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## The unwanted guests of hermits: A global review of the diversity and natural history of hermit crab parasites

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## ABSTRACT

Hermit crabs (superfamily Paguroidea), by their typical nature as inhabitants of mobile, protective domiciles, are a unique source for studying symbiotic relationships. A great variety of symbionts attach, bore into or live free in the lumen of shells harboring hermit crabs, and hermit crabs themselves as hosts for a variety of parasites and potential parasites are the subject of this review. Approximately 130–140 species of the >850 known hermit crab species are parasitized by 149 species in 9 phyla, and 27 species are hosts for 17 potential parasites in 5 phyla. Among the confirmed parasites, 30 species of parasitic barnacles (Rhizocephala) and 83 species of parasitic Isopoda are known. Species in other groups of parasites are few in number: Apicomplexa 2, Dinoflagellata 1, Microsporidia 2, Ascomycota 1, Platyhelminthes 8, Acanthocephala 2, Nematoda 3, and Nematomorpha 2. Fifteen species of ectosymbiotic mites are obligate associates, but little is known of their possible parasitic tendencies. In terms of trophic strategies, the rhizocephalans, nematomorphans and two flatworm species are complete parasitic castrators and the parasitic isopods are partial parasitic castrators. The rest of the species are trophically transmitted parasites (Apicomplexa, Platyhelminthes, Acanthocephala and Nematoda) or are classified as pathogens (Apicomplexa, Dinoflagellata, Microsporidia, and Ascomycota). Limited information shows that hermit crabs are first or second intermediate hosts for coccidians, cestodes, trematodes, acanthocephalans and nematodes. The importance of hermit crabs as definitive and intermediate hosts is greatly underestimated due to insufficient worldwide sampling for parasites. The ten most well-studied hermit crab host species are from European waters, the western Atlantic and the eastern Pacific. In contrast, the lower parasite diversity of the Indo-West Pacific region is presumably due to limited sampling. Hermit crabs are also known to host at least 17 species of obligate, intimate associates (not presently considered parasites), but further analyses are required to more fully clarify their symbiotic relationships. Among these potential parasites are four mesomycetozoans that are found in the digestive tract of hosts and four apistome ciliates whose reproduction is synchronized with the host's molting. Symbiotic nemertean and octolasmid barnacles that are common associates of decapods have, surprisingly, yet to be discovered associated with hermit crabs. In total, at least ten species of hyperparasites are found infesting primary associates (mostly rhizocephalans and bopyrids) of hermit crabs. Hyperparasitism involves: 1) rhizocephalans as hosts for one described species of amoeba and four species of cryptoniscid isopods, 2) bopyrid isopods as hosts for three described species of cabriopid isopods and one rhizocephalan (Akentrogonida), and 3) a burrowing barnacle (Trypetesidae) as host for one species of hemioniscid isopod. The biology and life histories of most hermit crab parasites, with the exception of rhizocephalans and some isopods, are poorly known and the role of crabs as intermediate hosts is especially in need of study. The information presented herein on geographical distribution of host species, the prevalence of their parasites, and known host-parasite relationships should be useful for developing models that will elicit a greater understanding of hermit crab parasitism. Such information, along with morphological and molecular analyses might lead to a better understanding of the evolution of anomurans and decapods as a whole.

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## 1. Introduction

Hermit crabs act as hosts in a variety of symbiotic relationships, due to their typical behavior of inhabiting domiciles (usually empty gastropod shells) that act as a refuge or space for settlement. Hermit crabs are considered allogenic ecosystem engineers and through their use of shells they prevent shell resources from being buried (Williams and McDermott, 2004; Wright and Jones, 2006). Since hard substrates such as rocks can be limited in many marine habitats, occupation of shells affords a stable but mobile substrate for epibiotic and endolithic species. Hence, many invertebrates have formed commensal or mutualistic relationships (both facultative and obligate) with these decapod hosts (Williams and McDermott, 2004).

The symbiotic relationships between hermit crabs and their associates are not always clearly defined and can change between commensalism, mutualism, and parasitism depending on environmental factors (both abiotic and biotic). For example, the hydroid *Hydractinia symbiolongicarpus* Buss and Yund, 1989 is a common associate of the hermit crab *Pagurus longicarpus* along its range on the east coast of the United States and has been the focus of numerous ecological, developmental and molecular studies (see Williams and McDermott, 2004). *Hydractinia symbiolongicarpus* is often classified as a commensal species. However, the hydroid is known to negatively

impact the reproductive output of *P. longicarpus* (Damiani, 2003) and to decrease the strength of shells, thus exposing hosts to increased chances of predation (Buckley and Ebersole, 1994; Bach et al., 2006). The association is further complicated by findings that suggest the hydroid confers protection to the host from certain predators (Brooks and Mariscal, 1985). This system shows how the classification of symbiotic relationships can be difficult and it is better to view these associations as symbiotic continuums rather than concrete categories (Bush et al., 2001; Williams and McDermott, 2004). In contrast, there are confirmed parasites of hermit crabs that, regardless of environmental factors, negatively influence fitness of hosts. Among these, species of parasitic isopods and barnacles are relatively common and their detrimental impacts on host reproduction (e.g., parasitic castration) are particularly evident.

Lafferty and Kuris (2002) do not consider parasitic associations as parts of continua, but instead view such associations as involving distinct trophic strategies that can be compared to other natural enemies such as predators. Parasites and predators are distinguished by the fact that parasites attack only one host during each of their life-history stages whereas predators typically consume multiple prey. Eight types of parasites can be defined: typical parasites, trophically transmitted typical parasites, pathogens, trophically transmitted pathogens, partial castrators, parasitic castrators, trophically transmitted

parasitic castrators, and parasitoids (Kuris and Lafferty, 2000; Lafferty and Kuris, 2002). Some of these parasites block reproduction or kill their hosts (parasitic castrators, trophically transmitted parasitic castrators, and parasitoids) whereas the rest typically do not kill their hosts or shut down their reproduction completely. Most trophically transmitted parasites and parasitoids cause the death of their hosts (intermediate hosts for the former) whereas the remainder does not. A final distinction within the parasites can be made between those that have intensity-dependent effects on hosts, i.e., host fitness decreases with increasing intensity of the parasites (found in typical parasites, trophically transmitted typical parasites, partial castrators, and trophically transmitted parasitic castrators) versus those that appear to be intensity-independent, i.e., impacts of multiple infections are overshadowed by the ability of these parasites to multiply in the host once infected (found in pathogens, trophically transmitted pathogens, parasitic castrators, and parasitoids) (Kuris and Lafferty, 2000).

The purpose of the present study is to provide a review of the biology and natural history of all hermit crab parasites, including well-known taxa and groups in need of further study. The combination of Williams and McDermott's (2004) previous review of the biology of hermit crab symbionts (commensal and mutualistic species) with the present study represents a nearly complete view of the symbiotic relationships involving hermit crabs (flora are not covered in either work). Whereas lists of certain hermit crab parasites have been compiled [e.g., protozoan parasites (Sprague and Couch, 1971) and isopod parasites (Markham, 2003)] and parasite reviews of individual host species are known [e.g., parasites of *Pagurus bernhardus* (Lancaster, 1988) and *P. longicarpus* (McDermott, 2001)], this paper is the first to provide a comprehensive review of all known hermit crab parasites worldwide.

Due to their relative ease in collection and extensive literature on their ecology and behavior, hermit crabs provide an excellent model system for experimental studies on host/parasite interactions. For example, research on the host specificity of parasites could be explored with parasitic isopods and barnacles. Such studies investigating the encounter/capability paradigm of rhizocephalans and other parasites of crustaceans are rare (Kuris et al., 2007). Hermit crabs are ripe for this type of research and would expand our understanding of the mechanistic basis for the specificity of parasites that have evolved to infest a limited range of host species within hermit crab assemblages. Complementary studies could explore the coevolution of hermit crabs and these parasites to determine the degree of congruence in their phylogenies (as explored for decapods as a whole by Boyko and Williams, 2009).

The trophic strategies of hermit crab parasites (including species with potential parasitic tendencies) and impacts on hosts are evaluated in this review, providing a basis for studies directed at more accurately defining these complex relationships. Finally, aspects of the biology and ecology of hermit crab parasites in need of study are highlighted. For example, poorly known aspects of their life histories and their impacts on hermit crabs as parasitic castrators are evaluated. As found for commensal and mutualistic symbionts, parasites may have important impacts on the populations of hermit crab hosts, which are important members of food webs in a variety of marine habitats (Williams and McDermott, 2004). Through their influence on hermit crabs, parasites can impact marine communities, either directly (via trophic interactions) or indirectly (via the action of hermit crabs as ecosystem engineers) (Mouritsen and Poulin, 2002). In applied settings hermit crabs could be used as a model system to study *Hematodinium* spp. and other parasites that impact commercially important species such as tanner (*Chiononecetes* spp.), snow (*C. opilio* (Fabricius, 1788)), and blue crab (*Callinectes sapidus* Rathbun, 1896) fisheries. In addition, hermit crabs can be used as indicators for stormwater runoff (Dunbar et al., 2003) and parasites may make them more susceptible to contaminants in such waters (Williamson et al., 2009).

## 2. Analysis

Data on the parasites of hermit crabs were gathered from the literature since 1864 (inception of the Zoological Record). Parasites of the atypical "free-living" lithodid paguroids (Lithodidae + Hapalogastriidae) are not included in this review. Transient parasites such as egg predators are excluded from this analysis (see Williams and McDermott, 2004 for review), as are viruses and bacteria associated with hermit crabs (see Leu et al., 2009; Klaphake, 2009). We have used the following definitions for the habitus of the hermit crab parasites: endoparasites are found within the body of hosts, ectoparasites are attached to the surface of hosts, and mesoparasites are found within the body of hosts and span to the external environment (e.g., Rhizocephala). Ectoparasites are further subdivided into those species that are found attached within the branchial chamber and those attached to the abdomen. For trophic strategies of the parasites we used the eight categories defined by Kuris and Lafferty (2000): typical parasites, trophically transmitted typical parasites, pathogens, trophically transmitted pathogens, partial castrators, parasitic castrators, trophically transmitted parasitic castrators, and parasitoids. In this review we used the term complete parasitic castrators (defined as parasites that completely block host reproduction) to distinguish these parasites from partial parasitic castrators (defined as parasites that have some less drastic, but negative impact on host reproduction). The trophic strategies of many of the species in the analysis are in need of further study. Where data are limited (e.g., in the delineation between partial and complete parasitic castrators), we have classified the trophic strategies of the species based on the present knowledge of the biology of these parasite groups and their impacts on hosts.

In addition to strict hermit crab parasites, we also include those species that are attached to or inside the bodies of hermit crabs and may have detrimental impacts on these hosts (as periodic or transient parasites). Most of the higher taxa used in the text and tables follow Brusca and Brusca (2003), Lee et al. (2000), and Martin and Davis (2001). We attempted to provide currently accepted names for all host and symbiont species; those species of unknown taxonomic status and/or questionable identity were noted but left as originally designated. Within the text, taxonomic authority and date are provided only for those species that do not appear in Tables 1–3. When reporting totals of species (parasites and hosts), we counted all described species and any undescribed species in genera not otherwise listed. For completeness of record, we note that Bukashkina (2004) reported on a fictitious colonial parasite of hermit crabs, considered to be related to the nose-walker group Rhinogradentia, a fictitious order of mammals (Stümpke, 1967).

## 3. Results

There are approximately 149 different species of parasites (representing 9 phyla) associated with hermit crabs worldwide (Fig. 1; Tables 1). This total includes one group (Acari) that we suspect are parasites, although no data have conclusively shown a negative impact on hosts. Whereas the Apicomplexa, Dinoflagellata, Microsporidia, Ascomycota, Platyhelminthes, Acanthocephala, Nematoda, and Nematomorpha are represented by 8 or fewer species each, the arthropods represent a major group of hermit crab parasites. Two arthropod groups, the parasitic barnacles (Rhizocephala) and parasitic isopods (Bopyridae and Etoniscidae), are represented by 30 and 83 parasite species, respectively (Table 1).

Five types of trophic strategies were found among the hermit crab parasites. In total, 117 (78.5%) of the species are parasitic castrators, reflecting the predominance of parasitic barnacles (complete parasitic castrators) and parasitic isopods (partial parasitic castrators); in addition, two flatworms and two nematomorphs are considered complete parasitic castrators (Fig. 1A). Twelve trophically transmitted



**Table 1**

Parasites of hermit crabs. Trophic: Trophic strategy (Pa: Pathogen; TtPa: Trophically transmitted Pathogen; TtTp: Trophically transmitted Typical parasite; CPc: Complete Parasitic castrator; PPc: Partial Parasitic castrator; Unk: Unknown); Hab: Habitus of parasite (Eca: Ectoparasitic, Abdominal; EcB: Ectoparasitic, Branchial; En: Endoparasitic; Meso: Mesoparasitic); Type: role of hermit crab in life-cycle of the parasite (Def: Definitive host; Int: Intermediate host; Unk: Unknown); Locality = geographic region where parasite collected. Genera and species of associates are listed under higher taxa in alphabetical order. “?” indicates questionable identification of host, parasite, or trophic strategy. \*Acari associated with hermit crabs have not been verified as parasites.

Associate species	Associate authority	Host hermit crab species	Host authority	Trophic	Hab	Type	Locality	Reference
<b>Phylum Apicomplexa, Class Sporozoea</b>								
<i>Aggregata vagans</i>	Léger and Duboscq, 1903	<i>Pagurus prideaux</i>	Leach, 1815	TtPa	En	Int	France	Léger and Duboscq, 1903
<i>Cephaloidophora ocellata</i>	(Léger and Duboscq, 1907)	<i>Pagurus prideaux</i>	Leach, 1815	Pa	En	Def	France	Léger and Duboscq, 1907
<b>Phylum Dinoflagellata</b>								
<i>Hematodinium</i> sp.		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)	Pa	En	Unk	Clyde Sea, Scotland	Hamilton et al., 2009
		<i>Pagurus prideaux</i>	Leach, 1815	Pa	En	Unk	Clyde Sea, Scotland	Hamilton et al., 2009
<b>Phylum Microsporidia</b>								
<i>Enterosporea</i> sp.		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)	Pa	En	Def	U.K. waters	Stentiford and Bateman, 2007
<i>Thelohania paguri</i>	Pérez, 1927	<i>Pagurus bernhardus</i>	(Linnaeus, 1758)	Pa	En	Def	France	Pérez, 1927a
<b>Phylum Ascomycota, Class Sordariomycetes, Order Hypocreales</b>								
<i>Fusarium solani</i>		<i>Pagurus pollicaris</i>	Say, 1817	Pa	Meso	Def	Massachusetts	Smolowitz et al., 1992
		? <i>Pagurus acadianus</i>	Benedict, 1901				Massachusetts	Smolowitz et al., 1993
		? <i>Pagurus longicarpus</i>	Say, 1817				Massachusetts	Smolowitz et al., 1993
<b>Phylum Platyhelminthes, Class Fecampiida</b>								
<i>Fecampia erythrocephala</i>	Giard, 1886	<i>Anapagurus hyndmanni</i>	(Bell, 1845)	CPC?	En	Def	France	Pérez, 1927a, 1934
		<i>Anapagurus hyndmanni</i>	(Bell, 1845)				Mediterranean, Tunisia	Mouchet, 1931
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)				France, English Channel	Giard, 1886
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)				France, English Channel	Pérez, 1934
<i>Kronborgia</i> -like species		<i>Pagurus trigonocheirus</i>	(Stimpson, 1858)	CPC?	En	Def	Alaska, Point Barrow	Christensen and Kannevorff, 1967
<b>Phylum Platyhelminthes, Class Cestoda</b>								
<i>Calliobothrium verticillatum</i>	(Rudolphi, 1819)	<i>Pagurus pollicaris</i>	Say, 1817	TtTp	En	Int	Massachusetts, Woods Hole	Caira and Ruhnke, 1991
		<i>Pagurus pollicaris</i>	Say, 1817				Massachusetts, Woods Hole	Cherry et al., 1991
		<i>Pagurus pollicaris</i>	Say, 1817				Massachusetts, Woods Hole	Smolowitz et al., 1992, 1993
<i>Calliobothrium</i> cf. <i>verticillatum</i>	(Rudolphi, 1819)	<i>Pagurus pollicaris</i>	Say, 1817	TtTp	En	Int	Connecticut, Long Island Sound	Fyler, 2007
<i>Rhynchobothrium</i> sp.		<i>Paguristes puncticeps</i>	Benedict, 1901	TtTp	En	Int	Florida, Dry Tortugas	Pearse, 1932
larval cestode		<i>Pagurus granosimanus</i>	(Stimpson, 1859)	TtTp	En	Int	California	Abbott, 1987
<b>Phylum Platyhelminthes, Class Trematoda</b>								
<i>Cymatocarpus solearis</i>	(Braun, 1899)	<i>Pagurus tinctor</i>	(Forskål, 1775)	TtTp	En	Int	Persian Gulf	Dollfus, 1927
<i>Derogenes varicus</i>	Müller, 1784	<i>Pagurus pubescens</i>	Krøyer, 1838	TtTp	En	Int	Russia, Barents Sea	Uspenskaya, 1960
<i>Microphallus pirum</i>	(Afanas'ev, 1941)	<i>Pagurus hirsutiusculus</i>	(Dana, 1851)	TtTp	En	Int	Alaska, Amchitka Island	Schiller, 1954
<i>Steganoderma formosum</i>	Stafford, 1904	<i>Pagurus acadianus</i>	Benedict, 1901	TtTp	En	Int	Nova Scotia, Canada	Marcogliese, 1996
		<i>Pagurus pubescens</i>	Krøyer, 1838	TtTp	En	Int	Russia, Barents Sea	Uspenskaya, 1960
<b>Phylum Acanthocephala</b>								
<i>Polymorphus</i> sp.		<i>Pagurus longicarpus</i>	Say, 1817	TtTp	En	Int	Massachusetts, Woods Hole	Reinhard, 1944
<i>Profilicollis botulus</i>	(Van Cleave, 1916)	<i>Pagurus pubescens</i>	Krøyer, 1838	TtTp	En	Int	Russia, Barents Sea	Uspenskaya, 1960
<b>Phylum Nematoda</b>								
<i>Ascarophis morrhuae</i>	Van Beneden, 1871	<i>Pagurus pubescens</i>	Krøyer, 1838	TtTp	En	Int	Russia, Barents Sea	Uspenskaya, 1953, 1960
<i>Ascarophis pacificus</i>	Zhukov, 1960	<i>Pagurus middendorffii</i>	Brandt, 1851	TtTp	En	Int	Russia, Sea of Okhotsk	Tsimbalyuk et al., 1970
<i>Ascarophis</i> sp.		<i>Pagurus granosimanus</i>	(Stimpson, 1859)	TtTp	En	Int	California, Bodega Bay	Poinar and Thomas, 1976
		<i>Pagurus samuelis</i>	(Stimpson, 1857)				California, Bodega Bay	Poinar and Thomas, 1976
		<i>Coenobita scaevola</i>	(Forskål, 1775)				Mediterranean, Egypt	El-Damhougy and El Alf, 2003
<i>Proleptus</i> sp.		<i>Dardanus lagopodes</i>	(Forskål, 1775)	TtTp	En	Int	Australia, Great Barrier Reef	Lester and Sewell, 1989
<b>Phylum Nematomorpha</b>								
<i>Nectonema agile</i>	Verrill, 1879	<i>Anapagurus hyndmanni</i>	(Bell, 1845)	CPc	En	Def	France	Pérez, 1927b, 1927c, 1934
		<i>Anapagurus hyndmanni</i>	(Bell, 1845)				Mediterranean, Tunisia	Mouchet, 1931
		<i>Anapagurus</i>	(Bell, 1845)				Mediterranean,	Feyel, 1936

(continued on next page)

Table 1 (continued)

Associate species	Associate authority	Host hermit crab species	Host authority	Trophic	Hab	Type	Locality	Reference
<b>Phylum Nematomorpha</b>		<i>hyndmanni</i>					Gulf of Naples	
		<i>Anapagurus laevis</i>	(Bell, 1845)				France, English Channel	Pérez, 1934
		<i>Diogenes pugilator</i>	(Roux, 1828)				France, English Channel	Pérez, 1934
		<i>Pagurus acadianus</i>	Benedict, 1901				Canada, Bay of Fundy	Leslie et al., 1981
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)				Mediterranean, Tunisia	Mouchet, 1931
<i>Nectonema munidae</i>	Brinkmann, 1930	<i>Pagurus bernhardus</i>	(Linnaeus, 1758)	CPc	En	Def	France, English Channel	Pérez, 1934
		<i>Pagurus cuanensis</i>	Bell, 1845				Norway, Bergen	Brinkmann, 1930
		<i>Pagurus cuanensis</i>	Bell, 1845				Norway, Bergen	Nielsen, 1969
		<i>Pagurus pubescens</i>	Krøyer, 1838				Norway, Bergen	Brinkmann, 1930
		<i>Pagurus pubescens</i>	Krøyer, 1838				Norway, Bergen	Nielsen, 1969
<b>Phylum Arthropoda, Infraclass Cirripedia, Superorder Clistosaccus</b>		<b>Rhizocephala, Order Akentrogonida</b>						
<i>Clistosaccus paguri</i>	Lilljeborg, 1860	<i>Anapagurus chiroacanthus</i>	(Lilljeborg, 1856)	CPc	Meso	Def	North Atlantic	Reinhard, 1944
		<i>Anapagurus laevis</i>	(Bell, 1845)				North Atlantic	Moore and Nickell, 1990
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)				North Atlantic	Høeg and Lützen, 1985
		<i>Pagurus capillatus</i>	(Benedict, 1892)				Alaska, Bering Sea	Reinhard, 1944
		<i>Pagurus dalli</i>	(Benedict, 1892)				Alaska	Reinhard, 1944
		<i>Pagurus forbesii</i>	Bell, 1845				North Atlantic	Reinhard, 1944
		<i>Pagurus pubescens</i>	Krøyer, 1838				North Atlantic	Høeg and Lützen, 1985
		<i>Labidochirus splendescens</i>	(Owen, 1839)				Alaska	Reinhard, 1944
		unidentified					Vostok Bay	Shukalyuk et al., 2007
<i>Thompsonia chuni</i>	Häfele, 1911	<i>Parapagurus sp.</i>		CPc	Meso	Def	Unknown	Høeg and Lützen, 1993
<i>Thompsonia japonica?</i>	Häfele, 1911	<i>Dardanus arrosor</i>	(Herbst, 1796)	CPc	Meso	Def	Japan	Potts, 1906; Shiino, 1943
<i>Thylacoplethus isaevae</i>	Rybakov and Shukalyuk, 2004	<i>Pagurus trigonocheirus</i>	(Stimpson, 1858)	CPc	Meso	Def	Sakhalin Island	Rybakov and Shukalyuk, 2004
<i>Thylacoplethus magellani</i>	Høeg and Lützen, 1993	<i>Pagurus forceps</i>	H. Milne Edwards, 1836	CPc	Meso	Def	Southern Chile	Høeg and Lützen, 1993
<i>Thylacoplethus orientalis</i>	Høeg and Lützen, 1993	<i>Dardanus arrosor</i>	(Herbst, 1796)	CPc	Meso	Def	Japan	Høeg and Lützen, 1993
<i>Thylacoplethus reinhardi</i>	(Lützen, 1992)	<i>Dardanus impressus</i>	(De Haan, 1849)				Japan	Høeg and Lützen, 1993
		<i>Discorsopagurus schmitti</i>	(Stevens, 1925)	CPc	Meso	Def	Puget Sound, WA	Høeg and Lützen, 1993; Gherardi and Cassidy, 1995
<b>Phylum Arthropoda, Infraclass Cirripedia, Superorder Angulosaccus</b>		<b>Rhizocephala, Order Kentrogonida</b>						
<i>Angulosaccus tenuis</i>	Reinhard, 1944	<i>Parapagurus benedicti</i>	de Saint Laurent, 1972	CPc	Meso	Def	Washington	Reinhard, 1944
<i>Dipterosaccus indicus</i>	van Kampen and Boschma, 1925	<i>Calcinus gaimardii</i>	(H. Milne Edwards, 1848)	CPc	Meso	Def	Sumatra	Shiino, 1943
		<i>Calcinus laevimanus</i>	(Randall, 1840)				Japan	Shiino, 1943
		<i>Calcinus latens</i>	(Randall, 1840)				Moluccas	Van Baal, 1937
		<i>Clibanarius striolatus</i>	Dana, 1852				Moluccas	Van Baal, 1937
		<i>Dardanus deformis</i>	(H. Milne Edwards, 1836)				Kei Islands	Boschma, 1931; Boschma, 1953
<i>Peltogaster aelaniticus</i>	Boschma, 1969	<i>Nematopagurus sp.</i>		CPc	Meso	Def	Red Sea	Boschma, 1969
<i>Peltogaster boschmae</i>	Reinhard, 1944	<i>Discorsopagurus schmitti</i>	(Stevens, 1925)	CPc	Meso	Def	Washington	Reinhard, 1944; Gherardi and Cassidy, 1995
<i>Peltogaster curvatus</i>	Kossmann, 1874	<i>Pagurus alatus</i>	(Fabricius, 1775)	CPc	Meso	Def	Mediterranean	Øksnebjerg, 2000
		<i>Pagurus cuanensis</i>	Bell, 1845				Northeast Atlantic, Mediterranean	Høeg and Lützen, 1985; Øksnebjerg, 2000
		<i>Pagurus excavatus</i>	(Herbst, 1791)				Northeast Atlantic, Mediterranean	Potts, 1906; Boschma, 1933; Øksnebjerg, 2000
		<i>Pagurus prideaux</i>	Leach, 1815				Northeast Atlantic, Mediterranean	Høeg and Lützen, 1985; Øksnebjerg, 2000
<i>Peltogaster depressus</i>	Reinhard, 1944	<i>Pagurus capillatus</i>	(Benedict, 1892)	CPc	Meso	Def	Alaska, Bering Sea	Reinhard, 1944
<i>Peltogaster latus</i>	Van Baal, 1937	<i>Calcinus laevimanus</i>	(Randall, 1840)	CPc	Meso	Def	Moluccas	Van Baal, 1937
		<i>Pagurus hirtimanus</i>	(Miers, 1880)				Moluccas	Van Baal, 1937
		<i>Clibanarius striolatus</i>	Dana, 1852				Moluccas	Van Baal, 1937
		<i>Calcinus latens</i>	(Randall, 1840)				Moluccas	Van Baal, 1937
		<i>Calcinus sp.</i>					Moluccas	Van Baal, 1937
<i>Peltogaster naushonensis</i>	Reinhard, 1946	<i>Pagurus annulipes</i>	(Stimpson, 1860)	CPc	Meso	Def	Massachusetts	Reinhard, 1946
<i>Peltogaster paguri</i>	Rathke, 1842	<i>Anapagurus chiroacanthus</i>	(Lilljeborg, 1856)	CPc	Meso	Def	Northeast Atlantic	Høeg and Lützen, 1985
		<i>Anapagurus laevis</i>	(Bell, 1845)				Northeast Atlantic	Høeg and Lützen, 1985
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)				Northeast Atlantic	Høeg and Lützen, 1985
		<i>Pagurus capillatus</i>	(Benedict, 1892)				Alaska	Reinhard, 1944
		<i>Pagurus cornutus</i>	(Benedict, 1892)				Bering Sea	Reinhard, 1944
		<i>Pagurus cuanensis</i>	Bell, 1845				Northeast Atlantic, Mediterranean	Høeg and Lützen, 1985; Øksnebjerg, 2000
		<i>Pagurus excavatus</i>	(Herbst, 1791)				Mediterranean	Øksnebjerg, 2000
		<i>Pagurus hirsutiusculus</i>	(Dana, 1851)				Alaska	Reinhard, 1944

Table 1 (continued)

Associate species	Associate authority	Host hermit crab species	Host authority	Trophic Hab	Type	Locality	Reference
<b>Phylum Arthropoda, Infraclass Cirripedia, Superorder Rhizocephala, Order Kentrogonida</b>							
		<i>Pagurus pubescens</i>	Krøyer, 1838			Norway	Dahl, 1950
		<i>Pagurus pubescens</i>	Krøyer, 1838			Maine	Reinhard, 1939
		<i>Pagurus samuelis</i>	(Stimpson, 1857)			Japan	Shiino, 1943
		<i>Pagurus trigonocheirus</i>	(Stimpson, 1858)			Bering Sea	Reinhard, 1944
		<i>Pagurus prideaux</i>	Leach, 1815			Mediterranean	Øksnebjerg, 2000
		<i>Pagurus maculosus</i>	Komai and Imafuku, 1996			Japan	Nagasawa et al., 1996
		<i>Parapagurodes gracilipes</i>	(Stimpson, 1858)			Japan	Krüger, 1912
<i>Peltogaster purpureus</i>	(Müller, 1862)	Paguroidea		CPc	Meso Def	Brazil	Müller, 1862
<i>Peltogaster reticulatus</i>	Shiino, 1943	<i>Pagurus constans</i>	(Stimpson, 1858)	CPc	Meso Def	Japan	Shiino, 1943
		<i>Pagurus proximus</i>	Komai, 2000			Vostok Bay	Kashenko and Korn, 2003
		<i>Pagurus proximus</i>	Komai, 2000			Vostok Bay	Isaeva et al., 2005
<i>Peltogaster rugosus</i>	Boschma, 1931	<i>Clibanarius sp.</i>		CPc	Meso Def	Kei Islands	Boschma, 1931
<i>Peltogaster senegalensis</i>	Guérin-Ganivet, 1911	<i>Clibanarius senegalensis</i>	Chevreaux and Bouvier, 1892	CPc	Meso Def	Senegal	Guérin-Ganivet, 1911
<i>Peltogaster sp.</i>		Pagurids		CPc	Meso Def	British Columbia	Boschma, 1931
<i>Peltogaster sp.</i>		<i>Diogenes sp.</i>		CPc	Meso Def	Moluccas	Van Baal, 1937
<i>Peltogaster sp.</i>		<i>Pagurus longicarpus</i>	Say, 1817	CPc	Meso Def	Wakulla Co., Florida	Wells, 1966
<i>Peltogaster sp.</i>		<i>Lophopagurus (Australeremus) kirkii</i>	(Filhol, 1883)	CPc	Meso Def	New Zealand Waters	Lützen et al., 2009
<i>Peltogasterella gracilis</i>	Boschma, 1931	<i>Discorsopagurus schmitti</i>	(Stevens, 1925)			Washington	Reinhard, 1944
		<i>Labidochirus splendescens</i>	(Owen, 1839)			Alaska	Reinhard, 1944
		<i>Pagurus ochotensis</i>	Brandt, 1851			Oregon, Washington, Alaska	Boschma, 1933; Reinhard, 1944
		<i>Pagurus aleuticus</i>	(Benedict, 1892)			Alaska	Reinhard, 1944
		<i>Pagurus dalli</i>	(Benedict, 1892)			Alaska	Reinhard, 1944
		<i>Pagurus edwardsi</i>	(Dana, 1852)			Chile, Peru	Boschma, 1931, 1959; Coloma and Moyano, 2003
		<i>Pagurus filholi</i>	(de Man, 1887)			Japan	Nagasawa et al., 1996
		<i>Pagurus hemphilli</i>	(Benedict, 1892)			California	Reinhard, 1944
		<i>Pagurus hirsutiusculus</i>	(Dana, 1851)			Alaska	Warrenchuk and Shirley, 2000
		<i>Pagurus lanuginosus</i>	De Haan, 1849			Japan	Yanagimachi, 1961
		<i>Pagurus maculosus</i>	Komai and Imafuku, 1996			Japan	Nagasawa et al., 1996
		<i>Pagurus middendorffii</i>	Brandt, 1851			Japan	Nagasawa et al., 1996
		<i>Pagurus pectinatus</i>	(Stimpson, 1858)			Vostok Bay	Kashenko and Korn, 2002
<i>Peltogasterella socialis</i>	(Müller, 1863)	Paguroidea		CPc	Meso Def	Brazil	Müller, 1863
		<i>Pagurus criniticornis</i>	(Dana, 1852)			Brazil	Faria et al., 2007
		<i>Pagurus lanuginosus</i>	De Haan, 1849			Japan	Ichikawa and Yanagimachi, 1957
<i>Peltogasterella sulcata</i>	(Lilljeborg, 1859)	<i>Anapagurus chiroacanthus</i>	(Lilljeborg, 1856)	CPc	Meso Def	Northeast Atlantic, Mediterranean	Hansson, 1998
		<i>Anapagurus hyndmanni</i>	(Bell, 1845)			France	Bourdon, 1963
		<i>Anapagurus laevis</i>	(Bell, 1845)			Northeast Atlantic, Mediterranean	Høeg and Lützen, 1985; Øksnebjerg, 2000
		<i>Pagurus alatus</i>	(Fabricius, 1775)			Northeast Atlantic, Mediterranean	Høeg and Lützen, 1985; Øksnebjerg, 2000
		<i>Pagurus cuanensis</i>	Bell, 1845			Northeast Atlantic, Mediterranean	Høeg and Lützen, 1985; Øksnebjerg, 2000
		<i>Pagurus excavatus</i>	(Herbst, 1791)			Mediterranean	Øksnebjerg, 2000
		<i>Pagurus prideaux</i>	Leach, 1815			Northeast Atlantic, Mediterranean	Høeg and Lützen, 1985; Øksnebjerg, 2000
<i>Pterogaster involvulus</i>	Van Baal, 1937	<i>Pagurus cuanensis</i>	Bell, 1845			France	Bourdon, 1960
<i>Pterogaster philippinensis</i>	(Kossmann, 1872)	<i>Clibanarius virescens</i>	(Krauss, 1843)	CPc	Meso Def	Moluccas	Van Baal, 1937
<i>Septosaccus cuenoti</i>	Duboscq, 1912	<i>Calcinus latens</i>	(Randall, 1840)	CPc	Meso Def	Moluccas	Van Baal, 1937
		<i>Clibanarius erythropus</i>	(Latreille, 1818)	CPc	Meso Def	Arcachon	Carayon, 1945
		<i>Diogenes pugilator</i>	(Roux, 1828)	CPc	Meso Def	Northeast Atlantic, Mediterranean	Duboscq, 1912; Øksnebjerg, 2000
<i>Septosaccus reticulatus</i>	van Kampen and Boschma, 1925	<i>Diogenes pugilator</i>	(Roux, 1828)			Black Sea	Codreanu, 1941
<i>Septosaccus rodriguezii</i>	(Fraisie, 1877)	<i>Dardanus deformis</i>	(H. Milne Edwards, 1836)	CPc	Meso Def	Moluccas	Van Baal, 1937
<i>Septosaccus snelli</i>	Van Baal, 1937	<i>Dardanus deformis</i>	(H. Milne Edwards, 1836)			Kei Islands	Van Baal, 1937
		<i>Clibanarius erythropus</i>	(Latreille, 1818)	CPc	Meso Def	Mediterranean	Øksnebjerg, 2000
		<i>Diogenes pugilator</i>	(Roux, 1828)			Northeast Atlantic	Bourdon, 1960, 1963
		<i>Clibanarius striolatus</i>	Dana, 1852	CPc	Meso Def	Moluccas	Van Baal, 1937
		<i>Clibanarius aequabilis</i>	Dana, 1851			Moluccas	Van Baal, 1937
		<i>Clibabarius padavensis</i>	de Man, 1888			New Guinea	Ball and Haig, 1972
<i>Temnascus foresti</i>	Boschma, 1951	<i>Calcinus spicatus</i>	Forest, 1951	CPc	Meso Def	Gambier Islands	Boschma, 1951

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Table 1 (continued)

Associate species	Associate authority	Host hermit crab species	Host authority	Trophic	Hab	Type	Locality	Reference
<b>Phylum Arthropoda, Infraclass Cirripedia, Superorder Rhizocephala, Order Kentrogonida</b>								
Unknown rhizocephalan		<i>Pagurus macLaughlinae</i>	García Gómez, 1982	CPc	Meso	Def	Florida, USA	Lemaitre et al., 1982
<b>Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea, Family Bopyridae, Subfamily Pseudioninae</b>								
<i>Asymmetrione aequalis</i>	Pardo, Boyko and Mantelatto, 2009	<i>Paguristes tomentosus</i>	H. Milne Edwards, 1848	PPc	EcB	Def	Pisco, Peru	Pardo et al., 2009
<i>Asymmetrione ambodistorta</i>	Markham, 1985	<i>Isocheles pilosus</i>	(Holmes, 1900)	PPc	EcB	Def	California	Markham, 1985c
<i>Asymmetrione asymmetrica</i>	(Shiino, 1933)	<i>Clibanarius bimaculatus</i>	(De Haan, 1849)	PPc	EcB	Def	Japan	Shiino, 1933
		<i>Clibanarius merguiensis</i>	de Man, 1888				Thailand	Markham, 1985a
		<i>Clibanarius merguiensis</i>	de Man, 1888				Thailand	Brunenmeister, 1980
<i>Asymmetrione clibanarii</i>	Markham, 1975	<i>Clibanarius tricolor</i>	(Gibbes, 1850)	PPc	EcB	Def	Florida, Bahamas	Markham, 1975
		<i>Clibanarius tricolor</i>	(Gibbes, 1850)				Colombia (Atlantic)	Markham, 1988
		<i>Clibanarius</i> sp.					Ascension Island	Markham, 1978
		<i>Clibanarius antillensis</i>	Stimpson, 1862				Colombia (Atlantic)	Markham, 1988
<i>Asymmetrione dardani</i>	Bourdon, 1968	<i>Dardanus arrosor</i>	(Herbst, 1796)	PPc	EcB	Def	Morocco	Bourdon, 1968
<i>Asymmetrione desultor</i>	Markham, 1975	<i>Iridopagurus</i> sp.?					Belize	Markham, 1988
		<i>Paguristes tortugae</i>	Schmitt, 1933				Brazil	Bourdon, 1979c
		<i>Pagurus brevidactylus</i>	(Stimpson, 1859)				Colombia (Atlantic)	Markham, 1988
		<i>Pagurus brevidactylus</i>	(Stimpson, 1859)				Bahamas	Boyko and Williams, 2004
		<i>Pagurus longicarpus</i>	Say, 1817				North Carolina	Markham, 1975
		<i>Pagurus provenzano</i>	Forest and de Saint Laurent, 1968				Antigua, Curacao	Markham, 1975, 1978
		<i>Pagurus stimpsoni</i>	(A. Milne Edwards and Bouvier, 1893)				Florida	Markham, 1975
<i>Asymmetrione foresti</i>	(Bourdon, 1968)	<i>Pylopagurus</i> sp.					Cal Say Bank	Markham, 1975
		<i>Paguristes eremita</i>	(Linnaeus, 1767)	PPc	EcB	Def	Mediterranean	Bourdon, 1968
<i>Asymmetrione nossibensis</i>	Bourdon, 1976	unknown		PPc	EcB	Def	Madagascar	Bourdon, 1976
<i>Asymmetrione sallyae</i>	Williams and Schuerlein, 2005	<i>Diogenes avarus</i>	Heller, 1865	PPc	EcB	Def	Singapore	Williams and Schuerlein, 2005
<i>Asymmetrione shiinoi</i>	Codreanu, Codreanu and Pike, 1965	<i>Clibanarius englaucus</i>	Ball and Haig, 1972	PPc	EcB	Def	Red Sea	Codreanu et al., 1965
<i>Bopyrissa dawydoffi</i>	(Codreanu and Codreanu, 1963)	<i>Clibanarius signatus</i>	Heller, 1861				Red Sea	Codreanu et al., 1965
		<i>Clibanarius merguiensis</i>	de Man, 1888	PPc	EcB	Def	Vietnam	Codreanu and Codreanu, 1963
<i>Bopyrissa diogeni</i>	(Popov, 1927)	<i>Diogenes pugilator</i>	(Roux, 1828)	PPc	EcB	Def	Notheastern Atlantic	Bourdon, 1963
		<i>Diogenes pugilator</i>	(Roux, 1828)				Black Sea	Popov, 1927
<i>Bopyrissa fraisei</i>	(Carayon, 1943)	<i>Clibanarius erythropus</i>	(Latreille, 1818)	PPc	EcB	Def	France	Carayon, 1943
<i>Bopyrissa liberorum</i>	Markham, 1985	<i>Clibanarius merguiensis</i>	de Man, 1888	PPc	EcB	Def	Thailand	Markham, 1985a
<i>Bopyrissa magellanica</i>	Nierstrasz and Brender à Brandis, 1931	<i>Clibanarius albidigitus</i>	Nobili, 1901	PPc	EcB	Def	Costa Rica	Nierstrasz and Brender à Brandis, 1931
<i>Bopyrissa pyriforma</i>	(Shiino, 1958)	<i>Clibanarius bimaculatus</i>	(De Haan, 1849)	PPc	EcB	Def	Hong Kong	Markham, 1982
		<i>Diogenes edwardsii</i>	(De Haan, 1849)				Japan	Shiino, 1958
<i>Bopyrissa wolffi</i>	Markham, 1978	<i>Clibanarius tricolor</i>	(Gibbes, 1850)	PPc	EcB	Def	Florida, Bermuda, Bahamas	Markham, 1978
		<i>Clibanarius vittatus</i>	(Bosc, 1802)				North Carolina, Texas	Markham, 1978
		<i>Clibanarius tricolor</i>	(Gibbes, 1850)				Quintana Roo, Mexico	Markham, 1990
		<i>Clibanarius tricolor</i>	(Gibbes, 1850)				Bahamas	Boyko and Williams, 2004
		<i>Clibanarius tricolor</i>	(Gibbes, 1850)				Bermuda	McDermott, 2002
<i>Bopyrophryxus branchiobdominalis</i>	Codreanu, 1965	<i>Oncopagurus monstrosus</i>	(Alcock, 1894)	PPc	EcB	Def	Indonesia	Bourdon and Boyko, 2005
		<i>Paragiopagurus acutus</i>	(de Saint Laurent, 1972)				Philippines	Bourdon and Boyko, 2005
		unidentified pagurid					Indonesia	Bourdon and Boyko, 2005
		<i>Pagurixus</i> sp.?					Guam	Bourdon and Boyko, 2005
		<i>Pagurixus anceps</i>	(Forest, 1954)				Tuamotu Archipelago	Bourdon and Boyko, 2005
<i>Pagurion tuberculata</i>	Shiino, 1933	<i>Dardanus scutellatus</i>	(H. Milne Edwards, 1848)	PPc	EcB	Def	Japan	Shiino, 1933
<i>Parapagurion calcinicola</i>	Shiino, 1933	<i>Calcinus elegans</i>	(H. Milne Edwards, 1836)	PPc	EcB	Def	Japan	Shiino, 1933
		<i>Calcinus linapropodus</i>	Morgan and Forest, 1991				Japan	Shiino, 1933



Table 1 (continued)

Associate species	Associate authority	Host hermit crab species	Host authority	Trophic Hab	Type	Locality	Reference	
<b>Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea Family Bopyridae, Subfamily Pseudioninae</b>								
		<i>Paguristes monoporos</i>	Morgan, 1987			Indonesia	Haig and Ball, 1988	
		<i>Paguristes</i> sp.				Thailand	Markham, 1985a	
		<i>Pagurus</i> aff. <i>hedleyi</i> or <i>kulkarnii</i>				Hong Kong	Markham, 1992	
<i>Parapagurion imbricata</i>	Markham, 1978	<i>Parapagurus</i> sp.		PPc	EcB	Def	Colombia (Atlantic)	Markham, 1978
		<i>Paguristes tortugae</i>	Schmitt, 1933				Cuba	Markham, 1978
<i>Parapseudione lata</i>	Shiino, 1958	<i>Pagurus middendorffii</i>	Brandt, 1851	PPc	EcB	Def	Japan	Shiino, 1958
<i>Pleurocryptella paguri</i>	Bourdon, 1979	<i>Parapagurus nudus</i>	(A. Milne Edwards, 1891)	PPc	EcB	Def	Azores	Bourdon, 1979b
<i>Pleurocryptella</i> sp.		<i>Oncopagurus bicristatus</i>	(A. Milne-Edwards, 1880)	PPc	EcB	Def	Azores	Bourdon, 1979b
<i>Propseudione rhombicosoma</i>	Shiino, 1933	<i>Calcinus laevimanus</i>	(Randall, 1840)	PPc	EcB	Def	Japan	Shiino, 1933
<i>Pseudione biacuta</i>	Bourdon, 1979	<i>Calcinus morgani</i>	Rahayu and Forest, 1999				Japan	Shiino, 1933
		<i>Paguristes robustus</i>	Forest and de Saint Laurent, 1967	PPc	EcB	Def	Uruguay	Bourdon, 1979a
<i>Pseudione brandaoi</i>	Brian and Dartevelle, 1941	<i>Clibanarius</i> sp.		PPc	EcB	Def	Zaire	Brian and Dartevelle, 1941
<i>Pseudione calcinii</i>	Shiino, 1958	<i>Calcinus latens</i>	(Randall, 1840)	PPc	EcB	Def	Japan	Shiino, 1958
<i>Pseudione clibanaricola</i>	Shiino, 1933	<i>Clibanarius bimaculatus</i>	(De Haan, 1849)	PPc	EcB	Def	Japan	Shiino, 1933
<i>Pseudione giardi</i>	Calman, 1898	<i>Pagurus aleuticus</i>	(Benedict, 1892)	PPc	EcB	Def	Alaska	Markham, 1974
		<i>Pagurus armatus</i>	(Dana, 1851)				Washington	Nyblade, 1974
		<i>Pagurus beringanus</i>	(Benedict, 1892)				Washington	Markham, 1974
		<i>Pagurus capillatus</i>	(Benedict, 1892)				Alaska	Markham, 1974
		<i>Pagurus hirsutiusculus</i>	(Dana, 1851)				Alaska, Washington	Markham, 1974
		<i>Pagurus ochotensis</i>	Brandt, 1851				Alaska	Markham, 1974
<i>Pseudione hyndmanni</i>	(Bate and Westwood, 1868)	<i>Anapagurus chiroacanthus</i>	(Lilljeborg, 1856)	PPc	EcB	Def	Notheastern Atlantic	Bate and Westwood, 1868
		<i>Anapagurus laevis</i>	(Bell, 1845)				Notheastern Atlantic	Pike, 1961a
		<i>Lophopagurus (Lophopagurus) lacertosus</i>	(Henderson, 1888)				New Zealand	Page, 1985
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)				Notheastern Atlantic	Bonnier, 1900
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)				Norway	Dahl, 1950
		<i>Pagurus prideaux</i>	Leach, 1815				Scotland	Henderson, 1886
		<i>Pagurus pubescens</i>	Krøyer, 1838				Notheastern Atlantic	Pike, 1961a
		<i>Pagurus</i> sp.					Japan	Shiino, 1936
		<i>Lophopagurus (Lophopagurus) lacertosus</i>	(Henderson, 1888)				New Zealand	Page, 1985
<i>Pseudione intermedia</i>	Nierstrasz and Brender à Brandis, 1932	<i>Pagurus cuanensis</i>	Bell, 1845				Notheastern Atlantic	Pike, 1961a
		<i>Lophopagurus (Australeremus) triserratus</i>	(Ortmann, 1892)	PPc	EcB	Def	Japan	Shiino, 1936
		<i>Pagurus</i> sp. ?					Japan	Nierstrasz and Brender à Brandis, 1932
<i>Pseudione kensleyi</i>	Williams and Schuerlein, 2005	<i>Clibanarius infraspinatus</i>	Hilgendorf, 1869	PPc	EcB	Def	Singapore	Williams and Schuerlein, 2005
<i>Pseudione nobili</i>	Nierstrasz and Brender à Brandis, 1923	<i>Trizacheles spinosus spinosus</i>	(Henderson, 1888)	PPc	EcB	Def	Indonesia	Nierstrasz and Brender à Brandis, 1923
<i>Pseudione novaeguineensis</i>	Danforth, 1971	<i>Clibanarius</i> sp. aff. <i>longitarsus</i>	(De Haan, 1849)	PPc	EcB	Def	New Guinea	Danforth, 1971
<i>Pseudione quasimodo</i>	Boyko and Williams, 2004	<i>Paguristes grayi</i>	Benedict, 1901	PPc	EcB	Def	Bahamas	Boyko and Williams, 2004
		<i>Paguristes invisicacculus</i>	McLaughlin and Provenzano, 1974				Bahamas	Boyko and Williams, 2004
<i>Pseudione</i> sp.		<i>Paguristes anahuachis</i>	Glassell, 1938	PPc	EcB	Def	Gulf of California	Brusca, 1980
		<i>Clibanarius digueti</i>	Bouvier, 1898				Gulf of California	Brusca, 1980
<i>Pseudionella akuaku</i>	Boyko and Williams, 2001	<i>Calcinus imperialis</i>	Whitelegge, 1901	PPc	EcB	Def	Easter Island	Boyko and Williams, 2001
<i>Pseudionella attenuata</i>	Shiino, 1949	<i>Pagurus</i> sp.		PPc	EcB	Def	Japan	Shiino, 1949
<i>Pseudionella deflexa</i>	Bourdon, 1979	<i>Pagurus brevidactylus</i>	(Stimpson, 1859)	PPc	EcB	Def	Bahamas	Boyko and Williams, 2001
		<i>Pagurus criniticornis</i>	(Dana, 1852)				Brazil	Bourdon, 1979a
<i>Pseudionella markhami</i>	(Adkison and Heard, 1978)	<i>Pagurus annulipes</i>	(Stimpson, 1860)	PPc	EcB	Def	North Carolina	Boyko and Williams, 2001
		<i>Pagurus brevidactylus</i>	(Stimpson, 1859)				Colombia (Atlantic)	Boyko and Williams, 2001
		<i>Pagurus stimpsoni</i>	(A. Milne Edwards and Bouvier, 1893)				Colombia (Atlantic)	Boyko and Williams, 2001
		<i>Iridopagurus iris</i>	(A. Milne Edwards, 1880)				Venezuela	Boyko and Williams, 2001
<b>Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea Family Bopyridae, Subfamily Athelginae</b>								
<i>Allathelges pakistanensis</i>	Kasmi and Markham, 1999	<i>Paguristes perspicax</i>	Nobili, 1906	PPc	EcA	Def	Pakistan	Kazmi and Markham, 1999
<i>Anathelges hyphalus</i>	(Markham, 1974)	<i>Parapagurodes laurentae</i>	McLaughlin and Haig, 1973	PPc	EcA	Def	California	Boyko and Willams, 2003
		<i>Parapagurodes markarovi</i>	McLaughlin and Haig, 1973				California	Boyko and Willams, 2003
<i>Anathelges hyptius</i>	(Thompson, 1902)	<i>Iridopagurus caribbensis</i>	(A. Milne Edwards and Bouvier, 1893)	PPc	EcA	Def	Florida	García Gómez, 1983

(continued on next page)

Table 1 (continued)

Associate species	Associate authority	Host hermit crab species	Host authority	Trophic	Hab	Type	Locality	Reference
<b>Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea, Family Bopyridae, Subfamily Athelginae</b>								
		<i>Iridopagurus margaritensis</i>	García Gómez, 1983				Curacao	Markham, 1978
		<i>Pagurus annulipes</i>	(Stimpson, 1860)				North Carolina	Adkison and Heard, 1978
		<i>Pagurus brevidactylus</i>	(Stimpson, 1859)				Florida	Markham, 1974
		<i>Pagurus brevidactylus</i>	(Stimpson, 1859)				Bahamas	Boyko and Williams, 2004
		<i>Pagurus longicarpus</i>	Say, 1817				Mass-NC, USA	Boyko and Williams, 2003
		<i>Pagurus macLaughlinae</i>	García Gómez, 1982				Florida	Markham, 1988
		<i>Pagurus provenzano</i>	Forest and de Saint Laurent, 1968				Curacao	Markham, 1978
		<i>Pagurus stimpsoni</i>	(A. Milne Edwards and Bouvier, 1893)				Florida	Markham, 1974
<i>Anathelges resupinatus</i>	(Müller, 1871)	<i>Pagurus</i> sp.		PPc	EcA	Def	Brazil	Boyko and Williams, 2003
<i>Anathelges thompsoni</i>	(Nierstrasz and Brender à Brandis, 1931)	<i>Pagurus</i> sp.		PPc	EcA	Def	Chile	Boyko and Williams, 2003
<i>Athelges aegypticus</i>	Codreanu, Codreanu and Pike, 1965	<i>Diogenes senex</i>	Heller, 1865	PPc	EcA	Def	Red Sea	Codreanu et al., 1965
<i>Athelges bilobus</i>	Sars, 1898	<i>Pagurus cuanensis</i>	Bell, 1845	PPc	EcA	Def	Northeastern Atlantic	Bourdon, 1967
<i>Athelges caudalis</i>	Barnard, 1955	<i>Diogenes senex</i>	Heller, 1865	PPc	EcA	Def	South Africa	Barnard, 1955
<i>Athelges cladophorus</i>	Gerstaecker, 1862	<i>Pagurus cuanensis</i>	Bell, 1845	PPc	EcA	Def	English Channel	Gerstaecker, 1862
		<i>Pagurus cuanensis</i>	Bell, 1845				Northeastern Atlantic	Bonnier, 1900
<i>Athelges guitarra</i>	Giard and Bonnier, 1890	<i>Pagurus</i> sp.		PPc	EcA	Def	Italy	Giard and Bonnier, 1890
<i>Athelges intermedius</i>	Hesse, 1877	<i>Pagurus cuanensis</i>	Bell, 1845	PPc	EcA	Def	France	Hesse, 1877
<i>Athelges japonicus</i>	Shiino, 1958	<i>Pagurus constans</i>	(Stimpson, 1858)	PPc	EcA	Def	Japan	Shiino, 1958
		<i>Pagurus lanuginosus</i>	De Haan, 1849				Japan	Shiino, 1958
		<i>Pagurus middendorffii</i>	Brandt, 1851				Japan	Shiino, 1958
<i>Athelges lacertosi</i>	Pike, 1961	<i>Lophopagurus</i>	(Filhol, 1883)	PPc	EcA	Def	New Zealand	Page, 1985
		<i>(Australeremus) cooki</i>						
		<i>Lophopagurus</i>	(Filhol, 1885)				New Zealand	Page, 1985
		<i>(Lophopagurus) thompsoni</i>						
<i>Athelges paguri</i>	(Rathke, 1843)	<i>Pagurus lacertosus</i>	(Henderson, 1888)				New Zealand	Page, 1985
		<i>Anapagurus laevis</i>	(Bell, 1845)	PPc	EcA	Def	Northeastern Atlantic	Nierstrasz and Brender à Brandis, 1926
		<i>Diogenes pugilator</i>	(Roux, 1828)				Northeastern Atlantic	Bourdon, 1967
		<i>Pagurus cuanensis</i>	Bell, 1845				France	Hesse, 1877
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)				Northeastern Atlantic	Bonnier, 1900
<i>Athelges pelagosae</i>	Babić, 1912	<i>Paguristes eremita</i>	(Linnaeus, 1767)	PPc	EcA	Def	Adriatic	Babić, 1912
<i>Athelges prideauxii</i>	Giard and Bonnier, 1890	<i>Pagurus prideaux</i>	Leach, 1815	PPc	EcA	Def	Northeastern Atlantic	Bourdon, 1963
		<i>Pagurus prideaux</i>	Leach, 1815				Italy	Giard and Bonnier, 1890
<i>Athelges</i> sp.		<i>Trizopagurus strigatus</i>	(Herbst, 1804)	PPc	EcA	Def	Indonesia	Haig and Ball, 1988
<i>Athelges takanoshimensis</i>	Ishii, 1914	<i>Diogenes edwardsii</i>	(De Haan, 1849)	PPc	EcA	Def	Hong Kong	Markham, 1982
		<i>Pagurus samuelis</i>	(Stimpson, 1857)				Japan	Ishii, 1914
		<i>Pagurus brachiomastus</i>	(Thallwitz, 1891)				Korea	Kim and Kwon, 1988
		<i>Pagurus filholi</i>	(de Man, 1887)				Korea	Kim and Kwon, 1988
		<i>Pagurus filholi</i>	(de Man, 1887)				Japan	Nagasawa et al., 1996
		<i>Pagurus japonicus</i>	(Stimpson, 1858)				Japan	Shiino, 1934
		<i>Pagurus maculosus</i>	Komai and Imafuku, 1986				Japan	Nagasawa et al., 1996
		<i>Pagurus middendorffii</i>	Brandt, 1851				Korea	Kim and Kwon, 1988
		<i>Pagurus dubius</i>	(Ortmann, 1892)				Korea	Kim and Kwon, 1988
		<i>Pagurus dubius</i>	(Ortmann, 1892)				Japan	Saito et al., 2000
		<i>Pagurus minutus</i>	Hess, 1865				Hong Kong	Williams, unpublished
		<i>Pagurus pectinatus</i>	(Stimpson, 1858)				Korea	Kim and Kwon, 1988
		<i>Pagurus pectinatus</i>	(Stimpson, 1858)				Japan	Shiino, 1937
		<i>Pagurus aff. geminatus</i>	McLaughlin, 2008				Hong Kong	Markham, 1982
		<i>Clibanarius</i> sp.					Hong Kong	Markham, 1990
		<i>Pagurus trigonocheirus</i>	(Stimpson, 1858)				Hong Kong	Markham, 1992
		<i>Diogenes</i> sp.					Hong Kong	Markham, 1992
		<i>Pagurus</i> sp.					China	Wei, 1991
		<i>Pagurodoefleinia doederleini</i>	(Doflein, 1902)				Taiwan	Boyko, 2004
<i>Athelges takanoshimensis</i> var. <i>tenuibranchiatus</i>	Shiino, 1936	unidentified					Vostok Bay	Shukalyuk et al., 2007
<i>Athelges tenuicaudis</i>	Sars, 1898	<i>Lophopagurus</i>	(Ortmann, 1892)	PPc	EcA	Def	Japan	Shiino, 1936
		<i>(Australeremus) triserratus</i>						
		<i>Anapagurus breviculeatus</i>	Fenzia, 1937	PPc	EcA	Def	Spain	García Gómez, 1994

Table 1 (continued)

Associate species	Associate authority	Host hermit crab species	Host authority	Trophic	Hab	Type	Locality	Reference
<b>Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea, Family Bopyridae, Subfamily Athelginae</b>								
		<i>Anapagurus chiroacanthus</i>	(Lilljeborg, 1856)				Northeastern Atlantic	Pike, 1961b
		<i>Anapagurus hyndmanni</i>	(Bell, 1845)				Northeastern Atlantic	Bourdon, 1960
<i>Falsanathelges muelleri</i>	(Nierstrasz and Brender à Brandis, 1931)	<i>Calcinus linapropodus</i>	Morgan and Forest, 1991	PPc	EcA	Def	Indonesia	Boyko and Williams, 2003
		<i>Clibanarius infraspinus</i>	Hilgendorf, 1869				Malaysia	Boyko and Williams, 2003
<i>Minimathelges minutus</i>	(Markham, 1992)	unidentified paguroid		PPc	EcA	Def	Hong Kong	Boyko and Williams, 2003
<i>Minimathelges nanus</i>	Boyko and Williams, 2003	? <i>Anapagrides</i> sp.		PPc	EcA	Def	Loyalty Islands	Boyko and Williams, 2003
<i>Parathelges aniculi</i>	(Whitelegge, 1897)	<i>Aniculus aniculus</i>	(Fabricius, 1787)	PPc	EcA	Def	Ellice Island	Whitelegge, 1897
<i>Parathelges cardonae</i>	Codreanu and Codreanu, 1968	<i>Clibanarius erythropus</i>	(Latreille, 1818)	PPc	EcA	Def	Corsica	Codreanu and Codreanu, 1968 (in Codreanu, 1968)
<i>Parathelges caroli</i>	Codreanu, 1968	<i>Dardanus arrosor</i>	(Herbst, 1796)	PPc	EcA	Def	Italy	Codreanu, 1968
<i>Parathelges enoshimensis</i>	Shiino, 1950	<i>Pagurus dubius</i>	(Ortmann, 1892)	PPc	EcA	Def	Japan	Shiino, 1950
		<i>Pagurus filholi</i>	(de Man, 1887)				Korea	Kim and Kwon, 1988
		<i>Pagurus vittatus</i>	(Bosc, 1802)				Korea	Kim and Kwon, 1988
<i>Parathelges foliatus</i>	Markham, 1972	<i>Clibanarius vittatus</i>	(Stimpson, 1859)	PPc	EcA	Def	Trinidad	Markham, 1972
		<i>Pagurus brevidactylus</i>	(Stimpson, 1859)				Barbados, Curacao	Markham, 1978
<i>Parathelges neotenuicaudis</i>	(Shyamasundari, Hanumantha-Rao, Jalajakumari, and Mary, 1993)	<i>Pagurus kulkarnii</i>	Sankoli, 1962	PPc	EcA	Def	India	Shyamasundari et al., 1993
<i>Parathelges occidentalis</i>	Markham, 1972	<i>Clibanarius tricolor</i>	(Gibbes, 1850)	PPc	EcA	Def	Florida, Bahamas	Markham, 1972
		<i>Clibanarius tricolor</i>	(Gibbes, 1850)				Quintana Roo, Mexico	Markham, 1990
		<i>Clibanarius tricolor</i>	(Gibbes, 1850)				Bahamas	Boyko and Williams, 2004
		<i>Iridopagurus margaritensis</i>	García Gómez, 1983				Venezuela	Markham, 1972
		<i>Manucomplanus unguatus</i>	(Studer, 1883)				North Carolina	Markham, 1978
		<i>Pagurus brevidactylus</i>	(Stimpson, 1859)				Bahamas	Boyko and Williams, 2004
<i>Parathelges piriformis</i>	Markham, 1972	<i>Paguristes oxyophthalmus</i>	Holthuis, 1959	PPc	EcA	Def	Colombia	Markham, 1978
		<i>Pagurus brevidactylus</i>	(Stimpson, 1859)				Bermuda	Markham, 1972
		<i>Pagurus provenzanoi</i>	Forest and de Saint Laurent, 1968				Bahamas	Markham, 1978
<i>Parathelges racovitzai</i>	Codreanu, 1940	<i>Diogenes pugilator</i>	(Roux, 1828)	PPc	EcA	Def	Black Sea	Codreanu, 1940
<i>Parathelges tumidipes</i>	Markham, 1972	<i>Dardanus fucosus</i>	Biffar and Provenzano, 1972	PPc	EcA	Def	Jamaica	Markham, 1972
		<i>Allodardanus bredini</i>	Haig and Provenzano, 1965				Bermuda	Markham, 1978
<i>Parathelges weberi</i>	Nierstrasz and Brender à Brandis, 1923	<i>Calcinus albengai</i>	Poupin and Lemaitre, 2003	PPc	EcA	Def	Indonesia	Poupin and Lemaitre, 2003
		<i>Calcinus laevimanus</i>	(Randall, 1840)				New Guinea	Danforth, 1971
<i>Parathelges whiteleggei</i>	Nierstrasz and Brender à Brandis, 1931	<i>Pagurus</i> sp.		PPc	EcA	Def	Indonesia	Nierstrasz and Brender à Brandis, 1931
		<i>Paguristes monoporus</i>	Morgan, 1987				Indonesia	Haig and Ball, 1988
<i>Pseudostegias atlantica</i>	Lemos de Castro, 1965	<i>Clibanarius</i> sp.		PPc	EcA	Def	Brazil	Lemos de Castro, 1965
<i>Pseudostegias dulcilaucum</i>	Markham, 1982	<i>Clibanarius merguiensis</i>	de Man, 1888	PPc	EcA	Def	Thailand	Markham, 1985a
<i>Pseudostegias macdermotti</i>	Williams and Boyko, 1999	<i>Diogenes</i> aff. <i>edwardsii</i>	(De Haan, 1849)	PPc	EcA	Def	Hong Kong	Markham, 1982
<i>Pseudostegias mossambica</i>	(Barnard, 1956)	<i>Calcinus morgani</i>	Rahayu and Forest, 1999	PPc	EcA	Def	Indonesia	Williams and Boyko, 1999
<i>Pseudostegias otagoensis</i>	Page, 1985	unidentified paguroid		PPc	EcA	Def	Mozambique	Boyko and Williams, 2003
<i>Pseudostegias setoensis</i>	Shiino, 1933	<i>Paguristes barbatus</i>	(Heller, 1862)	PPc	EcA	Def	New Zealand	Page, 1985
		<i>Clibanarius bimaculatus</i>	(De Haan, 1849)	PPc	EcA	Def	Japan	Shiino, 1933
		<i>Clibanarius bimaculatus</i>	(De Haan, 1849)				Hong Kong	Markham, 1982
		<i>Clibanarius padavensis</i>	de Man, 1888				Thailand	Markham, 1985a
		<i>Clibanarius ransonii</i>	Forest, 1953				Hong Kong	Markham, 1982
		<i>Clibanarius striolatus</i>	Dana, 1852				Taiwan	Shiino, 1958
		<i>Clibanarius taeniatus</i>	(H. Milne Edwards, 1848)				Queensland, Australia	Dunbar and Coates, 2000
		<i>Clibanarius virescens</i>	(Krauss, 1843)				Queensland, Australia	Dunbar and Coates, 2000
		<i>Strigopagurus boreonotus</i>	Forest, 1995				Chesterfield Islands	Markham, 1994
<i>Pseudostegias</i> sp.		<i>Clibanarius</i> cf. <i>merguiensis</i>	de Man, 1888	PPc	EcA	Def	Thailand	Brunenmeister, 1980
<i>Stegias andronophoros</i>	Nierstrasz and Brender à Brandis, 1923	unidentified paguroid		PPc	EcA	Def	Indonesia	Nierstrasz and Brender à Brandis, 1923
<i>Stegias angusta</i>	Nierstrasz and Brender à	unknown; presumed		PPc	EcA	Def	Costa Rica (Pacific)	Nierstrasz and Brender à

(continued on next page)

Table 1 (continued)

Associate species	Associate authority	Host hermit crab species	Host authority	Trophic	Hab	Type	Locality	Reference
<i>Stegias clibanarii</i>	Brandis, 1931 Richardson, 1904	paguroid <i>Clibanarius tricolor</i>	(Gibbes, 1850)	PPc	EcA	Def	Bermuda	Brandis, 1931 Richardson, 1904; McDermott, 2002
Unknown parasitic isopod		<i>Clibanarius tricolor</i> <i>Paguritta harmsi</i>	(Gibbes, 1850) (Gordon, 1935)	PPc	EcA	Def	Colombia Australia	Markham, 1988 Patton and Robertson, 1980
<b>Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea, Family Entoniscidae</b>								
<i>Diogenion vermifactus</i>	Codreanu, Codreanu and Pike, 1960	<i>Diogenes senex</i>	Heller, 1865	PPc?	En	Def	Red Sea	Codreanu et al., 1960
<i>Paguritherium alatum</i>	Reinhard, 1945	<i>Pagurus longicarpus</i> <i>Pagurus longicarpus</i> <i>Pagurus longicarpus</i> <i>Pagurus annulipes</i>	Say, 1817 Say, 1817 Say, 1817 (Stimpson, 1860)	PPc?	En	Def	North Carolina New Jersey Massachusetts North Carolina	Adkison and Heard, 1978 McDermott, 1998 Reinhard, 1945 Adkison and Heard, 1978
<b>Phylum Arthropoda, Order Acari*</b>								
<i>Andregamasus conchylidae</i>	(André, 1937)	<i>Coenobita</i> sp.		Unk	EcB	Def	Vanuatu	André, 1937
<i>Andregamasus steinitzii</i>	Costa, 1965	<i>Coenobita</i> sp.		Unk	EcB	Def	Red Sea	Costa, 1965
<i>Askinasia antillarum</i>	Fain, Yunker, van Goethem and Johnston, 1982	<i>Coenobita brevimanus</i>	Dana, 1852	Unk	EcB	Def	Lesser Antilles and Florida	Fain et al., 1982
<i>Askinasia aethiopicus</i>	Yunker, 1970	<i>Coenobita rugosus</i>	H. Milne Edwards, 1837	Unk	EcB	Def	Kenya	Yunker, 1970
<i>Askinasia sinusarabicus</i>	Yunker, 1970	<i>Coenobita scaevola</i>	(Forskål, 1775)	Unk	EcB	Def	Red Sea	Yunker, 1970
<i>Aspidilaelaps mirabilis</i>	Trägårdh, 1949	unidentified hermit crab		Unk	EcB	Def	Somoa	Johnston, 1960
<i>Aspidilaelaps pagurophilus</i>	(André, 1937)	<i>Coenobita</i> sp.		Unk	EcB	Def	Vanuatu	André, 1937; Johnston, 1960
<i>Caloglyphus birgophilus</i>	Vitzthum, 1937	<i>Birgus latro</i>	(Linnaeus, 1767)	Unk	EcB	Def	unknown	Vitzthum, 1937
<i>Cyclothorax carcinicola</i>	Frauenfeld, 1868	<i>Calcinus tibicen?</i>	(Herbst, 1791)	Unk	EcB	Def	Nicobars	Frauenfeld, 1868
<i>Cyclothorax latronis</i>	Vitzthum, 1937	<i>Birgus latro</i>	(Linnaeus, 1767)	Unk	EcB	Def	unknown	Vitzthum, 1937
<i>Ereynetes (Anereynetes) coenobitus</i>	Hunter and Poe, 1971	<i>Coenobita clypeatus</i>	(Fabricius, 1787)	Unk	EcB	Def	Puerto Rico	Hunter and Poe, 1971
<i>Ereynetes (Anereynetes) papuanus</i>	Fain and Van Goethem, 1977	<i>Coenobita rugosus</i>	H. Milne Edwards, 1837	Unk	EcB	Def	Papua New Guinea	Fain and Van Goethem, 1978
<i>Ewingia coenobitae</i>	Pearse, 1929	<i>Coenobita brevimanus</i> <i>Coenobita brevimanus</i> <i>Coenobita rugosus</i>	Dana, 1852 Dana, 1852 H. Milne Edwards, 1837	Unk	EcB	Def	Florida Florida Kenya	Pearse, 1932 Fain et al., 1982 Yunker, 1970
<i>Hoogstraalacarus tiwensis</i>	Yunker, 1970			Unk	EcB	Def		
<i>Physalozercos paguroxenus</i>	André, 1937	<i>Coenobita</i> sp.		Unk	EcB	Def	Vanuatu	André, 1937

parasites (8.1%) are found among the Apicomplexa, Platyhelminthes, Acanthocephala and Nematoda; the one apicomplexan is a trophically transmitted pathogen while the rest are trophically transmitted typical parasites. Finally, five pathogens (3.3%) are found among the Apicomplexa, Dinoflagellata, Microsporidia, and Ascomycota. The trophic strategy of the mites remains unknown. Although none of the species are considered strict parasitoids, some can cause the death of the hosts during development and thus can act in an analogous fashion to parasitoids (e.g., *Fecampia erythrocephala*).

The habitus of the parasites includes endoparasites, ectoparasites, and mesoparasites (Fig. 1B). Most of the arthropod parasites are mesoparasitic or ectoparasitic. Specifically, the rhizocephalans are all mesoparasitic, pseudionine bopyrids are ectoparasites within the branchial chamber of hosts, and athelgine bopyrids are ectoparasites on the abdomen of hosts. All of the rest of the parasitic groups are endoparasitic. In addition, arthropods are the only group known to frequently parasitize terrestrial hermit crabs. Specifically, 15 species of mites are found, either attached to the gills of such hosts or roaming over the body.

Most parasites associated with hermit crabs use them as definitive hosts (91.3%; 136 of 149 species) (Fig. 1C); only 12 species (represented by 1 coccidian, 2 tapeworms, 4 digenetic trematodes, 2

acanthocephalans, and 3 nematodes) use the crabs as the first or second intermediate hosts in their life cycles.

A total of 133 species of hermit crabs are hosts to these parasites; on average hermit crabs have been documented with  $2.1 \pm 1.7$  ( $n = 133$ ) parasite species over their geographic range (including mites). More than 850 species of hermit crabs have been described, but <16% of all hermit crabs have been described as hosts for parasites. This low percentage is most likely a reflection of lack of sampling for symbionts rather than a true indication of lack of parasites (except in the Coenobitidae, see discussion below). The ten most studied hermit crab species (those with 5 or more parasites) are known from European waters, the western Atlantic, and the eastern Pacific (Fig. 2). These species harbor an average of  $6.9 \pm 1.5$  ( $n = 10$ ) parasites, with *Pagurus bernhardus* and *P. cuanensis* hosting the most parasites (9 species each).

Among the six recognized families of non-lithodid hermit crabs, parasites are associated with a total of 26 genera. However, the parasites are not evenly distributed among the genera in these families: Coenobitidae (2 of 2 genera parasitized, if mites of *Birgus latro* are true parasites), Diogenidae (10 of 19), Paguridae (11 of 72), Parapaguridae (3 of 10), Pylochelidae (1 of 7), and Pylojacquesidae (0 of 2). Terrestrial hermit crabs have been successful in an ecological sense on tropical islands (Greenaway, 2003; Brodie, 2005). Perhaps



**Table 2**

Symbionts found attached to or on hermit crabs that are considered potential parasites. Hab: Habitus of parasite (C: on Crab; En: Endosymbiotic; El: Epibiotic, Internal to shell; FL: Free-Living, roaming in shell); Locality = geographic region where parasite collected. Genera and species of associates are listed under higher taxa in alphabetical order.

Associate species	Associate authority	Host hermit crab species	Host authority	Hab	Locality	Reference
<b>Class Mesomycetozoa, Order Eccrinales</b>						
<i>Arundinula capitata</i>	Léger and Duboscq, 1906	<i>Pagurus cuanensis</i>	Bell, 1845	En	France, Roscoff	Léger and Duboscq (1906)
		<i>Paguristes eremita</i>	(Linnaeus, 1767)		France, Roscoff	Léger and Duboscq, (1905, 1906, 1911)
		<i>Paguristes eremita</i>	(Linnaeus, 1767)		France, Roscoff	Duboscq et al. (1948)
		<i>Pagurus cuanensis</i>	Bell, 1845		France, Roscoff	Manier and Ormières (1962)
<i>Arundinula incurvata</i>	Léger and Duboscq, 1905	<i>Pagurus prideaux</i>	Leach, 1815	En	France, Roscoff	Léger and Duboscq (1905)
<i>Arundinula washingtoniensis</i>	Hibbitts, 1978	<i>Paguristes turgidus</i>	(Stimpson, 1856)	En	Washington, San Juan Islands	Hibbitts (1978)
<i>Taeniella carcini</i>	Léger and Duboscq, 1911	<i>Paguristes turgidus</i>	(Simpson, 1856)	En	Washington, San Juan Islands	Hibbitts (1978)
		<i>Pagurus beringanus</i>	(Benedict, 1892)		Washington, San Juan Islands	Hibbitts (1978)
		<i>Pagurus excavatus</i>	(Herbst, 1791)		France, Roscoff	Léger and Duboscq (1911)
		<i>Pagurus granosimanus</i>	(Stimpson, 1859)		Washington, San Juan Islands	Hibbitts (1978)
		<i>Pagurus kennerlyi</i>	(Stimpson, 1864)		Washington, San Juan Islands	Hibbitts (1978)
Unidentified sp.		<i>Pagurus capillatus</i>	(Benedict, 1892)	En	Washington, San Juan Islands	Hibbitts (1978)
Unidentified sp.		<i>Clibanarius tricolor</i>	(Gibbes, 1850)	En	Bermuda	McDermott (2002)
<b>Phylum Ciliophora, Class Phyllopharyngea, Subclass Apostomatia, Family Foettingeriidae</b>						
<i>Gymnodinioides inkystans</i>	Minkiewicz, 1913	<i>Clibanarius erythropus</i>	(Latreille, 1818)	C	France, Roscoff	Baccarani and Pessani (1997)
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)		France	Sprague and Couch (1971)
		<i>Pagurus longicarpus</i>	Say, 1817		Massachusetts, Woods Hole	Trager (1957)
		<i>Pagurus prideaux</i>	Leach, 1815		France	Sprague and Couch (1971)
<i>Gymnodinioides</i> sp.		<i>Pagurus ochotensis</i>	Brandt, 1851	C	Northeast Pacific (Washington and California)	Bradbury (1966)
		<i>Pagurus hirsutiusculus</i>	(Dana, 1851)		Northeast Pacific (Washington and California)	Bradbury (1966)
<i>Hyalophysa chattoni</i>	Bradbury, 1966	<i>Clibanarius vittatus</i>	(Bosc, 1802)	C	Alabama, Mobile Bay	Landers et al. (1999)
		<i>Clibanarius vittatus</i>	(Bosc, 1802)		North Carolina, Beaufort	Grimes (1976)
		<i>Pagurus annulipes</i>	(Stimpson, 1860)		Massachusetts	Bradbury and Clamp (1973)
		<i>Pagurus granosimanus</i>	(Stimpson, 1859)		Northeast Pacific (Washington and California)	Bradbury (1966)
		<i>Pagurus hirsutiusculus</i>	(Dana, 1851)		Northeast Pacific (Washington and California)	Bradbury (1966)
		<i>Pagurus longicarpus</i>	Say, 1817		North Carolina, Beaufort	Grimes (1976)
		<i>Pagurus ochotensis</i>	Brandt, 1851		Northeast Pacific (Washington and California)	Bradbury (1966)
		<i>Pagurus samuelis</i>	(Stimpson, 1857)		Northeast Pacific (Washington and California)	Bradbury (1966)
<i>Polyspira delagei</i>	Minkiewicz, 1912	<i>Clibanarius erythropus</i>	(Latreille, 1818)	C	France, Roscoff	Baccarani and Pessani (1997)
		<i>Pagurus bernhardus</i>	(Linnaeus, 1758)		France	Sprague and Couch (1971)
<b>Phylum Platyhelminthes</b>						
<i>Ectocotyla hirudo</i>	(Levinsen, 1879)	<i>Pagurus pubescens</i>	Krøyer, 1838	FL	Ellsworth, Maine	Hyman (1944)
		<i>Pagurus pubescens</i>	Krøyer, 1838		West Greenland	Fleming and Burt (1978)
		<i>Parapagurus pilosimanus</i>	Smith, 1879		Indian Ocean	Petrov (2000)
<b>Phylum Rotifera</b>						
<i>Proales paguri</i>	Thane-Fenchel, 1966	<i>Pagurus bernhardus</i>	(Linnaeus, 1758)	C	Denmark, Sweden, North Sea	Thane-Fenchel (1966)
<b>Phylum Arthropoda, Subclass Copepoda</b>						
unidentified copepod		<i>Paguristes puncticeps</i>	Benedict, 1901	C	Florida	Pearse (1932), Humes (1958)
<b>Phylum Arthropoda, Infraclass Cirripedia, Superorder Thoracica</b>						
<i>Pagurolepas atlantica</i>	Keeley and Newman, 1974	<i>Tomopagurus cokeri</i>	(Hay, 1917)	El	Florida	Keeley and Newman (1974)
<i>Pagurolepas conchicola</i>	Stubbings, 1940	<i>Sympagurus andersoni</i>	(Henderson, 1896)	El	Zanzibar	Stubbings (1940)
		unidentified hermit crab			Zanzibar	Zevina and Kolbasov (1997)
<i>Pagurolepas elongata</i>	Zevina and Kolbasov, 1997	unidentified hermit crab		El	Southeast Pacific, Nasca Ridge	Zevina and Kolbasov (1997)
<i>Pagurolepas utinomii</i>	Zevina and Kolbasov, 1997	<i>Dardanus aspersus</i>	(Berthold, 1846)	El	Japan	Utinomi (1970), Zevina and Kolbasov (1997)
<i>Pagurolepas zhadani</i>	Zevina and Kolbasov, 1997	<i>Paragiopagurus boletifer</i>	(de Saint Laurent, 1972)	El	Nasca Ridge	Zevina and Kolbasov (1997)

(continued on next page)

Table 2 (continued)

Associate species	Associate authority	Host hermit crab species	Host authority	Hab	Locality	Reference
<b>Phylum Arthropoda, Infraclass Cirripedia, Superorder Thoracica</b>						
<i>Poecilasma kaempferi novaeangliae</i>	Pilsbry, 1907	<i>Pagurus politus</i>	(Smith, 1882)	C	Massachusetts, Marthas Vineyard	Pilsbry (1907)
<b>Phylum Arthropoda, Order Diptera</b>						
<i>Lissocephala powelli</i>	Carson and Wheeler, 1973	<i>Birgus latro</i>	(Linnaeus, 1767)	C	Christmas Island	Carson and Wheeler (1973), Carson (1974)

the transition from water to land in the Coenobitidae had an added benefit of allowing for release from parasitism. Coenobitids are only parasitized by mites and no terrestrial hermit crabs are infested with parasites (e.g., bopyrids or rhizocephalans) that cause castration of hosts as found in their marine counterparts. In their review of burrowing brachyuran land crabs, Bright and Hogue (1972) found few parasites aside from dipterans, mites and copepods. Another partial release from parasitism is found within the Aeglidae, a family of anomurans entirely restricted to freshwater habitats in South America. While aeglids host a variety of commensals and a few parasites (Martin and Felgenhauer, 1986), none are found with parasitic isopods or barnacles as members of both these taxa are, with the exception of four species of rhizocephalans, not found breeding in fresh-water habitats. The aeglid release from parasitism is not directly comparable with hermit crabs in that only one hermit crab has ever been described from freshwater habitats (McLaughlin and Murray, 1990), probably due to osmoregulatory constraints (Dunbar et al., 2003).

In addition to the known parasites of hermit crabs, there are an additional 17 species that are suspected to have negative impacts on 27 hosts (Table 2; Section 3.10). Hermit crabs are also known to be hosts for 10 described species of hyperparasites (Table 3; Section 3.12).

### 3.1. Phylum Apicomplexa

Members of the Apicomplexa are all parasites in a great variety of invertebrates and vertebrates (Lee et al., 2000). The best studied members of this phylum are those that cause disease in man and domestic animals (e.g., malaria and coccidiosis). Less biological information is available for species that infect invertebrates, although hundreds of species of gregarines infect the digestive tracts or hemocoels of invertebrates from a wide variety of phyla. All cephaline gregarines that infect the intestine of crustaceans (cirripedes, decapods and amphipods) belong to four genera distributed in two families, Cephaloidophoridae and Porosporidae (Lee et al., 2000; Prasad and Janardanan, 2001). Among the 62 named species within the family Cephaloidophoridae, *Cephaloidophora ocellata* is the only gregarine known from hermit crabs (Fig. 3B); the species is found in the gut of the European species *Pagurus prideaux* (Sprague and Couch, 1971). Within the host, sporozoites are liberated and then enter and develop in epithelial cells of the digestive tract. Oocysts are produced by sporogony and, after release from infected animals, are ingested by new hosts. Nothing appears to be known of the biology and the relations of *C. ocellata* with hermit crab hosts.

*Pagurus prideaux* is also parasitized by the coccidian *Aggregata vagans* (Kamm, 1922; Sprague and Couch, 1971) (Fig. 3A). Goodrich (1950) indicated this species was found with three European species of hosts from the genus *Pagurus*, but did not indicate which species. The genus *Aggregata* (subclass Coccidiasina, order Eucoccidiorida) is composed of approximately 20 species whose life cycles involve two hosts, intermediate decapod crustacean hosts and definitive cephalopod hosts (Sprague and Couch, 1971;

Sardella and Martorelli, 1997; Lee et al., 2000). Thus, other paguroids may act as hosts in systems where cephalopods (e.g., octopus) prey on these potential crustacean hosts (e.g., Brooks and Mariscal, 1985).

### 3.2. Phylum Dinoflagellata

The endoparasitic dinoflagellate genus *Hematodinium* parasitizes a wide range of crustaceans (Fig. 3E, F), including hermit crabs (Hamilton et al., 2009; Jensen et al., 2010). Two species of hermit crabs, *Pagurus bernhardus* and *P. prideaux*, have been shown to harbor this parasite in waters of the Clyde Sea, Scotland (Hamilton et al., 2009). In this area, 23% of *P. bernhardus* were infected with the parasite and the parasite reached highest prevalence in April, at which time >50% of the crabs had the parasite (Hamilton et al., 2009). In the hermit crab hosts it invades cardiac muscle, gills, hepatopancreas, muscle, and stomach tissues (Hamilton et al., 2009). In commercially important crustaceans such as *Chionoecetes bairdi* Rathbun, 1893 and *C. opilio* (tanner and snow crabs, respectively), *Hematodinium* sp. causes Bitter Crab Disease (BCD) due to effects on flavor of the muscle tissue in these hosts (Stentiford and Shields, 2005). Molecular evidence shows the species that infects *P. bernhardus* is conspecific with *Hematodinium* infecting *Nephrops norvegicus* (Linnaeus, 1758), *Cancer pagurus* Linnaeus, 1758, and *Chionoecetes opilio* (Small et al., 2007). The complete life cycle of *Hematodinium* spp. is not known but may involve an additional planktonic host or a resting benthic phase (Stentiford and Shields, 2005; Hamilton et al., 2009). Whether the parasites causes death of large numbers of hermit crabs, as has been found in other hosts, remains unknown.

### 3.3. Phylum Microsporidia

Microsporidians are intracellular parasites found in most invertebrate phyla (mainly arthropods) and all classes of vertebrates (mainly fishes) (Lee et al., 2000). Most of the life cycles are unknown, but all involve a proliferative period (merogony) resulting in the production of the infective spores (sporogony). Identification usually requires detailed observations on the elaborate internal structure of mature spores. Presently there are two described species of microsporidians found with the hermit crab *Pagurus bernhardus*. Pérez (1927a) examined 838 specimens of *Pagurus bernhardus* of which four were infected with *Thelohania paguri*; the abdominal hemocoels of the host crabs were packed with large masses of spores. Approximately 17 other crustacean species, both fresh water and marine, are infected with at least nine other species of *Thelohania* (Sprague, 1965, 1970; Sprague and Couch, 1971). In crayfish, *Thelohania* causes porcelain disease (thelohaniasis) resulting in white coloration of the abdomen of infected individuals due to destruction of myofilaments by the parasite (Mori and Salvidio, 2000). More recently, Stentiford and Bateman (2007) described *Enterosporea* sp. as an intranuclear parasite that infects the hepatopancreatocytes of *Pagurus bernhardus* (Fig. 3C). The species found in *P. bernhardus* is similar to

**Table 3**

Hyperparasites associated with hermit crabs.

Primary parasite	Primary symbiont Authority	Hyperparasite	Hyperparasite Authority	Hermit crab	Locality	Reference
<b>Protozoa (incertae sedis)</b>						
<i>Peltogaster curvatus</i>	Kossmann, 1874	<i>Vahlkampfia paedophthora</i>	(Caullery, 1906)	<i>Pagurus excavatus</i>	Naples	Caullery (1906)
<i>Peltogaster paguri</i>	Rathke, 1842	Amoeba		<i>Pagurus pubescens</i>	Maine	Reinhard and von Brand (1942)
<b>Phylum Arthropoda, Order Isopoda, Superfamily Cryptoniscoidea, Family Cabiropidae</b>						
<i>Bopyrissa diogeni</i>	(Popov, 1927)	<i>Cabirops codreanui</i>	Bourdon, 1967	<i>Diogenes pugilator</i>	France	Bourdon (1967)
<i>Asymmetrione foresti</i>	(Bourdon, 1968)	<i>Cabirops ibizae</i>	Bourdon, 1967	<i>Paguristes oculatus</i>	Mediterranean	Bourdon (1967)
<i>Bopyrissa fraisei</i>	(Carayon, 1943)	<i>Cabirops perezi</i>	Carayon, 1942	<i>Clibanarius erythropus</i>	France	Carayon (1942), Bourdon (1964)
<i>Pseudionella deflexa</i>	Bourdon, 1979	<i>Cabirops</i> sp. B		<i>Pagurus brevidactylus</i>	Brazil	Boyko and Williams (2004)
<i>Athelges</i> sp.		<i>Cabirops</i> sp.		<i>Trizopagurus strigatus</i>	Indonesia	Haig and Ball (1988)
<b>Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea, Superfamily Cryptoniscoidea, Family Cryptoniscidae</b>						
<i>Peltogaster curvatus</i>	Kossmann, 1874	<i>Liriopsis monophthalma</i>	Fraisse, 1878	<i>Pagurus excavatus</i>	Italy	Altès (1962)
<i>Peltogaster paguri</i>	Rathke, 1842	<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Pagurus bernhardus</i>	France	Bourdon (1963)
		<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Pagurus bernhardus</i>	Norway	Dahl (1950)
		<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Pagurus hirsutiusculus</i>	Alaska	Warrenchuk and Shirley (2000)
		<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Orthopagurus schmitti</i>	Washington, USA	George and Strömberg (1968)
		<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Pagurus cuanensis</i>	United Kingdom	Marine Biological Association (1931)
		<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Anapagurus laevis</i>	Northeastern Atlantic	Pike (1961b)
<i>Peltogasterella gracilis</i>	Boschma, 1927	<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Pagurus pubescens</i>	Maine	Reinhard (1939)
		<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Pagurus ochotensis</i>	Washington, USA	George and Strömberg (1968)
		<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Pagurus hirsutiusculus</i>	Washington, USA	George and Strömberg (1968)
<i>Septosaccus cuenoti</i>	Duboscq, 1912	<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Diogenes pugilator</i>	France	Duboscq (1912)
<i>Septosaccus rodriguezi</i>	(Fraisse, 1876)	<i>Liriopsis pygmaea</i>	Rathke, 1843	<i>Diogenes pugilator</i>	France	Bourdon (1963)
<i>Septosaccus rodriguezi</i>	(Fraisse, 1877)	<i>Cryptoniscus paguri</i>	Fraisse, 1878	<i>Clibanarius erythropus</i>	Corsica	Codreanu (1968)
<i>Peltogaster purpureus</i>	(Müller, 1862)	<i>Cryptoniscus planarioides</i>	Müller, 1871	<i>Clibanarius</i> sp.?	Brazil	Altès (1962)
<b>Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea, Superfamily Cryptoniscoidea, Family Hemioniscidae</b>						
<i>Tomlinsonia mclaughlinae</i>	Williams and Boyko, 2006	<i>Hemioniscus paguophilus</i>	Williams and Boyko, 2006	<i>Calcinus gaimardii</i>	Philippines	Williams and Boyko (2006)
<b>Phylum Arthropoda, Infraclass Cirripedia, Superorder Rhizocephala, Order Akentrogonida</b>						
<i>Parathelges weberi</i>	Nierstrasz and Brender à Brandis, 1923	<i>Duplorbis smithi</i>	Nierstrasz and Brender-à-Brandis, 1923	Unknown	Unknown	Nierstrasz and Brender à Brandis (1923)

*Enterosporea canceri* Stentiford, Bateman, Longshaw and Feist, 2007 described from *Cancer pagurus* (Stentiford et al., 2007). In hermit crabs, the parasite causes no sign of disease externally but the hepatopancreas tubules are destroyed when the host epithelial cells are invaded by the parasite.

### 3.4. Phylum Ascomycota, Class Sordariomycetes, Order Hypocreales

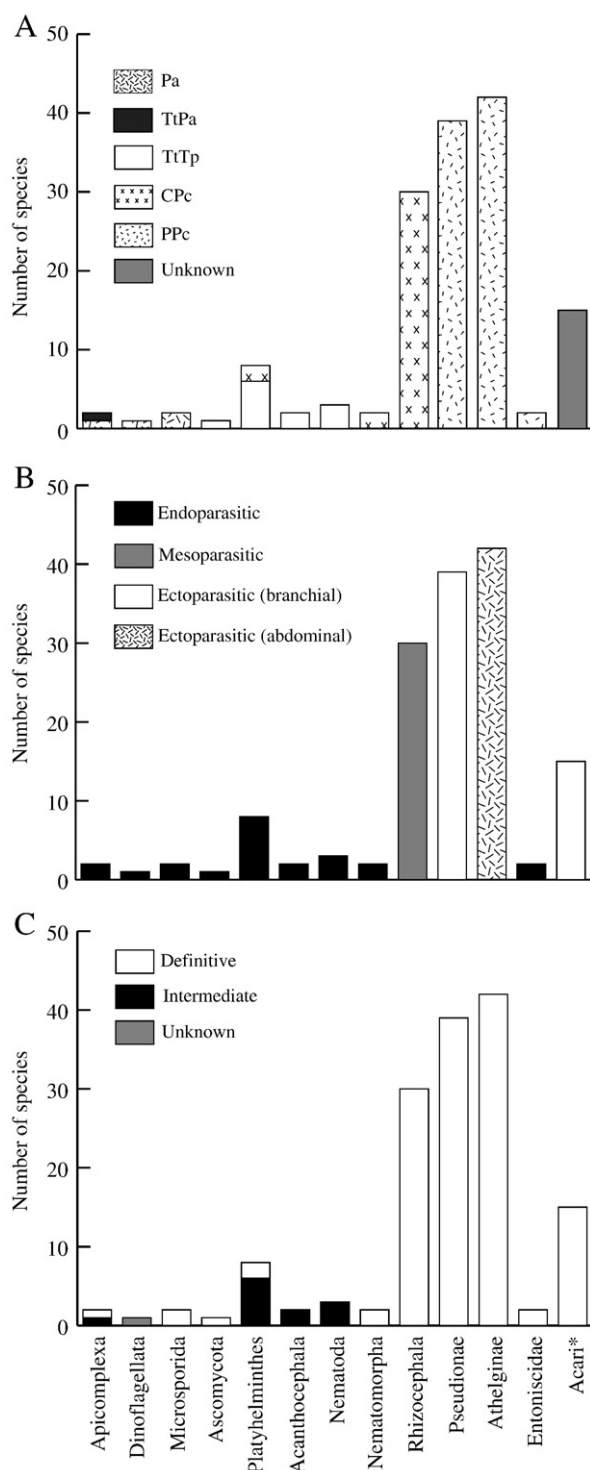
*Fusarium solani* is the only representative of the fungal phylum Ascomycota that has been found to parasitize hermit crabs. Specifically, Smolowitz et al. (1992) found *F. solani* in three species of *Pagurus* from the Woods Hole region (Fig. 3D). The species is also found in a wide range of crustacean hosts where it causes an inflammatory cell response (branchial mycosis), or black gill disease in shrimp [e.g., *Penaeus* spp. (Hose et al., 1984; Colorni, 1989; Aguirre Guzman and Ascencio Valle, 2000)]. In hermit crabs the fungus infects the gill filaments and invades the dermis of the branchial joints (Smolowitz et al., 1992). *Fusarium solani* is now considered to represent a species complex of potentially 45+ phylogenetic/biological species, many of which are of medical importance to humans since they can cause mycoses, especially in immunocompromised individuals (Zhang et al., 2006). Antimicrobial peptides

from penaeid shrimp are known to have antifungal properties to *Fusarium* sp. (Destoumieux et al., 2000; Tincu and Taylor, 2004) and similar antimicrobial defenses have been found in the hermit crab *Pagurus bernhardus* (Haug et al., 2002).

### 3.5. Phylum Platyhelminthes

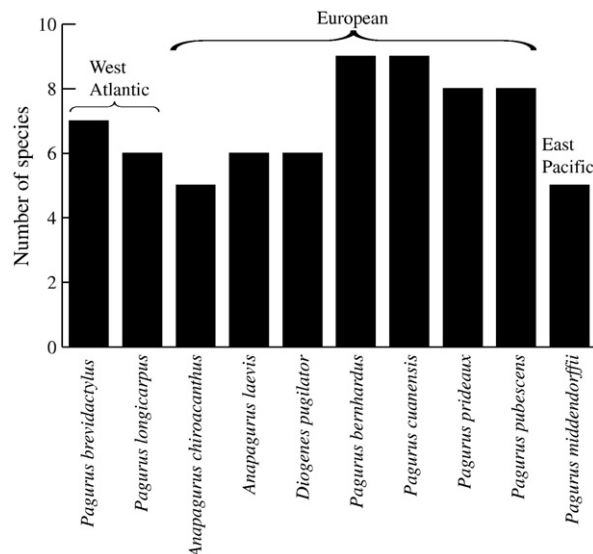
#### 3.5.1. Class Fecampiida

Parasitic platyhelminths belonging to the genus *Fecampia* were originally considered to be turbellarians (Jennings, 1971), but are now placed along with the genera *Kronborgia* and *Glanduloderma* in the Class Fecampiida (Rhode et al., 1994). These worms infect and grow to adulthood in a variety of marine crustaceans, generally killing and/or castrating their hosts. They eventually emerge as adults that produce cocoons filled with developing larvae (Fig. 4). Adults deposit the cocoon in a dying state or die within the cocoon. Competent, ciliated larvae in turn leave the cocoon and penetrate the exoskeleton of new hosts. Fecampids lack a digestive tract, and some species of the genus *Kronborgia* are dioecious (Christensen and Kannevorff, 1964, 1965; Kannevorff and Christensen, 1966; Christensen, 1976), whereas those in the genus *Fecampia* are hermaphroditic. *Fecampia erythrocephala* parasitizes



**Fig. 1.** (A) Number of hermit crab parasite species per major taxonomic grouping, showing the trophic strategies (Pa: Pathogen; TtPa: Trophically transmitted Pathogen; TtTp: Trophically transmitted Typical parasite; CPc: Complete Parasitic castrator; PPc: Partial Parasitic castrator; Unk = Unknown). To calculate total species, those parasites that were of questionable identity or not identified to the species level were not included (unless identified to genus and no additional members of that genus were represented). (B) Number of hermit crab parasite species per major taxonomic grouping, showing the habitus of parasites. (C) Number of hermit crab parasite species per major taxonomic grouping, showing the use of hermit crab hosts (as definitive hosts versus intermediate hosts). \*Mites associated with hermit crabs have not been verified as parasites.

the hermit crabs *Anapagurus hyndmanni* and *Pagurus bernhardus* (Fig. 4A), but also infects the brachyurans *Cancer pagurus* and *Carcinus maenas* (Linnaeus, 1758), and the caridean shrimp



**Fig. 2.** Number of parasite species associated with ten hermit crab hosts from three geographic regions: West Atlantic, European waters, East Pacific. These represent the most studied hermit crabs (all other species are known to host <5 parasites).

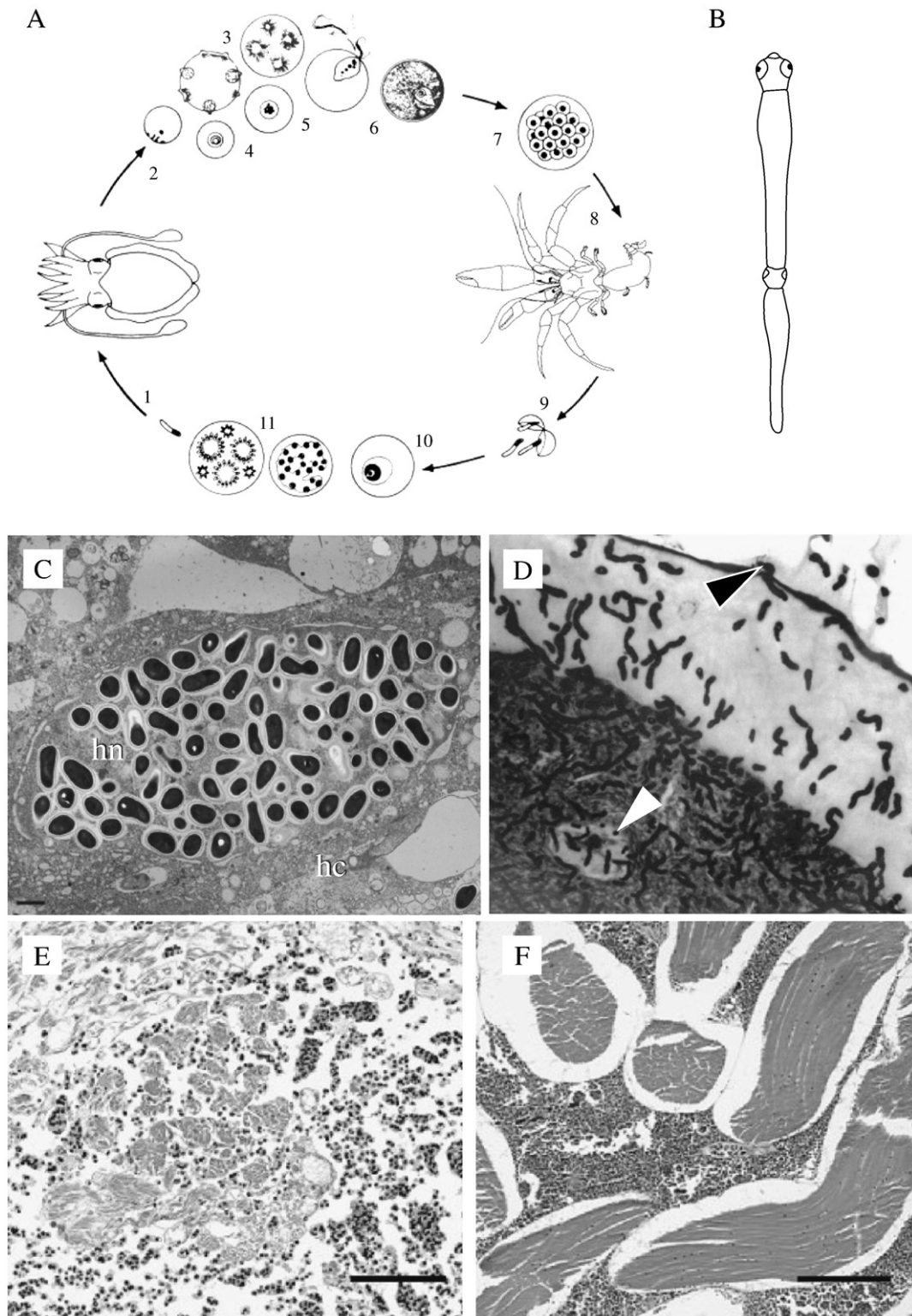
*Palaemon serratus* (Pennant, 1777) (Giard, 1886; Mouchet, 1931; Pérez, 1934; Bellon-Humbert, 1983). Pérez (1934) found that 25 of 1359 specimens of *A. hyndmanni* (1.8%) were infected with *F. erythrocephala* (two of these crabs were simultaneously parasitized with the nematomorph *Nectonema agile*). Kuris et al. (2002) suggested that *F. erythrocephala*, being very large in relation to the very young immature *C. maenas* that it infects and kills, acts like a parasitoid. Hermit crabs and caridean shrimp are infected as adults by *F. erythrocephala*, which may temporarily castrate their hosts but apparently cause less mortality than to *C. maenas* (Mouchet, 1931; Bellon-Humbert, 1983).

A curious hermit crab - fecampid (*Kronborgia* - like species) relationship was described by Christensen and Kannevorf (1967) (Fig. 4B). A sinistrally-coiled cocoon was found attached to and covering most of the shell of *Cryptonatica affinis* (Gmelin, 1791) (= *Natica clausa* Broderip & Sowerby, 1829) inhabited by *Pagurus trigonocheirus* from Point Barrow, Alaska (Fig. 4B). The authors indicated that the position of the cocoon left little doubt that *P. trigonocheirus* was host for this parasite. Furthermore, some other shells (*Buccinum scalariforme* Möller, 1842 and *Cryptonatica affinis*) without hermit crabs also harbored this distinctive cocoon. The deposition of the cocoons (designated as "type A" by Christensen (1981) and known from localities on both sides of the Bering Straits) on snail shells may be a behavioral adaptation by the fecampid. Unfortunately the species remains unknown beyond its egg masses and nothing more is known of its biology.

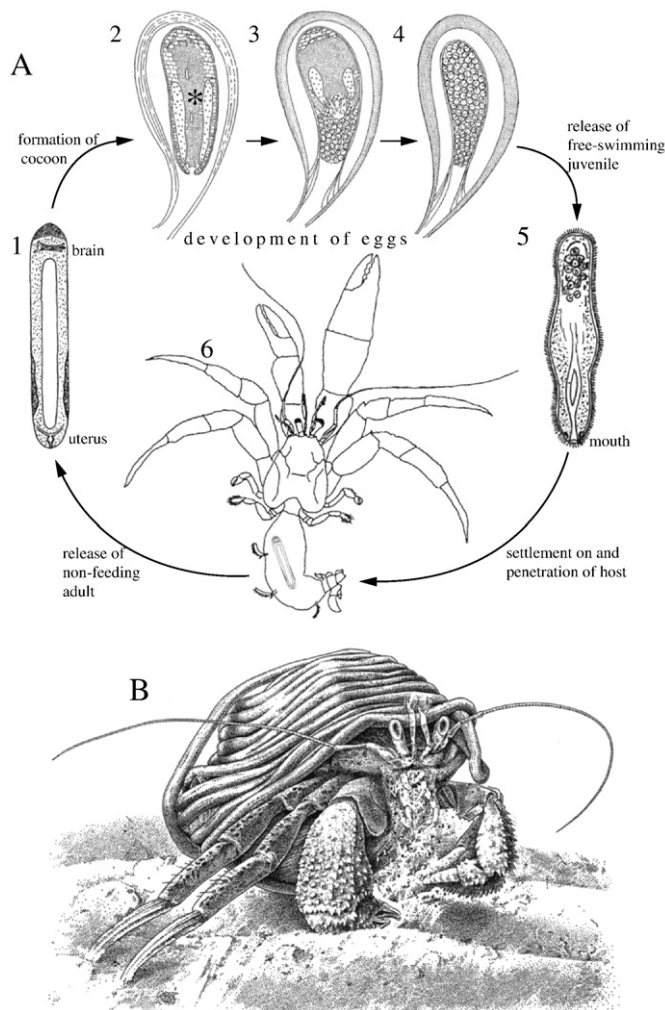
### 3.5.2. Class Cestoda

*Pagurus pollicaris* is an intermediate host for the tetraphyllidean tapeworm *Calliobothrium verticillatum* (Fig. 5), a parasite found as adults in the spiral valve of the smooth dogfish *Mustelus canis* (Mitchill, 1815) (Caira and Ruhnke, 1991; Cherry et al., 1991) and other species of elasmobranchs (Wardle and McLeod, 1952; Nasin et al., 1997; Pickering and Caira, 2008). This hermit crab is a known component of the dogfish's diet (Caira and Ruhnke, 1991; Cherry et al., 1991; Flyer, 2007). Smolowitz et al. (1993) showed, in histological sections, plerocercoid larvae within the lumina of the anterior and midgut ceca, but nowhere else in the bodies of *Pagurus* spp. collected in the Woods Hole region of Cape Cod, Massachusetts. They processed 39 crabs of which 24 had plerocercoids, but later unpublished studies showed that nearly all crabs





**Fig. 3.** Protistan and fungal parasites of hermit crabs. A) Hypothesized life cycle of the apicomplexan *Aggregata vagans* (based on *Aggregata eberthi* (Labbé, 1985) a parasite of portunid crabs): 1, cephalopods such as *Sepia* feed on hermit crabs and ingest merozoites; 2, within the intestinal mucosa the merozoites transform into gamonts; 3, microgametocyte; 4, macrogametocyte; 5, fertilization; 6, zygote; 7, oocysts containing the sporozoites that are released with feces of cephalopod host; 8, hermit crabs such as *Pagurus prideaux* ingest free sporozoites; 9, sporozoites excyst in gut; 10, sporozoites penetrate gut wall and produce meronts; 11, mature meront. B) Paired gamonts of the gregarine *Cephaloidophora ocellata*; C) The microsporidian *Enterospora* sp. in the hepatopancreatic epithelia of *Pagurus bernhardus*, showing host nuclei during advanced infection; host nucleoplasm (hn) with mature spores and host cytoplasm (hc) unaffected. D) The ascomycotan fungus *Fusarium solani* parasitizing *Pagurus pollicaris*, showing hyphae penetrating the arthropod membrane (black arrowhead) and the dermal tegmental gland (white arrowhead). E) The dinoflagellate *Hematodinium* sp. in the hemal sinuses of *Chionoecetes opilio*. F) Claw muscle of *C. opilio* showing degeneration caused by the dinoflagellate *Hematodinium* sp. (Fig. A, life cycle modified from Lee et al. (2000), hermit crab from Lancaster (1988); Fig. B modified from Kamm (1922); Fig. C modified from Stentiford and Bateman (2007); Fig. D modified from Smolowitz et al. (1992); Figs. E, F modified from Stentiford and Shields (2005)). Scale bars C = 1  $\mu$ m; E, F = 300  $\mu$ m; rest not to scale.



**Fig. 4.** Fecampid flatworm parasites of hermit crabs. A) Diagrammatic life cycle of *Fecampia erythrocephala*: 1, adult *F. erythrocephala* emerged from parasitized host *Pagurus bernhardus*; 2, early cocoon formed by *F. erythrocephala* (worm shown with asterisk); 3, production of eggs by *F. erythrocephala* and shrinking of flatworm body; 4, cocoon at end of spawning, filled with eggs; 5, free-swimming larva of *F. erythrocephala* released from cocoon; 6, *P. bernhardus* infected with *F. erythrocephala* (shown within abdomen of host). B) *Pagurus trigenocheirus* in gastropod shell *Cryptonatica affinis* with spiral cocoon of unidentified fecampid on top. (Fig. A (1, 5) modified from Hyman (1951); Fig. A (2–4) modified from Bellon-Humbert (1983); Fig. B modified from Christensen and Kannevorf (1967)). Not to scale.

harbored these larvae. Unfortunately, the 39 crabs were a mixture of *Pagurus acadianus*, *P. longicarpus* and *P. pollicaris*, and the infected crabs were not specifically identified. However, it is likely that at least some of the illustrated histological sections containing plerocercoids were from *P. pollicaris* (as evidenced by the hermit crab in Fig. 1a of Smolowitz et al. (1993) that is identifiable as this species). In addition, Cherry et al. (1991) noted plerocercoids were present in over 95% of *P. pollicaris* from the Woods Hole region, Massachusetts. The plerocercoids of *C. verticillatum* induce an inflammatory response due to an infiltration of hemocytes an encapsulation of the parasites, melanization and necrosis. Some crabs were found to have concurrent infections with a fungus (mycotic branchitis) and the cestode (Smolowitz et al., 1992; Smolowitz et al., 1993). Plerocercoids of *C. verticillatum* have been recorded from the brachyuran crab *Carcinus maenas* in Europe. Fyler (2007) examined the morphology of plerocercoid and adult forms of *Calliobothrium* cf. *verticillatum*. As indicated by Fyler (2007), *C. verticillatum* is in need of additional taxonomic study based on research suggesting that it may represent a species complex (Nasin et al., 1997). There is also evidence

that *P. pollicaris* may act as a host to more than one species of cestode (J. Caira, pers. commun.). Two other species of hermit crabs have been recorded as hosts for cestodes. Pearse (1932) found an unidentified species of *Rhynchobothrium* in *Paguristes puncticeps* from Florida and Abbott (1987) recorded an unidentified larval cestode (plerocercoid) in *Pagurus granosimanus* from California.

### 3.5.3. Class Trematoda

Hermit crabs may serve as second intermediate hosts in the life cycles of digenetic trematodes, but only four species of trematode metacercariae are known to infect hermit crabs (Fig. 6). Over 100 species of teleost fishes and the cuttlefish *Sepia officinalis* Linnaeus, 1758 are definitive hosts of *Derogenes varicus* (Køie, 1979) (Hemiuridae). Cystophorous cercariae released from gastropod intermediate hosts (three species of Naticidae) are consumed by a variety of crustaceans. The cercarial body is injected via the unique delivery tube into the body cavity of the host where it remains unencysted. Fish are parasitized by ingesting infected crustaceans. Uspenskaya (1960) recorded the metacercariae of *D. varicus* from the body cavity of *Pagurus pubescens* (Fig. 6A). Other intermediate hosts include pelagic, benthic and parasitic copepods and chaetognaths (Køie, 1979). Køie was able to experimentally infect six species of calanoid copepods, harpacticoid copepods and barnacle nauplii with the cercariae of *D. varicus* (Fig. 6B–D). She was unsuccessful, however, in infecting two species of amphipods, an isopod, a mysid, a chaetognath and two decapods, one of which was *Pagurus bernhardus*.

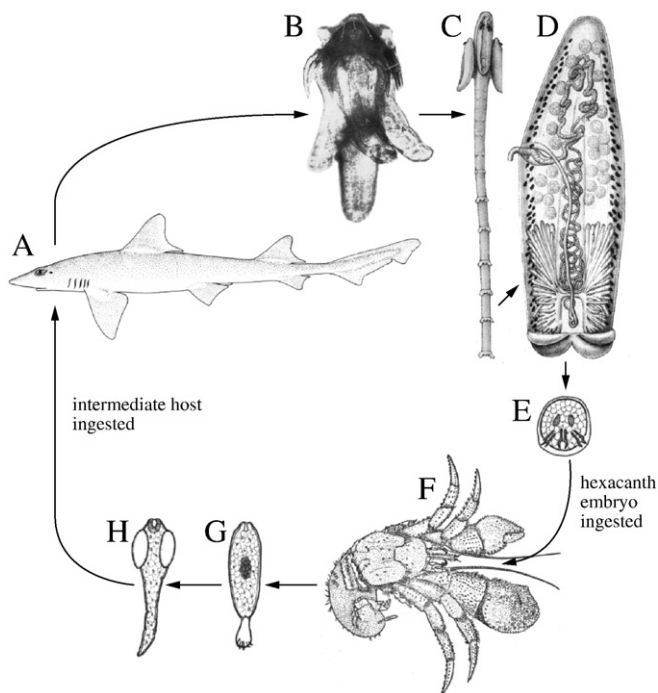
The definitive hosts of *Microphallus pirum* (Microphallidae) are the sea otter *Enhydra lutris lutris* (Linnaeus, 1758) and the Arctic fox *Vulpes lagopus* (Linnaeus, 1758) (Rausch, 1953). Metacercariae of this trematode are found in the abdominal hemocoel of *Pagurus hirsutiusculus* from Alaskan waters (Schiller, 1954) (Fig. 6E–H). Ninety percent (46 of 51) of the sampled hermit crabs had metacercariae, averaging 87 per crab with a maximum intensity of 382.

Schiller (1959) experimentally infected vertebrate hosts (including hamsters, foxes, and gulls) with metacercariae of *Microphallus pirum* from *P. hirsutiusculus*. Schiller also experimentally infected the gastropod *Purpura emarginata* Deshayes, 1839 with mature eggs from the experimental definitive hosts (miracidia released after eggs ingested). This snail is sympatric with the hermit crab, and its shell serves as one of the crab's domiciles. However, Stunkard (1968) and others have indicated that Schiller's experimental infections of the snails were confounded by the apparent presence of two different species of trematodes in the snails; some of the snails to be experimentally infected presumably harbored a second species of parasite. Thus, of the two types of cercaria reported by Schiller (1959) only the "early stage" cercaria represents *M. pirum* (Fig. 6H).

Metacercariae of *M. pirum* are also found in the brachyuran *Telmessus* sp., probably *T. cheiragonus* (Tilesius, 1812) (Schiller, 1954). Microphallid metacercariae are known to cause behavioral changes in host crabs and may cause mortality at high intensities (Shields and Overstreet, 2007).

Uspenskaya (1960) recovered the metacercariae of *Steganoderma formosum* Stafford, 1904 (originally cited as *Nordostrema messjatzevi* (Issaitchikov, 1928), a junior synonym of *S. formosum* fide Bray, 1987) from *Pagurus pubescens* as well as from the caridean shrimps *Sabinea septemcarinata* (Sabine, 1824) and *Sclerocrangon boreas* (Phipps, 1774) from the Barents Sea. Larvae of this species have also been found in 5 other caridean shrimp and probably in one brachyuran (Bray, 1987). The definitive hosts are mostly bony fish in the families Pleuronectidae, Cottidae and Gadidae, although a few species in four other families are known to be infected, as well as infections in a shark and a ray (Bray, 1987; Moles, 2007). More recently, Marcogliese (1996) found metacercaria of *S. formosum* in *Pagurus acadianus* collected from Nova Scotia. In contrast to its apparent low host specificity in the Barents Sea, *S. formosum* on the Scotian Shelf was found on average in 5% of the *P. acadianus* but not in any other hermit





**Fig. 5.** Life-cycle of the tetraphyllidean cestode *Calliobothrium verticillatum*. A) The smooth dogfish *Mustelus canis* (and other elasmobranchs) acts as definitive host. B) Immature adults of *C. verticillatum* mature in the spiral valve. C) Mature adults of *C. verticillatum* produce hexacanth embryos that are released from gravid proglottids. D) Single proglottid of *C. verticillatum*. E) Hexacanth (representative example). F) *Pagurus pollicarius* (and other crustaceans) acts as intermediate host after ingesting hexacanths; within the body of the hermit crab the parasite forms proceroids and then plerocercoids. G) Proceroid (representative example). H) Plerocercoid (representative example). The life cycle is completed when infected hermit crabs are ingested by sharks. (Fig. A modified from Compagno (1984); Fig. B modified from Cherry et al. (1991); Figs. C, D modified from van Beneden (1850); Figs. E, G, H modified from Caira and Reyda (2005); Fig. F modified from Miner (1950)). Not to scale.

crabs collected (*P. arcuatus* and *P. pubescens*) and in less than 0.1% of *Crangon septemspinosa* Say, 1818 sampled (Marcogliese, 1996). The definitive hosts for *S. formosum* are bony fish including commercially important species from the north-west Atlantic such as Greenland halibut *Reinhardtius hippoglossoides* (Walbaum, 1792) and winter flounder *Pleuronectes americanus* Walbaum, 1792 (Bray, 1987; Boje et al., 1997; McClelland et al., 2005).

Dollfus (1927) reported metacercariae of *Cymatocarpus solearis* (Braun, 1899) (as *Cymatocarpus undulatus*) in the abdominal musculature of *Pagurus tinctor* from the Persian Gulf. This trematode typically has been found in lobsters as intermediate hosts; ~35–50% of the spiny lobsters in regions of the Caribbean may harbor metacercariae of the parasite (del Carmen Gómez del Prado-Rosas et al., 2003; Grano-Maldonado and Álvarez-Cadena, 2010). Several species of turtles are known as definitive hosts for *C. solearis*, including the loggerhead turtle *Caretta caretta* (Linnaeus, 1758) (Blair and Limpus, 1982). The first intermediate host of *C. solearis* remains unknown (Cheng and Provenza, 1960; del Carmen Gómez del Prado-Rosas et al., 2003). Experiments showing adult stages of *C. solearis* can be cultivated in yolk of chicken eggs (Grano-Maldonado and Álvarez-Cadena, 2010) could lead to studies that will provide a more complete understanding of its life cycle.

### 3.6. Phylum Acanthocephala

There are about 1150 described species of acanthocephalans (spiny-headed worms) (Bush et al., 2001). They possess a unique eversible hooked proboscis used to secure them to the intestinal walls

of definitive vertebrate hosts. Without mouth or digestive tracts, they absorb their host's nutrients, and following copulation, their fertilized eggs are released and carried out of the host in its feces. The eggs are ingested by aquatic and/or terrestrial arthropod intermediate hosts where they develop into oval or fusiform cystacanth larvae capable of parasitizing the definitive host upon ingestion. Two species of hermit crabs are known hosts of two closely related species of acanthocephalan larvae in the Polymorphidae (Nickol et al., 1999) (Fig. 7).

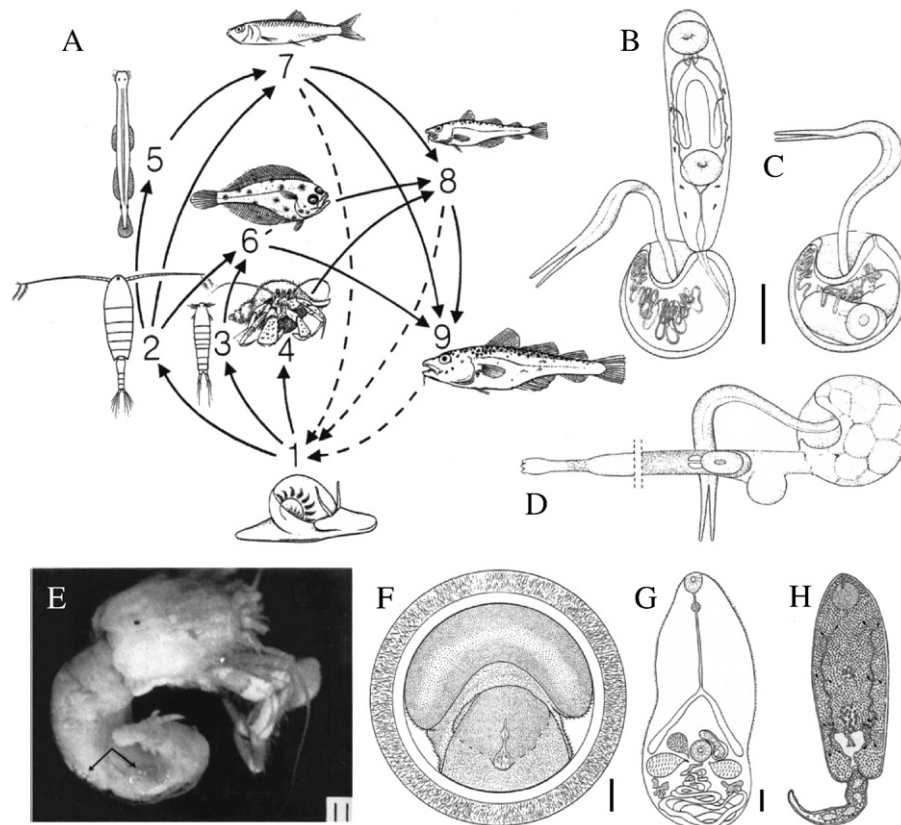
Reinhard (1944) recovered cystacanths of *Polymorphus* sp. from the abdominal hemocoel of *Pagurus longicarpus* collected in the Woods Hole area. Approximately 1% of >8000 crabs examined were infected. Usually there was one cystacanth per crab but some crabs had three. Because of the cystacanth's large size (2–3 mm long), coloration and the relative transparency of the host's abdominal wall, cystacanths were easily detected without dissection when viewed with a low power microscope. Nothing further is known of this acanthocephalan's life history (McDermott, 2001).

*Profilicollis botulus* is a parasite of many species of ducks living in the eastern and western north Atlantic, northeastern Pacific and the Arctic Oceans, but the common eider, *Somateria mollissima* (Linnaeus, 1758), appears to be the primary definitive host (Van Cleave, 1916; Uspenskaya, 1960; Ching, 1989). The European hermit crab, *Pagurus pubescens*, is an intermediate host in the life cycle of *P. botulus* (Uspenskaya, 1960) (Fig. 7), but another anomuran (*Paralithodes camtschaticus* (Tilesius, 1815) and four brachyurans (*Carcinus maenas*, *Necora puber* (Linnaeus, 1767), *Hyas araneus* (Linnaeus, 1758), *Hemigrapsus oregonensis* (Dana, 1851)) also harbor the cystacanths of this parasite (Uspenskaya, 1960; Nickol et al., 1999). Both *C. maenas* and *H. araneus* appear to be the principal intermediate hosts for *P. botulus* in northern Europe and the Arctic region (Nickol et al., 1999). Whereas Uspenskaya (1960) found only 12% (n = 1284) of *P. pubescens* infected with *P. botulus* in the Barents Sea, nearly all specimens of *H. araneus* were infected. Similarly, high prevalences were found for *C. maenas* in many northern European studies (Torchin et al., 2001).

### 3.7. Phylum Nematoda

Species of *Ascarophis* (Order Spirurida) parasitize the intestinal tracts of marine fishes (Ko, 1986) (Fig. 8A). Hermit crabs and other decapod crustaceans may harbor the juvenile stages of these nematodes, thus serving as intermediate hosts in their life cycles (Uzmann, 1967; Petter, 1970; Poinar and Kuris, 1975; Poinar and Thomas, 1976; Moravec et al., 2003). *Pagurus pubescens* as well as *Carcinus maenas* and various species of caridean shrimp (*Eualus gaimardi* (H. Milne Edwards, 1837), *Lebbeus polaris* (Sabine, 1824), *Pandalus borealis* Krøyer, 1838, *Spirontocaris spinus* (Sowerby, 1805)) are infected with *A. morrhuae* (Uspenskaya, 1960; Petter, 1970). Uspenskaya (1960) failed to recover juveniles of the closely related *A. filiformis* Poljansky, 1952 from 1,284 specimens of *Pagurus pubescens*; this worm apparently utilizes only the above mentioned caridean shrimp as intermediate hosts. *Ascarophis pacificus* Zhukov, 1960 parasitizes the hemocoel of *Pagurus middendorffii* from the Sea of Okhotsk, but was more frequently found in amphipods and an isopod (Tsimbalyuk et al., 1970). Poinar and Thomas (1976) found encapsulated infective juveniles of an unidentified species of *Ascarophis* (possibly *A. morrhuae* or *A. pacificus*) in the abdomens of *Pagurus granosimanus* (1 of 19, 5.3%) and *P. samuelis* (7 of 81, 8.6%), but not *P. hirsutiusculus* (0 of 67), collected in the Bodega Bay area of California.

Lester and Sewell (1989) recorded larvae of *Proleptus* sp. from the digestive gland of *Dardanus lagopodes* collected on Heron Island, Great Barrier Reef, Australia. In the same region, they reported *Proleptus australis* Baylis, 1933 from the digestive gland of the elasmobranch *Hemiscyllium ocellatum* (Bonnaterre, 1788).



**Fig. 6.** Trematode parasites of hermit crabs. A) Life cycle of *Derogenes varicus*. Gastropod snails (*Natica* sp.) act as first intermediate hosts (1), miracidia develop into redial stages in the snails. After release of cercariae, the parasites are ingested by a variety of potential second intermediate hosts, including the hermit crab *Pagurus pubescens* (shown in 4; note that it appears larval stages of this hermit crab are infected, not adults). Within the second intermediate hosts the parasites form metacercariae; fish definitive hosts (6–9) become infected after ingesting hermit crabs or other second intermediate hosts (2, 3, 5). B) Intra-redial cercaria of *D. varicus*. C) Free-swimming cercaria of *D. varicus*. D) Cercaria of *D. varicus* with delivery tube evaginated. E) *Pagurus hirsutiusculus* with metacercaria of *Microphallus pirum* in the body (shown by arrows). F) Encysted metacercaria of *M. pirum* from body of *Pagurus hirsutiusculus*. G) Excysted metacercaria of *M. pirum*. H) Cercaria of *M. pirum*, after 61 days of development in *Purpura emarginata*. (Figs. A–D modified from Koie, (1979); Figs. E–G modified from Schiller (1954); Fig. H modified from Schiller (1959)). Scale bars B–D, F, G = 50  $\mu$ m; rest not to scale.

### 3.8. Phylum Nematomorpha

Members of the Nematomorpha (horsehair worms), the adults of which are dioecious, short-lived, long, slender animals, occur in freshwater and semiterrestrial habitats (Class Gordioida, approximately 320 species) and marine environments (Class Nectonemertoida, 1 genus, 5 species) (Bresciani, 1991; Poinar and Brockerhoff, 2001; Schmidt-Rhaesa, 2005). The larvae of freshwater species parasitize aquatic and terrestrial insects, whereas marine nematomorphs utilize a variety of decapod crustaceans as hosts. Development takes place in the host's hemocoel where nutriment is absorbed primarily through the worm's body wall rather than being taken up by the near-nonfunctional digestive tract (Bresciani, 1991). Juveniles close to maturity leave their hosts, become pelagic and mate. Females then release their embryos, which develop into infective larvae. The five marine species all belong to the genus *Nectonema*, two of which are known to undergo development in hermit crabs. Whereas the life cycle of freshwater species has been worked out, the complete life cycle of marine nematomorphs remains unknown (Hanelt et al., 2005; Schmidt-Rhaesa, 2005). There is no evidence that a paratenic host is involved in the life cycle of *Nectonema* (Schmidt-Rhaesa, 2005) and presumably the larval nematomorphs directly infect hermits (Fig. 8B).

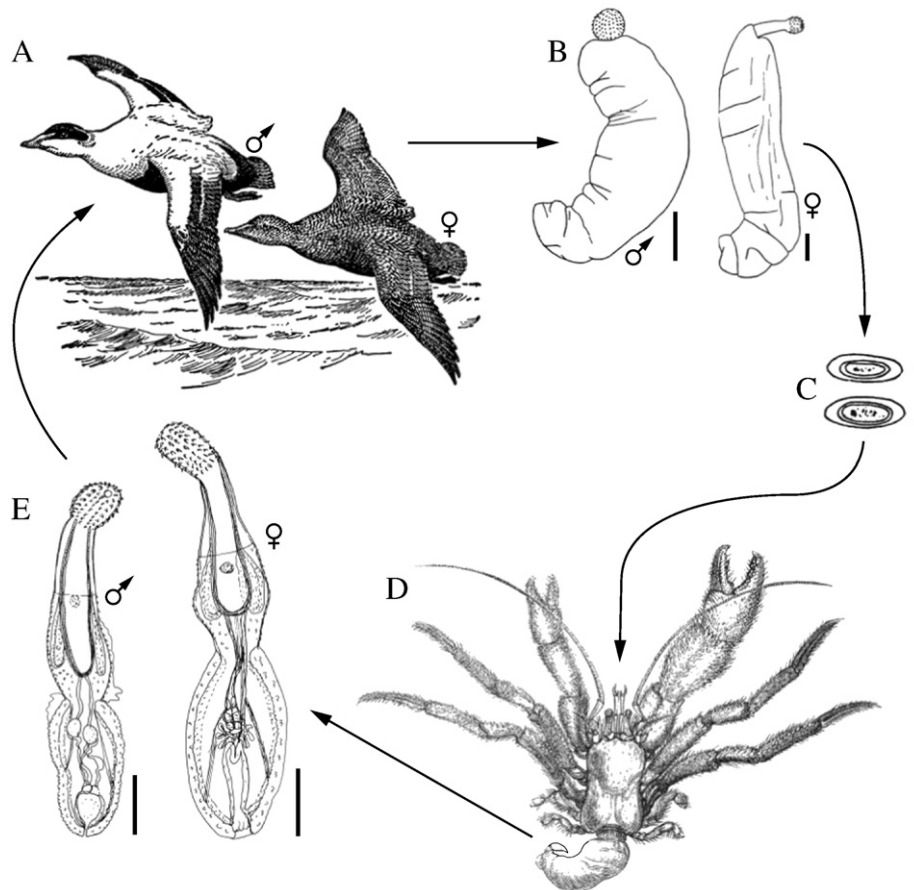
Both *Nectonema agile* and *N. munidae* are hermit crab parasites. Besides infecting at least five species of hermit crabs, *N. agile* also infects a penaeid shrimp (*Gennadas elegans* (S.I. Smith, 1882), seven caridean shrimp (*Lebbeus polaris*, *Palaemon elegans* Rathke, 1837, *P. serratus*, *Palaemonetes vulgaris* (Say, 1818), *Pandalus borealis*, *P. montagui* Leach, 1814, *Pontophilus norvegicus* (M. Sars, 1861)) and

five brachyurans (*Cancer borealis* Stimpson, 1859, *C. irroratus* Say, 1817, *Liocarcinus navigator* (Herbst, 1794), *L. pusillus* (Leach, 1815), *Macropodia rostrata* (Linnaeus, 1761)) (Arvy, 1963; Aguirre Guzmán and Ascencio Valle, 2000; Poinar and Brockerhoff, 2001). Pérez (1934) showed that *N. agile* infected 101 of 1359 (8.1%) specimens of its host *Anapagurus hyndmanni*, being nearly twice as common in males than females. Five crabs were each infected with two worms. Pérez also found that *N. agile* had a prevalence of 0.86% (20 of 2324) in *Pagurus bernhardus*. In the Bay of Fundy (Canada) the prevalence of *N. agile* in the abdominal hemocoel of *Pagurus acadianus* was 3.0% (18 of 591) (Leslie et al., 1981). Worms ranged in length from 8 to 25 cm and 0.5 mm in diameter, which was considerably smaller than the 30 to 65 cm long worms infecting the bodies of larger hosts such as the largely sympatric brachyurans *Cancer borealis* and *C. irroratus*. These rock crabs and another host, the pandalid shrimp *Pandalus montagui*, each had a prevalence of  $\approx$  20%. *Nectonema agile* has not yet been reported for crustaceans in the northeast Pacific Ocean (Kuris, 2007).

A similar lack of host specificity occurs in *Nectonema munidae* that parasitizes two species of hermit crabs, two galatheids (*Munida sarsi* (Huus, 1935) and *M. tenuimana* G. O. Sars, 1872), a sergestid shrimp (*Sergestes arcticus* Krøyer, 1855), and a caridean shrimp (*Pontophilus norvegicus*) (Poinar and Brockerhoff, 2001). Nielsen (1969) recorded a prevalence of 3.5% (2 of 58) for *N. munidae* in *Pagurus pubescens* and 0.2% (1 of 500) in *Pagurus cuanensis*.

Poinar and Brockerhoff (2001) described a new species, *Nectonema zealandica*, from the brachyuran *Hemigrapsus sexdentatus* (H. Milne Edwards, 1837) (= *Hemigrapsus edwardsii*; see McLay and Schubart,





**Fig. 7.** Life-cycle of the acanthocephalan *Profilicollis botulus*. A) Birds such as the common eider *Somateria mollissima* act as definitive hosts. B) Adult worms of *P. botulus* are found in the gastric caeca of definitive hosts. C) Eggs produced by females are shed with the feces of the hosts. D) The hermit crab *Pagurus pubescens* is infected when it ingests the eggs. E) Within the intermediate host the parasite forms male and female cystacanths (both shown evaginated). The definitive hosts are parasitized after ingesting infected hosts. (Fig. A modified from Pough (1951); Figs. B, C modified from Van Cleave (1916); Fig. D modified from Bell (1853); Fig. E modified from Ching (1989)). Scale bars B = 1 mm; C = 0.05 mm; E = 0.5 mm; rest not to scale.

2004). They suggested that this may not be the only host because other species of *Nectonema* lack host specificity; however, in their study hermit crabs were apparently not examined. Poinar and Brockerhoff provided a key for the identification of five known species of *Nectonema* (three mentioned above plus *N. melanocephalum* Nierstrasz, 1907 and *N. svensksundi* Bock, 1908, the hosts of which are not known).

*Anapagurus hyndmanni* and *P. bernhardus* parasitized with *N. agile* were found infested simultaneously with *Fecampia erythrocephala* (Pérez, 1927c, 1934; Mouchet, 1931). Although simultaneous infections with *F. erythrocephala* in the two hermit crab hosts of *N. munidae* have not been reported, Nielsen (1969) showed that the galatheid *Munida tenuimana*, infected with the same nematomorph, at times also harbored the branchial bopyrid isopod *Pseudione crenulata* G. O. Sars, 1898. *Nectonema munidae* was more prevalent in crabs infested with the bopyrid (16.3% versus 6.5%). Furthermore, multiple infections with the worm were more numerous in galatheids with the isopod (36.4% versus 2.5%). No suggestions were made by Nielsen to explain these differences, but it is possible that the bopyrid presence makes the host more vulnerable to infection by the nematomorph through impacts on the immune responses.

### 3.9. Phylum Arthropoda

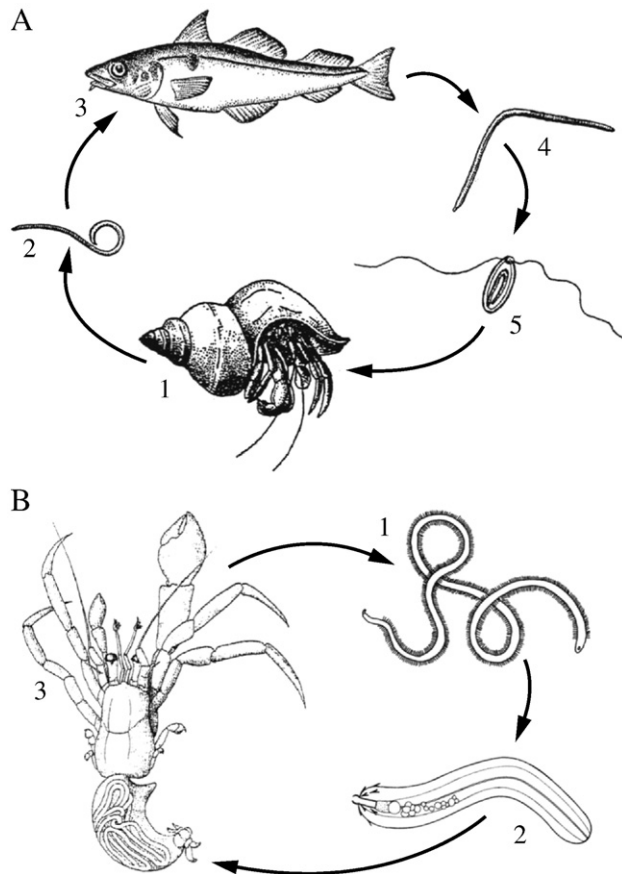
In total, 128 species of arthropods parasitize hermit crabs. This total includes mites (15 species), barnacles (30 species), and isopods (83 species). Mites are suspected ectoparasites strictly on land hermit

crabs, rhizocephalan barnacles are mesoparasites, and the isopods are ectoparasites and endoparasites.

#### 3.9.1. Phylum Arthropoda, Infraclass Cirripedia, Superorder Rhizocephala

Barnacles (Infraclass Cirripedia) belonging to the superorder Rhizocephala are parasites of a broad spectrum of their fellow crustaceans, and hermit crabs are relatively well-known hosts of these parasites. As a result, hermit crabs have been the source of considerable experimentation elucidating the life histories and host-parasite relationships of rhizocephalans. Infections impact overall host physiology as a result of castration and destruction of endocrine organs causing hormonal imbalance and resultant changes in secondary sex characteristics (Reinhard, 1942; Nielsen 1970; Høeg and Lützen, 1985; Raibaut and Trilles, 1993; Høeg et al., 2005). Pathology of the central nervous system affects neuroendocrine function producing behavioral abnormalities. Such debilitating changes produced by rhizocephalans have suggested the possibility that these parasites might be used in the control of harmful introduced brachyurans (Kuris et al., 2005, 2007; Goddard et al., 2005), although the level of host specificity is not known for most rhizocephalans.

Rhizocephalans are divided into two orders, Kentrogonida and Akentrogonida, distinguished primarily by larvae that hatch as nauplii or cyprids, respectively (Høeg, 1995). Hermit crabs are hosts to the Peltogastridae (Kentrogonida) and to the Clistosaccidae and Thompsoniidae (Akentrogonida). Thirty species of rhizocephalans are known to infect at least 55 species of hermit crabs belonging to the



**Fig. 8.** Life cycles of the nematode and nematomorph parasites of hermit crabs. A) Life cycle of the nematode *Ascarophis morrhuae*: 1) the hermit crab *Pagurus pubescens* acts as the intermediate host; 2) within the hermit crab the parasite forms an encapsulated larval form (unencapsulated larva shown); 3) definitive host fish such as the Atlantic cod *Gadus morhua* become infected when they feed on hermit crabs; 4) within the definitive host *A. morrhuae* reaches maturity within the intestinal tract; 5) adults of *A. morrhuae* produce eggs that are released with the feces of the fish and ingested by hermit crabs and other crustaceans. B) Hypothesized life cycle of the nematomorph *Nectonema agile*: 1) the non-feeding adult nematomorph worm is free-living; 2) adults produce larvae that penetrate hermit crabs such as *Pagurus bernhardus*; 3) the larvae develop into juvenile nematomorphs in the hemocoel of the hermit crabs and absorb nutrients across the worm's body wall. (Fig. A modified from Uspenskaya (1953); Fig. B modified from Pérez (1934) and Schmidt-Rhaesa (2005)). Not to scale.

Diogenidae, Paguridae and Parapaguridae (Table 1). At least 11 species (35%) of these barnacles parasitize more than one species of crab; *Peltogaster paguri* and *Peltogasterella gracilis* have the broadest host range, infecting 14 and 13 species of crabs, respectively. These host-parasite statistics were recorded primarily from Høeg and Rybakov (1992) and Øksnebjerg (2000).

Some of the rhizocephalan species within the three families that parasitize hermit crabs are considered gregarious or non-colonial whereas others are colonial (Høeg and Rybakov, 1992; Høeg and Lützen, 1993, 1995). For example, within the Kentrogonida, species of the genus *Peltogaster* are gregarious in that externae result from multiple crab invasions of cyprid larvae, each developing its own root system and emerging at different times. The number of externae per crab is relatively small (Fig. 9). In *Peltogaster paguri* infections of *Pagurus pubescens* for example, Reinhard (1942) found that 93.2% of the crabs examined (395 of 424) had only one externa (Fig. 9). *Peltogaster curvatus* usually produced single externae in its host *Pagurus cuanensis* in Scandinavian waters, whereas in the Mediterranean Sea one-third of its two hosts, *P. cuanensis* and *P. prideaux*, had two to four externae (Høeg and Lützen, 1985). The genus *Peltogasterella*, on the other hand, is colonial in that multiple externae are

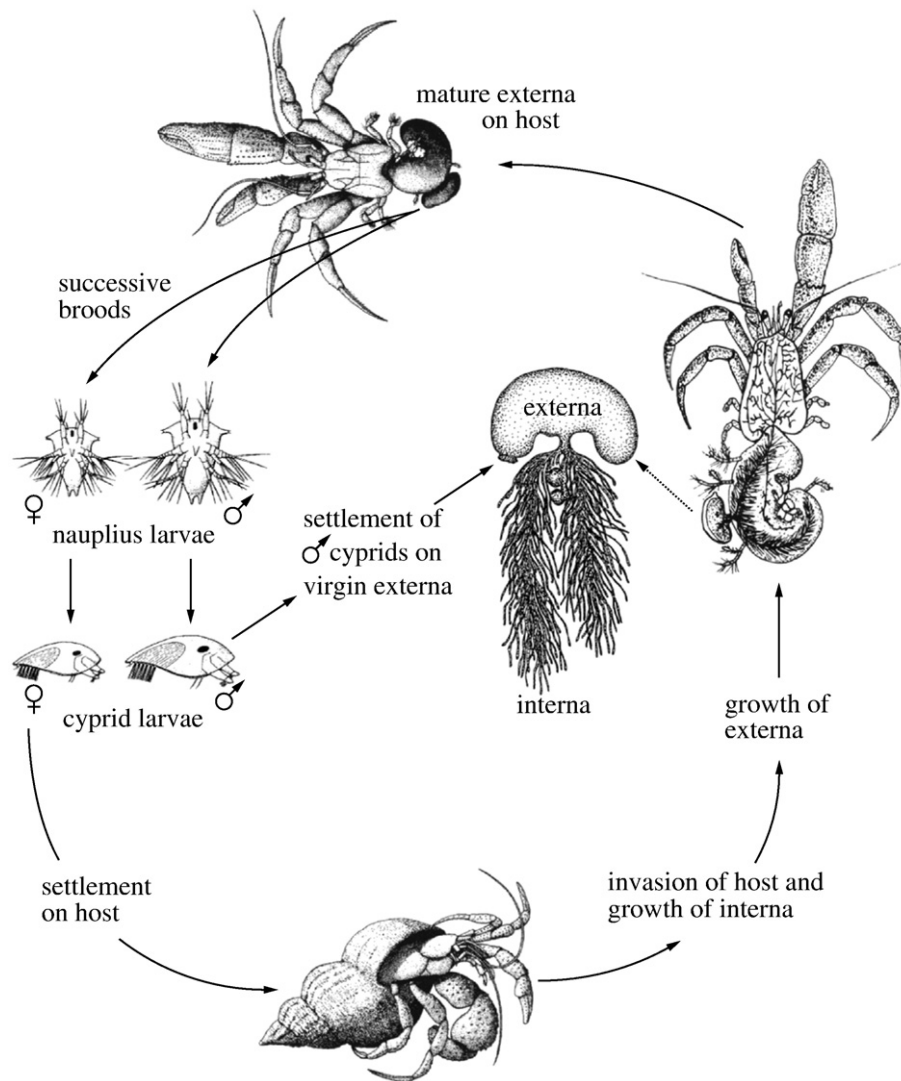
derived from a common root system produced by single cyprid larvae (Fig. 10D, E). These externae emerge simultaneously, and the number per crab is relatively large. Høeg and Lützen (1985) showed that *Peltogasterella sulcata* sometimes produced single externae, but 92.6% had >1 (50 of 54 specimens). Some crabs had 30 externae. The same dichotomy exists in hermit crab parasites within the Akentrogonida. *Clistosaccus paguri* is gregarious and usually produces one or two externae (87.4%, 90 of 103 crabs examined) (Høeg and Lützen, 1985; Glenner et al., 2010) (Fig. 10F). On the other hand, species of *Thylacoplethus* and *Thompsonia* are colonial and known to produce hundreds of externae (Fig. 10A–C). Lützen (1992) showed that *Thylacoplethus reinhardi*, a parasite of *Discorsopagurus schmitti*, always produced multiple externae with as many as 37 per host. *Thylacoplethus isaevae* produces >150 externae in its host *Pagurus trigonochirus* from Russian waters (Rybakov and Shukalyuk, 2004). This hermit crab also harbors *P. paguri* and *C. paguri*. Høeg and Lützen (1993) suggested that coloniality in *Peltogasterella* and members of the Thompsoniidae is a case of convergence, as the two are rather distantly related. One interesting feature of rhizocephalan infection on hermit crabs is that these hosts, like galatheids but unlike brachyurans, are able to continue molting even after the emergence of the externae (Potts, 2006; Pérez, 1931).

Infections of multiple species of rhizocephalans on a single host species, although usually not simultaneous, are possible, with as many as three species known from a single host taxon. Samuelsen (1970) reported 2.0% of *Pagurus cuanensis* in Norway being infected by *Peltogaster paguri*, whereas 5.5% bore *Peltogaster curvatus* and 1.7% had *Peltogasterella sulcata*.

Isaeva et al. (2005) found the kentrogonid rhizocephalan *Peltogaster reticulatus* in approximately 20% of *Pagurus proximus* sampled from Vostok Bay, Peter the Great Bay and Sea of Japan. Although *Peltogaster reticulatus* has only one externa visible on the abdomen of the infected hosts (Fig. 9), Isaeva et al. (2005) observed that the parasitic barnacle produces multiple supplementary primordial externae that are associated with the interna. These primordial externae can replace the original externa if it is damaged.

Reinhard (1942) studied the host–parasite relationship between *Pagurus pubescens* and *Peltogaster paguri* from several locations in Maine. He found that 424 of 3092 crabs were infected (13.7%, range 7.5 to 25.2%). Females were more frequently parasitized, and although castration occurred only in females, their secondary sexual characteristics were not affected. Earlier studies by others involving infections with *P. paguri* in three species of European hermit crabs showed some masculinization of infected females or feminization in males, as well as inhibition of gonad development in males and females of some species (Reinhard, 1942).

Walker and Pearse (1939) collected *P. pubescens* from Maine and recorded *P. paguri* in 10 of 29 crabs (34.5%), but they found no infections among *P. acadianus* from Maine or Newfoundland. At approximately the same time and place, Reinhard (1942) also found that *P. acadianus* was not infected with *P. paguri* (>3000 crabs examined). These results suggest that there are species-specific differences in congeneric (and sympatric) hermit crab hosts in their susceptibility to rhizocephalan infections. *Pagurus pubescens* is the only trans-oceanic species of *Pagurus* in the northern Atlantic. Its geographical distribution in the western Atlantic is from western Greenland, Foxe Basin, Hudson Bay to Cape Hatteras, and in the eastern Atlantic at Spitzbergen, Barents Sea to the Faeroes, the Hebrides, England and Ireland (Williams, 1984). Although *P. pubescens* is morphologically similar to the European species *P. bernhardus*, McLaughlin (1973) claimed the species to be distinct and unlikely to have been involved in hybridization as suggested by Jennings (1972). *Peltogaster paguri* is known to parasitize many species of hermit crabs from the eastern Atlantic, viz., 12 other members of the genus *Pagurus*, *Parapagurodes gracilipes*, and two species of *Anapagurus* (Høeg and Lützen, 1985; Table 1). Hermit crab species from the western Atlantic



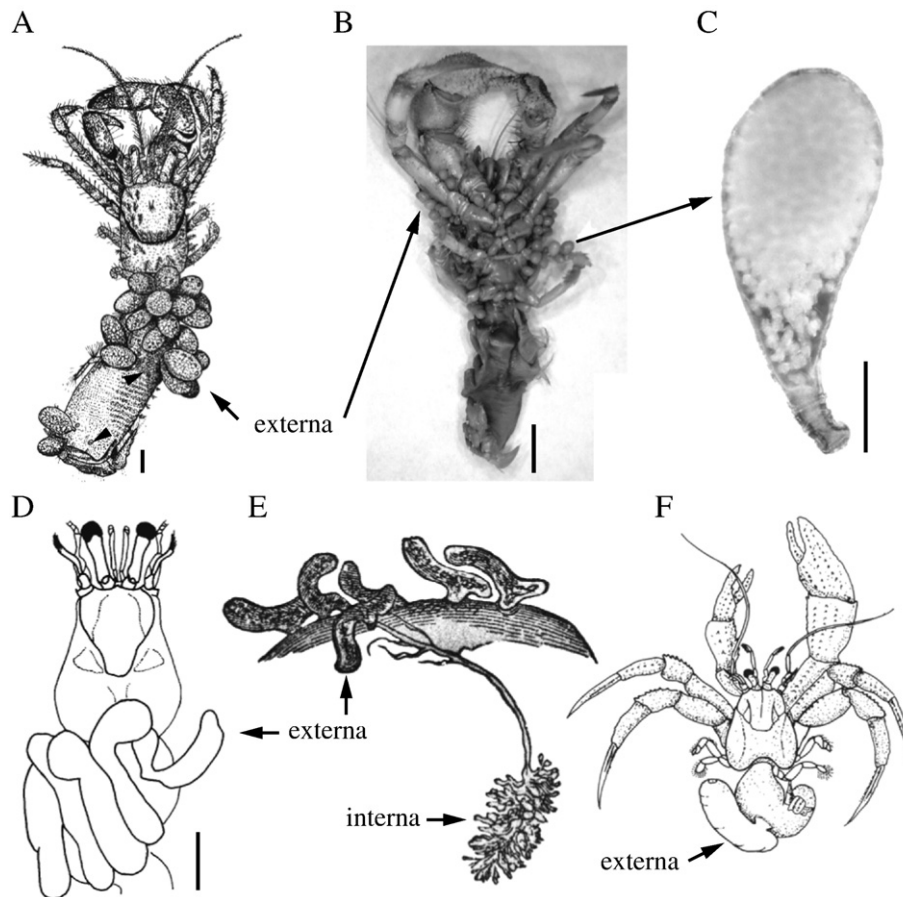
**Fig. 9.** Life-cycle of rhizocephalan barnacles that infest hermit crabs. Mature externa of parasitized host releases nauplius larvae that develop into cyprids (rhizocephalans of the Akentrogonida lack free-swimming naupliar stages). Female cyprids settle on new hosts whereas male cyprids settle on 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 (dotted arrow indicates magnified view of rhizocephalan taken out of hermit crab host). 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)). Not to scale.

that overlap in their geographic distributions with *P. pubescens* and *P. acadianus* but apparently do not harbor *P. paguri* are: *P. annulipes*, *P. arcuatus*, *P. longicarpus*, *P. politus*, and *P. pollicaris*. Thus, only the trans-Atlantic hermit crab species is host to *P. paguri*. What does this say about the evolution of host relations or specificity of this rhizocephalan? Are these six other western Atlantic species so physiologically different from *P. pubescens* and the eleven other European members of the same genus that they resist infection with this barnacle? Are gill-cleaning mechanisms that remove invasive cyprid larvae in the western Atlantic species superior to those of the other pagurids? This seems unlikely as studies of grooming appendage morphology in porcelain crab species (Anomura: Galatheaidea) showed no differences between those species susceptible to rhizocephalan attack and those that are resistant, and suggested that behavioral adaptations may be responsible for the differential success of congeneric hosts at avoiding parasitization (Fleischer et al., 1992). Although *P. paguri* has not been reported from *Pagurus annulipes*, the latter is vulnerable to *Peltogaster naushonensis*, described by Reinhard (1946) from crabs collected in the Woods Hole area of Massachusetts. Its prevalence was

4.2% (3 of 71 crabs examined). Is there natural immunity to the parasite or are there unique host internal cellular reactions that might lyse and melanize the invading parasites? Were the number of crabs examined by Reinhard and Walker and Pearse adequate to detect a possibly low prevalence in the western Atlantic species? This seems unlikely if we consider that many thousands of specimens of *P. longicarpus* and *P. pollicaris* have been examined in the past for various species of symbionts (Reinhard, 1945; Lytwyn and McDermott, 1976; McDermott, 1998, 2001).

Morphological and physiological changes in the hosts infected by rhizocephalans are dramatic and well documented for a variety of relationships (Reinhard, 1956; Nielsen, 1970; Høeg, 1995; Raibaut and Trilles, 1993; Høeg et al., 2005), although these studies do not appear to show as great an effect on the hosts as is seen in galatheid or shrimp species. These particularly involve the reproductive biology and growth of infected hosts and can be illustrated with observations on a variety of hermit crab hosts. Potts (1906) stated that *Pagurus excavatus* with *Peltogaster* developed an intersexual condition capable of producing both sperm and eggs in the testes. Reinhard (1956)





**Fig. 10.** Rhizocephalan parasites of hermit crabs. A) *Thylacoplethus reinhardi*, a colonial akentrogonid rhizocephalan with multiple externae on *Discorsopagurus schmitti* (dorsal view); scars of externae shown on abdomen of host by arrowheads. B) *Thylacoplethus isaevae*, a colonial akentrogonid rhizocephalan with multiple externae on *Pagurus trigonocheirus* (ventral view). C) Single externa of *T. isaevae* removed from host, developing larvae within externa. D) *Peltogasterella socialis*, a colonial kentrogonid rhizocephalan with multiple externae on *Pagurus criniticornis*. E) *P. socialis*, showing interna and externa of barnacle. F) *Clistosaccus paguri*, an akentrogonid rhizocephalan with a single externa on the abdomen of *Pagurus bernhardus*. (Fig. A modified from Raibaut and Trilles (1993); Figs. B, C modified from Rybakov and Shukalyuk (2004); Figs. D, E from Faria et al. (2007); Fig. F modified from Høeg (1990)). Scale bars A = 1 mm, B–D = 0.15 mm; rest not to scale.

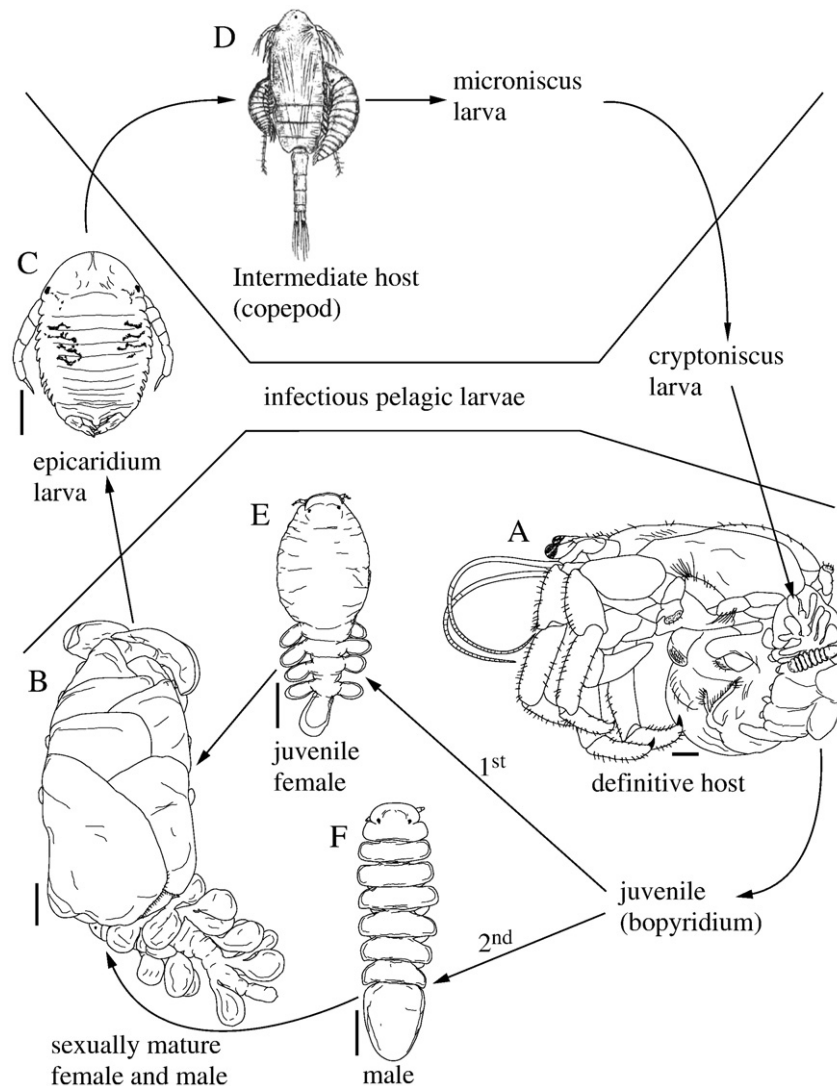
considered the body of evidence for sex reversal caused by parasitic castration to be scanty, as Potts' observations have never been documented for any other hermit crab.

The effects of *Peltogaster paguri* and *Peltogasterella sulcata* on five species of hermit crabs belonging to two genera collected in western Scotland, western Sweden and southern Norway were described by Nielsen (1970). Two species (*Anapagurus laevis*, *Pagurus prideaux*) are hosts for both parasites, two hosts (*P. bernhardus*, *P. pubescens*) are found only with *P. paguri*, and one (*P. cuanensis*) is a host for *P. sulcata*. Effects on the primary and secondary sexual characteristics of the hosts varied considerably. In all infected crab species, ovaries and testes were reduced or virtually absent, except for *P. pubescens* infected with *P. paguri* where there was no noticeable effect in males. The latter verified Reinhard's (1942) earlier observations with the same host-parasite relationship in Maine. In the two crab species that hosted both species of parasites, *Peltogaster* had a greater effect on the gonads in *A. laevis*, whereas *Peltogasterella* had the greater effect in *P. prideaux*. Secondary sexual characteristic changes in males involved reduced or missing gonopores, extra pleopods, and feminization of pleopods (i.e., elongated endopods). In the male of *A. laevis* there is a copulatory organ (external vas deferens on the coxopod of the left fifth pereopod), and both *Peltogaster* and *Peltogasterella* cause a partial reduction or absence of this structure. In female hosts there may be a reduction in the size of whole pleopods or a reduction in the length of the endopods, reduction in the length or number of the embryo-bearing setae on the pleopods, reduction in the size of the fourth

pleopod, and gonopores may be modified or absent. Reinhard (1956), in a summary of the effects of parasitism on sexual function in crustaceans, noted that most studies on secondary sexual character modification in pagurids by rhizocephalans (*Peltogaster* and *Septosaccus* spp.) showed a tendency for pleopods of infected males to become more like those of females, whereas there was little evidence for females becoming more masculinized. Some hosts appear to show little to no modification of the secondary sexual features, despite suffering complete parasitic castration by the rhizocephalan.

As is the case in the more well studied brachyuran-rhizocephalan relationships, the hermit crab parasites obviously upset the hormonal system of their hosts (Warner, 1977; Høeg, 1995; Høeg et al., 2005). The root-like parasitic interna affects the normal functioning of the gonads, causes degeneration of the androgenic gland in males, and produces extensive destruction of the central nervous system and ventral ganglionic mass with the accompanying loss of important neurosecretory functions. All may lead to the well-documented physiological, morphological and behavioral changes that have been observed. The lithodid crab parasite *Briarosaccus callosus* Boschma, 1930, produces high-affinity hemoglobin that circulates through the interna and externa of the barnacle (Terwilliger et al., 1986). The hemoglobin of the rhizocephalan appears to aid in transfer of oxygen to the developing barnacle embryos (Terwilliger, 1998). Although physiological effects of these parasites on their hosts have been long recognized, some of the data regarding their impacts on hosts is contradictory. For example, Reinhard and von Brand (1944) detected lower levels of fat in the liver of





**Fig. 11.** Life cycle of the athelgine bopyrid isopod *Athelges takanoshimensis*. A) Sexually mature female and male pair of isopods attached to the abdomen of the definitive host *Calcinus minutus*. B) Ovigerous female isopod and male removed from host; female releases epicaridium larvae (C) that seek out a copepod intermediate host (D) in the water column, upon which they are ectoparasitic. The epicaridium larva metamorphoses into a microniscus larva that eventually transforms into a cryptoniscus larva. The cryptoniscus detaches and after a free-swimming period settles onto a suitable definitive host (A). E) If the first recently settled juvenile (bopyridium) infests a novel host, the isopod becomes female. F) Subsequent isopods become dwarf males that live on the female and fertilize the developing eggs in the marsupium. (Drawing of infested copepod modified from Sars (1899)). Scale bars: 1 mm for definitive host and sexually mature female and male pair; 0.5 mm for juvenile and male isopod; 0.05 mm for the epicaridium larva (infested copepod not to scale).

*Pagurus pubescens* infested with *Peltogaster paguri* using both morphological and chemical methods of detection. In contrast, Rudolff and Veillet (1954) found an increase in fat for both male and female *Diogenes pugilator* bearing *Septosaccus cuenoti*.

Certain behavioral changes in brachyuran and porcellanid hosts of rhizocephalans are more easily documented than those observed in infected shell-inhabiting hermit crabs. For example, parasitized female brachyurans may undergo “brood grooming behavior” on their externae located under the abdomen where their embryos are normally attached to the pleopods (Ritchie and Høeg, 1981; Høeg and Lützen, 1995; Takahashi et al., 1997; Innocenti et al., 1998). Such abnormal behavior has been recorded also in infected, feminized males that have developed broader abdomens. Thus, the surfaces of externae are kept free of epibionts (Takahashi et al., 1997). Crabs parasitized with sacculinids also aid in the release of nauplii from the externae by undergoing the typical abdominal flexing employed in the release of crab zoeae. The question is: do parasitized hermit crabs exhibit similar behaviors? Aside from removing infected hermit crabs from their shells for such observations, it may be possible to approach

this problem under more natural conditions by providing crabs with fabricated transparent, glass or plastic shells (Brightwell, 1951; Lytwyn and McDermott, 1976; Gravel et al., 2004).

### 3.9.2. Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea, Family Bopyridae

The Bopyridae are by far the largest family of epicarideans and one of the largest families within the Isopoda. It is comprised of approximately 600 described species that are all parasites of decapod crustaceans as adults and calanoid copepods as larvae (Boyko and Williams, 2009). The adult females of all species are highly modified for their parasitic existence, with distorted, non-symmetrical bodies, non-motile pereopods, reduced or lacking eyes, reduced or absent cephalic appendages, and a disproportionately large and well-developed marsupium devoted to the brooding of large numbers of eggs (Fig. 11).

The family is currently divided into 9 subfamilies. The Pseudioninae is the largest subfamily (ca. 215 spp.) and is considered the most primitive taxon within the Bopyridae, both by virtue of morphology, which is less derived from the isopod bauplan,

and by host selection, which is broadly based (caridean shrimp, nephropid lobsters, thalassinidean shrimp, anomuran and brachyuran crabs) (Shiino, 1952, 1965; Markham, 1986). Approximately 18% (39 of 215 species) of pseudionine species parasitize hermit crabs. Forty-three of the 44 species in the Athelginae parasitize hermit crabs (95.5%), with the other being a parasite of a lithodid. There are two sites of bopyrid infestation on hermit crab hosts: in the branchial chamber (Pseudioninae) or on the abdomen (Athelginae). The subfamily Bopyrophryxinae, which contained one species occurring simultaneously in the branchial chamber and on the abdomen of their hermit crab hosts, was shown to be a highly derived member of the Pseudioninae, closely related to the genus *Asymmetrione*, and not representing a distinct subfamily (Bourdon and Boyko, 2005). Although the endoparasitic bopyrids of the genus *Entophilus* are now known from two major host groups (galatheid crabs and thalassinid shrimp), none are known from hermit crab hosts.

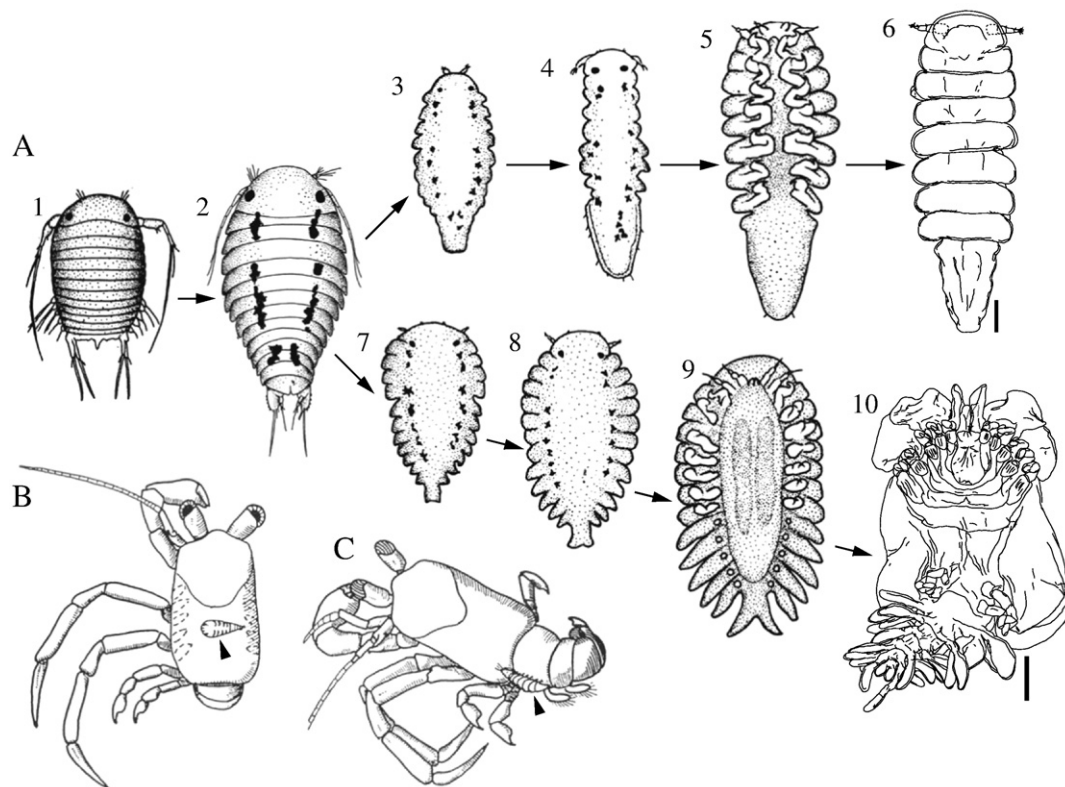
Bonnier (1900) compiled all of the data on the then known bopyrids in his monographic treatment of the Epicaridea, and there are several subsequent important regional taxonomic works (Bourdon, 1968; Markham, 1982, 1985a,b, 1988, 1990, 1992; Page, 1985; Kim and Kwon, 1988), many of which include data for species found on hermit crabs. Outside of taxonomic studies, there are some biological data on hermit crab bopyrids, although far less than that known about rhizocephalans on hermit crabs. Markham (2003) reviewed the known associations between bopyrids and hermit crab hosts.

Bopyrid fecundity is high in comparison to non-parasitic isopods of similar body size, and greatly increases with parasite size. For example, *Pseudione hyndmanni* females of 3 mm total length bear ca. 1000 eggs whereas those of 7 mm have in excess of 9000 eggs (Bourdon, 1968). Despite this, the usual host rates of infestation are rather low

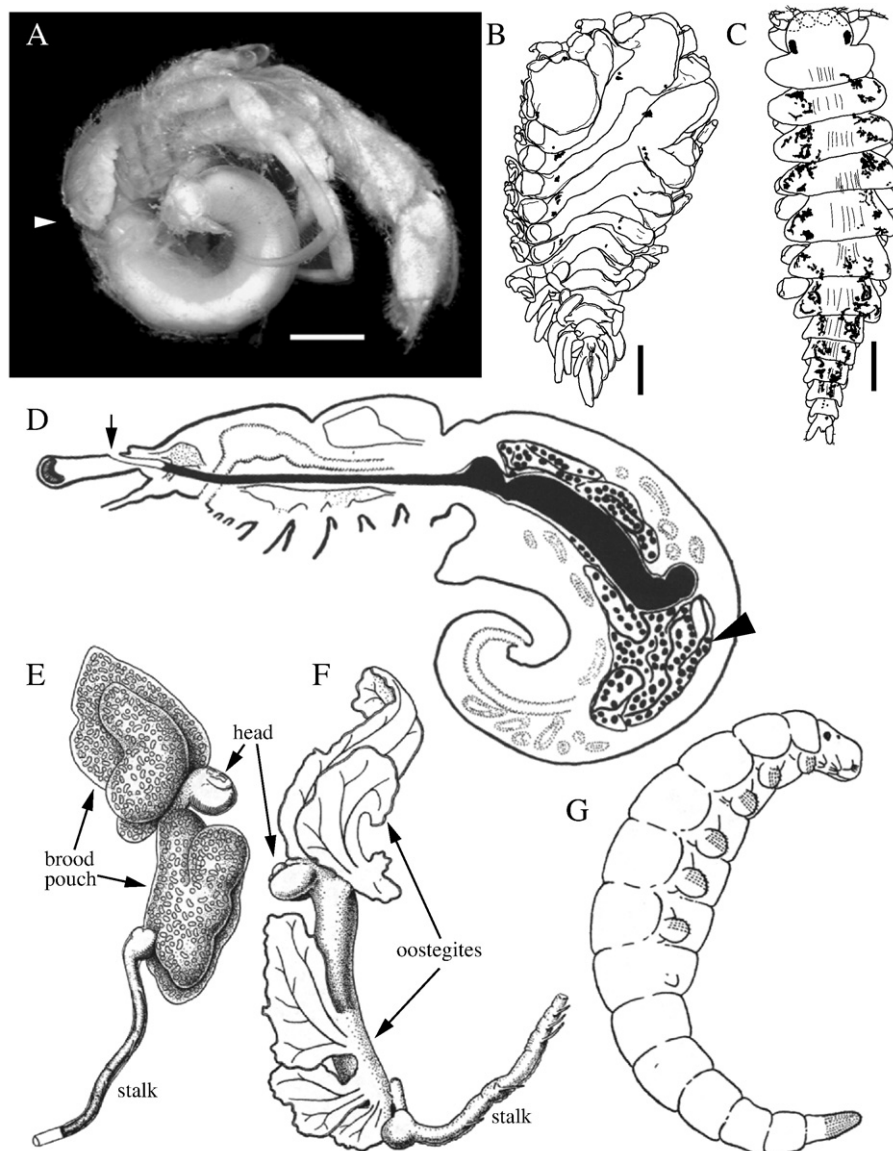
even when large numbers of hosts are examined (e.g., >9000 hermit crabs studied by McDermott, 1998), typically being anywhere from 0.1–3.8%, depending on species of host, parasite or locality (Bourdon, 1968; Samuelsen, 1970; McDermott, 1998). Records of higher infestation rates do, however, exist as with the 8.5% rate for *Pseudione diogeni* on *Diogenes pugilator* (Popov, 1927) or the 6.7–19.1% rate for *Asymmetrione foresti* on *Paguristes eremita* (Bourdon, 1968).

Although many species of hermit crab infesting bopyrids have only been recorded from one host species, some species are known to parasitize multiple hosts. *Athelges takanoshimensis* parasitizes at least 13 species of pagurid and diogenid hermit crabs from Japan, Korea, Hong Kong, and Taiwan (Boyko, 2004) (Fig. 11). Another athelgine bopyrid, *Anathelges hyptius* (Fig. 12A), parasitizing eight species of pagurid hermit crabs, has a range from Massachusetts, USA to Argentina (Boyko and Williams, 2003; Diaz and Roccatagliata, 2006), and perhaps extending all the way around the southern tip of South America to Chile (Diaz and Roccatagliata, 2006; Pardo et al., 2009). Some of these bopyrids have been found to occur on host individuals that also bear externae of rhizocephalans. Nagasawa et al. (1996) reported *Pagurus maculosus* with *Anathelges takanoshimensis* and 6 externae of *Peltogasterella gracilis*; similarly, Shiino (1958) reported *Pagurus japonicus* with *Athelges takanoshimensis* and *Peltogaster paguri*. In fact, co-occurrence of a bopyrid and a rhizocephalan has often been recorded, but never two female bopyrids and a rhizocephalan (e.g., Codreanu, 1941). The precise nature of the harm caused to hermit crab hosts by bopyrids, beyond suppression of reproduction, is unclear as, unlike with rhizocephalans, there is no evidence that fat content is decreased in the presence of a parasite (Reinhard and von Brand, 1944; Reinhard et al., 1947).

Modification of secondary sexual characters of hermit crabs by their bopyrid hosts appears to be far less evident than with rhizocephalans. Baffoni (1948) found no modifications in pleopods of *Pagurus prideaux*



**Fig. 12.** A) Development of athelgine bopyrid isopods of the genus *Anathelges*. *Anathelges hyptius*: 1) epicaridium larva, dorsal view; 2) cryptoniscus larva, dorsal view.; 3-6) developing male (3, 4 in dorsal view, 5 in ventral view); 6) mature male, dorsal view; 7-9) developing female, dorsal view. 10) mature female, dorsal view. B) Megalopa of *Pagurus bernhardus* with cryptoniscus larva of *Athelges paguri* on thorax (parasite shown by arrowhead). C) Juvenile *P. bernhardus* with bopyridium of *A. paguri* on abdomen (parasite shown by arrowhead). (Figures A1-5, 7-9 modified from Reinhard (1949); Figures A6, 10 from Boyko and Williams (2003); Figures B, C modified from Pike (1961a)). Scale bars A6 = 0.25 mm, A10 = 1 mm; rest not to scale.



**Fig. 13.** Pseudionine and entoniscid isopods parasitizing hermit crabs. A) The pseudionine *Asymmetrione sallyae* within the right branchial chamber of the host *Diogenes avarus*, arrow shows anterior end of isopod. B) Female of *A. sallyae*, dorsal view. C) Male of *A. sallyae*, dorsal view. D) The entoniscid *Paguritherium alatum* (body shown in black, arrowhead shows brood pouch with embryos) within the host *Pagurus longicarpus*. The parasite has a posterior stalk that typically extends to the eyestalk of the host where it communicates with the outside environment (shown by arrow). E) Ovigerous female of *P. alatum*, with embryos in brood pouch. F) Female of *P. alatum* with enclosing sheath and embryos within brood removed. G) Male of *P. alatum*, lateral view. (Figs. A–C modified from Williams and Schuerlein (2005), Figs. D–G modified from Reinhard (1945). Scale bars A = 2.0 mm, B = 0.5 mm, C = 0.2 mm; rest not to scale.

infested with *Athelges prideauxii*, nor did Thompson (1902) with *Pagurus longicarpus* bearing *Anathelges hyptius*. However, with regards to reproduction by hosts, a much clearer picture of the parasite's effect can be seen. Parasitism by *Athelges prideauxii* on *Pagurus prideaux* suppresses activity of the female crab's gonads, with some reduction also seen in male crabs (Baffoni, 1948). McDermott (2002) found only one ovigerous specimen among 100 females of *Clibanarius tricolor* parasitized by *Stegias clibanarii* in Bermuda, and the rest were devoid of gonads during the reproductive season. Furthermore, mean shield length of infested crabs was significantly less than in uninfested individuals.

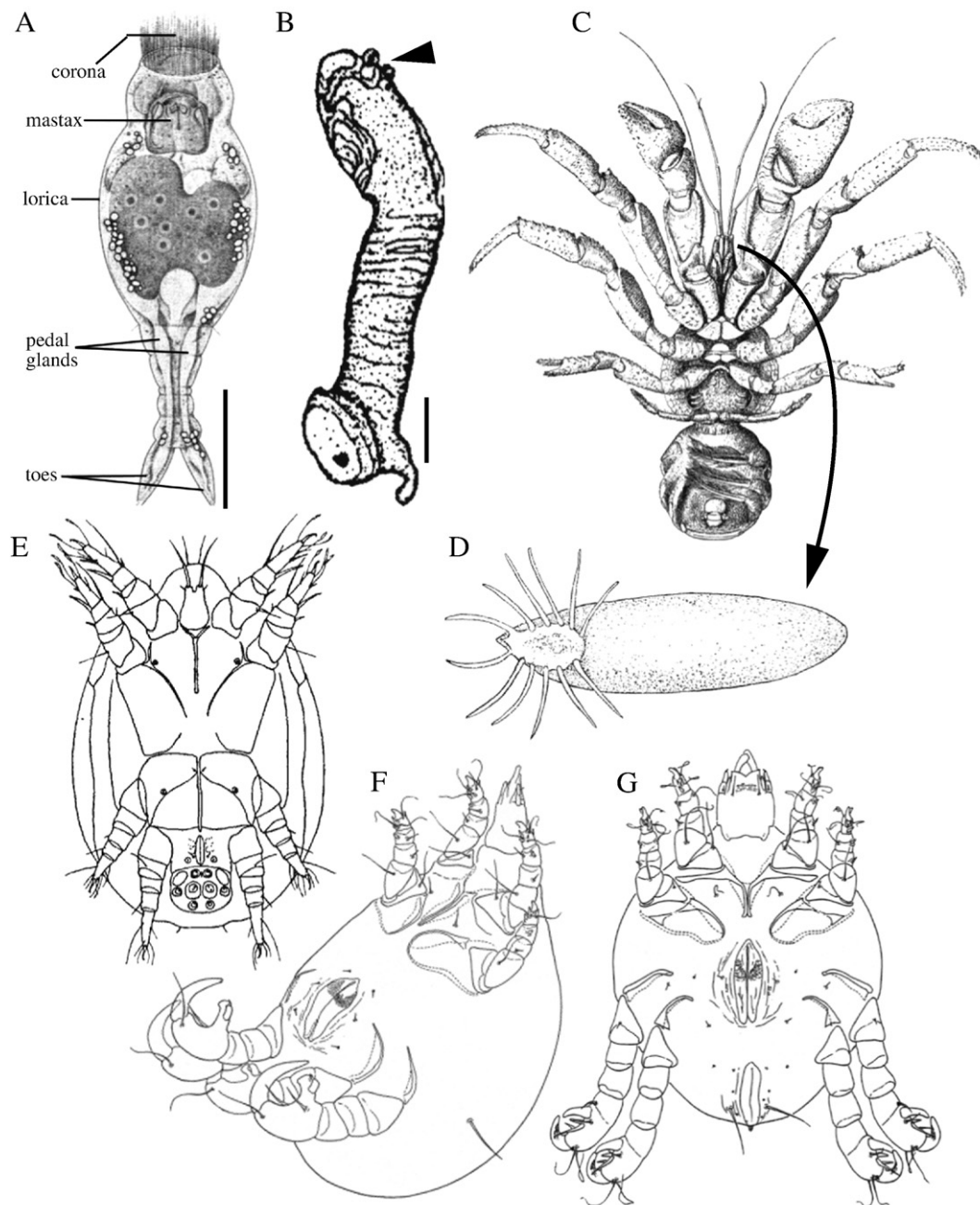
The development of some species of bopyrids found on hermit crab hosts has also been studied (Fig. 12). Pike (1961a), in one of the very few studies involving the rearing of hermit crab bopyrids, showed that *Athelges paguri* larvae survived only on *Pseudocalanus* copepods when used as intermediate hosts. Upon reaching their final host, the cryptoniscid larvae attached to thorax of megalopa of *Pagurus bernhardus*, molted once and remained in place for 11 days (Fig. 12B).

The parasite then moved to the abdomen when the hermit molted to the first crab stage (Fig. 12C). Indeed, even for those bopyrids found as mature adults on the abdomens of hermit crabs, thoracic attachment on megalopae or young crabs may well be the norm.

### 3.9.3. Phylum Arthropoda, Order Isopoda, Superfamily Bopyroidea, Family Entoniscidae

The Entoniscidae are comprised of 39 described species in 16 genera. Entoniscid isopods are parasites of decapod crustaceans and are fully endoparasitic (Kuris et al., 1980; McDermott, unpublished data). In hermit crabs, they communicate with the outside environment through a long posterior stalk which emerges in the vicinity of the host's eyestalks (Fig. 13D); this is in marked contrast to those entoniscids found in brachyuran crabs where a much shorter stalk emerges in the branchial region of the host. The location of the parasite differs: in hermit crabs it occupies the majority of the space within the abdomen, whereas in brachyuran crabs and shrimp it is





**Fig. 14.** Suspected parasites from hermit crabs. A) The rotifer *Proales paguri* from the gills of *Pagurus bernhardus*. B) The lepadomorph barnacle *Pagurolepas elongata*, arrowhead shows juveniles. C) The coconut crab *Birgus latro*, showing where eggs of the drosophilid fly *Lissocephala powelli* are oviposited at the base of the antennae; larvae then migrate to the gills. D) Egg of *L. powelli*. E) The mite *Caloglyphus birgophilus* (deutonymph, ventral view) from *Birgus latro*. F) The mite *Ewingia coenobitae* (female, lateral view) from the gills of the terrestrial hermit crab *Coenobita brevipennis*. G) The mite *Askinasia aethiopicus* (female, ventral view) from the gills of the terrestrial hermit crab *C. rugosus*. (Fig. A modified from Bush et al. (2001); Fig. B modified from Zevina and Kolbasov (1997); Fig. C modified from Smith and Weldon (1909); Fig. D modified from Carson and Wheeler (1973); Fig. E from Vitzthum (1937); Figs. F–G modified from Yunker (1970)). Scale bar A = 50  $\mu$ m; B = 1.7 mm; rest not to scale.

found in the thoracic space. Female entoniscids are so highly modified in their reduced worm-like morphology that they are difficult to recognize as isopods (Fig. 13E, F). However, males present typical isopod morphology (Fig. 13G) and larvae are of the epicaridean type.

Only two species of entoniscids have been reported from hermit crab hosts: *Paguritherium alatum* from the east coast of the United States and *Diogenion vermifactus* from the Red Sea. Little is known of the biology for *P. alatum* and nothing for *D. vermifactus*. Infestation rates for *P. alatum* are very low, even by epicaridean standards, at less than 1% (Reinhard, 1945; McDermott, 1998). Parasitism by *P. alatum* on *Pagurus longicarpus* suppresses activity of the female crab's gonads,

with some reduction also seen in male crabs (Reinhard and Buckeridge, 1950). Likewise, the secondary sexual characters of the female crabs are modified in the developmental process, whereas the male crabs appear unaffected in this regard (Reinhard and Buckeridge, 1950).

#### 3.9.4. Phylum Arthropoda, Order Acari

Although other marine decapods are known to be infested by parasitic mites of the Halacaridae (Dabert, 2005; Pepato et al., 2005; Bartsch, 2007), no hermit crabs have been found with mites of this family. However, 10 land hermit crabs of the family Coenobitidae (including the coconut crab *Birgus latro*) are infested by fifteen species



of mites from other families and the symbiotic relationship between these mites and hosts remains to be studied. The finding of *Cyclothorax carcinicola* associated with the subtidal hermit crab *Calcinus tibicen* from Nicobar is likely a misidentification; the true host may be a species of *Coenobita* (Johnston, 1960). Johnston (1960) further indicated that specimens identified as *Cyclothorax carcinicola* from hermit crabs collected in Sumatra by Vitzthum (1928) were misidentified. Unfortunately the original description of *C. carcinicola* does not allow for positive identification of the species but it could be a synonym of *Aspidilaelaps mirabilis*. The nature of the relationship between these mites and hermit crab hosts remains essentially unknown (O'Connor, 1982). However, the mites are obligate associates of the hermit crabs and are sometimes found in large numbers (see Williams and McDermott, 2004, for a review of their biology). Some of these mites (e.g., *Ewingia* and *Askinasia* spp.; see Fig. 14F, G) clutch onto the gills of infested hosts with their posterior tarsi whereas others (e.g., *Caloglyphus* and *Cyclothorax* spp.) are mobile over the surface of hosts (Fig. 14E).

Mites are a problem in the pet trade of hermit crabs such as *Coenobita clypeatus* (Fox, 2000; Wilkins, 2007; see Calado et al., 2003 for review of decapods, including hermit crabs, in the aquarium trade industry). Although *Coenobita* spp. are naturally infested with the mites (Hunter and Poe, 1971), it appears that many mite infestations of *Coenobita* spp. reported by pet owners are opportunistic associations resulting from mites that are attached to materials (substrates, food) and brought into aquaria housing hermit crabs. Some authors in the pet trade of hermit crabs have claimed that these mites can cause the death of hermit crabs (Pavia, 2006) but no research has been undertaken to show the detrimental impact on hosts.

### 3.10. Potential parasites of hermit crabs

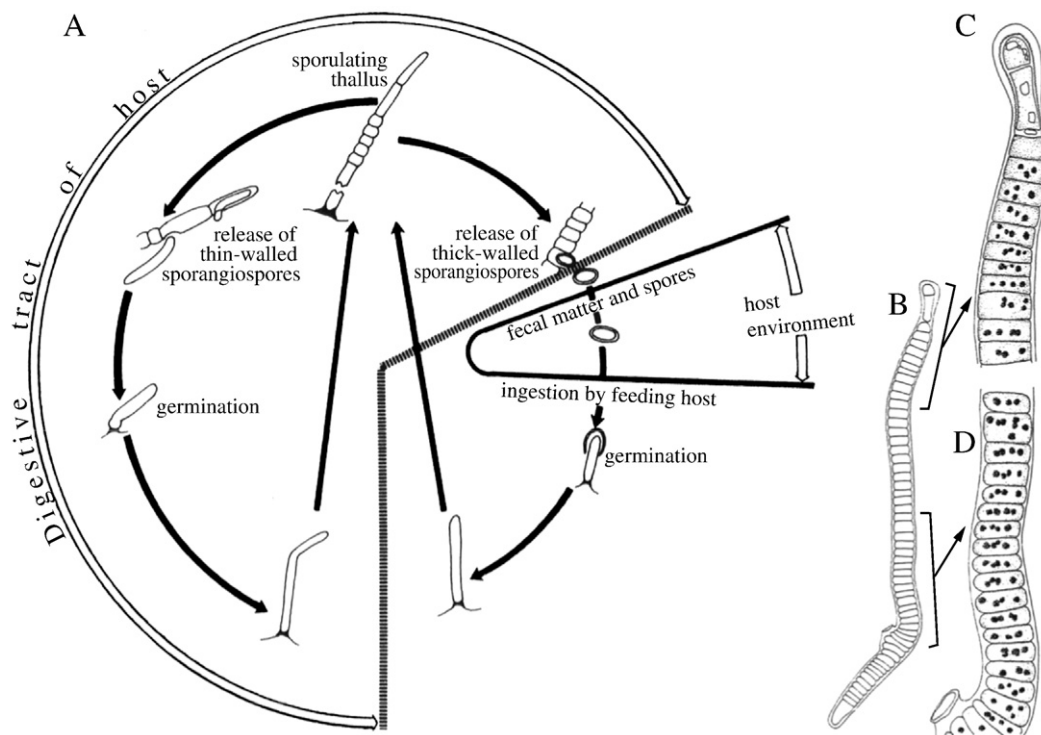
In the course of this review some symbionts were found that exhibited intimate obligate relationships with hermit crabs but no research has shown detectable harm to their hosts. These species are

considered as potential parasites, and we recommend that they receive additional study to clarify host relationships. In total, 17 taxa among 5 phyla are represented (Table 2). This includes 4 mesomycetozoans (obligate “fungal-like” inhabitants of hermit crab digestive tracts), 4 apistome ciliates, a flatworm, a rotifer, and arthropods (6 thoracican barnacles, a copepod and a fly).

#### 3.10.1. Class Mesomycetozoa, Order Eccrinales

Mesomycetozoans are primarily internal obligate symbionts in the digestive tracts of arthropods such as millipedes, insects and crustaceans (Moss, 1979; Lichtwardt, 1986; Mattson, 1988; Misra, 1998; Lichtwardt et al., 2001). Molecular research has showed that the order Eccrinales, as well as the order Amoebidiales (which contains ectosymbionts of arthropods), belongs to the protist class Mesomycetozoa (Cafaro, 2005); previously they were considered members of the fungal class Trichomycetes. Members of the Mesomycetozoa exhibit branched or unbranched thalli or filaments, attach by holdfasts to the chitinous lining of the gut and are shed with the host's molted exoskeleton; there appears to be no evidence that holdfasts penetrate to the living host tissue. Nutrition is dependent on the host's food. Reproduction takes place asexually with the production of a variety of sporangiospores, whereas sexual reproduction and the production of zygospores are much less common (Lichtwardt, 1986; Misra, 1998; Lichtwardt et al., 2001).

The relationships of these gut-inhabiting symbionts with their hosts range from commensalism to mutualism, but in most cases the nature of host relationships is not known (Moss, 1979; Misra, 1998). All evidence suggests that these species are non-parasitic; however, speculation abounds on the nutritional elements absorbed by these fungi. Kimura et al. (2002) studied the enzymatic activity involved in the digestion of detritus from the gut of the ghost shrimp *Nihonotrypaea harmandi* (Bouvier, 1901) with and without *Enteromyces callianassae* Lichtwardt, 1961. Aside from the enzymes secreted by the shrimp, the symbiont probably secretes peptidases, all of which could explain the greater rate of growth by infected



**Fig. 15.** Mesomycetozoan associates of hermit crabs. A) Generalized life cycle of the eccrinales. B) Thallus of *Arundinula washingtoniensis* from the foregut of *Paguristes turgidus*. C) Distal end of thallus, with spores. D) Lateral holdfast of thallus, with spores. (Fig. A modified from Moss (1979); Figs. B–D modified from Hibbits (1978)). Scale bar C, D = 50  $\mu$ m.

shrimp. They concluded that considerably more study was needed to understand the nature of this host-symbiont relationship. Thalli attached to the chitinous lining of the host's gut are lost at host ecdysis. This requires coordination between host and symbiont life cycles, e.g., rapid holdfast development of ingested spores, and coordination of the symbiont's growth and reproduction with metabolism and growth cycles of the host.

The order Eccrinales is the only taxon that includes marine crustaceans as hosts. Members of this order have unbranched, nonseptate and multinucleate thalli. Asexual reproduction occurs within the sporangia located at the distal ends of the thalli, and spores are released via rupture of the sporangial wall. Multinucleate, thin-walled spores germinate in the gut, thus adding to the infection of the same host, whereas the uninucleate, thick-walled spores may be expelled with the host's feces or with the ecdysed cuticle to infect other hosts upon ingestion.

Members of the family Eccrinaceae belonging to two genera, *Arundinula* and *Taeniella*, are hermit crab symbionts (Fig. 15). *Arundinula washingtoniensis* is the only member of the genus known to live in hermit crabs (*Paguristes turgidus*) from the western hemisphere (Hibbitts, 1978). Different types of thalli are found in the foregut and the hindgut. *Arundinula hapalogaster* Hibbitts, 1978 infects a related anomuran, the lithodid crab *Hapalogaster mertensii* Brandt, 1850. *Taeniella carcini* appears to be much less host specific than the two species of *Arundinula* in that it has been recorded from five species of hermit crabs as well as two other species of anomurans (Galatheididae and Lithodidae), several species of thalassinidean shrimp (Callinassidae and Upogebiidae) and nine brachyurans (Cancridae, Grapsidae, Portunidae, Xanthidae) (Hibbitts, 1978; Lichtwardt, 1986; Lichtwardt et al., 2001). *Taeniella carcini* was also found to co-occur with *Arundinula washingtoniensis* in *Paguristes turgidus* (Hibbitts, 1978). Besides the four hermit crab hosts of identified eccrinids, Hibbitts (1978) noted that *Pagurus capillatus* is a host for an unidentified species and examined five additional species of Paguridae all of which were not infected. *Clibanarius tricolor* hosts an unidentified, non-branching species of eccrinid from Bermuda (McDermott, 2002). A total of 11 species of hermit crabs (3 genera) are known hosts of eccrinids (Table 2); *Arundinula incurvata* (reported from *Pagurus prideaux*) is considered a *nomen nudum* (Lichtwardt, 1986; Lichtwardt et al., 2001).

Prevalence of the species from *Clibanarius tricolor* was 1.5% at one collecting site in Bermuda (25 of  $\approx 1700$  crabs examined) and 7.6% at another (8 of 105 crabs) (McDermott, 2002). Literature dealing with identified Eccrinales species from other hermit crabs does not record their prevalence. On the other hand, the prevalence of eccrinids in other marine crustaceans is often 50–100% (Van Dover and Lichtwardt, 1986; Mattson, 1988).

### 3.10.2. Phylum Ciliophora

**3.10.2.1. Class Oligohymenophorea.** Members of the Subclass Apostomatia, an unusual group of ciliates symbiotic in hermit crabs, were discussed in the review of symbionts associated with hermit crab shells by Williams and McDermott (2004). As phoronts, these apostomes encyst on the gills. When the crab molts trophonts are released from the cysts, feed on the exuvial fluids, and form free-living cysts or tomonts from which, after a series of divisions, they release small dispersal, infective stages called tomites (Bradbury, 1966; Lee et al., 2000). Three species of exuviotrophic apostomes infest ten species of hermit crabs (Table 2).

The three apostomes are apparently not specific for hermit crab hosts. *Gymnodinioides inkystans* also infests gammarid amphipods (Fenchel, 1965), five species of brachyurans (*Armases cinereum* (Bosc, 1802), *Callinectes sapidus*, *Panopeus herbstii* H. Milne Edwards, 1834, *Sesarma reticulatum* (Say, 1817), *Uca pugilator* (Bosc, 1802) (Grimes, 1976)) and two species of caridean shrimp (*Hippolyte zostericola* (Smith,

1873), *Tozeuma carolinense* Kingsley, 1878 (Landers, 2004)). *Halophysa chattoni* infests the fresh water caridean shrimp *Palaemonetes paludosus* (Gibbes 1850), the estuarine species *P. intermedius* Holthuis, 1949, *P. pugio* Holthuis, 1949, and *Alpheus* sp., as well as the brachyurans *Glebocarcinus oregonensis* (Dana, 1852), *Carcinus maenas* and *Lophopaneopeus bellus* (Stimpson, 1860) (Bradbury, 1966; Bradbury and Clamp, 1973). In addition to hermit crabs, *Polyspira delagei* is found in the galatheid crab *Galathea squamifera* Leach, 1814 and the brachyuran *Macropodia rostrata* (Minkiewicz, 1912; Sprague and Couch, 1971).

The development of the apostome ciliates infesting hermit crabs is intimately involved with the hosts' growth (molting cycles), and is indicative of a lengthy evolution resulting mainly in non-parasitic relationships. Johnson and Bradbury (1976) have shown, however, that the apostome *Synophrya hypertrophica* Chatton and Lwoff, 1926 is parasitic in a number of brachyuran crab hosts. Tomites of this species burrow into gill lamellae where they feed on host tissues, may induce encapsulation by the host, and eventually encyst as phoronts. Trophonts are eventually released from the cysts as the host molts and feed on exuvial fluid (Johnson and Bradbury, 1976; Shields and Overstreet, 2007). *Petrochirus diogenes* (Linnaeus, 1758), the only hermit crab examined by Johnson and Bradbury, was not infested with *S. hypertrophica*. Perhaps further experimentation with supposed commensal relationships between hermit crabs and apostomes may yield indications of some pathogenicity.

### 3.10.3. Phylum Platyhelminthes

**3.10.3.1. Class Turbellaria.** The acoel flatworm *Ectocotyla hirudo* is a facultative symbiont of *Pagurus pubescens* and *Parapagurus pilosimanus*, but has also been reported from the bodies of two brachyurans (Fleming and Burt, 1978). A very similar species, *Ectocotyla multitesticulata* Fleming and Burt, 1978, is also associated with brachyurans, but as yet has not been found in hermit crabs. Williams and McDermott (2004) suggested that these symbionts may consume the host's embryos.

### 3.10.4. Phylum Rotifera

*Proales paguri*, the only known rotiferan symbiont of hermit crabs, is found on the gills of *Pagurus bernhardus* collected in the waters surrounding Denmark (Thane-Fenchel, 1966) (Fig. 14A). *Pagurus pubescens* from the Øresund, and *P. prideaux* and *Dardanus* (not *Pagurus*) *arrosor* and *Diogenes pugilator* from the Mediterranean Sea had no rotifers. The larger specimens of *P. bernhardus* were nearly all infested, and the intensity of infestation ranged from 1 to 40 per crab. This rotifer is an obligate symbiont that ingests epithelial cells from the gills, but further studies are needed to determine its impacts on hosts. Symbiotic rotifers (including the few parasites known) were reviewed by May (1998).

### 3.10.5. Phylum Nemertea

Gibson (1995) recognized approximately 1150 species within the phylum Nemertea. Most of these worms are marine, free-living predators (McDermott and Roe, 1985), and approximately 40 species appear to be in various symbiotic relationships with cnidarians, bivalve molluscs, ascidians, echinoderms and arthropods (Jensen and Sadeghian, 2005; Santos et al., 2006). All of these species belong to the order Hoplonemertea, suborder Monostyliifera, members of which have a protractile proboscis bearing a single stylet used for penetration. Decapod crustaceans, mainly species of Brachyura, but some Anomura, Thalassinidea and Palinura, are hosts for the well-known symbiotic relationships involving worms within the family Carcinonemertidae (genera *Carcinonemertes*, *Ovicides*); most are egg predators. Hermit crabs are not known hosts for these worms. The red king crab, *Paralithoides camtschaticus*, however, is host for *Carcinonemertes regicides* Shields, Wickham and Kuris, 1989.

What is it about hermit crabs that appear to resist infestation by nemertean egg predators? Is there some sort of natural immunity?

Are hermit crab's branchial chambers less suitable for worms than those in brachyurans or the more carcinized lithodids due to the gill cleaning activity of the fifth pereopods? We suggest that an effort be made to examine hermit crabs, especially ovigerous ones, for evidence of symbiotic Nemertea.

### 3.10.6. Phylum Arthropoda, Subclass Copepoda

Wilson (1913) described a new species of harpacticoid copepod, *Cancrincola jamaicensis*, from the white land crab, *Cardisoma guanhumi* Latreille, 1828, from Jamaica. This symbiont clings to the crab's gill filaments with its second antennae, infesting nearly 100% of the crabs examined with a maximum intensity of 30 per crab. Because this terrestrial crab spends only about 7–10 days per year in the ocean, the copepods must have developing ova in their egg sacs so that, when inundated, nauplii will hatch and proceed to reach the infective copepodite larvae and attach to a crab host during this short annual breeding season. Wilson found that female copepods from crabs examined before they enter the sea had their oviducts filled with ripe ova ready to be extruded into their egg sacs. As with free-living harpacticoids, this species is an able swimmer.

Morphologically *Cancrincola jamaicensis* is much like other harpacticoid copepods, but its movements on the host's gills during the crab's terrestrial phase must be limited. Wilson therefore suggested that, since its source of nutrition must be the host's blood or secretions, the relationship may be parasitic. If this were true, these copepods would be expected to cause only slight harm to these large crabs. Pearse (1932) identified what he believed to be the same copepod species from the gills of the hermit crab *Paguristes puncticeps* collected in the Dry Tortugas, Florida. His identification was from a single specimen and he provided no other information except that six crabs were examined. Later, Humes (1958) re-examined Pearse's material and found that the copepods did not belong to the genus *Cancrincola* but he did not identify them further. Although it appears that *C. jamaicensis* is restricted to the branchial chamber of semiterrestrial land crabs of the genera *Cardisoma* and *Sesarma* (see review in Huys et al., 2009), we suggest that with additional sampling it is likely that similar copepods will be found in association with hermit crabs. *Paguristes puncticeps* should be sampled to determine if the copepods found by Pearse (1932) represented an accidental association, erroneous record, or a true hermit crab symbiont.

### 3.10.7. Phylum Arthropoda, Infraclass Cirripedia, Superorder Thoracica

Thoracican barnacles of the genus *Poecilasma* (Poecilasmataidae) attach to the exoskeleton of a variety of decapod crustaceans (Williams and Moyse, 1988). Pilsbry (1907) considered the populations that attached to *Pagurus politus* to represent a distinct subspecies (*Poecilasma kaempferi novaeangliae*). *Poecilasma* species attach to the base of limbs, often in high numbers. However, negative impacts on hosts have not been shown and they are generally considered opportunistic commensals of these hosts.

The stalked barnacle genus *Pagurolepas* (closely related to the family Poecilasmataidae) contains five species that attach to the inside of gastropod shells inhabited by hermit crabs (Zevina and Kolbasov, 1997) (Fig. 14B). Although Anderson (1994) indicated *Pagurolepas* possess vestigial cirri and may be ectoparasitic on host hermit crabs, the interactions between these species and hosts remains unknown. Zevina and Kolbasov (1997) speculated that species of *Pagurolepas* might feed on "scraps" from the host hermit crabs but researchers should consider the possibility that the barnacles are egg predators of host hermit crabs (Williams and McDermott, 2004).

Members of the symbiotic, pedunculate, gooseneck barnacle genus *Octolasmis* (Poecilasmataidae) have been found in association with corals, echinoderms, molluscs, marine arthropods, fish and sea snakes, but the only common hosts with the largest populations are the decapod crustaceans (Jeffries and Voris, 1996, 2004). The gill chambers and the mouth parts are the sites for attachment of these barnacles on their

decapod hosts. In a recent survey of 122 species of crustaceans from the northern Gulf of Mexico, Jeffries and Voris (2004) found species of *Octolasmis* mainly among 9 families of brachyurans, whereas 3 species of hermit crabs were negative (*Clibanarius vittatus* (Bosc, 1802),  $n = 85$ ; *Dardanus insignis* (de Saussure, 1858),  $n = 9$ ; *Paguristes erythrops* Holthuis, 1959,  $n = 4$ ). The same was true for other anomurans examined, e.g., 2 species of Albuneidae, 1 species of Hippidae, 5 species of Galatheidae and 2 species of Porcellanidae. In an earlier survey of crustaceans from the waters of Singapore, Jeffries et al. (1982) found 10 species of *Octolasmis* infesting members of 6 families of brachyurans and 2 families of lobsters, but not in 3 species of Porcellanidae. Jeffries (personal communication, 2006), who has surveyed the world literature on *Octolasmis*, has yet to find references relating to hermit crab infestations. The nature of this resistance needs investigation. Is the gill or gill chamber morphology or gill cleaning behavior of hermit crabs associated in some way with this resistance? Are there some innate aspects in the biology of anomurans that are responsible for their resistance to infestations by octolasmids? Some simple infestation experiments are suggested employing the methods for laboratory culture of *Octolasmis* nauplii developed by Jeffries et al. (1995). It is unclear if species of *Octolasmis* should be considered parasitic. Studies of *Octolasmis* infestations in the blue crab *Callinectes sapidus*, however, have shown behavioral changes, increased ventilation, heart rates and mortality (Gannon and Wheatly, 1992, 1995; Shields and Overstreet, 2007).

### 3.10.8. Phylum Arthropoda, Order Diptera

One dipteran fly *Lissocephala powelli* (Drosophilidae) is known to complete its larval stages on a pagurid, the host being the robber or coconut crab *Birgus latro* (Carson and Wheeler, 1973; Carson, 1974; Stensmyr and Hansson, 2007; Stensmyr et al., 2008). Unlike the other terrestrial hermit crabs in the family Coenobitidae, *B. latro* only occupies shells when young whereas adults are found free-living on tropical islands (Sato and Yoseda, 2008; Drew et al., 2010). On Christmas Island in the Indian Ocean *L. powelli* oviposits on the base of the second antennae of the crab (Fig. 14C, D). The hatched larvae move to the gills of the crab where they develop before dropping to the ground and pupating in the soil. Other hosts of *L. powelli* are terrestrial brachyurans of the families Gecarcinidae and Grapsidae: *Discoplax hirtipes* (Dana, 1852), *Cardisoma carniflex* (Herbst, 1796), *Gecarcinoidea lalandii* H. Milne Edwards, 1837, *G. natalis* (Pocock, 1888) and *Geograpsus crinipes* (Dana, 1851) (Hicks et al., 1990). Fly larvae in these brachyurans develop mainly under the third maxillipeds in the nephric grooves (site of nephric pores) and less often among the gills, whereas in the robber crab, which lacks external nephric grooves, developing larvae are found only in the gill chambers. Irrespective of the anomuran or brachyuran hosts, third stage larvae pupate off the hosts.

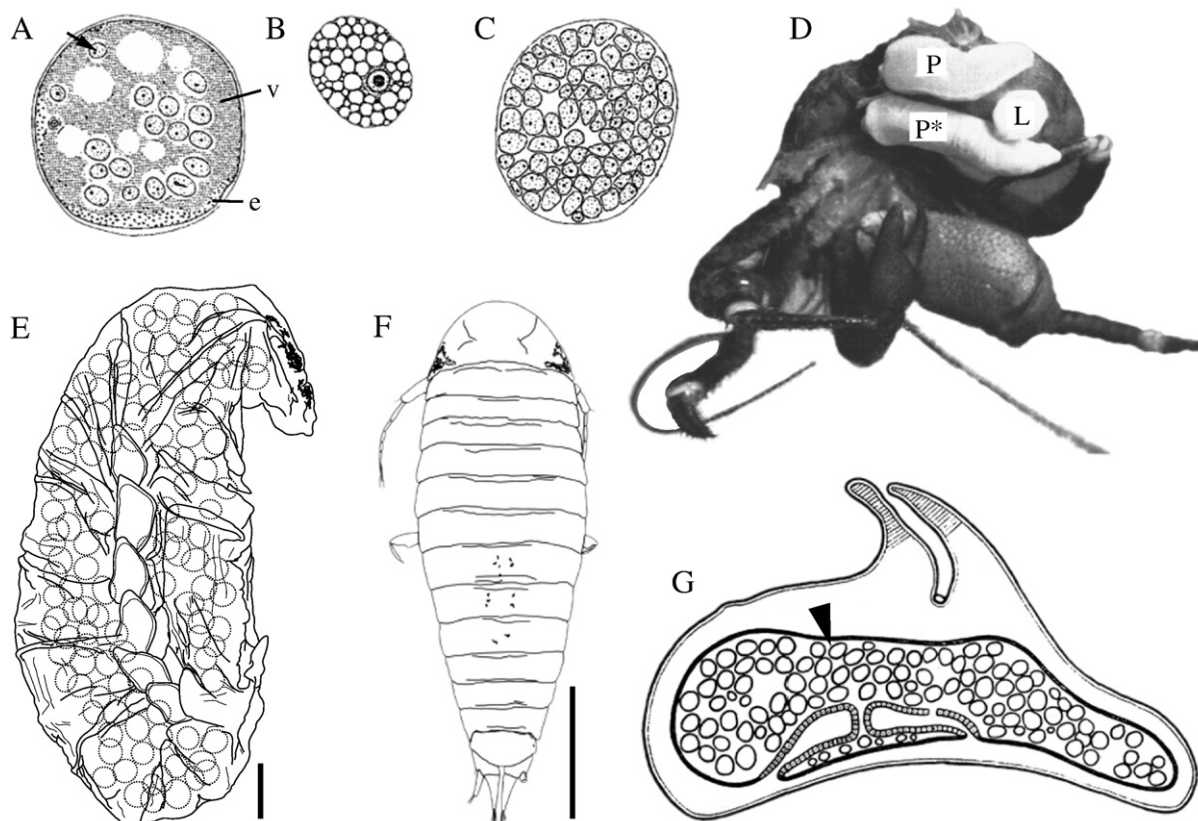
The life history of *Lissocephala powelli* differs from that of *Drosophila carcinophila* Wheeler, 1960, a symbiont of the brachyuran mountain land crab, *Gecarcinus ruricola* (Linnaeus, 1758) an inhabitant of the Bahamas and the Greater and Lesser Antilles. In this relationship, mature larvae that develop under the maxillipeds attach to and pupate on the undersides of these appendages (Carson, 1967, 1974; Stensmyr and Hansson, 2007). Thus, infested crabs are detected easily in living or museum specimens by noting the presence of puparia or eclosed (exuviated) puparia attached to the maxillipeds.

There is no indication in any of the drosophilid fly-crab relationships that harm is done to the host resulting from the adults or larvae feeding on body exudates. Mutualism is unlikely as some crab populations are without flies (Carson, 1967). Thus, these curious drosophilids are considered commensal symbionts but researchers should further examine their potential negative impact on hosts.

### 3.11. Hyperparasites

Of the ten species of described hyperparasites eight are hyperparasitic isopods. This includes Cabiropidae that infect parasitic isopods





**Fig. 16.** Hyperparasites associated with hermit crabs. (A–C) *Vahlkampfia paedophthora*, an endoparasite of the eggs of the rhizocephalan primary parasite *Peltogaster curvatus*. A) Cross section of egg of *P. curvatus* early after infection by *Vahlkampfia paedophthora* (shown by arrow), v = vitelline, e = “tissus de l’embryon”. B) *V. paedophthora*. C) Cross section of egg of *P. curvatus* with advanced infection by *V. paedophthora*, host egg filled with parasite cells. D) *Liriopsis pygmaea*, a hyperparasitic isopod infesting the rhizocephalan primary parasite *Peltogaster paguri* on the host hermit crab *Pagurus hirsutiusculus*; the host has two externa of *P. paguri*, one externa (P) that is unparasitized and one externa (P\*) with *L. pygmaea* (L). E) Female *Cabirops* sp., a hyperparasitic isopod that infests the bopyrid primary parasite *Pseudionella deflexa*. F) Male *Hemioniscus paguophilus*, a hyperparasitic isopod that infests the burrowing barnacle *Tomlinsonia mclaughlinae*. G) *Duplorbis smithi*, a hyperparasitic barnacle that infests the bopyrid primary parasite *Parathelges weberi*; section of mature externa with developing eggs in brood chamber (shown by arrowhead). (Figs. A–C modified from Caullery (1906); Fig. D modified from Warrenchuk and Shirley (2000). Figs. E, F from Boyko and Williams (2004); Fig. G modified from Nierstrasz and Brender-à-Brandis (1923)). Scale bars F, G = 0.25 mm; rest not to scale.

of the subfamily Pseudioninae and Cryptoniscidae that are found in rhizocephalan or acrothoracican barnacles associated with hermit crabs (Table 3). One species of akentrogonid rhizocephalan is found in a parasitic isopod of the subfamily Athelginae. Finally, one described and one undescribed species of amoeboid protozoans of uncertain phylum are been found in parasitic barnacles of the genus *Peltogaster*.

### 3.11.1. Protozoa (incertae sedis)

The hyperparasitic amoeboid protozoan *Vahlkampfia paedophthora* is found as an endoparasite within the eggs of *Peltogaster curvatus*, a rhizocephalan barnacle parasitizing *Pagurus meticulosus* from Naples (Caullery, 1906) (Fig. 16A–C). A similar hyperparasitic relationship exists in *Peltogaster paguri* associated with *Pagurus pubescens* from Maine (Reinhard and von Brand, 1942); however, the identity of the amoeboid protozoan found within the eggs of the parasitic barnacle remains unknown.

### 3.11.2. Phylum Arthropoda, Order Isopoda, Superfamily Cryptoniscoidea, Family Cabiropidae

The Cabiropidae comprise 31 described taxa that are parasites occurring within the brood chambers of isopod crustaceans. Females of all species are highly degenerate as adults, being reduced to saclike bodies with only faint segmentation bearing witness to their isopod affinities. The males are immediately recognizable as isopods, albeit they exhibit neoteny, being in all external appearances identical with cryptoniscid larval stages. In fact, the cryptoniscus larvae, functional males, and immature females are all indistinguishable with light microscopy.

As with all Cryptoniscoidea, the life cycle involves 2 hosts and 3 larval stages in much the same fashion as with bopyrid isopods, except the definitive hosts are mostly not decapods. The current taxonomic framework is based entirely on the cryptoniscus stage due to the reduced morphology of adult females and the fact that functional males are indistinguishable from the larvae. The family is currently divided into 13 genera, the species of which are all apparently specific to one sub-group of isopods (e.g., *Cabirops* on bopyrid isopods), although the taxonomic scheme is, at least in part, based on final host choice and so the phylogeny of the group is in need of much more study. Very little has been published on species in this family (see Nielsen and Strömberg, 1973; Williams and Boyko, 2004); however, the number of known, but undescribed species of Cryptoniscoidea far exceeds those described and may number in the hundreds (Boyko and Williams, pers. obs., Bourdon, pers. commun.). Only three species of *Cabirops* have been described from pseudionine bopyrids infesting hermit crabs (Fig. 16E), whereas a further two putative species have been recorded, but not named, from another hermit crab pseudionine and an athelgine (Table 3). Little is known about their prevalence or biology.

### 3.11.3. Phylum Arthropoda, Order Isopoda, Superfamily Cryptoniscoidea, Family Cryptoniscidae

About half of the 25 or so species in the Cryptoniscidae are hyperparasitic on various species of rhizocephalans found on decapod crustaceans with the remainder being directly attached to their decapod hosts. There is disagreement on whether parasitism of the decapod



occurs after the death of the rhizocephalan host within the lifespan of an individual hyperparasite or if, on an evolutionary scale, some species have secondarily adapted to direct parasitism of decapods and no longer require rhizocephalan hosts (Smith, 1906). Examples have been noted of cryptoniscids effectively replacing the externa of the rhizocephalan, leaving little more than the stalk and roots (Lützen et al., 2009), and this may have misled some observers into thinking that the isopod was directly parasitizing the host. However, direct parasitism of some cryptoniscids on decapods does occur without any internal or external evidence of a rhizocephalan. The life cycle of these species is similar to that of the other “epicarideans” and involves a copepod intermediate host (Caullery, 1908). Only four species have been reported from hermit crab rhizocephalans and none are known to directly attach to the crabs. Two of these species (*Cryptoniscus planaroides* and *Liriopsis monophthalmus*) have never been convincingly recorded subsequent to their original descriptions and nothing is known of their biology. *Liriopsis pygmaea* (Fig. 16D) has a circumboreal distribution on one species each of *Peltogaster* and *Peltogasterella*, with a further occurrence in European waters only on two species of *Septosaccus*. This can be an abundant hyperparasite, reaching prevalences of up to 36% on *Peltogaster paguri* in Alaska (Warrenchuk and Shirley, 2000) and, in some European populations of *P. paguri*, may occur on most of the specimens in an area (Høeg and Lützen, 1985). The effects of *Liriopsis* and *Cryptoniscus* on the rhizocephalans is likely to weaken the parasite and perhaps allow for establishment of additional rhizocephalans on the same host, due to compromise of the naturally competitive abilities of the healthy parasite (Warrenchuk and Shirley, 2000). *Liriopsis pygmaea* also has been recorded from *Briarosaccus callosus* infesting the false king crabs *Paralomis granulosa* (Hombron and Jacquinot, 1846) collected in the Beagle Channel, Argentina (Peresan and Roccatagliata, 2005). Kuris (1974) used the term hypercastrator in referring to *Liriopsis*, indicating their impacts on the primary castrator.

#### 3.11.4. Phylum Arthropoda, Order Isopoda, Superfamily Cryptoniscoidea, Family Hemioniscidae

Members of the Hemioniscidae are parasites of barnacles, including thoracican and acrothoracican barnacles. One hyperparasitic species, *Hemioniscus pagurophilus*, infests the acrothoracican barnacle *Tomlinsonia mclaughlinae* described as an obligate symbiont of hermit crabs from the Philippines (Williams and Boyko, 2006) (Fig. 16F). In this region, nearly 10% of the barnacles found burrowing in gastropod shells inhabited by hermit crabs harbored *H. pagurophilus*. The primary symbiont is suspected to be an egg predator of the hermit crab hosts, as documented in other species of trypanetid barnacles (Williams and McDermott, 2004).

#### 3.11.5. Phylum Arthropoda, Infraclass Cirripedia, Superorder Rhizocephala, Order Akentrogonida

Members of the akentrogonid family Duplorbidae parasitize various peracarids, including both free living hosts and parasitic isopods (Bresciani and Høeg, 2001). The only described species found as a hyperparasite of hermit crabs is *Duplorbis smithi* that infests the primary parasite *Parathelges weberi* (Fig. 16G). Knowledge on its biology and ecology are lacking but the ultrastructure and impacts on hosts of other duplorbid species have been studied (Mourey, 1991; Bresciani and Høeg, 2001).

## 4. Discussion

### 4.1. Scarcity of hermit crab parasites

This worldwide analysis of hermit crab literature reveals that the low numbers of parasite species (<16% of hermit crab species with parasites;  $n = 133$  or 149 if Acari included) is due to the small fraction of the >850 known species of hermit crabs studied in this regard. Most species of the relatively numerous rhizocephalan and bopyrid isopods have been

detected and often described during taxonomic studies of host crabs rather than in parasitological surveys of crab populations. Thus, the biology and host-parasite relations are poorly known for the majority of these parasites, being particularly true for the bopyrid parasites. These two taxa comprise ~74–83% (111 of 149 species versus 111 of 133) of parasite species known from hermit crabs. It is not surprising that bopyrids and rhizocephalans are known from more species of hermit crabs than the other recorded species. The former are relatively large ectoparasites, and the latter, while endoparasitic in development to maturity, produce relatively large conspicuous externae.

The other parasites of hermit crabs (not including the Acari) are endoparasitic, so that their detection and identification usually demand dissection of the host and histological preparations. Experience with parasitic taxa is another requirement for the detection of internal parasites, and especially for the detection of hyperparasites. Detection of hermit crabs infected with nematomorphans and entoniscids may be facilitated by isolating crabs and looking for the emergence of adults and epicaridium larvae, respectively.

Many endoparasites may have low prevalences in hermit crab hosts, thus requiring the examination of large number of crabs. For example, recorded prevalences of the entoniscid isopod *Paguritherium alatum* in *Pagurus longicarpus* from different locations along the western Atlantic coast from Massachusetts New Jersey and North Carolina were 0.8% ( $n = 4,600$ ), 0.1% ( $n = 3,703$ ) and 3.0% ( $n = 300$ ) (Reinhard, 1943, 1945; McDermott, 1998; Adkison and Heard, 1978, respectively). The same may be true for ectoparasitic isopods, e.g., the bopyrid *Anathalgas hyptius*, also a parasite of *P. longicarpus*, had prevalences of 1.25% ( $n = 8,748$ ) in Massachusetts (Reinhard, 1943) and 0.15% ( $n = 9,111$ ) in New Jersey (McDermott, 1998). The cystacanth larvae of the acanthocephalan *Polymorphus* sp. had a prevalence of ~1% ( $n = >8,000$ ) in *P. longicarpus* from Massachusetts (Reinhard, 1944). Although McDermott (2001) found no digenetic metacercariae in thousands of specimens of *P. longicarpus*, high prevalences have been recorded in some other hermit crabs, e.g., Schiller (1954) found the metacercariae of *Microphallus pium* in 90% ( $n = 51$ ) of *Pagurus hirsutiusculus*. Unfortunately, information on prevalence of parasites utilizing hermit crabs as intermediate hosts is very limited.

### 4.2. Hermit crabs as intermediate hosts: effects and specificity of their parasites

Hermit crabs serve as prey for a variety of vertebrate species, particularly fishes and birds. Various species of cartilaginous and bony fishes are known predators of hermit crabs (Verrill, 1873; Reid, 1954; McDermott, 1964; Sikora et al., 1972; Stickney et al., 1974; Hamilton, 1976; Overstreet and Heard, 1978, 1982; Jewett and Feder, 1980; Bertness, 1981; Heck and Wilson, 1987; Lancaster, 1988; Caira and Ruhnke, 1991; Kuhlmann, 1992; Clark et al., 2006) as are several kinds of sea birds (Lancaster, 1988; Litzow et al., 1998). Great black-backed gulls (*Larus marinus* Linnaeus, 1758) and herring gulls (*L. argentatus argentatus* Pontoppidan, 1763) are common predators of *Pagurus pollicaris* along the Atlantic coast, extracting the crab from their protective shells which are cracked by dropping them onto hard surfaces from several meters aloft (authors' personal observations). The crustacean predators of hermit crabs serving as intermediate hosts may themselves serve as paratenic hosts for parasites prior to their transfer to definitive fish or avian hosts. Some of the crustaceans that are notable predators of hermit crabs include cold water and warm water lobsters (*Homarus americanus* H. Milne Edwards, 1837; *Panulirus argus* (Latreille, 1804)) (McLean, 1983; Elner and Campbell, 1987), and many species of brachyuran crabs (e.g., *Calappa flammea* (Herbst, 1794), *Callinectes sapidus*, *Cancer borealis*, *C. irroratus*, *Eriphia squamata* Stimpson, 1860, and *Ovalipes ocellatus* (Herbst, 1799)) (McLean and Mariscal, 1973; Bertness, 1981; Drummond-Davis et al., 1982; Kuhlmann, 1992; Stehlik, 1993; Tirelli et al., 2000; Stehlik et al., 2004). Hermit crabs are also common prey of octopuses (Ross, 1971; McLean, 1983; Kobayashi,

1986; Brooks, 1988) and coccidian parasites of the genus *Aggregata* may be transferred to octopuses through hermit crabs.

Considering their importance as a food source for the aforementioned predators, hermit crabs have the potential to act as first or second intermediate hosts in the life cycles of coccidians, cestodes, trematodes, acanthocephalans and nematodes, but the literature implicating them as host for these parasites is very sparse. In total, hermit crabs are known to act as first or second intermediate hosts for 12 species, including one coccidian, two cestodes, four species of digenetic trematodes, two acanthocephalans, and three species of nematodes. Hermit crabs have seldom been implicated as second intermediate hosts in the life cycles of parasites (but see Køie, 1979; Marcogliese, 1996). The literature documenting the role of hermit crabs as intermediate hosts is generally inadequate for critically evaluating possible parasite-induced morbidity, mortality, pathology and host resistance to infections in hermit crabs. Thus, it is necessary to refer to literature dealing with the host-parasite relationships of similar parasites that infect other species of crustaceans in order to speculate on possible effects in hermit crabs.

In addition to describing details in the life history of the trematode *Derogenes varicus*, Køie (1979) also experimented with infecting second intermediate hosts (mainly calanoid copepods) other than the hermit crab host *Pagurus pubescens*. Copepods exposed to cercariae released from snail hosts were readily infected, but mortality in these much smaller hosts was high, especially if they were infected by several metacercariae. The fact that the metacercariae of *D. varicus* do not encyst in the body cavity of second intermediate hosts, as well as its relatively small size, may make it more difficult to detect in dissected hosts as compared to the more typical encysted stages of other species of trematodes. Because Køie could not directly infect the chaetognath *Parasagitta elegans* Verrill, 1873, she suggested that chaetognaths in nature became infected by consuming copepods; thus, a third intermediate host or paratenic may sometimes be involved in the life-cycle of this trematode. Since Køie could not experimentally infect *Pagurus bernhardus* with cercariae of *D. varicus*, it may be that hermit crabs are not the preferred hosts. Marcogliese (1996) showed that *Pagurus acadianus* is the predominant second intermediate host for the trematode *Steganoderma formosum* on the Scotian Shelf. The life cycles of *Steganoderma* spp. associated with hermit crabs are poorly known but the parasite exhibits progenetic development in *P. acadianus* (Marcogliese, 1996). Both *S. formosum* and *D. varicus* have been used as a biological tags to delineate commercially important fish populations (Boje et al., 1997; McClelland et al., 2005).

The cercariae of *Microphallus pirum* encyst in its second intermediate host, *Pagurus hirsutiussculus*. Schiller (1954) found up to 382 cysts per crab, but did not detect any negative effects. Species of microphallid trematodes are very numerous and their metacercariae are found in a wide variety of crustacean hosts. The fact that only one species of hermit crab has been reported with microphallids is likely due to inadequate study. Encysted metacercariae are usually easy to detect, especially in dissections of small crustaceans (McDermott, 2005).

Changes in the behavior of hosts due to parasitic infections have received much attention in recent decades (Moore, 2002). It is known that infections with metacercariae may change the normal behavior of crustacean hosts, in some cases making these hosts more susceptible to consumption by definitive hosts. For example, caridean shrimp, *Palaemonetes pugio*, infected with the metacercariae of *Microphallus turgidus* (Heard and Overstreet, 1983) were eaten more readily by a fish predator than uninfected shrimp (Kunz and Pung, 2004). This was apparently due to the infected crustacean's excessive swimming in the presence of a predator compared to the more subdued activity of uninfected shrimp. Specimens of the amphipod *Corophium volutator* (Pallas, 1766) infected with the metacercariae of *Gynaecotyla adunca* (Linton, 1905) were more active in the field than uninfected animals that remained burrowed and

were more susceptible to predation by shore bird definitive hosts (McCurdy et al., 1999). Precocious reproduction in female amphipods after infection with cercariae was a host adaptation to this parasitism (McCurdy et al., 1999, 2000). Although documented in other species, behavioral changes due to metacercarial infections have not been reported in hermit crabs.

*Calliobothrium verticillatum* is the only cestode parasitizing hermit crabs that has been studied in detail. The plerocercoids of this worm infected nearly 100% of *Pagurus* spp. in the Woods Hole region of Massachusetts (Cherry et al., 1991). Smolowitz et al. (1993) suggested that the pathology produced in the anterior midgut cecae might have been responsible for mortality of crabs crowded in holding tanks at the Marine Biological Laboratory. Severe mycotic branchitis, however, was also responsible for crab mortality (Smolowitz et al., 1992). Possible changes in the behavior of crabs infected with plerocercoids that may make them more vulnerable to predation by definitive hosts were suggested for future study by Smolowitz et al. (1993). Behavioral changes in copepod intermediate hosts infected with proceroids of cestodes in the order Pseudophyllidea have also been demonstrated (Poulin et al., 1992; Urdal et al., 1995). Pearse (1932) found an unidentified cestode of the genus *Rhynchobothrius* associated with *Paguristes puncticeps* but nothing is known of its impacts on this intermediate host.

Crustaceans are involved as intermediate hosts in most of the known acanthocephalan life cycles. Surely, among the 850+ species of hermit crabs, it is highly unlikely that *Pagurus longicarpus* and *P. pubescens* are the only species harboring cystacanth larvae (Reinhard, 1944; Uspenskaya, 1960). Cystacanths are relatively easy to recognize in dissected tissue and inducing the evagination of the characteristic thorny proboscis confirms their identity. Infected hosts may be detected without dissection because cysts may be seen through the poorly calcified integument of living, small crustaceans such as amphipods and isopods or, as Reinhard (1944) noted, the semi-transparent abdominal wall of small hermit crabs such as *P. longicarpus*. Cysts are easily dissected from the intermediate host and may be fed to potential vertebrate hosts to determine the specific identity of adult worms. Behavioral changes may occur in infected hermit crabs just as they have been demonstrated in smaller intermediate hosts such as amphipods and isopods (Moore, 2002) and some brachyurans (Latham and Poulin, 2002).

It is also likely that more species of hermit crabs are involved as intermediate hosts in nematode life cycles than have been recorded in the literature. Adverse effects of the two species of *Ascarophis* larvae on hermit crabs and their other crustacean hosts are not known. Poinar and Kuris (1975) studied the relationship of an unidentified species of *Ascarophis* larvae with its brachyuran host *Hemigrapsus oregonensis* from coastal California. Up to 24 worms were found in the crab's hemocoel, but usually only 1 to 5 larvae occurred. They showed that these worms interfered with the crab's growth and induced mortality. In addition, the encapsulation of third-stage juveniles with host tissue demonstrated some host resistance.

The nematodes *Pseudoterranova decipiens* (Krabbe, 1878) and *Anisakis simplex* (Rudolphi, 1809) are found in a wide range of crustacean intermediate hosts and probably use hermit crabs as well (Bush et al., 2001; McClelland, 2005). These nematodes are trophically transferred to commercially important fishes or squid as their second intermediate host and then marine mammals as their definitive hosts. The parasitic worms are of medical concern because they can cause Anisakiasis when humans ingest raw fish.

Another nematode of potential medical importance is *Anatrichosoma cutaneum* (Swift, Boots, and Miller, 1922) which causes nasal and cutaneous Anatrichosomiasis in monkeys and, although extremely rare, cases have also been reported in humans (Kessler, 2005; Berger and Marr, 2005). *Coenobita clypeatus* from Cayo Santiago, Puerto Rico are known to feed on the feces of rhesus monkeys *Macaca mulatta* (Zimmermann, 1780) and the eggs may pass through the digestive

tract of the hermit crabs and remain viable (Rowland and Vandenberg, 1965; Kessler, 2005). The complete life cycle of the parasite is unknown and the hermit crabs might act as an intermediate host for the parasite (Kessler, 2005). Semi-terrestrial *Coenobita* spp. in other regions (e.g., Mozambique) are known to feed on human feces (Barnes, 1997) but no studies have examined their potential role in transfer of parasites. Rowland and Vandenberg (1965) showed that cysts of *Entamoeba coli* (Grassi, 1879), ova of *Strongyloides* sp., and ova of *Hymenolepis diminuta* (Rudolphi, 1819) were present in the feces of rhesus monkeys and these stages remained viable after ingestion by *Coenobita clypeatus*.

#### 4.3. Hermit crabs as definitive hosts: effects and specificity of their parasites

This review shows that hermit crabs are important definitive hosts for only the Rhizocephala and certain parasitic isopods, primarily bopyrids. Host specificity is highly variable, with some species parasitizing as many as fourteen different species of hermit crabs (e.g., *Peltogaster paguri*, *Athelges takanoshimensis*). Although some species are known from a single host species, it is clear that the “one host species – one parasite species” rule of Giard and Bonnier is not correct. However, all species of rhizocephalans, bopyrids, and entoniscids known from hermit crabs have been found only on these hosts and never on species of other decapods (e.g., brachyurans, carideans). Bopyrids, entoniscids and rhizocephalans are parasitic castrators of hosts (Lafferty and Kuris, 2009), but whereas rhizocephalans and entoniscids always sterilize hosts of both sexes, some bopyrids allow for reproduction by host females (albeit with smaller clutch sizes) and may not interfere with male reproductive ability (Van Wyk, 1982; Calado et al., 2005), thus they are considered partial castrators in this review.

Rhizocephalans modify their hosts both physiologically and behaviorally through hormonal influence (Høeg et al., 2005). The developing female interna is intimately associated with the nervous system of the host and via chemical secretion, simultaneously suppresses female host reproduction while also altering the behavior of the host so that the externa, when extruded, will be cared for by the host with the same kind of grooming behaviors of the pereopods normally reserved for the host's own clutch of eggs. When the host is a male, the rhizocephalan actively modifies the sexual identity of the host through a process of chemically induced feminization (internally and externally), accompanied by the grooming behaviors displayed by females towards their eggs. In an evolutionary sense, rhizocephalans and other complete parasitic castrators kill their hosts and the hosts act as an extended phenotype of the parasite (Kuris, 1974; Kuris and Lafferty, 2000; Lafferty and Kuris, 2009). Most of what is known of rhizocephalan effects on hosts is derived from studies on brachyurans, but the same kinds of effects, in terms of feminization and behavior, can be seen in hermit crabs as well as other anomurans (Brinkmann, 1936). Although rhizocephalans and parasitic isopods do not typically cause the death of hosts, their impacts could make hosts more vulnerable to contaminants such as pesticides (Williamson et al., 2009) that are common in intertidal areas where hermit crabs can be found in abundance.

In contrast to our rather robust understanding of the mechanisms by which the parasitic barnacles affect their hosts, the chemical basis for the impacts of bopyrids and entoniscids on hosts remains largely unknown (but see Baffoni, 1948; Lester, 2005; Calado et al., 2008). Parasitic isopods clearly do alter the fitness of their hosts, and their ability to remain attached while being within reach of host pereopods suggests a chemical modification of host behavior. The observable decrease or cessation of host reproduction could also be influenced by chemical modification. The branchial bopyrids strongly modify the branchiostegite in which they are living, giving the host a lopsided appearance. In contrast, there are no obvious external modifications from abdominal bopyrids on hermit crabs, aside from some reports of

modifications, although not necessarily feminization, to host pleopods (but see Reinhard 1942 for examples of these modifications not caused by parasites). Bopyrids are known to shut down reproduction in other host groups (e.g., O'Brien and Van Wyk, 1985), sometimes with apparent impacts on the populations of hosts (e.g., Smith et al., 2008; Griffen, 2009; Williams and An, 2009). Further experimental and field studies are needed to determine if and how bopyrids parasitizing hermit crabs shut-down host reproduction and the potential impacts they have on host populations.

Entoniscids in hermit crabs are poorly known, but they occupy a very large portion of the host's hemocoel and suppress development of gonad tissue (Reinhard and Buckeridge, 1950). Entoniscids in other groups have been shown to be complete castrators (Kuris et al., 1980).

The five marine species of nematomorphans within the class Nectonematoida are all in the genus *Nectonema*. Two of the species (*N. agile* and *N. munidae*) use a total of seven species of hermit crabs as hosts for their development to free-living adults, but these parasites apparently complete their life cycles equally well in penaeid and caridean shrimp and brachyuran crabs. This lack of host specificity suggests that hermit crabs are not essential hosts for these parasites. However, because so little is known of *Nectonema* life cycles and distribution, it is possible that in some geographic regions, where other suitable hosts are in low abundance or lacking, hermit crab hosts may be essential.

Developing nematomorphs occupy a large portion of the hemocoel volume of arthropod hosts and interfere with their reproduction (Bush et al., 2001). *Nectonema agile* castrates and modifies the secondary sexual characters of *Anapagurus hyndmanni* and *Pagurus bernhardus* (Pérez, 1927b,c; Mouchet, 1931). Female caridean shrimp hosts (*Palaemon serratus* and *Palaemonetes vulgaris*) are subject to castration (Nouvel and Nouvel, 1934; Born, 1967). Males of *P. vulgaris* are apparently not similarly affected. Born also examined ~100 specimens of *Pagurus longicarpus* from the same location; none was infected.

Nielsen (1969) found that *Nectonema munidae* did not castrate its galatheid hosts (*Munida sarsi* and *M. tenuimana*), nor was there any negative effects on their growth or normal behavior. He did not detect parasitic castration in the two hermit crab hosts of *N. munidae*, both of which had low prevalence of the parasite compared to *M. tenuimana*. Host resistance by *Hemigrapsus sexdentatus* to *N. zealandica* was suggested by Poinar and Brockerhoff (2001) as 95.7% of parasitized crabs had encapsulated juveniles in their hemocoels. Poinar and Brockerhoff further suggested that the high prevalence of worm encapsulation indicates that this grapsid crab is not the normal or preferred host, although the congeneric hosts *Hemigrapsus oregonensis* and *H. nudus* (Dana, 1851) are known to encapsulate individuals of an entoniscid isopod for which they are the known preferred hosts (Kuris et al., 1980).

As in the Nematomorpha, the life cycles in the class Fecampiida involve only one host, and for *Fecampia erythrocephala* these hosts are decapod crustaceans. Developing *F. erythrocephala* occupy a large fraction of the host's hemocoel where they displace organs, absorb nutrients and affect gonadal development (Kuris et al., 2002). Upon release of the hermaphroditic adults from their hosts, they produce cocoons in which eggs develop into infective larvae. The release process involves puncturing the host's body wall, which may cause death especially in small hosts such as amphipods infected with the dioecious *Kronborgia amphipodicola* Christensen and Kannevorff, 1964 (Christensen and Kannevorff, 1964, 1965). Kuris et al. (2002) found *F. erythrocephala* mainly in juvenile specimens (<10–12 mm carapace width) of *Carcinus maenas*, and indicated that the release of adults was an important source of crab mortality. No such information is available for the two hermit crab hosts (*Anapagurus hyndmanni* and *Pagurus bernhardus*) of this parasite, but we suggest that the body wall damage produced by these large worms may be similarly detrimental.



*Fecampia erythrocephala* appears to castrate its two hermit crab hosts and modifies their secondary sexual characters (Giard, 1886; Mouchet, 1931). Histological studies of *Palaemon serratus* infected with this same fecampid have shown that its oocytes and follicular cells are diminished compared to normal and that there is a hemocyte infiltration into the gonads (Bellon-Humbert, 1983). Not all shrimp were killed by release of the adult worms and the permanence of this condition was not determined. Parasites did not cause abnormal behaviors in the shrimp, but there was some delay in the molt cycle and a greater mortality upon molting. In this host and in all other fecampid hosts, adverse effects must be due to the absorption of nutrients from the hemocoel fluid during the long developmental period and possibly due to the release of harmful metabolites by the parasites.

Mesomycetozoa are symbiotic in eleven species of hermit crabs. *Taeniella carcini*, aside from infecting five species of hermit crab hosts, also infects many other different kinds of crustaceans. It remains to be determined, however, how many of the other three known species and unidentified species of these potential parasites from hermit crabs show a similar lack of host-specificity.

Hermit crabs are apparently not important definitive hosts for the Apicomplexa and Microsporida since only three species of these parasites have been recorded from just two species of crabs. However, difficulty in detecting and identifying these microscopic organisms, as well as the limited research designed to study such hermit crab parasites, may account for their scarcity in the literature.

The ciliated protozoan ectosymbionts found on hermit crabs are not classified as parasites even though many have been designated as being obligate (Williams and McDermott, 2004). Among the apostome ciliates, however, there are relationships that are distinctly obligate since they include intimate contact with the hermit crab's gills as well as a life cycle synchronized with the host's growth cycles (molting) (Trager, 1957; Bradbury, 1966; Morado and Small, 1995). Because host mortality due to *Gymnodinioides inkystans* and *Hyalophysa chattoni* has not been observed in hermit crabs, their classification as parasites remains uncertain. Grimes (1976), experimenting with brachyurans (*Armases cinereum*, *Sesarma reticulatum*, *Uca pugnax* (Smith, 1870)) infested with *Hyalophysa trageri* Grimes, 1976, found that crabs often died after two molting cycles, but suggested that some of the mortality may have been due a poor diet. Other species of apostomes, such as *Synophrya hypertrophica*, parasitic in brachyurans and *Collinia* spp. in amphipods and euphausiids, are pathogenic and lethal (Haefner and Spacher, 1985; Morado and Small, 1995). In brachyurans there may be perforations of gill cuticle, melanization of infected filaments and gill autotomy. Both *G. inkystans* and *Hyalophysa chattoni* are not host-specific; the former infesting four species of hermit crabs and the latter infects eight species of hermit crabs and two species of brachyurans (Bradbury, 1966; Bradbury and Trager, 1967; Baccarani and Pessani, 1997).

#### 4.4. Evolutionary Considerations

The parasite fauna of anomurans could be used as an independent test of the hypotheses on the evolution of hermit crabs and king crabs (Lithodidae). Whereas multiple lines of evidence support the hypothesis that king crabs evolved from a hermit crab ancestor in the Paguridae (Cunningham et al., 1992; Richter and Scholtz, 1994; Harvey, 1998; Tudge et al., 1998; Morrison et al., 2002; Ah Yong et al., 2009), a few morphological analyses support the hypothesis that hermit crabs and lithodids represent distinct monophyletic groups, with lithodids more closely related to members of the Hippoidea (McLaughlin et al., 2007; see also review of anomuran phylogeny in Lemaitre and McLaughlin, 2009). Lithodids are hosts to a variety of parasites (Zaklan, 2002) including bopyrid isopods and rhizocephalans. Markham (2003) noted that all branchial and abdominal parasites of lithodids are within genera also found associated with

hermit crabs. However, the phylogenetic relationships of the bopyrids associated with lithodids and hermit crabs, such as the likely polyphyletic genus *Pseudione*, are unknown and require morphological and molecular analysis before conclusions can be made on their coevolution with hosts. Similar data on the rhizocephalans associated with these hosts would also be informative. In order to fully evaluate the hypotheses on the evolution of hermit and king crabs, a broader sampling of parasites would have to be made within the Anomura (for reviews of other parasites in other anomuran groups see Martin and Felgenhauer, 1986; Aeglididae; Boyko 2002: Hippoidea). Some molecular analyses have suggested hermit crabs (*sensu lato*) may be polyphyletic (see Ah Yong et al., 2009), in which case study of the coevolution of hermit crab and their parasites could shed light on this question as well. Coevolutionary analyses also could have commercial implications for king crab fisheries since researchers could use hermit crabs or other more easily collected anomurans as model systems for examining impacts of parasites on king crab hosts (Shukalyuk et al., 2005).

The evolutionary history of hermit crabs and their parasites cannot be ascertained from examination of the fossil record. Although hermit crabs are known from the early Jurassic (Jagt et al., 2006), intact hermit crab fossils are exceedingly rare, due to the poorly calcified nature of much of hermit crab anatomy, and most of the known examples are represented only by chelae and other disarticulated pieces (Van Bakel et al., 2003). Therefore, there are no hermit crab fossils known which bear evidence of parasitism. This is in marked contrast to the situation for other anomurans such as galatheids and porcellanids, as well as several brachyuran groups that have a long history of fossilized swellings that presumably indicate bopyrid infestation (Radwanski, 1972; Conway Morris, 1981; Markham, 1986; Weinberg Rasmussen et al., 2008). At least one fossilized species of brachyuran shows feminized male anatomy indicative of rhizocephalan infection (Feldman, 1998). In no case, however, is there any direct evidence of parasitism by bopyrids or rhizocephalans in the fossil record, as no fossils of these taxa have ever been reported.

Despite the lack of a fossil record for bopyrids or rhizocephalans on hermit crabs, some inferences can be drawn based on the identities of the taxa that are found on this host group. For the bopyrids, only members of the Pseudioninae and Athelginae are known to occur on hermit crab hosts. This is of interest particularly as these two subfamilies are quite different in terms of their position relative to each other in the overall evolution of the Bopyridae. The Pseudioninae is considered by most researchers to be a basal taxon with a suite of pleisiomorphic characters, whereas the Athelginae is clearly a derived taxon showing the expected modifications and loss of characters possessed in the ancestral *bauplan* (e.g., Shiino, 1952, 1965; Markham, 1986; Boyko and Williams, 2009). It should be noted, however, that the Pseudioninae is almost certainly para- or polyphyletic (Boyko and Williams, 2009) and the hermit crab-infesting genera like *Bopyrissa*, *Asymmetrione*, and *Bopyrophryxus* are probably among the most derived forms in the subfamily as currently defined. Current evidence suggests that the bopyrids initially invaded the decapod crustaceans via the Anomura, which are relatively derived host taxa (Boyko and Williams, 2009), and later switched to more primitive hosts, such as those in the Penaeoidea and Caridea. Although they have also invaded the Brachyura, they have not been as successful as in the anomurans, possibly due to the general heavier calcification of the true crabs, or perhaps a combination of this and more acute behavioral responses by the crab hosts to larval attempts at parasitism than are seen in the anomurans. Among the anomurans, the putatively more basal bopyrids occur on the galatheids, with the more advanced forms being found on the hermit crabs as well as the lithodids.

The phylogenetic relationships of the rhizocephalan barnacles have been recently analyzed based on the molecular data of Glenner and Hebsgaard (2006). These researchers found that the

Peltoastridae and Lernaodiscidae were basal within the Rhizocephala and the ancestral host of rhizocephalans therefore appears to be anomuran. The more derived Akentrogonida, containing *Thompsonia* and *Thylacoplethus*, appears to have reinvaded anomurans, including hermit crabs, as the intermediate clade between the Peltoastridae + Lernaodiscidae and the Akentrogonida is composed entirely of brachyuran parasites. Subsequently, Glenner et al. (2010) updated this work with the addition of the hermit crab parasite *Clistosaccus paguri* and the barnacle parasite *Chthamalphilus delagei* (Bocquet-Védrine 1967) in a new molecular analysis and study of larval forms. This study confirmed that Rhizocephala are composed of a paraphyletic “Kentrogonida” within which is nested the Akentrogonida. In contrast to earlier predictions, the barnacle parasite *C. delagei* was found to represent a derived member of the Akentrogonida. The hermit crab parasite *C. paguri* was most closely related to a shrimp parasite *Sylon hippolytes* Sars, 1870, forming a monophyletic Clistosaccidae (Glenner et al., 2010).

## 5. Conclusions

Hermit crabs have formed relationships with a wide range of symbionts. Among these, hermit crabs are host to parasites with a wide range of trophic strategies (partial and complete parasitic castrators, pathogens, trophically transmitted pathogens, and trophically transmitted typical parasites). Hermit crabs also harbor some symbionts presently considered commensals but that should be further investigated to rule out parasitism. As found in other symbioses, the nature of these relationships could change depending on biological and environmental conditions, thus requiring challenging experimental studies to determine their potentially varied impacts on hosts. Among the confirmed parasites, this review shows that while some groups are well known from these hosts (e.g., rhizocephalan barnacles and bopyrid isopods), other taxa are underrepresented based on their prevalences recorded from other decapod hosts. Some of this lack of diversity may represent the unique ecological and behavioral adaptations of hermit crabs. However, it is apparent that many hermit crab species have been poorly sampled for parasites. The finding that European hermit crabs harbor larger number of parasite species than hermit crabs from highly diverse areas such as the Indo-West Pacific most likely reflects a lack of this type of study. The bias in sampling efforts towards temperate zone hermit crabs in North America and Europe is likely due to the many years of intensive parasitological research on marine species that has been performed at institutions in these regions (e.g., Woods Hole, Roscoff). Thus, the differences in number of parasite taxa associated with the hermit crabs could represent a disparity in sampling efforts rather than a real difference in diversity patterns. This is similar to findings based on commensal and mutualistic species associated with hermit crabs (Williams and McDermott, 2004). In addition, impacts of sampling efforts are found in other crustacean groups such as penaeid prawns where up to nine parasite species have been found in a single well-studied host species, whereas the parasite fauna of the Indo-West Pacific host taxa remain largely unknown (Owens, 1987). We predict that additional studies will show the numbers of parasites associated with hermit crabs from less studied regions, including the Indo-West Pacific and deep-sea habitats, will be considerably higher than is presently known. For example, ~15% of all described hermit crabs are known to harbor parasites but there is no reason to conclude that the 700+ marine hermit crab species that are not listed in the present work are parasite free. Most likely each harbors one or more parasites as is thought to be the case with all organisms (Bush et al., 2001), many of which will be new to science. A better understanding of the true diversity of the parasites of hermit crabs will also lead to additional lines of fruitful research in host-specificity studies, coevolution of parasites and hosts, and perhaps even give greater insight into the

phylogeny of host taxa. In addition, hermit crabs could be used as model organisms for studies on parasites that impact commercially important decapods.

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