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

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ABSTRACT

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 callianideid, *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 (Anacalliacinae, Callianopsinae, Ctenochelinae, and the recently suggested Gourretinae) was not supported. Three callianassid subfamilies (Callianassinae, Cheraminae, and Eucalliacinae) 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*, *Anacalliax*, 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 "*Callianassa*" 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 *Anacalliax* 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 typa* 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 specimens 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 typa* 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

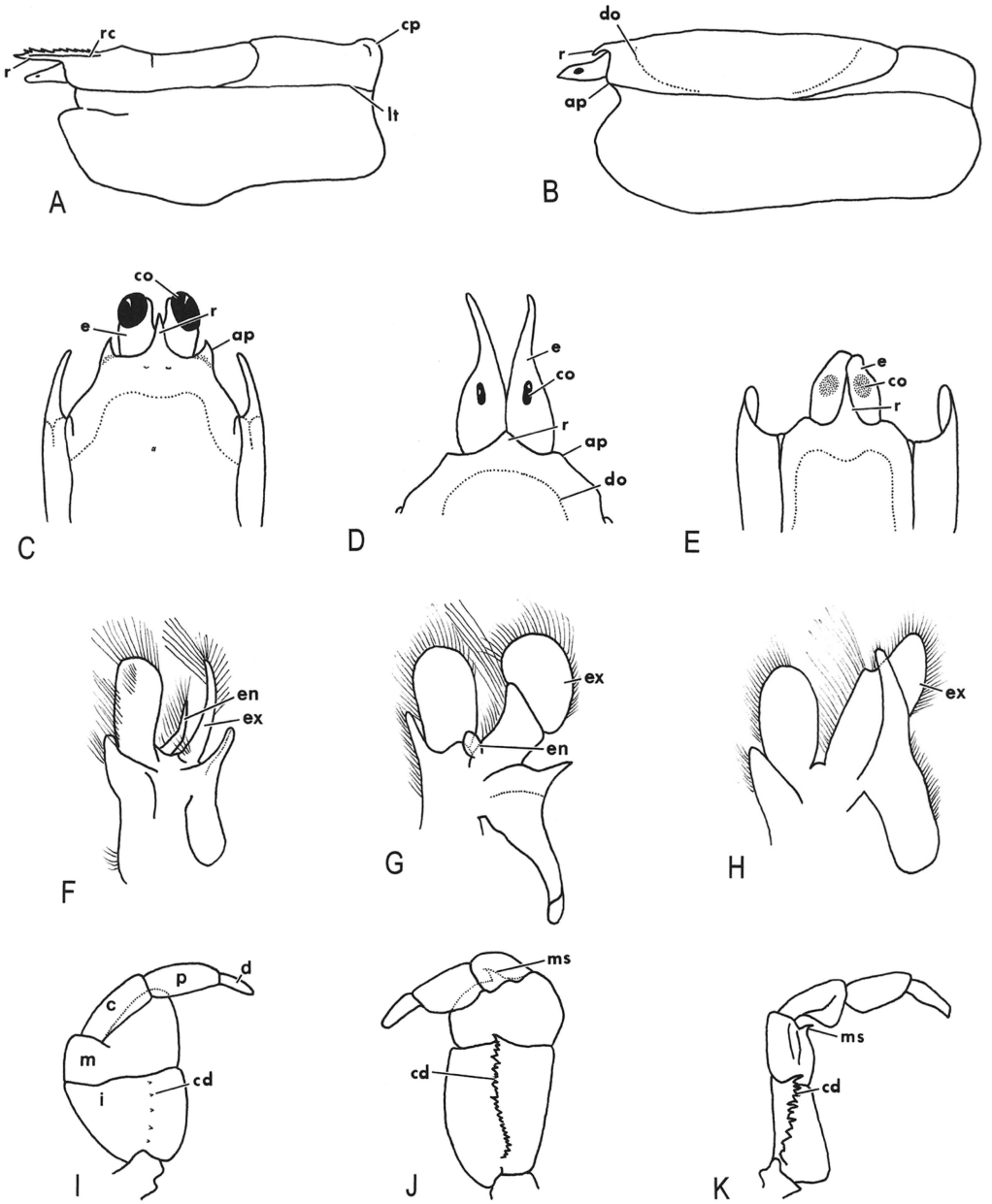

Fig. 1. Diagrammatic representation of selected ctenochelid and callianassid morphological character states. A, B, Lateral view of carapace: A, *Ctenocheles serrifrons*; B, *Biffarius biformis* (both after Manning and Felder, 1991a). C–E, Dorsal view of rostral region and eyestalks: C, *Corallichirus xuthus* (after Manning and Felder, 1991a); D, *Callichirus 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.

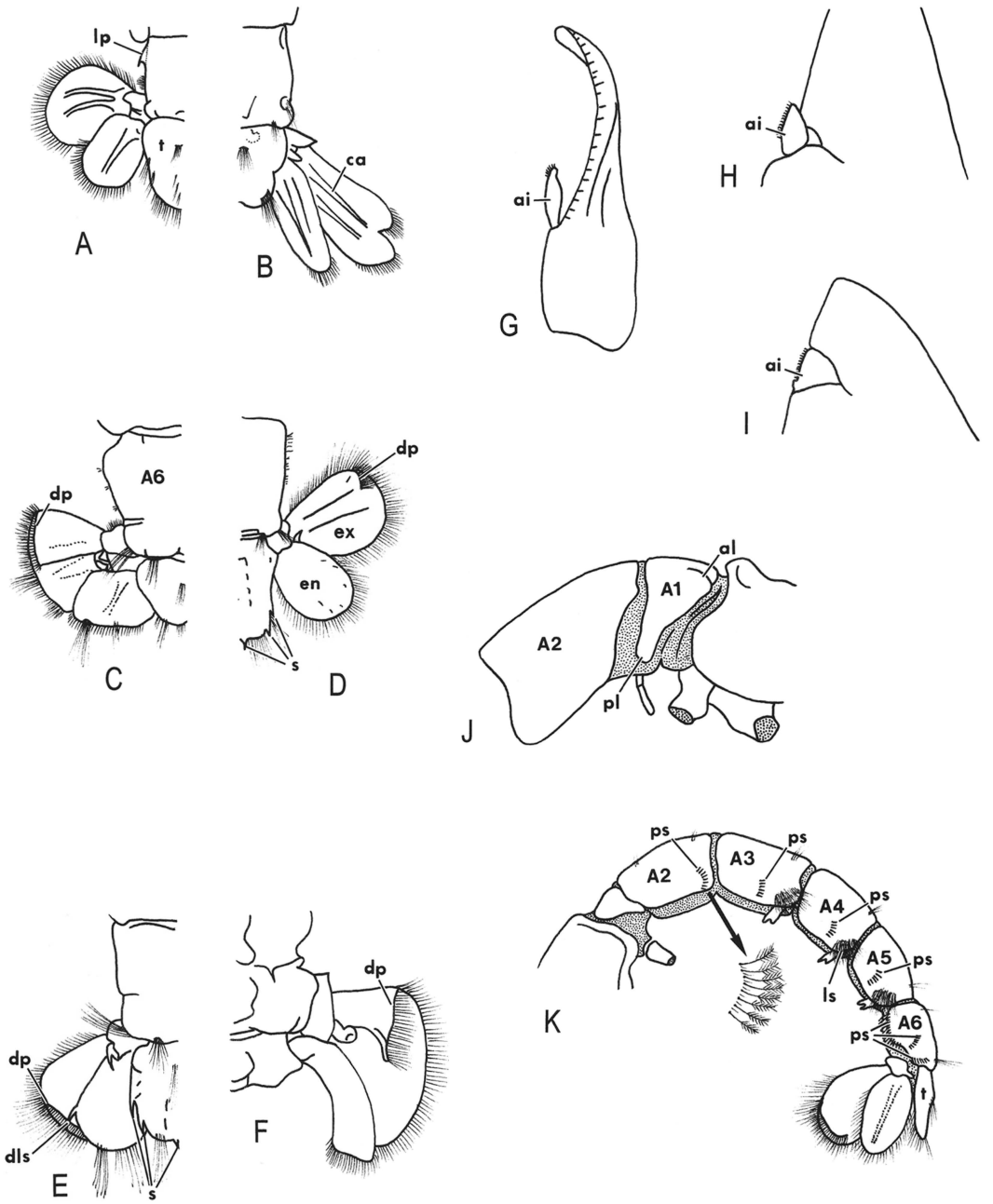

Fig. 2. Diagrammatic representation of selected ctenochelid and callianassid morphological character states. A–F, Uropods, telson, and 6th abdominal somite: A, *Dawsonius latispina* (after Biffar, 1971b); B, *Ctenocheles maorianus* (after Dworschak, 1992); C, *Neocallichirus lemaitrei* (after Manning, 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, *Notiax 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.

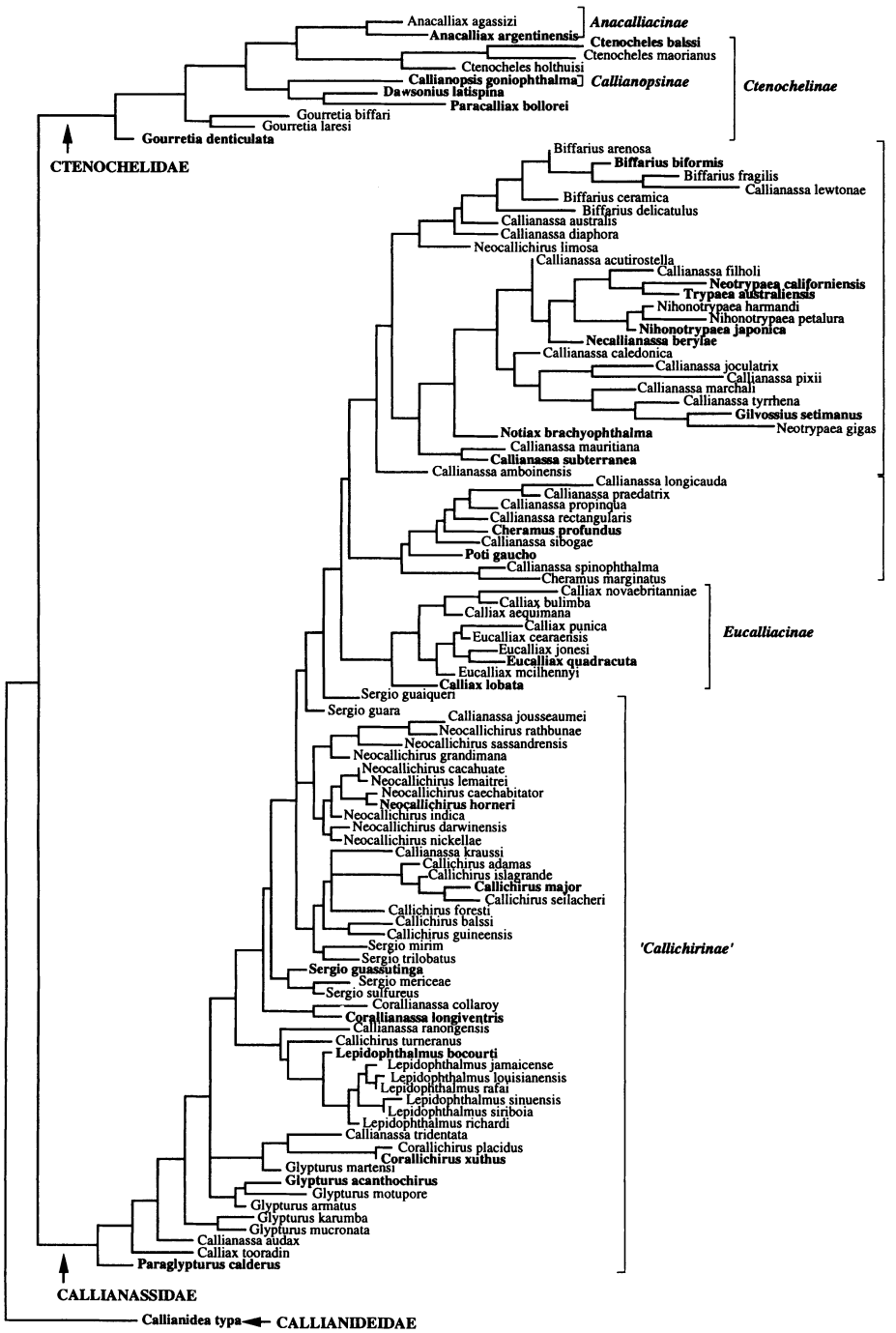

Fig. 3. Phylogram of 50% majority rule consensus tree of 1,700 equally parsimonious trees obtained from an heuristic analysis of 107 thalassinidean taxa using 93 morphological characters and using the out-group method. Tree length = 838 steps; consistency index (CI) = 0.905. Some higher taxonomic categories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

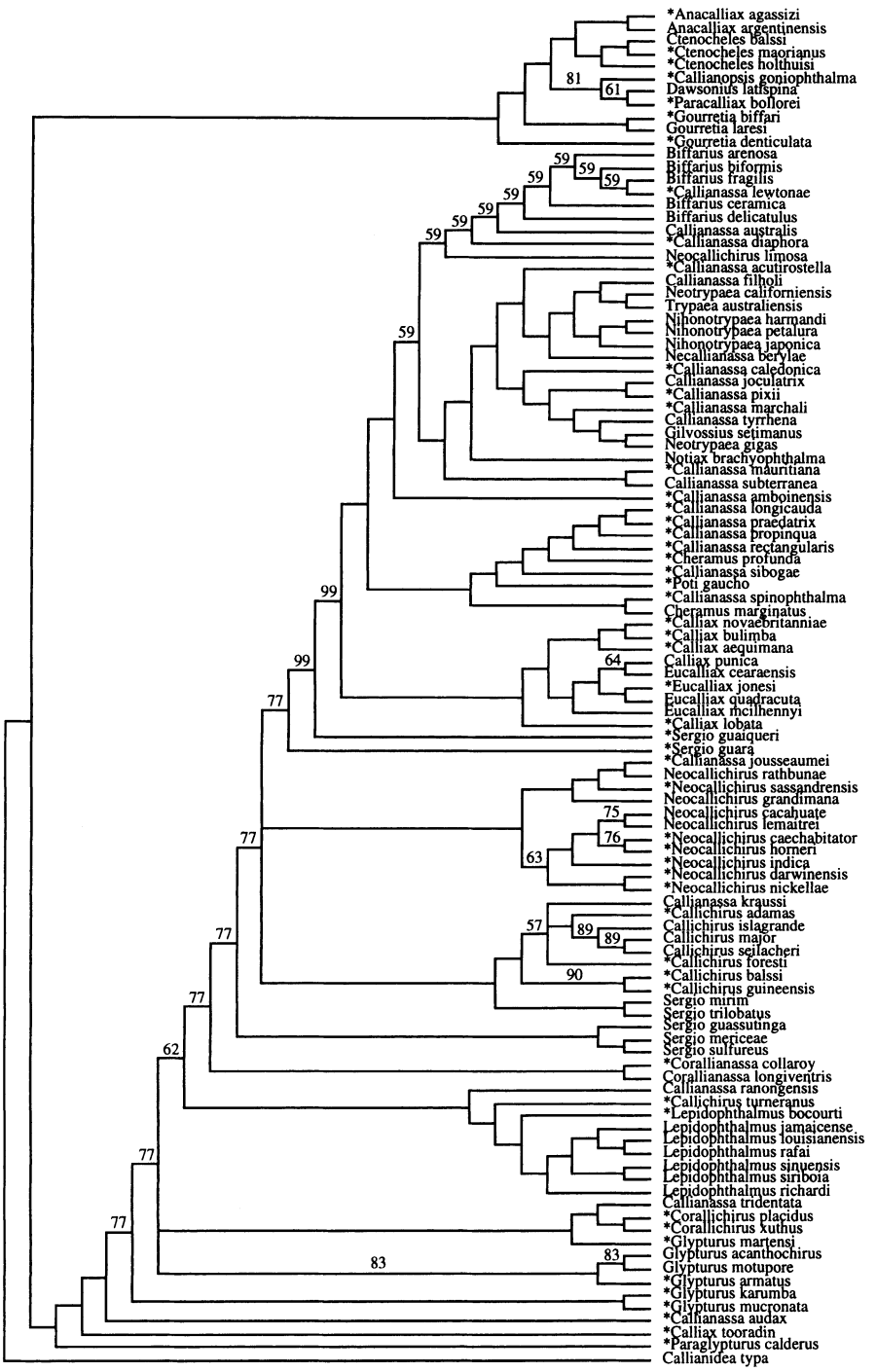

Fig. 4. Cladogram of 50% majority rule consensus tree of 1,700 equally parsimonious trees obtained from an heuristic analysis of 107 thalassinidean taxa using 93 morphological characters and using the out-group method. Tree length = 838 steps; consistency index (CI) = 0.905. Species without a full complement 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 (Anacalliacinae, Callianopsinae, Ctenochelinae, Gourretinae) (Manning and Felder, 1991a; Sakai, 1999) are not monophyletic in the present analysis. The subfamily Anacalliacinae, 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 pereiopod 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, Eucalliacinae) (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 pereiopod 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.

Eucalliacinae

A monophyletic clade comprises all the investigated members of the subfamily Eucalliacinae, 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 pereiopod 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" jousseaumei*. Nearly half of the character data are missing for this species. However, *C. jousseaumei* 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.*" *jousseaumei* 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 pereiopod 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 diagnosed, 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.

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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 kempi* Sakai, 1999a; *Neocallichirus raymanningi* 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 Eucalliacinae is similar to that subfamily in our analysis. Within this subfamily he has synonymised *Eucalliax* 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. novaebrittaniae*) 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, Anacalliacinae, 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 raymanningi*, 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.

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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 musuem 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 Anacalliacinae 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 *Gourretia* de Saint Laurent, 1973
Gourretia barracuda Le Loeuff and Intès, 1974
**Gourretia biffari* Blanco Rambla and Linero Arana, 1994 [Blanco Rambla and Linero Arana, 1994; USNM]
Gourretia coolibah Poore and Griffin, 1979
Gourretia crosnieri Ngoc-Ho, 1991
**Gourretia denticulata* (Lutze, 1937) TYPE SPECIES [de Saint Laurent and Bozic, 1972; Le Loeuff and Intès, 1974; USNM]
Gourretia lahouensis Le Loeuff and Intès, 1974
**Gourretia laresi* Blanco Rambla and Linero Arana, 1994 [Blanco Rambla and Linero Arana, 1994; USNM]
Gourretia 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 Intés, 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 joculatrix* de Man, 1905 [Poore and Griffin, 1979; Ngoc-Ho, 1991; USNM]
{**Callianassa jousseaumei* 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 gaucho* 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 borradailei (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 laurae (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 jamaicense* (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 cacahuate* Felder and Manning, 1995 [Felder and Manning, 1995; USNM]
**Neocallichirus caechabitator* 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 jousseaumei (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 pachydactylus (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 guassutinga* (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 Eucalliacinae 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 Lagardere, 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 *Eucalliax* Manning and Felder, 1991a
**Eucalliax cearaensis* Rodrigues and Manning, 1992 [Rodrigues and Manning, 1992a; USNM]
**Eucalliax jonesi* (Heard, 1989) [Heard, 1989; Felder and Manning, 1994; USNM]
**Eucalliax mcilhennyi* Felder and Manning, 1994 [Felder and Manning, 1994; USNM]
**Eucalliax 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 pereiopod 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, uniramus (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, uniramus (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).

Appendix 3. Data matrix. ($\frac{0}{1}$ = 0/1, an equivocal character state assignment)

```
Character number              111111111222223333333344444555556666666666667777777777777777777788888888888889999999999900000
Taxa                          ABCDEFGHIABCDEABCDEFGHABCDEABCDEABCDEFGHIJKLABCDEFGHIJKLMNOPQRSTABCDEFGHIJKLMABCDEFGHIJKABCDE
-----------------------------------------------------------------------------------------------------------------------------
Anacalliax agassizi           01?10011011112????001?2111100101011102011000112210110100000?22?113?001110??0120010021000?????
Anacalliax argentinensis      010101110112220102001121111101010111021110001122100101001001221112200112011012000002102010000
Biffarius arenosa             01112312111111110010013112110020111220111001133101000011011220113103311011001111101100010100
                                                           1                                    2

Biffarius biformis            01112312111111110000012112110102011122111110103310100001101122111220331101100111110110001010 0
Biffarius ceramica            011111121111111100100131121101020111220111001132101000001011220113202211011011111100100010100
                                                                                                  3

Biffarius delicatulus         011123121111111101000121121101010101221111101033101100000111220113201211011011110101100010100
                                                                1                                 2

Biffarius fragilis            011123111111101101000131121100020111220110101030101000011011221112203311011011112002101010100
                                                                       1

Callianassa acutirostella     0?110112111111??????01??????0001????22011200????????????????????1?????130???11120021021?????
Callianassa amboinensis       0?112312111111???1??0???????0001011122011200112110110000000122?1122012110???11120021021?????
                                  34                                                             12

Callianssa audax              01112312111111??????0???????0101????12?11110112010110000111??2??1?????11011??11120021020?????
Callianassa australis         0111231211111211001001211111010101111201100011311010000001011220113201211011011111101102210110
                                                                                                  2

Callianassa caledonica        01110011111111???1??0???????0000?11?0201100011331011000110012 2??1????110???11120021021?????
                                                                  1

Callianassa diaphora          0111231111111???0??0?21111?0101010102011000113110000000101122011220??11011011010?021001?????
                                     2                                                         3 1          1

Callianassa filholi           0111111111111111001100121121100010111220111001132100000001011220113203313011011110000001010100
Callianassa joculatrix        0111001111112221101100121121102010110020110001131100000001001220111213312011011111002101110100
                                     2                                                 1

Callianassa jousseaumei       0?110111112111??????0???????0002????120112101120101100001????2?????????????????111021000?????
Callianassa kraussi           011123111101111101100121121100020110221110101111101000001011221113203312011021112002102010100
                                     2                                      2

Callianassa lewtonae          01111012110111???2??0?3?????0002?11?22011200?01110110001000?22????????????11001?120011010?????
Callianassa longicauda        01110210111110????????31121?0101????12100200?1?31????1????0??1??122011130???01120001011?????
Callianassa marchali          011100111211111???1100?21111?010101010201100011311001000000112201100233130110110 10?001001?????
                                                                                                            1

Callianassa mauritiana        01112312111111?????????????????1????120110001131100?00010?1??2??142001130???11110021010?????
Callianassa pixii             011110110122222????????311?1?000?0211021110000010100100011001220112300?100111311120021030?????
                                                           2                 1

Callianassa praedatrix        01110011111110???0??01??????0101????22000200??2?10110?0010???2??123002130???11120001121?????
Callianassa propinqua         01110011111111??????0?211?1?0102?11112000200112210110000000121??123002110110011120001102?????
Callianassa ranongensis       0111001111111111100000121111101010110121101111131101101000001221112300113011021111002101010010
                                                                                      1

Callianassa rectangularis     01110011111111???0??0?21????0001?111220112001?2210100000100122??????????????11120001122?????
Callianassa sibogae           01110211011111???0??0???????0101????02011000?12210110001000??1??1??00?1?01100111100010 21?????
                                                                                                                     2

Callianassa spinophthalma     0111021111111101100000???????0201????12011100?1211010000010 0??1??????????????11120021021?????
                                                                            3              2

Callianassa subterranea       011123111111101101100121121101010101120110001131100100000001220112300210011011111001100210110
                                     2                                                            23             2  1

Callianassa tridentata        011102101111111101100131121100120100121111101131101000001001221112300211011001112002100010110
Callianassa tyrrhena          011123111111111111100131121100010101220112001131100100001111220110023313011011112001100010110
                                                                                                                 2

Callianidea typa              211023121101121101000001101001011011000110001111101100011111101032002110000101120001000000 10
Callianopsis goniophthalma    0111001102111201110011211310110000100200101111011011000010002111123001??0110000120011010 00011
                                                         1

Calliax aequimana             0?11231111111????00???????11010100211111110011100100001 00?22111230011101 1??11120021020?????
                                                                   2

Calliax bulimba               0?11231111111??????0???????1102????221111110?2210110000100?????123001???????11120021010?????
Calliax lobata                0?1?2311111112??????0???????1101????12011011112110110000100121??123001130110111020021000?????
                                                                                           2                         2

Calliax novaebritanniae       01110010101111???1??0?2?????110101102111121100221010000010012201141001130110011120021020?????
Calliax punica                011023111111111101000120121111010110100110110011101100001001221113100211011021112002101010110
                                 1

Calliax tooradin              0?11231111111??????0?2?????0100011010111011111110010000011?????100202110???11120021000?????
                                     2

Callichirus adamas            01112311112111???1110?21111?000100102111111010211010010010112211133002130110210130021020?????
                                         222                12     2                 1                      1

Callichirus balssi            01111111111111??????0?21111?0001010002111110113110010000101??2??133022110???11120021020?????
Callichirus foresti           01112312111111???1100?21111?0011011002111000112110100000101122111330121111102111200210 20?????
                                                                                                                 2

Callichirus guineensis        0?11231111111??????0?21111?00010110021110001121100100001011221?11312213011021112002102 0?????
Callichirus islagrande        011123111121111101110121111100010100221101101021101001021011221112300211011021113002102010111
                                                                      1

Callichirus major             0111231111111111011101211111001101002211111011311000000001011221112300211011021113002102010111
                                                             2

Callichirus seilacheri        011123111121111100110121111100110100221111101021100100010011221112300211011021113002102010111
                                                                                                                    3

Callichirus turneranus        011100111111111110010 0?21111?000101102211101011331010000010 11?21?1230021101???11120021030?????
Cheramus marginatus           011101111111110000000131131001010111120110001111100001011001110111303311011100112001102110000
                                             1                                                 2           1

Cheramus profundus            01110011111111????00013112100102011112011000 0?22101100001 00?11?1123002???11001112000211 2?????
                                                                                          2

Corallianassa collaroy        0?11001010110 0?????00?311?1?0100010022000110112210110000000122111330021 30???11120021020?????
                                       1  1

Corallianassa longiventris    011102101011101101100131111111020110220110101122101100001001221113300212011021112002102010100
                                       1

Corallichirus placidus        0?11001010001 0?????00???????0112????12?11010??2210110000?00??2???????????????11120021010?????
Corallichirus xuthus          0111001010001011001001311211001202001201101 0?12210110000100122111?????1101101111200210000000 0
Ctenocheles balssi            010002020011121010001130121011000011020010001100100010131111210114300113011002001001002100000
                                                                 2

Ctenocheles holthuisi         010002100111120??0001?311210100001020200100011321001101310012111022001??000000000002000000000
Ctenocheles maorianus         01000011011222110010013012101100000002011000110010011012111121011220 01???11002002002102000???
Dawsonius latispina           011001110211120000001131111001010010020010001133100100011001211113200111011000010001000010011
                                                                                           2

Eucalliax cearaensis          0110231111111111101000121111112020110120100110011101100001001221113300111011001112002101010110
                                                                      1                                             2
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Appendix. 3. Continued