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MARINE, BENTHIC OSTRACOD ECOLOGY, TAPHONOMY AND EVOLUTION - STUDIES FROM THE SOUTH WEST PACIFIC

BY

KERRY MICHAEL SWANSON

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ABSTRACT

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Results of over twenty five years of ostracod (Crustacea) research in the south west Pacific, especially the New Zealand region are documented. These studies have focussed on three themes which may be broadly categorised as: a) systematics, b) ecology/taphonomy and c) evolution.

With respect to the systematics of Ostracoda, forty nine new species, one new subgenus and five new genera have been described. From Lower Miocene shelf sediments of the Middle Waipara District of north Canterbury I have described as new (Swanson 1969), the following taxa: *Cytherella elongata, Cytherella hemipuncta, Cytherelloidea willetti, Bairdia canterburyensis, Callistocythere hanaii, Munseyella rectangulata, Hemicythere hornibrooki, Waiparacythereis joanae, Waiparacythereis caudata, Waiparacythereis decora, Urocythereis? opima, Quadracythere claremontensis, Cytheridea symmetrica, Neocytherideis mediata* and *Cytheropteron mosaica.* The new genus *Waiparacythereis* described at that time was subsequently found by me living in littoral sediments at many localities throughout the New Zealand region. My description of the soft anatomy of that animal published in 1982, confirmed the assignment of those taxa to the subfamily Hemicytherinae. Involvement with a University of Otago led to an investigation of the benthos of the Otago Shelf and resulted in more precise determinations of distribution of the ostracod biocoenose and the description of nineteen new species, one subgenus and one new genus. The species described by me as new in New Zealand oceanographic Memoir 78 were: *Anchistrocheles araforma, `Bythocythere' bulba, Pseudocythere (Plenocythere) fragilis, Munseyella brevis, `Munseyella' arca, Munseyella modesta, `Munseyella' tumida, Kotoracythere formosa, Callistocythere neoplana, Callistocythere obtusa, Hemicythere munida, Bradleya opima, Hermanites andrewsi, Hermanites briggsi, Jacobella papanuiensis, `Cythereis' incerta, Ponticocythereis decora, Semicytherura arteria* and *Semixestoleberis taiaroaensis.* The hemicytherinid genus *Jacobella* and bythocytherinid subgenus *Pseudocythere (Plenocythere)* were new to science. Benthic samples from the most southern of New Zealand's three main islands were also examined for ostracods and from that assemblage, five new species and one new genus were described (Swanson, 1980): *Tanella dedeckkeri, Kangarina unispinosa, `Loxoconcha' tubmani, Microxestoleberis triangulata* and the new monospecific, bythocytherinid genus *Microceratina* with *M. quadrata* as the type species. Involvement in a project examining late Pleistocene carbonate lake deposits from alpine South Island resulted in the discovery of a new freshwater ostracod species of the genus *Paralimnocythere.* Subsequently, living representatives of the new species *Paralimnocythere vulgaris* were recovered by me from a small pond near Lake Tekapo, South Island. This material enabled a detailed description of both the carapace and soft anatomy of that species to be made (McKenzie and Swanson, 1981). The ostracod assemblage of the Australasian region remains poorly known with many new and interesting taxa yet to be described. Co-operative projects examining ostracods from Cenozoic sediments of South Island and recent material from offshore sites in the Tasman Sea have, to date, resulted in the description of two new ostracod

genera and six new species (Ayress & Swanson, 1991). One new genus *Bisulcocythere* was based on descriptions of five species *B. novaezealandiae, B. eocenica, B. micropuncta, B. compressa* and *B. campbelli*, the other *Clinocythereis* is at present represented only by the type species *C. australis*. In 1989 after a detailed examination of carapace morphology, soft anatomy and ontogeny, I became the first researcher to publish details of a new living species of punciid ostracod *Manawa staceyi.*

With respect to the distribution and ecology of the extant, marine podocopid ostracod fauna, significant tracts of the shelf and slope off Otago and Westland have been examined and the hydrologic/sedimentologic character of some niches defined (Swanson, 1979 and 1993 unpub. thesis). Such data is of considerable value for continuing studies of the deep-sea record of latest Quaternary climatic events, and of ostracod shell-chemistry as a paleothermometric tool. Syndiagentic alterations of both shallow and deep water, benthic, podocopid ostracods have been identified establishing a) a more vigorous routine for sample selection for shell chemistry and b) a new hypothesis relating to the evolution of carapace architecture (Swanson & van der Lingen, 1994; Swanson, in press). It is probable that the need to evolve a dissolution-resistant exoskeleton in an environment in which alkalinity fluctuated significantly has been a key determinant with respect to ostracod evolution and, the invasion of the psychrosphere by that group. A statistical measure of ostracod carapace corrosion (CI) is not only useful for paleothermometric studies, but also provides useful proxy data for fluctuating levels of paleoproductivity in surface waters (Swanson & van der Lingen, 1994; in press).

The discovery of living representatives of the enigmatic punciid ostracod *Manawa* in very shallow waters of northernmost New Zealand is of considerable scientific interest (Swanson, 1985a and 1987). Results of this research have established (a) that the gait of *Manawa staceyi* is found in no other extant ostracod and (b), that condition (valves fully extended horizontally) is plesiomorphic for ostracods - an observation confirmed by the fact that open-gapedness is recorded commonly in Cambrian palaeocopid assemblages (Swanson, 1989a). I have also concluded the existence of a dome-shaped valve on some larval stages and the subsequent development of bivalvedness provides a window to the evolution of both the hinge and sensory systems in `modern' podocpid ostracods (Swanson, 1989a and 1990a). With respect to the soft anatomy, the trunk of *Manawa* has ten segments (herein considered plesiomorphic for ostracods), but reported homologies with *Cytherella* are now considered superficial (Swanson, 1990b). Determination of the exact position of attachment (vis. thoracid segmentation) of the copulatory apparatus of the playtcopids and punciids is of considerable importance with respect to the phylogeny of Crustacea in general and Ostracoda in particular. However, my studies have shown that such a result is most likely to be achieved by a histological examination of specimens rather than observation of external morphology. Unexpectedly, the latter approach did establish a new technique for differentiation of various species of *Cytherella* using differential interference contrast and SEM examination of the adult hemipene (Swanson, 1991). The fact that *Manawa* carries three cephalic limb pairs and four on the thorax is at odds

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with prevailing views - the `normal` configuration being four cephalic, two to the thorax and one to either the thorax or the cephalon. However, this apparent contradiction is explained by observations made on one specimen of Cambrian phosphatocopine `ostracod' in which four `thoracic' indentations were observed on the interior surface of the carapace (Jones & McKenzie, 1980). Thus, in the living punciid ostracod we are able to observe the last remaining renmant of a group of ostracods whose decline was initiated over 500 million years ago.

INTRODUCTION

Published results of investigations of both the marine and freshwater components of the New Zealand ostracod fauna are few - a true reflection of the state of knowledge of that assemblage. With respect to the fossil, marine ostracod assemblage, it was, and still is, unlikely that that group would ever supercede the foraminifers as the key biostratigraphic species. Using foraminifers, New Zealand micropalaeontologists have developed a series of biostratigraphic `zones' for both the Cretaceous and the Cenozoic, recognised internationally for their precision and utility. To a large extent, it was the early recognition of this utility which provided the impetus for the establishment of foraminifers as the most important biostratigraphic marker. In a bid to reduce its dependence on imported fossil fuels, the post-war government of New Zealand established exploration for oil and gas as a key objective. The then New Zealand Geological Survey was given as one of its briefs, the scientific support of that programme. As a consequence, a significant part of the total micropalaeontological research effort was directed to that end - foraminiferal research progressed at the expense of less favoured or less well-known taxa. In almost two decades from 1950, only three significant publications on New Zealand marine ostracoda were published (Hornibrook 1962, 1953 & 1963).

In 1965, this writer initiated a research project with the objective to investigate ostracodal biostratigraphic precision in Miocene sediments of the Middle Waipara District. The results, published in 1969 will be discussed more fully later in this text. Increasingly during that time, sedimentologists and field geologists mapping the vast expanse of Cenozoic sediments in New Zealand were calling for more and more precise palaeoenvironmental data. The quality of such information is only as good as data which defines constraining environmental parameters for the extant equivalents of the fossil assemblage being studied. Although, as will become evident through this text, a number of other research objectives have temporarily diverted my attention, ultimately such efforts have proved to be of value with respect to improving the knowledge of extant, marine podocopid ostracods in the New Zealand Region.

As a result of both a long isolation (at least 80 million years according to Fleming, 1987), and significant climatic differences in the recent geological past, the flora and fauna of New Zealand contrasts sharply with that of the nearest landmass, Australia. As a consequence of this isolation, a significant proportion of the New Zealand flora and fauna is endemic and novel - the focus of much scientific attention. Additionally, the New Zealand subcontinental landmass straddles a very active plate boundary, this also has profoundly affected the character of the New Zealand biota. With respect to the marine realm for example, the sedimentary record in parts of the Tasman Sea (adjacent to that active plate boundary) is a continuous, late Cretaceous - Cenozoic sequence of flat-lying, little deformed, predominantly deep-marine sediments. Faunal and floral components of these sediments will exhibit a progressively oceanic aspect as sea-floor spreading progressed. Additionally, the character of marine filter barriers affecting migration routes into and out of the region will be altered by the dynamics of tectonic

activity associated with both sea-floor spreading and transform plate boundary processes.

Thus, ostracod research in New Zealand over the last three decades has been influenced by a perception of utility amongst geoscientists in general which was prejudiced in favour of foraminifera. Superimposed on this, has been an increasing awareness amongst members of the international scientific community that this land, Aotearoa is biogeographically unique. A vibrant, relatively unpolluted, living laboratory. The marine, podocopid ostracod fauna illustrates all those characteristics which differentiate the New Zealand biota from those found elsewhere. Endemism is common, mesozoic relics still survive on the shelf and slope and representatives of the once dominant paleocopids, survive at only a few localities in the littoral environment of northern New Zealand. As work progresses it is becoming increasingly apparent that much of the unique character of the marine podocopid fauna in this region is a direct result of habitation in an unstable environment. The origin of some now cosmopolitan deep-water ostracod genera can be traced to early Cenozoic sediments of the Tasman Sea - submergence of these taxa being achieved in a sense passively as sea-floor spreading progressed (Whatley, 1985; Whatley & Ayress, 1988; Ayress, 1994). Additionally adaptive responses associated with habitation in a bathymetrically and physico-chemically unstable environment are expressed in the morphology of the ostracod carapace. From an evolutionary point alone, such features are worth study. Increasingly however, such proxy data is being used to interpret the development of the oceans is general and the marine sedimentary record of Quaternary climate-change in particular.

IMPROVING TAXONOMIC PRECISION AND ECOLOGICAL DATA

During the period 1950 - 1965, a quiet revolution occurred is ostracodology. Increasingly, researchers adopted a `holistic' approach to systematic determinations, such, that all carapace characters were considered important. Prior to that, many taxonomic publications overemphasised one morphological feature (hingement especially), providing minimal descriptive information on other structures. Hornibrook's 1952 publication was significant for two main reasons. It was the first attempt to document in detail the New Zealand Cenozoic ostracod fauna, and secondly, it established a `style' of research and presentation with respect to carapace architecture in particular, worthy of duplication.

In an attempt to improve both taxonomic and, as a consequence, biostratigraphic precision, this writer undertook a study of marine, podocopid ostracods preserved in Lower Miocene sediments of the Middle Waipara District, New Zealand (Fig. 1). Results of this research were published in 1969. From a taxonomic perspective the research effort was well rewarded with 15 new species and one new genus being described amongst a total of 39 ostracod species discriminated (Pls 1 - 6). The new hemicytherid genus *Waiparacythereis* which exhibited considerable morphologic novelty with respect to both the marginal pores and muscle scars, has subsequently

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proved to be a key indicator of littoral depositional environments in New Zealand Cenozoic sediments. With respect to biostratigraphy, results from this study were disappointing. Of the 24 species originally described by Hornibrook and now recovered from Middle Waipara, ranges for 21 remained unchanged and for an additional 3, were extended.

About 1967, the late Dr Betty Batham (Director, Portobello marine Station, University of Otago) approached Dr Peter Andrews (Sedimentation laboratory, New Zealand Geological Survey) to promote a co-operative survey of the benthos of a large tract of shelf and slope adjacent to the Otago Peninsula. The present writer agreed to participate, encouraged by the fact that most samples would be preserved and that reoccupation of some sites a possibility. A total of 163 samples from water depths of 3 -750 metres were scanned for both `live' (soft anatomy present) ostracods, and valves (Fig. 2). Sixty three species were recognised of which, nineteen were described as new (Swanson, 1979a). One new genus *Jacobella* and one new subgenus *Pseudocythere* (*Plenocythere*) were proposed. Data from this project confirmed the enormous potential exhibited by ostracods for use as paleoenvironmental indicators (Table 1).

As a result of that Otago Shelf study, it was made abundantly clear that reliable distributional data for the extant ostracod population could only be achieved if living and dead populations of each species were discriminated. In fact, it was possible to distinguish four quite distinct ostracod populations, acknowledging the geographic limits of each population often merge. By plotting the occurrence of living specimens (in this study `living' was conservatively defined as ... appendages intact, internal musculature present), it became immediately obvious that in most cases, valves were distributed over a much wider area than the living equivalent (Figs. 3 - 6). That the biocoenose (living) is more restricted geographically than the thanatocoenose (death assemblage) is not a novel observation. What was worthy of note however was the fact that representatives of each assemblage could be found in most other assemblages - often as a significant component of that assemblage. Valves of *Waiparacythereis joanae*, a littoral species normally found living at depths of <30 metres, occurred quite commonly in samples straddling the edge of the continental shelf (120 - 155 metres). In contrast, valves of *Bairdoppilata* sp. an outer shelf species, were distributed over the entire inner-shelf to depths as shallow as 3 metres.

In an attempt to compare and contrast the effects of current reworking and sea-level change on present-day ostracod distribution on the Otago Shelf, it was necessary to also examine individual ostracod specimens with respect to preservation `state'. Relict and reworked populations being evidenced by abraded surfaces, opaqueness and corrosion. Once that had been achieved, it was then possible to not only accurately define the distribution of both the biocoenose and thanatocoenose for each species but also to document a depositional sequence for each assemblage.

A) **Dead `concentrations' directly associated with living species (biocoenose)**.
Unless affected by transport after death, it is expected that large accumulations of

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valves will occur in the area in which a particular species is living. For the majority of species on the Otago Shelf this has proved to be the case (Fig. 7). Such concentrations are generally larger in size (representing many generations of accumulation) and cover a slightly larger geographic area than that of the living equivalent. Very little, if any, post-mortem modification of these dead concentrations has occurred and for this reason they are considered a true biocoenose (see Fig. 7; traverse a-a, *Cytherella* sp., *Loxocythere crassa*, *Copytus novaezealandiae* and *Munseyella brevis*.

B) <u>**Dead `concentrations' associated with, but geographically displaced from the living counterpart (thanatocoenose**</u>). The effectiveness of various transporting agents in the dispersal of ostracod valves on the Otago Shelf is well illustrated by Assemblage 1 species (Table 1). Generally, large discrepancies between the biocoenose and the thanatocoenose exist. In most cases, living forms are restricted to shallow, near-coastal waters of the Otago Peninsula (see Figs. 5 & 6). Dead specimens however, are distributed over much of Blueskin Bay and the innermost part of the shelf. The dispersal of these dead forms and the formation of a thanatocoenose probably involves two phases of transport. Back eddies from the Southland Current (a northward flow with a core centred at about 50 metres and located over the 100 metre isobath), remove dead specimens from live populations, and transport them as detritus to a more northerly site. A second phase of transport involves wave action which distributes this material eastward and northeastward over the entire sea-floor of Blueskin Bay and parts of the inner shelf.

Some species living on the mid and outer-shelf (for example *Cytherella hemipuncta* Fig. 3) were also recovered from sediments of the inner-shelf and Blueskin Bay. Such occurrences are also attributed to reworking by both Southland Current eddies and north-easterly waves. Almost certainly, it would appear that Type B populations are relatively stable since at present only fine sand, very find sand and silt are being transported by the Southland current. Such a conclusion is recognised as tentative, for although there has been much speculation, little factual information has been published on the dynamics of ostracod carapace transport by hydraulic agencies.

C) <u>**Relict populations**</u>. Geological and sedimentological evidence suggest the likely occurrence of relict populations. Bathymetry indicates drowned shorelines at 56 - 59 metres, 84 - 110 metres and less clearly at 108 - 133 metres. Andrews (1973) concluded, on the middle and outer shelf off the Otago Peninsula, where the percentage of organic skeletal debris is greater than 20 - 30%, the sediments may be regarded as largely relict, having been deposited during times of lowered sea level. The distribution of most Otago mid-shelf and outer-shelf ostracod populations is consistent with this concept. In each assemblage, almost complete sequences illustrating the gradual deterioration of the ostracod valves occur. Opaque, yellow-brown strained (often matrix filled) valves representing forms of earlier generations, transparent shells and valves belong to more recent generations.

Interestingly, distribution of some relict forms indicates mixing of depth-controlled species has occurred. The presence of dead concentrations of shallow-water species of *Waiparacythereis joanae* (Fig. 6) and *Loxocythere crassa* (Fig. 7) at extreme depths, and often in isolation with respect to the living counterpart, excludes the possibility that these concentrations have been transported. The presence of thin-shelled, shallow-water species such as *Anchistrocheles arcaforma* reinforces this observation. For some years a somewhat heated debate amongst sedimentologists focussed on the origin of carbonate-rich sediments commonly found on the shelf around New Zealand. Andrews and his supporters favoured such deposits as relict, Schofield and his associates on the other hand attributed all the morphological features of the modern shelf as lag, separated by modern, fine-grained sediments the geometry of which reflects the long-shore course of the Southland Current. The present study contributed significantly to this debate providing evidence which substantiated the presence of relict deposits. Schofield (1976) indicated a virtual absence of shallow-water species in the documented offshore malacology, however, most of that data was for relatively small subsamples herein considered inadequate for a comprehensive study of the extant molluscan fauna. As previously indicated, the ostracod fauna gave a clear indication that relict deposits did occur on the Otago Shelf - an observation exemplified by the distribution of *Waiparacythereis joanae* (Fig. 6).

D) **Dead `concentrations' occurring in Canyons**. Specimens contribution to this type of accumulation have been displaced from the biocoenose which occurs on the eastern margins of the mid and outer shelf. Dispersal of sediments in and around canyon heads is not well understood but, work by van der Linden (1969) on offshore sediments of north-west Nelson, New Zealand, suggests that the sudden break in continental slope may give rise to considerable turbulence.

In 1975, the Portobello marine Station extended its survey of the marine benthos of South Island to include littoral sediments of Stewart Island. A total of 27 samples from Port Pegasus were made available to this writer but unfortunately none were preserved. A total of sixty one described species were listed from the southern-most part of New Zealand (excluding dependencies and protectorates), the 1979b publication being the first to illustrate a New Zealand ostracod fauna using scanning electron microscopy. In 1980, five new species of ostracod were described from the Stewart Island study area and, a peculiar bythocytherid was described as the type species of a new genus *Microceratina* (Pls 7, 8 & 9). Concerns expressed about the musculature (the Stewart Island material presenting variable dorsal adductor scars) and the resultant taxonomic determination were unwarranted. Recently, Yassini (1995) described two new species of that genus from recent sediments of the south-east coast of Australia and, in doing so confirmed the original systematic placement. A record of the genus *Tanella* is the most southern for this taxon originally described from Indonesia by Kingma (1949).

In 1979, the then New Zealand Oceanographic Institute initiated a seasonal study of productivity in waters off the west coast, South Island (WESP). This long-term program was to focus on primary productivity; this writer assumed responsibility for benthic

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samples, specifically sediment analysis and ostracods. Analysis of the soft anatomy of the New Zealand marine ostracod fauna had, to that point, never been attempted. From a paleontological perspective such research is warranted since almost universally, neontologists rarely describe the ostracod carapace in a manner appropriate for the study of fossil equivalents. The first full description of ostracod soft anatomy by this writer was in fact a joint effort (McKenzie & Swanson, 1981) which established a new freshwater species *Paralimnocythere vulgaris*. Dissecting skills developed during that research were then applied to *Waiparcythereis joanae*, results published in 1982 being the first independent confirmation of the status of that group as the thaerocytherids (Pls 10 & 11). Initial results from the WESP program indicated widespread occurrences of living specimens of the ostracod *Cytherella*. The fact that these ostracods presented a smooth, often heavily calcified carapace has led to the fact that genus is probably the poorest understood with respect to taxonomic precision and ecology. Because large numbers of specimens were available for study, it was possible to develop through experimentation a set of preparatory and microscopic routines unsurpassed in terms of detail and with few induced artefacts. Differential interference contrast for instance is an optical train configured in such a way that optical sectioning (based on variations of refractive index) of mounted appendages is possible. Such a technique not only improves chaetotaxic detail, but also allows investigation of both internal musculature and chitinous fabric (Pl. 12, Figs. F & H; Pl. 13, Figs B & H). Preparation of soft-part material for scanning electron microscope examination has always been recognised as time consuming and technically demanding. A relatively simple fixation-dehydration regime in preparation for critical point drying of entire ostracods has been repeatedly tested and documented (Swanson 1989b). As a result of both the geometry and chemical makeup of the ostracod body, lack of earthing (even with sputter coating) consistently results in inferior secondary electron imagery. Experimentation with back-scattered electrons, using gun voltages to control beam penetration and signal intensity has led to the development of a technique which now routinely produces micrographs of the highest quality (see Pl. 12, Fig. 2d). Using these techniques, it has been possible to describe the morphology and evolution of the male copulatory apparatus (hemipene) of *Cytherella* in detail (Swanson, 1991). Significantly as this work progressed, it became evident that using hemipene morphology it was possible to discriminate five new species of *Cytherella* and, to accurately determine their distribution in the eastern Tasman Sea (Swanson, 1993). The fact that, prior to this study, so many cytherelline ostracods were seen as cosmopolitan, was a direct reflection of poor taxonomic precision rather than a consequence of arrested development.

From a total of 26 Tasman Sea (Fig. 8) samples ranging in depths from 41 to 1050 metres, 63 benthonic ostracod species were discriminated. Eleven of these species were new to science. Using the same strategies developed for the Otago Shelf, bathymetric constraints for the biocoenose of most species were defined. Significantly, a number of `deep-water' genera were found living at quite shallow depths (100 - 200 metres) on the Westland Shelf. It is probable that the distribution of these taxa reflects the combined influence of upwelling and high nutrient levels in an area around the Hokitika Canyon. The species concerned with their revised upper depth limits (UDL) are

as follows: *Legitimocythere horrida* (135 metres), *Henryhowella tumida* (187 metres), *Krithe* sp. (135 metres) and *Cytheropteron wellmani* sp. aff. *testudo* (41 metres). The geometry and hydrology of the Hokitika Canyon area suggests a significant volume of cold, oxygenated water is intermittently moved onto the shelf via the canyon. Whether such an event is continuous enough to depress bottom water temperatures to a level which could be tolerated by up-slope migrating, psychrospheric ostracods is open to question. Especially since inherent in that statement, is the assumption that temperature is the limiting parameter. The discovery of such `anomalous' occurrences of deep-water ostracods is of considerable importance for paleothermometric studies in particular. Using live material reared in aquaria, a number of key assumptions relating to deep-water ostracodal physiology and taphonomy could be studied. For example once a breeding population of *Krithe* is established, by varying dissolved oxygen levels in the tank it should be possible to prove/disprove that vestibule size and complexity are affected by such variations. Confirmation would establish a new, unique and cost-effective tool for paleoceanography made more attractive by the fact that *Krithe* is both cosmopolitan and commonly preserved in deep-sea carbonates. Similarly, aquaria-based breeding populations of other deep-water taxa could be exposed to varying alkalinity to examine the effects of same on carapace chemistry and degradation - the results of this study having considerable value with respect to paleothermometry and ostracodal dissolution signals (see Part 2, this chapter).

NEW INVESTIGATIVE TOOLS FOR PALEOCEANOGRAPHY

Researchers at the Australian National University have, as part of the Australian Marine Quaternary program, developed an international expertise in the use of benthic deep-sea ostracod valves for paleothermometry. An integral part of this technique is the calculation of a partition number for extant representatives of the taxon under study. The data required includes an accurate measurement of the Ca:Mg of the carapace, equivalent chemistry for ambient sea-water and, a precise temperature record for the water at the site in which that species is living. The fact a large volume of environmental data was available for the ostracods of the Tasman Sea meant that fauna was a natural candidate for continued paleothermometric studies. Additionally, a number of cores from the Challenger Plateau (Fig. 9) had been made available or were collected by this writer as part of a detailed examination of the latest Quaternary climate-change record. Such a study, by being incorporated into the Australian National University program would establish a more regional base for faunal and paleothermometric studies of the deep-sea climate-change record in the South West Pacific.

The use of ostracod valves for paleothermometry is based on the premise that the extracted Ca:Mg is a primary signal. At the time of calcification, the ratio of calcium to magnesium in the carapace is determined primarily by ambient water-temperature. Clearly, since the object of such studies is to construct accurate profiles for bottom-water temperature through time, controls relating to the potential for taphonomic

modification of that primary chemical signature must be rigorous and precise. To that end, the data base for WESP benthic samples was extended towards the Challenger Plateau and would now include piston-cores and water-chemistry. The fact that taphonomic processes can severely alter the fabric and distribution of calcareous biogenic remains is well documented and in fact first observed by members of the "*Challenger*" expedition over 100 years ago. With respect to paleothermometric studies, the objective was to determine at what point does dissolution of the ostracod carapace alter the `primary' chemical signature and, what are the processes which produce such effects?

Examination of the preservation state of many thousands of ostracod valves, both modern and fossil resulted in a number of important conclusions: a) resistance to dissolution varies between species and between representatives of one species collected from different localities, b) the most dramatic effects are syndiagenetic i.e. occur at or near the sediment/water interface, c) living ostracods from almost every marine environment exhibit some carapace corrosion or recrystallisation and, d) foraminiferal dissolution signals reflect not only differences in the ability of the skeletal fabric to react to variations in sea-water alkalinity but also to variations in the source of the chemical fluctuation giving rise to the calcite dissolution. The fact that profiles of carapace dissolution for *Krithe* spp. (Fig. 16) accurately track the `equivalent' $\delta^{13}C$ profile is interpreted as indicating that the ostracod signal is a direct reflection of variations in local, surface-water primary production (analyses of benthic $\delta^{13}C$ were incomplete at the time of writing). In contrast, planktonic foraminiferal fragmentation profiles for the Challenger Plateau at least, more closely resemble that for $\delta^{18}O$ (Fig. 15) and in consequence are interpreted as more `oceanic' and regional (Swanson, 1994; Swanson and van der Lingen, *in press*).

Micropaleontologists studying foraminifers were first to conclude that distribution patterns of deep-sea benthic foraminiferal assemblages were a reflection of the physico-chemical character of surrounding water-masses. As this controversial conclusion is examined in more detail, a number of accepted generalisations are proving false. Similarly, with respect to deep-sea Ostracoda a number of workers have described distribution patterns as directly attributable to water-mass characteristics. (Dingle and Lord 1990; Cronin *et al*., 1994 for example). In many respects, the original sampling strategies used for such studies are flawed. As previously indicated (Swanson, 1993), the aerial distribution of valves of individual taxa on the sea-floor is a poor indication of the geography of the biocoenose. Additionally and more importantly, it is a scientific nonsense to attribute a single data point as characterising a particular water-mass when most physico-chemical parameters are known to fluctuate significantly both temporally and spatially. For example, dissolved oxygen content at the sediment/water interface of a particular water-mass will be dramatically affected by the organic rain rate, which in turn may reflect quite localised fluctuations of primary, surface-productivity. Additionally, if the vestibule of *Krithe* is a sensitive indicator of dissolved oxygen as suggested by Peypouquet (1977, 1979) the utility of such an important paleoecological tool will neither be proved or disproved when a) vestibule size is desensitized by adopting a hierarchy of classes to ease statistical manipulation of the

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data and b) in-situ measurements of dissolved oxygen and seasonal collections of target species are not made (for example see Whatley & Zhao 1993 and Coles et al., 1993).

Notwithstanding such provisos, it has been possible to re-evaluate distribution patterns of some deep-sea, benthic ostracods with respect to upper depth limits and water-mass (Ayress *et al.*, *in press*). Results from this study show that unlike previous studies in the South Atlantic Ocean (Dingle et al., 1989 and Dingle and Lord, 1993), the bathymetric ranges of selected taxa cannot be used to distinguish watermasses in the five areas studied (Figs. 12 - 14). Significantly, at least 2 cosmopolitan species not previously studied in detail (i.e. **Cytheropteron testudo - wellmani** complex and **Henryhowella asperrima**) show considerable potential for determining the relationship between water-mass and the deep-ocean ostracodal biocoenose on a global scale (Swanson & Ayress, in progress).

Clearly, this initiative has resulted in two significant contributions to paleoceanography. A new tool to investigate fluctuating alkalinity signals at the sea-floor (and the coupled, surface primary-productivity) has been developed and a simple method which constrains paleothermometric sample selection described (Swanson and van der Lingen 1994). less obvious, although no less important, has been the impact such studies have had on concepts of ostracod evolution.

EVOLUTION OF THE PODOCOPID OSTRACOD CARAPACE - A NEW CONCEPT

Although foraminiferal workers in particular have recognised and used evidence of calcite dissolution as a paleoceanographic tool for many decades, the effects of variations of ocean alkalinity on living, calcareous shell-building organisms has been neglected. For benthic components of the deep-sea flora and fauna such effects are exaggerated because a) older deep-water is undersaturated with respect to calcite and b) the metabolism of a fluctuating organic rain at or near the seafloor will profoundly affect the ΣCO_2 of that water. A natural consequence of this observation must be that the `metabolic stress' associated with a constantly varying alkalinity at or near the sediment/water interface has a significant impact on the evolution of the architecture of the calcitic, ostracod carapace (Swanson in press (a)).

To a significant degree, progress with respect to understanding the ostracod carapace has been stifled by two commonly held beliefs. Firstly that the psychrosphere is a uniform remarkably stable environment and secondly that `ostracods like oceans are steady-state systems' (Benson, 1976). The concept I wish to emphasise, of the chemistry of the deep-ocean in a constant state of flux is not new. However, by focussing on aspects of alkalinity it is apparent that most existing viewpoints relating to ostracod evolution do not adequately explain the character of the extant, marine, ostracod assemblage. Prior to this work, the ostracod was seen as a crustacean with

a static-frame (the carapace) - an exoskeleton which functioned to resist pressure and predation in a harsh but uniform environment (Benson & Sylvester-Bradley, 1971; Benson, 1976; Leibau, 1977 and Whatley, 1988). From that it was concluded, that deep-sea ostracods are not particularly useful biostratigraphically because in an evolutionary sense in such an environment the need to change is minimised. Accepting that other environmental factors (e.g. pressure) may have presented significant barriers to the invasion of the deep-sea by benthic ostracods, results from the present study indicate that existence as an inhabitant of `shallow' water (especially the continental shelf) established an architectural *bauplan* for the carapace which made such migrations possible. The almost universal acceptance that dissolution (and to a lesser extent precipitation) of calcite are only worth consideration with respect to deep-sea sediments and its biota are patently wrong. Evidence is presented (Swanson, in press (a)) which illustrates that dissolution and reprecipitation of calcium carbonate occurs on the valves of *living* ostracods in water depths as shallow as 110 metres (Tables 2 & 3). This observation confirms the potential within the shallow-marine ostracod assemblage to overcome those chemical barrier/s (specifically related to ΣCO_2) which must be penetrated if migration into the psychrosphere is to be achieved.

The platycopid response

The fact that many mid and deep-water species of **Cytherella** and **Cytherelloidea** possess very heavily calcified valves seems almost a contradiction. As marine biologists, we believe evolution progresses in a way which leads to an economy of purpose - extraction of carapace building calcium from an aquatic environment which chemically promotes dissolution of such materials is metabolically taxing. Yet, these animals have survived in the marine realm longer than most extant ostracods, accepting that the fossil record appears to indicate a progressive decline in importance. Certainly the key to understanding the platycopid `success' lies in the fossil record, the problem is have we interpreted that record correctly?

Using primarily the soft-anatomy, I have been able to discriminate six species of **Cytherella** living in the eastern Tasman Sea. It is probable that the final tally will be twice that number. More significantly, however, at least two thirds of those species have extremely broad depth ranges (150 - 1000+ metres). In many dredge samples **Cytherella** was the dominant living ostracod. Counts made on box-core subsamples from equivalent sites are however more in line with observations elsewhere, i.e. although **Cytherella** is an important component of the ostracod assemblage it is not the dominant taxon.

To explain such an apparent anomaly, we must first examine the valves of living cytherelline ostracods. Of all the marine ostracods examined by this author, **Cytherella** is the most susceptible to carapace degradation whilst the animal is still alive (Table 3. Alive = carapace intact, soft anatomy intact and with well-preserved internal musculature). Significantly, a large number of specimens of **Cytherella** recovered from the upper-most box-core samples, collapsed once moistened with a picking brush. In all probability therefore, a greater proportion of that population would have been lost

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during sample collection and processing. After a detailed SEM examination of valves of a number of living species of *Cytherella*, it appears most likely that such a widely distributed phenomena can be attributed to (1) epicuticular coatings, and (2) the internal crystal fabric. In the eastern Tasman Sea study area, examples of live individuals of *Cytherella* with incomplete or damaged epicuticles occur commonly in most environments. As illustrated (Pl. 14 Fig. f) a natural consequence of the loss of this protective layer is the degradation and dissolution of the crystal fabric and cuticular coatings of the protoostracum (equivalent to the `epicuticle' plus `exocuticle' of Bate & East, 1972). Initiation of this process is not restricted to these outer layers however; Pl. 14. Fig. e, illustrates the effect of severe chitinoclastic `grazing' immediately underneath the remnants of an assumed epi-exocuticular layer. Most of the outermost carapace layer has disappeared because `grazing' has resulted in the collapse and loss of coherence in the supporting crystalline fabric below. In fact, in many ostracod genera (especially *Krithe*, this study and Whatley et al. 1982), it is only by examining valves in transmitted light that the effects of attack by chitinoclastic organisms become apparent; externally, the shell appears to be well preserved. Consistently in living *Cytherella*, crushing of the carapace results in the formation of three crystalline `terraces' (Pl. 14, Figs. g & h), the surfaces of which replicate the contours of the external shell. These `terraces' are separated in part from their neighbours by an elongate cavity and become more `porous' and coarsely crystalline towards the interior. Greatest protection of the carapace fabric must of necessity be afforded by the outermost shell layer - once this outer layer is breached and dissolution initiated in the exocuticle, valve degradation will proceed quite rapidly. Either cytherelline Ostracoda are genetically predisposed to laying down incomplete cuticular coatings during valve calcification or, more probably, structural/chemical peculiarities of that cuticle encourage microbial/biochemical attack. Certainly many living specimens of *Cytherella* examined have an array of epibionts on the external surface, many of which are firmly rooted to the cuticle (Pl. 14, Fig. b). Additionally, `grazing' trails can also be distinguished morphologically, suggesting the assemblage of chitinoclastic organisms attacking deep-sea Ostracoda is also diverse.

Why do so many deep-sea representatives of *Cytherella* possess such heavily calcified shells? In relation to available shell-building material, I have indicated that even in the deep-oceans, the ease with which such a resource may be extracted from the sea-water fluctuates. At shallower depths (slope and shelf), such fluctuations may be a response to periodic upwelling and/or productivity increases for example. On that basis, one could postulate therefore that in these environments the platycopid life-cycle has evolved to be in phase with oscillations in bottom-water chemistry. Moulting for instance could be achieved most efficiently (in a metabolic sense) immediately after a period of strong dissolution when surrounding waters are saturated with respect to calcite. The subsequent laying down of a heavily-calcified carapace being one evolutionary solution to the problem of dissolution. Just as marine engineers attach `sacrificial' metal to the hull of a steel ship to overcome problems of electrolysis, in *Cytherella* sufficient `sacrificial' reserves exist within the mass of the carapace to ensure total dissolution of the protective exoskeleton is unlikely to occur within the animal's life-time.

A second evolutionary pathway to solving the problem of shell-dissolution is illustrated by some punctate platycopids. This metabolically efficient strategy involves the substitution of shell-building material with more easily dissolved fine-grained, calcareous components of the surrounding sedimentary substrate. For example, coccoliths trapped within each puncta (Pl. 14. Fig a) will preferentially dissolve thus reducing the corroding effects of `aggressive' undersaturated water on the fabric of the valve (Fig. 11).

The obvious contrast in calcite saturation state within that zone inhabited by benthic ostracods must offer some opportunity for exploitation by an animal whose survival is dependent on the maintenance of a calcitic exoskeleton. The platycopids for example are all equipped with a pair of extremely strong furca. The present consensus amongst ostracodologists would appear to be that these `appendages' function as devices for cleaning domiciliary spaces within the carapace, acknowledging that behavioural studies of deep-sea ostracods have not yet been undertaken. On that basis, one could, with equal conviction, promote the idea that strong furcae on the platycopids provide that group with a mechanism by which exposure to temporarily high levels of undersaturation may be avoided - by burrowing into the substrate. Studies using microelectrodes to trace chemical-change at or near the deep-sea sediment/water interface indicate that calcite dissolution is most intense in a zone which extends from, to only a few centimetres above the sea-floor (Keir, 1982 & Jahnke et al. 1989). In general, within the sediments immediately below, however, dissolution of calcite very quickly moves interstitial waters towards a saturated state at which point they stabilise (Morse & McKenzie, 1990). The presence of branchial plates could therefore have been anticipated since such respiratory organelles would increase the throughput of low-oxygen interstitial water during periods of burial.

Why are *Krithe*-related species dissolution resistant?

Earlier (Swanson and van der Lingen, 1994) I suggested one reason why **Krithe** are so well represented in deep-sea core material (accepting that they are normally a significant part of the biocoenose) relates to the observation that valves of that group appear to be dissolution resistant. Certainly the shell-fabric of these Ostracoda is quite distinct from that found in the platycopids. The protoostracum is extremely fine-grained and that, along with the cuticular envelope surrounding each calcite crystal, ensures this layer acts as a barrier to dissolution (Pl. 15, Figs b,c,d & e). This feature is well illustrated in many valves, by the presence of residual rims of fine-grained normal-pore lining on many heavily corroded valves of **Krithe** spp (Pl. 15, Figs. b & e). Again, once perforation of the protoostracum is initiated, carapace degradation should proceed rapidly. Interestingly, valves from which almost the entire protoostracum has been removed (Pl. 15, Fig. h) still remain structurally coherent. This strength is clearly afforded by a thick layer of densely-interfingered laminar calcite crystals which make up the bulk of the carapace wall (Pl. 15, Figs c & d) and line the domicilium (Pl. 15, Fig. g). Resistance to dissolution of this layer is again related to the cuticular envelope associated with each calcite lath. Once degradation of that envelope begins, dissolution will in all probability proceed more rapidly than that associated with

platycopids for two reasons: (a) the crystals are larger and as a consequence perforation of the cuticle exposes a larger surface area of calcite, and (b) once the intracrystalline network of cuticular fibrils is removed the total surface area of calcite exposed to dissolution increases enormously (Pl. 15 Figs. f & g). It is now apparent from the present study and that of Whatley et al. (1982) that *Krithe*-related taxa provide an ideal substrate for chitinoclastic organisms. Significantly, almost all such activity appears to occur within the coarsely-crystalline layer beneath the protoostracum. As a consequence the protoostracum remains intact and thus impervious to potentially damaging, `aggressive' sea-water.

Reticulation - mechanical strength and/or chemical resistance?

It is now known that different faces of the calcite crystal have different solubilities, with faces of the c-axis being the most soluble (Suess, 1970). On the basis of kinetics alone therefore, it could be postulated that reticulate and spinose Ostracoda are more likely to resist dissolution than smooth-shelled forms, simply because in the more complex configuration, valves will present a greater variety of crystal faces and axes to `aggressive' solutions. Jørgensen (1970) suggested in `unornamented forms (ostracods) smaller and larger crystal units occur together and are generally not distributed according to size'. In ornamented forms segregation of crystals into layers of various sizes is common with usually the finest laths occurring near the shell surfaces (Jørgensen, 1970., Sylvester-Bradley & Benson, 1971, Langer, 1973). Langer gave a clear indication of how crystal orientation (and as a consequence exposure of the C-axis) may vary around valve surfaces (see Langer, 1973; Figs. 5 & 7). Valve architecture may not only be an efficient mechanical solution to a structural problem (*sensu* Benson, 1981) but may additionally minimise dissolution during periods of exposure to undersaturated water.

The strength of the dissolution gradient at, or near the external carapace surface will be considerably reduced by carapace architecture (Fig 10). Evidence of dissolution around the distal extremities of muri on living, reticulate Ostracoda occurs commonly (Pl. 16, Figs. a & h). Dissolution of shell-material and `entrapped' fine carbonate debris (Pl. 16, Figs. c & d) leading to a reduction in the undersaturation of those waters within and around the reticular mesh. Preferential dissolution of fine-grained, carbonate material within the test of some porous, thin-walled, planktonic foraminifers has been given as one reason why such taxa are not more readily removed from deep-sea sediments (Kier and Hurd, 1983). Additionally, Morse (1978; p.345) after a laboratory study of deep-sea carbonate dissolution kinetics concluded that one reason why published rates of dissolution varied so dramatically was almost certainly a reflection on the methods used. "Berger's 1967 samples may have dissolved at a slower rate because circulation of water through his chambers was inhibited enough to allow a change in the saturation state of the waters passing through the chambers". Similar effects should in theory also be initiated by the hydraulic `dams', `barriers' and `sills' created by topographic irregularities on the ostracod carapace such as muri and spines. Diffusion, and the fact that ostracods are mobile will result in a continuous, though

markedly reduced, chemical exchange between the undersaturated sea-water and the external valve surface.

Spines, turrets, clavae and bullae

The advent of the SEM has been of immense importance to the biological sciences in general and to micropaleontology in particular. However, the never ending search for greater detail and resolution has, I believe, a negative aspect. Techniques for the preparation of material for scanning electron microscopy are many and varied but, "One of the major problems in preparing crustaceans for SEM is the removal of accumulated debris" (Felgenhauer, 1987; p.71). Accepted, the removal of such materials is necessary if one is to examine the biological make-up of selected taxa in the detail instrumentation such as the electron microscope affords, but who amongst us has bothered to examine and ponder the significance of the so-called "debris?"

Few organisms I believe have achieved the level of "debris" attachment and cartage exhibited by living representatives (especially adults), of the deep-sea Ostracoda *Legitimocythereis* and *Henryhowella*. In many instances, only the outer-most extremities of spines and other protuberances are exposed; all remaining carapace surfaces (excluding the contact margins), being masked by a loosely woven mat of phytoplanktonic debris (Pl. 17, Figs. c & d). Much of this material is entangled or trapped behind a network of papillate spines and/or multilobate tubercles (Pl. 17, Figs. a, b & c). Spines may be anti-predatory or, on deep-sea ostracods, devices to facilitate the extension of sensory setae (Benson, 1975). Alternatively, they may represent another architectural response to the problem of maintaining a calcareous shell in an environment undersaturated with respect to calcite. Indeed, the pedestal of each spine does appear to allow the extension of sensory setae (Pl. 17, Figs. a & c). Significantly, in relation to present discussion (also see p.15 on possible behavioural responses), the setae are thus extended to that area of the carapace outside the zone of particle entrapment (Fig. 11). As for reticulate species the preferential dissolution of fine-grained calcareous particles (especially coccoliths), lodged between the spines, shifts the zone of calcite undersaturation away from exposed valve surfaces. Examination of the truncated, distal ends of many vertical primary spines on living specimens of *Legitimocythere* spp. give clear indication that at that point, dissolution occurs commonly. Thus, the entrapment of fine calcareous particulates by spines, tubercles and other irregularities on the external surfaces of the ostracod carapace, establishes a zone between the surface of the carapace and the surrounding sea-water in which the level of undersaturation is buffered. Such a mechanism is not only economic in a metabolic sense, but also in respect to the sacrificial component (the calcareous debris), since that resource is renewable.

Conclusion

The podocopid Ostracoda are faced with total carapace reconstruction about nine times in their lives. I have already indicated that in those environments where the ease with which carapace building material can be extracted fluctuates seasonally (in areas of

upwelling, for example), the life-cycle could become synchronised with environmental change to ensure moulting occurs during those times when bottom-waters are saturated with respect to calcite. Alternatively, burrowing or excavation would provide access to interstitial waters also at equilibrium with calcite. Here, new shell material could be laid down in conditions which in a metabolic sense, were less taxing. Ostracoda also carry a diverse array of sensillary hairs and pores on the external surfaces of both the carapace and most limbs - some such devices are tactile, but many are chemo-sensory (Broadbakker & Danielopol, 1982). Setae, afforded additional length as a result the exit position on a tubercle or spine (Fig. 11) may be part of an` early-warning' system which provides information on chemical change in the surrounding waters. Clearly, avoidance by burrowing is a response which may be widespread amongst Ostracoda in general. Similarly, replenishment of `sacrificial' debris by spinose or reticulate species may also be a behavioural response triggered by signals from chemo-sensory setae and/or pores.

Increasingly, ostracodologists are being `surprised' by the apparent diversity of the deep-sea ostracod fauna. "Until recently it was doubted by few that the ocean-floors were dark and gloomy deserts of extremely low biological diversity. Recent research has clearly shown however that the floor of the world's ocean is in fact home to a profusion of genera and species and that single samples may compare in variety with those from shallower waters" (van Harten, 1990; p.327). Additionally, we are now aware that in some situations (e.g. areas of upwelling), presumed `deep-water' taxa may be found living at quite shallow depths. On the west coast of South Island, New Zealand for instance, I have found **Bradleya arata** living at 187 metres, a new species of **Legitimocythere** living at 135 metres and live **Krithe** spp. at 138 metres. Thus, it could be concluded that (a) the deep-ocean benthic environment is both dynamic and ecologically variable, and (b) that migration through such highly refractive transition zones (*sensu* Benson, 1976) as the thermocline has been achieved repeatedly by Ostracoda.

The thesis of the present study was to establish carbonate saturation as a significant though not the only determinant influencing both the direction and `success' of various evolutionary strategies within marine, podocopid Ostracoda. Modern carbonate saturation levels vary from ocean to ocean. These variations are determined by physico-chemical characteristics peculiar to each ocean and by interactions with other oceans, seas and surrounding land/masses. Throughout geological history, carbonate saturation levels in the oceans have fluctuated, often asynchronously, at other times with apparently predictable lag times, relative to neighbouring water-bodies (for example see Martinez 1994).

Ironically, some sense of how such fluctuations might have impacted on the evolution of the architecture of marine, benthic Ostracoda can be gained by the examination of data resulting from the study of extant species of the freshwater genus **Limnocythere** (Carbonel et al. 1990). In Lake Titicaca, as a result of photosynthetically-driven productivity in surface waters during spring and summer, an increasing detritus/nutrient load is delivered to the lake floor. Progressively, bottom-water becomes undersaturated

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with respect to calcite. Initially valves are large and well-calcified, however, successive populations of **Limnocythere** living in increasingly undersaturated water present individuals with spines, and then spinose/nodose morphs appear. Finally, when stratification is complete and anoxic conditions prevail, precipitation of calcium carbonate ceases.

That the modern, psychrospheric, podocopid fauna retains an amalgam of carapace-characters (some now `exaggerated') inherited from ancestral stock more attuned to survival in pre-Paleocene, thermospheric seas and oceans is now well established in the literature (see for example, Benson, 1990 and Coles, 1990). In thermospheric seas, calcium has always been a readily available resource, as a consequence the valves of Ostracoda associated with that environment tend to be thick-walled and reticulate, often with mural thickening and/or fossal infilling, whilst in other forms, spines and tubercles occur. This was the *bauplan* of the ancestral stock for much of the extant, psychrospheric, podocopid fauna. Immediately after the establishment of the psychrosphere in the Late Eocene (according to Benson, 1976), within the Ostracoda, a number of lineages exhibit consistent evolutionary trends. "These changes most dramatically appear in the increase in reticulation which is one of several means of selectively reinforcing shell-wall structure over an area with less mass", and "On first view, the effect of great depth on architecture of skeletons seems to be one of character exaggeration" (Benson, 1976; p.386). Additionally, valves become larger and in many species, spines larger, longer or more densely packed.

That **Bradleya** and **Poseidonamicus** originated in Paleocene shelf seas in the Australian region is now well-documented (Whatley et al. 1983; Whatley, 1985). It was suggested that "the mode of entry into the deep sea of these two genera and many others was by means of subsidence of areas of continental shelf at a rate slow enough for at least part of the fauna to survive and adjust to the new environmental conditions". With respect to **Bradleya** and **Poseidonamicus** it was noted by those authors that both genera showed progressive size increases with time. **Bradleya**, however, was `extremely conservative with respect to ornamental change'. Character exaggeration, therefore, must be seen as only one possible evolutionary solution to the problem of carapace maintenance in deep-water. In those cases where `character exaggeration' is demonstrated, associated structures may represent metabolically efficient solutions to internally generated mechanical stress (Benson, 1976); they may also reflect an increasing need to incrementally shift reactant, undersaturated sea-water away from critical valve surfaces as the solution potential of bottom-water increases.

`LIVING FOSSILS' AND CRUSTACEAN EVOLUTION

In 1949, Hornibrook described a new ostracod family (Punciidae) from the Three Kings Islands area off Northland, New Zealand. Although recognising quite remarkable similarities in shape and ornament with some frilled Paleozoic ostracods he was, "reluctant to assert that a representative of a group of Ostracoda which apparently died out elsewhere, in the Devonian, is still living in the South Pacific". He did conclude however that a) **Puncia** most closely resembled members of the Palaeozoic (Lower Ordovician - Upper Devonian) ostracod family Eurychilinidae. Later, after a more detailed re-examination of the 1949 specimens and additional fossil material of **Puncia**

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from the Miocene of New Zealand, he stated "the only feasible conclusion is to regard the Punciidae as a relict group of Paleocopida, which were the dominant order of ostracods in the Palaeozoic" Hornibrook (1963). From the time of their discovery, *Manawa* and *Puncia* have been recognised as animals whose biology once documented, could have profound effects in areas much broader than the discipline of ostracodology from whence such data was generated. In the last two decades punciid valves have been recovered from the Late Cretaceous of Germany (Herrig, 1988), the Miocene of Australia (McKenzie and Neil, 1983), the Pliocene of Japan ((Ishizaki, 1973; Nohara and Nakasone, 1982) and the Holocene of Australia (Blom, 1988) and New Zealand (Swanson 1989 a & b). Living material however has only ever been recovered in a few sites from northern New Zealand (Swanson, 1985, 1989a, 1989b, 1990a & 1990b).

Recovery of live specimens of *Manawa staceyi* is very time consuming with an average return of one specimen for every three hours at the microscope. For that reason, experimentation with routines for preparing material for electron microscopy had to be minimised. New, secondary and backscattered electron microscopy techniques have however been developed and described (Swanson, 1985a; 1985b and Moore & Swanson, 1993). Attempts at histological sectioning for transmission electron microscopy have thus-far produced unsatisfactory results. It is this writer's belief that a wealth of phylogenetic material will become available as an examination of punciid embryological development at the cellular level progresses. For that reason, this research objective will be one priority for future work. The release of backscattered electron imagery of the soft anatomy of *Manawa staceyi* has had a significant impact on concepts of ostracod evolution and crustacean phylogeny. Novelties with respect to carapace gait and morphology were however discovered quite early as a result of theoretical modelling of a soft anatomy constrained by those shell-features which were uniquely punciid.

The concept of the frill cavities of *Puncia* and the ventral `lunettes' of *Manawa* as structures associated with reproduction and/or brooding can be traced to observations relating to fossil palaeocope ostracods. In contrast I concluded (Swanson, 1985a), that dolonic dimorphism displayed by a number of Palaeozoic eurychilinids is not found on the frill of *Puncia* and that the frill cavities are closed dorsally by a fine calcareous membrane (Pl.20, Fig. b). With respect to *Manawa*, the 8-9 `lunettes' open internally only (Pl.19, Figs. a & c) and, since both sexes of that genus (using the criteria of Nohara & Nakasne, 1982) exhibit ventral cavities, it is unlikely that such structures have any reproductive significance. In podocopids the duplicature is the zone of contact during carapace closure, and sensory setae tend to be concentrated peripherally along the lateral extremities of each valve. In *Manawa* (see discussion of gait p.22), the duplicature acts as the major source of sensory information relating to the external environment and possibly during copulation (Swanson, 1989a). As indicated by Benson (1981), the most economical structure for spanning and enclosing a considerable area is a dome. In the case of *Manawa*, both valves combine to form an elongate dome (Pl. 19, Figs b, c; Pl. 26, Figs 23a, 23b). Compressive forces on the external carapace are dispersed through the heavily buttressed duplicature. The added

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weight also lowers the centre of gravity of the carapace thus improving positional stability. The `lunettes' therefore are simply an economic architectural solution to the stresses imposed on an animal inhabiting a high-energy environment.

The punciid carapace:

The single, dome-shaped carapace carried by the nauplius of *Manawa staceyi* (Pl. 19, Figs. e, f; Pl. 23, Figs. 1a, 2a, 3a, 3b; Pl. 24, Figs. 4a, 5, 6a, 6b) is unique for ostracods and possibly for Crustacea. Significantly, small larval forms (*Melopetasus*) from Upper Ordovician erratics of the Isle of Sylt (Schallreuter, 1979) display quite remarkable similarity to the carapace of the manawan nauplius (Pl. 19, Figs. g, h). I believe these remains are punciid-like and ostracodal rather than trilobitan as suggested by some authors. That being the case the position of the phaselus (a bilaterally symmetrical body created by the folding of a dome along a `dorsal' axis) becomes problematic. In *Manawa staceyi* during the transition from nauplius to metanauplius, the naupliar dome occasionally shows evidence of slight infolding (Pl. 19, Fig. d); however examples of the exaggerated phaselus-type fold have never been recovered from modern sediments. Either the phaselus is unrelated to the manawan-type naupliar dome (favoured by this writer) or it may represent an additional larval stage which has subsequently been eliminated from the `punciid' ontogeny.

In some respects the recovery of these enigmatic larval remains from Upper Ordovician sediments gives some credibility to the thesis of Becker that the punciids represent `The only living palaeocopines' (Becker & Swanson, 1992). In other words they are a true palaeozoic remnant, the punciid carapace architecture being truly plesiomorphic whilst the Kirkbyacea display a number of apomorphic features and cannot therefore be considered an appropriate root stock for the Punciacea. To a large extent, the debate will continue until functional aspects of the punciid adductorial musculature are resolved. In the opinion of Becker "The obvious similarities in carapace architecture do not convincingly close relationships between both superfamilies and are considered to be homoeomorphic: i.e. plesiomorphic in ostracods. In particular, the carapace closure mechanism (position of the adductor muscle scar, vertically oriented carapace with reduced gape) in the extinct Superfamily Kirkbyacea is, in terms of efficiency, more advanced than that in the extant Superfamily Punciacea Hornibrook (1949)".

According to Becker, the kirkbyaceans have Early Devonian drepanellid ancestors; the Punciacea are presumably the only living palaeocopines. The fossil evidence relating to the evolution of adductorial muscle patterns is inconclusive with respect to lines or trends. The fact that Healdiid-type patterns occur in all Palaeozoic ostracod groups and is the plesiomorphic condition is equivocal, since within that group representatives presenting a primitive open-gape and the modern vertically-oriented `podocopid' condition exist. With respect to the palaeozoic ostracods, taphonomic considerations may also play in important part in how that group is assessed in an evolutionary sense. Most specimens (fossil and living) of punciid ostracods display a full complement of well-preserved muscle scars; in contrast representatives of the Palaeozoic Kirkbyacea, although nearly always presenting the characteristic `Kirkbyan pit' externally, more often

than not have the internal muscle scar detail obliterated as a result of imperfect preservation. That poor resolution with respect to those scars results from taphonomic processes is indicated by the fact that in one species of *Aurikirkbya* the muscle scars were described as a subcentrally located adductor muscle scar field consisting of ten to twenty irregularly aggregated spots (Becker & Fohrer, 1990). After a re-examination of Sohn's (1954) material, I concluded that group exhibits a variety of muscle scar types as diverse as that expected for `modern' podocopid ostracods. The complete muscle scar pattern for punciids consists of a central adductor group of six scars arranged biserially, two dorsal scars (the larger occurring on an elevated node) and a single mandibular scar. Becker (1992) on the one hand argues that healdiid adductor muscle scars and the punciid condition are plesiomorphic yet, on the other states a key character of the Kirkbyacea is not the scar detail but rather the position of the scar field relative to the lobes and the dorsal (hinge) margin. In the case of the latter, the Kirkbyiids possess a more ventrally located field than the punciids and are therefore more advanced - the extreme carapace gap of punciids can only be achieved if the adductor muscles are attached close to the dorsal-line and that condition is plesiomorphic. As previously indicated, functional aspects of the ostracodal external musculature are poorly understood. It is possible for instance that closure of the punciid-shell from a position of extreme open-gapedness is achieved by the central muscle-block operating not in unison, but rather sequentially, dorsal-most first. This mechanism would overcome at least some of the difficulties associated with the need for exceedingly long and tensible muscle blocks when punciid carapace gape is interpreted using a `podocopid' framework. It is still the thesis of this writer that contrasts in central muscle scar fields, as they are presently understood, cannot be used reliably as evidence against a kirkbyacean-punciacean continuum. Additionally, as noted by McKenzie and Neil (1983), *Promanawa australiensis* (a punciid) does present a well developed Kirkbyid pit externally; other members of the Punciidae do not, presumably because they have a much weaker reticulum.

Discussion of the relationship between the extant Punciidae and a possible Palaeozoic predecessor has invariably been dominated by the presence/absence of homologeous structures in the frill (see Pls. 18 & 20). In most respects, our assessment of the Palaeozoic ostracod frill has changed little over the last 30 years, acknowledging that `the ability of forming adventral extensions has been acquired independently in different remotely related groups of Palaeocopa' (Jaanusson, 1957). The total number of chambers in each frill is quite variable; 31 - 55 in the Kirkbyacea and 28 - 43 in the Punciacea. In *Puncia* and *Promanawa* the septa which divide the frill into approximately 40 chambers are not radial pore canals (Swanson, 1985) but rather a calcareous bridge connecting what may loosely be described as the outer and inner lamella (Pl. 20, Fig. c). Additionally, access to the domicilium via these chambers is prevented by a thin, calcareous (?) wall or membrane (Pl. 20, Fig. b). At the ventral edge of the frill each chamber may be completely or only partially sealed, the latter resulting from incomplete calcification or dissolution (Pl. 20, Fig. b). A similar situation occurs in most Kirkbyacea, in the hollinacean *Oepikium* and in eurychilinids (Jaanusson, 1957), noting however that in those Palaeozoic taxa most chambers are circular/ovoid in section rather than rectangular. Although some specimens give an

indication that the Kirkbyid frill is composed of a row of distinct tubules (Pl. 20, Fig. d), I suspect this may be an artefact of preservation/extraction and that in life the gaps between chambers were closed by a thin calcareous bridge. Ventral chamber exits, where present, were also extremely small since in many instances the ventral extremity of the calcareous bridge is tapered to a fine edge (Becker, 1978). Determination of the function of the frill must await the discovery of living specimens of *Puncia* or *Promanawa*, however the possibility that these structures perform a dual role as both a benthic support and gas-filled floating aid cannot be excluded. Adamczak (*pers. comm*) has also found a membranous (?) closure in the crumen of the Ordovician genus *Craspedobolbina*; this he felt could indicate a ballast/brooding function for that structure. Although McKenzie and neil (1983) suggested the punciid frill did not appear till quite late in ontogeny (`until after the development of the anlages of reproductive characters in the soft anatomy'), evidence from imperfect ontogenetic sequences for *Puncia* (Pl. 18, Figs. a - e), *Aurikirkbya* and *Coronakirkbya* (Becker, 1978) indicate that it is carried by `early' juvenile stages as well. Informally, I have suggested that perhaps *Puncia* represents a planktonic, dispersive stage of the manawan ontogenetic sequence. Such a mechanism would at least account for a) the global distribution of that group and b) the fact that remains of Puncia occur so rarely. That being the case, we must either accommodate the sequence (Pl. 18, Figs a - e) into the ontogeny of *Manawa*, or accept that those specimens represent 5 distinct species of *Puncia*. Accepting some variation in the mid-dorsal admarginal structures, in general the increase in length and height and proportions of other carapace structures indicate this as normal and monospecific. The valves of *Puncia* cannot be considered a part of the *manawan* ontogenetic sequence because a) the smallest valve of *Puncia* recovered is smaller than the adult *Manawa* (compare Pl. 18, Fig. a and Pl. 19, Fig. a) and b) the introduction of additional moult stages into an `ostracodal' development sequence is clearly at odds with established principles. An intriguing possibility, and one which will be investigated is that *Puncia* is planktonic throughout its life.

Marginal pore canals with their associated setae, as found in most podocopid ostracods, do not occur within the Punciidae. The stratigraphic record of ostracods gives clear evidence that the contact margin between the two valves has been a zone of considerable evolutionary innovation. Increasingly, workers on Palaeozoic assemblages are recognising a wealth of structural detail in the calcified inner-lamella and it is now established that the lack of a duplicature is not a determinant of the `palaeocopid' condition (Gramm, 1988; Schallreuter, 1988). In *Manawa* and *Puncia* the upper surfaces of the carapace are pierced by evenly-spaced, small, simple sensilla or `normal' pores. The sole of the manawan valve displays an inner and outer row of pores from which moderately long sensory setae exit (Pl. 19, Fig. c, Pl. 20, Fig. f). A single row of between 12 - 15 equivalent pores and setae may be found on the proximal edge of the upper surface of the sole (Pl. 19, Fig. a; Pl. 26, Figs. 22 & 24).. Examination of the carapace of *Puncia* between the frill and the contact zone clearly indicates that the manawan pore pattern is repeated in this genus (Pl. 20, Fig. a).

Significantly, the outermost row of setae on the ventral (when the carapace is gaping) surface of the frill are extremely long (equal to the total width of the frill in most cases).

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The flexibility of these setae suggests a sensory role within the cavity created by the frill and the substrate, rather than one associated with the lateral extremities of the frill. Clearly as the carapace gape is increased, the distance between the contact margin (and therefore the animal) and the substrate is reduced to a point where such setae would no longer drape; in fact during ambulatory excursions it is likely that they are drawn across the substrate. If the punciids are capable of dispersal by floatation, it seems likely that the animal would then assume a passive/defensive mode (i.e. the carapace would be closed); during such times extreme setal length in an area surrounding the carapace opening would obviously be advantageous.

Details of pore types and their distribution for Palaeozoic ostracodes remain scanty. From an examination of micrographs of **Coronakirkbya fimbriata** I see no evidence of pore-exits similar to those found on the underside of the punciid frill. In all instances, however, specimen/detector angles were not optimal for such a search. One row of assumed pore exists (Pl. 20, Fig. d) does clearly duplicate that found on **Puncia** close to the contact margin (Pl. 20, Fig. c). Because of their position close to the contact margin/sole, these may be considered analogues of `modern' podocopid marginal pores which penetrate the carapace between the outer lamella and the duplicature. There is some evidence to suggest that the oldest `ostracods' (see discussion Swanson, 1989a) were also open-gaped with pore exits concentrated on the carapace sole in a fashion similar to that exhibited by **Manawa**. The setal arrangement in **Puncia** therefore could represent an evolutionary intermediate step appropriate to a wide-gaped ostracod, in which a domiciliar `early-warning' system is afforded by the frill and extremely long setae. In extant benthic podocopid ostracods, because of their vertical orientation, carapace shape and narrow gape, the greatest concentration and most diverse sensory receptors (marginal pores and their setae) occur around the valve periphery near the contact margin.

In both the Kirkbyacea and the Punciacea some representatives carry externally, near their dorsal margins, structures ranging from lobes as in **Aurikirkbya** and **Coronakirbkya** to bulbs, ridges and spines as in **Puncia** (Pl. 18, Figs, e, g, h.). An incomplete developmental sequence for Puncia (Pl. 18, Figs, a - e) clearly illustrates the progressive reduction in relief of two, perforated, mid-dorsal, admarginal ridges. Although equivalent hollows are found on the interior of the valves, they are poor reflections of the external condition, especially in juvenile valves. Structural duplicates (for which subsurface and internal carapace detail is not available) in the Kirkbyacea show a similar developmental pattern through ontogeny. In **Manawa** (Pl. 19, Fig. a), **Promanawa** (Pl. 18, Fig. i) and **Puncia** (Pl. 18, Fig. j) lobate surface-swellings may occur in zones equivalent to L1 and L3 on palaeocopids. Functionally, the more compact and defined ridges, knobs and spines remain a mystery. The fact that their surface expression is more pronounced earlier in ontogeny suggests some form of larval aid, noting that subsurface detail in adults has not been investigated. Shape does not appear to influence the basic pattern of the components making up the larval admarginal `lobe'. The dome or roof is always smooth and unlike the rest of the carapace, unperforated; the lobal floor has a rough texture, which suggests the epicuticle envelopes the entire structure. Lastly, the basal periphery of the lobe is

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interrupted by a number of portals in which the carapace perforations are organised in a roughly semi-circular pattern (Pl. 20, Fig. g). A detailed examination of these structures is warranted since they are a) clearly important in the earlier stages of ontogeny and b) maybe homologous with `equivalents' found of the valves of some carboniferous Kellettinidae (tentatively placed in the Superfamily Kirkbyacea by Becker & Wang, 1992). Becker has consistently used the location of the adductor scar field as evidence of a relationship with the Kirkbyacea and, because in Punciidae that field is located the `primitive' positon (i.e. above mid-valve height) they are unlikely to be Kirkbyid. Two research objectives therefore should be given priority. Firstly determine the functional aspects of the external, admarginal ridges of the punciids and, examine the ontogeny of the punciid adductorial musculature and the relationships of these structures to the lobes and ridges described above. When that data is available, then functional aspects of the kirkbyacean carapace and its novelty may be able to be described and discussed with more certainty.

In both *Manawa* and *Puncia*, numerous small (1 - 5µm) `ducts' perforate the carapace wall perpendicular to the external surface, excluding lobes and frills or their equivalents (Pl. 20, Figs. b, i). In benthic podocopid ostracods, the calcified portion of the carapace consists of a reticular chitin fabric the interstices of which are filled with fine crystals of calcium carbonate; in those ostracods (e.g. pelagic myodocopids) for which flexibility and/or low weight seem a priority, a lamellar chitin structure similar to that found in decapod Crustacea occurs (Bate & East, 1972, 1975). The carapace of most podocopid ostracods is also pierced by small `normal' pores which display an enormous variety of form. Generally such structures provide a) exits for sensory setae and b) accommodation for basal accessories of such setae. Both *Manawa* and *Puncia* have normal pore exists but these are easily distinguished from the perforations presently under discussion (Pl. 20, Figs. f, i) by the fact the latter do not have setae. They may be densely-packed, simple, vertical tubules (*Puncia*, Pl. 20, Figs. a, b) or large countersunk manawan forms in which the external rim is either papillate or spinose. Both manawan types of duct are extremely complex internally with `epicuticular' lining forming 2 - 3 continuous membranous bridges across each duct. In general the *bauplan* of the carapace of benthic ostracods is internally coherent with few breaks (normal pores) interrupting that continuity and often with external beams and ridges providing additional strength at a minimum cost physiologically. Why have the punciids taken the development of carapace perforations to such extremes? One possible answer lies in the unique gait of the animal. Whilst walking, both valves are carried aloft and extended, presumably supported by relatively thin and poorly chitinised chepalic and thoracic appendages. The pivotal, side to side, rocking motion of *Manawa staceyi* as it walks, would suggest that weight loss resulting from possession of a densely perforated valve, may provide a partial solution to some locomotory problems. The relatively high density of perforations in *Manawa* may also be used as additional evidence to indicate the value of the frill of *Puncia* as a bouyant, balancing aid. Almost all Kirkbyacea present a punctate pattern externally which duplicates that described for punciids. Whether these negative carapace features penetrate the entire thickness of the carapace wall in the Palaeozoic forms is unknown.

In some kirkbyids (and extinct hollinaceans and eurychilinids according to Becker), the external expression of the reticulum (if it exists) is often masked by a very thin, `calcified' membrane which may represent an extension of the inner lamella (Pl. 20, Fig. h). Such a membranous layer is commonly encountered on specimens of punciid ostracod and although extremely thin and transparent, is sufficiently electron dense to obscure structural detail below (Pl. 20, Fig. i). I am unaware of the existence of equivalent structures in any other extant ostracods.

The punciid soft anatomy:

Although a histological examination of **Manawa staceyi** is incomplete, SEM examination of maxillary ontogony indicates that limb as thoracic; in fact its origin, development and pediform nature initiates a pattern duplicated as each thoracic leg is subsequently added (Pl. 23, Fig. 2c; Pl. 24, Fig. 6c; Pl. 26, Fig. 17). Thus in **Manawa staceyi** only the first three limb pairs (antennule, antenna and mandible) are cephalic, the remaining four being thoracic and pediform in origin; adaptions for feeding (the maxilla/maxilliped and to a lesser extent thoracopid 1) and reproduction (maxilla/maxilliped only) being derived secondarily. The boundary between the head and trunk is most obvious in the first metanauplius (Pl. 23, Fig. 2c) and allocation of only three limb pairs to the cephalon clearly at odds with established views. "It is clear that the first four limbs belong to the cephalon and the last two to the thorax, but the fifth limb has been claimed for both." (Maddocks, 1982). However Jones and McKenzie (1980) noted that ancestral ostracodal forms may have had four thoracic limbs, a maxillar pair being lost during evolution; this observation being based on the presence of four, elongate internal identations on a single valve of the Cambrian phosphatocopine **Oepikaluta dissuta**. Significantly the appendage configuration in adult specimens of **Manawa staceyi** masks the thoracic origin of the maxilla since, during ontogeny cephalic elements in particular migrate foward as somites are added.

The development of a complex mandibular gnathobase in the first metanauplius (Pl. 23, Figs. 2c, 2d) is interpreted as indicating that such larvae are capable of feeding. Whether the distal claws of the mandible assist during feeding is not known, however, the remaining setal elements associated with the palp have an obvious rotatory component which could sweep food particles/detritus off the ventral surface of the body into the oral region (Pl. 23, Fig. 2d). Interestingly, it has been observed that whilst swimming calanoid nauplii hold the posterior of the body in a near vertical position, creating a `post-oral basket' from which food particles are gathered by a horizontal sweep of the manibles. Such a posture could also aid early manawan metanauplii in food gathering and manipulation since a well-developed ventral food groove is achieved only after most thoracic somites have been added (Pl. 24, Figs. 8, 10a). The progressive inclusion of thoracic limbs in the food gathering effort is most dramatically illustrated in the transition from metanauplius `1' to `2'. The earlier larval stage is at least setally equipped for feeding (Pl. 23, Figs. 2b - d), however, once the first thoracic

limb rudiments appear (noting that even at that early stage the gnathobasic components are functionally well advanced) a number of striking changes occur in the mandibular setal array. Endopodial setae in particular undergo a reduction in both size and complexity as food moving/grappling responsibilities are shifted posteriorly (compare Pl. 23, Fig. 2b - d and Pl. 24, Figs. 6c, 8). The ambulatory nature of the maxilla is maintained through ontogeny and illustrates how little modification is requred to allow a simple, uniramous thoracic limb perform both walking and feeding functions simultaneously.

Ostracoda are generally regarded as non-segmented and cephalised (McKenzie, 1983), and their trunk and abdominal reduction, as a result of segmental loss, is the most extreme of any crustacean. Nevertheless, after a study of the chitino-skeleton of several living taxa, Schulz (1976) concluded that ostracods had abdominal segmentation earlier in their phylogeny. On the basis of this evidence and the possession of other `primitive' limb and carapace characters, at least five groups of ostracods are repeatedly utilised as providing bauplans (acknowledging such constructions only as indications of what is possible) from which `modern' ostracods may have evolved. I have excluded the Polycopidae from this discussion because they have fewer segments in the trunk (Pl. 22, Fig. d). Saipanettid ostracods will be discussed only in a general sense because detailed election micrographs were not abailable. As noted by Maddocks (1982), Schulz considered *Saipanetta* to represent a phylogenetic intermediate between the ancestral Platycopina and descendant Podocopina. On the basis of carapace detail Schallreuter and Jones 1984, included the Punciocopa (Kirkbyacea and Punciacea, *their definition*) in the extant Playtcopa. Discussion of the abdomen of the platycopid *Cytherella* is warranted because superficially, at least, it appears to resemble that described for *Manawa staceyi* (Swanson, 1989a).

The trunk of male cytherellids is dominated by paired hemipenes which are attached to the body on or near segments 5 to 7 (Pl. 21, Fig. e; Pl. 22, Figs. a, b, c). Chitinous skeletal elements of the abdomen are produced anteriorly to provide what may be structural support for each hemipenis and genital lobe (in females). From my studies, the precise origin of each hemipenis could not be determined; what is encouraging however is a) its structural variation between taxa and b) the existance of `segmentation' (Pl. 21, Figs, e, f) indicating a potential source of important taxonomic and phylogenetic information. The anlage of the hemipenis appears quite early in ontogeny (A-3 or A-4), as does abdominal segmentation (Pl. 22, Fig. c).

Kornicker (1975) argued that the positon of the furca relative to the anus should be given more emphasis in ostracod classification. Schulz (1976) figured the cytherellid trunk as being composed of ten segments, a telson and furca; according to him the anus was located between the tenth segment and the telson, dorsal to the furca. Kornicker (1975) also placed the cytherellid anus dorsal to the furca but behind the telson. Scanning electron microscope examination of *Cytherella* confirms Kornicker's view. The anus occurs after the last full segment and an anal flap is present (Pl. 21, Fig. c). Also of interest is the presence of a `faecal' pellet composed almost entirely

of coccolith remains which may indicate that cytherellids operate as `collectors' (Kornicker, 1975) rather than as efficient benthic filterers (Cannon, 1933). Note also that the posterior-most (in life position) ventral elements of the furca may also function as `housekeeping' accessories (Pl. 21, Fig. f).

Members of the Punciidae also have ten trunk segments with a poorly understood `reproductive' element between segments 5 and 7. Both *Cytherella* and *Manawa* carry paired lamelliform furca the setae of which differ numerically (more in *Cytherella*) and structurally (derived?). The anal position in *Manawa* duplicates that found in *Cytherella* although in the former the anal flap occurs after the `telson' (Pl. 21, Fig. b). Both Kornicker (1975) and Schulz (1976) indicated that in *Saipanetta* the anus exits dorsal to the furca. This was seen by Kornicker (1975) as confirmation of the podocopid status of the saipanettids, since members of the Myodocopida (with which *Saipanetta* has some furcal similarity) have the anus ventral to the furca. The fact that *Saipanetta* has six trunk segments and a telson shows that its abdominal condition is more derived than that of platycopid or punciid ostracods but less than that of most extant ostracods.

Abdominal evidence for a direct punciid-platycopid link (Schallreuter and Jones, 1984) is not convincing; when combined with substantial contrasts in anatomy and carapace structure it seems unlikely. I suggest that segmentation of the trunk and abdominal configuration as found in *Cytherella* and *Manawa* is the pleisomorphic condition for ostracods. This does not exclude the possibility that both lineages developed independently.

Punciid appendage configuration through ontogeny provides a new insight into evolution of ostracods in general, but more specifically within the subclass Podocopina. The most primitive crustaceans are cephalic feeders with trunk limbs usually dedicated to locomotion. As the group evolved, trunk limbs developed increasingly as food processors assisting the limbs of the cephalon, in some cases such modified trunk limbs, behind the maxillary segment, have become fused to the head. The punciid cephalon with only three limb pairs is clearly larval in contrast, the trunk with four homonomous, pediform, thoracic limbs and full segmentation is adult and primitive (for maxillopods at least). The development of a masticatory gnathobase on the first thoracic leg illustrates how trunk limbs can become progressively involved in feeding. The extreme consequence of this pathway would be the fusion of that thoracic segment to the head and dedication of the limb to food sorting and grappling (= maxillule). The fact that for most podocopid ostracods the second maxillae are alternatively described as a maxilliped or first thoracic leg may confirm that such a developmental sequence is more pervasive in ostracods than can reasonably be anticipated from the results of this study.

Punciid research - new directions

Anderson (1965, 1967) acknowledged that embryological studies of post-mandibular segment formation is of little value in assessing phylogenetic affinities amongst non-

brachiopods because the possibility of paraphyletic derivation can never be excluded. Equivalent studies may however, prove useful in some areas of punciid biology (especially the segmental origin of limbs) and phylogeny. The fundamental difficulty associated with the concept of a specific group of limbs allocated to specific tagma is how does one prove it and to what end? In most crustacea, the mesoderm of the post-naupliar region even in its earliest stages gives evidence of differentiation into somite rudiments of post-maxillulary segments; i.e. differentiation of some mesodermal tissue into cellular clumps from which thoracic elements are derived is initiated during the naupliar stage. Consequently, it would be difficult to divide such a developmental sequence, when it is effectively a continuum.

In terms of `phylogenetic' studies, Anderson (1965, 1967) gave indication of an embryological developmental progression from that of the cephalocarids in which `mesodermal segmentation precedes ectodermal segmentation in the primitive manner`; to the derived malacostracan condition in which 8 mesoteloblasts `.....bud off successive rows of 8 cells which form the somite rudiments of individual segments, and a corresponding row of ectoteloblasts bud off ectoderm which lies outside the somite rows and becomes segmentally associated with them.' Embryological studies of `primitive' and `modern' ostracods should give an indication of polarity within Anderson's sequence and as a result confirm or refine present concepts of ostracod phylogeny and relationships with other Crustacea.

I have indicated previously that the development of a histological regime appropriate for studies of embryology, musculature and taxonomy has been only partially achieved. It must be accepted that during this process, a number of specimens are `sacrificed' as procedures are tested. Clearly with respect to rare, live punciids the time penalty associated with such objectives is substantial. On that basis the most obvious solution is an aquarium based breeding/behavioural study. If successful, material would then be available for histology and for live observation. Some indication of the potential of live observation for improving knowledge of these unique crustaceans was achieved in January 1995. In 1987 I wrote `Carapace shape and copulatory position are intimately linked with each other in ostracodal life and evolutionary history. Copulation venter-to-venter has been observed on only one living species. Similarly in the fossil record, particularly the Palaeozoic, carapace shape is such that hemipene extension required to form venter-to-venter copula would be extreme. Dorsal and postero-dorsal mating is therefore accepted as normal for ostracods. Such mechanical constraints are overcome by the adoption of the manawan gait since, in that position, the entire body is exposed. Consequently a venter-to-venter copulatory position may have occurred quite commonly amongst primitive ostracods'. This year a co-operative study of live punciids was initiated with Professor N. Ikeya and Dr K. Abe (Shizuoka University, Japan). Specimens were observed and significant behavioural/locomotory events recorded on video tape, at other times the camera was simply left to record for extended periods of time. Examination of tape from one such session gave clear evidence of the formation of an assumed venter-to-venter copula between two specimens of *Manawa staceyi*. Significant not only because it provides good evidence that laboratory breeding should be possible but also for the first time we have witnessed

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a style of reproduction more appropriate for an ostracod assemblage which existed over 500 million years ago.

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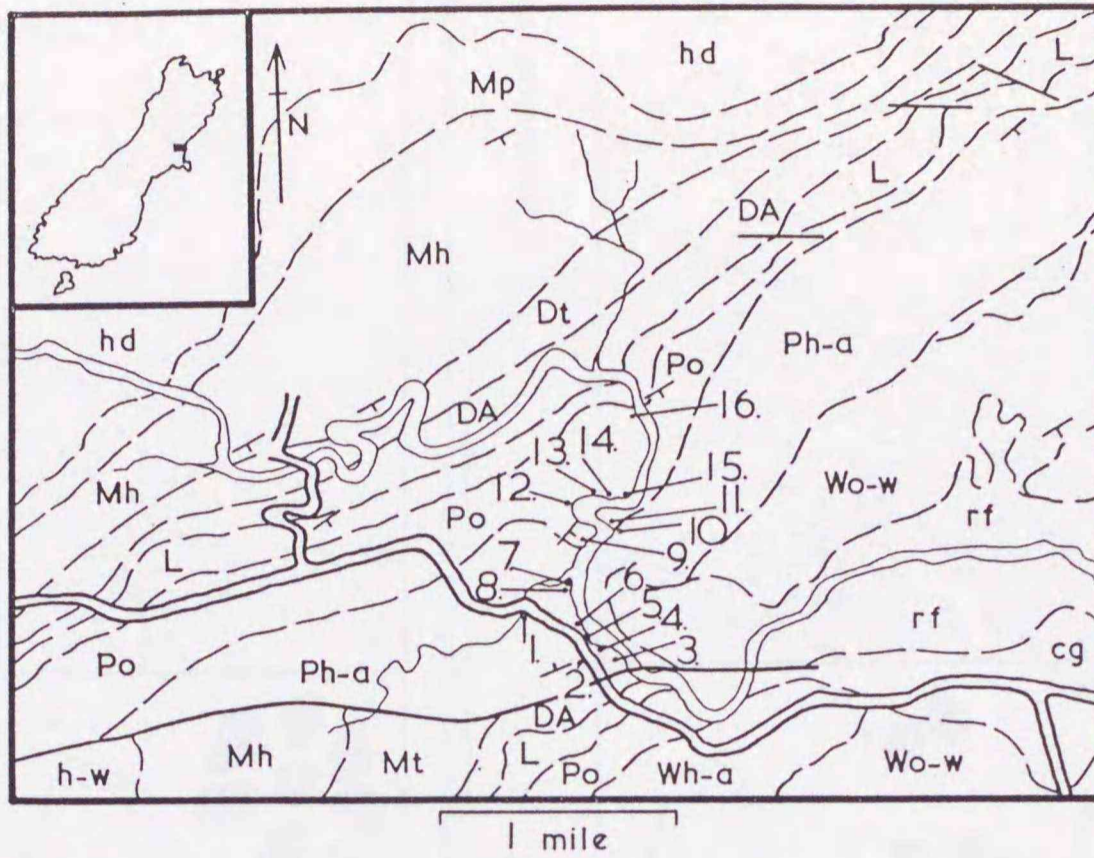
FIG. 1.—Geological map of the Middle Waipara district (after Wilson, 1963).

1–16	Sample positions	
rf	Flood plain gravels	Holocene
Cg	Gravels and loess deposits	Pleistocene
Wo-w	Marine silts, sands, and conglomerates	Pliocene
Ph-a	Blue siltstones and sandy limestones	
Po	Calcareous siltstones	Miocene
L	Limestones and marls	Oligocene
D-A		
Dt	Glauconitic mudstones and siltstones	
Mh	Glauconitic mudstones, siltstones,	Eocene and Paleocene
Mp	Sandstones and occasional coal seams	Maastrichtian
hd	Compacted sandstones and siltstones	Cretaceous and Jurassic

Inset: the Waipara district, South Island of New Zealand.

from Swanson, 1969
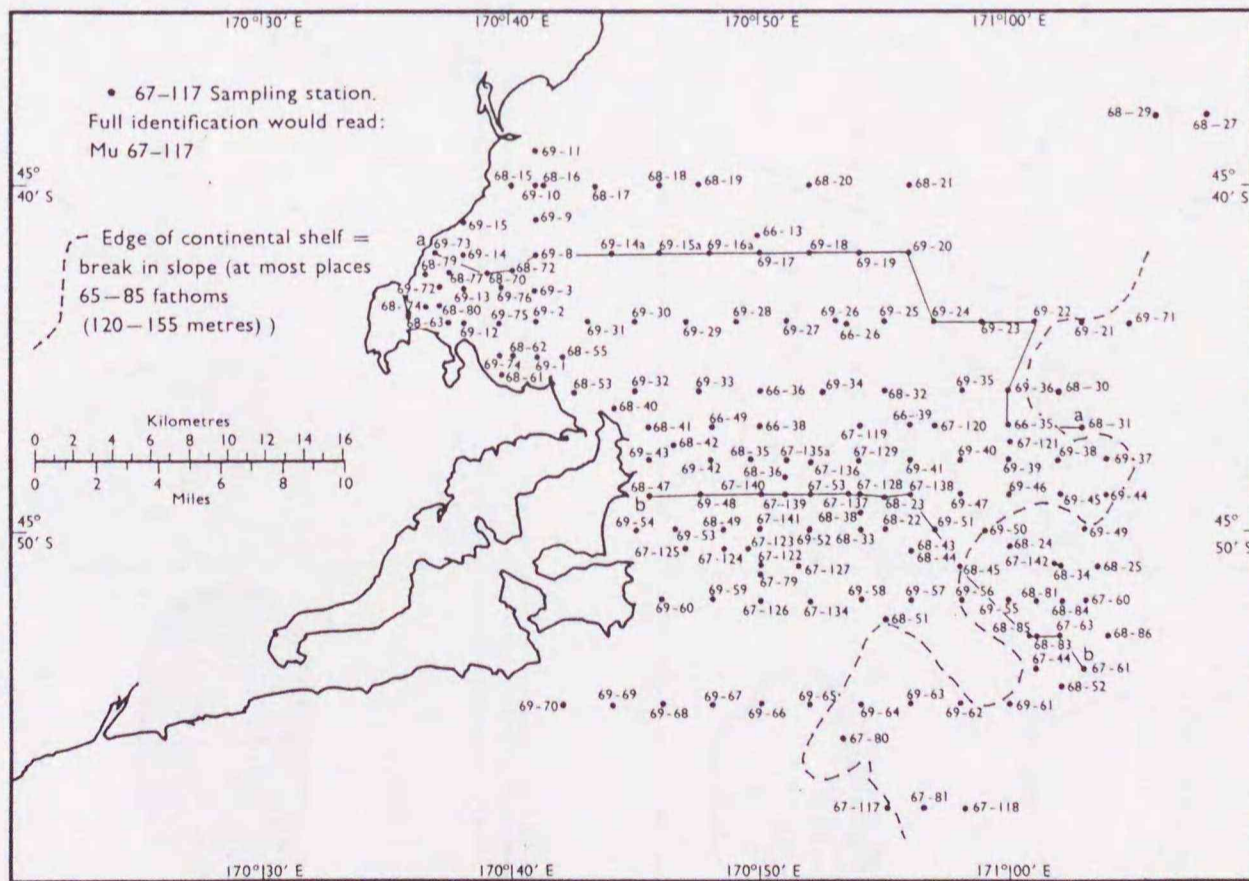
Fig. 2   Sampling stations. Lines a–a and b–b are sample traverses for Fig. 58 (i, ii).

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from Swanson, 1979a

Fig. 4.

Bairdoppilata (Bairdoppilata) sp (N.Z. Geological Survey Cat. No. OP 1031): a, external view of right valve showing left valve overlap, x 70; b, internal view of right valve, x 70; c, muscle scars, x 200; d, geographic distribution.

from Swanson, 1979a

Fig. 6.

Waiparacythereis joanae Swanson (N.Z. Geological Survey Cat. No. OP 1050): a, internal view of right valve, x 60; b, dorsal view of entire (female?) valve, x 60; c, muscle scars, x 200; d, external view of right valve, x 60; e, geographic distribution.

Fig. 3.

Cytherella hemigymna Swanson (N.Z. Geological Survey Cat. No. OP 1029): a, internal view of female right valve, x 70; b, external view of female right valve, x 70; c, dorsal view of entire (female?) carapace, x 70; d, geographic distribution.

Fig. 5.
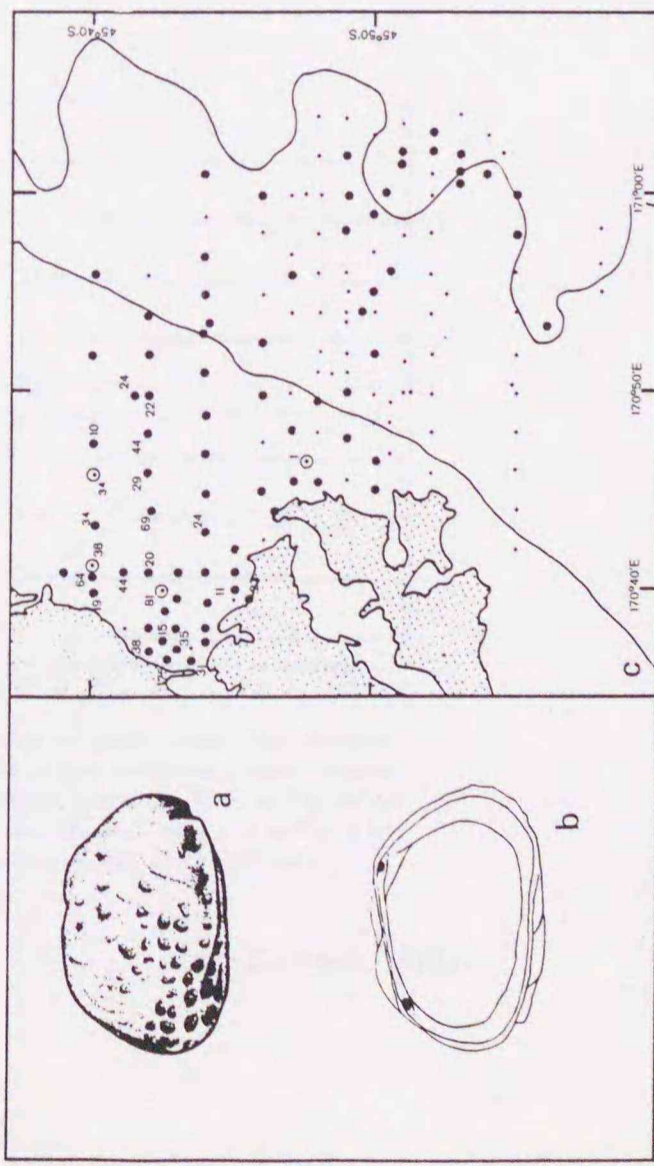
Loxoconcha crasta Hornibrook (N.Z. Geological Survey Cat. No. OP 1048): a, external view of left valve, x 60; b, internal view of left valve, x 60; c, geographic distribution.

39

SPECIES — DEPTH (m)

Left chart (traverse a–a):
Cytherella sp.
Cytherella hemipuncta
Cytherelloidea willetti
Bairdoppilata (Bairdoppilata) sp.
Loxocythere crassa
Eucythere gravepuncta?
S. taiaroaensis n.sp.
Copytus novaezealandiae
Pontocythere hedleyi
Oculocytheropteron acutangulum
O. confusum
O. fornix
Semicytherura arteria n.sp.
S. sencava
Hemicytherura gravis
Hemicythere munida
Waiparacythereis joanae
Callistocythere obtusa n.sp
C. neoplana n.sp
'Munseyella' aegua n.sp
M. brevis n.sp
Kotoracythere formosa n.sp
'M' tumida n.sp
Hermanites briggsi n.sp
Bradleya opima n.sp
'Cythereis' incerta n.sp
Quadracythere truncula
Semicytherura cf. C. costeliata

Right chart (traverse b–b):
Cytherella hemipuncta
Cytherelloidea willetti
Bairdoppilata (Bairdoppilata) sp.
Propontocypris (P) sp.
Propontocypris (E) epicyrta?
Argilloecia cf. pusilla
Argilloecia sp.
Loxocythere crassa
Eucythere gravepuncta?
Pontocythere hedleyi
Oculocytheropteron acutangulum
O. mosaica
O. fornix
Semicytherura arteria n.sp.
Hemicytherura gravis
Hemicythere munida n.sp
Waiparacythereis joanae
Callistocythere obtusa n.sp.
'Munseyella' aequa n.sp.
M. brevis n.sp.
Kotocythere formosa n.sp.
'M' tumida n.sp
Trachyleberis lyttletonensis
Hermanites briggsi n.sp.
Bradleya opima n.sp.
'Cythereis' incerta n.sp.
Quadracythere truncula
Semicytherura cf. C. costeliata

Fig 7. Bathymetric distribution of some Otago Shelf ostracod species : closed circles indicate living specimens present, crosses indicate sample points containing no specimens. Refer to Fig. 59 for explanation of sediment textures (mS, gmS, etc.) and to Fig. 2 for location of stations along traverse a–a (left) and b–b (right).

from Swanson, 1979a

40
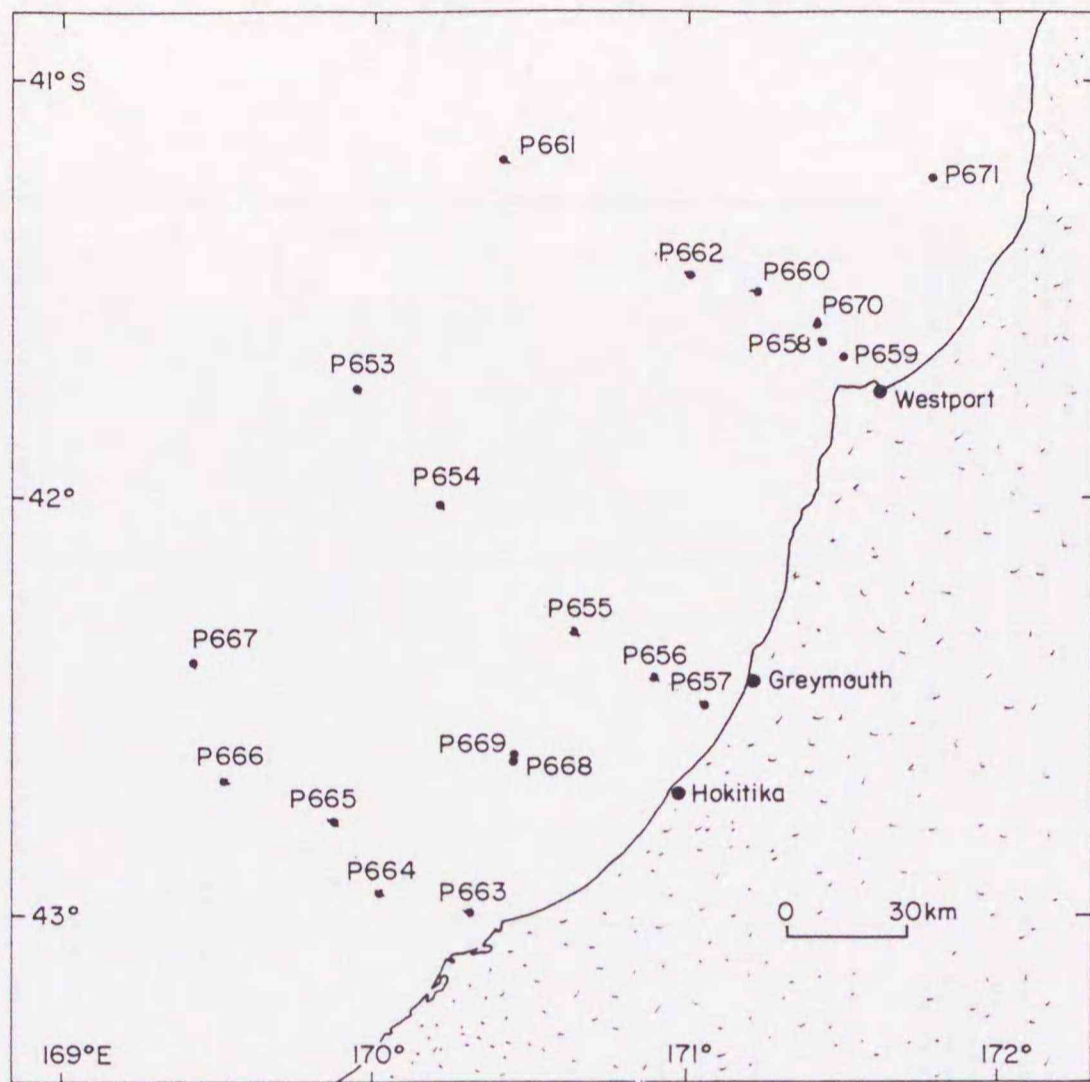
Fig. 8.   Box-core and anchor-box dredge localities, west coast South Island, New Zealand.
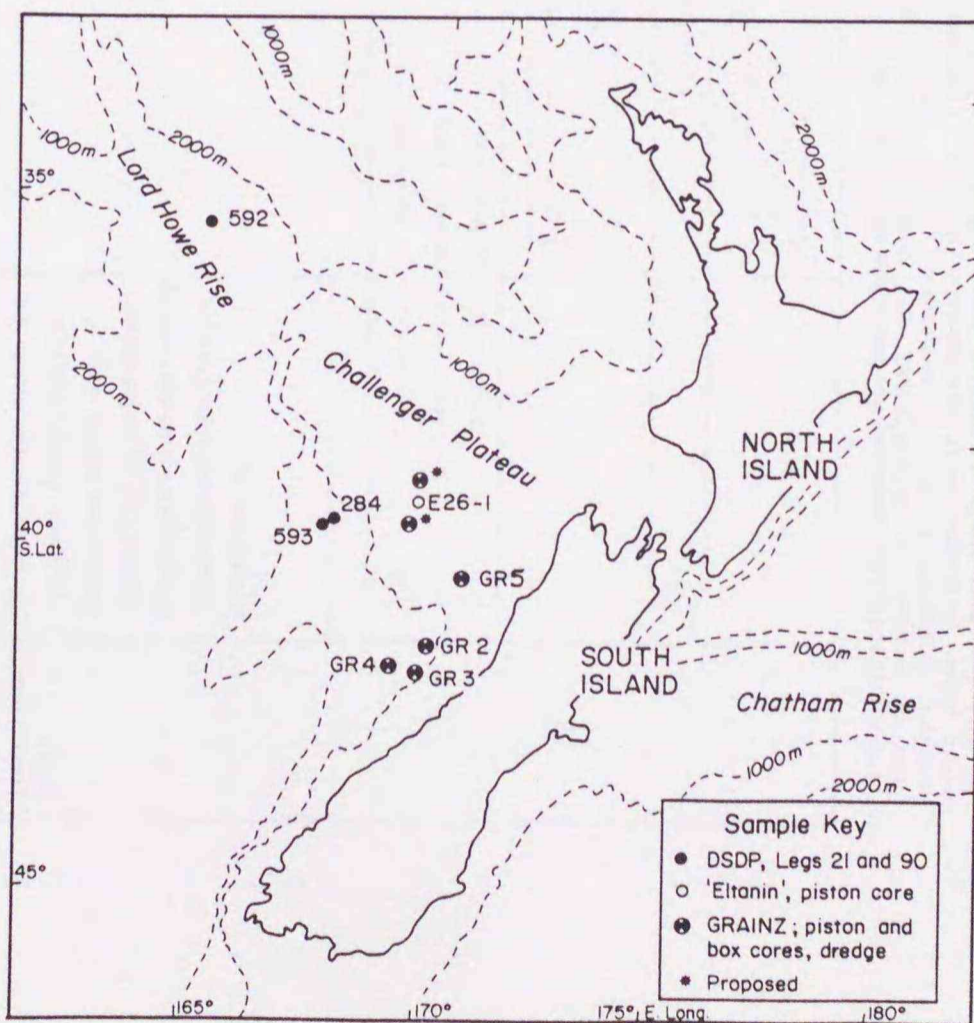
Fig. 9.   Box/piston-core localities for samples used for ostracod dissolution/shell-chemistry studies.

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TABLE 1. Ostracod assemblage zones.

	ASSEMBLAGE 1	ASSEMBLAGE 2	ASSEMBLAGE 3	ASSEMBLAGE 4	ASSEMBLAGE 5
Depth range	0-35m	0-46 m	46-95 m	95-155m	150-750 m
Dominant sediment class	sand	muddy sand	none: varies from gravelly muddy sand to sandy gravel	gravelly sand, sandy gravel	none: varies from muddy sand to sandy gravel
Mean size	$2\,0\text{-}3\,0\,\theta$ $(0\,25\text{-}0\,125mm)$	$3\,0\text{-}4\,0\,\theta$ $(0\,125\text{-}0\,062mm)$	$2\,0\text{-}3\,0\,\theta$ $(0\,25\text{-}0\,125mm)$	$-2\,0\text{-}2\,0\,\theta$ $(4\,00\text{-}0\,25mm)$	
Percentage gravel	0%	0%	25-60%	0-75%	0 50%
Percentage organic detritus	0-2%	0-20%	40-60%; minor occurences 60-100%	40-80%, minor occurrences 100%	20-60%
Sorting	well and very well sorted	moderately well - well sorted	poorly-moderately sorted	Extremely poorly-poorly sorted	Extremely poorly-poorly sorted

Characteristic species:

(a) *Semixestoleberis taiaroaensis* n.sp.
Pontocythere hedleyi (Chapman)
Hemicythere munida n.sp.
Ambostracon cf. *pumila* (Brady)
Waiparacythereis joanae Swanson
Loxoconcha punctata Thomson
Xestoleberis sp.

(b) *Loxocythere crassa* Hornibrook
Copytus novaezealandiae Brady
Callistocythere neoplana n.sp.

(c) *Munseyella brevis* n.sp.
Cytherella sp.

(d) *Kotoracythere formosa* n.sp.

(e) *Munseyella tumida* n.sp.

(f) *Cytherella hemipuncta* Swanson
Bairdoppilata sp.
Sclerochilus sp.b

(g) *Macrocypris* sp.
Argilloecia sp.

(a) The majority of species comprising this assemblage are forms of medium size (0.50-0.75 mm) with thick carapaces. *Hemicythere munida* and *Ambostracon* cf. *pumila* display moderately heavy ornamentation, the remaining five have faintly ornamented or smooth carapaces.

(b) All species small to medium in size. Both *Loxocythere crassa* and *Callistocythere neoplana* have extremely thick carapaces. *L. crassa* is the only heavily ornamented form in this group.

(c) Both *Cytherella hemipuncta* and *Munseyella brevis* have extremely thick shells. The largest populations of *Munseyella brevis* occurred in coarse sands and gravel. *Cytherella* sp. has a large smooth shell of medium thickness. Largest populations occurred in muddy sands, but the species was also common in gravelly sands.

(d) *Kotoracythere formosa*, a thick, smooth shelled form of medium size which occurs commonly in muddy sands, gravelly muddy sands, and muddy sandy gravel.

(e) A species of medium size with a thin, moderately heavily reticulate carapace. Occurs commonly in muddy sandy gravel and rarely in gravelly sand.

(f) Both species are smooth shelled : *Sclerochilus* sp.b has an extremely thin, medium sized carapace and occurs rarely in gravelly sand; *Bairdoppilata* sp. occurs commonly in sandy gravel and rarely in gravelly sand.

(g) *Argilloecia* sp and *Macrocypris* sp. display large, smooth carapaces of medium thickness. Occur only rarely.

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SAMPLE	DEPTH in metres	SED. TYPE	SETAE ✓ present x absent	CUTICLE thallophyte– bacterial degradation	RECRYST- ALLIZATION ✓ present x absent	SHELL evidence of dissolution
P657	41	detrital	✓	✓	x	✓
Q726	51	detrital	✓	✓	x	✓
P671	123	detrital	✓	✓	x	✓
P656	138	carbonate	✓	x	✓	✓
P659	152	detrital	✓	✓	x	✓
P664	187	detrital	✓	✓	✓	✓
Q693	297	detrital	✓	✓	x	✓
P654	769	carbonate	✓	✓	x	x
Q697	910	detrital	✓	✓	x	x

Note: all specimens presented here contained well–preserved soft anatomies

TABLE 2.   Ostracodal biocoenose – evidence of modification of platycopid valves in contrasting sedimentary environments

from Swanson, in press

GENUS	SAMPLE	DEPTH in metres	SED. TYPE	SETAE ✓ present x absent	COCCO. evidence of reprecipitation	SHELL evidence of dissolution
Cytheropteron	Q691	109	carbonate	✓	✓	x
Eucythere	P660	154	detrital	x	✓	x
Bradleya	P693	297	detrital	✓	x	✓
'Henryhowella'	P693	297	detrital	✓	✓	x
Bradleya	P661	621	carbonate	x	✓	✓
Bradleya	P661	621	carbonate	x	✓	✓
'Henryhowella'	P661	621	carbonate	x	✓	x
Bradleya	P654	769	carbonate	x	x	✓
Cytheropteron	P654	769	carbonate	x	x	✓
Parakrithe	P654	769	carbonate	x	x	✓
'Henryhowella'	Q719	793	carbonate	✓	x	✓
Actinocythereis	P667	1047	detrital	x	✓	✓
Argilloecia	P667	1047	detrital	x	x	✓
Bradleya	P667	1047	detrital	x	x	✓
Bradleya	P667	1047	detrital	x	✓	✓
Legitimocyther.	Q698	1100	detrital	✓	x	✓

Ostracodal biocoenoes – evidence of modification of podocopid valves in contrasting sedimentary environments

TABLE 3.

from Swanson, in press

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UNDERSATURATED SEAWATER

CaCO₃

CaCO₃

CaCO₃
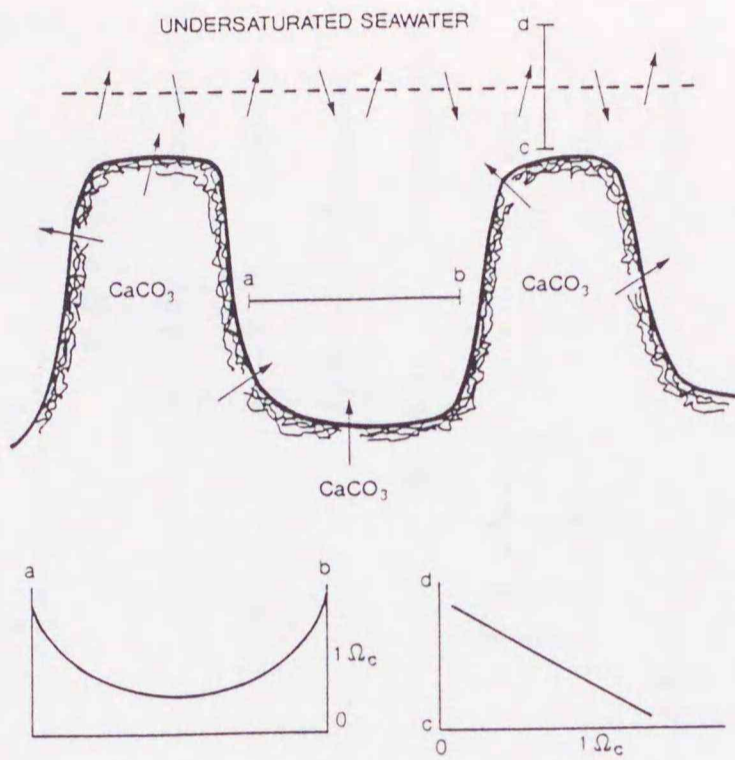
$$\Omega_c = \frac{(Ca^{2+})(CO_3^{2-}) \text{ sea water}}{(Ca^{2+})(CO_3^{2-}) \text{ sea water saturated with calcite}}$$

Fig. 10. :Theoretical calcite saturation flux at and near
the external surface of an ornate
podocopid ostracod carapace

UNDERSATURATED SEAWATER
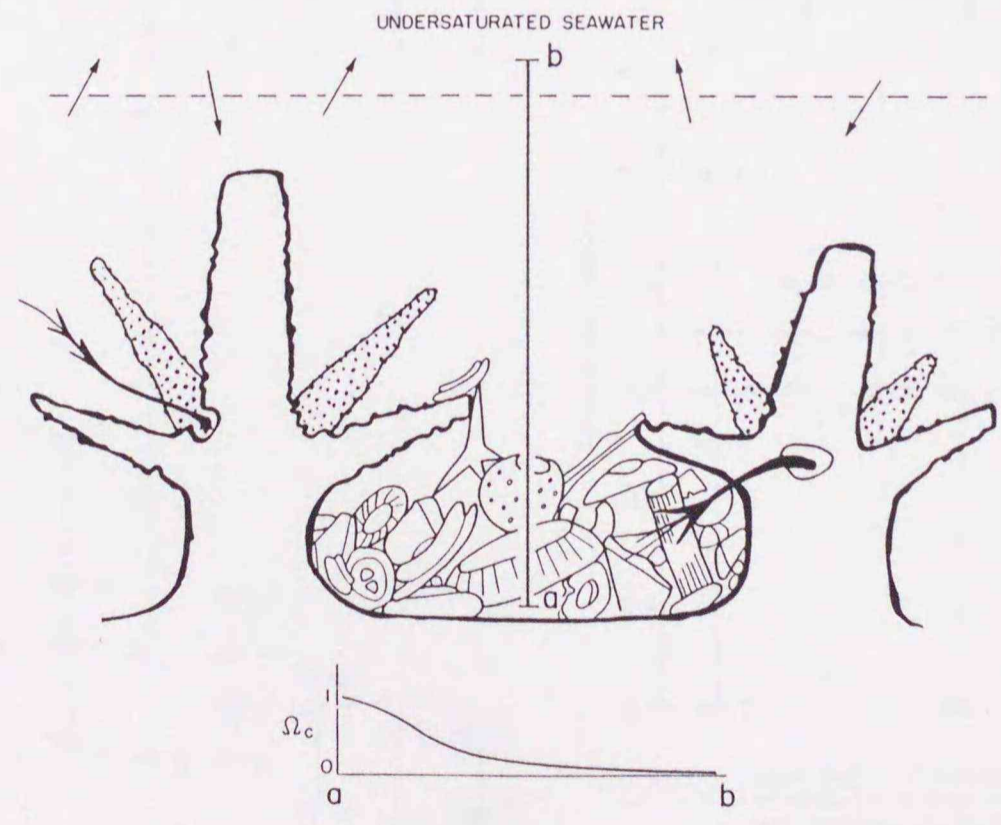
Fig. 11. :Modifying effects of calcareous particle entrapment
on the theoretical calcite saturation flux near the
external surface of a spinose podocopid ostracod

from Swanson, in press

Fig. 12.

Water depth (m.)

Krithe
Philoneptunus
L. acanthoderma
H. dasyderma
Poseidonamicus
B. audax
D. suhmi
P. mucronalatum

0

1000

2000

3000
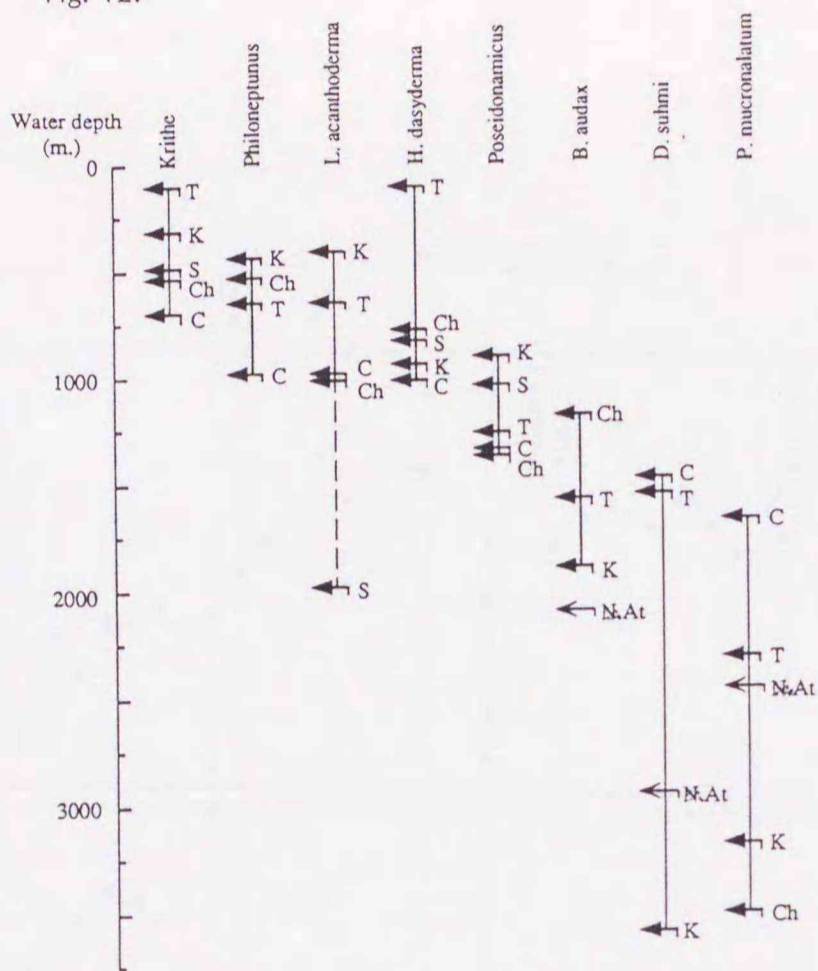
Fig. 12.   Difference in upper depth limit of studied taxa between the study regions. The shallowest upper depth limit of abyssal taxa recorded in the Atlantic (Dingle et al., 1990) is also shown for comparison. Key to abbeviation: C= Coral Sea,   Ch = Chatham Rise,   K - Kerquelen Plateau, S = Southeast Australian Continental Slope,   T = Tasman Sea, At = Alantic

Fig. 13.

Krithe
Philoneptunus
L. acanthoderma
H. dasyderma
Poseidonamicus
B. audax
D. suhmi
P. mucronalatum

Water temperature at upper depth limit (°C)

14

12

10

8

6

4

2

0
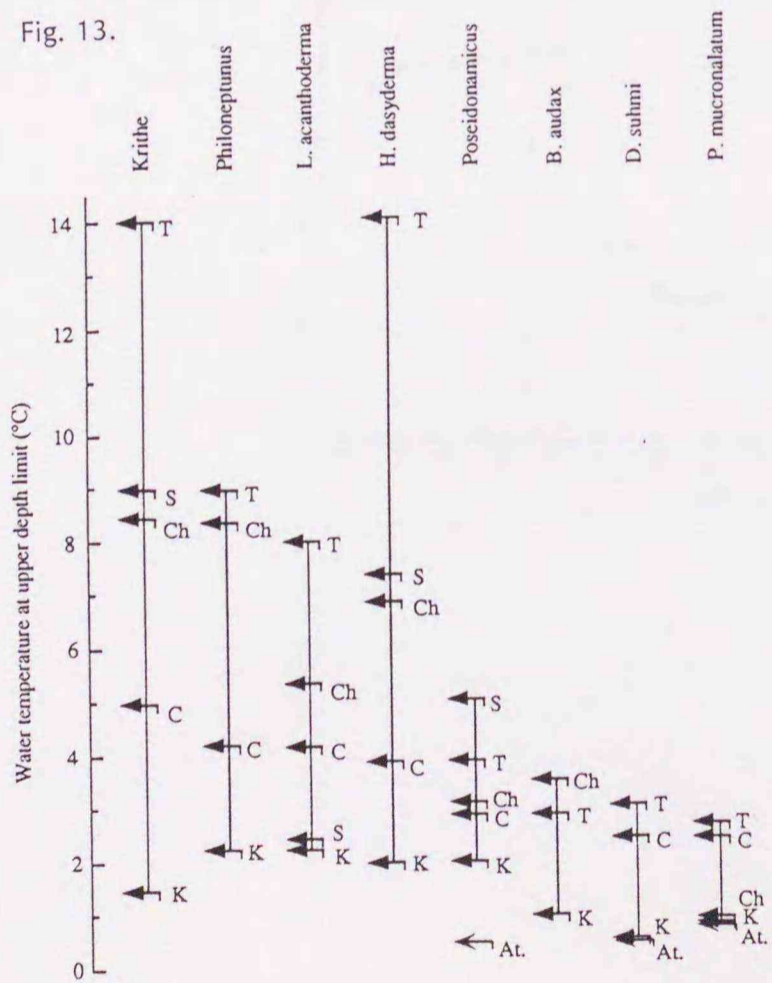
Fig. 13.   Upper depth limits of studied taxa with respect to water temperature (°C) in each of the five study regions. Levels corresponding to shallowest Atlantic occurrences (see Fig. 12) are also shown.

Fig. 14.

Krithe
Philoneptunus
L. acanthoderma
H. dasyderma
Poseidonamicus
B. audax
D. suhmi
P. mucronalatum

Salinity at upper depth limit ( )

34.0

34.2

34.4

34.6

34.8

35.0

35.2
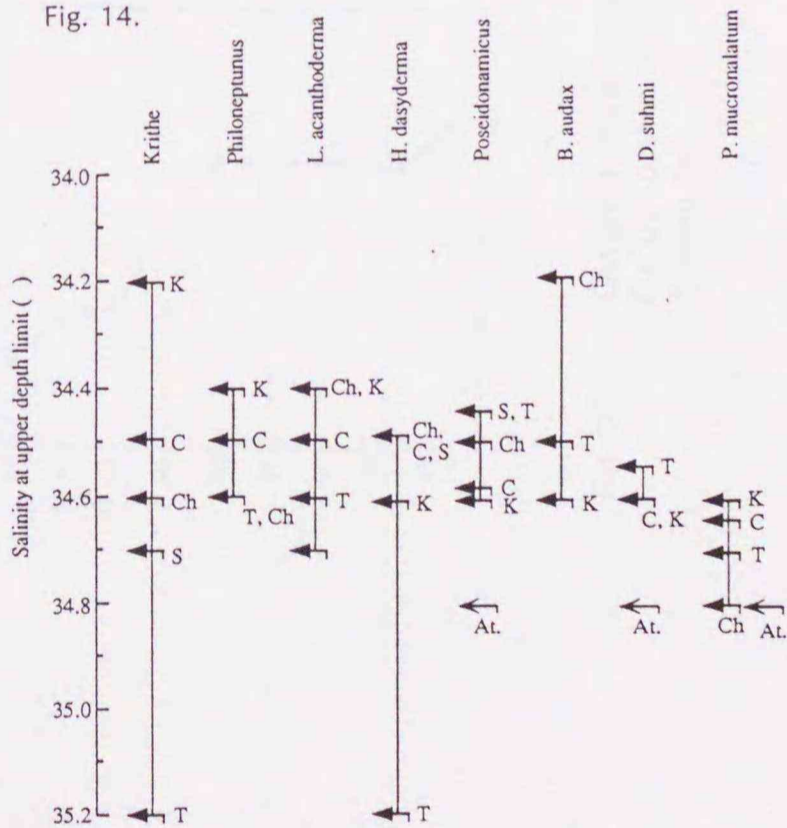
Fig. 14.   Upper depth limits of studied taxa with respect to salinity (parts per thousand) in each of the five study regions. levels corresponding to shallowest Atlantic occurrences (see Fig. 12) are also shown.

45

from Ayress, Neil, Passlow and Swanson, in press
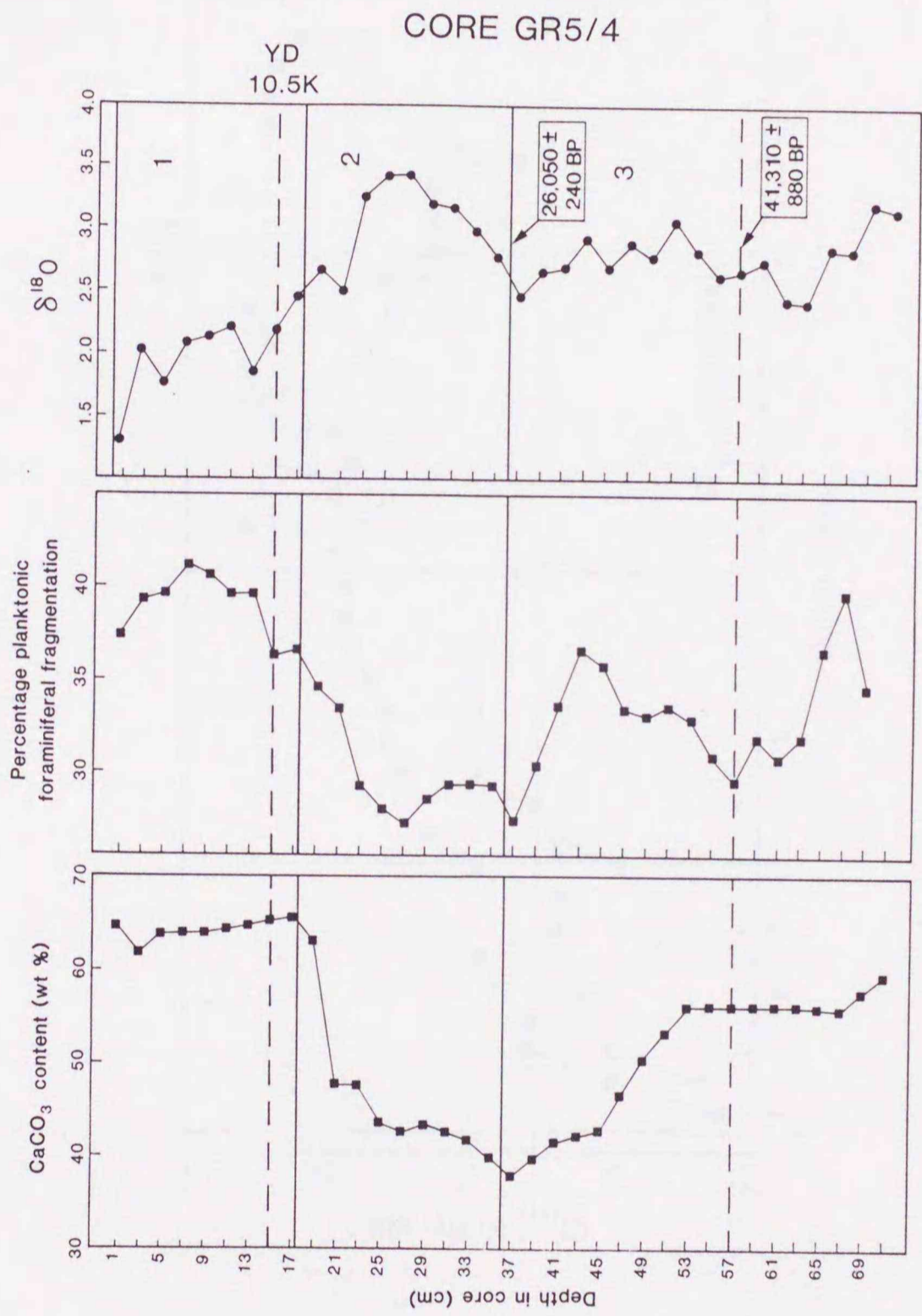
Fig. 15. Oxygen isotope stratigraphy, planktonic foraminiferal fragmentation and CaCo$_3$ content in core GR5/4 (686 metre water depth) in the eastern Tasman Sea.

from Swanson and van der Lingen, in press

46
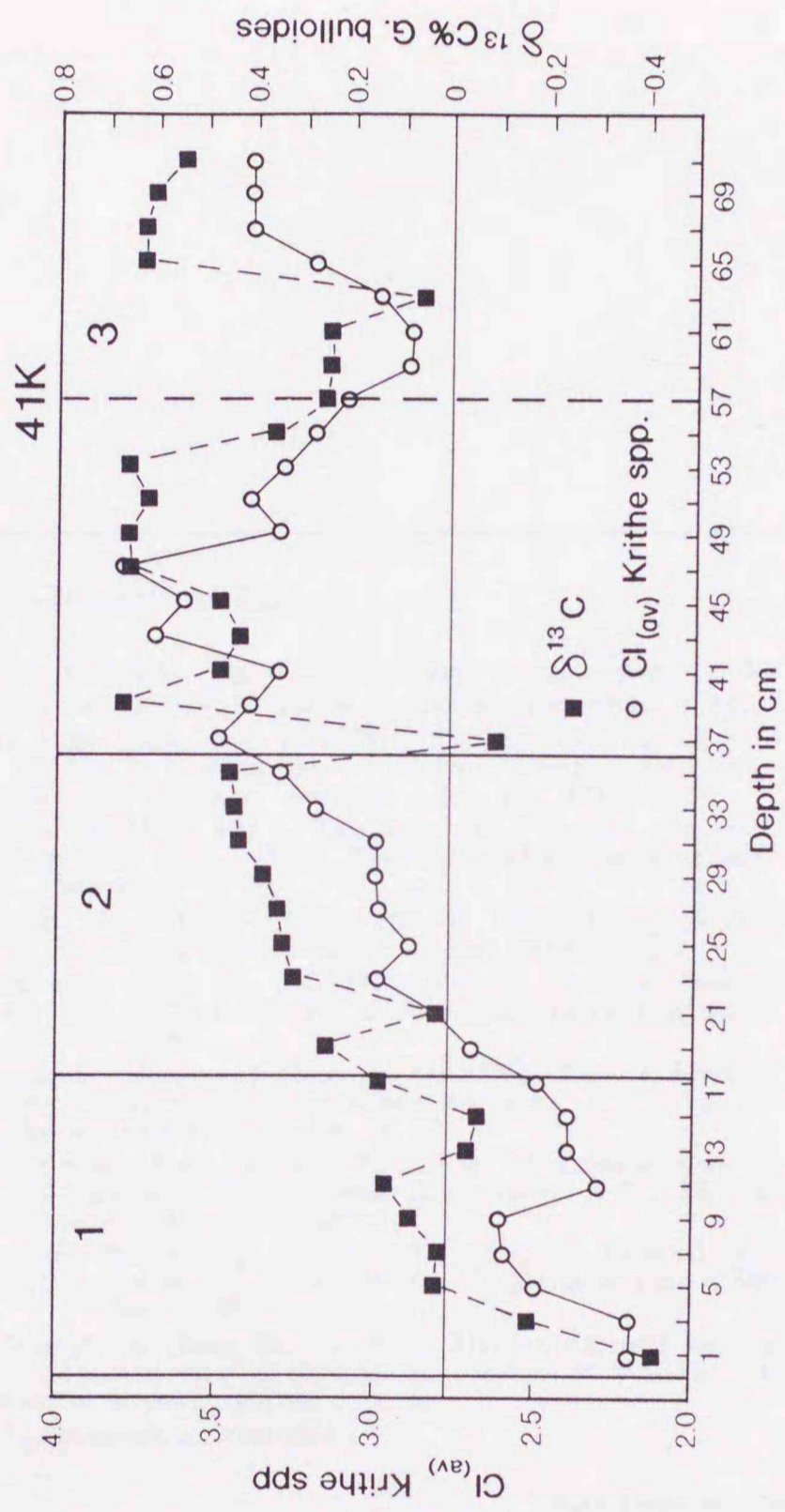
Fig. 16. Corrosion index for *Krithe* spp and planktonic foraminiferal $\delta^{13}C$. Core GR5/4, eastern Tasman Sea.

from Swanson and van der Lingen, in press

47

Description of Plate 1

Figs. 1–3.—*Cytherella* sp.a (Reg. No. OP1004). Fig. 1. External view of right valve. × 50. Fig. 2. Internal view of right valve. × 50. Fig. 3. Dorsal outline of right valve. × 50.

Figs. 4–6.—*Cytherella hemipuncta* n.sp. (Reg. No. TO1003). Fig. 4. External view of holotype. Female? right valve. × 30. Fig. 5. Internal view of holotype. Female? right valve. × 30. Fig. 6. Dorsal outline of entire carapace. Paratype (Reg. No. TO1003/2).

Figs. 7–9.—*Cytherella* sp.b (Reg. No. OP1005). Fig. 7. External view of female? left valve. × 50. Fig. 8. Internal view of female? left valve. × 50. Fig. 9. Dorsal outline of female? left valve. × 50.

Figs. 10–11.—*Cytherella elongata* n.sp. (Reg. No. TO1002). Fig. 10. External view of holotype. Left valve. × 30. Fig. 11. Dorsal view of holotype. Left valve. × 30.

Figs. 12–13.—*Cytherelloidea willetti* n.sp. (Reg. No. TO1004). Fig. 12. External view of holotype. Female right valve. × 45. Fig. 13. Internal view of holotype. Female right valve. × 45.

Figs. 14–16.—*Cytherelloidea praeauricula* (Chapman) (Reg. No. OP1006). Fig. 14. External view of female right valve. × 30. Fig. 15. Internal view of female left valve. × 30. Fig. 16. Dorsal outline of female right valve. × 30.

Figs. 17–19.—*Bairdia canterburyensis* n.sp. (Reg. No. TO1005). Fig. 17. External view of holotype. Right valve. × 30. Fig. 18. Internal view of holotype. Right valve. × 30. Fig. 19. Dorsal outline of holotype. Right valve.

Figs. 23–25.—*Phlyctenophora zealandica* Brady (Reg. No. OP1007). Fig. 23. External view of left valve. × 30. Fig. 24. Internal view of left valve. × 30. Fig. 25. Dorsal outline of left valve. × 30.

Figs. 20–22.—*Loxocythere crassa* Hornibrook (Reg. No. OP1008). Fig. 20. External view of female? right valve. × 50. Fig. 21. Internal view of female? right valve. × 50. Fig. 22. Dorsal outline of female? right valve. × 50.

(Magnifications approximate.)

from Swanson, 1969

48
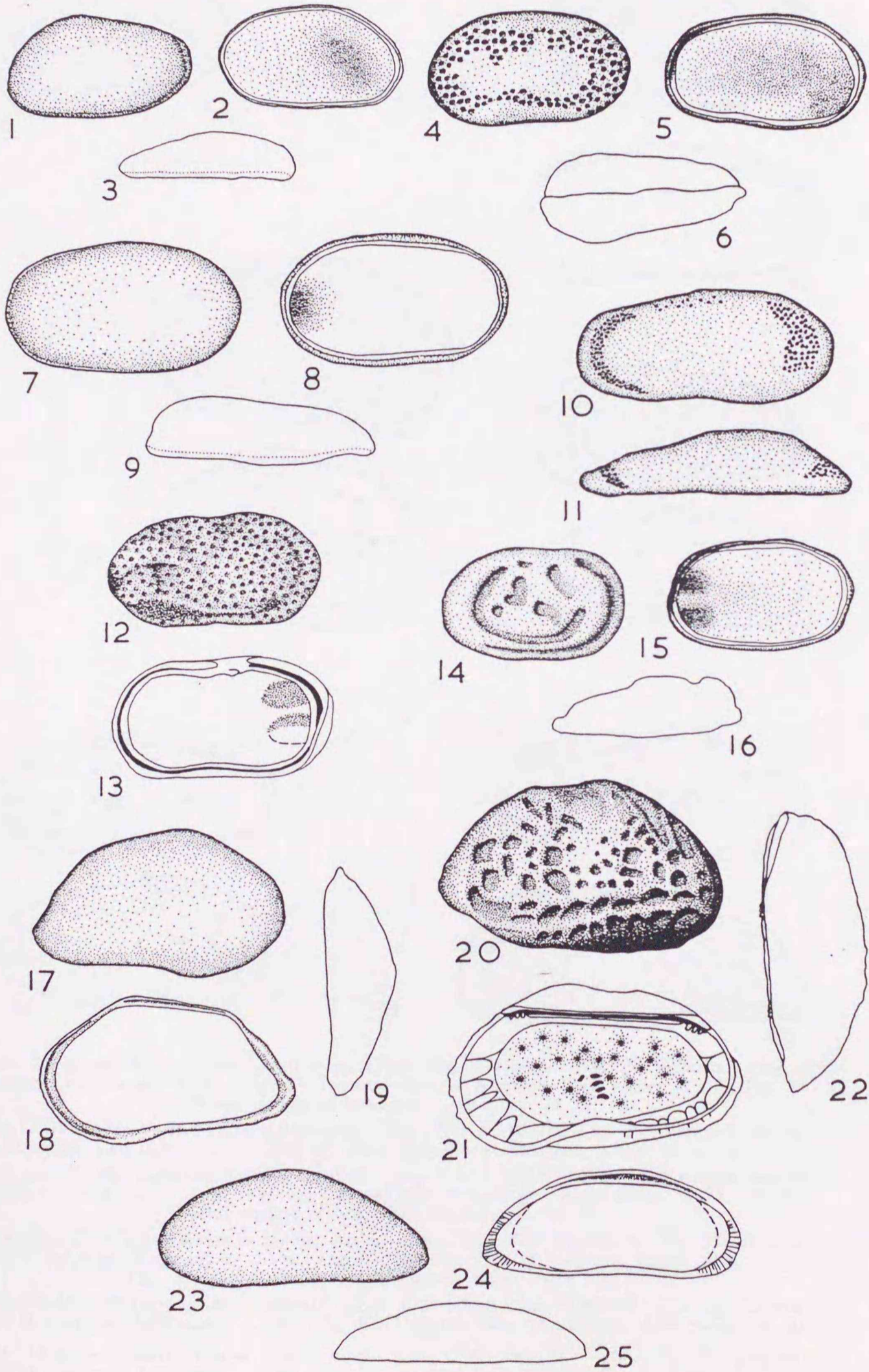
PLATE 1

PLATE 2
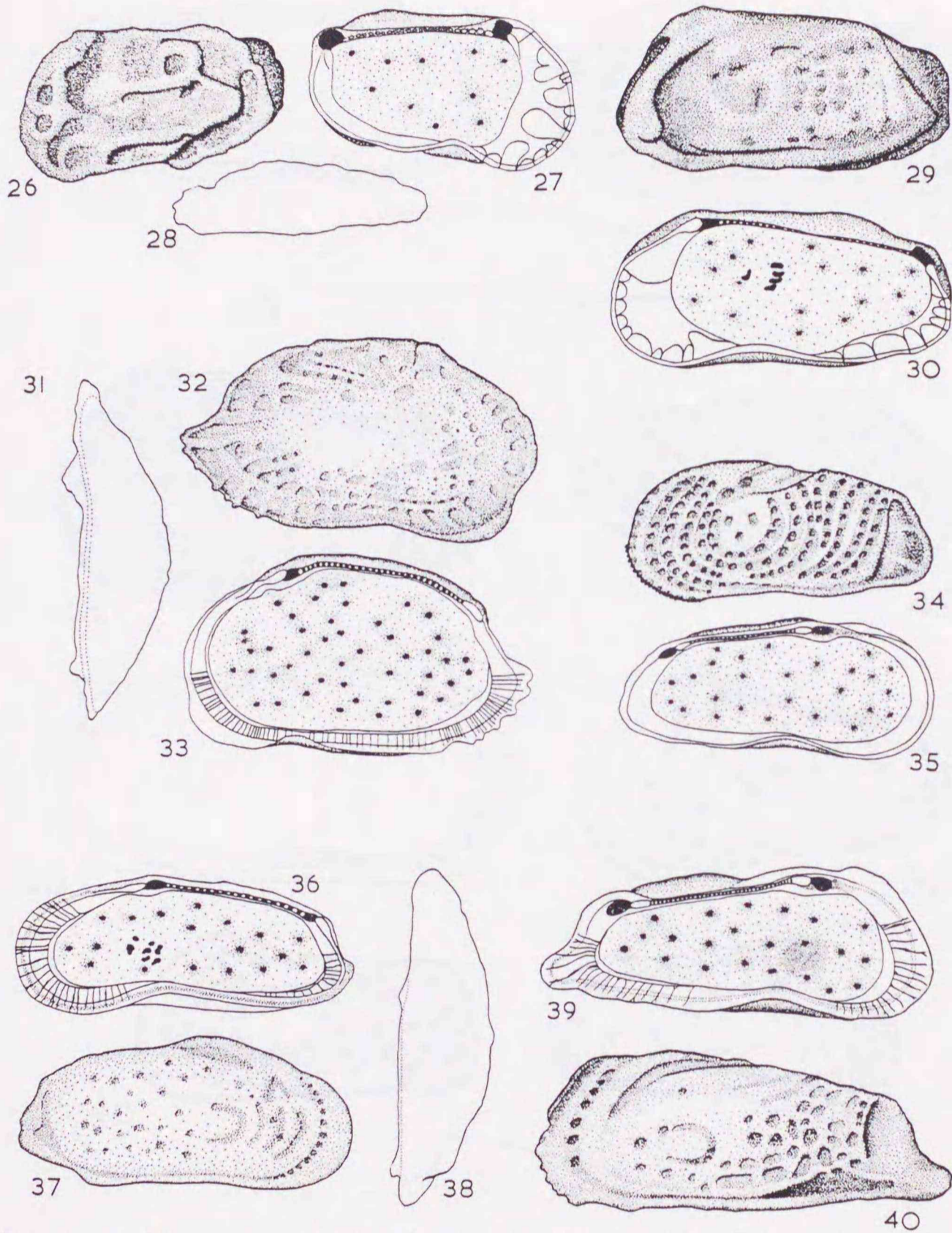
FIGS. 26–28.—*Callistocythere hanaii* n.sp. (Reg. No. TO1006). Fig. 26. External view of holotype. Left valve. × 50. Fig. 27. Internal view of holotype. Left valve. × 50. Fig. 28. Dorsal outline of holotype. Left valve. × 50.

FIGS. 29–30.—*Munseyella rectangulata* n.sp. (Reg. No. TO1007). Fig. 29. External view of holotype. Left valve. × 75. Fig. 30. Internal view of holotype. Right valve. × 75.

FIGS. 31–33.—*Hemicythere hornibrooki* n.sp. (Reg. No. TO1008). Fig. 32. External view of holotype. Right valve. × 75. Fig. 33. Internal view of holotype. Right valve. × 75. Fig. 31. Dorsal outline of holotype. Right valve. × 75.

FIGS. 36–38.—*Waiparacythereis joanae* n.gen. n.sp. (Reg. No. TO1009). Fig. 36. Internal view of holotype. Right valve. × 50. Fig. 37. External view of holotype. Right valve. × 50. Fig. 38. Dorsal outline of holotype. Right valve. × 50.

FIGS. 39–40.—*Waiparacythereis caudata* n.gen. n.sp. (Reg. No. TO1010). Fig. 39. Internal view of holotype. Left valve. × 50. Fig. 40. External view of holotype. Left valve. × 50.

FIGS. 34–35.—*Waiparacythereis decora* n.gen. n.sp. (Reg. No. TO1011). Fig. 34. External view of holotype. Left valve. × 60. Fig. 35. Internal view of holotype. Left valve. × 60. (Magnifications approximate.)

from Swanson, 1969

PLATE 3
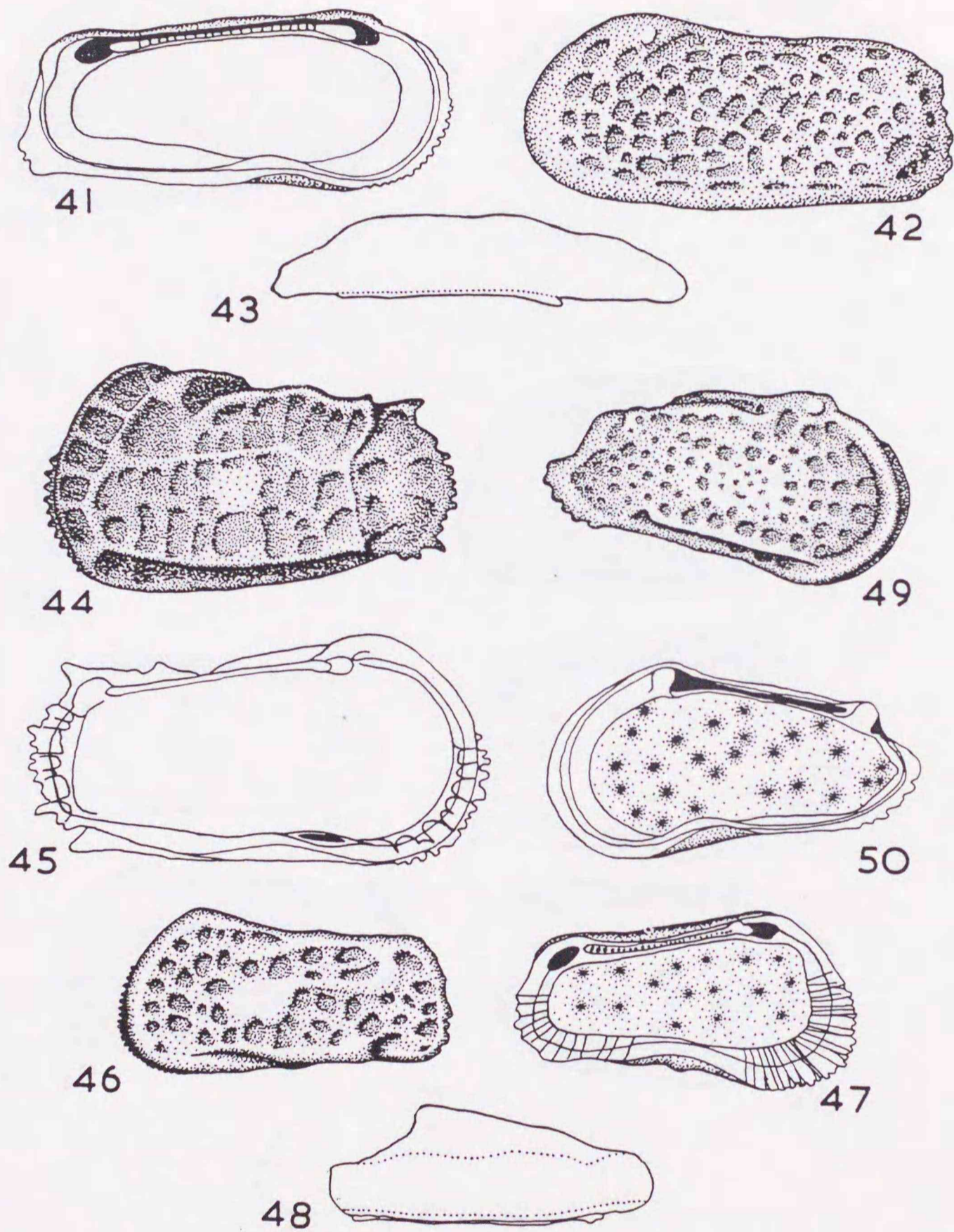
FIGS. 41–43.—*Urocythereis ? opima* n.sp. (Reg. No. TO1012). Fig. 41. Internal view of holotype. Left valve. × 50. Fig. 42. External view of holotype. Left valve. × 50. Fig. 43. Dorsal outline of holotype. Left valve. × 50.

FIGS. 44–45.—*Bradleya dictyon* (Brady) Hornibrook (Reg. No. OP1009). Fig. 44. External view of left valve. × 60. Fig. 45. Internal view of left valve. × 60.

FIGS. 46–48.—*Bradleya cuneazea* Hornibrook (Reg. No. OP1010). Fig. 46. External view of left valve. × 60. Fig. 47. Internal view of left valve. × 60. Fig. 48. Dorsal outline of left valve. × 60.

FIGS. 49–50.—*Cletocythereis* cf. *bradyi* Holden (Reg. No. OP1012). Fig. 49. External view of right valve. × 60. Fig. 50. Internal view of right valve. × 60.

(Magnifications approximate.)

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Plate 4
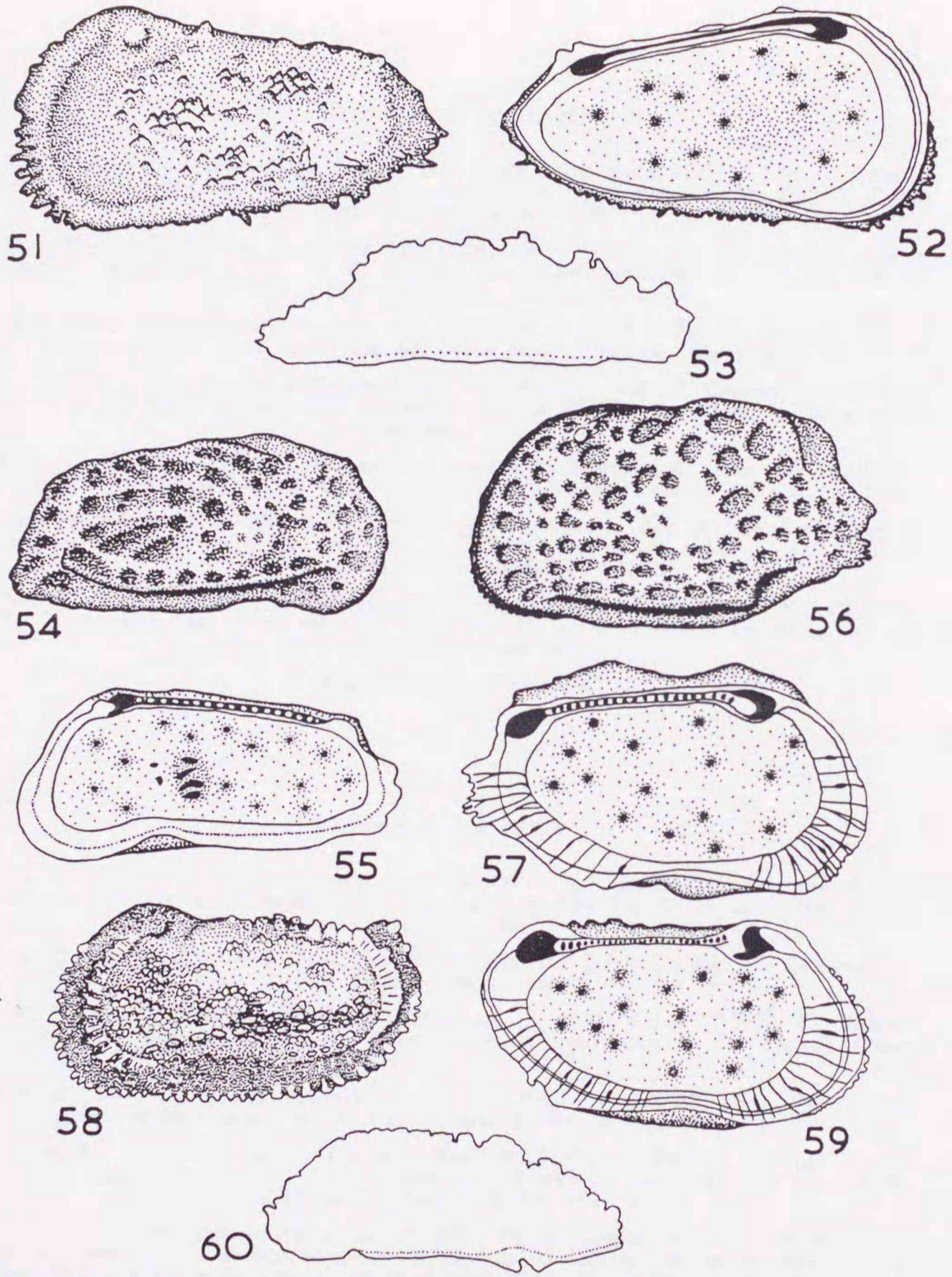
Figs. 51–53.—*Trachyleberis thomsoni* Hornibrook (Reg. No. OP1011). Fig. 51. External of view of male? left valve. × 50. Fig. 52. Internal view of male? left valve. × 50. Fig. 53. Dorsal outline of male? left valve. × 50.

Figs. 54–55.— *Quadracythere claremontensis* n.sp. (Reg. No. TO1013). Fig. 54. External view of holotype. Right valve. × 60. Fig. 55. Internal view of holotype. Right valve. × 60.

Figs. 56–57.—*Quadracythere mediaplana* Hornibrook (Reg. No. OP1013). Fig. 56. External view of left valve. × 75. Fig. 57. Internal view of left valve. × 75.

Figs. 58–60.—*Henryhowella rugibrevis* (Hornibrook) (Reg. No. OP1014). Fig. 58. External view of left valve. × 75. Fig. 59. Internal view of left valve. × 75. Fig. 60. Dorsal outline of left valve. × 75.

(Magnifications approximate.)

from Swanson, 1969

Description of Plate 5

Figs. 61–63.—*Clithrocytheridea marwicki* Hornibrook (Reg. No. OP1015). Fig. 61. External view of right valve. × 50. Fig. 62. Internal view of right valve. × 50. Fig. 63. Dorsal outline of right valve. × 50.

Figs. 64–66.—*Cytheridea symmetrica* n.sp. (Reg. No. TO1014). Fig. 64. External view of holotype. Left valve. × 50. Fig. 65. Internal view of holotype. Left valve. × 50. Fig. 66. Dorsal outline of holotype. Left valve. × 50.

Figs. 67–68.—*Neocytherideis mediata* n.sp. (Reg. No. TO1015). Fig. 67. External view of holotype. Right valve. × 30. Fig. 68. Dorsal view of holotype. Right valve. × 30.

Figs. 69–71.—*Copytus rara* McKenzie (Reg. No. OP1016). Fig. 69. External view of right valve. × 30. Fig. 70. Internal view of right valve. × 30. Fig. 71. Dorsal outline of entire carapace. × 30.

Figs. 72–73.—*Eucythere (Rotundracythere) subovalis* Hornibrook (Reg. No. OP1017). Fig. 72. Internal view of left valve. × 100. Fig. 73. External view of left valve. × 100.

Figs. 74–76.—*Eucythere (Rotundracythere) mytila* Hornibrook (Reg. No. OP1018). Fig. 74. External view of left valve. × 100. Fig. 75. Internal view of left valve. × 100. Fig. 76. Dorsal outline of entire carapace. × 100.

Figs. 77–79.—*Eucythere (Rotundracythere) gravepuncta* Hornibrook (Reg. No. OP1019). Fig. 77. Internal view of left valve. × 100. Fig. 78. External view of left valve. × 100. Fig. 79. Dorsal outline of left valve. × 100.

(Magnifications approximate.)

Description of Plate 6

Figs. 80–82.—*Cytherura clausi* Brady (Reg. No. OP1020). Fig. 80. Internal view of right valve. × 100. Fig. 81. External view of right valve. × 100. Fig. 82. Dorsal outline of right valve. × 100.

Figs. 83–84.—*Hemicytherura gravis* Hornibrook (Reg. No. OP1021). Fig. 83. External view of left valve. × 100. Fig. 84. Internal view of left valve. × 100.

Figs. 85–87.—*Cytheropteron improbum* Hornibrook (Reg. No. OP1022). Fig. 85. Internal view of right valve. × 75. Fig. 86. External view of right valve. × 75. Fig. 87. Dorsal outline of right valve. × 75.

Figs. 88–89.—*Cytheropteron wellmani* Hornibrook (Reg. No. OP1023). Fig. 88. External view of right valve. × 75. Fig. 89. Internal view of right valve. × 75.

Figs. 90–92.—*Cytheropteron mosaica* n.sp. (Reg. No. TO1016). Fig. 90. External view of holotype. Right valve. × 60. Fig. 91. Internal view of holotype. Right valve. × 60. Fig. 92. Dorsal outline of holotype. Right valve. × 60.

Figs. 93–95.—*Loxoconcha* sp. (Reg. No. OP1027). Fig. 93. Internal view of left valve. × 75. Fig. 94. Dorsal outline of entire carapace. × 75. Fig. 95. External view of left valve. × 75.

Figs. 96–97.—*Loxoconcha propunctata* Hornibrook (Reg. No. OP1024). Fig. 96. Internal view of left valve. × 60. Fig. 97. External view of left valve. × 60.

Figs. 98–100.—*Cytheralison pravacauda* Hornibrook (Reg. No. OP1025). Fig. 98. Internal view of left valve. × 30. Fig. 99. External view of left valve. × 30. Fig. 100. Dorsal outline of left valve. × 30.

Figs. 101–102.—*Saida torresi* (Brady) (Reg. No. OP1026). Fig. 101. External view of right valve. × 75. Fig. 102. Internal view of right valve. × 75.

(Magnifications approximate.)

PLATE 5

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PLATE 6

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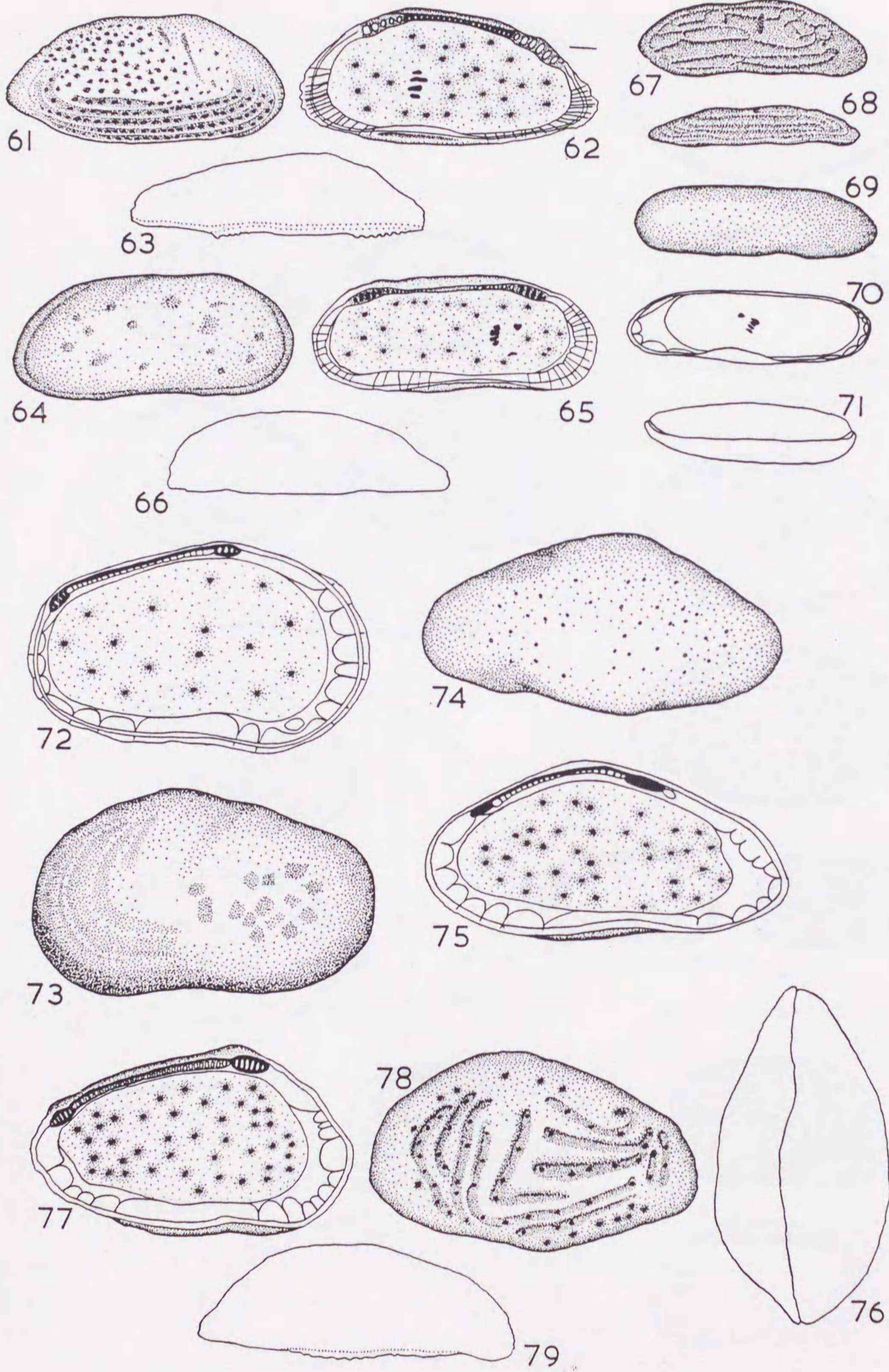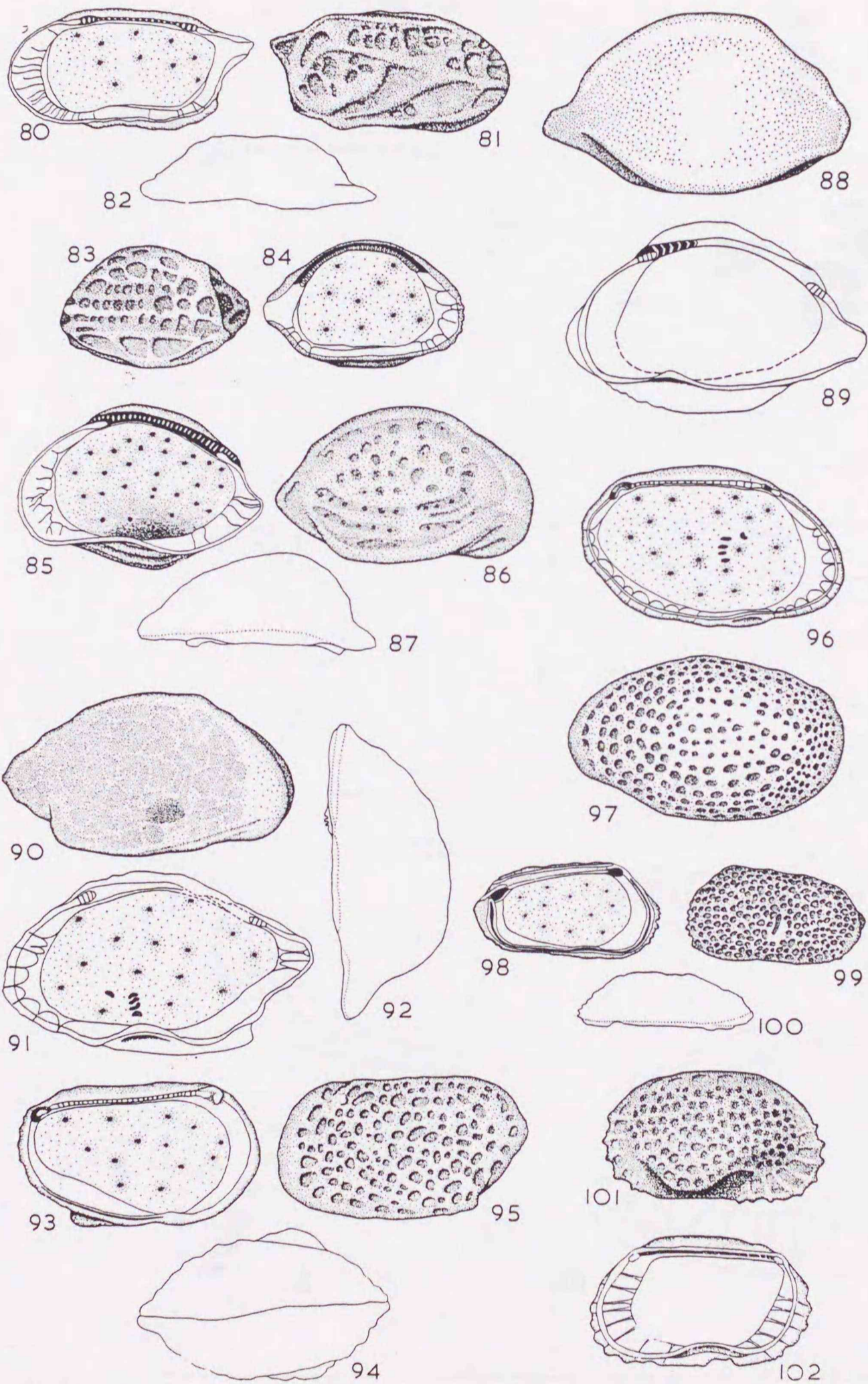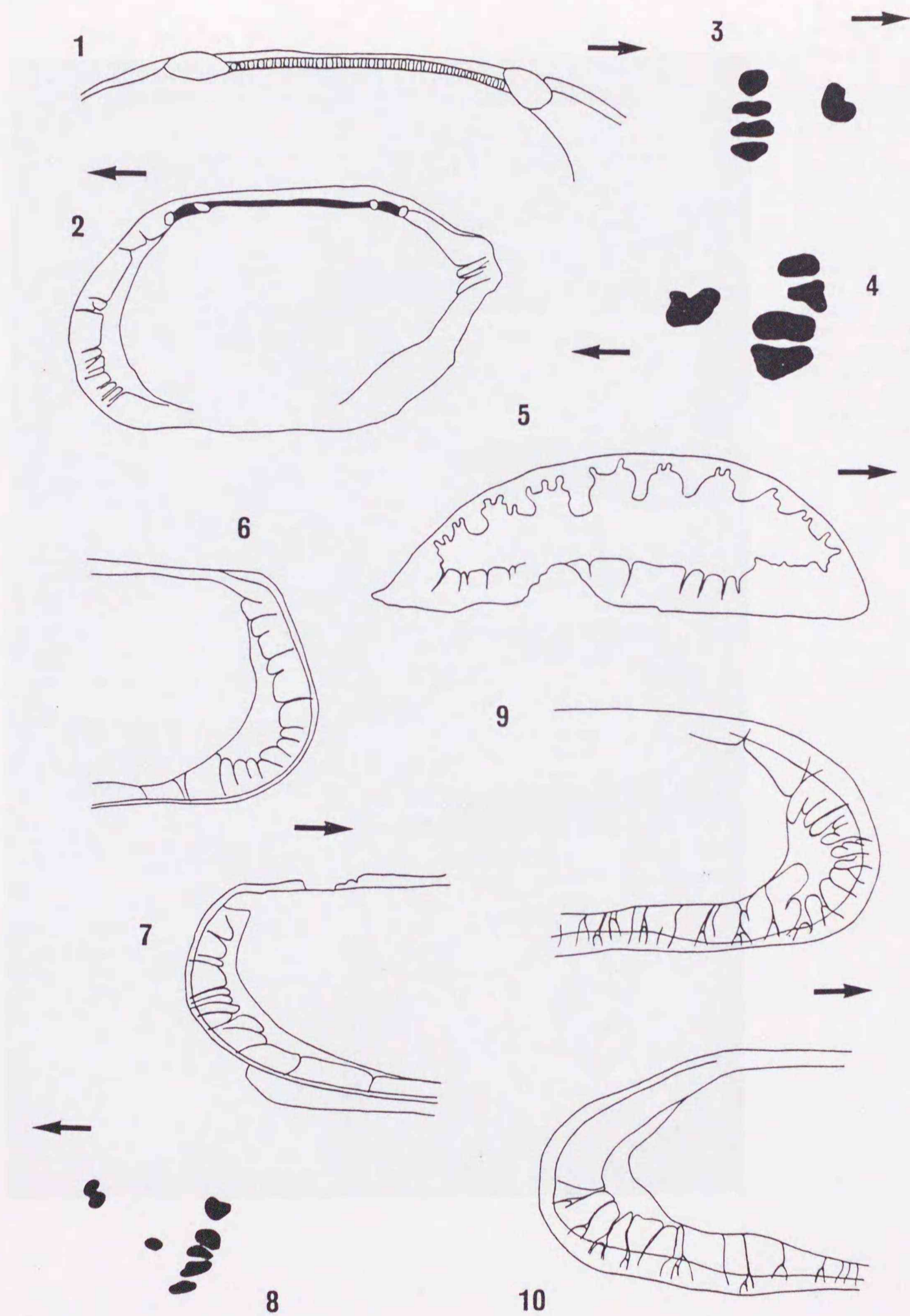
from Swanson, 1980

Plate 7. _(opposite)_ (all magnifications approximate).   **(1–3)** _'Loxoconcha' tubmani_ n.sp.: **1**, hingement, left valve (×300); **2**, internal view of right valve showing marginal pores and hingement (×200); **3**, muscle scars, left valve (×450). **(4,5)** _Microxestoleberis triangulata_ n.sp.: **4**, muscle scars (×300); **5**, ventral view of marginal pores (×100). **(6–8)** _Microceratina quadrata_ n.sp.: **6**, internal view of left valve, anterior, showing marginal pores (×100); **7**, internal view of left valve, posterior, showing marginal pores (×100); **8**, muscle scars (×100). **(9,10)** _Tanella dedeckkeri_ n.sp.: **9**, internal view of left valve, anterior, showing marginal pores (×150); **10**, internal view of left valve, posterior, showing marginal pores (×150).
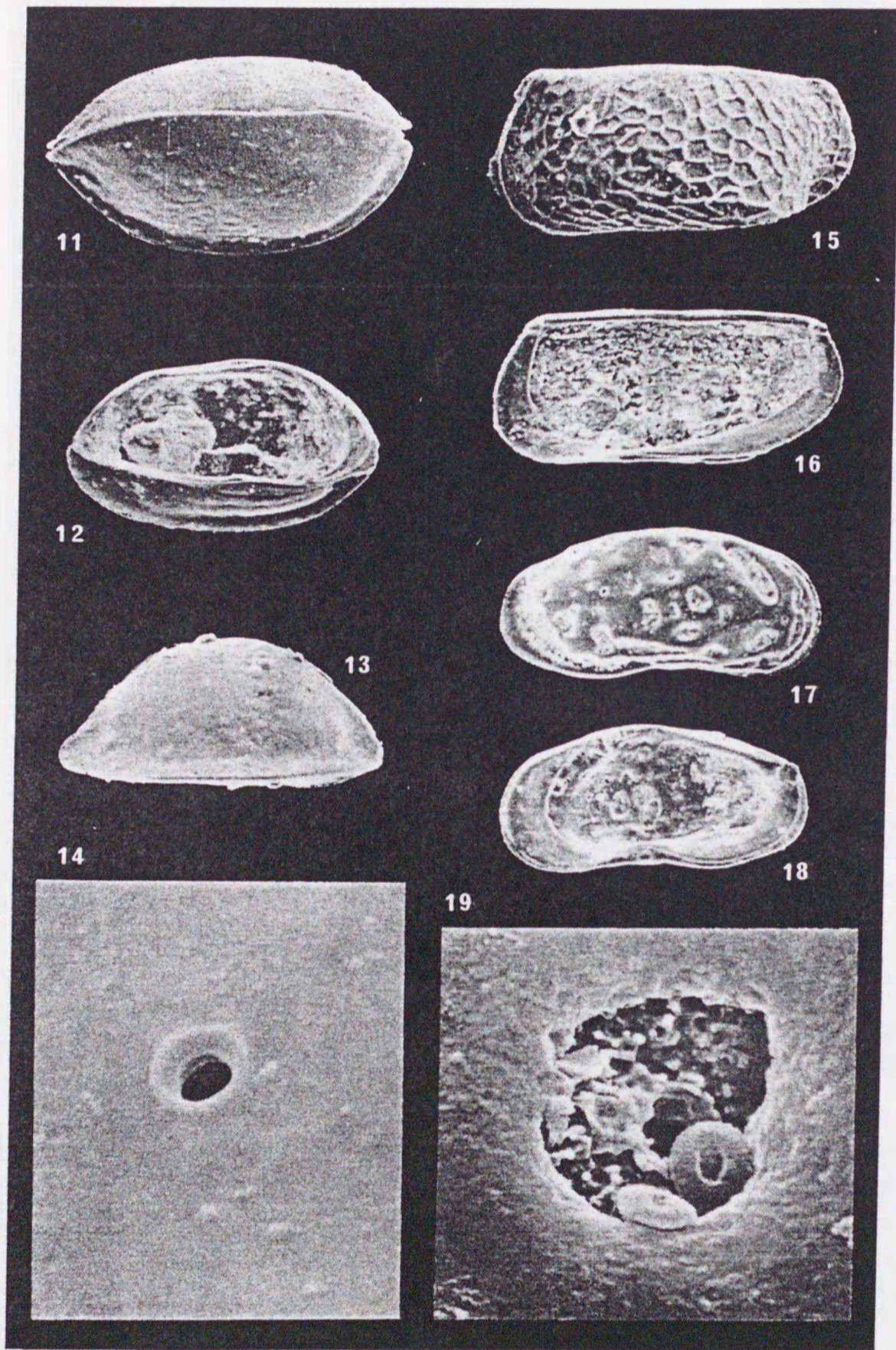
Plate 8. (all magnifications approximate). (11–14,19) *Microxestoleberis triangulata* n.sp.: 11, dorsal view of entire carapace (×80); 12, internal view of right valve (×80); 13, external view of left valve (×80); 14, normal pore exit (×1200); 19, internal carapace, showing structural fabric surrounding normal pore (×1200). (15,16) *Microceratina quadrata* n.sp.: 15, external view of left valve (×80); 16, internal view of right valve (×80). (17,18) *Tanella dedeckkeri* n.sp.: 17, external view of right valve (×100); 18, internal view of right valve (×100).

from Swanson, 1980
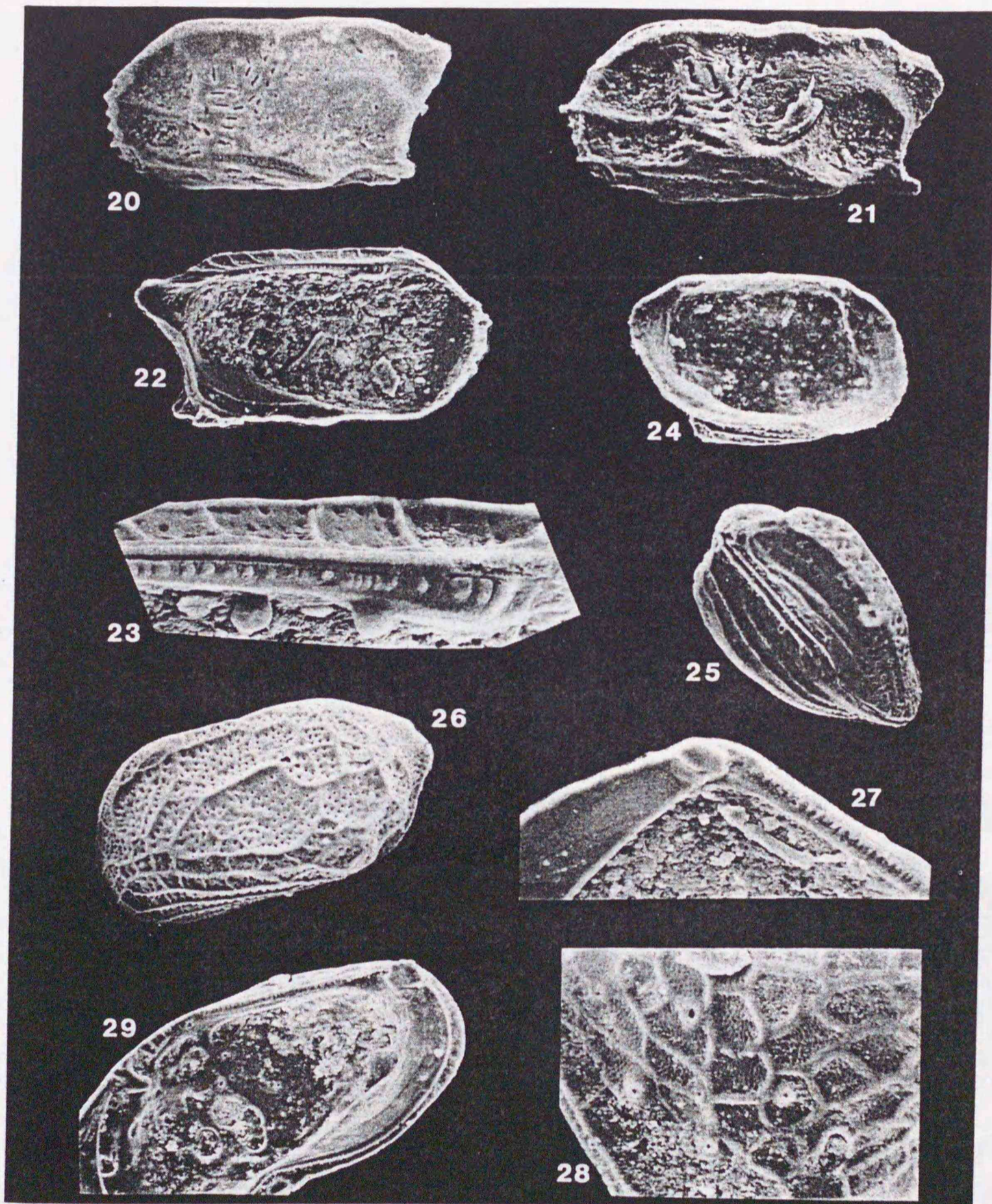
Plate 9. (all magnifications approximate). (20–23) *Kangarina unispinosa* n.sp.: 20, external view of left valve (×150); 21, same, showing surface relief and ornamentation (×150); 22, internal view of left valve (×150); 23, anterior hinge element, left valve (×600). (24–26) *'Loxoconcha' tubmani* n.sp.: 24, internal view of left valve (×150); 25, ventral view of entire carapace (×150); 26, external view of left valve (×175). (27,28) *Microceratina quadrata* n.sp.: 27, detailed view of anterior hinge elements, right valve (×500); 28, detailed view of anterior, showing normal pore exits and ornamentation (×300). 29, *Tanella dedeckkeri* n.sp.; internal view of right valve, showing hingement and 'snap tooth' (×200).

from Swanson, 1980

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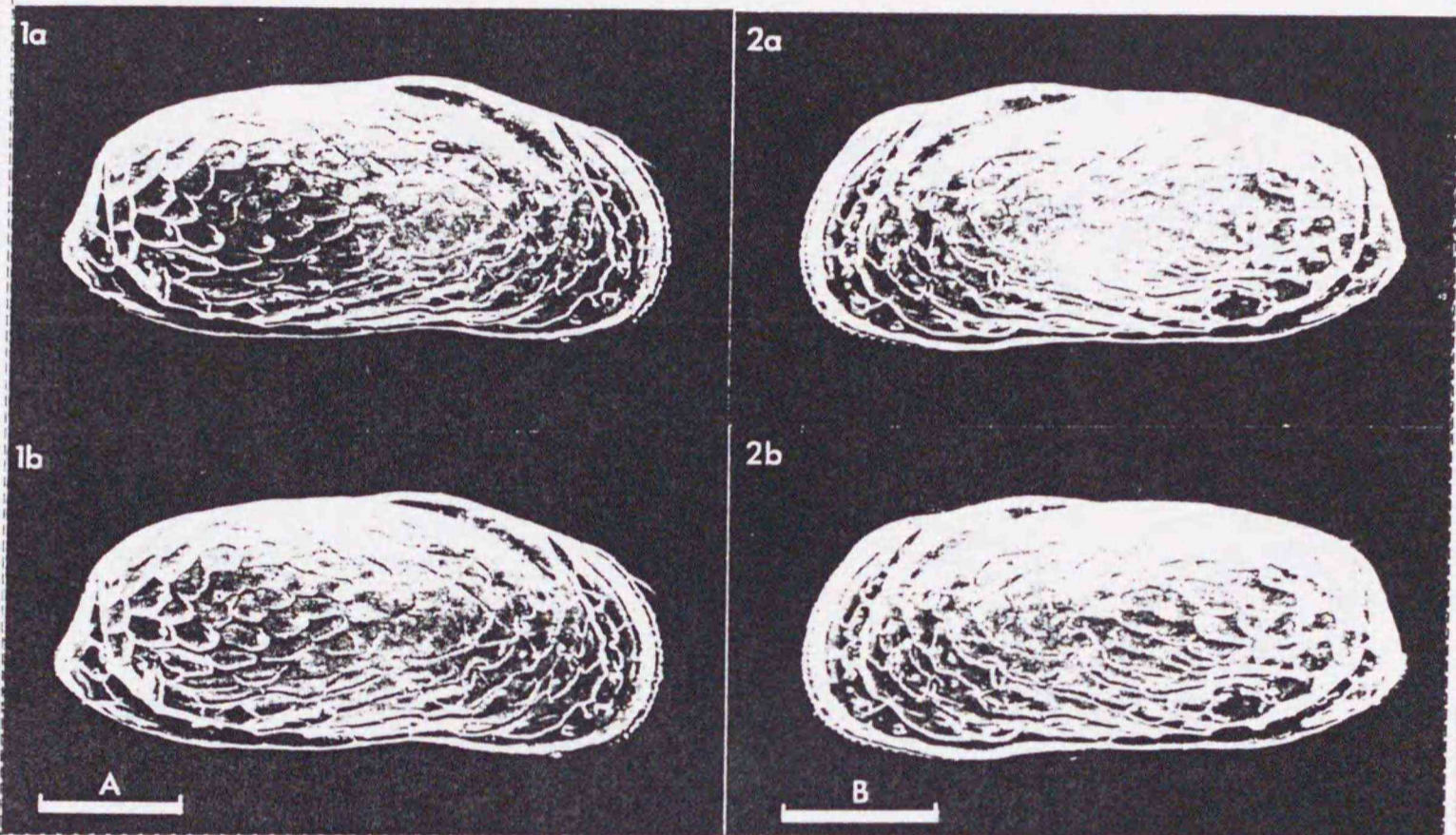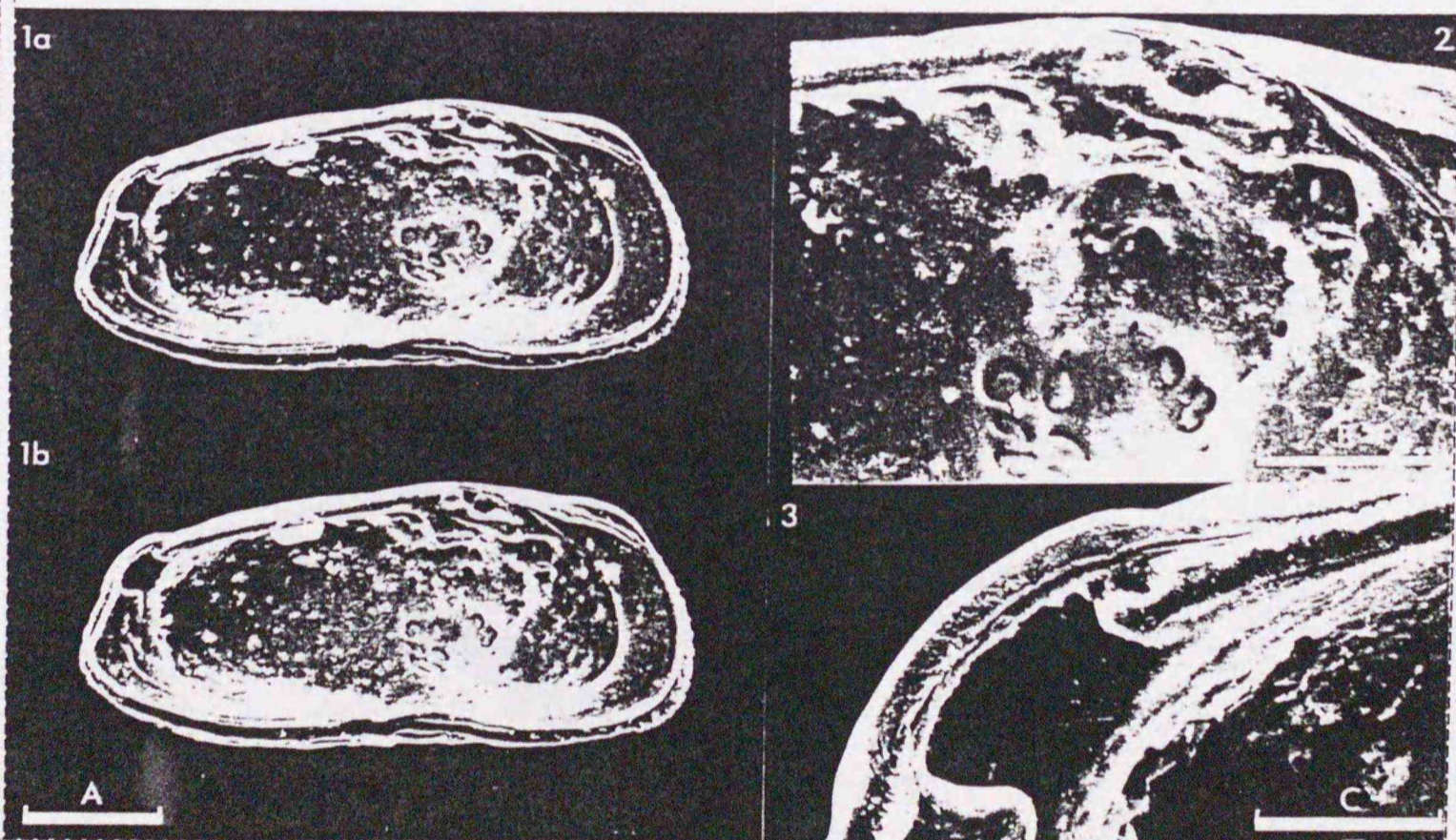
Plate 10.   (top) Stereopairs of right (Figs. 1a, 1b) and left valves of female
Waiparacythereis joanae. Scale = 200μm.
(bottom) Stereopair of internal left valve (Figs. 1a, 1b), anterior hinge
element (2) and posterior hinge element (3). Scale bar A = 200μm;
B = 100μm; c = 50μm

1a

100μm

1b

1c
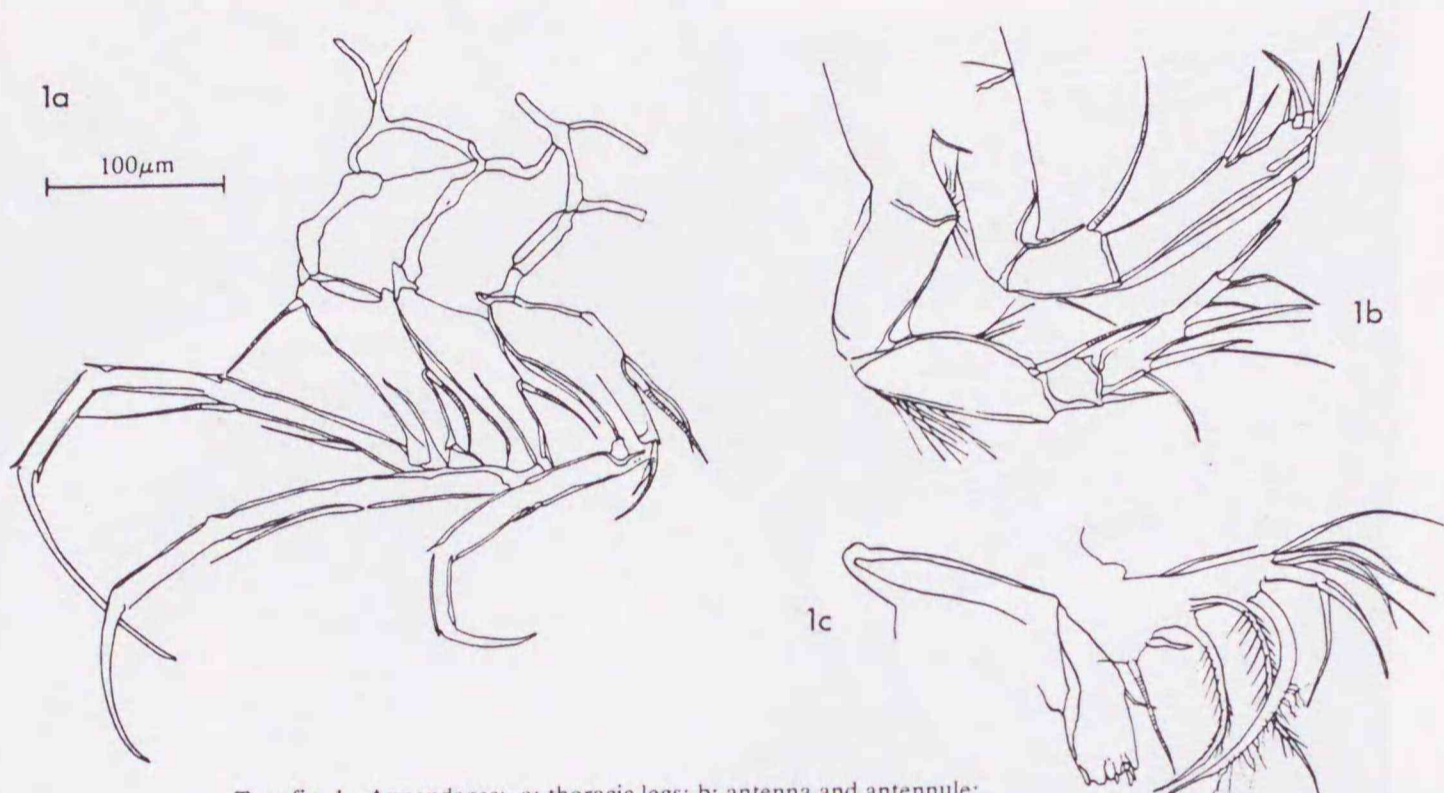
Text-fig. 1. Appendages: a: thoracic legs; b: antenna and antennule; c: mandible.

2a

2b

75μm

75μm

2c

60μm

2d

60μm
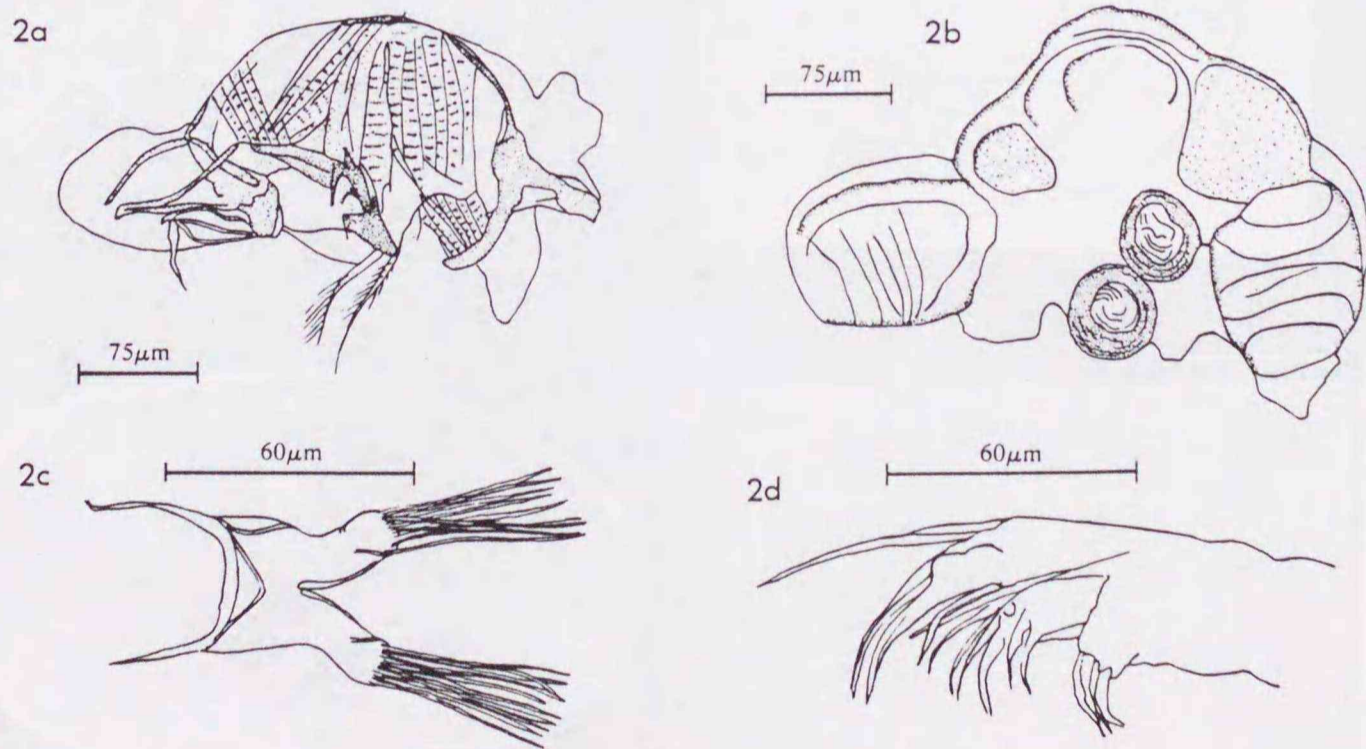
Text-fig. 2. Appendages: a: copulatory apparatus; b: posterior of body; c: brush organ; d: maxilla
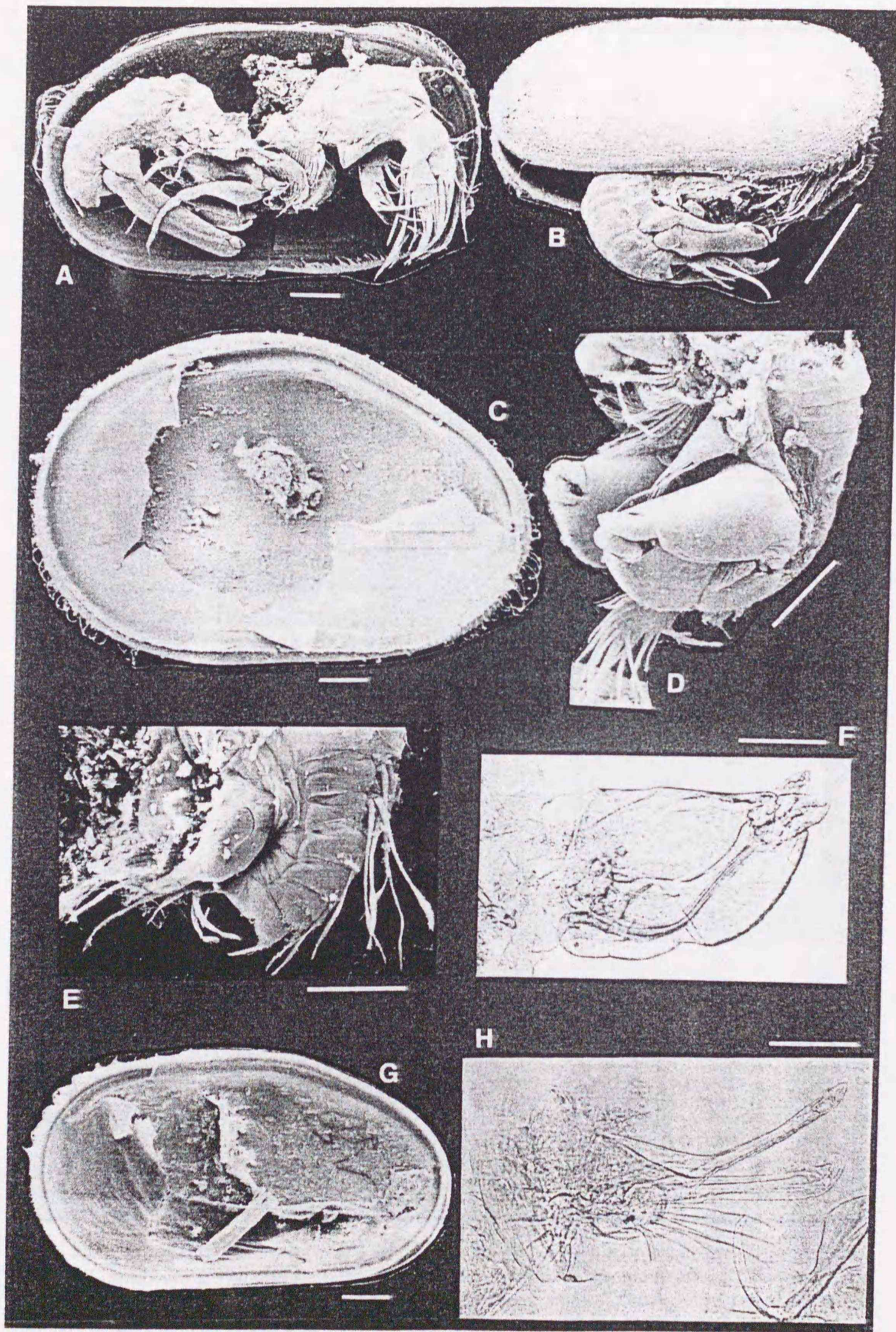
Figure 2. A, *Cytherella* n. sp. *B*, Kaikoura Benthic 82 Station U259 (100 m), male LV, internal view. B, *Cytherella* sp., WESP Station Q693 (297 m), male carapace, oblique ventral view. C-F: *Cytherella* n. sp. *A*, male RV, WESP Station Q693 (297 m). C, internal view. D, anterior oblique view of paired hemipenes. E, lateral view of female left genital lobe. F, transmitted light (DIC) image of left hemipenis. G,H: *Cytherella* n. sp. *D*, male RV, WESP Station P664 (187 m). G, internal view. H, transmitted light (DIC) image of paired hemipenes. All scale bars = 100µm.
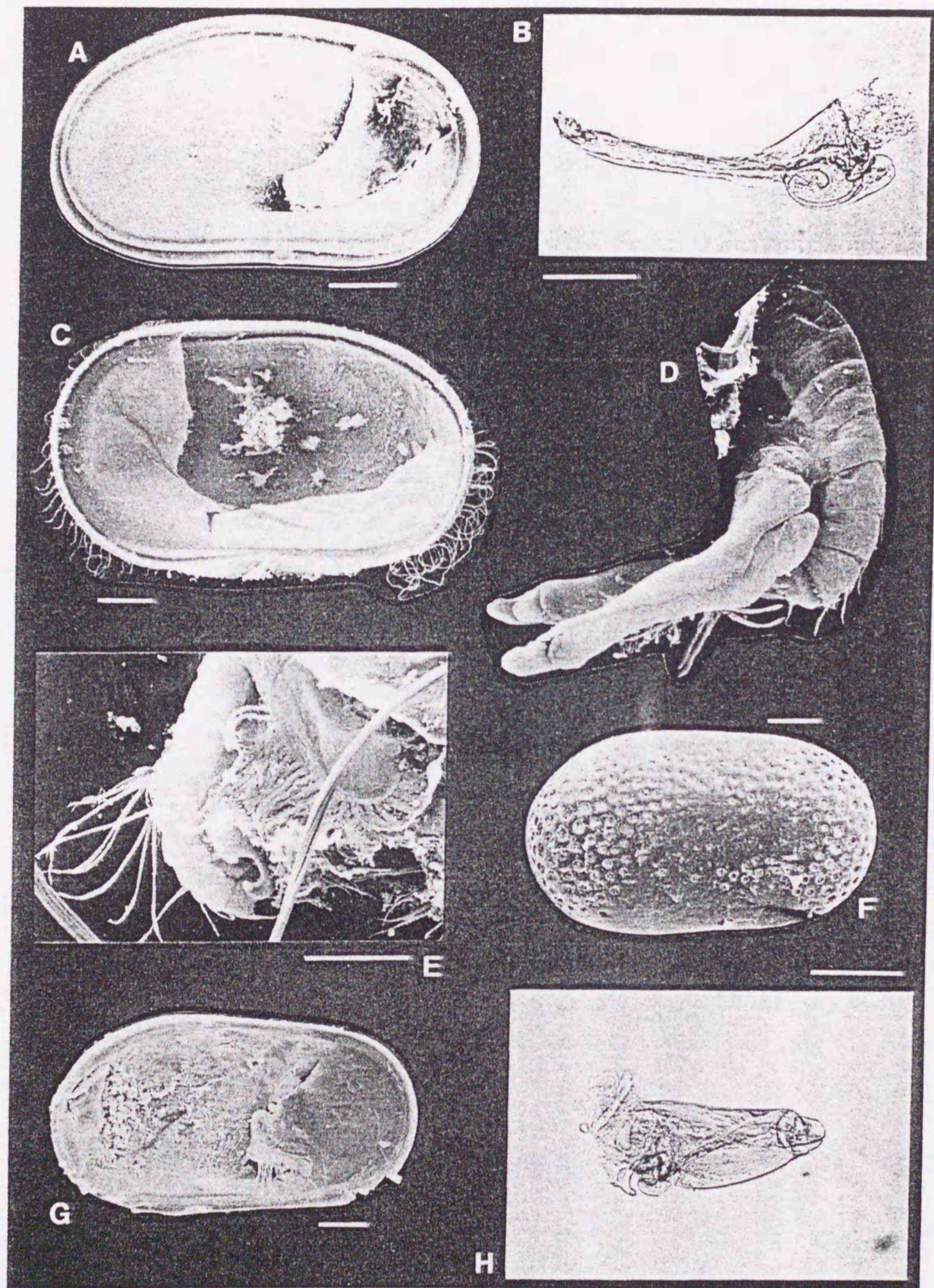
Figure 3. A,B: *Cytherella* n. sp. *C*, male LV, WESP Station Q761 (51 m). A, internal view. B, transmitted light (DIC) image of right hemipenis. C-E: *Cytherella* sp., male RV, Kaikoura Benthic 82 Station U264 (680 m). C, internal view. D, abdomen and paired hemipenes. E, as for C, female abdomen and genital lobe (arrowed). F-H: *Cytherella* n. sp. *E*, male RV, WESP Station P657 (41 m). F, external view. G, internal view. H, transmitted light (DIC) image of right hemipenis. All scale bars = 100μm.

Plate 14.

Fig. a: *Cytherella hemipuncta* Swanson. Living specimen: debris infilled fossae, antero-ventral area of left valve. Station Q693, eastern Tasman Sea, 297 metres. Scale bar = 20 μm. GR1/03. Fig. b: *Cytherella* n.sp. a. Living specimen; external posterior surface displaying setae, biogenic debris and epibiontic 'protozoans'. Station P664, eastern Tasman Sea, 187 metres. Scale bar = 40 μm. GR1/04. Fig. c: *Cytherella hemipuncta* Swanson. Living specimen: view of postero-ventral angle showing debris and contact margin entangled in exceedingly long, normal pore setae. Station Q693, eastern Tasman Sea, 297 metres. Scale bar = 40 μm. GR1/03. Fig. d: *Cytherella* n.sp. b. External surface, central area of left valve showing intense, chitinoclastic fungal 'microboring'. Station Gr5/4, eastern Tasman Sea, 686 metres. Piston-core subsample, depth 8-10cm. Scale bar = 20 μm. GR1/02. Fig. e: *Cytherella* n.sp. b. External surface, central area of right valve showing effects of intense chitinoclastic fungal or bacterial 'grazing'. Note that most of the primary protoostracum has disappeared. Station Gr 5/4, eastern Tasman Sea, 686 metres. Piston-core subsample, depth 8-10cm. Scale bar = 20 μm. GR1/06. Fig. f: *Cytherella* n.sp. c Living specimen: external surface, central area of left valve showing severe delamination and corrosion. Station P671, eastern Tasman Sea, 123 metres. Scale bar = 20 μm. GR1/07. Fig. g: *Cytherella* n.sp. b. Living specimen: delaminated carapace fragment. Note increasing porosity with depth, primary shell layer situated at top left-hand third of micrograph. Station P665, eastern Tasman Sea, 768 metres. Scale bar = 20 μm. GR1/08. Fig. h: *Cytherella* n.sp. b. Living specimen: oblique view of fracture through contact margin, external carapace at bottom, right-hand corner of micrograph. Note open texture and cavities delineating internal carapace layers. Station Q698, eastern Tasman Sea. 1120 metres. Scale bar = 20 μm. GR1/09.

from Swanson, in press
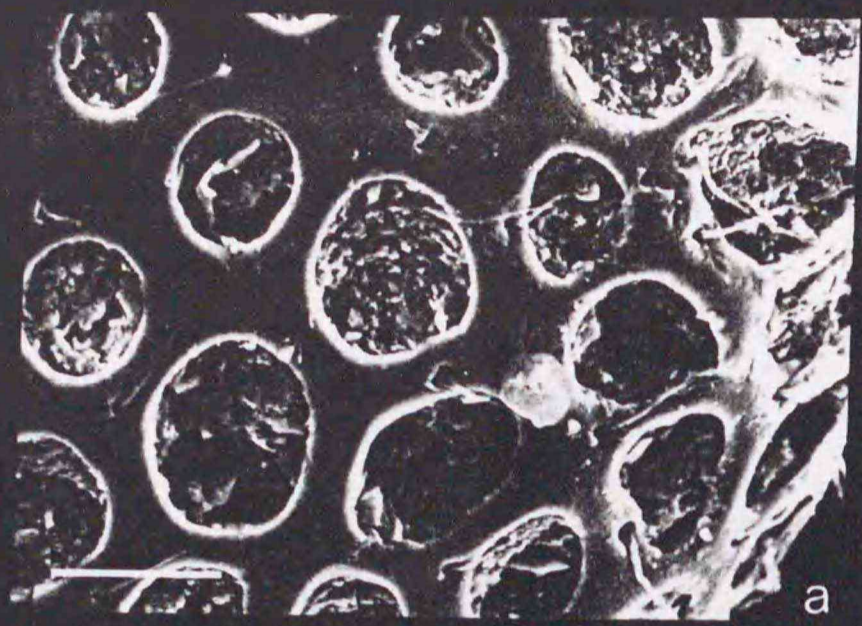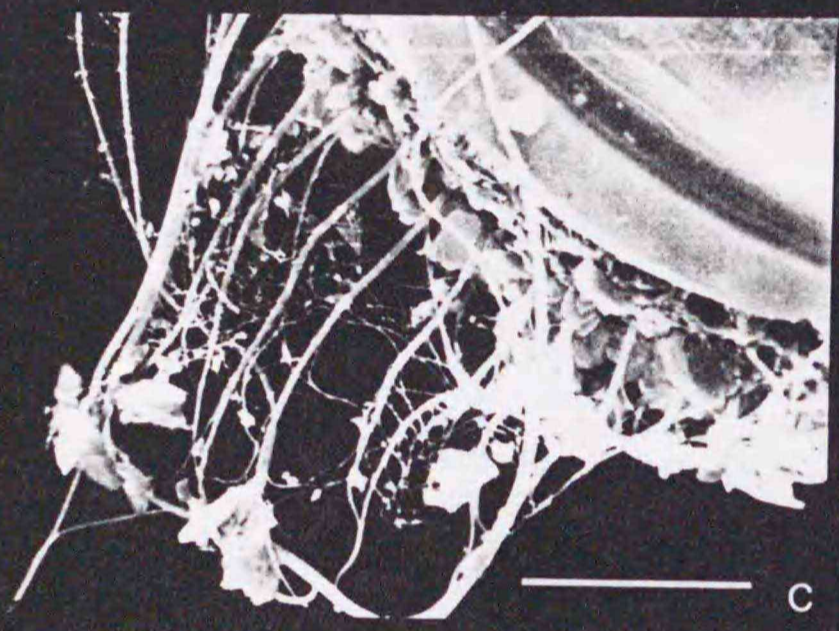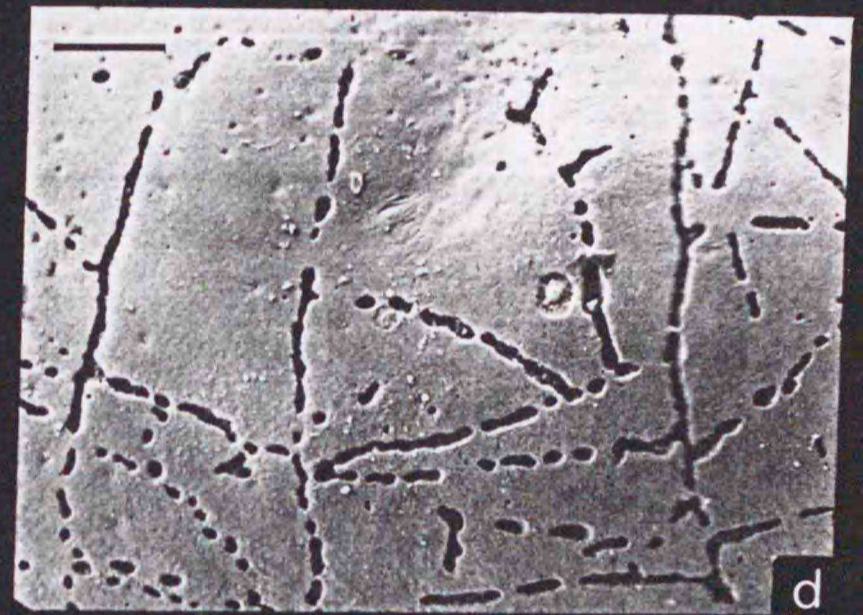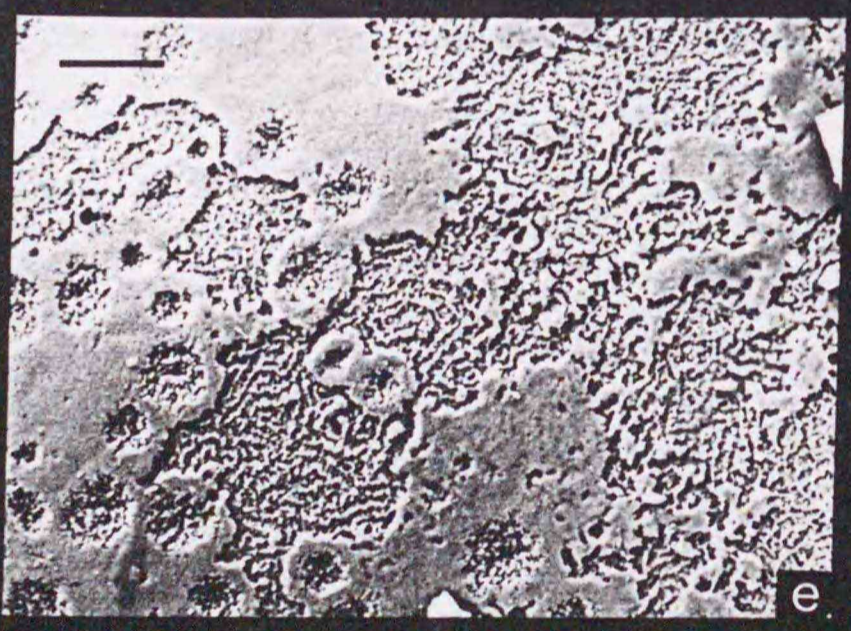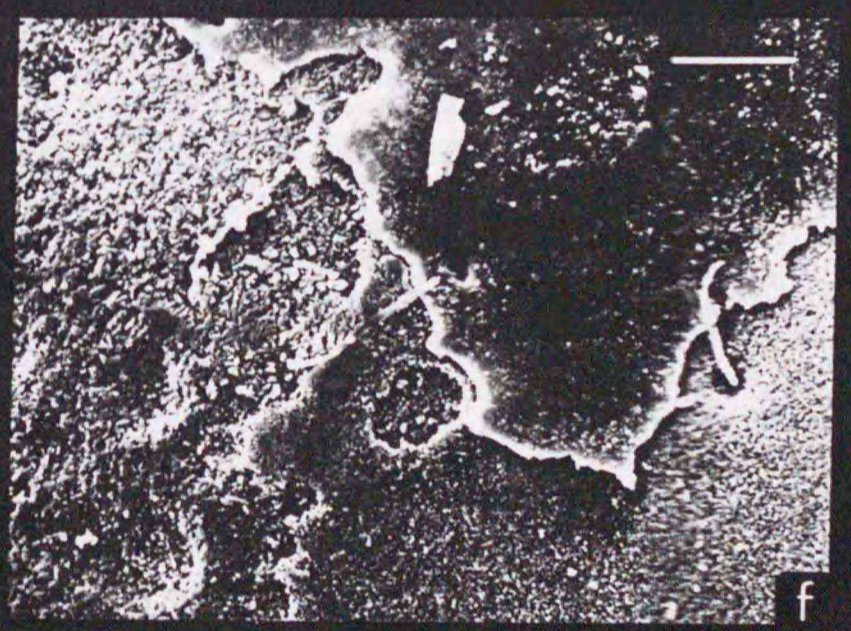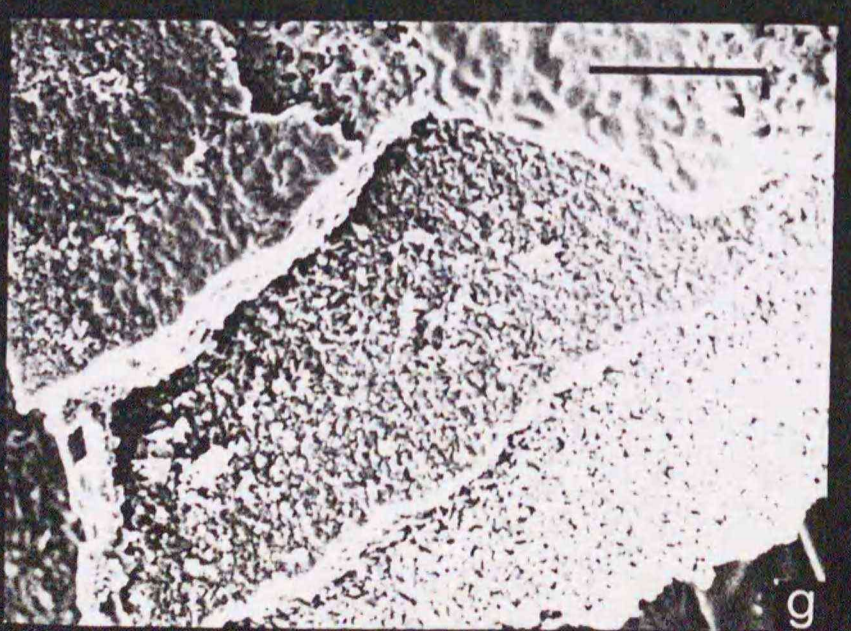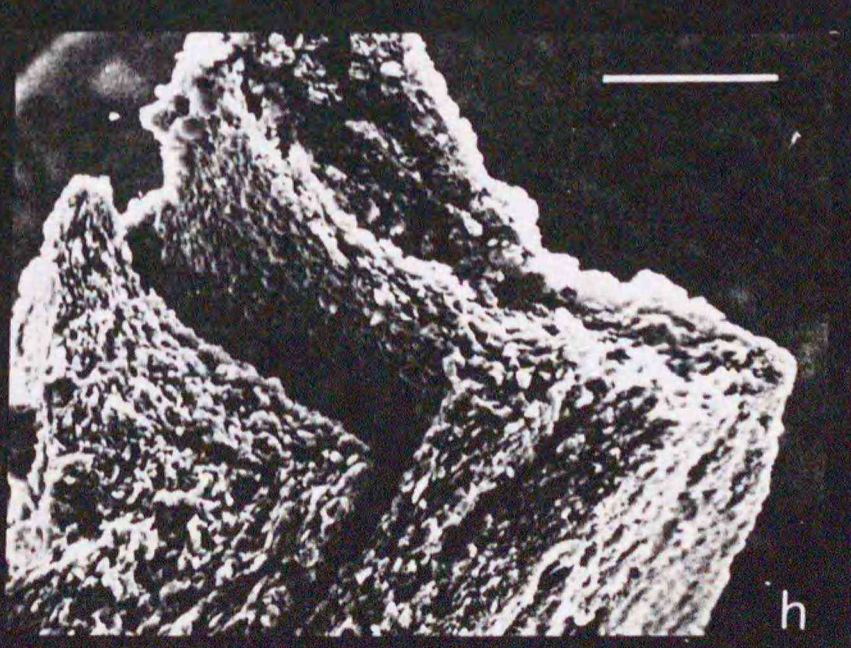
Plate 15.

Fig. a: **Krithe** sp. a. Internal view of central carapace area showing plate-like calcite crystal laths. Station Gr5/4, eastern Tasman Sea, 686 metres. Piston-core subsample, depth 4-6cm. Scale bar = 20 μm. GR1/012. Fig. b: **Krithe** sp. b. External carapace surface showing partial removal of etched primary protoostracum. Station Q696, eastern Tasman Sea, 960 metres. Scale bar = 20 μm. GR1/016. Fig. c **Krithe** sp. c. External surface of fragmented carapace. The protoostracum has been completely removed, note contrasting crystalline fabric. Station P665, eastern Tasman Sea, 768 metres. Scale bar = 10 μm. GR1/015. Fig. d **Krithe** sp. b. Internal carapace surface, showing internal layer of plate-like calcite laths, and more finely crystalline, porous intermediate layer which underlies the protoostracum. Station Q696, eastern Tasman Sea. 960 metres. Scale bar = 4 μm. GR1/020. Fig. e. **Krithe** sp. b. Heavily corroded carapace from which the entire protoostracum has dissolved. Note that finer crystals lining the walls of the normal pore canals are clearly more resistant to dissolution. Station Q696, eastern Tasman Sea, 960 metres. Scale bar = 4 μm. GR1/022. Fig. f: **Krithe** sp. a. Inner lamella, antero-ventral area of left valve. Note dissolution effects are not distributed evenly and dense pattern of striation. The latter are interpreted as dissolution features rather than biotic 'grazing' trails. Station Gr5/4, eastern Tasman Sea, 686 metres. Piston-core subsample, depth 22-24cm. GR 1/023. Scale bar = 40 μm. GR1/023. Fig. g: **Krithe** sp. a. Specimen as for Fig. f. Postero-dorsal region of interior of carapace. Plate-like crystal layer showing effects of severe dissolution; compare with Fig. a. Station Gr5/4, eastern Tasman Sea, 686 metres. Piston-core subsample, depth 22-24cm. Scale bar = 40 μm. GR1/023. Fig. h: **Krithe** sp. a. Heavily corroded external carapace surface on which only a small remnant of the protoostracum remains. Station Gr5/4, eastern Tasman Sea, 686 metres. Piston-core subsample 28-30cm. Scale bar = 10 μm. GR1/027.

from Swanson, in press
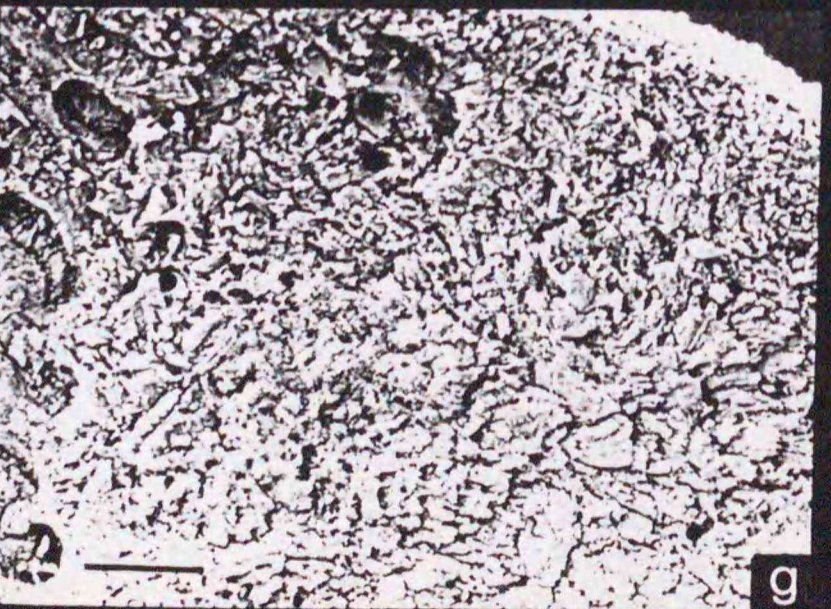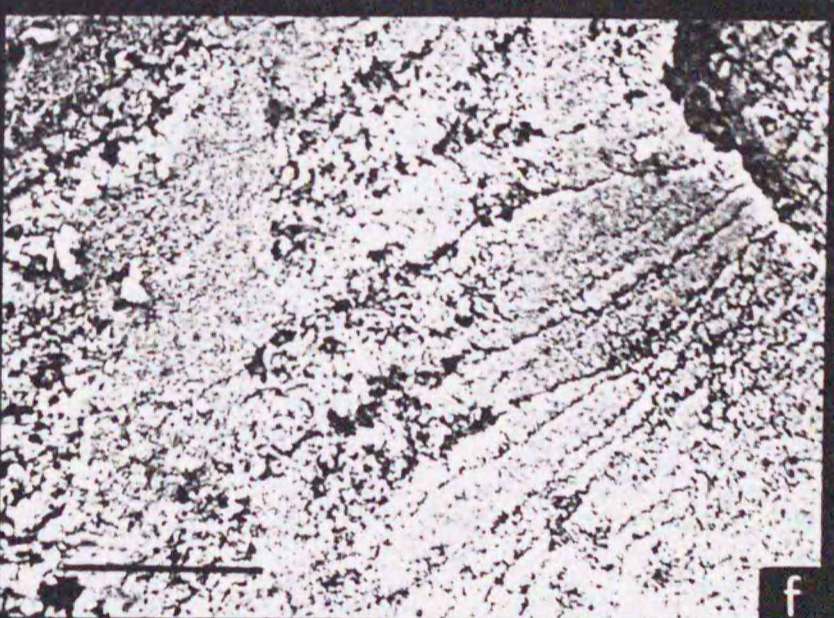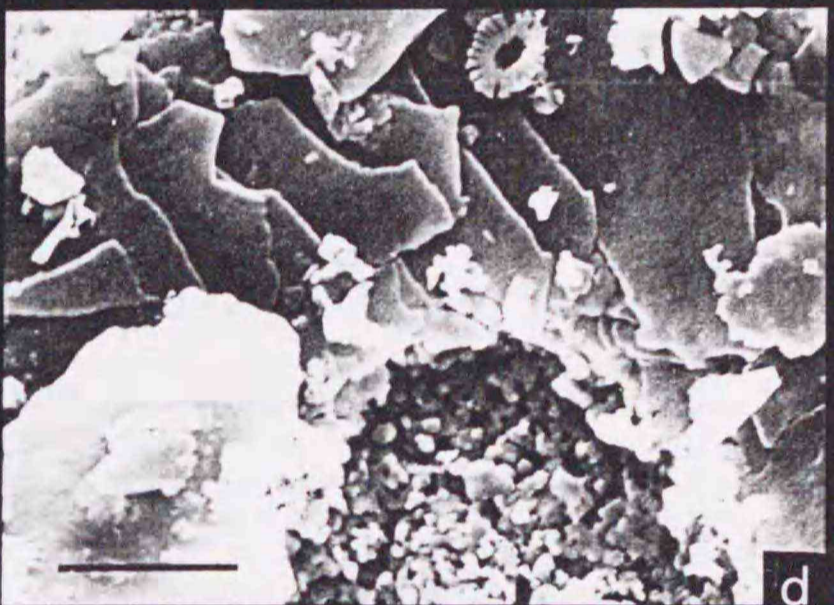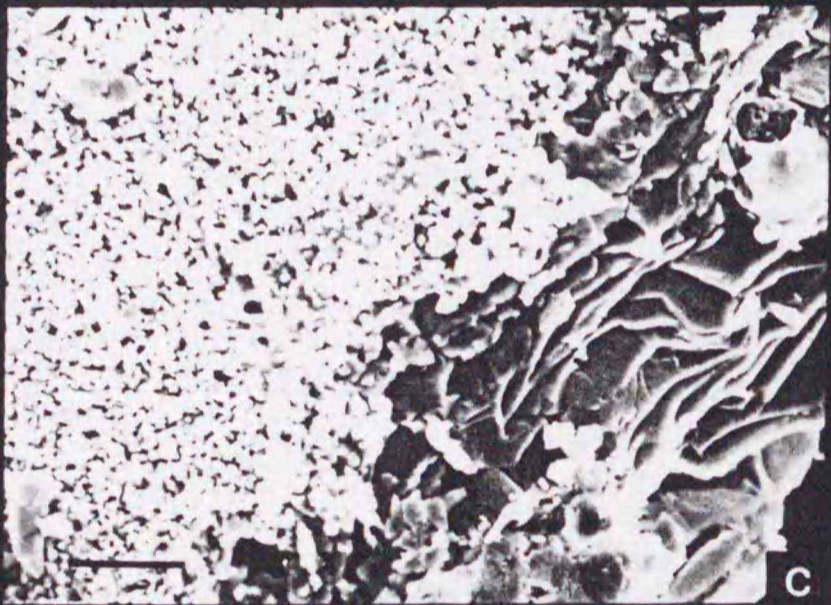
Plate 16.

Fig. a: *Bradleya* n.sp. Living specimen. Elements of the reticulum on the external carapace. Note biogenic debris lodged on the mural walls and solum, and evidence of dissolution on upper surfaces of muri. Station P666, eastern Tasman Sea, 925 metres. Scale bar = 10 μm. GR1/033. Fig. b: *Bradleya* sp. External carapace in which dissolution has removed part of the protoostracum, undercut it elsewhere and removed mural elements. It seems probable such severe degradation may be initiated by dissolution in areas such as those illustrated in Fig. a. Station Q696, eastern Tasman Sea, 960 metres. Scale bar = 10 μm. GR1/034. Fig. c: *Bradleya* sp. Biogenic debris infilling a single fossa. Station Q696, eastern Tasman Sea, 960 metres. Scale bar = 10 μm. GR1/032. Fig. d: *Bradleya* sp. Specimen as for Fig. c. Biogenic debris infilling a single fossa, note evidence of solution/reprecipitation especially in top left-hand corner of micrograph. Station Q696, eastern Tasman Sea, 960 metres. Scale bar = 10 μm. GR1/032. Fig. e: *Bradleya* sp. Section through carapace wall from which the bulk of the internal fabric of the shell has been removed by dissolution. Station Q696, eastern Tasman Sea, 960 metres. Scale bar = 20 μm. GR1/044. Fig f: *Bradleya* sp. Cross-section through a corroded mural wall. Dissolution has resulted in the exposure of crystal surfaces on the protoostracum and more importantly, increased porosity within the coarser 'procuticle'. Station Q696, eastern Tasman Sea, 960 metres. Scale bar = 4 μm. GR1/040. Fig. g: *Bradleya* sp. Living specimen. Cementation of biogenic debris to the solum and mural wall of a single fossae. Station P666, eastern Tasman Sea, 925 metres. Scale bar = 10 μm. GR1/047. Fig. h: *Bradleya* sp. Living specimen. Cementation of biogenic debris to mural surfaces. Note outlines of individual nannofossils in bottom left-hand corner. Station P666, eastern Tasman Sea, 925 metres. Scale bar = 10 μm. GR1/045

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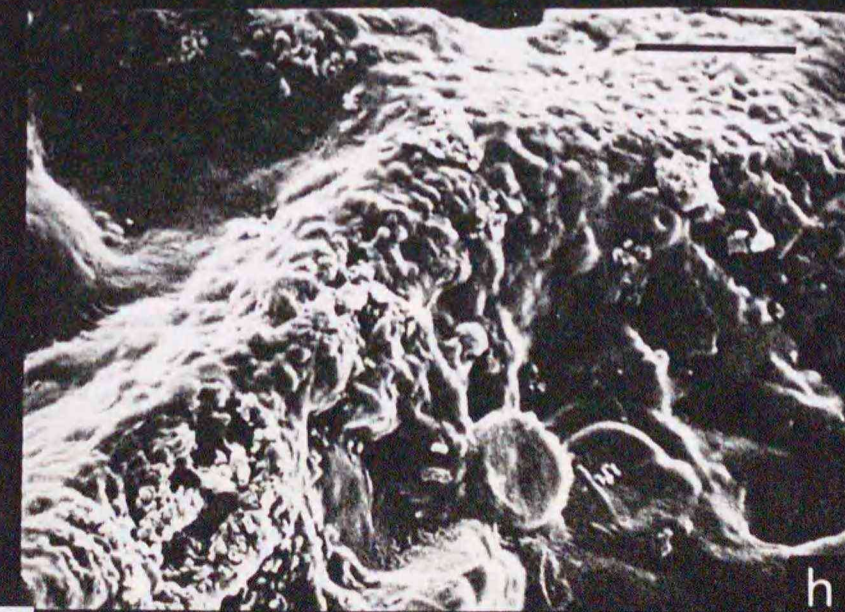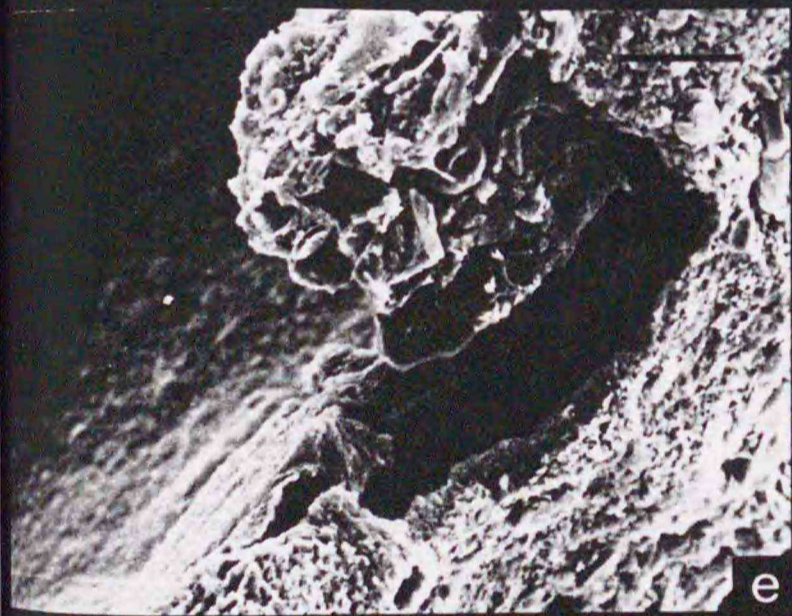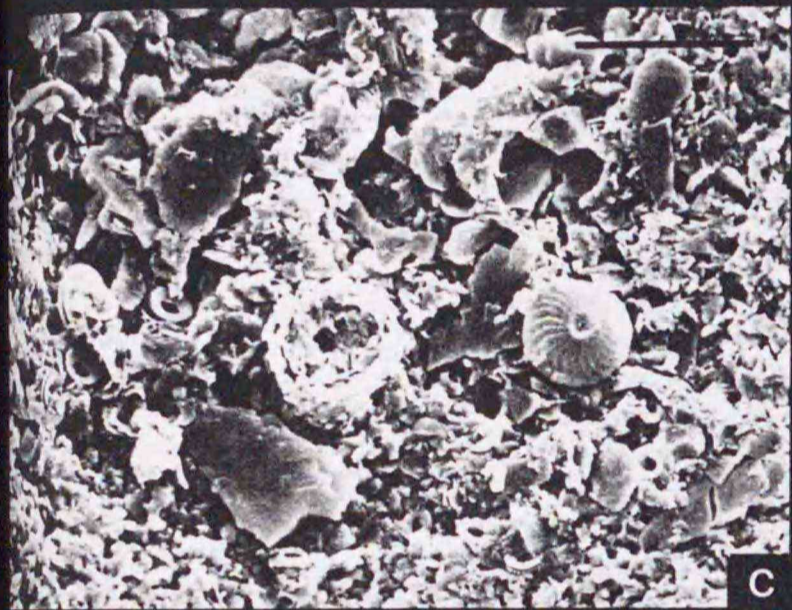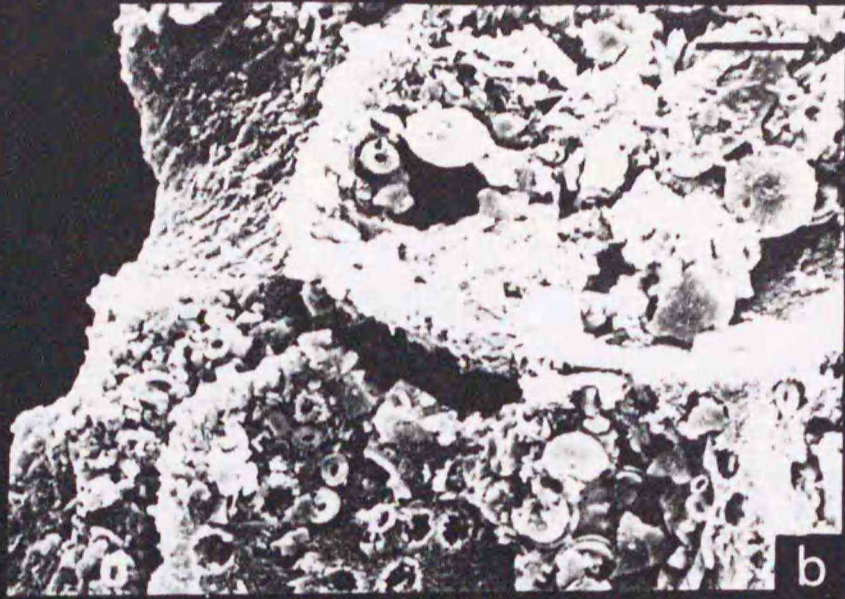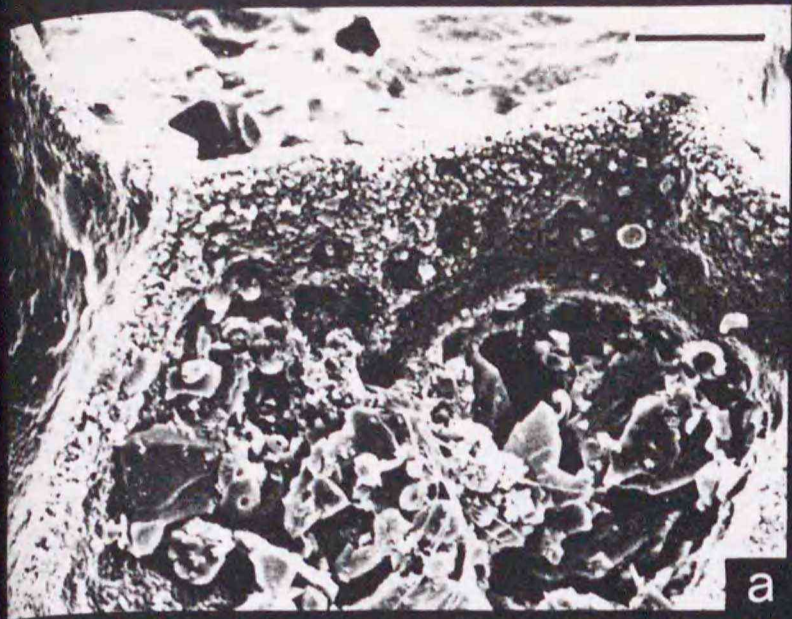
Plate 17.

Fig. a *Legitimocythere* sp. a. Living adult. Particle entrapment around posterior margin, also note dissolution effects on spinal extremities. Station Q719, eastern Tasman Sea, 750 metres. Scale bar = 40 μm. GR1/058. Fig. b: *Legitimocythere* sp. a. Living adult. Fragmented carapace showing particle entrapment by spines. Station Q695, eastern Tasman Sea, 808 metres. Scale bar = 20 μm. GR1/050. Fig. c: *Legitimocythere* sp. a. Living specimen. 'Castellate' spines along ventral margin, note sensory setae. Station Q693b, eastern Tasman Sea, 297 metres. Scale bar = 10 μm. GR1/055. Fig. d: *Legitimocythere* sp. a. Living specimen. External carapace surface showing fibrous mat binding biogenic debris. Station Q696, eastern Tasman Sea. 960 metres. Scale bar = 10 μm. GR1/051. Fig. e: *Legitimocythere* sp. b. Posterior of carapace showing dense network of thallophyte 'grazing trails'. Station Gr5/4, eastern Tasman Sea, 686 metres. Scale bar = 20 μm. GR1/060. GR1/060. Fig. f: *Legitimocythere* sp. a. Living juvenile. Fragmented carapace showing internal fabric. Note coarse crystals and nannofossils. Station Q695, eastern Tasman Sea, 790 metres. Scale bar = 10 μm. GR1/057. Fig. g: *Legitimocythere* sp. a. Living juvenile. Fragmented carapace showing coarsely crystalline internal fabric and entrapped biogenic debris. Station Q695, eastern Tasman Sea, 790 metres. Scale bar = 4 μm. GR1/056. Fig. h: *Legitimocythere* sp. b. Living adult. Cementation of biogenic material by secondary precipitation on and between spinal surfaces. Station P666, eastern Tasman Sea, 925 metres. Scale bar = 20 μm. GR1/062.

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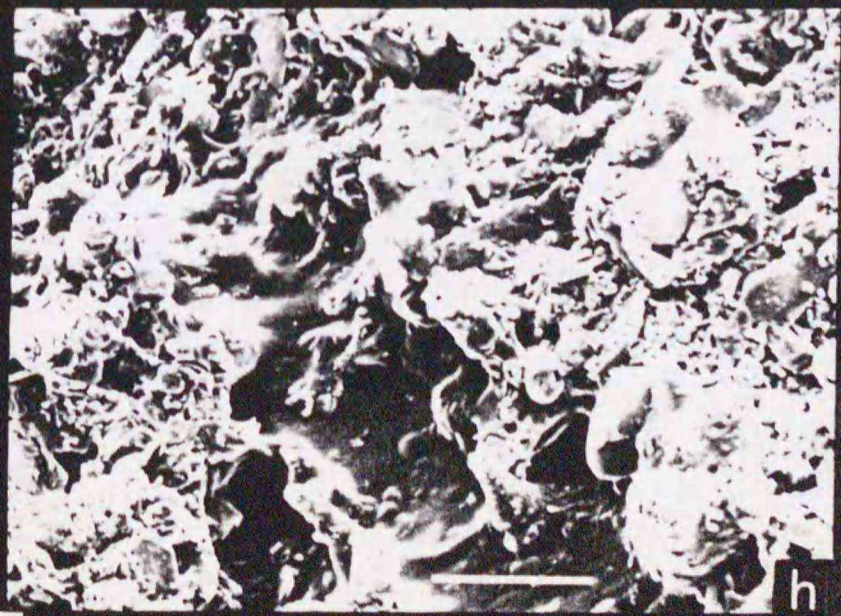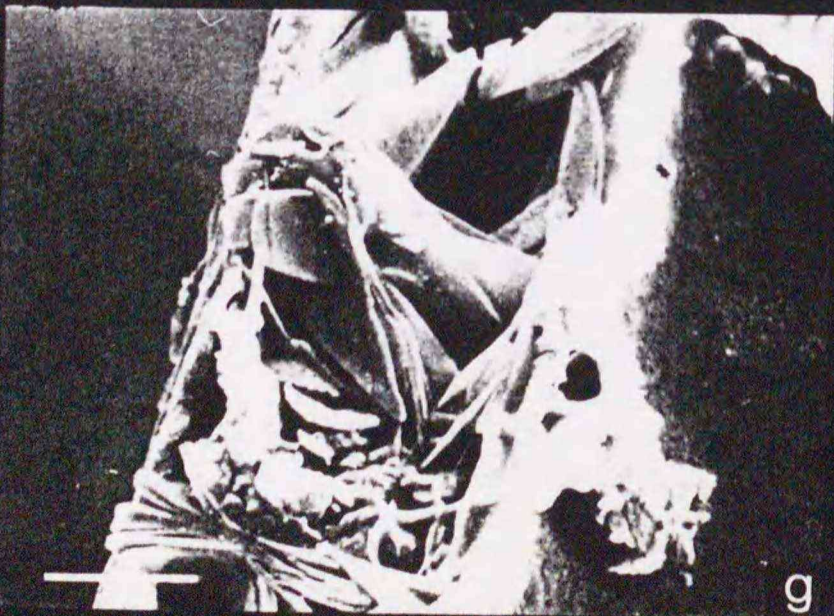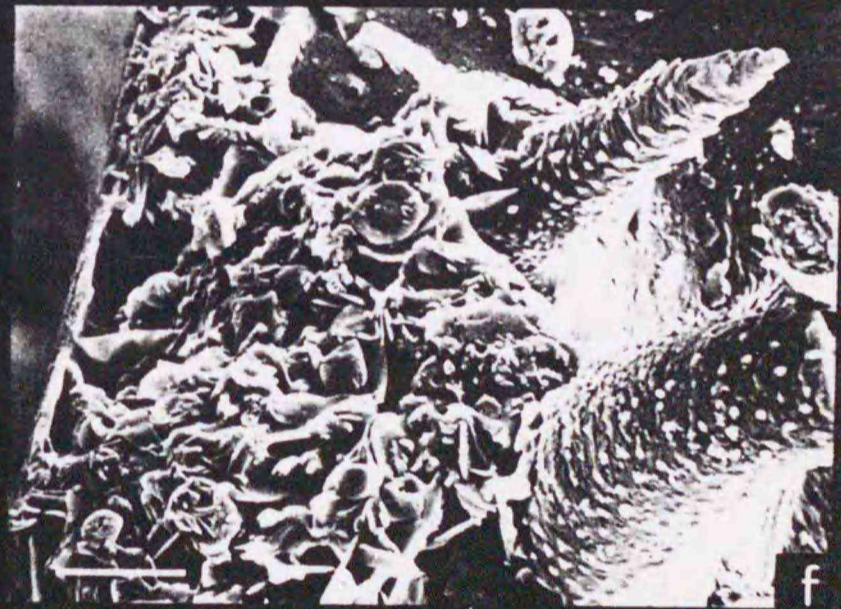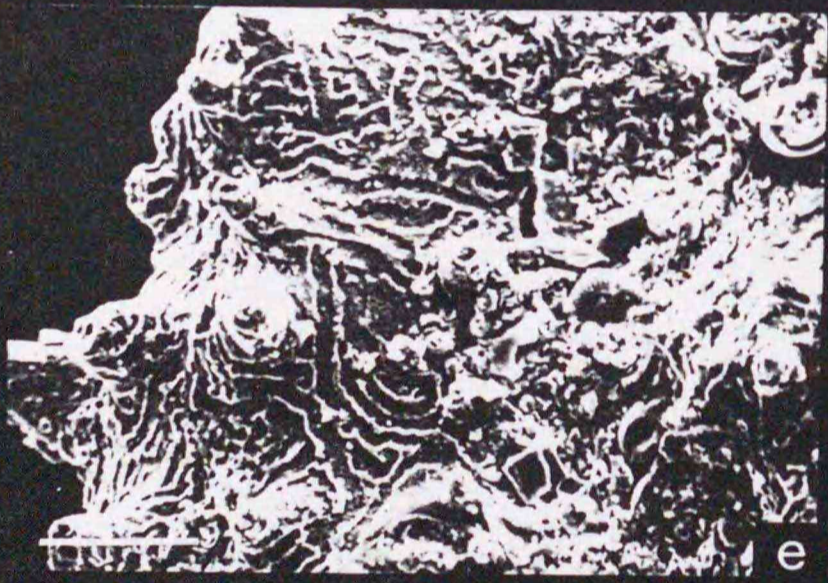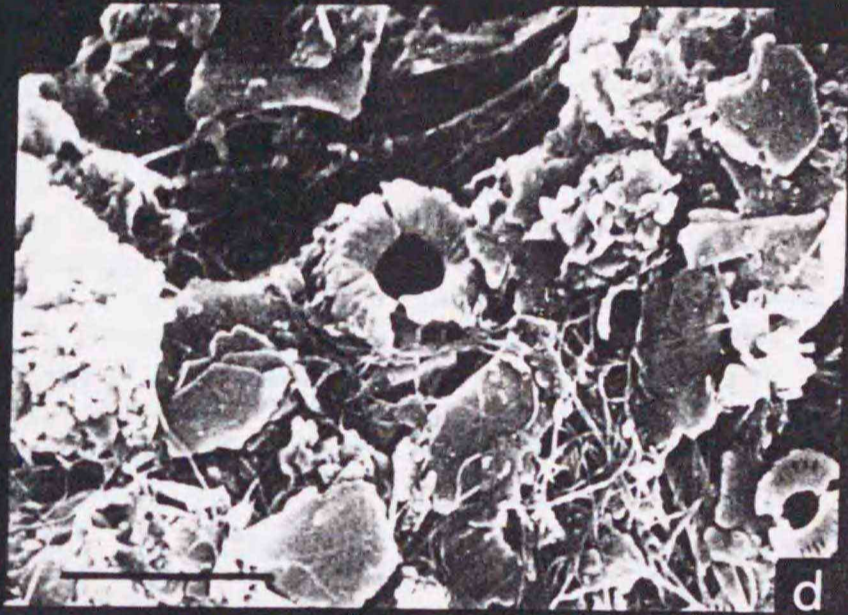
Plate 18.

Scale bar = 200μm unless otherwise stated. A-E incomplete ontogenetic sequence for *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Note progressive reduction in sub-dorsal protuberance towards adulthood. F, **Coronakirkbya fimbriata** juvenile paratype, Lower Permian, West Texas. USNM 118486. Scale bar = 300μm. G, *Puncia* sp.B. Cavalli Islands, New Zealand, 17 metres. Juvenile? Compare and contrast sub-dorsal nodes with Figs. B and H. Scale bar = 100μm. H, **Puncia novaezealandica** Cavalli Islands, New Zealand, 17 metres. Note sub-dorsal spines. Scale bar = 100μm. I, **Promanawa exposita** Upper Cretaceous erratic, Insel Rügen, Jasmund, Germany. Scale bar = 100μm. J. **Puncia levis** Upper Cretaceous erratic, Insel Rügen, Jasmund, Germany. Scale bar = 100μm.

from Swanson, 1990b

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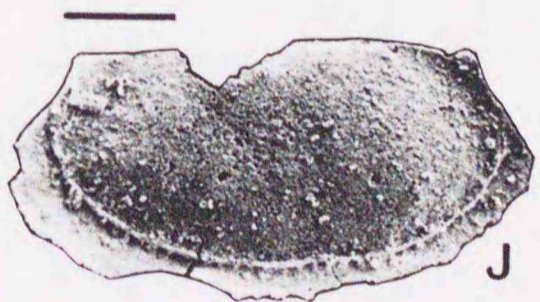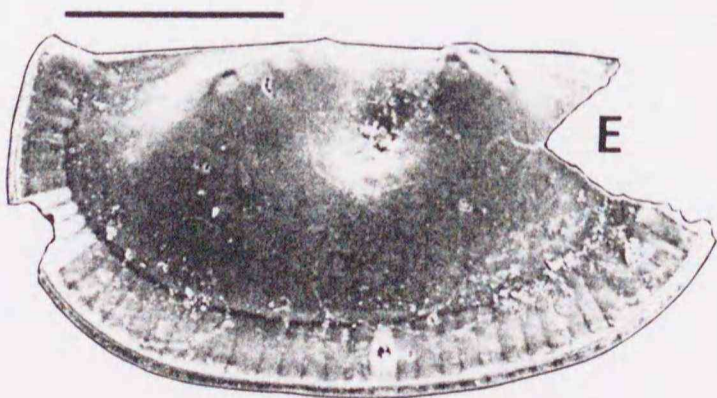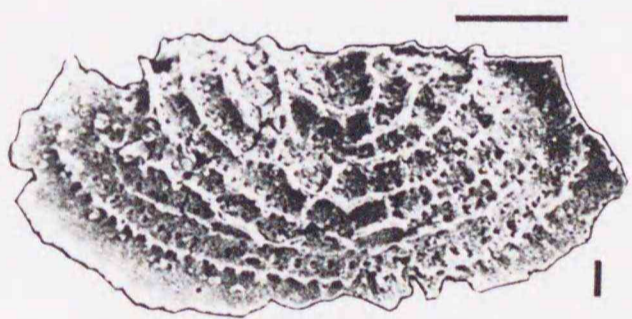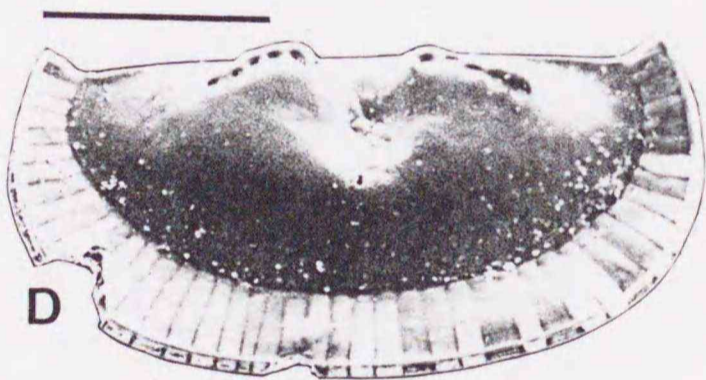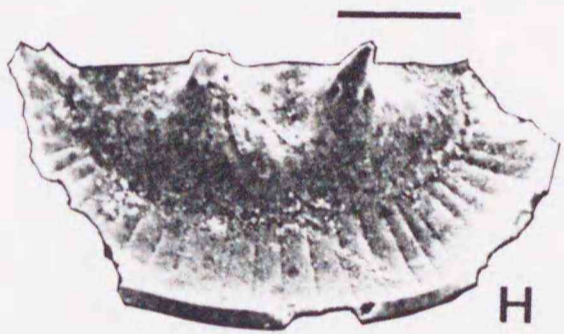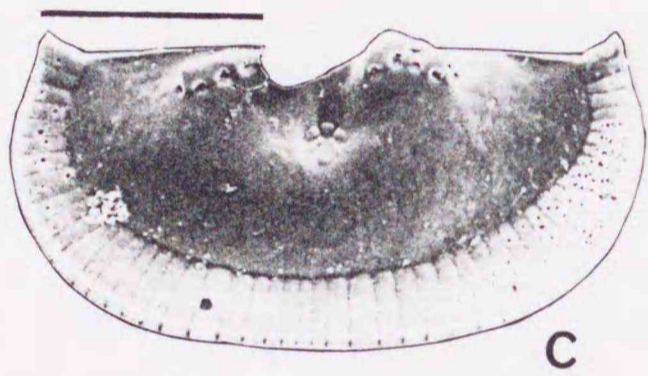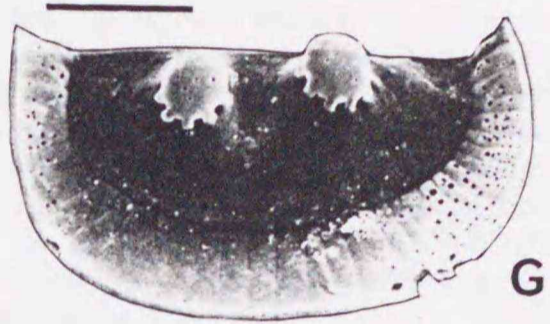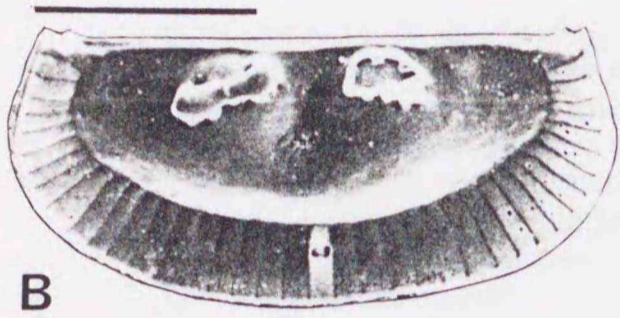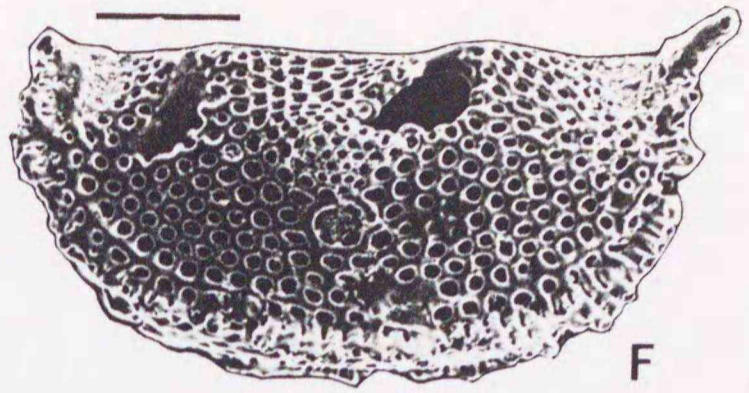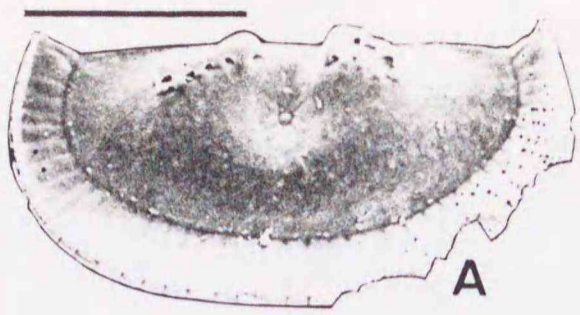
Plate 19.

Scale bar = 100μm unless otherwise stated. A, **Manawa tryphena** Cavalli Islands, New Zealand, 8 metres. B, **Manawa staceyi** Cavalli Islands, New Zealand, 17 metres. Entire carapace in life position. C. **Manawa staceyi** Cavalli Islands, New Zealand, 17 metres. Entire carapace in life position inverted to expose soft anatomy. D, **Manawa staceyi** Cavalli Islands, 17 metres. Nauplius. Note slight bending of carapace. E, **Manawa staceyi** Cavalli Islands, 17 metres. Naupliar carapace. Arrow indicates double-walled nature of sole. F, **Manawa staceyi** Cavalli Islands, 17 metres. Metanaupliar carapace. G, **Melopetasus syltensis** Ordovician, Isle of Sylt, North Sea. Geologisch - Paläontologisches Institut der Universität Hamburg (GPIH 2223). Oblique view of "larval" carapace, H, Vertical view, specimen as for 3G.

from Swanson, 1990b

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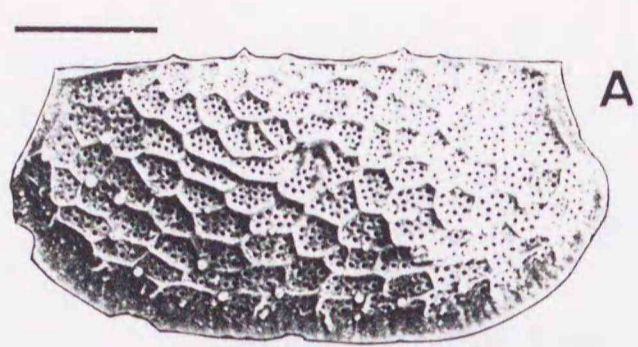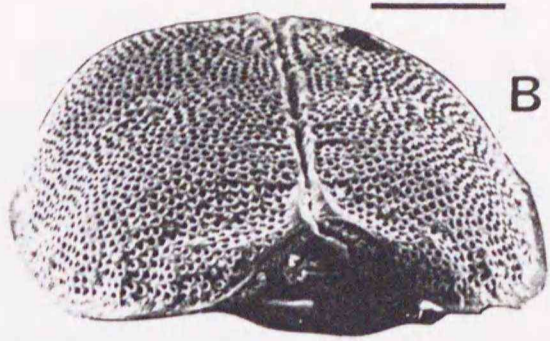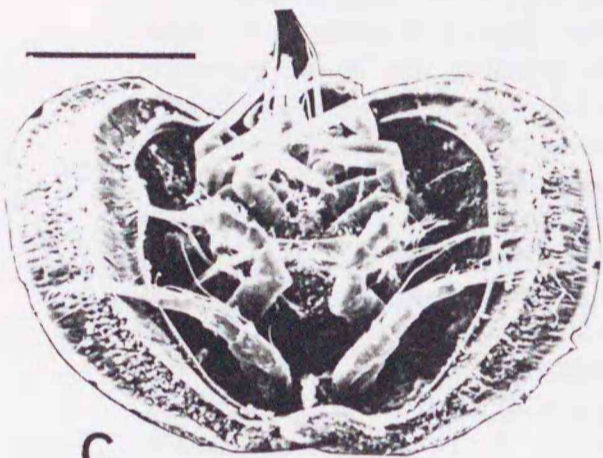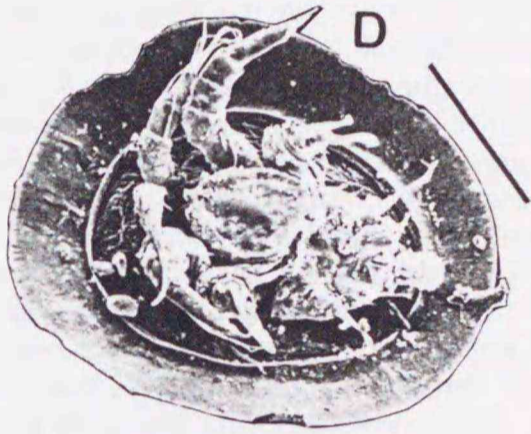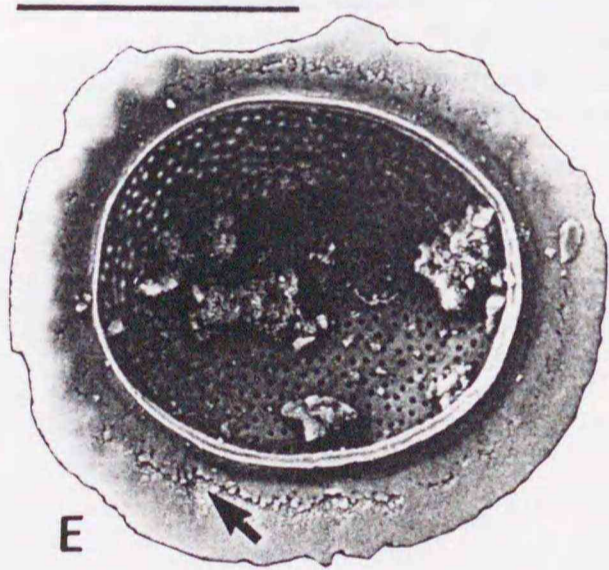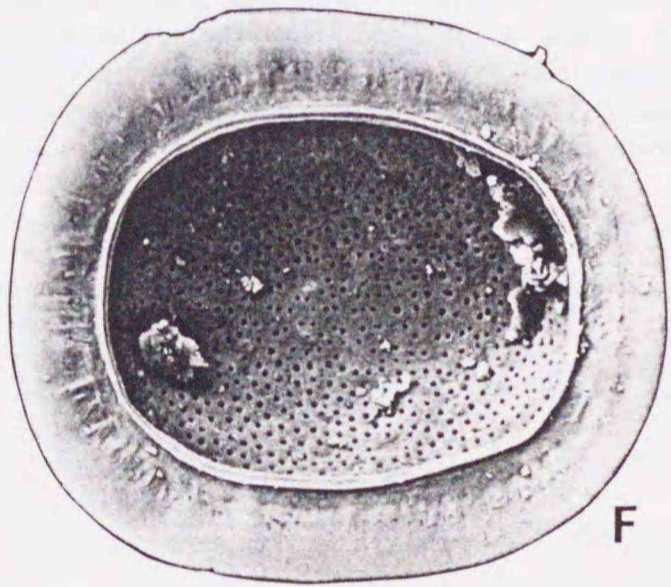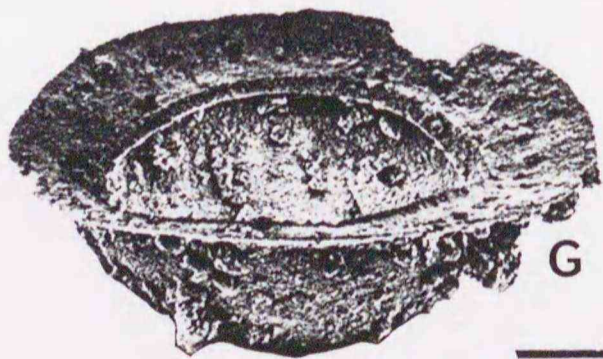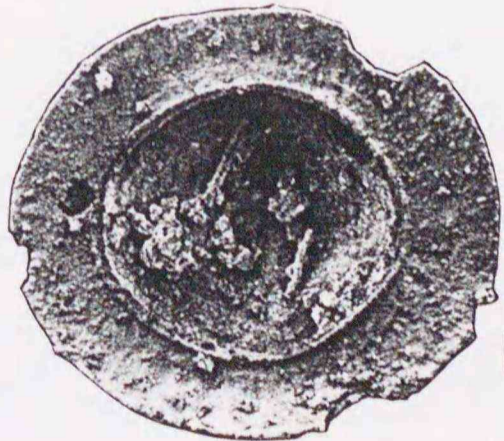
Plate 20.

A, *Puncia* sp. A. Cavalli Islands, New Zealand 17 metres. Internal surface of frill (left = ventral) showing pore exit and seta (arrowed). Scale bar = 20μm. B, *Puncia* sp. A. Cavalli Islands, New Zealand, 17 metres. Longitudinal section of frill showing exposed chamber and septa (upper surface = ventral). Note break is slightly oblique therefore top of next chamber also exposed. Arrow indicates 'calcareous' membrane which closes the domicilum to the frill. Note also imperfect calcification of frill at distal (right hand) extremity. Scale bar = 20μm. C, *Puncia* sp. A. Cavalli Islands, New Zealand, 17 metres. Frill and external ventral periphery of domicilium. Note pore exists and setae (arrowed) below carapace sole. D, *Coronakirkbya fimbriata* Lower permian, West Texas. USNM 118488. Ventral view of entire carapace, contact margin at top of picture. Scale bar = 300μm. E, *Coronakirkbya fimbriata* Lower Permian, West Texas. USNM 118488. Ventral view of entire carapace, contract margin at top of picture. Scale bar = 300μm. F, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Contact zone or sole of left valve showing two rows of pores and associated setae. Scale bar = 20μm. G, *Puncia* sp. A. Cavalli Islands, New Zealand, 17 metres. Subdorsal protuberance. Note carapace perforations continue under portal (arrow) and contrasting texture of external carapace surface and protuberance floor. Scale bar = 20μm. H, *Aurikirkbya wordensis*. Middle Permian, West Texas, USNM 110232a. Partial view of surface reticulation. "Membranous" closure (partial) at base of each reticulation arrowed. Scale bar = 60μm. I. *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Note "equivalent" partial closure of one reticulation (arrowed). Scale bar = 4μm.

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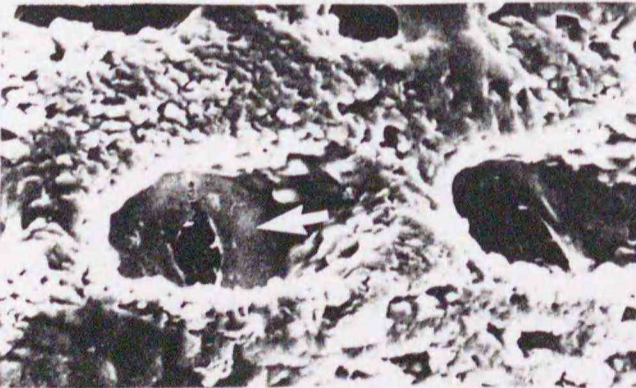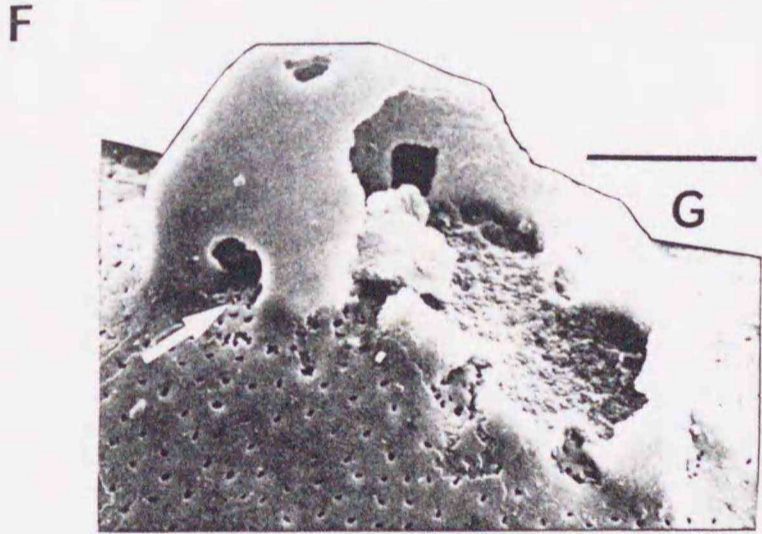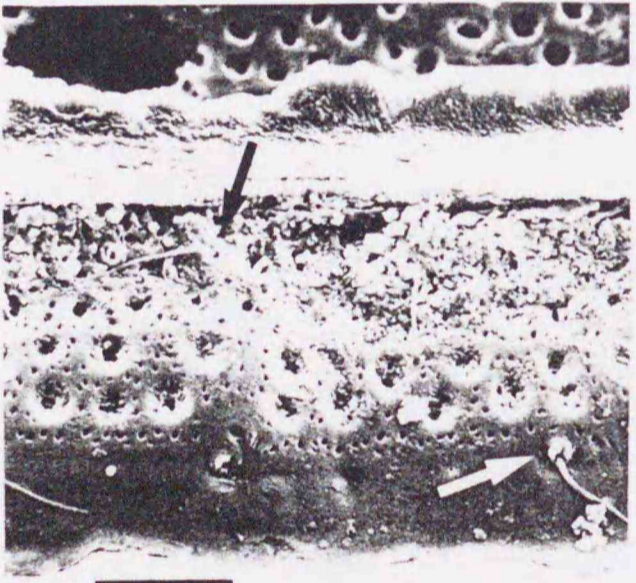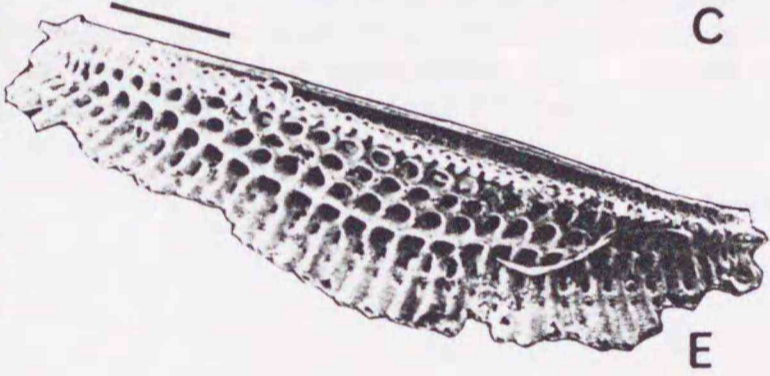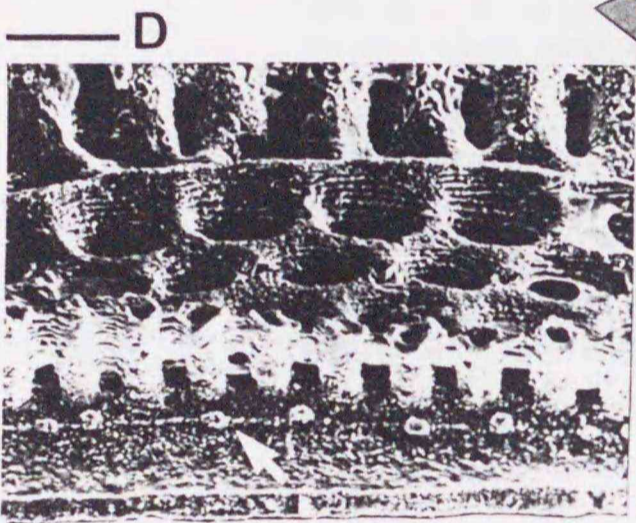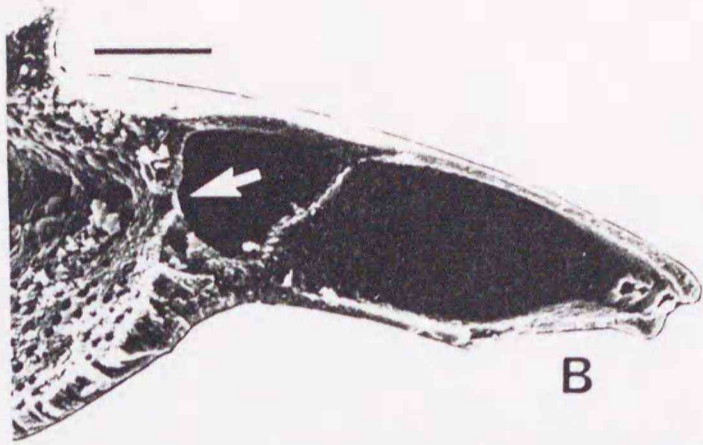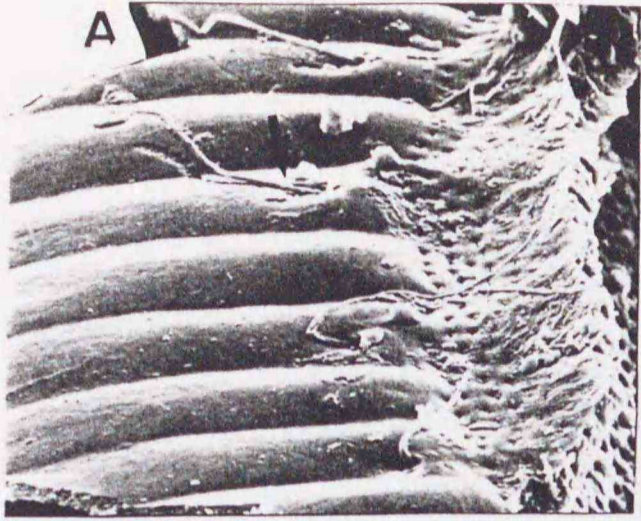
Plate 21.

Scale bar = 100μm unless otherwise stated. A, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Posterior of body (male) including thoracic/abdominal elements and right valve. Scale bar = 40μm. B, *Manawa staceyi* Cavalli Islands, New Zealands, 17 metres. Vental oblique view of abdominal segments and furca. Anal flap arrowed. Scale bar = 20μm. C, *Cytherella* sp. A. West Coast South Island, New Zealand 500 metres. Posterior-most abdominal segments and furca (male). Note anal flap and faecal pellet (arrowed). Scale bar = 40μm. D, *Cytherella* sp. B. Off Kaikoura, South island, New Zealand, 380 metres. Trunk showing segmentation and genital lobe, gravid female. E, *Cytherella* sp. B. Off Kaikoura, South Island, New Zealand, 380 metres. Trunk showing abdominal and thoracic (incomplete) segmentation and hemipenes, male F, *Cytherella* sp. C. West Coast South Island, New Zealand, 910 metres. Ventral oblique view of furca, trunk and hemipene.

from Swanson, 1990b

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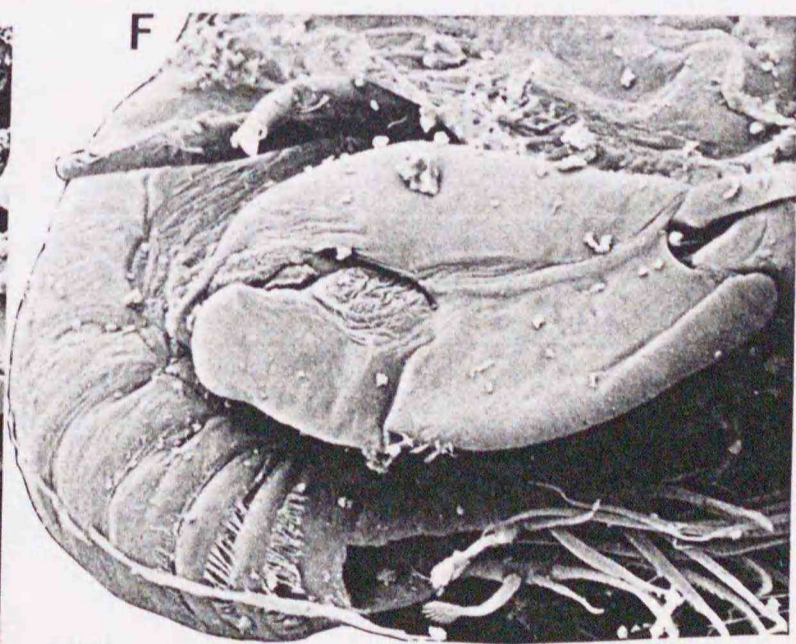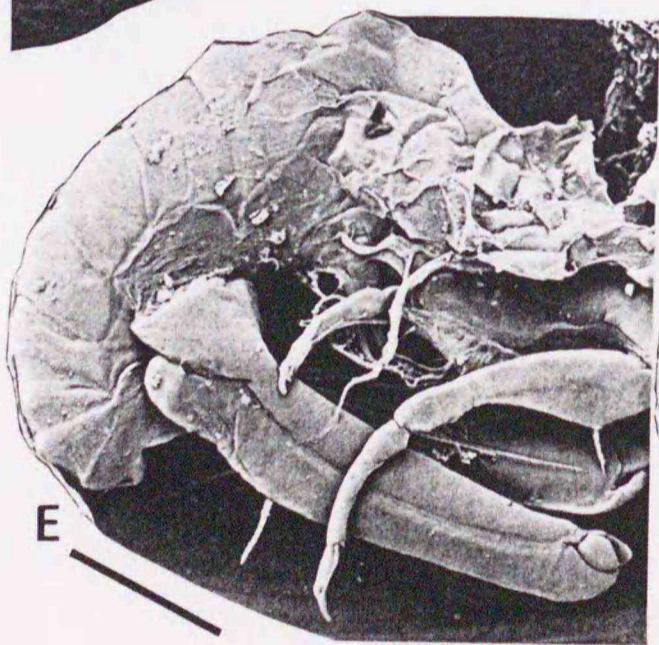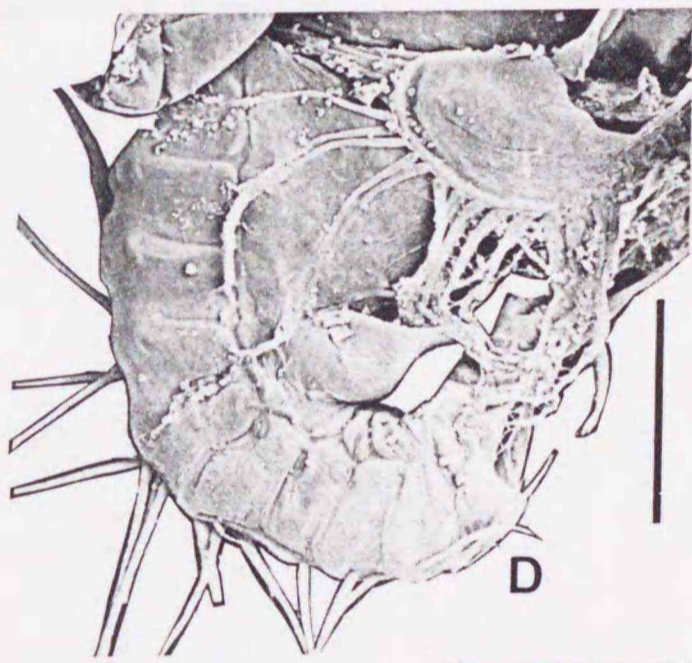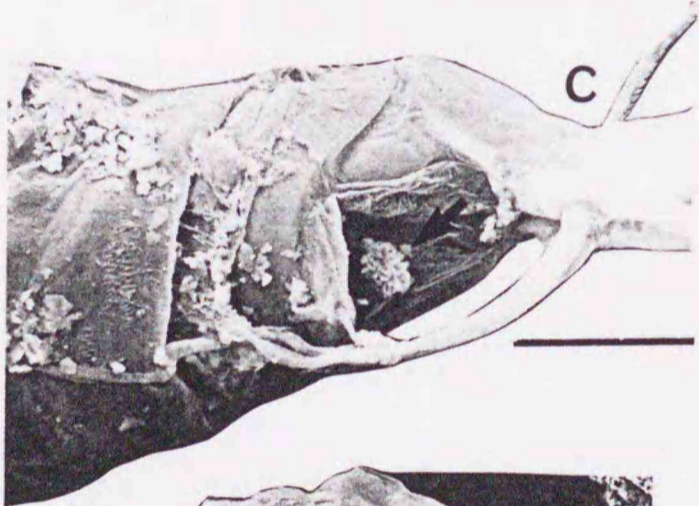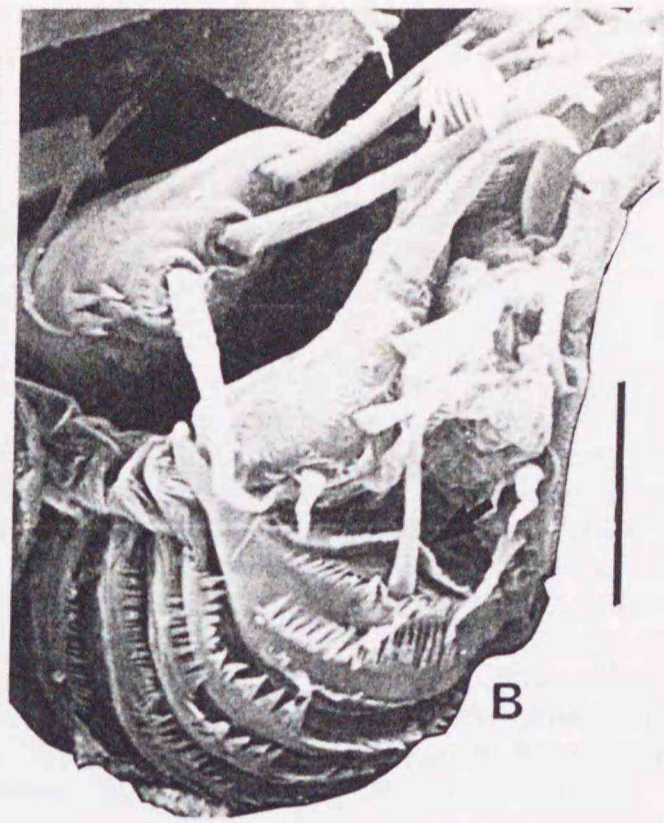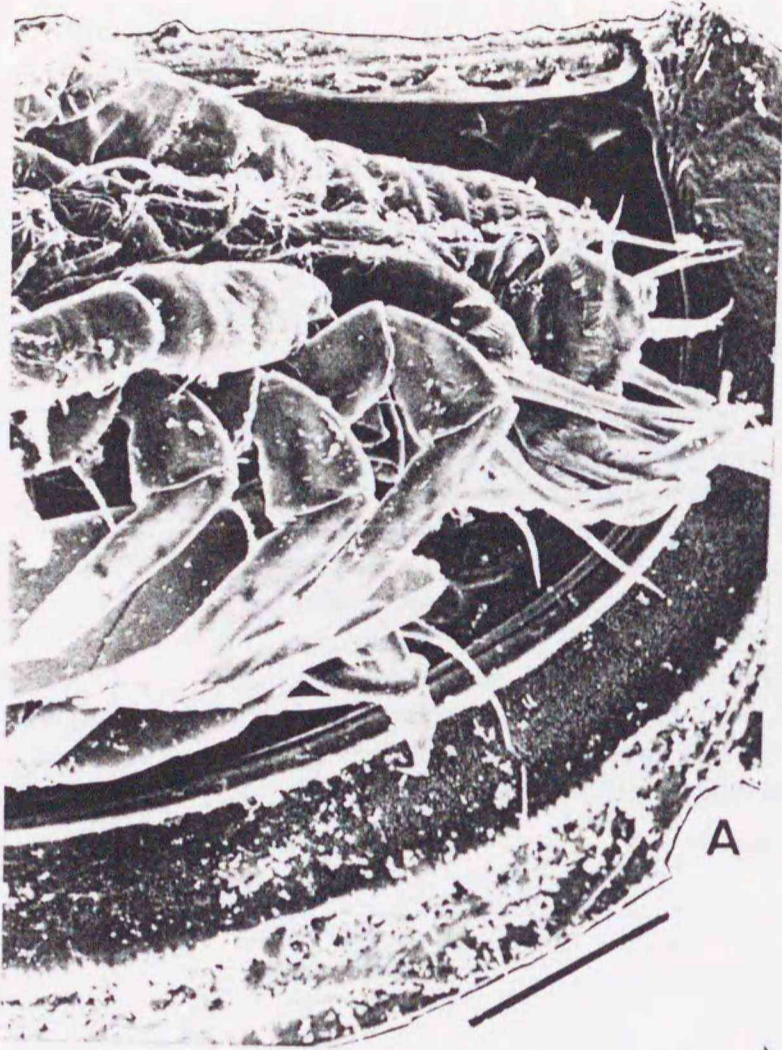
Plate 22.

Scale bar = 100μm unless otherwise stated. A, *Cytherella* sp. D. West coast South Island, New Zealand 320 metres. Ventral oblique view of male abdominal segments, furca and hemipenes. B, *Cytherella* sp. E. West Coast South Island, New Zealand 320 metres. Hemipenes and abdomen (male). C, *Cytherella* sp. B. Off Kaikoura, South Island, New Zealand 380 metres. Trunk and hemipene of juvenile male. C, *Polycope* sp. Inside Crayfish Reef, Kaikoura, South Island, New Zealand, 14 metres. Entire adult enclosed in right valve, abdominal segments arrowed. E, *Polycope* sp. Inside Crayfish Reef, Kaikoura, South Island, New Zealand, 14 metres. Entire juvenile enclosed in right valve, abdominal segments arrowed. F, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Metanauplius 3, anal segment and furcal anlage. Scale bar = 10μm.
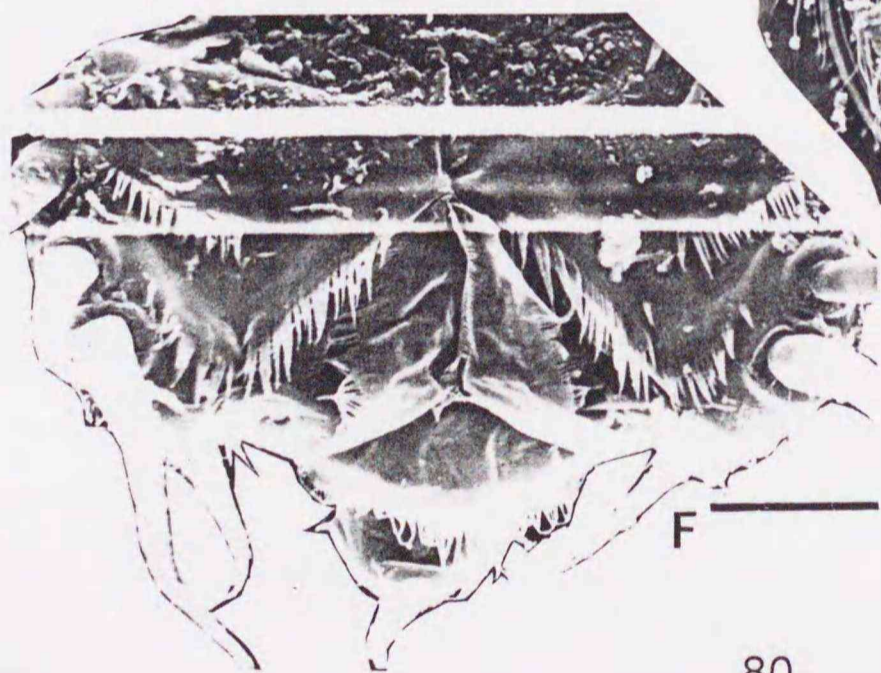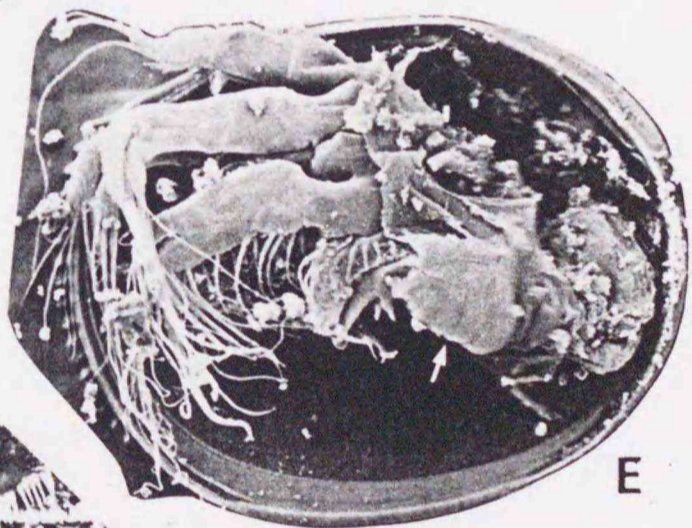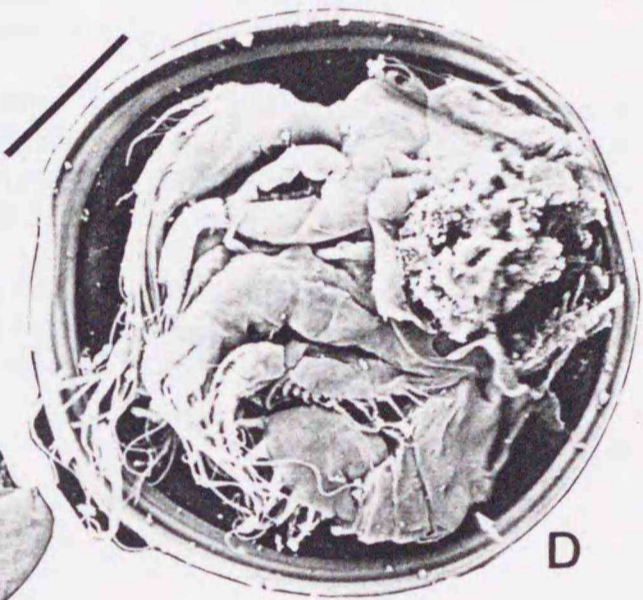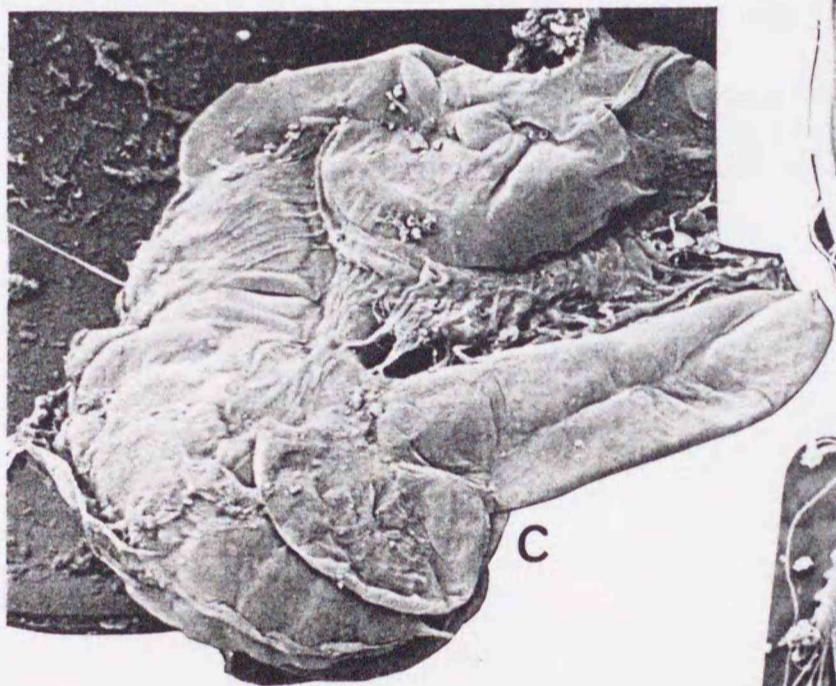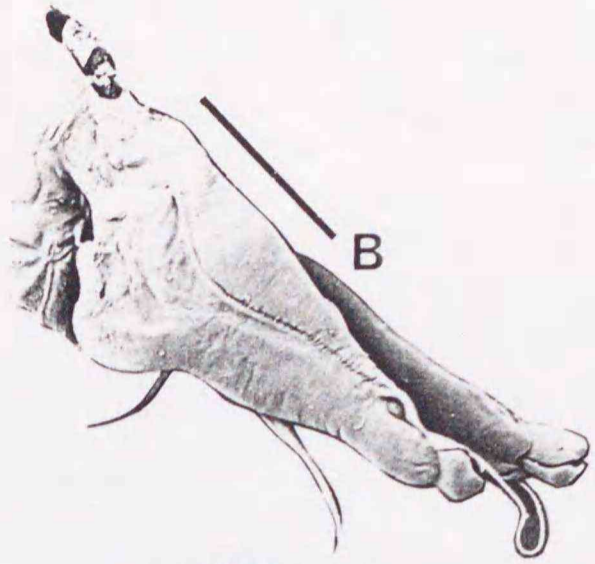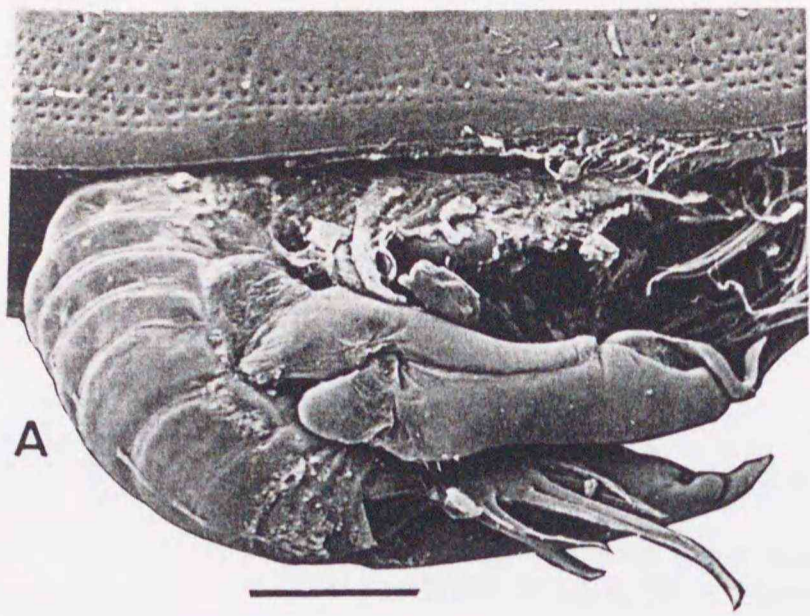
Plate 23, Figs. 1 - 3.

Manawa staceyi n.sp

Leigh, New Zealand; "megaripple zone", 17 metres.

1. a) "Nauplius", scale bar = 40μm, b) detail of flange sole, showing incomplete calcification, scale bar = 10μm; N.Z.G.S. No. OP 1126.

2. "Metanaupilus 1", a) ventral view, scale bar = 40μm, b) detail showing the left mandible in ventral view, scale bar = 10μm, c) secondary image of soft anatomy, scale bar 20μm, d) labrum, mandibles and posterior of body, posterior oblique view, scale bar = 10μm' N.Z.G.S No. op 1124.

3. "Metanauplius 1", a) ventral view, secondary image (note absence of "faecal pellet"), scale bar = 40μm, b) ventral view, secondary image with 45° rotation, scale bar = 40μm, N.Z.G.S. No. OP 1125.

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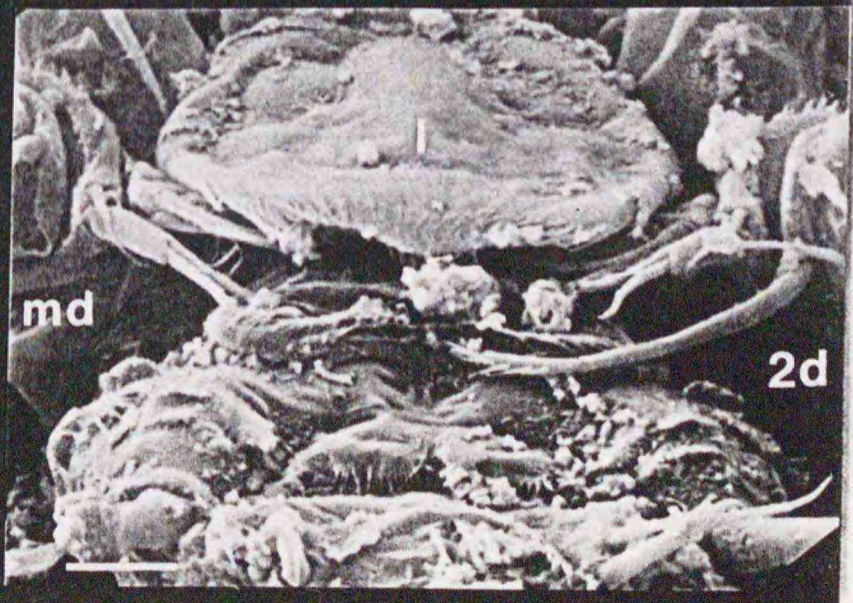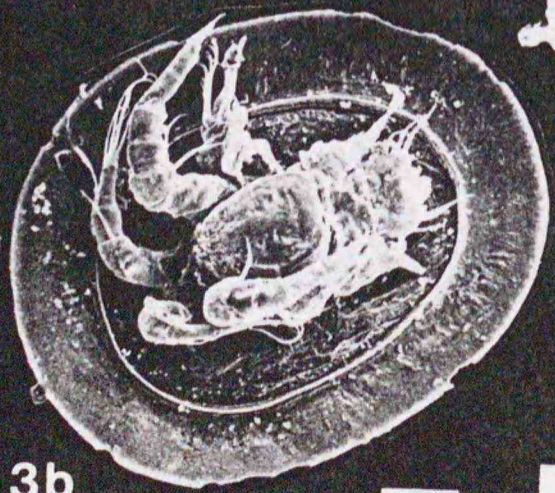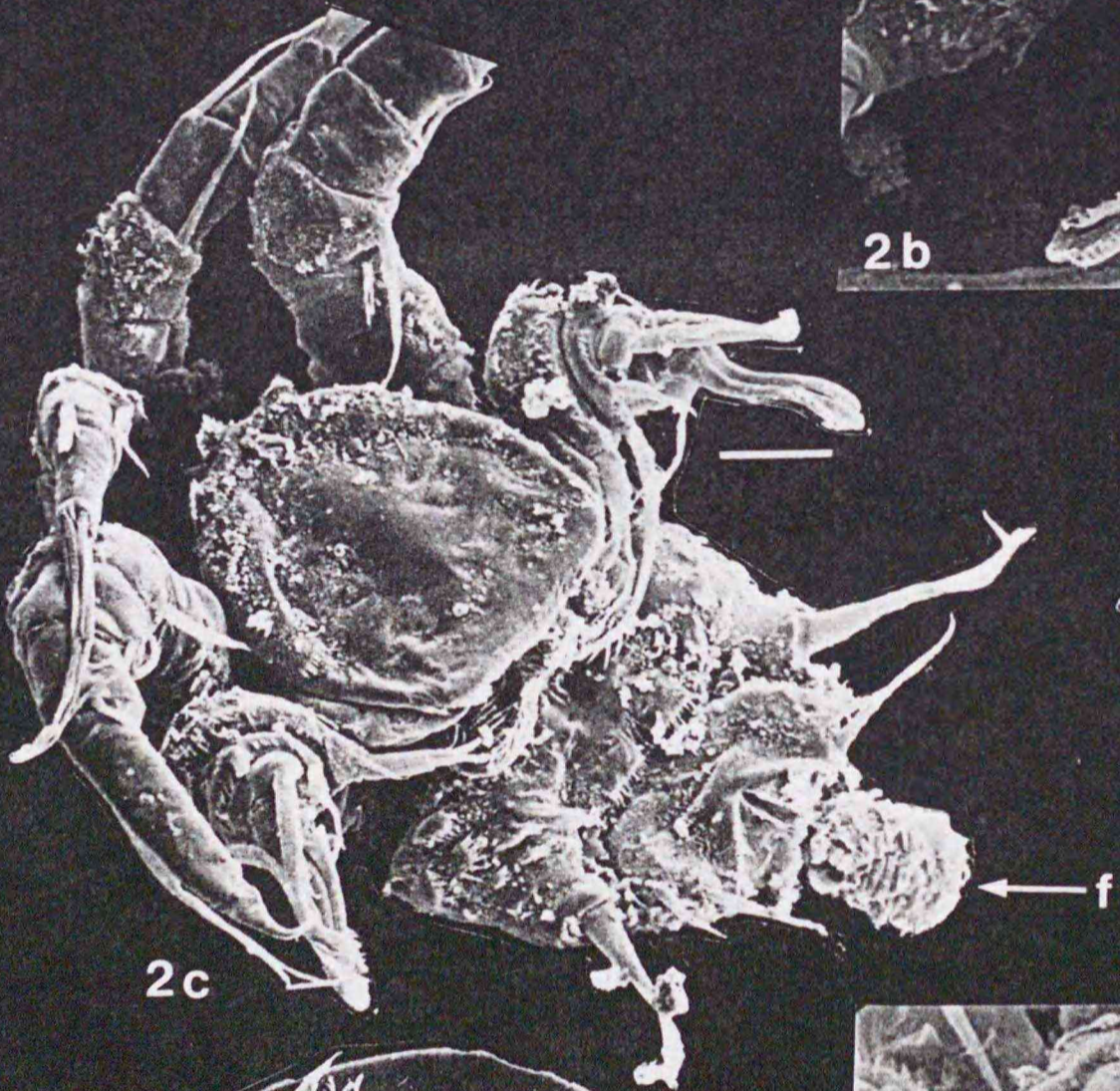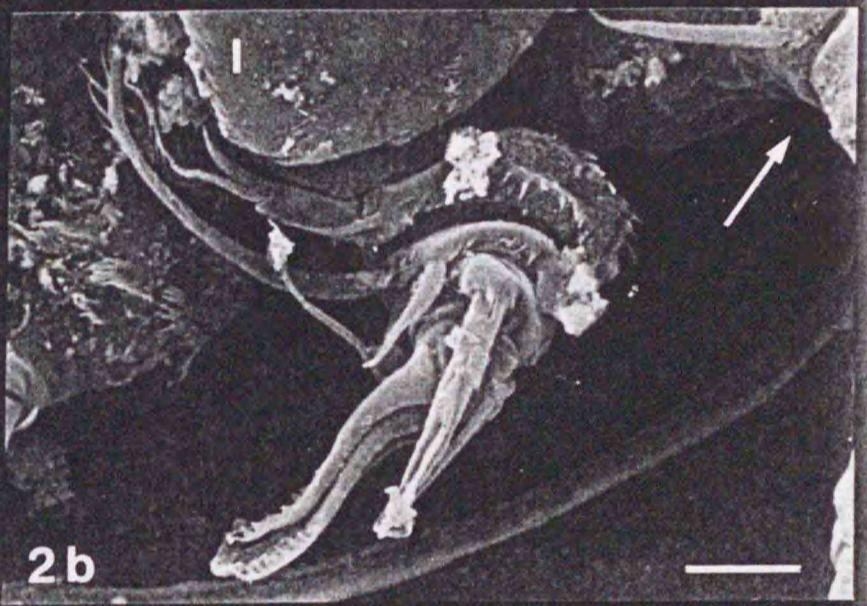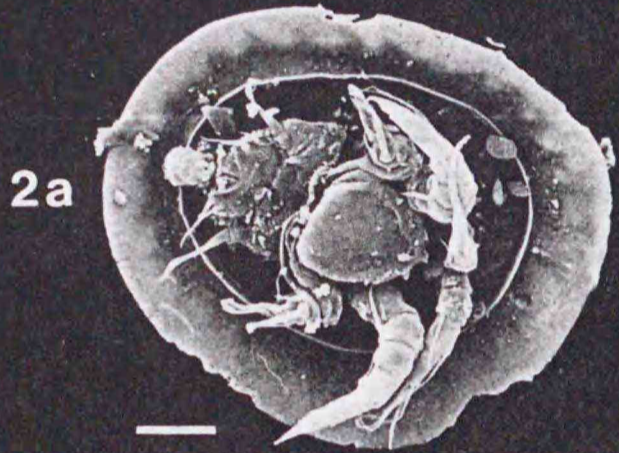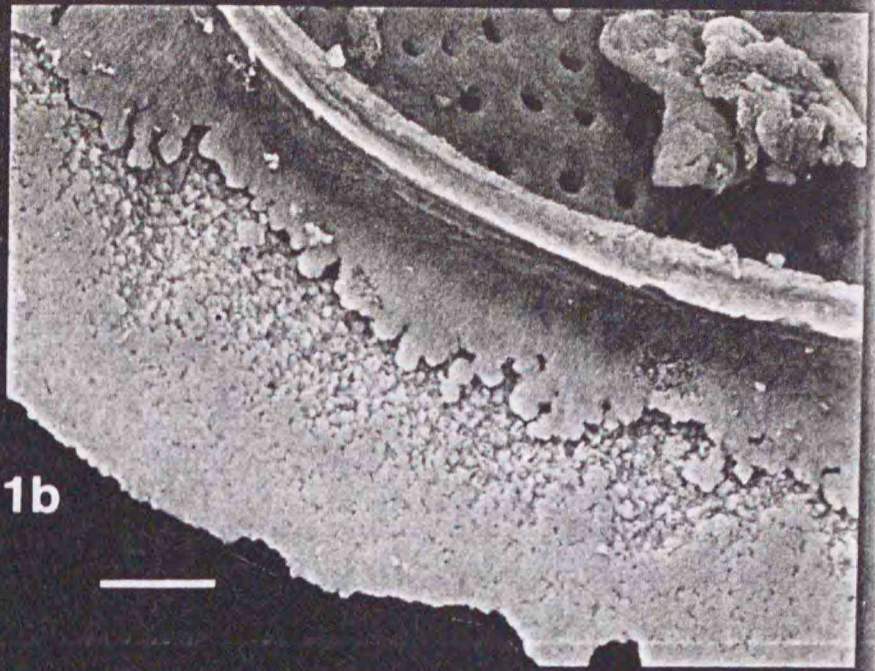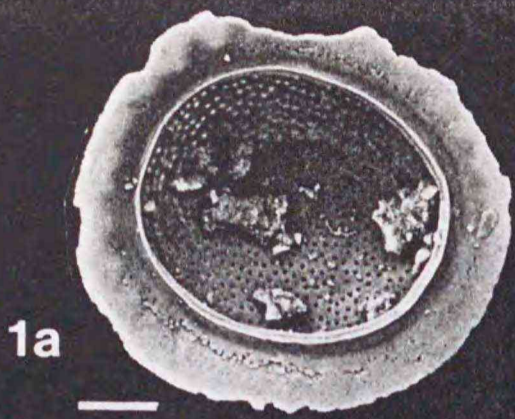
Plate 24, Figs. 4 - 10

Manawa staceyi n.sp.

Leigh, New Zealand; "megaripple zone", 17 metres.

4.   "Metanauplius 2", a) dorsal view of entire carapace, scale bar = 100μm, b) external carapace, pore with seta exiting above flange, scale bar = 10μm; N.Z.G.S. No. OP 1130 (specimen lost).

5.   "Metanauplius 2", ventral view of entire carapace, scale bar = 100μm; N.Z.G.S. No. OP 1131.

6.   "Metanauplius 2", a) carapace and soft anatomy, ventral view, scale bar = 40μm, b) carapace and soft anatomy, anterior oblique view, scale bar = 40μm, c) ventral view, anlage of 1st thoracid legs, scale bar = 20μm; N.Z.G.S. No. OP 1123.

7.   "Metanauplius 2", oblique view of fractured carapace showing flange and domicilium, scale bar = 4μm, N.Z.G.S. No. OP 1129.

8.   "Metanauplius 2", labrum, mandible and gnathobasic maxillae, posterior oblique view, scale bar = 10μm, N.Z.G.S. No. OP 1136 (specimen destroyed during manipulation).

9.   "Metanauplius 3", hinged carapace and soft anatomy, scale bar = 40μm; N.Z.G.S. No. OP 1127.

10.   "Metanauplius 3", a) posterior oblique view of labrum, gnathobasic maxilla and basal segments of 1st thoracic legs, scale bar = 10μm; N.Z.G.S. No. OP 1128. For Fig. 10b see Pl.25.

from Swanson, 1989b

4a

5

6a

7

fl

do

8

6b

4b

6c

9

max

st

st1

10a
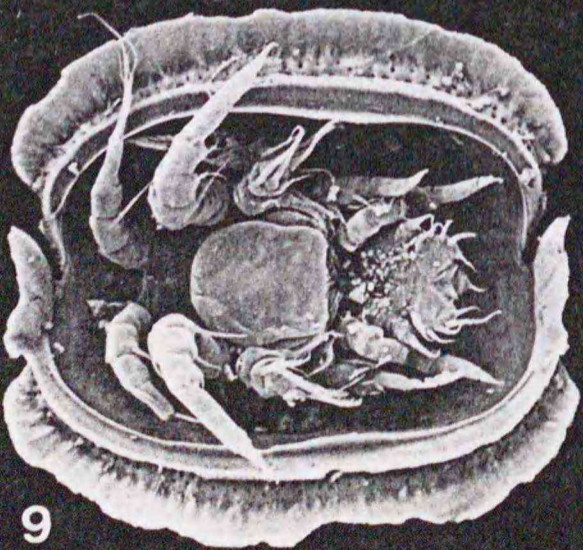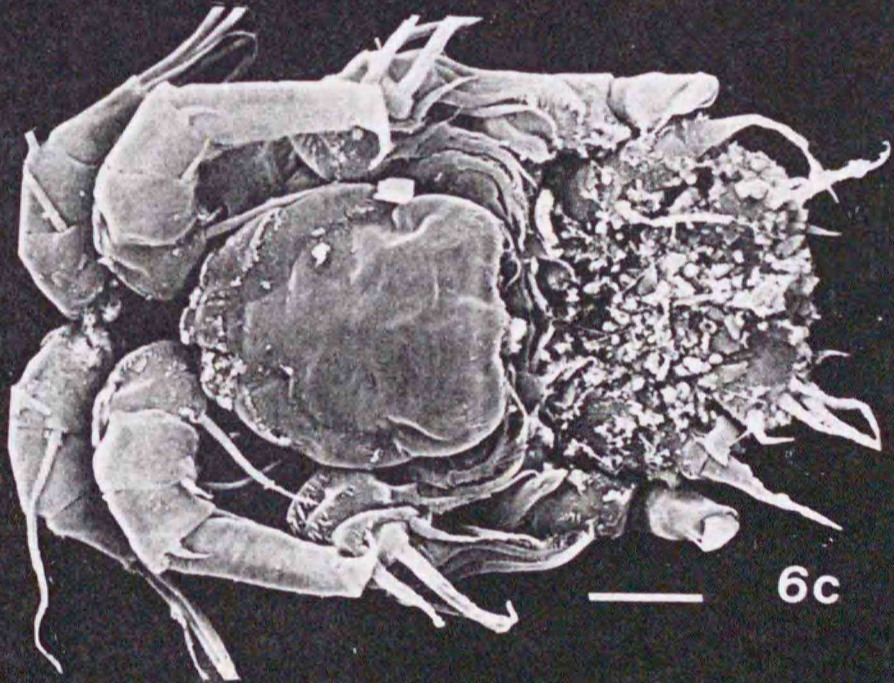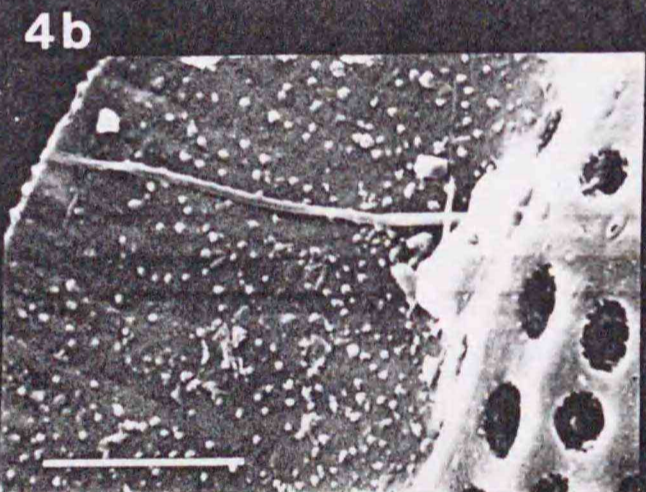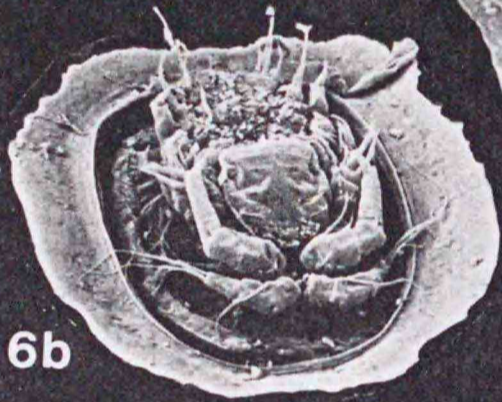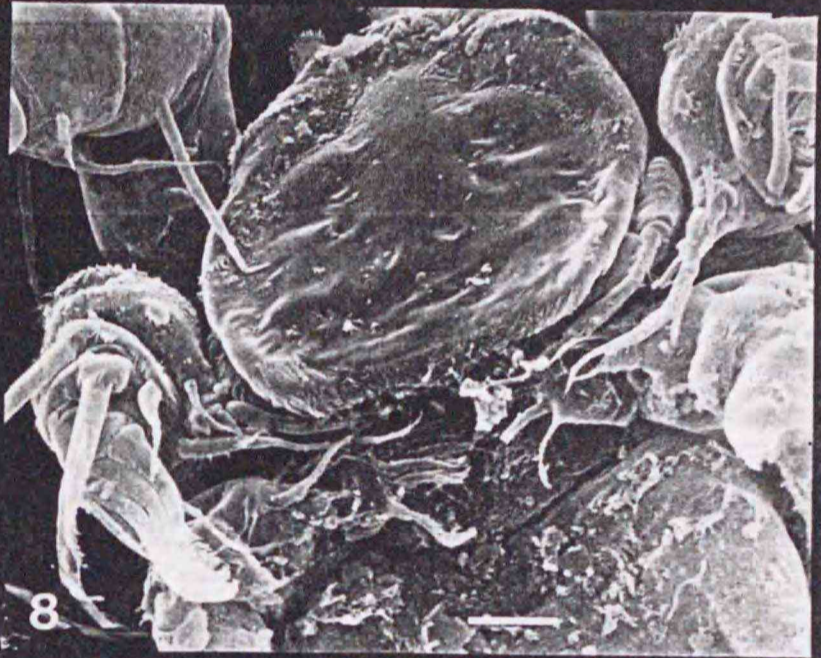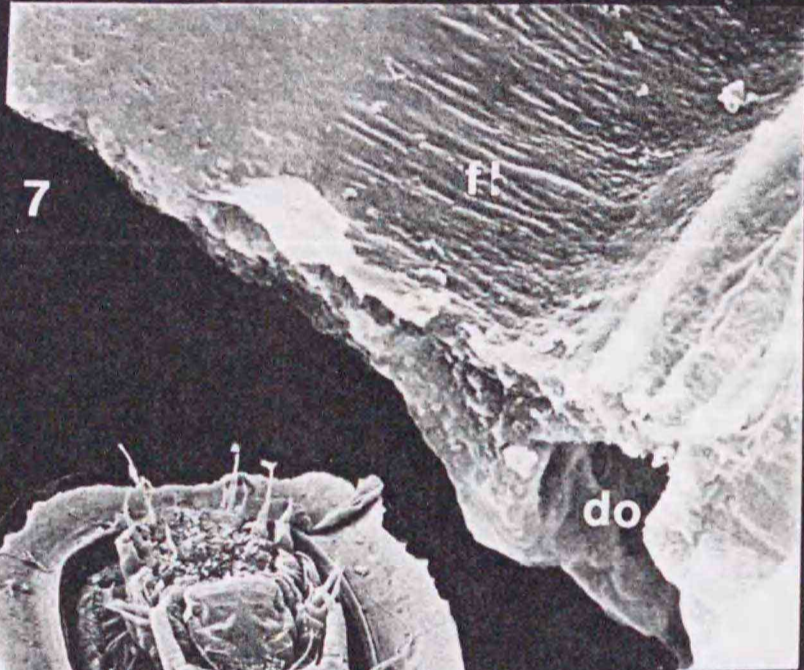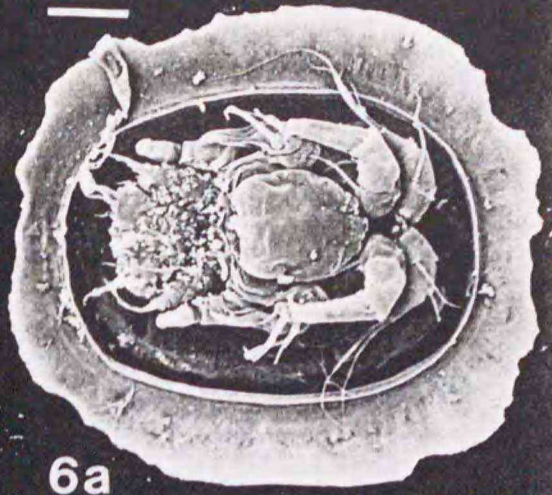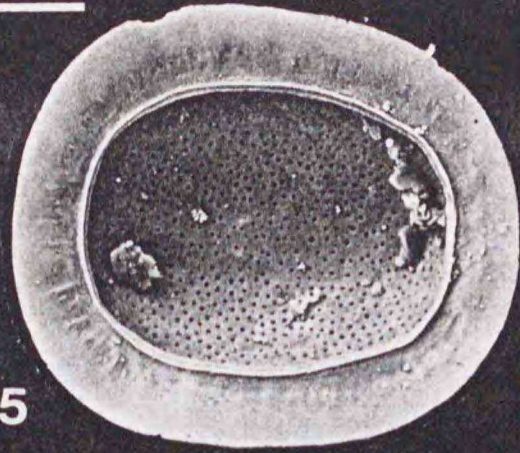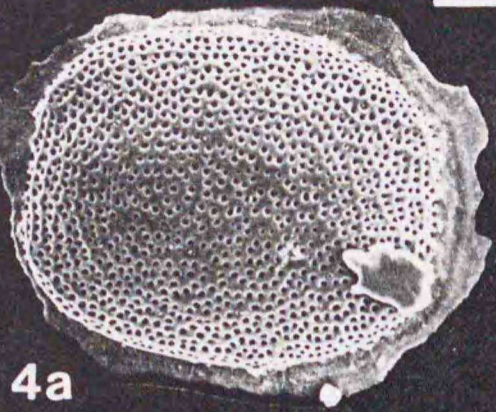
Plate 25, Figs. 10 - 16.

Manawa staceyi n.sp.

Leigh, New Zealand; "megaripple zone", 17 metres.

10.   "Metanauplius 3", b) posterior view, soft anatomy - note anlage of 2nd thoracic leg developing posteriorly, scale bar = 20μm; N.Z.G.S. No. OP 1128 - For Fig. 10a see Pl. 24.

11.   "Metanauplius 3", posterior oblique view, soft anatomy - note abdominal spine, scale bar = 20μm; unregistered specimen.

12.   "Female", anterior view, secondary image, scale bar = 100μm; unregistered specimen.

13.   "Female", holotype, oblique ventral view, scale bar = 100μm; N.Z.G.S. No. TO 1153/1. (Same specimen Pl. 26, Fig. 17).

14.   "Male", ventral view, scale bar = 100μm; N.Z.G.S. No. OP 1121.

15.   Secondary image of right antenna with branched exopodite, scale bar = 20μm; unregistered specimen.

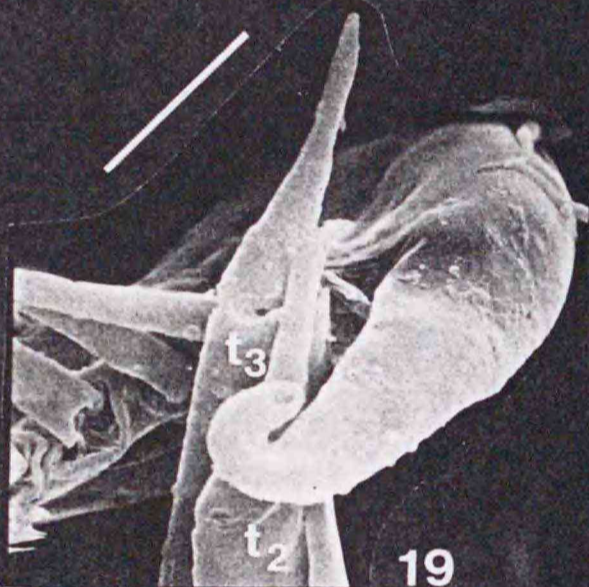16.   "Male", paratype, secondary image showing abdominal segments = note also thoracic legs clasping a large grain of biogenic detritus; N.Z.G.S. No. to 1153/4.

from Swanson, 1989b

10b

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12

13

14

15

16

86
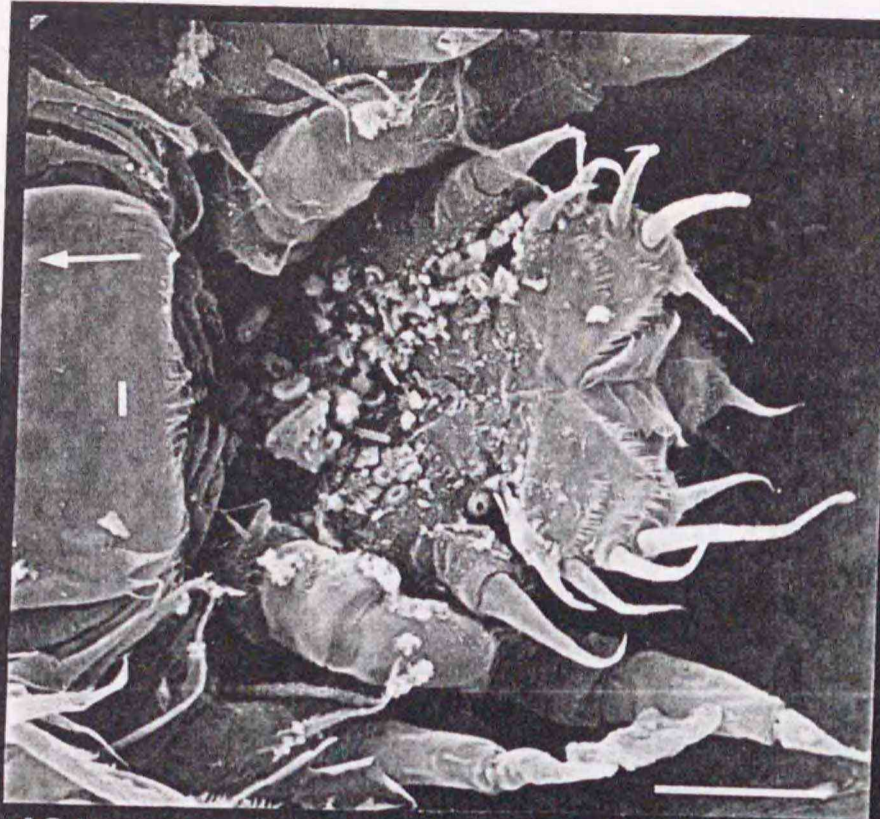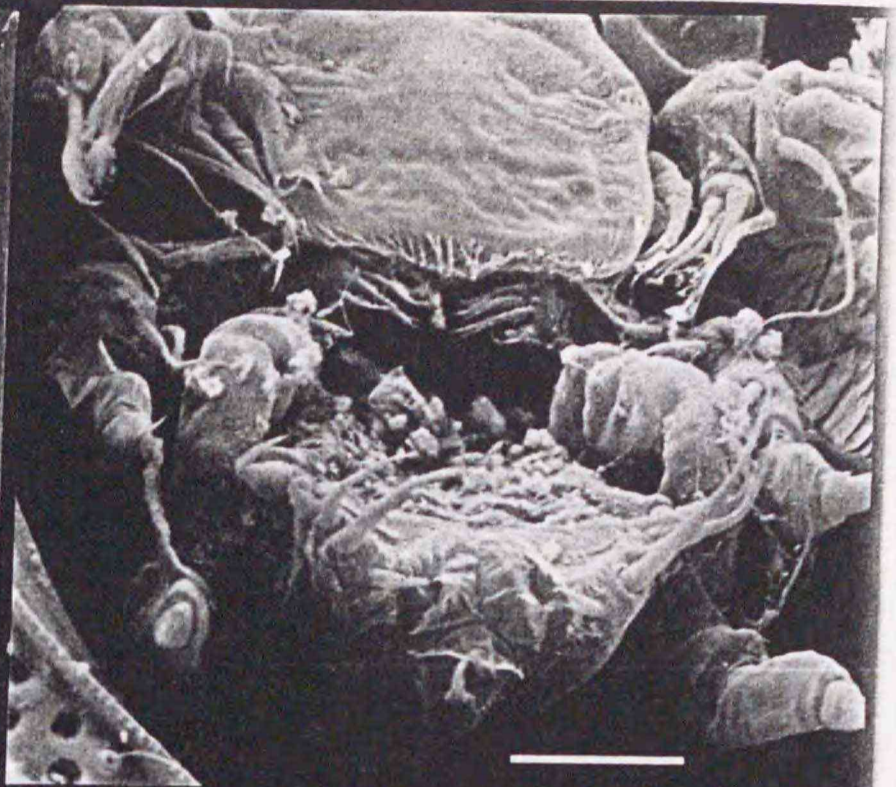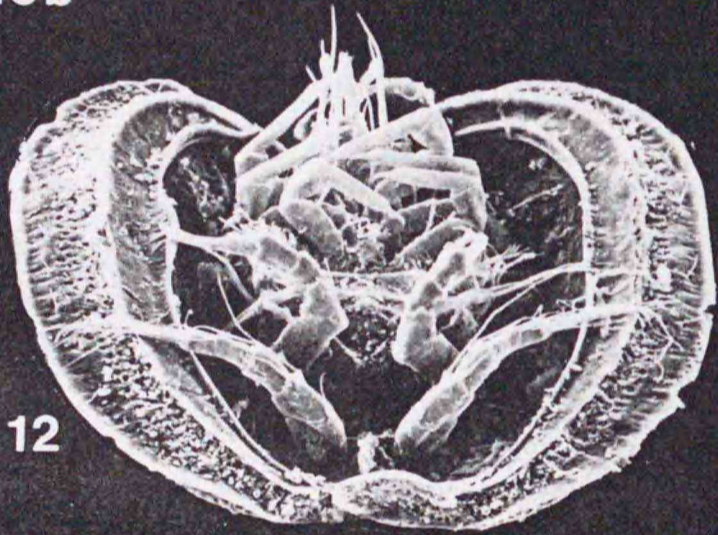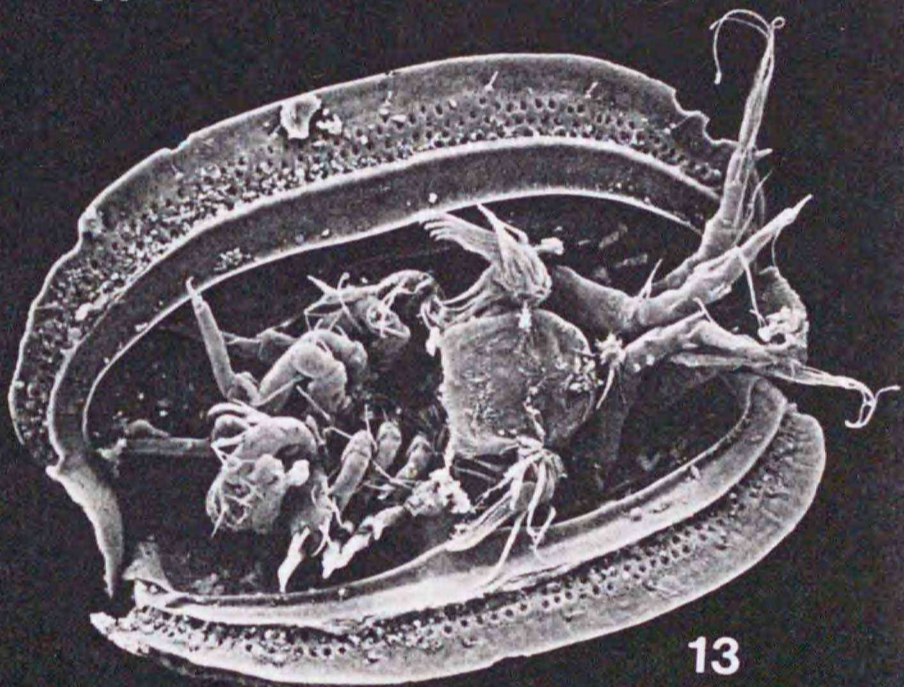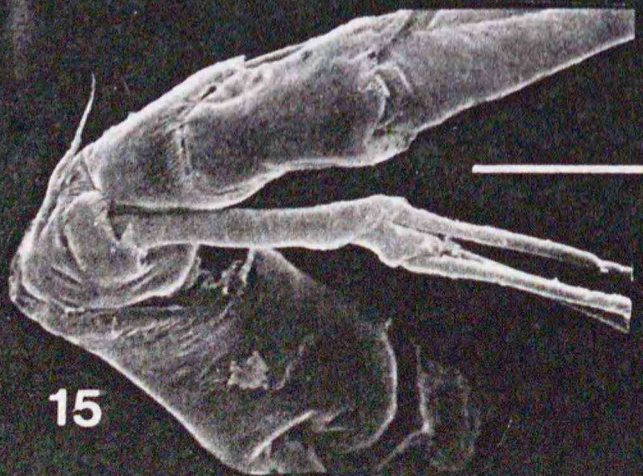
Plate 26, Figs. 17 - 24.

Manawa staceyi n.sp.

Leigh, New Zealand; "megaripple zone", 17 metres.

17. "Female", holotype, basal segments of thoracic appendages, scale bar = 10μm; (Same specimen Pl. 25, Fig. 13).

18. "Male", secondary image terminal segment of maxilla with clasper, scale bar = 20μm; unregistered specimen.

19. "Male", secondary image "copulatory apparatus", scale bar = 10μm; unregistered specimen.

20. "Female", paratype, abdominal segments and furca, scale bar = 10μm; N.Z.G.S. No. TO 1153/3.

21. "Female" paratype, furca - note extremely thin "transparent" seta, scale bar = 20μm; N.Z.G.S. No. TO 1153/2.

Cavalli Islands; 13 metres.

22. Left valve, secondary image, scale bar = 100μm; N.Z.G.S. No. OP 1134.

23. Entire carapace in "life" position, a) posterior oblique view, scale bar = 40μm, b) anterior view, scale bar = 40μm; unregistered specimen (destroyed).

Leigh, New Zealand; "megaripple zone", 17 metres.

24. Right valve, secondary image, scale bar = 100μm; N.Z.G.S. No. OP 1122.

from Swanson, 1989b

17

18

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20

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23a

23b

24

88.