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(DECAPODA: ANOMURA: AEGLIDAE), WITH
COMMENTS ON ANOMURAN PHYLOGENY

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PHYLOGENETIC RELATIONSHIPS OF THE GENUS *AEGLA* (DECAPODA: ANOMURA: AEGLIDAE), WITH COMMENTS ON ANOMURAN PHYLOGENY

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ABSTRACT

Anomuran decapods in the family Aeglidae are ecologically and morphologically distinct from other members of the Galatheoidea (Galatheidae, Chirostylidae, Porcellanidae). Among the morphological characters distinguishing aeglids from other galatheoids are several characters seen in the hermit crab families (Paguroidea). The hypothesis that aeglids are members of the Paguroidea rather than the Galatheoidea was tested using numerical phenetic and cladistic methods. Fifty-four morphological and ecological characters were scored for all families that are now or have been previously included among the Anomura. Aeglids are shown to be primitive members of the Galatheoidea, in accordance with traditional classifications of the Anomura, although other traditional groupings within the Anomura are questioned. A proposed hypothesis of anomuran phylogeny separates thalassinoids from Anomura *sensu stricto*, places aeglids with other galatheoids, and removes lithodids and *Lomis* from the paguroid line. The need for increased and improved basic morphological monographs of decapod families is stressed.

Phylogenetic relationships within the decapod Crustacea have been the subject of controversy since the establishment of the taxon Decapoda by Latreille (1803). Although some groupings appear to reflect "natural" (i.e., monophyletic) lineages, such as the Dendrobranchiata and Brachyura, other recognized assemblages are generally conceded to be unnatural (i.e., para- or polyphyletic). The infraorder Anomura MacLeay, 1838, is an example of a taxon that has undergone considerable revision and rearrangement since its conception (see McLaughlin, 1983b; McLaughlin and Holthuis, 1985). Modern classifications of the Anomura vary according to author. The scheme of Glaessner (1969) follows that of Borradaile (1907) and includes as anomurans the superfamilies Thalassinioidea, Paguroidea, Galatheoidea, and Hippoidea. Most modern workers exclude the thalassinoids from the Anomura; McLaughlin and Holthuis (1985) list as constituent superfamilies the Galatheoidea, Hippoidea, Lomoidea, and Paguroidea.

The anomuran family Aeglidae Dana, 1852, consisting of the single genus *Aegla*, is usually placed in the superfamily Galatheoidea Samouelle, 1819, along with the Galatheidae, Chirostylidae, and Porcellanidae (e.g., Balss, 1957; Glaessner, 1969; Bowman and Abele, 1982). Aeglids are unique ecologically (the only family of the Anomura restricted to fresh water), biogeographically (endemic to temperate South America), and morphologically (see Martin and Abele, in press). A recent morphological study (Martin and Abele, in press) questions the traditional classification on the basis of several characters, most salient of which are: (1) the gills of *Aegla* are trichobranchiate, whereas all other galatheoids have well-developed phyllobranch gills, and (2) the carapace of *Aegla* is subdivided by a series of sutures (lineae) unlike those seen in other galatheoids. These characters suggest the possibility of common ancestry with the hermit crab families, nearly all of which possess carapace lineae similar to those seen in *Aegla* and some of which possess trichobranch gills. In this paper we address the possible phylogenetic relationships of *Aegla* by comparing morphological and ecological characters of *Aegla* with those of representatives of all families that are now or have been previously included among the Anomura.

MATERIALS AND METHODS

Anomuran and thalassinoid decapods in our collections or in the holdings of the Smithsonian Institution's National Museum of Natural History were examined and scored for 54 characters (Appendices I, II). We examined firsthand representatives of all families with two exceptions. The Axi-anassidae of the Thalassinoidea were excluded because it is likely that this group will be reassigned to the Laomedidiidae (personal communication, Richard Heard; B. Kensley and R. Heard, manuscript in preparation). The thalassinoids of the family Callianideidae, previously a subfamily of the Callianassidae, were excluded because of a shortage of specimens. The morphology of callianideids is very similar to that of the Callianassidae and Axiidae, from which they possibly were derived (see de Saint Laurent, 1979), and it is unlikely that this highly specialized group bears on the question at hand. Although individuals from every other family were examined, the rareness of some specimens precluded dissection. Therefore, some characters in rare taxa (e.g., the Pomatochelidae) have been taken from the literature. The family Lithodidae was scored separately for both its constituent subfamilies (Lithodinae and Hapalogastrinae) because we felt that these two groups differed significantly. Similarly, the genus *Probebe* of the Parapaguridae was treated as a separate entity because of its unusual morphology (see Wolff, 1961). Selected characters of each family, when not adequately illustrated in existing literature, were described with the aid of a Wild M-5 stereoscope and drawing tube. Specimens used for scanning electron microscopy (SEM) were fixed in 10% Formalin or 3% glutaraldehyde in 0.1 M phosphate buffer for 3 h and postfixed in 2% osmium tetroxide for 1.5 h at room temperature. Fixed tissue was cleaned by sonication, dehydrated in a graded ethanol series, and critical-point dried. Specimens were then mounted on stubs and sputter coated with 20 nm of gold palladium for observation in a Cambridge S4-10 and a JEOL 840 scanning electron microscope at accelerating voltages of 5-30kV.

The resulting data matrix (21 taxa including *Penaeus* for comparative purposes; 54 characters) was subjected to a numerical phenetic analysis and used to estimate minimum-length Wagner trees by cladistic methods. For the phenetic analysis, the data matrix (Appendix III, minus *Penaeus*) was used to perform a cluster analysis using the unweighted pair-group method with arithmetic averages (UPGMA) based on Euclidean distances (Sneath and Sokal, 1973). Cladograms were constructed using computer algorithms based on the Wagner ground plan analysis (see Wiley, 1981). Computer programs used were WAGNER78 (Farris, 1970), MINT (mini numerical taxonomy system of Rohlf, 1971), and PHYLIP (Felsenstein, 1984). The trees were rooted by out-group comparison with the genus *Penaeus* following the procedures of Wiley (1981). For all cladistic analyses the order of entry of the taxa was shuffled and the analysis run a minimum of 10 times.

CHARACTER SELECTION AND SCORING

Characters employed in the analyses (Appendix II) were selected from a larger initial set of characters. Characters were discarded when it became apparent that the state of the character was the same for all operational taxonomic units (OTUs), and thus was of no value for the analysis. Polarity of a character state was determined by comparison with the shrimp genus *Penaeus* or by available ontogenetic data (see Wiley, 1981). *Penaeus* was chosen as an out-group because the characters of the Dendrobranchiata are conceded by most workers to be primitive relative to characters of other infraorders (see Felgenhauer and Abele, 1983). We scored apparent plesiomorphies 0 and derived states 1-3, although in some cases we feel it unlikely that these numbers reflect a transitional series of character states. For the PHYLIP program it was necessary to rescore multistate characters (0-3) as binary numbers according to Sneath and Sokal (1973: 150). We should point out that many characters used here and in other decapod studies are not clear-cut. Often our judgement was used as to whether, for example, a rostrum was well developed, a pereopod reduced, or a maxilliped pediform. It is probable and indeed desirable that many of our decisions will be questioned by future workers. The characters used, and our reasons for scoring them as primitive (plesiomorphic, p) or advanced (apomorphic, a), are discussed below. Numerals in brackets refer to characters in Appendices II and III.

Rostrum [1].—A well-developed rostrum (p) occurs in *Penaeus* and in all of the thalassinoids except the Callianassidae (see Biffar, 1972), although in some upo-

gebiids the rostrum is wide and blunt and could possibly be considered reduced (see Williams, 1986). In the Anomura, it is reduced (a) in the hippoids (Fig. 1*b*) and paguroids (Fig. 1*g-i*), with two exceptions: the paguroid family Lithodidae (although it is reduced in the subfamily Hapalogastrinae; Fig. 1*f*) and the parapagurid genus *Probeebe* (see Wolff, 1961). Although variable in form, the rostrum of the Galattheoidea is well developed (e.g., chirostylids, Fig. 1*c*) with the exception of most of the crablike Porcellanidae (Fig. 1*d*).

Eyes.—The presence of ocular acicles [2] is difficult to determine. They are lacking (p) in *Penaeus* and in all of the Thalassinoida and Galattheoidea, so that their presence (a) probably represents a derived condition. In the Paguroidea they are almost always present (Fig. 1*g-i*), except in the Lithodidae and some parapagurids. Makarov (1962) noted their absence in lithodids, although McLaughlin (1983*b*) felt that they were present in some species but reduced or absent in others. We have scored them as absent in lithodids, on the basis of our admittedly cursory examination (1 species each) of the Lithodinae and Hapalogastrinae (Fig. 2*a, b*), and present in the Albuneidae (Fig. 2*d*). The small ossicles on the albuneid eyestalks may be pieces of the ocular plate and not true ocular acicles (McLaughlin, 1983*b*), but we are unsure about the difference between small ocular acicles and pieces of the ocular plate. Although McLaughlin (1983*b*) noted that ocular acicles may be reduced or absent in some parapagurids, we scored this family as having ocular acicles present because this condition is seen in the majority of species.

The eyestalks [3] are well developed (p) in most of the anomuran families and *Penaeus*. They are flattened (a) in the Callianassidae, and flattened and enlarged in the Albuneidae (Fig. 2*d*) (with several exceptions; see Eford and Haig, 1968) and *Lomis* (Fig. 2*c*). This condition is approached in certain lithodids as well (e.g., Fig. 2*b*), but we scored the family as a whole with normal development of the eyestalks.

Antennule [4].—The ventral flagellum of the decapod antennule is almost always reduced relative to the dorsal flagellum (Fig. 3*a-h*). In the Coenobitidae, this flagellum is compressed, short, and lacking segmentation (Fig. 3*g*), a condition we feel is derived (a). It is further modified in the albuneids, where the ventral flagellum is usually vestigial or lost (Fig. 3*b*) (although not in *Blepharipoda* or *Lophomastix*).

Antenna.—The peduncle of the antenna bears a well-developed scaphocerite [5] in *Penaeus*. Its presence (p) and development is variable in the thalassinoids and anomurans. In the thalassinoids a scaphocerite is seen in the Axiidae (but is often reduced; see Kensley and Gore, 1981), Laomediidae (Wear and Yaldwyn, 1966), and Thalassinidae (Fig. 4*a*), but again may be reduced in some species. It is apparently always reduced or absent (a) in the Callianassidae and Upogebiidae, and thus we feel these two families are derived for this character. Among the anomurans it is always present in the Hippoidea (Fig. 4*b*) and the Paguroidea, with the exception of the terrestrial Coenobitidae (Fig. 4*h*). It is absent in *Lomis* and all the Galattheoidea, with the exception of the Chirostylidae where it can be either well developed (e.g., Fig. 4*c*) or reduced or absent (e.g., *Gastroptychus cavimurus*; see Baba, 1977*c*).

The number of segments of the antennal peduncle [6] in *Penaeus* is usually given as five. McLaughlin and Provenzano (1974*a*) and McLaughlin (1974) described an additional “supernumerary” segment between the third and fourth segments of the peduncle in several genera of the Paguroidea. McLaughlin (1983*b*) later modified this definition as “between the typical second and third segments”

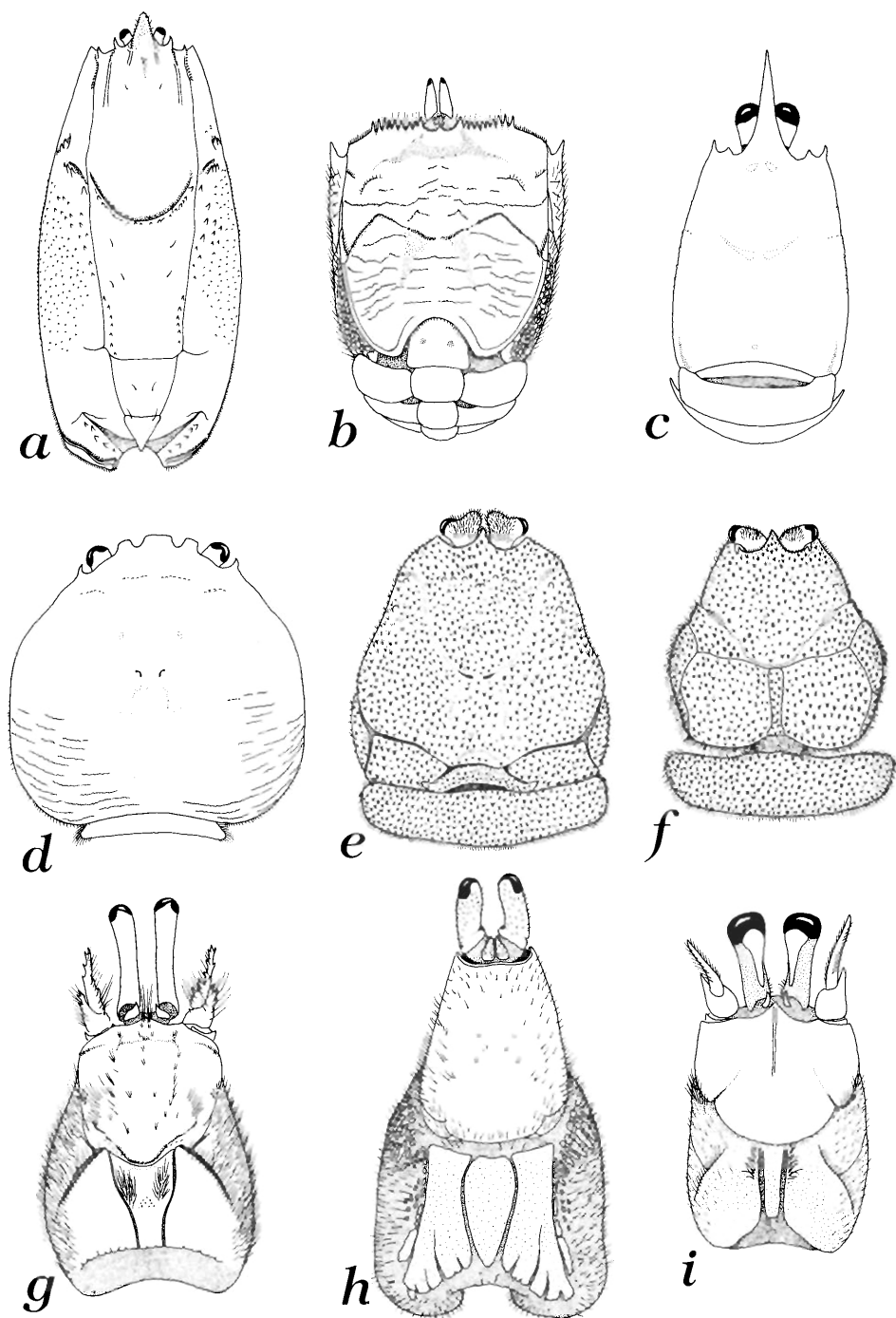


Fig. 1. Carapace of selected thalassinoids and anomurans, dorsal view. *a*, *Thalassina squamifera* (Thalassinioidea, Thalassinidae); *b*, *Albunea paretii* (Hippoidea, Albuneidae); *c*, *Uroptychus nitidus* (Galatheoidea, Chirostylidae); *d*, *Petrolisthes tuberculatus* (Galatheoidea, Porcellanidae); *e*, *Lomis hirta* (Lomoidea, Lomidae); *f*, *Hapalogaster cavicauda* (Paguroidea, Lithodidae, Hapalogastrinae); *g*, *Mixtopagurus paradoxus* (Paguroidea, Pomatochelidae); *h*, *Coenobita clypeatus* (Paguroidea, Coenobitidae); *i*, *Parapagurus pictus* (Paguroidea, Parapaguridae). Not drawn to scale.

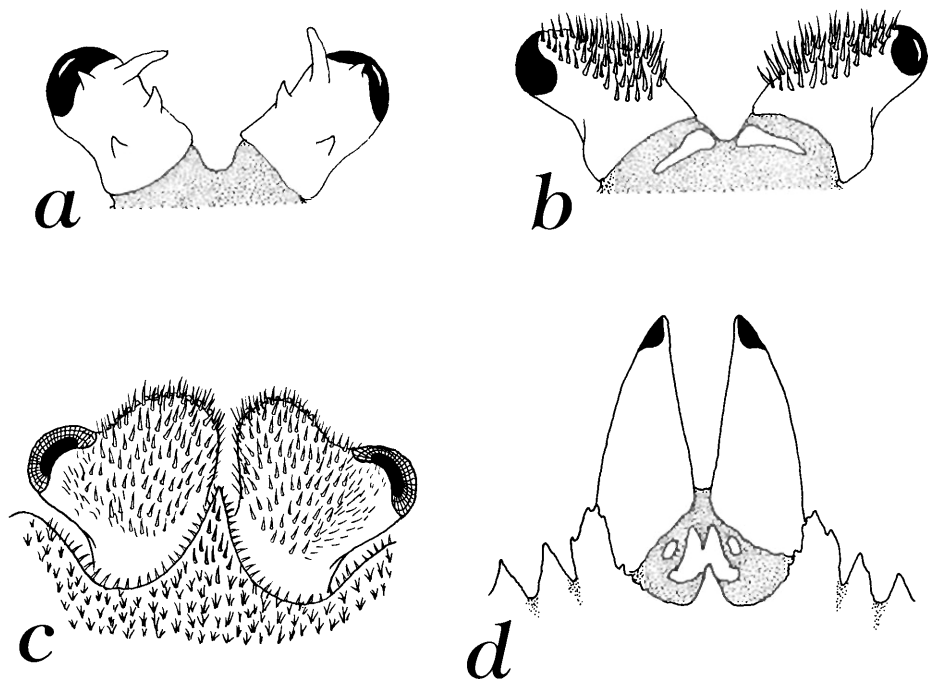


Fig. 2. Ocular region of selected anomurans. *a*, *Neolithodes agassizii* (carapace removed); *b*, *Haplogaster cavicauda* (carapace removed); *c*, *Lomis hirta*; *d*, *Albunea paretii*. Not drawn to scale.

and considered the presence of the supernumerary segment the plesiomorphic condition. This segment is found in the Thalassinioidea in the families Thalassinidae (Fig. 4a), Callianassidae, and Axiidae, but we did not detect it in the Laomediidae or Upogebiidae. In the Anomura this additional segment is present in all families of the Paguroidea except the lithodids, where we did not find it in our specimens (Appendix I) (but see McLaughlin, 1983a, b). In the galatheoids the number of segments is clearly five, with the exception of the porcellanids, all of which have only four segments (Fig. 4d). Like McLaughlin, we feel that the "supernumerary" condition (more than five segments) is likely the primitive (p) condition. Although Young (1959) described five segments in the peduncle of *Penaeus setiferus*, his figure (1959: fig. 18) shows a small unlabeled segment between the second and third segments. Our specimens of *Penaeus* agree with Young's figure. In addition, Calman (1909: 265) figured a strikingly similar (to anomurans) segment for the caridean *Athanas*.

Epistome.—Epistomal spines [7] have been reported for the labrum or interantennular area of some pomatochelids (de Saint Laurent, 1972), some parapagurids (de Saint Laurent, 1972), and the lomoids (McLaughlin, 1983a, b). The epistomal spine of *Parapagurus pictus* is a single sharp projection of the lower epistomal border. This is not the case in *Lomis*, which has only a blunt interantennular projection and no true spines on the epistome. Although this character has not been described for many species (and thus any decision by us is likely a gross generalization), we scored the Pomatochelidae and Parapaguridae as having true epistomal spines based on the findings of de Saint Laurent (1972) and on our examination of *Parapagurus pictus*. True epistomal spines (a) also occur in certain

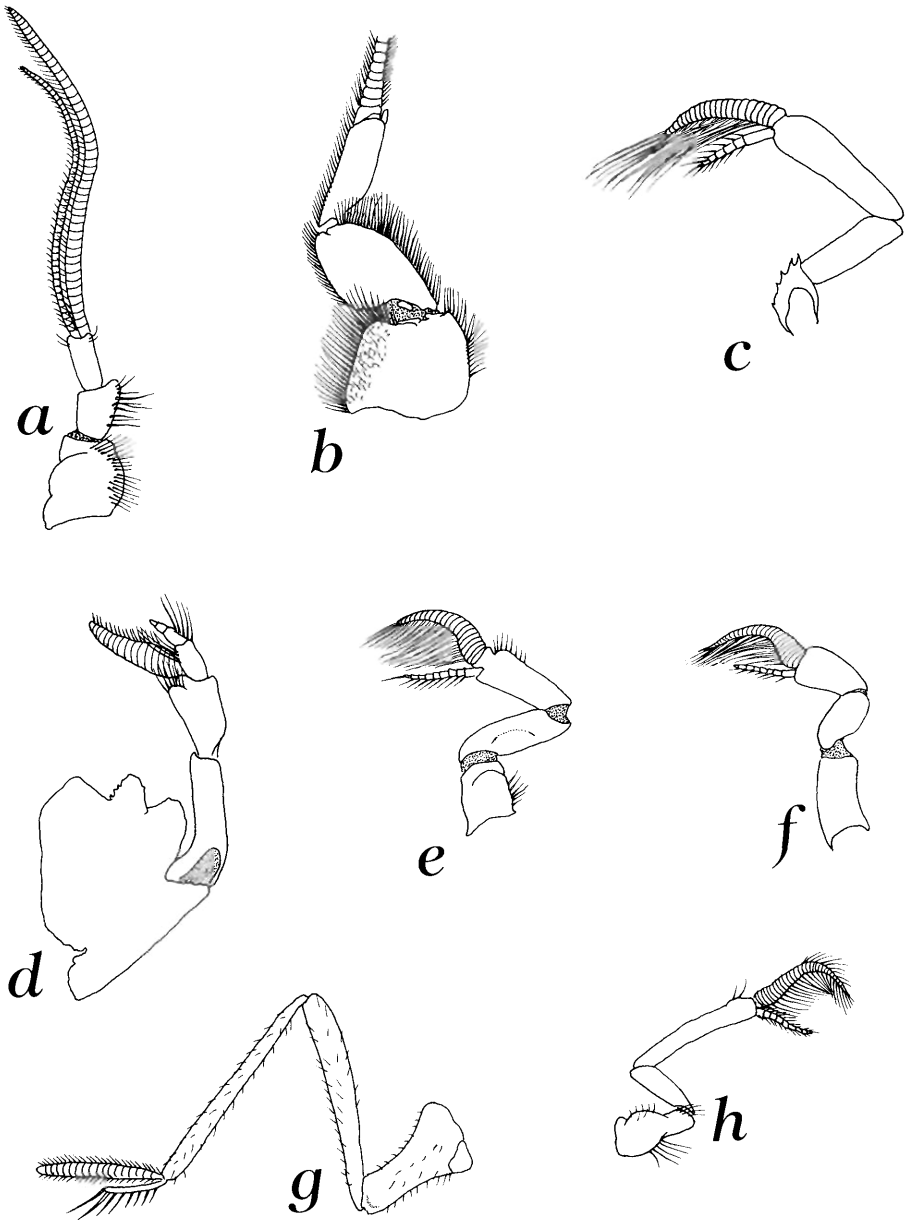


Fig. 3. First antennae (antennules) of selected thalassinoids and anomurans. *a*, *Thalassina squamifera*; *b*, *Albunea paretii*; *c*, *Uroptychus nitidus*; *d*, *Petrolisthes tuberculatus*; *e*, *Lomis hirta*; *f*, *Haplogaster cavicauda*; *g*, *Coenobita clypeatus*; *h*, *Parapagurus pictus*. Not drawn to scale.

members of the Axiidae, where they may be large paired spines situated below the articulation of the antenna. They are absent (p) in *Penaeus* and in all other families of the Anomura and Thalassinoida.

Maxillule.—The first maxilla (=maxillule) of reptants always bears a small dorsal palp (an apparent exception is the maxillule of an axiid illustrated by Kensley

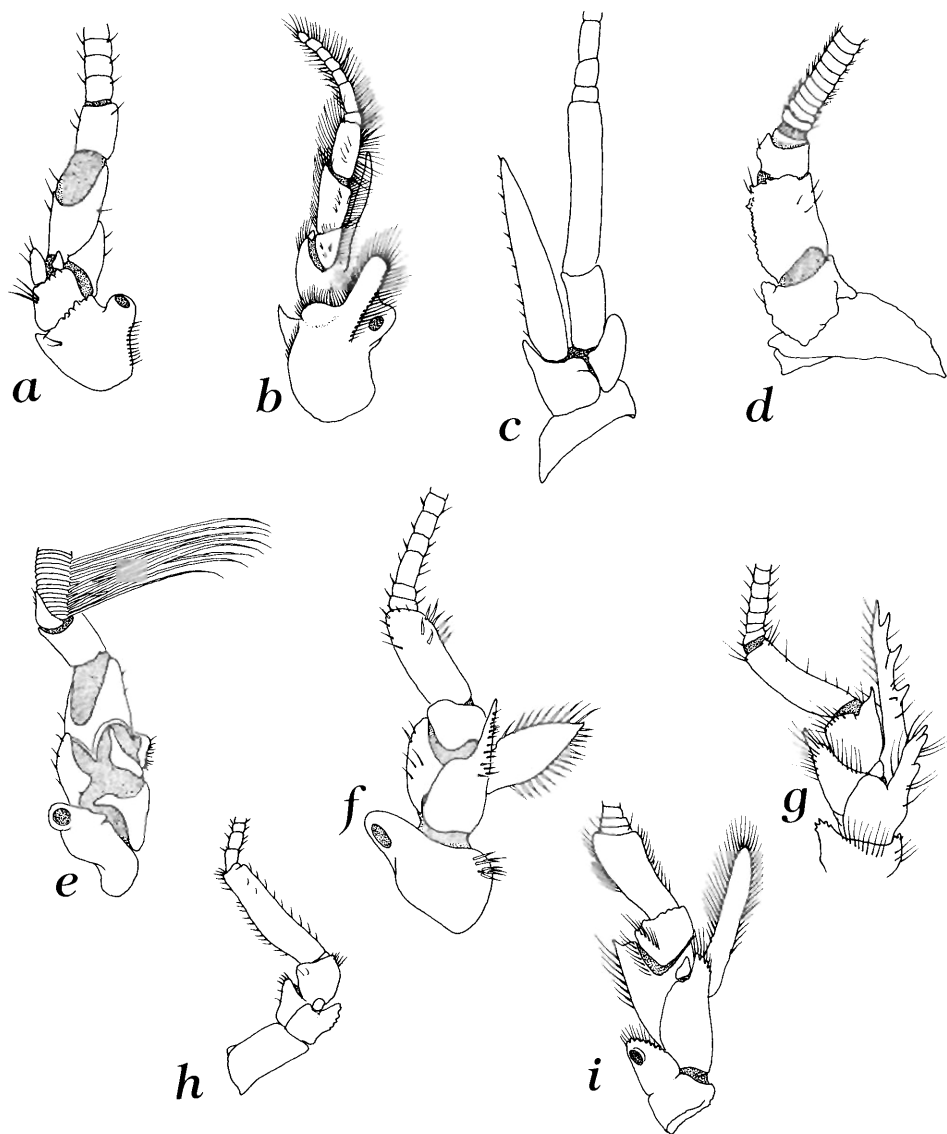


Fig. 4. Second antennae of selected thalassinoids and anomurans. *a*, *Thalassinina squamifera*; *b*, *Albunea paretii*; *c*, *Uroptychus nitidus*; *d*, *Petrolisthes tuberculatus*; *e*, *Lomis hirta*; *f*, *Hapalogaster cavicauda*; *g*, *Mixtopagurus paradoxus*; *h*, *Coenobita clypeatus*; *i*, *Parapagurus pictus*. Not drawn to scale.

and Gore, 1981). In many anomurans this palp bears a posteriorly directed lobe [8] which Pilgrim (1965), working with *Lomis*, called an "appendage" (Fig. 5*e*). It is difficult to determine if the lobe is a modification of the distal segments of the palp or is an extension of the basal segment. The lobe is absent (p) in *Penaeus*, but present (a) in all of the Thalassinioidea (e.g., Thalassinidae, Fig. 1*a*), although it may be greatly reduced in the Upogebiidae (see Williams, 1986). In the Hippoidea it is large in the Albuneidae (Fig. 5*b*) but absent in the Hippidae (Snodgrass,

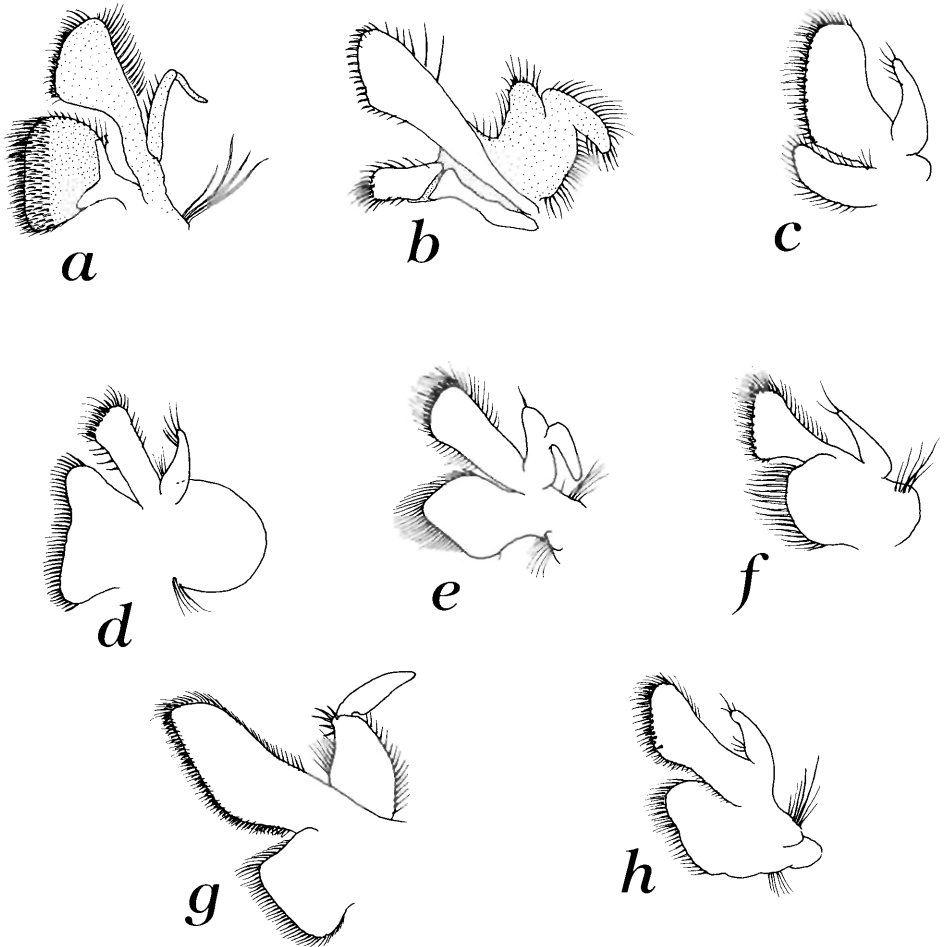


Fig. 5. First maxilla (maxillule) of selected thalassinoids and anomurans. *a*, *Thalassina squamifera*; *b*, *Albunea paretii*; *c*, *Uroptychus nitidus*; *d*, *Petrolisthes tuberculatus*; *e*, *Lomis hirta*; *f*, *Hapalogaster cavicauda*; *g*, *Coenobita clypeatus*; *h*, *Parapagurus pictus*. Not drawn to scale.

1952: 18, fig. 6A). It is absent in all of the Galattheoidea (e.g., Fig. 5*c*, *d*, Fig. 7*a*; Pike, 1947; Martin and Abele, in press), and present in most of the Paguroidea (e.g., Fig. 5*g*) with exceptions in the Lithodidae (Fig. 5*f*), several diogenids (e.g., *Aniculus*, see Forest, 1984), and apparently the pagurid genera *Nematopagurus* (see McLaughlin and Brock, 1974: 252) and *Lithopagurus* (see Provenzano, 1968). Although it is present in some of the Parapaguridae (e.g., *Typhlopagurus* and some *Parapagurus*; see de Saint Laurent, 1972) we scored it as absent (see Fig. 5*h*) for the family.

First Maxilliped.—In *Penaeus* the exopod of the first maxilliped (terminology after Young, 1959) bears a well-developed setose flagellum [9]. In the thalassinoids, it appears as if the endopod, rather than the exopod, is segmented (e.g., *Thalassina*, Fig. 6*a*). This condition has been illustrated by Boas (1880: pl. II) for *Axius*, *Thalassina*, and *Upogebia*. We are hesitant to score this condition as different from that of *Penaeus*, because of difficulties in interpretation of the segments of

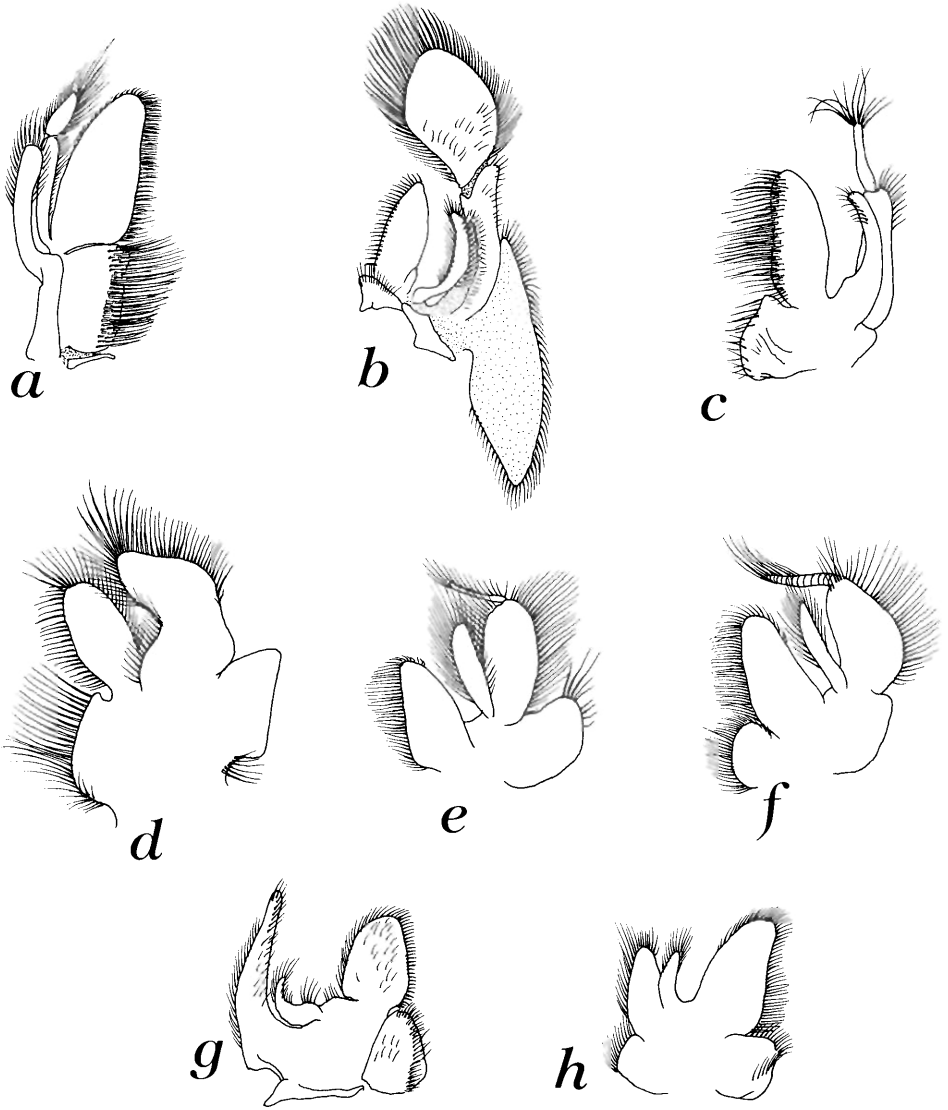


Fig. 6. First maxilliped of selected thalassinoids and anomurans. *a*, *Thalassina squamifera*; *b*, *Albunea paretii*; *c*, *Uroptychus nitidus*; *d*, *Petrolisthes tuberculatus*; *e*, *Lomis hirta*; *f*, *Hapalogaster cavicauda*; *g*, *Coenobita clypeatus*; *h*, *Parapagurus pictus*. Not drawn to scale.

this appendage (see Abele and Felgenhauer, 1986). It is possible that the segmented process in these groups is indeed the exopod, and that the unsegmented lateral process is a coxal exite rather than an unsegmented exopod. Thus, we have scored this condition as equal to that of *Penaeus*, recognizing that this interpretation may be questioned. Exceptions occur in the Callianassidae (see Biffar, 1972) and in some species of the Axiidae (e.g., Kensley and Gore, 1981) which have no palp, and in some upogebiids that have an exopod similar to that of *Penaeus* (e.g., see Williams, 1986). In the Hippoidea the exopod is expanded and ovate, but is setose and well developed (Fig. 6*b*). In the Porcellanidae, Coenobitidae, and Parapa-

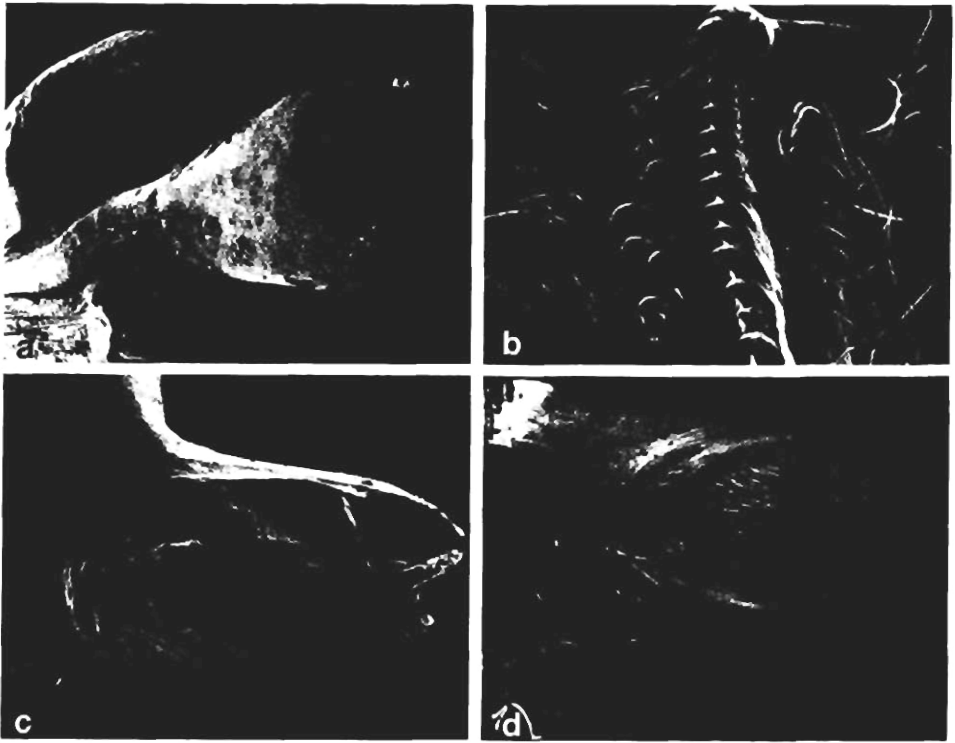


Fig. 7. Scanning electron micrographs of mouthparts and modified coxal segments of *Aegla* (a-c) and *Coenobita* (d). a, first maxilla (maxillule) of *Aegla* ($\times 60$); b, ischium of third maxilliped of *Aegla* showing crista dentata ($\times 55$); c, modified coxa of fifth pereopod of *Aegla* showing spoonlike medial projection presumably used in sperm transfer ($\times 75$); d, modified coxa of fifth pereopod of *Coenobita* ($\times 50$).

guridae (including *Probeebei*) (Fig. 6d, g, h) the exopod and endopod are reduced, neither are segmented, and thus there is no palp. Among the Galatheoidea, one subfamily (Munidopsinae) of the Galatheidae lacks the flagellum entirely (Barnard, 1950: 482).

Second Maxilliped.—The flagellum of the exopod of the second maxilliped [10] is well developed (p) in *Penaeus* and in all the thalassinoids except the Callianassidae. In the Anomura, the exopod is somewhat reduced (a) in the Coenobitidae.

Third Maxilliped.—The flagellum of the third maxilliped [11] is well developed (p) in *Penaeus* and in all thalassinoids except some upogebiids (Williams, 1986) and all callianassids. In the Anomura, it is reduced or absent in the Hippoidea (Fig. 8b; Barnard, 1950; Snodgrass, 1952) and Coenobitidae (Fig. 8g).

The ischium of the third maxilliped of many reptants bears a row of sclerotized teeth on the medial margin. This row, usually termed the crista dentata (7b), is absent (p) in *Penaeus*, the Upogebiidae, and some of the Callianassidae. It is present (a) in all of the anomuran families except for the Hippidae and most of the Albuneidae (Fig. 8b) (it is present in *Blepharipoda* and *Lophomastix*). Another exception is the galatheoid family Porcellanidae (Fig. 8d). It may be reduced in

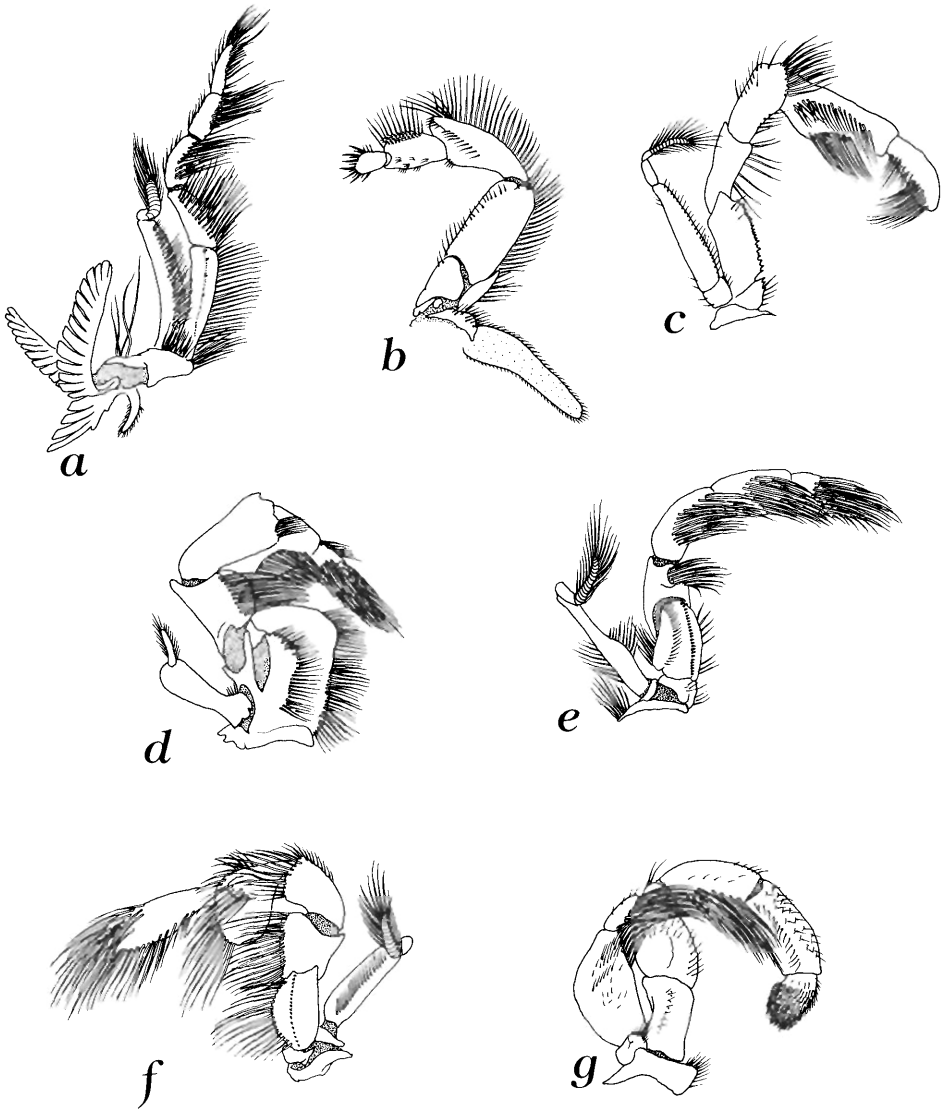


Fig. 8. Third maxillipeds of selected thalassinoids and anomurans. *a*, *Thalassina squamifera*; *b*, *Albunea paretii*; *c*, *Uroptychus nitidus*; *d*, *Petrolisthes tuberculosus*; *e*, *Lomis hirta*; *f*, *Hapalogaster cavicauda*; *g*, *Coenobita clypeatus*. Not drawn to scale.

some of the Paguroidea (e.g., *Coenobita*, see Fig. 8g), but was scored as present by us in all paguroid families.

The epipod [13] of the third maxilliped is present (p) in *Penaeus* and in all the thalassinoids (e.g., *Thalassina*, Fig. 8a) except the Callianassidae. In the Anomura it is present in the Hippoidea (Fig. 8b) and present (although reduced) in the Aeglidae, Galatheidae, and Pomatochelidae. In all other families the epipod is absent (a). The shape of the third maxilliped [14] may be long and pediform (p) or flattened and operculate (a). It is pediform in *Penaeus* and most of the thalassinoids, paguroids, galatheoids, and the Albuneidae (Fig. 8b). It is flattened

and nonpediform (at least, not so much as in other thalassinoids) in the Upogebiidae and Callianassidae, in the hippoid family Hippidae (Snodgrass, 1952), and in the Porcellanidae (Fig. 8*d*).

The position of the bases of the third maxillipeds [15] has been used in the past as a character of familial importance within the Anomura (see discussion in McLaughlin, 1983*b*). The plesiomorphic condition, seen in *Penaeus* and in all the Thalassinoidea, is one in which the maxillipeds are approximate basally (p). The derived condition has the bases widely separated (a), a condition seen in the Hippoidea (Fig. 9*b*), Paguridae, Parapaguridae (including *Probebebi*), Lithodidae (Fig. 9*g*), and *Lomis* (Fig. 9*f*). The condition is variable in the Galatheoidea; aeglids, porcellanids, and galatheids have the plesiomorphic condition, but in chirostylids the bases of the third maxilliped may be approximate or widely divergent (e.g., Fig. 9*d*).

Carapace.—Although the earliest fossil decapod had lineae [16] on the carapace (the Devonian *Palaeopalaemon*; see Schram *et al.*, 1978), penaeids lack dorsal carapace sutures (p). There is some confusion as to the identity of the lineae on the carapace of the Pleocyemata (see Martin and Abele, in press). Many authors (e.g., Boas, 1880; Calman, 1909) refer to the linea thalassinica and linea anomurica as separate characters, although others (e.g., Glaessner, 1969) use the two terms interchangeably. In the Thalassinoidea, with the exception of the Callianideidae and Axiidae, there is a pair of sutures (the “lineae thalassinicae”) extending posteriorly from the antennal region along the dorsum of the carapace (Figs. 1*a*, 10*a*). A similar condition is seen in many anomurans (e.g., *Albunea*, Fig. 10*b*) but here the “lineae anomuricae” are displaced laterally and are not apparent in dorsal view (compare Fig. 1*a*, *b*). We do not know if these two types of lineae are homologous. This latter type of carapace linea is seen in the Hippoidea, Galatheoidea (except *Aegla*), and the lithodid subfamily Lithodinae. The carapace of the Aeglidae (Fig. 11*a*, *b*) has a series of lineae not seen in other members of the Galatheoidea. Martin and Abele (in press) argued that this character was of sufficient significance to question the traditional placement of the aeglids within the Galatheoidea. Dorsal carapace lineae demarcating the branchial region occur also in every family of the Paguroidea, except the Lithodinae, and in *Lomis* (Figs. 1*e*, 10*e*). Again, we do not know whether this condition is derived from the “linea anomurica” condition, but we have scored these latter carapace types as the most derived in a transitional series.

The dimensions of the carapace [17] vary somewhat among and within families. Those families with a carapace of roughly equal width throughout length (p) include all the thalassinoids, the hippoid family Albuneidae, and many members of the Porcellanidae. Other anomuran families tend to be slightly wider posteriorly than anteriorly (a) (Fig. 1*c*, *e-i*).

The shape of the carapace [18] may be laterally compressed to subcylindrical (p), as in *Penaeus* and all the Thalassinoidea, or dorsoventrally compressed (a). We scored the carapace of the thalassinoids, hippids, galatheids, and chirostylids as subcylindrical, and all other families dorsoventrally compressed (Fig. 10*a-i*). Although few of the galatheids are as dorsoventrally depressed as *Aegla*, this difference is slight and probably of little importance.

Thorax.—The eighth thoracic somite [19], which bears the fifth pereopods, is fused (p) with the anterior thoracic somites in *Penaeus*. In all families of the Thalassinoidea and Anomura, this somite is unfused (a) and is connected to the preceding somites by a membranous articulation (Fig. 9*a-i*).

The pereopods of *Penaeus* and most of the thalassinoids bear epipods [20] of

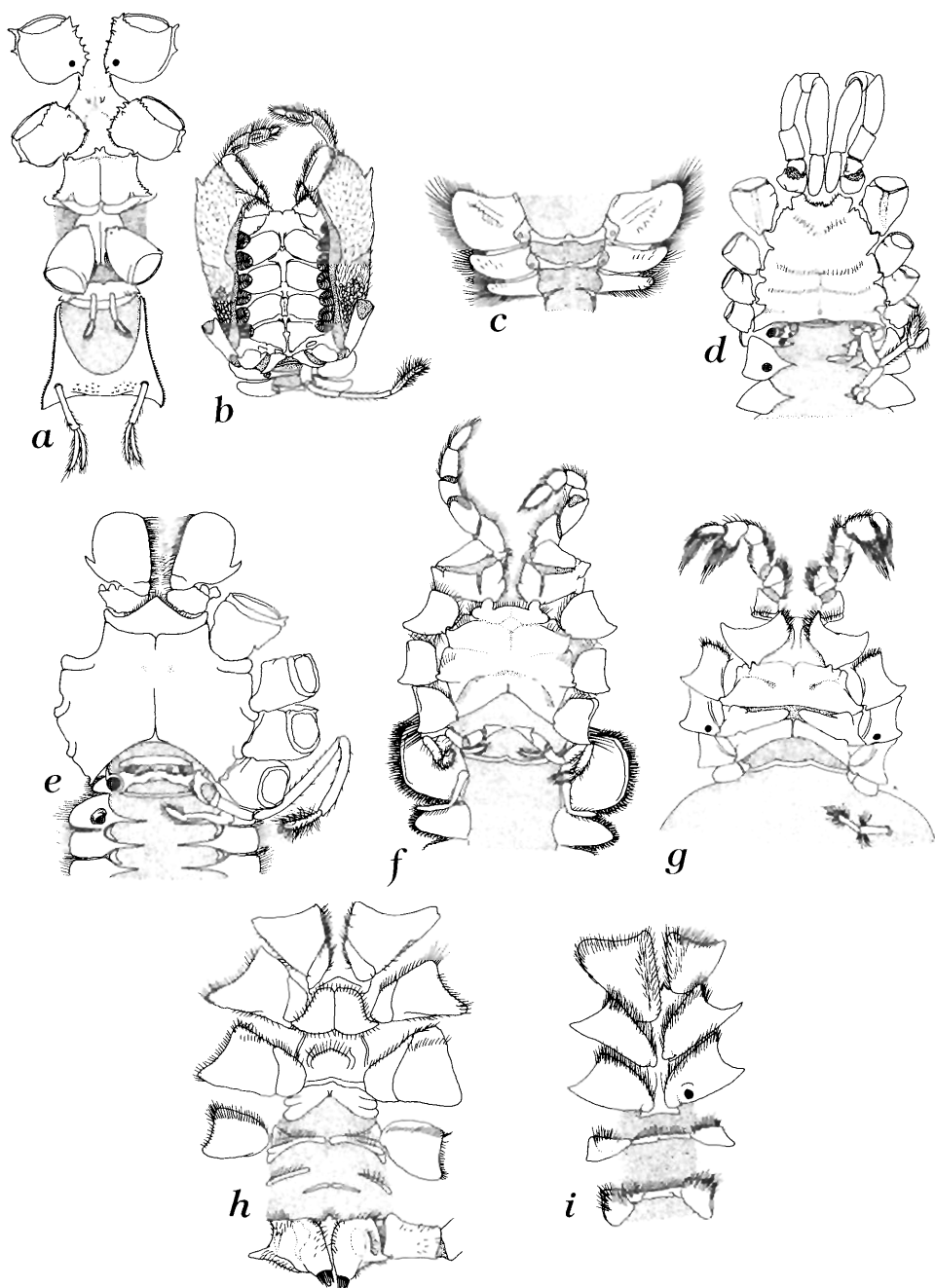


Fig. 9. Ventral view of thorax/abdominal region in selected thalassinoids and anomurans. *a*, *Thalassinina squamifera*; *b*, *Albunea paretii*; *c*, close-up of abdominal somites of *Albunea* showing complete sternal processes; *d*, *Uroptychus nitidus*; *e*, *Petrolisthes tuberculosus*; *f*, *Lomis hirta*; *g*, *Hapalogaster cavicauda*; *h*, *Coenobita clypeatus*; *i*, *Parapagurus pictus*. Not drawn to scale.

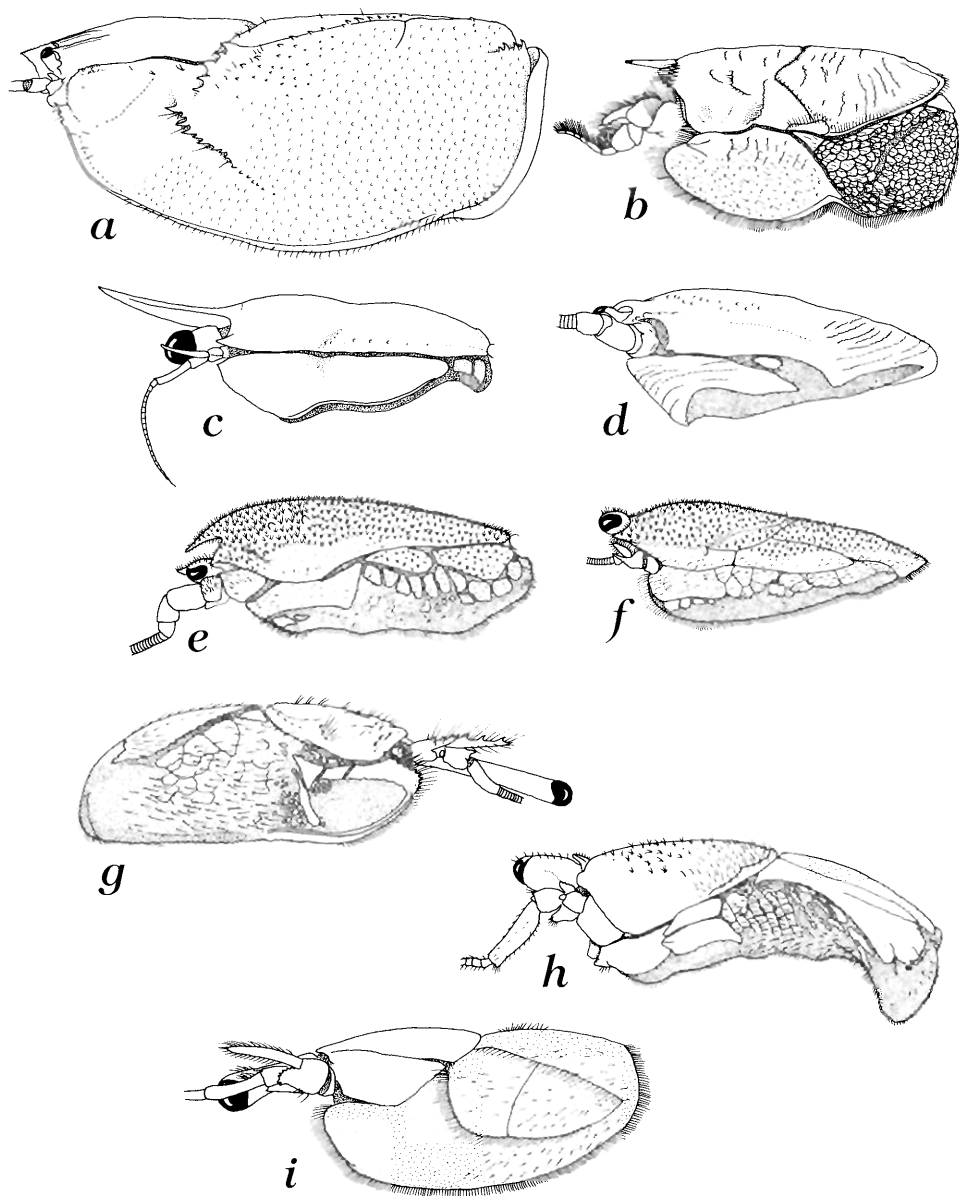
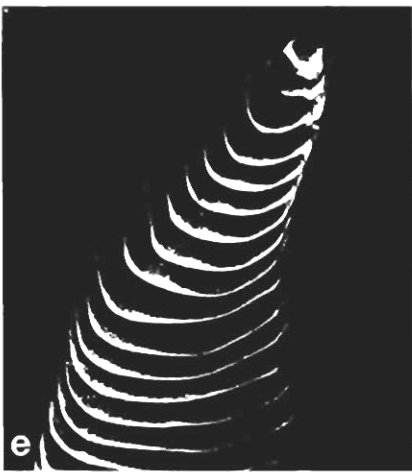


Fig. 10. Carapaces of selected thalassinoids and anomurans, lateral view. *a*, *Thalassinina squamifera*; *b*, *Albunea paretii*; *c*, *Uroptychus nitidus*; *d*, *Petrolisthes tuberculosus*; *e*, *Lomis hirta*; *f*, *Hapalogaster cavicauda*; *g*, *Mixtopagurus paradoxus*; *h*, *Coenobita clypeatus*; *i*, *Parapagurus pictus*. Not drawn to scale.

varying length and development. They are present (p) in the Axiidae, Laomedidae, and Thalassinidae (Fig. 12a), but presumably have been lost in the Callinassidae and Upogebiidae. Epipods are absent (a) in all the hippoids, galatheoids, and paguroids, with one exception: some galatheids have small epipods (see Pike, 1947: pl. VI; Baba, 1977b) and we therefore scored them as present for the family.



First Pereiopod [21].—In *Penaeus* and most of the thalassinoids and anomurans the first pereiopods are chelate. In *Aegla*, the borders of the chelae bear numerous sclerotized scales (Fig. 13a), a character shared with the Parapaguridae, including *Probeebe*, although not figured by Wolff (1961). Barnard (1950: fig. 77) figured a similar chela border for *Neolithodes* (Lithodidae), and Wass (1963) described this condition in several pagurids. In the Thalassinidae and Upogebiidae the first pereiopod is subchelate, a condition we feel is derived. In the Hippoidea, the first pereiopod is subchelate in the Albuneidae but simple (further derived) in the Hippidae.

Symmetry of the first pereiopods [22] was used by McLaughlin (1983b) as a character separating hermit crab families. In *Penaeus* the chelipeds are equal in size (p). We scored as plesiomorphic those families with equal chelipeds and also those families in which "handedness" was variable (e.g., porcellanids and callianassids). The derived conditions of "handedness" are seen in the Coenobitidae, Diogenidae, and Aegliidae, which tend to be left-handed (with several exceptions among the Diogenidae), and the Lithodidae, Paguridae, and Parapaguridae, which tend to be right-handed (see Makarov, 1962). The right cheliped of *Lomis* was very slightly larger than the left in all specimens examined (10) but the difference was so slight that we scored this family as having equal chelipeds.

Pereiopods 2-4.—The second [23] and third pereiopods [25] of *Penaeus* are chelate. In the Thalassinioidea, chelate or subchelate second pereiopods (p) are seen in the Axiidae, Callianassidae, and Thalassinidae. In all other families this leg is simple (nonchelate) (a). A chelate third pereiopod (p) does not appear in thalassinoids or anomurans. Thus, a nonchelate third pereiopod (a) is derived for these groups.

The fourth pereiopod [28] is simple (p) in *Penaeus* and all the thalassinoids except the Callianassidae. In the Anomura it is simple in the Hippoidea, Galathea-idea, *Lomis*, and the Lithodidae. In all other families (the hermit crab families) the fourth leg is subchelate (a) and bears sclerotized scales (Figs. 12g, 13d, 14g, h), although it is barely subchelate in some families while fully subchelate in others (compare Figs. 14g, h and 13d). The fourth leg in the hermit crab families is also reduced relative to the other legs [30] (an exception is the terrestrial genus *Birgus*, with a secondarily slightly enlarged fourth leg), a derived condition seen in none of the other groups. The dactylus of pereiopods 2-4 [24, 26, 29] is usually sharp and clawlike (p). The derived condition, flat paddlelike dactyli on these legs (a), is seen in both families of the Hippoidea only (Fig. 14b). A final character of pereiopods 2-4 is the number of female genital apertures (gonopores) [27]. In almost all decapods these openings are paired (p) and are found on the coxa of the third pereiopod (e.g., *Hapalogaster*, Fig. 9g). In the Parapaguridae (including *Probeebe*) the right gonopore is lost (a) (Fig. 9i). This condition is also seen in a few diogenid and pagurid genera (e.g., see de Saint Laurent, 1968).

Fifth Pereiopod.—In *Penaeus* and several families of the Thalassinioidea, the fifth leg is achelate [31] (p) (Fig. 14a). It is minutely chelate (a) in the Axiidae, Callianassidae, and every anomuran family (Fig. 14b-h). The dactylus [32] may be unarmed (p) as in *Penaeus*, Upogebiidae, Thalassinidae, and Laomediidae. The

←

Fig. 11. Scanning electron micrographs of carapace and gills of selected anomurans. a, carapace of *Aegla*, dorsal view showing suture lines ($\times 10$); b, close-up of sutures in area indicated by arrow in a ($\times 130$); c, trichobranch gill of *Aegla* ($\times 40$); d, phyllobranch gill of *Petrolisthes* ($\times 40$); e, thickened phyllobranch gill of *Coenobita* ($\times 65$); f, distal tip of phyllobranch gill of *Coenobita* ($\times 50$).

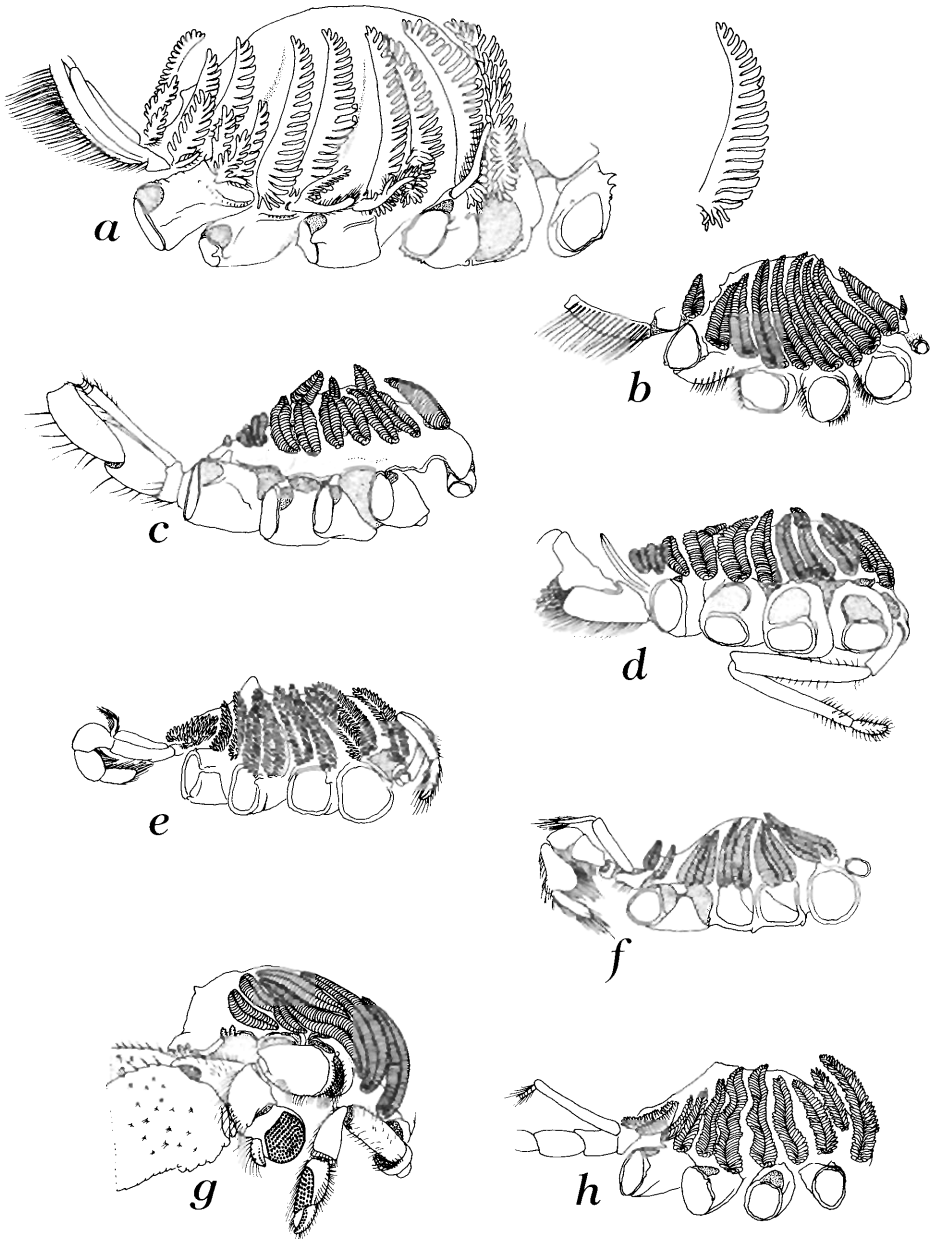


Fig. 12. Branchial arrangement and morphology in selected thalassinoids and anomurans. *a*, *Thalassinina squamifera*, with single thalassinobranch gill enlarged on right; *b*, *Albunea paretii*; *c*, *Uroptychus nitidus*; *d*, *Petrolisthes tuberculosus*; *e*, *Lomis hirta*; *f*, *Hapalogaster cavicauda*; *g*, *Coenobita clypeatus*; *h*, *Parapagurus pictus*. Not drawn to scale.

derived condition is with corneous scales along the cutting borders (a), as seen in the Axiidae, Callianassidae, *Lomis*, the Lithodidae (both subfamilies), the parapagurid genus *Probeebei*, all hippoids, and all galatheoids (Figs. 13b, c, 14b-f). The remaining families (the hermit crab families) have, in addition to a chelate

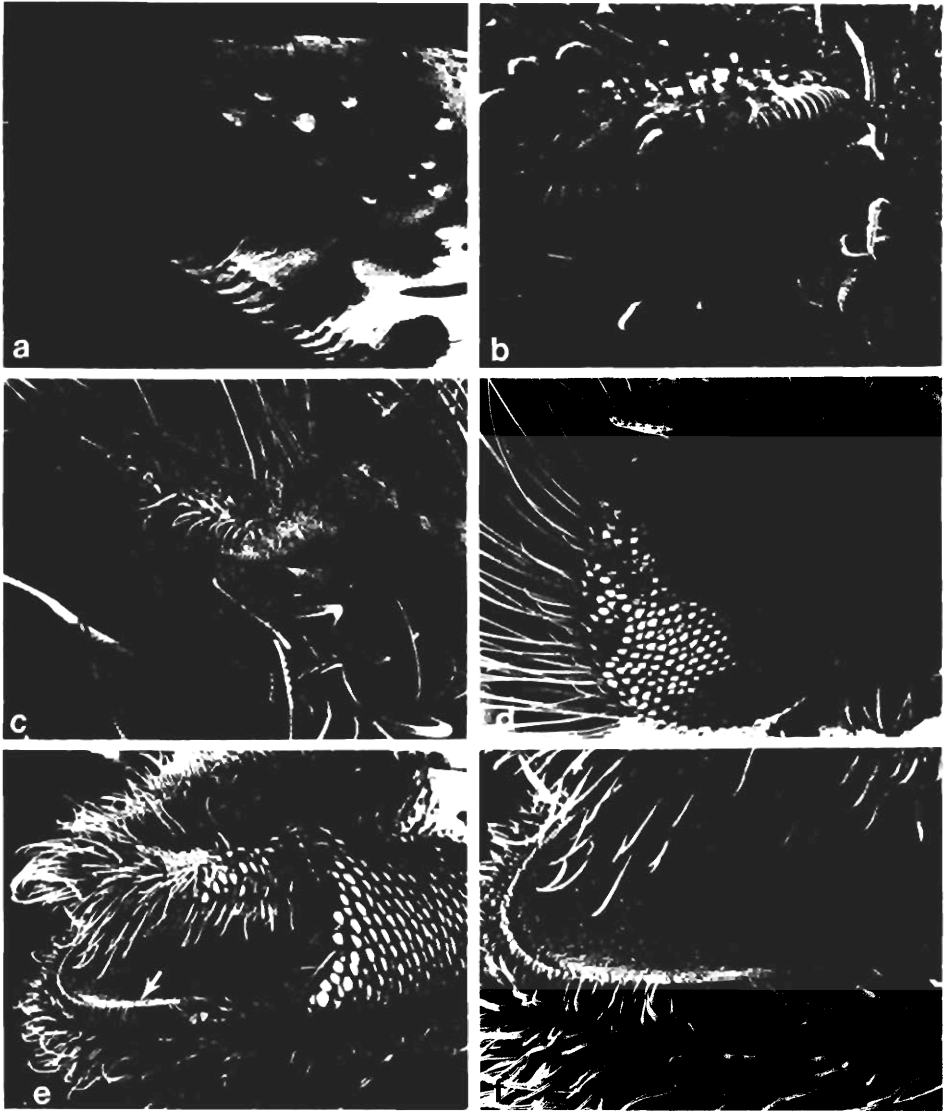


Fig. 13. Scanning electron micrographs of dactylus and propodus of cheliped and fifth pereiopod of selected anomurans. a, *Aegla*, dactylus of cheliped showing sclerotized teeth on cutting border ($\times 90$); b, *Aegla*, chela of fifth pereiopod ($\times 180$); c, *Petrolisthes*, chela of fifth pereiopod ($\times 75$); d, *Coenobita*, subchelate fourth pereiopod with scales ($\times 30$); e, *Coenobita*, chela of fifth pereiopod ($\times 35$); f, close-up of area indicated by arrow in e, showing transition of sclerotized teeth on chela border to flattened scales on propodal surface ($\times 75$).

cutting border, the further derived condition of a “rasp” of small scales on the lateral surface of the dactylus and propodus (Figs. 13d–f, 14g, h), although presence and location of these scales may vary.

The fifth pereiopod when chelate is often reduced and may be inserted beneath the carapace [33]. It is normally developed (p) in *Penaeus* and all of the thalassinoids, although it could be argued that this leg is slightly reduced in the upo-

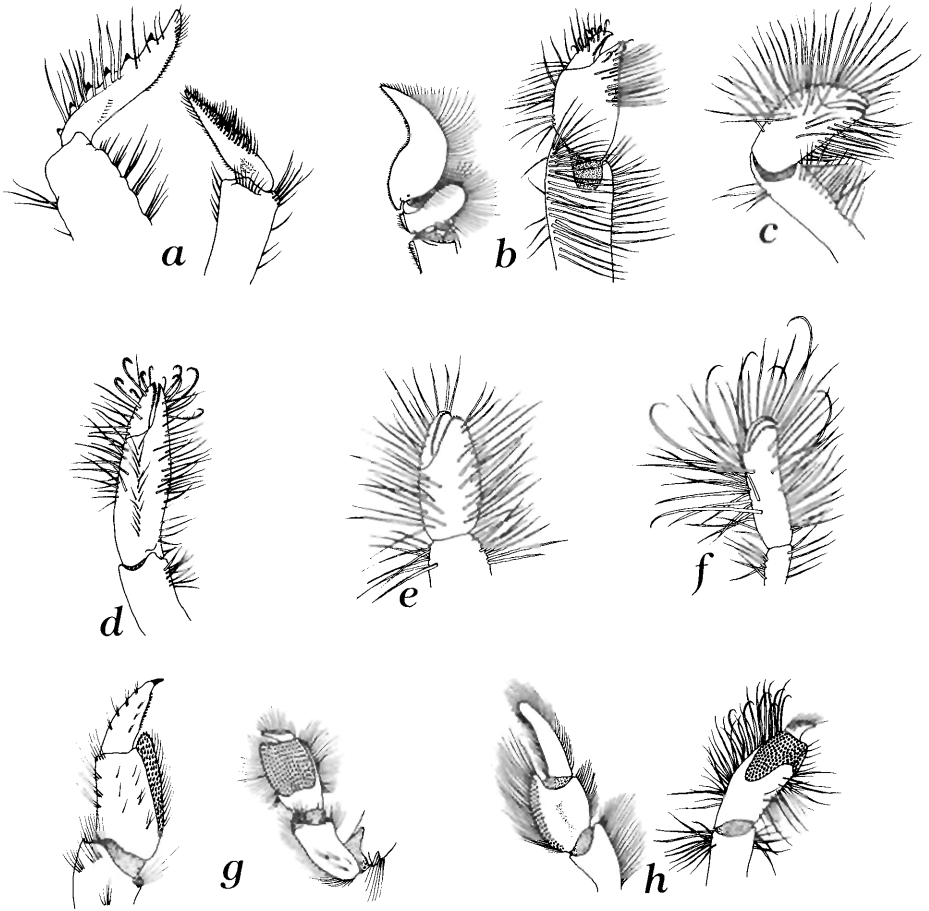


Fig. 14. Distal segments of posterior pereiopods of selected thalassinoids and anomurans. *a*, *Thalassinia squamifera*, fourth and fifth (smaller) pereiopods; *b*, *Albunea paretii*, fourth (flattened) and fifth pereiopods; *c*, *Uroptychus nitidus*, fifth pereiopod; *d*, *Petrolisthes tuberculatus*, fifth pereiopod; *e*, *Lomis hirta*, fifth pereiopod; *f*, *Hapalogaster cavicauda*, fifth pereiopod; *g*, *Mixtopagurus paradoxus*, fourth (larger) and fifth pereiopod; *h*, *Parapagurus pictus*, fourth (larger) and fifth pereiopods.

gebiids and callianassids. We considered the leg reduced (a) in the Coenobitidae, Diogenidae, Pomatochelidae, Paguridae, and Parapaguridae (including *Probeebei*). In these groups the fifth leg may be inserted beneath the carapace but is usually carried outside the branchial cavity. A more derived condition is seen in *Lomis*, the Lithodidae, the Hippoidea, and the Galattheoidea, all of which have a reduced fifth leg normally carried within the branchial cavity.

In the Aeglidae, Coenobitidae, and Hippidae (see Snodgrass, 1952: 24) the coxa of the fifth pereiopod is modified for sperm transfer [34]. The posteromedial surface is produced into a spoonlike apparatus (*Aegla*) or an elongate tube (*Coenobita*) (Fig. 7c, d). Although this is likely coupled with loss of male pleopods, it has not occurred in all families in which the male pleopods are lost. A modified male coxa (sometimes extremely modified) is seen also in many pagurid genera, on right, left, or both coxae (see de Saint Laurent-Dechancé, 1966; de Saint Laurent, 1968), but we scored pagurids as having an unmodified male coxa be-

cause, to our knowledge, the majority of species are not modified. Future workers may wish to reconsider our scoring of this character for pagurids. The plesiomorphic condition, seen in *Penaeus* and all other anomurans and thalassinoids, is with a normal (unmodified) coxa.

Abdomen.—The abdomen in *Penaeus* and all thalassinoids, hippoids, galatheoids, and lomoids is well developed (p) with distinct overlapping somites [35]. This condition is seen also in the paguroid families Lithodidae (except the Hapalogastrinae) and Pomatochelidae. The genus *Probeebei* of the Parapaguridae also has a well-developed abdomen with distinct calcified somites; we believe this to be a case of character reversal. All other anomuran families, as well as the lithodid subfamily Hapalogastrinae (Fig. 9g), have weakly calcified membranous abdomens with indistinct somites.

The development (shape) of the abdomen [36] is in most groups straight (p). In the hermits, including both subfamilies of the Lithodidae, the abdomen is asymmetrically twisted (a), although some pagurid genera exhibit nearly complete symmetry (e.g., *Porcellanopagurus*; see Kensley, 1977). We scored the Pomatochelidae as having a straight symmetrical abdomen, but this may be a mistake. Some pomatochelids are slightly twisted, with modified asymmetrical uropods like the other hermits (e.g., *Mixtopagurus paradoxus*, Fig. 17g), while others (e.g., *Pylocheles*) display the plesiomorphic condition with a symmetrical abdomen and uropods (Benedict, 1901; Milne Edwards and Bouvier, 1893). Changing the scoring of this character did not affect the numerical results.

The lithodid subfamily Lithodinae displays two autapomorphies of the abdomen: tergal plates that are subdivided [37] and supplemental tergal calcification [38] in the form of ossicles (see McLaughlin, 1983b; Makarov, 1962).

The abdominal sterna [39] may be entire (p), as in *Penaeus* and all thalassinoids (Fig. 9a) and hippoids (Fig. 9c), or incomplete (a) as in all other anomurans (e.g., see Fig. 9d–g). In the Galatheidae these sterna are most often incomplete and therefore similar to other galatheoids. However, we scored galatheids as having complete sterna because of this condition in certain species of *Munida* in our collections (not illustrated).

Pleopods.—The pleopod of the female first abdominal somite [40] has been lost in many anomurans. It is present (p) in *Penaeus*, all families of the Thalassinoidea, the Pomatochelidae, *Lomis*, and some members (e.g., *Paguristes* and *Paguroopsis*) of the Diogenidae. It is lost (a) in all other anomuran families, except several pagurid genera (e.g., the *Pylopagurus* complex, McLaughlin, 1981; see also Alcock, 1905: 24–27).

Female pleopods 3–5 [41] are paired (p) in the thalassinoids, hippoids, galatheoids, *Lomis*, and in the paguroid family Pomatochelidae. In all other families, these pleopods are unpaired (a) presumably as a result of abdominal asymmetry.

The rami of the female pleopods [42], primitively biramous (p), are uniramous (a) in the Hippoidea, Galatheoidea, and the Lithodidae (both subfamilies) (Fig. 15b, c, f). In the Parapaguridae, the pleopodal rami tend to be crossed or twisted (Fig. 15i; see also McLaughlin, 1983b).

Male pleopods [43] on all abdominal somites are present (p) in *Penaeus* and most of the thalassinoids. They are present also in the Galatheidae and Pomatochelidae. They are reduced in number (a) in the Laomediidae and Axiidae, where the first pleopod is lost, and in the Porcellanidae, Chirostylidae, Parapaguridae (including *Probeebei*), Paguridae, Diogenidae, and *Lomis*, where all except the first two pleopods are usually lost. Complete loss of male pleopods is seen in the hippoids, lithodids (both subfamilies), coenobitids, some pagurids, and *Aegla*.

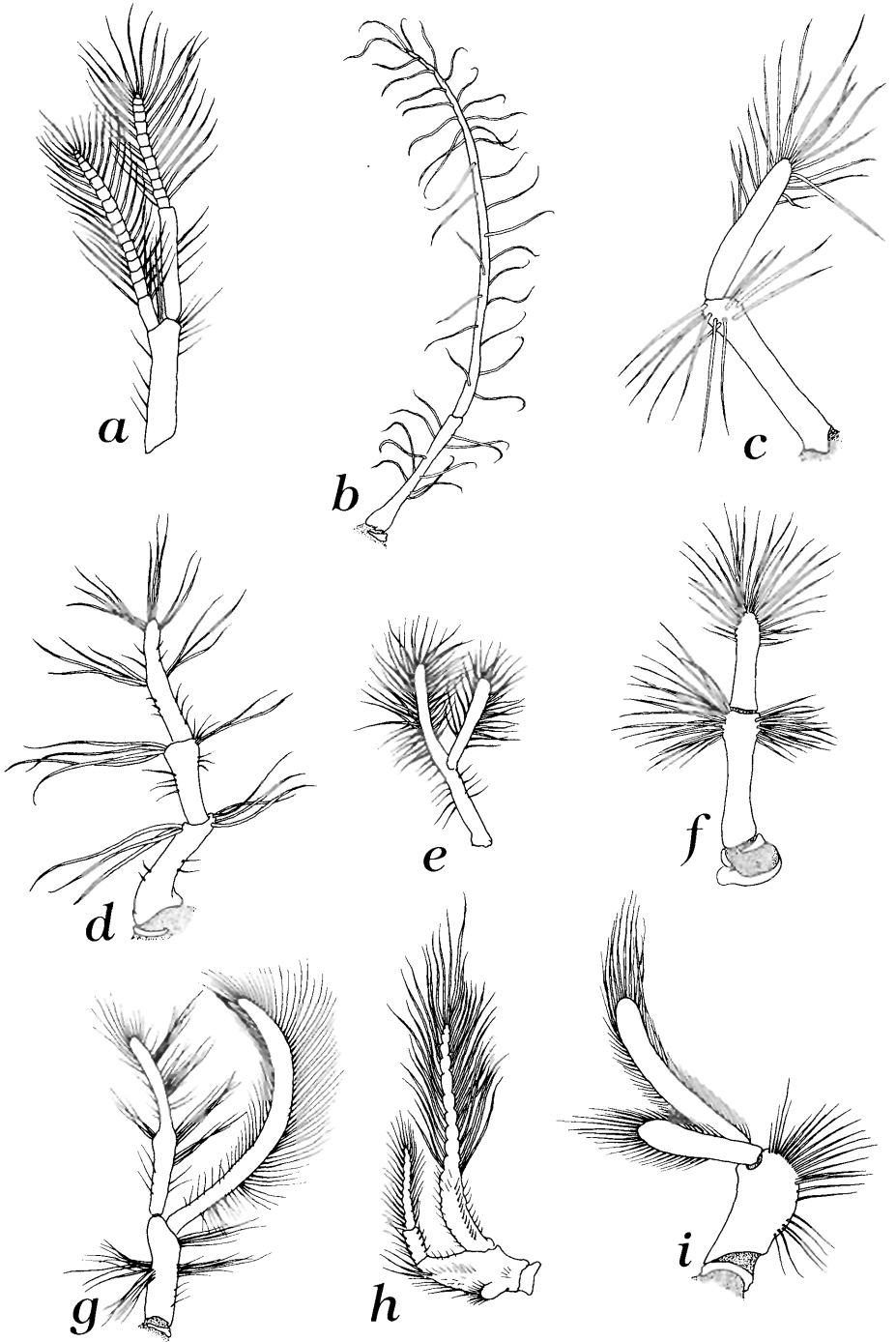


Fig. 15. Female pleopods of selected thalassinoids and anomurans. *a*, *Thalassina squamifera*, from third abdominal somite; *b*, *Albunea paretii*, third somite; *c*, *Uroptychus nitidus*, fourth somite; *d*, *Petrolisthes tuberculatus*, second somite; *e*, *Lomis hirta*, third somite; *f*, *Hapalogaster cavicauda*, second somite; *g*, *Mixtopagurus paradoxus*, second somite; *h*, *Coenobita clypeatus*, third somite; *i*, *Parapagurus pictus*, third somite. Not drawn to scale.

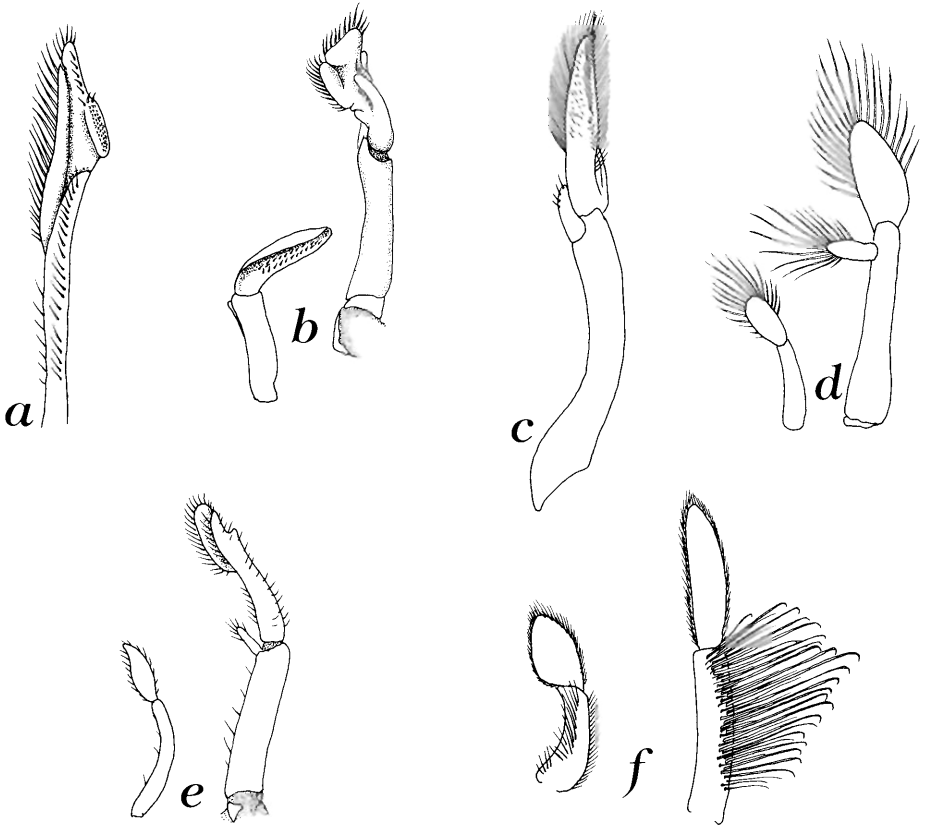


Fig. 16. Male gonopods (sexually modified pleopods) in selected thalassinoids and anomurans. *a*, *Thalassinina squamifera*, first pleopod; *b*, *Uroptychus nitidus*, first (smaller) and second pleopods; *c*, *Petrolisthes tuberculatus*, second pleopod; *d*, *Lomis hirta*, first (smaller) and second pleopods; *e*, *Mixtopagurus paradoxus*, first (smaller) and second pleopods; *f*, *Parapagurus pictus*, first (smaller) and second pleopods. Not drawn to scale.

Male pleopods are often modified as intermittent organs termed gonopods [44]. These are absent (p) in *Penaeus* (although a portion of the pleopod is developed for sperm transfer, the entire appendage is not) and all of the thalassinoids, with the exception of the Thalassinidae (Fig. 16*a*). In the Anomura they are absent in those groups lacking male pleopods (above) and in diogenids (except *Paguristes*; see McLaughlin and Provenzano, 1974b) and most pagurids. They are present (a) in the Pomatochelidae, Parapaguridae (including *Probeebei*), *Lomis*, and all of the galatheid families except the aeglids (Fig. 16*b–f*).

Telson.—The telson and uropods form a tail fan [45] in most Thalassinioidea and all Galattheoidea (including *Aegla*). They do not form a tail fan (a) in the Thalassinidae, where they are styliform (Fig. 17*a*), in the Hippoidea, where they are modified for burrowing (Fig. 17*b*), the Lithodidae and *Lomis*, where they are absent (Fig. 17*e, f*) (except for females of *Lomis*), or any of the Paguroidea where the uropods are modified for adhering to cochleate surfaces (Fig. 17*g–i*).

The lateral margin of the telson [46] may be entire (p), as in *Penaeus*, all thalassinoids, all hippoids, *Lomis*, and most galatheoids, or it may be indented to various degrees (a). This derived condition is seen in most paguroids, with the

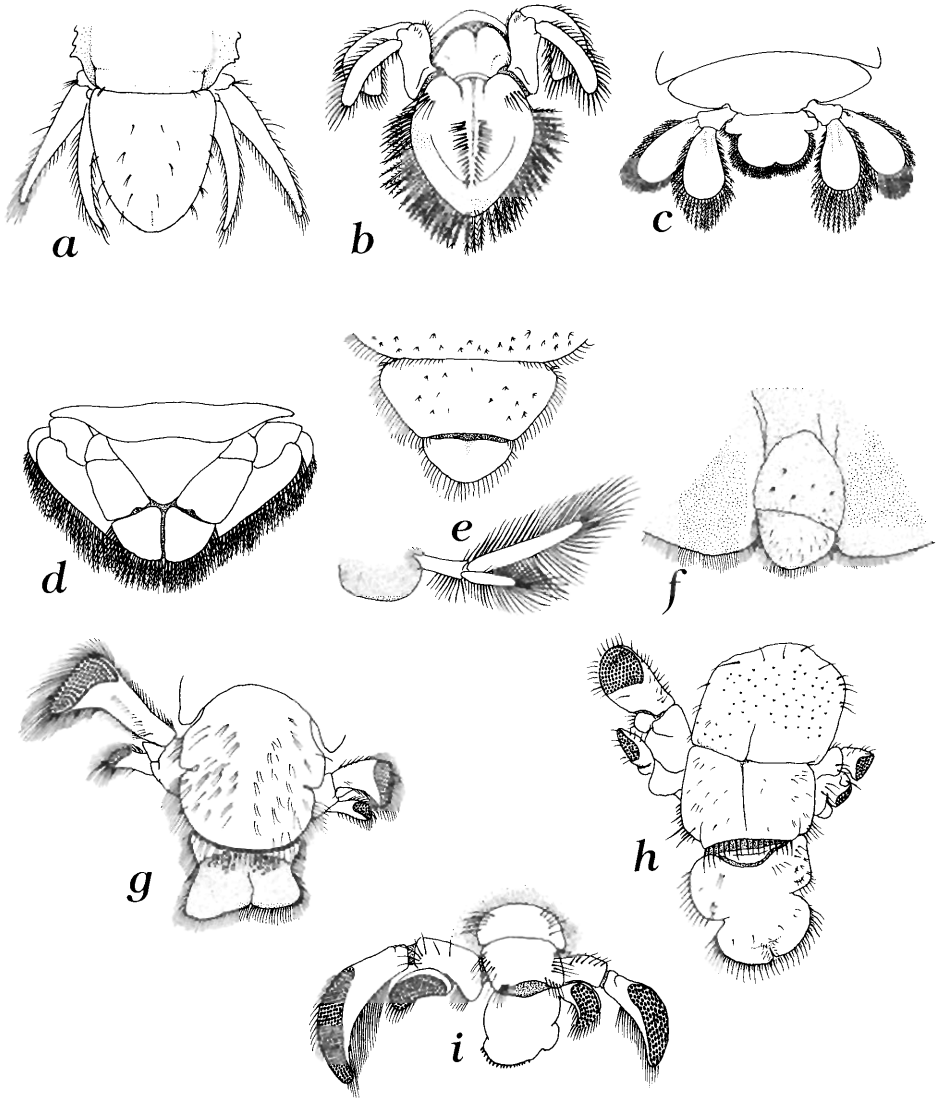


Fig. 17. Telson and uropods of selected thalassinoids and anomurans. *a*, *Thalassinia squamifera*; *b*, *Albunea paretii*; *c*, *Uroptychus nitidus*; *d*, *Petrolisthes tuberculosus*; *e*, *Lomis hirta*, male (above, lacking uropods, dorsal view) and female (below, with only left uropod illustrated, ventral view); *f*, *Hapalogaster cavicauda*, dorsal view, lacking uropods; *g*, *Mixtopagurus paradoxus*; *h*, *Coenobita clypeatus*; *i*, *Parapagurus pictus*. Not drawn to scale.

exception of the lithodids, the genus *Probeebei*, and several other parapagurids (see de Saint Laurent, 1972), the diogenid genera *Cancellus* and *Diogenes*, and several pagurid genera (e.g., *Discorsopagurus* and *Enallopagurus*, see McLaughlin, 1974, 1981). An indented telson is seen also in the galatheoid family Chirostylidae (Fig. 17c).

The dorsal surface of the telson [47] is primitively entire (p). In the Pomatochelidae and Aeglidae the telson is longitudinally divided (a), and in several other

families there is at least a median indentation. In the Porcellanidae and Galatheidae the telson may be subdivided into as many as 7 plates (Fig. 17*d*).

Uropods.—The uropods [48] of *Penaeus* are well developed and have a slight transverse groove (diaeresis) (p). A diaeresis is also seen in the thalassinoid families Laomediidae and Axiidae. In the remaining thalassinoid families and in all hippoids and galatheoids, and also in the paguroid genus *Probeebei*, a diaeresis is lacking and the uropods are unspecialized (a). A further development is seen in the paguroids (except lithodids and *Probeebei*), which lack a diaeresis but have the pleopodal rami specialized as organs of adherence. This occurs even in those perfectly symmetrical members of the Pomatochelidae (see Benedict, 1901). Uropods are completely lost in the Lithodidae and in males of *Lomis*.

Branchiae.—Pleurobranch gills on at least one of pereopods 2–4 [49] are present in *Penaeus*, all paguroids, all galatheoids, and *Lomis* (Table 1). We believe it is significant that no pleurobranches exist in any of the Thalassinioidea or Hippoidea. (Pereopod 5 was excluded from this scoring because it is often difficult to determine whether the reduced gill there is a pleurobranch or arthrobranch.)

Gill formula varies within families and according to author. We have used reduction in gill number [50] by scoring as primitive (p) all families with 14 or more pairs of gills (excluding podobranchiae) and as derived (a) all families with less than 14 pairs. Thus, even though they may have a large number of gills, the thalassinoids are “reduced” by our scoring on the basis of their lack of pleurobranches (Table 1, Fig. 12*a*). Families with 14 or more pairs of gills are the lomids, pomatochelids, galatheids, porcellanids, and *Penaeus*.

Our findings (Table 1) differ slightly from reported gill formulas of previous workers (Huxley, 1878; Calman, 1909). In the Thalassinioidea, Huxley (1878) and Calman (1909) reported 10 gills in upogebiids and callianassids. Although we found 10 gills in upogebiids, we noted one arthrobranch on the third maxilliped and a single small pleurobranch on the fifth pereopod; Huxley and Calman scored *Upogebia* as having no pleurobranches, and two (rather than one) arthrobranches on the third maxilliped. Huxley reported the identical formula for callianassids (as did Biffar, 1972), whereas we found only nine gills, the difference being one versus two arthrobranches on the third maxilliped. We report more gills for *Thalassinina* (16 versus Huxley's total of 15 plus 3 epipods, and Calman's total of 15 plus 6 mastigobranchs), differing in the number of podobranchs on the second maxilliped (1 versus 0) (Fig. 12*a*). We report 17 gills for the Axiidae, versus Huxley's 19 (plus 2 epipods). Here, the difference lies in the number of pleurobranches (1 versus Huxley's 3). Calman (1909) also found pleurobranches on pereopods 2–4 in *Axius*. Kensley and Gore (1981) noted the absence of all pleurobranches in four genera and six species of axiids, a condition more similar to our findings. The number and location of gills in the Laomediidae in Table 1 is in agreement with the majority of genera described by Le Loeuff and Intes (1974). It is also clear from the table of Kensley and Gore (1981: 1292) and from the compilation of laomediid gill formulas by Le Loeuff and Intes (1974: 23) that there is considerable variation in gill formula within thalassinoid families, and that summary tables like ours (Table 1) and that of Burkenroad (1981) are somewhat misleading.

Within the Anomura, our findings are in agreement with those of Calman (1909), with only slight differences. For the Lithodidae, Calman scored the second maxilliped as lacking gills, and the third maxilliped as having a pair of arthrobranches. Although it is difficult to determine because of the crowding of segments in carcinization, we believe that there is a single arthrobranch on each of these

Table 1. Gill formula in the Anomura. *With several exceptions; see text.

		Maxillipeds									Pereiopods									Total										
		I			II			III			IV			V			VI			VII			VIII			Σ				
		Podobranch	Arthrobranch	Pleurobranch	Podobranch	Arthrobranch	Pleurobranch	Podobranch	Arthrobranch	Pleurobranch	Podobranch	Arthrobranch	Pleurobranch	Podobranch	Arthrobranch	Pleurobranch	Podobranch	Arthrobranch	Pleurobranch	Podobranch	Arthrobranch	Pleurobranch	Podobranch	Arthrobranch	Pleurobranch					
Anomura	Faguroidea	Coenobitidae	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	2	1	0	2	1	0	0	1	0	8	3	11
		Diogenidae	0	0	0	0	0	0	0	2	0	0	2	0	0	2	1	0	2	1	0	2	1	0	0	0	0	10	3	13 *
		Pomatochelidae	0	0	0	0	0	0	0	2	0	0	2	0	0	2	1	0	2	1	0	2	1	0	0	1	0	10	4	14
		Lithodidae	0	0	0	0	1	0	0	1	0	0	2	0	0	2	0	0	2	0	0	2	1	0	0	0	0	10	1	11
		Paguridae	0	0	0	0	0	0	0	2	0	0	2	0	0	2	0	0	2	0	0	2	1	0	0	0	0	10	1	11 *
	Lomoidea	Parapaguridae	0	0	0	0	0	0	0	2	0	0	2	0	0	2	0	0	2	0	0	2	1	0	0	0	0	10	1	11
		Lomidae	0	0	0	0	0	0	0	2	0	0	2	0	0	2	1	0	2	1	0	2	1	0	0	1	0	10	4	14
		Aeglidae	0	0	0	0	0	0	0	1	0	0	2	0	0	2	1	0	2	1	0	2	1	0	0	1	0	9	4	13
		Chirostylidae	0	0	0	0	0	0	0	1	0	0	2	0	0	2	1	0	2	1	0	2	1	0	0	1	0	9	4	13
		Galatheidae	0	0	0	0	0	0	0	2	0	0	2	0	0	2	1	0	2	1	0	2	1	0	0	1	0	10	4	14
	Galatheaidea	Porcellanidae	0	0	0	0	1	0	0	1	0	0	2	0	0	2	1	0	2	1	0	2	1	0	0	1	0	10	4	14
		Albuneidae	0	0	0	0	0	0	0	1	0	0	2	0	0	2	0	0	2	0	0	2	0	0	0	1	0	9	1	10
		Hippidae	0	0	0	0	0	0	0	1	0	0	2	0	0	2	0	0	2	0	0	2	0	0	0	0	0	9	0	9
		Axiidae	0	0	0	0	1	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	0	0	1	5	11	1	17
		Callianassidae	0	0	0	0	0	0	0	1	0	0	2	0	0	2	0	0	2	0	0	2	0	0	0	0	0	9	0	9
Thalassinidea	Laomedidae	0	1	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	0	2	0	0	0	0	5	13	0	18	
	Thalassinidae	0	0	0	1	2	0	1	2	0	1	2	0	1	2	0	0	2	0	0	2	0	0	0	0	4	12	0	16	
	Upogebiidae	0	0	0	0	0	0	0	1	0	0	2	0	0	2	0	0	2	0	0	2	0	0	0	1	0	9	1	10	

appendages. Our findings for the pagurids and galatheids agree exactly with those of Calman. Our formula for the Coenobitidae differs slightly from Calman's. We report 11 gills, with paired arthrobranchs present on pereopods 2-4 (although rudimentary on 1 and 2), and pleurobranchs on pereopods 3-5 (see Fig. 12g). Calman reported 14 gills, with a pleurobranch on pereopod 2 and rudimentary paired arthrobranchs on maxilliped 3 and pereopod 1. Forest (1984: 10) noted that several diogenid genera (e.g., *Cancellus*, *Aniculus*, *Dardanus*, etc.) have 14 gills, rather than the 13 listed in our Table 1; the difference is the presence of a pleurobranch on the fifth pereopod. Gill formula in the Paguridae varies widely. We list (Table 1) the most commonly occurring gill number (11), but species with 9, 10, and 13 pairs are known (e.g., see de Saint Laurent-Dechancé, 1966: 259).

Gill morphology [51] has played an important role in the development of decapod systematics (e.g., see Huxley, 1878; Bate, 1888; Burkenroad, 1963, 1981). Although several recent workers have discounted the importance of gill structure because it varies within groups, we believe gill morphology to be important. In *Penaeus* the gills are dendrobranchiate (p). This condition is not seen in any of the thalassinoids or anomurans. Trichobranch gills are possibly derived from dendrobranchiae, and almost certainly gave rise to phyllobranch gills several times in different lineages. In the Thalassinioidea, trichobranch gills have been reported for thalassinids, upogebiids, and axiids (see Abele and Felgenhauer, 1982). The gills of *Thalassina* (Fig. 12a) are not trichobranch, but conform to no other known gill type. We score them as trichobranchs here, since it is likely that they are not far removed from true trichobranchs, but introduce the term *thalassinobranch* to describe these vertically flattened foliaceous gills. The gills of upogebiids are trichobranchiate, but the filaments are slightly flattened and not far from a primitive phyllobranch (as seen in *Parapagurus*, Fig. 12h). A similar condition is seen in axiids. Among the Anomura, trichobranch gills are known for the Pomatochelidae, *Lomis* (Fig. 12e), some parapagurids, and *Aegla* (Fig. 11c). All other families have well-developed phyllobranch gills (Fig. 12b-d, f-h), consisting of biserial rows of horizontally flattened gill rami. These may be thin and delicate (e.g., porcellanids, Fig. 11d) or thickened as in the terrestrial coenobitids (Fig. 11e, f).

Carcinization [52].—Carcinization (reduction and folding of the abdomen beneath the thorax) probably has occurred several times in the Decapoda. We scored carcinization as absent (p) in *Penaeus* and all of the thalassinoids, and in the hermit crab families (except lithodids). We scored it as "present in varying degrees" in the Galattheoidea (except porcellanids) and as "marked" (a) in lithodids, porcellanids, *Lomis*, and the hippoids (Figs. 1, 10).

Osmoregulation [53].—The vast majority of decapods are adapted to marine environments (p). Among the Anomura the Coenobitidae are unique in their terrestrial existence (a) and the aeglids, possibly coming from a terrestrial ancestor, are the only truly fresh-water representatives.

Development [54].—Although important information is likely to be gained from a study of larval and postlarval characters and their ontogeny, such an analysis for this data set was not possible. Larval development is not known for the pomatochelids or *Lomis* (Gore, 1985) and *Aegla* lacks larval stages. Assuming that larval development in pomatochelids and in *Lomis* is zoeal (p), as in the majority of anomurans, we scored all thalassinoid and anomuran families plesiomorphic and aeglids apomorphic because of their direct development. The distinction between naupliar (Penaeoidea) and zoeal eclosion, which separates the penaeoids from all other decapods, was not used.

RESULTS AND DISCUSSION

The UPGMA phenogram (Fig. 18) is in general agreement with traditional classifications of the Anomura (e.g., Bowman and Abele, 1982; Glaessner, 1960, 1969), especially at higher taxonomic levels. The thalassinoids cluster together as the sister group of all the remaining families, supporting their exclusion from the Anomura *sensu stricto* (McLaughlin and Holthuis, 1985). An arbitrary phenon line (see Sneath and Sokal, 1973) drawn at the 0.7 distance mark would separate the taxa into the traditionally recognized clusters Thalassinoidea, Hippoidea, Galatheoidea, and Paguroidea. The Hippoidea are shown to be the sister group of the remaining anomurans (galatheoids and paguroids), and within the Galatheoidea the genus *Aegla* is depicted as the most primitive offshoot of that lineage. At higher taxonomic levels this arrangement is similar to that proposed by McLaughlin (1983b) in a cladistic approach to anomuran phylogeny. At lower taxonomic levels the phenogram breaks with tradition and with McLaughlin's proposed phylogeny. The lithodids, instead of clustering with the pagurids and parapagurids, appear as the sister group to all of the "Paguroidea." *Lomis*, considered to represent a separate superfamily by McLaughlin (1983a, b) and McLaughlin and Holthuis (1985), is grouped with the lithodids. Although this at first might seem an artificial grouping caused by the extreme carcinization in lithodids and *Lomis*, this arrangement is not without merit. In addition to their crablike forms, the Lithodidae and Lomidae lack ocular acicles (but see McLaughlin, 1983b), do not have a reduced fourth pereopod, and have completely lost the uropods (except for females of *Lomis*), conditions which are seen in no other paguroid. The phenogram requires the evolution of asymmetry in two separate lines (lithodids and paguroids) (or the unlikely secondary acquisition of symmetry in *Lomis*). The phenogram differs from tradition also by grouping diogenids with pagurids, rather than with coenobitids, but McLaughlin (1983b) notes that only one character (handedness) was synapomorphic to the diogenid-coenobitid line. The lack of previous attempts to estimate phylogenies within the Galatheoidea and Thalassinoidea prevent us from making comparisons of these groupings. We do feel that, within the Galatheoidea, the galatheids are more closely related to porcellanids than to chirostylids (as the phenogram suggests), and that the characters associated with carcinization in porcellanids caused this clustering. Galatheids and porcellanids both have subdivided telsons and lack scaphocerites; the chirostylids differ in both characters. Interpretation of intrathalassinoid relationships is beyond the scope of this paper.

The most parsimonious cladogram (Fig. 19) entailed 187 steps. As with the phenetic analysis, the thalassinoids are shown to be a primitive group relative to the Anomura *sensu stricto*, although intrathalassinoid relationships differ greatly from those suggested by the phenogram. Within the Anomura, the cladogram suggests a marked departure from traditional classifications. The Galatheoidea, Hippoidea, and Lomoidea, along with the Lithodidae, are seen as the sister group of all Paguroidea (minus the lithodids). This would necessitate asymmetry arising twice to explain the asymmetrical lithodids, but, as discussed above, lithodids differ in several characters from their supposed relatives in the Paguroidea. Within the "hermit crab" group, the cladogram is in exact agreement with the proposal of McLaughlin (1983b), except that the lithodids have been removed to the non-paguroid line. Within the Galatheoidea, the aeglids are shown as intermediate between chirostylids and galatheids-porcellanids. We think this arrangement is possible, as chirostylids show several characters (e.g., retention of the antennal scale) that appear primitive. However, we feel it unlikely that the aeglid tricho-

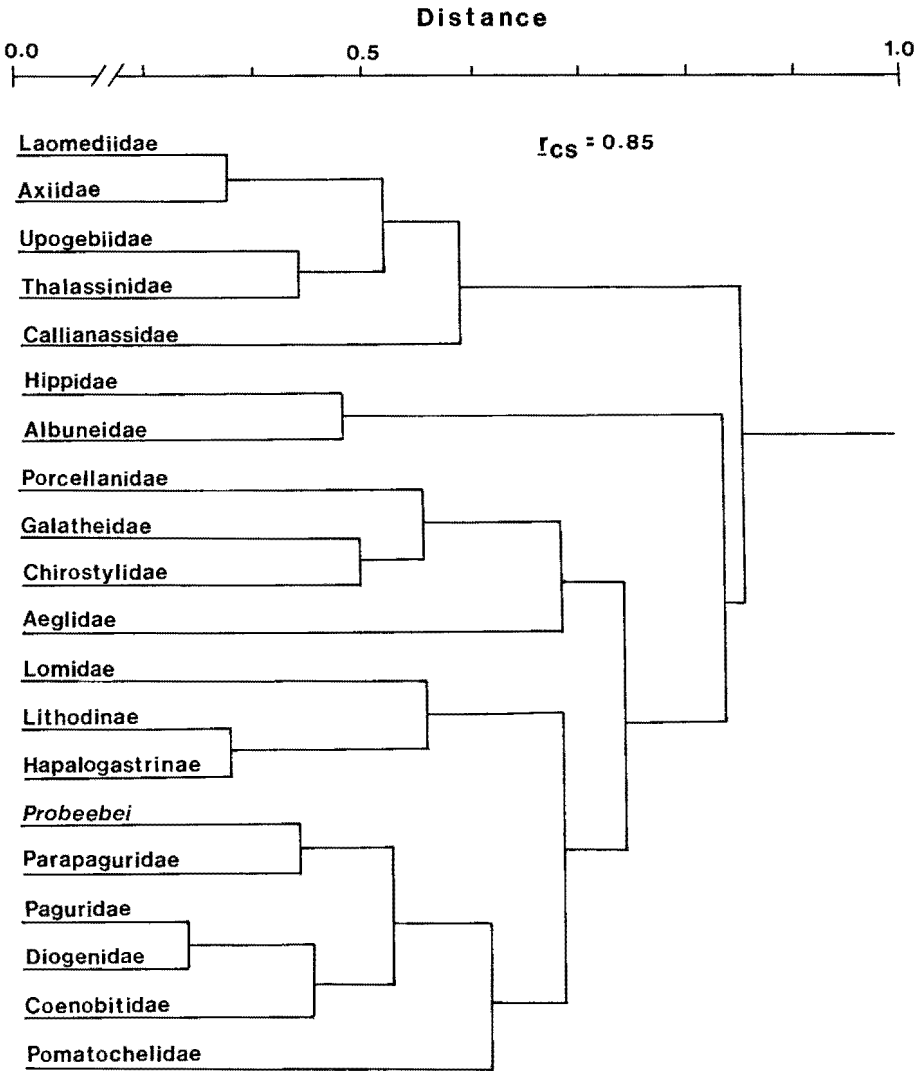


Fig. 18. Phenogram produced by UPGMA clustering (MINT program). r_{CS} = cophenetic correlation coefficient; see Sneath and Sokal, 1973: 278-279.

branch gill condition could have arisen from the well-developed phyllobranchs seen in chirostylids (compare Figs. 11c and 12c), or that the complex sutures on the carapace of *Aegla* could have come from a chirostylid-like ancestor. It should be noted, of course, that this cladogram is only one of many possible, and not necessarily the most plausible by our estimation.

These analyses draw attention to some salient points: (1) In every analysis the following groupings occur: (a) the genus *Probeebei* with the Parapaguridae, (b) the Hapalogastrinae with the Lithodinae, and (c) the albuneids with the hippids; (2) The thalassinoids were always excluded from the Anomura, although the internal arrangement of thalassinoid taxa varied considerably, emphasizing the need for further studies on these groups; (3) The pomatochelids were always depicted as

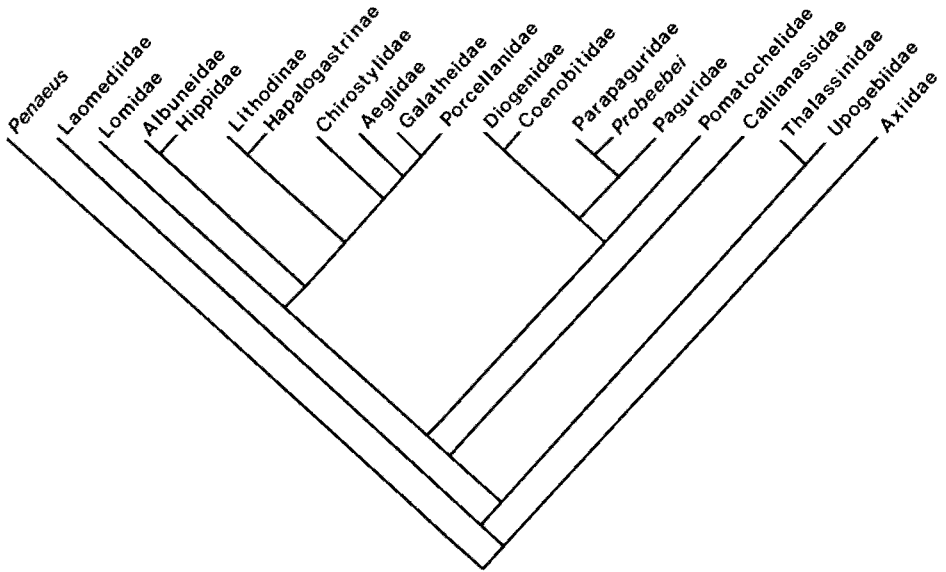


Fig. 19. Most parsimonious cladogram obtained (produced by PHYLIP program).

the most primitive of the paguroids, whether or not lithodids were included or excluded from the paguroids; (4) The position of the genus *Lomis* varied, as did the placement of the lithodids; and (5) Without exception, the Aeglidae were grouped with the Galatheoidea and not with the Paguroidea.

We propose a phylogeny of the Anomura (Fig. 20) that combines some features of both the phenogram and cladogram discussed above. As in both numerical analyses, the thalassinoids are depicted as the sister group of the Anomura sensu stricto. Relationships among the thalassinoids are unsure and are not dealt with here. Among the Anomura, the hippoids are arguably the closest relatives of the thalassinoids. Of particular interest is the loss in both groups of all pleurobranch gills, and the retention of complete abdominal sterna in the hippoids even though they have undergone considerable carcinization. Our proposed phylogeny differs most in the placement of the crablike lithodids and *Lomis*. We place them on a separate line because the preponderance of characters seems to disallow their inclusion with the other Paguroidea. *Lomis* is suggested to be an earlier offshoot of this lithodid line, before asymmetry was attained, and thus not a separate superfamily. Among the Galatheoidea we consider the aeglids the most primitive. This does not agree with several of our cladograms (e.g., Fig. 19) which place chirostylids at the base of the galatheid line. Although chirostylids have antennal scales, a primitive character, many of their other characters are very specialized and not reminiscent of other galatheoids. By placing the aeglids at the galatheid stem we avoid having to explain how a well-developed phyllobranch gill could have given rise to a trichobranch such as that seen in *Aegla*. One problem with this arrangement is that the telson of *Aegla* is longitudinally subdivided and thus similar to galatheids and porcellanids, whereas the telson of chirostylids is entire (not divided).

Despite the above discrepancies between our proposed phylogeny and the most parsimonious cladogram, the difference in the number of steps is slight (191 versus 187 in Fig. 19). The remainder of our suggested anomuran tree is in agreement

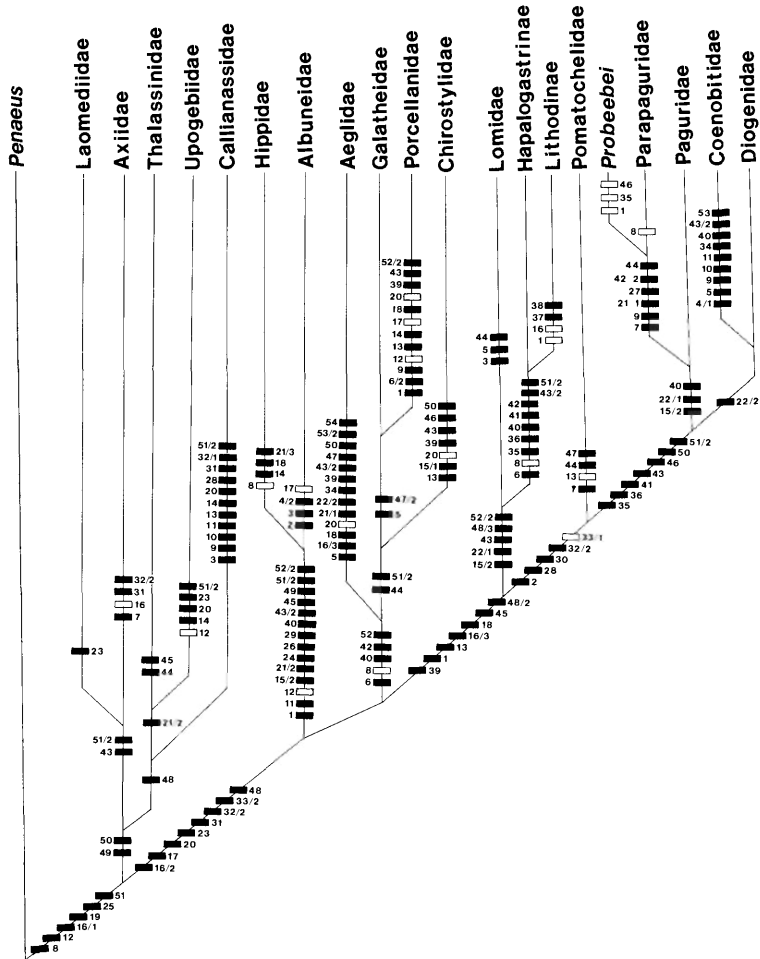


Fig. 20. Suggested hypothesis for anomuran phylogeny. Numbers refer to characters listed in Appendix II. Open rectangle = presumed character reversal.

with the cladogram of McLaughlin (1983b). We refer the reader to that paper and to McLaughlin and Holthuis (1985) for an introduction to the history of anomuran phylogeny.

Few works exist that discuss the possible origins of the Aegidae. Dana (1852) recognized the distinct nature of the group and placed them in a subtribe separate from the Galatheoidea within his "Anomura inferiora." Schmitt (1942) stated that "its nearest relatives are marine and probably to be found somewhere among the Galatheidae (tribe Galatheidea)." This view has gone unchallenged almost since Latreille first described an *Aegla* under the name *Galathea*, not knowing that his specimen was from fresh water. Since that time most workers have included aeglids as constituent members of the Galatheoidea (e.g., Borradaile, 1907; Kaestner, 1970). Our findings do not disagree with this grouping, but seem to indicate a more remote origin for aeglids than the modern galatheoids. Of the characters believed by Martin and Abele (in press) to be significant in separating aeglids from other galatheoids, we believe that the sutures of the carapace are not

as important as we first thought. Although these sutures appear in no other galatheoids, and although Dana (1852) noted (as did Martin and Abele) the remarkable similarity between sutures of the aeglid carapace and those of certain hermit crabs, an overview of all anomurans (Fig. 1) shows that most groups have some dorsal sutures, although not always in the same location. We believe that the trichobranch gills are an important character and that their presence in a group should not be taken lightly. We concede that although trichobranchs could give and undoubtedly have given rise to phyllobranch gills, the reverse does not seem likely, so that a member of a decapod assemblage with trichobranch gills is likely a primitive member of that taxon.

The phylogenies presented in this paper are not meant to be replacements for existing classifications. We feel strongly that our literature review has been too shallow, our illustrations too sketchy, and our employment of numerical methodologies too superficial to lay the question of anomuran phylogeny to rest. Felsenstein (1978) noted that, for 21 taxa as in the present case, there are over 3.19×10^{23} possible trees, if only bifurcations are considered, and of course only one of these can be correct. Instead, we hope that our proposed phylogeny (Fig. 20) is accepted only as a hypothesis to be tested by future workers. In closing, we make a plea for an increase in basic morphological studies of crustaceans. The amount of time it takes to search through (often incorrect) literature to score character states is prohibitive for most workers, and illustrating every character used in a large analysis is not possible. Only by comprehensive studies of major groups, such as that of Pike (1947) on *Galathea*, will we ever achieve the compendium needed to undertake constructing accurate phylogenies within the decapod Crustacea.

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Appendix I. Material and main references consulted for scoring characters in Appendix II. PO = personal observation; USNM = catalog numbers of specimens in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Superfamily Paguroidea Latreille, 1803	
Family Coenobitidae Dana, 1851	
<i>Birgus latro</i>	PO
<i>Coenobita clypeatus</i>	PO
Family Diogenidae Ortmann, 1892	
<i>Clibanarius vittatus</i>	PO
Forest, 1984 (<i>Aniculus</i>)	
Mayo, 1973 (<i>Cancellus</i>)	
McLaughlin, 1974 (several species)	
McLaughlin and Provenzano, 1974a (<i>Paguristes</i>)	
McLaughlin and Provenzano, 1974b (<i>Paguristes</i>)	
Family Pomatochelidae Miers, 1879	
<i>Mixtopagurus paradoxus</i> USNM 92321	PO
Benedict, 1901 (several species)	
Makarov, 1962 (several species)	
McLaughlin, 1983b (several species)	
Milne Edwards and Bouvier, 1893 (several species)	
Pilgrim, 1965 (<i>M. paradoxus</i>)	
Wass, 1959 (<i>Pylocheles inarmatus</i>)	
Family Lithodidae Samouelle, 1819	
<i>Hapalogaster cavicauda</i> USNM 207834	PO
<i>Neolithodes agassizii</i> USNM 333646	PO
Haig, 1974 (several species)	
Makarov, 1962 (several species)	
Family Paguridae Latreille, 1803	
<i>Pagurus pollicaris</i>	PO
Kensley, 1977 (<i>Porcellanopagurus</i>)	
McLaughlin, 1974 (several species)	
McLaughlin, 1981 (<i>Pylopagurus</i> complex)	
McLaughlin and Brock, 1974 (<i>Nematopagurus</i>)	
McLaughlin and Haig, 1973 (several species)	
Milne Edwards and Bouvier, 1893 (several species)	
Provenzano, 1968 (<i>Lithopagurus</i>)	
Wass, 1959 (several species)	
Wass, 1963 (several species)	
Family Parapaguridae Smith, 1882	
<i>Parapagurus pictus</i> USNM 9640	PO
<i>Probeebei mirabilis</i> USNM uncatalogued	PO
de Saint Laurent, 1972 (several species)	
Wolff, 1961 (<i>Probeebei mirabilis</i>)	
Superfamily Lomoidea Bouvier, 1895	
Family Lomidae Bouvier, 1895	
<i>Lomis hirta</i> USNM 125380	PO
McLaughlin, 1983a (<i>L. hirta</i>)	
Pilgrim, 1965 (<i>L. hirta</i>)	
Superfamily Galattheoidea Samouelle, 1819	
Family Aegliidae Dana, 1852	
<i>Aegla platensis</i>	PO
<i>Aegla uruguayana</i>	PO
<i>Aegla jujuyana</i>	PO
Martin and Abele (in press)	
Martin and Felgenhauer (in press)	

Appendix I. Continued.

Family Chirostylidae Ortmann, 1892	
<i>Uroptychus nitidus</i>	PO
Baba, 1977a (several species)	
Baba, 1977c (<i>Gastroptychus</i>)	
Baba, 1981 (several species)	
Benedict, 1902 (several species)	
Haig, 1979 (<i>Pseudomunida</i>)	
Kensley, 1977 (<i>Uroptychus</i>)	
Family Galatheidae Samouelle, 1819	
Baba, 1977b (several species)	
Benedict, 1902 (several species)	
Mayo, 1974 (<i>Munidopsis</i>)	
Pike, 1947 (<i>Galathea squamifera</i>)	
Family Porcellanidae Haworth, 1825	
<i>Petrolisthes tuberculosus</i>	PO
Chace, 1959 (several species)	
Glassell, 1938 (several species)	
Haig, 1956 (several species)	
Haig, 1960 (several species)	
Haig, 1981 (<i>Petrolisthes</i>)	
Makarov, 1962 (several species)	
Superfamily Hippoidea Latreille, 1825	
Family Albuneidae Stimpson, 1858	
<i>Albunea paretii</i>	PO
Efford and Haig, 1968 (several species)	
Family Hippidae Latreille, 1825	
<i>Emerita rathbunae</i> USNM 300691	PO
Snodgrass, 1952 (<i>Emerita talpoida</i>)	
Superfamily Thalassinoidea Latreille, 1831	
Family Axiidae Huxley, 1879	
<i>Axius (Neaxius) vivesi</i> USNM 189040	PO
Kensley and Gore, 1981 (several species)	
Makarov, 1962 (<i>Axiopsis</i>)	
Poore and Griffin, 1979 (several species)	
Family Callianassidae Dana, 1852	
<i>Callianassa jamaicensis</i>	PO
Biffar, 1972 (several species)	
de Man, 1928a, b (several species)	
Kensley, 1974 (several species)	
Kensley, 1975 (several species)	
Le Loeuff and Intes, 1974 (several species)	
Poore and Griffin, 1979 (several species)	
Schmitt, 1935 (several species)	
Family Laomediidae Borradaile, 1903	
<i>Naushonia crangonoides</i> USNM 170634	PO
Goy and Provenzano, 1979 (<i>Naushonia</i>)	
Le Loeuff and Intes, 1974 (<i>Laurentiella</i>)	
Martin and Abele, 1982 (<i>Naushonia</i>)	
Sakai, 1962 (several species)	
Wear and Yaldwyn, 1966 (<i>Jaxea novaezealandiae</i>)	
Family Thalassinidae Latreille, 1831	
<i>Thalassina squamifera</i> USNM 152523	PO
de Man, 1928a (<i>T. anomala</i>)	
Poore and Griffin, 1979 (<i>T. squamifera</i>)	

Appendix I. Continued.

Family Upogebiidae Borradaile, 1903

Upogebia africana USNM 105367

PO

de Man, 1927 (several species)

Le Loeuff and Intes, 1974 (several species)

Poore and Griffin, 1979 (several species)

Thistle, 1973 (several species)

Williams, 1986 (several species)

Appendix II. Characters and character states employed.

CHARACTER	CHARACTER STATES
ROSTRUM	
1. Development	0 well developed 1 reduced
EYES	
2. Ocular acicles	0 absent 1 present
3. Eyestalks	0 normally developed 1 flattened, large
ANTENNA 1	
4. Flagella	0 well developed 1 compressed, truncate 2 ventral flagellum vestigial
ANTENNA 2	
5. Scaphocerite	0 present, well developed 1 reduced or absent
6. Peduncle segments	0 with "supernumerary" segment (>5) 1 5 segments 2 4 segments
EPISTOME	
7. Epistomal spines	0 absent 1 present
MAXILLA 1 (MAXILLULE)	
8. Palp of maxillule	0 without lobe 1 with lobe
MAXILLIPED 1	
9. Flagellum of exopod	0 well developed 1 reduced or absent
MAXILLIPED 2	
10. Flagellum	0 well developed 1 reduced or absent
MAXILLIPED 3	
11. Flagellum	0 well developed 1 reduced or absent
12. Crista dentata	0 absent 1 well developed
13. Epipod	0 present 1 reduced or absent

Appendix II. Continued.

CHARACTER	CHARACTER STATES
14. Shape	0 pediform 1 non-pediform
15. Basal separation	0 approximate basally 1 variable condition 2 divergent basally
CARAPACE	
16. Lineae	0 absent 1 present, linea thalassinica 2 present, linea anomurica 3 present, transverse linea delineating branchial region
17. Dimensions	0 equal width throughout length 1 wider posteriorly
18. Shape	0 laterally compressed to subcylindrical 1 dorsoventrally compressed
THORAX	
19. Thoracic somite 8	0 immobile (fused) 1 mobile (unfused)
20. Pereiopods	0 with epipods 1 epipods absent or reduced
PEREIOPOD 1	
21. Condition	0 chelate, without corneous scales 1 chelate, with scales 2 subchelate 3 loss of chelae
22. Symmetry	0 symmetrical or variable 1 right-handed 2 left-handed
PEREIOPOD 2	
23. Condition	0 chelate or subchelate 1 achelate
24. Dactylus	0 sharp, clawlike 1 flat, paddlelike
PEREIOPOD 3	
25. Condition	0 chelate 1 achelate
26. Dactylus	0 sharp, clawlike 1 flat, paddlelike
27. Female gonopores	0 paired 1 on left side only
PEREIOPOD 4	
28. Condition	0 achelate 1 chelate or subchelate
29. Dactylus	0 sharp, clawlike 1 flat, paddlelike
30. Development	0 normally developed 1 reduced
PEREIOPOD 5	
31. Condition	0 achelate 1 subchelate or chelate
32. Dactylus	0 lacking corneous scales 1 with corneous scales

Appendix II. Continued.

CHARACTER	CHARACTER STATES
33. Development	0 normally developed 1 reduced 2 reduced and inserted beneath carapace
34. Coxa	0 unmodified 1 modified for sperm transfer
ABDOMEN	
35. Calcification	0 strong, somites distinct 1 weak, integument often membranous, somites poorly defined
36. Development	0 normal (not reduced), straight 1 usually reduced and/or twisted
37. Abdominal terga	0 entire 1 divided
38. Supplemental tergal calcification	0 absent 1 present
39. Abdominal sterna	0 entire 1 incomplete, except for first somite
PLEOPODS	
40. Female first pleopod	0 present 1 absent
41. Female pleopods 3-5	0 paired 1 unpaired
42. Rami of female pleopods 2-5	0 biramous 1 uniramous 2 crossed or twisted
43. Male pleopods	0 present 1 reduced in number 2 absent
44. "Gonopods" (modified first or first and second pair)	0 not present 1 present
TELSON	
45. With uropods	0 forming tail fan 1 not forming tail fan
46. Lateral margin	0 entire 1 indented
47. Dorsal surface	0 entire 1 longitudinally divided 2 divided into >2 plates
UROPODS	
48. Condition	0 present, with diaeresis 1 present, without diaeresis, rami unspecialized 2 present, without diaeresis, rami specialized 3 uropods absent
BRANCHIAE	
49. Pleurobranchs on legs 2-4	0 present 1 absent
50. Gill formula (excluding podo-branchiae)	0 at least 14 pairs of gills 1 reduction in gill number (less than 14 pairs of gills)

Appendix II. Continued.

CHARACTER	CHARACTER STATES
51. Gill structure	0 dendrobranchiate 1 trichobranchiata 2 phyllobranchiate
CARCINIZATION	
52. Carcinization	0 absent 1 present in varying degrees 2 marked
OSMOREGULATION	
53. Osmoregulation	0 marine adapted 1 terrestrial adapted 2 fresh-water adapted
DEVELOPMENT	
54. Eclosion from egg	0 zoal 1 "advanced" (postlarval)

