Decapod Crustacean Phylogenetics

edited by

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Contents

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A Preliminary Phylogenetic Analysis of the Dendrobranchiata Based on Morphological Characters

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ABSTRACT

Dendrobranchiata currently is composed of two superfamilies, Penaeoidea (families Aristeidae, Benthesicymidae, Penaeidae, Sicyoniidae, and Solenoceridae) and Sergestoidea (families Sergestidae and Luciferidae). Although the monophyly of Dendrobranchiata is rather firmly established, little is known about the relationships among its families. We analyzed 24 taxa of Dendrobranchiata using three different combinations of outgroups, with differing results. In the majority of the most parsimonious trees, Dendrobranchiata, Penaeoidea, and Sergestoidea appear monophyletic, as do the families Aristeidae, Solenoceridae, Sicyoniidae, Sergestidae, and Luciferidae. The families Penaeidae and Benthesicymidae are not monophyletic. Dendrobranchiata is defined by having dendrobranchiate gills, prominent pleonic hinges, larvae hatching as nauplii or protozoeae, and the presence of a petasma in males. Sergestoidea is defined primarily by "lost" characters, including the loss of the exopod on maxilliped 3, the absence of a dactyl on P1, and the related absence of a P1 chela. Penaeoidea is defined by the presence of a tubercle on the terminal article of the eyestalk and the presence of a branchiocardiac carina. There are no clear synapomorphies defining the Aristeidae. Solenoceridae is defined by the presence of a postorbital spine and the presence of a distolateral projection on the male pleopod 2. Sicyoniidae is defined by many characters, including the presence of an ocular stylet. Sergestidae and Luciferidae also are defined by many characters, such as the presence of a clasper organ on the male antenna 1 in the sergestids and the brooding of eggs on the female pereopods in luciferids.

1 INTRODUCTION

The decapod suborder Dendrobranchiata contains some 500 species of shrimps, including most of the 10–15 commercially important species worldwide. Dendrobranchiates also play important ecological roles in estuaries and other marine systems. Species range from shallow waters in the tropics to depths of 1000 m or more on the continental slopes (Pérez Farfante & Kensley 1997).

These shrimps have had a somewhat confusing taxonomic history. Boas (1880) divided the Decapoda into the Natantia, a "swimming" group that included all shrimps and shrimp-like forms, and the Reptantia for the remaining (crawling) species of decapods. Bate (1888) first recognized the different types of gills among the Natantia and divided the group into three subgroups: Dendrobranchiata, Phyllobranchiata, and Trichobranchiata. Bate (1888) also divided the "tribe Penaeidea" into the families Penaeidae and Sergestidae. Calman's (1909) treatment of the Dendrobranchiata (as Tribe Penaeidea) included the family Penaeidae (with the subfamilies Aristeinae, Sicyoninae, and Penaeinae) and the family Sergestidae (with subfamilies Sergestinae and Leuciferinae). Much

later, Crosnier (1978) treated Penaeidae as consisting of two families: Aristeidae, containing the subfamilies Aristeinae, Benthesicyminae, and Solenocerinae, and Penaeidae containing the subfamilies Penaeinae, and Sicyoninae. Crosnier (1978) also suggested that most or all of the penaeid subfamilies should be raised to familial level, an action finally taken by Pérez Farfante & Kensley (1997).

Currently, the suborder Dendrobranchiata contains two superfamilies: Penaeoidea and Sergestoidea. The Penaeoidea includes the families Aristeidae, Benthesicymidae, and Solenoceridae, species of which are found in the deep sea, and the Penaeidae and Sicyoniidae, found more often on the continental shelf. The Sergestoidea includes only two families, the Sergestidae (mostly in the deep sea but with some freshwater species) and the highly aberrant and exclusively planktonic Luciferidae.

The first phylogenetic hypothesis for any dendrobranchiate taxa was proposed in 1983, when Burkenroad (1983) presented a more or less intuitively based hypothesis, unfortunately without a corresponding character matrix. Since then there have been many papers published on the relationships of these shrimp, and nearly all of these studies have agreed that the Dendrobranchiata is a basal group among the Decapoda and is the sister group to the Pleocyemata (e.g., Burkenroad 1981; Felgenhauer & Abele 1983; Schram 1984; Abele & Felgenhauer 1986; Abele 1991; Wills 1997; Richter & Scholtz 2001; Dixon et al. 2003). Reviewing the details of all of these studies is beyond the scope of this paper, but noteworthy contributions include Felgenhauer & Abele's (1983) recognition of the Dendrobranchiata as a natural group and their addition of other important characters to the diagnosis of the suborder; Abele's (1991) first molecularly derived phylogeny of the Dendrobranchiata and his comparison of that tree to a morphology-based phylogeny, strongly supporting the monophyly of the dendrobranchs; and Wills's (1997) support of dendrobranchiate monophyly in his analysis of all major crustacean taxa (extant and fossil). Most recent studies have assumed or supported monophyly of the Dendrobranchiata, such as Dixon et al. (2003), who considered monophyly of the group probable from their analysis of ordered characters, while at the same time emphasizing that the clade was not recovered in all of the most parsimonious trees in that study.

Defining morphological characters of the Dendrobranchiata (based primarily on the works of Pérez Farfante & Kensley 1997; Burkenroad 1981, 1983; Dixon et al. 2003) are: 1) the presence of gills that are "dendrobranchiate" (defined as "secondarily branching;" see Martin et al. 2007); 2) the presence of chelae on the first three pairs of pereopods (with some exceptions); 3) the pleura of the second abdominal somite not overlapping those of the first (as opposed to the situation in the caridean shrimps); 4) the presence of prominent hinges between the pleonic somites; 5) the direct release of eggs into the water (as opposed to being carried on the female pleopods) and the subsequent hatching of the eggs as nauplii or protozoeae; 6) the presence of a petasma in males; and 7) the absence of an appendix interna on the pleopods (with the exception of a vestigial structure found in some males). Here, we use morphological characters and cladistic methods to establish a preliminary phylogeny of the Dendrobranchiata and to test the monophyly of the two superfamilies and seven families currently treated as dendrobranchiates.

2   MATERIALS AND METHODS

The material used in this study was obtained from three institutions: Museu Nacional/UFRJ, Brazil; FURG (Fundação Universitária Rio Grande), Brazil; and NMNH (National Museum of Natural History, Smithsonian Institution), USA (Appendix 1). For the ingroup, 24 species distributed among the seven families of Dendrobranchiata were examined. For the outgroups, 3 species of Caridea, one of Stenopodidea, and one of Nephropidea were examined, in three different combinations: one with Caridea alone, another with Caridea and Stenopodidea, and a third with Caridea, Stenopodidea, and Nephropidea.

For selection of the morphological characters, specimens of Dendrobranchiata were examined using compound and stereoscope microscopes. Drawings of most of the phylogenetically
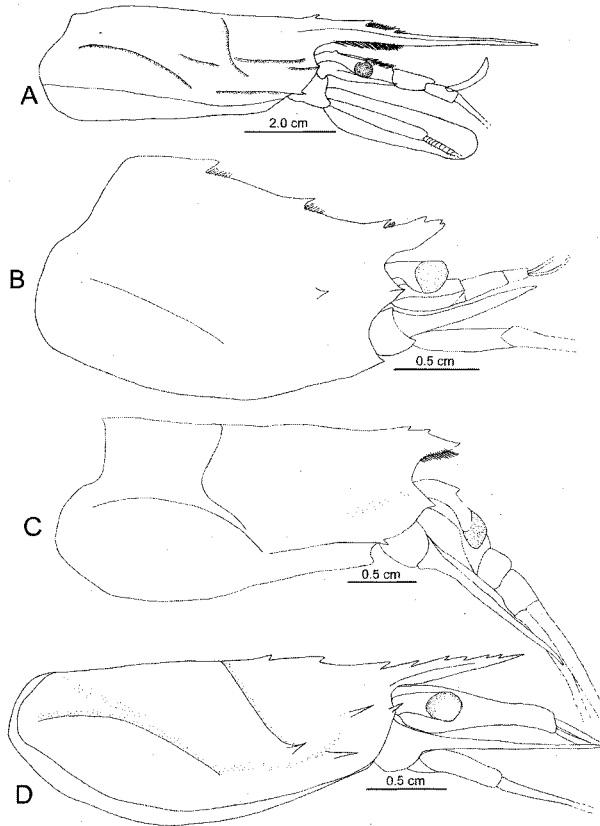
Figure 1. Selected morphological characters. Rostrum length. (A) *Plesiopenaeus coruscans*, surpassing antennular peduncle. (B) *Sicyonia typica*, not surpassing antennular peduncle, reaching cornea. (C) *Benthesicymus bartletti*, not surpassing antennular peduncle, not reaching cornea. (D) *Hymenopenaeus debilis*, not surpassing antennular peduncle, surpassing cornea.

informative characters are provided (Figs. 1–4). A total of 102 morphological characters was selected. When appropriate, characters were combined into multistate groupings to avoid overly dependent characters. This combining into multistate characters resulted in a matrix of 68 binary characters and 34 multistate characters. Of the 34 multistate characters, 8 were regarded as continuous characters. These characters were split into multistate characters following an arbitrary method in which we took the range between the lowest and the highest values and divided that range into three equal parts; each of these parts was then treated as one character state. All characters were unordered.

The data matrix was assembled using the program Delta (Dallwitz et al. 1993, 1998). This program allows users to prepare a dataset and export it as a nexus format. The cladistic analysis was performed using PAUP 4.0 Beta version (Swofford 2000), with a heuristic search option, in stepwise addition, with 1000 replicates. Bootstrap analysis and Bremer support (Bremer 1994) also were performed using PAUP 4.0.

For character optimization we used the tool trace character of MacClade 4.03 (Maddison & Maddison 2001). For character polarization we followed Nixon & Carpenter (1993) for outgroup comparisons.
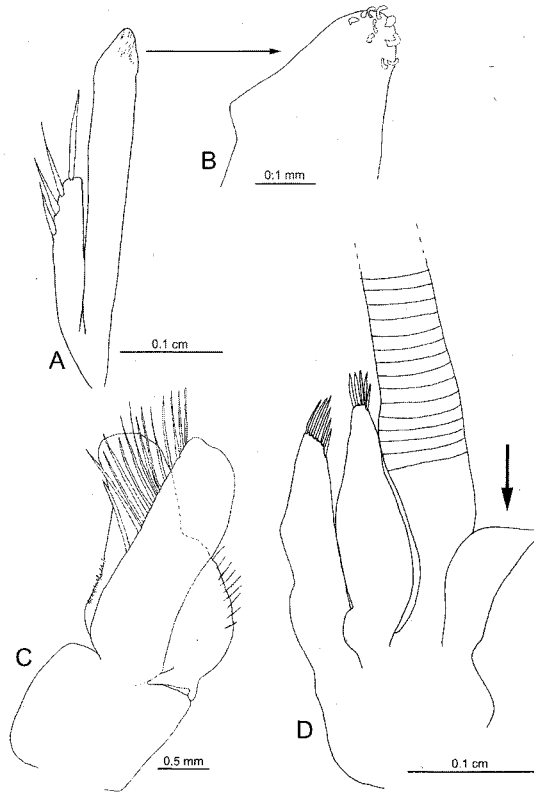
Figure 2. Selected morphological characters. Hook setae on male appendix interna. (A) *Pasiphaea princeps*, present. (B) *Pasiphaea princeps*, present, detailed. (C) *Benthesicymus bartletti*, absent. Disto-lateral projection on male pleopod 2. (D) *Hymenopenaeus debilis*, present.

3 RESULTS

3.1 *Description and optimization of characters*

Characters used and explanations of their distribution and polarity are given in Appendix 2. Because Dendrobranchiata is widely recognized as a basal group within Decapoda, it is difficult to find true synapomorphies for the group. For this reason, character optimization was performed by comparison with the three outgroups, meaning that some characters appearing here as "apomorphic" to (or within) the Dendrobranchiata may in fact be plesiomorphic in the Decapoda as a whole. One example is the second abdominal pleuron overlapping the first, a character that is clearly derived (occurring only in the Caridea) but that appears "plesiomorphic" here when the Caridea is used as the outgroup for the dendrobranchs. The same problem occurs with characters 38 (releasing eggs freely into the water as opposed to carrying them on the pleopods), 40 (hatching as nauplius larvae), and 83 (absence of hook setae on the male appendix interna), in which states treated in this analysis as apomorphic for the Dendrobranchiata are actually plesiomorphic among the Decapoda as a whole.

3.2 *Analysis 1 - Caridea as the outgroup*

Sixty-nine equally most parsimonious trees were found (for indices see Table 1), and from these two consensus trees were calculated (strict and majority rule) (Figs. 5, 6). Character states
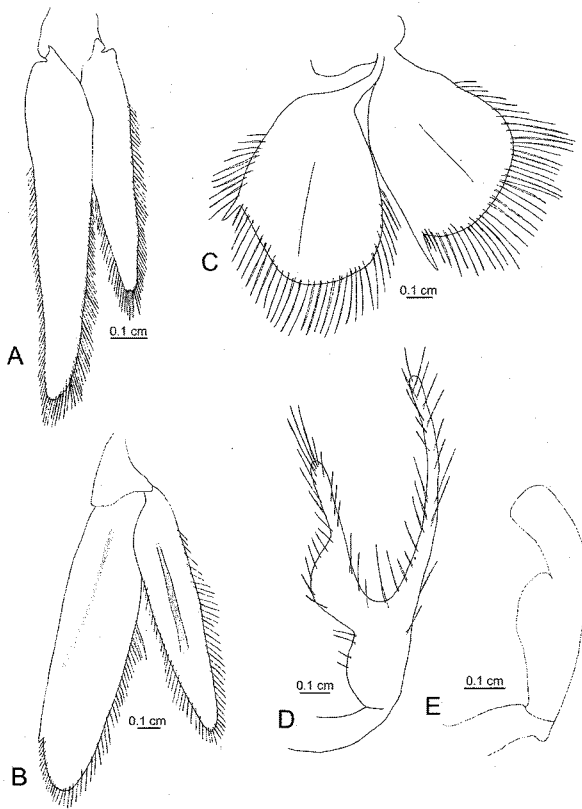
Figure 3. Selected morphological characters. Uropods. (A) *Sergestes armatus*. (B) *Artemesia longinaris*. (C) *Nephropsis agassizi*. Epipod shape. (D) *Haliporoides sibogae sibogae*, bifid. (E) *Litopenaeus schmitti*, foliaceous.

considered non-homoplastic are depicted in bold. For the majority rule consensus tree, we obtained the following results:

Dendrobranchiata (clade 3) is a monophyletic group. The suborder is defined by 6(2), 30(1), **31(2)**, **39(1)**, 79(1), **80(2)**, **83(1)**, **84(1)**. Luciferidae (clade 5) is a monophyletic group, defined by **6(1)**, 26 (2), **38 (3)**, **41(1)**, **49(1)**, **51(1)**, 58(1), 59(1), **64(1)**, **65(1)**, **72(1)**, **76(1)**. Sergestoidea is not a natural group. Sergestidae (clade 7) is a natural group defined by 32(4), **42(2)**, 58(1), 59(1), **73(1)**, **77(1)**. Penaeoidea (clade 8) is a natural group defined by 9(2); 23(2); 44(2); 54(2); 99(4). Benthesicymidae is not a natural group. Sicyoniidae (clade 17) is a natural group defined by **8(2)**, **32(3)**, **37(2)**, **81(4)**, **101(2)**. Penaeidae is not resolved, with members of the family in a trichotomy with Sicyoniidae in clade 12. Solenoceridae (clade 19) is a natural group defined by **14(2)**, **90 (2)**. Aristeidae (clade 24) is a natural group. Characters 22 (3), 61 (1), 67 (1), 85(1) characterize the family, but it is not possible to determine plesiomorphic vs. apomorphic states.

Other clades (most of which are currently not defined taxonomically) resulting from the analysis were: Clade 2: All species except *Pasiphaea princeps*. This clade is characterized by 8(1), 16(2), 22(1), 47(2), 48(2), 53(1), 54(2), 61(3), 67(2), 92(2), 97(2). Clade 6: All Dendrobranchiata except the family Luciferidae, defined by 24(2), **55(1)**, **70(2)**. Clade 9: Penaeoidea except for *Benthesicymus* sp., defined by 1(2), 4(2), 28(2). Clade 10: Penaeoidea except for *Benthesicymus bartletti* and *Benthesicymus* sp., defined by 17(2), 32(4). Clade 11: Penaeoidea except for Benthesicymidae and Aristeidae, defined by 10(2), 23(1), **40(2)**, 93(1). Clade 12: Sicyoniidae and

Figure 4. Selected morphological characters. Telson posterior margin. (A) *Pasiphaea princeps*, cleft. (B) *Rimapenaeus constrictus*, with robust setae only. (C) *Stenopus hispidus*, truncate. Telson ornamentation. (D) *Penaeopsis serrata*, with spines and robust setae. (E) *Xiphopenaeus kroyeri*, unarmed, with spines only. Telson robust setae position. (F) *Lucifer typus*, lateral and terminal. (G) *Oplophorus spinosus*, lateral and dorsal.

Penaeidae, defined by 99(3), 100(1). Clade 13: *Penaeopsis serrata* and *Artemesia longinaris*, defined by 46(2), 93(3). Clade 14: *Farfantepenaeus paulensis, Litopenaeus schmitti, Parapenaeus americanus, Xiphopenaeus kroyeri* and *Rimapenaeus constrictus*, defined by 19(1). Clade 15: *Farfantepenaeus paulensis* and *Litopenaeus schmitti*, defined by 1(3). Clade 16: *Parapenaeus americanus, Xiphopenaeus kroyeri* and *Rimapenaeus constrictus*, defined by 13(2).

3.3 Analysis 2 - Caridea and Stenopodidea as outgroups

Ninety-three equally most parsimonious trees were found (for indices see Table 1), and from these two consensus trees were calculated (strict and majority rule) (Fig. 7). Character states considered non-homoplastic are depicted in bold. For the majority rule consensus tree, we obtained the following results:

Dendrobranchiata (clade 3) is monophyletic, defined by 6(2), **30(1)**, 38(1), **39(1)**, 45(1), **80(2)**, 90(2). Luciferidae (clade 5) is monophyletic, defined by **6(1)**, 19(1), 26(2), **38(3)**, **41(1)**, **51(1)**, **64(1)**, **65(1)**, **72(1)**, **76(1)**. Sergestoidea (clade 28) is a natural group, now with the families Luciferidae and Sergestidae in a monophyletic clade, defined by 57(1), **58(1)**, **59(1)**. Sergestidae (clade 7) is a natural group defined by 32(4), **42(2)**. Penaeoidea (clade 8) is a natural group defined by 9(2), 23(2), 33(4), 82(2). Benthesicymidae is not a natural group. Sicyoniidae (clade 17) is a natural

Table 1. Some values of the three different analyses. NT = total number of trees; Tl = total length; CI = consistency index; RI = retention index; RC = rescaled consistency index.

Analysis	NT	TI	CI	RI
1	69	290	0.50	0.64
2	93	304	0.49	0.63
3	69	319	0.49	0.63

group defined by the following apomorphies: **8(2)**, **33(3)**, **37(2)**, 57(1), **81(4)**, **101(2)**. Penaeidae (clade 29) is a natural group characterized by 81(4), although optimization is not possible. Solenoceridae (clade 19) is a natural group defined by **14(2)**, **90(2)**. Aristeidae (clade 24) is a natural group. As in analysis 1, characters 22(3), 61(1), 67(1), 85(1) characterize the family but cannot be optimized.

Figure 5. Analysis 1 majority rule consensus of 69 equally parsimonious trees (length = 290), with clade numbers (black squares), bootstrap and MR (percentage of appearance of each clade in all original trees, in italics) values.

Pasiphaea princeps

4 ┌ Heterocarpus inopinatus
  └ Oplophorus spinosus

Aristaeomorpha foliacea

Plesiopenaeus coruscans

Hymenopenaeus debilis

1 Solenocera necopina

Mesopenaeus tropicalis

Pleoticus muelleri

1 ┌ Sicyonia burkenroadi
6 └ Sicyonia dorsalis

Sicyonia typica

1 ┌ Farfantepenaeus paulensis
  └ Litopenaeus schmitti

Penaeopsis serrata

Parapenaeus americanus

Artemesia longinaris

Xiphopenaeus kroyeri

Rimapenaeus constrictus

Hymenopenaeus aphoticus

Haliporoides sibogae sibogae

Benthesicymus bartletti

Benthesicymus carinatus

5 ┌ Sergia regalis
  └ Sergestes armatus

12 ┌ Lucifer faxoni
   └ Lucifer typus

Figure 6. Analysis 1, strict consensus of 69 equally parsimonious trees (length = 290), with Bremer support index values.

Other clades (not taxonomically defined or named) in the analysis are: Clade 9: Penaeoidea except for *Benthesicymus* sp., defined by 1(2), 4(2), 28(2). Clade 10: Penaeoidea except for *Benthesicymus bartletti* and *Benthesicymus* sp., defined by 17(2), 32(4). Clade 11: Penaeoidea except for Benthesicymidae and Aristeidae, defined by 10(2), **40(2)**, 93(1). Clade 12: Sicyoniidae and Penaeidae, defined 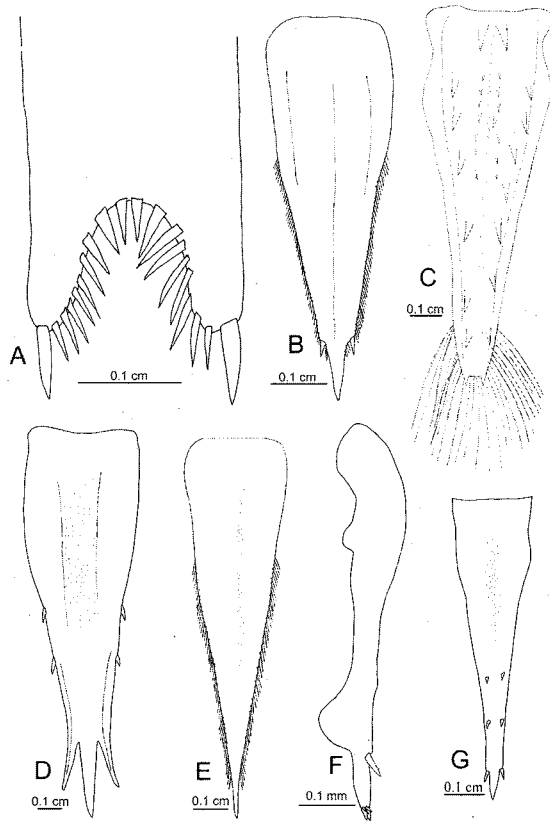by 82(1), **99(3)**, 100(1). Clade 13: *Penaeopsis serrata* and *Artemesia longinaris*, defined by 46(2), **93(3)**. Clade 14: *Farfantepenaeus paulensis, Litopenaeus schmitti, Parapenaeus americanus, Xiphopenaeus kroyeri* and *Rimapenaeus constrictus*, characterized by 19(1). Clade 15: *Farfantepenaeus paulensis* and *Litopenaeus schmitti*, defined by 1(3). Clade 16: *Parapenaeus americanus, Xiphopenaeus kroyeri* and *Rimapenaeus constrictus*, defined by 13(2). Clade 27: Dendrobranchiata and *Stenopus hispidus*, defined by 31(2), 55(1), 70(2), 79(1), 82 (1), 84(1).

3.4 *Analysis 3 - Caridea, Stenopodidea and Nephropidae as outgroups*

Sixty-nine equally most parsimonious trees were found (for indices see Table 1) and, from these, two consensus trees were calculated (strict and majority rule) (Figs. 8, 9). Character states considered non-homoplastic are depicted in bold. For the majority rule consensus tree, we obtained the following results:
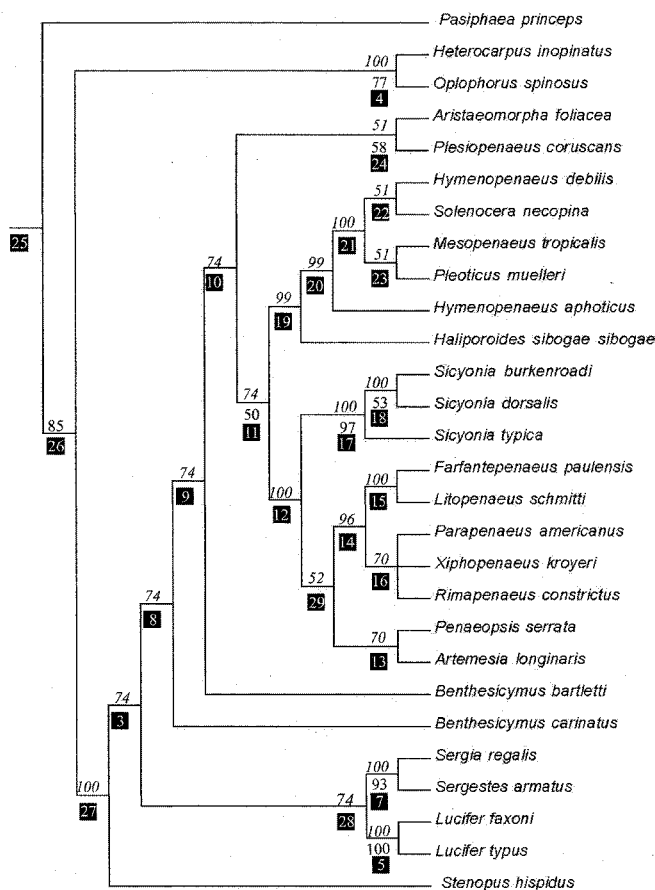
Figure 7. Analysis 2, majority rule consensus of 93 equally parsimonious trees (length = 304), with clade numbers (black squares), bootstrap and MR (percentage of appearance of each clade in all original trees, in italic) values.

Dendrobranchiata (clade 3) is monophyletic, defined by 6(2), **30(1)**, 38(1), **39(1)**, 45(1), **80(2)**. Luciferidae (clade 5) is a monophyletic group, defined by **6(1)**, 19(1), 26(2), **38(3)**, **41(1)**, **49(1)**, **51(1)**, **64(1)**, **65(1)**, **72(1)**, **76(1)**. Sergestoidea (clade 28) is a natural group. As in analysis 2, the families Luciferidae and Sergestidae constitute a monophyletic clade defined by 57(1), **58(1)**, 59(1). Sergestidae (clade 7) is a natural group defined by 32(4), **42(2)**. Penaeoidea (clade 8) is a natural group defined by 9(2), 15(2), 25(2), 46(2), 82(2). Benthesicymidae is not a natural group. As in analysis 1 and 2, the benthesicymid species do not appear together. Sicyoniidae (clade 17) is a natural group defined by **8(2)**, 32(3), **37(2)**, 57(1), **81(4)**, **101(2)**. Penaeidae could not be evaluated (as in analysis 1). Solenoceridae (clade 19) is a natural group defined by **14(2)**, **90(2)**. Aristeidae (clade 24) is a natural group characterized (as in analyses 1 and 2) by 22(3), 61(1), 67(1), 85(1), but optimization of characters is not possible.

Other clades depicted in this analysis are: Clade 9: Penaeoidea except for *Benthesicymus* sp., defined by 1(2), 4(2), 28(2). Clade 10: Penaeoidea except for *Benthesicymus bartletti* and *Benthesicymus* sp., defined by 17(2), 32(4). Clade 11: Penaeoidea except for Benthesicymidae and Aristeidae, defined by 10(2), **40(2)**, 93(1). Clade 12: Sicyoniidae and Penaeidae, defined by 82(1), **99(3)**, 100(1). Clade 13: *Penaeopsis serrata* and *Artemesia longinaris*, defined by 46(2), **93(3)**. Clade 14: *Farfantepenaeus paulensis, Litopenaeus schmitti, Parapenaeus americanus, Xiphopenaeus kroyeri*
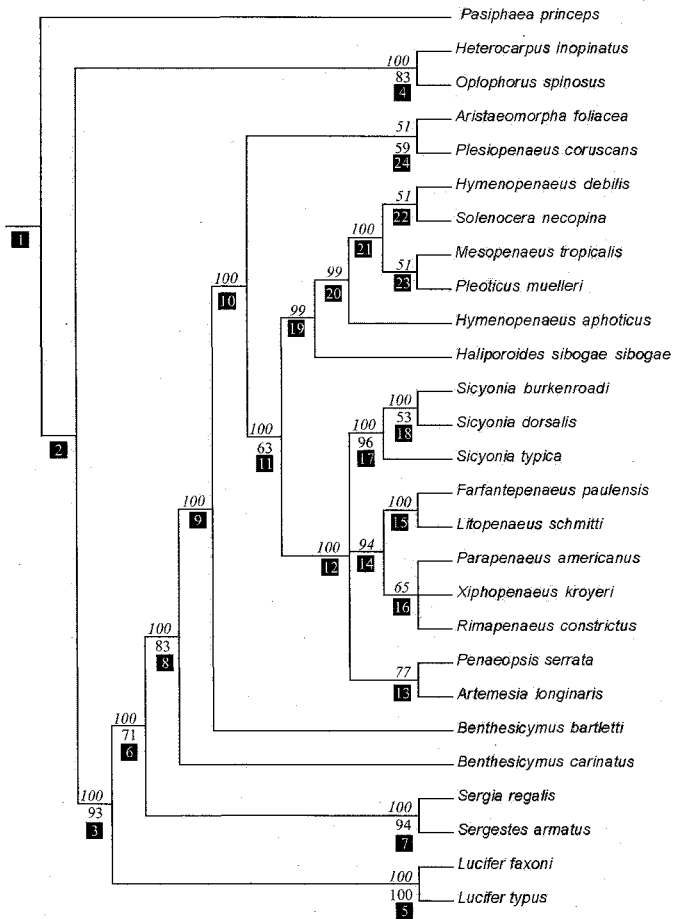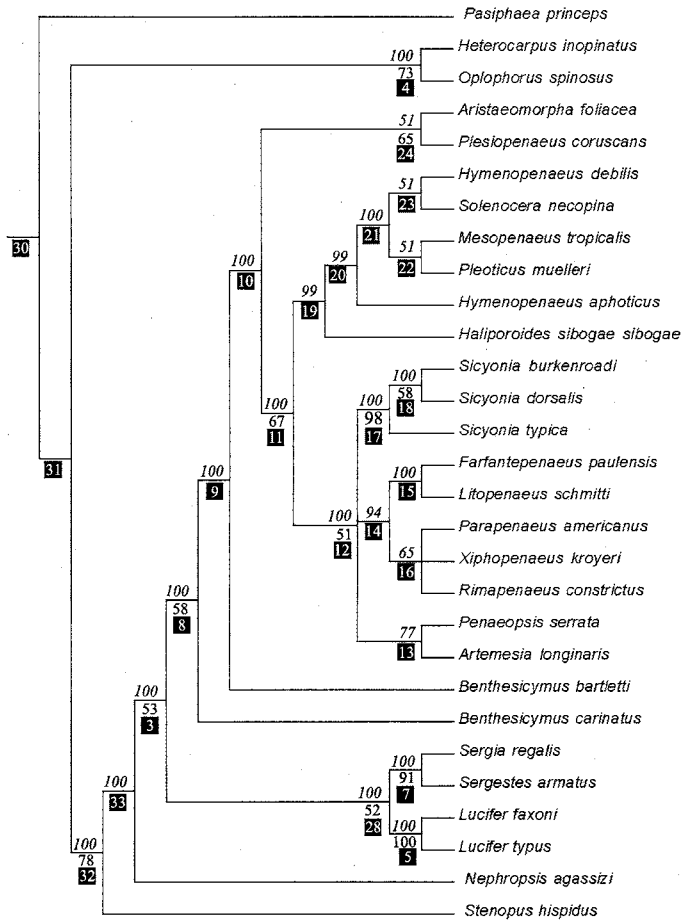
Figure 8. Analysis 3, majority rule consensus of 69 equally parsimonious trees (length = 319), with clade numbers (black squares), bootstrap and MR (percentage of appearance of each clade in all original trees, in italic) values.
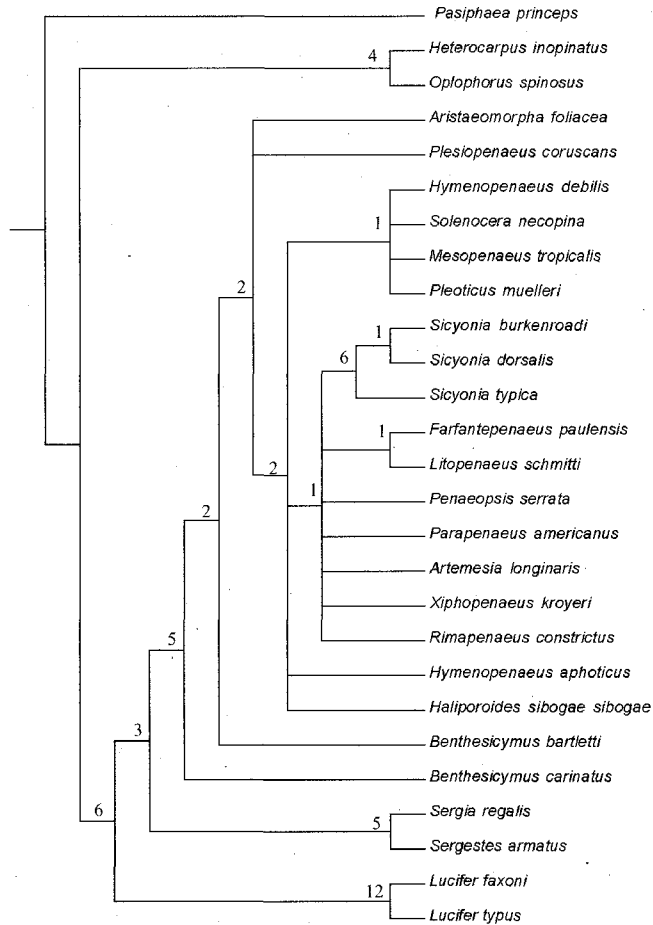
and *Rimapenaeus constrictus*, characterized by 19(1). Clade 15: *Farfantepenaeus paulensis* and *Litopenaeus schmitti*, defined by 1(3). Clade 16: *Parapenaeus americanus*, *Xiphopenaeus kroyeri* and *Rimapenaeus constrictus*, defined by 13(2). Clade 33: Dendrobranchiata and *Nephropsis agassizi*, defined by 31(2), 55(1), 70(2), 79(1), 82(1), 84(1).

4   DISCUSSION

4.1   *Choice of outgroup and different analyses*

Selecting the best outgroup for phylogenetic analysis is often a difficult decision, and this was true in our case as well. Although Pleocyemata is often depicted as the sister group to Dendrobranchiata in the literature, that group (Pleocyemata) is highly diverse, and it is unclear which group among the Pleocyemata should be used. Consequently, we prepared three different analyses using different Pleocyemata groups. Interestingly, although some topologies are similar, all three analyses differed. When we compared clades that appeared in two or all three analyses, sometimes character polarity differed. Analysis 3 is perhaps the most realistic in that more pleocyemata taxa are included,
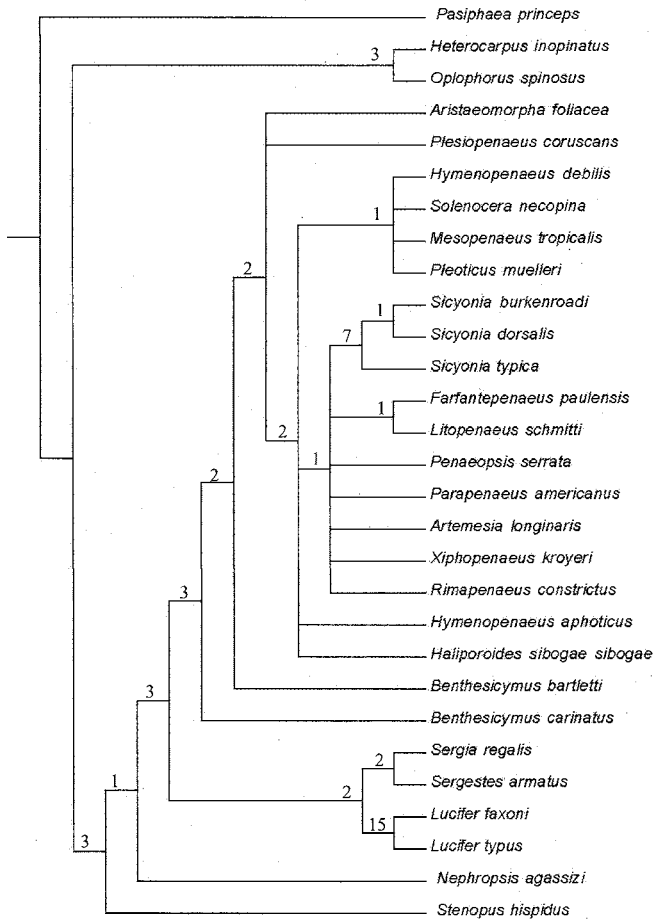
Figure 9. Analysis 3, strict consensus of 69 equally parsimonious trees (length = 319), with Bremer support index values.

although all three analyses are valuable in highlighting characters and polarities that might be important in dendrobranchiate phylogeny. Euphausiids, another potential outgroup choice, were not used in this study.

4.2 *Dendrobranchiata as a monophyletic group*

We began with the hypothesis that the suborder is monophyletic, as indicated in the literature (e.g., Burkenroad 1983; Felgenhauer & Abele 1983; Dixon et al. 2003), and with the suborder defined by the presence of 1) dendrobranchiate gills (but see Martin et al. 2007); 2) the first three pairs of pereopods usually chelate; 3) the pleura of the second abdominal somite not overlapping those of the first; 4) prominent hinges between their pleonic somites; 5) eggs released directly into water (rather than carried by females); 6) larvae hatching as nauplii or protozoea; 7) a petasma in males; and 8) pleopods without an appendix interna, except for some vestigial structure found in males. In our analyses, only the following characters proved to be synapomorphies of Dendrobranchiata: dendrobranchiate gills [6(2)], prominent pleonic hinges [30(1)], larvae hatching as nauplii or protozoea [39(1)], and the presence of a petasma in males [80(2)]. All species we examined have the first two pereopods chelate (except for Sergestoidea). A distinctive character of the

dendrobranchiates (as noted in previous studies) is the presence of a chelate third pereopod [70(2)]. However, although this character is "typical" of Dendrobranchiata, in analysis 1 it appears as a synapomorphy of clade 6 (Penaeoidea + Sergestidae), and in analyses 2 and 3 as a synapomorphy of clades 27 and 32, respectively. The pleura of the second abdominal somite not overlapping those of first [31(2)] is apomorphic only in analysis 1; in analyses 2 and 3 this character appears as a synapomorphy of clades 27 and 32. Eggs released directly into the water [38(1)] vs. being retained on the female pereopods [38(3)] is a synapomorphy for Dendrobranchiata only in analyses 2 and 3. The ratio between scaphocerite and antennae 1 peduncle [45(1)] is a synapomorphy for Dendrobranchiata also in analyses 2 and 3. The absence of hook setae on the male appendix interna [83(1)] is apomorphic only in analysis 1; in analyses 2 and 3 this character is a synapomorphy of clades 27 and 32.

Despite the fact that there is much evidence to indicate that the suborder is monophyletic, in the strict consensus of analysis 2, the dendrobranchiate species appear as a non-monophyletic clade, grouped with *Stenopus hispidus* as the sister group to the Caridea. Similarly, Dixon et al. (2003) did not recover Dendrobranchiata in the most parsimonious trees in their ordered analysis. Yet we think it unlikely that Dendrobranchiata is non-monophyletic, with most of the above discrepancies explained by outgroup choice or character polarity. Here, we accept the monophyly and current classification of Dendrobranchiata, divided into two superfamilies, Sergestoidea and Penaeoidea, as discussed below.

The position of Luciferidae is a salient question in any consideration of dendrobranchiate phylogeny. The family is extremely different from other Dendrobranchiata, with most of the differences assumed to be modifications for a planktonic life. Although the inclusion of Luciferidae within Dendrobranchiata by Bate (1988) was not based on cladistic methods, it was assumed (then and now) that most of the family's unusual features represented simple character loss. In all of our analyses, the family clustered with the other families of Dendrobranchiata; for this reason we feel that Luciferidae should be maintained for now as a Dendrobranchiata family.

4.3   *Sergestoidea as a natural group*

Sergestoidea includes two families, Sergestidae and Luciferidae. Traditionally, the superfamily has been poorly defined, often by such different character states as having pereopods 4 and 5 reduced or absent and/or having the antennular flagellum modified or absent. In analysis 1, Sergestoidea appears as non-monophyletic. However, in analyses 2 (except for strict consensus) and 3 these families appear together in clade 28, defined by the absence of the exopod on maxilliped 3 [57(1)], the absence of a dactyl on P1 [58(1)], and the absence of a chela on P1 [59(1)]. The absence of a P1 dactyl and consequently the chela is scored here as non-homoplastic, but from the literature we know that this is indeed homoplastic, as other sergestid genera not treated here (e.g., *Acetes*, *Peisos*, *Sicyonella*) possess a minute chela on P1. Although these characters have been described in the literature, they were never used to define the superfamily.

4.4   *Penaeoidea as a natural group*

The superfamily Penaeoidea contains five families: Aristeidae, Benthesicymidae, Penaeidae, Sicyoniidae, and Solenoceridae. In all analyses, the superfamily was monophyletic (clade 8), with the exception of the strict consensus of analysis 2. In the literature the superfamily is defined by having all five pereopods well developed, at least some somites with three branchiae on each side, and at least 11 well-developed gills on each side. None of these characters was found as a synapomorphy here, where the superfamily is defined instead by the presence of a tubercle on the terminal article of the eyestalk [9(2)] and the presence of the branchiocardiac carina [23(2)].

4.5   *Benthesicymidae as a non-natural group*

In all trees, this family did not appear as a monophyletic clade. Characters used in the literature to define the family (e.g., the presence of an open petasma [82(1)] and the presence of a tubercle on the eyestalk [9(2)]) are not synapomorphies, as they are shared by other species within the Penaeoidea. It is important to notice that the two species used in this study belong to two different groups among the genus *Benthesicymus*. The first group is defined in the literature by the following characters: presence of marginal branchiostegal spine, with branchiostegal carina not sharp; exopods of first maxilliped narrowing abruptly to tip; merus of second maxilliped expanded laterally; dactylus of third maxilliped triangular, with only one spine at tip; exopods of all pereopods small but easily perceptible. The second group is defined by the following characters: presence of non-marginal branchiostegal spine, with very sharp branchiostegal carina; exopods of first maxilliped tapering to tip; merus of second maxilliped not expanded laterally; dactylus of third maxilliped subrectangular, distal margin bearing more than 1 strong spine; exopods of all pereopods minute (Burkenroad 1936; Kikuchi & Nemoto 1991; Dall 2001). Our study suggests that this morphological separation is in accordance with evolutionary patterns within the genus *Benthesicymus*. However, very few species of the family, which includes some 40 species, were used in our analyses, so our results have to be considered preliminary.

4.6   *Penaeidae as a non-natural group*

Most studies on penaeid phylogeny have indicated that the family is not monophyletic (Quan et al. 2004; Vázquez-Bader et al. 2004; Voloch et al. 2005). Characters previously used to diagnose the family are not always synapomorphs; e.g., the presence of an ocular scale [10(2)] is synapomorphic to clade 11, not to Penaeidae only. Similarly, the exopods of maxilliped 2 [54(2)] and maxilliped 3 [57(2)] are characteristic of clade 10, not just the Penaeidae. Other characters are "one time" occurrences with no phylogenetic signal, such as the semi-open petasma [80(3)] found only in *Litopenaeus schmitti* (a semi-closed petasma [81(3)] is characteristic of clade 29). Analyses 1 and 3 resulted in a trichotomy (clade 12) of two groups of Penaeidae (clades 13, 14) and a group of Sicyoniidae (clade 17); no further resolution was possible here. On the other hand, in analysis 2 the majority rule consensus Penaeidae clades are nested in a monophyletic clade 29, characterized by the presence of a semi-closed petasma [81(3)]; however, clade 29 is not supported by either Bremer index or bootstrap analysis. Regardless of whether Penaeidae is monophyletic, two groups emerged consistently: clade 14 (*Farfantepenaeus paulensis, Litopenaeus schmitti, Parapenaeus americanus, Xiphopenaeus kroyeri*, and *Rimapenaeus constrictus*), defined by the absence of a branchiocardiac carina [19(1)], and clade 13 (*Penaeopsis serrata* + *Artemesia longinaris*), defined by the presence of the parapenaeid spine [46(2)] and a telson armed with spines and robust setae [93(3)]. The close relationship between sicyoniids and penaeids shown here was suggested earlier by both Crosnier (1978) and Burkenroad (1983).

4.7   *Solenoceridae as a natural group*

Although this clade is present only in majority rule consensus trees (99%) and additionally was not supported by Bremer index and bootstrap analysis, we continue to consider the family monophyletic based on two non-homoplastic synapomorphies (presence of a postorbital spine [14(2)] and presence of a distolateral projection on male pleopod 2 [90(2)]), as has been noted previously in the literature. The position of the family among Dendrobranchiata in all analyses obtained here showed solenocerids closer to penaeids and sicyoniids (as in clade 11), in contrast with some previous authors (e.g., Crosnier 1978; Burkenroad 1983) who placed solenocerids closer to aristeids.

4.8   *Status of the Aristeidae*

This clade is present in all majority rule consensus trees, although it was not supported by Bremer index and has a low bootstrap value (58%). Additionally, no synapomorphies were found to define or characterize the family. Characters used to describe the family in the past, such as the presence of an ocular tubercle and an open petasma, are present also in clades 8 and 9. Because of the preliminary nature of this analysis, we are leaving the question of aristeid monophyly unanswered for now.

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APPENDIX 1

List of species examined in this study with specimen collection numbers. MNRJ = UFRJ collection, Museu Nacional, Brazil; FURG = Fundação Universitária Rio Grande, Brazil; USNM = National Museum of Natural History, Smithsonian Institution, USA.

Suborder Dendrobranchiata Bate, 1888
Superfamily Penaeoidea Rafinesque-Schmaltz, 1815
 Family Aristeidae Wood-Mason, 1891
  Aristaeomorpha foliacea (Risso, 1827) MNRJ 13775, MNRJ14561
  Plesiopenaeus coruscans (Wood-Mason, 1891) MNRJ 14522, MNRJ 14577
 Family Benthesicymidae Wood-Mason, 1891
  Benthesicymus bartletti Smith, 1882 MNRJ 19167, MNRJ19164
  Benthesicymus carinatus Smith, 1884 MNRJ 14731
 Family Penaeidae Rafinesque-Schmaltz, 1815
  Artemesia longinaris Bate, 1888 MNRJ 1653
  Farfantepenaeus paulensis (Pérez Farfante, 1967) MNRJ 28
  Litopenaeus schmitti (Burkenroad, 1936) MNRJ 15835
  Parapenaeus americanus Rathbun, 1901 MNRJ 14815
  Penaeopsis serrata Bate, 1881 MNRJ 14784
  Rimapenaeus constrictus (Stimpson, 1874) MNRJ 1680
  Xiphopenaeus kroyeri (Heller, 1862) MNRJ 49
 Family Sicyoniidae Ortmann, 1898
  Sicyonia burkenroadi Cobb, 1971 MNRJ 14632
  Sicyonia dorsalis Kingsley, 1878 MNRJ 68, MNRJ 1656
  Sicyonia typical (Boeck, 1864) MNRJ 63, MNRJ 1692
 Family Solenoceridae Wood-Mason, 1891
  Haliporoides sibogae sibogae (De Man, 1907) USNM 261459
  Hymenopenaeus aphoticus Burkenroad, 1936 FURG 1609, FURG 2681
  Hymenopenaeus debilis Smith, 1882 - MNRJ 14794, MNRJ 14796, MNRJ 14798, MNRJ, 14807
  Mesopenaeus tropicalis (Bouvier, 1905) FURG 220
  Pleoticus muelleri (Bate, 1888) - MNRJ 39
  Solenocera necopina Burkenroad, 1939 MNRJ 14631, MNRJ 14630
Superfamily Sergestoidea Dana, 1852
 Family Luciferidae Thompson, 1829
  Lucifer typus H. Milne Edwards, 1837 MNRJ 18048, MNRJ 18050
  Lucifer faxoni Borradaile, 1915 MNRJ 18046, MNRJ 18054
 Family Sergestidae Dana, 1852
  Sergestes armatus Kroyer, 1855 MNRJ 15505
  Sergia regalis (Gordon, 1939) MNRJ 15507, MNRJ 15508, MNRJ 15509
Suborder Pleocyemata Burkenroad, 1963
Infraorder Caridea Dana, 1852
Superfamily Pandaloidea Haworth, 1825
 Family Pandalidae Haworth, 1825
  Heterocarpus inopinatus Tavares, 1999 MNRJ 14693
Superfamily Oplophoroidea Dana, 1852
 Family Oplophoridae Dana, 1852
  Oplophorus spinosus (Brullé, 1839) MNRJ 14874
Superfamily Pasiphaeoidea Dana, 1852
 Family Pasiphaeidae Dana, 1852
  Pasiphaea princeps Smith, 1884 MNRJ 19525, MNRJ 19522
Infraorder Stenopodidea Bate, 1888
 Family Stenopodidae Claus, 1827
  Stenopus hispidus (Olivier, 1811) MNRJ 2288
Infraorder Astacidea Latreille, 1802
Superfamily Nephropoidea Dana, 1852
 Family Nephropidae Dana, 1852
  Nephropsis agassizii A. Milne-Edwards, 1880 MNRJ 19232

APPENDIX 2

Morphological characters used in the analyses. Although some characters listed below proved to be uninformative, we have listed them here for informational purposes and the possibility of future analyses.

1. Rostral spines: (1) absent; (2) present, dorsal only; (3) present, dorsal and ventral; (4) present, dorsal and lateral; (5) present, lateral only.
2. Number of dorsal rostral spines: (1) up to 5; (2) 6–9; (3) 10 or more.
3. Number of ventral rostral spines: (1) up to 4; (2) 5–7; (3) 8 or more.
4. Post-rostral spines: (1) absent; (2) present.
5. Number of post-rostral spines: (1) up to 2; (2) 3; (3) 4 or more.
6. Gills: (1) absent; (2) dendrobranch; (3) phyllobranch; (4) trichobranch.
7. Number of gills: (1) at least 11 on each side of the body; (2) from 1 to 8 on each side of the body.
8. Ocular stylet: (1) absent; (2) present.
9. Ocular tubercle: (1) absent; (2) present.
10. Ocular scale: (1) absent; (2) present.
11. Ocelo on eye: (1) absent; (2) present.
12. Rostrum length: (1) surpassing antennular peduncle (Fig. 1A); (2) not surpassing antennular peduncle, reaching cornea (Fig. 1B); (3) not surpassing antennular peduncle, not reaching cornea (Fig. 1C); (4) not surpassing antennular peduncle, surpassing cornea (Fig. 1D).
13. Orbital spine: (1) absent; (2) present.
14. Post-orbital spine: (1) absent; (2) present.
15. Adrostral carina: (1) absent; (2) present.
16. Antennal spine: (1) absent; (2) present.
17. Antennal carina: (1) absent; (2) present.
18. Cervical sulci: (1) absent; (2) present; (3) reduced.
19. Branchiocardiac carina: (1) absent; (2) present.
20. Hepatic sulci: (1) absent; (2) present.
21. Hepatic spine: (1) absent; (2) present.
22. Branchiostegal spine: (1) absent; (2) present, marginal; (3) present, not marginal.
23. Branchiostegal carina: (1) absent; (2) present.
24. Post-cervical sulci: (1) absent; (2) present.
25. Gastro-orbital sulcus: (1) absent; (2) present.
26. Pterygostomian spines: (1) absent; (2) present.
27. Longitudinal carina on carapace: (1) absent; (2) present.
28. Thoracic sternites width: (1) sternites 3–8 narrow; (2) sternites 3–5 narrow; (3) sternites 3–6 narrow.
29. Pleon: (1) laterally compressed; (2) dorso-ventral compressed.
30. Pleonic hinges: (1) prominent; (2) hidden; (3) slight.
31. Second abdominal pleura: (1) overlapping first; (2) not overlapping first.
32. Posterior spines on abdominal pleura: (1) absent; (2) present on somites 3–6; (3) present on somites 5–6; (4) present on somite 6.
33. Dorso-abdominal carina: (1) absent; (2) present on somites 2–6; (3) present on somites 3–6; (4) present on somites 4–6; (5) present on somite 6; (6) present on somites 1–6; (7) present on somites 3–5; (8) present on somites 5–6.
34. Dorso-posterior spines on abdominal somites: (1) absent; (2) 3–6; (3) 4–6; (4) 6; (5) 5; (6) 1,5,6.
35. Abdominal somite 6 with posterior dorso-lateral spines: (1) absent; (2) present.
36. Ventral projections on male abdominal somite 6: (1) absent; (2) present two rounded big projections and without a small disto-ventral projection; (3) present two sharp-pointed big projections and with a small disto-ventral projection.
37. Pleopods 3–5: (1) biramous; (2) uniramous.
38. Eggs: (1) released free in water; (2) brooded in female pleopods; (3) brooded in female pereopods.
39. Larvae: (1) hatch as nauplius; (2) hatch as protozoea.
40. Antenna 1 prosartema: (1) absent; (2) present.
41. Antenna 1: (1) uniflagellate; (2) biflagellate.
42. Male antenna 1: (1) without clasper organ; (2) with clasper organ.
43. Scaphocerite: (1) absent; (2) present.

44. Antenna 1 first article: (1) without disto-lateral spine on outer margin; (2) with disto-lateral spine on outer margin.
45. Ratio scaphocerite/antenna 1 peduncle: (1) up to 1.39; (2) 1.4–1.98; (3) 1.99 or more.
46. Ventromesial (parapenaeid) spine: (1) absent; (2) present.
47. Mandible: (1) only with incisor process; (2) with molar and incisor processes together; (3) with molar and incisor processes separated.
48. Mandibular palp: (1) absent; (2) present.
49. Maxilla 1 palp: (1) absent; (2) present.
50. Maxilla 2: (1) with two bilobed setose endites; (2) with one bilobed and one unilobed setose endites; (3) with reduced endites; (4) with one bilobed and one reduced endites.
51. Maxilla 2 palp: (1) absent; (2) present.
52. Number of maxillipeds: (1) 0; (2) 3.
53. Maxilliped 1 endite: (1) oval; (2) reduced, no defined sharp; (3) absent.
54. Maxilliped 2 exopod: (1) absent; (2) present.
55. Articles of maxilliped 3 endopod: (1) separated; (2) fused.
56. Maxilliped 3 dactyl: (1) with only one article; (2) with 5 articles.
57. Maxilliped 3 exopod: (1) absent; (2) present.
58. Pereopod 1 dactyl: (1) absent; (2) present.
59. Pereopod 1: (1) without chela; (2) with chela.
60. Pereopod 1 without chela: (1) with a subchela formed by a row of strongly flexed robust setae present on distal margin of carpus and proximal margin of propodus; (2) without subchela.
61. Pereopod 1 merus: (1) with a sub-distal robust setae; (2) with a sub-distal spine; (3) unarmed; (4) with a row of 5 spines; (5) with a sub-distal robust setae and a row of 3 spines.
62. Pereopod 1 ischium: (1) unarmed; (2) with a mesial spine; (3) with a distal spine.
63. Right and left pereopod 2: (1) of equal size; (2) of unequal size.
64. Pereopod 2 dactyl: (1) absent; (2) present.
65. Pereopod 2: (1) without chela; (2) with chela.
66. Pereopod 2 carpus: (1) divided; (2) entire.
67. Pereopod 2 merus: (1) with a sub-distal robust seta; (2) unarmed; (3) with a disto-lateral row of 5–7 robust setae.
68. Pereopod 2 ischium: (1) unarmed; (2) with one spine.
69. Pereopod 3 dactyl: (1) absent; (2) present.
70. Pereopod 3: (1) without chela; (2) with chela.
71. Pereopod 3 merus: (1) with a robust setae row; (2) without a robust setae row.
72. Pereopod 4: (1) absent; (2) present.
73. Pereopod 4 dactyl: (1) absent; (2) present.
74. Pereopod 4 merus: (1) with a robust setae row; (2) without a robust setae row.
75. Ratio P4/ P3: (1) up to 1.1; (2) 1.11–1.6; (3) 1.61 or more.
76. Pereopod 5: (1) absent; (2) present.
77. Pereopod 5 dactyl: (1) absent; (2) present.
78. Ratio P5/ P3: (1) up to 1.19; (2) 1.2–1.98; (3) 1.99 or more.
79. Exopods on pereopods: (1) absent; (2) present, reduced; (3) present, not reduced.
80. Petasma: (1) absent; (1) present.
81. Petasma present: (1) open; (2) semi-open; (3) semi-closed; (4) closed.
82. Male appendix interna: (1) absent; (2) present only on pleopod 2; (3) present on pleopods 2–5.
83. Hook setae on male appendix interna: (1) absent (Fig. 2C); (2) present on pleopods 2–5 (Fig. 2A,B).
84. Female appendix interna: (1) absent; (2) present on pleopods 2–5.
85. Appendix masculina: (1) smaller than appendix interna; (2) about the same size as appendix interna; (3) bigger than appendix interna.
86. Appendix masculina size: (1) longer than wide; (2) as long as wide.
87. Appendix interna size: (1) as long as wide; (2) longer than wide.
88. Thelycum: (1) absent; (2) present.
89. Thelycum present: (1) open; (2) closed.
90. Disto-lateral projection on male pleopod 2: (1) absent; (2) present, near appendix interna and appendix masculine (Fig. 2D).
91. Uropods: (1) exopod and endopod unarmed (Fig. 3A); (2) exopod with an outer lateral spine, endopod unarmed (Fig. 3B); (3) endopod and exopod with an outer lateral spine both (Fig. 3C).
92. Telson posterior margin: (1) cleft (Fig. 4A); (2) pointed (Fig. 4B,D,E,G); (3) truncate (Fig. 4C,F).
93. Telson ornamentation: (1) only with spines (Fig. 4C); (2) only with robust setae (Fig. 4A,B,F,G); (3) with spines and robust setae (Fig. 4D); (4) unarmed (Fig. 4E).

94. Robust setae position: (1) lateral (Fig. 4B); (2) terminal (Fig. 4A); (3) lateral and terminal (Fig. 4F); (4) lateral and dorsal (Fig. 4G).
95. Number of robust setae on each side of telson: (1) up to 4; (2) 4.1–7.1; (3) 7.2 or more.
96. Number of spines on each side of telson: (1) up to 3.6; (2) 3.7–6.3; (3) 6.4 or more.
97. Photophores: (1) absent; (2) present.
98. Pesta organ: (1) absent; (2) present. (uninformative)
99. Epipods on pereopods 1–5: (1) absent; (2) present on P1–P5; (3) present on P1–P3; (4) present on P1–P4.
100. Epipods on pereopods 1–5 shape: (1) bifid (Fig. 3D); (2) foliaceous (Fig. 3E).
101. Abdominal somites with antero-dorsal spines: (1) absent; (2) present on somite 1.
102. Abdominal pleurae with lateral carina: (1) absent; (2) present.

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