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Decapod Crustacean Phylogenetics

edited by

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The Bearing of Larval Morphology on Brachyuran Phylogeny

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ABSTRACT

Obtaining all developmental stages from an ovigerous decapod female is common in the laboratory. This is a significant advance for larval taxonomic studies, morphological descriptions, systematics, phylogenetics and evolutionary theory. Yet for such studies reliable data must be founded on quality observations and interpretation of setotaxy using a modern high-powered microscope equipped with differential interference contrast. Incorrect setal counts are problematic, especially since first-stage zoeas of congeneric brachyuran species appear to have identical setotaxy. This similarity provides such a high degree of predictability within a taxon that setal differences (incongruence) in a group may suggest incorrect assignment of taxa. However, relationships based on differences and similarities are not necessarily founded on shared derived characters, and instead may be supported by symplesiomorphies. The methodology involved in larval phylogenetics is also problematic. For example, oligomerization is considered to be an evolutionary trend within Crustacea. Decapod larval development suggests that heterochronic processes may provide a dominant evolutionary mechanism influencing loss of characters. Although using an unordered transformation series in a phylogenetic analysis is acknowledged to generate the most parsimonious trees, such an assumption does not necessarily represent a linear evolutionary pathway towards gradual terminal delay of characters as postulated by heterochrony for decapod larvae. A mosaic of heterochronic processes provides a complex evolutionary mechanism influencing oligomerization (reduction and loss) within brachyuran zoeae. This is best captured in a phylogenetic analysis by using "irreversible-up" (terminal delay, not terminal addition) transformation series. Reconstruction of trees using this assumption about character evolution generates longer trees and frequently involves more evolutionary steps to compensate for homoplasy. Yet there is evidence to suggest that homoplasy is common within many brachyuran larval lineages. Nonetheless, larval phylogenetics does appear to have advantages since all decapod zoeal stages are adapted to a planktonic existence, and therefore setal patterns are subject to similar selection pressures. Morphological differences among larvae may provide additional phylogenetic information as compared to possibly convergent adult characters that are more the product of the interaction between genotype and environment.

1 WHY STUDY LARVAE?

Historically, decapod systematics has been established on the basis of adult morphology, but these phenotypic characters are the end product of the interaction between genotype and environment. Consequently, relationships within and between taxa may be postulated on convergence between adults. Another valuable and often-overlooked source of information is the morphology of decapod larvae. Larvae are adapted to the same habitat, a uniform planktonic environment, and as such setal patterns should be subjected to more or less constant selection pressures. Therefore, larval characters may reflect relationships better than the morphology of the adults (see Williamson 1982; Rice 1980; Felder et al. 1985).

The majority of decapod larval studies have addressed relationships within the Brachyura, and these have been based mostly on zoeal characters. As with the adults, larval relationships have normally been established on similarity and difference of morphologically features (e.g., Rice 1980; Martin 1984; Martin et al. 1985; Felder et al. 1985; Ng & Clark 2000; Clark & Ng 2006). But relationships founded on similarities among taxa may be based on ancestral characters and not necessarily those that are shared and derived. With this in mind, several studies have conducted phylogenetic analyses of zoeal characters with a view to confirming or testing relationships based primarily on adult morphology (e.g., Rice 1980; Clark 1983; Clark & Webber 1991; Marques & Pohle 1998; Ng & Clark 2001; Clark & Guerao 2008).

The purpose of this paper is to use a restricted set of data associated with brachyuran (mostly pilumnoid) zoeal stages to review some of the problems identified with constructing phylogenies using setotaxy. The study also aims to show that phylogenetic analysis of Xanthoidea and Pilumnoidea zoeal characters can provide a new insight into a classification traditionally founded on adult convergent morphology.

2 COLLECTING LARVAE

Rearing decapod larvae was once considered difficult, but the use of *Artemia* nauplii as a food source has opened up the field. All aspects of larval biology, including biochemistry, ecology, endocrinology, growth, metabolism, moulting, physiology, ultrastructure and other topics (see Anger 2001 for details) can now be more easily studied. Obtaining all developmental stages from an ovigerous female is now common in the laboratory. This is a significant advance for descriptive studies (alpha taxonomy), systematics, phylogenetics and evolutionary theory. However, larval rearing is not without its disappointments and failures. Collecting ovigerous target species still depends on sampling effort and a measure of luck; success is never guaranteed. Once the specimens are safely ensconced in a constant temperature room, rearing is time-consuming, requiring dedication and discipline to see it through to completion. Even then, for no apparent reason, larval cultures occasionally crash. These frustrations aside, there are distinct advantages to rearing larvae in the laboratory as opposed to studying plankton-collected material, such as collecting all life stages with verification from exuvia, providing sufficient specimens for morphological studies, and confirming the identification of the larvae by examining the spent female. The ability to positively identify the species is the distinct advantage that laboratory-reared material has over describing plankton-caught larvae. Confident identification of such larvae to species level is still problematic (e.g., the third and fourth zoeal stages of crab larvae from Atlantic Seamounts described by Rice & Williamson 1977 are still unidentified).

3 SETAL OBSERVATIONS

After completing the task of laboratory rearing, many larval morphologists proceed to produce poor descriptions, typically by missing increasing numbers of setal characters during zoeal development. Reliable data are everything, and setotaxy must be founded on high-quality observations and interpretation. Although Rice (1979) and Clark et al. (1998a) made pleas for improved standards in descriptions of crab zoeas, some studies are still inadequate. Zoeal and megalopal characters are still being either overlooked or ignored, for example, the development of the third maxilliped through successive zoeal moults. This situation must be resolved if there is to be progress in brachyuran larval research. A modern-day high-powered microscope equipped with differential interference contrast (DIC) is fundamental to these studies if setal ambiguities are to be resolved. Using lesser microscopes is inadequate for modern larval studies. Additionally, some larval characters, such as the endopod spine on the antennal protopod of xanthoid larvae, may be resolved only by using a scanning electron microscope.

4 ZOEAL SIMILARITY

Brachyuran first-stage zoeas of congeneric species appear to have virtually identical setotaxy (Christiansen 1973; Clark 1983, 1984; Ng & Clark 2000). This similarity provides a high degree of predictability within a taxon. Setal differences (incongruence) within a group suggest incorrect assignment of taxa and lack of systematic compatibility. For example, the first stage zoeas of *Chlorodiella nigra* (Forskøal, 1775), *Cyclodius monticulosus* (Dana, 1852), *Pilodius areolatus* (H. Milne Edwards, 1834), *Pilodius paumotensis* Rathbun, 1907 and *P. pugil* Dana, 1852 are similar, if not identical, in terms of setotaxy. Their zoeas cannot be identified to species level. An example shows the usefulness of this similarity: Serène (1984), based on adult features, felt that *Chlorodiella bidentata* (Nobili, 1901) did not belong in *Chlorodiella* and should perhaps be referred to its own genus within the Chlorodiinae Alcock, 1898 (now Chlorodiellinae Ng & Holthuis, 2007). If the hypothesis of Serène (1984) were correct, then the first-stage zoeas of *C. bidentata* would possess a setotaxy identical to those of the other species assigned to the subfamily. According to Ng and Clark (2000), this was not the case. In fact, based on larval characters, especially the antenna, Ng & Clark (2000, table 6) showed that *C. bidentata* was not even a xanthid but a member of the Pilumnidae (now Pilumnoidea Samouelle, 1819; see Ng et al. 2008).

According to Clark & Ng (2004b) there were 72 genera and 408 species of Pilumnoidea known, and of these the zoeas of approximately 30 species (Table 1) are described. The pilumnoid zoeal antenna is a conservative character in that, except for the development of the endopod, its morphology remains unchanged with successive moults and defines all species attributed to this superfamily. It is characteristic of all 30 species listed in Table 1. According to Martin's (1984: 228, Fig. 1H) definition of xanthid group II, pilumnids are characterized by an acutely tipped antennal exopod, about equal in length to or slightly longer than the protopod, armed with small spinules distally, and with a prominent outer seta about halfway along its length; additionally, the antennal protopod is usually longer than the rostrum. However, Martin overlooked a second smaller medial seta on the exopod. Two medial setae on the antennal exopod are diagnostic of this family (Fig. 1A). Furthermore, the exopod is distally bilaterally spinulate, as is the protopod. Interestingly, the antenna exopod of *Aniptumnus quadridentatus* (De Man, 1895) (Fig. 1B) is more elongate than in the other pilumnoids described, but it still retains the two medial setae.

Eumedonic crabs provide another example. Adult eumedonids are associates of echinoderms. Many brachyuran systematists have found their morphology confusing, resulting in their placement in various families, including the Majidae, Parthenopidae, Xanthidae, Pilumnidae, Trapeziidae, Portunidae, Pinnotheridae and Eumedonidae. Ng & Clark (2001) considered the first-stage zoeas of five eumedonid species: *Echinoecus pentagonus* (A. Milne Edwards, 1879), *Harrovia albolineata* Adams & White, 1849, *Permanotus purpureus* (Gordon, 1934), *Rhabdonotus pictus* A. Milne Edwards, 1879 and *Zebrida adamsii* White, 1847. All five possessed the same type of antenna (as in Fig. 1A). On similarity of the zoeal antenna, Ng & Clark (2001) challenged the validity of the Eumedonidae as a distinct (e.g., Martin & Davis 2001) family and suggested that these cryptic crabs were in fact pilumnoids. Their study of eumedonid first-stage zoeas is a classic example of larvae setal patterns resolving the classification of a difficult group of brachyuran species that was previously based on deceptive adult morphology.

Comparisons based on differences and similarities of morphology are of interest because they provide an expectancy (predictability) that the first-stage zoeas of closely related species will share a suite of characters. However, these characters are not necessarily shared derived characters, and therefore relationships founded on similarities among taxa may be based on symplesiomorphic characters.

Table 1. References to descriptions of larvae in the brachyuran family Pilumnidae.

Species	Reference	Stage	Remarks
Actumnus setifer (de Haan, 1835)	Aikawa 1937	ZI	
Actumnus setifer (de Haan, 1835)	Clark & Ng 2004b	ZI-ZIII, Meg.	
Actumnus squamosus (de Haan, 1835)	Terada 1988	ZI-IV, Meg.	
Aniptumnus quadridentatus (De Man, 1895)	Ng 2002	ZI	
Aniptumnus quadridentatus (De Man, 1895)	Ng & Clark 2008	ZI	
Benthopanope eucratoides (Stimpson, 1858)	Lim et al. 1986	ZI-III, Meg. as	*Pilumnopeus eucratoides*
Benthopanope indica (De Man, 1887)	Takeda & Miyake 1968	ZI	as *Pilumnopeus indicus*
Benthopanope indica (De Man, 1887)	Terada 1980	ZI-IV	as *Pilumnopeus indicus*
Benthopanope indica (De Man, 1887)	Ko 1995	ZI-IV, Meg.	
Galene bispinosa (Herbst, 1794)	Mohan & Kannupandi 1986	ZI-IV, Meg.	
Halimede fragifer de Haan, 1835	Terada 1985	ZI-II	
Heteropanope glabra Stimpson, 1858	Aikawa 1929	ZI	
Heteropanope glabra Stimpson, 1858	Lim et al. 1984	ZI-IV, Meg.	
Heteropanope glabra Stimpson, 1858	Greenwood & Fielder 1984a	ZI-IV, Meg.	
Heteropilumnus ciliatus (Stimpson, 1858)	Takeda & Miyake 1968	ZI	
Heteropilumnus ciliatus (Stimpson, 1858)	Ko & Yang 2003	ZI-III	
Latopilumnus conicus Ng & Clark, 2008	Ng & Clark 2008	ZI	
Lobopilumnus agassizi Stimpson, 1871	Lebour 1950	ZI	
Pilumnopeus granulata Balss, 1933	Ko 1997	ZI-IV, Meg.	
Pilumnopeus makianus (Rathbun, 1929)	Lee 1993	ZI-IV	
Pilumnopeus serratifrons (Kinahan, 1856)	Wear 1968	ZI	
Pilumnopeus serratifrons (Kinahan, 1856)	Greenwood & Fielder 1984b	ZI-III	
Pilumnopeus serratifrons (Kinahan, 1856)	Wear & Fielder 1985	ZI	
Pilumnus dasypodus Kingsley, 1879	Sandifer 1974	ZI-IV, Meg.	
Pilumnus dasypodus Kingsley, 1879	Bookhout & Costlow 1979	ZI-IV, Meg.	
Pilumnus hirtellus (Linnaeus, 1761)	Williamson 1915	ZI	
Pilumnus hirtellus (Linnaeus, 1761)	Boraschi 1921	ZI,	
Pilumnus hirtellus (Linnaeus, 1761)	Lebour 1928	ZI-IV, Meg.	
Pilumnus hirtellus (Linnaeus, 1761)	Bourdillon-Casanova 1960	ZI	
Pilumnus hirtellus (Linnaeus, 1761)	Salman 1982	ZI-IV, Meg.	

Table 1. continued.

Species	Reference	Stage	Remarks
Pilumnus hirtellus (Linnaeus, 1761)	Ingle 1983	Meg.	
Pilumnus hirtellus (Linnaeus, 1761)	Ingle 1991	ZI-IV, Meg.	
Pilumnus hirtellus (Linnaeus, 1761)	Ng and Clark 2000	ZI	
Pilumnus hirtellus (Linnaeus, 1761)	Clark 2005	ZI-IV	
Pilumnus kempi Deb, 1987	Siddiqui & Tirmizi, 1992	ZI-II, Meg.	
Pilumnus lumpinus Bennett, 1964	Wear 1967	Meg.	
Pilumnus lumpinus Bennett, 1964	Wear & Fielder 1985	?ZI Meg.	
Pilumnus longicornis Hilgendorf, 1879	Prasad & Tampi 1957	ZI	
Pilumnus longicornis Hilgendorf, 1879	Hashmi 1970	?ZI	
Pilumnus longicornis Hilgendorf, 1879	Clark & Paula 2003	ZI	
Pilumnus minutes de Haan, 1835	Aikawa 1929	ZI	
Pilumnus minutes de Haan, 1835	Terada 1984	ZI-IV	
Pilumnus minutes de Haan, 1835	Ko 1994b	ZI-IV	
Pilumnus minutes de Haan, 1835	Ko 1997	Meg.	
Pilumnus novaezealandiae Filhol, 1885	Wear 1967	Meg.	
Pilumnus novaezealandiae Filhol, 1885	Wear & Fielder 1985	Meg.	
Pilumnus sayi Rathbun, 1897	Bookhout & Costlow 1979	ZI-IV, Meg.	
Pilumnus scabriusculus Adams & White, 1849	Terada 1990	ZI-IV	
Pilumnus sluiteri De Man, 1892	Clark & Ng 2004a	ZI-II, Meg.	
Pilumnus trispinosus (T. Sakai, 1965)	Terada 1984	ZI-IV	as *Parapilumnus trispinosus*
Pilumnus trispinosus (T. Sakai, 1965)	Quintana 1986	Meg.	as *Parapilumnus trispinosus*
Pilumnus trispinosus (T. Sakai, 1965)	Ko 1994a	ZI-IV, Meg.	as *Parapilumnus trispinosus*
Pilumnus vespertilio (Fabricius, 1793)	Aikawa 1929	ZI	
Pilumnus vespertilio (Fabricius, 1793)	Lim & Tan 1981	ZI-III, Meg.	
Pilumnus vespertilio (Fabricius, 1793)	Terada 1990	ZI-III	
Pilumnus vespertilio (Fabricius, 1793)	Clark and Paula 2003	ZI	
Pilumnus vestitus Haswell, 1882	Hale 1931	Meg.	
Tanaocheles bidentata (Nobili, 1901)	Ng & Clark 2000	ZI	

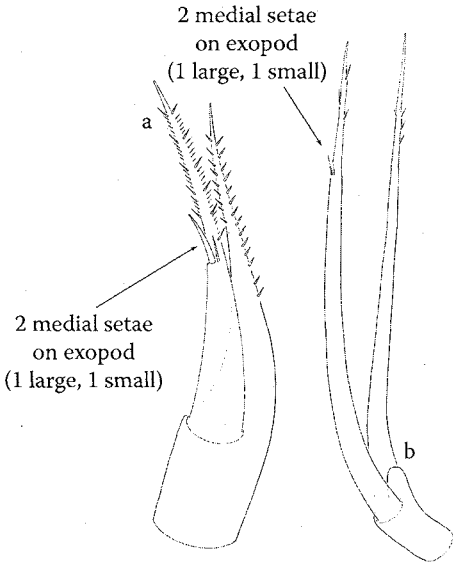

Figure 1. Diagnostic characters of the pilumnoid antenna, first-stage zoea. (A) *Pilumnus hirtellus*. (B) *Aniptumnus quadridentatus*.

5 HETEROCHRONY

Clark (2001) analyzed patterns in setotaxy and segmentation associated with abbreviated zoeal development in three higher taxa of brachyuran crabs — two portunids, two xanthoids and a number of majids — with different numbers of larval stages. Included were laboratory-reared larvae of species with six zoeal stages [*Charybdis helleri* (A. Milne Edwards, 1867) by Dineen et al. 2001], five stages [*Liocarcinus arcuatus* (Leach, 1814) by Clark 1984], four stages [*Lophozozymus pictor* (Fabricius, 1798) by Clark & Ng 1998], three stages [*Actumnus setifer* (de Haan, 1835) described later by Clark & Ng 2004b], and two stages [*Macrocheira kaempferi* (Temminck, 1838) by Clark & Webber 1991, *Libinia spinosa* H. Milne Edwards, 1834, by Clark et al. 1998b, and *Inachus dorsettensis* (Pennant, 1777) and *Inachus leptochirus* Leach, 1817 both by Clark 1980, 1983]. Comparing these life cycles, Clark (2001) concluded that the development of different characters occurred at different times and/or rates, suggesting that the evolutionary history of brachyuran zoeas provided robust examples of heterochrony. However, Clark (2001) made no attempt to relate his zoeal theory to the heterochronic processes described by McKinney & McNamara (1991).

Heterochrony can be defined as an evolutionary change in the timing of the development of a character between an ancestor and descendant. McKinney & McNamara (1991) illustrated a hierarchical classification of heterochrony, reproduced here in Fig. 2A. They considered that between an ancestor and its descendant, development can be either reduced or increased. Accordingly, a reduction in development resulted in paedomorphosis (child formation), i.e., the retention of juvenile characters of the ancestral forms by adults of their descendants. An increase in development resulted in peramorphosis, i.e., the descendant incorporating all the ontogenetic stages of its ancestor, including the adult stage, in its ontogeny, so that the adult descendant "goes beyond" its ancestor. McKinney & McNamara (1991) recognized three basic types of change for paedomorphosis and peramorphosis: change in rate, change in offset time, and change in onset time. Consequently, six kinds of developmental change were recognized: (1) the rate of change in the descendant can be slower (neoteny) or faster (acceleration) than the ancestor; (2) the onset time in the descendant can be later (postdisplacement) or earlier (predisplacement) than in the ancestor; and (3) the offset time

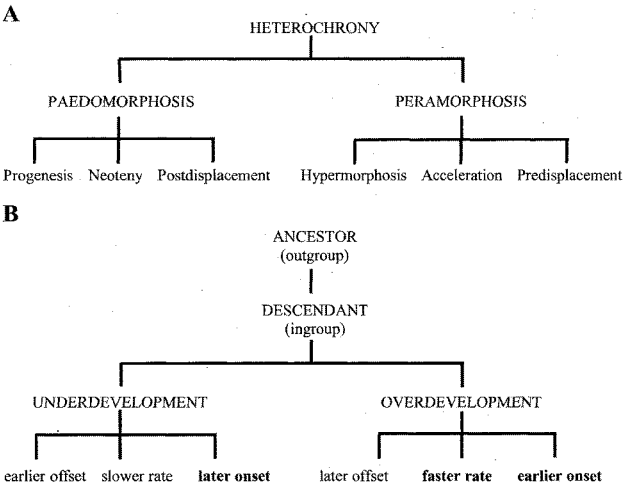

Figure 2. Heterochrony. (A) The hierarchical classification of heterochrony (after McKinney & McNamara 1991). (B) Simplified version with the three heterochronic processes associated with brachyuran zoeas highlighted in bold.

in the descendant can be earlier (progenesis) or delayed (hypermorphosis) than in the ancestor. The heterochronic system proposed by McKinney & McNamara (1991) is summarized here in Fig. 2B.

The problem with the hierarchical system of heterochrony as proposed by McKinney & McNamara (1991) in relation to larvae, in particular to zoeal characters, is that three processes are usually associated with sexual maturity, namely progenesis, neoteny and hypermorphosis. Functionally, Decapoda larvae are developmental and dispersal stages and are not influenced by sexual maturity, which develops during the postlarval phase and is continued in the juveniles and adults. Therefore, only three heterochronic mechanisms (see Clark 2005) appear to relate to brachyuran zoeal development (see bold typeface in Fig. 2B): postdisplacement (Table 2), predisplacement (Table 3) and acceleration (Table 4). In addition, the terms onset and offset used by McKinney & McNamara (1991) can be used to describe the presence (expressed) or absence (delayed) of individual setae, segments and even developmental phases/stages.

Table 2. Postdisplacement (underdevelopment): four setae are present (expressed, onset) in the ancestor compared to 3 setae (seta 4 absent or delayed) and 2 setae (setae 3 and 4 absent or delayed, offset) in descendants 1 and 2, respectively.

	Seta 1	Seta 2	Seta 3	Seta 4
ANCESTOR	**present onset expressed**	**present onset expressed**	**present onset expressed**	**present onset expressed**
DESCENDANT 1	**present onset expressed**	**present onset expressed**	**present onset expressed**	absent offset delayed
DESCENDANT 2	**present onset expressed**	**present onset expressed**	absent offset delayed	absent offset delayed

onset of first zoeal stage (hatching) ↑ *offset of first zoeal stage (molt to second zoeal stage)* ↑

Table 3. Predisplacement (overdevelopment): four setae are present (expressed, onset) in the ancestor compared to 5 setae (seta 5 present or expressed) and 6 setae (setae 5 and 6 present or expressed, onset) in descendants 1 and 2, respectively.

	Seta 1	Seta 2	Seta 3	Seta 4	Seta 5	Seta 6
ANCESTOR	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**	absent offset delayed	absent offset delayed
DESCENDANT 1	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**	absent offset delayed
DESCENDANT 2	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**	**present** **onset** **expressed**

onset of first zoeal stage (hatching) ↑ *offset of first zoeal stage (molt to second zoeal stage)* ↑

Table 4. Acceleration (overdevelopment) faster rate: four steps are required in the ancestor to fully develop an appendage from hatching to the offset of the zoeal phase compared to three and two steps in descendants 1 and 2, respectively (see third maxilliped, Clark 2005: 441, fig. 14).

	ACCELERATION			
ANCESTOR	UNIRAMOUS	BIRAMOUS	BIRAMOUS with EPIPOD	BIRAMOUS with EPIPOD and ARTHROBRANCH
DESCENDANT 1	BIRAMOUS	BIRAMOUS with EPIPOD	BIRAMOUS with EPIPOD and ARTHROBRANCH	
DESCENDANT 2	BIRAMOUS with EPIPOD	BIRAMOUS with EPIPOD and ARTHROBRANCH		

onset of hatching and zoeal phase ↑ *offset of zoeal phase, onset of megalopal phase* ↑

6 POLARITY OF SETAL CHARACTERS

Brachyuran zoeal molts are associated with body growth, division of somites, appearance and development of appendages, and appearance (expression) of setae. On certain body somites and appendage segments, the number of some setae does not increase after successive zoeal moults (stages) and can be considered conservative. For example, the setal patterns on the second maxilliped endopod of xanthoids (Fig. 3A) remain constant (conservative) throughout zoeal development (e.g., *Lophozozymus pictor* as described by Clark & Ng 1998). When analyzing these conservative setal characters for possible phylogenetic significance, a number of brachyuran workers (e.g., Lebour

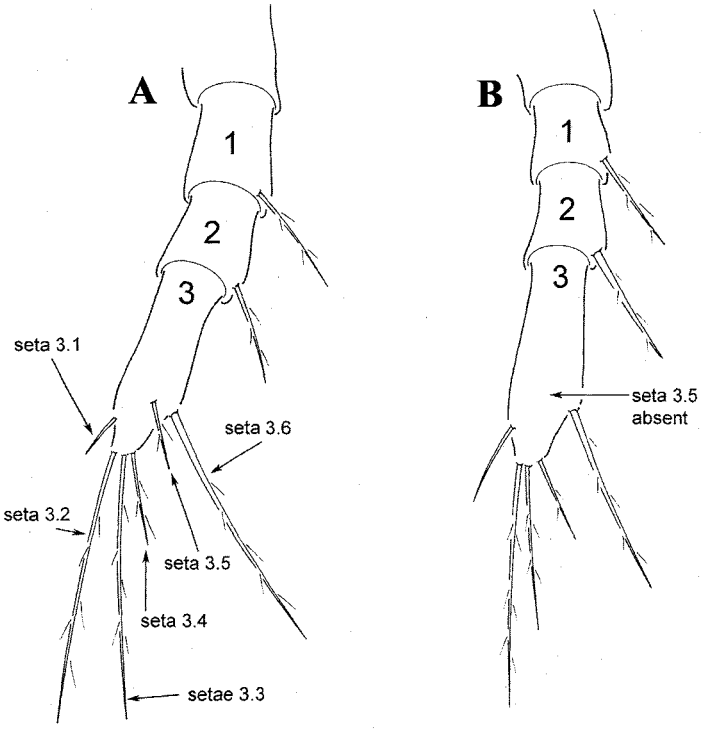

Figure 3. First-stage zoea, second maxilliped, setation patterns on the three-segmented endopod. (A) *Pilodius pugil*: seta 3.5 is present (expressed) and is considered to be the ancestral condition. (B) *Banaria subglobosa*: seta 3.5 is lost (absence or delay in appearance) and is regarded as the derived state for this character.

1928, 1931; Bourdillon-Casanova 1960; Kurata 1969; Clark 1980, 1983; Rice 1980, 1983, 1988; Clark & Webber 1991; Ng & Clark 2001) have assumed that zoeal evolution has proceeded by loss or reduction of setae. Under such an assumption, the presence (expression) of a seta would be considered the ancestral state, and its absence (loss or delay in appearance) is considered derived. For example, seta 3.5 is present (expressed) and considered to be the ancestral condition (Fig. 3A), while its loss (absence or delay in appearance) is regarded as the derived state for this character (Fig. 3B).

In contrast to such conservative characters, there are some somites and appendage segments that accumulate setae at successive zoeal moults. Scoring and polarizing these characters is not straightforward. When Clark & Webber (1991) first analyzed majid zoeae using PAUP, they simply counted the setae on each appendage article. As a consequence, five setae on a segment for one species was considered ancestral when compared to the same segment of another species with only four setae (derived). Such an assumption does not take into account which seta had been lost (absent or delayed). Neither did such counting take into account the influence of abbreviated zoeal development on expression of setae (Clark 2005). For example, with reference to the third endopod segment of the first maxilliped in the first stages of *Charybdis helleri* (Portunoidea Rafinesque, 1815; see Ng et al. 2008) and the xanthoid *Chlorodiella nigra*), at first glance a seta is present in ZI of the latter and absent in the former, suggesting that *C. helleri* is the derived condition (compare Fig. 4A with 4E). However, when Dineen et al. (2001) reared *C. helleri* in the laboratory through to stage ZVI, they showed that this seta appeared (was expressed) later (in ZIV) during development (Fig. 4A–D). Reassessing this character now (Fig. 4E), it is clear that the seta on endopod segment 3 has appeared (expressed) early, in ZI, of *Chlorodiella nigra* compared to the outgroup (possible ancestor) of *Charybdis helleri*. From McKinney & McNamara (1991), this early

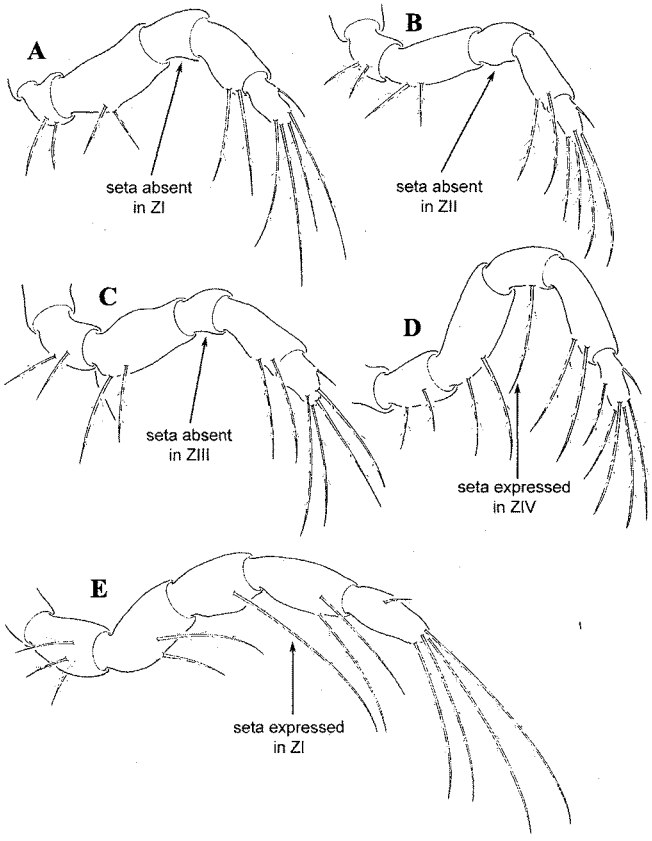

Figure 4. First maxilliped, expression (appearance or presence) of the seta on third endopod segment. (A–D) *Charybdis helleri* zoeas I–IV, respectively. (E) *Chlorodiella nigra* zoea I.

expression relates to predisplacement of the seta, overdevelopment (peramorphosis) in *Chlorodiella nigra*, and its early onset is the derived condition. The absence of the seta in ZI of *Charybdis helleri* is therefore the plesiomorphic (ancestral) condition.

Accumulative setae, such as the armature of the maxilla proximal coxal endite in brachyuran zoeas, also are of interest with regard to hetrochrony and polarization. Figure 5A–F illustrates the accumulative setae on the maxilla proximal coxal endite during the development of ZI–VI for *Charybdis helleri* by Dineen et al. (2001); stages ZI to ZVI bear 3,3,3,3,4,5 setae, respectively. Comparison of this accumulation sequence with the zoeal development of *Nanocassiope melanodactyla* (A. Milne Edwards, 1867) by Dornelas et al. (2004), which consists of only four zoeas with setation arranged 4,4,5,6 (Fig. 5G–J), shows that the appearances of 4 (ZI) and 6 (ZIV) setae are both expressed (present) early compared to what is seen in the zoeal stages of *C. helleri* (ZV and ZVI).

Scoring the accumulative setae on the maxilla proximal coxal endite for a phylogenetic analysis with reference to the first-stage zoeas of *C. helleri*, *N. melanodactyla*, *Pilumnus hirtellus* (Linnaeus, 1761) and *Eriphia scabricula* Dana, 1852 is difficult (Fig. 6A–D, respectively). Considering *C. helleri* as the outgroup (ancestor), the character could be scored simply as a multistate character, with the 3 setae of this species being the ancestral condition and accumulation of setae being increasingly more derived.

However, these accumulative setae also could be scored individually with respect to the principles of heterochrony and overdevelopment (peramorphosis). The individual setae can be identified

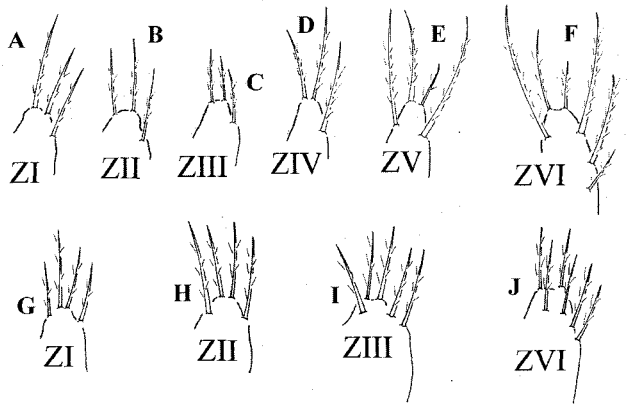

Figure 5. Maxilla, setation of proximal coxal endite. (A–F) *Charybdis helleri* (Portunidae). (G–J) *Nanocassiope melanodactyla* (Xanthidae).

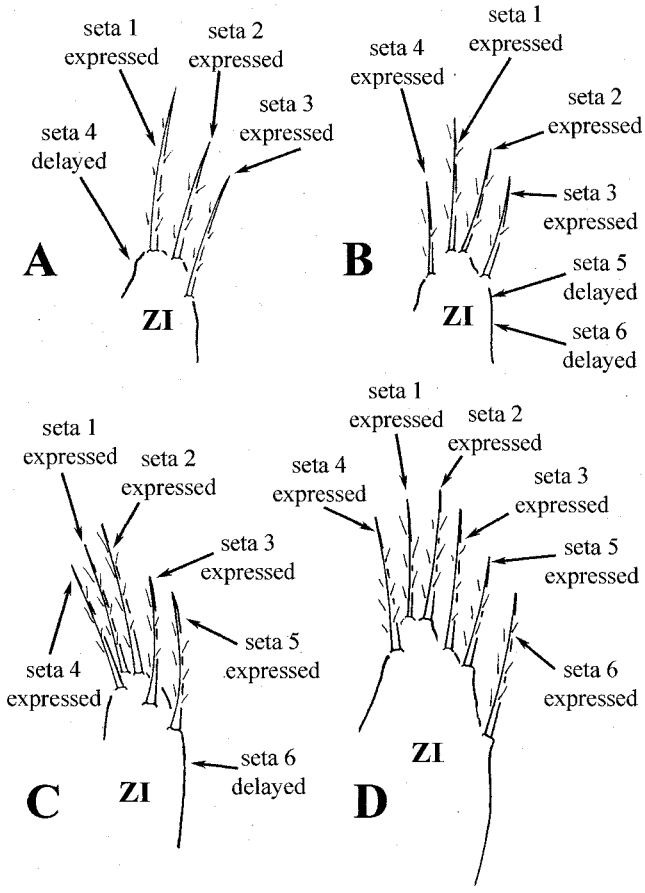

Figure 6. Maxilla, setation of proximal coxal endite. (A) *Charybdis helleri*. (B) *Nanocassiope melanodactyla*. (C) *Pilumnus hirtellus*. (D) *Eriphia scabricula*.

and their expression (presence) correlated to an outgroup (possible ancestor) species with a longer zoeal development phase, e.g., *Charybdis helleri* with six zoeal stages. Thus, instead of being a single multistate character, three characters can be scored. In Figure 6A–D, the setae are numbered from 1 to 6. Setae 1–3 are present (expressed) in *C. helleri*, *N. melanodactyla*, *P. hirtellus* and *E. scabricula*. Seta 4 is absent (delayed) in *C. helleri* (the outgroup and ancestor), but is expressed (overdeveloped when compared to the ancestor) in *N. melanodactyla*, *P. hirtellus* and *E. scabricula*. Seta 5 is delayed in *C. helleri* and *N. melanodactyla* but is expressed in *P. hirtellus* and *E. scabricula*, with seta 6 being delayed in *C. helleri*, *N. melanodactyla* and *P. hirtellus* but expressed in *E. scabricula*. These characters therefore could be scored as delayed (0) vs. expressed (1) for each of the three setae (seta 4, 5 and 6).

7 TRANSFORMATION TYPES

The choice of transformation types is important because such decisions affect the number of evolutionary steps in a phylogenetic analysis. Using "irreversible-up" with respect to brachyuran zoeal phylogeny is widely regarded as introducing an element of subjectivity because it does not necessarily produce the shortest (most parsimonious) trees, as postulated by Marques & Pohle (1998).

A problem for the present study is that according to Maddison & Maddison (1992: 79), when using unordered characters, ". . . a change from any state to any other state is counted as one step" (referred to as "Fitch parsimony"; see Fitch 1971; Hartigan 1973). Thus, a change from 0 to 1, or from 0 to 8 or 7 to 4, is each counted as one step. A five-state unordered character can be represented diagrammatically (Fig. 7A), where change between any two states involves only one step (i.e., only one line has to be traversed in the diagram). An unordered transformation series does not reflect the course of evolution as proposed for decapod larvae and based on heterochrony (Clark 2005). Heterochrony suggests a gradual progressive loss (delayed expression) of characters in a linear transformation series, such as the loss of one seta at a time from the proximal basial endite of the maxilla (Clark 2005: 437, table 19; and fig. 16). Individual setae can be scored (Fig. 6), i.e., the six setae on the proximal basial endite of the maxilla are numbered individually 1 to 6. Empirical observations suggest that seta 6 is lost, then seta 5, then seta 4 and so on in the last zoeal stage of the descendant in relation to the ancestor. Heterochrony within decapod larvae provides no support for the suggestion that any one state can transform to any other state in a single step, e.g., 1 to 4 or 3 to 0. Indeed, heterochrony appears to support a linear transformation series, of which there are two types: ordered and irreversible.

Maddison & Maddison (1992: 79) define an ordered transformation series: "For characters designated as ordered, the number of steps from one state to another state as the (absolute value of the)

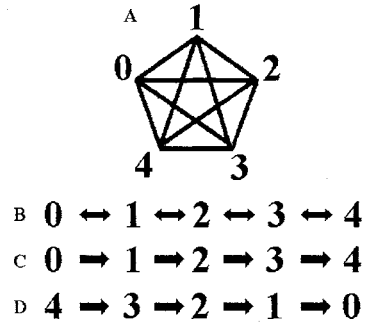

Figure 7. Transformation series: (A) unordered. (B) ordered. (C) irreversible-up terminal addition. (D) irreversible-up terminal delay = oligomerization.

difference between their state numbers" ("Wagner parsimony"; Farris [1970]; Swofford and Maddison [1987]). Thus, a change from 0 to 1 is counted as one step, from 0 to 8 as eight steps, from 7 to 4 as three steps. Thus, a five-state ordered character can be represented diagrammatically as shown in Fig. 7B. In this diagram, the number of steps in the change between any two states is equal to the number of lines on the path between the two states; thus, from 1 to 4 is three lines or three steps. The analysis of heterochrony (Clark 2005) provides no support for the existence of ordered transformation of character types in decapod larvae. In the absence of any supporting evidence, it is problematic to accept that zoeal characters once lost in a specific lineage or taxon, e.g., 4 to 3 to 2 to 1 to 0 (Fig. 7B), can then reappear again as 0 to 1 to 2, etc. Within the decapods a number of traits have been lost and not reappeared. For example, the Dendrobranchiata release their eggs directly into the water column, whereas all derived decapods (Pleocyemata) spawn their eggs onto the pleopods, where they remain with parental (female) care until hatching. This strategy, the release of eggs into the sea, has not been reversed in derived decapods. Further, the Dendrobranchiata have a nauplius larval phase, which is lost (present in embryonic development) in the more derived decapods (Pleocyemata) where larvae hatch in a more advanced stage of development as zoeas. Nauplii have not reappeared in the Pleocyemata.

Maddison & Maddison (1992: 79-80) define irreversible as: "For characters designated as irreversible, the number of steps from one state to another state is counted as the difference between their state numbers, with the restriction that decreases in the state number do not occur" ("Camin-Sokal parsimony"; Camin and Sokal [1965]). Thus, a change from 0 to 1 is counted as one step, from 0 to 8 as eight steps, but changes from 1 to 0 or 8 to 0 are impossible. Multiple gains (increases) are allowed, but no losses (decreases) are allowed. A five-state irreversible character can be represented diagrammatically (Fig. 7C). However, this figure represents terminal addition (Clark 2005: 438), whereas the linear transformation series described by Fig. 7D seems to best fit the theories that a mosaic of several heterochronic processes provides a dominant evolutionary mechanism influencing oligomerization within brachyuran zoeae. Terminal delay of characters is represented by Fig. 8 (see also Clark 2005). Once decapod larval characters are lost in any lineage, they are not expressed again.

8 HOMOPLASY

Although scoring characters as "irreversible-up" does reflect reduction or abbreviation, ultimately resulting in terminal delay (oligomerization), this option, in general, does not allow reversals in character state changes and forces additional homoplasy. But homoplasy does appear to be extremely widespread in brachyuran zoeal lineages; many derived character states have evolved more than once within different branches (clades). For example, seta 3.5 (Fig. 3B) has been lost (delayed or absent) a number of times in brachyuran zoeal evolution. Examples are found in the Pilumnidae as in *Tanocheles bidentata* (described by Ng & Clark 2000); within the Xanthidae as in *Leptodius exaratus* (H. Milne Edwards, 1834) and *Lybia plumose* Barnard, 1947 (both by Clark & Paula 2003); within the Majidae as in *Inachus* (by Clark 1983) and *Libinia spinosa* H. Milne Edwards, 1834 (by Clark et al. 1998b); and within the Grapsoidea as in *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (by Min-Shiou et al. 2004). As with the second maxilliped, the expression of the seta on the first endopod segment (Fig. 3) also has been lost (delayed or absent) a number of times in brachyuran zoeal evolution. Examples occur within the Trapezioidea as in *Trapezia richtersi* Galil & Lewinsohn, 1983 (by Clark & Ng 2006); within the Majidae as in *Inachus* (by Clark 1983) and *Libinia spinosa* (by Clark et al. 1998b); and within the Grapsoidea as in *Armases miersii* (Rathbun, 1897) (by Cuesta et al. 1999). Such derived characters have not just evolved once within brachyuran zoeas; they have evolved in many different lineages. Consequently, homoplasy appears to be the norm in the evolution of brachyuran zoeas, not the exception.

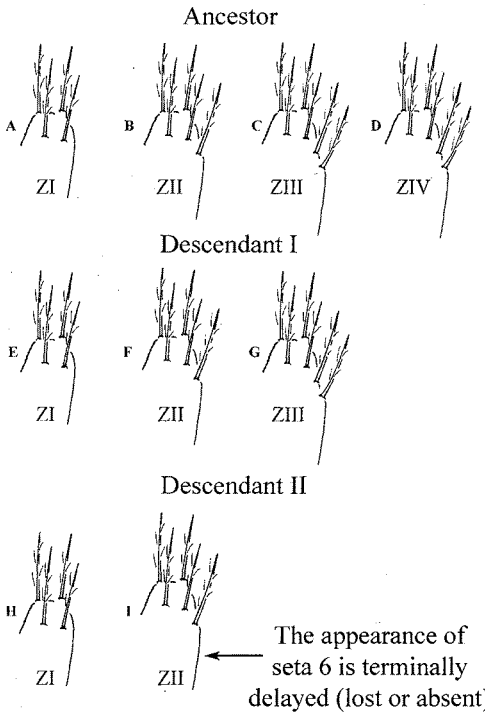

Figure 8. Maxilla, proximal basial endite, a representation of terminal delay with respect to seta 6. (A–D) *Pilumnus hirtellus*. (E–F) *Actumnus setifer*. (H–I) *Pilumnus sluiteri* (see Clark 2005).

9 PHYLOGENETICS

Our understanding of larval morphology bears not only on classification but also on phylogeny. For example, on the basis of adult morphology, *Tanaocheles bidentata* was originally assigned to the xanthoidean subfamily Chlorodiellinae, and the "Eumedoninae" species have been assigned to various taxa including Eumedonidae, Xanthoidea, Trapezioidea and Portunoidea (for details see Ng & Clark 2000, 2001). However, similarity of the zoeal antenna morphology (Fig. 1) suggests that *T. bidentata* and the "eumedonids" should be assigned to the Pilumnoidea. In order to test this hypothesis, 18 synapomorphic characters of first-stage zoeas from representative taxa were analyzed, including: two xanthids, *Actaea areolatus* (Dana, 1852) and *Chlorodiella nigra*; one tetraiid, *Tetralia cavimana* Heller, 1861; one Portunoidea, *Charybdis helleri* (also the outgroup); four pilumnoids, *Benthopanope indica* (De Man, 1887), *Glabropilumnus edamensis* (De Man, 1888), *Pilumnus hirtellus* and *P. vespertilio* (Fabricius, 1793); and three "eumedonids," *Echinoecus pentagonus*, *Zebrida adamsi* and *Rhabdonotus pictus*. *Rhabdonotus pictus* is used to represent the first-stage zoeas of *Harrovia albolineata* and *Permanotus purpureus* because the setal arrangement of all three larvae is identical.

For this brief example, the data matrix was constructed in MacClade 4.08 OSX (Maddison & Maddison 2000), the trees were generated in PAUP* 4.0b10 (Swofford 2002), and the data set was analyzed using Branch and Bound. One of the 18 characters included in the analysis was treated as unordered because of the difficulty in determining the polarity of exopod antennal spinulation (Clark & Guerao 2008), and the remaining 17 were treated as "irreversible-up." A 50% majority rule consensus was generated from two trees with a consistency index = 0.5714 and tree length of 35.

The resulting tree supported the inclusion of *Tanaocheles bidentata* within the Pilumnoidea (Fig. 9) and in the same clade as *Pilumnus hirtellus*, the type species of the superfamily. There is no

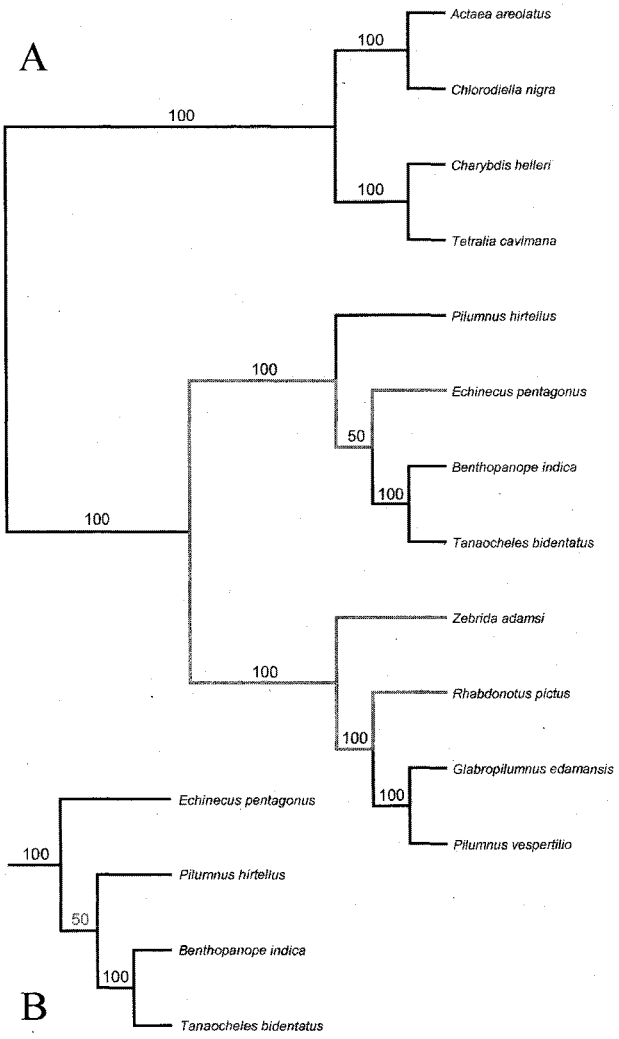

Figure 9. Phylogenetic analysis of first-stage zoeas (1) supports the morphological comparisons based on similarity and difference in that *Tanaocheles bidentata* is not a member of a xanthoidean subfamily but should be assigned to the Pilumnoidea Samouelle, 1819; (2) indicates that eumedonid crabs should be assigned to the Pilumnoidea Samouelle, 1819, rather than to a distinct family within the Xanthoidea; and (3) suggests that the Eumedonidae Dana, 1852, may not be a monophyletic taxon because *Echinoecus pentagonus* appears in a separate pilumnoidean clade. Competing topologies for the pilumnoid lineages of tree A are shown in tree B.

phylogenetic support for assigning this species to the Chlorodiellinae, represented in the analysis by the type species *Chlorodiella nigra*. Similarly, there is no support for placing *T. bidentata* in the Trapezioidea Miers, 1886 (represented by *Tetralia cavimana*) as suggested by Kropp (1984) for *Tanaocheles stenochilus* (see Ng and Clark 2000 for details). Although *T. bidentata* possesses some unique larval characters, such as loss of lateral spines and reduced rostral spine, on the basis of this limited analysis there appears to be little support for the assignment of *Tanaocheles* to a new subfamily, Tanaocheleinae (now Tanaocheleidae Ng & Clark 2000, see Ng et al. 2008), as

proposed by Ng & Clark (2000). However, more taxa will need to be included to resolve intrafamilial relationships.

In Figure 9, the "eumedonid" taxa represented by *Echinoecus pentagonus*, *R. pictus* and *Z. adamsi* (including *Harrovia albolineata* and *Permanotus purpureus*) were located within the Pilumnoidea clade. There is no support from the first zoeas that the eumedonids were related to the Trapezioidea (represented by *Tetralia cavimana*), the Xanthoidea (represented by *Chlorodiella nigra* and *Actaea areolatus*), or the Portunoidea (represented by *Charybdis helleri*). Furthermore, this analysis suggests that the "eumedonids" may be polyphyletic. These commensal crabs are associated with echinoderms. *Echinoecus pentagonus* is found internally in sea urchins such as *Diadema savignyi*, *Echinothrix calamarix* and *Echinothrix diadema*; *H. albolineata*, *P. purpureus* and *R. pictus* are found on crinoids; and *Zebrida adamsi* is located externally on sea urchins such as *Asthnosoma ijimai* and *Diadema setosum*. From the tree (Fig. 9), *E. pentagonus* and *Z. adamsi* + *R. pictus* (representing *H. albolineata* and *P. purpureus*) are placed in separate clades. Biologically, these two clades correspond to the externally inhabiting eumedonids and the internally associated *E. pentagonus*. Moreover, the externally inhabiting eumedonids appear to be subdivided into those crabs that live on crinoids (*R. pictus* representing *H. albolineata* and *P. purpureus*) and *Z. adamsi*, which is found on sea urchins. More larval descriptions of sea-urchin associates are required to confirm this division. The non-monophyly of the eumedonids also has implications for the subfamily Eumedoninae as proposed by Števčić (2005) and Ng et al. (2008), as two of the genera that they assign to this subfamily, namely *Echinoecus* and *Zebrida*, are in separate clades (Fig. 9). This analysis supports the views expressed by Chia & Ng (1995), who questioned the divisions of the Eumedonidae proposed by Števčić et al. (1988). The larvae of the type species, *Eumedonus niger* H. Milne Edwards, 1835, are not known but are of interest, for if these are similar to those of *Z. adamsi*, *R. pictus*, *H. albolineata* and *P. purpureus*, it would suggest that *E. pentagonus* is not a eumedonine as presently defined. In fact, *E. pentagonus* shares two synapomorphies — absence of dorolateral spines on somites four and five — with the three taxa in the clade (*B. indica*, *T. bidentatus* and *Pilumnus hirtellus*). In summary, this limited phylogenetic analysis of first-stage zoeas supports the inclusion of *T. bidentatus* and the eumedonines within the Pilumnoidea, but suggests the latter taxon may not be monophyletic.

10 CONCLUSIONS

Studying only first-stage zoeas or obtaining the complete larvae development from an ovigerous decapod female in the laboratory has one distinct advantage: the species can be subsequently positively identified. A modern high-powered microscope with DIC is essential for basic alpha taxonomy and descriptions of setal patterns.

Brachyuran zoeas of congeneric species appear to have identical setotaxy. This similarity provides a degree of predictability within a taxon. Setal differences (incongruence) within a group are indicative of systematic non-compatibility; they suggest incorrect assignment of taxa. However, similarity does not provide a measure of relationship, which can only be achieved by analyzing shared derived characters.

Oligomerization is considered to be an evolutionary trend within the Crustacea. Study of decapod larval development suggests that heterochronic processes may provide a dominant evolutionary mechanism influencing oligomerization within brachyuran zoeas.

On some body somites and appendage segments, setae do not increase in number after successive zoeal moults, so these are considered conservative characters. When analyzing conservative setal characters for possible phylogenetic significance, their presence (expression) can be considered the ancestral state and their absence (loss or delay) derived. In contrast, there are some somites and segments that accumulate setae; numbers of these setae increase with successive zoeal moults. A method of phylogenetically interpretating these accumulative setae may be to identify individual

setae and correlate their expression or delay with respect to an outgroup (possible ancestor) species with a long zoeal development phase.

Unordered characters generate the shortest number of evolutionary steps and produce the most parsimonious trees. However, an unordered transformation series does not represent the linear evolutionary steps toward gradual loss of characters as postulated here by heterochrony. A mosaic of several heterochronic processes provides an evolutionary mechanism influencing oligomerization (reduction and loss) in brachyuran zoeas, and this is best represented by an irreversible transformation series. But reconstruction of trees using "irreversible up" does not necessarily produce the most parsimonious trees and frequently involves more evolutionary steps to compensate for homoplasy. There is evidence that suggests homoplasy is widespread within many brachyuran lineages.

With respect to a classification based on decapod adult morphology, brachyuran larval descriptions can be used to provide an additional perspective on conventional systematics and evolutionary processes.

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