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A re-evaluation of the Gondwanan invertebrate *Waiparaconus* as a coelenterate

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Abstract

The remains of *Waiparaconus*, an enigmatic calcareous invertebrate, have been known from Palaeocene deposits in the Middle Waipara Gorge of Canterbury, New Zealand, since the early 1870s. More recently, similar material has been collected from the late Cretaceous of Antarctica and Western Australia, and the Eocene of South America, demonstrating a Gondwanan distribution. These marine fossils have previously been interpreted as either rudistid molluscs or lepadomorph cirripedes, and even though it is clear that the remains are neither of these, many writers continue to include them within the Cirripedia. This paper re-examines the disposition of *Waiparaconus* from the Waipara Greensands, analyses gross morphology, and concludes these remains are most reasonably interpreted as an internal skeleton. It is proposed that *Waiparaconus* lies within the Waiparaconidae, a new family of the Anthozoa. At ordinal level, *Waiparaconus* shows similarity to the pennatulacean octocorals, but inclusion within this order is not warranted, both because of the uniquely waiparaconid imbrications (which are interpreted as attachment sites for rachides or polyps), and an unclear understanding of its mode of life. The austral endemism, and age of *Waiparaconus* suggest a Gondwanan origin for the family.

Introduction

In 1871 Julius von Haast described some "fossil shells" he had collected from the "....thick greensand strata overlying the Septarian clays..." of the middle Waipara Gorge, Canterbury, New Zealand, as "....allied to *Radiolites*", a rudistid bivalve. The same horizons were later collected by Thomson (1920) who, after rejection of any affinities with the Plantae, classified them as inorganic. Their similarity to the heavily calcified lepadomorph peduncles such as *Euscalpellum eocenense* (Meyer) from the southern United States prompted Withers (1951) to ally them with other "monstrously developed peduncles" within the cirripede genus *Euscalpellum*. Withers acknowledged that although none of the "peduncles" were associated with capitular valves, they were sufficiently like *Euscalpellum eocenense* to be included within the same genus. The position in the Lepadomorpha was maintained by Newman, Zullo and Withers (1969), although they gave only very brief reference to the solid peduncles. Buckeridge (1983) re-examined the material and concluded that it was not cirripede. In doing so, he proposed the replacement name *Waiparaconus*, but did not pursue formal systematic location. This paper specifically addresses the issue of systematic placement.

Buckeridge (1983) noted that the reconstruction proposed by Withers (1951) identified the broader end as the upper (= younger) part of the structure. This gave rise to

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confusion with respect to the direction of "plate" (= imbrication) growth, for if Withers' plan were adopted, it would follow that these imbrications must all have been pendant, a condition unknown amongst cirripedes. Further, no known *confirmed* cirripede, either fossil or extant, possesses a solid calcareous peduncle.

Subsequently, Seilacher (1984), and Seilacher and Seilacher-Drexler (1986) have again placed *Waiparaconus* within the Cirripedia, this interpretation being based primarily upon what they considered to be isolated capitular valves found with the New Zealand material.

Since Haast's original report, similar material has been described from a number of regions: Antarctica, New Zealand and South America (Withers 1951); Antarctica (Newman and Ross 1971); New Zealand and Australia (Buckeridge 1983). All of this material has been recovered from late Cretaceous-Eocene strata, and has a distinct "southern oceans" distribution. This paper has arisen following extensive fieldwork at New Zealand locations (during 1985-1992), study of the Western Australian specimens, the material described by Withers (1951), and that collected by W.J. Zinsmeister from Seymour Island, Antarctica (Zullo, Feldmann and Wiedman 1988).

Waiparaconus has been recovered from strata with complex faunal assemblages at Seymour Island, Antarctica, and at Kaynaba, near Dandaragan, Western Australia. In New Zealand it occurs very abundantly in restricted horizons in the Waipara Greensands of Canterbury, thousands being preserved in thanatocoenoses as the sole macrofossil (Figure 1). An examination of the inferred "capitular valves" of Seilacher and Seilacher-Drexler (1986) and of similar material, including that held at the Canterbury Museum, Christchurch, N.Z., suggests that they may better be interpreted as broken fragments of the broader ends of the stalks. Although most stalks appear to be remarkably well preserved, some, especially from the Waipara type location, are fractured around the broader end. The resultant fragments are arcuate, and in thin section could appear similar to cross-sections through cirripede capitular valves, especially when fragments of smaller individuals have been entrapped within the internal cavity of larger stalks. Excavation of specimens held both by Canterbury Museum and the New Zealand Institute of Geological and Nuclear Sciences, Lower Hutt, plus further field collecting, has failed to reveal any material that possesses the shape or growth patterns characteristic of lepadomorph capitular valves.

Systematics

Phylum Cnidaria Hatschek, 1888

Class Anthozoa Ehrenberg, 1834

Subclass Octocorallia? Haeckel, 1866

Order Incertae sedis

Discussion

Waiparaconus Buckeridge, 1983, is represented in the fossil record as arcuate, calcareous, non septate, conical tubes. In section, the tubes are comprised of concentric

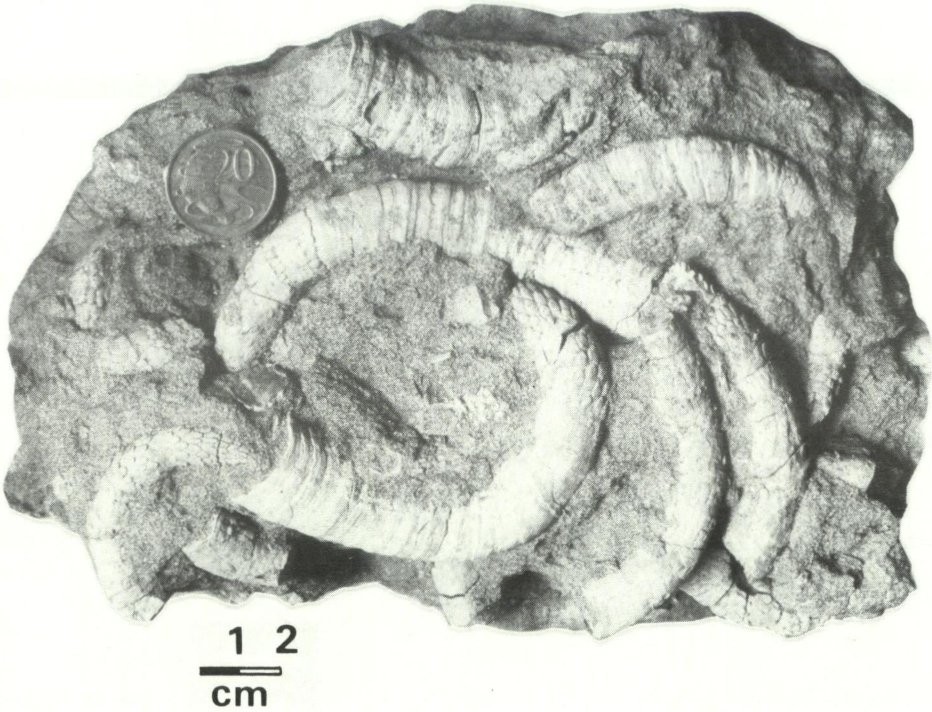

Figure 1 *Waiparaconus zelandicus* (Withers). **G050d:** Numerous stalks from the Waipara Greensands (Landenian), Middle Waipara Gorge, New Zealand, showing preservational disposition. The rigid calcareous stalks are relatively brittle, and are likely to have either been protected by soft tissue during transportation, or to have only been transported a short distance.

laminae of fine radiating calcite crystals, features which can be interpreted as anthozoan. *Waiparaconus* is unlike any known octocoral, particularly in its gross morphology and symmetry; it seems however, to represent an octocoral-like internal skeleton. It was developed as a series of concentric calcareous cones, and retains structures that can be interpreted as attachment sites for polyps, or polypiferous rachides. The informal ordinal location, and the tentative inclusion within Subclass Octocorallia reflect the uncertainty that still surrounds not only the total morphology of the organism but detail of its mode of life.

Family Waiparaconidae fam. nov.

Diagnosis

Massive, calcareous, internal skeleton comprising an elongate, semicircular, arcuate cone, with a central cavity, opening from a fine tube at the narrower, (proximal) end to occupy the entire diameter at the broader (distal) end; length characterised by medium to small imbrications, (possibly attachment sites for polypiferous rachi), each of which may

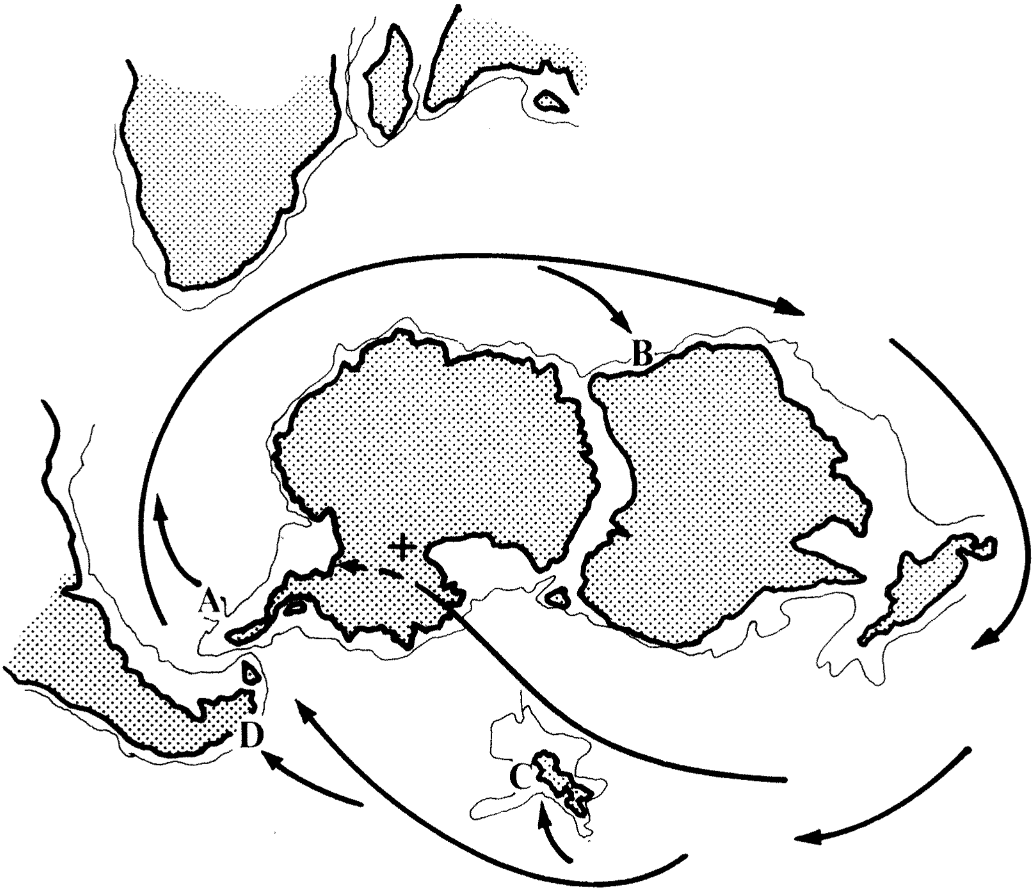

Figure 2 Known distribution the Waiparaconidae. Palaeogeographic reconstruction of the southern hemisphere at the close of the Cretaceous. The fine line surrounding the stippled areas represents the continental shelf at that time, with the "+" marking the south pole location. Arrows show oceanic circulation routes for the period Campanian-Maastrichtian, as inferred from foraminiferal biogeography (adapted from Huber, B T, 1988; BMR Palaeogeographic Group, 1990). An origin for *Waiparaconus* near Antarctica (site "A"), or Australia (site "B"), is likely, with subsequent colonization of New Zealand (site "C") at the close of the Cretaceous, and southern South America (site "D") in the early Cainozoic.

be totally or partially fused to adjacent imbrications; in fully fused varieties, imbrications become less abundant toward the distal end, where they are also increasingly submerged beneath more recently deposited calcareous lamellae.

Discussion

Amongst living octocorals, *Waiparaconus* shows greatest similarity to the Pennatulacea (sea pens), an order characterised by a calcareous or horny shaft, surrounded by coenenchyme which may contain calcareous spicules. Polypiferous rachi arise from the upper (proximal) part of the shaft, with the lower portion anchoring the colony in the bottom sediment. In the pennatulaceans, the rachi are generally arranged bilaterally, whereas in *Waiparaconus* rachi would have emerged from all sides of the shaft, each attached directly to an "imbrication". Like the pennatulaceans, the lower (distal) part of the shaft was probably buried in sediment, acting to anchor the colony. Most specimens show greater wear (corrosion?) at the distal end, suggesting that the protective soft tissue may have been restricted to the middle and upper portions of the stalk. A cross-section through the stalk of *Waiparaconus zelandicus* with its fine radiating calcite crystals superimposed on concentric growth rings (Figure 3) is very like the structure observed the New Zealand Oligocene pennatulacean *"Graphularia" longissima* Squires. The lack of imbrications on any pennatulacean shaft is the prime reason for excluding *Waiparaconus* from that order.

Distribution

Late Cretaceous (Santonian) to Palaeocene (Landenian), ?Upper Eocene (Bartonian); austral. Associated with glauconitic or glauconitic chalk horizons.

New Zealand, Teurian (= Landenian). Australia, Santonian. Antarctica, Middle Campanian. South America, ?Bartonian.

Palaeogeographic reconstructions of the late Cretaceous to early Palaeocene show only a partial break-up of the Gondwana supercontinent (Figure 2) at this time. The dispositions of the continents provide a continuity for *Waiparaconus* to range from Western Australia to the southern, circum-Pacific Weddellian Province of Zinsmeister, (1976). Circum-polar currents are inferred from foraminiferal studies (Huber, 1988), and may have provided a opportunity for *Waiparaconus* to disperse.

Palaeoecology

All material recovered to date is associated with glauconitic and glauconitic chalk sediments. Glauconite typically forms near the edge of the continental shelf, in warm waters (15-20° C), with low sedimentation rates. Similar conditions, resulting in glauconite formation, occur today off the west coast of Australia. The Western Australian *Waiparaconus* is preserved in the slightly glauconitic Gingin Chalk (Carter and Lipple, 1982), and water depths in that region during the late Cretaceous are interpreted as having been mid shelf or shallower, with widespread carbonate shoals (BMR Palaeogeographic Group, 1990). The New Zealand *Waiparaconus* shows strong evidence of having been transported, and is restricted to thin horizons adjacent to scour-and-fill and cross bedding. Most of the specimens lie sub-parallel to bedding planes, and are randomly oriented in this plane (Figure 1).

Waiparaconus from Waipara is less well preserved than specimens from other localities, and show characteristics that have been interpreted by Withers (1951) as weathering. This surface damage is however better described as solution pitting, a diagenetic feature, as pits tend to form where quartz grains, (which are common in the Waipara Greensand at this locality), come in contact with the calcareous stalks (Figure 4).

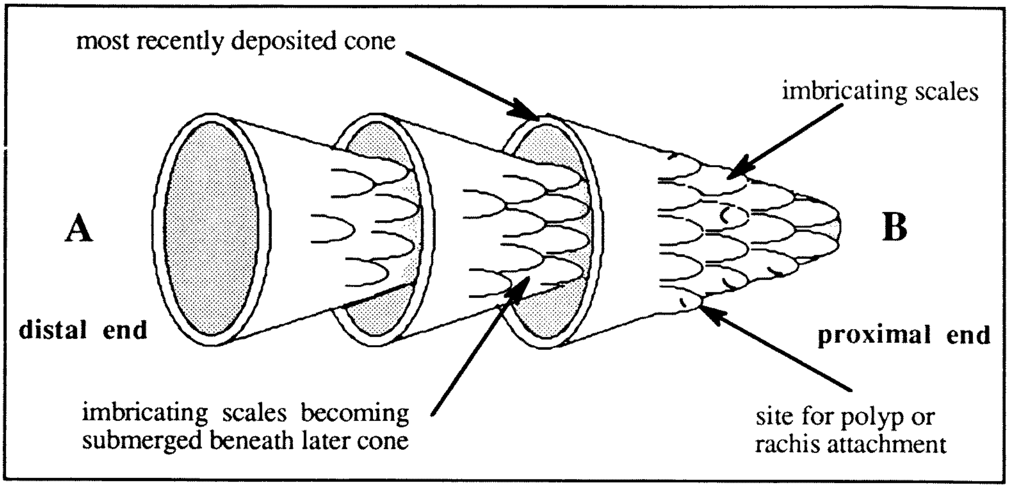

Figure 3 *Waiparaconus* structure. Exploded diagram of "Model 1", illustrating sequential growth in *Waiparaconus zelandicus*. Growth was accompanied by the deposition of successive cones of calcite with associated imbrications. In this process, older cones and imbrications (at end A) become submerged beneath younger (at B). Calcite deposition occurred over most of the shaft length, and although new layers thinned out toward the distal end, this part became broader as the structure lengthened.

Morphology

Buckeridge (1983) dealt specifically with the New Zealand and Australian material, all of which possess fully fused stalks. Further consideration of the specimens described in Withers (1951) shows that stalks in material from outside Australasia were less completely fused. In light of this, and to more fully appreciate the systematic location of *Waiparaconus*, specimens from the Lopez de Bertodano Formation, Seymour Island, Antarctica were examined. Unfortunately the South American (Tierra del Fuego) specimen could not be located.

In all specimens, the stalks are composed of calcite. The manner in which this was laid down may be interpreted in two different ways: In "Model 1", deposition occurred as a series of concentric cones, each cone being made up of fine calcite needles radiating out from about the geometric centre of the structure (Figure 3). These cones developed a series of imbrications on the outer surface, and these are particularly well preserved at the proximal end of all stalks. In specimens from New Zealand and Australia, the imbrications become progressively isolated towards the distal end. This is interpreted as being due to burial beneath successive, newer layers of calcite as the structure increased in size.

In "Model 2", growth would have occurred in precisely the opposite direction. This plan is favoured by Seilacher (1984), and Seilacher and Seilacher-Drexler (1986) who interpreted the "imbricated end" as the portion buried in the sediment, with filamentous anchors extending out from the imbrications. Seilacher proposed that the open end (here termed distal) housed diminutive capitular valves and associated soft parts.

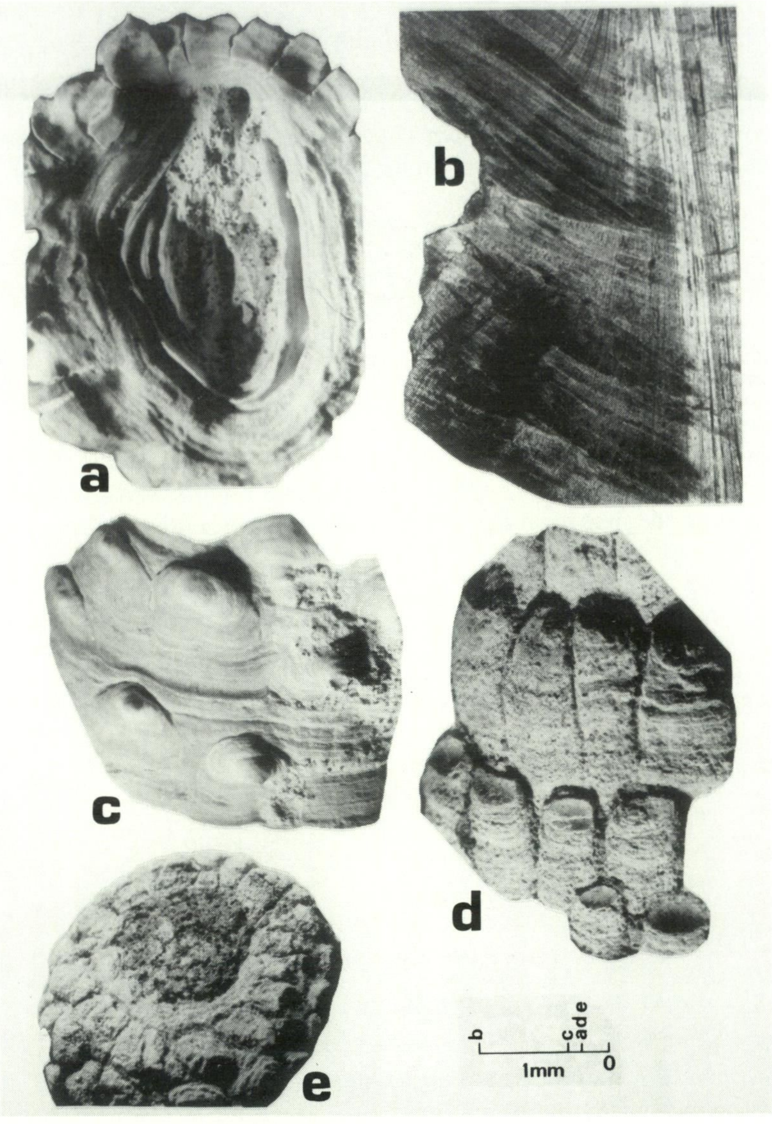

Figure 4 Morphology of *Waiparaconus* imbrications. **a:** apex of specimen **G071a** from the Gingin Chalk, Dandaragan, Western Australia. Santonian. **b:** Longitudinal section through **77.3532b,** from Kaynaba Homestead, Dandaragan, Western Australia. Santonian. **c:** detail of imbrications on **G071a,** showing proposed attachment sites for rachi; note that the distal part of imbrications may be reflexed. **d,e:** Portion of stalk from **G050a,** showing decortication of, and pressure solution effects on, the imbrications. **e:** apical region of **G050b**, showing development of new imbrications. Both G050a and G050b from Middle Waipara Gorge, Canterbury, New Zealand. Landenian.

Analysis

"Model 1" is supported by thin section analysis of material from New Zealand and Western Australia. Conic growth lines pass through imbrications, and thus represent the main structural element. This interpretation appears consistent with the Antarctic specimens, where although imbrications appear to retain much greater integrity, growth lines clearly pass through them to the more solid inner structure (Figure 4).

Genus *Waiparaconus* Buckeridge, 1983

Waiparaconus Buckeridge, 1983: 116.

Waiparaconus, Seilacher and Seilacher-Drexler, 1986:79

Diagnosis and Distribution

As for family.

Composition

At present a monospecific genus: *Waiparaconus zelandicus* (Withers). Type locality: Waipara River, North Canterbury, New Zealand. *W. zelandicus* is selected as type by precedence, being the first form described by Withers (1951).

Waiparaconus zelandicus (Withers, 1951)

Figures 1, 4a-e, 5a-h, 6a-f

Euscalpellum zelandicum Withers, 1951: 155-157, Pl.11, figs 1-3, Pl.12 fig. 1.

Euscalpellum antarcticum Withers, 1951: 157-158, Pl.12, figs 2-4.

Euscalpellum crassissimum Withers, 1951: 161-162, Pl.14, figs 1-5.

"Cirripede peduncle" Glaessner, 1956: 33, figs. 2a-2d.

Waiparaconus zelandicus (Withers), Buckeridge, 1983: 116, Pl.13a-f.

Diagnosis

Stalks massive, arcuate; imbrications with a single terminal tubercle; interior with longitudinal grooves, produced by fusion/partial fusion of adjacent imbrications.

Distribution

Late Cretaceous to Palaeocene, ?Upper Eocene; austral.

Discussion

Three distinct morphotypes of *Waiparaconus zelandicus* exist, and these have previously been recognised as different species (Withers, 1951). Distinction was made on the basis of the imbrications, i.e. whether they were completely or partially fused, and/or were narrow or broad. Material examined from Australia by Buckeridge (1983), and further specimens collected by Zinsmeister from Seymour Island, have shown the distinctions between the different forms to be less clear than originally thought, with a continuous sequence now being discernible: from a form with adjacent imbrications being weakly fused to one in which fusion (and subsequent calcite deposition) almost obliterates traces of older imbrications (Table 1). Rather than representing an

Table 1 Distribution of *Waiparaconus zelandicus* with known ranges in imbrication morphology from each region. The Antarctic (Seymour Island) material (Figures 5a-f, 6e,h) shows by far the greatest morphological variation, and if the new material from this location, and that from Australia had been available to Buckeridge (1983) and perhaps to Withers (1951), it is unlikely that specific separation would have been mentioned.

location	imbricating scales	age
Australia	moderately narrow; almost completely fused into the stalk, suture lines very fine, traceable for short distances; apex wide.	Santonian
Antarctica	moderately narrow; partially or almost completely fused into the stalk, sutures traceable for almost entire length; apex narrow to wide.	Campanian - Maastrichtian
New Zealand	moderately narrow; completely fused into the stalk, sutures traceable for very short distances only; apex narrow or wide.	Landenian
South America	broad; incompletely fused into stalk, nature of apex unknown.	Bartonian

evolutionary change, it is suggested that these differences would better be interpreted as reflecting variations in environmental conditions.

The Seymour Island material includes a stalk with the greatest known diameter (Figure 5a-c). In this specimen, the number of imbrications increases in proportion to the diameter: in early stages up to twenty imbrications appear in cross-section, this number increasing to over fifty with a doubling of the diameter. This type of growth, with the insertion of "secondary imbrications", is analogous to septa addition in anthozoans but is not a characteristic of the lepadomorph cirripedes. Withers (1951) discussed the similarity of this material to the Eocene lepadomorph *Euscalpellum eocenense* (Meyer), a peduncle of which (No. Z. 672) from the Cook Mountain Formation, Mississippi, was examined. *E. eocenense* peduncular scales are more discrete than *Waiparaconus* imbrications, they possess no terminal tubercles and their growth lines can be traced between adjacent scales. The growth lines do not arc inwards, but run parallel to the side of the peduncle, as would be anticipated if growth had occurred from the base. More importantly, the scales in *E. eocenense* are oriented in precisely the opposite direction to the imbrications of *Waiparaconus*, i.e. the peduncle increases in diameter from the base to the capitular end, with all scales erect.

Note: Other cirripede remains (capitular valves) that occur in the Cook Mountain Formation, are not intimately associated with this material. In light of this, it remains to be confirmed that the valves and the peduncle attributed to *E. eocenense* are of the same taxon.

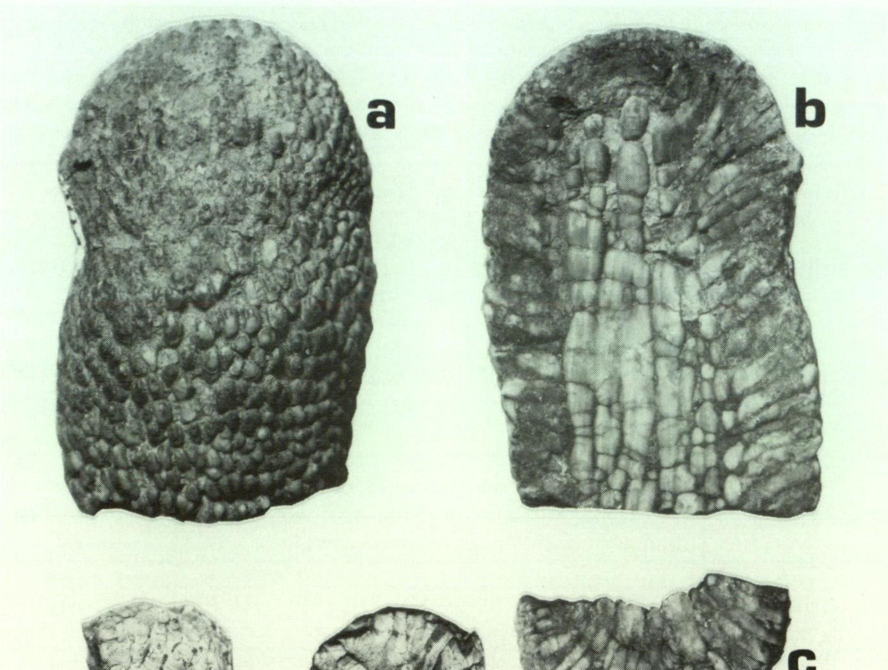

Figure 5 Antarctic *Waiparaconus*. **a,b,c:** external view, longitudinal section and cross section of specimen **1115**, Dagger Peak, Seymour Island. Campanian-Maastrichtian. **f:** Specimen **508** from same locality. **d,e:** Specimen **In 43813.** Stalk showing weakly cemented imbrications with external view, (d) and longitudinal section (e). From slope between Dagger Peak and Comb Ridge, Seymour Island. Campanian-Maastrichtian. Note: This specimen was initially figured as the holotype of *Euscalpellum antarcticum* Withers, in Withers (1951).

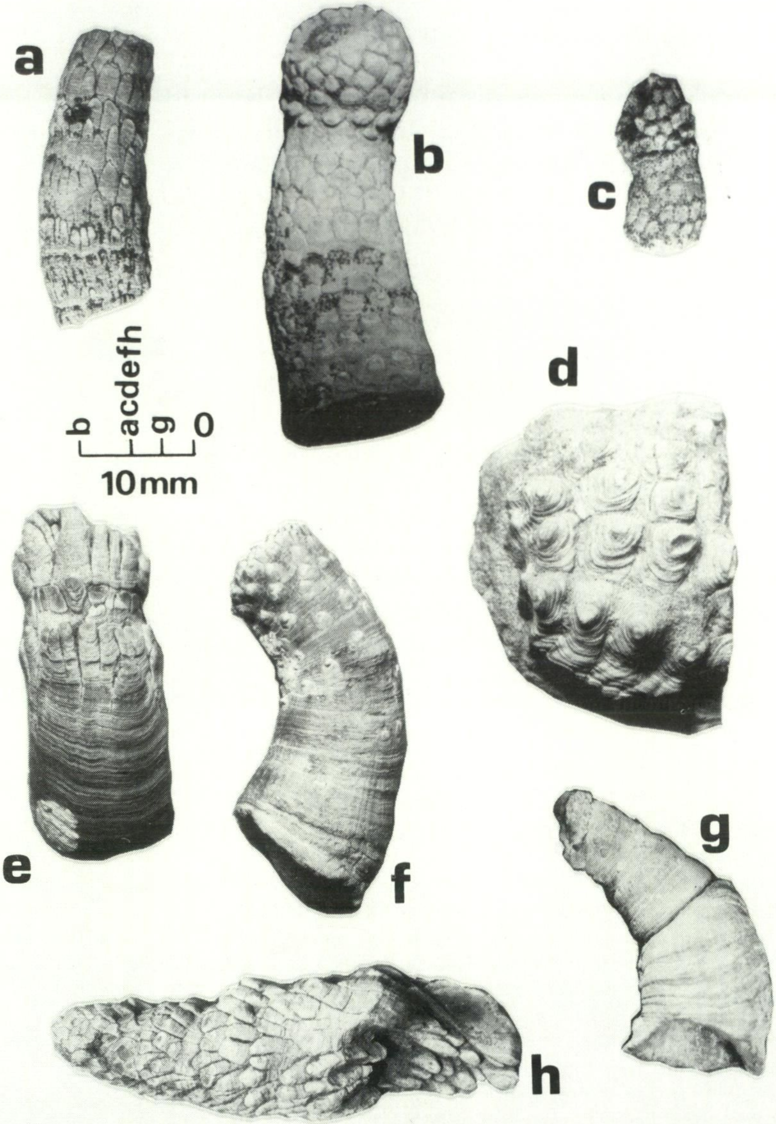

Figure 6 *Waiparaconus* stalk variation. a: Specimen **G050a**; **b:** Specimen **G050b**; **c:** Specimen **G050c** both from Middle Waipara Gorge, New Zealand. Landenian. **d:** Large "globular" specimen, **AR 2095** from Old Claverley Stream, Canterbury, New Zealand. ?Maastrichtian. **e,h:** Seymour Island material from Dagger Peak, **82a** showing extensive (e), and **82b,** partial fusion (h), of imbrications. Campanian-Maastrichtian. **g:** Large specimen with distally expanded base and almost complete fusion of imbrications. **77.3532a**, from Kaynaba, Dandaragan, Western Australia. Santonian. **h:** Well fused specimen with weakly expanded distal portion. **G070a** from Gingin Chalk, Dandaragan, Western Australia. Santonian.

Repositories

Material referred to in this paper was sourced from the following institutions: The Natural History Museum, London, for all specimen numbers prefixed by **In**; the Western Australian Museum, Perth for specimen numbers with no prefix, but typically **77.3532a**; the New Zealand Institute of Geological and Nuclear Sciences for specimen numbers prefixed by **AR**; specimens from the William J Zinsmeister Collection have three or two digits with no prefix, e.g. **1115**, and these are all held by Professor V. A. Zullo, University of North Carolina. All other material, prefixed by **G** is held by the author at Carrington Polytechnic.

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