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Papers from the Conference on the Biology and Evolution of Crustacea

HELD AT THE AUSTRALIAN MUSEUM
SYDNEY, 1980

Edited by
JAMES K. LOWRY

The Australian Museum

Memoir 18

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FOREWORD

The first international conference on Crustacea to be held in Australia took place at the Australian Museum, Sydney in May 1980. More than 160 carcinologists from 15 countries attended. Ninety papers and posters were presented. In general the conference was concerned with the biology and evolution of Crustacea and papers were presented on evolution, physiology, community ecology, behaviour, biogeography, reproductive biology and taxonomy. The twenty contributions presented in this volume represent a cross-section of the papers presented at the conference.

The conference organisers were excited by its success and appreciate the efforts made by all who attended. We are particularly grateful to the Australian Museum Trust for financial support, to the Australian Museum Society for organising teas and lunches and to the New South Wales Department of State Fisheries for allowing us to use the FRV Kapala for a conference field trip to collect crustaceans.

J.K. Lowry
Editor

CONTENTS

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ALTERNATIVES IN MALACOSTRACAN EVOLUTION

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SUMMARY

The Malacostraca appear to have been derived from epibenthic ancestors with many caridoid features. Despite their very long palaeontological record the Phyllocarida differ in so many respects from the basic eumalacostracan morphological and functional plan that they are regarded as unlikely ancestors and more probably an early diverging branch.

The general morphology of the malacostracan cephalothorax and carapace is discussed and it is shown that the concept of a maxillary segment carapace common to all Crustacea is not valid. The malacostracan dorsal shield is produced by a fusion of terga and a free carapace fold is sometimes formed at its posterior margin.

Some functional systems of the various caridoid Malacostraca are discussed. Attention is drawn to the unsolved problem of secondary segmentation after the alleged loss of a cephalothorax, e.g. in the Syncarida.

The unsatisfactory status of the diagnosis of the superorder Peracarida is pointed out and a revision recommended.

Introduction

Since Calman (1909) presented his views on the 'caridoid facies' and the 'generalised malacostracan' the position of a crustacean of this general type as ancestral to the Malacostraca has remained practically unchallenged, accepted also by more recent revisors (Siewing, 1956, 1963; Fryer, 1964). Nevertheless certain observations, old and new, are not easy to reconcile with this traditional concept of the ancestral caridoid.

Similarly, the higher systematics of the Malacostraca proposed by Calman (l.c.) has remained unshaken and as far as its fundamentals are concerned is likely to remain so. Recently, however, the position of the Hoplocarida within the framework of this system has been questioned by Schram (1969). The current definition of the Peracarida, too, appears more and more unsatisfactory (Dahl and Hessler, 1982).

The aim of the present paper is to focus attention on a number of areas within which a fresh evaluation of current interpretations appears desirable.

Diagnostic features of the Malacostraca

Malacostracans have stalked eyes with a unique neuronal pattern, biramous antennules, tagmatisation of the postcephalic body, fixed number of segments, fixed position of gonopores, respiratory thoracopod epipods, and natatory pleopods. These characteristics are shared by less derived members of all four eumalacostracan superorders and by the leptostracans. The position of the Malacostraca as a natural taxon is secure.

The Eumalacostraca are further defined by the presence of ambulatory endopods and natatory exopods on the thoracopods, as well as by fan-shaped uropods.

Many of the traits enumerated above are more or less typically caridoid. There can be little doubt that Crustacea with these basic morphological traits were originally epibenthic swimmers and walkers.

Cephalothorax and carapace in the Malacostraca

The presence of a cephalothoracic shield is a prominent feature of the typical caridoid. This shield is often referred to as the 'carapace' but this is not wholly correct.

The carapace, by definition, is a fold growing out from the posterior border of the maxillary segment. It is to be found in its typical form in the Notostraca. In *Triops* it starts growing in connection with metamorphosis towards a benthic mode of life. It grows backwards more rapidly than the body itself and soon covers most of it. However, the carapace is not attached to the maxillary segment in all non-malacostracans. In the Cladocera one, two, or, in *Leptodora,* more segments are fused to the head, and the carapace fold is attached to the last of these segments. Similar conditions appear to prevail in ostracods.

In the Malacostraca the formation of branchiostegal folds always precedes possible carapace formation. Lateral folds grow out from the cephalon and thorax of the embryo (Manton, 1934; further instances in Anderson, 1973). The folds grow out laterad and ventrad, and in the peracarids, where they are always short, sometimes also posteriad beyond their point of attachment to the body wall.

These folds form the branchiostegal chambers. Generally within these chambers segment borders disappear and the segments fuse to become integrated into the cephalothorax. In the Leptostraca, however, where the large folds envelop not only the body but also the thoracopods, lateral segment borders are retained. Dorsad to the folds the tergal parts fuse and thus complete the cephalothorax.

Sometimes, in the Leptostraca, certain Peracarida, and larvae of stomatopods and penaeid decapods, there are not only lateral branchiostegal folds but also continuous with them a transversal dorsal fold projecting posteriad over a varying number of segments. This dorsal part of the fold is attached to the posterior margin of the dorsal shield formed by the fused terga. Consequently the position of this attachment varies from group to group—in the Mysidacea, where a variable number of segments are included in the dorsal shield, even from genus to genus. Considering what has been stated above concerning carapace attachment in the non-Malacostracan groups, this structure can also be regarded as a carapace.

In decapods the fused dorsal shield comprises the entire thorax, in the peracarids a varying but lower number of segments, in *Nebalia* only the first thoracic segment. No adult malacostracan has a carapace attached to the maxillary segment, not even the Leptostraca, although this is stated in practically every text-book. Only stomatopod larvae are reported to have a carapace fold attached to the maxillary segment (Calman, 1909).

It is also frequently stated that in malacostracans with a dorsal shield this shield is formed by the fusion of the maxillary segment carapace to the dorsum.

This is not so. A histological investigation of representatives of leptostracans, mysids, euphausians, and decapods at various stages of their development has nowhere revealed any sign of integumental folding in the dorsal shield region. As already stated the dorsal shield is formed by a fusion of the segments involved and this gives as its result a simple and continuous dorsal body integument.

The alleged omnipresent maxillary carapace has profoundly influenced the discussion of malacostracan derivation and evolution but can and should now be relegated to history. What remains is a tendency among the Malacostraca to form thoracic shields and folds fulfilling various important functions. In the Malacostraca they are generally part of the respiratory system, and their high degree of development in pelagic forms indicates little-investigated hydrodynamic functions.

Phyllocarida and Eumalacostraca

Mainly owing to their antiquity the Phyllocarida have often been supposed to be ancestral to the Eumalacostraca. However, the phyllocarid functional pattern with non-locomotory respiratory and filtering thoracopods, absence of an independent cephalic feeding mechanism, and, throughout the known record, an abdomen of a very special type, differs very much from any known eumalacostracan pattern and indicates differentiation in a diverging direction. Preliminary observations on the Devonian *Nahecaris* from an investigation carried out together with Professor Stürmer and Dr Bergström give a wealth of new data but no promise of information on the origin of the Eumalacostraca.

Following Calman (1909) I regard the Phyllocarida as an early diverging branch of the Malacostraca, and with Burnett and Hessler (1973) I do not find a separate phyllocaridan derivation of the Hoplocarida probable. In this connection I wish to stress the importance of the new results published by Schram (1978, 1979) which indicate that eumalacostracan radiation took place much earlier than generally presumed.

Eumalacostracan caridoids

Typical caridoid forms are found among eucarids and peracarids and as larvae in the Hoplocarida. Also the anaspidacean syncarids, although lacking a branchiostegal cephalothorax, have a general resemblance to caridoids (Calman, l.c.; Manton, 1930). Between the various caridoid types, however, differences exist which are probably of evolutionary significance.

Eucarida

The eucaridan cephalothorax comprises the whole or nearly the whole thorax. In the Euphausiacea locomotion is effected by pleopod and exopod swimming, partly integrated with respiratory ventilation. The respiratory epipods lie outside the non-respiratory branchiostegal chambers. The function of the cephalothoracic shield is unknown but probably hydrodynamic. In caridoid decapods swimming is effected by the pleopods and respiration by highly developed epipods enclosed in branchiostegal chambers and ventilated by the maxillary scaphognathite. Thus segregation between locomotion and respiratory ventilation is complete.

Peracarida

The cephalothorax is short, comprising at most 4 segments (certain Cumacea), generally fewer. A free carapace fold sometimes occurs. The Lophogastrida are unique within the group in possessing a full set of thoracic epipods. The function of their exceptionally large carapace seems to be the enclosing of these epipods within the branchiostegal chambers so that ventilation by means of the maxilliped epipod may become effective. Swimming in the lophogastrids is effected by pleopods and exopods. A branchiostegal respiratory system is found also in Mysidacea (s.s.), Cumacea, Tanaidacea, Spelaeogriphacea, and Thermosbaenacea. In connection with a more benthic life the pleopods tend to become reduced, especially in the females. Natatory exopods are found in the epibenthic—pelagic mysids. Of thoracopod epipods only the ventilatory and respiratory maxilliped endopod is retained, supplemented by a respiratory branchiostegal wall and sometimes by respiratory exopods. However, there are strong reasons to presume that in the peracarids it is the proximal epipod of certain female thoracopods that has been transformed into an oostegite.

The divergent functional and morphological patterns of isopods and amphipods will be discussed in the next section.

Syncarids

In the paleocaridacean syncarids all eight thoracic segments were free (Brooks, 1969). Also the Anaspidacea appear to be in many respects very primitive. Manton (1930) noted the surprisingly high degree of locomotory integration between thorax and abdomen, which she tentatively interpreted as a sign of incomplete tagmatisation. In any case it is unique within the Malacostraca. Respiration is effected by means of double pairs of epipods, ventilated by autochonous vibration and exopod beating. At least some exopods are also respiratory.

The peracarid concept

Within the Peracarida all the orders except the Isopoda and Amphipoda represent a natural group centred around a functional model which recurs in easily recognisable forms within the various orders, and the main characteristics of which were described in the previous section.

The lophogastrids, probably representing a separate order, stand a little apart from the other members of this group. Their internal morphology is characterised by many primitive traits (Siewing, 1956), and they have a very peculiar type of mandible (Dahl and Hessler, 1982), thoracic epipod respiration, pleopod and exopod swimming, remnants of a seventh abdominal segment, and a telson with what appears to be remnants of a furca. Probably they were at a very early stage adapted for a pelagic mode of life, and within the peracarid assemblage they may possibly link up more closely with the pygocephalomorphs than with the more derived orders.

Mysids are generally supposed to have descended from lophogastrids, but morphologically they are not very close to them, and the tendency to reduction of pleopods points to a more benthic mode of life, although they are in many respects less modified in this direction than the other orders.

The isopods have traditionally been considered to form the terminal link in an evolutionary chain going from mysids via tanaids. This, however, demands the loss in isopods of the peracarid respiratory system and its replacement by pleopod respiration, the retention of natatory pleopods, and, in connection with the loss of the branchiostegal cephalothorax, the establishment of a secondary segmentation.

The amphipods have the thoracopod epipod respiration, which is probably plesiomorphic in malacostracans, and lack a maxilliped epipod. They have developed a unique ventilation system, integrated with pleopod swimming, and they have a subtagmatisation of the abdomen without counterpart among the Malacostraca. A derivation from the characteristic peracarid model discussed above offers difficulties. The thoracic respiratory epipods remain in what must be considered to be their original position—identical with that found in the Anaspidacea—and have not been displaced ventrally as suggested by Grindley and Hessler (1971). Considering this and the absence of a maxilliped epipod it is very difficult to see any functional reason for the existence of a peracarid type cephalothorax-carapace and its subsequent disappearance. Hessler (in press) in his comprehensive investigation of the walking mechanisms of the Eumalacostraca found a general peracarid pattern in the hinge structures. But in this respect also those of the amphipods stand somewhat apart and permit different interpretations. The current definition of the Peracarida appears far from satisfactory and a revision of the higher systematics of the group appears desirable. It is not impossible that such a revision may lead to a subdivision or even a splitting of the superorder.

The direction of eumalacostracan evolution

What one is tempted to call the most perfect manifestations of the caridoid facies as we see them in decapods, euphausians, and certain peracarids display a high degree of outward conformity. However, if we look into the functional systems involved in and partly responsible for the establishment of these manifestations we find that they are by no means uniform. If derived from a basic caridoid stock they must have diverged fairly early. The best argument for the existence of such a basic caridoid stock appears to be provided by the Euphausiacea, retaining basic modes of locomotion and respiration and having a cephalothorax without recognised functional differentiation.

This, however, leaves the Syncarida unexplained. As pointed out above they appear to be plesiomorphic with respect to segmentation, locomotion, respiration, respiratory ventilation, and, possibly, tagmatisation. At the same time recent results presented by Schminke (1978) indicate a close relationship between syncarids and penaeid decapods. Theoretically it is not very difficult to visualise the evolutionary steps by which the various caridoid types could have been derived from a syncarid-type ancestor. Reversing the process appears a good deal more difficult and once more forces us to solve the problem of the loss of a cephalothorax and the establishment of a secondary segmentation. In connection with the Syncarida such processes have repeatedly been referred to (among others by Manton, 1930; Siewing 1958, 1963; Hessler and Grindley 1973). With respect to amphipods Bousfield (1978) also considered a derivation from carapace-bearing ancestors as the most likely alternative, and this confronts us with the same problem. Siewing (1958) expressed the opinion that the establishment of a secondary segmentation is a much more difficult problem than the loss of segmentation, but nobody has really seriously faced it. Yet this is what we have to do if the concept of the caridoid ancestor shall be either vindicated or rejected and if, on the whole, we wish to understand the course of malacostracan evolution.

Conclusions

In concluding this brief review it appears to the writer—who has to some extent deliberately acted the part of the *advocatus diaboli*—that, although many problems concerning crustacean relationships have found solutions, we have during a long time tended to bypass or sweepingly explain away some of the most crucial problems inherent in the study of malacostracan evolution.

Attention has been drawn to some of the alternatives with which we have to deal. Many of the problems have become apparent during an attempt to think in terms not only of comparative anatomy, but also of functional systems and the integration and segregation of such systems. This seems to be a tool useful not only in the identification but also in the solution of problems.

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CATOMERUS POLYMERUS AND THE EVOLUTION OF THE BALANOMORPH FORM IN BARNACLES (CIRRIPEDIA)

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SUMMARY

On the basis of comparative anatomy, Darwin proposed that the catophragmid *C. polymerus*, representing the basic form among balanomorphs, had evolved from a scalpellid lepadomorph ancestry. This hypothesis has since been supported by fossil evidence, but has not been tested by the techniques of comparative functional morphology.

Functional studies of *C. polymerus* and *Calantica villosa* have now shown that an evolution of catophragmid balanomorphs from calanticine scalpellids is functionally feasible, upholding Darwin's proposal. *C. polymerus* retains the scalpellid mode of planktivorous extension feeding, except for further modification of the first two pairs of cirri as short maxillipeds acting in forward food transfer in a limited space. The basic adaptive significance of the foreshortened form and flattened operculum of *C. polymerus* lies in allowing a species with this mode of feeding to inhabit a high energy intertidal environment. Protection against certain kinds of predation may also have been important.

The development of the opercular valves from capitular plates and their changed orientation relative to the wall is accommodated by further modification of a hinge mechanism already present in calanticine scalpellids. The closure mechanism of the operculum involves supplementation of the action of the adductor scutorum by the downward pull of large tergal depressor muscles, evolved as a modification of the peduncular longitudinal muscles of calanticines.

Massive tergal and small scutal depressor muscles, a basic balanomorph condition, are functionally associated with a large prosoma and paired branchiae occupying the rostral part of the limited mantle cavity.

Introduction

Catomerus polymerus (Darwin) is a common balanomorph barnacle on the rocky shores of southeastern Australia (Pope, 1965), easily distinguished by its eight wall plates supplemented by several concentric whorls of marginal plates (Fig. 1a). The recent revision of the Balanomorpha by Newman and Ross (1976) follows Utinomi (1968) and places *C. polymerus* in the family Catophragmidae of the superfamily Chthamaloidea. The species was first described by Darwin (1854) in his monograph on the Balanidae, from specimens collected from Twofold Bay, N.S.W. Darwin placed his specimens in the genus *Catophragmus,* previously erected by Sowerby (1826) for a similar animal, *Catophragmus imbricatus* Sowerby, known as two shells from Antigua in the West Indies in the collections of the British Museum. Pilsbry (1916) with more material of *C. imbricatus* at his disposal from Bermuda, recognised a difference between the two species sufficient to require transfer of *C. polymerus* to another genus, which he named *Catomerus.* A difference already noted by Darwin, is the presence in *C. imbricatus* of a pair of caudal appendages, absent in *C. polymerus.* The distinction between the two is otherwise minor, comprising slight differences in the operculum and basis. In a personal communication, W.A. Newman writes "I have despaired of finding much if any differences in the appendages between the two." At the same time, it has been recognised recently that *C. imbricatus* is now confined to the tropical W. Atlantic (Antigua and Bermuda), while the animals on the other side of the isthmus, in Panama and Costa Rica, are a distinct species, *C. pilsbryi* Broch (Southward and Newman, 1977).

The Catophragmidae also includes another surviving form, *Chionelasmus darwini* (Pilsbry), which apparently has a disjunct distribution, Hawaii and New Zealand in the Pacific Ocean and the Rodriguez

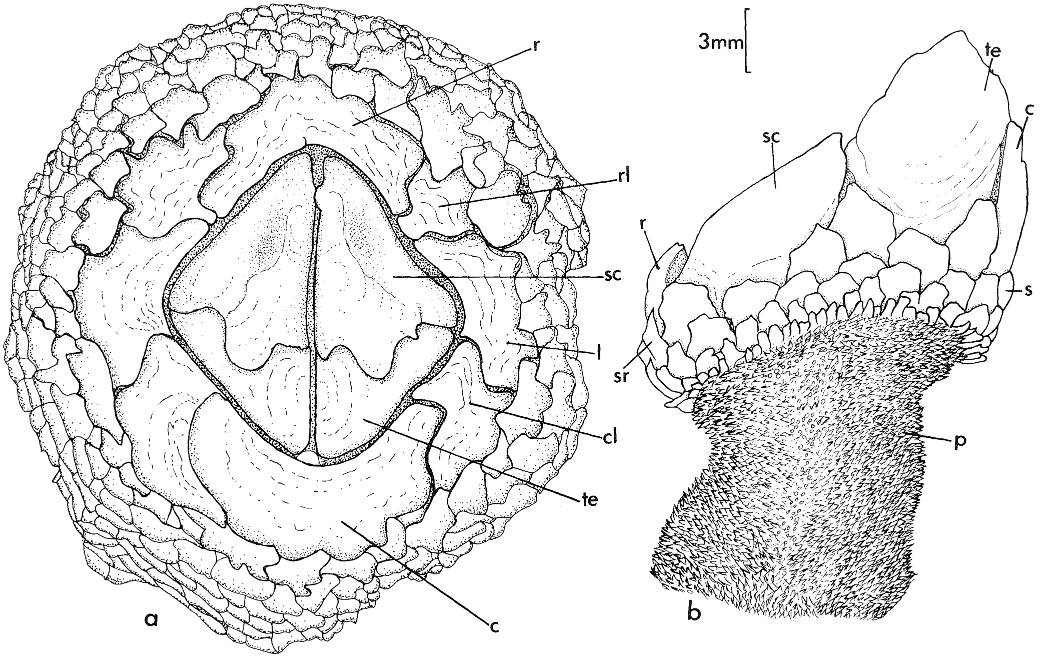

Fig. 1. **a,** *Catomerus polymerus,* apical view. **b,** *Pollicipes polymerus,* right lateral view. *c,* carina; *cl,* carinolateral; *l,* lateral; *p,* peduncle; *r,* rostrum; *rl,* rostrolateral; *s,* subcarina; *sc,* scutum; *sr,* subrostrum; *te,* tergum.

Islands in the Western Indian Ocean, as a benthic shelf form at 450–460 m (Stanley and Newman, 1980). *Chionelasmus* is more advanced than *Catophragmus* or *Catomerus* in some features of its carapace. The wall plates are 6 in number, as in most balanomorphs, and there is only a single whorl of supplementary plates outside the primary wall plates. The general anatomy of the body and limbs, however, remains catophragmid.

Catomerus polymerus is therefore a typical representative of the Catophragmidae. Darwin, in a delightful example of his thinking in evolutionary terms, recognised immediately the phylogenetic importance of this animal, which "forms in a very remarkable way the transitional link between" the lepadomorphs and the balanomorphs, "for it is impossible not to be struck with the resemblance of its shell with the capitulum of *Pollicipes*" (see Fig. 1b). "In *Pollicipes,* at least in certain species, the scuta and terga are articulated together—the carina, rostrum and three pairs of latera, making altogether eight inner valves, are considerably larger than those of the outer whorls—the arrangement of the latter, their manner of growth and union,—all are as in *Catophragmus.* If we, in imagination, unite some of the characters found in the different species of *Pollicipes,* and then make the peduncle so short (and it sometimes is very short in *P. mitella*) that the valves of the capitulum should touch the surface of attachment, it would be impossible to point out a single *external* character by which the two genera in these two distinct families could be distinguished."

While Darwin went on to recognise that there were some fairly major internal differences, especially in the arrangement of the mantle musculature, that he was unable to explain, he saw *Catomerus* not only as an indicator of a scalpellid ancestry for the balanomorph form, but also as a form ancestral to other balanomorphs. "Considering the whole structure, external and internal, of *Catophragmus,* with the great exception of the exterior whorls of valves, there is hardly a single generic character by which it can be separated from *Octomeris* and *Pachylasma*"; and the generalised position of *Octomeris* and *Pachylasma* at the base of the balanomorph stock continues to be recognised to this day (Newman and Ross, 1976).

Darwin, then, presented a hypothesis of the origin of the Balanomorpha—that they had evolved from a scalpellid ancestry via forms represented today by the catophragmids, which in turn gave origin to the other balanomorphs.

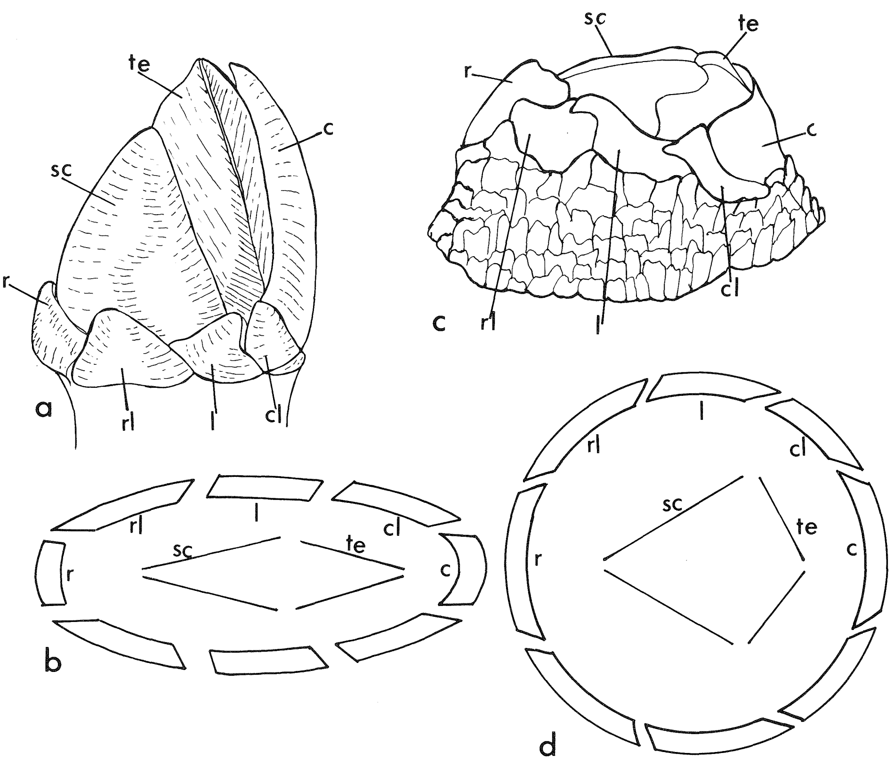

Fig. 2. **a**, *Scillaelepas dorsata*, right lateral view. **b**, *S. dorsata*, plan of capitular plates. **c**, *Catomerus polymerus*, right lateral view. **d**, *C. polymerus*, plan of wall plates. (From Newman, Zullo and Withers, 1969, reproduced with permission, courtesy of the Geological Society of America and University of Kansas.) *c*, carina; *cl*, carinolateral; *l*, lateral; *r*, rostrum; *rl*, rostrolateral; *sc*, scutum; *te*, tergum.

In the years since 1854 this hypothesis, based on comparative anatomy, has gained further support from fossil evidence. Withers (1935) described from the Cretaceous of Sweden a fossil catophragmid, *Pachydiadema cretaceum*, which remains the only known Mesozoic balanomorph. This discovery placed the catophragmids chronologically at the base of balanomorph evolution in the later Mesozoic, a time of abundant and diverse scalpellids (Newman, Zullo and Withers, 1969). *P. cretaceum*, furthermore, shows opercular features more like those of scalpellids than the modern catophragmids, which can now be recognised as relicts of a family of once widespread distribution (Stanley and Newman, 1980). Newman *et al.* (1969) following Aurivillius (1894), developed the idea of a scalpellid ancestry further in a comparison (see Fig. 2) of the plate arrangements of *C. polymerus* and the Eocene calanticine *Scillaelepas dorsata* (Steenstrup). Allowing for only a minor modification of the position of the laterals in relation to the rostrolaterals and carinolaterals, the arrangement of the capitular plates in *C. dorsata* is one which can be easily envisaged, with foreshortening of the stalk, to have become modified to that of the wall plates of *C. polymerus*. Since *Scillaelepas* and *Calantica* are thought to be central and early evolved genera within the calanticine scalpellids, first appearing in the Upper Jurassic (Newman, 1979), Darwin's hypothesis gains further support from this evidence, as it does from the cirral and mouthpart anatomy of the two groups. Pollicipoid scalpellids, including calanticines and pollicipines (Zevina, 1978), show some modification of the first and to a lesser extent the second pair of cirri as maxillipeds (Figs 3a, 3d), and have a characteristic setation of the four posterior pairs of cirri (Fig. 4b). Each cirral segment carries several pairs of long setae anterolaterally and has a bunch of short, forwardly projecting setae between them on the anterior face of the segment. *C. polymerus* shares this feature in the setation of the four posterior pairs of cirri (Fig. 4a), but it exhibits a greater modification of the first two pairs (Figs 3b, 3c) as short maxillipeds (Darwin, 1854; Pope, 1965). A striking similarity also attends the

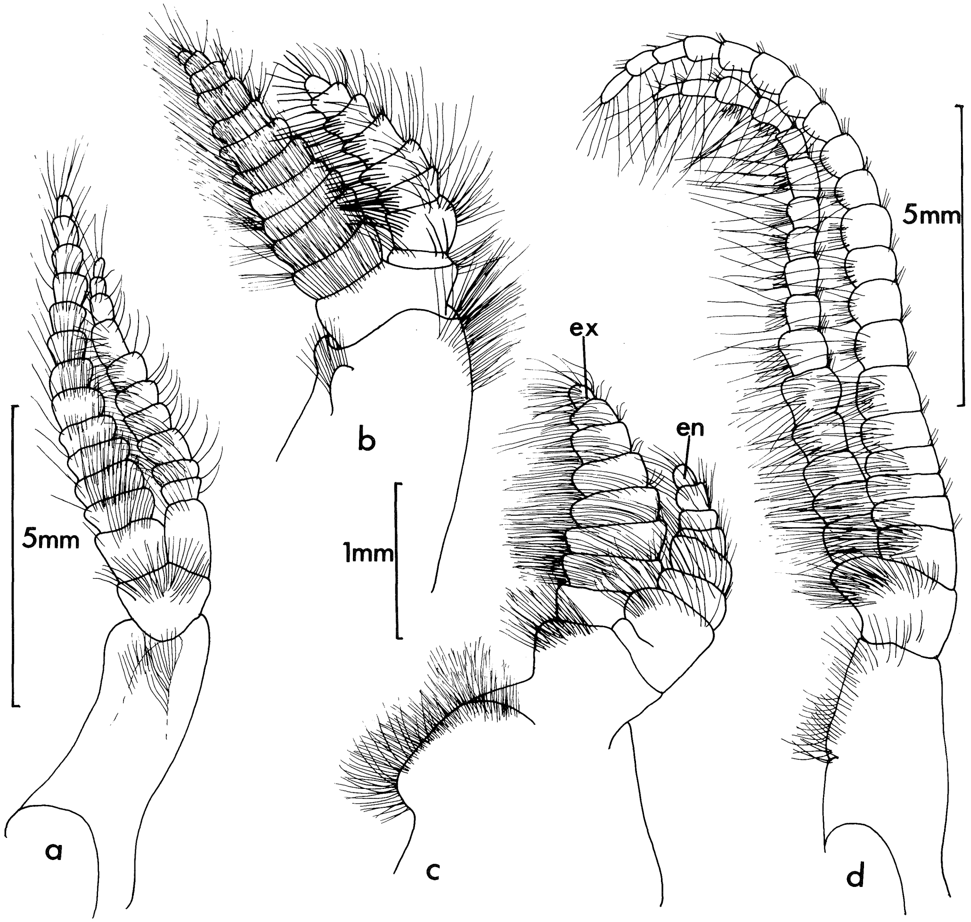

Fig. 3. **a**, Left cirrus I of *Calantica villosa,* median view. **b**, Left cirrus I of *Catomerus polymerus,* median view. **c**, Left cirrus II of *C. polymerus,* median view. **d**, Left cirrus II of *C. villosa,* median view. *en,* endopod; *ex,* exopod.

oral cone and mouthparts (Fig. 5) (Darwin, 1854; Pilsbry, 1916; Nilsson-Cantell, 1926; Pope, 1965; Newman and Ross, 1976; Foster, 1978). The labrum is bullate. The palps are simple, and setose mainly at the tips. The mandibles are tri- or quadridentoid, with a well developed incisor tooth and a strong, setose or pectinated molar process. The maxillules have a large seta on the lateral angle, a fringe of numerous marginal setae, and some development of a double prominence at the median angle. The maxillae are bilaterally flattened, with a fringe of setae around the angulate margin. The mouthparts of *C. polymerus* are more strongly toothed and setose in general than those of *Calantica* or *Scillaelepas,* but the anatomical resemblance between the two types of oral cone is striking and undeniable. Cirral and mouthpart anatomy therefore accord with the idea of a scalpellid ancestry for catophragmids.

Since catophragmids show so much evidence of being foreshortened descendants of calanticoid scalpellids, originating during the Mesozoic, what is the adaptive significance of the foreshortened form? Commonsense would suggest an adaptation to rocky, exposed, intertidal habitats and this view has been maintained from Darwin to the present day. The catophragmid facies, according to Newman and Ross (1976), was apparently an adaptation to high energy conditions along the shore. In terms of the protective modification of the closable carapace, this interpretation is appropriately functional. It is also supported by the fact that balanomorphs have become extraordinarily diverse and successful in the littoral environment, in a Tertiary radiation that has its zenith in the present day, whereas the lepadomorphs

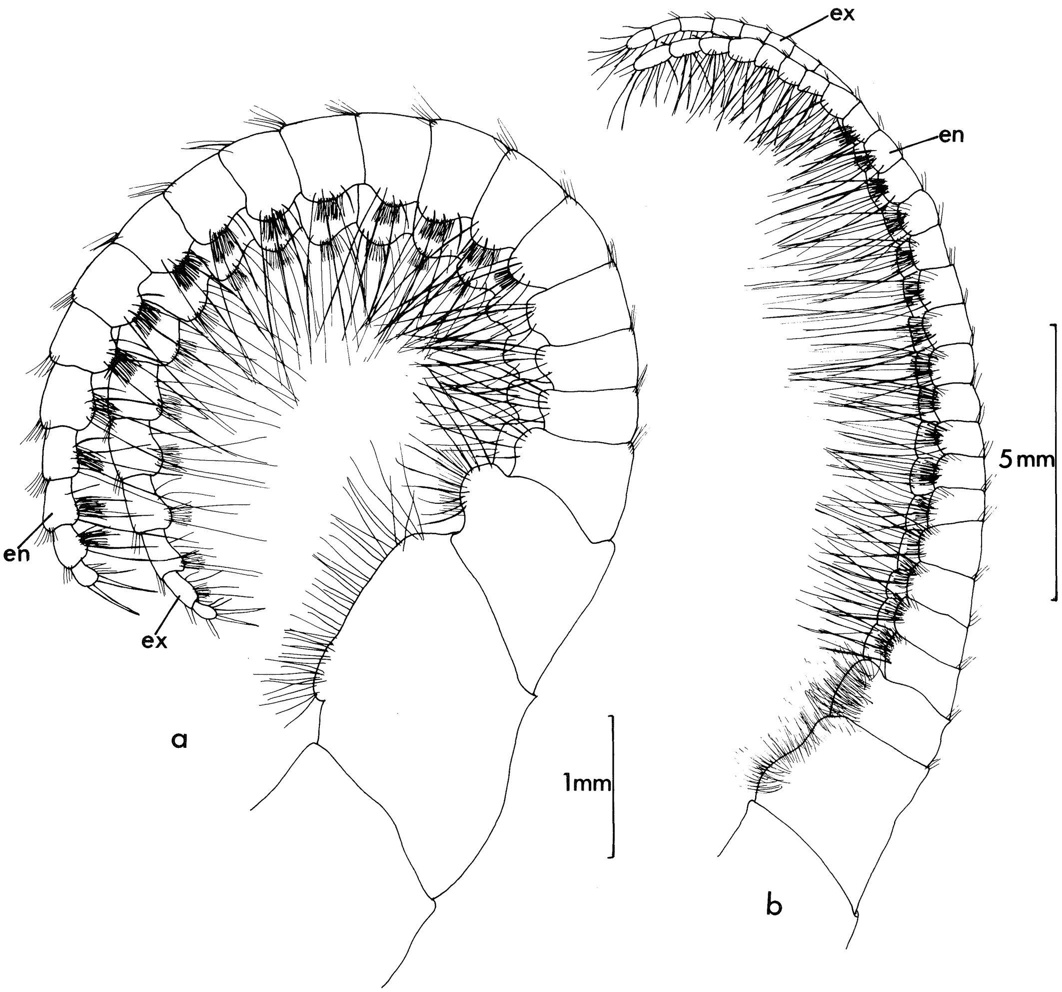

Fig. 4. **a,** Right cirrus IV of *Catomerus polymerus,* lateral view. **b,** Left cirrus IV of *Calantica villosa,* median view. *en,* endopod; *ex,* exopod.

have penetrated this environment only sporadically. Intertidal lepadomorphs are either cryptic, like *Ibla quadrivalvis* Cuvier (Fig. 6a) and *I. cumingi* Darwin, or armour-plated in shaded habitats, like *Pollicipes polymerus* J.B. Sowerby (Fig. 1b) and *Calantica villosa* (Leach) (Fig. 6b), or functionally convergent with balanomorphs, like *Calantica spinosa* (Quoy and Gaimard). The latter species, occurring mid-tidally on exposed rocks in New Zealand, is short and squat, with a reduced capitulum and an exceptionally thick and tough integument on the pedicel (Fig. 6c).

Accepting the assumption that the balanomorph form originated as an intertidal adaptation, and recognising that the anatomical modifications of catophragmids as compared with scalpellids are post-settlement modifications (basically, the form in adult barnacles is established through developmental events which begin *after* settlement of the cyprid larva has occurred), the calanticoid-catophragmid evolutionary hypothesis raises a number of questions. First, what is the major thrust of the adaptation, functionally? Is it trophic, or protective, or both? Protection in this context encompasses resistance both to high energy water movements and to the desiccation resulting from aerial exposure. Secondly, if this question can be resolved satisfactorily, what functional modifications of structure were involved

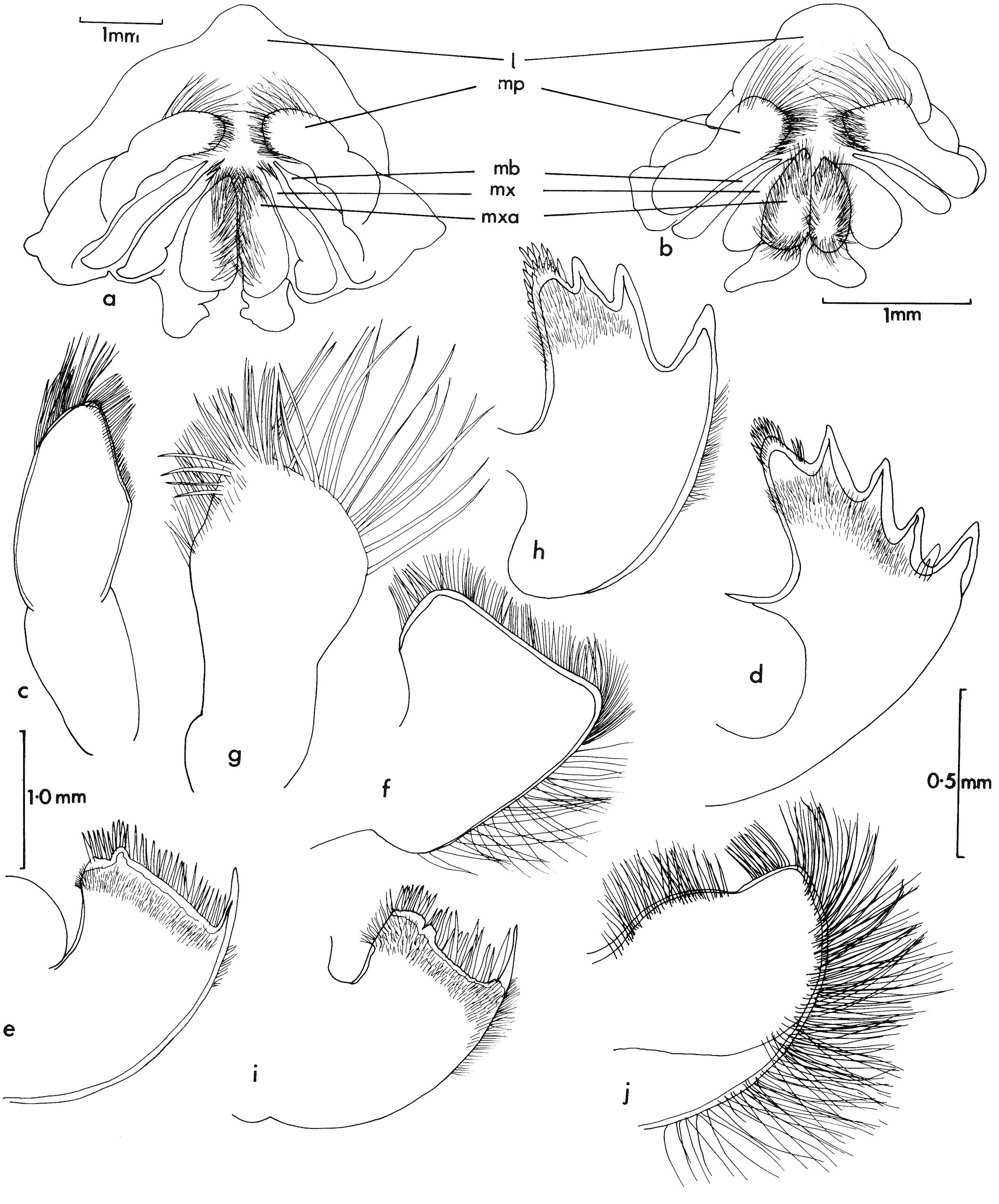

Fig. 5. **a,** Oral cone of *Calantica villosa,* posterior view. **b,** Oral cone of *Catomerus polymerus,* posterior view. **c–f,** the mouthparts of *C. villosa,* right side, lateral view (**c,** mandibular palp; **d,** mandible; **e,** maxillule; **f,** maxilla. The scale of these diagrams is indicated on the left of the figure). **g–j,** The mouthparts of *C. polymerus,* left side, median view (**g,** mandibular palp; **h,** mandible; **i,** maxillule; **j,** maxilla. The scale of these diagrams is indicated on the right of the figure). *l,* labrum; *mb,* mandible; *mp,* mandibular palp; *mx,* maxillule; *mxa,* maxilla.

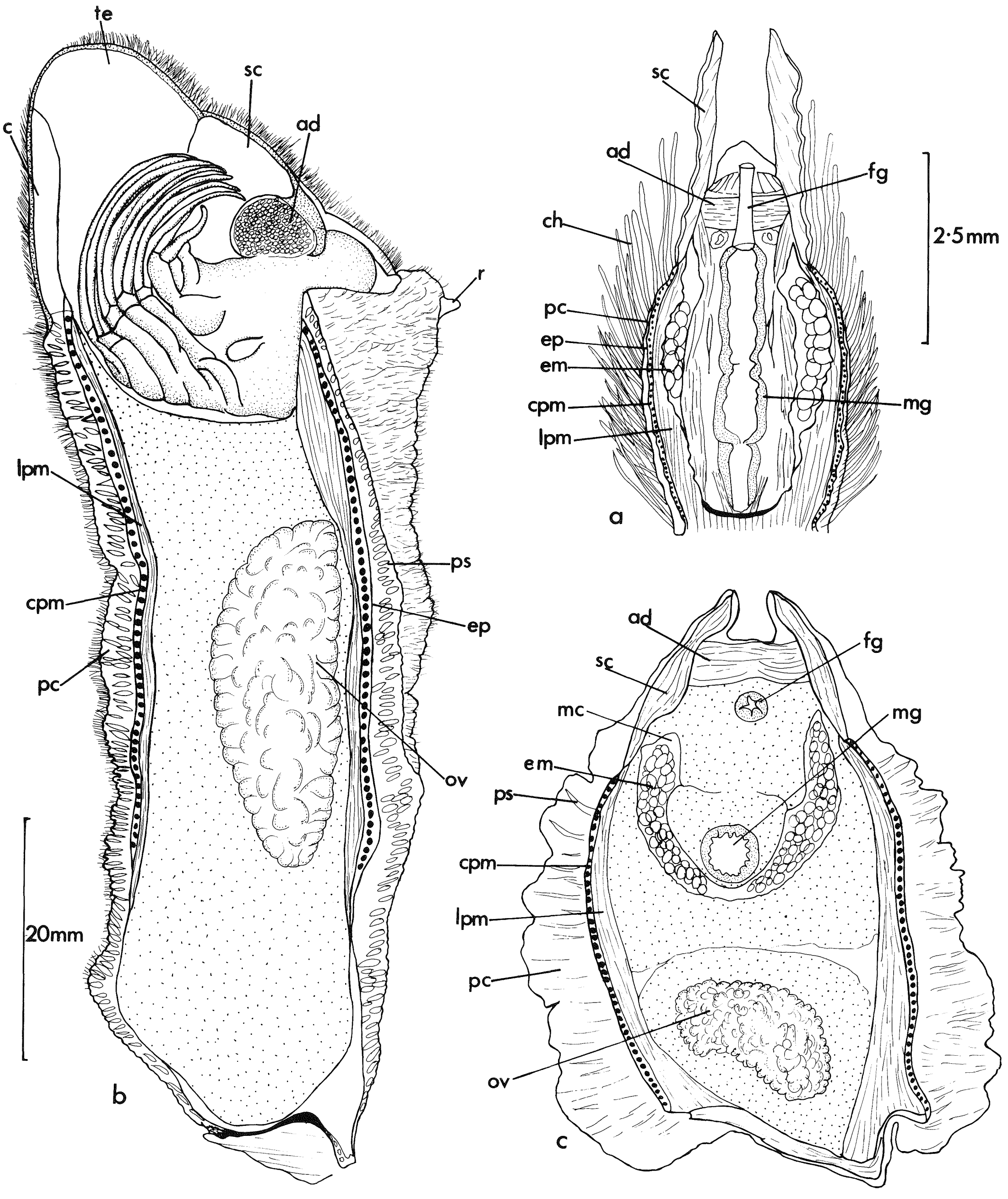

Fig. 6. **a,** Longitudinal frontal section through the apical half of *Ibla quadrivalvis.* **b,** Longitudinal sagittal section through *Calantica villosa.* **c,** Longitudinal frontal section through *Calantica spinosa. ad,* adductor scutorum; *c,* carina; *ch,* cuticular hair; *cpm,* circular peduncular muscle; *em,* embryos; *ep,* surface epithelium; *fg,* foregut; *lpm,* longitudinal peduncular muscle; *mg,* midgut; *ov,* ovary; *pc,* peduncular cuticle; *ps,* peduncular spine; *r,* rostrum; *sc,* scutum; *te,* tergum.

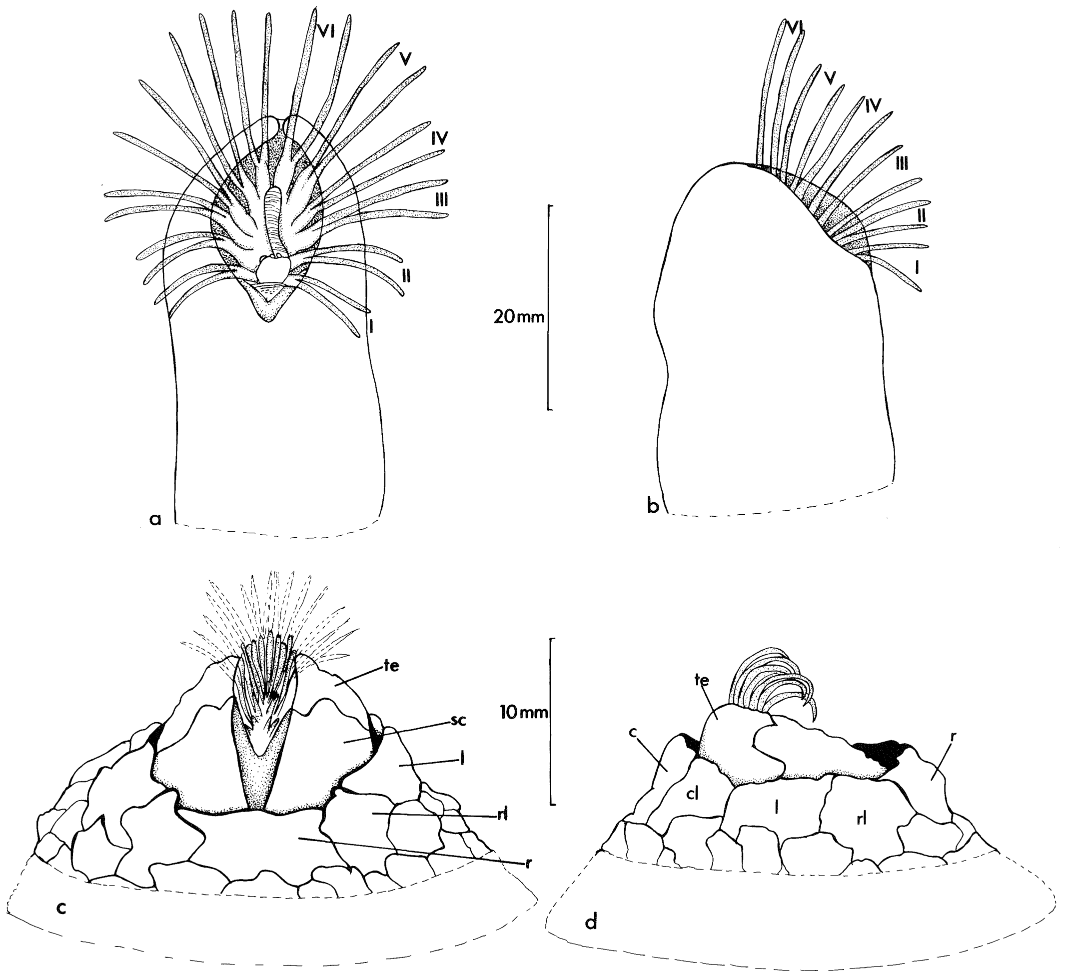

Fig. 7. **a** and **b**, Rostral and left lateral views of *Calantica villosa* during cirral extension. **c** and **d**, Rostral and left lateral views of *Catomerus polymerus* during cirral extension. I-VI, cirri I-VI; *c,* carina; *cl,* carinolateral; *l,* lateral; *r,* rostrum; *rl,* rostrolateral; *sc,* scutum; *te,* tergum.

in the transformation, through time, of stalked barnacles into sessile barnacles? In order to answer these questions, it is necessary to have some understanding of the functional morphology of both types of animal.

Functional morphology of *Catomerus polymerus*

Structure and function have been explored to some extent in the Scalpellidae, though very little in the calanticoids until now, but the catophragmids have never been examined in a functional way. The results reported in the following lines were obtained through an investigation of specimens of *C. polymerus* collected from the rock platform at Harbord, N.S.W. during 1978 and 1979 and examined by the methods reported in previous papers (Anderson, 1978, 1980a, b, 1981). Similar observations on specimens of *Calantica villosa* collected at Warrington, Otago, New Zealand in January 1979 provided a supplement to previous knowledge of the functional morphology of pollicipoid scalpellids and a basis for comparison with *C. polymerus.*

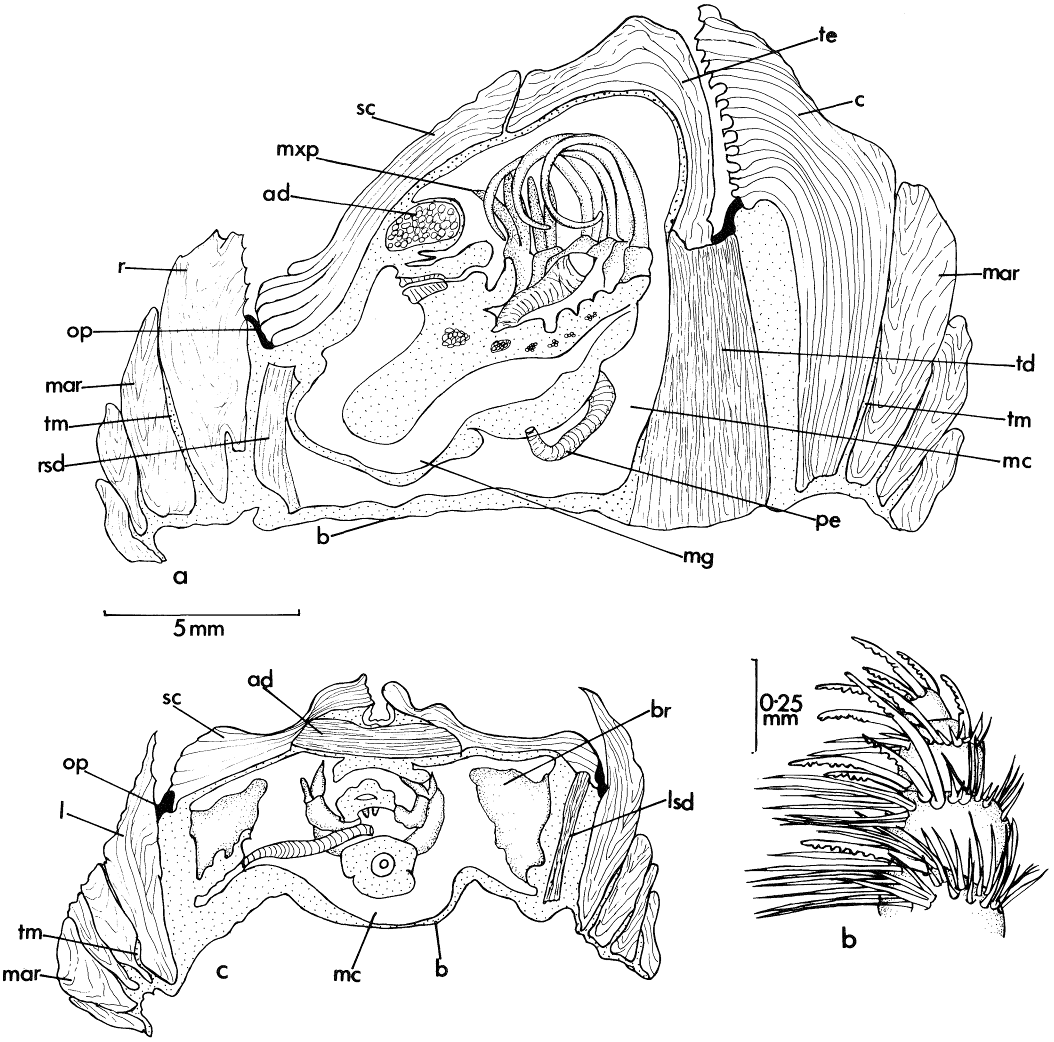

Fig. 8. **a**, Sagittal section through a decalcified specimen of *Catomerus polymerus*. **b**, Specialised setation at the tip of cirrus II of *C. polymerus*. **c**, Transverse section through a decalcified specimen of *C. polymerus* at the level of the adductor scutorum. *ad*, adductor scutorum; *b*, basis; *br*, branchia; *c*, carina; *l*, lateral; *lsd*, lateral scutal depressor muscle; *mar*, marginal wall plate; *mc*, mantle cavity; *mg*, midgut; *mxp*, maxilliped; *op*, opercular membrane; *pe*, penis; *r*, rostrum; *rsd*, rostral scutal depressor muscle; *sc*, scutum; *td*, tergal depressor muscle; *te*, tergum; *tm*, mantle tissue.

(a) Feeding

Feeding in scalpellids was described in detail for *Pollicipes polymerus* by Barnes and Reese (1959). Feeding in *Calantica villosa* is similar and so, judging by the brief comments provided by Batham (1946), is feeding in *C. spinosa*. All three species are extension-feeding planktivores, preying on small to moderate size plankton, mainly crustaceans, the remains of which can be easily identified in the stomach contents. The aperture being on the rostral margin of the capitulum, the long cirri are slowly extended and held as an apico-rostrally projecting fan, with the shorter cirri extending more laterally towards the basal end of the aperture (Figs 7a, 7b). Prey organisms are captured either by individual rami of the long cirri or, if larger, by the cirral net as a whole. The captorial cirri coil down and are cleaned off by the maxillipeds, which transfer the food to the mouthparts. Cirral extension is maintained for long periods provided there are water currents. In still water, the cirri are usualy withdrawn and the aperture closed, as is also the case when the animal is exposed to air. Withdrawal of the cirri is a relatively faster movement than cirral extension, but still occurs quite slowly as compared with the corresponding movement in advanced balanomorph barnacles. For example, in *Calantica villosa* at 15°C, extension of the cirral net in response to a water current takes 4.0 s, withdrawal 0.95 s. In *C. spinosa* at the same temperature the corresponding figures are extension 2.94 s, withdrawal 1.76 s. The advanced balanomorph *Balanus perforatus,* at 21°C, in contrast, extends its cirri in 0.17–0.23 s and withdraws them in 0.06–0.14 s on each beat (Anderson, 1981).

Investigation of *Catomerus polymerus* has now revealed that the scalpellid mode of feeding is also a feature of this species. On immersion in water, the aperture slowly opens and the long cirri are extended to project as a partly curled fan at the carinal end of the aperture (Figs 7c, 7d). When a water current flows over the aperture, the cirri extend to a more upright position, though still maintaining an apico-rostral posture. Food in the form of small planktonic prey such as copepods, cyprid larvae and other crustaceans of similar size is captured, usually by the curling down of a single cirral ramus. Larger prey are occasionally engulfed by contraction of the whole cirral net. The maxillipeds transfer the captured prey from the coiled long cirri to the mouthparts. In association with the horizontal posture of the body relative to the basis and aperture and the more posterior placement of the long cirri (Fig. 8a), the process of forward food transfer by the maxillipeds is more complex than in scalpellids. The long cirri coil down mainly in a position behind the oral cone. The short maxillipeds with their dense setation, including a number of comb-like, stout serrate spines (Fig. 8b) on the distal segments of the second maxillipeds ("grapples" of Pope, 1965; "cards" of Newman, 1967a), are adapted to a forward combing action in the limited space between the coiled long cirri and the apex of the oral cone. Allowing for this functional adaptation related to changed body posture, however, *C. polymerus* has retained the feeding mechanism seen in scalpellids. The rate of cirral extension is comparable, though the withdrawal process is accelerated. At 20°C, extension in *C. polymerus* takes 2.8 s, withdrawal 0.33 s. Since *P. polymerus, C. villosa, C. spinosa* and *C. polymerus* are all intertidal and all feed in the same way, it can be concluded that the evolution of the balanomorph form in the catophragmids was not a functional correlate of the evolution of a new feeding mechanism. The diversification of feeding mechanisms in balanomorphs (e.g. Crisp and Southward, 1961; Anderson, 1978, 1981) is a result of further evolution after the balanomorph form had been attained.

(b) Protection

It follows, therefore, that the modifications leading from calanticine to catophragmid were functionally associated with a changed role of the peduncle and capitular plates. Some of this is evident from the anatomical considerations set out earlier in this paper. The long peduncle, with its obvious advantages for a subtidal extension feeder, is disadvantageous in exposed intertidal situations and is vulnerable to predators such as crabs. Elimination of the peduncle, resulting in a squat, conical form with a broad circular basis, is clearly advantageous. The extension of the basal capitular plates downwards to meet the basis as an interlocking vertical wall of 8 plates (Fig. 2) is also advantageous in terms of protection from desiccation, predation and mechanical damage, and is only a minor structural change, given a virtual cessation of peduncular growth. The lateral displacement of the pedunculo-capitular scales as concentric whorls of marginal plates is a corollary of this modified growth pattern, the marginals being turned to grow upright and imbricating, rather than lateral (Figs 8a, 8c). The progressive elimination of these marginals, even within the catophragmids, is indicative of their vestigiality of function as well as of structure.

As part of the process of evolution of the wall plates as a short upright cylinder, there has been a reduction in height of the ancestral carina. At the same time, the apical margin of the wall has expanded laterally, from the oval shape of the basal capitular region in calanticines to the diamond shape of the orifice in *Catomerus*. Both of these changes are associated with modifications of the opercular valves. In calanticines, as mentioned above, the aperture is rostral (Figs 1b, 2a, 6b). The scuta and terga are tall, arising from that basal part of the capitulum which is bordered by a horizontal row of 7 small plates (rostrum and latera) and the base of the carina. The carina, extending apically from this level, supports the junction between the terga along their carinal margins. The scuta, with their apical umbones and adductor muscle, cover the rostral halves of the valves. The terga, again with apical umbones, are taller and narrower than the scuta and cover the carinal halves of the valves. In some species of *Calantica,*

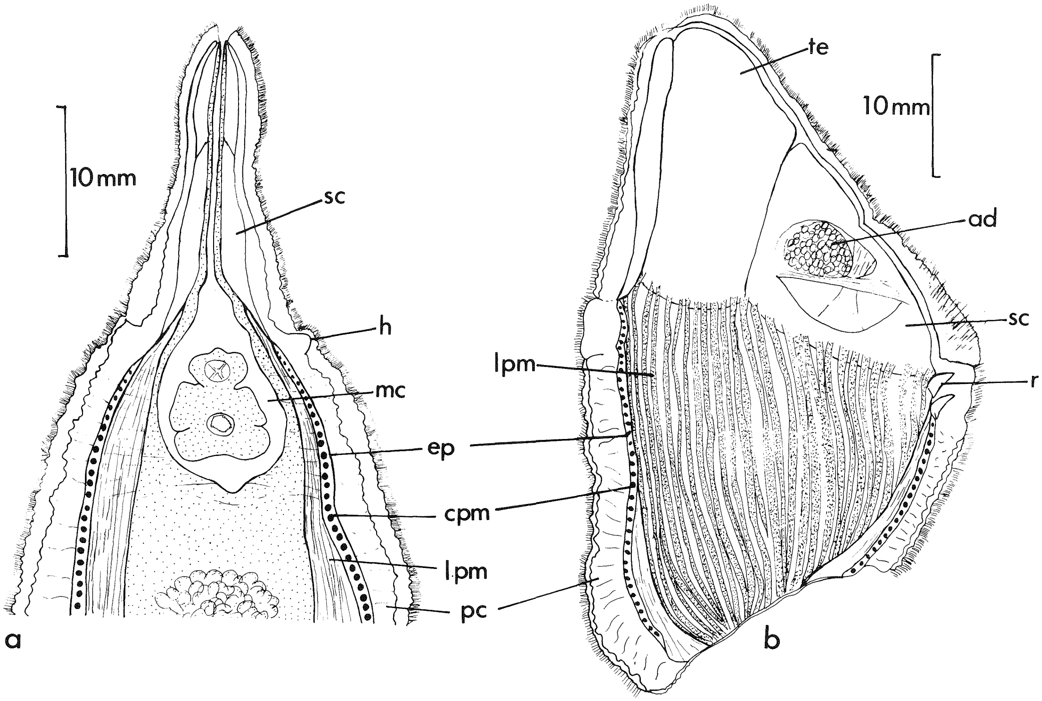

Fig. 9. **a**, Frontal section through the apical half of a decalcified specimen of *Calantica villosa*. **b**, Median view of the left half of a decalcified specimen of *C. villosa*, bisected sagittally and dissected to expose the longitudinal peduncular muscle. *ad*, adductor scutorum; *c*, carina; *cpm*, circular peduncular muscle; *ep*, surface epithelium; *h*, hinge; *lpm*, longitudinal peduncular muscle; *mc*, mantle cavity; *pc*, peduncular cuticle; *r*, rostrum; *sc*, scutum; *te*, tergum.

as noted by Darwin (1854), the scutum and tergum of each side are articulated together along their apposed margins.

In relation to the intertidal habitat, the calanticoid capitular plates have certain functional disadvantages. They project upwards as a bilaterally flattened cone and their mechanism of aperture closure is simple and potentially leaky. In catophragmids, through *P. cretaceum* to *C. polymerus*, a functional transformation of capitular plates to opercular valves has occurred. While retaining the capacity for opening to produce a widish aperture, the valves now have a low profile (Figs 1a, 2c), especially in the closed position, and can clamp tightly shut. It is to be noted, however, that the latter involves no interlocking of the aperture margins. These are still straight, so the tight closure of the aperture is a matter of bringing the aperture margins harder together.

The first consideration in understanding this change is to examine the modifications of the valves themselves. With the foreshortening of the carina, the aperture is rotated from a rostral to an apical position. It is in connection with this change that the body, within the mantle cavity, is also rotated from an oblique to a horizontal position, displacing the long cirri postero-basally and necessitating a functionally correlated modification, shortening of the maxillipeds, as illustrated by Newman (1967b).

At the same time, with a broadening of apical margin of the wall, the valves are canted from an upright to an oblique position, with the establishment of a sharp angle at the junction with the wall. The angled region acts as a hinge for the opening and closure of the opercular valves on the now rigid wall (Fig. 8c). Certain changes in the shape and growth pattern of the scuta and terga are a part of this general modification (Fig. 2). The scutal umbones are displaced carinally, so that the scuto-tergal junctions slope obliquely in a carinal direction and the scuta grow mainly in a rostral direction. The tergal umbones are also displaced carinally, maintaining their position behind the carinal end of the aperture, and the terga themselves are now relatively short and broad.

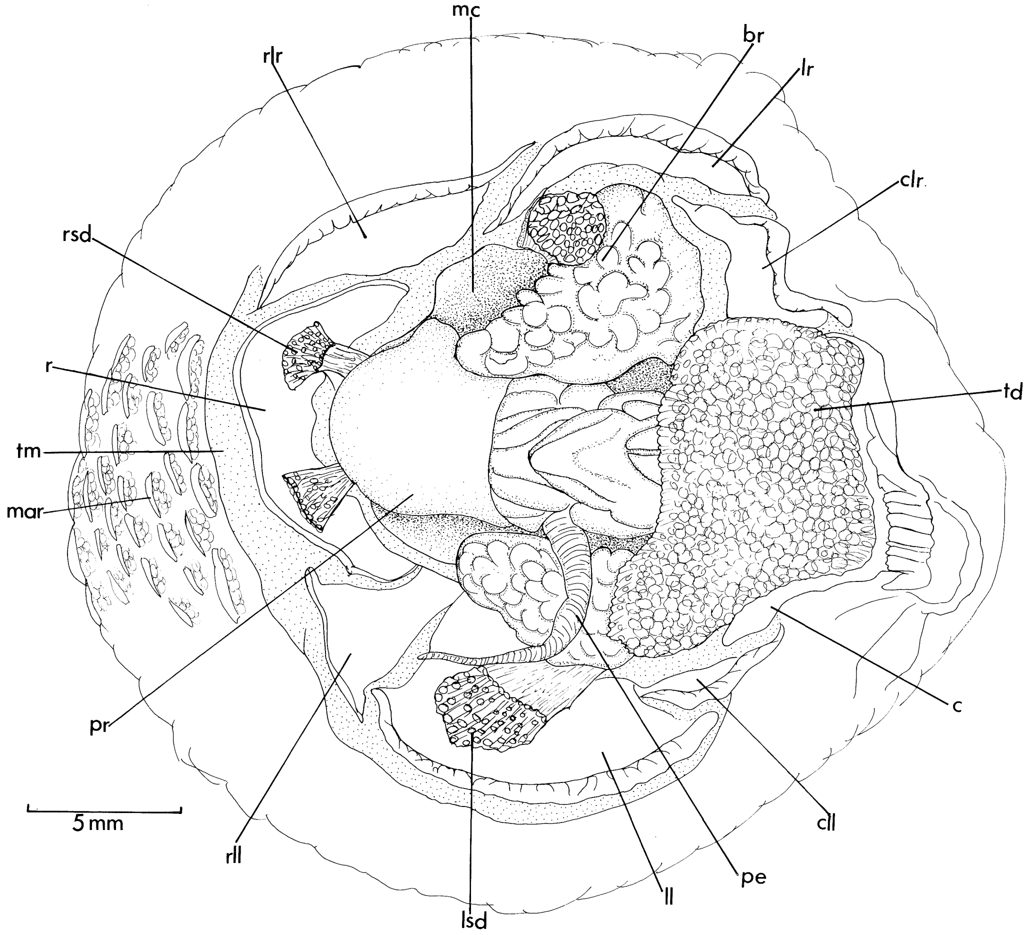

Fig. 10. *Catomerus polymerus,* basal view with basis removed. *br,* branchia; *c,* carina; *cll,* left carinolateral; *clr,* right carinolateral; *ll,* left lateral; *lr,* right lateral; *lsd,* lateral scutal depressor muscle, *mar,* marginal wall plates, *mc,* mantle cavity; *pe,* penis; *pr,* prosoma; *r,* rostrum; *rll,* left rostrolateral; *rlr,* right rostrolateral; *rsd,* rostral scutal depressor muscle; *td,* tergal depressor muscle; *tm,* mantle tissue.

The changes in growth pattern that transform upright capitular plates into a flattened operculum are readily understandable. The resulting low profile of the valves is functionally sensible. The opening mechanism of the valves, operating through hydraulic inflation of the mantle tissue underlying the scuta and terga (Burnett, 1972, 1977), remains unchanged. Attention needs to be paid, however, to the form and origin of the opercular hinge and the closure mechanism of the balanomorph operculum.

The hinge, as it happens, is not an innovation. A fully developed hinge is present between the basal margins of the scuta and terga and the more basal capitular plates in *Calantica* (Fig. 9a). Thus the hinge mechanism was already present before the balanomorph form evolved.

The closure mechanism, however, is more complex. In calanticines, closure is brought about in part by the scutal adductor muscle, working at good mechanical advantage, but also in part by the strongly developed sheath of longitudinal muscles in the peduncle (Fig. 9b). These muscles, lying within a sheath of connective tissue, are able to effect slow shape changes of the peduncle, but from the present point of view the significant feature is that their apical ends insert on the inner basal margins of the scuta and terga. In this position, contractions of these muscles can assist in closure, though at poor mechanical advantage.

A calanticine–catophragmid evolutionary transition requires that this system of closure should have been functionally transformed into the system present in *C. polymerus*. Previously, no details of the opercular closure mechanism in this species were available. Opercular closure remains a slow process, proceeding at about the same rate as in *Calantica villosa*. The adductor muscle remains an important functional component of valve closure, but in relation to the new position of the valves its efficiency would appear to be diminished (Fig. 8c). Valve closure is more of a downward swing than a bilateral apposition, and yet the adductor muscle retains its transverse orientation. It cannot therefore be as effective in valve closure as it is in scalpellids.

On the other hand, the downward swing of the closing valves in *Catomerus* is an exaggeration of that component of calanticine closure which is brought about by the peduncular longitudinal muscles, namely, a swing on the hinge due to an apicobasal pull of muscles inserted on the inner side of the hinge. The peduncular longitudinal muscles, instead of remaining as a muscle sheath, are transformed in *Catomerus* into a massive block of tergal depressor muscles extending from the terga to the basis (Fig. 8a) and two pairs of much smaller depressor muscles extending from the rostral and tergal corners of the scuta to the basis. The wall of the carapace no longer retains any pliability and these modified longitudinal muscles function solely in clamping down the opercular valves into the closed position. Because of their direction of pull, apicobasal, they play a major role at excellent mechanical advantage in swinging the valves downwards and shut. The same pull also serves to bring the occludent margins hard together in the closed position and hold them tightly shut.

One question remains to be examined. Why is it that the tergal depressor muscles in *C. polymerus* are so large and the two pairs of scutal depressor muscles quite small, when the ancestral form had an equal development of longitudinal muscles all round the peduncle? Functional considerations make it clear that the answer to this lies in the availability of space within the modified external wall (Fig. 10).

Allowing for the foreshortening of the mantle cavity and the rotation of the body to a horizontal position, the rostral half of the mantle cavity is almost entirely taken up by the large prosoma, and the lateral parts by the branchiae. The need for enlarged branchiae is correlated with the reduction in the surface area and exposure of the inner surfaces of the opercular valves as respiratory surfaces (see Burnett, 1972, 1977 for details of vascularisation of these surfaces). In this configuration, the only possibility for the development of large, longitudinal opercular muscles exists at the carinal end of the mantle cavity. A whole series of consequent proportional and functional changes in the prosoma relative to the mantle cavity has been associated with the subsequent evolution of the opercular depressor muscles in balanomorphs as three more or less equally developed pairs (Crisp and Southward, 1961; Anderson, 1978, 1981) but, like the evolution of the feeding mechanisms of balanomorphs, these changes have post-dated the establishment of the basic balanomorph form.

Thus in its opercular mechanism and every other aspect of its functional organisation, the balanomorph form as expressed in *C. polymerus* is a functional modification of the calanticine form, and Darwin's hypothesis withstands the functional test. The balanomorph modification is basically adaptive to enhanced protection in the high energy, stressful and predator-rich environment of the rocky intertidal. Feeding, in the early evolution and establishment of the balanomorph form, remained basically unchanged.

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ON THE ORIGIN OF CRUSTACEA

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SUMMARY

Crustaceans are predominantly aquatic arthropods with a characteristic naupliar stage. Their known evolutionary history extends at least from the Early Cambrian. They display many features convergent with the chelicerates, uniramians and trilobites and formerly were classified with these groups in Arthropoda.

It seems more appropriate to study the origins of Crustacea by reference to their Cambrian representatives than by seeking to establish particular intuitions concerning early crustaceans based on a knowledge of living forms only.

Among Cambrian fossils, the lobopod *Aysheaia* is irrelevant to crustacean origins. Similarly, the living Tardigrada are best consigned to a separate phylum although they seem to be a related group with several primitive characters and are likely, on zoogeographic grounds, to have had a long evolutionary history.

Assuming that Crustacea are monophyletic, the existing fossil record dictates that the ancestral taxon possessed a complex of characters out of which evolved (during Cambrian times) at least: bradoriids and other primitive ostracode-like animals; *Canadaspis* and other phyllocarid-like forms; *Branchiocaris* and similar notostracan-like forms. Several other Cambrian taxa may be either true crustaceans or examples of convergence. Some show similarities to anostracans and conchostracans.

The diversity and complexity of the Cambrian fossils suggest that a basic crustacean facies was already established by the Late Precambrian (Ediacaran).

Introduction

Most crustaceans are aquatic invertebrates, inhabiting marine or continental athalassic and freshwater environments, although many terrestrial-adapted species are known. The total of crustacean species is not known definitively but has been conservatively reported at 40,000 (Gruner and Holthuis, 1967, cited in Moore, 1969, p. R59). This number is near the known species of Ostracoda alone (McKenzie, 1973). Probably, the total number of described crustacean species is nearer 100,000. This larger figure takes into account the rich fossil record of Crustacea which extends from the Early Cambrian to Recent, i.e. spans over 550 million years.

It is scarcely surprising that such a large pool of species embraces a remarkable diversity of forms. Nevertheless, the homogeneity of Crustaceans as a group has rarely been questioned. A particularly powerful argument in favour of the unity of Crustacea is adduced from embryology. Thus, ". . . the mode of development in Crustacea is based on spiral cleavage and a configuration of presumptive areas whose subsequent development is as a nauplius . . ." (Anderson, 1973, p. 471). The typical crustacean nauplius (metanauplius) is an ontogenetic stage which, embryologically at least, may be considered to possess a basic segmentation that includes antennular, antennal and mandibular segments (McKenzie, 1972, p. 172).

With some major exceptions (e.g. Ostracoda), most mature crustaceans possess three more or less well-defined tagmata—cephalon, thorax and abdomen—analogously with the non-related Trilobita. In general, cephalic features tend to be conservative among the several crustacean groups and typically include two pairs of antennary appendages. Behind these are segments which carry gnathobasic mandibles and up to two pairs of maxillae (in some groups one pair is interpreted as having been lost during evolution). The total possible number of cephalic segments is thus six but some or all may be fused.

On the other hand, the crustacean thorax is rather variable both in its segmentation and appendages but usually displays metamery. Some conception of its variability may be gained by study of Table 1, which lists the number of serially homologous thoracic limb pairs in carapace-bearing crustaceans and in some Burgess Shale (Middle Cambrian) arthropods with affinities to Crustacea. Likewise, the abdomen is variable and terminates either in an anal segment plus uropods or in a telson with or without uropods (Bowman, 1971).

Crustaceans often possess a carapace, although many groups lack one. It may be bivalved and enclose all or most of the body (Ostracoda, Conchostraca, Cladocera and cirripede cyprid larvae), or be a simple head-shield (Notostraca), or be bivalved and cover only the anterior part of the body (Phyllocarida). When bivalved it articulates either along a ligament or through hinge structures (Ostracoda). It seems best to consider the carapace as representing a grade of evolution (Manton, 1969)* rather than as indicating relative ancestry between groups being compared, although the fossil record clearly indicates that the most ancient preserved crustaceans all had carapaces (Table 1).

Table 1. Numbers of serially homologous paired thoracic appendages and segments in carapace-bearing crustaceans (modified from Jones and McKenzie, 1980).

Anderson (personal communication, June 1980) has noted that in all Malacostraca the number is 8, even though some of the anterior segments may have their limbs modified as maxillipeds.

Other ancient crustacean groups, e.g. Anostraca/Lipostraca (Devonian-Recent) and Syncarida (Carboniferous-Recent) lack a carapace.

Group	Serially homologous paired thoracic appendages and segments	Geologic range
Bradoriida	4	Cambrian-Ordovician
Ostracoda	3	Cambrian-Recent
Phyllocarida	8	(?) Cambrian-Recent
Branchiocaris	12-13	Middle Cambrian
Burgessia	3+7	Middle Cambrian
Waptia	10	Middle Cambrian
Cirripedia	6	(?)Cambrian-Recent
Eocarida	6-8	Devonian-Permian
Conchostraca	10-30	Devonian-Recent
Notostraca	11	Devonian-Recent
Hoplocarida	4+4	Devonian-Recent
Decapoda	5	Devonian-Recent
Peracarida	5-7	Carboniferous-Recent
Cladocera	6	Permian-Recent
Argulidae	4	Mesozoic-Recent
Euphausiacea	8	(?)-Recent

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* This concept apparently is confusing for some workers who correlate functional morphologic equivalence with taxonomic hierarchies. Such correlations may occur but are not necessarily a corollary of the concept, which holds that functional equivalence (grade) may be attained in different lines at about the same or at different times depending on their several evolutionary rates.

Summarising, crustaceans have in common a characteristic embryology and naupliar stage (sometimes as a metanauplius: Sanders, 1963, p. 14); characteristic cephalic features which include biramous antennae, biramous gnathobasic mandibles and a more or less common number of partially or wholly fused head segments; and, often, a carapace.

Early crustaceans or pre-crustaceans

All discussions on origins have a common problem: whether to concentrate on the conditions leading up to a particular event or on the earliest expressions of that event. This problem is well expressed in current research on the origin of life where two distinct schools have arisen: one prebiological, represented by the work of chemists such as Ponnamperuma and Fox; the other early organic, and represented by the work of biologists such as Margulis and Schopf. Both groups use the uniformitarian approach of comparisons with modern phenomena and living organisms (Margulis, 1970).

With respect to the origins of Crustacea, such a problem is resolved by the fact that virtually nothing is known of a crustacean record prior to the Early Cambrian although the complex organisations of Cambrian Crustacea suggest that there must have been one. *Parvancorina*, a carapace-bearing (?) taxon in the famous Ediacaran fauna of South Australia, is the only conceivable Precambrian candidate—its age is about 680 x 10^6 years—but Delle Cave and Simonetta (1975) compare it with *Skania* and argue against it being a crustacean.

Skania is a member of the later, equally famous, Middle Cambrian Burgess Shale fauna of western Canada which has a highly diverse arthropodan assemblage that includes several distinct stocks of carapace-bearing crustaceans; and there are numerous other Cambrian crustacean records. Most notable of these latter is the recent description of phosphatocopine ostracodes from the Late Cambrian of Sweden and from Late Cambrian rocks which have been re-sorted into Pleistocene drift deposits of northern Germany (Müller, 1979). The apatite preservation of the appendages of these ancient ostracodes is excellent.

Thus there are a number of well-preserved early crustaceans. This paper will consider some of them. It will also use an uniformitarian approach and study their living descendants, the objective being to develop ideas on the likely characteristics of the early Crustacea.

En route to my conclusions, it will be necessary to deal in a definitive manner with the relevance or otherwise for crustacean evolution of the bilaterally symmetrical lobopodial coelomate *Aysheaia*, another of the exotic suite of animals from the Burgess Shale.

Homeomorphy with other arthropodans

In 1973, Sidnie Milana Manton formalised taxonomically the concepts which she had pursued vigorously over five decades (Manton, 1973). In consequence, the phylum Crustacea is nomenclaturally available and, more importantly, its relationships with other arthropodans are better understood. These relationships were elaborated in greater detail by Manton in her classic book "The Arthropoda" published shortly before her untimely death (Manton, 1977).

The concept of polyphyly in arthropodans depends upon the elucidation of numerous homeomorphic characters. This fact remains not widely appreciated so that some workers persist in proposing a monophyletic origin for Arthropoda (Simonetta and Delle Cave, 1978). Presumably, such workers regard these characters as homologous rather than homeomorphic. Quoting Simonetta and Delle Cave (op. cit., p. 88), ". . . gli Artropodi paleozoici mostrano possedere una base morfologica comune che depone per l'essenziale monofiletismo del phylum . . ."

The difference between homology and homeomorphy can be demonstrated by considering in some detail the crustacean mandible and by contrasting this type with the homeomorphic mandibles of other arthropodans. That these basically different structures can have the same function, i.e. can operate as one or another kind of jaws to bite, triturate or pierce food, demonstrates a generally similar grade of evolution, but this is not homology.

Crustacean mandibles

In a major paper, Hessler (1964) discussed the comparative skeleto-musculature of Crustacea in support of the thesis that Cephalocarida are the most primitive living members of the phylum. I later applied Hessler's results to a comparison between the extrinsic musculature of Ostracoda and Cephalocarida (McKenzie, 1972) with the assistance of two recently published studies (Kesling, 1965; Smith, 1965). It seems fruitful to review the topic as an example of homology between groups of Crustacea.

Crustacean mandibles are the third pair of adult appendages from the front. It is important to understand this homology of position for two reasons. First, in some early well-preserved crustaceans (ostracodes) the third pair of appendages is not yet adapted for specialised functions with regard to feeding (Müller, 1979). Secondly, even in modern crustaceans the mandibles may not be so adapted. This is the case, for example, with the mandibles, maxillae and fifth limbs of adult males in the ostracode family Sarsiellidae; when examined the guts of these males were found to be empty, i.e. adult sarsiellid males do not feed. On the other hand, mature sarsiellid females have limbs adapted for food-gathering and examination of gut contents has indicated that they and juveniles of both sexes feed voraciously (Kornicker, 1969).

Crustacean ontogeny indicates that the mandible retains the classic grundplan of a crustacean biramous limb: it comprises a protopod, endopod and exopod. This is well illustrated by Sanders (1963, Figs 14, 16, 28–30) for the nauplii of several groups and has been documented for ostracodes by several authors (Kesling, 1951; Tseng, 1976). Note that for Ostracoda, even in some ancient groups, the exopod is usually reduced or lacking—except in Bradoriida (Müller, 1979).

Although crustacean mandibles are homologous and conform to the common scheme for a crustacean appendage they can differ considerably, their morphologic variety representing the grade of evolution reached by each group in terms of its feeding pattern. Some idea of how these patterns can differ is given by the résumé below with respect to Ostracoda.

For Bradoriida, Müller (1979, p. 23) has suggested that the animals were nectobenthic and fed on plankton which they filtered through bristles on their cephalic limbs. Podocopida are usually benthic or epibenthic omnivorous detrital scavengers, carnivores (I have observed them prey on a weakened anostracan), suctorial feeders by special adaptations of the mouthparts associated with mandible coxales having the form of piercing stylets (McKenzie, 1969) or filter feeders. The latter adaptation, involving a previously undescribed organ (filter fan) on the hypostome, ". . . may be taken for the initial stage of development of a new large group with a new adaptational level . . ." (Schornikov, 1976). Myodocopida are benthic, epibenthic and pelagic detrital scavengers, mud ingesters, filter feeders, predators and collectors (Kornicker, 1975, pp. 39-42). Platycopida are filter feeders with different adaptations for this mode from cylindroleberidid myodocopids and the specialised podocopids mentioned above, as Schornikov illustrates (op. cit., pp. 248-249). In terms of the fossil record, the most ancient surviving ostracode stock is Podocopida.

Figure 1 illustrates the mandibles of the podocopids *Renaudcypris* (Cypridacea) and *Paralimnocythere* (Cytheracea), representing the two most numerous groups of living Podocopida adapted to marine and freshwater aquatic environments respectively—probably interstitial in the case of *Renaudcypris*. *

The general morphology of the mandible is illustrated for *Paralimnocythere*. The protopod, as usual, is 2-segmented, with a powerful gnathobasic coxale oriented vertically against the body; the basale is attached to it medially and dorsally bears a setose vibratory epipod; the palp (endopod) is 2-segmented (3-segmented in many other podocopids); and the exopod is interpreted as either absent or reduced to a powerful plumose annulated dorsal bristle (illustrated). The extrinsic musculature of this limb is shown for *Renaudcypris* (McKenzie, in press) and conforms to that described for other podocopids (Kesling, 1965, etc.). This musculature attaches the limb to the endoskeleton, the dorsal internal surface of a carapace valve and the anteromedial mandibular scars; additionally, the rounded top edge of the coxale is rotated against the internal cuticular lining of the valve as the limb works and develops a mandibular fulcral callus which can be seen on well-preserved material. The most powerful muscles are those to the endoskeleton and two of the dorsally attached muscles. This muscular array allows both backward–forward and outward–inward movement of the coxale. Since *Renaudcypris* is a scavenger/browser among the relatively large interstices of a coarse coralline littoral sand, the mandibles function to gather (grasp) bits of foodstuff and proffer them to the mouth. The food current is ventral and moves from the posterior forwards.

Unlike Ostracoda, which is the largest group in Crustacea, the Cephalocarida comprises only eight known species in four genera. The tagmata are clearly defined: cephalon; thorax of 7–8 segments; abdomen of 11–12 segments, plus an anal somite with long uropods. The mandible is not described

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* Usually, cypridaceans are athalassic or freshwater-adapted and cytheraceans are marine (both groups are marine *in origin*). Nevertheless, the examples illustrated here display the typical mandibular morphology among Podocopida. Even Schornikov's newly described abyssal filter feeding podocopid has a mandible of this type (1976, p. 253) as does the most ancient surviving podocopid stock, *Bairdia* (Maddocks, 1969). So too does the metacopine 'living fossil' *Saipanetta* (McKenzie, 1967).

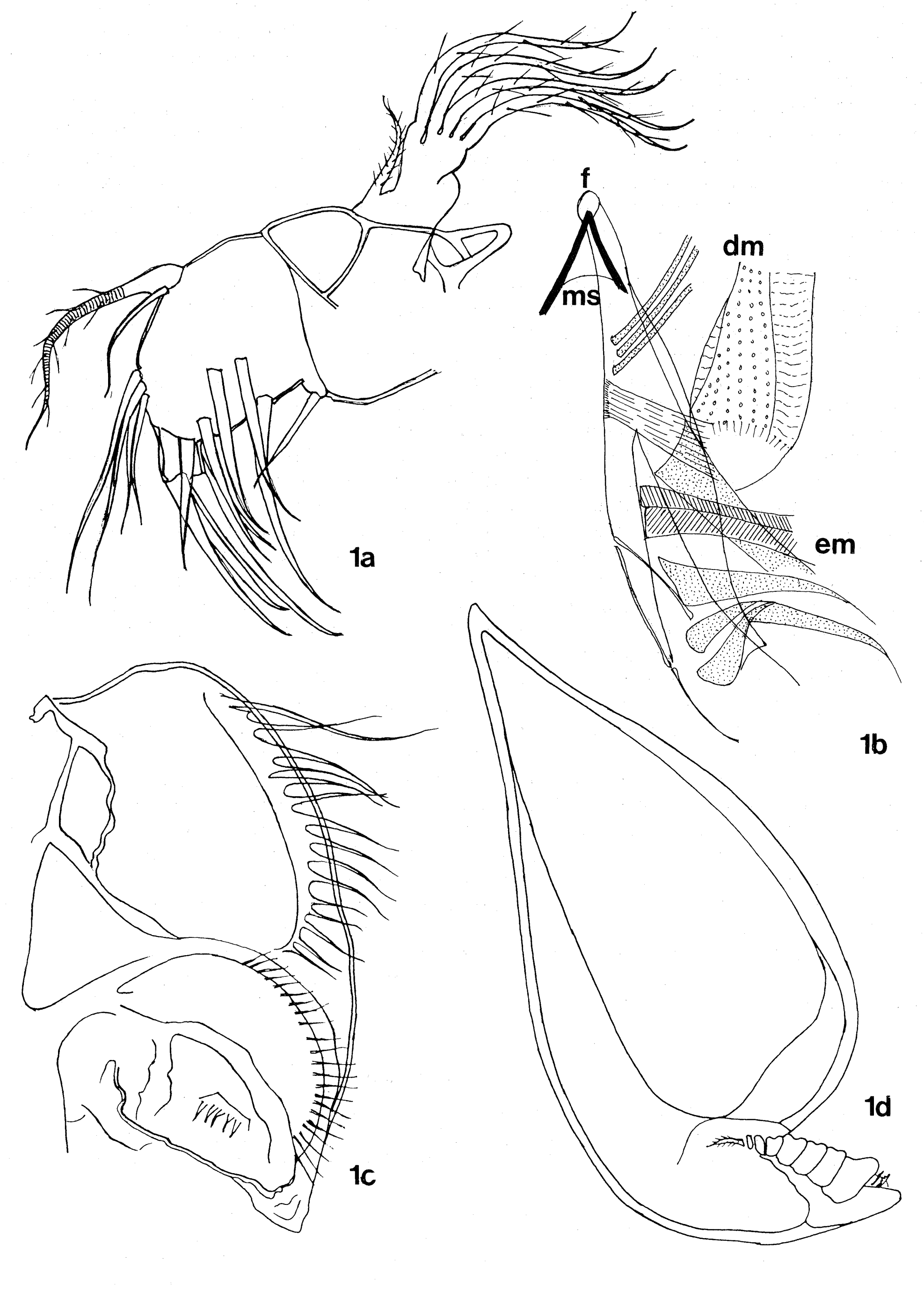

Fig. 1. Feeding apparatus of *Paralimnocythere* sp. and of *Renaudcypris gorongae* McKenzie. 1a, mandible basis, epipod and endopod of *Paralimnocythere*. 1b, part of mandible coxale of *Renaudcypris*: dm, muscles to the dorsal scar field of the carapace; em, muscles to the endoskeleton (= endosternite, = ventral cephalic tendon); ms, chitinous mandible supports to the mandibular scars in front of and below the central rosette of adductor scars; f, fulcral point. One slender front edge muscle to the dorsal scar field is not illustrated. With this array, the coxale is capable of both adductor-abductor and promotor-remotor, i.e. of slightly rotary, movement. 1c, labrum of *Paralimnocythere*. 1d, mandible coxale of *Paralimnocythere*.

or referred to in the latest genus to be erected, *Chiltoniella* (Knox and Fenwick, 1977), but its extrinsic musculature has been carefully illustrated by Hessler (1964, Fig. 12). Comparison with the extrinsic musculature of *Candona suburbana* Hoff 1942 made earlier (McKenzie, 1972, pp. 173-175) clearly sustains the conclusion that there are numerous and important correspondences between the extrinsic muscles of ostracodan and cephalocarid mandibles.

Functionally too the cephalocarid mandible is similar to its podocopid counterpart. Of the known cephalocarids, *Hutchinsoniella* at least is a non-selective deposit feeder, ingesting diatom frustules, sand, silt and detritus. Its food comes from the flocculent zone of subtidal muds. When feeding, the mandibles present to the mouth detritus captured on the gnathobases which has been passed forward to them by the posterior limbs along a ventral food groove. The movement of the gnathobases during feeding is both backward–forward and outward–inward, i.e. slightly rotary; again similar to *Renaudcypris* (Sanders, 1963), pp. 9, 12, 13).

Other detailed studies of crustacean mandibular musculature have been made by Manton (1964, Figs 3, 7–9, 11) for the animals *Chirocephalus*, (Anostraca), *Anaspides* and *Paranaspides* (Syncarida), *Ligia* (Isopoda) and *Calanus* (Copepoda); and *Nebalia* (Phyllocarida) (op. cit., p. 22).

All these mandibular musculatures display the following common features: a powerful set of muscles uniting the inner face of the coxa above the gnathobase with the endoskeleton; at least two powerful muscles, one of them often divided, which join the central-upper inner face of the coxa with the dorsal surface of the valve, cephalon, head capsule or head-shield; a fulcral point at the rounded upper edge of the coxa allowing backward–forward and outward–inward, slightly rotary, movements (Fig. 2).

This basically similar musculature can serve different functions in different animals. As indicated, it enables "secondary transverse biting" (grasping) of foodstuff in Cephalocarida and Ostracoda; a similar function characterises its operation in syncarids, isopods and copepods. But in Anostraca and Phyllocarida the functional effect is a grinding-rolling movement achieved mainly by promotor-remotor movements which are derived, according to Manton, from ancestral locomotory movements. Manton suggests that the grinding-rolling mandible is primitive but there is no explanation for this preference in her papers (e.g. Manton, 1963, p. 113). I repeat, the extrinsic musculature is similar for both types of movement—transverse biting and grinding-rolling.*

What differs is the gnathobase. Plate 1 shows that anostracan and notostracan mandibles are superbly adapted for a grinding-rolling function. But they may take other roles.

Observations of the feeding behaviour of the notostracan *Triops* indicate that it can be a savage carnivore.† I once collected *Triops granarius* (Lucas, 1864) and the anostracan *Streptocephalus dregei* Sars 1899 in the same sample jar from a pond on the Dwyka Tillite, near Grahamstown, South Africa. The *Streptocephalus*, unable to take avoiding action in the confined space and weakened by reduced oxygenation, proved no match for the *Triops* and were unrecognisable within half an hour. Thus, these broad corrugated, mandibular coxal gnathobases can hold and assist to rip soft animal tissue as well as grind and squeeze soft food (such as the green algae favoured by many anostracans). In their predatory role, notostracans also employ maxillary gnathobases which resemble (are homeomorphic with) the mandibular gnathobases of other crustaceans and make efficient grasping appendages (Plate 1).

Summarising, this brief review suggests that grinding-rolling and transverse biting are equally primitive adaptations of the third pair of appendages for feeding and require essentially the same extrinsic musculature. In every case the gnathobase is coxal, near the body, part of the protopod of a biramous limb.

Other arthropodan mandibles

Considering the other arthropodan groups, it is apparent that different feeding habits are involved.

Among chelicerates, the longest surviving group is the Merostomata (Silurian–Recent, a span of over 400 million years), represented in modern seas by the limulid horseshoe crabs. These marine and

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*"The explanation, I think, is that the promotor-remotor rolling action is assumed to be primitive because it is derived from a prior (hypothetical) condition in which the limbs of the 'mandibular' segment were walking limbs. The transverse biting action, on this view, is emphasised secondarily in association with the modification of these limbs as mandibles, though it probably had its origins in the transverse movements of the limb bases of walking limbs." (Anderson, personal communication, June, 1980.)

† Elsewhere (California, China) *Triops* is feared as a major ricefield pest because it tears at the young plants during the aquatic cycle of the crop. Probably, it is best thought of as a predatory omnivore.

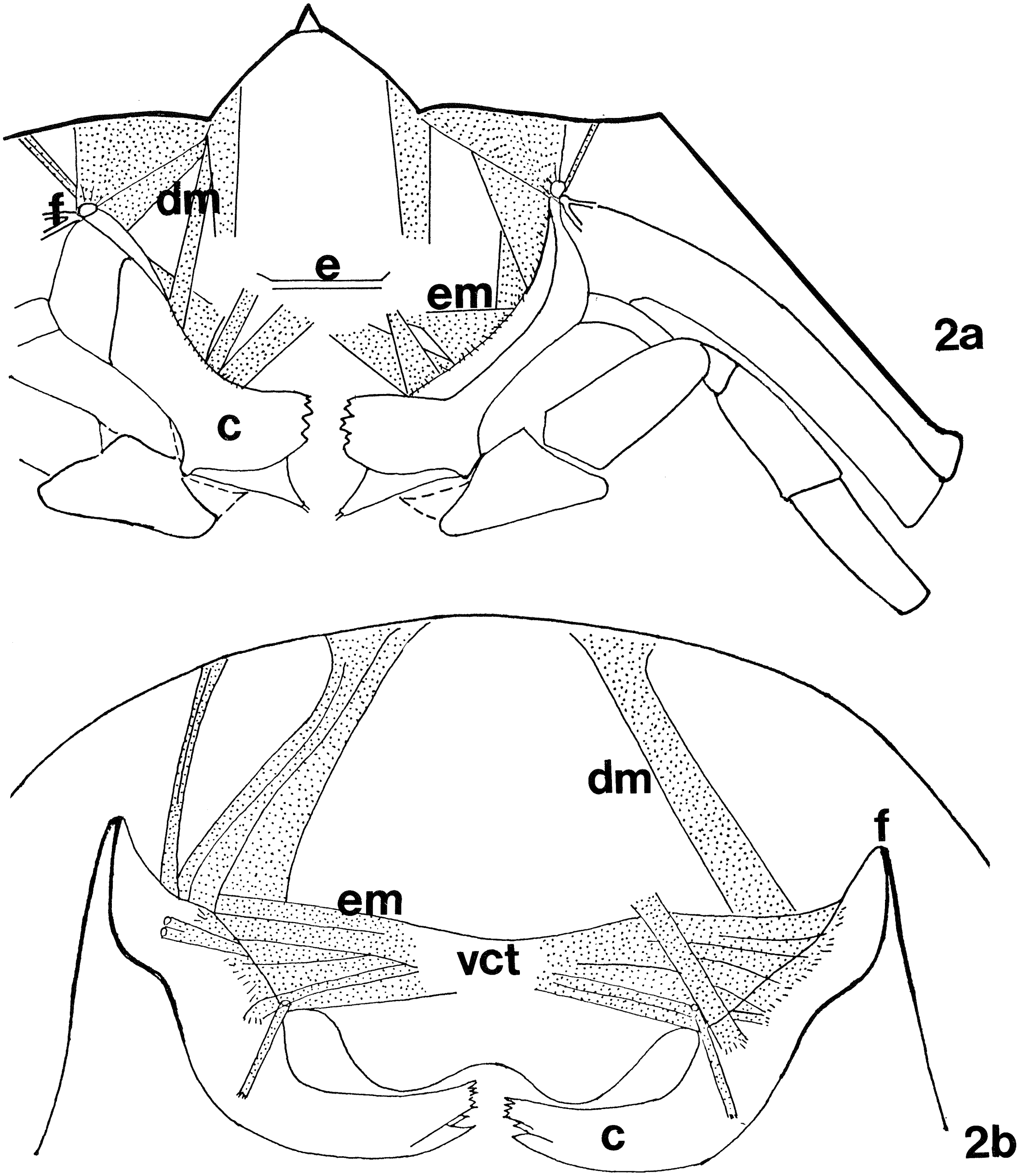

Fig. 2. Feeding apparatus of chelicerates (*Tachypleus tridentatus* Leach) and cephalocarids (*Hutchinsoniella macrocantha* Sanders) after Manton (1964, 1977) and Hessler (1964) respectively. c, coxale; dm, dorsal muscles; em, muscles to the endosternite (*Tachypleus*) or ventral cephalic tendon (*Hutchinsoniella*); e, endosternite; vct, ventral cephalic tendon; f, fulcral point. In *Tachypleus*, Y-shaped pleurite and large fan-shaped dorsal muscles both articulate at the fulcral point region. 2a, *Tachypleus*. 2b, *Hutchinsoniella*.

nearshore adapted animals represent more nearly the ancestral chelicerate stock than any order of the other major branch, Arachnida, including the scorpions which were about to embark upon the transition to a terrestrial environment when they first appear in the fossil record—somewhat later than the xiphosurids. Störmer (1970) notes, ". . . Characteristic of the scorpions is the external digestion of prey." None of the adaptations of either fossil or living scorpions to achieve this (suctorial) feeding mode have any similarities with the structures or musculature described for Crustaces (Störmer, op. cit., pp. 345-348).

The feeding pattern of horseshoe crabs is grossly similar to that of some crustacean predators such as the decapod crabs but, as pointed out by Manton (1964, pp. 34-37), differs in details. It consists of the provision of food via chelipeds to gnathobases which then push it into an oval food basin where they shred and chew it before it is ingested. There is no ventral food current carrying food forwards to these coxae. The chelipeds take up food directly below themselves as the animals burrow and grub in the substrate. The gnathobases of horseshoe crabs are homeomorphic with crustacean coxal gnathobases, not homologous. The extrinsic musculature of limulid coxae includes a large fan-shaped dorsal coxal muscle which is not present in crustaceans (Manton, op. cit., Fig. 15). This and other dorsal muscles articulate via characteristic Y-shaped pleurites with the under surface of the carapace where it joins the pleural arthrodial membrane (Manton, op. cit., fig. 17); see also Fig. 2 this paper). This differs from the crustacean musculature described above as one would expect from the basically different feeding habits.

As far as the other living arthropodan groups are concerned—Onychophora, Myriapoda and Insecta—their evolution is inextricably linked to the invasion of the land and a subsequent radiation into the extensive newly available soil and vegetative niches. Not only can we not identify the immediate ancestors of these early uniramians, we have similar difficulties with the immediate ancestors of some crustacean geoups which made the same transition, e.g. Lipostraca/Anostraca, Notostraca and Conchostraca. This chorologic criterion has rarely been given its full weight (McKenzie, 1970; Simonetta and Delle Cave, 1975; McKenzie, 1977). As I concluded earlier, ". . . considerations pertaining to the evolution of the predominantly terrestrial uniramians, therefore, need not cloud the perceptions of workers interested in the older predominantly aquatic crustaceans" (McKenzie, 1977, p. 269).

Manton, without reference to any chorologic principle, has dissected the detailed skeletomusculature and evaluated the form and habits of all orders of Myriapoda, of Onychophora and of a sufficient number of the insect (hexapod) groups to satisfy the most persistent advocate of detail. With respect to mandibular mechanisms her classic paper for the Royal Society makes clear that, ". . . since the crustacean mandible is primarily a gnathobase and the hexapod mandible a whole limb it would be surprising to find more than convergent resemblances between them . . ." Manton, 1964, p. 101). In her summation, Manton extends this conclusion to the Myriapoda and Onychophora (p. 106).

Aysheaia

Unless one has seen fossils of *Aysheaia* from the celebrated Middle Cambrian Burgess Shale of western Canada and has some knowledge of living Onychophora it is difficult to appreciate the long enduring supposition that *Aysheaia* represents an ancestral onychophoran stock. Indeed, this remains a common textbook dogma and at one time or another Calman, Cannon and Manton all subscribed to it.

However, there are several objections to such an hypothesis. As already mentioned, Onychophora are terrestrial and thus could not antedate the first life on land (Latte Silurian-Early Devonian). Next, unlike some other groups with similar characters, e.g. Tardigrada, which are adapted for respiration in aquatic and semi-aquatic environments, Onychophora are physiologically incapable of life in water. They breathe in air with the assistance of tracheae and in a marine environment would quickly drown. The fantasy of a horde of land-dwelling *Aysheaia* crawling across the littoral to their certain doom in a Mid-Cambrian Canadian sea, like lemmings, is exciting but is dissipated by the abundant evidence that *Aysheaia* was part of a rich sublittoral biocoenose engulfed by a catastrophic submarine mudflow (Briggs, 1976 and references cited therein). No trace of jaws or jaw-like structures has ever been found in the *Aysheaia* fossils and the latest interpretation of their feeding habits is that they may have preyed on sponges, using their spinose antennae to lacerate these organisms and then feeding suctorially (Whittington, 1978); i.e. the position of the mouth is terminal in *Aysheaia* not ventral as in Onychophora. Finally, the movement of *Aysheaia* must have been dissimilar in detail to that of Onychophora. About these latter animals, Manton (1977, p. 284) has written ". . . the use of exploratory sensory antennae to find narrow crevices or paths of least resistance may have led to the extreme powers of the Onychophora to distort their bodies, without pushing, so penetrating through narrow channels leading to more commodious spaces where larger predators could not follow . . ." As pointed out by Della Cave and Simonetta (1975, p. 76), the Burgess Shale substratum was a fine mud—its texture suggests the flocculent

Table 2. Comparative morphology and habits of *Aysheaia* (A), Onychophora (O), Tardigrada (T), Elasipoda (E): an example of common evolutionary grades leading to (convergent) common characters. X = present; — = absent.

Characters	**A**	**O**	**T**	**E**
marine habitat	X	—	X[1]	X
bilateral symmetry	X	X	X	X
terminal mouth	X	—	X	X
posterior anus	X	X	X	X
gut, a simple straight tube	X	X	X	X[2]
jaw apparatus	—	X	—	—
oral papillae	X	X	X	X
eyes	—	X	X	—
annulated body	X	X	X	X[3]
annulated limbs	X	X	X	X[4]
dorsal spines, tubercles, etc.	X	X	X	X
frontal structure[5]	X	X	X	X
pairs of lobopodial feet	10	14–43	4	4–5
terminal or near terminal claws	X	X	X	—
posterior of body projecting	—	X	—	X
longitudinal, transverse and dorsal-ventral musculature[6]	X	X	X	X
slow, non-pushing gait[7]	X	X	X	X
feeding habits[8]	suct.	pred.	suct.	suct.
moulting (vs continuous growth)	—	—	X	—
metameric characters	X	X	X	X
size (mm)	10-60	14-150	0.01-1.2	5-50
distribution[9]	rest.	rest.	cosmop.	cosmop.
Cambrian fossils	X	—	?	X

1. Terrestrial aquatic and semi-aquatic tardigrades are also known.
2. cf. discussion in text (*Aysheaia*).
3, 4. The elasipodid *Scotoplanes* has a pseudosegmented body; several elasipodid genera have annulated lobopodial limbs.
5. Interpreted as anterior appendage in *Aysheaia* (Whittington, 1978); an antenna in Onychophora; tardigrades have antero-lateral cirri, some complex, e.g. in *Parastygarctus*; in Elasipoda, complex frontal structures are known in e.g. *Periamma, Periagone.*
6 cf. discussion in text (Tardigrada).
7. Implies a capacity to vary limb length when walking and to allow promotor-remotor swing.
8. *Aysheaia* has been interpreted as preying on glass sponges suctorially (Whittington, 1978); most onychophorans prey on small invertebrates, using jaw blades (see Manton, 1977, pp. 97-99 for discussion and illustrations) and a labral 'sucking tube'; tardigrades use their stylets to pierce plant tissue and extract the juices; elasipodids are suctorial deposit feeders and mud ingesters.
9. cf. discussions in text (*Aysheaia*).

zone of sublittoral ooze—and the associated organisms were often sponges (Whittington, 1978, pp. 192-194, fig. 90); there was no need for *Aysheaia* to negotiate narrow passages.

These important differences suggest to me that any apparent resemblances between *Aysheaia* and Onychophora are instances of convergence between stocks far removed in time and phylogeny and all subsequent research has sustained this opinion.

This objection to any close relationship between *Aysheaia* and Onychophora is reinforced by the fact that *Aysheaia* also has many characters in common with other lobopodial animals which, unlike Onychophora, are known to inhabit marine environments similar to that in which *Aysheaia* lived before it was catastrophically buried. Previously, a possible affinity with Tardigrada has been discussed (Delle

Cave and Simonetta, 1975; Whittington, 1978), a possibility which I had suggested independently in correspondence with Whittington. I shall discuss this in more detail in the next section. But the resemblances between *Aysheaia* and yet another group of little known marine animals, the echinoderm Elasipoda, have hitherto been ignored (McKenzie, in correspondence with Whittington and Belyaev, 1975).

Table 2 compares about twenty characters of *Aysheaia*, Onychophora, Tardigrada and Elasipoda and indicates that the latter have many features in common with the other three taxa, including a comparable size range to *Aysheaia*—the minute size of Tardigrada has been cited as an objection to *Aysheaia* having tardigradan affinities.

The great variety of living Elasipoda is such that it does not require an extraordinary stretch of the imagination to place *Aysheaia* among them although some objections to such a conclusion will be discussed. What may not be widely appreciated, however, is that the holothuroid Elasipoda are considered to be one of the most ancient echinoderm stocks.

While other Cambrian echinozoan fossils, such as *Helicoplacus* and *Eothuria* exhibit a distinct anti-clockwise torsion in their preserved tests, no traces of such torsion exist in restorations of ancient holothuroid echinozoans such as *Protocaudina*, a Carboniferous elasipodid-like animal in which the bilateral symmetry remains undistorted. Earlier fossils, such as *Laggania* and *Mackenzia* (like *Aysheaia* components of the Burgess Shale fauna) once thought to be holothuroids, are now classified elsewhere (Croneis and McCormack, 1932); but *Louisella*, a bilaterally symmetrical lobopod also from the Burgess Shale, seems clearly an elasipodid (Durham, 1974).

The evidence from biogeography indicates that both marine Tardigrada and the exclusively marine Elasipoda are cosmopolitan—unlike *Aysheaia* and Onychophora. While many gaps remain in our understanding of their dispersal patterns, it is already clear that several tardigrade marine genera have Tethyan affinities (Renaud-Mornant, 1979), i.e. they are distributed from the Central Pacific coasts to Indonesia and Australia; and that Elpidiidae, the largest of the elasipodid families, probably dispersed from a parental stock in the southern Indian Ocean (Belyaev, 1974). These patterns suggest a Palaeozoic origin for both groups with dispersive radiations during the Mesozoic—early Tertiary when Tethys was a major seaway, the Gondwana continents were drifting apart and the southern Atlantic and Indian Ocean had their origins. The best current interpretations of distributions of land and sea in the Palaeozoic (Smith, Briden and Drewry, 1973; Scotese, Bambach, Barton, van der Voo and Ziegler, 1979) suggest that the most favourable period for dispersive radiations between the southern and northern hemispheres was during the Middle Ordovician (about 450 million years ago).

While such an analysis is hypothetical it is at least anchored plausibly in time and space and environment. The dogma which relates *Aysheaia* and Onychophora is founded only on a morphological resemblance.

Considering life habits and morphologic characters, a principal objection to the possibility that *Aysheaia* could have been an echinoderm stock related to Elasipoda is that, although both have terminal mouths (unlike Onychophora), living elasipodids are deposit feeders and mud ingesters with a long coiled alimentary canal whereas the fossils of *Aysheaia* clearly show a short straight food tract free of mud.* But early echinoderms probably had simpler alimentary systems and this hypothesis, that all echinoderms arose from a bilaterally symmetrical ancestor with a short straight food tract and a dipleurule larva stage, is still favoured in the literature (e.g. Fell, in Marshall and Williams, 1974). The most recent analysis of *Aysheaia*'s feeding habit suggests that it preyed on sponges (Whittington, 1978) but nowhere in the detailed descriptions of the remarkably preserved *Aysheaia* fossils is there any reference to the contents of the animals' alimentary canals although it is hypothesised that these were not mud-filled (Whittington, 1978, p. 192).

Of the remaining distinctions between *Aysheaia* and elasipoda listed in Table 2, the numbers of pairs of lobopodial feet does not seem of great significance since *Aysheaia* is midway between the other taxa in this respect. The posterior projection of the body in Elasipoda is a common character with Onychophora hence should not make the possibility of an elasipodid affinity any less likely than that of an onychophoran one. This leaves the absence of terminal claws on the lobopodial limbs as the sole important distinguishing character.

On balance, it seems that a possible affinity between *Aysheaia* and elasopodid echinoderms is worthy of more detailed study. On the other hand, no firm new evidence can be adduced for a link between *Aysheaia* and the Crustacea.

* Further with respect to elasipodid feeding, it has been suggested that their highly aqueous tissue and the low ambient (deep sea) temperatures probably enable them to live without much food.

Tardigrada

As noted in the previous section, Delle Cave and Simonetta (1975) first drew attention to the similarities between Tardigrada and *Aysheaia* which were later discussed by Whittington (1978). The discussion by these authors was relatively superficial, however, and this section intends to treat the possible relationships in greater detail, drawing on recently published work and personal confirmatory research.

Tardigrada are a phylum of minute aquatic and semi-aquatic animals which formerly were considered to be mostly terrestrial but are now known to include numerous marine species, mainly from nearshore and interstitial environments. They have been recorded on every continent but are well-known only from northern hemisphere terrestrial ecosystems. Southern hemisphere terrestrial species have been neglected. Marine taxa, although long passed over, are now being carefully studied and it is already clear from their morphology, diversity and widespread distribution that the primitive tardigrades were marine. This being so, the phylum must antedate the Cretaceous, from which the first fossil tardigrade, a terrestrial species trapped in amber, was described (Cooper, 1964).

Living descendants of the ancestral stock belong in the wholly marine suborder Arthrotardigrada of the order Heterotardigrada. Some general information on the embryonal onotgeny of tardigrades is provided in Cuenot (1932, pp. 12-13) and the moult ontogeny of heterotardigrades has been studied for the genera *Batillipes* and *Stygarctus* (McGinty and Higgins, 1968; Renaud-Mornant and Anselme-Moizan, 1969).

By embryonal stage V, several tardigradan characteristics are already present, namely: the buccal region and stylets; the pharyngeal bulb; and the four trunk segments. Developed embryos use their stylets to hatch. The earliest larval stage of *Stygarctus*, however, shows no segmentation and (although all four pairs are developed) the lobopodial limbs have only two terminal claws each. Complete segmentation in *Stygarctus* is attained by the third larval stage and the four pairs of feet now have the adult number of claws (four each) but the adult size and reproductive capability are not acquired until the next (fourth) stage (Renaud-Mornant and Anselme-Moizan op. cit., pp. 885-887). *Batillipes* also reaches adulthood in the fourth larval stage then undergoes a fifth (adult) developmental stage (McGinty and Higgins, 1968). The number of moults to adulthood in these taxa is rather fewer than for most crustaceans (Sanders, 1963, p. 69; McKenzie, 1972, pp. 182-183).

Tardigrade have a terminal or ventroterminal mouth (Table 2) and feed suctorially via protrusible stylets powered by specialised muscles in the body (Fig. 3). This buccal apparatus is clearly visible through the transparent body in many tardigrades but may be obscured by the exoskeletal segmental armour (cuirass) of others, such as *Stygarctus*. The whole structure is cast off in an initial phase of moulting but the musculature remains behind with the body and attaches itself to the newly formed buccal apparatus of the next stage. Once the buccal apparatus has reformed, the rest of the body cuticle moults. This two-phase moulting pattern is unknown in Crustacea.

Tardigrade excretion is incompletely understood. It includes defecation into an old moult as the new moult casts it off, and excretion via the epidermis where the excretory products accumulate as granules (Ramazotti, 1972). Such habits are not known in Crustacea.

All tardigrades have a slow non-pushing gait (Table 2) which facilitates their identification under the microscope when examining mosses and fine marine detritus for living specimens. Indeed, it is responsible for their common name: water bears. There is no basic difference between this gait and that of the Onychophora or that hypothesised for *Aysheaia* (Whittington, 1978, p. 192) or that of the echinozoan elasipodid *Scotoplanes* as recently photographed at 1060 m depth in the San Diego Trough, off California (Hansen, 1972).

But crustaceans move differently although retaining the basic metachronal rhythm, promotor-remotor swing and more or less well developed adductor-abductor movements. In the simplest case—walking/swimming—the coxa of a segmented crustacean limb swings transversely through a narrow arc against flexible cuticle around the body joint. A pivot joint at the distal end of the next segment (basis) favours limited adductor-abductor movements of the endopod and/or exopod (in modern crustaceans, usually one branch of the standard biramous limb is precociously adapted for locomotion and the other branch is adapted for a different function). Further small movements in the vertical plane are accomplished via intersegmental hinge joints of the endopod/exopod. All these movements are implemented by the limb's extrinsic and intrinsic flexor and extensor muscles (Manton, 1977, pp. 39-48).

The mechanisms which power such gaits are hydrostatic for all the groups cited but in the case of Tardigrada there is a basic difference in the intrinsic musculature of the locomotory lobopods. As first illustrated by Renaud-Mornant (1965) and confirmed in her laboratory by this author working

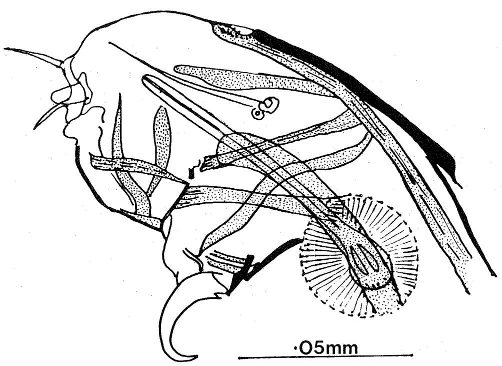

Fig. 3 (above). Feeding apparatus of a tardigrade, *Echiniscus* sp., drawn in the retracted position. When feeding, the muscles illustrated power the protrusion of the stylet from the head.

Fig. 4 (right). Telescopic limbs of a tardigrade, *Florarctus hulingsi* Renaud-Mornant. Both protruded and retracted states are shown. Note also the powerful transverse muscles. (The anterior leg pair and the terminal claws of some legs not illustrated.)

on a different specimen, the limbs of Tardigrada are telescopic. Thus, they shorten and extend in a manner basically unlike the lobopods of Onychophora because the muscles are differently disposed (Fig. 4)—I cannot comment on the comparison with Elasipoda due to a lack of reference material and no musculature is preserved for *Aysheaia*. On the other hand, the extrinsic musculature of these limbs in Tardigrada is similar to that for many arthropodans (Fig. 5).

Body turgor in tardigrades is maintained by several groups of muscles: dorsolateral and ventrolateral; transverse, dorsoventral. The musculature of the tardigrades was first figured (diagrammatically) by Marcus (1929) for several taxa and Fig. 6 is my confirmatory, more explicit drawing of part of the musculature of *Batillipes pennaki* Marcus 1947. Although several muscles are not illustrated in this drawing (particularly some transverse muscles), it is sufficiently clear that the muscular orgainsation is similar in pattern to that of many arthropods (cf. Hessler, 1964)—again I cannot comment with respect to Elasipoda and *Aysheaia*, for the same reasons as cited earlier.

As regards the types of muscles involved, the (more primitive) marine heterotardigrades have cross-striated muscles like many arthropodans, including Pentastomida, but unlike Onychophora which have obliquely striated muscles (Kristensen, 1978). Eutardigrades, however, have smooth or obliquely-striated muscles, except for the pharyngeal bulb and stylet muscles which are cross-striated (Walz, 1975). In explication, Kristensen (p. 182) suggests, ". . . the ancestral tardigrades had arthropod cross-striated muscles, these were transformed (by functional requirements), when tardigrades adapted to the terrestrial biota . . ." Thus, muscle types may fail to substantiate oft-stated claims on the primitiveness of onychophoran organisation vis-a-vis primitive tardigrades and the early marine crustaceans which will be considered later.

Some other characteristics of Tardigrada can be considered more briefly. They serve either to separate tardigrades from Crustacea or to suggest further possible links with *Aysheaia*, sometimes both at once.

Returning to ontogeny, a feature of tardigrade larval development is that all four pairs of limbs are present in the first stage and there is no subsequent addition of limbs during the larval ontogeny.

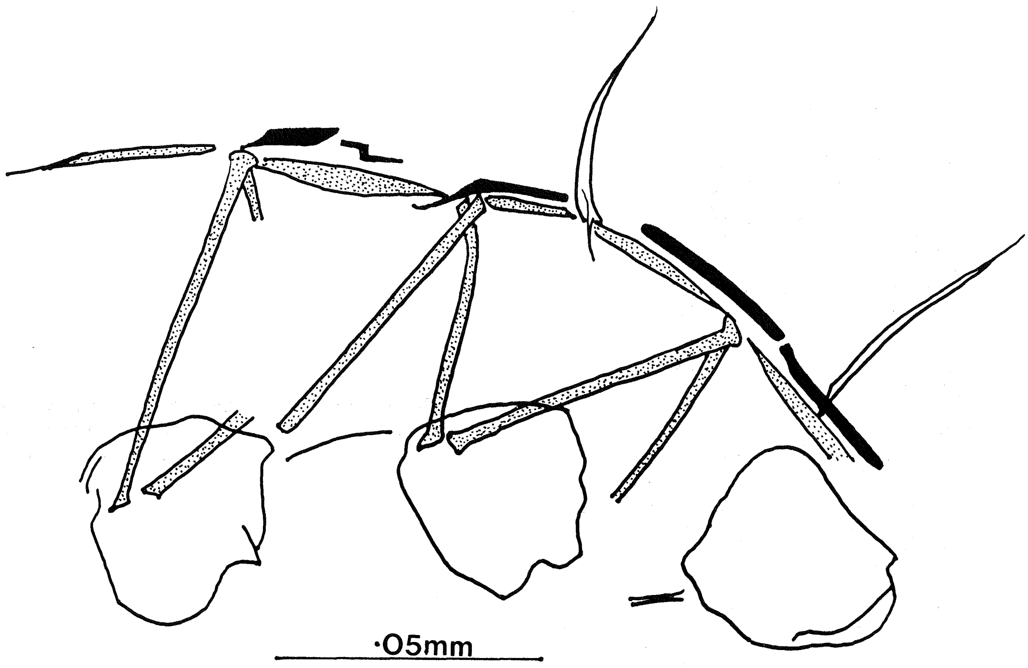

Fig. 5. Extrinsic leg muscles of a tardigrade, *Echiniscus* sp. (see also Marcus 1929), anterior to the left.

This is unlike the situation in Crustacea but is comparable with the fossil record of *Aysheaia*. A second point is that larval size increases in Tardigrada are not consistent with the crustacean Law of Growth, originally proposed by Brooks (1886) as "... the length of the larvae increases uniformly at each moult by one-fourth of its length before the moult ..." Subsequent research (Skogsberg, 1920, pp. 123-147) has shown that hardly any taxa develop with such regular size increments throughout their larval ontogeny but nonetheless the Law is approximately correct. The growth factor in Tardigrada does not conform to this crustacean pattern (Renaud-Mornant and Anselme-Moizan, 1969).

An important factor of similarity between Tardigrada and *Aysheaia* (and one which distinguishes between Tardigrada and Crustacea) is the disposition of their posterior pair of limbs. In *Aysheaia* and Tardigrada these are terminal; In Crustacea, the body terminates in a telson, anal segment, posterior lobe, furca, uropods, but never in a pair of locomotory limbs. Earlier authors have given due weight to this factor (Delle Cave and Simonetta, 1975).

These authors have also drawn attention to the common possession of oral papillae in *Aysheaia* and Tardigrada. The observation can be extended also to Onychophora and to Elasipoda (Table 2.)

A final brief comment on sight. While Tardigrades are commonly thought to possess eyes, many interstitial species lack them, including *Stygarctus* and many other arthrotardigradan heterotardigrades. While *Aysheaia* is illustrated as blind (Whittington, 1978, pp. 187, 192, 193) the evidence is insufficient to support such an interpretation. The flocculent texture of the Burgess Shale sediment is such that if small eyes were present in *Aysheaia* they would not necessarily be preserved. This factor, therefore, cannot be considered to contribute either way—for or against a possible relationship between Tardigrada and *Aysheaia* or Crustacea.

Conclusions about *Aysheaia*

The extended and relatively detailed discussion of *Aysheaia* and some taxa homeomorphic with it has shown that the similarities of this celebrated Burgess Shale animal to such phyla as Echinodermata and Tardigrada are at least as worthy of attention as its much touted relationships with arthropodans, especially Uniramia but including also the Crustacea.

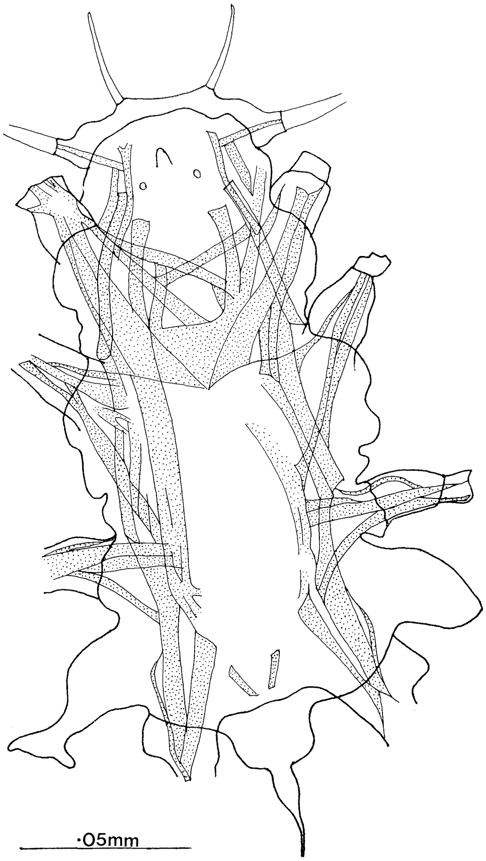

Fig. 6. Musculature of a tardigrade, *Batillipes pennaki* Marcus, posterior transverse muscles not shown. The general organisation is rather similar to that of many arthropodans.

In respect of some fundamental habits of life, the similarities are obviously due to convergence. Thus, in considering locomotion, the intrinsic musculature of a tardigrade lobopod is shown to differ basically from that of the uniramian Onychophora, i.e. the lobopods in these two groups are homeomorphic not homologous (Fig. 4). Further, the musculature which powers the feeding stylets of Tardigrada is not recapitulated in that which activates elasipodid ingestion or the ventroterminal jaw blades of onychophorans. Again, each of the three groups with which *Aysheaia* has been compared respires differently, with the most specialised adaptation among them being the air-breathing tracheae if onychophorans.

In the light of such data (cf. also Table 2), the relevance of *Aysheaia* to the evolution of any of the arthropod phyla can be considered minimal. Few crustacean workers should quarrel with such a conclusion.

Early crustaceans

The irrelevance of *Aysheaia* to the origins of Crustacea does not mean that there is now a lack of material on which to base some ideas on the topic. On the contrary, the marine Cambrian sediments of the world hold a rich diversity of early crustaceans and there are many other early fossils which can be considered as crustacean in their affinities rather than, say, trilobitan or cheliceratan.

Considering true Crustacea first, the major early fossil group is undoubtedly the bivalved ostracodan Bradoriida. Once considered to be conchostracans (Ulrich and Bassler, 1931), these animals are now generally confirmed as phosphatocopid ostracodes (Müller, 1964) although Jones and McKenzie (1980) warn that, as presently understood, bradoriids are probably polyphyletic and include phyllocarid-like or branchiopod-like species.

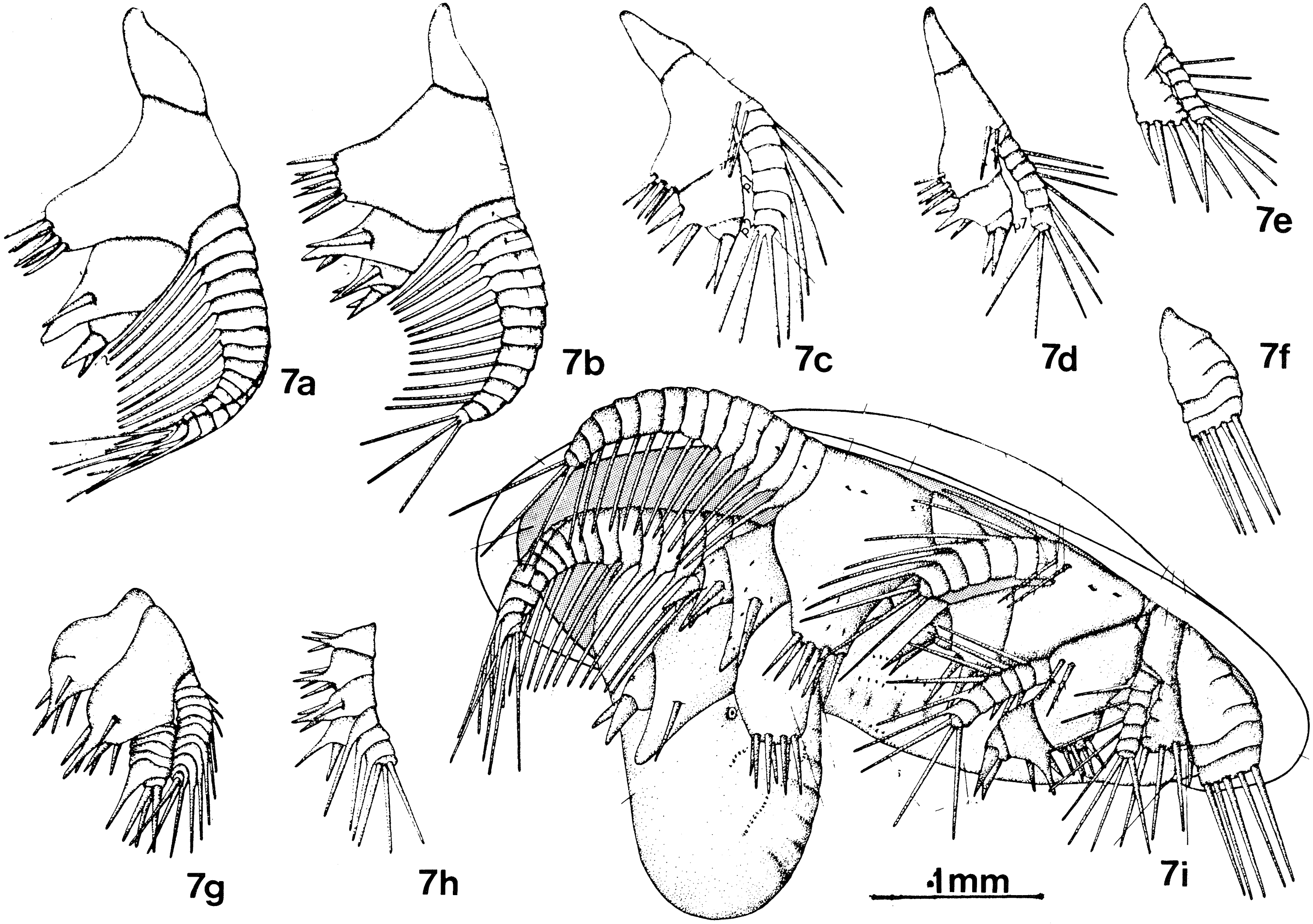

Fig. 7. Anatomy of a Cambrian bradoriid ostracode, *Vestrogothia spinata* Müller (after Müller 1979). 7a, first appendage; 7b, second appendage; 7c, third appendage; 7d, fourth appendage; 7e, fifth appendage; 7f, sixth appendage, (all the same specimen); 7g, fourth appendage; 7h, fifth appendage (both from another specimen of *Vestrogothia* sp.). 7i, reconstruction of the animal. Note that the first appendage of *Vestrogothia* is the antenna. This animal lacks an antennule. However, a uniramous antennule is present in *Hesslandona unisulcata* Müller, another Cambrian bradoriid (Müller, 1982).

This notwithstanding, over 260 species in about 60 genera have been described as bradoriids from Cambrian and Early Ordovician sequences (Jones and McKenzie, op. cit.). The group is cosmopolitan and its environmental associations include nearshore phosphorites as well as sublittoral mudstones and shales, indicating an adaptative range from the shoreline to well offshore. The taxonomy appears to be plagued by over-zealous splitting but it is nevertheless true that bradoriid assemblages commonly comprise a diversity of species and genera. Obviously, they were as well adapted for life in the Cambrian as the more widely known Trilobita.

Knowledge about the habits of life of Bradoriida remained sketchy until the recent publication of high quality micrographs of entire animals including their soft anatomy (Müller, 1979). Müller's rich collections of over 400 specimens with preserved soft parts and several thousands of empty carapaces came from four different localities in Sweden and northern Germany. Subsequently, further bradoriid material with traces of the soft anatomy preserved has been discovered in Ausralia (McKenzie and Jones, 1979) and has added significantly to our understanding of the group.

Morphologically, the major new data are that ostracodan phosphatocopine bradoriida had uniramous antennules, biramous antennae and mandibles plus at least four other pairs of appendages behind these (Müller, 1982), and that the thorax was probably four-segmented (McKenzie and Jones, op. cit.). The multi-segmented limbs were not modified for specialised functions except that the segments bore numerous long setae (Müller, 1979, pp. 21-23). As Müller expresses it (p. 1), the animals were ". . . nectobenthic filtering plankton feeders." These features are illustrated in Fig. 7.

Additionally, there are occasional records from the Cambrian of ostracodes belonging to groups other than Bradoriida. Possibly, these were benthic detrital scavengers.

At least two other crustacean groups are represented in the Cambrian faunas of the world but specimens with well-preserved appendages are practically confined to the Middle Cambrian Burgess Shale of Canada.

The richest material is of the phyllocarid-like *Canadaspis perfecta* (Walcott, 1912) of which some 5000 specimens have been collected (Briggs, 1978). *Canadaspis* and *Perspicaris*, the latter represented by about a dozen specimens also from the Burgess Shale, are the best authenticated possible Cambrian phyllocarids, since the assignments of other taxa, such as, *Isoxys, Odaraia, Plenocaris, Saccocaris, Tuzoia,* to this group are all more uncertain (Rolfe, in Moore, 1969; Whittington, 1974; Briggs, 1977; Glaessner, 1979).

Of the two supposed Cambrian phyllocarids, *Perspicaris* may have been nectobenthic (Briggs, 1977) while *Canadaspis* probably lived benthically (Briggs, 1978). Both animals were part of the rich arthropodan biocoenose of a flocculent sublittoral mud and ooze which owes its exceptional preservation to a fortunate accident of burial. The feeding mode of *Perspicaris* is unknown, but the sclerotised gnathobasic mandible coxae of *Canadaspis* and its spinose thoracic appendages suggest that it was a detrital scavenger over the substrate mud and that food particles were directed forwards to the mouth via a ventral feeding current generated by epipodial fans.

The remaining crustacean group, of branchiopod-like animals, is represented in the Burgess Shale by the genera *Protocaris* and *Branchiocaris*, but the appendages are preserved only in *Branchiocaris* (Briggs, 1976). This animal is considered to have been benthic and to have fed on substrate detritus by using antennary appendages; apparently it lacked gnathobasic mandible coxae (Briggs, op. cit., pp. 11-12).

Other Burgess Shale taxa may show affinities to Crustacea but their precise relationships are obscure and, since their redescription is in train, analyses based on the old literature are premature. They include the genera *Waptia* and *Burgessia* of which *Waptia* appears to be bivalved (Whittington, 1974, pl. 18, fig. 5) and *Burgessia* univalved (Simonetta and Delle Cave, 1975, pl. 5, fig. 5). Simonetta (personal communication, April 1980) links *Burgessia* with Notostraca, and *Waptia* with the evolution of Cirripedia, especially Ascothoracica. Having dissected both notostracans and ascothoracic cirripedes (McKenzie, 1972, fig. 3 which is diagrammatic only), I do not subscribe to either of these interpretations. Among other discrepancies, *Waptia* lacks the large, flexed and forwardly pointing antennules with terminal adhesive organs which are characteristic of Ascothoracica (Tessmann, 1904, pp. 1, 2, fig. 11); and *Burgessia* differs so widely from Notostraca in antennules, labrum, headshield, number of segments, telson, etc., that I do not consider them even remotely connected. *Waptia* may well be a crustacean but *Burgessia* appears to be cheliceratan and too clumsy to have had the life habits of Notostraca (cf. Fox, 1949). The difficulties of assigning any of these arthropodans to the major modern groups are also discussed by Manton and Anderson (1979).

Of the numerous genera assigned uncertainly to Phyllocarida, one at least may belong elsewhere;

this is the genus *Isoxys* Walcott 1890. Glaessner (1979) places it tentatively with phyllocaridans but Simonetta and Delle Cave (1975) give it separate ordinal status,* and Simonetta (pers. comm., April 1980) now wonders if in fact it is arthropodan. Of living crustaceans, *Isoxys* most nearly resembles the pelagic halocyprid Ostracoda, especially the genera *Euconchoecia* Müller 1980 and *Conchoecia* Dana 1849 (cf. Müller, 1906). However, the fossil record of halocyprids only goes back to the Cretaceous; and as *Isoxys* can be an order of magnitude larger than both *Euconchoecia* and *Conchoecia* its similarity to these taxa is probably due to convergence.

As new Cambrian faunas are studied, many other taxa with affinities to Crustacea undoubtedly will be described. In particular, the faunas of Cambrian phosphorites should prove rewarding because of the astonishing detail of apatite preservation. Figure 8 indicates that one such study is already under way. It includes the first record of a presumably telescopic limb for the Cambrian, plus assorted appendages, limb segments and abdominal segments all of which appear to be arthropodan. The preservation is so faithful that some pieces retain traces of musculature, and others may preserve muscle attachment sites. When the host rock is sectioned, parts of setiferous limbs and bivalves with an indistinct internal soft anatomy can be identified on slides viewed by transmitted light. This rich material comes from the Middle Cambrian Duchess Phosphorite of Queensland, but almost 100 other localities are recorded by Notholt, in Cook and Shergold (1979, pp. 71-86, fig. 13) who lists all known early phosphorites for the world. A further factor in favour of more detailed work on phosphorite faunas is that this rock type extends into the Precambrian so it may well yield well-preserved Crustacea and other arthropodans which are more primitive than any hitherto known.

The origin of crustacea

We know that Cambrian fossil Crustacea are abundant and may expect to find new, well-preserved Late Precambrian taxa. Unfortunately, the best known Precambrian material, South Australia's notable Ediacaran fauna, does not include Crustacea, with the possible exception of *Parvancorina* (Glaessner, 1962), although other arthropodans are present.

We can, however, make some reasonable assumptions concerning the characteristics of the primitive crustaceans.

Firstly, Manton (1977) has demonstrated the unity of crustaceans as a major group of invertebrate animals. Her conslusions have been underlined by the work of Anderson (1973, p. 467): ". . . the basic theme of crustacean embryonic development is seen to differ fundamentally, not only from the clitellate-like mode of development underlying the development of onychophoran embryos, but also from the basic annelid mode of development itself. The interpolation of a nauplius stage in the developmental sequence itself is fundamentally different and could not posssibly be a modification of any annelid mode of development."

Apart from their embryology, the later development of crustaceans has some common characteristics. Anderson (1973, pp. 290-308) notes that after the nauplius hatches all post-mandibular segments are developed from the short post-naupliar region. He did not discuss Ostracoda in this context, but ostracodes have a mode of post-naupliar segment development similar to that of other generalised Crustacea, though the bivalve carapace, antennules, antennae and mandibles are developed precociously in the embryo to yield a distinctive nauplius. Taking absolute body length as the criterion, proportionate development of ostracode cephalic limbs (antennule, antennae and mandibles) is complete even at this naupliar stage (McKenzie, 1973, p. 184, Table III), after which Ostracoda add appendages more regularly than any other crustacean group until adulthood is reached (McKenzie, 1972, pp. 182-183, Tables I, II). Although Ostracoda are regarded as non-segmented and highly cephalised—both interpreted as specialisations—the Bradoriida clearly have at lease four thoracic segments (McKenzie and Jones, 1979) and the posterior chitinoskeletons of several living taxa suggest that ostracodes had abdominal segmentation also earlier in their phylogeny (Schulz, 1976). There is no reason to doubt that this thoracic and abdominal development took place from the post-naupliar region as for other Crustacea.

Anderson (1973, p. 301) goes on to hypothesise six pairs of trunk (thoracic) limbs as the basic adult number, the argument being based on metamorphosis in cephalocarids where all limbs are involved in all functions. Functionally, these limbs are thought of as responsible for swimming, crawling and feeding movements and their rhythm is metachronal. Mechanically, the lowest number of limb pairs

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* Specimen 189301 from the Walcott collection in the Smithsonian Institute, Washington D.C., does not seem an *Isoxys* in my opinion although recorded as such by Simonetta and Delle Cave (1975, pl. 54), but I have not checked the original material.

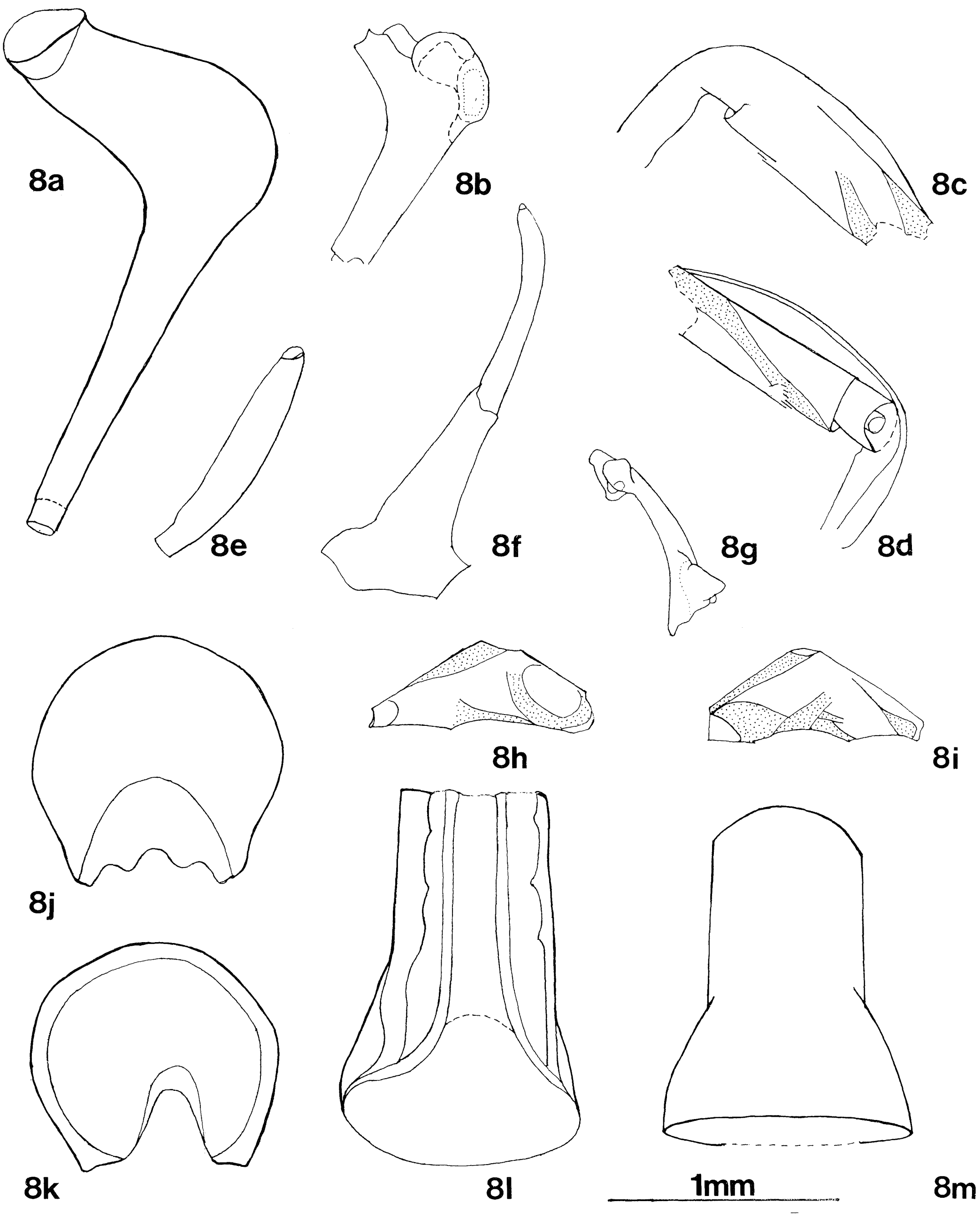

Fig. 8. Bits of arthropodans from the Cambrian phosphorites near Duchess, Queensland. 8a, movable, pleural(?) spine; 8b, ball-headed joint of movable spine; 8c, part of thoracic limb; 8d, other side of 8c, showing probably telescopic limb segments; 8e, segment of walking leg, with hinge joints at each end; 8f, sensory spine; 8g, "rib", with pivot joints at each end; 8h, "trochanter", showing supposed muscles (transmitted light); 8i, other side of 8h, showing other supposed muscles; 8j, posterior(?) face of abdominal segment; 8k, anterior(?) face of abdominal segment; 8l, ventral view of same segment as 8j, 8k; 8m, dorsal view of same segment. Published with the permission of the Director, Bureau of Mineral Resources, Geology and Geophysics, Canberra.

which can work metachronally is three, and as Table 1 indicates this is the number of serially homologous thoracic limb pairs in modern Ostracoda (Podocopa). Bradoriida have at least four such limb pairs behind the cephalic limbs but as only juveniles with well-preserved appendages have been recovered so far the adult number is possibly greater (Muller, 1979). The difference between podocopid Ostracoda and other crustaceans may be due to a reduction to the lowest mechanically possible number of metachronal, locomotory thoracic limb pairs, imposed by the necessity to maintain a capacity for all functions within the relatively restricting valves of the carapace.

Very many ostracodes display adaptations of the thoracic region for other purposes than locomotion. These include: adaptation to interstitial environments, e.g. Cladocopa, Parvocytheridae; clasping during copulation and cleaning, e.g. Cypridacea; food forwarding of filtered or grasped substrate detritus, e.g. Platycopa, Myodocopa. The latter adaptations are particularly pertinent since it is debatable whether locomotion is a more primitive necessity than feeding. Rather, both functions are equally vital and in many ostracodes the antennae bear the burden of swimming, e.g. Myodocopa, or crawling, e.g. Platycopa.

A further criterion is adult size. Here the primitive fossil crustaceans differ markedly. The hypothesised phyllocaridans *Canadaspis* and *Perspicaris* range from about 10 mm to more than 50 mm (Briggs, 1977, 1978) and the branchiopod-like taxa *Protocaris* and *Branchiocaris* from 43 mm to 87 mm (Briggs, 1976). The Cambrian ostracodes, however, are all much smaller, ranging from less than 1 mm to about 2 mm. Presumably, all three groups and the numerous other early arthropodans which have been described meet the biochemical criteria imposed by Towe (1970) for the synthesis of collagen and cuticle and fall within his definition of small and simply structured metazoans. The size of the only possible Precambrian crustacean, *Parvancorina*, is about 3 cm but no appendages of this taxon are preserved to link it with any of the three Cambrian groups.

Considering these three groups, only the Bradoriida juveniles had a biramous antennule; and only in the Bradoriida was the third appendage from the front a generalised biramous limb rather than a specialised mandible (Fig. 7). In fact, all the first three limb pairs were very similar in their organisation. It is difficult to explain away such general characters as indicating an embryonisation of development, or specialisation, or oligomerisation from some earlier more complex condition. The bradoriid thorax had at least four segments. The bradoriid abdomen is unknown but by analogy with modern ostracodes may have had a chitinous exoskeleton indicating at least six segments, followed by a telson and laminate uropods (Schulz, 1976, figs 2, 12, 13, 17-20). The entire soft anatomy was fully enclosed within a bivalved chitinophosphatic carapace. If an eye was present, it was naupliar.

In the branchiopod-like *Branchiocaris*, the first two limbs of a mature specimen were uniramous but the remainder of the soft anatomy was biramous and serially homologous and the body ended in a telson plus uropods. The division between the cephalon and thorax is unknown and that between the thorax and abdomen poorly defined, but probably it lies at about the 12th or 13th segment. The combined thorax-abdomen had 46 segments. A bivalved carapace covered the anterior of the body. If eyes were present they were located beneath the carapace.

In the mature *Canadaspis*, the first two limbs were likewise uniramous and the mandible had a sclerotised gnathobase of the transverse-biting type. There were two postmandibular maxillae and eight serially homologous thoracic limb pairs. The abdomen had seven segments and the body ended in a telson with uropods. A bivalved carapace covered the cephalothorax. There were two simple stalked eyes.

These groups form the basis for an interpretation of the origin of Crustacea. It may well be, as Anderson concludes (1973, p. 471) that ". . . the metamerically segmented coelomates which gave rise to the Crustacea cannot be identified . . .", but these groups afford the most secure basis for any such attempt.

Manton (1973, p. 128) states ". . . we can do no fossil embryology . . ."; nevertheless, of the three groups both phyllocaridans and ostracodes are known to hatch as young adults, and the Cambrian Bradoriida at least followed such a developmental scheme. Because we are less sure of the relationship betweeen *Branchiocaris* and modern branchiopods it is not possible to extend this suggestion with confidence to *Branchiocaris*. Clearly, however, even in the Early Cambrian crustaceans exhibited some embryonisation of development. The adults were specialised in relation to active swimming and plankton filter-feeding in the case of bradoriids and for benthic grubbing and detrital scavenging in the case of the phyllocaridan-like taxa. *Brachiocaris*, with its small mouth and lack of mandibles, presumably used its large antennary appendages to grasp and gather food. Both sexes were probably present in all three groups although we can only be sure of this in the case of the ostracodes (Müller, 1964).

Extrapolating from these data, the ancestral types probably exhibited the following common features: a bilateral symmetry; uniramous antennules; biramous antennae and mandibles, developed as generalised biramous limbs in the adult form; some embryonisation of naupliar development, possibly including the early secretion of a carapace; thoracic and abdominal development from the post-naupliar region; more or less well-expressed sex dimorphism; discontinuous growth by moulting. The habits of life of these small earliest crustaceans would have been appropriate to marine epibenthic or nektobenthic niches, adapting them for bottom scavenging, predation or filtatory feeding, in the main via generalised limbs and a ventroterminal mouth. Their basic movements were promotor-remotor and adductor-abductor and were accomplished via serially similar cross-striated muscles. Turgor was maintained hydrostatically and by longitudinal and transverse muscle bundles. They had naupliar eyes.

Such ancestral animals should be looked for in deposits no older than the Ediacaran (680 m.y. BP) in which as we have observed there is yet no obvious crustacean taxon. The reason for such a choice is geochemical not biological. Holser (1974), in a paper culminating two decades of painstaking research, has established the occurrence of a major catastrophic event in the history of the world ocean between about 650 to 550 m.y. BP (op. cit., fig. 1). Towards the end of this period, abundant fossil evidence has convinced us of an explosive radiation in many groups of invertebrates, notably trilobitans, cheliceratans and carapace-bearing crustaceans. It seems plausible that the beginning of this catastrophic period was the era during which Crustacea commenced their evolution towards dominance among invertebrate metazoans of the world's aquatic environments.

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Prof. D. T. Anderson F.R.S. kindly refereed the original manuscript.

This paper is dedicated to the memory of that tireless worker on arthropodans, the late Dr Sidnie Milana Manton (Mrs J. P. Harding) F.R.S.

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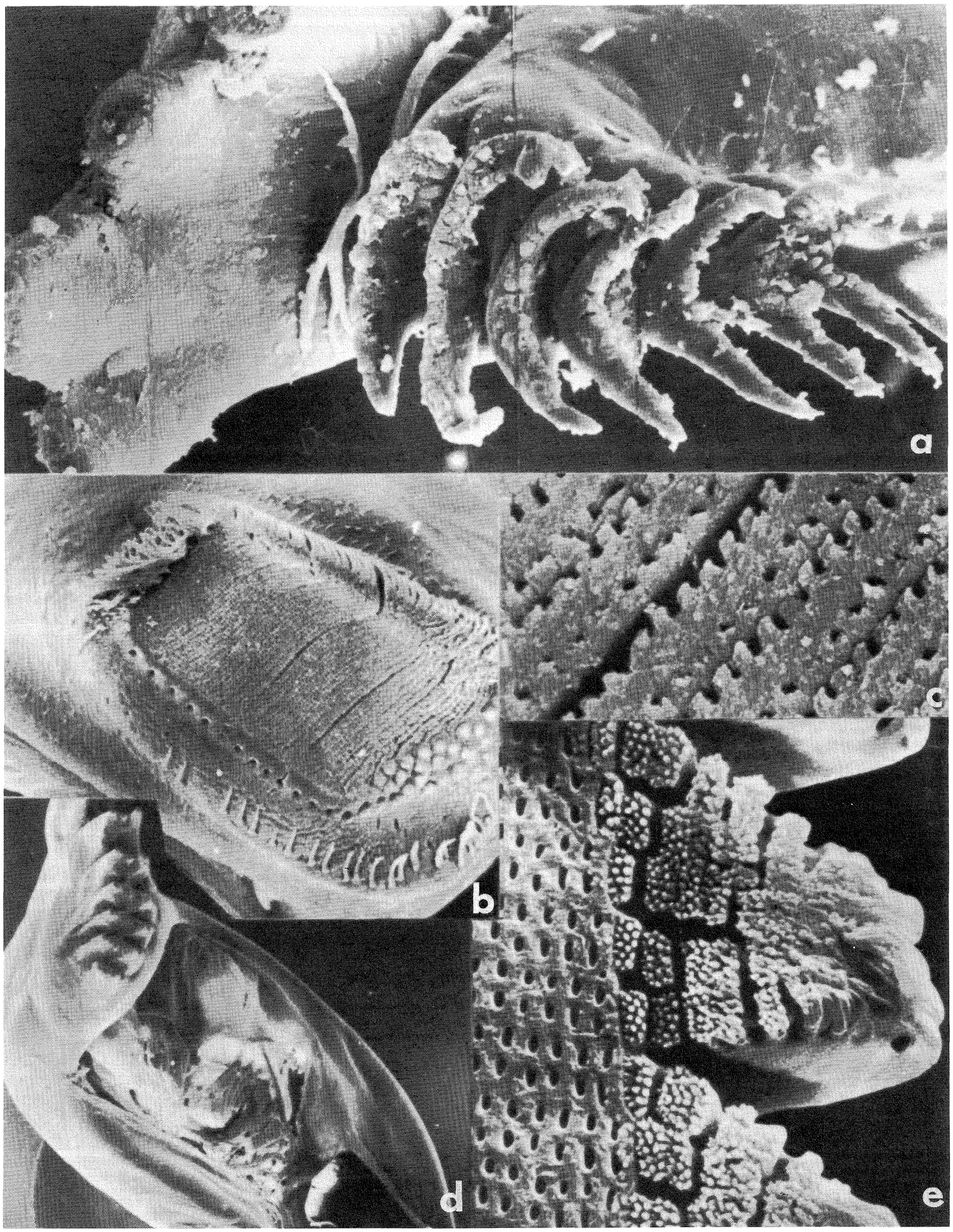

Plate 1. Feeding in Recent Notostraca and Anostraca. **A-C**, *Lepidurus* (Notostraca) gnathobases; **A**, biting gnathobase × 440; **B**, grinding-rolling gnathobase × 180; **C**, detail of grinding-rolling gnathobase × 1800; **D**, *Triops* (Notostraca), biting gnathobase × 28; **E**, *Dendrocephalus* (Anostraca), detail of grinding-rolling gnathobase × 1800.

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AUSTRALIA AS A MAJOR EVOLUTIONARY CENTRE FOR AMPHIPODA (CRUSTACEA)

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SUMMARY

The morphology of modern amphipods is used in place of a cogent fossil record to conclude that amphipods existed in the early Mesozoic during Pangaea. A freshwater group called crangonyctids was distributed at that time over most of the continental coagulum. Freshwater amphipods abhor tropical environments so that the modern dispersal of continents has resulted in widely dispersed relict fragments of crangonyctids. North America remains heavily populated with these animals whereas South Africa and Australia are now poorly endowed owing to climate. Eurasia is poorly endowed with crangonyctids because of the later evolution of more successful freshwater amphipods such as gammarids and niphargids, neither of which reached the southern hemisphere. South America lacks any of the mentioned groups, having a freshwater amphipod fauna of unique character except for bogidiellids shared with other world regions.

Marine amphipods also are cold-adapted. This characteristic in part provides a global ecological effect best represented in Australia and known as ends-of-the-earth phenomenon. The warm-temperate region of southern Australia therefore comprises a large isolated reservoir of amphipods dominated by groups poorly represented elsewhere. Parts of certain families have exploded evolutionarily in Australia. These include Phoxocephalidae, Dexaminidae and Urohaustoriidae. Australia is seen primarily as a huge environment capable of containing a diverse assemblage of these taxa and is not necessarily the place of origin for these and other taxa. However, Australia retains the most primitive living phoxocephalid (*Pontharpinia*).

A new classification of amphipods based on fleshy telson is promulgated and criticised. Two new families and two new genera are also created to fill obvious gaps in Australian taxonomy.

A prospectus treats new research needed, especially that which requires morphofunctional investigation.

Introduction

Evidence that Australia is a major evolutionary centre and refugium for both freshwater and marine Amphipoda (Crustacea) is presented in this paper. The evidence thrusts the presumed origins of the group back into the early Mesozoic during the time of Pangaea.

The evolutionary system, dispersal knowledge recently gained about Australian amphipods, and new ideas on classification are all interrelated. Two data bases, on freshwater and marine facts, will be presented here, then discussed and problems raised. The faunule in Australia is summarised and a prospectus treats the many investigations now required to clarify not only certain facts but the tentative conclusions drawn herein. Research to be done in the Australian region is of major importance.

A new subordinal classification of the order Amphipoda based on telson is presented in which the group is reduced to 3 suborders, Corophiidea, Gammaridea, and Hyperiidea, part of the old Gammaridea being removed to join Caprellidea to form the Corophiidea.

Objections to certain hypotheses and alternative explanations for several conditions are provided by the second author, Karaman, in Notes a, b, c, and d in Appendix 2.

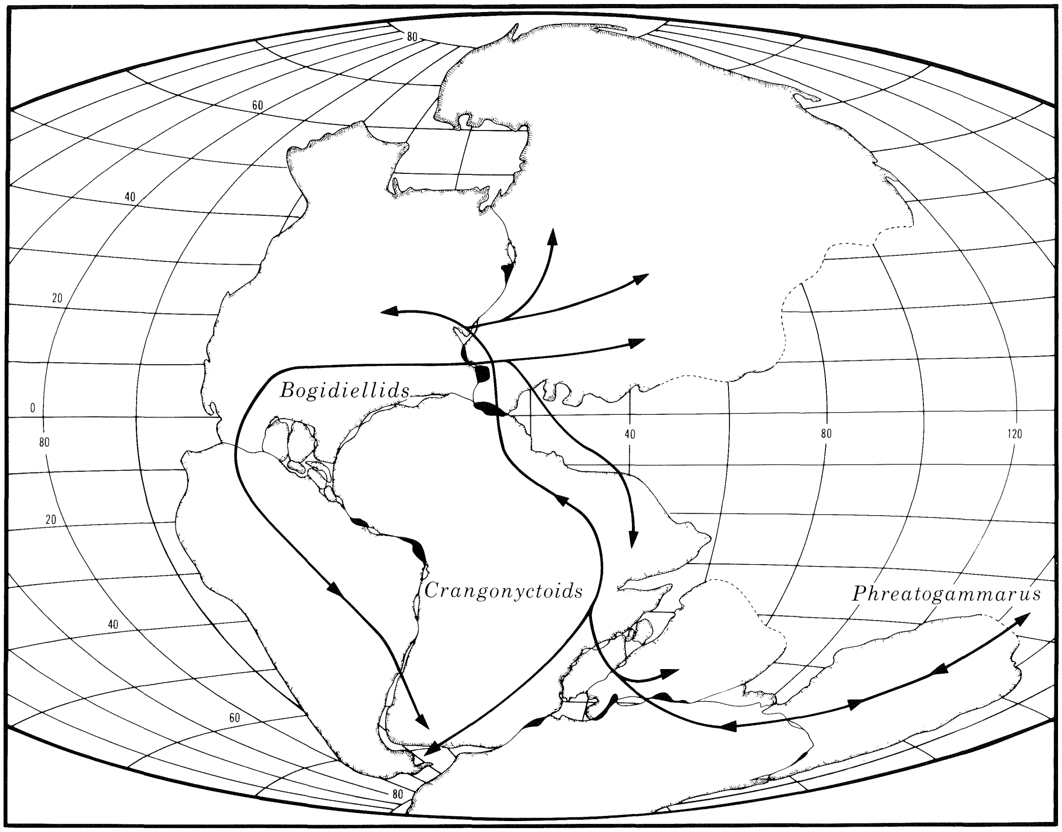

Fig. 1. Pangaea. Hypothetical pathways of amphipod groups based on modern distributional remnants.

Methods and procedures

The adjectival ending "id" refers to a group of amphipods conceivably at the level of family; "oid" refers to a group at the level of superfamily; "in" refers to a group at subfamily level.

The intent of this work is neither to create nor honour nor perhaps misuse many family and superfamily names published by others. Our concept of these categories is almost completely distinct from that of others and we often disagree between ourselves (see Appendix 2). We believe that a cluster to be honoured with a family name (*sensu lato*) should have a positive, describable and keyable distinction from other similar clusters and that all of the members of the cluster be so endowed. Clusters should be monophyletic.

This work borrows heavily from 2 unpublished books, "The Freshwater Amphipoda of the World" by J.L. Barnard and C.M. Barnard, in press, and "The Families and Genera of Gammaridean Amphipoda" by J.L. Barnard and G.S. Karaman, in preparation (since 1973, not yet completed).

Freshwater data base

1. Australia (=Notogaean), South Africa (=Ethiopian), Eurasia (=Palearctican) and North America (=Nearctican) have freshwater amphipods with many characters in common, including the presence of sternal gills. These amphipods are classified by Bousfield (1977) as Crangonyctidae. Several taxa of crangonyctids actually lack sternal gills but can be included in the group by internal goodness of fit through cladistic (descent and apomorphy) or phenetic (similarity) clustering. Actually they can be included by the simple phyletic process of finding their grossly closest morphological relatives which are themselves crangonyctids. Crangonyctids without sternal gills technically fall into the classic family Gammaridae which is restricted by Bousfield (1977) to a narrower content than in earlier times.

2. No modern marine pathways for crangonyctids are known to occur between Australia and South Africa, nor between Australia and Eurasia, nor between South Africa and North America, nor any mixture among these elements (J.L. Barnard, 1972b). In other words, there are no living marine relatives of crangonyctids in the seas around Australia or South Africa. In the context of marine groups identified through an extensive literature there appear to be no possible connections between freshwater crangonyctids of Holarctica and the southern hemisphere by oceanic connections in modern seas.

3. Freshwater amphipods of the gammarid-crangonyctid family group abhor the tropics. They apparently are adapted to cold waters and cold climates. However, a closely descendent group, the bogidiellids, has invaded subterranean habitats in tropical South America. Tropical epigean amphipods are absent in Asia, Africa and Australia at least in rainforest regimes or in the wettest northern parts of Australia. In the South American tropics the family Hyalellidae, with sternal gills independently evolved, has invaded certain epigean habitats. A modern tropical freshwater pathway for gammarids and crangonyctids does not exist because these taxa cannot cross the "Sonoran" deserts nor the equatorial rainforests nor tropical seas. In a few places some marine taxa have emerged into freshwater habitats and have converged towards the gammarid morphology but these apparently can be sorted away from the truly crangonyctid groups.

4. The crangonyctids can be considered to be plesiomorphic to gammarids in light of the general structure of amphipods which seems to have an evolutionary deployment proceeding from morphologically complicated to morphologically simplified (Barnard, 1969). Most of the characters for which one can construct plesiomorphic-apomorphic sequencing proceed from complex to simple and this dominantly fits a parsimonious and logical biogeographic picture. For example, the basic crustacean biramous antennal condition is progressively reduced to uniramous; the basic body segmentation is reduced; the fleshy uncleft telson is progressively laminated and cleft; the mouthparts are progressively degenerated; etc. One must note that amphipods generally are poor material for cladogenesis because of this negative progression (noting Ashlock, 1974).

5. Freshwater amphipods of a group known as austroniphargids occur in Madagascar. They bear coalesced urosomites and supposedly lack sternal gills. They could either be marine crawlouts or more parsimoniously they could be considered descendents of African crangonyctoids. No absurdities in phenetics, cladistics or evolutionary methods are known to prevent this assumption.

6. Freshwater amphipods of India and at least one genus of Australian freshwater amphipods (*Giniphargus*) are likewise assumed to be marine crawlouts because their closest ancestors morphologically and geographically live in the sea. There are very few and poorly studied taxa yet known in this category so that much more information needs to be gathered in this regard.

7. All insular freshwater amphipods from places such as Reunion, Andaman, Java, Bismarck, Hawaii, and Galapagos, can be parsimoniously best related to adjacent marine taxa. These are genera such as *Paraniphargus, Psammoniphargus, Galapsiellus, Anchialella, Rotomelita.*

8. The hadziids, which occur predominantly in limestone aquifers of central America, Caribbean Sea islands (Stock, 1977), margins of Mediterranean Sea and some Pacific coral atolls, have several blind marine species also. This distribution is predominantly Tethyan. A tightly parallel group with parsimonious ancestry in the marine ceradocids (*Ceradocus*) is the weckeliids, which occur only in the Caribbean part of the Tethyan sphere. Their ecology is similar to hadziids.

9. The Pontocaspian basin, today composed of remnants such as the Caspian, Black and Aral Seas has a diverse amphipod fauna. Part of the fauna is clearly of marine origin, genera such as *Corophium* and *Pseudalibrotus* being invaders either directly from the sea or from glacial sluicing which brought them from the shallow arctic sea into the drainage pattern of the Pontocaspian basin (Segerstrale, 1962). *Corophium* may be a holdover from Tethyan eras but if a Tethyan connection was supreme at one time the evidence is now poor. Many other possible marine and brackish Gondoasiatic genera simply left no impact on this basin (for example *Grandidierella* is not represented). The marine influence to us therefore appears to be entirely post-Tethyan, or at least the survivors have that character. The great majority of the fauna is of gammarid morphology, being composed of apomorphic genera from ancestors like *Gammarus* and *Echinogammarus.* But one group, which we call gmelinids, has a fossil ancestry in Miocene imprints (*Andrussovia, Praegmelina*). If these fossils clearly have aequiramous uropod 3 then their gmelinid descendents do not pass through *Echinogammarus* and therefore they form a subsidiary group. They may be an earlier holdover and be in the process of extirpation by the echinogammarids such as *Dikerogammarus* and *Niphargoides.* The sequencing descent is very good in these organisms, so close at times that Karaman and Barnard (1979) implied a large share of the species could be included within a few supergenera, themselves blending together.

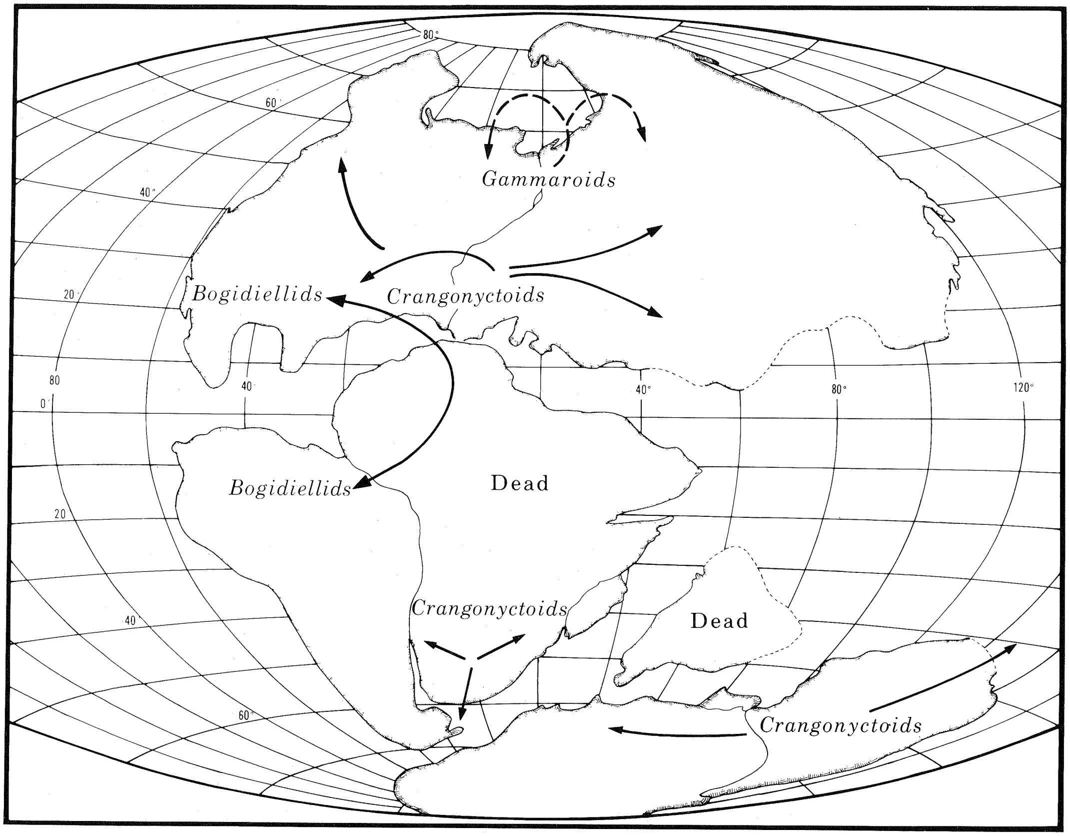

Fig. 2. Later Tethyan era. Crangonyctids now disjuncted. Gammaroid group (or *Gammarellus*) possibly developing now in northern sinuses.

The Pontocaspian amphipods are dominated by fossorial (burrowing) kinds owing to the great shallowness of the system and the high proportion of benthos to water volume. There are many congruencies in morphology between pontogammarids and Phoxocephalidae (Barnard and Drummond, 1978) but the ecological and biogeographic facts are all wrong at present to justify this relationship. Most taxonomists, including Karaman, believe that the congruencies between phoxocephalids and pontogammarids are entirely due to their similar ecological requirements and their remarkable similarities are a result of convergence. Once again, an amazing parallelism has arisen in Amphipoda, similar to that between the west Palearctic gammarids and the Baikalian microcosm.

10. Lake Baikal in Siberia, just north of Mongolia, contains more than 40 genera and about 300 species of gammarids. One of these, *Macrohectopus,* is so bizarre that it may have a distinctive origin but all others can be envisioned as having one ancestor. Again, most taxonomists believe this genus is autochthonous. The Baikalian faunule has diverged into pelagic, nestling, fossorial, and inquilinous kinds of taxa, with pelagic and nestling kinds dominant because of the high proportion of water to benthos in this deep lake (containing 20 per cent of the world's fresh water). The fossorial kinds are so close morphologically to Pontocaspian fossorial types that if they are polyphyletic and simply convergent then little damage would be done internally to the gammarid classificatory system. On the other hand, Bazikalova (1945), Koshov (1963), and others have proposed 4–6 ancestral kinds to the Baikalian amphipod fauna with biogeographic pathways from Pontocaspian and glacial lakes through Siberian ice lakes. Neither alternative, the mono- or the polyphyletic view, is empirically supported at present and these may be only tempests in a teacup.

The immense diversification seen in west Palearctic gammarids out of *Gammarus* and *Echinogammarus* and the fossil *Andrussovia* and *Praegmelina* through various sarothrogammarids, and dikerogammarids, into gmelinids, pontogammarids, and compactogammarids is so overwhelming that to have this repeated in the Baikalian microcosm with results selected by the environment is not difficult to accept.

Marine data base

1. The data bases for Gammaridea presented by Barnard (1962, 1965, 1969, 1976) remain mostly true, having been diversified and strengthened through subsequent description of numerous new taxa in a field (amphipodan systematics) that has exploded in the past decade. This data base shows that at generic level Gammaridea are more poorly developed in the tropics than one might expect (but notice the positive statement of item 2 below and that the taxa of the deepest seas are more apomorphic than those of the upper deep sea just below the continental shelf). In other words, the Bruun (1957) idea of ancient deep-sea taxa being displaced upward by cooling of the deep seas has not yet been disputed, at least in Gammaridea. One major modification now must be added; herein we realign the Amphipoda to make Corophioidea the most plesiomorphic of groups and this adds a strong tropical aspect to normalise the plesiomorphic content of the tropical fauna as in other groups. Taxa orbiting about the old Gammaridae (*sensu lato*) are still considered to be the most plesiomorphic of the Gammaridea but not of the Amphipoda as a whole (but see Note b, Appendix 2).

2. About 68 marine families of amphipods (barring hyperiidean kinds) occur today (J.L. Barnard, 1969, 1977, Bousfield, 1979) (see Appendix 1, taxa marked with *). About 35 of these are believed to be tropically plesiomorphic, whereas most of the remainder have their most primitive members in cold waters (J.L. Barnard, 1976) (Appendix 1, herein, cold taxa marked with †). About one third of the 33 coldwater taxa occur mainly in the deep sea or in cold pelagic waters. The 21 families of hyperiids listed in Bowman and Grüner (1973) could be added to this total. There is also strong coldwater representation in 7 of the 35 tropically plesiomorphic families mentioned above. Therefore Amphipoda are strongly developed in cold waters.

3. In Australia there is strong centrifugal character to 12 of the 68 families, here listed in order from strongest to weakest in focus: Dexaminidae, Phoxocephalidae, Urohaustoriidae, Zobrachoidae, Paracalliopiidae, Exoedicerotidae, Ochlesidae, Phliantidae, certain parts of Podoceridae and Stenothoidae (especially the thaumatelsonins), very weakly Platyischnopidae and Colomastigidae.

Australia is a centre or subsidiary centre for these families because of occurrence of plesiomorphs and/or great diversity of familial components or because of the occurrence of deployment sequences (Fig. 4 shows some of the strongest examples of these taxa). The "ends-of-the-earth" phenomena in marine amphipods discussed by Barnard (1972a, 1972b, 1974, 1976) prevail.

4. Other areas of the world do not have such a broad and sharp focus on families, the following notable exceptions being: Bateidae—Central America; Haustoriidae—New England (North America); Pontoporelidae—North Atlantic; Mesogammaridae, Gammaroporeidae, Anisogammaridae, Dogielinotidae and Najnidae—North Pacific; Hadziidae—Tethyan; Ceinidae—New Zealand; Plioplateidae, Temnophliidae, Kuriidae—South Africa (or Africa). Some of these are also shown on Fig. 4. Urohaustoriidae and Zobrachoidae are new families in press by Barnard and Drummond.

5. The fossil record for amphipods (Hurley, 1973) is confined to (1) Baltic ambers of Eocene age in which are well preserved such taxa as *Paleogammarus balticus* Lucks, a species so close superficially to modern crangonyctids that no justification for the genus can be made apart from great age; and (2) imprints in Miocene Sarmatian sediments near the Caspian Sea, contain taxa completely united to the special elements now living in the modern Pontocaspian basin. No fossils with plesiomorphic content are known. The occurrence of sternal gills on the Eocene amber fossils has not been demonstrated.

6. One genus of corophiidean amphipod, *Paracorophium,* is found in Australia, New Zealand and South America. This genus is largely limited to freshwater and is an exceptional genus in this superfamily, which is composed largely of marine taxa. One assumes the distribution of *Paracorophium* to be a result of continental drift.

Discussion

If the information presented in the data bases above is true the only pathway for crangonyctids between Holarctica and Notogea would have occurred in the Paleozoic or early Mesozoic when continental coalescence occurred at a time often denoted as Pangaean (including Laurasian). At that time the Indian subcontinent was near South Africa, Antarctica and Australia (Fig. 1); South America was pressed near Africa; and Eurasia and America were contiguous. A continuous pathway would have been provided for freshwater animals to disperse elsewhere.

The modern distribution of freshwater amphipods suggests that crangonyctids were widespread in Pangaea, never reached or died out from South America but bloomed in North America (Figs. 2, 3). Owing to severe ecological changes they exist only as remnants in Australia and South Africa. Owing to the evolution of competitive gammarids and niphargids which took hold primarily in Palearctica, crangonyctids have almost reached extinction there (but see Note c, Appendix 2). Only a few species survive in west Palearctica, whereas the east margin of Palearctica retains some highly derived, mostly subterranean crangonyctids such as *Pseudocrangonyx* and *Protocrangonyx.*

Problems: Today freshwater gammarid-crangonyctid amphipods abhor the tropics. One must therefore presume a cool-water pathway between Holarctica and Notogaea existed earlier. Today gammarid-crangonyctid amphipods live in South America only as descendent hypogean bogidiellids; and in India and middle Africa they are extinct. Either the amphipods or Pangaean environmental conditions were different then from what they are today. Just because marine crangonyctids do not exist today we cannot assume they did not exist during Pangaea. Thus, Australian and Nearctic freshwater crangonyctids could be relicts of pandemic marine forms now extinct. This is supported by the lack of primary freshwater fish interchange north to south in the fossil record (Darlington, 1957). The absence of crangonyctids in South America matches the situation in spiders noted by Besch (1969), who thought that South Africa pulled away early. But too many diverse and conflicting distribution patterns that could have been affected by continental drift exist in animal and plant groups so that virtually any desirable solution can be extracted from general biotic data (Keast, Erk and Glass, 1972).

The gammarids and their immediate descendents probably had a Laurasian origin. None has ever been found south of the Sahara or "Sonoran" deserts. A few of them retain or acquired a salt tolerance so that a few species of *Gammarus* and *Echinogammarus* have been able to penetrate into the very shallow seas and their margins in Holarctica. One suspects a case could be made for descent of gammarids from crangonyctids through loss of sternal gills, thereby improving physiological adaptations to osmotic problems such that a few could invade the sea. This may all have occurred during the breakup of Laurasia when so many rift lakes became brackish. Gammarids exploded in southwest Palearctica and escaped to, but poorly bloomed in, Nearctica where crangonyctids have been able to hold on and diversify. In west Palearctica, gammarids (*Gammarus, Echinogammarus*) spun off numerous genera into marginal ecoisolates such as estuaries, pebble-beach aquifers, and the great Pontocaspian basin where dozens of genera were spawned. The salt tolerance again is apparent but we believe that the amphipod fauna of Pontocaspia, apart from the obvious marine imports such as *Corophium,* is strictly of freshwater origin, from gammarids working outward towards salty waters. This is entirely opposite to all other opinions heretofore offered. We think this argument is strengthened by the inability of any gammarids to escape by sea routes outside Holarctica and for any but the most plesiomorphic (*Echinogammarus*) to escape out of the Pontocaspian Basin into the Mediterranean Sea.

Gammarids cannot even compete with their close vicariants, the Anisogammaridae, in the Pacific Ocean. And the anisogammarids have not escaped the North Pacific shallows.

Problems: If Corophioidea (see following chapter) are to be accepted as a good plesiomorphic marine group representing to some extent the best ancestral content of the order Amphipoda, then the direction from corophiideans to gammarideans is well expressed in the *Gammarellus* group where the telson is uncleft but no longer fleshy. *Gammarellus* could, at the very least, form a model for this evolutionary stage. It retains an accessory flagellum and can thus form a mode ancestral to both crangonyctids and gammarids and the various calliopiid-eusirid taxa (the latter mostly marine and showing loss of accessory flagellum but frequent retention of uncleft telson). *Gammarellus* survives today in the icy brackish shallows of the Arctic Ocean and coasts of Mediterranean Sea and Black Sea also. This jogs one's intuitive idea that crangonyctids had a Gondwanan origin from a *Gammarellus-Gammaropsis*-like ancestor, whereas gammarids (*Gammarus*) were spun off evolutionarily from crangonyctids during a brackish cycle through some tectonic rift or sinus borealis. Sites of origin and flow of distribution are therefore contentious at the moment.

Sternal gills are another problem. They occur in various crangonyctids but are lost in highly apomorphic members in both Australia and west America. They also occur in the remote hyalellids of South America and in a few other taxa such as *Sternomoera* (a pontogeneiid) of subterranean Japan and brackish *Pontoporeia* of the North Atlantic Ocean. One may construct an immense tree (not a true cladogram) to get from crangonyctids to hyalellids while retaining sternal gills, but it is preposterous and nonparsimonious. A much simpler system can be envisioned to get from crangonyctids to *Sternomoera* and *Pontoporeia* (indeed we herein remove the pontoporeiids from separate superfamilial status to low position near the gammarids). One must nevertheless conclude that sternal gills have arisen more than

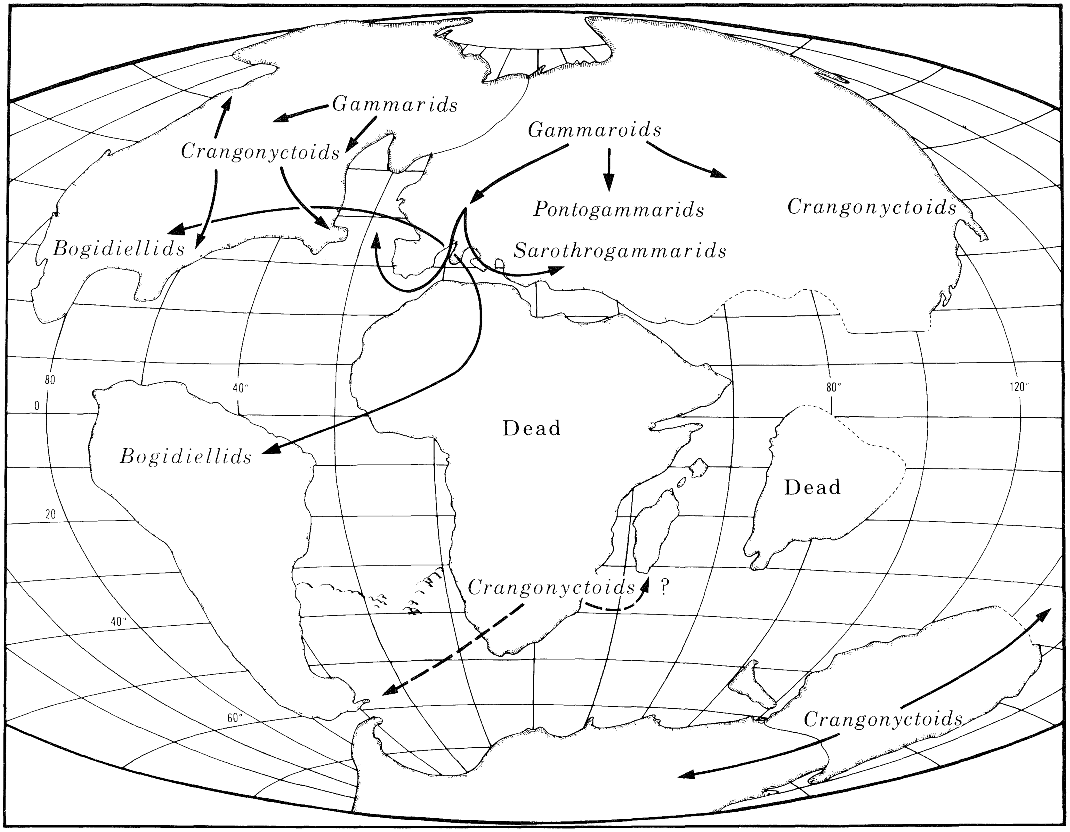

Fig. 3. Crangonyctids close to being split into 4 modern disjunctions (Nearctica, Palearctica, Ethiopian = South Africa, and Notogaean, with outposts in Falklands and Madagascar). Gammaroids will be split later by Nearctic part remaining poorly developed. Bogidiellids probably is a diversely polyphyletic group but one genus, *Bogidiella*, has definite intercontinental distribution as shown.

once in amphipods. Therefore, one must ask if sternal gills did not arise separately in Laurasia and Gondwanaland to produce parallel apomorphs (but see Note c, Appendix 2). We have no answer.

Classification and phylogeny

An evolutionary pattern in gammaridean Amphipoda was produced by Barnard (1969) and then updated by Barnard (1974). A revised classification and phylogeny of Amphipoda were produced by Bousfield (1978). Barnard's evolutionary tree was based on the plesiomorphy of accessory flagellum, 'basic' mouthparts, large coxae and dominance of gnathopod 2 in males, and worked outward towards specialisations such as pygidisation (modification of pleon by losses and fusions) and losses of structures such as in mouthparts and accessory flagellum.

Bousfield's tree and classification are based on the morphology of the reproductive male in which 4 kinds are recognised.

Both schemes recognise what has long been known, that there are corophioid (podocerid) amphipods which are clearly the ancestors of Caprellidae (Note a, Appendix 2), and that there is a greater Talitroidea group, and the following smaller groups conform: oedicerotids, stegocephalids, bogidiellids, and lysianassoids, ampeliscids, etc. Otherwise there is little but occasional similarity in certain juxtapositions. Barnard's scheme is mainly classificatory (rigid definitions) but has the advantage that all members in a group bear the class characters, whereas Bousfield's scheme is mainly evolutionary (indefinable clusters) and has the disadvantage that most of the individuals in a species lack the group characters

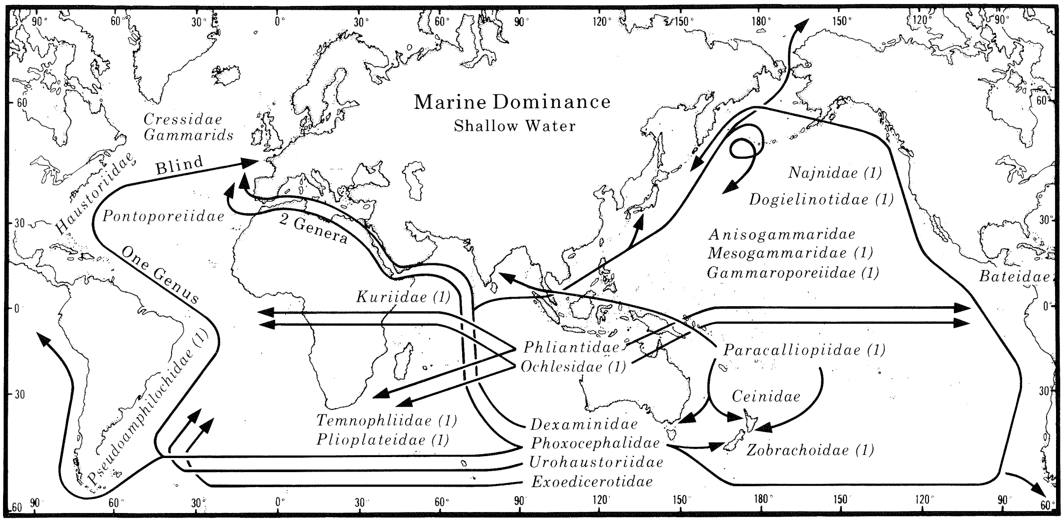

Fig. 4. Marine dominance by families in Australia. All but one North Pacific family are monotypic. Arrows show apomorphic shoots outward from Australia. Most other marine families have much wider distributions than those shown.

(since only terminal males of a few plesiomorphic species in each group have the class characters; other specimens have to be identified by approximations).

Barnard now proposes another scheme which reconstructs the Amphipoda at suborder level but which downgrades the significance of Bousfield's superfamilies and maintains some of the web-like structure of the earlier Barnard schemes.

This proposal recognises the plesiomorphy of the solid fleshy telson in Corophioidea and Caprellidea and joins them together into a suborder Corophiidea (but see Karaman's Note b, Appendix 2). This removes the Corophioidea and the Caprogammaridae from the suborder Gammaridea and leaves it to hold other amphipods. The suborder Hyperiidea is maintained as an assemblage which early lost the palp of the maxilliped and the suborder Ingolfiellidea is placed under Gammaridea as nothing more than a bogidiellin with altered operation of dactyls on gnathopods (but see Note e, Appendix 2).

The order Amphipoda is therefore reduced to 3 suborders on fleshiness (Corophioidea, Hyperiidea) and lamination (Gammaridea) of telson. Forms with fleshy telson are considered plesiomorphic because the laminar telson is considered to be a specialisation abnormal to basic crustaceans. Though not Hennigian, Barnard believes this to be a very workable classification because more than 95 per cent of all amphipod specimens can be classified instantly into suborders.

The classification is presented in Appendix 1 and Fig. 5. It places the suborder Corophiidea first (upper left) as most plesiomorphic, showing that these amphipods represent only a small part of the total order and are divisible into only 2 superfamilies, the Corophioidea and the Caprelloidea, neither of which is worth much because the two groups grade into each other so broadly through the Podoceridae, Caprogammaridae and Caprellidae (with 4 other residual families not mentioned).

The Corophiidae was divided into additional families by Bousfield (1973) and although Bousfield's method has great interest and possible merit we have not reanalysed this situation.

The suborder Gammaridea continues to have the Gammaridae or similar taxa at its base, for example, those taxa that resemble primitive corophioids (such as *Gammaropsis*) except in telson. In other words, gnathopod 2 is fully developed and strongly prehensile (Barnard, 1969) but the telson is laminar, not fleshy.

At the base of the Gammaridae are placed the crangonyctids which contain relict sternobranchiate genera now confined to freshwaters of southern Australia, southern Africa, sketchily in Palearctica and in a blooming condition in Nearctica. Their descendents, various subterranean bogidiellins, occur prominently in the west Tethyan region but especially in South America where orthodox crangonyctids have disappeared. The dispersal of crangonyctids had to occur when all the continents were coalesced as they have no connection whatsoever with marine amphipods. Neither the crangonyctids nor the

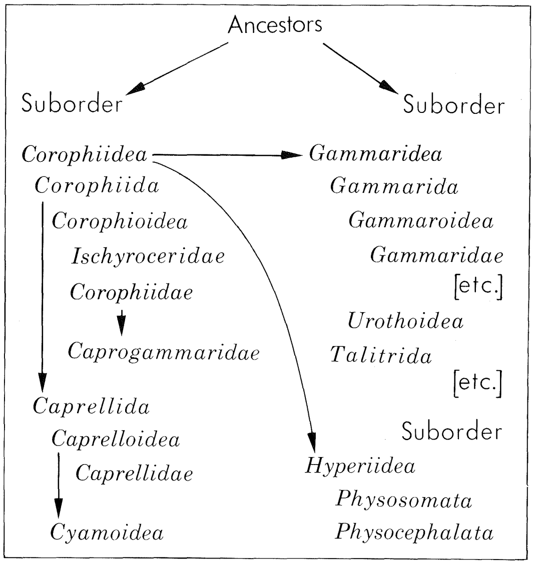

Fig. 5. Higher groups of order Amphipoda.

bogidiellids can be recognised nominally as families because neither of them has technical definitiveness. They simply represent large diffuse clusters of genera which can be interrelated by use of phyletics, phenetics or cladistics when seeking nearest relatives but a crangonyctids without sternal gills or one without notched spines on the palms of the gnathopods is not definitively distinct from gammarids.

New groups of crangonyctids are proposed to clean up the evolutionary classification and to show the phyletic order Barnard conceives. But none of these is a very good group beyond cluster level although one can clearly invoke such 'all or none' characters as bifidation of coxal gill 2 in *Allocrangonyx* to raise it so as to typify family level or the fusion of urosomites to validate Austroniphargidae. Barnard and Karaman (1974) warned against premature formalisation of names but this has not been taken seriously by anybody. We are now beginning to be burdened by many superfluous and even foolish names as high as at superfamily level (for example Niphargoidea, a cluster not worth recognition at more than supergeneric level).

The old Gammaridae, *sensu lato,* of Stebbing's (1906) concept was narrowed stringently by Bousfield (1973, 1978) but in reality about all that has happened is that it has been upgraded to a superfamily (or it could be elevated to a section* "Gammarida" if one could define it in some way). It remains as indefinable as it ever was, regardless of categorical level. Our concept of the contents and their phyletic order is presented in Appendix 1 in very skeletal form, taken from the Barnards' (in press) forthcoming book "The Freshwater Amphipoda of the World". As in almost all other Gammaridea at any level, there is very little complete discontiguity between or among groups. Gaps between clusters are not absolute, only pinched places between clumps. For example, we follow the convention of European specialists that strongly honours the parviramous uropod 3 of *Echinogammarus* as a strong distinction from *Gammarus,* but only with tongue in cheek, because so many bridges occur across this boundary (for example, *Gammarus roeseli* to *Echinogammarus annandalei*).

The old Gammaridae contained some clusters or cluster fragments that can be removed, such as Anisogammaridae, about the only group that can be rigidly defined (with accessory coxal gills), or the Macrohectopinae (based on the mysidiform Baikalian genus *Macrohectopus,* raised to family level by Sowinsky, 1915, honoured by Bousfield, 1978, but here removed to the vicinity of weyprechtiins in the Melphidippidae). Here, Bousfield must be looking at reproductive males while we are looking at gnathopods and telson.

Proceeding past the Melphidippidae, a rather strong cluster, one finds the Hadziidae, a weak cluster with little to recommend it except some ecological facts. Bousfield recognises it as a family in Melitoidea, a superfamily which we here reduce to family or lower level and equate with and then rename as hadziids (which has priority). We can't define this melitid-hadziid group in more than negative terms; the

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*The term "section" is a taxonomic category between suborder and superfamily.

component taxa are largely in the ocean or in Tethyan nearshore limestones and lack coxal gill 7, lack sternal gills, lack calceoli, and lack notched spines on gnathopods (or do they?). Without any positive features they are simply a residue of indefinable things. Some of these leftovers are worse (more degenerate) than others and therefore can be clustered: for example, the *Metacrangonyx* group lacking inner ramus on uropod 3.

There are scarcely any but ecological reasons to recognise hadziids, weckeliids and melitids and out of all of this, the completely negative niphargids, which are only barely definable from eriopisellids, are here reduced from superfamily level to supergeneric level.

Having lost almost everything, coxal gill 7, sternal gills, differentiated gnathopods, notched gnathopodal spines, thick bodies, deep coxae and long inner ramus of uropod 3, and having developed only in a majority of taxa a long article 2 on the outer ramus of uropod 3, a character replicated in eriopisellids and certain crangonyctids, niphargids are the ultimate evolute in the gammaroids, *sensu lato*. Apart from ingolfiellids and crangonyctids (and bogidiellids) they also have the strangest ecology (stygobionts) and perhaps strangest behaviour (errant) of any gammaroids. But they are not a good, definable cluster and there is no evidence they are not simply one more variation on a theme, similar to eriopisas and eriopisellins.

All of the other families listed in sequence in Appendix 1 starting with Eusiridae also form an outline of taxa listed for the purpose of item 2 of Marine Data Base showing total marine families. The Gammaroidea contain a wide assortment of families besides the classical Gammaridae. The Talitroidea contain several families already consolidated earlier in the literature. The remaining families must remain unordered until they are better understood.

The Australian faunule

The freshwater Amphipoda of Australia today are strongly constrained descendents of a fauna common to much of Pangaea of pre-Jurassic times (Figs 1-3). These crangonyctids today bloom in North America, are holding on in east Palearctica but are almost or fully extinct elsewhere, except for the remarkable and primitive New Zealand *Phreatogammarus*. Crangonyctids are antitropical and one would expect their environment to disappear if Australia pushes northward completely into the tropics. In Australia crangonyctids can be described as relicts because one assumes they were much more diverse when the Australian climate was wetter and colder. In Europe they have been largely extirpated by gammarids and niphargids (but see Karaman's Note c, Appendix 2). Australian and South African crangonyctids are very closely connected. As far as is known, crangonyctids never reached South America or went extinct, but may be represented by the apomorphic *Spelaeogammarus* and various bogidiellins which one presumes were also in existence and distributed among the continental fragments during Pangaea. The austroniphargids of Madagascar have the appearance of apomorphic crangonyctids.

Approximately 12 of the 68 major family groups of so-called gammaridean amphipods in the sea have a strong focus on Australian shores, especially in the warm-temperate outpost of the southern half (Fig. 4). This may both be a place of action and a refugium for the remnants of evolutionary deployment in all of certain families and subdivisions of other families. No other marine place on earth holds even half as many such family centres; of course, a significant share of the marine families is either subcosmopolitan or confined to cold waters. This makes the Australian dominance more superior.

We have reconstructed the order Amphipoda on the basis of telsonic apomorphy to proceed from a primitive suborder Corophiidea, containing former gammarideans with fleshy telson and including the Caprellidea, outward to the newly restricted Gammaridea, from which the corophioids have been removed (Fig. 5). The Ingolfiellidea are sunk into the Gammaridea and the Hyperiidea are retained as an early branch from Corophiidea in which the telson retains more of its plesiomorphy than does the average gammaridean telson and in which the maxillipedal palp is lost. New taxa described are Paracalliopiidae, Exoedicerotidae, and *Austrocrangonyx* (Appendix 3). We have also proposed a system of evolutionary deployment within the section Gammarida, distinct from the Bousfieldian system (Appendix 2 and Fig. 6). Much of this is based on knowledge of Australian taxa.

Prospectus

1. Continue study of morphology, function and ecology of crangonyctoids to find proof whether or not Nearctic and Notogaean taxa are homologous or monophyletic or at least sister groups with a common ancestor.

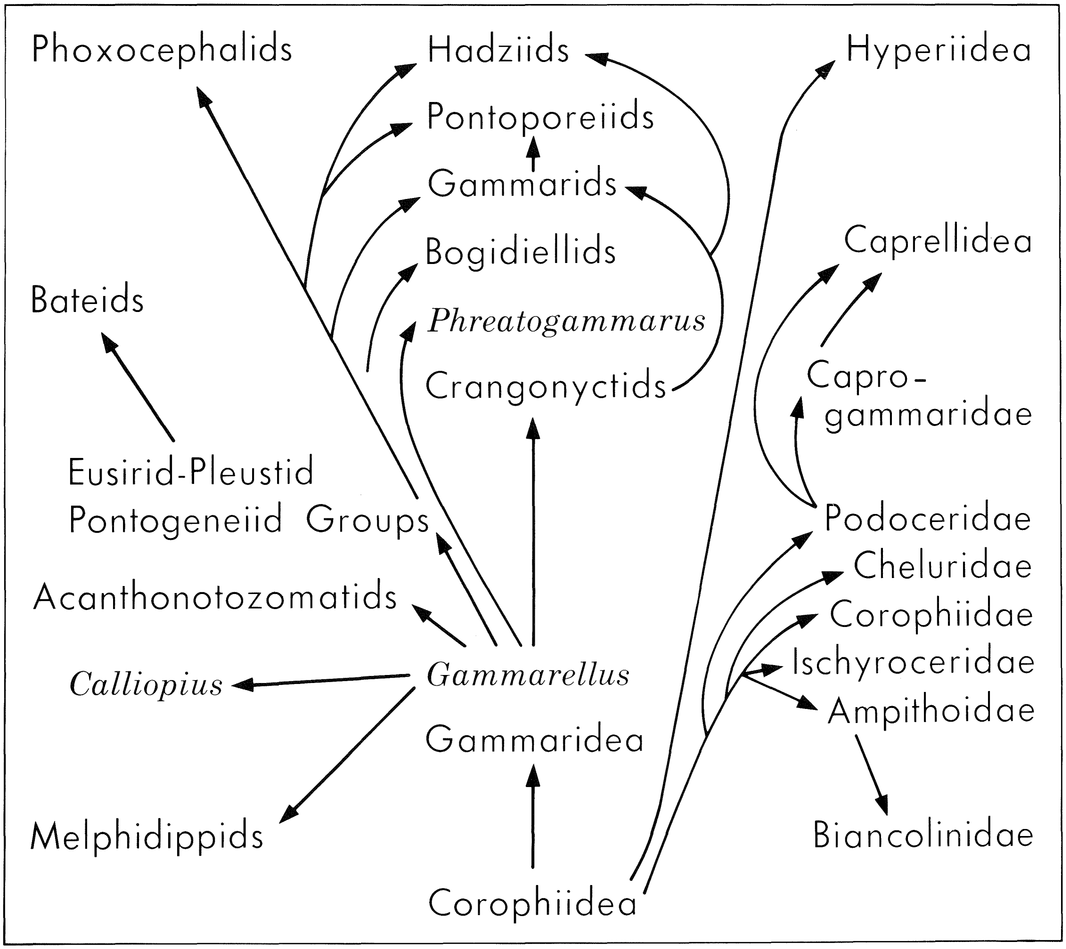

Fig. 6. Tree of relationships showing mostly primitive amphipod groups. Many apomorphs such as *Talitroidea* are omitted. Made to show total contrast with tree of Bousfield (1978).

2. Work out a theory of the development of sternal gills in amphipods. Are sternal gills of crangonyctoids and hyalellids and other amphipods homologous or are they structurally distinct and of differing origins? How can apomorphic species of *Stygobromus* survive without sternal gills? Drummond (*in litt.*) has suggested to us they may be mainly osmotic rather than respiratory as in certain insects. How useful are they to the species known to have them? Can they be removed and not affect survival?

3. Develop ecological theory on sequential relationships between crangonyctids and gammarids. Is one or the other plesiomorphic or are they sister groups with a common ancestor? Develop a model of an ancestor and its ecology, especially its osmotic problems and potential.

4. How are gammarids better adapted than crangonyctids in west Palearctica and why are gammarids so much less well adapted than crangonyctids in Nearctica? Is this entirely the late arrival of gammarids?

5. Reconstruct all osmotic sequencing and other data to test the hypothesis that marine species of *Gammarus* have ultimate freshwater ancestry. Ditto for various Pontocaspian taxa.

6. Study the functional reasons for tropical antipathy in freshwater gammarids. Make ecological comparison between general gammaroid facies and talitroid facies (the freshwater hyalellids of Neotropica).

7. Intensify study of the rare tropical freshwater gammarids such as *Indoniphargus* and

Paraniphargus and in the former make ecofunctional and morphologic analyses seeking links to crangonyctoids. The purpose is to determine if *Indoniphargus* is a relict of Gondwanan crangonyctoids. How do marine taxa such as *Paraniphargus* and *Rotomelita* so easily invade freshwater? *Paracalliope,* a non-gammarid but potentially remote descendent of crangonyctoids, needs strong focus. That genus may also be interpreted as a freshwater relict of the basal stock near marine Oedicerotidae.

8. Focus on *Phreatogammarus,* the New Zealand endemic with 3 species. Do the many generalised plesiomorphic characters imply a transitional mode between marine and freshwater crangonyctoids, or is *Phreatogammarus* simply a relict now moving outwards to the sea on an impoverished archipelago?

9. Is the generally low generic diversity (and relatively low morphologic diversity) of Notogaean-New Zealand-South African-Falklandian crangonyctoids evidence of eternal Gondwanan stagnation of environment? Balance this diversity against the similar low Nearctic diversity and then compare to the Baikalian explosion in gammarids. West Palearctic gammarid diversity, though reduced recently by us through synonymies, is also very striking. Are these diversities simply the result of Hennigian commonness or (more probably) certain favourable ecological circumstances?

10. Balance the roots of stenothermy and competition in assessing the reasons for tropical abhorrence in amphipods. This abhorrence in epigean forms is close to 100 per cent (except hyalellids, one tropical genus so far) but at generic level it is also rather high in marine shallows. Is there such a thing as stenothermy—a genetically controlled intolerance of tropical waters for thermal reasons—or is there a stenocompetitive factor also involved? To what extent do these factors explain the absence of amphipods in African rift lakes? One must note generally that amphipods are of low diversity in freshwater lakes other than Baikal, Titicaca, Ohrid and Pontocaspia.

11. Determine the lowest thermal limits of a cold era fossil pathway between Laurasia and Gondwana during which time freshwater amphipods could migrate between Nearctica and Notogaea.

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APPENDIX 1, GROUPS OF AMPHIPODS

Nomenclature often restricted to "in", "id" and "oid" endings so as not to create or submerge taxa; comments in parentheses show subordination of groups considered by Bousfield (1978) to be situated at higher level. * = Marine Family Group; † = Cold Centre.

Suborder Corophiidea
  Superfamily Corophioidea (at best gradational)
    *Corophiidae (Aorids, Photids, Isaeids)
    *Ischyroceridae
    *Ampithoidae
    *Biancolinidae
    *Cheluridae
    *Podoceridae
    *Caprogammaridae
  Superfamily Caprelloidea (at best gradational)
    *Caprellidae (and 4 residual families)
    *Cyamidae
Suborder Gammariidea
  Superfamily Gammaroidea
    Crangonyctids (reduced from superfamily level)
      Phreatogammarins (new) (Phreatogammarus group of Bousfield)
      Paramelitins
      Neoniphargins (reduced)
      Sternophysingins (new)
      Crangoncytins (reduced)
      Pseudocrangonyctins (new)
      Allocrangonyctins (new)
      Austroniphargins (new)
      Spelaeogammarins (new)
      Bogidiellins (reduced from superfamily level)
    Gammaridae
      Gammarins (Gammarus group)

    - Brandtia group
    - Echinogammarus group
    - Metohia group (vaguely Typhlogammaridae of Bousfield)
    - Fluviogammarus group (artificial)
    - Acanthogammarus group (Acanthogammaridae of Bousfield)
    - Dikerogammarus group
      - Gmelina subgroup
      - Dikerogammarus subgroup
    - Pontogammarus group (Pontogammaridae of Bousfield 1978)
      - Pontogammarus subgroup
      - Compactogammarus subgroup
    - Cardiophilus group (gradational) (Behningiella-Zernovia group of Bousfield)
    - †*Pontoporeia group (reduced from superfamily level)
    - Macropereiopus group
    - Micruropus group
    - Hyalellopsis group
  - †*Mesogammaridae
  - †*Gammaroporeiidae
  - †*Eoniphargids (new)
  - †*Anisogammaridae
  - †*Melphidippidae
    - Weyprechtiins (new)
    - Cheirocratins (new)
    - Hornelliins (new)
    - Megaluropins (new)
    - Argissins
    - Melphidippins
    - Macrohectopins
  - *Hadziids
    - Ceradocins (new)
      - Ceradocus group (or to include Paraweckelia subgroup)
      - Paraceradocus group
      - Maera group
        - Maera subgroup
        - Elasmopus subgroup
        - Beaudettia subgroup
      - Parapherusa group
    - Ceradocopsins (new)
    - Gammarellins (new)
    - Weckeliins (new) (founder is Paraweckelia subgroup above)
        - Paraweckelia subgroup
        - Weckelia group
    - *Hadziins
    - Metacrangonyctins
    - *Melitins
      - Melita group
      - Eriopisella group
      - Salentinella group
      - Pseudoniphargus group
      - Niphargus group (Niphargoidea and Niphargidae of Bousfield)
  - †*Eusiridae (= Calliopiidae, Pontogeneiidae)
  - †*Bateidae
  - †*Pleustidae
  - †*Carangoliopsidae
  - †*Laphystiopsidae
  - †*Acanthonotozomatidae (= Paramphithoidae) (= Amathillopsidae)
  - *Urothoidae
  - †*Phoxocephalidae
  - *Platyischnopidae
  - *Urohaustoriidae (new)
  - †*Haustoriidae
  - †*Zobrachoidae (new)
- Superfamily Talitroidea

*Hyalidae
*Hyalellidae (also has freshwater taxa)
Talitridae
†*Dogielinotidae
†*Najnidae
†*Ceinidae
  Chiltoniinae
*Plioplateidae
*Phliantidae
*Kuriidae
†*Temnophliidae
Unordered families
*Liljeborgiidae
*Sebidae
†*Lysianassidae
†*Synopiidae
†*Pardaliscidae
†*Stilipedidae
†*Hyperiopsidae
†*Astryridae
†*Maxillipiidae
†*Vitjazianidae
†*Dexaminidae (submerging all other dexaminoids)
*Colomastigidae
*Ampeliscidae
†*Exoedicerotidae (new)
†*Oedicerotidae
†*Paracalliopiidae (new)
†*Stegocephalidae
†*Ochlesidae
†*Lafystiidae
†*Pseudamphilochidae
*Amphilochidae
†*Pagetinidae
*Nihotungidae
*Leucothoidae
*Anamixidae
*Stenothoidae (= Thaumatelsonidae)
†*Cressidae

APPENDIX 2, KARAMAN'S ANTITHESIS

Note a: Karaman believes that Caprogammaridae do not support the opinion that Corophioidea are ancestral to Caprellidea; he remarks they are close to Podoceridae but Barnard puts Podoceridae in the Corophioidea despite certain problems such as absence of tube-forming glands in various taxa. Barnard remarks that we may simply be failing to communicate to each other that Podoceridae are corophioideans.

Note b: Karaman does not accept the theory of telsonic fleshiness having any high taxonomic validity. The telson is so variable even within one genus that its value is questioned. For example, *Niphargus duplus* has a fleshy telson in a genus otherwise defined as having a laminar telson; in *Bogidiella* the telson has progressed and regressed from fleshy to laminar; certain talitroids have a fleshy telson. Karaman continues to accept the standard classification within amphipods, 4 suborders of equivalent status, Hyperiidea, Gammaridea, Ingolfiellidea and Caprellidea. Caprogammaridae form the link between Gammaridea and Caprellidea. Corophioidea must be retained in Gammaridea. They are not the oldest of living amphipods and are only one additional adaptation of primary gammaridean amphipods with highly specialised characters. There are no fossil records to substantiate any theories of evolution within amphipods.

Note c: Karaman believes the opposite; crangonyctids have arrived in Europe much later than gammarids. Most crangonyctids, especially *Synurella,* are now expanding because of their high vitality and resistance to variables in oxygen tension and temperature and other exigencies of subterranean life.

For example, certain crangonyctids have recently been imported by humans from America to England and Holland and are expanding. Probably crangonyctids arrived in America first but gammarids arrived in Europe first. This explains the differing dominances of the groups.

Note d: Variability within amphipod genera is high; for example, coxal gill 7 is present or absent within the basic European genus *Echinogammarus* and this is just one of the many anomalies within amphipods that prevent any clear classification in higher categories.

Note e: Karaman states that Ingolfiellidea are not as close to Gammaridea as they seem to be at first glance. Ingolfiellidea are well-defined in the special shape of gnathopods 1-2, having coalesced with the head the first and sometimes the second thoracic segments and often having articulate ocular lobes in marine species. In contrast there are so many other ill-defined amphipod groups that it is inappropriate now to deal with ingolfiellids in this way.

APPENDIX 3, NEW TAXA

Exoedicerotidae, new family

Type genus: *Exoediceros* Stebbing, 1899.

Composition: *Exoediceropsis* Schellenberg, 1931; *Bathyporeiapus* Schellenberg, 1931.

Diagnosis. Gammaridean Amphipoda with urosomites 1-3 separate, pereopod 7 elongate as in Oedicerotidae, dactyl elongate and setose; head ordinary (not galeate); eyes 2 and fully lateral. Accessory flagellum vestigial or absent, antennae of general gammaroid form, often with calceoli on flagella in one or both sexes. Mouthparts of primitve form, thus with all palps present and fully articulate or divided, all medial setae present; inner lobes of lower lip present. Gnathopods sexually diverse, wrists lobate or not, mittenform or not, palms obsolescent or poorly defined. Coxae overlapping, medium to elongate, sometimes variable between the sexes. Pereopods 3-4 with vestigial dactyls; except for pereopod 7 no pereopods with fossorial mechanisms. Pleopods and peimera ordinary. Outer rami of uropods 1-2 not shortened, rami well spinose. Uropod 3 magniramous, aequiramous, peduncle elongate, rami slender, lanceolate. Telson laminar, leaf-like, entire. Coxal gills sac-like, subovate, oostegites narrow, setose.

Relationships. Like Paracalliopiidae but dactyls of pereopods 3-4 vestigal, outer rami of uropods 1-2 not shortened, urosomites all free. Like Oedicerotidae but eyes paired and lateral. *Metoediceros* Schellenberg (1931) is like this taxal group but uropod 3 is severely reduced.

Paracalliopiidae, new family

Type genus: *Paracalliope* Stebbing, 1899. Unique.

Diagnosis. Gammaridean Amphipoda with urosomites 2-3 fused together, pereopod 7 elongate as in Oedicerotidae, dactyl elongate and setose; head ordinary (not galeate); eyes 2 and fully lateral. Accessory flagellum vestigial or absent, antennae of general gammaroid form, with calceoli on both flagella in one or both sexes. Mouthparts of primitve form, thus with all palps present and fully articulate or divided, all medial setae present; inner lobes of lower lip present. Gnathopods sexually diverse, wrists lobate, in female very small, mittenform, in male of enlarged mittenform kind, hands thus softly ovate, palms poorly defined except by unarmed corners. Coxae overlapping, medium to elongate, variable between the sexes (coxae 2-4 elongate in female). Pereopods 3-4 with normal dactyls; except for pereopod 7 no pereopods with fossorial mechanisms. Pleopods and epimera ordinary. Outer rami of uropods 1-2 slightly shortened, otherwise well spinose; uropod 3 magniramous, aequiramous, peduncle elongate, rami slender, lanceolate. Telson laminar, leaf-like, entire. Coxal gills sac-like, subovate, oostegites expanded, setose.

Relationships. Like Exoedicerotidae but dactyls of pereopods 3-4 well developed, urosomites 2-3 fused.

Austrogammarus Barnard and Karaman, new genus

Type species: *Gammarus australis* Sayce, 1901.

Diagnosis: Urosomites occasionally with transverse posterodorsal setation. Rostrum weak to obsolescent, lateral cephalic lobes weakly projecting, subrounded. Eyes potentially present or absent.

Antennae 1-2 elongate, antenna 1 longer than 2, ratio of peduncular articles generally = 22:15:7, accessory flagellum 3-6 articulate. Antenna 2 usually bearing paddle-shaped calceoli (at least in male).

Ratio of mandibular palp articles generally = 7:20:17, article 3 weakly falcate, setae = BDE. Labium lacking inner lobes. Maxillae medially setose, inner plate of maxilla 1 triangular, fully setose medially, outer plate with ?7 spines, palps ?symmetric. Inner plate of maxilla 2 with oblique facial row of setae. Maxillipedal palp articles 2-3 densely setose laterally or ventrally.

Coxae 1-4 elongate, strongly setose, coxa 1 not expanded below, not prominent, coxa 4 lobate, coxa 5 much shorter than 4. Gnathopods 1-2 of medium size, alike but male gnathopod 2 slightly enlarged and with shortened wrist, article 5 of gnathopod 1 and female gnathopod 2 as long as article 6, poorly lobed, article 6 alike in both pairs, palms weakly oblique, lacking bifid spines.

Pereopods 5-7 not elongate, article 2 weakly expanded, ovate to pyriform, lobed or unlobed, dactyls not spinose.

Epimera lacking vertical rows of setae on lateral faces. Rami of uropods 1-2 extending subequally, margins spinose, uropod 2 ?with basofacial armaments. Uropod 3 weakly extended, variramous, peduncle short, outer ramus 2-articulate, article 2 short, inner ramus generally reaching to M. 67 on article 1 of outer ramus in male but only to M. 50 in female. Telson short, cleft to base, lobes tumid, with dorsal and apical spination.

Variants. Anterior coxae often with posteroventral spines; peduncle of uropod 2 often setose.

Relationships. Differing from *Phreatogammarus* in the diverse rami of uropod 3 (they are unequal in size and armaments), short article 1 of mandibular palp and poorly spinose palms of the gnathopods; from *Paramelita* in the diversity of male and female gnathopods; longer inner ramus of uropod 3, more strongly setose maxillae and lack of vertical facial rows of epimeral setae. Differing from *Crangonyx* in the elongate inner ramus of uropod 3, fully cleft telson and absence of bifid spines on the gnathopodal palms.

Species: *australis* (Sayce, 1901); *haasei* (Sayce, 1902); Australia, Victoria, epigean, 2.

Austrocrangonyx Barnard and Karaman, **new genus.**

Type species: *Gammarus barringtonensis* Chilton, 1916.

Diagnosis: Like *Austrogammarus* but uropod 3 fully parviramous; maxillae poorly setose medially.

Variants. Accessory flagellum only 3-4-articulate; inner plate of maxilla 1 with only 3-7 setae; article 2 on outer ramus of uropod 3 present or absent; eyes occasionally absent.

Relationships. Differing from *Paramelita* in the similarity of male and female gnathopods and absence of facial epimeral setae.

Species: *antipodeus* (G.W. Smith, 1909): *barringtonensis* (Chilton, 1916); *mortoni* (Thomson, 1893); *?niger* (G.W. Smith, 1909); *ripensis* (G.W. Smith, 1909); Southeastern Australia and Tasmania, epigean to hypogean, 4 species and one probable species.

ACOUSTIC 'CALLING' BY FIDDLER AND GHOST CRABS

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SUMMARY

Male fiddler and ghost crabs are unique among the Crustacea in their use of acoustical signals to call females during the breeding season. This paper reviews what has been learned about the sound-producing mechanisms, signal characteristics, calling range, detection abilities and the behavioural responses of the crabs to the calls. Evidence is also presented to suggest that species differences in call structure are heritable.

Recent studies indicate that differences in calling behaviour in the two groups can be related to burrow zonation and access to water, and are best conceived as representing a continuum of change rather than two (or more) distinct patterns. Finally, directions of future research are outlined which emphasise where needed experimental studies would be most appropriate.

I. INTRODUCTION

It has been about thirty years since the importance of nocturnal sound production in the courtship of fiddler and ghost crabs became apparent. I do not mean to imply that nothing was known beforehand. On the contrary, a number of earlier, largely anecdotal accounts by naturalists documented the occurrence of ghost crab 'choruses', heard on quiet tropical nights by keen listeners. Anatomical studies revealed the well-developed stridulatory and 'tympanal' organs of ghost crabs and their relatives. But the widespread use of sound among these animals and its role in communication were matters for speculation. Indeed, virtually nothing was known about hearing in terrestrial crabs, whether sounds were produced by one or both sexes, or how the crabs themselves responded to the acoustic stimuli emitted by conspecifics. The answers had to await the development of suitable tape recorders, transducers, and speakers, none of which were available until the 1950's.

Many of these questions can now be partly answered; others still remain. My purpose in this paper is to summarise the present state of our knowledge, emphasising where the gaps have been filled and where they still remain. I will also indulge in some speculation which I hope may form the basis for hypothesis-testing by future workers. I shall not attempt to cite the historically pertinent literature, as most of this is referred to in my earlier reports, those of my collaborators, or reviews (Schöne, 1968; Salmon and Atsaides, 1968; Horch, 1971, 1975; Crane, 1975; Weygoldt, 1977). Rather, this paper will emphasise significant contributions over the last 20 years.

Before proceeding, a few words are necessary to place this particular topic in its biological perspective. The use of sound as a *calling* signal is a rare phenomenon among the Crustacea. It is unknown among the marine forms. Acoustic *calling* (spontaneous sound production by a single crab, usually male) occurs only in the subfamily Ocypodinae, though other Ocypodids, as well as terrestrial crabs (Gercarcinidae, Grapsidae), use sound during *courtship* interactions (i.e. when one crab, usually a male, has detected the presence of another, usually a female). Why these differences exist is a puzzle requiring more detailed study of the groups involved. In any event, the rarity of this behavioural adaptation invites comparison between acoustic calling in the Crustacea, with their unique marine heritage, and analogous systems in terrestrial forms such as insects and frogs. Are similar mechanisms involved in the coding of species-typical information within calls? What sort of adaptations minimise the effects of noise? How are sound sources localised? What types of central processes underlie decoding and recognition? Are stimuli detected as air- or substrate-borne signals? This is not a complete list of questions, but it emphasises the rationale behind these studies. We hoped through an analysis of acoustic calling in *Uca* and *Ocypode* to simultaneously contribute toward an understanding of their specific adaptations, and also of the general features common to calling systems in a variety of animals.

II. SIGNAL PRODUCTION, TRANSMISSION AND DETECTION

Acoustic calling by fiddler and ghost crabs is only performed by males in possession of special 'mating' burrows. The burrows are distinguished from those of non-calling males by their location and/or their structure (Linsenmaier, 1967; Lighter, 1974; Christy 1980). Calling also is most prevalent for a few days twice each month (a semi-lunar rhythm), though the exact timing with reference to lunar phase varies with species. In fiddler crabs (Christy, 1978) calling activity coincides with the timing of ovarian ripening of females. The driving force for timing display activity in males is thought to be this ovarian cycle in females. But the significance of the female rhythm itself is not understood. Zucker (1978) and Christy (1978) have hypothesised that females synchronise reproduction so as to release their larvae during optimal tides some days later. However, these authors disagree on whether tidal flow optimises larval dispersion, or prevents the larvae from being scattered too far from protected shorelines.

Fiddler crabs call by 'rapping' or by 'honking', depending upon species (Fig. 1). Rapping species rapidly 'vibrate' their major cheliped against the substrate. The sounds are composed of a series of pulses, each of which represents one strike between the base of the claw and the substratum. Species differ in such temporal features as the number and regularity of the pulses within each sound, the pulse repetition rate, the duration of each sound, and the interval between consecutive sounds.

Honking sounds are also composed of pulses, but each pulse is many times longer than the brief, plosive strikes typical of rapping species. The physical structure of the pulse is complex. It consists of harmonically related, low frequency (150-800 Hz) sounds, not unlike a brief buzz of a flying insect. In some species, the harmonics are intermingled with 1–4 brief higher-frequency pulses. The former are correlated with rapid up-and-down movements of some of the walking legs, held off the substrate; the latter, with rapid taps of individual legs against the substrate. These may not be the only structure involved in generating honking calls. Von Hagen (1975) believes that the major chela also contributes. However, I have not seen this structure move while males make honking calls. The matter will only be resolved through experiment. Honking species differ not only in the temporal patterning of their sounds, but also in the spectral energy distribution of the honk.

Calling male fiddler crabs make their sounds just outside the entrance of their mating burrows, where the movements involved can be observed. In contrast, ghost crabs call from well within the burrow so that designation of the method employed in signal production is based upon sonic structure. *Ocypode quadrata, O. ceratophthalmus,* and *O. pallidula (= O. laevis)* are designated as 'rappers' on this basis, but whether one claw or both are involved in calling is unknown. In *O. pallidula* and *O. ceratophthalmus,* there is also a lower-amplitude stridulatory component which occurs before the first pulse (Fig. 1). The rasp sounds of *O. cordimana* appear as 'pure' stridulations. Yet this species is the only ghost crab lacking a stridulatory ridge (Horch, 1975)! Regardless of the proposed mechanism for call production, each ghost crab species has a unique temporal pattern of pulses.

How are the sounds detected? Horch (1971) showed that the receptor in *Ocypode* was Barth's myochordotonal organ (MCO). Parallel studies by Salmon, Horch and Hyatt (1977) demonstrated the same receptor was used by the fiddler crabs *Uca pugilator* and *U. minax.* In both genera, the receptor is located on the merus of each walking leg. Externally, it is marked by a thin-walled 'window' or 'tympanum'. When this structure is destroyed acoustic sensitivity of the operated walking leg is reduced by up to 20 dB, especially at the higher range of frequencies the crabs can detect. At frequencies below about 300 Hz, Barth's organ is only slightly more sensitive, at least to vibrations, than other sensory units which are stimulated (probably joint proprioceptors). Barth's organ operates, then, to increase sensitivity to a higher range of frequencies than can be detected by other sensory systems. The significance of this adaptation will be discussed shortly.

An important issue centred upon whether the crabs responded to substrate or air-borne sound. In our laboratory experiments we recorded sensory input from acoustic interneurones in the supraoesophageal ganglion when stimuli were presented either through a vibrating platform or a speaker located some distance away. These tests indicated that both genera could respond to sufficient amplitudes of either sound or vibration. This was especially the case in *Ocypode,* which was somewhat more sensitive to all acoustic stimuli. Thus to resolve the question we had to measure the actual amplitudes of sound and vibration generated by the animals under natural conditions.

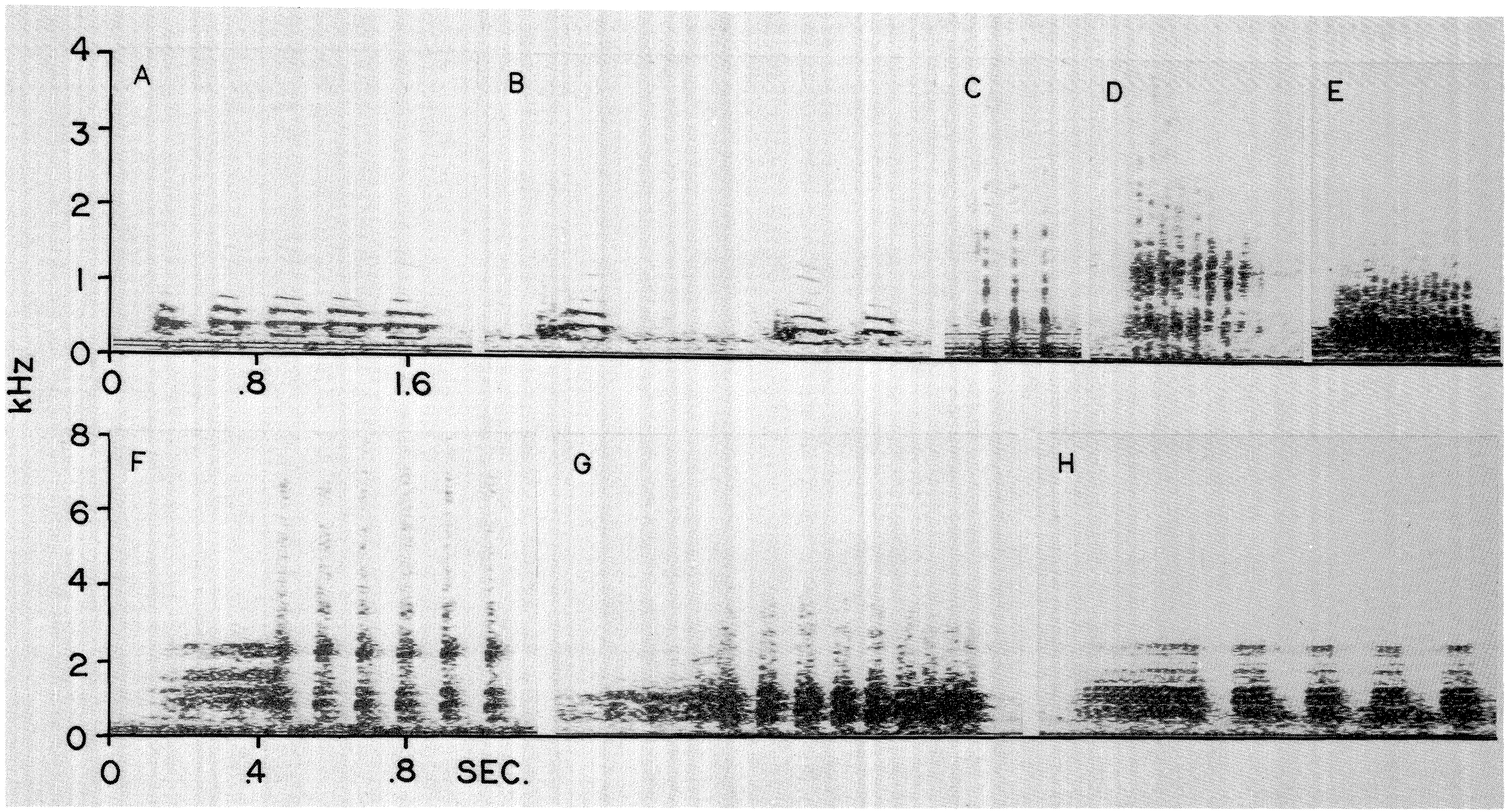

Fig. 1. Spectographs of calling sounds produced by fiddler and ghost crabs. **A,** a honking sound of *Uca rapax.* **B,** two honking sounds of *U. pugnax.* The first consists of one pulse, the second of two. **C-E,** rapping sounds of *U. speciosa, U. spinicarpa,* and *U. panacea,* respectively. The pulse repetition rate for these species ranges from average values of 5 Hz (*U. speciosa*) to 23 Hz (*U. panacea*), **F-G,** rapping sounds of *Ocypode ceratophthalmus* and *O. pallidula.* Note that first rap is preceded by a lower amplitude component, probably stridulatory. **H,** rasping sound of *O. cordimana.*

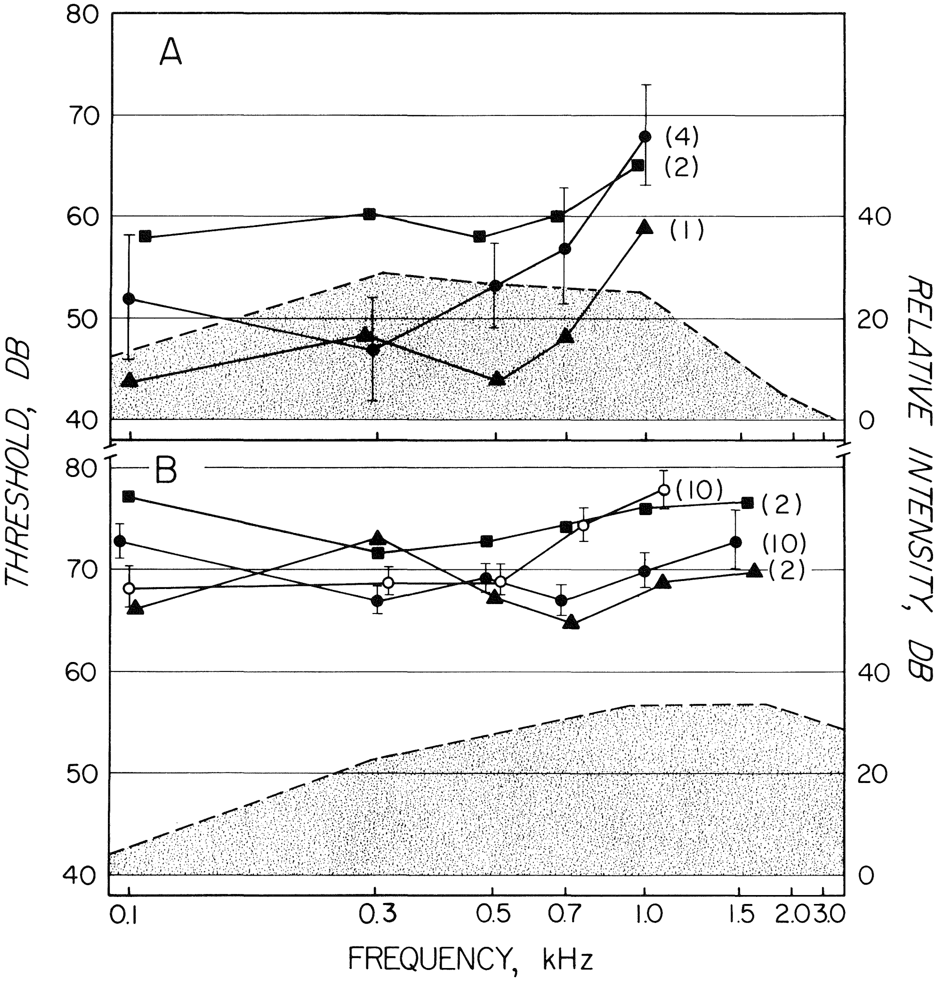

Fig. 2. Spectral energy distributions (shaded) of the sounds of *Uca minax* (A) and *U. pugilator* (B), plotted relative to background levels in the field (right scale). Superimposed on the area are thresholds (mean ± SE) for acoustic interneurones to pure tones in dB re: 10^{-3}cm/sec^2 (left scale). Values in parentheses indicate number of cells in the sample, ○, ●, tonic cells; ▲, inhibited cells; ■, phasic cells. From Salmon and Horch, 1976.

These measurements indicated that only on the quietest nights were the air-borne components of the calls above background and even then, scarcely so. When noise from such sources as wave action or wind completely masked the air-borne component, males continued to call. On the other hand, the substrate proved to be amazingly noise-free, even on windy nights. Horch and Salmon (1971) found that the relatively loud sounds of *O. ceratophthalmus* existed at suprathreshold amplitudes 8-10 metres away from calling males, when measured as vibration. For the smaller fiddler crabs, the calling distance was much less; 50-100 cm (Salmon and Horch, 1972). These results suggested that the biologically significant channel was substrate vibration.

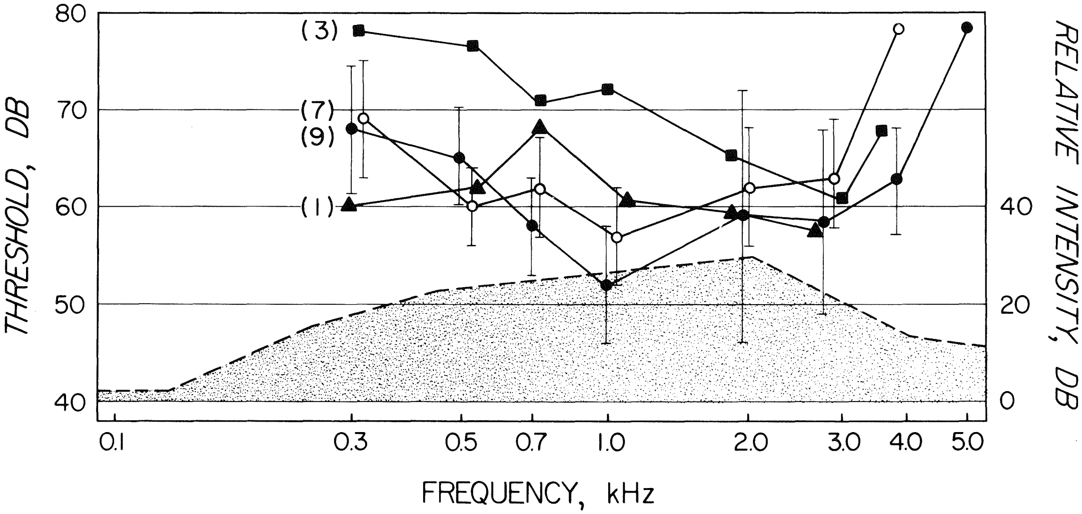

Fig. 3. Spectral energy distribution (shaded) of rapping sounds of *Ocypode quadrata,* plotted in conjunction with thresholds of its acoustic interneurones. Format as in Fig. 2. From Salmon and Horch, 1976.

Horch (1975) also found that the substrate had two additional properties which heightened its utility as a communicatory channel. First, when the substrate was damp, vibrations attenuated much more slowly than when it was dry. This finding suggested why all male ghost crabs called from lower regions of the supralittoral zone where the substrate was moist. Secondly, he found that the velocity of substrate-borne vibration was slower than air-borne sound (200 m/s vs. 350 m/s). Arrival time cues therefore may be important in localising vibration sources. For fiddler crabs, legs nearest a source of vibration would be stimulated about 0.25 ms before those farthest; in the larger ghost crabs, the difference would be about 0.5 ms. These values are well within the range of resolution by other arthropods such as scorpions which locate prey by vibrational cues (Brownell and Farley, 1979).

In calling systems of other animals there is a matching between the sensitivity of the receptors and the spectral energy distribution of the sounds produced during communication. We were therefore anxious to determine if similar relationships existed in the fiddler and ghost crabs. Figures 2 and 3 show spectral sensitivities for three representative species: *Ocypode quadrata* and *Uca pugilator* (rappers) and *U. minax,* a honking species. For the two rappers, vibration sensitivity was more restricted in range than the spectral energy composition of the sounds. However, the high-frequency components of rapping sounds attenuate rapidly and, at near-threshold distances, are not present. Thus, the tuning curves are centred upon the lower frequencies that are most useful for distance communication. The situation for *U. minax* was different. Here, the sensitivity curve more closely matched the spectral composition of the sounds near the calling male. In this species, however, sounds were produced by males only when they detected the movements of another crab nearby; thus attenuation effects were of little consequence.

The significance of Barth's MCO may be appreciated by considering signal-to-noise conditions under which the crabs must detect vibration. The substrate is a relatively noise-free environment compared to the sound channel in air, but noise is still present. It is confined to the very low frequencies (500 Hz and below). If the crabs were to depend upon joint proprioceptors for detecting signals, they would by necessity have to produce signals which fell within this band of noise. Barth's MCO, by extending the range of frequencies upward, allows the crabs to signal and detect just above this band of noise, where frequency-dependent attenuation effects are minimised. In the ghost crabs, which have the largest calling range, sensitivity below 500 Hz is poor. This adaptation should actually improve detection by excluding competing noise, thus improving the signal-to-noise ratio.

III. INFORMATION CONTENT AND BEHAVIOURAL RESPONSE

It is one thing to note correlations between male calling and female reproductive cycles, call structure and species, or sound production and exquisite abilities to detect these signals. It is quite another to

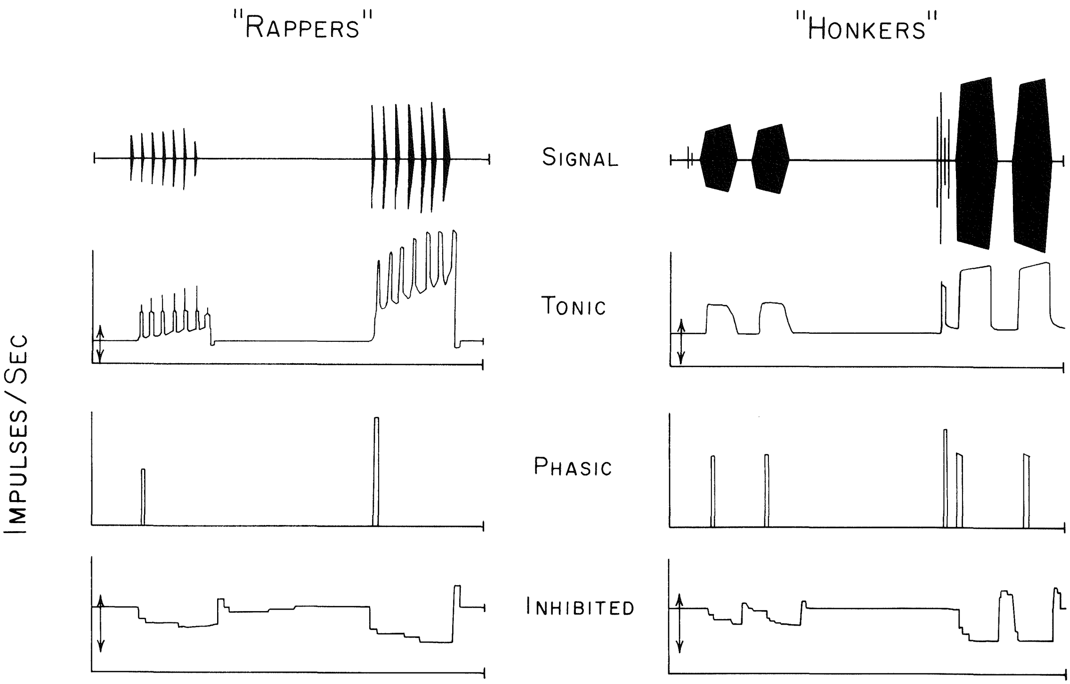

Fig. 4. Responses of tonic, phasic and inhibited units to rapping and honking sounds (signal) of two amplitudes. Data based upon presentations of signals to preparations under laboratory conditions. Tonic cells code pulse number; phasic cells, sound onset; and inhibited cells, sound duration. All cells show stronger responses to louder signals. Vertical, double-pointed arrow indicates cell shows variable rate of spontaneous firing.

prove that the crabs respond to the calls or can appreciate call differences. Sound lends itself nicely to experiments testing these features, since it can be presented as a playback either to crabs in the field or to preparations, while excluding other parameters of calling males such as their associated visual or chemical cues. In this section I will review our electrophysiological studies which indicate how the crabs process features of the sounds. Then I will summarise field data from experiments with males which show how they respond to one another's calls.

A. Electrophysiological experiments

Barth's MCO is innervated by clusters of two cell types which differ in size. These send axons into the leg nerve which enters the thoracic ganglion. In our initial experiments (Salmon and Horch, 1973) done with *U. minax,* we recorded from preparations eviscerated to expose the thoracic ganglion and the proximal portion of the leg nerves. When electrodes were inserted into the nerve, two classes of units were found: tonic and phasic. The former responded to vibrational stimuli with a continuous burst of impulses. The latter were at least 10 dB less sensitive and responded with many fewer impulses of much greater impulse amplitude. Both types of units continued to respond when walking leg segments distal to the merus were removed. However, the response was abolished when ablation included the merus. Latencies for these fibres were typically 3-5 ms.

Eviscerated preparations, while allowing us to identify the properties of sensory units, were of limited utility because we could not keep the animals alive. Thus thresholds we obtained were abnormally high, probably because the walking legs were resting limply upon the testing surface used to present vibrations. It proved rather simple to make a small hole in the exoskeleton just above the mouthparts to expose the supraoesophageal ganglion and record from acoustic interneurones located there or in the connectives. The crabs were relatively unaffected by this operation and remained vigorous during the recordings. Not only were thresholds much lower, but the units themselves proved especially interesting, responding to different features of the sounds. We used *U. minax, U. pugilator,* and *O. quadrata* as subjects. All three species possessed the same types of units: tonic, phasic, and inhibited (Salmon and Horch, 1976).

Tonic cells were similar to those found at the sensory level. They responded with a burst of impulses throughout the course of stimulation. They differed from sensory units by showing varying amounts of spontaneous firing. Inhibited units were spontaneously active prior to stimulation. This activity was decreased during stimulation, the amount depending upon stimulus amplitude. Phasic units responded with a single impulse to a vibrational stimulus, provided it occurred with a rapid onset. After firing they required at least a second to recover. None of the units coded tonal frequency; that is, it was impossible to distinguish between responses to 400 Hz from those of 700 Hz or 1 kHz. However, the units were tuned to respond best to certain frequencies, typically those most prevalent in the species' sounds (Figs 2 and 3).

Figure 4 summarises the responses of the units to stimulation by natural sounds and shows the manner in which temporal features of the calls are coded at low (i.e., some distance from the male) as well as higher stimulus levels. It is clear that most of the significant temporal properties of the calls are resolved.

Several other features of these neurones should be mentioned. First, all the cells were non-habituating. By this, we mean they continued to respond to consecutive presentations of crab sounds (or pure tones), delivered at biologically appropriate rates. Secondly, in their non-habituation, as well as their particular response characteristics, they were remarkably similar to the pulse- and chirp-coding neurones found in female crickets by Stout and Huber (1972). We therefore consider the crab interneurones to be vibration-sensitive analogues of the cricket cells. Thirdly, the cells were non-specific in the sense that those of one species responded to the calls of the other species we tested. Thus, these interneurones are not those used in making discriminations, though they probably supply information to the cells that do. Lastly, all the interneurones ceased to respond to acoustic input when the animals moved (began walking). During locomotion, therefore, input is somehow blocked. No doubt this is a form of 'overload protection', since during walking Barth's MCO is subjected to mechanical stimulation many times more powerful than that associated with the calls. This finding suggests that the crabs can detect calls only during pauses in movement, and that vibrational orientation must involve successive temporal comparisons interspersed between movements toward or away from the source. One can only wonder if overload protection also operated within the nervous system of calling males to shield them from their own sounds.

B. Behavioural responses

The majority of crustaceans pair briefly. The sexes then separate and females brood their eggs until they hatch. The larvae enter the plankton. These facts bias most crustaceans toward polygynous mating systems, in which males are most successful if they outcompete other males for access to females, and females enhance their reproductive success by selecting the 'best' males. The criteria used by female ghost crabs in mate selection are unknown. In the fiddler crabs *U. rapax* and *U. pugilator,* the largest males seemed to be preferred (Greenspan, 1975; Hyatt, 1977). However, for *U. pugilator,* Christy (1980) found this to be an oversimplification. Females preferred to mate with males possessing mating burrows above the intertidal because these burrows did not collapse at high tide. Christy found that after mating, females remained within a side branch of the male's burrow where they extruded and incubated their eggs. It took several days for newly extruded eggs to become firmly attached to the female's pleopods. If the burrow collapsed, most of the eggs were lost during this critical stage. In crowded colonies, males competed aggressively for access to high beach areas and only the largest were successful in obtaining and holding burrows there. However, if a smaller male could hold a high beach burrow, he was selected by a female as often as a larger male.

Competitive interactions between males are not confined to the daylight hours. Acoustic interactions occur during nocturnal periods which are analogous to similar phenomena in insect (Alexander, 1975) and anuran (Wells, 1977) choruses. Natural selection should favour a male who can alter his signalling behaviour so as to minimise the effects of competitors. Doing so makes his own signal more conspicuous and might coax a female away from a neighbouring male and toward him. A number of these responses have been documented in ghost and fiddler crabs, and some have been experimentally induced through playback experiments. The responses fall into the following categories:

(1) **Induced calling responses.** Male crabs of both genera call in bouts lasting several minutes. They pause to feed, modify their burrows, or perhaps rest. Should a neighbouring male within acoustic detection range begin calling more vigorously, the temporarily silent male will often join in. Presumably, the neighbour's behaviour indicates a female is nearby. The response of the silent male increases his probability of attracting her too. Since females usually visit several males before making a final selection, this response

is obviously adaptive. Salmon (1965) demonstrated this response somewhat indirectly. He frightened calling males (*U. pugilator*) into their burrows, then timed their return to the surface and subsequent calling with and without a playback of another crab's sounds. Those males receiving the playback began calling significantly sooner.

(2) **Changes in calling 'vigour'.** Neighbouring groups of calling males will often increase their rate and amplitude of sound production for a few seconds, then return to a previous lower 'spontaneous' rate. These changes only involve males which can detect one another's calls. In fiddler crabs (and presumably ghost crabs), such shifts are initiated by one male which has been stimulated either by nearby walking movements of another crab or by actual contact between a wanderer and the caller. Salmon (1965) did playback tests in which calling males were presented with sounds of a single male that varied in tempo, from the usual (16 sounds/min) to the calling rate of stimulated individuals (24/min). Only the latter induced tested males to significantly increase their calling rate over the pre-playback level. After the playback (which lasted one minute), the test male quickly returned to his ambient rate of calling.

(3) **Avoidance of call overlap.** Horch (Horch and Salmon, 1971; Horch, 1975) has documented changes in the inter-call intervals by neighbouring ghost crabs that result in avoidance of call overlap. Playback tests were used to show that the changes in a male's behaviour are deliberate, i.e. that overlap was avoided significantly more often than predicted by chance. These responses occur not only within species, but also in mixed species assemblages (*O. ceratophthalmus* and *O. cordimana* in Enewetok, Marshall Islands; *O. ceratophthalmus* and *O. pallidula* in Hawaii).

Overlap avoidance probably has several advantages. First, and most obviously, a male that avoids overlap between his calls and those of a conspecific presents a distinct signal, most easily evaluated by a prospecting female. But this explanation does not account for responses to heterospecifics, as males of another species are not reproductive competitors. Though each species of ghost crab produces sounds with a distinctly different temporal pattern, all calls have been shaped by natural selection to maximise transmission range. This is accomplished by concentrating most of the spectral energy of the call in the lowest frequencies just above background (500 Hz–3 kHz). For this reason, the sounds of all three species of ghost crabs are remarkably similar in their spectral energy distribution (Fig. 1), and thus constitute a masking noise for one another. Interspecific call avoidance responses preclude such masking effects.

It is curious that overlap avoidance does not occur in North American fiddler crabs. One possible reason is the much closer spatial proximity of calling males which may result in acoustic contact between too many neighbours for a call avoidance response to evolve.

IV. EVOLUTION OF ACOUSTIC DISPLAY

It has been largely assumed that the particular characteristics of each species' calling display are heritable, and therefore shaped by natural selection. However, the relationships between genome and behaviour within the Crustacea are virtually unknown. Selection experiments have never been done. Behavioural analyses of hybrids and their backcrosses, comparable to the work of Bentley and Hoy (1972), were until recently limited to non-calling species (e.g. Solignac, 1976).

In this section I will review recent work which provides some insight into heritable components of acoustic display, as well as an example of microevolutionary changes in call structure. Then, I will critically evaluate some old hypotheses and present some new ones which seek to explain how basic patterns of display in fiddler and ghost crabs might have evolved.

A. Reproductive isolating mechanisms in *Uca*

Uca pugilator was once believed to be a single species extending from Massachusetts to Florida on the Atlantic coast and from Florida into Mexico along the Gulf coast. However, field studies showed that in northern Florida it was replaced by a structurally similar species (*U. panacea*) which is the most ubiquitous form west of Florida. The two species overlap from Cedar Key to Pensacola, Florida. The distribution of *U. pugilator* west of Florida is unknown, except that it is rare.

While the two species are difficult to separate on the basis of morphology, they are easily distinguished by their premating displays. The rapping sounds of *U. panacea* contain over twice as many pulses, produced at about twice the rate (Fig. 5). The waving displays of the two forms are similar, though they can be separated on the basis of subtle differences in form and emphasis (Salmon *et al.*, 1978).

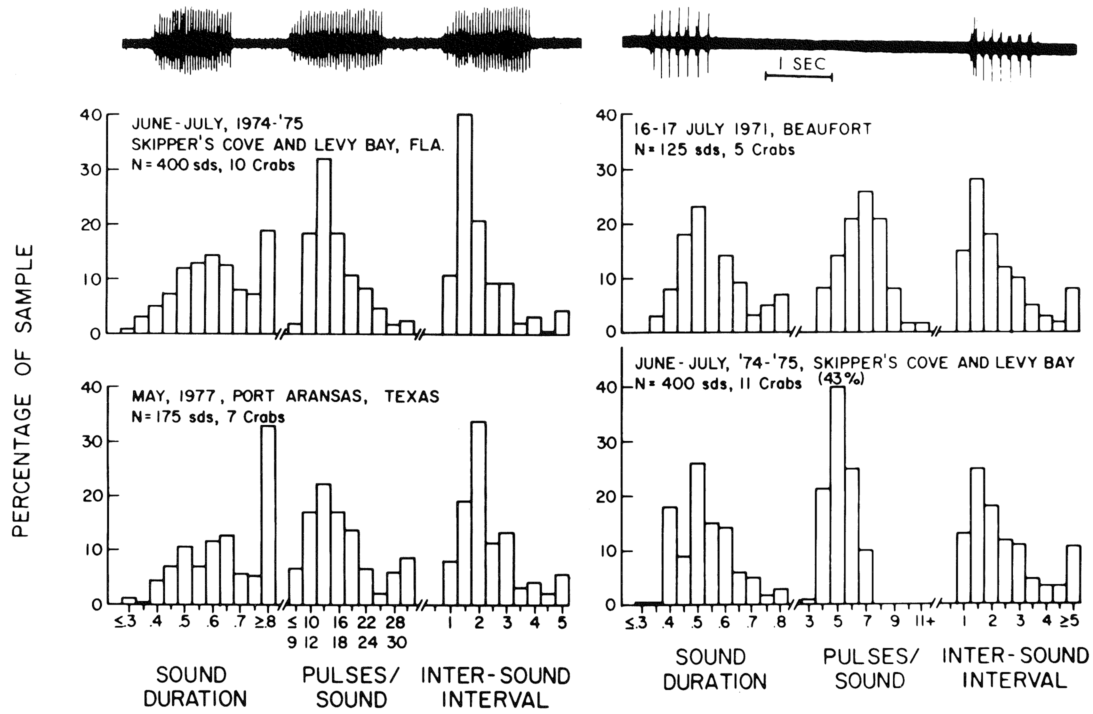

Fig. 5. Temporal properties of rapping sounds produced by *Uca panacea* (left) and *U. pugilator* (right). The pulse repetition rate for the former averages about 23 Hz throughout its range. For the latter, it is 12 Hz in Beaufort, N.C., where *U. panacea* does not occur; it averages 9.5 Hz at Skipper's Cove and Levy Bay, Florida, where *U. panacea* is sympatric. Note also that the number of pulses per sound is reduced in the overlap zone. See text for further details. Modified from Salmon *et al.*, 1978.

I believe that the two species diverged from common stock and then came in contact before they were capable of avoiding interbreeding. Evidence in support of this hypothesis comes from an analysis of their call structure. Male *U. pugilator* from North Carolina produce sounds with an average pulse repetition rate of 12 Hz, but when they are sexually stimulated, the rate may go as high as 17-18 Hz. The latter falls close to the lower range of variation shown by male *U. panacea* (21 Hz). A comparison between the calls of *U. pugilator* in the overlap zone and those in North Carolina indicated significant change. The former called at a reduced pulse repetition rate (mean of 9.5 Hz) and their sounds were composed of fewer pulses. Both changes made their calls more distinct from those of *U. panacea.*

I presume that selection by females has been the driving force altering the call structure of conspecific males in Florida. But what are the penalties against indiscriminate females? Hybrids have not been found in nature, but under laboratory conditions males occasionally succeeded in forcing interspecific copulations. The offspring suffered higher mortality through the developmental stages and as adults were sterile (Salmon and Hyatt, 1979).

The call structure of the hybrids is shown in Fig. 6. We (Salmon and Hyatt, 1979) found that the pulse repetition rate was intermediate between the two parental forms. Note that there are also distinct difference between the reciprocal crosses in sound duration as well as the number of pulses/sound. These data strongly support the notion that call structure is under close genetic control.

B. Patterns of display in fiddler and ghost crabs

There is general agreement that fiddler and ghost crabs are more closely related to one another than to any other group (Crane, 1975). But they show many differences in their ecology and behaviour. In the past, their sexual behaviour patterns have been treated separately, as if few similarities existed and as if no general inferences could be drawn to relate differences along a continuum of selection

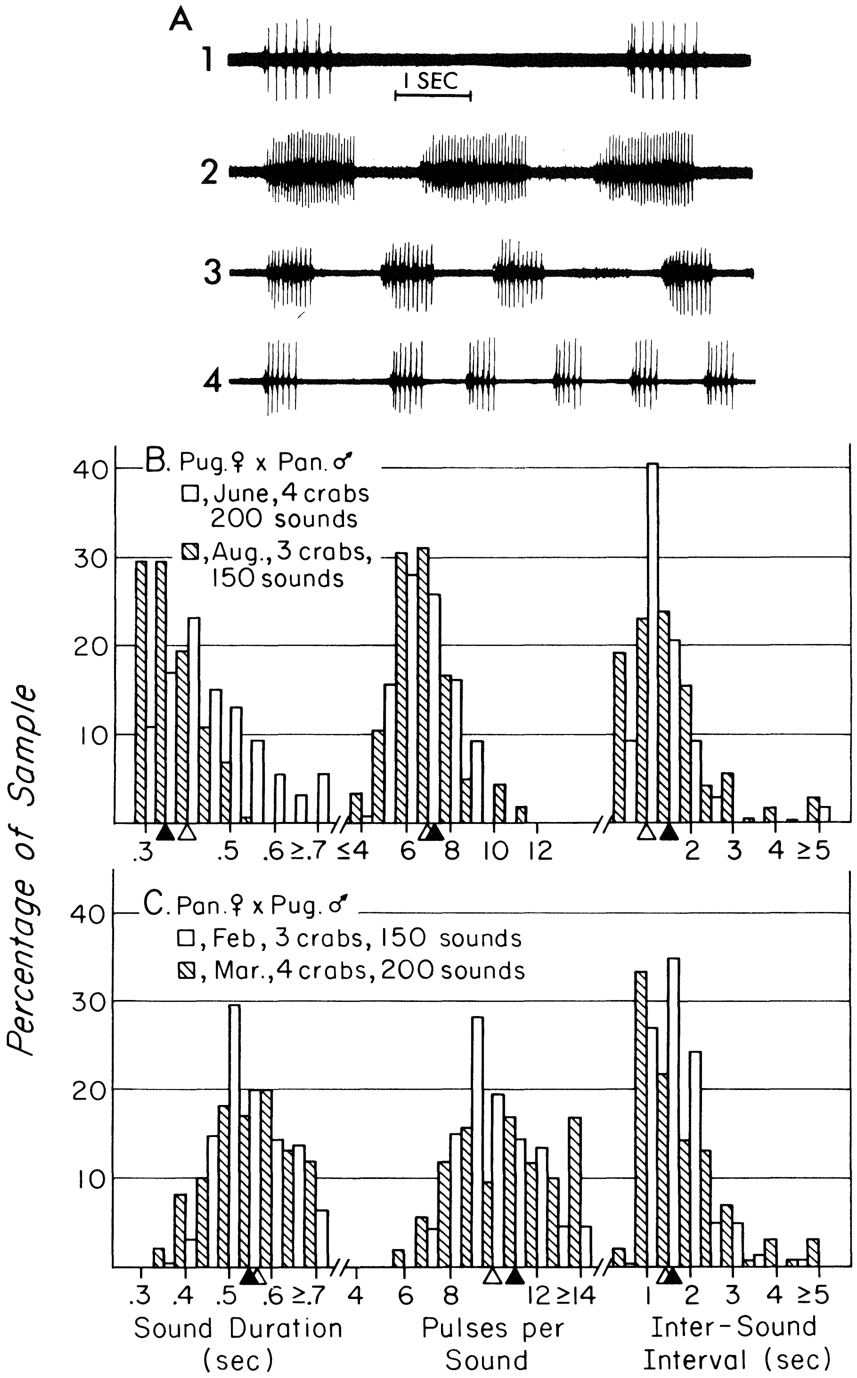

Fig. 6. Temporal properties of the calling sounds produced by hybrids between *Uca panacea* and *U. pugilator*. **A**, oscillographs of rapping signals produced by *U. pugilator* (1), *U. panacea* (2), panacea ♀ × pugilator ♂ (3), and pugilator ♀ × panacea ♂ (4) hybrids. **B**, **C**, quantitative analysis of the sound structure for each cross during the first year of development. △, ▲, median category. Modified from Salmon and Hyatt, 1979.

pressures. Enough new information has been gathered now to suggest that the two genera should be conceived of as overlapping in some features of their ecology and reproductive behaviour. In this section I will first review courtship patterns in fiddler crabs, then present evidence which supports the above claim.

(1) Courtship patterns in fiddler crabs. Based upon present information, fiddler crabs show three basic patterns of courtship display. The first of these is typical of tropical species found in the Indo-Pacific, called the 'narrow fronts' by Crane (1957). These species tend to mate on the beach surface. Sound plays no role in calling, and waving occurs only as a courtship signal. Typically a male leaves his burrow, approaches a nearby female, and waves as he moves toward her. A receptive female does not retreat, allowing the male to grasp her and manoeuvre her into a copulatory position.

The second pattern is characteristic of New World tropical species where mating takes place in the male's burrows. Waving occurs as both a calling and a courtship signal. That is, males will wave when no female is present, but in response to a wandering female, waving becomes much more vigorous. Should the female be attracted, the male precedes her into his mating burrow and begins producing sonic signals. The latter are presumed to induce the female to follow and also present additional cues for species identification.

The third pattern is found in most (but not all) of the subtropical and temperate species. It differs from the second pattern by the addition of a nocturnal phase of courtship, employing sound as a calling signal. But this adaptation is probably associated with latitude rather than species composition. For example, *U. rapax* in Trinidad shows a typical second pattern there; it courts only during the day. Florida populations, however, show nocturnal activity and acoustic calling (Salmon, 1967). At the same time, latitude is not the only factor. *Uca minax,* which occurs as far north as Massachusetts, shows strong tendencies toward nocturnal locomotor activity, but males do not call. They do, however, court with sound at night.

A major question, currently unanswered, is that of the selection pressures responsible for these different courting patterns. Crane (1957) proposed that the surface-mating species of the Indo-Pacific were most primitive, both structurally and behaviourally, while the New World forms were phylogenetically advanced. There is some question, however, whether the genus *Uca* is really a monophyletic assemblage of species (M. Türkay, pers. comm.) which can be placed on such a 'primitive' to 'advanced' continuum. One could also argue that the differences represent alternative ecological solutions. For example, Christy (1980) hypothesises that many fiddlers may exist under one of two types of ecological conditions; those in which the food supply is spatially separated from areas where mating takes place, and those where it is not. In the former, typical of many broad front *Uca* and the ghost crabs, females feed at the lower intertidal but select mates with high beach burrows. In the latter, typical of the narrow fronts, burrows are located in organically rich, muddy substrates where they rarely collapse and are also safe incubation sites. As a result, females are relatively sedentary and 'defendable'. The 'broad front' pattern, then, with its emphasis upon dramatic male display, may be an outcome of male–male competition for high beach mating burrows and the necessity of attracting undefendable females from a distance; the 'narrow front' pattern, with its surface matings and simple waves, may result because males can defend a harem of sedentary females which the males visit at intervals for the purpose of mating.

But why did the nocturnal calling phase evolve among some of the broad fronts? Some years ago I (1965) proposed that the evolution of nocturnal calling might enable some temperate populations to complete fertilisation and reproduction more rapidly in a breeding season shortened by climatic extremes. Christy (1980) criticised this hypothesis, arguing that reproductive rates were limited by how quickly females could convert food to egg clutches and implying that male behaviour could not speed the process. He is, of course, correct with regard to ultimate limits on fecundity. But, once a female is receptive, she must find a high quality mate if she is to maximise her reproductive success. Since a male who has attracted a female into his mating burrow is 'out of circulation' for at least one low tide, the supply of optimal males may in fact be limiting. But if males could return to courtship by the next low tide, *regardless if it occurred at night or during the day,* the turnover time for optimal paired males would be shortened. This adaptation would increase the reproductive success of both sexes. The net effect would be more matings of higher quality per unit time.

The matter will only be resolved when experiments are done. But until they are, I believe this explanation is at least plausible. Christy's alternative, that nocturnal activity is linked to a poorer food supply, seems inadequate to me. There is no reason to assume all northern habitats are depauperate in this regard. They may, in fact, be more productive.

(2) Display patterns in ghost crabs, and an attempt at a synthesis. There are 19 species of ghost crabs, most of which occur in the Indo-Pacific (Bliss, 1968). The group, as a whole, spans a wider range of habitats than the fiddler crabs: from the extralittoral (*O. cordimana*) to the intertidal (*O. gaudichaudi*). The few species studied in any detail also show great flexibility in their locomotor activity patterns (reviewed in Vannini, 1976) as well as display format (Linsenmaier, 1967). Thus, a more complete study of the entire genus might provide insights into the selective forces shaping not only their behaviour, but also the behaviour of their intertidal relatives. For example, do intertidal *Ocypode* show calling behaviour patterns similar to the fiddlers? How do these patterns change as species preferences become more terrestrial? To answer these questions a survey of the admittedly fragmentary information is in order.

The ghost crabs can be divided into three groups of species, differing in zonation of their burrows, activity, and reproductive behaviour. For example, *O. gaudichaudi* and *O. ryderi* occur in the intertidal to low supralittoral zones (Crane, 1941; Vannini, 1976). Both species are active during diurnal and, in some locales, nocturnal low tides. Nothing is known about the reproductive behaviour of the former, but male *O. ryderi* court females with waving signals during the day (Vannini, 1976). Both *O. ceratophthalmus* and *O. saratan* are exclusively supralittoral as adults. As a rule, neither species shows tidal rhythms of activity. Rather, adults are predominantly active at night, though diurnal activity occurs in some populations under some conditions (cloudy skies, beaches devoid of human disturbance, etc.; Fellows, 1966; Linsenmaier, 1967). Males attract females during the day with sand pyramids near their mating burrows, and at night with acoustic signals (Linsenmaier, 1967; Horch and Salmon, 1971). The most terrestrial ghost crabs, *O. cordimana* and *O. pallidula,* dig burrows in the extralittoral zones (Fellows, 1966; Rao, 1968) and are exclusively nocturnal in activity. Reproductively active males move down to the supralittoral, establish mating burrows, and call at night with acoustic signals.

Viewed from the standpoint of male behaviour, the differences between the display patterns of low supralittoral, supralittoral, and extralittoral species of ghost crabs appear very profound. However, I suggest that this approach is not the most productive, as it deals with the *consequence* of evolution and not the actual *causes* of the differences (the selection pressures themselves). As an alternative, I would argue along the following lines. First, the fiddler and ghost crabs, for unknown reasons, possess a genetic tendency to use acoustic and visual displays as both calling and/or courtship signals to a degree unparalleled by any other semiterrestrial crustaceans. Second, when and how these signals are used by males must depend upon when females can search for mates. This searching exposes females not only to predators, but also to temperature and humidity conditions more extreme than those encountered within a protective burrow. Third, for any given species, zonation of female burrows will determine when they can search for mates. If females reside near the intertidal, they can easily dig burrows reaching damp sand or mud and expect that supplies of moisture will also be available in male burrows (even if the male is later rejected as a mate). Such females can prospect during the day and or at night if conditions dictate. On the other hand, females of extralittoral species can only search for mates at night when temperatures are low and humidity is high. For species in intermediate positions in the supralittoral, females might be able to search during the day in some locales but not in others, depending upon beach slope, depth to water level, climatic factors, and other variables. Nocturnal searching, however, should be common. Fourthly, the format of a male's display should optimise his chances of attracting a female, given the characteristics of her searching pattern. For diurnally active females, visual displays, such as waving, are optimal as a male calling signal, provided the habitat is relatively flat and unobstructed by vegetation. For nocturnally active females, acoustic calling by males is clearly best. And for supralittoral species where some females can risk daytime searches, as in *O. saratan* and *O. ceratophthalmus,* the male solution is a visual signal not requiring his extended exposure—the sand pyramid.

Viewed in this manner, the major differences between ghost and fiddler crab reproductive behaviour, and even between the less and more terrestrial ghost crabs, seem natural outcomes of a continuum of selection pressures. Whether these ideas will prove correct must depend upon the results of future studies, carried out with other species of ghost crabs residing in a wide range of habitats.

V. DIRECTION FOR FUTURE RESEARCH

This review has exposed a number of issues which remain for further study. Among the most important, in my view, are behavioural, ecological, and anatomical investigations of the fiddler crabs to clarify phyletic relationships and place patterns of display into a proper perspective. The physiology of vibration reception has only been analysed in a few species of ghost and fiddler crabs. Other members of the group, such as *Tympanomerus* and *Scopimera,* possess enlarged tympana whose functional significance is unknown. Relationships between zonation, water balance, and behaviour may provide major insights into patterns of display and their evolution. Finally, the study of female behaviour, including criteria for mate selection, orientation to sound sources, and discrimination capabilities, is ripe for further work. I hope that if nothing else the reader now understands why so many have found these animals particularly fascinating and useful as experimental subjects.

ACKNOWLEDGEMENTS

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This paper is dedicated to my parents, Walter and Bess.

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A REVISION OF THE FAMILY PODOCERIDAE (AMPHIPODA: GAMMARIDEA)

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SUMMARY

The podocerid genera *Cyrtophium, Icilius, Laetmatophilus, Leipsuropus,* and *Podocerus* have been investigated to elucidate their generic characters. Four of these genera are very closely related, with only minor differences between them; *Icilius* has proved to be non-corophioidean and is removed from Podoceridae. The family Iciliidae, and a new podocerid genus *Styloxenodice,* to accommodate *Xenodice macrophthalma,* are diagnosed. Four groups of genera are recognised within Podoceridae, and are given subfamilial status: Podocerinae, Xenodicinae, Neoxenodicinae, and Dulichiinae. It is suggested that Podoceridae is derived from a basic corophioidean *Gammaropsis*-type ancestor through an ancestral form that would have been similar to *Styloxenodice.*

INTRODUCTION

The gammaridean amphipod family Podoceridae is diagnosed as a corophioidean having a depressed urosome with the first urosomite more than twice as long as the second. As currently constituted the family contains eleven genera, all of which are marine. The relationships of the six cold water, slender bodied genera (*Dulichia, Dulichiopsis, Dyopedos, Neoxenodice, Paradulichia,* and *Xenodice*) were discussed recently by Laubitz (1977, 1979). At that time it was concluded that there was insufficient information available on the five flat-bodied, warm water genera (*Cyrtophium, Icilius, Laetmatophilus, Leipsuropus,* and *Podocerus*) to include them in the discussion.

I have recently had the opportunity to study specimens of all five of these warm water genera. The result of this investigation made it apparent that the whole family needed to be reassessed, and an attempt needed to be made to determine the relationships between the genera currently placed therein.

OBSERVATIONS

The five depressed-bodied genera *(Cyrtophium, Icilius, Laetmatophilus, Leipsuropus,* and *Podocerus)* classically assigned to the family Podoceridae are superficially very similar. However, study of specimens of these genera produced rather startling results. It quickly became apparent that the genus *Icilius* not only was not a podocerid, but also that it was not even a member of the superfamily Corophioidea. As a result of this discovery it seemed essential to reconsider the characters of all of the genera assigned to Podoceridae and to see whether they could be considered a unique group forming a single family unit, and could be linked together in a logical evolutionary sequence.

The characters of *Icilius* are such that this genus cannot be placed in any of the currently accepted gammaridean families, so that the family Iciliidae (Icilidae of Dana) must be reinstated. Characters that specifically bar the Iciliidae from being included in the Corophioidea are: antenna 1 with short peduncular articles; gnathopods slender, simple, and alike; coxal plate 4 excavate; coxal gill on pereopod 7; uropod 3 well developed, inner ramus much longer than outer; telson entire, not fleshy.

TAXONOMY

Iciliidae Dana 1849, **emend.**

Body strongly depressed, may be posteriorly processiferous, urosomite 1 elongate. Antenna 1 shorter than antenna 2, both with well-developed flagellum, accessory flagellum minute. Buccal mass small. Upper lip notched, lobes symmetrical. Lower lip, inner lobes developed. Mandibular molar and incisor strong, palp slender with segment 2 the longest. Maxilla 1 inner plate setose, outer plate with 11 apical spines. Maxilla 2 inner plate setose. Maxilliped plates and palp strong. Coxal plates small, processiferous, overlapping slightly; 4th slightly excavate, 5–7 anterolobate. Gnathopods 1 and 2 similar, small, simple. Pereopods 5–7 similar, 7 slightly the longest, bases with processiferous posterodistal lobes. Coxal gills simple, on pereopods 2–7; brood plates large, with simple marginal setae, on 2–5. Pleopods with medially broadened peduncles, long rami. Rami of uropods 1 and 2 linear, unequal, apically spinose; uropod 3 inner ramus lanceolate, outer ramus linear, unsegmented, about as long as peduncle. Telson not fleshy, short and entire, pointed ovate to bluntly rounded.

Remarks. The relationship of the family to the superfamilies proposed by Bousfield (1979) is obscured by its adaptive characters. Iciliidae appears to be closest to the family Paramphithoidae on the basis of the acuminate coxae, vestigial accessory flagellum, combination of mouthparts, and simple gnathopods, and must therefore be assigned to the Eusiroidea. The atypical appearance and characters of Iciliidae are presumed to be the result of adaptation to an as yet unknown way of life.

Icilius Dana 1849

Head flat, rostrum small, eyes round and lateral. Accessory flagellum one-segmented. Maxilliped palp 4 falcate. Coxae 1 and 2 small; 3 and 4 larger, posteroventrally acuminate; 5 large and anteroventrally acuminate. Gnathopods 1 and 2 simple, with articles 5 and 6 elongate and setose. Pereopods 3 and 4 strongly grasping; 5-7 without palmar development. Epimeral plates with pointed posteroventral corners. Pleopod peduncle may be very greatly broadened. Urosomite 1 more than twice as long as urosomite 2. Uropods 1 and 2, peduncle depressed, outer ramus shorter than inner; uropod 3 inner ramus longer than outer, lanceolate, and strongly spinose apically.

Type species. *Icilius ovalis* Dana 1852.

Remarks: There are currently four species in this genus; material of *I. australis* Haswell and *I. danae* Stebbing was examined. The extremely depressed body, simple gnathopods, and subchelate pereopods 3 and 4 make this genus easily recognisable. Stebbing (1910) discussed the four species, which he had previously treated as one (1906), remarking that the incomplete state of all collected specimens made a final decision on their status impossible. Current knowledge of this genus is no further advanced than in Stebbing's day.

Podoceridae Leach 1814, emend. Stebbing 1906. **Revised.**

Diagnosis. Corophioidea with urosomite 1 more than twice as long as urosomite 2, and uropod 3 reduced or absent. Body variable, either broadly depressed or slender cylindrical, occasionally processiferous; pereonites and urosomites variously fused; abdomen flexed beneath pereon. Antenna 1 and 2 elongate, setose, flagellum shorter than peduncle, accessory flagellum present or absent. Upper lip bilobed; mandibular molar strong, palp variable; maxilla 1 inner plate strongly setose to absent, outer plate with 9 (rarely 8 or 10) apical spines; maxilla 2 inner plate setose, sometimes with facial setae; maxilliped plates and palp strong. Coxal plates small, usually discontiguous; coxal gills simple, 3-6 pairs; brood plates 3-4 pairs. Gnathopods variable, 2 the larger, subchelate. Pereopods 3 and 4 sometimes glandular. Pleopods with slender peduncle. Urosomite 1 at least more than twice as long as urosomite 2; uropod 1 normal; uropod 2 biramous, vestigial or absent; uropod 3 uniramous, vestigial or absent. Telson fleshy, short, entire.

Podocerinae n. subfam.

Diagnosis. Podoceridae with strongly depressed body, head anterodorsally elongate, coxal plates equal to or longer than pereonites. Antenna 1 shorter than antenna 2; accessory flagellum 1-segmented or absent. Mandibular palp heavy, strongly setose; maxilla 1 inner plate reduced and non-setose, or absent. Pereopods 3-7 essentially similar, non-glandular, without propodal palm; gills on pereopods 2-6. Pleosome not greatly reduced; urosomite 1 shorter than or equal to pleosomites 2 + 3.

Podocerus Leach 1814.

Pereon depressed, with 5-7 segments; urosome of 3 segments. Accessory flagellum present; maxilla 1 inner plate reduced and non-setose or absent, outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; brood plates on pereopods 2-4 or 2-5; uropod 2 biramous, uropod 3 without rami.

Remarks. There are about 30 species currently recognised in this genus, which is badly in need of revision. Specimens of seven species were examined: *P. andamanensis* (Giles), *P. brasiliensis* (Dana), *P. chelonophilus* (Chevreux & Guerne), *P. cristatus* (Thomson), *P. inconspicuus* (Stebbing), *P. septemcarinatus* Schellenberg, and *P. variegatus* Leach. The genus shows variation in the degree of fusion of the posterior pereonites; the brood plate on pereonite 5, when present, is very small.

Laetmatophilus Bruzelius 1859.

Pereon depressed, with 5-7 segments; urosome of 2 segments. Accessory flagellum absent; epistome produced; maxilla 1 inner plate greatly reduced, non-setose, outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; gnathopod 2 of female nearly as large as that of male; brood plates on pereopods 2-4; uropod 2 without rami, uropod 3 absent.

Remarks. There are currently seven species in this genus. Specimens of four species were examined: *L. durbanensis* K. Barnard, *L. leptocheir* K. Barnard, *L. purus* Stebbing, and *L. tuberculatus* Bruzelius (includes *L. armatus*). The tendency to fusion of the posterior pereonites appears to be non-specific, some specimens of *L. durbanensis* having pereonites 6 and 7 fused while others did not.

Cyrtophium Dana 1852.

Pereon depressed, with 7 segments; urosome of 3 segments. Accessory flagellum absent; epistome produced; maxilla 1 inner plate absent, outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; gnathopod 2 of female nearly as large as that of male; brood plates on pereopods 2-4; uropod 2 biramous, uropod 3 without rami.

Remarks. There are two currently accepted species in this genus; material of *C. minutum* Haswell was examined.

Leipsuropus Stebbing 1899.

Pereon depressed with segments 6 and 7 incompletely fused; urosome of 3 segments. Accessory flagellum absent; epistome produced; maxilla 1 inner plate absent, outer plate with 8 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; gnathopod 2 of female nearly as large as that of male; brood plates on pereopods 2-4; uropod 2 absent, uropod 3 without rami.

Remarks: This genus had been considered to be of doubtful status (e.g., Barnard, 1969) because of the peculiar conformation of the urosome as described in the literature. However, information received from J.L. Barnard (personal communication) and subsequent study of specimens of the single species in the genus, *L. parasiticus* (Haswell), have supported the absence of any sign of uropod 2, and thus the correctness of the original description.

Xenodicinae n. subfam.

Diagnosis. Podoceridae with cylindrical body, head anterodorsally elongate, coxal plates equal to or shorter than pereonites. Antenna 1 longer than antenna 2; accessory flagellum comparatively long, 4- or 5-segmented. Mandibular palp heavy, strongly setose; maxilla 1 inner plate strongly setose. Pereopods 3-7 essentially similar, increasing in length posteriorly, non-glandular, without propodal palm; gills on pereopods 2-6. Pleosome not reduced; urosomite 1 shorter than pleosomites 2 + 3.

Xenodice Boeck 1870.

Pereon cylindrical, with 7 segments; urosome of 3 segments. Maxilla 1 outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; brood plates on pereopods 2-5; gnathopods 1 and 2 subequal in male and female; uropod 2 biramous, uropod 3 without rami.

Remarks. Specimens of the single species in this genus, *X. frauenfeldti* Boeck, were examined.

Styloxenodice n. gen.

Diagnosis. Xenodicinae with uropod 3 with single, styliform ramus; anterior coxal plates closely contiguous; maxilla 1 outer plate with 10 apical spines; maxilla 2 with facial setae.

Description. Pereon cylindrical, with 7 segments; urosome of 3 segments. Maxilla 1 outer plate with 10 spines; maxilla 2 inner plate with facial setae; maxilliped palp 4 blunt; brood plates on pereopods 2-5; gnathopods 1 and 2 subequal in male and female; uropod 2 biramous, uropod 3 uniramous.

Type species. *Xenodice macrophthalma* Schiecke 1976.

Etymology: The genus name is based on the Greek word 'stylos', which describes the uropod 3 ramus, plus *Xenodice.*

Remarks. The well-developed uropod 3 ramus is the most obvious character distinguishing *Styloxenodice* from *Xenodice;* other characters include the long accessory flagellum, closely contiguous coxae, 10 spines on maxilla 1 outer plate, and facial setae on maxilla 2. I have not seen any specimens of the single species in this genus, and the diagnosis is based on Schiecke's (1976) very complete description of that species.

Neoxenodicinae n. subfam.

Diagnosis. Podoceridae with cylindrical body having greatly elongated anterior pereonites, head anterodorsally elongate, coxal plates equal to or shorter than pereonites. Antenna 1 longer than antenna 2; accessory flagellum 1-segmented. Mandibular palp heavy, strongly setose; maxilla 1 inner plate reduced, non-setose. Pereopods 3-7 dissimilar, non-glandular, without propodal palm; gills on pereopods 2-4. Pleosome reduced; urosomite 1 shorter than pleosomites 2 + 3.

Neoxenodice Schellenberg 1926.

Pereon cylindrical, with 7 segments; urosome of 3 segments. Maxilla 1 outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; brood plates on pereopods 2-4; pereopods 3 and 4 very small; uropod 2 biramous, uropod 3 without rami.

Remarks. The genus comprises two species; specimens of *N. cryophile* Lowry were examined.

Dulichiinae n. subfam.

Diagnosis. Podoceridae with cylindrical body, head triangular to rectangular, coxal plates equal to or shorter than pereonites. Antenna 1 longer than antenna 2; accessory flagellum short, 1- to 5-segmented. Mandibular palp slender, sparsely setose; maxilla 1 inner plate reduced, non-setose. Pereopods 3-7 dissimilar, 3 and 4 glandular, 5-7 with or without propodal palm; gills on pereopods 2–5 or 3-5. Pleosome reduced; urosomite 1 longer than or much longer than pleosomites 2 + 3.

Remarks. Laubitz (1979) stated that the subfamily is confined to the colder waters of the northern hemisphere. During examination of collections from Australian waters, I came across one specimen of a *Dulichiopsis* species from Bass Strait (841 m) and many specimens of a *Dulichia* species from Western Port, Victoria. The zoogeographical status of Dulichiinae is thus less clear than was previously thought.

Dulichia Kroyer 1845, redefined Laubitz 1977.

Head triangular; pereon cylindrical, with 6 segments; urosome of 2 segments, urosomite 1 longer than pleosome. Accessory flagellum with 3 articles; maxilla 1 outer plate with 9 spines; maxilla 2 inner plate with facial setae; maxilliped palp 4 blunt; gills on pereopods 2-5, brood plates on 2-4; pereopods 5-7 without propodal palm; uropod 2 biramous, uropod 3 absent.

Remarks. There are five species in the genus; for material examined see Laubitz, 1977.

Dulichiopsis Laubitz 1977.

Head rectangular; pereon cylindrical, with 6 segments; urosome of 2 segments, urosomite 1 longer than pleosomites 2 + 3. Accessory flagellum with 3-4 articles; maxilla 1 outer plate with 9 spines; maxilla 2 inner plate with facial setae; maxilliped palp 4 falcate; gills on pereopods 2-5, brood plates on 2–4; pereopods 5-7 with propodal palm; uropod 2 biramous, uropod 3 absent.

Remarks. There are six species in the genus; for material examined see Laubitz, 1977.

Dyopedos Bate 1857.

Head triangular to rectangular; pereon cylindrical, with 6 segments; urosome of 2 segments, urosomite 1 longer than pleosomites 2 + 3. Accessory flagellum with 1-4 articles; maxilla 1 outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; gills on pereopods 3-5, brood plates on 2-4; pereopods 5-7 without propodal palm; uropod 2 biramous, uropod 3 absent.

Remarks. There are nine species in the genus; for material examined see Laubitz, 1977.

Paradulichia Boeck 1870.

Head rectangular; pereon cylindrical, with 6 segments; urosome of 2 segments, urosomite 1 longer than pleosome. Accessory flagellum with 3-5 articles; maxilla 1 outer plate with 9 spines; maxilla 2 without facial setae; gills on pereopods 2-5, brood plates on 2-4; gnathopods 1 and 2 subequal in male and female; pereopods 5-7 without propodal palm; uropod 2 minute, with 1 or no rami, uropod 3 absent.

Remarks. There is one species in the genus; for material examined see Laubitz, 1977.

Key to the subfamilies and genera of Podoceridae

1. Head triangular or rectangular; mandibular palp slender, sparsely setose; pereopods 3 and 4 glangular; gills on pereonites 2-5 or 3p5; urosomite 1 longer than pleosomites 2 + 3. **(Dulichiinae)** 4

— Head anterodorsally elongate; mandibular palp heavy, strongly setose; pereopods 3 and 4 not glandular; gills on pereonites 2-4 or 2-6; urosomite 1 no longer than pleosomites 2 + 3 2

2. Pereon strongly depressed; antenna 1 shorter than antenna 2; pereopods 3-7 similar; gills on pereonites 2-6; maxilla 1 inner plate reduced or absent. **(Podocerinae)** 7

— Pereon cylindrical; antenna 1 longer than antenna 2; pereopods 3-7 of increasing length; if gills present on pereonites 2-6 then maxilla 1 inner plate setose 3

3. Pereopods 3 and 4 greatly reduced in size; anterior pereonites elongate, pleosome reduced; accessory flagellum short, of 1 article; gills on pereonites 2-4; maxilla 1 inner plate reduced .... **Neoxenodicinae**

— Pereopods 3 and 4 not reduced in size; anterior pereonites not elongate, pleosome well developed; accessory flagellum long, of 4-5 articles; gills on pereonites 2-6; maxilla 1 inner plate well developed and setose **(Xenodicinae)** 10

4. Uropod 1 normal, uropod 2 rudimentary; gnathopods 1 and 2 of equal size in male and female .... *Paradulichia*

— Uropods 1 and 2 normal; gnathopods 1 and 2 of equal size in female, grossly unequal in male 5

5. Gills on pereonites 3-5; basis of pereopods 3 and 4 greatly expanded; maxilla 2 inner plate without facial setae .... *Dyopedos*

— Gills on pereonites 2-5; basis of pereopods 3 and 4 not greatly expanded; maxilla 2 inner plate with facial setae 6

6. Eyes large, strongly convex; pereopods 5-7 without propodal palm; maxilliped palp with short stout terminal article .... *Dulichia*

— Eyes abnormal, poorly developed, or absent; pereopods 5-7 with propodal palm; maxilliped palp with long slender dactyl .... *Dulichiopsis*

7. Urosome with only two urosomites, uropod 2 without rami .... *Laetmatophilus*

— Urosome with three urosomites, uropod 2 either biramous or absent 8

8. Uropod 2 absent, uropod 3 present; maxilla 1 outer plate with eight apical spines .... *Leipsuropus*

— Uropod 2 biramous, uropod 3 present; maxilla 1 outer plate with nine apical spines 9

9. Accessory flagellum 1-segmented .... *Podocerus*

— Accessory flagellum absent .... *Cyrtophium*

10. Uropod 3 uniramous; maxilla 1 outer plate with ten apical spines; maxilla 2 inner plate with facial setae .... *Styloxenodice*

— Uropod 3 without rami; maxilla 1 outer plate with nine apical spines; maxilla 2 inner plate without setae .... *Xenodice*

DISCUSSION

The four warm-water depressed-bodied podocerid genera (Group 1 in Table 1) appear to be closely similar and are herein designated subfamily Podocerinae. They share the following characters: there is a tendency for the posterior two or three pereonites to become fused; antenna 2 becomes large and heavy, with loss of setation, in mature specimens; pereopods 3 and 4 are non-glandular; the female gnathopod 2 is comparatively large, particularly in *Cyrtophium, Laetmatophilus,* and *Leipsuropus,* where the propodus approximates the male form; also in these three genera, and occasionally in *Podocerus,* the epistome is produced into a point. Within the group the evolutionary trend is toward: exaggerated flattening of the body; loss of urosomites, accessory flagellum, and maxilla 1 inner plate; and development of the female gnathopod 2 with its large propodus and elongated, distally extended article 4. Distribution is temperate-cosmopolitan to southern subtropical.

The slender-bodied podocerid genera were discussed recently by Laubitz (1979), and it was then suggested that *Xenodice macrophthalma* Schiecke might not belong in that genus. Further study of the characters of *Xenodice* indicates that *X. macrophthalma* should indeed be placed in a new genus, *Styloxenodice,* as defined above. This genus is close to *Xenodice* but differs in several basic characters, such as the well-developed uropod 3 ramus and the facial setal row on the inner plate of maxilla 2. Both *Xenodice* and *Styloxenodice,* subfamily Xenodicinae (Group 2 in Table 1), differ from other podocerids in having: a long multisegmented flagellum on antenna 1 and 2, with a long accessory flagellum (i.e. longer than the basal two segments of the primary flagellum); a well-developed, strongly setose inner plate on maxilla 1; slender oostegites; and a comparatively strongly developed pleosome. These genera show the greatest number of primitive characters and the closest resemblance to other corophioids. Currently-known distribution is limited to the northeastern Atlantic and the Mediterranean.

The *Dulichia* group (Table 1, Group 4) of cylindrical-bodied genera (Laubitz, 1979), the Dulichiinae, is characterised by head shape, slender mandibular palp, glandular pereopods, very long urosomite 1, and climbing behaviour. The distributional limits of this group are currently uncertain.

Neoxenodice (Table 1, Group 3) differs from the other podocerids by its greatly elongated anterior pereonites, very small anterior coxal plates, gills on pereonites 2-4, and minute pereopods 3 and 4, and is assigned to the subfamily Neoxenodicinae. The genus is morphologically distinct and geographically isolated from the other cylindrical podocerids, having a subantarctic-antarctic distribution.

Laubitz (1979) concluded that the family Podoceridae contained three, and probably four, groups of genera, based on morphology, behaviour, and distribution. It has been shown above that the family can indeed be divided into four groups of different body types (Figure 1), a division supported by analysis of specific morphological characters (Table 1, Figure 2). These four groups are considered to be sufficiently distinctive that they are herein designated subfamilies.

Apart from their corophioidean characters, and the elongation of urosomite 1 and reduction of uropod 3, the podocerid genera share other characters to a greater or lesser degree. Gnathopod 2 much larger than gnathopod 1 in male (Groups 1, 3, 4) and female (Groups 1, 3); pereopods 3 and 4 reduced in size (Groups 3, 4); pereonite 1 short and oriented toward the head (Groups 1, 4); some pereonites elongated (Groups 3, 4); maxilla 1 inner plate reduced and non-setose, or lost (Groups 1, 3, 4); number of gills (Groups 3, 4) and brood plates (Groups 1, 3, 4) reduced.

The main diagnostic character of the Podoceridae has always been the elongate urosomite 1. The presence of this long urosomite in *Icilius,* which has had to be removed from the family, shows that it is not an exclusive taxonomic character; unfortunately, its functional significance is unknown. Since the long urosomite 1 thus cannot be of major taxonomic significance, one must question whether Podoceridae is not just a heterogeneous collection of subfamilies sharing a convergent character. Xenodicinae, for example, would appear to fit quite well into Aoridae (of Bousfield, 1973) along with *Neohela* and *Unciola;* however, Aoridae as defined has such excluding characters as gnathopod 1 larger than gnathopod 2, mandibular palp tapering, and pereopods 3 and 4 glandular. Similarly, Podocerinae is strongly reminiscent of *Jassa* in Ischyroceridae; but the similar, non-glandular pereopods, non-setose maxilla 1 inner plate, and reduced uropods of Podocerinae militate against a close relationship.

TABLE 1. Morphological characters of the Podoceridae, with the genera arranged by subfamily

4. Dulichiinae; 3. Neoxenodicinae; 2. Xenodicinae; 1. Podocerinae

+ = present; 0 = not developed; – = absent

4				3	2		1				
Dulichiopsis	*Dulichia*	*Dyopedos*	*Paradulichia*	*Neoxenodice*	*Xenodice*	*Styloxenodice*	*Podocerus*	*Laetmatophilus*	*Cyrtophium*	*Leipsuropus*	
triangular-rectangular				← recessed →							Head shape
← slender →				← expanded →							Md. palp
+	+	+	+	–	–	–	–	–	–	–	Pereopod glands
← U1 at least > P2+3 →				← U1 shorter or equal P2+3 →							Urosome: Pleosome
2-5	2-5	3-5	2-5	2-4	2-6	2-6	2-6	2-6	2-6	2-6	Coxal gills[1]
6	6	6	6	7	7	7	5-7	5-7	7	(6)	No. of pereonites
2	2	2	2	3	3	3	3	2	3	3	No. of urosomites
–	–	–	–	0	0	1	0	–	0	0	Uropod 3 rami
← cylindrical →							← flat →				Body shape
← Antenna 1 > Antenna 2 →							Antenna 1 < Antenna 2				Antennae
0	0	0	0	0	0	0	0–+	+	+	+	Epistome produced
← reduced →					setose		reduced-absent		absent		Mx. 1 inner plate
3-4	3	1-4	3-5	1	long 4-5	long 4-5	1	–	–	–	Acc. flag. segments
2>>1	2>>1	2>>1	2≥1	2>>1	2≥1	2≥1	2>>1	2>>1	2>>1	2>>1	♂ Gn. 2: Gn. 1
2>1	2≥1	2≥1	2≥1	2>>1	2≥1	2≥1	2>1	2>>1	2>>1	2>>1	♀ Gn. 2: Gn. 1
2-4	2-4	2-4	2-4	2-4	2-5	2-5	2-(5)	2-4	2-4	2-4	Brood plates[1]
S-E	S-E	S-E	S-E	S	E-S	E	E	E	E-L	E-L	Coxa size[2]
← strongly dissimilar →					of increasing length		← similar →				Pereopods 3-7
2	2	2	0-1	2	2	2	2	0	2	–	Uropod 2 rami
9	9	9	9	9	9	10	9	9	9	8	Mx. 1 apical spines
+	+	–	–	–	–	+	–	–	–	–	Mx. 2 facial setae
falcate	← blunt →										Mxpd. palp 4
+	0	0	0	0	0	0	0	0	0	0	Pereopod 5-7 palm

1. Pereopods on which coxal gills and brood plates are present.
2. S-shorter than, E-equal to, L-longer than, pereonite.

Despite the differences between the subfamilies, the podocerids do have a number of shared, although not necessarily exclusive, characters other than the urosomite 1. Antenna 1 and 2 are strongly developed; gnathopod 2 is dominant, usually strongly; the coxae are reduced, frequently greatly; and, most significant, uropod 3 (and sometimes uropod 2) is reduced or lost. The structure of the head is hard to interpret, but appears to have been caused by the posteriad deepening of the inferior antennal sinus to create on the one hand the 'recessed' head (defined by Barnard, 1973) of Groups 1, 2, and 3, and

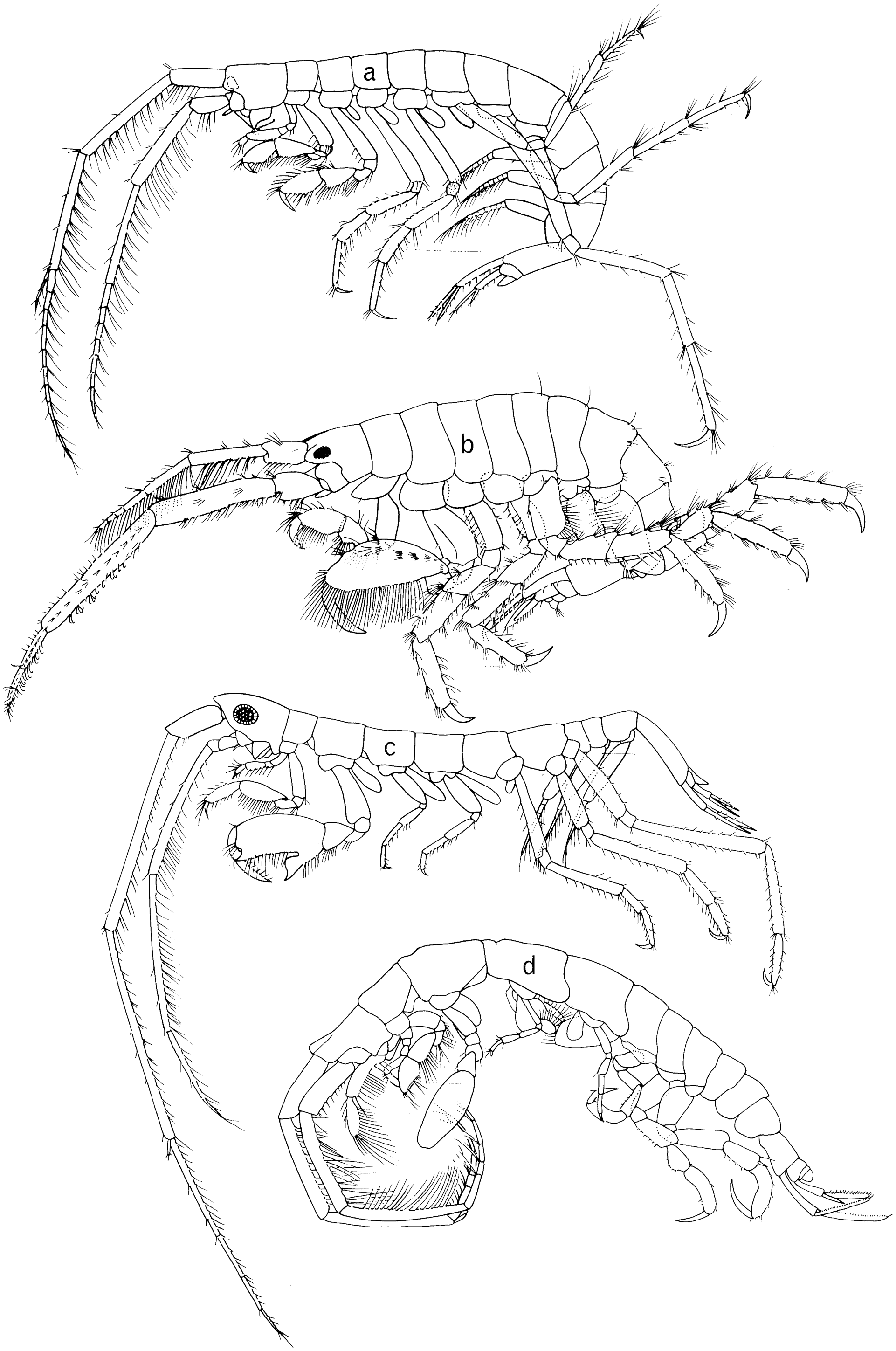

Fig. 1. Gross morphology of the four subfamilies of Podoceridae. **a** Xenodicinae. **b** Podocerinae. **c** Dulichiinae. **d** Neoxenodicinae. (Redrawn from Baranard, Sars)

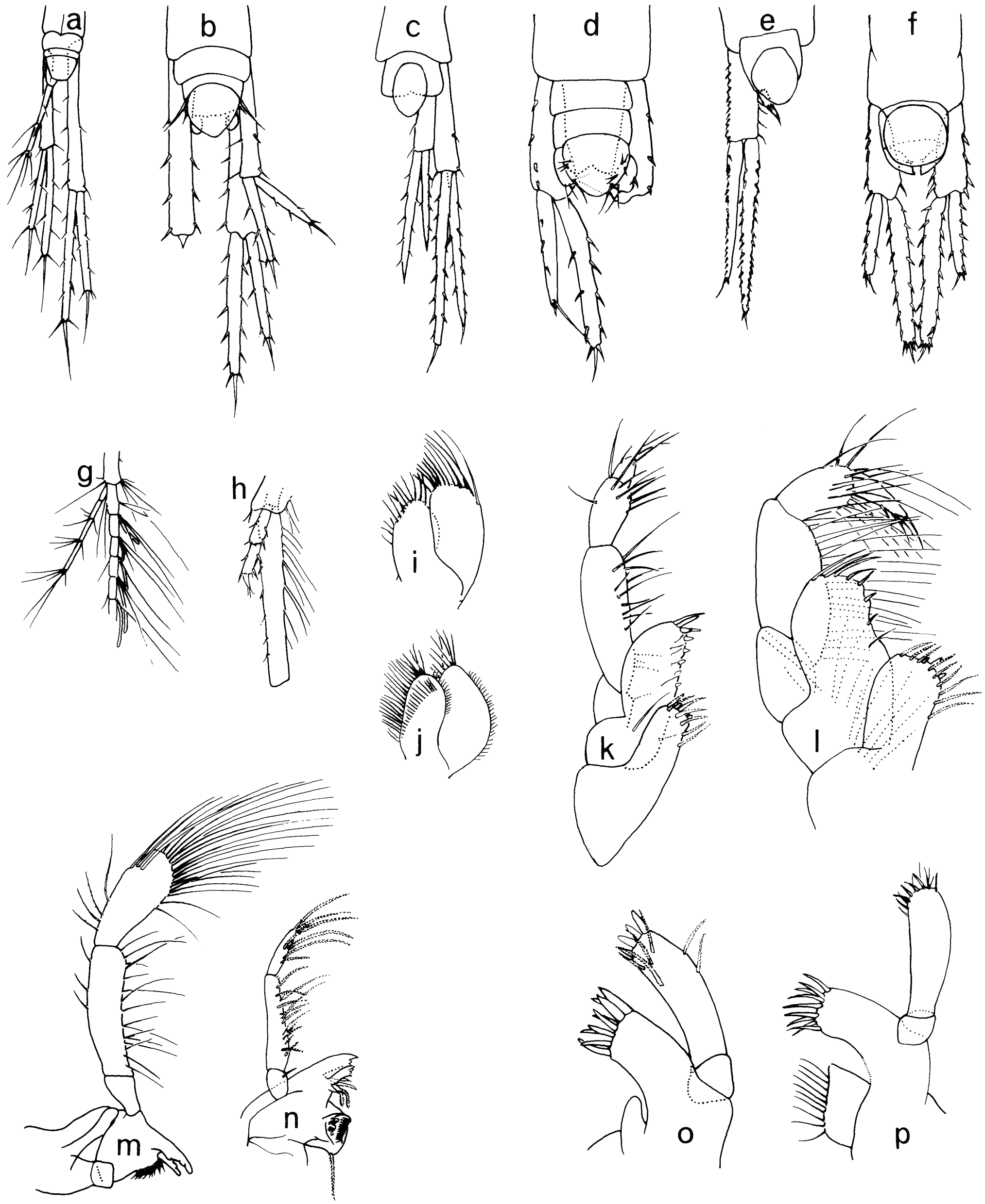

Fig. 2. Posterior urosome of **a** *Styloxenodice,* **b** *Xenodice,* **c** *Dulichia,* **d** *Leipsuropus,* **e** *Paradulichia,* **f** *Laetmatophilus.* Accessory flagellum of **g** *Styloxenodice,* **h** *Dulichia.* Maxilla 2 of **i** *Podocerus,* **j** *Styloxenodice.* Maxilliped of **k** *Neoxenodice,* **l** *Dulichiopsis.* Mandible of **m** *Styloxenodice,* **n** *Dulichia.* Maxilla 1 of **o** *Styloxenodice,* **p** *Neoxenodice.* (Redrawn from Barnard, Laubitz, Lowry, Sars, Schiecke, Stebbing; d original.)

on the other hand the even more exaggerated distinctive head of Group 4. Certainly, the combination of characters exhibited by the podocerids is unique, and although both the Xenodicinae (with long flagella and strong pleosome) and the Neoxenodicinae (with almost caprellidean gross morphology) are atypical, they can be assumed to show the two extremes of degree of evolutionary development within the family.

The highly adaptive characters of most podocerid genera tend to obscure their relationship with and evolution from other corophioids. However, the combined characters of gnathopod 2 dominance, long article 3 on antenna 1, and recessed head all point to a *Gammaropsis* type ancestor (Barnard, 1973). Assuming that the family originated in the temperate Pacific (Laubitz, 1979), distribution (north-eastern Atlantic) and characters (e.g., loss of glandular pereopods) make *Styloxenodice* itself an unlikely ancestral podocerid. One can, however, visualise a *Styloxenodice*-like form, still retaining glandular pereopods, from which all four generic groups could have been derived. While it is possible, perhaps even probable, that Podoceridae is polyphyletic, it would at present be premature to subdivide it at the family level when we have limited knowledge of many aspects of the constituent genera and species. The genera currently accepted within the family are all sufficiently distinctive to be readily recognisable, by their combination of characters, as Podoceridae.

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TERRESTRIAL OSTRACODS IN AUSTRALIA

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SUMMARY

Two new species of terrestrial ostracods are described from Australia: *Mesocypris australiensis* n.sp., mainly recorded from near the east and south coast of eastern Australia, and *M. tasmaniensis* from south-west Tasmania. An additional species *Scottia audax* is also recorded from Queensland and New South Wales.

Ecological notes on *M. australiensis* are given and the distribution of the terrestrial ostracods found only in the southern hemisphere is discussed.

INTRODUCTION

Ostracods occur in most aquatic environments ranging from typically marine to freshwater. They are present in interstitial and non-marine saline waters and are also found outside the typical aquatic habitats, living among moss and leaf litter characterised by a high moisture content. The term 'terrestrial' used here refers to that particular environment. Such cases of terrestrial adaptation for ostracods have been recorded from African forests by Klie (1939) with *Mesocypris pubescens* Daday, 1908 and by Lawrence (1953) and Harding (1953) with *Mesocypris terrestris* Harding, 1953, from New Zealand native forests by Chapman (1960, 1961) with *Scottia audax* (Chapman, 1961), and from a variety of terrestrial environments in Madagascar by Danielopol and Betsch (1980) who described *Mesocypris madagascariensis* and *M. pauliani* and also *Terrestricandona minuta*. Additionally, Schornikov (1969) described a highly adapted terrestrial ostracod *Terrestricythere ivanovae* Schornikov, 1969 living in vegetal debris of marine origin on a beach of the Kuril Archipelago. It is only recently that ostracods have also been recorded from litter and soil in wet sclerophyll forests in Victoria (as *Mesocypris* sp. by Ahern and Yen, 1977) and Queensland (no identification given by Plowman, 1979) and New South Wales (De Deckker, 1980).

All the ostracods found in terrestrial environments, including the Australian species here, belong to the family Cyprididae Baird, 1845, which groups non-marine ostracods with the exception of *Terrestricythere ivanovae* and *Terrestricandona minuta*. The former belongs to the superfamily Terrestricytheracea, which has marine affinity, and the latter belongs to the Candonidae, which groups mainly freshwater and some marine forms. Danielopol and Betsch (1980) claim that *T. minuta* originates from a typical interstitial freshwater candonid ancestor.

In Australia there are three species of terrestrial ostracods known: *Mesocypris tasmaniensis* n.sp from SW Tasmania, *M. australiensis* n.sp from northern Queensland to New South Wales and Victoria (see Table 1, Fig. 6) and *Scottia audax* (Chapman, 1961) from Queensland and New South Wales. The latter species has recently been re-examined by De Deckker (1980).

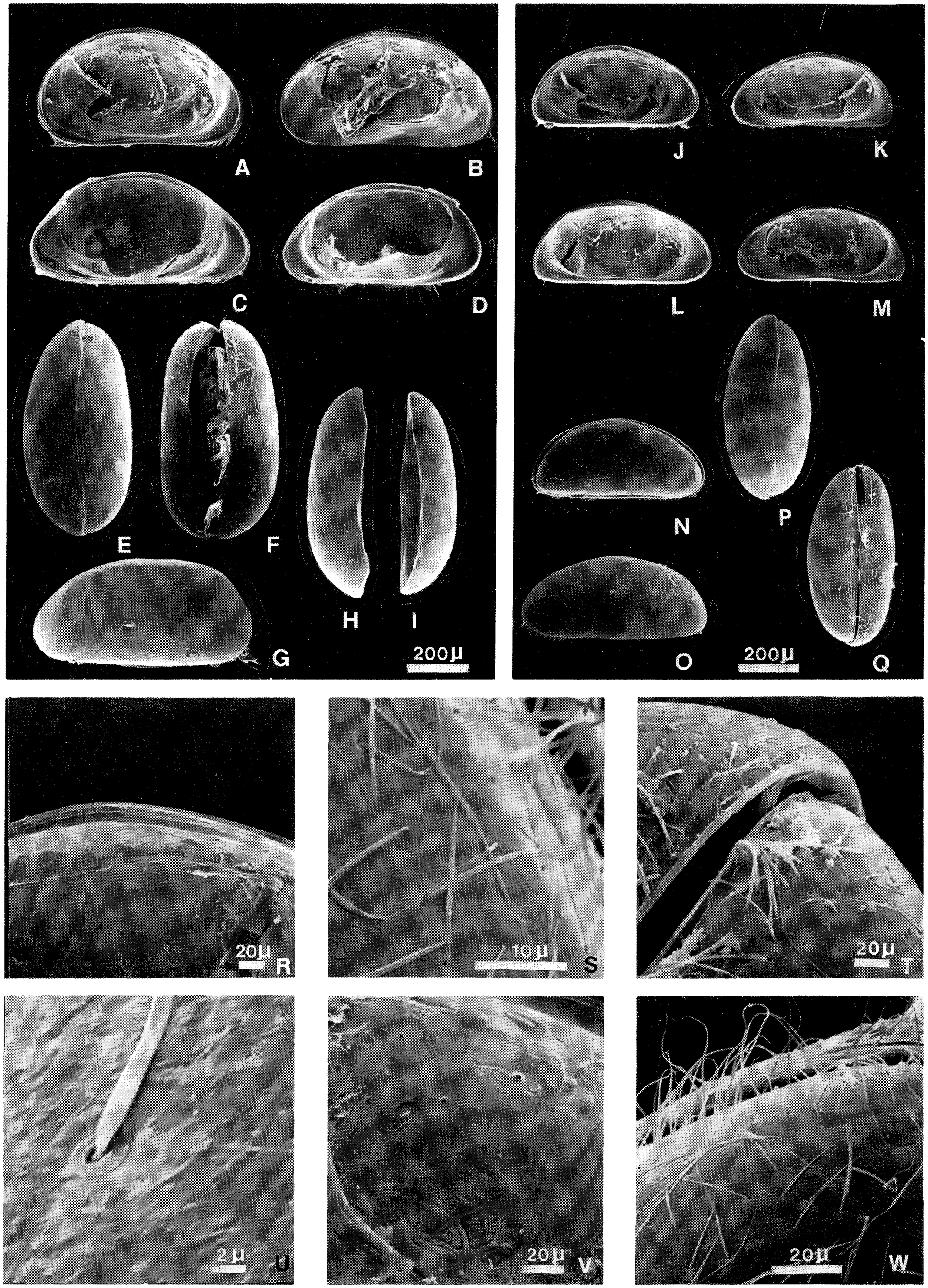
SYSTEMATICS

Superfamily Cypridacea Baird, 1845

Family Cyprididae Baird, 1845

Subfamily Scottinae Bronstein, 1947

Remarks: This subfamily is characterised by: smooth oviform shell, dorsally arched and ventrally flat and often densely pilose, especially in the ventral area. Central muscle field consisting of an almost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vertical row of 3 large rectangular scars with a smaller one below plus 2 others behind, the top one often being the largest. Natatory bristles of the antenna strongly reduced. Furca strongly chitinised and with 2 thick and strong denticulated claws. Zenker organ with one rounded, globular end. (Modified from Hartmann and Puri, 1974.) *Scottia* Brady and Norman, 1889 and *Mesocypris* Daday, 1908 are grouped in this subfamily as discussed by De Deckker (1979a).

Mesocypris Daday, 1908

Remarks: Shell smooth or pseudopunctate and often strongly pilose, especially in the ventral area; left valve larger than right one especially at both anterior and posterior ends. Thoracopod I with segments 2 and 3 fused and a small seta on the outside of the 4th segment; furcae asymmetrical: right one with strongly denticulated shaft, left one finely pectinated.

Mesocypris australiensis n.sp

Figs 1, 2, 5A-G

Types. *Holotype:* ♂ adult, Beauchamp Falls, Otway Ranges, Victoria—collected on moss. South Australian Museum, C3922.

Paratype: ♀ adult, same data, C3923.

Diagnosis: *Mesocypris* with furcae consisting each of 2 short, stout and strong and almost equal denticulated claws plus a long plumose anterior seta which is often much longer than the claws. The posterior setae are dissimilar: a thin (at least twice thinner and shorter than the claws) and pectinate one on the left furca which has a shaft with fine hairs; a short (almost half the length of the claws) stout and thick one on the right furca which possesses a coarse and irregular denticulation along its shaft.

Dimensions:

			Length (μm)	Height (μm)
Holotype	♂	LV	710	400
		RV	690	380
Paratype	♀	LV	690	370
		RV	670	340

Description

Carapace: *external:* oval in shape with almost flat ventral area; length about twice the height and the width; greatest height usually in middle. Shell smooth or finely pseudopunctate. Pilosity of shell variable but hairs always more prominent ventrally; hairs thin at their base. Left valve (LV) overlapping right valve (RV) all around its periphery except in the hinge area where both valves join at the same level. In dorsal view, strong overlap of LV over RV anterior and posterior to hinge and more extensive posteriorly. Normal pores commonly rimmed and often arranged in rows parallel to the long axis of the shell ventrally. Colour of shell white with pale yellow colouring occasionally noticed on live specimens from Mt Wilson, N.S.W. in the vestibulum areas both anteriorly and posteriorly.

internal: hinge adont; central muscle field consisting in front of an almost vertical row of 3 large rectangular scars plus a narrower one below and two more rounded placed behind. Mandibular scars elongated and almost as long as the rectangular scars above. Calcareous part of the inner lamella broad, especially in the postero-ventral area. Selvage faint in right valve and more evident in left valve where

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Fig. 1 (facing). *Mesocypris australiensis* n.sp **A-I, U**—Beauchamp Falls, Otway Ranges, Vic. **A-B**—Holotype male, internal lateral view of LV and RV; **C-D**—Paratype female, same data; **E**—Female, dorsal view of carapace; **F**—Female, ventral view of carapace; **G**—External lateral view of carapace (note slight deformation of the shell in posterodorsal area); **H-I**—Male, dorsal view of LV and RV separated; **U**—Detail of E to show rimmed normal pore and pseudopunctation of shell. **J-T, V-W**—Gold Hill, McDonald Range (16° 05'S 145° 17'E), Qld. **J-K**—Male, internal lateral view of LV and RV; **L-M**—Female, same data; **N**—Male? external lateral view of carapace showing RV; **O**—Female? external lateral view of carapace showing LV; **P**—Female, dorsal view of carapace; **Q**—Female, ventral view of carapace; **R**—Detail of J to show fine groove in hinge area and below it a sperm thread; **S**—Detail of N to show rimmed normal pores and ? sensory hairs; **T**—Detail of Q to show normal pore canals with and without protruding hairs (note pores aligned parallel to long axis of the shell); **U**—Detail of E to show rimmed normal pore with hair and pseudopunctation of shell; **V**—Detail of K to show central and part of dorsal muscle field and internal pores; **W**—Detail of N to show hairs in dorsal area of shell. LV-left valve, RV-right valve.

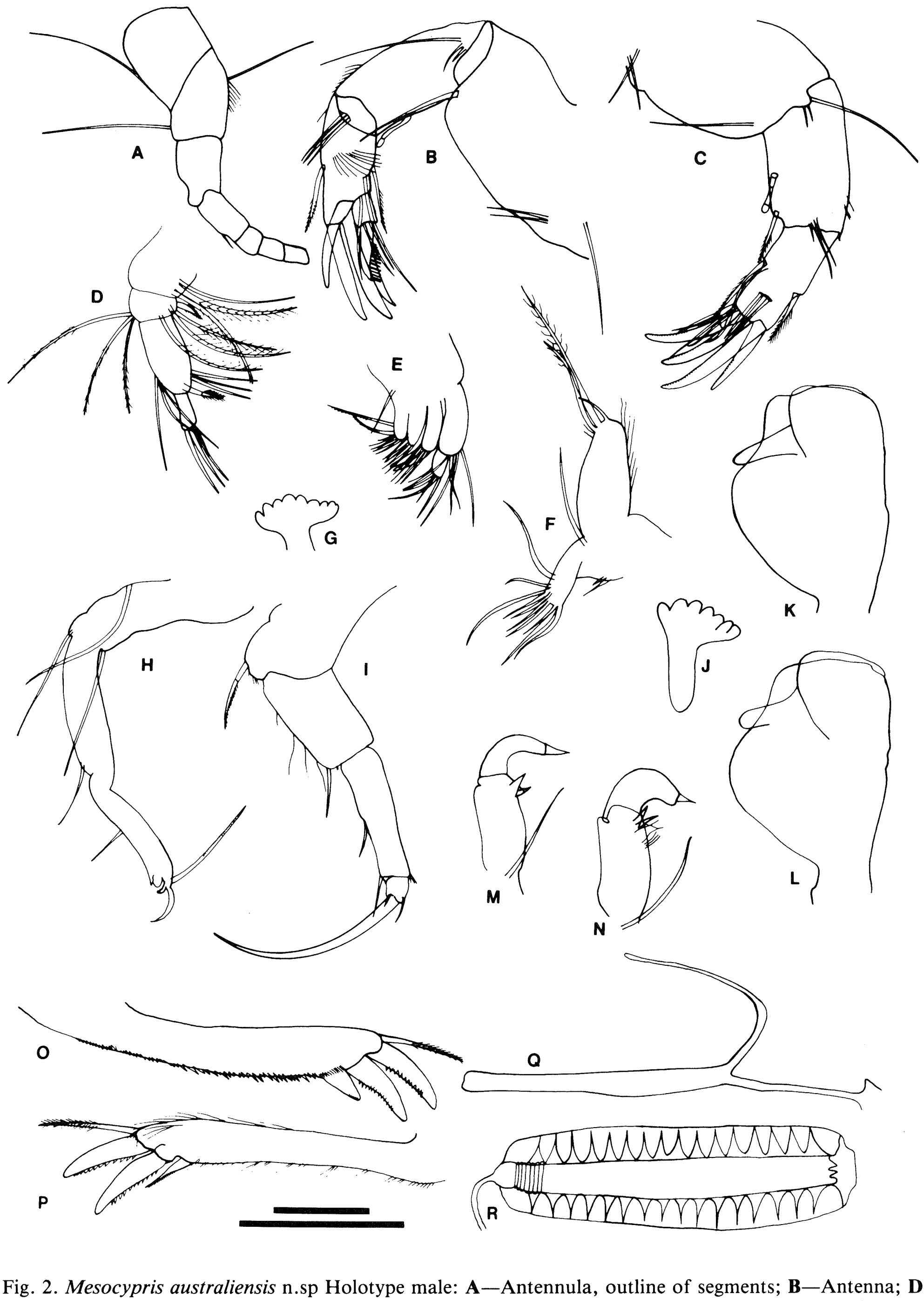


Fig. 2. *Mesocypris australiensis* n.sp Holotype male: **A**—Antennula, outline of segments; **B**—Antenna; **D**—Mandibular endopod; **E**—Maxillular palp with lobes; **H**—Thoracopod II; **I**—Thoracopod I; **J**—Rake-like organ; **K-L**—Hemipenis outline; **N-M**—Maxilla, detail of palp; **O**—Right furca; **P**—Left furca; **Q**—Furcal attachment; **R**—Zenker organ. Paratype female: **C**—Antenna; **F**—Maxilla; **G**—Rake-like organ.
Scales: small one (25 μm) for Figs 2G, J; large one (100 μm) for others.

it is narrow anteriorly and broader posteriorly. Width between inner margin and selvage often twice that of distance between selvage and outer margin. Edge of outer margin slightly curved outwards especially in LV.

Appendages. Only the characteristic features will be described here. For details see Fig. 2 and Fig. 5A-G.

Antennula: 7-segmented; segments 4–7 strongly chitinized; segment 4 longer than 5 and 6 together. The distal setae are as long as all the segments together.

Antenna: sexual dimorphism present: 4 short strong claws in both sexes plus an additional smaller one in male which has a broad comb-like denticulation (this claw is thought to help during copulation for the male to trap hairs protruding on the outside of the female carapace in order to remain in a stationary position). 'Natatory' setae very small.

Mandible: coxa with 7 molars; distal molar longer than previous 3 and next to it there is a slightly longer pectinate seta. Mandibular palp 4-segmented with last segment narrow and twice as long as 2nd one; α seta very long and smooth, β seta short and pectinate, γ seta thin and shorter than 4th segment and with brush-like hairs. Respiratory plate normally developed.

Rake-like organ: in holotype only 7 teeth present whereas in females 7–8 teeth seen with outside one bifid.

Maxillula: second segment of palp narrow and small: 2 smooth *Zahnborsten* on 3rd endite and on external side of 1st endite and 2 thick pilose setae, one about the length of the endite and the other about double in length. Respiratory plate normally developed.

Maxilla: strong sexual dimorphism: in male, end segment of prehensile palps slightly asymmetrical: one broader than the other; in female, endopodite with 3 plumose bristles of different lengths, the smallest one being 4 times shorter than the longest one. Long seta at the base of the endopodite in both sexes. Near the tip of the protopodite there are 11 bristles and 2 smaller ones near its base.

Thoracopod I: segments 2 and 3 fused; posterior seta on 4th segment very small (about length of that segment).

Thoracopod II: segments 2 and 3 fused; terminal segment with one pincer and 2 unequal setae.

Hemipenis: for outlines see Fig. 2K-L.

Zenker organ: 16 rosettes in holotype but the number can vary between 9 and 16. Central tube finely ribbed transversally. One end globular.

Furca: see diagnosis. The length of the anterior setae is very variable and occasionally they can be different on a single specimen (Fig. 5H).

Furcal attachment: strongly chitinized; long and straight median branch; ventral branch with broad apex; dorsal branch long and strongly curved.

Eye: dark brown in colour.

Remarks. Variation in hemipenis outline is noticeable especially in the protrusion of the lateral lobe and on the external edge of the median lobe (see Fig. 5A-B). Because of such variations, no constant diagnostic feature could be selected for differentiating *M. australiensis* from *M. tasmaniensis.* This phenomenon is rather unusual as the outline of the hemipenis is normally an excellent taxonomic feature and is used for species differentiation for many cypridid ostracods (see discussions in De Deckker, 1978, 1979). In general, the lateral lobe of *M. australiensis* does not protrude as much as for *M. tasmaniensis.*

Specimens of *M. australiensis* from Gold Hill, Queensland (see Fig. 1J-Q) are much smaller than those from the type locality and others in southern Australia. This is also reflected in the size of the furca (compare Figs 2O-P and 5H); similarly, reduction in size of the animal appears to be associated with a reduction in rosette number in the Zenker organ (9 and 10 rosettes found in specimens from Gold Hill).

Distribution. See Table 1.

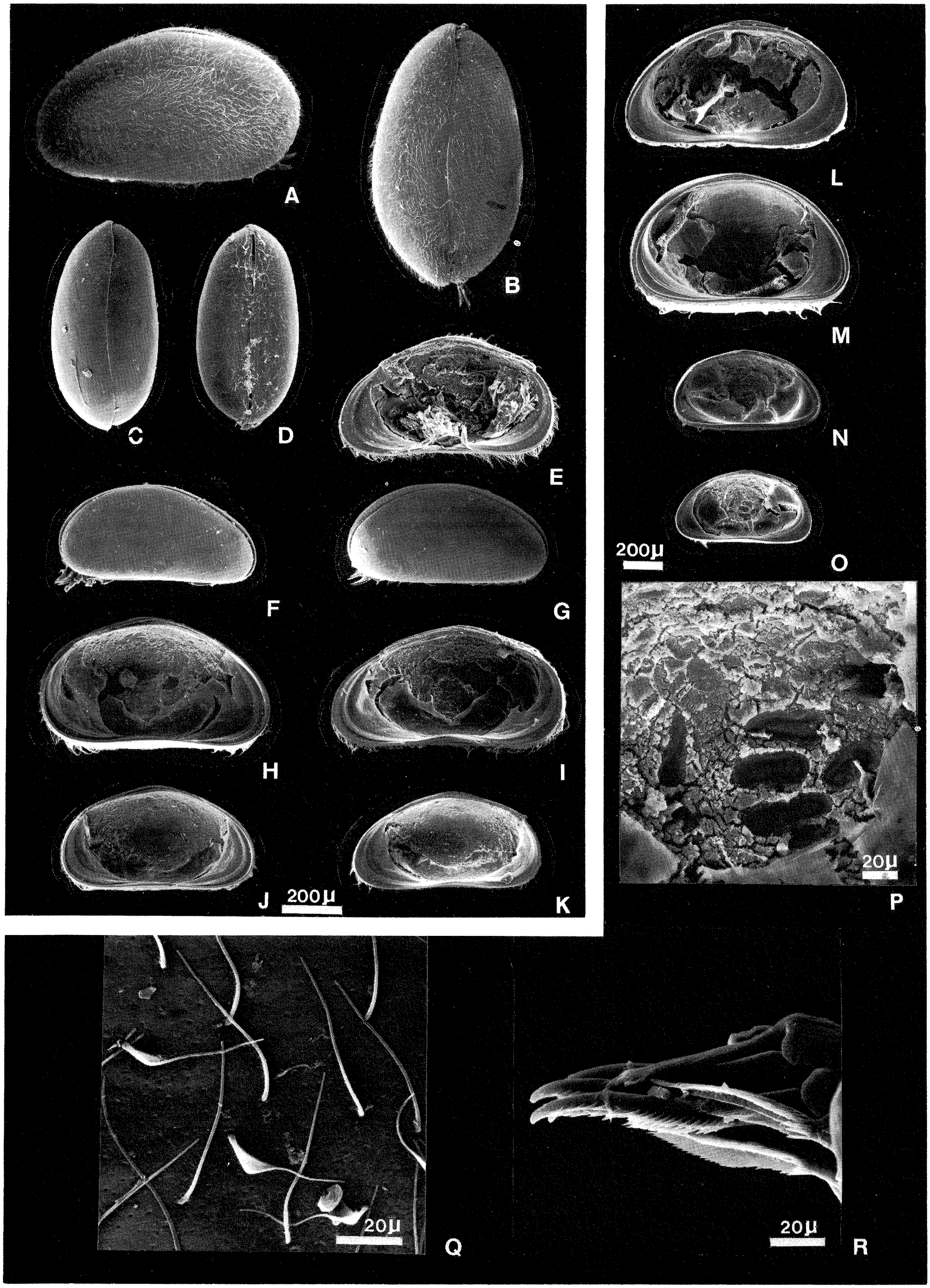
Mesocypris tasmaniensis n.sp.

Figs 3A-K, 4, 5I-N

Types. *Holotype:* ♂ adult, broken valves, wet sclerophyll litter, lower Gordon River area in SW Tasmania (42° 51′S, 145° 50′E). Tasmanian Museum, G2237.

Paratype: ♀ adult, same data, G2238.

Diagnosis. *Mesocypris* with furca with similar claws and setae: 2 almost equal, short, stout and strong claws and a thin anterior seta often longer than the claws and a pectinate posterior seta, coarser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than the anterior one and about half to ¾ the length of the claws. Right furcal shaft with coarse irregular denticulation and left shaft with fine hairs.

Dimensions:	Length (μm)	Height (μm)
Paratype ♀: carapace	600	300
Paratype ♂: carapace	580	300
Paratype ♀ (unusually large): carapace	840	440

Description

Only the features of the carapace and the anatomy which are different from those of *M. australiensis* are presented.

Carapace: *externally:* the height and width of the carapace are slightly less than half the length; the greatest height is usually at 3/5 from the anterior.
internally: the selvage is broader and more prominent in both valves.

Appendages. The main anatomical feature distinguishing *M. tasmaniensis* from *M. australiensis* is the morphology of the posterior setae of the furcae. For description see diagnosis. The minor differences seen in the Tasmanian species are:
—on the antennae, the natatory setae are very short in the male;
—on thoracopod I, the posterior seta on segment 4 is slightly longer;
—in the male maxilla, the broadening of both palps is almost identical;
—the lateral lobe on the hemipenis is usually longer;
—the furcal attachment has a ventral protrusion at mid-length on the median branch and the apex of the ventral branch is knob-shaped;
—the main tube of the Zenker organ is transversely ribbed.

Remarks. Occasionally unusually large specimens of *M. tasmaniensis* have been found in the Tasmanian collections. The carapaces of these are more hairy (see Fig. 3A-B). No difference in morphology has been noticed for these specimens. It is thought that they represent animals which could have undergone an additional moult but there is no evidence to substantiate this.

Distribution. Lower Gordon River and tributaries area in SW Tasmania. Found in 122 samples taken in that area by members of the Zoology Department, University of Tasmania. Fossil specimens, which have been recovered in many samples from Mowbray and Pulbeena Swamps from NW Tasmania (formed during the Late Quaternary—De Deckker, 1982), are tentatively included in this species even though it is necessary to have soft parts to distinguish species of *Mesocypris* in Australia, as quite a few fossil specimens have large valves as seen in some of the living samples taken in the lower Gordon area (see remarks above).

General remarks about *M. australiensis* and *M. tasmaniensis*

Anatomically both species are very similar except for the morphology of the posterior setae of the furcae. The general shape of the shell varies from one locality to another but there does not seem to be any distinctive taxonomic difference except that the selvage is much broader in both valves of *M. tasmaniensis*. The difference in size between specimens from different populations is likely to be caused by varying ecological parameters.

The two Australian species differ from *M. terrestris* mainly in that the latter has no eye and a much higher number of rosettes on the Zenker organ. The outline of the hemipenis is also different. The shell and the anatomy of *M. terrestris* are generally more pilose.

For discussion of other *Mesocypris* species see Danielopol and Betsch (1980).

Fig. 3. (facing) **A-K**—*Mesocypris tasmaniensis* n.sp, from various localities in the lower Gordon River area, SW Tas. **A-B**—(loc. 42° 41′S 145° 39′33″E) Female: lateral and dorsal view of carapace; **C-G**—(Type locality: 42° 51′S 145° 50′E): **C-D**—Male?, dorsal and ventral view of carapace; **E**—Males, internal lateral view of RV; **F**—Female?, external lateral view of RV; **G**—Male, same data; **H-K**—(loc. 42° 43′S 145° 50′E): **H-I**—Large female, internal lateral view of LV and RV; **J-K**—Small female, same data.
L-R—*Scottia audax* (Chapman, 1961). **L-P**—Joalah National Park, rainforest (loc. 27° 55′S 153° 12′E), Qld: **L-M**—Female, internal lateral view of RV and LV; **N-O**—Juvenile, same data; **P**—Detail of O to show central muscle field; **Q-R**—Dorrigo National Park, N.S.W.: **Q**—Detail of shell to show normal pores and different types of hairs; **R**—Detail of claws and setae of furcae.

Fig. 4. *Mesocypris tasmaniensis* n.sp. Paratype female: **A**—Antennula, outline of segments; **C**—Antenna; **D**—Mandibular endopod; **E**—Maxilla; **I**—Thoracopod I; **M**—Right furca; **N**—Left furca; **O**—Furcal attachment. Holotype male: **B**—Antenna; **F**—Hemipenis outline; **G**—Maxillular palp with lobes; **H**—Part of rake-like organ; **J-K**—Maxilla, detail of palp; **L**—Thoracopod II; **P**—Zenker organ. **Scales:** small one (25 μm) for Fig. 4H; large one (100 μm) for others.

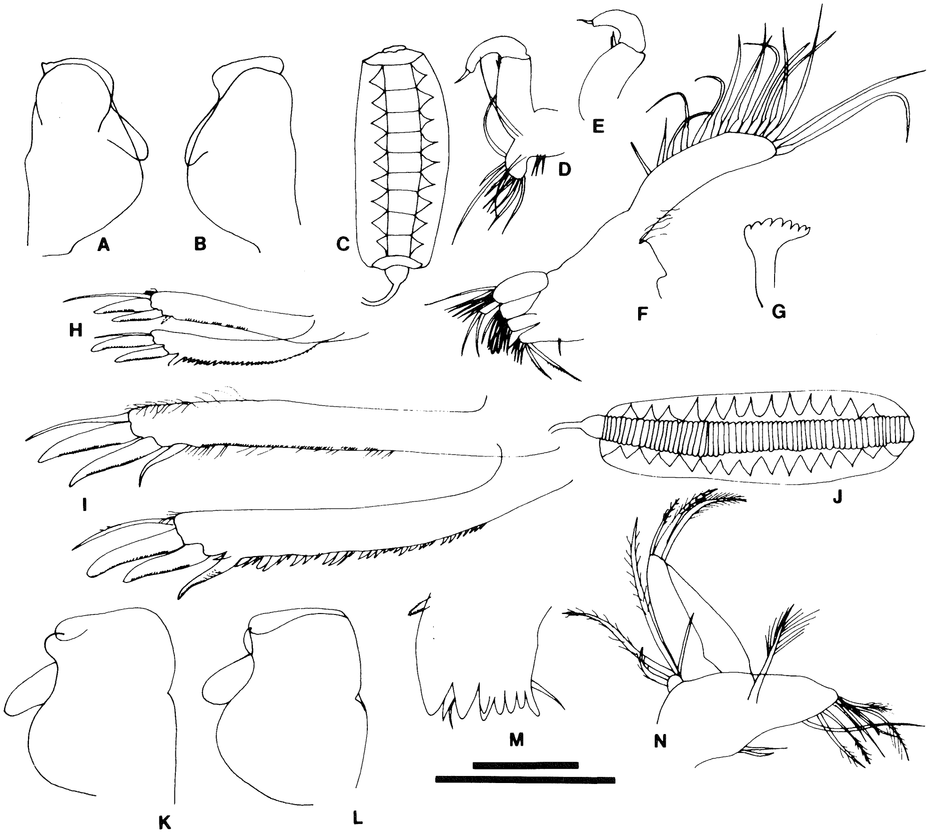

Fig. 5. *Mesoscypris australiensis* n.sp. Gold Hill, McDonald Ranges (loc. 16° 05′S 145° 17′E). Male: **A-B**—Hemipenis outline; **C**—Zenker organ; **D**—Maxilla; **E**—Maxilla, detail of palp; **H**—Furcae. Female: **F**—Maxillula; **G**—Rake-like organ.

Mesocypris tasmaniensis n.sp. Type locality (42° 51′S 145° 50′E), Lower Gordon River area, SW Tas.: Female: **I**—Furcae. Male: **J**—Zenker organ: **M**—Mandibular coxale, detail. (Loc. 42° 37′S 145° 45′E) Lower Gordon River area, SW Tas.: Male **K-L**—Hemipenis outline (Loc. 42° 41′ 30″S 145° 54′E) SW Tas.: Female **N**—Maxilla.

Scales: small one (25 μm) for Figs 6 J-M; large ones: (100 μm) for others.

Scottia Brady and Norman, 1889

Remarks. The genus is characterised by a thoracopod I with well defined (not fused) segments 2 and 3 and with a terminal claw and a long thick seta, often longer than half the length of the claw. The furcae are symmetrical and the furcal shafts are much broader than for *Mesocypris* species. So far there are only 3 known living *Scottia* species: *S. pseudobrowniana* Kempf, 1971, *S. audax* (Chapman, 1961) and *S. insularis* Chapman, 1963.

S. audax, recently re-examined by De Deckker (1980), is a terrestrial species; the female anatomy of that species is almost identical to that of *S. pseudobrowniana. S. insularis* could not be examined as the type material is at present missing from the Otago Museum. From Chapman's (1963) description, which is the only one available for that species, De Deckker (1980) has cast doubts on its generic affinity. Eagar's (1969) description of mummified parts of the soft anatomy of *S. insularis* from Pleistocene sediments does not provide additional details as many appendages were partly damaged.

Scottia audax differs from the two Australian *Mesocypris* species on the following characters:

—*shell*—thicker shell which is usually coloured in brown or light grey.

—some hairs protruding from the normal pores are broad at their base.

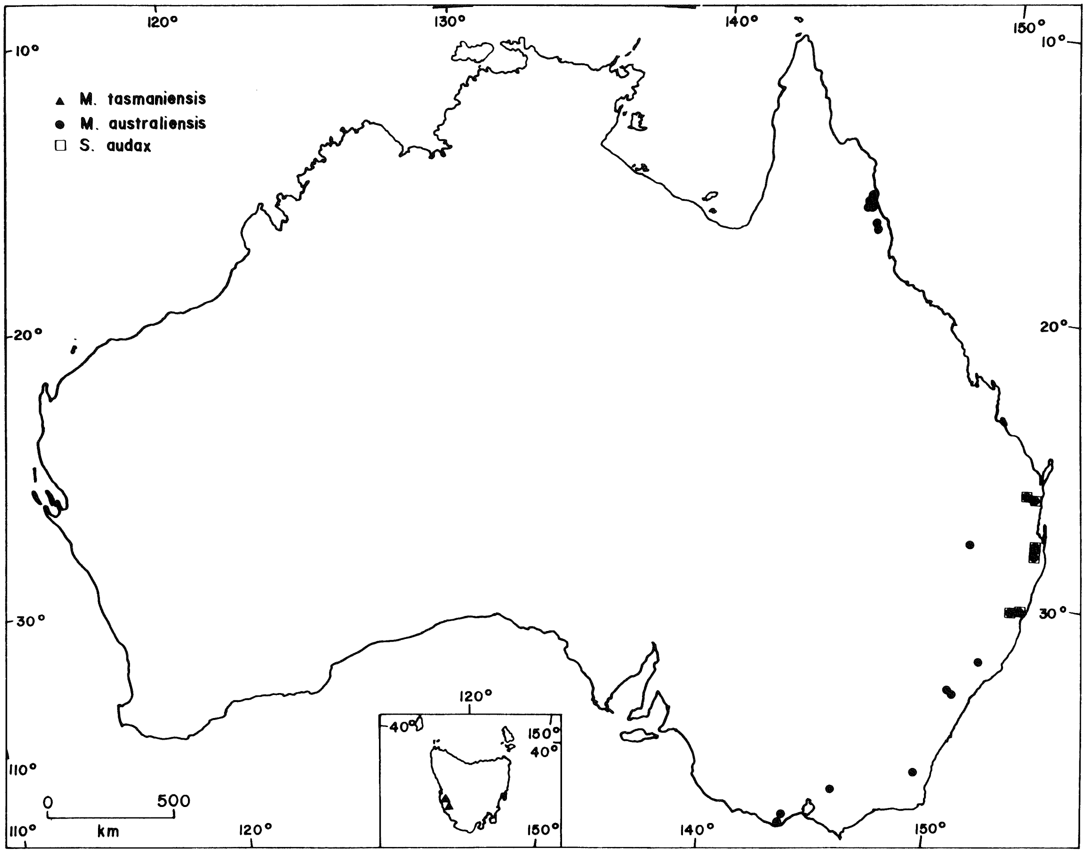

Fig. 6. Distribution of the terrestrial ostracods in Australia. See Table 1 for further details.

—mandibular scars below the central muscle field are very small.

—selvage more prominent in LV and closer to the edge of the shell anteriorly, whereas in the right valves it is thin and far away from the edge of the shell posteriorly.

—*anatomy:* see different generic details mentioned above; in general the appendages are more pilose and many setae are more plumose.

Ecological notes

Terrestrial ostracods in Australia have only been found in wet sclerophyll and rain forests. Live specimens of *Mesocypris australiensis* found in *Sphagnum* moss collected on the side of the road near a small creek (where light penetration was poor) at Mt. Wilson near Lithgow, N.S.W., were examined in the laboratory. The following observations were made:

—when fully immersed in water *M. australiensis* did not swim freely. This is probably due to the atrophy of 'natatory' setae on the antennae and the small number of long setae on the antennulae. When put in an upside-down position at the bottom of a glass petri dish of water, the animal did not return to the normal upright position. At the time, it was possible to see through the white translucent shell the maxillular respiratory plates vibrating between the body and the valves. Rate of beating of the plates increased when the shell was either open or about to open. Immediately after closing of the valves, beating stopped for a short period of time.

—locomotion occurred on any surface by slight opening of the shell and movement of the strongly chitinised antennae and furcae. The use of these two parts of appendages is similar for benthic ostracods. In *M. australiensis* the furcae move together, although they are slightly dissociated from one another, they are welded at their base (for that reason they are hard to separate during dissection).

Table 1. List of Occurrences of Terrestrial Ostracods in Australia

M.a. = *M. australiensis*
M.t. = *M. tasmaniensis*
S.a. = *S. audax*

Queensland

Joalah National Park, altitude c. 380 m, rainforest, 27° 55'S 153° 12'E, **M.a.** + **S.a.**
Dingo Creek, 1 km E of Traverton, c. 80 m, rainforest, 26° 18'S 152° 48'E, **M.a.**+ **S.a.**
Cooran Plateau, near Traverton, c. 400 m, rainforest, 26°17'S 152°50'E, **M.a.**
Lamington National Park, c. 920 m, 28° 14'S 153° 09'E, **M.a.** + **S.a.**
Mt Haig, c. 1150 m, 17° 06'S 145° 36'E, **M.a.**
Mt Lewis, 970 m, 16° 33'S 145° 13'E, **M.a.**
Mt Lewis, 960 m, 16° 35'S 145° 17'E, **M.a.**
Mt Lewis Road, near Julatten, 9 km from grid, **M.a.**
Mt Lewis Road, near Julatten, c. 500 m, c. 1000 m, c. 1200 m, c. 1300 m, **M.a.**
Eacham National Park, 760 m, rainforest, 17° 18'S 145° 37'E, **M.a.**
Cammoo Caves near Rockhampton, 28° 10'S 150° 28'E, **M.a.**
Gold Hill, McDonald Range, 550 m, 16 05'S 145° 17'E, **M.a.**

New South Wales

Dorrigo National Park, rainforest, 30° 21'S 152° 45'E, **M.a.** + **S.a.**
Dorrigo National Park, Wonga Walk, rainforest, c. 850 m, **S.a.**
Bruxner Park near Coffs Harbour, rainforest, **M.a.** + **S.a.**
Tuckers Knob, 21 km SW of Coffs Harbour, 760 m, **M.a.**
Upper Allyn Valley, near Eccleston, c. 650 m, rainforest leaf mould, **M.a.**
Brown Mountain, near Nimmitabel, Rutherford Creek, c. 820 m, rainforest, **S.a.**
Clyde Mountain, 600 m, c. 800 m, rainforest, **M.a.**
Mt Tomah, E of Lithgow, from beside a natural spring, wet sclerophyll forest, **M.a.**
Mt Wilson, E of Lithgow, creek along side of road, **M.a.**

Victoria

Beauchamp Falls, Otway Ranges, moss, **M.a.**
8 km SSE of Beech Forest, Otway Ranges, leaf litter and soil sample, **M.a.**
9.5 km SSE of Beech Forest, Otway Ranges, leaf litter and soil sample, **M.a.**
Acheron River, 500 m, trailing vegetation in leafy liverwort, wet sclerophyll forest, **M.a.**

Tasmania

Lower Gordon River and tributaries, 122 samples from moss and leaf litter, **M.t.**

—movement of the animal can be rapid and continuous. When the antennae are moving, the brown eye, with its 2 lateral lenses which can be seen through the carapace, is also moving sideways.

—*M. australiensis* was never seen moving backward or rotating completely.

—when taken out of the water in the petri dish, the ostracod closes its valves immediately and no appendages are seen to move inside the carapace.

—when the ostracod is moving on moss, a film of water surrounds the bottom part of the carapace. The trapping of water is caused by the abundant hairs which are most common ventrally and laterally to mid-height. When the shell is seen from above, hairs are very noticeable at both anterior and posterior ends. Some hairs can reach 100 μm in length (this is often the case in *S. audax*). When *M. australiensis,* surrounded by a bubble of water, is put on a dry petri dish, the animal can be mobile but it cannot retain the whole amount of water which was around it prior to motion. This indicates that hairs can trap water and retain it only when moving on moist ground.

—the position of the animal during motion or at rest is vertical upright at most times. This is achieved by the broadening of the shell near its base (when seen from the anterior, the shell is triangular in shape) and by the abundance of hairs which help in retaining a constant vertical position—other ostracods usually do not retain the vertical position on a hard surface but lie on their side, particularly when feeding.

—the strong pilosity seen on some of the appendages is likely to help in the retention of additional water.

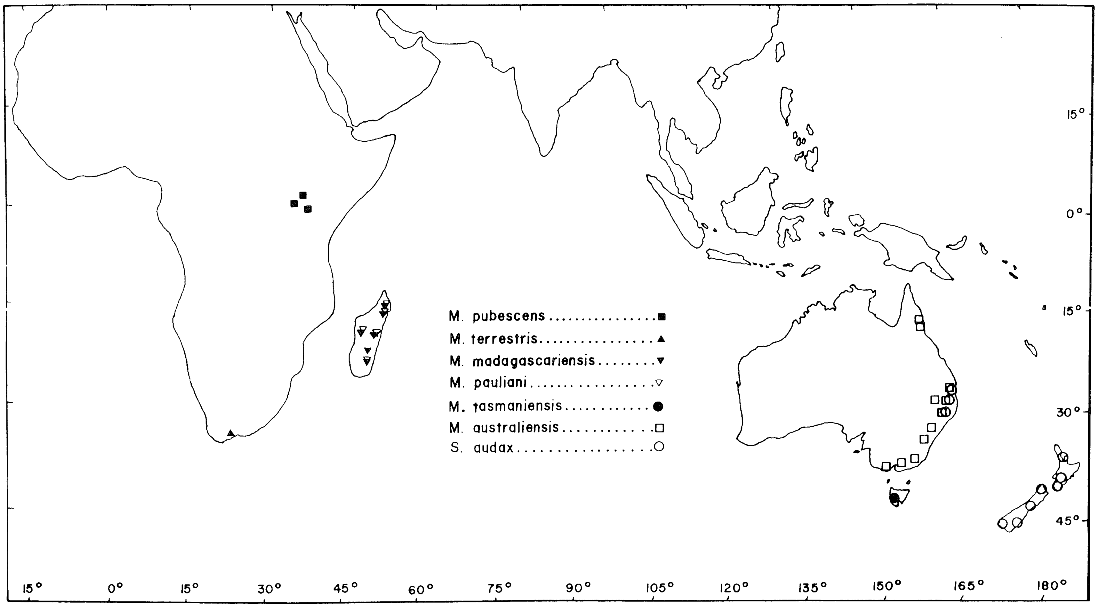

Fig. 7. Distribution of the terrestrial cypridid ostracods for the world. Data from Kile (1939), Harding (1953), Chapman (1961) and Danielopol and Betsch (1980).

Distribution

In Australia (see Fig. 6 and Table 1). In Queensland and some localities in northern New South Wales, *M. australiensis* was collected together with *S. audax* from the same samples of moss. They could usually be easily differentiated because *S. audax* is larger and is coloured light brown or grey. *M. australiensis* has a white shell through which occasionally pale yellow pigmentation is visible. Juveniles of *S. audax* of similar shell length to adults of *M. australiensis* can be distinguished from the latter because of their greater height.

In Tasmania, only *M. tasmaniensis* has been found. In the 122 samples collected, a few unusually large specimens of that species were noticed among others of the normal size. These were always females. No specimens in the Tasmanian collections had furcae similar to those of *M. australiensis* although many specimens had dried up prior to preservation in alcohol and proper dissection therefore was very difficult or impossible.

The presence of a Tasmanian species distinct from the one found on the mainland, and the absence of the latter in Tasmania can be understood as the 2 geographical areas probably always remained separated: during high sea levels marine water covered Bass Strait and during low sea levels, when Bass Strait was dry, arid climatic periods occurred. During the latter period, desert dunes were present even in NE Tasmania at some stage (Bowler, 1976 and Sprigg, 1979) and consequently no birds or transporting agents for ostracods from wet sclerophyll or rain forests were likely to have crossed the natural arid barrier. Recolonisation of the Australian mainland along the entire Great Dividing Range by passive or active migration of *M. australiensis* after arid episodes in the Pleistocene at least could have been achieved more easily than the crossing of Bass Strait, either dry or covered by the sea. A much wider marine barrier, however, separating Australia from New Zealand did not prevent *S. audax* from occurring in both countries (see discussion below).

Outside Australia. The known distribution of terrestrial ostracods is restricted to some of the areas which formed part of Gondwanaland: Africa, Madagascar, Australia and New Zealand. So far there have been no reports of terrestrial ostracods from South America or India. *Mesocypris* groups terrestrial species in Africa, Madagascar and Australia (see Fig. 7). Apparently, *Mesocypris* does not seem to have evolved rapidly since the breakup of the 'super land mass': anatomical specialisation and habitat restriction probably restrained additional specific radiation. The presence of *S. audax* in Australia and New Zealand (female specimens found in both countries possess identical anatomies and features of the shell) cannot be easily understood unless migrating birds crossing the Tasman Sea or other carrying agents could have existed to transport the animals or their eggs. It is strange, however, that transport only occurred one way, probably from New Zealand to Australia, as *M. australiensis* is absent from New Zealand.

Scottia pseudobrowniana, which is widely distributed in Europe (Löffler and Danielopol, 1978), is closely related to *S. audax* anatomically. It is not surprising therefore to learn of a record of *S. pseudobrowniana* from floating fen in the Danube Delta in Romania by Danielopol and Vespremeanu (1964). The same species is usually recorded from peaty swamps in Europe, as is *S. insularis* in New Zealand.

ACKNOWLEDGEMENTS

I would like to thank the following people and their respective institutions for the loan of specimens: Dr J. Lowry (Australian Museum), Dr R. Swain and C. Howard (University of Tasmania), W. Ziedler (South Australian Museum), Mrs A. Ralph, J. Nicholson, L. Macmillan, L.D. Ahern and A.L. Yen.

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Note added in proof

Since the submission of this paper for publication (May 1980) a significant article by Schornikov (1980) on ostracods in terrestrial biotopes has been published. It describes a new species of *Terrestricythere* from among meadow plants on saline soil near Vladivostok. From south-west Pacific islands, 3 ostracod species (*Darwinula malayica* Menzel, 1923, *Callistocypris zlottini* Schornikov, 1980 and *Terrestricypris arborea* Schornikov, 1980 [the latter 2 being new genera]) are also described from a variety of terrestrial habitats (soil, decayed wood and rhizosphere of a fern epiphyte on a tree at a height of 2 m above ground).

GEORGEOPLAX, NEW GENUS FOR *LITOCHEIRA GLABRA* BAKER, 1906 (CRUSTACEA: DECAPODA: BRACHYURA)

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SUMMARY

Georgeoplax new genus is proposed for *Litocheira glabra* Baker, 1906, as the shape of the male first pleopod is different from that of *Litocheira bispinosa* Kinahan, 1856. Both genera share the primitively catometopan configuration of the male reproductive system with coxal genital openings and the penis situated in a groove between the seventh and eighth sternites, as well as the general torsion of the basal part of the first male pleopod as shown by the direction of the sperm channel. For these reasons both genera are monotypic.

INTRODUCTION

Litocheira glabra was first described by W.H. Baker (1906) in his ''Notes on South Australian Crustacea'' from a female specimen dredged in St Vincent's Gulf (South Australia). Baker placed his species in the genus *Litocheira,* as he found close resemblence to its type-species *L. bispinosa.* He pointed out the two main differences in gross morphology between *L. bispinosa* and *L. glabra:* the former has a well-developed spine on the antero-lateral borders of the carapace behind the exorbital corner and has a double-edged front, while the latter has an indentate antero-lateral border of the carapace and a simple front.

Baker's specimen remained the only one known for a very long time. Hale (1927: 170, 171) mentioned the species in both his key and the current text, but had only the type before him. He suggested that *glabra* might be merely a variety of *L. bispinosa.* Griffin & Yaldwyn (1971: 57) repeated the differences between *L. bispinosa* and *L. glabra,* but had no material of the latter. Türkay (1975) revised the genus *Litocheira,* which was very heterogenous, and excluded all species but *L. bispinosa* and *L. glabra.* The latter was provisionally left in the same genus, because there was no material of it available, and a superficial similarity could be concluded from Baker's original description and figure. As the holotype was a female no better judgement would have resulted from its examination.

Recently a good series of *L. glabra* including male specimens was dredged between Rottnest Island and Fremantle (Western Australia) and made available for study by R.W. George of the Western Australian Museum. The present study is based on this material and the holotype, which was borrowed from the South Australian Museum (SAM). The recently collected specimens are deposited in the Western Australian Museum (WAM) and a pair has been deposited in the Senckenberg Museum, Frankfurt (SMF).

SYSTEMATIC ACCOUNT

Georgeoplax n. gen.

Type species: *Litocheira glabra* Baker, 1906 (by monotypy).

Diagnosis. Carapace glabrous, front simple-edged, antero-lateral borders indentate. Male genital opening coxal, penis situated in a groove. First male pleopod twisted with sperm channel beginning dorsally and ending in the ventrally situated distal opening; distal end of the pleopod flattened and provided with broad, scale-like structures. Second male pleopod distinctly shorter than first.

Remarks. The present new genus is still allied to *Litocheira.* It is a rather primitive catometopan crab as shown by the organisation of the male reproductive system. The male genital openings are coxal, but the penis is already situated in a groove between 7th and 8th sternites. This configuration is identical in *Litocheira* and shows both genera to have the same evolutionary rank. Moreover the torsion of the basal part of the first male pleopod shown by the direction of the sperm channel is identical in both genera, but the distal part of the pleopod is more twisted in *Litocheira,* and the distal opening is dorsal, while the opening in *Georgeoplax* is situated medio-ventrally.

In spite of these fundamental common features there are also some important differences, which suggest the separation of both genera. The endpiece of the male first pleopods is of very different shape (cf. Figs. 1-2) and there are other differences in gross morphology, which are helpful for the recognition of the genus. A list of the differences is given below:

Georgeoplax	*Litocheira*
(1) Front simple.	(1) Front double-edged.
(2) Antero-lateral borders of carapace at most with a faint knob.	(2) Antero-lateral borders of carapace with a sharp spine.
(3) Ambulatory legs naked.	(3) Ambulatory legs rather conspicuously hairy.
(4) Propodi of ambulatory legs considerably enlarged; posterior border of last one distinctly convex.	(4) Propodi of ambulatory legs slender; posterior border of last one nearly straight.
(5) First male pleopod with flattened distal end. (Fig. 1).	(5) First male pleopod with cylindrical distal end. (Fig. 2).

Derivation of name: This new genus is dedicated to R.W. George (Western Australian Museum), who provided the material for this study, in appreciation of his work on Western Australian and Indo-Pacific decapods. *Gender:* feminine.

Georgeoplax glabra (Baker, 1906)

Figs 1, 3-4

Litocheira glabra Baker, 1906: 110-112, pl. 2 figs 1-1a, pl.3.—Hale, 1927: 170, 171.—Griffin & Yaldwyn, 1971: 57.—Türkay, 1975: 124-125, 128-129.

Material examined. South Australia: St Vincent's Gulf, Dredged by Dr Verco (1♀ Holotype SAM C 1483).—Western Australia: Between Rottnest Isle and Fremantle, FRV "Flinders", 10–20 m (2 ovig. ♀ WAM 230-79, 2 ovig. ♀ WAM 231-79, 2 ♂ 2 ovig. ♀ WAM 233-79, 2♂ 2 ovig. ♀ WAM 234-79, 1♂ 2 ovig. ♀ SMF 9220).—Western Australia: off Fremantle, 14 m (1 ovig. ♀ WAM 232-79).

Remarks. The species shows considerable variation in the prominence of the front, which in comparison to the holotype is much more advanced in some of the Western Australian specimens (cf. Figs 3a, 4a). However, the variability of this feature becomes evident in the series WAM 233-79 and 234-79, in which no specimens are similar in that respect. Also no connection of the prominence of front with either size or sex is evident. The larger of the two female specimens of WAM 230-79 has a front identical to the holotype's, so that all intergradations from a less to a much advanced front exist.

Another variable feature is the distinctness of the faintly marked knob on the antero-lateral borders, which is rather pronounced in the holotype and several other specimens, but nearly extinct in others.

Usually the right cheliped is slightly larger than the left, but in some specimens (1 ♂ and 1 ♀ of WAM 234-79, and 1 ♀ of WAM 230-79) the left one is larger than the right.

Size. A small species. Holotype: Carapace breadth = 9.0 mm, Carapace length = 8.0 mm. Largest specimen (a male out of WAM 234-79): carapace breadth: 12.1 mm, carapace length: 10.2 mm.

Distribution: The species is known only from its type-locality (St Vincent's Gulf) and southwestern Australia (near Fremantle). It is possibly a southern faunal element, but this can only be concluded after examining more material.

ACKNOWLEDGEMENTS

Thanks are due to R.W. George (Western Australian Museum) for making the Western Australian material available for study and loaning material of *Litocheira bispinosa* for comparative study, to W.

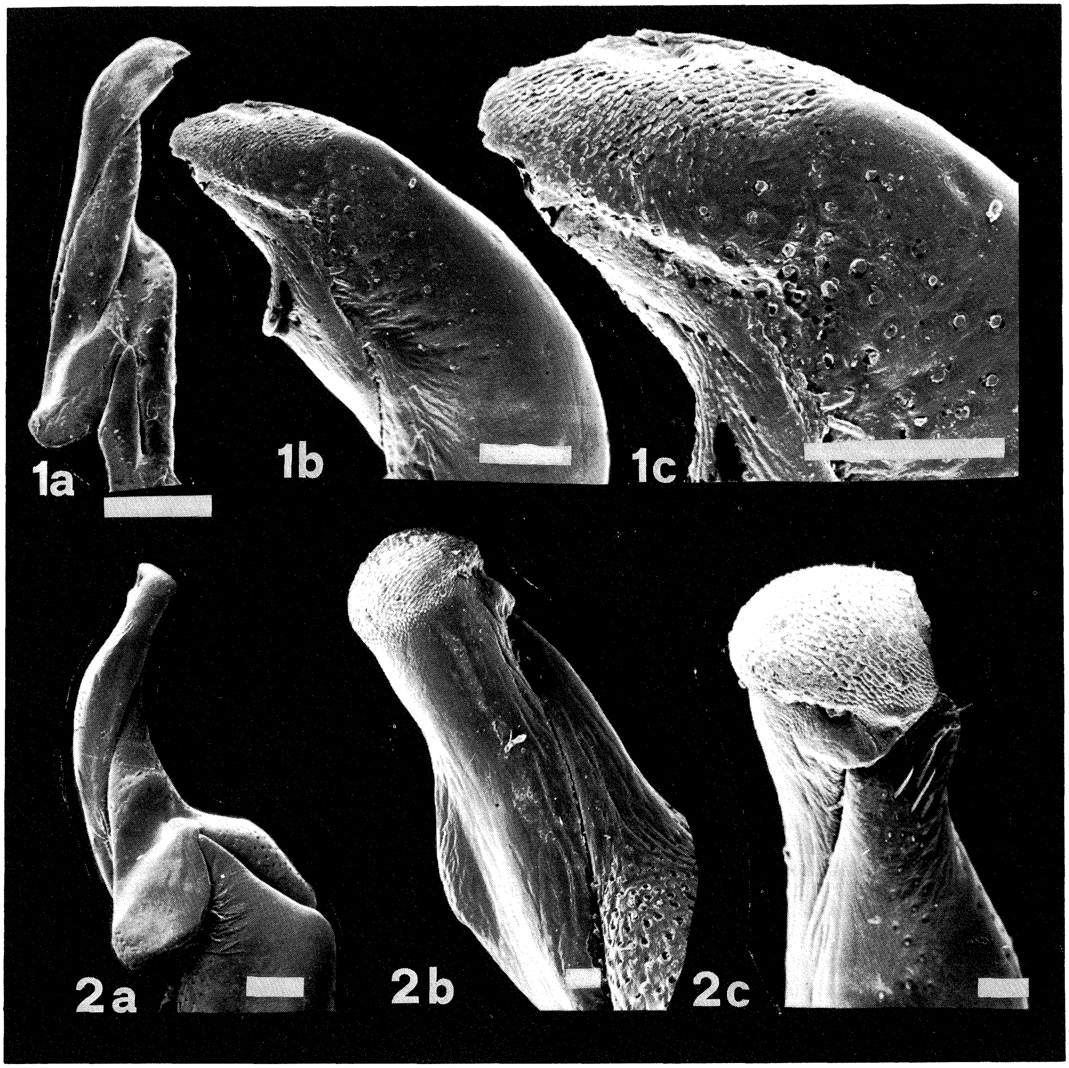

Fig. 1 (upper). *Georgeoplax glabra* (Baker, 1906), male, right first pleopod (SMF 9220): **a**, total organ, lateral aspect; **b**, distal part, fronto-median aspect; **c**, endpiece, fronto-median aspect. (Scales: total organ 1/2 mm, all others 1/10 mm.)

Fig. 2 (lower). *Litocheira bispinosa* Kinahan, 1856, male, right first pleopod (WAM 237-79): **a**, total organ, lateral aspect; **b**, distal part, median aspect; **c**, endpiece, medio-ventral aspect. (Scales: total organ 1/2 mm, all others 1/10 mm.)

Zeidler (South Australian Museum) for loaning the holotype of Baker's species and to D.J.G. Griffin and J.K. Lowry (both Australian Museum, Sydney) for loaning material of *L. bispinosa* for comparison.

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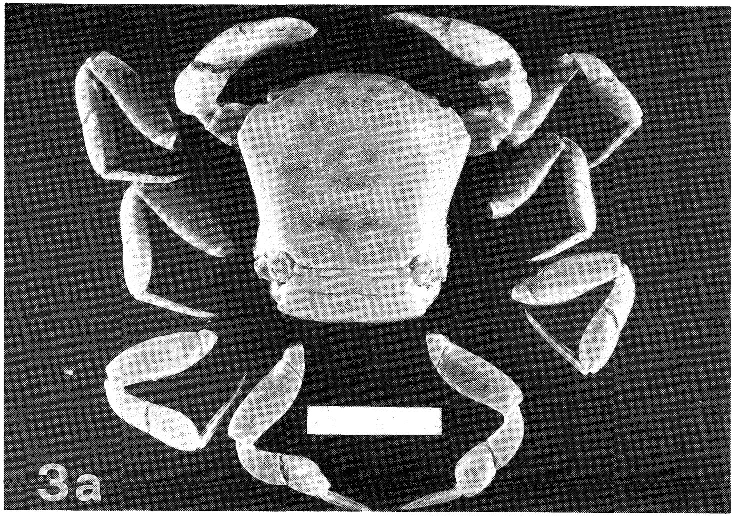

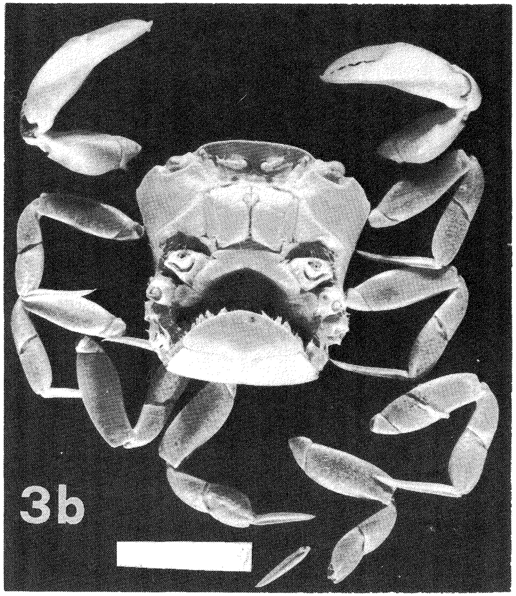

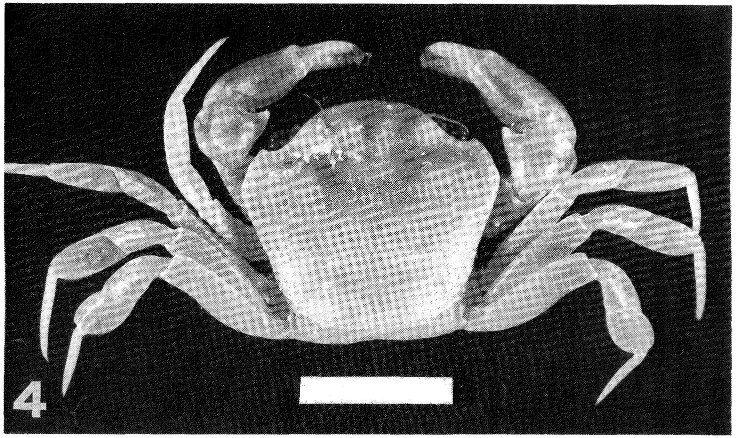

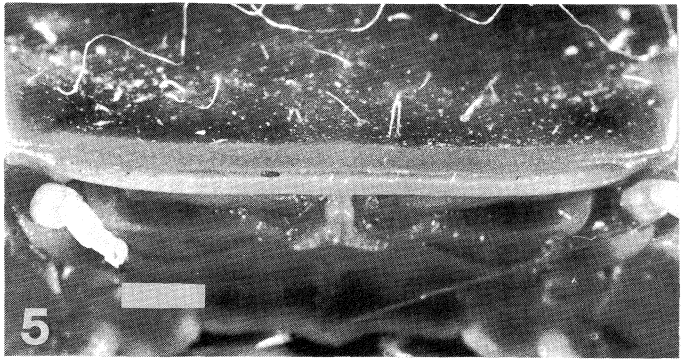

Fig. 3. *Georgeoplax glabra* (Baker, 1906) (Holotype SAM C 1483): **a**, dorsal aspect; **b**, ventral aspect. (Scale: 5 mm.)
Fig. 4. *Georgeoplax glabra* (Baker, 1906) (male specimen SMF 9220), dorsal aspect. (Scale: 5 mm.)
Fig. 5. *Litocheira bispinosa* Kinahan, 1856 (male specimen WAM 237-79), front. (Scale: 1 mm.)

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THE SYSTEMATIC POSITION OF AN AUSTRALIAN MANGROVE CRAB *HELOECIUS CORDIFORMIS* (CRUSTACEA: DECAPODA: BRACHYURA)

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SUMMARY

Males of *Heloecius* possess a coxo-sternal genital opening. This character suggests that *Heloecius* is the most primitive crab within the classical Ocypodidae. It is therefore excluded from the Ocypodinae and a new subfamily, the Heloecinae, is proposed for it. The relationships of this subfamily are discussed and *Ucides*, an American genus of mangrove crab, is provisionally included in the new subfamily.

Introduction

The name *Heloecius* was introduced by Dana (1852a: 248) for *Gelasimus cordiformis* H. Milne-Edwards 1837. Dana (1852b: 319) identified the main characteristic of the species as follows: "Second joint of male abdomen narrower than sternum behind". He also stated that *Gelasimus* was significantly different in this and in other respects. However, the general appearance of the species as well as several other similarities in position and direction of antennal and antennular appendages, led him to conclude that *Heloecius* might be closely allied to *Gelasimus*. Therefore, he left the former in subfamily Ocypodinae.

The position of the genus in the subfamily Ocypodinae has remained unquestioned by subsequent workers. For example Alcock (1900) and Borradaile (1907) left *Heloecius* with *Ocypode* and *Uca* in the subfamily. This classification was also used by Tesch (1918), who, however, used the ratio abdomen:sternum to separate *Heloecius* from the two other Ocypodinae genera. Balss (1957) also accepted the mentioned classification without change.

A number of characters have been used for distributing the ocypodid genera to subfamilies. Many of these, however, are only applicable to certain genera within each subfamily and are of no help in differentiating between the subfamilies. There are, however, three characters which together have historically been used to separate the subfamilies: the mode of folding of the antennules, the breadth of the interantennular septum, and the existence and position of the supplementary respiratory openings. The latter have hair-tufts at their sternal ends, which have been found to function as organs of moisture uptake from damp substrata (see Verwey, 1930 and Bliss, 1968). The three subfamilies of the Ocypodidae were defined as follows:

	Ocypodinae	**Scopimerinae**	**Macrophthalminae**
1)	Antennules folded lengthwise or oblique.	Antennules folded lengthwise or oblique.	Antennules folded transversely or slightly oblique.
2)	Interantennular septum broad.	Interantennular septum broad.	Interantennular septum very narrow.
3)	A hairy-edged pouch leading into the branchial cavity between the bases of third and fourth pereiopods.	A hairy-edged pouch between bases of second and third pereiopods or none at all.	No hairy-edged pouch present at the base of of any pereiopod.

This classification is not satisfactory, as the main characters of the frontal appendages (1 and 2 above) do not clearly differentiate the subfamilies. The remaining character (3) will be discussed later.

The basic trend in evolution of crabs is the adjustment to a construction permitting highly efficient and rapid locomotion. This led to the evolution of such advanced forms as *Ocypode* and other terrestrial crabs. It must be concluded that the direction of evolution of the group is dominated by the enlargement of the sternum. This modification results in the distribution of the body weight on a larger surface and the movement of the centre of gravity farther back between the walking legs. As a result, the whole locomotory system becomes more efficient as the body can be more easily balanced and, at the same time, there is more room in the enlarged thoracic system for a more complex endoskeletal musculature. This trend seems basic in the evolution of the Decapoda and Brachyura, though it takes place along different phylogenetic lines. Many of these evolutionary lines and the effect of the enlargement of the sternum on the external reproductory system have been discussed by Guinot (1969, 1978, 1979).

Because of these circumstances, the classification of the grapsoid crabs must be revised, largely on the basis of evolutionary characters drawn from the thoracic and genital configuration. A new classification for the Brachyura has been recently outlined by Guinot (1978), but the grapsoid groups within this revision still need further investigation.

These considerations led me to reexamine the status of *Heloecius* and the results lead to some surprising conclusions.

Structure of the male reproductive system of *Heloecius cordiformis*

(Figs 1–3)

Superficially, the male genital opening seems to be coxal as the base of the penis is connected with the coxa of the fifth pereiopod (Fig. 2). The eighth sternite does not meet the seventh above the penis so that there is no purely sternal arrangement. But when the penis is removed it becomes apparent that the genital opening is not merely coxal, but coxo-sternal (Fig. 3). That is, the lateral part of the genital opening arises from the coxa, while the medial and caudal part is bordered by the eighth sternite at the fronto-lateral border where the genital opening is situated. The border between the seventh and eighth sternite forms the frontal margin of the opening. This configuration is much more primitive than that ordinarily encountered in the Ocypodidae. The latter are normally advanced forms with a clearly sternal genital opening. For this reason, the abdomen covers nearly the whole space between the coxae of the fifth pereiopods in *Heloecius*, while it is much narrower in comparison to the hind part of the sternum in all other ocypodids.

The first male pleopod of *Heloecius* has a unique shape and construction. Evidently there is a torsion of the distal part, as the sperm channel begins dorso-laterally, then turns to dorsal, and just behind the palp passes to the ventral side where it enters the terminal horny piece and meets the distal opening terminally (Fig. 1). The terminal piece is thus fronto-laterally directed.

Discussion

Since the genus *Heloecius* shows primitive features that are unique among the Ocypodidae and never encountered in *Ocypode* and *Uca* s.l., and as its first male pleopod shows a particular construction, the genus must be excluded from the Ocypodinae. However, it can not be included in any other classic subfamily. Therefore, a new subfamily is proposed.

Heloecinae n. subfam.

Type genus: *Heloecius* Dana, 1852

This subfamily clearly differs from the other generally recognised subfamilies by its posteriorly narrow sternum, which must be considered a more primitive catometopan feature. Supplementary characters, such as the obliquely folded antennulae and the tufts of setae between the coxae of the third and fourth pereiopods, may be used to distinguish the subfamily from the Scopimerinae and Macrophthalminae.

With the exclusion of *Heloecius* from the Ocypodinae, the classical characters of this subfamily must be discussed. The main characters also shared by *Heloecius* are listed in this paper. The obliquely folded antennulae are also shared with the Scopimerinae and some Macrophthalminae so that it would be more accurate to state that the latter have more transversely oblique folding, while the former two may have more lengthwise folding. In practice, there is no problem distinguishing between these two kinds of obliqueness but it is questionable whether such intergrading characters are of sufficient significance to be used for the definition of such high ranks. In any case, they can not outweigh the

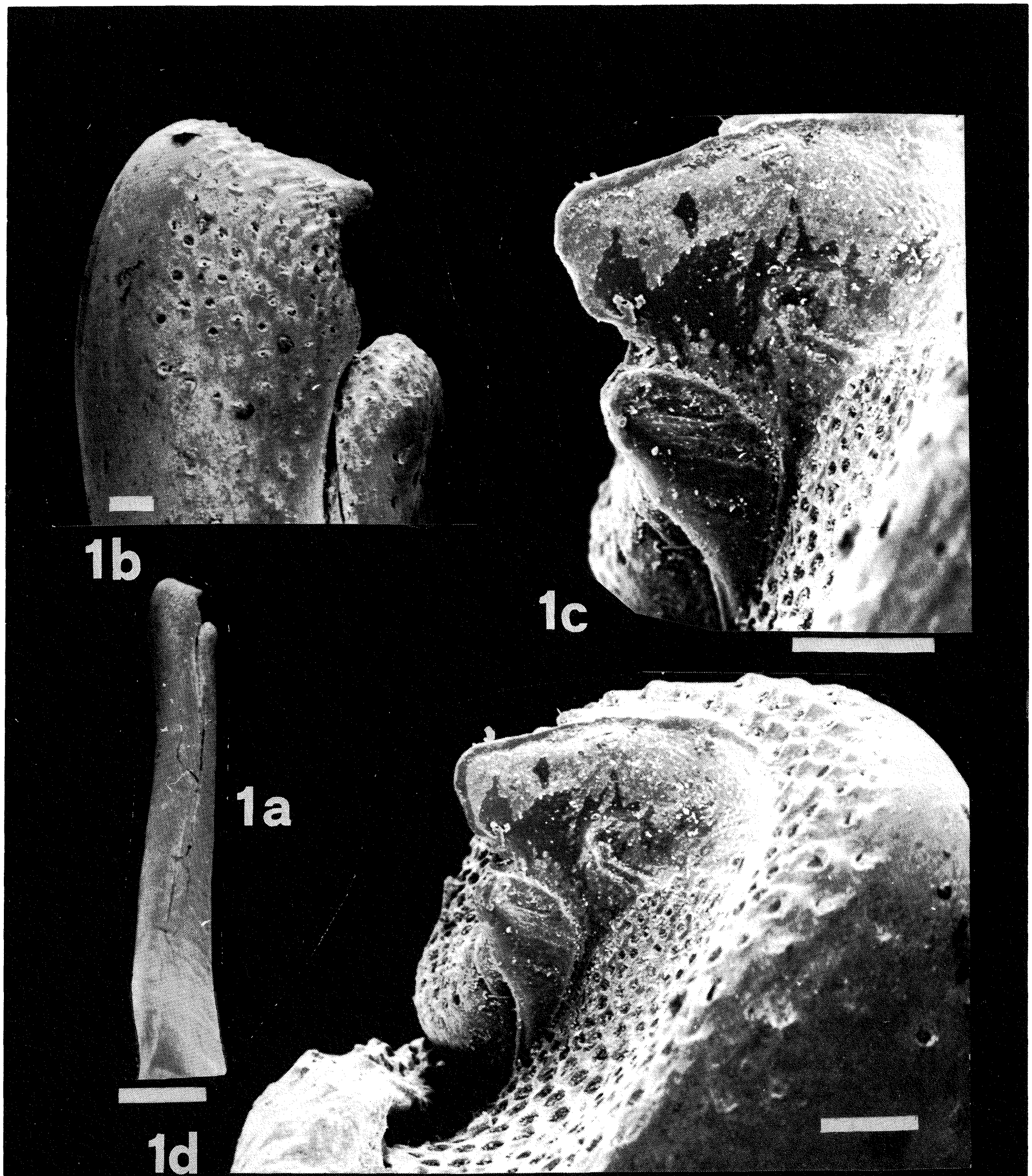

Fig. 1. *Heloecius cordiformis* (H. Milne-Edwards, 1837), right first male pleopod (from specimen in Australian Museum, Sydney, catalogue number P. 3839): **a**, total organ, dorso-lateral aspect; **b**, distal part, dorso-lateral aspect; **c**, horny terminal piece, ventral aspect; **d**, distal portion, ventral aspect. (Scales: total organ, 1 mm; all others, 1/10 mm).

importance of structural differences in the male genital system between *Heloecius* and the remaining Ocypodinae.

The same applies to several other characters which I believe represent convergence due to adaptations to certain common modes of life and not to phylogenetic relationships, or which upon further analysis are not diagnostic. For example, the breadth of the interantennular septum does not show significant

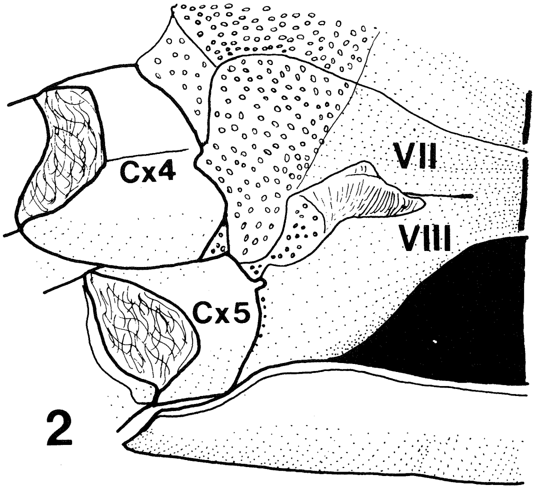

Fig. 2. *Heloecius cordiformis* (H. Milne-Edwards, 1837), latero-caudal part of sternum showing the coxae of the fourth (Cx 4) and fifth (Cx 5) pereiopod and the penis. VII and VIII indicate the last two thoracic sternites.

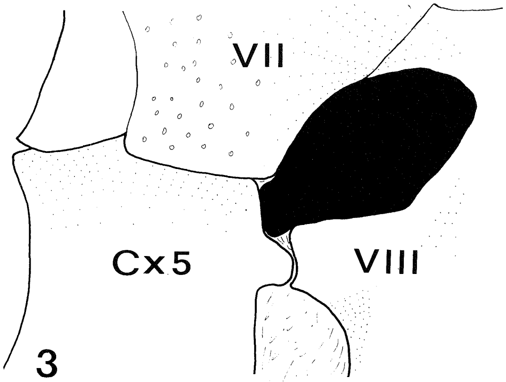

Fig. 3. *Heloecius cordiformis* (H. Milne-Edwards, 1837), situation of the male genital opening (black) after the removal of the penis. All symbols as in Fig. 2.

differences between the subfamilies. The tuft of setae between the coxae of the third and fourth pereiopods occurs not only in *Ocypode*, *Uca* and *Heloecius*, but also in several grapsid genera such as *Geograpsus* and *Goniopsis* (see Balss, 1944: 557). They also occur in *Scopimera*, where they are situated between the coxae of the second and third pair of pereiopods, but are absent in all other crabs actually grouped in the Scopimerinae, a fact ignored when the latter genera are included in this subfamily. At the same time, the tufts have been considered reliable characters for the remaining subfamilies. Griffin (1968) mentioned some common features in the behaviour of *Heloecius* and the two other ocypodine genera. However, none of these are restricted to this genus and thus they cannot form a basis for relationships (Crane, 1975).

As stated above, *Heloecius* is not only distinct from the other classical ocypodine genera, but also from the Scopimerinae and the Macrophthalminae which have a typical, highly advanced, catometope organisation.

The American genus *Ucides* is another group of species with an uncertain position within the Ocypodidae. It was transferred from the Gecarcinidae to the Ocypodidae by Chace & Hobbs (1969: 219-223), a view which I also support (Türkay, 1970: 350). The former authors mentioned several similarities between *Ucides* and *Heloecius*, but stated that there was no pronounced tuft of hairs at the base of the third and fourth pereiopods. Therefore, they did not include the genus in the Ocypodinae. A close examination of the male reproductive system shows several similarities to *Heloecius*, but also some differences. The male genital opening in this genus is sternal, but the sternum is oval and narrowed behind. This means that the eighth sternites is much narrower than in typical ocypodid crabs. Thus, the abdomen, as in *Heloecius*, covers nearly the whole space between the coxae of the fifth pereiopods. In spite of this difference in the position of the male genital opening, *Ucides* does in fact show a similar configuration to *Heloecius* in that the sternal position of the former is the result of the meeting of the seventh and eighth sternites over the base of the penis, while both sternites are already apporoximated in *Heloecius*. Thus, *Ucides* is more advanced in that the hind part of the sternum is a little broader than in *Heloecius*. In this respect, the gap between the two genera is less than that between *Ucides* and the remaining Ocypodidae. In addition, the first male pleopods of *Ucides* show considerable resemblance to *Heloecius*, i.e. the parts of the organ are oriented in nearly the same plane. This is also reflected by the directions of the slits of the female vulvae which are identical in both genera. However, the torsion of the distal part of the pleopod is much stronger in *Heloecius*, where the sperm channel is fronto-ventrally situated, while it remains rather dorsal in *Ucides*. Otherwise, the torsion of the pleopod is identical in both, as shown by the direction of the sperm channel.

In evaluating these differences, I conclude that *Ucides* is more closely related in evolutionary rank to *Heloecius* than to other ocypodid genera. It should therefore be provisionally included in the Heloecinae, which would then contain the more primitive members of the family. These are characterised by a male abdomen which covers nearly all the space between the coxae of the fifth legs. However, the different torsion of the distal part of the first male pleopods is a difficulty which can not be overlooked. As, at the moment, there is no functional or evolutionary explanation for pleopod torsion, either in the *Ucides-Heloecius* complex or in such genera as *Uca* s.l., the question must be left open. For this reason, I stress the provisional character of the inclusion of *Ucides* in the Heloecinae. A more detailed study of the male reproductive system, and of the sternal construction of the grapsoid crabs, will enable us to answer these questions more definitely than is now possible. Such studies could, of course, also lead to the creation of a new group for *Ucides*, as apart from the different torsion of the male pleopod tips, there are other differences in gross morphology, e.g. the folding mode to the antennulae, which must also be resolved.

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SIZE COMPOSITIONS OF LYSIANASSID AMPHIPODS IN COLD AND WARM WATER HABITATS

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SUMMARY

Since the family Lysianassidae is one of the largest and most diverse in the order Amphipoda it is suitable for the study of adaptations to different zoogeographic regions. The fauna is best known in regions of cold water (polar oceans and deep sea). Here most species are relatively small (6–13 mm) but a small number of large species are also found. In tropical waters such as the Indo-Pacific lysianassids are less well known and less conspicuous. The species are smaller and there is an apparent lack of large species. The problem is therefore not the occurrence of giants in cold water habitats but rather the small size of tropical species. While increased predation or competition could be responsible it is suggested here that the differences are probably due to shorter life spans at the higher temperatures in tropical waters. The species mature at a small size and produce small clutches of small eggs. In cold water survival is greater and the species mature at a larger size and infrequently produce large clutches of large eggs.

INTRODUCTION

One of the most striking features of marine amphipods is that they tend to be small in shallow tropical water but rather large in the Arctic, Antarctic and the deep sea. The reasons for these differences remain unknown but the apparent gigantism in the cold water habitats has been the subject of considerable speculation (Barnard, 1962, De Broyer, 1977 and Menzies, George and Rowe, 1973). The present contribution presents a different approach to this question by considering the size compositions of the faunas rather than just the occurrence of giants.

Species of the amphipod family Lysianassidae are suitable for making interhabitat comparisons since they are numerous at all depths in all oceans and many have the same life style—scavengers of freshly killed or wounded animals—and are either pelagic or benthic burrowers in soft sediments. Other lysianassids that are parasitic or commensal will not be considered here.

MATERIALS AND METHODS

In the present analysis the midpoint of the size range of mature females has been used as a measure of size. Mature females are readily recognised by the presence of setose oostegites and are usually reported in the literature. Mature males are typically smaller than females and can be recognised by their elongate calceolate antennae but are rarely reported in the literature. The midpoint of the size range is considered to be more representative of the size of mature animals than is the maximum. Since the maximum is determined by post-maturation survival it can be biased by an individual who survives longer than normal (personal observation) and is therefore not representative of the adult size of most individuals of the species. The maximum and the midpoint are similar in species with short reproductive lives. Size at maturity (Steele and Steele, 1975) and mean adult size would give a more precise measurement of size but neither is available for many lysianassid amphipods.

Total length was measured from the anterior margin of the head at the base of any rostrum, to the tip of the telson. Small individuals and hatched young from the brood pouch were measured with an eyepiece micrometer. Egg diameter is the average of the length and width of early (Stage A (Steele and

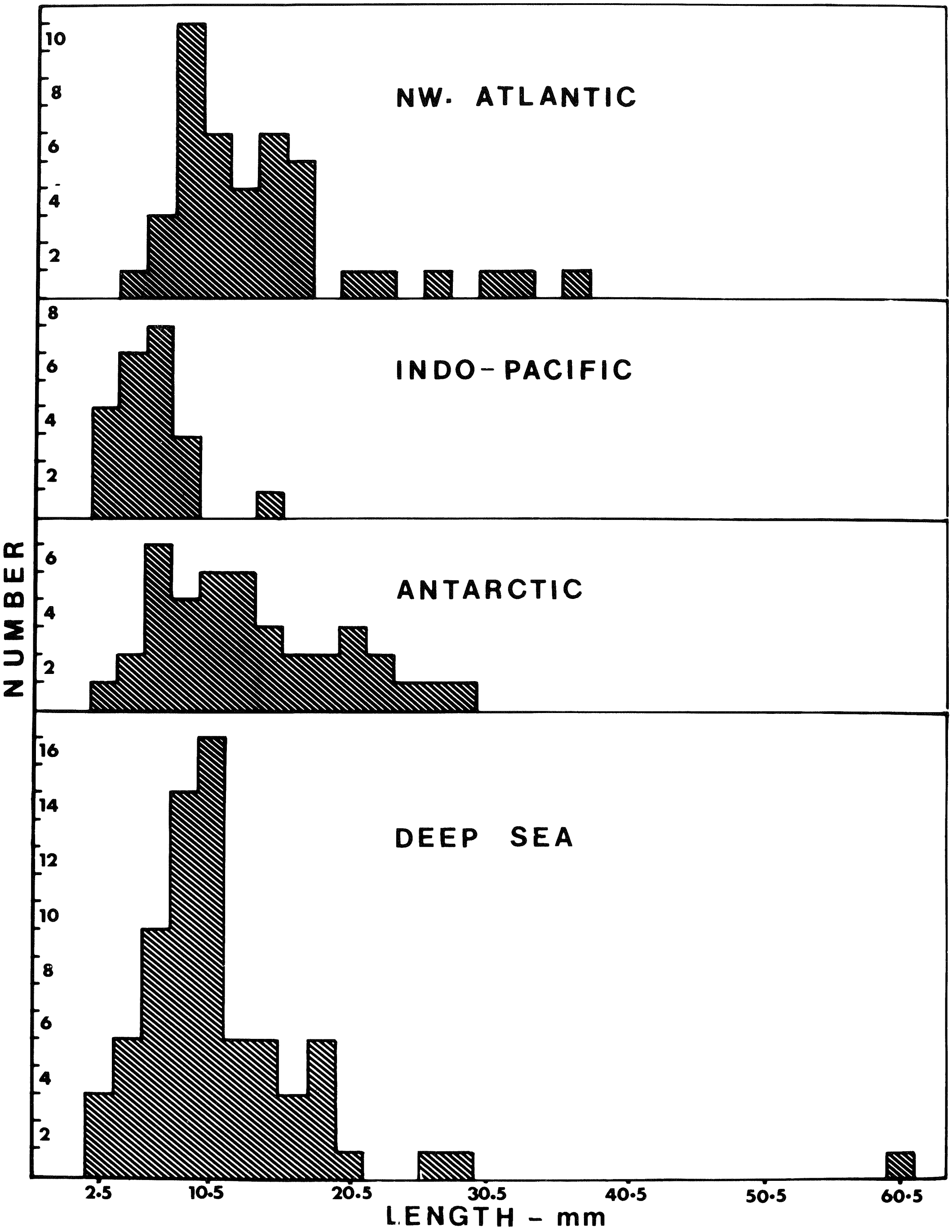

Fig. 1. Size compositions of mature female lysianassid amphipods.

Table 1. Body lengths of lysianassid amphipods

Area	N	Number <10 mm	%	Number >10 mm	%
N.W. Atlantic	42	14	33	28	67
Indo-Pacific	22	21	95	1	5
Antarctic	39	13	33	26	67
Deep Sea	69	31	45	38	55

Steele, 1969)) embryos taken from the brood pouch of ovigerous females. These measurements were also made with an eyepiece micrometer.

Measurements of specimens from the northwestern Atlantic (between the Bay of Fundy and the Alaskan border and including the Canadian Arctic Archipelago) were made by the author on specimens in the author's collections. Those from the Indo-Pacific, as delineated by Abbott (1959) are based on specimens of species collected at Nosy-Bé, Madagascar, by the author plus data extracted from a review of the literature on Indo-Pacific lysianassids. Data from the Antarctic are for species listed by Lowry and Bullock (1976) and were obtained in the literature. Those from the deep sea are for both bathypelagic and benthic species and are also from the literature. The literature consulted is not listed here but is available from the author. The species for which there is information on the sizes of mature females represent only a portion of the species known from each habitat but are considered to be a random selection and hence to be representative.

RESULTS

Examination of the size frequencies (Fig. 1) shows that most lysianassids in the northwestern Atlantic, the Antarctic and the deep sea are relatively small (6–13 mm). Large species are present but their numbers are relatively few and while the size frequencies are skewed to the right, large species are probably not more frequent than one would expect in a group of organisms in a habitat. In contrast, the Indo-Pacific lysianassids are almost all small and with a lower modal size than those from the cold water regions. What is most striking, however, is an apparent complete lack of large species. The frequency curve is truncated and almost no species is more than 10 mm in length (Table I). It appears therefore that giants are not more frequent than might be expected in cold water habitats and that their size compositions are similar to the theoretical model developed by Hutchinson and MacArthur (1959). The questions to be answered concern tropical waters: (1) why is the modal size reduced there and (2) why are large species apparently absent?

DISCUSSION

Body size is probably the most easily varied species characteristic and varies both within a species and between closely related species, as for example in *Anonyx* spp. (Steele and Brunel, 1968). Thus there is no reason to expect that large species could not evolve in tropical water, expecially as some lysianassid genera have species in both warm and cold water habitats.

There are at least three possible explanations of the small sizes of species in the Indo-Pacific. They are not mutually exclusive.

1. *Predation Hypothesis*

Many recent studies, reviewed by Hall *et al.* (1976), have documented how selective predation by fish in fresh water lakes can result in zooplankton populations with small body sizes compared to those in fishless lakes where such predation is absent.

A similar phenomenon could be postulated to occur in the oceans since fish species diversity varies in different habitats. It is highest in warm tropical habitats (Table II) and there fish predation is considered a highly significant factor in organising the fish communities themselves (Johannes, 1978). The number of species is much less in the northwestern Atlantic and in the deep sea and declines with latitude and depth respectively. Thus it is possible that predation may be less in the cold water habitats where large

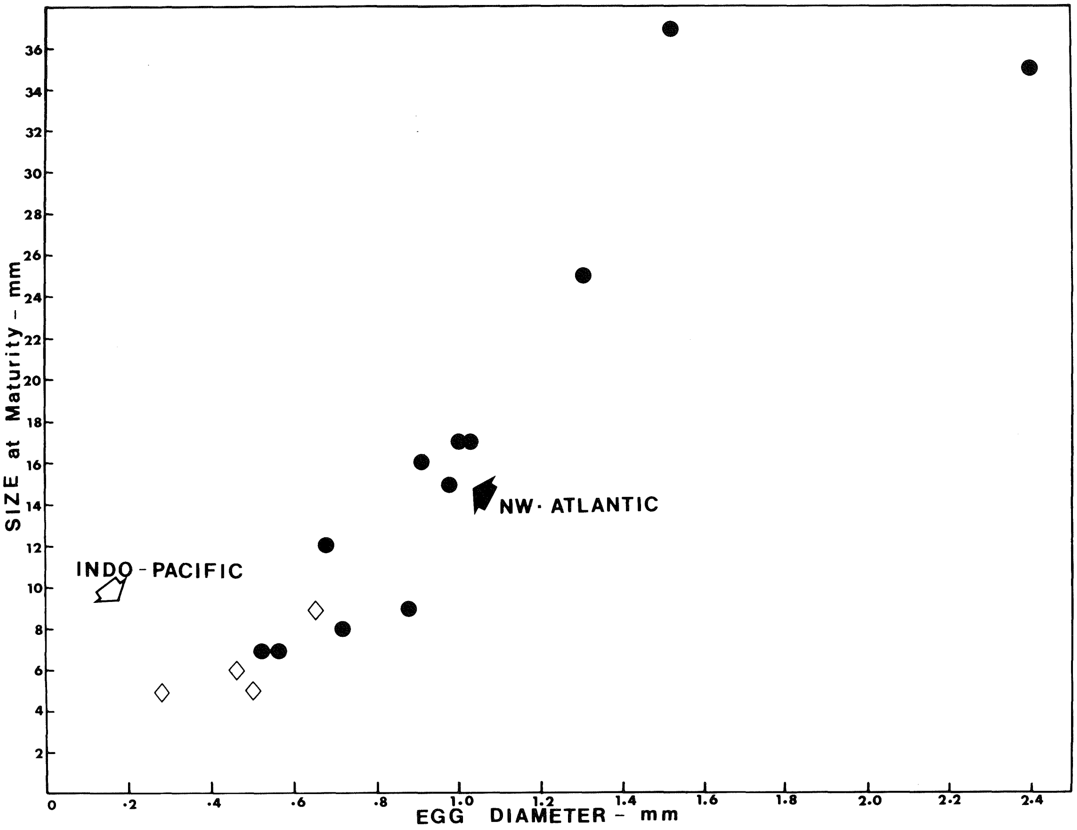

Fig. 2. Size at maturity of females related to egg diameters in lysianassid amphipods.

Table II. Numbers of fish species

Area		N	Source
N.W. Atlantic	>60°N	90	Leim & Scott, 1966
	Total	325	
Indo-Pacific		3000+	Briggs, 1974
Deep Sea	>2000m	100 pelagic 260 benthic	Marshall, 1963
	Total	2000	

amphipods are found. Nelson (1980) has made a similar suggestion to explain the decrease in size with latitude of epifaunal amphipods in eelgrass beds.

However, this simple correlation between amphipod size and number of fish species is confounded by differences in fish density in the different habitats, and it is not clear for example, how predation by large populations of certain species, such as cod (*Gadus morhua*) which passes through several growth stanzas, compares to the predation by the many species of fish in the Indo-Pacific. In addition, predation on lysianassids is limited by the fact that most species spend most of their time burrowed in the substrate and hence are unavailable to predators. Also the predation hypothesis is difficult to reconcile with the

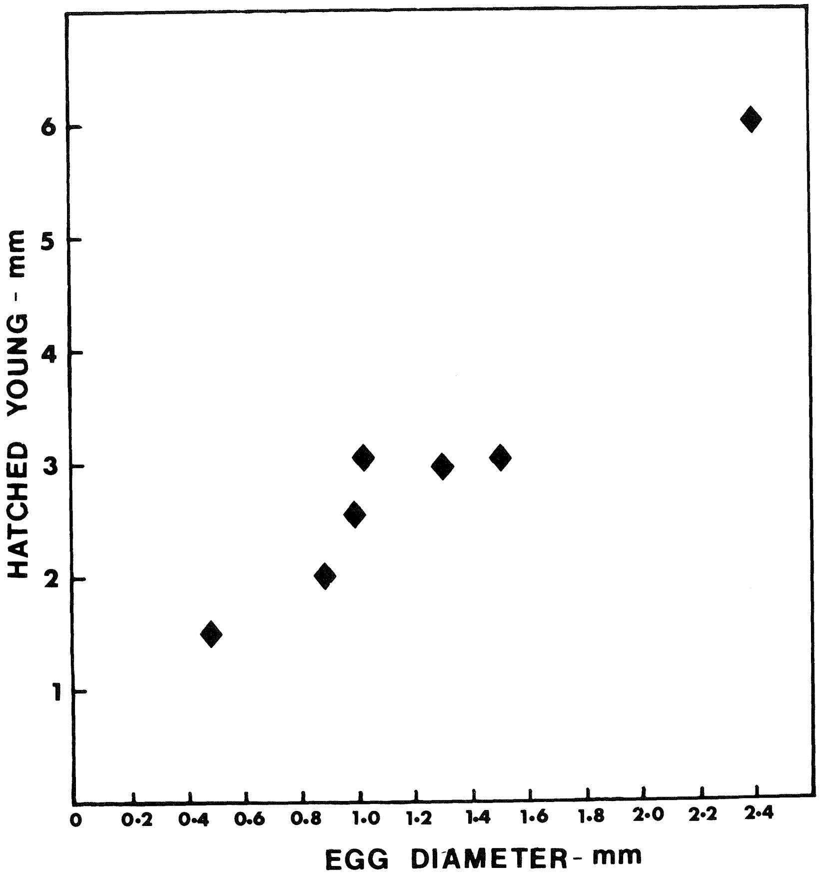

Fig. 3. Sizes of hatched young in the brood pouch related to egg diameters of lysianassid amphipods.

distribution of the decapod Crustacea which are also preyed on by fish. These are most numerous and also small in size in warm tropical waters where fish predation should be most intense (personal observation).

2. *Competition Hypothesis*

The scavenging habits of lysianassids in the Arctic, Antarctic and deep sea are legendary and one of the easiest methods to catch them in large numbers in these areas is with baited traps. However, in warm water habitats such as the Indo-Pacific, competition from fish and decapod Crustacea must increase considerably for this type of food. Both fish and decapods are probably better competitors than the lysianassids since they are more mobile, have better visions and are typically larger and they are what is usually attracted to bait in the warm water habitats.

3. *Reproductive Strategy Hypothesis*

Studies of *Gammarus* spp. (Steele and Steele, 1975) and haustoriid amphipods (unpublished) indicate that small size is an advantage in warm habitats with a long period of food availability, since reducing generation time, which can be accomplished simply by reducing size at maturity and egg size, produces more offspring than increasing clutch size by growing larger. This seems to have been at least part of the reason why the introduced *Gammarus tigrinus* has displaced the native *Gammarus* spp. in parts of Holland (Pinkster, Dieleman and Platvoet 1980). On the other hand, large size and a resulting high

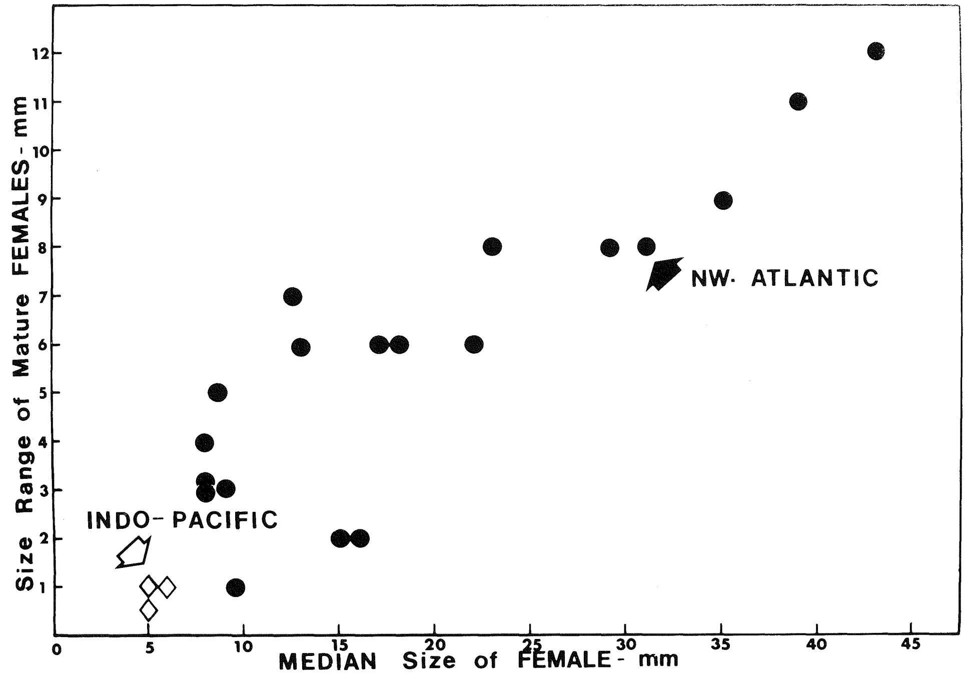

Fig. 4. Size ranges of mature females related to their median sizes in lysianassid amphipods.

fecundity will be an advantage in a cold habitat where there is a short period of food availability. If a species can produce only a single brood per year but can survive to produce later broods then larger broods are advantageous.

Data for the Indo-Pacific lysianassids are incomplete and the life cycle of no species is known, but is it possible to extrapolate from known species in other areas in order to determine if they follow this scheme.

The small Indo-Pacific lysianassids (Fig. 1) obviously mature at a small size and age. Egg sizes which are correlated with size at maturity in lysianassids (Fig. 2), as they are in *Gammarus* spp. (Steele and Steele 1975), are also small, which indicates that development time will be short at the high tropical temperatures. Both of these factors will result in a short generation time in this region as has been found in other amphipod species (Steele 1973). Clutch sizes are small (4–22 eggs in females 4–8.5 mm long) and the young when they hatch will also be small (Fig. 3).

Survival rates are unknown for any of the amphipods but an indication can be obtained by determining the size ranges of the mature animals since they will be greater if the animals survive to breed more than once rather than producing only a single brood. Figure 4 shows that the size ranges of the mature females are correlated with their sizes. In part this will be due to the cumulative effects of differences in growth rates and measurement errors for large individuals but the ranges of the large species are too great to be accounted for by these factors alone and suggest that the large species, with some exceptions, apparently do survive to produce more than one brood whereas the small species do not. The Indo-Pacific species with their small size ranges are at the low end of the scale and probably do not survive long after they mature. Unlike the decapods, the lysianassids seem to lack specific reproductive adaptations for life in warm water such as pelagic larvae and their small sizes are therefore explicable in the advantages they obtain from having short generation times in the warm water of this region. This agrees with what has been suggested for other amphipod groups elsewhere (Steele and Steele 1975). On the other hand, the relatively small size of many lysianassids in the northwestern Atlantic and other cold water areas is unlike the situation in *Gammarus* spp. or the haustoriids where the body size increases with latitude. The only explanation that can be offered for this difference is that the lysianassids as benthic scavengers may have suitable food available for a longer period during the year then is the case for the *Gammarus* or haustoriid species that are more dependent on ephemeral algae for food.

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STRATEGIES OF CRUSTACEAN GROWTH

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SUMMARY

The various species of Crustacea display great differences in maximum size, and the means by which this is delimited have been investigated. Two distinct strategies of growth exist. Some species have indeterminate growth and continue moulting indefinitely. In these the percentage moult increment declines and the intermoult period increases with size, thereby limiting growth: the respective rates of decline and increase determine the final size. Others have determinate growth and eventually cease moulting, usually at the time of maturity: this termination of moulting stops growth, and in such species the percentage moult increment does not decline appreciably with size. The advantages and disadvantages of the two strategies of growth are discussed.

Introduction

There is great variation in maximum size both within the Crustacea as a whole, and within restricted taxa of the class. Thus within the Crustacea there is a range from small copepods with a length of the order of a millimetre to the giant Japanese spider crab *Macrocheira,* with a carapace length of 400 mm and a chelar span of nearly 4 m. Within the Brachyura sizes range from *Macrocheira* down to the ectocommensal *Dissodactylus* with a carapace length of 3 to 4 mm, or the males of some Hapalocarcinidae with a carapace length of only 1 mm. Within the Majidae there is a range from *Macrocheira* to species of *Eurynome, Pelia* and *Thoe* with carapace lengths of 10 to 12 mm. There is also variation in the relationship between maximum size and the size at sexual maturity. Some species become sexually mature and then continue moulting (and growing) for prolonged or indefinite periods afterwards. Others cease moulting and growth at the time when sexual maturity is achieved.

Clearly the Crustacea employ diverse strategies of growth, and two questions can be asked in relation to this diversity:

1. How are the strategies effected? What are the patterns of growth which produce the desired end results?
2. Why do the various strategies exist? What are the selective advantages of one strategy over another?

This paper is mainly directed towards answering the first of these questions, and consists essentially of an analysis of the patterns of growth. At the present it is not possible to say much concerning the more fundamental subject of the physiological mechanisms which underlie these patterns. The second of the questions is dealt with only briefly. As necessary prerequisites some further detail must first be provided on the form of growth, and on the components of which growth is composed.

The pattern of growth

Although tissue growth is essentially a continuous process in Crustacea, the accompanying increase in external dimensions is discontinuous. This proceeds by a series of moults or ecdyses, when the old integument is cast off and a rapid increase in size occurs before the new integument hardens and becomes inextensible. These moults are separated by intermoults, periods when the integument is hard and no external growth occurs. During periods of growth the intermoults are relatively short, and are termed diecdyses. Between two growing seasons there is a prolonged intermoult known as an anecdysis. If moulting ceases altogether the condition is a terminal anecdysis. There are three main variables in the pattern of crustacean growth:

1. Is moulting continued indefinitely, or is there a terminal anecdysis?
2. If there is a terminal anecdysis, is the onset of sexual maturity before or after the start of the terminal anecdysis?
3. In the event of a terminal anecdysis is it preceded by a fixed or variable number of instars?

Given these variables, then the following hierarchy of patterns becomes possible. Examples are given for those patterns which are known to exist.

- Indeterminate growth, no terminal anecdysis (*Daphnia, Balanus, Homarus*)
- Determinate growth, with terminal anecdysis
  - Maturity before final moult
    - Instar number variable (*Carcinus, Portunus*)
    - Instar number fixed
  - Maturity after final moult
    - Instar number variable (*Corystes, Maja*)
    - Instar number fixed (Ostracoda, Copepoda)

There is no clear relation between taxonomic groups and growth pattern: both determinate and indeterminate growth occur in a wide range of primitive and advanced taxa, and both can occur within the same small taxon. If indeterminate growth is primitive, as seems likely, then determinate growth must have evolved independently on a number of occasions.

The components of growth

The growth rate in Crustacea results from the interaction of the two variable components of growth. One is the interval separating successive moults—the intermoult period. This can vary from less than a day in the early instars of the ostracod *Cyprinotus* (Kurata, 1962) to two to three years in mature females of large decapods such as *Cancer* (Pearson, 1908). The period is markedly affected by extrinsic factors, notably temperature and food supply, but in the present context it is the influence of intrinsic factors that is more relevant. In general the intermoult period becomes longer with increasing size, and the duration may be further extended by sexual maturity: this intrinsic variation will be analysed in detail in later sections.

The second component is the increase in size that occurs at a moult—the moult increment. This may be expressed in absolute or relative terms, and the most convenient is to present it as a percentage of the pre-moult dimension. It varies from as much as 83% in *Daphnia* (Green, 1956) to as little as zero at the moult preceding laying in some female decapods (Mauchline, 1977). Within a species the percentage moult increment usually decreases with increasing size.

In the two following sections the interaction of intermoult period and moult increment will be analysed to see how growth is regulated. This will be done first for Crustacea showing indeterminate growth, and secondly for those with determinate growth.

Regulation of indeterminate growth

The fact that growth is indeterminate in many Crustacea, in the sense that moulting does not stop, does not mean that size is unrestricted. Far from it. The changes in intermoult period and moult increment with size interact to set an upper limit which will not be appreciably exceeded in practice. However the nature of this interaction differs markedly from species to species, and so very different maximum sizes are attained. Thus indeterminate species range from *Daphnia* spp with maximum lengths of 2.5 mm (Anderson, 1932; Green, 1956) to *Homarus americanus* which exceeds 900 mm (Wilder, 1957). Exactly how is this brought about?

The intermoult period tends to increase with size, this being a very consistent phenomenon throughout the Crustacea (Hartnoll, 1982) with only a few exceptions. Several proposals have been put forward to describe the relationship of intermoult duration to size, namely the linear regressions of:

1. Intermoult period on length (Mauchline, 1977)
2. Intermoult period on length^3 (Kurata, 1962)
3. Log intermoult period on $\sqrt[3]{\text{weight}}$ (Hewett, 1974) or, much the same, log intermoult period on length (Mauchline, 1976, 1977).

There is no *a priori* reason to favour any particular regression, so the one which provides the best fit to a wide range of observations is to be preferred: this is the regression of log intermoult period on length. The slope of this regression for a selection of species is presented in Table 1, and there is great variation. Some have a steep slope which indicates a rapid lengthening of the intermoult as size

Table 1. The slope of the regression of $\log_{10}$ intermoult period (days) on reference length (mm) for various Crustacea with indeterminate growth. In the last column one, two and three asterisks indicate significance at the 5%, 1% and 0.1% levels respectively.

Species	Source	Reference dimension	Maximum size	Slope and significance
Porcellio scaber Latreille	Kurata, 1962	Head width	2 mm	0.41***
Daphnia longispina Müller	Ingle *et al.,* 1937	Total length	3 mm	0.22***
Daphnia carinata King	Navaneethakrishnan & Michael, 1971	Total length	4 mm	0.27**
Metamysidopsis elongata (Holmes)	Clutter & Theilacker, 1971	Total length	7 mm	0.085***
Rhithropanopeus harrisii (Gould)	Hartnoll, 1978	Carapace width	10 mm	0.25***
Cyclograpsus punctatus Milne-Ed.	Broekhuysen, 1941	Carapace width	25 mm	0.036***
Hemigrapsus sanguineus (de Haan)	Kurata, 1962	Carapace width	26 mm	0.025***
Crangon crangon (L.)	Meixner, 1969	Total length	55 mm	0.011***
Jasus lalandei (H. Milne Edw.)	Fielder, 1964	Carapace length	90 mm	0.007*
Panulirus argus (Latreille)	Travis, 1954	Carapace length	90 mm	0.004***
Cancer anthonyi Rathbun	Anderson & Ford, 1976	Carapace width	110 mm	0.023***
Homarus americanus Milne Edw.	Templeman, 1948	Carapace length	130 mm	0.013***

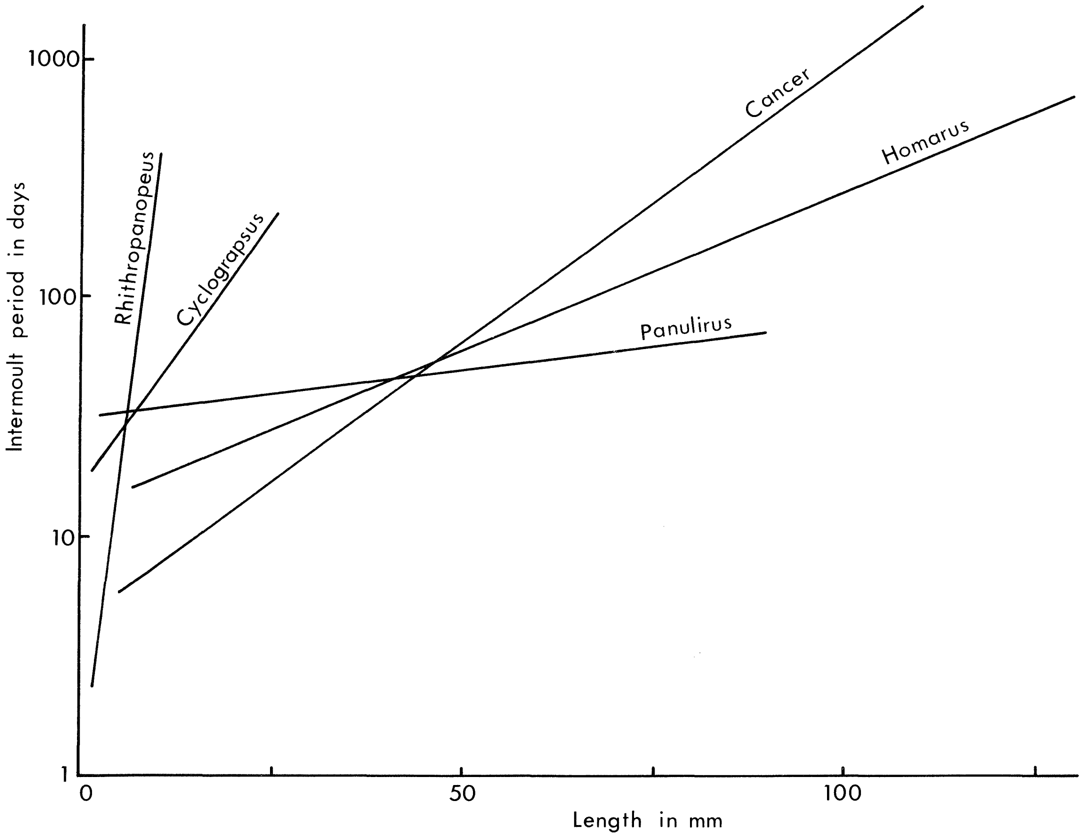

Fig. 1. The regressions of log intermoult period on carapace size for *Rhithropanopeus harrisii, Cyclograpsus punctatus, Cancer anthonyi, Homarus americanus* and *Panulirus argus.* Sources of data in Table 1.

Table 2. The slope of the regression of $\log_{10}$ percentage moult increment on reference length (mm) for various Crustacea with indeterminate growth.

Species	Source	Reference dimension	Maximum size	Slope and significance
Porcellio scaber	Kurata, 1962	Head width	2 mm	−0.37***
Daphnia pulex (de Geer)	Anderson *et al.*, 1937	Total length	2 mm	−1.72***
Gastrosaccus vulgaris Nakazawa	Matsudaira *et al.*, 1952	Carapace length	5 mm	−0.18***
Rhithropanopeus harrisii	Hartnoll, 1978	Carapace width	10 mm	−0.14**
Hymenosoma orbiculare Desm.	Broekhuysen, 1955	Carapace width	25 mm	−0.026*
Pachygrapsus crassipes Randall	Mauchline, 1976	Carapace width	38 mm	−0.019***
Crangon crangon	Lloyd & Yonge, 1947	Total length	68 mm	−0.019***
Panulirus homarus (L.)	Mauchline, 1977	Carapace length	94 mm	−0.014***
Jasus lalandei	Newman & Pollock, 1974	Carapace length	105 mm	−0.004***
Homarus americanus	Templeman, 1948	Carapace length	130 mm	−0.005***
Cancer pagurus L.	Mauchline, 1977	Carapace width	150 mm	−0.002***
Cancer magister Dana	Poole, 1967	Carapace width	190 mm	−0.002***

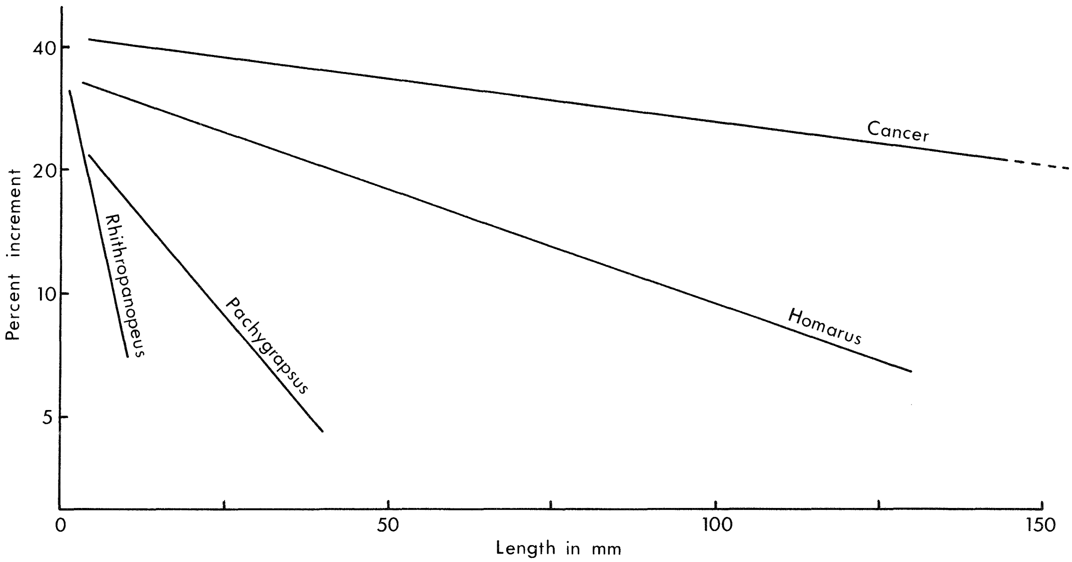

Fig. 2. The regressions of log percentage moult increment on carapace size for *Rhithropanopeus harrisii, Pachygrapsus crassipes, Homarus americanus* and *Cancer magister.*

increases, others a gentle slope. Small species (in terms of the reference dimension) generally have steep slopes, large species gentle ones (Fig. 1).

The percentage moult increment tends to decrease with size, and although not as universal a trend as the increase in intermoult period, this is the prevalent condition (Hartnoll, 1982). Since first pointed out by Olmstead & Baumberger (1923) it has been observed in many species from all crustacean groups. Various approaches have been adopted to try and quantify the relationship of moult increment to size. One was to plot post-moult against pre-moult size (Hiatt, 1948; Kurata, 1962) to produce a 'Hiatt growth diagram': when a linear relationship exists it is expressed by the equation:

$$L = a_{n+1} + b.L._{n}$$

b is known as the growth coefficient, but it is not easily interpreted. Also the method is unsatisfactory in that L_n is contained within L_{n+1}, making a degree of correlation inevitable. A more rigorous approach is to examine the relationship between percentage moult increment and pre-moult length

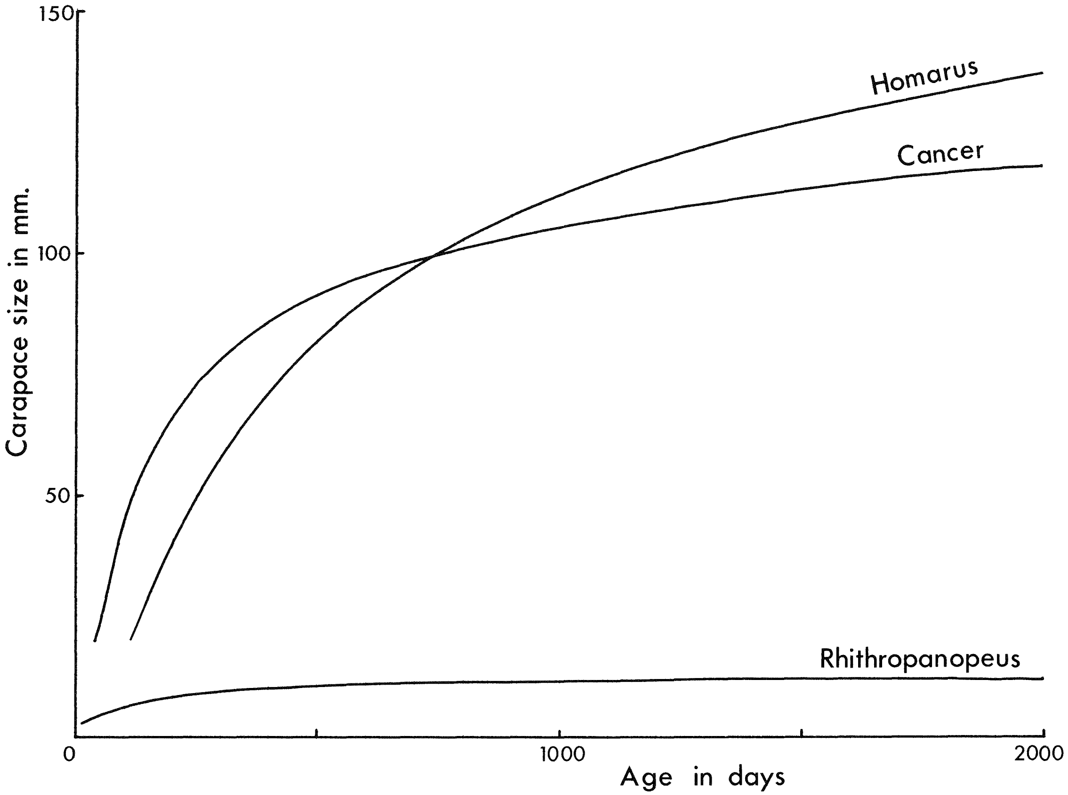

Fig. 3. Growth curves for *Homarus americanus, Cancer anthonyi* and *Rhithropanopeus harrisii* generated from the regressions of log intermoult period and log per cent increment on carapace size.

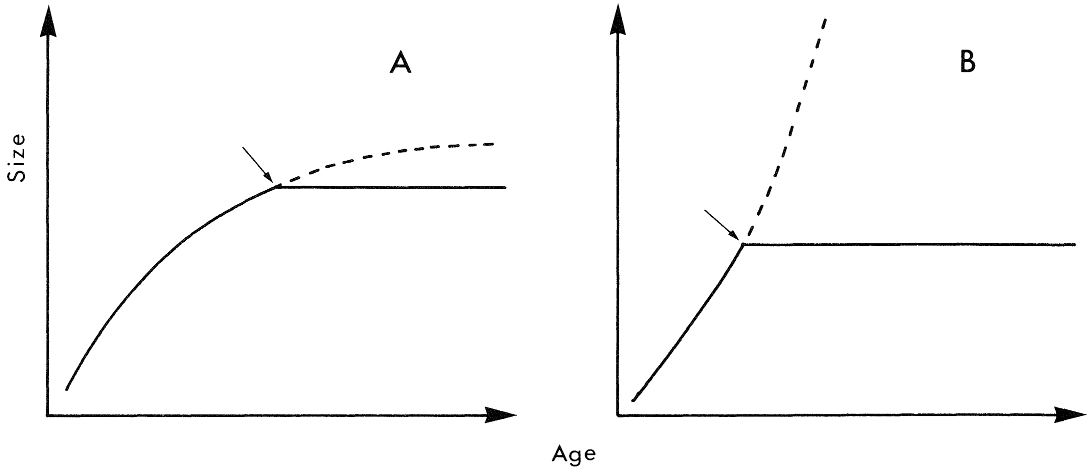

Fig. 4. Two possible formats for Crustacea with definitive growth, showing actual (solid line), and potential growth (broken line) if the terminal anecdysis did not occur. The start of the terminal anecdysis is arrowed.

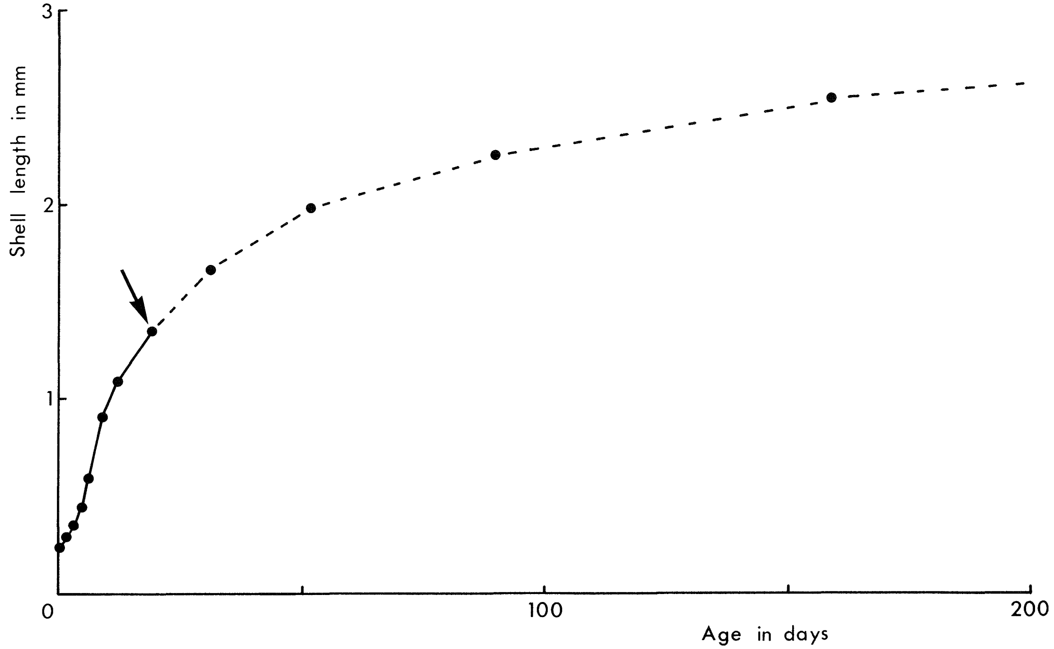

Fig. 5. Actual (solid line) and extrapolated (broken line) growth of *Cyprinotus* sp. at 21°C: the eighth and final instar is arrowed. Data from Kurata (1962).

(Mauchline, 1976), best expressed as the linear regression of log percent increment on pre-moult length (Mauchline, 1977). The slopes of this regression for a series of species with indeterminate growth are listed in Table 2, and several species compared in Fig. 2. The regression has a negative slope, since increment decreases with size. As in the case of intermoult period, small species tend to have a steep slope and large species a gentle one.

It is apparent that in species with indeterminate growth there is a measure of correlation between the slopes of intermoult period and moult increment on size: for a given species both slopes tend to be either steep or gentle (or intermediate). In the former event intermoult period will increase and moult increment decrease rapidly with size, so that however long the species lives it can never reach a very large size. On the other hand, if both slopes are gentle, then growth will continue at an appreciable rate, permitting a large maximum to be attained. Thus in twenty moults from hatching *Porcellio scaber* reaches a body length of 11 mm, compared with 180 mm for *Homarus americanus* after the same number of moults. If the regressions for both log intermoult period and log per cent increment on size are available they can be used to generate growth curves. These are highly simplified in that they ignore seasonal influences and the effects of sexual maturity, but they are adequate to indicate the maximum size attainable. Such curves have been produced for one small and two large species (Fig. 3). Despite the simplifications the indicated maximum sizes are well in agreement with those which occur.

Thus in crustacean species with indeterminate growth the regulation of size is brought about through the mediation of both components of growth. These are regulated in such a way as to set a size limit beyond which the species is effectively unable to grow, irrespective of how long it survives. These growth tendencies are identifiable even in the early post-larval instars, and regressions calculated from such instars can, when extrapolated, give acceptable estimates of maximum size (Hartnoll, 1978).

Regulation of determinate growth

In determinate species, which eventually cease moulting after either a fixed or variable number of moults, the limitation of growth appears extremely simple at first sight: a series of moults occur until the required size is attained, whereupon moulting and growth stop. There is, however, considerable

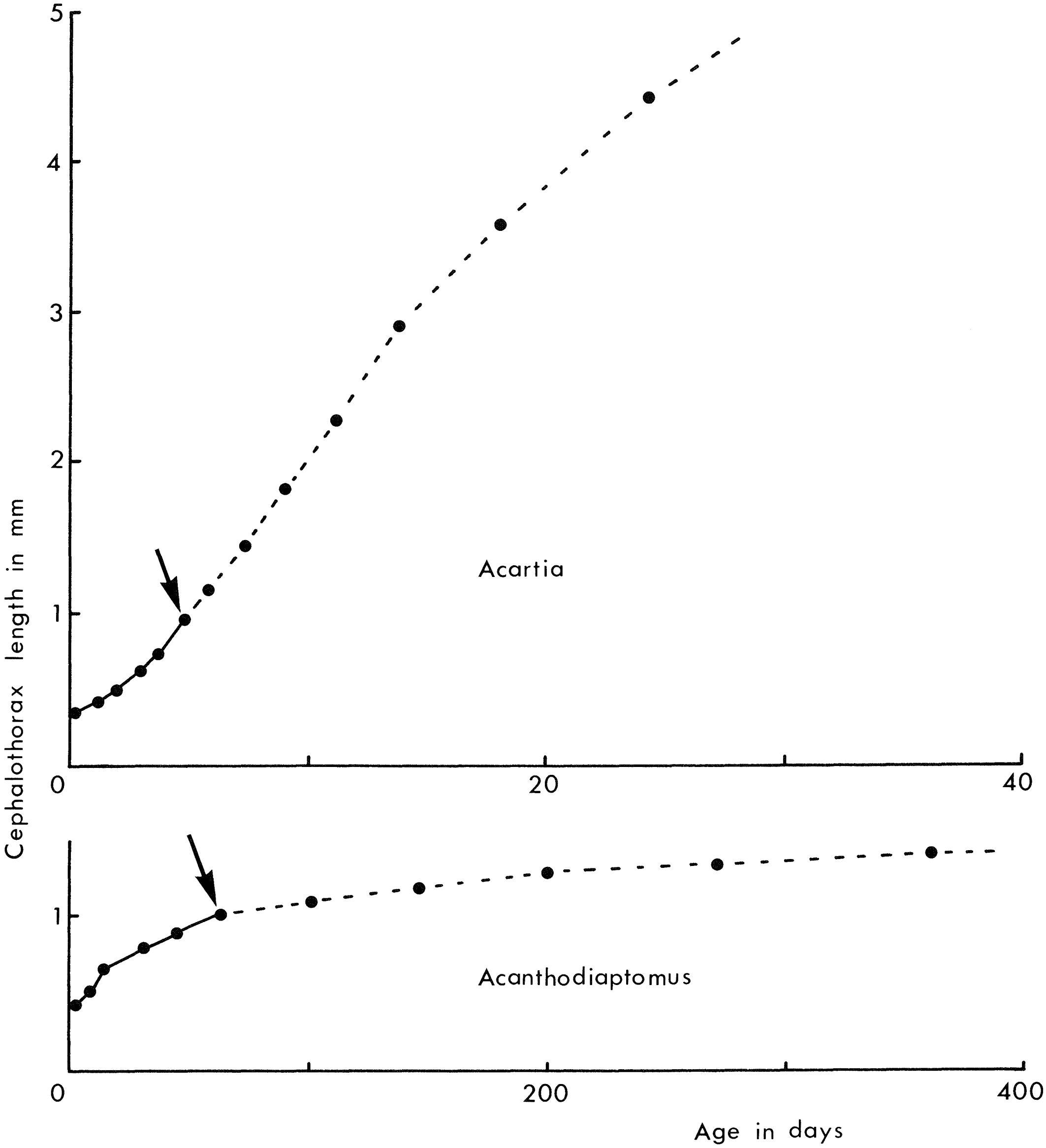

Fig. 6. Actual (solid lines) and extrapolated (broken line) growth for *Acartica tonsa* (data from Miller *et al.*, 1977) and *Acanthodiaptomus denticornis* (data from Ivanova, 1973). Final instar arrowed.

variation in the pattern of growth which precedes the terminal moult, and this deserves closer examination. Do the components of growth respond to increasing size in a similar way to that seen in indeterminate species, or are they freed from such restraints, and does the limitation of size depend entirely upon the terminal anecdysis? The two possible situations are shown in Fig. 4. The pattern of growth in Fig. 4A is similar to that already observed in indeterminate species, and the intervention of the terminal anecdysis causes only a modest truncation of the potential growth. That shown in Fig. 4B is unrestricted, and the terminal anecdysis is the important limiting factor. The pattern of determinate growth will be examined in Ostracoda, Copepoda and certain Brachyura, to see how it relates to the two alternatives.

Table 3. The slopes of the regressions of $\log_{10}$ percentage moult increment and $\log_{10}$ intermoult period (days) on carapace size (mm) for several crabs with determinate growth.

Species	Source	Maximum size	Slope and significance
Increment			
Pisa tetraodon (Pennant)	Vernet-Cornubert, 1960	45 mm	- 0.002 ns
Carcinus mediterraneus Czerniavsky	Veillet, 1945	50 mm	- 0.003***
Carcinus maenas (L.)	Crothers, 1967	50 mm	♂ - 0.003 ns
			♀ - 0.005**
Callinectes sapidus Rathbun	Tagatz, 1968	140 mm	♂ - 0.0004 ns
			♀ 0.0011***
Intermoult period			
Pisa tetraodon	Vernet-Cornubert, 1960	45 mm	0.010*
Carcinus maenas	Meek, 1918	70 mm	0.020***
Callinectes sapidus	Tagatz, 1968	140 mm	0.005***

Cyprinotus sp. is an ostracod with a fixed number of eight instars (Kurata, 1962). The intermoult period lengthens sharply with size, the regression of log period on body length having a slope of 0.76 to 1.14 depending upon temperature: a comparison with Table 1 shows this slope to be steep. On the other hand the percentage moult increment does not decline consistently with size—it in fact increases for the first five moults, and only declines over the final two. Fig. 5 is an extrapolated curve for growth at 21 °C calculated from the observed relationships of moult increment and intermoult period with size. This indicates a levelling off at about 2.5 mm, compared with an actual length in the terminal instar of 1.35 mm. The terminal anecdysis obviously truncates growth to a degree, though it would apparently cease eventually in any case.

The Copepoda have a fixed sequence of six post-larval instars, but display considerable variation in the pattern of growth. In species such as *Acanthodiaptomus denticornis* (Wierzejski) (Ivanova, 1973) the increment declines and the intermoult lengthens with size, and the extarapolated growth curve (derived similarly to Fig. 5) flattens off in typical fashion (Fig. 6). The potential maximum of 1.5 mm cephalothorax length is not greatly in excess of the actual final instar length of 1.0 mm, and growth is of the pattern depicted in Fig. 4A. In other species such as *Acartia tonsa* Dana the per cent increment and intermoult period both change little with increasing size, giving 'isochronal development' (Miller *et al.,* 1977). The extrapolated growth curve is still rising sharply at 5 mm cephalothorax length (Fig. 6), whilst the length of the final instar is only 0.93 mm: this is a marked truncation of growth by the terminal anecdysis as in Fig. 4B.

In crabs with definitive growth there is a tendency, as in *Acartia,* for the percentage moult increment not to decrease with size. This is true of *Carcinus maenas* (Crothers, 1967; Hogarth, 1975; Meek, 1918; Needham, 1950), *Carcinus mediterraneus* (Veillet, 1945), *Maja squinado* (Carlisle, 1957) and *Pisa tetraodon* (Vernet-Cornubert, 1958). In *Callinectes sapidus* the increment is constant in males, but even increases with size in females (Haefner & Shuster, 1964; Leffler, 1972; Tagatz, 1968). The slopes of the regressions of log percentage moult increment on size are gentle, and sometimes not significant (Table 3), and clearly nowhere near as steep as those of indeterminate species of comparable size (Fig. 7). On the other hand the intermoult period increases with size in the normal way, and the slopes of the regressions of log intermoult period on size (Table 3) are comparable with indeterminate species of similar size. The overall effect is that growth is not as potentially unrestricted as in 'isochronal' copepods, but does eventually level off. In *Callinectes sapidus* the extrapolated curve flattens at a carapace width of about 250 mm, whereas specimens in the final instar may measure only 100 mm (Tagatz, 1968).

So although maximum size in determinate species is controlled by the termination of moulting, there is considerable variation in the extent to which this truncates the potential growth were moulting to continue indefinitely. Where, as in 'isochronal' species, the components of growth change little with size, the truncation of potential growth is extreme. However, this situation is unusual in determinate

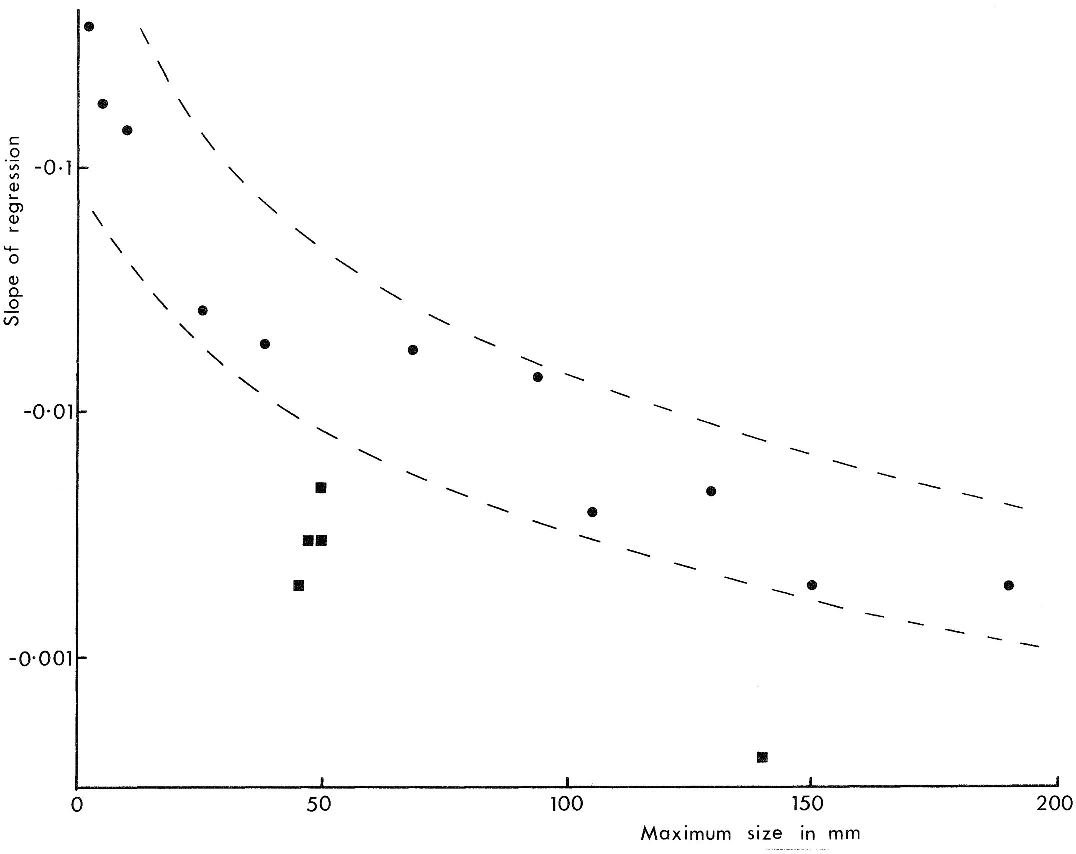

Fig. 7. The log of the slope of the regression of log per cent moult increment on length plotted against maximum size. ●—species with indeterminate growth listed in Table 2. ■—species with determinate growth listed in Table 3.

species, for although the per cent increment tends not to decline with size as it does in indeterminate ones, the intermoult period does lengthen. So the growth curve levels off in due course, and the truncation of growth can be quite modest.

DISCUSSION

It has been shown that there are various patterns of growth in Crustacea which can be responsible for determining the size which a species attains. It must be emphasised that this account has been limited to a description of the patterns of growth as they have been observed, and there has been no attempt to explain the underlying physiological mechanisms. That would be exceedingly difficult. Something is known of the endocrinal control of the terminal anecdysis in crabs (Carlisle, 1957; Hartnoll, 1972), but nothing of that in other determinate Crustacea. Nothing is known of the mechanisms which cause intermoult period and moult increment to change with size.

It remains to consider briefly the adaptive advantage of the alternative strategies of growth which have been described. Assuming that a particular maximal size is optimal for a species which fills a given ecological niche, there are basically two alternative ways by which this size can be assured. One is by indeterminate growth, with the growth rate levelling off in response to changes in the components of growth operative from the early post-larval stages (Fig. 8A). The other is determinate growth, levelling off more slowly, and with growth stopped at a certain size by the cessation of moulting (Fig. 8B). What are the advantages of each strategy?

Indeterminate growth:

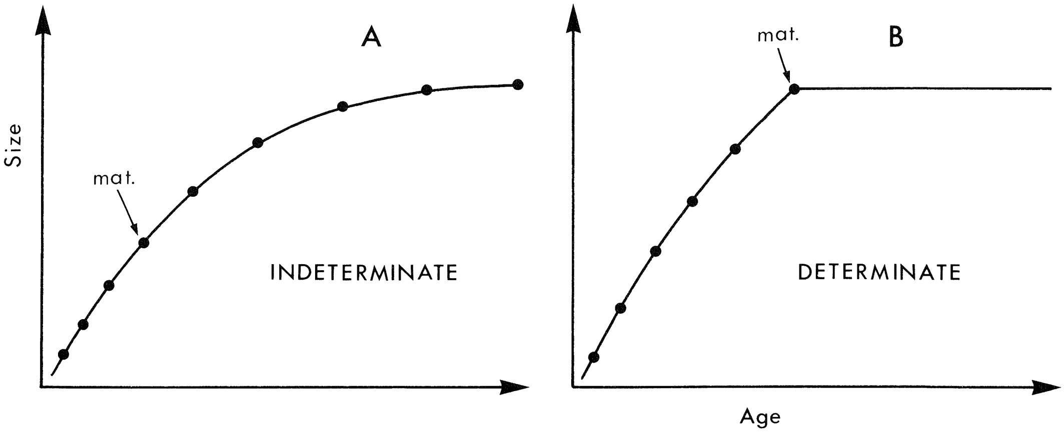

Fig. 8. Growth curves indicating the sequence of instars for species with A, indeterminate, and B, determinate growth. Onset of maturity arrowed.

1. Sexual maturity is early, so there is an ability to reproduce even if mortality occurs before full size is reached.
2. The mature phase is prolonged by post-pubertal moulting, which allows the repair of damage, regeneration of appendages and elimination of metabolites.
3. A pre-ovigerous moult, providing a clean surface for the attachment of eggs, can precede each incubation.

Determinate growth:

1. Growth to full size can be faster.
2. In the mature phase all resources can be concentrated on reproduction, and none diverted to growth. Moulting does not interrupt breeding.
3. During the mature phase there is no mortality induced by moulting.

The selection of one strategy in preference to the other presumably depends upon the balance of the cost-benefit effects of these various factors. At present the information is not available in order to attempt such an analysis.

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COMPLEMENTAL MALES IN THE BARNACLE *BATHYLASMA ALEARUM* (CIRRIPEDIA: PACHYLASMIDAE)

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SUMMARY

Complemental males are described for the first time in this deepwater family of balanomorph barnacles. The males are usually lodged externally on the tergum, in the angle formed between the articular margin and the articular ridge. Sometimes they occur in the apex angle of the carina. Compared with similar-sized individuals attached to the outside of the parietal shell plates, the body of the male is dominated by testes and seminal vesicles, the latter packed with sperm, and the penis is 4 to 5 times longer. The sexual condition is compared with that in other barnacles, and the mode of sex determination is discussed.

Introduction

Most barnacles (Cirripedia Thoracica) are simultaneous hermaphrodites. A less common sexual condition of some barnacles first fascinated Darwin (1851), who described in the genera *Ibla* and *Scalpellum (sensu lato)* little individuals associated with either larger hermaphrodites or, more rarely, females. Darwin ascertained they were males of the same species and called them dwarf and complemental males respectively. Subsequently, such males have been described in two other species of *Ibla,* in numerous scalpellids, and in 4 species of archeobalanid barnacles (McLaughlin and Henry, 1972). This paper describes a new case of complemental males, of a different sort to those in the archeobalanids, and in a different balanomorph family.

Is the more common hermaphrodite condition or the rarer separate-sex condition primitive? Newman (1974, p. 444) was of the opinion that barnacles with separate sexes are primitive, which accords with the views of Broch (1922) that complemental males represent the last vestiges of ancestral dioeciousness prior to the establishment of the more prevalent hermaphrodite condition. However, this may not be so. Independent development of complemental males in diverse families of barnacles, from a more basic hermaphrodite condition, may have arisen to improve reproductive performance in sublittoral barnacles. Whereas a gregarious settling response (Knight-Jones, 1953) must improve the opportunities for cross-fertilisation of hermaphrodites, the advantage of complemental males possibly lies in the speeding up of reproduction of already mature individuals that the little males associate with. The abolishment of the male function of the larger partners in certain scalpellids and species of *Ibla* amounts to a restoration of a precirriped dioecious condition, but with female dominance. This theory is expounded in the discussion.

Material

Thirty-five free-living specimens of *Bathylasma alearum* (Foster), on a boulder collected by "Tangaroa" from New Zealand Oceanographic Institute Stn R6: 42° 29.2′S, 176° 06.3′E, 1568 m, northern Mernoo Slope.

Deposited: National Museum BS648.

These mostly disarticulated specimens range in size from 10 mm to about 30 mm basal rostrocarinal diameter. As well, 3 small specimens and two recently metamorphosed spat (Fig. 2a) were attached to the outside of the parietes of larger specimens. A total of 35 males were present on the terga of 21 of the hermaphrodites, the latter all more than 14 mm shell diameter; 8 hermaphrodites had males on both terga. Of the 29 individual terga with males, 24 had one male, 4 carried 2 males, and one had 3 males. In addition, 2 hermaphrodites bore a small male in the internal groove at the apex of the carina.

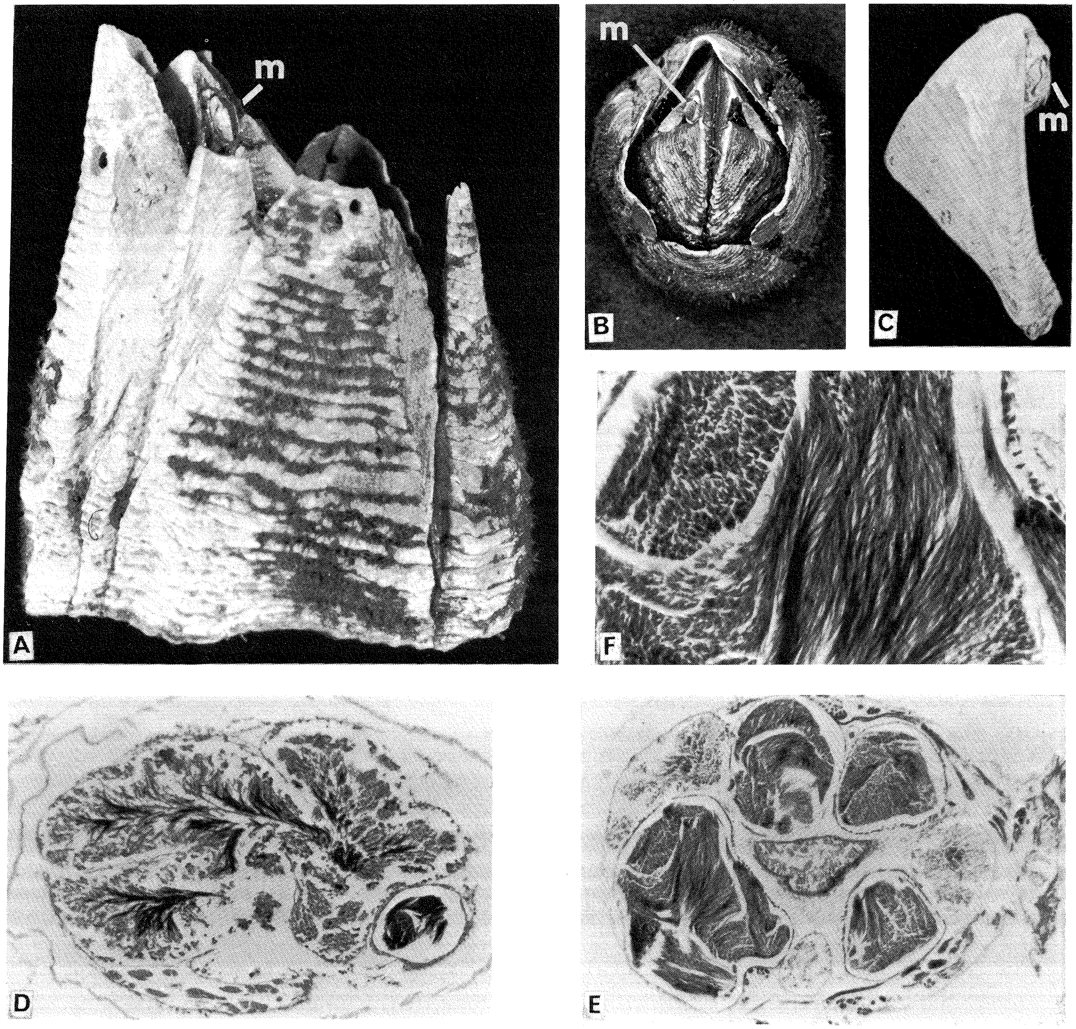

Fig. 1. *Bathylasma alearum:* **A,** lateral view of hermaphrodite showing small male (m) in tergal niche, plus whelk-drilled holes in apical parts of parietes; **B,** apical view of another hermaphrodite with a male (m) on right tergum; **C,** dissected tergum with male (m); **D,** section through prosoma of tergal male, mostly of testis (t) undergoing spermatogenesis and sperm in one seminal vesicle: **E,** section through another male showing distended seminal vesicles with sperm, three marginal testis lobes and centrally the stomach; **F,** aligned sperm in seminal vesicles of specimen E.

The males ranged in size from 1.0 mm (recently metamorphosed) to 4.0 mm rostrocarinal length. The largest males were solitary in their niche, occupying most of the niche.

Note on the taxonomy

Bathylasma alearum was first described as *Hexelasma alearum* by Foster (1978) from two intact specimens and copious shell plates collected on the New Zealand shelf. Since the preparation of my earlier paper, and with extra material, I have reconsidered the taxonomy of the *Bathylasma/Hexelasma/Aaptolasma* section of the Pachylasmidae (Foster, 1981) and now uphold *Bathylasma* of Newman & Ross (1971). *Hexelasma* is the senior synonym of *Aaptolasma.*

B. alearum (Fig. 1a) is very closely related to the large fossil *B. aucklandicum* (Hector), now known from the Oligocene to the Pliocene of New Zealand (Mr John Buckeridge, pers. comm.). I earlier

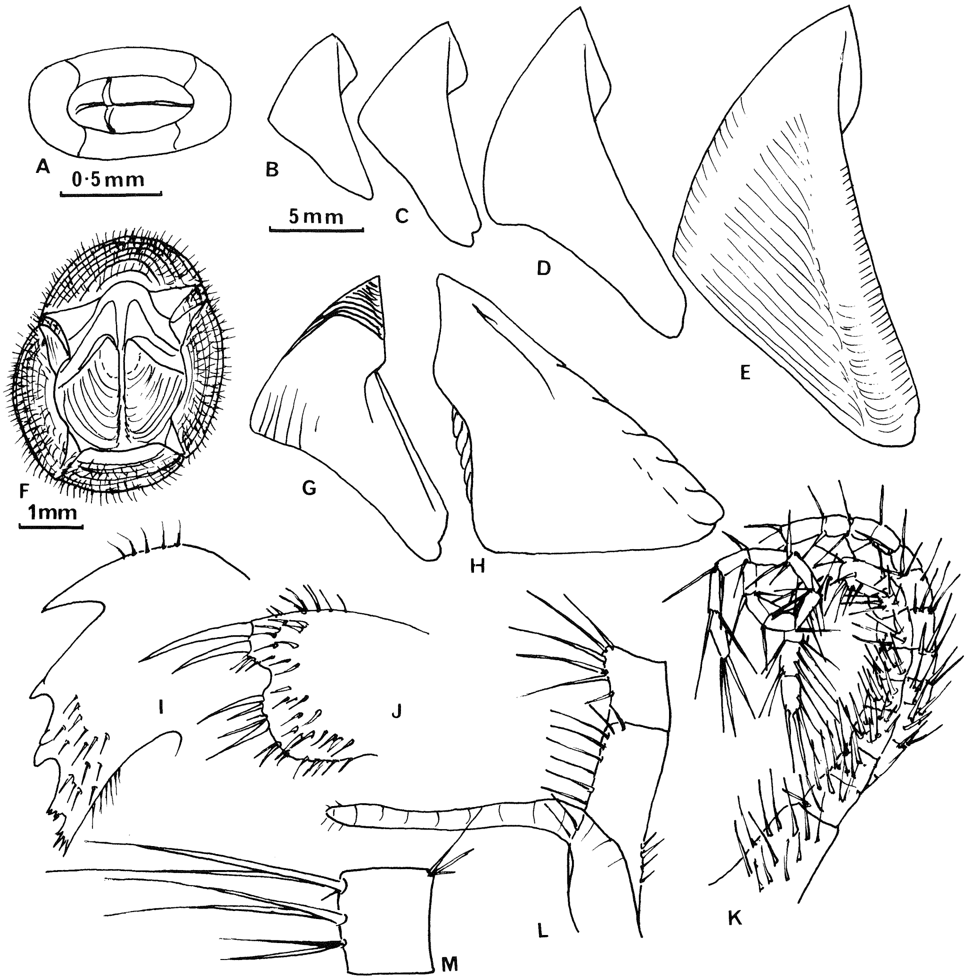

Fig. 2. *Bathylasma alearum:* **A**, apical view of spat; **B-E**, external views of terga of range of specimens to show appearance of articular ridge, to same scale; **F**, apical view of juvenile; **G-M**, details of this juvenile; **G**, tergum; **H**, scutum; **I**, mandible; **J**, maxillule, **K**, cirrus III with antenniform posterior ramus; **L**, penis and pedicel of cirrus VI; **M**, intermediate segment of cirrus VI.

distinguished the two species by the shape of the tergal articular ridge, but it is clear from the present material that the triangular articular ridge of *B. alearum* becomes truncated in larger specimens (Fig. 2b–e), as it is in the relatively massive tergum of *B. aucklandicum* (see Foster, 1978, plate 10D). *B. alearum* is conceivably descended from the fossil species with a concomitant reduction of the maximum size attainable.

Description of males

Males laterally compressed with the rostrocarinal axis aligned with either the articulation between the tergum and scutum of the 'host' (Fig. 1a–c) or the longitudinal groove of the carina for those seated on a carina. Parietes often cracked and deformed. Opercula embryonic, often deformed. Internal appendage series complete. Mouthparts and appendages as shown in Fig. 3, with cirral segment counts in Table 1. Penis longer than cirrus VI. Prosomata of 1 carinal and 2 tergal males were sectioned; found to be mostly occupied with seminal vesicles containing sperm masses (Fig. 1e–f) and testes undergoing spermatogenesis (Fig. 1d); gut with food remains.

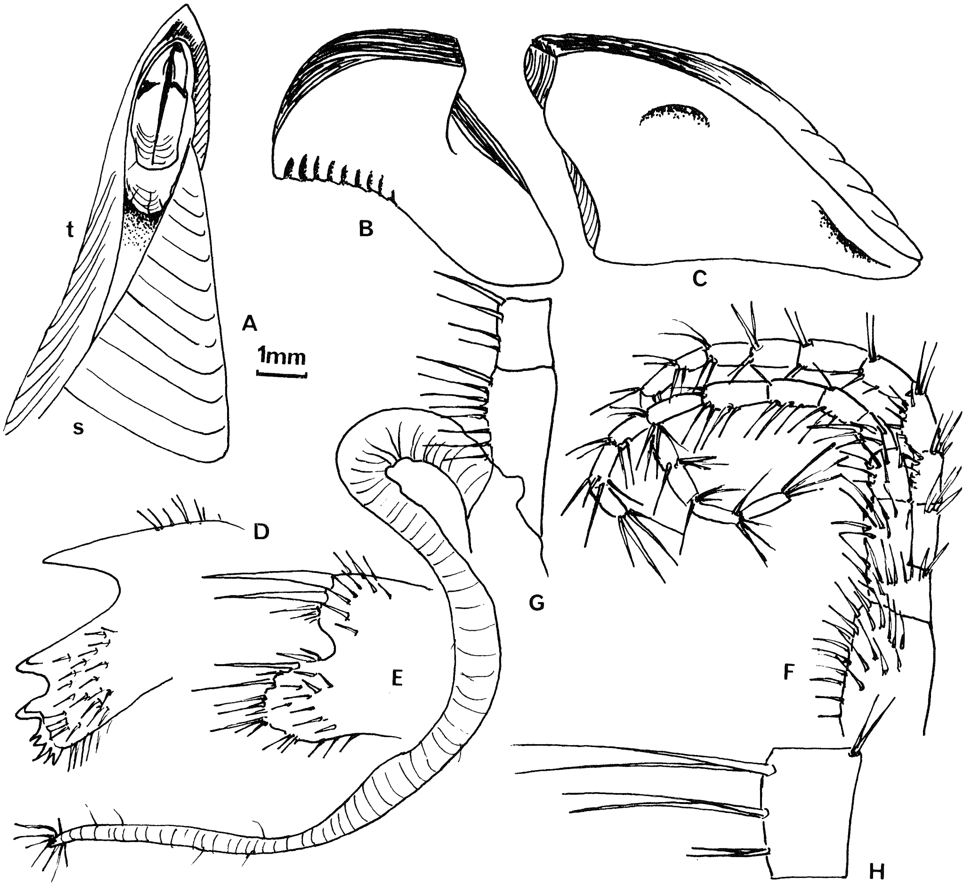

Fig. 3. *Bathylasma alearum:* **A**, apical view of male in tergal niche of a larger specimen, t-tergum, s-scutum; **B-H**, details of male; **B**, tergum; **C**, scutum; **D**, mandible; **E**, maxillule; **F**, cirrus III; **G**, penis and pedicel of cirrus VI; **H**, intermediate segment of cirrus VI.

Comparison with juveniles and hermaphrodites

Shell and appendages of a similar-sized specimen attached on the outside of parietes are shown in Fig. 2f–m, with cirral counts included in Table 1. Penis ⅓ length of cirrus VI. Testes primordia present, but insignificant in comparison with size of gut. Seminal vesicles small, without sperm.

In larger specimens, the number of segments in the cirri increases (Table 1). In the present material, the posterior ramus of cirrus III is antenniform, with numerous distal elongate segments such that the ramus is as long or longer than cirrus IV. (In the type material there was no evidence of antenniformy). In large specimens the penis is shorter than cirrus VI, sometimes stout and 0.7 × the length of cirrus VI, sometimes degenerate and <0.1 × cirrus VI.

Table 1. Numbers of segments in the rami of cirri of specimens of *Bathylasma alearum,* anterior ramus first.

	rostro-carinal length	NZOI Stn	Cirrus					
			I	II	III	IV	V	VI
male	0.4 mm	R6	5,5	5,7	9,14	13,14	15,19	16,19
juv.	0.4 mm	R6	8,6	7,12	11,22	16,17	21,19	19,21
herm.	9 mm	F132	8,8	11,18	19,19	18,22	21,22	21,26
herm.*	16 mm	F132	12,11	18,22	24,24	33,27	31,34	35,33
herm.	22 mm	R6	15,14	23,23	29,49	37,35	39,39	34,41

*holotype (Foster, 1978).

DISCUSSION

None of the specimens of the present suite possessed any embryos or larvae in the mantle cavity; many had well developed ovarian tissue. It is suspected that free-swimming nauplius and normal cypris stages are involved in the life cycle of *B. alearum,* because planktotrophic nauplii are known for *B. corolliforme* from Antarctic seas (W. Newman, pers. comm.).

It is postulated that the larvae are potentially sexually hermaphrodite, but the cyprids that settle in the carinal and tergal apical niche of conspecific adults metamorphose there to feed and grow to about 4 mm length, and become precocious males. Cyprids that settle elsewhere within the orifice could be in danger of destruction by the rocking movements of the opercula, known to keep the orifice clear of encroaching organisms (Tait & Emmons, 1925; Crisp & Southward, 1961). Cyprids that settle beyond the orifice, whether on conspecific adults or not, develop to hermaphrodites if they escape the attentions of predatory whelks.

An alternative theory is that the larvae are incipient males or hermaphrodites and the former kind are compelled to find a niche in the orifice for their subsequent functioning.

To consider these alternatives, it is profitable to recapitulate the types of complemental males amongst barnacles, which can be classified as follows:

1. Those that have trophi and are essentially minute forms of their associate hermaphrodites:
   a) males attached among the rostral plates of *Scillaelepas* (Newman, 1980);
   b) males attached to the integument between the terga below the orifice of species of *Calantica, Smilium* and *Euscalpellum* (see Foster, 1978);
   c) males of *Bathylasma alearum.*
2. Those with degenerate trophi and occurring in special pouches near the orifice of their ‘host’:
   a) sac-like males of scalpellids, in pouches on the inside near the umbo of the scuta of scalpellids with hermaphrodites in some species (e.g. *Graviscalpellum pedunculatum*), but mostly with females in most species of arcoscalpellids (Foster, 1980);
   b) small degenerate males in pouches on the inside of the rostrum of three species of *Solidobalanus* and one of *Conopea* (McLaughlin & Henry, 1972).
3. Those of *Ibla* spp. that reside inside the mantle cavity, with degenerate trophi or without trophi and then either attached or lying loosely respectively (Darwin, 1815; Batham, 1945).

Within the family Scalpellidae, the most primitive genera like *Lithotrya, Capitulum* and *Pollicipes* (Foster, 1978; Newman, 1979) do not have males and are hermaphrodites. Somewhat more advanced genera like *Calantica, Scillaelepas* and *Smilium* have males of types 1a and 1b. Finally, the scalpellids that lack subcarinae and subrostra (226 species assigned to 29 genera by Zevina, 1978 a, b), and probably variously evolved from a calanticid ancestor, are of type 2a. The phylogenetic trend shown in the scalpellids is towards an association with complemental males, perhaps facultative in calanticids (see Foster, 1978) but obligatory for cross-fertilisation in the ‘higher’ arcoscalpellids where the larger and more normal partner lacks a male reproductive system. If this is the correct sequence of evolution, and the phylogeny is compelling, then it follows that instances of complemental males in other families have been independently evolved.

Looking beyond the barnacles (Thoracica) to the semi-parasitic and morphologically more primitive Ascothoracica, it is noteworthy that the most generalised genus, *Synagoga,* exists as sequential protandric hermaphrodites (Newman, 1974), giving a superficial impression of there being two similar sexes. The Cirripedia may be fundamentally hermaphrodite, even though they may have originally derived from the isomorphic dioecious condition of other Maxillopoda. The advent of hermaphroditism may have been associated with a parasitic life of the first cirripeds, but subsequent radiation has involved changing the protandric hermaphroditism to simultaneous hermaphroditism or, at various times, to a complemental partnering arrangement. But what are the selective advantages in the latter option?

An ability of cyprids of parasitic species to detect hosts could, with a shift in the chemical basis of that response, have changed to the gregarious response that has been demonstrated to operate in some barnacle species (Knight-Jones, 1953). The gregarious response enhances opportunities for cross-fertilisation. If an already established hermaphrodite not only attracts a conspecific neighbour but also controls its sexual identity so that it becomes sexually functional very quickly after settlement, then cross-fertilisation can be effected much more quickly. The second-comer is forced to be precocious and protandric. Otherwise the hermaphrodite would have to wait for the new-comer to grow and mature with increased chance of predation. Judging from the number of drill holes in the plates of pachylasmid barnacles (see e.g. in Fig. 1a) whelks are predators as much for sublittoral barnacles as for shore barnacles, and in sublittoral environments there can be no respite during low tides. Many shallow water fouling barnacles increase the onset of reproduction by growing rapidly and maturing at small size. In the deepsea, low food levels would not favour fast growth; the precocious complemental male possibly enhances reproduction in slow-growing species in low food environments.

If the development of complemental males is viewed as the influence of an existing barnacle over a cyprid that settles on it, the mechanism may involve a sex pheromone that operates only on cyprids that settle in close proximity to the orifice, or crawl inside the mantle as in *Ibla.* This environmental influence is what was concluded by Callan (1941) for the situation in *Scalpellum scalpellum.* There is, nevertheless, growing opinion that sex in barnacles is genotypically determined in so far as larvae exist in two types: those that will develop into males only, and those that are destined to be normal-form hermaphrodites or females (Veillet, 1956; Gomez, 1973). These latter conclusions have been based on studies of species of type 2 above, where the degree of degeneration of the male is more advanced than in *B. alearum,* or in others of type 1. Where complemental males have become obligatory for reproduction it could well be that there is an underlying early sex-determining mechanism of a different nature to the conventional chromosome one. However, because complemental males have arisen separately on at least 7 occasions in the Cirripedia, there may be as many mechanisms.

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ASSOCIATIONS BETWEEN AMPHIPODS (CRUSTACEA: AMPHIPODA) AND SEA ANEMONES (ANTHOZOA, ACTINIARIA)

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SUMMARY

Published and unpublished records of amphipod–sea anemone associations are reviewed. They involve at least 22 amphipod species in 7 families, and 8 families of sea anemones. The associations are of 4 main types: protection only, ectocommensals, endocommensals and micropredators.

Morphological adaptations are not conspicuous, except for the specialised mouthparts of *Acidostoma* spp., but most obligate symbionts show inborn immunity against the toxic substances released by the host. Sex ratios are normal, sexual dimorphism small, and fecundity low compared to related free-living species.

The obligate commensal associates are usually host-specific, although able to survive in alternative hosts in the laboratory, while the micropredators and the facultative associates show low host specificity. The amphipod symbionts usually do not occupy the entire geographical and ecological range of their hosts' distribution.

Amphipod–sea anemone associations have evolved independently many times and do not seem to be of great evolutionary antiquity.

INTRODUCTION

The crustaceans of the order Amphipoda are according to most biology textbooks free-living animals, with some old and invariably cited exceptions such as the whale-lice on whales, *Hyperia* species on medusae and some Dexaminidae in sponges and tunicates. This view is certainly incorrect for the suborder Hyperiidea, most of which are obligate symbionts of gelatinous zooplankton (cf. Laval, 1980). Also among the Gammaridea and Caprellidea a large number of species live in association with a wide spectrum of invertebrates (e.g. Arndt, 1933; Vader, 1970b, 1971a–c, 1972, 1979, in prep.), fish (no review paper published) or even sea turtles (Barnard, 1967). These associations have in the past been largely overlooked or looked upon as incidental, in part because amphipods generally become easily dislodged from their host on capture, in part because most amphipod workers were museum taxonomists. With the advent of SCUBA-diving as a biological tool, large numbers of amphipod associations are now being discovered, although only few have been studied thoroughly.

Sea anemones are well-known as hosts of many symbionts: fishes (cf. Allen, 1972), shrimps, porcelain crabs, hermit crabs and spider crabs (Ross, 1967, 1971, 1974; Wolff, 1972; Suzuki & Hayashi, 1977), mysids (Clarke, 1955) and copepods (Bouligand, 1966; Gotto, 1979; Humes, 1982); such associations seem to be especially common in tropical waters. These associations occur in spite of the fact that most anemones are active predators and often feed on prey in the same size ranges as the associates, which they catch with the help of numerous batteries of toxic nematocysts and clinging spirocysts. Furthermore, digestion is largely extracellular and large amounts of proteolytic enzymes, also containing chitinases, are secreted into the gastrovascular cavity. The copious mucus production of sea anemones may also pose problems.

Once symbionts have been able to overcome these barriers, however, sea anemones offer many obvious advantages as hosts. They are long-lived animals and offer excellent protection, even to such large associates as hermit crabs (Ross, 1971; McLean & Mariscal, 1973). Sea anemones may collect more food than they can eat quickly, while the semi-digested and ejected food remains are also of high nutritive

Table 1 KNOWN SEA ANEMONE HOSTS AND THEIR AMPHIPOD PARTNERS. For further data see text.

ACTINIARIA	AMPHIPODA	
Tribe Subtribe Family Species	Family	Species
Athenaria		
Haloclavidae		
Peachia hastata Gosse	Lysianassidae	*Acidostoma obesum* (B & W)
Haliactiidae		
Haliactis arctica Carlgren	Stenothoidae	*Stenothoe* sp.
Thenaria		
Endomyaria		
Actiniidae		
Anemonia sulcata (Pennant)	Caprellidae	*Caprella acanthifera* Leach
	Melitidae	*Melita obtusata* (Montagu)
Anthopleura artemisia (Pickering in Dana)	Lysianassidae	*Orchomene recondita* (Stasek)*
A. elegantissima (Brandt)	Lysianassidae	*Orchomene recondita* (Stasek)
A. xanthogrammica (Brandt)	Pleustidae	Pleustidae indet.
Bolocera tuediae (Johnston)	Leucothoidae	*Leucothoe spinicarpa* (Abildgaard)
	Lysianassidae	*Aristias neglectus* Hansen
	Lysianassidae	*Onisimus normani* G.O. Sars*
Liponema multicornis (Verrill)	Lysianassidae	*Onisimus normani* G.O. Sars
Condylactis aurantiaca (Della Chiaje)	Lysianassidae	*Acidostoma obesum* (B & W)
Tealia coriacea (Cuvier)	Pleustidae	Pleustidae indet.
T. felina (Linnaeus)	Melitidae	*Melita obtusata* (Montagu)
Stoichactiidae		
Stoichactis haddoni Saville Kent	Leucothoidae	*Leucothoe* sp.
Mesomyaria		
Actinostolidae		
Actinostola callosa (Verrill)	Lysianassidae	*Acidostoma nodiferum* Stephensen
	Lysianassidae	*Onisimus normani* G.O. Sars
	Stenothoidae	*Stenothoe brevicornis* G.O. Sars
Acontiaria		
Hormathiidae		
Hormathia nodosa (Fabricius)	Lysianassidae	*Onisimus normani* G.O. Sars*
Calliactis armillatus Verrill	Melitidae	*Elasmopus calliactis* Edmondson
Calliactis sp.	Leucothoidae	*Leucothoe spinicarpa* (Abildgaard)
Metridiidae		
Metridium senile (Linnaeus)	Stenothoidae	*Metopa solsbergi* Schneider
Metridium sp.	Lysianassidae	*"Orchomene"* n.sp
Aiptasiidae		
Aiptasia couchii Cook)	Caprellidae	*Caprella acanthifera* Leach
Bartholomea annulata (Leseur)	Amphilochidae	*Amphilochus neapolitanus* Della Valle
	Stenothoidae	*Stenothoe* n. sp
host unknown	Lysianassidae	*Acidostoma laticorne* G.O. Sars
	Lysianassidae	*Onisimus turgidus* G.O. Sars
	Stenothoidae	*Stenothoe barrowensis* Shoemaker

* = probably rare alternative host.

value and in fact constitute the main food source for many associates. Finally, and this is important especially for smaller symbionts, the copious mucus secretions of the host are a high-quality source of food and are used as such by many copepods (Briggs, 1976, 1977; Gotto, 1979) and also by amphipods. A further step, feeding directly on host tissues, apparently has been taken by many copepods (e.g. Vader, 1970; Gotto, 1979; Lönning & Vader, in prep.), by the Pycnogonida, and by at least one genus of amphipods.

The present review of associations between amphipods and sea anemones is admittedly very incomplete. I know of the existence of a number of other such associations, usually involving Leucothoidea, which have been observed by divers in Caribbean waters and in the NE Pacific, but where the identity of the amphipod partners has not yet been established.

The known records of amphipod-sea anemone associations are listed below in alphabetical order of the families of the amphipod partners. Table 1 lists the known sea anemone hosts according to Carlgren's classification (Carlgren, 1949).

THE AMPHIPOD ASSOCIATES

Amphilochidae

Amphilochus neapolitanus Della Valle

This species was recently discovered to be quite common on *Bartholomea annulata* in southern Florida. "Each anemone has at least 1–2 specimens and some of the larger ones were host to as many as twelve specimens. The species also occurs on several other species of anemones and on the soft coral *Pterogorgia anceps*." (J. D. Thomas, pers. comm. 1980).

The biotope of *A. neapolitanus* is generally listed as among algae on rocks (Lincoln, 1979) and it has also been reported from sea urchins (cf. Vader, 1979).

Caprellidae

Caprella acanthifera Leach

This common and widespread caprellid has been found on sea anemones only in the western Mediterranean (Stroobants, 1969; R. Patzner, pers. comm. 1979); the hosts are *Anemonia sulcata* and *Aiptasia couchii*. Stroobants (1969) has described how the caprellids live among the tentacles and on the column of their host, where they apparently largely catch their own food, independent of the host.

Most caprellids are apparently free-living but a number of species are associated with starfish (cf. Vader, 1979; see also McCain, 1979); *C. ungulina* lives on a crab (Griffiths, 1977) and *G. gorgonia* is an obligate associate of soft corals (Laubitz & Lewbel, 1974).

Leucothoidae

Leucothoe spinicarpa (Abildgaard)

This well-known and apparently cosmopolitan species (or superspecies) shows a high tendency toward inquilinism, but with very low host specificity. It has twice been found on sea anemones: once on *Bolocera tuediae* in the northern North Sea (Vader, unpubl.), and once on *Calliactis* sp. in Cuban waters (Ortiz, 1975).

Leucothoe spinicarpa usually lives in sponges (cf. Connes, 1967) or tunicates, but it has also been found in molluscs (Ortiz, 1975; Vader & Beehler, in press) and brachiopods (cf. Vader, 1970d). The feeding biology of *Leucothoe* species is still unknown, but the closely related *Leucothoides*, likewise an inquiline of sponges and tunicates, has recently been shown to be a microphagous commensal (Thomas, 1979).

Leucothoe sp.

A single specimen of a *Leucothoe* species allied to *L. richiardii* Lessona has been collected from *Stoichactis haddoni* on the Great Barrier Reef by Dr S. Losey and sent to me.

Lysianassidae

Acidostoma Lilljeborg

The nomenclature of the European representatives of this genus has recently been revised by Lincoln (1979). He showed that *A. obesum* (Bate & Westwood) is a senior synonym of *A. neglectum* Dahl, and coined the name *A. sarsi* Lincoln for *A. obesum* auct., non Bate & Westwood. Lincoln also synonymised *A. nodiferum* Stephensen with *A. sarsi*, incorrectly under the latter name. To avoid further confusion, *A. nodiferum* is here provisionally kept apart.

Acidostoma laticorne G. O. Sars

Dahl (1964) found the proctodaeum of museum specimens filled with nematocysts, most probably of anthozoan origin.

Acidostoma nodiferum Stephensen

This species was found on the large sea anemone *Actinostola callosa* in deep water in western Norway (Vader, 1967). The faeces of the amphipods contained numerous nematocysts.

Acidostoma obesum (Bate & Westwood) (= *A. neglectum* Dahl)

Della Valle (1893) collected this amphipod from the column of the sea anemone *Condylactis aurantiaca* in the Gulf of Naples, while Ansell (1969) found some specimens within the burrow of *Peachia hastata* in Scotland.

Dahl (1964) has studied the structure and function of the mouthparts of this and other species of *Acidostoma*. He concluded that the mouthparts are apparently adapted for sucking and that *Acidostoma* species live as ectoparasites on anthozoans.

Aristias neglectus Hansen

This is, like *Leucothoe spinicarpa*, a common inquilinous species with low host specificity. It is found sparsely but regularly in the gastrovascular cavity of the large mud-living sea anemone *Bolocera tuediae* in western Norway (Vader, 1970b). No egg-bearing females have been found inside the sea anemones.

A. neglectus usally lives in sponges and tunicates, but is has also been found in Brachiopoda (Vader, 1970d) and on echinoderms (cf. Vader, 1979).

Lysianopsis sp.

Dr E.L. Bousfield (pers. comm. 1980) has told me that he has several times collected an undescribed species of this genus on the Canadian Pacific coast from around the base of *Anthopleura xanthogrammica*, where gravel and sand had collected, but not in any other intertidal locations.

Onisimus Boeck (= *Boeckosimus* Barnard)

Barnard (1969) has pointed out that the name *Onisimus* Boeck is a senior synonym of *Pseudalibrotus* Della Valle, and he has coined the new name *Boeckosimus* for *Onisimus* auct. As pointed out by Just (1978, p. 10), this move disrupts the stability of an extensive literature and the problem should be referred to ICZN. In the meantime, I use the name *Onisimus* in the 'classic' sense.

Onisimus normani G. O. Sars

This N. Atlantic species appears to be an obligate inquiline of sea anemones. The normal host is *Bolocera tuediae*, but in northern Norway *O. normani* has also been found in *Actinostola callosa, Hormathia nodosa* and *Liponema multicornis* (Vader, unpubl.). The biology of the association has been studied by Vader (1967, 1970; Vader & Lönning, 1973). *Onisimus normani* live in the gastrovascular cavity among the mesenterial filaments and apparently feed mainly on the semi-digested prey of their host. They have a 2-year life cycle and exhibit seasonal reproduction. The amphipods enter the sea anemones as c. 3 mm young juveniles in spring and grow to fully adult size within the host in c. 18 months. They then leave their host and disappear; no ovigerous *O. normani* have ever been found within the host, and very few have been found elsewhere. Circumstantial evidence indicates that the species is single-brooded. Infection rates may be high: in a deep fjord in western Norway 70% of the *Bolocera* contained *Onisimus*, with a mean incidence of c. 3. The amphipods are strictly host-specific in western Norway, but much less so in northern Norway, although the same host species in about the same relative numbers occur in both areas.

Onisimus turgidus G. O. Sars

This little-known arctic species was originally described as parasites on a large actinian in the Barents Sea (Sars, 1885, p. 147); the specific identity of the host remains unknown (Vader, 1967). Later records confirm the association, but add no further details.

Orchomene recondita (Stasek)

This species was originally described in the primarily Antarctic genus *Allogausia* Schellenberg (Stasek, 1958) but it is certainly not congeneric with its type, *A. paradoxa* Schellenberg (Vader, unpubl.). I therefore provisionally follow Barnard (1964, 1969b), who combined a number of genera into *Orchomene* s.l., although this enlarged genus is clearly not homogeneous (see e.g. Oleröd, 1975).

Orchomene recondita lives inside the gastrovascular cavity of the intertidal sea anemone *Anthopleura elegantissima* (a very few specimens have been found in *A. artemisia*). It has hitherto been found only at a few localities near San Francisco. The biology of the association has recently been studied by Vader & Lönning (in prep.). The amphipod spends its entire life cycle within its host. It feeds mainly on the half-digested prey of its host, probably augmented with mucus secretions and zooxanthellae, but usually not host tissues. *O. recondita* has seasonal reproduction and a 1-year life cycle. The females have several consecutive broods of 8–15 young in early spring and then die. Both young and adult amphipods spend long periods within a single host, although amphipods kept without a host are clearly night-active. The distribution of *O. recondita* is extremely patchy. Within patches, the infection rate may be as high as 80% with a mean incidence of up to 6 amphipods per sea anemone.

Orchomene (s.l.) n. sp.

A sample from Alaska in the National Museum of Natural Sciences, Ottawa, contained 1 ♂ and 1 ♀ of this undescribed species labelled as having been collected 'among tentacles of *Metridium*'. Further specimens of this taxon have been collected from an intertidal habitat in Washington (E.L. Bousfield, pers. comm.). Off the northern California coast white *Orchomene*-like lysianassids have been noted among the tentacles of *Metridium*, which had been dredged from deep water, but no material is extant (J. Chapman, pers. comm. 1980).

Melitidae

Elasmopus calliactis Edmondson

This little-known species was described by Edmondson (1951) as an obligate associate of a hermit crab–sea anemone symbiosis in Hawaii, but the role of the sea anemone partner, *Calliactis armillatus*, in the biology of the amphipod is not known.

Melita obtusata (Montagu)

This common European amphipod is best known as a regular associate of starfish, but it has also been found apparently free-living, as well as on other echinoderms and on hermit crabs (for ref. see Vader 1979), and on the sea anemones *Anemonia sulcata* (Brady & Robertson, 1869; Hartnoll, 1971) and *Tealia felina* (Reid, in Sanderson 1973). Hartnoll (1971) found the amphipods among the tentacles. He speculated that they perhaps feed upon the remains regurgitated by the anemone.

Pleustidae

Several as yet undescribed species of Pleustidae, among them at least one *Parapleustes* sp. (alluded to in Barnard, 1972, p. 17) and a *Pleusymtes* sp., have been observed by divers on subtidal Californian sea anemones, especially *Anthopleura xanthogrammica* and *Tealia coriacea* (D. Wobber, unpubl. rep. 1968; J. Ratliff, unpubl. rep. 1974; T. Chess, pers. comm. 1978). They appear to move away from the sea anemones frequently and to find most of their own food, but they flee to their host when danger threatens.

Stenothoidae

Metopa solsbergi Schneider

This is one of the many rarely collected *Metopa* species from the North Atlantic. Elmhirst (1925) found numbers of this amphipod to be present on *Metridium senile* on pier piling in western Scotland, the only known record from Great Britain (Lincoln, 1979). The amphipods crawled about on the oral disc and the tentacles and also entered and left the stomodaeum unharmed. Elmhirst stated that the slime of the host, enriched with trapped food particles, constituted the natural food of the amphipods, but he did not say how he arrived at that conclusion.

The same association has recently also been found off the coast of Newfoundland, Canada (Fenwick & Steele, in prep.).

Stenothoe barrowensis Shoemaker

This species, known only from the two type specimens from off Point Barrow, Alaska (Shoemaker, 1955), is apparently closely related to *Stenothoe brevicornis* G. O. Sars and may likewise be an associate of sea anemones. The types were taken from a dredge haul which contained among other things 22 unidentified sea anemones (MacGinitie, 1955, p. 77).

Stenothoe brevicornis G. O. Sars

This amphipod, widely distributed in the North Atlantic, in northern Norway is an obligate associate of the large sea anemone *Actinostola callosa*. The biology of the association is being studied by Vader (in prep.). *Stenothoe brevicornis* spends its entire life-cycle among the tentacles and on the oral disc of its host, where it crawls about unhampered. I have never seen the amphipods enter the stomodaeum. They apparently mainly feed on the mucus secretions of the sea anemones. Females with eggs are present among the tentacles at all seasons, but the number of broods is not yet known. Frequency of infection at the study-site in northern Norway is from 40–70%, with a mean of 1–4 amphipods per host. Many other populations of *Actinostola callosa* in the Norwegian fjords were examined, but most did not contain any *Stenothoe.*

Stenothoe n.sp.

An undescribed species of *Stenothoe* is apparently common on the sea anemone *Bartholomea annulata* in S. Florida waters (Vader, 1971c, in prep.; K. Cairns pers. comm. 1979; J.D. Thomas pers. comm. 1980). It lives among the tentacles of its host and may attain high frequencies: up to 70 specimens (including ovigerous ♀♀) have been collected from a single host. The association seems to be similar to that of *Stenothoe brevicornis* with *Actinostola callosa.*

Stenothoe sp.

A sample of 3 specimens collected off Point Barrow, Alaska in 1959 of an unidentified *Stenothoe* species in the collections of the National Museum of Natural History in Washington is labelled 'from coelenteron of *Haliactis arctica*'.

TYPES OF ASSOCIATIONS

The associations between amphipods and sea anemones as yet are little studied and any classification must therefore be regarded as preliminary. There seem, however, to be four categories.

I. *Protection only*

These amphipods find protection on their sea anemone host, but they collect all or most of their food independently; ejected food-remains may play a role in nutrition. The amphipods in this category are generally not very host specific and most are facultative symbionts. *Caprella acanthifera, Melita obtusata* and probably the as yet unstudied pleustid and *Lysianopsis* associations belong in this category.

This type of association is equivalent to that of clownfishes, porcelain crabs and spider crabs with sea anemones.

II. *Ectocommensals*

These amphipods live on the tentacles and oral disc of their host and feed primarily on host secretions, probably enriched with detritus and, in microphagous hosts, small prey animals. They usually do not penetrate into the gastrovascular cavity, although some apparently are able to do so with impunity. These amphipods spend their entire life cycle on their host.

To this category belong the amphilochid and stenothoid associates and probably also the leucothoids. Most stenothoids seem to be host-specific obligate symbionts, while the amphilochids and leucothoids have a low host specificity and are facultative.

This type of association is equivalent to that of many lichomolgid copepods on sea anemones (Briggs, 1976), to the stenothoids living among *Tubularia* polyps (Pirlot, 1932) and to the caprellids on starfish (cf. Vader, 1979).

III. *Endocommensals*

These amphipods live mainly in the gastrovascular cavity of their host and their main food is the semidigested prey of the sea anemone. In some cases the mucus secretions of the host mesenteria also may play a role in nutrition. The amphipods spend most or all of their lives inside their host, but in some cases the adults leave the host just prior to egglaying.

To this category belong the *Onisimus* species and *Orchomene recondita*, possibly also '*Orchomene*' sp. and *Aristias neglectus*, although the latter seems to be mostly microphagous. *Aristias* has a very low host specificity, while the others are obligate, host specific symbionts.

This type of association is roughly equivalent to the mouth-living isopods in fishes and the food-stealing lysianassids in the stomachs of starfish (cf. Vader, 1979, p. 131), although the latter apparently do not consort permanently with their hosts.

IV. *Micropredators*

These amphipods live on the column or in the burrows of sea anemones and feed on host tissues; their mouthparts are strongly modified to this end. It is uncertain whether they live permanently on their hosts or leave them periodically.

To this group belong the lysianassid amphipods in the genus *Acidostoma*. They do not seem to be very host-specific, but information is as yet very scanty.

This type of association is equivalent to that of the sea spiders of the *Pycnogonum* type on sea anemones.

There are also endoparasitic crustaceans, chiefly copepods, in sea anemones (cf. Bouligand, 1966; Vader 1970c; Humes, 1982), but this type of association does not seem to have an equivalent among the Amphipoda. This reflects the general rule that associated amphipods usually are morphologically less altered in their adaptation toward symbiosis than are Copepoda, Cirripedia or Isopoda. The endoparasitic copepods in sea anemones are so apomorphic that it has not yet been possible to find their proper place in the copepod classification system (cf. Gotto, 1979).

Caprella acanthifera and *Melita obtusata* are here considered to belong to category I on the strength of the published descriptions of these associations (Stroobants, 1969; Hartnoll, 1971). It should be kept in mind, however, that *M. obtusata* and a number of *Caprella* species also occur on starfish (cf. Vader, 1979) where they have been shown to derive a large part of their nutrition from the skin secretions of their hosts. Further research may show that also in the sea anemone symbionts mucus secretions are more important than hitherto assumed.

Although leucothoid and stenothoid amphipods often are found inside sponges and tunicates, and some species even live within the mantle cavity of bivalve molluscs and brachiopods (Vader & Beehler, in press; Vader, in prep.), on sea anemones these groups are mostly restricted to the tentacles and oral disc of their hosts and generally do not penetrate into the gastrovascular cavity, with the possible exception of *Metopa solsbergi* and *Stenothoe* sp. Lysianassid amphipods, on the other hand, are most often endocommensals.

ADAPTATIONS

Morphological adaptations

Clearcut morphological adaptations are only found in the micropredators in the genus *Acidostoma* which have their mouthparts clearly specialised for piercing and sucking (Dahl, 1964). Similar mouthparts are found in a number of related lysianassid genera, but their biology is as yet unknown.

An obvious adaptation, but one that is found in most associates of soft-bodied invertebrates, is the generally weak development of the armament of the distal parts of the pereopods and, with the exception of chemosensory setae, of the antennae. This no doubt decreases the chance of becoming entangled in mucus, apparently a real danger. I have repeatedly found specimens especially of *Orchomene recondita* so covered with mucus that they were unable to extricate themselves. The lysianassids use their second gnathopod in trying to remove mucus from the body, but these appendages do not deviate in any obvious way in either form or armaments in the associates of sea anemones.

The obligate amphipod symbionts of sea anemones belong to the leucothoid-stenothoid group of amphipods (the Leucothoidea of Bousfield, 1978) or the lysianassids (the Lysianassoidea of Bousfield, 1978). The Leucothoidea as a group are adapted (or preadapted) towards associations with soft-bodied, mucus-producing invertebrates. They are smooth-bodied animals with large, shield-like coxal plates and sparsely spinose antennae and pereopods. They also have specialised mouthparts, often with reduced mandibular molars and palps, and small, more or less fused maxillipedal plates. They usually feed on fine flocculant detritus, host secretions or the food of microphagous hosts. The species on sea anemones do not show any obvious special adaptations to these particular hosts.

The Lysianassoidea as a group are adapted toward a scavenging way of life, although they are very diverse in their feeding ecology. This group, which is generally considered to be plesiomorphic (Bousfield, 1978), is characterised by smooth bodies, short and stout antennae with many chemosensory brush setae (especially in the males), mouthparts adapted for biting and chewing large pieces of food, and a highly specialised gnathopod 2, used for grooming.

The large genera *Onisimus* and *Orchomene* s. l. are both made up mainly of species which are generalised free-living scavengers. *Onisimus* species are most common in arctic and subarctic shallow seas. The mouthparts of *Onisimus normani* do not deviate in any obvious way from those of its scavenging congener, *O. edwardsi* Kröyer.

Orchomene s. l. is bipolar arctic/antarctic and cold-temperate, in both shallow and deep water, with a number of species in the deep sea. The fine structure and functional morphology of the mouthparts of *Orchomene* species have recently been studied by Oleröd (1975) and Dahl (1979). Briefly, *Orchomene* s. l. are quite generalised lysianassids in the structure of their mouthparts. The incisor of the mandible is quite narrow and the molar triturative, and as a whole the mouthparts are well able to shear off, chew and process large food items, but without the extreme adaptations of specialised necrophages like the deep sea genera *Hirondellea* (Hessler *et al.* 1978; Dahl, 1979) or *Paralicella* (Dahl, 1979; Thurston, 1979).

In *Orchomene recondita* the mouthparts are of the generalised *Orchomene*-type, although differing in several details from *Orchomene* s. s. (Oleröd, 1975). The mandibular molar is triturative, but lacks a border of setae, and the triturative elements are quite flat. The incisor is short, smooth, convex and not very sharp. There is no excessive development of the proctodaeum for food-storage in *O. recondita*, such as is found in some specialised necrophagous *Orchomene* species (Dahl, 1979).

Physiological adaptations

Sea anemones are predators and they often feed on prey of the same size-range as the associates. Some type of adaptation is therefore necessary. As shown by Mariscal (cf. 1970) and Schlichter (cf. 1976) the fish symbionts of sea anemones go through a long and gradual acclimatisation process, in which they gradually become covered with the mucus secretions of the tentacles of their host. When completely 'camouflaged' they are no longer recognised by the sea anemones as something extraneous and can move among the tentacles at will. It is the prudence and perseverance of the fishes, and not any special physiological or biochemical characteristics of their skin, that result in the association becoming established, and the adaptations are therefore primarily behavioural.

With the exception of the somewhat aberrant hermit crab associations little research has as yet been carried out on the many decapod symbionts of sea anemones, but the available evidence suggests that also in these cases a similar protective mucus covering is acquired. Apparent acclimatisation behaviour has been described for spider crabs by Schrieken (1966). *Inachus phalangium*, on the other hand, does not, as far as is known, show acclimatisation behaviour (Hartnoll, 1971). There are also some indications that spider crabs, dropped upon the oral disc of sea anemones, elicit less forceful reactions than do *Carcinus* species (cf. Davenport, 1962; Hartnoll, 1971). It is not quite clear, however, whether the spider crabs used in these experiments were thoroughly cleansed of their slime-cover. There is some old evidence that certain hermit crabs possess immunity against the nematocyst toxin of their host (Cantacuzène, 1925; Rey, 1940), but I know of no recent research on this subject.

For amphipod symbionts no acclimatisation behaviour has been described and all the available evidence suggests that the adaptations for these associates are not primarily behavioural, but physiological and/or biochemical. Stroobants (1969) and Hartnoll (1971) have shown that the facultative associates *Caprella acanthifera* and *Melita obtusa* elicit far lesser reactions from the tentacles of the host than do free-living amphipods from the same biotope, but the possible presence of a protective mucus covering was not excluded by the experimental design.

Our own work has mainly been with the endocommensals *Aristias neglectus, Onisimus normani* and *Orchomene recondita* (Vader & Lönning, 1973, in prep.). When e.g. *O. recondita* is dropped on the oral field of its host *Anthopleura elegantissima* there is some reaction by the tentacles. As the amphipod actively crawls down into the stomodaeum, the role of the tentacles is hard to determine; however, dead or narcotized *O. recondita* are swallowed. Tidepool amphipods of the genus *Hyale* are caught and swallowed quickly by *Anthopleura*, but the isopod *Exosphaeroma inornatum* Dow, which is often found among the debris surrounding the sea anemones, elicits less reaction and usually manages to escape. *Onisimus normani* is caught and swallowed by its host *Bolocera tuediae* in exactly the same way as prey animals.

The nematocysts of these sea anemones stun their prey animals, making it possible for the mesenterial filaments to adpress closely, but they usually do not kill them outright. If *Hyale* specimens are retrieved shortly after having been swallowed, they usually recover.

In order to separate the effect of the nematocyst toxin from that of the secretions of the mesenterial filaments, amphipods and isopods of different species were tied in cloth or nylon gauze bags and pushed directly into the gastrovascular cavity. After 6–9 hours, the free living amphipods and isopods were invariably dead, fragmented and often more or less digested, while there was no appreciable mortality among the symbionts. This 'immunity' is not confined to the proper host, but exists in all other sea anemones tested.

Extracts of the mesenterial filaments of *Bolocera tuediae* were tested in a series of bioassays, using *Aristias neglectus, Onisimus normani* and free-living Lysianassidae (Vader & Lönning, 1973). The results showed that under these circumstances, where behavioural responses were completely ruled out, *Aristias* and *Onisimus* survived quite high concentrations of the extracts, while the free-living lysianassids were invariably killed.

The secretions of the mesenterial filaments contain at least three substances: nematocyst toxin (but extracts of the tentacles were not toxic), mucus substances secreted by at least two different types of mucus cells, and proteolytic enzymes (Vader & Lönning, 1975). Further bioassays made it highly probable that the toxicity of the extracts was primarily caused by their proteolytic enzymes (Vader & Lönning, 1973).

The specimens of *Aristias neglectus* used in these experiments had been collected from sponges and had probably never been in contact with sea anemones. Nevertheless, tolerance of these amphipods to the extracts was very high. This tolerance thus appears to be genetically determined and is not acquired during the life of the individual.

The mechanism of this 'immunity' is, unfortunately, still unknown. Briggs (1978) has recently published a study of the fine structure of the integument of *Paranthessius anemoniae*, a copepod associate of sea anemones. He discovered subcutaneous glands opening through pores in the cuticle that appeared to secrete substances that he claimed may be responsible for the immunity of *Paranthessius* to the nematocysts of their host. Such cuticular pores also exist in *Orchomene recondita* and the fine structure of its cuticle is under further study.

Reproductive adaptations

Many endocommensal decapods have enlarged abdomens and thus higher fecundity than free-living relatives of the same size (cf. Patton, 1967). The same is true for parasitic and commensal copepods (Gotto, 1962, 1979).

The endocommensal amphipod *Orchomene recondita*, on the other hand, has a low fecundity compared to free-living amphipods of the same size (c. 5 mm): each female produces 2–3 broods of only 8–15 young each (Vader & Lönning, in prep.). *Onisimus normani* has a two-year life-cycle and probably only a single brood of eggs. The ectocommensal *Stenothoe brevicornis* has 7–15 eggs per brood (Vader, in prep.), less than the far smaller *S. monoculoides* (Montagu) (cf. Krapp-Schickel, 1976), but the number of broods is still unknown.

The low fecundity of the symbiotic amphipods is probably made possible by the protection afforded by the host. Moreover in *O. recondita* the reproductive season of the amphipod coincides with the period of maximum asexual reproduction of *Anthopleura elegantissima*.

The sex ratio in those investigated more closely, viz. *Onisimus normani, Orchomene recondita* and *Stenothoe brevicornis*, does not deviate significantly from 1:1, although males of *O. recondita* die slightly earlier than females. In the lysianassids the females are only a little larger than the male, while the difference is more clearcut in *Stenothoe*. In other *Orchomene* species, *O. gerulicornis* and *O. cavimanus*, the sex-ratio is clearly skewed in favour of the females and the females are markedly larger than the males (Thurston, 1979). Thurston explained this as an expression of the greater energy involvement of the double-brooded *Orchomene* females (compared to single-brooded genera with normal sex ratio). However, *O. recondita* also produces several broods.

Bousfield (1978) has discussed plesiomorphic and apomorphic characters in the Amphipoda. Among the important primitive characters present in the Lysianassoidea he enumerated the presence of terminal pelagic males, calceoli, and coxal gills on pereopod 7. Many *Orchomene* species do have such calceolate terminal males, but *O. recondita* shows very little sexual dimorphism, is acalceolate and lacks a coxal gill on pereopod 7. It is possibly the most apomorphic species in *Orchomene* s.l. Sexual dimorphism is also very slight in *Onisimus normani* and much less obvious than usual for the genus in *Stenothoe brevicornis*.

RELATIONS BETWEEN AMPHIPOD AND HOST

Host specificity

Of the four groups used in the preliminary classification of amphipod associates of sea anemones (see p.146), the amphipods in categories I and IV do not appear to be strongly host specific. Among the commensal symbionts in categories II and III *Orchomene recondita* and *Stenothoe brevicornis* are strongly host-specific. *Onisimus normani* is almost exclusively found on *Bolocera tuediae* in western Norway (Vader, 1970b), but is much less host-specific in northern Norway, although the same sea anemone species occur in both areas. *Aristias neglectus* has been found on only one species of sea anemone, but this species also inhabits a wide spectrum of other invertebrates (cf. Vader, 1979). For most partnerships, the available data are not sufficient to allow any conclusions.

The strongly host-specific Lysianassidae are also able to survive for considerable periods in alternate hosts, if given no choice. *Metopa solsbergi*, on the other hand, was eaten 'without hesitation' when tested on an alternate host, *Tealia felina* (Elmhirst, 1925).

Preliminary experiments designed to test distant host location of *Anthopleura elegantissima* by *Orchomene recondita* have hitherto given inconclusive results. When visual and tactile clues are also available, *O. recondita* strongly prefers its own host in aquarium tests (Vader & Lönning, in prep.).

Variations in host infection

Many amphipod associates do not inhabit their sea anemone host throughout the latter's geographical and ecological range. Although *Anthopleura elegantissima* is a common sea anemone from southern Alaska to northern Mexico (Hand, 1955), *Orchomene recondita* has hitherto only been found at a few sites near San Francisco, in spite of several attempts to collect it further south (Barnard, 1969a; Vader & Lönning, unpubl.). In the San Francisco area *O. recondita* has a much more restricted ecological distribution than its host, being absent from exposed sites and from sand-embedded colonies of the host (Vader & Lönning, in prep.).

Onisimus normani occurs in western Norway in *Bolocera tuediae* at depths of 200–700 m, but not in shallower water, and in some fjords it seems to be absent altogether, in spite of the common occurrence of its host at appropriate depths (Vader, 1970b, in prep.).

There may also be large variations through time in infection rate. Mean incidence of infection of *Bolocera* with *Onisimus* in deep fjords in western Norway was, from 1967–1970, c. 3 amphipods per host. In 1970–1977 the mean incidence of infection was as low as 0.01 amphipods per host.

Effects on host

In no case do the amphipods seem to have any appreciable effect on the vitality or reproduction of the host. This is in spite of the fact that the total symbiont load may be appreciable. I have found *Aristias neglectus* and *Onisimus normani* within the same specimen of *Bolocera tuediae*, which also was heavily infested by the large endoparasitic copepod *Antheacheres duebeni* (Vader, 1970 b, c). In northern Norway *Actinostola callosa* may hold both *Onisimus normani* and *Stenothoe brevicornis*, and in California *Anthopleura elegantissima* is often host to both *Orchomene recondita* and the lichomolgid copepod *Metaxymolgus confinis* (Lönning & Vader, in prep.).

GENERAL CONCLUSIONS

Associations between amphipods and sea anemones are probably quite common, although as yet little known. They occur in arctic, temperate and tropical waters, and from the intertidal zone to depths of at least 1000 m.

When we compare the amphipod fauna of sea anemones with that of echinoderms (Vader, 1979) the most striking difference is the prominence of the Leucothoidea which are virtually unknown as echinoderm symbionts. The two faunas agree, however, in being very diverse, thus having evolved independently many times, and in not having developed dramatic morphological adaptations. Thus, although the sea anemones are among the oldest known multicellular groups and the amphipods may be of much greater antiquity then previously thought (cf. Dahl, 1977, 1979; Schram, 1979), symbiotic associations between the two groups show no evidence of great evolutionary age.

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BIOGEOGRAPHY AND ECOLOGY OF AUSTRALIAN ANOSTRACA (CRUSTACEA: BRANCHIOPODA)

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SUMMARY

Three anostracan genera occur in Australia, the native genera *Branchinella* and *Parartemia* and the introduced genus *Artemia*. The nineteen described species of *Branchinella* include some that are widely distributed within Australia, especially *B. australiensis,* and others of local occurrence. Of the eight species of *Parartemia* five occur in south-western Australia, one occurs across southern Australia, another is found in the south-east, and one occurs in the north-east. *Branchinella* species usually occur in ephemeral freshwater pools while *Parartemia* is halobiont, but some species from both genera occur in brackish water. Cladocerans and calanoid copepods generally occur with *Branchinella* and notostracans and conchostracans are often present. *Parartemia* generally occurs with halobiont copepods and ostracods. Some samples contained more than one species of *Branchinella* but there were no co-occurrences of *Parartemia* species. The Australian anostracan fauna is compared with that from other continents and factors influencing the distribution of anostracans are discussed.

Introduction

Three genera of Anostraca occur in Australia, the genera *Branchinella* and *Parartemia* established for Australian material by Sayce (1903) and *Artemia* Leach. *Parartemia,* in the family Branchipodidae, is an endemic genus and is most closely related to the freshwater genus *Branchipodopsis* which is distributed in arid regions of Africa and Asia (Linder, 1941). *Branchinella,* in the family Thamnocephalidae, occurs in Africa, America, Europe and Asia, although most species (19 of 26 described) are Australian (Fig. 1). Other genera in the Thamnocephalidae, *Thamnocephalus* and *Dendrocephalus,* occur in central and South America and Linder (1941) suggests that *Branchinella* may also occur in South America. Australian species of *Branchinella* are endemic. The taxonomy of *Artemia,* family Artemiidae, is presently confused, with what was once considered a single cosmopolitan species now recognised as several sibling species separated on biochemical and chromosomal characters (Bowen *et al.,* 1978). The populations in Australia will, therefore, be referred to as *Artemia* sp.

The taxonomy of the Australian Anostraca is relatively well studied. Linder (1941) revised previous work and described seven new species of *Branchinella* and six new species of *Parartemia,* bringing the number of Australian species in the two genera to nineteen and seven respectively. Since then four new species of *Branchinella* have been described, three others put into synononymy and one declared *nomen dubium* (Geddes, 1981), one new species of *Parartemia* has been described (Geddes, 1973a) and the occurrence of *Artemia* in Australia has been documented (Geddes, 1979). However, other aspects of the biology of the Australian Anostraca are poorly known. This paper aims to show the distributions of the various genera and species in Australia and to discuss their biogeography. Some aspects of anostracan ecology will also be considered.

Distribution

The distribution of the various species of *Branchinella* within Australia is shown in Figure 2. Several species are widely distributed (Fig. 2A): *B. lyrifera* and *B. probiscida* in central Australia, *B. occidentalis* in central and western Australia, *B. frondosa* and *B. affinis* in south-eastern and south-western Australia

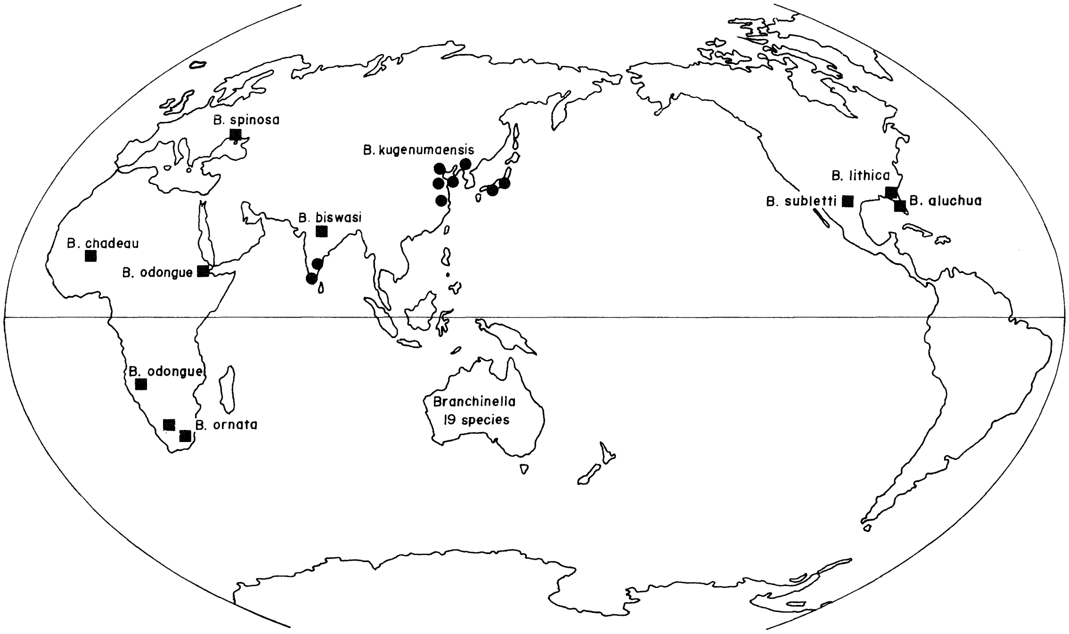

Fig. 1. Distribution of the various species of *Branchinella.*

and *B. australiensis* from most of the continent. Several other species appear to have restricted distributions (Fig. 2B): *B. longirostris* in south western Australia, *B. latzi* in central Australia and *B. compacta* in south eastern Australia. The remaining five species (Fig. 2C) have been collected only once or twice and are probably of local occurrence; all are from Western Australia.

The distribution of *Artemia* and the various species of *Parartemia* is shown in Fig. 3. All *Artemia* collections are from coastal ponds that presently are, or previously were, used for salt production. Two groups of populations are identifiable. Those in the west are parthenogenetic and electrophoretic studies show them to be closely related to parthenogenetic populations in Asia, Europe and Africa (Bowen *et al.,* 1978), while those in Queensland reproduce sexually and are electrophoretically identical to populations from Great Salt Lake, Utah and San Francisco Bay, California (Bowen *et al.,* 1978). The Western Australian populations probably arrived with European man, and those in Queensland certainly represent inoculations of commercial *Artemia* eggs from the U.S.A. (Geddes, 1980). The origin of the single population in South Australia is obscure.

Species of *Parartemia* occur in all of the series of natural salt lakes that have been studied (Fig. 3). In Western Australia there are 6 described species, and two undescribed species also occur (Geddes *et al.,* 1981). Most of these species have fairly restricted distributions and there is little overlap between the three most commonly occurring species, *P. informis* in the north, *P. serventyi* near Kalgoorlie, and *P. longicaudata* in southern coastal areas. One species, *P. cylindrifera,* occurs in south-western Australia and south-eastern South Australia, although it is apparently absent from Victoria and Tasmania. The common species in south-eastern Australia is *P. zietziana* while *P. minuta* is known from one locality, L. Buchanan, in Queensland.

The distribution maps (Figs 2 and 3), when considered together, point to shortcomings in the collecting of Australian anostracans. As might be expected the group is generally restricted to arid and semi-arid regions, with no anostracans known from the tropical north of Australia and only a few collections from the relatively well watered island of Tasmania. However the absence of anostracans from large areas of apparently suitable habitat in central and north-western Australia is a reflection of incomplete sampling. Australia does not appear to have any Anostraca adapted to pools that freeze in winter and are available to aquatic animals in summer, although small areas in which these habitats

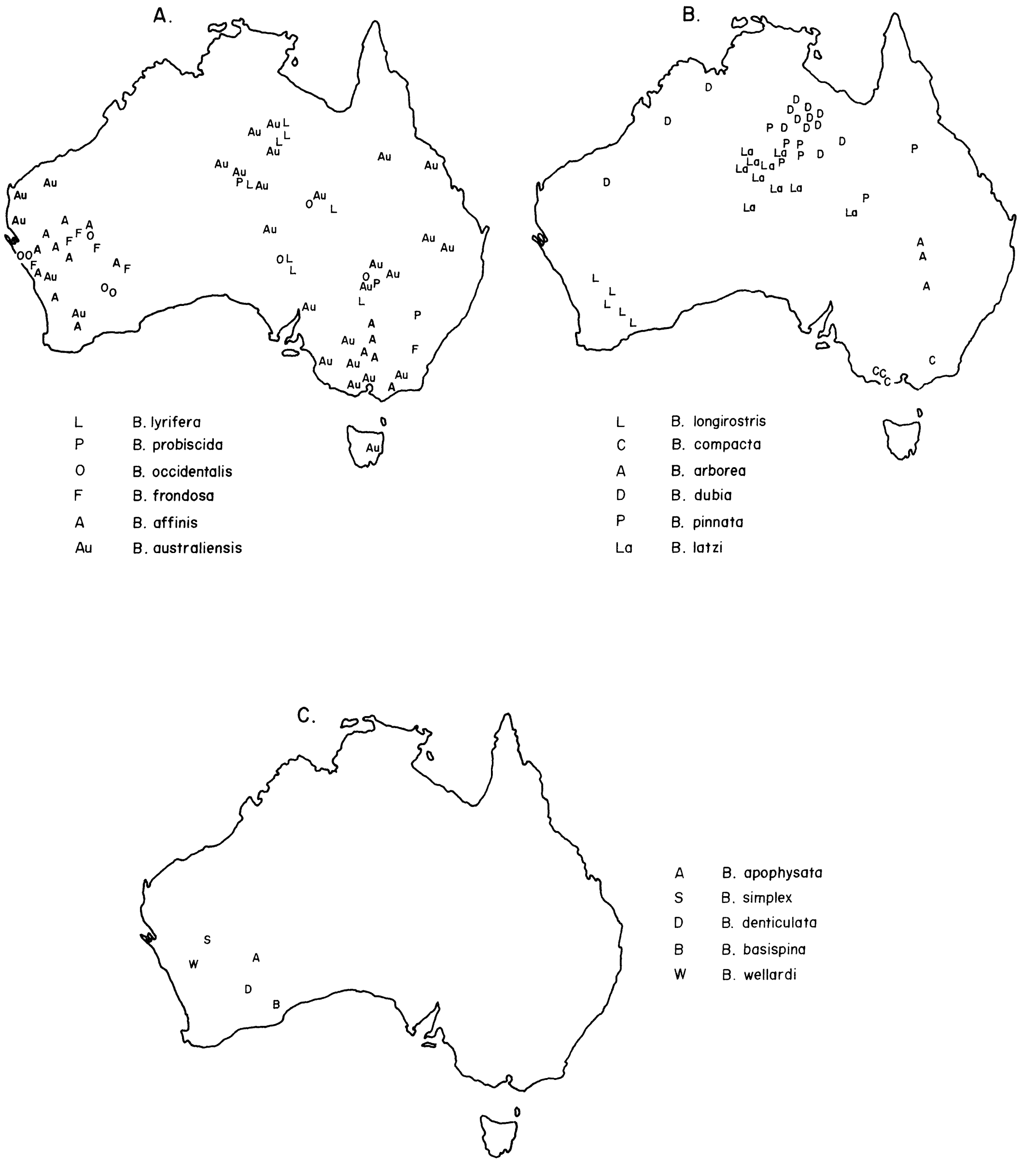

Fig. 2. Distribution of the Australian species of *Branchinella.*

occur do exist in the Australian Alps and in Tasmania. In the northern hemisphere many species and some genera occur in, and are restricted to, such environments (Pennak, 1978).

Ecology

Branchinella species typically occur in small (<2 ha), shallow (<1 m) temporary pools that persist from two to ten months, although some records are from permanent but very astatic pools. In northern

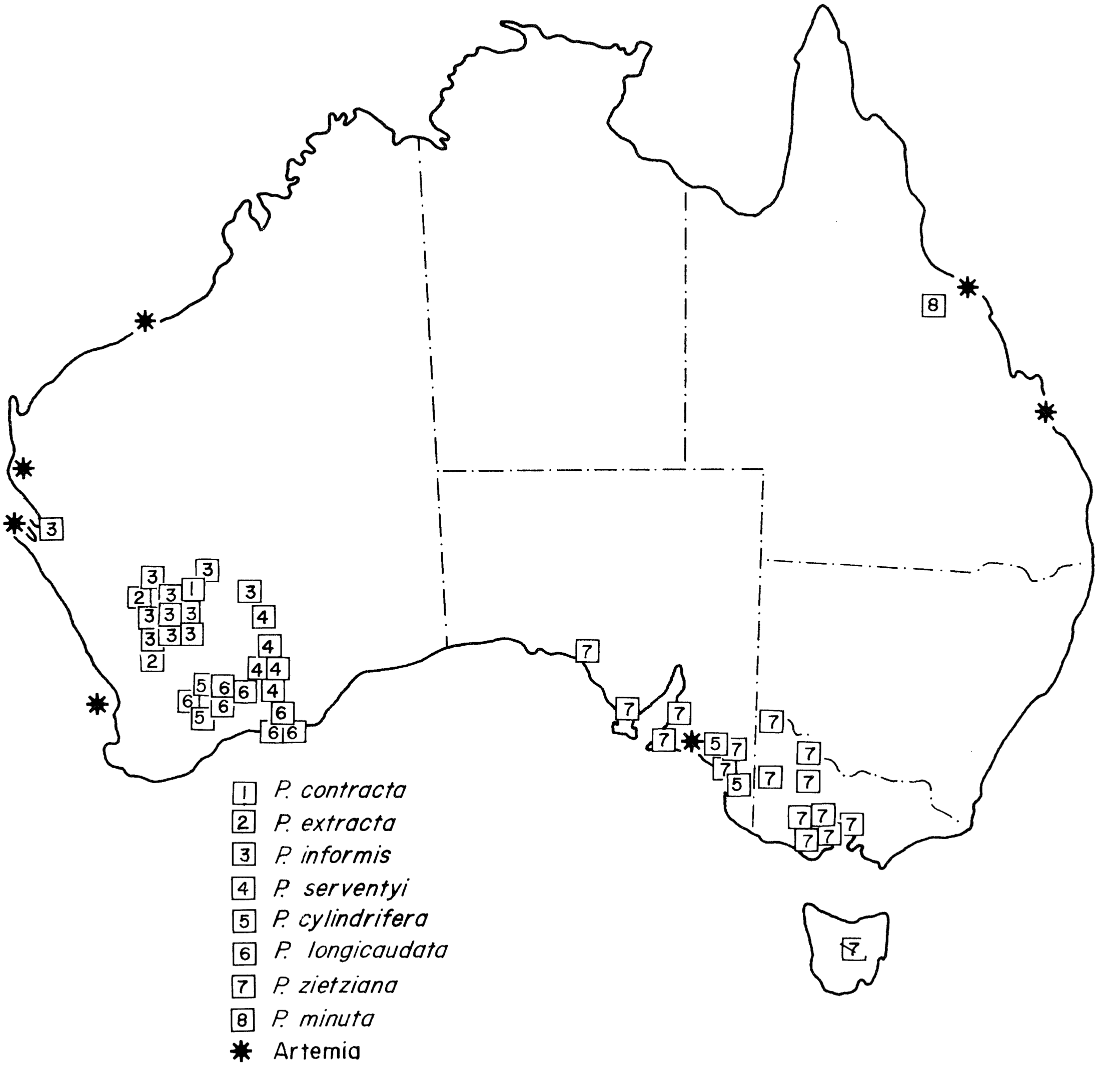

Fig. 3. Distribution of *Artemia* sp.(*) and the various species of *Parartemia* (□) in Australia.

Australia, where temperatures and evaporation rates are particularly high, *Branchinella* spp. were collected from considerably deeper (to 4 m) and larger (to several hundred ha) pools. In fact, in the north anostracans were generally absent from small shallow pools possibly as they were too short-lived. *Branchinella* habitats are usually turbid and have considerable diurnal fluctuations in temperature. Fish are usually absent but may be present in habitats that are formed by river flooding. Some examples of environments from which *Branchinella* has been collected are roadside ditches, claypans, natural depressions on volcanic or clay soils, temporary farm dams, temporary lagoons beside streams, and pools in the channels of intermittent streams (especially in northern and central Australia).

Parartemia typically occurs in ephemeral saline lakes which are less than 1.5 m deep when full and covered by a salt crust when dry. Some localities (e.g. Pink L., western Victoria) do not dry out every year but do have wide fluctuations in salinity and occasional desiccation. However, *Parartemia* does not occur in the more eustatic salt lakes in western Victoria (Geddes, 1976). *Parartemia* localities vary greatly in surface area from less than 1 ha to very large playa lakes like L. Monger and L. Moore in Western Australia.

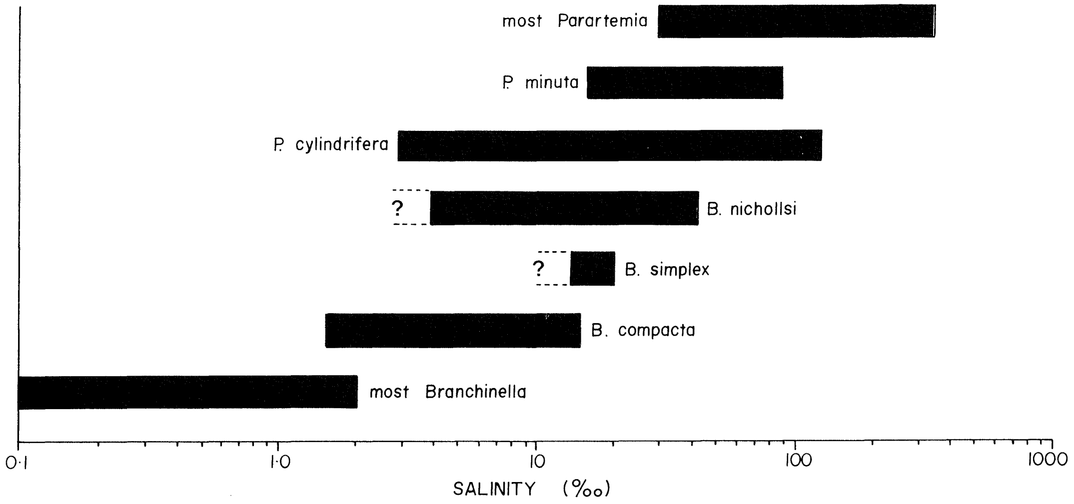

Fig. 4. Field salinity ranges for various species of Australian Anostraca.

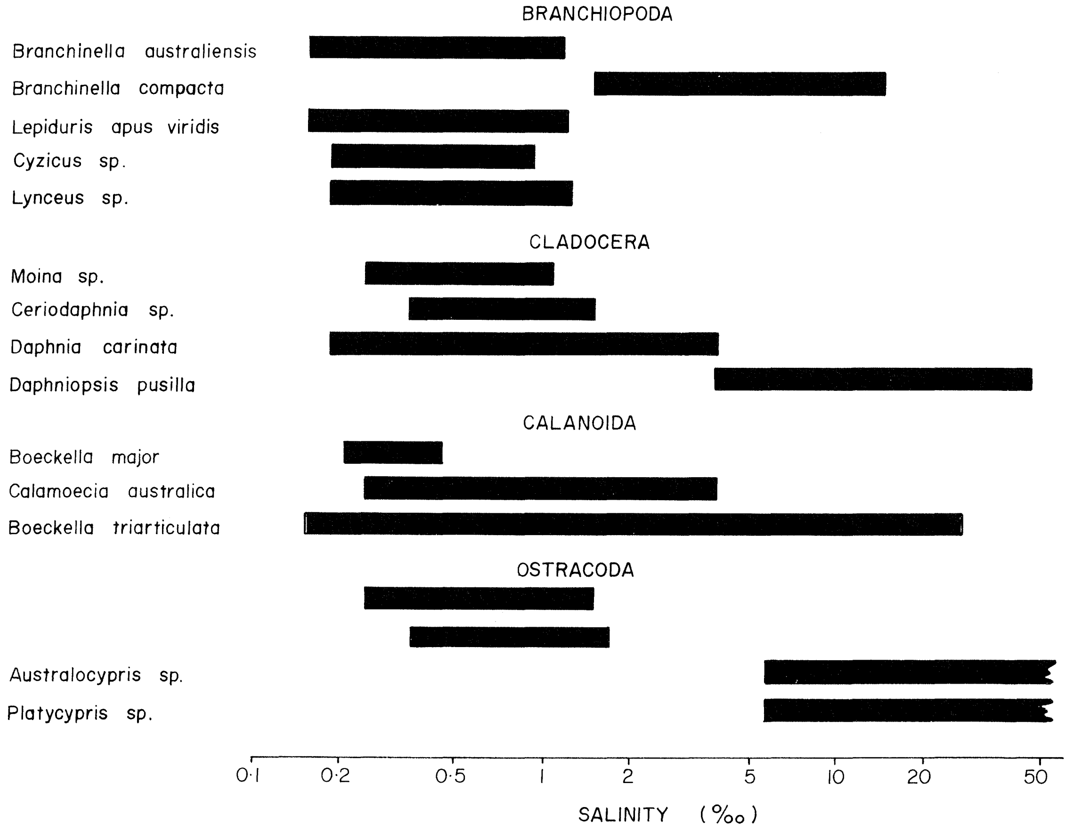

Fig. 5. Field salinity ranges for various crustaceans in temporary pools in western Victoria.

The field salinity ranges for the various species of Anostraca in Australia are shown in Fig. 4. Basically, *Branchinella* is a freshwater genus and *Parartemia* is halobiont. However at least three species of *Branchinella, B. compacta, B. simplex* and *B. nichollsi,* show tolerance to intermediate salinities and *P. minuta* and *P. cylindrifera* penetrate to slightly saline water. In L. Buchanan, Queensland, *B. nichollsi* occurred with *P. minuta* at salinities of 15.7 and 42.6°/oo (Geddes, 1973a). A similar mixture of stenohaline freshwater and euryhaline species of anostracans was reported by Hartland-Rowe (1966) in the temporary waters of western Canada.

Tables 1 and 2 show the fauna collected in association with several anostracans and so provide descriptions of the communities of ephemeral waters. Several studies have been made on the fauna of ephemeral saline lakes (Geddes, 1976; De Deckker and Geddes, 1980; Geddes *et al.,* 1981) and so the communities associated with *Parartemia* are well known. However little work has been done on ephemeral freshwaters and the only published record of communities containing *Branchinella* is by Morton and Bayly (1977).

Table 1 shows the fauna collected with several species of *Branchinella* in western Queensland and the Northern Territory, with *B. australiensis* in three areas in south-eastern Australia and with *B. compacta* in western Victoria. In all cases the communities were dominated by crustaceans, especially cladocerans and calanoid copepods. *Daphnia* (generally *D. carinata* s.l.) and *Boeckella* (generally *B. triarticulata*) almost always occurred with species of *Branchinella.* Notostraca and Conchostraca often occurred but they were not always present, and were usually absent in the larger, deeper *Branchinella* habitats in Queensland and the Northern Territory. A restricted fauna occurs in the slightly saline pools inhabited by *B. compacta* and presence of particular species appears to depend on salinity. The salinity range of *B. australiensis* and *B. compacta* and their associated faunas in western Victoria is shown in Figure 5. *Daphniopsis pusilla, Boeckella triarticulata* and ostracods make up the halophilic community associated with *B. compacta.*

The fauna collected with various species of *Parartemia* is shown in Table 2. *Parartemia zietziana* in south-eastern Australia and the halobiont species of *Parartemia* in Western Australia occur with halobiont copepods and ostracods. *P. cylindrifera* in South Australia occurs in pools with a much wider range of species including the cladoceran *Daphniopsis pusilla,* the amphipod *Austrochiltonia australis,* the isopod *Haloniscus searlei,* the gastropod *Coxiella* sp., and a polychaete worm. These pools generally have rich beds of the aquatic grasses *Ruppia* and *Lepilaena.*

Many of the localities sampled contained more than one species of *Branchinella.* Some co-occurrences are listed in Table 3. Most co-occurrences are of a large species, *B. australiensis* or *B. occidentalis,* with a smaller species, and it may be this size difference that makes co-existence possible. No co-occurrences of *Parartemia* species are known, although the distributions of several species in Western Australia overlap. A *Parartemia* species does co-occur with a species of *Branchinella* in at least one locality.

Discussion

Perhaps the most notable features of the Australian anostracan fauna are the low diversity at the generic level and the high degree of endemism. Whereas only two anostracan genera occur naturally in Australia, ten are known in North America (Belk, 1975), ten in Europe (Daday, 1910) and five in South Africa (Barnard, 1929). No Australian anostracan species occur outside Australia, and the otherwise cosmopolitan genus *Artemia* was apparently absent from the continent before the arrival of European man. Low diversity of higher taxonomic categories and high endemism are well known phenomena in Australia, but are somewhat surprising in a group of the age and supposedly high dispersal ability of the Anostraca. It should be recognised that the Australian anostracan fauna is isolated by climatic barriers as well as geographic ones, as no suitable environments exist in tropical northern Australia or in New Guinea and south-east Asia to allow movement of anostracans into Australia from Asia. Several authors (e.g. Bishop, 1967; Belk and Cole, 1975) have suggested that the dispersal ability of phyllopods may not be universally high. The world-wide distribution of *Branchinella* suggests that it is a very old genus which may have dispersed when geographic and climatic conditions were more favourable.

It is interesting to contrast the high degree of speciation in the Australian brine shrimp *Parartemia,* with the situation in *Artemia* where populations throughout the world are morphologically alike, although genetically somewhat different. *Artemia* is unusual among anostracans in that its resistant eggs generally float and are blown to the edge of lakes from where they are easily dispersed by wind and/or birds. The eggs of *Parartemia,* like those of most anostracans, sink and are bound up in the sediments of the lake, thus limiting their chances of dispersal.

Table 1. Zooplankton with species of *Branchinella* in various parts of Australia. (M) present in many localities; (F) few localities; (S) single locality; (X) only one or two localities investigated, and so no estimate of frequency of occurrence.

Taxa	*Branchinella* Qld. & N.T.	*B. australiensis* Carrieton, S.A.	*B. australiensis* western Victoria	*B. australiensis* Gippsland, Vic.	*B. compacta* western Victoria
Branchiopoda					
Cyzicus	F	X	M		
Eulimnadia	S				
Lynceus	F		M	X	
Triops	F				
Lepidurus		X	F	X	
Cladocera					
Daphnia	M	X	M	X	F
Moina	M		F		
Diaphonosoma	F	X			
Ceriodaphnia			F		F
Daphniopsis					M
Saycia				X	
Neothrix	S				
Alona				X	
Biapertura				X	
chydorids	F		M		F
Copepoda					
Boeckella	M	X	M	X	M
Diaptomus	M				
Hemiboeckella				X	
Calamoecia	M	X	F		S
Mesocyclops	M	X	M	X	
Microcyclops			F	X	
Attheyella				X	
Other				the following	
rotifers	F		M	ostracods:	
ostracods	F		M	*Newnhamia*	M
notonectids	M	X	M	*Cypretta*	F
corixids			F	*Cypris*	F
dytiscids	M	X	M		

In Australia anostracans occur more commonly in warm, arid and semi-arid areas than in cooler well-watered ones. Thus of 53 temporary freshwater pools in coastal eastern Victoria only three contained anostracans (Morton and Bayly, 1977), while they were present in most temporary pools investigated in the Northern Territory and western Queensland.

The distribution of anostracan species appears to be related to temperature and water chemistry (Belk, 1977; Hartland-Rowe, 1966), and also to other factors such as chance and food availability (Daborn, 1978). The effect of salinity on the distribution of Australian species is clearly shown in Figure 4. The restriction of some species of *Branchinella (B. dubia, B. latzi, B. pinnata)* to northern Australia where rainfall coincides with high temperature, and others *(B. compacta, B. longirostris)* to winter rainfall areas in southern Australia may be the result of temperature-dependent egg development as shown by Belk (1977).

The diversity of anostracans in any one area has been related to the chemical heterogeneity among habitats, especially in relation to salinity, and thermal variation resulting from ponds refilling in different seasons and from distribution of ponds along altitudinal and latitudinal gradients (Belk, 1977). In Australia the effect of variation in salinity on species diversity is clearly seen. In western Victoria three species of anostracan occur, with *B. australiensis* in fresh pools (<1°/oo), *B. compacta* in adjacent slightly saline pools (2-15°/oo) and *P. zietziana* in highly saline pools (Geddes, 1973b, 1975). In the

Table 2. Zooplankton with species of *Parartemia* in various parts of Australia. (M) present in many localities; (F) few localities; (S) single locality; (X) only one locality investigated.

Taxa	*P. zietziana* western Victoria	*P. zietziana* South Australia	*Parartemia* spp. Western Australia	*P. cylindrifera* South Australia Qld.	*P. minuta* L. Buchanan,
CLADOCERA					
Daphniopsis				M	
COPEPODA					
Calamoecia	M	M	F	M	
Boeckella				S	
Microcyclops	M	M	M	M	
Apocyclops					X
Mesochra	M	M		M	
Schizopera				S	
OSTRACODA					
Platycypris	M	M	M	M	
Diacypris	M	M	M	M	
Australocypris	M	M	M	M	
Reticypris		M	M	M	
Mytilocypris				F	
Limnocythere				S	
OTHER					
	Ephydrella S chironomid S		*Coxiella* F	*Austrochiltonia* M *Haloniscus* F *Coxiella* M polychaete F	*Branchinella*

Table 3. Co-occurrences of species of *Branchinella*.

locality	species present
Brunette Downs, N.T.	*B. lyrifera, B. dubia, B.* sp., *B. australiensis*
Hatches Ck Mine, N.T.	*B. pinnata, B.* sp., *B. australiensis*
Napperby Station, N.T.	*B. latzi, B.* sp., *B. australiensis*
Alice Springs, N.T.	*B. pinnata, B. australiensis*
Mt Doreen Station, N.T.	*B. latzi, B. australiensis*
Tenant Creek, N.T.	*B. dubia, B. australiensis*
nr Prairie, Qld.	*B. dubia, B. australiensis*
nth Barringun, Qld.	*B. arborea, B. australiensis*
L. Buchanan, Qld.	*Parartemia minuta, B. nichollsi*
nr Stratford, Vic.	*B. affinis, B. australiensis*
claypan nr L. Eyre, S.A.	*B. lyrifera, B. occidentalis*

Coorong region of South Australia a similar pattern occurs except that *P. cylindrifera* occupies the pools of intermediate salinity (De Deckker and Geddes, in press). The greatest diversity of Anostraca in Australia is found in Western Australia with 11 species of *Branchinella* and 6 species of *Parartemia* recorded. At least three factors appear to be operating to produce this diversity: (1) there is considerable variation in the salinity of the waters, (2) the semi-arid region extends over a considerable latitudinal gradient and is affected by both winter rain from the south-west and summer rain from the north, resulting in ponds filling under various thermal conditions, (3) the area is one of long continued geological stability and aridity (van de Graaff *et al.,* 1977). The first two factors provide habitat heterogeneity, while the third provides the time necessary for speciation to proceed within the area.

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REVISION OF THE CALAPPIDAE

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SUMMARY

The brachyuran Calappidae *sensu* Balss (1957) is composed of three subfamilies, Calappinae, Matutinae and Orithyinae. However, an examination of the history of the comprehension of these three groups shows that they have been interpreted in various ways. From critical re-examination of Balss's diagnosis and from reconsideration of all available data, it can be concluded that because of the considerable differences in shape, structures and functions of adults and larvae, as well as their mode of life, these three groups, in spite of their several similarities, are not closely related, as believed before, and therefore their unity on a higher systematic level is questionable. The available data permits the conclusion that these three groups form separate well-delimited families, as originally stated by Ortmann (1892), i.e., Calappidae De Haan, 1833, Matutidae De Haan, 1833, and Orithyiidae Dana, 1852.

Introduction

As with all animal taxa, the brachyuran family Calappidae (*sensu* Balss, 1957), has been interpreted systematically in various ways. Comprehension of its status and position has varied from author to author. The group has been considered to be either a family or a superfamily, and it is interesting that for more than 140 years its sub-groups have been classified together, implying their close affinity. Because of increasing overall knowledge of crab biology, as well as theories of systematics and evolution, it is necessary from time to time to re-examine earlier concepts and test their conformity to modern views of science. Accordingly, I here present a solution of the problem posed by the calappids.

Balss (1957), in the last great monograph on decapod Crustacea, included in the family Calappidae Alcock, 1896 three subfamilies: Calappinae Alcock, 1896; Matutinae Alcock, 1896; Orithyinae Ihle, 1918. However, neither all previous authors, nor all subsequent ones, have invariably accepted such a classification, and so it is better at the outset to give a historical review of the knowledge of these groups from a systematic point of view.

The first classification of higher taxa that included calappids as such was that of de Haan (1833), who distinguished within the Oxystomata two relevant families, Calappidea and Matutoidea. Shortly after, H. Milne Edwards (1837) distinguished within the Oxystomata the tribe Calappiens comprising of the genera *Calappa, Platymera, Mursia, Orithyia, Matuta* and *Hepatus*. Macleay (1838) united the families Calappidae and Matutidae into one systematic unit—stirpe Calappina. Dana (1852) distinguished again within the subtribe Leucosoidea two relevant families, Matutidae and Calappidae, with two subfamilies within the latter, Calappinae and Orithyinae. Miers (1886) accepted the classification of Dana and further divided Matutidae into two subfamilies, Matutinae and Hepatinae. Ortmann (1892) established the subdivision Calappinea, composed of three families: Calappidae, Matutidae, and Orithyidae. Alcock (1896) united all these groups into a single family Calappidae, with two subfamilies, Calappinae and Matutinae; the subfamilies of Miers thus were reduced to the status of alliances, i.e. Calappoida, Orithyoida, Matutoida and Hepatoida. Later, Ortmann (1901) subdivided the Calappidae into three subfamilies: Calappinae, Orithyinae and Matutinae. The latter classification was accepted by Borradaile (1907), Ihle (1918), and Balss (1957), as mentioned before. It is noteworthy that Ihle, after detailed morphological analysis, although accepting the latter classification, has expressed a doubt about the inclusion of *Orithyia* within Calappidae. Glaessner (1969) first used the category of superfamily, Calappoidea, for this group, but included in it only the family Calapppidae, with two subfamilies, Calappinae and Matutinae. Recently Guinot (1978) has radically revised this group, excluding from it *Hepatus* and allied genera, and has included in the superfamily Calappoidea two families, Orithyiidae and Calappidae, the latter composed of Calappinae and Matutinae. Most of the authors have placed these families in Oxystomata, either at the beginning or at the end of the brachyuran system. Only Guinot (1978) has rejected the Oxystomata as a taxon, and has established her own classification in which Calappoidea are placed in Heterotremata, and at the beginning of the phylogenetic scheme, following only Dorippoidea.

Having considered the historical development of the conceptions of the group, we can now pass to analysis of similarities and differences, and then set down a conclusion.

The unity of the groups considered is based on their common characters, which are as follows: front narrow; orbits incomplete; antennulae obliquely plicated; antennal basal article large; antennal flagella reduced in size; endostome elongated and epistome very much reduced; exostegal channel (formed by pterygostome and chelipeds) exists; inhalant respiratory openings in the front of the basis of the chelipeds; coxae of Mxp$_3$ enlarged on basis and placed on the entrance of inhalant opening; exhalant respiratory opening near and beneath the front; endopodite of first maxilliped forms the ventral floor of the exhalant channel; chelipeds pressed tightly against the anterolateral part of the carapace; male abdomen composed of 5 segments (3–5 fused), that of the female of 7 segments; sterno-abdominal cavity well developed; male sexual opening coxal; first pair of male pleopods with simple top; second pair of male pleopods long; female sexual opening sternal; 9 branchiae on each side.

Moreover, there are also similarities between the particular groups when considered in pairs:

Calappa–Matuta. (Pseudo)rostrum absent; orbital fissures present; supra-orbital tooth absent; antennulo-orbital septum present; antero-lateral spines absent (in some genera epibranchial spine present); longitudinal respiratory gutter on the endostome present; last part of the exhalant channel covered by the elongated endopodite of the third maxilliped; retaining mechanism of the abdomen present.

Matuta—Orithyia. Merus of third maxilliped elongated and acute; palp of the exopod of the third maxilliped absent; inhalant opening at the ocular cavity; last pair of walking legs paddle-like; sternum flat and rounded; episternites present; a part of 8th sternite visible from above.

Orithyia—Calappa. Third maxilliped does not cover completely the mouthparts; palp of third maxilliped not concealed by merus joint.

In order to better illuminate the similarities and differences between the three groups, we shall here adopt the method of considering some parts of the body as morphological- physiological and adaptive unities, since the shape of an organism depends, according to Hadži (1944), upon its organisation, (macro) habitat and mode of life. But at the outset it must be noted that although the mode of life of *Calappa* and *Matuta* is known to some degree, that of *Orithyia* is completely unknown. Concerning the habitat, all three groups occur mostly in shallow littoral waters, sometimes in tidal flats; exceptionally, some calappids enter deeper waters. They usually occur on sandy or sandy-muddy bottoms, with or without sea grass (Klunzinger, 1906; Thomassin, 1974; Mergner and Schumacher, 1974; Seidel, 1976; Hong, 1976; Basson et al., 1977).

Insofar as the mode of life includes the mode of locomotion, feeding, respiration, defence, reproduction, orientation and regulation (Števčić, 1974), we shall be able to analyse only some of these, but the data should be sufficient to show the principal similarities and differences important for our considerations.

Respiration

The mode of respiration is very different in these groups.

Calappa

The respiration of *Calappa* was described in detail by Garstang (1897). The direction of respiratory currents is very complicated, and in the first (afferent) part is connected with the function of the chelipeds. The chelipeds are very heavily developed and flattened, and in flexion are pressed tightly against the pterygostomial region of the carapace, completely covering the mouthparts, leaving only a slit between the upper anterolateral margin of the carapace and the serrated crest of the upper margin of the chelipeds. The inner face of the propodus is smooth and slightly concave, and is closely apposed to the pterygostomial region, forming an accessory channel—the "exostegal channel" of Garstang (1898). The serrated upper margin forms a sieve for sand particles, and the hairs on the pterygostomial region aid in better filtration of the water. The inhalant apertures are in front of the chelipeds, and are protected by the bases of exopodites of the third maxillipeds, which are furnished with hairs. The exhalant part is formed on the endostome, which has two gutters separated by a septum, directing the exhalant water anteriorly.

The ventral floor of the gutter is the endopod of the first maxilliped, which is not covered by the third pair of maxillipeds; the other mouthparts are not covered completely by these maxillipeds either.

Matuta

The respiratory mechanism of this genus was also described by Garstang (1898). The respiratory water currents enter the orbital cavity, the margins of which are provided with hairs, thus forming a sieve. Afterwards, the water travels down and backwards through the orbital gutter. The first part of the gutter is furnished with long interlocked hairs, and the following portion is covered by the chelipeds, which are closely apposed to the pteryogostomial region. The latter is also covered by a carpet of hairs, as in *Calappa*, wth the difference that the chelipeds do not cover all the mouthparts. The gutter becomes less defined in this region, and the water enters into an afferent aperture of the branchial chamber through an auxiliary channel formed by chelipeds and carapace. The exhalant part of the respiratory system is different from that of *Calappa*. The exhalant opening is underneath and near the front, and the endostomial gutter is not divided. Moreover, the endopod of the first maxilliped which forms the floor of the exhalant channel is completely covered by the third maxilliped—so completely that its palp is also concealed in the special groove. The flagellum of the exopod is also reduced.

Orithyia

As with *Matuta*, the inhalant water current enters the orbital cavity, which is furnished with marginal hairs. Subsequently, the current follows a different course from that in *Matuta*. The orbital gutter is situated between supra- and suborbital spines, and is covered by the usual hairs in this group. This first part is very short, and it is immediately covered by enlarged inner parts of the meri of the chelipeds, which are smooth, enlarged and flat. On the anterior part of this plate is a small groove. Many hairs on the outer margins of this plate enhance water filtration. The exhalant current is again different from those of the two previous species. The water passes through a tunnel, a special structure of the endostome, which opens near the front. The exhalant aperture is again protected by many long hairs. The first maxilliped is short, but serves also as the floor of the respiratory channel. The exhalant orifice is not covered by the third maxilliped, and the latter is not long and does not cover completely other mouthparts.

Locomotion

Calappa

All walking legs of this crab are unmodified and lack specialised structures. This means that they are used only for more or less sideways movements.

A special feature of this group, however, is the ability to bury in the substrate. The crab buries itself by means of the chelipeds (Schmiedlein, 1879; Schäfer, 1954), and remains partly buried so that only the anterior portion of the body protrudes from the sand bottom.

Matuta

This genus differs from all other crabs in having all legs modified into paddles or spades, especially the enlarged terminal articles of the second and fifth pairs. These crabs can swim, using all walking legs, but the second and the fifth pair are especially efficient in this mode of locomotion. Although all authors agree that they are able to swim, opinions differ on whether they can swim quickly or not. Some earlier authors such as Klunzinger (1906) cite others to the effect that they can swim very slowly, but later researchers, such as Seidel (1976) and Basson *et al.* (1977), claim that they can swim very rapidly. Morevoer, these crabs have been observed swimming near the surface (Delsman and de Man, 1925). In Ras Burqa (Red Sea, near Eilat), however, I have observed *Matuta lunaris* swimming slowly in water only about several centimeters deep over the sand. The same observation has been made by Dr R.G. Wear in Hong Kong (pers. comm.). Additional observations on different *Matuta* species need to be performed in the field.

These crabs exhibit the ability to bury themselves backwards very quickly in the sand (Seidel, 1976; Basson *et al.,* 1977). For this they use the paddle-like legs. As with *Calappa*, they only partly embed in the substrate. It is interesting to note that Seidel (1976) and I observed *Matuta*, just as with *Calappa* (described by Schäfer, 1954), vigorously throwing out a jet of water mixed with sand immediately after digging in.

Orithyia

Locomotion in *Orithyia* is totally unknown.

Feeding

Calappa

Those parts of the feeding complex (Števčić, 1967) that have been analysed here include food, chelipeds and stomach structures. The feeding of *Calappa* has been described in detail by Shoup (1968). It feeds upon molluscs, and also upon hermit crabs protected in gastropod shells. This has been confirmed by Thomassin (1974). The claws of *Calappa* are somewhat different in size and have differing dentition on the occlusive surface. The right claw is usually the stronger one and is provided with a special crushing tooth (*Klöppelzahn* in Schäfer, 1954) that is used for destroying the shells of prey: it is the 'crusher claw'. The left claw is smaller, with more or less equal teeth; it is a 'cutter' or 'pincer'. Especially relevant stomach structures are the meso-cardiac (dorsal) teeth and a pair of lateral teeth of zygocardiac ossicles. The type of stomach structure is similar to that of the great majority of Oxystomata and Cyclometopa (Nauck, 1880), and is of a Platystilidea type, i.e. the dorsal tooth has no sharp ridges. The anterior (cusp) of the lateral tooth is very robust and strong. On the ventral part of the tooth there are many ridges, and on the ventral margin there are two ill-defined lobes.

Matuta

The manner of feeding of *Matuta* is poorly known, and the data are somewhat contradictory. Thomassin (1974) reported that the main food of *Matuta* is gastropod and bivalve molluscs, while Seidel (1976) observed that *Matuta lunaris* feeds on marine plants. However, my examination of the stomach contents of *Matuta lunaris* from the Red Sea (Ras Burqa) revealed the following components in eight specimens: sand (7); Polychaeta (5); undetermined organic matter (5); Decapoda: Natantia (4); Decapoda: Brachyura (4); vascular marine plants (2); Amphipoda (2); Gastropoda (2); Pagurida (1); Copepoda (1). From this, it is clear that *Matuta* is a very active predator within its surrounding area on the sand substrate. It is also an omnivorous species, with a preference for higher caloric animal food. Further knowledge will require continued observations on its food selection. The claws of *Matuta* species are symmetrical (i.e. monomorphic) and in this connection functionally identical, so that during feeding, the crabs use them alternately. It is interesting to note that all of my 12 male specimens from the Red Sea have chelipeds a little different in size. The teeth of the occlusive surface of the claws are very different in form and size, and likely have various functions, since crab claws, as established by Brown *et al.* (1979), are polyfunctional organs. The stomach ossicula are very similar to those of *Calappa*, although there are some differences. The tooth of the zygocardiac ossicula is not robust, but narrow and elongate, with a great number of sharp ridges. Two ventral lobes are only feebly developed.

Orithyia

The food of this crab is not known, but it will be useful to describe its chelipeds and stomach structure. The chelipeds in both sexes are different in size, the right chela being greater than the left one. On the bigger claw there are various types of teeth, and one tooth (crusher) is bigger than the others. The teeth of the big claw are not laterally compressed on the top; they are equally wide at base and top. On the smaller claw the teeth are unequal and are laterally compressed on the top. The stomach is generally similar to those of the crabs described earlier. The dorsal tooth (medio-cardiac) is relatively very robust. The lateral teeth also have well developed anterior cusps, the dorsal ridges are not numerous, and two ventral lobes are a little stronger and extend over all the ventral margin of the tooth. Altogether the teeth are all robust, and the food of this crab might be expected to be sturdy.

Defence

The main organs of defence (and attack), as in all other crabs, are the chelipeds. These are very efficient in *Calappa* (Schmiedlein, 1879) and in *Matuta* (pers. observation). Although in *Orithyia* there are no direct observations from the field, there is no doubt that they use the chelipeds in defence. Moreover, in order to protect themselves they are able to bury into the (sedimentary) bottom on which they occur. Doubtless, the bigger body size of adults of some *Calappa* species and of *Orithyia*, as well as lateral spines of *Acanthocarpus, Matuta*, and to some degree of *Orithyia*, contribute in their defence against potential predators. Concerning the colour in the genera mentioned, it is impossible to suggest without direct field observations of their habits in the natural habitats, whether or not it is cryptic.

Reproduction and development

The reproductive complex of these three groups is still insufficiently known. The reproductive behaviour of all of them is not yet known. There are only some data concerning larval development. In the older literature there are some data concerning the genus *Calappa* and one reference to *Mursia* (Raja Bai, 1959; Motoh, 1977). The zoeal stages of *Matuta* were first described by Raja Bai (1959). She pointed out some differences between the larvae of *Calappa lophos* and *Matuta lunaris*, but without making any systematic inferences. Recently, Hong (1976) described all three zoeal stages of *Orithyia sinica*. From the description it is clear that larvae of *Orithyia* are very different from those of the other crabs, especially in the shape of rostrum and telsom. But the differences between *Matuta* and *Calappa*, although notable, are not as remarkable as with *Orithyia*. It is very difficult to evaluate these differences and derive systematic consequences, because only the larvae of some of the crabs are known, and the functional meaning and systematic value of some structures remains unclear.

General Discussion

From the above it can be seen that the mode of life, and many structures and functions, both of adults and of larvae, are insufficiently known or completely unknown, and therefore it is very difficult to assess completely their systematic status and phylogenetic importance. Subsequent examinations will doubtless reveal a number of similarities, but especially differences, as has already been seen in the work of Ihle (1918) and of Guinot (1979). However, even a non-specialist can see at first glance, that these three groups are basically different. *Calappa* and related genera (*Mursia, Acanthocarpus, Paracyclois, Cyclöes, Platymera*) are recognisable by means of their broadened carapace, specific shape and form and position of chelipeds; *Matuta* species by the fact that all walking legs are transformed into paddles; and *Orithyia* by the rounded carapace, fifth pair of walking legs transformed into paddles and specific form of cheliped. *Calappa* with related genera are adapted specifically to burying, *Matuta* to burying-swimming using all walking legs, and *Orithyia* can probably bury and maybe swim. Their shape and structures could be understood only in connection with these key adaptations, which are, as we have seen, different.

In the organisation of these three groups there are several structures whose function is not clear, e.g. flat and rounded thoracic sterna *Orithyia* and *Matuta,* the episternites, or postero-lateral vault-like expansion of the carapace over the walking legs of *Calappa* and others. Nevertheless, we can see that in all the vital functions we have considered there are differences.

Although at the beginning of the analysis of these groups some similarities were pointed out, a large number of them (e.g. position of genital openings, number of branchiae, incomplete orbits, etc.) are not specific to these three groups, but are well-known to be common among many groups of Heterotremata. Many similarities can be considered to be convergences arising from adaptation to similar mode of life (e.g. respiratory systems). The differences are also numerous. Most of them have been mentioned before in connection with analysis of their mode of life. Furthermore, a great number of differences occur in some structures analysed earlier by Ihle (1918) and by Guinot (1978) (front, orbits, anterolateral spines, retaining system of abdomen, thoracal sternum, female genital opening, etc.). These facts show that the differences are very numerous, especially between the *Orithyia* and the other two groups, and to a lesser degree between the *Matuta* and *Calappa* with related genera. It can be concluded that these three groups are morphologically, physiologically and ecologically so different that they should not be accommodated within a single family, and that they represent three quite distinct families: Calappidae de Haan, 1833; Matutidae de Haan, 1833; and Orithyiidae Dana, 1852, as established by Ortmann (1892). Unity on a higher systematic level is somewhat questionable because their differences are very considerable.

Their evolution is very obscure, but there are some indirect indications of their evolutionary trends, seen for instance in their fossil records, geographical distribution, and diversity. Concerning the palaeontological evidence their fossils are not numerous, and those known need revision. They are, however, relatively old groups. The first Calappidae are known from Eocene, Orithyiidae from Cretaceous (Albian, Turon), and Matutidae from the Miocene.

Their geographical distribution is rather limited. *Orithyia* is known only from Chinese waters, from Korea (Hong, 1976) to Hong Kong (A. J. Bruce, pers. comm.), and *Matuta* in tropical waters, chiefly of the Indo-Pacific region. Only calappids have a wide distribution in temperate and tropical waters of the Indo-Pacific, Eastern Pacific and Atlantic Oceans.

The number of subtaxa is very limited. Orithyiidae has only one species, Matutidae only one genus with about ten species, and Calappidae has six genera with about forty species.

These facts suggest that the evolution of these three groups has not been particularly successful, and that they have remained, in Mayr's (1969, p. 595) terms, only a limitedly successful 'evolutionary experiment', because after the occupation of the present adaptive zone, subsequent adaptive radiation has not occurred. For a better illustration of these terms, I would like to quote Mayr's statements that: "Each major shift of habitat is an evolutionary experiment" (p. 595) and later "However, not all such shifts are equally successful. No spectacular adaptive radiation has followed the invasion of the sand niche by a coelenterate. The shift of a carnivore (Giant Panda) to herbivorous diet has not led to a new phylogenetic breakthrough" (Mayr, 1960). The same could also be said for the three groups under consideration here in which each of them occupied its own "structural-functional and adaptive zone" (Simpson, 1963, p. 26) which is indeed, particular and peculiar, and therefore they occupy an isolated position in the system of the brachyuran crabs. Their "evolutionary experiments" to occupy new adaptive zones were also of limited success, as is evident from their limited diversity, distribution and also abundance and biomass. However, these three groups do not represent an isolated case in the brachyuran crabs. On the contrary, there are a great number of taxa with a very low number of subtaxa, for instance Dorippidae, Palicidae, Retroplumidae, Belliidae, Thiidae, Pirimelidae, Mimilambridae, Mictyridae, and others. On the other hand, some brachyuran taxa as Xanthidae, Majidae, Portunidae, Leucosiidae, Pinnotheridae, Potamidae, Grapsidae and Ocypodidae were extremely successful, having a great number of subtaxa, especially species, with high expressed biomass, abundance and distribution.

Conclusions

All available data show that the Calappidae *sensu* Balss (1957) are not a homogeneous, i.e. natural, group-taxon. *Calappa, Matuta* and *Orithyia* and their related genera form at least three separate families, as originally stated by Ortmann (1892). Future examination not only of these three groups, but also of all other crabs, with special attention to their habitat and way of life, will permit the reorganisation of brachyuran systematics and phylogenetic trees. This, however, must await future investigations.

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BIOGEOGRAPHICAL RELATIONSHIPS OF SOME SOUTHERN AFRICAN BENTHIC CRUSTACEA

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SUMMARY

A brief discussion of benthic amphipods, isopods, and decapods deals with the distribution of the Atlantic, Indo-Pacific, and endemic components of each group around the southern African coastline. This distribution is related to faunal provinces of the area. It is concluded that for the two peracaridan groups, the South Coast Warm Temperate province was an evolutionary centre. Although there is a considerable number of endemic species in the decapods, recruitment from the Indo-Pacific accounts for the major component of this group.

INTRODUCTION

Although the southern African marine region has received considerable attention from zoogeographers (see Ekman, 1967, and Briggs, 1974, for references), seldom have either the Crustacea as a whole or any section of them been dealt with from a zoogeographical point of view. Ortmann (1896) was one of the exceptions. In his "Grundzüge der marinen Tiergeographie", Ortmann used the Decapod Crustacea as the basis for his ideas. Hartmann-Schröder and Hartmann (1974) have dealt briefly with the zoogeography of southern African Ostracoda. But even K.H. Barnard with his unsurpassed knowledge of the southern African crustacean fauna ventured few opinions on the distribution and affinities of this group. Several of the southern African crustacean groups have reached a point of taxonomic maturity where zoogeographic speculation can begin to have meaning. These groups include the Cumacea, Amphipoda, Isopoda, and Decapoda. I shall concentrate on the latter three groups, the raw data for these being relatively easily accessible.

Data sources and limitations.

Raw data for the gammarid and caprellid Amphipoda used in this paper come from Griffiths (1973, 1974a, 1974b, 1974c, 1975, 1976a, 1976b); for the Isopoda, Kensley (1978); for the Decapoda, Kensley (1981, in press).

In the following discussion, I have limited myself to animals occurring above the 200 m line, so little being known about the fauna beyond that depth. Also, amongst the decapods, the true pelagic forms such as the sergestids, aristeids, and the oplophorids have been excluded.

DISCUSSION

The geographic area under discussion stretches from the Kunene River on the west coast to Vilanculos on the east (Fig. 1) and is dominated by two major current systems. On the west, the Benguela system flows northwards and is characterised by strong upwelling of cold Subantarctic water. On the east coast the Agulhas current sweeps down the Mozambique Channel, at varying distances from the coast depending on the width of the continental shelf.

The question of faunal provinces is a contentious one, but for the purposes of this paper, I shall follow Brown and Jarman (1978). If we superimpose the various faunal provinces of the area on the coastline (Fig. 2) we see that five provinces are involved: (1) Tropical West African (2) Cold Temperate Namaqua (3) Warm Temperate South Coast (4) Subtropical East Coast (5) Tropical East Coast.

The overall composition of the amphipod, isopod, and decapod fauna (as circumscribed above) may be represented in Table 1.

Fig. 1. Locality map of area discussed.

Table 1. Overall composition of southern African Decapoda, Isopoda, and Amphipoda from less than 200 m.

	Decapoda	Isopoda	Amphipoda
Families	62	26	34
Genera	234	105	144
Species	494	266	297

If the total numbers of species for these groups are represented in bar graphs (Fig. 3), and the major components of each is indicated, we see that the Indo-Pacifics form the most important segment of the decapods, while the endemics form the major components for the two peracarid groups. (The 'other' component represents those species which are either 'cosmopolitan' or austral in distribution, or of uncertain affinity.)

Taking these three major components and looking at their distribution around the coastline, some interesting patterns emerge. The number of species of each component at eight localities around the coast is given as a percentage of the total for that component. The eight localities, chosen because of good collecting data, are the Kunene River Mouth, Lüderitz, Saldanha Bay, False Bay, Port Elizabeth, East London, Durban, and Inhaca Island.

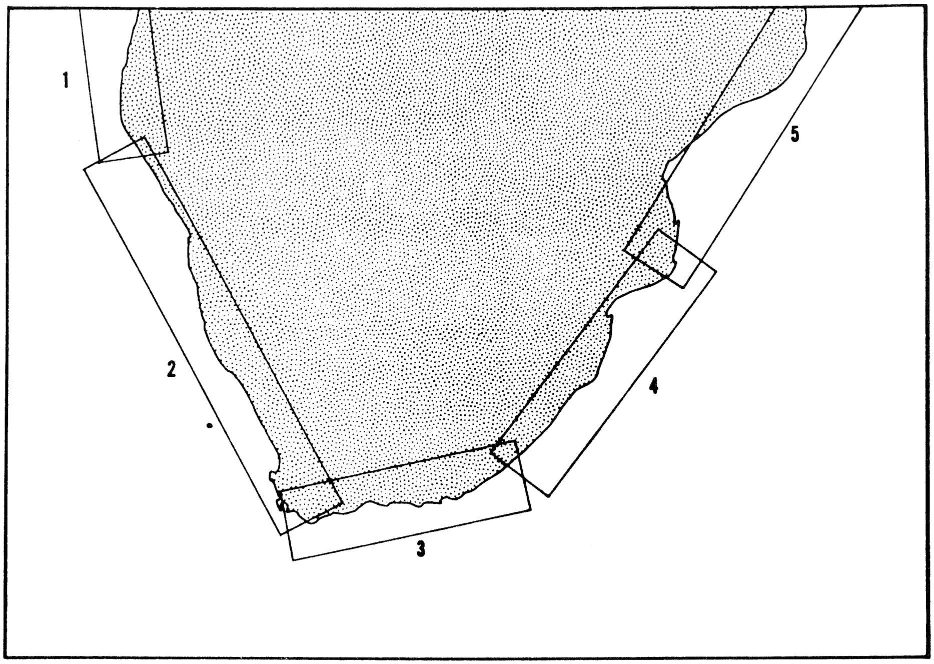

Fig. 2. Faunal provinces along the southern African coastline: 1 Tropical West African; 2 Cold Temperate Namaqua; 3 Warm Temperate South Coast; 4 Subtropical East Coast; 5 Tropical East Coast. (After Brown & Jarman, 1978).

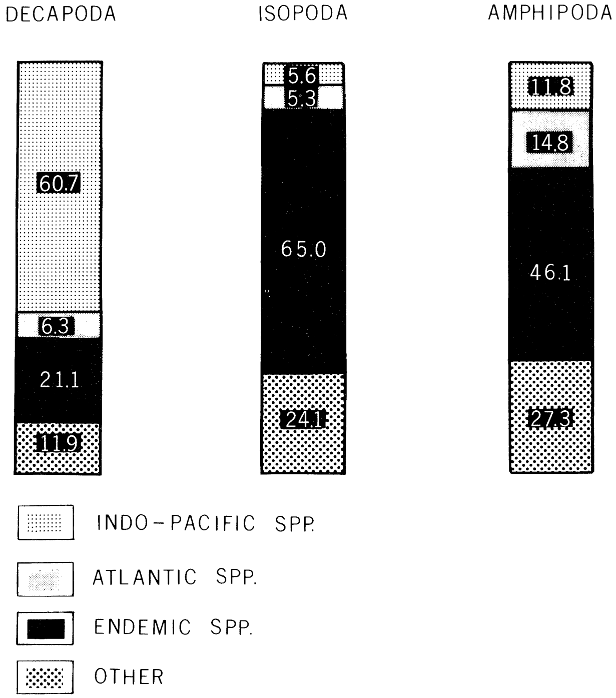

Fig. 3. Faunal components in percentages.

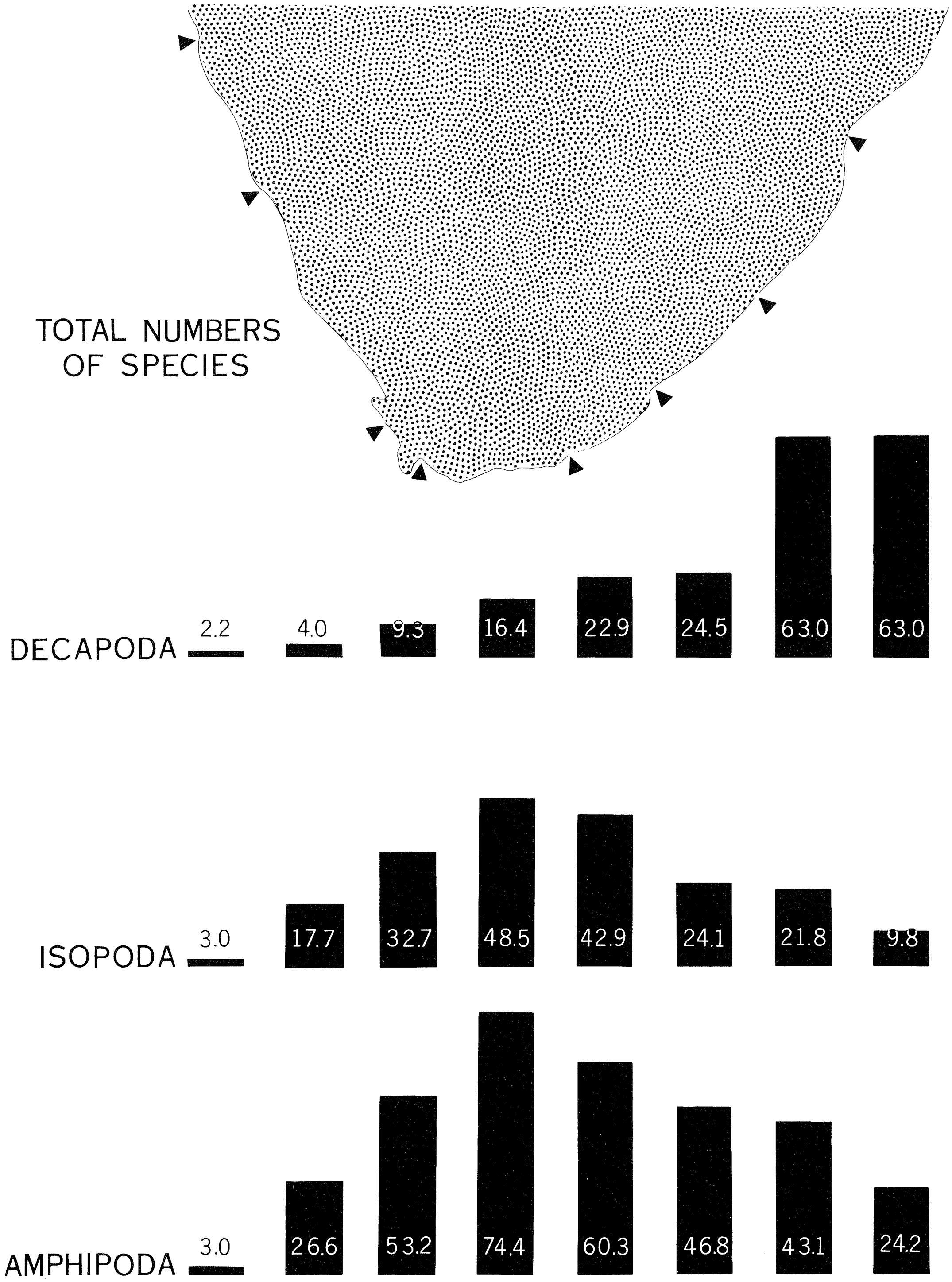

Fig. 4. Distribution of species around the southern African coastline (figures in percentages of total number of species).

For total number of species, (Fig. 4) we find, not surprisingly, that the decapods increase in number as we move into the subtropical east coast Indo-West-Pacific region. Both the amphipods and isopods reach peaks in the Agulhas Bank area, perhaps confirming the reality of the Warm Temperate South Coast Province. Looking at the distribution of Indo-Pacific species (Fig. 5), this trend in the decapods is even more marked, with very few species reaching the west coast. For the isopods and amphipods there is a fairly even spread, with a small percentage reaching as far as Lüderitz on the west coast. Even though several Atlantic species penetrate as far as Mozambique, for all three groups the Atlantic species reach a peak in the South Coast Agulhas Bank area. (Fig 6). This may be explained by regarding these south coast forms as relicts from warmer conditions on the west coast during the Quarternary, or we may regard the south coast as closer to the optimum conditions for the Atlantic species, with the upwelling of cold water on the west coast exercising a limiting effect on some species.

The distribution of the endemic component (Fig. 7) is perhaps the most interesting pattern. High endemism for the isopods and amphipods occurs in the Agulhas Bank area, again confirming the reality of the Warm Temperate South Coast Province. These species concentrations probably indicate a centre of evolutionary radiation, the basic stock of which was derived from less well-adapted species of both Atlantic and Indo-Pacific origin. Day (1978) came to a similar conclusion with regard to the cumaceans. As the eggs and larval stages of peracaridans are retained in a brood pouch, and thus lack a planktonic stage, these groups would need to resort to a slow step-by-step invasion of new territory. This reduced dispersal rate would perhaps predispose populations to becoming better adapted to the habitats into which they were moving than if they were relying on repeated waves of pioneer larval forms. The decapods show a less marked peak in the Agulhas area, to some extent reflecting the role of planktonic larvae in being able to populate an area, and another peak in the Durban area. It may be argued that this latter peak reflects concentrated collecting: alternatively, this may be a real peak, representing well-adapted species of the subtropical east coast province, derived from Indo-Pacific ancestors. (Almost all the endemic species of decapods from this area belong to Indo-Pacific genera.)

It is difficult to make any comparison of southern African amphipods, isopods, or decapods with the faunas of other southern hemisphere regions, because of lack of data. However, comparison of two well documented decapod groups—the Majidae (Griffin, 1966) and the Thalassinidae (Poore & Griffin, 1979)—from Australia and South Africa may reflect the overall situation: see Table 2. (It is of interest to note here that the Australian decapod fauna, which is basically Indo-Pacific in nature, is over twice the size of that of southern Africa.) Not surprisingly in the light of length of coastline and proximity to the tropics, both in overall numbers and in percentage endemism the Australian fauna is significantly richer than the southern African.

Table 2. Comparison of Majidae and Thalassinidea from southern Africa and Australia.

MAJIDAE

	Genera	Species	Endemic	Species
Southern Africa	28	42	11	(26%)
Australia	45	95	37	(39%)

(Australian figures from Griffin, 1966)

THALASSINIDEA

	Families	Genera	Species	Endemic Species
Southern Africa	3	7	18	10 (55%)
Australia	6	10	40	28 (70%)

(Australian figures from Poore and Griffin, 1979)

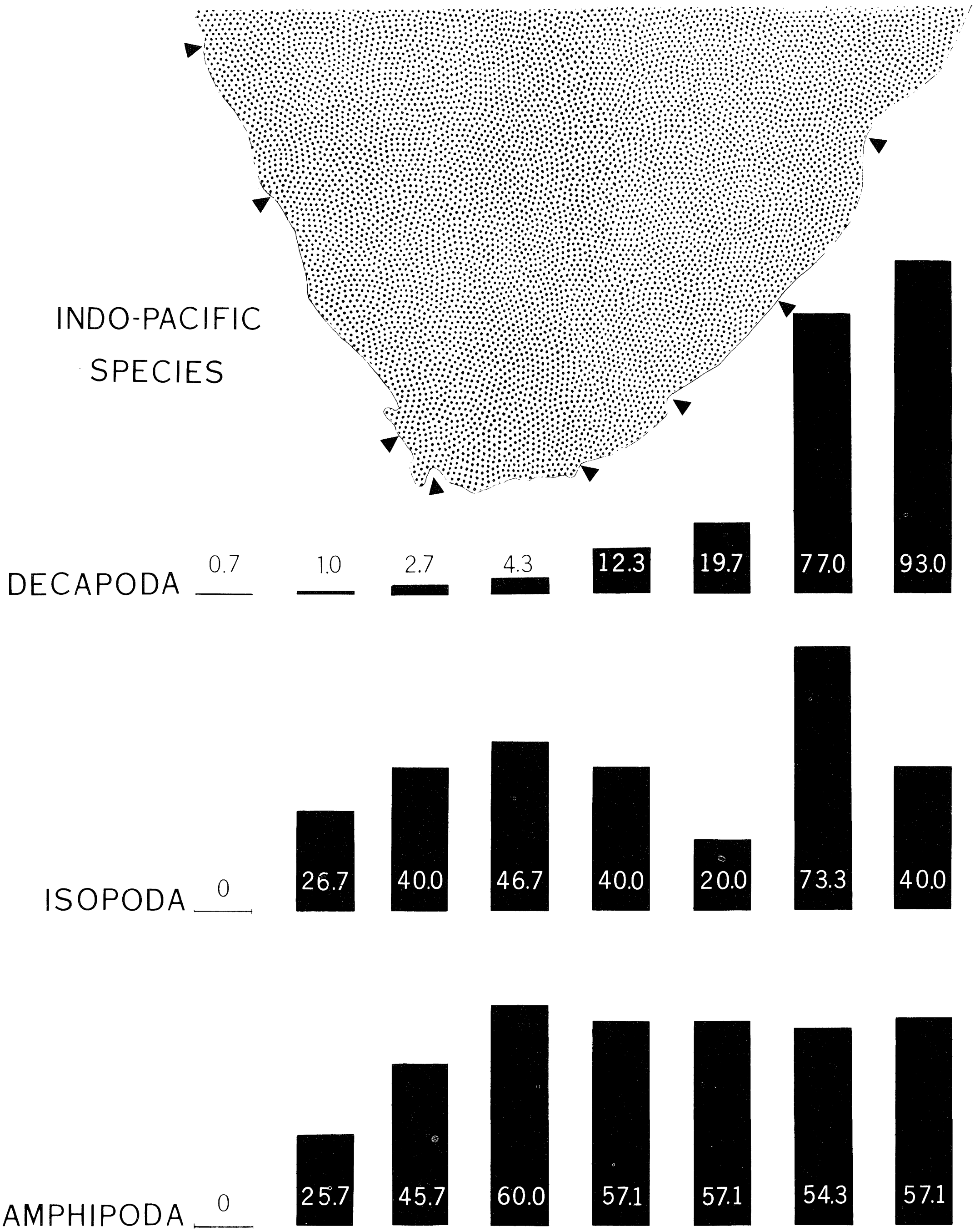

Fig. 5. Distribution of Indo-Pacific species around the southern African coastline (figures in percentages of total number of species).

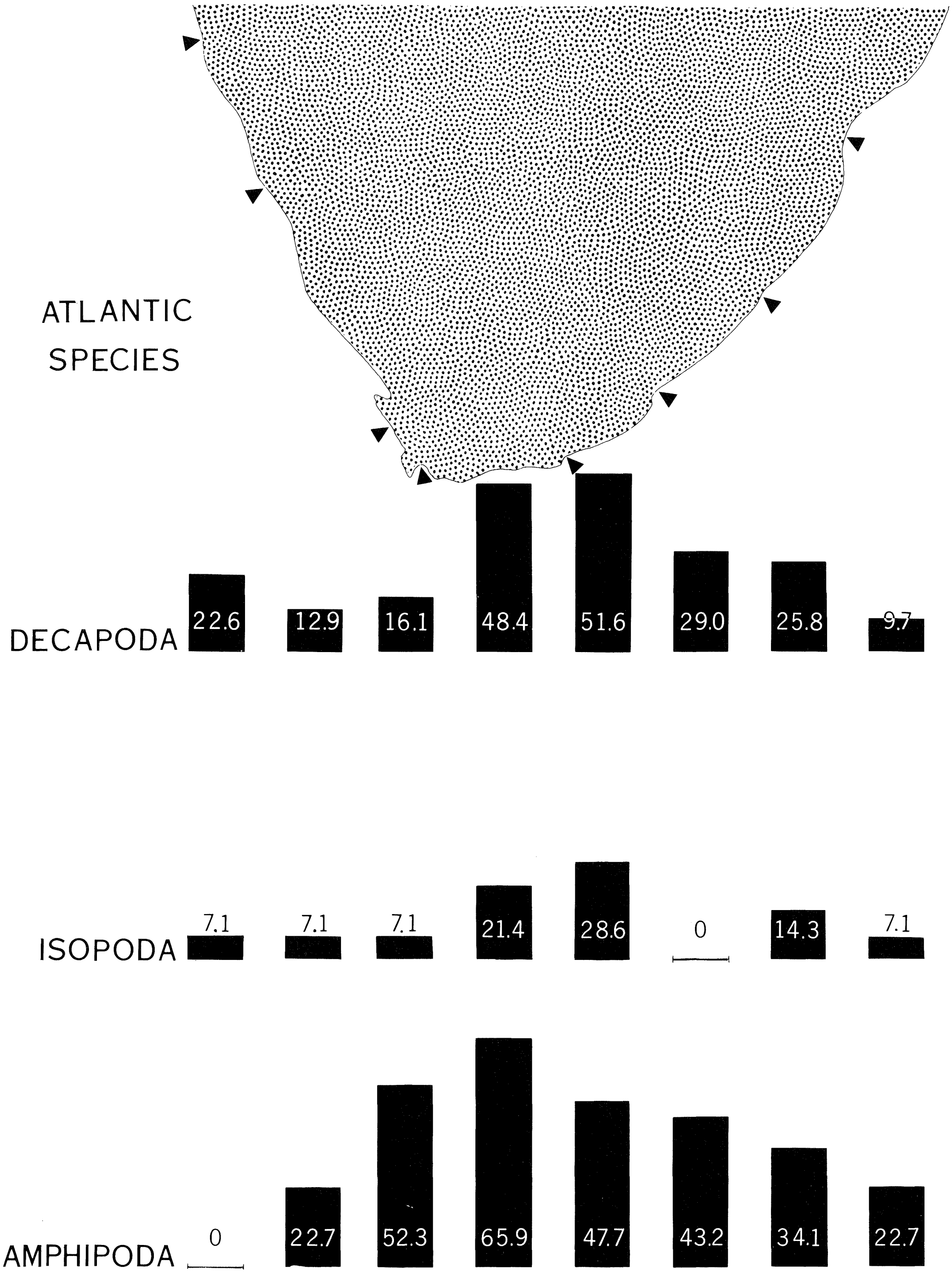

Fig. 6. Distribution of Atlantic species around the southern African coastline (figures in percentages of total number of species).

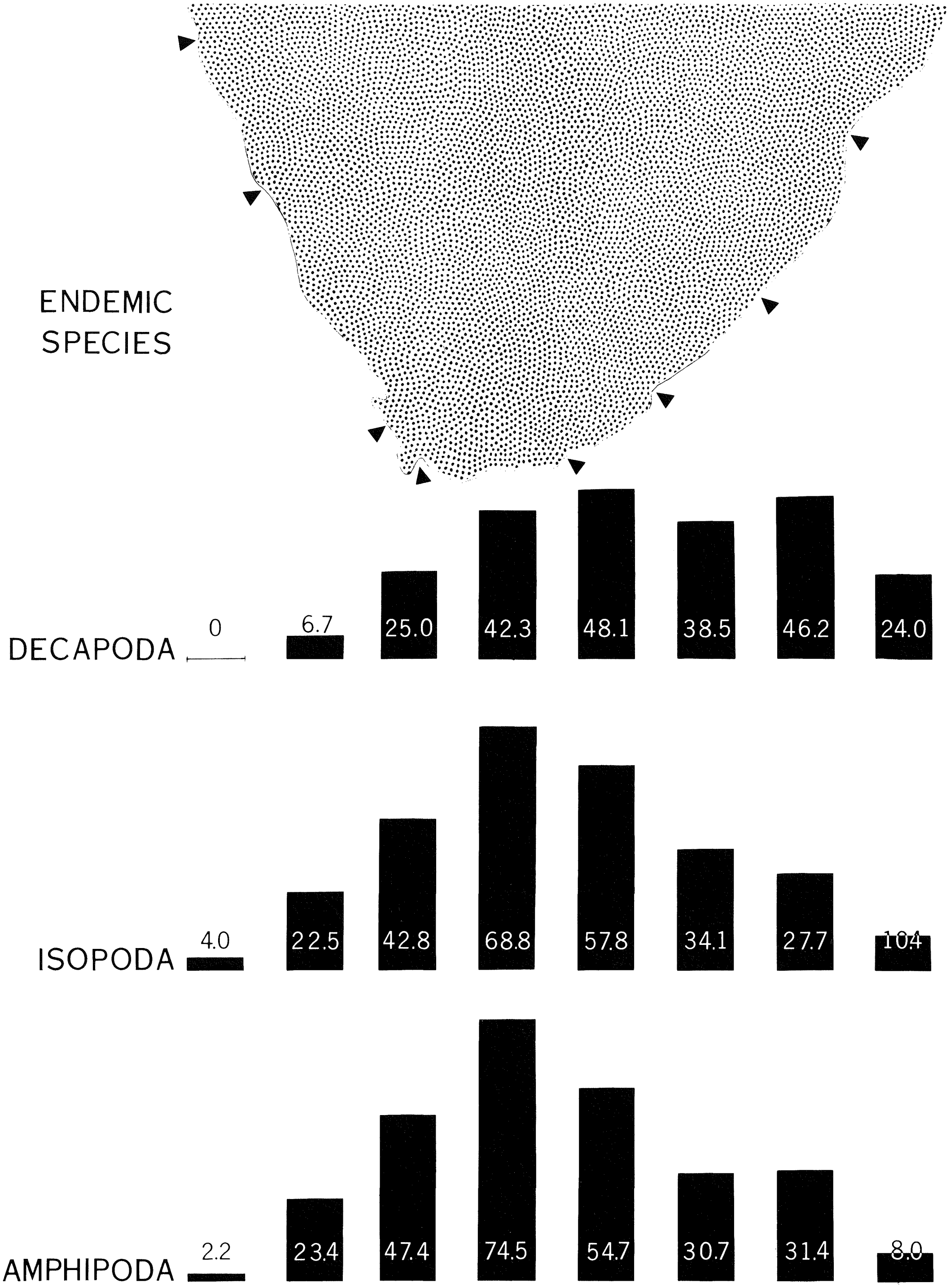

Fig. 7. Distribution of endemic species around the southern African coastline (figures in percentages of total number of species).

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REPRODUCTION CYCLES IN SOME FRESHWATER AMPHIPODS IN SOUTHERN AUSTRALIA

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SUMMARY

Reproduction patterns in three populations of southern Australian amphipods were examined to investigate the suggestion that a basic difference exists in reproduction patterns between northern hemisphere and southern hemisphere stream invertebrates. The species considered were *Pseudomoera gabrieli,* sampled in Sassafras Creek, Victoria, and *Austrochiltonia australis,* sampled at Dandenong Creek, Victoria, and Aldgate Creek, South Australia. The former species showed continuous breeding, the latter, seasonal. These results, together with a review of published studies, indicated that for Amphipoda no such basic reproductive difference exists.

INTRODUCTION

The study of stonefly life cycles on the mainland of south-eastern Australia by Hynes and Hynes (1975) is of considerable interest for they found that, unlike most stoneflies of the northern hemisphere, the stoneflies investigated by them had life cycles which lacked precise seasonal timing. A similar finding was obtained for a wide variety of benthic invertebrates, including a species of amphipod, in New Zealand streams (Towns, 1976; Winterbourn, 1978). Hynes and Hynes concluded that although some of the flexibility in the life-cycle patterns was a response to temperature, an important determinant was the uncertain Australian climate. In the New Zealand aquatic studies, on the other hand, the flexibility in life cycles has been attributed to New Zealand's mild climate (Devenport and Winterbourn, 1976; Towns, 1976).

A further explanation unrelated to climate may be advanced for both studies. It is that the pattern of invertebrate life cycles in streams, if not rivers, is linked to the seasonal pattern of allochthonous organic input in the form of leaf-fall. Such input is known to be an important source of energy for maintaining stream ecosystems. In contrast to the situation in the northern hemisphere, the input in Australia and New Zealand mostly occurs over a long and imprecisely timed period: both countries lack native trees deciduous in the northern sense of that word. In the northern hemisphere, leaf-fall from deciduous trees provides massive and precisely timed allochthonous inputs to streams in autumn.

Drawing on the (then) unpublished work of Hynes and Hynes on Australian stoneflies, Williams and Wan (1972) hypothesised that the lack of a precisely timed autumnal leaf-fall would be reflected in poorly synchronised life cycles for Australian stream invertebrates (and in lowered species diversities) but this hypothesis was not taken up by Hynes and Hynes (1975) in their explanations of stonefly life-cycle flexibility.

Against this background, it is of interest to consider the life-cycle patterns of two species of amphipod known from Australian streams. One, *Pseudomoera gabrieli* Sayce (Eusiridae), is known thus far only from upland streams in Victoria. The other, *Austrochiltonia australis* (Sayce) (Ceinidae), with its congener *A. subtenuis* (Sayce), is widespread in south-eastern Australia (Williams, 1962) and occurs in many freshwater habitats, both lotic and lentic. The two known species of *Austrochiltonia* are by far the most common freshwater amphipods of temperate Australia. Amphipods from fresh waters in the northern hemisphere are claimed to exhibit seasonality in life-cycle patterns, as do stoneflies there.

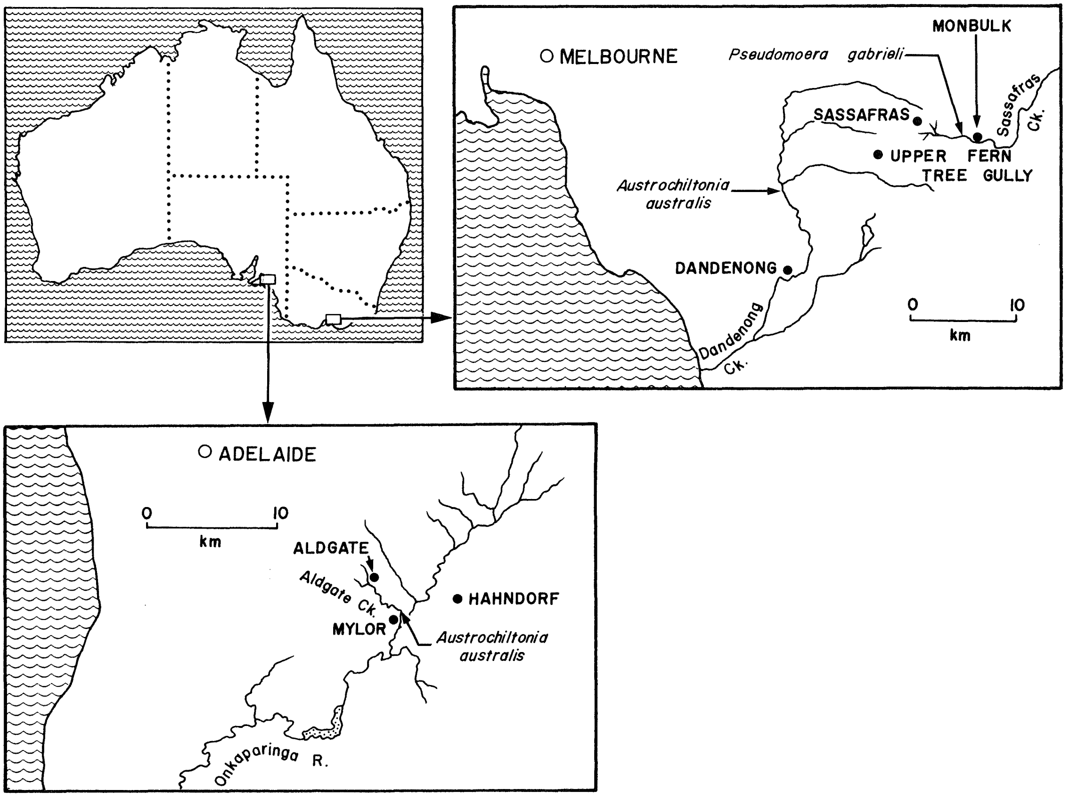

Fig. 1. Location of the three sampling sites.

LOCALITIES

Pseudomoera gabrieli was collected from Sassafras Creek, near The Patch, east of Melbourne, Victoria. *Austrochiltonia australis* was collected from Dandenong Creek, at Wellington Road, south-east of Melbourne, Victoria, and from Aldgate Creek, Mylor, south-east of Adelaide, South Australia (Fig. 1).

Sassafras Creek, at an altitude of 300 m above sea-level, is a typical stream of the Dandenong Hills, and maintains more or less constant flows throughout the year. Four to 5 m wide, it comprises pools with substrate of gritty silt and plant detritus and riffle areas with substrate of silt, stones and cobbles. The water is often turbid and rarely clear. Temperatures recorded during the study period were 9 to 15.5°C. Total dissolved solids were about $60\ \mathrm{mg\ l^{-1}}$. Whilst *P. gabrieli* was the most abundant amphipod species in the creek, another species, *Neoniphargus* sp., also occurred at a low frequency in most samples. Only *P. gabrieli* provided sufficient animals for analysis. Collections were made at monthly intervals over an 18-month period from September 1961 to February 1963.

Dandenong Creek at the sampling point is 50 m above sea-level and about 6 m wide, a moderately large coastal lowland stream. Its flow is strongly seasonal with maximum discharge values recorded in early spring (September) and minimal ones in late summer/early autumn (February, March) (State Rivers and Water Supply Commission, 1965); minimal discharge values are only about 5 per cent of maximal values, and at times of low flow little water movement downstream is visible. The substratum is mud and there is much submerged and emergent macrophytic growth. The water is almost always turbid. Total dissolved solids were about $400\ \mathrm{mg\ l^{-1}}$, and temperature during the study period was from 9 to 20°C. As in samples from Sassafras Creek, a species of *Neoniphargus* was also present, but at densities too low for adequate analysis. Samples were obtained at monthly intervals over a 16-month period from September 1961 to December 1962.

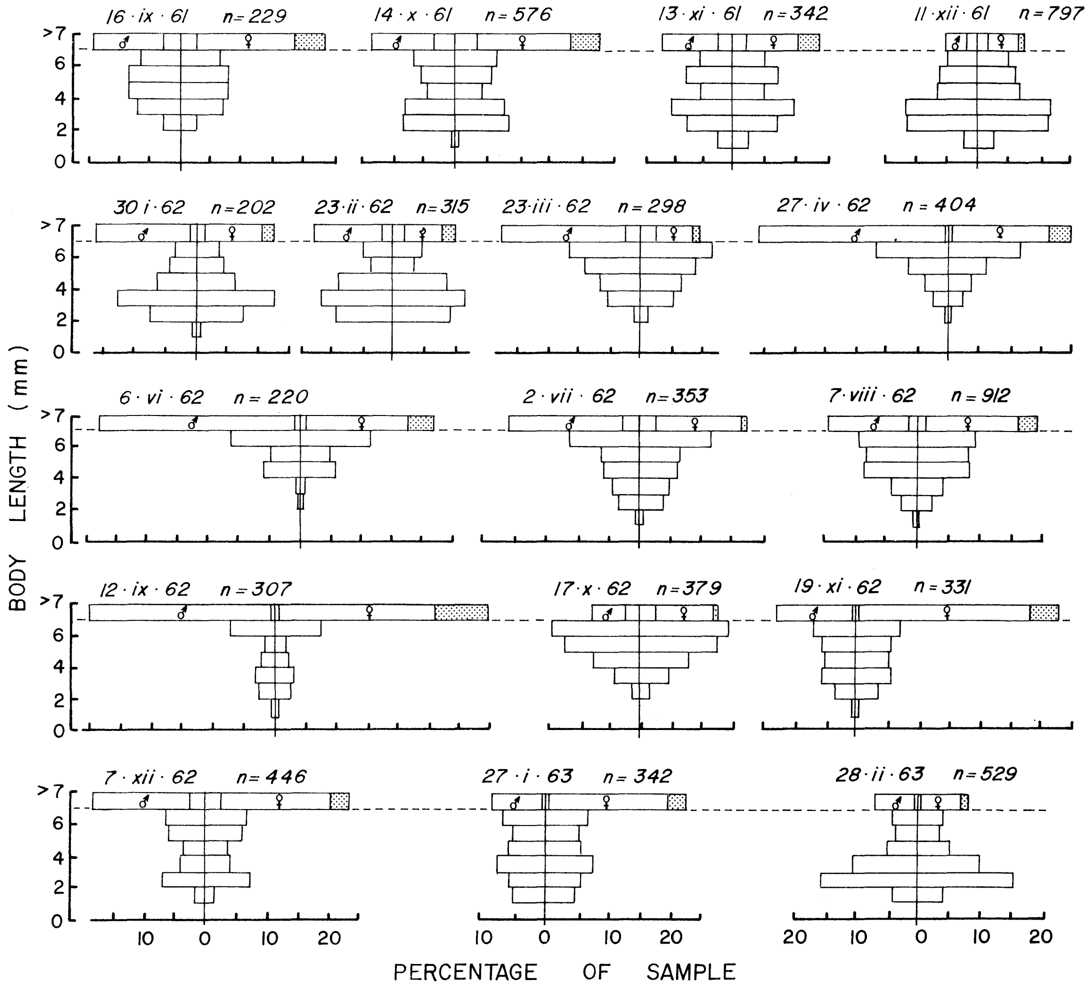

Fig. 2. Size and sex distribution of *Pseudomoera gabrieli* samples from Sassafras Creek, Victoria. The lengths of the specimens are given by the vertical scale and the length of each horizontal size-group block represents the percentage of the total in that size group. The horizontal dashed line shows the lower limit of sex distinction; below this line the blocks are centred; above it, males are shown on the left, females on the right. Females shown by the stippled areas are ovigerous.

Aldgate Creek, at 300 m above sea-level, is a small upland stream in the Mount Lofty Ranges. As in Dandenong Creek, flow shows a strong seasonality with minimal flows in late summer, and maximal ones in spring. Relatively deep pools with sandy substrata are connected by shallow riffle regions of approximate width 3 m. The water is moderately clear and during the study period temperatures varied from 7 to 17°C. Total dissolved solids were about 190-260 mg l^{-1}. Whilst *A. australis* was the abundant amphipod, a few individuals of *Neoniphargus* sp. were found in most samples. Samples were obtained monthly over a 15-month period, from October 1977 to December 1978.

METHODS

The collecting technique in all sampling was the same. A stramin hand-net was vigorously moved amongst bottom detritus, stones and other material in the stream for a few minutes. Net contents were transferred to containers at intervals. Preservation was in the field in 70 per cent ethanol. Temperature was measured with a mercury in glass thermometer at the time of sampling.

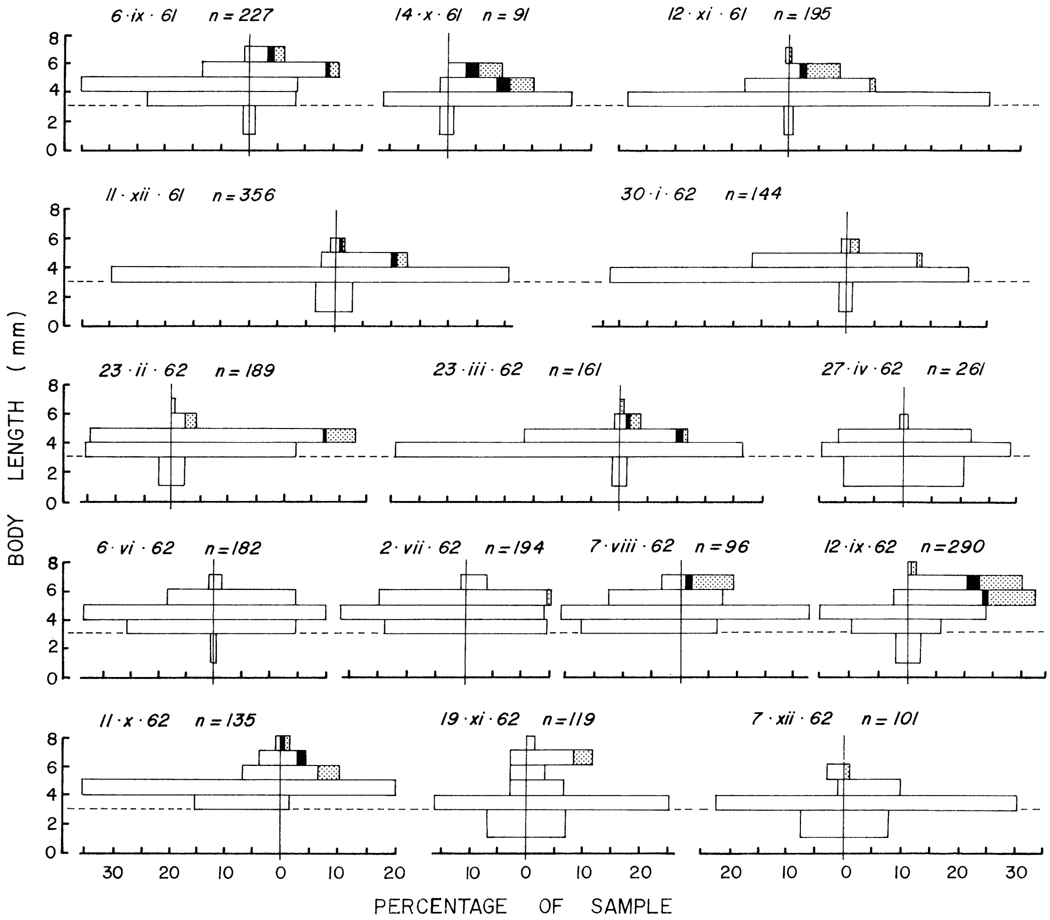

Fig. 3. Size and sex distribution of *Austrochiltonia australis* from Dandenong Creek, Victoria. The arrangement is as in Fig. 2, and the solid blocks represent pouched females.

In the laboratory, specimens were removed from field samples by hand and arranged into 1 mm size groups by comparison with a series of measured specimens. Ovigerous or pouched females of *A. australis* were directly measured with an eyepiece graticule. Adults were sorted into three main categories: males, non-breeding females (without brood pouch or eggs), reproductive females (with empty brood pouch or eggs). Eggs in brood pouches were counted except when pouches were damaged or partly empty, indicating egg loss during preservation or storage.

Pseudomoera gabrieli was distinguished from the other Australian eusirid, *Paramoera fontana* (Sayce), by the presence of 5 or fewer setae on the inner plate of maxilla 1. The sex of individuals of this species was very difficult or impossible to tell in specimens less than 7 mm long, and even in some longer neither oostegites nor male genital papillae could be distinguished without dissection. No female less than 7 mm long was found to be ovigerous. Hence, specimens of *P. gabrieli* over 7 mm long were classed as adults, those smaller as immatures. The largest specimens found were over 12.0 mm long.

Austrochiltonia australis was distinguished from *A. subtenuis* by examination of the third uropod, which is 2-segmented in *A. australis* and 1-segmented in *A. subtenuis.* Because both species may occur together, care was taken to ascertain that mixed populations did not occur at Dandenong Creek and Aldgate Creek. All specimens examined from both localities had 2-segmented third uropods. The sex of individuals over 3 mm long could be determined by examination of second gnathopods, which are enlarged in males. The largest specimens found did not exceed 8.00 mm in length.

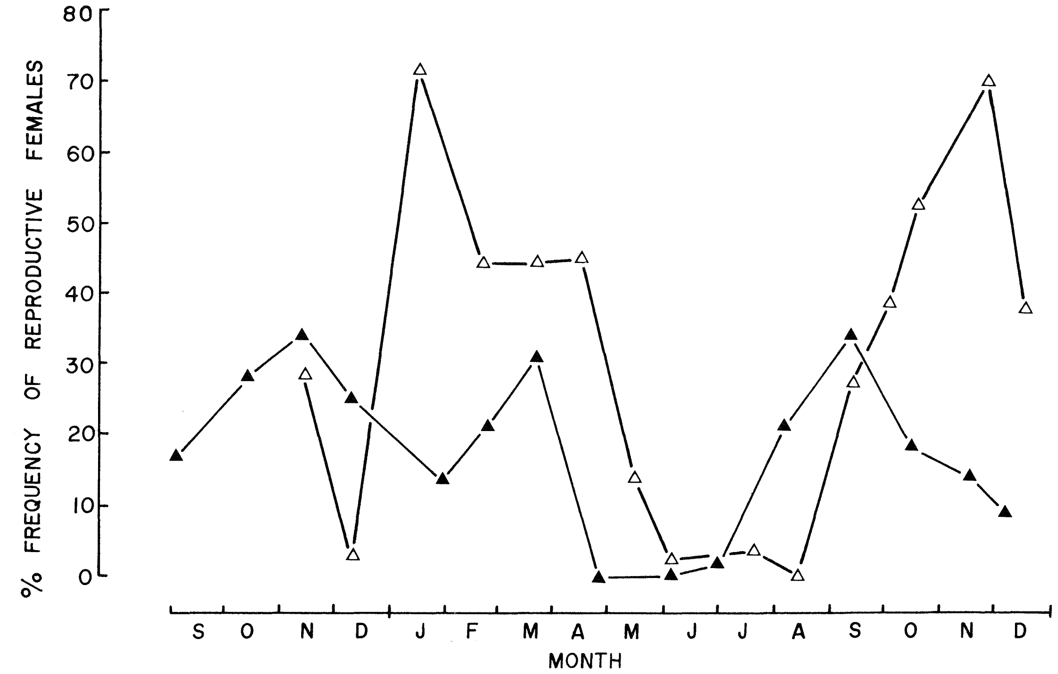

Fig. 4. Annual variation in breeding intensity of *Austrochiltonia australis* from Dandenong Creek (▲) and from Aldgate Creek (△). The symbols represent reproductive females (ovigerous or with empty brood pouch) expressed as a percentage of all females > 4.0 mm.

Representative specimens from each locality are lodged in the South Australian Museum, with register numbers C3871 to C3873.

RESULTS

(a) *Pseudomoera gabrieli*

Ovigerous females were present in all samples, their frequency varying from a low in July 1961 of 1.6% of total adults to a maximum in September 1962 of 14.6% (Table 1). In no sample did ovigerous females exceed 30% of total females. The continuous presence of ovigerous females was reflected in the relatively small changes in size-structure of the population throughout the year (Fig. 2). Small specimens, less than 3 mm long, composed less than 10% of the population in autumn and winter, but were more abundant in summer (Table 1).

Brood size varied between 19 and 62 eggs, the larger broods being carried by the larger females.

The ratio of males to females varied from 2.95 in March 1962 to 0.36 in January 1963. The fluctuations in sex ratio could not be related to other changes in population structure or to season.

(b) *Austrochiltonia australis* in Dandenong Creek

Changes in the size-frequency of the population and in the proportions of pouched and ovigerous females indicate a seasonal cycle (Fig. 3, Table 2). No females were ovigerous or pouched between April and June 1962, and only one was ovigerous in July 1962. In August 1962 and during the spring and summer months and in March 1962 reproductive females made up 20% or more of adult females in most samples (Fig. 4). The halt in breeding activity came abruptly. Juveniles reached their greatest relative abundance in April 1962 and were absent from the population in July and August 1962. Immatures also reached their greatest abundance in April, but the immature size class was never absent (Fig. 3).

Adults composed a large proportion of the population in winter and early spring, their frequency reaching a maximum of 83% in early November 1962. Many specimens that reached adult size by autumn survived the winter and were represented in the 6.0–7.0 mm and 7.0–8.0 mm size classes in the following

Table 1. Details of regular samples of *Pseudomoera gabrieli* from Sassafras Creek, Victoria.

	1961				1962											1963	
Date of sampling	6 Sept	14 Oct	13 Nov	11 Dec	30 Jan	23 Feb	23 Mar	27 Apr	6 June	2 July	7 Aug	12 Sept	17 Oct	19 Nov	7 Dec	27 Jan	28 Feb
Total specimens	229	576	342	797	202	315	298	404	220	353	912	307	379	331	466	342	529
Immatures	148	390	265	695	144	242	203	200	100	227	604	102	302	179	271	239	451
Males	26	59	31	27	31	34	59	121	70	65	121	93	21	41	76	27	35
Nonovigerous ♀♀	37	73	29	41	19	20	17	64	36	49	141	78	37	91	82	64	35
Ovigerous ♀♀	10	12	12	6	4	6	3	12	10	2	25	30	2	16	13	10	5
Spec. <3 mm as % total	5.7	18.3	19.0	28.0	16.3	18.7	2.0	0.7	0.5	7.9	5.1	5.5	2.4	6.9	17.8	19.6	39.1
Immatures as % total	64.6	67.7	77.5	87.2	71.3	76.8	68.1	49.5	45.5	64.3	66.2	33.2	79.7	54.1	58.2	69.9	85.3
Ovigerous ♀♀ as % adults	12.3	6.5	13.8	5.9	6.9	8.2	3.2	5.9	8.3	1.6	8.1	14.6	2.6	10.5	6.7	9.7	6.4
Ovigerous ♀♀ as % total females	21.3	14.1	29.3	12.8	17.4	23.1	15.0	15.8	21.7	3.9	15.1	27.8	5.13	15.0	13.7	13.5	12.5
Males/females	0.55	0.69	0.76	0.57	1.35	1.31	2.95	1.59	1.52	1.27	0.73	0.86	0.54	0.38	0.80	0.36	0.88

Table 2. Details of regular samples of *Austrochiltonia australis* from Dandenong Creek, Victoria.

Date of sampling	1961 6 Sept	14 Oct	12 Nov	11 Dec	1962 30 Jan	23 Feb	23 Mar	27 Apr	6 June	2 July	7 Aug	12 Sept	11 Oct	19 Nov	7 Dec
Total specimens	227	91	195	356	144	189	161	261	182	194	96	290	135	119	101
Juveniles	9	4	6	44	6	18	7	111	1	0	0	25	0	33	32
Immatures	60	33	124	251	91	71	98	86	56	56	23	46	23	49	54
Males	87	11	15	9	25	29	30	31	59	72	35	52	63	9	4
Nonovigerous ♀♀	59	31	32	39	19	57	18	33	66	65	30	110	40	24	10
Ovigerous ♀♀	8	6	15	8	3	14	5	0	0	1	7	49	6	4	1
Pouched ♀♀	4	6	2	5	0	1	3	0	0	0	1	8	3	0	0
Juveniles as % total	4.0	4.4	3.1	12.4	4.2	9.5	4.4	42.5	0.5	0	0	8.6	0	27.7	31.7
Immatures as % total	26.5	36.3	63.6	70.5	63.2	37.6	60.9	77.5	30.8	28.9	24.0	15.9	17.0	41.2	53.5
Ovigerous ♀♀ as % adults	5.1	11.1	23.1	13.1	6.4	14.0	8.9	0	0	0.7	9.5	22.4	5.4	10.8	6.7
Ovigerous ♀♀ as % adult females	11.3	14.0	30.0	15.4	13.6	19.7	19.2	0	0	1.5	18.4	29.3	12.2	14.3	9.1
Males/females, adult	1.22	0.26	0.30	0.17	1.14	0.41	1.15	0.94	0.89	1.09	0.92	0.31	1.28	0.32	0.36
Av. length ovig. ♀♀ (mm)	6.1	6.1	4.9	4.7	5.2	4.9	5.0			6.07	6.1	5.1	4.6	4.5	4.0
Av. length pouched ♀♀ (mm)	6.4	5.8	5.1	4.7		4.7	4.5				6.4	5.2	6.7		
Av. no. eggs/ovig. ♀	39(7)*	26(4)	35(13)	24(5)	—	27(9)	22(2)			—		48(48)	43(6)	39(3)	18(1)

*Figure in parentheses is the number of broods in which eggs were counted.

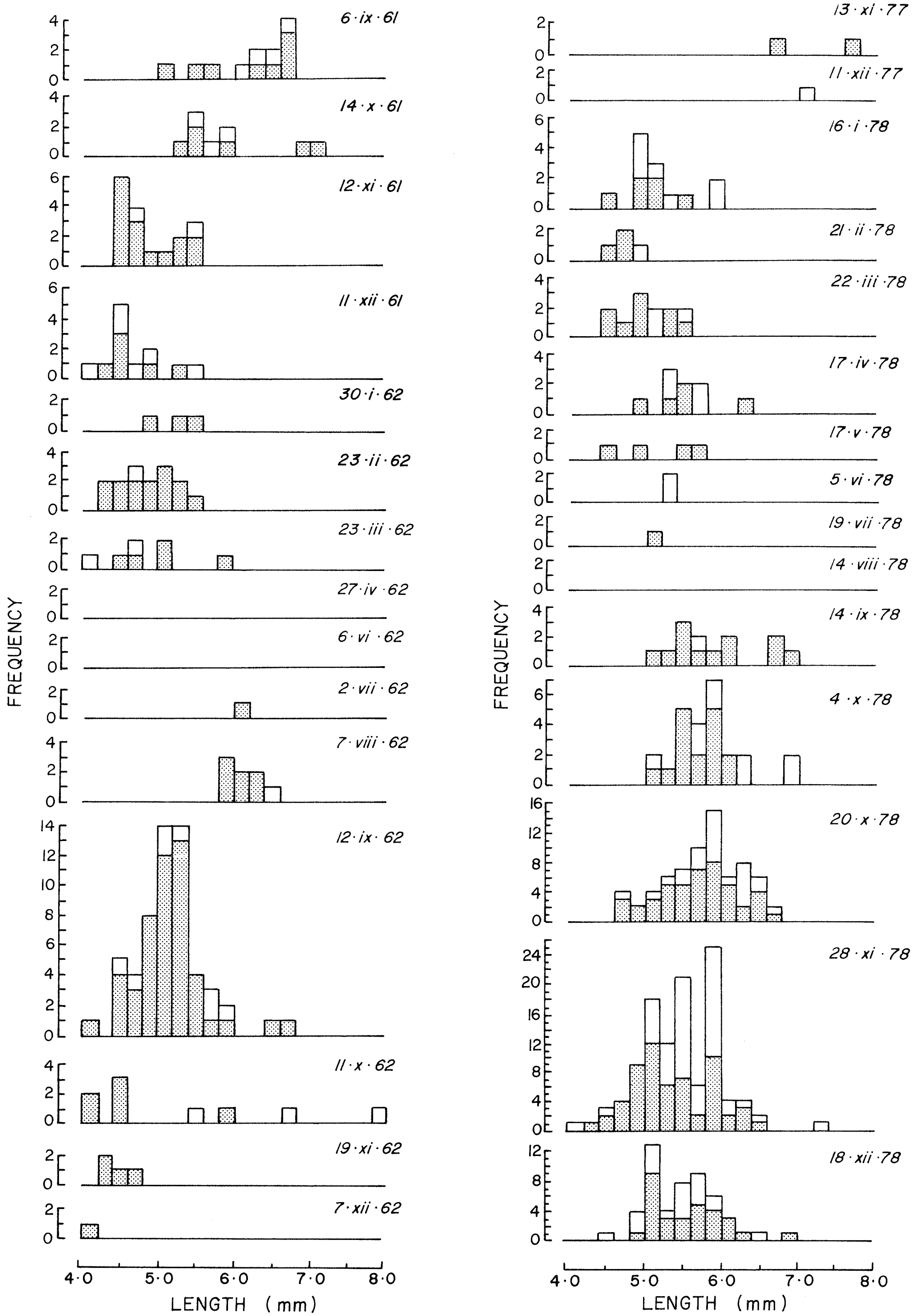

Fig. 5. Size distribution of ovigerous females of *Austrochiltonia australis* in each sample from Dandenong Creek (left) and from Aldgate Creek (right). Stippled blocks, ovigerous females; open blocks, pouched females.

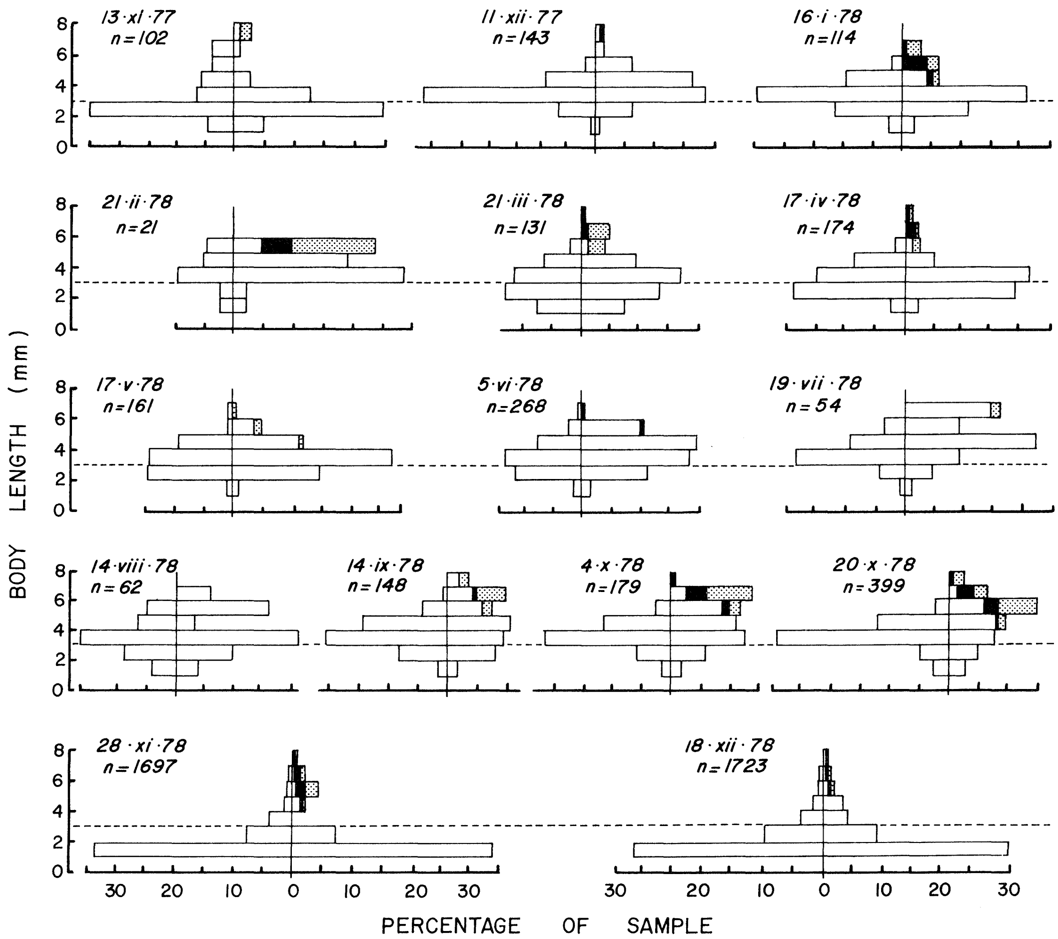

Fig. 6. Size and sex distribution of *Austrochiltonia australis* from Aldgate Creek, South Australia. The arrangement is as in Fig. 3.

spring. They apparently did not survive beyond November, and by December the largest animals were in the 5.0–6.0 mm size class. Females grew to larger size than males, the largest observed female being 7.9 mm, the largest male 6.5 mm. Also, fewer males than females reached the 6.0–7.0 mm size class. The females that became ovigerous in August and early spring were large, and the average size of reproductive females declined during the breeding season (Fig. 5). The small females breeding in December 1961 and 1962 probably were born in August-September of the same years. However, the average size of ovigerous females began to fall as early as September in 1962, and this must have resulted from slower ovarian development in females reproducing for the first time. The number of eggs per brood was so variable that although there was a trend towards larger females carrying more eggs, the average brood size varied erratically throughout the breeding season. The range in brood size was from 10 to 76.

(c) *Austrochiltonia australis* in Aldgate Creek

There was a seasonal cycle, with an almost complete absence of reproductive females in June, July and August 1978 (Fig. 6). Ovigerous females became abundant in September and their frequency increased during spring (Table 3). In January and November 1978 more than 70% of adult females were ovigerous or pouched (Fig. 4). Hence the non-breeding season occurred one month later than at Dandenong Creek, and the maximum frequency of reproductive females was much higher. In other respects the annual

Table 3. Details of regular samples of *Austrochiltonia australis* from Aldgate Creek, South Australia.

Date of sampling	10 Oct	1977 13 Nov	11 Dec	16 Jan	21 Feb	22 Mar	17 Apr	17 May	5 June	1978 19 July	14 Aug	14 Sept	4 Oct	20 Oct	28 Nov	18 Dec
Water temp °C	13	13	17	16	16	15	13	10	12	10	7.5	9	9.1	10.1	7	15
Total specimens	6	102	143	114	21	131	174	161	268	54	62	148	179	399	1697	1723
Juveniles	0	61	20	31	2	56	74	50	71	6	16	29	27	61	1405	1427
Immatures	1	20	72	52	8	38	63	66	86	15	23	44	61	148	100	132
Males, adult	4	14	14	13	2	10	17	17	28	7	7	28	24	56	34	29
Nonovigerous ♀♀	1	5	36	5	5	15	11	24	81	25	16	34	41	64	47	84
Ovigerous ♀♀	0	2	0	6	3	9	5	4	0	1	0	12	17	45	59	30
Pouched ♀♀	0	0	1	7	1	3	4	0	2	0	0	1	9	25	52	21
Juveniles as % total	0	59.8	14.0	27.2	9.5	42.7	42.5	31.1	26.5	11.1	25.8	19.6	15.1	15.3	82.8	82.8
Immatures as % total	16.7	19.6	50.3	45.6	38.1	29.0	36.2	41.0	32.1	27.8	37.1	29.7	34.1	37.1	5.9	7.7
Ovigerous ♀♀ as % adults	0	9.5	0	19.4	27.3	24.3	13.5	8.9	0	3.0	0	16.0	18.7	23.7	30.7	18.3
Ovigerous ♀♀ as % adult females	0	28.6	0	33.3	33.3	33.3	25.0	14.3	0	3.8	0	25.5	25.4	33.6	37.3	22.2
Males/females, adult	4.0	2.0	0.38	0.72	0.22	0.37	0.85	0.61	0.34	0.27	0.44	0.60	0.36	0.42	0.22	0.21
Av. length ovig. ♀♀ (mm)		7.3		5.0	4.7	4.92	5.5	5.1		5.2		5.9	5.7	5.7	5.3	5.6
Av. length pouched ♀♀ (mm)			7.1	5.2	4.8	5.2	5.5		5.3			5.7	6.0	5.9	5.6	5.4
Av. no. eggs/ ovig. ♀		76(2)*		26(3)	18(3)	30(9)	16(5)	15(4)		25(1)		54(11)	44(16)	48(37)	35(32)	35(27)

*Figure in parentheses is the number of broods in which eggs were counted.

cycle of *A. australis* at Mylor was similar to that of the Dandenong Creek population. The largest female was 7.8 mm long and the largest male 6.6 mm. The range in brood size was from 8 to 91 eggs.

DISCUSSION

A review of freshwater amphipod life cycles in the northern hemisphere showed that while in many localities stream amphipods display marked seasonality in reproduction, breeding is continuous in others (Hynes, 1955). Strictly seasonal breeding is shown by *Gammarus lacustris lacustris* in Wales and *G. pseudolimnaeus* in Ontario, both species having a simple annual cycle, with young being released in late spring and early summer, overwintering as immatures and breeding in the following spring (Hynes and Harper, 1972). Variations on this pattern are the two-year life cycle of *G.l. limnaeus* in Ontario, and, on the other hand, the rapid development to maturity before overwintering shown by *G. fasciatus* in England. Non-seasonal breeding is exemplified by *Crangonyx gracilis* (Hynes, 1955). Different populations of the same species may even have different reproductive patterns, this being shown by *G. pulex* which has a resting period in November in Cheshire, whilst in Dorset and on the Isle of Man, reproduction continues throughout the year (Hynes, 1955; Welton, 1979).

The lack of seasonality in the life cycles of *P. gabrieli* agrees with the findings on the life-cycle patterns of Australian mainland stoneflies (Hynes and Hynes, 1975) and of the amphipod *Paracalliope fluviatilis* in New Zealand (Towns, 1976). However, the agreement contributes no useful evidence for the hypothesis that the absence in Australia of a precisely timed autumnal leaf fall results in more flexible life cycles. It seems likely that the reproductive strategy adopted by *P. gabrieli* in Sassafras Creek is similar to that of those northern hemisphere amphipods which breed continuously, and is basically a response to the absence of marked seasonal variations in temperature and flow rates. There is no evidence to suggest that the strategy is a response either to the absence of an autumnal leaf fall or to the uncertainty of the Australian climate.

On the other hand, seasonality in the life cycle of *A. australis* in both upland and lowland streams is scarcely evidence against the hypothesis. Both localities where *A. australis* was studied displayed marked seasonal changes in flow regime and it seems likely that these would affect the life-cycle patterns of stream inhabitants. In other words, even if the lack of a precisely timed autumnal leaf fall represents the absence of a condition which induced life cycle seasonality, another condition, marked seasonal changes in flow regime, operates to induce it. The marked seasonality in the intensity of reproduction of *A. subtenuis* in Lake Modewarre (Lim and Williams, 1971) might be a reflection of recent derivation from a stream-dwelling population or frequent genetic interchange with a stream population.

Whilst our findings provide no direct information on the relationships between the patterns of life cycle and leaf fall, they do contribute in a general sense to our limited knowledge of invertebrate life cycles in Australian streams. When such knowledge is more taxonomically and geographically comprehensive, more insight into the factors controlling life cycle patterns may then be possible.

ACKNOWLEDGEMENTS

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THE PONTONIINE SHRIMP FAUNA OF AUSTRALIA

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Introduction

The caridean family Palaemonidae Samouelle consists of two major subfamilies. The Palaemoninae are conspicuous in tropical freshwater and temperate marine habitats and are almost entirely free-living. The Pontoniinae are almost exclusively tropical and subtropical marine commensals and are rarely found in temperate or fresh waters. They occur most abundantly in the warm shallow waters of tropical coral reefs and the species probably present in deeper waters here have so far been little studied. The use of scuba-diving as a collecting method in recent years has greatly increased the efficiency of sampling coral reefs and other shallow water marine animals. Precise information can now be obtained for many species with regard to their habitats or associations. Many of the more cryptic species could not be reliably collected by any earlier method and so remained 'rare' and little known. Coral reefs are famous for the diversity of the fauna that they support, and the Great Barrier Reef and the caridean shrimps are no exception to this generalisation. Among the marine shrimps in Australian seas only the snapping shrimps of the family Alpheidae exceed the number of species of the subfamily Pontoniinae.

The continent of Australia is provided with a richer fauna of pontoniine shrimps than has been reported from any other major geographical area. At present some 136 species have been recorded (and numerous new species, particularly of the genera *Periclimenaeus* and *Pontonia,* remain to be described).

The majority of these are well-known Indo-West Pacific species and they have been recorded principally from the shallow waters of Queensland and the associated Great Barrier Reef.

The fauna is represented by 36 genera, all except two of which are considered to contain species adapted to a 'commensal' way of life. That is to say, the adults live in permanent obligatory associations, often of a high degree of specificity, with a wide variety of other marine animals, particularly sponges, coelenterates, molluscs, echinoderms and ascidians. The hosts of many species are inadequately known, so that information concerning the degree of host-specificity between closely related species is incomplete.

The first pontoniine shrimp recorded from Australia was *Periclimenes aesopius,* described by Bate in 1863, and still known only from St. Vincent Gulf, South Australia from a small number of specimens. Although it is probably an associate of a coelenterate, its host animal has yet to be identified and the shrimp remains one of the least-known Australian species. Saville-Kent (1893) in his monograph of the Great Barrier Reef next illustrated the well-known species *Periclimenes brevicarpalis,* an associate of giant anemones, such as *Stoichactis* spp., throughout most of the Indo-West Pacific region. Miers (1884) reported on four species collected from Australian waters by H.M.S. "Alert", and Baker (1907) described the unusual and possibly endemic species *Pontonia minuta* from South Australia. Two species, *Anchistus custos* and *Periclimenes brevicarpalis* were reported from the Monte Bello Islands, Western Australia by Rathbun (1914). Balss (1921) reported a further six species from Cape Jaubert in the same state, in his report on the results of Dr E. Mjöberg's 1910-1913 Swedish Expedition. McCulloch and McNeill (1923) recorded more *Periclimenes brevicarpalis* from a number of Queensland localities and McNeill (1926) recorded *Periclimenes spiniferus, P. elegans* and *Conchodytes tridacnae* from North-West Island in the Capricorn Islands, at the southern end of the Great Barrier Reef. Hale (1927) confirmed the presence of these species in South Australian waters. The first detailed information concerning the coral-associated species in Queensland waters was provided by Patton (1966), and McNeill (1968) provided details of eight species collected mainly from the Low Isles by the Great Barrier Reef Expedition, 1928-1929. Preliminary descriptions of five new species of *Periclimenaeus* were provided by Bruce (1969b, 1970a), and details of a further eight species from Queensland waters and a report on pontoniine material in the Australian Museum (Bruce, 1971, 1977c). Several other papers dealing with isolated species have also appeared. Wadley (1978) recorded several species of *Periclimenes* from Moreton Bay, Queensland. The fauna has been studied in most detail at Heron Island, the Capricorn Islands, in subtropical waters, at the southern end of the Great Barrier Reef. Over a hundred species occur at this locality and have been reported upon by Bruce (in press f).

The present report includes details of ten species not previously recorded from Australian waters. These are:

Dasycaris zanzibarica Bruce
Hamodactyloides incompletus (Holthuis)
Mesopontonia gorgoniophila Bruce
Periclimenaeus rastrifer Bruce
Periclimenes alcocki Kemp
Periclimenes attenuatus Bruce
Periclimenes investigatoris Kemp
Periclimenes kororensis Bruce
Periclimenes pectiniferus Holthuis
Periclimenes platycheles Holthuis

Further information on most of these shrimps, including descriptions, illustrations and synonymies are to be found in the works of Borradaile (1917), Kemp (1922) and Holthuis (1952).

Key to the genera of the pontoniine shrimps of Australia

1.	Telson with at least three distinct pairs of posterior marginal spines	2
——	Telson with fewer than three pairs of posterior marginal spines	36
2.	Mandible with palp	*Palaemonella*
——	Mandible without palp	3
3.	Maxilla with basal endite absent	4
——	Maxilla with basal endite present	9
4.	Rostrum absent, scaphocerite rudimentary; inhabiting galls in *Acropora*	*Paratypton*
——	Rostrum present, scaphocerite distinct	5
5.	Rostrum toothless; body form strongly depressed; second pereiopods with large subequal similar chelae; associated with Scleractinia	*Platycaris*
——	Rostrum with several distal teeth; body not strongly depressed	6
6.	Third maxilliped with fully functional exopod	8
——	Third maxilliped with exopod greatly reduced or absent	7
7.	Body compressed; lateral border of exopod of uropod dentate; associated with oculinid corals	*Anapontonia*
——	Body not compressed; lateral border of exopod of uropod not dentate; associated with Alcyonaria	*Propontonia*
8.	Dactyls of ambulatory pereiopods with rounded basal protuberance; several small post-antennal spines present; associated with Scleractinia	*Fennera*
——	Dactyls of ambulatory pereiopods without basal protuberances, single large acute antennal spine present; associated with Corallimorpharia	*Pliopontonia*
9.	Third maxilliped with fully functional exopod	10
——	Third maxilliped lacking fully functional exopod	14
10.	Dactyls of ambulatory pereiopods with distinct basal process	11
——	Dactyls of ambulatory pereiopods without distinct basal process	18
11.	Basal process of ambulatory dactyls compressed	12
——	Basal process of ambulatory dactyls hoof-like	13
12.	Basal process of ambulatory dactyls rounded; third maxilliped with an arthrobranch; movable hepatic spine present; associated with Ascidiacea	*Dasella*
——	Basal process of ambulatory dactyls acute or angular; third maxilliped without arthrobranch; hepatic spine absent; associated with Bivalvia	*Conchodytes*

13. Hepatic spine present; second pereiopods with chelae unequal and dissimilar; rostrum dorsally and ventrally dentate; associated with Scleractinia .... *Jocaste*

—— Hepatic spine absent; second pereiopods typically equal, similar; rostrum dentate or edentate; associated with Scleractinia .... *Coralliocaris*

14. Dactyls of ambulatory pereiopods simple 15

—— Dactyls of ambulatory pereiopods biunguiculate 17

15. Rostrum short, with lateral carinae broadly expanded, toothless; chelae of second pereiopods unequal; associated with Gorgonacea, Antipatharia, Scleractinia .... *Pontonides*

—— Rostrum normal, compressed, dorsally toothed, without expanded lateral carinae 16

16. Second pereiopods greatly reduced; dactyls of ambulatory pereiopods slender without basal swelling; associated with Gorgonacea, Alcyonacea .... *Hamodactylus*

—— Second pereiopods not reduced, normal size, unequal; dactyls of ambulatory pereiopods proximally swollen; associates of *Millepora* hydroids .... *Hamodactyloides*

17. Rostrum well developed, compressed, toothed; telson with three pairs of posterior spines; of slender body form; associated with Gorgonacea .... *Mesopontonia*

—— Rostrum short, stout, swollen and toothless; telson with about six pairs of posterior spines; of stout body form; possibly associated with Annelida *"Pontonia" minuta*

18. Hepatic spine present 19

—— Hepatic spine absent 26

19. Hepatic spine mobile 20

—— Hepatic spine fixed 22

20. Rostrum with a few small or minute teeth only; associates of Bivalvia .... *Paranchistus*

—— Rostrum with numerous acute teeth dorsally 21

21. Fingers of chela of first pereiopods spatulate with pectinate cutting edges; associates of Asteroidea .... *Zenopontonia*

—— Fingers of chela of first pereiopods subspatulate, cutting edges entire; associates of Echinoidea .... *Allopontonia*

22. Postero-ventral angles of pleura of fourth and fifth somites rounded 23

—— Postero-ventral angles of pleura of fourth and fifth somites acutely produced 25

23. Second pereiopods with chelae markedly unequal and dissimilar; rostrum toothless with broadly expanded lateral carinae; associated with Echinoidea ..*Stegopontonia*

—— Second pereiopods generally with chelae subequal and similar 24

24. Rostrum generally strongly dentate; epistomal horns absent; associated with Porifera, Coelenterata, Nudibranchia and Echinodermata ....*Periclimenes*

—— Rostrum toothless, supra-orbital spines and epistomal horns present; associated with Crinoidea ....*Parapontonia*

25. Rostrum compressed, ventral teeth present; second pereiopods subequal in size, similar in form; dactyls of ambulatory pereiopods laterally twisted, carinate; associates of Scleractinia .... *Harpiliopsis*

—— Rostrum styliform, ventral teeth absent; second pereiopods unequal; dactyls of ambulatory pereiopods not twisted or carinate; associates of Pennatulacea .... *Dasycaris*

26. Second pereiopods generally markedly unequal, dissimilar; fingers of major chela with a pit and hammer mechanism; associates of Porifera and Ascidiacea .... *Periclimenaeus*

—— Fingers of major second pereiopod without pit and hammer mechanism 27

27. Maxilla with basal endite simple 28

—— Maxilla with basal endite bifid or bilobed 32

28. Fourth thoracic sternite with conspicuous median process; associated with Scleractinia .... *Philarius*

—— Fourth thoracic sternite without conspicuous median process 29

29. Body strongly compressed; rostrum with numerous dorsal teeth; second pereiopods subequal, similar, elongate; dactyls of ambulatory pereiopods simple; exopod of uropod with strong hooked disto-lateral spine; associates of Scleractinia .... *Ischnopontonia*

—— Body not strongly compressed, rostrum generally feebly toothed or toothless; dactyls of ambulatory pereiopods biunguiculate 30

30. Scaphocerite rudimentary; second pereiopods with chela generally unequal in size and dissimilar; associates of Porifera .... *Typton*

—— Scaphocerite normal or small; second pereiopods with chelae equal or subequal in size and generally similar in form 31

31. Chelae of second pereiopods short, with deep strongly compressed palm, subspatulate fingers, with a small lateral accessory flange on the fixed finger of minor chela; associates of Porifera .... *Oxycocaris*

—— Chelae of second pereiopods elongate, palm subcylindrical, fingers simple and without accessory flanges; associates of Porifera .... *Onycocaridella*

32. First pereiopod with carpus segmented; associates of Porifera .... *Thaumastocaris*

—— First pereiopod with carpus entire 33

33. Dactyl of third pereiopod biunguiculate, with additional accessory spines 34

—— Dactyl of third pereiopod biunguiculate, without additional accessory spines 35

34. Second pereiopods with chelae generally large, unequal in size and dissimilar in form; associates of Ascidiacea and Bivalvia .... *Pontonia*

—— Second pereiopods with chelae small, subequal in size and similar in form; associates of Porifera .... *Apopontonia*

35. Rostrum short, slender, acute, edentate; lateral carinae broadly expanded forming deep orbits; associates of Crinoidea .... *Pontoniopsis*

—— Rostrum not slender, acute; lateral carinae and orbits obsolete; associates of Bivalvia .... *Anchistus*

36. Telson with a pair of stout hook-like terminal processes; associated with Scleractinia and Actiniaria .... *Hamopontonia*

—— Telson with two pairs of stout posterior spines only; associates of Porifera ... *Anchistioides*

CHECKLIST OF THE PONTONIINE SHRIMPS OF AUSTRALIA (PALAEMONIDAE SAMOUELLE, 1819; PONTONINAE KINGSLEY, 1878)

Allopontonia Bruce, 1972

1. *Allopontonia iaini* Bruce, 1972

A. iaini is the only species in the genus. It is known from Heron Island where two specimens have been collected from the echinoid *Salmacis sphaeroides* at 24 m. It is also known from the western Indian Ocean.

Anapontonia Bruce, 1966

2. *Anapontonia denticauda* Bruce, 1966.

A. denticauda is the only species in the genus. It is recorded only from Orpheus Island in association with the oculinid coral *Galaxea fascicularis* in shallow water. It is otherwise known from Zanzibar and Singapore living on the same host.

Anchistioides Paulson, 1875

3. *Anchistioides australiensis* Balss, 1921

This species is known in Australian waters from two juvenile specimens reported from Cape Jaubert, Western Australia. The only other record is from Bensback River, New Guinea.

4. *Anchistioides compressus* Paulson, 1875

A. compressus is recorded in sponges from the reef flat to 4.5 m from Heron Island, Wilson Island and Dunwich, Moreton Bay. It is also known from the Red Sea and western Indian Ocean to the South China Sea, Japan and the Tuamotu Islands.

5. *Anchistioides willeyi* (Borradaile, 1899)

In Australian waters *A. willeyi* is known from sponges on the reef slope at Heron Island from 9 to 12 m at One Tree Island and also in sponges from sea grass flats at Dunwich, Moreton Bay. It is otherwise known from the western Indian Ocean, Indonesia, the South China Sea and New Britain.

Anchistus Borradaile, 1898

6. *Anchistus australis* Bruce, 1977a

The type specimens of *A. australis* were collected from Capre Cay, Swain Reefs. The species has subsequently been recorded from Heron Island, and specimens from Michaelmas Reef have been examined. The species is otherwise known only from the Great Astrolabe Reef, Fiji. The hosts are the giant clams, *Tridacna derasa* and *T. squamosa.*

7. *Anchistus custoides* Bruce, 1977a

This species was first described from specimens collected at Gillet Cay, Swain Reefs. It is also found at Heron Island in the fan mussel *Atrina vexillum* from 3 to 6 m, and is otherwise known only from the Palau Islands.

8. *Anchistus custos* (Forskål, 1775)

The species was first recorded in Australian waters by Miers (1884) from Port Molle and Bowen, Queensland, and Shark Bay, Western Australia. It was later reported from Monte Bello Islands, Western Australia (Rathbun, 1914) and from St. Vincent Gulf, South Australia (Hale, 1927). Other Australian records are the Low Isles, Magnetic Island and Swain Reefs. The species is common and widespread throughout the Indian Ocean and most of the western Pacific Ocean east to the Fijian Islands. It occurs mainly in association with bivalves of the genus *Pinna.*

9. *Anchistus demani* Kemp, 1922

Anchistus demani is recorded from One Tree Island in association with the giant clam *Tridacna maxima.* Specimens have also been examined from Heron Island and Michaelmas Reef from *T. maxima* and *T. gigas.* The species is otherwise known from the western Indian Ocean to the Marshall Islands.

10. *Anchistus gravieri* Kemp, 1922

In Australian waters *A. gravieri* is known only from the Herald Islands in association with a type of giant clam *Hippopus hippopus.* The species is otherwise recorded from the type locality Vanikoro, Santa Cruz Islands and from New Caledonia.

11. *Anchistus miersi* (de Man, 1888)

This species is recorded only from Tijou Reef in Australian seas, living at 2 m in the giant clam *Hippopus hippopus.* Specimens have also been examined from the giant clam *Tridacna gigas* at Magnetic Island. *Anchistus miersi* is otherwise known throughout the Red Sea, Indian Ocean and the Pacific Ocean to the Gambier Archipelago in association with species of *Tridacna.*

12. *Anchistus pectinis* Kemp, 1925

First reported from Keppel Bay and Magnetic Island with the scallop *Amusium balloti,* additional specimens have since been examined from the same host collected off Townsville and from Bowden Reef at about 30 m. *Anchistus pectinis* is also known from Zanzibar, the Nicobar Islands and Japan.

Apopontonia Bruce, 1976

13. *Apopontonia falcirostris* Bruce, 1976

Two separate collections of this species have been made at Heron Island and at One Tree Island. The Heron Island specimen was from a sponge in the genus *Psammascus.* The One Tree specimen came from an unidentified sponge collected at 18 m. Outside Australian waters, this species is known only from Madagascar.

Conchodytes Peters, 1852

14. *Conchodytes biunguiculatus* Paulson, 1875

The records of Miers (1844) of *Conchodytes tridacnae* from a bivalve in the genus *Pinna,* may refer to the occurrence of *C. biunguiculatus* at Keppel Island, Queensland. *Conchodytes biunguiculatus* has not been reported outside the Indian Ocean, Taiwan and Indonesia. However, Miers' (1884) specimens may have been examples of *Conchodytes monodactylus* or even *Anchistus custos.* Two specimens from King Sound, Western Australia are also provisionally referred to *C. biunguiculatus.* The specimens are in the collections of the British Museum (Natural History), registration number 86:20. The host was not recorded.

15. *Conchodytes meleagrinae* Peters, 1852

Conchodytes meleagrinae is common in Australian waters in association with pearl oysters in the genus *Pinctada.* It has been reported from several localities along the Great Barrier Reef (the Low Isles, Swain Reefs, Capricorn Islands), Bathurst Island and North West Cape, and occurs widely from the Red Sea to Hawaii.

16. *Conchodytes monodactylus* Holthuis, 1952

This species is recorded only from Magnetic Island, Queensland (Bruce, 1977) in association with a species of the bivalve *Atrina.* It is otherwise known from Taiwan, Hong Kong, Singapore and Indonesia, generally in association with bivalves in the genus *Pinna.*

17. *Conchodytes nipponensis* (de Haan, 1844)

Conchodytes nipponensis is reported only from Keppel Bay, Queensland, where it occurs with a scallop, *Amusium balloti.* It is otherwise known only from Japanese waters where it is also found in pectinid hosts.

18. *Conchodytes tridacnae* Peters, 1852

The species has been reported from several Great Barrier Reef localities. Miers (1884) recorded a specimen of *Pontonia tridacnae* from Keppel Island, Queensland, from a giant clam *Tridacna* sp., which is probably referable to this species. Other examples are known from Torres Strait, Warrior Reef, Tijou Reef, Herald Island, Swain Reefs and One Tree Island, usually in association with *Tridacna squamosa*. *Conchodytes tridacnae* is found throughout the Indian Ocean, and western Pacific Ocean east to the Marshall Islands.

Coralliocaris Stimpson, 1860

19. *Coralliocaris brevirostris* Borradaile, 1898

This rare species was reported by Patton (1966) from Willis Island, Coral Sea, in an *Acropora* coral. The species is otherwise known only from the type locality in the Ellice Islands.

20. *Coralliocaris graminea* (Dana, 1852)

First reported from the Palm Islands by Boone (1935) and later from numerous localities on the Great Barrier Reef, *C. graminea* occurs commonly in association with many species of the coral genus *Acropora*. It is found throughout the Indo-West Pacific region with the exception of the Hawaiian Islands.

21. *Coralliocaris superba* (Dana, 1852)

C. superba was first recorded in Australian seas by Patton (1966) with numerous specimens from Great Barrier Reef localities in association with *Acropora* corals. The species is known throughout the Indo-West Pacific region from the Red Sea to the Society Islands but is absent from the Hawaiian Islands.

22. *Coralliocaris venusta* Kemp, 1922 (α form)

C. venusta (α form) occurs at Heron Island, Queensland, on several *Acropora* coral species. It is not distinguishable from preserved specimens of the β form but each form has a characteristic colour pattern in life. The colour pattern of the type material was not recorded. The α form is characterised by conspicuous patches of white on the body and appendages. The distribution of the two forms is uncertain but both may occur at the same localities.

23. *Coralliocaris venusta* Kemp, 1922 (β form)

This form also occurs at Heron Island, Queensland, on several *Acropora* coral species, and may be distinguished in life by the absence of conspicuous white colour patches. The combined distribution of the two forms extends from the Red Sea to the Samoan Islands.

24. *Coralliocaris viridis* Bruce, 1974

Known in Australian seas only from Heron Island and One Tree Island, Queensland, but probably of widespread occurrence in *Acropora* corals, *C. viridis* also occurs at several localities in the western Indian Ocean and in the Ryukyu Islands.

Dasella Lebour, 1945

25. *Dasella herdmaniae* (Lebour, 1938)

A single damaged female specimen has been collected from the ascidian *Herdmania momus* at Heron Island, Queensland. The species has been previously recorded only from the type locality, Tuticorin, southern India, living in the same host.

Dasycaris Kemp, 1922

26. *Dasycaris ceratops* Holthuis, 1952

First recorded from Lodestone Reef, Queensland, from an unidentified antipatharian coral at 35 m, *D. ceratops* has since been found at Wistari Reef, Heron Island, on the pennatulacean *Pteroides bankanense* at 24 m. The species is otherwise known from Zanzibar and Indonesia.

27. *Dasycaris zanzibarica* Bruce, 1973b

D. zanzibarica has not previously been recorded from Australian waters, but specimens have been examined in the collections of the Australian Museum from Lizard Island and from Wheeler Reef off

Townsville at 12 m. The Lizard Island example was associated with an antipatharian coral of the genus *Cirripathes*. *D. zanzibarica* has previously been recorded only from the type locality, Zanzibar, on *Cirripathes anguinis*.

Fennera Holthuis, 1951

28. *Fennera chacei* Holthuis, 1951

Recorded from Willis Island, Coral Sea, by Patton (1966) on a coral, *Pocillipora verrucosa,* this species has recently been found at Heron Island, Queensland, on a pocilloporid coral *Stylophora pistillata* at 14 to 15 m. *F. chacei* has been reported from numerous localities in the western Indian Ocean and from the tropical western American seaboard.

Hamodactyloides Fujino, 1973

29. *Hamodactyloides incompletus* (Holthuis, 1958)

This species has not previously been recorded from Australian seas. Several examples have been found in association with *Millepora* hydrocorals at Lizard Island, Queensland. It is known elsewhere only from the Red Sea, Kenya, Zanzibar and La Reunion.

Hamodactylus Holthuis, 1952

30. *Hamodactylus aqabai* Bruce and Svoboda, in press

Known in Australian waters only from Heron Island, where it occurs in association with alcyonarians *Nephthea* spp., from 4 to 11 m. The species is otherwise known only from the type locality, Aqaba, Gulf of Sinai.

31. *Hamodactylus boschmai* Holthuis, 1952

Specimens have been collected from Heron Island, Queensland, in association with the gorgonians *Subergorgia reticulata* and *Melithea ocracea,* from 4 to 25 m. *H. boschmai* is otherwise known only from Zanzibar, Kenya, Madagascar, Indonesia and New Caledonia.

32. *Hamodactylus noumeae* Bruce, 1970

In Australian waters, this species is recorded only from Heron Island, Queensland, where it is found in association with a variety of gorgonian hosts, including species of *Euplexaura, Rumphella, Pseudopterogorgia* and *Subergorgia* from 4 to 27 m. It is also known from New Caledonia, Indonesia, Kenya, Tanganyika and Zanzibar.

Hamopontonia Bruce, 1970b

33. *Hamopontonia corallicola* Bruce, 1970b

This species has been recorded intertidally at Heron Island in association with scleractinian corals of the genus *Goniopora,* and in deeper water from *Heliofungia* and on an unidentified anemone. A specimen from a fungiid coral from 10 m at Lizard Island has also been examined. *H. corallicola* was first recorded in Australian waters from Peloris Island, Queensland, from 10 m on *Heliofungia actiniformis.* It is also known from Hong Kong and Japan.

Harpiliopsis Borradaile, 1917

34. *Harpiliopsis beaupresii* (Audouin, 1825)

H. beaupresii is abundant on corals of the genera *Pocillopora* and *Stylophora* at Heron Island, where it was first recorded from Australian seas by Patton (1966). There have been no subsequent records of this common species, which is found throughout the whole Indo-Pacific region and on Easter Island.

35. *Harpiliopsis depressa* (Stimpson, 1860)

H. depressa was also first recorded from Heron Island by Patton (1966) and later from Swain Reefs. It is much less common than *H. beaupresii* but not rare. *H. depressa* is found throughout the Indo-West Pacific region to the Galapagos Islands and on to the tropical western American seaboard. It is normally associated with pocilloporid corals.

36. *Harpiliopsis spinigera* (Ortmann, 1890)

Uncommon on *Stylophora* corals at Heron Island, *H. spinigera* also occurs on *Seriatopora*. It has been recorded from numerous localities in the western Indian Ocean, from Indonesia, the Loyalty and Samoan Islands, and from Panama. This species closely resembles *H. depressa* and many records of that species may refer to *H. spinigera*.

Ischnopontonia Bruce, 1966

37. *Ischnopontonia lophos* (Barnard, 1962)

Known from Great Palm, Orpheus, Fantome and Heron Islands, Queensland, *I. lophos* is found in association only with the oculinid coral *Galaxea fascicularis* to a depth of 15 m. It is otherwise recorded extensively from the western Indian Ocean, from Singapore and from the Great Astrolabe Reef, Fiji.

Jocaste Holthuis, 1952

38. *Jocaste japonica* (Ortmann, 1890)

Recorded by Patton (1966) from Willis Island, Restoration Rock, and Heron Island, *J. japonica* is also known from Swain Reefs. All records are from corals of the genus *Acropora* to a depth of 15 m. The species is found throughout the Indo-West Pacific region, excluding the Red Sea, east to New Caledonia and the Marshall Islands.

39. *Jocaste lucina* (Nobili, 1901)

J. lucina was also first recorded from Australian waters by Patton (1966) with material from Heron Island, Moreton Bay, Willis Island and Restoration Rock. Material was later collected from Swain Reefs. These shrimps are common associates of *Acropora* corals and occur throughout the Indo-West Pacific region with the exception of the Hawaiian Islands.

Mesopontonia Bruce, 1967

40. *Mesopontonia gorgoniophila* Bruce, 1967

This species has not been previously recorded from Australian seas. One ovigerous female was identified from an unidentified gorgonian from 270 m, collected by the F.V. "Nimbus" on 5 August 1968 at 26° 27′S 153° 51′E. It is otherwise known only from the northern South China Sea.

Onycocaridella Bruce, in press, d

41. *Onycocaridella monodoa* (Fujino and Miyake, 1969)

O. monodoa has been recorded twice from Heron Island and once from Tryon Island, Queensland, in association with sponges of the genus *Paraesperella* from the reef flat. It is otherwise known from the Ryukyu Islands, Pacific Ocean, and La Reunion, Indian Ocean.

42. *Onycocaridella prima* Bruce, in press, d

This species is known only from the type locality, Wistari Reef, Heron Island, where it was found in the sponge *Mycale sulcata,* from a depth of 12 m.

Onycocaris Nobili, 1904

43. *Onycocaris amakusensis* Fujino and Miyake, 1969

In Australian waters this species is recorded only from the reef flat at Heron Island in association with the sponge *Callyspongia* sp. It is also recorded from Zanzibar, Hong Kong, Japan and Hawaii.

44. *Onycocaris oligodentata* Fujino and Miyake, 1969

O. oligodentata has been recorded only once from Heron Island, Queensland, at a depth of 17 m, in association with a sponge, *Spongionella* sp. It is also known from Japan and Hong Kong.

45. *Onycocaris quadratophthalma* (Balss, 1921)

In Australian seas this species is known only from Cape Jaubert, Western Australia, the type locality. It has subsequently been reported from the Ryukyu Islands, Wake Island and Hawaii. *Onycocaris quadratophthalma* is probably also an associate of sponges but no hosts have yet been identified.

Palaemonella Dana, 1852

46. *Palaemonella pottsi* (Borradaile, 1915)

First recorded by Borradaile from Torres Strait and later from One Tree Island, Queensland, *P. pottsi* is common at Heron Island in association with the crinoids *Comanthus parvicirrus* and *Comanthina schlegli* to depths of 29 m. It is widespread in Indo-West Pacific waters from East Africa to the Marshall Islands.

47. *Palaemonella rotumana* (Borradaile, 1898)

Palaemonella rotumana is one of the commonest and most widely distributed pontoniine shrimps. It was first reported from the Low Isles (McNeill, 1968, as *Periclimenes rotumanus*) and has since been reported from One Tree Island and Heron Island in the Capricorn Islands and from Moreton Bay, Queensland. This free-living species occurs throughout the Indo-West Pacific region from the Red Sea to Hawaii in shallow water to about 125 m. It also extends into the eastern Mediterranean Sea.

48. *Palaemonella spinulata* Yokoya, 1936

A few specimens of this species have been reported from about 25 m at Heron Island, Queensland, and specimens have subsequently been examined from two intertidal localities at Dulwich, Moreton Bay. Previously recorded only from Japan, Tanganyika and La Réunion.

Paranchistus Holthuis, 1952

49. *Paranchistus armatus* (H. Milne-Edwards, 1837)

Paranchistus armatus was first recorded from Australian waters by McNeill (1968) with a specimen from Undine Reef, Cape Tribulation, in association with *Tridacna gigas*. The shrimps are apparently abundant in this host and numerous examples from the Cairns area, Michaelmas Cay and Arlington Reef, all from the same host species, have been examined. The distribution of this species is related to that of its single host and it has been recorded from the Moluccan Islands to the Marshall Islands.

50. *Paranchistus pycnondontae* Bruce, 1978a

This species is known only from the holotype collected at Heron Island, Queensland, in association with a bivalve *Hyotissa* sp.

Parapontonia Bruce, 1968

51. *Parapontonia nudirostris* Bruce, 1968

Parapontonia nudirostris has been recorded from a variety of crinoid hosts at Heron Island, One Tree Island and Stradbroke Island, Queensland. Additional specimens have been examined from Lizard Island and Sudbury Reef in association with the crinoids *Tropiometra afra* and *Himerometra robustipina.* It is otherwise known only from New Caledonia.

Paratypton Balss, 1914

52. *Paratypton siebenrocki* Balss, 1914

Since its being recorded by Patton (1966) from *Acropora squamosa* at Heron Island, there have been no more records of this species in Australian waters. It is known from numerous localities, from the Red Sea to La Réunion and eastwards to the Samoan Islands.

Periclimenaeus Borradaile, 1915

53. *Periclimenaeus arabicus* (Calman, 1939)

This species is recorded in Australian waters from four specimens collected in association with sponges at Heron Island, Queensland, between 1 and 30 m depth. One host has been subsequently identified as *Callyspongia* sp., and several additional examples have been obtained. The species is known sparsely from southern Arabia and Djibouti to Japan and New Caledonia.

54. *Periclimenaeus ardeae* Bruce, 1970a

P. ardeae was first reported from Heron Island, Queensland, where it occurs in association with the sponge *Jaspis stellifera.* It has been subsequently recorded from Kenyan waters from a different sponge host.

55. *Periclimenaeus bidentatus* Bruce, 1970a

Since this species was originally reported from Heron Island further examples have been collected from sponges in the genera *Arenochalina, Jaspis* and *Sponginella.* One example from Dunwich, Moreton Bay, has also been examined. The species has been otherwise recorded only from Zanzibar and Kenya.

56. *Periclimenaeus diplosomatis* Bruce, 1980

This species is known only from the type locality, Heron Island, Queensland, where a pair was collected from the colonial ascidian *Diplosoma rayneri.*

57. *Periclimenaeus djiboutensis* Bruce, 1970a

Two specimens of this species have been reported from sponges at Heron Island, Queensland. The identity of the hosts has not yet been established. *Periclimenaeus djiboutensis* is known from Djibouti, Eilat, Zanzibar and Madagascar.

58. *Periclimenaeus gorgonidarum* (Balss, 1913)

In Australian waters this species is known only from Heron Island, Queensland. An ovigerous female and a pair of specimens have been collected from 18 and 24 m off Heron Island and Wistari Reef. The latter were associated with a sponge of the genus *Siphonochalina. Periclimenaeus gorgonidarum* is otherwise known only from East Africa and Japan.

59. *Periclimenaeus hecate* (Nobili, 1904)

Periclimenaeus hecate was first recorded from Cape Jaubert, Western Australia by Balss (1921). It was reported later from Heron Island and Wistari Reef, Queensland, in association with encrusting colonial ascidians, such as *Diplosoma* spp. Balss' specimen should be re-examined to confirm its initial identification. *P. hecate* has otherwise been recorded only from the western Indian Ocean and Indonesia.

60. *Periclimenaeus odontodactylus* Fujino and Miyake, 1968

A pair of specimens from an unidentified sponge collected at 11 m off Wistari Reef, Heron Island, has been reported. A further pair of specimens has also been examined from a sponge collected at 20 m depth, 8 km off Lizard Island. This species has been previously recorded only from Japan and the Philippine Islands.

61. *Periclimenaeus orbitospinatus* Bruce, 1969b

This species was first recorded from the Gulf of Carpentaria near Mornington Island, in a sponge from 15 m. There have been no further records.

62. *Periclimenaeus ornatus* Bruce, 1970a

P. ornatus was initially described from Heron Island, Queensland. Further examples have since been obtained from the reef flat in association with the sponge *Jaspis stellifera,* often with *Periclimenaeus ardeae.* Elsewhere, this species has been reported only from Zanzibar.

63. *Periclimenaeus pachydentatus* Bruce, 1969b

First described from material collected at the Low Isles in association with the colonial ascidian *Sigillina deerata,* this species has since been reported from the south-eastern Gulf of Carpentaria and from Heron Island at 12 to 15 m. It is known from other parts of the Great Barrier Reef, from the same host. *Periclimenaeus pachydentatus* has not been recorded outside Australian waters.

64. *Periclimenaeus rastrifer* Bruce, 1980a

Recently found in sponges from 12 to 15 m around Heron Island, this species has not been previously recorded in Australian waters. Hosts include sponges of the genus *Ulosa. Periclimenaeus rastrifer* was previously known only from New Caledonia.

65. *Periclimenaeus rhodope* (Nobili, 1904)

A single pair of specimens has been recorded at Heron Island, Queensland, in an encrusting sponge on a reef flat coral. It has been reported elsewhere from several localities in the western Indian Ocean.

66. *Periclimenaeus tridentatus* (Miers, 1884)

The type locality for this species is Murray Island, Torres Strait. Further specimens have since been obtained from Heron Island and Wistari Reef, Queensland, at 7 to 12 m depth from species of encrusting colonial ascidians in the genus *Diplosoma.* The species is otherwise known with certainty only from the Sulu Archipelago and Singapore, with several other doubtful reports.

67. *Periclimenaeus tuamotae* Bruce, 1969b

This species has been recorded from Heron Island, Queensland, where seven specimens were found in an unidentified sponge at 12 m. It is otherwise known only from Mururoa Atoll, Kenya and Tanganyika.

Periclimenes Costa, 1844

68. *Periclimenes aesopius* (Bate, 1863)

Periclimenes aesopius was the first pontoniine shrimp recorded from Australian waters, from St. Vincent Gulf, South Australia. The species has not been reported subsequently from any other locality and its associations remain unknown.

69. *Periclimenes affinis* (Zehntner, 1894)

Several examples of this species have been recorded from Wistari Reef, Heron Island, Queensland, from 25 to 30 m, in association with the crinoids *Comatula cratera* and *Comanthina schlegeli* which they closely resemble in coloration. This rare species has otherwise been reported only from New Caledonia and the South China Sea.

70. *Periclimenes alcocki* Kemp, 1922

This species has not been previously recorded from Australian waters. A single female specimen has been collected from 330 m off Bateman's Bay, New South Wales, by the F.V. "Kapala" in May 1977. The host animal was not collected and the host of this shrimp is yet to be determined. *P. alcocki* has been recorded from Madagascar, the Laccadive Sea, the Philippine Islands and Japan.

71. *Periclimenes amboinensis* (de Man, 1888)

Periclimenes amboinensis is a rare species, of which the type material from Ambon, Indonesia, is no longer extant. One female and a pair of specimens have been collected from 15 to 23 m at Wistari Reef, Heron Island on the crinoids *Comanthina briareus* and *Comaster bennetti.*

72. *Periclimenes amymone* de Man, 1902

This species was first recorded from Heron Island, by Patton (1966) and also from One Tree Island, Queensland, from *Pocillopora, Stylophora* and *Acropora* corals. It is common on the branching corals of the Heron Island reef flat. *Periclimenes amymone* is distributed from the Nicobar Islands to the Samoan Islands.

73. *Periclimenes attenuatus* Bruce, 1971a

Periclimenes attenuatus has not been previously recorded from Australian waters. One male has been examined from an unidentified crinoid collected from 15 m at Lizard Island, Queensland. The species has been previously recorded only from the Duke of York Island, Bismarck Archipelago.

74. *Periclimenes brevicarpalis* (Schenkel, 1902)

First recorded in Australian waters by Saville-Kent (1893) from several Great Barrier Reef localities, *P. brevicarpalis* is also known from several northern Queensland localities and the Monte Bello Islands, Western Australia. It has been recorded from most of the Indo-West Pacific region, excluding Hawaii and south-eastern Polynesia, in association with species of the giant anemone genus *Stoichactis,* and with other anemones.

75. *Periclimenes brocketti* Borradaile, 1915

Three specimens from Heron Island, associated with a yellow crinoid, probably *Comanthina schlegeli,* have been provisionally referred to this little-known species, which is know with certainty only from the holotype from the Maldive Islands, and which may be synonymous with *P. affinis* (Zehntner).

76. *Periclimenes carinidactylus* Bruce, 1969a

Periclimenes carinidactylus is known from two examples only. One specimen was collected in Port Jackson, New South Wales, and the other came from Kangaroo Island, South Australia, collected at a depth of 9 m. The latter specimen was associated with the crinoid *Comanthus trichoptera.*

77. *Periclimenes ceratophthalmus* Borradaile, 1915

First recorded in Australian waters from One Tree Island on the crinoid *Himerometra robustipinna* at 43 m, this species was later recorded from Heron Island at 18 m on the same host. *P. ceratophthalmus* is distributed from Zanzibar and Kenya to the Solomon Islands.

78. *Periclimenes colemani* Bruce, 1975

This species was first discovered at Heron Island in association with the echinoid *Asthenosoma intermedium* at 11 m depth. One further example has since been obtained from the same host. It has yet to be recorded at any other locality.

79. *Periclimenes commensalis* Borradaile, 1915

Initially recorded from Murray Island, Torres Strait, this species is one of the commonest crinoid associates. It has since been reported from Heron Island and from Bribie Passage and Myora in Moreton Bay, Queensland. The hosts include *Comanthus parvicirrus, Comanthina schlegeli, Comaster multifidus* and *Lamprometra palmata,* a new host record. It has been found to a depth of 30 m. The species is widely distributed from the western Indian Ocean to the Great Astrolabe Reef, Fiji.

80. *Periclimenes consobrinus* (de Man, 1902)

This species is recorded in Australian waters only from Heron Island, Queensland, in association with the coral *Pocillipora damicornis,* from the reef flat. It is otherwise known only from several localities in the western Indian Ocean and the Moluccan Islands.

81. *Periclimenes cornutus* Borradaile, 1915

Specimens reported from Wistari Reef, Heron Island, Queensland, collected on the crinoid *Himerometra robustipinna* at 12 to 14 m, have been provisionally referred to this species, which may be a synonym of *P. amboinensis* (de Man). *P. cornutus* is known only from the holotype from the Maldive Islands.

82. *Periclimenes cristimanus* Bruce, 1965

Periclimenes cristimanus has been recorded from Heron Island, Queensland, in association with the echinoid *Echinothrix calamaris* from 3 to 17 m depth. It is otherwise recorded only from Singapore, Malaysia and Hong Kong.

83. *Periclimenes diversipes* Kemp, 1922

First recorded from Australia by Patton (1966) with specimens from Restoration Rock, Queensland, *P. diversipes* was later recorded from Heron Island where it occurs sparsely with a variety of hosts including species in the coral genera *Porites* and *Goniopora.* The species is known from the Red Sea to La Réunion and as far east as the Coral Sea.

84. *Periclimenes elegans* (Paulson, 1875)

This is a free-living species first recorded in Australia from Cape Jaubert, Western Australia, by Balss (1921), and later from the Capricorn Islands, Low Islands, Swain Reefs and Heron Island, Queensland. Its distribution extends from the Red Sea to the Marshall Islands.

85. *Periclimenes galene* Holthuis, 1952

Periclimenes galene is known in Australian waters from three specimens collected separately at Heron Island, Queensland, on the hydroid *Lytocarpus philippinus* at 18, 24 and 26 m depths. Originally reported from Indonesia, this species is now known also from Zanzibar, Tanganyika and Kenya, in association with the hydroid genus *Aglaophenia*.

86. *Periclimenes gonioporae* Bruce, in press, a

This species is recorded only from Heron Island, Queensland, in Australian waters, where a small number of specimens have been collected from the reef flat to 6 m depth, in association with a variety of coral genera including *Montipora, Goniopora, Galaxea* and *Porites*. The only previous records of this species are from Kenya and La Reunion.

87. *Periclimenes granulimanus* Bruce, 1978

A single specimen of this species is reported from Wistari Reef, Heron Island, Queensland, collected at 24 m in association with the hydroid *Lytocarpus philippinus*. The species is known by only one other specimen from Tany Keli, Madagascar, found on an antipatharian host.

88. *Periclimenes hertwigi* Balss, 1913

Periclimenes hertwigi was first recorded from Australia on the basis of specimens collected off Mooloolaba, Queensland, at a depth of 500 m, in association with the echinoid *Aerosoma thetidis*. There have been no subsequent records of this species from Australia. It has otherwise been recorded only from Japan, the East China Sea and the Kei Islands.

89. *Periclimenes holthuisi* Bruce, 1969a

First recorded in Australia from Bowen Island and later Peloris Island and Moreton Bay, Queensland, *P. holthuisi* has more recently been recorded from Heron Island where it occurs to a depth of 25 m in association with the coral genera *Goniopora* and *Catalaphyllia* and the anemone *Dofleinia armata*. It is otherwise known from Zanzibar to the Caroline Islands and from Hong Kong to New Caledonia.

90. *Periclimenes imperator* Bruce, 1967

This species was first recorded from Heron Island, Queensland, on the nudibranch *Hexabranchus sanguineus*, and has since been recorded from Undine Reef, Orpheus Reef and Lizard Island. Specimens have also been examined from Bligh Reef, associated with the holothurian *Bohadschia argus* and from Heron Island on another holothurian *Thelonota ananas*. *Periclimenes imperator* is extensively distributed throughout the Indo-West Pacific region from the Red Sea and Zanzibar to Hawaii.

91. *Periclimenes incertus* Borradaile, 1915

Reported from Cape Jaubert, Western Australia, by Balss (1921) (as *Palaemonella biunguiculatus*), *P. incertus* is also known from Heron Island, Queensland, in association with sponges of the genera *Arenochalina* and *Leucetta*, from 12 to 15 m. The species is distributed from Aden to Madagascar, east to Indonesia and New Caledonia.

92. *Periclimenes indicus* (Kemp, 1915)

Periclimenes indicus has been recorded from Moreton Bay, Queensland, in association with the intertidal anemone *Macrodactyla aspera*. It is otherwise known only from India, Singapore and Indonesia.

93. *Periclimenes inornatus* Kemp, 1922

Specimens have been recorded from Heron Island, Queensland, from giant anemones of the genus *Radianthus* in depths of 9 to 18 m. It is also known from Kenya and Zanzibar east to the Great Astrolabe Reef, Fiji.

94. *Periclimenes investigatoris* Kemp, 1922

This species has not been previously recorded from Australian waters. One specimen has been examined from an unspecified locality in Queensland, where it was collected in association with a telestacean host in the genus *Solenocaulon*. The species is otherwise known only from the type locality in the Arabian Gulf at 24 m depth.

95. *Periclimenes kempi* Bruce, 1969a

Periclimenes kempi has been reported in association with a variety of reef flat and shallow water alcyonarians, including *Sarcophyton, Limnalia, Macrospicularia* and *Nephthea*, only from Heron Island, Queensland. It is otherwise known from the Red Sea, Zanzibar, Andaman Islands and Singapore.

96. *Periclimenes kororensis* Bruce, 1977

Although not previously recorded from Australia, a pair of specimens of *P. kororensis* have been examined from Broadhurst Reef, Queensland. They were associated with the coral *Heliofungia actiniformis* from a depth of 17 m. The species has been previously recorded only from the type locality, Koror Island, in the Palau Islands, in association with the same host species.

97. *Periclimenes lanipes* Kemp, 1922

First noted in Australian waters from Double Island Point, Queensland, in association with the basket star *Euryale aspera,* further specimens of *P. lanipes* have been recorded from Heron Island on the same host species. *Periclimenes lanipes* is otherwise known from Somalia to Madagascar, east to the South China Sea and New Caledonia. It is the only pontoniine shrimp known to associate with an ophiuroid host.

98. *Periclimenes longirostris* (Borradaile, 1915)

Periclimenes longirostris is known in Australian waters from a single example reported from North East Cay, Herald Islands. The species has otherwise been recorded sparsely from the Red Sea, Zanzibar, Maldive, Seychelle and Andaman Islands, Papua, the Philippines and Enewetak Atoll.

99. *Periclimenes lutescens* auct.

Recorded from Heron Island by Patton (1966) and from Swain Reefs, with further material from Heron Island (Bruce, in press, f), *P. lutescens* lives in association with a variety of *Acropora* coral species. It is common throughout most of the Indo-West Pacific region from the Red Sea to Tonga and probably further east.

100. *Periclimenes madreporae* Bruce, 1969a

The type locality of this species is Erskine Island, Queensland. It is also known from Willis Island, Bet Reef, Restoration Rock, Heron Island, Wistari Reef and Myora, Moreton Bay (Patton, 1966) where it occurs in a wide variety of coral hosts. Outside Australian waters *P. madreporae* has been reported only from La Réunion and the Solomon Islands.

101. *Periclimenes magnificus* Bruce, 1979

This species was first described from specimens collected at Heron Island, Queensland, at 24 m depth, in association with the coral *Catalaphyllia plicata* and is also found in association with the anemone *Dofleinia armata.* Further specimens have since been collected at Heron Island, including four examples from a species of *Cerianthus* anemone. Outside Australian waters, it is known only from southern Japan.

102. *Periclimenes nilandensis* Borradaile, 1915

Periclimenes nilandensis is known in Australia from 14 specimens collected from the hydroid *Lytocarpus philippinus* at 24 m on Wistari Reef, Heron Island, Queensland. It is usually found with gorgonian hosts. The species has been reported from Zanzibar, Kenya, Madagascar, Maldive Islands, Indonesia and the South China Sea.

103. *Periclimenes ornatellus* Bruce, 1971a

This species is known in Australian waters from a single example from an unidentified anemone on the reef flat at Heron Island, Queensland. It is otherwise known only from Enewetak Atoll, on the anemone *Radianthus malu.*

104. *Periclimenes ornatus* Bruce, 1969a

In Australian waters this species is known only from Heron Island, Queensland, in association with anemones of the genus *Radianthus* to a depth of 6 m. It is otherwise known only from Kenya, Hong Kong, Japan and Enewetak Atoll.

105. *Periclimenes pectiniferus* Holthuis, 1952

A single ovigerous female was collected in 30 to 35 m depth, 50 km east of Townsville, Queensland, and represents the only occurrence of this rare species in Australian seas. It was previously known only from the type material from Kabala Dua Island, Indonesia. The host of this species has yet to be identified.

106. *Periclimenes platycheles* Holthuis, 1952

This species has not been previously recorded from Australia. One male and two ovigerous females from Lizard Island, Queensland, have been examined. They were collected from a colony of *Acropora* in 14 m depth. The species has previously been recorded only from Indonesia and the Palau Islands.

107. *Periclimenes psamathe* (de Man, 1902)

Numerous specimens of this species, found in association with the hydroid *Lytocarpus philippinus,* have been reported from 24 to 26 m at Heron Island, Queensland. Although not recorded elsewhere in Australia, this species is known from East Africa, Madagascar, Chagos and Maldive Islands, Indonesia, South China Sea, Japan, Palau and New Caledonia.

108. *Periclimenes ruber* Bruce, in press, c

At present known only from Australian waters, this species was first reported in association with the crinoid *Zygometra microdiscus* from 9 m in Bribie Passage, Queensland.

109. *Periclimenes seychellensis* Borradaile, 1915

Periclimenes seychellensis has been reported in Australian waters in numbers on the reef flat at Heron Island. This free-living micropredator, usually found in algal communities, is also known from the Red Sea to Mozambique, east to Indonesia and Papua.

110. *Periclimenes soror* Nobili, 1904

First recorded in Australian waters from Green and Fairfax Islands, Queensland, on the seastar *Acanthaster planci,* this species has subsequently been recorded from Chapman Island, Beaver Reef and Heron Island in Queensland, Cuwatong in New South Wales, and Exmouth Gulf and Dampier Islands in Western Australia. Specimens have also been examined from Lizard Island and Wreck Island, Queensland. The species associates with a wide variety of asteroid hosts, most commonly *Acanthaster* and *Culcita* but also species of *Plecaster, Halityle, Echinaster* and also *Nardoa novaecaledoniae,* a new host record. *Periclimenes soror* occurs throughout the whole Indo-West Pacific region from the Red Sea to Hawaii and the Tuamotu Islands, and also occurs in the Gulf of Panama.

111. *Periclimenes spiniferus* de Man, 1902

McNeill (1926) first recorded *P. spiniferus* in Australia from Northwest Islet, Capricorn Island and later from Heron Island and the Low Isles. The species is abundant on the Heron Island reef flat, and specimens have also been examined from Lizard Island. *Periclimenes spiniferus* is present throughout most of the Indo-West Pacific region with the exception of the north-west Indian Ocean and Red Sea. It is a free-living species commonly found sheltering in coral colonies.

112. *Periclimenes tenuipes* Borradaile, 1898

Four specimens have been reported from Wistari Reef, Heron Island, Queensland from 14 to 24 m. It is also known from Zanzibar, Kenya, Madagascar and east to Palau Islands and Enewetak Atoll. *Periclimenes tenuipes* is apparently a free-living, nocturnally active animal, but it has been reported as an anemone associate at Palau Islands (Read, 1974).

113. *Periclimenes tenuis* Bruce, 1969a

A few examples of this species have been reported from Heron Island, Queensland, in association with crinoids, including *Himerometra magnipinna.* It is known elsewhere only from Zanzibar and Eilat.

114. *Periclimenes toloensis* Bruce, 1969a

Periclimenes toloensis has been recorded from Wistari Reef and Heron Island, Queensland, on the hydroid *Lytocarpus philippinus* from 24 m depth. It is otherwise known only from the type locality, Hong Kong, and from Zanzibar.

115. *Periclimenes zanzibaricus* Bruce, 1969

This species is recorded in Australia only from Geraldton, Western Australia (Bruce, 1973) in association with the echinoid *Centrostephanus tenuispinus.* It is otherwise recorded only from Zanzibar, Kenya and the Seychelles.

Philarius Holthuis, 1952

116. *Philarius gerlachei* (Nobili, 1905)

Philarius gerlachei has been recorded by Patton (1966) from Willis Island, Bet Reef, Restoration Rock and Heron Island, Queensland, in association with *Acropora* corals. Further examples have since been examined from Heron Island. This species extend from the Red Sea to the Samoan Islands.

117. *Philarius imperalis* (Kubo, 1940)

Three examples of *P. imperialis* were recorded by Patton (1966) from reef flat Acropora colonies at Heron Island and three from Restoration Rock, Queensland. Further specimens from Heron Island and Lizard Island have since been examined. This species is found to depths of 20 m, from the Red Sea to the Marshall Islands.

118. *Philarius lifuensis* (Borradaile, 1898)

Several examples of this little-known species have been reported from Wistari Reef and Heron Island, Queensland, from *Acropora* corals between 6 and 18 m depth. The species has been previously recorded from Heron Island and Erskine Island in the Capricorn Island and is otherwise known only from the type locality in the Loyalty Islands.

Platycaris Holthuis, 1952

119. *Platycaris latirostris* Holthuis, 1952

This species was recorded from Australia on the basis of a single pair of specimens collected at 15 m from Heron Island, Queensland, in the oculinid coral *Galaxea fascicularis.* There have been no further examples collected. The species is otherwise known from Kenya to La Réunion, east to the Great Astrolabe Reef, Fiji.

Pliopontonia Bruce, 1973a

120. *Pliopontonia furtiva* Bruce, 1973a

Pliopontonia furtiva was first recorded from Australia by Coleman (1977) from Heron Island, Queensland. Further specimens have since been recorded from 8 m at Wistari Reef, Heron Island and a single example has been examined from 5 m at Cook Island, Tweed Heads, New South Wales. The species is known elsewhere only from the type locality in Kenya.

Pontonia Latreille, 1829

121. *Pontonia ardeae* Bruce, in press, b

This species was recently described from Heron Island, Queensland, at 18 m depth, in association with the bivalve *Chama reflexa.* It has not yet been recorded from any other localities.

122. *Pontonia katoi* Kubo, 1940a

Pontonia katoi was initially reported in Australia from Coil Reef, Queensland, and later from Wistari Reef and Heron Island, in association with species of solitary ascidians in the genera *Herdmania, Cnemidocarpa, Polycarpa* and *Styela.* Other examples have been examined from Lizard Island, Queensland, in *Polycarpa aurata* and from Cockburn Sound, Western Australia, in *Polycarpa pedunculata.* The species is otherwise known from Tanganyika, Japan, Indonesia and New Caledonia.

123. *Pontonia minuta* Baker, 1907

This species has been recorded only from an indefinite locality in South Australia and from Meroo Point, New South Wales. There have been no reports from outside Australia. A colour slide of a pair of pontoniine shrimps associated with the polychaete *Eunice aphroditois* is provisionally referred to *P. minuta*—the shrimps were not preserved. They were collected by Ms J. Hunter on 18 February 1973 from Long Reef, Sydney, New South Wales. They were uniformly bright red with the outer parts of the fingers of the second pereiopods, propod and carpus of the ambulatory pereiopods, and distolateral part of the exopod of the uropod white. There are no confirmed records of associations between annelids and pontoniine shrimps. *Pontonia minuta* is the only pontiine shrimp known to have abbreviated larval development. The species differs in a number of small morphological characters from all other species of this genus and these, together with abbreviated larval development and possible association with an annelid host suggest that this taxon should probably be placed in a separate genus (Bruce, 1972d).

124. *Pontonia okai* Kemp, 1922

Specimens have been recorded at Heron Island at depths of 15 m, in association with ascidians, including a species of *Ascidia. Pontonia okai* is otherwise known from Kenya, Burma, the Lesser Sunda Islands and the South China Sea.

125. *Pontonia sibogae* Bruce, 1972b

Pontonia sibogae is recorded in Australia only from Port Curtis and Lodestone Reef, Queensland. The Port Curtis material, from 3 to 6 m depth, was associated with the ascidian *Styela whiteleggii.* The species is also known from Madagascar and Indonesia.

Pontonides Borradaile, 1917

126. *Pontonides* sp., aff. *unciger* Calman, 1939

A pair of specimens has been collected from 23 m at Wistari Reef, Heron Island, Queensland, in association with the whip coral *Cirripathes anguina.* These specimens are considered to be distinct from *P. unciger* Calman s.s. Similar material from Lizard Island has also been examined. This species of *Pontonides* occurs extensively throughout the Indo-West Pacific region. *P. unciger* s.s. is known only from the Red Sea and Kenya.

Pontoniopsis Borradaile, 1915

127. *Pontoniopsis comanthi* Borradaile, 1915

First described from specimens collected at Mabuaig, Torres Strait, the species has since been reported from Wistari Reef and Heron Island at a depth of 6 to 21 m. *Pontoniopsis comanthi* usually occurs on crinoids including *Comatula pectinata, C. purpurea* and *Capillaster multiradiatus.* Outside Australia the species ranges from the Red Sea to the Gilbert Islands.

Propontonia Bruce, 1969

128. *Propontonia pellucida* Bruce, 1969

A pair of specimens has been recorded from the reef flat at Heron Island, in association with a species in the alcyonarian genus *Lobophyton.* The species is known otherwise from several western Indian Ocean localities.

Stegopontonia Nobili, 1906

129. *Stegopontonia commensalis* Nobili, 1906

A single specimen of this species has been reported from Australia, in association with the echinoid *Diadema setosum* at Heron Island (Gillet and McNeill, 1959). This species has not been found subsequently on Heron Island. It has been rarely reported from Kenya to Hawaii and the Tuamotu Islands.

Thaumastocaris Kemp, 1922

130. *Thaumastocaris streptopus* Kemp, 1922

Thaumastocaris streptopus has been previously recorded from Heron Island and Wistari Reef, Queensland, from 12 m in the sponges *Arenochalina flammula* and *Leucetta microraphis.* A few further specimens have since been collected. The species is known elsewhere from Zanzibar, Kenya, Somalia, Madagascar, Indonesia, New Caledonia and Enewetak Atoll.

Typton Costa, 1944

131. *Typton anomalus* (Bruce, 1979)

This species is known only from the type locality, Darwin, Northern Territory, from three ovigerous females collected between 5 and 13 m, probably from sponge hosts. There have been no further reports of this species, which was originally placed in the genus *Onycocaris.*

132. *Typton australis* Bruce, 1973c

Typton australis was first described from Chinaman's Reef, Queensland, and has since been reported from Heron Island reef flat in association with a sponge in the genus *Psammopemma*. There have been no records of this species outside Australian waters.

133. *Typton bawii* Bruce, 1972c

One specimen has been reported from an unidentified sponge on the Heron Island Reef flat. There have been no subsequent specimens collected. The species is elsewhere known only from Zanzibar and Kenya.

134. *Typton dentatus* Fujino and Miyake, 1969

A pair of specimens has been reported from the reef flat at Heron Island, Queensland, in a sponge in the genus *Reniera*. There have been no further records and the species is otherwise known only from the type locality in the Ryukyu Islands.

135. *Typton wasini* Bruce, 1977b

Numerous specimens have been recorded from Heron Island, Queensland, from the reef flat, crest and slope, in a variety of small encrusting sponges, including a species of *Dysidea*. The species has been recorded elsewhere only from Kenya and La Reunion.

Zenopontonia Bruce, 1975

136. *Zenopontonia noverca* (Kemp, 1922)

Zenopontonia noverca was first reported from Bowen, Queensland, and from Wistari Reef and Heron Island, on the asteroid *Pentaceraster regularis*. There have also been no other Australian records but the species is also known from Zanzibar, Madagascar and New Caledonia.

DISCUSSION

The subfamily Pontoniinae is at present represented by 136 species, belonging to 36 genera, in the waters of the Australian continent. Of these genera, 18 are monotypic, in most cases highly modified morphologically and specialised in their associations with a restricted range of hosts. The fauna is dominated by the genus *Periclimenes* with 48 species, 6 of which are free-living while the others are associated with a wide variety of host animals including particularly sponges, corals, anemones and crinoids. The genus *Periclimenaeus* is also well represented by 15 species, 11 of which are associates of sponges and 4 of colonial ascidians. *Coralliocaris* is represented by 6 species, all associated with corals in the genus *Acropora*. *Typton* is represented by 5 species, all associated with sponges. *Conchodytes* also with 5 species, is associated with bivalves. *Pontonia* has 3 species found in association with solitary ascidians, one with a bivalve mollusc and one species of rather uncertain systematic position possibly associated with an annelid.

Of the species recorded in this report 13 have not yet been found to occur outside Australian waters. Several have recently been described from Queensland waters and may be expected to occur elsewhere but the species from Australia's southern waters may be endemic (indicated by asterisks in the following list):

Onycocaridella prima; Paranchistus pycnodontae; Periclimenaeus diplosomatis, P. orbitospinatus, P. pachydentatus; Periclimenes aesopius, P. carinidactylus*, P. colemani, P. ruber; Pontonia ardeae, P. minuta*. Typton anomalus, T. australis.*

With the exception of 8 species (2 *Palaemonella*, 6 *Periclimenes*) regarded as free-living browsers, scavengers or micropredators, all other species are considered to be 'commensals' of other marine invertebrates, although the hosts of 3 species are yet to be identified. These associations are summarised in Table 1.

Coelenterates predominate among the hosts of pontoniine shrimps. They are hosts to 50 shrimp associates in 18 genera; of these 50 shrimp species, 29 (in 11 genera) are associated with scleractinian corals. Sponges are the hosts of 27 species in 8 genera and echinoderms are host to 23 species in 11 genera.

Only very general comparisons of the diversity of the Australian fauna with other regions are yet possible as few regions have been investigated to the same level. The Indonesian Archipelago has a pontoniine fauna of 67 species (Holthuis, 1952), Zanzibar Island has 87 species (Bruce, 1974a), the

Table 1. THE ASSOCIATIONS OF THE AUSTRALIAN PONTONIINE SHRIMPS

Host	**Number of associates**	**Genera associated (number of species in parentheses)**
Porifera	27	
Demospongiae	27	*Anchistioides (3); Apopontonia (1); Onycocaridella (2); Onycocaris (3); Periclimenaeus (11); Periclimenes (1); Thaumastocaris (1); Typton (5)*
Coelenterata	50	
Hydroida	6	*Hamodactyloides (1); Periclimenes (5)*
Antipatharia	2	*Pontonides (1); Dasycaris (1)*
Alcyonacea	3	*Hamodactylus (1); Periclimenes (1); Propontonia (1)*
Telestacea	1	*Periclimenes (1)*
Gorgonacea	4	*Hamodactylus (2); Mesopontonia (1); Pontonides (1)*
Pennatulacea	1	*Dasycaris (1)*
Corallimorpharia	1	*Pliopontonia (1)*
Actiniaria	3	*Periclimenes (3) (+2*)*
Scleractinia	29	*Anapontonia (1); Coralliocaris (6); Fennera (1); Hamopontonia (1); Harpiliopsis (3); Ischnopontonia (1); Jocaste (2); Paratypton (1); Periclimenes (9); Philarius (3); Platycaris (1)*
Mollusca	16	
Gastropoda	1	*Periclimenes (1)*
Bivalvia	15	*Anchistus (7); Conchodytes (5); Paranchistus (2); Pontonia (1)*
Annelida	1?	
Polychaeta	1?	*?Pontonia minuta*
Echinodermata	22	
Crinoidea	13	*Palaemonella (1); Parapontonia (1); Periclimenes (10); Pontoniopsis (1)*
Holothuroidea	1	*Periclimenes (1)**
Echinoidea	6	*Allopontonia (1); Periclimenes (4); Stegopontonia (1)*
Asteroidea	2	*Periclimenes (1); Zenopontonia (1)*
Ophiuroidea	1	*Periclimenes (1)*
Chordata	9	
Ascidiacea	9	*Dasella (1); Periclimenaeus (4); Pontonia (4)*
Host unknown	3	*Periclimenes (3)*
Free-living	8	*Palaemonella (2); Periclimenes (6)*
Total	136	

*paratenic association only.

Seychelle Islands 50 species (Bruce, in press, e) and Japan 33 species. The central East African fauna (Kenya and Tanzania) consists of 134 species (Bruce, 1974a). In all these areas the pontoniine fauna is still inadequately known.

The distribution of most of the 'commensal' species will be largely determined by the distribution of their host animals and their adaptability in utilising other types of host animals. The preponderance of species from Queensland waters reflects the amount of study this region attracts and is not an accurate measure of their relative diversity or of their geographical distribution, although undoubtedly these shrimps do reach their maximum diversity in the coral reef biotope. The caridean fauna of the tropical northern waters in Western Australia and the Northern Territory has still only been cursorily studied. Undoubtedly many or even most of the species known from Queensland will also occur in these regions, probably with additional species.

At present only 13 species have been recorded in Australia from outside Queensland waters, mainly from single occurrences at scattered localities, but 6 species were reported by Balss (1921) from Cape Jaubert, Western Australia.

Note added in proof. The following publications listed as being in press in the "References" section have now been published.
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————in press, c: *Mem. Aust. Mus.* 16: 191-216 (1982).
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