

Cuticular ultrastructure of fossil and living homolodromiid crabs (Decapoda: Brachyura)

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Comparison of cuticular ultrastructure in *Antarctidromia inflata* Förster, 1985 from the Miocene Cape Melville Formation on King George Island, Antarctica, with that of the confamilial, extant *Homolodromia paradoxa* A. Milne Edwards, 1880 suggests that the more rigid carapace of the fossil form results from a relatively thicker, more strongly calcified exocuticle. Epicuticle, exocuticle, and endocuticle are all recognizable on the fossils; however, adherence of the epicuticle to the counterpart may result in misinterpretation of the fine sculpture on the carapace. Absence of dissolution features in the endocuticle confirm conclusions, based upon completeness of remains, that the specimens of *Antarctidromia inflata* represent corpses, not molts.

Key words: Decapoda, Homolodromiidae, cuticular ultrastructure, Miocene, Antarctica, Caribbean Sea.

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Introduction

Antarctidromia inflata Förster, 1985 is a decapod crustacean known only from the early Miocene Cape Melville Formation, King George Island, South Shetland Islands, Antarctica (Fig. 1). The species is one of three known occurrences of the ‘primitive’ crab family Homolodromiidae in the fossil record. It is also one of only three known occurrences of benthic decapod crustaceans known from Antarctica in post-Eocene rocks. In the time interval spanning the Cretaceous to Eocene, the decapod crustacean record was relatively robust; however, general deterioration of oceanographic conditions concomitant with the initiation of the circum-Antarctic circulation had a profound effect on this group. As a result, only two species of decapods from the Miocene of King George Island, one currently under study, and *Antarctidromia inflata* Förster,

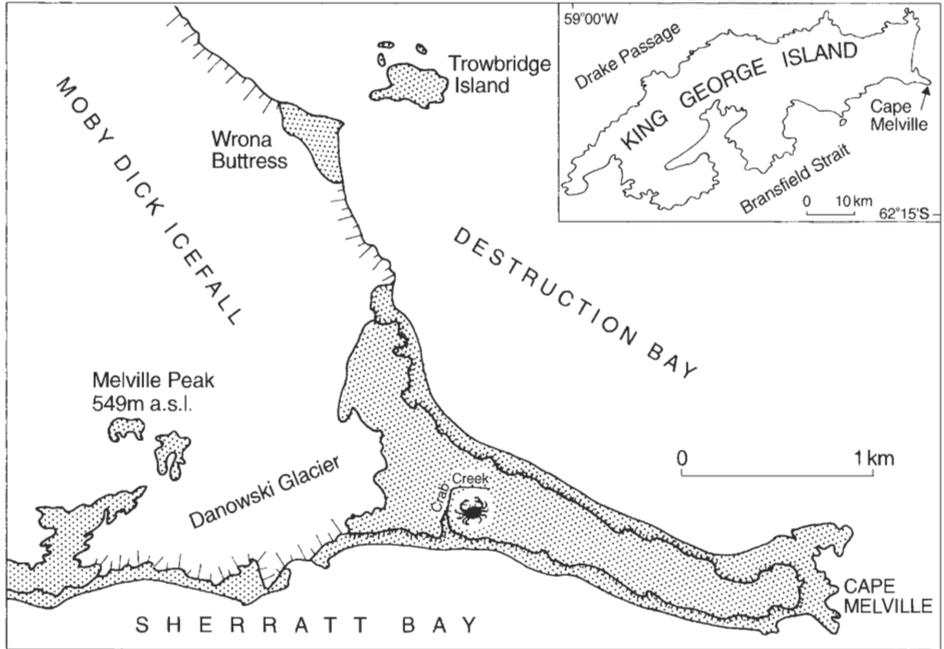


Fig. 1. Map of Cape Melville (King George Island), showing the aerial extent of the Tertiary strata of the Moby Dick Group and the position of Crab Creek from which specimens of *Antarctidromia inflata* were collected. Inset map shows location of Cape Melville on King George Island (South Shetland Islands).

1985 represent the only significant younger record of crabs and lobsters. The third taxon, an incomplete, poorly preserved fragment of a palinurid lobster has recently been reported from the Pliocene of the Marine Plain, Princess Elizabeth Land (Feldmann & Quilty 1997).

A. inflata is documented by a large number of remarkably well preserved individuals, rivaled only by the occurrences of the crab, *Lyreidus antarcticus* Feldmann & Zinsmeister, 1984, from the Eocene of Seymour Island and *Hoploparia stokesi* (Weller, 1903), from the Cretaceous and Paleocene of the James Ross Basin. Finally, most of the specimens of *Antarctidromia inflata* (Fig. 2A) are preserved in association with burrow structures that may be attributable to their activity (see also Förster *et al.* 1987). Thus, details of life habits of *A. inflata* and nearly complete understanding of its anatomy can be explored.

Roer & Dillaman (1984) and Feldmann & Thsudy (1987) summarized key studies on the ultrastructure on cuticle in extant decapods. These works described the details of ultrastructure using both light and electron microscopy which provide a framework for the investigation of fossil cuticular structure.

Ultrastructure in fossils has been less well studied and, for the most part, work has been devoted to the examination of macrurans, the lobsters. Schäfer (1972) implied that cuticular ultrastructure would not be useful in distinguishing corpses from exuviae, indicating that the fossil properties of the two types of remains were identical. Glaessner (1969) reinforced this observation by noting that, during the molting pro-

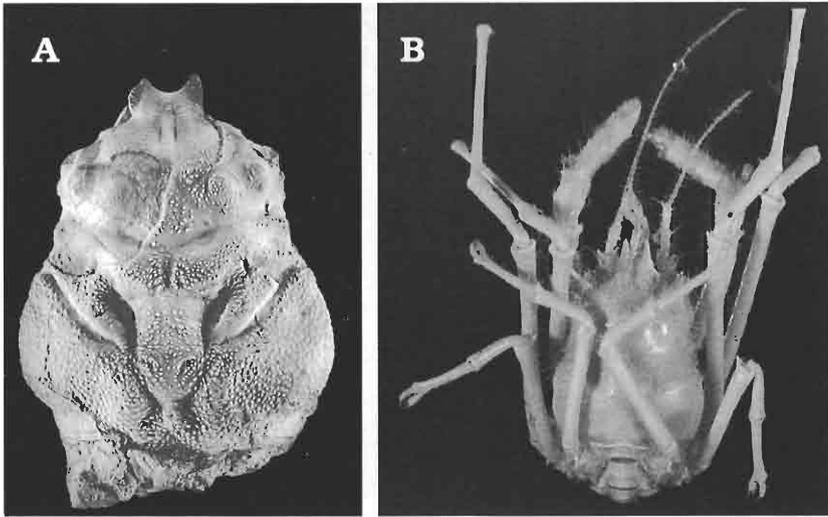


Fig. 2. **A.** *Antarctidromia inflata* Förster, 1985 (ZPAL Cr. I/63) showing the general conformation of the carapace and the fine details of preservation. King George Island, Cape Melville; Cape Melville Formation (early Miocene). **B.** *Homolodromia paradoxa* A. Milne Edwards, 1880, showing the overall morphology of a female specimen. Carribean Sea 'Oregon' Sta. 6703 (Recent). Both in natural size.

cess, whatever decalcification of endocuticle occurred, it would not be noticeable in comparison to the effects of preservation. However, Neville & Berg (1971) recognized extremely finely preserved exocuticle and endocuticle in the Jurassic macruran, *Eryma stricklandi* (Phillips, 1871). They described helicoidal structures extending transversely across the cuticle and interpreted them to represent helically coiled pore canals. Taylor (1971) recognized the presence of saprotrophic fungus borings in the Cretaceous lobsters, *Hoploparia stokesi* (Weller, 1903) and *Glyphea georgiensis* Taylor, 1979 collected from Alexander Island, Antarctica. The recognition of well preserved cuticle in these species prompted a further study (Taylor 1973) in which Taylor recognized clear differentiation of epicuticle, exocuticle, and endocuticle in *Hoploparia stokesi* and *Glyphea alexandri* Taylor, 1979. Details of the morphology of pore canals and smaller tubules within Cretaceous macruran, *Hoploparia longimana* (Sowerby, 1826), permitted Dallingwater (1977) to make detailed comparisons between the architecture of cuticle in fossil and extant decapods.

Feldmann & Tshudy (1987) demonstrated that molted cuticle could be identified in the fossil record. *Hoploparia stokesi*, collected from the James Ross Basin, Antarctica, was observed to be preserved commonly in Salter's position; that is, the abdomen is rotated away from the cephalothorax in the position that would be anticipated as the animal lay on its side and worked its way out of the exuvia. Scanning electron microscopy of one such specimen demonstrated dissolution of the lower parts of the endocuticle in a fashion that would be anticipated for a molted specimen and, therefore, confirmed that Salter's position was an indication of molting.

The first study of cuticular structure in brachyurans, to our knowledge, was that of Vega *et al.* (1994) in which the structure of *Costacopluma mexicana* Vega & Perrilliat,

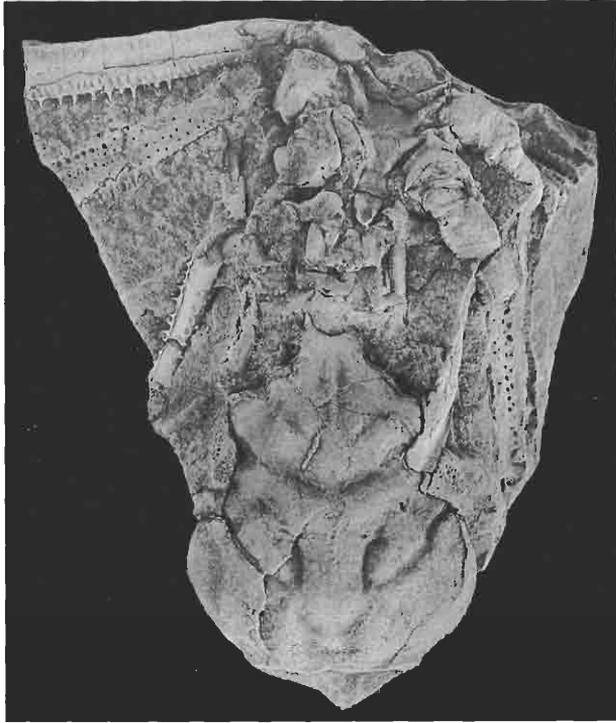


Fig. 3. *Antarctidromia inflata* (BAS P.2702.902) in which the rotation of the abdomen, sternum, and appendages into the same plane as the cephalothorax reflects the molted condition. King George Island, Cape Melville; Cape Melville Formation (early Miocene). Natural size.

1989, was recognized as having not only the three calcified layers of cuticle present, but also the membranous layer. This material, from the Maastrichtian of Mexico, exhibited no evidence of molting and the observation of the cuticular structure confirmed that conclusion.

The purpose of the present work is to examine the details of cuticular ultrastructure of homolodromiid crabs and to compare the structure with that of the living representative within the same family, *Homolodromia paradoxa* A. Milne Edwards (Fig. 2B).

Material and methods

Over 280 specimens of *Antarctidromia inflata* have been collected from the early Miocene Cape Melville Formation at Cape Melville, King George Island by A. Gaździcki and R. Wrona during the Fifth Polish Antarctic Expedition to Arctowski Station in 1980–81 (Birkenmajer *et al.* 1983; Förster *et al.* 1985, 1987). The collection is housed at the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw (abbreviated ZPAL). One specimen of *A. inflata* (Fig. 3) was collected by Dr J. A. Crame, Jr. on an expedition of the BAS and is deposited in the British Antarctic Survey,

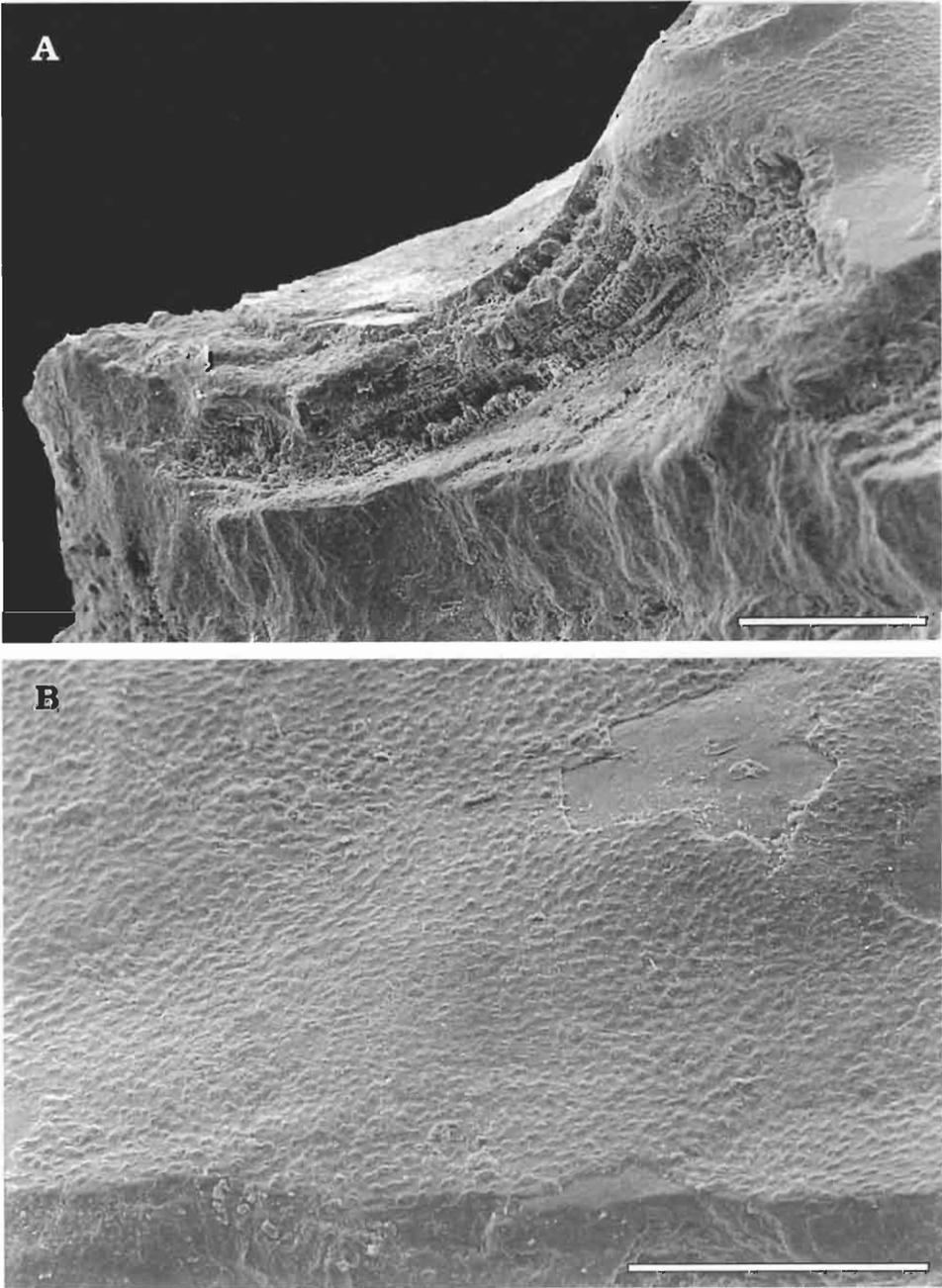


Fig. 4. SEM micrographs of cuticular structure of *Antarctidromia inflata* (ZPAL Cr. I/7). King George Island, Cape Melville; Cape Melville Formation (early Miocene). **A.** Oblique view of edge with most of the surface bearing epicuticle and well defined, layered exocuticle and endocuticle. **B.** Surface in same region showing details of surface ornamentation on epicuticle contrasted with that in a region in which the epicuticle is absent. Scale bars – 200 μm .

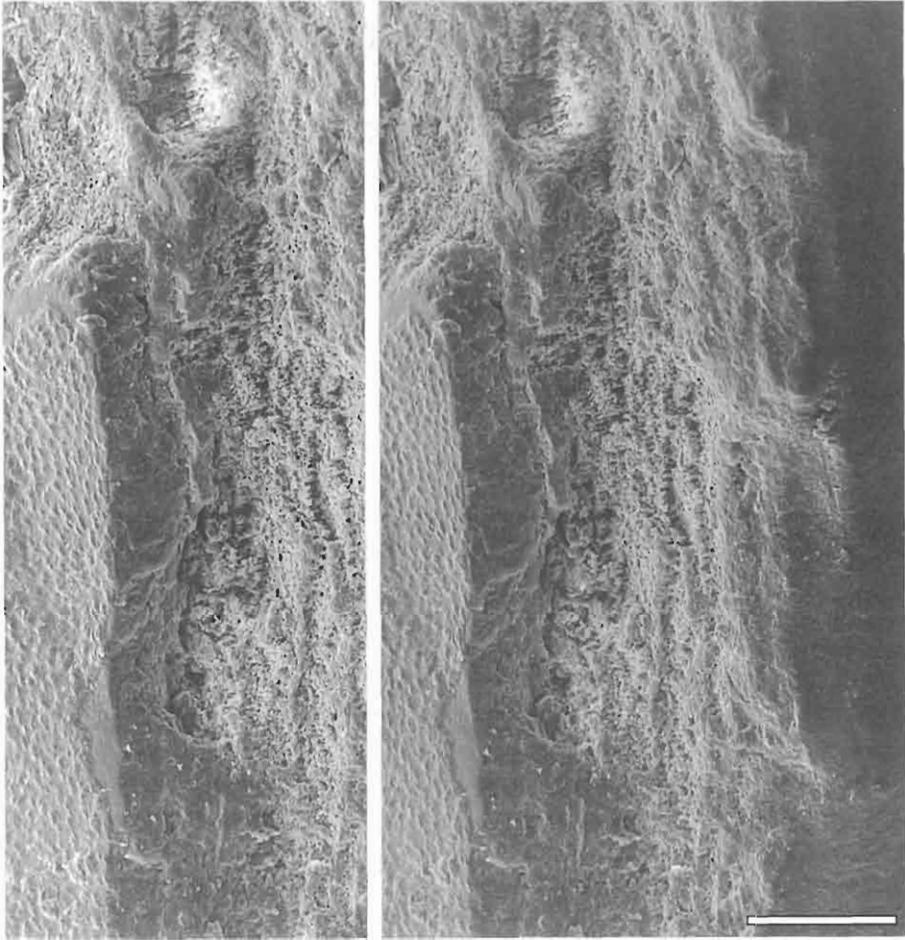


Fig. 5. Stereoscopic SEM micrographs of broken edge of cuticle of *Antarctidromia inflata* (ZPAL Cr. I/96) showing surface of epicuticle (left), relatively dense exocuticle (center), and distinctly laminar endocuticle (right). Scale bar – 100 μ m.

Cambridge (abbreviated BAS). The specimen of extant *Homolodromia paradoxa* (Fig. 2B) from Caribbean Sea, 'Oregon' Sta. 6703 is housed at the National Museum of Natural History, Washington (abbreviated USNM).

The study was conducted using a Philips XL-20 scanning electron microscope on broken and polished specimens. Polished specimens were treated in 1% HCl for 30 seconds.

Preservation of Miocene *Antarctidromia*

The geologic occurrence, anatomy, and paleoecology of *Antarctidromia inflata* have been discussed by Förster *et al.* (1985, 1987). They concluded that the majority of the

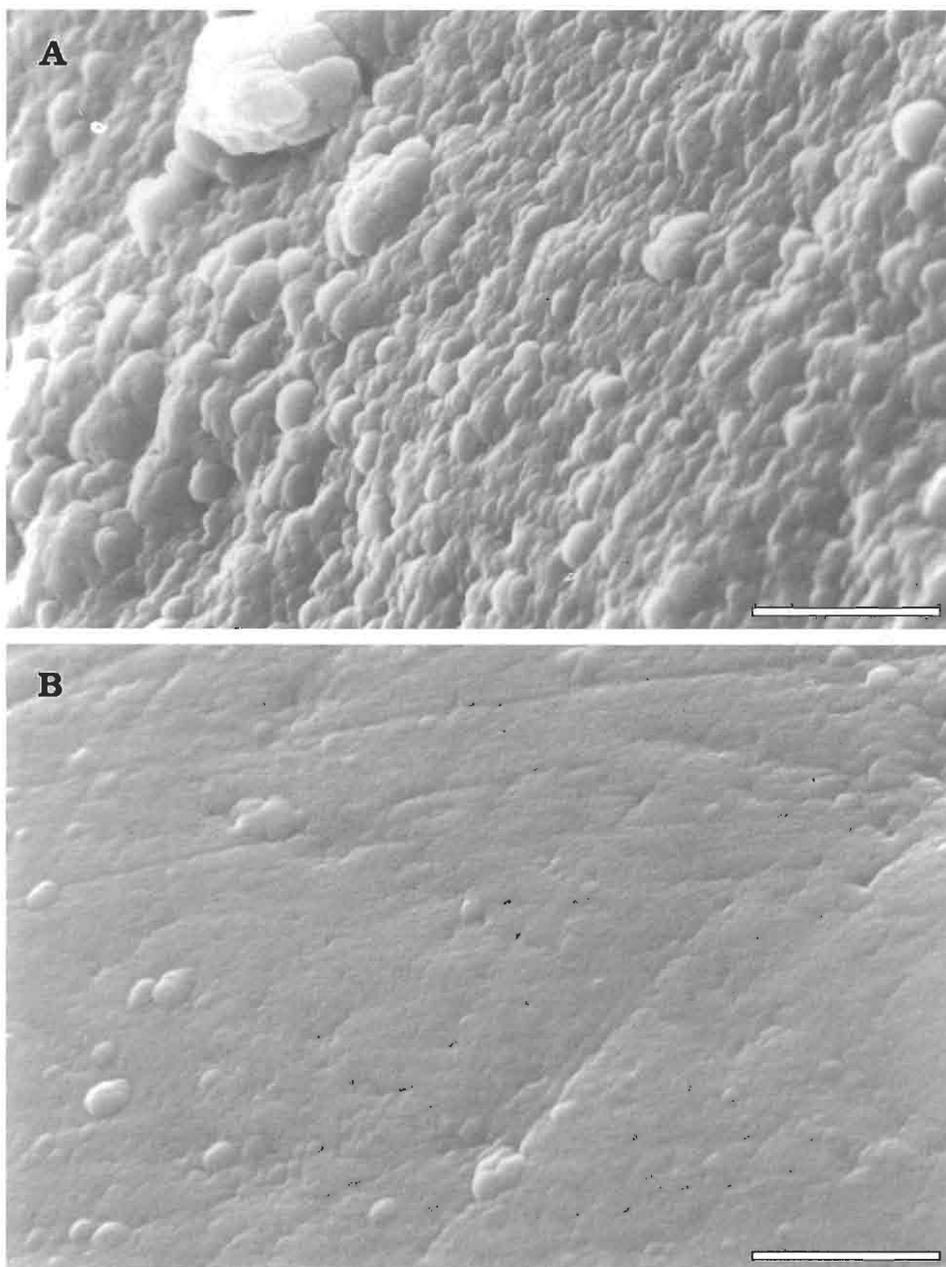


Fig. 6. SEM micrographs of the surface of *Antarctidromia inflata* (ZPAL Cr. I/7). **A.** Pustulose surface of integument between bosses. **B.** Smooth, perhaps abraded, surface of a boss. Scale bars – 2 μm .

specimens represented corpses based upon the observation that nearly all specimens were complete; that is, the abdomen, sternum, and appendages were attached and in life position relative to the cephalothorax. Reexamination of the collection in ZPAL



Fig. 7. SEM micrograph of cross-section of cuticle of *Antarctidromia inflata* (ZPAL Cr. I/7) showing relative thickness of exocuticle (above) and endocuticle (below).

and BAS, convinced us that this conclusion is valid. Only one specimen of *A. inflata* (that collected by Dr. J. Alistar Crame, Jr.) can be considered a molt (Fig. 3). It differs from all the others in having the abdomen, sternal plastron, and appendages articulated, but rotated 180° out of their life-plane and attached to the cephalothorax only in the area of the front; cuticle was entirely absent from this specimen. This unusual orientation of the preserved parts is rarely observed. The orientation has been recognized by Feldmann (1998, in press) in the large xanthid crab, *Tumidocarcinus giganteus* Glaessner, 1960, from New Zealand.

Nearly all of the specimens are preserved with a large amount of cuticle intact, which is preserved as a dark, lustrous, bluish-black layer.

Cuticle of *Antarctidromia*

Three discrete cuticular layers can be identified in scanning electron micrographs of *Antarctidromia inflata* (Fig. 4A). The epicuticle consists of a very thin unilamellar layer that exhibits a fine, wavy sculpture on the outer surface and appears to be smooth on its lower surface (Figs 4, 5). Epicuticular material is well preserved over some of

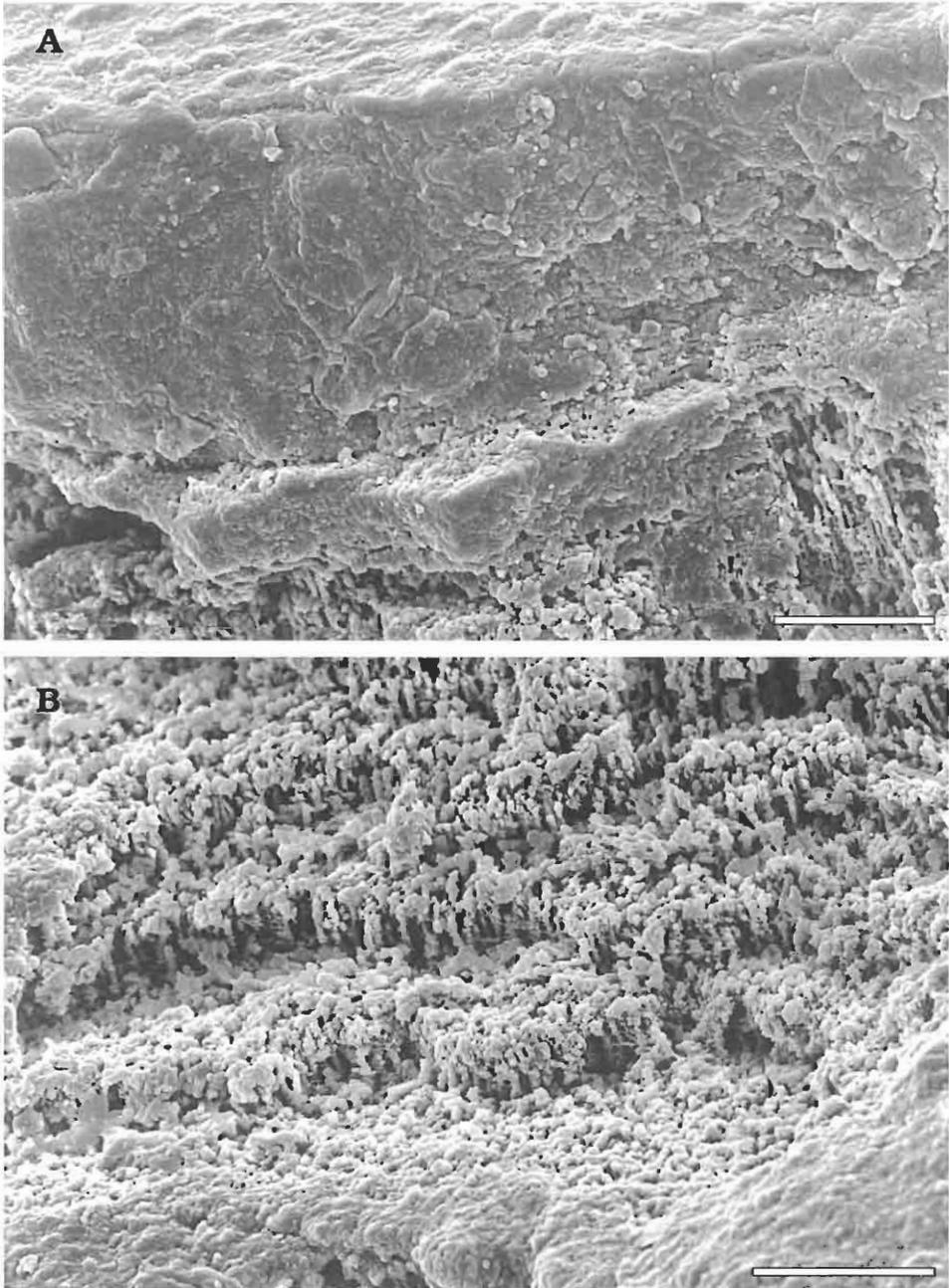


Fig 8. SEM micrograph of cuticular structure of *Antarctidromia inflata* (ZPAL Cr. I/96). **A.** Extremely thin epicuticle and nearly massive exocuticle. **B.** Fibrous nature of ultrastructure of endocuticular layers. Scale bars – 25 μm .

the carapace of many specimens, however, it does appear to be selectively abraded from the surfaces of elevated regions or nodes (Fig. 6).

Beneath the epicuticular layer, the exocuticle is a dense, multilamellar layer which is readily distinguishable from the much more obviously lamellar and less dense endocuticular region. The layers within the endocuticle are uniform from top to bottom, no evidence of dissolution of the lower layers is evident; however, no membranous layer was observed at the base of the endocuticle. Throughout the specimen (ZPAL Cr. I/7) examined, the exocuticle appeared to be about one-fourth the total thickness of the cuticle and, where measured, the exocuticle was 50.2 μm thick whereas the underlying endocuticle was 150 μm in thickness (Fig. 7).

Closer examination of the layers of cuticle (Fig. 8A) confirms that the epicuticle is unilamellar, that the exocuticle is layered, but that the calcification of this layer has rendered laminations obscure. In marked contrast, the layering of the endocuticle is evident at all magnifications. Calcification of the endocuticular layer appears to have been preceded by precipitation around discrete centers situated on a fine, reticulate, chitinous matrix (Fig. 8B). This matrix is defined as a series of dense layers extending parallel to the surface of the cuticle and separated from one another by transverse rods forming an open meshwork.

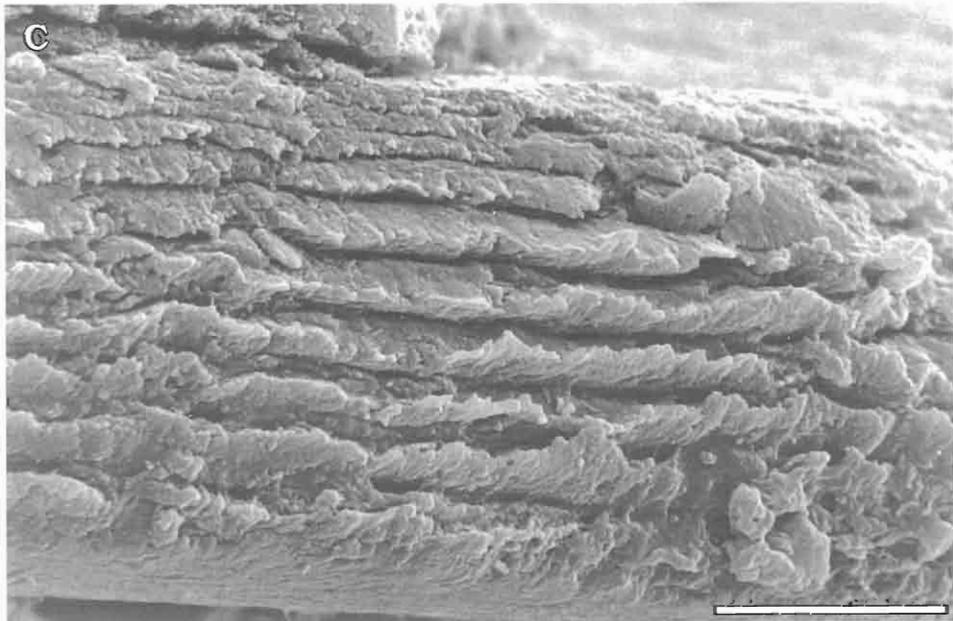
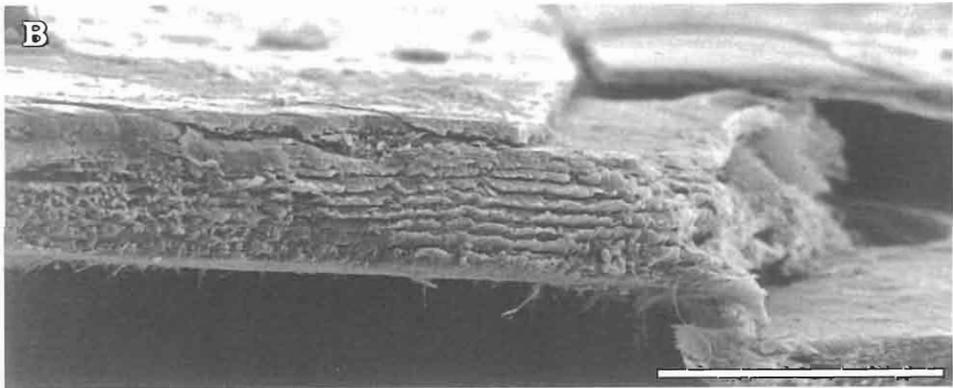
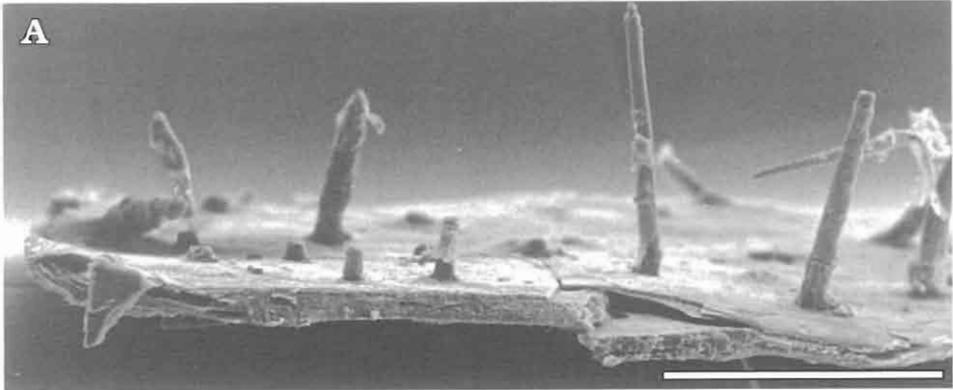
Throughout the areas examined, no evidence for vertical structures, rods, or setal pores was observed. The surfaces tended to be quite uniform and thickness varied only slightly, increasing in the area of nodes.

Ultrastructure of extant *Homolodromia*

The ultrastructure observed in *Antarctidromia inflata* was contrasted with that seen on the preserved specimen of the extant *Homolodromia paradoxa* from Caribbean Sea (Figs 9–11). Although the same three typical cuticular layers are present in *H. paradoxa*, some important differences could be observed. The epicuticle appears to be a single layer which exfoliated readily from the surface of the exocuticle and, therefore, was not preserved in such a way that it could be examined at high magnification. It is (Fig. 9A) an extraordinarily thin, unilamellar layer that appears as a kind of film over the surface. The exocuticular layer is coarsely laminated and appears to contain three or four obscure laminations. Laminations within the endocuticle (Fig. 9B, C) are much more obvious and comprise about 10 layers. The relative thickness of exocuticle and endocuticle is about 1:7 as opposed to 1:3 as observed on *Antarctidromia inflata*. As in *A. inflata*, the exocuticle appears to be much more densely calcified (Fig. 10A) than the endocuticle (Fig. 10B). Endocuticular layers consist of a series of dense mats separated by a more open structure of vertical chitinous members about which calcification has occurred. A thin membranous layer consisting of very finely laminated material was evident at the base of the endocuticle.

The density of calcification of cuticle varied considerably over carapace surface in *Homolodromia paradoxa*. The sample collected for examination was taken from the left posterolateral margin of the branchial chamber and, consistent with the visual

Fig. 9. SEM micrograph of cuticle of *Homolodromia paradoxa* taken from the left branchial region. **A.** Oblique view of cuticle showing cut edge and projecting setal hairs. Scale bar – 500 μm . **B.** Enlargement of edge showing relatively dense exocuticle and more distinctly laminated endocuticle. Epicuticle is evident



in the upper right corner. Scale bar equals 100 μm . C. Enlargement of lower part of exocuticle and all of endocuticle showing increase in thickness of laminations from exterior to interior. Scale bar – 20 μm .

observation, the branchial region was most strongly calcified axially and became progressively less calcified laterally. Thus, examination of the lateral regions provided a somewhat different perspective on cuticular ultrastructure. The exocuticle was, again, the most densely calcified of the layers (Fig. 11A); the endocuticle was calcified hardly at all (Fig. 11B). More detailed examination of the endocuticle clearly shows the chitinous framework upon which calcification occurs. The calcification in this region was confined to a series of globular excrescences, which had not coalesced sufficiently to form a rigid framework for the cuticle. Thus, the cuticle in the region was quite flexible. Throughout the examination of cuticular calcification in *Antarctidromia inflata* as well as *Homolodromia paradoxa*, there was no evidence of pitting or etching that would be suggestive of dissolution of previously precipitated calcium carbonate. Instead, the surfaces of the calcified globules appeared to be unpitted and therefore, it may be concluded that openness within the framework of the endocuticle in particular was a result of lack of growth of calcium carbonate rather than dissolution of a previously more dense structure.

Taphonomic effects on *Antarctidromia*

During the scanning electron microscopic examination of *Antarctidromia inflata*, both the surface of the carapace and the surface of the corresponding counterpart were examined. The examination revealed that, over much of the surface of the carapace, the epicuticular material was absent (Fig. 12). As a result, the surface of the carapace in these regions appears to be relatively smooth in the regions between carapace nodes. Examination of the surface of the counterparts, however, suggested that the actual outer surface, that is, the outer surface of the epicuticle, was not present on the carapace but, instead, was adherent to the mold of the exterior. Examination of this surface (Fig. 13) revealed that the underside of the exocuticle exhibited a polygonal structure which, upon closer examination, bounded a very finely wavy surface. The overall appearance was that of desiccation features and it is possible that the separation of epicuticle from exocuticle may have resulted from a differential shrinkage of material during early diagenesis which produced a plane of weakness facilitating separation of part and counterpart. Examination of the edge of this mold of the exterior (Fig. 14) clearly shows the unilamellar, thin exocuticular lining of the counterpart.

The implications of this method of preservation are significant. Variations on surface sculpture are frequently used as species-level characters and there is no reason to argue that surface ornamentation cannot be considered a useful character. However, extreme caution must be used when doing so as indicated by the discussion of the material herein. If the actual surface of the epicuticle is examined, the overall texture of the carapace would be described as, 'coarsely nodose on a field of extremely fine granules,' whereas if the surface of the specimen illustrated in Fig. 6 were taken to be the outer surface of the carapace, the texture would be described as, 'nodes developed on an otherwise smooth surface.'

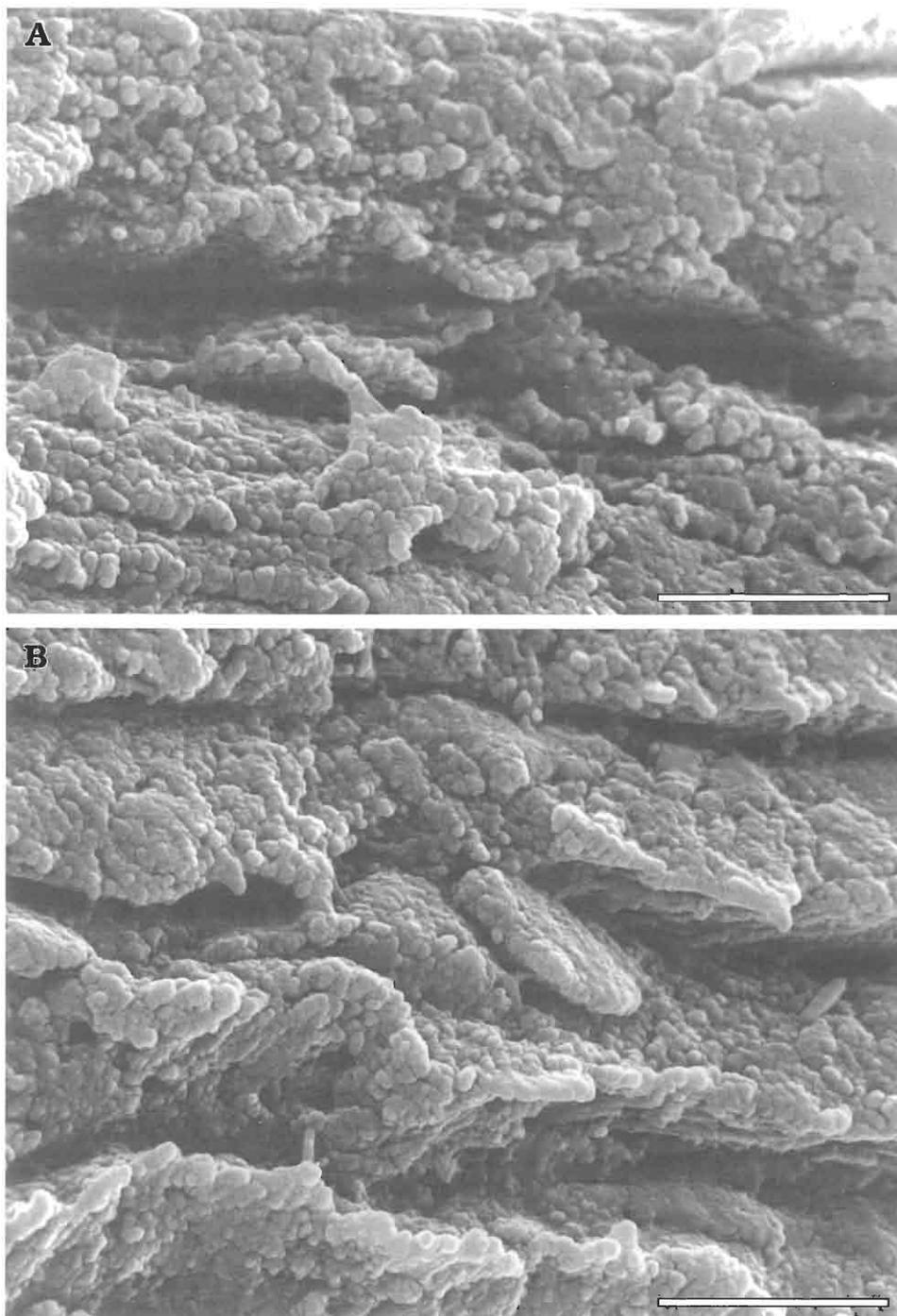


Fig. 10. SEM micrograph of cuticular structure of *Homolodromia paradoxa*. **A.** Nearly massive nature of exocuticle showing coalescence of globose calcareous deposits. **B.** More open structure of endocuticular layers showing generally linear arrangement of globose calcareous deposits within layers. Scale bars – 5 μm .

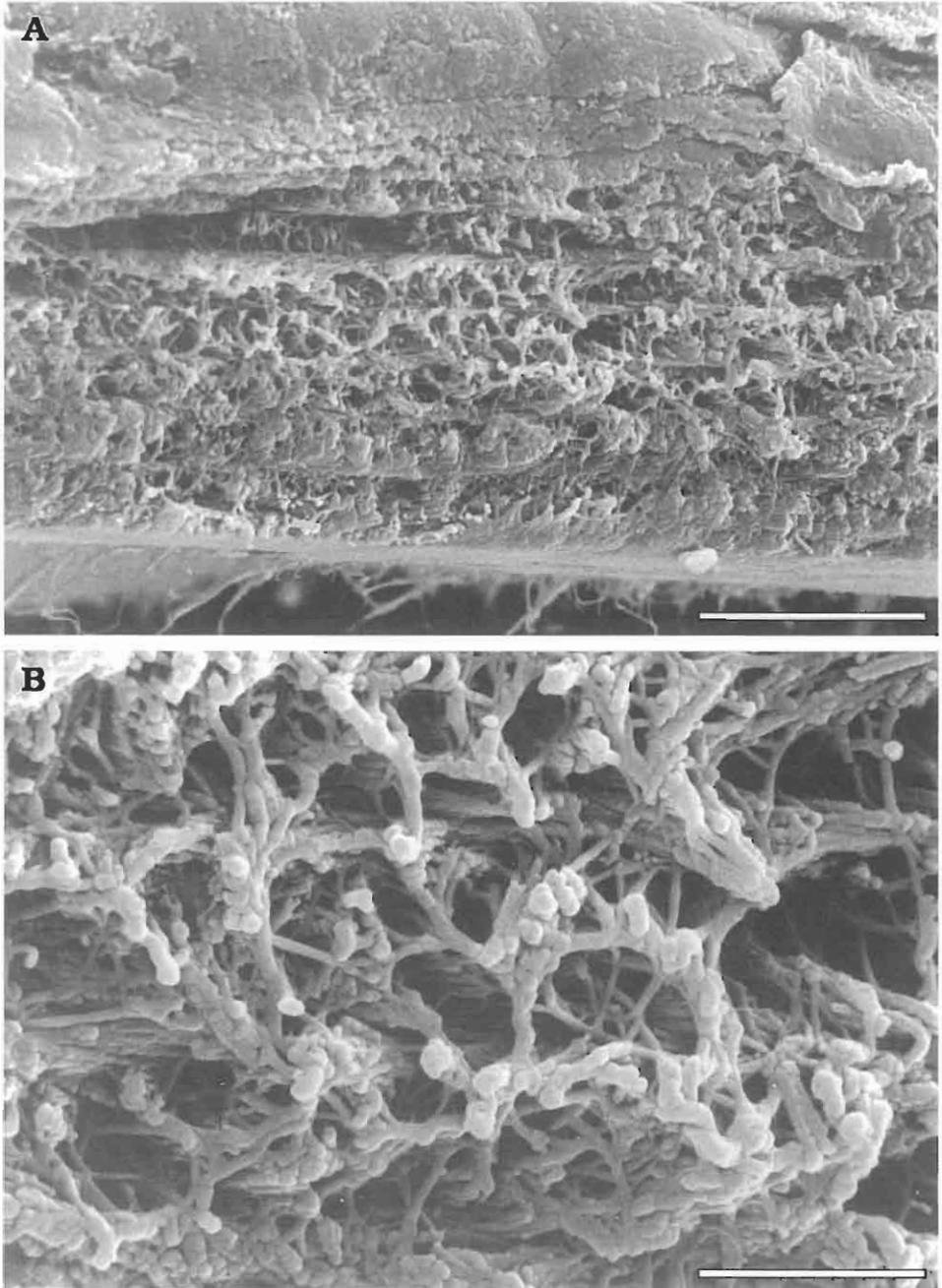


Fig. 11. SEM micrograph of cuticular structure in weakly calcified branchial margin of *Homolodromia paradoxa*. **A.** Relatively dense exocuticular region (above) and open, fibrous endocuticular layer (below). Scale bar – 20 μm . **B.** Enlargement of endocuticular region showing fibrous chitinous reticulum and incipient calcification. Scale bar – 5 μm .

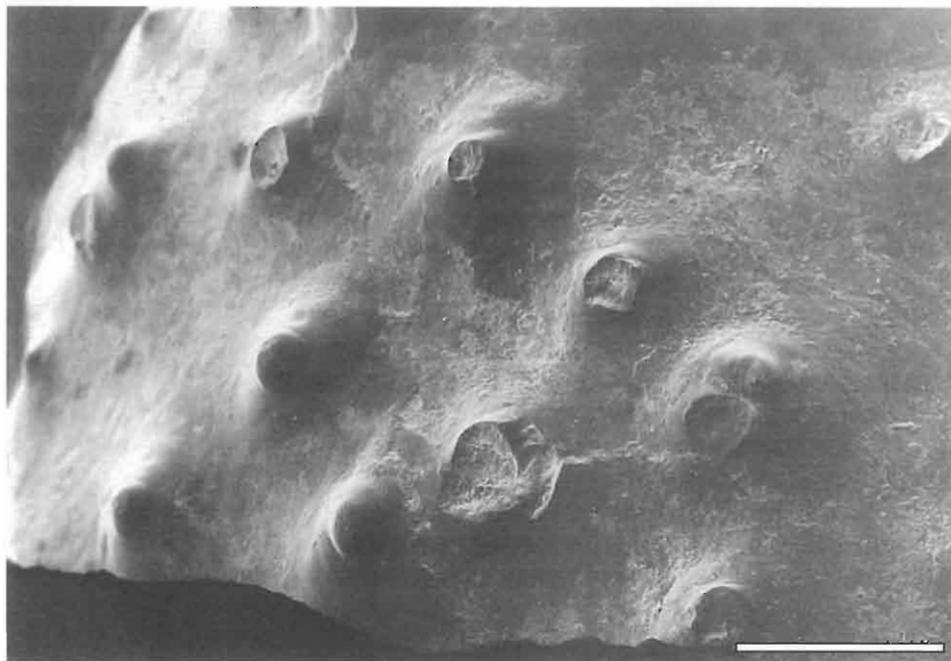


Fig. 12. SEM micrograph of a portion of the branchial region of *Antarctidromia inflata* (ZPALCr. I/7). Scale bar – 1 mm.

Conclusions

Visual examination of fossil material of *Antarctidromia inflata* suggests that the cuticle was relatively rigid. There was very little indication of deformation of the carapace. The relatively thick, dense exocuticular layer within this species tends to corroborate that observation. The entire carapace of *Homolodromia paradoxa*, by contrast, was somewhat flexible, becoming more so in the uncalcified margins of the branchial region. The flexibility of the carapace of *H. paradoxa* may be attributed to relatively weak calcification coupled with a relatively thin exocuticular layer. Thus, although the general ultrastructure of the two species is similar, the carapaces did differ in the important aspects of relative thickness of layers and degree of calcification.

Contrary to some early observations (Glaessner 1969) it is possible to recognize cuticular layering in decapod cuticle at a wide range of magnifications, given sufficiently good quality preservation. Examination of the lower layers within the endocuticle, noting the presence or absence of dissolution, can permit distinction between molt and intermolt conditions. Although the membranous layer has been observed previously (Vega *et al.* 1994), it cannot be anticipated under any but the most unusual preservational circumstances.

Whereas the epicuticular layer in fossil and extant homolodromiids appears to be extremely thin, unilamellar, and weakly adherent to the underlying cuticular layers, the relative proportions and the degree of calcification of exocuticle and endocuticle varies

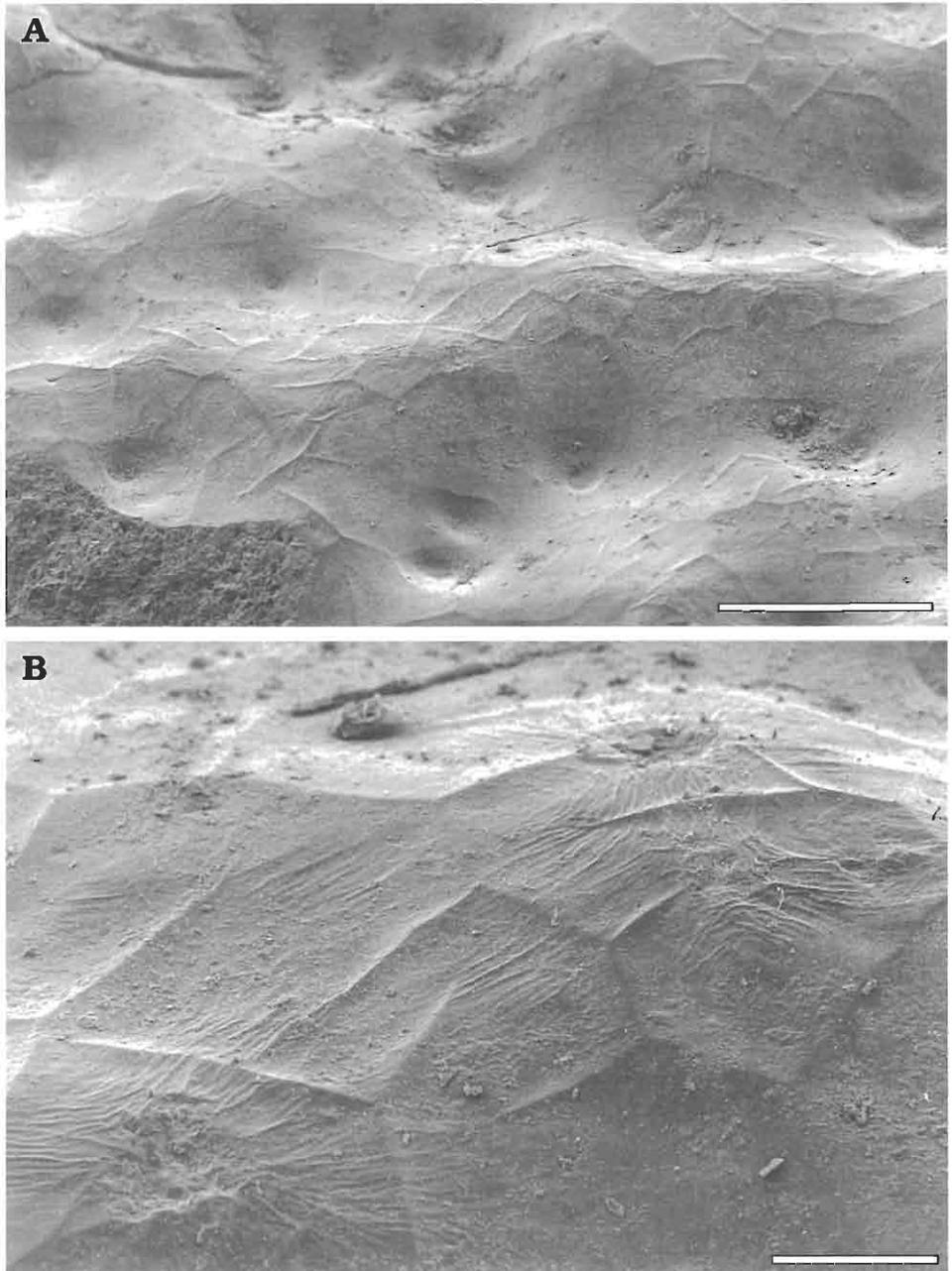


Fig. 13. SEM micrographs of counterpart surface of the branchial region of *Antarcticidromia inflata* (ZPAL Cr. I/7). **A.** Undulose surface of counterpart with position of bosses appearing as depressions. Scale bar – 1 mm. **B.** Enlargement of surface between bosses showing details of wrinkled surface. Scale bar – 200 μ m.

widely between the two species examined. The relatively thick exocuticle of *Antarcticidromia* overlies a moderately densely calcified endocuticle which results in a rigid carapace.

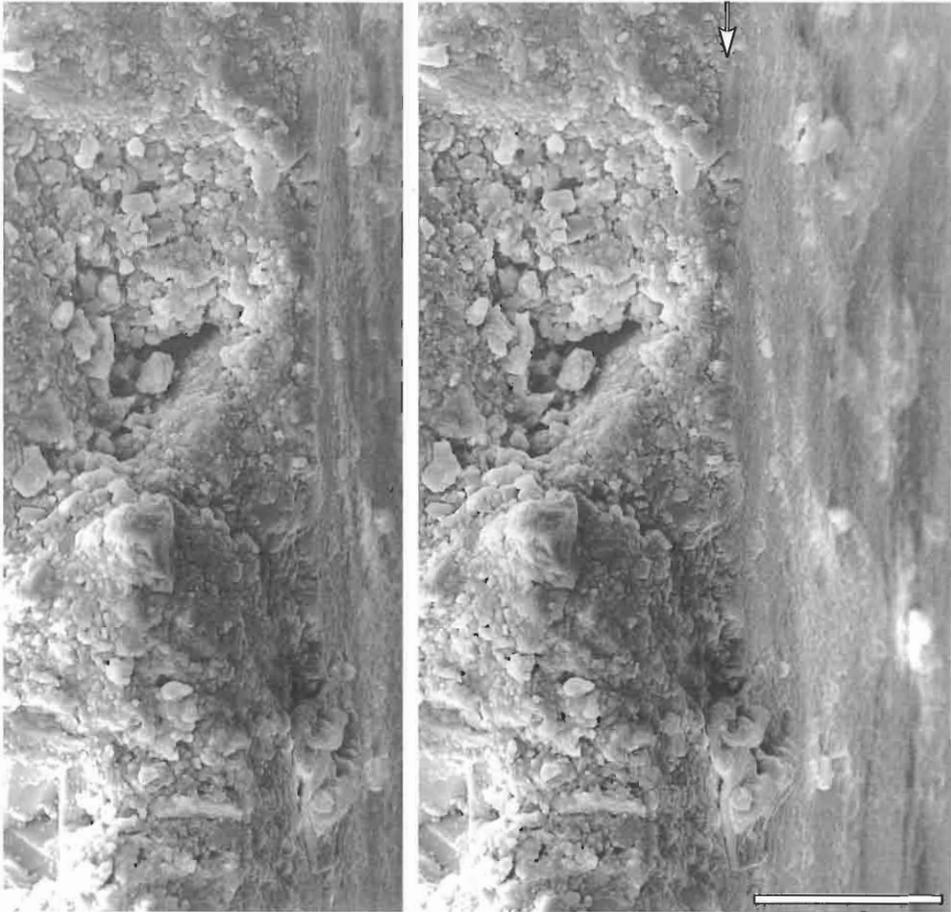


Fig. 14. SEM stereo-micrograph of broken edge of counterpart of *Antarctidromia inflata* (ZPAL Cr. 1/7) showing the thin layer of epicuticle (arrow) adherent to the rock surface. Scale bar – 20 μm .

The proportionately thinner exocuticle of *Homolodromia* and the more weakly calcified endocuticle of that species produces a more flexible carapace. The carapace becomes even more flexible in marginal regions of the branchial chambers where calcification is limited to precipitation of discrete nodes on the chitinous framework. The differences in degrees of calcification may reflect differences in ecological setting of the two species. The bathymetric setting of the Cape Melville Formation on King George Island, Antarctica, has been interpreted (Gaździcki 1987; Hara 1994) to be no deeper than an outer shelf or uppermost continental shelf, whereas *Homolodromia paradoxa* is known to range from outer shelf depths into bathyal environments. Rathbun (1937) recorded a depth range for *H. paradoxa* as 651–863 m. A second species, *H. bouvieri* Doflein, 1904, ranges through depths of 850–960 m (Martin 1992).

The absence of evidence for decalcification of the lower layers of endocuticle in *Antarctidromia inflata* corroborates observations on the general morphology of the

fossils that the specimens from the Cape Melville Formation are largely of corpses rather than molts. The specimen that was sectioned was buried during its intermolt phase. Only one specimen can positively be identified as a molt.

Exfoliation of the epicuticle in *Homolodromia paradoxa* suggests that two different types of surface texture might be recognized on extant material. Extreme caution must be applied when examining fossil decapods preserved in manners similar to that of *Antarctidromia inflata*. Because the epicuticle may separate readily from the exocuticle, it is possible that details of surface sculpture might be overlooked resulting in misleading descriptions.

Acknowledgements

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Mikrostruktura pancerzy kopalnych i współczesnych krabów z rodziny Homolodromiidae

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Streszczenie

Badania mikrostruktury pancerzy krabów z rodziny Homolodromiidae Alcock, 1899 oparto na pochodzącym z utworów wczesnego miocenu Wyspy Króla Jerzego (Antarktyka) gatunku *Antarctidromia inflata* Förster, 1985 oraz żyjącej współcześnie w rejonie Karaibów *Homolodromia paradoxa* A. Milne Edwards, 1880.

U okazów kopalnych rozpoznano, na podstawie porównania z okazami współczesnymi, epikutykulę, egzokutykulę i endokutykulę oraz przedstawiono ich charakterystykę w oparciu o badania w mikroskopie skaningowym.

Kompletne zachowanie okazów, a także obecność endokutykuli u *Antarctidromia inflata* wskazuje, że reprezentują one zespół pogrzebanych osobników, a nie wylinki.