AUSTRALIAN FOSSIL DECAPOD CRUSTACEA: FAUNAL AND ENVIRONMENTAL CHANGES

by

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Frontispiece

Upper: A male specimen of the extant *Ommatocarcinus macgillivrayi* White, 1852, from near Sydney, New South Wales.

Lower: The probable ancestor of *Ommatocarcinus macgillivrayi*, the fossil species *Ommatocarcinus corioensis* (Creswell, 1886) from the approximately Middle Miocene Port Campbell Limestone at Gravell Point, southeast of Port Campbell, Victoria. Specimen collected by Dr. G. Baker, 1965.

SUMMARY

Fossil decapod Crustacea are known from the Mid-Cretaceous and Tertiary of Australia. Most of those from the Tertiary are described here for the first time. Conclusions are drawn concerning factors in the history of the southern Australian marine decapod fauna.

The Decapoda from the Cretaceous occur in the northern, northeastern and eastern parts of the continent and comprise macrurans and brachyurans; both cosmopolitan and endemic genera are represented, but strictly Tethyan genera are absent.

The Decapoda known from the Australian Tertiary are mainly from the southeastern part of the continent. Sparse assemblages of thalassinids and a few brachyurans are known from the Paleocene and Eocene. A diverse assemblage of brachyurans and anomurans occurring in the Middle Oligocene of the Gambier Embayment probably inhabited an outer-neritic or upper continental-slope environment. This assemblage is essentially modern in aspect, with about 60% of its species related to living Australian forms, and most of the remainder resembling modern Indo-Pacific species not occurring in Australian waters. Thus some Indo-Pacific lineages represented in the Australian Oligocene have apparently become extinct locally.

Early Miocene brachyuran and anomuran assemblages known chiefly from the Murray Basin and a small mid-Lower Miocene assemblage from the Gambier Embayment probably inhabited mid- or inner-neritic environments. They

comprise genera present in earlier Australian assemblages and immigrant Tethyan and Indo-Pacific genera no longer known in southern Australian waters. The occurrence of these genera is probably related to climates considerably warmer than at present.

The widespread occurrence of the crab *Ommatocarcinus corioensis* in southeastern Australia in approximately the Middle Miocene is striking because the southern limit of the range of its modern relative *Ommatocarcinus macgillivrayi* is north of Cronulla (Sydney) off eastern Australia. Its widespread occurrence may therefore be linked to sub-tropical water temperatures and its local abundance to its burrowing habits in the moderately fine grained sediments which were deposited prevalently at this time.

Brachyurans and anomurans comprising late Upper Miocene and Pliocene assemblages are mostly closely related to or represent extant Australian species. These faunas are from near-shore environments.

It is concluded that the present Australian decapod fauna has been derived largely from the Indo-Pacific region but that most cool water Australian species have evolved locally. Some taxa apparently migrated from Australia to New Zealand and limited migration seems to have taken place in the reverse direction.

Inferences made about past climates of Australia from fossil decapods, from other sections of the fossil biota and from oxygen isotope palaeotemperature work are in close agreement. Apparently the continent was

largely extratropical in the Cretaceous; there was a trend towards increasing temperature from the Paleocene to the Early Miocene and a decline in temperature since. These changes may be related to world-wide fluctuations in climate and also to a progressive northward movement of Australia since the Cretaceous or early Tertiary.

Taxonomic studies of newly collected materials and museum collections from the Oligocene to Pliocene of southeastern Australia led to the recognition of 50 decapod species within 26 genera; 39 species are new. A subspecies of a crab and a new genus and species of macruran are described from the New Zealand Tertiary.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University nor, to the best of my knowledge and belief, does it contain any material previously published or written by another person, except where due reference is made in the text.

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INTRODUCTION

Interest in the modern decapod Crustacea of the Australasian region has increased greatly in the past few years, partly perhaps because of a concomitant increase in the numbers of Australasian biologists and the realization of the economic importance of decapods in fisheries, but also because these commonly occurring, diverse and structurally complex animals, with their often ordered and involved patterns of behaviour, provide a rich field for scientific investigation. The taxonomy of these animals in Australasia is becoming increasingly complete (Griffin and Yaldwyn, 1968; Dell, 1968a; Yaldwyn, 1971) and is now leading to questions as to the origin of the faunas, and the evolutionary and ecological relationships of the different taxa which comprise them. Palaeontology offers the only factual method of studying the origin and evolution of these faunas.

Fossil decapods occur in Australia in Cretaceous and Cainozoic rocks. Those from the Cretaceous have been relatively well documented by several authors. Undescribed materials from the Cretaceous of Melville and Bathurst Islands may increase this knowledge.

The Tertiary faunas, which are of the greatest significance for studies of the origin of the modern faunas, have received little attention except in a few instances. This thesis is an attempt to help fill this gap in knowledge.

Numerous authors have briefly mentioned the occurrence of crustacean remains in the Australian Tertiary. Investigations carried out initially by Professor Glaessner of the University of Adelaide, and continued by the author have shown that brachyurans and anomurans occur as quite common fossils in most local marine Tertiary deposits. A few weeks' collecting by the author in the Gambier Embayment, Murray Basin and Otway Basin (eastern part) sufficed to bring to light a diverse collection of many hundreds of specimens; mostly these consist of various fragments of appendages but they also include numerous carapaces. These specimens, together with material collected by Professor Glaessner, and museum collections which he brought together from South Australia, Victoria and Tasmania, form the basis of the present study.

This investigation is in no way exhaustive but attempts to document the most common members of the local Tertiary decapod faunas; this involves about 70% of the taxa represented in the materials at hand and perhaps 60% of the taxa actually preserved in the rocks so far studied.

A historical outline of previous works concerning fossil decapods from Australia follow this introduction. The body of the thesis is divided into two parts, the first of which is a discussion of various aspects of the Australian fossil Decapoda, and the second largely taxonomic. Chapter I outlines the stratigraphic distribution of the Tertiary decapods described in this work and includes remarks on their palaeoecology. Chapter II gives an outline of all the fossil decapods and fossil decapod faunas known from Australia, and an attempt is made to analyse the faunas with respect to the evolutionary and geographic relationships of the taxa comprising them, and their possible palaeoclimatic significance. In the third chapter the faunal and palaeoclimatic inferences made are compared to similar observations which have been made (mainly in the literature) on other sections of the Australian fossil biota, to relate these observations to physical studies of past climates, and to assess the results of these comparisons in relation to the geological hypothesis that Australia has moved progressively northwards since the Cretaceous or Early Tertiary, and that Australia and Antarctica separated in the Eocene.

HISTORICAL

Fossil decapod remains were first reported from Australia by Bell (1844, 1845). These remains, a subfossil thalassinid probably from northern Australia, were initially referred to by Bell (1844) as Thalassina antiqua (nomen nudum) and subsequently described formally by him (Bell, 1845) as Thalassina emerii. However it was not until 41 years later that a pre-Pliocene decapod from Australia was recorded when Cresswell (1886) described the fossil crab Goneplax corioensis from specimens preserved in nodules collected at Curlewis and North Geelong on Corio Bay, Victoria. Cresswell also mentioned that he had been told that the same species had been found at Beaumaris, near Melbourne, Victoria; this has since been substantiated. Both at Beaumaris and in the Geelong area the crabs occur in remanié phosphatic nodules at the base of marine late Miocene sediments.

Wintle (1886, 1887) described subfossil remains of crabs and mentioned a freshwater crayfish from the estuarine deposit at the mouth of the Yarra River, Victoria.

Woodward (1893) described a fossil crab, Prosopon etheridgei from a carapace which had been found in the Cretaceous of central Queensland. In an appendix to the same work, Etheridge Jr. suggested that P. etheridgei was probably from the Lower Cretaceous Rolling Downs Series; Etheridge also mentioned a large chela of a macruran-like decapod from the Cretaceous of the Walsh River district of northern Queensland. Etheridge and Dun (1902) mentioned both of these remains again in a list they give of Australian Cretaceous fossils.

Hall (1904) referred *Goneplax corioensis* Cresswell to the genus *Ommatocarcinus* White and redescribed it from some of the original materials from Curlewis and from other well preserved examples which he collected from the Miocene Port Campbell Limestone, near Port Campbell, Victoria. He suggested that the very complete preservation of the specimens from the latter locality was due to the crabs becoming "entombed in their burrows".

Chapman (1914), in his book reviewing Australasian fossils, mentions and figures *Prosopon etheridgei* and *Ommatocarcinus corioensis*. He also referred to other more or less fragmentary remains of decapods occurring in the Tertiary of Victoria and noted the occurrence of another crab in the late Miocene marine sediments at Beaumaris, Victoria (a note on a label suggests that this was the specimen here described as *Ovalipes victoriensis* sp. nov.).

Etheridge (1914) described the greater portion of a macruran carapace from the Cretaceous of the Barcoo River Watershed in south-central Queensland as *Enoploclytia terrareginae*.

Etheridge and McCulloch (1916) reidentified *Thalassina emerii* Bell as *Thalassina anomala* (Herbst) and described other subfossil remains of a number of still-living crabs from coastal sediments located in northeastern, northern, eastern, and southeastern Australia. The one new species which they described, *Paracycloïs grandispinis* (here referred to *Calappilia* A. Milne-Edwards) was stated to be from the estuarine deposits of the Yarra Delta, Melbourne. In the present study it is suggested that this species is of Miocene age.

Etheridge (1917) described the limbs and figured specimens of *Prosopon etheridgei* Woodward (referred to *Homolopsis* Bell by van Straelen, 1928) from the Rolling Downs Series at Beaconsfield near Longreach, central Queensland, and described the macruran *Hoploparia mesembria* from the same locality and another lobster *Glyphea arborinsularis*, from the Cretaceous of the Maryborough Basin of Queensland. He also described *Callianassa* (?) sp. from the Rolling Downs Series at either the Walsh or Mitchell River, north Queensland; this was the claw to which he had referred in the appendix to the paper of Woodward (1893). He noted that the hind limbs of the beautifully preserved examples of *P. etheridgei* which he figured have their basal attachments raised, and inferred that they may have functioned to hold protective material above the animal. This habit persists in modern homolids (present study p.156).

Maitland (1919) referred to various molluscan remains and "the great chela of a burrowing crab *Callianassa*, ... or *Thalassina*" from between depths of 1,505 and 1,831 feet (460 and 560 metres) in the Tertiary of the South Perth Bore, Perth, Western Australia.

Coulson (1932) and Keble (1932) described the occurrence of Ommatocarcinus corioensis in the bed of phosphatic nodules at the base of the Pliocene sequence in the Geelong district, Victoria. They suggested that the crabs were remanié from a bed which formed in narrow arms of the sea after the major phase of Miocene deposition and prior to a Pliocene transgression.

A number of thalassinids from Paleocene strata in the vicinity of Princetown, Victoria, were described by Glaessner (1947). The species described comprised Callianassa bakeri from the Middle Paleocene Pebble Point Formation and Callianassa cf. lacunosa Rathbun, Callianassa sp., and Ctenocheles victor from the Upper Paleocene Rivernook Member of the Dilwyn Formation; fossil burrows attributed to Callianassa were also described from the Pebble Point Formation.

Crespin (1947) described a fossil crab "Harpactocarcinus" victoriensis from the Lakes Entrance Oil Shaft, Gippsland, Victoria. The crab is from the Lakes Entrance Formation and is considered here to be of early Lower Miocene age.

Woods (1953, 1957) reviewed the Cretaceous fossil decapod remains then known from Australia and described a number of new forms. In his work of 1953, Woods redescribed Homolopsis etheridgei (Woodward) and erected new genera and species for Doratiopus salebrosus and Torynomma quadrata, the remains of all of these forms being from the Albian of Central Queensland.

In his 1957 paper Woods redescribed the macrurans Enoploclytia terrareginae Etheridge (referred to Palaeastacus Bell by Förster, 1966) and Hoploparia mesembria Etheridge, and described Astacodes sp. and the new species Glyphea oculata and Tillocheles shannonoae from the Albian of Central Queensland; redescribed Glyphea arborinsularis Etheridge from the Aptian of North-Central Queensland and the Maryborough Formation (? Neocomian-Aptian) in southeastern Queensland; and described the new species Enoploclytia tenuidigitata from the Aptian of North Queensland, and referred Callianassa (?) sp. Etheridge, from sediments of similar age in the same area, to Enoploclytia sp. (this is more likely Palaeastacus).

Gill and Baker (1955) mentioned the occurrence of the crab Pseudocarcinus H. Milne-Edwards at West Essendon, Melbourne, Victoria in sediments of approximately Lower Miocene age.

Glaessner (1957) described the thalassinid Protocallianassa australica from the South Perth Bore, Perth, Western Australia. This material is from the Kings Park Shale which is now considered as being of late Middle to early Upper Paleocene age (McGowran, 1964, 1968).

Gill (1957) reported the occurrence of a fossil crab Persephona sp. nov. (reidentified here as a species of Philyra Leach), in the late Miocene at Beaumaris, Victoria.

In his monographic study of New Zealand fossil decapod Crustacea, Glaessner (1960) made several references to Australian forms; the occurrence of Ctenocheles in the Australian Eocene (actually Paleocene) and Miocene, the presence of Lyreidus in the Oligocene to Miocene Gambier Limestone near Mount Gambier, South Australia, the representation of his new genus Tumidocarcinus in the early Lower Miocene of southeastern Australia, the wide distribution of Ommatocarcinus corioensis and Calappa (species here referred to Calappilia A. Milne-Edwards) in the Miocene, and the recognition of Pseudocarcinus in the Miocene and Pliocene of southern Australia. He reidentified "Harpactocarcinus" victoriensis Crespin as Tumidocarcinus tumidus (Woodward) and noted the occurrence of another example of this crab from rocks of early Miocene age near Longford, Gippsland. He also mentioned the occurrence of Pseudocarcinus in the Miocene of Melbourne, Victoria (the same material to which Gill and Baker (1955) referred). This record is substantiated in the present work, but remains of the same genus Glaessner noted from the Pliocene of Adelaide, Aldinga and Surveyors Point, near Port Vincent, South Australia, are here tentatively referred to Ozius.

Bowler (1963) remarked on the remanié preservation of Ommatocarcinus corioensis in phosphatic nodules occurring in the Pliocene nodule bed of the Geelong area, and stated that he had observed crab remains in phosphatic concretions in situ in Tertiary sediments (Oligocene-Miocene) at Torquay and Shelford, Victoria. These occurrences have been investigated by the author and found to comprise mainly the thalassinid Ctenocheles Kishinouye.

O. P. Singleton (1967) suggested that the complete preservation of specimens of *Ommatocarcinus corioensis* in the Port Campbell Limestone, which occurs in the Otway region, Victoria, and is here considered approximately Middle Miocene in age, indicated an extremely quiet, off-shore environment of deposition for this formation. Spencer-Jones (1967) noted an occurrence of the same crab in the Miocene Fyansford Clay on the sea-coast at Geelong.

Many of the Cretaceous fossil decapods from Queensland have been refigured by Hill, Playford and Woods (1968). The same authors (1970) have also figured decapod remains from the fresh-water Lower Tertiary (parastacid claw) and from the ? Pleistocene-Recent of Queensland.

Von der Borch (1970) recorded the occurrence of the crab *Ommatocarcinus corioensis* in phosphatic nodules dredged from the upper continental slope off northern New South Wales. The crab and other fossils in the incorporated sediment in the nodules indicate a possible Middle Miocene age; the core of the nodules is probably remanié material winnowed from Miocene sediments of the continental slope.

The studies made in this thesis rest heavily on knowledge of the modern decapod faunas of Australasia. A recent summary of studies made on the modern Australian decapod fauna is given by Griffin and Yaldwyn (1968) and a similar review for New Zealand brachyurans is presented by Dell (1968a).

PART 1

Chapter I

STRATIGRAPHIC AND PALAEOECOLOGICAL FRAMEWORK

Introduction

The fossil Decapoda described in this work are all from the marine Tertiary of southeastern and eastern Australia. The different occurrences are indicated in Figure 1. The stratigraphic occurrence of the different species is summarized in Table 1.

This chapter is principally a description of the different localities where the fossil decapods described in the present study have been found and an attempt to place these occurrences in stratigraphic perspective. Most of these localities have been described by previous workers, but it is considered necessary to bring the relevant parts of this rather scattered literature together in order to provide a coherent stratigraphic framework against which the occurrence of the decapods can be viewed. New investigations of foraminifera at some of the localities enable the rocks at these sites to be more precisely dated than has previously been possible. These studies and other recent micropalaeontological work (chiefly McGowran *et al*., 1970) provide, for the first time, a basis for tentatively correlating the rocks at the sites described with a detailed, modern, world chronostratigraphic scheme (Figure 4). New geological data is presented for some of the localities and, where possible, inferences are made concerning the palaeoenvironments in which the decapods lived.

Sequences of zones based on the ranges of planktonic foraminifera (Carter, 1958, 1958a, 1959, 1964; Wade, 1964, 1966; Taylor, 1966, in O. P. Singleton, 1967, and in McGowran et al., 1970; Ludbrook and Lindsay, 1969) provide the most precise time-stratigraphic framework yet available for the Tertiary of southern Australia. Harris (in McGowran et al., 1970) has erected a zonal scheme based on palynological data from the southern Australian Tertiary. McGowran et al. (1970) tentatively correlated the local foraminiferal and palynological biostratigraphic systems with the numbered P-zones and N-zones which Banner and Blow (1965) and Blow (1969, 1970) erected for Palaeogene and Neogene tropical planktonic foraminiferal sequences; this correlation was placed in chronostratigraphic and radiometric perspective following Berggren (1969a). Other foraminiferal studies by Lindsay (1970) and McGowran (1970a), and foraminiferal studies which the author has made, especially on some Otway Basin sediments collected by Dr. Mary Wade, have furnished additional information concerning the biostratigraphy of the local Oligocene and Miocene, particularly with respect to the ranges of key Lower and early Middle Miocene foraminifera (Figure 2).

Ludbrook (1967) and Ludbrook and Lindsay (1969) have correlated sequences of foraminiferal zones erected for the Tertiary of southern Australia with the marine stages of the same period recognized in New Zealand, where various palaeoclimatic events of relevance to the present work are better documented than in Australia. The recent geochronological studies of Page and McDougall (1970) and Bandy et al. (1970) shed further light on

Australasian chronostratigraphy, particularly for the late Oligocene and Miocene.

The biostratigraphic scheme presented in Figure 3 is based largely on the work of McGowran *et al.* (1970), but also attempts to take into account the other recent works mentioned above. Several problems within this scheme warrant at least a brief further discussion.

McGowran *et al.* (1970) consider that the *Globigerina euapertura*/*Globoquadrina dehiscens* zone boundary of Ludbrook and Lindsay (1969) is high within the tropical standard zone N4 of Banner and Blow (1965), Blow (1969) (hereafter the tropical standard zones erected by these later authors are indicated by the abbreviation "T.S. zone"). Geochronological studies lend support to this argument. The Maude Basalt (Bowler, 1963) which occurs in the eastern part of the Otway Basin, lies near the boundary of faunal unit 5 and faunal unit 6 of Carter (1964) and has been dated as 21.1 ± 0.3 m.y. old by K-Ar, whole-rock studies (Page and McDougall, 1970). Carter (1959, 1964) indicated that the first appearance of *Globoquadrina dehiscens* (Chapman, Parr and Collins), which marks the zone boundary mentioned above, occurs early in his faunal unit 6. The appearance of *Globoquadrina dehiscens* closely corresponds to the Duntroonian/Waitakian Stage boundary in New Zealand (D. G. Jenkins, 1971; Ludbrook, 1967; Ludbrook and Lindsay, 1969). Datings of 20.8 m.y. for the Whaingaroan-Duntroonian interval and 19.4 ± 1.2 m.y. for the Waitakian (Funnel, 1964; Page and McDougall, 1970) accord well with this correlation (Figure 3).

McGowran *et al.* (1970) indicate that in the Otway Basin the evolutionary appearance of *Globoquadrina dehiscens* occurs after the disappearance of *Globorotalia* (*Turborotalia*) *kugleri* Bolli, but that this order is apparently reversed in the Gippsland Basin (zonation of D. Taylor) and in New Zealand. Berggren (1969) and Blow (1969) indicate that *G.* (*T.*) *kugleri* has a short range from within T.S. zone N3 to the end of T.S. zone N4. Scott (1968), however, states that this species also occurs at the type locality of the *Catapsydrax dissimilis* zone (Bolli, 1957) in Trinidad (i.e. T.S. zone N5). It seems probable that the occurrences of *G.* (*T.*) *kugleri* in the Gippsland Basin and New Zealand correspond to this later part of its range. *G.* (*T.*) *kugleri* occurs in the Otaian stage in New Zealand (D. G. Jenkins, 1967, 1971; Scott, 1968a, 1970), and Scott (1968, 1968a, 1969) has shown that a population of *Globigerinoides altiaperturus* Bolli from this stage closely compares with those from the *Catapsydrax dissimilis* zone in Trinidad.

In New Zealand rare morphotypes approaching *Globigerinoides sicanus* de Stefani (= *Globigerinoides bisphericus* Todd) first appear in the Hutchinsonian or Awamoan and radiometric work indicates that this event occurred about 16.8 ± 0.4 m.y. ago (Bandy *et al.*, 1970). McGowran *et al.* (1970) regarded the appearance of *G. sicanus* as being an important stratigraphic marker. Wade (1964, 1966) and Scott (1969), however, indicated that in Australasia the development of the *Globigerinoides trilobus-sicanus* lineage is different from that in the tropics; the value of *G. sicanus* as a tie between these regions thus seems doubtful. Scott (*in* Bandy *et al.*, 1970) considered that the taxonomic distinction between *G. trilobus* and *G. sicanus* is imprecise and the author concurs with this opinion.

The interval from the later part of T.S. zone N9 to the early part of T.S. zone N12 is not subdivided in local zonal schemes. The zones of Banner and Blow (1965) and Blow (1969) younger than T.S. zone N13 have not apparently been recognized in Australia.

The late Middle Miocene to Pleistocene in Australia is divided into local stages which are dated principally by molluscan assemblages (Wilkins, 1953; Ludbrook, 1963, 1967, 1969). Two foraminiferal "zonules" are recognized within this time interval (McGowran *et al.*, 1970).

These observations are taken into consideration in a correlation chart for the rocks which contain the decapod remains described in this work (Figure 4) and in illustrating the time ranges of known decapod fossils from Australia (Figure 19).

Two factors which are important in controlling the distribution of decapods and of particular relevance to the present study are water-temperature and water depth. Water-temperature appears to be the most obvious influence controlling the broad provincial distribution of modern, marine, shallow-water decapods. Warm tropical seas are characterized by rich diverse assemblages while cooler waters at high latitudes contain less diverse assemblages (Ekman, 1953). George (1969) suggested that the diversity of tropical assemblages reflected the variety of different environments found in the equatorial region. This is certainly an over-simplification as similar environments (sandy littoral zone for example) in tropical and temperate areas support faunas of quite different diversity. However, while water-temperature may control the limits of distribution of taxa, the abundance of individuals of any given species seems greatly dependent on factors largely or completely unrelated to temperature, such as the amount of available food, of weed or crevices in which to hide, or the mechanical properties of the substrate with respect to burrowing.

Vaughan (1940) recognized five marine zones which can be defined by seasonal temperature fluctuations within certain limits: polar, -1.9 to 5°C; temperate, 10 to 25°C; subtropical 15 to 30°C; and tropical, 25 to 31°C. With the exception of the polar zone, these climatic divisions are all represented in the Australasian region where they are clearly characterized by the different decapod assemblages which they contain (for distribution of taxa see Griffin, 1966; Dell, 1968, 1968a; Griffin and Yaldwyn, 1968; and George, 1969; for hydrological data concerning New Zealand waters, see Garner, 1961). The species most typical of a particular zone are presumably the very shallow-water forms as these are adapted to the near-surface temperature. The vertical temperature gradient which exists everywhere in the sea except perhaps the polar regions enables temperate and even subpolar organisms to live at depth in areas with a much warmer surface climate (Ekman, 1953).

If the distribution of modern decapod taxa is dependent on temperature, then presumably water-temperature was an important influence controlling the provincial distribution of decapods in the past. Conversely it follows that fossil Crustacea can be used to make inferences about past water-temperatures. Benthonic shelf decapods at least seem a rather slowly evolving group and forms dating back to the mid-Tertiary commonly resemble modern species. It seems likely that their similar appearance reflects their adaptation to environments comparable to those which the modern species inhabit. Thus the Decapoda are potentially useful for recognizing equivalents of present temperature zones from the mid-Tertiary onwards. Present and past temperature zones are described in this work by the usage of Vaughan's (1940) terminology; for past temperature zones the implied limits of water-temperature are only approximate.

Dell (1968a) showed that the crabs occurring in the New Zealand region can be grouped in five depth zones: the intertidal zone, from 0 to 50 fathoms (0-91 m), 0 to 100 fathoms (0-183 m), below 100 fathoms, and occurring on the shelf and extending deeper than 100 fathoms. The lower depth limit of any species was 435 fathoms (786 m) but a number of forms ranged down to 300-400 fathoms (550-730 m). Depth data for species from other parts of the world suggests a comparable zonation. It seems likely that ancient populations of decapods were also restricted in their depth range, and hence that fossil decapods may indicate past water depths. The same assumptions apply here as for their use in indicating past water-temperatures.

A variety of factors control the depth distribution of decapods. As already mentioned warm-water species are necessarily restricted to near-surface waters. Ability to withstand exposure is probably a major restriction for littoral species, while those of the turbulent surf zone must withstand strong currents and high turbidity. Seaweed growth to the depth of effective light penetration offers shelter for slow moving species. Bryozoal fields occurring on the outer part of the continental shelf, at least in the southern Australian area (Conolly and Von der Borch, 1967; Wass, Conolly and MacIntyre, 1970) may also form a kind of shelter. Wide areas of loose or soft sediment occur over much of the outer part of the continental shelf and bathial region and are probably the habitat of species which burrow for protection and the various spiny and long-legged forms known from these depths.

The different bottom environments recognized in the present study are summarized in Figure 5, which is modified after Ager (1963). It is notable that the bottom zones indicated on this diagram approximate the depth zones recognized by Dell (1968a) in his study of the New Zealand decapod fauna.

The different localities at which the decapod remains described in the present work have been found are described below. The different finds are grouped with respect to their age and the sedimentary basins in which they are sited.

Middle Oligocene

Otway Basin - Gambier Embayment

Vicinity of Mount Gambier

A rich decapod faunule has been collected from the lower part of the Gambier Limestone of the Gambier Embayment in building stone quarries 12 km west of Mount Gambier, on sections 26, 28, 29, 30, 144 and 145, Hundred of Blanche, South Australia (Figure 6). At this occurrence the Gambier Limestone is folded into a gentle anticline, the axial trace of which trends N.W.-S.E. The quarrying operations have been carried out along the axis of this anticline. A representative stratigraphic sequence for this locality was measured on section 28 in a small quarry about 600 m W.S.W. of the Marte railway siding (Figure 7). The sequence consists almost entirely of bryozoal grainstones. The rock contains only an extremely small amount of terrigenous (acid insoluble) material (on average 1×10^{-3} parts by weight clay and 1×10^{-4} parts fine angular quartz, feldspar and mica sand). Evidently deposition occurred in extremely clean water. The lower 6.7 m of the sequence, the part quarried for building stone, is remarkably uniform and is composed of a criss-cross mesh of nearly flat-lying fragments of vinculariiform bryozoa (4-10 mm long branches 0.5-1 mm in diameter) and less abundant fragments of adeoniform bryozoa (terminology after Wass, Conolly and MacIntyre, 1970). The fragments are cemented at points of contact by finely crystalline calcite. Only the nearly flat orientation of the bryozoal fragments and slight changes in average grain size indicate bedding. Bowl shaped or branching colonies of the large bryozoan Cellepora gambierensis Busk occur in life position. Large irregular echinoids (about 10 cm in diameter) occur complete or partly broken; the corona of these specimens is little more than 1 mm thick. Rarely, complete individuals of a large starfish belonging to the genus Pentagonaster Gray (span across arms about 26 cm) are found, the unjointed ossicles positioned just as in the living animal. These occurrences give evidence of a low energy environment of deposition.

Coarse grained (grains 1 mm by 4-10 mm) to very coarse grained (grains 1-15 mm by 10-15 mm up to plates 1.5 mm by 40-80 mm) beds occur between 7 and 9 m above the base of the section. The finer grained beds in this interval are again composed predominantly of fragmented vinculariiform bryozoa and less abundant adeoniform bryozoa and seem to have been deposited during times of gentle current activity.

The coarser grained beds in the interval just noted show well developed crossbedding. Fragments of vinculariiform bryozoa still predominate but adeoniform, reteporiform and lunulitiform types are well represented. Numerous other shelly fossils are present: disarticulated bivalve shells, complete brachiopods and isolated valves of brachiopods, irregular echinoids and their broken remains, and isolated plates and spines of cidaroid echinoids. These beds appear to be lag deposits from which fines have been winnowed by strong currents.

Fine vinculariiform bryozoa predominate in the thick bedded calcarenites at the top of the sequence. This interval was probably deposited in a low energy régime.

The decapods from this sequence are mainly epifaunal species. An anomuran, Munida martensis sp. nov., occurs rarely in the lower 5 m of the section. The crab Psudocarcinus parvus sp. nov. is reasonably common (6 or 8 specimens) in the interval from 5 to 7.5 m above the base of the section. The richest assemblage of species (Table 3) is from the interval between 7.5 and 9 m. For convenience in later discussion this part of the section is hereafter termed the crab-bed. Brachyura predominate in this assemblage. The decapod remains are commonest in the very coarse grained beds of this interval, but specimens also occur in the finer grained interbeds. Elements of this rich fauna (Carcinoplax woodsi sp. nov., Pseudocarcinus parvus and Tutankhamen hieracodes sp. nov.) occur much less abundantly in the part of the sequence above the disconformity at 9 m.

The decapod remains mostly consist of isolated carapaces or claws. As the pleural sutures of the carapaces are never found intact it seems likely that most of the remains are of moults. Most specimens are broken. This damage is almost certainly due to current transportation. However, as the specimens are very fragile it seems likely that they could not have been moved more than a few hundreds of metres without disintegrating. Thus the fossils probably represent populations which lived near or at the site of deposition. Decapod remains are considerably more numerous in the crab-bed than is usual in other marine Tertiary sediments in southern Australia. The abundance of remains in this interval is possibly due to a low rate of sedimentation. Slow sedimentation would not mask the accumulation of relatively rare remains. Current sorting probably concentrated the specimens in the very coarse grained beds.

A size frequency histogram based on measurements of the width of the carapace of 75 specimens of <u>Carcinoplax</u> <u>woodsi</u> from exposures of the crab-bed throughout the locality under consideration is presented in Figure 8. This graph is distinctly polymodal and shows perhaps seven maxima. It seems likely that the maxima correspond to successive moult stages or instars of the crab. The enveloping curve generated from this data is essentially a bell-shaped distribution, but is skewed towards smaller individuals as in the curve which Boucot (1953) predicted for a "life assemblage". Boucot considered that the symmetrical normal distribution was characteristic of assemblages which had been affected by sorting processes. A considerable degree of sorting has apparently occurred in the present instance, probably as a result of movement by currents.

The depth distribution of the modern species which the present decapod fossils most closely resemble is shown in Figure 9. The greatest amount of overlap in the depth range of these modern species is between about 90 and 350 m. It seems likely that this is the approximate depth range in which the fossil faunule lived. As already indicated the decapod fossils occur in bryozoal grainstones in which fragments of vinculariiform bryozoa predominate and adeoniform zoarial varieties occur commonly. In the present day seas of southern Australia, living bryozoa abound at depths of 90 to 220 m and forms with adeoniform and vinculariiform zoaria occur commonly at depths greater than 180 m (Wass, Conolly and MacIntyre, 1970).

The sediments of the present section contain only sparse assemblages of planktonic foraminifera. This is probably due to current winnowing of the sediment. The foraminifera identified in four selected samples (mainly by McGowran, 1970a) are indicated in Figure 10. McGowran indicates that the differences in the assemblages in the samples are probably not significant as they are limited to rare or very rare forms. The planktonic forms actually present in the samples suggest possible correspondence with either the *Globigerina labiacrassata* zone or the *Globigerina euapertura* zone of Ludbrook and Lindsay (1969). The presence of "*Globorotalia*" *munda* D. G. Jenkins is some evidence for the *Globigerina labiacrassata* zone, and the occurrence of *Globigerina juvenilis* Bolli is suggestive of the *Globigerina euapertura* zone. With reference to McGowran (1971a), assignment to the *Globigerina labiacrassata* zone seems more probable.

The association of *Globigerina euapertura* D. G. Jenkins, *Globigerina officinalis* Subbotina, *Globigerina ampliapertura* Bolli, *Globigerina* aff.

senilis Bandy, Globigerina prasaepis Blow, "Globorotalia" munda, Globorotalia (Turborotalia) opima Bolli s.s., and Globigerinita unicava unicava (Bolli, Loeblich and Tappan), along with the absence of Globigerina angiporoides Hornibrook on the one hand and Globigerina angulisuturalis Bolli on the other, is suggestive of an approximate correlation with T.S. zone P19/20. However negative evidence must be suspect in the case of these sparse faunas and the dating given is tentative. In general terms, foraminiferal evidence thus suggests an approximately Middle Oligocene age.

Mr. S. G. Shafik kindly examined nannoplankton assemblages from several of the same samples and, on rather limited evidence, also suggested a Middle Oligocene age (late Rupelian).

Upper Oligocene to early Lower Miocene

Otway Basin - eastern portion

Vicinity of Torquay

Raggatt and Crespin (1952, 1955) described the geology of Tertiary exposures in the sea-cliffs between Torquay and Eastern View, Victoria. Their work has been revised by O. P. Singleton (1967). Opposite Bird Rock, which is situated about 2.4 km S.W. of Torquay, the lower 9.5 m of the cliff are formed by the Jan Juc Marl, a richly fossiliferous marl. The Puebla Clay, which rests conformably on the Jan Juc Marl and consists of siltstone, clayey siltstone and thin beds of concretionary limestone, forms the upper

27 m or so of the cliff. An additional 8.5 m of the Jan Juc Marl is exposed at the centre of an anticline situated about .6 km S.W. of Bird Rock, and a further 21 m of this formation is known in a bore near this site.

F. A. Singleton (1941) defined the Janjukian Stage as being represented by the marine rocks of this section. However, Raggatt and Crespin (1952, 1955) considered that the upper part of the Puebla Clay was Balcombian and restricted the Janjukian Stage to the "stratigraphic interval represented by the Jan Juc Marl". The age relationships which recent authors have suggested for the sequence in the vicinity of Bird Rock are summarized in Figure 11. The exposed part of the Jan Juc Marl at Torquay is apparently either late Upper Oligocene or early Lower Miocene in age. The Puebla Clay is apparently Lower Miocene.

Fingers of claws of *Ctenocheles fragilis* sp. nov. occur in the cliff near Bird Rock. Specimens have come from about 4 m below the top of the Jan Juc Marl and apparently from the uppermost bed of this unit. The author has collected specimens in concretionary structures within a limestone bed occurring in a large fallen block of the Puebla Clay. The concretionary structures apparently developed around the infilling of animal burrows. It seems probable that these burrows were excavated and occupied by *Ctenocheles* (see pp.130-131).

A fossil crab cf. *Portunites* Bell occurs in the Jan Juc Marl in the cliffs opposite Bird Rock (M. F. Glaessner, pers. comm.). Another crab occurring in the same formation at this locality belongs to the Carcinoplacinae.

Bass Basin - southern margin

Vicinity of Wynyard

A single damaged specimen of the fossil crab *Ommatocarcinus corioensis* (Cresswell) (preserved mainly as an internal mould) is known from the Fossil Bluff Sandstone, at Fossil Bluff, near Wynyard in northwestern Tasmania. Quilty (1966) considered the basal part of this unit to be early Lower Miocene in age and within the *Globigerina woodi* zone of D. G. Jenkins (1960) or faunal unit 6 of Carter (1964). The exact interval in which the fossil occurred is not known and hence its age can only be given in general terms as probably early Lower Miocene. As such the specimen is the earliest record of *Ommatocarcinus* in Australia.

Middle Lower to early Middle Miocene

Otway Basin - Gambier Embayment

Vicinity of Mount Gambier

A small decapod assemblage is known from quarries in the Gambier Limestone on sections 601 and 606, Hundred of Blanche, 6.4 km south of Mount Gambier (Figure 6). The sequence exposed at this locality is illustrated in Figure 12. The species *Lyreidus tridentatus* de Haan and

Axius wadeae sp. nov. occur commonly in the bryozoal, foraminiferal calcarenite interval present at the base of the sequence. *Ovalipes denticulatus* sp. nov. has been found in the shelly limestone bed 1.8 m above the base of the sequence. *Paromala* cf. *pritchardi* sp. nov. also occurs at this locality but it is not known precisely from which part of the sequence; a specimen in a loose piece of rock was found about 7 m above the base of the section.

The calcarenite interval in which *L. tridentatus* and *A. wadeae* occur numerously is appreciably finer grained than the remainder of the section. Both of these species belong to families which have burrowing habits and their abundance in this relatively fine grained interval may be linked to the original suitability of the sediment for their burrowing activities.

Rich assemblages of planktonic foraminifera occur in the sediments at this site. McGowran (1970a) assigned these assemblages to the *Globigerina woodi woodi* zone of Ludbrook and Lindsay (1969) or the *Globigerina woodi connecta* zone of D. G. Jenkins (1967). In terms of the zonation of Blow (1970) they probably are in the vicinity of the lower part of T.S. zone N6, or middle Lower Miocene.

Murray Basin - western portion

Downcutting by the River Murray in the western part of the Murray Basin has exposed a nearly flat-lying or very gently folded Oligocene to late

Lower Miocene sequence of richly fossiliferous limestones, clays and marls (Ludbrook, 1961, 1969; here Figure 4). The Ettrick Formation, the oldest unit exposed in this sequence, is regarded as extending in age from the Janjukian to possibly the early Longfordian (Ludbrook, 1967, 1969; Ludbrook and Lindsay, 1969). The Janjukian begins approximately in the Middle Oligocene and the Longfordian starts in the early Lower Miocene (McGowran *et al.*, 1970; here Figure 3). The Ettrick Formation is succeeded by the Murray Group. Three units belonging to the Murray Group are exposed, the Mannum Formation, Finniss Clay and Morgan Limestone. The Murray Group is entirely marine in origin and seems to have been deposited mainly in the inner-neritic zone. The rocks of the Murray Group show a general paucity of pelagic foraminifera, suggesting that a basement high (Padthaway Horst) on the seaward side of the basin restricted circulation at the time of their deposition (Ludbrook, 1961). Different intervals in the river cliff exposures of the Murray Group contain numerous decapod remains; these occurrences are described below.

Nildottie - Swan Reach area

Abundant remains of decapods occur in exposures of the Mannum Formation in the river cliffs of the area of Nildottie and Swan Reach, South Australia (Figure 13). The Murray Group sediments exposed in this area are nearly flat-lying. The Mannum Formation forms the lower 29 m or so of the cliffs and is overlain conformably by an 8-14 m thick interval of the Morgan Limestone. The sequence exposed near Greenways Landing, about 3 km north of Nildottie, is summarized in the stratigraphic column presented in Figure 14.

The lower 24 m of the Mannum Formation in this vicinity consists of medium to thick bedded (.3-1.5 m thick beds), richly fossiliferous calcarenites (skeletal grainstones). The grains composing these calcarenites consist mainly of curved plates and tubules of fragmented bryozoa, but also include calcite rhombs from disintegrated echinoid tests, broken foraminifera, and slivers of shell from juvenile molluscs. Typically the rock contains numerous subvertical burrows filled with finer argillaceous calcarenite. Irregular cavities and "potholes" with a filling of coarse skeletal debris are also present. On weathering this rock forms a "raggy limestone" (Tate, 1885:p.39)which contains numerous cavities. Decapod remains (Anomura and Brachyura, Figure 14) occur numerously in this raggy limestone facies between about 6 and 21 m above the normal water level of the Murray River (the normal river level is used here as an arbitrary reference mark and is designated N.R.L. in the rest of this work). Up to about 6 m above N.R.L. the rocks have been leached by river water during times of flood and decapod remains are difficult to find. Above the 6 m level the remains tend to weather free of the enclosing sediment.

The decapod fossils consist mostly of isolated carapaces or claws and are usually broken. The damage to the remains is probably due to movement by currents. The pleural sutures of carapaces are either intact or broken, indicating that dead animals and probably moults are represented.

The top part of a number of beds in the raggy limestone interval is penetrated by numerous burrows and is more strongly lithified than the rest of the sequence. Subrounded fragments eroded from the top of such beds sometimes occur at the base of the immediately overlying stratum. In one other instance the top 30 cm of a bed is intensively burrowed and bioturbated. These more strongly lithified or burrowed surfaces and "hard-grounds" are regarded as marking significant diastems. They evidently represent appreciable time breaks as differences occur in the decapod faunas above and below the surfaces.

Figure 15 shows the depth ranges inhabited by the living species which the decapod fossils from the raggy limestone facies most clearly resemble. There is considerable overlap in the depth ranges from the intertidal down to about 110 m and it seems likely that this was the depth range which the populations represented by the fossils inhabited. The high content of bryozoal detritus in the raggy limestone facies suggests that deposition occurred in the lower part of the depth range suggested by the decapods (see above p.23). The reasonably abundant occurrence of planktonic foraminifera in marly beds within the raggy limestone interval is consistent with this inference. Mollusca occur very frequently in the facies and amongst the species which reach dimensions of more than several centimetres thin shelled forms are common (Chlamys, "Pecten"). Similar molluscan assemblages occur below the sublittoral zone (see Figure 5) on the continental shelf of southern Australia today (data: Cotton, 1961). Thus it seems likely that the raggy limestone facies represents a shelf-environment and was deposited in water perhaps 50-110 m deep.

Periodic deposition, animal activity, and processes of lithification, solution and erosion seem to have been involved in producing the raggy limestone facies (Figure 16). If the environment of deposition of the raggy limestone was at an appreciable depth of water as suggested above, the lithification, solution and erosion which occurred at the time of formation of the facies presumably resulted from submarine processes: the intraformational lithification seems to be mainly due to the envelopment and cementation of grains by finely crystalline calcite. Usually the formation of this calcite has only weakly indurated the sediment. Patchy recrystallization throughout the facies probably resulted from postdepositional processes.

Submarine lithification of Recent deep-sea carbonate oozes has been demonstrated in the Atlantic Ocean, Red Sea and elsewhere (Fischer and Garrison, 1967). The lithification is thought to occur where sedimentation is virtually absent over long periods of time. The cementing agents involved are either aragonite or high-magnesium calcite. Comparable processes of lithification occur in shallow or relatively shallow marine environments in the Bahamas, off Barbados, and in the Mediterranean

(Taft et al., 1968; Macintyre, Mountjoy and D'Anglejan, 1968; Alexandersson, 1969). In the Persian Gulf the process of submarine cementation of carbonate sediments seems to be operating over wide areas at water-depths down to 30 m (Shinn, 1969; de Groot, 1969). Aragonite and high-Mg calcite are again the cementing agents. Shinn found that light aragonitic cementation of sediment around modern artefacts may occur in as short a time as 20 years. However, he deduced that the principal factors necessary for cementation are a relatively low rate of sedimentation, absence of disturbance, and a high initial sediment permeability. The source of the cementing material was inferred to be sea water supersaturated in carbonates. De Groot (1969) found that water samples from uncemented sediment between cemented layers contained hydrogen sulphide. This water dissolved carbonates. De Groot supposed that both carbon dioxide and hydrogen sulphide are released from decaying organic matter present in the sediment and that they act to inhibit further precipitation of carbonate and cementation.

By analogy with these modern examples of submarine lithification it seems likely that the raggy limestone facies of the Mannum Formation formed in a régime of slow deposition. By means of foraminifera the section measured near Nildottie can be approximately referenced to the chronostratigraphic scheme presented in Figure 3; this correlation (detailed below, p.34) is shown in Figure 14. The part of the section between 7 and 36 m above N.R.L. may represent a time span of about 3 m.y. The mean sedimentation rate indicated by this data is approximately 1 cm/1000 years.

This is an exceptionally low rate and compares with values of 1-1.5 cm/ 1000 years which Peterson et al. (1970) give for rates of Eocene and later Tertiary carbonate sedimentation in the central part of the North Atlantic Ocean. It seems possible that acidic solutions formed in the manner suggested by de Groot (1969) dissolved the numerous cavities occurring in the raggy limestone facies. Most of the cavities are elongate in shape and probably formed along pre-existing animal burrows.

The poorly consolidated calcarenites which form the top 5 m of the Mannum Formation at Nildottie (Figure 14) do not show evidence of the complex intradepositional processes which the raggy limestone facies underwent. Alternating beds of recrystallized limestone and soft calcarenite occur at the base of the Morgan Limestone. As one of the more weakly recrystallized limestone beds has cut and fill structures developed on its upper surface, the recrystallization process was evidently intraformational. The remainder of the interval of the Morgan Limestone present is composed of calcarenite and moderately well indurated limestone beds. No decapod remains have been found in the top part of the Mannum Formation and the Morgan Limestone at Nildottie. Possibly most of this interval was deposited at a more rapid rate than the preceding raggy limestone facies.

The decapod assemblages present in the Mannum Formation in the Nildottie-Swan Reach area change significantly in different intervals of the formation. These changes are documented in Figure 14. The most pronounced of these changes occur at the diastems which have been described above. However, some of the changes appear to be progressive, particularly in the interval from about 12 to 16 m above N.R.L. *Ctenocheles sclephros* sp. nov. first appears and is common in the marl bands between 11 and 12 m. As this is almost certainly a burrowing form its entry is probably related to the originally softer nature of the marl compared to the earlier calcarenites.

The foraminifera of chronostratigraphic importance identified in the present section (partly by Lindsay (1970) and partly by the author) are indicated in Figure 14. The interval from 7 to 8.5 m above N.R.L. contains the benthonic species *Operculina victoriensis* Chapman and Parr and *Sherbornina cuneimarginata* Wade, and the planktonic forms *Globigerina woodi* s.s. and *Globigerina woodi connecta* D. G. Jenkins, and rare (one specimen per sample) *Globigerinoides altiaperturus*. This assemblage is consistent with the later *Globigerina woodi s.s.* zone of Ludbrook and Lindsay (1969), or the *Globigerina woodi connecta* zone of D. G. Jenkins (1971). The specimens of *Globigerinoides altiaperturus* present have the primary aperture about half as high as wide. Specimens with approximately the same height/width ratio for the primary aperture are well represented or modal in populations of *Globigerinoides altiaperturus* from the Lower Hutchinsonian-Otaian of New Zealand or the *Catapsydrax dissimilis* zone (Bolli, 1957; = T.S. zone N5) in Trinidad (Scott, 1968, 1968a, 1969).

Globigerinoides trilobus immaturus Le Roy appears at 11.5 m above

N.R.L. in the Nildottie section; it enters in the early Hutchinsonian in New Zealand and at about the boundary of the *Catapsydrax dissimilis* and *Catapsydrax stainforthi* zones (Bolli, 1957) in Trinidad (Scott, 1968b, 1969, 1970, 1970a). The first appearance of *Globigerinoides trilobus* (Reuss) *s.s.* at 13 m above N.R.L. can be equated to the beginning of the *Globigerinoides trilobus s.s.* zone of Ludbrook and Lindsay (1969). Rare specimens (1 to 3 individuals per sample) referable to *Globigerinoides sicanus* occur in the interval between about 16 and 18 m above N.R.L. The rare appearance of *Globigerinoides sicanus* in the Hutchinsonian-Awamoan of New Zealand about 16.8 m.y. ago (Bandy *et al.*, 1970) has already been discussed above (p.14). *Globigerina woodi connecta* disappears from the present section at about 18.5 m. above N.R.L. The same form disappears in New Zealand towards the end of the Awamoan (D. G. Jenkins, 1965, 1967). *Globigerinoides sicanus* occurs commonly in the Nildottie section at 20 m above N.R.L. This level corresponds to the start of the *Globigerinoides sicanus* zone of Ludbrook and Lindsay (1969). D. G. Jenkins (1967, 1971) indicated that *Globigerinoides sicanus* becomes common in the Altonian stage of New Zealand. The benthonic foraminifera species *Lepidocyclina howchini* Chapman and Crespin occurs in a narrow interval between 5.5 and 7 m above the base of the Morgan Limestone. This species seems to have a very restricted range in the western part of the Murray Basin and is a useful marker. Ludbrook (1961, 1963) has previously reported its occurrence in the Morgan Limestone at Caloote (8 km S.W. of Mannum), Mannum, Blanchetown, and in a bore near Loxton, South Australia.

The appearance of *Lepidocyclina* in the Murray Basin probably approximates closely to the start of the Batesfordian Stage (equated by Carter (1959) to his faunal unit 9) in the Otway Basin (Wade, 1964). In the Nildottie section early forms of *Praeorbulina glomerosa curva* Blow are present immediately above the *Lepidocyclina* interval. The appearance of *Praeorbulina* marks the start of the *P. glomerosa curva* zone of Ludbrook and Lindsay (1969). In New Zealand *Praeorbulina* appears at the start of the Clifdenian Stage (D. G. Jenkins, 1967, 1971). Thus the start of the Batesfordian Stage approximately corresponds to the beginning of the New Zealand Clifdenian. According to Berggren (1969) and Blow (1969) *Praeorbulina glomerosa curva* appears early in T.S. zone N8. This zone possibly began about 15 m.y. ago (Figure 3).

The correlations just advanced enable the Nildottie section to be referenced to the oxygen isotope palaeotemperature data which Dorman and Gill (1959) and Dorman (1966, 1968) have given for the Tertiary of south-eastern Australia and the similar data which Devereux (1967, 1968) presented for the New Zealand Tertiary (Figure 14). The relevant data given by these authors is reinterpreted here in the light of new stratigraphic information available for Australia (numerous authors) and New Zealand (work of Scott, 1966, 1968b, 1969a, 1970a). Only data for which the stratigraphic control seems to be good has been used. The New Zealand data considered was limited to that which Devereux used to construct his palaeotemperature curve. All determinations were normalized to the latitude of Nildottie (approximately 35°S) by adding a correction factor of .7°C for each 1° of latitude that the site of a determination was to the south of Nildottie (correction averaged to nearest 1°C). It can be seen from Figure 14 that if the original palaeotemperature values are thus corrected, the higher Australian results concord excellently with the New Zealand determinations for the same approximate time interval. The Australian data is mainly for bivalves and the low values are possibly from the remains of animals which lived in the deeper parts of the depositional basins in which they occur. The New Zealand data is mainly for planktonic organisms (foraminifera). The palaeotemperature trend drawn through the data places reliance on the lowest New Zealand values and the means of the higher Australian determinations.

The method of determining palaeotemperatures from measurements of the oxygen isotope composition of carbonate fossils is reviewed by Garlick (1969). The hypothesis that the oxygen isotope composition of such fossils could be used to provide realistic estimates of past palaeotemperatures has been championed by Emiliani (1966) and others; this hypothesis is lent support by detailed palaeontological studies (for example Lidz, 1966). Shackleton (1967), however, considered that oxygen isotope fluctuations in shell materials were due largely to variations in the isotopic composition of sea water caused by changes in the extent of glaciation. Nevertheless it seems probable that if oxygen isotope studies do not provide realistic palaeotemperatures, the apparent temperature trends suggested by this data correspond closely to actual climatic changes experienced by the earth and related changes in the extent of glaciation.

The apparent disappearance of *Callianassa bulwara* sp. nov., *Callianassa* cf. *aequimana* Baker, *Ebalia nildottiensis* sp. nov., *Ebalia sturti* sp. nov., *Maja robinsoni* sp. nov., *Leptomithrax elegans* sp. nov., and *Naxia* sp. just before or at the diastem at 9 m above N.R.L. in the Nildottie section can be tentatively correlated to a falling trend in palaeotemperature. The reappearance of most of these species between about 12 and 14 m above N.R.L., and the appearance of *Ebalia tatei* sp. nov. and the short ranging *Schizophroida tertiaria* sp. nov. in this interval apparently correlates to a rising trend in palaeotemperature. *Maja robinsoni* is a fossil member of a modern, tropical or subtropical species-group and probably was itself a warm-water species; this inference concords with the observations made above. *Ebalia sturti* and *Schizophroida tertiaria* both resemble modern subtropical forms. Of the five forms known to range through the interval between 9 and 12 m above N.R.L. four, *Paguristes brevirostris antiqua* subsp. nov., *Ovalipes costatus* sp. nov., *Nectocarcinus granosus* sp. nov. and *Notomithrax angustifrons* sp. nov., resemble modern species which extend from the tropics to the temperate regions or are temperate.

The disappearance of *Calianassa bulwara*, *Calianassa* cf. *aequimana*, *Paguristes chondrochelus* sp. nov., *Paguristes brevirostris antiqua*, *Ebalia nildottiensis*, *Ovalipes costatus*, *Schizophroida tertiaria*, *Leptomithrax* *elegans* and *Naxia* sp. between about 13 and 17 m above N.R.L., and the sudden appearance of *Pagurus greenwayensis* sp. nov., *Pagurus murrayensis* sp. nov., *Calappilia australis* sp. nov., and *Ovalipes eamesi* sp. nov. in the stratum overlying the diastem surface at 14.5 m above N.R.L., correlate to a continuing upward trend in palaeotemperature. The increase in abundance of *Calappilia australis* up to 20 m above N.R.L. also follows this trend. It seems probable that *Calappilia* has been predominantly a tropical or subtropical genus throughout its history (p.180). One specimen of *Nucia rhomboidea* sp. nov., which is a fossil representative of a modern tropical species-group, was found in the lower part of the range of *Calappilia australis* at Big Bend Reserve, 8 km south of Swan Reach.

Mannum

An internal mould of a specimen of *Calappilia australis* has been collected from the Mannum Formation at Mannum, South Australia. No additional information is available concerning the stratigraphic position of this specimen.

Blanchetown

Several specimens of *Calappilia australis* have been collected from the lower part of the cliff on the western side of the River Murray near the old ferry crossing and new bridge at Blanchetown, South Australia. The sequence at this site is subhorizontal. The medium to thick bedded (.3-1 m thick beds) calcarenite which forms the lower 18 m of the cliff is equivalent to the upper part of the Mannum Formation (Dr. M. Wade, pers. comm.). The overlying highly fossiliferous limestone and calcarenite beds which form the next 12 m of the cliff have been placed in correlation with the Morgan Limestone (Ludbrook, 1957, 1958). The decapod remains were from 3 to 4.5 m above N.R.L. in the interval equivalent to the upper part of the Mannum Formation.

Morgan area

Numerous remains of decapods have been collected from exposures of the Morgan Limestone in the river cliffs in the vicinity of Morgan, South Australia. Most of these remains are from the type section of the Morgan Limestone. This exposure is situated on the eastern side of the River Murray on section C, Hundred of Cadell, about 6.4 km south of Morgan (Ludbrook, 1957, 1958, 1961, 1969). The Cadell Marl Lens occurs within the Morgan Limestone at this site (Figure 17). The basal part of the Morgan Limestone is below the level of the river in this section. At Blanchetown and Nildottie _Lepidocyclina howchini_ occurs in a narrow interval between about 5.5 and 7 m above the base of the Morgan Limestone. _Lepidocyclina_ has not been found in the present section.

Crespin (1944) reported the occurrence of the benthonic foraminifera species _Cycloclypeus victoriensis_ Crespin, 1941, in a rock sample from the present locality; her description of the lithology of this sample suggests that it was collected from the lower member of the Morgan Limestone.

Carter (1964) indicated that Lepidocyclina and Cycloclypeus occur together in the Otway Basin in his faunal unit 9.

The lower member of the formation contains a shelf fauna which includes Bryozoa, Mollusca and brachiopods. The presence of occasional calcareous algae indicates that deposition occurred within the photic zone (according to Ager (1963: p.28) the photic zone generally extends down to about 100 m depth in the open ocean).

The Cadell Marl Lens contains a rich fauna of Mollusca (Ludbrook, 1961, 1969). The planktonic foraminifera species Praeorbulina transitoria Blow occurs in the basal part of this unit; the appearance of this species marks the start of Carter's faunal unit 10. The benthonic foraminifera species Marginopora vertebralis Blainville occurs in the middle part of the Cadell Marl Lens and the upper member of the Morgan Limestone (Ludbrook, 1961). In modern seas Marginopora occurs most commonly in very shallow water down to a depth of about 27 m (Adams, 1965).

Ludbrook (1961) noted that the upper member of the Morgan Limestone contains only a sparse planktonic foraminiferal assemblage and suggested that it was regressive. Alternating beds of sandy limestone and calcareous sandstone occur in the top 1.8 m of the upper member. The fauna of this interval includes several varieties of Bryozoa, the brachiopod Magellania macleani Tate, the Mollusca Turritella Lamarck and Ostrea Linnaeus and Cirripedia. Small branching coralline algae occur quite commonly in life orientation. Cut and fill structures associated with these beds are filled with sandy limestone which contains innumerable randomly orientated shell moulds; originally this fill was a coquina. The moulds are mostly of thick-shelled bivalves. This part of the sequence may have been deposited in a subtidal environment. Johnson (1961) indicated that coralline algae mainly occur in the intertidal zone down to 30 m depth. Movement of tidal waters might have formed the cut and fill structures; the assemblage of thick-shelled bivalves in the fillings of these structures is suggestive of a high-energy, in-shore environment as the source of the fill material.

The presence of *Praeorbulina transitoria* in the upper member of the Morgan Limestone at the type section (Ludbrook, 1961) indicates a late Lower or early Middle Miocene age. Elsewhere in the Murray Basin, *Orbulina* d'Orbigny appears immediately above the upper boundary of the Morgan Limestone (Ludbrook, 1961). The appearance of *Orbulina* is equated to the start of the Middle Miocene by Berggren (1969) and Blow (1969).

The distribution of the decapod remains known from the present section is indicated in Figure 17. Thalassinids occur in most parts of the section; they are represented by more or less fragmentary remains of their claws. Thalassinids often occur numerously in the subtidal and intertidal regions today and their abundance in the top part of the upper member of the Morgan Limestone is consistent with the shallow depositional environment postulated for this interval. *Ommatocarcinus corioensis* is represented in the lower member of the Morgan Limestone by isolated fingers of claws; complete specimens of this crab occur commonly in the middle and upper part of the upper member of the Morgan Limestone. The complete specimens are usually preserved in a life-like attitude similar to the example figured in the frontispiece. Although the pleural sutures are invariably broken, the ventral parts of the exoskeleton are usually almost in their life position. It seems likely that these are remains of animals which died after burying themselves in the substrate. Sediment compaction and post-mortal decalcification may have led to the broken sutures. A specimen of Calappilia grandispinis (Etheridge and McCulloch) from 3/4 km north of the present section is probably from the upper part of the upper member of the Morgan Limestone.

A finger of the larger claw of Ctenocheles sclephros has been collected from the Morgan Limestone at North West Bend, about 2 km N.E. of Morgan.

River cliffs between Mannum and Wongulla

Fingers of the claws of Ctenocheles compressus sp. nov. have been collected by F. A. Cudmore from the "lower beds" of the River Murray cliffs between Mannum and Wongulla (8 km E.S.E. of Nildottie). In the Morgan area this species occurs in the Cadell Marl Lense and the upper member of the Morgan Limestone. An interval of the Morgan Limestone overlies the Finniss Clay and the Mannum Formation in the river cliffs in the area of present consideration. Probably Cudmore's material is from the Morgan Limestone.

Fragmentary fingers of the smaller claw of a *Ctenocheles* sp. indet. are known from Fromm's Landing, 29 km N.E. of Mannum. This material may be from either the Mannum Formation or the lower part of the Morgan Limestone.

Otway Basin

Vicinity of Hamilton

Examples of the carapace of both *Calappilia australis* and *Calappilia grandispinis* have been collected from the Muddy Creek Marl (Gill, 1957) at Muddy Creek, 6.4 km south of Hamilton, Victoria. The age of the Muddy Creek Marl at this locality is within the lower part of Carter's faunal unit 10.

Vicinity of Shelford

At the Amphitheatre on the Leigh River 6.4 km north of Shelford, Victoria, a section of about 30 m of Tertiary sediments is exposed. The lower 25 m of the section consists of yellow, white or grey silty clays and occasional thin beds of silty limestone. This lower sequence is disconformably overlain by some 5 m of white or ferruginous clay-rich gravelly sands which Bowler (1963) considered equivalent to the Moorabool Viaduct Sands of the Geelong area, Victoria. Foraminiferal assemblages from the upper part of the lower sequence are indicative of a Longfordian age, probably late in faunal unit 7 of Carter (1964). Possibly the lower sequence can be correlated with the Lower Maude Limestone (Bowler, 1963), the type section of which is near Maude, about 13 km east of the present locality. A single specimen of *Ommatocarcinus corioensis* has been found in a thin limestone bed in the upper part of the lower sequence.

Geelong - Maude area

The Dog Rocks Granite, which is apparently Devonian in age, forms an outcrop 2.5 by 1 km near Batesford, about 5.5 km N.W. of Geelong, Victoria (Foster, 1970). The southeastern part of this granite is overlain unconformably by the Batesford Limestone, a localized unit consisting of sandy limestone, bryozoal limestone and foraminiferal limestone (Bowler, 1963; Foster, 1970). The Batesford Limestone is in excess of 70 m thick in the vicinity of the Batesford Quarry. The upper part of the formation intergrades and intertongues with the overlying Fyansford Clay. Carter (1964) summarized the ranges of stratigraphically important foraminifera present in the sequence in the Batesford Quarry and indicated that his faunal units 8, 9, 10 and 11 are represented in this section. The upper part of the Batesford Limestone and the lowermost part of the Fyansford Clay contain *Lepidocyclina howchini* and *Cycloclypeus victoriensis*; this interval is the type section of the Batesfordian Stage of F. A. Singleton (1941). Carter (1959) equated his faunal unit 9 to the Batesfordian. Foster (1970) studied the echinoid fauna of the Batesford Limestone and concluded that the unit was deposited below the littoral zone in water 20-200 m deep.

A well preserved specimen of the carapace of *Calappilia australis* has been collected at the Batesford Quarry from the *Lepidocyclina-Cycloclypeus* interval at the top of the Batesford Limestone.

The Fyansford Clay, a marine unit consisting of calcareous clays and thin argillaceous limestone beds, occurs throughout the Geelong-Maude area and reaches a maximum known thickness of 91 m (Bowler, 1963). The older part of the unit (late in faunal unit 9 to faunal unit 11 of Carter (1964)) was apparently deposited in a deep neritic (shelf) environment and the younger part of the unit (within Carter's faunal unit 11) in a shallow neritic environment.

The crab Ommatocarcinus corioensis occurs in this formation at several places. Near the junction of Bruces Creek and the Barwon River in the vicinity of Murgheboluc it has been collected in situ in phosphatic concretions at the top of a thin limestone bed within the Fyansford Clay. Foraminiferal samples date this occurrence as near the boundary of Carter's faunal units 10 and 11. Several other specimens from Murgheboluc have been dated as being from within Carter's faunal unit 10. Ommatocarcinus corioensis has also been reported as occurring with Hinnites corioensis in a limestone bed within the Fyansford Clay at North Shore, Geelong (Spencer-Jones, 1967). Bowler (1963) dated this occurrence of the Fyansford Clay as being within Carter's faunal unit 11.

Melbourne area

The hand of the right cheliped and a fragment of the carapace of a large crab here identified as Pseudocarcinus cf. gigas (Lamarck) have been collected from an excavation in Buckley Street, West Essendon, Melbourne, Victoria (Gill and Baker, 1955). The sediments at this site are part of the Newport Formation (Kenley, 1967) and T. Darragh (pers. comm.) considers that they are probably of Balcombian age (late Lower to early Middle Miocene). Deposition may have occurred almost at low tide level (Gill and Baker, 1955).

Balcombe Bay

Specimens of the fossil crabs Calappilia grandispinis and Notomithrax angustifrons are known from Balcombe Bay, Victoria, apparently from the lower fossiliferous facies of the Balcombe Clay. This occurrence is dated at being within the early part of Carter's faunal unit 10 (Gostin, 1966).

Grices Creek

Remains of the chelae of a specimen of Ommatocarcinus corioensis have been found in the Balcombe Clay at the downstream section of Grices Creek, 4.8 km N.N.E. of Mornington, Victoria. The age of the Balcombe Clay at this locality is probably early Bairnsdalian (Carter's faunal unit 11) (Gostin, 1966).

Bass Basin - southern margin

Cape Grim

A marine Tertiary sequence of about 45 m of breccias, conglomerates and fossiliferous calcarenites exposed at Cape Grim, northwestern Tasmania, comprises the Cape Grim Beds (Banks, 1962; Quilty, 1969; Southerland and Corbett, 1967). Quilty (1966) suggested that these sediments are probably equivalent in age to faunal unit 7 or 8 of Carter (1958).

A specimen of the propodus of a right (larger) claw and other fragmentary remains of chelae known from this locality are identified as *Pseudocarcinus* cf. *parvus* in the present work. One of the specimens just referred to is a fragment broken from a claw which must have had the manus 50 or 55 mm long.

Middle Miocene

Otway Basin

Port Campbell area

The geology of the Port Campbell area, Victoria, has been described by Baker (1945, 1950, 1953) and summarized by Bock and Glenie (1965) and O. P. Singleton (1967). In the sea cliffs at Glenample Steps, 11 km east of Port Campbell, the Glenample Clay, which consists of yellow and blue-grey clays, is overlain conformably by the Port Campbell Limestone. The lower part of this latter unit consists of argillaceous limestone; purer limestones form the top part of the unit. An interval of up to 4.6 m of fossiliferous, calcareous clay present within the lower part of the Port Campbell Limestone at Rutledges Creek and the Amphitheatre, respectively 6 km and 4.4 km east of Port Campbell, comprises the Rutledges Creek Member. The total thickness of the Port Campbell Limestone is of the order of 90 to 120 m.

The Port Campbell Limestone is laterally continuous with the Portland Limestone Member (Glenie and Reed, 1960) of the Portland district, Victoria

(Bock and Glenie, 1965). Reed (1965) indicated on the basis of foraminifera that the Portland Limestone Member in the Heywood Bore may have been deposited in water 35 to 95 m deep. His calculation seems applicable to the Port Campbell Limestone.

Foraminiferal studies (Wade, 1964, 1966; Taylor, 1966, *in* O. P. Singleton, 1967, *in* McGowran *et al*., 1970; McGowran *et al*., 1970) indicate a Middle Miocene age for the Glenample Clay and Port Campbell Limestone (Figure 18). The probable relationship between these formations and the marine stages recognized in New Zealand is also shown on this figure.

Numerous specimens of *Ommatocarcinus corioensis* have been collected from the Port Campbell Limestone at the Port Campbell coastal section. The species occurs in the argillaceous limestone which forms the lower part of the unit and in the purer limestone of the upper part of the formation. Localities include the top of London Bridge, the cliff top at Point Hesse, Two Mile Beach (Hall, 1904), Gravel Point, the notch on the east side of the Amphitheatre, and the mouth of the Sherbrook River. Baker (1945) has also recorded the crab in the cliffs at Beacon Steps and opposite Sentinel Rock. Most specimens are preserved in a life-like attitude (frontispiece) and their mode of preservation is similar to the examples of the same species from the top part of the Morgan Limestone in the Murray Basin. Hall (1905) suggested that the animals died in "burrows". Seilacher (1953) and Ager (1963) distinguish between burrows (excavations, holes) made by organisms as dwelling structures (Seilacher's *Wohnbauten*) and structures made by organisms moving through sediments during the course of their normal life activities (Seilacher's *Fressbauten*). The attitude in which the crabs are preserved in the present instance indicates that their appendages have been supported by the sediment enclosing them. No traces of *dwelling structures* are however associated with the remains. It seems probable that the animals died after burying themselves below the surface of loose sediment. Members of the genus *Macrophthalmus* Desmarest (Ocypodidae) which parallel *Ommatocarcinus* in having greatly developed eyestalks, a low, markedly broadened carapace, and slender pereiopods with styliform dactyli, bury themselves in the sediment by side-ways digging motions and leave only the tips of the eyes projecting above the surface (Kesling, 1958; Barnes, 1967).

The burrowing activity of *Ommatocarcinus corioensis* could probably have only been carried out on a soft bottom and in this regard it is significant that the remains of this crab typically occur within relatively fine grained sediments (calcareous silts, calcilutites and fine calcarenites). Such sediments were deposited widely in the slowly regressing, southeastern Australian seas of the Middle Miocene.

Inland from Port Campbell, *Ommatocarcinus corioensis* occurs in exposures of the Port Campbell Limestone at the lime works at Curdies River and at a location 3.2 km west of Timboon.

Late Miocene

Otway Basin

Vicinity of Hamilton

At Grange Burn and Muddy Creek, near Hamilton, the Grange Burn Coquina (Gill, 1957) rests disconformably on Lower and Middle Miocene sediments. A volcanic tuff, a fossil soil and basalt flows overlie the Grange Burn Coquina (Gill, 1957, 1964). The molluscan fauna of the Grange Burn Coquina is considered to be of Kalimnan (Lower Pliocene) age (Gill, 1957). However pelagic foraminifera from the lower part of the formation are of Upper Miocene aspect (D. Taylor, pers. comm.).

The base of the Grange Burn Coquina is characterized by an accumulation of water-worn phosphatic nodules and phosphatized whalebone (Gill, 1957). The accumulation of nodules rests in the surface of disconformity between the earlier Miocene sediments and the younger formation and appears to be a lag deposit. The nodules are probably abraded concretions which have been eroded from the older sediments (see also Bowler, 1963). The term *nodule* is restricted here to discrete structures with a water-worn or abraded surface, while *concretion* is used to mean a chemical aggregation of material formed *in situ* within a parent matrix or sediment.

Several joints of appendages of *Ommatocarcinus corioensis* are known from the nodule accumulation at the base of the Grange Burn Coquina.

These specimens are partly enclosed in phosphatic material and are almost certainly remanié in origin. Two other specimens of the same crab have been found in phosphatic concretions within the Grange Burn Coquina 1 m above (normal?) creek level at Forsyths Bank, Grange Burn. This is probably a late Miocene occurrence.

Geelong - Shelford area

Middle Miocene and older Tertiary rocks occurring in the Geelong area are overlain disconformably by the Moorabool Viaduct Sands (Bowler, 1963). This unit occurs over a wide area and usually is relatively thin (its maximum known thickness is 24 m). It consists of argillaceous sands with minor calcareous and ferruginous phases; gravelly beds and concentrations of water rounded phosphatic nodules are present locally at the base. Molluscan faunas from the lower part of the formation are now regarded as being of probable late Upper Miocene age (T. Darragh, pers. comm.).

Between 10 and 20% of the phosphatic nodules which occur in local concentrations at the base of the unit enclose fossils of *Ommatocarcinus corioensis* and considerably less commonly, remains of *Ctenocheles fragilis* and *Ctenocheles sclephros*. Bowler's opinion that the nodules both with and without decapod remains, were derived from the Fyansford Clay and older sediments is accepted here in contradistinction to the suggestion of Coulson (1932) and Keble (1932) that the decapod containing nodules formed during a later transgression which predated the deposition of the Moorabool

Viaduct Sands. The free joints of appendages of O. corioensis which Keble noted in association with the nodules may have been derived from unphosphatized remains in soft beds of the Fyansford Clay, or possibly represent a Late Miocene occurrence.

In the immediate vicinity of Geelong, nodules containing O. corioensis occur at North Shore, Western Beach, Fyansford and Cowies Creek. Nodules which contain the same crab also occur at the Amphitheatre 6.4 km north of Shelford, at Murghebolue, Batesford and near Fenwick, and at the sea coast near Curlewis (the location of the lectotype). Nodules containing Ctenocheles have been found near Fenwick and near Curlewis.

Beaumaris - Melbourne

At Beaumaris, 21 km S.S.E. of the city centre of Melbourne, Victoria, the Black Rock Sandstone, which consists of ferruginous sandstone and marly sands, rests disconformably on marly sands comprising part of the Newport Formation (Gill, 1957; Kenley, 1967). In the vicinity of the Beaumaris boatsheds the lower 6 m of the Black Rock Sandstone contains marine fossils and is the type section of the Cheltenhamian Stage of F. A. Singleton (1941); this stratigraphic interval is considered as being probably of late Miocene age (Kenley, 1967; Simpson, 1970). A bed of phosphatic nodules occurs at the base of the Black Rock Sandstone at this locality. At the same site the Newport Formation is apparently of late Lower to early Middle Miocene age.

Phosphatized segments of the appendages of Ommatocarcinus corioensis and specimens of this crab in nodules occur plentifully in collections from Beaumaris. These remains are probably from the basal nodule bed of the Black Rock Sandstone and are most likely of remanié origin. Several more or less fragmentary remains preserved as the natural skeletal material in limey siltstone are of uncertain stratigraphic level; they may indicate a Cheltenhamian occurrence of O. corioensis or could also be remanié. Gill (1957) reported a specimen (N.M.V. P.15863) of "Persephona sp. nov." from this locality. This specimen is here identified as belonging to the genus Philyra Leach. Other examples of Philyra sp. known from this site occur both as phosphatized remanié specimens and as unaltered remains; the latter may represent an in situ occurrence in the lower part of the Black Rock Sandstone. The one known specimen of Ovalipes victoriensis sp. nov. was also collected at Beaumaris; its preservation is suggestive of an in situ occurrence in the Black Rock Sandstone.

Several specimens of Ommatocarcinus corioensis in phosphatic nodules are known from a Railway Cutting at South Yarra, near Melbourne. These nodules are remanié and probably came from a nodule bed similar to that at Beaumaris.

Pliocene

St. Vincent Basin

Vicinity of Port Willunga

An interval of up to 6 m of interbedded, grey, white or yellow quartzose sand, calcareous sandstone and arenaceous limestone is present in the sea-cliffs extending between Blanche Point and Snapper Point, in the vicinity of Port Willunga, South Australia (Reynolds, 1953). Crespin (1954) included this interval in the Hallett Cove Sandstone. It is generally agreed that the Hallett Cove Sandstone is equivalent to the Dry Creek Sands (Glaessner, 1961) of the Adelaide Plains Basin (Ward, 1966). This latter unit contains a distinctive assemblage of large warm-water molluscs (Yatalan fauna) and is considered late Pliocene in age (Ludbrook, 1963, 1967, 1969).

The exposure of the Hallett Cove Sandstone in the cliffs about 1.4 km S.W. of Port Willunga contains numerous isolated valves of _Ostrea arenicola_ Tate and complete, articulated specimens of _Pinna_ cf. _dolabrata_ Lamarck; the latter sometimes occur in life orientation. _Ostrea_ and _Pinna dolabrata_ occur in association just below low tide mark and down to a few metres depth off southern Australia today. The present exposure of the Hallett Cove Sandstone was possibly deposited in a similar depth range.

Decapod remains occur numerously in the Hallett Cove Sandstone at Port Willunga. The most common species is _Calianassa aequimana_ Baker. As many as 5 or 6 crushed individuals of this species can be counted in a square metre area under overhanging bedding planes at about the middle of the formation. Modern callianassids are specialized for a burrowing habit. The fossils in question almost certainly died in burrows, though no obvious sign of these structures now remains. Fingers and other more or less fragmentary remains of *Nectocarcinus amathitus* sp. nov. also occur very frequently. Probably many of these specimens were originally more complete, but leaching seems to remove all but the most heavily calcified parts of their exoskeleton. *Nectocarcinus* cf. *integrifrons* (Latreille) is represented by rare remains of its fingers and a species of *Ovalipes* is also present. Another moderately common brachyuran species is represented by heavily calcified fingers which reach a length of perhaps 100 mm. The taxonomic affinities of this form are uncertain, but it is described here as ?*Ozius macrochelus* sp. nov. The large fingers of its claws seem well adapted for crushing the shells of the large molluscs which occur commonly in the fauna with which it is associated. Extensive wear on the teeth of some specimens of the fingers indicates their function in crushing hard objects.

The assemblage of genera just noted is entirely characteristic of a subtidal environment (see Figure 5). *Nectocarcinus amathitus* and ?*Ozius macrochelus* also occur at Blanche Point and Snapper Point.

Kangaroo Island, Adelaide and Surveyors Point

Apart from the Port Willunga locality, ?*Ozius macrochelus* occurs in the St. Vincent Basin,in outcrops of the Hallett Cove Sandstone,on Kangaroo Island and at Adelaide and Surveyors Point, near Port Vincent.

Western part of Murray Basin

Morgan area and Devlins Pound

?*Ozius macrochelus* occurs in the Murray Basin in a Pliocene oyster bed on the east side of the Murray River, 6.4 km south of Morgan, and in the upper part of the cliffs at Devlins Pound, 13 km west of Overland Corner, South Australia. Ludbrook (1961) equated the oyster bed south of Morgan with the Norwest Bend Formation. This unit has been correlated with the Dry Creek Sands and is considered Upper Pliocene in age (Ludbrook, 1963, 1967). The stratigraphic position of the material from Devlins Pound is not known, but it is likely that the occurrence is also Pliocene.

Gippsland Basin

Bunga Creek

The palm of a cheliped of an *Ommatocarcinus* sp. has been found at Bunga Creek, 5.6 km E.N.E. of Lakes Entrance, Victoria. The specimen came from the upper shell bed in the exposure of the Jemmys Point Formation at the road cutting for the Princes Highway on the western side of Bunga Creek. The age of the bed which contained the palm is latest Kalimnan (Wilkins, 1963).

Chapter II

REVIEW OF AUSTRALIAN FOSSIL DECAPODA: THEIR HISTORY AND PALAEOCLIMATIC SIGNIFICANCE

Introduction

This chapter presents an outline of the decapod fossils and fossil decapod faunules known from Australia and is an attempt to collate available data concerning the history of the Decapoda in the Australian region. The evolutionary and geographic relationships of the fossil species are reviewed and an assessment is made of their possible palaeoclimatic significance.

In order to trace the history of the faunas represented by the fossils, the various fossils are discussed in the sequence of their geological age. Their occurrence is reviewed in the perspective of the time-stratigraphic framework outlined in Chapter I and additional chronostratigraphic data given chiefly by Casey (1964), Funnel (1964), Berggren (1969a) and McGowran et al. (1970): this relationship is indicated in Figure 19. The geographic distribution of the fossils is summarized in Figure 20.

Assessment of the palaeoclimatic significance of the fossil species is based on study of the geographic distribution of the modern species to which the fossils seem most closely related. Reference has already been made in Chapter I to the possible palaeoclimatic significance of fossil decapods. While such data may be derived from study of the distribution of single species, investigation of the biogeographic relationships of **fossil** assemblages seems more likely to give realistic information concerning past water-temperatures.

A factor controlling patterns of distribution of decapods is oceanic circulation. The larvae of decapods are pelagic and thus drift with currents. This is undoubtedly the reason for the wide distribution of many shallow-water (neritic) species. Alternatively larvae or juveniles may become entangled in masses of seaweed torn up in storms and rafted with the floating weed for long distances (see also George, 1969). The probability of a given taxon being weed-rafted at any particular time is small, but becomes increasingly likely over the geological time span of species (perhaps $5-15\times10^6$ years for benthonic decapods, Appendix 1). Bennett (1964) and Dell (1968) consider that a number of elements in the New Zealand decapod fauna crossed the Tasman from Australia. In several instances this is now substantiated by fossils.

The terms assemblage and faunule in reference to fossils, are used here in a rather broad sense to include collections of fossils of the same age (within the limits of geological accuracy) from several localities in a restricted geographical area (for example, the southern part of southeastern Australia). The earliest fossil decapods known from Australia are Cretaceous.

Cretaceous

Woods (1953, 1957) described and revised the Decapoda from the Cretaceous of the northeastern sector of Australia (Queensland). The eleven species discussed by him represent probably nine genera (Table 2) and occur in the Aptian or Albian of the northern part of the Great Artesian Basin. *Glyphea arborinsularis* Etheridge also occurs in the Aptian of the Maryborough Basin (its type locality). *Doratiopus* Woods is also known from the Albian-Cenomanian of Melville Island, and *Torynomma* Woods has been found in the Albian-lower Turonian of Bathurst Island (M. F. Glaessner, pers. comm.).

The form which Woods (1953) described as *Astacodes* sp. is probably a palinurid, but seems of rather doubtful generic identity as only imperfect remains of the abdomen are known. Of the other eight genera represented by the species Woods (1953, 1957) discussed, one is cosmopolitan (*Hoploparia* McCoy) and three others are also rather widely distributed (*Enoploclytia* McCoy, *Palaeastacus* Bell, *Glyphea* von Meyer), one occurs in eastern, central and western North America and northern Europe, as well as Australia (*Homolopsis* Bell), and three are apparently endemic to the Australian region (*Tillocheles* Woods, *Doratiopus*, *Torynomma*). The absence of genera which have a limited Tethyan distribution is possible evidence for cool (extra-tropical) conditions.

Paleocene

Apart from a few sporadic records, little is known about the decapod faunas which must have existed in the Australian region from the Paleocene to the early Oligocene. The total number of genera known from the Paleocene is three.

A thalassinid, *Protocallianassa australica* Glaessner occurs in the Kings Park Shale in the South Perth Bore, Perth Basin, Western Australia. From foraminiferal studies McGowran (1964, 1968) concluded a late Middle-early Upper Paleocene age for the Kings Park Shale. Elsewhere in the world *Protocallianassa* Beurlen occurs in the ? Lower and Upper Cretaceous of Europe and the Upper Cretaceous of North America (Glaessner, 1957, 1969).

Several thalassinids are also known from the Paleocene of the southern part of the Otway Basin, near Princetown, Victoria. *Callianassa bakeri* Glaessner (with which *Ctenocheles glaessneri* Via is synonymous) is represented by numerous remains of claws from the Pebble Point Formation, which is considered Middle Paleocene in age (McGowran, 1965). Cylindrical and bifurcating fossil burrows with which these claws are associated were suggested by Glaessner (1947) to have been made and inhabited by *Callianassa*. *Callianassa* sp. Glaessner, *Callianassa* cf. *lacunosa* Rathbun, and *Ctenocheles victor* Glaessner occur in the Rivernook Member of the Dilwyn Formation (O. P. Singleton, 1967), which rests conformably on the Pebble Point Formation. The Rivernook Member is presently regarded as being Upper Paleocene in age (McGowran, 1970).

While common along the present-day shores of northern and eastern Australia, thalassinids seem rather rare in most southern Australian waters and apparently do not extend further south than off northeastern Tasmania. Thus the abundance of thalassinids in the Paleocene might be interpreted as indicating water-temperatures no cooler than in the vicinity of Bass Strait today (12-16°C).

Eocene to Lower Oligocene

One specimen of a fossil crab, yet undescribed, is known from the Upper Eocene in the Ashmore Reef No. 1 oil bore, off northwestern Australia. This fossil is a primitive member of the Goneplacidae and probably represents a new genus.

In southeastern Australia there are apparently no exposures of marine Lower Eocene rocks and only marginal marine facies representing the Middle Eocene. No decapods of these ages are known.

Several decapod species have been discovered in the Upper Eocene of the eastern margin of the St. Vincent Basin, South Australia (M. F. Glaessner, pers. comm.). The carapace and claws of a species of a genus aff. *Titanocarcinus* A. Milne-Edwards occur quite commonly in the Tortachilla Limestone at Witton Bluff, Christies Beach. One specimen of the same species and a carapace of a dromiid crab are known from the Tortachilla Limestone at Maslins Beach. Rare claws of *Callianassa* Leach occur in the lower part of the Blanche Point Marl, which conformably overlies the Tortachilla Limestone. The Upper Eocene age of both formations has been confirmed by recent studies of foraminifera (Wade, 1964; Ludbrook and Lindsay, 1969; McGowran *et al.*, 1970).

The claw of a parastacid from the Lower Tertiary of Queensland has been figured by Hill, Playford and Woods (1970). This is the oldest recorded occurrence of this freshwater family.

Middle Oligocene

The rich Middle Oligocene decapod assemblage from the Gambier Limestone near Mount Gambier, gives an insight into the outer neritic or upper bathyal fauna of southern Australia at this time. The species present and the percentage of the assemblage which each constitutes (averaged for two well-collected sites) are shown in Table 3. The world distribution and time range of the genera represented, and the modern species which the individual fossils most closely resemble are shown in Table 4.

Only four of the genera, *Pagurus* Fabricius, *Munida* Leach, *Lyreidus* de Haan and *Carcinoplax* H. Milne-Edwards, are known elsewhere from Middle Oligocene and older strata. The species which represent *Pagurus*, *Munida* and *Lyreidus* in the Mount Gambier assemblage differ significantly from these older or contemporaneous fossils. *Carcinoplax praevictoriensis* sp. nov., however, shows a marked similarity to *Carcinoplax* ("*Pilumnoplax*") *urpiniana* (Via) from the Middle Eocene of Spain. Thus with the exception of the possibly Tethyan genus *Carcinoplax* the origin of the assemblage is unknown.

Four of the species in the faunule, *Paromola pritchardi* sp. nov., *Lyreidus tridentatus*, *Ovalipes primitivus* sp. nov., and *Pseudocarcinus parvus* are known either to have time ranges which extend later than the Oligocene, or to have fossil descendants in Australia.

All of the identified genera in the assemblage have surviving representatives, though not necessarily in the Australian region. *Tutankhamen* Rathbun is a Recent genus not reported in present Australian seas; it is known only from Japan, Hawaii and the West Indies. Its fossil occurrence reported here is suggestive of a wider distribution in the mid-Tertiary. The species of *Leptomithrax* Miers in the assemblage appears to belong to a species-group recognized here as the *Leptomithrax longimanus* group, and which is now restricted to the New Zealand region. Presumably this species-group crossed directly from Australia to New Zealand. Probably the West Wind Drift was the medium of this dispersal. The species of *Leptomithrax* which occur in Australia today all apparently belong to a section of the genera identified here as the *Leptomithrax tuberculatus* species-group. Competition from the ancestors of these may have caused the extinction of the *L. longimanus* group in Australia. *Carcinoplax woodsi*, the commonest species in the fossil faunule, appears to be the direct ancestor of *Carcinoplax* ("*Homoioplax*") *haswelli* (Miers) which apparently occurs at the present time only to the north of Australia. Possibly the niche the fossil form occupied in the southern Australian region is now filled by other species of *Carcinoplax*. Only one truly endemic genus occurs in the faunule, *Pseudocarcinus*.

All but one of the fossil species closely resemble and are probably related to living species (Table 4). This indicates that the assemblage is essentially modern in aspect. The distribution of the modern species which the fossils resemble is shown in Figure 21. Eight of the fossil species (53% of the total number) resemble modern species known to occur in the

Australian region, one (7%) resembles a New Zealand species, and five (33%) resemble Indo-Pacific species not occurring in Australian waters. This suggests that some modern Indo-Pacific lineages occurring in Australia in the Oligocene have since become extinct locally; several examples of this have already been discussed.

None of the modern relatives of the fossil species can be described as exclusively tropical as all extend into at least subtropical regions. Ten of the living forms are however warm-water or subtropical species and five are temperate or cool-water species. Thus it can be inferred that the fossil faunule is a mixed group of warm- and cool-water forms. The number of forms related to modern warm-water species is suggestive of a warmer climatic régime than at present; the mixed warm- and cool-water aspect of the assemblage is consistent with water-temperatures in the lower (cooler) part of the subtropical range.

It seems significant that the modern cool-water species related to the fossils are restricted to southern Australia and New Zealand. This suggests that these species are endemic to Australasia and have evolved within this area rather than migrating to it from some other cool-water province.

Late Oligocene to early Lower Miocene

Species of a genus cf. Portunites another crab belonging to the Carcinoplacidae, and remains of Ctenocheles fragilis occur in the upper part of the

Jan Juc Marl at Torquay, Victoria, an occurrence of Late Oligocene or early Lower Miocene age (Chapter I). *Ctenocheles fragilis* also occurs in the Lower Miocene Puebla Clay at the same locality, and it is considered to have made and inhabited burrows preserved in both the Jan Juc Marl and Puebla Clay.

Ommatocarcinus corioensis occurs in the probably early Lower Miocene Fossil Bluff Formation near Wynyard, Tasmania. The oldest known *Ommatocarcinus* is *O. zariquieyi* Via, a Tethyan species from the Middle Eocene of Spain. *O. corioensis* is closely related to the modern *O. macgillivrayi* White, a sub-tropical species from off eastern Australia and Japan.

The fossil crab "*Harpactocarcinus*" *victoriensis* Crespin which was tentatively referred to the species *Tumidocarcinus tumidus* (Woodward) by Glaessner (1960), is known from the Lakes Entrance Formation in the oil shaft at Lakes Entrance, Victoria. This occurrence is here considered early Lower Miocene.

Tumidocarcinus tumidus has also been found in the Longford Limestone at Dowd's Quarry, near Longford, Gippsland (Glaessner, 1960). Carter (1964) dated this locality as early in his faunal unit 6; this unit represents part of the early and middle Lower Miocene. The occurrences just mentioned are the only records of *Tumidocarcinus* Glaessner in Australia.

Glaessner (1960) indicated that *Tumidocarcinus* is endemic to Australia and New Zealand, where it is known from Middle Eocene to late Middle or early Upper Miocene rocks. He documented the occurrence of _T. tumidus_ in the Upper Eocene and Oligocene of New Zealand; it last occurs in the Duntroonian Stage, which D. G. Jenkins (1971) places in the late Oligocene; in the present study the upper part of this stage is suggested to span the Oligocene-Miocene boundary (Figure 3). As the Australian occurrences of _Tumidocarcinus_ are apparently restricted both in space and in time it seems improbable that the genus migrated from Australia to New Zealand, but far more likely that it reached Australia from New Zealand. The mechanism of transportation for this dispersal may have been the anticlockwise circulation of the northern part of the Tasman Sea. In New Zealand _T. tumidus_ is restricted to the South Island, suggesting perhaps that it was a moderately cool-water species.

Middle Lower Miocene to early Middle Miocene

Four successive shelf assemblages of fossil decapods can be recognized in the middle Lower Miocene to late Lower or early Middle Miocene of southern Australia:

1. Assemblage M.1. This is middle Lower Miocene (Figure 19) and is known from the Gambier Embayment in the Gambier Limestone near Mount Gambier.

2. Assemblage M.2. This assemblage is also of middle Lower Miocene age (Figure 19) and is best represented in the western portion of the Murray Basin in the middle part of the Mannum Formation in the Nildottie-Swan Reach area.

3. Assemblage M.3. *Calappilia australis* assemblage. This is of middle to late Lower Miocene age (Figure 19) and again is best represented in the middle part of the Mannum Formation in the Nildottie-Swan Reach area.

4. Assemblage M.4. This is a late Lower Miocene to possibly early Middle Miocene assemblage and is best represented in the western portion of the Murray Basin in the upper member of the Morgan Limestone, near Mannum.

The assemblage M.1. is known from only one locality. While best documented from the western portion of the Murray Basin, the other three assemblages are further represented by various elements from the southern part of the Murray Basin, the Otway Basin in southern Victoria, and the northwestern part of Tasmania.

Assemblage M.1.

This faunule (Table 5) occurs in the Gambier Limestone at the locality on the Mount Gambier-Port Macdonnell Road 6.4 km south of Mount Gambier. In Chapter I the sediments at this locality were suggested to have been deposited in a mid-neritic environment. All of the identified genera in the assemblage except *Axius* Leach are represented in the Oligocene assemblage which occurs nearby. The only older species of *Axius* known is from the Oligocene of Panama.

Lyreidus tridentatus is present in the nearby Oligocene assemblage and the remains identified as *Paromola* cf. *pritchardi* greatly resemble the species of *Paromola* represented in that assemblage. *Ovalipes denticulatus* and *Nectocarcinus* sp. may be descendants respectively of *Ovalipes primitivus* and *Nectocarcinus cafpercoensis* sp. nov. of the same Oligocene faunule.

All of the fossils in assemblage M.1. seem to be related to present-day Australian species. *Lyreidus tridentatus* is a subtropical species today and does not occur off southern Australia (Griffin and Yaldwyn, 1968; Griffin, 1970). Thus its occurrence in the assemblage suggests a climate warmer than at present.

Assemblage M.2.

This assemblage is present in the middle part of the Mannum Formation in the Nildottie-Swan Reach area. The sediments at this occurrence were probably deposited in an inner-neritic environment. Twelve genera belonging to the assemblage are recognized in this area (Table 6). Eight of these, *Callianassa*, *Ctenocheles*, *Paguristes* Dana, *Ebalia* Leach, *Leptomithrax*, *Ovalipes* Rathbun, *Nectocarcinus* A. Milne-Edwards and *Pilumnus* Leach are represented by older or contemporary species either in the Australian region or elsewhere.

Callianassa appears to have been cosmopolitan throughout its history. *Callianassa bulwara*, which has elongate hands, seems closely similar to *Callianassa longa* Noetling from the Upper Eocene of Egypt. Glaessner (1947) and Via (1970) indicate that elongate *Callianassa*-chelae of this type occur quite widely in the Older Tertiary of the world (*Callianassa bakeri*, from the

Paleocene of Victoria, belongs in this group). Their distribution suggests that they represent mainly warm-water species. Ctenocheles occurs in the Tethyan and West Pacific areas (including Australia) in the Palaeogene. Paguristes is recorded from the Upper Cretaceous and Paleocene of southern North America. The genus Ebalia is represented by the species in the Oligocene faunule from Mount Gambier and is also known from the Lower Miocene (Burdigalian) of Mediterranean Europe and the Miocene of Burma. However the section of Ebalia occurring in the present assemblage (Phlyxia Bell) is apparently endemic to the Australian region.

Earlier species of Leptomithrax, Ovalipes and Nectocarcinus occur in the Australian region. However the species-group of Leptomithrax represented (L. longipes group) is not recorded earlier. Pilumnus is known from the Oligocene of the West Indies. Thus while half of the present assemblage consists of genera which occurred in Australia at earlier times, the possibility of a significant exotic component still remains.

At the generic or subgeneric level, all of the taxa in the assemblage except Schizophroida Sakai and the L. longipes group of Leptomithrax occur in the Australian region today. The modern Schizophroida hilensis, which is seemingly a close ally of the fossil, is known from the Kermadec Islands and Hawaii. Schizophroida also occurs in Japan. The pattern of dispersal of this genus has probably been complex. The L. longipes group of Leptomithrax is monospecific today and is recorded from Macquarie Island and the southern

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half of the New Zealand region. As for the *L. longimanus* group of *Leptomithrax*, it seems likely that the West Wind Drift was an agent in its eastward migration.

Perhaps the most interesting genus in the faunule is *Maja* Lamarck. The species representing it, *Maja robinsoni*, is the commonest form in the assemblage during the time immediately prior to the appearance of *Globigerinoides trilobus immaturus* and is possibly a warm-water form (see below, p.230). The only modern record of *Maja* in the Australian region is from off the north-western part of the continent. Possibly the commonest spider crab genus in southern Australia today is *Leptomithrax* (*L. tuberculatus* species-group, (Table 9) and as this taxon shows a general morphological similarity to *Maja* it seems not unreasonable to suppose that it fills the niche occupied by *Maja* in the Lower Miocene.

The *Pilumnus* sp. of the present assemblage is also known from the southern part of the Murray Basin in the middle Lower Miocene Naracoorte Limestone, near Naracoorte, South Australia. It also occurs later than assemblage M.2. in the Murray Basin and elsewhere.

Most of the fossil decapods in the assemblage resemble various living species (Table 6). The world distribution of these modern relatives of the fossils is shown in Figure 22. Two of the modern relatives of the fossils are apparently tropical species, three seem subtropical, one, *Ovalipes iridescens* (Miers), occurs both in tropical and temperate waters, and seven occur in the region of southern Australia, Macquarie Island and southern New Zealand and hence seem to be cool-water species. It thus seems likely that the fossil assemblage is composed of a mixture of warm- and cool-water species. The proportion of the fossils resembling modern warm-water species suggests climatic conditions warmer than in equivalent latitudes today.

The composition of assemblage M.2. changes significantly with time. These changes have been outlined in Chapter I, where it was suggested that they related to a decrease and then an increase in water-temperature.

Assemblage M.3: Calappilia australis assemblage

Twelve of the genera representing this assemblage, which is named after one of the more common and distinctive species within it, have been recognized at its occurrence in the middle part of the Mannum Formation in the Nildottie-Swan Reach area (Table 7). Nine of these, Callianassa, Ctenocheles, Paguristes, Ebalia, Maja, Notomithrax, Ovalipes, Nectocarcinus and Pilumnus, are represented in the earlier assemblage M.2. which occurs in the same area. The genera not present in the earlier assemblage are Pagurus, Calappilia A. Milne-Edwards and Nucia Dana. The one species of Nucia present is very rare. However Pagurus is represented by two common species and Calappilia by a single species which is the most numerous element in the assemblage. Thus the appearances of the two Pagurus species and Calappilia seem striking and real events. At the same time a new species of Ovalipes appears. Like assemblage M.2., the Calappilia australis assemblage probably inhabited an inner-neritic environment.

The species of *Pagurus* from the Oligocene near Mount Gambier is quite distinct from the two species in the present assemblage. *Calappilia*, which ranges from the Upper Paleocene to the present, is represented outside of Australia by fossil remains from North and South America, Europe, southern Africa and the East Indies. Its distribution during the Older Tertiary is essentially Tethyan. The two known modern representatives of the genus, respectively from the West Pacific and East Indies, are both tropical and it seems probable that the genus has been largely restricted to tropical and relatively warm waters throughout its history (p.180). The time range of the genus in Australia documented in this study corresponds closely to the Miocene temperature maximum which Dorman (1966), and Devereux (1967, 1968) have documented from $O^{16}/_{18}$ isotope studies in southern Australia and New Zealand. A record of *Calappilia* in the Pleistocene of Australia (Etheridge and McCulloch, 1916) seems incorrect (pp.184-185). *Calappilia australis* resembles *Calappilia dacica* Bittner from the Eocene of Hungary; the latter is probably close to the ancestor of *C. australis*. *Nucia rhomboides* belongs to a section of *Nucia* comprising modern tropical species.

Calappilia australis also occurs in the Mannum Formation at Mannum, South Australia. An occurrence of the same species about the same age as present assemblage is in the upper part of the Mannum Formation at Blanchetown, South Australia. Several occurrences of the species younger than at

Nildottie and Blanchetown are known, but these discoveries pertain to the next assemblage and will be discussed with it.

A single specimen of Ommatocarcinus corioensis contemporaneous with the C. australis assemblage has been found in the eastern part of the Otway Basin near Shelford, Victoria. This was possibly a subtropical species (below, p.77).

Remains of the claws of Pseudocarcinus cf. parvus from Cape Grim, north-western Tasmania, are apparently of about the same age as the present assemblage. Pseudocarcinus gigas Lamarck, the one known extant representative of Pseudocarcinus occurs mainly in outer-neritic and upper bathial waters.

The distribution of the different extant species which the fossils of the Calappilia australis assemblage most closely resemble is shown in Figure 23. This distribution again suggests that the fossil faunule comprises a mixture of cool- and warm-water species. However the large proportion of the fossils resembling living warm-water species is interpreted as indicating a warmer climate than at present, probably well within the subtropical range. The section of Nucia present suggests that the climate may have been almost tropical.

Assemblage M.4.

This assemblage (Table 8) comprises the species which have been collected from the Morgan Limestone at its stratotype 5 km south of Morgan.

The lower member of the Morgan Limestone, and the Cadell Marl Lens which occurs within the Morgan Limestone at this locality, are thought to have been deposited in an inner-neritic environment; the top part of the upper member of the Morgan Limestone may represent a subtidal environment (Chapter I). The claws of *Ctenocheles compressus*, rare fingers of claws probably referable to *Ommatocarcinus corioensis*, and occasional as yet unidentified crab claws are known from the lower member of the Morgan Limestone. *Ctenocheles compressus* and *Ctenocheles sclephros* occur together in the Cadell Marl Lens. Assemblage M.4. is however best represented in the top part of the Morgan Limestone. The species just mentioned are all present at this level.

Of the total of seven decapod genera comprising the faunule, all but one, the leucosiid *Pariphiculus* Alcock, occur earlier in Australia. *Pariphiculus* is also known from the Lower Miocene of Madura Island, Indonesia. Today this genus has an Indo-West-Pacific distribution. It apparently has not been recorded from modern Australian seas.

Only three of the species present (other than that representing *Pariphiculus*) are not known earlier in Australia: *Axius morganensis*, *Ctenocheles compressus* and *Calappilia grandispinis*. However these all resemble older Australian fossils; *Axius morganensis* sp. nov. is rather similar to *Axius wadeae* from the Oligocene near Mount Gambier, *Ctenocheles compressus* is closely similar to and probably descended from *Ctenocheles fragilis* from the late Oligocene to early Miocene of Torquay, and *Calappilia grandispinis* resembles and is almost certainly the descendant of *Calappilia australis* (which is also present). Thus with the exception of *Pariphiculus* the fauna appears to be endemic in aspect.

Ommatocarcinus corioensis is one of the more common species in the upper member of the Morgan Limestone. Its abundance at this level is noteworthy as it becomes common in rocks of about the same age (late Lower to possibly early Middle Miocene) in the Otway Basin.

Ctenocheles sclephros also occurs in the Morgan Limestone at North West Bend, near Morgan. *Ctenocheles compressus* has been found in the river cliffs between Wongulla and Mannum, apparently in the Morgan Limestone. *Calappilia australis* and the *Pilumnus* sp. of both assemblage M.2. and the present assemblage are known from the Otway Basin in the upper part of the Batesford Limestone at Batesford; this occurrence is probably equivalent in age to the lower member of the Morgan Limestone. *Calappilia australis*, *Calappilia grandispinis*, and *Paguristes brevirostris antiqua* (of assemblage M.2. and M.3.) occur in the Muddy Creek Marl, at Muddy Creek, near Hamilton. The age of this occurrence is probably comparable to that of the upper member of the Morgan Limestone. *Pseudocarcinus* cf. *gigas*, from the Newport Formation at Melbourne is also apparently of similar age (late Lower to early Middle Miocene).

Figure 24 shows the distribution of the modern species which the fossils in assemblage M.4. most closely resemble. The fossils predominantly resemble living warm-water species and this is very suggestive of a warm, possibly subtropical climate.

Middle Miocene

Only a single decapod species is definitely known from the Middle Miocene of southeastern Australia, the crab *Ommatocarcinus corioensis*. It has a widespread occurrence at this time. Specimens occur in the eastern part of the Otway Basin in early to mid-Middle Miocene exposures of the Fyansford Clay near Murgheboluc and Geelong, and in an early Middle Miocene interval of the Balcombe Clay, at Grices Creek, near Mornington. The older of these localities quite possibly overlap the age of the occurrence of *O. corioensis* in the upper part of the Morgan Limestone, near Morgan in the Murray Basin. The crab also occurs abundantly in the southern part of the Otway Basin in the approximately Middle Miocene Port Campbell Limestone. Remanié occurrences of the crab from the margin of the continental slope in the region of Coffs Harbour and Port Macquarie, New South Wales (von der Borch, 1970) indicate that the species ranged well up the eastern Australian coast.

Ommatocarcinus macgillivrayi, a closely related modern ally of *O. corioensis*, occurs in Australian waters between Cronulla, Sydney, New South Wales and Port Curtis, Queensland at depths of from shoal-water to 80 metres and water-temperatures from about 14-17°C to above 27°C. The fossil species was probably adapted to temperatures similar to those in the area and depths inhabited by this extant crab and it seems likely that its widespread distribution in southeastern Australia during approximately the Middle Miocene was linked to a subtropical climate.

Upper Miocene

The Upper Miocene seems to have been a time of general regression in southern Australia and is represented by rather limited exposures. For this reason relatively little is known about the decapod faunas of this time.

The different late Miocene occurrences from which fossil decapods are known (all in the Otway Basin in Victoria) have already been described in Chapter I. *Ommatocarcinus corioensis* occurs *in situ* as a rather rare element in sediments of this age at Grange Burn and possibly in the Geelong area and at Beaumaris. *Philyra* sp. and *Ovalipes victoriensis* also occur at Beaumaris.

The *Philyra* sp. resembles *Philyra undecimspinosa* (Kinahan) which occurs today off southern Australia. *Ovalipes victoriensis* is possibly the ancestor of the living *Ovalipes elongatus* Stephenson and Rees, which is known from Lord Howe Island and the Kermadec Islands. Thus the occurrence of *Ovalipes victoriensis* together with rare remains of *Ommatocarcinus* is suggestive of water-temperatures at least in the lower part of the subtropical range.

Pliocene

Decapod remains are numerous in the Pliocene of the St. Vincent Basin and are probably also common in sediments of similar age in the Murray Basin. However compared to some of the earlier Tertiary occurrences (for example the Lower Miocene of the Murray Basin) the number of species known is considerably less.

The occurrences of all of the Pliocene decapod species known are described in Chapter I. The species are *Callianassa aequimana*, *Ovalipes* sp., *Nectocarcinus integrifrons*, *Nectocarcinus amathitus* and ? *Ozius macrochelus* from the Murray Basin, and *Ommatocarcinus* sp. from the Gippsland Basin. The occurrences in the St. Vincent and Murray Basins are in near-shore deposits.

C. aequimana, *Nectocarcinus integrifrons*, *Ovalipes*, and *Ozius* Desmarest occur in southern Australian waters today. Thus the faunule from the Saint Vincent Basin suggests climatic conditions not greatly different to the modern climate of this area. The presence of *Ommatocarcinus* in the Gippsland Basin indicates water-temperatures probably 2 or 3°C warmer than off this region at present.

Conclusions

The Cretaceous fossil decapods from Australia occur in the northern, northeastern and eastern parts of the continent and comprise a mixture of cosmopolitan and endemic genera of macrurans and brachyurans; the absence of genera with a restricted Tethyan distribution is notable and might be interpreted as indicating an extratropical climate.

The fossil decapods from the Tertiary are mainly from the southeastern part of the continent. The assemblages known from the Paleocene and Eocene are too sparse to be of much significance zoogeographically; however the occurrence of thalassinids in the Paleocene of the Otway and Perth Basins and the Upper Eocene of the Saint Vincent Basin suggests water-temperatures no cooler than in the region of Bass Strait and northeastern Tasmania today (12-16°C). The Eocene species require further study.

A diverse assemblage of brachyurans and anomurans from the Middle Oligocene of Mount Gambier is probably representative of the outer-neritic or upper continental slope environment of southern Australia at this time; this faunule is remarkably modern in aspect with about 50% of its species related to living Australian forms and most of the remainder resembling modern Indo-Pacific species not occurring in Australian waters. Thus some Indo-Pacific lineages represented in the Australian Oligocene have apparently become extinct locally. The number of fossils resembling living warm-water species is interpreted as indicating subtropical water-temperatures.

Few decapod remains are known from the Upper Oligocene and earliest Miocene. Tumidocarcinus, which is represented in the early Lower Miocene of Gippsland, is otherwise well known in the Upper Oligocene to Miocene of New Zealand. It seems probable that it reached Australia from New Zealand, perhaps via the counterclockwise circulation of the northern part of the Tasman Sea.

Successive, diverse Early Miocene, brachyuran and anomuran assemblages known chiefly from the Murray Basin and a small decapod assemblage from near Mount Gambier probably inhabited mid- or inner-neritic environments. They comprise genera present in earlier Australian assemblages and immigrant Tethyan and Indo-Pacific genera (Maja, Calappilia, Nucia and Pariphiculus) no longer known in southern Australian waters. The composition of these faunules is interpreted as indicating subtropical water-temperatures in the middle Lower Miocene and an almost tropical climate in the late Lower Miocene.

The widespread occurrence of Ommatocarcinus corioensis in southeastern Australia during approximately the Middle Miocene is striking as the genus is today subtropical. The occurrence of the fossil is thus probably linked to subtropical water-temperatures; its local abundance may be related to its burrowing habits in the moderately fine grained sediments which were deposited commonly at this time.

The members of Late Miocene and Pliocene assemblages are mostly related to or actually represent present-day Australian species. These faunules are from near-shore environments. Water-temperatures in the lower (cooler) part of the subtropical range can be tentatively inferred for part of the Late Miocene; the Pliocene data suggests a temperature only a few degrees warmer than at present.

Griffin and Yaldwyn (1968) conclude that the modern "Australian decapod fauna appears to have been derived almost entirely from the tropical

Indo-Pacific region" and that "there seems to be no good evidence to suggest that temperate species have reached Australia directly from temperate areas outside Australia". These findings are largely supported by the present work. However, the ultimate origin of the Indo-Pacific fauna has probably been largely from the Tethys (Ekman, 1953) and several of the fossil decapod genera occurring locally are represented at an earlier time in the Tethyan region (Carcinoplax, Ommatocarcinus, Calappilia). Some migration seems to have occurred between Australia and New Zealand in both directions. Sections of Leptomithrax and other taxa probably reached New Zealand from Australia; Tumidocarcinus possibly migrated from New Zealand to Australia.

Chapter III

RELATIONSHIP OF FOSSIL DECAPODA TO CRETACEOUS AND CAINOZOIC PALAEOCLIMATIC AND GEOLOGICAL HISTORY OF AUSTRALIA

Introduction

Studies of the past distribution and palaeoecology of particular organisms become more meaningful when compared to the distribution and ecology of other unrelated taxa, and placed in perspective against the geological changes occurring in the area in which they lived. Only by comparing the results of such studies can assessment of the ecological data be made.

It is now generally accepted that some continents have moved large distances relative to each other (Vine, 1970). Palaeomagnetic data suggests that Australia occupied a sub-polar position in the Mesozoic and has moved progressively northwards since the mid-Cretaceous (Wellman, McElhinny and McDougall, 1969). Sea floor magnetic data suggests that Australia and Antarctica were joined in the mid-Eocene but have since separated and moved apart (Le Pichon and Heirtzler, 1968). With regard to Australia at least (Antarctica apparently remained in a near polar position) these changes might be evidenced by significant changes in climate and biota. Conversely, study of the latter should test and add to the understanding of the movements which the continent has undergone.

Modern decapods are sensitive indicators of environment (Ekman, 1953; Dell, 1968a; George, 1969, and others) and probably fossil decapods are similarly useful as environmental indicators. This thesis extends the knowledge of these fossils during the critical interval when Australia and Antarctica drifted away from one another and provides new palaeoecological information for this time. Hence it seems important to attempt to compare the palaeoecological inferences made from fossil decapods with the results of ecological studies based on other sections of the Australian fossil biota of comparable age, and to assess the geophysical hypothesis that Australia has moved progressively northwards since the Cretaceous.

Geophysical Data

Two lines of geophysical evidence have been regarded as indicating large scale movement between Australia and Antarctica. The first of these is palaeomagnetism and the second is the study of linear magnetic anomalies on the deep sea floor.

a) Palaeomagnetism

The theory of deriving the past latitudinal position of continents from the directions of remnant magnetism "frozen" into their rocks is now well known and has been reviewed by Irving (1964) and others. Wellman, McElhinny and McDougall (1969) review the palaeomagnetic data for the Jurassic, Cretaceous and Tertiary of southeastern Australia and present new information for geochronologically dated eastern Australian Tertiary volcanic complexes. They suggest that the palaeolatitude of the present site of Canberra was about 72°S in the Middle Jurassic, approximately 70°S in the mid-Cretaceous, about 52°S in the (lower) Eocene and close to 45°S in the (lower) Oligocene. Estimates for later times progressively approach the present latitude of Canberra (35°S). The 95% confidence limits for these results are of the order of ± 7-10° for the Mesozoic data and ± 3-5° for the Tertiary data.

b) Linear magnetic anomalies on the sea floor

Drilling in the deep sea has now virtually confirmed that patterns of linear magnetic anomalies on the sea floor resulted from processes of sea floor spreading and can be related closely to continental fragmentation and continental drift (Vine, 1970). Study of the pattern of linear magnetic anomalies in the middle and southern part of the Indian Ocean led Le Pichon and Heirtzler (1968) to conclude that the present ocean basin between Australia and Antarctica began to open at the time of anomaly 18. In the magnetic reversal time scale of Heirtzler et al. (1968) anomaly 18 is dated as being about 46 million years old. With reference to the chronostratigraphic scheme of Berggren (1969a), anomaly 18 is latest Middle Eocene.

In the South Indian Ocean the linear magnetic anomalies younger than anomaly 18 show almost the same proportionate spacing as their counterparts in the South Atlantic (Le Pichon and Heirtzler, 1968: 2113-2114, Figure 9). The results of deep sea drilling are indicative of a nearby constant rate of sea floor spreading in the South Atlantic since the late Upper Cretaceous or early Tertiary (Vine, 1970). It is thus likely that the rate of sea floor spreading in the South Indian Ocean has also been relatively constant since the time of anomaly 18. A further inference is that the relative rate of movement apart of Australia and Antarctica has been approximately constant since their initial separation.

Polar Climates

The tilt of the Earth's rotational axis to the ecliptic leads to the seasonal nature of present climates. At the same time it causes the polar regions of the globe (area within the polar circles) to be totally shaded from solar radiation during at least part of the winter period. This lack of insolation must result in conditions of intense cold and the development of sea ice, or of frost or ice cover on land. Cyclic growth stages in many fossils (corals, bivalves, belemnites, fossil woods) indicate seasonal climates during the geological past and it is contended that because of the seasonal shading of the poles they will always have experienced cold or glacial climates. This implies that world climates will always have been zoned latitudinally.

Cretaceous

Scheibnerová (1970, 1971) has made a detailed review of the palaeoecology and palaeogeography of the marine Cretaceous deposits of the Great

Artesian Basin, and the marine Cretaceous of the rest of Australia. She considers that the foraminiferal assemblages of the Aptian to Lower Cenomanian of the Great Artesian Basin show similarities to those of the Cretaceous of the West Siberian Lowland, western and northwestern North America, and northern Europe (Anglo-Paris Basin, N.W. Germany, N. Poland). She regards these northern hemisphere assemblages as being representative of a cold-water Boreal régime and concludes that the Great Artesian Basin assemblages were indicative of a similar environment. In her view, this finding accords well with the inference from palaeomagnetic data that the Great Artesian Basin lay between 50 and 70°S in the Cretaceous. A Tethyan aspect in Upper Cretaceous foraminiferal faunas from western, northwestern and northern Australia is recognized and it is suggested that these assemblages indicate the influence of warm currents. Scheibnerová (1971) considers that the nature of Cretaceous macrofossil assemblages (depleted ammonite and belemnite populations in the Great Artesian Basin) and oxygen-isotope palaeotemperature data support her conclusions.

The decapod faunules from the Great Artesian Basin are relatively sparse. They include several rather widely distributed genera (Enoploclytia, Palaeastacus, Homolopsis, Glyphea, ?Astacodes Bell) which are well represented in Scheibnerová's (1971) Boreal and Austral provinces, and one genus which is otherwise restricted to her Boreal province (Homolopsis). These faunules are probably extratropical (above, p.60) and lend support to Scheibnerová's conclusions.

A moist subtropical climate is postulated from late Upper Jurassic or early Lower Cretaceous plant fossils from the southwestern part of the Great Artesian Basin (Harris *in* Wopfner *et al.*, 1970). The diversity of the microfloras described from the Lower Cretaceous of the Great Artesian, Otway and Gippsland Basins, and the Upper Cretaceous of southeastern Australia (Dettman, 1963; Dettman and Playford, 1968; Harris *in* Wopfner *et al.*, 1970) might also be considered as indicating at least a temperate climate. Pollen showing a close relationship to that of the *Nothofagus brassi* group occurs in the Upper Cretaceous (Senonian and later) of the Otway Basin (Dettman and Playford, 1968). The *N. brassi* group is restricted to New Caledonia and New Guinea at the present time (Darlington, 1965).

Scheibnerová (1970, 1971) interprets the oxygen-isotope palaeotemperature data for the Cretaceous of Australia (Lowenstam and Epstein, 1954; Dorman and Gill, 1959; Bowen, 1961; Dorman, 1966, 1968) as showing a possible climatic zonation from S.S.E. (cold-water) to N.N.W. (warm-water). The palaeotemperatures for the Lower Cretaceous of the Great Artesian Basin certainly suggest cooler conditions than in present seas at the same latitudes but the difference seems only of the order of 3-5°C. The 'seasonal' palaeotemperature ranges of 9-17, 13-17, and 16-21°C measured in Aptian and Lower Cretaceous belemnites from the Lake Eyre region (Dorman and Gill, 1959) are closely comparable to the present seasonal range of water-temperatures off the southern coast of mainland Australia. Dorman (1966) records palaeotemperatures of 16.5 and 19.5°C for the Santonian of the Otway Basin. A value of 28°C, which he records for the Turonian of the same basin, was measured on Inoceramus. Lowenstam and Epstein (1954) have shown that this genus may give high results compared to other fossils (belemnites) in certain instances.

These inferences about Australian Cretaceous climates are broadly in mutual agreement. The foraminiferal data presented by Scheibnerová (1970, 1971) clearly indicates that southern Australia and most of the Great Artesian Basin were extratropical in the Cretaceous; she interpreted the foraminifera populations of these regions as being of "cold-water" character. However, the evidence for floral diversity and the palaeotemperature data seem suggestive of temperate conditions in the southeastern half of Australia. Warmer climates apparently obtained towards the northwestern part of the continent (Scheibnerová, 1970, 1971).

These findings can be interpreted as indicating a more southerly position for Australia if world climatic conditions as warm as or warmer than today are assumed for the Cretaceous. It now seems well established that during past climatic optima the world's warm climatic zones have increased in width (for a recent view, see Dorf, 1970). On the other hand a temperate climatic régime for southeastern Australia seems inconsistent with the very high Cretaceous palaeolatitudes of more than about 70°S suggested for this region by palaeomagnetic studies.

Paleocene to Eocene

Paralic and marine sedimentation occurred in the Otway Basin in the Middle and Upper Paleocene (McGowran, 1970). Assemblages of foraminifera from the marine intervals are distinctly cosmopolitan in general aspect, but taxonomically separate from the diversified Tethyan faunas (McGowran, 1965, 1970). The closest comparison is with other mid-latitude, early Tertiary assemblages. McGowran (1965) and McGowran and Wade (1967) note marked latitudinal changes in the Paleocene foraminiferal populations from southern Australia, the Carnarvon Basin and New Guinea; the large benthonic species of the latter locality do not reach the Carnarvon Basin. McGowran and Wade (1967) consider that these changes reflected a temperature gradient.

The occurrence of the decapods Callianassa and Ctenocheles in the marine phases of the Paleocene of the Otway Basin is suggestive of a temperate or warmer climate (above, p.61). Oxygen-isotope data given by Dorman and Gill (1959) and Dorman (1968) support this and indicate palaeotemperatures in the range 11-18°C.

From palynological studies, Harris (1965) suggests a general rise in temperature during the deposition of the Paleocene sequence of the Otway Basin. This agrees with data from Europe and North America (Dorf, 1970).

McGowran (1971) has reviewed the evidence for Eocene climatic conditions in Australia. He suggests a warm interval in the Lower Eocene, a cooler period in the early Middle Eocene, and a time of marked warmth in the Upper Eocene. His findings are in close agreement with those of Hornibrook (1971) for New Zealand.

The late Middle and Upper Eocene of Australia is marked by widespread marine transgression (McGowran, 1971). A minor transgression in the early Middle Eocene apparently preceded the main transgression which began in the late Middle Eocene and reached , maximum extent in the Upper Eocene.

Reference to the chronostratigraphic scheme of Berggren (1969a) indicates that this transgression spans the time of magnetic reversal event 18 (late Middle Eocene) and hence closely corresponds to the time when Australia and Antarctica are thought to have separated. McGowran (1971) considered that the transgression may have been largely tectono-eustatic in nature, and related to the formation of a new mid-oceanic rise. The widespread evidence of transgression in many parts of the world during the Middle and Upper Eocene (Gignoux, 1955; Frerichs, 1970) lends some support to this hypothesis. However rates of sea floor spreading seem to have been relatively constant after the Eocene and a similar mechanism cannot be used to explain the equally widespread mid-Miocene transgression (Frerichs, 1970), which in southern Australia at least, was more extensive than that of the Eocene.

The rather meagre palaeomagnetic data available for Antarctica suggests that it has been situated in an approximately polar position from the mid-Cretaceous to the present (McElhinny and Wellman, 1969). In this thesis it is accepted that Australia may have been further south than at present in the Cretaceous and early Tertiary, but that no part of the mainland experienced a polar climate or overlapped the Antarctic Circle. If Antarctica and Australia were joined in the early Tertiary (Le Pichon and Heirtzler, 1968) and probably the Cretaceous, it follows from the above argument that the geometry of the join of these continents is only possible if Greater Antarctica was then situated north (towards Australia) of its present position. A great part of the Antarctic land area (perhaps about half) would still be within the Antarctic Circle. An early Tertiary pollen flora from the vicinity of McMurdo Sound lends support for an extrapolar climate in part of Greater Antarctica (Cranwell, 1969). The part of the continent within the polar circle was possibly ice-covered. Following its separation from Australia, Antarctica probably drifted south to its present position. Margolis and Kennett (1971) document ice rafting of sediment in the South Pacific and sub-Antarctic Pacific at different times in the Tertiary from the Lower Eocene onwards. They argue that this is only possible if an Antarctic ice-cap existed. They also review on-shore evidence for an Antarctic ice-cap, the oldest datable record for which is Upper Eocene, in West Antarctica. Melting of an Antarctic ice-sheet and a consequent eustatic rise in sea level during the period of warm climate in the latter half of the Eocene provides a possible explanation for the transgression at this time and is favoured here.

Late Eocene to Early Oligocene

Oxygen-isotope palaeotemperatures which Dorman and Gill (1959) and Dorman (1966, 1968) give for the middle Upper Eocene and late Upper Eocene to Lower Oligocene of southeastern Australia are suggestive of relatively cool conditions. From his oxygen-isotope work in New Zealand Devereux (1967, 1968) deduced a sharp fall in temperature in the late Upper Eocene and a temperature minimum in the Lower Oligocene. McGowran and Wade (1967) also postulated a Lower Oligocene palaeotemperature minimum to explain the extinction of various Eocene foraminifera. A sharp temperature drop early in the Oligocene has also been recorded in North America (Wolf and Hopkins, 1967; Wolf, 1971); part of the Upper Eocene was also characterized by a relatively cool climate.

Another line of evidence assists in determining the palaeoclimates of Australia at this time, the appearance of the earliest penguins in Australia, New Zealand, and probably Seymour Island. Recent biostratigraphic studies (Edwards, 1971; D. G. Jenkins, 1971) provide a basis for the dating of the New Zealand remains. *Palaeeudyptes marplesi* Brodkorb and *Palaeeudyptes* sp. occur in the middle Upper Eocene of New Zealand (cf. Simpson, 1971). The remains of the giant *Pachydyptes ponderosus* Oliver can be firmly dated as latest Upper Eocene and early Oligocene, and seemingly postdate the sharp fall in palaeotemperature which Devereux (1967, 1968) recorded in the late Eocene. The Australian Upper Eocene penguin remains occur in two horizons within the Blanche Point Marls (Reynolds, 1953) in the St. Vincent Basin. The lower horizon is middle Upper Eocene and the higher horizon may be only slightly younger. *Palaeendyptes* sp. and a new species of *Pachydyptes* (manuscript in preparation) occur at both levels. Nannofloral studies (Mr. S. G. Shafik, pers. comm.) correlate the relevant part of the Blanche Point Marls with part of the Browns Creek Clay of the Otway Basin. Dorman and Gill (1959) and Dorman (1966, 1968) give a number of relatively low palaeotemperature determinations (12-14°C) from this latter formation and several higher values (16.5-17°C). It is possible that the interval of low temperature suggested by this data corresponds to the low temperature recognized by Wolf (1971) in the Upper Eocene of North America. The extreme rarity of the penguin fossils in the Blanche Point Marl and their restricted distribution in southern New Zealand in the Eocene suggests that they indicate the approximate northern limits of penguin distribution. This, in conjunction with the low palaeotemperatures, suggests that they were adapted to cool or cold waters. Simpson (1971) concedes that modern penguin species show a (rather weak) trend towards increasing size with increasing latitude and that the largest species are restricted to Antarctic and sub-Antarctic seas.

Middle Oligocene to Recent

By the Middle Oligocene the climate of southeastern Australia again seems to have been subtropical. This is shown by the assemblage of fossil decapods from the Oligocene of the Mount Gambier area (above, p.65). Middle and Upper Oligocene oxygen-isotope palaeotemperature data given by Dorman (1966) also suggests this, and indicates water-temperatures possibly of the order of 23°C. However no biotic evidence substantiating such a high value is apparently yet known. The oxygen-isotope data of Devereux (1967, 1968) and the foraminiferal abundance curve of D. G. Jenkins (1968) indicate a rise in temperature in New Zealand during the Middle Oligocene.

The occurrence of the fossil crab <u>Tumidocarcinus tumidus</u> in the early Lower Miocene of the Gippsland Basin is possible evidence for a temperate climate. Decapod assemblages from the middle Lower Miocene of the Gambier Embayment and Murray Basin suggest subtropical conditions. The disappearance of various taxa at a slightly later time may reflect the episode of cooling noted by Devereux (1967, 1968).

The high temperature peak of the late Lower Miocene now seems well documented on a world wide basis. It is indicated by studies of flora in Europe and North America (Dorf, 1969). In New Zealand it is shown by oxygen-isotope studies, a maximal Tertiary peak in foraminiferal abundance, and the incursion of large, benthonic, tropical foraminiferal species (Devereux, 1967, 1968; D. G. Jenkins, 1968; Hornibrook, 1971). Oxygen-isotope studies on fossils from southeastern Australia (Dorman, 1966) are indicative of water-temperatures of perhaps 25°C. The incursion of benthonic, tropical foraminifera occurred in southern Australia (McGowran and Wade, 1967; this work p.25, 40, 45) and the warm-water crabs (<u>Calappilia</u> and a tropical section of <u>Nucia</u>) appeared. Conditions were favourable for reef building corals and the development of algal reefs in the Eucla Basin (Ludbrook, 1957). The common occurrence of the crab *Ommatocarcinus corioensis* in the Middle Miocene may be interpreted as indicating a subtropical climate at this time. Similar conditions are indicated by the oxygen-isotope data of Dorman (1966).

Dorman's (1966) palaeotemperature work suggests a decline in temperature in the Upper Miocene. Possibly an increase in temperature occurred in the late Upper Miocene, when southeastern Australian crab assemblages suggest water-temperatures in the lower part of the subtropical range. A warm interval in the Pliocene is reflected by the occurrence of an assemblage of large molluscs and the foraminifera species *Marginopora vertebralis* Blainville in southern, but apparently not southeastern Australia (Ludbrook, 1961; McGowran and Wade, 1967). The decapod faunule associated with this assemblage is essentially modern in aspect and hence suggests a climate not unlike that of the present time. However the abundance of the thalassinid *Callianassa aequimana* and presence of a large species ?*Ozius* are possible indicators of a slightly warmer climate than today. The rare occurrence of *Ommatocarcinus* in the Gippsland Basin supports this conclusion.

An Upper Miocene temperature low and Pliocene high are also suggested by the foraminiferal abundance curve of D. G. Jenkins (1968) and by data for floras from the mid-west of North America (Wolf and Hopkins, 1967). Dorman's oxygen-isotope data suggests a decline in temperature at the end of the Pliocene.

Palaeoclimatic data for the Australian Tertiary and significant Tertiary events are summarized in Figure 25. Certain New Zealand data is included for comparison. A general record of the history of transgression and regression in southern Australia is also shown. Although the inferred palaeotemperature record for southern Australia fluctuates markedly there appears to be a trend towards increasing temperature from the Paleocene to the late Lower Miocene; thereafter temperature tends to decrease. The trend towards increase in temperature for the older three-quarters of the Tertiary is consistent with the contention of the geophysicists that Australia has moved progressively northwards during this time. Assuming that the world climate of the Tertiary was for the most part markedly warmer than at present, early Tertiary biological data for the climate of southern Australia can probably be reconciled with palaeomagnetic data which indicates that this region was situated at more than 45 to 50°S at this time.

One feature of interest which emerges from the summary presented in Figure 25 is the close correspondence between the record of transgressions or regressions in southern Australia and the fluctuations in climate. Transgressions coincide with data suggestive of relatively high temperatures and episodes of regression correspond with data suggestive of low temperatures. It seems well established that the detailed pattern of transgression and regression in the different sedimentary basins concerned is controlled by tectonic movements. However except for the Paleocene, most of the transgressive and regressive episodes shown can be documented in **several** sedimentary basins. The relationship just noted between the extent of the sea and palaeotemperature suggests that a significant component of the transgressions and regressions is due to glacial eustatism. This implies that there has been a large reservoir of land ice throughout the Tertiary. As indicated above the most probable site for such an ice reservoir is on Antarctica.

Conclusions

Inferences made about past climates of Australia from fossil decapods are in close agreement with the results of similar studies made on other sections of the fossil biota and oxygen-isotope palaeotemperature work. The results from decapods are most conclusive from the Oligocene onwards, when many of the fossil taxa closely resemble living forms.

Foraminiferal studies (Scheibnerová, 1970, 1971) and inferences made from decapods indicate extratropical climates for the Great Artesian Basin in the Cretaceous. However palaeobotanical and oxygen-isotope palaeotemperature data for the Cretaceous suggest that no part of Australia was within the high latitudes of 68-73°S which Wellman, McElhinny and McDougall (1969) indicate from their review of palaeomagnetic studies.

Climatic inferences made from the study of Early Tertiary decapods and other fossils can probably be reconciled with suggestions of palaeomagnetists (Wellman, McElhinny and McDougall, 1969) that southern Australia was situated at latitudes of more than 45-50°S at that time. The inferred trend towards increasing temperature in the mid-Tertiary is consistent with Australia having drifted progressively northwards.

Appearances and disappearances of warm-water genera of decapods (*Ommatocarcinus*, *Maja*, *Calappilia*, *Nucia*, *Pariphiculus*) in the mid-Tertiary of southeastern Australia lend support to the idea that palaeotemperatures fluctuated during that time rather than remaining relatively constant or increasing at a constant rate. An interpretive curve of the climatic changes which have occurred in southern Australia during the Tertiary is notable in that it shows a close parallelism with the record of transgression and regression in the same region. This suggests that the transgressions were principally a result of glacial eustatism, and implies the existence of a Tertiary ice-cap on at least part of Antarctica.

PART II

SYSTEMATICS

Taxonomy

The suprageneric taxonomy used in this work is that of Glaessner (1969). No new genera are recognized amongst the Australian materials at hand, and as the fossils described mostly resemble present day species seemingly little light is shed on the problems of suprageneric relationships.

Terminology

The terminology used here chiefly follows that of Glaessner (1969) and Moore and McCormick (1969). For the oxyrhynchous crabs some terms which Griffin (1966a) applied to the anterior parts of the carapace have been adopted. Notwithstanding the wealth of terminology provided by these authors, it was considered necessary to define or redefine several terms as follows:

Margin - a free edge of the exoskeleton or a hypothetical line marking the outline of a particular region or area of the exoskeleton.

Border (or marginal border) - a peripheral ridge or a line of thickening at a free edge of the exoskeleton.

Inner-branchial lobe - a small swelling (or one of several small swellings) located on the most medial part of the branchial regions of the carapace immediately adjacent to either the metagastric or urogastric region (branchial lobe in figure 220C of Glaessner, 1969).

Measurements

Dimensions are provided for the most complete individuals or representative specimens of the species described. All measurements are given in millimetres. Except where stated otherwise measurements given for the carapace are maximal dimensions *excluding* lateral spines, tubercles or granules (which may be readily abraded or broken, and in any event tend to be very variable between individuals). Measurements of joints of appendages are again maximal dimensions excluding ornamentation; length is measured between the extreme ends of the articulating processes of the said joint. For the palm of a chela the length is taken as the distance between the symphysis of the fingers and the extreme margin of the lower, proximal articulation.

Preparation of material, photography and reconstructions

Specimens were developed from the matrix (usually bryozoal limestone or calcarenite) chiefly with the aid of steel needles held in a pin-chuck. Several applications of thin shellac were found useful in hardening fragile specimens. The larger specimens were whitened with ammonium chloride for photography; specimens less than 10 mm in diameter were whitened with magnesium oxide smoke from burning magnesium: with both techniques care had to be exercised to maintain a thin coating without obscuring details. A "Leica" 35 mm camera on a vertical stand and oblique lighting (three or four lamps) were used for photography. Reconstructions were drawn from representative photographs enlarged to a suitable scale. Small objects were drawn with the aid of a camera lucida.

Abbreviation of localities

In order to minimise repetition the following abbreviations have been used to indicate certain key localities (see also Figures 6 and 13):

Nildottie loc. 1: cliff forming east bank of River Murray about .8 km south of Nildottie, South Australia.

Nildottie loc. 2: road cutting leading to Greenways pumping station and adjacent cliff, east side of River Murray, section 140, Hundred of Nildottie, 2 km north of Nildottie.

Nildottie loc. 3: cliff on east side of River Murray immediately north of Greenways Landing, section 190, Hundred of Nildottie, 3 km north of Nildottie.

Nildottie loc. 4: cliff on east side of River Murray immediately north of Big Bend Reserve, section 64, Hundred of Nildottie, 7 km N.N.W. of Nildottie.

Morgan loc. 1: cliff and ravine on east side of River Murray, section C, Hundred of Cadell, 6.4 km south of Morgan, South Australia.

(This locality is also the type section of the Morgan Limestone).

Mount Gambier loc. 1: building stone quarries in vicinity of Marte railway siding on sections 26, 28, 29, 30, 144 and 145, Hundred of Blanche, 12 km west of Mount Gambier, South Australia.

Mount Gambier loc. 2: quarries adjacent to Port Macdonnell Road on sections 601 and 606, Hundred of Blanche, 7 km south of Mount Gambier.

Location of collections

The materials studied in this thesis either belong to or have been lodged in various museum and university collections. The following abbreviations indicate the institute in which they are registered:

A.U. - Palaeontological collection of the Department of Geology and Mineralogy, The University of Adelaide, Adelaide, South Australia.

N.M.V. - Palaeontological collection of the National Museum of Victoria, Melbourne, Victoria.

N.Z.G.S. - Register of fossil Crustacea, New Zealand Geological Survey, Wellington, New Zealand.

S.A.M. - Palaeontological collection of the South Australian Museum, Adelaide, South Australia.

U.T.G.D. - Palaeontological collection of the Geology Department of The University of Tasmania, Hobart, Tasmania.

Order DECAPODA
Suborder PLEOCYEMATA
Infraorder ANOMURA
Superfamily Thalassinoidea
Family Axiidae Huxley, 1879
Genus Axius Leach, 1815

Type species: Axius stirhynchus Leach, 1815, by monotypy.

Axius Leach, 1815. De Man, 1925: 1 (in key), 3 (list of then known extant species), 8 (review, key to extant species). Zariquiey Alvarez, 1968: 228 (generic description: key to extant Spanish species). Glaessner, 1969: R477.

Axius wadeae sp. nov.

Plate 1 figures 1 - 4a,b

Name

Named after Dr. Mary Wade of the Queensland Museum, Brisbane, the original discoverer of the locality where the species was collected.

Material

An almost complete specimen of the chela of the right (large) cheliped, the holotype S.A.M. P15797, and a nearly complete example of a left (large) chela, paratype S.A.M. P15798. Three more or less incomplete specimens of the large chela, paratypes S.A.M. P15799-P15801. A dactylus of a right (large) chela, paratype S.A.M. P15802. An incomplete propodus of a right chela (? smaller claw of first pair of pereiopods), paratype

S.A.M. P15803. Specimens all preserved as the original shell material and coll. R.J.F.J., 1970.

Occurrence

Between 8 and 9 m below the ground surface in quarry on section 601, Hundred of Blanche, Mount Gambier loc. 2.

Stratigraphic Position and Age

Gambier Limestone. Middle Lower Miocene.

Description

Palm of large chela subquadrate, about 1.1 times as long as high, moderately compressed; upper margin gently convex, rounded above, but with a fine sharp ridge on inner side, a row of four fine pores in narrow groove on outer side of this ridge, a similar row of four pores on inner side of ridge, several pores grouped together at distal termination of ridge; lower margin with a flat keel, on either side of keel a groove containing a line of pores, the inner row of pores continuing along whole length of fixed finger; distal margins of palm nearly at right-angles to upper and lower margins, the outer distal margin notched at point where movable finger articulates; outer face moderately convex, mostly smooth, but with 16 or so lipped pores in an area of reticulate granulation on lower, distal part of face, two large granules on either side of a conspicuous pore near distal margin, and a single pore above notch where movable finger articulates; inner face gently convex, also mostly smooth but with a small area of reticulate granulation on middle of distal portion, a pore on lower distal part of face. Fixed finger more than .8 length of palm, tapered, smooth; outer face with a row of three conspicuous pores at upper 1/3 of height and several pores near ridged proximal portion of lower margin; several widely spaced pores on inner face; prehensile margin with a few obscure granules on proximal portion and a single tooth at about 3/5 length from proximal end. Movable finger robust, slightly curved, with distal part of upper margin curved downwards; a line of three conspicuous pores on lower part of outer face; upper margin formed into a strong ridge with a groove on either side, two or three pores on outer side of proximal portion of this ridge and a single pore near tip of finger, a line of five or so lipped pores in groove on inner side of ridge; inner face with a row of three pores at lower 1/3 of height and a fine pore on middle of proximal portion; prehensile margin with a flat basal tooth and a smaller tooth at about 3/5 length, distal part of margin sharp edged.

Propodus of smaller first pereiopod similar to that of large claw, but with the fixed finger more slender.

Measurements

The holotype S.A.M. P15797, a right (large) chela, has the propodus 20 mm long (incomplete) with the palm 12 mm long (incomplete) and 11 mm high and the dactylus 12 mm long. The other specimens of the large chela collected are either approximately the same size or smaller than this. Paratype S.A.M. P15803, the propodus of right chela (? smaller first pereiopod), is 8 mm long (incomplete) with the palm 4 mm long (incomplete) and 4.8 mm high.

Remarks

The oldest fossil species of Axius yet described and the only previously recorded mid-Tertiary representative of this genus is Axius reticulatus Rathbun, 1919, from the Oligocene of Panama. Axius wadeae is distinguished from A. reticulatus by the more nearly quadrate form of its palm and by having only a single tooth on the prehensile margin of the fixed finger. The hands of A. wadeae are rather similar to those of the extant species Axius plectrorhynchus Strahl, 1862, from southern, southeastern and eastern Australia, Amboina and Luzon, but differ in having granulate areas on the distal parts of the palm, a fine ridge on the inner, upper aspect of the palm, a ridge on the outer, proximal part of the fixed finger, and a well defined ridge on the upper margin of the movable finger.

Axius morganensis sp. nov.

Plate 1 figures 5 - 7a-c

Name

Named after Morgan, South Australia, the town nearest to the locality where the species occurs.

Material

A nearly complete specimen of the right (large) chela, the holotype S.A.M. P15810; an incomplete left (large) chela, paratype S.A.M. P15811; and numerous dissociated fingers of the claws. Specimens preserved as the original shell material and coll. Bret Robinson, 1967 (P15810 and P15811) and R.J.F.J., 1966-1968.

Occurrence

Morgan loc. 1.

Stratigraphic Position and Age

Morgan Limestone, upper 3 m of upper member. Late Lower or early Middle Miocene.

Description

Palm of large chela subquadrate, about 1.2 times as long as high, moderately biconvex; upper margin slightly convex, rounded distally and with a fine, sharp ridge on proximal portion, a row of five or so pores on outer side of this proximal ridge; lower margin gently recurved and carinate, the carina finely serrate and with a pore on distal side of each serration; distal margins slightly oblique; outer face moderately convex, smooth for most part, but finely granulate at base of fixed finger, with three or four pores together in a short line just above point where movable finger articulates and a line of widely spaced pores near lower margin; inner face gently convex, mostly smooth, obscurely and finely granulate at base of fixed finger, with a row of pores near upper margin, one pore a short distance from articulation of movable finger, and several pores near base of fixed finger. Fixed finger .7 length of palm, slightly deflexed relative to palm, tapered, smooth; outer face with a row of four pores at upper 1/3 of height and several pores near ridged, proximal part of lower margin of finger; inner face with a line of three widely spaced pores; sharp prehensile margin obscurely granulate proximally and with a single tooth at about 2/5 length from proximal end. Movable finger robust, tapered, gently curved; a line of three pores on lower part of outer face, two pores on upper, proximal portion of face and another pore on upper aspect near tip of finger; upper margin forming a rounded ridge with a groove on inner side and a weak groove on proximal part of outer side; a row of six to seven pores on inner side of this ridge; inner face with a row of four pores at lower 1/3 of height and a single pore on middle portion at about 1/3 length of finger from proximal end; prehensile margin with an elongate basal tooth and a smaller tooth at about ½ length, distal part of margin sharp edged.

Fingers of chela of smaller first pereiopod more slender than those of large claw, and more rounded in section.

Measurements

The holotype S.A.M. P15810, the remains of a right (large) chela, has the propodus 25 mm long and the palm 15 mm long and 14 mm high. Paratype S.A.M. P15811 an incomplete left (large) chela, has the propodus 33 mm long (incomplete), the palm 21 mm long (incomplete), and the dactylus 18 mm long (extreme tip broken away).

Remarks

These remains resemble the equivalent parts of both _A. wadeae_ and the modern _A. plectrorhynchus_. They differ from the claws of _A. wadeae_ as follows:

(a) The lower margin of the palm of the large chela is serrate rather than smooth.

(b) Only one or two pores are associated with the granulate area on the lower, distal part of the outer face of the palm of the large chela and the granulation is finer.

(c) The tooth on the prehensile margin of the fixed finger of the large claw is situated in a more proximal position.

(d) The grooves on the upper part of the movable finger of the large claw are weaker.

(e) The fixed finger of the claw of the smaller of the anterior pair of pereiopods is more slender.

The large claw of the *A. morganensis* differs from either hand of *A. plectrorhynchus* in features (a) and (c) above and in having parts of the palm granulate rather than smooth.

Family Callianassidae Dana, 1852
Subfamily Callianassinae Dana, 1852
Genus *Callianassa* Leach, 1814

Type species: *Cancer* (*Astacus*) *subterraneus* Montagu, 1808, by monotypy.

Callianassa Leach, 1814. Barnard, 1950: 505 (generic synonymy, generic description, key to extant South African species). Zariquiey Alvarez, 1968: 288 (generic description, key to extant Spanish species). Glaessner, 1969: R477. Vía, 1970: 33.

Callianassa bulwara sp. nov.

Text-figure 26a,b, plate 1 figures 8a,b - 11

Name

Named after the property "Bulwara", near the locality where the species was collected.

Material

Incomplete propodus of the right (large) cheliped, holotype S.A.M. P15627. Incomplete propodus of right (large) cheliped, paratype S.A.M. P15628. Fixed finger of right and left (large) chelae, paratypes S.A.M. P15629-30. Specimens all preserved as the original shell material and coll. R.J.F.J., 1968.

Occurrence

Between 7 and 8.5 m (P15627-29) and at 14 m (P15630) above N.R.L., Nildottie loc. 3.

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Palm of large chela subrectangular, 1.6 times as long as high, slightly decreasing in height distally, moderately compressed laterally; upper margin forming a fine, sharp, longitudinal ridge with a row of 11 or so fine pores on outer side; lower margin a sharp crest with a row of small denticles which each have a conspicuous pore on distal side of base; distal margins slightly oblique; a notch above base of fixed finger; smooth, moderately convex outer face of palm with three pores on upper distal portion, one or two pores on posterior position, a longitudinal row of four widely spaced pores at about a 1/3 of height from lower margin, and a row of quite closely spaced pores adjacent to lower margin; gently convex inner face smooth except for a few granules near notch above base of fixed finger, and with a row of pores near upper margin and a longitudinal line of four widely spaced pores near middle of face. Fixed finger slender about half length of palm, tapered, slightly deflexed relative to palm basally, gently curved upwards and inwards distally; lower margin rounded and with a row of large pores, outer surface with one row of pores on lower part and another row near prehensile margin; several widely spaced pores on inner surface; sharp prehensile margin with a line of 5-10 minute granules on proximal half and a slight prominence at about 3/5 length of finger from proximal end.

Measurements

The palm of the holotype propodus S.A.M. P15627 is 10 mm long and 6.3 mm high. The paratype propodus S.A.M. P15628 is 15 mm long (incomplete) with the palm 11 mm long (incomplete).

Remarks

These remains are closely similar to the corresponding parts of

Callianassa longa Noething, 1885, from the Upper Eocene of Egypt. They differ, however, in having the upper margin of the palm nearly straight rather than gently convex, the base of the fixed finger slightly less deflexed, and the row of pores near the lower margin of the palm continued along the ventral aspect of the fixed finger. They differ from *Callianassa bakeri* Glaessner, which occurs in the Middle Paleocene of Victoria, in the more elongate form of the palm and in having the upper margin of the palm smooth rather than serrate and the lower margin more conspicuously serrate.

Elongate *Callianassa* chelae of the *C. bakeri*, *C. longa*, *C. bulwara* type are widely distributed in the Early Tertiary of the world and are known also from the Upper Oligocene of Panama and the Miocene of Java (Glaessner, 1947; Vía, 1970). Their distribution suggests that they are mostly warm-water species.

The present remains are moderately similar to the propodus of the large claw of an unidentified modern species of *Callianassa* which Professor Glaessner collected from the intertidal mud flats of Port Moresby, New Guinea. This extant species differs from the fossil form in having the upper and lower margins of the palm of the large claw rounded for most of their length, the prehensile margin of the fixed finger smooth, and the hair pores on the upper aspect of the same finger more numerous. A sketch of the distal elements of the large cheliped of this New Guinea species is given here for comparison (Figure 27).

Callianassa aequimana Baker, 1907

Plate 1 figure 12a,b; Plate 2 figure 1

Callianassa aequimana Baker, 1907: 182, pl. 24 figs. 1-8. Hale, 1927: 87, fig. 87.

Material

Isolated specimens of the claws and numerous remains of the two chelipeds and associated fragments of the carapace. Complete propodus of left chela, hypotype S.A.M. P15890. Carpus and hand of right cheliped, and hand of left cheliped associated, hypotype S.A.M. P15889. Specimens all preserved as the original shell material and coll. R.J.F.J., 1970-1971.

The author has also examined the spirit-preserved types of the extant C. aequimana; the holotype S.A.M. C901, and the paratype specimens S.A.M. C902.

Occurrence of Fossil Material

Sea-cliffs about 1 km south of Port Willunga.

Stratigraphic Position and Age

Middle part of Hallett Cove Sandstone. Pliocene.

Measurements

The propodus of a left chela, S.A.M. P15890, is 14 mm long, with the palm 10 mm long and 8.5 mm high. The propodus of the right claw of S.A.M. P15889 is 15 mm long.

Remarks

These remains are indistinguishable from the corresponding parts of the modern *C. aequimana*. This species was first described from specimens collected near Kingston, South Australia (Baker, 1907). A dried specimen, S.A.M. C899 in the South Australian Museum, was taken from the stomach of a fish caught at a depth of 18 m in King George Sound, southwestern Western Australia.

Callianassa cf. *aequimana* Baker, 1907

Plate 1 figure 13a,b

Material

Propodus of right claw, S.A.M. P15551, and damaged palm of left claw, S.A.M. P15552, coll. R.J.F.J., 1967, 1969.

Occurrence

From 7 m (P15551) and about 16 m (P15552) above N.R.L., Nildottie loc. 3.

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Remarks

The preserved parts of this fossil form closely resemble the corresponding elements of *C. aequimana*, but differ in having the median groove on the distal part of the outer face of the palm slightly closer to the lower margin of the hand and an obtuse prominence rather than an acute denticle on the basal part of the prehensile margin of the fixed finger. The hands of the two are so similar in other respects that it can hardly be doubted that this fossil form is the ancestor of C. aequimana.

Genus Ctenocheles Kishinouye, 1926

Type species: Ctenocheles balssi Kishinouye, 1926, by monotypy.

Ctenocheles Glaessner, 1947: 4 (generic synonymy). Imaizumi, 1957: 299. Secretan, 1964: 148, 149 (generic diagnosis). Holthuis, 1967: 377. Glaessner, 1969: R478. Vía, 1970: 65, 78 (review). Rasmussen, 1971: 207.

Remarks

A number of forms belonging to Ctenocheles are not mentioned in the review of this genus given by Viá (1970), or have been described since; for the sake of completeness these are listed here:

Ctenocheles maorianus Powell, 1949

Extant: North Is. and northern South Is. of New Zealand; 35-73 m. Apparently a deep burrower in soft mud (Powell, 1949).

Ctenocheles cf. maorianus Powell. Glaessner, 1960

Castlecliffian, Upper Pleistocene: Wanganui, North Is. of New Zealand.

Ctenocheles sujakui Imaizumi, 1957

Eocene: Kyushu, Japan.

Ctenocheles madagascariensis Secretan, 1964

Upper Cretaceous; Madagascar.

Ctenocheles A Holthuis, 1967

Extant: Straits of Florida near Bimini Group, 297-406 m; off the north coast of Panama, west of the entrance of the Panama Canal, 109-295 m.

Ctenocheles B Holthuis, 1967

Extant: Off Cartagena, Columbia, 81-100 m; off Cordoba State, Columbia, 62-65 m.

Ctenocheles. Rasmussen, 1971

Lower Danian. Stevns Klint, Denmark.

In addition to these records of the genus, Ctenocheles cultellus (Rathbun) has been reported from New Jersey (Roberts, 1956) in rocks of Upper Paleocene age.

Ctenocheles victor, from southern Victoria, was originally described as being of Eocene age, but is now known to be from the Upper Paleocene (above, p.61).

Via (1970:pp.62,75) erected a new species Ctenocheles glaessneri for a propodus of a chela included by Glaessner (1947) in Callianassa bakeri (the specimen is that illustrated in Glaessner's plate 1 figure 4a,b). All the material which Glaessner included in *Callianassa bakeri* is from the Middle Paleocene of southern Victoria (above, p.61). The author has examined the specimen for which Via erected *Ctenocheles glaessneri* and finds that its palm has the sharp upper and lower margins typical of *Callianassa*, and that it is in no way different from the other specimens in the type series of *Callianassa bakeri*. Thus *Ctenocheles glaessneri* Via is a synonym of *Callianassa bakeri* Glaessner.

Ctenocheles fragilis sp. nov.

Text-figure 28a-f , plate 2 figures 2 - 8a,b

Name

From the Latin *fragilis*, meaning fragile.

Material

A number of more or less incomplete fingers of the chelae of the first pair of chelipeds and several examples of the palm of the large claw. Incomplete fixed finger of left (large) chela, holotype N.M.V. P29352, and various remains of fingers of the large chela, paratypes N.M.V. P29353-P29357. Incomplete fixed finger of chela of right (smaller) first pereiopod, S.A.M. P15884. Various remains of the claws preserved in phosphatic nodules, paratypes N.M.V. P29358-P29362, S.A.M. P15887-88. All specimens preserved as the original shell material; N.M.V. P29358-P29362 coll. Rev. A. W. Creswell; S.A.M. P15888 in collection of R. Tate; N.M.V. P29352-P29357 coll. F. A. Cudmore; S.A.M. P15884 and P15887 and several other specimens coll. R.J.F.J., 1966.

Occurrence and Stratigraphic Position

(Top of Jan Juc Marl) The Ledge, cliffs opposite Bird Rock, Torquay (N.M.V. P29352-P29357); and from a fallen block of the Puebla Clay at the same locality (S.A.M. P15884).

Beds of remanié phosphatic nodules at base of (Late Miocene to Pliocene) Moorabool Viaduct Sands, at Geelong (S.A.M. P15888) and Corio Bay, Geelong (N.M.V. P29358-P29362), and at "Rugby Park" at Fenwick, near Geelong (S.A.M. P15887).

Age

Late Upper Oligocene or early Lower Miocene, to middle Lower Miocene. The specimens from the nodule beds at the base of the Moorabool Viaduct Sands are probably remanié from the late Oligocene or Early Miocene.

Description

Fingers of chela of larger first pereiopod slender, elongate, strongly compressed laterally for greater part of length; distal portions tapered and curved to form pincers; prehensile margins armed with numerous slender, slightly curved, conical teeth. Fixed finger progressively tapering for whole length, deflexed relative to palm; lower margin forming a distinct keel continuous onto proximal part of palm;

on inner side of lower margin a row of more than 28 small, conspicuous nodes which each have a fine pore on the distal side; outer and inner faces of finger each with several irregular longitudinal rows of fine pores, a row of very distinct pores near lower margin of outer face; prehensile margin bearing 32 or so teeth, six or seven large, elongate primary teeth spaced at not quite regular intervals with two to four (usually three to four) rather even-sized, small, secondary teeth between. Movable finger with basal portion compressed dorsoventrally and expanded laterally, more distal parts of finger strongly compressed laterally, plate-like beyond middle of the length; distal extremity rather abruptly tapered as it curves to pincer; upper margin with a line of more than 17 fine pores which each have their proximal lip slightly raised to form a weak node; outer and inner faces each with several irregular rows of fine pores, both faces have a row of conspicuous pores near upper margin; prehensile margin bearing more than 31 teeth, the seven or more large, elongate primaries not quite regularly spaced and with three or four rather even-sized, small, secondary teeth between.

Palm of large chela inflated, 1.1 times as long as high, decreasing in height distally; upper and lower margins broadly rounded for most of their length and each with a line of obscure pores; inner face more convex than outer; distal margin of palm with a large, convex prominence on either side and a short flange above the inner of these prominences; a few granules on surface immediately proximal to inner prominence of distal margin and associated flange, remainder of palm smooth.

Incomplete finger of smaller first pereiopod slender, suboval in section with two rows of pores on either side; non-occludent margin with a row of elongate depressions which each contain a pore; small, triangular teeth on prehensile margin, every third or fourth tooth larger.

Measurements

The holotype N.M.V. P29352, a fixed finger of the large claw, is 27 mm long (incomplete). Paratype N.M.V., P29362 a fixed finger of the large claw, is 34 mm long (incomplete). Paratype N.M.V. P29358, a dactylus of the large claw, is 37 mm long (incomplete). Paratype N.M.V. P29360, a palm of the large claw, is 20 mm long, 18 mm high and 12 mm in width.

Remarks

The claw of the larger first pereiopod of this species seems closely similar to that of the Eocene Japanese fossil C. sujakui, but appears to differ in having the movable finger more slender, and the secondary teeth on both fingers slightly smaller. The fixed finger of the claw of its smaller first pereiopod lacks the obtuse tooth which appears to be present on the equivalent digit of C. sujakui (see Imaizumi, 1957: pl.44, fig.2). A more detailed and meaningful comparison is not possible because of the incomplete and fragmentary nature of the remains in either case. The fingers of the larger first pereiopod of C. fragilis have more numerous secondary teeth than in the Middle Oligocene, Hungarian C. rupeliensis, the only previously described mid-Tertiary representative of the genus.

Ctenocheles compressus sp. nov.

Text-figure 29a-f, plate 2, figures 9a,b - 14

Name

From the Latin compressus meaning compressed; in reference to the shape of the fingers of the larger claw of the first pair of pereiopods.

Material

Numerous specimens of the fingers of the chelae of the anterior pair of chelipeds. Specimens of the incomplete dactylus of the right (large) chela, the holotype S.A.M. P15872 and paratype N.M.V. P29351. Examples of incomplete dactylus of the left (large) chela, paratypes S.A.M. P15873 and P15876. Several examples of the fixed finger of the large chela including paratype S.A.M. P15875. A fixed finger of smaller first cheliped tentatively assigned to this species, paratype S.A.M. P15881. All specimens preserved as the original shell material. S.A.M. P15872-73 and various other specimens coll. R. Tate; N.M.V. P29351 and a number of other materials coll. F. A. Cudmore; S.A.M. P15881 and other specimens coll. Bret Robinson, 1967; S.A.M. P15875 and a number of other remains coll. R.J.F.J., 1966-1967.

Occurrence and Stratigraphic Position

Cliffs along River Murray, South Australia, stratigraphic position unknown (S.A.M. P15872-73). Cadell Marl Lens (N.M.V. P29351 and S.A.M. P15875, P15881) and upper member of the Morgan Limestone (S.A.M. P15876) at Morgan loc. 1. Apparently from the Morgan Limestone in the river cliffs between Wongulla and Mannum.

Age

Late Lower Miocene to possibly early Middle Miocene.

Description

General features of fingers of chela of larger first pereiopod as for *C. fragilis*. Fixed finger with a row of 19-26 conspicuous pore-nodes on keeled lower margin; inner and outer faces of finger each with several irregular longitudinal rows of fine pores, the pores numerous near prehensile margin but very widely spaced in more ventral rows; about 30 teeth on prehensile margin, seven large primaries spaced at rather regular to quite variable intervals with two to three to two to six much smaller secondary teeth between. Height of dactylus apparently about 1.4 times that of fixed finger at middle of length of both. Dactylus with a line of about 22 conspicuous pore-nodes on upper margin; inner and outer faces with several rows of fine pores; a row of distinct pores near upper margin of outer face; prehensile margin bearing more than 31 teeth, eight large primaries spaced at not quite regular intervals with two or three (usually three) smaller secondaries between, in each group of three secondaries the middle tooth larger.

Fixed finger of smaller first pereiopod, tapered, suboval in section with two rows of pores on either side; non-occludent margin with a row of pores; small, subtriangular teeth on prehensile margin, every third to fifth tending to be larger.

Measurements

The holotype S.A.M. P15872, a dactylus of the large claw, is 25 mm long (incomplete). Paratype S.A.M. P15875, a fixed finger of the large claw, is 28 mm long (incomplete). Paratype S.A.M. P15881, a fixed finger of the smaller of the anterior pair of claws, is 8.3 mm long.

Remarks

This is a close ally and probable descendant of the previous species *C. fragilis*. Its large claw differs from that of *C. fragilis* as follows:

(a) The height of the dactylus is greater.

(b) A much more conspicuous row of pore-nodes is present on the upper margin of the dactylus.

(c) A row of pores near the upper margin of the inner face of the dactylus of *C. fragilis* is missing in the present species.

(d) The pores on the lower two-thirds of both the inner and outer face of the fixed finger are much more widely spaced.

(e) The primary teeth on the fixed finger tend to be spaced at less regular intervals.

Ctenocheles sclephros sp. nov.

Text-figure 30a-f , plate 3 figures 1 - 12

Name

From the Greek *sclephros*, meaning slender; with reference to the fingers of the large claw.

Material

Numerous more or less fragmentary remains of the chelae and fingers of the first pair of chelipeds; an incomplete fixed finger of a left (large) chela, the holotype S.A.M. P15854, coll. R.J.F.J., 1968; an incomplete fixed finger of a left (large) chela and other remains preserved in a phosphatic nodule, paratype N.M.V. P29350, coll. F. A. Singleton, 1916; proximal part of dactylus of left (large) chela, paratype S.A.M. P15859, and various other fingers of chela coll. R. Tate; fixed finger of left (smaller) chela of anterior pair of pereiopods, paratype S.A.M. P15879, coll. Bret Robinson, 1967. Largely intact propodus of right (large) chela, paratype S.A.M. P15862 and palm of right (large) chela, paratype S.A.M. P15865, as well as various other materials, coll. R.J.F.J., 1967-1968. All specimens are preserved as the original shell material.

Isolated examples of dactyli of the large chela referred to this species are identified on the basis of their similarity to fixed fingers of this claw. Isolated examples of the fingers of the smaller claw of the anterior pair of pereiopods referred to this species are from the same stratigraphic horizon as remains definitely belonging to the species.

Occurrence

Murray Basin

Cliffs along the River Murray, South Australia, S.A.M. P15859. At 19-20 m above N.R.L., Nildottie loc. 2 (S.A.M. P15862). Between

11 and 19 m above N.R.L., Nildottie loc. 3 (S.A.M. P15858). From Morgan loc. 1 (S.A.M. P15865, P15879). From North-west Bend, 3 km N.E. of Morgan, S.A.M. P15857.

Otway Basin

Curlewis near Geelong (N.M.V. P29350).

Stratigraphic Position and Age

Murray Basin

Middle part of Mannum Formation (Nildottie area); from the middle part of the lower member and the top part of the upper member of the Morgan Limestone, and also in the Cadell Marl Lens (Morgan area). Middle Lower Miocene to late Lower or possibly early Middle Miocene.

Otway Basin

Bed of phosphatic nodules at base of (Late Miocene to Pliocene) Moorabool Viaduct Sands (Curlewis). Probably remanié from the Miocene.

Description

Fingers of chela of larger first pereiopod slender, elongate, about $2^1/_4$ times length of palm, gently bowed outwards, oval in section for greater part of length; distal portions tapered and smoothly curved to form elongate pincers; prehensile margins armed with numerous slender, slightly curved, conical teeth which usually have an extremely fine, sharp marginal ridge. Fixed finger progressively tapering for whole length, deflexed relative to palm; proximal portion of its lower margin forming a distinct keel continuous onto distal portion of palm, remainder of lower margin rounded; a line of about 14-18 conspicuous pores along inner side of lower margin, the proximal lip of each of these pores usually raised to form a small node; outer and inner faces of finger each with three irregular, longitudinal rows of pores, lowermost row on outer face most distinct; prehensile margin bearing 38-41 teeth, six to seven large, elongate primaries variably spaced with one to six different sized smaller secondaries in each interval. Dactylus with basal portion compressed dorsoventrally and expanded laterally, more distal parts of finger moderately compressed laterally; upper margin with a row of pores set in depressions; inner and outer faces each with two irregular longitudinal rows of pores; lateral prominences at base of finger perforated below; large primary teeth on prehensile margin spaced at rather regular intervals with four to five different sized, smaller secondaries between.

Palm of large chela inflated, 1.1-1.2 times as long as high, its upper and lower margins markedly convergent distally, broadly rounded for most of their length and each with a line of rather obscure pores; distal margins with a prominence at place of articulation of dactylus; surface of palm smooth.

Fingers of chela of smaller first pereiopod nearly round in section, and tapering to form curved pincers; fixed and movable finger each with two longitudinal rows of pores on both inner and outer surfaces and another row of pores on non-occludent margins; small, subtriangular teeth on prehensile margins, slightly larger teeth set at rather regular intervals with two or three to five or six smaller teeth between in different specimens.

Distal portion of palm of smaller first pereiopod compressed laterally and decreasing in height distally; outer face with a few scattered pores on distal portion and a row of pores near lower margin; another row of pores on lower margin of palm; inner face with a row of pores near upper margin; greater part of both inner and outer faces of palm obscurely wrinkled or roughened.

Measurements

The holotype S.A.M. P15854, a fixed finger of the large claw, is 29 mm long (incomplete). Paratype S.A.M. P15862, a propodus of the large claw, has the fixed finger 29 mm long (incomplete), and the palm 13 mm long (incomplete), 12 mm high and 8.4 mm wide (slightly distorted). Paratype S.A.M. P15865, a palm of the large claw, is 12 mm long and 9.2 mm high. Paratype S.A.M. P15879, a fixed finger of the smaller claw of the anterior pair of the pereiopods, is 8.7 mm long.

Remarks

The large claw of this species is readily distinguished from its equivalent in *C. fragilis* and *C. compressus* by the more ovate section of the fingers, the less regular arrangement of the teeth on the fixed finger, the larger number of secondary teeth on this same finger (31-34 in present species, about 25 in *C. fragilis*, about 23 in *C. compressus*) and the greater average size of the secondary teeth on both fingers. The upper margin of its palm is longer than in *C. fragilis*. The upper margin of its dactylus lacks the conspicuous pore-nodes present in *C. compressus*.

The remains of *C. sclephros* are quite closely similar to the corresponding parts of *C. maorianus*. However the large claw of *C. sclephros* differs from that of this modern species in lacking a large number of pores on the upper, inner part of the palm, in the more elongate and slender form of the fixed finger and in the same finger being a little less strongly deflexed relative to the palm and having a larger number of secondary teeth (this finger has 24-25 secondary teeth in *C. maorianus*). The arrangement of the pores on both the fingers of the large claw of the two also differs.

Palaeoecology of *Ctenocheles*

The fossil remains of the species of *Ctenocheles* described above often occur as associations of two or more individuals. As the remains of the chelae present in these associations are usually almost equal-sized and often show opposite heterochely, there can be no doubt that several individuals are involved. These associations occur in three different ways:

(a) The claws of several individuals *in situ* in animal burrows which have formed centres of concretionary phosphatisation.

(b) The remains of several individuals *in situ* in sediments where no burrow structures are visible and phosphatisation is apparently absent.

(c) The remains of several individuals within water-rounded, remanié phosphatic nodules.

Remains in animal burrows

Straight or curved animal burrows up to a metre long and parallel to the bedding are common in bedding plane exposures of the Jan Juc Marl on the wave cut platform below the cliffs adjacent to Bird Rock at Torquay, Victoria, and on fallen blocks of the Puebla Clay at the same locality. The burrows are filled with differently coloured sediment to the enclosing matrix and are often the sites of formation of dense, black, elongate phosphatic concretions. A concretion of this kind formed around a burrow in a fallen block of the Puebla Clay contained the remains of the claws of a number of individuals of *C. fragilis*. Fragmentary fingers of claws of the same species occurred in other similar concretions in this block and in a concretion in the cliff at the top of the Jan Juc Marl.

The infillings of the burrows at the locality just mentioned are suboval in section, 5 or 6 cm wide and several centimetres high. Compaction of the enclosing matrix may have distorted them from an originally more rounded shape. Comparison between the size of the *Ctenocheles* claws contained in the burrows and those of modern species of the genus suggests that the animals to which the former belonged were 18 to 20 cm long, including the outstretched chelipeds, and with the cephalothorax about 2 cm high. As thalassinids are adapted to a burrowing mode of life and the dimensions inferred for the animals represented by the fossils are comparable to the observed size of the burrows, it seems likely that these structures were made and inhabited by *Ctenocheles*.

Probably the *Ctenocheles* were trapped in their burrows by unusually rapid deposition of sediment and penetration of this material into the burrows. The occurrence of the remains of several *Ctenocheles* in the one burrow suggests that the animals were gregarious.

Burrows attributed to *Ctenocheles* have recently been described from the Maastrichtian-Danian boundary at Stevns Klint, Denmark (Rasmussen, 1971). These burrows are of comparable size to the ones described here but differ in having numerous, narrow, blind-ended branches.

Associations in unaltered sediments

An association of *Ctenocheles* remains in unaltered sediment was found in the Cadell Marl Lens within the Morgan Limestone at its type section, 6.4 km south of Morgan, South Australia. In this instance the remains of both claws of two equal-sized individuals of *C. sclephros* occurred with a fixed finger of the larger claw of a much smaller individual of *C. compressus* in a small patch of sediment (4-5 cm diameter). No sign of a burrow structure was evident. These remains might represent the regurgitated or defecated remains of a meal of a larger animal. It is notable, though, that these fragile fossils are preserved largely intact and show no etching by digestive juices, and that both of the anterior chelae of the individuals of *C. sclephros* are present. Another and probably more tenable explanation for the association is that two individuals of *C. sclephros* were living together and were trapped in their burrow after feeding on a smaller individual of *C. compressus*.

Other occurrences of the remains of several individuals of *Ctenocheles* together in small patches of sediment have been illustrated by Glaessner (1947) and Imaizumi (1957).

Associations in remanié phosphatic nodules

The water-rounded phosphatic nodules which occur at the base of the Late Miocene-Pliocene Moorabool Viaduct Sands in the Geelong district, Victoria (Bowler, 1963; here p.52) occasionally contain the remains of the chelae of *C. fragilis* and, more rarely, *C. sclephros*. Several such nodules included the remains of two individuals of *Ctenocheles* and scattered fish scales and bones, the latter up to about 1 cm long.

The nodules occurring at the base of the Moorabool Viaduct Sands are considered to be remanié and to have been derived from concretions eroded from the pre-Late Miocene Tertiary sediments which the Moorabool Viaduct

Sands disconformably overlie. It seems likely that the nodules with *Ctenocheles* represent parent concretions identical to those formed around the animal burrows in the sediments of the cliffs at Torquay. Their included fish scales are interpreted as further evidence of the feeding habits of *Ctenocheles*.

It is concluded that *Ctenocheles* probably excavated and inhabited burrows preserved in the sediments of the cliffs at Torquay. Associations of the remains of more than one individual in a burrow suggest gregarious habits. Other occurrences in sediments where the burrows are not visible indicate at least a pair of animals living together. Remains associated with *Ctenocheles* in sediments and nodules may indicate that they fed on like species and small fishes.

It might be supposed that the soft bodied *Ctenocheles* feeds by waiting at the top of its hole with the dagger-tipped and sharp-toothed fingers of its larger chela spread wide as a trap for unwary visitors. Powell (1949) remarked of the living New Zealand form *Ctenocheles maorianus* that "this species is apparently a deep burrower in soft mud, for chela are frequently torn off by trawl nets, but the dislodgement of a complete animal is a rare occurrence".

Superfamily Paguroidea
Family Paguridae Latreille, 1802
Subfamily Pagurinae Latreille, 1802
Genus *Pagurus* Fabricius, 1775
(= *Eupagurus* Brandt, 1851)

Type species: *Cancer bernhardus* Linnaeus, 1758, subsequent designation by Latreille, 1810.

Pagurus Fabricius, 1775. Fize and Seréne, 1955: 155 (generic synonymy, generic description, history, key to extant species from Vietnam). Forest and Saint Laurent, 1967: 116 (discussion, key to extant species from the Atlantic coast of South America). Zariquiey Alvarez, 1968: 243 (in key, generic description, key to extant Spanish species). Glaessner, 1969: R479.

Pagurus gambierensis sp. nov.
Plate 5 figure 2a,b

Name

Named after Mount Gambier, South Australia, the largest town near the locality where the species occurs.

Material

Two specimens of the propodus of the right (?larger) chela, the holotype S.A.M. P15770 and paratype S.A.M. P15771. Both specimens preserved as the original shell material and coll. R.J.F.J., 1968.

Occurrence

Quarry on northeastern part of section 26, Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Palm of right chela about 1.2 times as long as high, highest at about 4/5 of its length from proximal end, markedly biconvex; upper margin gently arched, bluntly ridged and with a line of spiniform granules; lower margin gently convex, rounded proximally, bluntly crested distally, this crest bearing a line of coarse, spiniform granules and continuing below fixed finger; distal margins slightly oblique, notched at point where movable finger articulates; outer face ornamented by rather widely spaced, coarse, spiniform granules; inner face obscurely roughened, with two or three granules adjacent to upper margin and a few low granules near proximal part of lower margin. Fixed finger about .5 length of palm, curved inwards, weakly spooned above; outer face ornamented by a few scattered granules and with a line of obscure pores near upper margin; inner face obscurely roughened and with a few pores on distal portion; dorsal surface very slightly concave above basal $\frac{1}{2}$ of finger and with a small rounded depression above distal portion of finger; prehensile margin nearly smooth; an opening at tip of finger.

Measurements

The holotype propodus S.A.M. P15770 is 17 mm long (incomplete), with the palm 11 mm long (incomplete) and 9.2 mm high. The paratype propodus S.A.M. P15771 is 14 mm long (incomplete).

Remarks

This species resembles the equivalent parts of the hand of Pagurus alabamensis Rathbun, 1935, from the Eocene of Alabama, but differs in having the lower margin of the propodus more convex and the outer surface less densely granulate or spinulose. The granulation is coarser and more sparsely distributed than in Pagurus merceti Vía, 1959, from the Middle Eocene of Spain and Pagurus marini Vía, 1959, from the Middle and Upper Eocene of Spain.

The propodus of the present species also resembles that of the right claw of the extant Pagurus provenzanoi Forest and Saint Laurent, 1967, from off Brazil and Uruguay. It differs from the latter in its narrower and straighter fixed finger, in the almost smooth rather than dentate prehensile margin of this finger, in the less oblique distal margins of the palm, and in apparently having several more granules or spinules in the row on the upper margin of the palm.

Pagurus greenwayensis sp. nov.

Plate 4 figures 5a,b - 8

Name

Named after the locality "Greenways Landing", where the species is found.

Material

Seven specimens of the propodus of the right (? larger) chela. Relatively complete specimens, the holotype S.A.M. P15903, and paratype S.A.M. P15906. Two examples of the palm of the same claw, paratypes S.A.M. P15904-05. All specimens preserved as the original shell material, and collected by R.J.F.J., 1968-1969.

Occurrence

At 19-20 m above N.R.L., Nildottie loc. 2 (P15908). Between 14.5 and 17 m above N.R.L., Nildottie loc. 3 (P15903-06).

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle to late Lower Miocene.

Description

Palm of right chela subrectangular, 1.3 times as long as high, markedly biconvex; upper margin downcurved proximally, otherwise nearly straight, forming an obtuse ridge which bears a line of fine granules; lower margin gently convex, rounded; distal margins moderately oblique, notched at point where movable finger articulates; outer face ornamented by nearly vertical, indistinct, discontinuous striae and four weak longitudinal ridges; the striae each with a line of minute, low granules; the longitudinal ridges each bearing a line of fine granules; first ridge on upper portion of face, second and third joined distally on middle of face, the fourth moderately oblique, situated on lower portion of face and continuing below fixed finger; upper portion of inner face ornamented with oblique rows of obscure granules, lower portion with faint, obscurely granulate, vertical striae. Fixed finger short, .4 length of palm, curved inwards, and with a slight hollow above basal portion; outer face finely and obscurely granulate or smooth, and with a line of four or five pores near upper margin; lower margin of finger angulate, with a narrow rib bearing a line of small granules; inner face smooth, with a row of four pores near upper margin; a few small rounded denticles on both inner and outer margins of hollow above basal part of finger, distal part of finger apparently with a few very small denticles.

Measurements

The holotype propodus S.A.M. P15903, from a right (? larger) chela, is 11 mm long, with the palm 8.2 mm long and 5.7 mm high. The other specimens known are about the same size or smaller.

Remarks

The propodus of Pagurus greenwayensis closely resembles its equivalent in the extant species Pagurus nana (Henderson, 1888), from Port Jackson to Beachport, southeastern Australia. Noted differences between the two are:

(a) A much less conspicuous ridge is present on the outer side of the upper margin of the palm of the fossil species.

(b) The ridge on the outer side of the lower part of the palm of the fossil species is weaker and the ridge on the upper part of the outer side of the fixed finger is also less pronounced.

(c) In *P. greenwayensis* the base of the fixed finger is appreciably wider.

As the similarity between the two species is otherwise very marked, it seems likely that the *P. greenwayensis* is near the ancestor of *P. nana*.

Pagurus murrayensis sp. nov.

Plate 5 figure 1a,b

Name

Named after the River Murray, on which the locality of the species is situated.

Material

Seven specimens of the propodus of the right (? larger) chela. Relatively complete examples, the holotype S.A.M. P15891, and paratypes S.A.M. P15892-94. Specimens all preserved as the original shell material and coll. R.J.F.J., 1968-1969.

Occurrence

Between 14.5 and 16.5 m above N.R.L., Nildottie loc. 3 (P15892-94). At 15-18 m above N.R.L., Nildottie loc. 4 (P15891).

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Palm of right chela as long as high, gradually increasing in height distally, robust; upper margin curved downwards proximally, otherwise almost straight, forming a blunt ridge which bears a line of small spinules; lower margin smoothly convex, forming a sharp angulation which bears a line of spiniform granules and continues below whole length of fixed finger; distal margins slightly oblique, notched at point where movable finger articulates; outer face obtusely angled to form a median ridge which bears a line of spiniform granules, flattish surfaces above and below this ridge ornamented by even-sized, low granules which each have a pore at apex; inner face strongly convex, the upper half bearing low, obscure tubercles and with a band of granules near upper margin, the lower half smooth except for a group of fine granules near proximal part of lower margin of palm, all tubercles and granules having one or several pores on distal aspect. Fixed finger stout, .65 length of palm, curved inwards to a moderate degree, spooned above; on upper part of outer face an obtusely angled longitudinal ridge bearing a line of spiniform granules, surface below this ridge ornamented by low granules which each have a large apical pore, a row of conspicuous pores adjacent to prehensile margin; inner face fairly smooth and with a row of pores near upper margin and a group of large pores near tip of finger; inner and outer margins of hollowed upper surface of finger with low, rounded, close-set denticles, the denticles on outer side of prehensile margin tending to be elongated.

Measurements

The holotype propodus S.A.M. P15891, the largest specimen found, is 13 mm long, with the palm 8.7 mm long and 7.6 mm high.

Remarks

Pagurus murrayensis and P. greenwayensis occur together in the same part of the Mannum Formation at Nildottie. The remains of claws attributed to P. murrayensis may, however, at once be distinguished from those of P. greenwayensis by the strong angulation of the middle of the outer surface of the palm, the more sharply carinate upper margin of the palm and the marginal position of the lower carina on the palm. Both species are represented by remains of the right (larger) chela.

Subfamily Diogeninae Ortmann, 1892

Genus Paguristes Dana, 1851

Type species: Paguristes hirtus Dana, 1851, subsequent designation by Stimpson, 1858.

Paguristes Dana, 1851. Forest and Saint Laurent, 1967: 67 (generic diagnosis, distribution, key to extant species from the Atlantic coast of South America). Zariquiey Alvarez, 1968: 233 (in key), 235 (generic description). Glaessner, 1969: R480.

Paguristes chondrochelus sp. nov.

Plate 3 figures ~~14 - 17a,b~~
13 - 16 a, b

Name

From the Greek chondros, granular, and chelè, claw; in reference to the granulation of the hands.

Material

Three specimens of the propodus of the left (larger) chela; holotype S.A.M. P15570; paratypes S.A.M. P15572 and P15574. Two specimens of propodus of right (smaller) chela, paratypes S.A.M. P15571 and P15573. Specimens all preserved as the original shell material and coll. M. F. Glaessner (P15572) and R.J.F.J., 1968-1970.

Occurrence

At 10 m (P15573) and 16.5 m above N.R.L., Nildottie loc. 3. Between 7.5 and 15 m above N.R.L., Nildottie loc. 4 (P15570-01). Swan Reach, from east side of River Murray in lower part of cliff immediately north of ferry (P15572).

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Palm of left chela 1.1 times as long as high, markedly biconvex; upper margin forming a ridge which bears a line of four or five pointed tubercles; lower margin broadly rounded, a nearly smooth area extending below finger and bounded on either side by irregular rows of coarse granules and tubercles; distal margins oblique, the outer distal margin with a line of three or four minute denticles near base of fixed finger; outer face closely covered by variably sized, moderately fine to fine, low granules; inner face ornamented by scattered low tubercles, three or four conspicuous tubercles in a vertical row adjacent to thickened upper portion of inner distal margin. Fixed finger stout, .6 length of palm, slightly deflexed, curved inwards, spooned above; outer face finely granular with two pits at about middle of height and a row of four or five pores adjacent to prehensile margin; inner face bearing a few scattered granules and with several pores near upper margin; spooned upper surface with a row of three pores; proximal $^2/_3$ of prehensile margin arched and bearing a line of six to nine close-set, small, rounded denticles; a row of seven or eight perforations following curved margin of blunt tip of finger.

Propodus of right chela much resembling that of left, but with the ornamentation less accentuated; lower $^1/_3$ of outer surface of manus smooth, remainder of outer surface of propodus covered by weak granules which each have a fine pore on distal side. Prehensile margin of fixed finger arched basally and with a row of 17 or so close-set, small, rounded denticles.

Measurements

The holotype S.A.M. P15570, a propodus of the left (larger) claw, has the palm 7.5 mm long and 6.2 mm high, and the fixed finger 4.6 mm long.

Paratype S.A.M. P15574, also a propodus of the left (larger) claw, has the palm 7.6 mm long and 6.8 mm high, and the fixed finger 5.5 mm long. Paratype S.A.M. P15573, a propodus of the right (smaller) claw, has the palm 5 mm long (incomplete) and 4.9 mm high, and the fixed finger 3.8 mm long.

Remarks

The propodi of the claws of Pagurus chondrochelus are similar to those of Paguristes johnsoni Rathbun, 1935, from the Paleocene of Alabama, but differ in having a row of pointed tubercles on the upper margin of the palm and in the convex rather than straight upper margin of the fixed finger of the smaller chela and the denser granulation of the middle part of the outer face of the larger chela. Its fingers are apparently less conspicuously dentate and more bluntly terminated than in the form Paguristes sp. Rathbun, 1926, from the Miocene of California.

The left propodus (larger claw) of the fossil species resembles that of the modern Paguristes triangulopsis Forest and Saint Laurent, 1967, from off Brazil, but differs in having the outer surface granulate, rather than ornamented by small conical tubercles.

Paguristes brevirostris Baker, 1905

Paguristes brevirostris Baker, 1905: 256, pl.33, figs 1, la. Hale, 1927: 90, fig.86.

Paguristes brevirostris antiqua subsp. nov.

Plate 4 figures 1a,b - 4a,b

Name

From the Latin *antiquus*, ancient.

Material

Three well preserved examples of the propodus of the left (larger) chela; holotype S.A.M. P15577; paratypes S.A.M. P15575-56. One damaged example of the same propodus, paratype S.A.M. P15578, and a fixed finger, paratype S.A.M. P15582. Two specimens of the propodus of the right (smaller) chela, paratypes S.A.M. P15579 and N.M.V. P29363 and a palm of this claw, paratype S.A.M. P15580. All specimens preserved as the original shell material; N.M.V. P29363 coll. G.B.Pritchard; other specimens coll. R.J.F.J., 1968-1970.

Occurrence

Murray Basin

From 19-20 m above N.R.L., Nildottie loc. 2 (P15582). Between 7 m (holotype) and 15 m (P15578) above N.R.L., Nildottie loc. 3 (P15575-80).

Otway Basin

From Muddy Creek, near Hamilton (N.M.V. P29363).

Stratigraphic Position and Age

Murray Basin:

Middle part of Mannum Formation. Middle to late Lower Miocene.

Otway Basin:

Muddy Creek Marl. Late Lower Miocene.

Description

Palm of left chela 1.5 times as long as high, markedly biconvex; outer surface ornamented by stout spinules which each have a minutely perforate, V-shaped areole encompassing distal aspect of base; four similar spinules on bluntly ridged upper margin of palm; lower margin broadly rounded and with a wide band of coarse granules which also have a group of minute pores on distal side; distal margins of palm oblique, finely granulate near base of fixed finger; inner face smooth for greater part, but with several low tubercles on upper distal portion and a few conspicuous tubercles which all have a group of minute pores on distal side. Fixed finger .5 length of palm, tapered, slightly deflexed, curved inwards; outer face closely covered by granules and with a row of three or four pores adjacent to prehensile margin; lower margin forming a blunt ridge which bears a line of spinules; two rows of pores on inner-ventral aspect of distal portion of finger; smooth, slightly hollowed upper part of inner face with a row of three pores; prehensile margin notched basally and then forming a crest armed with 10-11 small, rounded denticles; an opening at tip of finger.

Propodus of right chela very similar to that of left except for the ornamentation being slightly less accentuated.

Measurements

The holotype S.A.M. P15577, which is from a left (larger) chela, is 11 mm long, with the palm 6.9 mm long and 5.9 mm high. Paratype propodus S.A.M. P15579, from a right (smaller) chela, is 8 mm long (incomplete) with the palm 5 mm long (incomplete) and 4.8 mm high. Paratype propodus N.M.V. P29363, from a right (smaller) chela, is 8.6 mm long, with the palm 5.1 mm long and 4.5 mm high.

Remarks

The propodi of the claws of the present form differ only slightly from those of the living Paguristes brevirostris Baker, 1905, which inhabits Gulf St. Vincent and Spencer Gulf, South Australia. The spines on the outer surface and especially the lower aspect of the propodus of both claws of the fossil form are a little more numerous and are positioned slightly closer together than in the extant species. In the propodi of the fossil form the lip of the palm above the articulation with the movable finger is smooth or bears a line of weak granules; in P. brevirostris the equivalent lip bears a line of distinct granules and an associated row of hair pores. These differences are regarded as being only of subspecific importance.

Genus Trizopagurus Forest, 1952

Type species: Clibanarius melitai Chevreux and Bouvier, 1892, subsequent designation by Forest, 1952.

Trizopagurus Forest, 1952: 255; 1952a 1-40 (review).

Trizopagurus sp.

Plate 4 figure 9a-c

Material

Two incomplete specimens of the merus of the chelipeds. Right merus S.A.M. P15785. Fragmentary left merus, S.A.M. P15786. Specimens preserved as the original shell material and coll. R.J.F.J., 1968.

Occurrence

Quarry on northeastern part of section 26 (P15785) and quarry near centre of section 28 (P15786) Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Merus apparently quite short; rather high, moderately compressed laterally; upper margin convex, formed into a rounded crest ornamented distally by three short, oblique, granulose ridges; outer face gently convex, ridged and granulate towards distal portion of dorsal margin, otherwise obscurely striated or almost smooth; inner face smooth, almost flat with a deeply incised suture adjacent to lower margin; ventral aspects broadly rounded, granulose on either side, apparently with a prominent central tubercle. A deeply incised transverse groove on distal portion of merus marks off a wide marginal border; upper outer margin of border with a line of granules; ventral areas of border isolated by further grooves.

Measurements

The merus, specimen S.A.M. P15785, is 17 mm long (incomplete), 12 mm high (incomplete) and 8 mm in width.

Remarks

These remains greatly resemble the equivalent parts of specimens of the extant _Trizopagurus_ _strigimanus_ (White, 1847) taken in the waters off eastern and southern Australia. The merus fossil of the form differs from that of this extant species only in having the lower margins smooth rather than granulate, and in seeming to have the upper distal part of the outer surface less spinose.

Although too fragmentary to be named formally these remains are important in showing that the interesting genus _Trizopagurus_, which has evolved a complex pattern of stridulating ridges on the inner surface of the chelae, ranges back to the Oligocene.

Superfamily Galatheoidea
Family Galatheidae Samouelle, 1819
Subfamily Galatheinae Samouelle, 1819
Genus *Munida* Leach, 1820

Type species: *Pagurus rugosus* Fabricius, 1775, by monotypy.

Munida Leach, 1820. Barnard, 1950: 482 (in key), 488 (generic synonymy, generic diagnosis, key to extant South African species). Zariquiey Alvarez, 1968: 268 (in key), 281 (generic description, key to extant Spanish species). Glaessner, 1969: R482.

Munida monowalana sp. nov.

Text-figure 31; plate 5 figures 3 - 5

Name

Named after the property "Monowalana" which is near the locality where the species is found.

Material

Thirteen more or less fragmentary remains of the carapace; specimen showing left half of carapace with frontal region missing, holotype S.A.M. P15666; specimen showing right half of carapace with lateral rostral spine present, paratype S.A.M. P15667. Specimens all preserved as the original shell material and coll. R.J.F.J., 1967-1968.

Occurrence

Quarry on northeastern part of section 26, Hundred of Blanche, Mount Gambier loc. 1 (P15666-67). Quarry near centre of section 28, Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed and rarely in underlying beds in Gambier Limestone. Middle Oligocene.

Description

Carapace subquadrate, about as wide as long, slightly narrowed anteriorly, almost flat longitudinally, gently convex transversely; across middle of length a rearwardly arched, deeply impressed transverse groove forked laterally; a transverse row of spinules on anterior portion of carapace; rest of dorsal surface ornamented by 22-30 fairly continuous transverse ribs, every second, third or fourth more prominent, crest of each rib with a row of minute pores which probably bore fine hairs during life; a few other spinules and tubercles present.

Rostrum not known. Lateral rostral spines directed forward, slender, compressed dorsoventrally.

Supraorbital margins gently concave. Lateral margins of carapace with seven forwardly directed spinules, three hepatic, two on interval of margin between lateral branches of transverse carapace groove, and two behind; first spinule on hepatic margin minute, size of following spinules variable; posteriorly the lateral margins curve inwards. Nearly straight posterior margin of carapace with wide border which bears two secondary ribs.

Anterior margin of gastric region with a transverse row of 10 short spinules which progressively decrease in size laterally. A deep depression above outer extremity of orbit; a single tubercle behind this depression. Each side of carapace with three small spinules spaced at equal intervals behind oblique lateral portion of transverse carapace groove: one at place where groove branches and the other two on region between lateral branches of groove. Cardiac region indistinct, subtriangular, its lateral boundaries convergent rearward and marked only by a series of slight irregularities in transverse ribs ornamenting carapace.

Measurements

The carapace of the holotype S.A.M. P15666 is 18 mm long (incomplete) and originally was approximately 20 mm wide; this specimen represents the largest individual known.

Remarks

The carapace of *Munida monowalana* is rather similar to that of the living *Munida japonica* Stimpson, 1858, which is known from Halmahera (Indonesia), New Britain, Formosa, Korea Strait, and Japan. It differs in its greater relative breadth, in the straighter posterior margin and in the detailed arrangement of the spinules on the carapace: no distinct spinules are present on the mid-line behind the rostrum, an additional spinule is positioned behind the lateral part of the anterior branch of the transverse carapace groove, and two rather than three spinules are situated on the part of the lateral margin between the branches of the carapace groove.

Munida spriggi sp. nov.

Text-figure 32; plate 5 figures 6 & 7

Name

Named after Mr. R. C. Sprigg, who investigated and described the geology of the Mount Gambier area.

Material

Three incomplete specimens of the carapace; broken right half of carapace with frontal region and parts of lateral aspect missing, holotype S.A.M. P15657; carapace with interior surface exposed, the margins all damaged, paratype S.A.M. P15658; broken specimen showing interior surface of posterolateral aspect, paratype S.A.M. P15659. All specimens preserved as the original shell material and coll. R.J.F.J., 1968-1969.

Occurrence

Quarry on northeastern part of section 26, Hundred of Blanche, Mount Gambier loc. 1 (P15657-58). Quarry on southwestern part of section 30, Hundred of Blanche, Mount Gambier loc. 1 (P15659).

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Carapace subrectangular, about as wide as long, nearly flat longitudinally, gently convex transversely; across middle of length a rearwardly arched, deeply impressed transverse groove forked laterally; anterior sixth of carapace ornamented by low, squamose ridges and with a few spinules; major portion of carapace ornamented by approximately 25 fairly continuous transverse ribs, every second to fifth rib more prominent.

Lateral margins of carapace with five or more forwardly directed spinules, at least two hepatic, two known on interval of margin between lateral branches of transverse carapace groove, and one behind; posteriorly the lateral margins curve inwards. Posterior margin of carapace moderately concave and with a wide border which bears two secondary ribs.

Gastric region with a slight median axial ridge; anterior part of region bearing four small spinules in a medially positioned T-shaped arrangement, four prominent spinules at corners of a rectangle, and several tubercles situated laterally; lateral extent of region marked by short longitudinal grooves. Hepatic regions obscurely tuberculate before and bearing several small spinules behind. On each half of carapace three small spinules behind oblique lateral portion of transverse carapace groove: one near place where groove branches and the other two on region between lateral branches of groove. Cardiac region slightly raised, subtriangular, its lateral margins convergent rearward and marked by conspicuous irregularities in transverse ribs ornamenting carapace.

Interior surface of carapace with a pair of dash-shaped muscle attachments below middle of ridge marking external transverse carapace groove.

Measurements

The carapace of the holotype S.A.M. P15657 is 8.5 mm long (incomplete). The carapace of paratype S.A.M. P15659 is 19 mm long (incomplete).

Remarks

The carapace of *Munida spriggi* closely resembles that of the extant species *Munida andamanica* Alcock, 1901, which is known from the East African Coast, the Arabian Sea, the Coromandel Coast of India, the Andaman Sea, the vicinity of the islands of Nias and Siberut (Indonesia), and Japan. It differs principally in the detailed arrangement of the spinules on the dorsal aspect: the fossil species lacks the minute median spinule which is present between the posterior submedian pair of gastric spinules in *M. andamanica*, but has another further forward; several extra spinules are situated on the posterior part of the hepatic region and one additional spinule is positioned behind the lateral part of the anterior branch of the transverse carapace groove. *M. spriggi* may well be the ancestor of *M. andamanica*.

Infraorder BRACHYURA
Section DROMIACEA
Superfamily Dromioidea
Family Dynomenidae Ortmann, 1892
Genus *Dynomene* Latreille *in* Desmarest, 1825

Type species: *Dynomene hispida* H. Milne-Edwards, 1837, subsequent designation H. Milne-Edwards, 1837.

Dynomene Latreille in Desmarest, 1825. Sakai, 1965: 12 (generic synonymy). Glaessner, 1969: R487.

Carapace flattish, subcircular or polygonal, slightly broader than long, pilose in extant species. Front broadly and bluntly triangular, more or less distinctly notched or divided anteriorly, medially grooved above. Tips of fingers of chelae of first pair of pereiopods spooned. (After Rathbun (1937) and Barnard (1950)).

The following previously described extant forms belong to this genus:

Dynomene hispida Desmarest, 1825

Mauritius; Coetivy; Timor; Amboina; Solomon Is.; New Caledonia; southern Japan; Hawaiian Is. This species inhabits coral reefs or crevices in rock at a depth of about 10 fathoms (18 m) (Sakai, 1936).

Dynomene ursula Stimpson, 1860

Galapagos Is. to west coast of Mexico; 4-104 m.

Dynomene praedator A. Milne-Edwards, 1879

Madagascar; Coetivy; Postiljon Is.; Obilatu I.; Amboina; New Caledonia; Samoa; southern Japan.

Dynomene filholi Bouvier

Cape Verde I.; Principe I.; Annobón I.; from 23 to 150-275 m and rarely to 477 m.

Dynomene pugnatrix de Man,

Mauritius.

subsp. *D. pugnatrix brevimana* Rathbun, 1911

Providence Is., 91-143 m.

Dynomene pilumnoides Alcock, 1899

Natal, 91 m. Laccadive Is., 57-91 m. Japan, 80-150 m.

Dynomene spinosa Rathbun, 1911

Coetivy.

Dynomene tanensis Yokoya, 1933

Japan, 219 m.

Dynomene ovata sp. nov.

Text-figure 33; plate 5 figures 8 & 9

Name

From the Latin *ovatus*, ovate; in reference to the subovate outline of the carapace.

Material

One almost complete specimen and five other more or less fragmentary remains of the carapace; the holotype S.A.M. P15671, a carapace with most of the right side and posterior part broken away; paratype S.A.M. P15672, an almost complete carapace. Specimens all preserved as the original shell material. Fossil P15672 coll. M. F. Glaessner, 1953; P15671 and remaining specimens coll. R.J.F.J., 1968.

Occurrence

Quarry near middle of section 28, Hundred of Blanche, Mount Gambier loc. 1 (P15672). Quarry on northeastern part of section 26, Hundred of Blanche, Mount Gambier loc. 1 (P15671 and remaining specimens).

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Carapace subovate, .85 times as wide as long, gently convex above; regions distinct, delimited by shallow grooves; surface finely pitted, otherwise smooth.

Front projected forwards, broadly rounded, weakly notched anteriorly, medially grooved above.

Orbits transversely ovate and without an extraorbital tooth; supraorbital margins slightly raised, gently concave, singly and faintly notched; suborbital margins notched near antennal hiatus and with inner part forming a broad triangular tooth which projects well in advance of supraorbital margin in small individuals (Plate 5, Figure 9). Frontoorbital margin about .5 width of carapace.

Anterolateral margins rounded, each bearing five spinules, two hepatic, two epibranchial, and the last mesobranchial; second and third spinules a little more widely spaced and with a rounded tubercle just below interval, third and fourth slightly more prominent, fifth reduced. Posterolateral margins markedly convergent rearwards, gently convex for greater part of length, rounded posteriorly. Posterior margin about .4 width of carapace, slightly concave, and with a weak, narrow border.

Epibranchial regions small, swollen, separated from front by a deep transverse groove, and with an incised longitudinal groove between. Protogastric regions large, moderately inflated. Hepatic regions small, faintly marked. A short median groove bisects posterior part of mesogastric region. Lateral portions of cervical groove shallowly impressed, median portion deeply incised and containing slit-like posterior gastric pits. Metagastric region formed into two distinct transverse lobes. Shallow, curved grooves on either side of urogastric region. Cardiac region slightly raised, weakly two-lobed. Intestinal region indistinct. Epibranchial regions divided into two lobes by an oblique shallow groove.

Outer portion of branchiocardiac groove broad, moderately deeply impressed, extending from anterolateral corner of cardiac region to interval between fourth and fifth marginal spinules. Mesobranchial regions weakly ridged adjacent to branchiocardiac furrow. Posterolateral regions sloping obliquely downwards and outwards.

Material

The carapace of the holotype S.A.M. P15671 was originally 17 mm wide (excluding lateral spinules). The carapace of paratype S.A.M. P15672 is 8.4 mm long and 9.5 mm wide. Fragmentary remains indicate that the carapace may reach a width of approximately 23 mm.

Remarks

Dynomene ovata is closest to and almost certainly the ancestor of the modern species *D. pilumnoides*. The two are distinguished by the following differences:

(a) The spinules on the anterolateral margins of the carapace of the fossil species are much less prominent than the sharp teeth present in *D. pilumnoides*.

(b) The posterior margin of the carapace is nearly straight in the fossil species but is moderately concave in *D. pilumnoides*.

(c) Both the fossil form and the modern crab have one large suborbital tooth; this tooth seems to be much more protrusive in the fossil.

Superfamily Homoloidea

Family Homolidae White, 1847

(=Thelxiopeidae Rathbun, 1937)

Genus Paromola Wood-Mason and Alcock, 1891

Type species: Dorippe cuvieri Risso, 1816, by monotypy.

Homola (Paromola) Alcock, 1899: 156; Alcock, 1901: 64; Ihle, 1913: 69 (in key); Sakai, 1936: 47.

Thelxiope (Moloha) Barnard, 1946: 371; 1950: 341.

Description

Carapace urn-shaped or subrectangular, longer than broad, widest across branchial regions; rostrum a simple spine flanked on either side by a single supraorbital spine (occasionally with small side branches) of equal or greater size; lineae homolicae conspicuous, well inside lateral margins; regions well marked; surface usually granulate with scattered spinules, spines and tubercles, smooth in one extant species. Merus of third maxilliped elongate with a dentate prominence or a spine near middle of length of outer margin; inner margin of joint usually denticulate. Meri of pereiopods usually spinose along their length. Palms of chelae of first pair of pereiopods smooth or granulate. Extant species with 13-14 gills plus five or six epipods.

Remarks

In the literature Paromola has often been confused with two other genera of homolids, Homola Leach, 1815 (=Thelxiope Rafinesque, 1814) and

Latreillopsis Henderson, 1888. These genera all have an urn-shaped or subrectangular carapace and slender, elongate pereiopods.

In *Paromola* and *Homola* the meri of the pereiopods are spinose. The branchial formula of extant species of *Homola* is 13-14 gills plus six epipods, similar to or little different from that in *Paromola* (see Bouvier, 1940, p.191-193; and Gordon, 1950, p.220, 221). The following differences between *Paromola* and *Homola* may be noted:

(a) In *Paromola* a single supraorbital spine is situated above the orbital foramen on either side of the rostrum. In *Homola* two spines project above the orbit, a lateral rostral spine near the base of the rostrum and a supraorbital spine positioned a little more distant.

(b) Usually no conspicuous tubercles or spines are situated on the epigastric regions of *Paromola*. In *Homola* a pair of epigastric tubercles or spines are positioned a short distance behind the lateral rostral spines.

(c) In *Paromola* the rostrum is invariably a single spine. The rostrum of *Homola* is sometimes single but usually bidentate.

(d) The palms of the chelae of the first pair of pereiopods of *Paromola* are either smooth or carry pointed granules. Those of *Homola* are often spinose.

Diagnoses of *Paromola* given by Alcock (1899) and Rathbun (1937) state that the second article of the antennal peduncle is not produced or specially acute at the antero-external angle. However this angle is produced to a stout spine in *Paromola japonica* Parisi, 1915 (see Edmondson, 1932: p.5, text-fig.la; Edmondson's species is synonymous with *P. japonica* Parisi according to Sakai, 1936).

The extant species *Paromola spinimana* Griffin, 1965, from New Zealand waters, is referable to *Homola* Leach.

The genus *Latreillopsis* Henderson is here restricted to two extant species, the type *L. bispinosa* Henderson, 1888, from the Kei Is., the Andaman Sea, the Philippine Is., and Japan, and *L. laciniata* Sakai, 1936, from Japan. These two species are distinguished from *Paromola* by their branchial formula of 10 gills plus four epipods (Gordon, 1950, p.220). However the gill structure is not preserved in fossils. The following external morphological differences between *Paromola* and *Latreillopsis* are apparent:

(a) The carapace of *Paromola* is usually considerably more spinose than that of *Latreillopsis*.

(b) Except in juveniles, the carapace of *Paromola* is widest across the branchial regions. In apparently mature individuals of *Latreillopsis* the carapace is widest across the hepatic regions which are very swollen.

(c) In *Paromola* the merus of the third maxilliped is elongate and bears a dentate prominence or a spine near the middle of the length of the outer margin, while the external distal angle of the ischium is sometimes produced to a spine; the inner margin of both joints is usually denticulate. In *Latreillopsis* the merus of the third maxilliped is quadrate in shape; both the merus and ischium are without any spines.

(d) The meri of the pereiopods are usually spinose along their length in *Paromola*, but bear only a terminal spine in *Latreillopsis*.

Within the homolid crabs two families have been erected, the Homolidae White, 1847 (type genus *Homola* Leach, 1815), and the Latreilliidae (corrected from Latreillidea) Stimpson, 1858 (type genus *Latreillia* P. Roux, 1830). Wood-Mason and Alcock (1891) included *Paromola* in the Homolidae. Alcock (1899) retained *Paromola* within his restricted usage of the family Homolidae and included *Latreillopsis* in the Latreilliidae. Barnard (1950) similarly included *Latreillopsis* in the Latreilliidae. Ihle (1913), Gordon (1950), Balss (1957) and Williamson (1965) argued that the division of the homolids is much less clear than had been supposed and included the Latreilliidae within the family Homolidae.

The resemblance evident in the external morphology of *Paromola* and *Latreillopsis* strongly suggests that these two genera have a common ancestry. Separation of these genera into different families is here considered unjustified.

The following previously described extant species have been included in *Paromola* or appear referable to this genus:

Paromola cuvieri (Risso, 1816)

Mediterranean (excluding the Adriatic) and eastern Atlantic, from Angola, Cape Bojador and the Azores north to Cork, The Shetland Is. and the west coast of Norway; 150-1320 m, rarely wandering into shallower waters.

Paromola profundorum (Alcock and Anderson, 1899)

Travancore coast of India; 786 m. Maldive area; 256 m. East African Coast; 1362 m.

Paromola petterdi (Grant, 1905)

Pl.1, fig.7; Pl.2, figs.7a-b.

Paromola petterdi. Gordon, 1950, p.220

Southern and southeastern Australia, from Sydney south to Bruny I., Tasmania, and west to Eucla; 91-1460 m. North Island of New Zealand, from the Cavalli Is. to Banks Peninsula; 183-541 m. The specimen photographed S.A.M. C,83 is a male with the carapace 37 mm long (excluding the rostrum) and was taken 32 km S.W. of Cape Everard, Victoria, at a depth of 164 m.

Paromola rathbuni Porter, 1908

Isla de Mas-Afuera, Juan Fernández, Chile.

Latreillopsis multispinosa Ihle, 1912

Kei Is.; 204 m.

Paromola japonica Parisi, 1915

(=*Latreillopsis hawaiiensis* Edmondson, 1932) Japan: Tanega Shima I., Izu Peninsula, Sagami Bay; 183-392 m. Hawaii; 55 m. According to Sakai (1936) the species inhabits a rocky bottom.

Paromola alcocki (Stebbing, 1920)

(Apparently = *Latreillopsis major* Kubo, 1936; ? = *Homola* (*Parhomola*) *majora*, Edmondson, 1951) Southern Africa: Algoa Bay, South Africa; Mozambique; 73-312 m. Maldive area; 229 m. Japan (*Paromola major* (Kubo)): Izu Peninsula, Sagami Bay, Tokyo Bay; 100-200 m. ? Hawaii (*Homola* (*Parhomola*) *majora* Edmondson); 12-107 m. The Japanese form inhabits a muddy bottom (Sakai, 1936).

Paromola faxoni (Schmitt, 1921)

Off San Diego, California; 122-370 m. A remarkable recent photograph of this species in its natural environment at a depth of 370 m (Church, 1971: p.113) clearly shows how the subchelate hind limbs may be used to hold a piece of sponge above the back of the animal.

Paromola macrochira Sakai, 1962

Japan: Tosa Bay and Kii Peninsula.

Homola (*Moloha*) *acutispinosa* Sakai, 1962

Japan: Tosa Bay.

One previously described fossil species can probably be referred to *Paromola*:

Homolopsis japonicus Yokoyama, 1911

Homolopsis japonicus Yokoyama, 1911: 12, pl.3, fig.4. Paleocene or Eocene. Miike Coalfield, Japan.

The single median portion of a carapace from which this species was described unfortunately has the frontoorbital region damaged, but closely resembles *P. pritchardi* and *P. petterdi* in the shape of the other regions and in the positioning of the major tubercles.

The modern species belonging to *Paromola* can be divided into three informal species-groups which may be characterized as follows:

1. *P. cuvieri* group

Carapace more or less covered by granules and spinules and bearing short to moderately long spines on lateral and anterior-dorsal aspects. Palms of chelipeds smooth or bearing pointed granules, particularly in mature individuals.

P. cuvieri, *P. petterdi*, *P. rathbuni*, *P. japonica*, *P. alcocki*, *P. faxoni*, *P. macrochira*.

2. *P. profundorum* group

Carapace mainly smooth, with one hepatic spine and one denticle on branchial margin. Palms of chelipeds smooth.

P. profundorum.

3. *P. multispinosa* group

Carapace bearing elongate spines, between which it is mainly smooth. Palms of chelipeds smooth.

P. multispinosa, *P. acutispinosa*.

The Early Tertiary *Paromola japonicus* (Yokoyama) is a fossil member of the *P. cuvieri* group.

Paromola pritchardi sp. nov.

Text-figure 34; plate ~~1~~ 6 figures 1 - 5; plate ~~2~~ 7 figures 1 - 5

Name

Named after Pritchards Quarry, on section 28, Hundred of Blanche, South Australia.

Material

Seventeen incomplete specimens of various parts of the carapace and four specimens of isolated abdominal tergites. Holotype S.A.M. P15631, median part of carapace with rostrum and supraorbital spines lacking; paratype S.A.M. P15632, median part of carapace with most of skeletal materia exfoliated to leave a thin remaining layer partly covering an internal mould, the rostrum intact; paratype S.A.M. P15639, fragmentary remains of median part of carapace with rostrum and one supraorbital spine present; paratypes S.A.M. P15633, P15638 and P15646, all incomplete remains of median part of carapace; paratypes S.A.M. P15635, P15642 and P15643, all incomplete remains of lateral aspect of carapace from right side; paratype S.A.M. P15637, lateral aspect of carapace from left side; paratype S.A.M. P15636, fragment of lateral aspect of carapace from left side; other more or less fragmentary remains of the carapace; paratype ♀, S.A.M. P15634, tergite of fourth segment of abdomen; paratype ♂, S.A.M. P15640, tergite of third segment of abdomen; paratypes S.A.M. ♂, P15641 and ♂, P15647, tergite of fifth segment of abdomen. Specimens preserved as the original shell material; P15633 coll. Glaessner, 1953; other specimens coll. R.J.F.J., 1967-1970.

Occurrence

Quarries on northeastern part of section 26 (P15631, P15638, P15640 and P15646-47), section 28 (P15632-35, P15637, P15639 and P15641-43) and southwestern part of section 30 (P15636), Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Gambier Limestone. Middle Oligocene.

Description

Carapace subrectangular, gently convex above, extremely deep in lateral aspect; regions well marked, delimited and subdivided by moderately deep grooves; greater part of surface covered by variably sized granules and spinules, nine short spines on dorsum in advance of cervical groove, lateral aspects of carapace ornamented by short spines and blunt spinules. Portion of carapace between lineae homolicae 1.5 times as long as wide, broadest across mesobranchial regions.

Rostrum a single, forwardly directed, slender spine about a sixth length of carapace, subtriangular in section and slightly deflexed basally, round and smoothly upcurved distally.

Orbits forwardly directed and with a large supraorbital spine above; inner part of supraorbital margin smoothly concave and with a narrow border; supraorbital spine directed obliquely upwards, forwards and slightly outwards, about twice length of rostrum, with a lateral spinule at about half length; a short spine on lower corner of lateral margin of orbit.

Epigastric regions relatively small, slightly raised, with only a few granules. Protogastric regions each subdivided into three lobes by an oblique Y-shaped groove; anteromedial lobe with a central spine and two spinules on posterior part; anterolateral lobe with a single prominent spine; posterolateral lobe with a prominent spine on lateral aspect, a lesser spine on inner portion, and several small spinules between. Hepatic regions strongly inflated, bearing a crescentic row of four acute spines on anterolateral aspect and a group of spinules behind. Mesogastric region with a median spine set at centre of a circlet of five or a triangular arrangement of three small spinules; a pair of granulate ridges adjacent to posterior margin of region. Cervical groove strongly impressed, containing slit-like posterior gastric pits at .50-.52 length of carapace. Metagastric region in form of two oblique, elongated, granulate lobes and with a pair of more prominent granules positioned submedially. Urogastric region saddle-shaped, its lateral margins marked by two incised, crescentic grooves. Cardiac region moderately inflated, subtriangular, with three prominences, two side by side before and one behind. Intestinal region depressed, progressively broadened rearwards. Epibranchial regions obliquely elongated, with a spine just outside linea homolica and an irregular line of spinules on lateral aspect. Innerbranchial lobes on either side of urogastric region obliquely elongated and with one more prominent granule. Branchiocardiac groove well marked. Mesobranchial regions gently inflated, each with a line of at least three short spines just outside linea homolica, most anterior of these spines the largest and situated on a slight ridge behind lateral portion of branchiocardiac groove. Metabranchial regions relatively small, two-lobed, with a spinule on posterolateral portion of inner lobe. Sub-branchial margin with a narrow border. Posterior margin fairly wide, raised, with median third indented.

A spinule at anterolateral corner of buccal frame.

Muscle attachment scars only faintly marked on interior surface of carapace except for the two distinct, small depressions which form the gastric apodemes.

Third and fifth segments of male abdomen each with a prominent median lobe and a spinule at centre of each of the lateral lobes. Fifth segment subrectangular, with posterior angles slightly produced; median lobe apparently bearing a few scattered granules and with a spinule on anterior portion; lateral lobes obliquely sulcate and apparently ornamented by coarse granules.

Fourth segment of female abdomen with the lateral lobes slightly inflated and curved downwards (if abdomen was straightened behind crab) and the surface nearly smooth except for a few, scattered weak granules; an obscure tubercle on anterior portion of median lobe.

Measurements

Holotype (P15631), length of carapace excluding rostrum, 18 mm; width of median part of carapace between lineae homolicae at level of mesobranchial regions, 12 mm. Paratype (P15632), length of carapace excluding rostrum, 23 mm ; length of rostrum (incomplete), 3.6 mm; width of median part of carapace between lineae homolicae at level of mesobranchial regions, 16 mm. The largest individual known is represented by an incomplete carapace (paratype P15638) approximately 1.3 times the size of that of P15632.

Remarks

The precise arrangement of the minor spinules on the carapace of the fossil *P. pritchardi* is very variable and the relief of the regions also varies slightly in different specimens.

P. pritchardi belongs to the *P. cuvieri* species-group and closely resembles *P. petterdi* and *P. alcocki*. It seems slightly more similar to *P. petterdi* than to *P. alcocki*, but is possibly ancestral to both. It is distinguished from *P. petterdi* by the following differences:

(a) The carapace is more rectangular.

(b) The posterior gastric pits are situated at about .50-.52 the length of the carapace in *P. pritchardi* but at about .41-.43 the length in *P. petterdi*.

(c) In *P. pritchardi* the rostrum is directed forwards and is upcurved distally. In *P. petterdi* the rostrum is slightly deflexed.

(d) In the fossil species a prominent spine is situated on the anterolateral lobe of the protogastric regions; in *P. petterdi* a small tubercle corresponds to this spine.

(e) The mesobranchial regions of the carapace are not so strongly sculptured as in *P. petterdi*.

Differences between the fossil species and *P. alcocki* are as follows:

(a) The carapace is more rectangular.

(b) In *P. alcocki* the posterior gastric pits are situated at about .43 the length of the carapace.

(c) The supraorbital spines of *P. pritchardi* are longer than in *P. alcocki*.

(d) The branchial regions of *P. pritchardi* lack many of the numerous spinules present in the extant species.

It is not unlikely that the different positioning of the posterior gastric pits in *P. pritchardi* is a function of differential growth of the carapace; the specimens of the fossil carapace are considerably smaller than the individuals of the two modern species to which they were compared.

P. pritchardi apparently differs from the Eocene or Paleocene *Homolopsis japonicus* Yokoyama in lacking a distinct transverse ridge over the anterior part of each mesobranchial region and in bearing several additional spines. The differences which occur between *H. japonicus* and *P. pritchardi*, and between these fossils and the modern species, *P. petterdi* and *P. alcocki* seem relatively minor and are indicative of an extremely slow rate of evolutionary change. If this rate of change is at all comparable to rates of evolutionary change experienced by *Paromola* prior to the Eocene or Paleocene, then the genus may date from a much earlier time, probably from within the Mesozoic. Glaessner (1969) indicates that the fossil record of the family Homolidae extends back to the Upper Jurassic. None of the other fossil genera of homolids yet described, however, appears likely to be the direct ancestor of *Paromola*.

Paromola cf. *pritchardi*

Plate ~~1~~ 6 figure 6; plate ~~2~~ 7 figure 6

Material

A fragment of the median part of a carapace, S.A.M. P15806, and a fragment of the lateral part of a carapace, S.A.M. P15805. Remains preserved as the original shell material; P15805 coll. M. Wade, 1955; P15806 coll. R.J.F.J., 1970.

Occurrence

Both specimens from quarry on section 606, Hundred of Blanche, Mount Gambier loc. 2; P15806 from a loose piece of rock 3.5 m below the ground surface.

Stratigraphic Position and Age

Gambier Limestone. Middle Lower Miocene.

Measurements

Specimen P15806, width of median part of carapace between lineae homolicae, approximately 13 mm. Specimen P15805, height of lateral part of carapace approximately 8 mm.

Remarks

These remains are too fragmentary to be positively identified to the level of species, but in all features closely resemble the corresponding parts of *P. pritchardi*.

Section OXYSTOMATA
Superfamily Calappoidea
Family Calappidae de Haan, 1833
Subfamily Calappinae de Haan, 1833
Genus *Calappilia* A. Milne-Edwards, 1873

Type species: *Calappilia verrucosa* A. Milne-Edwards, 1873, by monotypy.

Calappilia A. Milne-Edwards, 1873, *in* Bouillé: 8. Noetling, 1885: 122 (generic description, discussion). Glaessner, 1929: 73 (list of fossil species); 1969: R494. Lőrenthey and Beurlen, 1929: 126 (generic description, discussion). Rathbun, 1931: 7.

Paracycloïs Miers, 1886: 228

Carapace subcircular, strongly convex, widest slightly in advance of middle of length; front narrow, three-lobed; orbits obliquely ovate, relatively large; posterolateral margins with five to seven triangular teeth; broad, deep grooves isolate axial regions of carapace, other regions not clearly marked; surface granulate and tuberculate, the tubercles not showing a marked tendency to be arranged in sublongitudinal rows. Chelipeds greatly resembling those of *Calappa* Weber, 1795; inner surface of palm with a finely ribbed, nearly vertical stridulating ridge which opposes a line of prominent elongate granules on suborbital region of carapace.

Remarks

Calappilia and the genus *Calappa* are closely allied, but differ in the following features:

(a) In Calappilia the front is distinctly three-lobed. In Calappa the front is two-lobed.

(b) The carapace of Calappilia is widest a little in advance of the middle of the length. In most species of Calappa the carapace is widest across the posterolateral clypeiform expansions.

(c) Species of Calappa apparently lack the stridulating device present in Calappilia.

(d) Tubercles on the carapace of Calappilia are usually arranged in a rather irregular pattern. In a number of species of Calappa the tubercles are positioned in more or less longitudinal rows.

The stridulating device present in Calappilia greatly resembles that of the genus Acanthocarpus Stimpson, 1810 (see Guinot-Dumontier and Dumontier, 1960: p.129 and fig.7). The oldest species of Calappilia for which the stridulating device can be inferred to have been present is the Lower Oligocene C. perlata Noetling. It is documented here from the Australian fossil species of Calappilia and has been described in "Paracycloïs" atlantis Chace. This confirms Glaessner's (1969) placement of this living genus the synonymy of the Tertiary genus Calappilia.

The following previously described forms have been included in Calappilia or appear to belong to this genus:

Calappilia verrucosa A. Milne-Edwards, 1873

Middle Oligocene. Southwest France.

Calappilia sexdentata A. Milne-Edwards, 1873

Middle Oligocene. Southwest France.

Calappilia perlata Noetling, 1885

Lower Oligocene. Northern Germany.

Calappilia incisa Bittner, 1886

Middle Eocene. Northern Italy.

Paracycloïs milneedwardsii Miers, 1886

Extant. Admiralty Is., 247 m.

Calappilia dacica Bittner, 1893

Upper Eocene. Hungary.

Calappilia dacica lyrata Lörenthey and Beurlen, 1929

Upper Eocene. Budapest.

Calappilia vicetina Fabiani, 1910

Upper Oligocene. Northern Italy.

Paracycloïs grandispinis Etheridge and McCulloch, 1916

Late Lower Miocene to possibly early Middle Miocene. Southeastern Australia.

Calappilia borneoensis Van Straelen, 1924

Middle Eocene. Borneo.

Calappilia böhmi Glaessner, 1929

Upper Eocene. Java.

Calappilia hondoensis Rathbun, 1931

Upper Eocene. Lower California (Mexico).

Calappilia diglypta Stenzel, 1934

Middle Eocene. Texas.

Paracycloïs atlantis Chace, 1939

Extant. Cuban seas; 272-329 m.

Calappa tridentata Beurlen, 1939

Middle Oligocene. Hungary.

Calappilia sp. Roberts, 1956

Upper Paleocene. New Jersey.

Calappa circularis Beurlen, 1958

Upper Oligocene or Lower Miocene. Pará, northern Brazil.

Calappa matzkei Bachmayer, 1961

Tortonian. Austria.

Calappilia brooki Ross and Scolaro, 1964

Eocene. Florida.

Although most of the fossil records of this genus are from what are now temperate latitudes, the occurrences from Texas, Florida, northern Brazil, Java and Borneo suggest that its range in the Tertiary was continuous latitudinally through the tropics. North America and Europe, where the largest number of fossil species occur, have apparently experienced significantly warmer climates during most of the Tertiary than at present (Dorf, 1970). It thus seems likely that the past distribution of *Calappilia* was restricted to relatively warm waters and tropical seas. The two surviving representatives of the genus "*Paracycloïs*" *milneedwardsii* and "*Paracycloïs*" *atlantis* both occur in tropical regions.

Calappilia cf. *matzkei* (Bachmayer, 1961).

cf. *Calappa* *matzkei* Bachmayer, 1961: 43, text-fig.1, pl.3.

An internal mould of the carapace of a species of *Calappilia* from the Burdigalian of Uloa, Zululand, Natal, has been loaned to Professor Glaessner by Professor L. C. King, of the University of Natal, Durban. In its shape and ornamentation this carapace, which is 23 mm wide, greatly resembles *Calappilia matzkei*. It seemingly differs from the latter only in being a little broader relative to its length. This difference seems about the same magnitude at the limits of intra-specific variability which the author has observed in the dimensions of an Australian species of

Calappilia. However, as *C. matzkei* and the Zululand specimen are both rather incompletely known from single examples of internal moulds of the carapace, the latter is identified only as *Calappilia* cf. *matzkei*.

Calappilia grandispinis (Etheridge and McCulloch, 1916)

Plate 8 figure 7a-f; plate 9 figures 2 & 3

Paracycloïs grandispinis Etheridge & McCulloch, 1916: 8, text-fig.1, pl.II, fig.3.

Material

Three incomplete specimens of the carapace; a specimen with the right posterolateral aspect broken away, hypotype N.M.V. P29346, coll. F. A. Cudmore, 1934; a carapace with the anterolateral aspects and front broken away, hypotype N.M.V. P16192; the fragmentary remains and a partial internal mould of the lateral aspect of a carapace, hypotype S.A.M. P15902, coll. M. Wade, 1955.

Occurrence of present materials

Otway Basin

Balcombe Bay (N.M.V. P29346). Muddy Creek, near Hamilton (N.M.V. P16192).

Murray Basin

Old kiln just south of "Brenda Park", west bank of River Murray, 5 km south of Morgan (S.A.M. P15902).

Stratigraphic Position and Age

Otway Basin

Balcombe Clay. Late Lower Miocene. Muddy Creek Marl. Late Lower Miocene.

Murray Basin

Morgan Limestone (? upper member). Late Lower to early Middle Miocene.

Description

The above listed specimens closely agree with the description and figures given by Etheridge and McCulloch except for slight differences in the ornamentation. The following observations are intended to supplement the original description.

Carapace about 1.05 times as wide as long. Anterior half of carapace varying from finely and evenly granulate to finely and obscurely granulate in different individuals, and with prominent broadly conical to broadly rounded tubercles which decrease in size towards margins. Posterior half of carapace covered by variably sized granules and bearing numerous discrete tubercles which decrease in size rearwards. An obscure marginal prominence at widest part of carapace. Short posterior margin of carapace with three slight prominences.

Protogastric regions each with a broad central tubercle; a group of four small tubercles at corners of a trapezoid between. A large, broad tubercle at centre of mesogastric region; posterior gastric pits distinct; a small tubercle at centre of metagastric region; two pairs of pits or deep depressions lateral to mesogastric region and metagastric region respectively. A slight prominence at middle of urogastric region; lateral urogastric grooves short, crescentic, deeply impressed. Cardiac region elongate and with an obscure median prominence on anterior portion. Epibranchial regions each with three oblique pitted grooves; between the middle and inner grooves a large tubercle nearly in line with that at centre of mesogastric region.

Submarginal areas of carapace finely granulate. Below orbit and anterior part of anterolateral margin a stridulating plectrum formed by an angulate ridge bearing about nine evenly spaced, elongate, oblique granules.

Epistome apparently arched forwards and deeply indented behind, its lateral parts furrowed transversely and sparsely granulate; anterior process of epistome acutely triangular and weakly hollowed below; a sharp median carina on anterior portion of endostome. Lateral margins of buccal frame moderately convergent forwards and with a well marked border, anterior and posterior parts of border finely granulate.

Sub-branchial regions very broad, with the middle part finely and sparsely granulate and the anterior and posterior portions smooth, inner margin deeply concave lateral to base of cheliped and with a well marked finely granulate border.

Interior surface of carapace with nearly hemispherical depressions corresponding to external tubercles. Position of muscle attachments shown by shallow pits, pitted areas and slight depressions with a reticulate ornamentation; two pitted, triangular attachments below posterior part of mesogastric region and a conspicuous depression corresponding to each posterior gastric pit; elongate attachments adjacent to urogastric region and anterior half of cardiac region, a faintly pitted area below grooves on either side of posterior half of cardiac region and anterior part of intestinal region; lines of small, shallow pits below epibranchial grooves and several small groups of similar pits nearby.

Measurements

The carapace of hypotype N.M.V. P29346 is 33 mm long (incomplete) and 35 mm wide. The carapace of specimen N.M.V. P16192 was in excess of 20 mm wide (incomplete). The carapace of hypotype S.A.M. P15902 was more than 24 mm long (incomplete).

Remarks

The one specimen from which Etheridge and McCulloch (1916) originally described this species was stated by them to be sub-fossil from estuarine deposits excavated during the construction of the Coode Canal in the Yarra Delta, Melbourne, Victoria. With reference to the description of the geology of the Yarra Delta given by Neilson and Jenkin (1967), the stratigraphic data presented by Etheridge and McCulloch would indicate that their specimen was probably from the Fishermans Bend Silt, a marine or possibly estuarine deposit dated within the Riss-Würm Interglacial of the Pleistocene.

The present three specimens date from the late Lower Miocene or late Lower to possibly early Middle Miocene. Their resemblance to the holotype is strongly suggestive of conspecificity. In view of the considerable apparent difference in age between the holotype and the present series it seems possible that the holotype has been mis-located and is actually of Tertiary age. It is improbable that it is a long ranging form present in the late Pleistocene of Melbourne because the only present-day Australasian record of "*Paracycloïs*", which is synonymous with *Calappilia*, is from equatorial waters.

Calappilia australis sp. nov.

Plate 8 figures 1 - 6a,b; plate 9 figure 1

Name

From the Latin *australis*, meaning southern; in reference to the occurrence of the species being near the southernmost known limit of distribution of the genus.

Material

Numerous remains of the carapace and parts of the chelipeds. The remains of the chelipeds have not been found in direct association with the carapace but occur in the same beds. Carapace with left side damaged, holotype S.A.M. P15610, and another carapace with part of shell material exfoliated from internal mould, paratype M.U.G.D. 3772. Other remains of the carapace, all more or less incomplete, paratypes S.A.M. P15611, P15618-19, P15622, P15625-26, and N.M.V. P29347. Damaged internal mould of carapace, S.A.M. P15617. Articulated carpus and propodus of left (smaller) cheliped, paratype S.A.M. P15614, and almost complete right (larger) chela, paratype S.A.M. P15624. All specimens except moulds preserved as the original shell material; P15617 coll. R. Tate; N.M.V. P29347 coll. G. B. Pritchard; M.U.G.D. 3772 coll. a student, 1954; P15625 coll. R. C. Sprigg, 1958; P15618 coll. Bret Robinson and H. Eames, 1967; P15624 coll. R. Foster, 1969; remainder coll. R.J.F.J., 1967-1970.

Occurrence

Murray Basin

Vicinity of Mannum (P15617).

At approximately 20 m above N.R.L., Nildottie loc. 1 (P15618). At 19-20 m (P15610-11, P15614) and up to 24 m above N.R.L., Nildottie loc. 2. Between 15 m (P15619) and 17 m above N.R.L., Nildottie loc. 3. At 16-20 m above N.R.L., Nildottie loc. 4 (P15622).

High in cliff on west bank of River Murray just south of Swan Reach (P15624).

At 2.7 m (P15625) and 4.6 m above N.R.L. in cliff on west side of River Murray 100 m north of punt landing, Blanchetown.

From 2 m below top of upper member of the Morgan Limestone, Morgan loc. 1 (P15626).

Otway Basin

At Muddy Creek, near Hamilton (N.M.V. P29347). New Quarry at Batesford, near Geelong (M.U.G.D. 3772).

Stratigraphic Position and Age

Murray Basin

Mannum Formation at Mannum. Middle and upper part of Mannum Formation at Nildottie and Swan Reach. Upper part of Mannum Formation at Blanchetown. Upper member of Morgan Limestone in vicinity of Morgan. Middle to late Lower Miocene or early Middle Miocene.

Otway Basin

Muddy Creek Marl at Muddy Creek. Batesford Limestone (foraminiferal limestone) at Batesford. Late Lower Miocene.

Description

The overall shape and the outline of the carapace almost the same as for Calappilia grandispinis. Surface of carapace bearing numerous distinct tubercles and closely granulate; the tubercles conical or rounded, decreasing in size posteriorly and towards margins, tending to be arranged in irregular longitudinal rows on branchial regions and forming a row on mid-line of carapace; the granulation variable, ranging from fine to moderately coarse to coarse to very coarse in different individuals, and usually becoming coarser towards posterior of carapace.

Principal tubercles on gastric and epibranchial regions arranged as in *C. grandispinis*, but smaller and more distinct than in that species. Protogastric regions each with two small tubercles before and a much larger tubercle behind. Cardiac region with one to three tubercles on mid-line. Intestinal region sometimes with four tubercles at corners of a trapezoid. Epibranchial regions usually without well marked oblique grooves.

Submarginal areas of carapace finely granulate anterolaterally, smooth below posterolateral teeth. Below orbit and anterior portion of anterolateral margin a stridulating plectrum formed by a prominent crest bearing five or more evenly spaced, oblique ovate granules.

Interior surface of carapace with conical pits corresponding to external tubercles. Muscle attachment scars similar to those in *C. grandispinis*.

Carpus and hand of chelipeds compressed laterally and deep vertically. Carpus subtriangular, with outer face tuberculate and sparsely granulate, inner face sculptured and smooth except for a few obscure granules; upper margin forming a sharp crest which bears a line of variably sized spinules. Palm with a high dorsal crest cut into seven sharp teeth; a flattened triangular tooth on outer-ventral-proximal corner of joint; outer face convex,ornamented by irregular rows of discrete tubercles with variably sized granules between; ventral aspects of palm closely and coarsely granulate; inner face sculptured, a sharp, ventral ridge ornamented by a line of pointed granules, a broad, finely granulate longitudinal ridge about 1/3 the distance between lower and upper margins of face, a nearly vertical stridulating ridge with 51 to 60 fine transverse striae extends below fourth tooth of dorsal crest, another small area of striae present on third tooth of dorsal crest from proximal end, surface distal to stridulating ridge obscurely and finely granulate, remaining areas smooth. Left palm with a large rounded prominence above articulation of movable finger, right palm with a smaller prominence in same position and a large, blunt, tooth-like protuberance on outer face near base of fixed finger. In both chelae the fixed finger extremely short and deep and projecting moderately downwards, with outer face coarsely granulate and inner face doubly ribbed; a large, flattened basal tooth and several smaller blunt teeth beyond on prehensile margin of right hand fixed finger, left with five or six small teeth. Movable finger of right chela curved, moderately compressed laterally; upper margin serrated and granulate, with a conspicuous rounded tooth above base; low flat teeth on prehensile margin; a large curved tooth on outer side of base of finger opposes blunt protuberance on distal part of palm, this arrangement identical to the shell opening device in the genus Calappa (see Shoup, 1968).

Measurements

The carapace of the holotype S.A.M. P15610 is 7 mm long and was originally 18 mm wide. The carapace of paratype M.U.G.D. 3772 is 23 mm long and 24 mm wide. The carapace may reach about 24 mm in width (paratype S.A.M. P15619). Paratype S.A.M. P15624, a right (larger) chela, has the propodus 18 mm long (incomplete), the palm 16 mm long and 12 mm high (excluding teeth on upper margin), and with the dactylus 9.1 mm long (incomplete). Paratype S.A.M. P15625, the remains of a left (smaller) cheliped, has the propodus 18 mm long and the palm 16 mm long and 13 mm high.

Remarks

The one carapace from the Batesford Limestone in the eastern part of the Otway Basin (M.U.G.D. 3772, pl.8, fig.4a,b) is virtually identical in all its features with specimens from the Mannum Formation in the Murray Basin. The carapace from the Muddy Creek Marl in the northern, central part of the Otway Basin (N.M.V. P29347) has its outer surface worn and abraded, but a latex mould of its interior surface shows features typical of the species.

Calappilia australis greatly resembles and is almost certainly the ancestor of *C. grandispinis*. The two are distinguished by features of their ornamentation, which differs as follows:

(a) The principal tubercles on the anterior half of the carapace of *C. australis* are considerably smaller and stand in sharper relief than in *C. grandispinis*.

(b) The granulation on the anterior part of the carapace of *C. australis*, although rather variable, is appreciably coarser than in *C. grandispinis*.

(c) Latex or natural internal moulds of the carapace of *C. australis* show bluntly conical prominences corresponding to the principal tubercles (Plate 9 figure 1); appreciably larger, nearly hemispherical prominences indicate the principal tubercles in similar moulds of *C. grandispinis* (Plate 9 figure 2). Many more small prominences representing minor tubercles are evident on the internal mould of *C. australis*.

(d) The denticles in front of the principal posterolateral spines are less conspicuous in the present species than in *C. grandispinis*.

C. australis also closely resembles the Upper Eocene, Hungarian, *Calappilia dacica*, but differs in the smaller size of the tubercles on the carapace, in not having discernible bosses on the anterolateral margins of the carapace, in having five rather than seven conspicuous posterolateral spines, and in having the larger of these spines more protrusive laterally. Nevertheless it is likely that *C. dacica* is close to the ancestor of *C. australis*.

The extant "*Paracycloïs*" *milneedwardsi*, from the Admiralty Islands, has the posterior part of the carapace weakly ornamented and in this regard is dissimilar from the Australian fossil species of *Calappilia* described here. Instead it seems markedly similar to "*Calappa*" *tridentata* from the Middle Oligocene of Budapest and is very probably a direct descendant of the latter.

Family Leucosiidae Samouelle, 1819

Genus Ebalia Leach, 1817

Type species: Cancer tuberosus Pennant, 1777, subsequent designation by Rathbun, 1922.

Ebalia Leach, 1817. Sakai, 1965: 25 (generic synonymy, discussion on Japanese species). Gordon in Zariquiey Alvarez, 1968: 322 (generic description, discussion). Glaessner, 1969: R496.

Remarks

This genus is today widely distributed (western north America, Atlantic, Mediterranean, Indo-Pacific) and includes numerous named forms. Barnard (1950) indicated that the species of the genus tend to show considerable intraspecific variation and hence were often difficult to identify. For this reason no revision of Ebalia is attempted here.

Subgenus Ebalia Leach

Ebalia (Ebalia) restricted by Bell, 1855: 303

Ebalia (Ebalia) spanios sp. nov.

Text-figure 35a,b; plate 9 figure 4

Name

From the Greek spanios, meaning rare.

Material

One specimen of the carapace, the holotype S.A.M. P15656, preserved as the original shell material and coll. R.J.F.J., 1968.

Occurrence

Quarry southeast of centre of section 28, Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Carapace subcircular, about as wide as long, strongly convex above; regions tumid and conspicuous; surface openly covered by rather coarse mushroom-shaped granules and with a number of prominences and tubercles paved by close-set granules.

Front narrow, projected forwards, bi-lobed.

Orbits small, rounded; supraorbital margins deeply concave, terminated laterally in a blunt extraorbital tooth; supraorbital regions each with two faintly marked sutures; suborbital margins projected beyond supraorbital margins in dorsal view and forming a right-angular prominence adjacent to antennal hiatus.

Hepatic regions isolated from rest of carapace by deep grooves and with a large anterolateral prominence. Protogastric regions swollen, each with an elongate, oblique median prominence; these prominences convergent rearwards. Posterior part of mesogastric region slightly swollen and with a small median tubercle. Cardiac region strongly inflated. Branchial regions inflated, each with two tubercles on dorsal aspect and apparently four tubercles on lateral margin, the second in this marginal series situated at widest part of carapace. A tubercle on either side of short posterior margin of carapace.

Antennulary fossae formed by obliquely arched anterior margin of front. Antennal hiatus apparently of moderate width.

Measurements

The carapace of the holotype is 10 mm long and 11 mm wide, including the marginal tubercles.

Remarks

The carapace Ebalia spanios resembles that of the extant Japanese species Ebalia yokoyai Sakai, 1965 (for Ebalia tuberculata Yokoya, 1933, non Ebalia tuberculata Miers, 1881). The following differences between the two may be noted:

(a) The carapace of the fossil species is about as wide as long, not slightly broadened as in the extant species.

(b) Elongate, oblique prominences on the protogastric regions are convergent rearwards in E. spanios, but convergent forwards in E. yokoyai.

(c) The branchial regions of *E. spanios* have two dorsal tubercles rather than three.

(d) The cardiac region of the fossil species lacks the posterior tubercle present in *E. yokoyai* (note: the author's usage of "cardiac region" = "intestinal region" in description of *E.* "*tuberculata*" given by Yokoya (1933: 121)).

(e) The carapace of *E. spanios* is covered by moderately coarse, mushroom-shaped granules while that of *E. yokoyai* is apparently "minutely granular".

Subgenus *Phlyxia* Bell, 1855

Type species: *Phlyxia crassipes* Bell, 1855, subsequent designation by Rathbun, 1922.

Phlyxia Bell, 1855: 303. Miers, 1886: 304, 305. Haswell, 1882: 124. Hale, 1927: 198. Tyndale-Biscoe and George, 1962: 72 (diagnosis).

Ebalia (*Phlyxia*) *sturti* sp. nov.

Text-figure 36a,b; plate 9 figures 7 & 8

Name

Named after Charles Sturt, who in 1829 led the first expedition to navigate the Murray River, and who first reported on the fossiliferous strata exposed along its course.

Material

Two specimens of the carapace; holotype S.A.M. P15562, with ornamentation well preserved; paratype S.A.M. P15563, slightly abraded and with frontal region damaged. Both specimens coll. R.J.F.J., 1968.

Occurrence

From 7.5 m (P15562) and 8.5 m (P15563) above N.R.L., Nildottie loc. 3.

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Carapace subcircular in outline, about as wide as long, strongly convex above; frontoorbital region produced forwards to form a short "snout"; other regions well marked, tumid, delimited by distinct grooves; surface granulate and spinulose with a variable number of denticles and short spines more or less covered by granules and spinules.

Front narrow, truncated, notched medially and quadridentate before, bi-lobed above.

Orbits small, round; supraorbital margins deeply concave, doubly fissured, terminated laterally in a small, acute extraorbital spine; suborbital margins also deeply concave, produced to a conspicuous spine adjacent to antennal hiatus.

Hepatic regions each forming an anterolateral prominence and bearing one to three spines or denticles. Protogastric regions swollen, each with a large spine on posterior portion and up to five subsidiary spines, one situated anteriorly the most prominent. Wedge-shaped anterior portion of mesogastric region with one or two median spines; one or two median spines on moderately inflated posterior part of region. Cardiac region strongly inflated, with a prominent median spine above followed by a much larger spine directed rearwards and slightly upwards; this second spine ornamented by club-shaped spinules and mushroom-shaped granules. Branchial regions inflated with two to four spines on dorsal aspect and four denticles on lateral margin, second denticle in marginal series at widest part of carapace. Sub-branchial margins slightly arched above base of each limb and with a finely granulate narrow border. A spine on either side of short posterior margin of carapace.

Antennulary fossae formed by obliquely arched anterior margin of front.

Pterygostomial regions subtriangular, produced to a blunt spine below orbit and with another spine on lateral aspect below hepatic region.

Buccal frame slightly narrowed anteriorly; lateral margins sharply kinked at about a third their length from proximal end, with adjacent gutters of moderate width representing inhalant canals. Middle part of epistome weakly ridged medially; posterior processes narrow, with their inner margin raised to form a flange; median posterior embayment nearly semicircular.

Measurements

The carapace of the holotype S.A.M. P15562 is 6.6 mm long and was originally 6.6 mm wide (excluding marginal spines). The carapace of paratype S.A.M. P15563 is 7.1 mm long (incomplete) and 7.5 mm wide.

Remarks

Ebalia (Phlyxia) sturti closely resembles the extant form Ebalia (Phlyxia) quadridentata spinifera Miers, 1886, from Port Jackson. The two differ as follows:

(a) The carapace of the fossil species is about as wide as long, not a little elongated as in the extant form.

(b) The spines on either side of the posterior margin are narrow-based in E. (P.) sturti, but very broad based in the extant form.

(c) The front of E. (P.) sturti is less conspicuously quadridentate.

(d) A subdorsal spine present on the posterior part of the branchial region in the fossil species appears to be missing in the extant form.

Ebalia (Phlyxia) tatei sp. nov.

Text-figure 37a-c; plate 9 figures 5 & 6

Name

Named after Professor R. Tate, an early student of the geology and palaeontology of the sediments of the River Murray cliffs.

Material

Two specimens of carapace; holotype ♀, S.A.M. P15560, well preserved but with front damaged; paratype S.A.M. P15561, with rear part of carapace damaged and posterolateral regions preserved as an internal mould. Specimens coll. R.J.F.J., 1968-1969.

Occurrence

From 7 m (P15561) and 13 m (P15560) above N.R.L., Nildottie loc. 3.

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Carapace subcircular, about as wide as long, strongly convex above; frontoorbital region produced forwards to form a short "snout"; other regions well marked, tumid, delimited by distinct grooves; surface openly covered by coarse mushroom-shaped granules and with several prominences and tubercles paved by close-set granules; lateral aspects each with five conspicuous, rounded bosses.

Front narrow, truncated, notched medially and apparently quadridentate before, bi-lobed above.

Orbits small, round; supraorbital margins deeply concave, doubly sutured, terminated laterally in a short extraorbital tooth; suborbital margins also deeply concave, produced to a conspicuous tooth adjacent to antennal hiatus.

Hepatic regions isolated from rest of carapace by deep grooves and each with a large anterolateral prominence. Protogastric regions moderately inflated, with a small prominence before and a much larger granulated tubercle behind. Mesogastric region wedge-shaped before, moderately inflated posteriorly. Strongly inflated cardiac region outlined by grooves and with a prominent tubercle on posterior aspect. Branchial regions inflated, each bearing two large bosses on anterolateral aspect, two small tubercles on posterolateral aspect, and another small tubercle just behind centre of upper surface of region; the second of the large anterolateral bosses situated at widest part of carapace. Subbranchial margins arched above base of each limb and with a well marked granulate border. On either side of short posterior margin of carapace a conspicuous protrusion paved by close-set granules.

Antennulary fossae formed by obliquely arched anterior margin of front. Antennal hiatus of moderate width. Epistome short, relatively narrow, arched forwards.

Pterygostomial regions narrowly subtriangular; anterior margin three-lobed, a small, rounded outer lobe separated by a fissure from two weaker inner lobes; on lateral aspect a rounded boss below hepatic prominence. Anterior part of pleural suture faintly marked.

Lateral margins of buccal frame moderately convergent forwards, finely granulate for anterior half of length, smooth behind. Moderately wide gutters adjacent to lateral margins of mouthfield represent inhalant canals. Endostome with anterior part concave, but ridged medially; posterior processes narrow, with their inner margin raised to form an obtuse angled prominence.

First large segment of female sternum projected forwards and upwards, with a deep median channel and a deep, broad depression behind to accommodate abdomen; anterior margin of segment obtusely angulate medially and with a deep furrow and notch at posterolateral corners of mouthfield; a line of fine granules on a ridge just behind anterior margin of segment, lateral parts of segment conspicuously granulate.

Measurements

The carapace of the holotype ♀, S.A.M. P15560 is 6.9 mm long and 7.2 mm wide excluding peripheral bosses and tubercles. The carapace of paratype S.A.M. P15561 is 7.6 mm wide.

Remarks

This species differs from _Ebalia_ (_P._) _sturti_ with which it may occur in association, in lacking numerous conspicuous spines on the dorsal aspect of the carapace, in having rounded bosses rather than spines ornamenting the lateral margins of the carapace, and in its considerably coarser dorsal granulation.

Ebalia (Phlyxia) nildottiensis sp. nov.

Text-figure 38a,b; plate 9 figure 9

Name

After the town of Nildottie, South Australia, the principal settlement near the locality where the species occurs.

Material

Three specimens of the carapace; holotype S.A.M. P15564, well preserved; paratype ♂, S.A.M. P15565, abraded and damaged carapace with sternum attached; paratype S.A.M. P15566, broken left half of a carapace. Specimens coll. R.J.F.J., 1969-1970.

Occurrence

From 19-20 m above N.R.L., Nildottie loc. 2 (P15566). From 12-14 m (P15565) and 16 m (holotype) above N.R.L., Nildottie loc. 3.

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle to late Lower Miocene.

Description

Carapace subcircular, convex above; frontoorbital region projected upwards and forwards; other regions delimited by distinct grooves; surface covered by small club-shaped granules (mostly broken away in available material); several spinules on lateral parts of carapace, three spines on posterior aspect, these spinules and spines also ornamented with club-shaped granules.

Front narrow, truncated, notched medially, obscurely quadridentate before, bi-lobed above.

Orbits small, round; supraorbital margins deeply concave, doubly fissured, terminated laterally in a small, rounded extraorbital tooth, produced to a blunt tooth adjacent to antennal hiatus.

Hepatic and protogastric regions clearly marked but not prominent. Posterior part of mesogastric region inflated. Strongly inflated cardiac region outlined by grooves and with a prominent rearwardly directed spine on posterior aspect. Branchial regions inflated, each with a series of four spinules on lateral aspect, the spinules increasing in size posteriorly. Sub-branchial margins slightly arched above base of each limb and with a well marked granulate border. A triangular spine on either side of short posterior margin of carapace.

Subfrontal region similar to that of *E.* (*P.*) *tatei*. Pterygostomial regions narrowly subtriangular, with a central spine. Mouthfield and endostome also similar to those of *E.* (*P.*) *tatei*.

Sternum of male longitudinally oval and with a deep median groove to receive abdomen, sternites apparently ornamented by low, flat granules; posterior margin of first large sternite gently convex rearwards, posterior margin of next sternite also slightly convex, hind margin of following sternites increasingly concave (rearwards); episterna triangular.

Measurements

The carapace of the holotype S.A.M. P15564 is 6.7 mm long and 6.9 mm wide (excluding peripheral spines). The carapace of paratype S.A.M. P15565 is 6.3 mm long (incomplete).

Remarks

Ebalia (Phlyxia) nildottiensis most closely resembles E. (P.) sturti from which, however, it differs in having the hepatic and epigastric regions less swollen and the dorsal profile of the carapace flatter in lateral view, and in lacking conspicuous spines on the dorsal aspect of the carapace. It differs from Ebalia (P) tatei in its less swollen hepatic and epigastric regions, in having the dorsal aspect of the carapace appreciably flatter, more finely granulate and without any distinct prominences, and in the margins of the carapace being ornamented by relatively slender granulate spines rather than prominent rounded bosses.

The bosses and prominences present on E. (P.) tatei and the spines on E. (P.) nildottiensis can each be matched to analogous spines on E. (P.) sturti. This and other similarities indicate that these three species are closely allied.

Genus Nucia Dana, 1852

Type species: Nucia speciosa Dana, 1852, by monotypy.

Nucia Dana, 1852. Serene, 1954: 480 (generic synonymy, diagnosis, key to species); 1955: 153 (revised key to species). Sakai, 1965: 37. Glaessner, 1969: R498.

Remarks

The works of Seréne (1954, 1955) omit to mention the one previously described fossil species referred to this genus, *Nucia fennemai* Böhm, 1922, from the Lower Miocene of Java. The present-day species of *Nucia* are Indo-Pacific in distribution and are apparently restricted to tropical and subtropical waters.

Nucia rhomboides sp. nov.

Plate 9 figure 10a,b

Name

From the Greek *rhomboides*, meaning rhomboidal; in reference to the shape of the outline of the carapace.

Material

One well preserved carapace, holotype S.A.M. P15567, coll. R.J.F.J., 1968.

Occurrence

Approximately 18-20 m above N.R.L., Nildottie loc. 4.

Stratigraphic Position and Age

Middle part of Mannum Formation. Late Lower Miocene.

Description

Carapace rhomboidal, 1.1 times as wide as long, convex dorsally; regions well marked, tumid, the branchial regions with several conspicuous swellings; surface paved with fine, flattish, low granules.

Front projected forwards, narrow, .2 width of carapace, forming two rounded lobes separated by a fine median groove; behind front a median crest extends backwards to gastric regions.

Orbits small, ovate, without distinct sutures.

Anterolateral margins very convergent forwards, a large hepatic prominence followed by a small protuberance on anterior part of branchial region. A bluntly pointed tubercle at widest part of carapace. Posterolateral margins very convergent rearwards, each with two rounded prominences. Rear margin of carapace with a well marked, wide border.

A deep hollow behind orbits and above hepatic regions. Protogastric regions strongly inflated. Anterior portion of mesogastric region acutely triangular; a median swelling on posterior part of region. Cardiac region greatly inflated, nearly hemispherical, outlined by distinct grooves. Branchial regions each with two swellings on dorsal aspect. Sub-branchial margins slightly arched over base of each limb and with a well marked border.

Antennular-antennal fossae small, rounded-subtriangular. Antennal hiatus narrow. Epistome short, arched forwards.

Pterygostomial regions subtriangular; anterior margin bluntly rounded; a slight protuberance directly below anterolateral hepatic prominence. Anterior portion of pleural suture well marked.

Lateral margins of buccal frame moderately convergent forwards; adjacent narrow gutters represent inhalant canals; anterior part of endostome with a low, median ridge.

Measurements

The carapace of the holotype is 9.3 mm long and 11 mm wide.

Remarks

This fossil most closely resembles the extant Nucia bouvieri Ihle, 1918, from off Rott I. and Semau I. near Timor and off South Vietnam. However it is distinguished by the more rhomboidal outline of the carapace and its relatively narrower front.

Genus Pariphiculus Alcock, 1896

Type species: Randallia coronata Alcock and Anderson, 1894, by original designation.

Pariphiculus Alcock, 1896: 257. Ihle, 1918: 248. Sakai, 1937: 103, 129; 1965: 43. Beets, 1949: 351. Glaessner, 1969: R498.

Carapace subcircular or oval-elongate, globular; frontoorbital region produced forwards to form a short "snout", cardiac region inflated and isolated by grooves, other regions more or less indistinct; surface usually granulate and often finely perforate (bearing a sparse tomentum in extant species); margins with short spines; infraorbital lobes low and obtuse; anterior margin of pterygostomial regions formed into two lobes notched between. Palm swollen proximally, shorter than fingers.

The genus contains four previously described species:

Pariphiculus mariannae (Herklots, 1852)

Extant. Coromandel and Malabar Coasts of India; 46-82 m. North of Madura I., East Indies; 82 m. China. The species inhabits soft, muddy bottoms (Alcock, 1896).

Pariphiculus coronatus (Alcock and Anderson, 1894)

Extant. Red Sea; 800 m. Bay of Bengal, off Coromandel Coast; 205 m. Great Nicobar I.; 296 m Sumbawa I.; 274 m. Japan; coast of Kyusyu to Sagami Bay; 65-250 m. The species inhabits a mud or sandy mud bottom (Sakai, 1937).

Pariphiculus agariciferus Ihle, 1918

Extant. Between Timor and Rott I.; 216 m. Japan: Kii Peninsula, Tolsa Bay and Sagami Bay; 65-209 m.

Pariphiculus oselli Beets, 1949

Lower Miocene (Rambangan), Madura I.

Pariphiculus coronatus (Alcock and Anderson, 1894)

Randallia coronata Alcock and Anderson, 1894: 174.

Pariphiculus coronata (Alcock and Anderson, 1894) Alcock, 1896: 258.
Sakai, 1965: 43, pl.17, fig.4 (synonymy).

Pariphiculus coronatus spinosus subsp. nov.
Text-figure 39a,b; plate 9 figure 11a,b

Name

From the Latin _spinosus_, spiny.

Material

One specimen of the carapace, the holotype S.A.M. P15790, with the orbits damaged and most of the granules and spines on the surface broken away. Specimen preserved as the shell material and coll. R.J.F.J., 1966.

Occurrence and Stratigraphic Position

From 0.5 m below the top of the upper member of the Morgan Limestone, Morgan loc. 1.

Age

Late Lower Miocene or early Middle Miocene.

Description

Carapace subcircular, globular, about as broad as long excluding peripheral spines; frontoorbital region produced forwards to form a short "snout", only posterior regions well marked on rest of carapace; surface closely covered by variably sized, coarse, rounded granules and bearing numerous tubercles; 16 short spines peripheral.

Front narrow, bidentate, medially grooved above.

Orbits damaged, small, apparently round; supraorbital margins each with two deep fissures.

Hepatic and protogastric regions separated by a fine shallow groove which extends rearwards and slightly outwards from lateral part of fronto-orbital margin. Hepatic regions with a tubercle on inner portion and two spines near lateral margin. Protogastric regions each bearing five tubercles arranged in a V-shaped pattern. Mesogastric region slightly raised, bounded laterally by two short, deeply incised grooves, and with a single tubercle positioned medially. Cardiac region swollen, isolated by distinct grooves, and bearing two tubercles on mid-line. Branchial regions each with two tubercles positioned subdorsally and four spines on lateral aspect, second spine in this lateral series at widest part of carapace. Sub-branchial margins with a prominent flange gently arched above base of each limb. A spine on either side of short posterior margin of carapace.

Epistome short, arched upwards and forwards.

Pterygostomial regions expanded to protrude slightly beyond hepatic regions, separated from latter by a shallow groove containing pleural suture; anterior margin formed into a prominent, forwardly directed, external spine and a short, rounded, inner denticle, the two separated by a deep notch between; one spine on anterolateral aspect.

Lateral margins of buccal frame moderately convergent forwards and with a narrow border.

Measurements

The carapace of the holotype is 18 mm long and 19 mm wide (excluding peripheral spines).

Remarks

The only differences observed between the present specimen and the extant P. coronatus are:

(a) Two additional spines appear to be present on the lateral aspect of the hepatic regions of the fossil form.

(b) The lateral lobe on the anterior margin of the pterygostomial region is more elongated in P. coronatus spinosus.

(c) On the present specimen the tubercles on the dorsal aspect of the anterior half of the carapace seem more distinct.

The features of P. coronatus spinosus seem identical in all other respects with those discernible in published illustrations of P. coronatus. It seems clear that P. coronatus spinosus represents the direct ancestor of the modern form.

Superfamily Raninoidea de Haan, 1841
Family Raninidae de Haan, 1841
Genus *Lyreidus* de Haan, 1841

Type species: *Lyreidus tridentatus* de Haan, 1841, by monotypy.

Lyreidus de Haan, 1841. Glaessner, 1929: 241 (list of fossil species); 1960: 16, 17 (discussion concerning fossil species): 1969 R500 (diagnosis). Griffin, 1970: 93 (diagnosis, review of modern species).

Tribolocephalus Ristori, 1886: 127. Van Straelen, 1927: 85. Glaessner, 1929: 387.

Ranidina Bittner, 1893: 33. Glaessner, 1929: 360 (species listed). Lörenthey and Beurlen, 1929: 120. Glaessner, 1969: R501.

Remarks

Tribolocephalus is represented by only one species, *T. laevis* Ristori, 1886, from the Pliocene of Italy. This form greatly resembles the modern *Lyreidus channeri* Wood-Mason, 1885, except for lacking spines on the lateral margins; probably these have been broken away.

Ranidina (type species *R. rosaliae* Bittner, 1893, from the Miocene of Austria) is said to differ from *Lyreidus* in features of its sternum and in possessing two longitudinal grooves on the dorsal aspect of its carapace (Lörenthey and Beurlen, 1929; Glaessner, 1969). However in the illustration of the ventral aspect of its type species given by Lörenthey and Beurlen (1929: plate 5, figure 8b) the sternum is not markedly different from that of Lyreidus tridentatus (except for some probable breakage). The longitudinal grooves on the carapace were originally described by Bittner (1893) as "cracks". Possibly they correspond to the supraorbital sutures and the faint branchiocardiac grooves evident in some specimens of Lyreidus.

Lyreidus tridentatus de Haan, 1841

Plate 10 figures 2 - 6a,b

Lyreidus tridentatus de Haan, 1841. Griffin, 1970: 94, text-figs.6a,e, f,j-o, 7a,b, 8a,b,f,g; pl.1, fig.A (synonymy, remarks, biometry, distribution).

Material

A number of specimens of the carapace and one specimen of the articulated carpus and manus of a cheliped. A carapace with the frontoorbital region damaged and the skeletal material exfoliated from the median part of the dorsal aspect, hypotype S.A.M. P15772; a carapace with the rostrum missing and the anterolateral aspects damaged, hypotype S.A.M. P15773; three complete specimens of the carapace, S.A.M. P15791-92 and hypotype S.A.M. P15793; seven broken specimens of the carapace, S.A.M. P15794, P15796A-F; the carpus and manus of a right cheliped, hypotype S.A.M. P15795; a carapace with the frontoorbital margin broken away, hypotype

S.A.M. P15820. Specimens all preserved as original shell material, P15773 coll. R. Tate; P15794 coll. M. Wade, 1955; remainder coll. R.J.F.J., 1970.

Occurrence and Stratigraphic Position

Gambier Embayment, Otway Basin

Crab bed, Gambier Limestone, in quarry near middle of section 28, Hundred of Blanche, Mount Gambier loc. 1 (P15772). Gambier Limestone, Mount Gambier area, precise locality unknown (P15773). Gambier Limestone, between 8.5 and 10.5 m below ground surface in quarry on section 601, Hundred of Blanche, Mount Gambier loc. 2 (P15796A-F, P15795). Gambier Limestone, precise stratigraphic level unknown, quarry on section 606, Hundred of Blanche, Mount Gambier loc. 2 (P15794).

Murray Basin

From 3.5 m below top of upper member of Morgan Limestone, Morgan loc. 1 (P15820).

Age

Gambier Embayment

Middle Oligocene (P15772); Middle Oligocene - early Middle Miocene (P15773); middle Lower Miocene (P15794, P15795, P15796A-F).

Murray Basin

Late Lower to possibly early Middle Miocene (P15820).

Measurements

The carapace of P15772 is 22 mm long (including rostrum) and 13 mm wide (excluding lateral spines; the frontoorbital margin is 5.7 mm wide). Specimen P15793 has the carapace 15 mm long, 9.2 mm wide, and the frontoorbital margin 4.1 mm wide. Specimen P15820 has the carapace 29 mm long (incomplete), 18 mm wide, and the frontoorbital margin 7.4 mm wide (incomplete). The carpus of P15795 is 11 mm long and the palm is 13 mm long and 7.6 mm high.

Remarks

The materials listed above are indistinguishable from modern specimens of *Lyreidus tridentatus*. At the present time this species occurs widely in the western and central Pacific at depths of between 27 and 380 m (Griffin, 1970). In the Australasian region it occurs off southwestern and eastern Australia, New Zealand and New Caledonia. The modern New Zealand population differs slightly from the extant Australian form; the width of the frontoorbital margin of the carapace tends to be a little greater, the lateral spines of the carapace project a little further laterally and the merus of the cheliped is slightly more slender. Griffin demonstrated that the populations just noted overlap in these features and considered that the differences represent only regional intraspecific variation. Bennett (1964) described the carapace of the New Zealand specimens as being "finely and uniformly punctulated" and fine pitting as clearly evident in his figure 106. In contrast the few modern Australian specimens which the author has seen have the carapace polished and only faintly pitted. Sakai (1937) remarked on the "smooth and polished" surface of the carapace in specimens from Japan, the region from which the types of the species were obtained. The variability of the surface pitting in regional populations has not been described.

The relative width of the frontoorbital margin of the Middle Oligocene specimen P15772 (with frontoorbital margin/width carapace = 0.43) is closely comparable to that of relatively wide fronted, similar sized specimens from the present New Zealand population. The width of the frontoorbital margin of the mid Lower Miocene specimens falls within the limits of variation of either the extant New Zealand or eastern Australian populations. All of the fossil specimens from the Gambier Embayment have the surface of the carapace finely and distinctly pitted as in the modern New Zealand individuals described by Bennett (1964). It thus seems likely that the modern New Zealand population descended directly from and is virtually identical to populations which existed off southern southeastern Australian in the Middle Oligocene and early Miocene (Figure 40).

The late Lower Miocene specimen P15820 has the carapace smooth and polished as in the present Australian population. The specimen apparently evolved from older forms represented in the Gambier Embayment. In turn the population from which it was derived was almost certainly the forerunner of the extant Australian population. The present fossil materials thus suggest that the ancestral (Oligocene) form of L. tridentatus in Australasia survives today in New Zealand and that the modern Australian form has diverged from this original stock. This viewpoint contrasts with the suggestion made by Griffin (1970:p.109) that the living New Zealand population of Lyreidus is in the course of becoming a distinct species from the form to which the extant Australian populations belong.

Lyreidus brevifrons Sakai, 1937

Plate 10 figure 1a-d

Lyreidus brevifrons Sakai, 1937. Griffin, 1970: 104, text-figs.6b,g,p, 7d, 8c, pl.1, fig.B (synonymy, remarks, distribution).

Time Range

Extant

Geographic Distribution

Indo-West-Pacific; Dar-es-Salaam; west of the Philippines; near Hong Kong; and southeastern Japan; 188-394 m (Griffin, 1970).

Lyreidus brevifrons elegans Glaessner, 1960

Lyreidus elegans Glaessner, 1960: 16, text-fig.5, pl.2, figs.15,16.

Material

A well preserved carapace associated with the sternum and fragmentary remains of the appendages, N.Z.G.S. DC 359. The specimen is probably a moult. The extraorbital spines are broken.

Occurrence and Stratigraphic Position

0.8 km south of Perpendicular Point, near Porarari, west coast of South Island of New Zealand. From upper part of Arnold Series.

Age

Runangan, late Upper Eocene.

Measurements

The carapace of DC 359 is 32 mm long (including rostrum), 16 mm wide (excluding lateral spines), and with the frontoorbital margin 7 mm wide (incomplete). The distance from the hind margin of the orbits to a line drawn between the lateral spines (between anterior margin of base of either spine) is 11 mm.

Remarks

Glaessner (1960) described Lyreidus elegans from two specimens respectively from the late Lower Miocene (Altonian Stage) and late Lower to possibly Middle Miocene of the northwestern part of the South Island of New Zealand. Both of these specimens have the frontoorbital margin broken away and the holotype is apparently fractured and distorted (see Glaessner's plate 2 figure 16). The present specimen is also from the northwestern part of the South Island of New Zealand and its features correspond closely to those which Glaessner gives for L. elegans. Its proportions are similar to those of the paratype of the latter (measured from enlargements of photographs which Professor Glaessner kindly made available). Thus although the new specimen is appreciably older than the type material of L. elegans there seems no reason to regard it as being other than conspecific.

The frontoorbital margin of the present specimen is complete except for the extraorbital spines (Plate 10, Figure 1c,d). The orbits seem to have been relatively deep and the rostrum is slightly longer than wide. The extraorbital spines have strong bases and may have been relatively long; their lateral margins are parallel or even slightly divergent forwards. A small notch and fissure is present in each lateral suborbital margin; this notch seems to have been well behind the posterior margin of the cornea of the eye.

Glaessner (1960) suggested that L. elegans was the ancestor of the modern Lyreidus tridentatus. He distinguished L. elegans from L. tridentatus by its relatively wider frontoorbital margin, its less strongly converging anterolateral margins, and the more posterior position of its lateral teeth. Griffin (1970) considered it doubtful that L. elegans and L. tridentatus were distinct species.

The new specimen differs from L. tridentatus in the features which Glaessner noted for his material, and in addition, in its more elongate rostrum, the more nearly parallel lateral margins of its extraorbital spines and the notched or fissured lateral suborbital margins. These differences are regarded as being of specific importance and L. elegans and L. tridentatus are considered to be separate species.

The proportions of the present specimen and Glaessner's paratype of L. elegans are closely similar to those of the living species Lyreidus brevifrons. The rostrum and the preserved parts of the extraorbital spines of the present specimen resemble their counterparts in L. brevifrons. The new specimen appears to differ from L. brevifrons only in the notched form of the lateral suborbital margins, in having the posterior gastric pits positioned slightly more towards the rear of the carapace, and possibly in having the second segment of the antenna somewhat shorter and broader. It thus seems likely that L. elegans is the direct ancestor of L. brevifrons and that the two are conspecific; the differences noted between them are regarded as being probably of subspecific importance.

Evolution of the genus Lyreidus

Griffin (1970) recognizes a total of five living species belonging to this genus, namely:-

Lyreidus tridentatus de Haan, 1841

Eastern Indian Ocean, Western and Central Pacific Ocean; 27-384 m.

Lyreidus bairidii Smith, 1881

West Indies and off eastern North America; 119-475 m.

Lyreidus channeri Wood-Mason, 1885

Northern Indian Ocean and Western Pacific Ocean; 366-740 m.

Lyreidus stenops Wood-Mason, 1887

Western Pacific Ocean; 55-141 m.

Lyreidus brevifrons Sakai, 1937

Western Indian Ocean and Western Pacific Ocean; 188-395 m.

The following fossil forms apparently belong to the genus:-

Lyreidus tridentatus de Haan, 1841

Middle Oligocene and Lower Miocene to possibly early Middle Miocene. Southern Australia.

Tribolocephalus laevis Ristori, 1886

Pliocene. Italy.

Ranidina rosaliae Bittner, 1893

Tortonian. Austria.

Lyreidus paronai Crema, 1895

Burdigalian and Helvetian. Italy.

Lyreidus fastigatus Rathbun, 1919

Oligocene. West Indies.

Lyreidus hungaricus Beurlen, 1939

Middle Oligocene. Hungary.

Lyreidus brevifrons elegans Glaessner, 1960

Upper Eocene and Lower to possibly Middle Miocene. New Zealand.

All of these forms except *L. fastigatus* are represented by specimens of the carapace. *L. fastigatus* was described from only the carpus of the left cheliped. While it apparently shows similarities to other (modern) species of *Lyreidus*, this remains is perhaps too fragmentary to provide a positive identification of the genus.

The status of *Lyreidus alseanus* Rathbun, 1932, which was described from a single badly fractured and incomplete carapace from the Lower Oligocene of Oregon, is uncertain. A literal interpretation of the description and figures given by Rathbun (1932) suggests that it may belong to the genus *Ranilia* H. Milne-Edwards.

In its upward and outwardly directed outer-orbital tooth *Ranidina willapensis* Rathbun, 1926, from the Oligocene of Washington resembles species of *Raninoides* H. Milne-Edwards. Griffin (1970: p.107) notes that the raninid species occurring in the eastern Pacific today are quite unlike *Lyreidus*.

Griffin (1970) considers that the living Indo-West-Pacific species of *Lyreidus* could be divided into three groups. The extant American species constitutes a fourth group. These divisions can be characterized as follows:

L. tridentatus group

Anterolateral margins of carapace straight or uniformly curved, terminating posteriorly in a single short lateral spine. *L. tridentatus*, *L. brevifrons*.

L. bairdii group

Anterolateral margins of carapace sinuous, a convex protruberance immediately in front of a single short lateral spine. *L. bairdii*.

L. channeri group

Lateral margins of carapace with two spines, one large and situated at posterior termination of anterolateral margin, the other smaller or considerably smaller and a little further forward. Extraorbital spines and rostrum elongated. *L. channeri*.

L. stenops group

Lateral margins of carapace smoothly curved, without spines. Frontoorbital margin relatively narrow. *L. stenops*.

The fossil remains of *L. tridentatus* and *L. brevifrons elegans* from the Tertiary of Australia and New Zealand respectively, clearly extend the time range of the *L. tridentatus* group back to the Upper Eocene (Figure 40). The degree of similarity exhibited between these fossils and modern populations of their respective nominate species indicates that evolutionary change has been minimal in this section of *Lyreidus* over the 40 million year time span from the Late Eocene to the present and the group must surely rank as one of the most conservative divisions of known crustaceans. Raninids are burrowing crabs and evidently the *L. tridentatus* group has achieved a nearly perfect state of adaptation to this mode of life. Griffin (1970) indicates that *L. tridentatus* has the widest geographic distribution of any extant member of the genus and this probably reflects the degree to which it is fitted to its way of living. *L. tridentatus* and *L. brevifrons* overlap in their depth range (Griffin, 1970; above, pp.220, 221). The geographic ranges of these species overlap in southeastern Japan and it seems not unlikely that the two are actively competing in this region. The fossil remains of *L. tridentatus* known lend support to the idea that this species reached New Zealand from Australia. Competition from *L. tridentatus* may have led to the extinction of the earlier New Zealand form *L. brevifrons elegans*.

L. rosaliae resembles *L. tridentatus* and thus probably belongs to the same group. The anterior part of the carapace of *L. rosaliae* is not markedly produced; this is possibly a primitive feature.

The resemblance between L. laevis and L. channeri has been noted already, and hence L. laevis can be considered a representative of the L. channeri group. In the general shape of the carapace and in the arrangement of the lateral spines and teeth L. hungaricus also closely resembles L. channeri. Unfortunately, however, the frontoorbital margin is broken away in the one specimen of L. hungaricus known. Nevertheless it seems probable that L. hungaricus was near the ancestor of the L. channeri group.

L. paronai also seems rather similar to L. hungaricus and L. channeri. It differs from the latter, however, in having a small ancillary tooth on the inner side of each of the extraorbital teeth. In this it resembles spines of Ranilia (for example Ranilia vareolata Lörenthey and Beurlen, 1929, from the Eocene of Hungary). It thus seemingly provides an evolutionary link between Ranilia and the L. channeri group.

The anterolateral margins of the carapace of L. hungaricus are also reminiscent of the similarly sinuous anterolateral margins of L. bairdii. Hence it is possible that the L. channeri and L. bairdii groups are quite closely related and had a common ancestry.

No fossil material of the L. stenops group is known. The elegant, bottle-shaped carapace of L. stenops is suggestive of a relationship with the L. tridentatus group. Illustrations given by Griffin (1970) show that L. stenops particularly resembles L. tridentatus in the general shape of the manus of the cheliped and the form of the dactyl of the third ambulatory leg; to a lesser degree the two are similar in the outline of the anterior portion of the sternum and the shape of the male first pleopod (resemblance evident to pleopod of Japanese *L. tridentatus*). Possibly *L. stenops* and *L. tridentatus* have a common ancestor.

If *Lyreidus* evolved from *Ranilia* as has been suggested, then the main evolutionary trends which occurred during the history of this evolution were for the anterior part of the carapace to become elongated and the frontoorbital margin narrowed with a consequent loss of supraorbital teeth or denticles. If *Lyreidus* burrows rearwards into the substrate to leave only the extreme anterior part of the carapace protruding (Bourne, 1922), the changes would be of obvious advantage for concealment. These changes were essentially complete in the *L. tridentatus* group by the Upper Eocene, but seem to have been more gradual in the other sections of the genus.

Section OXYRHYHCHA

Family Majidae Samouelle, 1819

Subfamily Majinae Samouelle, 1819

Genus *Maja* Lamarck, 1801

Type species: *Cancer squinado* Herbst, 1788, by designation under Plenary Powers, Opinion 511, *Opin. Decl. int. Commn. zool. Nom.*, 2nd May, 1958.

Maja Lamarck, 1801. Sakai, 1965: 83 (generic synonymy). Zariquiey Alvarez, 1968: 444, 445 (generic description). Glaessner, 1969: R502.

Carapace pyriform; rostral (pseudorostral) spines elongate, projected forwards, subparallel or divergent; orbits consisting above of supraorbital eave, intercalated spine and postorbital spine, the three separated by deep fissures; supraorbital eave lamellate, bearing a spine at posterior corner (antorbital spine), intercalated spine of moderate size, postorbital spine large, acute, limiting rear of orbit, either hollowed or not hollowed anteriorly; infraorbital margins formed by basal antennal article and a flattened prominence near base of postorbital spine; orbital foramen ovate, notched behind; regions indistinct to moderately well marked; surface of carapace usually closely covered by granules, tubercles and spinules; lateral margins and median line usually bearing spines; basal antennal article of moderate width with anterior angles spinose, foramen for flagellum included within lip of orbit. Palms of chelae usually slender, sometimes short and inflated.

The genus includes the following forms:

Maja _squinado_ (Herbst, 1788)

Lower Pliocene: England.

Pleistocene: Sicily.

Extant: Eastern Atlantic north of Guinea to Ireland and Marche, France; Mediterranean.

Maja _squinado_ _distefanoi_ Gemmellaro, 1914

Pleistocene: Sicily.

Maja verrucosa H. Milne-Edwards, 1834

Pliocene: England.

Extant: Eastern Atlantic from the Cape Verde Is. and Cape Blanco to Portugal; Mediterranean.

Maja spinigera de Haan, 1837

Extant: Beluchistan; Formosa; and Japan.

Maja orbignyana Millet, 1854

Helvetian: France.

Maja sp. Woodward, 1873

Miocene: Malta.

Maja miersii Walker, 1887

Extant: Cape Jaubert, northwestern Australia; Singapore; Japan; sublittoral to 148 m.

Maja goltziana d'Oliveira, 1888

Extant: Eastern Atlantic from the Congo and Principe I. north to Portugal; Mediterranean, Israel.

Maja gibba Alcock, 1895

Extant: Andaman Sea; 457 m.

Maja miocenica Lörenthey, 1909

Tortonian: Sardinia.

Maja suluensis Rathbun, 1916

Extant: Philippines, Sulu Archipeligo; 16 m.

Maja linapacanensis Rathbun, 1916

Extant: Philippines, Linapacan St.; 84 m.

Maja bisarmata Rathbun, 1916

Extant: Philippines, off northern Mindanao; 333 m in water at a temperature of 12.4°C.

Maja biaënsis Lörenthey and Beurlen, 1929

Tortonian: Hungary.

Maja hungarica Lörenthey and Beurlen, 1929

Tortonian: Hungary.

Maja japonica Rathbun, 1932

Extant: Japan; 57-203 m.

Maja japonica Sakai, 1934 (non *M. japonica* Rathbun, 1932)

Extant: East China Sea.

Maja laddi Rathbun, 1934

Neogene: Fiji.

Maja _kominatoensis_ Kubo, 1936

Extant: Japan; 366 m.

Maja _arambourgi_ Van Straelen, 1936

Pliocene: Algeria.

Maja _austriaca_ Bachmayer, 1953

Tortonian: Austria.

Maja _oroszyi_ Bachmayer, 1953, also from the Tortonian of Austria, appears referable to _Pisa_ Leach, 1815.

The above data indicates that at the present time the distribution of the genus extends through the tropics. The northern limit of its species appears to be related to the presence and extent of warm currents. The latitudinal extent of fossil representatives of the genus is comparable to that of the modern forms. Thus _Maja_ was probably restricted chiefly to tropical and subtropical waters throughout its history.

Maja _robinsoni_ sp. nov.

Plate 11 figures 1a-e, 2

Name

Named after Mr. Bret Robinson who in conjunction with Mr. H. Eames found the holotype specimen; this discovery was the first made in what is now known to be a rich fossil decapod occurrence.

Material

Nine specimens of the carapace, three almost complete and the remainder more or less fragmentary. Holotype S.A.M. P15679 a well preserved virtually complete carapace, but with the surface ornamentation slightly abraded. Paratypes S.A.M. P15680 and P15683 nearly complete carapaces with the surface ornamentation undamaged. Specimens all preserved as the original shell material. Holotype coll. Bret Robinson, 1968; other examples coll. R.J.F.J., 1968-1969.

Occurrence

At 12-15 m above N.R.L., Nildottie loc. 1 (holotype). From 19-20 m above N.R.L., Nildottie loc. 2. Between 7 m (P15680) and 9 m and at 15 m above N.R.L., Nildottie loc. 3. Between 7 and 9 m above N.R.L., Nildottie loc. 4 (P15683).

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle to late Lower Miocene.

Description

Carapace broadly pyriform, 1.3 times as long as wide, slightly constricted behind hepatic regions, broadly convex longitudinally and transversely; regions distinct, delimited by shallow grooves; surface closely covered by coarse granules, spinules and small rounded tubercles and bearing a few short, slender spines; granules and tubercles each with a group of fine pores which probably bore hairs during life.

Rostral spines projected forwards, slender, tapered, about $\frac{1}{8}$ length of carapace, round in section.

Orbits consisting above of a supraorbital eave, an intercalated spine and a postorbital spine, the three separated by deep fissures; supraorbital eave wide, lamellate, rounded before, strongly arched, granulate above, bearing a prominent antorbital spine directed obliquely outwards and forwards; intercalated spine short, flattened, extending only slightly beyond base of antorbital spine; postorbital spine about $1\frac{1}{2}$ times size of intercalated spine, acute, directed forwards and outwards, limiting rear of orbit, with upper anterior margin sharp-crested and anterior face hollowed. Infraorbital margins fairly complete, formed by basal antennal article and a short flattened prominence adjacent to base of postorbital spine. Orbital foramen oval, notched behind so that eyestalk could probably fold rearwards in life.

Frontal region of carapace moderately narrow, medially depressed between two longitudinal ridges bearing two or three small tubercles. Protogastric regions rounded, with several small tubercles near upper margin. Narrow anterior portion of mesogastric region with a conspicuous median tubercle; two short spines, the second more prominent, on mid-line of posterior part of region; posterior gastric pits distinct. Hepatic regions inflated with a single short marginal spine followed by several spinules; sub-hepatic regions each weakly subdivided into two by a shallow groove and densely spinulose. Mesogastric region weakly bi-lobed, a distinct pit on either side of posterior part of region. Urogastric region constricted, bearing a median spinule; lateral urogastric grooves well marked, crescentic. Cardiac region expanded, subhexagonal in outline, surmounted by a short median spine. Intestinal region elongate, with two small tuberoles positioned submedially on anterior portion and another situated at centre of region. Epibranchial regions only faintly marked. Two small branchial lobes adjacent to metagastric region and urogastric region respectively. Mesobranchial regions swollen, bearing two short spines and several spinules between on anterolateral aspects; another spine positioned subdorsally, level with cardiac spine. Metabranchial regions each forming a low swelling lateral to posterior part of cardiac region and with a second swelling behind. Sub-branchial margins with a distinct narrow border. Short posterior margin of carapace projecting slightly rearwards and bearing two spines.

Basal antennal articles of moderate width, concave on either side, fused to frontoorbital region along an incised suture; outer margin smooth and lamellate, inner margin granulate; anterior angles toothed; anteromedial tooth small, spinous, directed downward and forward; anterolateral tooth about twice size of anteromedial, flattened, directed outward; foramen for flagellum included just within margin of orbit, facing forward and upward. Openings of antennal glands subtriangular.

Antennular fossae broad, an inverted V-shape before, rounded behind; interantennular spine well developed, directed downward, curved, bluntly pointed, with anterior face weakly excavated; anterior process of epistome narrow and crested. Epistome (excluding anterior process) 2½ times as wide as long.

Pterygostomial regions subtriangular, flattened, separated from subhepatic regions by a deep groove; a small spine on lateral margin.

Buccal frame subrectangular; anterior margin transverse, gently sinuous, fissured medially and at about 1/6 width from either side; lateral margins subparallel, with a narrow border which dilates anteriorly. Endostome with posterior processes pointed behind; median embayment a broad inverted U-shape and with a narrow border bearing two small prominences.

Measurements

The carapace of the holotype S.A.M. P15679 is 31 mm long (excluding rostral spines) and 24 mm wide. The carapace of paratype S.A.M. P15680 is 30 mm long (excluding rostral spines) and 23 mm wide.

Remarks

Five similar extant species of *Maja* occurring in the Indo-West Pacific area, *M. gibba*, *M. japonica* Rathbun, *M.* "*japonica*" Sakai (*non M. japonica* Rathbun), and *M. miersi*, form a well defined group. The carapace of these species is densely and coarsely granulate or closely tuberculate, and bears very short to moderately long, slender spines on the branchial regions and median line.

M. robinsoni is a fossil member of this group closely resembling *M. gibba* and *M. japonica* Rathbun. It differs from *M. gibba* in having more slender rostral spines, a less prominent supraorbital intercalated spine, and one marginal hepatic spine rather than two. It differs from *M. japonica* in having the carapace slightly more elongate and the rostral spines subparallel, not divergent. The postrostral spine is hollowed anteriorly in *M. robinsoni*, but not hollowed in *M. japonica*. The basal antennal articles of the fossil are broader and more concave on either side than in either *M. gibba* or *M. japonica*.

Amongst the previously described fossil members of the genus *M. robinsoni* most closely resembles the Miocene species *M. miocenica* and *M. austriaca*. The arrangement of some of the spinules and principal tubercles on the carapace is similar to that in *M. miocenica*, but the rostral spines are considerably smaller and the postorbital spine less elongate. *M. robinsoni* resembles *M. austriaca* in the outline of the carapace and again in the positioning of spines and tubercles, but the marginal hepatic and branchial spines of *M. robinsoni* are smaller. The lateral spines of the carapace of *M. robinsoni* are smaller than in *M. orbignyana*, *M. biaënsis*, *M. hungarica*, *M. squinado*, *M. verrucosa* and seemingly *M. laddi*, which is probably too incomplete to be definitely identified as *Maja*. *M. arambourgi* is a form with extremely prominent carapace spines.

Genus Notomithrax Griffin, 1963

Type species: Paramithrax peronii H. Milne-Edwards, 1834, by original designation.

Notomithrax Griffin, 1963: 231 (generic diagnosis, key to species); 1966: 283 (in key to species of Australian majid spider crabs); 1966a: 49 (generic description, discussion, key to New Zealand and Australian species).

Remarks

Griffin (1963, 1966, 1966a) includes five extant species in this genus and indicates that it occurs off eastern and southeastern Australia, Norfolk Island, New Zealand, and Juan Fernandez, Chile.

Notomithrax angustifrons sp. nov.

Text-figure 41a-c; plate 12 figures 1a,c - 7a,b

Name

From the Latin angustus, narrow, and frons, front; in reference to its narrow frontal region.

Material

Three relatively complete specimens of the carapace and numerous fragments; various isolated parts of chelipeds attributed to this species. Holotype S.A.M. P15587, carapace with mid-dorsal portion fractured and eroded and the rostral (pseudorostral) spines broken; paratype S.A.M. P15588, carapace with anterior part broken away; paratype N.M.V. P29349, carapace largely preserved as an internal mould; specimens of broken anterior portion of carapace, paratypes S.A.M. P15589, P15592-93. Claw of left cheliped, paratype S.A.M. P15590; articulated carpus and propodus of left cheliped, paratype S.A.M. P15591; carpus of left cheliped, paratype S.A.M. P15595; propodus of right cheliped, paratype S.A.M. P15594; isolated movable finger of right claw, paratype S.A.M. P15596. All specimens other than moulds preserved as the original shell material. Specimen N.M.V. P29349 coll. F. A. Cudmore; other materials coll. R.J.F.J., 1968-1969.

Occurrence

Murray Basin

At 19-20 m above N.R.L., Nildottie loc. 2 (P15594-95). From 7 m (P15591) to 15 m (P15592) above N.R.L., Nildottie loc. 3 (P15587-93). Between 12 and 15 m above N.R.L., Nildottie loc. 4 (P15596).

Otway Basin

Balcombe Bay (N.M.V. P29349).

Stratigraphic Position and Age

Murray Basin

Middle part of Mannum Formation. Middle to late Lower Miocene.

Otway Basin

Balcombe Clay. Late Lower Miocene.

Description

Carapace broadly pyriform, about 1.3 times as long as wide, slightly constricted behind hepatic regions, moderately convex in longitudinal profile, strongly convex transversely; regions distinct, delimited by shallow grooves, greater part of protogastric regions smooth except for numerous fine pores, rest of carapace covered by variably sized, rounded tubercles and bearing a few inconspicuous spinules at margins, tubercles each with a group of fine pores which probably bore hairs in life.

Rostral spines projected forwards and slightly downwards, a little more deflexed distally, tapered, acuminate, about 1/10 length of carapace, compressed dorsoventrally; inner margins moderately divergent, outer margins not quite parallel; numerous fine pores on upper surface.

Orbits consisting above of a supraorbital eave, an intercalated spine and a postorbital spine, the three separated by deep fissures, but closely approximated; supraorbital eave lamellate, rounded before, strongly arched, bearing a short antorbital spine, surface of eave with scattered pores; intercalated spine reaching just beyond tip of antorbital spine, flattened dorsoventrally or conical; postorbital spine about 1.5 times size of intercalated spine, conical, not limiting rear of orbit. Infraorbital margin incomplete, formed by basal antennal article and a small rounded tubercle behind. Orbital foramen round, a slight posterior lip probably restricting rearward movement of eyestalks in life.

Frontal region of carapace narrow, grooved medially between two longitudinal ridges bearing a line of three or four tubercles which progressively increase in size rearwards. Several pairs of tubercles positioned submedially above protogastric regions. Mesogastric region with two prominent tubercles in mid-line; gastric apodemal pits indistinct. Hepatic regions swollen, with a group of four to seven small spinules on lateral aspect. Metagastric region sub-lunate, with two deep pits on either side. Urogastric region constricted, with a single median tubercle. Cardiac region elevated, subhexagonal, slightly elongated, covered by numerous low tubercles, two slightly more prominent tubercles positioned submedially, grooves lateral to posterior part of region crenulate. Intestinal region with two conspicuous tubercles submedian before and another positioned centrally. Epibranchial regions not well defined, a small triangular depression on anterolateral portion. Two small inner-branchial lobes each with a large rounded tubercle. Mesobranchial regions expanded with five or six small spinules on lateral periphery and a conspicuous tubercle on innermost portion. Metabranchial regions with a slight swelling adjacent to cardiac region. Sub-branchial margins with a narrow border. Short posterior margin of carapace with a small spinule on either side.

Basal antennal articles of moderate width, elongate, slightly tapered, fused to frontoorbital region along an incised suture; anterior angles toothed, anteromedial tooth short, acute, directed downward and forward, anterolateral tooth bluntly rounded, projected laterally; foramen for flagellum excluded from orbit, facing forwards and upwards.

Antennular fossae narrow, an inverted V-shape anteriorly; inter-antennular spine short, directed downward and rearward, and with anterior face weakly excavated.

Chelipeds robust. Carpus 1.8 times as long as high, increasing in height distally, smooth, with upper margin rounded, lower margin distinctly ridged, and outer face broadly ridged medially. Palm subrectangular, 1.5 to 1.7 times as long as high, biconvex, smooth; upper margin gently convex and forming a rounded ridge; lower margin gently convex and rounded; both inner and outer face with several pits near points where movable finger articulates. Fingers slender, tapered, separated by a broad diastema at base; fixed finger imperfectly known, smooth basally, apparently with distal portion of prehensile margin sharp edged; movable finger about .7 length of palm, and with a single tooth at about .3 length from proximal end, more distal part of prehensile margin sharp and very finely granulate, a single pit on dorsal aspect of basal portion of finger.

Measurements

The carapace of the holotype S.A.M. P15587 is 24 mm long (excluding the rostral spines) and 18 mm wide. The carapace of N.M.V. P29349 is 21 mm long and 17 mm wide. The carapace is known to reach approximately

26 mm long. The palm of the left claw S.A.M. P15590 is 15 mm long and 9.9 mm high.

Remarks

The claws referred to this species occur in the same stratigraphic interval as specimens of the carapace in exposures of the Mannum Formation in the Nildottie-Swan Reach area, but have not been found in direct association with the carapace. The claws are more numerous in intervals in which remains of the carapace are plentiful. Several claws are found for every carapace.

The one carapace (N.M.V. P29349) from the Balcombe Clay of the Otway Basin is very similar to the type material except for the intercalated and postorbital spines being more elongated and sharp-pointed.

Notomithrax angustifrons most closely resembles the extant species *Notomithrax minor* (Filhol, 1885), from Port Curtis, Queensland, to Tasmania, and New Zealand. The fossil species differs from *N. minor* in the following particulars:

(a) The frontal region of the carapace is relatively narrower.

(b) No spines are situated on the dorsal aspect of the carapace; numerous dorsal spines are present in *N. minor*.

(c) The spinules on the hepatic and branchial margins of the fossil species are much smaller than the spines on these margins in *N. minor*.

(d) The antennal fossae are narrower.

(e) The basal antennal articles are narrower and differ in the accentuation of the anterior angles.

(f) The carpus of the chelipeds is much more weakly ridged.

Genus Leptomithrax Miers, 1876

Type species: Paramithrax (Leptomithrax) longimanus Miers, 1876, subsequent designation by Miers, 1879.

Leptomithrax Miers, 1876. Griffin, 1966a: 60 (generic synonymy, generic description, discussion, key to extant New Zealand and Australian species). Glaessner, 1969: R502.

Remarks

Bennett (1964) divided the extant Australian and New Zealand species of this genus into three subgenera, Leptomithrax sensu stricto (type species L. longimanus Miers), Australomithrax (type species L. (A.) mortenseni Bennett, 1964, a subspecies of L. tuberculatus (Whitelegge, 1900) according to Griffin (1966a)), and Zemithrax (type species L. longipes (Thomson, 1902)). These subgenera were distinguished on the basis of features of the basal antennal article and the position of the antennal flagellum relative to the orbit, the form of the supraorbital margin, the degree of development of a swelling on the third maxilliped at the articulation of the ischium and merus, and the presence or absence of excavations in the sternum and abdomen. Griffin (1966a) rejected this formal subdivision, and instead recognized five informal groups or sections which show various lines of development in the features of the orbit and basal antennal article. The relationships between Bennett's subgenera and the informal sections distinguished by Griffin are shown in Table 9.

Griffin's second group is characterized by a strong anterolateral spine on the basal antennal article; his third group is distinguished by the tuberculate or spinose nature of the postorbital lobe. The author does not agree that the division between these two sections is particularly clear. The basal antennal article is rather similar in the members of both groups (excluding P. parvispinosus which the author has not seen): it is of moderate width or relatively broad, the anterior spines are prominent, and the anterolateral spine is appreciably larger than the anteromedial; the forward, upward and outward direction of the anterolateral spine causes it to lie against the anterior margin of the supraorbital eave so that the antennal peduncle is widely excluded from the orbit (Bennett, 1964: p.51 and fig.36). Also the prominences on the postorbital lobe of L. sternocostulatus closely approximate the tubercles or spinules present in L. gaimardii; this is particularly evident in juveniles of these species. The rostral (pseudorostral) spines of these two crabs have a rather distinctive shape and are extremely similar; other more general similarities also suggest that the two are allies. It should be noted that the sternal excavations of L. sternocostulatus are not "wholly segmental" as stated by Griffin (1966a: p.61), but are intersegmental just as in L. tuberculatus.

Thus the formal subdivisions erected by Bennett (1964) probably do represent natural groupings within the genus, and this is further supported by the known fossil remains. Nevertheless this formal nomenclature is based on features which are potentially intergradational and implies a rigid distinction between otherwise very similar species. For these reasons the author concurs with Griffin in rejecting Bennett's nomenclature, but continues to recognize Bennett's divisions at the status of informal species-groups (Table 9).

Three extant species from outside the region of Australasia appear to belong to the *L. tuberculatus* group. They are *Leptomithrax sinensis* Rathbun, 1916, from the Philippines, and the two Japanese species *Leptomithrax edwardsi* (de Haan, 1839) and *Leptomithrax bifidus* (Ortmann, 1893).

The previously described fossil species referred to the genus are:

Leptomithrax atavus Glaessner, 1960

Late Miocene (Kapitean). Makino River, North Island of New Zealand.

Leptomithrax uruti Glaessner, 1960

Upper Miocene (Upper Tongaporutuan). Urati and Upper Waitara S.D., North Island of New Zealand.

Leptomithrax irirangi Glaessner, 1960

Lower Pliocene (Opoitian), near Waioura, North Island of New Zealand.

L. uruti closely resembles the modern New Zealand species *L. richardsoni* and is moderately similar to the Australian *L. gaimardii*. It differs from *L. richardsoni* in lacking a conspicuous preorbital spine on the anterior part of the supraorbital eave. It is distinguished from *L. gaimardii* by its slightly narrower frontal region, by the more conspicuous lobes of the metagastric region, and by the deeper groove separating the mesobranchial and metabranchial regions.

L. irirangi resembles *L. gaimardii* and another living Australian species, *L. waitei*. It is distinguished from both by its narrower front and by the smaller number of tubercles or spines on the dorsal surface of its carapace.

L. atavus has a narrower front than either *L. uruti* or *L. irirangi* but seems more similar to these than to any of the known extant species of the genus.

Leptomithrax martensis sp. nov.

Text-figure 42a-c; plate 13 figures 1 - 4

Name

Named after Marte, a railway siding adjacent to the locality where the species is found.

Material

Eleven remains of the carapace, all damaged or more or less incomplete. The holotype S.A.M. P15650, an incomplete left half of a carapace with part of orbital region present. Specimens preserved as the original shell material and coll. R.J.F.J., 1967-1968.

Occurrence

Quarry on northeastern part of section 26, Hundred of Blanche, Mount Gambier loc. 1 (P15650). Quarries near middle and immediately southeast of middle of section 28, Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Carapace broadly pyriform, about 1.1 times as long as wide, slightly constricted behind hepatic regions, moderately convex in longitudinal profile, strongly convex transversely; regions well marked; surface covered by rounded tubercles, pointed tubercles and broad conical spines, rounded tubercles each with a group of fine pores which probably bore hairs during life.

Orbits consisting above of a supraorbital eave, an intercalated spine and a postorbital spine, the three separated by wide deep fissures; supraorbital eave wide, lamellate, bearing a short antorbital spine; intercalated spine slender and extending only slightly beyond base of antorbital spine; postorbital spine positioned slightly below intercalated spine and about twice as long, partially limiting rear of orbit, slightly flattened anteriorly. Orbits apparently incomplete below, a rounded denticle near base of postorbital spine.

Frontal region of moderate breadth, grooved medially between two longitudinal ridges bearing several tubercles. Protogastric regions with three prominent tubercles adjacent to inner margin. Hepatic regions inflated and with a single prominent lateral spine. Narrow anterior portion of mesogastric region with a line of three median spinules; posterior part of region with two median spines and a pair of conspicuous tubercles on lateral aspect. A pit in grooves lateral to posterior part of mesogastric region; posterior gastric pits distinct. Metagastric region bi-lobed with two prominent tubercles positioned submedially; a deep pit adjacent to anterolateral corner of region. Urogastric region greatly constricted, with a single conical median tubercle; lateral urogastric grooves crenulate. Cardiac region subhexagonal, markedly expanded, with a pair of spines positioned submedially. A double tubercle before and a spine at centre of intestinal region. A crescentic row of four prominent spines on lateral aspect of mesobranchial regions, last spine in series largest, subdorsal, level with spines on cardiac region; a small spine positioned dorsally. Two small inner-branchial lobes each with a prominent conical tubercle. Metabranchial regions slightly depressed with two or three conspicuous tubercles on anterior portion and several more on postero-lateral aspect. Sub-branchial margins with a distinct border. Posterior margin of carapace short and with a stout conical spine on each end.

Measurements

The carapace of the holotype S.A.M. P15650 is 21 mm long (incomplete).

Remarks

Leptomithrax martensis closely resembles and is possibly the ancestor of the extant New Zealand species *Leptomithrax longimanus* Miers, 1876. It differs from *L. longimanus* as follows:

(a) The postorbital spine is only weakly flattened anteriorly, not moderately excavated.

(b) The mesogastric region of *L. martensis* has two conspicuous tubercles on either side. Analogous tubercles present in *L. longimanus* are much smaller.

(c) In the fossil species a prominent conical tubercle is present on both of the inner-branchial lobes. No large tubercles are present on these lobes in *L. longimanus*.

Leptomithrax elegans sp. nov.

Plate 13 figures 5a-d & 6

Name

From the Latin *elegans*, meaning elegant; in reference to the form of the carapace.

Material

Four specimens; holotype S.A.M. P15553, an almost complete carapace; two specimens showing lateral portion of carapace, paratypes S.A.M. P15554-45;

part of the anterior half of a carapace, paratype S.A.M. P15556. Specimens preserved as the original shell material and coll. R.J.F.J., 1967-1970.

Occurrence

Between 8 m (P15554) and 14 m (P15555) above N.R.L., Nildottie loc. 3.

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Carapace pyriform, 1.3 times as long as wide, (excluding rostral spines), constricted behind hepatic regions, moderately convex above; regions distinct, mostly delimited by shallow grooves, the lateral margins of cardiac and intestinal regions marked by deep grooves; protogastric regions obscurely tuberculate and sparsely pitted; remainder of carapace closely and coarsely pitted, with a few tubercles on dorsal surface and short, acute spines on marginal aspects.

Rostral spines large, projected forward, 1/4 length of carapace, tapered, flattened dorsoventrally, subtriangular in section; inner margins divergent, outer margins subparallel, the tips slightly more divergent; upper surface smooth, with margins finely pitted, flat lower surface closely and coarsely pitted.

Orbits consisting above of a supraorbital eave, an intercalated spine, and a postorbital spine, the three separated by narrow fissures; supraorbital eave of moderate width, lamellate, obtuse-angled before, arched above, bearing a short laterally directed antorbital spine; intercalated spine minute, compressed dorsoventrally; postorbital spine acute, triangular in section, flattened before and limiting rear of orbit, with a minute angulation on basal part of upper anterior margin. Infraorbital margins moderately complete, formed by basal antennal article; suborbital prominence minute, positioned below postorbital spine and remote from orbit. Orbital foramen oval, depressed behind so that eyestalks could probably fold rearwards in life.

Frontal region of carapace moderately narrow, slightly depressed medially between two weak longitudinal ridges which each bear two small tubercles. Another two small tubercles positioned near upper margin of each protogastric region. On mid-line of mesogastric region two elongate tubercles, the second more prominent; posterior gastric pits distinct. Hepatic regions with a pitted depression at inner corner and a single marginal spine. Crescentic metagastric region with two weak tubercles positioned submedially and a pit at either lateral extremity. Urogastric region with a small, median tubercle and a crescentic row of deep pits on either side. Cardiac region subhexagonal, inflated, with a high median prominence bearing two tubercles side by side. Intestinal region narrow, with a spine on posterior portion. Epibranchial regions not well marked. Adjacent to urogastric region a small inner-branchial lobe bearing a conspicuous tubercle. Mesobranchial regions strongly inflated, bearing a few small tubercles above and four spines on lateral aspect, the fourth spine subdorsal and often reduced. Metabranchial region with its posterior portion forming a low transverse lobe. Sub-branchial margins slightly arched above bases of pereiopods and without a border. Posterior margin of carapace short, arched rearwards, unarmed.

Basal antennal articles of moderate width, subrectangular, slightly concave on either side, pitted below, fused to frontoorbital region along an incised suture; anterior angles dentate, small anteromedial denticle projected forward and downward, slightly larger anterolateral denticle forwardly and outwardly directed; foramen for flagellum excluded from orbit and facing forward. Openings of antennal glands subtriangular.

Antennular fossae of moderate width, a narrow inverted V-shape before, and with a slightly oblique margin behind; interantennular spine well developed, triangular, directed rearward and downward, blunt tipped, weakly hollowed and coarsely pitted anteriorly; anterior process of epistome narrow, medially grooved. Epistome (excluding anterior process) twice as wide as long, smooth medially.

Pterygostomial regions subtriangular, flattened, separated from hepatic regions by a deep groove; surface pitted, a small spinule on lateral margin.

Buccal frame widened anteriorly; anterior margin almost transverse, gently arched rearwards, kinked laterally, sutured medially and at about 1/4 width from either end; lateral margins with a narrow border. Endostome grooved laterally and with pointed tips of posterior processes directed slightly outward; median embayment a widening inverted U-shape and with a narrow border bearing two small prominences before.

Measurements

The carapace of the holotype is 22 mm long (excluding rostral spines) and 17 mm wide. The rostral spines are 5.1 mm long.

Remarks

Leptomithrax elegans resembles juveniles of the modern *L. longipes* which is known from Macquarie Island, the South Island of New Zealand north to Cook Strait, and the Chatham Islands. It differs in the following particulars:

(a) The anterior half of the carapace is relatively narrower.

(b) The spines on the branchial margins are much shorter.

(c) The supraorbital spines are smaller.

(d) A double cardiac prominence is present in the fossil species. This prominence is single in *L. longipes*.

(e) The antennular foramina are more narrowly V-shaped before.

(f) In the fossil species the carapace is coarsely pitted and bears only a few low tubercles. The carapace of juveniles of *L. longipes* bears groups of well marked tubercles and is apparently smooth between.

L. elegans differs from mature individuals of *L. longipes* in features (d), (e) and (f) above and in the more narrowly pyriform outline of the carapace and the elongate form of the rostral spines.

Evolution of *Leptomithrax*

Inferred evolutionary lineages within *Leptomithrax* are shown in Figure 43. *L. longimanus*, *L. australis* and *L. garricki*, the known extant species belonging to the *L. longimanus* group, are confined to the New Zealand region and nearby islands. The author's new species *L. martensis* is a fossil representative of this group. The other fossil described here, *L. elegans*, is near the ancestor of *L. longipes*, the one known modern species belonging to the *L. longipes* group. *L. longipes* is recorded from Macquarie Island and again the New Zealand region. It seems likely that the *L. longimanus* and *L. longipes* groups reached New Zealand from Australia where they are now extinct. Dispersal from Australia to New Zealand probably resulted from current transportation and chance landfall of pelagic larvae or rafting of juveniles on floating masses of seaweed. The prevailing West Wind Drift of the southern oceans at the present time is favourable to such a pattern of dispersal and has probably existed for most of the Tertiary period. Large seaweed rafts are characteristic of the southern latitudes today (George, 1969).

The six modern species known from the Australian region, *L. tuberculatus*, *L. sternocostulatus*, *L. parvispinosus*, *L. gaimardii*, *L. waitei* and

L. globifer, all belong to the *L. tuberculatus* group (except possibly *L. parvispinosus*). A subspecies of *L. tuberculatus*, *L. t. mortenseni*, occurs in the New Zealand region and the Kermadec Islands. *L. uruti*, *L. atavus* and *L. irirangi* document the Upper Miocene and Pliocene occurrence of this group in New Zealand. These fossils probably evolved from the stocks which gave rise to *L. gaimardii* and *L. waitei*. In turn *L. uruti* is near the ancestor of the New Zealand *L. richardsoni*, the one modern representative of the *L. richardsoni* group. It is curious that no fossil representatives of the *L. tuberculatus* group have been found in Australia. As many of the better known marine Tertiary exposures in Australia predate the Upper Miocene it is tempting to suppose that the *L. tuberculatus* group reached this region at some later time. At present the *L. tuberculatus* group seems to range north of Australia to the Philippines and Japan. The place and time of origin of the group is unknown.

Genus *Schizophroida* Sakai, 1933

Type species: Here designated *Schizophroida simodaensis* Sakai, 1933.

Schizophroida Sakai, 1933: 137 (generic description, key to species); 1938: 304; 1965; 89.

Carapace elongate pyriform, smooth and nongranulate or mostly smooth with some areas weakly granulate, finely pitted (hirsute in extant species), a few small spines present. Rostral (pseudorostral) spines elongate, slender, slightly divergent. Elongate supraorbital eave ending in a spine at posterior corner; slender postorbital spine concave before, an intercalated spine between the two. Lateral aspects with five to seven short spines or spinules behind postorbital spines; another two short spines on posterior margin. Basal antennal article stout, armed with two acute terminal spines.

(Modified after Sakai (1933))

Three extant forms belong to this genus:

Schizophroida hilensis (Rathbun, 1906)

Hawaiian Is.

Schizophroida simodaensis Sakai, 1933

Japan: Kii Peninsula, Nagashima, Izu Peninsula, Sagami Bay; 10-50 m. The species inhabits a rocky weedy bottom (Sakai, 1938).

Schizophroida manazuruana Sakai, 1933

(Possibly = Schizophroida hilensis Chilton, 1911, non Rathbun, 1906, according to Buitendijk (1939:p.251)).

Kermadec Is. Near the Sulu Is., 70-80 m. Japan: Kii Peninsula, Izu Peninsula, Sagami Bay; 50-100 m. From rocky or sandy-mud bottoms (Sakai, 1938).

Schizophroida tertiaria sp. nov.

Text-figure 44a-d; plate 14 figures 1a,b - 3

Name

In reference to its Tertiary age.

Material

Four specimens; holotype S.A.M. P15583, carapace of a small individual, the rostral spines missing; two remains of broken anterior portion of carapace, paratypes S.A.M. P15585-86; fragment broken from region of orbit, paratype S.A.M. P15584. All specimens preserved as the original shell material and coll. R.J.F.J., 1968-1969.

Occurrence

From 12-13 m (P15584-85) to 14 m (P15583) above N.R.L., Nildottie loc. 3. Between 12 and 15 m above N.R.L., Nildottie loc. 4 (P15586).

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Carapace narrowly pyriform, about 1.5 times as long as wide, slightly constricted behind hepatic regions, gently convex in longitudinal profile, strongly convex transversely; regions distinct, delimited by shallow grooves; surface bearing a few small spines and occasional tubercles, mostly smooth between, rear part of carapace sparsely granulate; surface of hepatic regions and posterior half of carapace closely and finely pitted.

Rostral spines projected forwards and slightly upwards, tapered distally, about 1/5 length of carapace, a little divergent, compressed dorsoventrally.

Orbits consisting above of a supraorbital eave, an intercalated spine and a postorbital spine, the three separated by deep fissures; supraorbital eave lamellate, rounded before, strongly arched, obscurely granulate above, bearing a short to moderate sized antorbital spine directed outwards and slightly rearwards; intercalated spine widely separated from eave, compressed dorsoventrally, blunt tipped, reaching slightly beyond base of antorbital spine; postorbital spine close to intercalated spine and about twice size of latter, slender, pointed, partially limiting rear of orbit, with upper anterior margin crested for outer 3/4 of length and anterior face shallowly hollowed. Infraorbital margin incomplete, formed by basal antennal article and a small rounded tubercle behind. Orbital foramen round with posterior lip slightly depressed.

Frontal region of carapace narrow, grooved medially between two longitudinal ridges bearing a conspicuous tubercle behind. A transverse row of four tubercles across anterior 1/3 of protogastric regions. Mesogastric region with two small, broadly conical spines in mid-line; posterior gastric pits distinct. Hepatic regions inflated, obscurely tuberculate above, with one short, blunt, dorsoventrally compressed marginal spine followed by a minute spinule. Metagastric region obscurely granulate. Urogastric region depressed, with an impressed crescentic groove on either side. Cardiac region subhexagonal, broadly conical, with a single small median spine; grooves marking posterolateral margins of region weakly crenulate. Intestinal region small, raised, with several small tubercles. Epibranchial regions distinct, bearing three or four obscure tubercles. A small inflated branchial lobe on either side of urogastric region. Mesobranchial regions expanded with a row of five small spines on lateral aspect, last spine in series subdorsal, slightly behind level of spine on cardiac region; marginal part of mesobranchial regions sparsely granulate. Metabranchial regions divided into two parts by a transverse depression, anterior part obscurely granulate, posterior part bearing several small tubercles. Sub-branchial margins with a distinct narrow border. Posterior margin of carapace very short with a small spine on either side.

Basal antennal articles of moderate width, elongate, tapered towards anterior end; inner margin weakly concave, outer margin moderately concave; anterior angles produced to elongate, slender spiniform teeth of about equal size, anteromedial tooth directed forwards, downwards and slightly outwards, anterolateral tooth outwardly directed; foramen for flagellum excluded from orbit, facing forwards. Openings of antennal glands subtriangular.

Antennular fossae of moderate breadth, a rounded, inverted V-shape before, with a slightly oblique margin behind; interantennular spine well developed, directed rearwards and downwards, curved, its anterior face weakly excavated; anterior process of epistome strong, grooved medially. Epistome (excluding anterior process) about 2½ times as wide as long.

Anterior margin of buccal frame transverse, gently sinuous, sutured at about 1/5 length from either end. Endostome with tips of posterior processes directed slightly outwards; median embayment a broad inverted U-shape and with a low border.

Measurements

The carapace of the holotype S.A.M. P15583 is 13 mm long (excluding rostral spines) and 8.7 mm in width. The carapace of the species apparently reaches a length of about 30 mm.

Remarks

Schizophroida tertiaria seems nearest to *S. hilensis* (Rathbun). The two differ as follows:

(a) *S. tertiaria* has several additional tubercles on the anterior portion of the carapace, two on the frontal region and one at the centre of each protogastric region. The fossil species also has an extra spinule on the mid-line of the mesogastric region.

(b) In *S. tertiaria* the cardiac region bears one tubercle, not two.

(c) The carapace of *S. tertiaria* has one or several extra spinules on the lateral aspects.

Subfamily Inachinae Macleay, 1838

Genus Naxia Latreille, 1825

Type species: Pisa aurita Latreille, 1825, by monotypy.

Naxia Latreille, 1825. Griffin, 1966a: 29 (generic synonymy, generic description, discussion, key to species).

Griffin (1966a) included five extant species in this genus. It is presently known from southwestern, southern and southeastern Australia (including Tasmania), the Kermadec Islands, and New Zealand.

Naxia sp.

Plate 14 figures 4 - 6

Material

Three specimens; broken posterior portion of carapace, S.A.M. P15557, two fragments broken from the median part of the carapace, S.A.M. P15558-59. Remains coll. Miss P. E. Lim, 1970 and R.J.F.J., 1969.

Occurrence

Between 8 m (P15558) and 14 m (P15559) above N.R.L., Nildottie loc. 3.

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Carapace with posterior part rounded in outline and convex above;

regions apparently distinct, delimited by shallow grooves; surface bearing a number of rather slender spines and a few granules and tubercles, smooth between, smooth areas and surfaces of tubercles and spines all minutely pitted.

A small median spine on posterior part of mesogastric region; posterior gastric pits distinct. A low tubercle on lateral portions of rather flat metagastric region. Urogastric region not clearly marked, but limited laterally by several deep pits. Cardiac region strongly inflated, conical, and bearing a prominent central spine. Intestinal region narrow, raised, bearing two acute spines on mid-line, the second spine broad based and projecting rearwards above posterior margin of carapace. A conspicuous rounded tubercle on small inner-branchial lobe lateral to urogastric region. Mesobranchial regions swollen and bearing a few scattered small tubercles and granules above and three slender spines on lateral aspect, the spines increasing in size posteriorly, the last spine in series sub-dorsal. A small obscurely granulate swelling on posterior parts of meta-branchial regions. Sub-branchial margins with a narrow border.

Measurements

Specimen S.A.M. P15557 represents a carapace which was originally 13 mm wide.

Remarks

This form resembles the extant <u>Naxia aries</u> (Guerin, 1825), a littoral species from southern and southeastern Australia. It is distinguished from *N. aries* by the following differences:

(a) The posterior part of the carapace appears to have been more strongly convex.

(b) A more prominent spine is situated on the cardiac region.

(c) The two intestinal spines are more widely separated. The first of these spines is more slender than its counterpart in *N. aries*.

(d) The three mesobranchial spines increase in size rearwards, not the reverse.

Family Parthenopidae Macleay, 1838
Subfamily Parthenopinae Macleay, 1838
Genus *Tutankhamen* Rathbun, 1925

Type species: *Mesorhoea cristatipes* A. Milne-Edwards, 1880, designated by Rathbun, 1925.

Tutankhamen Rathbun, 1925: 511, 530. Sakai, 1938: 339; 1965: 89.

Carapace broadly triangular; rostrum large, three-lobed, produced medially; gastric and cardiac regions strongly elevated to form a prominent median crest; three tubercles on gastric regions, two side by side before and one behind; two or three tubercles on mid-line of cardiac region; surface smooth, pitted or granulate. Extant species with short deep afferent channels. Chelipeds long and strong.

Two previously described species, both extant, belong to this genus:

Tutankhamen cristatipes (A. Milne-Edwards, 1880)

St. Vincent, Windward Islands; Pourtales Plateau, Florida Straits; 226-366 m.

Tutankhamen pteromerus (Ortmann, 1893)

Japan; 85-296 m; Hawaii; 95-570 m.

Tutankhamen hieracodes sp. nov.

Text-figure 45; plate 14 figures 7 & 8

Name

From the Greek *hieracodes*, meaning hawk-like; with reference to the outline of the carapace which is reminiscent of a diving hawk with the wings half closed.

Material

Twelve specimens of the carapace, all to varying degrees incomplete. The holotype S.A.M. P15660, a carapace with the front damaged. Two isolated fragmentary remains which appear to represent the palm of parthenopid like chelipeds are also attributed to this species, paratypes S.A.M. P15663-64. All materials preserved as the original shell material (or as moulds where this has exfoliated) and coll. R.J.F.J., 1967-1969.

Occurrence

Quarry near middle of section 28, Hundred of Blanche, Mount Gambier loc. 1 (holotype and P15663-64). Quarry on northeastern part of section 26, Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Carapace broadly triangular, 1.3 times as wide as long (including median lobe of front); gastric and cardiac regions strongly elevated and coarsely pitted, other regions moderately well marked and with surface pitted or nearly smooth, a few tubercles and spinules present.

Front large, forwardly projected, three-lobed; median lobe depressed, produced forwards; lateral lobes arched above deep, divergent, subfrontal-antennular grooves.

Orbits small, rounded; supraorbital margins raised, deeply concave, singly fissured; suborbital margins projected forwards slightly to form a right-angular tooth adjacent to antennal hiatus.

Hepatic margins divergent rearwards and with a median spinule. A distinct inflexion in outline of carapace behind hepatic regions. Anterolateral branchial margins moderately convex, sharply angulate, and with a line of denticles; every second denticle enlarged. Branchial expansions terminated laterally in a broad spine. Posterolateral margins moderately concave, with a prominent spinule at about 2/3 of their length. Posterior margin narrow, gently convex, with a median spinule and one on either side.

Frontal region with two slightly divergent crests separated by a deep depression containing several minute granules and two pits at centre. A tubercle near upper margin of each protogastric region; a central tubercle on indistinctly defined mesogastric region; posterior gastric pits distinct. Urogastric region saddle-shaped and with a deep pit at either lateral margin. Cardiac region with two rounded tubercles in mid-line above, and one behind; several deep pits positioned on either side of region. Intestinal region strongly depressed. Mesobranchial regions inflated above, with two indistinct ridges extending from near margin of hepatic region obliquely outwards towards posterolateral extremity of carapace; each ridge with a central tubercle, that on the hinder ridge sometimes spiniform. Metabranchial regions with a tubercle or spinule near prominent spinule on posterolateral margin. Posterolateral regions down-curved, vertical.

Palm of cheliped apparently angulate in section with upper face gently convex and pitted and upper margins bearing tubercles and blunt spinules; a large, blunt projection towards distal end of upper-inner margin.

Measurements

The carapace of the holotype S.A.M. P15660 is 15 mm long (incomplete) and 19 mm wide (incomplete). The carapace of paratype S.A.M. P15662 (Plate 14, Figure 8) is 14 mm long and 18 mm wide. The carapace reaches a width of more than 24 mm. The fragmentary remains of a cheliped palm, paratype S.A.M. P15663, is 14 mm long (incomplete).

Remarks

The tubercles on the dorsal surface of the carapace are rather variable in expression. In the holotype the submedian tubercles above the protogastric regions are nearly obsolescent. In paratype S.A.M. P15661, an internal mould, these same tubercles were apparently quite prominent.

Tutankhamen hieracodes is very similar to the modern _T. pteromerus_ Ortmann, but differs from it in the following particulars:

(a) The central portion of the hind margin of the carapace projects more rearwards relative to the large lateral angulations.

(b) The large lateral angulations do not have a small subsidiary spine behind as in _T. pteromerus_.

(c) The mesobranchial regions seem much less distinctly ridged.

(d) The tubercle on the hinder mesobranchial ridge is positioned further forwards and inwards than in _T. pteromerus_.

Section BRACHYRHYNCHA

Superfamily Portunoidea

Family Portunidae Rafinesque, 1815

Subfamily Macropipinae Stephenson and Campbell, 1960

Genus Ovalipes Rathbun, 1898

Type species: Cancer ocellatus Herbst, 1799, by original designation.

Ovalipes Rathbun, 1898. Stephenson and Rees, 1968: 215 (generic synonymy, generic description, revision). Stephenson, 1969: 43-69 (stridulating structures in genus).

Carapace a little broader than long; front not prominent, rather narrow, cut into three or four teeth; anterolateral margins each with five forwardly directed teeth (including extraorbital angle); surface granulate without transverse ridges. Palms of chelae carinate, often with conspicuous striae below; fingers also ribbed or carinate, dactylus with upper, inner carina usually bearing a line of conspicuous spinules or several prominent spines.

A detailed revision of Ovalipes by Stephenson and Rees (1968) describes ten extant species and indicates the possible occurrence of an eleventh form. Two species have previously been recorded as fossils, both from fingers of chelae:

Ovalipes catharus (White, 1843)

Ovalipes cf. punctatus (de Haan), Glaessner, 1960: 22, pl.3, fig.8. Castlecliffian, Pleistocene; subfossil. North Island of New Zealand.

Stephenson and Rees (1968: p.227) suggest that the finger illustrated in pl.3, fig.8 of Glaessner (1960) belongs to O. catharus. Records of this species in present seas are from the south coast of southeastern Australia, New Zealand, and the Chatham Islands.

Ovalipes sp. a Glaessner, 1960

Ovalipes sp.a Glaessner, 1960: 23, pl.3, fig.9.

Waitotarian, Upper Pliocene. South Island of New Zealand.

According to Stephenson and Rees (1968) this fossil does not appear to belong to any present-day species, but resembles the corresponding element in the living forms O. punctatus (de Haan, 1833), from Japan and China, and O. australiensis Stephenson and Rees, 1968, from the southern half of Australia and Lord Howe Island.

Ovalipes primitivus sp. nov.

Text-figure 46; plate 15 figures 1 - 4

Name

From the Latin primitivus, primitive.

Material

Holotype S.A.M. P15719, the greater part of a carapace showing the dorsal aspect. Seven other specimens of the carapace, all more or less incomplete; paratypes S.A.M. P15720, P15723, P15725 and P15727 show the dorsal aspect and paratypes S.A.M. P15722, P15724 and P15726 the interior surface only. Two isolated fragmentary remains of the fixed finger of chela, paratypes S.A.M. P15721 and P15727; these resemble the fingers of other species of Ovalipes and are assumed to belong to the present form because they occur at the same stratigraphic level. All materials preserved as original skeletal material and coll. R.J.F.J., 1967-1969.

Occurrence

Quarry near middle of section 28, Hundred of Blanche, Mount Gambier loc. 1 (P15719-20, P15725-27). Quarry on southwestern part of section 30, Hundred of Blanche, Mount Gambier loc. 1 (P15721). Quarry on northeastern part of section 26, Hundred of Blanche, Mount Gambier loc. 1 (P15722-24, P15727).

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Carapace subhexagonal, about 1.1 times as wide as long, gently convex above; regions distinct, bounded by moderately deep to shallow grooves; surface finely granulate with several small spinules and tubercles.

Front projected forwards, approximately .3 width of carapace, its median portion evidently more forwardly produced than its lateral part which is marked by a small raised tooth.

Orbits forwardly directed and relatively large; supraorbital margins slightly raised, mainly concave, doubly fissured with a short tooth between fissures; outer-orbital extremity apparently angulate. Fronto-orbital margin approximately .7 width of carapace.

Anterolateral margins long, gently curved, moderately convergent anteriorly, bearing five teeth (including angulate extraorbital tooth); second to fifth teeth broad based, compressed, directed forwards, their lateral margins crested and smooth, the second to fourth progressively increasing in size rearwards and convex laterally, the fifth smaller, slightly concave behind tip. Posterolateral margins gently recurved and moderately convergent rearwards, sharply ridged for anterior 1/3 of their length. Rear margin of carapace wide, recessed to accommodate bases of fifth pereiopods, and with a narrow border.

Epibranchial regions small, raised. A tubercle or spinule just behind centre of each protogastric region and another smaller tubercle between on narrow anterior extension of mesogastric region; a central spinule on posterior part of mesogastric region; posterior gastric pits indistinct. Hepatic regions slightly elevated behind. Cervical groove well marked to margin of carapace, its lateral portions directed outwards and slightly forwards. Urogastric region depressed, a well marked curved groove on either side. Cardiac region weakly subdivided into three lobes, axial lobe raised with a forwardly directed, spiniform median tubercle on anterior portion. Epi-, meso- and metabranchial regions separated by slight depressions; two small inner-branchial lobes adjacent to urogastric region and mesogastric region respectively, anterior lobe with an obscure median tubercle.

Muscle attachments on interior surface of carapace generally indistinct; those recognizable are represented by shallow grooves or depressions.

Outer-distal portion of palm of cheliped sparsely and finely granulate. Fixed finger tapered with two prominent, rounded ribs on outer face and a less distinct rib below; ribs obscurely granulate proximally, smooth distally; grooves on either side of ribs each with a line of pores; teeth on prehensile margin compressed laterally and arranged in groups of three to five with one tooth in each group enlarged.

Measurements

The carapace of the holotype S.A.M. P15719 is 14 mm long (incomplete) and prior to breakage measured 16 mm in width (excluding lateral teeth). The carapace may reach a length of approximately 20 mm. The fixed finger of the left (? smaller) claw, paratype S.A.M. P15721, is 12 mm long (incomplete).

Remarks

The holotype specimen, on which the description and figure are largely based, is not full-sized and may show some juvenile features.

Ovalipes primitivus somewhat resembles two modern species, *Ovalipes* elongatus Stephenson and Rees, 1968, from Lord Howe Island and the Kermadec Islands, and Ovalipes georgei Stephenson and Rees, 1968, from off Rottnest Island, Western Australia. It particularly resembles O. elongatus in the general outline of the carapace and in the broad-based form of the anterolateral teeth. The two also have the fixed finger of the chela quite similar. O. primitivus differs from O. elongatus in the following features:

(a) The carapace regions are much more clearly marked.

(b) Spinules or tubercles present on the gastric regions, inner branchial lobes and cardiac region of O. primitivus are apparently absent in the modern crab.

(c) The carapace of O. primitivus is more coarsely granulate.

O. primitivus and O. georgei also have the outline of the carapace similar. Both have the carapace regions well marked and the surface of the carapace conspicuously granulate. Each has prominences on the gastric regions. Notable differences between the two are:

(a) The anterolateral teeth of the carapace of O. primitivus are more widely based.

(b) The outer part of the cervical groove is directed outwards and slightly forwards in O. primitivus, but outwards and markedly rearwards in O. georgei.

(c) While the cardiac region of the carapace of O. primitivus is weakly divided into three lobes, that of O. georgei is conspicuously three-lobed.

(d) In the fossil species the branchial regions lack the granulated stridulating ridge present in O. georgei.

(e) The fixed finger of the chelae of the two differs in the form of the ribbing and the extent and coarseness of the granulation.

Ovalipes denticulatus sp. nov.

Text-figure 47; plate 15 figures 5 & 6

Name

From the Latin denticulatus, small-spined; in reference to the small anterolateral spines of the carapace.

Material

Two specimens of the carapace; one almost complete but with the outermost layer of shell material exfoliated, holotype S.A.M. P15568; the other incomplete, paratype S.A.M. P15569. Specimens coll. R.J.F.J., 1968-1970.

Occurrence

Holotype from a fallen block which possibly came from 12-15 m above N.R.L., Nildottie loc. 4. Paratype from 8 m below ground surface in quarry on section 601, Hundred of Blanche, Mount Gambier loc. 2.

Stratigraphic Position and Age

Holotype: Mannum Formation. Middle to late Lower Miocene.
Paratype: Gambier Limestone. Middle Lower Miocene.

Description

Carapace subhexagonal, 1.1 times as wide as long, gently convex above; regions well marked, delimited by moderately deep grooves; surface covered by rather even sized granules, several tubercles on gastric regions.

Front projected forwards, obtusely triangular, notched medially and furrowed in mid-line above, bearing four small denticles, .24 width of carapace; submedian denticles very close together and well in advance of laterals; median notch minute; lateral denticles without subsidiary lobes below.

Orbits transversely ovate; supraorbital margins concave, minutely granulate, doubly fissured, terminated laterally in a short extraorbital tooth; infraorbital margins forming a large right-angular tooth which projects well in advance of supraorbital margins. Frontoorbital margin .6 width of carapace.

Anterolateral margins long, curved, moderately convergent anteriorly, bearing five teeth (including extraorbitals); base of extraorbitals triangular, tips broken away; following teeth small, narrow based, aculminate, directed more or less forwards except for the fifth which projects outwards. Posterolateral margins slightly concave, moderately convergent rearwards, sharp crested for a short distance behind last anterolateral tooth. Rear margin of carapace apparently recessed to accommodate bases of fifth pereiopods.

Epigastric regions small, indistinct. A small tubercle just behind centre of each protogastric region and another between on narrow anterior extension of mesogastric region; a central tubercle on posterior part of mesogastric region; posterior gastric pits indistinct. Hepatic regions slightly elevated. Cervical groove well marked to margin of carapace, its lateral portions directed outwards and slightly forwards. Metagastric region short, wide, constricted medially. Urogastric region depressed, a crescentic groove on either side. Cardiac region forming three distinct lobes, axial lobe with an obscure median prominence on anterior portion. Epibranchial regions slightly swollen, divided into an inner and outer lobe by a shallow groove. Two small branchial lobes lateral to urogastric region and metagastric-mesogastric regions respectively, anterior lobe considerably larger. Mesobranchial and metabranchial regions separated by a slight depression.

Measurements

The carapace of the holotype S.A.M. P15568 is 15 mm long and 16 mm wide excluding the lateral spines. The carapace of paratype S.A.M. P15569 is 13 mm long (incomplete).

Remarks

The specimen from the Mount Gambier area does not differ significantly from the holotype. Both these specimens may be young individuals. The front is very similar to that of juveniles of the extant crab *Ovalipes australiensis* Stephenson and Rees, 1968. Juveniles of this modern species also have the anterolateral teeth narrow-based; these teeth become much broader-based as the crab increases in size.

Ovalipes denticulatus resembles *O. primitivus* and the living *O. georgei*. It is distinguished from *O. primitivus* by the narrow-based form of the anterolateral teeth, the much more conspicuously trilobate cardiac region, and the more prominently granulate surface of the carapace.

The main differences between *O. denticulatus* and *O. georgei* are:

(a) The branchial regions of the fossil species lack the granular stridulating ridge present in *O. georgei*.

(b) The outer part of the cervical groove is directed outwards and slightly forwards in *O. denticulatus*, but outwards and markedly rearwards in *O. georgei*.

(c) The mesogastric, metagastric, urogastric and cardiac regions of the carapace of the fossil species are appreciably wider than in the extant species.

Ovalipes costatus sp. nov.

Plate 16 figures 1a,b - 5a,b

Name

From the Latin *costatus*, ribbed; in reference to the ornamentation of the fingers of the chelae.

Material

Numerous specimens of separated or disarticulated fingers of claws. The holotype S.A.M. P15602, coll. R.J.F.J., 1968, is a fixed finger of a left (smaller) claw. Other isolated fixed or movable fingers of either claw showing similar ornamental features to the holotype and from the same, an equivalent, or an adjacent stratigraphic level are assumed to belong to this species.

Occurrence

Between 7 and 12 m above N.R.L., Nildottie loc. 3 (includes holotype). Between 7 and 14 m above N.R.L., Nildottie loc. 4. Lower 4 m of cliff on east side of River Murray at Swan Reach.

Stratigraphic Position and Age

Middle part of Mannum Formation. Middle Lower Miocene.

Description

Fingers of the chelae elongate, tapered, and ribbed. Fixed finger straight, laterally compressed, ornamented by five broad, low, rounded ribs, three on inner face and two on outer face, lower margin of finger sharply carinate; ribs and marginal carina granulate proximally and smooth distally, separated by shallow grooves which each contain a line of distinct pits. Movable finger curved and subtriangular in section; a rounded, granulate rib on outer face, two weak, minutely granulate or smooth ribs on lower part of inner face, and two granulate, angular carinae marginal to upper surface; inner upper carina bearing a line of six prominent spines, surface between upper carinae smooth, grooves on either side of ribs on inner and outer faces each containing a row of distinct pits. Teeth on prehensile margins of both fingers more or less widely spaced and arranged in groups of three with middle tooth in each group much more prominent; fingers of one claw, usually the left, with sharp edged teeth; fingers of other claw with distal teeth sharp edged and basal teeth rounded.

Measurements

The holotype S.A.M. P15602, a fixed finger from a left (smaller) chela is 19 mm long. The fixed finger of the same (equivalent) claw represented by paratype S.A.M. P15603, is 23 mm long. Paratype S.A.M. P15607, a dactylus of a left (smaller) claw is 23 mm long.

Remarks

The fingers of the claws of O. costatus seem most closely similar to those of the extant species Ovalipes iridescens (Miers, 1886), from the waters of South Africa, Indonesia, Japan and southeastern Australia. The following differences between the two may be noted:

(a) The inner upper carina on the movable finger of the claws of the fossil species bears a series of six spines, rather than four or five.

(b) The movable finger of *O. costatus* is more curved in shape and the granulation on the lower, proximal part of the outer surface is apparently coarser.

(c) Whereas Stephenson and Rees (1968) describe one pitted groove on the outer face of the fixed finger of the claws of *O. iridescens*, three such grooves are present in *O. costatus*; the granulation on the ribs on the outer face of this finger may be coarser in the fossil species.

(d) The teeth on the prehehsile margins of both of the fingers of either claw of *O. costatus* are two or three fewer in number than in the modern crab.

Ovalipes eamesi sp. nov.

Plate 15 figures 7a-c; Plate 16 figures 6a,b - 8

Name

Named after Mr. H. Eames who in conjunction with Mr. Bret Robinson, discovered the first specimen.

Material

A propodus of the right (larger) chela, holotype S.A.M. P15597, coll. H. Eames, 1967, and various separated or disarticulated fingers of chela, coll. R.J.F.J., 1967-1969. Isolated fingers or movable fingers of either claw showing similar ornamental features to the holotype and from the same, an equivalent, or an adjacent stratigraphic level are assumed to belong to the present form.

Occurrence

From 15-20 m above N.R.L., Nildottie loc. 1 (holotype). From 19-20 m above N.R.L., Nildottie loc. 2. From 15-16 m above N.R.L., Nildottie loc. 3.

Stratigraphic Position and Age

Upper middle part of Mannum Formation. Middle to late Lower Miocene. This species occurs at a higher stratigraphic level than O. costatus and it and the latter's stratigraphic ranges are mutually exclusive.

Description

Right palm about twice as long as high, gradually widening distally; inner face gently convex, lower margin rounded proximally, crested distally, outer face convex, angled in a line through point of articulation with movable finger, a weak, central longitudinal ridge on upper aspect of palm, inner upper margin forming a distinct crest which protrudes slightly over inner face; surfaces of palm covered by coarse spiniform granules, a row of seven to eight spinules along inner, upper crest and a few spinules nearby on dorsal aspect.

Fingers of both hands elongate, tapered, and ribbed. Fixed finger nearly straight, laterally compressed, ornamented by five distinct, narrow ribs, three on inner face and two on outer surface, lower margin of finger carinate, ribs and marginal carina granulate proximally and smooth distally; flutes between ribs smooth or with closely spaced fine pores. Movable finger curved and subtriangular in section; a distinct granulate rib on outer face, two conspicuously granulate ribs on inner face near prehensile margin, and two granulate, angular carinae marginal to upper surface, the inner upper carina bearing a line of six prominent, distally directed spines; surface between ribs and carinae smooth or with closely spaced fine pores. Teeth on prehensile margins of fingers arranged in groups of three or four with a central tooth in each group enlarged and prominent, minute teeth sometimes placed in intervals. Teeth on fingers of left chela sharp edged and slightly separated; fingers of right chela with rounded, closely spaced teeth.

Measurements

The holotype S.A.M. P15597, the remains of a right (larger) claw, has the propodus 37 mm long (incomplete), and the palm 21 mm long (incomplete) and 11 mm high. Paratype S.A.M. P15598, a dactylus of a right (larger) claw, is 23 mm long (incomplete).

Remarks

The fingers of the chelae of Ovalipes eamesi are very similar to those of O. costatus. The hand as a whole most resembles the chelae of O. iridescens. The fingers of O. eamesi differ from those of O. costatus in the following features:

(a) The ribs on the inner and outer surfaces of the fixed finger are narrower and stand in sharper relief.

(b) The ribs on the lower part of the inner face of the movable finger are stronger and more conspicuously granulate.

(c) In O. eamesi the ribs and carinae on both fingers are separated by flutes which are smooth or closely and finely pitted. In O. costatus the ribs are separated by shallow grooves which each contain a line of distinct pits.

(d) The teeth on the prehensile margins of the fingers are closer together in O. eamesi.

The principal differences between the chelae of O. eamesi and O. iridescens are:

(a) The central ridge on the upper aspect of the palm is less distinct in O. eamesi.

(b) Several very faint ribs are present on the inner and outer faces of the palm of O. eamesi. These ribs are apparently more distinct in O. iridescens.

(c) The inner upper crest on the palm of _O. eamesi_ bears seven or eight spinules rather than four as in the extant crab.

(d) The inner upper carina of the movable finger of the fossil species bears six spines, not four or five.

(e) The ribbing on the faces of both the fingers of the fossil species is apparently more distinct than in _O. iridescens_.

(f) Fluted intervals between the ribs on the fingers of _O. eamesi_ are smooth or closely and finely pitted, not with a line of distinct pits.

Ovalipes victoriensis sp. nov.

Text-figure 48; plate 15 figure 8

Name

For the place of occurrence, Victoria.

Material

An incomplete carapace with the front and most of the left lateral aspect preserved; holotype N.M.V. P25841.

Occurrence

At Beaumaris, near Melbourne, Victoria.

Stratigraphic Position and Age

Black Rock Sandstone. Late Upper Miocene.

Description

Carapace apparently subhexagonal, gently convex in longitudinal profile, almost flat transversely; regions distinct, delimited mostly by rather shallow grooves; surface coarsely granulate anteriorly, becoming more finely and closely granulate posteriorly, several tubercles and obscure prominences on gastric regions and branchial lobes.

Front flat, four toothed, .9 width of carapace; submedian teeth close together, short, pointed, broadly separated from and produced further forwards than laterals; median notch deep; lateral teeth also quite sharp, a blunt subsidiary lateral lobe on a lower plane and visible on inner side of lateral tooth; frontal indentations with a finely granulate, narrow marginal border.

Orbits somewhat elongate transversely; supraorbital margins broadly concave, granulate, doubly fissured, toothed between fissures, terminated laterally in a large extraorbital tooth; infraorbital margins each forming a large, elongate flattened tooth which projects forwards and slightly inwards far in advance of supraorbital margins. Frontoorbital margin about half width of carapace.

Anterolateral margins long, moderately convergent forwards, gently curved, each cut into five large, narrowly separated teeth (including extraorbital teeth); each tooth broad based and apparently directed forwards and acute, with its gently convex outer margin weakly crested and finely granulate; extraorbital tooth large, following two teeth slightly smaller, last tooth in series the smallest and directed more outwards and upwards. Posterolateral margins slightly recurved, moderately convergent rearwards, and with a thin, granulate marginal ridge.

Epigastric regions small, expanded. Protograstric regions each with an obscure central prominence. Mesogastric region with a small tubercle on narrow anterior portion and a broadly conical, bluntly pointed, forwardly directed median tubercle on posterior part of region; posterior gastric pits indistinct. Hepatic regions slightly swollen. Cervical groove moderately deeply impressed behind protogastric regions, deeply impressed lateral to mesogastric region. Metagastric region indistinct. Urogastric region slightly depressed; lateral urogastric grooves curved, deeply incised. Cardiac region slightly swollen, subhexagonal. Branchial regions mostly following general curvature of carapace, sloping downwards posterolaterally; two small branchial lobes lateral to urogastric region and metagastric-mesogastric regions respectively, the anterior lobe larger and with an obscure central prominence.

Measurements

The incomplete holotype specimen N.M.V. P25941, represents a carapace 41 mm wide, excluding lateral teeth.

Remarks

This species closely resembles and is possibly the ancestor of

Ovalipes elongatus. The two differ as follows:

(a) Tubercles or prominences present on the gastric regions and inner branchial lobes of *O. victoriensis* carapace are apparently absent in *O. elongatus*.

(b) The surface of carapace of the fossil species seems to be more coarsely granulate.

(c) The submedian teeth of the front are acuminate in *O. victoriensis*, but are somewhat blunted in *O. elongatus*.

Phylogeny of *Ovalipes*

Stephenson and Rees (1968) divided the extant species of *Ovalipes* into two groups (A and B) which were each further subdivided into two subgroups thus:

Group A

1. *O. punctatus* subgroup containing *O. punctatus* and *O. trimaculatus* (de Haan), *O. catharus*, *O. australiensis*, and *O. elongatus*.
2. The monospecific *O. georgei* subgroup.

Group B

1. *O. iridescens* subgroup containing *O. iridescens* and *O. molleri* (Ward).
2. *O. ocellatus* subgroup comprising *O. ocellatus* (Herbst) and two forms of *O. quadulpensis* (Saussure).

Three of the fossil species, *O. primitivus*, *O. denticulatus*, and *O. victoriensis*, belong to Group A. *O. primitivus* resembles *O. elongatus* in the shape of its carapace and broad based lateral carapace spines and *O. georgei* in its distinct granulation and presence of well marked tuberoles or spinules on the carapace. Possibly *O. primitivus* is near the ancestor of both the *O. punctatus* and *O. georgei* subgroups (Figure 49). *O. denticulatus* markedly resembles *O. georgei* and is probably the ancestor of the latter. Notably *O. denticulatus* lacks the distinctive branchial stridulating ridge present in *O. georgei*. Fragmentary and complete remains of a species of *O. georgei* occur as rare elements in the Pliocene Hallett Cove Sandstone at Port Willunga. *O. victoriensis* resembles *O. elongatus* and may be its progenitor.

O. costatus and *O. eamesi* belong to the *O. iridescens* subgroup of Group B. The fingers of the chelae of *O. costatus* resemble those of *O. iridescens* and it is probable that this fossil is near the ancestor of *O. iridescens*. While the fingers of *O. eamesi* are similar to those of *O. costatus*, they do not appear to closely resemble those of either *O. iridescens* or *O. molleri*. *O. eamesi* evidently represents an extinct lineage which evolved from the same stock as *O. costatus*.

Group A of *Ovalipes* appears to have evolved more rapidly than some of the other genera represented by fossils documented in the present work; this almost certainly reflects the adaptation of most of the species within it to relatively changeable nearshore environments and its very widespread distribution (circum-global excepting North America and the North Atlantic and Mediterranean).

Subfamily Carcininae Macleay, 1838

Genus *Nectocarcinus* A. Milne-Edwards, 1860

Type species: *Portunus integrifrons* Latreille, 1825, selection by Dell, Griffin and Yaldwyn (1970: 52).

Nectocarcinus A. Milne-Edwards, 1860. Stephenson and Campbell, 1960: 82 (generic synonymy, generic description). Bennett, 1964: 65. Dell, Griffin and Yaldwyn, 1970: 50 (review, description of new species).

Remarks

The six modern species recognized (Dell, Griffin and Yaldwyn, 1970) variously occur off southwestern, southern and southeastern Australia, New Zealand and nearby islands, and the Juan Fernandez Islands off Chile.

Nectocarcinus cafpercoensis sp. nov.

Text-figure 50; plate 16 figures 9 - 11

Name

For the area in which the quarries containing it occur, the Cafperco district, to the west of Mount Gambier, South Australia.

Material

Thirty specimens of the carapace of which 22 are more or less complete and the remainder fragmentary. Holotype S.A.M. P15728, coll. R.J.F.J., 1968. Paratypes S.A.M. P15733-34, coll. Glaessner, 1953. Remainder of material coll. R.J.F.J., 1967-1969. All specimens preserved as the original shell material.

Occurrence

Quarries on sections 26, 28 and 30, Hundred of Blanche, Mount Gambier loc. 1. Holotype from quarry near middle of section 28. P15733-34 from quarry on northeastern part of section 26.

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Carapace subhexagonal, slightly wider than long, gently convex above; regions lobate, inflated, very clearly marked; surface of different specimens smooth or finely granulate with coarser granulation at centres of inflated regions and at periphery of carapace.

Front projected well forwards, nearly flat, .3 width of carapace, notched medially, weakly furrowed in mid-line above, four weak denticles and a line of granules on anterior margin, a conspicuous antennal notch on either side.

Orbits large, transversely oval, supraorbital margins raised, slightly oblique, concave, doubly fissured, terminated laterally in a prominent extraorbital tooth; suborbital margins projecting beyond supraorbital margins in dorsal view, singly fissured just below extraorbital tooth, produced to form a prominent triangular denticle adjacent to antennal hiatus. Frontoorbital margin about .7 width of carapace.

Anterolateral margins long, gently curved, moderately convergent forwards, bearing four teeth (including extraorbital tooth), first three teeth in series directed forwards or forwards and outwards, the second tooth reduced, fourth tooth slightly smaller than third and pointed outwards and upwards. Posterolateral margins gently convex and moderately convergent rearwards for anterior 3/4 of their length, curved inwards and gently arched behind. Posterior margin .4 width of carapace, gently concave, with a narrow border extending over rear 1/4 of posterolateral margins and bearing a line of granules above, or smooth.

Epigastric regions small, raised, distinct. Protogastric regions subcircular in outline, elevated, conspicuous. Hepatic regions nearly flat, slightly depressed relative to adjacent regions. Mesogastric region tumid, a clearly marked narrow extension reaching forwards to epigastric regions; posterior gastric pits distinct. Urogastric region depressed and constricted; lateral urogastric grooves well marked, gently convex inwards. Cardiac region inflated, subpentagonal. Intestinal region flat, indistinct. Branchial regions lobate, subdivided by broad open grooves. Epibranchial regions transversely elongate, with a prominent transverse swell extending inwards from near rearmost anterolateral tooth. A small indistinct inner-branchial lobe adjacent to urogastric region. Mesobranchial regions with a conspicuous oblique swell extending rearwards and outwards. Metabranchial regions swollen.

Places of muscle attachment on interior surface of carapace marked by small pits and shallow depressions with a reticulate ornamentation (Plate 16 Figure 11);

Measurements

The carapace of the holotype S.A.M. P15728 is approximately 13 mm long (front and posterior margin incomplete) and is 14 mm wide (excluding lateral teeth). The carapace of paratype S.A.M. P15729 is 14 mm long and 14 mm wide. The largest specimen found has the carapace 19 mm wide.

Remarks

Nectocarcinus cafpercoensis is most closely similar to the extant species *Nectocarcinus spinifrons* Stephenson, 1961, which is known from off Shark Bay, Western Australia, and Greenly Island, South Australia. The fossil species differs from the modern crab in the following particulars:

(a) The third and fourth teeth on the anterolateral margins of the carapace are more widely separated in *N. cafpercoensis*. The fourth tooth tends to be directed outwards in *N. cafpercoensis* but more forwards in *N. spinifrons*.

(b) In *N. cafpercoensis* the antennal notch lateral to the front seems to be less pronounced.

(c) The protogastric regions of *N. cafpercoensis* are relatively larger and possibly less swollen, and their anterior margin is positioned further forwards.

(d) In *N. cafpercoensis* the groove behind the epibranchial lobe is directed laterally and slightly rearwards, not obliquely rearwards as in the photograph of *N. spinifrons* given by Dell, Griffin and Yaldwyn (1970: pl.3, fig.B).

Nectocarcinus granosus sp. nov.

Plate 16 figures 12 - 14; plate 17 figures 1a,b & 2a,b

Name

From the Latin *granosus*, granular; referring to the ornamentation.

Material

Several remains of the carpus, palm or propodus, and isolated fingers of chelipeds. Holotype S.A.M. P15896, coll. R.J.F.J., 1968, a palm of the right (larger) cheliped. Paratype S.A.M. P15897, coll. Bret Robinson, 1967, carpus and palm of right cheliped. Specimens all preserved as original shell material.

Occurrence

Between 7 and 14 m above N.R.L., Nildottie loc. 3 (holotype, 11-14 m above N.R.L.). From 19-20 m above N.R.L., Nildottie loc. 2. Between 7 and 20 m above N.R.L., Nildottie loc. 4. Cliff at Morgan loc. 1 (P15897).

Stratigraphic Position and Age

Nildottie. Middle part of Mannum Formation. Middle to late Lower Miocene.

Morgan. Upper 2.4 m of upper member of Morgan Limestone. Late Lower or early Middle Miocene.

Description

Carpus essentially the same as its equivalent in the larger cheliped of the extant Australian species Nectocarcinus integrifrons (Latreille, 1825). General features of hand also as in larger cheliped of N. integrifrons. Palm with ventral aspect ornamented by numerous, granulate, transverse ribs; outer face of palm conspicuously granulate, the granules tending to be arranged in discontinuous transverse rows; most of inner face sparsely and moderately finely to closely and coarsely granulate in different specimens, the granules tending to be arranged in wavy, discontinuous transverse rows. Fingers with prominent longitudinal ridges; greater part of length of ridges finely granulate to smooth, proximal part of ridges more coarsely granulate, grooves between ridges smooth. Prehensile margin of fixed finger with two small, rounded teeth on either side of extreme basal portion, two large, broad teeth on proximal half of length and five or so small, unequal sized rounded teeth beyond. Prehensile margin of movable finger with a large, protrusive basal tooth and about nine smaller, unequal sized rounded or sub-conical teeth beyond, a rather conspicuous tooth at about middle of length of finger.

Measurements

The palm of the holotype S.A.M. P15896 is 21 mm long and 15 mm high. The palm of paratype S.A.M. P15897 is approximately 31 mm long and 20 mm high. The propodus of paratype S.A.M. P15901 (Plate 16, Figure 13) is 25 mm long with the palm 17 mm long (approximately) and 13 mm high. The dactylus of paratype S.A.M. P15899 (Plate 16, Figure 12) is 14 mm long.

Remarks

Nectocarcinus granosus closely resembles the modern *Nectocarcinus integrifrons* (Latreille, 1825). The two differ as follows:

(a) Discontinuous transverse ridges which ornament the inner and outer surfaces of the palm of the larger chela of *N. integrifrons* are absent or much more weakly developed in the fossil species.

(b) In *N. integrifrons* there are two narrow smooth bands on the lower half of the outer face of the larger chela; these bands are not clearly marked in *N. granosus*.

(c) The teeth on the fingers of the larger chela of *N. granosus* are apparently one or two fewer in number and are lower and more rounded.

Nectocarcinus amathitus sp. nov.

Plate 17 figures 3a-d, 4, 5

Name

From the Greek *amathites* meaning sand-dweller; in reference to the sandy sediments in which this species occurs and on which it apparently lived.

Material

Fragment of anterolateral portion of carapace, merus and incomplete chela of right (larger) cheliped, holotype S.A.M. P15845, coll. Glaessner, 1951. Several specimens of the distal part of the claws or of the fingers of a claw associated together. Numerous isolated fingers of claws. Specimens coll. R. Tate, W. J. Kimba, 1913, Mr. Wilson, Glaessner, 1951, 1953, 1959, South Australian Museum staff, R.J.F.J., 1970. All specimens preserved as original shell material; the fingers commonly show traces of the original colouration.

Occurrence

Sea cliffs in vicinity of Port Willunga, from Blanche Point to Snapper Point. Holotype from cliffs south of Port Willunga.

Stratigraphic Position and Age

Hallett Cove Sandstone. Pliocene.

Description

Surface of carapace apparently ornamented by low, nearly smooth, discontinuous transverse ridges. Lateral margins of carapace rounded; anterolateral teeth directed forwards, very broad based, weakly granulate above, and with outer margin gently convex.

General features of merus and hand of holotype specimen much the same as in equivalent elements of larger cheliped of N. integrifrons. Merus subtriangular in section, the distal part of its upper margin with a large, nearly right-angular tooth directed distally; surface of joint mostly smooth, inner ventral margin sparsely and coarsely granulate. Outer and ventral aspects of palm ornamented by low, smooth discontinuous transverse ridges.

Fingers of both chelae very similar to those of N. integrifrons. Ribs on fingers narrow, minutely granulate for greater part of length when not abraded; proximal part of these ridges often finely granulate; grooves between ridges finely to coarsely pitted. The greater (distal) part of the fingers was dark coloured in the same pattern as in N. integrifrons.

Measurements

In the holotype S.A.M. P15845, the propodus of the right (larger) claw is more than 60 mm long and the palm 46 mm long and more than 29 mm high. Paratype S.A.M. P65 has the fixed finger of the right (larger) claw 24 mm long. Paratype S.A.M. P15842 has the fixed finger of the left (smaller) claw 27 mm long and the dactylus 37 mm long.

Remarks

The present species is closely related to N. integrifrons but the two differ in the following features:

(a) The upper margin, upper part of the outer face and lower-outer margin of the merus of the larger chela of N. amathitus are almost smooth; the corresponding surfaces in N. integrifrons are ornamented by short, granulate transverse ridges.

(b) In N. amathitus the greater part of the lower margin of the merus of the larger chela is smooth; the equivalent surface in N. integrifrons is conspicuously granulate.

(c) The low, discontinuous transverse ridges which ornament the outer surface of the palm of the larger chela of N. amathitus lack the row of granules present in the extant species.

(d) The distal parts of the palm of the larger chela are more sparsely and weakly granulate than in N. integrifrons.

(e) In both claws of N. integrifrons the fixed finger has a line of conspicuous granules on either side of the row of teeth on the prehensile margin; these lines of granules are absent or very much finer in N. amathitus.

(f) The ribs on the fingers of the fossil species are more finely granulate than in the modern crab.

Nectocarcinus integrifrons (Latreille, 1825)

Plate 18 figure 1

Nectocarcinus integrifrons (Latreille, 1825). Stephenson and Campbell, 1960: 83, text-fig.2B, pl.1, fig.2, pl.5, fig.B, pl.6, fig.A (synonymy, male pleopod).

Material

Broken dactylus of right (larger) claw, hypotype S.A.M. P15840 and incomplete dactylus of left (larger) claw, S.A.M. P15841.

Occurrence

Sea cliffs in vicinity of Port Willunga.

Stratigraphic Position and Age

Hallett Cove Sandstone. Pliocene.

Measurements

The dactylus, specimen S.A.M. P15840, is 27 mm long (incomplete). The fragmentary dactylus, S.A.M. P15841, is 15 mm long (incomplete).

Remarks

These dactyli are indistinguishable from the corresponding parts of modern specimens of *N. integrifrons* from South Australian waters. In present seas *N. integrifrons* occurs off southwestern, southern and south-eastern mainland Australia, and Tasmania, and is known from the intertidal region down to a depth of about 13 m.

Phylogeny of Nectocarcinus

The living species of Nectocarcinus can be divided into several groups of closely similar forms (Dell, Griffin and Yaldwyn, 1970). Four such groups are recognized here:

1. N. integrifrons group including N. integrifrons and the southeastern Australian N. tuberculosus A. Milne-Edwards.
2. Monospecific N. spinifrons group.
3. N. antarcticus group comprising N. antarcticus (Jacquinot, 1853) from New Zealand, islands of the New Zealand Plateau and the Chatham Islands, and N. bennetti Takeda and Miyake, 1969, from the Auckland and Campbell Islands and the Chatham Rise.
4. N. bullatus group containing only N. bullatus Balss, 1924, from the Juan Fernandez Islands off Chile.

The Oligocene N. cafpercoensis shows features which might be expected in a primitive ancestral member of this genus; a medially notched weakly quadridentate front, four well developed relatively narrow-based antero-lateral teeth, and smooth, lobate carapace-regions with little secondary ornamentation. It most closely resembles the living N. spinifrons, to which it may be directly ancestral (Figure 51). A species of Nectocarcinus allied to N. cafpercoensis is known from the middle Lower Miocene exposure of the Gambier Limestone at the quarries on sections 601 and 606, Hundred of Blanche, 6.4 km south of Mount Gambier.

N. granosus and N. amathitus are fossil representatives of the N. integrifrons group. The chelipeds of N. granosus resemble the corresponding parts of N. integrifrons particularly and to a lesser degree those of N. tuberculosus; it is probably the ancestor of both of these species. N. amathitus appears to represent an extinct side branch off the N. granosus, N. integrifrons lineage.

Remains of N. amathitus and N. integrifrons occur together in the Hallett Cove Sandstone in the vicinity of Port Willunga. The remains of N. amathitus are, however, about 30 times more frequent than those of N. integrifrons and it is probable that the two species inhabited different micro-environments. As more or less complete remains of N. amathitus are sometimes found, it almost certainly lived at the immediate site of deposition of the Hallett Cove Sandstone, a near-shore or sublittoral deposit.

No fossils representing the N. antarcticus and N. bullatus groups are known and thus only speculative remarks can be made about the origin of these sections. Their narrow quadridentate front is an exaggeration of the frontal features of N. cafpercoensis and might be interpreted as indicating that this fossil is near their ancestral stock. The overall shape of the carapace and the short, broad-based form of the anterolateral spines in the N. antarcticus group is suggestive of a common ancestry with the N. integrifrons group. Dell, Griffin and Yaldwyn (1970) consider that N. bullatus is related to the N. antarcticus group.

If the evolutionary scheme just proposed is to any degree realistic, then it is interesting to note that the specific diversification of the genus appears to be coupled with a progressive eastwards migration (Figure 51). It is speculated that the major influence on the direction of this migration has been the West Wind Drift.

Superfamily Xanthoidea
Family Xanthidae Dana, 1851
Genus *Ozius* Leach, 1825

Type species: *Ozius tuberculosus* H. Milne-Edwards, 1834, subsequent designation by Rathbun, 1930.

Ozius Leach in Desmarest, 1825: 105. H. Milne-Edwards, 1834: 404. Haswell, 1882: 62. Rathbun, 1930: 539. Bennett, 1964: 69.

?*Ozius macrochelus* sp. nov.

Plate 18 figures 2 - 8

Name

From the Greek *makros*, large, and the Greek *chele*, claw; in reference to the large size of the claws of this species.

Material

Numerous specimens of the fingers of the claws of the larger cheliped. Holotype S.A.M. P15821a,b, two fingers of right (larger) cheliped, coll. H. Eames, 1970. Large incomplete dactylus of right (larger) cheliped, paratype S.A.M. P15822, coll. Mr. Wilson. Broken distal part of dactylus of right (larger) cheliped, paratype S.A.M. P15823, coll. R. Tate. Specimens of dactylus of larger chela: paratype S.A.M. P15829, coll. W. G. Kimba and paratype S.A.M. P15834, coll. M. F. Glaessner, 1956. Specimens of fixed finger of larger chela, paratype S.A.M. P15827, coll. C. A. Kruger. Other materials R. Tate, W. G. Kimba, M. F. Glaessner, 1953-1954, Bret Robinson, 1967 and R.J.F.J., 1966-1971.

Occurrence and Stratigraphic Position

St. Vincent Basin:

Hallett Cove Sandstone, sea cliffs in vicinity of Port Willunga; at Blanche Point (P15821a,b); at Port Willunga (P15822, P15823, P15827, P15829, P15831); in road cutting leading to Port Willunga Jetty; at Aldinga Bay; and at Snapper Point, 2 km S.W. of Port Willunga (P15834).

Hallett Cove Sandstone, Adelaide.

Hallett Cove Sandstone, Surveyor Point, near Port Vincent, Yorke Peninsula.

Kangaroo Island.

Murray Basin:

Norwest Bend Formation, Morgan loc. 1. Upper parts of cliffs at Devlins Pound, 13 km west of Overland Corner, South Australia.

Age

Pliocene.

Description

Fixed finger of larger claw elongate, curved and tapered, subtriagonal in section at base, suboval in section distally, the shell material thick; outer and inner faces each somewhat flattened and with a line of pits in a shallow groove near middle of height; prehensile aspect also somewhat flattened, two small rounded teeth on either side of extreme basal portion followed by two larger, flattened, confluent teeth side by side, a single large domed tooth just beyond, on remainder of prehensile margin, five or so small, blunt teeth, every second more prominent; longitudinal spacing between all teeth increases in larger specimens.

Movable finger of larger claw elongate, tapered, curved, suboval to ovate-triagonal in section; shell material very thick; outer face flattened medially, with a row of conspicuous pores in a slight groove at about 1/3 height from upper margin and a few scattered pores on proximal portion; upper part of inner face rounded or bluntly angled, a row of pores just below middle of height of face; on basal part of prehensile margin an extremely large tooth which usually has its proximal aspect worn and flattened; remainder of prehensile margin with eight or nine low rounded teeth which become progressively lower and less distinct in larger specimens, each third to fourth tooth in series larger.

Measurements

The holotype (P15821) has the fixed finger 47 mm long and the dactylus also 47 mm long (incomplete). The largest specimen known is represented by a broken dactylus (P15822) 70 mm long. This specimen was perhaps 100 mm long originally.

Remarks

Large specimens of these fingers are considerably more elongate relative to their width than small examples. This is probably a function of differential growth.

Materials of this form from the Pliocene of Adelaide, Aldinga and Surveyors Point were suggested by Glaessner (1960: p.24) to belong to the genus *Pseudocarcinus*. Admittedly the present fingers resemble those of *Pseudocarcinus* in their elongation, large size, and heavy calcification of the shell. However in their shape and the arrangement of the teeth, particularly in small examples, they much more closely resemble the corresponding fingers of the modern *Ozius truncatus* H. Milne-Edwards, 1834, which occurs in southern and eastern Australia, New Zealand and the Kermadec Islands. As various genera allied to *Ozius* have the fingers of the claws very similar to the latter, the above noted resemblance cannot be accepted as the basis of a definite generic identification. However until more is known about the crab concerned a tentative placement in *Ozius* seems appropriate.

The fossil fingers reach a much larger size than those of *O. truncatus* or any other extant species of *Ozius* which the author knows of. They are further distinguished from the fingers of *O. truncatus* by their relatively more elongate form, especially the larger specimens, and by their broader teeth; the large tooth at the base of the movable finger is more prominent and the same finger has two or three more small teeth on the distal part of the prehensile margin. The degree of calcification of the fossil fingers is similar to that in *O. truncatus*.

Genus *Pseudocarcinus* H. Milne-Edwards, 1834

Type species: *Cancer gigas* Lamarck, 1818, selection by Miers, 1886.

Pseudocarcinus H. Milne-Edwards, 1834: 407. Haswell, 1882: 52. Miers, 1886: 141, *nota* 1. McCoy, 1889: 293. Hale, 1927: 156.

Carapace 1.2-1.4 times as wide as long, broadly rounded in outline before, narrowed behind; front .3-.13 width of carapace, nearly horizontal, notched medially, with four projecting denticles on anterior margin and a transverse row of six prominences or tubercles above; orbits relatively small; anterolateral margins obscurely to distinctly four-lobed, each lobe bearing two or five spiniform teeth; protogastric regions and a large epibranchial lobe inflated and prominent, other regions lobate and conspicuous; surface smooth, granulate or tuberculate above regions, intervening grooves smooth.

Chelipeds robust; one claw unusually large in mature males of extant species. Merus with a serrate crest above. Carpus with two to three or more spines grouped about internal angle, surface of joint tuberculate or nearly smooth. Palm with three prominences on inner side of upper aspect; outer face ornamented by longitudinal rows of more or less obscure tubercles, or smooth. Fingers with few blunt teeth on prehensile margins; old males of extant species have fingers of larger claw greatly elongated.

The one known extant species of this genus and the several fossil occurrences previously recorded are as follows:

Pseudocarcinus gigas (Lamarck, 1818)

Extant. Southern and southeastern Australia, from the Great Australian Bight to Tasmania, and off Wollongong, New South Wales; 91-822 m.

Pseudocarcinus sp. Glaessner, 1960

Uppermost Miocene to Pliocene (Kapitean). Near Goldsborough, South Island of New Zealand.

This identification is based on a single incomplete cheliped dactylus. The specimen is not particularly similar to the corresponding part of P. gigas and could well belong to a different genus. Pseudocarcinus has never been recorded in the present-day seas of New Zealand.

Glaessner (1960) also stated that Pseudocarcinus occurs in the Miocene of Melbourne, Victoria, and in the Pliocene of Adelaide, Aldinga and Surveyors Point near Port Vincent, South Australia. The material from Melbourne certainly belongs to this genus and is described below. The Adelaide, Aldinga and Surveyors Point specimens to which Glaessner was referring all consist of isolated and incomplete fingers of chelae. Several more complete fingers from near Aldinga have since come to hand. Although they reach a relatively large size (dactylus perhaps 10 cm long), these specimens seem more similar to the fingers of *Ozius* Leach than to those of *Pseudocarcinus* and are tentatively referred to Ozius here (p.304).

Pseudocarcinus parvus sp. nov.

Text-figure 52a-c, plate 19 figures 1 - 7; plate 20 figures 1 - 3

Name

From the Latin *parvus*, small; in reference to the small size of this species compared to the modern *P. gigas*.

Material

More than seventy specimens of the carapace of which eleven are more or less complete and the rest variously broken. Fourteen more or less incomplete specimens of different parts of the chelipeds have been found. All the specimens are preserved as the original shell material and were coll. R.J.F.J., 1967-1969.

Occurrence

From quarries on sections 26, 28, 29, 30, 144 and 145, Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed and immediately underlying and overlying strata in Gambier Limestone. Middle Oligocene.

Description

Carapace 1.2 times as wide as long, moderately convex in longitudinal section, nearly flat transversely; protogastric regions greatly inflated, epibranchial regions with a large prominent lobe, other regions lobate, separated or subdivided by distinct grooves; prominences of regions either obscurely granulate or coarsely granulate with occasional tubercles, margins of prominences and grooves between smooth.

Front .3 width of carapace, projected forwards, almost square cut viewed from above, deeply notched medially; anterior margin with four projecting, rounded denticles, two large and submedial, one less prominent at either lateral extremity; immediately above anterior margin a transverse row of six prominences or tubercles.

Orbits comparatively small, transversely ovate; supraorbital margins concave, doubly fissured, terminated laterally in a short, extraorbital tooth; suborbital margins also concave.

Anterolateral margins broadly rounded and divided into four rather obscure lobes by three grooves; each lobe with two or three prominent spiniform teeth. Posterolateral margins markedly convergent rearwards. Posterior margin .4 width of carapace, nearly straight, with a prominent border bearing a line of distinct granules.

Epigastric regions small, expanded, with several granules arranged in a longitudinal line. Extremely prominent protogastric regions each with a low, granulate, transverse, crescentic ridge on anterior portion and an obscure indistinctly granulate ridge behind. Hepatic regions divided in two by an oblique shallow groove which terminates behind at a deep pit; lobes on either side of this groove with prominences or tubercles on anterior portion. Hind part of mesogastric region bi-lobed; posterior gastric pits distinct. Metagastric region bi-lobed; urogastric region constricted, with a slight median expansion on anterior portion. Cardiac region three-lobed, two lobes side by side before and one less prominent behind. Intestinal region not clearly delimited. Branchial regions subdivided into numerous lobes by shallow grooves. Epibranchial regions with a large, inflated central lobe and two smaller lateral lobes, all three lobes coarsely granulate and sparsely tuberculate. Two small inner-branchial lobes adjacent to metagastric region and urogastric region respectively. Mesobranchial regions each forming a large, low, coarsely granulate lobe which bears several tubercles. Metabranchial regions with a prominence adjacent to posterior part of cardiac region and a transversely elongate, granulate lobe behind.

Interior surface of carapace with a number of positions of muscle attachment indicated by small depressions, areas with a reticulate ornamentation, and slight prominences, the arrangement being as shown in Figure 52b.

Chelipeds robust. Merus short, broad, moderately inflated; upper margin formed into a longitudinal crest with five dentiform prominences, a single triangular spine positioned distally. Carpus rhomboidal, its upper-outer surface openly tuberculate with a few scattered granules between, upper angle of joint with a prominent conical spine central to a group of four to five lesser spines and spinules. Palm broadened distally; blunt, inner-upper crest bearing two spiniform tubercles and a stout spine between; outer face rounded and ornamented by six or seven longitudinal rows of tubercles which become progressively more obscure as joint increases in size. Fixed finger of right (larger) chela .3-.4 length of palm, stout, tapered, with a line of indistinct pits on middle of outer face and two broad, blunt, rounded teeth on prehensile margin; a large pore at tip of finger.

Measurements

The carapace of the holotype S.A.M. P15686 is 22 mm wide (excluding lateral spines) and 17 mm long. The carapace of paratype S.A.M. P15688 is 30 mm long. Fragmentary remains indicate that the carapace may reach a width of approximately 60 mm. The propodus of the largest chela known, paratype S.A.M. P15705, is 33 mm long.

Remarks

This species greatly resembles and is almost certainly the direct ancestor of *Pseudocarcinus gigas*. Unfortunately all of the specimens of the latter available for comparison are much larger than the fossil species. The fossil form differs from the smallest of these specimens of *P. gigas* (a female with the carapace 124 mm wide) in the carapace being slightly flatter, the protogastric regions appreciably larger (relatively) and more swollen, the cardiac region less elongated, the surface of the carapace less granulate and smoother, and the marginal spination of the carapace more conspicuous. The outer surface of the largest specimens of the chelae of the fossil species (Plate 20, Figure 3) is nearly smooth rather than closely and conspicuously granulate and tuberculate.

Some of these differences undoubtedly result from allometric changes which occur during the growth of _P. gigas_. Rathbun (1923) describes small specimens of _P. gigas_ (carapace down to 12.3 mm wide) as having the carapace "roughly granular" and with all the spines on the animal and the teeth on the fingers more conspicuous than in large examples. The author's material would appear to differ in having much of the carapace relatively smooth and the teeth on the fixed finger, at least, very weak.

Pseudocarcinus cf. _parvus_

Plate 20 figures 4 & 5

Material

A nearly complete right (larger) claw, U.T.D.G. 53683A, a fragment broken from the upper outer part of the palm of a right (larger) claw, U.T.D.G. 53683B, and three fingers of claws, U.T.D.G. 53683C-D.

Occurrence

Cape Grim, northwestern Tasmania.

Age

Approximately middle to late Lower Miocene.

Measurements

The claw 53683A has the palm 27 mm long and 21 mm high (incomplete), and the fixed finger 13 mm long. The fragment 53683B is from a claw with the palm 50-55 mm long.

Remarks

These remains seem quite similar to the chelae of *P. parvus* in the shape and ornamentation, but evidently reached a much larger size. In this regard they approach *P. gigas*. The tuberculation on the nearly complete claw is much better developed than in comparable sized claws of *P. parvus*. This feature again is approaching the condition in *P. gigas*. There thus seems little doubt that these fossils represent an intermediate form on the lineage between *P. parvus* and *P. gigas*.

Pseudocarcinus gigas (Lamarck, 1818)

Plate 19 figure 9; plate 20 figure 7

Pseudocarcinus gigas (Lamarck, 1818). McNeill, 1920: 108 (synonymy, remarks); 1927: 8, fig. page 7. Rathbun, 1923; 104. Hale, 1927: 157, fig.158.

Material

Fossil: broken fixed finger of a right (larger) chela, hypotype S.A.M. P15912, coll. D. Schultz, 1961.

Extant: a dozen or so specimens, some in the South Australian Museum but most in the private collection of Mr. D. R. Delaine.

Occurrence

Fossil from shelly lime sand inland from Woakwine Dune, 6 m below ground surface in excavation for Hatherleigh Drain, 1.4 km N.N.W. of Rendelsham railway siding and 13.5 km W.N.W. of Millicent, South Australia.

Modern examples from off the coast of Southern Australia.

Age of Fossil

Quaternary.

Measurements

The length of the fossil finger is 142 mm.

Remarks

The fossil is virtually identical to the fixed finger of the larger chela of males of P. gigas.

Pseudocarcinus cf. gigas (Lamarck, 1818)

Text-figure 53a,b, plate 19 figure 8; plate 20 figure 6

Material

Broken piece of limonitic internal mould and partial cast of lateral portion of a carapace, N.M.V. P29348a. Limonitic internal mould and partial cast of carpus, palm and basal parts of fingers of right (larger) chela, N.M.V. P29348b. Both specimens apparently belonged to a single individual and were collected by Mr. Eric Nielsen (Gill and Baker, 1955).

Occurrence

Excavation, Buckley Street, West Essendon, Melbourne.

Stratigraphic Position and Age

Newport Formation. Late Lower or early Middle Miocene.

Description

Anterolateral margins of carapace apparently very convergent forwards, acutely angulate in profile, evidently cut into well defined lobes by deep notches; rearmost lobe apparently at widest part of carapace and about 1/3 length of preceding lobe; margin of each lobe dentate. Posterolateral margins evidently very convergent rearwards, gently sinuous, rounded in profile. Dorsal surface of lateral portion of carapace nearly smooth; a conspicuous depression behind hepatic region; large central lobe of epibranchial region gently domed; several broad, low prominences near anterolateral margin of carapace, area below this margin apparently tuberculate.

Carpus and chela of larger claw massive. Carpus rounded externally. Palm increasing in height distally and with upper and lower margins rounded; a large tubercle on inner side of upper margin at about ½ length of palm; outer face convex, with most of interior surface covered by a reticulate pattern of muscle attachments, a wide, deep vertical groove near articulation with movable finger; inner face gently convex. Fixed finger slightly deflexed relative to palm and evidently with a large basal tooth; preserved stub of movable finger strongly downsloping relative to upper margin of palm.

Measurements

The fragment representing the lateral part of a cephalothorax (N.M.V. P29348a) is from a carapace 160-170 mm wide. The palm of the claw (N.M.V. P29348b) is 100 mm long and more than 67 mm in height.

Remarks

The preserved parts of this fossil resemble the corresponding portions of males of P. gigas, but indicate an individual considerably smaller than the average size reached by the latter (carapace about 290 mm wide). The features of the fragment of the carapace of the fossil are within the limits of variability in shape which the author has observed in P. gigas. The claw of the fossil differs from its counterpart in the male P. gigas only in having a deeper vertical groove on the outer, distal part of the palm. Very probably the fossil form is a direct ancestor of P. gigas, but it is too fragmentary to be either identified as belonging to the modern species or distinguished as a separate taxon.

(Females of P. gigas differ from males in having much of the dorsal aspect of the carapace tuberculate rather than nearly smooth, the epibranchial regions slightly less swollen, and the anterolateral margins of the carapace more weakly notched. Their claws are also more equal sized and the fingers of the larger claw are not especially elongated).

Phylogeny of Pseudocarcinus

The different fossil remains here referred to this genus are all considered to be on the direct lineage leading to the modern P. gigas. P. gigas occurs most frequently on the outer part of the continental shelf and upper bathial region, but apparently occurs rarely in in-shore waters. The past distribution of the genus seems to have been similar. P. parvus was also probably an outer-continental shelf or upper bathial species. The beds from which P. cf. gigas was obtained at Essendon, Melbourne, have been considered as representing a near-shore environment (Gill, 1957).

Gigantism and allometry in Pseudocarcinus

The extant Pseudocarcinus gigas is one of the largest living arthropods in the world. It is said to weigh as much as 13 kgm and to reach up to 41 cm across the carapace (Hale, 1927). The outstretched claws of such a giant would probably span 1.5-1.8 m. Amongst the Decapoda it is only exceeded in size by the giant Japanese spider crab Macrocheira kaempferi de Haan which may reach 46 cm across the carapace and 3.7 m across the outstretched arms (Healy and Yaldwyn, 1970). The fossil remains of Pseudocarcinus indicate that this genus has experienced a persistent phylogenetic trend towards an increase in size since the Oligocene. Various changes in the carapace and claws have accompanied this size increase.

Presentation of data

Size of different species

Figure 54 shows a graph of the width of the carapace (excluding lateral spines) against geological time (Tertiary time scale of Berggren, 1969a) for the estimated dimensions of the largest example of P. minor collected and the specimen of P. cf. gigas, and the average size of eight mature individuals of P. gigas. The assumption is made that the fossil remains approximate the average size of mature individuals in the original populations to which they belonged. A similar graph for the length of the palm of the larger cheliped of the various fossil forms and the male of the modern species is also shown.

Allometry

The growth of different parts of many organisms can be approximated by the empirical formula

$$y = bx^h$$

$$\text{or} \quad \log y = h \log x + \log b,$$

where y and x are respective magnitudes of the parts of the organism under consideration, h is a constant (coefficient of differential growth or growth coefficient) and b is a constant (Huxley, 1932; Gould, 1966). This equation describes the line of best-fit or reduced major axis of plots of the dimensions of the organism on orthogonal logarithmic coordinates, or of plots of logarithms of the dimensions of the animal on scalar (non logarithmic) coordinates.

Figure 55 shows plots of various dimensions of the carapace versus its length, on logarithmic ordinates, for P. minor and P. gigas respectively. For each equivalent set of plots for the two species, the data for the largest individuals of each species have been joined to provide inter-specific regressions. Figure 56 shows similar plots of the length of the propodus of the chela versus the length of the carapace, and the length of the fixed finger of the chela versus the length of the palm; for this last category data for the claw of P. cf. minor has been included.

Discussion

Size attained by different species

The data for the plot of the width of the carapace against geological time for P. parvus, P. cf. gigas and P. gigas (Figure 54) indicates a gentle curve and suggests that Pseudocarcinus has increased at a gradually increasing rate since the Middle Oligocene. As numerous examples of the carapace of P. parvus (more than seventy) have been found, this apparent change in size can hardly be due to accidents in collecting and must be regarded as a real phylogenetic size increase. The rate of increase in width of the carapace indicated by the graph is between 6 and 9 mm per 10^6 years.

The chelipeds also show a progressive increase in size, but at a more rapidly changing rate than the carapace. This is consistent with their growth being allometric relative to the carapace.

Ontogenetic allometry in P. parvus

The coefficients of differential growth between different dimensions of the carapace are slightly greater than 1 or not quite isometric in each instance. This suggests that physiological stresses resulting from the increase in size of the animal are minimal over the size range involved and necessitate no obvious morphological changes in the carapace with growth.

The limited data on the chelae indicate a marked positive allometric relationship between the length of the fixed finger of the larger claw and the length of the palm. In P. gigas the most marked allometric changes with growth apparently occur in the larger claw of males and this is probably also true for the fossil. The functional significance of this change in the relatively small claws of P. parvus is not obvious.

Ontogenetic allometry in P. gigas

Again the growth coefficient for the width of the carapace versus the length is slightly greater than 1, not quite isometric. The actual value, 1.06, is virtually identical to that for P. parvus (1.04). However, the relationship for the width of the epigastric regions versus the length of the carapace is negatively allometric ($h = .88$) and the differential growth between the height of the carapace (above the pleural suture) and the length of the carapace is to a slight degree positively allometric ($h = 1.10$). These changes are brought about by a disproportionate increase in the area of the branchial regions at the expense of the more medial regions, as the carapace increases in size, and by a disproportionate swelling of the carapace and particularly the branchial regions with growth. It seems probable that various physiological stresses are induced during the growth of P. gigas. The disproportionate increase in height of the carapace may occur partly to accommodate larger muscles to move the limbs. The increase in area and swelling of the branchial regions is almost certainly related to a disproportionate increase in the size of the gills, a change brought about by the need to maintain a satisfactory respiratory level in an animal of much greater body weight (about 8 kg, ignoring exoskeleton, in a male with the carapace 29 cms wide and apparently over 13 kg in a male with the carapace 40 cms wide).

Information concerning the growth of the claws is again relatively meagre. It is clear however that for females the increase in length of the propodus of the claws relative to the length of the carapace is almost isometric (h = .93). For the same sex, the increase in length of the fixed finger versus the length of the palm of the claw is to a slight degree positively allometric (h = 1.09).

The right (usually) claw of mature males is greatly enlarged compared to the left and the fingers are considerably lengthened, often by a somewhat disproportionate amount so that the pincers do not meet (Hale, 1927: figure 158). The growth of these elements relative to the carapace is almost certainly allometric, at least in sub-mature individuals, but unfortunately the data available to the author is inadequate to show this. The growth of the smaller claw in males is apparently also allometric, but to a less marked degree.

Interspecific allometry between P. parvus and P. gigas

The value of h for the width of the carapace versus the length (1.06) is almost the same as the corresponding parameter for P. parvus (1.04) and identical to that for P. gigas. The value of the growth coefficient for the length of the fixed finger versus the length of the palm of the larger claw of males (1.50) is also virtually the same as in the equivalent relationship for P. parvus (1.48). The regression for the length of the fixed finger versus the length of the palm between a small claw of P. parvus and claws of females of P. gigas (h = 1.14) is closely comparable to the equivalent regression for the claws of females of P. gigas alone (h = 1.09). The fact that these regressions form nearly rectilinear series lends strong support to the idea that P. parvus is the direct ancestor of P. gigas.

Each of the other interspecific growth regressions plotted for the carapace closely parallels its ontogenetic equivalent for P. gigas. Thus the allometry of the carapace which occurs during the growth of P. gigas very closely follows the apparent evolutionary changes between P. parvus and itself. This seemingly is an example of recapitulation, the ontogeny of the individual recapitulating the phylogeny of the lineage (Arkell, 1957: L107). Given phylogenetic size increase, it seems likely that the allometric changes in the carapace between these two species occurred in response to the same physiological stresses which acted during the growth of P. gigas.

Conclusions

It is suggested that Pseudocarcinus has increased in size at a gradually increasing rate from the Middle Oligocene to the present. During this time the growth coefficients for the width of the carapace versus its length (1.04-1.06), and for the length of the fixed finger versus the length of the palm of the larger claw of males (1.48-1.50) and for the same relationship in both claws of females (≏ 1.14-1.09) remained relatively constant. This suggests that these changes were occurring in response to a selection pressure or various selection pressures of virtually constant intensity. As Pseudocarcinus seems typically to have inhabited outer continental shelf and upper bathial environments which probably changed little over long periods of time, this finding is not altogether unexpected.

Family Goneplacidae Macleay, 1838

Subfamily Goneplacinae Macleay, 1838

Genus Ommatocarcinus White, 1852

Type species: Ommatocarcinus macgillivrayi White, 1852, by monotypy.

Ommatocarcinus White, 1852: 393. H. Milne-Edwards, 1852: 163. Miers, 1886: 246. Stebbing, 1893: 92. Alcock, 1900: 280, 293. Tesch, 1918: 181, 186. Barnard, 1950: 282, 285. Glaessner, 1960: 28; 1969: R525. Bennett, 1964: 74.

Carapace trapezoidal or pentagonal, width between tips of large, single extraorbital spines more than 1.6 times length; front narrow, less 1/4 width of carapace between tips of extraorbital spines, usually deflexed and more or less truncate; inner-orbital notches generally well indented; orbits elongated transversely, trough-like to accommodate greatly elongated eyestalks; extraorbital spines usually directed laterally; pterygostomial region with an anterior ridge which may or may not be transversely ribbed for stridulating. Basal three segments of male abdomen occupying all of width between coxa of last pereiopods or reduced in width. Chelipeds, particularly those of males, usually sub-equal and strongly elongated, the palms compressed and the fingers elongate. Ambulatory legs slender.

Remarks

Miers (1886) considered Ommatocarcinus most nearly allied to Goneplax Leach. Both genera are characterized by having the frontoorbital margin the widest or nearly the widest part of the carapace, the orbits trough-like for accommodating greatly elongated eyestalks, the anterolateral angles produced to a spine, and the chelipeds elongated. Tesch (1918) and Bennett (1964) indicated that some members of both genera have the basal segments of the male abdomen reduced in width, not occupying the full distance between the coxa of the last pair of legs as suggested by Miers.

Ommatocarcinus differs from *Goneplax* in having a relatively narrower front which generally has well defined inner-orbital notches. The more typical forms of *Ommatocarcinus* have the extraorbital spines strongly produced and directed laterally, not short and forwardly directed as in *Goneplax*. Apparently no members of *Goneplax* have a stridulating device.

Ommatocarcinus corioensis (Cresswell, 1886)

Frontispiece, plate 21 figures 1 - 3

Gonoplax (sic) *corioensis* Cresswell, 1886: 90, 91.

Ommatocarcinus corioensis (Cresswell) Hall, 1904: 356, pl.23, figs.1-5. Chapman, 1914: 247, text-fig. 120B. Glaessner, 1960: 29, text-fig.12c.

Material

Over one hundred and seventy specimens, including the types in the National Museum of Victoria were examined.

The lectotype, here designated as N.M.V. P7665, is in a water-rounded phosphatic nodule collected by the Rev. A. W. Cresswell at Curlewis near Geelong, Victoria. Specimen N.M.V. P7666, also in a nodule collected by Cresswell at Curlewis, is designated the paralectotype.

Three hypotypes of T. S. Hall; ♂, N.M.V. P7667; ♀ N.M.V. P7668; N.M.V. P7669, are from (the Port Campbell Limestone) Two Mile Beach, Port Campbell, Victoria.

Occurrence and Stratigraphic Position

This species is known from numerous widely distributed localities in southeastern Australia (including Tasmania) and also from the upper part of the continental slope off northern New South Wales. Its distribution and stratigraphic occurrence are outlined in the chapters I and II.

Age

Middle Lower Miocene to late Upper Miocene, ? middle Pliocene.

Diagnosis

Carapace trapezoidal with two transverse ridges. Anterior margin of front gently sinuous, slightly concave on either side of a median convexity. Supraorbital margins acute or subrounded in profile, with a row of spinules. Extraorbital spines laterally directed, strongly produced, and narrow based. Well developed anterolateral rises coarsely granulate. Basal segment of eyestalks concealed. Pterygostomial region with a stridulating ridge bearing about 76 short transverse striae. Male abdomen seven-segmented; the first three segments just reaching coxae of last pereiopods. Mature cheliped meri with a basal stridulating plectrum, an evenly spaced row of spinules on anterior margin, three spinules on distal part of ventral margin, and a spinule half way along dorsal margin.

Remarks

The chelipeds of this species, particularly in mature males, are often very elongated. Usually large males have the right chela the major, but in about one in five specimens the heterochely is reversed. One specimen, A.U. F17220, in a phosphatic nodule from Coghills near Geelong has the left cheliped about half the size of the right. This may be an example of regeneration.

Male crabs from the Morgan Limestone in the Murray Basin differ from most of the males from the eastern part of the Otway Basin in having somewhat shorter and broader chelipeds. However several males from the Otway Basin also have short, broad chelipeds. A gradational series appears to exist between the crabs from the Otway Basin with long chelipeds and the specimens from the Morgan Limestone. It is thus considered impracticable to separate the two forms. The growth of the chelipeds in all of the male individuals is an allometric function.

O. corioensis closely resembles and is the probable ancestor of _Ommatocarcinus macgillivrayi_ White, which occurs sub-fossil in nodules dredged from Moreton Bay, Queensland, and lives today off eastern Australia, Japan and probably Natal (*O. pulcher* Barnard, 1950) at depths of from shoal water to 274 m. It differs from *O. macgillivrayi* in having the anterior margin of the front sinuous but not doubly notched, the anterolateral margins of the carapace straighter and sharper and coarsely spinulate, the three basal segments of the male abdomen reaching the full distance between the coxae of the last pair of legs, not reduced in width, and the meri of the chelipeds with an anterior row of spinules. In *O. corioensis* the basal segment of the eyestalks is apparently covered by the front; the basal segment is exposed in *O. macgillivrayi*.

Subfamily Carcinoplacinae H. Milne-Edwards, 1852

Genus *Carcinoplax* H. Milne-Edwards, 1852

Type species: *Cancer* (*Curtonotus*) *longimanus* de Haan, 1835, subsequent designation by Glaessner, 1929.

Carcinoplax H. Milne-Edwards, 1852. Imaizumi, 1960: 219 (discussion concerning fossil species); 1961: 163 (fossil and modern Japanese species reviewed, Japanese fossil forms described). Sakai, 1965: 166 (generic synonymy). Glaessner, 1969: R526.

Carapace transversely ovate, subhexagonal or subquadrangular, gently to moderately convex above; front square cut and nearly straight, often faintly notched medially or longitudinally grooved in mid-line above, .2-.4 width of carapace, with or without shallow antennal notches on either side; orbits moderately large and transversely ovate; short basal joint of antennal flagellum standing loosely in orbital hiatus in present-day species; frontoorbital margin .6-.9 width of carapace; anterolateral margins each with three or fewer spines or teeth or nearly smooth, the second and third anterolateral teeth of type species, *C. longimanus*, reduced to slight prominences in mature individuals; carapace regions only faintly marked, surface smooth or finely granulate. Chelipeds either very long, particularly in mature males, or quite short and robust; sides of fingers of chelae smooth or shallowly grooved.

The taxon *Homoioplax* Rathbun, 1914, which was erected for the single extant species *Pseudorhombilia haswelli* Miers, 1884, greatly resembles *Carcinoplax*. Rathbun (1914) distinguished it from *Carcinoplax* on the basis of the third segment of the male abdomen being reduced in width, not spanning the full distance between the coxae of the last pair of legs. This difference is of equivocal significance, however, as in the Goneplacid genus *Ommatocarcinus* White (1852), the width of the basal segments of the male abdomen varies in different species. *Homoioplax* otherwise appears to differ from *Carcinoplax* only in having the orbits slightly more elongated. This feature is potentially gradational between the two and *Homoioplax* is here considered a synonym of *Carcinoplax.*

Carcinoplax differs from *Carcinoplacoides* Kesling, 1958, in not having the carapace so markedly broadened, and is further distinguished, at least in immature specimens, by the anterolateral margins of the carapace being toothed rather than entire.

Pilumnoplax sulcatifrons Stimpson, 1858, which Rathbun (1918: p.21) designated the type species of *Pilumnoplax* Stimpson is now included in *Eucrate* de Haan, 1835 (Campbell, 1969). Thus *Pilumnoplax* is a synonym of the latter genus. Hence the generic status of most of the species previously included in "*Pilumnoplax*" is uncertain. *Carcinoplax* differs from *Eucrate* in having three rather than usually four anterolateral teeth on the carapace, and in the antenna standing free in the open antennal hiatus, not with the flagellum excluded from the orbit by a process of the basal antennal article.

At least sixteen modern forms, from the western coast of Africa, the Indian Ocean, southern Australia and New Zealand, the Philippine Islands, southern China and Japan have been referred to *Carcinoplax*. To the author's knowledge, however, nearly half of these forms have never been figured. It would thus be presumptuous to attempt any meaningful review of these forms without a study of a complete series of representative specimens. Such an investigation is beyond the scope of the present work.

The following species belong or appear to belong to the genus and have been found as fossils:

Carcinoplax longimanus de Haan, 1835

Extant: Southern Africa, Natal, Mozambique; 73-238 m. Gulf of Martaban and Andaman Sea; 97-110 m. Southern China. Kyushu to

Hakodate, Japan; 30-324 m.

Younger Tertiary. Dredged from sea-bottom off Shikoku, Japan.

Carcinoplax antiqua (Ristori, 1899)

Lower Miocene. Japan.

Pilumnoplax urpiniana Vía Boada, 1959

Middle Lutetian (Middle Eocene). Cataluna, Spain.

Carcinoplax prisca Imaizumi, 1960

Middle Miocene. Japan.

Carcinoplax senecta Imaizumi, 1960

Middle Miocene. Japan.

Carcinoplax praevictoriensis sp. nov.

Text-figure 57; plate 21 figures 4 - 6

Name

From the Latin *prae*, meaning before, and *victoriensis*, a specific name; in reference to the suggestion that this fossil is the ancestor of *Carcinoplax victoriensis* Rathbun.

Material

Six specimens preserved as the original shell material; the holotype S.A.M. P15674, and paratypes S.A.M. P15677, P15913, examples of the carapace showing the external aspect, coll. R.J.F.J., 1968; paratype S.A.M. P15676, a carapace showing interior surface and partly preserved as an external mould, coll. M. F. Glaessner, 1963; paratypes S.A.M.

P15675, P15678, broken examples of carapace with interior surface exposed, coll. R.J.F.J., 1967.

Occurrence

From quarries on sections 26 (P15675-78) and 28 (P15674), Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed in Gambier Limestone. Middle Oligocene.

Description

Carapace ovate-subquadrate, 1.2 times as wide as long, with two gently curved, low, transverse swells at .4 and .7 length of carapace over posterior part of protogastric regions and anterior 1/3 of cardiac region respectively; longitudinal profile moderately down-sloping in advance of first transverse swell and behind second, a transverse depression between; carapace gently convex from side to side; regions faintly marked; surface minutely granulate or smooth.

Front .35-.36 width of carapace, truncate, projected forwards and slightly downwards, straight except for a faint median notch and doubly marginate; slight antennal notches at anterolateral extremities; a weak longitudinal groove in mid-line above; a shallow transverse depression behind.

Orbits apparently transversely ovate; supraorbital margins slightly raised, concave, with two faint sutures. A small denticle or extraorbital tooth adjacent to lateral extremity of each orbit. Frontoorbital margin .7 width of carapace.

Anterolateral margins short, rounded in outline, convergent forwards, with a small prominence just behind extraorbital tooth, a small, forwardly directed spine at about middle of length, and a slightly larger spine behind; this posterior spine directed forwards and upwards and situated a little in advance of first transverse swell across carapace. Posterolateral margins moderately convergent rearwards for anterior $\frac{1}{2}$ of their length, curved progressively inwards and broadly rounded behind. Posterior margin about .4 width of carapace, slightly concave, with a narrow border which extends onto rear part of each posterolateral margin.

Epigastric regions small, slightly inflated. Protogastric regions large, gently domed. Hepatic regions almost flat, slightly depressed relative to adjacent regions. Mesogastric region slightly raised. A depression on either side of urogastric region. Cardiac region broad, subhexagonal. Intestinal region narrow, slightly raised. Epibranchial regions swollen. Mesobranchial regions shallowly concave before, expanded behind. Rear part of branchial regions and down-sloping posterolateral regions meeting in a short longitudinal crest.

Places of muscle attachment on interior surface of carapace marked by pits, grooves, and lines of depressions; their position as indicated in Figure 57.

Measurements

The carapace of the holotype S.A.M. P15674 is 20 mm wide, excluding the lateral spines, and 17 mm long. Paratype S.A.M. P15676 has the carapace 19 mm wide and 16 mm long. The carapace may reach a width of about 25 mm.

Remarks

The carapace of *Carcinoplax praevictoriensis* greatly resembles that of the modern *Carcinoplax victoriensis* Rathbun, 1923, which occurs off eastern Victoria at depths of 128 to 366 m and in the region of the Chatham Rise and Chatham Islands, New Zealand, at 402 to 604 m. The two differ as follows:

(a) The carapace of the fossil species is slightly narrower (ratio of width versus length 1.2 in the fossil and 1.3 in *C. victoriensis*).

(b) The anterolateral margins of *C. praevictoriensis* are slightly less convergent forwards.

(c) In the fossil species a small denticle is situated at the extra-orbital angle. In *C. victoriensis* the extraorbital angle is bluntly obtuse.

(d) The anterolateral margins of *C. praevictoriensis* have a small prominence just behind the extraorbital angle; this prominence is absent or much less conspicuous in the extant species.

(e) In the carapace of *C. praevictoriensis* the second anterolateral spine is positioned a little further rearwards than its counterpart in *C. victoriensis*.

The overwhelming similarity between the carapace of these two forms leaves little room for doubt that *C. praevictoriensis* is the direct ancestor of *C. victoriensis*.

Carcinoplax woodsi sp. nov.

Text-figure 58; plate 21 figures 7 - 10

Name

Named after the Rev. J. E. Tenison Woods, who first studied the limestones of the Mount Gambier district and collected and described fossils from them in the late 1850's and 1860's.

Material

More than 110 specimens of the carapace, about half of which are more or less complete and the remainder variously broken. The first specimens were collected by M. F. Glaessner in 1953. All examples are preserved as the original shell material.

Occurrence

From quarries on sections 26, 28, 29, 30, 144 and 145, Hundred of Blanche, Mount Gambier loc. 1.

Stratigraphic Position and Age

Crab bed and immediately overlying strata in Gambier Limestone. Middle Oligocene.

Description

Carapace subquadrangular, 1.2 times as wide as long, with two gently curved, transverse swells at .4 and .75 length of carapace over posterior part of protogastric regions and anterior 1/3 of cardiac region respectively; longitudinal profile moderately down-sloping in advance of first transverse swell and behind second, depressed and shallowly concave between; transverse profile gently convex; regions mainly indistinct; surface smooth.

Front .37 width of carapace, truncate, hardly deflexed, straight and doubly marginate before, gradually widening behind, weakly furrowed above just behind either anterolateral extremity.

Orbits moderately elongated transversely, their outer 3/5 hollowed to receive ocular cornea; supraorbital margins raised, slightly oblique, weakly sulcate above at about 2/5 length, terminated laterally in a short, pyramidal extraorbital tooth; suborbital margins projected forwards a little beyond supraorbital margins in dorsal view and with two slight bulges. Frontoorbital margin .87-.84 width of carapace.

Anterolateral margins short, nearly straight, slightly convergent forwards, sharp crested anteriorly, bearing a small tooth at about 2/5 length, terminated behind at a prominent forwardly and upwardly directed tooth situated just in advance of end of first transverse swell across carapace. Posterolateral margins gently convex and slightly convergent rearwards for anterior 3/4 of their length, curved inwards and slightly arched behind. Posterior margin about .4 width of carapace, slightly concave, with a narrow border which extends over rear part of posterolateral margins.

Protogastric regions faintly marked, slightly expanded. Hepatic regions almost flat. Posterior part of mesogastric region slightly elevated, subtriangular; posterior gastric pits distinct. Urogastric region depressed; lateral urogastric grooves faintly marked or quite distinct in different specimens. Cardiac region slightly elevated, subhexagonal, a depression on either side behind. Intestinal region indistinct. Epibranchial regions swollen. Mesobranchial regions shallowly concave before, swollen behind. Rear part of branchial regions and down-sloping posterolateral regions meeting in a short longitudinal crest.

Muscle attachment areas on interior surface of carapace similar to those in previously described species of <u>Carcinoplax</u>. Lateral-urogastric attachments impressed as distinct grooves and strongly curved.

Measurements

The carapace of the holotype S.A.M. P15747 is 17 mm wide, excluding the lateral teeth, and 15 mm long. The carapace of paratype S.A.M. P15749 is 16 mm wide and 13 mm long.

Remarks

The carapace of this little crab is very closely similar to that of the modern "*Homoioplax*" *haswelli* (here referred to *Carcinoplax*, p.328) which is known from Madura Strait, the Arafura Sea, and Japan at depths of from 18 to 384 m. The only features at variance with published figures of *Carcinoplax haswelli* seem to be that the carapace is very slightly narrower relative to its length, the transverse ridges are possibly more accentuated, particularly the median part of the anterior one, and the middle anterolateral tooth is slightly less conspicuous. In addition *C. haswelli* is described as having a slight notch in the middle of the anterior margin of the front, and the surface of the carapace granulate; the fossil species has the anterior margin of the front almost perfectly straight, and the surface of the carapace is smooth.

If these seemingly quite trivial differences were widespread in two separate modern populations, they might possibly be accorded subspecific importance. However considering the long time interval which has elapsed between the present fossil form and *C. haswelli* (of the order of 30 million years), these features can be justifiably rationalized as indicating a real specific difference. There can be no doubt that *Carcinoplax woodsi* is the direct ancestor of the modern species.

Phylogeny of *Carcinoplax*

The similarity in the outline of the carapace of "*Pilumnoplax*" *urpiniana*, from the Middle Eocene of Cataluna, Spain, to that of the modern species Carcinoplax meridionalis Rathbun, 1923, from off southern Australia, and Carcinoplax surugensis Rathbun, 1932, from Japanese waters, is suggestive of a direct phylogenetic relationship (Figure 59). C. praevictoriensis and C. victoriensis, and to a lesser degree C. woodsi and C. haswelli, resemble C. meridionalis and probably share its ancestry.

While C. woodsi is common in the mid-Oligocene at Mount Gambier, C. praevictoriensis is relatively rare. The modern descendant of C. woodsi, the species C. haswelli, apparently occurs only to the north of Australia, although it is present in subtropical régimes off Japan. C. meridionalis and C. victoriensis probably now fill the position which C. woodsi formerly occupied in the southern Australian fauna.

The different living forms mentioned above have relatively short chelipeds; in this regard they contrast with the Indo-West Pacific C. longimanus and the Japanese fossil species C. antiqua, C. prisca and C. senecta, which have elongate chelipeds, particularly in mature males. The length of the chelipeds thus can be used to divide the genus into two sections. This division cannot itself be regarded as being of generic importance, however, as Carcinoplax indica Doflein, 1904, from the Nicobar Islands has the nearly oval carapace similar to that of C. longimanus, but robust chelipeds of only moderate length.

Imaizumi (1960, 1961) suggested that C. antiqua is the ancestor of C. prisca and C. senecta and that C. longimanus evolved from C. prisca.

The main evolutionary trends amongst these species appear to be for the carapace, originally subhexagonal, to become more ovate in outline and more strongly swollen, and for the chelipeds to increase in length. The extraordinary length which the chelipeds reach in males of *C. longimanus* is shown in the illustration given by Doflein (1904: pl.36). The shape of the carapace of some of the smaller specimens of *C. antiqua* which Imaizumi (1961) illustrates is similar to that of members of the "*Pilumnoplax*" *urpiniana*, *C. meridionalis*-*surugensis* lineage and it is probable that this is the stock from which the *C. antiqua*-*prisca*-*senecta*-*longimanus* group evolved.

APPENDIX I

Abridged transcript of paper in press
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METANEPHROPS, A NEW GENUS OF LATE PLIOCENE TO RECENT LOBSTERS (DECAPODA, NEPHROPIDAE)

Introduction

In 1966 the carapace of a fossil lobster was discovered by Mr. and Mrs. W. Elliot in a loose cobble on Motunau Beach, about 39 miles N.N.E. of Christchurch, South Island of New Zealand. Subsequently six more specimens of the lobster, also in loose cobbles, were collected at the same locality by Miss H. D. Adams, Mrs. J. R. Taggart, and Messrs. J. Cairney, S. A. Chidgey and L. Tregoning. Mr. D. R. Gregg, Keeper of Geology, Canterbury Museum, Christchurch, sent this material to Professor M. F. Glaessner, of the University of Adelaide, South Australia, who suggested the present study.

The fossil is a new species but is clearly related to extant lobsters which occur in the Indo-West-Pacific region, the West Indies, and off the southeast coast of South America. Previously these Recent species were referred to the genus Nephrops Leach, 1814. They and the new species are here accommodated in a new genus, Metanephrops, while Nephrops is restricted to contain only the extant N. norvegicus (Linnaeus) and one certain fossil species.

The cobbles enclosing the specimens of the present fossil were probably derived from concretions in the Greta Siltstone which forms the coastal cliffs at Motunau Beach (Mr. D. R. Gregg, pers. comm.). Fleming (1963) considered the faunule from Motunau to be Waitotaran and suggested it was no younger than the middle of this stage. D. G. Jenkins (1967) places the Waitotaran in the late Pliocene.

The specimens studied are deposited in the Canterbury Museum, Christchurch, New Zealand (indicated C.M. in the rest of this paper), and are catalogued in the 'Canterbury Museum register of fossil Arthropoda'.

Terminology

The terminology used for the carapace grooves in the descriptive parts of this paper follows the notation for Nephrops norvegicus given by Glaessner (1960, text-fig.18, drawing 10). This notation differs radically from that traditionally used by zoologists in descriptions of 'Nephrops' species; in particular the hepatic and cervical grooves are now considered the cervical and postcervical grooves respectively.

Subfamily Nephropinae Dana, 1852

Metanephrops gen. nov.

Designated type species: Nephrops japonicus Tapparone Canefri, 1873.

Diagnosis

Carapace slightly compressed laterally; rostrum elongate with a single pair of lateral spines; dorsolateral margins of rostrum continued back onto carapace as more or less parallel ridges bearing three to five pairs of prominent spines; antennal spine greatly expanded, lamellate; usually seven longitudinal ridges on carapace posterior to postcervical groove. Scaphocerite broad, often circular in shape. First pair of pereiopods almost symmetrical.

Remarks

It has long been recognized that extant Indo-West-Pacific and American nephropsids assigned to Nephrops Leach differ in several important features from the European type species Cancer norvegicus Linnaeus, 1758 (see de Man, 1916: p.98; Yaldwyn, 1954: p.730). This problem is resolved by the removal of the Indo-West-Pacific and American forms to Metanephrops gen. nov., and restriction of Nephrops to the extant type species and the Pliocene fossil N. reedi Carter, 1898, from Suffolk, England. Other fragmentary fossils referred to Nephrops either cannot be identified from literature, or belong to different genera (see p.345).

Nephrops differs from Metanephrops in the following features; the rostrum has three pairs of lateral spines instead of one and the dorsolateral margins of the rostrum are not continued back onto the carapace as more or less parallel ridges, the antennal spine is small, only five longitudinal ridges are present on the carapace posterior to the postcervical groove, the scaphocerite is narrow and lanceolate, and the first pair of pereiopods are distinctly heterochelous.

The previously described extant forms listed below are here referred to Metanephrops. These forms are each distinguished by combinations of differences and thus seem valid species.

Nephrops japonicus Tapparone Canefri, 1873

Japan: Market, Mitani, Aiti-ken; east of Owase, 180-379 m; off Lake Hamana-ko, 100-189 m; Suruga Bay; Sagami Bay; Tokyo Bay.

Nephrops thomsoni Spence Bate, 1888

Between Samboangan and Manila, Philippine Islands; Formosa; northern part of South China Sea; southern part of South China Sea off Sarawak and North Borneo; 159-314 m.

Nephrops andamanicus Wood-Mason, 1892

S.E. Africa; Andaman Sea; north of Bali I., Indonesia; 186-840. The specimen from north of Bali Island was taken on a bottom of mud and broken shells (de Man, 1916). The material mentioned by Holthuis (1964: p.71) from off Eucla, Western Australia at 219-820 m is a new species according to Dr. A. J. Bruce (pers. comm.). Dr. Bruce reached this conclusion after comparing additional material of the Australian form with specimens of N. andamanicus from South Africa and the Bay of Bengal.

Nephrops rubellus Moreira, 1903

S.E. coast of South America, roughly between 23° and 38°S; 50-150 m.

Nephrops arafurensis de Man, 1905

Kei Islands, Moluccas, 560 m. Taken from a bottom of liquid brown mud above solid bluish grey mud (de Man, 1916).

Nephrops challengeri Balss, 1914

New Zealand. Tasman Sea off Cook Strait, E. coast of North Island north to Hawke Bay; Chatham Is.; 146-503 m.

Nephrops sibogae de Man, 1916

Off Kei Islands, 310 m. Taken from a bottom of fine grey mud (de Man, 1916).

Nephrops sagamiensis Parisi, 1917

(= N. japonicus Balss, 1914 = N. intermedius Balss, 1921) Sagami Bay, Japan. 250 m; northern part of South China Sea.

Nephrops binghami Boone, 1927

British Honduras; north coast of Cuba; Bahama Is.; 438-885 m. Bahama Is. specimens from a bottom of grey sand (Holthuis, 1964).

Nephrops boschmai Holthuis, 1964

Off Eucla, Western Australia, 220-823 m.

Nephrops neptunus Bruce, 1965

Northern part of South China Sea, 731-795 m.

Nephrops sinensis Bruce, 1966a

Northern part of South China Sea, 205-391 m. Mud was brought up on the sole of the trawls used to take the species (Bruce, 1966a).

Nephrops australiensis Bruce, 1966b

N.E. of Port Hedland, Western Australia, 434 m. Greenish brown, *Globigerina* ooze was sampled near where the species was taken (Bruce, 1966b).

None of the several fossil species referred to *Nephrops* appears to belong to *Metanephrops*. *N. reedi* Carter from the Pliocene (probably Boytonian), at Boyton, Suffolk, England, is known from incomplete chelae; according to Woods (1931) it is allied to *N. norvegicus*. The Pleistocene forms *N. costatus* and *N.* sp. Rathbun, 1918, from the Panama Canal Zone and the Oligocene or Miocene species *N. maoensis* and *N. aequus* Rathbun, 1920, from the Dominican Republic, all described from more or less fragmentary fingers or chelae, show only a casual resemblance to either *N. reedi* or *N. norvegicus*, and hence are of questionable identity. *N. shastensis* Rathbun, 1929, from the Cretaceous of California appears referable to the genus *Hoploparia* McCoy. The short, stout fingers of *N. americanus* Rathbun, 1935, from the Cretaceous of Texas, are quite unlike those of *N. norvegicus* or any of the known members of *Metanephrops* (the fingers of *Nephrops reedi* are imperfect).

Metanephrops motunauensis sp. nov.

Text-figure 60, plates 22 & 23

Material

Seven specimens, six with all or part of the abdomen visible. Five specimens have the abdomen similarly sculptured and are thought to be female; one has the abdomen more complexly sculptured and is probably a male. Bruce (1965) described a comparable sexual dimorphism in M. neptunus.

The holotype ♀, C.M. zfc 201 and one paratype ♀, C.M. zfc 170 show most of the body and fragments of the pereiopods. The allotype ♂, C.M. zfc 202 has several abdominal segments, a portion of one uropod and most of the right first pereiopod visible. One paratype ♀, C.M. zfc 193 has the carapace, the anterior portion of the abdomen and the left and a fragment of the right first pereiopod exposed, and is associated with the fragmentary remains of a crab. One paratype C.M. zfc 40 is a carapace with the tip of the rostrum and the ventral and posterior margins damaged. Two paratypes ♀, C.M. zfc 134; ♀, zfc 183 show the abdomen with the first segment and portions of the telson and uropods eroded.

The matrix of all specimens is a grey calcareous siltstone. The exoskeleton is usually replaced by a brown phosphatic mineral, and occasionally by pyrite which also forms small crystalline aggregates and films adjacent to the fossil. In one instance (zfc 202) areas of the natural skeletal material showing traces of colouration are preserved. One specimen (zfc 40) is slightly compressed dorsoventrally while the others are all compressed laterally and are asymmetrically distorted or fractured.

The positioning of one of the more complete remains (zfc 170; Plate 23, Figure 1a) resembles that of the partly completed reptantian macruran moults illustrated by Hale (1927, fig.11) and Thomas (1966, pl.1, fig.2).

Thomas indicated that moulting occurred while the animal lay on its side. In the fossil exuviae the carapace has moved back towards the abdomen. Specimens zfc 40, zfc 134, zfc 183, and zfc 202 may also be parts of moults. The holotype zfc 201 and specimen zfc 193 show little displacement of the different parts of the body and are probably remains of dead animals.

Diagnosis

Anterior two thirds and lateral aspects of posterior third of carapace spinulose; dorsal aspect of posterior third smooth or finely granulate with a few scattered larger granules and spinules. Tergum of sixth somite of female abdomen with five spinules on each lateral aspect and three pairs of submedian spinules. Palms of first pair of pereiopods with a broad dorsal ridge ornamented by a dense band of spinules.

Remarks

The extant species here assigned to *Metanephrops* can be divided into four main groups (de Man, 1916; Yaldwyn, 1954; and later authors). These groups are characterized as follows:

Carapace smooth or finely granulate. Terga of second to fifth abdominal somites conspicuously furrowed with arched or oblique lateral grooves and a submedian pair of longitudinal grooves. Palms of chelae of first pair of pereiopods with prominent spinulose ridges; fingers slender, gently curved or nearly straight, carinate basally. *M. japonicus*; *M. andamanicus* (Wood-Mason, 1892); *M. sagamiensis*; *M. andamanicus* (*sensu* Holthuis, 1964).

Carapace finely granulate. Terga of abdominal somites not conspicuously furrowed. Palms of chelae of first pair of pereiopods with prominent spinulose ridges; fingers strong, with spinulose carinae. *M. rubellus*, *M. binghami*.

Carapace spinulose. Terga of second to fifth abdominal somites conspicuously furrowed, but without prominent submedian longitudinal grooves. Palms of chelae of first pair of pereiopods angulated or ridged dorsally, convex ventrally, and coarsely or finely granulate; fingers either strong, curved and feebly carinate, or slender, straight and rounded in section. *M. arafurensis*, *M. neptunus*, *M. australiensis*. The single known specimen of *M. arafurensis* is mutilated and lacks the posterior portion of the abdomen, the first pair of pereiopods and the antennal flagella.

Carapace smooth or finely granulate. Terga of second to fifth abdominal somites smooth or punctate, with or without a single transverse furrow interrupted medially. Palms of chelae of first pair of pereiopods weakly ridged, finely granulate; fingers slender, straight, rounded in section. *M. thomsoni*, *M. challengeri*, *M. sibogae*, *M. boschmai*, *M. sinensis*.

M. motunauensis resembles members of both the "*japonicus*" and "*arafurensis*" groups. *M. motunauensis* resembles *M. japonicus* and *M. andamanicus* in the form of the abdominal sculpture and in having prominent spinose ridges on the chelae of the first pair of pereiopods. It resembles *M. arafurensis* and *M. neptunus* in the general form of the abdominal sculpture and in having the carapace spinulose. The spinulation of the sixth abdominal tergum of *M. motunauensis* somewhat resembles that in *M. neptunus*, as illustrated on pl.XV of Bruce (1965), while the fingers of the first pair of pereiopods are quite similar.

M. motunauensis is readily distinguished from *M. japonicus* by the following characters:

(a) The anterior two thirds and the lateral aspects of the posterior portion of the carapace of *M. motunauensis* are spinulose. The carapace of *M. japonicus* is not spinulose.

(b) The fossil has four pairs of teeth on the postrostral ridges while *M. japonicus* has five.

(c) The submedian raised areas on the second to fifth abdominal terga of *M. motunauensis* are not further subdivided as in *M. japonicus*.

(d) Five spinules are situated on the lateral aspects of the sixth abdominal tergum in the fossil. Only a single spinule is situated in this position in *M. japonicus*.

(e) In *M. motunauensis* the median dorsal ridge on the palms of the first pair of pereiopods is ornamented by a dense band of spinules. The equivalent ridge on the chelae of *M. japonicus* bears a single row of spinules except near the distal end.

Clear differences between *M. motunauensis* and *M. andamanicus* are:

(a) The carapace of *M. andamanicus* is not spinulose.

(b) *M. andamanicus* has only three pairs of teeth on the postrostral ridges.

(c) The sixth abdominal tergum of the fossil has five spinules situated on the lateral aspects and three pairs of spinules positioned submedially. The same abdominal tergum in *M. andamanicus* has one spinule near the middle of the lateral margin and lacks paired submedial spinules.

(d) The median dorsal ridge on the palms of the first pair of pereiopods of *M. andamanicus* bears one or two rows of spinules, not a dense band of spinules as in the fossil.

The principal differences between *M. motunauensis* and *M. arafurensis* are:

(a) The dorsal aspect of the posterior third of the carapace of *M. motunauensis* is smooth or finely granulate with only a few scattered larger granules and occasional spinules. The same region in *M. arafurensis* is strongly spinulose.

(b) *M. arafurensis* has five pairs of spines on the postrostral ridges, not four as in the fossil.

(c) The inner lateral grooves on the second and third abdominal terga of *M. arafurensis* are directed obliquely downwards and forwards. The equivalent grooves on the same somites of *M. motunauensis* are arched upwards.

(d) On the third abdominal tergum of *M. arafurensis* no longitudinal submedian grooves are present as in the fossil.

The following main differences between *M. motunauensis* and *M. neptunus* may be noted:

(a) The dorsal aspect of the posterior two thirds of the carapace of *M. neptunus* is densely spinulose.

(b) The postrostral ridges bear only three pairs of teeth in *M. neptunus* and are divergent rearwards for most of their length, not slightly convergent as in the fossil.

(c) *M. neptunus* lacks the uppermost branchiostegal ridge present in the fossil.

(d) The second to fifth abdominal terga of *M. neptunus* have an additional pair of transverse grooves not present in *M. motunauensis*. Short submedian longitudinal grooves are developed only on the second and third abdominal terga of males of *M. neptunus*.

(e) The sixth abdominal tergum of *M. neptunus* apparently has a series of five or six submedian pairs of spinules, not three pairs as in *M. motunauensis*.

(f) The palms of the first pair of pereiopods of the fossil are elongate and have prominent spinulose ridges on the dorsal and ventral surfaces. In *M. neptunus* the palms are relatively short, convex ventrally and coarsely granulate.

M. motunauensis is clearly intermediate between the modern "*japonicus*" and "*arafurensis*" species groups, suggesting that these two sections had a common ancestry. Studies the author has made of other fossil Decapoda suggest that new species evolve from a single lineage at intervals of the order of 5-15 x 10^6 years. The relatively youthful geologic age of *M. motunauensis* (about 3 x 10^6 years) precludes it being directly ancestral to the "*japonicus*" and "*arafurensis*" groups as these each contain several quite distinct species. Rather the fossil is considered to have retained many of the characters of an earlier form near the ancestry of these two groups. Somewhat closer affinity between *M. motunauensis* and the "*arafurensis*" group is inferred from the incompletely spinulose carapace of the fossil.

Distribution and Evolution of *Metanephrops*

The geographic distribution of species of *Metanephrops* is summarized in Figure 61. The modern species have been taken at depths between 50 and 885 metres, the majority of records being deeper than about 150 metres (Figure 62). Typically the modern species are found on soft muds, and rarely sand, on the outer edge of the continental shelf and the upper part of the continental slope (see also Bruce, 1966). The matrix of the specimens of *M. motunauensis* also indicates a fine-grained substrate. The relatively limited occurrence, in the geological record, of exposed sediments deposited on the margin of the continental shelf and the upper part of the continental slope is the probable reason why only one fossil member of the genus is yet known.

Geographic records of several extant species and each of the four main species groups are widely scattered. However, recent systematic surveys in the South China Sea and investigations off New Zealand and Australia suggest species may be more widespread and abundant than indicated by the older records, and show that the distribution of single species is probably fairly continuous (Bruce, 1966).

The "*japonicus*" group seems the most widely distributed of the extant species groups. The distributions of the "*japonicus*" and "*thomsoni*" groups are apparently largely exclusive. Members of these two groups inhabiting the same or adjacent regions are found at similar depths; for example off the east coast of Asia and Japan *M. japonicus*, *M. sagamiensis*, *M. thomsoni* and *M. sinensis* are all known at depths within the range 100 to about 400 metres. Three of these species, *M. sagamiensis*, *M. thomsoni* and *M. sinensis* occur in the northern part of the South China Sea (Bruce, 1966, 1966a, 1966b). *M. thomsoni* is the most numerous species in this area. *M. sinensis* is almost equally abundant, but tends to be taken at greater depths than *M. thomsoni*, although both have been taken in the same trawl. It is suggested that a northwards invasion of species of the "*thomsoni*" group into the South China Sea may be actively displacing members of the "*japonicus*" group from the area. Similarly the ancestor of *M. challengeri* probably reached New Zealand in the late Tertiary and replaced the Pliocene *M. motunauensis*.

Members of the "*arafurensis*" group occupy part of the same region as the "*thomsoni*" group. The species of the "*arafurensis*" group are known at depths within the range 434-795 metres; *M. thomsoni*, *M. sinensis* and *M. sibogae* are not known deeper than 310-391 metres.

The American species occupy ranges fairly symmetrically positioned on either side of the equator. It seems possible that this resulted from splitting of a single species formerly occupying an equatorial range.

The inferred phylogenetic relationships of the different members of the genus are indicated in Figure 63. No direct ancestor to the genus is known. It is inferred from the large number of Indo-West-Pacific species that the genus originated in this province. The "*japonicus*" and "*arafurensis*" sections are suggested to be the oldest of the modern species groups as they include the most diverse species. *M. neptunus* is the most aberrant member of the "*arafurensis*" group. The American species seem most closely allied to the "*japonicus*" group (see also de Man, 1916: p.97); the carapace and first pair of legs are quite similar in these forms. *Metanephrops* possibly reached the Atlantic around southern Africa, but more probably migrated through Tethys prior to or during the Lower Miocene. The sea connection between the Indian and Atlantic Oceans through Tethys was lost in the late Lower Miocene (Ruggieri, 1967). The "*thomsoni*" group appears more closely allied to the "*arafurensis*" group and probably evolved from near the ancestor of *M. australiensis*, off northern Australia or in the Indonesian region, central to the present distribution of these two groups. Members of the "*thomsoni*" group and *M. australiensis* have the abdomen comparably furrowed and the first pair of legs extremely similar.

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