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Decapod Crustacean Phylogenetics

edited by

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Evolution and Radiation of Shrimp-Like Decapods: An Overview

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ABSTRACT

The shrimp-like Decapoda currently include the suborder Dendrobranchiata and the infraorders Caridea and Stenopodidea within the suborder Pleocyemata. Their phylogenetic relationship with the other Decapoda, as well as previously proposed internal phylogenies, are reviewed. This review shows that only a small percentage of the shrimp-like decapod taxa is incorporated in phylogenetic analyses at higher to lower taxonomic levels and that there remain numerous controversies between and within analyses based on morphological characters and molecular markers. The morphological and molecular characters thus far used in phylogenetic reconstructions are evaluated. It is suggested that when a robust morphological matrix is available, the addition of fossil taxa will be worthwhile, in view of their unique morphology and ecology. A review of potentially phylogenetically informative characters across all caridean families is sorely lacking; such a review needs to be instigated to assess foregut morphology and the mastigobranch–setobranch complex, to name but a few important characters.

1 INTRODUCTION

Three groups of shrimp-like decapods are currently recognized (Martin & Davis 2001): the suborder Dendrobranchiata and the infraorders Caridea and Stenopodidea of the suborder Pleocyemata. A count of the number of taxa recognized in these groups shows that the Caridea are by far the largest group with more than 3100 species (Table 1).

The discovery curves in all three groups do not show any sign of reaching a plateau (Fig. 1), suggesting we are a long way off from knowing the true species richness for all groups. Although Stenopodidea are far less species rich than the other two taxa, the median date of description (1978), and the steep incline since then, indicates that many more species remain to be described even in this group—not surprising given the deep-water habitat of many of its constituent species. Focusing on the Caridea, at the end of the 19th century and the beginning of the 20th century, the number of species described increased distinctly to about 25 species per year, mainly due to the publication of the results of major oceanographic expeditions like the “Challenger,” “Discovery,” and “Siboga.” Around 1910, the increment of species slowed down to about 12 species a year until around 1970 when the description rate increased again to a mean of 33 per year. The fossil record of shrimp-like decapods is meager, especially in the Caridea, for which relatively few fossil taxa are known compared to the large number of extant taxa (Crandall et al. in prep).

Table 1. Number of extant and extinct (†) taxa within the three shrimp-like decapod groups (current as of August 2008).

Taxon level	Dendrobranchiata	Caridea	Stenopodidea
Superfamilies	2	16 (1 †)	0
Families	9 (2 †)	36 (1 †)	3
Genera	56	361	10 (2 †)
Species	505 (74 †)	ca. 3108 (46 †)	58 (2 †)

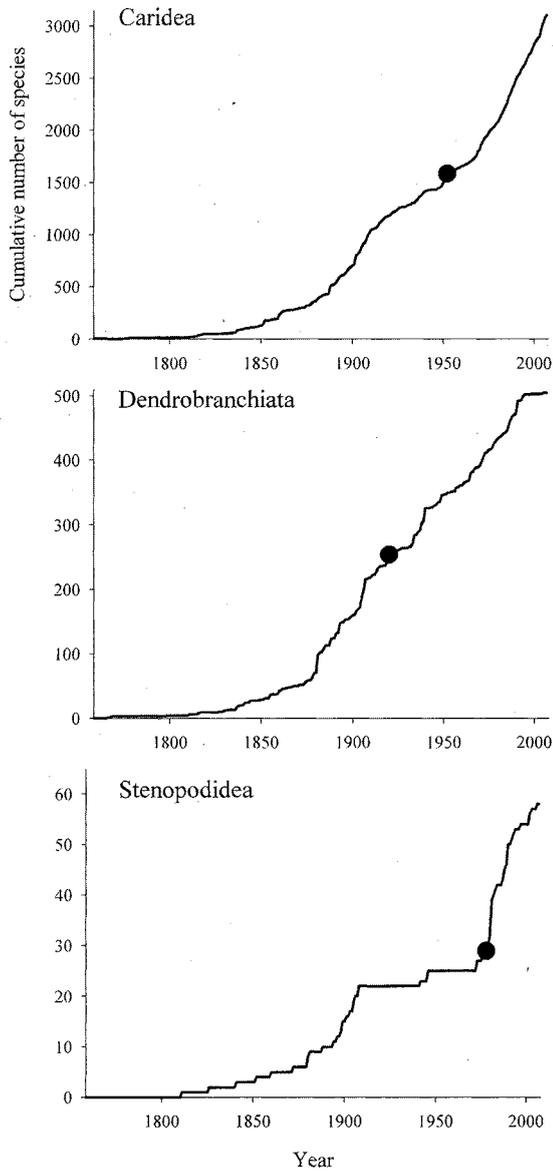


Figure 1. Cumulative numbers described for shrimp-like Decapoda per taxon per annum; circle indicates median date of description.

2 POSITION OF THE SHRIMP-LIKE DECAPODS WITHIN THE DECAPODA

Ever since Dana (1852) and Huxley (1879) recognized the artificial nature of the Natantia, there has been controversy over the relationships between the shrimp-like decapods as well as their relationship to the remaining groups. Despite this uncertainty, most recent studies demonstrate that the shrimp-like decapods are basal to the other decapod lineages (Richter & Scholtz 2001; Schram 2001; Dixon et al. 2003; Porter et al. 2005). In contrast to these studies, however, the molecular tree presented by Bracken et al. (this volume) indicates that the Stenopodidea might not be as basal as previously assumed.

Earlier classifications, from the 1800s up to 1981, have been succinctly reviewed by Felgenhauer & Abele (1983) and Holthuis (1993), and there appears to be no need to repeat this information here. Burkenroad (1963) firmly established the separate status of the Dendrobranchiata as a suborder, containing the Penaeidae and Sergestidae (now usually treated as the superfamilies Penaeoidea, with 5 families, and the Sergestoidea, with 2 families). Both Burkenroad (1981) and Felgenhauer & Abele (1983) discussed the differences between the Dendrobranchiata and the other shrimp-like decapods, primarily the presence of dendrobranchiate gills, egg broadcasting and the pleonic hinges. Recently Martin et al. (2007) have demonstrated considerable variation in dendrobranch gill morphology. Following on from their study, we recommend that the other distinguishing characters should also be re-studied.

The separate status of the Stenopodidea has long been recognized and is supported by morphological and developmental studies (Felgenhauer & Abele 1983). With the exception of trichobranchiate gills, many of the proposed characters do exhibit some overlap with either Dendrobranchiata or Caridea. Nevertheless, all phylogenetic studies have supported their status as a separate lineage.

The internal classification of the Caridea and their relationship to the other lineages currently appears far from settled, although it is generally accepted that they do constitute a separate lineage (Burkenroad 1963; Felgenhauer & Abele 1983; Abele & Felgenhauer 1986). Of specific interest is the position of the family Procarididae, which remains controversial to date. Prior to the discovery of *Procaris* in 1972, Caridea were characterized by one or both of the two anterior pairs of legs being chelate (Burkenroad 1981), easily differentiating them from the other two lineages, which have the first three pairs nearly always chelate. *Procaris*, and the later discovered *Vetericaris*, not only are achelate but share a number of characters with the Dendrobranchiata (e.g., a well developed gastric mill, L-shaped mastigobranchs, and appendices internae absent) and with Caridea *sensu stricto* (phyllibranchiate gills, wide second abdominal pleuron). Much has been written on whether they should be considered a superfamily within the Caridea (Abele & Felgenhauer 1986; Abele 1991; Chace 1992; Holthuis 1993) or be considered a separate lineage. Felgenhauer & Abele (1983) were the first to address their position, and, although not based on a cladistic analysis, they considered them a separate lineage, branching off earlier than the Caridea. This was opposed by Christoffersen (1988) who, using manual parsimony, considered procaridids as a sister group to the Caridea. Using more objective computer-based methods, Abele & Felgenhauer (1986) reached the same conclusion and considered both taxa closely related, but they did not assign a formal rank to either clade. Bracken et al. (this volume) support the treatment of the Procaridoidea as a sister group to the remaining carideans on the basis of a phylogenetic analysis based on both mitochondrial and nuclear genes.

Both morphological (Dixon et al. 2003; Schram & Dixon 2004) and molecular (Porter et al. 2005) analyses support positioning of the shrimp-like decapods as the most basal clades within the Decapoda. However, the relationships of the three (or four) separate lineages to each other, and indeed to the other Decapoda, are far from settled. All phylogenetic analyses, be they morphological (Abele & Felgenhauer 1986; Dixon et al. 2003; Schram & Dixon 2004) or molecular (Porter et al. 2005), support positioning of the Dendrobranchiata as the most basal clade within the Decapoda. The position of the Stenopodidea and Caridea (including the Procaridoidea or not) remains

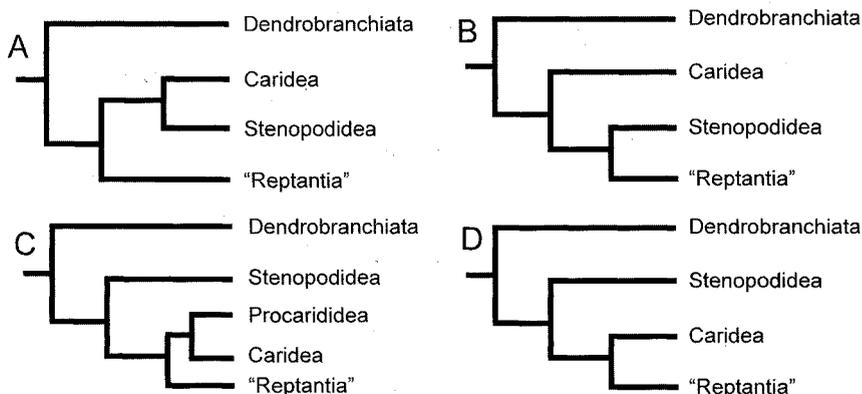


Figure 2. Position of the shrimp-like groups within the Decapoda according to (A) Burkenroad (1963), (B) Abele & Felgenhauer (1986), (C) Christoffersen (1988) and (D) Porter et al. (2005).

unsettled. Burkenroad (1963) regarded the Caridea + Stenopodidea as a sister group to the Reptantia (Fig. 2). On the basis of morphological cladistic analyses, two hypotheses have been put forward. Abele & Felgenhauer (1986) considered the Stenopodidea as a sister group to the reptant decapods, preceded by the branching off of the Caridea *sensu lato* (Fig. 2); in contrast, Christoffersen (1988) offered the reverse situation, and considered the Caridea + Procarididea as a sister group to the reptant decapods (Fig. 2). The molecular study by Porter et al. (2005), using representatives of all three shrimp-like taxa as well as a score of reptant taxa, resolved a caridean + reptant clade, but it was not statistically different from a stenopodidean + reptant clade (Fig. 2). Interestingly, a caridean + stenopodidean clade, as used by Burkenroad (1963, 1981), was rejected by their analysis (Porter et al. 2005). The analysis by Bracken et al. (this volume) indicates a position of the Stenopodidae within the Reptantia, which has been suggested before on the basis of larval development (see Seridji 1990, and references therein). Thus, the exact position of these two shrimp-like taxa in relation to the reptant decapods and indeed to each other remains debated.

From this brief overview, it is evident that more rigorous and more inclusive cladistic analyses are needed to resolve the position of the Caridea and Stenopodidea within the Decapoda.

3 PHYLOGENETIC RELATIONSHIPS WITHIN STENOPODIDEA

Saito & Takeda (2003) have published the only phylogeny within the Stenopodidea. Analyzing the family Spongicolidae, they used a morphological matrix composed of 38 characters of 32 species, which resulted in a consensus tree with mainly paraphyletic genera. The phylogeny shows a tendency from primitive "shallow water free living species" towards a more derived group of "deep water sponge-associated" species. All genera and nearly all species in this family are included in this phylogeny. Thus, about half of the genera and species for the infraorder as a whole have been subjected to a cladistic analysis.

4 PHYLOGENETIC RELATIONSHIPS WITHIN DENDROBRANCHIATA

In their excellent book on penaeoid and sergestoid shrimps, Pérez Farfante & Kensley (1997) recognized two superfamilies: the Penaeoidea and Sergestoidea, with the Sergestoidea consisting of two families and the Penaeoidea of five distinct families (Table 2). The position of the enigmatic genus *Lucifer* remains problematic (Tavares et al. this volume) due to its aberrant adult morphology. The relation between the two superfamilies has not been treated in any phylogenetic study to date.

Table 2. Number of genera and species in the suborder Dendrobranchiata (as of August 2008).

Superfamily	Family	Genera	Species
Penaeoidea	Aristeidae	9	26
	Benthescymidae	4	21
	Penaeidae	26	215
	Sicyoniidae	1	44
	Solenoceridae	9	80
Sergestoidea	Luciferidae	1	9
	Sergestidae	6	90
		56	505

Several phylogenies within the Penaeoidea have appeared in the last four decades (Mulley & Latter 1980; Palumbi & Benzie 1991; Tam & Chu 1993; von Sternberg & Motoh 1995; Baldwin et al. 1998; Tong et al. 2000; Quan et al. 2001; Maggioni et al. 2001; Quan et al. 2004; Lavery et al. 2004; Vazquez-Bader et al. 2004; Voloch et al. 2005; and Chan et al. 2008); however, the relationships within Sergestoidea have not been examined.

Phylogenetic relationships among the five penaeoid families were tackled by Vazquez-Bader et al. (2004), using a partial sequence of about 300 bps of the 16S mitochondrial gene. Their results support monophyly of the superfamily, but they show the Penaeidae to be paraphyletic with regard to the closely related Solenoceridae. This was confirmed by Voloch et al. (2005) using the two mitochondrial markers 16S and COI, although the separate family status of Aristeidae, Benthescymidae, and Sicyoniidae was questioned, as they form a compact group separated by small genetic distances. These somewhat preliminary results require confirmation based upon more conservative markers, as already acknowledged by Voloch et al. (2005) themselves.

All other phylogenetic studies within the superfamily deal with the family Penaeidae. Crosnier (1987, 1991, 1994a, 1994b) revised the genus *Metapenaeopsis*. He proposed a grouping primarily based on the morphology of the petasma and a subgrouping based on the presence/absence of a stridulating organ. A preliminary phylogeny of selected species within this genus (based on mitochondrial markers) published by Tong et al. (2000) confirms the views of Crosnier. All other studies have focused on the generic division proposed by Pérez Farfante & Kensley (1997), which was, and is, debated by both the fishing industry and the scientific community (Flegel 2007; McLaughlin et al. 2008). An overview of molecular research on this topic was published by Dall (2007). He concluded that some of the genera recognised by Pérez Farfante & Kensley (1997) are not monophyletic with regards to the molecular markers used in other analyses (e.g., *Penaeus* and *Melicertus*). More studies using nuclear genes are needed to elucidate the systematic position of these genera and their constituent species groups. In a recent contribution, Chan et al. (2008) studied the phylogenetic relationships of 20 genera of the 26 recognized by Pérez Farfante & Kensley (1997), supporting Burkenroad's (1983) original three-tribe scheme (Peneini, Parapeneini, and Trachypeneini) and synonymizing the genus *Miyadiella* with *Atypopenaeus*. Within the Penaeidae nearly all genera and just over 20% of the species have been the subject of phylogenetic analyses. See also Tavares et al. (this volume) for a preliminary morphological analysis of penaeoid families and genera.

5 PHYLOGENETIC RELATIONSHIPS WITHIN CARIDEA

The internal classification of the Caridea by Chace (1992) and Holthuis (1993), which is largely followed by Martin & Davis (2001), is widely used today (Table 3). Minor recent changes are the addition of the family Pseudocheilidae (De Grave & Moosa 2004) and the non-recognition of the

Table 3. Number of genera and species in the suborder Dendrobranchiata (as of August 2008).

Superfamily	Family	Genera	Species
Procaridoidea	Procarididae	2	6
Galatheacaridoidea	Galatheacarididae	1	1
Pasiphaeoidae	Pasiphaeidae	7	97
Oplophoroidea	Oplophoridae	10	73
Atyoidea	Atyidae	40	395
Bresilioidea	Agostocarididae	1	3
	Alvinocarididae	6	18
	Bresiliidae	3	9
	Disciadidae	3	10
	Pseudochelidae	1	3
Nematocarcinoidea	Eugonatonotidae	1	2
	Nematocarcinidae	4	44
	Rhynchocinetidae	2	24
	Xiphocarididae 1	2	
Psalidopodoidea	Psalidopodidae	1	2
Stylodactyloidea	Stylodactylidae	5	33
Campylonotoidea	Bathypalaemonellidae	2	11
	Campylonotidae	1	5
Palaemonoidea	Anchistoididae	1	4
	Desmocarididae	1	2
	Euryrhyndidae	3	6
	Gnathophyllidae	5	13
	Hymenoceridae	2	3
	Kakaducarididae	3	3
	Palaemonidae	116	876
	Typhlocarididae	1	3
Alpheoidea	Alpheidae	43	614
	Barbouriidae	3	6
	Hippolytidae	36	302
	Ogyrididae	1	10
Processoidea	Processidae	5	66
Pandaloidea	Pandalidae	23	189
	Thalassocarididae	2	4
Physetocaridoidea	Physetocaridae	1	1
Crangonoidea	Crangonidae	22	190
	Glyphocrangonidae	1	77
		360	3108

Mirocarididae. Studies dealing with phylogenetic relations among the superfamilies and families are scarce. Christoffersen's (1987, 1988, 1989, 1990) contributions, using manually constructed phylogenies, indicate the non-monophyletic nature of the traditional classification. The first comprehensive molecular phylogeny of the group is presented by Bracken et al. (this volume), and suggests polyphyletic and paraphyletic relationships among genera within the families Atyidae, Pasiphaeidae, Oplophoridae, Hippolytidae, Gnathophyllidae, and Palaemonidae. Phylogenetic research has

been carried out on 7 of the 36 families within the Caridea, amounting to less than perhaps 3-4% of all species. Christoffersen performed manual and computerized morphological cladistic analyses among the hippolytid (1987), crangonid (1988), and pandaloid (1989) genera.

Within the predominantly freshwater family Atyidae, molecular studies on selected species within genera like *Paratya* (Page et al. 2005; Cook et al. 2006), *Troglocaris* (Zaksěk et al. 2007), and *Caridina* (Chenoweth & Hughes 2003; Roy et al. 2006; Page et al. 2007; von Rintelen et al. 2007a, b) in relation to biogeographical issues, as well as the regional study of several genera by Page et al. (2008), have been published.

The phylogenetic relationships among the deep-sea hydrothermal vent shrimp belonging to the Alvinocarididae were analyzed by Shank et al. (1998) using the COI mitochondrial gene. Their molecular phylogeny is consistent with the higher-level taxonomy based on morphology, and demonstrates that the Alvinocarididae form a monophyletic group in relation to the outgroup shrimp taxa used.

A morphological hypothesis about the phylogenetic relationships within the Palaemonoidea (currently containing 910 species) was presented by Pereira (1997), who concluded that both the superfamily Palaemonoidea and the family Palaemonidae (*sensu* Chace 1992) are natural groups, but that a rearrangement of palaemonid subgroups would better reflect their phylogenetic relationships. However, if the classification of Martin & Davis (2001) were to be superimposed upon Pereira's cladogram, the Palaemonidae (*sensu* Martin & Davis 2001) become paraphyletic. Pereira (1997) also indicated that several genera in the subfamily Palaemoninae, such as *Macrobrachium*, *Cryphiops*, *Palaemon*, *Palaemonetes*, and *Pseudopalaemon*, are paraphyletic. The subfamily Pontoniinae remains monophyletic in his view, although several genera, now included in the Palaemoninae (e.g., *Brachycarpus*, *Leander*, *Leandrites*), should be transferred to the Pontoniinae. Page et al. (2008) showed the genera *Kakaducaris* and *Leptopalaemon* (currently in the family Kakaducarididae) as a strongly supported clade within the Palaemoninae that is closely related to the genus *Macrobrachium*. This result is confirmed by Bracken et al. (this volume).

Recent work by Mitsuhashi et al. (2007), using the nuclear 18S rRNA and 28S rRNA genes, showed the families Hymenoceridae and Gnathophyllidae to be closely related and nested within the Pontoniinae, which is also confirmed by the study of Bracken et al. (this volume). This clade is clearly distinct from the clade with representatives of the Palaemoninae, in accordance with the relationships among the families as suggested by larval characters (Bruce 1986; Yang & Ko 2002). A review of the literature on the first zoea shows that the characters suggested by Yang & Ko (2002) to separate palaemonine and pontoniine genera hold true except for five genera: *Leander*, *Leandrites*, *Harpilius*, *Kemponia*, and *Philarius*. Such a shift of several genera from the Palaemoninae to the Pontoniinae is in line with the ideas put forward by Pereira (1997). Future molecular work including representatives of these genera should elucidate the boundaries between the Pontoniinae and Palaemoninae and their relationship to the other palaemonoid clades, including the Anchistioididae, with its peculiar larval development.

Within the Pontoniinae, a phylogeny of 72 genera based on 80 morphological characters was published by Li and Liu (1997). They regard the subfamily, as currently defined, to be a monophyletic group but suggest that the status of some newly erected genera should be reexamined. They further conclude that commensal Pontoniinae are evolved from free-living Palaemoninae, and they propose the genus *Periclimenes* to be the evolutionary link between free-living and commensal taxa. As currently much taxonomic work is focused around the paraphyletic genus *Periclimenes sensu lato*, this conclusion seems premature. Fransén (2002) published a morphological phylogeny of the genus *Pontonia* s.l., splitting the genus into six genera, with species in these genera associating either with bivalves or ascidians. Molecular work on selected genera using 16S and COI mitochondrial genes in relation to certain host groups is in progress, providing building blocks for a molecular phylogeny within this subfamily.

Within the Palaemoninae, several phylogeographical studies on *Macrobrachium rosenbergii* have been published in recent years by de Bruyn and coworkers (2004a, 2004b, 2005, 2007). Additionally, Murphy & Austin (2002, 2004) studied the origin and classification of Australian species of *Macrobrachium* using the 16S gene.

Anker et al. (2006) presented the first phylogenetic hypothesis of relationships among 36 extant genera of alpheid shrimps based on a cladistic analysis of 122 morphological characters from 56 species. In that study there is strong support for the monophyly of the family. Nodes defining genera were relatively well supported, though many basal nodes showed weak support. Six genera appeared paraphyletic, the large genus *Alpheus* (276 species) being amongst these. As suggested by the authors, the remaining uncertainties in the phylogenetic relations among the genera would benefit from tests with independent larval and molecular data.

Molecular phylogenies of alpheids also have been produced as a component of studies on eusociality among species of *Synalpheus* by Duffy et al. (2000) and Morrison et al. (2004). Williams et al. (2001) used one mitochondrial (COI) and two nuclear genes (GPI, EF-1 α) to analyze the status of the 7 morphological groups within the genus *Alpheus* recognized by Coutière (1905). This analysis showed the existence of three major clades within the genus; these clades showed no particular relationship to the groupings of Coutière (1905). Finally, a morphological phylogeny of the genus *Athanopsis* was presented by Anker & Ahyong (2007).

6 MORPHOLOGICAL CHARACTERS

The monophyly of both the Dendrobranchiata and the Stenopodidea is uncontroversial and is supported by several characters, of which the following can be considered to be of phylogenetic significance: the dendrobranchiate gill, male petasma, naupliar egg eclosion, and pleonic hinge structure in the Dendrobranchiata (Felgenhauer & Abele 1983; Abele & Felgenhauer 1986; Abele 1991; Dixon et al. 2003); and the enlarged third pereopod and spherical spermatozoa in the Stenopodidea (Felgenhauer & Abele 1983; Abele & Felgenhauer 1986; Abele 1991; Dixon et al. 2003). As Martin et al. (2007) recently described considerable variation in dendrobranch gill morphology, a fresh look at some of the generally accepted characters may reveal further incongruities.

The monophyly of the Caridea is harder to address, as it is based on a large number of variable morphological characters (Felgenhauer & Abele 1983). Bracken et al. (this volume) consider the taxon as monophyletic, but perhaps excluding Procarididae. The true position of the family Procarididae, although unquestionably closely related to other carideans, remains unresolved. Procaridids share only one character with the other caridean families, the second abdominal pleuron overlapping the first and third somites, which is however variable in Glyphocrangonidae and Psalidopodidae. Procaridids differ from carideans in the attachment position of the phyllobranch gills, which is precoxal in *Procaris* versus higher on the body wall in Caridea, whereas other characters are similar to Dendrobranchiata (e.g., the foregut; see Felgenhauer & Abele 1983).

Currently the family level classification of Caridea is based primarily on the structure of the propodus and dactylus of the first two pereopods, non- or multi-articulated carpus of the second pereopod, features of the mandible, second and third maxilliped, and the number of epipods and branchial formula (Chace 1992; Holthuis 1993). Although these characters are of considerable use in the identification of Caridea, their phylogenetic significance at the family level appears uncertain. It is far beyond the current review to highlight all discrepancies, and we can only discuss a few salient ones. The chelae of carideans come in a bewildering variety of shapes and sizes, ranging from the relatively unspecialised examples in Palaemoninae, Processidae, and Pandalidae (the latter two with a multiarticulated carpus) to the specialized structures in Alpheidae, Atyidae, and Disciidae, the homologies of these structures remaining unclear. Burkenroad (1981) proposed that the plesiomorphic gill formula in Caridea is one arthrobranch and one pleurobranch on thoracic segments 3 to 7, which is reduced in various ways to a minimum formula of a single pleurobranch each on thoracic segments 4 to 7, considered the most derived condition (Bauer 2004). However, within

families there exists much variation in this character, especially in the Atyidae, and its phylogenetic usefulness remains to be proven.

Several authors (Thompson 1967; Felgenhauer & Abele 1983; Christoffersen 1990; Bauer 2004) have offered their opinion on which characters could be phylogenetically useful. Thompson (1967) placed much emphasis on the mandible, considering a fused molar and incisor process, combined with a 3-segmented palp, to be ancestral. Although there exists considerable variation at the generic level in some families, this could indeed be a valuable phylogenetic character. Felgenhauer & Abele (1983) and Abele & Felgenhauer (1986) discussed the protocephalon, pleonic hinges, and the gastric mill. These characters also may prove to be of value, but a survey of their variation across all families is still lacking. Christoffersen (1990) used a combination of previously highlighted characters (e.g., mandible, telson armature), with a score of "new" characters (e.g., corneal ocellus, bifid dorsal carina on the third abdominal somite, and a distolateral tooth on the basicerite) in his new superfamily/family arrangement. Many of Christoffersen's characters do, however, appear to be of low phylogenetic value. Finally, Bauer (2004) reviewed some of the above characters and emphasized the mandible, first to third maxillipeds, first and second pereopods, pereopodal exopods, gills, and the mastigobranch-setobranch complex. Currently, there is not enough information on the evolutionary polarity and indeed on even the mere occurrence of many of these characters across (and within) all families to address their phylogenetic usefulness, although work on this is now in progress by one of the authors.

7 MOLECULAR MARKERS

Several mitochondrial genes have been used for phylogenetic studies of shrimp-like decapods. Cytochrome C Oxidase Subunit I (COI) is a protein coding gene that has been used in more than 30 studies. COI is especially informative at low taxonomic levels with good resolution among populations of a species and sometimes at the family level. The protein coding gene Cytochrome B has been used in a few studies at the species and infraspecific levels of, for instance, *Typhlatya* (Webb 2003; Hunter et al. 2008). The non-protein coding 16S ribosomal RNA (16S) gene is slightly more conservative than COI with good resolution at species to family levels. The 12S ribosomal RNA (12S) gene has been applied to study infraspecific variation in a penaeid species (Palumbi & Benzie 1991; Bouchon et al. 1994). The complete mitochondrial genome of 6 shrimps has been sequenced: *Penaeus monodon* by Wilson et al. (2000), *Marsupenaeus japonicus* by Yamauchi et al. (2004), *Litopenaeus vannamei* by Xin Shen et al. (2007), *Fenneropenaeus chinensis* by Xin Shen et al. (2007), *Macrobrachium rosenbergii* by Miller et al. (2005), and *Halocaridina rubra* by Ivey & Santos (2007). As only a few complete mitochondrial sequences of species from different higher taxa are yet available, phylogenetic analyses have been performed only on these taxonomic levels.

Nuclear genes have been applied in a few phylogenetic studies of shrimp-like decapods so far. The following protein coding genes have so far been used: Myosin Heavy Chain (MyHC) for cryptic diversity and phylogeography in an *Alpheus* species-complex (Mathews, 2006); Glucose-6-phosphate isomerase (GPI) to analyze the status of the species-groups within the genus *Alpheus* (Williams et al. 2001); Elongation factor-1 α (EF-1 α) for infraspecific variation in penaeid species (Duda & Palumbi 1999; France et al. 1999); and the analysis of *Alpheus* species-groups (Williams et al. 2001). Histone H3 was used by Porter et al. (2005) in combination with 3 other genes for the elucidation of phylogenetic relations among the higher Decapod taxa. Non-coding nuclear genes used are: Internal Transcribed Spacer (ITS), applied in analysis of infraspecific variation in penaeid species (Chu et al. 2001; Wanna et al. 2006); 18S ribosomal DNA gene, used at higher taxonomic levels among families to orders (Kim & Abele 1990; Porter et al. 2005; Mitsuhashi et al. 2007; Bracken et al. this volume); and the 28S ribosomal DNA gene, also used at higher taxonomic levels (Porter et al. 2005; Mitsuhashi et al. 2007), although Zaksčik et al. (2007) used it within the cave-shrimp genus *Troglocaris*.

8 FOSSILS

The fossil record of the shrimp-like decapods is particularly scant, due to their poorly calcified exoskeleton and perhaps also to their mode of life. Of the three groups, the Dendrobranchiata has the best fossil record with 74 fossil taxa known. Examples of extant families extend only as far back as the lower Cretaceous (100 mya), but the extinct Aegeridae range from the upper Triassic to the upper Jurassic, and a few species of the extinct Carpopenaeidae are present in the mid-Cretaceous. Two families of Stenopodidea contain a single extinct species each, both of lower Cretaceous age, one of which is a freshwater form. The Caridea have an extraordinarily poor fossil record, with a mere 46 extinct species compared to more than 3100 extant taxa. Taxa positively assigned to extant families occur only from the lower Cretaceous and later. In contrast to these confirmed ages, Porter et al. (2005) estimate the origin of the Dendrobranchiata to be in the early Silurian (437 mya) and the origin of the Caridea to be in the Devonian (417–423 mya), leaving a considerable gap in the historical record between the appearance of fossils and the estimated origin of the major lineages.

Although a good proportion of fossil taxa can be placed confidently within extant families, several remain enigmatic. This is particularly the case in the Caridea, with 9 fossil genera unplaced within any recent family, whilst the Udorellidae cannot be assigned to a superfamily (Crandall et al. in prep.). Interestingly, the achelate first and second pereopods of the Udorellidae have led to speculation that they are related to the Procarididae (Abele & Felgenhauer 1983).

Several positively assigned fossil taxa exhibit features that are not present in modern-day lineages. For instance, the Carpopenaeidae, currently assigned to the Dendrobranchiata, harbor a multiarticulate carpus on the second and third pereopods. Equally incongruous, the recently erected caridean superfamily Pleopteryxoidea (erected for *Pleopteryx kuempeli*) differs from all known carideans by the multiarticulate first pereopod combined with achelate second pereopods (Schweigert & Garassino 2006).

A robust, combined cladistic analysis of extant and extinct taxa in the shrimp-like decapods currently appears difficult to achieve, as classification of extant forms is largely based on rarely fossilized structures such as mouthparts, epipods, and gill structure/formulae (Holthuis 1993). Such studies are further hindered by the current lack of a robust phylogeny for the extant forms themselves. When a robust phylogeny of recent forms does become available, it would be instructive to pursue experimental analyses akin to Schram & Dixon (2004), by incorporating selected fossil taxa. Certainly, Solnhofen-type taxa (the origin of many fossil shrimp) may be of sufficient preservation status to circumvent the “vraagteken effect” (see Schram & Hof 1998). Equally, the addition of characters lacking in extant taxa may shed light on evolutionary pathways, whilst the addition of non-extant ecological niches (such as the freshwater Dendrobranchiata and Stenopodidea) could contribute interesting information.

9 CONCLUSION

This overview shows that relatively few representatives of shrimp-like decapod taxa thus far have been incorporated into phylogenetic analyses at higher to lower taxonomic levels and that controversies remain between the outcomes of various morphological and molecular analyses.

A survey of many morphological characters across (and within) families is sorely needed. These surveys should target characters previously suggested to be of phylogenetic importance, such as the mandible, the mastigobran- setobran complex, and pleonic hinges, but they should also include other characters known to vary among genera and families, such as the carpo-propodal brush and the setal brush on the fifth pereopod in carideans. Additionally, the homology of certain characters needs to be put on a firmer footing, such as the L-shaped mastigobran in Dendrobranchiata, Procarididae, and basal Caridea. Certain characters have been dismissed as being of phylogenetic value and should be re-appraised, including the structure of the gastric mill. This structure is generally assumed to be lacking in all carideans, but Felgenhauer & Abele (1983) discuss its occurrence in

several families. Comparative morphological studies across all taxa, both at the family level within the Caridea and across all shrimp-like taxa, are urgently needed for morphological phylogeny to progress and to keep pace with the predictable flood of molecular phylogenies.

Currently, molecular phylogenetic work lags behind the amount of effort devoted to the Brachyura, but it is rapidly gaining momentum, with a score of new studies appearing in print each year. Nevertheless, the range of taxa included in molecular work, and their systematic breadth and scope, must be further expanded.

In other decapod groups, an interesting body of literature exists on various systematically informative biological attributes, such as larval development, spermatozoan ultrastructure, and even evo-devo processes. Works of this nature in shrimp-like Decapoda are few and far between. These will need to be integrated with molecular and morphological studies, underpinned by continued morphological studies, in order for the decapod Tree of Life to fully embrace available technologies for integrative systematics.

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