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Decapod Crustacean Phylogenetics

edited by

Joel W. Martin, Keith A. Crandall, and Darryl L. Felder



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Edited by

Joel W. Martin

Natural History Museum of L. A. County
Los Angeles, California, U. S. A.

Keith A. Crandall

Brigham Young University
Provo, Utah, U. S. A.

Darryl L. Felder

University of Louisiana
Lafayette, Louisiana, U. S. A.



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Phylogeny of the Infraorder Caridea Based on Mitochondrial and Nuclear Genes (Crustacea: Decapoda)

HEATHER D. BRACKEN¹, SAMMY DE GRAVE² & DARRYL L. FELDER³

¹*University of Louisiana at Lafayette, Department of Biology, Lafayette, Louisiana, U.S.A.*

²*Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, United Kingdom*

ABSTRACT

Shrimps of the infraorder Caridea occur commonly throughout marine and freshwater habitats. Despite general knowledge of the group, phylogenetic relationships within the infraorder remain poorly known. The few studies that have focused specifically on the classification and evolutionary history within the Caridea have relied entirely on morphological characters and suggest conflicting phylogenetic relationships. Robust molecular analysis is required to test current hypotheses. We present the first comprehensive molecular phylogeny of the group, combining nuclear and mitochondrial gene sequences, to evaluate the relationships among 14 superfamilies and 30 families. Bayesian and likelihood analyses were conducted on a concatenated 18S/16S alignment composed of 1835 basepairs. Results indicated no evidence contrary to hypotheses of monophyly within the families Alpheidae, Processidae, and Alvinocarididae. Ogyrididae is resolved as a sister clade to the Alpheidae, as has been previously suggested. Our findings raise questions as to the systematic placement of the Procarididae within Caridea and suggest polyphyletic and paraphyletic relationships among genera within the families Atyidae, Pasiphaeidae, Oplophoridae, Hippolytidae, Gnathophyllidae, and Palaemonidae, as currently defined. Our results in some cases confirm and in others reject placements of controversial taxa within higher-level phylogeny and provide new insights for classifications within the Caridea.

1 INTRODUCTION

The range of adaptation and biological diversity within the infraorder Caridea is remarkable among the decapod crustaceans. While many caridean families inhabit marine shallow tropical and subtropical waters, some can be found associated with hydrothermal vents and hydrocarbon seeps, while others occur in freshwater lakes, mountain streams, anchialine caves, and deep-sea basins (Shank et al. 1999; Anker & Iliffe 2000; Komai & Segonzac 2003; Cai & Anker 2004; Martin & Wicksten 2004; Alvarez et al. 2005; Richardson & Cook 2006; Komai et al. 2007; Page et al. 2007; De Grave et al. 2008). With approximately 36 families, 361 genera, and 3,108 species (Fransen & De Grave this volume), carideans dominate the natantian decapods in terms of morphological and ecological diversity (Martin & Davis 2001; Bauer 2004; De Grave & Moosa 2004).

Members of the infraorder Caridea are abundant in epifaunal and fouling communities and contribute to the structure and function of aquatic ecosystems (Richardson & Cook 2006). They commonly establish temporary or lifelong associations with other organisms including cnidarians, sponges, molluscs, echinoderms, echiurans, stomatopods, fish, and other crustaceans (Knowlton 1980; Knowlton & Keller 1983; Pratchett 2001; Duffy 2002; Hayashi 2002; Khan et al. 2003; Silliman et al. 2003; Bauer 2004; Marin et al. 2005; Macdonald et al. 2006). Many aspects of these

unique associations make caridean shrimps ideal organisms for studies of symbiosis, communication, behavioral ecology, and evolutionary biology.

1.1 *Evolutionary history of the Caridea*

Over the last five decades, several studies have addressed the systematic placement of the infraorder Caridea within the decapods (Burkenroad 1963, 1981; Abele & Felgenhauer 1982; Christoffersen 1988a; Abele 1991; Chace 1992; Porter et al. 2005), but phylogenetic relationships within the infraorder remain poorly known. Few studies have specifically examined the systematic arrangements and evolutionary relationships among superfamilies and families within the Caridea (Holthuis 1955; Thompson 1967; Christoffersen 1986, 1987, 1988b, 1989, 1990; Chace 1992; Holthuis 1993). Although these studies were crucial in contributing to an evolutionary understanding of the group, they relied entirely on morphological characters and resulted in conflicting patterns of phylogeny.

Difficulties in determining relationships among carideans have been attributed to inconsistent and insufficient coding of morphological characters, lack of comparative larval and molecular studies, a limited fossil record (Thompson 1967; Schram 1986; Christoffersen 1990), and a general dearth of phylogenetic work. One study examined evolutionary relationships using 16S data but lacked sufficient taxon sampling ($n = 20$) and showed little support for the resulting phylogeny (Xu et al. 2005). Some workers have attempted classifications at the superfamilial and familial levels with relative trepidation, all acknowledging that further work is necessary to validate current hypotheses (Holthuis 1955; Thompson 1967; Christoffersen 1990; Chace 1992; Holthuis 1993). Here we acknowledge a few studies that were essential to constructing the currently applied classification of the Caridea (for a further summary of early studies, see Christoffersen 1987).

Early comparative work by Thompson (1967) divided the Caridea into 10 superfamilies and 23 families on the basis of adult morphology. In this account, he suggested a suite of evolutionarily informative characters, such as chelae adaptations, mandible shape, telson armature, and branchial formula, and proposed an updated classification of Caridea. Thompson assumed the group to be a monophyletic unit, and his hypothesized evolutionary tree suggested an early branching of the families Pasiphaeidae, Styrodactylidae, Glyphocrangonidae, and Crangonidae, while postulating that the remaining families arose from an oplophorid-like ancestor. Thompson's diagram included what are now regarded as some unnatural groupings, such as the polyphyly of Heterocarpoidea, Bresilioidea, and Oplophoroidea, but did provide hypotheses for subsequent testing and called attention to morphological characters later used in cladistic analyses.

During the 1980s and early 1990s, Christoffersen conducted a series of cladistic analyses examining the phylogenetic relationships within the Caridea (Christoffersen 1986, 1987, 1988a, 1988b, 1989, 1990). During the course of his work, he resurrected, revalidated, rejected, restricted, and re-assigned many groups to construct a new superfamily and family level classification of the Caridea. In his final contribution, he divided the Caridea into eight superfamilies and 36 families using 19 adult and larval synapomorphies (Christoffersen 1990). Unfortunately, this classification was based on a limited number of characters. Furthermore, the characters for a number of species were scored using available literature only, which even the author conceded to be inadequate and subject to possible misinterpretation. Christoffersen's work was not accepted at the time but is slowly gaining some recognition. He was the first to attempt a true phylogenetic analysis of the group, using cladistic methods and establishing polarities for morphological characters. As did Thompson (1967), he offered a potential explanation for the evolutionary transition from a pelagic to benthic lifestyle, proposing a suite of morphological characters that were derived from this adaptation.

Two years later, a strikingly different classification of the Caridea was presented, which grouped superfamilies and families on the basis of morphological similarity (Chace 1992). Primarily based on the three anterior pairs of pereopods and six pairs of mouthparts, the infraorder was divided into 15 superfamilies and 28 families. It was acknowledged that this arrangement might not necessarily indicate relationships, since superfamilial and familial arrangements were constructed using relative

similarity. However, with minor alterations, the currently used caridean classification stems from this work, and it has yet to be challenged by molecular systematists or morphological cladists.

A recently published consensus on classification divided the Caridea into 36 families (Martin & Davis 2001) after a review of varied morphologically based analyses (Holthuis 1955; Thompson 1967; Christoffersen 1986, 1987, 1988a, 1988b, 1989, 1990; Chace 1992; Holthuis 1993), which we follow as our frame of reference, with two minor revisions. It should be noted that since this publication the family Mirocarididae has been synonymized with Alvinocarididae, and a new family, Pseudochelidae, has been described (De Grave & Moosa 2004).

The current subdivision of the infraorder may not reflect phylogenetic relationships, given aforementioned limitations of cladistic morphological analyses and the lack of previous studies examining higher-level caridean relationships on the basis of molecular data. Here, we present the first comprehensive molecular phylogenetic analysis for the infraorder Caridea, combining nuclear and mitochondrial sequences, to investigate relationships among 30 families, 75 genera, and 104 species. It is intended to identify monophyletic and polyphyletic groups and highlight congruence or incongruence between molecular phylogenies and currently applied classifications.

2 MATERIALS AND METHODS

2.1 *Ingroup taxa and outgroup selection*

Representatives from 30 families, 75 genera, and 104 species of caridean shrimp were used in this analysis. Families containing a greater number of genera and species were sampled more extensively than others. Sequences of the families Galatheacarididae, Bresiliidae, Pseudochelidae, Campylonotidae, Barbouriidae, and Physetocarididae were not available for inclusion in the analyses because material was unattainable. Specimens were collected during cruise and field expeditions or requested on loan from various museums (National Museum of Natural History—Smithsonian Institution, Oxford University Museum of Natural History, Universidad Nacional Autónoma de México). Sequences from 18 of the 104 caridean species used in this study were obtained from GenBank (Table 1). Fresh specimens were either frozen in glycerol at -80°C and later transferred to 80% ethyl alcohol (EtOH) or placed directly into 80% EtOH. Identifications of all materials were confirmed by two or more authors to limit the chance of misidentifications.

Since the identity of the sister group to the Caridea remains debatable, we included 10 outgroup taxa to represent all of the other presently recognized decapod suborders, infraorders, and superfamilies (Penaeoidea, Sergestoidea, Anomura, Brachyura, Stenopodidea, Astacidea, Palinuroidea, and Thalassinidea). Additionally, we included one representative of the order Euphausiacea, putative sister order to the Decapoda within the superorder Eucarida. Sequences representing the putative sister order Amphionidacea were not available for inclusion in the analysis. Sequences for eight of the ten outgroup taxa were obtained from GenBank (Table 1).

2.2 *DNA extraction, PCR, and sequencing*

Total genomic DNA was extracted from the abdomen, gills, pereopods, and pleopods under one of three different extraction protocols. Extraction kits included the Genomic DNA Extraction Kit for Arthropods (Cartagen Cat. No. 20810-050) and Qiagen DNeasy[®] Blood and Tissue Kit (Cat. No. 69504). For some extractions, we used an isopropanol precipitation as follows: Muscle was ground and then incubated for 12h in 600 μl of lysis buffer (100 mM EDTA, 10 mM tris pH 7.5, 1% SDS) at 65°C ; protein was separated by the addition of 200 μl of 7.5 M ammonium acetate and subsequent centrifugation. DNA was precipitated by the addition of 600 μl of cold isopropanol followed by overnight refrigeration (4°C) and later centrifugation (10–30 min at 14,000 rpm); the

Table 1. Taxonomy, voucher catalog numbers, and GenBank accession numbers for gene sequences used in study. An "N/A" designates gene sequences we were unable to acquire. ULLZ = University of Louisiana at Lafayette Zoological Collection; USNM = National Museum of Natural History, Smithsonian Institute Invertebrate Collection; OUMNH = Oxford University Museum of Natural History, Zoological Collection; CNCR = Colección Nacional de Crustáceos, Universidad Nacional Autónoma de México. Catalog numbers accompanied by asterisk (*) represent cataloged tissue specimens (isolated appendages, gills, eggs, or abdomens) originating from presently uncataloged specimens at OUMNH.

| Taxon | GenBank Nos. | | |
|---|------------------|-----------|----------|
| | Voucher Cat. No. | 16S | 18S |
| Outgroups | | | |
| Euphausiacea Dana, 1852 | | | |
| Euphausiidae Dana, 1852 | | | |
| <i>Euphausia</i> sp. | ULLZ 8093 | EU868655 | EU868746 |
| Decapoda Latreille, 1802 | | | |
| Dendrobranchiata Bate, 1888 | | | |
| Penaeoidea Rafinesque, 1815 | | | |
| <i>Penaeus semisulcatus</i> de Hann, 1844 | GenBank | DQ079731 | DQ079766 |
| Sergestoidea Dana, 1852 | | | |
| <i>Sergia</i> sp. | ULLZ 8089 | EU868710 | EU868807 |
| Pleocyemata Burkenroad, 1963 | | | |
| Brachyura Latreille, 1802 | | | |
| <i>Dromia dehaani</i> Rathbun, 1923 | GenBank | AY583899 | AY583972 |
| Stenopodidea Claus, 1872 | | | |
| <i>Stenopus hispidus</i> (Olivier, 1811) | GenBank | AY583884 | AY743957 |
| Astacidea Latreille, 1802 | | | |
| <i>Enoplometopus occidentalis</i> (Randall, 1840) | GenBank | AY583892 | AY583966 |
| <i>Procambarus clarkii</i> (Girard, 1952) | GenBank | DQ666844 | AF436001 |
| Anomura MacLeay, 1838 | | | |
| <i>Pagurus longicarpus</i> Say, 1817 | GenBank | NC_003058 | AF436018 |
| Achelata Scholtz & Richter, 1995 | | | |
| <i>Panulirus argus</i> (Latreille, 1804) | GenBank | AF337966 | AY743955 |
| Thalassinidea Latreille, 1831 | | | |
| <i>Upogebia affinis</i> (Say, 1818) | GenBank | AF436047 | AF436007 |

Table 1. continued.

| Taxon | Voucher Cat. No. | GenBank Nos. | |
|--|------------------|--------------|----------|
| | | 16S | 18S |
| Ingroups | | | |
| Decapoda Latreille, 1802 | | | |
| Pleocyemata Burkenroad, 1963 | | | |
| Caridea Dana, 1852 | | | |
| Alpheoidea Rafinesque, 1815 | | | |
| Alpheidae Rafinesque, 1815 | | | |
| <i>Alpheopsis trigonus</i> (Rathbun, 1901) | ULLZ 7283 | EU868633 | EU868723 |
| <i>Alpheus packardii</i> Kingsley, 1880 | ULLZ 7248 | EU868630 | EU868720 |
| <i>Alpheus vanderbilti</i> Boone, 1930 | ULLZ 7461 | EU868639 | EU868730 |
| <i>Automate rectifrons</i> Chace, 1972 | ULLZ 7303 | EU868631 | EU868721 |
| <i>Automate</i> sp. | ULLZ 7754 | EU868635 | EU868725 |
| <i>Betaeus</i> sp. | CNCR16850 | N/A | EU868726 |
| <i>Coronalphheus natator</i> Wicksten, 1999 | ULLZ 8938 | EU868636 | EU868727 |
| <i>Coutieralphheus</i> sp. | ULLZ 8939 | EU868637 | EU868728 |
| <i>Fenneralphheus chacei</i> Felder & Manning, 1986 | ULLZ 4559 | EU868638 | EU868729 |
| <i>Leptalphheus forceps</i> Williams, 1965 | ULLZ 5594 | EU868670 | EU868763 |
| <i>Leptalphheus axitamassae</i> Dworschak & Coelho, 1999 | ULLZ 5913 | EU868671 | EU868764 |
| <i>Synalphheus bousfieldi</i> (Chace, 1972) | ULLZ 7137 | EU868646 | EU868737 |
| <i>Synalphheus fritzmuelleri</i> Coutière, 1909 | ULLZ 7136 | EU868642 | EU868733 |
| <i>Synalphheus hemphilli</i> Coutière, 1909 | ULLZ 7147 | EU868643 | EU868734 |
| <i>Synalphheus pandionis</i> (Coutière, 1909) | ULLZ 7241 | EU868647 | EU868738 |
| <i>Yagerocaris cozumel</i> Kensley, 1988 | ULLZ 8883 | EU868645 | EU868736 |
| Hippolytidae Dana, 1852 | | | |
| <i>Hippolyte varians</i> Leach, 1814 | ULLZ 6970 | EU868662 | EU868753 |
| <i>Hippolyte obliquimanus</i> Dana, 1852 | ULLZ 9137 | EU868661 | EU868752 |
| <i>Hippolyte pleuracanthus</i> (Stimpson, 1871) | GenBank | N/A | AY743956 |
| <i>Latreutes fucorum</i> (Fabricius, 1798) | ULLZ 9135 | EU868664 | EU868755 |
| <i>Lysmata</i> cf. <i>wurdemanni</i> | ULLZ 7433 | EU868666 | EU868757 |

Table 1. continued.

| Taxon | Voucher Cat. No. | GenBank Nos. | |
|---|------------------|--------------|----------|
| | | 16S | 18S |
| <i>Lysmata</i> sp. | UJLLZ 8931 | EU868665 | EU868756 |
| <i>Lysmata boggei</i> Rhyné & Lin, 2006 | GenBank | DQ079719 | DQ079753 |
| <i>Lysmata debelius</i> (Bruce, 1983) | GenBank | DQ079718 | DQ079752 |
| <i>Thorulus cranchii</i> (Leach, 1817) | UJLLZ 6969 | EU868667 | EU868758 |
| <i>Tozeuma</i> cf. <i>carolinense</i> | UJLLZ 7445 | EU868669 | EU868760 |
| <i>Tozeuma serratum</i> A. Milne-Edwards, 1881 | UJLLZ 7446 | EU868668 | EU868759 |
| <i>Trachycaris rugosa</i> (Bate, 1888) | UJLLZ 7425 | N/A | EU868761 |
| <i>Trachycaris</i> sp. | UJLLZ 7749 | N/A | EU868762 |
| Ogyrididae Holthuis, 1955 | | | |
| <i>Ogyrides</i> sp. | UJLLZ 7755 | EU868679 | EU868772 |
| <i>Ogyrides</i> sp. | UJLLZ 7756 | EU868680 | EU868773 |
| Atyoidea de Hann, 1849 | | | |
| Atyidae de Haan, 1849 | | | |
| <i>Antecaridina</i> sp. | | EF173754 | EF173850 |
| <i>Atya scabra</i> Leach, 1815 | CNCR 17094 | EU868632 | EU868722 |
| <i>Atyoida bisulcata</i> (Randall, 1840) | GenBank | DQ079704 | DQ079738 |
| <i>Atyopsis</i> sp. | UJLLZ 9174 | EU868634 | EU868724 |
| <i>Halocaridina rubra</i> Holthuis, 1963 | GenBank | EF173749 | EF173848 |
| <i>Halocaridinides trigonophthalma</i> (Fujino & Shokita, 1975) | GenBank | EF173752 | EF173849 |
| <i>Paratya australiensis</i> Kemp, 1917 | USNM 1073432 | EU868640 | EU868731 |
| <i>Potimirim mexicana</i> (De Saussure, 1857) | CNCR 17140 | EU868641 | EU868732 |
| <i>Typhlatya mitchelli</i> Hobbs & Hobbs, 1976 | CNCR 22696 | EU868644 | EU868735 |
| <i>Typhlatya pearsei</i> Creaser, 1936 | GenBank | DQ079735 | DQ079770 |
| Bresilioidea Calman, 1896 | | | |
| Agostocarididae Hart & Manning, 1986 | | | |
| <i>Agostocaris</i> sp. | USNM 1014071 | EU868626 | EU868716 |
| Alvinocarididae Christoffersen, 1986 | | | |
| <i>Alvinocaris muricola</i> Williams, 1988 | CNCR 24875 | EU868627 | EU868717 |

Table 1. continued.

| Taxon | Voucher Cat. No. | GenBank Nos. | |
|---|------------------|--------------|----------|
| | | 16S | 18S |
| <i>Alvinocaris muricola</i> Williams, 1988 | CNCR 24873 | EU868628 | EU868718 |
| <i>Chorocaris chacei</i> (Williams & Rona, 1986) | GenBank | AM087922 | AM087653 |
| <i>Rimicaris exoculata</i> (Williams & Rona, 1986) | GenBank | AM076958 | AM087652 |
| Discidiidae Rathbun, 1902 | | | |
| <i>Discias atlanticus</i> Gurney, 1939 | ULLZ 8953 | EU868652 | EU868743 |
| Campylonotoidea Sollaud, 1913 | | | |
| Bathypalaemonellidae de Saint Laurent, 1985 | | | |
| <i>Bathypalaemonella</i> sp. | ULLZ 8929* | EU868648 | EU868739 |
| Crangonoidea Haworth, 1825 | | | |
| Crangonidae Haworth, 1825 | | | |
| <i>Crangon crangon</i> (Linnaeus, 1758) | ULLZ 696Z | EU868649 | EU868740 |
| <i>Crangon franciscorum</i> Stimpson, 1856 | GenBank | N/A | AY859567 |
| <i>Pontophilus gracilis</i> Smith, 1882 | ULLZ 8287 | EU868650 | EU868741 |
| Glyphocrangonidae Smith, 1884 | | | |
| <i>Glyphocrangon alispina</i> Chace, 1939 | ULLZ 7878 | EU868656 | EU868747 |
| <i>Glyphocrangon alispina</i> Chace, 1939 | ULLZ 8084 | EU868657 | EU868748 |
| Nematocarcinoidea Smith, 1884 | | | |
| Nematocarcinoidea Chace, 1937 | | | |
| <i>Eugonatonotus chacei</i> Chan & Yu, 1991 | ULLZ 8880* | EU868653 | EU868744 |
| Nematocarcinidae Smith, 1884 | | | |
| <i>Nematocarcinus cursor</i> A. Milne-Edwards, 1881 | ULLZ 8044 | EU868673 | EU868766 |
| <i>Nematocarcinus rotundus</i> Crosnier & Forrest, 1973 | ULLZ 7736 | EU868672 | EU868765 |
| <i>Nematocarcinus rotundus</i> Crosnier & Forrest, 1973 | ULLZ 7736 | EU868674 | EU868767 |
| Rhynchocinetidae Ortmann, 1890 | | | |
| <i>Cinetorhynchus manningi</i> Okuno, 1996 | ULLZ 7414 | N/A | EU868805 |
| Xiphocarididae Ortmann, 1895 | | | |
| <i>Xiphocaris elongata</i> (Guérin-Méneville, 1856) | ULLZ 8882* | EU868714 | EU868809 |
| Oplophoroidea Dana, 1852 | | | |

Table 1. continued.

| Taxon | Voucher Cat. No. | GenBank Nos. | |
|--|------------------|--------------|----------|
| | | 16S | 18S |
| Ophiophoridae Dana, 1852 | | | |
| <i>Acanthephyra</i> sp. | ULLZ 8026 | EU868675 | EU868768 |
| <i>Acanthephyra curtirostris</i> Wood-Mason, 1891 | ULLZ 6702 | EU868676 | EU868769 |
| <i>Acanthephyra purpurea</i> A. Milne-Edwards, 1881 | ULLZ 7579 | EU868677 | EU868770 |
| <i>Ephyrina figueirai</i> Crosnier and Forest, 1973 | GenBank | AM076960 | AM087654 |
| <i>Meningodora</i> sp. | ULLZ 7738 | EU868678 | EU868771 |
| <i>Systellaspis debilis</i> (A. Milne-Edwards, 1881) | ULLZ 7854 | EU868682 | EU868775 |
| <i>Systellaspis debilis</i> (A. Milne-Edwards, 1881) | ULLZ 6713 | EU868678 | EU868771 |
| Palaemonoidea Rafinesque, 1815 | | | |
| Anchistioidea Borradaile, 1915 | | | |
| <i>Anchistioidea antiguensis</i> (Schmitt, 1924) | ULLZ 7454 | EU868629 | EU868719 |
| Desmocarididae Borradaile, 1915 | | | |
| <i>Desmocarid</i> sp. | ULLZ 8358 | EU868651 | EU868742 |
| Euryrhynchidae Holthuis, 1950 | | | |
| <i>Euryrhynchus wrzesniewskii</i> Miers, 1878 | ULLZ 9070 | EU868654 | EU868745 |
| Gnathophyllidae Dana, 1852 | | | |
| <i>Gnathophyllodes mineri</i> Schmitt, 1933 | ULLZ 8596 | EU868658 | EU868749 |
| <i>Gnathophyllodes mineri</i> Schmitt, 1933 | ULLZ 8932 | EU868659 | EU868750 |
| <i>Gnathophyllum americanum</i> Guérin-Méneville, 1855 | ULLZ 8597 | EU868660 | EU868751 |
| Hymenoceridae Ortmann, 1890 | | | |
| <i>Hymenocera picta</i> Dana, 1852 | ULLZ 8595 | EU868663 | EU868754 |
| Kakaducarididae Bruce, 1993 | | | |
| <i>Leptopalaemon gagadju</i> Bruce & Short, 1993 | ULLZ 9120 | EU868693 | EU868787 |
| Palaemonidae Rafinesque, 1815 | | | |
| <i>Brachycarpus biunguiculatus</i> (Lucas, 1846) | ULLZ 7382 | EU868685 | EU868778 |
| <i>Brachycarpus biunguiculatus</i> (Lucas, 1846) | ULLZ 7430 | EU868686 | EU868779 |
| <i>Brachycarpus biunguiculatus</i> (Lucas, 1846) | ULLZ 7426 | EU868684 | EU868777 |
| <i>Coralliocaris graminea</i> (Dana, 1852) | GenBank | N/A | AM083319 |

Table 1. continued.

| Taxon | Voucher Cat. No. | GenBank Nos. | |
|--|------------------|--------------|----------|
| | | 16S | 18S |
| <i>Creaseria morleyi</i> (Creaser, 1936) | CNCR 22720 | EU868687 | EU868780 |
| <i>Creaseria morleyi</i> (Creaser, 1936) | CNCR 22732 | EU868688 | EU868781 |
| <i>Cryphiops caementarius</i> (Molina, 1782) | GenBank | DQ079711 | DQ079747 |
| <i>Kemponia americana</i> (Kingsley, 1878) | ULLZ 7431 | EU868701 | EU868795 |
| <i>Leander tenuicornis</i> (Say, 1818) | ULLZ 7765 | EU868690 | EU868783 |
| <i>Macrobrachium ohione</i> (Smith, 1874) | ULLZ 8715 | EU868694 | EU868788 |
| <i>Macrobrachium potiuma</i> (Müller, 1880) | GenBank | DQ079721 | DQ079756 |
| <i>Palaemon elegans</i> Rathke, 1837 | ULLZ 6968 | EU868696 | EU868790 |
| <i>Palaemonetes pugio</i> Holthuis, 1949 | ULLZ 7458 | EU868697 | EU868791 |
| <i>Palaemonetes vulgaris</i> (Say, 1818) | GenBank | N/A | AY743941 |
| <i>Periclimenaeus wilsoni</i> (Hay, 1917) | ULLZ 7384 | EU868702 | EU868797 |
| <i>Periclimenes pedersoni</i> Chace, 1958 | GenBank | N/A | AY743954 |
| <i>Pontonia</i> sp. | ULLZ 8886 | EU868706 | EU868801 |
| <i>Pontonia manningi</i> Fransen, 2000 | ULLZ 8536 | EU868705 | EU868800 |
| Typhlocarididae Ammandale & Kemp, 1913 | ULLZ 9152* | EU868713 | EU868808 |
| <i>Typhlocaris salentina</i> Caroli, 1924 | | | |
| Pandalioidea Haworth, 1825 | | | |
| Pandalidae Haworth, 1825 | | | |
| <i>Heterocarpus ensifer</i> A. Milne-Edwards, 1881 | ULLZ 8362 | EU868689 | EU868782 |
| <i>Heterocarpus ensifer</i> A. Milne-Edwards, 1881 | GenBank | AMO76962 | AMO83320 |
| <i>Pandalus montagui</i> Leach, 1814 | ULLZ 6966 | EU868698 | EU868792 |
| <i>Parapandalus richardi</i> (Coutière, 1905) | ULLZ 6706 | N/A | EU868793 |
| <i>Plesionika holthuisi</i> Crosnier & Forrest, 1968 | ULLZ 7953 | EU868703 | EU868798 |
| <i>Plesionika longipes</i> (A. Milne-Edwards, 1881) | ULLZ 8363 | EU868704 | EU868799 |
| Thalassocarididae Bate, 1888 | | | |
| <i>Thalassocaris crinita</i> (Dana, 1852) | ULLZ 8359 | EU868712 | EU868810 |
| Pasiphaeoidea Dana, 1852 | | | |
| Pasiphaeidae Dana, 1852 | | | |

Table 1. continued.

| Taxon | Voucher Cat. No. | GenBank Nos. | |
|---|------------------|--------------|----------|
| | | 16S | 18S |
| <i>Leptochela carinata</i> Ortmann, 1893 | ULLZ 7232 | EU868692 | EU868786 |
| <i>Leptochela bermudensis</i> (Gurney, 1939) | ULLZ 7888 | EU868691 | EU868785 |
| <i>Leptochela papulata</i> Chace, 1976 | ULLZ 8614 | N/A | EU868784 |
| <i>Paspiphaea merriami</i> Schmitt, 1931 | ULLZ 6703 | EU868700 | EU868796 |
| <i>Paspiphaea merriami</i> Schmitt, 1931 | ULLZ 8088 | EU868699 | EU868794 |
| Procaridoidea Chace & Manning, 1972 | | | |
| Procarididae Chace & Manning, 1972 | | | |
| <i>Procaris mexicana</i> Sternberg & Schotte, 2004 | ULLZ 9224 | EU868715 | EU868811 |
| Processoidea Ortmann, 1890 | | | |
| Processidae Ortmann, 1890 | | | |
| <i>Ambidexter symmetricus</i> Manning & Chace, 1971 | ULLZ 6432 | EU868683 | EU868776 |
| <i>Nikoides schmitti</i> Manning & Chace, 1971 | ULLZ 7441 | EU868695 | EU868789 |
| <i>Processa guyanae</i> Holthuis, 1959 | ULLZ 7378 | EU868707 | EU868802 |
| <i>Processa guyanae</i> Holthuis, 1959 | ULLZ 7150 | EU868708 | EU868803 |
| Psalidopodoidea Wood Mason & Alcock, 1892 | | | |
| Psalidopodidae Wood Mason & Alcock, 1892 | | | |
| <i>Psalidopoda barboursi</i> Chace, 1939 | ULLZ 7805 | EU868709 | EU868804 |
| Stylodactyloidea Bate, 1888 | | | |
| Stylodactylidae Bate, 1888 | | | |
| <i>Stylodactylus multidentatus</i> Kubo, 1942 | ULLZ 8881* | EU868711 | EU868806 |
| <i>Stylodactylus libratus</i> Chace, 1983 | GenBank | AM076943 | AM083323 |

resulting pellet was rinsed in 70% EtOH, dried in a speed vacuum system (DNA110 Speed Vac[®]), and resuspended in 10–50 μ l of nanopure water (Robles et al. 2007).

One mitochondrial gene and one nuclear gene were selected due to their utility in resolving phylogenetic relationships at different taxonomic levels (Spears et al. 1992; Spears et al. 1994; Giribet et al. 1996; Schubart et al. 2000; Stillman & Reeb 2001; Tudge & Cunningham 2002; Porter et al. 2005; Mantelatto et al. 2006; Mantelatto et al. 2007; Robles et al. 2007). The 16S large ribosomal subunit (~550 bps) was selected as our mitochondrial gene, and the complete 18S, large ribosomal subunit (~1850 bps) was selected as the nuclear gene. Targeted sequences were amplified by means of the polymerase chain reaction (PCR). The mitochondrial gene, 16S, was amplified with the primers 16SL2, 16S-ar, and 1472 to create one overlapping region of approximately 550 basepairs in length (Palumbi et al. 1991; Crandall & Fitzpatrick 1996; Schubart et al. 2002). The nuclear gene, 18S, was amplified with the primers A–L, C–Y, and O–B to yield three overlapping regions of approximately 600–700 basepairs in length each (Medlin et al. 1988; Apakupakul et al. 1999). Additionally, slightly shorter internal 18S primers (B–D18s1R, D18s2F–D18s2R, D18s3F–D18s3R, D18s4F–D18s4R, and D18s5F–A) were designed to yield five overlapping regions ranging from approximately 450–600 basepairs in length each (all primers listed in Table 2).

Reactions were performed in 25 μ l volumes containing 0.5 μ M forward and reverse primer for each gene, 200 μ M each dNTP, PCR buffer, magnesium chloride, 5 M betaine, 1 unit AmpliTaq-GOLD[®] polymerase, and 30–50 ng extracted DNA. The thermal cycling profile conformed to the following parameters: initial denaturation for 10 min at 94°C followed by 40 cycles of 1 min at 94°C, 1.5 min at 46–58°C, 1.5 min at 72°C, and a final extension of 10 min at 72°C. PCR products were purified using filters (Microcon-100[®] Millipore Corp., Billerica, MA, USA or EPOCH GenCatch PCR Clean-up Kit Cat. No. 13-60250) and sequenced with ABI BigDye[®] terminator mix (Applied Biosystems, Foster City, CA, USA). A Robocycler 96 cyler was used in all PCR and cycle sequencing reactions and sequencing products were run (forward and reverse) on a 3100 Applied Biosystems automated sequencer.

Table 2. 16S and 18S primers used in this study.

| Gene | Primer | Primer Pair | Sequence 5' → 3' | Ref. |
|------|--------|---------------|---------------------------------------|------|
| 16S | 16S-ar | 1472 | CGC CTG TTT ATC AAA AAC AT | (1) |
| 16S | 16S-L2 | 1472 | TGC CTG TTT ATC AAA AAC AT | (2) |
| 16S | 1472 | 16S-ar/16S-L2 | AGA TAG AAA CCA ACC TGG | (3) |
| 18S | 18S-A | 18S-L | AAC CTG GTT GAT CCT GCC AGT | (4) |
| 18S | 18S-L | 18S-A | CCA ACT ACG AGC TTT TTA ACT G | (5) |
| 18S | 18S-C | 18S-Y | CGG TAA TTC CAG CTC CAA TAG | (5) |
| 18S | 18S-Y | 18S-C | CAG ACA AAT CGC TCC ACC AAC | (5) |
| 18S | 18S-O | 18S-B | AAG GGC ACC ACC AGG AGT GGA G | (5) |
| 18S | 18S-B | 18S-O | TGA TCC TTC CGC AGG TTC ACC T | (4) |
| 18S | D18s1R | 18S-B | CTT AAT TCC GAT AAC GAA CGA GAC TCT G | New |
| 18S | D18s2F | D18s2R | TCT AAG GGC ATC ACA GAC CTG | New |
| 18S | D18s2R | D18s2F | AGA TAC CGC CCT AGT TCT AAC C | New |
| 18S | D18s3F | D18s3R | GGT TAG AAC TAG GGC GGT ATC | New |
| 18S | D18s3R | D18s3F | TGG AGG GCA AGT CTG GTG | New |
| 18S | D18s4F | D18s4R | GCA ACA AAC TTT AAT ATA CG | New |
| 18S | D18s4R | D18s4F | TGG TAA TTC TAG AGC TAA TAC | New |
| 18S | D18s5F | 18S-A | GTT ATT TTT CGT CAC TAC CTC CC | New |

References: (1) Palumbi et al. 1991, (2) Schubart et al. 2002, (3) Crandall & Fitzpatrick 1996, (4) Medlin et al. 1988, (5) Apakupakul et al. 1999.

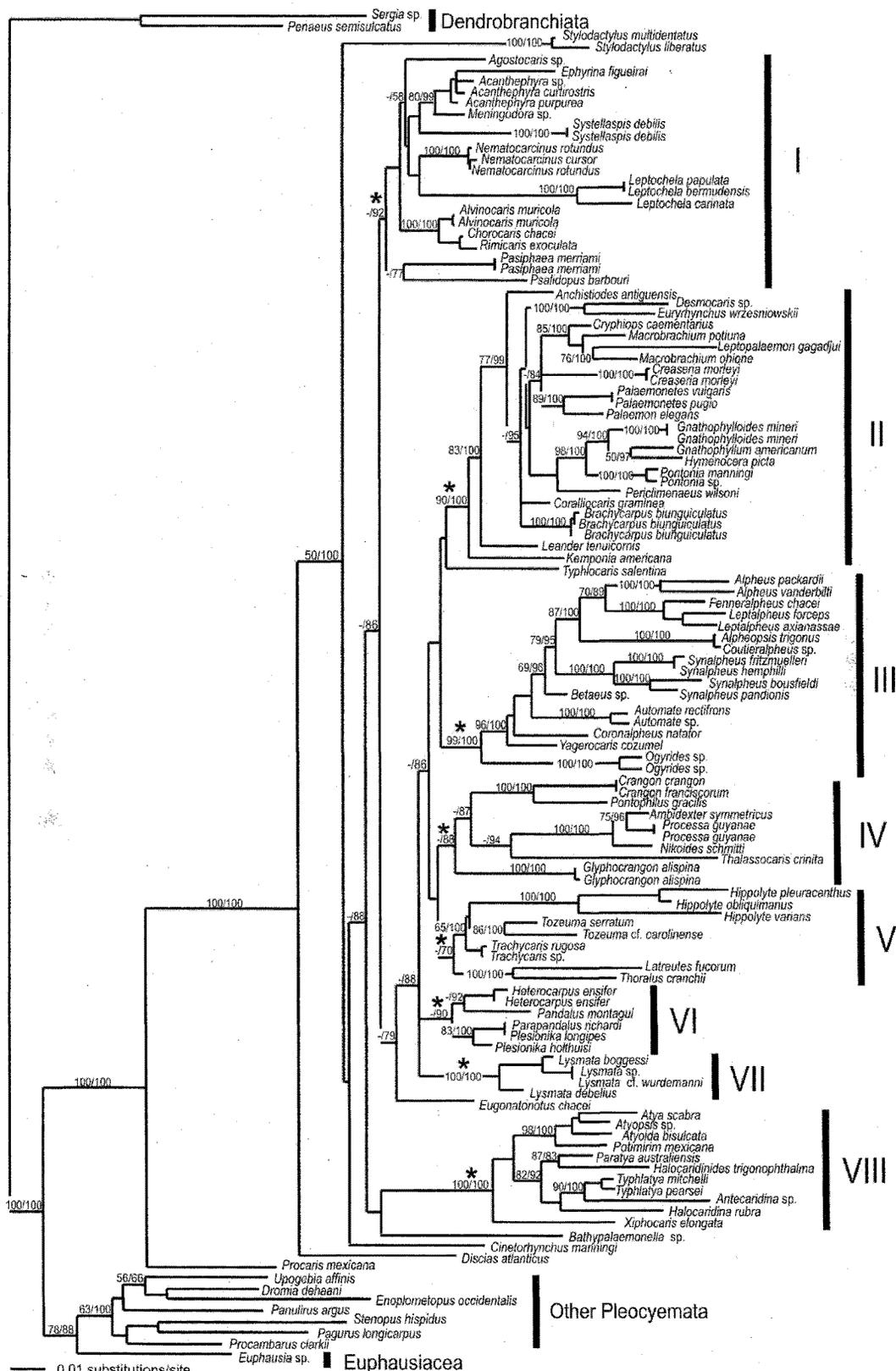
2.3 Phylogenetic analyses

Sequences were assembled using the computer program Sequencher 4.7 (GeneCodes, Ann Arbor, MI, USA). Once assembled, sequences were aligned using MUSCLE (multiple sequence comparison by log-expectation), a computer program found to be more accurate and faster than other alignment algorithms (Edgar 2004). Since many regions within the 16S and 18S datasets were extremely divergent and difficult to align, we used GBLOCKS v0.91b (Castresana 2000) to omit poorly aligned positions (GBLOCKS parameters optimized for dataset and modeled after previous studies (Porter et al. 2005): minimum number of sequences for a conserved position = 62/57; minimum number of sequences for a flanking position = 104/95; maximum number of contiguous non-conserved positions = 8/8; minimum length of a block = 6/6; allowed gap positions = half/half). GBLOCKS pruned approximately 400 and 170 basepairs from the 18S and 16S alignments, resulting in two datasets composed of 1458 and 377 characters, respectively. Recent studies have shown an increase in phylogenetic resolution when multiple genes are combined in phylogenetic analyses. These approaches have gained popularity over single gene studies because of their potential to resolve phylogenies at different taxonomic levels (Ahyong & O'Meally 2004; Porter et al. 2005). For these reasons, we concatenated our 18S and 16S datasets into a single alignment consisting of 1835 basepairs and 122 sequences. We conducted a partition test of heterogeneity (incongruence length difference test (ILD)) (Bull et al. 1993), as implemented in PAUP* (Swofford 2003), and results indicated that the two gene regions could be combined. Before concatenation, we generated single gene trees (16S and 18S). Although we observed similar patterns of phylogeny, the 18S tree showed better resolution at the deeper nodes, while the 16S tree showed higher resolution between species.

The model of evolution that best fit the individual datasets (18S, 16S) was determined by MODELTEST 3.06 (Posada & Crandall 1998) before conducting maximum likelihood (ML) and Bayesian Inference (BAY) analyses. The ML analysis was conducted using RAxML (Randomized Axelerated Maximum Likelihood) (Stamatakis et al. 2005) with computations performed on the computer cluster of the Cyberinfrastructure for Phylogenetic Research Project (CIPRES) at the San Diego Supercomputer Center. The BAY analysis was conducted in MrBayes v3.0b4 (Huelsenbeck & Ronquist 2001). Each analysis was run three times to evaluate the consistency among runs.

Likelihood settings followed the General Time Reversible Model (GTR) with a gamma distribution and invariable sites and RAxML estimated all free parameters following a partitioned dataset. Confidence in the resulting topology was assessed using non-parametric bootstrap estimates (Felsenstein 1985) with 1000 replicates. Values > 50% are presented on the BAY phylogram (Fig. 1). The BAY analysis was performed using parameters selected by MODELTEST. A Markov chain Monte Carlo (MCMC) algorithm ran for 2,000,000 generations, sampling one tree every 100 generations. Preliminary analyses and observation of the log likelihood (L) values allowed us to determine burn-ins and stationary distributions for the data. Once the values reached a plateau, a 50% majority rule consensus tree was obtained from the remaining saved trees. Clade support was assessed with posterior probabilities (pP), and values > 0.5 are presented on the BAY phylogram (Fig. 1). Trees were initially generated as unrooted phylograms to help designate outgroup taxa. Ten taxa showed a clear separation from the Caridea and were selected as outgroups (Table 1).

Figure 1. (Opposite Page) Bayesian (BAY) phylogram for the infraorder Caridea ($n = 112$) and selected outgroups ($n = 10$) based on 18S (rDNA) and 16S (rDNA) concatenated dataset. ML bootstrap values and BAY posterior probabilities are noted above branches (ML/BAY). Values < 50% are not shown. Vertical black bars indicate 8 major clades within the Caridea. Clades I–IV and VIII represent multiple families and Clades V–VII represent a single family or genus. * = node for each clade.



3 RESULTS

Our study included representatives from 14 of the 16 superfamilies and 30 of the 36 families presently encompassed in the infraorder Caridea. In total, we generated 87 new complete 18S (~1850 bps), 7 new partial 18S (~700-1450 bps), and 88 new partial 16S sequences (~550 bps) (Table 1). Missing data were designated as a “?” for partial sequences. The ILD test showed no significant incongruence ($P = 0.65$) between datasets, so the 18S and 16S alignments were combined. After the 18S and 16S alignments were run through GBlocks, they were concatenated; of the 1835 basepairs for 122 sequences used in the phylogenetic analyses, 1458 were for 18S and 377 for 16S gene sequences. The optimal model of evolution selected in MODELTEST for the individual datasets was the General Time Reversible (GTR) model (18S) with gamma-distributed among-site rate heterogeneity and invariant sites (base frequencies = 0.2639, 0.2217, 0.2725, 0.2419; Rmat = 1.4462, 2.6478, 1.2472, 1.1228, 4.5836; gamma shape parameter = 0.4927; proportion of invariable sites = 0.3884) and the Transition (TIM) model (16S) with gamma-distributed among-site rate heterogeneity and invariant sites (base frequencies = 0.3833, 0.1700, 0.0553, 0.3914; Rmat = 1.0000, 8.9199, 0.7503, 0.7503, 4.2441; gamma shape parameter = 0.4938; proportion of invariable sites = 0.2420). ML and BAY analyses showed similar tree topologies, but because the ML phylogeny was less resolved at deeper nodes, the BAY tree is presented (Figs. 1, 2).

3.1 *Monophyly, paraphyly, and polyphyly of the infraorder Caridea*

Our results can be interpreted to support monophyly of the infraorder Caridea as presently constituted, but at the same time they offer support for treatment of the family Procarididae as a separate infraorder (Fig. 1). While the basally positioned procaridids grouped more closely to carideans than to any other represented infraorder of pleocyemates, branch length between the procaridids and carideans was comparable to branch lengths between different infraorders of outgroup taxa, rather than those between other families of carideans. Furthermore, in unrooted trees (not shown here) the procaridids were positioned as a distinct lineage, separated from the remaining carideans.

There was no overwhelming support for the monophyly of the currently proposed superfamilies (those containing > 1 family). However, our analyses strongly suggested (bootstrap values > 0.9, $pP = 1.0$) three major multi-familial clades within the infraorder Caridea (Clades II, III, VIII, Figs. 1, 2). Additionally, there was weaker support ($pP \geq 0.88$) for the formation of two additional assemblages composed of two or more families (Clades I, IV, Fig. 1). Our analysis provides some evidence for a relationship between the families Agostocarididae, Oplophoridae, Nematocarinidae, Pasiphaeidae, Psalidopodidae, and Alvinocarididae (Clade I, $pP = 0.92$). There is significant support for Clade II, which includes all families within Palaemonoidea, excluding Typhlocarididae, and there is no support for the inclusion of the typhlocaridids within the Palaemonoidea, as presently classified. The Ogyrididae is resolved as a sister clade to the Alpheidae (Clade III), and Atyidae + Xiphocarididae (Clade VIII) form a monophyletic assemblage with high support. Clade IV, uniting Crangonidae, Processidae, Thalassocarididae, and Glyphocrangonidae, has low support ($pP = .88$), but the subclade grouping Processidae and Thalassocarididae is marginally significantly supported with posterior probabilities ($pP = 0.94$). The remaining clades (V–VII) represent single families; two are weakly supported (Clade V: $pP = 0.70$, Clade VI: $pP = 0.90$) and one is strongly supported (Clade VII: bootstrap values = 1.0, $pP = 1.0$). The Hippolytidae, as currently defined, is split between clades V and VII, and Clade VI is limited to the Pandalidae.

Although superfamilial support is missing or low, our analyses suggest that many families form monophyletic units. Approximately 8 of 16 proposed superfamilies within the Caridea each contain a single family. Our present observations are limited to those families that have multiple genera represented in our tree, and thus we cannot comment on the monophyly of families represented by a single genus (i.e., Stylocladidae, Rhynchocinetidae, Bathypalaemonellidae, Agostocarididae,

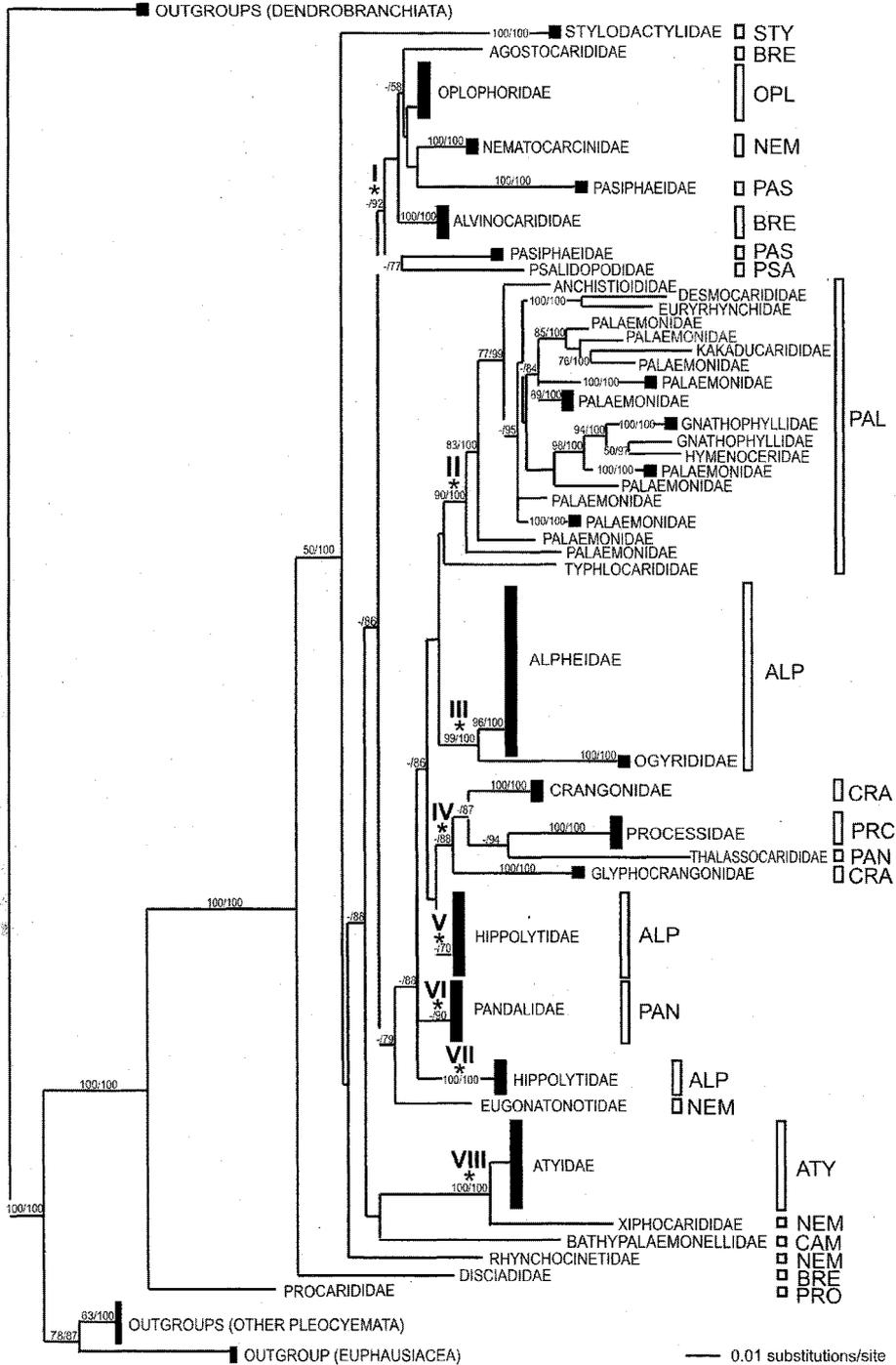


Figure 2. Bayesian (BAY) phylogram for the infraorder Caridea and selected outgroups based on 18S (rDNA) and 16S (rDNA) concatenated dataset. ML bootstrap values and BAY posterior probabilities are noted above the branches (ML/BAY). Values < 50% are not shown. For ease of interpretation, branches are collapsed to show caridean families (solid bars), superfamilies (open bars), and outgroup taxa (solid bars). I–VIII indicate the 8 major clades within the Caridea. * = node for each clade. STY = Stylo-dactyloidea, NEM = Nematocarcinoidea, CAM = Campylonotoidea, BRE = Bresilioidea, OPL = Oplophoroidea, PAS = Pasiphaeidea, PSA = Psalidopodoidea, PAL = Palaemonoidea, ALP = Alpheoidea, CRA = Crangonoidea, PRC = Processoidea, PAN = Pandaloidea, ATY = Atyoidea, PRO = Procaridoidea.

Nematocarinidae, Psalidopodidae, Anchistioididae, Hymenoceridae, Desmocarididae, Kakaducariidae, Euryrhyndidae, Typhlocarididae, Ogyrididae, Thalassocarididae, Eugonatonotidae, Disciadidae, Procarididae, and Glyphocrangonidae). Results are congruent with hypotheses of monophyly within the families Alvinocarididae, Alpheidae, Crangonidae, and Processidae. The monophyly of the Pandalidae is only marginally supported with posterior probabilities. Our findings suggest polyphyletic relationships among genera within the families Pasiphaeidae, Oplophoridae, Hippolytidae, and Palaemonidae (both Palaemoninae and Pontoniinae) and paraphyletic relationships within Gnathophyllidae and Atyidae (Figs. 1, 2).

Systematic placement of Typhlocarididae and Eugonatonotidae is unclear considering there is little support for their position in relation to other families within the tree's topology. The families Procarididae, Disciadidae, Rhynchocinetidae, Stylodactylidae, Bathypalaemonellidae, Atyidae, and Xiphocarididae represent basal (less derived) lineages, which we address in the discussion.

4 DISCUSSION

Aside from the phylogenetic discussions that follow, it does not escape our attention that euphausiaceans are positioned as a sister clade to the non-caridean pleocyemate outgroups included in the analysis. This is not entirely unexpected, because we did not enforce rooting to only the Euphausiacea as in a previous analysis by colleagues (Porter et al. 2005). While it is not our primary interest to resolve phylogenetic positioning of this group, it is noteworthy that other recent molecular studies have also yielded enigmatic placements for this putative sister group of the decapods. While sometimes at low support values, positioning in trees based on protein-coding genes can place euphausiaceans as an immediate sister group to the decapods or outside the eucarids altogether as a sister group to stomatopods (Podsiadlowski & Bartolomaeus 2006). Somewhat controversially, euphausiaceans, on the basis of 28S rDNA sequences, have been allied more closely to the mysidaceans than to dendrobranchiate decapods, but no pleocyemate decapods were included in that analysis (Jarman et al. 2000). Recent ontogenetic studies do not support a closer phylogenetic relationship to mysids than to dendrobranchiate decapods (Casanova et al. 2002).

4.1 *Procaridoidea + Caridea clade?*

Ever since the discovery of the anchialine shrimp *Procaris ascensionis* Chace & Manning, 1972, there has been a debate as to its systematic position in relationship to other shrimp-like decapods. Initially, procaridids were placed within their own family (Procarididae) and superfamily (Procaridoidea) within the infraorder Caridea (Chace & Manning 1972). Over the years, many studies have retained procaridids within the carideans (Chace & Manning 1972; Holthuis 1973; Abele & Felgenhauer 1986; Kensley & Williams 1986; Kim & Abele 1990). Kensley & Williams (1986) described a new genus and species of procaridid shrimp, *Vetericaris chaceorum*, and based on a suite of morphological characters agreed with the phylogenetic placement proposed by Chace & Manning some years earlier. Moreover, a phenetic and cladistic analysis suggested the procaridids be placed within the carideans on the basis of a single shared morphological character, the 2nd abdominal pleura overlapping the 1st and 3rd somites without the 1st being reduced (Abele & Felgenhauer 1986). In 1988, Felgenhauer & Abele discovered that *Procaris ascensionis* carried its eggs attached to the pleopods and secured the group's placement within the Pleocyemata. Molecular evidence presented by Kim & Abele (1990) again suggested a close affinity between the carideans and procaridids. However, this study lacked robust representation of caridean groups ($n = 2$), mandating a more thorough molecular investigation. While many studies position procaridids basally within the Caridea, there is some morphological evidence for the separation of the two groups (Felgenhauer & Abele 1983, 1985, 1989; Schram 1986). In foregut morphology, procaridids appear to be more like dendrobranchiates than carideans (Felgenhauer & Abele 1983, 1985, 1989), and after review of several morphological characters (e.g., gills, protocephalic, and foregut) Felgenhauer & Abele (1983)

concluded that the procaridids be elevated to infraordinal level. Other characters potentially supporting separation of procaridids and carideans include distinct cephalic and thoracopodal anatomy (Fransen & De Grave this volume; Schram 1986).

Present results strongly separate (long branch length) procaridid shrimp basally as a sister group to all other putative carideans. The group is separated, along with carideans *sensu stricto*, from all other pleocyemate infraorders. This could be interpreted as support for treatment of the Procarioidea at the infraordinal level within the Pleocyemata, especially if substantiated by analysis of additional genes and a more robust representation of pleocyemate taxa.

4.2 Superfamily Palaemonoidea

The superfamily Palaemonoidea is an extremely diverse group, currently composed of eight families, including Anchistoididae, Gnathophyllidae, Hymenoceridae, Palaemonidae, Desmocarididae, Kakaducarididae, Euryrhynchidae, and Typhlocarididae. Representatives from all the aforementioned families are presented in our analysis, and, with the exclusion of Typhlocarididae, Palaemonoidea is strongly supported.

Throughout the years, the systematic position of the freshwater troglobitic family, Typhlocarididae, has been controversial. Until recently, the typhlocaridids were thought to be close relatives of the euryrhynchids on the basis of overall mouthpart similarity (Chace 1992, 1993; Holthuis 1993). However, a recent review of morphological characters identifies a suite of fundamental differences between the two families and confirms that similarity in mouthpart structure is shared amongst many genera within Palaemonidae (De Grave 2007). Our analyses reject a close relationship between Euryrhynchidae and Typhlocarididae and question the systematic position of Typhlocarididae within Palaemonoidea, as defined by Chace (1992). Instead, our results strongly suggest Desmocarididae as the sister clade to Euryrhynchidae. Both families inhabit freshwater in South America (Euryrhynchidae) and West Africa (Euryrhynchidae, Desmocarididae) (De Grave et al. 2008) and share the presence of cuspidate setae on their appendix masculina in addition to other morphological features (De Grave 2007).

Leptopalaemon gagadju, an Australian freshwater representative of the family Kakaducarididae, forms a strong affinity with the freshwater genera *Macrobrachium* and *Cryphiops*, which agrees with a recent molecular study (Page et al. 2008b). Although the placement of the Kakaducarididae in relation to these genera appears unclear in our analyses, Page et al. (2008) demonstrate how the use of many genes (16S/18S/28S/H3) help clarify the monophyletic position of this family.

The radiantly beautiful coral reef families, Gnathophyllidae and Hymenoceridae, had long been recognized as a single family (Gnathophyllidae) until Chace (1992) once again separated the two on the basis of the 3rd maxilliped. They both share morphological characteristics such as a broadened 3rd maxilliped and similarity in mandible structure (Holthuis 1993). Our analyses strongly support an affinity between Gnathophyllidae and Hymenoceridae, which is in accordance with results found by Mitsuhashi et al. (2007). However, our study includes the genus *Gnathophylloides*, which was lacking in the former study. This inclusion identifies Gnathophyllidae to be a paraphyletic assemblage with the genus *Gnathophyllum* more closely related to *Hymenocera* than to *Gnathophylloides*. Mitsuhashi et al. (2007) grouped the Gnathophyllidae + Hymenoceridae clade within the subfamily Pontiinae, while providing evidence for the paraphyly of the Pontiinae. Larval morphology corroborates the close relationship among the three aforementioned taxa (Bruce 1986, 1988; Yang & Ko 2002). Our analyses show an obvious association between Hymenoceridae, Gnathophyllidae, and the genus *Pontonia*, but we do not find strong support for the inclusion of the other pontoniine taxa (*Kemponia*, *Coralliocaris*, *Periclimenaeus*). This may be due to the limited number of pontoniine taxa in our analysis ($n = 4$ genera).

Our results suggest a polyphyletic Palaemonidae, which is not unexpected due to the high degree of morphological diversity found within this family. However, definitive conclusions about

phylogenetic relationships cannot be drawn until a broader representation of taxa is included in the analysis, especially of the Pontoniinae. Undoubtedly, this group is ripe for multiple systematic and taxonomic revisions in the future.

4.3 Superfamily Alpheoidea

Currently, the superfamily Alpheoidea contains the families Alpheidae, Ogyrididae, Hippolytidae, and Barbouriidae. Our tree contains representatives from all families except Barbouriidae, and results reject the monophyly of Alpheoidea. It is evident the family Hippolytidae represents a polyphyletic assemblage that qualifies for partitioning into several families as formerly suggested (Kemp 1914; Gurney 1942; Christoffersen 1987, 1990; Chace 1997; Posada et al. 2002). Our tree infers a strong relationship between the genera *Thoralus* and *Latreutes*, while *Hippolyte*, *Tozeuma*, and *Trachycaris* fall out as a supported single unit. Moreover, the genus *Lysmata* forms a distinct clade, clearly separated from the remaining hippolytids. In the past, Christoffersen (1987, 1990) placed *Lysmata* with other related genera within the family Lysmatidae Dana, 1952, and our analysis supports this division. Since then, several studies have recognized unique morphological and reproductive traits (Bauer 2000; Lin & Zhang 2001; Bauer 2004) of these shrimp.

Results support Ogyrididae as a sister clade to Alpheidae, confirming proposals of previous workers (Banner & Banner 1982; Christoffersen 1987; Anker et al. 2006). Recently, Anker et al. (2006) performed a cladistic analysis on the family Alpheidae, examining the phylogenetic relationships among genera. Our results suggest some congruence with their morphological analysis such as the basal position of *Yagerocaris cozumel* and close associations between *Fenneralpheus* and *Leptalpheus*. However, our analysis does not place *Synalpheus* (including some representatives assigned to *Zuzalpheus* (Ríos & Duffy 2007)) as sister taxon to *Alpheus*, as Anker et al. (2006) previously concluded. While the snapping claw, which is thought to have facilitated rich diversification found within *Alpheus* and *Synalpheus*, is concluded by morphological analyses to have evolved only once within the Alpheidae, our molecular evidence suggests this key innovation may have arisen more than one time.

4.4 Atyidae + Xiphocarididae clade

The genus *Xiphocaris* was formerly considered a primitive atyid by Bouvier (1925), and morphological studies have placed the xiphocaridids as a subfamily within the Atyidae (Christoffersen 1986). These taxa inhabit freshwater and possess a dactylar grooming comb on the 5th pereopod. However, other caridean families have dactylar grooming combs (e.g., palaemonids and campylonotids) and xiphocaridids lack the unique cheliped setal brushes used in filter feeding, a diagnostic character used to define membership in the family Atyidae. In 1992, Chace grouped xiphocaridids within the superfamily Nematocarcinoidea, because they shared large epipods on the anterior pereopods and similar mouthparts. Recently, a molecular analysis of atyid shrimp questioned the relationships between selected genera and revisited the issue of possible relationships between xiphocaridids and atyids (Page et al. 2008a). Due to the phylogenetic resolution of the genes used in that study (16S, COI), the position of Xiphocarididae remained unclear, and the authors recommended “the addition of more highly conserved nuclear genes . . . to resolve the deeper nodes fully” (Page et al. 2008a). Our analysis clearly places the xiphocaridids as close relatives of the atyids, with *Xiphocaris* being positioned as the basal lineage of the group or nested within the Atyidae in many of our reconstructions.

With the exclusion of the enigmatic position of *Xiphocaris elongata*, the division of the genera concurs with the findings of Page et al. (2008a). While delimitation of subfamilies within the Atyidae is yet to be taxonomically resolved, two clades are strongly supported in our topology, one

representing the subfamily Atyinae and the other containing members of the other three subfamilies within the Atyidae.

4.5 *Crangonidae + Processidae + Thalassocarididae subclade*

Our analysis suggests a weak affinity among the families Crangonidae, Processidae, and Thalassocarididae, and similar arrangements have been suggested in the past. The first proposed classification for the Caridea (Dana 1852) placed the processids with the crangonids, along with other selected taxa, in the family Crangonidae. More recently, in a cladistic analysis based on morphological characters, Christoffersen (1987) noted a relationship between the two groups and transferred the family Processidae from the Alpheoidea into the Crangonoidea. Christoffersen (1990) again treated the crangonids and processids within the superfamily Crangonoidea, uniting the taxa on the basis of the length of pereopod 2. Molecular evidence lends some support for a relationship between Crangonidae and Processidae. However, our subclade includes the family Thalassocarididae, a group traditionally assumed related to Pandalidae on the basis of mouthparts (Chace 1985). Other workers have suggested a close affinity between Thalassocarididae and Oplophoridae on the basis of larval morphology (Menon & Williamson 1971). The undivided carpus of the 2nd pereopod within some thalassocaridids (exception seen in *Chlorotocoides*) may suggest remote evolutionary ties with crangonids, and molecular evidence supports this grouping. Nevertheless, systematic placement of thalassocaridids remains controversial, and a more robust examination of this family is required.

4.6 *Basal lineages*

Felgenhauer & Abele (1989) suggested that morphological attributes of the foregut may provide insights into the evolutionary relationships among the carideans. They argued the armament of the foregut to be a conserved trait, more related to the phylogenetic history of the group than to feeding behavior and diet. In comparisons to the putatively ancestral state in the Dendrobranchiata, the least derived foregut among the carideans was thought to be a complete set of ossicles and a well-developed gastric mill. Any progressive reduction of chitinized structures was thus considered a derived feature. Felgenhauer & Abele (1983, 1985, 1989) reported primitive states of caridean foreguts to occur in the families Atyidae, Nematocarcinidae, Stylodactylidae, and Rhynchocinetidae, with the least derived state found within the Procarididae. In our analysis, each of these families, and to a lesser extent the Nematocarcinidae, represents a basal lineage in the phylogeny. Furthermore, this morphological observation concurs with molecular results that imply separation of the procaridids from the infraorder Caridea. To our knowledge the foreguts in the other basally positioned lineages such as *Discias* and *Bathypalaemonella* have not been examined, but it would appear worthwhile to determine if they follow the same trends. Derived foreguts were reported from families such as Alpheidae, Crangonidae, Palaemonidae, Hippolytidae, Gnathophyllidae, and Oplophoridae (Felgenhauer & Abele 1983, 1985, 1989). With the exception of the oplophorids, all these families can be considered derived within our phylogeny.

Perhaps more intriguing are observations Felgenhauer & Abele (1989) noted within the Pasiphaeidae. While the genus *Leptochela* was reported to have a primitive well-developed foregut, the foregut within *Pasiphaea* appeared less chitinized and thus more derived. Our analysis suggests the Pasiphaeidae to be polyphyletic, despite the striking similarities in mouthparts and pectinate nature of the anterior chelipeds (Holthuis 1993). This result is in congruence with the findings of Felgenhauer and Abele (1989) and appears to argue for the separation of this family.

Our findings argue that foregut morphology should be thoroughly revisited and considered as a potentially informative character in morphological cladistic analyses. Concordance between earlier reported trends in foregut morphology and our present molecular phylogenetic tree appears to be more than coincidental.

4.7 *Testing morphological hypotheses with molecular data*

Although our phylogeny is not in complete congruence with the classifications and/or relationships proposed by Thompson (1967), Christoffersen (1990), or Chace (1992), the current molecular analysis provides fresh insights on long-debated issues related to the evolution of caridean morphological characters and can also be used to formulate new testable hypotheses bearing on caridean phylogeny. For example, Thompson (1967), among others, believed an oplophorid-like ancestor gave rise to many lineages within the carideans. Our analyses show the Oplophoridae nested within a larger clade and do not support this hypothesis. In fact, we find the oplophorids to be a polyphyletic group that requires more examination. Other hypotheses have suggested the superfamilial grouping of Crangonidae and Glyphocrangonidae on the basis of the subchelate 1st pair of pereopods. Our results would argue against the aforementioned superfamily classification and position us to test for convergent evolution among those groups. Finally, there is widely held consensus that subdivision of the 2nd pereopod (polycarpidean lineage) occurred only once in the evolution of caridean families (Christoffersen 1990). Our tree suggests this trait arose multiple times throughout caridean history, a finding that agrees with Thompson's work (1967). Should these and other findings hold up to more exhaustive phylogenetic scrutiny, we are challenged, on a case-by-case basis, to find explanations in biology and evolutionary history, as well as to reflect them in taxonomic revisions.

5 CONCLUSIONS

Our study presents the most comprehensive treatment to date of caridean phylogeny. Results suggest the monophyly of the Caridea but also propose that this group may represent two separate infraorders. We find little congruence with present hypotheses of higher-level relationships among caridean families. There is no support for the current superfamily classification, and only the Alpheidae, Alvinocarididae, Crangonidae, and Processidae are retained as strongly supported monophyletic assemblages. Morphology has long suggested the procaridids may represent a distinct lineage separate from the remaining carideans, and molecular data provide evidence to justify this division.

Our phylogeny is not expected to resolve all debates currently surrounding classification of the group but, rather, should be treated as a milepost in our ongoing studies. It is intended to provide initial insights on a molecular genetic basis and lay groundwork for further testing. Our findings add validity to some current phylogenetic hypotheses while calling others into question, and in several cases suggest phylogenies that are difficult to rectify with morphological evidence and assumed biogeographic history. However, apparent polyphyletic and paraphyletic compositions of some caridean superfamilies and families are not surprising and have been suggested by previous morphological and molecular systematists.

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