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AMPHIPODS AS ASSOCIATES OF OTHER CRUSTACEA: A SURVEY

Wim Vader [1] and Anne Helene S. Tandberg [2,*]

[1] Tromsø Museum – University Museum, NO-9037 Tromsø, Norway
[2] Natural History Collections, University Museum of Bergen, P.O. Box 7800, NO-5020 Bergen, Norway

ABSTRACT

This paper presents an overview of the known associations between amphipods and other crustaceans. Such associations are quite common and widely distributed among the different amphipod clades, and in most cases show a high degree of host specialisation. They can roughly be divided into 5 groups: 1) living among the epifauna of large Crustacea, 2) living directly on the surface or appendages of their crustacean hosts, 3) living among the eggs of their crustacean hosts, 4) living in the permanent burrows of infaunal crustaceans, and 5) living on or in gastropod shells tenanted by hermit crabs. This survey concentrates on groups 2-4.

KEY WORDS: Amphipoda, associations, Crustacea

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INTRODUCTION

Although Amphipoda are now generally considered to be a crustacean group of considerable antiquity and diversity (Schram, 1986; Bousfield and Shih, 1994), the morphological and physiological adaptations towards a parasitic lifestyle that we find in this group are far less drastic than those that occur in some other groups of associated Crustacea (Vader and Lønning, 1973; Vader, 1983b). There is nothing comparable to the strange forms and life-cycles of many associated and parasitic Copepoda, to Tantulocarida or Rhizocephala, or to the epicaridean Isopoda; even many symbiotic shrimps have undergone far greater morphological specializations than have most amphipods. In the amphipods, the primary thrust of evolutionary diversification has gone towards adaptation to different habitats (freshwater, interstitial, soft-bottom, scavenging, tube-living, etc.) (Steele, 1988). Only secondarily and probably much later, except in the case of the whale-lice and maybe the pelagic amphipods, have some taxa developed further towards a symbiotic life-style.

Nevertheless, the frequency of occurrence of symbiotic associations involving Amphipoda has been seriously underestimated and is not fully realized always even by many amphipod workers. Especially since scuba diving came into common use as an observational tool, new associations are being discovered at a rapid pace.

This does not, however, apply equally to all amphipod habitats. No associations with subterranean amphipods have as yet been described, nor do there seem to be symbiotic terrestrial species, although several intertidal Hyalidae habitually seek protection underneath intertidal molluscs (Vader and Tandberg, 2013), while another hyalid, *Hyachelia tortugae* Barnard, 1967, has become an apparently obligate associate of sea turtles, even penetrating into the buccal cavity (Barnard, 1967). In surface freshwater habitats, except Lake Baikal, the incidence of associated amphipods is also very low, although species of *Iphigenella* occur on crayfish in the Ponto-Caspian region (Behning, 1924). In the extremely diversified and ancient amphipod fauna of Lake Baikal associated amphipods are clearly more frequent, but little seems to be known as yet about the biology of most of these species (Kamaltynov et al., 1993; Takhteev and Mekhanikova, 1993; Mekhanikova, 2010; Daneliya and Väinölä, 2014). As regards the frequency of occurrence of amphipod associations in the deep sea, present collecting methods are much too coarse to make a reliable evaluation possible.

There are many associated amphipods in hard-bottom epifaunas, and also quite a number in soft-bottom infaunas. In the pelagic realm many, if not most, amphipods are facultative or obligate associates at least during part of their life-cycle, i.e., if we define the term associate broadly enough to encompass also the parasitoid lifestyle of many Hyperiidea and pelagic Lysianassoidea (Harbison et al., 1977; Laval, 1980; Bowman and Wasmer, 1984).

The first author has during many years collected data on occurrences of associated amphipods living on or in several groups of marine invertebrates as well as fishes: molluscs (Vader and Tandberg, 2013), sea anemones (Vader, 1983b; De Broyer and Vader, 1990; Vader and Krapp-Schickel, 1996; Krapp-Schickel and Vader, 2009), echinoderms (Vader, 1978; Berge et al., 2004), sponges and tunicates (Vader, 1984), hermit crabs (Vader, 1996; Vader and Myers, 1996), king crabs (Vader and Krapp, 2005), and fish (Vader and Romppainen, 1984). In the present paper we shall give a survey of the occurrence of amphipods as associates of other crustaceans; we have, however, partly excluded the hermit crab associates (except those living directly on the hermit crabs themselves), as these associations often are of a different type (Vader, 1996).

* Corresponding author; e-mail: pansdamen@gmail.com

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We have in this paper used the neutral term "associates" and largely avoided "commensals," since the term commensalism is used differently by different authors. Facultative associates are also found free-living, while obligate associates are always found together with a host, not necessarily only on a single host species. True commensals feed on the food collected by the host.

Survey of Amphipod-Crustacean Associations

Associations between amphipods and other crustaceans can roughly be divided into 5 groups, although the boundaries between groups may be a bit fuzzy here and there:

1. Amphipods living among the epifauna of heavily overgrown large crustaceans.
2. Amphipods living directly on the surface of their crustacean hosts.
3. Amphipods living primarily among the eggs of the host.
4. Amphipods living in the permanent burrows of infaunal Crustacea.
5. Amphipods living on or in gastropod shells tenanted by hermit crabs.

Group 1: Epifauna

Many amphipods live among the often luxuriant epifauna covering spider crabs or hermit crabs and their 'houses.' Good examples are the spider crab *Maja squinado* (Herbst, 1788) on European coasts (Chevreux, 1908; Parapar et al., 1997) and the heavily overgrown hermit crabs *Pagurus cuanensis* Bell, 1846 and *Paguristes eremita* (Linnaeus, 1769) (formerly *Paguristes oculatus* (Fabricius, 1775)) in the Adriatic Sea described by Stachowitsch (1980). Such associations are almost never obligatory; the amphipods found here are generally not very different from those found among the general epifauna of rocky substrates, and they will not be considered further here. It should be kept in mind, however, that a few amphipod species, such as *Jassa pusilla* (Sars, 1894) (Ischyroceridae) and *Monocorophium sextonae* (Crawford, 1937) (Corophiidae) in Europe, seem to have a preference for 'moving substrates'; the recently described *Jassa kjetilanna* Vader and Krapp, 2005 from Falkland Islands' king crabs and spider crabs may be in the same category, although it has weakly prehensile pereiopods and therefore has been listed in Table 1.

Group 2: Direct Associates

This is a very diverse group of amphipods, belonging to many different families and occurring on many different hosts, all over the world (Table 1). Most of the hosts are slow-moving hermit crabs, king crabs and spider crabs, but there are also a few macrurans and a single portunid, *Chaceon affinis* (Milne-Edwards and Bouvier, 1894). Most of the amphipods in this group are characterized by having prehensile pereiopods (Fig. 1), clearly an adaptation to the frequent grooming of the host (Vader, 1983a). In one species, the pleustid *Myzotarsa anaxiphilius* Cadien and Martin (1999), the pereiopods are even more specialized (Fig. 2): the dactyli bear sucker-like structures for clinging. Intriguingly, this species is in most cases found on king crabs that are parasitized by the rhizocephalan *Briarosaccus callosus* Boschma, 1930 and the authors surmise that the associate may feed on the eggs of the rhizocephalan. No such connection has been found in any of the other king crab associates.

The most cited representatives of this group are the isaeids of the genus *Isaea*, especially the European *I. montagui* Milne-Edwards, 1830 from the spider crab *Maja squinado* (Herbst, 1788) (for references, see Vader, 1983a), and *I. elmhirsti* Patience, 1909 from the European lobster *Homarus gammarus* (L., 1758) (Moore, 1983, see also Williamson, 1916 sub. nom. *Amphipoda montagui*). In Australia and New Zealand, species of the closely related genus *Pagurisaea* Moore, 1983 live a similar life, but in their case the known hosts are all hermit crabs (Moore, 1983; Vader, unpublished data). There does not seem to be a single published study on the biology and diet of any of these species. *Isaea montagui* often is found clustered around the mouthparts of its host and might well be a true commensal. *Pagurisaea schembrii* Moore, 1983, however, seems to live on various areas on the body of the host hermit crab and 'has not been observed to interact with the host while it is feeding' (Schembri in Moore, 1983).

Many of the pleustid associates of king crabs and spiny lobsters cling to the pleopods of their hosts (Table 1), a position which is not easy to reconcile with true commensalism. (NB: the *Pleusymtes* species described by Gurjanova (1938) and Marin et al. (2013) from large hermit crabs in the Sea of Japan do not have prehensile pereiopods, and probably belong in group 5). Nothing seems as yet to be known about the very interesting freshwater pendant of this type of associations, i.e., that of *Iphigenella acanthopoda* Sars, 1896 on *Astacus leptodactylus* Eschscholtz, 1823; but also *Iphigenella* has prehensile pereiopods.

The choice of location on the host is probably primarily decided by protection from water currents and predators, possibly also to areas that are less efficiently groomed by the host (pleopods!), although the prehensile pereiopods of most of these associates appear to convey adequate protection against dislodgement by grooming.

Most amphipods in this group appear to be obligate symbionts and most are quite host-specific, being found on only one, or on a few closely related host species. The exceptions are the very widely distributed *Caprella ungulina* Mayer, 1903 and *C. bathytatos* Martin and Pettit, 1998, which have been found on a considerable number of king crab hosts (and even on a spider crab).

Group 3: Egg Associates

These associates are listed in Table 2. They form a most heterogeneous group, ranging from the specialized egg predators in the Lake Baikal pachyschesid genus *Pachyschesis* to diverse tubicolous taxa, which might not really be egg-predators. In the case of some other species that have often been found among the eggs of their hosts, such as the lysianassid *Acosta* [formerly *Pardia*] *punctata* (A. Costa, 1851) from hermit crabs, and the aberrant ischyrocerid *Isaeopsis tenax* K. H. Barnard, 1916 from spiny lobsters, their biology is completely unknown. In many cases the amphipods occur primarily on other parts of the hosts (most Photidae) and thus cannot really be called 'egg associates.'

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Table 1. Amphipods living as direct associates on other crustaceans.

Amphipod taxon	Species	Host taxon	Host group	Geographic origin	Where on host	Reference
Amphilochidae	*Gitanopsis iseebi* Yamato, 1993	*Panulirus japonicus* (von Siebold, 1824)	Macrura	Japan	Branchial chambers	Yamato (1993)
	Gitanopsis paguri Myers, 1974	*Dardanus megistos* (Herbst, 1804)	Paguridea	Kenya	Body and branchial chambers	Myers (1974)
Calliopiidae	*Bouvierella carcinophila* (Chevreux, 1889)	*Chaceon affinis* (A. Milne-Edwards and Bouvier, 1894)	Portunida	Azores	On carapace	Chevreux (1927)
		(crab pots)		British Columbia	"Crab pots"	Shaw (1988)
	Dolobrotus mardeni Bowman, 1974	(lobster pots)		NE USA	"Lobster pots"	Bowman (1974)
	Oradarea longimana (Boeck, 1871)	*Macroregonia macrochira* Sakai, 1978	Majoidea	British Columbia		Shaw (1988)
Caprellidae	*Caprella bathytatos* Martin and Pettit, 1998	*Macroregonia macrochira* Sakai, 1978	Majoidea	British Columbia	Mouthparts	Marin and Pettitt (1998)
		Lithodes santolla (Molina, 1782)	Lithodidea	Uruguay	"Clinging to"	Verdi and Celentano (2008)
	Caprella ungulina Mayer, 1903	*Paralomis multispina* (Benedict, 1895)	Lithodidea	California	Legs, mouthparts	Wicksten (1982), Baldinger (1992)
		Lithodes aequispinus Benedict, 1895	Lithodidea	Sea of Okhotsk	Mouthparts	Takeuchi et al. (1989)
				Japan	"Clinging to"	Takeuchi et al. (1989)
		Neolithodes asperrimus K. H. Barnard, 1946	Lithodidea	South Africa	On appendages	Griffiths (1977)
		Paralomis formosa Henderson, 1888	Lithodidea	Brazil	"Together with"	Sittrop and Serejo (2006)
Iphigenellidae	*Iphigenella acanthopoda* Sars, 1896	*Astacus leptodactylus* Eschscholtz, 1823	Macrura	Caspian Sea		Sars (1896)
				Wolga Delta	"Clinging to"	Behning (1924)

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Table 1. (Continued.)

Amphipod taxon	Species	Host taxon	Host group	Geographic origin	Where on host	Reference
Isaeidae	*Isaea concinna* Gurjanova, 1938	"hermit crab with *Suberites*"	Paguridea	Japan Sea		Gurjanova (1951)
				Russian Far East		Kudrajschov (1968, 1972)
	Isaea elmhirsti Patience, 1908	*Homarus gammarus* (L., 1758)	Macrura	Scotland	Mouthparts, midventral sternum	Patience (1909), Williamson (1916)
				France	Mouthparts	Chevreux and Fage (1925), Toulmond and Truchot (1964)
	Isaea montagui Milne-Edwards, 1830	*Maja squinado* (Herbst, 1788)	Majoidea	W. Europe	Mouthparts	Several authors
	Pagurisaea schembrii Moore, 1983	*Aeropaguristes pilosus* (H. Milne-Edwards, 1836)	Paguridea	New Zealand	Chelipeds, walking legs and cephalothorax	Moore (1983)
	Pagurisaea spp.	hermit crabs	Paguridea	Tasmania, S. Australia	Hermit crab rinses	Vader, unpublished
Ischyroceridae	*Jassa kjetilanna* Vader and Krapp, 2005	*Paralomis granulosa* (Jacquinot, 1852)	Lithodidea	Falkland Islands	Around mouthparts and sternum	Vader and Krapp (2005)
		Eurypodius latreillii Guérin, 1828	Majoidea	Falkland Islands	On body	Vader and Krapp (2005)
Pleustidae	*Commensipleustes commensalis* (Shoemaker, 1952)	*Panulirus interruptus* (Randall, 1840)	Macrura	California	Pleopods	Shoemaker (1952)
	Domicola lithodesi Pretus and Abello, 1993	*Lithodes ferox* Filhol, 1885	Lithodidea	Namibia	Pleopods	Pretus and Abello (1993)
		Paralithodes californiensis (Benedict, 1895)	Lithodidea	Namibia	Pleopods	Pretus and Abello (1993)
	Gnathopleustes pugettensis (Dana, 1853)	various hermit crabs	Paguridea	NE Gulf of Alaska	Rinsed from hermit crabs	Hoberg et al. (1982)
	Myzotarsa anaxiphilius Cadien and Martin, 1999	*Paralithodes rathbuni* (Benedict, 1895)	Lithodidea	California	Pleopods	Cadien and Martin (1999)
Stenothoidae	*Metopelloides paguri* Marin and Selnikov, 2012	*Elassichirus cavimanus* (Miers, 1879)	Paguridea	Russian Far East	Inside gastropod shells	Marin and Shielnikov (2012)
		Pagurus pectinatus (Stimpson, 1858)	Paguridea	Russian Far East	Sponge on gastropod shells	Marin and Shielnikov (2012)
	Stenothoe symbiotica Shoemaker, 1956	*Stenocionops spinimana* (Rathburn, 1892)	Majoidea	Caribbean	"Exterior"	Shoemaker (1956), Thomas and Cairns (1984)

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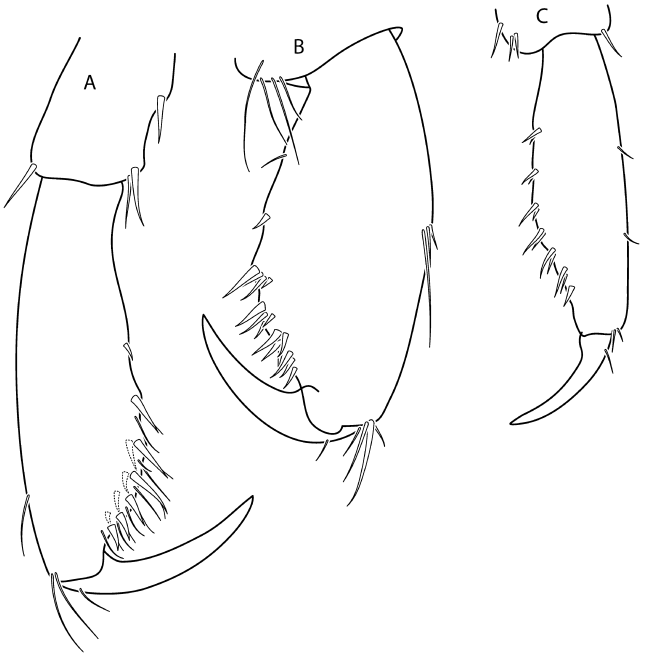

Fig. 1. Prehensile pereiopods in amphipods living in direct association with crustaceans. A, *Isaeopsis tenax*; B, *Isaea elmhirsti*; C, *Gitanopsis paguri*. Redrawn after Vader (1983).

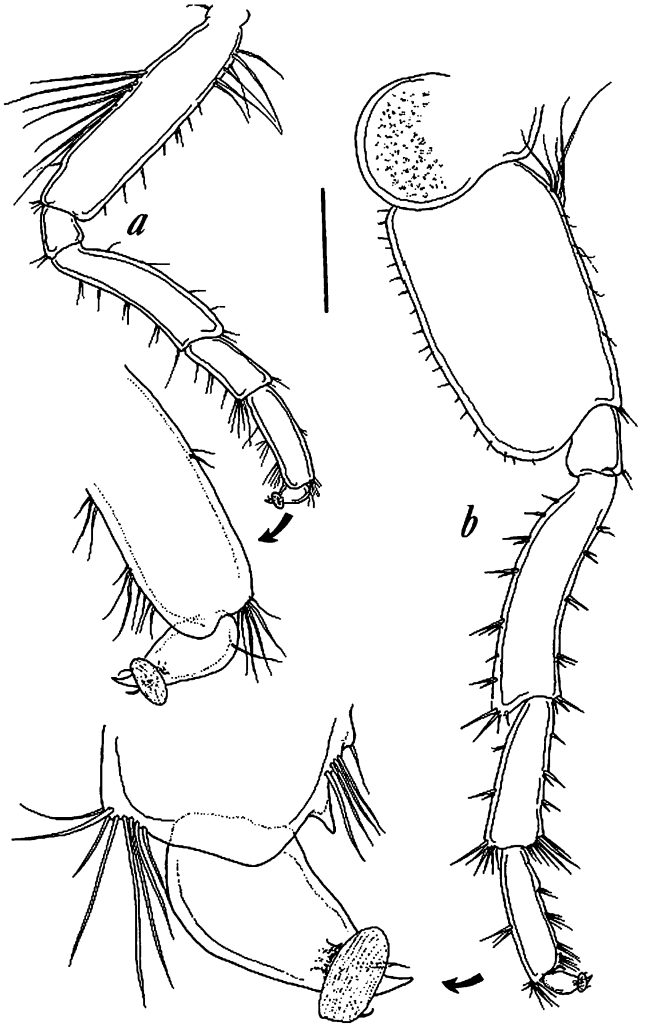

Fig. 2. Specialised sucker-like structures on pereiopods of *Myzotarsa anaxiphilius* Cadien and Martin, 1999. Redrawn after Cadien and Martin (1999).

The many species of *Pachyschesis* (Takhteev, 2000) are almost all species-specific symbionts on other amphipods of the Baikal Sea; they live in the marsupium of their hosts and their mouthparts (Fig. 3) are clearly specialized for piercing the eggs of the hosts (Takhteev and Mekhanikova, 1993; Mekhanikova, 2010). A somewhat similar specialization may have occurred in the pelagic cebocarid *Paracyphocaris praedator* Chevreux, 1905 that has been found in the marsupium of *Oplophorus* shrimps (Bowman and Wasmer, 1984); those authors consider these amphipods to be egg-mimics, but they may as well be egg-predators. Virtually all Cebocaridae are of largely unknown biology (Lowry and Stoddart, 2011) but most have prehensile pereiopods and they may well have a similar biology as *Paracyphocaris*.

In the case of Ischyroceridae, their reputation as egg-predators rests largely on the paper by Kuris et al. (1991), who examined samples of the red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), from many different localities in Alaska, infested with both various Nemertea and the amphipod *Ischyrocerus* sp. The authors showed considerable egg-mortality in the king crabs and also found rests of egg membranes in the digestive system of the amphipods. They concluded that both the nemerteans and the amphipods were important egg predators, but do not seem to have realized the possibility that the nemerteans were the main predators and that the amphipods just fed on the ruined eggs. The association between *Ischyrocerus* spp. (mainly *I. commensalis* Chevreux, 1900) and red king crabs has in recent years been studied in a long series of papers by Dvoretsky and Dvoretsky (2009a, b, c, 2010, 2011a, b, 2012) and Dvoretsky et al. (2007). Their conclusion is that the amphipods in the Barents Sea area do not feed on eggs; they are mostly distributed on the gills (juveniles) and on the mouthparts (adults) of the crabs and feed on the host's food remains, i.e., as true commensals. Also Steele et al. (1986), who found *Ischyrocerus commensalis* and the photid *Podoceropsis inaequistylis* Shoemaker, 1930 on spider crabs in Newfoundland, concluded with a commensal lifestyle. The same, or detritus-feeding, may be the case in the other *Podoceropsis* species found on spider crabs and king crabs (Table 2). Dick et al. (1998) reported large numbers of what they call "tube-living amphipods" on the Tanner crab *Chionoecetes bairdi* Rathbun, 1924 from Kodiak Island, Alaska; these may well also have been species of *Ischyrocerus*. The domicolous amphipods in this group seem to be less species-specific than the amphipods in group 1, and in many cases they are not obligate symbionts either. In the case of *Paramoera falklandica* Vader and Krapp, 2005, it is unknown whether this species only occurs on the crustacean hosts, or is a normal part of the local bottom-fauna.

A very special case is that of the Ponto-Caspian behningiellid *Cardiophilus baeri* Sars, 1896, a species that as adult lives as a symbiont in the mantle cavity of cardiid bivalves (Mirjazani and Vonk, 2006), but which as juveniles has been several times found in the marsupium of *Corophium* species (Osadchikh, 1977); little is known about its biology.

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Table 2. Amphipods found associated with the eggs of other crustaceans.

Amphipod taxon	Species	Host taxon	Host group	Geographic origin	Reference	Comment
Behningiellidae	*Cardiophilus baeri* Sars, 1896	*Chelicorophium curvispinum* (Sars, 1895)	Amphipoda	Black Sea	Osadchikh (1977)	In marsupium
		Chelicorophium spinulosum (Sars, 1895)	Amphipoda	Black Sea	Osadchikh (1977)	In marsupium
Cebocaridae	*Paracyphocaris praedator* Chevreux, 1935	*Oplophorus novazeelandiae* (De Man, 1931)	Caridea	Off Chile	Bowman and Wasmer (1984)	In marsupium
Ischyroceridae	*Isaeopsis tenax* K. H. Barnard, 1916	*Jasus lalandii* H. Milne-Edwards, 1837	Palinura	S. Africa	Barnard (1916)	Among egg clusters
	Ischyrocerus anguipes (Krøyer, 1838)	*Paralithodes camtschaticus* (Tilesius, 1815)	Lithodidea	Barents Sea	Dvoretsky and Britayev (2009)	Gills, mouthparts
	Ischyrocerus commensalis Chrevreux, 1900	*Chionoecetes opilio* (Fabricius, 1788)	Majoidea	Newfoundland	Steele et al. (1986)	Various places on body and legs
		Paralithodes camtschaticus (Tilesius, 1815)	Lithodidea	N. Norway	Johnsen and Vader, unpublished, Haugen et al. (1998)	Amongst eggs
		Hyas araneus (L., 1758)	Majoidea	N. Norway	Johnsen and Vader, unpublished, Haugen et al. (1998)	Amongst eggs
		Paralithodes camtschaticus (Tilesius, 1815)	Lithodidea	Barents Sea	Dvoretsky and Dvoretsky – several papers	Various places on host
	Ischyrocerus sp.	*Paralithodes camtschaticus* (Tilesius, 1815)	Lithodidea	Alaska	Kuris et al. (1991)	Amongst eggs
Lysianassidae	*Acosta punctata* (Costa, 1851)	*Pagurus prideaux* Leach, 1815	Paguridea	Mediterranean	Ruffo (1987)	Amongst eggs
		Petrochirus pustulatus (H. Milne-Edwards, 1848)	Paguridea	Senegal	Ruffo (1987)	Amongst eggs
Pachyschesidae	*Pachyschesis branchialis* (Dybowsky, 1874)	*Brachyuropus grewingkii* (Dybowsky, 1874)	Amphipoda	Lake Baikal	Takhteev and Mekhanikova (1993)	In marsupium
	P. bazikalovae Karaman, 1976	*Garjajewia cabanisii* (Dybovsky, 1874)	Amphipoda	Lake Baikal	Takhteev and Mekhanikova (1993)	In marsupium
	P. 15 further species	various gammarids	Amphipoda	Lake Baikal	Takhteev (2000)	In marsupium
Photidae	*Gammaropsis monodi* (Schellenberg, 1931)	*Eurypodium latreillei* Guerin, 1828	Majoidea	Magellan Straits	Schellenberg (1931)	
		Eurypodium latreillei Guerin, 1828	Majoidea	Falkland Islands	K. H. Barnard (1932) Vader and Krapp (2005)	On carapace and legs
		Paralomis granulosa (Jacquinot, 1852)	Lithodidea	Falkland Islands	Vader and Krapp (2005)	On carapace and legs
	Podoceropsis chionoecetophila Conlan, 1983	*Chionoecetes tanneri* Rathburn, 1893	Majoidea	Oregon	Conlan (1983)	Amongst eggs
	Podoceropsis grasslei (Soto and Corona, 2007)	*Neolithodes diomediae* (Benedict, 1894)	Lithodidea	Gulf of California	Soto and Corona (2007)	On carapace
	Podoceropsis inaequistylis Shoemaker, 1930	*Paralithodes camtschaticus* (Tilesius, 1815)	Lithodidea	Newfoundland	Steele et al. (1986)	Base of walking legs, marginal groove of carapace
		Hyas araneus (L., 1758)	Majoidea	Newfoundland	Steele et al. (1986)	Base of walking legs, marginal groove of carapace
Pontogeneiidae	*Paramoera falklandica* Vader and Krapp, 1005	*Paralomis granulosa* (Jacquinot, 1852)	Lithodidea	Falkland Islands	Vader and Krapp (2005)	On carapace and legs
		Eurypodium latreillei Guerin, 1828	Majoidea	Falkland Islands	Vader and Krapp (2005)	On carapace and legs

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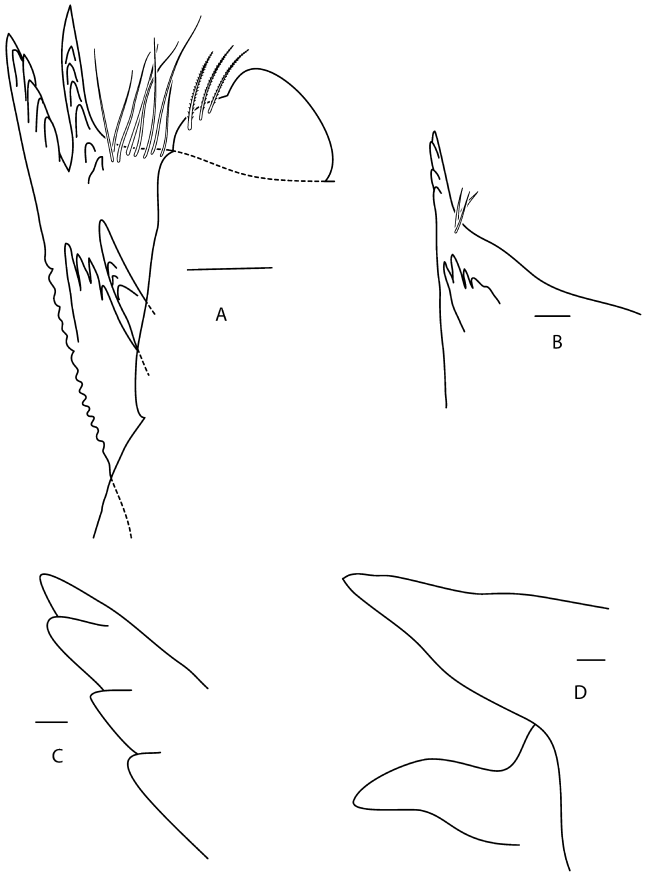

Fig. 3. Specialised mandible for piercing eggs in *Pachyschesis bazikalovae* Karaman, 1976 in Lake Baikal. Redrawn after Mekhanikova (2000).

Group 4: Associates of Infaunal Crustaceans

This is a group that could be much more common than we think in areas with a diverse and stable infauna. In the same way that various *Urothoe* have been found to occur in the burrows of *Arenicola* (Lackschewitz and Reise, 1998), other infaunal amphipods probably live in crustacean burrows. Fox and Bynum (1975) found an undescribed species of the liljeborgiid *Idunella* in the burrows of the mud shrimp *Upogebia affinis* (Say, 1818); this species is apparently still undescribed. Also, diverse *Listriella* species often live together with burrowing invertebrates (Vader, 1996), and we predict that similar associations with burrowing decapods will be discovered also in other genera, such as *Urothoe*. The associates in such cases can be called 'energy commensals': they live in an oxygenated and food-enriched environment where they are more or less safe from predators.

Interestingly, there is also in this group a freshwater equivalent: the paraleptamphopid *Rudolphia macrodactylus* Grosso and Peralta, 2009 is found in the burrows of the crayfish *Virilastacus rucapihuelensis* Rudolph and Crandall, 2005 in Chile (Grosso and Peralta, 2009).

Group 5: Amphipods Living on or in Gastropod Shells Tenanted by Hermit Rrabs

Those amphipod species that live directly on the hermit crabs themselves, which usually have prehensile pereiopods, have been included in group 2, and the amphipods from the often luxuriant epifauna of the gastropod shells tenanted by hermit crabs belong in group 1. There is, however, a further large group of amphipod species that has been found on or in the shells tenanted by hermit crabs, where in most cases we do not as yet know the nature of the association. There are a number of surveys listing associates of hermit crabs from western Europe (Chevreux, 1908; Jensen and Bender, 1973), the Mediterranean (Cuadras and Pereira, 1977; Patzner, 2004), eastern Canada (Besner, 1976), Alaskan waters (Hoberg et al., 1982), and eastern Australia (Vader, 1996; Vader and Myers, 1996). Williams and McDermott (2004) have published a general survey on hermit crab biocoenoses, where many amphipods are listed; in their later paper on 'the unwanted guests of hermits' (McDermott et al., 2010) they concentrate on undoubted parasites and all amphipods are omitted.

Liljeborgia spp. are often found (Vader, 1996) in the top whorls of shells tenanted by hermit crabs (Fig. 4), and a number of other species have been described as 'associated with hermit crabs' (Vader, 1971; McGrath, 1978; Moore, 1985; Vader and Myers, 1996; Marin et al., 2013). Some domicolous amphipod species make their tubes around the mouth of the shells, while others, e.g., the stenothoids, seem to be primarily associated with the hydroids covering the shells. All these species have had to be excluded from this survey because too little is known about them and the boundaries with the species in group 1 are often very vague.

Discussion

Amphipod symbionts of Crustacea are very widely and seemingly almost randomly spread among the various amphipod clades, and there is little doubt that associations between amphipods and crustaceans are generally of no great antiquity and have developed independently many times in many different evolutionary lineages. A convincing argument for this is the case of the Caspian *Iphigenella acanthopoda* Sars, 1896 that lives on freshwater crayfish in a way apparently directly comparable to the associations of for example *Gitanopsis iseebi* Yamato, 1993 (Amphilochidae) or *Commensipleustes commensalis* (Shoemaker, 1952) (Pleustidae) on *Panulirus* spp. in the sea. Also the occurrence of basically similar associations among *Caprella* spp. (Table 1) is proof of the several convergent pathways to the 'lice on large crabs' niche.

Most hosts seem to be slow-moving, often ornamented king crabs, hermit crabs, and spider crabs, although there are also a few lobsters and the swimming crab *Chaceon affinis* (A. Milne-Edwards and Bouvier, 1894) (also slow-moving); we know of no records of amphipod symbionts on other Brachyura. It is as yet completely unknown whether this difference is connected with the diet of the hosts, the texture and ornamentation of their carapace, or differences in grooming behaviour and intensity.

The group of direct associates might well have arrived at this niche by different routes. Especially the Calliopiidae and the atylopsine Pleustidae seem to be taxonomically closely related to more general scavengers that are not permanently associated with any hosts, such as *Leptamphopus sarsi* Vanhöffen, 1897 (Vader, 1972) and *Dolobrotus mardeni* Bowman, 1974. As scavenging could be a pathway towards

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Fig. 4. *Liljeborgia aequabilis* Stebbing, 1888 from the hermit crab *Dardanus arrosor* (Herbst), off Bermagui NS Wales, Australia. Photo W. Vader.

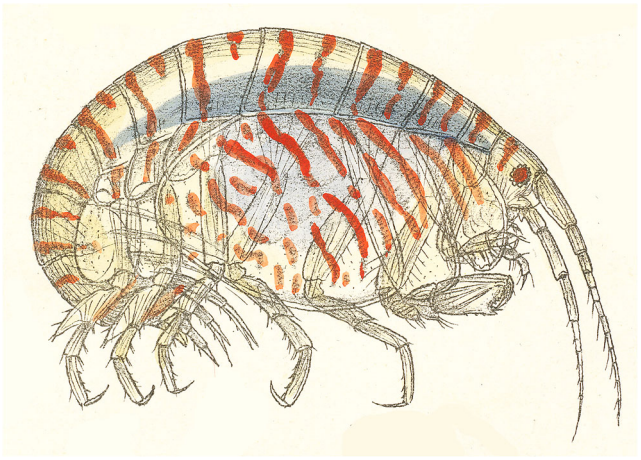

Fig. 5. Hand coloured drawing of *Stenula rubrovittata* as *Metopar* by G. O. Sars in his Amphipod monograph of 1890-1895.

association with large invertebrates, it is unexpected to find that the main group of amphipod scavengers, a group well-known from other associations, Lysianassoidea, is virtually absent among the associates of large Crustacea. The only exceptions known to us are *Acosta punctata* (A. Costa, 1851) of the Mediterranean and West Africa that is often found among the egg-clusters of hermit-crabs and even mimics them in colour (Della Valle, 1893; Ruffo, 1987), and probably *Paracyphocaris praedator* Chevreux, 1905 – and quite possibly other cebocarids – that are accused of being egg predators of pelagic shrimps (Bowman and Wasmer, 1984).

The amphilochids, stenothoids, and also the caprellids may have arrived via the route of association with the epifauna of the large decapods, especially hydroids and bryozoans. The isaeids might have come via the same route, but their relatives are also very commonly represented among the next group, the egg associates, which may well be the older type of association, even though the amphipod species in this group are usually less species-specific than the direct associates.

Among the egg associates domicolous forms predominate. The *Podoceropsis* species are probably mainly general deposit feeders; they are also often found on and in the shells of hermit crabs, both in Alaska (Hoberg et al., 1982), in western Europe (Vader, 1971; Fernandez-Laborans et al., 2013), and in Australia (Vader, personal observation). The studies by Dvoretsky and Dvoretsky (2010) show that the same is the case in the *Ischyrocerus*-associates of king crabs.

An intriguing problem is that of the colour of amphipods that are associated with Crustacea, particularly with hermit crabs; many are uncommonly colourful, most often with a pattern of reddish colours (Figs. 4, 5) (Della Valle, 1893; Myers, 1974; McGrath, 1978; Vader and Myers, 1996; Marin and Sinelnikov, 2012). The obvious explanation at first thought is that these colours serve as camouflage on the usually also colourful and reddish hosts. This presupposes, however, that there are predators that 'delouse' hermit crabs and other large crustaceans and that hunt by eye. Especially baffling is the case of the spectacularly patterned *Liljeborgia*'s of hermit crabs from Australia, New Zealand, Japan and California (Fig. 4) (Vader, 1996), as these amphipods almost invariably are found 'behind the host,' in the top whorls of the gastropods tenanted by the hermit crab, where it is dark and where one would suppose they would be well protected, so that colour would be largely immaterial.

What we need most of all, however, in order to further unravel the historic evolution of the associations between amphipods and large Crustacea, is thorough biological studies of the food, dispersal, and life cycle of some common associated amphipod species. Except for the work of the Dvoretsky brothers, such studies are until now completely absent.

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