

# AN EOCENE ARTICULATED POLYPLACOPHORA (MOLLUSCA) FROM THE LA MESETA FORMATION, ANTARCTICA AND THE STRATIGRAPHY OF THE FOSSIL-BEARING STRATA

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**ABSTRACT**—An exceptionally well-preserved specimen of *Leptochiton* sp. attached to a brachiopod valve is described from the early Eocene beds of the La Meseta Formation, Seymour Island. It records the first fossil Polyplacophora from Antarctica. The small specimen has eight imbricating valves, rounded lateral margins, ribs of fine granules, and growth marks in all valves. It strongly resembles extant Antarctic and South American species of *Leptochiton* Gray. The record of articulate valves in fossil Polyplacophora is rare and requires exceptional preservational conditions. *Leptochiton* sp. is associated with well preserved bryozoans, brachiopods, asterozoan echinoids, and serpulids, among other organisms that inhabited hard substrates in normal marine conditions, and probably lived attached to the side walls of an incised valley eroded in Cretaceous sediments. The well-preserved fossils were probably removed from their attachment site during storm events and, after a short transportation, rapidly buried within the early Eocene valley-fill deposits. The fossil-bearing beds are included in the Telm 2 or Acantilados Allomember of the La Meseta Formation.

## INTRODUCTION

POLYPLACOPHORAN ARE primitive marine animals with a characteristic elliptical or elongate body outline and eight overlapping calcareous valves surrounded by a marginal muscular band called the girdle. They live mostly at shallow water, in high littoral to intertidal zones of rocky shores but also in deep chemosynthetic environments and on the continental slopes down to the abyssal and even hadal plains (Schwabe, 2008 and references therein). Modern Polyplacophora have a worldwide distribution from the Arctic to the Antarctic; fossil Polyplacophora are known since the Cambrian–Ordovician and have also a wide geographic distribution with records in all modern continents (Sirenko, 2006a; Puchalski et al., 2008) except for Antarctica, but most of the fossil record of Polyplacophora consists of disarticulate valves. To the authors' knowledge, four examples of fully articulate specimens are known in the Cenozoic fossil record and the preservation of these extraordinary examples are related to exceptional conditions of fossilization (Itoigawa, et al., 1977; Ivany et al., 1990; Squires and Goedert, 1995; Dell'Angelo et al., 2003).

In this study we report the first fossil record of Polyplacophora from Antarctica. The material consists of a single, fully articulated specimen of the genus *Leptochiton* Gray, 1847, attached to the pedicle valve interior of the brachiopod *Liothyrella*? sp. *Leptochiton* sp. was recorded at the westernmost outcrops of the La Meseta Formation, Eocene, Seymour Island, Antarctica at the top of a small outcrop situated at about 42 m above sea level, known as Bill Hill (Fig. 1), after Bill Zinsmeister who discovered the locality in 1985 (Sadler, 1988). Just above the basal unconformity of the La Meseta Formation, the Bill Hill strata (Figs. 1, 2) have provided a diverse, well-preserved invertebrate fauna that includes, among others, 22 species of brachiopods (Bitner, 1996), 40 species of bryozoans (Hara, 2001), asterozoan echinoids (Blake and Zinsmeister, 1988), serpulids, corals, regular echinoids, crinoids, and mollusks (Sadler, 1988). However, the precise stratigraphic position of the Bill Hill beds within the La Meseta Formation is not well known.

The aims of this study are to document the record of fossil Polyplacophora from Antarctica and to discuss the systematic,

paleoecology and taphonomy of the fossil specimen, and the stratigraphic position of the fossil-bearing Bill Hill strata within the La Meseta Formation.

## STRATIGRAPHY AND PALEOENVIRONMENTS OF THE LA MESETA FORMATION

The Eocene La Meseta Formation (Elliot and Trautman, 1982) crops out in northeastern Seymour Island at the northeastern tip of the Antarctic Peninsula (Fig. 1.1). An angular unconformity separates La Meseta Formation from gently tilted strata of the Maastrichtian–Danian López de Bertodano Formation and the Paleocene Sobral and Cross Valley Formations (Figs. 1.2–1.5, 2.1) forming a trough-like major erosive surface that is 7 km wide and with more than 70 m vertical relief. The beds of the La Meseta Formation lap onto the steep-sided trough walls with variable dips, ranging from 15° near the unconformity to less than 3° toward the trough axis (Sadler, 1988; Marenssi, 2006).

The La Meseta Formation consists of a complex stack of large, lenticular, channel-form elements separated by unconformities (Sadler, 1988). Individual elements are composed of variable proportions of silty sandstone and mudstone heterolith; fine-grained sandstone; and shelly conglomerate that accumulated in deltaic, estuarine, and wave-influenced tidal-shelf settings (Sadler, 1988; Porebski, 2000; Marenssi et al., 2002). Due to the complex, lenticular geometry of the sedimentary filling, no single section can represent the total thickness of the La Meseta Formation. Its aggregate thickness is estimated to be over 700 m (Marenssi et al., 1998, 2002; Marenssi, 2006). Overall, the La Meseta Formation is thought to represent a composite incised valley cut into an emergent shelf, filled with deltaic, estuarine, and shallow marine deposits during several, eustatically controlled episodes of fluvial incision and accumulation (Sadler, 1988; Marenssi et al., 2002; Marenssi, 2006). Conversely, Porebski (2000) and Ivany et al. (2008) interpreted that the La Meseta Formation accumulated within a fault-bounded basin where erosion and accumulation were controlled by a combination of tectonic subsidence and sea-level changes.

The formation was divided in seven informal map units, including from base to top Telm 1 to Telm 7 (Sadler, 1988) or

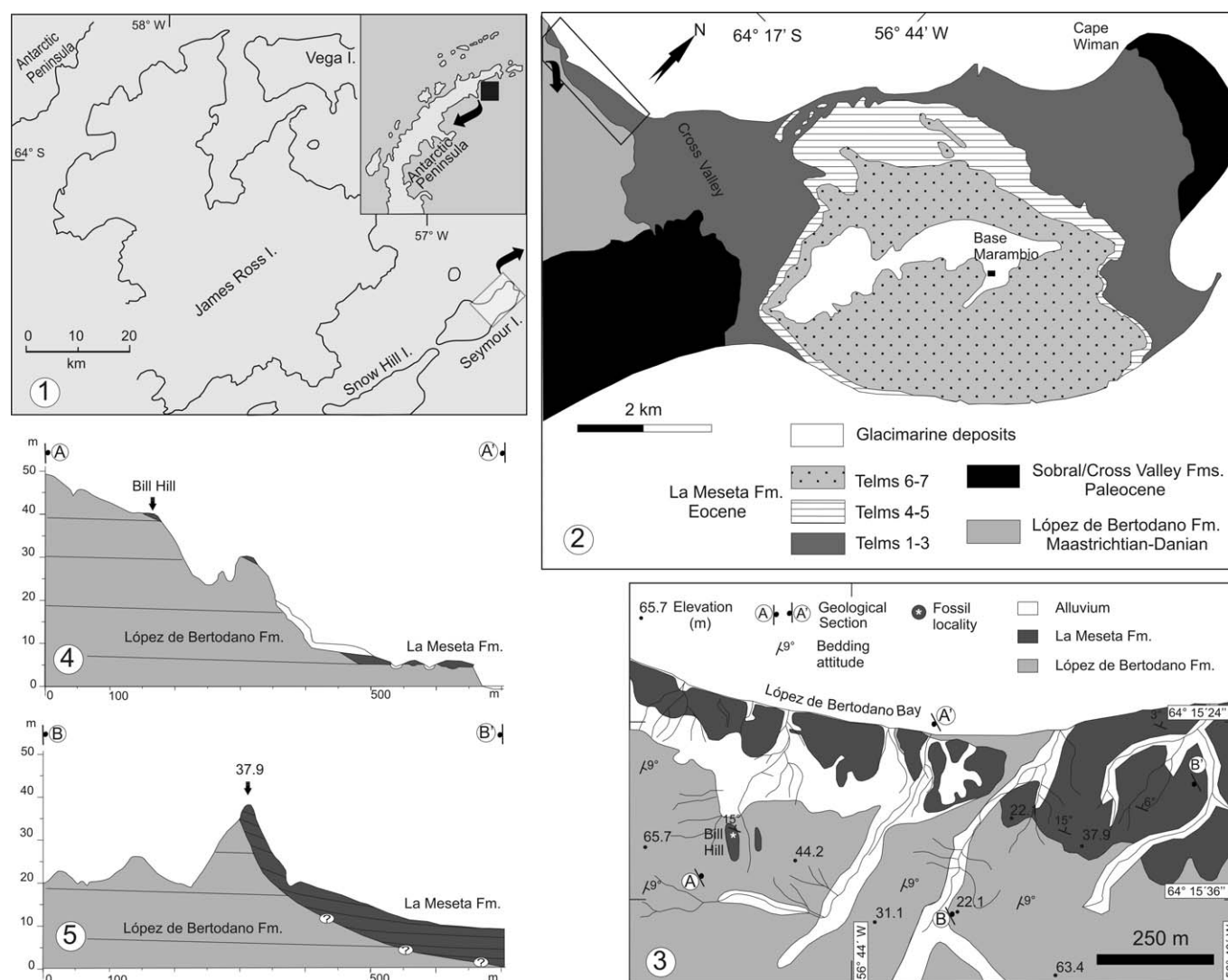


FIGURE 1—Geographic situation and schematic geology of the studied area: 1, relative situation of the James Ross archipelago and Seymour Island in the Antarctic Peninsula; 2, schematic geology of northeastern Seymour Island showing the distribution of the La Meseta Formation and Paleocene and Maastrichtian rocks, after Sadler (1988) and Marensi et al. (1998), the inset shows the situation of Figure 1.3; 3, detailed geological sketch of the fossil-bearing strata at Bill Hill area; 4, 5, geological sections of Bill Hill and 37.9 elevation hill showing the geometry of the unconformity between the López de Bertodano and La Meseta Formations, note in Figure 1.5 that the La Meseta beds lap on the unconformity, exposing successively younger beds at higher elevations. Topography after the U.S. Geological Survey (USGS) topographic map 64056-T5-TM-010 produced in 1995.

six, unconformity-bounded allomembers, including the Valle de las Focas (roughly equivalent to Telm 1); Acantilados (Telm 2 and partly Telm 3); Campamento (partly Telm 3); Cuccullaea I (Telm 4 and 5); Cuccullaea II (Telm 6); and Submeseta (Telm 7) Allomembers (Marensi et al., 1998; Marensi, 2006). Biostratigraphic studies of dinoflagellates (Wrenn and Hart, 1988; Cocozza and Clarke, 1992), and mollusks (Stilwell and Zinsmeister, 1992) suggest early Eocene, late middle Eocene, and late Eocene ages for different intervals of the La Meseta Formation. These biostratigraphic results are supported by Sr isotope stratigraphy data reviewed by Ivany et al. (2008). Additional, detailed Sr isotope stratigraphy from numerous samples collected from Telm 2 to Telm 7 (Ivany et al., 2008) indicates an early Eocene age for Telm 2 (54 Ma), Telm 3 (53.5–52.8 Ma) and Telm 4 (52.5 Ma); an early Eocene to early middle Eocene age for Telm 5 (51 to 48.8 Ma); a late middle Eocene age for Telm 6 (41 Ma) and a late middle Eocene to latest late Eocene age for Telm 7 (39.1 to 34.0 Ma).

In the studied area the contact between the López de Bertodano Formation and La Meseta Formation is well exposed at Bill Hill and at the 37.9 m elevation hill (Fig. 1). The basal part of the La Meseta Formation at the Bill Hill locality (Fig. 1.3, 1.4) is about 2 m thick and consists of a basal conglomeratic sandstone bed including lenses of fine-grained, shelly hash conglomerate (Figs. 2, 3) that bear isolated, well-rounded slate and volcanic clasts; rhythmically interbedded mudstone and silty sandstone heterolith; and thick sandstone beds with shelly hash lenses bearing sparse, well-preserved fossils (Fig. 4), including serpulids, brachiopods, bryozoans, *Leptochiton* sp., and echinoids. At the top of the section is a hard, parallel laminated and wave-rippled, fine-grained sandstone that bears the trace fossils *Lockeia* James 1879 and *Protovirgularia* McCoy, 1850. At the 37.9 m locality, the basal part of the La Meseta Formation consists of a rhythmic alternation of silty fine-grained sandstones and silty and muddy heterolith, about 5 m thick (Fig. 2.4).



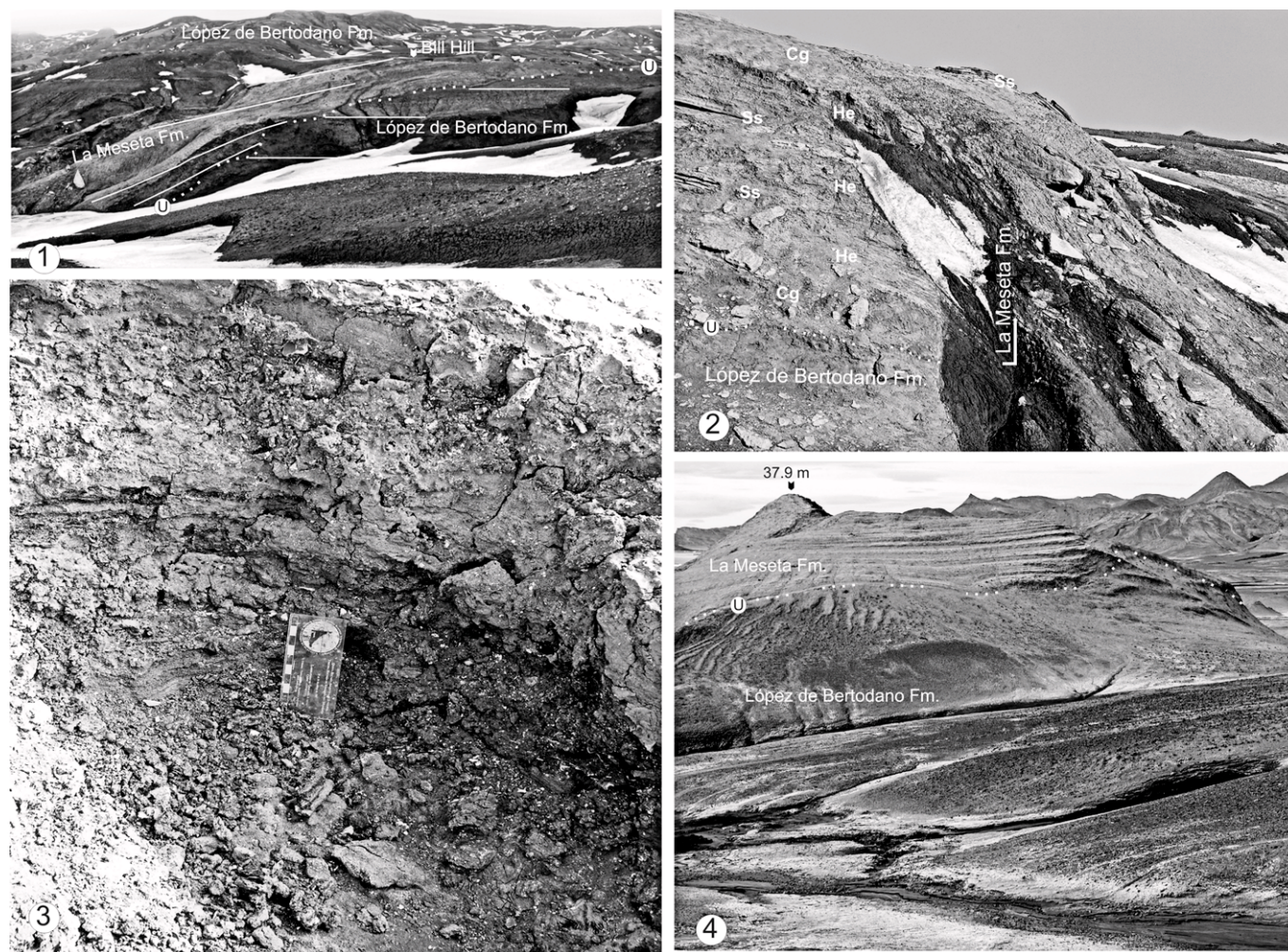


FIGURE 2—Geometry of the unconformity between the López de Bertodano and La Meseta Formations and lithology of the basal beds of La Meseta Formation: 1, the fossil-bearing Bill Hill locality, note the angular unconformity (U) and the onlap geometry of the basal beds (white lines) of the La Meseta Formation; 2, lithology of the basal beds of the La Meseta Formation at Bill Hill locality (Cg: shelly hash conglomerate; Ss: laminated fine-grained sandstone; He: silty sandstone-mudstone heterolith, total thickness is about 2 m, see Figure 3; 3, detailed view of the basal shelly hash conglomerate of the La Meseta Formation, light particles are bivalve shell fragments; 4, the unconformity between the López de Bertodano and the La Meseta Formations at the 37.9 elevation hill.

The fossiliferous strata cropping out at Bill Hill were referred to Telm 1 (Sadler, 1988; Bitner, 1996; Hara, 2001) or Valle de las Focas Allomember (Marenssi et al., 1998) and the strata of the 37.9 m hill to Telm 2 (Sadler, 1988; Ivany et al., 2008) or Acantilados Allomember (Marenssi et al., 1998; Marenssi, 2006). However, the strict correspondence of Bill Hill and 37.9 m hill strata with Telm 1 (Valle de las Focas Allomember) is questionable on the basis that the reference sections for Telm 1/Telm 2 and the Valle de las Focas/Acantilados allomembers are located on the opposite side of the incised valley, near Cape Wiman, and the strata do not have physical continuity across the valley axis. Assuming that the 37.9 m hill beds correspond to Telm 2 (Acantilados Allomember) as suggested by the Sr isotope age of 54.0 Ma obtained from nearby strata at Cross Valley (Ivany et al., 2008), then the Bill Hill beds should be younger than Telm 1 (Valle de las Focas) strata. This seems apparent from the geological sections (Fig. 1.4, 1.5) that show how the strata of the La Meseta Formation lap onto the basal unconformity, implying that younger beds are located successively at higher topographic levels, as they

climb the basal unconformity during the filling of the incised valley. Hence, we interpret that the Bill Hill strata are probably intercalated within Telm 2 (Acantilados Allomember).

#### MATERIALS

The studied material comes from the Bill Hill locality (Lat. S 64°15'33.1"; Long. W 56°44'22.7"), located at the western boundary of the La Meseta Formation on Seymour Island, Antarctica (Fig. 1). The illustrated material is housed with the paleontological collections of the Laboratorio de Geología Andina, Centro Austral de Investigaciones Científicas (CADIC-CONICET), Ushuaia, Tierra del Fuego Argentina, numbered with the prefix CADIC-PI.

#### SYSTEMATIC PALEONTOLOGY

Class POLYPLACOPHORA Gray, 1821  
Family LEPTOCHITONIDAE Dall, 1889  
Genus LEPTOCHITON Gray, 1847

*Types species.*—*Chiton cinereus* Linnaeus, 1767 sensu Montagu, 1803 by subsequent designation of Gray (1847).



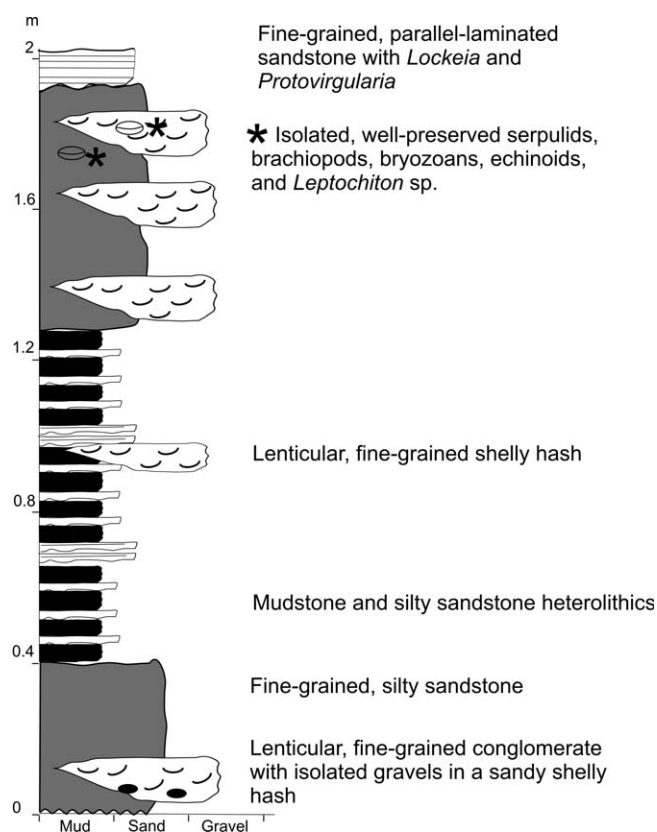


FIGURE 3—Sedimentary log of the 2-m-thick basal La Meseta section at Bill Hill locality depicted in Figure 2.2.

#### LEPTOCHITON sp. Figure 5

**Material.**—One well-preserved specimen with the eight articulate valves CADIC-PI 151.

**Occurrence.**—Bill Hill locality, Seymour Island, Antarctica. Early Eocene, probably from Teln 2 beds of the La Meseta Formation.

**Description.**—Specimen of elongate outline and small size—9.4 mm in length, 3.8 mm in width, and 2.1 mm in height—preserving the eight imbricated valves and well-marked sculpture on all valves. Head valve (HV) semicircular in outline, posterior part slightly V-shaped, with 40 to 50 fine, radial ribs of fine granules distributed in closer set than those of intermediate valves. Intermediate valves (IV) rectangular in outline with rounded lateral margins and straight posterior margin; apex absent, central area with about 30 longitudinal ribs of fine granules; lateral area slightly raised covered by seven diagonal ribs of fine granules; diagonal ridge not prominent. Width ratio of second IV/HV is about 1.13. Tail valve semicircular, mucro in central position, post mucronal area with steep slope and sculpture as on the head valve. Faintly preserved growth lines present in all valves.

**Discussion.**—The Eocene Antarctic polyplacophora is referred to *Leptochiton* Gray, 1847 by the apparent lack of insertion plates and its resemblance in shell form and sculpture to extant species of this genus that inhabit the Magellan region and Antarctica (Castellanos, 1988; Sirenko, 2006b). Of the recent species of *Leptochiton*, *L. medinae* Plate, 1899 exhibit close similarity to *Leptochiton* sp. (B. Sirenko, personal commun., 2009); they are small in size, the valves bear sculpture of ribs of fine granules and growth lines are present in all valves. However, *Leptochiton* sp. differs from *L. medinae*

(cf. Schwabe et al., 2006) by having less number of ribs of fine granules: *Leptochiton* sp. has 40–50 ribs on the HV, c. 30 in the central area and 7 in the lateral area of the IV and *L. medinae* has 80 ribs on the HV; c. 70 in the central area and 15 in the lateral area of the IV. Also the V-shaped posterior part of the HV in *L. medinae* bear a distinct notch not observed in *Leptochiton* sp. These features also differentiate *Leptochiton* sp. from other modern, deep water *Leptochiton* species of the Chilean region (Kaas and Van Belle, 1985; Schwabe and Sellanes, 2010) as *L. laurae* Schwabe and Sellanes, 2010 and *L. americanus* Kaas and Van Belle, 1985. *L. laurae* also has an irregularly arrangement of granules on the HV. *L. americanus* differs from *Leptochiton* sp. by the well-raised granular sculpture, a small HV with granules arranged quincuncially, and by a set of finer granulate ribs on the jugum. *Leptochiton kerguelensis* Haddon, 1886 of wide Magellan and Antarctic distribution differs from *Leptochiton* sp. by the small size, up to 5 mm long, and weaker valve sculpture bearing roundish flat granules arranged in quincunx (Kaas and Van Belle, 1985). The fossil Antarctic *Leptochiton* sp. also differs from modern species of South Atlantic distribution, such as *L. chariessa* Barnard, 1963 and *L. denhartogi* Strack, 2003. *L. chariessa* from South Africa has 60–70 ribs on the HV and 40–45 ribs in the central area of the IV, also the carinated IV bear a small pointed apex (Kaas and Van Belle, 1985). *L. denhartogi* from Angola has IV of similar rectangular and rounded margins but differs from *Leptochiton* sp. by the small size, up to 4.2 mm in length and 2.9 mm in width, and denser sculpture with coarse elevate granules in the ribs. In addition, the interspace between the rows in the central area of the IV is slightly latticed (Strack, 2003).

The fossil Antarctic *Leptochiton* sp. differs clearly from other fossil or modern species of the genus. However, as only one specimen was recovered and the morphological variability cannot be evaluated, we prefer not to erect a new species. The genus *Leptochiton* has a fossil record spanning the Eocene–Recent (Schwabe and Sellanes, 2010) including a fully articulate specimen reported from Oligocene deep-water cold seeps deposits in North America (Squires and Goedert, 1995).

#### PALEOECOLOGY AND TAPHONOMY

Two contrasting modes of fossil preservation characterize the upper levels of the 2 m-thick Bill Hill strata: 1) abundant, small fragments of mollusks within the conglomeratic shelly hash lenses (Figs. 2.3, 3); and 2) sparse, very well-preserved specimens of delicate fossils, including branched, reticulated, and massive multilamellar colonies of bryozoans; articulate or complete single valves of brachiopods; complete specimens of goniasterid asterozoan echinoids; articulate *Leptochiton* sp.; and encrusting serpulids (Figs. 3, 4, 5). These two contrasting preservational modes probably reflect both different sources for the fossil material and taphonomic pathways.

The shell fragments within the conglomeratic lenses belong mostly to bivalves but, with the exception of relatively larger fragments of pectinids and ostreids, the majority of the shell fragments are generally less than 10 mm in diameter and a more precise classification is not possible. Shell fragmentation suggests an allochthonous concentration, derivation of the fossil material from high-energy, near-shore settings, and probably transportation by storm processes to the depositional site. Conversely, the well-preserved specimens represent a diverse, paleoecologically consistent, autochthonous or parautochthonous group of taxa that typically lives on hard substrates in areas of low sedimentation rates. In this regard, Hara (2001), in her comprehensive study of the La Meseta





FIGURE 4—Well-preserved early Eocene fossils of the La Meseta Formation at Bill Hill locality, including massive (ma), multilamellar (ml), reticulated (re), and branched (br) bryozoan colonies; brachiopods (bp); serpulid tubes (se); and the asterozoans *Pentagonaster elegans* (Blake, 1988) (Pe) and an indeterminate goniasterid (Go), the white arrow points to the *Leptochiton* sp. specimen attached to the inner valve of *Liothyrella*? sp. Scale bar is 10 cm.

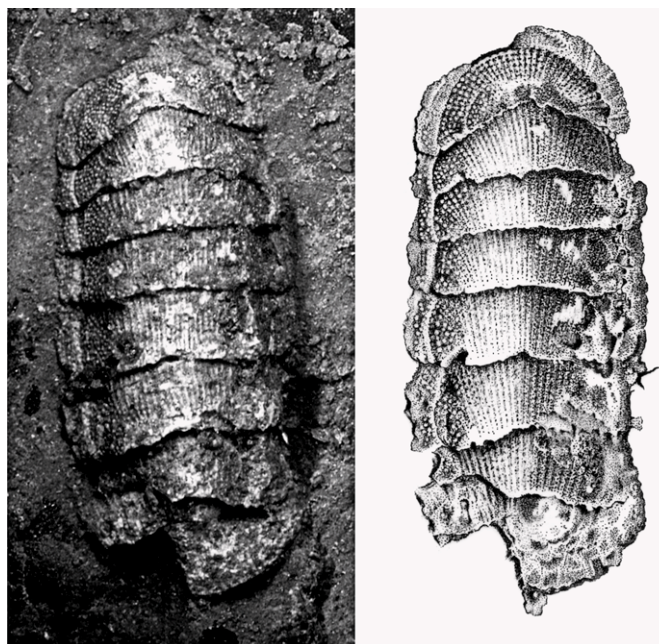


FIGURE 5—*Leptochiton* sp. from the La Meseta Formation, Bill Hill locality, Seymour Island, Antarctica, CADIC-PI 151. The drawing to the right is an exact reproduction of the original specimen highlighting its morphological features. The specimen is 9.4 mm in length.

Formation bryozoans, established that dominance in the Bill Hill bryozoans of multilamellar cerioporiform and celoporiform colonies; encrusting unilamellar sheet-like membrani-poriform colonies; erect, branching arborescent hornerid colonies; and erect, fenestrate retiform colonies, consistently indicate environmental settings characterized by hard substrate, limited available space, moderated energy, low turbidity, low sedimentation rate, and normal marine conditions. The accompanying fauna also indicates similar living conditions, particularly for the brachiopods (Bitner, 1996); asterozoan echinoids (Blake and Zinsmeister, 1988); crinoids and serpulids (cf. Hara, 2001). In addition, Hara (2001) concluded that the record of exceptionally well-preserved articulate crowns of isocrinids crinoids, numerous articulated brachiopod shells, and preservation of different ontogenetic stages of bryozoan colonies, suggest minimal postmortem transport, rapid burial, and preservation of a thanatocenosis.

The inferred mode of life and fossil preservation of *Leptochiton* sp. are both consistent with the paleoecological and environmental interpretations deduced by Hara (2001). Extant polyplacophora, the majority of which inhabits shallow tidal to subtidal settings, typically live on hard substrate and even the deep-sea species are reported to live on all kinds of hard substrates, including carbonate build-ups in cold-seeps; wood-falls; and whale-falls (see Squires and Goedert, 1995; Schwabe and Sellanes, 2010, and the bibliography therein). The exceptional preservation of *Leptochiton*



sp. with the eight articulate valves lying flat and adhered to the inner shell of a brachiopod, suggests that the organism was transported and rapidly buried still alive. Otherwise, post-mortem transportation and long exposure on the sea floor would result in the decay of the muscular girdle and subsequent loss of valve articulation. Preservation or disintegration of the girdle may still be possible in anoxic or dysoxic settings (Dell'Angelo et al., 2003), but in that case the post-mortem contraction of the muscular fibers would cause a curled preservation of the shell. As the shell of *Leptochiton* sp. is not curled or enrolled, this suggests transportation of a still alive organism adhered to the brachiopod shell.

The very-well preserved fossils of the Bill Hill locality are interpreted to represent a fully marine hard substrate community, probably with the organisms living in patches on the erosive valley sides, located at that time topographically above the Bill Hill depositional site, and attached to the sedimentites of the López de Bertodano Formation. In this scenario, the well-preserved fossil assemblage is thought to have been removed from the living site and emplaced at the depositional site during storm events, with only a short transportation and rapid burial. The same storm events could have produced the allochthonous concentration of bivalve fragments that characterizes the conglomeratic lenses at the Bill Hill section.

#### CONCLUSIONS

Fossil Polyplacophora have a worldwide distribution but they were not previously recorded from Antarctica. This study documents the discovery of an exceptional fossil Polyplacophora attached to the inner pedicle valve of the brachiopod *Liothyrella*? sp. The specimen that preserves the eight valves articulated is referred to *Leptochiton* sp. and was recorded in the Eocene La Meseta Formation of Seymour Island, Antarctica. *Leptochiton* sp. is similar to the modern species *L. medinae* Plate, 1899, which is common in subtidal and neritic settings of the Magellan region in South America and Antarctica (Schwabe et al., 2006; Sirenko, personal commun., 2009) but *Leptochiton* sp. has a fewer number of ribs of fine granules.

The Polyplacophora-bearing strata at the Bill Hill locality in Seymour Island are probably intercalated within the early Eocene Telm 2 (Sadler, 1988) or Acanitilados Allomember (Marenssi et al., 1998) of the La Meseta Formation. *Leptochiton* sp. is associated with a diverse and well-preserved assemblage of subspherical multilamellar, branched, and reticulate bryozoan colonies (Hara, 2001); articulate brachiopods (Bitner, 1996); crinoids; asterozoan echinoids; and serpulids, which together with *Leptochiton* sp. suggest a living community inhabiting hard substrates, with low sedimentation rates and normal marine conditions. This hard-substrate community was probably installed along the side walls of the incised valley elaborated in the Cretaceous sedimentites of the López de Bertodano Formation, topographically above the contemporaneous sedimentation surface of the Telm 2 that at that time was filling the valley. The well-preserved fossils probably represent removed specimens from the hard-bottom community during storm events, followed by short transport and rapid burial. Preservation of the articulate specimen of *Leptochiton* sp. is best explained by the rapid burial of a still alive organism.

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#### REFERENCES

- BITNER, M. A. 1996. Brachiopods from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula, p. 65–100. In A. Gaździcki, (ed.), Paleontological results of the Polish Antarctic Expeditions. Part. II. Palaeontologia Polonica 55.
- BLAKE, D. B. AND W. J. ZINSMEISTER. 1988. Eocene asteroids (Equinodermata) from Seymour Island, Antarctic Peninsula, p. 489–498. In R. M. Feldmann and M. O. Woodburne (eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America Memoir, 169.
- CASTELLANOS, Z. J. A. 1988. Catálogo Descriptivo de la Malacofauna Marina Magallánica I. Los Placoforos (Mollusca-Placophora). Comisión de Investigaciones Científicas, La Plata, Provincia de Buenos Aires, 41 p.
- COCOZZA, C. D. AND C. M. CLARKE. 1992. Eocene microplankton from La Meseta Formation, northern Seymour Island. Antarctic Science, 4:355–362.
- DELL'ANGELO, B., H. GALLORINI, AND M. TAVIANI. 2003. First Neogene record of an articulated polyplacophoran. Journal of Paleontology, 77:1193–1194.
- ELLIOT, D. H. AND T. TRAUTMAN. 1982. Lower Tertiary strata on Seymour Island. Antarctic Peninsula, p. 287–297. In C. Craddock (ed.), Antarctic Geoscience. The University of Wisconsin Press, Madison.
- GRAY, J. E. 1847. A list of the genera of recent Mollusca, their synonyms and types. Proceedings of the Zoological Society of London, 15:129–206.
- HARA, U. 2001. Bryozoans from the Eocene of Seymour Island, Antarctic Peninsula, p. 33–155. In A. Gaździcki, (ed.), Paleontological results of the Polish Antarctic Expeditions. Part. III. Palaeontologia Polonica 60.
- ITOIGAWA, J., H. NISHIMOTO, AND S. TOMIDA. 1977. *Lepidopleurus morozakiensis*, a new fossil Polyplacophora from the Miocene Morozaki group, central Japan. Bulletin of the Mizunami Fossil Museum, 4: 55–59.
- IVANY, L. C., R. W. PORTELL, AND D. S. JONES. 1990. Animal-plant relationships and Paleobiogeography of an Eocene Seagrass community from Florida. Palaios, 5:244–258.
- IVANY, L. C., K. C. LOHMANN, F. HASIUK, D. B. BLAKE, A. GLASS, R. B. ARONSON, AND R. M. MOODY. 2008. Eocene climate record of high southern latitude continental shelf: Seymour Island, Antarctica. Geological Society of America Bulletin, 120:659–678.
- JAMES, U. P. 1879. Description of new species of fossils and remarks on some others, from the Lower and Upper Silurian rocks of Ohio. Palaeontologist, 3:17–24.
- KAAS, P. AND A. VAN BELLE. 1985. Monograph of Living Chitons (Mollusca: Polyplacophora). Vol. 1. Order Neoloricata: Lepidopleurina. E. J. Brill/W. Backhuys, Leiden, 240 p.
- MARENSSI, S. M. 2006. Eustatically controlled sedimentation recorded by Eocene strata of James Ross Basin, Antarctica, p. 125–133. In J. E. Francis, D. Pirrie and J. A. Cramers (eds.), Cretaceous–Tertiary High-Latitude Palaeoenvironments, James Ross Basin, Antarctica. Geological Society, London, Special Publications, 258.
- MARENSSI, S. M., L. I. NET, AND S. N. SANTILLANA. 2002. Provenance, environmental and paleogeographic controls on sandstone composition in an incised-valley system: the Eocene La Meseta Formation, Seymour Island, Antarctica. Sedimentary Geology, 150:301–321.
- MARENSSI, S. M., S. N. SANTILLANA, C. A. RINALDI. 1998. Stratigraphy of the La Meseta Formation (Eocene), Marambio (Seymour) Island, Antarctica, p. 137–146. In Paleógeno de América del Sur y de la Península Antártica. Asociación Paleontológica Argentina, Publicación Especial, 5.
- MCCOY, F. 1850. On some genera and species of Silurian Radiata in the collection of the University of Cambridge. Annals and Magazine of Natural History, 6:270–290.

- POREBSKI, S. J. 2000. Shelf-valley compound fill produced by fault subsidence and eustatic sea-level changes, Eocene La Meseta Formation, Seymour Island, Antarctica. *Geology*, 28:147–150.
- PUCHALSKI, S. S., D. J. EERNISSE, AND C. C. JOHNSON. 2008. The effect of sampling bias on the fossil record of chitons (Mollusca, Polyplacophora). *American Malacological Bulletin*, 25:87–95.
- SADLER, P. M. 1988. Geometry and stratification of uppermost Cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula, p. 489–498. *In* R. M. Feldmann and M. O. Woodburne (eds.), *Geology and Paleontology of Seymour Island, Antarctic Peninsula*. Geological Society of America Memoir, 169.
- SCHWABE, E. 2008. A summary of reports of abyssal and hadal Monoplacophora and Polyplacophora (Mollusca). *Zootaxa*, 1866: 205–222.
- SCHWABE, E., G. FÖRSTERRA, V. HÄUSSERMANN, R. R. MELZER, AND M. SCHRÖDL. 2006. Chitons (Mollusca: Polyplacophora) from the southern Chilean Comau Fjord, with reinstatement of *Tonicia calbucensis* Plate, 1897. *Zootaxa*, 1341:1–27.
- SCHWABE, E. AND J. SELLANES. 2010. Revision of Chilean bathyal chitons (Mollusca: Polyplacophora) associated with cold-seeps, including description of a new species of *Leptochiton* (*Leptochitonidae*). *Organisms Diversity and Evolution*, 10:31–55.
- SIRENKO, B. 2006a. New outlook on the system of chitons (Mollusca: Polyplacophora). *Venus*, 65:27–49.
- SIRENKO, B. 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.
- SQUIRES, R. L. AND J. L. GOEDERT. 1995. An extant species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene and Oligocene Cold-Seep limestones, Olympic Peninsula, Washington. *The Veliger*, 38:47–53.
- STILWELL, J. D. AND W. J. ZINSMEISTER. 1992. Molluscan Systematics and Biostratigraphy, Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. *American Geophysical Union, Antarctic Research Series* 55, 192 p.
- STRACK, H. L. 2003. *Leptochiton denhartogi*, a new species of Polyplacophora (Mollusca) from Angola. *Journal Zoologische Verhandelingen*, 345:409–412.
- WRENN, J. H. AND G. F. HART. 1988. Paleogene dinoflagellated cyst biostratigraphy of Seymour Island, Antarctica, p. 321–447. *In* R. M. Feldmann and M. O. Woodburne (eds.), *Geology and Paleontology of Seymour Island, Antarctic Peninsula*. Geological Society of America Memoir, 169.

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