



Decapod Crustacean Phylogenetics

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Crustacean Parasites as Phylogenetic Indicators in Decapod Evolution

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ABSTRACT

The evolutionary history of decapods and their parasites is assessed with particular reference to the use of parasites as proxies for host phylogeny. We focused on two groups of obligate parasites that use decapods as their definitive hosts: parasitic isopods of the family Bopyridae and parasitic barnacles of the superorder Rhizocephala. Bopyrids and rhizocephalans differ in that the rhizocephalans have a direct life cycle whereas bopyrids require an intermediate host. In addition, rhizocephalans cause drastic impacts on hosts (including castration and behavioral modification) whereas bopyrids have less pronounced impacts but often also castrate hosts. The diversity and host specificity of both groups are reviewed and their patterns of association with decapod hosts are analyzed. Aside from the Dendrobranchiata (with 39 bopyrid species) and the Caridea (with 8 rhizocephalan and 203 bopyrid species), the more basal decapods are relatively unparasitized or completely lack representatives of these parasites. In contrast, the most derived decapod taxa (Anomura and Brachyura) host the largest number of parasites (233 rhizocephalan and 282 bopyrid species). Counterintuitively, when the phylogenies of the decapods and parasites are compared, some of the most basal parasite groups are found associated with more derived host groups. Our findings indicate a degree of cospeciation but suggest that host switching has been frequent in these parasites, with colonization of caridean shrimp occurring in both groups. Conclusions based on the coevolutionary analyses are complicated by the fact that comprehensive cladistic analyses of the parasites are presently lacking; our review can act as a catalyst for more directed studies analyzing the coevolution of these groups and testing particular hypotheses on their evolutionary history. Although the value of parasites in the elucidation of the phylogeny of decapods as a whole may be limited due to host switching, parasites may be informative *within* particular decapod taxa. We explore an example of this within the Anomura and indicate how such coevolutionary analyses may show host taxa that we would predict to have parasites but presently appear to be lacking them, likely due to limited sampling or evolution of anti-parasite defenses. In addition, these analyses are important in applied areas of decapod ecology (e.g., fisheries) and a brief discussion is provided on the role of coevolutionary studies in the use of bopyrids and rhizocephalans as biological control agents of invasive and/or pest decapod species.

1 INTRODUCTION

Recent attempts to elucidate the phylogenetic relationships among the decapod crustaceans have used a wide variety of characters, both morphological and molecular. However, one character with potentially informative phylogenetic signals has, to date, not been considered in the attempts at reconstructing decapod evolutionary history: parasites. Historically, parasites have been used to infer

the phylogeny of diverse host lineages, and within the past two decades methods for coevolutionary analyses have been developed to analyze and reconcile host and parasite lineages (see Brooks 1988; Brooks & McLennan 1993, 2002; Page & Charleston 1998; Legendre et al. 2002; Page 2002; Nieberding & Olivieri 2007; Poulin 2007). More recently, parasites have been used to determine demographic history and movement of their hosts (Whiteman & Parker 2005; Nieberding & Olivieri 2007). In the marine realm, the degree to which the phylogeny of parasites mirrors that of host(s) has been best studied in vertebrates (see review in Hoberg & Klassen 2002); there are few examples of coevolutionary analyses on parasites of invertebrates (e.g., Cribb et al. 2001). To our knowledge there are no coevolutionary studies on marine parasites (protozoan or metazoan) that infest invertebrates as their definitive hosts, although multiple host-parasite lineages have been analyzed separately and are amenable to future studies.

Decapod crustaceans are diverse and numerically dominant components of the marine environment, as well as being well represented in freshwater and terrestrial habitats (Bliss 1990). Many diverse groups of decapods harbor parasitic lineages that may provide phylogenetic signals that support or refute hypotheses of decapod evolution. However, it is essential to study and reveal the phylogenetic patterns within the parasite groups before attempting coevolutionary analyses of the parasites and their hosts. Many different types of organisms parasitize decapods, including bacteria, viruses, fungi (Johnson 1983), protozoans (Couch 1983), and metazoans including platyhelminths, acanthocephalans, nematodes, nematomorphs, and crustaceans (Overstreet 1983; Cressey 1983; Shields et al. 2006; Shields & Overstreet 2007). Within the crustaceans, there are only two parasitic lineages that are known to have evolved with decapod hosts: the rhizocephalan barnacles (Cirripedia) and the "epicaridean" isopods. Note that the classical term "Epicaridea" as a higher-level ranking within the Isopoda is not in current use, and the constituent taxa of Bopyroidea + Cryptoniscoidea are considered to be within the Cymothoida (Brandt & Poore 2003); the term "epicaridean" is used here to refer to both Bopyroidea and Cryptoniscoidea in shorthand, as the monophyly of the Epicaridea has not been demonstrated. However, since the Bopyridae (*sensu stricto*, not including Entoniscidae and Dajidae) is the most speciose and best studied family of epicaridean parasites of decapod hosts, the following analyses will be largely restricted to this group. Rhizocephalans and epicarideans also occur on non-decapod crustaceans, mostly peracarids and cirripedes, but the vast majority of species are known from decapod hosts. Copepods, although containing diverse lineages that parasitize many invertebrates and vertebrates, and being informative in coevolutionary analyses with their teleost hosts (e.g., Paterson & Poulin 1999), have not specialized on decapods. While commensal and mutualistic species also may be informative in coevolutionary analyses (e.g., Griffith 1987; Ho 1988; Cunningham et al. 1991), we focus on the parasitic barnacles and isopods.

Rhizocephalans and bopyrids are obligate parasites of their decapod hosts and are numerically dominant in terms of the parasite fauna on these hosts. As an example, in hermit crabs (Paguroidea), crustacean parasites make up 79% of the described parasite fauna, with bopyrids and rhizocephalans making up 57% and 21%, respectively, of the total number of parasite species (McDermott et al., unpublished data). Additionally, both bopyrids and rhizocephalans are macroparasites and are easily sampled, at least in their adult forms, as they are all either ectoparasitic (most bopyrids) or endoparasitic with an externa (rhizocephalans). This chapter summarizes what is known about the host specificity, diversity, and evolutionary history of rhizocephalans and bopyrids, and uses these data to provide a preliminary investigation of their coevolution with their decapod hosts.

1.1 A brief overview of coevolutionary theory

Host and parasite phylogenies may be in perfect agreement (i.e., they are congruent and follow Fahrenholz's Rule that the parasites track the phylogeny of hosts), indicating cospeciation of hosts and parasites. However, hosts and parasite lineages often do not exhibit perfect agreement or association by descent (Poulin 2007), and the resulting incongruence can be due to multiple factors, some

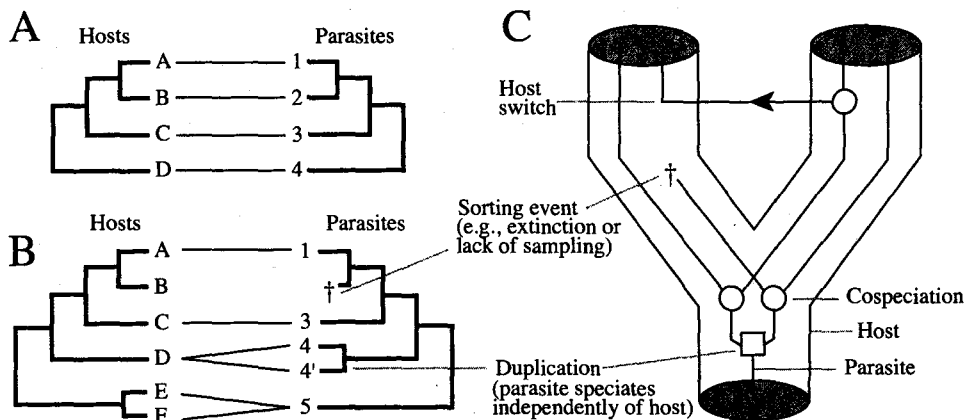


Figure 1. Host–parasite coevolution (association by descent) of hypothetical hosts and parasites. (A) Example of perfectly congruent host–parasite phylogenies (cospeciation of hosts and parasites) with all parasites specific to one host. (B) Example of incongruent host–parasite phylogenies, due to: sorting event† (extinction of parasite species or parasite species undetected due to lack of sampling of hosts), duplication (as in parasites 4, 4' that speciated independently of the host lineage and hosts E, F that speciated independently of the parasite lineage). (C) Embedding of a parasite tree inside a host tree. Shown is a duplication event in the parasite lineage and subsequent cospeciation of the resulting two parasite species. One parasite species goes extinct† and another parasite species undergoes a host switch (colonization or horizontal transfer). (A, B: modified from Poulin 2007; C, modified from Page & Charleston 1998.)

of which may represent the true historical associations of these groups (e.g., host switch, intra-host speciation) and others that may reflect our lack of knowledge (e.g., sampling efforts) (Fig. 1). To be able to map the host and parasite phylogenies and determine the degree of congruence present, three data sets must be considered (as indicated in Legendre et al. 2002): 1) association events for hosts and parasites, 2) host phylogenetic tree, and 3) parasite phylogenetic tree.

The first data set is only as good as our knowledge of the associations of the hosts and parasites, and requires accurate identifications of both, as well as reporting of these associations in the literature. To date, there are numerous gaps in our knowledge for this data set pertaining to decapods, as many hosts are reported with undescribed parasites and vice versa. It is important to note that the collection of accurate host/parasite data is essential, as assumptions about parasite occurrences on specific hosts should not be made. Indeed, potential host decapods may have the ability to block infestation by parasites that regularly infest congeners in other parts of the world or by parasite species that are common on sympatric species in the same area (Kuris et al. 2007).

Much progress has been made in the second data set, with many phylogenetic analyses of decapod groups being published in the past several years (e.g., Scholtz & Richter 1995; Pérez-Losada et al. 2002b; Dixon et al. 2003; Ahyong & O'Meally 2004; Porter et al. 2005; Tsang et al. 2008), although most studies have focused on evolutionary patterns above the family level. Although there is still no agreement on the placement of all the decapod constituent groups, a general consensus has developed on the monophyly of some (e.g., Brachyura, Caridea) and the relationships between others (e.g., Anomura+Brachyura, but see Porter et al. 2005).

The third data set is the principal sticking point in terms of generating coevolutionary hypotheses for rhizocephalan and bopyrid parasites and their decapod hosts. In the Bopyridae, no phylogenetic analyses have been performed to identify monophyletic units and there is no cladistic phylogeny for this family, or for the epicarideans as a whole. Cladistic analyses based on molecular and morphological data have shown that bopyrids appear to be derived from the Cymothoidea (isopod parasites

of fish) (Wägele 1989; Dreyer and Wägele 2001). However, sampling within the Bopyridae was too limited for any conclusions on the relationships of the bopyrid taxa to be made.

Similarly in the Rhizocephala, little work has been done above the species level (e.g., Høeg & Rybakov 1992; Høeg & Lützen 1993), and all of this has been confined to the Akentrogonida. However, two phylogenetic analyses have been published, one purely morphological (Høeg & Lützen 1993) and likewise restricted to the akentrogonids, and one molecular with limited sampling across the Rhizocephala (Glenner & Hebsgaard 2006). The molecular analysis indicated that several traditional groups of rhizocephalans were likely paraphyletic, including the genus *Sacculina*. One other study (Shukalyuk et al. 2007) has used genetic information from rhizocephalans and bopyrids but was conducted so as to produce a phylogeny of select genes, rather than organisms.

2 EVOLUTIONARY HISTORY, BIOLOGY, AND DISTRIBUTION OF CRUSTACEAN PARASITES

Several important questions can be asked about the utility of crustacean parasites in understanding decapod host evolution, including: 1) To what degree do the parasites cospeciate with decapod hosts? 2) Do different parasites show similar patterns of coevolution? and 3) Can biogeographic patterns tell us something about the evolutionary history of hosts and parasites?

In order to begin to provide answers to these questions, we summarize below what is known to date regarding relationships between parasites and hosts, both historically and today.

2.1 *The history of crustacean parasites of decapods*

Parasitization of decapods by bopyrids is evident from the fossil record and extends at least as far back as the Jurassic (ca. 145–199 mya) (Markham 1986). It is impossible, however, to identify the species of parasites in fossils as only the characteristic swelling of the branchial chambers is evident. Educated speculation about the identity of the parasites is possible (i.e., Ioninae likely in brachyuran fossils) but presently untestable. Some decapod families are known only to have bopyrids in their extant members, possibly due to limitations of fossil preservation, while others with numerous fossil records of parasites, such as the Raninidae (Brachyura), have never been found with bopyrids on members of extant species (Weinberg Rasmussen et al. 2008). The first clear evidence of rhizocephalans in decapods was demonstrated from the Miocene (ca. 5–23 mya) in fossil specimens of *Tumidocarcinus* (Xanthoidea), based on the presence of feminized abdominal segments on otherwise male crabs (Feldmann 1998). However, the origin of rhizocephalans is thought to be much more ancient (Walker 2001). As with bopyrids, there is no way to identify fossil rhizocephalan parasites beyond the higher taxonomic grouping. Although the oldest direct fossil evidences of bopyrids and rhizocephalans are separated by a large span of time, both groups clearly have a long history of association with their hosts.

2.2 *Overview of crustacean parasite biology*

Both bopyrids and rhizocephalans use decapods as definitive hosts; however, there are important differences in the two taxa in terms of their life histories. Bopyrids have an indirect life cycle with two hosts being externally parasitized, which is unusual among parasites in that there is no trophic transmission involved. Rhizocephalans, in contrast, have a free-living larval stage before completing their life cycle within a single definitive host. Both bopyrids and rhizocephalans are known to be parasitic castrators of hosts, but rhizocephalans cause more drastic impacts in terms of host modification (physiological and behavioral) through action of hormonal influence (Høeg et al. 2005); the chemical basis for the impacts of bopyrids on hosts remains largely unknown (Lester 2005; Calado et al. 2008). Some bopyrids do not cause “reproductive death” of their hosts, either allowing reduced reproduction by females (smaller clutch sizes) or not interfering with male reproductive

ability (Van Wyk 1982; Calado et al. 2005). Although theoretical predictions suggest that parasites with direct life cycles or free-living stages infecting hosts ectoparasitically are expected to exhibit greater congruence with hosts than parasites with indirect life cycles, this is not always the case (Paterson & Poulin 1999). Study of bopyrids and rhizocephalans can provide an additional test for this hypothesis.

2.2.1 Life cycles of the Rhizocephala

Rhizocephalans either release free-swimming nauplius larvae that develop in the water to the cyprid larval stage (all Akentrogonida and most Kentrogonida) or hatch cyprids directly from the eggs (a few Kentrogonida) that then settle on and initiate parasitism of the crustacean host (Fig. 2). Sexes are separate in rhizocephalans, and although sex determination of some species appears to be environmentally controlled (Walker 2001), the genetic basis for this process is not known for most species (Høeg et al. 2005). Female cyprids settle on new hosts, whereas male cyprids settle on the virgin rhizocephalan externa erupting from hosts. Female cyprids either directly inject

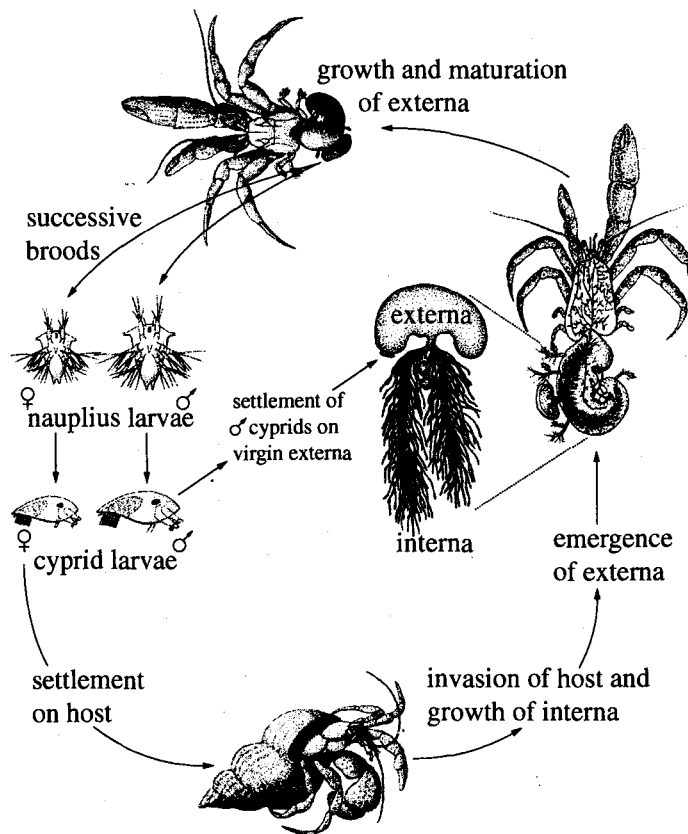


Figure 2. Generalized life-cycle diagram for rhizocephalan barnacles (Kentrogonid life cycle shown). Mature externa of parasitized host releases nauplius larvae that develop into cyprids (Akentrogonida lack free-swimming naupliar stages). Female cyprids settle on new hosts, whereas male cyprids settle on juvenile virgin externa. Female cyprids either directly inject inoculum into the host (Akentrogonida) or metamorphose into a kentrogon stage (not shown) that penetrates the host and injects the vermigon (Kentrogonida). Following invasion of the host, the rhizocephalan forms a branched nutrient-absorbing system of rootlets (interna) prior to forming the externa that emerges from the body. Male cyprids that settle on virgin externa will compete to inject generative cells into the female, becoming parasitic males (trichogon stage in the Kentrogonida). (Modified from the life cycle of *Peltogaster paguri* by Høeg (1992); with additional drawings of *P. reticulatus* by Isaeva et al. (2005) and *P. paguri* by Pérez (1937); figures not to scale).

female inoculum into the host (Akentrogonida) or metamorphose into a kentrogon stage that penetrates the host and injects the vermigon (Kentrogonida). The female grows inside the host, forming a branched nutrient-absorbing system of rootlets (interna) prior to forming an externa that emerges from the body. Male cyprids are attracted to settle on these virgin externa, competing to inject male generative cells that invade the female. In the Kentrogonida, a trichogon male stage invades and blocks the female receptacles with its shed cuticle (see fig. 4.21 in Høeg et al. 2005). In the Akentrogonida, the developing ovary or mantle cavity is typically invaded by the male generative cells (a trichogon stage is lacking) (Walker 2001). Eventually the externa matures, producing eggs that are fertilized and develop in the mantle cavity before being released as non-feeding nauplius or cyprid larvae into the water. Some rhizocephalans produce a single externa while others can undergo asexual reproduction where multiple externae are formed (Isaeva et al. 2005). Because rhizocephalans span both the external and internal environments of their hosts, they are sometimes termed mesoparasites, but their nutrition is taken up by the endoparasitic interna (Høeg 1992). The cues for location and recognition of hosts by rhizocephalans have been investigated (Boone et al. 2004; Pasternak et al. 2004a, b). In addition, cyprid settlement cues and host specificity of some rhizocephalans have been experimentally tested (e.g., Boone et al. 2003; Kuris et al. 2007).

2.2.2 Life cycles of the Bopyridae

Bopyrid isopods go through three different larval stages in their development. The epicaridium larva hatches from the egg and seeks out an appropriate intermediate host, always a copepod, where it metamorphoses into a microniscus larva and feeds on its hemolymph (Fig. 3). After this period of development on the intermediate host, the microniscus larva transforms into a free-swimming cryptoniscus larva that seeks out an appropriate definitive host, where it typically attaches to the gill filaments inside the branchial chamber or to the abdomen of the host. Species of the subfamily Entophilinae are endoparasites within the thorax or abdomen of hosts; some ectoparasitic species of the subfamily Pseudioninae (*Probopyrus*) are also known to be able to live initially as endoparasites of their hosts (Anderson 1990; Lester 2005). Once attached to their definitive hosts, the isopods transform into a juvenile bopyridium. In some species sex is epigametically or environmentally determined, that is, the first isopod to settle on a host will mature into a female, with any subsequent isopods settling on the same host becoming dwarf males. In some species the females appear to produce a masculinizing substance that reversibly restricts male sex change; when the female dies the males may change sex (Reinhard 1949). In other species determination of sex appears to be genetically controlled (Owens & Glazebrook 1985). Female bopyrids pierce the body of hosts and feed on hemolymph, eventually producing broods of eggs contained within the marsupium and fertilized by the dwarf males.

However, very few species of bopyrids have had their entire life cycles worked out; copepod host choice by epicaridium larva and the patterns of sex determination across the Bopyridae remain unclear. Limited research has investigated the interactions between bopyrids and their intermediate hosts, including the degree of intermediate host specificity (Anderson 1990; Owens & Rothlisberg 1991, 1995). Unfortunately, unlike for the Rhizocephala, little is known about the cues for location or settlement of isopod larvae on definitive hosts.

2.3 Parasite biogeography and host specificity

Although there have been numerous studies on the taxonomy and biology of bopyrids and rhizocephalans in European waters (e.g., Bourdon 1968; Høeg & Lützen 1985), the geographic ranges and degree of host specificity of many species in both groups are poorly known, especially in areas where sampling has been limited such as the Indo-West Pacific. In such regions, data on the host species may be extensive in taxonomic or ecological publications, but mention of the parasites is often omitted. From the limited worldwide data on the geographic distribution of decapod parasites,

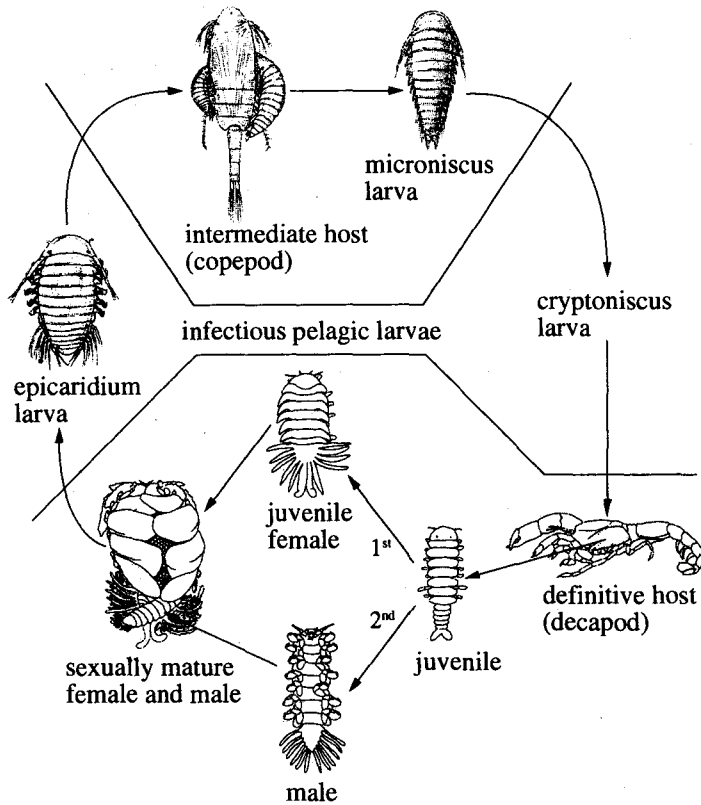


Figure 3. Generalized life-cycle diagram for bopyrid isopods. Mature male and female ectoparasitic isopods are typically found in the gill chamber or on the abdomen of decapod definitive hosts (members of the subfamily Entophilinae are endoparasites). Sexually mature females release epicaridium larvae that find a suitable copepod intermediate host, on which they attach and metamorphose into an ectoparasitic microniscus larva. After a period of development the microniscus larva transforms into a cryptoniscus larva that detaches and is free-swimming. The cryptoniscus settles onto suitable definitive hosts (recently settled juveniles are termed bopyridia). The first isopod to settle becomes female; subsequent isopods become dwarf males that live on the female and fertilize the developing eggs in the marsupium. (Modified from the life cycle of *Ione thoracica* by Wägele (1989), with additional drawings by Sars (1899); figures not to scale).

it appears that most species follow the classical pattern of having the parasite occur only within a portion of the range of the host species (Pielou 1974). However, it is clear that some species of bopyrids, at least, can parasitize multiple host species and extend their ranges by this means. As an example, *Athelges takanoshimensis* parasitizes at least 13 species of pagurid and diogenid hermit crabs from Japan, Korea, Hong Kong, and Taiwan (Boyko 2004). Another athelgine bopyrid, *Anathelges hyptius*, may have a range as great as from Massachusetts, USA, to Argentina (Boyko & Williams 2003; Diaz & Roccatagliata 2006) on eight species of pagurid hermit crabs, and perhaps extending all the way around the southern tip of South America to Chile (Diaz & Roccatagliata 2006). In contrast, many other species of bopyrids, as well as most rhizocephalans, appear to be more host-specific and have been found only on a single species of host.

One aspect of the life cycle of bopyrid isopods that may confound our understanding of the factors restricting their distribution is the inclusion of an intermediate copepod host in their life cycle. It is possible that the adaptation to the intermediate copepod host may be the key factor in the distribution of certain species or lineages of bopyrids. Other groups of parasites (e.g., digenean trematodes) have been shown to exhibit a narrower host range in their intermediate hosts than in

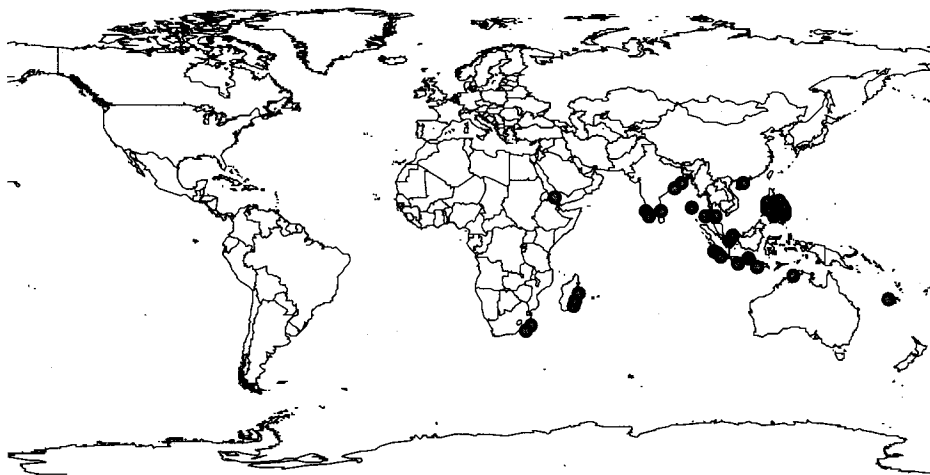


Figure 4. Geographic distribution of 36 species of parasitic isopods of the subfamily Orbioninae (each circle represents the type locality of one species; data largely from Bourdon 1979, 1981).

their definitive hosts, but the converse is also true (Cribb et al. 2001). In bopyrids of the subfamily Orbioninae, exclusively parasitic on penaeid shrimp, all of the species are found in the Indo-Pacific region (Fig. 4), despite the fact that penaeid shrimp are widely distributed in all the world's oceans. Bopyrid preference for certain species of copepod hosts may constrain their distribution, rather than the selection of definitive hosts, but this requires investigation. Unfortunately, little is known of the life cycles of Orbioninae or their specificity on copepod hosts. In fact, only a few studies have made direct observations on copepods parasitized by microniscus larvae (see Owens & Rothlisberg 1991, 1995). Coevolutionary analyses involving bopyrids and their intermediate copepod hosts may be informative, but this will require molecular studies to identify the parasites of copepods because bopyrids are typically not identifiable to species based on larval stages. It is notable that the diversity of the Orbioninae is highest in the Philippines, following the general pattern of highest diversity in this region of the Indo-West Pacific for free-living marine species (including invertebrates) (Carpenter & Springer 2005). Other parasitic isopod groups are predicted to exhibit higher diversity in this region (reflecting the diversity of their host groups), but this will require greater efforts in sampling (Markham 1986).

3 TAXONOMY AND PHYLOGENY OF DECAPOD CRUSTACEAN PARASITES

Identification of the monophyletic units within the bopyrids and rhizocephalans is essential before any testing of coevolutionary hypotheses can be undertaken. Unfortunately, this has not been done, and the process of identifying them is not simple.

3.1 *The phylogeny of the Rhizocephala*

While there is abundant morphological and developmental evidence supporting the monophyly of the Rhizocephala (Høeg 1992) and its placement within the Cirripedia as sister-taxon to the Thoracica (e.g., Billoud et al. 2000; Pérez-Losada et al. 2002a), there is a less clear picture regarding the relationships of its constituent taxa. An example of this can be seen in the genus *Sacculina*, which contains approximately 115 species, the most of any rhizocephalan genus. Species of *Sacculina*, as well as of the family Sacculinidae (including approximately 50 additional species in six genera), are

usually referred to as parasites of brachyurans (e.g., Walker 2001), but two of the species are known only from anomuran hosts (an albuneid and a galatheid) and one from a thalassinidean shrimp. These unusual host records suggest that a closer look at the genus should be undertaken to determine if it is monophyletic in its current configuration (see also Glenner & Hebsgaard 2006) or whether these unusual host associations reflect host switching within this parasitic taxon.

Almost all the species of rhizocephalans have been defined and described based solely on morphological criteria of the mature externa, despite the fact that these animals are among the most morphologically reduced in comparison to their non-parasitic relatives. This has resulted in there being only a limited suite of characters for identification of species, and it is unclear how many described species actually represent distinct taxa. Several recent studies have attempted to unite the limited morphological characters of adults with detailed cyprid morphology and molecular data in order to better define species boundaries and generate larger character selection options for phylogenetic analyses (e.g., Glenner et al. 2003; Chan et al. 2005).

A molecular study using 18S rDNA, 11 species of Sacculinidae, and 11 other rhizocephalans by Glenner & Hebsgaard (2006) resulted in a monophyletic Rhizocephala containing four clades of kentrogonids, with the two most derived being separated by the position of the Akentrogonida, thus rendering the Kentrogonida paraphyletic. The kentrogon stage was shown to be the primitive form of host invasion, with the akentrogonids being derived in their loss of the kentrogon, as well as in reduction in adult externa size. Perhaps most strikingly, *Sacculina carcini*, the type species of the genus, was separated from all other congeners by the position of the Akentrogonida, indicating paraphyly of *Sacculina* even with the limited taxon sampling.

3.2 The phylogeny of the Bopyridae

The "epicaridean" isopods are currently divided into the two lineages Cryptoniscoidea + Bopyroidea within the Cymothoida (Brandt & Poore 2003). While some of the cryptoniscoids are found parasitizing decapod hosts (e.g., *Danalia ypsilon* on *Galathea* spp.), most (ca. 88%) are known from peracarid, ostracod, or cirripede hosts. Members of the Bopyroidea, in contrast, are primarily known from decapod hosts. With 595 described species, the Bopyridae is the most speciose family in the Bopyroidea, as well as the most speciose family of isopods. Despite this large number of described taxa, the diversity in this group is largely underreported, and evidence for this can be gleaned from the more than 20% increase in the number of known species during the past 20+ years (subsequent to Markham 1986). Many new host records and new taxa await reporting and description, principally from tropical and deep-sea habitats (Bourdon, Markham, pers. commun.; Boyko, Williams, pers. obs.). The other two families of Bopyroidea are the Entoniscidae (ca. 35 spp.), which are endoparasites of decapods, and the Dajidae (ca. 50 spp.), which are ectoparasites of shrimp, mysids, and euphausiids. As with the Bopyroidea + Cryptoniscoidea grouping, Bopyridae + Entoniscidae + Dajidae has long been assumed to be monophyletic, based in large part on reproductive biology and the morphology of the males, but no cladistic phylogenetic analyses have ever been conducted for these taxa.

Currently, the Bopyridae is divided into nine subfamilies. A tenth, monotypic subfamily (Bopyrophryxinae) was synonymized with Pseudioninae (Bourdon & Boyko 2005). In the subfamilies Pseudioninae, Bopyrinae, Argeiinae, and Orbioninae, the adult female parasite is located on the decapod host in the right or left branchial chamber. The branchial chamber is also the usual site of attachment for members of the Ioninae, but species of *Rhopalione* are found under the abdomens of their pinnotherid hosts. In the Athelginae, the females are located on the dorsal abdomen of the host hermit or king crab, while in the Phyllodurinae, the female isopod is situated on the ventral surface of the thalassinidean host abdomen. Female isopods of the Hemiarthrinae are found either on the dorsal or ventral surface of the abdomen, laterally on the carapace, or in one species inserted into the mouth region of the host shrimp (Trilles 1999). The two species of Entophilinae are similar in habitat to entoniscid isopods, living as endoparasites in the thoracic or abdominal regions of their anomuran and thalassinidean hosts.

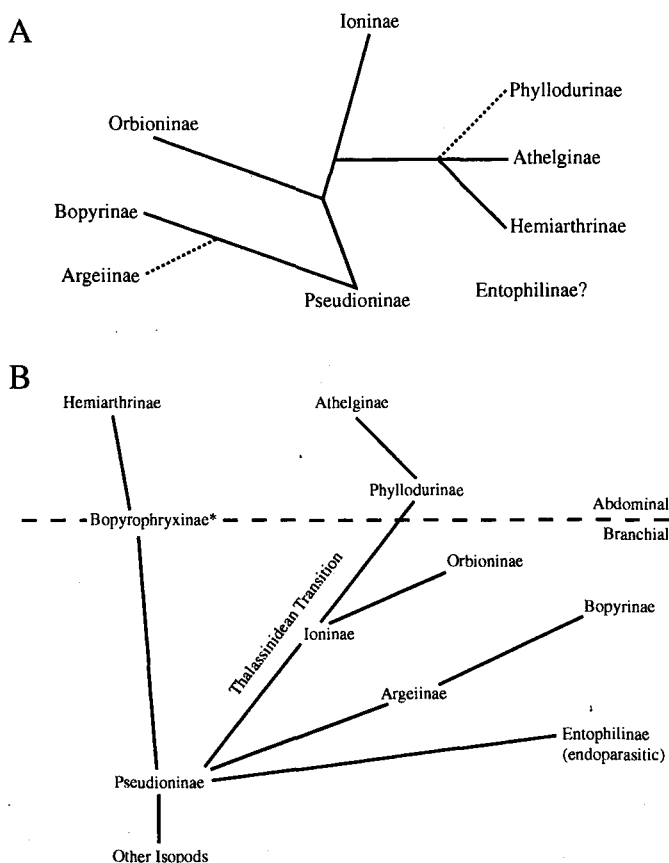


Figure 5. Hypotheses of the evolutionary relationships within the Bopyridae. (A) Proposed phylogeny based on Shiino (1965). Dotted lines indicate positioning of subfamilies based on the phylogeny from Shiino (1952); note that Entophilinae was not included in his trees and that subfamily names had not yet been proposed when these trees were originally presented. (B) Proposed phylogeny based on Markham (1986); horizontal dashed line indicates separation of isopods that infest the branchial chamber of hosts (bottom) or their abdomen (top). *Bopyrophryxinae are now members of the Pseudioninae; the Thalassinidean transition refers to those bopyrids that infest callianassid and upogebiid shrimp and are suspected to represent a link between the Pseudioninae and the Ioninae (Markham & Dworschak 2005).

No phylogenetic testing of the monophyly of the Bopyridae or any of its subfamilies has ever been attempted using morphological or molecular data. However, Shiino (1952, 1965) and Markham (1986) proposed evolutionary trees based on their years of research on this group (Fig. 5A & B, respectively). Both Shiino and Markham considered the Pseudioninae to be the basal group, based on morphology and broad range in host use. However, in many other features their trees are quite different. Shiino (1952, 1965) placed Athelginae and Hemiarthrinae (both abdominal parasites) as sister taxa, and showed only two lineages being derived from the Pseudioninae. Markham (1986), in contrast, showed four lineages arising from the basal taxon and placed Athelginae and Hemiarthrinae on two different branches. Additionally, while Shiino's (1952, 1965) trees can be converted into phylogenetic ones, albeit lacking a cladistic analysis, Markham's (1986) trees contain "transitional" taxa that are placed in direct line of descent from one subfamily to another. Specifically, he proposed that those bopyrids infesting callianassid and upogebiid shrimp represent a link between the Pseudioninae and the Ioninae — what he termed the "Thalassinidean transition" (see also Markham &

Dworschak 2005). Whether or not Markham's (1986) transitional forms may represent stem groups is not clear at this time.

Although there is a clear need for phylogenetic analyses of bopyrids, there are many taxonomic problems that need to be sorted out in order to make taxon sampling effective. Given the paucity of specimens for many described species, loss of type specimens, and lack of specimens properly preserved for molecular analysis, a phylogenetic analysis of the Bopyridae based on morphological and/or molecular data is a difficult task. One problem is exemplified by the type species of *Pseudione*, the largest genus in the family. The original description of *P. callianassae* by Kossmann (1881) was based only on an image of the ventral surface of the head of a male bopyrid, with no accompanying descriptive text. There are no useful characters present in the illustration, and this species is, based on this drawing, effectively unidentifiable. Only the choice of host is known (*Callianassa subterranea*), but two species of bopyrids are known from this European host species. On a morphological basis, it has long been suspected that *Pseudione* is paraphyletic, but the lack of an identifiable type species remains a barrier to resolving the taxonomic and phylogenetic issues of this large genus, as well for the Pseudioninae. A second problem is one of limited specimen collection and/or identification, which has resulted in lack of knowledge about the morphological boundaries of many species. In the case of *Metathelges muelleri*, described from a brachyuran host, the species was described from a single female specimen that was later determined to be likely developmentally aberrant (Boyko & Williams 2003). This resulted in the transfer of the genus from the Athelginae, where it was the only species ever reported from a brachyuran host, to the Ioninae, which are predominantly brachyuran parasites. A third potential difficulty, especially important in issues of coevolutionary analysis, is one of identification of the hosts. Usually, the problem is one of consistently recording the host identity and retaining this information with the parasite when it is separated. This has resulted in species' being described with unknown host data, or, occasionally, with incorrect host data, such as *Falsanathelges muelleri* being described by Nierstrasz & Brender à Brandis (1931) as collected from a "*Galathea*" (i.e., Galatheoidea), when it was in fact from a hermit crab collected by the vessel "*Galathea*"!

It is important to choose exemplar taxa for higher-level analyses carefully, as many genera of bopyrids have not been revised and may well be paraphyletic. An example is the genus *Gigantione*, which contains eight species known from brachyuran hosts, including three dromiids, and three species from thalassinoid hosts. This range of hosts may not accurately reflect patterns of host and parasite coevolution; examination of the original descriptions of all *Gigantione* species suggests that the brachyuran parasites and the thalassinoid parasites are not very similar to each other and appear to be currently placed in the same genus principally on the basis of females' having bifurcated uniramous uropods. If this genus is not monophyletic, any discussion of the coevolution of hosts and parasites would be confounded by the paraphyly of the parasite genus.

4 DECAPOD HOST AND PARASITE COEVOLUTION: INFERENCES BASED ON CURRENT DATA

Most of our discussion below is based on the decapod phylogeny of Dixon et al. (2003). However, we have also considered the findings of Porter et al. (2005) that present an alternative and dramatically different arrangement for many of the groups. It should be noted that our focus on Dixon et al. (2003) does not imply that we consider their study to be a more accurate representation of decapod phylogeny than other recent works (e.g., Ah Yong & O'Meally 2004; Tsang et al. 2008). At this point in time, it is probable that anyone who is "married" to any one particular decapod phylogeny is likely to suffer through a painful divorce at a later date.

In total, there are approximately 244 rhizocephalans and 586 bopyrids that parasitize decapods (representing 2.0 and 4.9% of the total number of decapods being infested by these two groups, respectively). The more derived decapods (Thalassinida + Achelata + Anomura + Brachyura) are host to 575 species of rhizocephalans and bopyrids, the bulk of which (515 species, ~90%) are found on

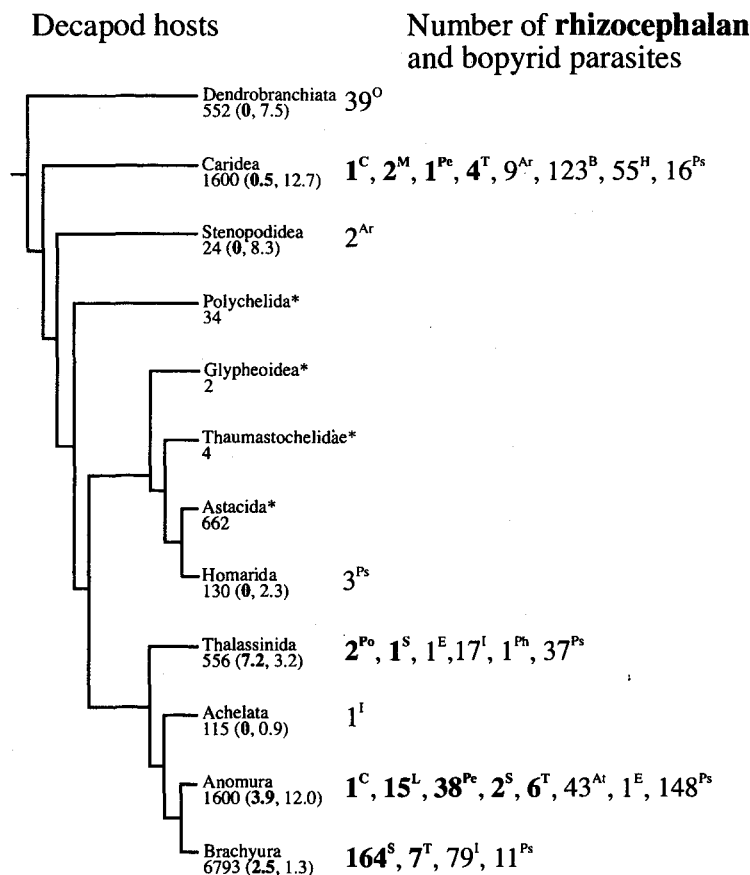


Figure 6. Phylogeny of the Decapoda showing numbers of rhizocephalan and bopyrid species that they host. Numbers under decapod groups indicate current estimates of total number of host species (numbers in parentheses indicate % of host species infested by rhizocephalans and bopyrids, respectively). Decapod phylogeny based on Dixon et al. (2003); *decapod taxa that do not host rhizocephalan or bopyrid parasites; rhizocephalan taxa (in bold): C = Clistosaccidae, L = Lernaediscidae, M = Mycetomorphidae, Pe = Peltogastridae, Po = Polysaccidae, S = Sacculinidae, T = Thompsoniidae; Bopyridae taxa: Ar = Argeiinae, At = Athelginae, B = Bopyrinae, E = Entophilinae, H = Hemiarthrinae, I = Ioninae, O = Orbioninae, Ph = Phylodurinae, Ps = Pseudioninae.

the Anomura and Brachyura (Fig. 6). In contrast, basal decapods (Dendrobranchiata, Caridea, and Stenopodidea) are host to less than half this number (252), the bulk of which (211 species, ~84%) are found on the Caridea. The relative diversity of rhizocephalans compared to bopyrids is low on the more basal decapods (8/252, ~3%) but is slightly less than half that of the bopyrids on the more derived decapods (236/575, ~41%). When the number of parasite species is standardized relative to the diversity of decapod host taxa, the host groups with highest percentages infested are: Anomura (15.9%), Caridea (13.2%), and Thalassinida (10.6%); the rest of the decapods have fewer than 10% infested in each taxon. Lack of parasites in some groups may represent sampling efforts, whereas others can be explained by their evolutionary history. For example, the Astacida harbor no definite parasites (although their commensal ostracods and annelids are thought by some to be parasitic), likely due to their invasion of freshwater habitats that provided a refuge from parasitism. As far as is known, most of the few species of rhizocephalans and bopyrids from hosts collected in freshwater are euryhaline and reproduce at the same time the hosts move towards the ocean to breed (Okada &

Miyashita 1935). There do not appear to be any bopyrids on hosts found in landlocked freshwater habitats, although there are truly freshwater rhizocephalans (Feuerborn 1931, 1933; Andersen et al. 1990). Below we discuss the host relations and coevolution for both these parasite groups.

4.1 *Rhizocephala*

Systematic work on the Rhizocephala subsequent to the contributions of Hildebrand Boschma, who worked on these organisms circa 1925–76, concentrated primarily on the non-Sacculinidae taxa. This has resulted in generation of morphological characters and life cycle data for many species in the Lernaediscidae, Peltogastridae, and Akentrogonida (e.g., Ritchie & Høeg 1981; Høeg & Lützen 1985; Lützen & Takahashi 1996). Therefore, there is a greater level of confidence in the monophyly of these groups than in the sacculinid taxa. Members of the Thompsoniidae, one of the most derived taxa in terms of reduced morphology, have the broadest diversity of host selection (four decapod groups plus Stomatopoda) (Fig. 6). This is a case, however, where diversity in host selection is not in conflict with the phylogeny of the group, as Glenner & Hebsgaard (2006) recovered a monophyletic Thompsoniidae. In fact, Glenner & Hebsgaard show a monophyletic Akentrogonida, if the poorly known monotypic *Parthenopea* is included, which generally supports prior morphologically based studies (e.g., Høeg & Rybakov 1992). In the Kentrogonida, Glenner & Hebsgaard (2006) support a monophyletic Peltogastridae + Lernaediscidae (which they label as Peltogastridae although there is not enough support or resolution in their tree to combine the two families) and the placement of *Peltogasterella* indicates that it may belong to a separate family. Except for the poorly known *Trachelosaccus* from a caridean, all the other peltogastrids and lernaediscids are known from anomuran hosts, a case of basal parasites targeting derived host taxa. The remainder of the Kentrogonida comprising the seven Sacculinidae genera is paraphyletic in Glenner & Hebsgaard's (2006) analysis, which, when combined with their placement of the Peltogastridae + Lernaediscidae, makes the Kentrogonida polyphyletic. Based on their results, the evolutionary pattern for the rhizocephalans appears to be: 1) an initial parasitism in anomurans (Peltogastridae + Lernaediscidae), 2) parasitism in brachyurans (a basal and a derived lineage of "Kentrogonida"), and 3) a lineage with great reproductive modification (loss of kentrogon) and a corresponding increase in host diversity across much of the Decapoda. One of the main difficulties with the kentrogonids, and the sacculinds in particular, is the high level of species diversity in the group, as compared to all other rhizocephalans. The average number of species per genus in the Sacculinidae is 23.8, but in reality more than 115 species occur in the single genus *Sacculina*. This is in marked contrast to the average number of species per genus in all the other rhizocephalan families that ranges from 1 (Clistosaccidae) to 6.3 (Thompsoniidae). In other words, in all families except the Sacculinidae, the genera are relatively small and better defined.

Several observations can be made from a comparison of the host and parasite phylogenies (Fig. 7), including that the most basal rhizocephalans do not parasitize basal decapods. In fact, none of the dendrobranchiate groups are known to host any rhizocephalans. The carideans are the most basal group to be parasitized, and then only by species of rhizocephalans from the derived akentrogonid genera *Pottsia* and *Sylon*. Species of the derived akentrogonid Mycetomorphidae and one species of the kentrogonid *Trachelosaccus* are also found on carideans, but these taxa were not sampled by Glenner & Hebsgaard (2006). A similar pattern of derived hosts being parasitized by primitive parasites with host-switching leading to invasion of a diverse range of taxa has been found in digenean trematode parasites of molluscs (Cribb et al. 2001).

Although no stenopodideans have been reported with rhizocephalans, one of us (CBB) has examined the stalked "bopyrid parasites" reported from a *Spongicoloides* species by Saito et al. (2006); and they are actually rhizocephalans that appear close to the genus *Trachelosaccus*, a poorly known possible member of the Kentrogonida. None of the polychelid lobsters or the Astacida are known to bear rhizocephalan parasites, making this the largest group of decapods not impacted by parasitic barnacles. Only four species of rhizocephalans are found on thalassinideans, but from three

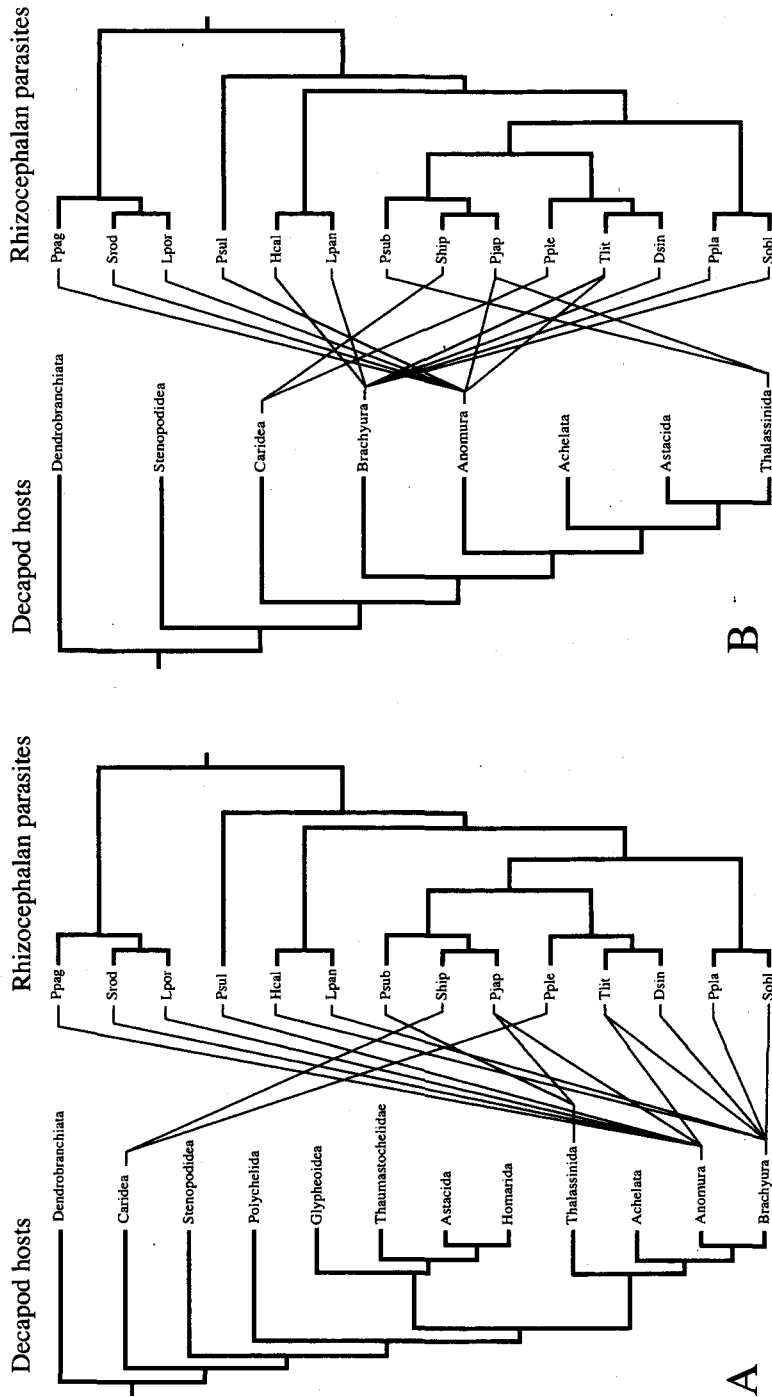


Figure 7. Phylogenies of decapod hosts and their rhizocephalan parasites. (A) Comparison of parasite phylogeny based on a subset of taxa from Glenner & Hebsgaard (2006) and host phylogeny based on Dixon et al. (2003). (B) Comparison of parasite phylogeny based on a subset of taxa from Glenner & Hebsgaard (2006) and host phylogeny based on Porter et al. (2005). Ppag = *Peltogaster paguri*, Srod = *Septosaccus rodriguezii*, Lpor = *Lernaodiscus porcellanae*, Psul = *Peltogasterella sulcata*, Hcal = *Heterosaccus californicus*, Lpan = *Loxothylacus panopaei*, Psab = *Parthenopea subterranea*, Ship = *Sylon hippolytes*, Ppap = *Polydora japonicus*, Pple = *Pottisia pleisonikae*, Tlit = *Thompsonia littoralis*, Dsin = *Diplothylacus sinensis*, Ppla = *Polydora plana*, Sobl = *Sacculina oblonga*.

different families. None of the Achelata have rhizocephalans and, if the spiny and slipper lobsters are indeed rather distant from the clawed lobsters, as born out by some recent analyses (e.g., Dixon et al. 2003), then perhaps the nature of their lobster-type morphology and ecology ("lobsterness") is resistant to rhizocephalan invasion. If, however, achelate lobsters are basal to the Astacura (Glypheidea + Astacidea), this resistance may be based on an evolutionary resistance derived from shared common ancestry. In fact, if considering only the lack of rhizocephalans in Polychelida, Achelata, and Astacura, the tree presented by Ah Yong & O'Meally (2004; fig. 3) is more parsimonious in uniting all the taxa above that are known to bear rhizocephalans in a single clade (Lineata) as opposed to that given by Dixon et al. (2003) where Achelata is positioned between Thalassinida and Anomura + Brachyura. This situation indicates the potential utility of parasites in analyzing phylogenetic relationships of host taxa.

4.2 Bopyridae

Based on host specificity alone, five of the bopyrid subfamilies are likely to be monophyletic: Bopyrinae, Hemiarthrinae, Athelginae, Orbioninae, and the monotypic Phylloporinae. The diversity of host taxa in the other four subfamilies, especially the Pseudioninae, does not in itself indicate polyphyly but suggests that those subfamilies are in need of rigorous analyses. Indeed, the Argeiinae and Pseudioninae have been suggested as being para- or polyphyletic on the basis of morphological characters (Adkison et al. 1982; Boyko & Williams 2001). However, all of the subfamilies need to have their monophyly tested by both morphological and molecular characters.

As with the Rhizocephala, the bopyrid parasites appear to have invaded relatively derived hosts (anomurans) first and later switched to other decapods (Fig. 8). These findings represent another potential parallel with results obtained by Cribb et al. (2001) in that eco-physiological similarities of hosts may play a role in associations over time. Specifically, the ecological niche of penaeids may have excluded most bopyrids, excepting the ancestral orbionines, from switching to these hosts. Likewise, the distinctive morphology of the relatively exposed abdomens of hermit crabs and carideans may have resulted in either convergent evolution of athelgine and hemiarthrine bopyrids (if they are not sister-taxa as per Markham 1986) or host switching from a putative paguroid host to a caridean one if they are closely related (as per Shiino 1952, 1965). At this juncture, however, the relationship between these abdominal parasite taxa is unclear.

There is a much greater diversity of host range within the Bopyridae than in the Rhizocephala, including several taxa (Dendrobranchiata, Homarida, Achelata) that are known to bear bopyrid parasites but not rhizocephalans. The parasites of homarids and achelates appear to be rather undifferentiated members of large genera (*Pseudione* and *Dactylokepon*), the majority of whose members infest other taxa (anomurans and brachyurans, respectively). In contrast, the parasites of dendrobranchiates are all members of a single lineage (Orbioninae) that has evolved to specialize on these shrimp and whose species are found parasitizing no other types of hosts.

4.3 An example of coevolution within the Bopyridae

An example of the potential of parasites as a phylogenetic character for decapod evolutionary studies can be seen in the three species of bopyrids found on albuneid crabs (Anomura: Hippoidea) (Fig. 9).

Each of the species of *Albunione* (Pseudioninae) shows the same relationships with respect to each other as their hosts in the genus *Albunea*. *Albunione australiana* is the sister species to the *A. indecora* + *A. yoda* clade, based on morphological characters of both males and females. Likewise, their hosts show the same pattern: *Albunea microps* is the sister species to the clade of *A. groeningi* + *A. paretii* (Boyko & Harvey, unpublished data). Although this analysis suggests some degree of cospeciation between parasites and hosts, reconciling their phylogenies requires the proposal of multiple species of hosts that lack parasites due to sorting events (extinction or

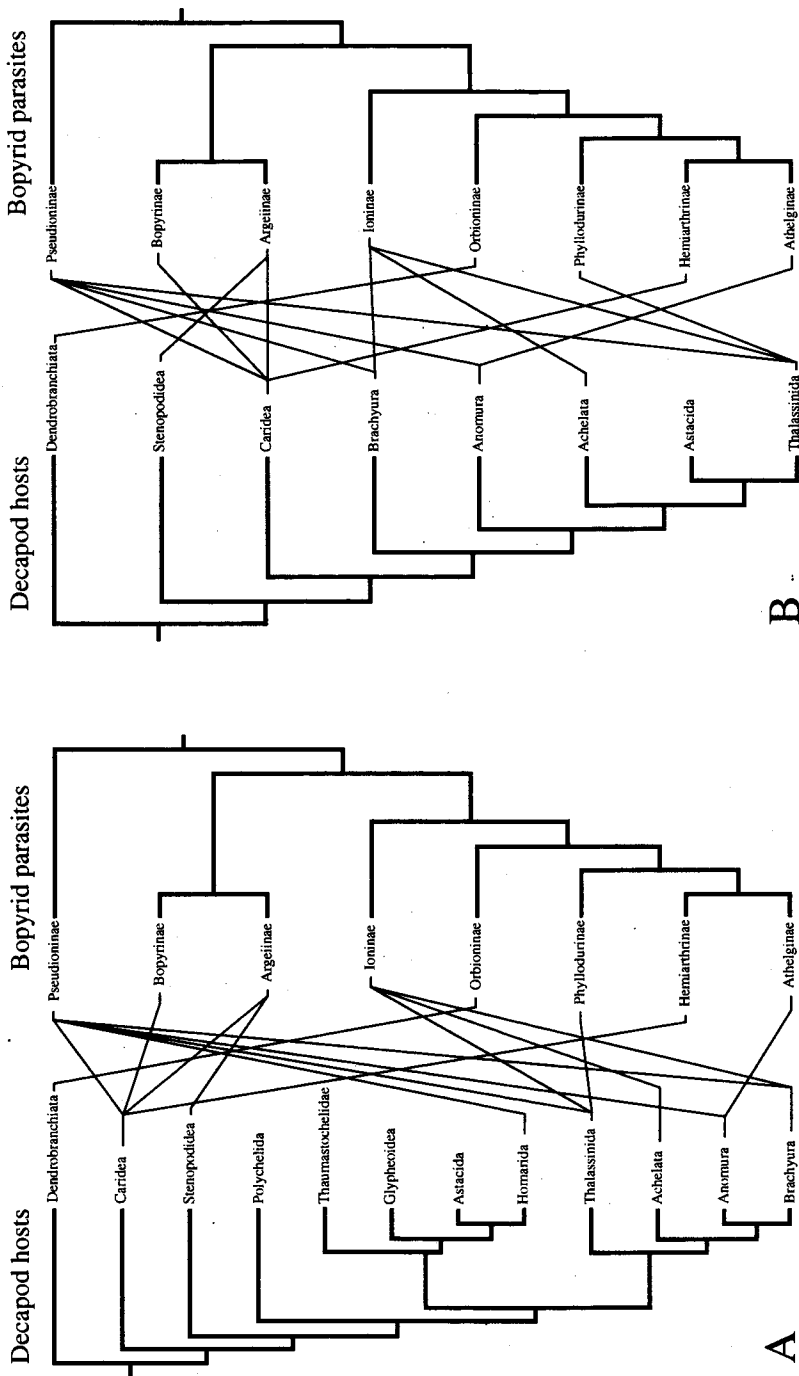


Figure 8. Phylogenies of decapod hosts and their bopyrid parasites (minus Entophilinae). (A) Comparison of parasite phylogeny based on Shiino (1952, 1965) and host phylogeny based on Dixon et al. (2003). (B) Comparison of parasite phylogeny based on Shiino (1952, 1965) and host phylogeny based on Porter et al. (2005).

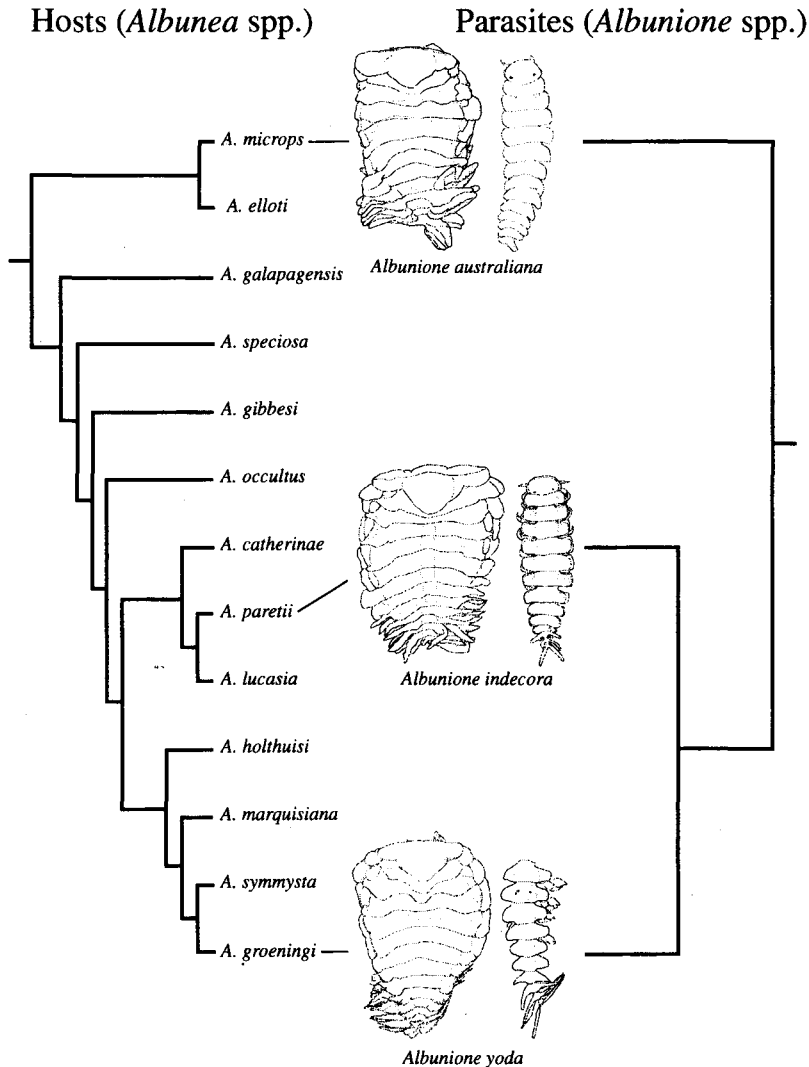


Figure 9. Phylogenies of the sand crab genus *Albunea* and the three species of branchial parasitic isopods (genus *Albunione*) that infest them. (Host phylogeny based on Boyko & Harvey, unpublished data; parasite phylogeny based on Markham & Boyko 2003).

lack of sampling). As indicated by Page & Charleston (1998), coevolutionary analyses can lead to hypotheses of hosts that apparently lack parasites but probably do so because they have not been extensively sampled. Given that only these three bopyrids parasitizing species in the Albuneidae are known, it is likely that our knowledge of the diversity of isopod parasites on these anomuran hosts is incomplete. Based on comparison of the analysis of the Shiino/Markham hypotheses with that of the *Albunea*/*Albunione* relationship, the coevolution of parasites and hosts may be more informative at the genus level than at higher taxonomic levels. However, more data must be gathered and analyzed to draw any general conclusions about this.

5 CONCLUSIONS

It is clear from the above discussion that we are only beginning to understand the coevolution between decapods and their crustacean parasites. Cross-phyletic comparisons between rhizocephalans and bopyrids are difficult to interpret due to the fact that the taxonomic levels of the parasites included in the analyses are different (species versus subfamilies). However, one common feature of the rhizocephalan and bopyrid coevolutionary analyses is that anomurans and other more derived host taxa are parasitized by members of basal parasite groups. Because the Anomura is among the more derived groups of decapods, they would be expected to have more derived parasites compared to, for example, penaeids that are more basal. It may be that anomurans, specifically galatheoids, are more susceptible to infestation by parasites than are other decapods. Evidence for this can be found in the robust fossil record for galatheid/bopyrid associations (Markham 1986) and in the large number of extant parasitized anomurans. Although there is clear evidence of some anomurans' having acquired the ability to mechanically resist parasite attack, at least against rhizocephalans (Ritchie & Høeg 1981; Høeg et al. 2005), further study needs to be undertaken to determine if this behavior is found within other decapod groups. Bauer (1981, 1989) hypothesized that selection pressures for natant decapods to remove epifauna that would impede swimming led to efficient mechanisms for removal of parasites, whereas in the more derived, generally non-swimming, decapods (e.g., Anomura and Brachyura) selection pressures to remove these parasites were reduced. One problem with this hypothesis is that, without experimentation, it is not possible to use absence of parasites on hosts as an indicator of their ability to deal with parasites. For example, is the presence of only two species of rhizocephalans (and no bopyrids) on cancrid crabs due to members of the Cancridae having experienced little to no historical parasitic pressure, or have they evolved effective defenses against the parasites? More data need to be collected across the spectrum of decapods in the context of their morphological, physiological, and particularly behavioral adaptations developed in the context of this evolutionary arms race (Ruiz 1991).

Coevolutionary analyses of these parasites of decapods go beyond "ivory tower" research and can inform future studies on the ecology of host-parasite relationships and applied areas of research, including fisheries. As in the *Albunione* example, studies of host/parasite coevolution may allow us to identify host lineages where parasites are unknown but, based on their shared histories, might be expected. Also, a robust understanding of these relationships would allow identification of hosts that are not impacted by parasites (such as the aforementioned cancrid crabs) and suggest the need for further study of the morphological, immunological, and/or behavioral methods they may utilize to resist attack.

These types of coevolutionary studies also can be used in light of the recent attention deservedly given to the problem of invasive species. Rhizocephalan parasites have been suggested as possible biological controls of decapods, in particular the green crab *C. maenas* that has been introduced from Europe to various parts of the world, including the east and west coasts of North America (see Griffen et al. 2007). The rhizocephalan *Sacculina carcini* has been evaluated as a biological control for *C. maenas* (Goddard et al. 2005; Lafferty & Kuris 1996; Thresher et al. 2000; Kuris et al. 2005; Kuris et al. 2007). Along the east coast of the United States, *Carcinus maenas* now competes with the Japanese shore crab *Hemigrapsus sanguineus*, which was first reported from New Jersey in 1988 (McDermott 1991) and has spread from North Carolina to Maine (McDermott 1998, 2000) and has been introduced to Europe and the Mediterranean (Breton et al. 2002; Schubart 2003). In its native habitat of Russia southward to Hong Kong and Japan, this crab is commonly parasitized by the rhizocephalan *Polyascus polygenea*, which sterilizes the crab hosts (Korn et al. 2004), but no rhizocephalans are found impacting the species in its introduced range (McDermott 1998, 2007). The recent rapid spread of *C. maenas* and *H. sanguineus* could reflect their release from parasite pressures (Torchin et al. 2001, 2003). However, introduction of native parasites as biocontrol agents requires detailed studies on host specificity of the parasites (e.g., Goddard et al. 2005; Kuris et al. 2005; Kuris et al. 2007). Given the paucity of our knowledge about the coevolutionary processes

that promote or inhibit tightly linked parasite/host relationships, the possibility of decapods being vulnerable to multiple parasite species (Tsuchida et al. 2006), and the ability of some rhizocephalan barnacles to parasitize novel hosts, it would be premature to allow such importation without additional study (Goddard et al. 2005). Even in the event of a controlled release of a rhizocephalan for a target invasive species, there may be little impact on the invader. The rhizocephalan *Heterosaccus dollfusi*, accidentally introduced into the Mediterranean over three decades after its host, has apparently not reduced populations of *Charybdis longicollis* in this region (Innocenti & Galil 2007). The only other known introduced rhizocephalan is *Loxothylacus panopaei*, a parasite of mud crabs that was accidentally introduced to the Chesapeake Bay from the Gulf of Mexico (see Kruse & Hare 2007), which also has limited impacts on host populations (Alvarez et al. 1995). These findings from “natural experiments” suggest that rhizocephalans may have limited utility in combating invasive hosts, and their potential impact on non-target species is far from clear.

The use of parasitic isopods as biological controls has received less attention than rhizocephalans, but some researchers have investigated the potential use of the entoniscid isopod *Portunion maenadis* for the control of *Carcinus maenas* (Høeg et al. 1997; Kuris et al. 2005) and the hyperparasitic cryptoniscid isopod *Cabirops orbionei* for the control of bopyrids on penaeid shrimp (Owens 1993). As indicated by Kuris et al. (2005), the use of epicaridean parasites requires careful evaluation and modeling due to their indirect life cycle and, as in the Rhizocephala, the potential for non-target hosts to be impacted.

In conclusion, parasitic crustaceans may offer insights into the evolutionary histories of their decapod hosts and vice versa. Although host switching among decapod host taxa appears to have occurred in both bopyrids and rhizocephalans, coevolutionary patterns may be more tightly linked at lower taxonomic levels (e.g., species, genera) than at higher ones (infraorders, families). More emphasis should be placed on generating cladistic analyses for parasite lineages, as well as on careful assessment of the status of some, particularly marine, potential host lineages that currently appear parasite-free. Results from these types of studies could be applied across disciplines of interest to crustacean biologists, such as ecological, developmental, and fisheries biology, as well as in the arena of crustacean systematics.

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