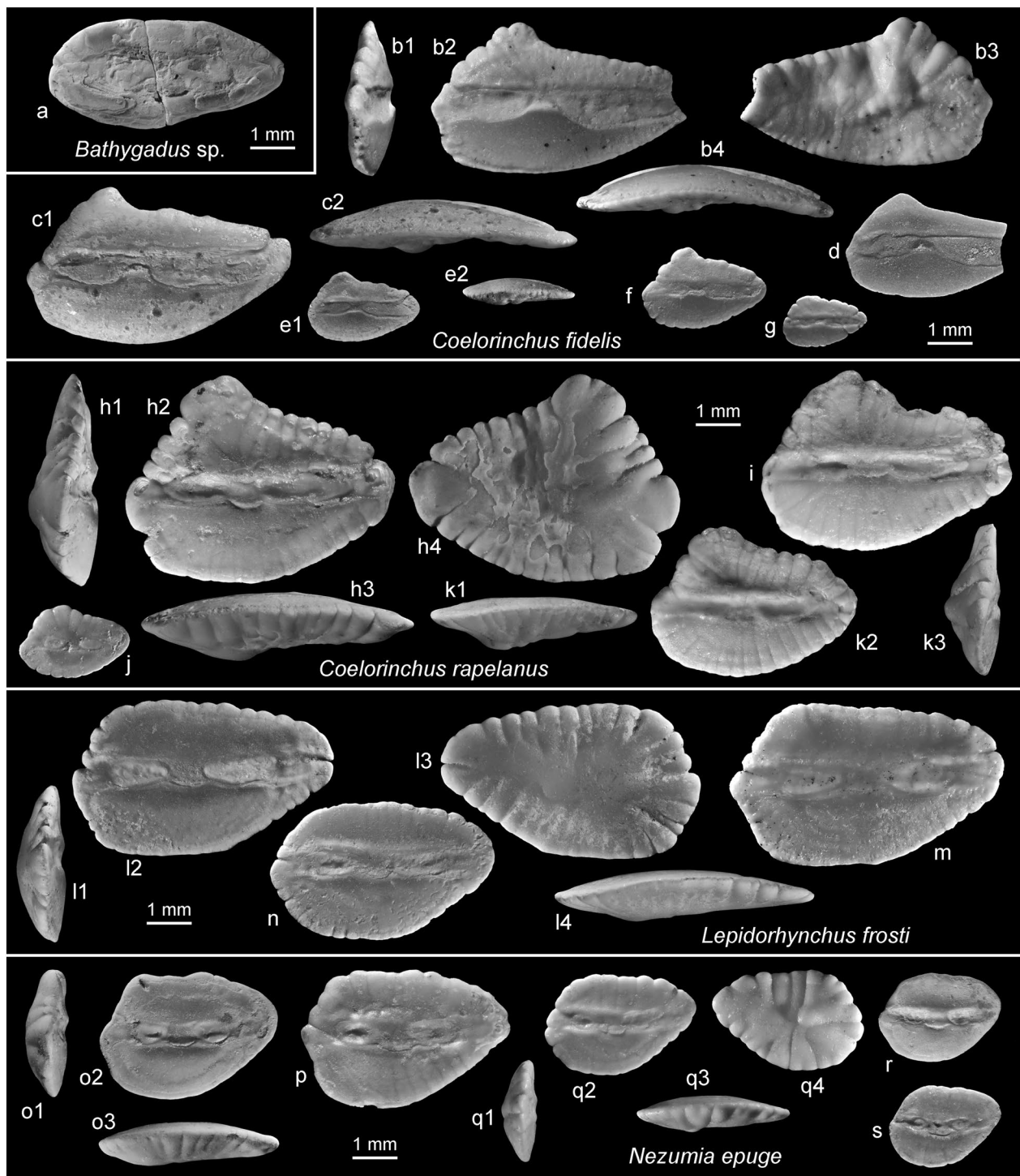
Fig. 13 a *Bathygadus* sp., IPN 16, SGO.PV.1660. **b–g** *Coelorinchus fidelis* n. sp.; **b** holotype, PPN, SGO.PV.1661; **c** paratype, PPN (reversed) SGO.PV.1662; **d, e** CUC (e reversed), SGO.PV.1663; **f, g** RAP (g reversed), SGO.PV.1664. **h–k** *Coelorinchus rapelanus* n. sp., PPP (reversed); **h** holotype, SGO.PV.1665; **i–k** paratypes, SGO.PV.1666. **l–n** *Lepidorhynchus frosti* Schwarzhans, 2019, MAT (l reversed), SGO.PV.1667. **o–s** *Nezumia epuge* n. sp.; **o** holotype, PPP, SGO.PV.1668; **p** paratype, PPP (reversed) SGO.PV.1669; **q, s** PPN, SGO.PV.1670; **r** paratype, PTA (reversed) SGO.PV.1671

0.85 to 1.05 (Fig. 13); that is the otoliths are higher than they are long. The otolith shape and ratio OL:OH transforms rapidly from the juvenile status at about 1 mm in length to the diagnostically mature status characterized above within the narrow size range between 1 and 3 mm in length (Figs. 12i, j, l, m, 13). If it were not for a continuous sequence of 51 measurable specimens (Fig. 12), one would have easily been tempted to recognize different taxa. Similarly small otolith specimens are not known from the extant *S. argentea* or the second fossil species *S. goederti*, and we, therefore, do not know whether they exhibit similar extreme ontogenetic changes. However, the smallest known specimens of *S. goederti*, which are about 3 to 4 mm in length (Fig. 12) and of the extant *S. argentea*, which are about 4 mm in length (from figures in Nolf, 2002), also show a decreasing OL:OH ratio in small specimens.

A further interesting aspect of the ontogenetic allometry observed in *S. svennielseni* is the fact that different size categories are not uniformly distributed throughout the studied locations. Most locations sampled from the Navidad Formation (FRM, MAT, PPN, PPP, PPS, and PTA) yielded only large specimens of generally more than 5 mm in length. One location in the Lacui Formation (CHO) yielded mainly intermediate-sized specimens of 3–6 mm in length, while the locations CUC in the Lacui Formation and RAP in the Navidad Formation are dominated by small specimens of mostly less than 3 mm in length. These findings indicate that *S. svennielseni* were fishes that lived in separate size classes or schools that were possibly segregated based on bathymetric conditions or depending on food availability given that zooplankton serves as the main food source for many larval and juvenile fishes (Hunter, 1981). The latter explanation is consistent with location CUC being the only one with, common, *Bregmaceros prosoponus,* since the Bregmacerotidae are also largely zooplankton feeders (Cohen, 1986).

Discussion: *Steindachneria svennielseni* differs from the coeval *S. goederti* in being distinctly more compressed (OL:OH < 1.6 vs 1.7–2.1) in all known size categories and showing a more developed predorsal lobe and a ventral furrow that is distinctly more distant from the ventral rim of the otolith (the latter, however, is also affected by ontogenetic changes). It appears to be more widespread than *S. goederti.* Specimens reported in open nomenclature from the early Miocene of Venezuela and the Mediterranean/Paratethys (Nolf, 2002) are here tentatively assigned to *S. svennielseni* too, with this placement, however, being subject to confirmation in future research. It appears that *S. svennielseni* may have been more tolerant

of warm water than its possibly antitropical early Miocene congener. *Steindachneria svennielseni* more closely resembles the extant *S. argentea* than *S. goederti*. Nolf (2002) recognized as main differences the more expanded and forward-leaning predorsal lobe in *S. argentea* and a distinct twist of the inner face in the horizontal axis as the main distinguishing characters.

Family Melanonidae

Genus *Karrerichthys* Schwarzhans, 1980

***Karrerichthys latisulcatus* (Frost, 1933)**
(Fig. 11o).
1933—*Otolithus (Macruridarum) latisulcatus*—Frost: figs. 35–36.
1980—*Karrerichthys latisulcatus* (Frost, 1933)—Schwarzhans: Fig. 604 (refigured holotype).
2019a—*Karrerichthys latisulcatus* (Frost, 1933)—Schwarzhans: Fig. 73.8.

Material: 1 specimen SGO.PV.1658, Ipún beds, Ipún Island (IPN 16).

Discussion: *Karrerichthys latisulcatus* is a rarely observed species in the middle Miocene of New Zealand and a single specimen has now been found in one of the southernmost early Miocene locations in Chile. It differs from the much more common coeval *K. tenuis* (see below) primarily in being somewhat more elongate compared to specimens of the same size (OL:OH = 1.5 vs 1.3–1.4) caused by a relatively low dorsal rim.

***Karrerichthys tenuis* (Stinton, 1957)**
(Fig. 11p–t).
1957—*Notothenia tenuis*—Stinton: fig. 14.
1984—*Melanonidarum* aff. *Karrerichthys admirabilis* Schwarzhans, 1980—Grenfell: Figs. 51, 154–155.
2019a—*Karrerichthys tenuis* (Stinton, 1957)—Schwarzhans: Figs. 73.9–13.

Material: 41 specimens: 39 specimens (figured specimens SGO.PV.1659), Navidad Formation, Punta Perro (PPP); 2 specimens Ipún Beds: 1 specimen SGO.VP.1753, Ipún Island (IPN 14), 1 specimen SGO.VP.1754, Lemo Island (LEM 01).

Discussion: *Karrerichthys tenuis* is fairly common in the early to early middle Miocene (Otaian to Lillburnian) of the northern, warm paleo-bioprovince of New Zealand. It differs from *K. latisulcatus* in being more compressed (see above), but there is a certain degree of ontogenetic

allometry observable as well. Specimens between 1.5 and 2 mm in length have a ratio OL:OH of 1.25–1.3, those of a length of 2 to 3 mm length a ratio of 1.3–1.4, and the largest specimen known (Fig. 11p) of about 4 mm length has a ratio OL:OH of 1.5. *Karrerichthys tenuis* is another mesopelagic fish identified on both sides of the southern Pacific during the early Miocene. Its distribution in Chile, however, is rather localized, and with two exceptions from the Ipún beds is restricted to a single location in the northern Navidad Formation.

Family Bathygadidae

Genus *Bathygadus* Günther, 1878

***Bathygadus* sp.**
(Fig. 13a).

Material: 1 specimen SGO.PV.1660, Ipún beds, Ipún Island (IPN 16).

Discussion: The single, broken and rather eroded specimen of 5.2 mm length probably represents and undescribed species of the genus *Bathygadus*, which are characterized by small colliculi positioned far from the anterior and posterior otolith rims and have a wide collum in between. Further characters are a nearly flat inner face and a distinct ventral furrow running at some distance from the ventral rim of the otolith. The specimen from Chile is not closely related to *Bathygadus waiohaensis* Schwarzhans, 2019 from the early Miocene (Otaian) of northern New Zealand.

Family Macrouridae

Genus *Coelorinchus* Giorna, 1809

***Coelorinchus fidelis* n. sp.**
(Fig. 13b–g).

Holotype: Fig. 13 b, SGO.PV.1661, Navidad Formation, Punta Perro (PPN).

Paratypes: 9 specimens: 3 specimens SGO.PV.1662, same data as holotype; 1 specimen SGO.PV.1755, Punta Perro (PPS); 2 specimens SGO.PV.1664, Navidad Formation, Rio Rapel (RAP); 3 specimens SGO.PV.1663, Lacui Formation, Cucao (CUC).
Further material: 55 specimens: 12 specimens Navidad Formation; 8 specimens, Rio Rapel (RAP), 4 specimens, same data as holotype; 40 specimens Lacui Formation: 14 specimens, Punta Chocoi (CHO), 26 specimens, Cucao

(CUC); 3 specimens Ipún Beds: 1 specimen, Ipún Island (IPN 18), 2 specimens, Lemo Island (LEM 01).

Name: From fidelis (Latin) = faithful, referring to its resemblance to the *C. australis* species group known from Australia and New Zealand, including the fossil *C. preaustralis*.

Diagnosis: OL:OH = 1.6–1.75. Dorsal rim with distinctly protruding and sharp predorsal expansion positioned above ostium and followed by distinct concavity above collum. Collum narrow, ventrally indented, without pseudocolliculum. Crista superior without bulge above ostium. Ostial colliculum slightly narrower than caudal colliculum and distinctly shorter; CCH:OCH = 1.1–1.2; CCL:OCL = 1.4–1.8. Ventral furrow very close to ventral rim of otolith.

Description: Elongate otoliths up to at least 6.6 mm length (reconstructed from largest incomplete specimen; holotype with missing posterior tip 5.7 mm; largest complete specimen in Fig. 13c 5.85 mm). OL:OH = 1.6–1.75, increasing with size; OH:OT = 2.5–3.0, increasing with size. Dorsal rim anteriorly high with prominent and sharp predorsal expansion positioned far anterior above ostium followed by distinct concavity above collum and in turn by depressed, nearly straight postdorsal region above cauda. Ventral rim moderately deep, gently curved, deepest below collum. Anterior rim blunt, with obtuse angle below tip of ostium; posterior rim tapering, somewhat pointed, positioned above tip of cauda. Dorsal rim and posterior part of ventral rim finely crenulated, diminishing with size.

Inner face distinctly convex with supramedian, moderately narrow sulcus. Colliculi well marked, with ostial colliculum slightly narrower than caudal colliculum, separated by narrow, ventrally indented collum. Ostium distinctly shorter than cauda, its colliculum slightly reduced anteriorly, particularly in small specimens. CCH:OCH = 1.1–1.2; CCL:OCL = 1.4–1.8. Colliculi well marked and slightly deepened. Dorsal field with indistinct depression above anterior part of sulcus and narrow and indistinct crista superior above ostium. Ventral field with variably strong ventral furrow very close to ventral rim of otolith. Outer face slightly convex in small specimens, becoming flat to concave in large ones, intensely ornamented with variably strongly developed radial furrows throughout and tubercular shallow umbo approximately opposite to collum of inner face.

Discussion: *Coelorinchus fidelis* resembles the coeval *C. preaustralis* from New Zealand in many aspects such as the elongate shape, the ostium being narrower than the cauda, the narrow, ventrally indented collum without pseudocolliculum or the strongly convex inner face (see Schwarzhans, 2019a). There are, however, also significant and consistent differences such as the distinct and sharp predorsal expansion (*vs* rounded and rather shallow), the ratio OL:OH (1.6–1.75 *vs* 1.75–1.85), the lack of a bulge of the crista superior above the ostium, the less narrowed ostium and the ratio CCL:OCL (1.4–1.8 *vs* 2.1–2.5). In conclusion, we assume that *C. fidelis* belongs to the *C. australis* group, which is restricted presently to off temperate Australia and New Zealand with two species. Most likely, *C. fidelis* in Chile represents the allopatric sister species of *C. preaustralis* from New Zealand.

Coelorinchus rapelanus n. sp.
(Fig. 13h–k).

Holotype: Fig. 13h, SGO.PV.1665, Navidad Formation, Punta Perro (PPP).

Paratypes: 6 specimens SGO.PV.1666, same data as holotype.

Further material: 8 specimens Navidad Formation; 6 specimens, Punta Perro (PPP), 1 specimen, Punta Perro (PPS), 1 specimen, Punta Alta (PTA).

Name: Referring to the type location on the banks of the river Rapel.

Diagnosis: OL:OH = 1.25–1.4. Dorsal rim high, with massive predorsal expansion positioned above rear part of ostium and collum. Inner face slightly bent. Collum narrow, with distinct pseudocolliculum. Crista superior without bulge above ostium. Ostial and caudal colliculi reduced towards outer otolith rims; CCL:OCL = 1.3–1.5. Ventral furrow indistinct.

Description: Compressed, high bodied otoliths up to about 6 mm length (holotype). OL:OH = 1.25–1.4, decreasing with size; OH:OT = 3.0. Dorsal rim high with prominent and broad predorsal expansion positioned above ostium and collum, followed by initially slightly concave then slightly convex, gently curved postdorsal region. Ventral rim deep, gently curved, deepest below collum. Anterior rim blunt, with rounded obtuse angle below tip of ostium; posterior rim tapering, rounded,

positioned at level of tip of cauda. Dorsal rim intensely and coarsely crenulated, ventral rim finely crenulated.

Inner face slightly bent in horizontal direction, almost not bent in vertical direction, with supramedian, narrow sulcus. Colliculi well-marked, slightly deepened, terminating distant from anterior and posterior tips, respectively, separated by narrow, ventrally slightly expanded collum bearing distinct pseudocolliculum. Ostium distinctly shorter than cauda; CCL:OCL = 1.3–1.5. Dorsal field with wide and indistinct depression and indistinct crista superior above ostium. Ventral field without clear ventral furrow. Numerous radial furrows ingressing on dorsal and ventral field from marginal crenulation. Outer face convex, intensely ornamented with variably strongly developed furrows extending orthogonally to otolith rims throughout, and distinct tubercular umbo approximately opposite to rear part of ostium on inner face.

Discussion: *Coelorinchus rapelanus* resembles *C. demonstratus* Schwarzhans, 1980 known from the early to middle Miocene (Altonian to Lillburnian) of northern New Zealand and *C. macruroloides* Brzobohatý, 1986 from the early and middle Miocene of Europe. From *C. demonstratus*, it differs in the anteriorly and posteriorly reduced colliculi and the much less bent inner face, particularly in the vertical direction. From *C. macruroloides*, it differs likewise in the anteriorly reduced ostial colliculum and the posteriorly reduced caudal colliculum, the lack of a ventral furrow, and the tendency to a lower ratio OL:OH (1.25–1.4 *vs* 1.35–1.5). It appears likely that all three species belong to a specific clade within the genus, caused by allopatric speciation. More distantly related may be *C. pakaurangiensis* Schwarzhans, 2019 from the late Oligocene and early Miocene (Duntroonian to Otaian) of New Zealand, from which it differs in the lower OL:OH ratio (1.25–1.4 *vs* 1.4–1.5) and the lower CCL:OCL ratio (1.3–1.5 *vs* 1.8). The relationships to any extant *Coelorinchus* species group remains elusive for now.

Coelorinchus rapelanus has been found only in the northern locations of the Navidad Formation and particularly in the location PPP (Punta Perro), where it completely replaces *C. fidelis*. This is also the location, which is dominated by *Karrerichthys tenuis* see above. The paleoenvironmental implications of these finds will be discussed in a later chapter.

Genus *Lepidorhynchus* Richardson, 1846

***Lepidorhynchus frosti* Schwarzhans, 2019**

(Fig. 13l–n).

1980—*Ventrifossa sagittiformis* (Frost, 1933)—Schwarzhans: Figs. 276–278.

2019a—*Lepidorhynchus frosti*—Schwarzhans: Figs. 70.4–10.

Material: 7 specimens, Navidad Formation: 2 specimens SGO.PV.1756, Punto Perro (PPP); 1 specimen Punta Perro (PPS); 4 specimens SGO.PV.1667, Matanzas (MAT).

Discussion: *Lepidorhynchus frosti* is a common species in the early Miocene (Altonian) of New Zealand. It is well recognized by its distinctive shape with an anteriorly pronounced ventral margin that is straight and horizontal at its deepest point, the low, nearly flat dorsal rim with an obtuse predorsal angle, and the sulcus with reduced ostial and caudal colliculi and a moderately wide collum. In New Zealand, the genus *Lepidorhynchus* has an almost continuous record from the early Miocene (Altonian) to present with *L. frosti* being its earliest representative. The extant *L. denticulatus* Richardson, 1846 is geographically restricted to temperate Australia and New Zealand on the continental slope, usually between 270 to 450 m (Froese & Pauly 2020). The record from the early Miocene of Chile shows that in the geological past its early ancestor was more widely distributed through the southern Pacific.

Genus *Nezumia* Jordan, 1904

***Nezumia epuge* n. sp.**
(Fig. 13o–s).

Holotype: Fig. 13 o, SGO.PV.1668, Navidad Formation, Punta Perro (PPP).

Paratypes: 4 specimens Navidad Formation: 1 specimen SGO.PV.1669, same data as holotype; 2 specimens SGO.PV.1670, Punta Perro (PPN); 1 specimen SGO.PV.1671, Punta Alta (PTA).

Further material: 20 specimens: 19 specimens Navidad Formation: 14 specimens, Punta Perro (PPP), 1 specimen, Punta Perro (PPN), 2 specimens, Punta Perro (PPS), 1 specimen, Punta Alta (PTA), 1 specimen, Matanzas (MAT); 1 specimen, Lacui Formation, Cucao (CUC).

Name: A combination of epu (Mapudungun) = two and ge (Mapudungun) = eye, referring to the two small and distantly positioned colliculi resembling the eyes of a face.

Diagnosis: OL:OH = 1.4–1.5. Dorsal rim low, nearly horizontal, with rounded predorsal angle. Ventral rim deep, deepest region anteriorly below ostium and collum. Inner face slightly bent. Collum almost as wide as colliculi long, with distinct pseudocolliculum. Ostial and caudal colliculi very small and oval; CCL:OCL = 1.0–1.1. Ventral furrow indistinct.

Description: Compressed otoliths up to about 4.6 mm length (holotype 4 mm). OL:OH = 1.4–1.5; OH:OT = 3.0. Dorsal rim low, nearly horizontal in mid-section, anteriorly with broadly rounded predorsal angle above anterior margin of ostial colliculum, and posteriorly gently curved. Ventral rim deep, gently curved, deepest anteriorly below ostial colliculum and collum, posteriorly ascending nearly straight. Anterior rim blunt, with rounded obtuse angle at or below tip of ostium; posterior rim tapering, rounded, positioned high, at level of tip of cauda or somewhat above. All rims variably crenulated.

Inner face slightly bent in horizontal direction, almost not bent in vertical direction, with supramedian, narrow sulcus. Colliculi well marked, slightly deepened, terminating distant from anterior and posterior tips, respectively, separated by wide collum bearing distinct pseudocolliculum. Ostial and caudal colliculi very small, oval, of about equal size, and only slightly longer than collum wide. Ostium slightly shorter than cauda; CaL:OsL (measured from center of collum) = 1.2–1.4; CCL:OCL = 1.0–1.1. Dorsal field with wide and indistinct depression. Ventral field without clear ventral furrow. Numerous radial furrows ingressing on dorsal and ventral field from marginal crenulation. Outer face slightly convex, intensely ornamented with variably strongly developed radial furrows, one or two vertical furrows going through center of otolith and shallow tubercular umbo in front, approximately opposite to ostial colliculum on inner face.

Discussion: Otoliths of *Nezumia* often reach only relatively small sizes and, therefore, we regard the specimens of 4 mm length and more as diagnostically mature. *Nezumia epuge* is characterized by its very small colliculi of about equal size which resembles *N. sagittiformis* (Frost, 1933) from the early and middle Miocene (Otaian to Lillburnian) of New Zealand, but differs in the more compressed shape (OL:OH = 1.4–1.5 *vs* 1.5–1.6), the wider collum and the CCL:OCL ratio of 1.0–1.1 (*vs* 1.1–1.4). The late Miocene *N. mangapariensis* Schwarzhans, 1980 from New Zealand is also similar, but differs in the rather smooth otolith rims, the more strongly convex inner and nearly flat outer face and the caudal colliculum being longer than the ostial colliculum (CCL:OCL = 1.2–1.3 *vs* 1.0–1.1).

Order Ophidiiformes

(See figure on next page.)
Fig. 14 **a** *Carapus* sp., CUC (reversed), SGO.PV.1672. **b, c** *Paracarapus chilensis* n. gen., n. sp.; **b** holotype, PPN (reversed), SGO.PV.1673; **c** paratype, PPS, SGO.PV.1674. **d–i** *Lepophidium chonorum* n. sp., CUC; **d** holotype, SGO.PV.1675; **e–i** paratypes (f, h, i reversed), SGO.PV.1676. **j–n** *Lepophidium mapucheorum* n. sp.; **j** holotype, PPS, SGO.PV.1677; **k, m** paratypes, RAP (m reversed), SGO.PV.1678; **l** paratype, PPP (reversed), SGO.PV.1679; **n** paratype, PPS (reversed), SGO.PV.1680. **o** *Ophidion* sp., PPS, SGO.PV.1681. **p, q** *Sirembola supersa* n. sp.; **p** holotype, CUC, SGO.PV.1682; **q** paratype, CHO, SGO.PV.1683. **r** *Spectrunculus sparsus* n. sp., holotype, PPP, SGO.PV.1684. **s–u** *Pseudonus humilis* n. sp., PPP; **s** holotype, SGO.PV.1685; **t, u** paratypes (u reversed), SGO.PV.1686

Suborder Ophidioidei

Family Carapidae

Genus *Carapus* Rafinesque, 1810

Carapus sp.
(Fig. 14a).

Material: 2 juvenile specimens SGO.PV.1672, Lacui Formation, Cucao (CUC).

Discussion: Two small otoliths of about 1.5 mm length from presumably juvenile fishes of an unknown *Carapus* species. They are characterized by a narrow and relatively short sulcus and are relatively thin, which, however, could be an early ontogenetic effect.

Genus *Paracarapus* n. gen.

Type species: *Paracarapus chilensis* n. sp., by monotypy.

Name: Combination of para (Greek) = next to, near and *Carapus* the type genus of the family indicating its relationships.

Diagnosis: A fossil otolith-based genus, of the family Carapidae with the following combination of characters: Compact otoliths with the inner face being bent along the horizontal axis and straight along the vertical axis, thickest portion of outer face slightly above its middle, leaving a relatively sharp dorsal rim and sulcus long, with parallel dorsal and ventral margins and slight indication of separation into ostium and cauda by incision of ventral sulcus margin; Osl:CaL ~ 3.0.

Discussion: *Paracarapus* is a typical carapid otolith in many aspects, such as the relatively flat inner face, the long and shallow sulcus, the outline with a shallow ventral rim and a distinct predorsal expansion and the thick outer face. Certain characters differ, however, and are interpreted as plesiomorphic in respect to carapid otoliths, such as the slightly bent inner face in horizontal direction, the parallel margins of the sulcus, and the thickest portion of the outer face in a more central position. In modern carapid taxa, the inner face is completely flat, the ventral sulcus margin is more or less straight and the dorsal sulcus margin domed, and the thickest portion of the outer face is positioned at the dorsal rim of the otolith resulting in the dorsal rim being very thick and the ventral rim sharp. We, therefore, consider *Paracarapus* as a genus at the stem of carapids and as a sister taxon to all modern carapids but at a higher branching level than the Pyramodontidae, which show a more basal otolith morphology. Since many modern carapid genera extend back in time considerably to at least early Oligocene, the occurrence of *Paracarapus* in the early Miocene of Chile might be interpreted as an evolutionary relict, i.e., as a 'living fossil' of its time. *Paracarpus* is established as a monospecific genus.

Paracarapus chilensis n. sp.
(Fig. 14b, c).

Holotype: Fig. 14b, SGO.PV.1673, Navidad Formation, Punta Perro (PPN).

Paratype: 1 specimen SGO.PV.1674, Navidad Formation, Punta Perro (PPS).

Name: Named after the country of Chile.

Diagnosis: See diagnosis of genus (monospecific genus).

Description: Compact, robust, and moderately large otoliths up to 4.1 mm length (holotype 3.9 mm). OL:OH = 1.5–1.6; OH:OT = 2.2–2.5. Dorsal rim anteriorly expanded in obtuse predorsal angle at about one third from anterior tip of otolith. Predorsal rim steeply inclined (~45°), postdorsal rim more gently inclined at ~20°, almost straight. Ventral rim shallow, somewhat flattened at mid-section. Anterior blunt, positioned below tip of sulcus; posterior tip slightly tapering, rounded positioned at level of caudal tip. All rims smooth, dorsal rim sometimes slightly undulating.

Inner face flat, smooth, only bent along horizontal axis. Sulcus slightly supramedian, long, shallow, at level with inner face. Sulcus margin more or less parallel, straight,
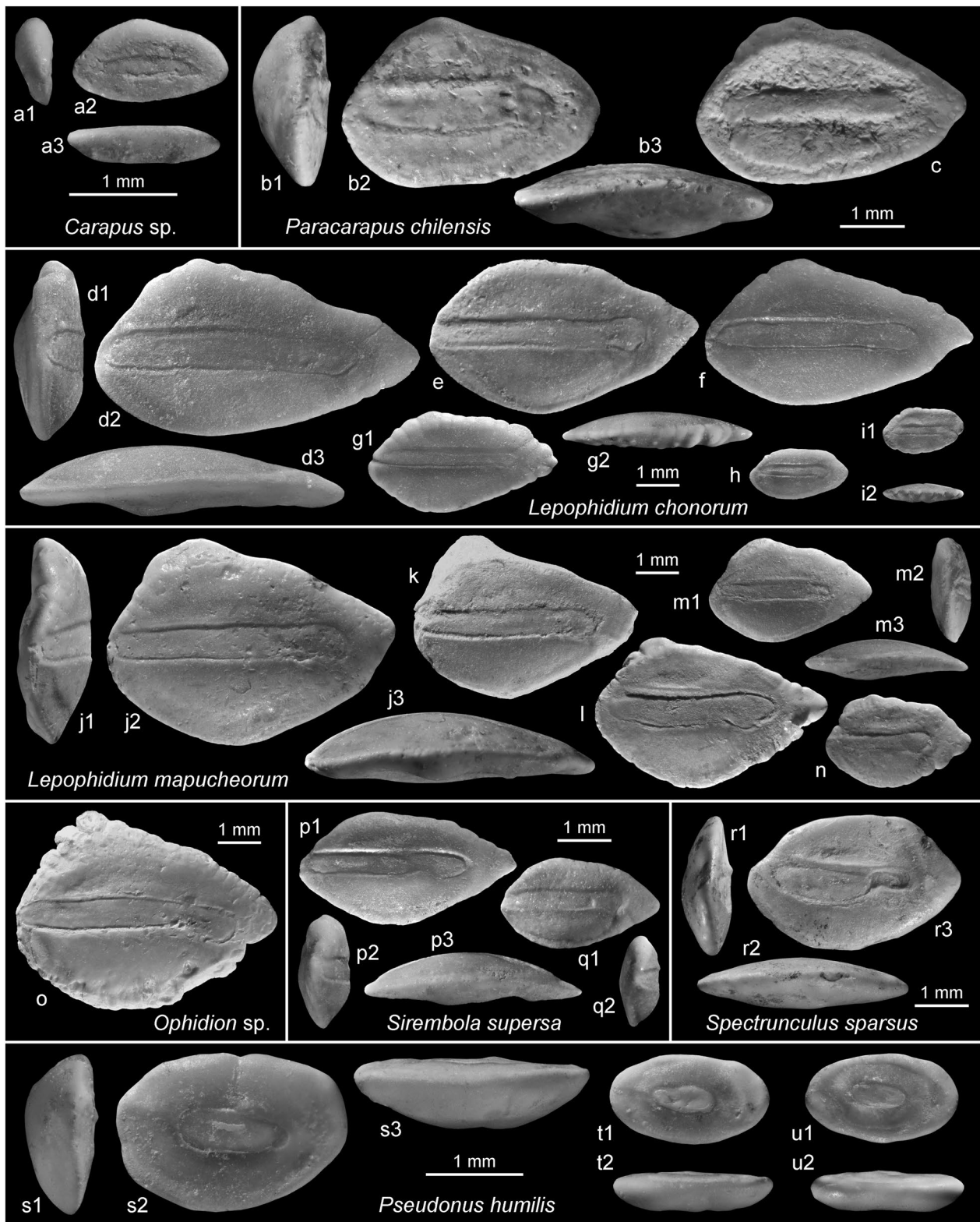
Fig. 14 (See legend on previous page.)

very slightly flexed at cauda, almost reaching anterior tip but at some distance from posterior tip. OL:SuL = 1.25–1.3. Distinction of ostium and cauda indicated by small indention of ventral margin and slight indication of fused colliculum. OsL:CaL ~ 3.0. Indistinct dorsal depression with moderate crista superior. Dorsalmost region slightly set off from inner face and bent outwards. Ventral field smooth, with variably developed ventral furrow at some distance from ventral rim of otolith. Outer face distinctly convex, smooth, its thickest portion slightly above middle of otolith. Dorsal rim slightly thicker than ventral rim.

Family Ophidiidae

Genus *Lepophidium* Gill, 1895

***Lepophidium chonorum* n. sp.**
(Fig. 14d–i).

Holotype: Fig. 14d, SGO.PV.1675, Lacui Formation, Cucao (CUC).

Paratypes: 10 specimens SGO.PV.1676, same data as holotype.

Further material: 99 specimens: 3 specimens Navidad Formation, 2 specimens, Punta Perro (PPN), 1 specimen, Matanzas (MAT); 98 specimens Lacui Formation: 5 specimens, Punta Chocoi (CHO), 91 specimens, Cucao (CUC).

Name: Named after the indigenous inhabitants of Chiloé, the type locality, the Chono.

Diagnosis: OL:OH = 1.7–1.8; OH:OT = 2.5–2.7. Predorsal expansion weak, positioned ~ 30% backwards from tip of otolith. Posterior tip expanded, pointed. Sulcus very narrow without clear separation in ostium and cauda and fused colliculi. OL:TCL = 1.25–1.3; TCL:TCH = 6.8–7.2.

Description: Slender, relatively thin otoliths up to at least 7.5 mm length (holotype). OL:OH = 1.7–1.8; OH:OT = 2.5–2.7. Dorsal rim low, nearly flat in specimens of 2.5 mm length or less and with weak to moderate, obtuse predorsal expansion in larger specimens, positioned far back from anterior tip of otolith (~ 30%). Predorsal rim inclined at 45–53°, postdorsal rim inclined at < 20°, with distinct postdorsal angle in small specimens. Ventral rim shallow, regularly curved, deepest at anterior of its midpoint. Anterior rim broadly rounded; posterior tip expanded, tapering, pointed in large specimens and rounded in small specimens. Rims smooth and dorsal rim slightly undulating in large specimens (> 5 mm length), crenulated dorsally stronger than ventrally in specimens smaller than 4–5 mm length.

Inner face moderately convex, smooth, with slightly supramedian sulcus. Sulcus long, very narrow, undivided but caudal area often somewhat widened, reaching very close to anterior tip of otolith. OL:TCL = 1.25–1.3; TCL:TCH = 6.8–7.2. Sulcus filled with single undivided shallow colliculum at level with inner face. No distinct dorsal depression; ventral furrow feeble and close to ventral rim of otolith or absent. Outer face flat, smooth in specimens > 5 mm, with numerous radial furrows in smaller specimens.

Discussion: *Lepophidium chonorum* is readily recognized by its extremely narrow sulcus, which it shares with *L. mapucheorum* n. sp. described below. The only extant species with nearly as narrow a sulcus are in the *L. microlepis* group (*L. microlepis* (Gilbert, 1905), *L. hubbsi* Robbins & Lea, 1978, *L. inca* Robbins & Lea, 1978; for figures see Schwarzhans & Aguilera, 2016) occurring as allopatric species along the shores of Pacific America from Baja California to Peru. *Lepophidium chonorum* differs from all of them in the much more elongate shape (OL:OH = 1.7–1.8 *vs* 1.5–1.6), the less sharply pointed posterior tip and the low, obtuse and far backward positioned predorsal expansion. It appears to be a species primarily distributed in the southern Chilean lower Miocene locations of the Lacui Formation.

***Lepophidium mapucheorum* n. sp.**
(Fig. 14j, n).

Holotype: Fig. 14j, SGO.PV.1677, Navidad Formation, Punta Perro (PPS).

Paratypes: 4 specimens Navidad Formation: 1 specimen SGO.PV.1680, same data as holotype; 1 specimen SGO.PV.1679, Punta Perro (PPP); 2 specimens SGO.PV.1678, Rio Rapel (RAP).

Further material: 37 specimens Navidad Formation: 4 specimens, Rio Rapel (RAP); 6 specimens, Punta Perro (PPP); 6 specimens, Punta Perro (PPN); 7 specimens, Punta Perro (PPS); 5 specimens, Punta Alta (PTA); 9 specimens, Matanzas (MAT).

Name: Named after the indigenous inhabitants of the area of the type locality, the Mapuche.

Diagnosis: OL:OH = 1.4–1.6; OH:OT = 2.5–2.8. Predorsal expansion prominent, positioned 20–25% backwards from tip of otolith. Posterior tip expanded, slightly

pointed. Sulcus very narrow without clear separation in ostium and cauda, widened cauda, and fused colliculi. OL:TCL = 1.25–1.4; TCL:TCH = 4.4–5.8.

Description: Moderately slender, and moderately thin otoliths up to at least 6.7 mm length (holotype). OL:OH = 1.4–1.6; OH:OT = 2.5–2.8. Dorsal rim relatively high, with prominent predorsal expansion positioned about 20 to 25% from anterior tip of otolith. Predorsal rim inclined at 55–65°; postdorsal rim inclined at 20–25°, with obtuse postdorsal angle in small specimens. Ventral rim deep, regularly curved, deepest at or slightly anterior of its middle. Anterior rim broadly rounded; posterior tip expanded, tapering, slightly pointed. Rims smooth, somewhat undulating, irregularly crenulated in small specimens.

Inner face moderately convex, smooth, with slightly supramedian sulcus. Sulcus long, very narrow, undivided but sometimes with indentation in ventral margin and widened caudal region, reaching very close to anterior tip of otolith. OL:TCL = 1.25–1.4; TCL:TCH = 4.4–5.8. Sulcus filled with single undivided shallow colliculum at level with inner face, sometimes with inclined furrow, leading from indentation of ventral margin of sulcus, indicating delimitation of ostium and cauda. No distinct dorsal depression; ventral furrow feeble and close to ventral rim of otolith or absent. Outer face flat, smooth or with few radial furrows in smaller specimens.

Discussion: *Lepophidium mapucheorum* differs from *L. chonorum* in being more compressed (OL:OH = 1.4–1.6 *vs* 1.7–1.8), which also results in a lesser TCL:TCH ratio of 4.4–5.8 (*vs* 6.8–7.2), and in the more strongly developed and more forwardly positioned predorsal expansion. *Lepophidium mapucheorum* appears to replace the southerly *L. chonorum* in the more northerly Navidad Formation. Both species probably form an allopatric pair characterized and differentiated from all extant species of the genus by their very narrow sulcus. The three species of the extant *L. microlepis* group (see above) resemble closest but it remains uncertain whether the early Miocene species from Chile would be related or represent an extinct group of their own.

Genus *Ophidion* Linnaeus, 1758

***Ophidion* sp.**
(Fig. 14o).

Material: A single specimen SGO.PV.1681, Navidad Formation, Punta Perro (PPS).

Discussion: This single specimen resembles in many aspects the coeval *L. mapucheorum* including the general outline and the very narrow sulcus, but differs in being slightly more compressed (OL:OH = 1.3 *vs* 1.4–1.6), the sulcus reaching close to the posterior tip of the otolith which results in a low OL:TCL ratio of 1.2 (*vs* 1.25–1.4), and the downward bending of the cauda. Because of the latter character we associate this otolith with the genus *Ophidion*.

Genus *Sirembola* Schwarzhans, 1981

***Sirembola supersa* n. sp.**
(Fig. 14p, q).

Holotype: Fig. 14p, SGO.PV.1682, Lacui Formation, Cucao (CUC).

Paratypes: 8 specimens Lacui Formation: 3 specimen SGO.PV.1683, same data as holotype; 5 specimens SGO.PV.1757, Punta Chocoi (CHO).

Name: From supersum (Latin) = surviving, referring to the occurrence of this genus in the early Miocene which previously was only known from Eocene strata.

Diagnosis: OL:OH = 1.75–1.9. No distinct predorsal expansion; dorsal rim slightly thickened. Posterior tip expanded, long, pointed. Sulcus very narrow with clear separation in ostium and cauda and separated colliculi. OL:TCL = 1.4; OCL:CCL = 2.5–2.7. Ventral field bulged.

Description: Elongate, fusiform otoliths up to 4 mm length (holotype). OL:OH = 1.75–1.9; OH:OT = 2.1–2.2. Dorsal rim relatively low with very low pre- and postdorsal angles; predorsal rim inclined at 45–50°, middorsal rim sloping at 5–10° and postdorsal rim inclined at 28–38°. Ventral rim slightly deeper than dorsal rim high, regularly curved, deepest at or slightly anterior of its middle. Anterior rim with obtuse angle at middle of section; posterior tip strongly projecting, tapering, distinctly pointed. All rims smooth, postdorsal rim sometimes slightly undulating.

Inner face strongly convex, smooth, with distinctly supramedian sulcus. Sulcus long, narrow, with long ostium and short cauda marked by separate colliculi and indentation at ventral sulcus margin. OL:TCL = 1.4; OCL:CCL = 2.5–2.7. Joint of ostial with caudal colliculum at collum, vertical or slightly forward inclined. No distinct dorsal depression; ventral furrow distinct, moderately close to ventral rim of otolith, posteriorly curving

upward to meet cauda. Ventral field slightly bulged below central portion of sulcus. Outer face flat, smooth; dorsal rim slightly thickened.

Discussion: *Sirembola supersa* resembles the parallel occurring *Lepophidium chonorum* at first sight but differs in the clearly separated ostial and caudal colliculum, the strongly bent inner face, and the slightly thickened dorsal rim. In these characters it resembles the European Eocene otoliths of *S. arcuata* (Stinton, 1966) and *S. spinosa* (Nolf & Cappetta, 1976) (see Schwarzhans, 1981 for figures) and is, therefore, considered to represent the youngest known species of this extinct otolith-based genus.

Genus *Spectrunculus* Jordan & Thompson, 1914

***Spectrunculus sparsus* n. sp.**
(Fig. 14r).

Holotype: Fig. 14r, SGO.PV.1684, Navidad Formation, Punta Perro (PPP).

Name: From sparsus (Latin)=rare, referring to the first fossil record of this genus.

Diagnosis: OL:OH=1.55. Postdorsal angle higher than predorsal angle. Inner face moderately bent in horizontal direction and nearly straight in vertical direction. Sulcus with wide, long ostium with convex lower margin and shallow colliculum. Cauda small, narrow, deepened. OL:TCL=1.6; OCL:CCL=2.5; OCH:CCH=2.0.

Description: Oval otolith of 4 mm length (holotype). OL:OH=1.55; OH:OT=2.6. Dorsal rim moderately high with depressed predorsal angle and elevated, obtuse postdorsal angle; predorsal rim inclined at 45°, long middorsal rim sloping upwards at 8° and postdorsal rim inclined at 50°. Ventral rim slightly deeper than dorsal rim high, regularly curved, deepest slightly anterior of its middle. Anterior rim with obtuse angle at middle of section; posterior tip nearly symmetrical to anterior tip in position and expression. All rims smooth.

Inner face slightly bent in horizontal direction, almost straight in vertical direction, relatively smooth, with slightly supramedian sulcus. Sulcus moderately long, slightly inclined against otolith axis at 4°, clearly divided in long ostium and short cauda marked by separate colliculi and a step in ventral sulcus margin. Dorsal margin of ostium straight, ventral margin expanded, curved; ostial colliculum distinct and shallow. Ostium not reaching anterior rim of otolith by some distance. Cauda very small and narrow, positioned along upper margin

of ostium, with deepened colliculum. OL:TCL=1.6; OCL:CCL=2.5; OCH:CCH=2.0. Dorsal depression wide, large, shallow, with indistinct margins except crista superior; ventral field smooth without clear ventral furrow. Outer face slightly convex, smooth.

Discussion: The two cosmopolitan extant species of the genus *Spectrunculus*, *S. grandis* (Günther, 1877) and *S. crassus* (Vaillant, 1888) belong to the largest benthopelagic ophidiiforms (see Schwarzhans, 1994a for otolith figures). Their otoliths achieve sizes of 15 to nearly 20 mm in length, which is up to five times the size of the holotype of *S. sparsus*. However, when comparing the otolith morphology of *S. sparsus* with that of various sizes of extant *Spectrunculus* otoliths including some of similar size (Schwarzhans, 1994a: Fig. 91) it is evident that the otolith of *S. sparsus* reflects a morphologically mature stage. Most likely, *S. sparsus* was a smaller species than the extant ones.

Despite the differences in size, there are several characters in *S. sparsus* that resemble extant *Spectrunculus* otoliths and thus support placing this species in that genus. These are the shape of the dorsal rim with the postdorsal portion being higher than the predorsal one, the proportions of the sulcus and the ostium with a straight dorsal and a convex ventral margin and the lack of a clear ventral furrow. *Spectrunculus sparsus* differs from the extant species in the cauda being considerably narrower and deeper than the ostium. The latter character is considered plesiomorphic.

Extant *Spectrunculus* otoliths show two different morphologies in otolith outline, which have been interpreted as an expression of sexual dimorphism by Schwarzhans (1994a) following a review of the genus by Nielsen and Hureau (1980) who recognized only a single valid species. A more recent review by Uiblein et al. (2008), however, resurrected *S. crassus*, which also led to previous morphological differences in otoliths thought to represent sexual dimorphism being submerged in the variability range of both species, leaving very little to distinguish both extant species by means of otoliths (see Uiblein et al., 2008). The fossil *S. sparsus* does not directly relate to either of the two extant species.

Suborder Bythitoidei

Family Bythitidae

Genus *Pseudonus* Garman, 1899

***Pseudonus humilis* n. sp.**
(Fig. 14 s−u).

Holotype: Fig. 14s, SGO.PV.1685, Navidad Formation, Punta Perro (PPP).

Paratypes: 10 specimens: 9 specimen SGO.PV.1686, same data as holotype; 1 specimen SGO.PV.1758, Ipún beds, Lemo Island (LEM 01).

Name: From humilis (Latin) = humble, referring to the unspectacular appearance of the otoliths.

Diagnosis: OL:OH = 1.45–1.75, decreasing with size. Outline regular oval. Inner face flat. Sulcus short, oval, undivided, located on center of inner face, inclined at 5–8° against otolith axis. OL:TCL = 1.8–2.2; TCL:TCH = 2.3–2.8. Sulcus connected to anterior rim of otolith by narrow, weak ridge. Ventral furrow indistinct, distant from ventral rim of otolith.

Description: Oval, moderately elongate otoliths up to 2.35 mm length (holotype). OL:OH = 1.7–1.75 in specimens up to 1.65 mm length, 1.45 in holotype of 2.35 mm length; OH:OT = 2.2–2.3. Oval outline without prominent angles; anterior and posterior rims regularly rounded; dorsal rim sometimes shallower than ventral rim. All rims smooth, dorsal rim sometimes slightly undulating.

  Inner face completely flat, with centrally positioned, short, oval, undivided, shallow sulcus. OL:TCL = 1.8–2.2; TCL:TCH = 2.3–2.8. Sulcus slightly inclined at 5 to 8° against otolith axis, with uniform, well-marked colliculum. Sulcus connected to tip of anterior rim by subtle narrow ridge. No distinct dorsal depression; ventral furrow indistinct, distant from ventral rim of otolith. Outer face convex, smooth.

Discussion: Bythitid otoliths exhibit a strongly simplified morphology concerning the otolith and sulcus outlines, which considerably hampers the allocation to specific genera. *Pseudonus humilis* is placed in the genus *Pseudonus* because of the similarity of the short, oval, and slightly inclined sulcus, the flat inner face, and the presence of the ridge connecting the sulcus with the anterior rim of the otolith, all of which resembles otoliths of the two extant species of *Pseudonus* (unpublished data) in this combination. *Pseudonus* is considered to be derived from *Cataetyx* according to Cohen and Nielsen (1978) and contains two extant species: *P. acutus* Garman, 1899 living bathydemersal at 915 to 1620 m in the Eastern Pacific from Panama to Peru (Froese & Pauly 2020) and *P. squamiceps* (Lloyd, 1907) occurring bathydemersal from 412 to 1270 m in the Indo-West Pacific (Froese & Pauly 2020). This is the first fossil record of the genus.

Order Trachichthyiformes

Family Trachichthyidae

Genus *Hoplostethus* Cuvier, 1829

***Hoplostethus* sp.**
(Fig. 15a)

Material: One specimen, SGO.PV.1687, Ranquil Formation, Lebu (LEB).

Discussion: The single eroded juvenile specimen of 2.65 mm length shows all the typical hallmarks of *Hoplostethus* otoliths in otolith shape and sulcus morphology, but because of its poor preservation cannot be identified in any further detail. Species of *Hoplostethus* occur with many species worldwide in the bathypelagic zone.

Order Zeiformes

Family Zeniontidae

Genus *Capromimus* Gill, 1893

***Capromimus undulatus* n. sp.**
(Fig. 15b).

Holotype: Fig. 15b, SGO.PV.1688, Navidad Formation, Punta Perro (PPP).

Name: From undulatus (Latin) = undulating, referring to the broadly and strongly undulating postventral rim.

Diagnosis: Very high bodied otolith; OL:OH = 0.7. Rostrum broadly rounded. Postventral rim steeply ascending, broadly and strongly undulating with two distinct and wide concave stretches. Colliculi very small, round, widely separated, not expanding into broad anterior and posterior excisurae. Ridge-like crista inferior below wide collum with underlying broad ventral concavity.

Description: Delicate and fragile otolith of about 2.35 mm length and 3.25 mm height. OL:OH = 0.7; OH:OT = 4.8. Dorsal rim high, regularly rounded (postdorsal region incomplete). Ventral rim very deep, anteriorly broadly rounded, with distinct projection below ostial colliculum; postventral rim broadly undulating with two distinct, long, regular, and deep concavities. Anterior rim with broadly rounded, blunt rostrum, shorter, rounded antirostrum and wide, regularly concave excisura. Posterior rim with wide posterior excisura, albeit less wide than anterior excisura and short rounded

(See figure on next page.)
Fig. 15 a *Hoplostethus* sp., LEB (reversed), SGO.PV.1687. **b** *Capromimus undulatus* n. sp., holotype, PPP, SGO.PV.1688. **c** Platycephalidae indet., PPN, SGO.PV.1689. **d** Scorpaenidae indet., PTA (reversed), SGO.PV.1690. **e–g** Scorpaenoidei indet., RAP (g reversed), SGO.PV.1691. **h–j** *Agonopsus cume* n. sp.; **h** holotype, RAP, SGO.PV.1692; **i** paratype, RAP (reversed), SGO.PV.1693; **j** paratype, PPN, SGO.PV.1694. **k** *Agonopsis vulsa* (Jordan & Gilbert, 1880), Recent, off California, coll. Schwarzhans, leg. Fitch. **l, m** *Normanichthys crockeri* Clark, 1937, Recent, off Lenga, Concepción, Chile, coll. Schwarzhans, leg. ZMH. **n–o** *Cottunculus primaevus* n. sp.; **n** holotype, CUC (reversed), SGO.PV.1695; **o** paratype, RAP (reversed), SGO.PV.1696. **p** *Cottunculus microps* Collett, 1875, Recent, 63°02′N—11°18′W, coll. Schwarzhans, leg. FBH. **q** *Cottunculus granulosus* Karrer, 1968, Recent, Walter Herwig st. 1029/78, coll. Schwarzhans, leg. FBH

section below. All rims smooth except undulations of postventral rim.

Inner face overall flat but dorsal and ventral tips slightly convex and sulcus and region below massive crista inferior broadly excavated. Sulcus anteriorly and posteriorly open (biostial), with small, round, widely separated colliculi opening to anterior and posterior excisurae, respectively, but without extruding out. Colliculi well marked by color difference in the unique holotype and slightly elevated. Collum distinctly wider than width of colliculi, underlain by strong, ridge-like crista inferior. No dorsal depression or ventral furrow. Outer face flat, smooth.

Discussion: Zeiform otoliths belong to the most spectacular morphologies in today's teleosts and the same is true for the species described here. Due to their fragility, they are rarely recorded in the fossil record. The specimen described here is a rather large specimen for the group and certainly fully diagnostically mature despite the fact that it partially lacks the postdorsal portion.

Nolf and Tyler (2006) conducted a comprehensive review of the otoliths of this group, in which they depicted the great diversity found in zeiform otoliths. Clearly, the morphologies found in otoliths of the Cyttopsidae (or Cyttopsinae of Parazenidae) and of certain genera of the Zeniontidae most closely resemble the fossil otolith from the early Miocene of Chile. Cyttopsid otoliths are ruled out based on their low dorsal rim and symmetrical ventral rim. Zeniontidae contain three genera, of which *Zenion* does not show a biostial sulcus organization, while the two other genera, *Capromimus* and *Cyttomimus*, do. *Capromimus* contains a single extant species, *Capromimus abbreviatus* (Hector, 1874), which is endemic to New Zealand, and *Cyttomimus* two species, *Cyttomimus stelgis* Gilbert, 1905, which is known from off Hawaii and Chile (see Nolf & Tyler, 2006: pl. 3, fig. 7), and *Cyttomimus affinis* Weber, 1913 from the West Pacific. Otoliths of *Cyttomimus* differ in the laterally reduced dorsal field and the large colliculi extending into the anterior and posterior excisurae. The otolith of *Capromimus abbreviatus* (see Nolf & Tyler, 2006: pl. 3, fig. 6), in contrast, closely resembles *Capromimus undulatus* from the early Miocene of Chile, specifically in the

high dorsal rim, the asymmetrical ventral rim, and the non-extruding colliculi. *Capromimus undulatus* differs in the broadly undulating postventral rim and the broadly rounded rostrum and posterior rostrum (*vs* angular) and in being even more compressed (OL:OH = 0.7 *vs* 0.9). *Capromimus undulatus* shows that *Capromimus*, presently a monotypic genus endemic to New Zealand, was more widely distributed in the South Pacific during the Miocene.

Order Scorpaeniformes

Suborder Scorpaenoidei

Family Scorpaenidae

Scorpaenidae indet
(Fig. 15d).

Material: 2 specimens, Navidad Formation: 1 specimen SGO.PV.1690, Punta Alta (PTA); 1 specimen SGO.PV.1759, Matanzas (MAT).

Discussion: The two rather poorly preserved otoliths may represent an unknown species of the Scorpaenidae.

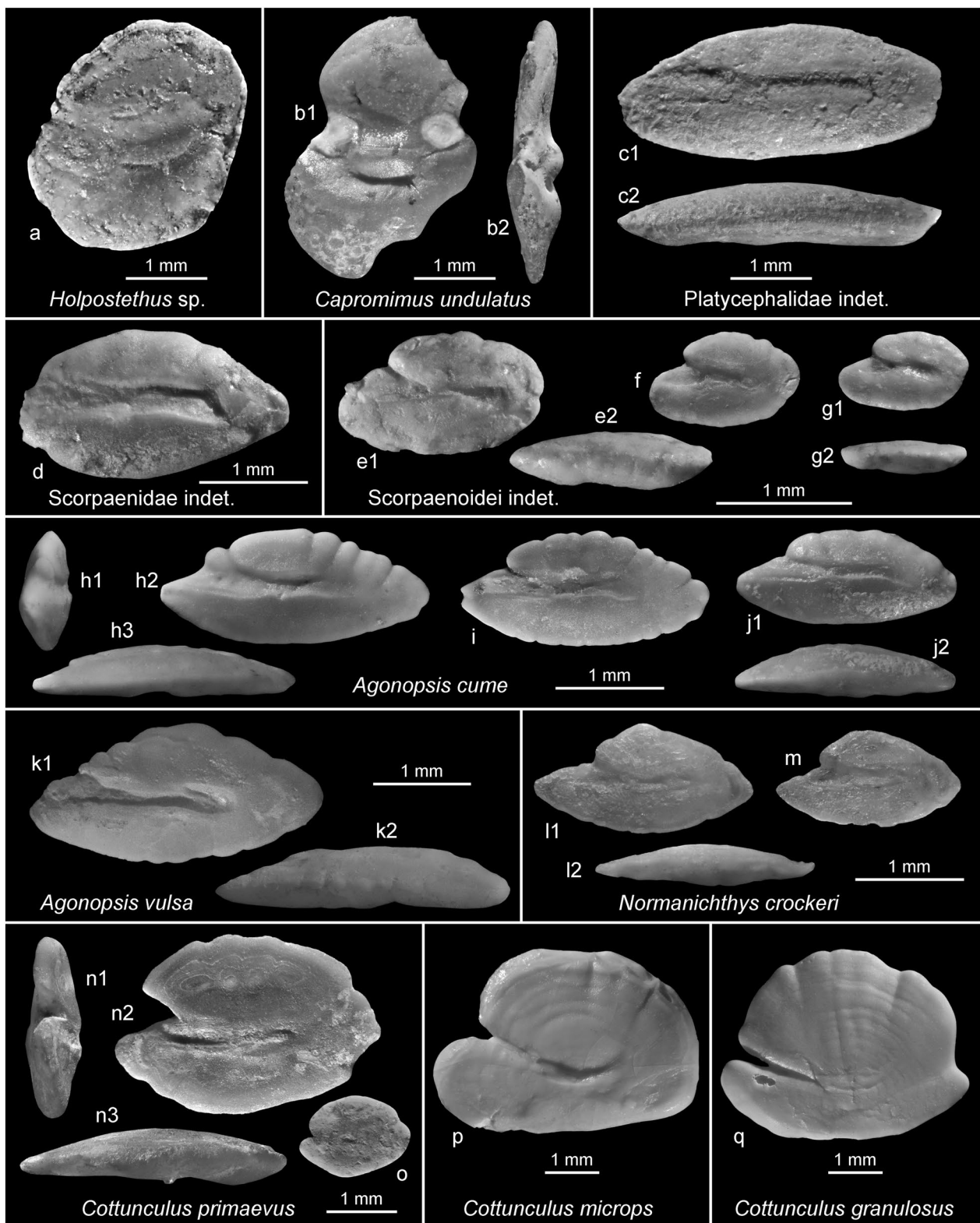### Family indet

Scorpaenoidei indet
(Fig. 15e–g).

Material: 5 specimens: 4 specimens SGO.PV.1691, Navidad Formation, Rio Rapel (RAP); 1 specimen SGO.PV.1760, Lacui Formation, Chiloé (CUC).

Discussion: Five surely juvenile specimens of about 1 mm length are grouped here that likely represent some sort of unresolved scorpaenoid fish.

Suborder Platycephaloidei

Family Platycephalidae

Genus indet.

Holpostethus sp.

Capromimus undulatus

Platycephalidae indet.

Scorpaenidae indet.

Scorpaenoidei indet.

Agonopsis cume

Agonopsis vulsa

Normanichthys crockeri

Cottunculus primaevus

Cottunculus microps

Cottunculus granulosus

Fig. 15 (See legend on previous page.)

Platycephalidae indet.
(Fig. 15c).

Material: 3 specimens: 2 specimens SGO.PV.1689, Navidad Formation, Punta Perro (PPN); 1 specimen SGO.PV.1761, Lacui Formation, Punta Chocoi (CHO).

Discussion: Three poorly preserved but relatively large sized specimens may represent an unresolved platycephalid species. This would represent the first East Pacific record for the family both extant and fossil.

Suborder Cottoidei

Family Agonidae

Genus *Agonopsis* Gill, 1861

***Agonopsis cume* n. sp.**
(Fig. 15 h–j).

Holotype: Fig. 15 h, SGO.PV.1692, Navidad Formation, Rio Rapel (RAP).

Paratypes: 5 specimens: 4 specimen Navidad Formation: 2 specimens SGO.PV.1693, same data as holotype; 1 specimen SGO.PV.1694, Punta Perro (PPN); 1 specimen SGO.PV.1762, Matanzas (MAT); 1 specimen SGO.PV.1763, Lacui Formation, Cucao (CUC).

Name: Short form of cumulatius (Latin) = cumulative, referring to the cumulative aspect of characters and possible interpretations.

Diagnosis: OL:OH = 2.15–2.35. Otolith shape fusiform with symmetrically pointed rostrum and posterior tip. Inner face distinctly convex; outer face flat. Ostium slightly widening towards anterior, particularly dorsally, longer than cauda; OsL:CaL = 1.1–1.2. Cauda slightly flexed close to termination.

Description: Small, elongate, fusiform otoliths up to 2.5 mm length (holotype). Dorsal rim shallow, gently curving, irregularly and rather strongly crenulated. Ventral rim shallow, gently curving, smooth or finely crenulated. Highest points of both rims approximately at middle. Rostrum long, sharply pointed, about 20% of OL. Antirostrum and excisura very small. Posterior tip expanded, pointed, almost symmetrical to rostrum.
  Inner face distinctly convex with slightly supramedian, slightly deepened, narrow sulcus. Sulcus anteriorly open, posteriorly terminating distant from posterior rim

of otolith. OL:SuL = 1.35–1.4. Ostium slightly longer than cauda; OsL:CaL = 1.1–1.2. Ostium slightly widened ventrally at collum and with horizontal ventral margin; dorsal margin of ostium slightly ascending towards tip of antirostrum. Cauda narrow, deeper than ostium, slightly flexed towards rear. Dorsal depression small, indistinct; ventral furrow indistinct or absent. Outer face flat with little ornamentation.

Discussion: *Agonopsis cume* is an unspectacular otolith resembling a variety of scorpaeniform morphologies. Two groups occurring presently in Chilean waters resemble it closest: species of the antitropical East Pacific and South–West Atlantic genus *Agonopsis* of the Agonidae and *Normanichthys crockeri* Clark, 1937, the sole species and genus of the enigmatic Normanichthyidae and suborder Normanichthyioidei known exclusively off southern Peru and Chile. For comparison, otoliths are figured of the extant species *Agonopsis vulsa* (Jordan & Gilbert, 1880) (Fig. 15 k) and *Normanichthys crockeri* (Fig. 15 l, m). Both are very similar to *Agonopsis cume* in shape and general sulcus organization, but in *Normanichthys* the cauda is even shorter (OsL:CaL = 1.3 *vs* 1.1–1.2) and the cauda is completely straight without any flexure towards its termination. Such flexure is present in *Agonopsis vulsa*, and we consider this character as most indicative for systematic allocation.

Family Psychrolutidae

Genus *Cottunculus* Collett, 1875

***Cottunculus primaevus* n. sp.**
(Fig. 15n, o).

Holotype: Fig. 15n, SGO.PV.1695, Lacui Formation, Cucao (CUC).

Paratype: 1 specimen SGO.PV.1696, Navidad Formation, Rio Rapel (RAP).

Name: From primaevus (Latin) = primeval, referring to the early occurrence of the species representing the earliest fossil record of the genus and family.

Diagnosis: Oval otolith with deep and wide excisura. OL:OH = 1.3–1.45. Ventral rim regularly curved. Ostium distinctly longer than cauda; OsL:CaL = 1.4.

Description: Oval otoliths with irregularly undulating rims up to 3.7 mm length (holotype). OL:OH = 1.3–1.45; OH:OT = 3.4. Dorsal and ventral rims regularly curved, dorsal rim higher than ventral rim. Anterior tip with

deeply incised and rather wide excisura, appearing like an incision into the oval shape; rostrum and antirostrum well developed, rostrum slightly longer than antirostrum. Posterior rim rounded.

Inner face distinctly convex with central to slightly inframedian positioned, short, narrow sulcus. OL:SuL = 1.6–2.0. Ostium longer than cauda, slightly widening anteriorly, its margins somewhat fading; cauda small, oval, deepened, centrally positioned on inner face, and well-marked. OsL:CaL = 1.4. No distinct dorsal depression; no ventral furrow. Outer face flat to slightly convex in small specimens, somewhat irregular but smooth.

Discussion: Psychrolutid otoliths are characterized by a narrow, mostly inframedian positioned sulcus with small and distinct cauda, and an ostium with fading margins that in some genera completely disappear. In *Cottunculus* the ostium is usually transformed to a poorly defined but deep furrow connecting the cauda with the excisura of the anterior otolith rim: see figures of *C. microps* Collett, 1875 (Fig. 15p) and *C. granulosus* Karrer, 1968 (Fig. 15q) for comparison. In *C. primaevus*, the expression of the ostium varies from rather well-defined in the large holotype (Fig. 15p2) to nearly absent in the small paratype of 1.6 mm length (Fig. 15q). It further differs from the extant species in the more strongly bent ventral rim. *Cottunculus* contains 8 recognized valid species (Froese & Pauly 2020) occurring bathydemersal on the lower shelf and continental slope from about 150 to 1300 m with a bipolar distribution pattern in polar to cold temperate climates, mostly in the northern hemisphere. The only species presently occurring off South America, off Argentina and Chile, is *C. granulosus*. The recognition of *C. primaevus* in the early Miocene of Chile indicates a long presence of the genus in South America.

Order Perciformes

Suborder Percoidei

Family Kuhliidae

Genus *Kuhlia* Gill, 1861

***Kuhlia orientalis* n. sp.**
(Fig. 16a–c).

Holotype: Fig. 16a, SGO.PV.1697, Navidad Formation, Rio Rapel (RAP).

Paratype: 7 specimens: 5 specimens Navidad Formation: 2 specimens SGO.PV.1699, Punta Perro (PPN); 2 specimens SGO.PV.1764, Punta Perro (PPS); 1 specimen SGO.PV.1698, Matanzas (MAT); 2 specimens SGO.PV.1765, Lacui Formation, Cucao (CUC).
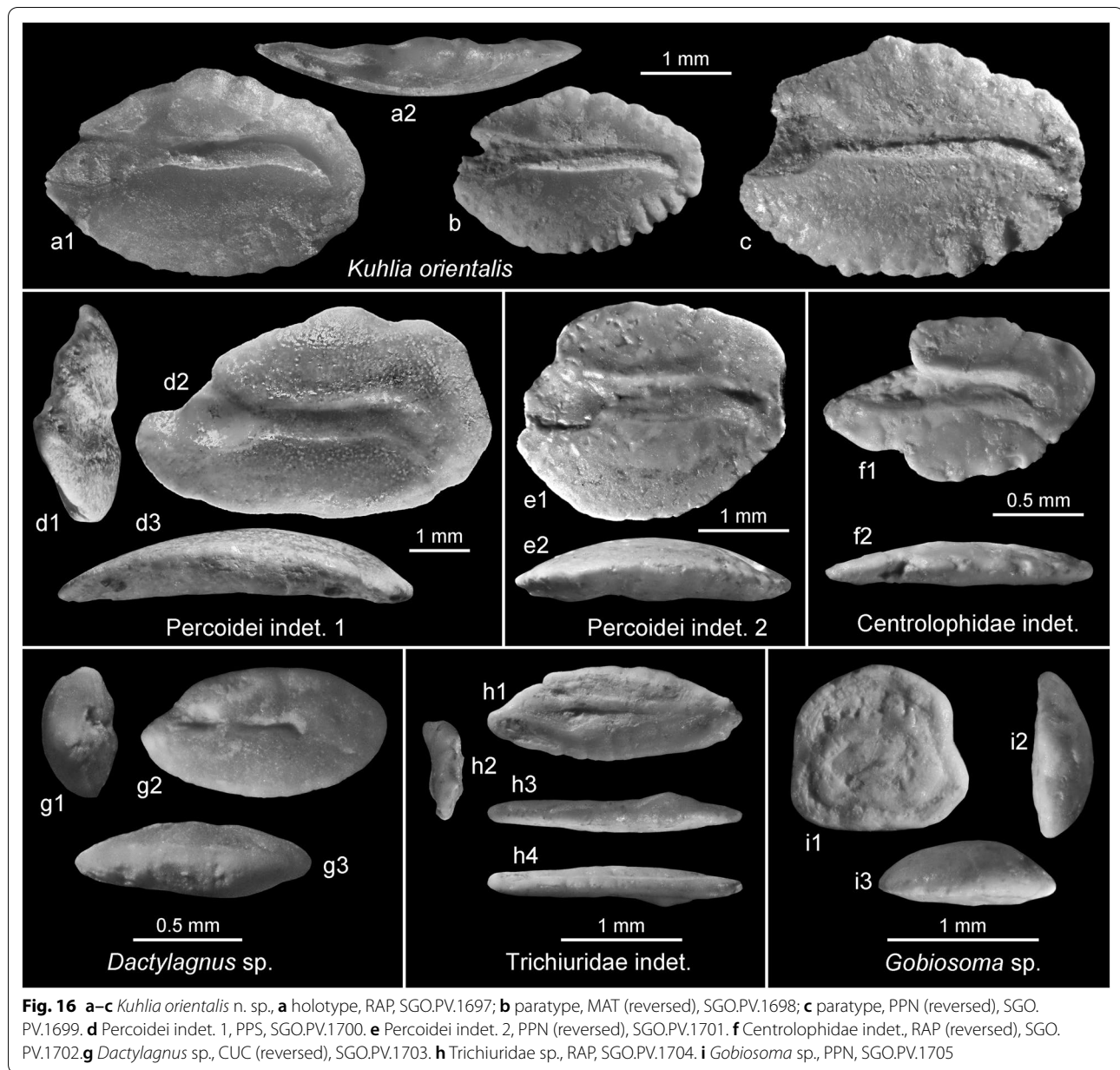
Name: From orientalis (Latin) = easterly, referring to the occurrence in the East Pacific.

Diagnosis: OL:OH = 1.5–1.55. Dorsal rim highest middorsal, irregularly undulating. Ventral rim regularly curved, postventral region crenulated or serrated. Cauda narrow, not widening anteriorly. Ostium ventrally widened and less so dorsally. CaL:OsL = 1.85–2.0; OsH:CaH = 2.0–2.1.

Description: Small, delicate, thin otoliths with elongate oval outline up to at least 4.1 mm length (reconstruction of largest specimen, Fig. 16c; holotype 3.55 mm). OL:OH = 1.5–1.55; OH:OT = 3.6. Dorsal rim shallower than ventral rim, highest middorsal, coarsely undulating or crenulated. Ventral rim relatively deep, regularly curved, anteriorly smooth or slightly undulating, posteriorly crenulated or serrated. Anterior rim with short, obtuse rostrum at middle of section; rostrum length about 12% of OL. Antirostrum and excisura small. Posterior tip somewhat tapering, rounded.

Inner face distinctly convex with narrow, moderately deep, and long supramedian sulcus. OL:SuL = 1.1. Ostium about half the length of cauda but twice as wide, particularly ventrally widened. CaL:OsL = 1.8–2.0; OsH:CaH = 2.0–2.1. Cauda long, slender, equally wide throughout, slightly flexed towards its termination, slightly swinging along its central section. Dorsal depression weak, indistinct; very feeble ventral furrow distant from ventral rim. Some radial furrows ingressing onto inner face, particularly ventrally and there extending up to ventral furrow. Outer face flat to slightly concave with some radial furrows.

Discussion: *Kuhlia* otoliths are relatively easily recognized by their very specific shape and proportions of the sulcus and its position on the inner face. So far, a single fossil otolith-based species has been described from the late Oligocene and early Miocene of Europe—*Kuhlia tenuicauda* (Schwarzhans, 1974) with *K. avitensis* Steurbaut, 1984 as junior synonym—and another occurrence has been recorded as *Kuhlia* sp. from the early Miocene (Altonian) of New Zealand by Schwarzhans (2019a). All these records are very similar in otolith shape and proportions. *Kuhlia orientalis* differs from *K. tenuicauda* in the lack of an anteriorly widening cauda and the rather strong ornamentation of the dorsal rim which also appears to be slightly higher. The specimen from New Zealand appears to have a comparatively longer cauda than the specimens from Chile (CaL:OsL = 2.2 *vs*

Fig. 16 a–c *Kuhlia orientalis* n. sp., **a** holotype, RAP, SGO.PV.1697; **b** paratype, MAT (reversed), SGO.PV.1698; **c** paratype, PPN (reversed), SGO.
PV.1699. **d** Percoidei indet. 1, PPS, SGO.PV.1700. **e** Percoidei indet. 2, PPN (reversed), SGO.PV.1701. **f** Centrolophidae indet., RAP (reversed), SGO.
PV.1702.**g** *Dactylagnus* sp., CUC (reversed), SGO.PV.1703. **h** Trichiuridae sp., RAP, SGO.PV.1704. **i** *Gobiosoma* sp., PPN, SGO.PV.1705

1.8–2.0) and has a dorsally shifted posterior tip and thus may not represent the same species.

Today, *Kuhlia*, the sole genus of the Kuhliidae, contains 12 recognized valid species living in shallow water marine to brackish and occasionally freshwater environments and chiefly distributed in the Indo-West Pacific with one species having extended its range to the tropical East Pacific.

Family indet.

Percoidei indet. 1

(Fig. 16d).

Material: One specimen SGO.PV.1700, Navidad Formation, Punta Perro (PPS).

Discussion: The single, relatively large otolith of 5.9 mm length is complete, robust, and somewhat leached on the surface. It shows a strongly undulating dorsal rim which is postdorsally pronounced, a shallow and smooth ventral rim, a long, massive, inferior rostrum and a broad, blunt posterior tip. On the distinctly convex inner face is a long sulcus with a shorter, anteriorly opening and widened

ostium, and a narrower and longer cauda, which is markedly flexed downwards towards its termination relatively close to the postventral corner of the otolith. This is a typical percoid otolith morphology found in many serranid or sparid fishes but also percichthyids, which for South America would offer a further alternative. No definitive allocation or diagnosis can be provided on the base of the single specimen.

Percoidei indet. 2
(Fig. 16e).

Material: 3 incomplete specimens Navidad Formation: 1 specimen SGO.PV.1701, Punta Perro (PPN); 2 specimens SGO.VP.1766, Rio Rapel (RAP).

Discussion: These compressed otoliths resemble morphologies found in certain Sparidae, Haemulidae, or Lactariidae.

Order Blenniiformes

Family Dactyloscopidae

Genus *Dactylagnus* Gill, 1863

Dactylagnus sp.
(Fig. 16 g).

Material: 1 specimen SGO.PV.1703, Lacui Formation, Cucao (CUC).

Discussion: A single, very small, elliptical otolith is interpreted to represent what would be the second fossil otolith record of a dactyloscopid, the other being from the late Miocene of the Dominican Republic (Nolf & Stringer, 1992). Dactyloscopid otoliths are indeed very small, characterized by rather deep ostium and cauda, often separated by a slightly elevated collum like in this specimen, whereby the ostium is anteriorly open and not substantially wider than the cauda, a narrow and short sulcus and a distinctly convex inner face. The otolith of *Dactylagnus* sp. has a ratio OL:OH of 1.9, a ratio OH:OT of 1.75 and a smooth elliptical outline without significant angles or incisions except for a very small excisura. The sulcus proportions are: OL:TCL = 1.55; OsL:CaL = 1.1. Otoliths of the only extant dactyloscopid from Chile—*Syndoscopus australis* (Fowler & Bean, 1923)—are not known.

Order Scombriformes

Family Centrolophidae

Genus indet

Centrolophidae indet
(Fig. 16f).

Material: 2 specimens SGO.PV.1702, Navidad Formation, Rio Rapel (RAP).

Discussion: Two small otoliths of 1.5 mm length might represent an unresolved centrolophid. The otoliths are thin, flat, and characterized by a long and sharp rostrum, deep and wide, almost orthogonal excisura, and a vaguely divided sulcus with the cauda slightly flexed towards its end.

Family Trichiuridae

Genus indet

Trichiuridae indet
(Fig. 16h).

Material: 2 specimens Navidad Formation: 1 specimen SGO.PV.1704, Rio Rapel (RAP); 1 specimen SGO.VP.1767, Punta Alta (PTA).

Discussion: Small, about 2 mm long and probably juvenile otoliths with a distinctive thickening of the postdorsal rim on the outer face represent a typical trichiurid morphology.

Order Gobiiformes

Family Gobiidae

Genus *Gobiosoma* Girard, 1858

Gobiosoma sp.
(Fig. 16i).
Material: 2 specimens SGO.PV.1705, Navidad Formation, Punta Perro (PPN).

Discussion: Small, somewhat eroded otoliths of 1.2 mm length, characterized by the ventral region of the otolith being wider than the dorsal region, a flat inner and convex outer face, a small sulcus without prominent ostial lobe or subcaudal iugum, probably represent an undescribed species of *Gobiosoma*. Recently, a similar looking otolith has been described as *Gobiosoma*? *axsmithi* Ebersole, Cicimurri & Stringer, 2021 from the Oligocene of Alabama, USA (Ebersole et al., 2021). However,

the preservation of the two unique specimens and their probably immature size do not allow a specific definition.

Order Pleuronectiformes

Suborder Pleuronectoidei

Family Paralichthyidae

Genus *Citharichthys* Bleeker, 1862

Citharichthys parvisulcus n. sp.
(Fig. 17a–g).

Holotype: Fig. 17 d, SGO.PV.1706, Navidad Formation, Punta Perro (PPS).

Paratypes: 6 specimens Navidad Formation: 2 specimen SGO.PV.1709, Rio Rapel (RAP); 1 specimen SGO.PV.1710, Punta Perro (PPN); 2 specimens SGO.PV.1708, Punta Alta (PTA); 1 specimen SGO.PV.1707, Matanzas (MAT).

Further material: 26 specimens: 22 specimens Navidad Formation: 13 specimens, Rio Rapel (RAP), 3 specimens, Punta Perro (PPP), 1 specimen, Punta Perro (PPN), 1 specimen, Punta Perro (PPS), 2 specimens, Punta Alta (PTA), 1 specimen, Matanzas (MAT); 2 specimens Ranquil Formation: 1 specimen, Ranquil (RQS), 1 specimen, Lebu (LEB); 2 specimens, Lacui Formation, Cucao (CUC); 1 specimen, Ipún beds, Lemo Island (LEM 01).

Name: From parvus (Latin) = small in combination with the morphological term sulcus referring to its small size.

Diagnosis: OL:OH = 0.95–1.0 in left otoliths, 0.97–1.05 in right otoliths. Dorsal rim much expanded, particularly postdorsal. Ventral rim with sharp angle anterior of its middle; postventral section straight, steeply inclined at 35–40°. Inner face flat. Sulcus very small; OL:TCL = 3.1–3.8. Distinct, wide diagonal furrow in circumsulcal depression postdorsal, inclined at 40–50°.

Description: Small, robust, high bodied, and rather thick otoliths up to 2 mm length (holotype 1.8 mm). OL:OH = 0.95–1.05, left otoliths tending to be slightly more compressed than right otoliths; OH:OT = 2.8–3.0. Outline spectacular with high dorsal rim, anteriorly slightly depressed, posteriorly broadly expanded. Ventral rim deep, with sharp angle slightly in front of its midpoint, anteriorly broadly rounded, posteriorly almost straight, inclined at 35–40°. Anterior rim blunt, broadly rounded, expanded dorsally as well as below sulcus; posterior tip short, angular, positioned at about level of sulcus at joint with straight postventral rim, and with variably shaped concavity towards dorsal rim.

Inner face flat with very small, centrally positioned, shallow, undivided sulcus with undivided colliculum. OL:TCL = 3.1–3.8. Circumsulcal depression very broad and complete except for small ridge-like feature connecting sulcus with anterior rim of otolith. Distinct, wide diagonal furrow in postdorsal position at angle of 40–50°, intersecting with posterior tip of sulcus. Outer face convex, smooth.

Side dimorphism: Pleuronectiform otoliths are the only ones that regularly exhibit side dimorphism to various degrees (Schwarzhans, 1999). In the case of *C. parvisulcus* only few left otoliths are available and they seem to show only minor differences to the right otoliths, mainly in being generally more compressed (OL:OH = 0.95–1.0 vs 0.97–1.05).

Discussion: These are very characteristic otoliths that are similar to extant otoliths of the nominal pleuronectiform genera *Citharichthys*, *Etropus*, and *Orthopsetta*. When compared to the extant otoliths figured in Schwarzhans (1999), those of *Orthopsetta* are the most similar due to their high body, expanded dorsal and deep ventral rim, and reduced sulcus. However, since Norman (1934), the genus *Orthopsetta* has been regarded as junior synonym of *Citharichthys* with the exception of Schwarzhans (1999) based on the study of otoliths of the Pleuronectiformes. We believe that further assessments of the validity of the three nominal genera involved should be delayed until such time as detailed results of molecular studies are available and have, therefore, refrained from using *Orthopsetta* at this time.

Citharichthys parvisulcus is readily recognized by the high body shape, the expanded dorsal rim, the asymmetrical ventral rim with the long straight postventral section, the wide and deep furrow in the postdorsal section of the circumsulcal depression, and the small sulcus. The closest extant species appears to be *Citharichthys cornutus* (Günther, 1880) from the Atlantic realms of South America (see Schwarzhans, 1999: Figs. 290–291), from which it differs in the forward position of the ventral angle and the long straight postventral rim and the postdorsal rim being higher than the predorsal section (*vs* predorsal section higher than postdorsal section). Other comparable otolith morphologies of extant species are observed in *C. sordidus* (Girard, 1856; see Schwarzhans,
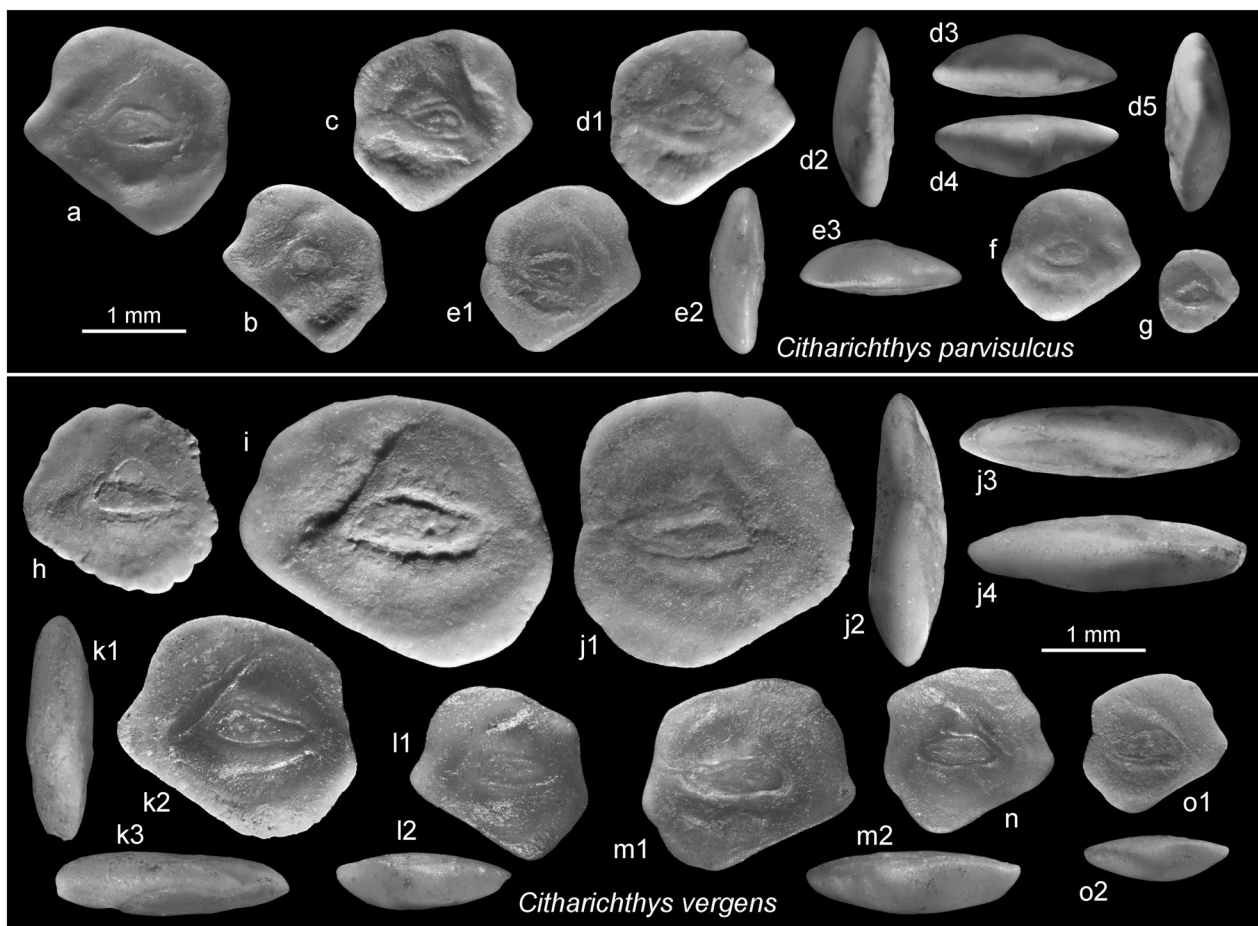
Fig. 17 **a–g** *Citharichthys parvisulcus* n. sp.; **d** holotype, PPS (right otolith), SGO.PV.1706; **a** paratype, MAT (left otolith), SGO.PV.1707; **b, c** paratypes, PTA (b left otolith, c right otolith), SGO.PV.1708; **e, g** paratypes, RAP (right otoliths), SGO.PV.1709; **f** paratype, PPN (right otolith), SGO.PV.1710. **h–o** *Citharichthys vergens* n. sp.; **k** holotype, CUC (left otolith), SGO.PV.1711; **h, j** paratypes, CUC (h left otoliths, j right otolith), SGO.PV.1712; **i** paratype, CHO (left otolith), SGO.PV.1713; **l–o** paratypes, RAP (l left otolith, m–o right otoliths), SGO.PV.1714

1999: Figs. 279–282) and *C. xanthostigma* (Gilbert, 1890) (see Schwarzhans, 1999: Figs. 284–285), both from the Pacific coast of North America, but these further differ in the shape of the ventral and posterior rims. There are no *Citharichthys* or *Etropus* species known today from off Chile, and otoliths known from those species occurring off Peru do not compare to that of *C. parvisulcus.*

Citharichthys vergens **n. sp.**
(Fig. 17h–o).

Holotype: SGO.PV.1711 (Fig. 17k), Lacui Formation, Cucao (CUC).

Paratypes: 7 specimens; 4 specimens Navidad Formation SGO.PV.1714, Rio Rapel (RAP); 3 specimens Lacui

Formation: 2 specimens SGO.PV.1712, same data as holotype; 1 specimen SGO.PV.1713, Punta Chocoi (CHO).

Further material: 156 specimens: 51 specimens Navidad Formation: 31 specimens, Rio Rapel (RAP), 1 specimen, Punta Perro (PPP), 12 specimens, Punta Perro (PPN), 4 specimens, Punta Perro (PPS); 105 specimens Lacui Formation: 17 specimens, Punta Chocoi (CHO), 88 specimens, Cucao (CUC).

Name: From vergens (Latin) = inclined, referring to the shape of the postventral rim.

Diagnosis: OL:OH = 1.0–1.15 in left and right otoliths. Dorsal rim much expanded, particularly postdorsal. Ventral rim with sharp angle anterior of its middle; postventral section straight, inclined at 25–32°. Inner face slightly convex. Sulcus small; OL:TCL = 2.2–2.6. Distinct,

relatively narrow diagonal furrow in circumsulcal depression postdorsal, inclined at 40–50°.

Description: Small, high bodied and moderately thick otoliths up to 3 mm length (holotype 2.3 mm). OL:OH = 1.0–1.15; OH:OT = 3.0–3.5, increasing with size. Outline spectacular with high dorsal rim, anteriorly slightly lower than posteriorly. Ventral rim deep, with rounded to moderately sharp angle slightly in front of its middle, anteriorly broadly rounded, posteriorly almost perfectly straight, inclined at 25–32°. Anterior rim blunt, broadly rounded, blunt tip well below sulcus; posterior tip short, rounded or angular, positioned at level slightly below sulcus.

   Inner face slightly convex with small, centrally positioned, shallow, undivided sulcus with undivided colliculum. OL:TCL = 2.2–2.6. Circumsulcal depression very broad and complete except for small ridge-like feature connecting sulcus with anterior rim of otolith. Distinct, mostly narrow diagonal furrow in postdorsal position at angle of 40–50°, intersecting with posterior tip of sulcus. Outer face slightly convex, smooth.

Side dimorphism: No specific side dimorphism evident.

Discussion: *Citharichthys vergens* is much more common than its coeval congener *C. parvisulcus* and appears to attain somewhat larger sizes (maximum observed size 3 mm length *vs* 2 mm length). It differs in several mostly subtle characters that taken together, however, give a stable diagnostic distinction, which in very small specimens may not be discernable (see below). These differences are (*C. parvisulcus* in parentheses): OL:OH = 1.0–1.15 (*vs* 0.95–1.05), inner face slightly convex (*vs* flat), postventral rim inclined at 25–32° (*vs* 35–40°), OL:TCL = 2.2–2.6 (*vs* 3.1–3.8).

Citharichthys parvisulcus or C. vergens (juveniles and eroded)

Material: 145 specimens: 71 specimens Navidad Formation: 64 specimens Rio Rapel (RAP), 5 specimens Punta Perro (PPP), 2 specimens Punta Perro (PPN); 70 specimens Lacui Formation: 4 specimens Punta Chocoi (CHO), 66 specimens Chiloé (CUC); 4 specimens Ipún beds, Ipún Island (IPN 14).

Discussion: A large number of very small otoliths of mostly less than 1 mm length and a few very eroded specimens cannot be attributed to either of the two parallel occurring species. Given their relative abundances, it

is likely though that they represent more often *C. vergens* than *C. parvisulcus*.

Suborder Soleoidei

Family Achiridae

Genus *Achirus* Lacepède, 1802

***Achirus australis* n. sp.**
(Fig. 18a–d).

Holotype: SGO.PV.1715 (Fig. 18b), Navidad Formation, Punta Perro (PPS).

Paratypes: 3 specimens; 2 specimens Navidad Formation SGO.PV.1716, Punta Perro (PPN); 1 specimen Lacui Formation SGO.PV.1717, Cucao (CUC).

Further material: 11 specimens: 6 specimens Navidad Formation: 4 specimen, Punta Perro (PPN), 1 specimen, Punta Perro (PPS), 1 specimen, Matanzas (MAT); 5 specimens Lacui Formation: 2 specimens, Punta Chocoi (CHO), 3 specimens, Cucao (CUC).

Name: From australis (Latin) = southerly, referring to the geographic occurrence.

Diagnosis: OL:OH = 1.2–1.35 in left and right otoliths. Dorsal rim with sharp orthogonal angle at intersection with near vertical posterior rim. Ventral rim relatively shallow, anteriorly ascending. All rims smooth. OCL:CCL = 1.3–1.8. Circumsulcal depression narrow except for region above cauda, distant from sulcus.

Description: Small, oval, and moderately thick otoliths up to 3.3 mm length (holotype 2.6 mm). OL:OH = 1.2–1.35; OH:OT = 2.5–3.0. Dorsal rim nearly straight, slightly ascending backwards to sharp, orthogonal angle at joint with posterior rim. Ventral rim moderately deep, anteriorly less strongly curved than posteriorly, anteriorly ascending, deepest point posterior of middle. Anterior rim broadly rounded, with inferior blunt tip below sulcus; posterior rim nearly vertical. All rims smooth.

   Inner face distinctly convex with relatively wide, straight, shallow, upward inclined sulcus with clearly distinct ostial and caudal colliculi. Sulcus inclination towards upward-posteriorly at 6–12°. Ostium distinctly longer than cauda and very slightly wider, anteriorly reaching very close to anterior rim of otolith but not
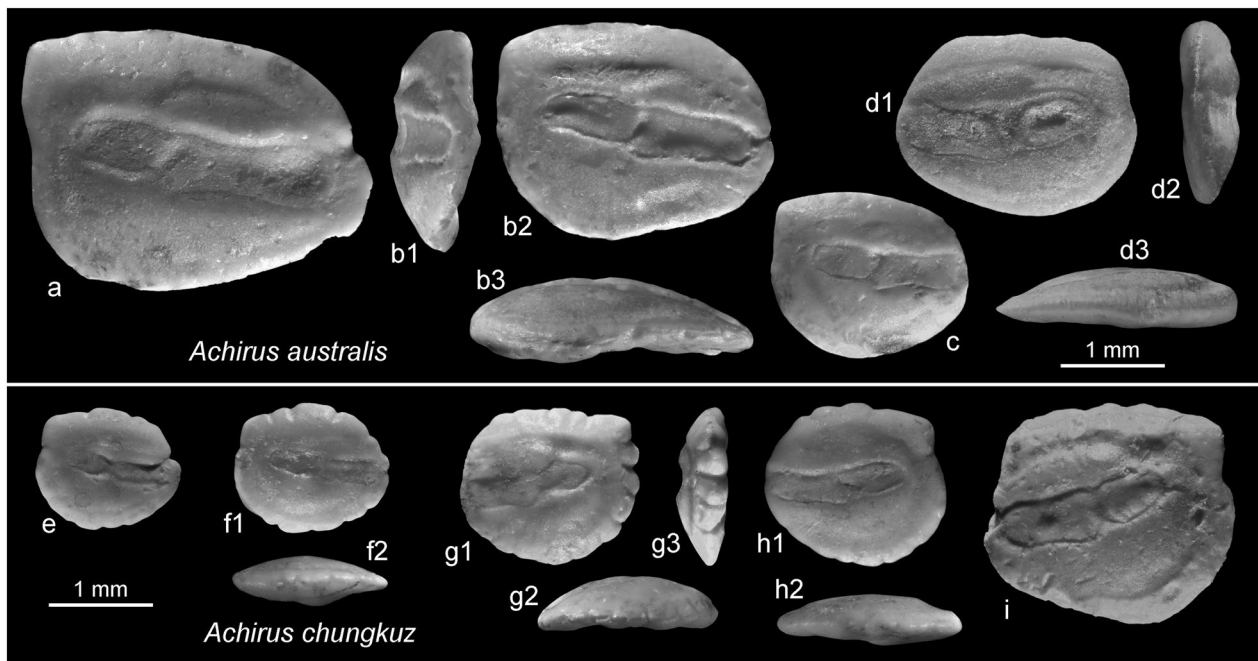
Fig. 18 a–d *Achirus australis* n. sp.; **b** holotype, PPS (left otolith), SGO.PV.1715; **a, c** paratypes, PPN (left otoliths), SGO.PV.1716; **d** paratype, CUC (right otolith), SGO.PV.1717. **e–i** *Achirus chungkuz* n. sp.; **g** holotype, PPN (right otolith), SGO.PV.1718; **e, f, h** paratypes, RAP (e–f left otoliths, h right otolith), SGO.PV.1719; **i** paratype, PPN (right otolith), SGO.PV.1720

open. OL:TCL = 1.3–1.35; OCL:CCL = 1.3–1.8. Circumsulcal depression very narrow resembling a furrow except for widened region above cauda, positioned halfway between sulcus and otolith rims. Outer face flat to slightly concave, smooth.

Side dimorphism: No distinct side dimorphism; right otoliths appear to have a somewhat stronger pronounced but rounded predorsal angle resulting in a nearly horizontal dorsal rim.

Discussion: *Achirus australis* differs from known otoliths of extant achirid species (see Schwarzhans, 1999) in the clearly ascending sulcus, which is also longer than in extant species and the long ostium. So far, no fossil achirid otoliths have been described, but a specimen figured as Soleidae indet by Nolf and Stringer (1992: pl. 17, fig. 19) from the late Miocene of the Dominican Republic may possibly represent an achirid. Presently, no achirid occurs off Chile, but two species of *Achirus* and three species of *Trinectes* are known off Peru. Otoliths are known from two of those (see Schwarzhans, 1999).

Achirus chungkuz n. sp.
(Fig. 18e–i).

Holotype: SGO.PV.1718 (Fig. 18g), Navidad Formation, Punta Perro (PPN).

Paratypes: 4 specimens Navidad Formation: 1 specimen SGO.PV.1720, same data as holotype; 3 specimens SGO.PV.1719, Rio Rapel (RAP).

Further material: 40 specimens: 35 specimens Navidad Formation: 26 specimens, Rio Rapel (RAP), 5 specimen, Punta Perro (PPN), 4 specimens, Matanzas (MAT); 1 specimen, Ranquil Formation, Ranquil (RQS); 4 specimens Lacui Formation: 2 specimens, Punta Chocoi (CHO), 2 specimens, Cucao (CUC).

Name: From chungkuz (Mapudungun) = round, referring to the shape of the otolith.

Diagnosis: OL:OH = 1.1–1.2 right otoliths more compressed than left otoliths. Dorsal rim with distinct angle at joint with near vertical posterior rim. Ventral rim deep, regularly curved. All rims undulating or crenulated. OCL:CCL = 1.4–1.8. Circumsulcal depression narrow except for region above cauda, distant from sulcus.

Description: Small, round, and moderately thick otoliths up to 2.4 mm length (holotype 1.7 mm). OL:OH = 1.1–1.2; OH:OT = 2.7–3.3. Dorsal rim nearly straight to

mildly curved, with orthogonal angle at joint with posterior rim. Ventral rim deep, regularly curved, deepest point at or posterior of middle. Anterior rim broadly rounded, with inferior blunt tip below sulcus; posterior rim nearly vertical, often with small indentation below postdorsal angle. All rims intensely crenulated in specimens smaller than 1.8 mm length and irregularly undulating in larger ones.

Inner face distinctly convex with straight, shallow, upward inclined sulcus with clearly distinct ostial and caudal colliculi. Sulcus inclination towards upward-posteriorly at 5–15°. Ostium distinctly longer than cauda and very slightly wider, anteriorly reaching very close to anterior rim of otolith, almost open. OL:TCL = 1.3–1.55; OCL:CCL = 1.4–1.8. Circumsulcal depression very narrow, indistinct or resembling a furrow except for widened region above cauda, positioned halfway between sulcus and otolith rims. Outer face convex in small specimens, flat to slightly concave in large ones, with irregular ornamentation.

Side dimorphism: Right otoliths appear to be more compressed than left otoliths and show less convexity on the outer face.

Discussion: *Achirus chungkuz* does not seem to grow to the same size as *A. australis* n. sp. and is also more common. It differs primarily in being more compressed (OL:OH = 1.1–1.2 *vs* 1.2–1.35) and in the more intense marginal ornamentation (*vs* smooth). Both characters could be interpreted as ontogenetic effects, but some specimens of comparable sizes (compare Fig. 18c, d with 18g–i) show that this is not the case.

Faunal composition and Paleoecology
Faunal composition
The most abundant family in the otolith associations of the early Miocene from Chile is the Myctophidae with an overall share of 44%, followed by the Paralichthyidae (16.2%), Ophidiidae (7.8%), Steindachneriidae (6.2%), and Macrouridae (5.3%). On the higher systematic level, the Myctophiformes (44%), Pleuronectiformes (19%) and Gadiformes (15%) constitute about 78% of the total assemblage. On the species level four of the eight most common species are from the Myctophidae (*Diaphus excisus* 23.1%, *Lampanyctodes scopelopsoides* 9.8%, *Diogenichthys aguilerai* 5.2%, and *Electrona subasperoides* 3%). The other four of the eight most common species are one each of the common families, that is, of the Paralichthyidae (*Citharichthys vergens*, including tentative juvenile and eroded specimens, 14.6%), the Ophidiidae (*Lepophidium chonorum* 5.2%), the Steindachneriidae (*Steindachneria svennielseni* 5%), and the Macrouridae

(*Coelorinchus fidelis* 3.1%). Other groups that are common in the shallow-water tropical Miocene environments of Central America are either very rare (many Perciformes and the Gobiiformes) or entirely absent (such as Sciaenidae, Batrachoididae, or Ariidae). In addition, moderately common groups are the Congridae, Sternoptychidae, Bregmacerotidae, Melanonidae, and Achiridae, as well as an enigmatic taxon described here as *Navidadichthys*, which is believed to represent an extinct Prototroctidae, a fresh and brackish water family exclusive to the southern temperate hemisphere. Except for the Congridae and *Navidadichthys*, the representatives of the other families listed above show a very localized distribution pattern given that they are only common in one or two locations. Of course, the faunal contents vary between locations and this is reflected in the following paleoecological discussion.
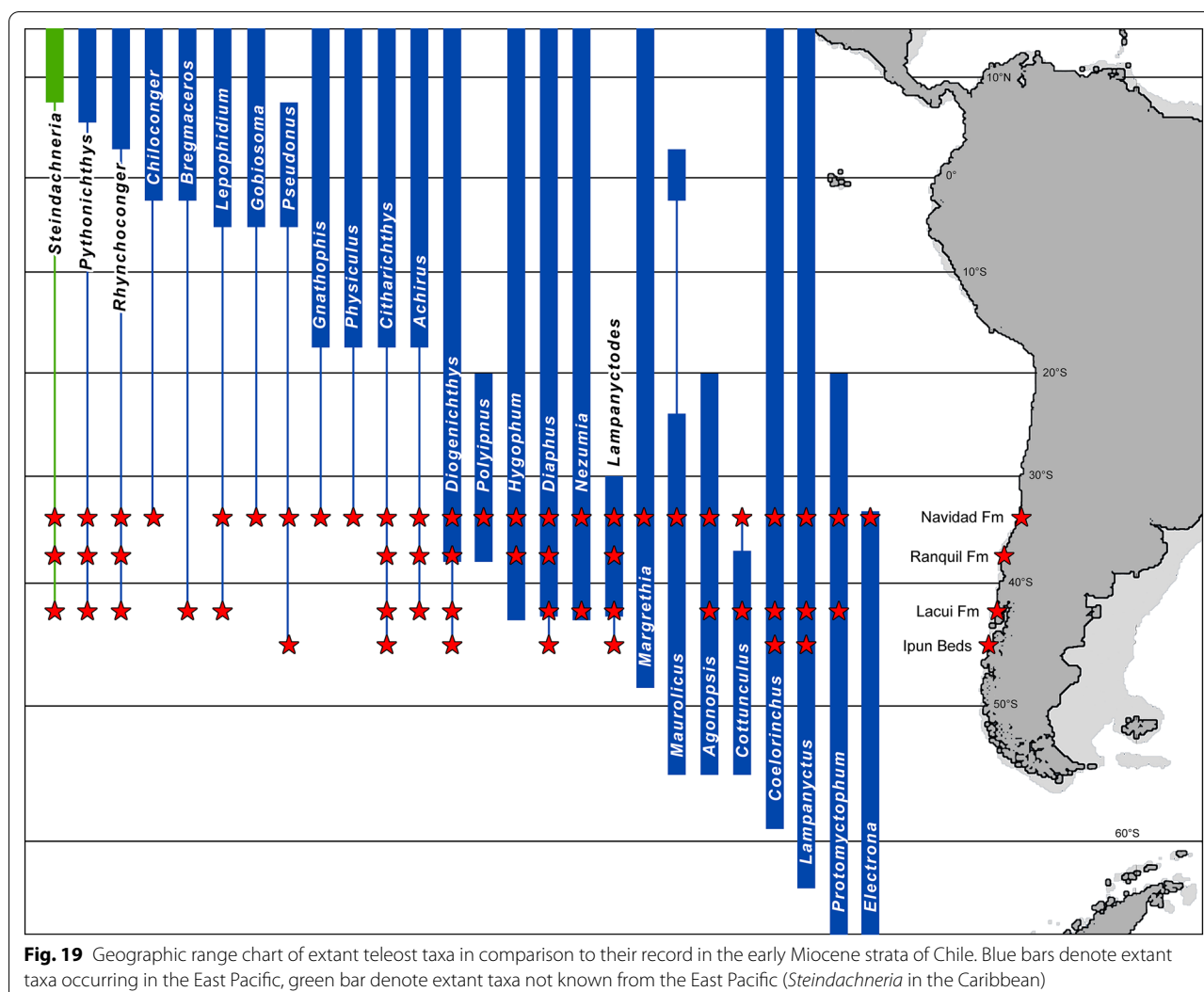
Paleotemperature
As indicated above, fish groups that are common in the tropical American sediments of Miocene age are generally rare or completely missing from the early Miocene of Chile. Even those that are well represented in tropical American sediments and Chile do not represent the same species (with one possible exception, see below) and, often, also not the same genera. In the Congridae, for instance, none of the three species from Chile described here are known from tropical America, and none of them appear to be related. Notably, the early Miocene of Chile contains the first fossil record of *Chiloconger*, a genus which is today known from two species, one from the central east Pacific, the other from the Philippines. In the Myctophidae, the richest and most diverse family in the early Miocene of Chile, only a single species is also known from tropical realms, namely *Diogenichthys aguilerai*, from the early Miocene of Angola (Schwarzhans, 2013c) and possibly also of Trinidad (as *Diogenichthys* sp. in Schwarzhans & Aguilera, 2013). No species are shared in the Miocene between tropical America and Chile for the families Bregmacerotidae, Macrouridae, Ophidiidae, Bythitidae, Gobiidae, Paralichthyidae, or Achiridae. For instance, the genus *Lepophidium* of the Ophidiidae is represented by two common species in the early Miocene of Chile and three species representing different clades of the genus in the middle and late Miocene of Panama and Ecuador (Schwarzhans & Aguilera, 2016). The only exception is the bathydemersal family Steindachneriidae, which has a single extant species in the Caribbean and at least three species in the Miocene with an extended distribution across America and Europe; thereof two otolith-based from America. The two otolith-based American species are *Steindachneria goederti* Nolf, 2002 and *S. svennielseni* Nolf, 2002. *Steindachneria goederti*

was originally described from the early Miocene of Oregon, USA, and is now also recorded from Chile, possibly indicating an antitropical distribution pattern in the East Pacific. *Steindachneria svennielseni* is more common in Chile and was possibly also present in Venezuela and the Mediterranean, where it was recorded as *Steindachneria* sp. (Nolf & Aguilera, 1998 and Nolf, 2002). If verified, *Steindachneria svennielseni* would be the only other species besides *Diogenichthys aguilerai* known from tropical America and Chile during the early Miocene.

In an assessment of paleotemperatures of the early Miocene in the southeast Pacific, Nielsen and Glodny (2009) concluded that the temperature of the region was at least about 5 °C higher than today as indicated by the occurrence of warm-water mollusks. A comparison of the distribution of extant fishes on the genus level with those from the early Miocene of the various locations in Chile reflects a comparable distribution background. Most genera found in the early Miocene today are restricted to warmer water, more northerly regions in the East Pacific. A number of genera today occur north of 18°S (e.g., *Gnathophis*, *Physiculus*, *Citharichthys*, and *Achirus*) and some are strictly tropic, occurring near or north of the equator (e.g., *Pythonichthys*, *Chiloconger*, *Rhynchoconger*, *Bregmaceros*, and *Lepophidium*; Fig. 19). The occurrence of these genera during the early Miocene off Chile indicates that the sea temperatures were higher than they are today, but by how much is difficult to judge. However, the lack of almost any overlap with the more or less coeval faunas from Venezuela and Trinidad (Aguilera et al., 2016; Nolf, 1976; Nolf & Aguilera, 1998; Schwarzhans & Aguilera, 2013, 2016) demonstrates that the regime was not strictly tropical. The restriction of certain genera to more northerly distribution patterns today in the East Pacific must have some other underlying causes than temperature alone. In addition, several genera occur in the early Miocene of Chile that today reach southwards to similar latitudes or are even restricted to the southeast Pacific temperate seas. Among the latter, truly temperate taxa are the most notable *Protomyctophum* (1%) and *Electrona* (3%) in myctophids, *Agonopsis* (Agonidae; 0.3%), which typically occur on the lower shelf, and the bathydemersal *Cottunculus* (Psychrolutidae; 0.1%) (Fig. 19). *Protomyctophum* and *Electrona* are abundant subantarctic mesopelagic fishes (Gon & Heemstra, 1990), with only few species extending northwards with cool water currents. *Agonopsis* and *Cottunculus* represent typical temperate to cold water demersal fishes, with *Agonopsis* distributed in the northern and southern reaches of America (Froese & Pauly 2020), and *Cottunculus* being found in boreal to temperate deep basins in all major oceans (Froese & Pauly 2020). We conclude from these distribution patterns that, when seen in combination, a

slightly warmer sea than today in the range as assessed from mollusks (Nielsen & Frassinetti, 2007b; Nielsen & Glodny, 2009) seems the most plausible, although past distribution patterns may not in all instances have been comparable to the recent temperature preferences of some fish groups. Interestingly and perhaps unexpectedly, we could not identify Miocene representatives of two of the most iconic endemic Chilean fishes, namely *Aplochiton* (Galaxiidae) and *Normanichthys* (Normanichthyidae, Scorpaeniformes).

The locations sampled for this study stretch across about 1,200 km in a north–south direction. Consequently, one would expect a certain degree of faunal variation that would probably be mainly temperature-driven. The density and abundance of otoliths in the sediments, however, are quite variable, and comparable amounts of otoliths have only been collected from the Navidad Formation in the north and the Lacui Formation on Chiloé Island. Significantly less information has been gathered from the Ranquil Formation and the southernmost locations of the Ipún beds, meaning that any faunal assessment is less reliable. Nevertheless, we find relatively little latitudinal diversification (Fig. 20). For the most part, we notice species occurring in the Navidad Formation and disappearing further to the south, such as, *Gnathophis quinzioi*, *Navidadichthys mirus*, sternoptychids, *Coelorinchus rapelanus*, and *Lepophidium mapucheorum*. Some others (e.g., *Diogenichthys aguilerai*, melanonids, *Nezumia epuge*, *Citharichthys parvisulcus*, and achirids) are still found in the south, for instance in the Lacui Formation, but are much less common than in the northern Navidad Formation. Certain species (e.g., *Pythonichthys panulus*, *Bregmaceros prosoponus*, *Steindachneria goederti*, *Coelorinchus fidelis*, and *Lepophidium chonorum*) increase in abundance in the southerly formations. Two pairs of species are of particular interest, because they seem to replace each other along the studied region (Fig. 20). The first consists of *Coelorinchus rapelanus*, which is more common in the north, and *C. fidelis*, which is more common in the south. However, *C. fidelis* also seems to have been living in a deeper paleoenvironment than *C. rapelanus*, which may have had an important effect on their distribution as well (see below). Even more latitudinal separation is evident for the pair consisting of *Lepophidium mapucheorum* and *L. chonorum*. Both species appear to be closely related. *Lepophidium mapucheorum* is only known from the Navidad Formation, while *L. chonorum* is very rare in the Navidad Formation but becomes the dominant ophidiid in the Lacui Formation (Fig. 20). In addition, in the case of the two *Lepophidium* species, bathymetric preferences may have played an additional role.

Fig. 19 Geographic range chart of extant teleost taxa in comparison to their record in the early Miocene strata of Chile. Blue bars denote extant taxa occurring in the East Pacific, green bar denote extant taxa not known from the East Pacific (*Steindachneria* in the Caribbean)

Paleobathymetry

A paleobathymetric assessment of fossil fish and otolith associations is difficult for several reasons. First, fishes are more flexible with respect to water depth than many other marine animals, which is primarily due to their agility in the water column and often wide vertical distribution range, as well as ontogenetically induced migrations. Second, depth-dependent speciation is a common phenomenon among many groups of fishes. Third, many fish groups are suspected of having substantially changed their bathymetric adaptation during their evolutionary history. Finally, otoliths in particular can be deposited away from the primary environment of fishes through predation and subsequent excretion, which is especially relevant for bathymetric evaluations. As a result, relatively few fishes can reliably be used as bathymetric indicators, and those that can are generally demersal. In the Neogene, the percentage of myctophid

otoliths, which dominate sediments below 200 m, is usually considered as a good indicator when they exceed 50% of the total otolith association (Schwarzhans & Aguilera, 2013; Schwarzhans, 2013a). Nolf and Cappetta (1989) have developed a method to arrive at a statistical value for a paleobathymetric characterization of fossil associations by plotting the depth distribution of the relevant extant genera. However, downslope transport by predators and synsedimentary re-deposition processes on the deep Chilean slope during the early Miocene may have played a considerable role in the composition of faunal associations (Finger, 2013; Finger et al., 2007; Nielsen & Frassinetti, 2007a, 2007b; Nielsen & Glodny, 2009). Nevertheless, we here employ Nolf & Cappetta's approach but with some quality weighing, whereby fish groups deemed to be of particular bathymetric value are preferentially used. This approach results in the recognition of
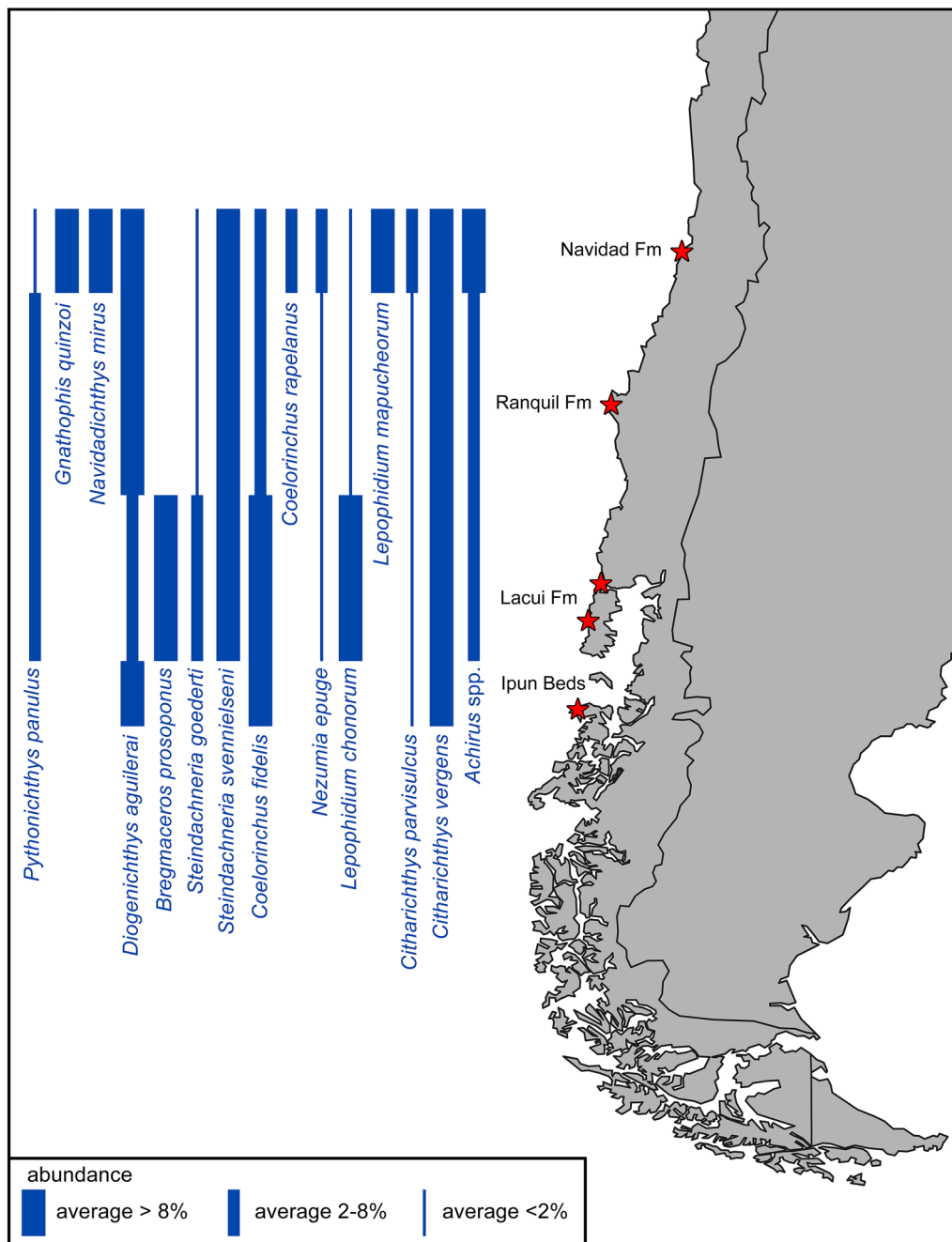
Fig. 20 Latitudinal distribution and abundance of selected otolith-based teleost taxa in the early Miocene of Chile

four different paleobathymetric associations, which are characterized as follows (Fig. 21).

The shallowest association, which is characteristic of middle to outer shelf positions is that of the LEB location in the Ranquil Formation. It is a very sparse association from which only a few species have been recovered, the most common being the heterenchelyid *Pythonichthys*

panulus. The Heterenchelyidae are one of the fish families that come closest to what can be described as an infaunal lifestyle, as they live buried in soft sediment for most of their lives (Eagderi & Adriaens, 2010) at depths of between 10 and 150 m. Myctophids and bathydemersal fishes are not present in LEB.

Most paleobathymetric associations from the early Miocene of Chile appear to be associated with positions on the continental slope between 200 and 1,000 m. The shallowest occur just below the shelf break at about 200 to 400 m and are thought to be the associations from PPS and MAT in the Navidad Formation. They are characterized by an abundance of congrids, particularly *Gnathophis quinzoi*, *Navidadichthys*, *Lepophidium*, *Diogenichthys*, *Diaphus*, *Lepidorhynchus*, and *Achirus*; *Diogenichthys* today usually occurs deeper, whereas *Achirus* appears on the shallow shelf. We interpret the abundance of *Achirus* as an expression of downslope transport, although there are no apparent erosional effects observable.

Associations, which presumably occurred on a middle slope position (400–600 m), are the most common in the early Miocene of Chile and are interpreted for the locations RAP and PPN in the Navidad Formation and CHO and CUC in the Lacui Formation. These associations are rich in a variety of myctophids of the genera *Diogenichthys*, *Lampanyctodes*, and *Diaphus*, as well as other groups such as *Maurolicus*, *Bregmaceros*, *Steindachneria*, *Coelorinchus*, and *Citharichthys*. *Steindachneria* and *Citharichthys vergens* and, in the Lacui Formation, also *Coelorinchus fidelis* and *Lepophidium chonorum* appear to be specifically indicative of this paleobathymetric interval. The occurrence of *Steindachneria* would be in good agreement with its extant depth distribution pattern (Cohen et al., 1990).

The locations PPP and PTA in the Navidad Formation and combined IPN, the Ipún beds, represent the deepest environments, presumably on the lower slope below 600 m and possibly reaching as deep as 1000 m or more. Again, myctophids (e.g., *Diogenichthys*, *Electrona*, *Lampanyctodes*, and *Diaphus*) are the dominant group. For *Lampanyctodes*, a pseudoceanic genus of the southern temperate oceans, this depth is already somewhat deeper than their usual occurrence. A unique and highly characteristic deep-water element is *Pseudonus* at the location PPP.

Comparing these estimates with previous interpretations based on other groups of organisms shows a generally good agreement. The shallowest location distinguished by otoliths, LEB, also yielded common vetigastropod limpets, which indicate nearby rocky substrate (Nielsen et al., 2004) and was considered to indicate a relatively coastal environment based on the gastropod fauna (Finger et al., 2007). The brachiopod *Kraussina chilensis* has been described from this location (Hiller et al., 2008); the genus now mostly lives in depths of less than 200 m. In the following group of locations, MAT was interpreted as relatively coastal due to its mollusk fauna (Frassinetti & Covacevich 1993, Finger et al., 2007), and the solitary

coral *Sphenotrochus* (which today lives in depths of less than 400 m) is common at PPS (Cairns, 2003); both findings agree with the fish-based interpretations. The presumably deeper locations (RAP, PPN, CHO, and CUC) show shallow-water and deeper-ranging components (Finger et al., 2007). The deepest locations identified based on otoliths (PPP, PTA) are also among those interpreted as comparatively deep-water based on the gastropods (Finger et al., 2007; Nielsen, 2005a, 2005b).

Faunal diversity

The characterization of the faunal diversity index follows the proposal of Schwarzhans (2010) and is measured by counting the number of the most common species until the level of 90% of the faunal composition is surpassed. The diversity index for the early Miocene of Chile is only calculated for locations, where more than 50 otoliths have been retrieved. The diversity index ranges from 8 (PPP, PTA) to 16 (PPS) (Fig. 21), which corresponds to a normal marine average for warm faunal associations (see Schwarzhans, 2019a). A latitudinal gradient could not be observed, but there appears to be a gradient from less diverse deeper environments to more diverse shallower environments (Fig. 21), which we consider a trend to be generally expected in marine environments.

Supraregional faunal correlation
Paleobiogeography

A total of 67 species of bony fishes, representing 45 genera, and together with 7 incertae sedis familial assignments belong to 36 families, have been identified based on otoliths from the early Miocene formations of Chile. Three families, namely the Steindachneriidae, the Dactyloscopidae, and the Achiridae, are today restricted to the seas surrounding the Americas. Of these, at least the Steindachneriidae were more widely distributed in the geological past. Of the 45 genera, four are extinct, and 26 are distributed over terrain encompassing several continental shelfs or ocean basins. Eight genera are endemic to the Americas, while one also occurs in West Africa (*Pythonichthys*). Of the remainder, two occur disjunctively in the East and West Pacific (*Chiloconger* and *Penopus*), and four are classified as "exotic." The latter are *Pterothrissus*, *Lepidorhynchus*, *Capromimus*, and *Kuhlia*, plus an unspecified platycephalid record, and they warrant a more specific discussion.

Pterothrissus is today restricted to the deeper shelf of Japan and a related genus (*Nemoossis*) to West Africa, but possibly enjoyed a cosmopolitan distribution during the late Cretaceous and Paleogene. In addition, during the Miocene its distribution was much wider but possibly already somewhat restricted and disjunctive. The record from the Navidad Formation represents the youngest
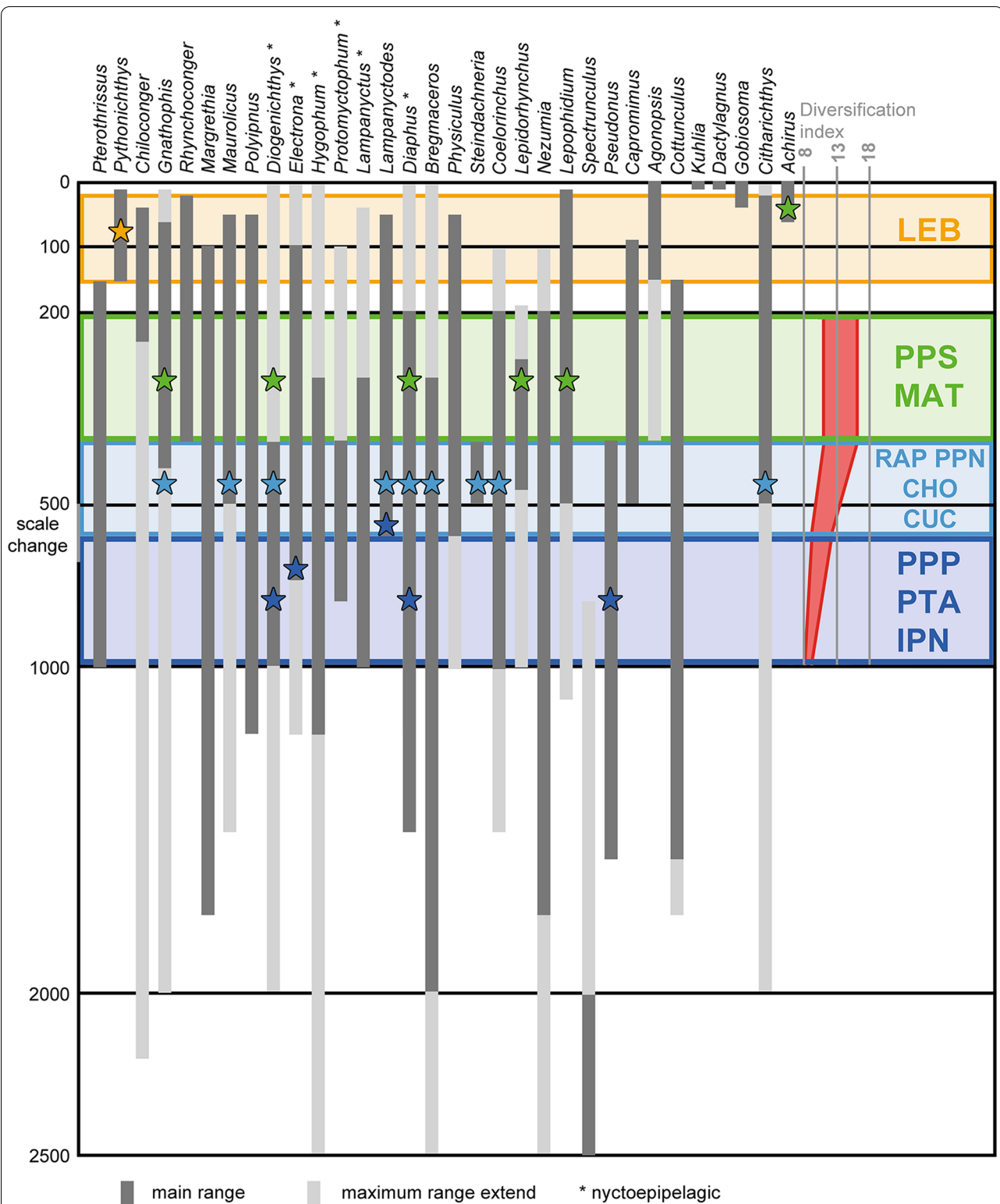
Fig. 21 Extant depth ranges of selected teleost taxa and their fossil occurrence in the early Miocene of Chile. Stars mark taxa considered indicative of certain depth intervals in the early Miocene of Chile; color of stars and abbreviated location names correlate with colors of depth zones. Diversification index ranges shown for locations with more than 50 otolith specimens, averaged per depth zone

record from the Americas (see also Müller, 1999). *Lepidorhynchus* is today endemic to New Zealand and temperate Australia, and *Capromimus* is endemic to New Zealand. The implications of their occurrence in the early Miocene of Chile are discussed in more detail below. Otoliths of *Capromimus* resemble those of the related *Cyttomimus* (see Nolf & Tyler, 2006), which is today more widely distributed in the Pacific Ocean including off Chile (for the reasoning behind the placement of the fossil record into *Capromimus* see the descriptive section above). Otoliths of the Cyttopsidae also resemble *Capromimus* to some extent, for example *Stethopristes* (Nolf & Tyler, 2006) which is also known from off Chile, but they differ in always having a much lower dorsal rim. The Kuhliidae, which consist of the single genus *Kuhlia*, are today restricted to shallow shelf and brackish to freshwaters of the Indo-West Pacific, with one very widely distributed species, *Kuhlia mugil* (Forster, 1801), that is also known from the tropical East Pacific along the central American shore. The occurrence of a species of *Kuhlia* in the early Miocene of Chile may, therefore, not be regarded as strictly "exotic," but it is here assumed that the wide distribution of *K. mugil* from East Africa to the tropical East Pacific is a rather exceptional modern achievement and is not connected to the occurrence of *Kuhlia orientalis*. Indeed, *Kuhlia* had a much wider geographical distribution and there is also a species, *K. tenuicauda* (Schwarzhans, 1974), known from the late Oligocene and early Miocene of Europe (Schwarzhans, 1974, 1994b, Steurbaut 1984). Finally, the Platycephalidae as a family are today widely distributed throughout the Indo-West Pacific and even have a single species in the East Atlantic, but representatives from the East Pacific are not known.

At the species level, as stated previously, there is almost no congruence between the early Miocene otolith association of Chile and the coeval ones from Venezuela or Trinidad with the exception of *Steindachneria svennielseni* and *Diogenichthys aguilerai*. In contrast, there is a certain degree of correlation with the extensive coeval fauna from New Zealand (Schwarzhans, 2019a), which, however, varies strongly depending on the lifestyle of each fish group. The correspondence of mesopelagic and bathypelagic fishes is very high between Chile and New Zealand but moderate for benthopelagic or shelf fishes (Figs. 22, 23). In fact, the correlation of mesopelagic fishes particularly of the Myctophidae is exceptional and perhaps somewhat unexpected. Sixteen of the 22 species in the mesopelagic and bathypelagic category of Chile are also known from New Zealand, and three more species appear to have allopatric counterparts in New Zealand. This extremely high congruence is interpreted as reflecting an already established southern Pacific mesopelagic bioprovince exceeding even the situation of today (Sutton

et al., 2017). However, it is interesting to note that the abundance of some species varies significantly on either side of the South Pacific. For instance, the most common species in Chile, *Diaphus excisus*, is uncommon in New Zealand, whereas the most common species in New Zealand, *Diaphus curvatus* and *D. marwicki*, are uncommon in Chile. Other species, such as *Electrona subasperoides*, *Lampanyctodes scopelopsoides*, and *Karrerichthys tenuis*, occur at similar frequency on both sides. Another interesting aspect is that the moderate distinction between a warm-water northern bioprovince in New Zealand with *Diaphus excisus* and *Karrerichthys tenuis* and a cooler southern province with *Diaphus curvatus*, and *D, marwicki*, is also reflected in Chile, but with more emphasis to the warmer bioprovince (Schwarzhans, 2019a). *Electrona subasperoides* and *Lampanyctodes scopelopsoides* are equally abundant in both provinces in New Zealand. Today, the Peru Upwelling/Humboldt Current regime along the southwestern region off Chile and Peru has led to the establishment of a mesopelagic biogeographic zone that is distinct from the southern central Pacific biogeographic region that includes northern New Zealand (Sutton et al., 2017). We interpret the high degree of congruence between the early Miocene mesopelagic fauna of Chile and New Zealand as an indication that the upwelling/cold current regime along the southwest South American shore was not (yet) established or at least was too weak to be of biogeographic significance.

In contrast to the mesopelagic fish fauna, the benthopelagic and bathydemersal fish fauna has only a single species among 17 in that category that occurs in Chile and New Zealand, namely *Lepidorhynchus frosti* (Fig. 22). Five more potential vicariant species pairs existed, but, overall, the level of divergence is much greater than the number of shared species. This suggests an effective separation of the continental slope environments of both continents. Unsurprisingly, the level of congruence is even less in the shallow shelf fauna. There is not a single shared species between Chile and New Zealand and only five out of 24 Chilean shallow water fishes appear to have had potential counterparts on the New Zealand shelf (Fig. 22). Again, this is in good agreement with the extant faunal distribution (see Froese & Pauly 2020, Roberts et al. 2015). We conclude that the biogeographical position of the Chilean sea during the early Miocene was similar to that of today.
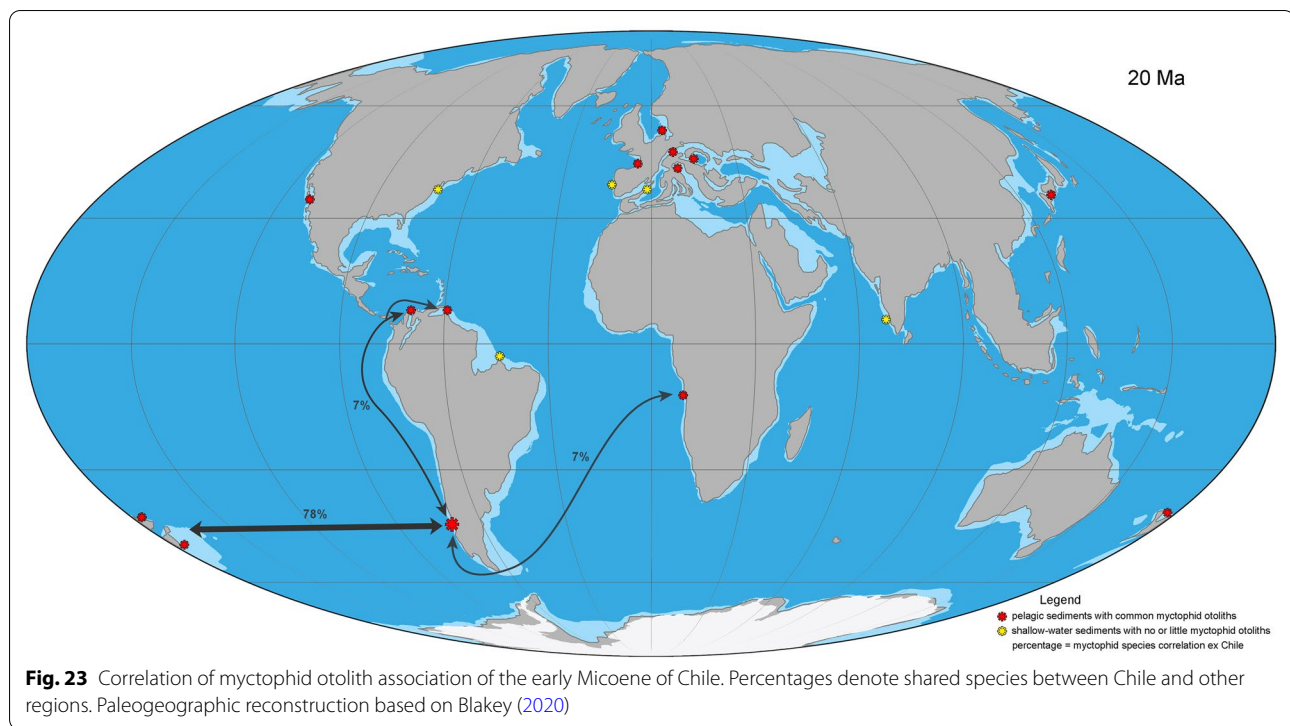
Biostratigraphic evaluation

The stratigraphic position of the Navidad Formation and the related formations in Chile was explained in the chapter "Geological Setting." According to the detailed analysis of planktonic foraminifera by Finger (2013), the actual biostratigraphic position of these formations is considered to be late Aquitanian to middle Burdigalian,
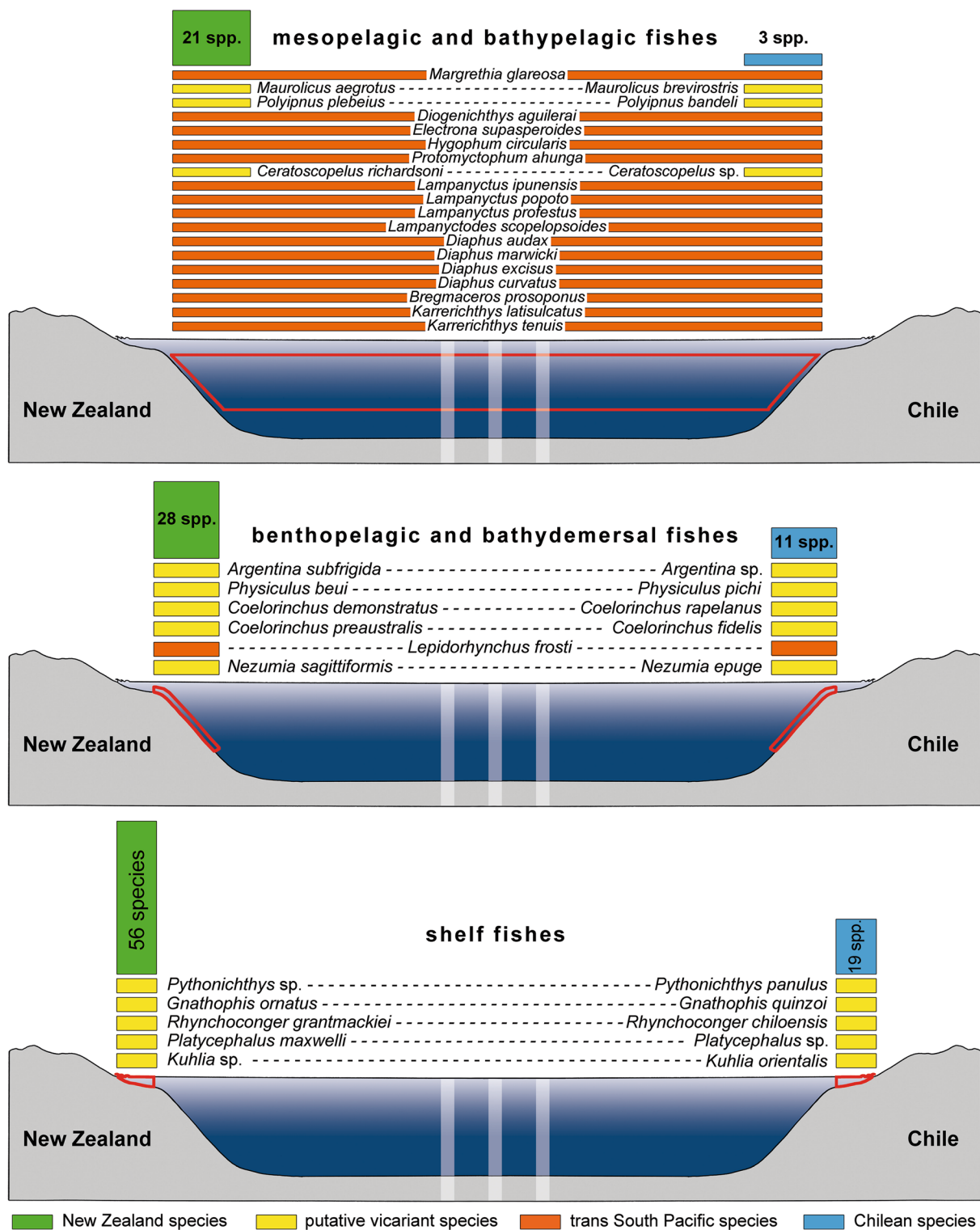
Fig. 22 Correlation of otolith-based teleost taxa across the southern Pacific between Chile and New Zealand. Horizontal distance not to scale (indicated by three light bars)

Fig. 23 Correlation of myctophid otolith association of the early Micoene of Chile. Percentages denote shared species between Chile and other regions. Paleogeographic reconstruction based on Blakey (2020)

that is, planktonic foraminifer biozones N5 to N6 (Fig. 24). The excellent correlation between the otoliths of mesopelagic fishes between Chile and New Zealand and the good and continuous database from New Zealand (Schwarzhans, 2019a) offer the opportunity to test this assumption with otoliths, primarily of the Myctophidae. In New Zealand, the foraminifer biozones N5 to N6 correspond to the Otaian and early Altonian. The correlation of the otolith associations between Chile and New Zealand reveals an excellent congruence with the one based on planktonic foraminifera (Fig. 24). Virtually all compared species co-occurred during the Altonian in New Zealand, except for *Karrerichthys latisulcatus*, which is, however, an extremely rare species known from only a single specimen in New Zealand. The stratigraphic range of *K. latisulcatus* is, therefore, expected to reach back into the Burdigalian (i.e., Altonian). The correlation with the Otaian is also high, but less than with the Altonian. However, one needs to remember that the Otaian otolith associations are much better known from northern New Zealand than from southern New Zealand, while the Altonian otolith associations are nearly equally well known from both islands of New Zealand (Schwarzhans, 2019a). Another caveat is that the samples studied from New Zealand did not allow for a more detailed stratigraphic differentiation within the Altonian. Nevertheless, the results from the foraminifer biozonation of Finger (2013) and the otolith zones after Schwarzhans (2019a)

produce a good overlap with biozone N6 corresponding to the middle Burdigalian (Fig. 24). In combination with the foraminifer biozonation, the biostratigraphic assessment of the otoliths effectively sharpens the stratigraphic resolution of the studied Chilean strata.

Conclusions and outlook

Fossil otoliths are an important resource for the reconstruction of fossil bony fish faunas. They are much more common than identifiable articulated fish skeletons, but exhibit fewer traits for a phylogenetic analysis in deep time. Their abundance, however, offers unique opportunities for the study of the evolutionary history and the paleoenvironmental and biostratigraphic records of fishes. Still, after more than 130 years of research on fossil otoliths, our knowledge has remained relatively confined both in a regional and a stratigraphic sense. This is primarily the result of otoliths having rarely been specifically collected. The early Miocene otolith association from Chile studied here, therefore, represents a unique data point with the nearest comparative assemblages known from New Zealand, about 9,000 km to the west, and Venezuela, about 5,000 km to the north. The main conclusions of this study are as follows:

1. With 67 identified species, the otolith-based fish fauna is highly diverse and is apparently composed of a mixture of shallow- and deep-water elements, of
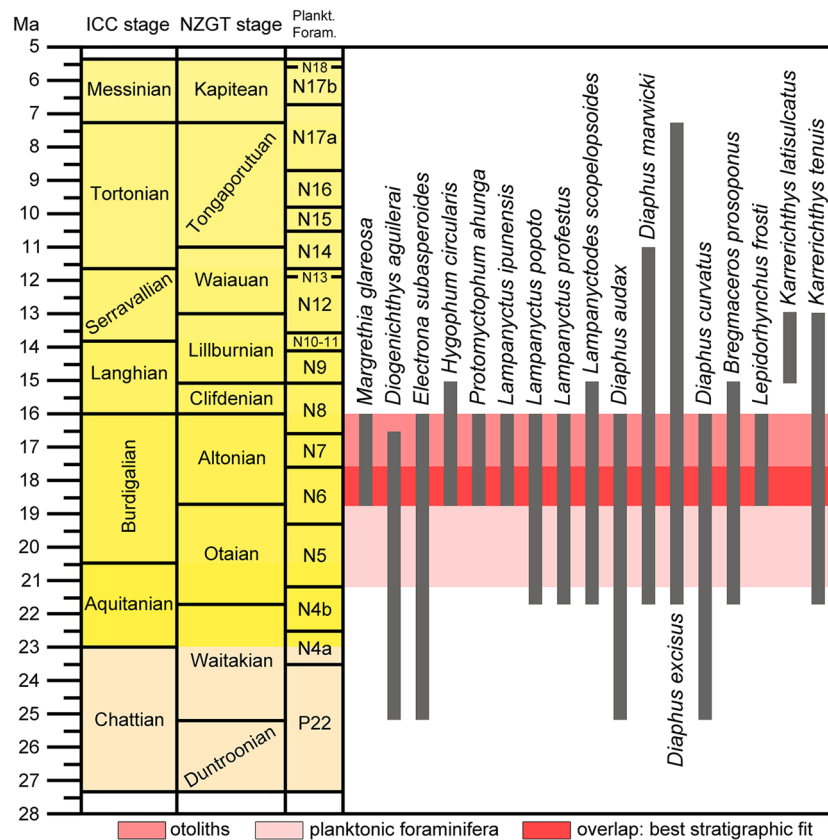
Fig. 24 Correlation of planktonic foraminifer biozone interpretation based on Finger (2013), and otoliths of mesopelagic fishes, mostly Myctophidae, known from New Zealand. Time scale after Gradstein et al., (2020: Fig. 29.10). Abbreviations used: ICC = International Chronostratigraphic Chart; NZGT = New Zealand Geological Time Scale

which the former were likely transported downslope due to the steep paleorelief and narrow shelf.

2. The mesopelagic faunal component, chiefly of the Myctophidae, shows a very high agreement on the species level with the coeval associations of New Zealand and is interpreted to represent an early Miocene South Pacific mesopelagic bioprovince.

3. The high degree of shared myctophid otolith-based species and its correlation with the Altonian stage of New Zealand allows a refinement of the stratigraphic position of the Chilean formations, as it was based on planktonic foraminfer biozonation, to middle Burdigalian (approximately 17.5 to 18.5 Ma).

4. The shallow-water faunal elements that pertain to shelf paleoenvironments show a high percentage of endemic American groups and a good relation to coeval faunas of Venezuela and Trinidad on the genus and family levels, but not on the species level.

5. The faunal composition indicates that the water temperature at the time of the early Miocene was warmer by about 5°C, but the faunal diversification along the roughly 1,200 km north-south extending outcrop section was nevertheless low.

Our investigations of the early Miocene otolith assemblage from Chile demonstrate the important contributions that can be expected when new regions of the world are studied for fossil otoliths. For instance, valuable new information has emerged concerning the potential of a supraregional biostratigraphic framework based on myctophid otoliths. New insights could be obtained concerning the evolution of the South American marine fish fauna. We believe that many more such unstudied opportunities exist around the world for collecting new and exciting otolith assemblages, and we hope that this study will encourage our colleagues to look for them.

Author details
[1]Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark. [2]Ahrensburger Weg 103, 22359 Hamburg, Germany. [3]Instituto de Ciencias de La Tierra, Universidad Austral de Chile, Valdivia, Chile.

References

Aguilera, O., & Rodriguez de Aguilera, D. (2001). An exceptional coastal upwelling fish assemblage in the Caribbean Neogene. *Journal of Paleontology, 73*, 732–742.

Aguilera, O. A., Schwarzhans, W., & Béarez, P. (2016). Otoliths of the Sciaenidae from the Neogene of tropical America. *Palaeo Ichthyologica, 14*, 7–90.

Antinao, J.L., Duhart, P., Clayton, J., Elgueta, S., & McDonough, M. (2000). Area de Ancud - Maullín, Región de Los Lagos. Escala 1:100.000. *Servicio Nacional de Geología y Minería, Chile. Mapas Geológicos, 17*.

Arenas, M. & Duhart, P. (2003). Geología del Área Castro—Dalcahue, Región de Los Lagos. *Servicio Nacional de Geología y Minería, Carta Geológica de Chile, Serie Geología Básica, 79*, 1–29, 1 map scale 1:100.000.

Arratia, G. (2015). Los peces osteíctios fósiles de Chile y su importancia en los contextos paleobiogeográfico y evolutivo. *Publicación Ocasional Del Museo Nacional De Historia Natural, Chile, 63*, 35–83.

Betancur, R. R., Broughton, R. E., Wiley, E. O., Carpenter, K., López, J. A., Li, C., Holcroft, N. I., Arcila, D., et al. (2013). The tree of life and a new classification of bony fishes. *Plos Currents Tree of Life*. https://doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288

Betancur, R. R., Wiley, E. O., Arratia, G., Acero, A., Bailly, N., Miya, M., Lecointre, G., & Orti, G. (2017). Phylogenetic classification of bony fishes. *BMC Evolutionary Biology, 17*(162), 1–40. https://doi.org/10.1186/s12862-017-0958-3

Blakey, R.C. (2020). Deep Time Maps. World Wide Web electronic service. https://deeptimemaps.com/ (purchased in March 2021).

Cairns, S. D. (2003). A New Species of *Sphenotrochus* (Scleractinia: Turbinoliidae) from the Late Miocene (Tortonian) of Chile. *Zoologische Verhandelingen, Leiden, 345*, 79–84.

Cecioni, G. O. (1978). Petroleum possibilities of de Darwin's Navidad Formation near Santiago, Chile. *Museo Nacional De Historia Natural Publicación Ocasional, 25*, 3–28.

Cecioni, G. (1980). Darwin's Navidad embayment, Santiago Region, Chile, as a model of the southeastern Pacific shelf. *Journal of Petroleum Geology, 2*, 309–321.

Chaine, J., & Duvergier, J. (1934). Recherches sur les otolithes des poissons. Etude descriptive et comparative de la sagitta des téléostéens. *Actes De La Société Linnéenne De Bordeaux, 86*, 1–254.

Chen, W.-J., Santini, F., Carnevale, G., Chen, J.-N., Liu, S.-H., Lavoué, S., & Mayden, R. L. (2014). New insights on early evolution of spiny rayed fishes (Teleostei: Acanthomorpha). *Frontiers in Marine Science, 1*(53), 1–17. https://doi.org/10.3389/fmars.2014.00053

Cohen, D. M. (1986). Bregmacerotidae. In P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen, & E. Tortonese (Eds.), *Fishes of the North-eastern Atlantic and the Mediterranean* (pp. 711–712). Paris: UNESCO.

Cohen, D. M., Inada, T., Iwamoto, T., & Scialabba, N. (1990). Gadiform fishes of the world. *FAO Species Catalogue, 10*, 1–442.

Cohen, D. M., & Nielsen, J. G. (1978). Guide to the identification of the fish order Ophidiiformes with a tentative classification of the order. *NOAA Technical Report NMFS Circular, 417*, 1–72.

Darwin, C. (1846). *Geological Observations on South America. Being the third part of the geology of the voyage of the Beagle, under command of Capt Fitzroy, R.N. during the years 1832 to 1836* (pp. 1–279). London: Smith Elder & Co.

Deng, X., Wagner, H.-J., & Popper, A. N. (2011). The inner ear and its coupling to the swim bladder in the deep-sea fish *Antimora rostrata* (Teleostei: Moridae). *Deep Sea Research I, 58*, 27–37. https://doi.org/10.1016/j.dsr.2010.11.001

Eagderi, S., & Adriaens, D. (2010). Cephalic morphology of *Pythonichthys macrurus* (Heterenchelyidae: Anguilliformes): Specializations for headfirst burrowing. *Journal of Morphology, 271*, 1053–1065. https://doi.org/10.1002/jmor.10852

Ebersole, J.A., Cicimurri, D.J. & Stringer, G.L. (2021). Marine fishes (Elasmobranchii, Teleostei) from the Glendon Limestone member of the Byram Formation (Oligocene, Rupelian) at site Awa-9, Washington County, Alabama, USA including a new species of gobiid (Gobiiformes: Gobiidae). *Acta Geologica Polonica*. https://doi.org/10.24425/agp.2020.134561.

Encinas, A., Le Roux, J. P., Buatois, L. A., Nielsen, S. N., Finger, K. L., Fourtanier, E., & Lavenu, A. (2006). Nuevo esquema estratigráfico para los depósitos mio-pliocenos del área de Navidad (33°00'-34°30'S), Chile central. *Revista Geológica De Chile, 33*, 221–246. https://doi.org/10.4067/S0716-02082006000200002

Encinas, A., Finger, K. L., Nielsen, S. N., Lavenu, A., Buatois, L. A., Peterson, D. E., & Le Roux, J. P. (2008). Rapid and major coastal subsidence during the late Miocene in south-central Chile. *Journal of South American Earth Sciences, 25*, 157–175. https://doi.org/10.1016/j.jsames.2007.07.001

Encinas, A., Folguera, A., Bechis, F., Finger, K.L., Zambrano, P., Pérez, F., Bernabé, P., Tapia, F., Riffo, R., Buatois, L., Orts, D., Nielsen, S.N., Valencia, V.V., Cuitiño, J., Oliveros, V., Del Mauro, L.G. & Ramos, V.A. (2018). The late Oligocene - early Miocene marine transgression of Patagonia. In: Folguera A. et al. (eds) The Evolution of the Chilean-Argentinean Andes Springer Earth System Sciences. Springer, Cham, pp 443–474. https://doi.org/10.1007/978-3-319-67774-3_18.

Encinas, A., Sagripanti, L., Rodríguez, M. P., Orts, D., Anavalón, A., Giroux, P., Otero, J., Echaurren, A., Zambrano, P., & Valencia, V. (2021). Tectonosedimentary evolution of the Coastal Cordillera and Central Depression of south-central Chile (36°30'-42°S). *Earth-Science Reviews, 213*, 103465. https://doi.org/10.1016/j.earscirev.2020.103465

Fahay, M.P. (1989). The ontogeny of *Steindachneria argentea* Goode and Bean with comments on its relationships. In: Cohen, D.M. (Ed.), Papers on the Systematics of Gadiform Fishes. *Natural History Museum of Los Angeles County, Science Series, 32*, 143–158.

Finger, K. L. (2013). Miocene foraminifera from the south-central coast of Chile. *Micropaleontology, 59*, 341–492.

Finger, K. L., Nielsen, S. N., Devries, T. J., Encinas, A., & Peterson, D. E. (2007). Paleontolgical evidence for sedimentary displacement in Neogene forearc basins of central Chile. *Palaios, 22*, 3–16. https://doi.org/10.2110/palo.2005.p05-081r

Fitch, J. E., & Barker, L. W. (1972). The fish family Moridae in the eastern Nort Pacific with notes on morid otoliths, caudal skeletons, and the fossil record. *Fishery Bulletin, 70*, 565–584.

Frassinetti, D. (2001). Moluscos bivalvos y gastrópodos del Mioceno marino de Isla Stokes, Sur de Chile. *Boletín Del Museo Nacional De Historia Natural De Chile, 50*, 73–90.

Frassinetti, D. (2004). Moluscos fósiles del Mioceno marino de Isla Ipún, Sur de Chile. *Boletín Del Museo Nacional De Historia Natural De Chile, 53*, 71–83.

Frassinetti, D., & Covacevich, V. (1982). Architectonicidae en la Formación Navidad, Mioceno, Chile central. Parte III. Architectonicinae (Mollusca: Gastropoda). *Boletín Del Museo Nacional De Historia Natural De Chile, 39*, 101–109.

Froese, R. & Pauly, D. (eds.) (2020) FishBase. World Wide Web electronic publication. www.fishbase.org, version (12/2020). http://www.fishbase.se/search.php (retrieved in January 2021).

Frost, G. A. (1924). Otoliths of fishes from the Tertiary formations of New Zealand. *Transactions and Proceedings of the Royal Society of New Zealand, 55*, 605–614.

Frost, G. A. (1933). Otoliths of fishes from the Tertiary formations of New Zealand. *Transactions and Proceedings of the Royal Society of New Zealand, 63*, 133–141.

García, F. (1968). Estratigrafía del Terciario de Chile Central. In: Cecioni G. (ed.), Simposio sobre el Terciario de Chile, Zona Central. Andres Bello, Santiago, 25–57.

Gon, O., & Heemstra, J. C. (Eds.). (1990). *Fishes of the Southern Ocean* (pp. 1–462). J.L.B. Smith Institute of Ichthyology.

Gradstein, F. M., Ogg, J. G., Schmitz, M. D., & Ogg, G. M. (2020). *Geologic Time Scale 2020* (pp. 1–1357). Elsevier.

Gregorová, R. (2008). *Steindachneria* sp. (Steindachneriinae, Merlucciidae, Gadiformes), a new fossil record of luminous hake from the outer Carpathians (Egerian, Ždánice-Hustopeče Formation, Czech Republic). *Acta Musei Moraviae, Scientiae Geologicae, 2008*, 219–224.

Grenfell, H. (1984). Early Miocene teleost otoliths from the Parengarenga Harbour, New Zealand. *New Zealand Journal of Geology and Geophysics, 27*, 51–96.

Grey, J. (1964). Fishes of the western North Atlantic, Part 4. (ed. Olsen, Y.M.). *Memoirs of the Sears Foundation Maritime Research Yale University, 1964*, 77–240.

Griffin, M., & Nielsen, S. N. (2008). A revision of the type specimens of Tertiary molluscs from Chile and Argentina described by d'Orbigny (1842), Sowerby (1846), and Hupé (1854). *Journal of Systematic Palaeontology, 6*, 251–316. https://doi.org/10.1017/S1477201907002374

Groves, L. T., & Nielsen, S. N. (2003). A new Late Miocene *Zonaria* (Gastropoda: Cypraeidae) from central Chile. *The Veliger, 46*, 351–354.

Gutiérrez, N., Hinojosa, L. F., Le Roux, J. P., & Pedroza, V. (2013). Evidence for an early-Middle Miocene age of the Navidad Formation (central Chile): Paleontological, paleoclimatic and tectonic implications. *Andean Geology, 40*, 66–78. https://doi.org/10.5027/andgeoV40n1-a03

Hidaka, K., Tsukamoto, Y., & Iwatsuki, Y. (2017). *Nemoossis*, a new genus for the eastern Atlantic long-fin bonefish *Pterothrissus belloci* Cadenat 1937 and a redescription of *P. gissu* Hilgendorf 1877 from the northwest Pacific. *Ichthyological Research, 64*, 45–53.

Hiller, N., MacKinnon, D. I., & Nielsen, S. N. (2008). (2007). A review of the systematics, biogeography, and evolutionary relationships of Recent and fossil brachiopods of the superfamily Kraussinoidea Dall, with descriptions of two new fossil species from New Zealand and Chile. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 98*, 379–390. https://doi.org/10.1017/S1755691007078474

Hughes, L. C., Orti, G., Huang, Y., Sun, Y., Baldwin, C. C., Thompson, A. W., Arcila, D., & Betancur-R., R., Li, C., Becker, L., Bellora, N., Zhao, X., Li, X., Wang, M., Fang, C., Xie, B., Zhou, Z., Huang, H., Chen, S., Venkatesh, B. & Shi, Q. . (2018). Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. *Proceedings of the National Academy of Sciences, 115*, 6249–6254. https://doi.org/10.1073/pnas.1719358115

Hunter, J. R. (1981). Feeding ecology and predation of marine fish larvae. In R. Lasker (Ed.), *Marine fish larvae. Morphology, ecology, and relation to fisheries* (pp. 33–79). Washington Sea Grant Program.

Ibaraki, M. (1992). Planktonic Foraminifera from the Navidad Formation, Chile: Their Geologic Age and Paleoceanographic Implications. In K. Ishizaki & T. Saito (Eds.), *Centenary of Japanese Micropaleontology* (pp. 91–95). Tokyo: Terra Scientific Publishing Company.

Karrer, C. (1971). Die Otolithen der Moridae (Teleostei, Gadiformes) und ihre systematische Bedeutung. *Zoologische Jahrbücher, Abteilung Für Systematik, 98*, 153–204.

Kiel, S., & Nielsen, S. N. (2010). Quaternary origin of the inverse latitudinal diversity gradient among southern Chilean mollusks. *Geology, 38*, 955–958.

Koken, E. (1884). Über Fisch-Otolithen, insbesondere über diejenigen der norddeutschen Oligocän-Ablagerungen. *Zeitschrift Der Deutschen Geologischen Gesellschaft, 36*, 500–565.

Kotlarczyk, J., Lerzmańka, A., Świdnicka, E., & Wiszniowska, T. (2006). A framework of ichthyofaunal ecostratigraphy of the Oligocene - early Miocene strata of the Polish outer Carpathian Basin. *Annales Societatis Geologorum Poloniae, 76*, 1–111.

Le Roux, J. P., Nielsen, S. N., Kemnitz, H., & Henriquez, Á. (2008). A Pliocene mega-tsunami deposit and associated features in the Ranquil Formation, southern Chile. *Sedimentary Geology, 203*, 164–180. https://doi.org/10.1016/j.sedgeo.2007.12.002

Lombarte, A., & Tuset, V. (2015). 3. Morfometría de otolitos. PIESCIIn A. V. Volpedo & A. M. Vaz-dos-Santos (Eds.), *Métodos de estudios con otolitos: Principios y aplicaciones* (pp. 60–90). Presidencia de la Nacíon.

Miya, M. & Nishida, M. (2014). The mitogenomic contribution to molecular phylogenetics and evolution of fishes: a 15-year retrospect. *Ichthyological Research, Review for IPFC9 special issue*. https://doi.org/10.1007/s10228-014-0440-9.

Möricke, W. (1896). Versteinerungen der Tertiärformation von Chile. *Neues Jahrbuch Für Mineralogie, Geologie Und Paläontologie Beilage-Band, 10*, 548–612.

Müller, A. (1999). Ichthyofaunen aus dem atlantischen Tertiär der USA. *Leipziger Geowissenschaften, 9*(10), 1–360.

Nelson, J. S. (2006). *Fishes of the world* (4th ed., pp. 1–601). John Wiley and Sons.

Nelson, J. S., Grande, T. C., & Wilson, M. V. H. (2016). *Fishes of the world* (5th ed., pp. 1–707). John Wiley and Sons.

Nielsen, J. G., & Hureau, J.-C. (1980). Revision of the ophidiid genus *Spectrunculus* Jordan and Thompson, 1914, a senior synonym of *Parabassogigas* Nybelin, 1957 (Pisces, Ophidiiformes). *Steenstrupia, 6*, 149–169.

Nielsen, S. N. (2005a). Cenozoic Strombidae, Aporrhaidae, and Struthiolariidae (Gastropoda, Stromboidea) from Chile: Their significance to the interpretation of southeast Pacific biogeography and climate. *Journal of Paleontology, 79*, 1120–1130. https://doi.org/10.1666/0022-3360

Nielsen, S. N. (2005b). *Exilia alanbeui*, new species, from the Neogene of central Chile: The first record of *Exilia* (Gastropoda: Ptychatractidae) from South America. *The Nautilus, 119*, 153–156.

Nielsen, S. N. (2013). A new Pliocene mollusk fauna from Mejillones, northern Chile. *Paläontologische Zeitschrift, 87*, 33–66. https://doi.org/10.1007/s12542-012-0146-0

Nielsen, S. N., & Ampuero, F. A. (2020). The lower Miocene Mitridae (Gastropoda) of Chile. *Ameghiniana, 57*, 255–265. https://doi.org/10.5710/AMGH.18.04.2020.3330

Nielsen, S. N., & DeVries, T. J. (2002). Tertiary Xenophoridae (Gastropoda) of western South America. *The Nautilus, 116*, 71–78.

Nielsen, S. N., & Encinas, A. (2014). The genus *Struthiochenopus* (Gastropoda, Aporrhaidae): New Miocene records from southern Chile. *Journal of Paleontology, 88*, 152–159. https://doi.org/10.1666/13-016

Nielsen, S. N., & Frassinetti, D. (2007a). The Neogene Volutidae (Gastropoda: Neogastropoda) from the Pacific coast of Chile. *Journal of Paleontology, 81*, 82–102. https://doi.org/10.1666/0022-3360

Nielsen, S. N., & Frassinetti, D. (2007b). The Miocene Architectonicidae (Gastropoda) of Chile. *Paläontologische Zeitschrift, 81*, 291–303.

Nielsen, S. N., & Glodny, J. (2009). Early Miocene subtropical water temperatures in the southeast Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology, 280*, 480–488. https://doi.org/10.1016/j.palaeo.2009.06.035

Nielsen, S. N., Frassinetti, D., & Bandel, K. (2004). Miocene Vetigastropoda and Neritimorpha (Mollusca, Gastropoda) of Central Chile. *Journal of South American Earth Sciences, 17*, 73–88. https://doi.org/10.1016/j.jsames.2004.05.005

Nielsen, S. N., Bandel, K., & Kröger, B. (2009). Palaeobiogeographical provenance, taphonomy, and mode of life of *Aturia cubaensis* (Lea, 1841) (Cephalopoda, Nautiloidea) from Cainozoic deposits of Chile. *Geobios, 42*, 73–88. https://doi.org/10.1016/j.geobios.2008.07.006

Nolf, D. (1976). Les otolithes de Téléostéens néogènes de Trinidad. *Eclogae Geologicae Helvetiae, 69*, 703–742.

Nolf, D. (2002). Fossil record and paleobiogeography of *Steindachneria* (Pisces, Gadiformes). *Courier Forschungsinstitut Senckenberg, 237*, 89–95.

Nolf, D. (2013). *The diversity of fish otoliths, past and present* (pp. 1–222). Royal Belgian Institute of Natural Sciences.

Nolf, D., & Aguilera, O. (1998). Fish otoliths from the Cantaure Formation (Early Miocene of Venezuela). *Bulletin De L'institut Royal Des Sciences Naturelles De Belgique, Sciences De La Terre, 68*, 237–262.

Nolf, D., & Brzobohaty, R. (2002). Otolithes de poissons du paléocanyon de Saubrigues (Chattien à Langhien), Aquitaine méridionale, France. *Revue De Micropaléontologie, 45*, 261–296.

Nolf, D., & Cappetta, H. (1989). Otolithes de poissons pliocènes du Sud-Ouest de la France. *Bulletin De L'institut Royal Des Sciences Naturelles De Belgique, Sciences De La Terre, 58*, 209–271.

Nolf, D., & Stringer, G. L. (1992). Neogene paleontology in the northern Dominican Republic 14. Otoliths of Teleostean fishes. *Bulletin of American Paleontology, 102*, 41–81.

Nolf, D., & Tyler, J. C. (2006). Otolith evidence concerning interrelationships of caproid, zeiform and tetraodontiform fishes. *Bulletin De L'institut Royal Des Sciences Naturelles De Belgique, 76*, 147–189.

Norman, J.R. (1934). A systematic monograph of the flatfishes (Heterosomata); Vol. 1: Psettodidae, Bothidae, Pleuronectidae. The trustees of the British Museum, London, 1–459.

Oliveros, V., Vásquez, P., Creixell, C., Lucassen, F., Ducea, M. N., Ciocca, I., González, J., Espinoza, M., Salazar, E., Coloma, F., & Kasemann, S. A. (2020). Lithospheric evolution of the Pre- and Early Andean convergent margin, Chile. *Gondwana Research, 80*, 202–227. https://doi.org/10.1016/j.gr.2019.11.002

Parin, N. V., & Kobyliansky, S. G. (1996). Diagnoses and distribution of fifteen species recognized in genus *Maurolicus* Cocco (Sternoptychidae, Stomiiformes) with a key to their identification. *Cybium, 20*, 185–195.

Pérez-Barría, L., & Nielsen, S. N. (2020). Solemyidae (Bivalvia, Protobranchia) from the lower Miocene of south-central Chile, with description of a new species. *Journal of Paleontology, 94*, 56–63. https://doi.org/10.1017/jpa.2019.60

Philippi, R. A. (1887). *Die Tertiären und Quartären Versteinerungen Chiles* (pp. 1–266). F.A. Brockhaus.

Philippi, R.A. (1897). Paleontología. In: R. Maldonaldo (ed.), Estudios geográficos é hidrográficos sobre Chiloé. Oficina Hidrográfica de Chile, Santiago, Chile, 365–370.

Quiroz, D., Duhart, P. & Crignola, P. (2004). Geología del Área Chonchi—Cucao, Región de Los Lagos. *Servicio Nacional de Geología y Minería, Carta Geológica de Chile, Serie Geología Básica, 86*, 1–33, 1 map scale 1:100:000.

Rees, D. J., Poulsen, J. Y., Sutton, T. T., Costa, P. A. S., & Landeata, M. F. (2020). Global phylogeography suggests extensive eucosmopokitanism in mesopelagic fishes (*Maurolicus*: Sternoptychidae). *Nature Research, Scientific Reports, 10*(20544), 1–12. https://doi.org/10.1038/s41598-020-77528-7

Roa-Varón, A., & Ortí, G. (2009). Phylogenetic relationships among families of Gadiformes (Teleostei, Paracanthopterygii) based on nuclear and mitochondrial data. *Molecular Phylogenetics and Evolution, 52*, 688–704.

Roberts, C. D., Stewart, A. L., & Struthers, C. D. (2015). *The fishes of New Zealand* (pp. 1–1748). Wellington: Te Papa Press.

Rojas, J., & Nielsen, S. N. (2020). Two new species of *Pratulum* from the lower Miocene of Chile - The first records of *Pratulum* (Bivalvia, Cardiidae) from South America. *Ameghiniana, 57*, 433–442. https://doi.org/10.5710/AMGH.20.05.2020.3290

Schmidt, W. (1968). Vergleichend morphologische Studie über die Otolithen mariner Knochenfische. *Archiv Für Fischereiwissenschaften, Hamburg, 19*, 1–96.

Schwarzhans, W. (1974). Die Otolithen-Fauna des Chatt A und B (Oberoligozän, Tertiär) vom Niederrhein, unter Einbeziehung weiterer Fundstellen. *Decheniana, 126*, 91–132.

Schwarzhans, W. (1978). Otolith-morphology and its usage for higher systematical units with special reference to the Myctophiformes s.l. *Mededelingen Van De Werkgroep Voor Tertiaire En Kwartaire Geologie, 15*, 167–185.

Schwarzhans, W. (1980). Die teritiäre Teleosteer-Fauna Neuseelands, rekonstruiert anhand von Otolithen. *Berliner Geowissenschaftliche Abhandlungen, A, 26*, 1–211.

Schwarzhans, W. (1981). Vergleichende morphologische Untersuchungen an rezenten und fossilen Otolithen der Ordnung Ophidiiformes. *Berliner Geowissenschaftliche Abhandlungen, A, 32*, 63–122.

Schwarzhans, W. (1994a). Sexual and ontogenetic dimorphism in otoliths of the family Ophidiidae. *Cybium, 18*, 71–98.

Schwarzhans, W. (1994b). Die Fisch-Otolithen aus dem Oberoligozän der Niederrheinischen Bucht; Systematik, Palökologie, Paläobiogeographie, Biostratigraphie und Otolithen-Zonierung. *Geologisches Jahrbuch, A, 140*, 1–248.

Schwarzhans, W. (1999). A comparative morphological treatise of recent and fossil otoliths of the order Pleuronectiformes. *Piscium Catalogus, Otolithi Piscium, 2*, 1–391.

Schwarzhans, W. (2008). Otolithen aus küstennahen Sedimenten des Ober-Oligozän der Niederrheinischen Bucht (Norddeutschland). *Neues Jahrbuch Geologie, Paläontologie Abhandlungen, 248*, 11–44.

Schwarzhans, W. (2010). The otoliths from the Miocene of the North Sea Basin. Backhuys Publishers, Leiden & Margraf Publishers, 1–352.

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

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

Schwarzhans, W. (2013c). Otoliths from the Miocene of West Africa, primarily from the Mandorové Formation of Gabon. *Palaeo Ichthyologica, 13*, 151–184.

Schwarzhans, W. (2018). A review of Jurassic and early Cretaceous otoliths and the development of early morphological diversity in otoliths. *Neues Jahrbuch Geology Und Paläontologie Abhandlungen, 287*, 75–121.

Schwarzhans, W. (2019a). Reconstruction of the fossil marine bony fish fauna (Teleostei) from the Eocene to Pleistocene of New Zealand by means of otoliths. *Memorie Della Società Italiana Di Scienze Naturali e Del Museon Di Storia Naturale Di Milano, 46*, 3–326.

Schwarzhans, W. (2019b). A comparative morphological study of Recent otoliths of the Congridae, Muraenesocidae, Nettastomatidae and Colocongridae (Anguilliformes). *Memorie Della Società Italiana Di Scienze Naturali e Del Museon Di Storia Naturale Di Milano, 46*, 327–354.

Schwarzhans, W. (2019c). A comparative morphological study of Recent otoliths of the Moridae (Gadiformes). *Memorie Della Società Italiana Di Scienze Naturali e Del Museon Di Storia Naturale Di Milano, 46*, 355–370.

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

Schwarzhans, W., & Aguilera, O. A. (2016). Otoliths of the Ophidiiformes from the Neogene of tropical America. *Palaeo Ichthyologica, 14*, 91–124.

Schwarzhans, W., Scofield, R. P., Tennyson, A. J. D., Worthy, J. P., & Worthy, T. H. (2012). Fish remains, mostly otoliths, from the non-marine early Miocene of Otago, New Zealand. *Acta Palaeontologica Polonica, 57*, 319–350.

Stinton, F. C. (1957). Teleostean otoliths from the Tertiary of New Zealand. *Transactions of the Royal Society of New Zealand, 84*, 513–517.

Stringer, G. L. (1998). Otolith-based fishes from the Bowden Shell Bed (Pliocene) of Jamaica: Systematics and palaeoecology. *Contributions to Tertiary and Quaternary Geology, 35*, 147–160.

Sutton, T. T., Clark, M. R., Dunn, D. C., Halpin, P. N., Rogers, A. D., Guinotte, J., Bogard, S. J., Angel, M. V., Perez, J. A. A., Wishner, K., Haedrich, R. L., Lindsay, D. J., Drazen, J. C., Vershchaka, A., Piatkowski, U., Morato, T., Błachowiak-Samołyk, K., Robison, B. H., Gjerde, K. M., … Heino, M. (2017). A global biogeographic classification of the mesopelagic zone. *Deep-Sea Research Part I, 126*, 85–102.

Świdnicki, J. (1990). Rewizja kopalnych Gadiformes z trzeciorzêdu Karpat (In Polish). Unpublished DSc. Thesis, University of Wrołcaw, 1–90.

Tavera, J. (1942). Contribución al estudio de la estratigrafía y paleontología del Terciario de Arauco. *Anales Del Primer Congreso Panamericano De Ingeniería De Minas y Geología, 2*, 580–632.

Tavera, J. (1979). Estratigrafía y paleontología de la Formación Navidad, Provincia de Colchagua, Chile (Lat. 30°50'-34°S). *Boletín Del Museo Nacional De Historia Natural De Chile, 36*, 1–176.

Uiblein, F., Nielsen, J. G., & Møller, P. R. (2008). Systematics of the ophidiid genus *Spectrunculus* (Teleostei: Ophidiiformes) with resurrection of *S. crassus*. *Copeia, 2008*, 542–551.

Valenzuela, E. A. (1982). Estratigrafía de la boca Occidental del canal de Chaco, X Región, Chile. *Congreso Geológico Chileno Actas, III*, A343–A376.

Villafaña, J. A., Nielsen, S. N., Klug, S., & Kriwet, J. (2019). Early Miocene cartilaginous fishes (Chondrichthyes: Holocephali, Elasmobranchii) from Chile: Diversity and paleobiogeographic implications. *Journal of South American Earth Sciences, 96*, 102317. https://doi.org/10.1016/j.jsames.2019.102317

Wiley, E. O., & Johnson, G. D. (2010). A teleost classification based on monophyletic groups. In S. N. Nelson, H.-P. Schultze, & M. V. H. Wilson (Eds.), *Origin and phylogenetic interrelationships of teleosts* (pp. 123–182). Verlag.

Whitehead, P.J.P. (1985). Clupeoid fishes of the world. Part 1 - Chirocentridae, Clupeidae and Pristigasteridae. *FAO Species Catalogue, 7.1*, 1–303.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.