

Borers and encrusters as indicators of the presence of hermit crabs in Antarctic Eocene gastropods shells

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Abstract: The community of encrusting and boring organisms developed on shells of the gastropod *Antarctodarwinella ellioti* from the lower section of the La Meseta Formation (Eocene) exposed on Seymour (Marambio) Island, Antarctic Peninsula, allows inference that the shells were inhabited by hermit crabs. A Chi-square Independence Test revealed that the community - dominated by polychaetes and bryozoans - shows preference for the aperture interior area of the shell. A subsequent Cochran Q Test indicated that the differences in frequency of encrusting and boring organisms as counted on the different interior sectors of the aperture were statistically significant. Thus, polychaetes, boring bryozoans, and encrusting bryozoans, do not show the same frequency in each interior sector of the aperture; they are more frequent on the columella ($P < 0.0001$, $P < 0.01$ and $P < 0.001$ respectively). Encrusting bryozoans also appear to show a preference - albeit not as high as on the columella - for the outer lip. This community of boring and encrusting organisms and their distribution on the shell confirms that the shells were inhabited by hermit crabs. The community is similar to that described in Recent hermitted shells from mid-latitude temperate water environments, suggesting that such communities were already established in the Eocene.

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Introduction

Eocene rocks from Seymour (Marambio) Island, at the northern tip of the Antarctic Peninsula (Fig. 1), contain a record of remarkable mollusc shell concentrations representing ecosystems with no Recent parallels, as they developed in a relatively warm (c. 14°C) shallow sea in a sunlight/darkness-stressed setting. Detailed study of fossil organisms as pointed out by Buick & Ivany (2004), from environments no longer extant is necessary if we are to understand the nature and degree of environmental control on their life history.

In this paper we describe and analyse the association of encrusting and boring organisms developed on the hermitted shells of the gastropod *Antarctodarwinella ellioti* Zinsmeister, 1976, from the lower section of the La Meseta Formation exposed along the northern tip of Seymour Island (Fig. 1). Hermitted will be used instead of hermit crab-occupied shell (after Vermeij 1978). The age of the rocks bearing the fossil fauna considered is Eocene, c. 52 Ma (Dutton *et al.* 2002).

Antarctodarwinella ellioti belongs in the Struthiolariidae (Fischer, 1884), a family of gastropods that evolved exclusively in the Southern Hemisphere since the Late Cretaceous. Modern representatives of this family still inhabit shelf environments in the circum-Antarctic realm. It is represented there by the genera *Struthiolaria* Lamarck,

1816, *Pelicaria* Gray, 1847, *Tylospira* Harris, 1897 and *Perissodonta* Martens, 1878. The Recent *Struthiolaria papulosa* (Martyn, 1784), *Pelicaria vermis* (Martyn, 1784), and *Tylospira scutulata* (Martyn, 1784) live in clean sandy environments in shallow to outer shelf marine settings. Being soft-bottom dwellers, most of these gastropods live generally buried in the sediment. They may be either deposit feeders, drawing their food directly from the substrate or else suspension-feeders, in which case they maintain the tips of their siphons above the sediment/water interface.

Encrusting and boring organisms are significant components of marine communities, interacting in different ways with either live or dead host substrates. They have proven to be useful tools in the understanding of the life habits and/or post-mortem histories of their hosts (Bottjer 1982, Bordeaux & Brett 1990, Bien *et al.* 1999, Taylor & Wilson 2003, Parras & Casadio 2006).

The community of encrusting and boring organisms dominated by polychaetes and bryozoans recorded on the studied specimens of *Antarctodarwinella ellioti* - and their distribution on the shells - allow us to infer that they were occupied by hermit crabs.

Hermit crabs are a very specialized group with a wide geographic distribution. They put back into circulation empty gastropod shells that would otherwise likely be

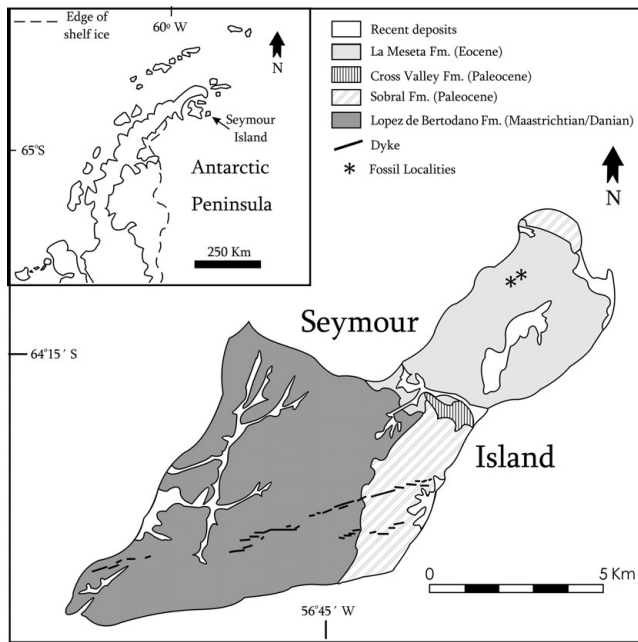


Fig. 1. Map showing study localities.

buried in the sediments (Walker 1989, Gutiérrez *et al.* 2003). Hermit crab assemblages can be considered examples of facilitation (Bruno *et al.* 2003) in which crabs extend the range of associated species through positive interactions (Reiss *et al.* 2003, Bell 2005). Over 180 Recent hermit crab species act as host for at least 550 invertebrate species, representing 16 phyla (Williams & McDermott 2004). Hermit crabs benefit from some symbionts, particularly bryozoans and hydractinians, through extension of shell apertures and by providing shelter from predators (Taylor *et al.* 1989, Olivero & Aguirre-Urreta 1994, Taylor 1994, Taylor & Schindler 2004). However, hermit crabs are also negatively impacted (e.g. reduction of reproductive success) by several symbionts (Buckley & Ebersole 1994, Williams 2000, 2002, McDermott 2001). Hermit crabs are common members of high-energy, shallow marine faunas (Hazlett 1981, Williams & McDermott 2004). They have been recorded in rocks as old as Lower Jurassic (Glaessner 1969) but their fossil record is poor and generally restricted to isolated claws. In contrast, indirect evidences of the presence of hermit crabs are abundant from the Middle Jurassic onwards (Walker 1992). Among the most important evidence used to recognize hermitted shells is the type and distribution of encrusting and boring organisms on their surface. In such shells, these organisms tend to colonize preferably the aperture periphery, apertural notch, callus, columella and the interior whorls of the shell. Boring or encrusting organisms that settle on these areas are mainly suspension-feeders that benefit from the water currents produced by the hermit crabs (Williams & McDermott 2004). However, the outer surface is colonized also (Walker 1988, 1998). Presumably colonization of the

outer shell surface is equally probable in hermitted epifaunal and infaunal gastropod shells. However, only those infaunal gastropod shells that are occupied by hermit crabs will show colonization of the outer surface as such surfaces are not available to bionts when the gastropod is alive.

The hermit crab record in Antarctica is poor and restricted to the Upper Cretaceous on Snow Hill and James Ross islands (Aguirre-Urreta & Olivero 1992, Olivero & Aguirre-Urreta 1994).

Geological setting

The La Meseta Formation (Elliot & Trautman 1982) is a clastic sedimentary unit exposed in the northern third of Seymour (Marambio) Island and in a small area of Cockburn Island. It takes its name from the plateau lying at the northern end of Seymour Island, where the 720 m type section of this unit is exposed. The La Meseta Formation unconformably overlies the López de Bertodano (Upper Cretaceous), Sobral (Palaeocene), and Cross Valley (Palaeocene) formations. It is unconformably overlain by late Cenozoic glacial beds.

The La Meseta Formation represents the upper part of the filling of a retroarc basin named the James Ross Basin by del Valle *et al.* (1992). It contains an abundant and well-preserved fauna of marine invertebrates and vertebrates, as well as terrestrial vertebrates and plants. The fossil content is a unique temporal window that allows the study of evolutionary and palaeobiogeographic events taking place during the early Palaeogene in the high latitudes of the Southern Hemisphere. The excellently preserved fossils occur mainly in remarkable accumulations dominated by mollusc shells. Such a unique fossil fauna was subject of numerous systematic studies (e.g. Wilckens 1910, Zinsmeister & Camacho 1982, Woodburne & Zinsmeister 1982, Feldmann & Woodburne 1988, Stilwell & Zinsmeister 1992, Radwańska 1996, Bitner 1996a, Goin *et al.* 1999, Casadio *et al.* 2001, Hara 2001). However, very few studies deal with the nature and origin of the shell concentrations from taphonomic and palaeoecologic perspectives (Zinsmeister 1987, Vizcaíno *et al.* 1998). Consequently, issues such as the taphonomic evolution biases of these concentrations remain virtually unknown.

Based on its fossil content, the La Meseta Formation was referred to the Lower Eocene–Upper Eocene or even Lower Oligocene by Stilwell & Zinsmeister (1992). Isotopic data suggest an Eocene age of *c.* 52 Ma (Dutton *et al.* 2002) for the lower part of the section. Elliot & Trautman (1982) interpreted this formation as a tide-influenced delta system in which they recognized a lower section attributed to a prodelta, a middle section representing the delta front and an upper part probably characterizing a subtidal delta platform. Pezzetti (1987) proposed a tidal-dominated delta as the origin of this formation, yet noted that only

delta-front deposits could be recognized. Doktor *et al.* (1988) suggested that the La Meseta Formation represented the progradation of a shallow marine environment, restricted by bars or barriers, under wave and tidal influence. Sadler (1988) recognized the lens geometry of this unit, and he proposed that such internal lens structure together with the sedimentologic setting could correspond to lagoon and barrier environments. Marensi (1995) and Marensi *et al.* (1998a, 1998b) concluded that the La Meseta Formation represented an incised valley system, where sedimentation took place in deltaic, estuarine and wave-influenced tidal-shelf environments. Porębski (2000) suggested that the La Meseta Formation represented a shelf valley-fill sequence, its development mainly governed by local subsidence along fault-controlled valley margins.

The overall depositional setting ranged from a prograding delta front to a storm-influenced sub aqueous delta plain dominated by tides after marine-flooding within an incised valley (Marensi 1995, Marensi *et al.* 1998a).

The studied samples come from the lower section of the La Meseta Formation (Fig. 2). These beds are included in the middle part of the T3 (Sadler 1988) or in the upper part of the Acantilados Allomember (Marensi *et al.* 1998b). This part of the succession is characterized by intercalated biogenic and sedimentologic concentrations where the brackish bivalve, *Eurhomalea* Cossmann, 1920, is dominant. Also present, but in greatly reduced numbers are other bivalves, gastropods and brachiopods. Biogenic concentrations consist of several dispersed to densely-packed and poorly-sorted lenses with fine sandstone matrix, ranging from 1 to 1.4 m thick, with sharp planar or undulating bottoms and sharp undulating tops. Most of the bivalves are articulated, many as the so-called “butterflied” bivalves. Fragmentation, abrasion, encrustation, and bioerosion are low. Bioturbated beds are common and consist of small-diameter (<2 mm) tubes perpendicular or inclined to stratification. These concentrations are interpreted as having formed in a delta plain environment during brief episodes of benthic colonization. Fossils are intercalated with sedimentologic concentrations formed by densely-packed to dispersed lens or beds, between 0.05 and 1.10 m thick, with fine to medium sandstone matrix and trough cross-stratification. Lithic clasts (up to 0.4 m), intraclasts (up to 0.5 m), concretions (between 0.05 and 0.2 m), and preserved burrows of the underlying beds are frequent. They are well- to poorly-sorted, and even bimodal (one mode represented by *Eurhomalea* spp. measuring 30 to 50 mm long, and the other one by juvenile veneroids and gastropods, all smaller than 5 mm long). The bottom and top surfaces are sharply undulose, and the bottom one is also sometimes bioturbated. Most of the bivalves are disarticulated, concordant or in chaotic position, sometimes arranged in stacking pattern. Fragmentation is low in some specimens to high in others; abrasion, encrustation and bioerosion are low. *Eurhomalea* species are all infaunal;

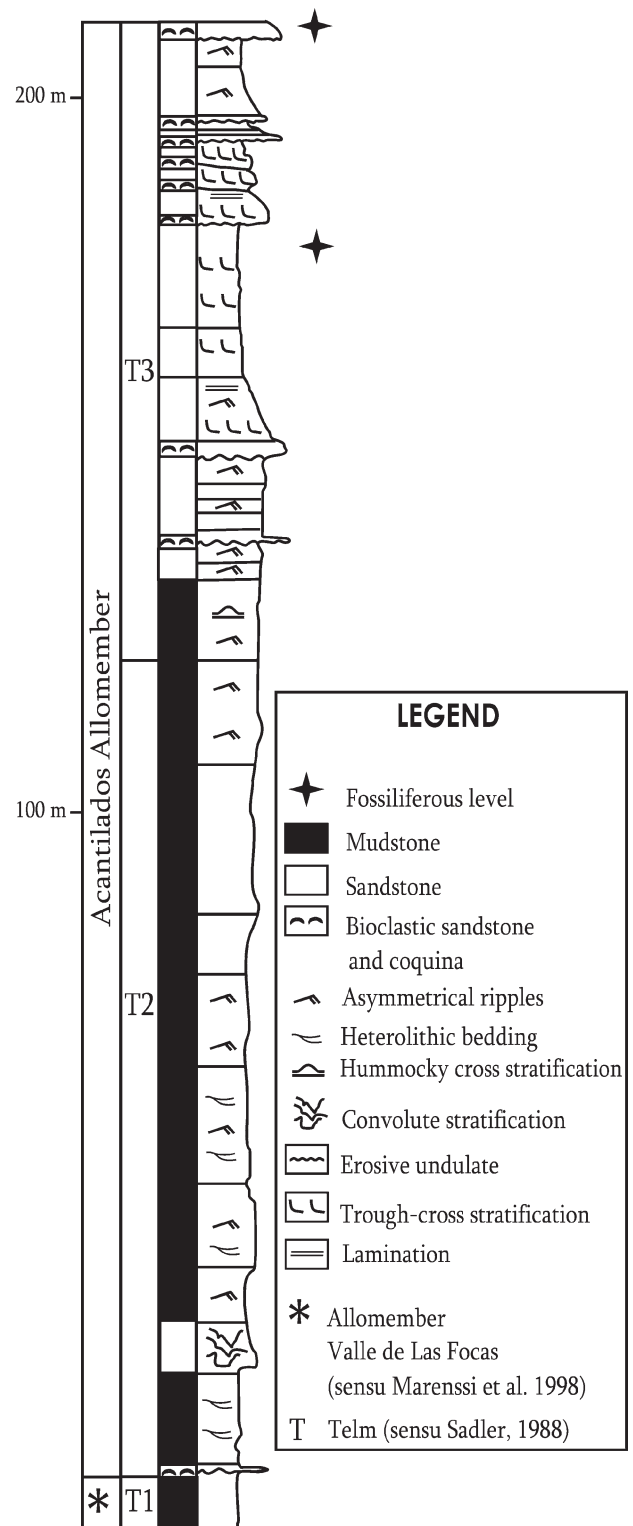


Fig. 2. Stratigraphic section of the La Meseta Formation showing the beds containing *Antarctodarwinella ellioti*.

thus some centimetres of sediment should have undergone erosion before the shells were finally deposited. The high proportion of disarticulated valves suggests that most

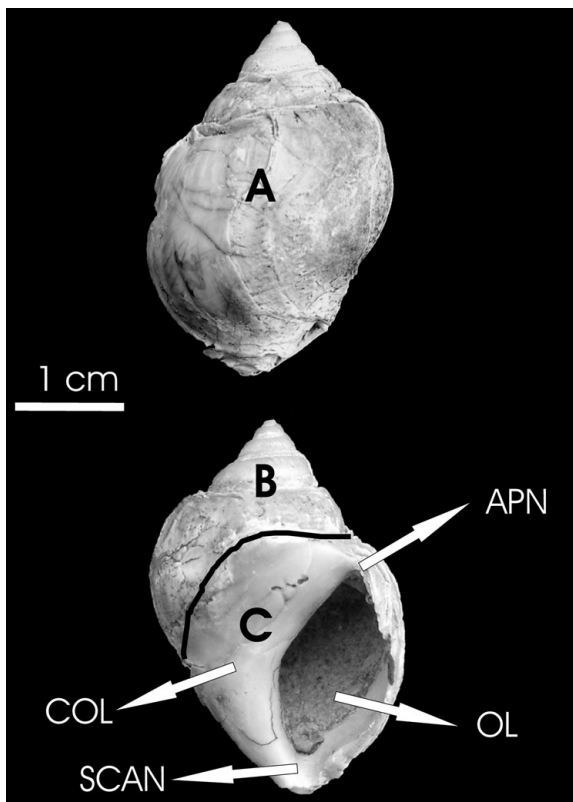


Fig. 3. Shell sectors on *Antarctodarwinella ellioti*. A = spire and abapertural exterior of last whorl, B = spire and adapertural exterior of last whorl, C = aperture interior. Aperture interior sectors: columella (COL), siphonal canal (SCAN), outer lip (OL) and apertural notch (APN).

individuals were dead at the time of exhumation. Furthermore, the scarcity of shell fragments suggests a single brief event of exhumation and exposure on the seafloor, as these large but thin and relatively fragile shells break easily. The distinctive stacking pattern and imbrications of disarticulated valves indicates highly turbulent conditions. Except for *Antarctodarwinella ellioti*, all invertebrate remains show few post-mortem borers and encrusters. This suggests minimal exposure time on the sea floor after exhumation. These concentrations are interpreted as composite or multiple-event concentrations deposited by tidal channels in a tidal-dominated sub aqueous delta plain.

Materials and methods

Thirty-three specimens of *Antarctodarwinella ellioti* were collected from two localities, 64°13'40"S, 56°39'05"W and 64°13'34"S, 56°38'56"W (Fig. 1), most from biogenic concentrations. Specimens were analysed under a binocular microscope and the kind and location of encrusters and borers was recorded for each one.

The number and percentage of specimens bored or encrusted by different organisms was calculated. To test

the hypothesis that a correlation exists between the sector of the shell considered and the presence/absence of the different encrusting/boring taxa - i.e. that there was preferential colonization - we defined three sectors reflecting distinct morphological features of the shells (Fig. 3). Sectors and percentage were: A = spire and abapertural exterior of last whorl (50%), B = spire and adapertural exterior of last whorl (25%), C = aperture interior (25%).

The presence of boring and encrusting organisms in each sector was recorded, and the frequency of shells with different taxa of encrusting or boring organisms was determined for each sector. Contingency tables were performed and a Chi-square Independence Test was used to ascertain whether or not these frequencies were non-randomly distributed among sectors. Methodological restrictions of the Chi-square Independence Test requires that all expected frequencies be 1 or greater and at most 20% of them be less than 5. Therefore, we performed this test using only the taxa that met these assumptions.

Because some of the boring or encrusting organisms showed preferential placement or at least high frequencies on area C, we divided this area into four sectors (Fig. 3): columella (COL), siphonal canal (SCAN), outer lip (OL) and apertural notch (APN). To test the hypothesis that the frequency of each of the boring/encrusting taxa is the same for each sector, we recorded the presence of boring and encrusting organisms in each sector, and subsequently performed a Cochran Q Test. Software packages used for statistical analyses and graphics were Excel XP and STATISTICA, version 99.

All specimens are housed at the Departamento de Ciencias Naturales, Universidad Nacional de La Pampa (GHUNLPam), Santa Rosa, La Pampa, Argentina, under numbers GHUNLPam 25205–25237.

Results

The fauna of encrusting and boring organisms recorded in the shells of *Antarctodarwinella ellioti* includes polychaetes, bryozoans, balanids, algae, and phoronids? (Table I and Fig. 4). Each case is described and discussed below and the distribution of each particular encruster/borer is also discussed.

Encrusting organisms - polychaetes

The first reference recording *Spirorbis* Daudin, 1800 in the La Meseta Formation was by Wiedman & Feldmann (1988). These authors described material attached primarily to other larger calcareous tube hosts collected from the top beds of this lithostratigraphic unit (Telm 7 *sensu* Sadler 1988). Bitner (1996b) later recorded *Spirorbis* encrusting brachiopods from different beds of the La Meseta Formation. Specimens referred to *Spirorbis* sp. and

Table I. Presence/absence of boring and encrusting organisms in each sector of the shell.

		No specimen (GHUNLPam)			25205			25206			25207			25208			25209			25210			25211			25212			25213			25214			25215		
Shell sector		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Encrusting organisms	Polychaetes	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
	<i>Leptichnus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0
	Bryozoans (organism)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Balanomorph	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Coralline algae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boring organisms	Polychaetes	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
	<i>Pinaceocladichnus</i>	1	1	1	0	0	0	1	1	1	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Talpina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		No specimen (GHUNLPam)			25216			25217			25218			25219			25220			25221			25222			25223			25224			25225			25226		
Shell sector		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Encrusting organisms	Polychaetes	0	0	1	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0
	<i>Leptichnus</i>	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Bryozoans (organism)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1
	Balanomorph	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Coralline algae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boring organisms	Polychaetes	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
	<i>Pinaceocladichnus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
	<i>Talpina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		No specimen (GHUNLPam)			25227			25228			25229			25230			25231			25232			25233			25234			25235			25236			25237		
Sector		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Encrusting organisms	Polychaetes	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
	<i>Leptichnus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	Bryozoans (organism)	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
	Balanomorph	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Coralline algae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boring organisms	Polychaetes	1	0	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0
	<i>Pinaceocladichnus</i>	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	1	0
	<i>Talpina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

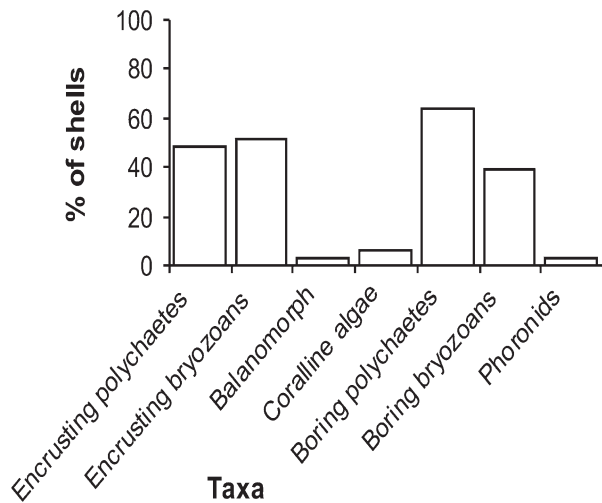


Fig. 4. Percentage of shells bored or encrusted by different organisms, $n = 33$.

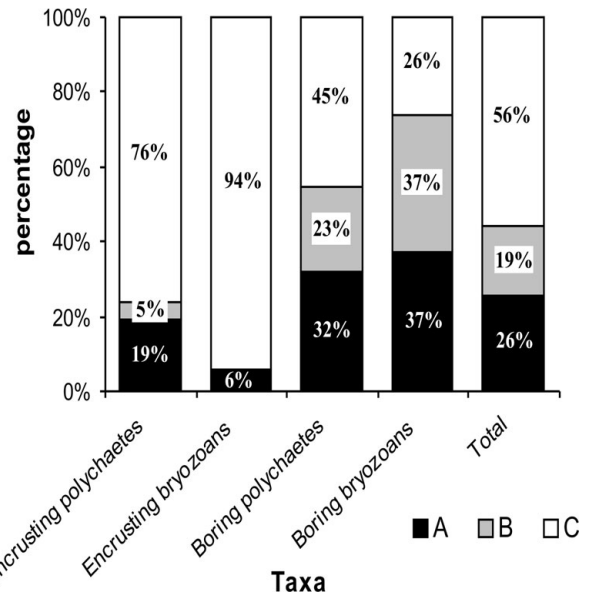


Fig. 6. Segmented bar graph showing the distributions of taxa according to shell sector.

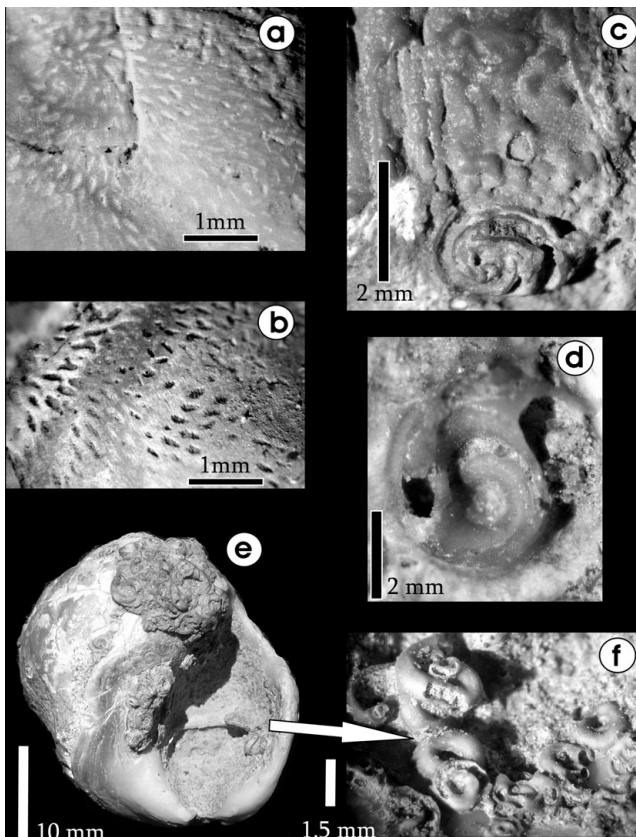


Fig. 5a. & b. *Leptichnus* isp. (GHUNLPam 25228), c. Coralline algae covering *Spirorbis* sp. (GHUNLPam 25205), d. & f. *Spirorbis* sp. (GHUNLPam 25205).

encrusting shells of *Antarctodarwinella ellioti* have a coiled calcareous tube, either evolute planispiral or trochoid, small (<0.2 cm diameter), with smooth outer and inner surfaces, with up to three whorls in the largest specimens, in which

each successive whorl is larger than the previous whorl (Fig. 5d–f). Some specimens of *Antarctodarwinella ellioti* (GHUNLPam 25214, 25217, 25218, 25219, 25222, 25224, 25227, 25228, 25236) record mutual overgrowth of *Spirorbis* sp. and cheilostome bryozoans. In such cases, instead of acquiring their typically spiral shape, polychaetes elevate their apertures away from the encroaching zooids. A similar behaviour was described by Lescinsky (1997) for Carboniferous “spirorbids” and by Stebbing (1973) for Recent spirorbids growing adjacent to bryozoan colonies.

Studies of settlement patterns of encrusting communities on extant marine species revealed that *Spirorbis* is the first in the succession (Chalmer 1982, Keough 1983, Walker & Carlton 1995). Ryland & Sykes (1972) found a positive correlation between the abundances of spirorbids and bryozoans in Recent encrusting communities. Taylor (1979) observed a similar correlation in middle Jurassic communities, as he described interspecific overgrowth of *Spirorbis* and several bryozoans taxa.

Numerous studies were published on the *Spirorbis* larval settlement behaviour and metamorphosis (Dirnberger 1990, Hamer & Walker 2001). Larvae of most species prefer settlement areas with poor illumination (Al-Ogily 1985). In the White Sea, *S. spirorbis* (Linnaeus, 1758) is present between 1 and 20 m deep and is affected by significant fluctuations of salinity and temperature (Ushakova 2003).

Spirorbid polychaetes are frequent inhabitants of hermitted shells (Williams & McDermott 2004). The most commonly colonized areas of the shells are the apertural notch, inner and outer lip, siphonal canal, and umbilicus (Walker 1992, Walker & Carlton 1995).

Table II. Contingency table of the shell sector and respective borers and encrusters for 33 randomly selected *Antarctodarwinella ellioti* specimens. Expected frequencies printed below observed frequencies, in brackets. χ^2 and *p* values with 6 df.

	Encrusting Polychaetes	Encrusting Bryozoans	Boring Polychaetes	Boring Bryozoans	Total
A	4 (5)	1 (5)	10 (8)	10 (7)	25
B	1 (4)	0 (3)	7 (6)	10 (5)	18
C	16 (12)	17 (10)	14 (17)	7 (15)	54
Total	21	18	31	27	97

$\chi^2 = 27.15$ *P* value = 0.000136

Spirorbis sp. occurs in 48% of the sampled specimens of *Antarctodarwinella ellioti* (Fig. 4) and shows a closer association (76%) with sector C of the shell (Fig. 6). Comparing observed and expected frequencies (Table II) of *Spirorbis* on this sector of the shell reveals that *Spirorbis* shows higher observed frequencies than expected, suggesting a preference for the aperture interior of the shell. However, *Spirorbis* showed the same frequency on all the sectors of the aperture (Table III). Walker (1992) reported a similar pattern in Recent hermitted shells from Mexico and northern California.

Encrusting organisms - bryozoans

Among the organisms living associated with hermit crabs, bryozoans are the best known. Many of them are multilayered, forming monticules, overgrowth of the gastropod shell aperture, and outward growth from the shell surface (Taylor 1994). However, not all bryozoans associated with hermit crabs form such a thick and conspicuous crust, as small multiserial encrusting colonies may also occur (Williams & McDermott 2004).

Encrusting bryozoans usually occur in the apertural notch, siphonal canal, and outer lip area of the shell (Walker 1992). On living hermitted shells their preferred settlement location may be limited to the aperture side for a variety of reasons, such as less susceptibility to dehydration, and competition between encrusting species (Walker 1992).

Encrusting cheilostome bryozoans on the studied shells of *Antarctodarwinella ellioti* are very poorly preserved and, in general, they are only revealed by small pits on the gastropod shell. This trace fossil is assigned to *Leptichnus* isp. and consists of pits that are sub-circular in cross section and are found in multiserial arrangements (Fig. 5a & b).

The oldest described *Leptichnus* is from the Upper Cretaceous, but the ichnogenus only became common during the Cenozoic. At least nine modern cheilostome taxa produce this trace (Taylor *et al.* 1999).

Cheilostome bryozoans (*Leptichnus* isp. or the organism itself) are the most abundant encrusting organisms on *Antarctodarwinella ellioti*. They are present on 52% of the gastropod shells (Fig. 4), and show a close association with sector C (94% of specimens) of the shell (Fig. 6).

Observed frequencies are higher than expected in this sector (Table II), suggesting a preference for the aperture interior of the shell. However, its greater abundance in this sector could also be explained if the interior acted as “taphonomic refuges”. When found in area C, they show highest frequencies on the columella and on the outer lip ($P < 0.001$) (Table III).

Encrusting organisms - balanomorph Cirripedia

Encrusting barnacles are present on hermitted shells in modern habitats but only two appear to be truly commensal (Williams & McDermott 2004). They are not frequent on similar shells in the fossil record. They occur on the external shell surface and sometimes near the apertural notch (Walker 1992, Fernandez-Leborans & Gabilondo 2006).

Two species of balanomorph barnacles were identified from the La Meseta Formation (Zullo *et al.* 1988). Amongst the studied specimens of *Antarctodarwinella ellioti*, only one carries barnacles (GHUNLPam 25219). These are completely re-crystallized and thus impossible to identify further. They are small, with a maximum diameter of 0.4 mm, and occur in areas A and C. One specimen was recorded from the aperture notch of area C.

Encrusting organisms - coralline algae

A few specimens of *Antarctodarwinella ellioti* (6%, Fig. 4) show non-geniculate coralline algae with crusts only a few microns thick. Crusts show cylindrical to compressed, non-branching protuberances less than 300 μm high (Fig. 5c). Their growth form falls within the “warty” type of Woelkerling *et al.* (1993).

Encrusting coralline algae are mainly restricted to normal marine water and are known to range from intertidal environments down to a depth of 250 m. However, the most common range in temperate-water environments is *c.* 20–40 m.

Boring organisms - polychaetes

Polydorids commonly inhabit gastropods shells, mainly in shells occupied by hermit crabs (Boekschoten 1966, 1967,

Table III. Presence/absence of boring and encrusting organisms in each sector of the aperture interior. Cochran Q test γ^2 and p values with 3 df.

No specimen (GHUNLPam)		25205				25206				25207				25208				25209				25210				25211							
Aperture sector		COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN				
Encrusting organisms	Polychaetes	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	Bryozoans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Boring organisms	Polychaetes	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Bryozoans	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No specimen (GHUNLPam)		25212				25213				25214				25215				25216				25217				25218							
Aperture sector		COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN
Encrusting organisms	Polychaetes	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0
	Bryozoans	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0
Boring organisms	Polychaetes	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1
	Bryozoans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No specimen (GHUNLPam)		25219				25220				25221				25222				25223				25224				25225							
Aperture sector		COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN
Encrusting organisms	Polychaetes	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	Bryozoans	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Boring organisms	Polychaetes	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	Bryozoans	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No specimen (GHUNLPam)		25226				25227				25228				25229				25230				25231				25232							
Aperture sector		COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN
Encrusting organisms	Polychaetes	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
	Bryozoans	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boring organisms	Polychaetes	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	Bryozoans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Specimen no. (GHUNLPam)		25223				25234				252235				25236				25237				Q (χ^2)		p value									
Aperture sector		COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN	COL	OL	SCAN	APN												
Encrusting organisms	Polychaetes	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0.428	0.9343									
	Bryozoans	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	18.927	<0.001										
Boring organisms	Polychaetes	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	25.325	<0.0001										
	Bryozoans	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	12	<0.01										

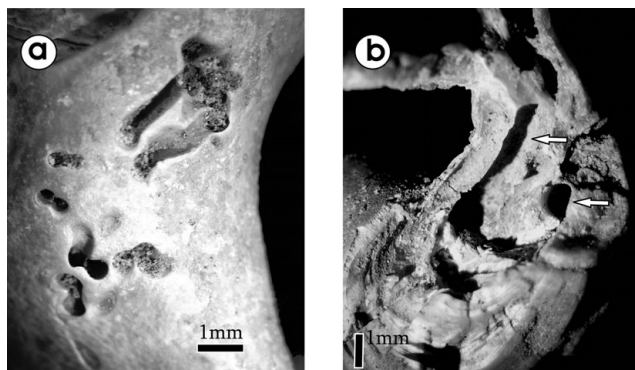


Fig. 7a. *Caulostrepsis* isp. (GHUNLPam 25228), **b.** Transverse section (GHUNLPam 25215) showing *Helicotaphrichnus* isp. (arrows).

Blake & Evans 1973, Walker 1988). They are commensals, feeding on materials captured by hosts or brought in through respiratory currents (Williams & McDermott 2004). According to Walker (1992), the most important feature suggesting that a shell was hermitted is the presence of the boring ichnogenus *Helicotaphrichnus* Kern, Grimmer & Lister, 1974. This boring is produced by spionids belonging to the genera *Polydora* Bosc, 1802 and *Dipolydora* Verrill, 1881. The boring produced by the extant *D. commensalis* (Andrews, 1891) is frequently associated with many species of hermit crabs and uniquely follows the columella of shells. According to Blake & Evans (1973) the spionid can only grow in hermitted shells and dies when the crab abandons the shell.

Helicotaphrichnus isp. and *Caulostrepsis* isp. (Fig. 7) are the most common boring ichnotaxa recorded and are present on 64% of the specimens of *Antarctodarwinella ellioti* (Fig. 4). Borings similar to those of *Caulostrepsis* isp. and *Helicotaphrichnus* isp. are produced by polychaetes of several families. *Polydora* is one of the better known extant boring Spionidae. The borings have a wall composed of mucus and fine sand particles. The infilling between the limbs consists of sand and detritus, cemented by mucus.

Polychaetes that bore in hermitted shells occur more frequently around the aperture, generally on the columella, apertural notch, and outer lip (Walker 1988, 1992, 1998). Blake & Evans (1973) and Kern *et al.* (1974) showed that boreholes produced on the columella by the spionid *Dipolydora commensalis* can be considered as the most important indicators of hermitted shells.

The boring polychaetes recorded in *Antarctodarwinella ellioti* show higher observed frequencies than expected in areas A and B (Table II). However, they are more abundant on area C, albeit not statistically significant. The frequency of polychaetes in area C is significantly higher on the columella than on other sectors of the interior aperture ($P < 0.0001$, Table III).

Boring organisms - bryozoans

Boring bryozoans included by Pohowsky (1978) in the Order Ctenostomata Busk, 1852, comprise a group of ethologically defined marine species whose members live immersed in mainly calcareous substrates, with the lophophores being the only exposed parts of the organism (Warme 1975). The substrates most frequently used by ctenostomes are gastropod and bivalve shells, although during the Palaeozoic they were colonizers of other organisms with calcareous parts, such as brachiopods and crinoids (Pohowsky 1978). Some taxa may show preference for a particular kind of shell. Several species inhabit live or dead mollusc shells. Silén (1947) pointed out that *Penetrantia concharum* Silén, 1946 inhabits only dead shells. It was suggested that larvae of this species avoid shells that still retain their periostracum (Pohowsky 1978). Information on the geographic range of living species of Ctenostomata is scanty and, according to Soule & Soule (1969), the known records are from latitudes lower than 64° for both hemispheres, and mainly from cold to warm temperate water.

Borings recorded on the shells of *Antarctodarwinella ellioti* and identified as ctenostomes consist of a regular system of tunnels and cavities. The tunnels are narrow, gently curved and branch off from a point in opposing directions at angles ranging from 20° to 40°. Primary openings are at the right or left side of the tunnels and are fusiform, tear-shaped or sub circular depending on the degree of wear. Their major axis attains a length of 0.25 mm and is aligned parallel to the tunnels. Cavities are placed in front of the bifurcation point and can be connected to each other by means of secondary subordinate tunnels (Fig. 8a–f). This trace is similar to borings produced by *Terebripora* d'Orbigny, 1847 and is referred to the ichnogenus *Pinaceocladichnus*. Most of the colonies are juxtaposed, rendering identification of ancestrulae difficult. In addition, wear contributes also to hamper accurate identification.

Pinaceocladichnus isp. appears in 39% of the studied specimens of *Antarctodarwinella ellioti* (Fig. 4) and shows higher observed frequencies than expected in areas A and B (Table II). When on area C, it appears more frequently on the columella ($P < 0.01$). Walker (1992) stated that boring bryozoans have been occasionally used to infer hermitted shells in the fossil record, and that in this case they penetrate areas thought to be inaccessible on living snails, such as the callus and parts of the columella.

Boring organisms - phoronids?

Only 3% of the studied specimens of *Antarctodarwinella ellioti* (Fig. 4) carried traces characterized by networks of multiapertural cylindrical borings of constant diameter and circular cross-section, showing a regular pattern involving a side branch and openings at regular intervals. This trace is

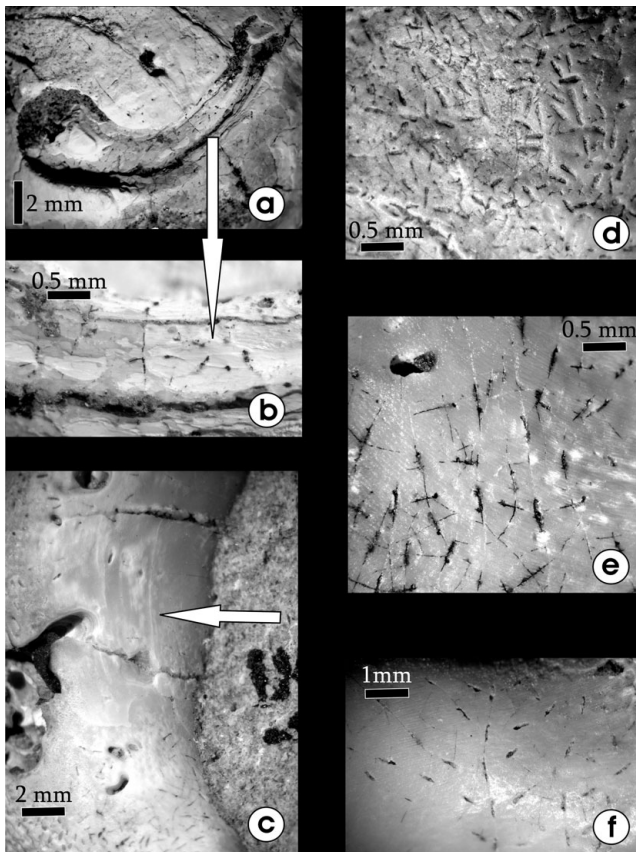


Fig. 8a. & b. *Pinaceocladichnus* isp. cutting through a polychaete boring (GHUNLPam 25207), **c.** Crab claw resting trace (arrow) delimited by *Pinaceocladichnus* isp. (GHUNLPam 25235), **d–f.** *Pinaceocladichnus* isp. (GHUNLPam 25235).

assigned to *Talpina* isp. According to Bromley (1994), *Talpina* is produced by phoronids. Casadio *et al.* (2001) documented the presence of this trace in shells of *Ostrea antarctica* Zinsmeister, 1984, from the lower part of the La Meseta Formation.

Diversity and community succession

Ninety four percent of the studied gastropod shells show at least one boring or encrusting organism. Most of the specimens of *Antarctodarwinella ellioti* (79%) show between 1 and 3 epizoans and/or ichnotaxa. Only 6% specimens show no boring or encrustation at all on their surface and 15% show the maximum diversity of 4 taxa (Fig. 9).

The segmented bar graph (Fig. 6) provides the conditional and marginal distributions of shell sectors for each one of the encrusters and borings. There is an association between some shell sectors and particular encrusters and borings. Thus, encrusting bryozoans and *Spirorbis* sp. have a closer association with sector C of the shell of *Antarctodarwinella ellioti* (94% and 76% respectively).

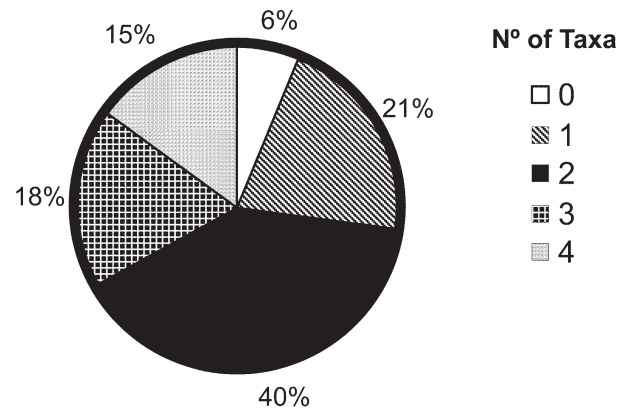


Fig. 9. Percentage of shells of *Antarctodarwinella* containing 0 to 4 encrusting and boring taxa.

The contingency table (Table II) shows that there is an association between shell sector and presence of borings and encrusters, i.e. certain parts of the shell were preferentially colonized ($P < 0.001$). Contrasting the observed and the expected frequencies, it is possible to establish that encrusting bryozoans and encrusting polychaetes (*Spirorbis* sp.) show higher observed frequencies than expected in sector C, suggesting a preference for the aperture interior of the shell. Boring polychaetes and boring bryozoans show higher observed frequencies than expected in areas A and B, although this difference in frequency is smaller than the previous one.

As some of the boring or encrusting organisms recorded on shells of *Antarctodarwinella ellioti* showed a clear preference (encrusting polychaetes and encrusting bryozoans) for or at least a higher frequency (boring polychaetes and boring bryozoans) in area C (aperture interior) - suggesting that the shells were hermitted - there also is an association between some of the aperture interior areas and particular encrusters and borers. Thus, boring polychaetes, boring bryozoans, and encrusting bryozoans, do not show the same frequency in each area of the aperture interior (Table III); they are more frequent on the columella ($P < 0.0001$, $P < 0.01$ and $P < 0.001$ respectively). The encrusting bryozoans also appear to show a preference - albeit not as high as on the columella - for the outer lip.

Recruitment of encrusting bryozoans and *Spirorbis* sp. was simultaneous, as mutual overgrowth was observed. Also observed were algae covering specimens of *Spirorbis* sp. Boring polychaetes were among the first to settle on the shells, as colonies of bryozoans were observed crossing through the eroded polychaete borings (Fig. 8a & b).

Conclusions

The identities and placement of encrusting and boring organisms, together with the inferred infaunal habit of

Antarctodarwinella ellioti, suggest that shell colonization began after the death of the gastropods.

A Chi-square Independence Test revealed that the community of encrusting and boring organisms recorded on *Antarctodarwinella ellioti* showed a clear preference for the aperture interior area of the shell. A subsequent Cochran Q Test indicated that the differences in frequency of encrusting and boring organisms as counted on the different aperture interior areas were statistically significant. Thus, boring polychaetes, boring bryozoans, and encrusting bryozoans are more frequent on the columella. Encrusting bryozoans also appear to show higher preference on the outer lip. This association of boring and encrusting organisms and their distribution on the shell support that the specimens of *Antarctodarwinella ellioti* were inhabited by hermit crabs.

The community of encrusting and boring organisms associated with shells of *Antarctodarwinella ellioti* is similar to those described in recent hermitted shells from temperate environments in mid-latitudes of the northern hemisphere (Stachowitsch 1980, Walker 1988, Walker & Carlton 1995). These similarities (predominance of spirorbids, spionids, and encrusting bryozoans) suggest that this type of community was already established in the Eocene. However, the Antarctic hermitted shells inhabited a temperate, shallow marine environment subject to long periods of darkness and low food availability, suggesting that one of the most important environmental factors conditioning the development of these communities was water temperature.

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References

- AGUIRRE-URRETA, M.B. & OLIVERO, E.B. 1992. A Cretaceous hermit crab from Antarctica: predatory activities and bryozoan symbiosis. *Antarctic Science*, **4**, 207–214.
- AL-OGILY, S.M. 1985. Further experiments on larval behaviour of the tubicolous polychaete *Spirorbis inornatus* L'Hardy & Quévrevreux. *Journal of Experimental Marine Biology and Ecology*, **86**, 285–298.
- BELL, J.J. 2005. Influence of occupant microhabitat on the composition of encrusting communities on gastropod shells. *Marine Biology*, **147**, 653–661.
- BIEN, W.F., WENDT, J.M. & ALEXANDER, R.R. 1999. Site selection and behavior of sponge and bivalve borers in shells of the Cretaceous oysters *Exogyra cancellata* and *Pycnodonte mutabilis* from Delaware, USA. *Historical Biology*, **13**, 299–315.
- BITNER, M.A. 1996a. Brachiopods from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula. In GAŹDZICKI, A., ed. *Palaeontological results of the Polish Antarctic Expeditions. Part II. Palaeontologia Polonica*, No. 55, 65–100.
- BITNER, M.A. 1996b. Encrusters and borers of brachiopods from the La Meseta Formation (Eocene), Seymour Island, Antarctica. *Polish Polar Research*, **17**, 21–28.
- BLAKE, J.A. & EVANS, J.W. 1973. *Polydora* and related genera: borers in mollusk shells and other calcareous substrates. *The Veliger*, **1**, 235–249.
- BOEKSCHOTEN, G.J. 1966. Shell borings of sessile epibiotic organisms as palaeoecological guides (with examples from the Dutch coast). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **2**, 333–379.
- BOEKSCHOTEN, G.J. 1967. Palaeoecology of some Mollusca from the Tielrode Sands (Pliocene, Belgium). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **3**, 311–362.
- BORDEAUX, Y.L. & BRETT, C.E. 1990. Substrate specific associations for paleoecology. *Historical Biology*, **4**, 221–224.
- BOTTJER, D.J. 1982. Paleoecology of epizoans and borings on some Upper Cretaceous chalk oysters from the Gulf Coast. *Lethaia*, **15**, 75–84.
- BROMLEY, R.G. 1994. The palaeoecology of bioerosion. In DONOVAN, S.K., ed. *The palaeobiology of trace fossils*. London: Belhaven Press, 134–154.
- BRUNO, J.F., STACHOWICZ, J.J. & BERTNESS, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, **18**, 119–125.
- BUCKLEY, W.J. & EBERSOLE, J.P. 1994. Symbiotic organisms increase the vulnerability of a hermit crab to predation. *Journal of Experimental Marine Biology and Ecology*, **182**, 49–64.
- BUICK, D.P. & IVANY, L.C. 2004. 100 years in the dark: extreme longevity of Eocene bivalves from Antarctica. *Geology*, **32**, 921–924.
- CASADÍO, S., MARENSSI, S. & SANTILLANA, S. 2001. Endolithic bioerosion traces attributed to boring bryozoans in the Eocene of Antarctica. *Ameghiniana*, **38**, 321–329.
- CHALMER, P.N. 1982. Settlement patterns of species in a marine fouling community and some mechanisms of succession. *Journal of Experimental Marine Biology and Ecology*, **58**, 73–85.
- DEL VALLE, R.A., ELLIOT, D.H. & MACDONALD, D.I.M. 1992. Sedimentary basins on the east flank of the Antarctic Peninsula: proposed nomenclature. *Antarctic Science*, **4**, 477–478.
- DIRNBERGER, J.M. 1990. Benthic determinants of settlement for planktonic larvae: availability of settlement sites for the tube-building polychaete *Spirorbis spirillum* (Linnaeus) settling onto seagrass blades. *Journal of Experimental Marine Biology and Ecology*, **140**, 89–105.
- DOKTOR, M., GAŹDZICKI, A., MARENSSI, S.A., PORĘBSKI, S.J., SANTILLANA, S.N. & VRBA, A.V. 1988. Argentine-Polish geological investigations on Seymour (Marambio) Island, Antarctica, 1988. *Polish Polar Research*, **9**, 521–541.
- DUTTON, A.L., LOHMANN, K.C. & ZINSMEISTER, W.J. 2002. Stable isotope and minor element proxies for Eocene climate of Seymour Island, Antarctica. *Paleoceanography*, **17**, 6.1–6.16.
- ELLIOT, D.H. & TRAUTMAN, T.A. 1982. Lower Tertiary strata on Seymour Island, Antarctic Peninsula. In CRADDOCK, C., ed. *Antarctic geoscience*. Madison, WI: University of Wisconsin Press, 287–297.
- FELDMANN, R.M. & WOODBURN, M.O., eds. 1988. *Geology and paleontology of Seymour Island Antarctic Peninsula*. Boulder, CO: Geological Society of America Memoirs, No. 169, 566 pp.
- FERNANDEZ-LEBORANS, G. & GABILONDO, R. 2006. Inter-annual variability of the epibiotic community on *Pagurus bernhardus* from Scotland. *Estuarine, Coastal and Shelf Science*, **66**, 35–54.
- GLAESSNER, M.F. 1969. Decapoda. In MOORE, R.C., ed. *Treatise on invertebrate paleontology. Part R, Arthropoda 4*. Lawrence, KS: University of Kansas Printing Service, R400–R651.
- GOIN, F.J., CASE, J.A., WOODBURN, M.O., VIZCAINO, S.F. & REGUERO, M.A. 1999. New discoveries of “opossum-like” marsupials from Antarctica (Seymour Island, Middle Eocene). *Journal of Mammalian Evolution*, **6**, 335–364.
- GUTIÉRREZ, J.L., JONES, C.G., STRAYER, D.L. & IRIBARNE, O.O. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos*, **101**, 79–90.

- HAMER, J. & WALKER, G. 2001. Avoidance of dried biofilms on slate and alga surfaces by certain spirorbis and bryozoan larvae. *Journal of Marine Biological Association of the United Kingdom*, **81**, 167–168.
- HARA, H. 2001. Bryozoans from the Eocene of Seymour Island, Antarctic Peninsula. In GAŹDZICKI, A., ed. *Palaeontological Results of the Polish Antarctic Expeditions. Part III. Palaeontologia Polonica*, **60**, 33–156.
- HAZLETT, B.A. 1981. The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics*, **12**, 1–22.
- KEOUGH, M.J. 1983. Patterns of recruitment of sessile invertebrates in two subtidal habitats. *Journal of Experimental Marine Biology and Ecology*, **66**, 213–245.
- KERN, J.P., GRIMMER, J.C. & LISTER, K.H. 1974. A new fossil spionid tube, Pliocene and Pleistocene of California and Baja California. *Journal of Paleontology*, **48**, 978–982.
- LESCINSKY, H.L. 1997. Epibiotic communities: recruitment and competition on North American Carboniferous brachiopods. *Journal of Paleontology*, **71**, 34–52.
- MARENSSI, S.A. 1995. *Sedimentología y paleoambientes de sedimentación de la Formación La Meseta, isla Marambio, Antártida*. PhD thesis, Universidad de Buenos Aires, 402 pp. [Unpublished].
- MARENSSI, S.A., SANTILLANA, S.N. & RINALDI, C.A. 1998a. Paleoambientes sedimentarios de la Aloformación La Meseta (Eoceno), isla Marambio (Seymour), Antártida. *Contribuciones del Instituto Antártico Argentino*, **464**, 1–51.
- MARENSSI, S.A., SANTILLANA, S.N. & RINALDI, C.A. 1998b. Stratigraphy of the La Meseta Formation (Eocene), Marambio Island, Antarctica. In CASADIO, S., ed. *Paleógeno de América del Sur y de la Península Antártica*. Buenos Aires: Asociación Paleontológica Argentina, Publicación Especial 5, 137–146.
- MCDERMOTT, J.J. 2001. Symbionts of the hermit crab *Pagurus longicarpus* Say, 1817 (Decapoda: Anomura): New observations from New Jersey waters and a review of all known relationships. *Proceedings of the Biological Society of Washington*, **114**, 624–639.
- OLIVERO, E.B. & AGUIRRE-URRETA, M.B. 1994. A new tube-builder hydractinian, symbiotic with hermit crabs, from the Cretaceous of Antarctica. *Journal of Paleontology*, **68**, 1169–1182.
- PARRAS, A. & CASADIO, S. 2006. The oyster *Crassostrea? hatcheri* (Ortmann, 1897), a physical ecosystem engineer from the upper Oligocene–lower Miocene of Patagonia, southern Argentina. *Palaio*, **21**, 168–186.
- PEZZETTI, T.F., 1987. *The sedimentology and provenance of the Eocene La Meseta Formation, Seymour Island, Antarctica*. MSc thesis, Ohio State University, 165 pp. [Unpublished].
- POHOWSKY, R.A. 1978. The boring ctenostomate bryozoa: taxonomy and paleobiology based on cavities in calcareous substrata. *Bulletins of American Paleontology*, **73**, 1–193.
- PORĘBSKI, 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.
- RADWAŃSKA, U. 1996. A new echinoid from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula. In GAŹDZICKI, A., ed. *Palaeontological results of the Polish Antarctic Expeditions. Part II. Palaeontologia Polonica* **55**, 117–126.
- REISS, H., KNÄUPER, S. & KRÖNCKE, I. 2003. Invertebrate associations with gastropod shells inhabited by *Pagurus bernhardus* (Paguridae) secondary hard substrate increasing biodiversity in North Sea soft-bottom communities. *Sarsia*, **88**, 404–415.
- RYLAND, J.S. & SYKES, A.M. 1972. The analysis of pattern in communities of bryozoa. I. Discrete sampling methods. *Journal of Experimental Marine Biology and Ecology*, **8**, 277–297.
- SADLER, P.M. 1988. Geometry and stratification of uppermost Cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula. In FELDMANN, R.M. & WOODBURNE, M.O., eds. *Geology and paleontology of Seymour Island Antarctic Peninsula. Memoir of the Geological Society of America*, No. 169, 303–320.
- SILÉN, L. 1947. On the anatomy and biology of Penetrantiidae and Immergentiidae (Bryozoa). *Arkiv för Zoologie*, **40**, 1–48.
- SOULE, J.D. & SOULE, D.F. 1969. Systematics and biogeography of burrowing bryozoans. *American Zoologist*, **9**, 791–802.
- STACHOWITSCH, M. 1980. The epibiotic and endolithic species associated with the gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*. *Marine Ecology Pubblicazioni della Stazione Zoologica di Napoli*, **1**, 73–104.
- STEBBING, A.R.D. 1973. Observation on colony overgrowth and spatial competition. In LARWOOD, G.P., ed. *Living and fossil Bryozoa*. London: Academic Press, 173–183.
- STILWELL, J.D. & ZINSMEISTER, W.J. 1992. Molluscan systematics and biostratigraphy, Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. *Antarctic Research Series*, **55**, 1–192.
- TAYLOR, P.D. 1979. Palaeoecology of the encrusting epifauna of some British Jurassic bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **28**, 241–262.
- TAYLOR, P.D. 1994. Evolutionary palaeoecology of symbioses between bryozoans and hermit crabs. *Historical Biology*, **9**, 157–205.
- TAYLOR, P.D. & SCHINDLER, K.S. 2004. A new Eocene species of the hermit-crab symbiont *Hippoporidra* (Bryozoa) from the Ocala Limestone of Florida. *Journal of Paleontology*, **78**, 790–794.
- TAYLOR, P.D. & WILSON, M.A. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews*, **62**, 1–103.
- TAYLOR, P.D., SCHEMBRI, P.J. & COOK, P.L. 1989. Symbiotic associations between hermit crabs and bryozoans from the Otago region, southeastern New Zealand. *Journal of Natural History*, **23**, 1059–1085.
- TAYLOR, P.D., WILSON, M.A. & BROMLEY, R.G. 1999. A new ichnogenus for etchings made by cheilostome bryozoans into calcareous substrates: *Palaeontology*, **42**, 595–604.
- USHAKOVA, O.O. 2003. Combined effect of salinity and temperature on *Spirorbis spirorbis* L. and *Circeus spirillum* L. larvae from the White Sea. *Journal of Experimental Marine Biology and Ecology*, **296**, 23–33.
- VERMEIJ, G.J. 1978. *Biogeography and adaptation: patterns of marine life*. Cambridge, MA: Harvard University Press, 332 pp.
- VIZCAINO, S.F., REGUERO, M.A., GOIN, F.J., TAMBUSI, C.P. & NORIEGA, J.I. 1998. Community structure of Eocene terrestrial vertebrates from Antarctic Peninsula. In CASADIO, S., ed. *Paleógeno de América del Sur y de la Península Antártica*. Buenos Aires: Asociación Paleontológica Argentina, Publicación Especial 5, 137–146.
- WALKER, S.E. 1988. Taphonomic significance of hermit crabs (Anomura: Paguridea): Epifaunal hermit crab - Infaunal gastropod example. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **63**, 45–71.
- WALKER, S.E. 1989. Hermit crabs as taphonomic agents. *Palaio*, **4**, 439–452.
- WALKER, S.E. 1992. Criteria for recognizing marine hermit crabs in the fossil record using gastropod shells. *Journal of Paleontology*, **66**, 535–558.
- WALKER, S.E. 1998. Endobionts on modern and fossil *Turritella* from the Northern Gulf of California Region. *Ichnos*, **6**, 99–115.
- WALKER, S.E. & CARLTON, J.T. 1995. Taphonomic losses become taphonomic gains: an experimental approach using the rocky shore gastropod, *Tegula funebris*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **114**, 197–217.
- WARME, J.E. 1975. Borings as trace fossils and the processes of marine bioerosion. In FREY, R.W., ed. *The study of trace fossils*. Berlin: Springer, 181–227.
- WIEDMAN, L.A. & FELDMANN, R.M. 1988. Ichnofossils, tubiform body fossils, and depositional environment of the La Meseta Formation (Eocene) of Antarctica. In FELDMANN, R.M., WOODBURNE, M.O., eds. *Geology and paleontology of Seymour Island Antarctic Peninsula. Memoir of the Geological Society of America*, No. 169, 531–539.
- WILCKENS, O. 1910. *Die Anneliden, Bivalven, und Gastropoden der antarktischen Kreideformation. Wissenschaftliche Ergebnisse der Schwedischen Südpolar-expedition, 1901–1903, unter der Leitung von Dr. Otto Nordenskjöld*. Stockholm: Stockholm Lithographisches Institut, **3**, 1–132.

- WILLIAMS, J.D. 2000. A new species of *Polydora* (Polychaeta: Spionidae) from the Indo–West Pacific and first record of host hermit crab egg predation by a commensal polydorid worm. *Zoological Journal of the Linnean Society*, **129**, 537–548.
- WILLIAMS, J.D. 2002. The ecology and feeding biology of two *Polydora* species (Polychaeta: Spionidae) found to ingest the embryos of host hermit crabs (Anomura: Decapoda) from the Philippines. *Journal of Zoology*, **257**, 339–351.
- WILLIAMS, J.D., McDERMOTT, J.J., 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. *Journal of Experimental Marine Biology and Ecology*, **305**, 1–128.
- WOELKERLING, W.J., IRVINE, L.M. & HARVEY, A.S. 1993. Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Australian Systematic Botany*, **6**, 277–293.
- WOODBURNE, M.O. & ZINSMEISTER, W.J. 1982. Fossil land mammal from Antarctica. *Science*, **21**, 284–286.
- ZINSMEISTER, W.J. 1987. Unusual nautilid occurrence in the upper Eocene La Meseta Formation, Seymour Island, Antarctica. *Journal of Paleontology*, **61**, 724–726.
- ZINSMEISTER, W.J. & CAMACHO, H.H. 1982. Late Eocene (to possibly earliest Oligocene) molluscan fauna of the La Meseta Formation of Seymour Island, Antarctic Peninsula. In CRADDOCK, C., ed. *Antarctic geoscience*. Madison, WI: University of Wisconsin Press, 299–304.
- ZULLO, V.A., FELDMANN, R.M. & WIEDMAN, L.A. 1988. Balanomorph Cirripedia from the Eocene La Meseta Formation, Seymour Island, Antarctica. In FELDMANN, R.M. & WOODBURNE, M.O., eds. *Geology and paleontology of Seymour Island, Antarctic Peninsula. Memoir of the Geological Society of America*, No. 169, 303–320.