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A Cretaceous hermit crab from Antarctica: predatory activities and bryozoan symbiosis

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Abstract: A hermit crab assigned to *Paguristes* sp. is described from James Ross Island, Antarctica. The fossil was obtained from the Gamma Member of the Santa Marta Formation of late Campanian age. The specimen is associated with an external mould of the gastropod *Taioma*, that was encrusted by a colony of ascophoran bryozoans. Another specimen of *Taioma* shows typical predatory marks in the outer lip that are attributed to the action of pagurids. It is concluded that the particular dwelling habits of the hermit crabs, their symbiosis with bryozoan, and their predatory activities were already established by the end of the Cretaceous.

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Key words: Antarctica, Cretaceous, Decapoda, Paguridae, hermit crabs, predation, symbiosis, palaeoenvironments

Introduction

The hermit pagurid crabs are a specialized group of decapod crustaceans commonly found around the world in near-shore, high energy environments. Perhaps reflecting the low potential of fossilization of these environments, their fossil record is scarce, especially in the Mesozoic (see Bishop 1983). Hermit crabs are known from the Jurassic (van Straelen 1925, Glaessner 1969), but their record is mostly confined to isolated claws, whose placement within the Paguridae is done by comparison with extant species. Evidence on the time of acquisition of the very specialized behaviour of hermit crabs is still more scarce. To the authors' knowledge, the only direct examples of a fossil pagurid connected to a gastropod shell were those presented by Mertin (1941), and Hyden & Forest (1980). Other evidence of the association of fossil pagurid crabs and gastropods has only been established indirectly by means of the predatory activity of pagurids (Papp *et al.* 1947, Schäfer 1972, Radwanski 1977), and by their particular symbiotic association with hydractinians and bryozoans (Ehrenberg 1931, Lecointre 1930, 1934, Kessel 1938, André & Lamy 1939, Papp *et al.* 1947, Schäfer 1939, 1972, Taylor & Cook 1981, Walker 1988).

During the 1986 Antarctic field season of the Instituto Antártico Argentino to James Ross Island, one of the authors (E.B.O.) found in a concretion a pair of crustacean claws associated with the external mould of the gastropod *Taioma* Finlay & Marwick. The taxonomic study of the specimen by the other author (M.B.A.U.) indicates that these claws can be placed within the Paguridae. A subsequent careful analysis of several specimens of *Taioma* from the same horizon has resulted in the recognition of typical predatory marks at the outer lip of the gastropod shells that can be attributed to pagurids, and of encrusting bryozoan colonies on the external part of the gastropod shells.

The main objectives of this study are to document the first record of hermit crabs from Antarctica, and to discuss the implications of this finding in connection with the time of acquisition of the specialized dwelling habit of hermit crabs, their predatory activities, and their symbiosis with bryozoans.

Repository

The specimens described here are deposited in the collections of the CIRGEO (Centro de Investigaciones en Recursos Geológicos), Ramírez de Velasco 847, Buenos Aires, 1414, Argentina.

Stratigraphy and age

Cretaceous sedimentary rocks, about 1200 m in thickness, exposed between Brandy Bay and Santa Marta Cove on James Ross Island, Antarctica, are included in the Santa Marta Formation (Fig. 1). The unit is divided into three members, from bottom to top: the Alpha, Beta, and Gamma members (Olivero *et al.* 1986). The Alpha Member, and part of the Beta Member, consist of a richly fossiliferous marine, volcaniclastic sequence deposited during a major transgressive episode spanning the Santonian–early Campanian. At the top of the Beta Member, the appearance of several coquina beds marks the beginning of an apparent regression that is documented throughout most of the Gamma Member with the deposition of quartzose sandstones (Olivero *et al.* 1989, Pirrie 1989, Scasso *et al.* 1991) in the late Campanian. In addition to their rich molluscan fauna, the Alpha and Beta members also preserve abundant decapod remains assigned to *Hoploparia* McCoy and *Callianassa* Leach (Scasso *et al.* 1991, Aguirre-Urreta 1989). Part of this material is being studied presently by Dr. R.M. Feldmann of

Kent State University, Ohio, U.S.A.

Fossils are very scarce in the quartzose, proximal marine sandstones of the lower part of the Gamma Member but minor fossiliferous horizons, dominated by the gastropod *Taioma* Finlay & Marwick and the bivalves *Cucullaea* Lamarck and *Nordenskjoldia* Wilckens, were recorded. Associated with these horizons are scarce remains of pagurids, *Hoploparia*, and *Callianassa*. However, trace fossils of *Ophiomorpha* Lundgren, *Thalassinoides* Ehrenberg, *Gyrolithes* de Saporta, *Skolithos* Haldemann, and an unknown pinecone-like trace are common (Scasso *et al.* 1991). In addition, the first Antarctic dinosaur (Ankylosauridae) was recorded in the Gamma Member (Gasparini *et al.* 1987, Olivero *et al.* 1991).

Stratigraphically above the gastropod-dominated beds a continuous coquina horizon, locally with well developed channels, and followed by fossiliferous mudstones and silty sandstones, marks the beginning of a new transgressive episode (Scasso *et al.* 1991). The ammonite assemblages at the top of the Gamma Member indicate an early Maastrichtian (or latest Campanian?) age. Thus, the age of the *Taioma* beds in which the pagurid specimen was found can be assigned to the late Campanian.

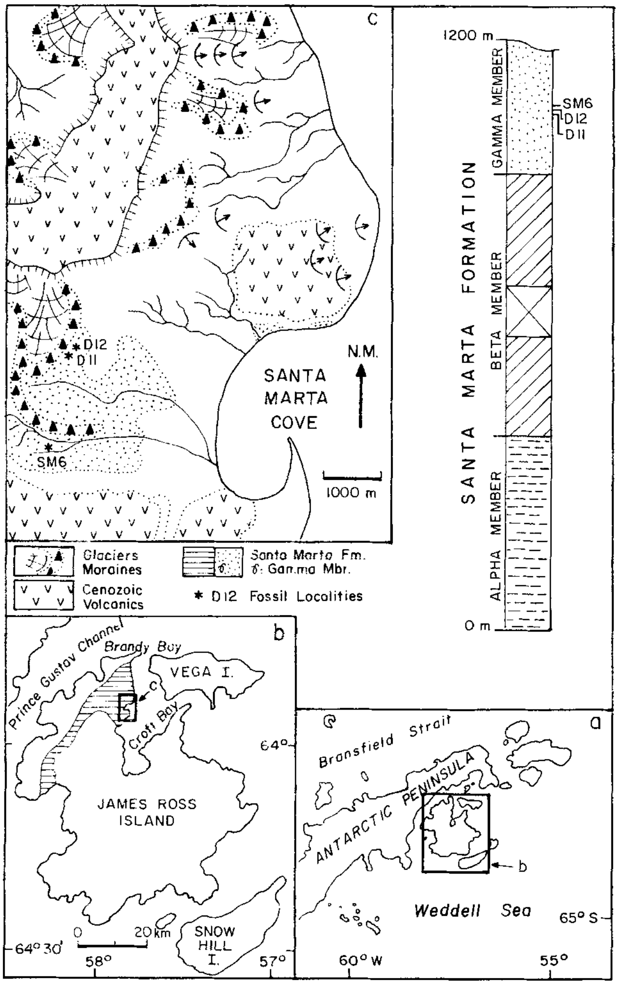


Fig. 1. Locality maps, showing the section where *Pagurites* sp. was collected, James Ross Island. ←= Slumps.

Description of the material

Methodology

The first impression when examining the specimen was that of a hermit crab, although the pagurids are very rare in the fossil record. Therefore, we have to eliminate the possibility of having just a post-mortem association of a brachyuran crab with a gastropod, though there are no records of brachyuran crabs in these deposits.

We first attempted to clean the fossil with mechanical methods, but the hardness of the matrix, and the fragility of the fossils made us abandon this cleaning, to avoid breaking the unique specimen. Then we tried chemical techniques, first with acetic acid (15%), and afterwards with a solution of thioglycolic acid (5%) and calcium ortho-phosphate (0.9%) in deionized water (ph 2.2–3.0), as the cement of the concretion was ferruginous. The results were of limited success. Finally, we took X-rays, using medical equipment, with 50 Kv, 24 MAS, fine focus and a 60 cm object distance. We obtained several good quality X-rays. They showed no trace of a carapace that could indicate the presence of a brachyuran in the concretion, but only the distinct view of both claws. A photographic print of the X-rays allowed us to demarcate some details of the dactylus and fixed finger (see below).

Systematics

Order DECAPODA Latreille, 1803

Suborder PLEOCYEMATA Burkenroad, 1963

Infraorder ANOMURA H. Milne-Edwards, 1832

Superfamily PAGUROIDEA Latreille, 1802

Family PAGURIDAE Latreille, 1802

Subfamily DIOGENINAE Ortmann, 1892

Remarks: The placement of isolated fossil claws within the Paguroidea is usually made by comparison with extant species. This treatment has created some problems (see Forest, in Bishop 1983), as the systematics of recent species seem to be in need of a revision, and it is based on morphological features commonly not preserved in the fossils. The assignment to the Subfamily Diogeninae is based on the equal size of both chelipeds, as compared with the Pagurinae, characterized by a right cheliped much larger than the left.

Genus *Paguristes* Dana, 1851

Type species: *Paguristes hirtus* Dana by subsequent designation of Stimpson 1858 (see Glaessner 1969, p. *R*480).

Diagnosis: Chelipeds similar, equal, unequal, or more commonly subequal, left usually larger. Carpal-propodal articulation oblique to strongly oblique. Propodal-dactylus articulation oblique, fingers closing horizontally (Bishop 1983).

Paguristes sp.

Figs 2a,b

Material: One specimen corresponding to the left and right chelipeds, and parts of the right and left pereiopods II and III; specimen CIRGEO 1474

Description: Small chelipeds similar in size. Carpus triangular, convex above, with the outer surface unevenly tuberculate. A ridge on the carpus borders the articulation with the propodus which is strongly oblique. Propodus squarish, outer surface rounded, covered with small tubercles. Rows of larger tubercles border both margins of outer surface, continuing in the fingers. Fixed finger longer than propodus, dactylus shorter, and curved.

Measurements of left cheliped (in mm)

Propodus length	7.3
Propodus maximum width	7.5
Fixed finger length	7.5
Dactylus length*	7.0
Carpus length	5.9
Carpus maximum width	7.0

* Measured on X-rays prints.

Remarks: Assignation of the specimen to *Paguristes* is mainly based on the equal size of the chelipeds, and the oblique carpal-propodal, and propodal-dactylar articulations. *Palaeopagurus* van Straelen, an extinct genus of uncertain affinities also shows oblique articulations, but the chelipeds are elongate with a rectangular propodus and a convex external surface (van Straelen 1925, p. 312). This genus is restricted to the European Jurassic, with a dubious mention from the Upper Cretaceous (Glaessner 1969, p. *R*481). Mertin (1941) described *Palaeopagurus cretaceus* Mertin, associated with an external mould of the gastropod *Turritella*, from the Upper Cretaceous of Salzberg but the photographs (Mertin 1941, pl. 5, figs. 13–14) are not good, and are very difficult to interpret.

Other Cretaceous records of *Paguristes* include *P. ouachitensis* Rathbun, 1935 from the Nacatoch Sand of Arkansas, and *P. whitteni* Bishop, 1983 from the Coon Creek Formation of Mississippi. This later species, characterized by subequal, heterochelous claws that are strongly convex, with dense randomly located coarse tubercles (Bishop 1983, p. 420, figs. 3E–F, 4A–I, 5), can be easily separated from the Antarctic *Paguristes* sp. which is typified by equal sized claws, with small tubercles, and rows of larger tubercles on both margins. *Paguristes ouachitensis* bears a typical scaly ornament totally different from that of *Paguristes* sp. (Rathbun 1935, p. 39, pl. 6, figs. 9–11).

Predation on gastropods by pagurids

The predation of fossil and recent gastropods by brachyuran decapods has received particular attention from the classic works of Vermeij (1976, 1977a, b, among others). The kind of predation is, in part, related to the size of the prey. If the prey is small enough, most crabs will crush completely the entire shell. Special adaptations to this durophagy are molar-like teeth in the proximal opposing surfaces of the dactylus and fixed finger of the master claw (Zipser & Vermeij 1978). Above the critical size, where the prey can not be completely crushed, different types of attack have been recorded in recent faunas. Commonly, the prey has to be held with both chelipeds: in the trans-apertural grip, each chela grips structures on the opposite sides of the aperture, while in the cis-apertural attack, both chelae grip a single structure (Zipser & Vermeij 1978), and act as a pair of scissors. In both kind of assaults, the prey is killed by progressive breaking of the body whorl.

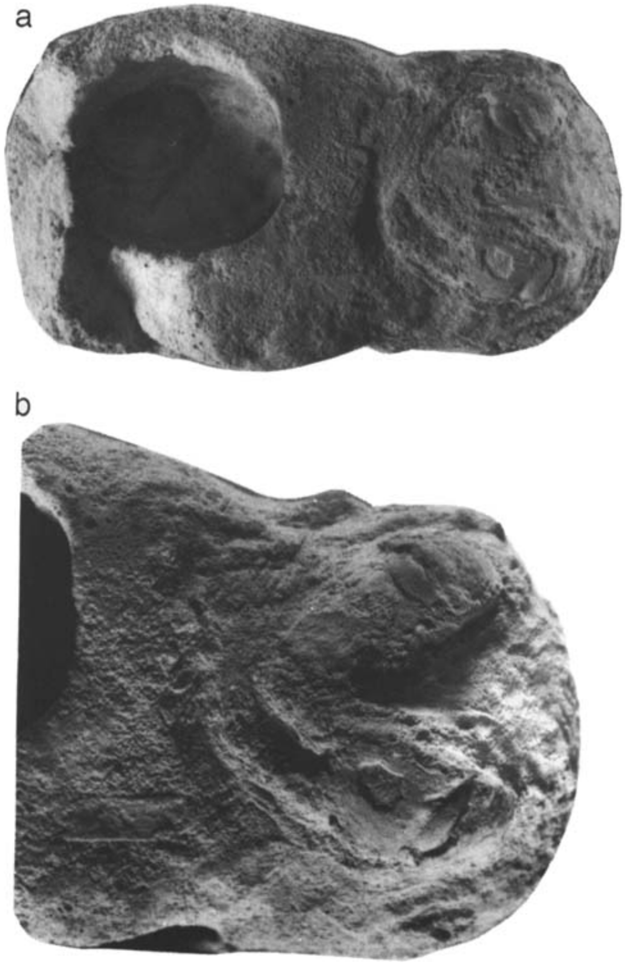


Fig. 2. *Paguristes* sp. CIRGEO 1474. Locality D11-D12. **a.** general view, also showing the external mould of *Taioma* sp. (×1). **b.** detailed view of same specimen showing both chelipeds (× 1.5).

Little has been written of the predatory activities of pagurid crabs on gastropods, either in recent species or in the fossil record, except for the papers of Ehrenberg (1931), and Papp *et al.* (1947) which seem to have been overlooked by many authors. Recent pagurids are mostly detrital or suspension-feeders. However, some species of *Petrochirus* and *Clibanarius* with strong claws are predators (Caine 1975, Hazlett 1981).

Papp *et al.* (1947) tested the predatory feeding habits of *Pagurus striatus* in aquaria with detailed descriptions of the behaviour of both predator and prey. The destruction of the gastropod shell begins with the breaking of the outer lip by means of both chelae. This forms a central sinus as the crab tries to reach the soft parts. This predatory behaviour has been called "cis-apertural grip" (Zipser & Vermeij 1978) and the resulting predatory mark "Band-schnitte" (Papp *et al.* 1947), "ribbon cut" (Schäfer 1972), or "nipping marks" (Radwanski 1977). The end of the process may be the abandonment of the shell with a still living gastropod inside (that can later regenerate its shell) or the exposure of the soft parts with the consequent death of the gastropod. It has also been observed that an empty damaged or regenerated shell can be used afterwards by other pagurids. Zapfe (in Papp *et al.* 1947) employed the results of Papp with recent gastropods and pagurids, for the study of injured gastropod shells from the Tortonian of Vienna, concluding that the pagurids were responsible for the predation.

Other Cretaceous durophages that employ a crushing attack include sharks, rays, bony fishes, and other decapods besides crabs and hermit crabs. Modern sharks and rays pluck off the prey from the bottom, which is then crushed by the strong teeth. The lobsters also shatter the shells, leaving only angular fragments (Carter 1967). Teleost fishes prey upon shelled organisms by crushing them with their mouth parts (Palmer 1979). In all these cases, the result of the predation is quite different from the "Band-schnitte" marks described by Papp *et al.* (1947).

We have a specimen of *Taioma* sp. (Fig. 3a. CIRGEO 1475) with an injured and regenerated shell, from a nearby level to that of our specimen of *Paguristes*. The geometry of the predatory marks is very similar to those described by Papp *et al.* (1947) and is attributed by us to the predatory activities of pagurids. The body whorl (see Fig. 3a) shows a series of cuts in the outer lip, forming a sinus near the suture with the previous whorl. The shell was regenerated, and the growth continued with minor modifications to the sculpture. Although we have a reasonable number of gastropods, most of them are preserved as moulds, and the presence of an injury in the shell cannot be detected.

According to Papp *et al.* (1947) the gastropods can be divided into three groups regarding their resistance to the attacks of hermit crabs: 1) gastropods that are easily attacked by pagurids possess thin outer lips, and large apertures. 2) gastropods that can escape the predators, and preserve the shell with signs of the injury possess either an operculum, or have a high spire where the animal can retract. 3) gastropods rarely attacked by pagurids have a thick shell, small aperture, and thick outer lip. *Taioma* sp. has a relatively large body whorl, with a wide, oval aperture, a thin outer lip only ornamented with small rounded tubercles, and a short spire. If we consider the classification of Papp *et al.* (1947), *Taioma* sp. was a gastropod poorly adapted to avoid the attack of predators like hermit crabs. Taking into consideration the presence of a damaged shell of *Taioma* sp. in a horizon nearby that of *Paguristes*, the similarity of the predation scar to the "Band-schnitte" marks (Papp *et al.* 1947), and the lack of evidences of any other possible predator, we can conclude that a pagurid crab was the responsible predator.

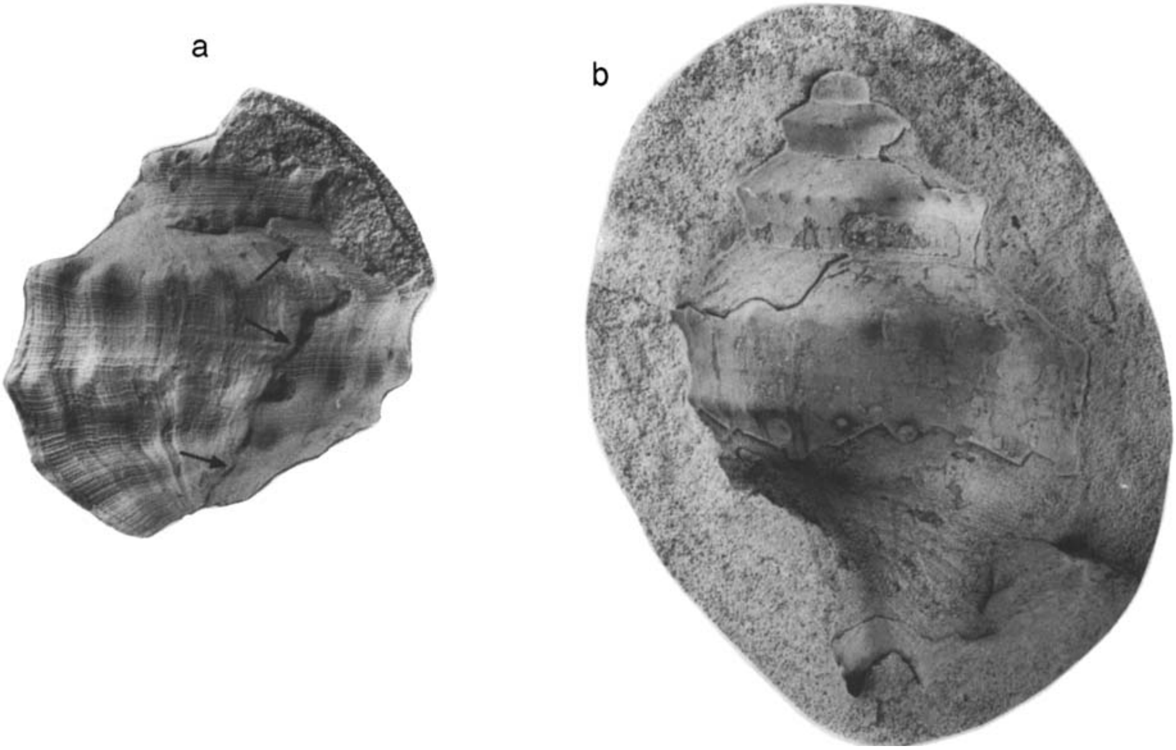
Pagurid and bryozoan symbiosis

In Recent seas, hermit crabs are usually associated with a variety of other invertebrates, and the benefits of this connection vary depending on the different partners. The most celebrated association is between hermit crabs and sea anemones, but there are also known attachments with hydractinians, polychaetes, and bryozoans (Dales 1971).

The sessile bryozoans need a solid substrate for settlement of their colony. Gastropod shells are good places in areas of fine sediments, and become the living substrate of the epizoic Bryozoa. The colony is protected from changes in the sea bottom, while probably providing concealment of the gastropod. Quite commonly the bryozoans settle over gastropod shells inhabited by hermit crabs. The degree of mutual need between the colony of bryozoans and the hermit crab is not fully understand, even in living forms. Thus, we would refer in general terms to a symbiotic relationship between the bryozoan and the pagurid crab. Abundant fossil records of this symbiosis are known from the Miocene and Pliocene of France (Lecointre 1930, 1934, Douvillé 1931) where the bryozoan are represented by several species of heavily encrusting celleporiform ascophorans such as *Hippoporidra*, among others (see also Taylor & Cook 1981).

Recently, Walker (1988) compared Recent and Pleistocene epibionts associated with the gastropod *Olivella biplicata* from California. Walker used the presence of encrusting bryozoa of the genus *Hippothoa* on the Pleistocene gastropods, to infer the contemporary existence of pagurids. In our *Taioma* collection at least six (including the pagurized shell) out of thirty specimens bear colonies of an encrusting ascophoran bryozoan. In all the encrusted gastropods, the bryozoan colonies are only visible on the external mould and are preferentially distributed on the body whorl, especially near the aperture. Remains on the original shell material as patches on the external mould, show that the inner shell surface is not encrusted indicating that the bryozoans encrusted only the external shell (see Fig. 3b).

The encrusting colony is mainly unilamellar with the basal walls of zooids partly immersed in the outer calcareous shell



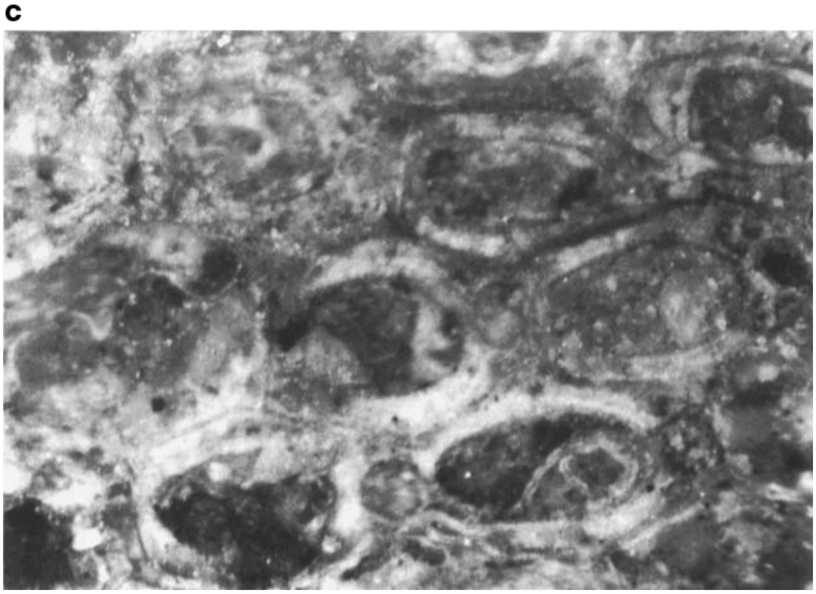


Fig. 3. *Taioma* sp. **a.** specimen showing the typical predatory marks on the outer lip, that was subsequently regenerated by the living gastropod (× 1). (CIRGEO 1475). Locality SM6. **b.** General view of the colony of encrusting ascophoran bryozoans on a shell of *Taioma* sp. CIRGEO 1476 (x 1). Locality D11. **c.** Detail of the basal view of the ascophoran bryozoan colony (× 45).

of the gastropod. Autozooids are more or less symmetrical and box-shaped. Smaller, interzooidal polymorphs are also present, probably including ovicells (see Figs 3c&4). Due to the preservation of the present material, further details are not discernible. On the gastropod mould, only the basal side of the colony is visible and, because the hardness of the matrix prevents cleaning, the diagnostic features of the upper side cannot be seen. However, two thin section of one *Taioma* mould (CIRGEO 1477), including transverse and longitudinal sections of autozooids, show diagnostic features. The original material is totally replaced by recrystallized calcite but, on the upper side of the zooids, a continuous, slightly convex or flat frontal shield that thickens around the small orifice of *c.* 0.11–0.12 mm in length, is present (see Figs 4a & b). On the basis of this feature the material is assigned to the ascophoran bryozoans (cf. Boardman *et al.* 1983).

In the fossil record, most of the bryozoans known to be associated with shells occupied by pagurids are ascophoran cheilostomates. Records from other bryozoan groups are very scanty and, to the authors' knowledge, only a Jurassic Cyclostomata has been reported so far (Buge & Fischer 1970). By contrast, recent studies have shown that a surprisingly diversity of bryozoan groups (including

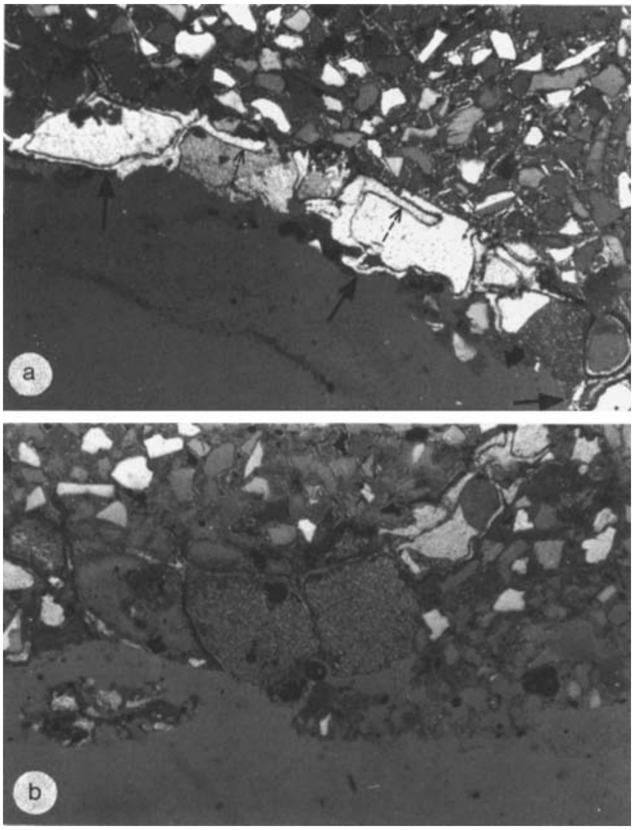


Fig. 4. Longitudinal **a.** and transverse **b.** sections of the colony of ascophoran bryozoans on a *Taioma* mould (CIRGEO 1477). Solid arrow points to the previous position of the shell material supporting the bryozoan colony (now disolved). Broken arrow indicates the frontal shield (× 21).

Cyclostomata and Cheilostomata) are symbiotically associated with living hermit crabs (see Taylor *et al.* 1989).

Two types of bryozoan colonies have been reported in the fossil record: heavily encrusting, multilayer, nodular colonies of "*Cellepora*"-*Hippoporidra* (Lecointre 1930, 1934, Douvillé 1931, Taylor & Cook 1981), and laminar, mostly single layer colonies of *Hippothoa* (Walker 1988). In our material, the growth pattern of the ascophoran colony is very similar to that of *Hippothoa*.

A careful analysis of all the collected bivalves and gastropods (including such minor components as *Turritella* and aporrhaids) suggests that only the *Taioma* shells were encrusted by the ascophoran bryozoans. Because of the type of preservation of the material it is not possible to assess the presence of the typical pagurid facets made by hermit crabs dragging the shell. These facets are expressed by the absence of epizoan growth or by abraded areas on the body whorl near the aperture (Ehrenberg 1931, Papp *et al.* 1947, Walker 1988). However, the preferential distribution of the colony near the aperture, the apparent restriction of the ascophorans to *Taioma* shells, and the presence of the encrusting Bryozoa in the one *Taioma* specimen preserving a hermit crab *in-situ* suggest that the ascophorans lived in association with gastropod shells occupied by pagurids (Fig. 5). The evidence is consistent with the results of the study made by Walker (1988) on Recent and Pleistocene pagurids that provides criteria useful for the recognition of pagurid-occupied shells on the basis of the associated epizoans. Except for a single record from the Jurassic (Buge & Fischer 1970), all previous records of bryozoans living in symbiosis with pagurids are from the Tertiary.

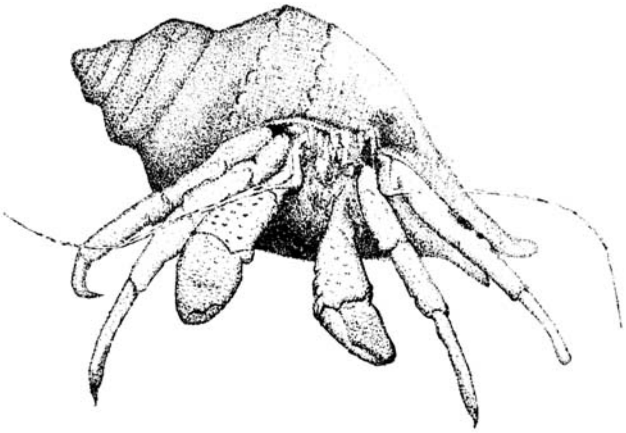


Fig. 5. Reconstruction of *Paguristes* sp. inhabiting an empty shell of *Taioma* sp. partly covered by encrusting ascophoran bryozoans. Natural size.

Palaeoenvironmental reconstruction

The late Campanian, lower part of the Gamma Member that records the *Paguristes-Taioma*-bryozoan association is characterized by distinctive lithofacies, biofacies, and trace fossils. Sedimentary facies and associated body and trace fossils reflect deposition in shallow marine environments at the regressive climax of the major Santonian-Campanian sedimentary cycle of the Santa Marta Formation (Scasso *et al.* 1991, see also Pirrie 1989).

Lithofacies are dominated by well-sorted, thick-bedded, fine quartzose and glauconitic sandstones with minor intercalations of thin-bedded, dark calcareous mudstones and stromatolites. Sandstones are massive or show parallel stratification, ripples, hummocky cross stratification and parting lineation. The marine invertebrate fauna, included in the *Taioma* biofacies by Scasso *et al.* (1991), is relatively scarce, has a low diversity and is mostly preserved as moulds in calcareous-ferruginous concretions. Bivalves (mainly *Cucullaea-Nordenskjoldia*) are commonly found with articulated valves and the dominant gastropod *Taioma* preserves the siphonal channel, suggesting a parautochthonous association. In sharp contrast with the underlying and overlying stratigraphical intervals, ammonites are very rare or are not present, whereas nautilids (*Cymatoceras* sp.) are relatively abundant. In addition to the

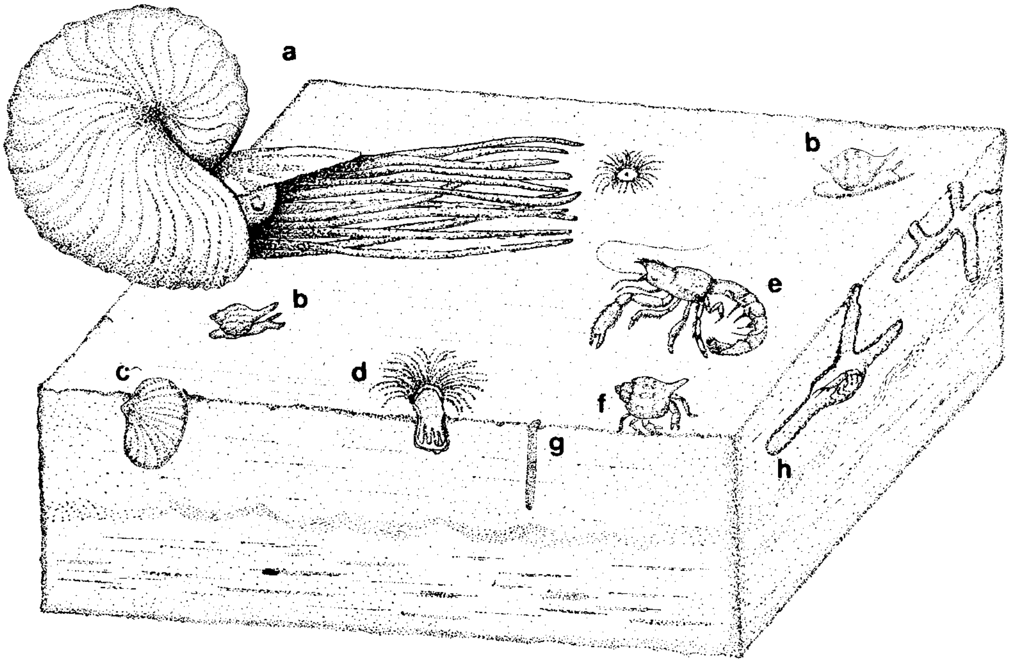


Fig. 6. Block diagram showing the main living conditions of *Paguristes* and the associated fauna in the late Campanian lower part of the Gamma Member, Santa Marta Formation of James Ross Island. **a.** *Cymatoceras* sp., **b.** *Taioma* sp., **c.** *Cucullaea* sp., **d.** actinid coral in pinecone-like burrow, **e.** *Hoploparia stokesi* (Weller), **f.** *Paguristes* sp. inhabiting an empty shell of *Taioma*. **g.** *Skolithos* sp., **h.** *Callianassa meridionalis* Ball inside *Ophiomorpha* burrows.

decapods, fish and shark remains, and a partial skeleton of an armoured dinosaur (Ankylosauridae) were also recorded (Gasparini *et al.* 1987, Olivero *et al.* 1991). Trace fossils are mainly Domichnia of suspension feeders, dominated by *Ophiomorpha*, an unknown pinecone-like burrow, *Thalassinoides*, and *Skolithos*. Less abundant are *Gyrolithes*, *Cylindrichnus*, *Taenidium*, and *Planolites* (Scasso *et al.* 1991). The pinecone-like burrow (Fig. 6d) is tentatively interpreted as the result of the activities of cnidarians (actinids or pennantulacean octocorals).

The described lithofacies, biofacies, and trace fossils are included in Facies Group V of the Santa Marta Formation (Scasso *et al.* 1991), and interpreted as representing near-shore, marine sedimentation within the shoreface and the transition zones. Dominant conditions of a relatively high energy and well-oxygenated environment are suggested by sedimentary facies, dominance of infaunal suspension feeder bivalves, and Domichnia trace fossils. A reconstruction of the living environmental conditions of the most common invertebrate and trace fossils during the deposition of the lower part of the Gamma Member is given in Fig. 6. Even though living pagurids are not exclusively restricted to the shelf, limited quantitative data indicate that most recent hermit crabs are preferentailly distributed between low tide and 40–50 m below sea level (Forest & Saint Laurent 1969, Schembri 1988). The inferred depositional setting for the beds preserving the *Paguristes-Taioma*-bryozoan association is consistent with the living environment of Recent pagurids (Hazlett 1981), suggesting that the preference of hermit crabs for near-shore, high energy habitats were already established by the Late Cretaceous.

Conclusions

A well-preserved specimen of a decapod crustacean in the Gamma Member of the Santa Marta Formation, late Campanian, Antarctica, is identified as *Paguristes* sp., a hermit crab. This is the first certain record of a fossil pagurid from the Cretaceous of Antarctica. The fossil specimen is associated with the external mould of the gastropod *Taioma*, that is encrusted by a colony of ascophoran bryozoans. Another specimen of *Taioma* shows typical predatory marks that have been ascribed to the action of pagurids. The evidence presented suggests that the particular dwelling habits of the hermit crabs, their specific predatory activities, and their symbiosis with encrusting bryozoans, were already established by the end of the Cretaceous.

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References

Aguirre-Urreta, M.B. 1989. The Cretaceous decapod Crustacea of Argentina and the Antarctic Peninsula. *Palaeontology*, **32**, 499-552.

Andre, M. & Lamy, E. 1939. Action des Pagures sur les coquilles qu'ils habitent. *Journal de Conchyliologie*, **83**, 234-242.

Bishop, G. 1983. Fossil decapod crustaceans from the Late Cretaceous Coon Creek Formation, Union County, Mississippi. *Journal of Crustacean Biology*, **3**, 417-430.

Boardman, R.S., Cheetham, A.H. & Cook, P.L. 1983. Introduction to the Bryozoa. *In* Robinson, R.A. *ed. Treatise on Invertebrate Paleontology. Part G (revised), Bryozoa*, Vol. 1, Lawrence, Kansas: Geological Society of America and University of Kansas Press, *G*3-*G*48.

Buge, E. & Fischer, J.C. 1970. *Atractosoecia incrustans* (d'Orbigny) (*Bryozoa Cyclostomata*) espèce bathonienne symbiotique d'un Pagure. *Bulletin de la Société Géologique de France*, Series 7, **12**, 126-133.

Caine, E.A. 1975. Feeding and masticatory structures of selected Anomura (Crustacea). *Journal of Experimental Marine Biology and Ecology*, **18**, 277-301.

Carter, R.M. 1967. On the biology and palaeontology of some predators of bivalved Mollusca. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **4**, 29-65.

Dales, R.P. 1971. Commensalism. *In* Hedgpeth, J.W. *ed. Treatise on Marine Ecology and Paleoecology. Memoir Geological Society America*, No. 67, 391-412.

Douvillé, H. 1931. Symbiose ou parasitisme. *Bulletin de la Société Géologique de France*, Série 5, **1**, 391-396.

Ehrenberg, K. 1931. Über Lebensspuren von Einsiedlerkrebsen. *Palaeobiologica*, **4**, 137-174.

Forest, J. & Saint Laurent, M. de. 1969. Crustacés décapodes: pagurides. *In* Campagne de la Calypso au large des cotes atlantiques de l'Amérique du Sud (1961-1962). *Annales de l'Institut Océanographique*, **45**(2), 49-169.

Gasparini, Z., Olivero, E.B., Rinaldi, C.A. & Scasso, R.A. 1987. Un ankylosaurio (Reptilia, Ornithischia) campaniano en el continente antártico. *Anais do X Congreso Brasileiro de Paleontologia*, Rio de Janeiro (1987) Vol 1, 131-141.

Glaessner, M.F. 1969. Decapoda. *In* Moore, R.C. & Teichert, C. *eds. Treatise on Invertebrate Paleontology, Part R. Arthropoda*, Vol. 4 Part 2, Lawrence, Kansas: Geological Society of America and University of Kansas Press, *R*400-*R*533.

Hazlett, B.A. 1981. The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics*, **12**, 1-22.

Hyden, F.M. & Forest, J. 1980. An *in situ* hermit crab from the early Miocene of southern New Zealand. *Palaeontology*, **23**, 471-474.

Kessel, E., 1938. Schneckenschalen, Krebse und Polypen. *Natur und Volk*, **68**, 428-430.

Lecointre, G. 1930. Symbiose des cellépores et des gastropodes dans les Faluns de Touraine. *Bulletin de la Société Géologique de France*, Série 4, **29**, 401-404.

Lecointre, G. 1934. Cellépores, gastropodes et pagures. *Bulletin de la Société Géologique de France*, Série 5, **3**, 485-486.

Mertin, H. 1941. Decapode Krebse aus dem subhercynen und braunschweiger Emscher und Untersenon sowie Bemerkungen über einige verwandte Formen in der ober Kreide. *Nova Acta Leopoldina*, N.F. **10**, 147-264.

Olivero, E.B., Scasso, R.A. & Rinaldi, C.A. 1986. Revisión del Grupo Marambio en la Isla James Ross, Antártida. *Instituto Antártico Argentino, Contribución*, No. 331, 1-29.

Olivero, E.B., Scasso, R.A. & Rinaldi, C.A. 1989. Shallow-water graded beds of the Santa Marta Formation (Upper Cretaceous, Antarctica): depth inferences from ammonite taphonomy. *Abstracts, 28th International Geological Congress,* Washington D.C., Vol **2**, 546.

Olivero, E.B., Gasparini, Z., Rinaldi, C.A. & Scasso, R.A. 1991. First record of dinosaurs from Antarctica (Upper Cretaceous, James Ross Island): palaeogeographical implications. *In* Thomson, M.R.A., Crame, J.A. & Thomson, J.E. *eds. Geological evolution of Antarctica*. Cambridge: Cambridge University Press, 617-622.

Palmer, A.R. 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution*, **33**, 697-713.

Papp, A., Zapfe, H., Bachmayer, F. & Tauber, A.F. 1947. Lebensspuren mariner Krebse. *Sitzungsberichte der Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse.* Wien Abteilung 1 Mineralogie, Biologie, Erdkunde, **155**, 281-317.

Pirrie, D. 1989. Shallow marine sedimentation within an active margin basin, James Ross Island, Antarctica. *Sedimentary Geology*, **63**, 61-82.

Radwanski, A. 1977. Present-day types of trace in the Neogene sequence; their problems of nomenclature and preservation. *In* Crimes, T.P. & Harper, J.C. *eds. Trace fossils*, Vol. 2, Liverpool: Seel House Press, 227–263.

Rathbun, M.J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America, Special Paper*, **2**, 1-160.

Scasso, R.A., Olivero, E.B. & Buatois, L. 1991. Lithofacies, biofacies, and ichnoassemblages evolution of a shallow submarine volcaniclastic fan-shelf depostional system (Upper Cretaceous, James Ross Island, Antarctica). *Journal of South American Earth Sciences*, **4**, 239-260.

Schäfer, W. 1939. Polypen-Kolonien im Watt. Zur Ökologie von *Hydractinia echinata* Flem. *Natur und Volk*, **69**, 408-412.

Schäfer, W. 1972. *Ecology and Paleoecology of Marine Environments.* Chicago: University of Chicago Press, 624 pp.

Schembri, P.J. 1988. Bathymetric distribution of hermit crabs (Crustacea: Decapoda: Anomura) from the Otago region, southeastern New Zealand. *Journal of the Royal Society of New Zealand*, **18**, 91-102.

Straelen, V. van. 1925. Contribution à l'étude des crustacés décapodes de la période jurassique. *Memoires Académie Royale de Belgique, Classes des Sciences.* Collection in 4°, **7**, 1-462.

Taylor, P.D. & Cook, P.L. 1981. *Hippoporidra edax* (Busk, 1859) and a revision of some fossil and living *Hippoporidra* (Bryozoa). *Bulletin of the British Museum (Natural History) (Geology)*, **35**, 243-251.

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.

Vermeij, G.J. 1976. Interoceanic differences in vulnerability of shelled prey to crab predation. *Nature*, **260**, 135-136.

Vermeij, G.J. 1977a. Patterns in crab claw size: the geography of crushing. *Systematic Zoology*, **26**, 138-151.

Vermeij, G.J. 1977b. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**, 245-258.

Walker, S.E. 1988. Taphonomic significance of hermit crabs (Anomura: Paguridea): epifaunal hermit crab-infaunal gastropod example. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **63**, 45-71.

Zipser, E. & Vermeij, G.J. 1978. Crushing behavior of tropical and temperate crabs. *Journal of Experimental Marine Biology and Ecology*, **31**, 155–172.