A PHYLOGENETIC ANALYSIS OF FOSSIL AND EXTANT SHRIMP-LIKE DECAPODS (DENDROBRANCHIATA AND CARIDEA)

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by

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Summary

Decapod crustaceans are of particular interest from both historical and modern perspectives due to their great diversity throughout their evolutionary history and as a food resource with great economic importance for both fisheries and aquaculture. The order's history can be traced back to the Late Devonian, but a good record of their diversity doesn't exist until the Mesozoic.

Decapods, for the most part, have moderate preservation potential, compared to most invertebrate groups, and have a rich fossil record which has allowed systematists to categorize large groups within the order through their evolutionary history and to compute intra-order phylogenies based on very apparent morphological characters. This, however, is not the case for the shrimp-like decapods, which have a significantly lower preservation potential due to their softer exoskeleton.

The late Jurassic Solnhofen Läggerstatte in southern Germany has yielded a very diverse and abundant record of shrimp-like decapods, among other animals. The exceptional preservation exhibited by these fossils allows the visualization of even some of the most discreet morphological features. In this work, a phylogenetic analysis was run using both fossil shrimp primarily from the Solnhofen Läggerstatte and extant species of shrimp-like decapods. The purpose of this work is to place both modern and fossil shrimp-like decapod species in a phylogenetic context through the comparison of their morphological characters. We believe this study offers fresh insight on the evolutionary relationships and character polarization within the decapod order.

139 characters (82 binary + 57 multistate; 45 from carapace, 19 from cephalic appendage, 47 from pereiopods, 18 from pleon, 8 from telson, and 2 others) were coded for 100 species (45 fossil + 55 extant). Specimens belong to several collections: The United States National Museum of Natural History, The Carnegie Museum, The Yale Peabody Museum, The Staatliches Naturwissenschaftliche Sammlungen Bayerns, and a private collection in Chicago.

Euphausia superba (Dana, 1850) was used as outgroup. The character matrix was generated in Microsoft Excel and Mesquite. Phylogenetic analysis was run in PAUP* 4.0b10. Character history was traced in Mesquite.

The current work does not support the monophyly of any currently accepted taxonomic levels within the order except for the dendrobranch superfamilies Penaeoidea and Sergestoidea and the family Aegeridae. The hypothesis that dendrobranchs are the plesiomorphic form for the group is partially supported due to the early branching of the sergestoid clade; however, many dendrobranch character states are considered to be homoplasic since penaeoids do not group together with sergestoids. The monophyly of dendrobranch superfamilies is supported, though the monophyly of family Penaeidae is challenged.

The monophyly of carideans as well as caridean superfamilies is challenged in the current work as well. Basal caridean (Atydae, Pasiphaeidae, and Procarididae) family placement with respect to other more derived families in this study is consistent with the results from previous phylogenetic works.

The inclusion of fossil species in a decapod shrimp phylogeny offers new insight to the order's evolutionary history. The difference in the extant only and the comprehensive phylogeny topologies results from different character polarization and clade groupings. This and the fact that nodes in both phylogenies have overall very little support suggests that reevaluation of character designation and species selection is necessary. Characters with too many states, multiple characters describing a single morphological aspect, and characters with unclear functions are some that will be reevaluated. Differential character weighting is also being considered. More taxa will be coded and included in the analysis to yield a more balanced representation of each suborder as well as to represent the morphological variation within each family.

Introduction

Decapod crustaceans are of particular interest from both historical and modern perspectives due to their great diversity throughout their evolutionary history and as a food resource with great economic importance for both fisheries and aquaculture. The history of the order can be traced back to the Late Devonian (Feldmann and Schweitzer, 2010; Jones *et al*., 2014), but a good record of their diversity doesn't exist until the Mesozoic (Glaessner, 1969; Bauer, 2004; Schweitzer and Feldmann, 2015).

Decapods, for the most part, have moderate preservation potential, compared to most invertebrate groups, and have a rich fossil record which has allowed systematists to categorize large groups within the order through their evolutionary history and to compute intra-order phylogenies based on very apparent morphological characters (Karasawa *et al*., 2013; Schweitzer *et al.*, 2016). This, however, is not the case for the shrimp-like decapods, which have a significantly lower preservation potential due to their softer exoskeleton. As a result the shrimp-like decapod fossil record is much more limited than that of the rest of the groups within the order and, thus, their evolutionary history has been much less studied. To date, no phylogenetic analysis has included shrimp-like decapod fossils due to the complexity of character and character state designation within the group.

Luckily, the Late Jurassic Solnhofen Läggerstatte in southern Germany has yielded a very diverse and abundant record of shrimp-like decapods, among other animals. The exceptional preservation exhibited by these fossils allows the recognition of even some of the least obvious morphological features. In this work, a phylogenetic analysis was run using both fossil and extant species of shrimp-like decapods. We believe this approach offers fresh insight on the evolutionary relations and character polarization within the decapod order.

Shrimp-like decapods.--Shrimp-like decapods are composed of what are considered the most basal groups within Decapoda. The term shrimp is used colloquially to reference crustaceans with long antennae, slender legs, and a laterally compressed pleon, and which are typically adapted to a nektic lifestyle. Besides decapods, it is also a term used to reference certain species of branchiopods, ostracods, hoplocarids, and euphasids (Bauer, 2004).

The shrimp-like decapods form a polyphyletic group comprising the suborder Dendrobranchiata and the infraorders Caridea and Stenopodidea, within the suborder Pleocyemata. All of these groups have the characteristic morphological features of decapods: carapace fused to thoracic segments, first three pairs of thoracopods adapted to handle food (maxillipeds), a pleon with six segments, and a telson. All of them also possess the typical shrimp features described above, but apart from these unifying characters, the morphological variation exhibited between and even within each of these groups is considerable (Fransen and De Grave, 2009).

An early classification of the decapod order grouped all shrimp-like decapods into a single taxon, Natantia, referencing the collective adaptation to swimming by all its members. The rest of the decapods were all grouped into the Reptantia, referencing the epibenthic nature of its members (Bauer, 2004). Since then, Natantia has been recognized as paraphyletic. The current decapod classification scheme includes two suborders: Dendrobranchiata and Pleocyemata. Dendrobranchiata is composed exclusively of shrimp-like decapod groups while Pleocyemata, aside from shrimp-like decapods (carideans and stenopodideans), includes lobster-like and crab-like decapods. The monophyly of Natantia has, therefore, been rejected, as pleocyemate shrimps are more closely related to crabs and lobsters than to dendrobranchiate shrimp (Burkenroad, 1983; Bauer, 2004; Fransen and De Grave, 2009; Tavares *et al*., 2009).

The common ancestor of all decapods is thought to have been shrimp-like. Lobster and crab groups, therefore, represent derived overall morphological conditions. Both morphological and molecular phylogenetic analyses support the basal positioning of shrimp-like decapods within the order (Abele and Felgenhauer, 1986; Chace, 1992; Porter *et al*., 2005) as does the fossil record (Feldmann and Schweitzer, 2010; Schweitzer *et al*, 2010; Jones *et al*., 2014). The relationships between and within the different shrimp-like decapod groups, however, are not conclusive. Though the monophyly of Dendrobranchiata and Pleocyemata are each well supported in previous works (Burkenroad, 1983; Chace, 1992; Bracken *et al,* 2009b, 2009c; Tavares *et al*., 2009), the precise relationship between Caridea, Stenopodidea, and Reptantia (a monophyletic group) is unclear, as is the relationships of the families within Dendrobranchiata, Stenopodidea, and Caridea (Fransen and De Grave, 2009).

Solnhofen.--The Solnhofen Plattenkalk is a lithographic limestone deposit located in the Southern Franconian Alb in Germany. The sediments of this unit were deposited in individual basins separated from the open ocean by algal-sponge and coral reefs in warm, anoxic, hypersaline conditions (Barthel *et al.,* 1994; Munnecke *et al.,* 2008). These conditions made this environment inhospitable to most life-forms. However, many organisms ended up falling or drifting into the hypersaline lagoons. The carcasses of these organisms were not scavenged by decomposers or transported by currents before being buried in the soft carbonate muds, and thus the Solnhofen Limestone has yielded fossils with exceptional preservation from the Late Jurassic (Barthel *et al.,* 1994; Munnecke *et al.,* 2008).

The world-famous Solnhofen fossils represent a variety of taxa including coccolithophorids, foraminiferans, phaeophytes, gymnosperms, cnidarians, annelids, molluscs, echinoderms, chondrichthyans, osteichthyans, reptiles, and the exquisite bird, *Archaeopteryx*. However, the greatest diversity of species in this site is seen in arthropods. Though most of these are species of insects, the Solnhofen Limestone is also extremely rich in crustacean fossils and is of great importance for the study of decapods, since it contains the first good fossil record for some of the most basal of the current decapod groups, including the shrimp-like decapods (Barthel *et al.,* 1994; Selden and Nudds, 2004). The great majority of shrimp-like decapod fossil specimens studied in this work come from the Solnhofen Limestone, which makes this location of great importance for this study.

Previous Work

Paleontological studies have been conducted on the Solnhofen Plattenkalk fossil assemblage focusing on several taxa (Viohl, 1994; Charbonnier and Garassino, 2012). In contrast, sedimentological aspects for the site have received relatively less attention, yet its depositional setting has been widely discussed (Werner Barthel, 1970; Munnecke et al., 2008).

Phylogenetic studies of the Dendrobranchiata are numerous, both using morphological characters (Abele and Felgenhauer, 1986; Martin et al., 2009) and (even more) using molecular characters (Vazquez-Bader et al., 2004; Voloch et al., 2005; Chan et al., 2008; Ma et al., 2009). Most studies support the monophyly of the superfamilies Sergestoidea and Penaeoidea within Dendrobranchiata, yet the monophyly and relationships of the families within these groups remains controversial, particularly on the basis of appropriate phylogenetically informative characters (especially morphological) and appropriate outgroup(s) in the study of these major groups.

The infraorder Caridea is currently the most diverse group of shrimp-like decapods. The group is for the most part considered monophyletic except for the family Procarididae which is considered to be either the basal–most group within the infraorder or the sister group to all carideans (Bauer, 2004). Many taxonomic paradigms have been proposed for Caridea, but currently around 36 families are accepted (Bauer, 2004). Several phylogenetic analyses, however, cast doubt on the monophyly of many of these groups. Both morphological (Burkenroad, 1983; Christoffersen, 1990; Martin and Davis, 2001) and molecular-based analyses

(Porter *et al*., 2005; Bracken *et al.,* 2009c) have been conducted to resolve internal relationships within the group, without a clear colclusions.

Stenopodidea phylogeny has not been investigated extensively. The most important work in this respect is probably that of Saito and Takeda (2003) where 38 characters from 32 extant species of the family Spongicolidae were analyzed. The results suggest that most accepted genera are paraphyletic.

Schram and Dixon (2004) performed cladistic analyses of decapods, particularly reptantians and not ably incorporated fossil species into the data set. Most of these fossils were collected from the Solnhofen Lagerstatte. They found that the inclusion of extinct species did not nullify or collapse clades based on extant forms. The current study would complement the work of Schram and Dixon, as they did not focus on the shrimp-like decapod species in their analyses.

Materials and Methods

The fossil samples that have been studied in this project belong to several collections: The United States National Museum of Natural History, Washington, DC, USA; The Carnegie Museum, Pittsburgh, PA, USA; The Staatliche Naturwissenschaftliche Sammlungen Bayerns, Munich, Germany; and a private collection in Chicago, IL, USA.

*Characters.***--**139 adult morphological characters were used in the analysis (Appendix 1). These characters were for the most part chosen based on previous work by Tavares *et al*. (2009) for dendrobranch characters and Chace (1992) for characters occurring in caridean shrimp (Fig. 1). Out of these, 82 are binary and 57 are multistate. 45 are derived from carapace characters, 19 are derived from cephalic appendage characters, 47 are derived from pereiopod characters, 18 are derived from pleonal characters, 8 are derived from telson characters and 2 are miscellaneous. Missing data was scored as "?", and inapplicable characters were scored as "-".

Character and character state selection is not a straightforward process. In this study, several characters and their states were taken from previous work (Chace, 1992; Tavares *et al*. 2009), and some were developed by the authors. The characters were intended to exhaustively represent as much of the morphological diversity within decapod shrimps as possible. Since all decapod shrimp phylogenetic work has been done exclusively with extant forms up until now, several of the characters were not observable on the fossil species.

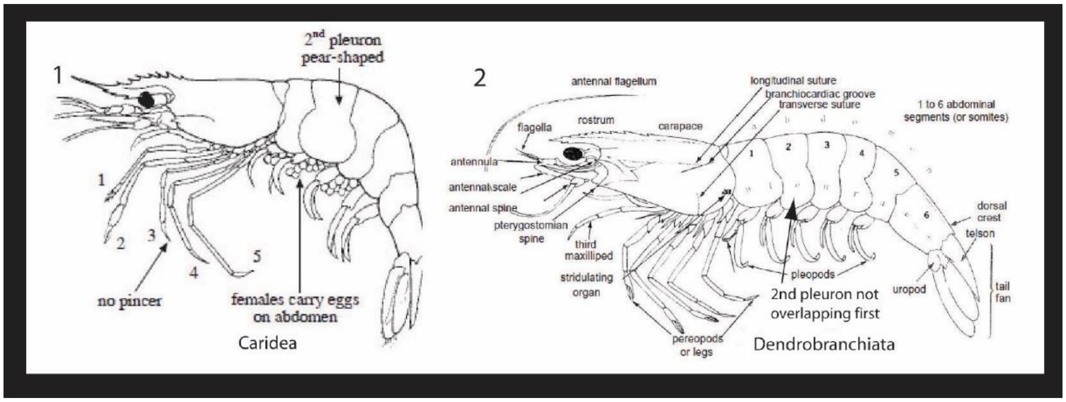

Figure 1. (1) caridean morphology (modified from Chan, 1998); (2) dendrobranch morphology (Modified from Tavares, 2003).

The first portion of the selected characters illustrate carapace variation within the group. The length, shape, and presence of spines on the rostrum are diagnostic features for many species, especially carideans (Chace 1992; Bauer, 2004). The exact function of the rostrum and its structures are inconclusive, though it is generally thought to play the role of a keel, along with the scaphocerite, during a shrimp's distress backward swimming (Bauer, 2004).

The bulk of the carapace (posterior to the rostrum) can bear a number of different spines and grooves arising from different sections of the carapace that are also diagnostic of certain species. These characters have previously been used to resolve phylogeny of higher decapods (Karasawa *et al.*, 2013); however, their homology across decapod infraorders has not been conclusively proven. Again, these characters' functions are elusive and are probably limited to species recognition.

Some of the characters are related to gill morphology and number. These are not observable in the fossils since gills have very low preservation potential. The gill morphology, however, defines one of the two decapod suborders, the

Dendrobranchiata. This character state and those associated to it (e.g. second pleonal pleura not overlapping first) are considered to be homologous arising from a single event (Chace 1992, Porter *et al*., 2005). Pleocyemate decapods for the most part bear phyllobranch gills, although a few groups have trichobranch gills; both are thought to be homologous between groups with a single event leading to their fixation.

The variation in morphology of the cephalic appendages is accounted for by several characters in our matrix. The variation in the forms of these structures is likely to reflect fine functional variation, undoubtedly tied to the particular feeding ecology and ethology of each species. As phylogenetically important as these structures might be, most of the cephalic appendages as well as the first two maxillipeds are virtually never preserved in the fossil forms, at least not to the degree where their morphology can be appreciated. Characters pertaining to the mandibles, maxillules, maxillae, and maxillipeds one and two are, thus, only observed in the extant species. There is considerable morphological diversity regarding these characters among the different extant shrimp taxa including the relative positioning and general form of the incisor and molar processes of the mandible, the endites, the maxillae and first maxillipeds, as well as the presence or absence of tactile palps, among others. Antennae and antennules, unlike the rest of the cephalic apendages, are usually preserved in most of the fossil forms since they are long and large and their flagellar portion is not usually overlain by any structure.

The pereiopods are the shrimp characters that best reflect their functional adaptation. These structures are usually observable in the fossil species, though it is difficult in some cases to discern which specific pereiopod one is observing. The homology between the different character states related to these structures is not established, and in some cases they are almost definitely homoplasic between certain groups. However, this is not reason enough to dismiss these characters for a phylogenetic analysis. Characters pertaining to the pereiopods include the relative lengths and robustness among the appendages, which are chelate, pseudochelate or achelate; the number and nature of the ornamentation on the different appendage segments, and further segmentation or fusion of the seven standard segments.

Characters pertaining to the pleon are comparatively fewer than those of the rest of the regions. This is due to the general lack of variation the pleon exhibits throughout the studied specimens. Most of the pleonal characters have reproductive functions and are miniscule to the point that they are unobservable on extant forms without the aid of specialized equipment (e.g. SEM). Many are not directly observable in the fossil specimens because of their difficulty to discern, but some cannot be coded for the fossils because their gender is unknown. Also, unlike the pereiopods, the pleopods exhibit comparatively little variation except between genera. The pleon, however, is the first structure to be observed in shrimp in order to determine their taxonomic allegiance, since it is the second pleura overlapping the first that is the most diagnostic character that helps differentiate between dendrobranchiate and pleocyemate shrimps.

The characters describing the tailfan (telson and uropods) of the shrimp species are also few, due to the relatively small size of the structure in relation to the rest of the animal. The function of the ornamentation is, again, unclear and the range of variation of the tailfan characters is not great.

Phylogenetic analysis

The morphological matrix was generated in Microsoft Excel and Mesquite (Appendix 3). The analysis was run in PAUP* 4.0b10. Heuristic search used Maximum Parsimony and the following options: random addition sequence, 1000 replications with random input order holding 1 tree at each stepwise addition. All characters were unordered and equally weighted. Relative clade stability was assessed using parsimony bootstrapping and jackknifing. Character history was traced using Mesquite. The analysis was rooted to *Euphausia superba* (Dana, 1850).

Fossil generic descriptions

The following are the fossil genera that were coded for the phylogenetic analysis. Additional specimen information may be found in Appendix 3.

Acanthochirana (Strand, 1928)

Diagnosis.-- Rostrum length variable from shorter than eyestalks to beyond antennular peduncle, straight or curved; up to five dorsal rostral spines in most cases. Post rostral spines present, variable in number. Carapace ornamentation variable, generally present hepatic sulci and spines as well as cervical sulci. Carapace generally twice as long (not including rostrum) as high. A swelling at the margin between the scaphocerite and the carapace characterizes the genus.

Pereiopods generally unadorned with first three pereiopods chelate, progressively increasing in length. Pereiopod 3 longer than pereiopods 4 and 5. Grooming setae present on pereiopod 1 merus. Maxilliped 3 longer than all pereiopods, adorned with thick grooming setae.

Ventral serrations present on pleonal pleura as well as a prominent pleonal hinge system. Diaeresis on uropod exopod lacking. Uropods occasionally setose.

Species examined.-- Acanthochirana angulatus, Acanthochirana cordata, Acanthochirana krausei, and *Acanthochirana longipes*.

Aeger (Münster, 1839)

Diagnosis.-- Rostrum length variable from shorter than eyestalks to beyond antennular peduncle, generally straight; up to 4 ventral rostral spines in most cases. Carapace ornamentation variable, generally present branchiocardiac and cervical sulci. Carapace relative dimensions variable from quadrate to elongate (Fig. 2).

First three pereiopods chelate, progressively increasing in length. Pereiopod 3 shorter than pereiopods 4 and 5. Grooming setae present on pereiopod 1 and 3 merus and pereiopod 2 merus and ischium. Maxilliped 3 longer than all pereiopods. Maxilliped 3 adorned with thick grooming setae.

Pleonal somite 1 narrower than the rest. Ventral serrations present on pleonal pleura as well as a prominent pleonal hinge system. Diaeresis present on uropod exopods. Uropods with soft setae. Telson occasionally spinose.

Species examined.-- *Aeger armatus, Aeger bronni, Aeger elegans, Aeger insignis, Aeger spinipes,* and *Aeger tipularius*.

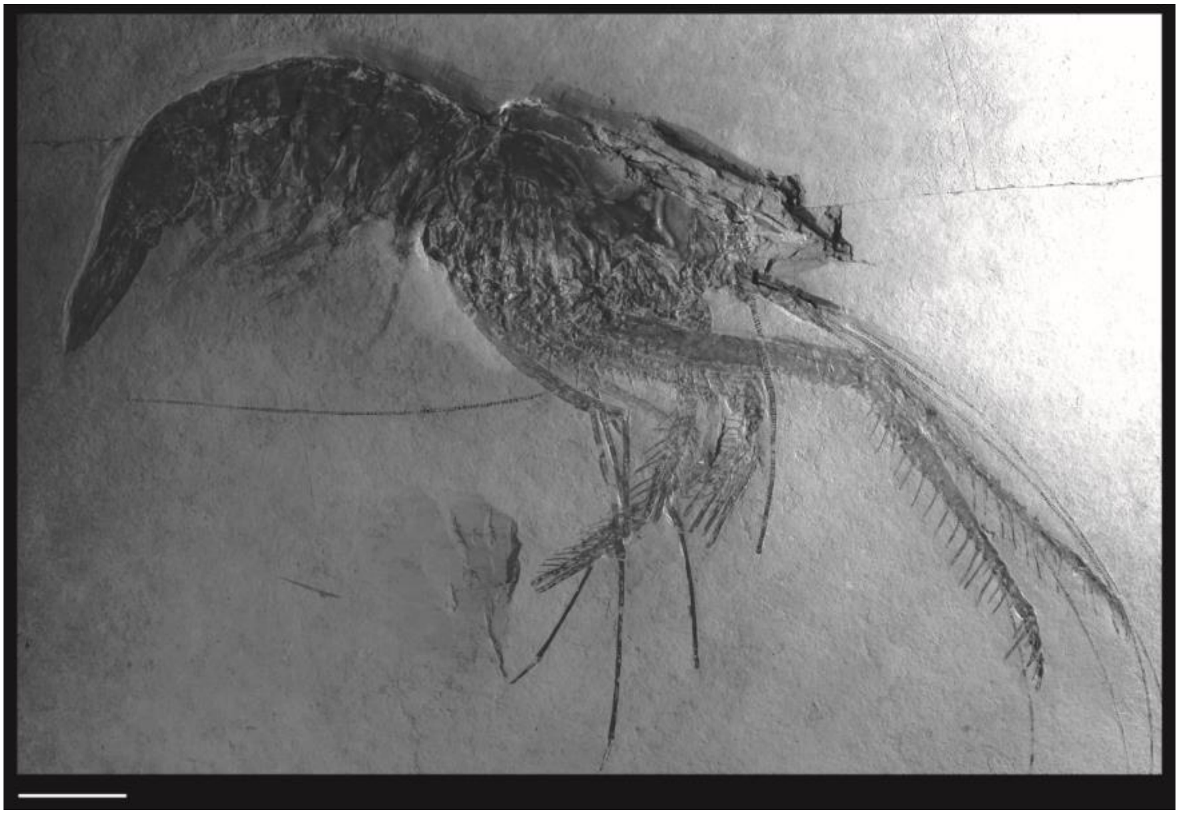

Figure 2. Solnhofen specimen of *Aeger tipularius* (AS I 959). Scale bar=1 cm.

Albertoppelia (Schweigert and Garassino, 2004)

Diagnosis.-- Rostrum extending beyond eye and antennular peduncle; ornamentation consists of dorsal and ventral rostral spines, up to five on the dorsal side and up to four on the ventral. Post rostral spines present, up to two. Carapace unadorned. Carapace height generally ¾ of length (not including rostrum). Exhibits swelling at the margin between the scaphocerite and the carapace as in *Acanthochirana*.

First three pereiopods chelate. Pereiopods unadorned with first three pereiopods chelate, progressively increasing in length. Pereiopod 3 longer than pereiopods 4 and 5. Pereiopod 1 most robust. Maxilliped 3 setose.

Pleonal somite 1 narrower than the rest.

Species examined.-- *Albertoppelia kuempeli.*

Anisaeger (Schweitzer *et al*., 2014)

Diagnosis.-- Rostrum length variable, generally straight; unarmed. Carapace ornamentation consists of postantennal spine and cervical and hepatic sulci.

Pereiopods 1 and 3 chelate, pereiopod 2 possibly chelate. First three pereiopods progressively increasing in length. Grooming setae present on pereiopod 1 and 2. Maxilliped 3 setose.

Pleonal somite 1 narrower than the rest. Dorsopleonal carina present on pleonites 5 and 6. Telson with lateral setae and spines.

Species examined.-- *Anisaeger brevirostris* and *Anisaeger spiniferus.*

Antrimpos (Münster, 1839)

Diagnosis.-- Rostrum length variable from shorter than eyestalks to beyond them, but not reaching antennular peduncle, generally curved; ornamentation consists generally of dorsal and ventral rostral spines, up to nine on dorsal side and up to four on ventral side. Carapace ornamentation variable, may include hepatic and pterygostomian spines and cervical groove, Carapace length about twice the height. Generally exhibits swelling at the margin between the scaphocerite and the carapace like *Acanthochirana*.

First three pereiopods chelate, progressively increasing in length. Grooming setae present on pereiopod 1 merus. Maxilliped 3 generally unadorned.

Pleonal somite 6 subquadrangular. Ventral serrations may be present on pleonal pleura, pleonal hinges slight. Diaeresis present on exopod of uropod. Tailfan structures may include setae on uropods.

Species examined.-- *Antrimpos intermedius, Antrimpos nonodon, Antrimpos senidens, Antrimpos speciosus*, and *Antrimpos udenarius.*

Blaculla (Münster, 1839)

Diagnosis.-- Rostrum length variable from shorter than eyestalks to beyond them, but not reaching antennular peduncle, curved; ornamentation variable. Carapace unadorned, length about twice the height (Fig. 3).

At least pereiopod 2 chelate with fingers strongly curved towards each other. Right and left second pereiopods unequal size with multisegmented carpus.

Second pleonal pleura apparently overlapping first and third. Pleonal somite 1 narrower than the rest. Tailfan unadorned.

Species examined.--*Blaculla nikoides* and *Blaculla sieboldi*

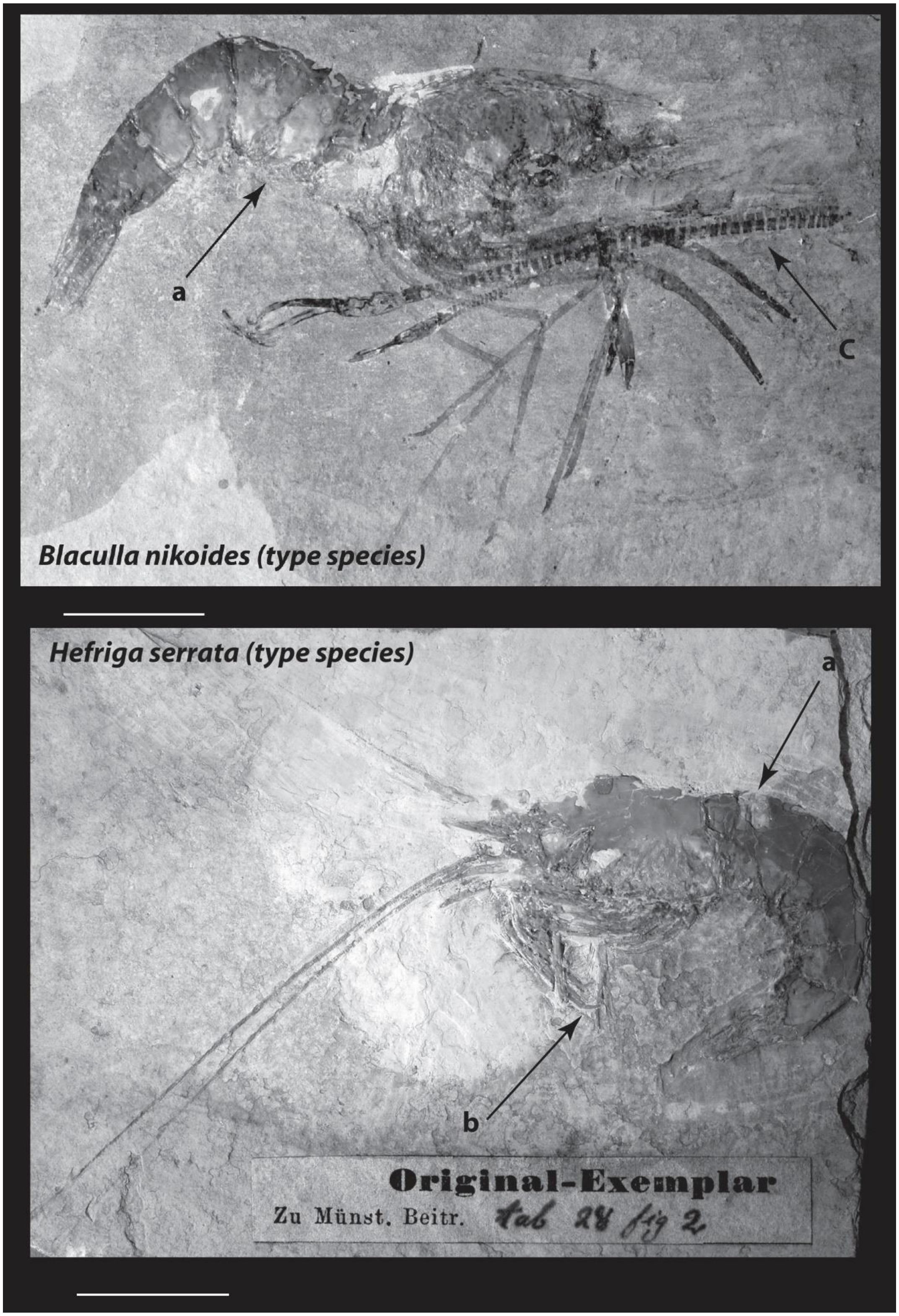

Figure 3. Solnhofen specimens of *Blaculla nikoides* (AS I 973) and *Hefriga serrata* (AS VII 722) type species. Scale bars=1 cm (a) indicates second pleonal pleura overlapping first (caridean character); (b) indicates *H. serrata* achelate third pereiopod; (c) indicates multiarticulate carpus of second pereiopod in *B. nikoides*.

Bombur (Münster, 1839)

Diagnosis.-- Rostrum not extending beyond eye, length, unarmed. Carapace ornamentation consists of pterygostomian and antennal spines. Carapace length about twice the height.

At least pereiopod 1 chelate; most robust. Middle pereiopod segments unadorned. Pereiopod 3 longest. Pereiopods 4 and 5 pseudochelate.

Second pleonal pleura apparently overlapping first and third. Tailfan unadorned.

Species examined.-- *Bombur complicatus.*

Buergerocaris (Schweigert and Garassino, 2004)

Diagnosis.-- Rostrum length extending beyond eyes and antennular peduncle, curved; ornamentation consists of dorsal and ventral rostral spines, more than 10 and up to 4 respectively. Carapace unadorned. Carapace about as high as it is long.

First three pereiopods chelate, progressively increasing in length. Pereiopod 4 longest. Pereiopod 1 most robust. Chelae of first two pereiopods bulbous.

Pleonal somite 1 narrower than the rest. Second pleonal pleura apparently overlapping first and third. Diaeresis present on exopods of uropods. Dorso-pleonal carina present on pleonal somites 3-6. Tailfan unarmed.

Species examined.--*Buergerocaris psittacoides.*

Bylgia (Münster, 1839)

Diagnosis.-- Rostrum length extending beyond eyes and antennular peduncle, curved; ornamentation consists of between 6 and 9 dorsal spines and up to 4 ventral rostral spines. Carapace unadorned. Carapace about 2/3 as high as it is long. Generally exhibits swelling at the margin between the scaphocerite and the carapace like *Acanthochirana*.

First three pereiopods chelate, progressively increasing in length. Pereiopod 3 longest; pereiopod 1 generally most robust. Pereiopod 1 chela occasionally bulbous. Maxilliped 3 adorned with thick grooming setae.

Pleonal somite 6 height greater than its length. Diaeresis present on exopod of uropods. Tailfan unarmed.

Species examined.-- *Bylgia haeberleini, Bylgia hexadon, Bylgia ruedeli,* and *Bylgia spinosa.*

Carpopenaeus (Glaessner, 1946)

Diagnosis.-- Rostrum length extending beyond eyes and antennular peduncle, curved; ornamentation consists of between 6 and 9 dorsal spines and up to 4 ventral rostral spines. Carapace with branchiocardiac groove and longitudinal carina. Carapace about half as high as it is long.

First three pereiopods chelate. Pereiopod 1 longest and most robust. Pereiopod 2 carpus multisegmented. Maxilliped 3 setose.

Pleura terminations sharp. Diaeresis present on exopod of uropods. Telson setose.

Species examined.-- *Carpopenaeus septemspinatus.*

Drobna (Münster, 1839)

Diagnosis.--Rostrum length extending beyond eyes and antennular peduncle, curved; ornamentation consists of dorsal rostral spines, up to five. Four or more post-rostral spines present as well. Carapace ornamentation consists of hepatic, pterygostomian and branchiocardiac spines as well as branchiocardiac crest. Carapace height ¾ of its length (Fig. 4).

Pereiopods unadorned; first three chelate, progressively increasing in length. Pereiopod 3 longest, pereiopod 1 most robust.

Pleonal somite 1 narrower than the rest, pleura terminations sharp. Diaeresis present on exopod of uropods. Telson and uropods unarmed.

Species examined.-- *Drobna deformis.*

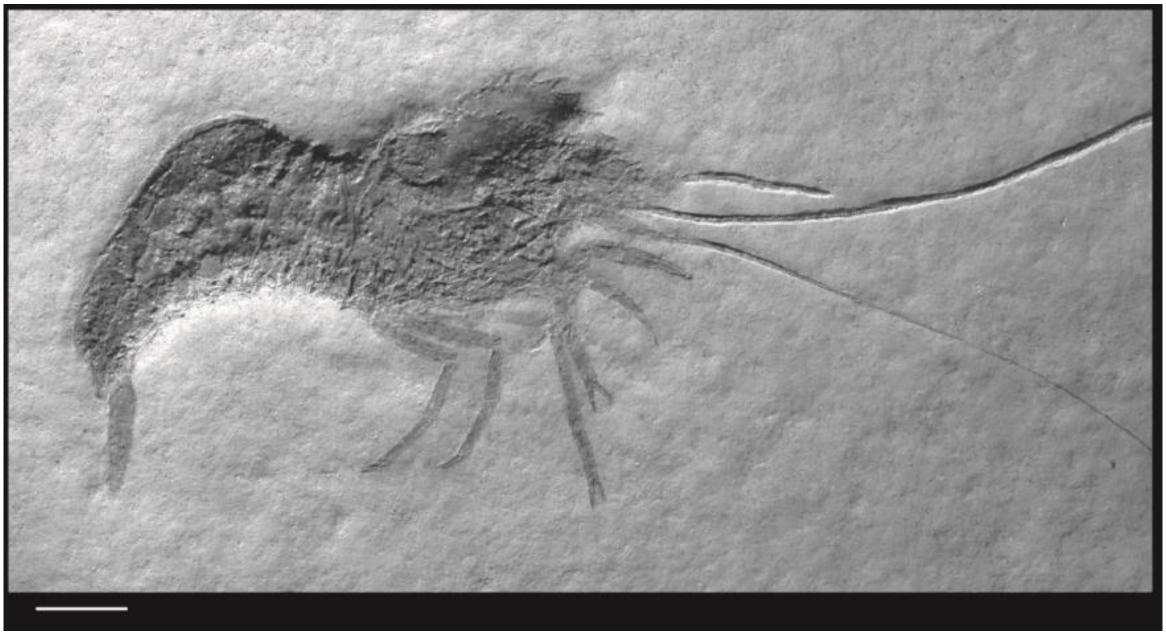

Figure 4. Solnhofen specimen of *Drobna deformis* (1986 XV 7). Scalebar=1cm

Dusa (Münster, 1839)

Diagnosis.-- Rostrum extending beyond eyes but not antennular peduncle; rostrum ornamentation variable, always including between 6 and 9 dorsal spines and occasionally up to four ventral spines. Includes more than 4 post-rostral spines. Carapace ornamentation variable but includes a pterygostomian spine. Carapace relative dimensions from quadrate to elongate.

Pereiopods unadorned; first three chelate, progressively increasing in length and robustness. Manus bulbous and chelae fingers strongly curved towards each other. Pereiopod 3 longest.

Pleonal somite 1 narrower than the rest; ventral serrations present on pleura. Telson armed with lateral and terminal spines.

Species examined.-- *Dusa denticulata,* and *Dusa monocera.*

Eystaettia (nomen nudum)

Diagnosis.-- Rostrum not extending beyond eyes; rostrum ornamentation consists of dorsal spines, up to 9. Up to 2 post rostral spines. Carapace unadorned. Exhibits swelling at the margin between the scaphocerite and the carapace like *Acanthochirana*.

First three pereiopods chelate, progressively increasing in length. Pereiopod 3 longest. Pereiopods and maxilliped 3.

Uropods setose. Telson bearing several lateral and terminal setae.

Species examined.--*Eystaettia intermedius.*

Francocaris (Münster, 1839)

Diagnosis.-- Rostrum absent. Carapace seemingly elongate and thinner than eyestalks. Poorly preserved specimens.

Species examined.--*Francocaris sp.*

Franconipenaeus (Oppel, 1862)

Diagnosis.-- Rostrum absent. Carapace ornamentation consists of hepatic spine. Exhibits swelling at the margin between the scaphocerite and the carapace like *Acanthochirana*.

First three pereiopods chelate, progressively increasing in length. Pereiopod 3 longest. First two pereiopods most robust. Maxilliped 3 spinose.

Uropods setose. Telson unarmed.

Species examined.-- Franconipenaeus meyeri.

Harthofia (Polz, 2007)

Diagnosis.-- Rostrum length extending beyond eyes but not antennular peduncle, curved; ornamentation consists of up to 5 dorsal and up to 4 ventral rostral spines. Carapace unadorned. Carapace about ¾ as high as it is long. Scaphocerite to antennular peduncle ratio variable from equal length to up to scaphocerite twice length of antennular peduncle.

First two pereiopods chelate. Pereiopod 1 generally most robust and longest.

Second pleonal pleura overlapping first and third. Pleonal somite 6 height greater than its length. Diaeresis present on exopod of uropods. Telson setose.

Species examined.--*Harthofia bergeri, Harthofia blumbergi*, and *Harthofia polzi.*

Hefriga (Münster, 1839)

Diagnosis.-- Rostrum length extending beyond eyes and antennular peduncle, straight; ornamentation consists of dorsal rostral spines, between 6 and 9. Carapace unadorned. Carapace about half as high as it is long. Sometimes exhibits swelling at the margin between the scaphocerite and the carapace like *Acanthochirana* (Fig. 3).

First two pereiopods occasionally chelate, bulbous and with highly curved fingers and more robust than the rest, otherwise achelate, not more robust.

Pereiopod 1 merus adorned with spines. Pereiopod 1 generally most robust and longest.

Second pleonal pleura overlapping first and third. Pleonal somite 6 quadrate. Uropods and telson setose.

Species examined.-- *Hefriga frischmanni,* and *Hefriga serrata.*

Koelga (Münster, 1839)

Diagnosis.-- Rostrum length extending beyond eyes but not antennular peduncle, curved or straight; ornamentation variable, always including dorsal rostral spines. Carapace generally unadorned, sometimes exhibits branchiostegal, postantennal or pterygostomian spines. Carapace generally about half as high as it is long. Exhibits swelling at the margin between the scaphocerite and the carapace like *Acanthochirana*.

First three pereiopods generally chelate, unarmed and progressively increasing in length; otherwise achelate. Pereiopod 3 longest.

Pleonal somite 1 occasionally narrower than the rest. Uropodal exopods setose in some species, telson usually unarmed.

Species examined.-- *Koelga curvirostris, Koelga muensteri*, and *Koelga quadridens.*

Occultocaris (Winkler, 2014)

Diagnosis.-- Rostrum length not extending beyond eyes or antennular peduncle, curved; unarmed. Carapace armed with antennal spine. Carapace generally about half as high as it is long. Exhibits swelling at the margin between the scaphocerite and the carapace like *Acanthochirana*.

First two pereiopods generally chelate, unarmed and progressively increasing in length. Pereiopod 4 longest, setose. Pereiopod 1 most robust with bulbous manus.

Second pleonal pleura overlapping first and third. Uropod exopods with distolateral spine.

Species examined.-- *Occultocaris frattigianii.*

Pseudodusa (Schweigert and Garassino, 2004)

Diagnosis.--Rostrum length extending beyond eyes but not antennular peduncle, curved; ornamentation consisting at least of ventral rostral spines. Carapace unarmed. Carapace height ¾ the length.

First three pereiopods generally chelate, unarmed and progressively increasing in length. Pereiopod 3 longest. First two pereiopods most robust. Tailfan unarmed.

Species examined.-- *Pseudodusa frattigianni.*

Rauna (Münster, 1839)

Diagnosis.-- Rostrum length variable; armed with dorsal spines, variable in number. Carapace unarmed. Carapace height ¾ the length.

Poorly preserved specimens. Uropods setose, telson unarmed.

Species examined.-- *Rauna angusta.*

T1

Diagnosis.-- Poorly preserved specimen from the Cenomanian of Tunisia; unidentified, but similar to *Acanthochirana*.

Rostrum not extending beyond eyes or antennular peduncle, curved; ornamentation consists of dorsal and postrostral spines. Carapace with hepatic spine and cervical sulcus, Carapace length about twice the height. Exhibits swelling at the margin between the scaphocerite and the carapace like *Macropenaeus* (Fig. 5).

First three pereiopods chelate, progressively increasing in length. Pereiopod 3 longest. Tailfan unarmed.

Species examined.-- Incertae sedis.

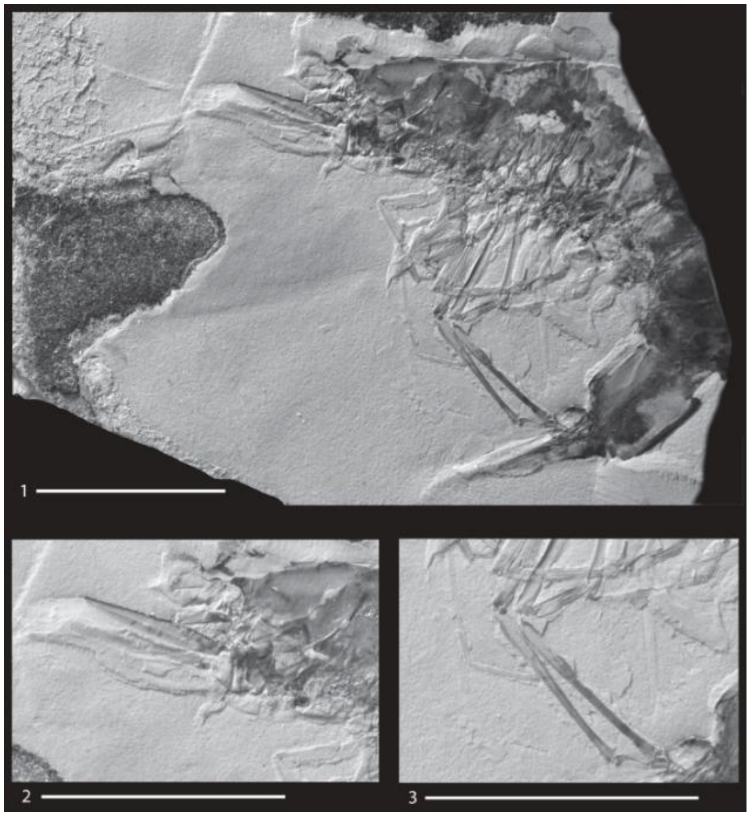

Figure 5. T1-Unidentified shrimp from the Cenomanian of Tunisia. Scalebars=1cm.

Udora (Münster, 1839)

Rostrum length extending beyond eyes but not antennular peduncle, curved; armed with up to 5 dorsal spines. Carapace unarmed. Carapace generally about 2/3 as high as it is long.

Pereiopods achelate and progressively decreasing in length and spinose. Maxilliped 3 setose. Ischium of pereiopods reduced.

Second pleonal pleura overlapping first and third. Diaeresis present on uropod exopods, exopods setose. Telson armed with several lateral spines.

Species examined.-- *Udora brevispina.*

Results

Extant phylogeny.--The phylogenetic analysis used *Euphausia superba* as an outgroup and therefore, the following character states are here considered plesiomorphic: a rostrum that does not surpass eyestalk length, acicular scaphocerite, straight rostrum, rows of setae on merus of pereiopods 1 through 4 as well as on ischium of pereiopods 2 and 3, tufts of setae on dactyls of pereiopods 1 and 2, first three pereiopods with equal relative length and robustness, and maxilliped 3 shorter than pereiopods. Also, a completely unadorned carapace is the plesiomorphic state in the analysis.

The first group to branch out (Fig. 6) embraced the members of the superfamily Sergestoidea (Clade 1). The clade forms an initial polytomy with the outgroup and the clade that includes the rest of the taxa (Clade 3). The characters that unite Sergestoidea are: dendrobranch gills, the absence of a dactyl on pereiopods 1, 4, and 5, the absence of tufts of setae on the first two pereiopod dactyls, the presence of a thelycum on females, and uropodal exopods with an outer lateral spine and unarmed endopods.

Clade 3 apomorphies include phyllobranch gills, attached ornamentation on maxilliped 3, foliaceous epipods on pereiopods, lack of a petasma, presence of a diaeresis on uropodal exopods, and spines on the telson.

The next clade to form contains a lophogastrid and a stomatopod (Clade 4). This clade's characteristics are a hepatic sulcus, a longitudinal and submarginal carina on the carapace, a ratio of height/length of pleonal somite 6 greater than 0.75 and a cleft posterior telson margin.

Clade 5 synapomorphies include an antennal flagellum longer than the entire body, exopods on maxillipeds 2 and 3, maxillipeds composed of less than 7 segments, rounded pleura terminations, and a second pleonal pleura overlapping the first.

Clade 6 apomorphies are: a distolateral spine on the outer margin of the first antennal article, chelate pereiopods 1 and 2, and lateral and terminal position of telson setae if present. The sister group to Clade 6 is the family Procarididae.

Clade 7 is distinguished from its sister group, a single member of the family Ogyridae, by the presence of post-rostral spines, a rostrum that surpasses the length of the eye stalks, but not of the antenullar peduncle, an antennal spine and a submarginal carina on the carapace.

Two clades form from Clade 7: Clade 8 is composed of two caridioid shrimp and an astacidean lobster. Their apomorphies are a triangular scaphognathite ventral lobe, a ratio of the height of the pleura of pleonal somite three/ total height of somite three greater than 0.5 and a rounded telson posterior margin. Clade 10 apomorphies include a ratio of height/length of carapace greater than 0.5 and the lack of tufts of setae on first two pereiopod dactyls.

Once again, two clades arise from the previous node, the first, Clade 11, is composed of a caridean shrimp as a sister taxon to the remaining dendrobranch species, the superfamily Penaeoidea. Clade 11 apomorphies include an antennal first article without a distolateral spine, chelate pereiopods 3, lack of grooming articles on pereiopod 2 and 3, and the lack of a diaeresis on the uropod exopods. The superfamily Penaeoidea apomorphies include: dendrobranch gills, a hepatic spine, longitudinal carina and the lack of a submarginal carina on the carapace, a prosartema, maxillipeds with 7 segments and without ornamentation, pereiopod 3 and 4 merus unarmed, the presence of a petasma in males and a thelycum in females, and a second pleonal somite not overlapping the first. This Clade has a bootstrap support of 87 and a jackknife support of 86.

Clade 16 is characterized by a rostrum length that exceeds the length of the antenullar peduncle and a lateral and terminal positioning of telson spines when present.

Two clades arise from the previous node. Clade 17 is composed of two caridioid superfamilies: Oplophoroidea and Stylodactyloidea. Their synapomorphies are narrow thoracic sternites 3 through 6 and the presence of pronounced dorsomedian reentrants in pleonal somites. Clade 20 apomorphies include a curved rostrum, mandibles with separated incisor and molar processes, a stouter first pereiopod relative to the second, and terminal position of telson setae when present.

Clade 21 synapomorphies include a hepatic sulcus on the carapace, a triangular scaphognathite ventral lobe, a pereiopod 1 merus armed with a subdistal spine and setae, and the presence of pleonal pleura ventral serrations.

Clade 22 is characterized by a ratio of scaphocerite/antennular peduncle length between 1.4 and 1.98, maxilliped 3 length greater than that of pereiopods, and between 3 and 6 spines on each side of telson.

Clade 23 apomorphies include unarmed pereiopod 1 and 2 merus and ischium, and a multi segmented carpus on pereiopods 2. Two clades arise from this node. Clade 24 is composed of a members of caridioid families Campylonotidae, Nematocarcinidae, Thalassocarididae, Glyphocrangonidae, and Barbouridae, the latter in its entirety. The clade is characterized by an antennal first article without a distolateral spine, setal brushes on pereiopod 3, and a ratio of height of pleura of pleonal somite three/ total height of somite three greater than 0.5. The next node up (Clade 25), which has a member of the family Thalassocarididae as its sister group, is characterized by the lack of a pterygostomian spine on the carapace, having narrow thoracic sternites 3 through 5, epipods present on all pereiopods, and a pleonal somite 1 not narrower than the rest.

Clade 29 is characterized by having fewer than 8 gills on each side, lacking a submarginal carina on the carapace, having narrow thoracic sternites 3 through 6, an unarmed pereiopod 4 merus, a lack of grooming articles on pereiopod 1, and a truncate posterior telson margin.

Clade 30 synapomorphies are a straight rostrum, a ratio of scaphocerite/antennular peduncle length lower than 1.4, a lack of grooming articles on pereiopod 3 and spines and soft setae on the telson.

Clade 31 synapomorphies include a rostrum length extending beyond that of the eye stalks but not the antennular peduncle, a well-developed incisor process, an unarmed merus on pereiopod 3 and setal brushes on pereiopod 2.

From the previous node two clades arise, Clade 32 synapomorphies are an androstral carina on the carapace, maxillae with one bilobed and one reduces endites, a triangular scaphognaithe ventral lobe, and a distal lash of the first maxilliped shorter that the caridean lobe on the same appendage. Another clade follows this one, Clade 33 synapomorphies include a mandibles with separated molar and incisor processes and a rounded telson posteriori margin.

The second clade that arises from Clade 31 is Clade 36. Its synapomorphies are the lack of a distolateral spine on the outer margin of the first antennal article, bifid epipods on pereiopods, and a ratio of height/length of pleonal somite 6 greater than 0.75.

Two clades arise from the previous node. The first one, Clade 37, is characterized by lacking a pterygostomian spine, having setal brushes on pereiopod 1, and having a lateral and terminal position of telson setae when present. The second group, Clade 39, is characterized by not having maxilliped 3 longer than the pereiopods, having a pointed telson posterior margin, and having up to three spines on each side of the telson.

Clade 40 synapomorphies are the lack of post rostral spines, an entire carpus on pereiopod 2, a slender pereiopod 1 with respect to pereiopod 2, and a terminal position of telson spines. From this node, two clades arise, the first, Clade 41, is characterized by having narrow widths of thoracic sternites 3 through 8, and a ratio of height/length of pleonal somite 6 lesser than 0.75. The second group, Clade 44, is characterized by lacking a mandibular palp, having a longer pereiopod 2 than 3, and having pereiopod 2 as its most robust.

Clade 46 is characterized by having an androstral carina and only spines as telson ornamentation. Clade 47 apomorphies include a rostrum length extending beyond that of the antennular peduncle, having narrow widths of thoracic sternites 3 through 8 and a ratio of height/length of pleonal somite 6 lesser than 0.75.

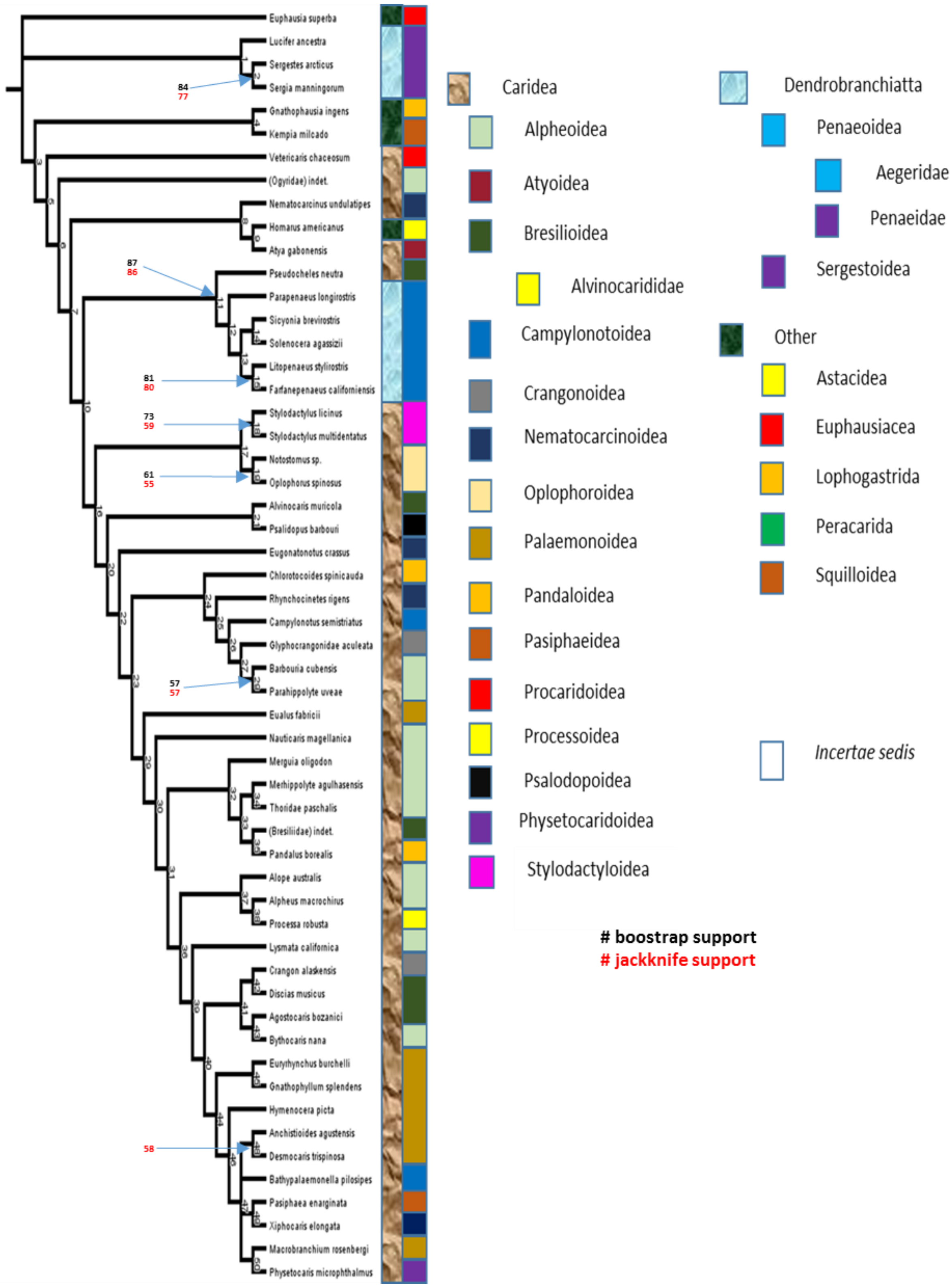

Figure 6. Extant shrimp-like decapod species cladogram. Left-most texture box indicates species infraorder or suborder (i.e. Caridea, Dendrobranchiata, other); right-most color box indicates species superfamily

Comprehensive phylogeny.--The resulting phylogeny for extant and fossil species combined group members into various clades (Fig. 7). The most significant clades and their respective apomorphies are described below.

Once again, the extant members of the superfamily Sergestoidea (Clade 1) formed an initial polytomy with the outgroup and the clade that includes the rest of the taxa (Clade 3). The characteristic synapomorphies are the same as the ones described above for the clade. This Clade has bootstrap support of 60.

The first distinct clade branching off the outgroup is Clade 3. It is characterized by possessing phyllobranch gills, a diaeresis in uropod exopods and spines on the telson. The clade is also characterized at this stage by lacking maxilliped ornamentation, petasma in males, and thelycum in females.

The next significant clade is Clade 11. This clade is also formed in the extant species phylogeny and is composed of two caridioid superfamilies: Oplophoroidea and Stylodactyloidea. Their synapomorphies are narrow thoracic sternites 3 through 6 and the presence of pronounced dorsomedian reentrants in pleonal somites.

The sister group to the previous clade is Clade 14 and it includes all the clades discussed below and is characterized by lacking exopods on pereiopods as well as possessing grooming articles on pereiopods 1 and 2. It is also characterized by having pereiopod 1 and 2 equally robust.

Clade 24 is the next clade of note and it is composed of various extant caridean species. It is characterized by having pereiopod 1 as the most robust and having a ratio of (height of pleonal somite pleura 3)/(total height of pleonal somite 3) greater than 0.5.

The sister group to the previous clade is clade 28 includes all the clades discussed below and is characterized by having up to two post rostral spines.

Two large clades branch out immediately after Clade 28: Clades 29 and 42. Clade 29 is composed of various caridean species, mostly pertaining to the superfamily Alpheoidea. The clade synapomorphies include the absence of rostral spines, having at least 11 gills on each side of the body, having relatively narrow thoracic sternites 3 through 6, having a divided carpus on pereiopod 2, and having maxilliped 3 be longer than pereiopod 1. Clade 42 includes all the subsequent clades described below and is characterized solely by having a rudimentary incisor process.

Once again, two large clades branch off immediately after Clade 42: Clades 43 and 52. Clade 43 is, once again, composed of various caridioid species as well as the American Lobster *Homarus americanus*. The clade is characterized by presenting a submarginal carina on the carapace, having separated incisor and molar processes on the mandible, having a triangular scaphognaithe ventral lobe, and foliaceous epipods on pereiopods. Clade 52 includes all the subsequent clades described below and is characterized by lacking an antennal spine and a diaeresis and having attached ornamentation on maxilliped 3.

The next clade of note is Clade 54. It is characterized by a curved rostrum, a chelate third pereiopod and a second pleonal pleura not overlapping the first. This clade is composed of all the extant dendrobranchiates and all fossil members.

From the previous node arises Clade 55, which is composed of all extant dendrobranchiates. Its synapomorphies are dendrobranch gills, at least 11 gills on each side of the body, an ocular scale, an antennal and hepatic spine, a longitudinal carina over the dorsal surface of the carapace, a prosartema on the antennule, setae rows on pereiopod 1 merus, epipods con pereiopods 1 through 3, exopods longer than pereiopod ischia, having all pereiopods of equal robustness, presenting a petasma in males, a thelycum in females and a dorsopleonal carina on somites 3 through 6. This Clade has a bootstrap support of 73 and a jackknife support of 76.

Clade 61 is the next clade of note. It is characterized by having a ratio of scaphocerite/antennular peduncle between 1.4 and 2, lacking grooming articles on the third maxilliped and a ratio of (height of pleonal somite pleura 3)/(total height of pleonal somite 3) greater than 0.5.

Two clades of note arise from Clade 61: Clades 62 and 81. Clade 62 is composed of various fossil species, most of which are classified as members of the family Penaeidae. The clade is characterized by having unarmed uropods. Clade 81 is characterized by having conspicuous dorsomedian reentrants between pleonal somites.

Clade 88 is composed exclusively of members of the extinct family Aegeridae. Is is characterized by having setae rows on pereiopod 1 merus and having maxilliped 3 longer than all pereiopods.

The last clade of note is Clade 92. It is composed exclusively of members of the genus *Aeger*. It is characterized by having having setae rows on pereiopods 1 through 3 and a Diaeresis on uropod exopods. This Clade has a bootstrap support of 76 and a jackknife support of 66.

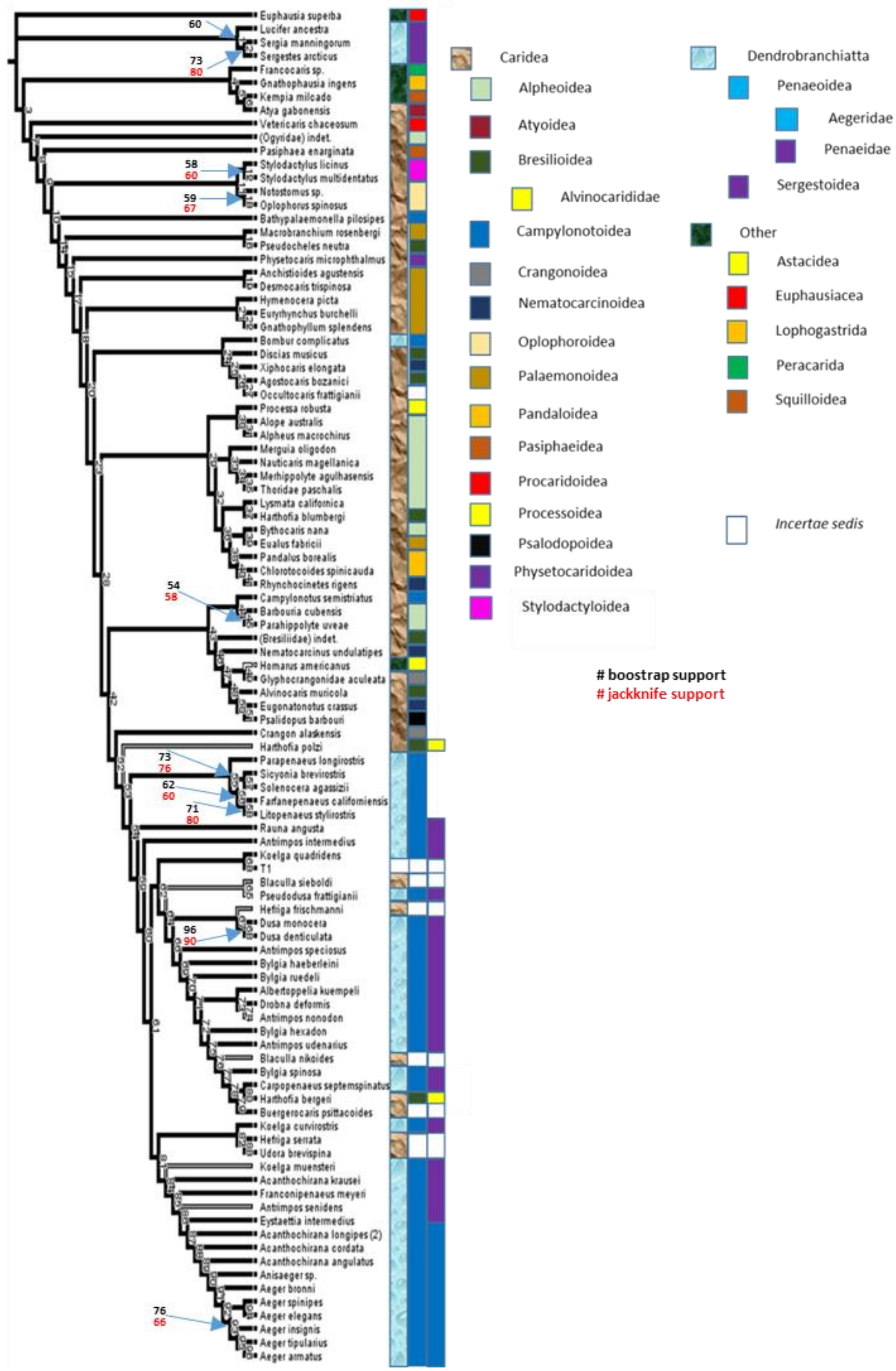

Figure 7. Comprehensive (extant and fossil) shrimp-like decapod species cladogram. Left-most texture box indicates species infraorder or suborder (i.e. Caridea, Dendrobranchiata, other); middle color box indicates species superfamily; right-most color box indicates species family.

Character history

Each of the characters considered in the analysis has some degree of impact in the resulting trees since their optimization, the character history with least number of character state shifts and reversals, is the route to finding the most parsimonious relation between the different taxa. Some of the characters most commonly used to describe and characterize taxa in previous systematic works are considered and traced throughout both the extant and comprehensive tree topologies. Autapomorphic occurrences of character states are, for the most part, not considered as they have little phylogenetic relevance. It must be mentioned, however, that most clades are not uniform regarding their character states and only broad patterns are discussed.

Rostrum.-- Character 1 describes the ornamentation on the rostrum. For the extant taxa tree, the ancestral state for this character is a lack of ornamentation (state 0). The state shifts to dorsal spine ornamentation (state 1) by Clade 6, though the character is not fixed since a reversal to state 0 and shift to lateral spines (state 4) are observed in Clade 8. When Clade 11 branches out, the group has members that are both strictly dorsally ornamented as well as both dorsally and ventrally (state 2). The sister group to Clade 11, Clade 16, is now characterized by having most of its members with both dorsal and ventral rostral spines. A reversal to state 1 and 0 occurs in Clade 39 and a reversal to state 0 occurs in Clade 41.

For the comprehensive tree the initial state is also a lack of ornamentation. By the branching of Clade 10, the character shifts to state 2, having both ventral and dorsal spines. This state is maintained till the branching of Clade 52, though a reversal to state 0 is occurs in Clade 24 and a shift to state 1 occurs in Clade 30. The most basal member of Clade 52 has a reversal to state 0, but by Clade 53, the character shifts to state 1, and strictly dorsal spines. The next change in character state occurs in two clades: Clade 66 and 67 which are subclades of Clade 62 and 69 respectively. In Clade 66 the character is reversed to state 2. In clade 91 the character is reversed to state 0, then shifts to state 5, ventral rostral spines only.

The next traced character is Character 11, rostrum length. For the extant tree (Fig. 8), the ancestral state is a rostrum that does not surpass the cornea (state 2). The character shifts to state 1, extending beyond the cornea, but not the antennular peduncle, at Clade 7. The character shifts to state 0, extending beyond the antennular peduncle, at Clade 16. The character then undergoes a reversal to state 1 at Clade 31, and finally returns once again to state 0 at Clade 47.

In the comprehensive tree (Fig. 9), the ancestral state is also a rostrum that does not surpass the cornea (state 2). The character shifts to state 0 at Clade 10 and then to state 1 at Clade 20. The state is maintained throughout most of the phylogeny after this with the exceptions of a reversal to state 2 in Clade 24, reversals to state 0 in Clades 38, 48 and 70. The character then undergoes various reversals and shifts throughout Clade 85 reversing to state 2, shifting to state 3 (gills absent), reversing to state 2, shifting again to states 1, then to state 0 and finally to state 2 again for the most derived members.

Overall, the rostral character traces on the extant tree suggest a polarization from a short and unadorned rostrum to a long and adorned one, passing through a medium length form (Character 11-state 1) and strictly dorsal ornamentation (Character 1-state 1). These characters undergo reversals in crown groups, making these homoplasic character states. In the comprehensive phylogeny these characters are not polarized in this manner and have more reversal episodes. These results suggest that rostral characters in this work are not phylogenetically informative, particularly with the inclusion of fossil species.

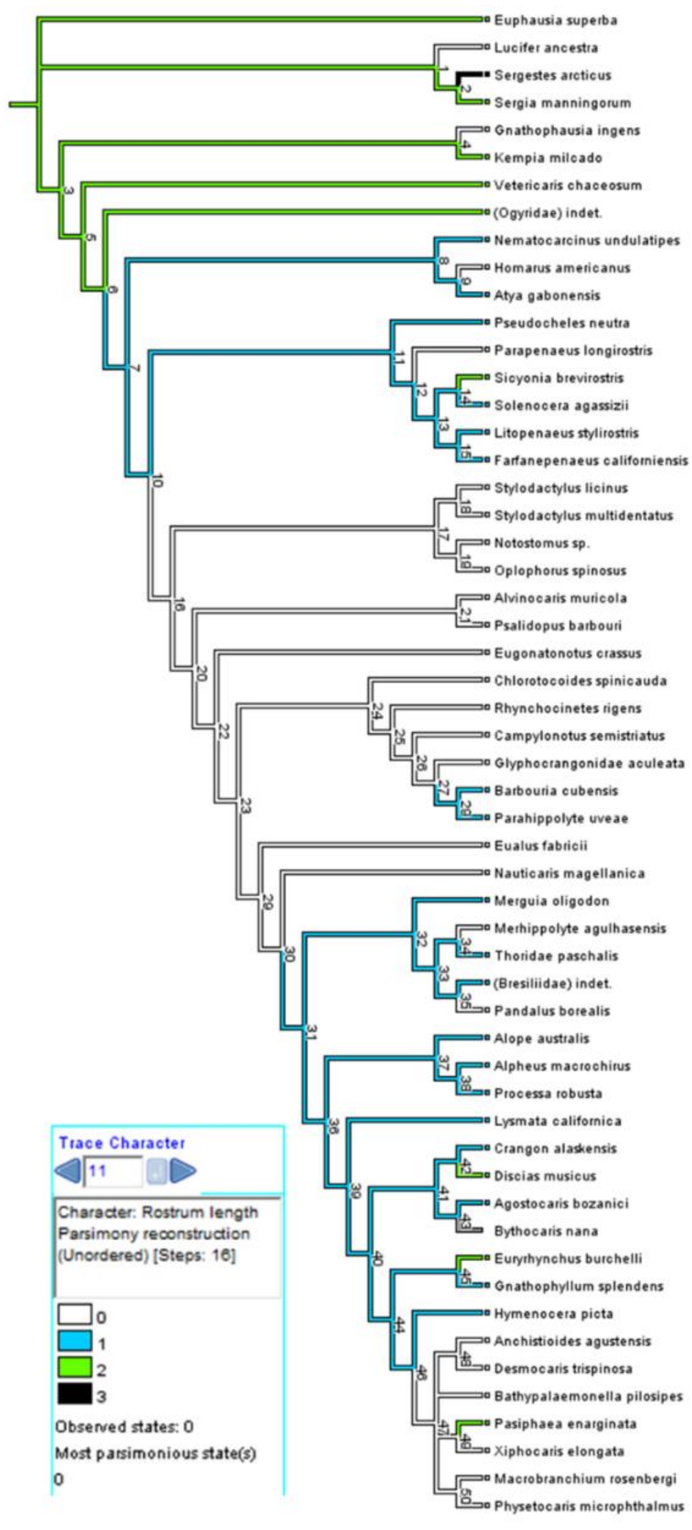

Figure 8. Extant shrimp-like decapod species cladogram tracing Character 11 (Rostrum length) history. Character states: 0-rostrum extending beyond antennular peduncle; 1-rostrum extending beyond eyestalk but not antennular peduncle; 2-rostrum not extending beyond eyestalk; 3-rostrum absent.

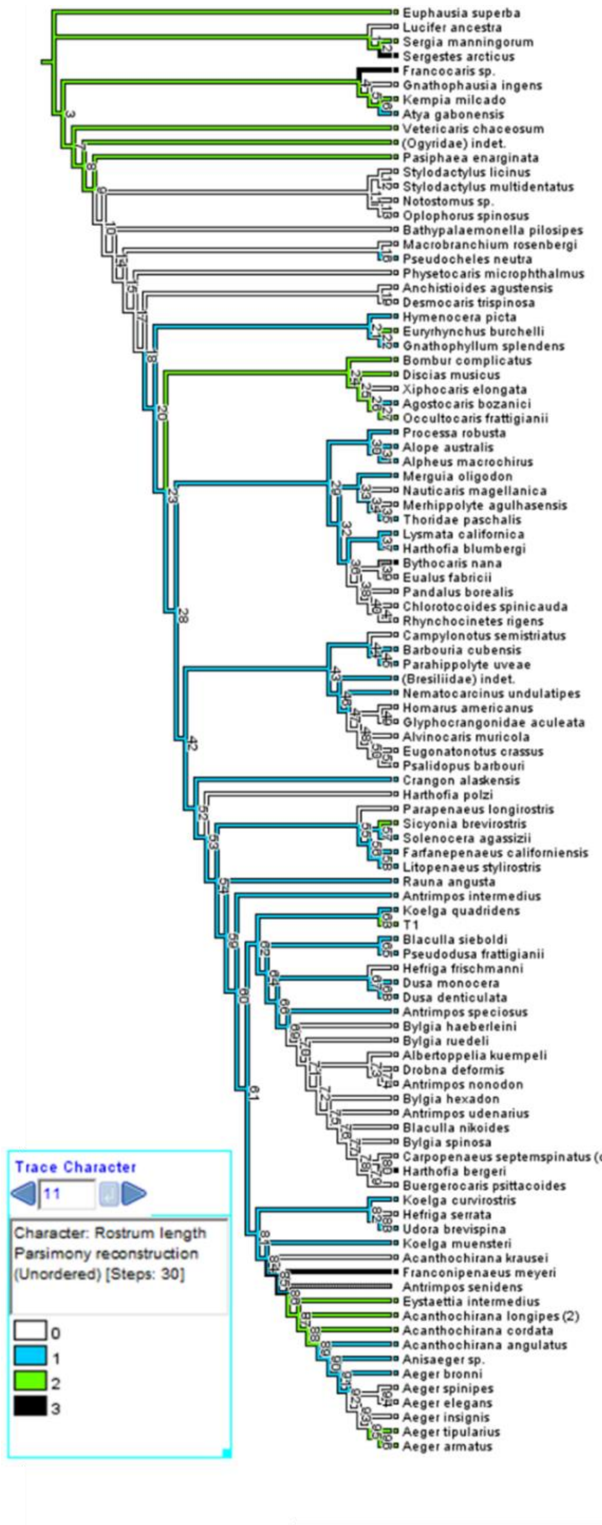

Figure 9. Comprehensive shrimp-like decapod species cladogram tracing Character 11 (Rostrum length) history. Character states: 0-rostrum extending beyond antennular peduncle; 1-rostrum extending beyond eyestalk but not antennular peduncle; 2-rostrum not extending beyond eyestalk; 3-rostrum absent.

Gills.-- The next traced character is Character 6, gill morphology. For the extant tree (Fig. 10) the ancestral states are trichobranch and dendrobranch gills because of the initial polytomy at the base of the tree. The character shifts to phyllobranch gills in Clade 1 and is maintained throughout, except for Clade 12, where there is a reversal to dendrobranch gills.

In the comprehensive tree (Fig. 11) the initial states are also trichobranch and dendrobranch gills because of the initial polytomy at the base of the tree. The character shifts to phylobranch gills by Clade 3. This state is maintained till Clade 53 where gill information in unavailable for all members, except for Clade 55, which undergoes a reversal to dendrobranch gills.

This character is for the most part constant except for the occurrences of two discrete dendrobranch clades in both trees that correspond to the sergestoids and the penaeoids. According to these results, the dendrobranchiate state is plesiomorphic, but not monophyletic, as there is a significant gap between both dendrobranch superfamilies.

Figure 10. Extant shrimp-like decapod species cladogram tracing Character 6 (Gill morphology) history. Character states: 0-gills absent; 1-dendrobranch gills; 2-phyllobranch gills; 3-trichobranch.

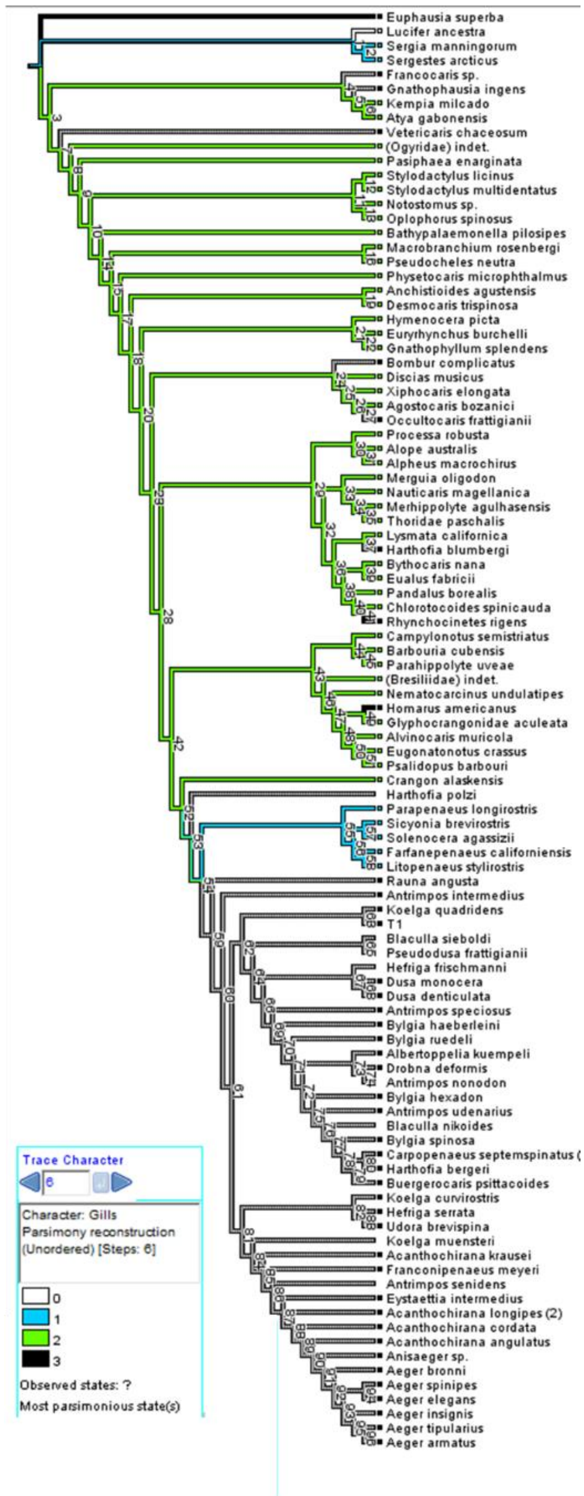

Figure 11. Comprehensive shrimp-like decapod species cladogram tracing Character 6 (Gill morphology) history. Character states: 0-gills absent; 1-dendrobranch gills; 2-phyllobranch gills; 3-trichobranch.

Carapace.-- The next set of characters that will be traced illustrates ornamentation on the carapace. These are the antennal and pterygostomian spines, the cervical sulcus and the swelling on the posteroventral margin of the carapace; characters 18 (Figs. 12 and 13), 29, 21 and 35, respectively. The discrete states are 0- absent and 1-present for all these characters.

The plesiomorphic state for all these characters is state 0-absent. For the extant tree (Fig. 12) the antennal spine appears and is maintained throughout Clade 7. The cervical sulcus appears in Clade 4 as well as in most members of Clade 13. The pterygostomian spine appears immediately within the ingroup and is maintained except for most members of Clade 25 and in Clade 39. The presence of a swelling in the posteroventral margin of the carapace was observed only for fossil forms, so it does not appear in the extant tree.

In the comprehensive tree (Fig. 13) the antennal spine appears in Clade 10; it is then lost again in Clade 52 and reappears once more in Clade 55. The cervical sulcus appears in Clade 56, and the sister groups of Clades 50 and 67. It appears once more in Clade 90 but is lost at Clade 95. The pterygostomian spine is present in most members of Clades 1 and 4 and its presence becomes fixed in Clade 7. The spine is lost afterwards in Clades 26, 30, 44 and 54. The swelling on the posteroventral margin of the carapace appears in Clade 60 and is then lost in Clades 64 and 91. It is momentarily lost for a section of Clade 62; from the node of Clade 64 to the node of Clade 71.

Overall the polarization for these ornamental characters is an unadorned plesiomorphic state with a marked shift towards ornamentation and some reversals to unadorned. The character states are, therefore, homoplasic, though the number of reversals for each character is not great.

Figure 12. Extant shrimp-like decapod species cladogram tracing Character 18 (Antennal spine) history.
Character states: 0- absent; 1-present.

Figure 13. Comprehensive shrimp-like decapod species cladogram tracing Character 18 (Antennal spine) history. Character states: 0- absent; 1-present.

Pereiopods.— Characters related to pereiopods describe the appendages based on a number of criteria including chelation, ornamentation, relative sizes and the presence of other unique features (e.g. pereiopod 2 carpus segmentation)

Characters 66, 72 and 77 describe the chelation for pereiopods 1, 2 and 3 respectively. For all of these state 0 is achelate, state 1 is pseudochelate and state 2 is chelate. In the extant tree, the ancestral state for characters 66, 72 and 77 is achelate. Characters 66 and 72 shift to a chelate state in Clade 6 and are maintained throughout. Character 77 (Fig. 14) shifts to chelate state occurs in Clade 24.

In the comprehensive tree, the ancestral state for characters 66, 72 and 77 (Fig. 15) is also achelate. Characters 66 and 72 shift to a chelate state in Clade 8 and is maintained throughout except for a reversal to achelate state in Clade 82. Character 77 shifts to a chelate state in Clade 59 and is maintained throughout except for a reversal to achelate state in Clade 82.

In all three cases, the character polarization is from an achelate state to a chelate one, not necessarily passing through a pseudochelate transition.

Characters 89, 90 and 91 describe the ratio between pereiopods: 1/2, 1/3 and 2/3 respectively. For all of these state 0 is less than 1, state 1 is greater than 1 and state 2 is 1. For the extant tree the ancestral state for all three characters is state 2, but is shifted to state 0 immediately after the outgroup, including the Clades 1 and 3. This state is maintained throughout for Characters 89 and 90. Character 91 undergoes a shift to state 1 in Clade 44.

For the comprehensive tree the ancestral state for all three characters is also state 2. These are also shifted to state 0 immediately after the outgroup, including Clades 1 and 3. This state is maintained throughout for Characters 89 and 90 except for Clade 82 which undergoes a shift to state 1 in Character 89. Character 91 undergoes a shift to state 1 in Clade 8 and is reversed to state 0 again in Clade 23.

Characters 89 (state 0; pereiopod 2 longer than pereiopod 1) and 90 (state 0, pereiopod 3 longer than pereiopod 1) are constant except for Character 91, which is clearly polarized from Pereiopod 2 being longer to Pereiopod 3 being longer in the extant tree. This is also the case for the comprehensive tree, but there is a group reversal in a higher node.

Characters 97, 98 and 99 describe the grooming articles for pereiopods 1, 2 and 3 respectively. States 0, 1 and 2 correspond to grooming articles absent, in the form of a comb, or in the form of setal brushes respectively. For the extant tree the ancestral state for all three characters is state 2. Character 97 shifts to state 0 in Clades 11 and 29. A reversal to state 2 occurs in Clade 37. Character 98 undergoes a shift to state 0 in Clades 11, 26 and 31. Character 99 shifts to state 0 in Clade 11 and to State 1 in Clade 16. A reversal occurs in Clade 24 and a shift to state 0 in Clade 30.

In the comprehensive tree, the ancestral state for all three characters is also state 2. Character 97 shifts to state 0 in Clade 14 and reversals to state 2 occur in Clades 43, 56 and 88. A shift to state 1 occurs in Clade 90. Character 98 shifts to state 0 in Clade 14, undergoes a reversal to state 2 in Clade 47 and a shift to state 1 in Clade 92. Character 99 shift to state 0 in Clade 9, a reversal to state 2 in Clade 47 and a shift to state 1 in Clade 92.

For all pereiopod ornamentation characters the polarization seems to be a plesiomorphic setose ancestral state which shifts early on in the cladogram to an unarmed state with punctual reversals or shifts to a combed state as with the aegerids in the comprehensive phylogeny (Clade 91).

Character 70 describes the symmetry between pereiopod 2 sizes on each side of the shrimps. State 0 is pereiopods of equal size, State 1 is pereiopod of unequal sizes. For both the extant and comprehensive tree this character appears only as homoplasic autapomorphies for select members.

Character 72 describes the multisegmentation of the carpus of pereiopod 2. State 0 is unsegmented carpus, state 1 is a segmented one. For the extant tree the ancestral state is an unsegmented carpus on pereiopod 2. The state shifts to a segmented carpus in Clade 23 and is reversed in Clade 40. In the comprehensive tree, the ancestral state for the character is also state 0; a shift to state 1 occurs in clade 29.

Character 101 describes the most robust pereiopod. The ancestral state in both trees is all pereiopods of equal robustness (state 0). In the extant tree a shift to pereiopod 1 being the most robust (state 1) occurs in Clade 20 and a shift to pereiopod 2 being the most robust (state 2) occurs in Clade 44. In the comprehensive tree shift to state 2 occurs in Clade 14 and in Clade 23 the character shifts to state 1. In Clade 53 pereiopods 1 and 2 are more robust than the rest. A reversal to state 0 occurs in Clades 55 and 81 and a reversal to state 1 in Clade 72.

Figure 14. Extant shrimp-like decapod species cladogram tracing Character 77 (Pereiopod 3) history. Character states: 0-achelate; 1-pseudochelae; 2-chelate.

Figure 15. Comprehensive shrimp-like decapod species cladogram tracing Character 77 (Pereiopod 3) history. Character states: 0-achelate; 1-pseudochelae; 2-chelate.

Maxilliped 3.-- Character 64 describes the grooming articles on maxilliped 3. In the extant tree the character state does not shift from having setal brushes (state 2). In the comprehensive tree the ancestral state is state 2, and a shift to lack of grooming articles (state 0) occurs in Clade 61. A reversal to state 2 occurs in Clade 85 with a shift to state 1 in Clades 78 and 88.

Character 102 describes maxilliped 3 length with respect to the pereiopods. In the extant tree (Fig. 16) the ancestral state is maxilliped 3 shorter than all pereiopods (state 0). A shift to maxilliped 3 longer that pereiopod 1 (state 2) occurs in Clade 22 and a reversal back to state 0 in Clade 39. In the comprehensive tree (Fig. 17) the ancestral state is also state 0. A shift to state 2 occurs in Clade 29 and a shift to maxilliped 3 longer than all pereiopods (State 1) in Clade 88.

Maxilliped 3 grooming articles are constant in the extant tree and polarized from setose to unarmed with intermittent reversals (like pereiopod grooming characters). Also, maxilliped 3 relative size seems to be shorter than pereiopods as a plesiomorphic state in both trees. In the comprehensive phylogeny, shifts in this character are sporadic, though homoplasic between certain groups. In the extant phylogeny, the ancestral state shifts to state 2 (maxilliped 3 longer that pereiopod 1) in the node of Clade 22 and then is reversed in a Clade 39.

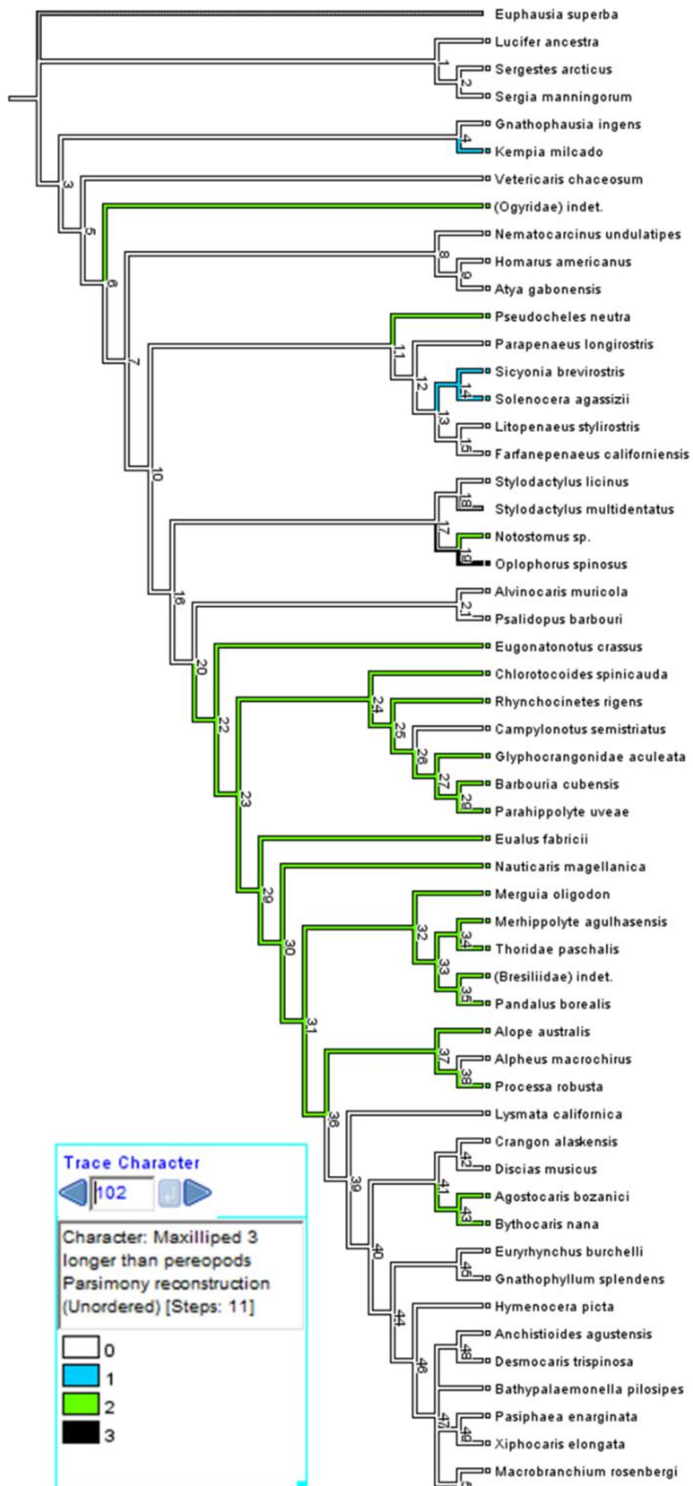

Figure 16. Extant shrimp-like decapod species cladogram tracing Character 102 (Maxilliped 3 longer than pereiopods) history. Character states: 0-Maxilliped 3 shorter than all pereiopods; 1-Maxilliped 3 longer than all pereiopods; 2-Maxilliped 3 longer than pereiopod 1 only; 3-Maxilliped 3 longer than pereiopods 1 and 2.

Figure 17. Comprehensive shrimp-like decapod species cladogram tracing Character 102 (Maxilliped 3 longer than pereiopods) history. Character states: 0-Maxilliped 3 shorter than all pereiopods; 1-Maxilliped 3 longer than all pereiopods; 2-Maxilliped 3 longer than pereiopod 1 only; 3-Maxilliped 3 longer than pereiopods 1 and 2.

Pleon.-- Character 127 describes whether the pleura of the second pleomere of the pleon overlaps the pleura of the first. The ancestral state in both trees is that it does not overlap (state 0). In the extant tree (Fig. 18) a shift to the second pleura overlapping the first (state 1) in Clade 5 and a reversal to state 0 occurs in Clade 12. In the comprehensive tree (Fig. 19) the character shift to state 1 in Clade 7. A reversal to state 0 occurs in Clade 59 and reversals to state 1 occur in Clades 79 and 82.

In both phylogenies, though a non-overlapping second pleura is the plesiomorphic state, after the early shift (Clade 5 and Clade 6 in the extant and comprehensive phylogenies respectively), there is a discrete group in both phylogenies that branches out with a reversed state: Clade 12 in the extant and Clade 54 in the comprehensive. This character's history is analogous to that of Character 6.

Figure 18. Extant shrimp-like decapod species cladogram tracing Character 127 (second pleonal pleura overlapping first) history. Character states: 0-absent; 1 present.

Figure 19. Comprehensive shrimp-like decapod species cladogram tracing Character 127 (second pleonal pleura overlapping first) history. Character states: 0-absent; 1 present.

Discussion

Little support.-- The clades resulting from both phylogenetic analyses have little support for the nodes throughout. Clades with bootstrap and jackknife supports greater than 50 are limited to Clades 4, 11, 15, 18, 19, and 28 in the extant phylogeny (Fig. 6) and Clades 2, 12, 13, 45, 55, 56, 58, 68 and 92 of the comprehensive phylogeny (Fig. 7). For the most part, these clades are terminal, comprised of only two members. This lack of support is due to a general lack of correlation between most of the characters which made it impossible to find complementary polarization between them since characters are not all optimized under a single topology. This suggests than many of the character states on the terminal nodes are homoplasic. It is not straightforward, however, to determine whether this result is due to the actual nature of the phylogenetic signal, or the arbitrary association of to some character state designations.

True homoplasy between taxa can, in most cases, be argued to arise from similar environmental pressures and available ecological niches. For instance, Characters 97, 98 and 99 describe the grooming articles for the first pereiopods. The plesiomorphic state for these characters in the comprehensive phylogeny was having setal brushes on pereiopods. When tracing the history for these characters we see instances where the setae are lost in some earlier node, but regained in a later one, and subsequently lost in a later one with a final shift to a unique synapomorphy, combed grooming articles, in one of the most terminal nodes. This could indicate specific episodes in which clades adapted to environments with different degrees of potential fouling. A possible interpretation could be the entire group evolved in an environment where setal brushes were crucial for cleaning themselves. Members from a specific clade were then subjected to conditions where grooming was not as important by either migrating or from environmental change and thus lost the grooming articles in their pereiopods. A group nested within this last clade was then subjected to the same initial conditions as the earliest taxa in the analysis and thus regained the articles.

Interpretations like these are, at this point, speculative since there are as yet no additional lines of evidence to support these hypotheses, and before further effort is placed in proactively looking for an evolutionary explanation for these convergences, more support is needed for the nodes in order to have a proper foundation for the character evolutionary history. This will likely be achieved by reevaluating the character state designations. For instance, in the same example with Characters 97, 98, and 99, a distinction between setal brushes and a comb is made in the character states. This distinction was, in some cases, very apparent to us, as in the case of most members of *Aeger* which have heavy ornamentation that seems to us more like spines than setae on pereiopods 1, 2, and 3 as well as on maxilliped 3, but in others not so much as in the case of various members of Penaeidae in which the distinction between spines and setae in the anterior appendages is not as apparent to us. There is a possibility that this distinction is arbitrary and phylogenetically uninformative and that the proper way to designate these character states would be to make no distinction between these two states. The designation scheme will be decided upon the iteration of different character designations until the non-arbitrary paradigm with the greatest number of optimized characters is found. If this revision were done, the resulting phylogenetic trees would very likely be different than the current ones and the character history for Characters 97, 98 and 99 would also change. The number of homoplasies would possibly decrease in this instance.

Character revisions.-- Several of the current characters and character states are being considered for revision in order to find a more balanced character set to analyze the taxa based on their morphology. The selection of these characters is based on various aspects of the character designation that have been deemed suboptimal for the analysis. These include characters related to ornamentation on any part of the morphology (e.g. Characters 21, 27, 67, 68, all describing carapace and pereiopod ornamental features), characters with numerous character states (e.g. Characters 1, 49, 86, 87, 101, describing rostral spine positions, maxillae endite morphology, position of epipod and exopods on pereiopods and pereiopod relative robustness respectively), character groups pertaining to a single morphological trait (e.g. Characters 65, 66, 67, 68, and 69, all describing pereiopod 1) and characters whose variability is observed only within a specific clade (e.g. Characters 115, 116, 117, 118, all describing dendrobranch sexual features).

The characters related to ornamentation present in our matrix are numerous and are descriptive primarily of the carapace and pereiopod segments. Because of the relative abundance of this type of character in the analysis, potentially unnecessary phylogenetic weight is placed on ornamentation and may be greatly affecting the topology. Making revisions of their designations may improve the resolution of discrete groups with better support for nodes. This is not to say that characters related to ornamentation will be removed from the analysis, but rather will be arranged in a different way. For instance, Characters 15 through 35 all pertain to ornamental features of the carapace, and most are dichotomous (presence-absence) types of characters. Grouping characters while increasing the number of character states would lessen the weight placed on carapace ornamentation. This might result, for instance, in a single character designated "carapace spines" with a state for each possible spine formula. If done properly, we hope that this change might eliminate error arising from morphological nomenclature which is sometimes unclear for certain taxa (e.g. distinctions between an orbital and antennal spine; a post-orbital and a post-antennal spine; an antennal and pterygostomian spine).

Another possible character designation revision is with regard to characters that are multistate. This paradigm decreases the probability of making group associations based on these characters since it is likelier each group will have its own character state. This revision is not straightforward since unwanted weight could be placed on a certain attribute if the trait were to be expanded to several characters. A possible solution to this problem would be to create fewer character states that encompass one or more of the previously existing states. For instance, character 128 (dorso-pleonal carina) has 8 character states depending, upon which pleonal somites the carina can be observed. This character was not phylogenetically informative possibly in part due to the numerous character states. If all of these states were to be collapsed onto a presence-absence designation, the character would likely be better optimized and polarized, adding support for specific clade differentiations.

We consider that the character groups pertaining to a single morphological trait are the ones that are in most dire need of revision. These are likely contributing to the error arising from unwanted weight to specific morphological aspects and would be relatively easy to revise. For instance, it has been observed empirically that for most cases the appendage ornamentation is relatively constant throughout the segments (e.g. species with ornamented merai on pereiopod 1 usually also have ornamentation on the other appendage segments; i.e. on the ischium). We, therefore, consider collapsing these groups (e.g. Characters 68 and 69; 74 and 75) into a single character (e.g. Pereiopod 1 ornamentation: absence-presence) for each trait would be beneficial in getting better topology resolution without losing significant information in the analysis.

Some characters in the analysis are applicable only to a single clade and are absent for the rest of the taxa. This results in having unequal criteria for phylogenetic grouping throughout the analysis and might have some effect on lowering the support for certain nodes. For instance, characters 115 through 118 describe sexual features for dendrobranchs and are inapplicable to carideans. It is likely due to characters like these that resolution within dendrobranchs is higher than that within the carideans.

Weight.-- Another aspect of the analysis that could be calibrated in order to attain better resolved results is that of the weight of the characters. The differential importance assigned to each character undeniably has an arbitrary component to it, and the whole practice is a matter of much controversy in the scientific world today (Lieberman, 2011). However, the notion that different characters have arisen at different times and have been fixed onto different clades throughout the evolutionary history is undeniable. We are, therefore, considering placing more relative weight on characters with important physiologic or ethologic implications with respect to characters more related to species recognition, sexual selection.

Outgroup selection.-- The selection of an outgroup for the current analysis was, as it is in all phylogenetic analysis, a key decision which had a direct and important influence on the outcome of the study. Since the general decapod shrimp morphology is considered to be plesiomorphic for the entire order, using another member of the order like a lobster or a crab would not, according to the current taxonomy, accurately polarize the characters and would result in an unordered resolution for the progressive clades. We thus turned to groups that prior to 2015 were3 considered to be the sister orders of Decapoda: Euphausiacea and Amphionidacea. Fortunately, while the outgroups were being considered, a paper by De Grave, *et al*. (2015) convincingly argued that the single species within Amphionidacea was a larval stage of a caridean shrimp. This narrowed our search for a suitable outgroup to the order Euphausiacea. We decided to use one of the most abundant species of the order, *Euphausia superba,* due to the abundance of available specimens, which would help us accurately code the species, and its manageable size, in contrast with most of the rest of the species of the order. For the continuation of the project we will test different topologies calibrated by different outgroups (e.g. mysids, phyllocarids, hoplocarids).

Homarus americanus.-- The American Lobster *Homarus americanus* was included in the analysis with the intention of visualizing the nature of the topology from the perspective of higher (more derived) decapods. In the extant phylogeny, the lobster is related to an early branching clade (Clade 8) along with two of the more morphologically uncommon caridean shrimps in the analysis, *Atya gabonensis* and *Nematocarcinus undulatipes* on the basis of their triangular scaphognathite ventral lobe, their ratio of the height of the pleura of pleonal somite three/total height of somite three greater than 0.5 and their rounded telson posterior margin. The following node is where the dendrobranch and the rest of the caridean shrimp diverge. This result does not support the monophyly of Pleocyemata, which might be due to inadequate character and character state designation. In the comprehensive phylogeny, the lobster branches out along with the most derived caridean clade before the dendrobranchs and the fossil species are derived. This topology suggests that Pleocyemata is paraphyletic and an ancestor to dendrobranchs.

Cladogram topology.-- Though numerous issues arose during the elaboration of this project that are potential sources of error in the resulting phylogenies, several clades grouped taxa in a way that is concurrent with previous work as well as with the current paradigm of the higher levels of the current taxonomy within the order.

Previous phylogenetic work done on higher level decapod taxa (Abele and Felgenhauer, 1986; Chace, 1992; Porter *et al*., 2005; Bracken *et al*., 2009b, 2009c) all support the monophyly of two distinct suborders: Dendrobranchiata and Pleocyemata. This is supported by aspects of morphology and physiology, primarily the fact that virtually all dendrobranchs have pereiopods 1, 2 and 3 chelate; dendritic gills (hence the name of the suborder) and the fact that dendrobranch species do not brood their eggs, but rather release them onto the water column which is not the case for pleocyemates. Carideans brood their eggs in the ventral portion of their pleon, which might be related to the development of a second pleonal pleura overlapping the first, which is considered a definitive character to distinguish dendrobranchiate and caridean shrimp. The results in the current project, however, do not support the monophyly of these suborders. This is partially due to the issues addressed above; however, we consider that our species selection also had a role in this result.

Dendrobranchs.-- For both the extant and comprehensive trees, suborder Dendrobranchiata is not supported due to the fact that superfamilies Sergestoidea and Penaeoidea do not group together. Sergestoidea, in both cases, branches out in the analysis on the same level as the outgroup. The monophyly of Sergestoidea, however, is very well supported because of this in both cases. Additionally, the members of the family Sergestidae form a distinct clade sister to the single representative of the only other sergestoid family, Luciferidae. These species have unique synapomorphies including the loss of terminal pereiopod segments as well as an elongate 6th pleonal somite which made the group branch out very early within the analysis.

In the extant tree, superfamily Penaeoidea also branches as a discrete group and is well supported by numerous characters (see Clades 11 and 12 in extant clade description); in the comprehensive tree, however, the monophyly of the group is questioned. *Bombur complicatus*, considered now as a single fossil dendrobranch species, lies quite removed from the terminal group composed mostly of dendrobranch species which corresponds to Clade 54. On this node two major clades form; one is composed of all extant dendrobranch species (Clade 55) and the other is composed of all the fossil species except *B. complicatus* and *Francocaris sp.*, an outgroup species (Clade 59).

In both trees the topology of the extant penaeoid species clades are identical. They do not support the monophyly of the family Penaeidae, which has been brought into question by numerous previous works (Voloch *et al*., 2005; Ma *et al*., 2009; Tavares *et al*., 2009), since a clade containing members of families Solenoceridae and Sicyonidae forms within the clade that contains the members of the family Penaeidae in the current study. We consider the family Penaeidae to be a "wastebasket taxon", in which various ambiguous species are placed, particularly fossil species. We consider this taxon to be in dire need of revision.

Carideans.-- In the comprehensive tree the infraorder Caridea groups as a paraphyletic grade sister to the clade that encompasses extant dendrobranchs and the fossil species. In this phylogeny, a single member of the family Atyidae (superfamily Atyoidea) is grouped with a lophogastrid, a stomatopod and a mysid in the first clade that branches off the outgroup complex (*Euphaisia superba* and dendrobranch superfamily Sergestoidea). The basal placement of superfamily Atyioidea has been observed in previous caridean phylogenetic analyses using both morphological (Christoffersen, 1990; Chace, 1992) and molecular (Porter *et al*., 2005; Bracken *et al*., 2009c; Li *et al*., 2011) characters. The morphology of the atyid coded in this analysis (*Atya gabonensis*) is unlike that of most decapod shrimps in the sense that it has a much more robust bodyplan reminiscent of a crayfish or a lobster. It also has very robust pereiopods 3 through 5 relative to pereiopods 1 and 2 and has an antennal flagellum that does not exceed body length. This family, however, has great morphological variability and some species are much more shrimp-like than species of the genus *Atya* (e.g. species of the genus *Jonga*).

The following taxa that branch out in the phylogeny are members of the families Procarididae (*Vetericaris chaceosum*), Ogyridae (indeterminate species), Pasiphaeidae (*Pasiphaea emarginata*) and a clade composed of members of superfamilies Stylodactyloidea (*Stylodactylus licinus* and *Stylodactylus multidentatus*) and Oplophoroidea (*Oplophorus spinosus* and *Notostomus sp*.). All of these groups, except for the species of Ogyridae which belongs to superfamily Alpheoidea and which is usually considered a more derived form, have been observed to branch out early in caridean phylogenetic analyses (Thompson, 1967; Christoffersen, 1990; Chace, 1992), especially the family Procarididae, whose placement within the infraorder Caridea is still disputed

(Bracken *et al*., 2009a). Most of these groups have distinct features that are likely the reason for their early divergence from the main phylogenetic body: Procarididae lacks a rostrum and chelate pereiopods; Pasiphaeidae has strongly curved chelipeds and well developed exopods on pereiopods; Ogyridae has exceedingly long eyestalks; and Stylodactilidae has well developed exopods on pereiopods and heavily setose pereiopods 1 and 2 and maxilliped 3.

Throughout the rest of the topology in the comprehensive tree, most caridean superfamilies are not well supported. Some members of superfamilies Alpheoidea and Palaemonoidea cluster as polyphyletic of paraphyletic groups. On Clade 16 up until Clade 20, a grade including all members of Palaemonoidea (except for *Eualus fabricii*) clusters with sporadic occurrences of members of superfamilies Physetocaridoidea (*Physetocaris microphthalmus*) and Bresilioidea (*Pseudocheles neutral*). This cluster is partially supported by the group's general lack of mandibular palps, but is most likely resulting from the optimization of other characters.

The grouping of members of Alpheoidea characterizes them as a relatively derived subgroup, which is observed in previous phylogenetic works (Christoffersen, 1990; Chace, 1992). This occurs for the most part in Clade 29, though members of superfamilies Processoidea, Bresiloidea, Palaemonoidea as well as a clade that groups members of superfamily Pandaloidea (*Pandalus borealis*, and *Chlorotocoides spinicauda*) as a grade containing also a member of Nematocarcinoidea (*Rhynchocinetes rigens*) are present as well. A separate terminal clade grouping two more members of Alpheoidea (*Barbouria cubensis* and *Parahippolyte uveae*) occurs in a separate phylogenetic line (Clade 46).

The comprehensive tree topology does not support the monophyly of superfamilies Nematocarcinoidea, Bresiloidea, Crangonoidea and Campylonotoidea.

The carideans in the extant tree exhibit in some cases, similar grouping patterns as the comprehensive tree. Members of families Procarididae, Ogyridae and Atyidae are the first to branch out. They are in this case accompanied by *Nematocarcinus undulatipes* (superfamily Nematocarcinoidea). However, *Pasiphaea emarginata* emerges as one of the most derived species.

Superfamilies Stylodactyloidea and Oplophoroidea group together, as in the case of the comprehensive tree. Their clade branches out after the emergence of the group that encompases the extant penaeoids.

Superfamily Alpheoidea is much more polyphyletic than in the comprehensive tree. Their members do group in discrete clades, but these are considerably removed from one another (Clades 28, 32 and 37). Members of superfamily Pandaloidea are also, very removed from each other.

Superfamily Palaeomonoidea groups as a polyphyletic clade (Clade 46) with sporadic ocurrences of superfamilies Campylonotoidea, Pasiphaeoidea, Nematocarcinoidea and Physetocaridoidea. This clade emerges as one of the most derived, which is not an observed result in previous work.

Conclusions

The inclusion of fossil species in a decapod shrimp phylogeny offers new insight into the order's evolutionary history. Comparison of extant and comprehensive phylogeny topology results in different character polarization and clade grouping. This and the fact that nodes in both phylogenies have overall very little support suggests reevaluation of character designation and species selection is necessary. Characters with too many character states, multiple characters describing a single morphological aspect, and characters with unclear adaptative functions are some of the characters that will be reevaluated. Differential character weighting is also being considered. More taxa will be coded and included in the analysis to give a more balanced representation of each suborder as well as to represent the morphological variation within each family.

The current work does not support the monophyly of any currently accepted taxonomic hierarchy within the order except for Aegeridae. The dendrobranch as plesiomorphic form hypotheses for the group is partially supported due to the early branching of the sergestoid clade, but the dendrobranch state is considered to be homoplasic since penaeoids do not group together with sergestoids. The monophyly of dendrobranch superfamilies is supported, though the monophyly of Penaeidae is challenged.

The monophyly of caridean superfamilies is challenged in the current work as well. Basal caridean families in this study (Atydae, Pasiphaeidae, and Procarididae) are consistent with the results from previous phylogenetic works.

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Appendix 1. Morphologic characters and character states coded for phylogenetic analyses.

1 Rostral spines: absent (0), dorsal only (1), dorsal and ventral (2), dorsal and lateral, (3) lateral only (4), ventral only (5), rostrum absent (6), ventral and lateral (7), dorsal, ventral and lateral (8)

2 Number of dorsal rostral spines: absent (0), <6 (1), 6-9 (2), >9 (3)

3 Number of ventral rostral spines: absent (0), <5 (1), 5-7 (2), >7 (3)

4 Post-rostral spines: absent (0), present (1)

5 Number of post-rostral spines: absent (0), <3 (1), 3 (2), >3 (3)

6 Gills: absent (0), dendrobranch (1), phyllobranch (2), trichobranch (3)

7 Number of gills: >10 on each side (0), <10 on each side (1)

8 Ocular stylet: absent (0), present (1)

9 Ocular tubercule: absent (0), present (1)

10 Ocular scale: absent (0), present (1)

11 Rostrum length: extending beyond antennular peduncle (0), extending beyond eyestalk but not antennular peduncle (1), not extending beyond eyestalk (2), rostrum absent (3)

12 Scaphocerite: absent (0), present (1)

13 Scaphocerite shape: acicular (0), flat (1)

14 Rostrum: straight (0), curved (1)

15 Orbital spine: absent (0), present (1)

16 Post-orbital spine: absent (0), present (1)

17 Androstral carina: absent (0), present (1)

18 Antennal spine: absent (0), present (1)

19 Antennal carina: absent (0), present (1)

20 Post-antennal spine: absent (0), present (1)

21 Cervical sulcus: absent (0), present (1)

22 Branchiocardiac groove: absent (0), present (1)

23 Hepatic sulcus: absent (0), present (1)

24 Hepatic spine: absent (0), present (1)

25 Branchiostegal spine: absent (0), present (1)

26 Branchiostegal carina: absent (0), present (1)

27 Post-cervical sulcus: absent (0), present (1)

28 Gastro-orbital sulcus: absent (0), present (1)

29 Pterygostomian spine: absent (0), present (1)

30 Longitudinal carina on carapace: absent (0), present (1)

31 Branchiocardial spine: absent (0), present (1)

32 Branchiocardiac crest: absent (0), present (1)

33 Dorsomedian ridge: absent (0), present (1)

34 Submarginal carina: absent (0), present (1)

35 Swelling on carapace anteroventral margin: absent (0), present (1)

36 Ratio carapace height/length: <0.5 (0), >0.5 (1)
37 Antennule prosartema: absent (0), present (1)
38 Antennule: biflagellate (0), uniflagellate (1)
39 Antennae: slender (0), robust (1)
40 Antennule: slender (0), robust (1), flattened (2)
41 Antennal flagellum length: not greater than total body length (0), greater than total body length (1)
42 Stylocerite: well defined (0), weakly defined (1)
43 Antennule first article distolateral spine: absent (0), present (1)
44 Ratio scaphocerite length/antennular peduncle length: <1.4 (0), 1.4-1.99 (1), >1.99 (2)
45 Thoracic sternites width: sternites 3-8 narrow (0), sternites 3-5 narrow (1), sternites 3-6 narrow (2), sternites 3-8 evenly wide (3)
46 Mandible: with molar and incisor processes together (0), with molar and incisor processes separated (1), only with incisor process (2), only with molar process (3)
47 Mandiblular palp: absent (0), present (1)
48 Maxillule palp: absent (0), present (1)
49 Maxilla: with two bilobed endites (0), with one bilobed and one unilobed endites (1), with reduced endited (2), with one bilobed and one reduced endite (3), with one unilobed and one reduced endites (4)
50 Maxilla palp: absent (0), present (1)
51 Number of maxillipeds: 0 (0), 3 (1), 4 (2), 5 (3)
52 Maxilliped 1 endite: absent (0), oval (1), reduced (2)
53 Maxilliped 2 exopods: absent (0), present (1)
54 Segments of maxilliped 2 exopod: separated (0), fused (1)
55 Maxilliped 3 dactyl: with one article (0), with 5 articles (1)
56 Maxilliped 3 exopod: absent (0), present (1)
57 Maxillipeds: with 7 segments (0), with less than 7 segments (1)
58 Attached ornamentation on maxilliped ending: absent (0), present (1)
59 Molar process: flat (0), laminar (1), vestigial (2), subtruncate (3), ridged (4), conical (5)
60 Incisor process perpendicular to molar: absent (0), present (1)
61 Perpendicular incisor process: rudimentary (0), well developed (1)
62 Scaphognathite ventral lobe: ronded (0), triangular (1)
63 Distal lash on maxilliped 1 shorter than caridean lobe: absent (0), present (1)
64 Maxilliped grooming articles: absent (0), comb (1), setal brushes (2), flaps (3)
65 Pereiopod 1 dactyl: absent (0), present (1)
66 Pereiopod 1: achelate (0), pseudochelate (1), chelate (2)
67 Pereiopod 1 achelate: with subchela formed by robust setae (0),

without subchela (1)

68 Pereiopod 1 merus: unarmed (0), with subdistal spine (1), with subdistal robust setae (2), with row of spines (3), with subdistal robust setae and row of 3 spines (4), with rows of setae (5), with subdistal spine and setae (6)

69 Pereiopod 1 ischium: unarmed (0), with mesial spine (1), with distal spine (2), with rows of setae (3), with row of spines (4)

70 Right and left pereiopods 2: of equal length (0), of unequal length (1)

71 Pereiopod 2 dactyl: absent (0), present (1)

72 Pereiopod 2: achelate (0), pseudochelate (1), chelate (2)

73 Pereiopod 2 carpus subdivisions: absent (0), present (1)

74 Pereiopod 2 merus: unarmed (0), with subdistal robust setae (1), with a disto-lateral row of 5-7 robust setae (2), with soft setae (3), with subdistal spine (4), with row of spines (5)

75 Pereiopod 2 ischium: unarmed (0), with one spine (1), with rows of setae (2), with severla spines (3)

76 Pereiopod 3 dactyl: absent (0), present (1)

77 Pereiopod 3: achelate (0), pseudochelate (1), chelate (2)

78 Pereiopod 3 merus: unarmed (0), with a robust setae row (1), with soft setae (2), with multiple spines (3), with sub-distal spine (4)

79 Pereiopod 4: absent (0), present (1)

80 Pereiopod 4 dactyl: absent (0), present (1)

81 Pereiopod 4 merus: unarmed (0), with a robust setae row (1), with soft setae (2), with multiple spines (3), with sub-distal spine (4)

82 Ratio length Pereiopod 4/ Pereiopod 3: <1 (0), 1-1.6 (1), >1.6 (2)

83 Pereiopod 5: absent (0), present (1)

84 Pereiopod 5 dactyl: absent (0), present (1)

85 Ratio length Pereiopod 5/ Pereiopod 3: <1.2 (0), 1.2-2 (1), >2 (2)

86 Exopods on pereiopods: absent (0), reduced (1), present (2), present only in pereiopod 1 (3), present in all except pereiopod 5 (4), present only in pereiopods 1 and 2 (5)

87 Epipods on pereiopods: absent (0), present on all pereiopods (1), present on pereiopods 1 through 3 (2), present on pereiopods 1 through 4 (3), present only on pereiopod 1 (4)

88 Pereiopod epipods shape: bifid (0), foliaceous (1), other (2)

89 Ratio length pereiopod 1/ pereiopod 2: <1 (0), >1 (1), 1 (2)

90 Ratio length pereiopod 1/ pereiopod 3: <1 (0), >1 (1), 1 (2)

91 Ratio length pereiopod 2/ pereiopod 3: <1 (0), >1 (1), 1 (2)

92 Pereiopod epipods with vertical appendix: absent (0), present (1)

93 Both fingers mobile on first pereiopod chela: absent (0), present (1)

94 Tufts of setae on pereiopods 1 and 2 ending: absent (0), present (1), present only on pereiopod 2 (2), present only on pereiopod 1 (3)

95 Pereiopod 1 stouter than pereiopod 2: absent (0), present (1)
96 Pereiopod exopods longer than ischium: absent (0), present (1)
97 Pereiopod 1 grooming articles: absent (0), comb (1), setal brushes (2)
98 Pereiopod 2 grooming articles: absent (0), comb (1), setal brushes (2)
99 Pereiopod 3 grooming articles: absent (0), comb (1), setal brushes (2)
100 Pereiopod 1 with respect to pereiopod 2: equal (0), more robust (1), more slender (2)
101 Most robust pereiopod: all equal (0), pereiopod 1 (1), pereiopod 2 (2), pereiopod 3 (3), pereiopod 1=pereiopod 2> pereiopod 3 (4), pereiopod 2=pereiopod 3>pereiopod 1(5)
102 Maxilliped 3 longer than pereiopods: absent (0), present (1), longer only than pereiopod 1 (2), longer than pereiopods 1 and 2 (3)
103 Pereiopod 4: achelate (0), pseudochelate (1), chelate (2)
104 Pereiopod 5: achelate (0), pseudochelate (1), chelate (2)
105 Pereiopod 1 manus narrowing proximally and distally (bulbous): absent (0), present (1)
106 Pereiopod 2 manus narrowing proximally and distally (bulbous): absent (0), present (1)
107 Pereiopod 3 manus narrowing proximally and distally (bulbous): absent (0), present (1)
108 Pereiopod 1 fingers strongly curved toward one another: absent (0), present (1)
109 Pereiopod 2 fingers strongly curved toward one another: absent (0), present (1)
110 Pereiopod 3 fingers strongly curved toward one another: absent (0), present (1)
111 Ischium very reduced: absent (0), present (1)
112 Petasma: absent (0), present (1)
113 Petasma present: open (0), semi-open (1), semi-closed (2), closed (3)
114 Male appendix interna: absent (0), present only on pleopod 2 (1), present on pleopods 2 through 5 (2)
115 Appendix masculina: smaller than appendix interna (0), same size as appendix interna (1), bigger than appendix interna (2)
116 Appendix interna size: londer than wide (0), as long as it is wide (1)
117 Thelycum: absent (0), present (1)
118 Thelycum present: open (0), closed (1)
119 Pleonal somite 3 bifid dorsal carina: absent (0), present (1)
120 Pleonal somite 1 narrower than the rest: absent (0), present (1)
121 Pleonal pleura serrations: absent (0), present (1)
122 Dorsomedial reentrant in pleonal somites: absent (0), present (1)
123 Ratio height pleura somite 3/somite three: <0.5 (0), >0.5 (1)
124 Pleura terminations: sharp (0), rounded (1)

125 Ratio pleonal somite 3 height/length: <0.75 (0), >0.75 (1)

126 Pleon: laterally compressed (0), dorsoventrally compressed (1)

127 Second pleonal pleura overlapping first: absent (0), present (1)

128 Dorso-pleonal carina: absent (0), present on somites 2 through 6 (1), present on somites 3 through 6 (2), present on somites 4 through 6 (3), present on somite 6 (4), present on all somites (5), present on somites 3 through 5 (6), present on somites 5 and 6 (7)

129 Pleopods 3 through 5: biramous (0), uniramous (1)

130 Diaeresis: absent (0), present unarmed (1), present armed (2)

131 Uropods: with exopod and endopod unarmed (0), exopod with an outer lateral spine, endopod unarmed (1), endopod and exopod with an outer lateral spine both (2), setae rows (3), exopod with spine, endopos and exopod with setae (4), several spines (5), exopod unarmed, endopod with setae (6), endopod and exopod with spines and setae (7)

132 Telson posterior margin: pointed (0), cleft (1), truncate (2), rounded (3)

133 Telson ormanentation: unarmed (0), only with robust setae (1), with spines and robust setae (2), only with spines (3), soft setae (4), with spines and soft setae (5)

134 Position of telson ornamentation; lateral (0), terminal (1), lateral and terminal (2), lateral and dorsal (3), lateral, dorsal and ventral (4)

135 Position of telson spones: lateral (0), terminal (1), lateral and terminal (2), lateral and dorsal (3), lateral, terminal and dorsal (4)

136 Number of setae on each side of telson: <5 (0), 5-7 (1), >7 (2), 0 (3)

137 Number of spines on each side of telson: <4 (0), 4-6 (1), >6 (2), 0 (3)

138 Photophores: absent (0), present (1)

139 Pesta organ: absent (0), present (1)

Appendix 2. Morphological matrix of extant species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Euphausia superba	0	0	0	0	0	3	0	0	0	0	2	1	1	0	0	0	0	0	0	0
Gnathophausia ingens	2	3	2	0	0	?	?	0	1	0	0	1	0	0	0	0	0	0	0	0
Homarus americanus	4	1	0	1	1	3	0	0	0	1	0	0	?	0	1	1	0	1	0	0
Kempia milcado	0	0	0	0	0	2	1	0	0	0	2	1	1	1	0	0	1	0	1	0
Farfantepenaeus californiensis	2	2	1	1	2	1	0	0	0	1	1	1	1	0	0	0	1	1	1	0
Litopenaeus stylirostris	2	2	1	1	1	1	0	0	0	1	1	1	1	0	0	0	1	1	1	0
Parapenaeus longirostris	1	2	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0
Sergia manningorum	0	0	0	0	0	1	1	0	0	0	2	1	1	0	0	0	0	0	0	0
Sergestes arcticus	0	0	0	0	0	1	1	0	0	0	3	1	1	-	1	1	0	0	0	0
Sicyonia brevirostris	1	1	0	1	2	1	0	1	0	0	2	1	1	0	0	0	0	1	0	0
Solenocera agassizii	1	1	0	1	2	1	0	0	0	1	1	1	1	1	1	1	0	1	0	0
Lucifer ancestra	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Notostomus sp.	2	3	1	1	3	2	0	0	1	0	0	1	1	1	0	0	1	1	0	0
Agostocaris bozanici	0	0	0	0	0	2	0	0	0	0	1	1	1	1	0	0	0	1	0	0
Alope australis	1	1	0	1	1	2	1	0	0	0	1	1	1	0	0	0	0	1	0	0
Alpheus macrochirus	0	0	0	0	0	2	1	0	0	0	1	1	0	0	1	0	1	0	0	0
Alvinocaris muricola	2	2	3	1	3	2	0	0	0	0	0	1	1	1	0	0	0	1	0	0
Anchistioides antiguensis	2	2	2	0	0	2	0	1	0	1	0	1	1	0	1	0	0	1	0	0
Atya gabonensis	0	0	0	0	0	2	0	0	0	0	1	1	2	0	1	0	1	1	1	0
Barbouria cubensis	2	1	1	1	2	2	1	0	0	0	1	1	1	0	0	0	1	1	1	0
Parahippolyte uveae	2	1	1	1	1	2	0	0	0	0	1	1	1	0	0	1	1	0	0	0
Bathypalaemonella pilosipes	2	3	3	0	0	2	0	0	0	0	0	1	1	0	0	0	1	1	0	0
(Bresiilidae) indet.	2	3	2	1	3	2	0	0	0	0	1	1	1	0	0	0	1	1	0	0
Bythocaris nana	0	-	-	-	-	2	1	0	1	0	-	1	1	-	0	0	0	1	0	0
Campylonotus semistriatus	2	1	1	1	1	2	0	0	0	1	0	1	1	1	0	0	0	1	1	0
Crangon alaskensis	0	-	-	-	-	2	1	0	0	0	1	1	1	0	1	0	0	0	0	0
Desmocaris trispinosa	2	2	1	0	0	2	1	0	0	0	0	1	1	0	0	1	0	1	0	0
Discias musicus	0	-	-	-	-	2	1	0	0	0	2	1	1	0	0	0	0	1	0	0

Appendix 2. Morphological matrix of extant species (cont.).

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Euphausia superba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnathophausia ingens	1	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1
Homarus americanus	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0
Kempia milcado	1	1	1	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0
Farfantepenaeus californiensis	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1
Litopenaeus stylirostris	1	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0
Parapenaeus longirostris	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0
Sergia manningorum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Sergestes arcticus	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1
Sicyonia brevirostris	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	0
Solenocera agassizii	1	0	1	1	0	1	0	0	1	2	0	0	0	0	0	1	1	0	0	0
Lucifer ancestra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Notostomus sp.	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1
Agostocaris bozanici	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Alope australis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Alpheus macrochirus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Alvinocaris muricola	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Anchistioides antiguensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Atya gabonensis	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	1	1
Barbouria cubensis	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Parahippolyte uveae	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Bathypalaemonella pilosipes	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
(Bresiilidae) indet.	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Bythocaris nana	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Campylonotus semistriatus	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Crangon alaskensis	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Desmocaris trispinosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Discias musicus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0

Appendix 2. Morphological matrix of extant species (cont.).

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Euphausia superba	0	1	0	0	0	?	?	?	?	?	0	-	-	-	-	-	-	-	?	?
Gnathophausia ingens	0	0	0	1	3	0	?	?	?	?	2	?	?	?	?	?	0	1	0	0
Homarus americanus	0	1	1	?	2	0	1	1	0	1	1	?	1	0	0	1	0	1	0	0
Kempia milcado	0	1	0	0	1	?	?	?	?	?	3	0	0	0	0	0	0	1	?	?
Farfantepenaeus californiensis	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	0
Litopenaeus stylirostris	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	0
Parapenaeus longirostris	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	0
Sergia manningorum	1	1	0	0	0	2	1	1	1	1	1	1	0	0	0	0	0	0	-	-
Sergestes arcticus	1	0	0	0	0	2	1	1	1	1	1	1	0	0	0	0	0	0	-	-
Sicyonia brevirostris	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	?	?
Solenocera agassizii	1	0	1	0	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	0
Lucifer ancestra	0	?	0	0	?	?	0	0	0	0	1	0	0	1	0	0	1	0	?	?
Notostomus sp.	1	0	1	2	3	0	1	1	1	1	1	2	1	0	0	1	1	1	0	0
Agostocaris bozanici	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	5	0
Alope australis	1	0	0	1	2	3	1	?	?	?	1	?	1	0	0	1	1	1	?	-
Alpheus macrochirus	1	0	0	0	0	0	1	?	0	1	1	?	1	1	0	1	1	1	0	0
Alvinocaris muricola	1	0	1	0	0	1	1	?	0	1	1	1	0	0	0	0	1	1	?	?
Anchistioides antiguensis	1	0	1	2	2	?	0	?	1	1	1	2	1	1	0	1	1	1	?	?
Atya gabonensis	0	1	0	0	0	1	0	0	0	1	1	1	1	0	0	1	1	1	?	?
Barbouria cubensis	1	0	0	1	1	?	?	?	?	?	1	1	1	0	0	1	1	1	?	-
Parahippolyte uveae	1	0	0	2	3	0	1	1	0	1	1	1	1	0	0	1	1	1	0	1
Bathypalaemonella pilosipes	1	0	0	2	0	0	1	1	0	1	1	1	1	0	0	1	1	1	4	0
(Bresiilidae) indet.	1	0	1	0	0	1	1	?	1	1	?	?	?	0	0	?	1	0	?	?
Bythocaris nana	?	0	0	2	0	3	0	1	3	1	1	?	1	0	1	1	1	1	?	-
Campylonotus semistriatus	1	0	0	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0
Crangon alaskensis	1	0	0	2	1	3	0	1	?	1	1	?	1	1	0	1	0	0	?	?
Desmocaris trispinosa	1	1	0	2	0	1	0	0	0	0	1	1	1	0	0	1	1	0	4	0
Discias musicus	0	1	0	1	0	1	1	?	1	1	1	?	1	0	0	1	1	0	?	?

Appendix 2. Morphological matrix of extant species (cont.).

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Euphausia superba	?	?	-	-	1	0	-	5	3	0	1	0	0	3	2	1	0	2	1	1
Gnathophausia ingens	?	?	-	-	1	0	-	5	3	0	1	0	0	3	2	2	1	0	1	1
Homarus americanus	?	?	?	2	1	2	?	3	4	0	1	2	0	0	0	1	2	0	1	1
Kempia milcado	?	?	-	2	1	0	1	5	3	0	1	0	0	3	2	1	0	0	1	1
Farfantepenaeus californiensis	-	0	-	2	1	2	-	5	2	0	1	2	0	0	0	1	2	0	1	1
Litopenaeus stylirostris	-	0	-	2	1	2	?	0	2	0	1	2	0	0	0	1	2	0	1	1
Parapenaeus longirostris	?	0	-	2	1	2	?	5	2	0	1	2	0	0	0	1	2	0	1	1
Sergia manningorum	-	0	-	2	0	0	0	5	0	0	1	0	0	3	2	1	0	2	1	0
Sergestes arcticus	-	0	-	2	0	0	1	5	3	0	1	0	0	3	2	1	2	2	1	0
Sicyonia brevirostris	?	0	0	2	1	2	-	5	3	0	1	2	0	0	0	1	2	0	1	1
Solenocera agassizii	0	0	-	2	1	2	-	5	0	0	1	2	0	3	2	1	2	0	1	1
Lucifer ancestra	?	-	-	2	0	0	?	5	3	0	0	0	0	3	0	1	0	1	0	0
Notostomus sp.	-	0	0	2	1	2	-	5	3	0	1	1	0	3	2	1	0	3	1	1
Agostocaris bozanici	-	1	0	2	1	2	-	0	0	0	1	2	0	0	0	1	0	0	1	1
Alope australis	-	?	?	2	1	2	-	0	0	0	1	2	1	3	0	1	0	0	1	1
Alpheus macrochirus	?	0	?	2	1	2	?	0	0	0	1	2	1	0	0	1	0	0	1	1
Alvinocaris muricola	?	1	1	2	1	2	-	6	3	0	1	2	0	3	2	1	0	2	1	1
Anchistioides antiguensis	?	0	?	2	1	2	-	0	0	0	1	2	0	0	0	1	0	0	1	1
Atya gabonensis	?	1	?	2	1	2	-	5	3	0	1	2	0	3	2	1	0	3	1	1
Barbouria cubensis	-	?	?	2	1	2	-	0	0	0	1	2	1	0	0	1	0	0	1	1
Parahippolyte uveae	0	0	?	2	1	2	-	5	0	0	1	2	1	0	0	1	0	0	1	1
Bathypalaemonella pilosipes	-	0	1	2	1	1	-	1	0	1	1	2	0	0	0	1	0	4	1	1
(Bresiilidae) indet.	?	1	?	0	1	2	-	0	0	0	1	2	0	0	0	1	0	0	1	1
Bythocaris nana	-	?	?	2	1	2	-	0	0	0	1	2	1	0	0	1	0	3	1	1
Campylonotus semistriatus	?	1	?	2	1	2	-	0	0	?	1	2	0	0	0	1	0	0	1	1
Crangon alaskensis	?	?	?	2	1	1	?	0	0	0	1	0	0	0	0	1	0	0	1	1
Desmocaris trispinosa	-	0	0	0	1	2	-	0	0	0	1	2	0	0	0	1	0	0	1	1
Discias musicus	?	0	?	0	1	2	-	0	0	0	1	2	0	0	0	1	0	0	1	1

Appendix 2. Morphological matrix of extant species (cont.).

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Euphausia superba	2	0	1	1	0	2	1	2	2	2	2	?	0	1	0	1	2	2	2	0
Gnathophausia ingens	2	0	1	1	0	2	0	0	0	0	0	-	0	0	0	1	2	2	2	0
Homarus americanus	0	0	1	1	0	0	1	1	1	1	1	0	0	2	1	-	0	2	2	1
Kempia milcado	0	1	1	1	1	0	0	2	1	1	1	-	-	1	0	?	2	2	2	0
Farfantepenaeus californiensis	0	0	1	1	0	1	2	0	0	0	0	0	0	0	0	0	2	0	0	0
Litopenaeus stylirostris	0	0	1	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Parapenaeus longirostris	0	0	1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Sergia manningorum	2	0	1	0	0	0	0	-	0	0	0	-	0	0	0	0	2	2	2	0
Sergestes arcticus	2	0	1	0	0	0	0	-	0	0	0	?	0	0	0	-	2	2	2	0
Sicyonia brevirostris	1	0	1	1	0	0	2	0	0	0	0	?	0	0	0	0	2	2	2	0
Solenocera agassizii	0	0	1	1	0	1	3	1	0	0	0	-	0	0	0	0	2	2	2	0
Lucifer ancestra	-	-	0	-	-	0	0	-	0	0	0	-	0	0	0	-	2	2	2	0
Notostomus sp.	3	0	1	1	0	2	2	2	0	0	0	0	0	0	0	1	2	2	0	0
Agostocaris bozanici	0	0	1	1	0	5	0	-	0	0	0	-	0	0	1	1	0	0	0	1
Alope australis	0	0	1	1	0	0	0	-	0	0	0	-	0	1	1	-	2	2	0	1
Alpheus macrochirus	0	0	1	1	0	0	0	0	0	1	1	?	0	0	1	-	2	0	2	1
Alvinocaris muricola	2	0	1	1	0	0	0	-	1	0	0	-	0	0	1	-	0	2	2	1
Anchistioides antiguensis	0	0	1	1	0	0	0	-	0	0	1	-	0	3	0	-	2	0	0	2
Atya gabonensis	3	0	1	1	0	1	0	-	0	0	0	-	0	1	0	1	2	2	2	0
Barbouria cubensis	0	0	1	1	0	0	1	1	0	0	0	?	0	0	1	-	0	0	0	2
Parahippolyte uveae	0	0	1	1	0	0	1	1	0	0	0	?	0	0	1	-	2	0	0	1
Bathypalaemonella pilosipes	4	0	1	1	0	0	0	-	0	0	1	-	0	0	0	-	0	0	0	2
(Bresiilidae) indet.	0	0	1	1	0	0	0	-	0	0	0	-	0	0	1	?	0	0	0	1
Bythocaris nana	3	?	1	1	?	0	0	-	0	?	?	-	0	0	1	-	0	0	0	1
Campylonotus semistriatus	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	-	0	0	2	2
Crangon alaskensis	0	0	1	1	0	3	0	-	0	0	0	-	0	0	1	1	0	0	0	1
Desmocaris trispinosa	0	0	1	1	0	0	0	-	0	0	0	-	0	3	0	-	2	0	0	2
Discias musicus	0	0	1	1	0	2	0	-	0	0	0	-	0	0	1	1	0	0	0	1

Appendix 2. Morphological matrix of extant species (cont.).

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Euphausia superba	0	-	0	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?	0
Gnathophausia ingens	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Homarus americanus	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	0	1
Kempia milcado	4	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	1	0
Farfantepenaeus californiensis	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	0	1	1	0	0
Litopenaeus stylirostris	0	0	0	0	0	0	0	0	0	0	0	1	1	1	-	0	1	0	0	0
Parapenaeus longirostris	0	0	0	0	0	0	0	0	0	0	0	1	?	0	1	1	1	?	0	0
Sergia manningorum	0	0	0	0	0	0	0	0	0	0	0	1	?	-	2	?	1	1	0	0
Sergestes arcticus	0	0	0	0	0	0	0	0	0	0	0	1	?	-	2	1	1	1	0	0
Sicyonia brevirostris	0	1	0	0	0	0	0	0	0	0	0	1	3	0	2	0	1	1	0	0
Solenocera agassizii	0	1	0	0	0	0	0	0	0	0	0	1	1	1	2	0	1	0	0	0
Lucifer ancestra	0	0	-	-	0	0	0	0	0	0	0	1	?	?	0	?	?	?	0	0
Notostomus sp.	4	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Agostocaris bozanici	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Alope australis	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Alpheus macrochirus	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	?	0
Alvinocaris muricola	1	0	0	0	0	0	0	0	0	0	0	0	0	2	?	?	0	0	0	0
Anchistioides antiguensis	2	0	0	0	0	1	0	0	0	0	0	0	0	?	?	?	0	0	0	1
Atya gabonensis	3	0	0	0	0	0	0	0	0	0	1	0	0	?	?	?	0	0	0	0
Barbouria cubensis	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Parahippolyte uveae	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Bathypalaemonella pilosipes	2	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
(Bresiilidae) indet.	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	1
Bythocaris nana	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Campylonotus semistriatus	2	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	1
Crangon alaskensis	1	0	0	0	1	0	0	1	0	0	0	1	0	0	?	?	0	0	0	1
Desmocaris trispinosa	2	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	1
Discias musicus	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0

Appendix 2. Morphological matrix of extant species (cont.).

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139
Euphausia superba	0	0	0	0	0	0	0	0	0	0	3	0	0	-	-	-	-	1	?
Gnathophausia ingens	0	1	1	0	1	0	0	0	0	1	3	1	3	0	0	-	2	?	?
Homarus americanus	1	1	1	0	1	1	1	0	0	1	3	3	5	2	0	2	0	?	?
Kempia milcado	0	0	0	0	1	?	0	5	0	1	5	1	3	4	5	-	2	?	?
Farfantepenaeus californiensis	0	0	1	1	1	0	0	2	0	0	3	0	4	2	-	2	-	0	0
Litopenaeus stylirostris	0	1	0	1	1	0	0	2	0	0	3	0	4	2	-	2	-	0	0
Parapenaeus longirostris	0	0	0	1	0	0	0	2	0	0	3	0	3	0	0	-	0	0	0
Sergia manningorum	0	0	1	1	0	0	0	0	0	0	1	0	0	-	-	-	-	1	0
Sergestes arcticus	0	0	1	1	0	0	0	0	0	0	1	0	4	2	-	2	-	0	1
Sicyonia brevirostris	0	0	1	0	1	1	0	5	1	1	3	0	4	2	0	2	0	0	0
Solenocera agassizii	0	0	0	1	1	0	0	2	0	0	3	0	3	0	0	-	0	0	0
Lucifer ancestra	0	0	0	0	0	0	0	0	0	0	1	0	3	?	?	?	?	0	0
Notostomus sp.	0	1	0	1	1	0	1	5	0	1	0	0	0	-	-	-	-	1	0
Agostocaris bozanici	0	0	0	1	1	0	1	0	0	1	4	3	5	1	1	0	0	0	0
Alope australis	0	0	0	1	1	0	1	0	0	1	4	2	5	2	2	2	1	0	0
Alpheus macrochirus	0	0	1	1	1	0	1	0	0	1	3	2	5	2	0	2	1	0	0
Alvinocaris muricola	1	0	1	0	0	0	1	0	0	1	4	3	2	1	3	1	2	0	0
Anchistioides antiguensis	0	0	0	1	0	0	1	0	0	1	3	0	3	-	3	-	0	0	0
Atya gabonensis	0	1	1	0	1	0	1	0	0	1	3	2	5	1	3	2	1	0	0
Barbouria cubensis	0	1	1	1	0	0	1	0	0	1	3	1	3	-	2	-	1	0	0
Parahippolyte uveae	0	1	1	1	1	0	1	0	0	1	3	0	5	0	2	2	1	0	0
Bathypalaemonella pilosipes	0	0	0	1	0	0	1	0	0	1	7	2	3	-	1	-	0	0	0
(Bresiilidae) indet.	0	0	0	1	0	0	1	0	0	1	3	3	3	-	2	-	2	0	0
Bythocaris nana	0	0	0	1	0	0	1	0	0	1	4	0	0	-	-	-	-	0	0
Campylonotus semistriatus	0	1	0	1	0	0	1	0	0	1	3	0	3	-	3	-	1	0	0
Crangon alaskensis	0	0	0	1	0	0	1	0	0	0	1	0	3	0	0	-	0	0	0
Desmocaris trispinosa	0	0	0	1	0	0	1	0	0	1	3	0	4	1	-	2	-	0	0
Discias musicus	0	0	1	1	0	0	1	0	0	1	3	3	4	1	-	2	-	0	0

Appendix 2. Morphological matrix of extant species (cont.).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Eugonatonotus crassus	2	2	2	1	3	2	0	0	1	1	0	1	1	1	0	0	0	1	1	0
Euryrhynchus burchelli	3	1	0	0	0	2	1	0	0	0	2	1	1	0	1	0	0	0	0	0
Glyphocrangonidae aculeata	3	1	0	1	3	2	0	0	1	0	0	1	1	1	0	0	1	1	0	0
Gnathophyllum splendens	1	1	0	0	0	2	1	0	0	0	1	1	1	0	0	0	0	1	0	0
Eualus fabricii	2	1	1	1	2	2	1	0	0	0	0	1	1	1	0	0	0	1	0	0
Hymenocera picta	2	1	1	1	1	2	1	0	0	0	1	1	1	0	0	0	1	1	0	0
Lysmata californica	2	1	1	1	1	2	1	0	0	0	1	1	1	0	0	0	0	1	0	0
Merguia oligodon	1	1	0	1	1	2	1	0	0	0	1	1	1	0	0	0	1	1	0	0
Merhippolyte agulhasensis	2	1	3	1	1	2	0	1	0	0	0	1	1	1	0	0	1	1	0	0
Nauticaris magellanica	2	1	1	1	1	2	1	?	?	?	0	1	1	0	0	0	0	1	0	0
Nematocarcinus undulatipes	1	1	0	1	3	2	0	0	0	0	1	1	1	0	0	0	1	1	0	0
(Ogyridae) indet.	1	1	0	1	1	2	1	0	0	0	2	1	1	0	1	0	0	0	0	0
Oplophorus spinosus	2	3	3	1	3	2	1	0	0	0	0	1	1	0	1	0	1	1	0	0
Macrobranchium rosenbergi	2	3	3	1	1	2	1	0	0	0	0	1	1	1	0	0	1	1	0	1
Pandalus borealis	2	3	2	1	3	2	0	0	1	0	0	1	1	1	0	0	1	1	0	0
Pasiphaea emarginata	0	-	-	-	-	2	0	0	0	0	2	1	1	0	0	0	1	0	0	0
Physetocaris microphthalmus	1	3	0	0	0	2	1	0	0	0	0	1	1	1	0	0	1	0	0	0
Vetericaris chaceosum	0	-	-	-	-	?	?	0	0	0	2	1	1	0	0	0	0	0	0	0
Processa robusta	1	1	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	1	0	0
Psalidopus barbouri	8	2	3	1	3	2	0	0	0	0	0	1	1	1	1	1	0	1	1	1
Pseudocheles neutra	2	2	1	1	1	2	?	0	0	0	1	1	1	0	0	0	0	1	0	0
Rhynchocinetes rigens	2	1	3	1	2	3	?	0	1	0	0	1	1	1	0	0	0	1	0	0
Stylodactylus licinus	2	3	3	1	3	2	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Stylodactylus multidentatus	2	3	3	1	3	2	0	0	1	0	0	1	0	0	1	0	0	1	1	0
Chlorotocoides spinicauda	2	1	1	1	2	2	0	0	0	0	0	1	0	1	1	0	0	1	0	0
Thoridae paschalis	1	1	0	0	0	2	1	0	0	0	1	1	1	1	0	0	1	1	0	0
Xiphocaris elongata	2	3	3	0	0	2	1	0	0	0	0	1	1	0	0	0	0	1	0	0

Appendix 2. Morphological matrix of extant species (cont.).

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Eugonatonotus crassus	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0
Euryrhynchus burchelli	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Glyphocrangonidae aculeata	1	0	1	1	1	1	0	0	1	1	0	1	1	1	0	1	0	0	0	0
Gnathophyllum splendens	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Eualus fabricii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1
Hymenocera picta	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2
Lysmata californica	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Merguia oligodon	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0
Merhippolyte agulhasensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Nauticaris magellanica	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Nematocarcinus undulatipes	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
(Ogyridae) indet.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Oplophorus spinosus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Macrobranchium rosenbergi	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Pandalus borealis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Pasiphaea emarginata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Physetocaris microphthalmus	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0
Vetericaris chaceosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Processa robusta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Psalidopus barbouri	1	1	1	1	1	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0
Pseudocheles neutra	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0
Rhynchocinetes rigens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Stylodactylus licinus	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Stylodactylus multidentatus	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Chlorotocoides spinicauda	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Thoridae paschalis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Xiphocaris elongata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2. Morphological matrix of extant species (cont.).

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Eugonatonotus crassus	1	0	1	1	0	3	1	?	0	1	1	1	1	0	0	1	1	1	?	?
Euryrhynchus burchelli	1	0	1	0	0	2	0	1	2	1	1	1	1	0	0	1	1	1	?	?
Glyphocrangonidae aculeata	1	1	0	0	1	3	0	1	2	1	1	1	1	0	0	1	1	1	5	-
Gnathophyllum splendens	1	0	0	0	2	3	0	?	2	1	1	1	1	0	0	1	1	0	?	-
Eualus fabricii	1	0	1	1	2	1	0	1	3	1	1	2	1	0	0	1	0	1	0	1
Hymenocera picta	0	0	0	0	2	3	0	?	2	1	1	1	1	0	0	1	1	1	?	-
Lysmata californica	1	0	0	0	2	3	1	1	1	1	1	1	1	0	0	1	1	1	0	-
Merguia oligodon	1	1	1	0	2	3	0	1	3	1	1	1	1	0	0	1	1	1	1	-
Merhippolyte agulhasensis	1	0	1	1	2	1	1	1	3	1	1	1	1	0	0	1	1	1	4	0
Nauticaris magellanica	1	0	1	0	0	3	1	?	?	?	1	?	?	0	0	1	1	1	?	?
Nematocarcinus undulatipes	1	0	1	2	1	1	1	1	0	1	1	0	1	0	1	1	1	1	1	0
(Ogyridae) indet.	1	0	1	0	1	1	1	?	1	1	1	1	1	0	0	1	1	1	?	?
Oplophorus spinosus	1	0	1	2	2	0	1	1	4	1	1	1	1	0	0	1	1	1	2	0
Macrobranchium rosenbergi	1	0	1	1	1	?	?	?	?	1	1	?	1	1	0	1	1	1	?	?
Pandalus borealis	1	0	0	2	2	1	1	1	3	1	1	1	1	0	0	0	1	1	4	1
Pasiphaea emarginata	0	0	0	0	0	2	1	1	2	1	1	0	0	0	0	1	1	1	-	-
Physetocaris microphthalmus	?	1	0	0	0	3	0	?	4	1	1	1	1	0	0	0	1	?	?	-
Vetericaris chaceosum	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	1	4	0
Processa robusta	1	1	0	0	2	3	0	?	?	1	1	?	1	1	0	1	1	1	?	?
Psalidopus barbouri	1	0	1	2	2	1	1	1	0	1	1	0	1	0	0	1	1	1	0	0
Pseudocheles neutra	1	0	0	1	0	0	1	1	3	1	1	2	1	0	1	1	1	1	2	0
Rhynchocinetes rigens	1	0	0	1	1	1	1	1	1	1	1	1	?	1	0	1	1	1	?	?
Stylodactylus licinus	0	0	0	1	2	0	1	1	?	1	1	?	1	1	0	0	1	1	0	?
Stylodactylus multidentatus	0	0	0	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chlorotocoides spinicauda	1	0	0	2	0	1	1	?	1	1	1	?	1	1	0	1	1	1	0	0
Thoridae paschalis	1	1	1	1	1	1	0	1	3	1	1	1	1	0	0	1	0	1	1	1
Xiphocaris elongata	1	0	0	0	0	0	1	1	1	1	1	0	1	1	0	1	1	1	5	1

Appendix 2. Morphological matrix of extant species (cont.).

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Eugonatonotus crassus	?	0	?	1	1	2	-	4	1	0	1	2	0	3	2	1	0	2	1	1
Euryrhynchus burchelli	?	0	1	2	1	2	-	0	0	1	1	2	0	0	0	1	0	0	1	1
Glyphocrangonidae aculeata	-	0	?	1	1	1	0	2	2	0	1	2	1	0	0	1	0	0	1	1
Gnathophyllum splendens	-	0	?	0	1	2	-	0	0	0	1	2	0	0	0	1	0	0	1	1
Eualus fabricii	0	0	0	2	1	2	-	0	0	0	1	2	1	0	0	1	0	3	1	1
Hymenocera picta	-	0	?	3	1	0	1	0	0	0	1	2	0	4	0	1	0	0	1	1
Lysmata californica	-	0	0	2	1	2	-	0	0	0	1	2	1	0	0	1	0	3	1	1
Merguia oligodon	-	1	1	2	1	2	-	5	4	0	1	2	1	0	0	1	0	0	1	1
Merhippolyte agulhasensis	-	1	1	2	1	1	-	5	0	0	1	2	1	0	0	1	0	4	1	1
Nauticaris magellanica	?	?	?	2	1	2	-	0	0	0	1	2	1	0	0	1	0	4	1	1
Nematocarcinus undulatipes	-	1	0	2	1	2	-	1	4	0	1	2	0	5	3	1	0	0	1	1
(Ogyridae) indet.	?	0	?	2	1	2	-	5	3	0	1	2	1	3	2	1	0	2	1	1
Oplophorus spinosus	-	0	-	2	1	2	-	5	3	0	1	2	0	5	2	1	0	2	1	1
Macrobranchium rosenbergi	?	?	?	2	1	2	?	0	0	0	1	2	0	2	3	1	0	0	1	1
Pandalus borealis	1	1	1	2	1	0	1	0	0	1	1	2	1	0	0	1	0	3	1	1
Pasiphaea emarginata	-	0	-	2	1	2	-	3	0	0	1	2	0	5	0	1	0	0	1	1
Physetocaris microphthalmus	-	0	?	?	0	0	0	5	4	0	1	2	1	0	2	1	0	0	1	1
Vetericaris chaceosum	?	0	?	2	1	0	?	5	3	0	1	0	0	3	2	1	0	2	1	1
Processa robusta	?	?	?	2	1	3	?	5	3	1	1	2	1	0	0	1	0	2	1	1
Psalidopus barbouri	?	1	?	2	1	2	?	6	2	0	1	0	0	0	1	1	0	2	1	1
Pseudocheles neutra	-	0	-	2	1	2	-	5	4	0	1	2	0	5	2	1	2	2	1	1
Rhynchocinetes rigens	?	?	?	1	1	3	?	0	0	0	1	2	0	0	0	0	0	3	1	1
Stylodactylus licinus	?	0	?	2	1	2	?	5	3	0	1	2	0	3	2	1	0	3	1	1
Stylodactylus multidentatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chlorotocoides spinicauda	?	0	?	2	0	0	?	0	0	0	1	2	1	0	0	1	0	3	1	1
Thoridae paschalis	1	1	1	2	1	2	-	0	0	0	1	2	1	0	0	1	0	0	1	1
Xiphocaris elongata	1	0	0	2	1	2	-	0	0	0	1	2	0	0	0	1	0	0	1	1

Appendix 2. Morphological matrix of extant species (cont.).

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Eugonatonotus crassus	2	0	1	1	0	2	3	1	0	0	0	0	0	1	1	0	2	2	1	1
Euryrhynchus burchelli	0	1	1	1	1	0	0	-	0	0	1	-	0	1	0	-	2	2	0	2
Glyphocrangonidae aculeata	0	0	1	1	0	0	0	-	0	0	0	-	0	0	1	-	1	0	2	1
Gnathophyllum splendens	0	0	1	1	0	0	0	-	0	0	1	-	0	0	0	-	0	0	0	2
Eualus fabricii	0	0	1	1	0	0	4	2	0	0	0	0	0	2	1	-	0	2	1	1
Hymenocera picta	0	0	1	1	0	0	0	-	0	0	1	-	0	0	0	-	0	1	0	2
Lysmata californica	3	0	1	1	0	0	3	1	0	0	0	0	0	0	1	-	0	0	1	1
Merguia oligodon	0	0	1	1	0	0	0	-	0	0	1	-	0	0	1	-	0	0	0	1
Merhippolyte agulhasensis	4	?	1	1	0	0	2	2	0	0	0	0	0	2	1	-	0	2	0	1
Nauticaris magellanica	4	0	1	1	0	0	3	2	0	0	0	0	0	2	1	-	0	2	0	1
Nematocarcinus undulatipes	0	0	1	1	0	4	3	1	2	0	0	0	0	1	0	0	2	2	2	0
(Ogyridae) indet.	2	0	1	1	0	0	0	-	0	1	1	-	0	1	0	-	2	2	2	0
Oplophorus spinosus	2	0	1	1	0	2	3	2	0	0	0	0	0	0	0	1	0	0	0	0
Macrobranchium rosenbergi	0	0	1	1	0	0	0	0	0	1	1	?	0	0	?	-	0	0	2	2
Pandalus borealis	3	0	1	1	0	0	1	2	0	0	1	0	0	0	1	-	0	0	0	1
Pasiphaea emarginata	0	0	1	1	0	2	0	-	2	1	1	-	0	0	0	1	1	1	0	0
Physetocaris microphthalmus	0	0	1	1	0	0	0	-	2	1	1	-	0	0	1	-	0	0	0	2
Vetericaris chaceosum	2	0	1	1	0	2	3	1	0	0	0	?	0	1	0	1	2	2	2	0
Processa robusta	0	0	1	1	0	0	?	?	0	0	1	?	0	3	1	-	2	0	2	1
Psalidopus barbouri	2	2	1	1	1	0	0	?	0	0	0	?	1	2	1	-	0	2	1	1
Pseudocheles neutra	2	0	1	1	0	2	0	-	0	0	1	-	0	0	0	1	0	0	0	2
Rhynchocinetes rigens	3	0	1	1	0	0	1	1	0	0	0	?	0	1	1	-	2	2	2	1
Stylodactylus licinus	3	0	1	1	0	0	0	?	0	0	0	?	0	0	0	-	2	2	1	0
Stylodactylus multidentatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chlorotocoides spinicauda	3	0	1	1	0	0	0	?	0	0	0	?	0	0	?	-	2	2	2	2
Thoridae paschalis	4	0	1	1	0	0	0	-	0	0	0	-	0	0	1	-	2	2	0	1
Xiphocaris elongata	0	0	1	1	0	2	0	?	0	0	0	?	0	0	0	0	0	0	0	0

Appendix 2. Morphological matrix of extant species (cont.).

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Eugonatonotus crassus	1	2	0	1	0	0	0	1	1	0	0	0	0	?	?	?	0	0	1	0
Euryrhynchus burchelli	2	0	0	0	0	1	0	0	1	0	0	0	0	?	?	?	0	0	0	1
Glyphocrangonidae aculeata	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	1
Gnathophyllum splendens	2	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Eualus fabricii	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Hymenocera picta	2	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Lysmata californica	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Merguia oligodon	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	1
Merhippolyte agulhasensis	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Nauticaris magellanica	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Nematocarcinus undulatipes	4	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	1
(Ogyridae) indet.	0	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Oplophorus spinosus	4	3	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Macrobranchium rosenbergi	2	0	0	0	0	0	0	0	0	1	0	0	0	?	?	?	0	0	?	0
Pandalus borealis	3	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Pasiphaea emarginata	4	0	0	0	0	0	0	1	1	0	0	0	0	?	?	?	0	0	0	0
Physetocaris microphthalmus	2	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Vetericaris chaceosum	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	?	0
Processa robusta	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	?	0
Psalidopus barbouri	1	0	0	0	0	0	0	1	0	0	0	0	0	?	?	?	0	0	?	1
Pseudocheles neutra	5	2	2	2	0	0	0	0	1	1	0	0	0	?	?	?	0	0	0	0
Rhynchocinetes rigens	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	?	1
Stylodactylus licinus	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	?	0
Stylodactylus multidentatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chlorotocoides spinicauda	2	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	?	0
Thoridae paschalis	1	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0
Xiphocaris elongata	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	0

Appendix 2. Morphological matrix of extant species (cont.).

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139
Eugonatonotus crassus	0	0	0	0	0	0	1	6	0	1	3	0	3	-	2	-	1	0	0
Euryrhynchus burchelli	0	0	0	1	1	0	1	0	0	2	3	3	5	1	1	1	0	0	0
Glyphocrangonidae aculeata	1	1	1	0	1	0	1	5	0	1	3	0	4	0	-	2	-	0	0
Gnathophyllum splendens	0	0	1	1	1	0	1	0	0	1	3	0	5	1	1	2	0	0	0
Eualus fabricii	0	0	0	1	0	0	1	0	0	1	3	2	3	-	2	-	2	0	0
Hymenocera picta	0	0	0	1	1	0	1	0	0	1	3	2	3	-	2	-	1	0	0
Lysmata californica	0	0	1	1	1	0	1	0	0	2	3	0	5	3	3	2	0	0	0
Merguia oligodon	0	0	1	1	0	0	1	0	0	1	3	2	5	2	2	2	0	0	0
Merhippolyte agulhasensis	0	0	0	1	0	0	1	0	0	1	4	3	5	1	1	0	0	0	0
Nauticaris magellanica	0	0	1	1	0	0	1	0	0	1	4	2	5	1	3	2	1	0	0
Nematocarcinus undulatipes	0	0	1	1	0	0	1	0	0	1	3	3	3	0	2	-	2	0	0
(Ogyridae) indet.	0	0	0	1	0	0	1	0	0	1	3	0	4	2	-	2	-	0	0
Oplophorus spinosus	0	1	1	0	1	0	1	6	0	1	3	0	3	-	1	-	0	1	0
Macrobranchium rosenbergi	0	0	0	1	1	0	1	0	0	1	3	0	0	-	-	-	-	0	0
Pandalus borealis	0	0	1	1	0	0	1	0	0	1	3	3	3	-	2	-	2	0	0
Pasiphaea emarginata	0	0	0	1	0	0	1	0	0	1	3	1	3	-	1	-	0	0	0
Physetocaris microphthalmus	0	0	0	1	0	0	1	0	0	0	3	0	0	-	-	-	-	0	0
Vetericaris chaceosum	0	0	1	1	1	0	1	0	0	1	4	2	3	0	1	?	0	0	0
Processa robusta	0	0	0	1	1	0	1	0	0	1	3	2	3	2	2	?	1	0	0
Psalidopus barbouri	1	0	0	1	0	0	1	5	0	0	3	0	4	4	?	2	?	0	0
Pseudocheles neutra	0	0	0	1	0	0	1	0	0	0	3	0	3	-	4	-	2	0	0
Rhynchocinetes rigens	1	0	1	1	0	0	1	0	0	1	4	0	3	2	2	?	2	0	0
Stylodactylus licinus	0	1	0	1	0	0	1	0	0	1	4	0	3	2	2	?	2	0	0
Stylodactylus multidentatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0
Chlorotocoides spinicauda	0	0	1	0	0	0	1	0	0	1	3	0	3	0	0	?	1	1	0
Thoridae paschalis	0	0	0	0	0	0	1	0	0	1	3	3	5	1	3	0	1	0	0
Xiphocaris elongata	1	0	1	0	1	0	1	0	0	0	4	1	0	?	?	?	?	0	0

Appendix 3. Morphological matrix of fossil species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Francocaris sp.	6	-	-	-	-	?	?	?	?	?	3	1	?	?	0	0	0	0	0	0
Acanthochirana cordata	1	1	0	0	0	?	?	?	?	?	2	1	0	1	0	0	0	0	0	0
Acanthochirana longipes	1	1	0	1	1	?	?	?	?	?	2	1	0	0	0	0	0	0	0	0
Acanthochirana angulatus	1	2	0	0	1	?	?	?	?	?	1	1	0	0	0	0	0	0	0	0
Acanthochirana krausei	1	1	0	?	?	?	?	?	?	?	0	1	0	0	?	?	0	?	?	?
Aeger spinipes	5	0	1	0	0	?	?	?	?	?	0	1	0	1	0	0	0	1	1	0
Aeger tipularius	5	0	1	0	0	?	?	?	?	?	2	1	0	0	0	0	0	0	0	0
Aeger bronni	0	0	0	0	0	?	?	?	?	?	1	1	0	0	0	0	0	0	0	0
Aeger elegans	5	0	1	0	0	?	?	?	?	?	0	1	0	0	0	0	0	1	0	0
Aeger insignis	5	0	1	0	0	?	?	?	?	?	0	1	0	0	0	1	0	0	0	0
Aeger armatus	0	0	0	0	0	?	?	?	?	?	2	1	0	0	0	0	0	0	0	0
Albertoppelia kuempeli	2	2	1	1	1	?	?	?	?	?	0	1	0	1	0	0	0	0	0	0
Anisaeger sp.	0	0	0	0	0	?	?	?	?	?	1	1	?	0	0	0	0	0	0	1
Antrimpos undenarius	2	2	1	0	0	?	?	?	?	?	0	1	0	1	0	0	1	0	0	0
Antrimpos speciosus	2	2	1	1	2	?	?	?	?	?	1	1	0	1	0	1	0	0	0	0
Antrimpos intermedius	1	1	0	1	1	?	?	?	?	?	1	1	0	1	0	0	0	0	0	0
Antrimpos nonodon	2	1	1	1	2	?	?	?	?	?	0	?	?	1	0	0	0	0	0	0
Antrimpos senidens	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0
Eystaettia intermedius	1	1	0	1	1	?	?	?	?	?	2	1	0	0	0	0	0	0	0	0
Franconipenaeus meyeri	6	-	-	-	-	?	?	?	?	?	3	1	0	-	0	0	0	0	0	0
Blaculla nikoides	?	?	?	0	0	?	?	?	?	?	0	?	?	0	?	?	?	?	?	?
Blaculla sieboldi	1	1	0	0	0	?	?	?	?	?	1	?	?	0	0	0	0	0	0	0
Bombur complicatus	0	0	0	0	0	?	?	?	?	?	2	1	1	0	0	0	0	1	0	0
Buergerocaris psittacoides	2	3	1	0	0	?	?	?	?	?	0	1	0	1	0	0	0	0	0	0

Appendix 3. Morphological matrix of fossil species (cont.).

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Francocaris sp.	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	-	?	?
Acanthochirana cordata	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	?	0	0	0
Acanthochirana longipes	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	?	0	0	0
Acanthochirana angulatus	1	0	0	1	0	0	0	0	1	0	?	?	?	?	1	1	?	0	0	0
Acanthochirana krausei	?	0	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?
Aeger spinipes	1	1	0	0	0	0	0	0	0	2	?	?	?	?	0	1	?	0	0	0
Aeger tipularius	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	1	?	0	0	0
Aeger bronni	1	1	1	0	0	0	0	0	0	0	?	?	?	?	0	1	?	0	0	0
Aeger elegans	1	1	0	0	0	0	0	0	1	0	?	?	?	?	0	1	?	0	0	0
Aeger insignis	0	0	0	0	1	0	0	1	0	0	?	?	?	?	0	1	?	0	0	0
Aeger armatus	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	1	?	0	0	0
Albertoppelia kuempeli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	0	0	0
Anisaeger sp.	1	0	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	0	0	0
Antrimpos undenarius	0	0	?	?	0	0	0	0	0	0	?	?	?	?	1	1	?	0	0	0
Antrimpos speciosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
Antrimpos intermedius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0
Antrimpos nonodon	0	0	0	0	0	0	0	0	0	1	?	?	?	?	1	1	?	0	0	0
Antrimpos senidens	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	?	?	0	0	0
Eystaettia intermedius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0
Franconipenaeus meyeri	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0
Blaculla nikoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?
Blaculla sieboldi	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	1	?	0	?	0
Bombur complicatus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	?	0	0	0
Buergerocaris psittacoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Appendix 3. Morphological matrix of fossil species (cont.).

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Francocaris sp.	?	?	-	-	?	?	?	?	?	?	?	?	?	?	?	?	-	-	?	?
Acanthochirana cordata	1	1	0	0	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Acanthochirana longipes	1	0	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Acanthochirana angulatus	1	1	0	0	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Acanthochirana krausei	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Aeger spinipes	1	1	0	0	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Aeger tipularius	1	1	0	0	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Aeger bronni	1	0	0	1	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Aeger elegans	1	1	0	0	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Aeger insignis	1	1	?	0	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Aeger armatus	1	1	0	0	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Albertoppelia kuempeli	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	?	?
Anisaeger sp.	1	1	?	2	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Antrimpos undenarius	1	0	?	1	?	?	?	?	?	?	1	?	?	0	0	?	0	1	?	?
Antrimpos speciosus	1	?	?	1	?	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?
Antrimpos intermedius	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Antrimpos nonodon	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	?	?
Antrimpos senidens	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eystaettia intermedius	1	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?
Franconipenaeus meyeri	?	?	?	0	?	?	?	?	?	?	?	?	?	0	0		0	1	?	?
Blaculla nikoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Blaculla sieboldi	1	?	0	?	?	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?
Bombur complicatus	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Buergerocaris psittacoides	1	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?

Appendix 3. Morphological matrix of fossil species (cont.).

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Francocaris sp.	?	?	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acanthochirana cordata	?	?	?	1	?	?	?	5	?	?	?	?	0	?	?	?	?	?	1	1
Acanthochirana longipes	?	?	?	1	1	2	1	5	?	0	1	2	0	0	?	1	2	0	1	1
Acanthochirana angulatus	?	?	?	1	?	?	?	5	0	0	?	?	0	0	0	?	?	0	1	?
Acanthochirana krausei	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
Aeger spinipes	?	?	?	1	1	2	?	5	3	0	1	2	0	2	2	1	2	1	1	1
Aeger tipularius	?	?	?	1	1	2	?	5	3	0	1	2	0	2	2	1	2	1	1	1
Aeger bronni	?	?	?	1	1	2	?	5	3	0	1	2	0	2	?	1	2	1	1	1
Aeger elegans	?	?	?	2	1	2	?	5	3	0	1	2	0	2	2	1	2	0	1	1
Aeger insignis	?	?	?	1	1	2	?	5	3	0	1	2	0	2	?	1	2	1	1	1
Aeger armatus	?	?	?	1	1	2	?	5	3	0	1	2	0	2	2	1	2	1	1	1
Albertoppelia kuempeli	?	?	?	0	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1
Anisaeger sp.	?	0	?	1	1	2	?	0	0	0	1	0	0	0	0	1	2	0	1	1
Antrimpos undenarius	?	?	?	1	1	2	?	2	0	0	1	2	0	0	0	1	2	0	1	1
Antrimpos speciosus	?	?	?	0	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1
Antrimpos intermedius	?	?	?	?	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1
Antrimpos nonodon	?	?	?	0	1	2	?	2	?	0	1	2	0	0	?	?	?	0	1	1
Antrimpos senidens	?	?	?	?	?	?	?	0	?	?	?	?	0	0	0	1	2	0	1	?
Eystaettia intermedius	?	?	?	?	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1
Franconipenaeus meyeri	?	?	?	2	1	2	?	0	0	?	1	2	0	0	0	1	2	0	1	1
Blaculla nikoides	?	?	?	?	1	2	?	0	0	?	1	0	0	0	0	1	0	0	1	1
Blaculla sieboldi	?	?	?	0	1	2	?	2	0	1	1	2	1	0	0	1	1	0	1	1
Bombur complicatus	?	?	?	?	1	2	?	0	0	?	?	?	0	0	0	1	0	0	1	1
Buergerocaris psittacoides	?	?	?	?	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1

Appendix 3. Morphological matrix of fossil species (cont.).

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Francocaris sp.	-	-	1	1	-	?	?	?	-	-	-	?	-	-	-	?	?	?	?	?
Acanthochirana cordata	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?
Acanthochirana longipes	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	2	0	0	0
Acanthochirana angulatus	0	0	1	?	0	?	?	?	0	0	0	?	?	?	?	?	1	0	0	?
Acanthochirana krausei	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aeger spinipes	0	1	1	1	0	?	?	?	1	0	0	?	0	0	1	?	1	1	1	1
Aeger tipularius	0	2	1	1	1	?	?	?	0	1	1	?	0	1	0	?	1	1	1	0
Aeger bronni	0	1	1	1	1	?	?	?	1	0	0	?	0	1	0	?	1	1	1	0
Aeger elegans	0	1	1	1	1	?	?	?	0	0	0	?	0	0	0	?	1	1	1	0
Aeger insignis	0	0	1	1	0	?	?	?	0	0	0	?	0	1	0	?	1	1	1	0
Aeger armatus	0	2	1	1	1	?	?	?	0	1	1	?	0	0	0	?	2	2	2	0
Albertoppelia kuempeli	0	0	1	1	0	?	?	?	0	0	0		0	0	1	?	0	0	0	1
Anisaeger sp.	0	?	1	1	?	0	?	?	?	0	0	?	0	?	0	?	2	2	0	?
Antrimpos undenarius	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	2
Antrimpos speciosus	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0
Antrimpos intermedius	0	2	1	1	1	?	?	?	0	0	0	?	0	0	1	?	0	0	0	1
Antrimpos nonodon	0	2	1	1	0	?	?	?	0	0	0	?	0	0	1	?	0	0	0	1
Antrimpos senidens	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?
Eystaettia intermedius	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0
Franconipenaeus meyeri	0	0	?	?	?	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0
Blaculla nikoides	0	0	1	1	0	?	?	?	0	0	0	?	0	?	?	?	0	0	0	0
Blaculla sieboldi	0	0	1	1	0	?	?	?	0	0	1	?	0	0	0	?	0	0	0	0
Bombur complicatus	0	0	1	1	0	?	?	?	0	0	0	?	0	?	?	?	0	0	0	1
Buergerocaris psittacoides	0	1	1	1	0	?	?	?	0	0	0	?	0	0	1	?	0	0	0	1

Appendix 3. Morphological matrix of fossil species (cont.).

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Francocaris sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0
Acanthochirana cordata	?	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	0	1
Acanthochirana longipes	0	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	?
Acanthochirana angulatus	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	1
Acanthochirana krausei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Aeger spinipes	3	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	1
Aeger tipularius	0	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	1
Aeger bronni	0	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	1
Aeger elegans	0	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	1
Aeger insignis	0	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	1
Aeger armatus	0	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	1
Albertoppelia kuempeli	1	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	1
Anisaeger sp.	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Antrimpos undenarius	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	0
Antrimpos speciosus	0	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Antrimpos intermedius	1	?	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	0	0
Antrimpos nonodon	1	0	?	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?
Antrimpos senidens	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eystaettia intermedius	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Franconipenaeus meyeri	4	0	0	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Blaculla nikoides	1	?	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	1
Blaculla sieboldi	4	0	1	1	0	0	0	0	1	0	?	?	?	?	?	?	?	?	0	1
Bombur complicatus	1	?	1	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Buergerocaris psittacoides	1	0	0	0	1	1	0	0	0	0	0	?	?	?	?	?	?	?	?	1

Appendix 3. Morphological matrix of fossil species (cont.).

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139
Francocaris sp.	0	0	?	?	?	0	0	0	0	?	0	1	3	0	?	0	0	?	?
Acanthochirana cordata	1	1	1	1	0	0	0	0	0	?	3	0	0	-	-	-	-	?	?
Acanthochirana longipes	1	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
Acanthochirana angulatus	1	0	0	1	1	0	0	0	?	0	3	0	0	-	-	-	-	?	?
Acanthochirana krausei	0	1	1	1	1	0	0	?	0	?	0	?	?	?	?	?	?	?	?
Aeger spinipes	1	1	1	1	1	0	0	0	0	1	3	0	0	-	-	-	-	?	?
Aeger tipularius	0	1	1	1	1	0	0	0	0	1	3	0	4	-	2	-	3	?	?
Aeger bronni	0	1	0	1	1	0	0	0	0	1	0	0	0	-	-	-	-	?	?
Aeger elegans	0	1	0	1	1	0	0	0	0	1	3	0	4	-	?	2	3	?	?
Aeger insignis	1	1	0	1	1	0	0	1	0	1	3	0	4	0	?	2	3	?	?
Aeger armatus	0	1	1	1	1	0	0	0	0	1	3	0	4	-	2	-	3	?	?
Albertoppelia kuempeli	0	0	1	1	1		0	0	?	?	?	0	?	?	?	?	?	?	?
Anisaeger sp.	0	1	?	?	?	1	0	7	1	?	0	0	5	0	0	2	0	?	?
Antrimpos undenarius	0	1	1	1	1	0	0	?	?	?	?	0	0	-	-	-	-	?	?
Antrimpos speciosus	0	0	0	1	1	0	0	0	?	1	0	0	0	-	-	-	-	?	?
Antrimpos intermedius	1	0	0	1	1	0	0	0	0	?	3	0	0	-	-	-	-	?	?
Antrimpos nonodon	?	1	1	1	1	0	0	?	0	0	0	0	0	-	-	-	-	?	?
Antrimpos senidens	?	?	1	1	1	0	0	?	0	?	?	0	?	?	?	?	?	?	?
Eystaettia intermedius	0	0	1	1	1	0	0	0	?	0	3	0	4	2	-	2	-	?	?
Franconipenaeus meyeri	0	1	1	1	1	0	0	0	0		3	0	0	-	-	-	-	?	?
Blaculla nikoides	0	0	1	?	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?
Blaculla sieboldi	?	0	1	?	0	0	?	0	?	?	0	0	0	-	-	-	-	?	?
Bombur complicatus	0	1	1	1	0	0	1	0	?	0	0	0	0	-	-	-	-	?	?
Buergerocaris psittacoides	0	0	1	1	1	0	1	3	?	1	0	0	0	-	-	-	-	?	?

Appendix 3. Morphological matrix of fossil species (cont.).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Bylgia spinosa	2	1	1	0	0	?	?	?	?	?	0	1	0	1	?	0	0	?	0	0
Bylgia haeberleini	2	2	1	1	1	?	?	?	?	?	0	1	0	1	0	0	0	?	0	0
Bylgia hexadon	2	2	1	0	0	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0
Bylgia ruedeli	2	2	1	1	1	?	?	?	?	?	0	1	0	1	0	0	0	0	0	0
Carpopenaeus septemspinatus	2	2	1	0	?	?	?	?	?	?	0	1	0	1	0	0	0	0	0	0
Drobna deformis	1	1	0	1	3	?	?	?	?	?	0	1	0	1	0	0	0	1	0	0
Dusa monocera	1	2	0	1	3	?	?	?	?	?	1	1	0	1	0	0	0	0	0	0
Dusa denticulata	2	2	1	1	3	?	?	?	?	?	1	1	0	0	0	1	0	0	0	0
Harthofia polzi	1	?	?	1	1	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0
Harthofia bergeri	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	0	0	0	0	0
Harthofia blumbergi	2	1	1	1	3	?	?	?	?	?	1	1	1	0	0	0	0	0	0	0
Hefriga serrata	1	2	0	1	3	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0
Hefriga frischmanni	1	2	0	1	3	?	?	?	?	?	0	?	?	0	?	0	0	0	0	0
Koelga quadridens	1	1	0	1	1	?	?	?	?	?	1	1	0	0	0	0	0	0	0	0
Koelga curvirostris	1	1	0	0	0	?	?	?	?	?	1	1	0	1	0	0	0	0	0	0
Koelga muensteri	1	1	0	1	1	?	?	?	?	?	1	?	?	0	0	0	0	0	0	0
Occultocaris frattigianii	0	0	0	0	0	?	?	?	?	?	2	1	?	1	0	0	0	1	0	0
Pseudodusa frattigianii	2	?	1	0	0	?	?	?	?	?	1	?	?	1	0	0	0	?	0	0
Rauna angusta	1	1	0	1	1	?	?	?	?	?	1	1	1	1	0	0	0	0	0	0
Udora brevispina	1	1	0	0	0	?	?	?	?	?	1	1	0	1	0	0	0	0	0	0
T1	1	?	?	1	1	?	?	?	?	?	2	1	1	1	1	0	0	1	0	0

Appendix 3. Morphological matrix of fossil species (cont.).

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Bylgia spinosa	0	0	0	0	0	0	0	0	?	0	?	?	?	?	0	1	?	0	0	0
Bylgia haeberleini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0
Bylgia hexadon	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	1	?	?	0	0
Bylgia ruedeli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	0	0	0
Carpopenaeus septemspinatus	0	1	0	0	0	0	0	0	0	1	?	?	?	?	0	1	?	0	0	0
Drobna deformis	0	0	0	1	0	0	0	0	1	0	1	1	?	?	0	1	?	0	0	0
Dusa monocera	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	?	0	0	0
Dusa denticulata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	?	0	0	0
Harthofia polzi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	?	?	?
Harthofia bergeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0
Harthofia blumbergi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0
Hefriga serrata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	0	0	0
Hefriga frischmanni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	0	0
Koelga quadridens	1	0	0	0	0	0	0	0	0	0	?	?	?	?	1	1	?	0	0	0
Koelga curvirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	0	0	0
Koelga muensteri	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	?	0	0	0
Occultocaris frattigianii	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	1	?	?	?	?
Pseudodusa frattigianii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0
Rauna angusta	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	1	?	?	0	0
Udora brevispina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	?
T1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?	?

Appendix 3. Morphological matrix of fossil species (cont.).

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Bylgia spinosa	1	0	1	0	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
Bylgia haeberleini	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bylgia hexadon	1	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?
Bylgia ruedeli	?	0	0	0	?	?	?	?	?	?	?	?	?	?	0	?	0	1	?	?
Carpopenaeus septemspinatus	1	1	0	0	?	?	?	?	?	?	1	?	?	0	0	?	0	1	?	?
Drobna deformis	1	0	0	1	?	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?
Dusa monocera	1	1	0	1	?	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?
Dusa denticulata	1	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Harthofia polzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Harthofia bergeri	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Harthofia blumbergi	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hefriga serrata	1	1	0	2	?	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?
Hefriga frischmanni	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?		1	?	?
Koelga quadridens	1	0	0	1	?	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?
Koelga curvirostris	1	?	0	0	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?
Koelga muensteri	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?
Occultocaris frattigianii	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?
Pseudodusa frattigianii	1	?	?	?	?	?	?	?	?	?	?	?	?	0	0		0	0	?	?
Rauna angusta	1	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?
Udora brevispina	?	1	0	2	?	?	?	?	?	?	?	?	?	0	0	?	0	1	?	?
T1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 3. Morphological matrix of fossil species (cont.).

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Bylgia spinosa	?	?	?	2	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1
Bylgia haeberleini	?	?	?	?	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1
Bylgia hexadon	?	?	?	0	1	2	?	2	?	0	1	2	0	0	?	1	2	0	1	1
Bylgia ruedeli	?	?	?	2	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1
Carpopenaeus septemspinatus	?	?	?	1	1	2	-	0	0	0	1	2	1	0	1	1	2	0	1	1
Drobna deformis	?	?	?	0	1	2	?	0	0	0	1	2	0	0	?	1	2	0	1	1
Dusa monocera	?	?	?	0	1	2	?	0	?	0	1	2	0	0	0	1	2	0	1	1
Dusa denticulata	?	?	?	?	1	2	?	0	?	0	1	2	0	0	0	1	2	0	1	?
Harthofia polzi	?	?	?	?	1	2	?	0	0	0	1	2	0	0	0	1	0	0	1	1
Harthofia bergeri	?	?	?	?	1	2	?	0	0	?	1	2	0	0	0	1	0	0	1	
Harthofia blumbergi	?	?	?	?	1	2	?	0	0	0	1	2	0	0	0	?	?	?	?	?
Hefriga serrata	?	?	?	0	1	0	?	2	0	0	1	0	0	1	0	1	0	1	0	1
Hefriga frischmanni	?	?	?	1	1	2	?	?	?	?	1	2	0	?	?	1	0	?	0	1
Koelga quadridens	?	?	?	0	1	2	?	0	?	0	1	2	0	0	?	1	2	0	?	?
Koelga curvirostris	?	?	?	0	1	0	?	0	0	0	1	0	0	0	0	1	0	0	1	1
Koelga muensteri	?	?	?	0	1	2	?	0	0	0	1	2	0	3	0	1	2	0	1	1
Occultocaris frattigianii	?	?	?	?	1	2	?	0	0	0	1	2	0	0	0	1	0	0	1	1
Pseudodusa frattigianii	?	?	?	0	1	2		0	0	0	1	2	0	0	0	1	2	0	1	1
Rauna angusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Udora brevispina	?	?	?	1	1	0	1	0	0	?	1	0	0	0	0	1	0	1	1	1
T1	?	?	?	?	1	2	?	0	0	0	1	2	0	0	0	1	2	0	1	1

Appendix 3. Morphological matrix of fossil species (cont.).

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Bylgia spinosa	0	0	1	1	0	?	?	?	0	0	0	?	0	0	1	?	0	0	0	0
Bylgia haeberleini	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0
Bylgia hexadon	0	0	1	1	0	?	?	?	0	0	0	?	0	0	1	?	0	0	0	0
Bylgia ruedeli	0	0	1	1	0	?	?	?	0	0	0	?	0	0	1	?	0	0	0	0
Carpopenaeus septemspinatus	0	?	1	1	?	?	?	?	1	1	0	?	0	?	1	?	0	0	0	1
Drobna deformis	0	0	1	1	0	?	?	?	0	0	0	?	0	0	1	?	0	0	0	1
Dusa monocera	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	2
Dusa denticulata	0	0	1	?	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	2
Harthofia polzi	0	?	?	?	?	?	?	?	1	?	?	?	0	0	0	?	0	0	0	0
Harthofia bergeri	0	?	1	1	?	?	?	?	1	0	0	?	0	0	1	?	0	0	0	1
Harthofia blumbergi	?	?	?	?	?	?	?	?	1			?	0	0	1	?	0	0	0	1
Hefriga serrata	1	?	0	1	?	?	?	?	?	?	?	?	0	0	0	?	0	0	0	0
Hefriga frischmanni	?	?	0	1	?	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0
Koelga quadridens	?	?	?	?	?	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0
Koelga curvirostris	0	0	1	1	0	?	?	?	1	0	0	?	0	0	0	?	0	0	0	0
Koelga muensteri	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0
Occultocaris frattigianii	1	1	1	1	0	?	?	?	0	0	0	?	?	?	?	?	0	0	0	1
Pseudodusa frattigianii	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0
Rauna angusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?
Udora brevispina	1	0	1	1	0	?	?	?	1	1	1	?	0	0	?	?	1	1	1	0
T1	0	0	1	1	0	?	?	?	0	0	0	?	0	0	0	?	0	0	0	0

Appendix 3. Morphological matrix of fossil species (cont.).

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Bylgia spinosa	1	0	0	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	1
Bylgia haeberleini	4	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	1
Bylgia hexadon	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?
Bylgia ruedeli	4	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Carpopenaeus septemspinatus	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	0
Drobna deformis	1	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	0	1
Dusa monocera	3	0	0	0	1	1	1	1	1	1	0	?	?	?	?	?	?	?	0	1
Dusa denticulata	3	?	?	?	1	1	1	1	1	1	0	?	?	?	?	?	?	?	0	1
Harthofia polzi	4	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Harthofia bergeri	1	?	?	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Harthofia blumbergi	1	?	?	?	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	0
Hefriga serrata	0	0	1	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	0	1
Hefriga frischmanni	4	0	0	0	1	1	0	1	1	0	0	?	?	?	?	?	?	?	0	0
Koelga quadridens	0	0	2	2	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	1
Koelga curvirostris	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Koelga muensteri	4	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	1
Occultocaris frattigianii	1	?	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Pseudodusa frattigianii	4	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0
Rauna angusta	?	?	?	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	0
Udora brevispina	0	0	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?	0	0
T1	0	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	0	1

Appendix 3. Morphological matrix of fossil species (cont.).

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139
Bylgia spinosa	?	0	?	?	?	0	0	0	?	?	0	0	0	-	-	-	-	?	?
Bylgia haeberleini	0	0	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?
Bylgia hexadon	0	0	0	1	1	0	0	0	0	?	0	0	4	0	?	2	?	?	?
Bylgia ruedeli	0	0	0	0	1	0	0	0	?	1	0	0	0	-	-	-	-	?	?
Carpopenaeus septemspinatus	0	0	0	0	1	0	1	0	0	1	0	1	1	?	?	?	?	?	?
Drobna deformis	0	1	1	0	1	0	0	0	0	1	0	0	0	-	-	-	-	?	?
Dusa monocera	1	1	0	1	1	0	0	0	0	0	0	0	4	2	-	2	-	?	?
Dusa denticulata	1	0	1	1	1	0	0	0	0	0	0	0	4	0	?	2	?	?	?
Harthofia polzi	0	0	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?
Harthofia bergeri	0	0	0	1	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?
Harthofia blumbergi	0	0	1	1	1	0	1	0	0	1	0	0	4	2	?	2	?	?	?
Hefriga serrata	0	1	1	1	1	0	1	0	0	0	?	0	?	?	?	?	?	?	?
Hefriga frischmanni	0	0	1	1	1	0	1	0	0	?	3	0	?	?	1	?	2	?	?
Koelga quadridens	?	0	1	0	1	0	0	?	0	?	0	0	0	-	-	-	-	?	?
Koelga curvirostris	0	1	0	1	1	0	1	0	?	0		0	0	-	-	-	-	?	?
Koelga muensteri	0	1	1	1	1	0	0	0	?	0	3	0	?	?	?	?	?	?	?
Occultocaris frattigianii	?	0	?	?	?	0	1	0	?	?	1	?	?	?	?	?	?	?	?
Pseudodusa frattigianii	0	0	1	1	0	0	0	0	0	0	0	0	0	-	-	-	-	?	?
Rauna angusta	0	1	0	1	1	0	0	0	0	0	3	0	?	?	?	?	?	?	?
Udora brevispina	0	1	1	1	1	0	1	0	0	1	3	0	4	0	-	2	-	?	?
T1	0	0	?	1	1	0	0	?	?	0	0	0	0	-	-	-	-	?	?

Appendix 4. Extant and fossil decapod shrimp specimens used for coding.

Abbreviations: CM- Carnegie Museum, KSU-Kent State University, LC-Lauer Collection SNSB-Staatliche Naturwissenschaftliche Sammlungen Bayerns, and USNM-United States National Museum of Natural History.
Extant

Species	Specimen ID #	Institution
Agostocaris bozanici	USNM 1007294	USNM
Alope australis	USNM 98871	USNM
Alpheus macrochirus	USNM 123598	USNM
Alvinocaris muricola	USNM 1175216	USNM
Anchistioides antiguensis	USNM 75901	USNM
Atya gabonensis	USNM 184863	USNM
Barbouria cubensis	USNM 184018	USNM
Bathypalaemonella pilosipes	USNM 285280	USNM
Bythocaris nana	USNM 222264	USNM
Campylonotus semistriatus	USNM 28346	USNM
Chlorotocoides spinicauda	USNM 205205	USNM
Crangon alaskensis	USNM 52837	USNM
Crangon alaskensis	USNM 26558	USNM
Desmocaris trisponosa	USNM 171373	USNM
Discias musicus	USNM 283599	USNM
Eualus fabricii	USNM 294	USNM
Eualus fabricii	USNM 192560	USNM
Eugonatonotus crassus	USNM 211231	USNM
Euphausia superba	KSU 2231	KSU
Euphausia superba	108	USNM
Euphausia superba	109	USNM
Euryrhynchus burchelli	USNM 1102281	USNM
Farfantepenaeus californiensis	USNM 255479	USNM
Glyphocrangon aculeata	USNM 11426	USNM
Gnathophausia ingens	USNM 283703	USNM
Gnathophyllum splendens	USNM 244019	USNM
Homarus americanus	KSU 2232	KSU
Hymenocera picta	USNM 138273	USNM
Indet (Bresiliidae)	USNM 378446	USNM
Indet (Ogyridae)	USNM 320261	USNM
Kempia milcado	KSU 2230	KSU
Litopenaeus stylirostris	USNM 254924	USNM
Lucifer ancestra	USNM 21230	USNM
Lysmata californica	USNM 6256	USNM
Macrobranchium rosenbergi	USNM 1151695	USNM
Merguia oligodon	USNM 169678	USNM

Merhippolyte agulhasensis	USNM 235112	USNM
Nauticaris magellanica	USNM 274258	USNM
Nematocarcinus undulatipes	USNM 221658	USNM
Notostomus sp.	USNM 1198404	USNM
Oplophorus spinosus	USNM 163964	USNM
Pandalus borealis	USNM 2566	USNM
Parahippolyte uveae	USNM 280216	USNM
Parapenaeus longirostris	USNM 255708	USNM
Pasiphaea emarginata	USNM 28264	USNM
Physetocaris microphthalmus	USNM 134716	USNM
Physetocaris microphthalmus	USNM 222478	USNM
Processa robusta	USNM 286618	USNM
Psalidopus barbouri	USNM 181283	USNM
Pseudocheles neutra	USNM 28394	USNM
Rhynchocinetes rigens	USNM 104753	USNM
Sergestes arcticus	USNM 152008	USNM
Sergia manningorum	USNM 163534	USNM
Sicyonia brevirostris	USNM 254684	USNM
Solenocera agassizii	USNM 253920	USNM
Stylodactylus licinus	USNM 266733	USNM
Stylodactylus multidentatus	USNM 252185	USNM
Thor paschalis	USNM 181194	USNM
Vetericaris chaceorum	USNM 205725	USNM
Xiphocaris elongata	USNM 125468	USNM

Fossil

Species	**Specimen ID #**	**Institution**
Acanthochirana angulatus	BSP AS VII 707	SNSB
Acanthochirana cordata	BSP AS VII 706 (syntype)	SNSB
Acanthochirana cordata	BSP AS VII 703	SNSB
Acanthochirana cordata	BSP AS VII 704	SNSB
Acanthochirana cordata	USNM 73857	USNM
Acanthochirana cordata	838	LC
Acanthochirana cordata	840	LC
Acanthochirana cordata	843	LC
Acanthochirana krausei	1967 I 90 (holotype	SNSB
Acanthochirana krausei	1967 I 88	SNSB
Acanthochirana longipes	BSP AS VII 705	SNSB
Acanthochirana longipes	1984 I 115	SNSB
Acanthochirana longipes	USNM 475693	USNM
Aeger armatus	BSP 1964 XXIII	SNSB
Aeger armatus	BSP AS I 1962 (syntype)	SNSB

Aeger bronni	BSP AS I 959 (holotype)	SNSB
Aeger elegans	BSP 1964 XXIII 90	SNSB
Aeger elegans	BSP 1964 XXIII 92	SNSB
Aeger elegans	BSP AS VII 712	SNSB
Aeger elegans	BSP AS I 963	SNSB
Aeger elegans	USNM 475724	USNM
Aeger elegans	USNM 475688	USNM
Aeger elegans	566	LC
Aeger elegans	2184	LC
Aeger insignis	BSP AS I 960 (syntype)	SNSB
Aeger insignis	856	LC
Aeger insignis	857	LC
Aeger insignis	1603	LC
Aeger spinipes	BSP 1882 XVI 13	SNSB
Aeger spinipes	BSP 1985 I 5	SNSB
Aeger spinipes	BSP 1984 I 105	SNSB
Aeger spinipes	BSP 1964 XXIII	SNSB
Aeger spinipes	BSP 1984 I 105	SNSB
Aeger spinipes	867	LC
Aeger spinipes	564	LC
Aeger spinipes	869	LC
Aeger spinipes	33222	CM
Aeger tipularius	2162	LC
Albertoppelia kuempeli	879	LC
Albertoppelia kuempeli	880	LC
Albertoppelia kuempeli	1671	LC
Anisaeger sp	LPI	Composite of published specimens
Antrimpos intermedius	BSP 1958 I 376	SNSB
Antrimpos intermedius	BSP 1964 XXIII	SNSB
Antrimpos intermedius	873	LC
Antrimpos intermedius	874	LC
Antrimpos intermedius	876	LC
Antrimpos nonodon	BSP AS VII 692 (lectotype)	SNSB
Antrimpos senidens	BSP AS VII 699	SNSB
Antrimpos speciosus	BSP 1986 XV 5	SNSB
Antrimpos speciosus	BSP AS V 43	SNSB
Antrimpos speciosus	BSP AS V 44	SNSB
Antrimpos speciosus	BSP 1964 XXIII	SNSB
Antrimpos speciosus	877	LC
Antrimpos speciosus	878	LC
Antrimpos undenarius	BSP 1964 XXIII 591	SNSB

Blaculla nikoides	BSP AS VII 729 (holotype)	SNSB
Blaculla nikoides	BSP 881	SNSB
Blaculla nikoides	BSP 882	SNSB
Blaculla sieboldi	BSP AS I 973 (holotype)	SNSB
Bombur complicatus	BSP AS VII 719 (holotype)	SNSB
Bombur complicatus	BSP AS VII 720 (holotype)	SNSB
Bombur complicatus	USNM 358138	USNM
Bombur complicatus	USNM 358137	USNM
Bombur complicatus	885	LC
Bombur complicatus	883	LC
Buergerocaris psittacoides	1605	LC
Buergerocaris psittacoides	1672	LC
Buergerocaris psittacoides	887	LC
Buergerocaris psittacoides	886	LC
Bylgia haeberleini	BSP AS VII 715 (holotype)	SNSB
Bylgia hexadon	BSP AS VII 714 (holotype)	SNSB
Bylgia hexadon	USNM 358139	USNM
Bylgia hexadon	USNM 475731	USNM
Bylgia hexadon	1688	LC
Bylgia ruedeli	1686	LC
Bylgia spinosa	BSP AS VIII 713 (holotype)	SNSB
Bylgia spinosa	BSP 1990 XVIII 45	SNSB
Bylgia spinosa	1840	LC
Carpopenaeus septemspinatus	BSP Hejoula 350	SNSB
Carpopenaeus septemspinatus	BSP Hejoula 356	SNSB
Carpopenaeus septemspinatus	BSP Hejoula 5b	SNSB
Carpopenaeus septemspinatus	BSP Hejoula 410	SNSB
Carpopenaeus septemspinatus	BSP Hejoula 411	SNSB
Drobna deformis	BSP AS VII 716 (holotype)	SNSB
Drobna deformis	BSP 1982 I 42	SNSB
Drobna deformis	BSP 1986 XV 7	SNSB
Drobna deformis	BSP 1983 I 144	SNSB
Drobna deformis	BSP 1983 I 12	SNSB
Drobna deformis	USNM 358146	USNM
Drobna deformis	USNM 475697	USNM
Drobna deformis	USNM 475720	USNM
Drobna deformis	USNM 358145	USNM
Drobna deformis	1848	LC
Drobna deformis	903	LC

Drobna deformis	411	LC
Dusa denticulata	BSP AS I 967	SNSB
Dusa denticulata	BSP AS VII 718	SNSB
Dusa denticulata	USNM 358147	USNM
Dusa denticulata	1944	LC
Dusa denticulata	898	LC
Dusa monocera	BSP AS VII 717 (holoype)	SNSB
Dusa monocera	BSP 1986 XV 9	SNSB
Dusa monocera	BSP AS I 966	SNSB
Dusa monocera	1426	LC
Eystaettia intermedius	BSP 1958 I 376	SNSB
Eystaettia intermedius	BSP 1964 XXIII	SNSB
Eystaettia intermedius	873	LC
Eystaettia intermedius	874	LC
Eystaettia intermedius	876	LC
Eystaettia intermedius	901	LC
Eystaettia intermedius	1595	LC
Eystaettia intermedius	589	LC
Francocaris sp	BSP 1919 I 5 (syntype)	SNSB
Francocaris sp	BSP 1917 I 2	SNSB
Francocaris sp	1843	LC
Francocaris sp	964	LC
Francocaris sp	1849	LC
Francocaris sp	1850	LC
Franconipenaeus meyeri	BSP AS V 42 (syntype)	SNSB
Franconipenaeus meyeri	BSP 1964 XXIII	SNSB
Franconipenaeus meyeri	BSP 1964 XXIII 32	SNSB
Franconipenaeus meyeri	BSP 1961 III	SNSB
Franconipenaeus meyeri	BSP 1960 XVIII 34	SNSB
Franconipenaeus meyeri	930	LC
Harthofia bergeri	935	LC
Harthofia bergeri	1505	LC
Harthofia blumenbergi	1504	LC
Harthofia blumenbergi	1509	LC
Harthofia polzi	1512	LC
Hefriga frischmanni	BSP AS I 972	SNSB
Hefriga frischmanni	923	LC
Hefriga frischmanni	924	LC
Hefriga frischmanni	921	LC
Hefriga frischmanni	1508	LC
Hefriga serrata	BSP AS VII 712 (holotype)	SNSB
Hefriga serrata	BSP AS VII 722	SNSB
Hefriga serrata	1516	LC

Hefriga serrata	918	LC
Hefriga serrata	920	LC
Koelga curvirostris	942	LC
Koelga curvirostris	943	LC
Koelga curvirostris	941	LC
Koelga curvirostris	944	LC
Koelga muensteri	945	LC
Koelga quadridens	BSP AS VII 697	SNSB
Occultocaris frattigianii	2198	LC
Pseudodusa frattigianii	948	LC
Pseudodusa frattigianii	947	LC
Pseudodusa frattigianii	750	LC
Rauna angusta	BSP AS VII 726	SNSB
Rauna multipes	BSP AS VII 724	SNSB
T1	unnumbered	
Udora brevispina	BSP AS VII 725	SNSB
Udora brevispina	BSP 1964 XXIII 593	SNSB