A new species of *Iothia* (Gastropoda: Lepetidae) from Chilean methane seeps, with comments on the accompanying gastropod fauna

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ABSTRACT

A new species of the limpet genus *Iothia*, *I. megalodon* new species, is described from a cold-seep locality in central Chile. It differs from other species of *Iothia* by the enlarged functional radular teeth. *Iothia megalodon* feeds on bacterial film and sediment as indicated by the gut content. *Iothia emarginuloides* (Philippi, 1868) is re-instated as the name to be used for the Antarctic–South American species previously known as *Iothia coppingeri* (E.A. Smith, 1881). A COI analysis of eight species of Lepetidae is included to elucidate the generic position of the new species. The gastropod fauna of the type locality, the recently discovered bathyal methane seeps off Central Chile, is reviewed in order to place *Iothia megalodon* in its ecological context. *Margarites huloti* Vilvens, 2006, *Bathybembix macdonaldi* (Dall, 1891), *Calliotropis ceciliae* Vilvens and Sellanes, 2010, and *Cantrainea panamense* (Dall, 1908) are known to have relatives in seeps or other chemosynthetic environments. The presence of *I. megalodon* within this community and its gut content support its inclusion as a member of the seep fauna.

Additional keywords: Molecular phylogeny, Chile

INTRODUCTION

The interest in chemosynthetic environments, hydrothermal vents, and various types of seeps has remained at a high level, ever since the discovery of vents in 1977 (Ballard, 1977; Lonsdale, 1977; Corliss et al., 1979). A few years later, the first sulphide seep locality off Florida (Paull, 1984) and methane seeps in the Gulf of Mexico (Brooks, Kennicut and Fay 1985) were discovered. In less than 30 years, these environments have become fairly well known, much better known than the surrounding deep-sea. The Gastropoda is richly represented in seeps and vents, both in number of species and specimens (Warén et al., 2006).

The fauna of vents and seeps to a high extent consists of species that have been found only in these environments (van Dover, 2000), more so in the vents. But there are also species that live in the adjacent deep-sea and seem to be attracted by the higher biomass and more complicated biotope, often with rocks, shells, and soft sediments mixed. To understand the ecology of these biotopes, it is therefore important to know which ones are its regular inhabitants and which are occasional intruders. Recognition of chemosynthetic biotopes is facilitated if this can be done simply from the presence of certain common genera or species when less sophisticated methods of investigation are used, which is the present case.

Already some time ago, species like *Calyptogena australis* Stuardo and Valdovinos, 1988 (Bivalvia, caught by long-line fishery), *Bathybembix macdonaldi* (Dall, 1891), and *Cantrainea panamense* (Dall, 1908) (Gastropoda, from side catches during trawling), started to become available on the commercial shell market. Their presence indicated that seep bottoms could occur off the Chilean coast. This was then confirmed by seismic surveys and trawling off Concépcion in depths between 650 and 930 m (Sellanes et al., 2004, 2008). So far, these seeps have been explored only by trawling and tube-coring.

In this paper, we describe a new patellogastropod from the methane seeps. The terminology largely follows Lindberg's (1998) review of the Patellogastropoda (=Docoglossa). To broaden our base for the systematic placement of the new species, we add some preliminary results from ongoing work on the phylogeny of the patellogastropods in hot vents and cold seeps (Nakano and Warén, unpublished).

To place *Iothia megalodon* in its ecological context, we summarize the gastropod fauna known from the Concépcion seeps, the type locality of *I. megalodon*, since the species have been described in several not easily accessible small papers. We review existing and new information on these species in order to single out which species may be considered "seep fauna".

MATERIALS AND METHODS

CHILEAN SAMPLING SITES

The seep specimens originate from several hauls with an Agassiz trawl with an opening of 1.5 × 0.4 m from R/V VIDAL GORMÁZ, off Concepción, central Chile. When the trawl came up, sediment samples were washed on board, specimens were picked out and preserved in 70% ethanol.

Cruise VG-03, 36°21.38′ S, 74°43.91′ W, 980 m depth, Nov. 2003 (*Iothia megalodon*, 2 paratypes, SMNH type collection 6784 and MNHC 6619)

Cruise VG-04, AGT 06, 36°21.75′ S, 73°43.55′ S, 800 m, Oct. 11, 2004. (*Cantrainea panamense* – 3 specimens, SMNH 103188)

Cruise VG-04, AGT 13, 36°21.91′ S, 73°43.21′ S, 843–728 m, Oct. 20, 2004 (*Bathybembix macdonaldi* – 2 specimens - SMNH 103189)

Cruise VG-06, AGT 6, 36°21.67′ S, 73°43.52′ W, 865 m, Sep. 01, 2006. (*Zetela alphonsi* – 2 specimens SMNH 103187)

Cruise VG-06 AGT 7-2, 36°32.19′ S, 73°40.65′ W, 764–843 m, Sep. 03, 2006 (*Iothia megalodon*, 2 paratypes SMNH type collection 7932)

Cruise VG-07, AGT 10, 36°22.01′ S, 73°43.10′ W, 764–843 m, Oct. 02, 2007, (*Iothia emarginuloides* – 1 specimen, SMNH 103936; *Iothia megalodon*, **holotype 6617**, 1 paratype MNHC 6618, 2 paratypes SMNH type collection 7933)

Cruise VG-07, AGT 11, 36°21.88′ S, 73°42.99′ W, 824–730 m, Oct. 03, 2007 (*Margarites huloti* Vilvens, 2006 – 3 specimens SMNH 103190, 103192 [dry]).

Work in the area has indicated several active methane seep sites with assumed chemoautotrophic communities, with chemosymbiotic clams like *Calyptogena*, *Lucinoma*, and *Thyasira* (Sellanes et al., 2004; Holmes, Oliver and Sellanes, 2005; Oliver and Sellanes, 2005; Sellanes and Krylova, 2005; Sellanes, Quiroga, and Neira, 2008). In addition, the heterotrophic fauna has high population densities within this area, probably benefiting from the abundance of food and by the habitat heterogeneity generated by the carbonate reefs associated with methane seepage (Sellanes et al., 2008).

MORPHOLOGY

For the systematic work, specimens of *Iothia*, *Margarites huloti*, *Cantrainea panamense*, and *Zetela alphonsi* were cleaned, soft parts extracted and critical point dried, and the gross anatomy examined with SEM. Radulae were prepared by dissection and cleaning in 1:50 commercial bleach (*Iothia megalodon*), or by dissolving bodies in 25% KOH at 40°C, cleaned, mounted, and examined with SEM.

For comparison with the new species of *Iothia*, DNA was extracted from pieces of foot tissue of the species listed in Table 1 where collection data and localities are listed. In total, 10 individuals were newly sequenced, and combined with published sequences of 9 individuals from Nakano and Ozawa (2007). Two species of *Emarginula* (Fissurellidae) and three species of the Cocculinidae were used as outgroup taxa.

DNA METHODS AND PHYLOGENETIC ANALYSIS

The procedures described by Nakano and Ozawa (2007) and Nakano et al. (2009) were used to extract DNA, amplify it using PCR, and determine the sequence of the COI and Histone H3 genes. All new sequences determined in this study have been deposited in GenBank (accession numbers in Table 1).

COI and Histone3 sequences were manually aligned using MacClade 4.03 (Maddison and Maddison, 2002), with reference to the translated amino acid sequence. Third-codon positions of both genes were retained in all phylogenetic analyses. The model of nucleotide substitution for the Bayesian analyses were selected using Modeltest (Posada and Crandall 1998), giving GTR+I+G for COI and Histone3. The partition-homogeneity test (Swofford 2002; the ILD test Farris et al. 1995) was performed to test whether the COI and Histone H3 sequences contained similar phylogenetic signal and could thus be analysed as a single data-set. Subsequent phylogenetic analyses were performed with PAUP* version 4b10 (Swofford 2002) for neighbor-joining (NJ) (Saito and Nei, 1987) (Kimura's two-parameter method; Kimura, 1980), equally weighted maximum parsimony (MP), as well as their associated bootstrap values (Felsenstein, 1985, 1988). MrBayes v.3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) was used to perform Bayesian analyses and to estimate posterior probabilities.

The NJ bootstrap analyses consisted of 10,000 replicates. The MP bootstrap analysis consisted of 1,000 replicates using heuristic search (with 10 random addition sequence replicates and TBR branch-swapping).

MrBayes was run with the following settings for the two partitions (i.e., genes), the maximum-likelihood model employed six substitution types (nst=6), rate variation across sites was modeled using a gamma distribution, with a proportion of the sites being invariant (rate=invgamma), the shape, proportion of invariable sites, state frequency, and substitution rate parameters were estimated for each partition separately. The Markov-chain Monte-Carlo search was run with four chains 3,000,000 generations, with trees being sampled every 100 generations and the first 5,000 trees (i.e., 500,000 generations) were discarded as burn-in.

Table 1. Specimens of Lepetidae sequenced for this study.

Species	Locality	Museum Registration	COI	Histone H3
Order PATELLOGASTROPODA				
LEPETIDAE				
Bathylepeta linseae Schwabe, 2006	Antarctica, 70°04.5'S, 03° 20'W, 2084–2163 m depth	ZSM Mol 20081168	AB543973	AB543983
Cryptobranchia kuragiensis (Yokoyama, 1920)	Aicappu, Akkeshi-cho, Hokkaido, Japan, 5–8 m depth.	NUGB-L505	AB238457	AB543984
Cryptobranchia kuragiensis (Yokoyama, 1920)	Aicappu, Akkeshi-cho, Hokkaido, Japan, 5–8 m depth.	NSMT-Mo76949	AB543974	AB543985
Iothia fulva (O.F. Müller, 1776)	Raunefjord, Norway, 50 m depth.	SMNH 107221	AB548309	AB548310
Iothia emarginuloides (Philippi, 1868)	Argentine, Beagle Channel, Bahia Lapataia, 54° 51'S, 068° 33'W, 15–18m depth	SMNH-103867	AB543975	AB543986
Iothia megalodon n. sp.	Chile, methane seep off Concepcion, AGT 10, 36° 22.01'S, 73° 43.10'W, 764–843 m depth.	UG07-AGT10	AB543976	AB543987
Lepeta caeca (O.F. Müller, 1776)	Koster Area, Bohuslän, Sweden	SMNH-65221	AB543977	AB543988
Lepeta caeca pacifica Moskalev, 1977	Aicappu, Akkeshi-cho, Hokkaido, Japan, 2–3 m depth	NUGB-L503	AB238458	AB543989
Lepeta caeca pacifica Moskalev, 1977	Aicappu, Akkeshi-cho, Hokkaido, Japan, 2–3 m depth.	NSMT-Mo76950	AB543978	AB543990
Limalepeta lima Dall, 1918	Urakawa-cho, Hokkaido, Japan, 150–300 m depth.	NSMT-Mo76951	AB543979	AB543991
Limalepeta lima Dall, 1918	Urakawa-cho, Hokkaido, Japan, 150–300 m depth.	NSMT-Mo76952	AB543980	AB543992
Sagamilepeta sagamiensis (Kuroda and Habe, 1971)	Off Hota, Chiba Pref., Japan, 200–270m depth.	NSMT-Mo76953	AB543981	AB543993
Sagamilepeta sagamiensis (Kuroda and Habe, 1971)	Off Hota, Chiba Pref., Japan, 200–270m depth.	NSMT-Mo76954	AB543982	AB543994
PECTINODONTIDAE				
Bathyacmaea nipponica Okutani, Tsuchida and Fujikura, 1992	Japan	NUGB-Ba1	AB238588	AB543995
Pectinodonta rhyssa (Dall, 1925)	Off Kiishirahama, Wakayama Pref., Japan	NUGB-L428	AB238589	AB543996
Order COCCULINIFORMIA				
COCCULINIDAE				
Coccopigya punctoradiata (Kuroda and Habe, 1949)	Kamikawaguchi, Kochi Pref., Japan	NUGB-L266	AB238590	AB543997
Cocculina sp. A	Kumanonada, Mie Pref., Japan	NUGB-L429	AB238591	AB543998
Cocculina sp. B	Tosa Bay, Kochi Pref., Japan	NUGB-L617	AB238592	AB543999
Order VETIGASTROPODA				
FISSURELLIDAE				
Emarginula foveolata fujitai Habe, 1953	Seto Inland Sea, Hiroshima Pref., Japan	NUGB-L277	AB238593	AB544000
Emarginula variegata A. Adams, 1852	Benoki, Okinawa Pref., japan	NUGB-L348	AB238594	AB544001

ABBREVIATIONS USED IN TEXT:

AGT – Agassiz trawl; MNHNCL – Museo Nacional de Historia Natural de Chile, Santiago; SEM – scanning electron microscopy; SMNH – Swedish Museum of Natural History; ZSM – Zoologische Staatssammlung, München

SYSTEMATICS

Family Lepetidae Gray, 1850

Remarks: This family contains species living in deep or cold waters. They live on pieces of old shells or on rocks, where they feed on precipitated detritus or, in shallow water, encrusting diatoms. Shallow water species occur only in high latitudes. The species of the family are most safely recognized by the radular morphology with a central complex of 4–6 sturdily built teeth and two feather-like ones on each side of the complex. The absence of ctenidium and secondary gills and the presence of well-developed oral lappets are more noticeable external characters, but these are not fully diagnostic, since they are shared with Neolepetopsidae. The shell usually has a better-defined sculpture of radiating ribs, often equipped with small scales or spine-like processes, when compared to other patellogastropods, but this is also shared with the Neolepetopsidae. Neolepetopsids, however, have a well-developed, perfectly transparent inner shell layer.

Species of Lepetidae are generally supposed to lack eyes, as indicated by their vernacular name "blind limpets", but this is not correct. Both *Iothia emarginuloides* and the type species *I. fulva* have very small black, pigmented eyes, situated on the tentacle bases, close to the head, having a diameter of 50–60 μm. According to Angerer and Haszprunar (1996: 173), they are supposed to be non-pigmented, but this is true only for *Lepeta caeca* (O.F. Müller, 1776) and *Propilidium ancyloides* (Forbes, 1840), among the species they investigated. The presence of eyes, however visible only in dorsal view, was confirmed both in *I. fulva* and in Chilean and Antarctic specimens of *I. emarginuloides*.

Generic level names included in Lepetidae: *Lepeta* Gray, 1847; *Propilidium* Forbes and Hanley, 1849; *Iothia* Forbes, 1849; *Cryptobranchia* Middendorff, 1851; *Sagamilepeta* Okutani, 1987; *Maoricrater* Dell, 1956; *Bathylepeta* Moskalev, 1977, and *Limalepeta* Moskalev, 1977. We are not convinced that all these generic names are needed to reflect the phylogeny of the family, but will refrain from making changes in their nomenclatural status at this point.

Genus *Iothia* Forbes, 1849

Type Species: *Patella fulva* O.F. Müller, 1776

Remarks: Species of this genus often have a shell with a distinctly yellowish or reddish color (Figure 9), but white or colorless shells also occur. The sculpture consists of distinct, scaly radial ribs, the apex is situated at the posterior third, and they have a distinctly convex posterior slope. Species have been reported from the North Pacific, North Atlantic, Antarctica, South America, and New Zealand (in this latter location as *Maoricrater* Dell, 1956).

Eight names have been used for species of Lepetidae in Antarctica and southern South America: **1.** *Patella albescens* Philippi, 1846 was placed in *Iothia* by Valdivinos (1999) and Forcelli (2000), but this species was described from "the shores in Central Chile" by Philippi (1846) and the description seems to be based on a young nacellid (Pilsbry, 1891: 36). The name has not been in modern use for any nacellids (Valdovinos and Rüth, 2005; Devries, 2008; De Aranzanmendi et al., 2009; González-Wevar et al., 2010), and is not discussed below; **2.** *Patella* (?) *emarginuloides* Philippi, 1868; **3.** *Tectura* (*Pilidium*) *coppingeri* (E.A. Smith, 1881); **4.** *Lepeta antarctica* E.A. Smith, 1907; **5.** *Propilidium pelseneeri* Thiele, 1912: 186, from the "Gauss Station" (68°S, 090°E), near Drygalski Island, Davis Sea; holotype in the Natural History Museum, Berlin, Mol 63.050; not seen; **6.** *Lepeta depressa* Hedley 1916: 42, from off the Schakleton Ice shelf in 220 m depth, has not been identified later. It was based on a single broken shell; not discussed below; **7.** *Pilidium fulviformes* Egorova, 1972; **8.** *Iothia coppingeri magellanica* Linse, 2002.

Bathylepeta is another lepetid genus with two species known from abyssal depths off Chile and in the Weddell Sea (ca. 5000 m). They differ by being quite large (25–30 mm) and having an almost smooth shell with central apex. One of them, *B. linsae* Schwabe, 2006 is included in the phylogenetic analysis.

Iothia emarginuloides (Philippi, 1868)
(Figures 5–6, 16–18, 23–26)

Patella (?) *emarginuloides* Philippi, 1868: 224. Type locality: "Magallanes, Potissimum Magellanicum [Magellan Strait], communicated by G. Acton". Type material: Museo Nacional de Historia Natural de Chile. Gueglielmo Acton was a Captain in the Neapolitanian Navy (Malakozoologische Blätter (1856) 3: 197). Transferred to *Iothia* by Pilsbry (1891: 72, as *Pilidium emarginuloides*.

Tectura (*Pilidium*) *coppingeri* E.A. Smith, 1881: Type locality: Eastern part of Magellan Strait, 16–18 m depth. Holotype: Natural History Museum, London, not examined. Transferred to *Iothia* by Pilsbry (1891: 72) as *Pilidium coppingeri*.

Lepeta (*Pilidium*) *antarctica* E.A. Smith, 1907: 12. Type locality: Hole 10 (McMurdo Sound), 130 fathoms. Holotype: Natural History Museum, London, not examined. Considered a synonym by Hain (1990: 37), validity questioned by Schwabe (2006: 43).

Pilidium fulviformes Egorova 1972: 384. Type locality: Davis Sea, 15 m depth. Type material: P.P. Shirshov Institute of Oceanology, Moscow. Synonymized with *Iothia coppingeri* (Moskalev 1977: 62)

Iothia coppingeri magellanica Linse, 2002: 62. Type locality: Beagle Channel (Chile and Argentina) 55° 07.30' S, 66°52.78' W, 25 m depth. Type material: Zoological Museum, Berlin.

Material Examined: SMNH 102837, Chile, Golfo de Ancud, 42°26.4' S, 072°59.0' W, 250–300 m, 3 specimens (Lund University Chile Expedition); SMNH 103289, Lazarev Sea, 70°19.0' S, 003°16.3' W, 191–204 m, 5 specimens; SMNH 103290, Lazarev Sea, 69°59.4' S, 008°00.3' E, 161–161 m, 2 specimens; SMNH 103291, Lazarev Sea, 69°57.4' S, 005°04.2' E, 210–210 m, 1 specimen; SMNH 103292, Lazarev Sea, 70°24.2' S, 006°08.1' E, 118–126 m, 1 specimen; SMNH 103293, Lazarev Sea, 70°19.0'S, 003°16.3' W, 191–204 m, 1 specimens; SMNH 103561, Chile, Magellan Strait, Punta Arenas, 13–15 m, 1895-12-04, Swedish Magellans Exp 1895-7#390, 2 specimens; SMNH 103562, Chile, Magellan strait, Romanche Bay, 21–27 m, dead shells on black clay (smooth, var. radiata Strebel), Swedish Magellans Exp 1895-7#665, 1 specimen; SMNH 103563, Chile, Magellan Strait, Punta Arenas, shell gravel, 27 m, Swedish Magellans Exp. 1895 #465, 1 specimen; SMNH 103564, Chile, Magellan Strait, Romanche Bay, 20 m, Swedish Magellans Exp. 1895-7#665, 2 specimens; SMNH 103689, Falkland Islands, Albermarle Harbour, 18–30 m, Swedish Antarctic Expedition 1901#57, 4 specimens;SMNH 103690, Chile, Otway Water, Puerto Toro, 1908-04-15, 20–30 m, Swedish Magellans Exp 1895-7#16, 2 specimens (smooth); SMNH 103936, Chile, off Concepcíon, 36°22.01' S, 073°43.10' W, 764–843 m, Leg Sellanes VG-07-AGT10, 1 specimen; SMNH 103867, Argentina, Tierra del Fuego, Beagle Channel, Bahia Lapataia, 54°51.5'S, 068°33.1' W, 15–18 m, Leg Diego
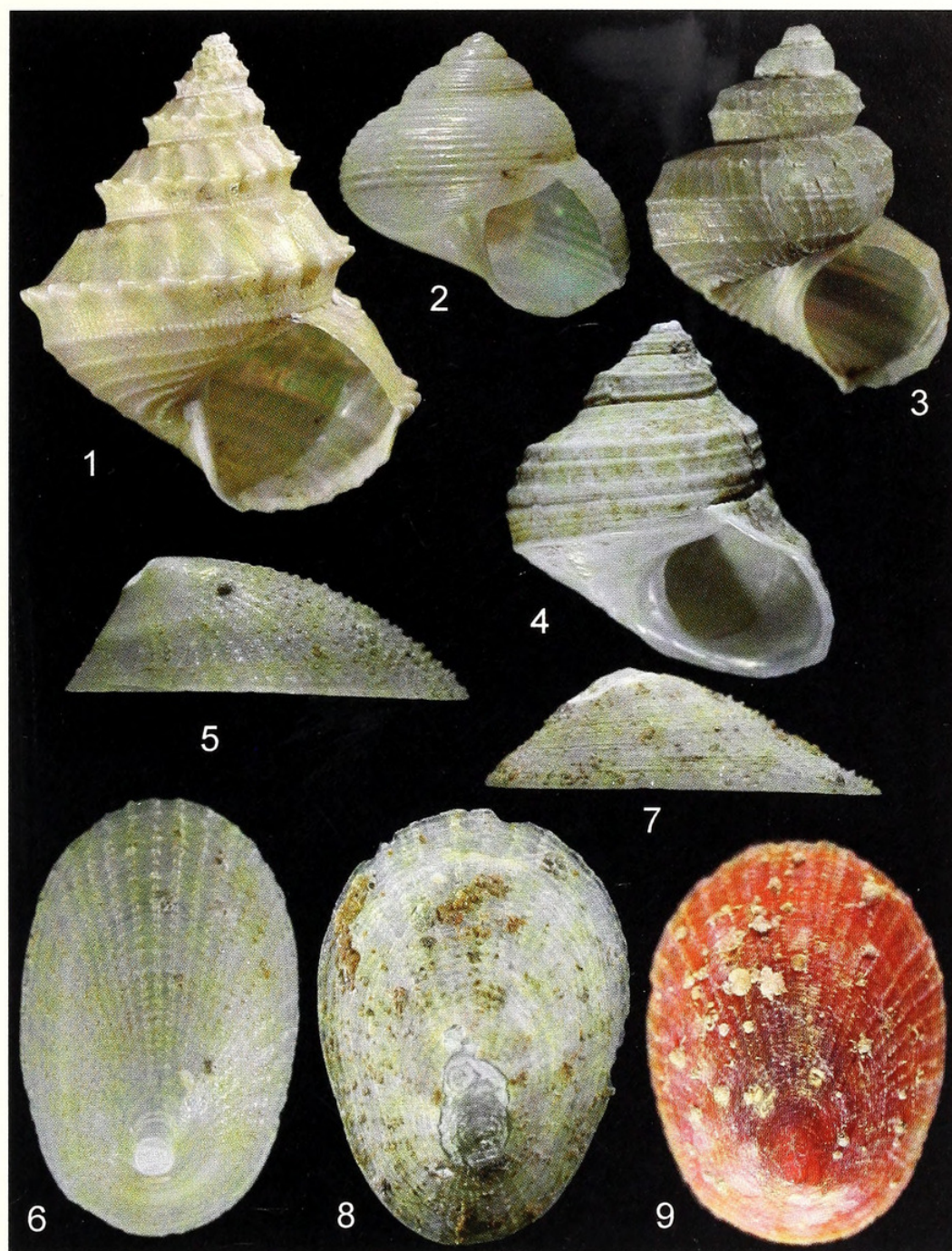
Figures 1–9. Gastropoda from Concepcion seeps, unless otherwise stated. **1.** *Bathybembix macdonaldi*, shell height 44.5 mm. **2.** *Margarites huloti*, shell height 23 mm. **3.** *Zetela alphonsi*, height 10.5 mm. **4.** *Cantrainea panamense*, shell height 21.8 mm. **5–6.** *Iothia emarginuloides*, length 5.8 mm. **7–8.** *Iothia megalodon*, holotype #6617, length 8.9 mm. **9.** *Iothia fulva*, Norway, Raunefjord, 50 m depth, length 5.7 mm.

Zelaya, 5 specimens, DNA extracted; ZSM Mol 20013014, Antarctica, 71°06.27′ S, 012°50.46′ W, 728–743 m , 1 specimen; ZSM Mol 20013011, Antarctica, 63°07.52′ S, 59°25.43′ W, 782 m, 1 shell; ZSM Mol 20013012, Antarctica, 71°06.27′ S, 012°50.46′ W, 728–743 m, 1 specimen.

Distribution: Antarctic circumpolar, the Subantarctic Islands and southern South America, north to Concepcíon (Chile), southernmost Argentina, the Falkland Islands, Kerguelen and Crozet Island (Dell, 1990; Linse, 2002; Aldea, Olabarria, and Troncoso, 2008), usually in 20–200 m depth.

Remarks: Supported by the fact that type specimens are very similar and were described from nearby localities (separated by maximum 400 km at the same latitude), we consider, as did Strebel (1907: 112), that *coppingeri* and *emarginuloides* are synonyms, and the consequence is that Philippi's name is the one to be used. Strebel

(1908), Egorova (1972), and Dell (1990) recognized this, but gave no reasons for their continued use of *coppingeri*. Philippi (1868) described the species as being similar to those in the genus *Emarginula*, but lacking gills. He also noticed that eyes were present in a specimen with dried soft parts, soaked in water. Both Chilean and Antarctic specimens have, contrary to common belief, small eyes, of 50–60 µm diameter, and visible only in dorsal view. In alcohol-preserved specimens, the eyes remain visible also after at least 100 years.

Schwabe (2006) reviewed some of the names supposed to be based on southern Lepetids, but did not change nomenclature.

Iothia coppingeri magellanica Linse, 2002 was described as new because its radula was said to differ from Hain's (1990) pictures of the radula of *coppingeri* by having two instead of a single feather-like marginal tooth. Linse also says there is only a single southern species of *Iothia*, viz. *I. coppingeri*. *Lepeta antarctica*, *Iothia emarginuloides*, *Lepeta depressa*, and *Pilidium fulviformes* are not mentioned. Linse has compared the teeth of her Magellanic specimens and found them to differ from the "high-Antarctic *Iothia coppingeri*". However, *Iothia coppingeri* is no more "high-Antarctic" than Linse's *magellanica*; if anything, *I. coppingeri* is more northern since it was described from the Strait of Magellan, not from Antarctica. It is obvious from Egorova's (1972) drawings and Hain's (1990) SEM pictures that Antarctic specimens of *Iothia* have two featherlike teeth. If there had been differences as assumed by

Linse, the Antarctic specimens would be the ones in need of a new name, but for them the name *antarctica* E.A. Smith, 1907 is available. Linse also stated (2002: 64) that her specimens could not be distinguished from *coppingeri* by shell morphology. Examination of the radula of a Chilean specimen and a specimen from Hain's collections in the Weddell Sea (partly kept in SMNH) did not show any obvious differences. The shells can usually be distinguished by the Antarctic specimens having a more vitreous shell but this is probably a result of the physical conditions when the shells were formed. We attempted to solve the problem by sequencing Antarctic specimens but no specimens available to us yielded a sequence.

If the Antarctic specimens are considered a distinct species, *Iothia antarctica* (E.A. Smith, 1907) is available for them (Zelaya, 2005).

Specimens from shallow water in the Magellan Strait often have an almost smooth shell (Figure 18), only indications of the ribs remain. Such specimens look very different from large Antarctic and deep water specimens, which are invariably sculptured (Figure 16).

Iothia megalodon new species
(Figures 7–8, 10–11, 12–14, 19–22)

Description: Shell (Figures 7–8, 14) limpet-shaped, thin, flat, dirty yellowish white. Protoconch unknown. Sculpture of 45–50 radiating ridges made more distinct by a series of low spines, knobs, or blisters on each. Apex situated at or just behind the anterior 1/3, height of shell
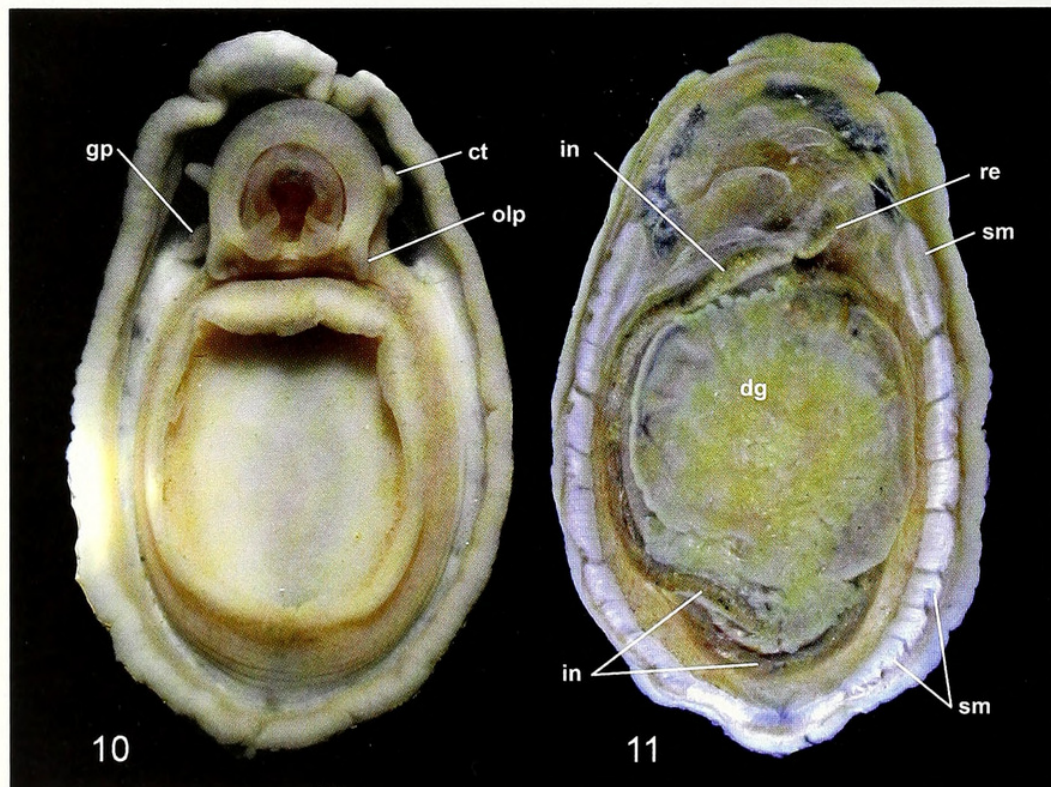
Figures 10–11. *Iothia megalodon*, holotype. **10.** Ventral; **11.** Dorsal view of soft parts. Length of body 7 mm. ct, cephalic tentacle; dg, digestive gland; gp, genital papilla; in, intestine; olp, oral lappet; re, rectum; sm, shell muscle.
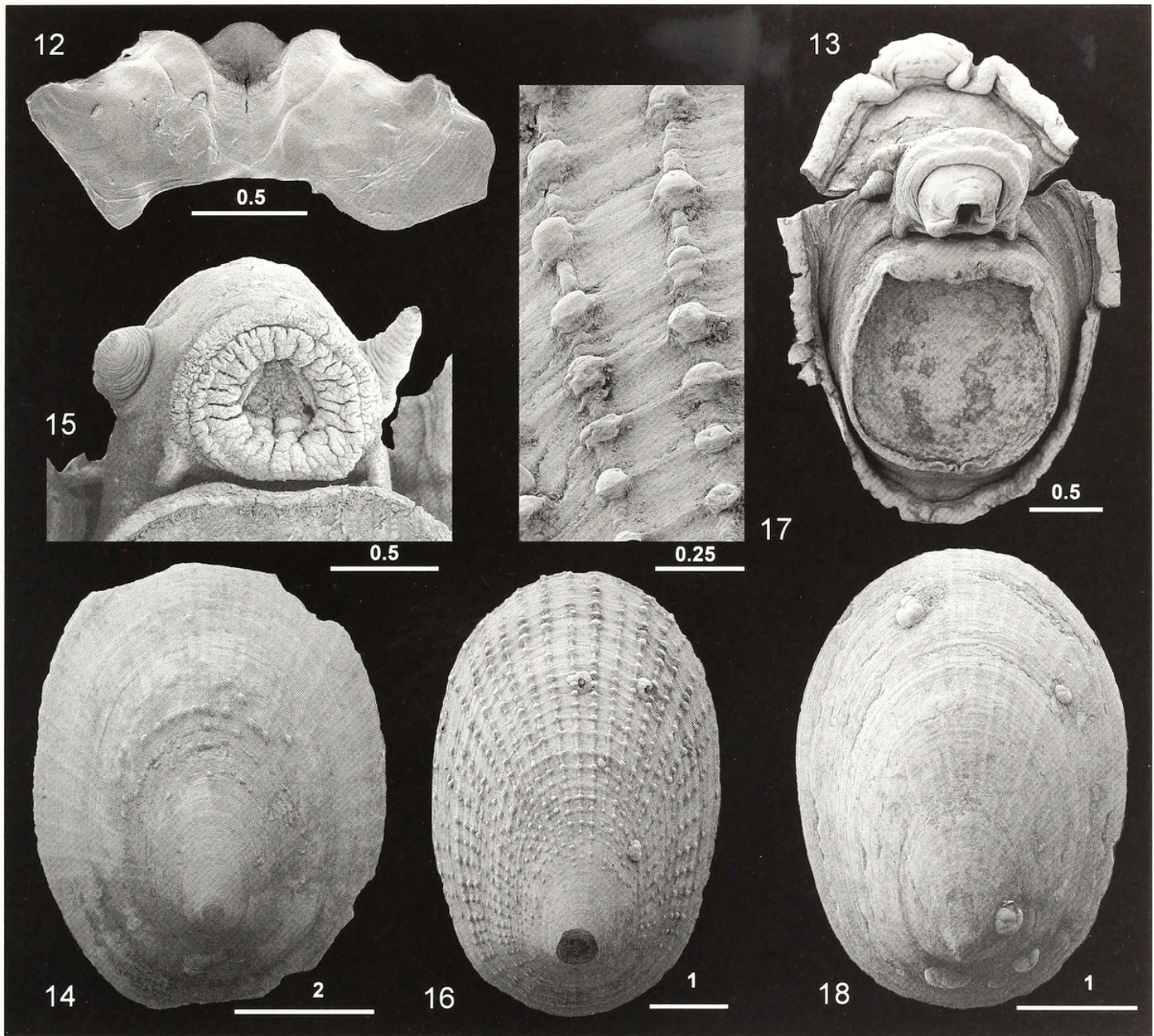
Figures 12–18. 12–14. *Iothia megalodon.* **12.** Jaw, inside, right side damaged. **13.** Body, critical point dried. **14.** Shell, paratype 6618, unusually smooth. **15.** *Iothia fulva*, head. **16–17.** *Iothia emarginuloides*, shell and detail of sculpture of strongly sculptured specimen from the type locality of *I. megalodon.* **18.** *Iothia emarginuloides*, Almost smooth specimen, SMNH 102837, from Chile, Golfo de Ancud, 250–300 m depth. Radula of this specimen, see Fig. 25, H. Scale bars in mm.

1/3 of length. Periphery of base maximum breadth ca. 72% of length and situated at posterior 2/5. Maximum shell length known 9.9 mm.

Soft Parts (Figures 10–11, 13): Pallial furrow and cavity shallow, the latter with conspicuous anal and genital papillae above right cephalic tentacle. Cephalic tentacles short, cylindrical, lacking any external trace of eye. Snout large with ventral mouth, posterior corners drawn out to small obtuse flaps. Gill absent.

Radula (Figures 19–22): Formula 2–2–0–2–2, not excessively long, 35 times as long as broad, length corresponding to 70% of length of shell. Posterior third with poorly developed teeth; middle third with normal lepetid type teeth, anterior third with ca. 25–30 teeth with very large, "inflated bases"; "median tooth" with a single large and smooth cusp, obviously formed by tooth 2 from both sides of the radula, while the original central tooth is reduced or invisibly incorporated. Second lateral tooth with two blunt denticles, possibly formed by fusion of teeth number 3 and 4 in other species of Lepetidae. Uncini soft and pliable, difficult to spread apart; outer one larger than inner one; margin of apical part smooth (Figure 22). Jaw very sturdily built (Figure 12).

Figures 19–26. Radular morphology. **19–22.** *Iothia megalodon*, holotype, 8.9 mm. **19.** 2.5 mm of the transitional zone. **20.** Transition to large teeth. **21.** Detail of radula, tilted backwards to show borders between teeth. **22.** Tips of feather-like marginals. **23–24.** *Iothia emarginuloides*, Concepcion, figured in Fig. 16 (shell 5.5 mm). **23.** Two rows in vertical view. **24.** Teeth tilted backwards to show demarcation. **25–26.** *Iothia emarginuloides*, Golfo di Ancud, SMNH 102837, (figured in Fig. 18, 4.5 mm). **25.** Two transverse rows in vertical view. **26.** Teeth tilted forwards to better show the feather-like structure of the two pairs of marginal teeth. Numbers on teeth or parts of teeth are counted with a hypothetical rhachidian as number 1. Scale bars in μm.

Type Material: Holotype, #6617 and 2 paratypes # 6618 and 6619 in MNHNCL; 5 paratypes SMNH type collection 6784, 7932, 7933 (for details see Materials and Methods).

Type Locality: Chile, methane seep off Concepción, 36°22.01′ S, 73°43.10′ W, 764–843 m.

Etymology: From *Carcharocles megalodon* (Agassiz, 1843), a fossil shark known from its large teeth.

Remarks: Differences in soft parts separate *megalodon* from *emarginuloides*: absence of eyes, abnormally large radular teeth in *megalodon* and the edge of the marginal teeth (uncini) being almost smooth in *megalodon*, not featherlike as in *emarginuloides* (Figures 23, 26). Additionally, the shell of the new species differs by being more depressed, having a less overhanging apex, and a pear-shaped circumference instead of elongate and regularly ovate. The presence of normal specimens of *Iothia emarginuloides* in the same trawl catch suggests that *megalodon* is not a local form.

The radular type, with enlarged, shield-like teeth on the anterior third (Figure 19) is unique. The mineralized part of the normal lepetid radula can be recognized in Figures 23 and 24 (*I. emarginuloides*), and is marked 2–4. These parts are assumed to correspond to three lateral teeth, whereas the rachidian tooth has been lost. They are attached to the radular membrane and are easily detached. The corresponding parts in *I. megalodon* (Figures 20–21, numbered 2–4) are also easily detached, but leave intact the whole shield-like area they are attached to. We consider this as an indication that the "shield" is formed by the basal membrane. The slender marginal teeth (or uncini, if one wants to refrain from homologizing) reach from the basal membrane to the tip of tooth 2 in lepetids in general; so they do also in *I. megalodon*, both before and after the development of the shield.

The loss of the rachidian tooth and fusion of the first lateral tooth from the two sides is obvious when the teeth are tilted backwards (Figures 21, 24). So is also the fusion of teeth number 3 and 4 in *Iothia emarginuloides* (Figure 24), while this is not obvious in *I. megalodon* (Figure 21).

Iothia megalodon usually had the gut full of white calcareous matter, sometimes with sections of the gut filled with grey sediment and mineral particles, and is evidently scraping off sediment from the shells and carbonate rocks where it lives. As in patellogastropods in other seep localities, the gut content occasionally was unexpectedly rich in radiolarian fragments.

DISCUSSION

Biotope and Fauna

A limited number of mollusk species regularly show up in vent or seep localities, often in high numbers and concentrated around the source(s) of effluents. They are usually distributed along or within a certain geologic structure, like a mid-ocean ridge, a coastline, or a series of seamounts. Their numbers invariably drop drastically to zero only a short distance from the source of the effluents. Among the bivalves, many have symbiotic bacteria (reviewed by Sibuet and Olu, 1998). Among gastropods, only a few have such associations but those that have are large and conspicuous (Warén and Bouchet, 2001) and are only known from vents. For the symbiotic species, it is not difficult to understand that they are vent/seep dependent, or favored by the presence of the effluents needed by the symbionts.

The vast majority of the vent/seep gastropods are grazers that utilize the rich bacterial growth on all surfaces, as well as material precipitated from the water (Warén and Bouchet, 1993, 2001, 2009). Among the seep gastropods, a few buccinids are scavengers and several species of the Conoidea, mainly belonging to the genus *Phymorhynchus*, are active predators. They can be assumed to profit from the much elevated biomasses (e.g., Levin and Michener, 2002).

The genera containing species favored by seeps are often distributed all over the world and their number is quite limited, about 25–30 "seep gastropod genera" (Warén and Bouchet, 1993, 2001, 2009; Sasaki et al., 2010). The proportion of these that is present at a given seep site is a good indication if it is a rich or poor seep fauna. More than half of them are present in the very rich seeps off the Pacific coast of Costa Rica (Warén unpublished).

Most of the vent/seep gastropod species are adapted to their environment by having different forms of haemoglobin as oxygen carrier or in simplification of the shell. Vent/seep species are rarely found outside the vent-seep sites, although Johnson et al. (2007) found a couple of species believed to be vent endemics on, sunken drift wood 2000 km north of the nearest vent where it is known to occur. The vent/seep species are often called "vent/seep-dependent" (Sibuet and Olu, 1998) even if the degree of dependency has not been quantified, and perhaps they should better be termed "favored by vents and seeps".

The main reason for our difficulty in recognizing the vent-seep components of the fauna is probably lack of knowledge of the fauna outside the seeps, which is more diverse, albeit poorer in specimens. As a rule of thumb, when visually directed collecting (manned submersibles, Video-monitored-grabs, or ROVs) is used in vents or seeps, the vast majority of the recovered specimens belong to the vent-seep fauna.

About 22 species of gastropods have been considered characteristic of the seep biota off Concepción (Sellanes, Quiroda and Gallardo, 2004; Sellanes et al., 2008, and listed below), which so far only have been explored by trawling and recently by TV-directed tube-coring (L. Levin, pers. comm).

Several genera of gastropods known to be common in seeps have not been found in the Chilean seeps, some of them perhaps because of their small size (species of *Hyalogyrina*, *Cima*, *Xylodiscula* ≈ 1–2.5 mm). Others

are of sizes similar to those of the known fauna (species of *Provanna*, *Paralepetopsis*, *Phymorhynchus*, and *Lepetodrilus* ≈ 6–20 mm), and are more likely to have been collected also with the limited resources at hand, if they were present. However, they may still be present since the site may not have been completely collected although a total of 13 trawls are believed to have passed across the seeps or their immediate neighborhood. During the French exploration of the seeps off West Africa (Warén and Bouchet, 2009), six hauls with a 5 m beam trawl and intensive sieving and search of the catch (von Cosel, pers. comm.), recovered only 4 out of 8 seep gastropod genera present at the site. The mesh of a trawl, in this case 10 mm, does not exclude smaller species; sediment is almost always caught and clogging the net, which then retains also small organisms.

Accompanying Gastropod Fauna

Margarites huloti Vilvens, 2006 (Family Trochidae) (Figures 2, 27–28) is not easily classified on shell characters alone and its radula is therefore figured (Figures 27–28). It is similar to that of species of Gazini (Trochidae). Few Gazini radulae have been figured but Hickman and McLean (1990: fig. 53) figured an unidentified species and *Gaza superba* (Dall, 1881), and Simone and Cunha (2006) reviewed the group. Species of *Margarites* and the Antarctic sister group *Margarella* have 4–6 lateral teeth, species of Gazinae have more, 7–8 laterals. Species of *Gaza* are sometimes common around carbohydrate seeps in the Gulf of Mexico (Warén and Bouchet, 1993, 2001). At present, there seems to be no generic name published for a genus where *M. huloti* fits, so we leave it in *Margarites*. The gut contained sediment in two specimens which were examined. Similar species are known from Japanese seeps and vents (*Margarites ryukyuensis* Okutani et al., 2000 and *M. shinkai* Okutani et al., 1992) and from the Manus Basin (Warén, unpublished) and we feel confident that this is a species adapted to and favoured by the seep environment.

Iothia emarginuloides (Philippi, 1868), *I. megalodon* new species (Lepetidae). Very similar, undescribed species are known from seeps in the Gulf of Mexico, off western Costa Rica, and off Oregon (Warén, unpublished). Therefore, we group *L. megalodon* as a seep species, while *I. emarginuloides*, which is mainly
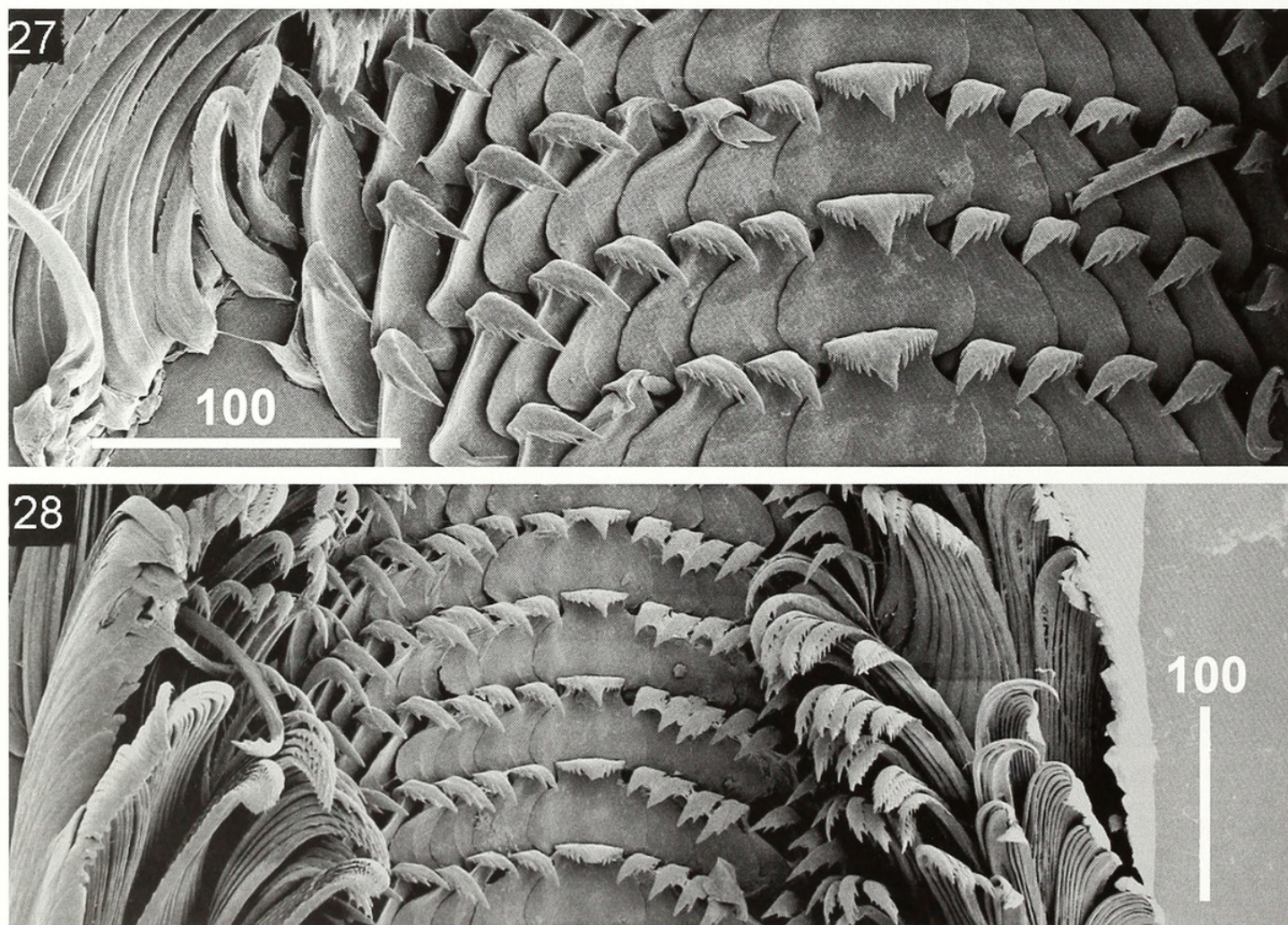
Figures 27–28.   *Margarites huloti*, radular morphology. **27.** Central Field. **28.** Whole width of radula. Scale bars in μm.

known from non-seep environments, probably is an occasionally occurring intruder.

Puncturella, (Family Fissurellidae). Two species found (Sellanes, unpublished) at Concépcion. Species of Fissurellidae seem to be regularly occurring in the outskirts of vents and in seeps, but they seem to be local species and no biotope specific radiation has been recognised, from seeps, vents or wood (Warén and Bouchet, 2009).

Cantrainea panamense (Dall, 1908) (Family Turbinidae (Colloniinae)) (Figure 4). May be a sister species to *Cantrainea macleani* Warén and Bouchet, 1993 described from Caribbean seeps (see also Garciá and Lee, 2002), since they are more similar to each other than to any other known Colloniinae. Species of *Cantrainea* are also known from Japanese hydrothermal vents (*Cantrainea jamsteci* (Okutani and Fujikura, 1990) and *C. nuda* Okutani, 2001) and fossil seeps in Japan (Kaim, pers. comm.). Several species of Colloniinae, including *C. panamense*, are also common on woodfalls (Warén, unpublished). From phylogeny and records, we consider this as a species with seep affinity.

Zetela alphonsi Vilvens, 2002 (Family Solariellidae) (Figure 3). Species of Solariellidae are occasionally found in cold seeps, sometimes more than single specimens, but no biotope specific radiation has been recognized and there is no indication of a solariellid species to be endemic to seeps. Therefore we believe this to be an occasional intruder.

Calliostoma chilena Rehder, 1971; *Calliostoma crustulum* (Vilvens, 2006) (Family Calliostomatidae). Species of Calliostomatidae are usually associated with sponges or hydroids and their occurrence may be related to occurrences of these. No radiation of calliostomatids has taken place in vents and seeps and no species of Calliostomatidae is known to be vent or seep dependent or even regularly occurring there.

Bathybembix macdonaldi (Dall, 1890) (Family Calliotropidae) (Figure 1). The distribution of the more northern relative *Bathybembix bairdii* (Dall, 1889) was reviewed by Hendrickx and Lopez (2006). Species of *Bathybembix* occur regularly in cold seeps, often in considerable quantities (Warén and Bouchet, 2001, 2009). The overview of these large calliotropids is obscured by the multiplication of generic names like *Ginebis* Noda, 1975, *Lischkeia* Fischer, 1880, *Bathybembix* Crosse, 1892, and *Bembix* Watson, 1879. These are all quite similar in shell and radular morphology and most likely closely related. This seems also to be the case with the fossil genus *Amberleya* Morris and Lycett, 1850, which comes close to *Lischkeia*, at least species like *A. dilleri* Stanton, 1895 and *A. morganensis* (Stanton, 1895), which occurred in a Late Jurassic to Lower Cretaceous seep environment along the North American West Coast. Kiel et al. (2008) drew the attention to this similarity, as well as to *Eucycloscala* Cossmann, 1895 and *Eucyclus* Eudes-Deslongchamps, 1860, and Janssen (1993) used the name *Bathybembix* for German Oligocene specimens. A careful comparison, based on

molecular methods where possible, is needed to better understand the relations among these groups.

Calliotropis ceciliae Vilvens and Sellanes, 2010 (Family Calliotropidae). One species of *Calliotropis* was reported from West African methane seeps (Warén and Bouchet, 2009) and AW has seen other species of *Calliotropis* from seeps in the Philippines and off Taiwan (unpublished). Species of *Calliotropis* invariably have their gut filled with sediment (Warén, unpublished), and are likely to gain from the rich bacterial growth. We therefore consider their presence indicative of seep environment and that they should be called "seep species" (althogh most species of the genus inhabit the normal deep-sea).

Caenogastropoda. The large species of predatory and scavenging Caenogastropoda are probably attracted by the increased biomasses and occurrence of possible prey. Here belong: Naticidae ("*Natica* sp.") Ranellidae (*Fusitriton magellanicus* (Röding, 1798)), Muricidae (*Trophon ceciliae* Houart, 2003; *Trophon condei* Houart, 2003; *Trophon* sp.; and *Pagodula concepcionensis* Houart and Sellanes, 2006), Buccinidae (*Kryptos explorator* Fraussen and Sellanes, 2008), Volutidae (*Miomelon philippiana* (Dall, 1890)), and the Conoidea (*Aforia* cf. *goniodes* (Watson, 1881) and two unidentified species of Conoidea).

Systematic Position of *Iothia*

The family Lepetidae is thought to be a sister group of the Acmaeidae and Lottiidae (Lindberg, 1988; Lindberg and Hedegaard, 1996), but anatomical characters such as the presence of a gill in Acmaeidae–Lottidae and the widely different radular morphology, separate Lepetidae from these families (Sasaki, 1998). Recent molecular work suggests that Lepetidae is closely related to Pectinodontidae and Nacellidae (Nakano and Ozawa 2007).

Moskalev (1977) reviewed the family Lepetidae worldwide and classified the species based on their radular characters. Later, Okutani (1987) proposed a new genus *Sagamilepeta* primarily on radular features. Angerer and Haszprunar (1996) summarized the anatomy of *Lepeta*, *Iothia*, and *Propilidium*. According to Sasaki (1998), eight genera are currently recognized within Lepetidae, but their relations are poorly understood. Only a few representatives of Lepetidae have been analysed using molecular data until now (Harasewych and McArthur, 2000; Nakano and Ozawa, 2007).

To stabilize our generic concept, we used some sequences from an ongoing project on the phylogeny of the Patellogastropods in seeps and vents (Nakano and Warén, unpublished) for a preliminary and simplified analysis (Figure 29). Our study includes the species belonging to six named genera, including the type species, *Lepeta caeca*, *Limalepeta lima*, *Sagamilepeta sagamiensis*, and *Iothia fulva*. Unfortunately, we were not able to include the type species of *Propilidium* and *Maoricrater* but the letter is very similar to and probably a synonym of *Iothia*.
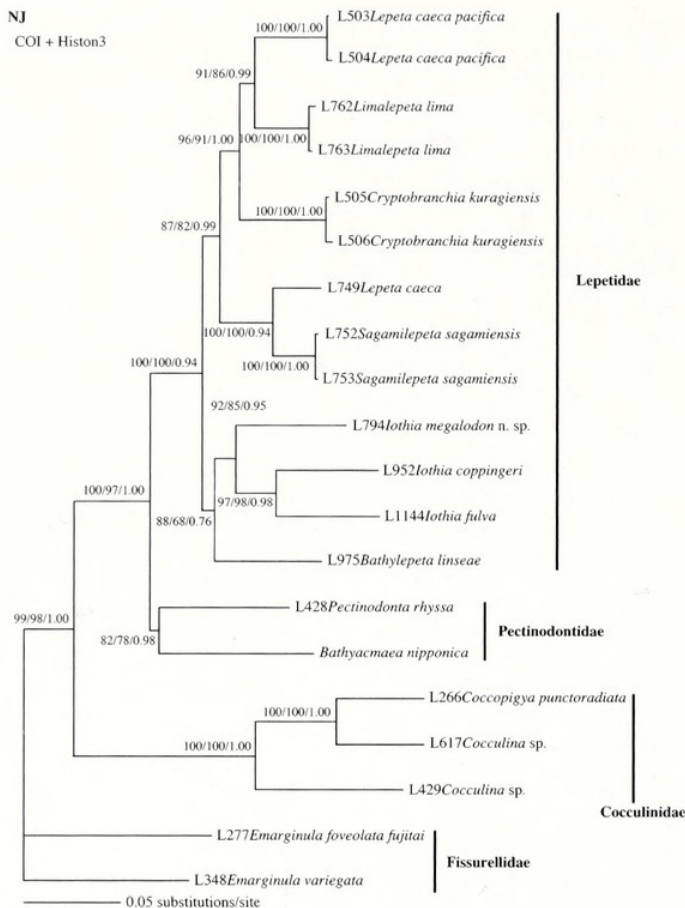
Figure 29. NJ phylogram generated from the 986 bp combined COI and Histone H3 data, showing NJ bootstrap, equally weighted MP bootstrap and Bayesian posterior probabilities.

The monophyly of Lepetidae is strongly supported (NJ=100%, MP=100%, PP=0.94) in the phylogenetic trees, as the results of Nakano and Ozawa (2007) suggest. This is also in agreement with the highly apomorphic radula which is quite uniform throughout the family. Two main clades are identified in the family Lepetidae corresponding to *Iothia* plus *Bathylepeta* and the remaing the Lepetidae (*Lepeta*, *Cryptobranchia*, *Limalepeta*, and *Sagamilepeta*) (Figure 29).

The monophyly of the genus *Iothia*, as used here was supported by NJ=92, MP=85, and PP=0.95, and the position of the new species in *Iothia* thus seems well supported.

Further work will be needed to evaluate the subdivision of Lepetidae.

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