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Revision of Chilean bathyal chitons (Mollusca: Polyplacophora) associated with cold-seeps, including description of a new species of *Leptochiton* (Leptochitonidae)

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Abstract The chiton fauna of Chile comprises 41 species, most of which inhabit shallow waters. The present paper gives a summary of all 14 chiton species reported from Chilean deep (bathyal to abyssal) waters, including some records that might be considered as doubtful. *Leptochiton laurae* n. sp. is formally established; it was formerly misidentified as *L. americanus* Kaas & Van Belle, 1985, but differs in the shape of the tail valve, less coarse sculpturing, in the girdle elements and radula armature. Two additional new species, *Leptochiton* sp. and *Placiphorella* sp., are discussed. For *Leptochiton medinae* Plate, 1899, a lectotype is designated. *Tripoplax balaenophila* (Schwabe & Sellanes, 2004) n. comb. is transferred from *Lepidozona* Pilsbry, 1892, due to coarse sculpturing in the central areas and multi-slit insertion plates. *Leptochiton belknapi* Dall, 1878 and *Tripoplax cowani* Clark, 2008 are reported from the study region for the first time. The majority of the Chilean deep-water polyplacophorans are associated with hard substrates (authigenic carbonates) near methane seeps. The present report raises the global number of chiton species inhabiting chemosynthetic environments from 10 to 18, including some overlooked literature records from other regions.

Keywords Polyplacophora · Systematics · Pacific Ocean · Chile · Deep water · Cold-seeps

Abbreviations

CASIZ	California Academy of Sciences, Invertebrate Zoology, San Francisco, USA.
CIEP	Centro de Investigación en Ecosistemas de la Patagonia, Coyhaique, Chile.
CMSA	Concepción Methane Seep Area.
FLMNH	Florida Museum of Natural History, Gainesville, USA.
JS	second author's reference collection.
MNHNCL	Museo Nacional de Historia Natural, Santiago de Chile, Chile.
NHM	National History Museum, London, United Kingdom.
spm(s)	specimen(s).
SIO	Scripps Institution of Oceanography, La Jolla, California, USA.
UDEC	Universidad de Concepción, Chile.
UF	University of Florida, Gainesville, USA.
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.
WAM	Western Australian Museum, Welshpool, Australia.
ZISP	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.
ZMB	Natural History Museum of Humboldt University, Berlin, Germany.

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Introduction

Among the molluscs the exclusively marine Polyplacophora may be considered as relatively species-poor. About 930 Recent species are considered as valid (Schwabe 2008a; authors' unpublished data), while 430 species (Puchalski et al. 2008) are known only as fossils (excluding 247 fossil taxa that are taxonomically unclear). The majority of Polyplacophora inhabit shallow waters, but 24 species are known from abyssal or even hadal depths (Schwabe 2008a). The scarcity of these records certainly reflects the expensive and time-consuming nature of deep-sea explorations, so that a considerable number of polyplacophorans in deep-sea benthic communities should still be awaiting discovery and characterization (see Schwabe 2008a).

Chitons usually inhabit all kinds of hard substrata, but some species appear restricted to such extreme habitats as wood falls (Sirenko 2004), whale-falls (Schwabe and Sellanes 2004) or even hot vents and cold-seeps (Saito et al. 2008).

Information on the shallow-water chitons of Chile is available from many works (e.g. Boudet Rommel 1945; Forcelli 1999; Frembly 1827; Leloup 1956; Marincovich 1973; Osorio Ruiz 2002; Otaíza and Santelices 1985; Plate 1897, 1899, 1901; Reid and Osorio 2000; de Rochebrune 1889; Schwabe et al. 2006; Sirenko 2006b; Zarges 1994). In contrast, bathyal species from off the Chilean coasts are poorly explored. The first of the few records dates back to Haddon (1886), who described *Lepidopleurus dallii* [= *Stenosemus exaratus* (G. O. Sars, 1878) fide Kaas and Van Belle (1990)] from a depth of 732 m in the South Chilean fjord region (51°27′30″S 74°03′W). Haddon also mentioned *Plaxiphora carmichaelis* (Gray 1828) [= *Plaxiphora aurata* (Spalowsky 1795)] from Southwest Chile and 630 m depth. Leloup (1956) recorded *Lepidopleurus medinae* Plate 1899 and *Callochiton puniceus* (Gould 1846) from 250–300 m in the Gulf of Ancud (42°26′40″S 72°59′W), and listed *Ischnochiton exaratus* from 225 m off the Bay of Puerto Montt (41°30′05″S 72°56′22″W). Osorio and Reid (2004) reported *Tonicia disjuncta* (Frembly 1827) from 300 m depth in the area between Boca del Guafo (43°39′S) and the Estero Elefantes (46°28′S). All of these records are from the fjord regions of the southwestern Chilean coast.

In 1962 during the "Cruise 3" of the USNS *Eltanin*, chitons were discovered for the first time in the Chile-Peru trench. Menzies (1963) mentioned five specimens of Polyplacophora from 2000–6000 m. The specimens were not identified, and it also remains unclear whether the single specimen Menzies mentioned from 3147–3255 m is part of this record (see also Schwabe 2008a)

Sellanes et al. (2004) and Schwabe and Sellanes (2004) provided the first comprehensive reviews of deep-water polyplacophoran species off the Central Chilean coast. These works also contain the first evidence of chitons from chemosynthetic habitats on the Southeast Pacific continental margin, especially off Concepción where a methane seep site was discovered. The generation of authigenic carbonate is a typical feature of the sites at which methane is expelled from the seafloor. Crusts form by precipitation of the methane-derived bicarbonate released to the pore water during the anaerobic oxidation of methane (AOM) via sulphate reduction. A recently identified consortium of archaea and bacteria mediates the process (Boetius et al. 2000). Blocks formed by carbonate-cemented mud, i.e. mud breccia, sometimes containing shell fragments of endemic seep-clams, are a typical feature of the seep site off Concepción (Sellanes et al. 2008).

The aims of the present paper are to: (1) compile all the available information on Chilean deep-water chitons, illustrating and referencing all species collected to date; (2) review their distribution; (3) describe a new species of *Leptochiton* Gray 1847; (4) document some new records of chitons from methane seep areas; and (5) summarize the information on chitons from chemosynthetic environments worldwide.

Material and methods

The new material presented herein was collected at depths from 240 to 922 m during several cruises along the Chilean margin, from Antofagasta (~23ºS) to Chiloé (~42ºS) (Table 1). The samples were gathered using a 1.5 m wide Agassiz trawl (AGT) operated in 20 min. hauls. The chitons were fixed in 4% buffered formalin and preserved in 75% ethanol. For each species description one specimen was disarticulated and prepared as described in Schwabe and Ruthensteiner (2001). The term "bathyal" is used for the zone extending from the shelf break at about 200 m to the lower continental slope at about 2000 m (Gage and Tyler 1991). The systematic classification follows Sirenko (2006a), with slight modifications.

Taxonomic section

Class Polyplacophora Gray, 1821
Subclass Neoloricata Bergenhayn, 1955
Order Lepidopleurida Thiele, 1909
Suborder Lepidopleurina Thiele, 1909
Family Leptochitonidae Dall, 1889

Table 1 Chiton sampling stations for the present study along the Chilean continental margin

Cruise	Vessel	Locality	Station	Lat. (S)	Long. (W)	Depth [m]	Habitat
Kay Kay	R/V *Kay Kay*	Concepción	–	36°29.9′	73°40.8′	240	whale bones
SO-156	R/V *Sonne*	Chiloé	7177	42°34.96′	74°50.22′	906	mid-slope
		Mejillones	7104	22°51.99′	70°29.40′	294	oxygen minimum zone
VG-04	AGOR *Vidal Gormáz*	Concepción	AGT 2	36°12.16′	73°39.15′	906–1000	methane seeps/carbonates
			AGT 8	36°21.80′	73°43.10′	854	methane seeps/carbonates
SeepOx	AGOR *Vidal Gormáz*	Concepción	AGT 6–8	36°21.93′	73°43.26′	843	methane seeps/carbonates
		Concepción	AGT 6–4	36°21.67′	73°43.52′	865	methane seeps/carbonates
		Concepción	AGT 6–6	36°21.65′	73°43.38′	878	methane seeps/carbonates
		Concepción	AGT 6–9	36°22.19′	73°43.36′	846	methane seeps/carbonates
VG-07	AGOR *Vidal Gormáz*	Constitución	AGT 4	34°42.84′	72°23.09	922	methane seeps/carbonates
		NW Concepción	AGT 8	36°00.23′	73°38.41′	922	methane seeps/carbonates
		Concepción	AGT 10	36°22.01′	73°43.10′	843	methane seeps/carbonates
		Concepción	AGT 12	36°21.98′	73°42.61′	760	methane seeps/carbonates
		Concepción	AGT 13	36°21.79′	73°43.38′	855	methane seeps/carbonates

Genus *Leptochiton* Gray 1847

Type species *Chiton cinereus* Linnaeus, 1767 sensu Montagu (1803) nec Linnaeus [= *Leptochiton asellus* (Gmelin, 1791)], by subsequent designation of Gray (1847).

Distribution Worldwide; Eocene–Recent.

Leptochiton americanus Kaas & Van Belle, 1985
(Figs. 1A–D, 2, 3)

Leptochiton (Leptochiton) americanus Kaas & Van Belle, 1985—Kaas and Van Belle (1985a: 91–93, fig. 40).

Name-bearing type Holotype (CASIZ 105889; formerly SIO M-559); examined.

Type locality East Pacific Ocean S of Gulf of Panama (5° 58.8′N 81°38.2′W), 1188 m.

Chilean deep-water records Ferreira (1981: 36; as "*Leptochiton rissoi*"): from 311–402 m, off Arica (18°30′S 70° 34.5′W); from 420–450 m, off Chile (21°23.7′S 70°18.2′ W). — Kaas and Van Belle (1985a: 93; figs. 40.1–40.6, 40.10, 40.11): from 311–402 m, off Arica (18°30′S 70° 34.5′W).

Additional material examined 1 spm (ZSM Mol 20033319), Peru, off Callao (12°32.5′S 77°29.6′W), 562 m, leg. R/V *Melville*, Jan. 1998, spade box-corer.

Remarks According to Kaas and Van Belle (1985a), *Leptochiton americanus* was partly misinterpreted by Ferreira (1981) as *L. rissoi* (Nierstrasz, 1905), a species that in fact occurs from the Philippines to New Guinea at depths between 216 and 2053 m, and was recently collected in SW Australia (WAM S11892, first author's unpublished data). In addition to the holotype of *L. americanus*, a specimen from Peru was examined with SEM (Figs. 2, 3). This represents the only record of the species from Peru. The reports from Chile by Schwabe and Sellanes (2004) and Sellanes et al. (2008) were misinterpretations of *L. americanus* prior to examination of the holotype (see under *Leptochiton laurae* n. sp. below). The distribution is given by Kaas and Van Belle (1985a) as ranging from Oregon (44°39′N) to SW of Iquique, Chile (21°23′S). Bathymetrically, the species lives between 400 and 1400 m depth. Our record from Peru thus falls within the previously known range.

Leptochiton belknapi Dall, 1878
(Fig. 1L–M)
Leptochiton belknapi Dall, 1878—Dall (1878: 1).

Name-bearing type Holotype (USNM 30972); not examined, figured in Ferreira (1979: fig. 10).

Type locality North Pacific Ocean (53°08′N 171°19′W), 1840 m, black sand and shells.

Chilean deep-water record Sellanes et al. (2004: 1066; as *Leptochiton* sp. (partim)): from 934 m, off Concepción (36º21′S 73º44′W).

Material examined 2 spms (ZSM Mol 20041050), Chile, off Antofagasta (23°39′S 70°24′W), 1300 m; 2 spms (ZSM Mol 20041049), Chile, off Chiloé (42°40′S 73°59′W), 906 m; 3 spms (JS), Chile, off Chiloé (42°40′S 73°59′W), 906 m; 1 spm (ZSM Mol 20070684), Chile, off Concepción (36º21.65′S 73º43.38′W), 878 m; 2 spms (ZSM Mol

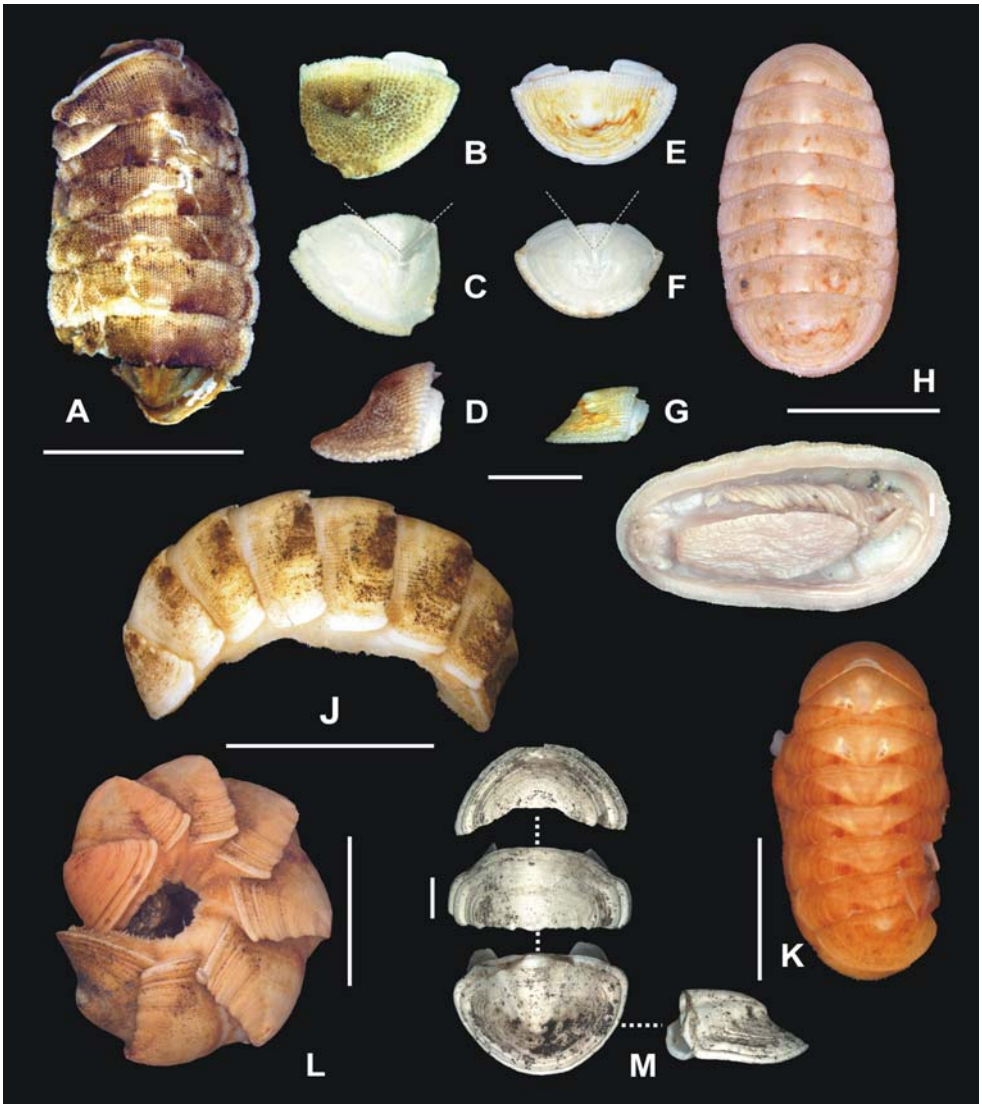

Fig. 1 Lepidopleurid deep-water Polyplacophora from Chile. (A–D) *Leptochiton americanus*, holotype; (E–I) *L.* sp., ZSM Mol 20070757; (J) *L. laurae* n. sp., holotype; (K) *L. medinae*, ZSM Mol 20070928; (L–N) *L. belknapi*, ZSM Mol 20070758 (L) and ZSM Mol 20041050. (A, H) Dorsal view of complete specimen, anterior at top; (B, E) dorsal view of tail valve; (C, F) ventral view of tail valve with angle of apophyses indicated (C=93°; F=77°); (D, G) right lateral view of tail valve; (I) ventral view of complete specimen, anterior at left, showing extent of ctenidia; (J, L) left lateral view of complete specimen; (M) top to bottom: dorsal views of head, second and tail valves; Scale bars: A, H–L=5 mm; B–G, M=2 mm

20041463), Chile, off Concepción (36º12.16′S 73º39.15′W), 906–1000 m; 2 spms (ZSM Mol 20041461), Chile, off Concepción (36º21.65′S 73º44.42′W), 900–904 m; 2 spms (ZSM Mol 20070687), Chile, off Concepción (36º21.67′S 73º43.52′W), 865 m; 1 spm (ZSM Mol 20070758), Chile, off Concepción (36º21.93′S 73º43.24′W), 843 m; 1 spm (ZSM Mol 20041048), Chile, off Concepción (36º21′S 73º44′W), 870–930 m, on pieces of carbonate crusts; 1 spm (ZSM Mol 20070761), Chile, W of Chiloé (42°34.96′S 74°50.22′W), 906 m; 1 spm (JS) Chile, NW off Concepción (36º00.23′S 73º38.41′W), 922 m; 3 spms (FLMNH UF 383787), off Peru, Peru-Chile Trench (*Anton Bruun* St. 144, 11°50′S 77°58′W), 907–935 m.

Remarks There are several published records of *Leptochiton alveolus* (Lovén, 1846) from the Pacific Ocean but, following Kaas and Van Belle (1987), we previously referred all Pacific Ocean records to *L. belknapi* (see Schwabe 2008a). The present material, tentatively determined after Wu and Okutani (1984) and Kaas and Van Belle (1987), includes the southernmost records with the first evidence from Chile, in particular off Concepción, and the first record from authigenic carbonates known to be associated with cold seeps.

Leptochiton medinae Plate, 1899
(Figs. 1K, 5E, F, 6, 7A, B)
Leptochiton medinae Plate, 1899—Plate (1899: 82–89; pl. 5., figs. 204–206).

Name-bearing type Lectotype (ZMB/Moll-102.045), designated here based on examination of digital images (Fig. 7A, B) provided by Diego Urteaga (Argentina), who currently has the material on loan.

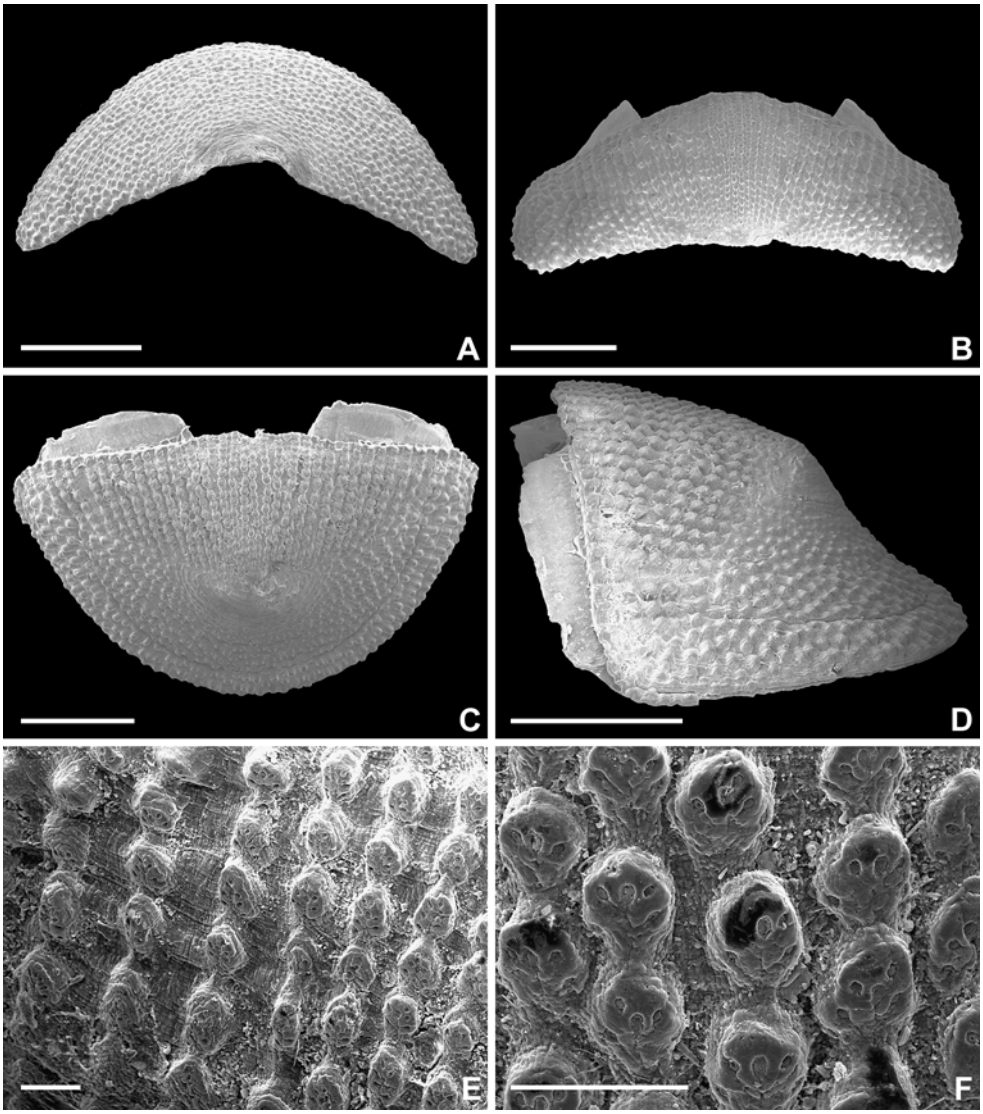

Fig. 2 Scanning electron micrographs of *Leptochiton americanus*, ZSM Mol 20033319. (A) Dorsal view of head valve. (B) Dorsal view of second valve. (C) Dorsal view of tail valve. (D) Left lateral view of tail valve. (E) Detail of B, showing granulation of left pleural area. (F) Detail of B, showing granulation of jugal area. Scale bars: A–D=1 mm; E, F=100 µm

Type locality Chile, Región Magallanes y de la Antártica Chilena, Punta Arenas harbour (53°09′S 70°55′W), 15–18 m (8–10 Faden), on stones and shells.

Chilean deep-water records Leloup (1956: 15; as "*Leptochiton medinae*"): from 270 m, near Cabo Valentin (53°34′S 70°32′W), and 250–300 m, E/SE of Isla Tac in Gulf of Ancud (42°26′40″S 72°59′W); the specimens from the latter record were examined and figured in Kaas and Van Belle (1985a: 80–83, figs. 1–13, 15); for further information see "Remarks" below. — Sirenko (2006b: 82), who stated that he had examined material from the Estados Islands and the Magellan Strait, bathymetrically ranging from 8 to 360 m.

Remarks Plate (1899) described the species based on more than 26 specimens ("... etwas mehr als 20 Exemplare im Hafen von Punta Arenas ..." and "... 6 Exemplaren im Admiralitätssund des Feuerlandes."), i.e. slightly more than 20 from the harbour of Punta Arenas, and six from Admiralty Sound at Tierra del Fuego. None of these specimens was selected as the sole name-bearing type. Kaas and Van Belle (1985a: 83) erroneously referred to a single type: "... of the type only the 8 shell plates are left (ZMHU)" (the collection mentioned is ZMB). The inconsistency became apparent when Kilias (1995) indicated that the ZMB owns six syntypes from the Admiralty Sound. A web source (http://www.biologie.uni-ulm.de/cgi-bin/query_ all/details.pl?id=38747&stufe=7&typ=ZOO&sid=T& lang=e&pr=nix), reveals that the six specimens mentioned by Kilias (1995) and the eight isolated valves referred to by Kaas and Van Belle (1985a) are all part of a single lot (ZMB/Moll-102.045). Under the current wording of the applicable nomenclature Code rule (ICZN 1999: Art. 74.5), use of the

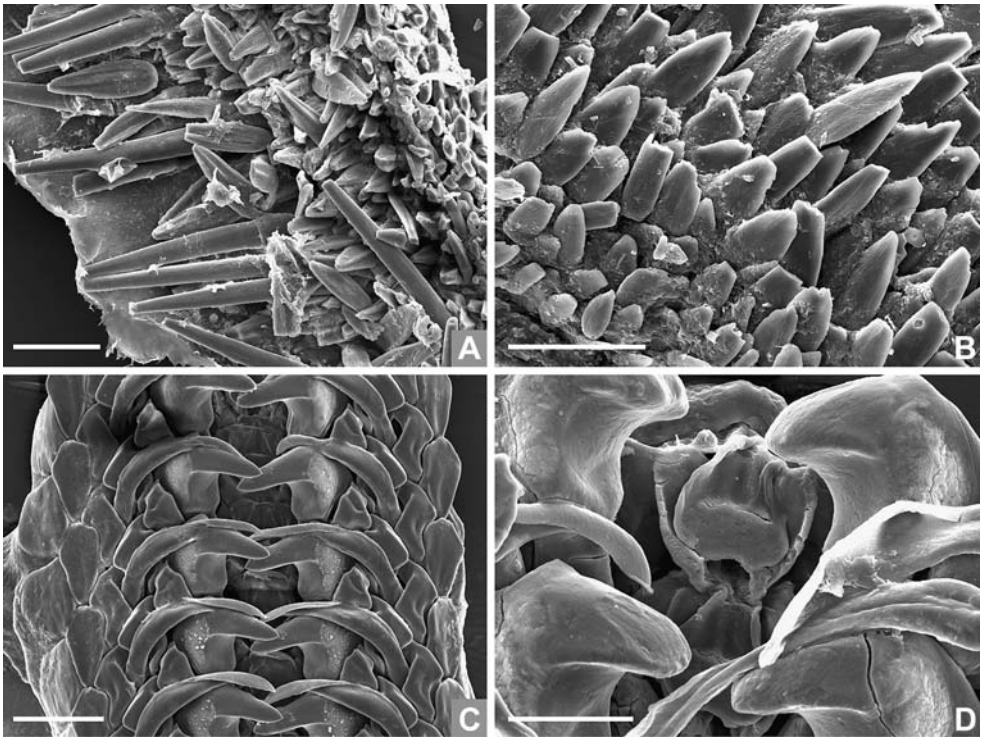

Fig. 3 Scanning electron micrographs of *Leptochiton americanus*, ZSM Mol 20033319. (A) Perinotum. (B) Hyponotum. (C) Anterior portion of radula. (D) Anteriormost row of radula, showing central, first and second lateral teeth. Scale bars: A, B, D=50 μm; C=100 μm

"type" term by Kaas and Van Belle (1985a) is not certain to constitute a valid lectotype designation, because the authors obviously were unaware of the original and continued existence of syntypes, thus could not possibly have intended to restrict name-bearing status to a single specimen. In order to remedy this uncertainty and the corresponding potential threat to the stability of nomenclature, we hereby designate the eight shell plates from Punta Arenas in the ZMB/Moll-102045 lot as the lectotype of *Leptochiton medinae* Plate 1899. Consequently, the six ethanol-preserved specimens from Admiralty Sound become paralectotypes. The whereabouts of the remaining original syntypes are unknown. We select the less well-preserved, fragmented specimen, because most probably Plate (1899) himself prepared it that way and based his description on it, and because Kaas and Van Belle's (1985a) interpretation hinges on it as well.

Leloup (1956) mentioned the species from deep water off Chile (Gulf of Ancud, 250–300 m, station M41); Kaas and Van Belle (1985a) later cited this with an SMNH registration number ("NHRM 792"). We re-examined this material in order to sort out discrepancies between the published information and the sample's label. Instead of station M41, the lot (comprising two intact specimens and a disarticulated one, including microslides of radula and girdle elements) originates from station M46. It shows that the material was collected in Chile, Canal Caicaen, W of Calbuco, 41°46′15″S 73°09′W, at 13 m depth. According to Karin Sindemark Kronestedt (SMNH; pers comm.), the museum does not hold additional material from that station, and the registration number given by Kaas and Van Belle (1985a) refers to this lot (formerly "NHRM 792", now SMNH 103021). We have not located the specimen(s) that Leloup (1956) mentioned from 270 m depth near Cabo Valentin. Consequently, we are listing Leloup's record with a question mark.

See also the "Remarks" under *Leptochiton laurae* n. sp. below.

Leptochiton sp.
(Fig. 1E–I)

Material examined 1 spm (ZSM Mol 20070757), Chile, off Mejillones (22°51.99′S 70°29.40′W), 294 m.

Remarks The specimen is coarsely sculptured and shows a strong similarity to *Leptochiton americanus*. Visual comparison with the holotype of *L. americanus* did not reveal any differences in the sculpturing. However, when we examined the only disarticulated valve available from the holotype, the tail valve, we noted some slight differences with the corresponding valve of our specimen in the development of the articulamentum. It is slightly more solid in the somewhat smaller holotype valve, and the apophyses diverge at a more acute angle in the valve of the Chilean specimen (Fig. 1F). In addition, the postmucronal slope in the latter is slightly steeper (Fig. 1G). It is

remarkable that the Chilean specimen (Fig. 1I) shows 21 instead of the 8–12 ctenidia originally mentioned for *L. americanus* (Kaas and Van Belle 1985a). The ctenidia of this specimen extend for more than two thirds of the foot length (Fig. 1I), which is unusual for the genus *Leptochiton*. The only other *Leptochiton* with a similarly extensive row of ctenidia is the Japanese hot-vent species *L. tenuidontus* Saito and Okutani 1990. In fact, the gill rows of *Leptochiton* sp. are longer than anywhere in the suborder Lepidopleurina, for which the known range of ctenidia length is 24–68% of foot length (Sigwart 2008). We hypothesize that the enhanced number and size of the ctenidia is an adaptation of this species to survival in oxygen-deficient waters. The habitat in which the specimen was collected lies in the permanent SE Pacific oxygen minimum zone (OMZ); bottom-water dissolved oxygen at this station was only 0.06 ml L^{-1}.

Superficially, *Leptochiton* sp. resembles *L. tenuidontus*. Compared to the original description of the latter (Saito and Okutani 1990), *L.* sp. has a larger tail valve, wich is nearly as long as wide (versus twice as wide as long in *L. tenuidontus*), the tail valve apophyses rectangular (vs. triangular), 49 radula rows (vs. 193), and the first uncinal tooth short (vs. toothpick-like). Interestingly, while the holotype of *L. tenuidontus* was described with 22 gills per side, reaching to the anterior third of the foot (Saito and Okutani 1990), nine more recently collected specimens (Saito et al. 2008) have only 6–8 gills per side. The holotype originates from a hot-vent site, whereas the remaining specimens were collected from methane seep areas. Whether the differences in gill number are an artefact or due to the varied chemosynthetic habitats could be clarified with more material from the hydrothermal locality.

Given the differences in valve morphology and gill arrangement, *Leptochiton* sp. could represent an undescribed species. This is currently under study by Dr. Boris Sirenko (ZISP; pers. comm.).

Leptochiton sykesi (Sowerby III, 1903)

Chiton (Hanleya) sykesi Sowerby III, 1903—Sowerby (1903: 225, pl. 5, fig. 13).

Name-bearing types Syntypes (NHM 1903.7.22.47, figured in original description; 2 x NHM 1903.7.22.45–46; 2 x SAMC A-5342). NHM material examined.

Type locality South Africa, "Cape Point Lighthouse (False Bay) bearing E.; distant 26.5 miles; depth, 210 fathoms. Also Vasco de Gama Pk. bearing S. 75°E; distant 13.5 miles; depth, 166 fathoms".

Chilean deep-water records Sirenko and Gallardo (2005: 89; as "*Leptochiton* cf. *sykesi*"): from about 450 m, near Valdivia, Punta Galera (39°59′S 73°43′W), and 438 m, in Canal Concepción (50°30′S 74°55′W).

Remarks Sirenko and Gallardo (2005) tentatively identified their material as this species, which had been known from the Cape region in South Africa only. Subsequently Sirenko (2006b) also mentioned the species from the Bransfield Strait (Antarctic Peninsula). If the species was identified correctly it would be only the second polyplacophoran, besides *Stenosemus simplicissimus* (Thiele, 1906), recorded from both South Africa and the Antarctic region (Schwabe 2008b).

Ashby (1931), Barnard (1963, 1974), and Kaas and Van Belle (1985a) speak of the type material either as "type" or as "holotype" and refer to the South African material only. However, Giles and Gosliner (1983) have pointed out that even the South African lot under the above-mentioned registration number contains two syntypes. Moreover, the material at the NHM was ignored.

Leptochiton laurae n. sp.
(Figs. 1J, 4, 5A–D)

Etymology The species is named after the first author's beloved girlfriend, Laura Würzberg.

Name-bearing type Holotype (ZSM Mol 20070760), partly disarticulated: head, second and tail valves, anterior portion of radula, and pieces of girdle SEM-mounted; remaining parts ethanol-preserved.

Type locality Chile, off Concepción (36º22.19′S 73º43.36′W), 846 m.

Chilean deep-water records Sellanes et al. (2004: 1066; as "*Leptochiton* sp." (partim)): from 934 m, off Concepción (36º21′S 73º44′W). — Schwabe and Sellanes (2004: 147), Sellanes et al. (2008: 1105), both as "*Leptochiton americanus*" (partim): see "Material examined" below.

Additional material examined Paratypes (all from Chile, off Concepción): 11 spms (ZSM Mol 20041046 + 20041047; two of them JS), 36º21′S 73º44′W, 870–930 m, on pieces of carbonate crusts; 9 spms (ZSM Mol 20041459 + 20041462; MNHNCL-6614), 36º12.16′S 73º39.15′W, 906–1000 m; 3 spms (ZSM Mol 20041460), 36º21.65′S 73º44.42′W, 900–904 m; 3 spms (ZSM Mol 20070688), 36º21.67′S 73º43.52′W, 865 m; 3 spms (ZSM Mol 20070756; MNHNCL-6615), 36º21.80′S 73º43.10′W, 708–854 m; 1 spm (MNHNCL-6616), 36º22.01′S, 73º43.10′W, 843 m.

Diagnosis Medium-sized; valves solid; sculptured with fine ribs of rounded granules; tail valve semicircular; apophyses

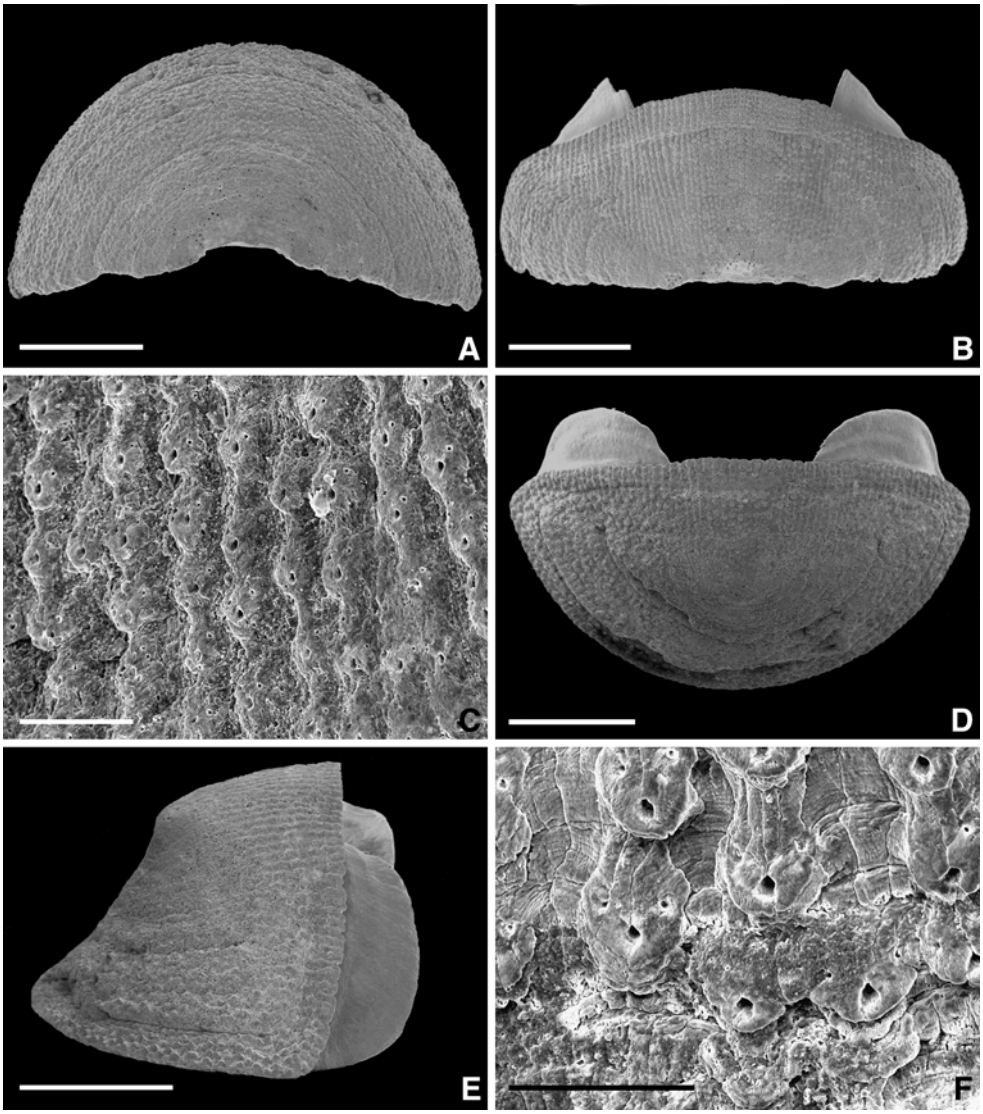

Fig. 4 Scanning electron micrographs of *Leptochiton laurae* n. sp., holotype. (A) Dorsal view of head valve. (B) Dorsal view of second valve. (C) Detail of left pleural area of second valve. (D) Dorsal view of tail valve. (E) Right lateral view of tail valve. (F) Detail of left antemucronal area of tail valve. Scale bars: A, B, D, E=1 mm; C, F=100 µm

short and widely separated; perinotum with short, elongate conical, nearly smooth, sharp-pointed spicules; hyponotum with elongate, distally ribbed scales; radula with bicuspid second lateral; articulamentum without insertion plates.

Description Data from holotype, unless otherwise mentioned. Medium body size, holotype (slightly curled; Fig. 1J) c. 11 × 5.3 mm, largest paratype (ZSM Mol 20070756) about 18 mm long. Grayish-white with remains of (probably) organic matter. Dorsum rounded, dorsal elevation quotient of valve ii=0.47. Head valve (Fig. 4A) semicircular, posterior margin very widely V-shaped, central part slightly notched. Second valve (Fig. 4B) rectangular, less than half as long as wide, posterior margin straight, without apex, anterior margin convex, lateral areas slightly elevated. Tail valve (Fig. 4D, E) semicircular, half as long as wide, posteriorly rounded, anterior margin straight, mucro slightly behind middle, postmucronal area steep, slightly concave behind posteriorly directed mucro.

Tegmentum generally very fine granulated, growth marks present in head valve, lateral areas and postmucronal area. Granules arranged irregularly in head valve, lateral areas and postmucronal area, hardly elevated, more or less round, one large, posteriorly situated megalaesthete and two micraesthetes in front forming a triangle (Fig. 4C, F). Pleural area and antemucronal area with longitudinal rows of granules (appearing as ribs), 70 in second valve, 52 in tail valve, 'ribs' always from anterior valve margin to diagonal ridge.

Articulamentum white, thin, and solid. Insertion plates lacking. Apophyses short and widely separated, triangular in second valve (Fig. 4B), trapezoidal in tail valve (Fig. 4D, E).

Perinotum (Fig. 5A, B) narrow, densely covered with elongate conical, sharply pointed, distally hardly sculptured

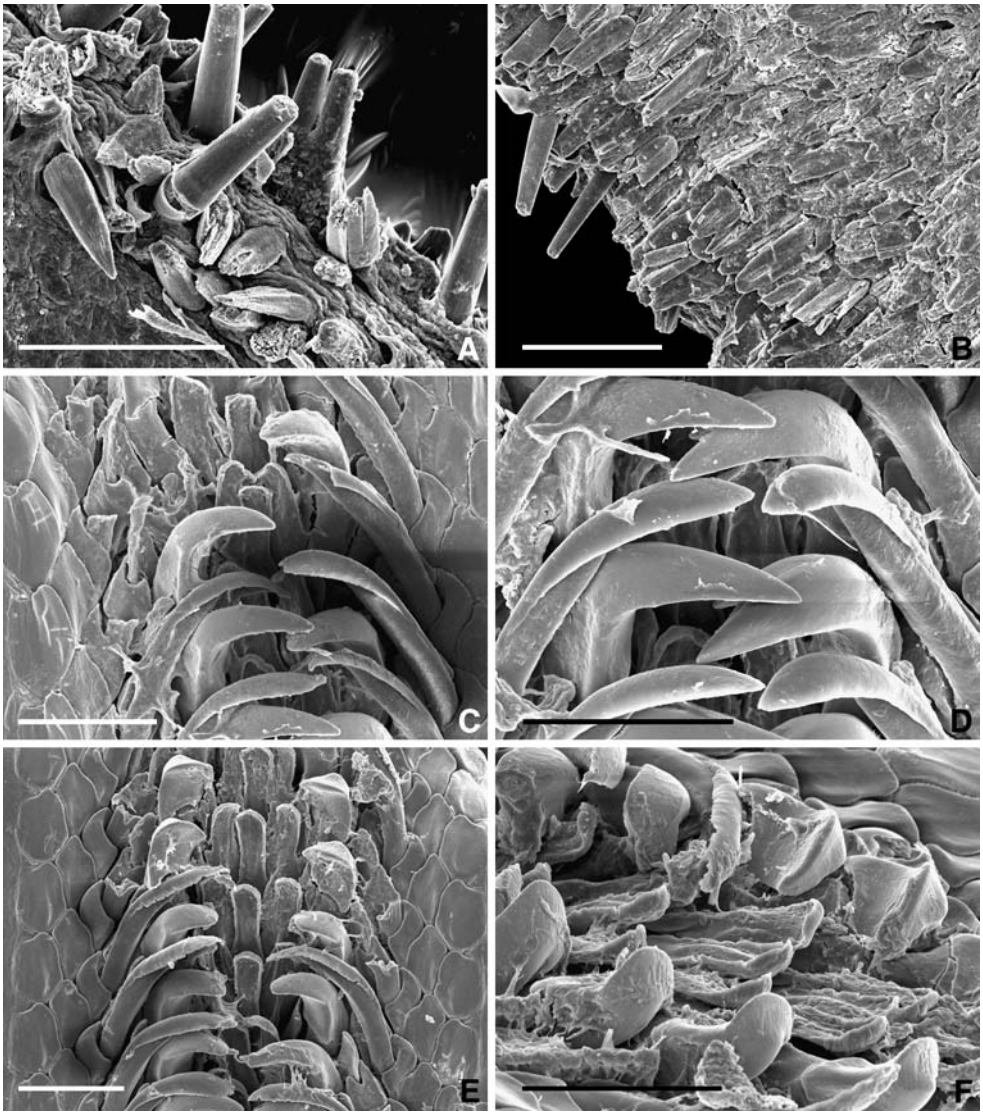

Fig. 5 Scanning electron micrographs of (A–D) *Leptochiton laurae* n. sp., holotype. (E, F) *L. medinae*, ZSM Mol 20070928. (A) Dorso-marginal girdle. (B) Ventro-marginal girdle. (C) Anterior portion of radula. (D) Detail of radula. (E) Anterior portion of radula. (F) Lateral view of anterior portion of radula. Scale bars: 100 μm

spicules measuring 65 × 20 μm. Where sculpturing is traceable, it comprises about 6–8 very faint longitudinal ribs. Randomly distributed straight and smooth needles up to 170 μm occur. Marginally with fringe of straight, smooth, obtuse-pointed spicules up to 88 μm. Hyponotum with elongated, flat, distally faintly ribbed, overlapping scales of about 73 × 24 μm, arranged in radial rows and directed outward.

Radula (Fig. 5C, D) 6.3 mm long, 2.1 mm (33%) occupied by cartilage; 69 rows of teeth, 57 of them (83%) with mineralized teeth. Central tooth rectangular-elongate, parallel-sided, with smooth, slightly bent blade, measuring 68 × 20 μm. First lateral similar in shape, at base with more pronounced keeled shaft, 88 × 27 μm. Second lateral with very slender shaft, slightly keeled at base, head hook-like, with bicuspid blade (Fig. 5D). Inner denticle much smaller than outer. Major uncinal tooth long, slender, spoon-like.

Ctenidia merobranchial, 8–9 on either side of foot, group of largest ctenidia in anterior third. Positions of nephridiopore and gonopore not discernible.

Remarks The new species strongly resembles *L. medinae* in general outline, but differs as follows (*L. laurae* vs. *L. medinae*): (1) anterior margin of tail valve straight vs. concave; (2) head of second lateral tooth bicuspid vs. unicuspid; (3) one megalaesthete plus two micraesthetes vs. four micraesthetes; (4) perinotum spicules hardly ribbed vs. strongly ribbed; (5) hyponotum scales elongate rectangular, obtusely pointed, hardly ribbed distally vs. short rectangular, sharply pointed, smooth (except at margin, where they are also sharply ribbed distally). The specimen of *L. medinae* illustrated in Kaas and Van Belle (1985a: fig. 35), from 250–300 m depth East/Southeast of Isla Tac in the Gulf of Ancud (42°26′40″S 72°59′W), shows a close

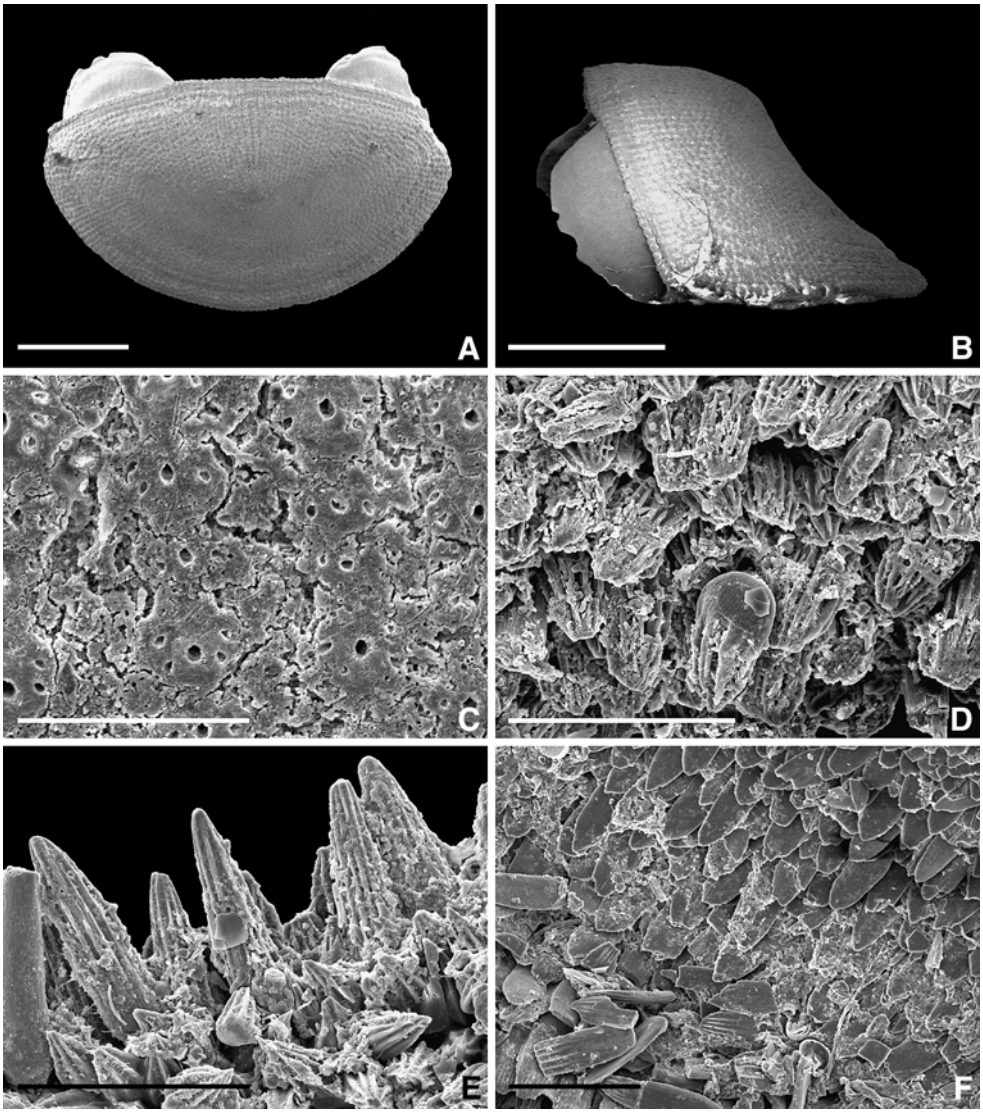

Fig. 6 Scanning electron micrographs of *Leptochiton medinae*, ZSM Mol 20070928. (A) Dorsal view of tail valve. (B) Left lateral view of tail valve. (C) Detail of antemucronal area of tail valve. (D) Perinotum. (E) Marginal fringe of girdle. (F) Hyponotum. Scale bars: A, B=1 mm; C–F=100 µm

relationship to the new species in general outline and the radula, but has distinctly ribbed perinotum spicules, a less steep postmucronal area, and a second lateral tooth with a bicuspid head with a shorter outer denticle. Plate (1899: pl. 5, fig. 205) illustrated a second lateral tooth with a tricuspid head, but emphasized in the description (p. 87) that the tooth is bicuspid, with two strong denticles of which one is substantially smaller, and that these are positioned very close together and difficult to separate. Our SEM images of *L. medinae* (Fig. 5E, F) show a unicuspid head with a narrow furrow (Fig. 5F) on the dorsal side, which could be misinterpreted as a gap between two denticles.

The co-occurring *L. americanus* differs from the new species in the proportionally longer tail valve, less steep postmucronal area, the rectangular apophyses, coarser sculpturing, wider distance between the longitudinally arranged granules, the smooth, sharp-pointed, little elongated hyponotum scales, the strongly ribbed perinotum spicules, unicuspid head of second lateral tooth, and the short rectangular central tooth. Larger specimens of *L. laurae* n. sp. might be mistaken for *L. belknapi*, but the latter has weaker raised sculpturing comprising triangular, quincuncially arranged granules; in addition, the radula has a square and short central tooth, a second lateral tooth with a unicuspid, sharp-pointed head, and distinctly radial ribbed scales at the hyponotum and perinotum.

The new species superficially resembles the North Pacific *Leptochiton rugatus* (Carpenter in Pilsbry 1892) as presented by Kaas and Van Belle (1985a), but the latter species has a long unicuspid (with a small denticle at the base) head of the second lateral tooth, a less steep postmucronal area, scale-like, sharp-ribbed perinotum spicules, and short-rectangular, longitudinally ribbed hyponotum scales.

The new species appears to be associated with the CMSA.

Order Chitonida Thiele, 1909
Suborder Chitonina Thiele, 1909
Superfamily Chitonoidea Rafinesque, 1815
Family Callochitonidae Plate, 1901

Genus *Callochiton* Gray, 1847

Type species Chiton laevis Pennant, 1777 sensu Montagu (1803) nec Pennant [= *Callochiton septemvalvis* (Montagu 1803) fide Kaas (1978)], by subsequent designation of Gray (1847).

Distribution Mostly tropical and subtropical regions of the Indo-Pacific (including Japan; absent from the northeastern Pacific), eastern and subantarctic parts of Atlantic Ocean; Neogene-Recent.

Callochiton puniceus (Gould, 1846)

(Figs. 7C–E, 8, 9)

Chiton puniceus Gould, 1846—Gould (1846: 143).

Chiton illuminatus Reeve, 1847—Reeve (1847: pl. 22, fig. 147).

Name-bearing type Holotype (USNM 5803), examined via digital image (Fig. 7D) provided by Diego Urteaga (Argentina).

Type locality "Orange Harbor" (Gould 1846), see "Remarks" below.

Chilean deep-water records Leloup (1956: 24): 2 specimens from 250–300 m, E/SE of Isla Tac in Gulf of Ancud (42°26′40″S 72°59′W), sand, clay, small stones and shells; one specimen from SMNH 94392 examined.

Additional material examined Holotype of *C. illuminatus* (NHM 1951.1.26.1), examined via digital image (Fig. 7E) provided by Roberto Portela Miguez (NHM). 1 spm (ZSM Mol 20070685), Chile, off Concepción, 36°21.67′S 73° 43.52′W, 865 m. 1 spm (ZSM Mol 20061006), Chile, Región de Magellanes y de la Antártica Chilena, Estero Montana (52°09′44″S 73°16′29″W), 20 m.

Remarks Our new specimen constitutes the northernmost record of the species and considerably extends its bathymetrical range from 300 to 865 m.

The type locality, "Orange Harbor" (Gould 1846), has been quite difficult to locate (see also Thiele 1908: 11, footnote 2). Gould (1852) added "Tierra del Fuego". Thiele (1908) modified Orange Harbor to Orange Bay (Strait of Magellan). Johnson (1964: 135) was the first time to provide more accurate information, stating that Orange Harbor, Tierra del Fuego, is located "on the west side of Bahía Nassau". The present authors searched the Gazetteer Server Client (http://middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp) and located the Orange Bay west of Bahía Nassau. Thus, we herewith specify the type locality of *Chiton puniceus* as Chile, Región de Magallanes y de la Antártica Chilena, Isla Hoste, Península Hardy, Bahia Orange (55°31′S 68°03′W).

The new specimen is only tentatively identified as *Callochiton puniceus* (Gould), following the concept of Suter (1909), who considered *Chiton illuminatus* Reeve, 1847 as conspecific with *Chiton puniceus* Gould 1846. This treatment was followed in the latest available revision of the species (Kaas and Van Belle 1985b), and the variability of the tegmentum was emphasized. We did not compare the holotypes of the two names directly, but had colour images of them available. Undoubtedly, the Chilean deep-water record of Leloup (1956) and our material belong to the same species. A comparison, including several shallow-water samples from the Magellan Strait (ZSM), shows closer similarity with the holotype (not "lectotype" as erroneously stated by Kaas and Van Belle 1985b) of *Chiton illuminatus* (see Fig. 7C, E). Our SEM images show differences between the deep-water (Fig. 8) and the shallow-water material (Fig. 9). However, more material is necessary to clarify whether *C. puniceus* is a variable species or part of a species complex, of which *C. illuminatus* would then be another, separate member.

Family Ischnochitonidae Dall, 1889

Genus *Stenosemus* von Middendorff, 1847

Type species Chiton albus Linnaeus, 1767, by subsequent designation of Winckworth (1926).

Distribution Worldwide in subtropical and tropical regions, in deep water only; Pliocene–Recent.

Stenosemus exaratus (G. O. Sars, 1878)

(Figs. 7F, 10, 11)

Lophyrus exaratus G. O. Sars 1878—Sars (1878: 113–114; pl. 8, figs. 1a–k; pl. II, fig. 1).

Lepidopleurus dallii Haddon, 1886—Haddon (1886: 19, pl. 1. fig. 6, pl. 3, fig. 6a–i); Kaas and Van Belle (1990): synonymization.

Lepidopleurus (Leptochiton) nicomedes Dall, 1919—Dall (1919: 501–502); Kaas (1979): synonymization.

Name-bearing types Syntypes (ZMO), not examined.

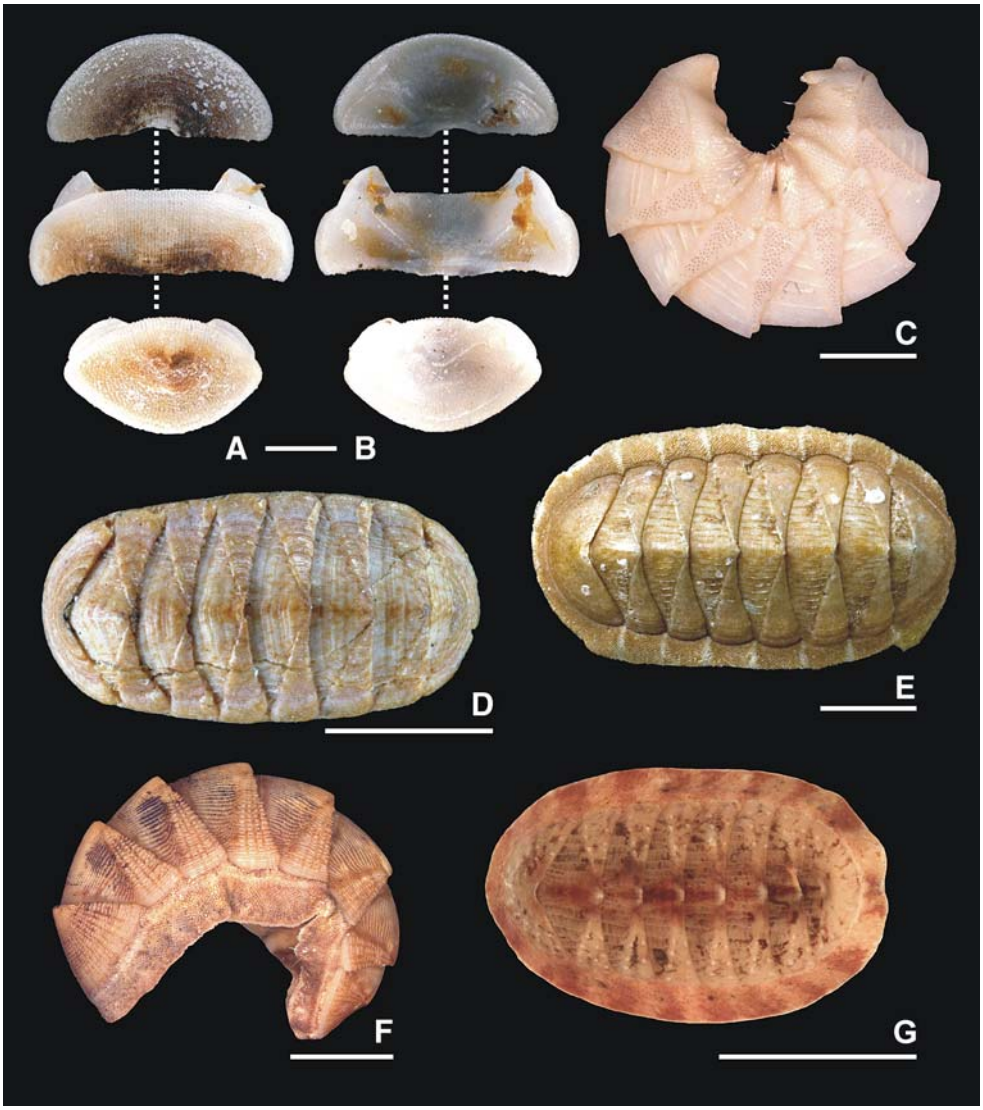

Fig. 7 Lepidopleurid, callochitonid and ischnochitonid deep-water Polyplacophora from Chile. (A, B) *Leptochiton medinae*, lectotype: dorsal (A) and ventral (B) views of (top to bottom) head, intermediate and tail valves. (C, D) *Callochiton puniceus*, complete specimens: (C) ZSM Mol 20070685, right lateral view; (D) holotype, dorsal view. (E) *Chiton illuminatus*, holotype; dorsal view of complete specimen. (F) *Stenosemus exaratus*, ZSM Mol 20070755; left lateral view of complete specimen. (G) *Lepidozona balaenophila*, holotype; dorsal view of complete specimen. Scale bars: A, B=1 mm; C–G=5 mm. (A, B, D) courtesy of D. Urteaga, (E) by R. Portela Miguez

Type locality Norway, Bodö and Florö, 180–360 m (Kaas and Van Belle 1990).

Chilean deep-water records Haddon (1886: holotype *Lepidopleurus dallii*, NHM 1889.11.9.9): from 732 m, Chile, Región de Magellanes y de la Antártica Chilena, S of Isla Evans (51°27.30′S 74°03′W). — Dall (1919; holotype *Lepidopleurus nicomedes*, USNM 96935): from 636 m, southern Chile, off Nelson Strait (51°52′S), not examined but photographed by Ferreira (1979: figs. 25–27). — Leloup (1956: 41; as *Ischnochiton exaratus*): from 225 m, Seno Reloncaví, bay off Puerto Montt, between Isla Tenglo and Punta Pilluco (41°30′05″S 72°56′22″W). — Sellanes et al. (2004: 1066; as *Stenosemus* sp.): from 934 m, off Concepción (36º21′S 73º44′W). — Sirenko (2006b: 84): from 78–360 m, in Magellan Strait; Sellanes et al. (2008: 1105): see "Material examined" below.

Material examined Holotype *Lepidopleurus dallii*; see the preceding text section. 1 spm (ZSM Mol 20041045) Chile, off Concepción (36º21′S 73º44′W), 870–930 m, on pieces of carbonate crusts; 1 spm (ZSM Mol 20041457) Chile, off Concepción (36º21.90′S 73º43.21′W), 713–850 m; 1 spm (ZSM Mol 20070686) Chile, off Concepción (36º21.67′S 73º43.52′W), 865 m; 1 spm (ZSM Mol 20070755) Chile, off Concepción (36º21.80′S 73º43.10′W), 708–854 m; 1 spm (JS) Chile, NW off Concepción (36º00.23′S 73º38.41′ W), 922 m; 1 spm (ZSM Mol 20050440) Chile, Región Aisén del General Carlos Ibánez del Campo, Canal Farguhar (48°26′54.7″S; 74°09′40.4″W), 23 m.

Remarks According to Kaas and Van Belle (1990) *S. exaratus* is a deep-water species, bathymetrically ranging from 100 to 2580 m (but see Schwabe 2008a). Sirenko (2006b) already found the species to range above the 100 m mark; the ZSM

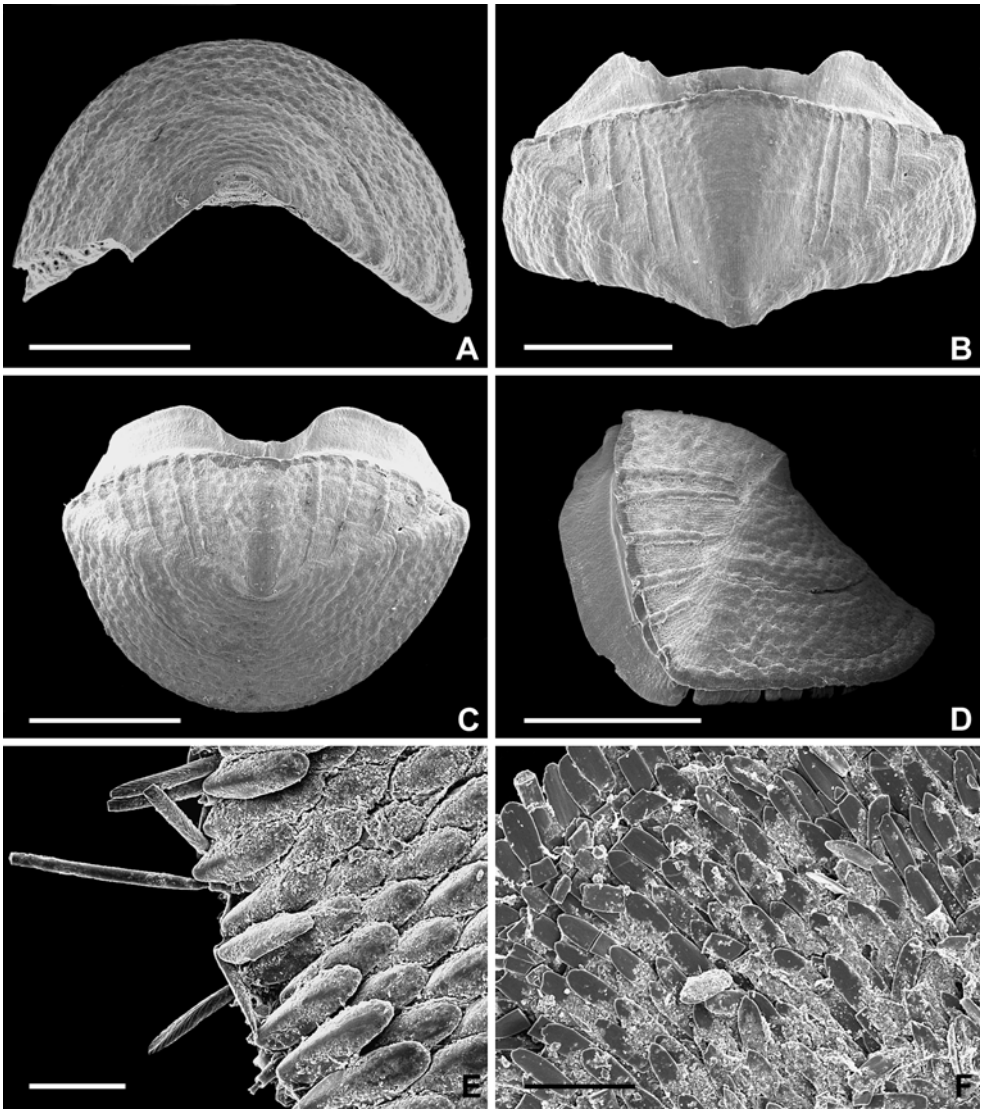

Fig. 8 Scanning electron micrographs of *Callochiton puniceus*, ZSM Mol 20070685. (A) Dorsal view of head valve. (B) Dorsal view of second valve. (C) Dorsal view of tail valve. (D) Left lateral view of tail valve. (E) Dorso-marginal view of girdle. (F) Hyponotum. Scale bars: A–D=1 mm; E, F=100 μm

holds a 7-valved specimen collected at 23 m depth. Hence, the present work extends the species' distribution range both by a new northernmost record in the Pacific Ocean and by one from the shallowest depth recorded so far. Sellanes et al. (2004, as *Stenosemus* sp.) already emphasized that the species can inhabit methane seep areas.

Genus *Tripoplax* Berry, 1919

Type species Trachydermon trifidus Carpenter, 1864, by original designation.

Distribution Southeastern and northern Pacific Ocean, mainly between 60°N and 36°N; Pleistocene–Recent.

*Tripoplax balaenophil*a (Schwabe & Sellanes, 2004) n. comb.

(Fig. 7G)

Lepidozona balaenophila Schwabe & Sellanes, 2004—Schwabe and Sellanes (2004: 149–152, figs. 1–10).

Name-bearing type Holotype (ZSM Mol 20034225), examined.

Type locality Chile, just beneath shelf break off Concepción (36°29.9′S 73°40.8′W), attached to osseous remains (mainly pieces of whale ribs) and rocks at 240 m depth.

Remarks The species has not been collected again since its original description. In accordance with Clark's (2008) redefinition of the genus *Tripoplax*, the species is transferred to this genus here.

Tripoplax cowani Clark, 2008

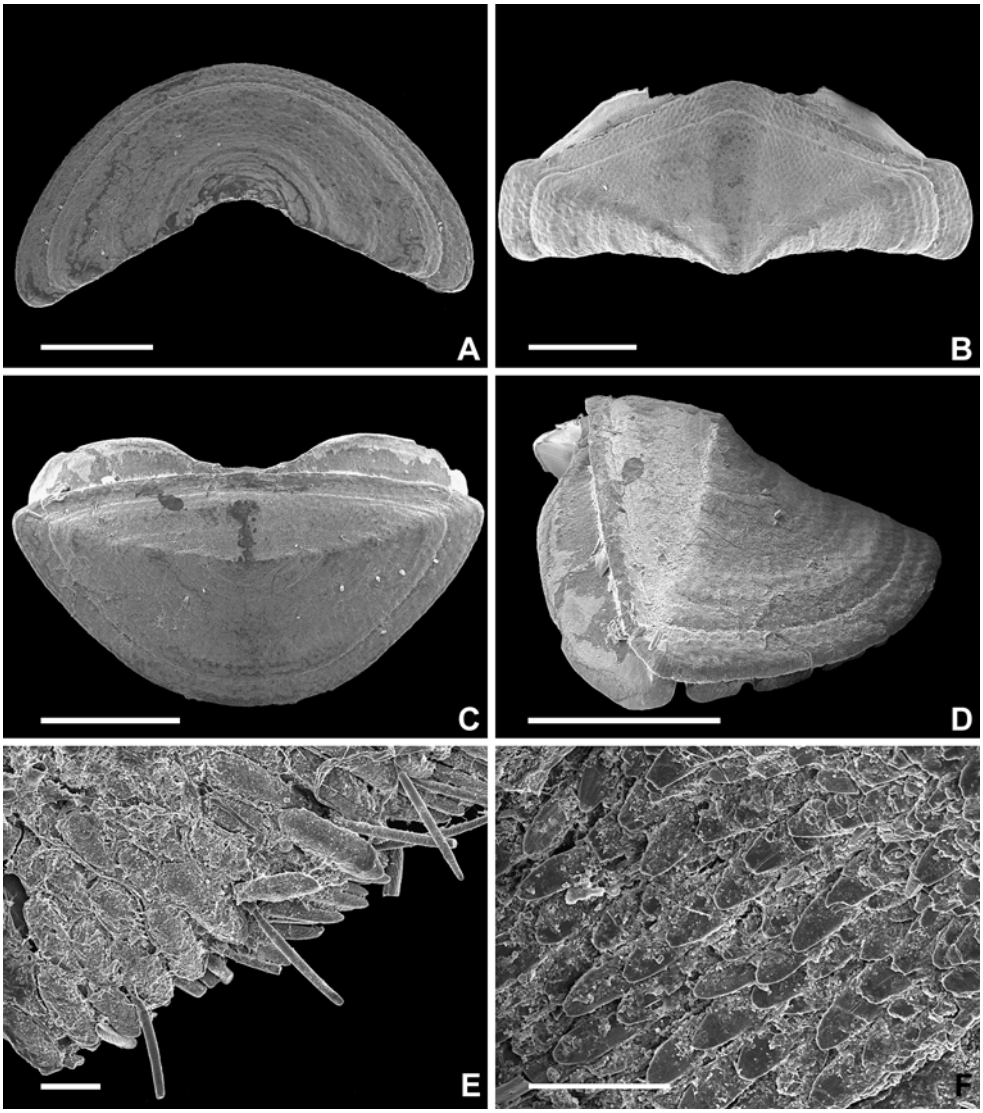

Fig. 9 Scanning electron micrographs of *Callochiton puniceus*, ZSM Mol 20061006. (A) Dorsal view of head valve. (B) Dorsal view of second valve. (C) Dorsal view of tail valve. (D) Left lateral view of tail valve. (E) Dorso-marginal view of girdle. (F) Hyponotum. Scale bars: A–D=1 mm; E, F=100 μm

(Figs. 12, 13, 14A–F)

Tripoplax cowani Clark, 2008—Clark (2008: 81–84, figs. 11–14).

Name-bearing type Holotype (CASIZ 11583), not examined.

Type locality USA, California, Monterey County, Carmel submarine canyon, 36°45.3′N 122°04.7′W, 954–1044 m depth.

Material examined 2 spms: 1 juvenile (ZSM Mol 20080792), 1 adult (ZSM Mol 20080793), Chile, NW of Concepción (36º00.23′S 73º38.41′W), 922 m.

Remarks Clark (2008) stated that the southernmost limit of the species is its type locality. The specimens presented here considerably shift the southern distribution limit to 36°S, and show that the species also lives on carbonate hard substrate associated with methane seep areas.

As the juvenile specimen does not show the sculpturing and peculiarities of adult specimens it is illustrated in detail (Figs. 12, 13, 14C–F). Roger Clark (USA) has confirmed the identification of this smaller specimen.

Family Chitonidae Rafinesque, 1815
Subfamily Toniciinae Pilsbry, 1893

Genus *Tonicia* Gray, 1847

Type species Chiton elegans Frembly, 1827 (homonym; nec *C. elegans* de Blainville, 1825) [= *Chiton chilensis* Frembly, 1827], by subsequent designation of Gray (1847).

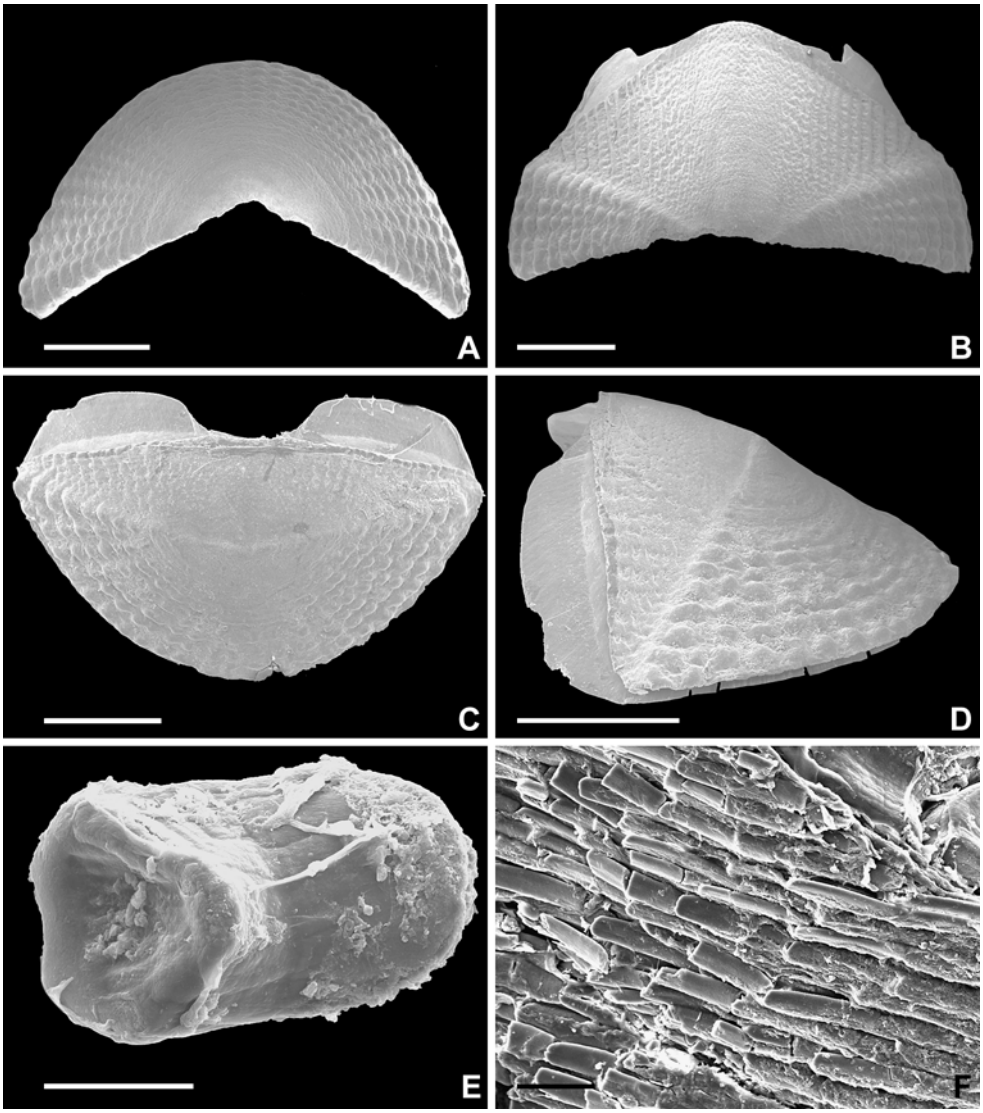

Fig. 10 Scanning electron micrographs of *Stenosemus exaratus*, ZSM Mol 20041045. (A) Dorsal view of head valve. (B) Dorsal view of second valve. (C) Dorsal view of tail valve. (D) Left lateral view of tail valve. (E) Isolated scale from perinotum. (F) Hyponotum. Scale bars: A–D=1 mm; E, F=50 μm

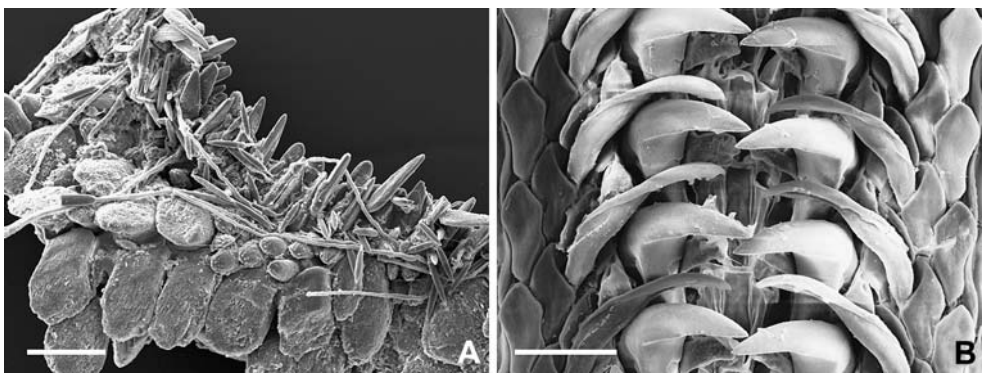

Fig. 11 Scanning electron micrographs of *Stenosemus exaratus*, ZSM Mol 20041045. (A) Dorso-marginal view of perinotum. (B) Anterior portion of radula. Scale bars: 100 μm

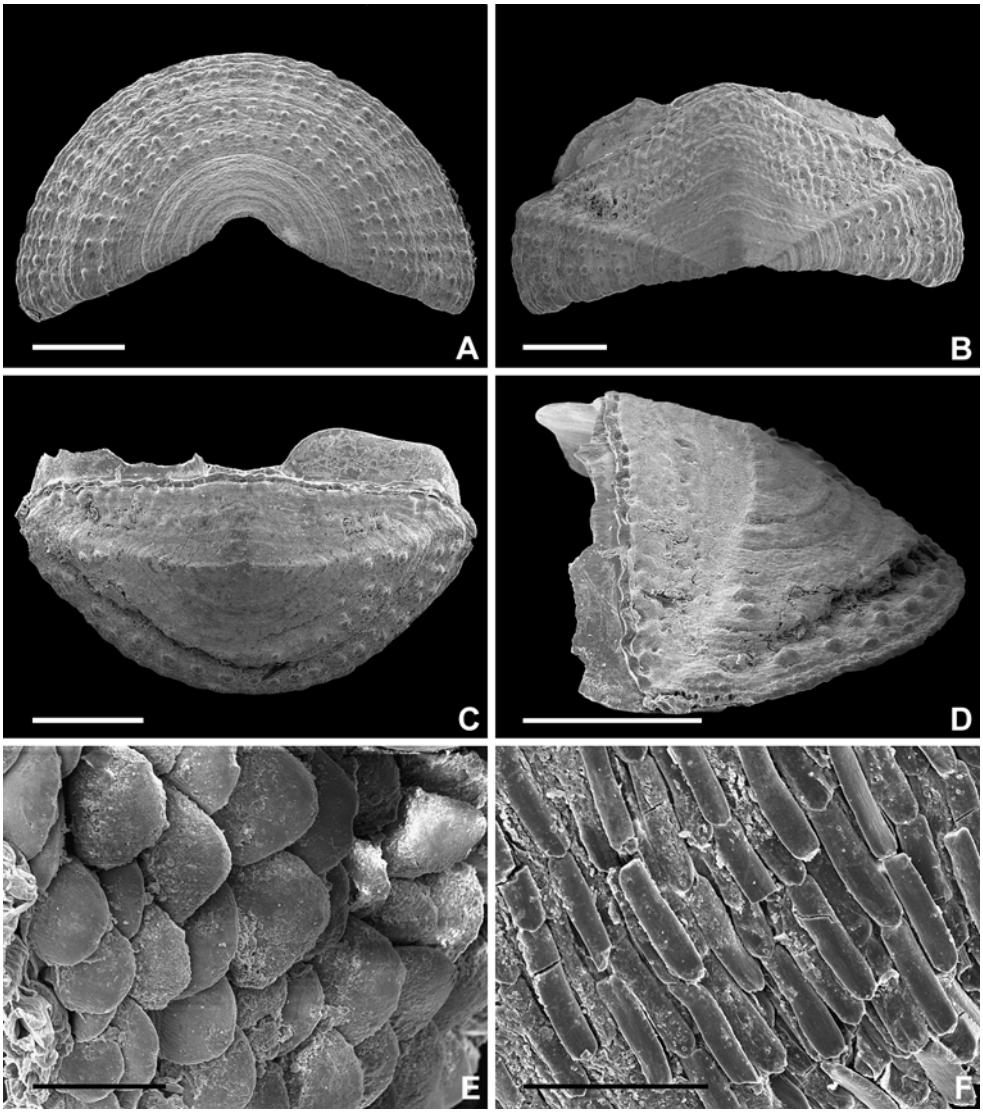

Fig. 12 Scanning electron micrographs of juvenile *Tripoplax cowani*, ZSM Mol 20080793. (A) Dorsal view of head valve. (B) Dorsal view of second valve. (C) Dorsal view of tail valve. (D) Left lateral view of tail valve. (E) Perinotum. (F) Hyponotum. Scale bars: A–D=1 mm; E, F=100 μm

Distribution Caribbean Sea, southeastern Atlantic Ocean via Strait of Magellan to coasts of tropical East Pacific; Miocene–Recent.

Tonicia disjuncta (Frembly, 1827)
(Fig. 14G)
Chiton disjunctus Frembly, 1827—Frembly (1827: 203; 1830–1831: pl. 17, fig. 5).

Name-bearing types 6 Syntypes (NHM 20080600), not examined.

Type locality Chile, Región de Valparaíso, Valparaíso (33° 02′S 71°37′W).

Chilean deep-water record Osorio and Reid (2004: 74): 1 specimen from 300 m, Región Aisén del General Carlos Ibáñez del Campo, Aisén (45°21′S 73°05′95″W).

Remarks Kaas et al. (2006) gave a bathymetric range from the intertidal zone down to 8 m depth.

Suborder Acanthochitonina Bergenhayn, 1930
Superfamily Mopalioidea Dall, 1889
Family Mopaliidae Dall, 1889

Genus *Plaxiphora* Gray, 1847

Type species *Chiton carmichaelis* Gray, 1828 [?=*Plaxiphora aurata* (Spalowsky, 1795) fide Pilsbry (1911)], by subsequent designation of Gray (1847).

Distribution Widespread in South Atlantic, Indian and Pacific Oceans (northern limit: Japanese Sea); Eocene–Recent.

Remarks The systematic position of this genus remains unsolved (Vendrasco et al. 2008).

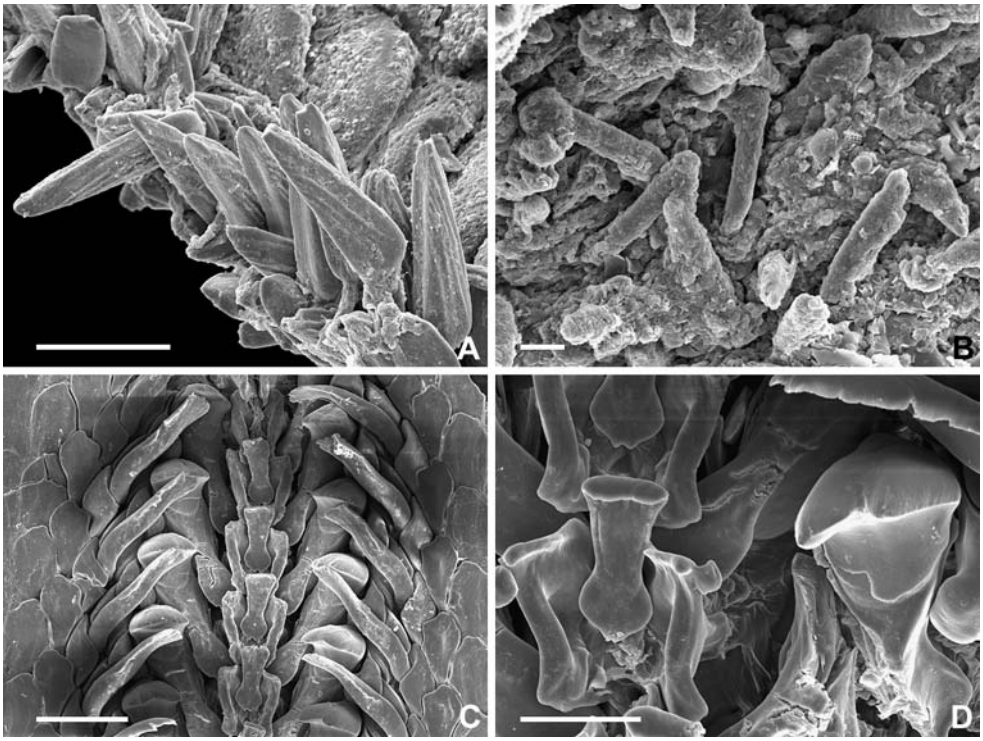

Fig. 13 Scanning electron micrographs of juvenile *Tripoplax cowani*, ZSM Mol 20080793. (A) Marginal fringe. (B) Spicules from mantle lappet. (C) Anterior portion of radula. (D) Detail of C, showing central, first and second lateral teeth. Scale bars: A, D=50 μm, B=10 μm, C=100 μm

? *Plaxiphora aurata* (Spalowsky, 1795)
(Fig. 14H)

Chiton auratus Spalowsky, 1795—Spalowsky (1795: 88, pl. 13, fig. 6).

? *Chiton carmichaelis* Gray, 1828—Gray (1828: 6).

Chiton setiger King & Broderip, 1831—King and Broderip (1831: 338).

Name-bearing type Probably lost (Kaas and Van Belle 1994).

Type locality "Mare Australe (ad insula Otaheiti?)" (Spalowsky 1795), see "Remarks" below.

Chilean deep-water record Haddon (1886: 2; as *Plaxiphora carmichaelis*): from 630 m, SW Chile. Pilsbry (1893 in 1892-1894), who saw Haddon's material, declared the species Haddon had interpreted as *Plaxiphora carmichaelis* (Gray) as undoubedtly conspecific with *Chiton setiger* King and Broderip 1831, and tentatively considered the nominal species, *Chiton carmichaelis* Gray, as also conspecific with *C. setiger*. Later, Pilsbry (1911) synonymized the latter name with "*Chiton aureus* Spalowsky".

Remarks Haddon's (1886) would be the only deep-water record of *Plaxiphora aurata*, which according to Kaas and Van Belle (1994) is an intertidal species. As the material and the species name are linked rather indirectly, we do not exclude the possibility that what Haddon examined should constitute the first record of a *Placiphorella* sp. from Chilean waters instead.

The type material of *C. auratus* is considered as lost, and the type locality remains unclear. Kaas and Van Belle (1994) speculated that the original locality information refers to the Falkland Islands.

Genus *Placiphorella* Dall, 1879

Type species Placiphorella velata Dall, 1879, by original designation.

Distribution Worldwide, except for polar regions; Pleistocene–Recent.

Placiphorella atlantica (Verrill & S. I. Smith in Verrill, 1882)
(Fig. 14K, L)

Placophora (Euplacophora) atlantica Verrill & S. I. Smith in Verrill, 1882—Verrill (1882: 365, footnote).

Name-bearing type Holotype (USNM 106921), examined from digital images provided by Yolanda Villacampa (USNM); also illustrated in Clark (1994).

Type locality USA, Massachusetts, off Nantucket (40°01′N 68°54′W), 1170 m.

Chilean deep-water records Clark (1994: 295): 1 specimen from 420–450 m, off Soutar. The present authors failed to

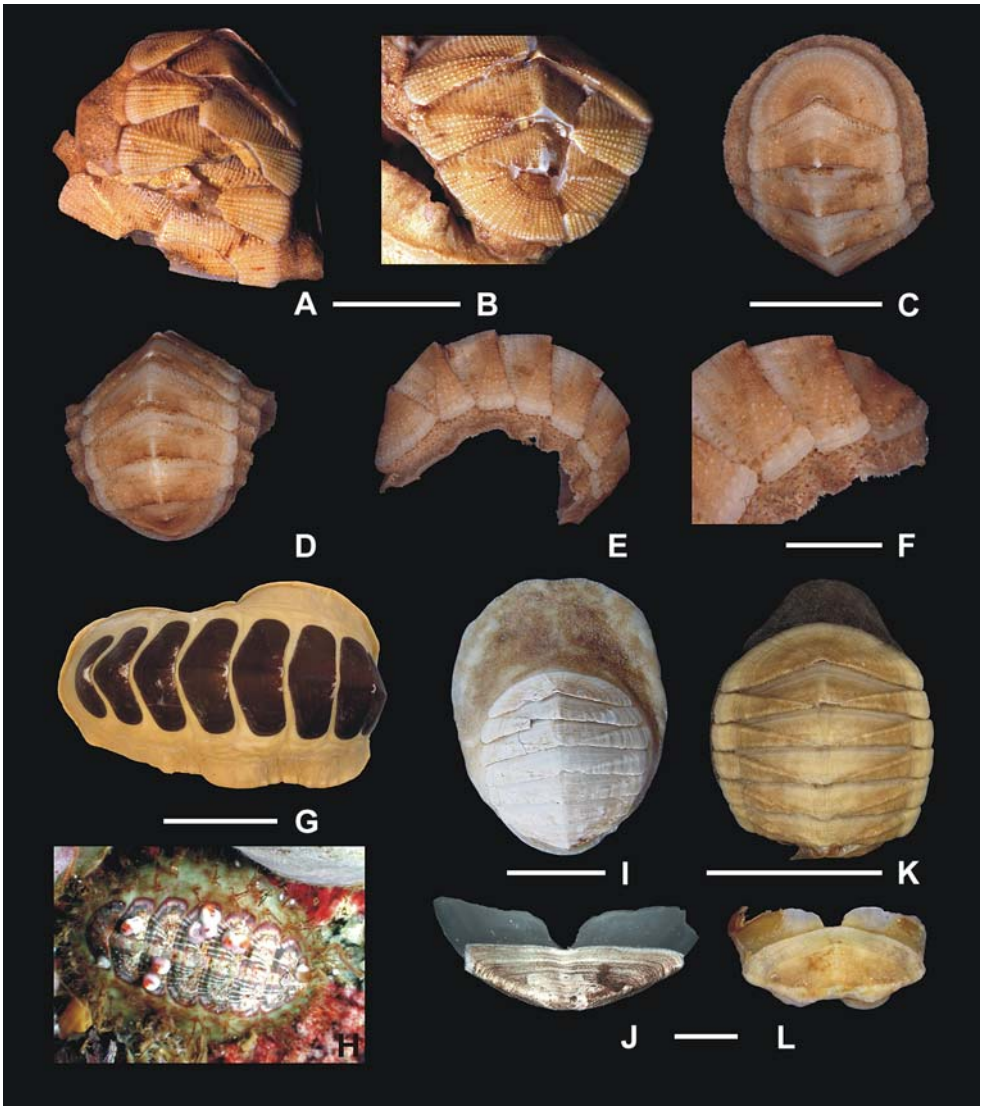

Fig. 14 Ischnochitonid, chitonid and mopaliid deep-water Polyplacophora from Chile. (A–F) *Tripoplax cowani*, adult, ZSM Mol 20080792 (A, B), and juvenile, ZSM Mol 20080793 (C–F): (A) valves i–v; (B) valves vi–viii; (C, D) dorsal views of anterior and posterior portions, respectively, of complete specimen; (E) left lateral view of complete specimen; (F) left lateral view of posterior portion, showing postmucronal slope of tail valve. (G) *Tonicia disjuncta*, ZSM Mol 20061008; dorsal view of complete specimen. (H) *Plaxiphora aurata*, ZSM Moll 20040961; complete specimen in situ (Chile, Punta Huinay, 42º22.483′S 072º25.693′W, 0–30.5 m), body length c. 24 mm. (I, J) *Placiphorella* sp., ZSM Mol 20041044; dorsal views: (I) complete specimen; (J) isolated tail valve. (K, L) *Placophora (Euplacophora) atlantica*, holotype; dorsal views: (K) complete specimen; (L) isolated tail valve. Scale bars: A, B, I, K=10 mm; C–E=5 mm; F, L, J=2 mm; G=20 mm. (K, L) courtesy of Y. Villacampa

locate this locality in Chile, but a search through the online database of the CASIZ (http://www.calacademy.org/ research/izg/iz_coll_db/Index.asp), where the specimen should be deposited, has yielded two specimens from off Chile: CASIZ 78505, from off Tarapaca (21°23.7′S 70°18.2′W), from 420–450 m; and CASIZ 82179, from off Chile, 768–823 m. Both records are attributed to *Placiphorella pacifica* Berry, 1919, which according to Clark (1994) is a synonym of *P. atlantica* (but see Saito et al. 2008).

Remarks We doubt that the identification of this material is correct (based on our own material, see the following species). Dr. Boris Sirenko (ZISP, pers. comm.), who has studied the material, supports our opinion. He is convinced that the species is new to science.

Placiphorella sp.
(Figs. 14I, J, 15)

Chilean deep-water records Sellanes et al. (2004: 1066; as "*Placiphorella* sp. nov."): from 934 m, off Concepción (36º21′S 73º44′W). — Sellanes et al. (2008: 1105; as "*Placiphorella atlantica*"): see "Material examined" below.

Material examined 3 spms (ZSM Mol 20080794 + 20080824) Chile, NW off Concepción (36º00.23′S 73º38.41′W), 922 m; 9 spms (JS) Chile, NW off Concepción (36º00.23′S 73º38.41′W), 922 m; 1 spm (ZSM Mol 20041044) from Chile, off Concepción, 36°21′S 73°44′W, 870–930 m.

Remarks This species was first mentioned from a methane seep area by Sellanes et al. (2004). Since then, Saito et al. (2008) have described *Placiphorella isaotakii*, which was collected at the Yaeyama Islands, also from a methane seep area, and *P. okutanii* from a potential hydrothermal

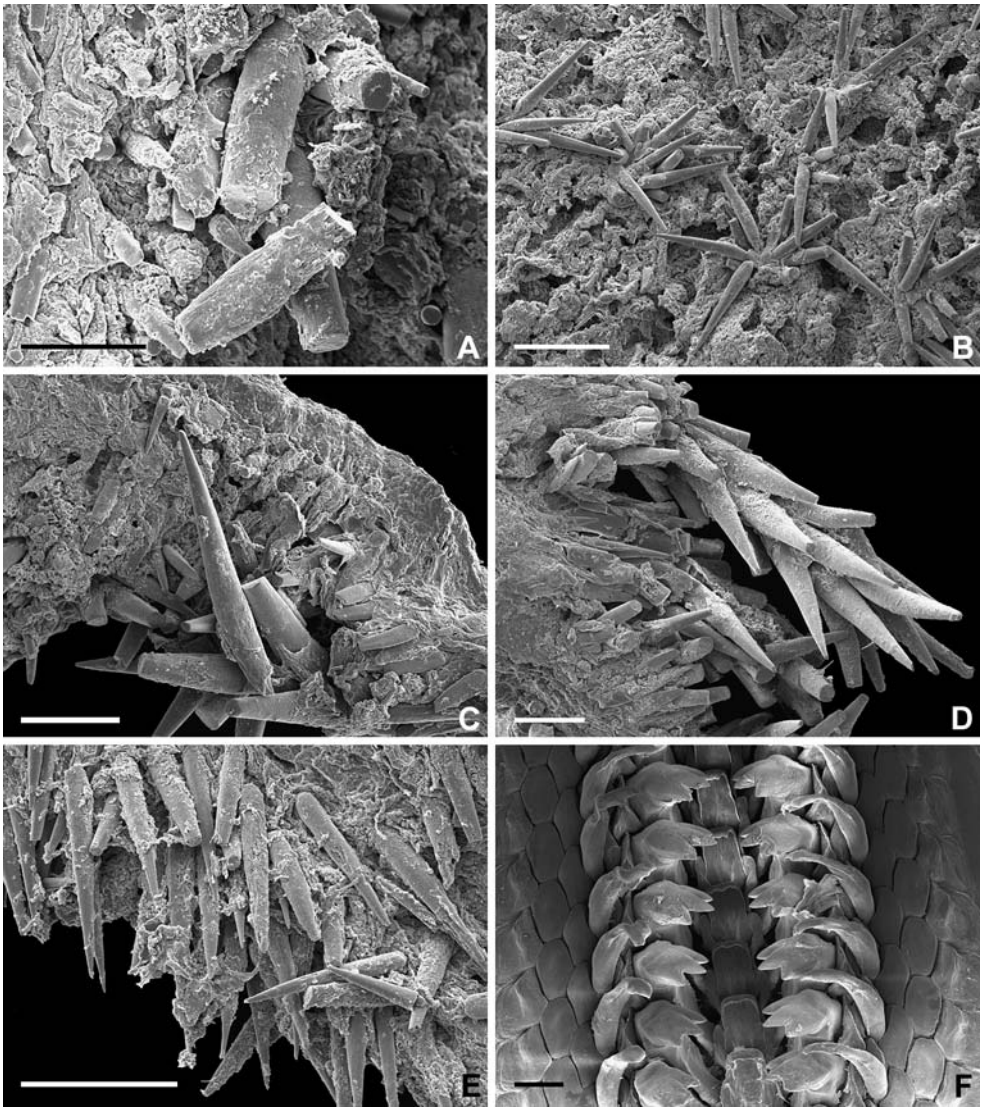

Fig. 15 Scanning electron micrographs of *Placiphorella* sp., ZSM Mol 20041044. (A, B) Perinotum spicules in situ. (C) Ventro-marginal girdle elements, in situ. (D) Bristle, view from ventro-marginal side of girdle. (E) Spicules of precephalic tentacles, in situ. (F) Anterior portion of radula. Scale bars: A=50 μm; B–F=100 μm

region near the Izu-Ogasawara Islands. Both species were regarded as possibly only guests in those habitats. The considerable number of specimens of the present species leads us to hypothesize that it is closely associated with, if not endemic to, the vicinity of the CMSA site. Our SEM images (Fig. 15) show close similarity to *Placiphorella okutanii*, but also distinct differences at least in the form of the tail valve (shorter in length relative to width in the present material). Our material may represent an undescribed species and is currently under study by Dr. Boris Sirenko (ZISP). A comparison with digital images of the holotype of *Placophora (Euplacophora) atlantica* (Fig. 14K, L; see preceding species) shows considerable differences in the shape of the tail valve. To make identification easier, SEM images of the girdle and the radula are also provided.

Discussion

The present work reviews older records of Chilean deep-water polyplacophorans and deals with the discovery of an interesting assemblage of bathyal chitons, which were mostly collected during the study of methane seep areas off South-central Chile. The Chilean chiton fauna comprises 41 species (Sirenko 2007; Sirenko and Gallardo 2005; two new shallow-water species, Sirenko pers. comm.), most of which inhabit shallow waters. Information on deep-water chitons from this region (as for invertebrates in general) has been scarce and partly questionable. Of the 14 named deep-water Polyplacophora from Chile (Table 2; excluded is the record of "Polyplacophora" from the Chile-Peru Trench, 2000–6000 m, by Menzies 1963), five are mentioned and illustrated here for the first time (*Leptochi-*

Table 2 Summary of Chilean deep-water Polyplacophora

Taxon	Distribution	Depth [m]	Chemo-synth. areas	Possibly endemic	References[a]	Remarks
Leptochiton americanus Kaas & Van Belle, 1985	East Pacific, 44°39′N to 21°23′S	400–1400	no	no	Ferreira (1981), Kaas and Van Belle (1985a)	partly as *Leptochiton rissoi* (Nierstrasz, 1905); not Schwabe and Sellanes (2004), Sellanes et al. (2008)
Leptochiton belknapi Dall, 1878	widespread in the Indo-Pacific	100–4400	partly	no	Kaas and Van Belle (1987), Sellanes et al. (2004), Schwabe (2008a)	partly as *Leptochiton* sp.
Leptochiton laurae n. sp.	Chile: off Concepción, 36°22′S to 36°12′S	708–1000	yes	yes	Schwabe and Sellanes (2004), Sellanes et al. (2004, 2008), present study	formerly reported as *Leptochiton* sp. or misinterpreted as *L. americanus*
Leptochiton medinae Plate, 1899	off South America (Pacific and Atlantic) from 42°S to Straits of Magellan	0–360	no	no	Kaas and Van Belle (1985a); Schwabe et al. (2006); Sirenko (2006b)	Leloup (1956) erroneously mentioned material from 250–300 m
Leptochiton sp.	Chile: off Mejillones, 22° 51.99′S 70°29.40′W	294	no	yes	present study	a new species currently under study
Leptochiton cf. *sykesi* (Sowerby III, 1903)	Chile: Valdivia and Canal Concepción in southern fjord region	438–450	no	no	Sirenko and Gallardo (2005)	the nominal species is known from Cape Province, South Africa, 70–433 m (Kaas and Van Belle 1985a)
Callochiton puniceus (Gould, 1846)	East Pacific, 36°21′S to 55°58′S; also southern Argentina and Falkland Islands	0–865	partly	no	Kaas and Van Belle (1985b), present study	most probably a complex of species
Stenosemus exaratus (G. O. Sars, 1878)	Pan-Atlantic; also Pacific along Chilean coast up to Concepción	23–2580	partly	no	Haddon (1886), Kaas and Van Belle (1990), Sirenko (2006b), present study	Haddon (1886) described this as *Lepidopleurus dallii*
Tripoplax balaenophila (Schwabe & Sellanes, 2004)	Chile: Concepción, 36°29.9′ S 73°40.8′W	240	yes	yes	Schwabe and Sellanes (2004)	
Tripoplax cowani Clark, 2008	East Pacific, 48°30′N to 36°S	432–1044	partly	no	Clark (2008), present study	
Tonicia disjuncta (Frembly, 1827)	Chilean coast, 33°S to 49°S	0–300	no	no	Osorio and Reid (2004), Kaas et al. (2006)	
Plaxiphora aurata (Spalowsky, 1795)	circum-subantarctic: Valparaíso via Magellan Straits to Falklands, Tristan da Cunha and Gough Islands; Neozelanic subantarctic islands	0–25 (630?)	no	no	Haddon (1886), Kaas and Van Belle (1994), Reid and Osorio (2000), Schwabe et al. (2006), Sirenko (2006b)	the deep-water record is likely based on a misidentification (possibly of *Placiphorella* sp.)
Placiphorella atlantica (Verrill & S. I. Smith in Verrill, 1882)	unclear, possibly cosmopolitan	155–2000	no	no	Clark (1994), Kaas and Van Belle (1994)	a species complex in urgent need of revision; Chilean deep-water records probably refer to the following species
Placiphorella sp.	Chile: off Concepción	870–934	yes	yes	Sellanes et al. (2004, 2008), present study	a new species currently under study; partly misidentified as *Placiphorella atlantica*

[a] Listed for general information, not limited to deep-water records

Table 3 Summary of Polyplacophora described from chemosynthetic environments

Taxon	Locality	Depth	Type of area			Possibly	References	Remarks
		[m]	HV	CS	WF	endemic		
LEPTOCHITONIDAE								
† *Leptochiton alveolus* (Lovén, 1846)	USA, Washington: Eocene and Oligocene limestones of Olympic Peninsula	unknown		+		no	Goedert and Campbell (1995), Squires and Goedert (1995)	partly as *Leptochiton* sp.; probably refers to the following species (see Schwabe 2008a)
Leptochiton belknapi Dall, 1878[a]	Chile: off Concepción	843–1000		+		no	Sellanes et al. (2004), present study	partly as *Leptochiton* sp.
Leptochiton binghami (Boone, 1928)	USA: Gulf of Mexico, Louisiana slope, 27° 44.7′N91°13.3′W and 27°44.5′N 91°19.1′W	528–571		+		no	Cordes et al. (2005), J. Sigwart (pers. comm., 04.12.2008)	as *Leptochiton* sp.
Leptochiton laurae n. sp.	Chile: off Concepción	708–1000		+		yes	Sellanes et al. (2004, 2008), present study	previously listed as either *Leptochiton* sp. or *L. americanus*
Leptochiton micropustulosus Kaas, 1994	South Barbados Prism, Domes 1 and 2 of El Pilar, ~11°13′N 59°21′W	1135–1236		+		yes	Kaas (1994), Olu et al. (1996)	special habitat neglected by Kaas (1994), subsequently indicated as a cold-seep area
Leptochiton pergranatus Dall, 1889	USA: Gulf of Mexico, Louisiana slope, 27° 44.7′N91°13.3′W and 27°44.5′N 91°19.1′W	528–571		+		no	Cordes et al. (2005), J. Sigwart (pers. comm., 04.12.2008)	
Leptochiton n. sp.	USA: Gulf of Mexico, Louisiana slope, 27° 44.7′N91°13.3′W and 27°44.5′N 91°19.1′W	528–571		+		yes	Cordes et al. (2005), J. Sigwart (pers. comm., 04.12.2008)	as *Leptochiton alveolus*
Leptochiton tenuidontus Saito & Okutani, 1990	East China Sea: Okinawa Trough, Iheya Small Ridge and off Kikaijima Island; Nansei Islds.	1395–1442	+	+		no	Saito and Okutani (1990), Saito et al. (2008)	
PROTOCHITONIDAE								
Deshayesiella sirenkoi Saito, Fujikura & Tsuchida, 2008	West Pacific: seamounts on Kasuga II, Nikko and Daikoku near northern Mariana Islands	400–460	+			yes	Saito et al. (2008)	
CALLOCHITONIDAE								
Callochiton puniceus (Gould, 1846)	Chile: off Concepción	865		+		no	present study	this specimen belongs to a species complex in need of revision
ISCHNOCHITONIDAE								
Ischnochiton dispar (Sowerby in Broderip & Sowerby, 1832)	USA: Gulf of Mexico, Louisiana slope, 27° 44.7′N91°13.3′W and 27°44.5′N 91°19.1′W	528–571		+		no	Cordes et al. (2005), J. Sigwart (pers. comm., 04.12.2008)	as *Leptochiton* sp.
Stenosemus exaratus (G. O. Sars, 1878)	Chile, off Concepción	708–930		+		no	Sellanes et al. (2004, 2008), present study	partly as *Stenosemus* sp.
Thermochiton undocostatus Saito & Okutani, 1990	East China Sea: Okinawa Trough, Iheya Small Ridge and off southern Nansei Islds.	686–1442	+	+		no	Saito and Okutani (1990), Saito et al. (2008)	
Tripoplax balaenophila (Schwabe & Sellanes, 2004)	Chile: off Concepción	240			+	yes	Schwabe and Sellanes (2004)	
Tripoplax cowani Clark, 2008	Chile: off Concepción	922		+		no	present study	

Table 3 (continued)

Taxon	Locality	Depth [m]	Type of area			Possibly endemic	References	Remarks
			HV	CS	WF			
MOPALIIDAE								
Placiphorella isaotakii Saito, Fujikura & Tsuchida, 2008	Kuroshima Knoll off Yaeyama Islds.	691–692		+		yes	Saito et al. (2008)	
Placiphorella okutanii Saito, Fujikura & Tsuchida, 2008	Hachijo Depression in Izu-Ogasawara Islds. area	817–926	+			no	Saito et al. (2008)	Saito et al. (2008) suggested the possibility of hydrothermal activity in this area
Placiphorella sp.	Chile: off Concepción	870–934		+		yes	Sellanes et al. (2004, 2008), present study	partly as *Placiphorella atlantica*
UNIDENTIFIED POLYPLACOPHORA								
"chitons"	USA, Oregon: continental shelf, ~45°50′N 124°40′W	100–700		+		?	Kulm and Suess (1990)	in holes of Cenozoic carbonate edifices, found around cold seeps

† fossil record; *CS* cold seep, *HV* hot vent, *WF* whale-falls

[a] Kiel and Goedert (2006) illustrated and listed *Leptochiton* sp. (most probably *L. belknapi*) from a bathyal Eocene–Oligocene whale-fall area at the Olympic Peninsula, Washington state, USA. We exclude this record here, as the authors mentioned that these whale-falls differ from modern ones in being a non-chemosynthetic food source (in the sense discussed in Schwabe and Sellanes 2004 and the references listed therein) for the discovered faunistic elements

ton belknapi, *L. laurae* n. sp., *L.* sp., *Tripoplax cowani*, *Placiphorella* sp.). Some of the previous records are considered as doubtful, e.g. Leloup's (1956) record of *Leptochiton medinae* is most probably in error, as the original labels for the sample indicate a different station. His *Callochiton puniceus* could also turn out to be a different species, as the variability of this species complex is not yet clarified. The record of *Plaxiphora aurata* based on Haddon (1886) is doubtful as well. The species involved could be a *Placiphorella* sp., as the two genera are superficially similar in size, valve morphology, and girdle armature. The material recorded as *Placiphorella atlantica* in Clark (1994) might also belong to the species we list as new (*Placiphorella* sp.).

None of the Chilean deep-water chitons was previously listed from chemosynthetic environments. The present data, which are mainly based on examinations of methane seep areas off South-central Chile (mostly Concepción), however, show that half of the Chilean deep-water chitons might be found in such extreme habitats. Moreover, four of the species are interpreted as potential endemics in this study, since they are known only from the present records. Thus, the new findings increase the number of worldwide chitons known from chemosynthetic areas to 18 (Table 3). This considerably increases the number over those reported by von Cosel (2006; two species) and Saito et al. (2008; ten). Regarding the systematic placement of those species from chemosynthetic environments, they comprise eight Lepidopleurina, one callochitonid, five ischnochitonids, and three mopaliids. The majority of them were found associated with cold seep areas (16 species); four species are known from hot-vent sites, whereas two have been reported from both habitats. So far, only one species is known to inhabit whale-fall communities. Table 3 illustrates that seven species are known from the corresponding environments exclusively, thus might be restricted to the respective habitats. We still do not have evidence for obligate dependence of any of those species on chemosynthetic environments. More likely they are not dependant on any chemosynthetic pathway per se but are just taking advantage of the enhanced availability of food or hard substrate or shelter provided by the seeps. This has been suggested for other non-chemosymbiotic invertebrates at the Concepción seep site based on stable isotope analysis of the local food webs (Sellanes et al. 2008). However, the biology of chitons from such extreme habitats is unknown, and certainly some explicit relationships could still be discovered. It is known that the radula of *Leptochiton tenuidontus* Saito and Okutani 1990 has a unique peculiarity. In contrast to other chitons, the first uncinal tooth in this species shows an elongate, toothpick-like tooth (Saito and Okutani 1990). Such a modification could be interpreted as

an adaptation to an unusual feeding behaviour. Another example may be the *Leptochiton* sp. reported here from off Mejillones; this species lives in an oxygen minimum zone and shows a higher number of ctenidia than usual for lepidopleurids. It shares this character with the previously mentioned *Leptochiton tenuidontus* Saito and Okutani 1990. Further analysis of this and other species from comparable extreme habitats may help clarify whether such modifications are correlated to the respective habitat.

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References

Ashby, E. (1931). Monograph of the South African Polyplacophora (Chitons). *Annals of the South African Museum, 30*, 1–59. pl. 1–7.

Barnard, K. H. (1963). Contributions to the knowledge of South African marine Mollusca. Part IV. Gastropoda: Prosobranchiata: Rhipidoglossa, Docoglossa. Tectibranchiata. Polyplacophora. Solenogastres. Scaphopoda. *Annals of the South African Museum, 47*, 201–360.

Barnard, K. H. (1974). Contributions to the knowledge of South African marine Mollusca. Part VII. Revised fauna list. *Annals of the South African Museum, 47*, 663–781.

Boetius, A., Ravenschlag, K., Schubert, C., Rickert, D., Widdel, F., Gieseke, A., et al. (2000). A marine microbial consortium apparently mediating anaerobic oxidation of methane. *Nature, 407*, 623–626.

Boudet Rommel, I. (1945). Los quitones Chilenos. *Revista Chilena de Historia Natural, 48*, 122–140.

Clark, R. N. (1994). Review of the genus *Placiphorella* Dall, 1879, ex Carpenter MS (Polyplacophora: Mopaliidae) with descriptions of two new species. *Veliger, 37*, 290–311.

Clark, R. N. (2008). Two new chitons of the genus *Tripoplax* Berry, 1919 from the Monterey Sea Canyon. *American Malacological Bulletin, 25*, 77–86.

Cordes, E. E., Hourdez, S., Predmore, B. L., Redding, M. L., & Fischer, C. R. (2005). Succession of hydrocarbon seep communities associated with the long-lived foundation species *Lamellibranchia luymesi*. *Marine Ecology Progress Series, 305*, 17–29. + suppl.

Dall, W. H. (1878). Descriptions of new forms of mollusks from Alaska contained in the collection of the National Museum. *Proceedings of the United States National Museum, 1*, 1–3.

Dall, W. H. (1919). Descriptions of new species of chitons from the Pacific coast of America. *Proceedings of the United States National Museum, 55*, 499–516.

de Rochebrune, A. T. (1889). Polyplacophores. In A. T. de Rochebrune & J. Mabille (Eds.), *Mission Scientifique du Cap Horn. 1882–1883. Tome VI. Zoologie. Mollusques*. Paris: Gauthier-Villars.

Ferreira, A. J. (1979). The family Lepidopleuridae (Mollusca: Polyplacophora) in the Eastern Pacific. *Veliger, 22*, 145–165.

Ferreira, A. J. (1981). Observations on the deep-water chiton, *Leptochiton rissoi* (Nierstrasz 1905) in the Eastern Pacific. *Bulletin of the Southern California Academy of Sciences, 80*, 36–41.

Forcelli, D. O. (1999). *Moluscos Magallanicos. Guía de Moluscos de Patagonia y Sur de Chile*. Buenos Aires: Vazquez Mazzni Editores.

Frembly, J. (1827). A description of several new species of Chitones, found on the coast of Chili, in 1825; with a few remarks on the method of taking and preserving them. *Zoological Journal (London), 3*, 193–205. Suppl. plates, 4th part, pl. 16–17 issued July 1830–Sept. 1831.

Gage, J. D., & Tyler, P. A. (1991). *Deep-sea biology: A natural history of organisms at the deep-sea floor*. Cambridge: Cambridge University Press.

Giles, E. K., & Gosliner, T. (1983). Primary type specimens of marine Mollusca (excluding Cephalopoda) in the South African Museum. *Annals of the South African Museum, 92*, 1–52.

Goedert, J. L., & Campbell, K. A. (1995). An early Oligocene chemosynthetic community from the Makah Formation, northwestern Olympic Peninsula, Washington. *Veliger, 38*, 22–29.

Gould, A. A. (1846). On the shells collected by the United States Exploring Expedition, commanded by Charles Wilkes U.S.N. *Proceedings of the Boston Society of Natural History, 2*, 141–145.

Gould, A. A. (1852). *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N., vol. XII. Mollusca & Shells*. Philadelphia: C. Sherman.

Gray, J. E. (1828). Family Chitonidae. In *Spicilegia zoologica; or original figures and short systematic descriptions of new and unfigured animals*, *vol. 1* (pp. 5–6, pl. 3, 6). London: Treuttel, Wurtz & Co.

Gray, J. E. (1847). A list of the genera of recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London, 15*, 129–206.

Haddon, A. C. (1886). Report on the Polyplacophora collected by H. M.S. "Challenger" during the years 1873–76. *Challenger Reports Zoology, 15*, 1–50. pl. 1–3.

ICZN = International Commission on Zoological Nomenclature. (1999). *International code of zoological nomenclature* (4th ed.). London: International Trust for Zoological Nomenclature.

Johnson, R. I. (1964). The recent Mollusca of Augustus Addison Gould. *United States National Museum Bulletin, 239*, 1–182. i–v.

Kaas, P. (1978). Notes on Loricata—10. On the European Callochiton species. *Basteria, 42*, 73–75.

Kaas, P. (1979). On a collection of Polyplacophora (Mollusca, Amphineura) from the Bay of Biscay. *Bulletin du Muséum National d'Histoire Naturelle, Section A, Zoologie, biologie et écologie animale, 4*, 13–31.

Kaas, P. (1994). A new species of *Leptochiton* Gray 1847 (Mollusca: Polyplacophora) from the South Barbados accretionary prism. *Zoologische Mededelingen, 68*, 45–47.

Kaas, P., & Van Belle, R. A. (1985a). *Monograph of living chitons (Mollusca: Polyplacophora). 1, Order Neoloricata: Lepidopleurina*. Leiden: E. J. Brill / W. Backhuys.

Kaas, P., & Van Belle, R. A. (1985b). *Monograph of living chitons (Mollusca: Polyplacophora). 2, Suborder Ischnochitonina, Ischnochitonidae: Schizoplacinae, Callochitoninae & Lepidochitoninae*. Leiden: E. J. Brill / W. Backhuys.

Kaas, P., & Van Belle, R. A. (1987). *Monograph of living chitons (Mollusca: Polyplacophora). 3, Ischnochitonidae: Chaetopleurinae, Ischnochitoninae (pars). Additions to vols 1 & 2*. Leiden: E. J. Brill / W. Backhuys.

Kaas, P., & Van Belle, R. A. (1990). *Monograph of living chitons (Mollusca: Polyplacophora). 4, Suborder Ischnochitonina: Ischnochitonidae: Ischnochitoninae (continued). Additions to vols 1, 2 and 3*. Leiden: E. J. Brill.

Kaas, P., & Van Belle, R. A. (1994). *Monograph of living chitons (Mollusca: Polyplacophora). 5, Suborder Ischnochitonina: Ischnochitonidae: Ischnochitoninae (concluded), Callistoplacinae; Mopaliidae. Additions to Volumes 1–4*. Leiden: E. J. Brill / W. Backhuys.

Kaas, P., Van Belle, R. A., & Strack, H. L. (2006). *Monograph of living chitons (Mollusca: Polyplacophora). 6, Suborder Ischnochitonina (concluded): Schizochitonidae; Chitonidae. Additions to Volumes 1–5*. Leiden: Brill NV.

Kiel, S., & Goedert, J. L. (2006). Deep-sea food bonanzas: early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. *Proceedings of the Royal Society of London, Series B, 273*, 2625–2631.

Kilias, R. (1995). Polyplacophora-Typen und -Typoide (Mollusca) im Zoologischen Museum in Berlin. *Mitteilungen aus dem Zoologischen Museum in Berlin, 71*, 155–170.

King, P. P., & Broderip, W. J. (1831). Descriptions of the Cirripedia, Conchifera and Mollusca in a collection found by the officers of H.M.S. “Adventure” and “Beagle” employed between the years 1826 and 1830 in surveying the southern coasts of S America, including the Straits of Magellan and the coast of Tierra del Fuego. *Zoological Journal (London), 5*, 332–349.

Kulm, L. D., & Suess, E. (1990). Relationship between carbonate deposits and fluid venting: Oregon accretionary prism. *Journal of Geophysical Research, B, Solid earth and planet section, 95*(B6), 8899–8915.

Leloup, E. (1956). Reports of the Lund University Chile Expedition 1948–49. 27. Polyplacophora. *Lunds Universitets Arsskrift, Avdelningen 2, Medicin samt matematiska och naturvetenskapliga ämnen (N. F.), 52*, 1–94.

Marincovich, L., Jr. (1973). Intertidal mollusks of Iquique, Chile. *Bulletin of the Los Angeles County Museum of Natural History, 16*, 1–49.

Menzies, R. J. (1963). General results of biological investigations on the deep-sea fauna made on the U. S. N. S. Elatnin (U. S. A. R. P.) during cruise 3 between Panama and Valparaiso, Chile in 1962. *Internationale Revue der Gesamten Hydrobiologie, 48*, 185–200.

Montagu, G. (1803). *Testacea Britannica or natural history of British shells, marine, land and freshwater, including the most minute, systematically arranged and embellished with figures*. London: J. White.

Olu, K., Sibuet, M., Hermegnies, F., Foucher, J. P., & Fiala-Medioni, A. (1996). Spatial distribution of diverse cold seep communities living on various diapiric structures of the southern Barbados prism. *Progress in Oceanography, 38*, 347–376.

Osorio, C., & Reid, D. G. (2004). Moluscos marinos intermareales y submareales entre la Boca del Guafo y el estero Elefantes, sur de Chile. *Investigaciones Marinas (Valparaiso), 32*, 71–89.

Osorio Ruiz, C. (2002). *Moluscos marinos en Chile: especies de importancia económica. Guía para su identificación*. Santiago de Chile: Universidad de Chile.

Otaíza, R. D., & Santelices, B. (1985). Vertical distribution of chitons (Mollusca: Polyplacophora) in the rocky intertidal zone of Central Chile. *Journal of Experimental Marine Biology and Ecology, 86*, 229–240.

Pilsbry, H. A. (1892–1894). Monograph of the Polyplacophora. In G. W. Tryon (Ed.), *Manual of Conchology* (14, 1–128, pl. 1–30 (1892); i–xxxiv, 129–350, pl. 31–68, 15, 1–64, pl. 1–10 (1893); 65–133, pl. 11–17 (1894)). Philadelphia, Academy of Natural Sciences.

Pilsbry, H. A. (1911). Notes. Chiton aureus Spalowsky. *Nautilus, 25*, 36.

Plate, L. H. (1897). Die Anatomie und Phylogenie der Chitonen. Fauna Chilensis 1 (1). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, 1*(Suppl. 4), 1–243. pl. 1–12.

Plate, L. H. (1899). Die Anatomie und Phylogenie der Chitonen. Fauna Chilensis 2 (1). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, 2*(Suppl. 5), 15–216. pl. 2–11.

Plate, L. H. (1901). Die Anatomie und Phylogenie der Chitonen. Fauna Chilensis 2 (2). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, 3*(Suppl. 5), 281–600. pl. 12–16.

Puchalski, S. S., Eernisse, D. J., & Johnson, C. C. (2008). The effect of sampling bias on the fossil record of chitons (Mollusca, Polyplacophora). *American Malacological Bulletin, 25*, 87–95.

Reid, D. G., & Osorio, C. (2000). The shallow-water marine Mollusca of the Estero Elefantes and Laguna San Rafael, southern Chile. *Bulletin of the Natural History Museum, Zoology Series, 66*, 109–146.

Saito, H., Fujikura, K., & Tsuchida, S. (2008). Chitons (Mollusca: Polyplacophora) associated with hydrothermal vents and methane seeps around Japan, with description of three new species. *American Malacological Bulletin, 25*, 113–124.

Saito, H., & Okutani, T. (1990). Two new chitons (Mollusca: Polyplacophora) from a hydrothermal vent site of the Iheya Small Ridge, Okinawa Trough, East China Sea. *Venus*, 165–179.

Sars, G. O. (1878). *Bidrag til kundskaben om norges arktiske fauna. I. Mollusca regionis Arcticae Norvegiae*. Brøgger: Christiania.

Schwabe, E. (2008a). A summary of reports of abyssal and hadal Monoplacophora and Polyplacophora (Mollusca). In P. Martínez Arbizu & S. Brix (Eds.), *Bringing light into deep-sea biodiversity. Zootaxa*, 1866, 205–222.

Schwabe, E. (2008b). Discovery of the South African polyplacophoran *Stenosemus simplicissimus* (Thiele, 1906) (Mollusca, Polyplacophora, Ischnochitonidae) in the Southern Ocean. *American Malacological Bulletin, 24*, 71–77.

Schwabe, E., Försterra, G., Häussermann, V., Melzer, R. R., & Schrödl, M. (2006). Chitons (Mollusca: Polyplacophora) from the southern Chilean Comau Fjord, with reinstatement of *Tonicia calbucensis* Plate, 1897. *Zootaxa, 1341*, 1–27.

Schwabe, E., & Ruthensteiner, B. (2001). *Callochiton schilfi* (Mollusca: Polyplacophora: Ischnochitonidae), a new species from Indonesian waters. *Vita Marina, 47*, 175–184.

Schwabe, E., & Sellanes, J. (2004). A new species of *Lepidozona* (Mollusca: Polyplacophora: Ischnochitonidae), found on whale bones off the coast of Chile. *Iberus, 22*, 147–153.

Sellanes, J., Quiroga, E., & Gallardo, V. A. (2004). First direct evidence of methane seepage and associated chemosynthetic communities in the bathyal zone off Chile. *Journal of the Marine Biological Association of the United Kingdom, 84*, 1065–1066.

Sellanes, J., Quiroga, E., & Neira, C. (2008). Megafauna community structure and trophic relationships at the recently discovered Concepción Methane Seep Area, Chile. *ICES Journal of Marine Science, 65*, 1102–1111.

Sigwart, J. D. (2008). Gross anatomy and positional homology of gills, gonopores, and nephridiopores in “basal” living chitons

(Polyplacophora: Lepidopleurina). *American Malacological Bulletin, 25*, 43–49.

Sirenko, B. I. (2004). The ancient origin and persistence of chitons (Mollusca, Polyplacophora) that live and feed on deep submerged land plant matter (xylophages). *Bollettino Malacologico, Supplemento, 5*, 111–116.

Sirenko, B. I. (2006a). New outlook on the system of chitons (Mollusca: Polyplacophora). *Venus, 65*, 27–49.

Sirenko, B. I. (2006b). Report on the present state of our knowledge with regard to the chitons (Mollusca: Polyplacophora) of the Magellan Strait and Falkland Islands. *Venus, 65*, 81–89.

Sirenko, B. I. (2007). New Chilean chiton-epizoophagus *Gallardoia valdiviensis* gen. et sp. nov. (Mollusca, Polyplacophora). *Ruthenica, 17*, 13–21.

Sirenko, B. I., & Gallardo, C. (2005). Chitons (Polyplacophora) of Chile. In *Poster Abstracts of the IVth International Congress of the European Malacological Societies, Oct. 10–14 2005 in Naples (Italy)*. *Notizario S.I.M., Supplemento, Bollettino Malacologico*, 23(5–8), 89.

Sowerby, G. B., III. (1903). Mollusca of South Africa. *Marine Investigations in South Africa, 2*, 213–232. pls 3–5.

Spalowsky, I. I. N. A. (1795). *Prodromus in systema historicum testaceorum. Vorschmack einer vollständigen systematischen Geschichte der Schalthiergehäuse*. Wien: Ignaz Alberti's Wittwe.

Squires, R. L., & Goedert, J. L. (1995). An extant species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene and Oligocene cold-seep limestones, Olympic Peninsula, Washington. *Veliger, 38*, 47–53.

Suter, H. (1909). Richtigstellung einiger Namen in Dr. Curt von Wissel's "Pacifische (sic) Chitonen" 1904. *Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 41*, 72–75.

Thiele, J. (1908). Die antarktischen und subantarktischen Chitonen. Deutsche Südpolar Expedition 1901–1903, 10. *Zoologie, 2*, 9–23. pl. 1.

von Cosel, R. (2006). Polyplacophora. In D. Desbruyères, M. Segonzac & M. Bright (Eds.), *Handbook of deep-sea hydrothermal vent fauna, second completely revised edition*. *Denisia*, 18, 80–81.

Vendrasco, M. J., Fernandez, C. Z., Eernisse, D. J., & Runnegar, B. (2008). Aesthete canal morphology in the Mopaliidae (Polyplacophora). *American Malacological Bulletin, 25*, 51–69.

Verrill, A. E. (1882). Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England, No. 7, and of some additions to the fauna of Vineyard Sound. *American Journal of Science, 24*, 360–371.

Winckworth, R. (1926). Notes on British Mollusca—1. *Journal of Conchology, 18*, 13–15.

Wu, S.-K., & Okutani, T. (1984). The deepsea chitons (Mollusca: Polyplacophora) collected by the R/V Soyo-Maru from Japan—I. Lepidopleuridae. *Venus, 43*, 1–31.

Zarges, C. V. (1994). Clave para la identificación de los poliplacoforos litorales de Chile Central (Mollusca: Polyplacophora). *Comunicaciones del Museo de Historia Natural de Concepción, 8*, 67–69.