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A PHYLOGENY OF THE FAMILIES OF THALASSINIDEA (CRUSTACEA: DECAPODA) WITH KEYS TO FAMILIES AND GENERA

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Abstract

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The confused taxonomy of the Thalassinidea (73 genera recognised here) is briefly reviewed. States of 93 characters are discussed with reference to five outgroup genera of reptant decapods. The linea thalassinica is concluded to be homologous with the linea anomurica of Anomura. Its loss in Axioidea is thought secondarily derived. Burrowing behaviour in callianassoids is coincident with loss of the interaction between the posterior margin of the carapace and anterolateral lobes on abdominal somite 1, and with loss of abdominal pleura. Characters from gills, mouthparts and pereopods are discussed. Pereopodal spiniform setae are a unifying feature of some axioids. Auxiliary surfaces on the margins of pleopods of *Callianidea* and *Michelea* are not homologous. Setal-rows, once thought to unite several genera into the Callianideidae are shown to be more widespread and this family, as previously conceived, to be polyphyletic.

A computer-aided phylogenetic analysis of the families, represented by 22 genera, has confirmed the monophyly of the infraorder, based largely on the unique possession of a setose lower margin to pereopod 2. The Thalassinidea are divided into three superfamilies: Thalassinoidea and Callianassoidea, more closely related to each other than to Axioidea. The Thalassinoidea contains a single family and single genus, *Thalassina*. Callianassoidea are divided into six families: Laomediidae, Upogebiidae, Callianideidae, Thomassiniidae, Ctenochelidae (paraphyletic), and Callianassidae. Axioidea contain four families: Calocarididae, Axiidae, Strahlaxiidae fam. nov. and Micheleidae.

The new classification differs from that of Borradaile (1903) only in the inclusion of many more taxa. The affinities between families suggested by Gurney (1938), de Saint Laurent (1973), Kensley and Heard (1991) and Sakai (1992a) are not supported.

Diagnoses and keys are presented for the families and all the currently accepted genera, largely based on review of the literature and reference to museum collections.

Contents

Introduction

The decapod infraorder Thalassinidea is a group of families of reptant or "tailed decapods which recall the hermit-crabs in some respects and the lobsters and crawfishes in others" (Borradaile, 1903). A satisfactory diagnosis of the group has never been given in spite of the attention of numerous workers. While preparing a contribution describing several new thalassinidean taxa it became clear that the Thalassinidea had never been unambiguously defined and the relationships between all the families had not been thoroughly investigated.

Several families have been assigned to the Thalassinidea but the number, and the genera contained therein, are somewhat contentious. Seventy-three genera are recognised here but the number of available names is larger. Three families, each well defined but themselves not apparently closely related, are:

Thalassinidae Dana, 1852 with two to four very similar species in one genus (fig. 1a; Poore and Griffin, 1979; Dworschak, 1992; Sakai, 1992a).

Laomediidae Borradaile, 1903 with 15 species in five diverse genera (fig. 1b; Kensley and Heard, 1990); and

Upogebiidae Borradaile, 1903 with over 100 species world-wide in seven quite similar genera (fig. 1c; Sakai, 1982; Ngoc-Ho, 1989; Williams and Ngoc-Ho, 1990; Sakai, 1993);

The monophyly of each of these three families is not disputed and each can be defined by numerous autapomorphies.

The remaining genera have been assigned to at least two and as many as 14 family-level taxa and their classification has been more unstable.

The largest of these families are Axiidae Huxley, 1879 (fig. 3a) and Callianassidae Dana, 1852 (fig. 2c). Both have from time to time included some forms which could not be clearly assigned. One genus, *Calocaris* Bell, 1853, was moved to its own family, Calocarididae Ortmann, 1891, but for most of this century has been treated as a member of the Axiidae. Ortmann's taxonomic judgement was supported by Kensley (1989) but was not followed by Sakai and de Saint Laurent (1989). Kensley (1989) included in the Calocarididae four genera previously included in the Axiidae. Sakai and de Saint Laurent (1989) separated *Coralaxius* Kensley and Gore, 1981 into a new subfamily, Coralaxiinae.

The Callianassidae and the smaller Callianideidae Kossmann, 1880 were first redefined in a modern context by de Saint Laurent (1973) who erected a new subfamily of the former, Thomassiniinae. This work was extended by Manning and Felder (1991, 1992), Manning (1992) and Rodrigues and Manning (1992) who erected four further callianassid subfamilies and several new genera. Manning and Felder (1991) implicitly raised Thomassininae to family rank. They added a new family Ctenochelidae (with three subfamilies) for four atypical genera.

Seven callianideid- and thomassiniid-like genera were grouped into the Callianideidae by Kensley and Heard (1991). Sakai (1992a) added another genus (here treated as a junior synonym of *Callianidea*) and divided the family into four subfamilies. Another is added in this work. Numerous new species are being described in work in progress. The genera of interest are: *Callianidea* Milne Edwards, 1837 (fig. 2a), *Crosniera* Kensley and Heard, 1991, *Marcusiaxius* Rodrigues and Carvalho, 1972 (fig. 3c), *Meticonaxius* De Man, 1905, *Michelea* Kensley and Heard, 1991 (fig. 3b), *Mictaxius* Kensley and Heard, 1991, *Tethisea* gen. nov. and *Thomassinia* de Saint Laurent, 1979a (fig. 2b).

The Thalassinidea have also included from time to time the genera *Enoplometopus* Milne Edwards, 1862 and *Hoplometopus* Holthuis, 1983 in the Axiidae (Balss, 1957; Holthuis, 1983) but these are now removed to their own family and superfamily (de Saint Laurent, 1988).

The definition of the Thalassinidea and the relationships between families, subfamilies and genera are now uncertain. There are competing definitions of Callianideidae, Thomassiniidae and their subfamilies. Examination of species of Axiidae, Calocarididae, Ctenochelidae and Callianassidae revealed that some of the characters used to define the callianideid and thomassiniid groups are more widespread than hitherto appreciated and that neither the schemes of Kensley and Heard (1991) nor of Sakai (1992a) seem to reflect the phylogeny of the infraorder.

It is the objective of this paper to attempt to define the Thalassinidea and to present a new hypothesis explaining family relationships. The work does not resolve generic definitions or relationships in the Axiidae and Calocarididae [dealt with by Sakai and de Saint Laurent (1989), Kensley (1989, work in progress)], and Callianassidae and Ctenochelidae [dealt with by Manning and Felder (1991, 1992), Manning (1992) and Rodrigues and Manning (1992)] although many taxa in these families have been examined in the course of this study. This need arose from the realisation that these families are not as homogeneous as current usage suggests.

A new classification and diagnoses of the superfamilies and families reflecting these relationships are offered. Keys, based mostly on recently published literature, to the superfamilies, families and genera of Thalassinidea in current use are presented.

Methods

Material for this study comes largely from the Muséum National d'Histoire Naturelle, Paris, and from the Museum of Victoria, Melbourne and checked for general consistency by reviewing the literature. Specimens of the rarest species will be listed in a paper nearing completion.

Hennigian phylogenetic (cladistic) methods were used to generate cladograms as hypotheses of the relationships of thalassinidean families. For families of undisputed monophyly, single genera were chosen for inclusion (Thalassinidae, Laomediidae and Upogebiidae). For others where subfamily relationships are unclear (Callianassidae, Axiidae, Ctenochelidae), or whose generic composition is controversial (Callianideidae, Thomassiniidae, Micheleidae), several or all genera were included in the analysis.

Outgroups were chosen from the reptant Decapoda in order to assess general evolutionary trends. These trends are assumed but are unlikely to be controversial. I contend that the primitive thalassinidean had the general habitus shown by the modern axiids, upogebiids, laomediids or thalassinids rather than by callianassids. In the axiids, for example, the cephalothorax is compact, little shorter than the abdomen, solid, with a prominent rostrum from which originate dorsolateral carinae running on to the carapace. The abdomen is firmly attached to the cephalothorax, has well developed pleura on all somites, and is strongly reflexed. In addition, the second abdominal pleuron overlaps the first anteriorly and the two abdominal somites articulate by means of a lateral condyle (cf. Burkenroad, 1981: 259–260). The pleopods 2–5 are similar and sexually unspecialised, and the pereopods 2–4 are typically cylindrical and linear rather than flattened for digging in soft sediments.

As far as is known axiids live in short burrows in hard or soft sediment, in crevices between rocks, or in cavities in sponges or corals. Kensley and Simmons (1988) described the straight 150-mm-long burrows of their new species *Axiorygma nethertoni*. Pemberton et al. (1976) reported that *Axius serratus* builds burrows up to 3 metres deep. *Calocaris macandrae* (Calocarididae) has also been reported to construct burrows (Atkinson and Taylor, 1988). In general they do not build complex lined burrows in muddy or sandy sediments as is the case for some callianassids (de Vaugelas and de Saint Laurent, 1984; Suchanek et al., 1986), a form of behaviour which is correlated with a more elongate body form, specialised fossorial pereopods, and considerable flexibility between the cephalothorax and first abdominal somites.

Discussion on character transformations is based on the assumption that the compact habitus is primitive and the elongate tube-dwelling habitus is derived. Many of the character transformations used in constructing the phylogeny reflect this assumed change in biology. Loss of rostrum and absence of armature on the carapace, abdomen and limbs seem correlated with a burrowing way of life. No assumption is made on the monophyly of the elongate forms.

The program, HENNIG86, was used to establish generic relationships and in order to derive a practical classification which as closely as possible reflected these relationships. Its results were confirmed with the program PAUP version 2.4 which was used to generate a list of apomorphies for each clade in the chosen tree.

The following sections describe the outgroups, taxa chosen and character transformations, before discussing the results and classification.

Outgroups

The living glypheid, *Neoglyphea inopinata*, described in detail by Forest and de Saint Laurent (1981, 1989) was selected as an outgroup and, because it scored zero (was plesiomorphic) for all characters except one, it became the effective 'ancestor' against which the trees were rooted. The genus *Enoplometopus* Milne Edwards (sometimes considered an axiid) to represent the superfamily Enoplometopoidea de Saint Laurent, 1988 and the nephropid, *Nephropsis stewarti* Wood-Mason, were also included. The Anomura were represented by a species of *Munida* (Galatheidae) and of *Dardanus* (Diogenidae).

Taxa chosen

Twenty-two genera representing at least 12 families or subfamilies were included in the phylogenetic analysis. The species from which data were gathered are listed in parentheses.

Three genera represent monophyletic families which, except for the Laomediidae, are relatively homogeneous: *Upogebia* Leach [*U. darwinii* (Miers) but see also Williams, 1986; Ngoc-Ho, 1989; Le Loeuff and Intès, 1974]; *Laomedia* De Haan [*L. healyi* Yaldwyn and Wear but see also Kensley and Heard, 1990]; and *Thalassina* Latreille [*T. squamifera* De Man].

The remaining families are much more diverse in form and with a complex nomenclature. Genera were selected to cover all nominate families and subfamilies.

The Axiidae (including Coralaxiinae) and Calocarididae include at least 30 genera (Sakai and de Saint Laurent, 1989; Kensley, 1989; Sakai, 1992b) but the monophyly of the two families is still questionable. Six very different genera were chosen: *Axiopsis* Borradaile [*A. serratifrons* Milne Edwards]; *Axius* Leach [*A. stirhynchus* Leach]; *Calocaris* Bell [*C. macandreae* Bell]; *Coralaxius* Kensley and Gore [*C. abelei* Kensley and Gore]; *Spongiaxius* Sakai and de Saint Laurent [an undescribed New Caledonian species]; *Strahlaxius* Sakai and de Saint Laurent [*S. plectrorhynchus* (Strahl)]. Because so few genera were selected from this group, the generic relationships of the family (or families) suggested by the analysis are only a weak hypothesis.

All genera of the Callianideidae in the sense of Kensley and Heard (1991) and Sakai (1992a) were included: *Callianidea* [*C. typa* Milne Edwards and *C. laevicauda* Gill]; *Thomassinia* [*T. gebioides* de Saint Laurent and *T.* sp. nov.]; *Crosniera* Kensley and Heard [*C. minuta* (Rathbun) and *C.* sp. nov.]; *Mictaxius* [*M.* sp. nov.]; *Marcusiaxius* [*M. lemoscastroi* Rodrigues and de Carvalho]; *Meticonaxius* [*M. monodon* De Man]; *Michelea* [*M. leura* (Poore and Griffin)]; *Tethisea* gen. nov. [*T. indica* sp. nov.]. Information for all genera was supplemented by other species examined for another work in preparation.

Four genera were selected from the Ctenochelidae as defined by Manning and Felder, 1991: *Anacalliax* de Saint Laurent [*Anacalliax agassizi* (Biffar)]; *Ctenocheles* Kishinouye [*C. collini* Ward]; *Gourretia* de Saint Laurent [an undescribed species]; *Paracalliax* de Saint Laurent [*P. bollorei* de Saint Laurent].

The Callianassidae were represented by *Trypaea* Dana [*Trypaea australiensis* Dana]. Detailed anatomical descriptions of several callianassid genera can be found in de Saint Laurent and Le Loeuff (1979) and Manning and Felder (1991). In fact, the characters scored were largely consistent throughout most callianassid genera, such as *Callianassa* Leach, *Callichirus* Stimpson and *Glypturus* Stimpson, as revealed by a review of extensive collections in the Museum of Victoria and the Muséum National d'Histoire Naturelle. It was not an objective to investigate the relationships of the genera of this large family, only to determine its affiliation to the other thalassinideans.

Character discussion

Ninety-three characters were used in the analysis and are discussed in turn. All are potential synapomorphic characters (i.e. none is apomorphic for a single genus). Their states are given in Table 1 and the data matrix in Table 2. Generic autapomorphies are not included in these tables.

Carapace, linea thalassinica and rostrum. The linea thalassinica (figs 1a–c, 2b, 2c) is said to characterise the Thalassinidea and much has been made of it in the classification of the families. The acquisition of a well-developed linea thalassinica which supposedly allows the lateral carapace to hinge for ventilation and cleaning of the gills would be of value to an animal in a burrow. Borradaile (1903) used the absence of a linea thalassinica to separate the Axiidae (also burrowers) from the other three families he recognised. However, the homology of the linea thalassinica with the linea anomurica in Anomura has never been convincingly demonstrated. I believe that the linea thalassinica is homologous throughout the thalassinidean genera in which it occurs and is homologous with the linea anomurica.

Four reference points on the anterior margin of the carapace (e.g. fig. 4m) serve to establish this homology: (1) median rostrum; (2) ocular lobe or spine (lateral to the eyestalk); (3) branchiostegal sclerite (a thickened more or less triangular marginal part of the branchial area attached to the epistome anteriorly, defined by weakly calcified grooves dorsally and ventrally, and to which a transverse muscle attaches posterior to the mouthparts); and (4) anterior branchiostegal lobe (a free lobe of the carapace enclosing the mouthparts anterolaterally). The linea anomurica and linea thalassinica start anteriorly as a line of weak calcification defining the dorsal margin of the branchiostegal sclerite. The cervical groove runs obliquely and converges with it.

The linea thalassinica runs the complete length of the carapace in Thalassinidae (fig. 1a), Laomediidae (fig. 1b), most Callianassidae (fig. 2c) and Ctenochelidae as does the linea anomurica in Galatheidae. In upogebiids the anterolateral margin of the cephalothorax is oblique, the branchiostegal sclerite is some distance posterior to the ocular spine, and the thoracic sternites very short (fig. 1c). As a consequence the linea thalassinica is depressed anterior to the point where the cervical groove meets it. The branchiostegal sclerite is more rounded anteriorly than in the Callianassidae but its relationship to the anterior branchial lobe is the same as in other families. An oblique branchiostegal ridge crosses and strengthens the branchiostegal sclerite and often appears as an extension of the cervical groove. The pattern in upogebiids varies between species and is complicated by failure of the linea to always reach the posterior margin of the carapace. An oblique ridge posteriorly on the branchial flap is variously developed in some species and may appear with an associated groove in place of the posterior section of the linea thalassinica. However, whatever the modification of the linea in more evolved upogebiids, there seems little doubt to me that the upogebiid pattern is primitively much the same as in other thalassinideans.

In Axiidae (figs 3a, 4a), Calocarididae and Micheleidae (figs 3b, c) the front of the carapace is simpler. The rostrum, weak ocular lobe and anterior branchiostegal lobe are clear but a defined branchiostegal sclerite is wanting. A very weak lobe near the base of antenna 2 may indicate its anterodorsal corner in some genera. The linea thalassinica is never visible.

Callianidea (fig. 2a) appears very similar to Axiidae but in one of the species (the most primitive on other counts — pleopodal lamellae, male pleopods), *C. laevicauda*, a short linea thalassinica is present and this is how the genus is scored.

In Thomassiniidae there is a linea thalassinica starting between the rostrum and a dorsolateral lobe next to the eyestalk (figs 4i, j). If this is a homologue of the linea thalassinica the lobe must be interpreted as the remnant of the branchiostegal sclerite and the ocular lobe must be absent. An alternative explanation is that the dorsolateral lobe is homologous to the ocular lobe usually found at that site, the true linea is lost, and the longitudinal groove is a new structure. The first explanation seems the simpler and is preferred.

Characters 1 and 2 in Table 1 describe the grooves on the carapace.

An armed rostrum is a usual feature of reptant decapods and its presence is assumed plesiomorphic. The thalassinidean rostrum is never strongly laterally compressed as in many carideans but is always dorsoventrally flattened or reduced. The most primitive condition is seen in axiids (figs 4a–e) and is similar to that in *Neoglyphea* in the possession of lateral carinae and a median carina which does not reach the anterior apex. Within the Thalassinidea the rostrum takes various forms many of which are probably independently derived from the primitive condition. In several genera, notably in the Callianassidae but also elsewhere, it is very reduced, triangular and shorter than the eyestalks (figs 4l, m; character 3); in others there is secondarily a spike-like rostrum (fig. 4i: character 4) and in many genera loss of armature (character 5).

Upogebia and *Thalassina* share a trilobed 'rostrum' of which the most lateral carinae are possibly derived from a ridge running back from the ocular spine. The origin of this cannot be seen in other reptants but the homologies of the structures involved are suggested by the possession of sublateral carinae meeting at the apex of the true rostrum and medial to the most lateral (ocular) ridges (figs 4o–q; character 6). The sides of the rostrum generally continue back on to the carapace as lateral carinae usually fringed by setae. Loss of the carinae in several genera is considered apomorphic (figs 4i–l; character 7). The median rostral carina seen in *Neoglyphea* is frequently lost (character 8).

In the Ctenochelidae the dorsal organ (see

Martin and Laverack, 1992, for a review of the structure and physiological functions of this sense organ) is raised on a cardiac prominence (Manning and Felder, 1991) (character 9).

Carapace-abdomen articulation. Life in long burrows demands a more elongate and flexible habitus than in a typical shrimp. This is best seen in the degree of articulation between the cephalothorax and abdominal somite 1. In the shrimp-like forms a pair of prominent anterolateral lobes on abdominal somite 1 ride on a thickened posterior margin of the cephalothorax and maintain the relative positions of the carapace and pleon. All reptants, such as *Neoglyphea inopinata*, all nephropids and astacideans, possess these anterolateral lobes in one form or another so they are undoubted plesiomorphies within Reptantia. These last named groups possess a posterior carapace margin which is regularly convex mid-dorsally and differs from that in many thalassinideans. In some thalassinidean families the posterior margin is similar and tripartite: on each side of the median convexity is a strong posterolateral lobe whose margin is strengthened by a smooth ridge on which the anterolateral lobes of abdominal somite 1 ride (figs 7a–d). Chace and Kensley (1992) discussed a similar arrangement in the alpheid shrimps and defined a 'cardiac notch' in this family. The pattern in the Thalassinidea is not thought homologous. The medial portion may be strongly depressed posteriorly in micheleids to enclose the midanterior sclerite of abdominal somite 1.

In the more shrimp-like forms abdominal somite 1 is half as long as the second, is sclerotised anterior to the anterolateral lobes, and possesses a prominent pleuron (fig. 7a). The anterior margin of the pleuron of abdominal somite 2 extends forward and covers the posterior margin of abdominal somite 1 (reptant- and caridean-like). Lateral condyles ensure that articulation between the first and second somites is in one plane.

In burrowing forms the cephalothorax-abdomen relationship is similar except that abdominal somite 2 is longer. Some species are more shrimp-like than others but there is a tendency for greater flexibility than in Axiidae, for example, by weakening of the lateral condyles. The pleuron of abdominal somite 1 is not prominent and is represented only by a non-projecting lateral plate. In callianassid-like genera the anterior sclerotisation is weak.

In the elongate burrowing families the anterolateral lobes on abdominal somite 1 and the posterolateral carapace ridges on which they ride in primitive forms are obsolete or absent. Abdominal somite 1 is elongate, almost or about as long as the second, and its pleuron obsolete. The anterior margin of abdominal pleuron 2 does not overlap anteriorly (figs 2b, 2c, 7e).

Characters 10–17 in Table 1 summarise evolutionary changes in the posterior carapace and abdominal somites 1 and 2.

Thoracic sternites. Thoracic sternite 7 is a complex structure which bears pereopods 4. In all thalassinideans, anomurans and in *Neoglyphea* it is separate from and more substantial than sternite 8 (character 18). Sakai and de Saint Laurent (1989) illustrated its variation in Axiidae but not very exactly in many cases. Homologies between the structures seen in Thalassinidea and in the other reptants are not clear. In *Neoglyphea* the articulation of coxa 4 is oblique on two condyles, and the sternite bears two sinuous episternal ridges which are well separate posteriorly (Forest and de Saint Laurent, 1989: fig. 2). In all thalassinideans the episternal ridges meet posteriorly where they are separated by a deep slit. There is a median ridge anterior to the coxal condyles (fig. 8a). There is a tendency in the burrowing forms for the episternal ridges to become obsolete posteriorly (the sternite to be smooth except for the median slit), for the anterior ridge to be broadened, and for the articulation between sternite and coxa to become weak (figs 8b, c). Rarely, for example in some apparently advanced thomassiniids, remnants of the hooks of the episternal ridges are seen. Coxa 4, more or less cylindrical in *Neoglyphea* and primitive thalassinideans, becomes flattened in the burrowers, especially with the development of an anteromedial lobe which may meet its pair medially.

Characters 19–24 in Table 1 explain changes in thoracic sternite 7 and coxa of pereopod 4.

Gills. The changes in shape of the elements of the gills and number of thoracic gills are complex.

In the non-thalassinidean reptants the epipods vary in form, the elements of the gills (podobranchs, arthrobranchs and pleurobranchs) are digitiform or lamellate and either regularly or irregularly arranged along a rachis. In anomurans and thalassinideans the gill elements are regularly arranged in pairs except in *Thalassina* where the gill elements are irregular filaments (fig. 6m). Paired lamellae would seem to be a strong unifying feature of many families (figs 6n, o). In some species of *Upogebia* each paired lamella appears divided into two. Ngoc-Ho (1981) hypothesised that this was a derived condition, subdivision of a broad lamella into two filaments, and correlated this with more advanced conditions such as a dorsal tooth on the mandible and absence of epipod on maxilliped 1. She contrasted this with the antithetical view of de Saint Laurent and Le Loeuff (1979) who viewed the four filamentous elements as more plesiomorphic than two lamellate elements. My examination of the underlying structure of the gills and correlation with other characters supports Ngoc-Ho's interpretation.

The most plesiomorphic condition of the number of gills is shown in *Neoglyphea* whose numbers of gills are as follows (Forest and de Saint Laurent, 1975):

Thoracomere:	1	2	3	4	5	6	7	8
Pleurobranchs	-	-	-	-	1	1	1	1
Arthrobranchs	1	1	2	2	2	2	2	-
Podobranchs	-	1	1	1	1	1	1	-
Epipods	-	1	1	1	1	1	1	1

The tendency for loss of thoracic branchiae throughout the Thalassinidea shows considerable homeoplasy and losses of different gills are not correlated. The absence of arthrobranch 1 and the loss or reduction of pleurobranch 8 are the only apomorphies common to all thalassinideans. *Thalassina* is unique in possessing a second smaller arthrobranch on thoracic somite 2. Epipods are primitively foliaceous at least posteriorly but become linear or lost in more apomorphic taxa. The presence of only a rudimentary gill is treated as an apomorphy in the same way as its loss in this analysis. In some genera, e.g. *Michelea*, *Crosniera* and *Mictaxius*, species exist with fewer gills than shown in Table 2. The most plesiomorphic condition known for the genus is that scored. Table 1 lists the characters 25–31 describing gills. In the first analysis charcters were treated as ordered and in an alternative, as unordered.

Cephalon and mouthparts. Long setae on the epistome are not widespread within the Reptantia; their presence is considered apomorphic (character 32) but their occurrence is irregular.

The cylindrical articulating eyestalk with a terminal cornea is the ancestral condition within the Decapoda (figs 4a–c, n). A flattened eyestalk with dorsal cornea is apomorphic (figs 4f, i–k; character 33).

An elongate waisted first article on antenna 1 is a peculiarity of micheleids (fig. 4f; character 34). Article 3 is primitively longer than the first two in outgroups and its shortening is a feature of axiids and micheleids (figs 4a, f; character 35). A similar situation is seen is some ctenochelids.

A scaphocerite (exopod) attached to the distal border of article 2 of antenna 2 is common in reptants and well developed in many carideans. It is accompanied often by the possession of a strong terminal spine (parallel to the scaphocerite) on article 2 and usually a small mesiodistal spine on article 3 (fig. 4a). Absence of the scaphocerite and spines is assumed to be apomorphic (fig. 4j; character 36). In the plesiomorphic state the scaphocerite is much longer than wide (fig. 4b) but its apomorphic states include a reduced but articulating acicle about as long as wide (figs 4i, k; state 1) or loss (fig. 4j; state 2). The character was treated as ordered and unordered in alternate analyses.

The mandibular incisor plesiomorphically, i.e. in outgroups and in most thalassinideans, has an anterior truncate blade-like part and a posterior toothed margin; the pair are symmetrical. Alternate apomorphic states are toothed along all the cutting edge (character 37) and asymmetrical (character 38).

The scaphognathite (epipod of maxilla 2) of reptants primitively has two lobes directed distally (or anteriorly) and proximally (or posteriorly into the branchial chamber). The latter lobe tapers and is fringed with setae which are longer apically. This is similar to the condition seen in thalassinids and laomediids but in these two families the posterior setae are thickened. In some thalassinidean families a long seta (or 2 setae in rare cases) on an acute apex of the proximal lobe extends the full length of the branchial cavity and interacts with the pereopodal epipods (fig. 6a). This was first recognised as a feature of axiids, *Callianidea* and *Thomassinia* (de Saint Laurent, 1979a). The presence of the seta was used as a defining character of the Callianideidae s.l. by Kensley and Heard (1991) and so is treated here as a synapomorphic state (character 39). The number, position, length and fine structure of the setae in Laomediidae and *Thalassina* suggest that they are not homologous. In most families the proximal lobe of the scaphognathite is shortened, rounded, and evenly fringed with plumose setae; this is treated as an apomorphy (fig. 6b;

character 40). However, there is strong evidence from the presence of a single long seta on the larvae of anomurans (Van Dover et al., 1982) that this may be a plesiomorphy.

The endopod of maxilliped 1 is 2-articled or elongate in the plesiomorphic state (fig. 6c) and minute when apomorphic (character 41). Its exopod is flagellate when plesiomorphic (fig. 6c) and 1-articled and foliaceous when apomorphic (character 42). Loss of the exopod is also apomorphic (character 43).

The plesiomorphic reptant maxilliped 3 endopod is a linear limb with elongate distal articles, with a well-developed crista dentata on the upper face, and spines along the mesial edges of the coxa-carpus (especially the merus) (fig. 6d). There are several apomorphic conditions most of which are frequently homeoplasic. As the proximal articles of the maxillipedal endopod become more operculiform in some callianassids the distal articles become more compact (fig. 6h; character 44). The exopod may become reduced or absent (figs 6f–i, k; character 45). The crista dentata is primitively a strong toothed ridge (fig. 6d; character 46) which may become a row of obsolete teeth or absent. Mesial spines on the merus are plesiomorphic (figs 4d, e) and one spine is common; absence of spines is apomorphic (character 47). Not all genera are consistent in this feature and even in callianassids where the maxilliped is often operculiform isolated cases of meral spines are recorded.

There is strong homeoplasy between and within genera in the loss of spines and exopods and as a consequence these are not considered of great evolutionary significance.

Pereopods. Fusion of the basis and ischium of all five pereopods is characteristic of all reptants except Glypheidae and Astacidea (character 48). A character state defining all Thalassinidea is the possession of a dense row of long setae on the lower basis-propodus margin of at least pereopod 2 (fig. 5h; character 49). In some families similar rows are well developed on other limbs (e.g., pereopods 1–4 in Upogebiidae). The setae are weaker on more posterior limbs in other families and the polarity of their development beyond pereopod 2 is uncertain.

The plesiomorphic reptant carpus and propodus of pereopod 1 are subcylindrical in cross-section and there is progressive flattening through the nephropids and thalassinideans. Flattening, especially of the carpus, and development of ridges on the upper and lower margins of both articles facilitates overlap between the merus and carpus when the leg is retracted and must help in burrow maintenance (fig. 5b; character 50). Articulation between the carpus and propodus of the primitive reptant allows movement through almost a right angle in a horizontal plane complementing vertical movement at the ischium-carpus joint; in all thalassinideans and hermit crabs movement here is considerably restricted (character 51). Equal chelipeds are plesiomorphic and unequal chelipeds apomorphic (character 52) but this character seems homeoplasic. Loss of spines from the lower margin of merus is apomorphic (character 53). The chelate nature of pereopod 1 is an apomorphic state shared with many reptants (character 54). I agree with Ngoc-Ho (1981) rather than de Saint Laurent and Le Loeuff (1979) that the chelate form in upogebiids is more plesiomorphic than the subchelate form (figs 5e, f) but this makes no difference to the character scores.

Although the first three pairs of pereopods of *Neoglyphea* are essentially simple each limb has an incipient thumb and it is easy to see how the chelate limb seen in many reptant groups arose. The Scyllaridea are the only other reptant group without chelate limbs; most (Anomura and Eubrachyura) have only the first pair of pereopods chelate; the Astacidea and Stenopodidea, with the non-reptant Penaeidea, have three pairs chelate; and the Eryonidea have four pairs chelate (de Saint Laurent, 1979b). The Thalassinidea all have a chelate or subchelate pereopod 1 but are variable for pereopod 2. De Saint Laurent (1979a) united the Axiidae, Callianassidae and Callianideidae, in part, on the chelate nature of pereopod 2 (fig. 5h). The most parsimonious hypothesis is that this is derived from the simple limb condition (character 55). *Thalassina* has a subchelate pereopod 2 but this is considered an independent autapomorphy (fig. 1a). Martin and Abele's (1986) phylogenetic analysis of the Anomura (including Thalassinidea) treated the absence of a chelate pereopod 3 an apomorphy of Thalassinidea, Upogebiidae and Laomediidae. The character is considered plesiomorphic in this analysis so does not feature here. Shortening of the fixed finger relative to the dactylus of pereopod 2 in *Michelea*, *Callianidea* and *Tethisea* is a character state differentiating these genera from the remaining thalassinideans (character 56). A strong proximal lobe or 'heel' on the lower margin of the propodus of pereopod 3 (fig. 5n) is a feature uniting the callianassid genera (de Saint Laurent and Le Loeuff, 1979: fig. 14). It is one of several characters uniting *Anacalliax* with the Callianassidae (character 57).

The presence of spiniform setae on distal articles of pereopods 3 and 4 is a feature of some thalassinidean genera but the homology and polarity of this character-suite is uncertain (fig. 5j, k). I assume that the acquisition of numerous spiniform setae is correlated with cryptic behaviour and that they have become lost in some burrowing forms. The numbers and position of spiniform setae vary considerably especially in the Axiidae and few characters are scored. The presence of spiniform setae on the dactylus of pereopods 3 and 4 is treated as an apomorphy (character 58). Similar spiniform setae in *Thalassina* and *Laomedia* are not considered homologous because of slight difference in position. Many axiid genera possess several rows of spiniform setae on the propodi of pereopods 3 and 4. Loss of these on pereopod 3 (character 59) and pereopod 4 (character 60) are apomorphies. In thomassiniids and callianideids a single spiniform seta on the lower margin of the propodus of pereopod 3 (fig. 5m; character 61) and of pereopod 4 (character 62) are treated as characters independent of the transverse rows of axiids and micheleids.

An apomorphy of the burrowing thalassinideans is broadening of pereopods 3 and 4 from a cylindrical to paddle shape (figs 5k–n; character 63). Pereopod 5 is short and able to be held closely posteriorly alongside abdominal somite 1 in thomassiniids and callianassids (character 64).

Body proportions. The ancestral reptant displays the typical caridoid facies, that is, the abdomen is strong and about as long as the cephalothorax, and the tail fan slightly reflexed to facilitate the reverse escape response. This body form is seen in *Neoglyphea*, upogebiids, laomediids and axiids (figs 1b, 1c, 3a). *Thalassina* is specialised only in having a narrow abdomen with narrow uropods (fig. 1a). In the burrowing forms the cephalothorax is a third or less of the total body length rather than half (character 65) but there is considerable variability. Elongation of the second abdominal somite relative to the first is a feature of micheleids (figs 3b, c; character 66) but there are some callianassid genera in which this abdominal somite is elongate. General flattening of the abdomen and loss of pleura accompanies elongation. This is most evident in some callianassids where abdominal somite 6 is especially flat and the lateral margin is a well defined setose ridge. Abdominal somites 3–5 or 3–6 are ornamented with dorsolateral dense tufts of plumose setae in some thalassinidean genera. This character is confined to the infraorder but polarity is uncertain (character 67).

Pleopods. Pleopods offer numerous characters for an understanding of the phylogeny of the Thalassinidea. The Callianassidae, with several genera (de Saint Laurent, 1979a; Manning and Felder, 1991, 1992; Manning, 1992; Rodrigues and Manning 1992) possess similar pleopods 3–5 and sexually dimorphic and diverse pleopods 1 and 2 (character 68). The endopods 3–5 are thickened, more or less triangular and, with the extended peduncles, meet along a straight mesial margin with their opposite pairs which are interlocked by means of appendices internae which are often minute (fig. 8k). The exopods are curved, foliaceous and envelope the endopods in such a way that each of the three pleopod pairs is a semicircular plate which could act as a ventilator in a narrow burrow. This condition is a synapomorphy for the family and is shared with *Anacalliax*. In all other Thalassinidea pleopods 2–5 are more or less similar and not modified in this way. The Calocarididae are also defined by a synapomorphic condition of pleopod 2: the endopod is not produced beyond the base of the complex appendix interna as it is in Axiidae (fig. 8g; Kensley, 1989).

In Axiidae, Calocarididae and Callianassidae subtle differences in the shape of the pleopods are useful generic characters but only more gross differences are useful at the family level.

The appendix interna on the inner margin of the pleopodal endopods is a feature of Glypheidae and all Thalassinidea except Thalassinidae, Laomediidae and Upogebiidae. The homology between curved hooks on male pleopod 1 and the same hooks on the elongate appendix interna of more posterior pleopods seems clear (Kensley, 1989). Because it was suspected that this might be a symplesiomorphy the presence of an appendix interna was not included in the analysis. A trial incorporating it as an apomorphy did not affect the resulting cladogram. Absence of the curved hooks on the male pleopod 1 in genera possessing an appendix interna on pleopods 2–5 is treated as an apomorphy (fig. 8d; character 69). In the Axiidae and related groups the second article of pleopod 1 is triangular (fig. 8d; character 70) with the minute hooks of the residual appendix interna on the mesial angle. In laomediids, upogebiids and callianassids the male pleopod 1 is lost or minute (character 71).

The plesiomorphic appendix masculina is an elongate setose structure diverging from the appendix interna on male pleopod 2 (figs 8e, f). There is no evidence of it in *Upogebia* or *Laomedia* (character 73) and in some thomassiniids it is fused to the internal margin of the appendix interna (fig. 8i; character 72).

The burrowing way of life has lead to the development of auxiliary respiratory surfaces on the margins of pleopods 2–5. These take the form of marginal simple or branching cylindrical filaments in *Callianidea* (fig. 8m) or as flat lamellae in *Michelea* (fig. 8o). In spite of fundamental differences between the appearance of the auxiliary surfaces the first species of *Michelea* were described as members of *Callianidea*. The marginal extensions are not treated as homologues as done by Kensley and Heard (1991) and the characters are autapomorphies which do not appear in this analysis. Treating the presence of an auxiliary respiratory surface as a homologous character state (adding one character) made no difference to the cladogram. Two steps were added, one for each genus, suggesting that the filaments were independently derived.

Shape of the pleopodal rami may be useful at a generic level within the Axiidae but the strong lateral lobes (subtriangular shape) of exopods 2–5 of the micheleid genera link this group (fig. 8l; character 74).

Tail fan. The most frequently encountered shape for the uropodal rami is ovate (figs 7f, i). Loss of the exopodal suture seen in *Neoglyphea* and some axiids is considered apomorphic (fig. 7g–j; character 75). A dorsal thickening of the setose anterolateral margin of the uropodal exopod is a callianassid character shared with *Anacalliax* (fig. 7h; character 76); a notch on the margin of the exopod in *Mictaxius* is not considered homologous. In *Upogebia*, *Strahlaxius*, *Meticonaxius*, *Marcusiaxius* and *Tethisea* the distal margin of the endopod is straight and ends laterally in a definite angle (figs 7g, j, k; character 77). In these same genera the telson tends to be shorter than wide.

Primitively the telson and uropods bear dorsal spines often along the ribs (fig. 7f). Loss of spination is apomorphic (character 78).

In the primitive condition abdominal somite 6 carries a well developed epimeron produced ventrally to enclose the base of the pleopods; it has a marginal row of setae. In the more advanced thalassinideans the epimeron and its marginal setae are lost and the area is receptive to the horizontal folding forward of the tail fan (character 79).

Setal-rows. Setal-rows characterise many thalassinidean genera and are much more widespread systematically and morphologically than previously appreciated. Setal-rows were defined by (Kensley and Heard, 1991: figs 1, 2) as tight rows of short plumose setae, each seta in a pit-like structure. They occur in several places:

a longitudinal row near the rostral carina (if present);

one, two or three vertical rows on the anterolateral cephalothorax: marginally, at the base of the eyestalk; an intermediate row; and a row near the cervical groove (fig. 6l);

dorsolateral row on abdominal somite 1;

lateral row on all or some of abdominal somites 2–5;

three rows, a longitudinal row on the margin of the pleuron, a transverse row along the posterior dorsolateral margin, and an oblique row in between, on abdominal somite 6;

short transverse row on the mesial face of the propodus of pereopod 2;

one or two rows on the mesial face of the propodus of pereopods 3 and 4 (figs 5k, l).

No species has all setal-rows. For this reason I treat them as 14 independent characters in which the apomorphic state is acquisition of the setal-rows. Table 1 explains the plesiomorphic and apomorphic states assumed (characters 80 to 93).

Results

The cladogram (ordered characters)

The matrix of 27 taxa by 93 characters was treated to phylogenetic analysis in the program HENNIG86 version 1.5 using the *mhennig** and *bb** (extended branch-swapping) options to find the most parsimonious trees. The results were confirmed using the *global* and *mulpars* multiple branch-swapping options in PAUP 2.4. In the first analysis all characters were treated as ordered.

Four equally short trees of 240 steps, with consistency and retention indices (ci and ri) of 41 and 75 respectively, were obtained. Only two clades, each of three genera, could not be fully dichotomously resolved. These were the genera of the Thomassiniidae and the three more advanced of the four genera of Micheleidae. These became resolved after successive weighting of the characters once with the *xs w* option in HENNIG86 to give a single fully dichotomous cladogram of the same length as the original four and with ci and ri of 63 and 87 respectively.

Weighting had the effect of removing nine characters, most of which reached their derived state independently in two or more genera or in small clades, and which would not intuitively be expected to define major taxa. Twenty-four characters (26%) retained ci and ri equal to 100 and are marked with * in Table 1. A further 31 characters (31%) had ci equal to 50, that is, changed from the plesiomorphic to apomorphic state only twice or reversed once.

The transformation series, apomorphic changes at all nodes of the cladogram, were investigated using the *apolist* option in PAUP 2.4 and with the program CLADOS. Ninety per cent of all steps in the cladogram were coincident in both transformation series but for 19 characters the nodes at which transformations took place were ambivalent. These were revealed with the *xs h* option in HENNIG86. The implication of this is that the state of 19 characters (in parentheses in Table 1) at some nodes was uncertain and they could not be used with certainty in defining supra-generic taxa. They are not included on fig. 9.

Character changes defining the clades and higher taxa

The cladogram derived using ordered characters resulted in several major clades for which taxonomic status exists or is proposed and which are discussed in detail. Clades are numbered as in fig. 9.

The Anomura and Thalassinidea (clade 51) share several apomorphies: possession of a linea thalassinica or linea anomurica (if considered homologous); free thoracic sternite 8; gill elements paired transversely along rachis; absence of podobranch 7; chelate or subchelate pereopod 1; and fused pereopodal basis–ischium. The cladogram suggests that the similar structure of the carpus–propodus joint of pereopod 1 may also be synapomorphic but convergence in thalassinideans and hermit crabs may be more probable. It is also hypothesised that the absence of a suture on the uropodal exopod is also a synapomorphy but this demands that the condition be reversed in some axiids and in Laomediidae.

Independent derivations of a linea thalassinica in non-axioid Thalassinidea and a linea anomurica in Anomura involve the same number of steps, two, as a single homologous structure lost in the axioids. Parsimony criteria cannot resolve this argument. Until it can be convincingly shown that there are fundamental structural differences between the linea anomurica and thalassinica which would support their independent evolution, I must assume their homology.

The synapomorphies of the Anomura (clade 29) are given in fig. 9 but are incomplete because this group was only an outgroup for this analysis. All are paralleled in the Thalassinidea.

The Thalassinidea (clade 50) share only a single synapomorphy which is never reversed, that is, a row of setae on the lower margin of ischium–propodus of pereopod 2. Other character changes are reversed in some genera or families: posterior margin of carapace with strong lateral lobes (lost in callianassoids); thoracic sternite 7, episternites contiguous posteriorly and flattened; and pleurobranchs absent (present in micheleids, some axiids and some upogebiids). A chelate pereopod 2 is a possible synapomorphy reversed partly in Thalassinidae and fully in Upogebiidae and Laomediidae.

Of the three clades here treated as superfamilies two, Thalassinoidea and Callianassoidea, are sister taxa (clade 49). Three clear character states define this clade: absence of medial rostral carina, reduced scaphocerite, and unarmed telson.

The first superfamily, Thalassinoidea, is represented by a single family and genus defined by numerous autapomorphies not included in this analysis and others which are convergent in other taxa: lateral ocular ridges on the rostrum; failure of the anterolateral margin of abdominal somite 2 to overlap somite 1; flattened coxa 4. The irregular and unique gill elements is a reversal.

The second superfamily, Callianassoidea (clade 48), is defined by one unquestionable synapomorphy: posterior margin of carapace soft and without ridges. Others are ambivalent. The reduced rostrum, unarmed and obtusely triangular (sometimes spike-like) and without lateral carinae, is seen in all families except Upogebiidae and may be independently derived in Laomediidae and the others (clade 46). However, the upogebiid rostrum is unique, not very similar to that of the axioids or of the thalassinids and may be an autapomorphy. Reduction or absence of the male pleopod 1 is a possible synapomorphy but this requires a reversal in Laomediidae.

The Callianassoidea comprise six groups at family level of which the Laomediidae and Upogebiidae are the least derived. Laomediidae are characterised by: thoracic sternite 7, episternites diverging posteriorly (reversal); podobranchs 3–7 present (reversal); absence of a meral spine on maxilliped 3; and uropodal exopod with a transverse suture.

Upogebiidae share numerous autapomorphies and, among the characters discussed here: the broad rostrum; appendix masculina absent; and uropodal endopod distally truncate.

The remaining callianassoids group strongly in successive clades 47 and 46. Clade 47 is defined by absence of anterolateral lobes on abdominal somite 1, reduction of epipods and podobranchs, and other character states which may be reversals. Clade 46 shares seven unambivalent character steps: coxa 4 flattened, with anteromesial lobe; eyestalk flattened; pereopod 1, carpus–propodus flattened, unequal; pereopods 3 and 4, propodus flattened; male pleopod 1, appendix interna absent; and abdominal somite 6 epimeron not ventrally produced. The derivation of a chelate pereopod 2 seems probable at this point.

Clade 46 supports two pairs of families: Ctenochelidae + Callianassidae (clade 42) and Callianideidae + Micheleidae (clade 38).

Ctenochelidae plus Callianassidae (clade 42) share: abdominal somite 1, tergite anterior to anterolateral lobes flexible; absence of epipod 3; and shortened cephalothorax. The three ctenochelid genera cluster paraphyletically and share only a cardiac prominence, a feature also seen in *Anacalliax* which has more callianassid characters.

Callianassidae (clade 39) are a well defined family which share: pereopod 3 propodus uniquely with heel on proximal corner of lower margin; pleopods 1 and 2 sexually modified, 3–5 uniquely similar and lamellar; male pleopod 2, appendix masculina absent; and uropodal exopod with unique anterodorsal setose thickening.

Callianideidae and Thomassiniidae (clade 38) are united on: coxa 4 immobile and with condyle obsolete; maxilla 2 scaphognathite with a long seta; pereopod 1, merus uniquely with convex lower margin; and pereopods 3 and 4, propodus uniquely with 1 spiniform seta distally on lower margin. The derivation of setal-rows on pereopods 2–4 and abdominal somites 1 and 6 may link these two families but they may have been derived independently in individual genera.

The Callianideidae, comprising only *Callianidea*, are defined most clearly on the autapomorphy of marginal pleopodal filaments. The most significant characters in the analysis are: loss of the condyle and overlap between abdominal somites 1 and 2; and loss of appendix masculina. *Callianidea typa* is the only callianassoid in which the linea thalassinica is completely absent and so resembles an axioid, but its presence in *C. laevicauda* reinforces the callianassoid affinities of the genus.

Clade 37 links the three genera of the Thomassiniidae which share three consistent characters: linea thalassinica displaced dorsally, ocular lobe substituted by branchiostegal sclerite; mid-dorsal tergite of abdominal somite 1 anteriorly depressed; and midanterior region of thoracic sternite 7 flattened and broadened (coxae secondarily separate). Other character states defining the family are: maxilliped 3 ischium–merus at least slightly broadened, carpus–dactylus compact (shorter than ischium–merus); its exopod reduced or absent; without crista dentata or meral spine; pereopod 5 short, compact and fitting into side of abdominal somite 1; carapace with at least one vertical setal-row; and abdominal somite 6 with one setal-row.

The relationships between the three thomassiniid genera were resolved by the cladogram only after character weighting.

The third superfamily, Axioidea (clade 45), is uniquely characterised by absence of the linea thalassinica. Although it may be argued that the axioids are not part of the anomuran-thalassinidean line on the grounds that there is no linea, there are so many other shared characters of gills, sternites and pereopods that this seems improbable. Other apomorphies of this group are: antenna 1 with article 3 only as long as article 2; and maxilla 2 scaphognathite with a long seta.

Five family-level clades are recognised within the Axioidea.

The first is Calocarididae (clade 8) which are best defined on the autapomorphic structure of the second male pleopods (Kensley, 1989). Continued recognition as a separate family is based on not sharing the synapomorphies of the Axiidae.

Remaining axioids (clade 44) share vestigial or absent podobranch 2, possibly loss or arthrobranch 2, and abdominal somite 6 with a setal row. These divide into Axiidae s.s. (clade 43) and Strahlaxiidae + Michcleidae (clade 35).

Two apomorphies define clade 43 containing the four genera of Axiidae: pereopods 3 and 4, dactylus and pereopod 4, propodus with spiniform setae. Review of the literature supports the fact that spiniform setae are variously developed throughout the family and that the character is an axiid synapomorphy. These two characters are shared with *Michelea* (Micheleidae) but not with other axioids. Because so few axiid genera were included, the relationships between them are not explored.

Strahlaxiidae and Micheleidae (clade 35) are particularly strongly linked and two character states are unique: abdominal somite 2 is more than twice as long as abdominal somite 1; and the exopod of pleopods 2–5 is laterally lobed. Other important characters are: coxa 4 flattened, with anteromesial lobe; pereopods 3 and 4, propodus flattened (less than twice as long as wide); uropodal endopod distally truncate, distolateral margin subacute; and pereopods 2–4 and abdominal somites 1–6 with setal-rows.

Strahlaxiidae (clade 13) share: abdominal somites 3–5 with dense tufts of lateral setae (although this may be a plesiomorphic condition appearing irregularly in the Thalassinidea); male pleopod 1 without appendix interna; and appendix masculina absent. The three genera placed in this family share a bifid apex on the rostrum and rugose gastric region of the cephalothorax.

The four genera comprising the Micheleidae (clade 34) are characterised by four unique synapomorphies, seven other synapomorphies and one reversal. The unique synapomorphies are: antenna 1, article 1 elongate and waisted; mandibular incisor asymmetrical; longitudinal carinal setal-row; and 2–3 carapace vertical setal-rows. Other important characters are: rostrum unarmed; pereopod 1, carpus-propodus flattened; cephalothorax less than one third body length; and telson and uropod unarmed. The reversal is the presence of pleurobranchs 5–7 (or at least 7).

Tethisea is the most primitive of the micheleids; the rest (clade 33) share five synapomorphies of which a second setal-row on pereopods 3 and 4 is unique. *Michelea* is characterised by 16 character changes among the suite listed here (notably absence of rostrum) but the most significant defining character is its marginal pleopodal lamellae. The relationships between *Michelea*, *Marcusiaxius* and *Meticonaxius* were resolved in the cladogram only after character weighting.

An alternate cladogram (unordered charaters)

An alternate analysis was run with multistate characters 27, 29, 30, 31 and 36 unordered. Characters 27–31 deal with the numbers of epipods and branchiae and 36 with the scaphocerite. Making them unordered means that a change from any one state to any other is treated as one step, equal to a change between sequential states. The alternate analysis resulted in four equally parsimonious trees of 234 steps (ci = 42, ri = 75) which were fully resolved with successive weighting.

This differed from the one obtained using unordered characters, in: 1, being 6 steps shorter; 2, the relationships between the major clades; and 3, relationships between the thomassiniid genera. The shorter length was accounted for in the epipods (character 27 four steps shorter) and branchiae (characters 29–31 each one step shorter). Character 36 was one step longer. This cladogram suggested that *Thalassina* is the sister taxon to Axioidea rather than Callianassoidea. However, the supposed synapomorphies of *Thalassina* and Axioidea are largely ambivalent characters. The only unique synapomorphies are the chelate pereopod 2 and triangular male pleopod 1. The chelate pereopod 2 is of doubtful homology and occurs in higher Callianassoidea also. The same may be said of the second character. The rearrangement of the thomassiniid genera was obtained only after successive weighting and remains questionable.

Ambivalent characters

Typically, ambivalent characters are explained by the inability of the phylogenetic programs to choose between one apomorphic step and one reversal, on the one hand, and two independent apomorphic steps, on the other. Both contribute two steps to tree length. Independent steps, which imply that these characters are non-homologous, is the commonsense interpretation for many. Others are more difficult to interpret. Character 3, for example, the flattened and shortened rostrum could have evolved independently in the Laomediidae and the non-upogebiid callianassoids, or been derived once in the Callianassoidea. In the latter case the upogebiid rostrum is a new character, and its specialised structure suggests this may be possible. A chelate pereopod 2 is another character about which the analysis was doubtful. Assuming it is apomorphic, which itself is uncertain, this character state could have arisen independently in Axioidea and advanced Callianassoidea, or have been lost in laomediids and upogebiids independently. The former is the more likely scenario since the condition in *Thalassina* is quite different from in other thalassinideans.

A new classification of the Thalassinidea

The generally high values of ci and ri give considerable confidence in the structure of the cladograms and it is used to hypothesise a classification as follows (clade numbers in fig. 9 in brackets). The alternate cladograms derived using ordered and unordered characters differ only in the relationships of the superfamilies and genera in one family, neither discrepancy affecting the classification.

Infraorder Anomura (29)
Infraorder Thalassinidea (51)
  Superfamily Thalassinoidea Dana, 1852 (6)
    Family Thalassinidae Dana, 1852 (6)
  Superfamily Callianassoidea Dana, 1852 (48)
    Family Laomediidae Borradaile, 1903 (7)
    Family Upogebiidae Borradaile, 1903 (21)
    Family Callianideidae Kossmann, 1880 (22)
    Family Thomassiniidae de Saint Laurent, 1979a (37)
    Family Ctenochelidae Manning and Felder, 1991 (42, 41, 40)
    Family Callianassidae Dana, 1852 (39)
  Superfamily Axioidea Huxley, 1879 (45)
    Family Calocarididae Ortmann, 1891 (8)
    Family Axiidae Huxley, 1879 (43)
    Family Strahlaxiidae fam. nov. (13)
    Family Micheleidae Sakai, 1992a (34)

The significant taxonomic changes proposed are:

1. Definition of the Thalassinidea as a monophyletic taxon distinct from the Anomura;
2. Division of the Thalassinidea into three monophyletic superfamilies;
3. Restriction of the Callianideidae to its type genus.
4. Confirmation and definition of the family groups Thomassiniidae and Micheleidae (incorporating Meticonaxiinae Sakai, 1992b).
5. Recognition of the Ctenochelidae as a paraphyletic family;
6. Erection of a new family, Strahlaxiidae.

Discussion

Although as many as 18 family-group taxa have been proposed for the Thalassinidea, their relationships are disputed. Discussion in the literature mostly concerns the similarities or differences between only two taxa (Callianassidae and Upogebiidae in particular). Few contributions have offered data on three or more taxa (necessary to resolve trees) and only recently have plesiomorphic and apomorphic similarities been distinguished.

The first synthetic work was that of Borradaile (1903) who recognised only four families: Axiidae, Laomediidae, Thalassinidae and Callianassidae. Most of the 23 genera and subgenera defined by him are still valid, the greatest divergences from present nomenclature being in the Callianassidae. Borradaile's tree of 'genealogical relations' is similar to that derived from my analysis; in fact, its basic dichotomies are identical. The tree and his key define one clade containing *Calocaris* and other axiid genera, and a second clade which splits off the Laomediidae, Thalassinidae, Upogebiidae, Callianideidae and Callianassidae in turn (as in my most parsimonious cladogram). The congruence between Borradaile's and my trees is remarkable especially given the greater number of taxa and characters used by me.

Borradaile's tree of generic and family relationships has not always been accepted.

Gurney (1938) tackled the problem of thalassinidean relationships by examining larval characters. He concluded that larval characters common to all thalassinideans are shared with the lobster *Homarus* but that the group is not homogenous. He recognised "two series of genera which might be regarded as Homarine and Anomuran respectively". In his tree the anomuran group (Upogebiidae and Laomediidae) are more closely related to the Anomura than to the homarine group (Axiidae and Callianassidae). Five larval characters were used to separate the two groups and some adult characters added to distinguish the Callianassidae and Upogebiidae. Much of his argument is taken up with the differences just between these last two families about which there is no dispute; only the affinities of Upogebiidae and Laomediidae to Anomura are relevant to thalassinidean phylogeny. Whether these characters are synapomorphies or shared plesiomorphies was not debated by Gurney and by his own admission the 'character . . . on which the greatest stress has been laid as evidence of relation to Anomura . . . is disputable'. Gurney's (1938) tree of affinities, which is very different from that proposed here, was criticised by Konishi (1989) on the basis of data from larvae of more families.

Gurney's tree of relationships proposes that the Thalassinidea are not monophyletic, rather, that the Axiidae + Callianassidae are the sister-group to the Anomura + Upogebiidae + Laomediidae. Such an arrangement presumes, as in my hypothesis, that the linea (thalassinica or anomurica) is homologous and was lost in the Axiidae. It assumes that the characters shared by Upogebiidae and Callianassidae arose independently: anterolateral lobes on abdominal somite 1 lost; reduction of epipods and podobranchs; and that the upogebiid rostrum is a unique apomorphy.

De Saint Laurent (1973) supported the differences between Callianassidae and Upogebiidae by raising the latter to full family rank but her grouping of the Callianideinae into Callianassidae was provisional. She too appeared to suspect that the callianassids have some axiid affinities but then offered no new evidence. She was uncertain about the affinities of the Upogebiidae but suspected they are close to Thalassinidae and Laomediidae, which is the case in my hypothetical tree.

De Saint Laurent (1979a, and in less detail in 1979b and in de Saint Laurent and Le Loeuff, 1979) grouped the Axiidae, Callianassidae and Callianideidae, in a superfamily, Axioidea, (or section Axiidea) which was defined as follows: reptant decapods with the epistome partially exposed, without a thelycum in the female, with pereopods 1–5 having the basis and ischium fused, with pereopods 1 and 2 chelate, pereopod 3 simple, pereopod 4 simple or subchelate, pereopod 5 chelate or subchelate, pleopods usually with an appendix interna, and maxilliped 1 always with a foliaceous epipod (my translation).

Several of these characters are true for all thalassinideans but the 'axioid' families as defined by de Saint Laurent (1979a) were said to differ from all others (Upogebiidae, Laomediidae and Thalassinidae) in the shape of the anterior region of the carapace, structure of the limbs and in larval morphology.

The peculiarities of the anterior margin of the carapace of 'axioids' were not defined. The most significant feature of the limbs distinguishing this superfamily group is that pereopod 2 is fully chelate, a condition never seen in other thalassinideans and is the only apomorphy shared. My analysis would suggest that chelate pereopods 2 have arisen independently in Callianassidae + Ctenochelidae (+ Thalassinidae) and Axioidea. Given the frequency of chelate limbs in the decapods this would not be a surprise.

Larval characters uniting the superfamily were listed by Gurney (1938) but plesiomorphic and apomorphic similarities of axiids and callianassids were not distinguished by him nor by subsequent authors. Because larvae of so few species are known with certainty, such characters cannot be easily investigated (Konishi, 1989). He tabulated the main zoeal characters of the Axiidae, Callianassidae, Upogebiidae, Thalassinidae and Laomediidae. He did not attempt to define relationships beyond stating his belief that the Axiidae are "most primitive and plesiomorphic in general feature" and that the upogebiids and laomediids are not grouped as in Gurney's (1938) scheme.

De Saint Laurent (1979b; reiterated in de Saint Laurent and Le Loeuff, 1979) ranked the Upogebiidae in a distinct section of Thalassinidea, Gebiidea, with Laomediidae and Thalassinidae. This was mainly on the basis of a simple pereopod 2 and convergence of habitus from a fossorial way of life. She noted the similarity of upogebiid larvae to those of 'Dromiacea' and the special 'trachelifer' larvae of laomediids without seeming to support Gurney's anomuran line.

De Saint Laurent's classification is not supported by parsimony criteria. Rearrangement of clades in my cladogram according to her scheme added 11 steps to the shortest tree. Significant homeoplasies added were: loss of posterolateral lobes on the carapace three times, in *Thalassina*, *Laomedia* and in Axioidea; loss of anterolateral lobes on abdominal somite 1 twice, in *Upogebia* and most callianassoids; loss of scaphocerite in two major clades; loss of podobranchs 3–6 twice, in *Upogebia* and higher callianassoids; and loss or armature on telson and uropod twice.

Ngoc-Ho (1981) demonstrated that the larvae of Laomediidae and of Upogebiidae could be divided into subgroups and discussed similarities between them and with adult Glypheidae. Her discussion did not offer an opinion on the position of these two families relative to other thalassinideans.

The first cladistic analysis of the Thalassinidea was that of Martin and Abele (1986) who used 54 characters in an analysis of 20 taxa in the 'Anomura'. The monophyly of their group of five thalassinidean families and of de Saint Laurent's (1979a) superfamily was not supported by the most parsimonious cladogram but they concluded that the Thalassinidea could be recognised in a slightly longer tree.

Martin and Abele (1986) defined the Thalassinidea on the basis of two apomorphies: absence of pleurobranchs on thoracic somites 5–7; and possession of fewer than 14 pairs of gills (podobranchs excluded). Neither of these conditions is in fact the most plesiomorphic state found in thalassinideans. They did not recognise the presence of a linea thalassinica, which might be thought to be diagnostic of the taxon, as an apomorphy but rather as a more plesiomorphic condition of the linea anomurica.

Their division of the families was first into Laomediidae + Axiidae which share reduced male pleopods and phyllobranchiate gills, both states which are widespread in other thalassinidean families. The second major clade, Thalassinidae + Upogebiidae + Callianassidae, shared uropodal rami without sutures. The first two of these were said to share a subchelate first pereopod. This is not so for most upogebiids and is probably not homologous in the two families. It is not surprising that with only four characters effectively distinguishing the families their tree is different from that presented here.

Kensley and Heard (1991) presented a cladistic analysis using PAUP of the Callianideidae, defined a priori as a family of 18 species in seven genera, united by the possession of rows of special plumose setae on the carapace, some abdominal somites, and the propodi of pereopods 2–4. Their analysis used Axiidae, Laomediidae and Callianassidae as outgroups; 21 characters were used. Their most parsimonious result (18 34-step trees which I have calculated from their data) did not resolve the relationships between *Callianassa*, *Crosniera*, *Mictaxius* and *Thomassinia*, demonstrated that these four together were the sister-group of *Callianidea*, and showed that all five were isolated from *Michelea*, *Marcusiaxius* and *Meticonaxius*. This result has some similarity to my phylogeny in that Callianideidae, Micheleidae and possibly Thomassiniidae appear monophyletic. The tree was dismissed by Kensley and Heard because 'the ingroup could not be rooted as monophyletic'. On the contrary, it demonstrates that on the basis of this small dataset the 'Callianideidae' s.l. are *not* monophyletic. In spite of this evidence Kensley and Heard (1991) insisted on the monophyly of their seven genera and removed *Callianassa* from the analysis. One effect of this was to reduce the number of informative characters to only 15. My calculation from their data produced two unresolved trees of 23 steps and I was not able to reproduce their cladograms (1991: fig. 25). However, some synapomorphies of each of the Callianideidae (s.s.), Micheleidae and Thomassiniidae are shown in spite of their interrelationships being misleading.

Kensley and Heard's (1991) revision and phylogenetic analysis of genera was accepted by Sakai (1992a) who recognised the callianassid affinities of the Thomassiniidae and the axiid affinities of the others. His 'cladogram' (Sakai, 1992a: fig. 1) was constructed in an unconventional manner in order to illustrate these affinities and is not based on phylogenetic principles. His opinion that the Thalassinidae are more closely related to the Callianideidae than to other families is not supported here. He noted that both groups have setal pits but their structure and positions differ.

There are two views of the relationship of the Calocarididae to the Axiidae. Sakai and de Saint Laurent (1989) and Sakai (1992b) did not recognise the family as distinct but Kensley's (1989) hypothetical scheme used three synapomorphies to separate its four genera from the Axiidae. My phylogeny supports this result and goes further in suggesting some synapomorphies for the other axiid-like genera.

The Strahlaxiidae have not been recognised as distinct before. *Strahlaxius* is a sister-group of the Micheleidae and the two families share several synapomorphies. It is their separation from the Axiidae which enables the new family to be recognised.

My analysis was not detailed enough to support or deny Manning and Felder's (1991) revision of the Callianassidae and introduction of the Ctenochelidae. For the time being, Ctenochelidae are recognised as a paraphyletic taxon. Its original diagnosis includes only two synapomorphies, a cardiac prominence and a uropodal exopod notch, neither present in all genera.

THALASSINIDEA Latreille

Diagnosis. Reptant decapods without a thelycum in the female; with pereopods 1–5 having the basis and ischium fused; with pereopod 1 chelate and carpus-propodus articulation slight; pereopod 2 chelate or simple; *always with dense row of long setae on lower margin*; pereopod 3 simple; pereopod 4 simple or subchelate; pereopod 5 chelate or subchelate; without arthrobranch on thoracomere 1.

Key to superfamilies and families of Thalassinidea

1\. Linea thalassinica absent; antenna 1 with article 3 about as long as article 2 (fig. 4a) .... Axioidea. 2

— Linea thalassinica present at least anteriorly (figs 4j, l–n) (if absent, with flattened eyestalks and cylindrical pleopodal marginal filaments (fig. 4k)); antenna 1 with article 3 usually longer than 2 5

2\. Pleopod 2 endopod simple, with terminal enlarged appendix masculina (fig. 8g); eye unpigmented; uropod exopod usually with suture .... Calocarididae

— Pleopod 2 endopod foliaceous with small appendix masculina attached mesially (figs 8e, l); eye usually pigmented; uropod exopod usually without suture 3

3\. Abdominal somite 2 less than twice as long as 3; exopods of pleopods 2–5 not laterally lobed (fig. 8e); pleuron of abdominal somite 1 produced; coxa of pereopod 4 more or less cylindrical; propodus of pereopods 3 and 4 more or less linear; uropodal endopod ovate (fig. 7f); pereopods 2–4 and abdominal somites without setal-rows .... Axiidae

— Abdominal somite 2 twice as long as 3; exopods of pleopods 2–5 laterally lobed (fig. 8l); pleuron of abdominal somite 1 not produced; coxa of pereopod 4 flattened; propodus of pereopods 3 and 4 more or less flattened (figs 5k, l); uropodal endopod triangular or ovate (fig. 7g); some of pereopods 2–4 (figs 5k, l) and abdominal somites with setal-rows 4

4\. Rostrum spinose, apically bifid (fig. 4d); longitudinal and vertical setal-rows on carapace absent; antenna 1, article 1 as long as 2; mandibular incisor toothed and symmetrical; epipods and podobranchs reduced posteriorly .... Strahlaxiidae

— Rostrum not spinose; longitudinal and vertical setal-rows on carapace present; antenna 1, article 1 longer than 2 (figs 4f, h); mandibular incisor not toothed and asymmetrical; epipods and podobranchs rarely reduced posteriorly .... Micheleidae

5\. Uropodal rami linear; gill elements irregular, filamentous proximally and plate-like distally (fig. 6m); rostrum spinose, narrow .... Thalassinoidea

[1 family: Thalassinidae; 1 genus: *Thalassina* (fig. 1a). See Poore and Griffin, 1979 and Dworschak, 1992 for separation of the species]

— Uropodal rami lamellate; gill elements regularly paired, lamellate (fig. 6o); rostrum flat or obsolete .... Callianassoidea. . . 6

6\. Posterior margin of carapace with lateral lobes (fig. 1b); abdominal somite 1 with anterolateral lobe; maxilla 2 scaphognathite with several long setae on posterior lobe .... Laomediidae

— Posterior margin of carapace evenly curved (fig. 2c); abdominal somite 1 without anterolateral lobes; maxilla 2 scaphognathite with 1 or without long seta on posterior lobe 7

7\. Pereopods 1 equal; pereopod 2 simple (fig. 5i); rostrum usually broad and setose (figs 4n–r); eyestalks cylindrical; coxa of pereopod 4 cylindrical .... Upogebiidae

— Pereopods 1 unequal, rarely equal; pereopod 2 chelate (fig. 4h); rostrum obsolete; eyestalks flattened (figs 4i–m); coxa of pereopod 4 flattened (figs 8b, c) 8

8. Maxilla 2 scaphognathite with long posterior seta (fig. 6a); pereopod 1 merus with convex lower margin; pereopod 3 (and sometimes 4) propodus with single distal spiniform seta on lower margin (fig. 5m); pereopods 2–4 and abdominal somites usually with setal-rows (figs 5k, l); abdominal somite 1 strongly chitinised anteriorly; cephalothorax half as long as total length; coxa of pereopod 4 immobile 9

— Maxilla 2 scaphognathite without long posterior seta (fig. 6b); pereopod 1 merus with straight or spinous lower margin; pereopod 3 propodus without distal spiniform seta on lower margin; pereopods 2–4 and abdominal somites without setal-rows; abdominal somite 1 weakly chitinised anteriorly; cephalothorax third as long as total length; coxa of pereopod 4 mobile 10

9. Linea thalassinica absent or short; pleopods with marginal filaments (fig. 8n); abdominal somite 1 with anterodorsal dome (fig. 2a); thoracic sternite 7 narrow (fig. 8c).......... Callianideidae
[1 genus: *Callianidea* (fig. 2a), 2 described species]

— Linea thalassinica present lateral to eyestalks (figs 4i, j); pleopods without marginal filaments; abdominal somite 1 anteriorly depressed (fig. 2b); thoracic sternite 7 broad, coxae 4 separate .... Thomassiniidae

10. Pleopod 2 similar to pleopods 3–5, rami lanceolate; pereopod 3 propodus linear or weakly ovate; uropodal exopod simply ovate .... Ctenochelidae

— Pleopod 2 reduced, sexually modified; pleopods 3–5 with broad interacting rami (figs 8j, k); pereopod 3 propodus with proximal heel on lower margin (fig. 5n); uropodal exopod with secondary setose lobe (fig. 7h) .... Callianassidae

AXIOIDEA Huxley

not Axioidea sensu de Saint Laurent, 1979a: 1395.

Diagnosis. Thalassinidea. Posterior margin of carapace with lateral lobes; *linea thalassinica absent*; pleuron of abdominal somite 1 more or less produced; eyestalks cylindrical; antenna 1 with article 3 about as long as article 2; maxilla 2 scaphognathite with 1–2 long setae on posterior margin; gill elements paired; pereopod 2 chelate; *pleopods with appendix interna*; pleopod 2 similar to pleopods 3–5; uropodal rami lamellate.

Axiidae Huxley

Diagnosis. Axioidea. Rostrum usually spinose, *apically acute*; eye usually pigmented; pleuron of abdominal somite 1 produced; abdominal somite 2 less than twice as long as 3; propodus of pereopods 3 and 4 linear or broadened; coxa of pereopod 4 more or less cylindrical; male pleopod 2 endopod foliaceous with small appendix masculina attached mesially; exopods of pleopods 2–5 not laterally lobed; *uropodal endopod ovate*; pereopods 2–4 without setal-rows, abdominal somite 6 with longitudinal setal-row.

Key to genera of Axiidae

The most recent key to the genera of this family (Sakai and de Saint Laurent, 1989) did not take into account the removal of genera to Calocarididae or the new family, Strahlaxiidae. The manuscript was published independently by K. Sakai and contains many errors (M. de Saint Laurent, pers. comm.). I am extremely grateful to M. de Saint Laurent for pointing out and correcting the errors; these improvements have been incorporated in this revised but pragmatic key. Nevertheless, many species still do not fit well with existing generic diagnoses and a reappraisal of the family is needed. Couplet 1 can be difficult if the uropodal exopod suture is obscure. If in doubt try the unusual genera leading from the first alternate before going to couplet 5.

1. Uropodal exopod without transverse suture (or suture obscure) 2
— Uropodal exopod with transverse suture (fig. 7a) (sometimes without) 5
2. Eyes weakly or not pigmented (rarely fully pigmented); rostrum level with carapace (fig. 4a) 3
— Eyes fully pigmented; rostrum significantly depressed below level of carapace (fig. 4c) 4
3. Pereopods 1 equal, fixed finger short; pleura of abdominal somites 3–5 posteriorly rounded .... *Anophthalmaxius* De Man, 1905
— Pereopods 1 unequal, fixed finger of smaller cheliped basally almost as broad as propodus (fig. 5g); pleura of abdominal somites 3–5 posteriorly angled .... *Eiconaxius* Bate, 1888
4. Male pleopod 1 present; median carina ends anteriorly in angle or tooth; submedian carinae present (fig. 4c) .... *Scytoleptus* Gerstaecker, 1856
— Male pleopod 1 absent; median carina rounded anteriorly; submedian carinae absent .... *Parascytoleptus* Sakai and de Saint Laurent, 1989
5. Pereopodal epipods absent (or vestigial on pereopods 4 and 5 only); rostrum a short acute spike; maxillipedal 3 exopod with clear bend (fig. 6e) .... Coralaxiinae . . . *Coralaxius* Kensley and Gore, 1981
— Pereopodal epipods present on 1–4 (fig. 6n); rostrum not a spike, usually broad, dentate, longer than eyes; maxillipedal 3 exopod not clearly bent (fig. 6d) 6
6. Pleopods 2–5 without appendix interna; antenna 2 scaphocerite usually bifurcate (fig. 4s) .... *Eutrichocheles* Wood Mason, 1876
— Pleopods 2–5 with appendix interna (fig. 8m); antenna 2 scaphocerite usually simple 7
7. Pleurobranchs 5–7 (above pereopods 2–4) present (absent in 1 undescribed species of *Spongiaxius*) 8
— Pleurobranchs 5–7 (above pereopods 2–4) absent 13
8. Supraocular spines absent, rostrum evenly and weakly dentate (fig. 4e) .... *Axius* Leach, 1815
— Supraocular spines present, i.e. basal rostral spine well developed, often larger than more distal spines (fig. 4b) 9
9. Male pleopod 1 present (sometimes absent in *Spongiaxius*) 10
— Male pleopod 1 absent 12
10. Antenna 2 scaphocerite short, comma-shaped in lateral view (fig. 4t); rostrum with lateral rows of several erect spines; living in sponges .... *Spongiaxius* Sakai and de Saint Laurent, 1989
— Antenna 2 scaphocerite as long as article 4; rostrum with 1 or 2 lateral spines only; not living in sponges 11
11. Eyes fully pigmented, rounded .... *Bouvieraxius* Sakai and de Saint Laurent, 1989
— Eyes weakly pigmented, anteriorly flattened .... *Levantocaris* Galil and Clark, 1993
12. Rostrum twice as long as eyestalks, not depressed, strongly dentate; carapace carinae armed; pereopod 1 spinose .... *Calaxius* Sakai and de Saint Laurent, 1989
— Rostrum little longer than eyestalks, depressed, not dentate; carapace carinae unarmed; pereopod 1 not spinose .... *Dorphinaxius* Sakai and de Saint Laurent, 1989

13. Antenna 2 scaphocerite rudimentary; eyes weakly pigmented; male pleopod 1 present .... *Paraxius* Bate, 1888
— Antenna 2 scaphocerite at least moderately long; eyes fully (rarely weakly or not) pigmented; male pleopod 1 absent (rarely present) 14
14. Carapace covered with scale-like tubercles; rostrum styliform, usually shorter than elongate eyestalks; pereopod 1 granulate, spinose on upper margins .... *Oxyrhynchaxius* Parisi, 1917
— Carapace smooth or spinose; rostrum not styliform (if narrow, longer than eyestalks which are not more than twice as long as wide); pereopod 1 spinose on upper margins or not 15
15. Eyestalks short (not more than half as long as rostrum); eyes weakly or not pigmented .... *Calocarides* Wollebaek, 1908
— Eyestalks long (at least half as long as rostrum); eyes fully pigmented 16
16. Rostrum narrow and acute (fig. 4b); supraocular spines present; pereopod 1 elongate, propodus and dactylus spinose or strongly setose on upper and lateral surfaces .... *Acanthaxius* Sakai and de Saint Laurent, 1989
— Rostrum broadly triangular; supraocular spines absent; pereopod 1 stout, propodus and dactylus smooth 17
17. Eyestalks elongate; median, submedian and lateral carinae unarmed ridges .... *Axiorygma* Kensley and Simmons, 1988
— Eyestalks stout; median, submedian and lateral carinae tuberculate, dentate or absent 18
18. Carapace carinae absent, strong paired tubercles instead; rostrum as long as or shorter than eyestalks .... *Allaxius* Sakai and de Saint Laurent, 1989
— Submedian carinae appear as horse-shoe-shaped line of weak tubercles; rostrum as long as or longer than eyestalks .... *Axiopsis* Borradaile, 1903

Calocarididae Ortmann

Diagnosis. Axioidea. Rostrum usually spinose, apically acute; *eye usually not pigmented*; pleuron of abdominal somite 1 produced; abdominal somite 2 less than twice as long as 3; propodus of pereopods 3 and 4 more or less linear; coxa of pereopod 4 more or less cylindrical; *male pleopod 2 endopod simple, with terminal enlarged appendix masculina*; exopods of pleopods 2–5 not laterally lobed; uropodal endopod ovate; pereopods 2–4 and abdominal somites without setal-rows.

Key to genera of Calocarididae

See Kensley (1989) and Sakai and de Saint Laurent (1989) for diagnoses of the genera and species and an entry to the literature. This key is a reconciliation of both works and adds the later genus of Sakai (1992b).

1. Uropodal exopod without transverse suture; sexes separate but some individuals hermaphroditic .... *Eucalastacus* Sakai, 1992
— Uropodal exopod with transverse suture; hermaphroditic 2
2. Carapace with strong post-cervical carina 3
— Carapace without post-cervical carina 4
3. Eyes flattened, mesially contiguous .... *Calocaris* Bell, 1853
— Eyes rounded, not mesially contiguous .... *Lophaxius* Kensley, 1989
4. Male pleopod 2 endopod with appendix interna and appendix masculina free, with 2 mesial rows of simple setae .... *Calastacus* Faxon, 1893
— Male pleopod 2 endopod with appendix interna and appendix masculina fused, with 2 mesial rows of spiniform setae 5

5. Appendix masculina elongate; podobranchs and arthrobranchs well developed.................................... *Calaxiopsis* Sakai and de Saint Laurent, 1989
— Appendix masculina boot-shaped; podobranchs and arthrobranchs rudimentary.................................. *Ambiaxius* Sakai and de Saint Laurent, 1989

Micheleidae Sakai

Micheleinae Sakai, 1992: 18.
Meticonaxiinae Sakai, 1992: 19.

Diagnosis. Axioidea. Rostrum *flat or obsolete*; eye usually pigmented; *antenna 1, article 1 longer than article 2*; *pleuron of abdominal somite 1 obsolete*; abdominal somite 2 twice as long as 3; propodus of pereopods 3 and 4 more or less broadened; coxa of pereopod 4 *flattened*; male pleopod 2 endopod foliaceous with small appendix masculina attached mesially; *exopods of pleopods 2–5 laterally lobed*; uropodal endopod *ovate*; *carapace, pereopods 2–4 and abdominal somites with some setal-rows.*

Remarks. Sakai (1992) erected the callianideid subfamily Micheleinae for genera without a linea thalassinica, with anterolateral lobes on abdominal somite 1, with a long scaphocerite, subequal first pereopods, with a small rostrum, and with normal propodus on pereopod 4. His second subfamily, Meticonaxiidae, differed mainly on the presence of a rostrum and absence of pleopodal filaments. The phylogenetic analysis suggests that the meticonaxiids are polyphyletic and must therefore be synonymised with Micheleidae. The subfamily is not related to the Callianideidae and is here elevated to family rank.

Key to genera of Micheleidae

The family is intended to include the two subfamilies of Callianideidae, Micheleinae and Meticonaxiinae, erected by Sakai (1992a). Its four genera include species have been variously included in Axiidae, Callianassidae and Callianideidae.

1. Rostrum minute, triangular (fig. 4f); without pleurobranchs; pereopods 3 and 4 with lateral spiniform setae (fig. 5k) ....*Michelea* Kensley and Heard, 1991
— Rostrum prominent, flat (figs 4g, h); with pleurobranchs; pereopods 3 and 4 without lateral spiniform setae 2
2. Cheliped with thickened setae in gape (fig. 5d); abdominal somites 3–5 without setal-rows; uropodal endopod with anterior margin convex, ending by curving to rounded posterior margin .... *Tethisea* gen. nov.
— Cheliped without thickened setae in gape; abdominal somites 3–5 with setal-rows; uropodal endopod with straight anterior margin ending sharply (fig. 7j) 3
3. Eyes visible in dorsal view, rostrum narrow (fig. 4g); cheliped fixed finger with major tooth two-thirds way along; maxilliped 2 exopod reduced ....*Meticonaxius* De Man, 1905
— Eyes not visible in dorsal view, rostrum wide (fig. 4h); cheliped fixed finger with major tooth one-third way along; maxilliped 2 exopod long ....*Marcusiaxius* Rodrigues and Carvalho, 1972

Tethisea gen. nov.

Type species. Tethisea indica. sp. nov.

Diagnosis. Micheleidae. Rostrum prominent, flat. Pleurobranchs 5–8 present. Pereopods 3 and 4 without lateral spiniform setae. Cheliped with thickened setae in gape. Abdominal somites 3–5 without setal-rows. Uropodal endopod with anterior margin convex, ending by curving to rounded posterior margin.

Etymology. From Tethys, the ancient ocean, alluding to the known distribution of this genus, and *Isea*, Guérin-Méneville's original genus of callianideid.

Remarks. *Tethisea* is most similar to *Marcusiax-*

ius and *Meticonaxius* in the possession of a rostrum and of pleurobranchs. The most obvious differences are the absence of setal-rows on abdominal somites 3–5, the presence of specialised thickened setae in the gape of pereopod 1, and the more ovate shape of the uropodal endopod.

Tethisea indica sp. nov.

Material examined. Holotype. Mozambique (24°64'S [sic], 35°20'E), 165 m, Agassiz trawl, 18 Aug 1964 (IIOE program, *Anton Bruun* cruise 7, stn 371D), National Museum of Natural History, Washington (USNM) 243552 (female, cl. 5.3 mm).

Paratypes. Mozambique, Mayotte, NNE of Récif Nord (12°31'S, 45°02'E), 300–350 m, course organic sand, dredge, 30 Mar 1977 (BENTHEDI stn 72DS), Muséum National d'Histoire Naturelle, Paris (MNHN) Th-1219 (2 males cl. 5.5 and 4.5 mm, female cl. 5 mm).

La Réunion (21°03.6'S, 55°09'E), 412-460 m, sand, Sanders dredge, 8 Sep 1982 (Cruise MD32 stn DS178), MNHN Th-1221 (1 specimen); MNHN Th-1223 (1 specimen).

Indonesia, Makassar Strait (0°54.2'S, 119°28.7'E), 170 m, 6 Nov 1980, grab (CORINDON 2 stn 248), MNHN Th-1216 (male cl. 6.5 mm, female, cl. 7 mm).

New Caledonia, E of SE corner of main island (22°15.32'S, 167°15.4'E), 440 m, Waren dredge, 5 Sep 1985 (MUSORSTOM BIOCAL stn DW77), MNHN Th-1226 (5 specimens); Museum of Victoria, Melbourne (NMV) J13268 (1 specimen).

Diagnosis. Rostrum triangular, 1.5 times as long as broad at base of eyes; posterior setal-row of 3 setae only. Maxilliped 3 merus without mesial tooth; exopod minute.

Cheliped merus with 2 spines on lower margin. Uropodal endopod with anterior margin convex, ending by curving to rounded posterior margin, 1.3 times as long as wide; exopod with concave anterior margin, apically rounded, posterior margin broadly lobed, 1.7 times as long as wide. Telson as long as wide, tapering to rounded–truncate apex beyond constriction one-third way along.

Remarks. The species and another in the same new genus will be described and figured in more detail in a later paper.

Strahlaxiidae fam. nov.

Type genus. Strahlaxius Sakai and de Saint Laurent, 1989.

Diagnosis. Axioidea. Rostrum usually spinose, *apically bifid*; eye usually pigmented; *antenna 1, article 1 as long as article* 2; pleuron of abdominal somite 1 *not* produced; abdominal somite 2 twice as long as 3; propodus of pereopods 3 and 4 broadened; coxa of pereopod 4 more or less flattened; male pleopod 2 endopod foliaceous with small appendix masculina attached mesially; *exopods of pleopods 2–5 laterally lobed*; *uropodal endopod triangular*; *pereopods 2–4 and abdominal somites with some setal-rows.*

Composition. Neaxius Borradaile, 1903; *Neaxiopsis* Sakai and de Saint Laurent, 1989; *Strahlaxius* Sakai and de Saint Laurent, 1989.

Remarks. The three strahlaxiid genera are superficially similar to some members of the Axiidae where they have traditionally been placed. The most significant diagnostic characters are the acute outer angle of the uropodal endopod, the bifid rostrum, rugose gastric region of the carapace, broad pleopodal rami, and possession of some setal-rows on some pereopods and abdominal somites. Absence of the appendix masculina is a synapomorphy but this is shared with some axiid genera.

The recognition of Axiidae, Calocarididae and Strahlaxiidae among the genera previously assigned to Axiidae s.l. does not deny the possible existence of other monophyletic taxa within this group. Strong evidence for the monophyly of the Calocarididae was argued by Kensley (1989) and unique diagnostic features of the Coralaxiinae were presented by Sakai and de Saint Laurent (1989). The existence of neither clade excludes the other, contrary to Sakai's (1992b) view, and my hypothesis is the first to attempt to relate them.

Key to genera of Strahlaxiidae

1. Antenna 2 scaphocerite toothed; pleurobranchs 5–7 (above pereopods 2–4) present; telson with 2 transverse ridges .... *Neaxius* Borradaile, 1903
— Antenna 2 scaphocerite simple; pleurobranchs 5–7 (above pereopods 2–4) absent; telson dorsally smooth (fig. 7g) 2
2. Male pleopod 1 present .... *Strahlaxius* Sakai and de Saint Laurent, 1989
— Male pleopod 1 absent .... *Neaxiopsis* Sakai and de Saint Laurent, 1989

CALLIANASSOIDEA Dana

Diagnosis. Thalassinidea. *Posterior margin of carapace with or without lateral lobes*; *linea thalassinica present*; pleuron of abdominal somite 1 weak; eyestalks cylindrical or flattened; antenna 1 with article 3 as long as or longer than article 2; maxilla 2 scaphognathite with or without long seta on posterior margin; gill elements paired; pereopod 2 simple or chelate; pereopods 3 and 4 propodus with or without spiniform setae; pereopods 2–4 and abdominal somites sometimes with setal-rows; pleopods with or without appendix interna, reduced if present; pleopod 2 similar or dissimilar to pleopods 3–5; uropodal rami lamellate.

Callianassidae Dana

Diagnosis. Callianassoidea. *Linea thalassinica present, lateral to antennae*; posterior margin of carapace evenly curved, rarely with cardiac prominence; rostrum obsolete or a spike; eyestalks flattened, rarely cylindrical; maxilla 2 scaphognathite without long seta on posterior lobe; abdominal somite 1 without anterolateral lobes, weakly chitinised; pereopods 1 unequal or equal; pereopod 1 merus with straight or toothed lower margin; pereopod 2 chelate; pereopod 3 propodus without distal spiniform seta on lower margin, *with proximal heel on lower margin*; coxa of pereopod 4 flattened, mobile; thoracic sternite 7 narrow; *pleopod 2 different from pleopods 3–5, sexually modified; pleopods 3–5 with broad interacting rami*; *uropodal exopod with thickened anterodorsal setose margin*; only abdominal somite 6 with setal-rows.

Key to genera of Callianassidae

The genera of the Callianassidae are poorly understood. De Saint Laurent and Le Loeuff (1979) provided a key to genera from the eastern Atlantic. Manning and Felder (1991, 1992), Manning (1992) Rodrigues and Manning (1992) and Manning and Lemaitre (1993) briefly diagnosed all the genera and gave keys to American forms. Both the French and American authors summarised earlier contributions but it is difficult to reconcile their two systems. The key here is based on both schemes and should be used for practical purposes only. The key seems unlikely to work for many Indo-West Pacific species.

1. Maxillipedal 3 dactylus ovate (fig. 6f); carapace lacking dorsal oval 2
— Maxillipedal 3 dactylus slender, digitiform (figs 6h, i); carapace with dorsal oval (fig. 2c) 3
2. Chelipeds equal, similar .... *Eucalliax* Manning and Felder, 1991
— Chelipeds unequal, dissimilar .... *Calliax* de Saint Laurent, 1973
3. Pleopods 3–5 with digitiform appendices internae (fig. 8j) 4
Pleopods 3–5 with stubby appendices internae (fig.8k 5
4. Maxilliped 3 without exopod; eyes subterminal, lateral .... *Cheramus* Bate, 1888
— Maxilliped 3 with exopod (fig. 6j); eyes terminal, subglobular .... *Scallasis* Bate, 1888
5. Eyes globular, terminal on cylindrical eyestalk; maxillipedal 3 merus with denticulate distal border .... *Calliapagurops* de Saint Laurent, 1973
— Eyes flattened, subterminal on flattened eyestalk; maxillipedal 3 merus without denticulate distal border 6
6. Maxillipedal 3 propodus oval, as broad as long, twice as wide as dactylus (fig. 6i) 7
— Maxillipedal 3 propodus slender, longer than broad, at most slightly wider than dactylus (fig. 6h) 14

7. Abdomen with strong pattern formed by symmetrical grooves on somites 3–5; uropodal endopod curved, strap-shaped ... *Callichirus* Stimpson, 1866

— Abdomen without pattern formed by symmetrical grooves on somites 3–5; uropodal endopod not curved or strap-shaped ... 8

8. Maxilliped 3 with exopod (fig. 6j); antenna 1 peduncle longer and stouter than antenna 2 peduncle ... *Lepidophthalmus* Holmes, 1904

— Maxilliped 3 without exopod; antenna 1 peduncle not longer and stouter than antenna 2 peduncle ... 9

9. Rostral spine absent or weak; front not or weakly trispinose ... 10

— Rostral spine distinct and upturned; front strongly trispinose (fig. 4l) ... 12

10. Linea thalassinica incomplete, not reaching to posterior margin of carapace ... *Poti* Rodrigues and Manning, 1992

— Linea thalassinica complete, reaching to posterior margin of carapace ... 11

11. Uropodal endopod broader than long, flattened distally; posterior margin of telson rounded or slightly indented ... *Neocallichirus* Sakai, 1988

— Uropodal endopod longer than broad, tapering distally; posterior margin of telson strongly excavate ... *Sergio* Manning and Lemaitre, 1994

12. Cheliped carpus and propodus with 3 spines on upper margin; eye disc-shaped, dorsal, narrower than eyestalk ... *Glypturus* Stimpson, 1866

— Cheliped carpus and propodus with unarmed upper margin; eye subglobular, distal, as wide as eyestalk ... 13

13. Abdominal somite 2 about as long as abdominal somite 6; carapace shorter than 10 mm ... *Corallichirus* Manning, 1992

— Abdominal somite 2 about as long as abdominal somite 6 plus telson; carapace about 25 mm ... *Corallianassa* Manning, 1987

14. Maxilliped 3 slender, pediform (fig. 6f) ... 15

— Maxilliped 3 broad, operculiform (figs 6h, i) ... 16

15. Cheliped with hook on merus (fig. 5b); male pleopod 2 vestigial or absent ... *Callianassa* Leach, 1814

— Cheliped without hook on merus; male pleopod 2 present, biramous ... *Anacalliax* de Saint Laurent, 1973

16. Maxillipedal 3 merus strongly projecting beyond articulation with carpus (fig. 6h); antenna 1 peduncle longer and stouter than antenna 2 peduncle ... 17

— Maxillipedal 3 merus barely or not projecting beyond articulation with carpus (fig. 6i); antenna 1 peduncle shorter and narrower than antenna 2 peduncle ... 18

17. Pleopods 3–5 with appendices internae embedded in endopod ... *Neotrypaea* Manning and Felder, 1991

— Pleopods 3-5 with appendices internae projecting from endopod ... *Trypaea* Dana, 1852

18. Carapace with rostral spine; male pleopod 2 present ... *Notiax* Manning and Felder, 1991

— Carapace without rostral spine; male pleopod 2 vestigial or absent ... 19

19. Antenna 1 peduncle longer and stouter than antenna 2 peduncle; telson shorter than long ... *Gilvossius* Manning and Felder, 1992

— Antenna 1 peduncle not longer and stouter than antenna 2 peduncle; telson as wide as long (fig. 7h) ... *Biffarius* Manning and Felder, 1991

Callianideidae Kossmann

Diagnosis. Callianassoidea. *Linea thalassinica absent or very short*; posterior margin of carapace evenly curved, abdominal somite 1 without anterolateral lobes; rostrum reduced; eyestalks flattened; maxilla 2 scaphognathite with 1 long seta on posterior lobe; *abdominal somite 1 with anterodorsal dome*; pereopods 1 unequal; pereopod 1 merus with convex lower margin; pereopod 2 chelate; pereopods 3 and 4 propodus with single distal spiniform seta on lower margin; pereopod 3 propodus ovate; coxa of pereopod 4 flattened, immobile; thoracic sternite 7 narrow; pleopod 2 similar to pleopods 3–5, rami lanceolate, *with marginal filaments*; uropodal exopod simply ovate; pereopods 2–4 and abdominal somites 1 and 6 with setal-rows.

Composition. One genus, *Callianidea* Kossmann, 1880; two species (Sakai, 1992a).

Ctenochelidae Manning and Felder

Diagnosis. Callianassoidea. *Linea thalassinica present, lateral to antennae*; posterior margin of carapace evenly curved, with cardiac prominence; rostrum obsolete or a spike; eyestalks flattened; maxilla 2 scaphognathite without long seta on posterior lobe; abdominal somite 1 without anterolateral lobes, weakly chitinised; pereopods 1 unequal; pereopod 1 merus with straight or toothed lower margin; pereopod 2 chelate; pereopod 3 propodus without distal spiniform seta on lower margin; pereopod 3 propodus linear or weakly ovate; coxa of pereopod 4 flattened, mobile; thoracic sternite 7 narrow; *pleopod 2 similar to pleopods 3–5, rami lanceolate*; uropodal exopod simply ovate; only abdominal somite 6 sometimes with setal-rows.

Key to genera of Ctenochelidae

The phylogenetic analysis suggested that Ctenochelidae are a paraphyletic family but its relationships will only be discovered with a more thorough investigation of its genera and those of the Callianassidae. *Anacalliax*, included by Manning and Felder (1991), is removed to Callianassidae. The key combines the characters used by de Saint Laurent and Le Loeuff (1979: 47) and Manning and Felder (1991).

1. Carapace with dorsal oval; abdominal somite 6 with lateral projections .... *Callianopsis* de Saint Laurent, 1973
— Carapace without dorsal oval; abdominal somite 6 without lateral projections 2
2. Abdominal somite 1 with well developed pleura; cheliped carpus with mesial hirsute triangular depression .... *Paracalliax* de Saint Laurent and Le Loeuff, 1979
— Abdominal somite 1 without pleura; cheliped carpus without mesial hirsute triangular depression 3
3. Larger cheliped with fingers at least twice as long as palm, with a comb of fine teeth (fig. 5c); smaller cheliped propodus not tapering; rostrum spike-like .... *Ctenocheles* Kishinouye, 1926
— Larger cheliped with fingers shorter than palm, without a comb of fine teeth; smaller cheliped propodus tapering; rostrum obsolete or triangular 4
4. Maxilliped 3 with exopod (fig. 6j); abdominal somite 6 without sharp lateral projections .... *Gourretia* de Saint Laurent, 1973
— Maxilliped 3 without exopod; abdominal somite 6 with sharp lateral projections .... *Dawsonius* Manning and Felder, 1991

Laomediidae Borradaile

Diagnosis. Callianassoidea. *Linea thalassinica present*; *posterior margin of carapace with lateral lobes, abdominal somite 1 with anterolateral lobes*; *rostrum minute*; eyestalks cylindrical; *maxilla 2 scaphognathite with several thickened setae on posterior lobe*; abdominal somite 1 chitinised; pereopods 1 equal; *pereopod 2 simple*; pereopods 3 and 4 propodus with few spiniform setae on lower margin; pereopod 3 propodus linear; coxa of pereopod 4 cylindrical; thoracic sternite 7 narrow; pleopod 2 similar to pleopods 3–5, rami lanceolate; pleopods without appendix interna; uropodal exopod ovate; pereopods 2–4 and abdominal somites without setal-rows.

Key to genera of Laomediidae

The key is derived from the table of Kensley and Heard (1990) who listed the recent literature.

1\. Uropodal rami both without transverse suture .... *Axianassa* Schmitt, 1924
— One or both uropodal rami with transverse suture 2
2\. Uropod with transverse suture on exopod only; pereopods 3 and 4 dactylus with corneous spiniform setae; maxilliped 3 without exopod .... *Laurentiella* Le Loeuff and Intès, 1974
— Uropod with transverse suture on both rami; pereopods 3 and 4 dactylus without corneous spiniform setae; maxilliped 3 with exopod 3
3\. Pereopod 1 subchelate; pereopods 2 and 5 simple; antenna 2 scaphocerite well developed .... *Naushonia* Kingsley, 1897
— Pereopod 1 chelate; pereopods 2 and 5 subchelate; antenna 2 scaphocerite reduced 4
4\. Pereopods 1 dissimilar; pereopods 2–5 with reduced exopods; antenna 1 article 4 and antenna 2 article 3 short .... *Laomedia* De Haan, 1849
— Pereopods 1 similar; pereopods 2–5 without exopods; antenna 1 article 4 and antenna 2 article 3 elongate .... *Jaxea* Nardo, 1847

Thomassiniidae de Saint Laurent

Diagnosis. Callianassoidea. *Linea thalassinica well developed, starting immediately lateral to eyes*; posterior margin of carapace evenly curved; rostrum minute or a spike; eyestalks flattened; maxilla 2 scaphognathite with 1 long seta on posterior lobe; abdominal somite 1 without anterolateral lobes; pereopods 1 unequal; pereopod 1 merus with convex lower margin; pereopod 2 chelate; pereopod 3 (and sometimes 4) propodus with single distal spiniform seta on lower margin; pereopod 3 propodus broad or ovate; coxa of pereopod 4 flattened, immobile; thoracic sternite 7 broad; pleopod 2 similar to pleopods 3–5, rami lanceolate; uropodal exopod simply ovate; carapace and abdominal somite 6 with setal-rows.

Key to genera of Thomassiniidae

The three genera included here have been previously included in Callianassidae and Callianideidae.

1\. Maxilliped 3 with brush of stiff setae on ischium and merus (fig. 6k); uropodal endopod with transverse row of spiniform setae .... *Thomassinia* de Saint Laurent, 1979
— Maxilliped 3 without brush of stiff setae on ischium and merus; uropodal endopod without transverse row of spiniform setae 2
2\. Rostrum spike-like (fig. 4i); maxillipedal 3 exopod as long as merus .... *Crosniera* Kensley and Heard, 1991
— Rostrum obsolete, maxillipedal 3 exopod vestigial or absent .... *Mictaxius* Kensley and Heard, 1991

Upogebiidae Borradaile

Diagnosis. Callianassoidea. *Linea thalassinica present, diverse*; posterior margin of carapace evenly curved, abdominal somite 1 without anterolateral lobes; *rostrum usually broad, spinose and dorsally setose*; eyestalks cylindrical; maxilla 2 scaphognathite without long seta on posterior lobe; abdominal somite 1 chitinised; *pereopods 1 equal*; *pereopod 2 simple*; pereopods 3 and 4 propodus without spiniform setae on lower margin; pereopod 3 propodus linear; coxa of pereopod 4 cylindrical; thoracic sternite 7 narrow; pleopod 2 similar to pleopods 3–5, rami lanceolate; pleopods without appendix interna; uropodal exopod triangular; pereopods 2–4 and abdominal somites without setal-rows.

Key to genera of Upogebiidae

The genera of the Upogebiidae are in flux and have not been analysed phylogenetically. This key summarises the recent contributions of Sakai (1982, 1993), Williams (1986), Ngoc-Ho (1989) and Williams and Ngoc-Ho (1990). *Gebicula* Alcock, 1901 is a senior subjective synonym of *Wolffogebia* Sakai, 1982. The subgenera *Calliadne* Strahl, 1862 and *Gebiopsis* Milne Edwards, 1868 are not in current usage but are available names.

1. Rostrum with 1 or more inferior spines (fig. 4n); distal margin of telson more or less concave; pereopod 1 subchelate, fixed finger short and spine-like, carpus and propodus with rows of strong spines on mesial and upper surfaces; uropodal exopod longer than telson .... *Gebiacantha* Ngoc-Ho, 1989

— Rostrum rarely with inferior spines; distal margin of telson usually convex; pereopod 1 chelate or subchelate (figs 5e, f), carpus and propodus smooth or with spines on upper surface; uropodal exopod rarely longer than telson 2

2. Anterior dorsal region of carapace and rostrum with scattered large yellow tubercles, lateral processes not differentiated from rostrum (fig. 4r) .... *Tuerkayogebia* Sakai, 1982

— Anterior dorsal region of carapace and rostrum usually with spines and/or setae, not tubercles, lateral processes differentiated or not (figs 4o-q) 3

3. Telson and uropods operculiform (fig. 7l).. *Pomatogebia* Williams and Ngoc-Ho, 1990

— Telson and uropods not operculiform (fig. 7k) 4

4. Anterior dorsal median region of carapace with low carina, without spines or setae (fig. 4o); pereopod 1 subchelate (fig. 5f) .... *Gebicula* Alcock, 1901

— Anterior dorsal median region of carapace with clear or obsolete furrow, with spines or setae (fig. 4p); pereopod 1 subchelate or chelate 5

5. Pereopod 1 simple, its dactylus without defined upper exterior plate; uropodal rami slender and leaf-like .... *Neogebicula* Sakai, 1982

— Pereopod 1 chelate (fig. 5e) or subchelate (fig. 5f), its dactylus with defined upper exterior plate; uropodal rami broad (fig. 7k) 6

6. Rostrum broadly separate from lateral crests (notch about as broad and deep as rostrum; fig. 4q); maxilliped 3 with crista dentata; maxilliped 2 dactylus subterminal; maxillipeds 2 and 3 exopods with 2-articled flagela .... *Acutigebia* Sakai, 1982

— Rostrum narrowly or only shallowly separate from lateral crests (notch usually narrower than rostrum; fig. 4p); maxilliped 3 with simple ischial hook, without crista dentata; maxilliped 2 dactylus terminal; maxillipeds 2 and 3 exopods with multiarticulate flagella .... *Upogebia* [Leach, 1814]

THALASSINOIDEA Dana

Diagnosis. Thalassinidea. Posterior margin of carapace with lateral lobes; linea thalassinica present; pleuron of abdominal somite 1 produced; eyestalks cylindrical; antenna 1 with article 3 about as long as article 2; maxilla 2 scaphognathite with thickened setae on posterior margin; *gill elements irregular, filamentous proximally and plate-like distally*; *pereopods 1 and 2 subchelate*; pereopods 3 and 4 propodus with spiniform seta; pereopods 2–4 and abdominal somites without setal-rows; pleopods 3–5 without appendix interna (vestigial on male pleopod 2); pleopod 2 similar to pleopods 3–5; *uropodal rami linear.*

Remarks. There is one family, Thalassinidae, with one genus, *Thalassina*. See Poore and Griffin, 1979 and Dworschak, 1992 for separation of the species. Sakai (1992a) described *T. anomala* in detail.

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Table 1. Character transformations used in the phylogenetic analysis of 22 taxa of Thalassinidea. Each character is numbered and described, the plesiomorphic state is followed by (0), and apomorphic states by (1) or for multiple state characters by higher numbers. Characters with consistency indices and retention indices of 100% after weighting by HENNIG86 are marked with *. Characters with ambivalent states at 2 or more nodes are in parentheses and are not included in fig. 9.

Carapace, linea thalassinica and rostrum

1.* Linea thalassinica or linea anomurica: absent (0); present (1).

2.* Linea thalassinica: typical (0); displaced dorsally, ocular lobes substituted by branchiostegal sclerite (1).

(3). Rostrum: longer than and covering eyestalks (0); reduced and obtusely triangular (sometimes spike-like) (1).

(4). Rostrum: flattened (0); spike-like (1).

5. Rostrum: spinose laterally (0); without armature (1).

6. Rostrum: simple (0); augmented by lateral ocular ridges (1).

7. Lateral carinae: present, with longitudinal row of setae (0); absent (1).

8. Medial rostral carina: present (0); absent (1).

9. Cardiac prominence: absent (0); present (1).

Carapace–abdomen articulation

10. Posterior margin of carapace: evenly convex (0); with strong lateral lobes (1).

11.* Abdominal somite 1 anterolateral lobes: present or indicated (0); absent (1).

12. Lateral articulation between abdominal somites 1 and 2: condyle present (0); condyle absent (1).

13. Posterior margin of carapace: ridged (0); soft, without ridges (1).

14.* Abdominal somite 1, tergite anterior to anterolateral lobes or their remnants: present and chitinised (0); absent, region flexible (1).

(15). Abdominal somite 1 pleuron: acute and projecting (0); blunt and obsolete (1).

16.* Abdominal somite 1 mid-dorsal tergite: anterior and posterior regions separate (0); regions amalgamated, anteriorly depressed (1).

17. Anterolateral margin of abdominal somite 2: overlaps abdominal somite 1 (0); does not overlap (1).

Thoracic sternites

18.* Thoracic sternite 8: fused to sternite 7 (0); free from sternite 7 (1).

19. Thoracic sternite 7, episternites: diverging posteriorly (0); contiguous posteriorly (1).

20. Thoracic sternite 7, episternites: acute (0); flattened (1).

21. Coxa of pereopod 4 posterior condyle: functional (0); obsolete or absent (1).

22. Coxa of pereopod 4: rectangular, without anteromesial lobe (0); flattened, with anteromesial lobe (1).

23. Coxa 4: mobile (0); immobile (1).

24.* Thoracic sternite 7, midanterior region: sharply ridged (0); flattened and broadened (coxae secondarily separate) (1).

Gills

25. Gill elements: irregularly arranged along rachis (0); paired transversely along rachis (1).

26. Epipods: broadly laminar (0); linear anteriorly and lost posteriorly (1).

(27). Epipods: 1–7 (rarely 2–7) present (0); 7 rudimentary or absent (1); 4–7 vestigial or absent (2); 3–7 absent (3); 2–7 absent (4).

(28). Podobranch 2: present (0); vestigial or absent (1).

29. Podobranchs 3–7: present (0); 7 absent (1); 3–7 absent or some rudimentary (2).

(30). Arthrobranchs on somites 1–7: 1122222 (0); 0122222 (1); 0022222 (2).

31. Pleurobranchs: 5–8 present (0); 5–7 (or rarely only 7) present, 8 rudimentary or absent (1); 5–8 absent (2).

Cephalon

(32). Epistome: without setae (0); with long setae (1).

33. Eyestalk: cylindrical, cornea terminal (0); flattened, cornea dorsal (1).

34.* Antenna 1, article 1: about as long as article 2 (0); elongate, waisted (1).

35. Antenna 1, article 3: longer than article 2 (0); as long as article 2 (1).

36. Antenna 2 scaphocerite: prominent, much longer than wide (0); reduced but articulating, about as long as wide (1); absent (2).

(37). Mandibular incisor: smooth anteriorly, denticulate posteriorly (0); toothed anteriorly and posteriorly (1).

38.* Mandibular incisor: symmetrical (0); asymetrical (1).

39. Maxilla 2 scaphognathite: without a long seta (0); with a long seta (1).

(40). Maxilla 2 scaphognathite, posterior lobe: tapering (0); rounded and evenly setose (1).

41. Maxilliped 1 endopod: 2-articled (or elongate and tapering) (0); minute (1).

(42). Maxilliped 1 exopod: 2-articled (with flagellum) (0); 1-articled (1).

43. Maxilliped 2 exopod: almost reaching to end of merus (0); reduced or absent (1).

44. Maxilliped 3: ischium–merus linear, carpus–dactylus linear (at least 6 times as long as wide) (0); ischium–merus at least slightly

broadened, carpus–dactylus compact (shorter than ischium–merus) (1).

(45).Maxilliped 3, exopod: reaching almost to end of merus (0); reduced or absent (1).

46. Maxilliped 3, crista dentata: prominent toothed ridge (0); obsolete or absent (1).

47. Maxilliped 3, meral spine: present (0); absent (1).

Pereopods

48.* Pereopodal basis — ischium: free (0); fused (1).

49.* Row of setae on lower margin of ischium — propodus of pereopod 2: absent (0); present (1).

50. Pereopod 1, carpus — propodus: cylindrical (0); flattened with upper and lower ridges (1).

(51).Pereopod 1, carpus — propodus: bending near right angles in horizontal plane (0); scarcely bending (1).

52.* Pereopod 1: equal (0); unequal (1).

53.* Pereopod 1, merus: with straight lower margin (0); with convex lower margin (1).

54.* Pereopod 1: simple (0); chelate or subchelate (1).

(55).Pereopod 2: simple (0); chelate (1).

56. Pereopod 2 dactylus: as long as fixed finger (0); longer than fixed finger (1).

57.* Pereopod 3 propodus: linear or oval (0); with heel on proximal corner of lower margin (1).

58. Pereopods 3 and 4, dactylus: without spiniform setae (0); with spiniform setae (1).

59. Pereopod 3, propodus: without spiniform setae (0); with rows of lower lateral spiniform setae (1).

60. Pereopod 4, propodus: without spiniform setae (0); with rows of lower lateral spiniform setae (1); with 1 spiniform seta distally on lower margin (2).

61.* Pereopod 3, propodus: without spiniform setae (0); with 1 spiniform seta distally on lower margin (1).

(62).Pereopod 4 propodus: without spiniform setae (0); with 1 spiniform seta distally on lower margin (1).

63. Pereopods 3 and 4, propodus: linear (on pereopod 3 more than 3 times as long as wide) (0); flattened (less than twice as long as wide) (1).

64. Pereopod 5: long and slender (0); short, compact and fitting into side of abdominal somite 1 (1).

Body proportions

65. Relative length of cephalothorax (cl/tl): half (0); third or less (1).

66.* Relative length of abdominal somite 2 to abdominal somite 1: less than 1.5 (0); more than 2 (1).

67. Abdominal somites 3–5: without setae laterally or at most sparse vertical rows (0); with dense tufts of lateral setae (1).

Pleopods

68.* Pleopods: 1 reduced, 2–5 similar and lamellar (0); 1 and 2 sexually modified, 3–5 similar and lamellar (1).

69. Male pleopod 1, appendix interna: present as minute hooks on ramus (0); absent (1).

(70).Male pleopod 1, second article: ovate (0); more or less triangular (1).

(71).Male pleopod 1: 1- or 2-articulate (0); minute or lost (1).

72.* Male pleopod 2, appendix masculina: present, prominent (0); fused to appendix interna (1).

73. Male pleopod 2, appendix masculina: present, prominent (0); absent (1).

74.* Pleopods 2–5 exopod: symmetrical (0); laterally lobed (1).

Tail fan

(75).Uropodal exopod: with transverse suture (0); without suture (1).

76.* Uropodal exopod: simply ovate (0); with anterodorsal setose thickening (1).

77. Uropodal endopod: distally rounded (0); distally truncate, distolateral margin subacute (1).

78. Telson and uropodal rami: with spines on surface (0); unarmed (1).

79. Abdominal somite 6 epimeron: ventrally produced, with mesial setae (0); not ventrally produced, without setae (1).

Setal-rows

80.* Longitudinal carinal setal-row: absent (0); present (1).

(81).Carapace vertical setal-row: absent (0); at least one present (1).

82.* Carapace vertical setal-rows: 1 present (0); 2 or 3 present (1).

(83).Pereopod 2 setal-row: absent (0); present (1).

(84).Pereopod 3 setal-rows: absent (0); 1 row present (1).

85.* Pereopod 3 setal-rows: 1 row only (0); second row present (1).

(86).Pereopod 4 setal-rows: absent (0); 1 row present (1).

87.* Pereopod 4 setal-rows: 1 row only (0); second row present (1).

88. Abdominal somite 1 setal-row: absent (0); present (1).

89. Abdominal somite 2 setal-row: absent (0); present (1).

90. Abdominal somites 3–5 setal-rows: absent (0); present (1).

91. Abdominal somite 6 longitudinal pleural setal-row: absent (0); present (1).

92. Abdominal somite 6, posterior setal-row: absent (0); present (1).

93. Abdominal somite 6, intermediate setal-row: absent (0); present (1).

Table 2. Genus-character matrix (27 genera by 93 characters) used in the HENNIG86 cladistic analysis of genera of the Thalassinidea. The first five taxa are outgroups. Unknown character states are shown by ?

	0	1	2	3	4	5	6	7	8	9
Neoglyphea	0000000000	0000000100	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	000
Enoplometopus	0000001000	0000000000	0000000002	0000000000	0000000000	0000000000	0000000001	0000000000	0000000000	000
Nephropsis	0000000000	0000000000	0000000002	0000000000	0000000000	0000000000	0000000000	0010000000	0000000000	000
Dardanus	1000000000	0000000100	0000111120	0000000000	0000000100	1001000000	0000000000	0000100000	0000000000	000
Munida	1000000000	0000000100	0000111120	0000000000	0000000100	0001000000	0000000000	0000100000	0000000000	000
Calocaris	0000000001	0000000111	0000100011	2000100010	0000000110	1001100000	0000000001	0000000000	0000000000	000
Coralaxius	0000000001	0000000111	0000102122	2000100010	0000000110	1001100111	0000000001	0000000000	0000000000	000
Axius	0000000001	0000000110	0000100011	1000100010	0000000110	1001100101	0000000001	0000000000	0000000000	010
Axiopsis	0000000001	0000000110	0000100012	2000100010	0000000110	1001100101	0000000001	0000000000	0000000000	010
Spongiaxius	0000000001	0000000111	0000100112	2000100010	0000000111	1001100111	0000000001	0000000000	0000000000	010
Strahlaxius	0000000001	0000100111	0100100112	2000100010	0000000110	1001100000	0010011010	0011101000	0011010110	011
Tethisea	0000100001	0000100111	0100100112	1001100110	0000100111	1001110000	0010110001	0001101111	1111010110	111
Marcusiaxius	0000100001	0000100111	0100100112	1101100110	0100111111	1001100000	0010110001	0001101111	1111111111	110
Meticonaxius	0000100001	0000100111	0100100112	1101100110	0110100111	1001100000	0010110001	0001101111	1111111111	111
Michelea	0010101101	0000100111	1110100122	1101110110	1010000111	1001110111	0010111001	0001101111	1111111111	011
Thalassina	1000010101	0000001111	0100000011	2000011000	0000000110	1001100000	0000000001	0000100100	0000000000	000
Laomedia	1010101101	0010000101	0000100001	2000011000	0000001110	1001000000	0000000000	1000000100	0000000000	000
Upogebia	1000011100	1010000111	0000112122	2000010001	0000000110	1001000000	0000000000	1010101100	0000000000	000
Callianidea	1010101100	1100101111	1110100122	2010010010	0100000111	1111110000	1110001010	0010100110	0011010100	010
Mictaxius	1110101100	1010110111	1111111121	2100011010	0101111111	1111100000	1111001010	0000100110	1011010111	011
Thomassinia	1110101100	1010110111	1111111122	2110021010	0101111111	1111100000	1011000010	0100100110	1000000100	111
Crosniera	1111101100	1010110111	1111110122	2110011010	0001010111	1111100000	1011001010	0100100110	1000000100	111
Paracalliax	1010101110	1011000111	0100113121	2110010001	0100000111	1101100000	00101000??	00?0100110	0000000000	000
Ctenocheles	1011101010	1111101111	0100114121	2110110001	0110100111	1101100000	0011100010	0000100110	1000000000	000
Gourretia	1011101110	1111101111	0100113121	2110110001	0101001111	1101100000	0011100010	0000100110	1000000000	111
Anacalliax	1010101010	1111101111	0100114122	2110110001	0001101111	1101101000	0001101110	0010110000	0000000100	111
Callianassa	1010101100	1111101111	0100113121	2110020001	1101101111	1101101000	0011101110	1010110110	0000000000	111

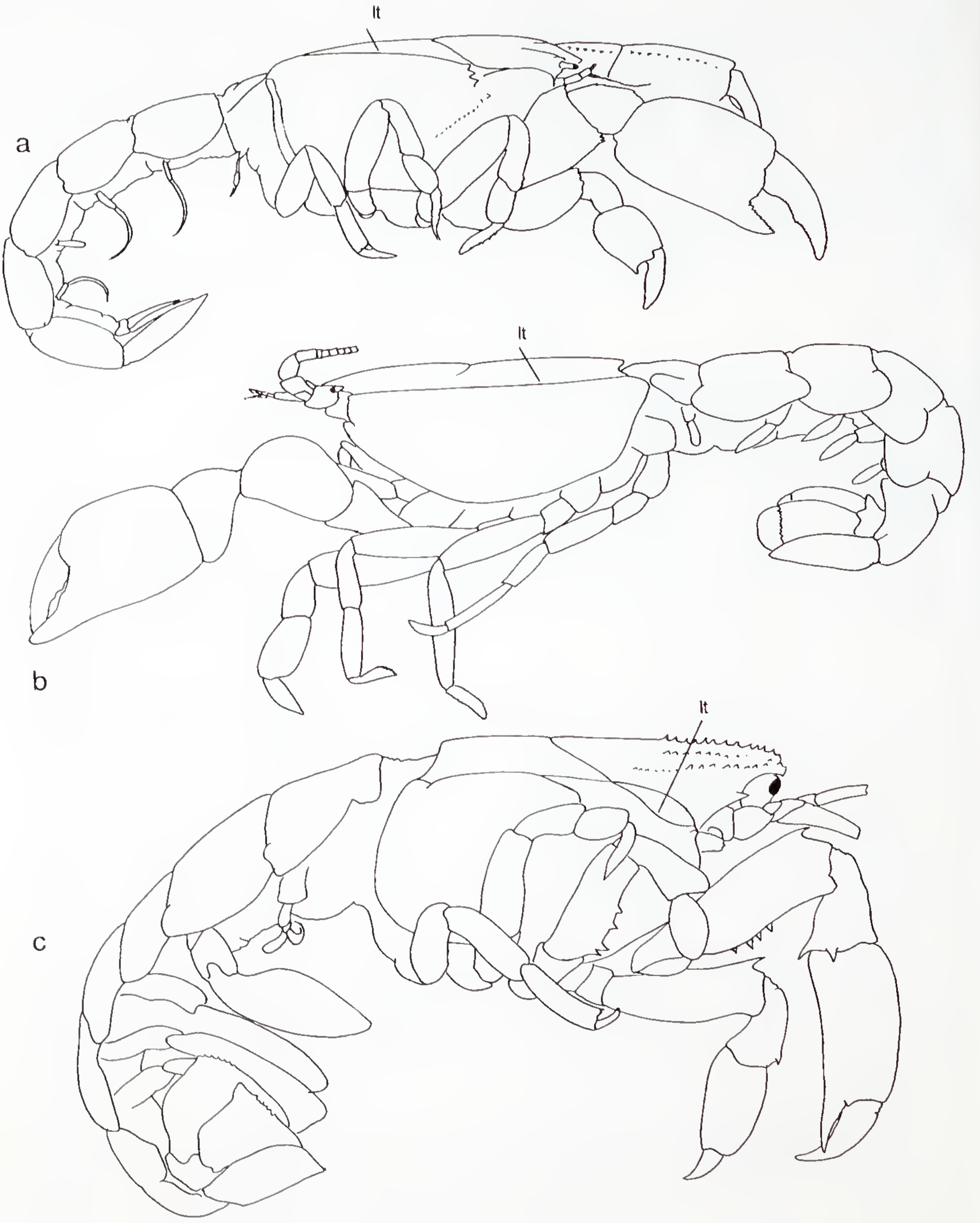

Figure 1. a, *Thalassina anomala* Herbst (Thalassinidae) [after Sakai, 1992a]; b, *Laomedia healyi* Yaldwyn and Wear (Laomediidae) [after Yaldwyn and Wear, 1972]; c, *Upogebia* species indeterminate (Upogebiidae) [after Williams, 1986].
lt = linea thalassinica.

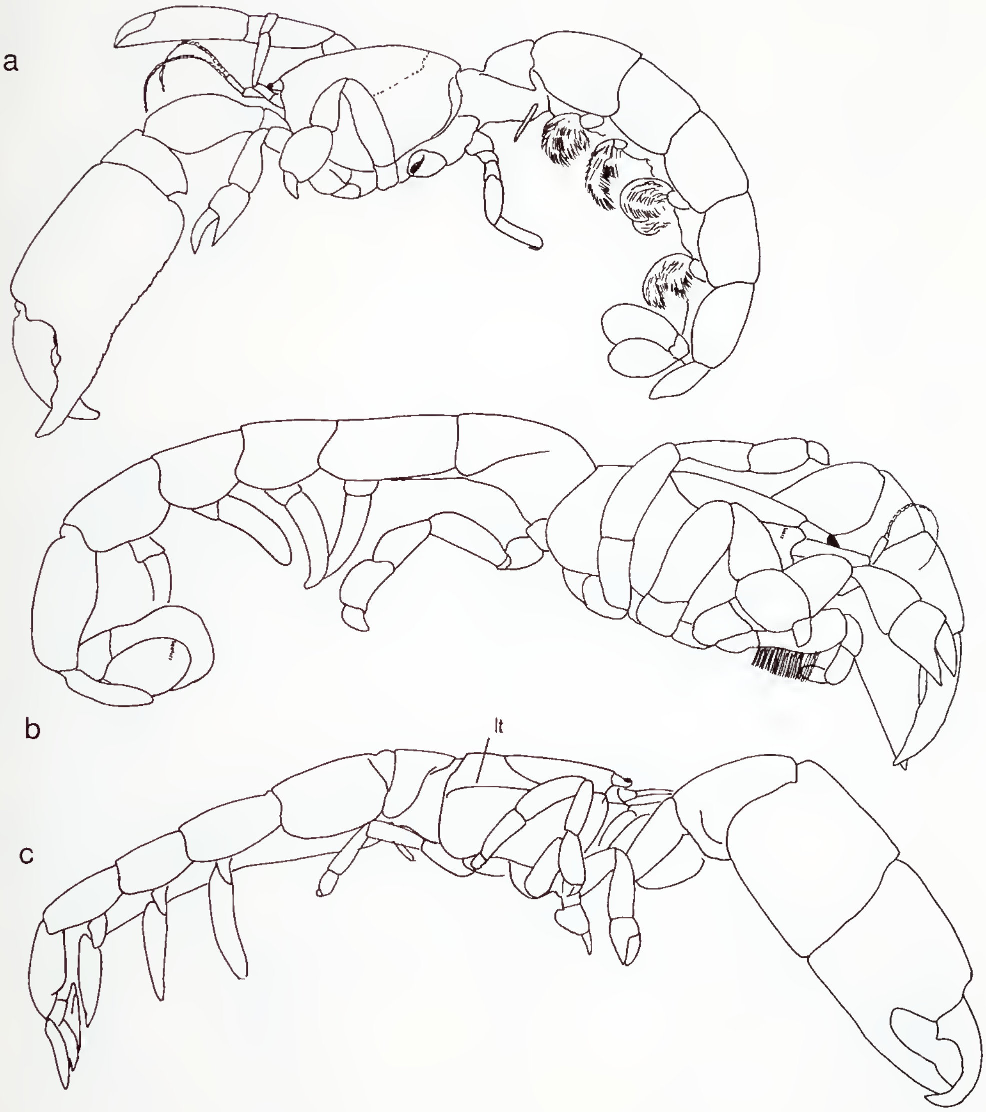

Figure 2. a, *Callianidea typa* Milne Edwards (Callianideidae) [after Sakai, 1992a]; b, *Thomassinia* sp. nov. (Thomassiniidae) c, *Trypaea australiensis* Dana (Callianassidae).
lt = linea thalassinica.

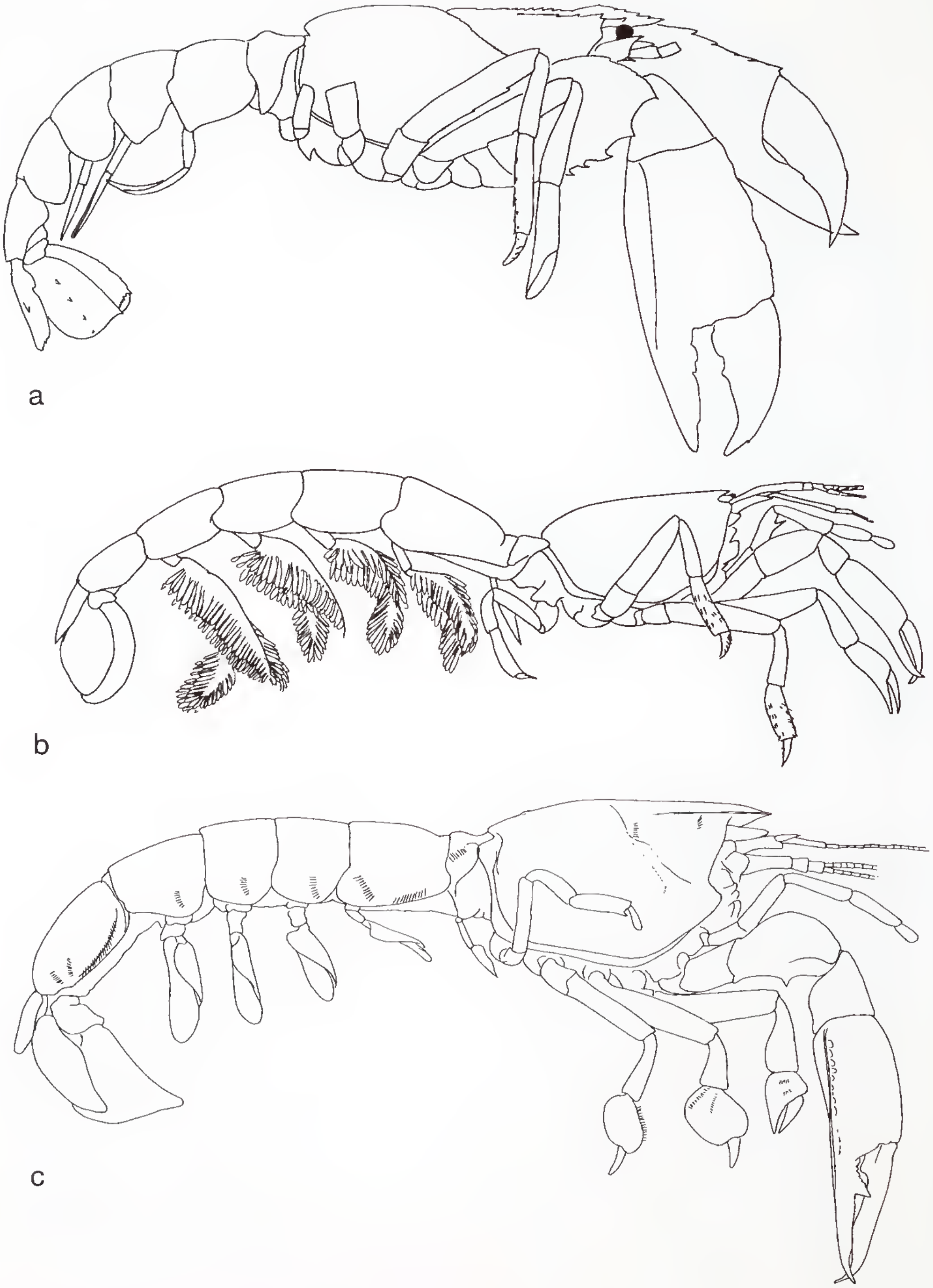

Figure 3. a, *Calaxius pailoeoensis* (Rathbun) (Axiidae) [after Sakai and de Saint Laurent, 1989]; b, *Michelea vanderoverae* (Gore) (Micheleidae); c, *Marcusiaxius lemoscastroi* Rodrigues and Carvalho (Micheleidae).

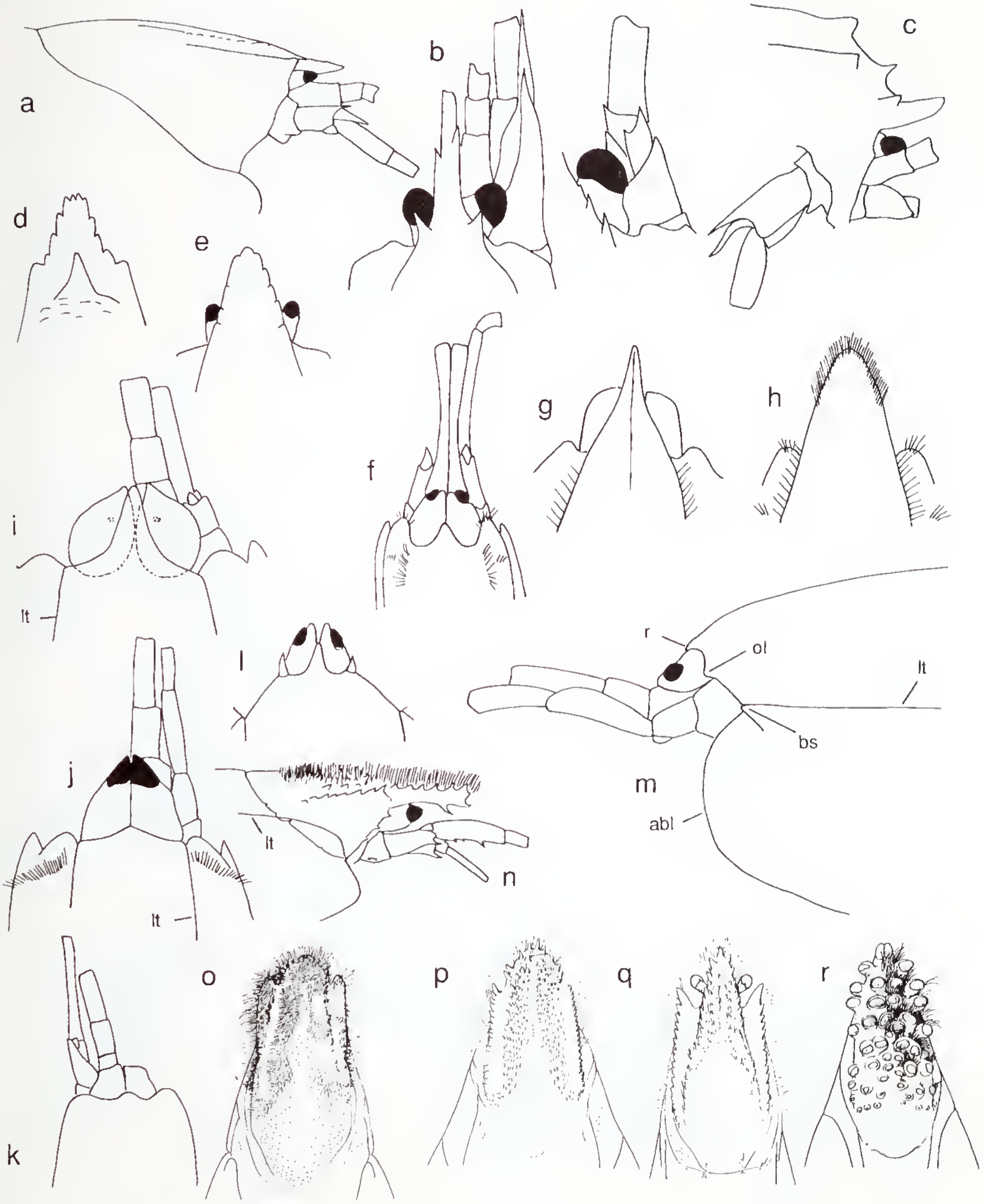

Figure 4. Anterior region of cephalothorax: a, *Axiopsis*; b, *Acanthaxius*; c, *Scytoleptus*; d, *Strahlaxius*; e, *Axius*; f, *Michelea*; g, *Meticonaxius*; h, *Marcusiaxius*; i, *Crosniera*; j, *Thomassinia*; k, *Callianidea*; l, *Corallianassa*; m, *Biffarius*; n, *Gebiacantha*; o, *Gebicula*; p, *Upogebia*; q, *Acutigebia*; r, *Tuerkayogebia* [o–r from Sakai, 1982]. Antenna 2 base and scaphocerite: s, *Eutrichocheles* (dorsal); t, *Spongiaxius* (lateral).

abl = anterior branchiostegal lobe; bs = branchiostegal scerite; lt = linea thalassiniea; o = ocular lobe; r = rostrum.

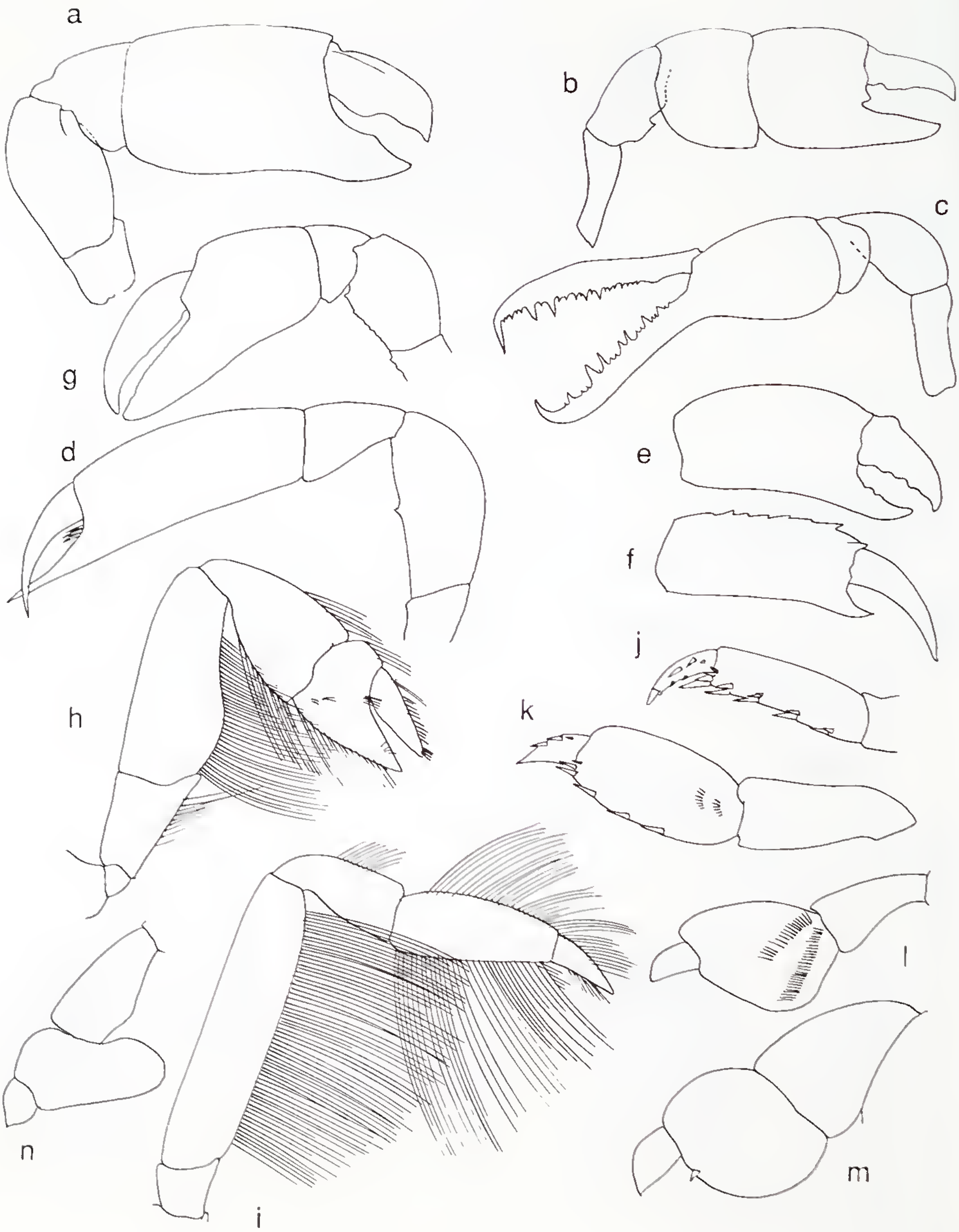

Figure 5. Major cheliped (pereopod 1): a, *Axius*; b, *Biffarius*; c, *Ctenocheles*; d, *Tethisea*; e, *Upogebia*; f, *Gebicula*.

Minor cheliped (pereopod 1): g, *Eiconaxius*.

Pereopod 2: h, *Callianassa*; i, *Upogebia*.

Pereopod 3 (distal articles showing spiniform setae and setal-rows): j, *Allaxius*; k, *Michelea*; l, *Marcusiaxius*; m, *Thomassinia*; n, *Callianassa*.

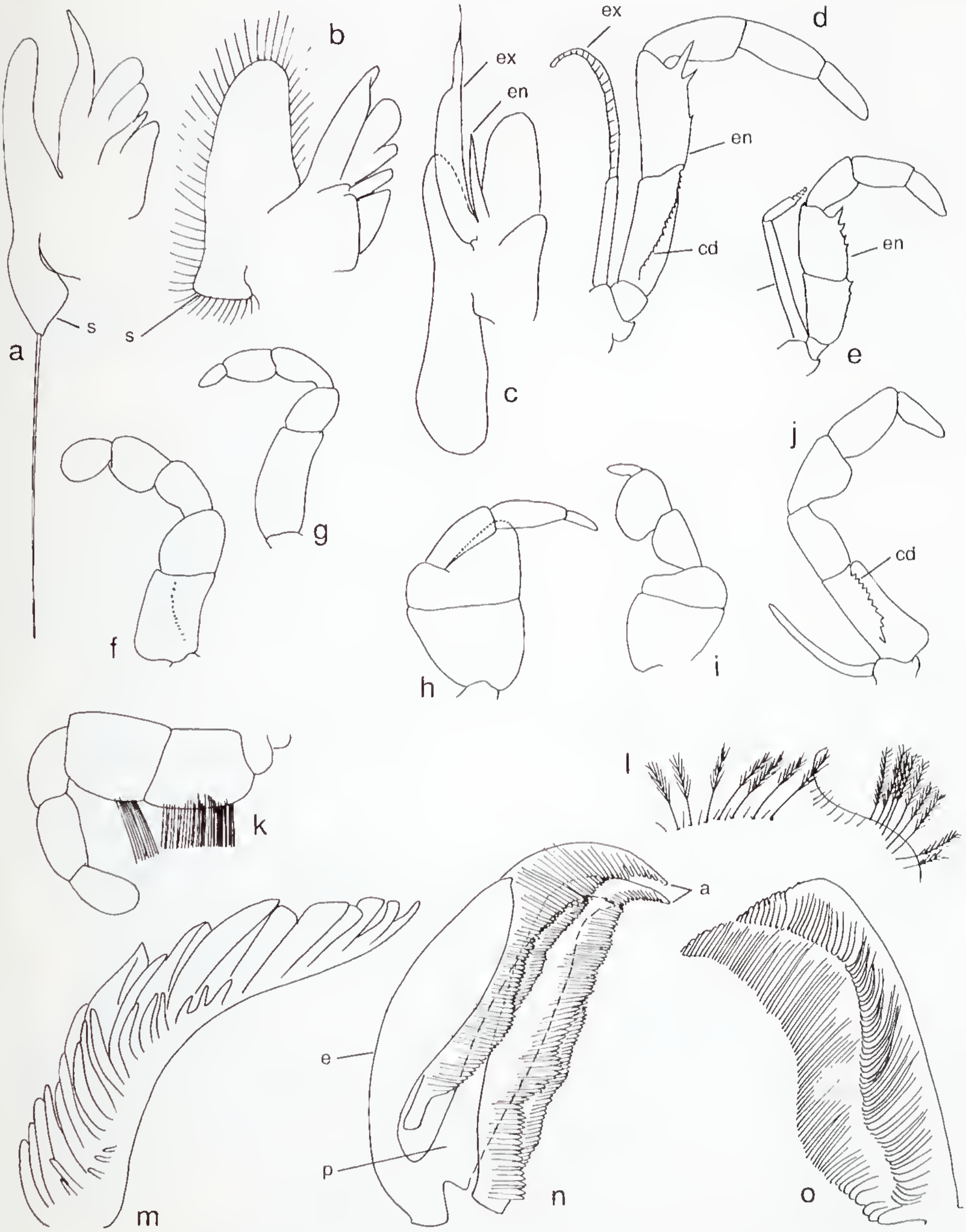

Figure 6. Maxilla 2: a, *Allaxius* (scaphocerite with long seta); b, *Callianassa* (scaphocerite with setose margin).
Maxilliped 1: c, *Allaxius* (with endopod and flagellate exopod).
Maxilliped 3: d, *Axiopsis*; e, *Coralaxius*; f, *Eucalliax*; g, *Anacalliax*; h. *Trypaea*; i, *Callichirus*; j, *Gourretia*; k, *Thomassinia*.
Setal-rows at anterior margin of carapace: l, *Michelea*.
Branchiae on thoracomere 7: m, *Thalassina* (1 of 2 arthrobranchs); n, *Axius* (2 arthrobranchs and broad epipod with podobranch, dotted); o, *Biffarius* (1 of 2 arthrobranchs).
a = arthrobranch; cd = crista dentata; e = epipod; n = endopod; p = podobranch; s = scaphocerite; x = exopod.

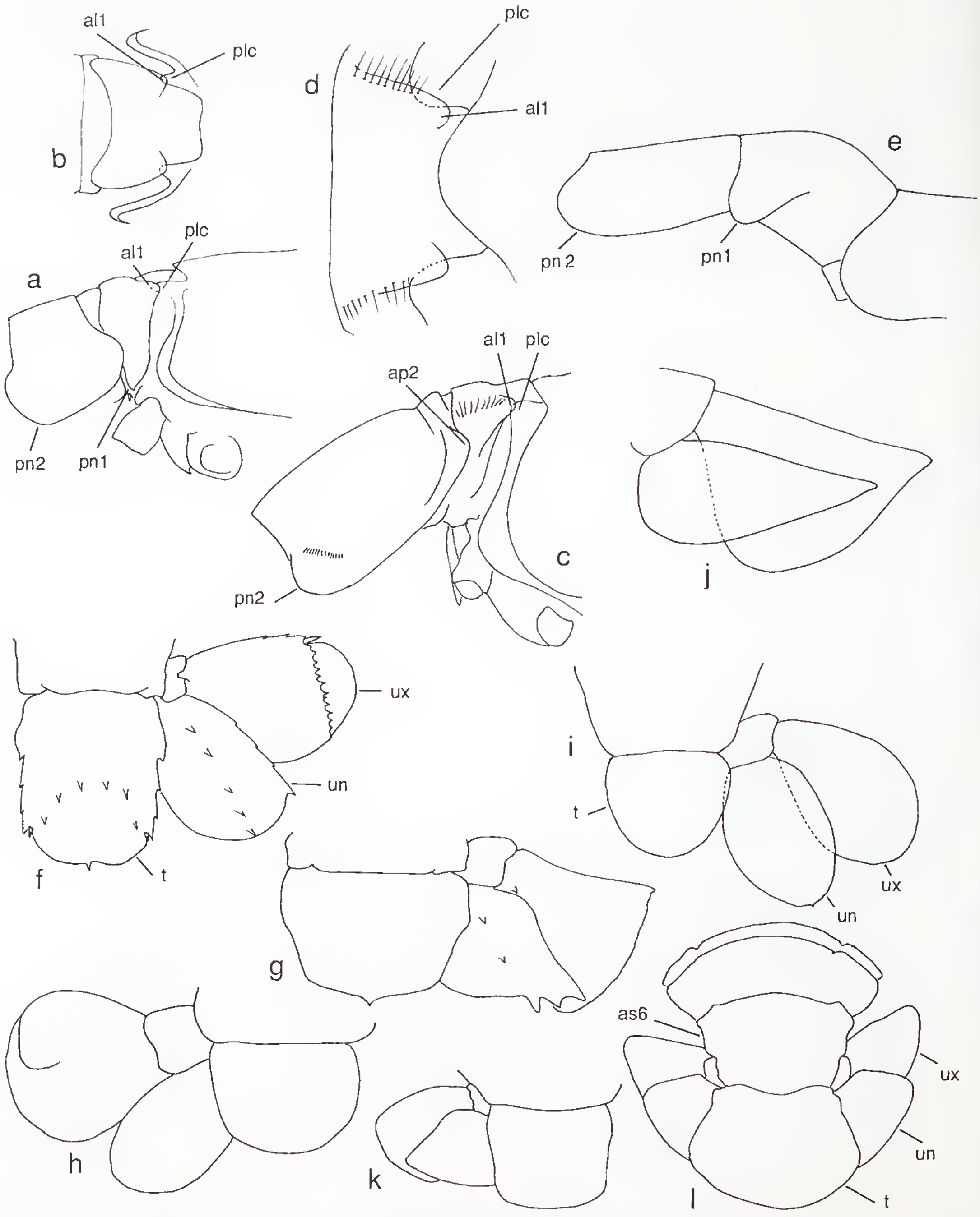

Figure 7. Posterior margin of carapace, abdominal somites 1 and 2: a, b, *Axius* (right and dorsal views); c, d, *Marcusiaxius* (right and dorsal views); e, *Thomassinia* (right view).

Telson and uropod: f, *Eutrichocheles*; g, *Strahlaxius*; h, *Biffarius*; i, *Michelea*; j, *Marcusiaxius* (right uropod only); k, *Upogebia*; l, *Pomatogebia*.

al1 = anterolateral lobe of abdominal somite 1; ap2 = anterior lobe of pleuron of abdominal somite 2; as6 = abdominal somite 6; dl = dorsal lobe; plc = posterolateral lobe of carapace; pn = pleuron; t = telson; un = uropodal endopod; ux = uropodal exopod.

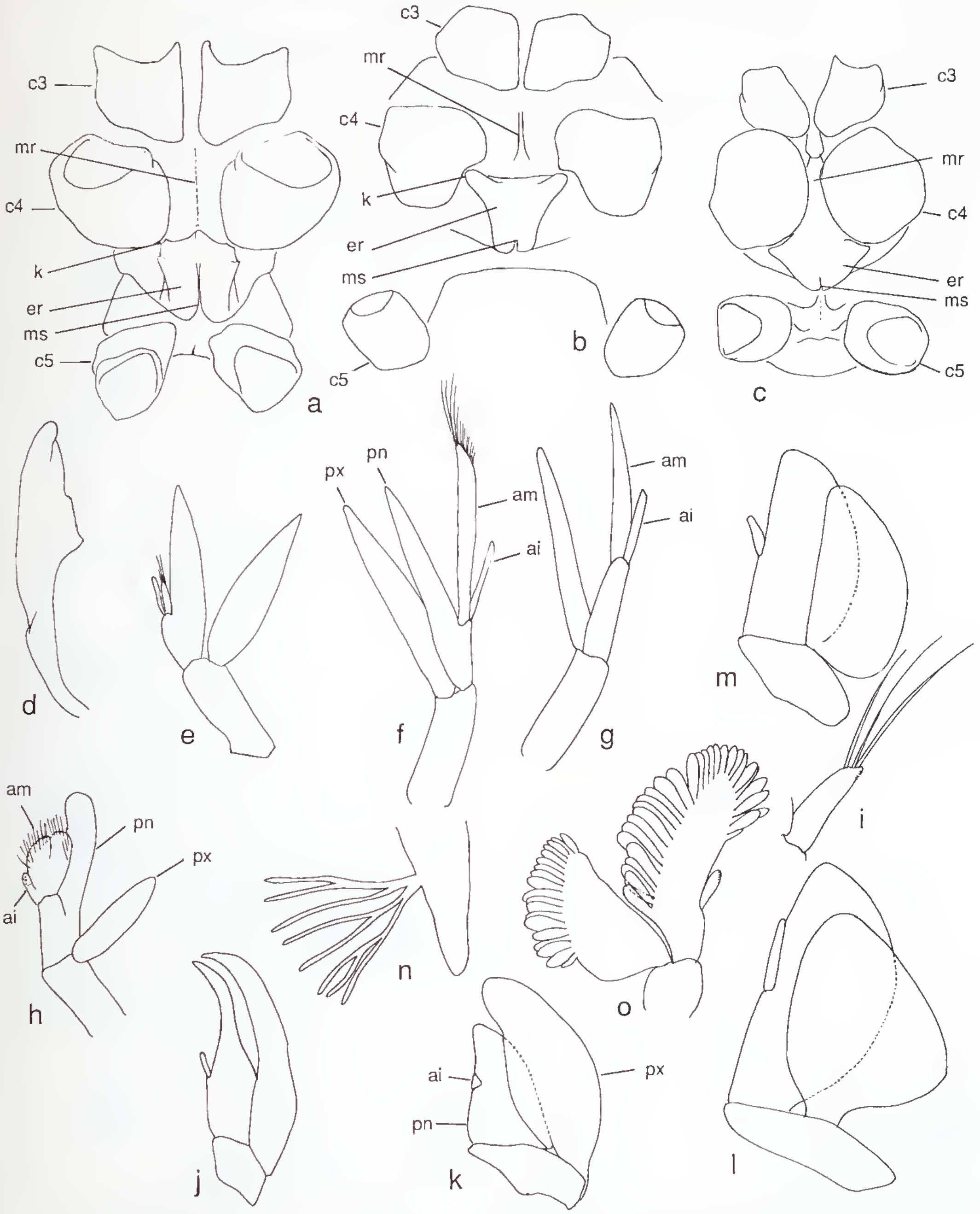

Figure 8. Sternites of thoracomeres 6, 7 and 8; coxae of pereopods 3 (top), 4 and 5 (bottom): a, *Axius*; b, *Biffarius*; c, *Callianidea*.

Pleopod 1 of male: d, *Bouvieraxius*.

Pleopod 2 of male, showing appendix interna and appendix masculina: e, *Axiopsis*; f, *Bouvieraxius*; g, *Calocaris*; h, *Coralaxius*; i, *Mictaxius* (combined appendices interna and masculina).

Pleopod 3, with appendix interna: j, *Biffarius*; k, *Anacalliax*; l, *Marcusiaxius*; m, *Neaxiopsis*.

Pleopodal marginal extensions: n, single branching filament on endopod of *Callianidea*; o, pleopod 2 of *Michelea* with marginal lamellae.

ai = appendix interna; am = appendix masculina; c3, c4, c5 = coxa of pereopods 3, 4, 5; er = episternal ridge (or plate); k = site of posterior condyle between sternite 7 and coxa 4; mr = median ridge of sternite 7; ms = median slit; pn, pleopodal endopod; px = pleopodal exopod.

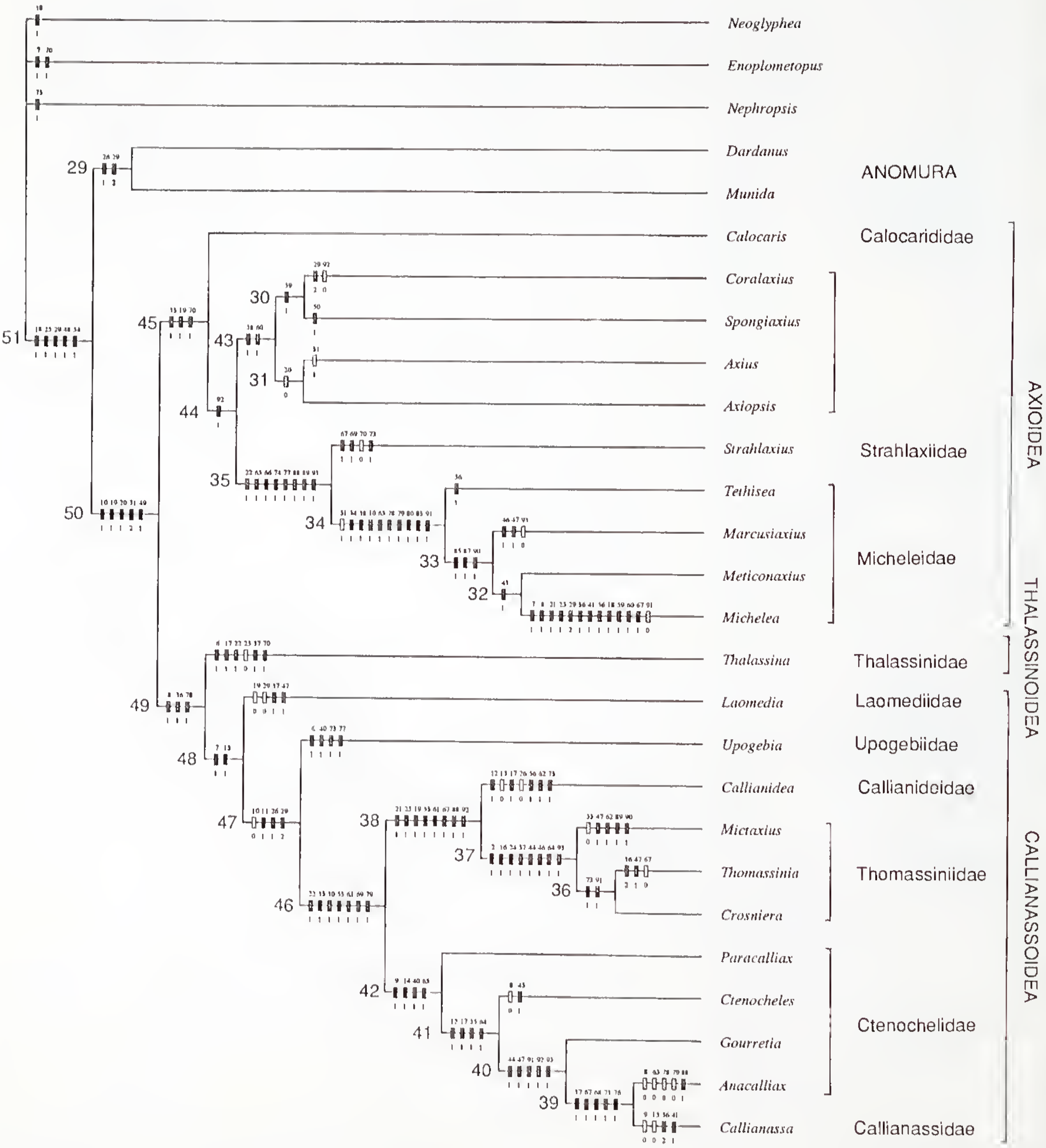

Figure 9. Cladogram of 22 selected genera of Thalassinidea and five outgroup genera generated from HENNIG86 using a single successive weighting of 97 characters. Unambivalent character changes are given for each ancestral clade. Clades are numbered at their stems and discussed in the text. Higher taxa are given at the right.