

PRELIMINARY PHYLOGENETIC ANALYSIS OF GENERIC RELATIONSHIPS
WITHIN THE CALLIANASSIDAE AND CTENOCHELIDAE (DECAPODA:
THALASSINIDEA: CALLIANASSOIDEA)

Christopher C. Tudge, Gary C. B. Poore, and Rafael Lemaitre

(CCT, GCBP) Crustacea Laboratory, Museum Victoria, P.O. Box 666E, Melbourne, Victoria 3001, Australia;
(CCT, RL) Department of Invertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560-0163, U.S.A.
(corresponding author (CCT) e-mail: tudge.christopher@nmnh.si.edu)

A B S T R A C T

A phylogenetic analysis of 106 representatives in the thalassinidean families Ctenochelidae and Callianassidae, based on 93 adult morphological characters, was performed to investigate the interrelationships between the 25 currently recognized genera. The callianeid, *Callianidea typa* H. Milne Edwards, was used as the out-group. The two in-group families, Ctenochelidae and Callianassidae, were both shown to be monophyletic. Monophyly of the four ctenochelid subfamilies (Anacalliinae, Callianopsinae, Ctenochelinae, and the recently suggested Gourretinae) was not supported. Three callianassid subfamilies (Callianassinae, Cheraminae, and Eucalliinae) were found to be monophyletic but with species compositions different from those presently understood. The fourth callianassid subfamily (Callichirinae) is paraphyletic and ancestral to the other subfamilies. Several species described as species of *Callianassa s.l.* were found to belong to other genera. Recent diagnosis of several small genera from the Americas and Japan has left larger traditional genera such as *Callianassa s.l.* and *Cheramus* paraphyletic. *Glypturus* is apparently paraphyletic as presently diagnosed. The taxonomic position of some species remains enigmatic largely because of missing data. A listing of all valid genera and species of Ctenochelidae and Callianassidae at the time of publication is provided.

Recent studies have greatly increased the number of known species in the thalassinidean families Ctenochelidae (e.g., Matsuzawa and Hayashi, 1997; Sakai, 1999), and Callianassidae (e.g., Ngoc-Ho, 1991, 1994, 1995; Sakai, 1992; Manning and Tamaki, 1998). The callianassids of the Americas in particular have received much attention (e.g., Manning and Felder, 1995; Lemaitre and Felder, 1996; Heard and Manning, 1998; Hernández-Aguilera, 1998). Various classification systems have been proposed for the decapod infraorder Thalassinidea. De Saint Laurent (1973) defined the Upogebiidae and Callianassidae and assigned those species previously in *Callianassa s.l.* to six distinct genera, *Callianassa*, *Callichirus*, *Gourretia*, *Calliax*, *Callianopsis*, *Anacalliix*, and created a seventh new genus *Calliapagurops*. Later Manning and Felder (1991a), focusing on the callianassids of the Americas, reviewed the genera in the Callianassidae, erected the new family Ctenochelidae, and concluded that the large and disparate genus *Callianassa s.l.* should be restricted to a few species in the eastern Atlantic, and that all other “*Cal-*

lianassa” species should be assigned to other genera. Poore (1994) presented a phylogeny of all the families of the Thalassinidea, confirmed the monophyly of the infraorder, established that it contained 11 families in three superfamilies, and that the families Callianassidae and Ctenochelidae are in fact sister taxa. His notable changes in the families Callianassidae and Ctenochelidae were the suggestion that the latter is paraphyletic and the reassignment of the genus *Anacalliix* from the Ctenochelidae to the Callianassidae. However, many carcinologists have experienced difficulties in applying the classifications of de Saint Laurent (1973) and Manning and Felder (1991a) (e.g., Poore, 1975, 1994; Poore and Griffin, 1979; Rabalais *et al.*, 1981; Williams, 1984; Ngoc-Ho, 1994; Sakai, 1999) and their global application has been questioned. Clearly, additional studies of genera in these two families are still required before true relationships can be ascertained.

A generic-level phylogenetic analysis of the Ctenochelidae and Callianassidae has not previously been attempted although various representatives have been used in investiga-

tions of relationships between other thalassinidean taxa (Borradaile, 1903; Kensley and Heard, 1991; Poore, 1994), or between thalassinideans and other decapods (Martin and Abele, 1986; Scholtz and Richter, 1995). These analyses were based on morphological characters, but others have used comparisons of 18s rRNA nucleotide sequences (Spears and Abele, 1988), neuroanatomy (Paul, 1989; Sandeman *et al.*, 1993), and ultrastructural morphology of spermatozoa and spermatophores (Tudge, 1997).

The objective of this paper is to subject the current taxonomy of the Callianassidae and Ctenochelidae to phylogenetic analysis based on existing, and readily available, character information. The aim is to highlight taxa where taxonomy may not be substantiated by parsimonious analysis rather than to provide a well-defined alternative classification for these two families. The current analysis is not intended for elucidation of species-level taxonomic groupings, and associations at this level should be treated with caution.

MATERIALS AND METHODS

The taxa included in this analysis are indicated by an asterisk (*) in the list of all valid species in the thalassinidean families Ctenochelidae and Callianassidae (Appendix 1). This list includes all valid species known to date (April 1999) arranged according to their most recent generic and subfamily assignments, and not according to their original combinations. The taxa selected for the analysis have greater than 50% of their character states able to be scored at this time (one exception being "*Callianassa*" *acutirostella* with 55% missing data). The largest genus is *Callianassa* *s.l.*, not because it is the largest monophyletic group of species but because many authors have used it as a default name until a more stable systematic arrangement becomes generally acceptable. In the text we use "*Callianassa*" in quotes where we suspect the generic placement is incorrect. The out-group taxon, *Callianidea* *typha* H. Milne Edwards, 1837, (family Callianideidae) is also included in Appendix 1. For each genus, the type species is indicated, and the source of morphological information is indicated in square brackets. Appendix 2 is a list describing the 93 adult somatic morphological characters used in the analysis and their suggested polarity. There are 56 binary characters and 37 multistate characters. There were no nonapplicable characters. This character list is a modified version of that used by Poore (1994). Throughout this paper the terms "antenna 1" and "antenna 2" refer to the antennule and antenna, respectively. Figures 1 and 2 illustrate some of the characters used. The complete data matrix is provided in Appendix 3. Of the characters employed in this analysis, 13 were considered to be phylogenetically uninformative due to their being autapomorphies or consistent in state across the included taxa. The missing character states (indicated by "?") indicate that the information was unable to be obtained from the literature or from the spec-

imens examined (e.g., incomplete specimens or only one sex available).

Phylogenetic Analysis

The phylogenetic analysis used PAUP version 3.1.1 (Swofford, 1993), utilizing a data matrix originating in MacClade version 3 (Maddison and Maddison, 1992). Heuristic search analyses were performed with the following options in effect: addition sequence, simple; one tree held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch-swapping performed; MULPARS option activated; steepest descent option inactive; branches having maximum length zero collapsed to yield polytomies; topological constraints not enforced; trees unrooted; multistate taxa interpreted as uncertainty; character-state optimization, accelerated transformation (ACCTRAN). All characters were unordered, unscaled, and equally weighted.

The large size of the data matrix excluded search strategies other than the heuristic method.

The callianideid *Callianidea* *typha* was selected as the out-group taxon because of its type species status and the undisputed, close sister-group relationship to the in-group families Ctenochelidae and Callianassidae (Borradaile, 1903; Kensley and Heard, 1991; Poore, 1994).

RESULTS

The 50% majority rule consensus tree calculated from the 1,700 equally parsimonious trees obtained from an heuristic analysis of the data matrix is shown in Figs. 3 and 4 and is the subject of our discussion. The tree length = 838 steps, and the consistency index (CI) = 0.905. Some higher taxonomic categories are shown with brackets and arrows (Fig. 3). Clades not supported by 100% of the trees are indicated (Fig. 4).

For brevity we will mostly discuss the systematic position of species that appear to lie outside the genera with which they are currently classified and apparently poly- or paraphyletic genera. Approximately half (51%) of the species in this analysis have incomplete data sets (Fig. 4, and Appendix 3), and therefore many of the contentious taxa also fall into this category. The average percentage of missing data in the matrix is only 11%, but in some species this percentage is as high as 30% or 50%. The placement of taxa with high proportions of missing data should be viewed with some reservation.

DISCUSSION

The two families Ctenochelidae and Callianassidae are both unambiguously monophyletic, and contrary to Sakai's (1999) view, warrant family rather than subfamily status. Poore (1994) considered the Callianassidae

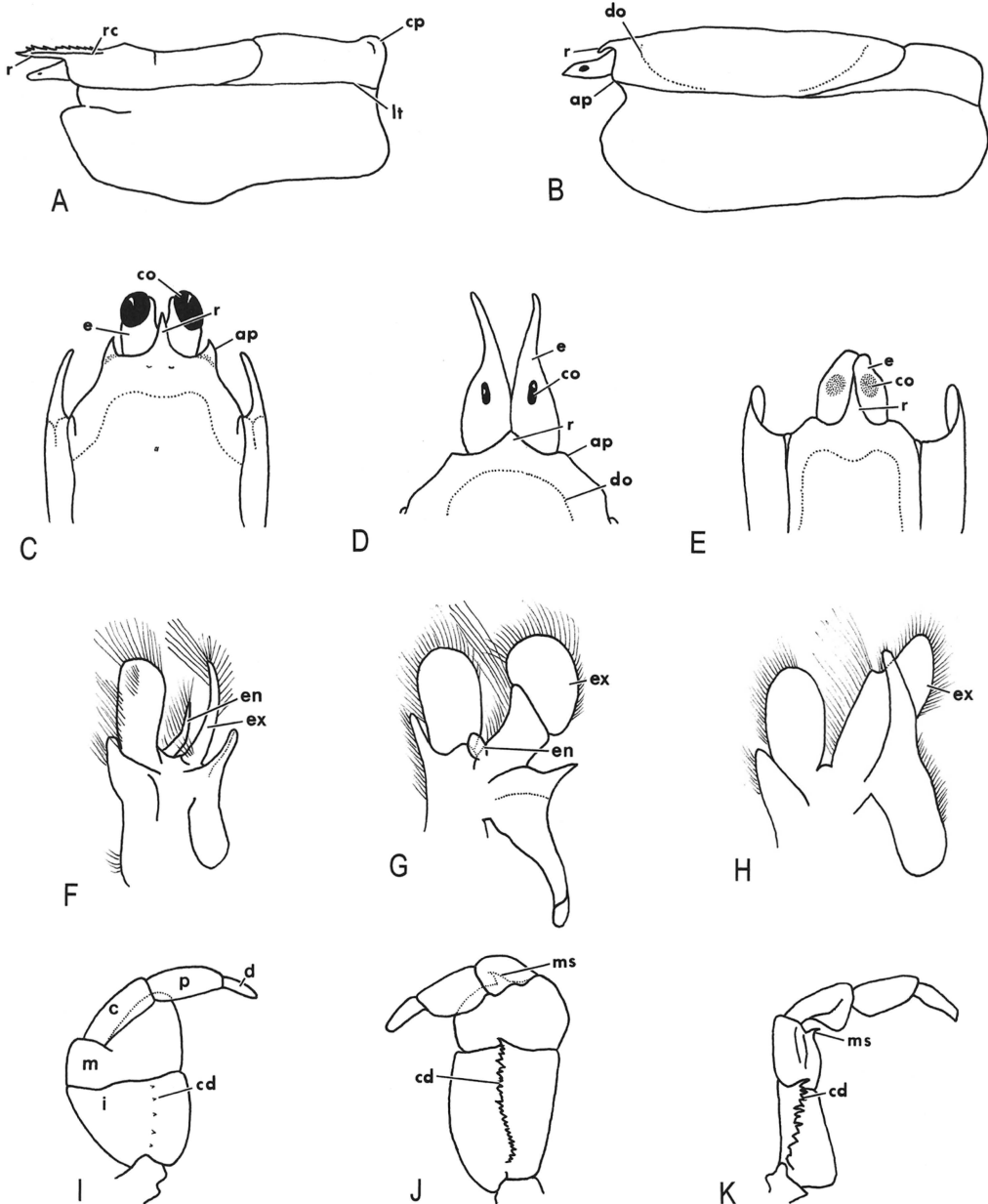


Fig. 1. Diagrammatic representation of selected ctenochelid and callianassid morphological character states. A, B, Lateral view of carapace: A, *Ctenocheles serrifrons*; B, *Biffarius bififormis* (both after Manning and Felder, 1991a). C–E, Dorsal view of rostral region and eyestalks: C, *Corallichirus xuthus* (after Manning and Felder, 1991a); D, *Callilichirus seilacheri* (after Manning and Felder, 1986); E, *Lepidophthalmus jamaicense* (after Manning and Felder, 1991a). F–H, Maxilliped 1: F, *Callianidea typa* (after Poore, 1997); G, *Biffarius delicatulus* (after Rodrigues and Manning, 1992a); H, *Glypturus acanthochirus* (after Biffar, 1971b). I–K, Maxilliped 3: I, *Trypaea australiensis* (after Poore and Griffin, 1979); J, “*Callianassa*” *praedatrix* (after Sakai, 1988); K, *Dawsonius latispina* (after Manning and Felder, 1991a). Not to scale. Abbreviations: ap, anterolateral projections; c, carpus; cd, crista dentata; co, cornea; cp, cardiac prominence; d, dactylus; do, dorsal oval; e, eyestalk; en, endopod; ex, exopod; i, ischium; lt, linea thalassinica; m, merus; ms, meral spine; p, propodus; r, rostrum; rc, median rostral carina.

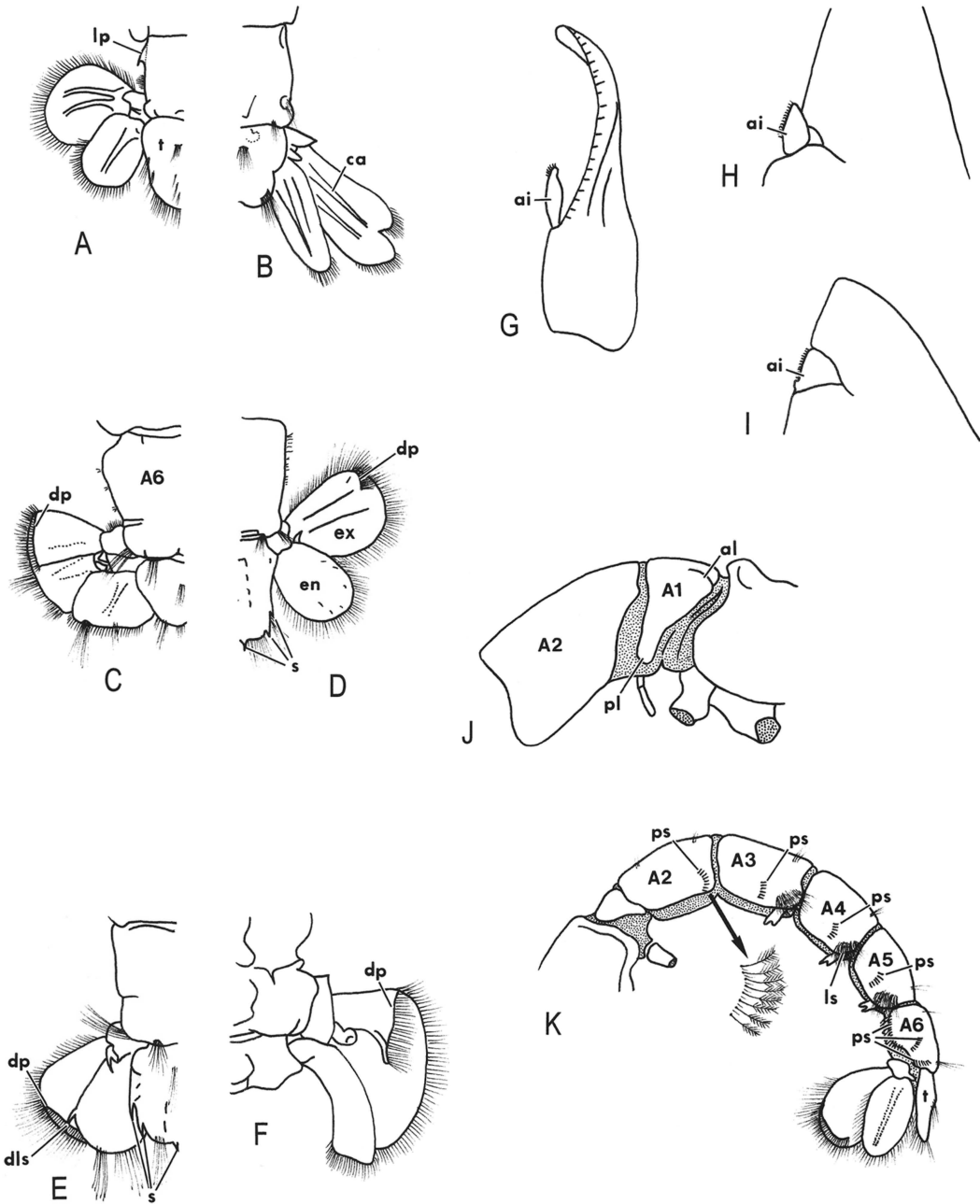


Fig. 2. Diagrammatic representation of selected ctenocheleid and callianassid morphological character states. A-F, Uropods, telson, and 6th abdominal somite: A, *Dawsonius latispina* (after Biffar, 1971b); B, *Ctenocheles maorianus* (after Dworschak, 1992); C, *Neocallichirus lemaitrei* (after Manning, 1993); D, *Cheramus profundus* (after Biffar, 1973); E, *Necallianassa berylae* (after Heard and Manning, 1998); F, *Callichirus islagrande* (after Manning and Felder, 1991a). G-I, Appendix interna on pleopods 3-5: G, *Cheramus marginatus*; H, *Callichirus seilacheri*; I, *Notiix brachyophthalma* (all after Manning and Felder, 1991a). J, Posterior margin of carapace and abdominal somites 1 and 2. K, Lateral view of abdominal segments 1-6 and tailfan, showing position of plumose setal rows on somites 2-6, and dense tufts of lateral setae on somites 3-5. Not to scale. Abbreviations: A1-6, abdominal somites; ai, appendix interna; al, anterolateral lobes; ca, carina; dls, distolateral spine; dp, dorsal plate; en, endopod; ex, exopod; lp, lateral projection; ls, lateral setal tufts; pl, pleuron; ps, plumose setal row; s, spine; t, telson.

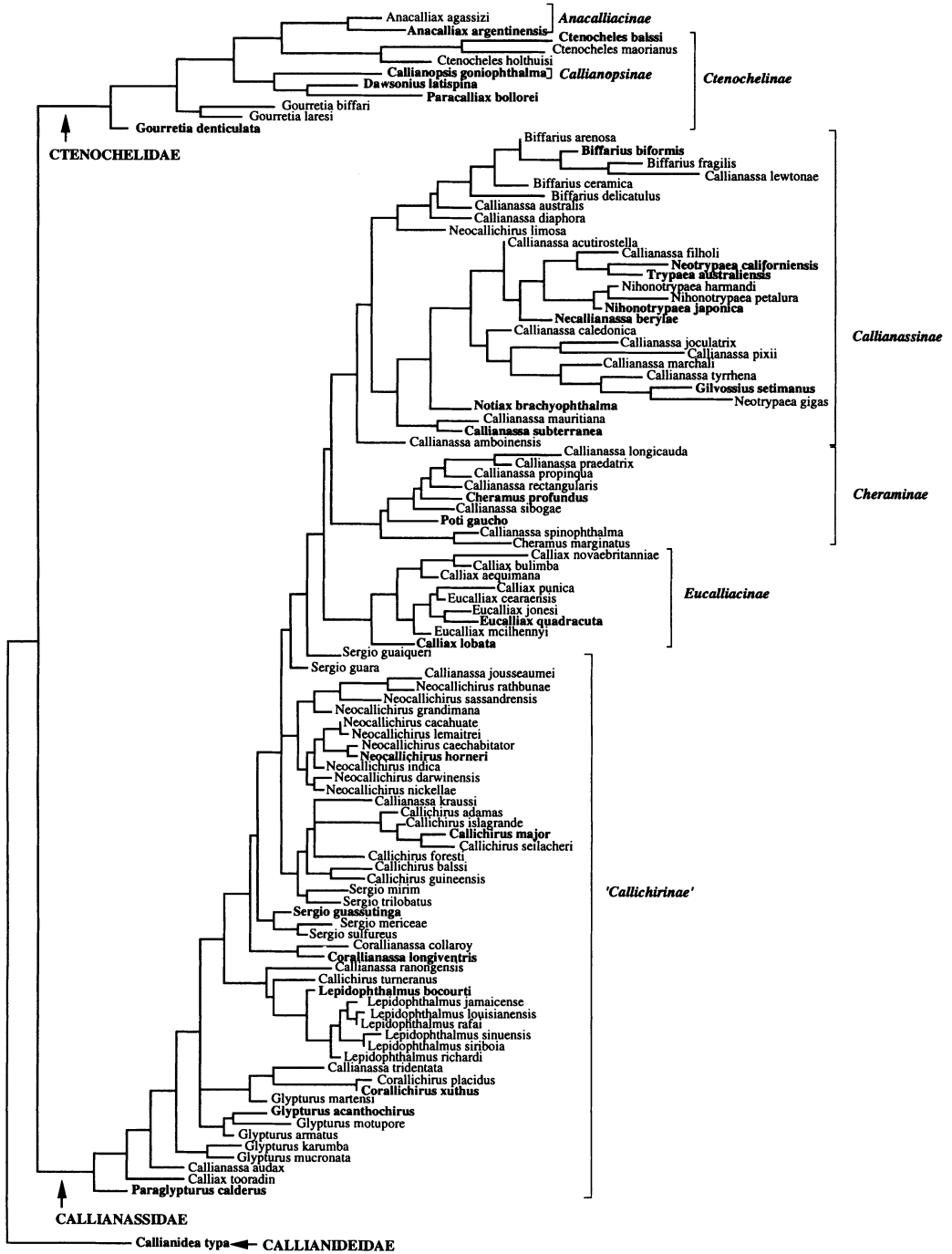
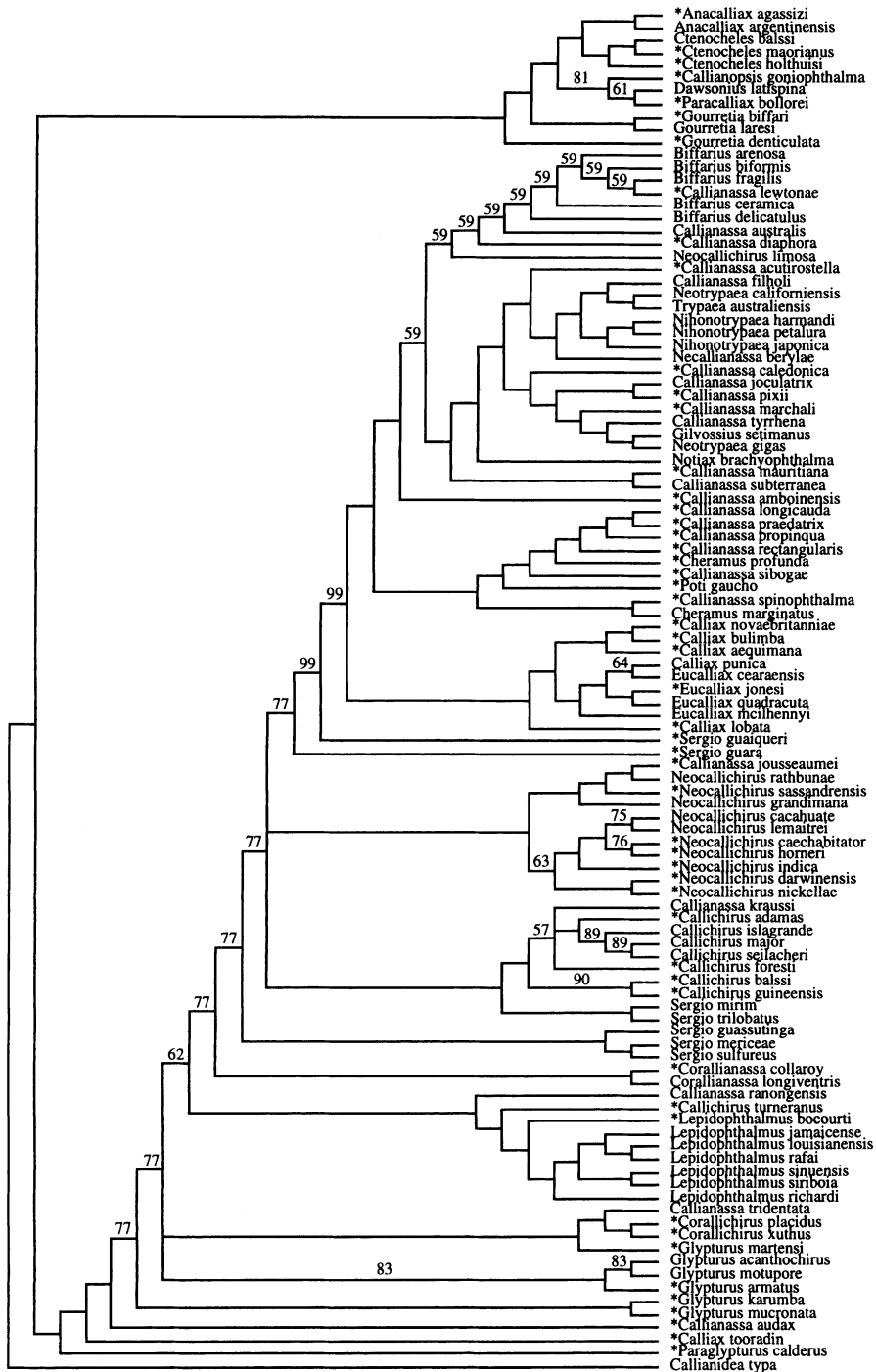


Fig. 3. Phylogram of 50% majority rule consensus tree of 1,700 equally parsimonious trees obtained from an heuristic analysis of 107 thalassinidean taxa using 93 morphological characters and using the out-group method. Tree length = 838 steps; consistency index (CI) = 0.905. Some higher taxonomic categories are indicated (arrows and brackets), as are type species (boldface).



Downloaded from https://academic.oup.com/jcb/article/20/5/129/2419506 by guest on 25 April 2024

Fig. 4. Cladogram of 50% majority rule consensus tree of 1,700 equally parsimonious trees obtained from an heuristic analysis of 107 thalassinidean taxa using 93 morphological characters and using the out-group method. Tree length = 838 steps; consistency index (CI) = 0.905. Species without a full complement of character states scored (missing data in the matrix) are indicated with an asterisk (*). Clades are supported by 100% of trees unless otherwise indicated.

paraphyletic, but the synapomorphies—presence of a dorsal plate on the uropodal exopod (= anterodorsal thickening), absence of dorsal carinae on the same uropodal exopod, and absence of a cardiac prominence—define the family.

Ctenochelidae

The four subfamilies (Anacalliinae, Callianopsinae, Ctenochelinae, Gourretinae) (Manning and Felder, 1991a; Sakai, 1999) are not monophyletic in the present analysis. The subfamily Anacalliinae, containing the single genus *Anacalliax*, is not a member of the Callianassidae, as suggested by Poore (1994). This analysis clearly shows that the genus (and subfamily) is part of the Ctenochelidae, supporting the placement of Manning and Felder (1991a) and Sakai (1999). However, most of the taxa used to represent this family in the present analysis have missing data, and the intergeneric relationships shown thus should be treated with caution.

The genus *Gourretia* is paraphyletic in this analysis, and it has previously been suggested that it comprises more than one genus (Manning and Felder, 1991a). In the analysis *G. denticulata*, the type species of *Gourretia*, does not group with the two other species of *Gourretia* (Figs. 3, 4). The type species differs from them in having a flatly spinose rostrum instead of an upturned one; it has no discernible antero-lateral projections on the frontal margin of the carapace (Fig. 1E); the endopod on maxilliped 1 is elongate (Fig. 1F) and not minute (Fig. 1G); there is a definite heel on the propodus of pereopod 3; the telson is longer than the uropods and has a rounded distal edge (Fig. 2A) instead of a flattened one; and lastly, transverse setal rows on abdominal somite 6 are absent (Fig. 2K).

Callianassidae

Three of the four subfamilies (Callianassinae, Cheraminae, Eucalliinae) (Manning and Felder, 1991a) are monophyletic in this analysis only after reappraisal of their constituent taxa. The fourth subfamily, Callichirinae, is paraphyletic.

Restriction of *Callianassa* (Manning and Felder, 1991a) to *Callianassa subterranea* is supported by the current analysis and suggests reassessment and reassignment of other *Callianassa s.l.*

Callianassinae

The clade of nine species and including the type species of *Biffarius* has 59% support. The genus may therefore include “*Callianassa*” *lewtonae*, “*C.*” *australis*, “*C.*” *diaphora*, and “*Neocallichirus*” *limosa* as well as those originally assigned to it. Although “*Callianassa*” *lewtonae* has less than half of the characters unscored, it shares 45 synapomorphies with the five *Biffarius* species. We consider at least five significant: absence of the anterolateral projections on the frontal margin of the carapace, equal or subequal chelipeds in the female, denticulate ischium of the minor cheliped, and a telson which is as long as broad but shorter than the uropods. “*Callianassa*” *lewtonae* is almost certainly a species of *Biffarius*.

The analysis also suggests that “*Neocallichirus*” *limosa* should not be in *Neocallichirus*, where it was placed by Sakai (1988) and Kazmi and Kazmi (1992), but perhaps should be considered as a member of *Biffarius*. This taxon has a full complement of characters and differs from the ten other species of *Neocallichirus* in presence of a distinct meral hook on the major cheliped, presence of ventral denticles on the ischium of the minor cheliped, a male first pleopod with the second segment triangular instead of ovate, a male second pleopod vestigial and not overtly biramous, pleopods 3–5 with the appendix interna a stubby projection and not embedded into the rami (Fig. 2H, I), and a terminally rounded telson (Fig. 2A) and not flat or slightly indented (Fig. 2B, C). Placement of “*Callianassa*” *limosa* in *Neocallichirus* is clearly erroneous, and it, “*C.*” *australis*, and *C. diaphora* are more probably species of *Biffarius*. All share similarities in rostral and anterolateral projection morphology, presence of a distinct meral hook on the major cheliped, telson and uropod characteristics, 2nd and 3rd maxilliped morphology and male pleopodal morphology.

Remaining clades within the Callianassinae are well supported.

Callianassa subterranea, type species of this genus, (currently grouping with *C. mauritiana*) is at the base of a clade that includes other species of *Callianassa s.l.* plus the genera *Notiax*, *Gilvossius*, *Neotrypaea*, *Necallianassa*, *Nihonotrypaea*, and *Trypaea*. The presence of other species of *Callianassa s.l.*

in other clades reflects the very broad way this genus name has been applied rather than misclassification. The smaller genera are specialized derivatives of *Callianassa* s.s. The genus *Neotrypaea* is not monophyletic, with *N. californiensis* the sister taxon of *Trypaea australiensis* and *N. gigas* the sister taxon of *Gilvossius setimanus*. Both associations are well supported. *Neotrypaea californiensis* differs from *N. gigas* in that abdominal somite 2 is greater in length than abdominal somite 6 (Fig. 2K) and not equal to it; abdominal somites 3–5 have dense tufts of lateral setae (Fig. 2K); antenna 1 peduncle is slightly longer than antenna 2 peduncle, rather than subequal; antenna 1 also has a reasonably dense brush of ventrally directed setae; a more prominent crista dentata is present (Fig. 2J); ischium of the minor cheliped lacks ventral denticulation; propodus of pereopod 3 has a distinct heel on the proximal corner of the lower margin whereas the same in *N. gigas* is more oval in shape; male pleopod 1 is present, but is unusually absent in *N. gigas*; female pleopod 1 is 2-segmented rather than 3-segmented; pleopods 3–5 have an embedded appendix interna (Fig. 2I), as opposed to a stubby projecting one (Fig. 2H); and finally, the telson has equal dimensions in *N. californiensis* and is broader than long in *N. gigas*.

Callianassa amboinensis sits in a clade remote from other taxa and may warrant separate generic status.

Cheraminae

A well-supported clade (here suggested to constitute the subfamily Cheraminae) is composed of six species of "*Callianassa*," *Poti gaucho*, *Cheramus profunda*, and *C. marginatus* (Figs. 3, 4). All except the last are missing significant character information (13% to 39%). "*Callianassa longicauda*," "*C. praedatrix*," and "*C. propinqua*" (all from the Southeast Asia region) share a similar rostral morphology, antennal proportions, denticulation of the ischium and merus of the major cheliped, and a distinctive tooth on the distal margin of the merus of the 3rd maxilliped (Fig. 2J). The importance of this latter character in linking these three taxa has previously been recognized (Sakai, 1988). Six of the nine species in this clade ("*Callianassa praedatrix*," "*C. propinqua*," "*C. rectangularis*," "*C. sibogae*," *Cheramus profunda*, and *C. marginatus*) are linked by the possession

of multiple spines on the distal and distolateral edges of the telson (Fig. 2D). Sakai (1970b) placed "*Callianassa spinophthalma*" in the subgenus *Cheramus*, and this genus name may be appropriate for all species in this clade.

Eucalliinae

A monophyletic clade comprises all the investigated members of the subfamily Eucalliinae, with the exception of *Calliax tooradin*. Although nearly a third of the character states are missing for *Calliax tooradin*, it differs from other members of its genus in nine characters (see Appendix 2, characters 1h, 5b, e, 7m–o, 8b–d). This species may not belong in *Calliax*, as previously suggested by Poore and Griffin (1979) and de Saint Laurent and Manning (1982). *Calliax punica* (the only member of this genus without missing data) appears as the sister taxon of *Eucalliax cearaensis*. The association has only 64% support, and a review of characters indicates that *C. punica* has no special affinities with *Eucalliax* that it does not share with its congeners. It differs from *E. cearaensis* in eight characters associated with abdominal somite setation, branchial formulae, and antennal, mouthpart, and pleopod morphology. However, Felder and Manning (1994) noted that *C. punica* shares the presence of one or two elongate setae on the propodus of pereopod 4 (not a character used in this analysis) with all known species of *Eucalliax*. The close relationship between *E. jonesi* and *E. quadracuta* was previously documented by Heard (1989), as were their differences from *Calliax lobata* and others. Differentiation of these two genera remain enigmatic.

Callichirinae

The paraphyletic Callichirinae are the least resolved subfamily and contain the only three polytomies in the consensus tree.

Sergio appears to be a paraphyletic genus with its seven species occurring on four clades. Character information is almost complete with only *Sergio guara* and *S. guaiqueri* each missing three characters associated with female pleopod morphology. The four-way split of the genus may be caused by a large polytomy (77% supported) at this point in the tree obscuring any characters that may unite the species. The three Brazilian species (*S. guara*, *S. mirim*, and *S. guassutinga*) occur

in three clades, while three species from Florida (*S. trilobata*, *S. guassutinga*, and *S. mericeae*) occur in two clades. The individual species groups can be identified by sets of characters, but these are not exclusive to each of the clades. *Sergio guara* and *S. guaiqueri* can be linked by eight characters (but are not sister taxa in this analysis); *S. mirim* and *S. trilobata* are linked by five characters; and *S. guassutinga*, *S. mericeae*, and *S. sulfureus* are linked by two characters. The latter two *Sergio* clades have 100% support, and the close association of *S. guassutinga*, *S. mericeae*, and *S. sulfureus* was supported by Manning and Felder (1995) and Lemaitre and Felder (1996). *Sergio* may be a paraphyletic genus, but it is possible that their uniting characters are outweighed by convergences elsewhere in this large cladogram.

A monophyletic clade (100% supported) containing 10 species of *Neocallichirus* also includes "*Callianassa*" *jousseamei*. Nearly half of the character data are missing for this species. However, *C. jousseamei* shares 39 of the remaining characters with *Neocallichirus*, of which four, associated with maxilliped 3 morphology and shape of the uropodal endopods, are not shared with *Callianassa* s.s. Biffar (1971b) noted that "*C. jousseamei* showed numerous morphological similarities with *Neocallichirus grandimana* (as *Callianassa branneri*) and *N. indica* (as *Callianassa indica*), so its membership of this genus seems certain.

Similarly, "*Callianassa*" *kraussi* shares a significant proportion of its characters with the members of *Callichirus* (seven exclusively), and the cladogram places it in this genus.

De Saint Laurent and Le Loeuff (1979) subdivided the then large genus *Callichirus* (15 species) into six categories, some upheld in the current analysis. Manning and Felder (1986) redefined *Callichirus* and restricted its species to *C. major*, *C. islagrande*, *C. seilacheri*, and *C. adamas*. They stated ". . . these four species comprise a distinctive group of species within the Callianassidae recognizable as a distinct genus, *Callichirus*." (Manning and Felder, 1986: 439). This analysis supports their statement, showing a distinct clade of these four taxa within *Callichirus*.

The two species of *Corallianassa* are sister taxa, and the genus is supported.

"*Callianassa*" *ranongensis* and "*Callichirus*" *turneranus* belong in the clade of seven of the eight published species of *Lepidophthalmus*, for they share a large proportion of their characters with members of this genus. Both can confidently be transferred to *Lepidophthalmus*.

The base of the Callianassidae is poorly resolved as most of its taxa have a high proportion of missing data (14% to 37%). "*Callianassa*" *tridentata*, with a full complement of character states, is sister taxon of the two investigated species of *Corallichirus* (*C. placidus* and *C. xuthus*). "*C.*" *tridentata* shares 71 characters with these two *Corallichirus* species, and it is possible that "*C.*" *tridentata* is a fourth species of *Corallichirus*.

Basally associated with *Corallichirus* is *Glypturus martensi*. With only 83% support for the association and with a significant proportion of the character states still missing, it is difficult to decide if this taxon is simply reflecting the lack of characters to link it with its congeners. It shares many character states with *Corallichirus* (including "*Callianassa*" *tridentata*) and differs in seven characters from the majority of *Glypturus*, of which only two are shared with *Corallichirus*. The seven character states in which *G. martensi* differs from the remaining species in *Glypturus* are: terminally rounded eyestalks (Fig. 1C) instead of pointed (Fig. 1D, E); antenna 1 peduncle is equal to or larger than antenna 2 peduncle rather than shorter; exopod of maxilliped 1 appears to be 2 or 3 segmented (Fig. 1G) and not consisting of a single segment (Fig. 1H); unlike the other species, the merus of maxilliped 3 projects beyond the articulation with the carpus (Fig. 2I, J); ventral margin of the merus of the minor cheliped has a convex margin (shared with *G. mucronata*) instead of a straight or toothed margin; fingers of the minor cheliped are longer than the propodal palm and not shorter than or equal to it; and finally, propodus of pereopod 3 would appear to lack the distinctive heel seen in the other five species (although this character state is ambiguously scored as oval or heeled in the data matrix, Appendix 3). *Glypturus* appears polyphyletic with or without the inclusion of "*G.*" *martensi*. *Glypturus karumba* and *G. mucronata* (both Australian and Southeast Asian species) form a small subclade separated from their congeners, a relationship supported by Poore and Griffin

(1979). These two species share a reduced but spinose rostrum, absence of anterolateral projections on the carapace, and absence of a scaphocerite on antenna 2. All are characters that differentiate them from the other *Glypturus* species studied (Poore and Suchanek, 1988).

"*Callianassa*" *audax*, at the base of the entire callianassid clade, may simply be a case of there being too much missing data to be effectively placed in the family. Of the 59 characters scored for "*C.*" *audax*, only four differ from the majority of the species currently in *Callianassa s.l.* Its basal position in the familial clade is enigmatic.

Paraglypturus calderus appears as the sister taxon to all other callianassids. It shares (among other characters) the presence of the anterodorsal thickening (dorsal plate) on the uropodal exopod with all other members of the family but possesses the primitive character of a large exopod on the third maxilliped. This latter character is observed in the out-group taxon, *Callianidea typa*, the ctenochelids *Gourretia* and *Anacalliax*, and the callianassid *Calliax tooradin*.

CONCLUSION

In spite of the high frequency of missing data (still to be obtained) the cladogram can be interpreted in a meaningful way which supports the existing systematic arrangements.

In the Ctenochelidae there is little justification for the subfamily arrangements recently proposed, and the genus *Gourretia* appears to be polyphyletic.

The traditional subfamily structure of the Callianassidae is revealed in the cladogram, and it is no surprise that one of the four subfamilies (defined in terms of plesiomorphies) is paraphyletic. The genus name *Callianassa* has been used loosely in the past, whereas smaller genera remained poorly defined or especially restricted to small, tightly diagnosed groups of species. There are two consequences of this. One is that our cladogram suggests the placement of several species of *Callianassa s.l.* in alternative monophyletic genera. This may necessitate the rediagnosis and/or subdivision of these genera. The other consequence is that *Callianassa* can be treated either as a very small genus (e.g., Manning and Felder, 1991a), in which case several new smaller genera need to be diag-

nosed, or as a large polyphyletic genus from which specialized clades (e.g., *Trypaea*, *Neotrypaea*) have derived.

Further progress on elucidating generic structure and relationships in these two families will be made by completing the data matrix, addition of new characters and taxa, and concentration on the better-defined clades in the tree presented here. Examination of specimens of type species of many of the included taxa should add most of the character data that is currently missing from the matrix. This character-state information, with the addition of new characters and the inclusion of newly described taxa, would form the basis for a more complete and rigorous analysis of these two thalassinidean families. Subsequent reanalysis of the individual clades presented in this consensus tree may lend support to the relationships shown and increase confidence in the systematic changes suggested.

We do not believe this cladogram is more than indicative of generic relationships, but hope it is a stimulus for further investigation.

ACKNOWLEDGEMENTS

The authors wish to acknowledge the assistance of B. Kensley and the late R. B. Manning (National Museum of Natural History, Smithsonian Institution) and the late A. B. Williams (National Oceanographic and Atmospheric Administration, National Marine Fisheries Service) for providing access to literature and specimens and advice on character-state assignments. Thanks are also extended to K. Fauchald (National Museum of Natural History, Smithsonian Institution) for facilitating the senior author's access to the Department of Invertebrate Zoology and its collections as a visiting researcher on two separate occasions in 1998 and 1999. The senior author was supported by an Australian Research Council Postdoctoral Research Fellowship (1996–1999). This paper is dedicated to R. B. Manning, in recognition of his many outstanding contributions to the taxonomy and systematics of the Thalassinidea and to the callianassoids of the Americas in particular. Credit is due also to his wife, Lilly King Manning, for preparing the illustrations that accompany many of her husband's papers.

LITERATURE CITED

- Barnard, K. H. 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps).—Annals of the South African Museum 38: 1–864.
 Bate, C. S. 1888. Report on the Crustacea Macrura collected by H.M.S. *Challenger* during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. *Challenger*.—Zoology 24: 1–192.
 Biffar, T. A. 1970. Three new species of callianassid shrimp (Decapoda, Thalassinidea) from the Western Atlantic.—Proceedings of the Biological Society of Washington 83: 35–50.

- . 1971a. New species of *Callianassa* (Decapoda, Thalassinidea) from the Western Atlantic.—*Crustaceana* 21: 225–236.
- . 1971b. The genus *Callianassa* (Crustacea, Decapoda, Thalassinidea) in South Florida, with keys to the Western Atlantic species.—*Bulletin of Marine Science* 21: 637–715.
- . 1973. The taxonomic status of *Callianassa occidentalis* Bate, 1888, and *C. batei* Borradaile, 1903 (Decapoda, Callianassidae).—*Crustaceana* 24: 224–230.
- Blanco Rambla, J. P., and I. Linero Arana. 1994. New records and new species of ghost shrimps (Crustacea: Thalassinidea) from Venezuela.—*Bulletin of Marine Science* 55: 16–29.
- , ———, and M. L. B. Lares. 1995. A new callianassid (Decapoda: Thalassinidea) from the southern Caribbean Sea.—*Proceedings of the Biological Society of Washington* 108: 102–106.
- Borradaile, L. A. 1903. On the classification of the Thalassinidea.—*Annals and Magazine of Natural History* (7) 12: 535–551.
- Chilton, C. 1906. Notes on the Callianassidae of New Zealand.—*Transactions of the New Zealand Institute* 39: 457–464.
- Dana, J. D. 1852. *Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carol Wilkes e classe reipublicae foederatae duce, lexit e descripsit.*—*Proceedings of the Academy of Natural Sciences, Philadelphia* 6: 6–28.
- Devine, C. E. 1966. Ecology of *Callianassa filholi* Milne-Edwards, 1878 (Crustacea, Thalassinidea).—*Transactions of the Royal Society of New Zealand* 8: 93–110.
- Dworschak, P. C. 1992. The Thalassinidea in the Museum of Natural History, Vienna; with some remarks on the biology of the species.—*Annalen Naturhistorischen Museums in Wien* 93(B): 189–238.
- Felder, D. L., and R. B. Manning. 1994. Description of the ghost shrimp *Eucalliax mcilhennyi*, new species, from South Florida, with reexamination of its known congeners (Crustacea: Decapoda: Callianassidae).—*Proceedings of the Biological Society of Washington* 107: 340–353.
- , and ———. 1995. *Neocallichirus cacahuete*, a new species of ghost shrimp from the Atlantic coast of Florida, with reexamination of *N. grandimana* and *N. lemaitrei* (Crustacea: Decapoda: Callianassidae).—*Proceedings of the Biological Society of Washington* 108: 477–490.
- , and ———. 1997. Ghost shrimps of the genus *Lepidophthalmus* from the Caribbean region, with description of *L. richardi*, new species, from Belize (Decapoda: Thalassinidea: Callianassidae).—*Journal of Crustacean Biology* 17: 309–331.
- , and ———. 1998. A new ghost shrimp of the genus *Lepidophthalmus* from the Pacific coast of Colombia (Decapoda: Thalassinidea: Callianassidae).—*Proceedings of the Biological Society of Washington* 111: 398–408.
- , and S. de A. Rodrigues. 1993. Reexamination of the ghost shrimp *Lepidophthalmus louisianensis* (Schmitt, 1935) from the northern Gulf of Mexico and comparison to *L. siriboia*, new species, from Brazil (Decapoda: Thalassinidea: Callianassidae).—*Journal of Crustacean Biology* 13: 357–376.
- Fulton, S. W., and F. E. Grant. 1906. Some little-known Victorian decapod Crustacea, with descriptions of new species.—*Proceedings of the Royal Society of Victoria* 19: 5–15.
- Gaillande, D. de, and J. P. Lagardère. 1966. Description de *Callianassa (Callichirus) lobata* nov. sp. (Crustacea Decapoda Callianassidae).—*Recueil des Travaux de la Station Marine d'Endoume* 40: 259–265.
- Heard, R. W. 1989. *Calliax jonesi*, n. sp. (Decapoda: Thalassinidea: Callianassidae) from the northwestern Bahamas.—*Gulf Research Reports* 8: 129–136.
- , and R. B. Manning. 1998. A new genus and species of ghost shrimp (Crustacea: Decapoda: Callianassidae) from the Atlantic Ocean.—*Proceedings of the Biological Society of Washington* 111: 883–888.
- Hernández-Aguilera, J. L. 1998. On a collection of thalassinids (Crustacea: Decapoda) from the Pacific Coast of Mexico, with description of a new species of the genus *Biffarius*.—*Ciencias Marinas* 24: 303–312.
- Holmes, S. J. 1904. On some new or imperfectly known species of West American Crustacea.—*Proceedings of the California Academy of Science, Zoology* 3: 307–328.
- Holthuis, L. B. 1967. A survey of the genus *Ctenocheles* (Crustacea: Decapoda, Callianassidae), with a discussion of its zoogeography and its occurrence in the Atlantic Ocean.—*Bulletin of Marine Science* 17: 376–385.
- . 1991. *FAO species catalogue. Vol. 13. Marine lobsters of the world.*—*FAO Fisheries Synopsis* No. 125, Volume 13: 1–292.
- Kazmi, Q. B., and M. A. Kazmi. 1992. A new species of a callianassid shrimp, *Neocallichirus manningi*, with a note on the genus *Neocallichirus* Sakai, 1988, not previously recorded from the Arabian Sea (Decapoda, Thalassinidea).—*Crustaceana* 63: 296–300.
- Kensley, B. 1974. The genus *Callianassa* (Crustacea, Decapoda, Thalassinidea) from the west coast of South Africa with a key to South African species.—*Annals of the South African Museum* 62: 265–278.
- . 1975. Records of mud-prawns (genus *Callianassa*) from South Africa and Mauritius (Crustacea, Decapoda, Thalassinidea).—*Annals of the South African Museum* 69: 47–58.
- , and R. W. Heard. 1991. An examination of the shrimp family Callianideidae (Crustacea: Decapoda: Thalassinidea).—*Proceedings of the Biological Society of Washington* 104: 493–537.
- Kishinouye, K. 1926. Two rare and remarkable forms of macrurous Crustacea from Japan.—*Annotationes Zoologicae Japonenses* 11: 63–70.
- Kossmann, R. 1880. *Reise in die Küstengebiete des Rothen Meeres, volume 2, part, 1, section III, Malacostraca.*—*Zoologische Ergebnisse einer im Auftrage der königlichen Academie der Wissenschaften zu Berlin* 1880: 67–140.
- Leach, W. E. 1814. *Crustaceology.*—*Edinburgh Encyclopedia* 7: 383–437.
- Le Loeuff, P., and A. Intès. 1974. Les Thalassinidea (Crustacea, Decapoda) du Golfe de Guinée. *Systématique-Écologie.*—*Cahiers O.R.S.T.O.M., série Océanographique* 12: 17–69.
- Lemaitre, R., and D. R. Felder. 1996. A new species of ghost shrimp of the genus *Sergio* Manning and Lemaitre, 1994 (Crustacea: Decapoda: Callianassidae) from the Caribbean coast of Colombia.—*Proceedings of the Biological Society of Washington* 109: 453–463.
- , and G. E. Ramos. 1992. A collection of Thalassinidea (Crustacea: Decapoda) from the Pacific coast

- of Colombia, with description of a new species and a checklist of eastern Pacific species.—Proceedings of the Biological Society of Washington 105: 343–358.
- , and S. de A. Rodrigues. 1991. *Lepidophthalmus sinuensis*: a new species of ghost shrimp (Decapoda: Thalassinidea: Callianassidae) of importance to the commercial culture of penaeid shrimps on the Caribbean coast of Colombia, with observations on its ecology.—Fishery Bulletin, U.S. 89: 623–630.
- Maddison, W. P., and D. R. Maddison. 1992. MacClade (Version 3). Analysis of phylogeny and character evolution. Sinauer Associates, Inc. Sunderland, Massachusetts, U.S.A.
- Man, J. G. de. 1928. A contribution to the knowledge of twenty-two species and three varieties of the genus *Callianassa* Leach.—Capita Zoologica II(6): 5–56.
- Manning, R. B. 1987. Notes on Western Atlantic Callianassidae (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 100: 386–401.
- . 1988. The status of *Callianassa hartmeyeri* Schmitt, 1935, with description of *Corallianassa xutha* from the west coast of America (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 101: 883–889.
- . 1992. A new genus for *Corallianassa xutha* Manning (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 105: 571–574.
- . 1993. Two new species of *Neocallichirus* from the Caribbean Sea (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 106: 106–114.
- , and D. L. Felder. 1986. The status of the callianassid genus *Callichirus* Stimpson, 1866 (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 99: 437–443.
- , and ———. 1991a. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 104: 764–792.
- , and ———. 1991b [1992]. *Gilvossius*, a new genus of callianassid shrimp from the eastern United States (Crustacea: Decapoda: Thalassinidea).—Bulletin of Marine Science 49: 558–561.
- , and ———. 1995. Description of the ghost shrimp *Sergio mericeae*, a new species from south Florida, with reexamination of *S. guassutina* (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 108: 266–280.
- , and R. W. Heard. 1986. Additional records of *Callianassa rathbunae* Schmitt, 1935, from Florida and the Bahamas (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 99: 347–349.
- , and R. Lemaitre. 1993 [1994]. *Sergio*, a new genus of ghost shrimp from the Americas (Crustacea: Decapoda: Callianassidae).—Nauplius, Rio Grande 1: 39–43.
- , and A. Tamaki. 1998. A new genus of ghost shrimp from Japan (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 111: 889–892.
- Martin, J. W., and L. G. Abele. 1986. Phylogenetic relationships of the genus *Aegla* (Decapoda: Anomura: Aegliidae), with comments on anomuran phylogeny.—Journal of Crustacean Biology 6: 576–616.
- Matsuzawa, K., and K.-I. Hayashi. 1997. Male of *Ctenocheles balssi* (Crustacea, Decapoda, Callianassidae) from off Muroto Peninsula, Shikoku, Japan.—Journal of National Fisheries University 46: 39–46.
- Ngoc-Ho, N. 1991. Sur quelques Callianassidae et Upogebiidae de Nouvelle-Calédonie (Crustacea, Thalassinidea). Pp. 281–311 in B. Richer de Forges, ed. Le benthos des fonds meubles des lagons de Nouvelle Calédonie. Vol. 1.
- . 1994. Some Callianassidae and Upogebiidae from Australia with description of four new species (Crustacea: Decapoda: Thalassinidea).—Memoirs of the Museum of Victoria 54: 51–78.
- . 1995. Une espèce nouvelle de *Neocallichirus* aux îles Tuamotu, Polynésie française (Crustacea, Decapoda, Thalassinidea).—Bulletin du Muséum national d'Histoire naturelle, Paris, série 4, 17: 211–218.
- Paul, D. H. 1989. A neurophylogenetist's view of decapod Crustacea.—Bulletin of Marine Science 45: 487–504.
- Poore, G. C. B. 1975. Systematics and distribution of *Callianassa* (Crustacea, Decapoda, Macrura) from Port Phillip Bay, Australia, with descriptions of two new species.—Pacific Science 29: 197–209.
- . 1994. A phylogeny of the families of Thalassinidea (Crustacea: Decapoda) with keys to families and genera.—Memoirs of the Museum of Victoria 54: 79–120.
- . 1997. A review of the thalassinidean families Callianassidae Kossmann, Micheleidae Sakai, and Thomassiniidae De Saint Laurent (Crustacea, Decapoda) with descriptions of fifteen new species.—Zoosystema 19: 345–420.
- , and D. J. G. Griffin. 1979. The Thalassinidea (Crustacea: Decapoda) of Australia.—Records of the Australian Museum 32: 217–321.
- , and T. H. Suchanek. 1988. *Glypturus motupore*, a new callianassid shrimp (Crustacea: Decapoda) from Papua New Guinea with notes on its ecology.—Records of the Australian Museum 40: 197–204.
- Powell, A. W. B. 1949. New species of Crustacea from New Zealand of the genera *Scyllarus* and *Ctenocheles* with notes on *Lyreidus tridentatus*.—Records of the Auckland Institute and Museum 3: 368–371.
- Rabalais, N. N., S. A. Holt, and R. W. Flint. 1981. Mud shrimps (Crustacea, Decapoda, Thalassinidea) of the northwestern Gulf of Mexico.—Bulletin of Marine Science 31: 96–115.
- Rodrigues, S. de A. 1971. Mud shrimps of the genus *Callianassa* Leach from the Brazilian coast (Crustacea, Decapoda).—Arquivos de Zoologia, Sao Paulo 20: 191–223.
- . 1978. *Ctenocheles holthuisi* (Decapoda, Thalassinidea), a new remarkable mud shrimp from the Atlantic Ocean.—Crustaceana 34: 113–120.
- , and R. B. Manning. 1992a. Two new callianassid shrimps from Brazil (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 105: 324–330.
- , and ———. 1992b. *Poti gaucho*, a new genus and species of ghost shrimp from southern Brazil (Crustacea: Decapoda: Callianassidae).—Bulletin of Marine Science 51: 9–13.
- Saint Laurent, M. de. 1973. Sur la systématique et la phylogénie des Thalassinidea: Définition des familles des Callianassidae et des Upogebiidae et diagnose de cinq genres nouveaux (Crustacea Decapoda).—Comptes rendus de l'Académie de Science, Paris (D) 277(1974): 513–516.

- . 1979. Sur la classification et la phylogénie des Thalassinides: Définitions de la superfamilles des Axioidea, de la sous-famille des Thomassiniinae et Deux genres nouveaux (Crustacea Decapoda).—Comptes rendus de l'Académie de Science, Paris (D) 288: 1395–1397.
- , and B. Bozic. 1972. Diagnoses et tableau de détermination des callianasses de l'Atlantique nord oriental et de Méditerranée (Crustacea, Decapoda, Callianassidae).—*Thalassia Jugoslavica* 8: 15–40.
- , and P. Le Loeuff. 1979. Crustacés Décapodes Thalassinidea. I. Upogebiidae et Callianassidae.—*Résultats Scientifiques des Campagnes de la CALYPSO* 11: 29–101.
- , and R. B. Manning. 1982. *Calliax punica*, espèce nouvelle de Callianassidae (Crustacea, Decapoda) des eaux méditerranéennes.—*Quaderni del Laboratorio di Tecnologia della Pesca* 3: 211–224.
- Sakai, K. 1966. On *Callianassa (Callichirus) novaebritanniae* Borradaile (Thalassinidea, Crustacea) from Japan.—*Journal of the Faculty of Agriculture, Kyushu University* 14: 161–171.
- . 1967a. Three new species of Thalassinidea (Decapoda, Crustacea) from Japan.—*Records of the Crustacea of Japan* 3: 39–51.
- . 1967b. Three new species of Thalassinidea (Decapoda, Crustacea) from South–West Japan.—*Publications of the Seto Marine Biological Laboratory* 15: 319–328.
- . 1970a. Supplementary description of *Callianassa (Callichirus) tridentata* von Martens (Crustacea, Thalassinidea). Noona Dan Papers No. 97.—*Publications of the Seto Marine Biological Laboratory* 17: 393–401.
- . 1970b. A small collection of thalassinids from the waters around Tsushima Islands, Japan, including a new species of *Callianassa* (Crustacea, Anomura).—*Publications of the Seto Marine Biological Laboratory* 18: 37–47.
- . 1983. On a new species of the genus *Callianassa* (Crustacea, Decapoda) from Thailand.—*Researches on Crustacea* 12: 111–115.
- . 1984. Some thalassinideans (Decapoda: Crustacea) from Heron Is., Queensland, Eastern Australia, and a new species of *Gourretia* from East Africa.—*The Beagle* 1: 95–108.
- . 1987a. On *Callianassa ranongensis* (Thalassinidea: Decapoda: Crustacea) from Halmahera, Indonesia.—*Reports of the Usa Marine Biological Institute, Kochi University* 9: 45–49.
- . 1987b. Two new Thalassinidea (Crustacea: Decapoda) from Japan, with the biogeographic distribution of the Japanese Thalassinidea.—*Bulletin of Marine Science* 41: 296–308.
- . 1988. A new genus and five new species of Callianassidae (Crustacea: Decapoda: Thalassinidea) from Northern Australia.—*The Beagle* 5: 51–69.
- . 1992. Notes on some species of Thalassinidea from French Polynesia (Crustacea: Decapoda).—*Senckenbergiana Maritima* 22: 211–216.
- . 1999. Redescription of *Ctenocheles balssi* Kishinouye, 1926, with comments on its systematic position and establishment of a new subfamily Gourretiinae (Decapoda, Callianassidae).—*Crustaceana* 72: 85–97.
- Sandeman, D. C., G. Scholtz, and R. E. Sandeman. 1993. Brain evolution in decapod Crustacea.—*The Journal of Experimental Zoology* 265: 112–133.
- Scholtz, G., and S. Richter. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca).—*Zoological Journal of the Linnean Society* 113: 289–328.
- Spears, T. and L. G. Abele. 1988. Phylogenetic relationships of crustacean anomurans based on partial 18S rRNA nucleotide sequences.—*American Zoologist* 29: 25A. [Abstract.]
- Stimpson, W. 1866. Descriptions of new genera and species of macrurous Crustacea from the coasts of North America.—*Proceedings of the Chicago Academy of Science* 1: 46–68.
- Swofford, D. L. 1993. PAUP: Phylogenetic analysis using parsimony, version 3.1.1 (computer program distributed by the Illinois Natural History Survey, Champaign, Illinois, U.S.A).
- Tirmizi, N. M. 1977. A redescription of the holotype species of *Callianassa mucronata* Strahl, 1861 (Decapoda, Thalassinidea).—*Crustaceana* 32: 21–26.
- Tudge, C. C. 1997. Phylogeny of the Anomura (Decapoda, Crustacea): spermatozoa and spermatophore morphological evidence.—*Contributions to Zoology* 67: 125–141.
- Türkyay, M., and K. Sakai. 1995. Decapod crustaceans from a volcanic hot spring in the Marianas.—*Senckenbergiana Maritima* 26: 25–35.
- Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C. 550 pp.

RECEIVED: 21 April 1999.

ACCEPTED: 21 December 1999.

NOTE ADDED IN PROOF

Three new genera and eight new species have been added to the callianassid fauna since this paper was first submitted: *Grynaminna* Poore, 2000 (type species *Grynaminna tamakii* Poore, 2000); *Podocallichirus* Sakai, 1999a (type species *Callianassa madagassa* Lenz and Richters, 1881); *Pseudobiffarius* Heard and Manning, 2000 (type species *Pseudobiffarius caesari* Heard and Manning, 2000); *Callianassa gruneri* Sakai, 1999a; *Callianassa ngochoae* Sakai, 1999a; *Callianassa poorei* Sakai, 1999b (probably a species of *Biffarius*); *Callianassa whitei* Sakai, 1999a; *Calliax doerjesti* Sakai, 1999a; *Grynaminna tamakii* Poore, 2000; *Neocallianassa kempii* Sakai, 1999a; *Neocallichirus raymanni* Blanco Rambla and Lemaitre, 1999.

Sakai's (1999a) synopsis of the Callianassidae has reached conclusions about the taxonomy of the family very different from those of our phylogenetic analysis and from those recently proposed (e.g., Manning and Felder, 1991a; Poore, 1994). Sakai recognizes four subfamilies of which only the Eucalliinae is similar to that subfamily in our analysis. Within this subfamily he has synonymised *Eucalliiax* with *Calliax* and included *Paraglypturus*. The four species assigned to this genus include two (*Calliax tooradin* and *Paraglypturus calderus*) which our analysis places basally within the Callianassidae clade and a third (*C. novaebritanniae*) which clusters with other species of *Calliax*.

The second of Sakai's subfamilies Calliapaguropsinae, for *Calliapaguropsis charcoti* only, is an unusual callianassid, hitherto poorly described and not included in our analysis.

The third subfamily, Anacalliinae, was erected in Ctenochelidae by Manning and Felder and treated within Callianassidae by Poore (1994). It contains a single genus which our analysis suggests is a highly derived clade of Ctenochelidae.

Sakai (1999a) treats all remaining callianassids as members of the Callianassinae. He did not recognise Cheraminae or Callichirinae. The former is a small, clearly monophyletic clade. The latter is probably paraphyletic but clearly defined (Poore, 2000).

Sakai's treatment of genera diverges from the results of our cladistic analysis. We agree on the monophyly of *Neocallichirus* but not on the assignment of some species of *Glypturus* to it. His synonymy of *Corallianassa* with *Glypturus* is not supported in our phylogeny. We agree too on the monophyly of *Lepidophthalmus*. Sakai's division of *Callichirus* into two genera, *Callichirus* and *Podocallichirus*, is not inconsistent with our analysis but is not supported by a clear dichotomy between species groups.

All remaining ten genera were synonymised by Sakai into *Callianassa*. While he recognised that some genera are "fundamentally different" from the type species of *Callianassa* or cited "the traditional generic criterion" to define this genus and highlighted differences in some characters, he appears so influenced by similarities in others and the presence of "intermediate forms" that synonymy seemed the simplest solution. Results of our phylogenetic analysis do not indicate monophyly of a large genus *Callianassa* but rather numerous monophyletic clades of few or several species, each supported by one or more synapomorphies. Generic names must be found for these, and we conclude that those erected so far should stand for the time being.

Blanco Rambla, J. P., and R. Lemaitre. 1999. *Neocallichirus raymanni*, a new species of ghost shrimp from the northeastern coast of Venezuela (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 112: 768–777.

Heard, R., and R. B. Manning. 2000. A new genus and species of ghost shrimp from Tobago, West Indies (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 113: 71–77.

Poore, G. C. B. 2000. A new genus and species of callianassid ghost shrimp from Kyushu, Japan (Decapoda: Thalassinidea).—Journal of Crustacean Biology 20 (Special no. 2): 150–156.

Sakai, K. 1999a. Synopsis of the family Callianassidae, with keys subfamilies, genera and species, and the description of new taxa (Crustacea: Decapoda: Thalassinidea).—Zoologische Verhandlungen, Leiden 326: 1–152.

———. 1999b. A new species, *Callianassa poorei*, sp. nov. (Decapoda: Crustacea: Callianassidae) from Tasmania.—Journal of the Marine Biological Association of the United Kingdom 79: 373, 374.

Appendix 1. List of valid species in the Ctenochelidae and Callianassidae, arranged according to their most recent revisions. * indicates taxa used in this analysis; sources of information, reference and/or museum collections are given in square brackets. Species in new combinations are in curly brackets. Collections are from USNM (National Museum of Natural History, Washington, D.C., U.S.A.) and NMV (Museum Victoria, Melbourne, Australia).

Family: Callianideidae Kossmann, 1880

Genus *Callianidea* Kossmann, 1880

**Callianidea typa* Milne Edwards, 1837 TYPE SPECIES [Poore, 1994, 1997; Kensley and Heard, 1991; USNM]

Family: Ctenochelidae Manning and Felder, 1991a

Subfamily Anacalliinae Manning and Felder, 1991a (as Anacalliinae)

Genus *Anacalliax* de Saint Laurent, 1973

**Anacalliax agassizi* (Biffar, 1971) [Biffar, 1971a]

**Anacalliax argentinensis* (Biffar, 1971) TYPE SPECIES [Biffar, 1971a; Manning and Felder, 1991a; USNM]

Subfamily Callianopsinae Manning and Felder, 1991a

Genus *Callianopsis* de Saint Laurent, 1973

**Callianopsis goniophthalma* Rathbun, 1902 TYPE SPECIES [Manning and Felder, 1991a; USNM]

Subfamily Ctenochelinae Manning and Felder, 1991a

Genus *Ctenocheles* Kishinouye, 1926

**Ctenocheles balssi* Kishinouye, 1926 TYPE SPECIES [Kishinouye, 1926; Matsuzawa and Hayashi, 1997; Sakai, 1999]

Ctenocheles collini Ward, 1945

**Ctenocheles holthuisi* Rodrigues, 1978 [Rodrigues, 1978]

Ctenocheles leviceps Rabalais, 1979

**Ctenocheles maorianus* Powell, 1949 [Powell, 1949; Dworschak, 1992; USNM]

Ctenocheles serrifrons Le Loeuff and Intès, 1974

Genus *Dawsonius* Manning and Felder, 1991a

**Dawsonius latispina* (Dawson, 1967) TYPE SPECIES [Biffar, 1971b; Manning and Felder, 1991a; USNM]

Genus *Gourettia* de Saint Laurent, 1973

Gourettia barracuda Le Loeuff and Intès, 1974

**Gourettia biffari* Blanco Rambla and Linero Arana, 1994 [Blanco Rambla and Linero Arana, 1994; USNM]

Gourettia coolibah Poore and Griffin, 1979

Gourettia crosnieri Ngoc-Ho, 1991

**Gourettia denticulata* (Lutze, 1937) TYPE SPECIES [de Saint Laurent and Bozic, 1972; Le Loeuff and Intès, 1974; USNM]

Gourettia lahouensis Le Loeuff and Intès, 1974

**Gourettia laresi* Blanco Rambla and Linero Arana, 1994 [Blanco Rambla and Linero Arana, 1994; USNM]

Gourettia manihinae Sakai, 1984

Genus *Paracalliax* de Saint Laurent, 1979

**Paracalliax bollorei* de Saint Laurent, 1979 TYPE SPECIES [de Saint Laurent and Le Loeuff, 1979]

Family: Callianassidae Dana, 1852

Subfamily Callianassinae Dana, 1852

Genus *Biffarius* Manning and Felder, 1991a

**Biffarius arenosa* (Poore, 1975) [Poore, 1975; Poore and Griffin, 1979; NMV; USNM]

**Biffarius australis* (Kensley, 1974), new combination

- **Biffarius biformis* (Biffar, 1971) TYPE SPECIES [Biffar, 1971a; Williams, 1984; Manning and Felder, 1991a; USNM]
- **Biffarius ceramica* (Fulton and Grant, 1906) [Fulton and Grant, 1906; Poore and Griffin, 1979; NMV; USNM]
- Biffarius debilis* Hernández-Aguilera, 1998
- **Biffarius delicatulus* Rodrigues and Manning, 1992 [Rodrigues and Manning, 1992a; USNM]
- **Biffarius diaphora* (Le Loeuff and Intès, 1974), new combination
- **Biffarius fragilis* (Biffar, 1970) [Biffar, 1970, 1971b; USNM]
- **Biffarius lewtonae* (Ngoc-Ho, 1994), new combination
- **Biffarius limosa* (Poore, 1975), new combination
- Genus *Callianassa* Leach, 1814
- Callianassa abdominalis* White, 1847
- **Callianassa acutirostella* Sakai, 1988 [Sakai, 1988]
- **Callianassa amboinensis* de Man, 1888 [de Man, 1928; Poore and Griffin, 1979; Sakai, 1984; Ngoc-Ho, 1991]
- Callianassa assimilis* (de Man, 1928)
- **Callianassa audax* de Man, 1911 [de Man, 1928; Dworschak, 1992]
- {**Callianassa australis* Kensley, 1974 [Kensley, 1974; de Saint Laurent and Le Loeuff, 1979; USNM]—removed to *Biffarius*}
- Callianassa bouvieri* Nobili, 1904
- Callianassa brevicaudata* (A. Milne-Edwards, 1870)
- **Callianassa caledonica* Ngoc-Ho, 1991 [Ngoc-Ho, 1991]
- Callianassa calmani* Nobili, 1904
- Callianassa candida* (Olivi, 1792)
- Callianassa carinaedoris* White, 1847
- Callianassa chilensis* A. Milne-Edwards, 1860
- Callianassa convexa* de Saint Laurent and Le Loeuff, 1979
- Callianassa coutierei* (Nobili, 1904)
- Callianassa cristata* (Borradaile, 1910)
- {**Callianassa diaphora* Le Loeuff and Intès, 1974 [Le Loeuff and Intès, 1974; de Saint Laurent and Le Loeuff, 1979]—removed to *Biffarius*}
- **Callianassa filholi* A. Milne-Edwards, 1878 [Chilton, 1906; Devine, 1966; NMV; USNM]
- Callianassa gilchristi* Barnard, 1947
- Callianassa grandidieri* Coutière, 1899
- Callianassa gravieri* Nobili, 1906
- Callianassa intermedia* de Man, 1905
- **Callianassa jocularis* de Man, 1905 [Poore and Griffin, 1979; Ngoc-Ho, 1991; USNM]
- {**Callianassa jousseumei* Nobili, 1904 [de Man, 1928; Dworschak, 1992]—removed to *Neocallichirus*}
- Callianassa kewalramanii* (Sankolli, 1971)
- {**Callianassa kraussi* Stebbing, 1900 [Barnard, 1950; Holthuis, 1991; USNM]—removed to *Callichirus*}
- {**Callianassa lewtonae* Ngoc-Ho, 1994 [Ngoc-Ho, 1994]—removed to *Biffarius*}
- Callianassa lignicola* Alcock and Anderson, 1899
- Callianassa lobetobensis* de Man, 1905
- {**Callianassa longicauda* Sakai, 1967 [Sakai, 1967b]—removed to *Cheramus*}
- Callianassa madagassa* Lenz and Richters, 1881
- Callianassa maldivensis* Borradaile, 1904
- **Callianassa marchali* Le Loeuff and Intès, 1974 [Le Loeuff and Intès, 1974; de Saint Laurent and Le Loeuff, 1979]
- Callianassa masoomi* (Tirmizi, 1970)
- **Callianassa mauritiana* Miers, 1882 [de Man, 1928; Kensley, 1975]
- Callianassa maxima* A. Milne-Edwards, 1870
- Callianassa modesta* de Man, 1905
- Callianassa nakasonei* Sakai, 1967 [Sakai, 1967a]
- Callianassa parva* Edmondson, 1944
- Callianassa parvula* Sakai, 1988
- **Callianassa pixii* Kensley, 1975 [Kensley, 1975]
- Callianassa pontica* Czerniavsky, 1884
- {**Callianassa praedatrix* de Man, 1905 [de Man, 1928; Sakai, 1988; Ngoc-Ho, 1994]—removed to *Cheramus*}
- {**Callianassa propinqua* de Man, 1905 [de Man, 1928; Ngoc-Ho, 1991]—removed to *Cheramus*}
- Callianassa pugnatrix* de Man, 1905
- Callianassa pygmaea* de Man, 1928
- {**Callianassa ranongensis* Sakai, 1983 [Sakai, 1983, 1987a; USNM]—removed to *Lepidophthalmus*}
- {**Callianassa rectangularis* Ngoc-Ho, 1991 [Ngoc-Ho, 1991]—removed to *Cheramus*}
- Callianassa rosae* Nobili, 1906
- Callianassa rotundicaudata* Stebbing, 1902
- {**Callianassa sibogae* de Man, 1905 [de Man, 1928; Ngoc-Ho, 1994]—removed to *Cheramus*}
- {**Callianassa spinophthalma* Sakai, 1970 [Sakai, 1970b]—removed to *Cheramus*}
- **Callianassa subterranea* (Montagu, 1808) TYPE SPECIES [de Man, 1928; de Saint Laurent and Bozic, 1972; de Saint Laurent and Le Loeuff, 1979; Manning and Felder, 1991a; USNM]
- Callianassa tonkinae* Grebenjuk, 1975
- {**Callianassa tridentata* Von Martens, 1868 [de Man, 1928; Sakai, 1970a; USNM]—removed to *Corallichirus*}
- **Callianassa tyrrhena* (Petagna, 1792) [de Saint Laurent and Bozic, 1972; Holthuis, 1991; USNM]
- Callianassa variabilis* Edmondson, 1944
- Callianassa vigilax* de Man, 1916
- Callianassa winslowi* (Edmondson, 1944)
- Genus *Calliapagurops* de Saint Laurent, 1973
- Calliapagurops charcoti* de Saint Laurent, 1973 TYPE SPECIES
- Genus *Gilvossius* Manning and Felder, 1991b
- **Gilvossius setimanus* (DeKay, 1844) TYPE SPECIES [Manning and Felder, 1991b; USNM]
- Genus *Necallianassa* Heard and Manning, 1998
- Necallianassa acanthura* (Caroli, 1946)
- **Necallianassa berylae* Heard and Manning, 1998 TYPE SPECIES [Heard and Manning, 1998]
- Necallianassa truncata* (Giard and Bonnier, 1890)
- Genus *Neotrypaea* Manning and Felder, 1991a
- Neotrypaea biffari* (Holthuis, 1991)
- **Neotrypaea californiensis* (Dana, 1854) TYPE SPECIES [Holthuis, 1991; Manning and Felder, 1991a; Dworschak, 1992; USNM]
- **Neotrypaea gigas* (Dana, 1852) [Holthuis, 1991; Dworschak, 1992; USNM]
- Neotrypaea rochei* (Bouvier, 1895)
- Neotrypaea uncinata* (H. Milne Edwards, 1837)
- Genus *Nihonotrypaea* Manning and Tamaki, 1998
- **Nihonotrypaea harmandi* (Bouvier, 1901) [de Man, 1928; Manning and Tamaki, 1998; USNM]
- **Nihonotrypaea japonica* (Ortmann, 1891) TYPE SPECIES [de Man, 1928; Manning and Tamaki, 1998; USNM]
- **Nihonotrypaea petalura* (Stimpson, 1860) [Holthuis, 1991; USNM]
- Genus *Notiax* Manning and Felder, 1991a
- **Notiax brachyophthalma* (A. Milne-Edwards, 1870) TYPE SPECIES [Manning and Felder, 1991a; USNM]

- Genus *Poti* Rodrigues and Manning, 1992
 {**Poti gauchoi* Rodrigues and Manning, 1992 TYPE SPECIES [Rodrigues and Manning, 1992b; USNM]—removed to Cheraminae}
- Genus *Trypaea* Dana, 1852
 **Trypaea australiensis* (Dana, 1852) TYPE SPECIES [Poore and Griffin, 1979; Holthuis, 1991; Poore, 1994; NMV; USNM]
- Subfamily Callichirinae Manning and Felder, 1991a
 Genus *Callichirus* Stimpson, 1866
 **Callichirus adamas* (Kensley, 1974) [Kensley, 1974; de Saint Laurent and Le Loeuff, 1979]
 **Callichirus balssi* (Monod, 1933) [Le Loeuff and Intès, 1974]
 **Callichirus foresti* Le Loeuff and Intès, 1974 [Le Loeuff and Intès, 1974]
Callichirus garthi (Retamal, 1975)
 **Callichirus guineensis* (de Man, 1928) [de Man, 1928; Le Loeuff and Intès, 1974]
Callichirus intesi de Saint Laurent and Le Loeuff, 1979
 **Callichirus islagrande* (Schmitt, 1935) [Manning and Felder, 1986; NMV; USNM]
 **Callichirus kraussi* (Stebbing, 1910), new combination
 **Callichirus major* (Say, 1818) TYPE SPECIES [de Man, 1928; Rodrigues, 1971; Williams, 1984; Manning and Felder, 1986; NMV; USNM]
Callichirus monodi de Saint Laurent and Le Loeuff, 1979
Callichirus pentagonocephala (Rossignol, 1962)
 **Callichirus seilacheri* (Bott, 1955) [Manning and Felder, 1986, 1991a; USNM]
Callichirus tenuimanus de Saint Laurent and Le Loeuff, 1979
 {**Callichirus turneranus* (White, 1861) [de Man, 1928; Le Loeuff and Intès, 1974; de Saint Laurent and Le Loeuff, 1979; Holthuis, 1991]—removed to *Lepidophthalmus*}
- Genus *Corallianassa* Manning, 1987
Corallianassa articulata (Rathbun, 1906)
Corallianassa borradalei (de Man, 1928)
 **Corallianassa collaroy* (Poore and Griffin, 1979) [Poore and Griffin, 1979; Sakai, 1992]
 **Corallianassa longiventris* (A. Milne-Edwards, 1870) TYPE SPECIES [de Man, 1928; Biffar, 1971b; USNM]
- Genus *Corallichirus* Manning, 1992
Corallichirus hartmeyeri (Schmitt, 1935)
 **Corallichirus placidus* (de Man, 1905) [de Man, 1928; Manning, 1988]
 **Corallichirus tridentatus* (Von Martens, 1868), new combination
 **Corallichirus xuthus* (Manning, 1988) TYPE SPECIES [Manning, 1988, 1992; USNM]
- Genus *Glypturus* Stimpson, 1866
 **Glypturus acanthochirus* Stimpson, 1866 TYPE SPECIES [Biffar, 1971b; Manning, 1987; USNM]
 **Glypturus armatus* (A. Milne-Edwards, 1870) [Kensley, 1975; Poore and Suchanek, 1988]
 **Glypturus karumba* (Poore and Griffin, 1979) [Poore and Griffin, 1979]
Glypturus laurac (de Saint Laurent, 1984)
 **Glypturus martensi* (Miers, 1884) [Poore and Griffin, 1979; Sakai, 1984; Dworschak, 1992]
 **Glypturus motupore* Poore and Suchanek, 1988 [Poore and Suchanek, 1988; NMV; USNM]
 **Glypturus mucronata* (Strahl, 1861) [de Man, 1928; Tirmizi, 1977; Poore and Griffin, 1979; Dworschak, 1992]
- Genus *Lepidophthalmus* Holmes, 1904
 **Lepidophthalmus bocourti* (A. Milne-Edwards, 1870) TYPE SPECIES [Lemaitre and Ramos, 1992; USNM]
Lepidophthalmus eiseni (Holmes, 1904)
 **Lepidophthalmus jamaicensis* (Schmitt, 1935) [Rodrigues, 1971; Manning and Felder, 1991a; Felder and Manning, 1997; USNM]
 **Lepidophthalmus louisianensis* (Schmitt, 1935) [Dworschak, 1992; Felder and Rodrigues, 1993; USNM]
 **Lepidophthalmus rafai* Felder and Manning, 1998 [Felder and Manning, 1998; USNM]
 **Lepidophthalmus ranongensis* (Sakai, 1983), new combination
 **Lepidophthalmus richardi* Felder and Manning, 1997 [Felder and Manning, 1997; USNM]
 **Lepidophthalmus sinuensis* Lemaitre and Rodrigues, 1991 [Lemaitre and Rodrigues, 1991; Felder and Manning, 1997; USNM]
 **Lepidophthalmus siriboia* Felder and Rodrigues, 1993 [Felder and Rodrigues, 1993; USNM]
 **Lepidophthalmus turneranus* (White, 1861), new combination
- Genus *Neocallichirus* Sakai, 1988
 **Neocallichirus cacahuatense* Felder and Manning, 1995 [Felder and Manning, 1995; USNM]
 **Neocallichirus caechabitor* Sakai, 1988 [Sakai, 1988]
 **Neocallichirus darwinensis* Sakai, 1988 [Sakai, 1988]
Neocallichirus denticulatus Ngoc-Ho, 1994
 **Neocallichirus grandimana* (Gibbes, 1850) [Manning and Felder, 1991a; Lemaitre and Ramos, 1992; Felder and Manning, 1995; USNM]
 **Neocallichirus horneri* Sakai, 1988 TYPE SPECIES [Sakai, 1988]
 **Neocallichirus indica* de Man, 1905 [de Man, 1928; Kensley, 1975]
 **Neocallichirus jousseumei* (Nobili, 1904), new combination
 **Neocallichirus lemaitrei* Manning, 1993 [Manning, 1993; Felder and Manning, 1995; USNM]
 {**Neocallichirus limosa* (Poore, 1975) [Poore, 1975; Poore and Griffin, 1979; NMV; USNM]—removed to *Biffarius*}
- Neocallichirus manningi* Kazmi and Kazmi, 1992
Neocallichirus moluccensis (de Man, 1905)
Neocallichirus natalensis (Barnard, 1947)
 **Neocallichirus nickellae* Manning, 1993 [Manning, 1993; USNM]
Neocallichirus pachyductylus (A. Milne-Edwards, 1870)
 **Neocallichirus rathbunae* (Schmitt, 1935) [Biffar, 1971b; Manning and Heard, 1986; USNM]
 **Neocallichirus sassandrensis* (Le Loeuff and Intès, 1974) [Le Loeuff and Intès, 1974]
Neocallichirus taiaro Ngoc-Ho, 1995
- Genus *Paraglypturus* Türkay and Sakai, 1995
 **Paraglypturus calderus* Türkay and Sakai, 1995 TYPE SPECIES [Türkay and Sakai, 1995]
- Genus *Sergio* Manning and Lemaitre, 1993
 **Sergio guaiqueri* Blanco Rambla, Linero Arana, and Lares M., 1995 [Blanco Rambla *et al.*, 1995; USNM]
 **Sergio guara* (Rodrigues, 1971) [Rodrigues, 1971; Manning and Lemaitre, 1993; USNM]
 **Sergio guassutanga* (Rodrigues, 1971) TYPE SPECIES [Rodrigues, 1971; Biffar, 1971b; Manning and Lemaitre, 1993; Manning and Felder, 1995; USNM]
 **Sergio mericeae* Manning and Felder, 1995 [Manning and Felder, 1995; USNM]
 **Sergio mirim* (Rodrigues, 1971) [Rodrigues, 1971; Manning and Lemaitre, 1993; USNM]

- **Sergio sulfureus* Lemaitre and Felder, 1996 [Lemaitre and Felder, 1996; USNM]
 **Sergio trilobatus* (Biffar, 1970) [Biffar, 1970, 1971b; Manning and Lemaitre, 1993; NMV; USNM]

Subfamily Cheraminae Manning and Felder, 1991a

Genus *Cheramus* Bate, 1888

- **Cheramus longicaudatus* (Sakai, 1967), new combination
 **Cheramus marginatus* (Rathbun, 1901) [Biffar, 1971b; Manning and Felder, 1991a; Blanco Rambla and Linero Arana, 1994; USNM]

Cheramus oblongus (Le Loeuff and Intès, 1974)

Cheramus orientalis Bate, 1888

- **Cheramus praedatrix* (de Man, 1905), new combination

**Cheramus profundus* Biffar, 1973 TYPE SPECIES [Biffar, 1973]

- **Cheramus propinquus* (de Man, 1905), new combination

**Cheramus rectangularis* (Ngoc-Ho, 1991), new combination

- **Cheramus sibogae* (de Man, 1905), new combination

**Cheramus spinophthalmus* (Sakai, 1970), new combination

Genus *Poti* Rodrigues and Manning, 1992

- **Poti gaucho* Rodrigues and Manning, 1992

Genus *Scallasis* Bate, 1888

Scallasis amboinae Bate, 1888 TYPE SPECIES

Subfamily Eucalliinae Manning and Felder, 1991a (as Eucalliinae)

Genus *Calliax* de Saint Laurent, 1973

- **Calliax aequimana* (Baker, 1907) [Poore and Griffin, 1979]

**Calliax bulimba* (Poore and Griffin, 1979) [Poore and Griffin, 1979]

- **Calliax lobata* (de Gaillande and Lagardère, 1966) TYPE SPECIES [de Gaillande and Lagardère, 1966; de Saint Laurent and Bozic, 1972]

**Calliax novaebritanniae* (Borradaile, 1899) [de Saint Laurent and Manning, 1982]

- **Calliax punica* de Saint Laurent and Manning, 1982 [de Man, 1928; de Saint Laurent and Manning, 1982; USNM]

Calliax sakai de Saint Laurent, 1979 [de Saint Laurent and Manning, 1982]

- **Calliax tooradin* (Poore and Griffin, 1979) [Poore and Griffin, 1979; de Saint Laurent and Manning, 1982]

Genus *Eucalliix* Manning and Felder, 1991a

- **Eucalliix cearaensis* Rodrigues and Manning, 1992 [Rodrigues and Manning, 1992a; USNM]

**Eucalliix jonesi* (Heard, 1989) [Heard, 1989; Felder and Manning, 1994; USNM]

- **Eucalliix mcilhennyi* Felder and Manning, 1994 [Felder and Manning, 1994; USNM]

**Eucalliix quadracuta* (Biffar, 1970) TYPE SPECIES [Biffar, 1970, 1971b]

Appendix 2. List of characters and their states used in analysis of genera of Ctenochelidae and Callianassidae. Alphanumeric character labels correspond with those in Appendix 3.

1. Carapace and rostrum

- a. Linea thalassinica: present and typically extending back to posterior edge of carapace (Fig. 1A) (0); present but incomplete (1); absent (2).

- b. Relative length of cephalothorax to total body length (cl/tl): approximately half (0); a third or less (1).
 c. Cardiac prominence (Fig. 1A): present (0); absent (1).
 d. Dorsal oval on carapace (Fig. 1B, D): absent (0); present (1).
 e. Rostrum: present, strongly spinose (Fig. 1A–C, E) (0); present, weakly spinose (1); present, nonspinose and broad (Fig. 1D) (2); absent (3).
 f. Rostrum: present, flatly spinose (Fig. 1A) (0); present, spinose but downturned (Fig. 1B) (1); present, spinose but upturned (2); present, nonspinose and broad (3); absent (4).
 g. Rostrum: dorsally armed with spines (Fig. 1A) (0); dorsally unarmed (1).
 h. Anterolateral projections on the frontal margin of the carapace: present, strongly spinose (Fig. 1C) (0); present, but poorly developed as blunt lobes (Fig. 1B, D) (1); absent (2).
 i. Median rostral carina: present (Fig. 1A) (0); absent (1).

2. Eyestalks and corneas

- a. Eyestalks: cylindrical (0); flattened (1); flattened but concave on dorsal surface (2).
 b. Eyestalks: terminally rounded (Fig. 1C) (0); terminally tapered to a blunt point (Fig. 1E) (1); terminally elongate and pointed (Fig. 1D) (2).
 c. Corneas: terminal on eyestalk (Fig. 1C) (0); subterminal on eyestalk (dorsally situated) (Fig. 1D, E) (1); absent (2).
 d. Corneas: equal to eyestalk width (Fig. 1C) (0); less than eyestalk width (Fig. 1D, E) (1); absent (2).
 e. Corneas: subglobular (Fig. 1C) (0); disc-shaped (Fig. 1B, E) (1); indistinct or absent (2).

3. Abdominal somites

- a. Abdominal somite 1, anterolateral lobes (Fig. 2J): present or indicated (0); absent (1).
 b. Abdominal somite 1, pleuron (Fig. 2J): acute and projecting (0); blunt and obsolete (1).
 c. Anterolateral margin of abdominal somite 2: does not overlap abdominal somite 1 (0); overlaps abdominal somite 1 (1).
 d. Abdominal somite 2: equal to length of somite 6 (0); greater than length of somite 6 (Fig. 2K) (1); less than length of somite 6 (2).
 e. Abdominal somites 3–5: without dense tufts of lateral setae or at most sparse vertical rows (0); with dense tufts of lateral setae (Fig. 2K) (1).
 f. Abdominal somites 3–5: not dorsally ornamented with distinct patterns of grooves and integumental glands (0); dorsally ornamented with strong symmetrical patterning of grooves and integumental glands (1).
 g. Abdominal somite 6: without lateral projections (Fig. 2B–F, K) (0); with lateral projections (Fig. 2A) (1).
 h. Coxa of pereopod 4: rectangular, without anteromesial lobe (0); flattened, with anteromesial lobe (1).

4. Gills

- a. Epipods: 1–7 (rarely 2–7) present (0); 4–7 vestigial or absent (1); 3–7 absent (2); 2–7 absent (3).
 b. Podobranch 2: present (0); vestigial or absent (1).
 c. Podobranchs 3–7: present (0); 3–7 absent or some rudimentary (1).
 d. Arthrobranchs on somites 1–7: 022 2222 (0); 012 2222 (1); 002 2222 (2); 001 2222 (3).
 e. Pleurobranchs: 5–7 absent, 8 rudimentary (0); 5–8 absent (1).

5. Epistome and antennae

- a. Epistome: without setae (0); with long setae (1).
- b. Antenna 1 (antennule), segment 3: longer than segment 2 (0); shorter than or about as long as segment 2 (1).
- c. Antenna 1 peduncle: longer than antenna 2 (antenna) peduncle (0); shorter than antenna 2 peduncle (1); as long as antenna 2 peduncle (2).
- d. Antenna 1, dense brush of ventrally directed long setae: absent (0); present (1).
- e. Antenna 2 scaphocerite: prominent, much longer than wide (0); reduced but articulating, about as long as wide (1); absent (2).

6. Mouthparts

- a. Maxilla 2 scaphognathite: without long setae (0); with one or more long seta(e) (1).
- b. Maxilliped 1 endopod: 2- or 3-segmented (or elongate and tapering) (Fig. 1F) (0); minute (Fig. 1G) (1); absent (Fig. 1H) (2).
- c. Maxilliped 1 exopod: 2- or 3-segmented (sometimes with flagellum) (Fig. 1G) (0); 1-segmented (Fig. 1F, H) (1).
- d. Maxilliped 2 exopod: equal to or longer than merus of endopod (0); shorter than merus of endopod (1); absent (2).
- e. Maxilliped 3: pediform, ischium-merus length more than 3 times merus width (Fig. 1K) (0); subpediform, ischium-merus length about twice merus width (Fig. 1J) (1); operculiform, ischium-merus length less than 2 times merus width (Fig. 1I) (2).
- f. Maxilliped 3, exopod: reaching almost to end of merus of endopod (0); reduced or vestigial (1); absent (Fig. 1I–K) (2).
- g. Maxilliped 3, crista dentata: as prominent toothed ridge (Fig. 1J, K) (0); obsolete or absent (Fig. 1I) (1).
- h. Maxilliped 3, meral spine (Fig. 1J, K): present (0); absent (1).
- i. Maxilliped 3, merus: with a denticulate distal border (Fig. 1J) (0); without a denticulate distal border (Fig. 1I) (1).
- j. Maxilliped 3, merus: not projecting beyond articulation with carpus (Fig. 1K) (0); barely projecting beyond articulation with carpus (Fig. 1J) (1); strongly projecting beyond articulation with carpus (Fig. 1I) (2).
- k. Maxilliped 3, propodus: slender, longer than broad, at most slightly wider than dactylus (Fig. 1I, K) (0); oval, as broad as long, or at least twice dactylus width (Fig. 1J) (1).
- l. Maxilliped 3, dactylus: digitiform and slender, longer than broad (Fig. 1I–K) (0); oval, as broad as long (1).

7. Pereiopods

- a. Pereiopod 1 (chela) in male: equal or subequal (0); unequal (1).
- b. Pereiopod 1 in female: equal or subequal (0); unequal (1).
- c. Pereiopod 1, merus of major cheliped: with straight lower margin (0); with convex lower margin (1); with toothed lower margin (2); with distinct meral hook (3).
- d. Pereiopod 1, merus of minor cheliped: with straight lower margin (0); with convex lower margin (1); with toothed lower margin (2); with distinct meral hook (3).
- e. Pereiopod 1: simple or subchelate (0); chelate (1).
- f. Pereiopod 1, major cheliped, carpus and propodus: without three spines on upper margin (0); with three spines on upper margin (1).

- g. Pereiopod 1, major cheliped, propodus: tapering distally (0); not tapering distally (1).
- h. Pereiopod 1, major cheliped; angle of fixed finger to palm: 90° or less (0); greater than 90° (1).
- i. Pereiopod 1, major cheliped, chelae fingers: shorter than, or approximately equal to palm (0); longer than palm (1).
- j. Pereiopod 1, minor cheliped, chelae fingers: shorter than or approximately equal to palm (0); longer than palm (1).
- k. Pereiopod 1, major cheliped, chelae fingers: without comb of fine teeth (0); with comb of fine teeth (1).
- l. Pereiopod 1, major cheliped, length-to-width ratio of propodus: 1.0–2.0 (0); 2.1–3.0 (1); 3.1–4.0 (2); 4.1–5.0 (3).
- m. Pereiopod 1, major cheliped denticulation: even (0); uneven (with occasional larger teeth) (1).
- n. Pereiopod 1, major cheliped, ventral teeth on ischium: present (0); absent (1).
- o. Pereiopod 1, minor cheliped, ventral teeth on ischium: present (0); absent (1).
- p. Pereiopod 2, row of setae on lower margin of ischium-propodus: absent (0); present (1).
- q. Pereiopod 2: simple (0); chelate, with dactylus longer than fixed finger (1); chelate, with dactylus as long as fixed finger (2).
- r. Pereiopod 3 propodus: linear (more than 3 times as long as wide) (0); oval (approximately twice as long as wide) (1); oval, but with prominent heel on proximal corner of lower margin (2).
- s. Pereiopod 4 propodus: linear (more than 3 times as long as wide) (0); oval and flattened (twice as long as wide or less) (1).
- t. Pereiopod 5: simple (0); chelate or subchelate (1).

8. Pleopods

- a. Pleopods: 1 absent or reduced, 2–5 similar and lamellar (0); 1 and 2 variously absent, reduced or sexually modified, 3–5 similar and lamellar (1).
- b. Male pleopod 1: absent (0); present, 1-segmented (1); present, 2-segmented, with the 2nd segment more or less triangular (2); present, 2-segmented, with the 2nd segment ovate (3); present, 3- or more segmented (4).
- c. Male pleopod 1: absent (0); present, with obvious appendix interna (1); present, appendix interna as minute hooks on ramus (2); present, appendix interna absent (3).
- d. Male pleopod 1: present, uniramous (0); present, but vestigial (1); absent (2).
- e. Male pleopod 2: present, biramous (0); present, uniramous (1); present, but vestigial (2); absent (3).
- f. Male pleopod 2: present, appendix masculina present (0); present, appendix masculina present and fused to appendix interna (1); present, appendix masculina absent (2); absent (3).
- g. Female pleopod 1: present, biramous (0); present, uniramous (1).
- h. Female pleopod 1: present, 1-segmented (0); present, 2-segmented, with the 2nd segment more or less triangular (1); present, 2-segmented, with the 2nd segment ovate (2); present, 3- or more segmented (3).
- i. Female pleopod 2: present, biramous (0); present, uniramous (1).
- j. Pleopods 3–5: rami lanceolate (0); rami broad (1).
- k. Pleopods 3–5, endopod and exopod: not a semisphere when combined (0); semispherical when combined (1).

- l. Pleopods 3–5: with appendix interna (Fig. 2G–I) (0); without appendix interna (1).
 - m. Pleopods 3–5, appendix interna: present and digitiform (Fig. 2G) (0); present but reduced and stubby (Fig. 2H) (1); present but embedded (Fig. 2I) (2); absent (3).
- 9. Uropods and telson**
- a. Uropodal exopod: simply ovate (Fig. 2A) (0); with anterodorsal setose thickening (= dorsal plate) (Fig. 2C–F, K) (1); bilobed, or markedly bipartite (Fig. 2B) (2).
 - b. Uropodal exopod: longitudinally carinate dorsally (Fig. 2A, B) (0); acarinate dorsally (Fig. 2C, E, F) (1).
 - c. Uropodal exopod, lateral notch or incision: present (Fig. 2B) (0); absent (1).
 - d. Uropodal endopod: oval, distally rounded, with similar length to width (Fig. 2A, D) (0); distally truncate, distolateral margin subacute, wider distally than proximally (Fig. 2C) (1); longer than broad, tapering distally (Fig. 2B, K) (2); much longer than broad, not tapering distally, strap-like (Fig. 2F) (3).
 - e. Uropodal endopod: longer than broad, tapering, or not tapering, distally (Fig. 2B, E, F) (0); broader than long, flattened distally (Fig. 2C) (1).
 - f. Uropodal endopod: without distinct distolateral spine (Fig. 2A–D, F, K) (0); with distinct distolateral spine (Fig. 2E) (1).
 - g. Telson: longer than broad (Fig. 2A, D) (0); as long as broad (Fig. 2B, E) (1); broader than long (Fig. 2C, F) (2).
 - h. Telson: longer than uropods (Fig. 2A, D) (0); shorter than uropods (Fig. 2B, F, K) (1); equal or subequal to uropods (Fig. 2E, C) (2).
 - i. Telson: without one or two lateral spines (Fig. 2A–C, F, K) (0); with one or two lateral spines (Fig. 2D, E) (1).
 - j. Posterior margin of telson: rounded (Fig. 2A, E) (0); flattened (Fig. 2D, F) (1), slightly indented (Fig. 2C) (2); strongly excavate (Fig. 2B) (3).
 - k. Posterior margin of telson: unarmed (Fig. 2A–C, F) (0); with one spine (1); with more than one spine (Fig. 2D, E) (2).
- 10. Setal rows**
- a. Abdominal somite 2, lateral setal row of plumose setae (Fig. 2K): absent (0); present (1).
 - b. Abdominal somites 3–5, lateral setal row of plumose setae (Fig. 2K): absent (0); present (1).
 - c. Abdominal somite 6, lateral setal row of plumose setae (Fig. 2K): absent (0); present (1).
 - d. Abdominal somite 6, transverse setal row of plumose setae on posterior dorsolateral margin (Fig. 2K): absent (0); present (1).
 - e. Abdominal somite 6, oblique setal row of plumose setae between lateral and transverse setal rows (above) (Fig. 2K): absent (0); present (1).

