

Original article

First Quaternary fossil record of Polyplacophorans from southern South America[☆]

Première mention de Polyplacophores fossiles quaternaires du sud de l'Amérique du Sud

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Received 6 November 2006; accepted 10 October 2008

Available online 21 February 2009

Abstract

A diverse assemblages of well-preserved polyplacophoran shell plates is present in Holocene marine deposits along the Beagle Channel, Tierra del Fuego (54°S). They represent the first fossil Quaternary report of polyplacophorans from southern South America. The taxa include *Callochiton puniceus* (Couthouy MS, Gould), *Plaxiphora aurata* (Spalowsky), *Plaxiphora* sp., *Tonicia atrata* (Sowerby), *Tonicia calbucensis* Plate, *Tonicia chilensis* (Frembly), and *Tonicia lebruni* de Rochebrune. The presence of these taxa in a transitory area between the Atlantic and the Pacific oceans suggests that, in the recent past, the Beagle Channel acted as a path that facilitated faunal dispersion between the two oceans. These records also show an apparent stability of these faunas over a period of several thousand years (from ca. 7500 years BP to present).

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Keywords: Quaternary; Polyplacophora; Systematics; Southern South America

Résumé

Un assemblage diversifié de plaques de polyplacophores bien préservées est présent dans des dépôts marins holocènes du Canal Beagle, Tierra del Fuego (54°S). Ils constituent le premier signalement de Polyplacophores fossiles quaternaires du sud de l'Amérique du Sud. Les taxons incluent *Callochiton puniceus* (Couthouy MS, Gould), *Plaxiphora aurata* (Spalowsky), *Plaxiphora* sp., *Tonicia atrata* (Sowerby), *Tonicia calbucensis* Plate, *Tonicia chilensis* (Frembly), et *Tonicia lebruni* de Rochebrune. La présence de ces taxons dans une aire de transition entre les océans Atlantique et Pacifique suggère que, dans un passé récent, le Canal Beagle a servi de route facilitant la dispersion de la faune entre les deux océans. Ces registres montrent également une apparente stabilité de ces faunes pendant plusieurs milliers d'années (depuis ca. 7500 ans BP jusqu'à maintenant).

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Mots clés : Quaternaire ; Polyplacophore ; Systématique ; Sud Amérique du Sud

1. Introduction

The Polyplacophora, or the so-called chitons, are a group of exclusively marine animals with a worldwide distribution. Their highest diversity is found in the Australasian and North-Pacific regions. Living chitons have a size range from a few

millimeters to about 150 mm. The world's largest species, however—*Cryptochiton stelleri* (von Middendorff, 1847) from the North Pacific—may attain a length of more than 300 mm.

Chitons have a long geological history from the Paleozoic (Vendrasco and Runnegar, 2004; Pojeta et al., 2005), with only about 370 known fossil species, and 914 living representatives (Schwabe, 2005). Although some fully articulated specimens have been reported (e.g., Dell'Angello et al., 2003), isolated plates are the rule in the fossil record. Chitons are a morphologically conservative group since the external anatomy has not changed significantly over time.

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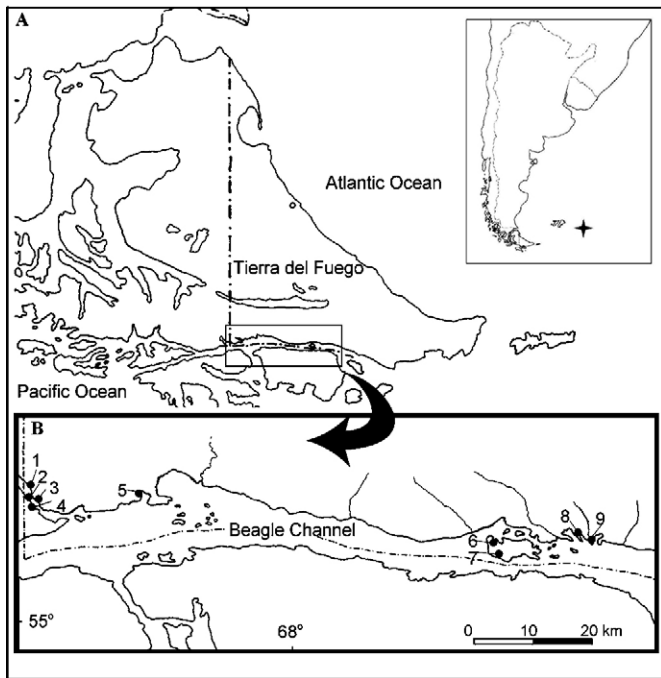


Fig. 1. Location map. **A.** Tierra del Fuego. **B.** Beagle Channel sector showing fossil localities. 1: Lago Roca; 2: Río Lapataia; 3: Alakush; 4: Río Ovando; 5: Península Ushuaia; 6: Isla Gable, northwestern coast; 7: Isla Gable, southern coast; 8: Harberton; 9: Río Varela.

The herein mentioned fossil chitons constitute the first Quaternary fossil record from southern Tierra del Fuego. This is a large island at the southernmost tip of South America located between the Pacific and the Atlantic oceans (Fig. 1). The island belongs to the Magellan Region, a wide cold-temperate region, which extends along the Pacific south of Isla Chiloé (42°S) to Cabo de Hornos (55°S) and from there, northward, along the Atlantic, as far as the Península Valdés (43°S).

The aim of this paper is to describe and illustrate the first fossil records of Quaternary chitons from a critical paleobiogeographic region located in southern South America, as it represents a connection between the Atlantic and the Pacific oceans.

2. Living chitons in the Magellan Region

In keeping with the worldwide trend, ecological research on molluscs from Tierra del Fuego also shows that chitons represent a minor fraction of the benthic communities (Ojeda and Santelices, 1984; Arntz et al., 1996; Linse, 1997). In relation to systematics, two expeditions in the middle of the 20th century are the source of most of the little existing knowledge of the chitons from Tierra del Fuego. First, a very important taxonomic work on polyplacophorans from the Magellan region by Leloup (1956) was based on material collected between Puerto Montt (41°S) and the Magellan Strait (52°–54°S) during the Lund University Chile Expedition in 1948–1949. Second, a review of the state of systematic malacology in southern Chile by Dell (1971) included chitons from Isla Navarino (54°S), in the Beagle Channel, southern

Tierra del Fuego. Another work compiled by Carcelles and Williamson (1951) made use of literature records to provide a non-illustrated checklist of the Magellan species. Zaixso (1974) described and illustrated five polyplacophoran species from Puerto Deseado, Patagonia. Also Brattström and Johanssen (1983) gave a non-illustrated checklist of 17 species, including their range of geographic distribution. Later, Castellanos (1988) published an illustrated catalogue of the Magellan chitons, including 31 species. More recent taxonomic reports on molluscs from the Magellan Region (i.e. Linse, 1999) excluded the systematics of chitons. One exception is the well-illustrated review by Reid and Osorio (2000) that provided the taxonomy of living chitons from the Parque Nacional Laguna Rafael (46°S). The most recent publication on southern Chilean chitons are provided by Sirenko (2006) and Schwabe et al. (2006), containing not only summarized information on the knowledge of chitons from the Magellanic and southern Chilean Fjord region, but also detailed descriptions and illustration of the relevant species. Some Magellan chiton groups (e.g., members of the genus *Tonicia*) show confusing variability in morphology and shell characteristics and numerous nominal species have been described previously. Thus, a basic work, based on local forms, should be a genetic one (Kelly and Eernisse, 2008; Kelly et al., 2007). The living chiton fauna of Tierra del Fuego includes at least 20 species listed in the Appendix A.

3. Quaternary fossil chitons

In southern Tierra del Fuego, Quaternary marine deposits containing chitons are located along the Beagle Channel. This channel, during the Quaternary glaciations, was repeatedly glaciated, at least in two major episodes (Rabassa et al., 2000). At about 9400 BP, the present Beagle Channel was occupied by a glacial lake, and before 8200 BP the lake water was replaced by seawater (Rabassa et al., 1986). A marine environment was fully established along this channel by 7900 BP, leaving Holocene raised beaches extended along the northern coast of the Beagle Channel (Rabassa et al., 1986; Gordillo et al., 1992; Gordillo et al., 1993).

Chitons from these deposits represent a minor fraction of the mollusc assemblages, mostly composed of bivalves and gastropods. These two mollusc groups were previously considered and described by Gordillo (1992), but polyplacophorans were only mentioned and never identified and/or described. Only one previous record of Holocene molluscs from Río Grande, northeastern Tierra del Fuego (Feruglio, 1950) proved the presence of one chiton species: *Plaxiphora aurata*.

Finally, other taxonomic reports from the Quaternary of Argentina include placophoran records from Buenos Aires, northern Argentina (Farinati, 1985; Aguirre, 1990), and from Patagonia, southern Argentina (Feruglio, 1950). Among them, the only systematic work centered on Holocene chitons (Farinati, 1995) described the presence of a species of *Chaetopleura Shuttleworth, 1853* in sediments from Bahía Blanca, Buenos Aires.

4. Material and methods

The material examined here was collected from nine sites located along the northern coast of the Beagle Channel (Fig. 1). Large sized chitons were sorted from entire bulk samples in the field. Small sized chitons were sorted from a sediment subsample under a stereoscopic microscope. The nine sites are:

- Lago Roca site (54°48'S, 68°36'W). This is a massive, greyish silty bed at 4 m a.s.l., radiocarbon dated at 7518 ± 58 years BP (date number #NZ 7730; Gordillo et al., 1993);
- Río Lapataia site (54°52'S, 68°32'W). This site is at 2 m a.s.l. and it was not dated;
- Alakush site (54°50'04''S, 68°34'W). This site yielded a radiocarbon date of 4400 ± 120 years BP at 5 m a.s.l. (#AC 0937; Figuerero and Mengoni, 1986);
- Río Ovando site (54°51'01''S, 68°35'W). This site at 3.1 m a.s.l. was dated at 4425 ± 55 years BP (# SI 6735; Rabassa et al., 1986);
- Península Ushuaia site (54°51'S, 68°18'W). The raised beach considered here at 2.5 m a.s.l. was not dated;
- NW Isla Gable site (54°53'S, 67°30'W). This marine deposit is located 5 m above the present sea level. Radiocarbon dating gave an age of 4790 ± 100 years BP (AECV 6480; Gordillo, 1991);
- SW Isla Gable site (54°54'S, 67°31'W). This deposit at 3.3 m a.s.l. has been described previously (Gordillo, 1991), but not dated;
- Harberton site (54°53'S, 67°24'W). This site, located at 1 m a.s.l., was not dated;
- Río Varela site (54°52'S, 67°11'W). This marine deposit located at 3 m a.s.l. was dated at 6240 ± 70 years BP (Coronato et al., 1999).

5. Systematic paleontology

All specimens are deposited in the Centro de Investigaciones Paleobiológicas (CIPAL), Universidad Nacional de Córdoba, Argentina. Figured specimens are housed under the prefix CEGH-UNC (22285, 22292, 22296, 22308, 22362, 22363, 22365, 22368, 22369, 22383, 22387, 22388, 22389, 22390, 22392, 22393, 22394).

Class POLYPLACOPHORA
Subclass NEOLORICATA
Order CHITONIDA
Family CALLOCHITONIDAE
Genus *Callochiton* Gray, 1847

Type species: *Chiton laevis*; Montagu, 1803; by subsequent designation (Gray, 1847) = *Callochiton septemvalvis* (Montagu, 1803).

Callochiton puniceus (Couthouy MS, Gould, 1846)

Fig. 2(A–C)

Material examined: Lago Roca: head plate (1); intermediate plates (3). Río Ovando: intermediate plates (21); tail plates (4).

Occurrence of the living species: Isla Navarino, in the Beagle Channel (54°55'S); Isla Bertrand, southern Navarino (55°15'S); intertidal rocks, boulders and *Macrocystis* holdfasts (Dell, 1971). Magellan Strait, 30–50 m (Ríos et al., 2003). Puerto Deseado, Patagonia; 3–9 m (Zaixso, 1974). Magellan Strait, 27 m; Islas Malvinas (51°45'S), 0–16 m (Dell, 1964). Range: according to Kaas and Van Belle (1985) the species occurs from 41° to 56°S (at the Pacific site) and northwards in the Atlantic to 47°S. Bathymetrically the species ranges from 0–300 m.

Diagnosis and description: Head plate semicircular in outline, with a slightly V-shaped posterior margin distinctly notched in the middle. Intermediate plates rectangular in outline, with the width at least twice the length; anterior margin straight to convex; posterior margin straight to somewhat concave on both sides of the protruding apex; lateral areas distinctly elevated showing some growth marks; pleural areas showing small grooves along the diagonal ridges; articulation well developed; apophyses rather short, rectangular and connected by a shallow jugal plate. Tail plate wider than long with mucro situated in the anterior third, directed forward and slightly elevated; postmucronal slope straight; antemucronal area sculptured like the pleural areas, while postmucronal area sculptured like the head plate. Slit formula variable: 15-16/1/11-14 (see Kaas and Van Belle, 1985).

Other fossil records: Unknown.

Family CHITONIDAE

Genus *Tonicia* Gray, 1847

Type species: *Chiton elegans* Fremby, 1827; by subsequent designation (Gray, 1847) = *Tonicia chilensis* (Fremby, 1827).

Tonicia atrata (Sowerby, 1840)

Fig. 2(D)

Material examined: Alakush: intermediate plate (1). Río Ovando: intermediate plates (5).

Occurrence of the living species: Isla Navarino, in the Beagle Channel (54°55'S); Isla Bertrand, southern Navarino (55°13'S); intertidal rocks, boulders and *Macrocystis* holdfasts (Dell, 1971). Magellan Strait, 30–50 m (Ríos et al., 2003). Fjordland of southern Chile (46°S); under stones, in pools; from mid to low eulittoral (Reid and Osorio, 2000; Schwabe et al., 2006). It is also recorded from the Islas Malvinas (Falkland Islands; Sirenko, 2006). Range: 15° to 55°S (Dell, 1971).

Diagnosis and description: Intermediate plates rectangular in outline; posterior margin slightly concave on both sides of the protruding apex; lateral areas slightly elevated, with ocelli restricted to the anterior half of the lateral areas; jugal area not elevated; solid articulation with one slit in the insertion plates; apophyses short and trapezoidal.

Comments: Uneroded specimens show normally a fine dentated jugal sinus between the apophyses.

Other fossil records: Unknown.

Tonicia calbucensis Plate, 1897

Fig. 2(G–I)

Material examined: Río Ovando: head plates (9); intermediate plates (9); tail plates (2).

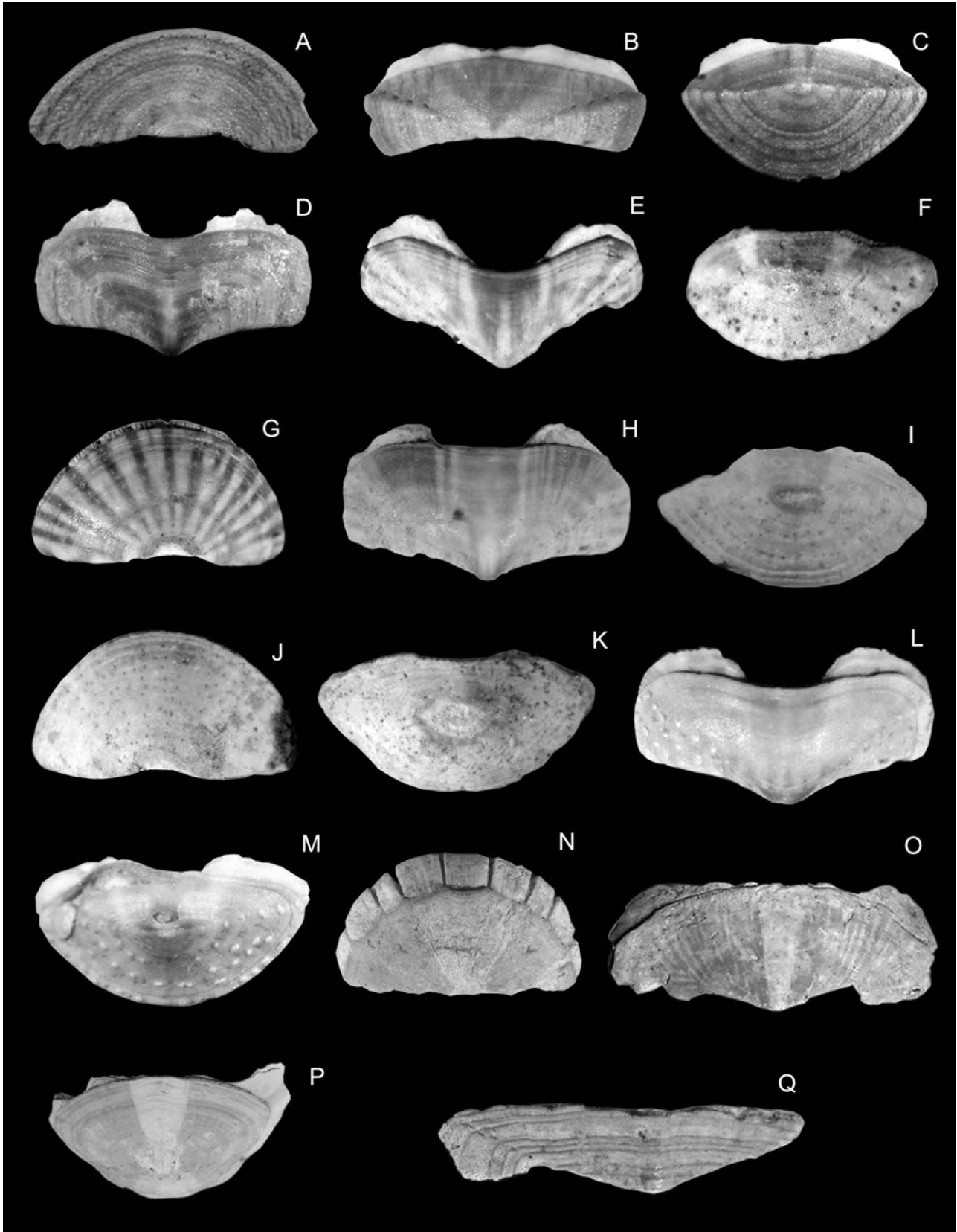


Fig. 2. A–C. *Callochiton puniceus* (Gould). A: head plate (CEGH-UNC22389), Lago Roca, $\times 13$; B: intermediate plate (CEGH-UNC22368), Río Ovando, $\times 10$; C: tail plate (CEGH-UNC22362), Río Ovando, $\times 9$. D. *Tonicia atrata* (Sowerby), intermediate plate (CEGH-UNC22369), Río Ovando, $\times 8$. E, F. *Tonicia chilensis* (Frembly). E: intermediate plate (CEGH-UNC22383), Río Ovando, $\times 13$; F: tail plate (CEGH-UNC22392), Río Ovando, $\times 15$. G–I. *Tonicia calbucensis* Plate: G: head plate (CEGH-UNC22285), Río Ovando, $\times 8$; H: intermediate plate (CEGH-UNC22296), Río Ovando, $\times 9$; I: tail plate (CEGH-UNC22365), Río Ovando, $\times 9$. J–M. *Tonicia lebruni* de Rochebrune. J: head plate (CEGH-UNC22393), Río Ovando, $\times 8$; K: tail plate (CEGH-UNC22394), Río Ovando, $\times 10$; L: intermediate plate

Occurrence of the living species: From Puerto Montt, Chile southwards to the Magellan Strait, between 0–35 m (Thiele, 1908) on different kind of hard substratum. According to Sirenko (2006) the species also lives in the Islas Malvinas (Falkland Islands).

Diagnosis and description: Head plate semicircular in outline, with posterior margin straight, showing typical texture of dark, radially arranged striations, where the ocelli occur; insertion plate with 9–10 slits. Intermediate plates showing a straight anterior margin, with posterior margin slightly concave on both sides of the protruding apex; jugal area not elevated but subcarinated; lateral areas moderately elevated showing anteriorly radial rows of ocelli, with striation oriented longitudinally on the pleural areas and radially on the lateral areas; apophyses short, widely separated and triangular in outline; insertion plates rather short and pectinated on the outside, with one slit. Tail plate nearly semicircular in outline with the mucro situated in the anterior half; postmucronal area showing concentrically arranged growth marks.

Comments: Tail plates collected lack the slits due to poor preservation of the margins. The head plate figured resembles the examined lectotype from the Natural History Museum Berlin ZMB Moll 102.006.

Other fossil records: Unknown.

Tonicia chilensis (Frembly, 1827) *s.l.*

Fig. 2(E, F)

Material examined: Río Ovando: intermediate plates (8); tail plates (2).

Occurrence of the living species: Magellan Strait, 30–50 m (Ríos et al., 2003). Fjordland of southern Chile (46°S); under stones, in pools; from the intertidal to 13 m (Reid and Osorio, 2000). Range: 12° to 54°S (Reid and Osorio, 2000). Schwabe et al. (2006) gave a bathymetric range from 0 to 28 m for this species.

Diagnosis and description: Intermediate plates rectangular in outline, with a protruding apex and concave posterior margins; lateral areas a little raised, with a slight depression along the diagonal ridge where the ocelli occur; jugum narrow and slightly elevated; faint concentric growth marks on the pleural area; apophyses short and rectangular; jugal sinus not visible; insertion plates with a single slit on both sides, and strongly pectinated on the outside. Tail plate rather worn, broad-oval in outline with the mucro nearly central; diagonal ridge moderately raised; number of slits indiscernible.

Other fossil records: Unknown.

Tonicia lebruni de Rochebrune, 1884

Fig. 2(J–M)

Material examined: Lago Roca: head plate (1). Río Ovando: head plates (10); intermediate plates (21); tail plates (4). Harberton: intermediate plate (1).

Occurrence of the living species: Isla Navarino, on the Beagle Channel (54°55'S); Isla Bertrand, southern Navarino

(55°13'S); intertidal rocks and *Macrocystis* holdfasts (Dell, 1971). Magellan Strait, 30–50 m (Ríos et al., 2003). In the Islas Malvinas (Falkland Islands) the species was found at 21 m (Sirenko, 2006). Range: 41° to 55°S (Dell, 1971).

Diagnosis and description: Intermediate plates broad, rectangular, rather highly elevated and not showing such a distinct jugal area as in *T. chilensis*; lateral areas not elevated but generally showing a row of rather high-elevated granules along the diagonal ridge, followed by ocelli and then again by granules, more distinct on the side margins; apex protruding with posterior margin straight; apophyses rather large, semi-rounded to trapezoid and connected by a sawed jugal sinus. Tail plates elliptic to trapezoid in outline, with a subcentral mucro; postmucronal area with concentric growth marks, granules and ocelli. Insertion plates short, with 8–9 slits in the head, one in the intermediate and 9–10 in the tail plate (Leloup, 1956).

Comments: The granulation on the tail plate together with the pectinated slits make the tail plate similar to that of *Chiton granosus* Frembly, 1827. However, *C. granosus* shows a striated antemucronal area, and the ocelli are lacking. Moreover *C. granosus* does not occur so far south. One peculiarity of the granules is that they are variable.

Other fossil records: Unknown.

Family MOPALIIDAE

Genus *Plaxiphora* Gray, 1847

Type species: *Chiton carmichaelis* Gray, 1828; by subsequent designation (Gray, 1847) = *Plaxiphora aurata* (Spalowsky, 1795).

Plaxiphora aurata (Spalowsky, 1795)

Fig. 2(N–P)

Material examined: Lago Roca: head plates (2); intermediate plate (1); tail plates (2). Río Lapataia: intermediate plates (2). Río Ovando: head plates (3); intermediate plates (10); tail plates (2). Península Ushuaia: intermediate plates (2). Harberton: head plate (1); intermediate plate (1). Río Varela: intermediate plate (1); tail plate (1). Isla Gable, NW: head plate (1). Isla Gable, SW: head plate (1).

Occurrence of the living species: Isla Navarino, in the Beagle Channel (54°55'S); Isla Bertrand, southern Navarino (55°13'S); intertidal rocks, grey mud, boulders and *Macrocystis* holdfasts (Dell, 1971). Bahía Ushuaia, Beagle Channel; pools (Zaixso et al., 1978). Magellan Strait, 30–50 m (Ríos et al., 2003). Fjordland of southern Chile (46°S); on and under stones, sheltered shores; from the intertidal to 10 m (Reid and Osorio, 2000). Puerto Deseado, Patagonia; intertidal, rocks and pools (Zaixso, 1974). Islas Malvinas (51°45'S) and Cockburn Channel (54°S) (Dell, 1964). Range: 31° to 55°S on the Pacific side and from there to 38°S on the Atlantic (Dell, 1971). The subantarctic distribution of the species is summarized in Sirenko (2006) and Schwabe et al. (2006).

Diagnosis and description: Head plate semicircular in outline, with a straight or slightly curved posterior margin, and

sculptured by eight slightly distinct radial folds; articulamentum solid, with eight rather deep slits in the insertion plate, extending longer than the tegmentum; teeth sharply edged and smooth on the outside. Intermediate plates rectangular in outline, and posterior margin concave on both sides of the protruding apex; anterior margin either straight or slightly convex (with a slightly extended anterior jugal area); lateral areas only slightly elevated, but easy to distinguish by the diagonal ridges; articulamentum forming large wing-like apophyses and long teeth in the insertion plates; apophyses large and wing-shaped, and the insertion plate forming an unslitted posterior callus. Tail plates elliptic in outline, with mucro in the posterior half.

Other fossil records: Río Grande, Tierra del Fuego; rare in raised beach (Feruglio, 1950).

? *Plaxiphora* sp.

Fig. 2(Q)

Material examined: Río Lapataia: intermediate plate (1). A single fragment.

Description: Intermediate plate much wider than long, slightly carinated showing very slightly raised lateral areas; plate surface smooth except for distinct concentric growth lines.

Comments: This latter feature leads us to separate this plate from *Plaxiphora aurata*, which does not show such growth marks. Unfortunately the articulamentum is too worn to allow specific systematic placement.

6. Concluding remarks

Seven species of chitons were collected from the Holocene marine deposits along the Beagle Channel, with only one species reported at the genus-level. All these taxa are mentioned for the first time in the Quaternary of southern South America. Considering that all of them are living species in the Beagle Channel, an apparent stability in these faunas over a period of several thousand years (from *ca.* 7500 BP to present days) is evidenced. The presence of these taxa in a transitory area between the Atlantic and the Pacific oceans also suggests that, in the recent past, the Beagle Channel acted as a path that facilitated faunal dispersion between the two oceans.

Acknowledgments

Thanks are extended to N.E. Vaccari (CICTERRA, CONICET, CIPAL, UNC) for assistance with the photos. We are grateful to Douglas J. Eernisse and the editor for their comments.

Appendix A. Living chitons from the Magellan Region

Family LEPTOCHITONIDAE Dall, 1889

1. *Leptochiton kerguelensis* Haddon, 1886.
2. *L. medinae* (Plate, 1899).
3. *Leptochiton* sp.
Family CALLOCHITONIDAE Plate, 1901

4. *Callochiton puniceus* (Couthouy MS, Gould, 1846).
Family ISCHNOCHITONIDAE Dall, 1889
5. *Ischnochiton pusio* (Sowerby in Broderip and Sowerby, 1832).
6. *I. stramineus* (Sowerby in Broderip and Sowerby, 1832).
7. *I. viridulus* (Couthouy MS, Gould, 1846).
8. *Stenosemus exaratus* (G.O. Sars, 1878).
Family CHAETOPLEURIDAE Plate, 1899
9. ? *Chaetopleura brucei* Iredale in Melvill and Standen, 1912.
Family CHITONIDAE Rafinesque, 1815
10. *Chiton bowenii* King and Broderip, 1831.
11. *Tonicia atrata* (Sowerby, 1840).
12. *T. calbucensis* Plate, 1897.
13. *T. chilensis* (Fremby, 1827).
14. *T. horniana* de Rochebrune in de Rochebrune and Mabilie, 1889.
15. *T. lebruni* de Rochebrune, 1884.
Family MOPALIIDAE Dall, 1889.
16. *Plaxiphora aurata* (Spalowsky, 1795).
17. *Nuttallochiton martiali* (de Rochebrune in de Rochebrune and Mabilie, 1889).
18. *N. hyadesi* (de Rochebrune in de Rochebrune and Mabilie, 1889).
Family ACANTHOCHITONIDAE Pilsbry, 1893
19. *Acanthochitona hirudiniformis peruviana* Leloup, 1941.
Family HEMIARTHURIDAE Sirenko, 1997
20. *Hemiarthrum setulosum* Carpenter in Dall, 1876.

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