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Amphipods and sea anemones, an update

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ABSTRACT

We present an updated survey of the Amphipoda that live in association with sea anemones. These amphipods can be divided into four groups: 1) symbiotic amphipods using sea anemones mainly for protection, but feeding largely independently; 2) amphipods feeding on sea anemones, but not permanently associated; 3) symbiotic amphipods living permanently among the tentacles of the sea anemones; and 4) symbiotic amphipods living permanently in the gastrovascular cavity of the sea anemones. Contrary to previous speculations, it appears that the amphipods in groups 3 and 4 mainly feed on host tissue, and the anemone-eating amphipods can therefore generally be classified as micropredators (group 2), ectoparasites (group 3), and almost endoparasites (especially those species in group 4 that spend their entire life cycle inside their hosts).

Although the associates in the latter two groups show various minor morphological, reproductive, and physiological adaptations to the symbiosis, these associations evolved many times independently. We provide new information on feeding ecology and a discussion of the evolution of these associations.

Key Words: Cnidaria, ectoparasitism, endoparasitism, micropredation, symbiosis

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INTRODUCTION

The first author published almost 40 years ago a survey of the associations between amphipods and sea anemones (Vader, 1983). The time seems ripe to update this survey as several new associations have been discovered, as well as new data collected on the nature of some of them. It follows similar surveys on amphipod associations with molluscs and with crustaceans (Vader & Tandberg, 2013, 2015). As much of the new information available on amphipod associations with sea anemones are on the diet of the amphipods, we present an updated classification of these associations from an ecological point of view.

Sea anemones are hosts for many symbionts. Their symbiosis with anemonefishes is well known and has been much studied (e.g., Fautin, 1991), while there also is an extensive literature about the associations between sea anemones and various decapod crustaceans, especially hermit crabs (cf. Ross, 1983), spider crabs (Wirtz & Diesel, 1983; Calado *et al.*, 2002; Briones-Fourzán *et al.*, 2012;

Landmann *et al.*, 2016), porcelain crabs (e.g., Valdivia & Stotz, 2006), and shrimps (e.g., Wirtz, 1997). Mysids (e.g., Wittmann, 2008, 2013) and copepods (e.g., Bouligand, 1966; Vader, 1970c; Gotto, 1979, 1993; Humes, 1982; Lønning & Vader, 1984) also regularly occur as symbionts of sea anemones.

At first sight sea anemones do not seem to be ideal hosts for amphipod associates. They are active predators that often feed on prey in the same size range as the associates, which they catch with the help of toxic nematocysts and clinging spirocysts. Digestion is largely extracellular and large amounts of proteolytic enzymes, also containing chitinases, are secreted into the gastrovascular cavity. In addition, most sea anemones produce a copious amount of mucus, creating further problems for would-be associates. Once symbionts have managed to overcome these barriers, however, sea anemones offer many advantages as hosts: they are very long-lived animals and offer excellent protection, even to large associates such as hermit crabs and shrimps (e.g., Ross, 1971, 1974; Suzuki & Hayashi, 1977). They catch more food than they can digest and

eat quickly, and ejected food remains are still of high nutritive value and are eaten by many symbionts. The copious mucus is in fact a high-quality food source and used as such by many copepods (e.g., Gotto, 1979; Lønning & Vader, 1984), pycnogonids, as well as by many amphipods.

As was discussed by Vader (1983), the amphipods that associate with sea anemones seem to be utilising the anemones very differently. Since 1983, much additional information about the feeding biology of several of the known associates has come about. We still think that amphipods associated with sea anemones can roughly be divided into four groups:

- Group 1. Amphipods using sea anemones mainly for protection, but feeding largely independently.
- Group 2. Amphipods feeding on sea anemones, but not permanently associated.
- Group 3. Amphipods living permanently among the tentacles of the sea anemones.
- Group 4. Amphipods living permanently in the gastrovascular cavity of the sea anemones.

In addition, of course, amphipods also play a more or less important role as food for sea anemones, a topic that will not be dealt with here.

TYPES OF ASSOCIATIONS

Group 1. Amphipods using sea anemones primarily for protection, but feeding largely independently

There are as yet not many recorded cases of amphipods belonging to this group. Most of these records, probably only the tip of the iceberg, are in fact very similar to the many cases where otherwise free-living shrimps (e.g., Stevens & Anderson, 2000; Jonsson *et al.*, 2001) and spider crabs (Schrieken, 1966; Hartnoll, 1970; Acuña *et al.*, 2003; Castro, 2015) have been found sheltering near large sea anemones. The symbionts find their own food in all these cases, independently from the sea anemones, and the association seems to be a temporary and not very specific one (Weinbauer *et al.*, 1982). Usually this type of associations is facultative: the species concerned are also found free-living or together with other hosts. They primarily obtain protection from their anemone hosts. (It must be admitted, however, that there are very few data on the diet of the amphipods concerned, and part of their food may therefore possibly in some cases be gained from the anemone hosts or they prey.)

This is clearly also the case with the amphipods in this group. *Caprella acanthifera* Leach, 1814 is normally free-living (Krappe-Schickel & Vader, 1998), but was reported by Stroobants (1969; see also Patzner, 2004) from the Mediterranean Sea moving with impunity among the tentacles of the sea anemones *Anemonia sulcata* (Pennant, 1777) and *Aiptasia couchii* Gosse, 1858. *Abludomelita obtusata* (Montagu, 1813) was similarly reported by Hartnoll (1970) from the Irish Sea as an associate of *Anemonia sulcata*; again, the amphipods, although they elicited some initial response from the tentacles, soon moved around unhindered, while e.g. different species of *Gammarus* Fabricius, 1775 were quickly caught and swallowed by the anemones. There is a single record of *A. obtusata* collected from another sea anemone, *Urticina felina* (Linnaeus, 1761) from the Scilly Islands (Sanderson, 1973). Again, *A. obtusata* is often found free-living, but it is also well known as associate of various echinoderms, especially starfishes (Vader, 1978).

There are also various pleustid amphipods probably belonging to this group, but details are as yet largely unknown (see Vader, 1983). *Chromopleustes lineatus* Bousfield & Hendrycks, 1995 has been reported from species of *Tealia* Gosse, 1858 in California, and the first author has seen both this species and another unidentified pleustid on *Tealia* sp. in the same area. Pleustid amphipods

belonging to species of *Stenopleustes* Sars, 1893 and *Pleusymtes* J.L. Barnard, 1969 have also been regularly found as associates of gorgonians (e.g. Brattegard & Vader, 1972; Gamo & Shinpo, 1992; Kumagai & Aoki, 2003; Buhl-Mortensen & Mortensen, 2004, 2005; Myers & Hall-Spencer, 2003; Kumagai, 2006), and of sponge-hermit crab symbioses (Gurjanova, 1938; Marin *et al.*, 2013). The diet of the pleustid amphipods is known in any of these cases, and there is generally little data on pleustid diets. Kodama *et al.* (2020) suggest that *Dactylopleustes yoshimurai* Tomikawa, Hendrycks & Mawatari, 2004, associated with the sea urchin *Strongylocentrotus intermedius* (Agassiz, 1864), feeds on host tissue. If the same should prove to be the case in the pleustid species associated with sea anemones, they would be best classified in group 2 among the amphipods feeding on sea anemones, but not permanently associated with them (see below) because as far as known, these associations are not obligatory.

A special case is that described by Moore & Cameron (1999), where the tube-building photid amphipod *Photis longicaudata* (Bate & Westwood, 1862), normally free-living, was found in high density on the outside rim of the tubes of the ceriantharian *Cerianthus lloydi* Gosse, 1859 in shallow water in the Clyde Sea area of Scotland. These authors speculate that also in this case protection from predators is the main advantage for the amphipods.

Group 2. Amphipods feeding on sea anemones, but not permanently associated with them

Surprisingly little is known about the food and feeding habits of most amphipod species, although a few authors have furnished many noteworthy data (Enequist, 1949; Schiecke, 1973; Guerra-García *et al.*, 2014). Many species of Stegocephalidae appear to feed on Cnidaria. The pelagic *Parandania boeckii* (Stebbing, 1888) feeds on medusae (Moore & Rainbow, 1989, 1992; Coleman, 1990), while *Stegocephaloides christianiensis* (Boeck, 1871) and *Andaniopsis nordlandica* (Boeck, 1871) clearly also are largely cnidarian feeders (Moore & Rainbow, 1989; 1994). Not all Stegocephalidae are cnidarian specialists, however, *Andaniopsis abyssii* (Boeck, 1871) and *A. lupus* Berge & Vader, 1997 being much more generalized feeders (Moore & Rainbow, 1992; Moore *et al.*, 1994 (as *Andaniopsis* sp.)). All these species occur bathypelagically or hyperbenthonically, and they are very rarely collected together with their prey. Another cnidarian feeder is the Antarctic iphimeidiid *Maxilliphimedia longipes* (Walker, 1906) (Coleman, 1989).

A very special case is that of the family Acidostomatidae (see Stoddart & Lowry (2012) for changes in the nomenclature), where the species appear to have their mouthparts highly specialized for piercing and sucking, and thus for feeding on the column of sea anemones (Dahl, 1964). Species of *Acidostoma* Lilljeborg, 1865 are usually found apparently free-living, but a number of reports of their connection with sea anemones has nevertheless been reported: Della Valle (1893) found *A. neglectum* Dahl, 1964 on *Condylactis aurantiaca* (Della Chiaje, 1825) in the Bay of Naples, while Ansell (1969) collected the same species from *Peachia hastata* Gosse, 1855 in Scotland, and Vader (1967) found *A. obesum* (Bate & Westwood, 1861) on the large sea anemone *Actinostola callosa* (Verrill, 1882) in western Norway. Many nematocysts were found in the stomach and faeces of the amphipods in several of these cases and in some preserved samples studied by Dahl (1964). Species of *Acidostoma* therefore seem to act as 'mosquitoes of the sea,' with sea anemones as their main food source and no great host specificity.

An intriguing record is the one by Ivanova & Grebelnyi (2017), who found apparently unharmed specimens of a species of *Conicostoma* in a study of the diet of the Antarctic sea anemone *Urticinopsis antarctica* (Verrill, 1922). Some Conicostomatidae Lowry & Stoddart, 2012 may well also be more or less obligate associates (see Lowry & Stoddart 1994, as *Phoxostoma* K.H. Barnard, 1925).

Group 3. Amphipods living permanently among the tentacles of sea anemones

Little is yet known about the biology of these associations. In most cases they seem to be obligatory and quite specific: the amphipods are rarely or never found apparently free-living and occur on only a single or very few host species of sea anemones. The amphipods appear to move around on the host, and often even stay on the tentacles when the sea anemone contracts. [Elmhirst \(1925\)](#) noted, however, that an alternate host, *Tealia felina* (Linnaeus, 1767), swallowed and killed the amphipod *Stenula solsbergi* ([Schneider, 1884](#)) ‘without hesitation.’

Most of the amphipods in this group belong to Stenothoidae ([Table 1](#)). In addition, there are as yet unconfirmed reports of an *Amphilocheus* sp. on *Bartholomea annulata* (Lesueur, 1817) in Florida, of ‘*Orchomene* s.l.’ on *Metridium senile* (Linnaeus, 1767) in Alaska and California, and *Lysianopsis* sp. together with *Anthopleura elegantissima* (Brandt, 1835) ([Vader, 1983](#)); a few specimens of *Leucothoe* sp. have also been found together with sea anemones ([Vader, 1983](#)). Many amphipods have also been reported from gorgonians. Most of these amphipods are members of Stenothoidae, but various species of Pleustidae have also been found in these associations. ([Brattegard & Vader, 1972](#); [Fenwick & Steele, 1983](#); [Buhl-Mortensen & Mortensen, 2004, 2005](#)).

Some additional information is known about the symbiosis between *Stenothoe brevicornis* Sars, 1883 and its host *Actinostola callosa* (Verrill, 1882) ([Vader & Krapp-Schickel, 1996](#)), although it was difficult to recreate the association in the laboratory because of the extreme fragility of the amphipods, who tolerate very little handling. The studied population lives in the Ullsfjord north of Tromsø in Northern Norway at approximately 100 m depth. From 30 to 70% of the *Actinostola* in this area carry between 1 and 20 amphipods, with more in the larger hosts; these numbers are minima, as the amphipods are easily dislodged from their host and there will therefore have been losses during the collecting process. The amphipods apparently live their entire lives on their hosts; they live for one year, the females are iteroparous, and ovigerous females can be found all year. The broods are small (6–10 eggs) in comparison to those of free-living species of *Stenothoe* [Dana, 1852](#). The food

appears, somewhat surprisingly, to consist mainly of tentacle tissue of the host (although a single harpacticoid copepod was also found) ([Moore et al., 1994](#)), and the amphipods therefore seem mainly to live as ‘lice’ on their host. Presumably the many other associated stenothoids have a similar lifestyle, but there are no data as yet.

Nothing seems to be known about the biology of *Elasmopus calliactis* [Edmondson, 1952](#) from the Hawaiian Islands, described as an associate of the sea anemone *Calliactis armillatus* Verrill, 1928; most species of *Elasmopus* are generalist shallow water algal dwellers.

Group 4. Amphipods living permanently in the gastrovascular cavity of their host

These amphipods belong to the infraorder Lysianassida, but to three widely different families: *Aristias neglectus* [Hansen, 1887](#) in Aristiidae [Lowry & Stoddart, 1997](#), *Orchomenella recondita* ([Stasek, 1958](#)) in Tryphosidae [Lowry & Stoddart, 1997](#), and *Onisimus normani* Sars, 1890 and *O. turgidus* (Sars, 1879) in Uristidae [Hurley, 1963](#). All have been almost exclusively collected from the gastrovascular cavity of their sea anemone hosts, but there are considerable differences in their biology.

Aristias neglectus is best known as an associate of Porifera and Ascidiacea, and it has also been found inside a brachiopod ([Vader, 1970a](#)). This species was regularly found, although in small numbers, in the gastrovascular cavity of the large sea anemone *Bolocera tuediae* (Johnston, 1832) at 240 m depth in the Bergen area in Western Norway ([Vader, 1970b](#)). No ovigerous females were found. An as yet unidentified *Aristias* sp. has also been found in sea anemones on the coast of Ghana (J.B. den Hartog, personal communication). Species of *Aristias* are generally considered to be microphagous associates, although we know of no research on the subject.

Orchomenella recondita (originally described in the Antarctic genus *Allogausia* [Schellenberg, 1926](#); see [De Broyer & Vader \(1990\)](#)) spends its entire life cycle within the gastrovascular cavity of the intertidal sea anemone *Anthopleura elegantissima* (Brandt, 1835) on the coasts of California and Oregon ([De Broyer & Vader, 1990](#)). Data on its biology have been collated by [Vader \(2020\)](#). The amphipods spend their entire life cycle within the host, moulting

Table 1. Overview of known associations where amphipods live permanently among the tentacles of sea anemones. *Originally described as *Metopa solsbergi*, but transferred to *Stenula* by [Krapp-Schickel & Vader \(2015\)](#). Later research by AHST (unpublished data) gives rise to the supposition that there may be sibling species present, one in *Metopa*, the other in *Stenula*, as appears to be the case in *Metopa rubrovittata* Sars, 1883 versus *Stenula latipes* ([Chevreux & Fage, 1925](#)) ([Krapp-Schickel & Vader, 2015](#))

Amphipod associate	Sea anemone host	Location	References
<i>Parametopella antholobae</i> Krapp-Schickel & Vader, 2009	<i>Antholoba achates</i> (Drayton, 1849)	Chile	Krapp-Schickel & Vader, 2009
<i>Stenothoe barrowensis</i> Shoemaker, 1955	unknown	Point Barrow, Alaska	Shoemaker, 1955 ; Vader, 1983 .
<i>Stenothoe bartholomea</i> Krapp-Schickel & Vader, 2015	<i>Bartholomea annulata</i> (Lesueur, 1817)	Florida Keys	Vader 1983 (as <i>Stenothoe</i> n. sp.), Krapp-Schickel & Vader, 2015
<i>Stenothoe boloceropsis</i> Krapp-Schickel et al., 2015	<i>Boloceropsis platei</i> McMurrich, 1904	Chiloe Island, Chile	Krapp-Schickel et al., 2015
<i>Stenothoe brevicornis</i> Sars, 1883	<i>Actinostola callosa</i> (Verrill, 1882)	Northern Norway	Vader & Krapp-Schickel, 1996
		Newfoundland, Canada	Fenwick & Steele, 1983
	<i>Liponema multicornis</i> (Verrill, 1880)	Stellwagen Bank, Canada	Auster et al., 2011
<i>Stenula pugilla</i> Krapp-Schickel & Vader, 2015	<i>Haliactis arctica</i> Carlgren, 1921	Chukchi Sea	Krapp-Schickel & Vader, 2015 , (see Vader, 1983 , as <i>Stenothoe</i> sp.)
<i>Stenula solsbergi</i> * (Schneider, 1884)	<i>Metridium senile</i> (Linnaeus, 1767)	Western Scotland	Elmhirst, 1925
		Newfoundland, Canada	Fenwick & Steele, 1983

and reproducing there. They live for a year and the females usually have two consecutive broods of 8–14 young, considerably less than in free-living congeners of similar size. The diet of *O. recondita* has not yet been elucidated. *Orchomenella recondita* has almost never been found in any other intertidal sea anemone on the California coast, in spite of extensive collecting (Lønning & Vader, 1984; Vader, 2020).

Onisimus normani Sars, 1891 was originally described by Sars (1890–95) from northern Norway, but it was later found to have its main distribution area in western Norway, north to about 68°N (W. Vader *et al.*, unpublished data). The species has later been reported from both the western Atlantic Ocean and from the northeastern Pacific Ocean, but Johnsen (2002) has shown that these populations in reality represent two different, as yet undescribed taxa, and that the species of *Onisimus* Boek, 1871 from sea anemones in northern Norway, earlier also considered to be *O. normani*, in reality belong to the almost forgotten *O. turgidus*, originally described from the Barents Sea.

O. normani was studied in western Norway, primarily in the 680m deep Korsfjorden near Bergen, where it was found in numbers inside the large mud sea anemone *Bolocera tuediae* (Vader, 1967, 1970b, 1983; Vader & Lønning, 1973). The amphipods appear to be obligatory and species-specific associates of *Bolocera*; they infest the host as juveniles and leave it as adults 1 1/2 years later; no ovigerous females have ever been found yet. The diet of *O. normani* has not yet been elucidated, but presumably the species feeds on the mesenteria of its host, as shown for the closely related *O. turgidus*.

Onisimus turgidus was studied in the Ullsfjord north of Tromsø, the same area where we also studied *Stenothoe brevicornis* (Vader, 1975; Moore *et al.*, 1994 (both as *O. normani*), W. Vader *et al.*, unpublished data). The amphipods in this area are most often found inside *Actinostola callosa* and only in small numbers in *Bolocera tuediae*, the exclusive host of *O. normani*. Its life cycle seems to be quite similar to that of *O. normani*; ovigerous females have not yet been found, while both species are parasitized by the cryptoniscid isopod *Parapodascon* Hansen, 1916. Moore *et al.* (1994) studied the diet of *O. turgidus* (sub. nom. *O. normani*) and found it to be a browser on the mesenterial filaments of its host.

DISCUSSION

The reported amphipod species in group 1 (protection only) are probably only a minority of such cases in nature. As is the case for similar associations involving decapods, few adaptations seem to have been necessary, and the species concerned are mainly found free-living and in other associations. In several cases (Stroobants, 1969; Hartmoll, 1970) the loosely associated amphipods are nevertheless reported to have been able to move among the host's tentacles unhindered.

The obligate symbionts of sea anemones (groups 3 and 4) almost all belong to either the Stenothoidea (mainly group 3) or Lysianassida (mainly group 4), but within these taxa the symbiosis with sea anemones appears to have evolved independently many times, as the symbionts are not close relatives, but scattered throughout particular taxonomic groups. The many stenothoid associates in group 3 are not each other's close relatives, and the lysianassids in group 4 even belong to different families.

In the earlier survey (Vader, 1983) it was surmised that the amphipod associates in groups 3 and 4 were mainly commensals, and that their diet consisted largely of 'host secretions and the semidigested prey of the hosts.' Subsequent research (Moore *et al.*, 1994) has shown that at least *Stenothoe brevicornis* and *Onisimus turgidus* largely feed on host tissue, and the same may well be true for many other Stenothoidea in group 3 and for *Orchomenella recondita* in group 4. These associates are therefore not commensals, and as such do not merely share food with their hosts,

but rather must be considered micropredators. We therefore suggest that group 2 may be classified as micropredators, group 3 as ectoparasites, and that group 4 may be considered close to endoparasites, especially for those species that spend their entire life cycle inside their hosts.

The number of morphological adaptations is modest among amphipod symbionts. Clearcut morphological adaptations in the mouthparts are only found in Acidostomatidae (and Conicostomatidae?), both in group 2, where these form a triangular bundle and are specialized for piercing and sucking.

A further obvious adaptation in most symbionts of sea anemones is the general paucity of setosity, probably connected to the danger of entanglement in mucus on or in the hosts. A less obvious trait, prevalent in Stenothoidea and Lysianassoidea, is the much-reduced sexual dimorphism in the obligate symbionts. There is little need for swimming males in species that spend almost their entire life as inquilines. The males of *Orchomenella recondita* have short second antennae (De Broyer & Vader, 1990), and even in the not-all-that-motile stenothoids, in which family sexual dimorphism usually is considerable, it is much reduced in many anemone symbionts as in the males of *Stenothoe brevicornis*, which were long considered as unknown (Vader & Krapp-Schickel, 1996). Sexual dimorphism is very slight in *S. boloceroopsis* (Krapp-Schickel *et al.*, 2015), while it is considerable, as is normal for the genus, in *Parametopella antholobae* (Krapp-Schickel & Vader, 2009). We can only speculate that stenothoids associated with sea anemones are less territorial than other associated stenothoids, who seem to be more territorial (Vader & Tandberg, 2013 (associations with molluscs) and Vader & Tandberg, 2015 (associations with crustaceans)). One reason for this might be that there is more space to share in a sea anemone than in a mollusc or on a crustacean.

Sea anemones are predators and often feed on prey of the same size-range as the amphipod associates. No acclimatization behaviour, as is well known from fish associates (Fautin, 1991) has ever been shown for amphipod associates, and all the available evidence suggests that in this case the adaptations are not so much behavioural, but rather physiological and/or biochemical. Vader & Lønning (1973) have shown, in a series of experiments, that when associated and free-living amphipods are kept together confined within the gastrovascular cavity of the sea anemone host, the free-living species quickly die and are digested, while most symbionts survive unharmed. This 'immunity' is not restricted to the proper host, but exists for many sea anemones (Vader & Lønning, 1973; Vader, 2020). Many individuals of *Orchomenella recondita*, however, were killed inside the corallimorpharian *Corynactis californica* Carlgren, 1936 (Vader, 2020). This difference persists, when the amphipods are tested in extracts from the mesenterial filaments, which contain proteolytic enzymes and chitinases (Vader & Lønning, 1973). The mechanism of this 'immunity' remains unknown.

There also appear to be reproductive adaptations. Many 'endocommusal' spider crabs have an enlarged pleon and higher fecundity than free-living relatives of the same size (Patton, 1979). The same is true for parasitic and commensal copepods (Gotto, 1962, 1979). But the opposite condition seems to apply to amphipod symbionts of sea anemones. Both in *Orchomenella recondita*, in contrast to free-living species of *Orchomenella* (De Broyer & Vader, 1990; Vader, 2020), and in *Stenothoe brevicornis*, in contrast to other species of *Stenothoe* (Vader & Krapp-Schickel, 1996), the sea anemone symbionts have clearly lower fecundity (as measured by number of eggs compared to body length) than free-living congeners. The low fecundity of the associated amphipods is probably made possible by the protection afforded by the host, and by these amphipods spending their entire life cycle on or in their hosts, whereas decapods and copepods have free-swimming larvae and need to find a new host for each generation. In the case of the symbiotic species of *Onisimus*, the juveniles need to find a new host

for each generation, but in these species ovigerous females have unfortunately not yet been found.

No doubt the associations reported herein only form the tip of an iceberg of as yet undiscovered cases. We also greatly need more research on the general biology and especially the diet of the associated amphipod species, on their dispersal from host to host, and on the whereabouts of the ovigerous *Onisimus* amphipods. This is hopefully just an interim report.

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REFERENCES

- Acuña, F.H., Excoffon, A.C. & Scelzo, M.A. 2003. Mutualism between the sea anemone *Antholoba achates* (Drayton, 1846) (Cnidaria: Actiniaria: Actinostolidae) and the spider crab *Libinia spinosa* Milne-Edwards, 1834 (Crustacea: Decapoda: Majidae). *Belgian Journal of Zoology*, **133**: 85–87.
- Ansell, A.D. 1969. Association of the amphipod *Acidostoma neglectum* Dahl with the anthozoan *Peachia hastata*. *Journal of Natural History*, **3**: 345–347.
- Auster, P.J., Heinonen, K.B., Watling, L., Parrish-Kuhn, C., Heupel, E. & Lindholm, J. 2011. A rare deep water anemone and its associates in the Stellwagen Bank National Sanctuary (Gulf of Maine, north-west Atlantic). *Marine Biodiversity Records*, **4**: e19 [doi: 10.1017/S1755267211000200].
- Barnard, J.L. 1969. The families and genera of marine gammaridean Amphipoda. *Bulletin of the United States National Museum*, **271**: 1–535.
- Barnard, K.H. 1925. Contributions to the Crustacean Fauna of South Africa n° 8. Further Additions to the List of Amphipoda. *Annals of the South African Museum*, **20**, 5: 319–380, pl. 34.
- Bate, C.S., Westwood, J.O. 1861. *A history of British sessile-eyed Crustacea, Parts 1–3*. John Van Voorst, London.
- Bate, C.S., Westwood, J.O. 1862. *A history of British sessile-eyed Crustacea, Parts 4–10*. John Van Voorst, London.
- Berge, J. & Vader, W. 1997. Atlantic and Mediterranean species of the genus *Andaniexis* Stebbing (Amphipoda: Stegocephalidae). *Journal of Natural History*, **31**: 1429–1455.
- Boeck, A. 1871. Crustacea Amphipoda Borealia et Arctica. *Forhandlinger i Videnskabs-Selskabet i Christiania*, **1870**: 83–280.
- Bouligand, Y. 1966. Recherches récentes sur les Copepodes associées aux Anthozoaires. *Symposium of the Zoological Society, London*, **16**: 267–306.
- Bousfield, E.L. & Hendrycks, E.A. 1995. The Amphipod family Pleustidae on the Pacific coast of North America. Part III. Subfamilies Parapleustinae, Dactylopleustinae and Pleusirinae: Systematics and distributional ecology. *Amphipacific*, **2**: 65–133.
- Brattegard, T. & Vader, W. 1972. A collection of Peracarida from Møre and Romsdal, northwestern Norway. *Sarsia*, **49**: 33–40.
- Briones-Fourzán, P., Pérez-Ortiz, M., Negrete-Soto, E., Barradas-Ortiz, C. & Lozano-Álvarez, E. 2012. Ecological traits of Caribbean sea anemones and symbiotic crustaceans. *Marine Ecology Progress Series*, **470**: 55–68.
- Buhl-Mortensen, E.L. & Mortensen, P.B. 2004. Crustaceans associated with the deep-water gorgonian corals *Paragorgia arborea* (L., 1758) and *Primnoa resedaeformis* (Gunn., 1763). *Journal of Natural History*, **38**: 1233–1247.
- Buhl-Mortensen, E.L. & Mortensen, P.B. 2005. Symbiosis in deep-water corals. *Symbiosis*, **37**: 33–61.
- Calado, R.J., Dionisio, G. & Dinis, M.T. 2002. Decapod crustaceans associated with the snakelocks anemone *Anemonia sulcata*. Living there or just passing by? *Scientia Marina*, **71**: 287–292.
- Castro, P. 2015. Symbiotic Brachyura. In: *Treatise on zoology – anatomy, taxonomy, biology. The Crustacea* (P. Castro, P.J.F. Davie, D. Guinot, F.R. Schram & J.C. von Vaupel Klein, eds.), Vol. **9C-II**, pp 543–582. Brill, Leiden & Boston.
- Chevreaux, E. & Fage, L. 1925. Amphipodes. *Faune de France*, **9**: 1–488.
- Coleman, C.O. 1989. On the nutrition of two Antarctic Acanthonotozomatidae (Crustacea: Amphipoda). Gut contents and functional morphology of mouthparts. *Polar Biology*, **9**: 287–294.
- Coleman, C.O. 1990. Anatomy of the alimentary canal of *Parandania boeckii* (Stebbing, 1888) (Crustacea, Stegocephalidae) from the Antarctic Ocean. *Journal of Natural History*, **24**: 1573–1583.
- Dahl, E. 1964. The amphipod genus *Acidostoma*. *Zoologische Mededelingen*, **39**: 48–58.
- Dana, J.D. 1852. Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wikles e classe Reipublicae Faederatae Duce, lexit et descripsit Jacobus D. Dana, Pars III (Amphipoda n°1). *Proceedings of the American Academy of Arts and Sciences*, **2**: 201–220.
- De Broyer, C. & Vader, W. 1990. Revision and notes on the biology of *Orchomenella recondita* (Stasek, 1958), an associate of sea anemones. *Beaufortia*, **41**: 31–38.
- Della Valle, A. 1893. Gammarini del Golfo di Napoli. *Fauna Flora Golf Neapel* **20**, I–XI, 1–948, I– LIV, Pls. I– LXI.
- Edmondson, C.H. 1952. Some Central Pacific crustaceans. *Occasional Papers, Bernice P. Bishop Museum*, **20**: 183–342.
- Elmhirst, R. 1925. Associations between the amphipod genus *Metopa* and coelenterates. *Scottish Naturalist*, **1925**: 149–150.
- Enequist, P. 1949. Studies on the soft-bottom amphipods of the Skagerak. *Zoologiska Bidrag från Uppsala*, **28**: 297–492.
- Fabricius, J.C. 1775. Systema Entomologiae, sistens Insectorum Classes, Ordines, Genera, Species, adjectis Synonymis, Locis, Descriptionibus, Observationibus. Officina Libraria, Kortii, Flensburgi et Lipsiae.
- Fautin, D.G. 1991. The anemonefish symbiosis. What is known and what not. *Symbiosis*, **10**: 23–46.
- Fenwick, G. D. & D. H. Steele. 1983. Amphipods of Placentia Bay, Newfoundland. *Memorial University Newfoundland, Occasional Papers in Biology*, **7**: 1–22.
- Gamo, S. & Shinpo, Y. 1992. A new gammaridean amphipod *Pleusymtes symbiotica*, ectosymbiotic with a Japanese gorgonacean octocoral, *Meliithaea flabellifera* (Kükenthal) from Sagami Bay. *Scientific Reports of Yokohama State University, Section B*, **39**: 1–11.
- Gotto, R.V. 1962. Egg number and ecology in commensal and parasitic copepods. *Annals and Magazine of Natural History*, Series 13, **5**: 97–107.
- Gotto, R.V. 1979. The association of copepods with marine invertebrates. *Advances in Marine Biology*, **16**: 1–109.
- Gotto, R.V. 1993. Commensal and parasitic copepods associated with marine invertebrates (and whales). *Synopses of the British Fauna* (New Series), **46**: 1–254.
- Guerra-García, J.M., Tierno de Figueroa, C., Navarro-Barranco, C., Ros, M., Sánchez-Morales, J.E. & Moreira, J. 2014. Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian peninsula. *Journal of Sea Research*, **85**: 508–517.
- Gurjanova, E. 1938. [Amphipoda Gammaridea of Siaukhu Bay and Sudzukhi Bay (Japan Sea).] *Reports of the Japan Sea Hydrobiological Expedition of the Zoological Institute of the Academy of Sciences USSR in 1934*, **1**: 241–404 [in Russian].
- Hansen H.J. 1887. Malacostraca marina Groenlandiae occidentalis. Oversigt over det vestlige Grønlands Fauna av malakostrake Havkrebsdyr. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, Series 4, **9**: 5–226.
- Hansen, H. J. 1916. Crustacea Malacostraca. III. V. The order Isopoda. *The Danish Ingolf-Expedition*, **3**(5): iii + 1–262.
- Hartnoll, R.G. 1970. The relationship of an amphipod and a spider crab with the snakelocks anemone. *Report of the Marine Biological Station, Port Erin*, **83**: 37–42.
- Humes, A.G. 1982. A review of Copepoda associated with sea anemones and anemone-like forms (Cnidaria, Anthozoa). *Transactions of the American Philosophical Society*, **72**(2): 1–120.
- Ivanova, N.Y. & Grebelnyi, S.D. 2017. On the food of the Antarctic sea anemone *Urticinopsis antarctica* Carlgren, 1927 (Actiniidae, Actiniaria, Anthozoa). *Journal of the Marine Biological Association of the United Kingdom*, **97**: 29–34.
- Johnsen, J.R. 2002. *The taxonomy of Onisimus*. M.Sc. thesis, University of Tromsø, Norway.
- Jonsson, L.G., Lundälv, T. & Johannesson, K. 2001. Symbiotic associations between anthozoans and crustaceans in a temperate coastal area. *Marine Ecology Progress Series*, **209**: 189–195.
- Kodama, M., Hayakawa, J. & Kawamura, T. 2020. Aggregation of *Dactylopleustes* (Amphipoda: Pleustidae) to diseased areas on the host sea-urchin. *Marine Biodiversity* [doi: 10.1007/s12526-020-01100-9].
- Krapp-Schickel, T. & Vader, W. 1998. What is, and what is not, *Caprella acanthifera* Leach, 1814 (Amphipoda, Caprellidea)? Part I: the *acanthifera* group. *Journal of Natural History*, **32**: 949–967.

- Krapp-Schickel, T. & Vader, W. 2009. A new *Parametopella* species (Crustacea, Amphipoda, Stenothoidae) from *Antholoba achates* (Anthozoa, Actiniaria) from Coquimbo, Chile (with remarks on *Parametopa alaskensis* (Holmes)). *Journal of the Marine Biological Association of the United Kingdom*, **89**: 1281–1287.
- Krapp-Schickel, T. & Vader, W. 2015. Stenothoids living with or on other animals. *Zoosystematics and Evolution*, **91**: 215–246.
- Krapp-Schickel, T., Häussermann, V. & Vader, W. 2015. A new *Stenothoe* species (Crustacea: Amphipoda: Stenothoidae) living on *Boloceropopsis platei* (Anthozoa: Actiniaria) from Chilean Patagonia. *Helgolander Marine Research*, **69**: 213–220.
- Kumagai, N.H. 2006. Distance effects on patterns and processes of dispersal in an octo-coral-associated amphipod. *Marine Ecology Progress Series*, **321**: 203–214.
- Kumagai, N.H. & Aoki, M.N. 2003. Seasonal changes in the epifaunal community on the shallow-water gorgonian *Melithaea flabellifera*. *Journal of the Marine Biological Association of the United Kingdom*, **83**: 1221–1222.
- Landmann, S.W., Meyer, R., Böttcher, A., Pfannkuchen, M. & Melzer, R.R. 2016. Field experiments on individual adaptation of the spider crab *Inachus phalangium* to its sea anemone host *Anemonia viridis* in the northern Adriatic Sea. *Mediterranean Marine Science*, **17**: 333–339.
- Leach, W.E. 1814. Crustaceology. *The Edinburgh Encyclopaedia*, **7**: 402–403, 429–434 [appendix].
- Lilljeborg, W. 1865. Bidrag till kännedomen om underfamiljen Lysianassina inom underordningen Amphipoda bland kräftdjuren. *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, **3**: 1–25.
- Lønning, S. & Vader, W. 1984. Sibling species of *Doridicola* (Copepoda: Lichomolgidae) from California sea anemones: biology and host specificity. *Journal of Experimental Marine Biology & Ecology*, **73**: 99–135.
- Lowry, J.K. & Stoddart, H.E. 1994. Taxonomy of the lysianassoid genera *Phoxostoma* K. H. Barnard, *Conicostoma* Lowry & Stoddart, and *Ocosingo* J. L. Barnard (Amphipoda, Gammaridea). *Crustaceana*, **47**: 192–208.
- Lowry, J.K. & Stoddart, H. E. 1997. Amphipoda, Crustacea IV. Families Aristiidae, Cyphocarididae, Endeavouridae, Lysianassidae, Scopelocheiridae, Uristidae. *Memoirs of the Hourglass Cruises*, **10**: 1–148.
- Lowry, J.K. & Stoddart, H.E. 2012. Australian and South African conicostomatine amphipods (Amphipoda: Lysianassoidea: Lysianassidae: Conicostomatinae subfam. nov.). *Zootaxa*, **3248**: 43–65.
- Marin, I., Sinelnikov, S. & Sokolova, A. 2013. Ecological remarks and re-description of the hermit-crab associated pleustid *Pleusymtes japonica* (Gurjanova, 1938) (Crustacea, Amphipoda, Pleustidae, Pleusymtinae) from the Sea of Japan. *Zootaxa*, **3640**: 581–588.
- Montagu, G. 1813. Descriptions of several new or rare animals, principally marine, discovered on the south coast of Devonshire. *Transactions of the Linnean Society of London*, **11**: 1–26.
- Moore, P.G. & Cameron, K.S. 1999. A note on a hitherto unreported association between *Photis longicaudata* (Crustacea: Amphipoda) and *Cerianthus lloydii* (Anthozoa: Hexacorallia). *Journal of the Marine Biological Association of the United Kingdom*, **79**: 369–370.
- Moore, P.G. & Rainbow, P.S. 1989. Feeding biology of the mesopelagic gammaridean amphipod *Parandania boeckii* (Stebbing, 1888) (Crustacea: Amphipoda: Stegocephalidae) from the Atlantic Ocean. *Ophelia*, **30**: 1–19.
- Moore, P.G. & Rainbow, P.S. 1992. Aspects of the biology of iron, copper and other metals in *Andaniopsis abyssii*, with notes on *Andaniopsis nordlandica* and *Stegocephalus inflatus*, from Norwegian waters. *Sarsia*, **76**: 215–225.
- Moore, P.G., Rainbow, P.S. & Vader, W. 1994. On the feeding and comparative biology of iron in coelenterate-associated gammaridean Amphipoda (Crustacea) from N. Norway. *Journal of Experimental Marine Biology & Ecology*, **178**: 2015–231.
- Myers, A.A. & Hall-Spencer, J.M. 2003. A new species of amphipod crustacean, *Pleusymtes comitari* sp. nov., associated with gorgonians on deep-water coral reefs off Ireland. *Journal of the Marine Biological Association of the United Kingdom*, **83**: 1029–1032.
- Patton, W.K. 1979. On the association of the spider crab, *Mithrax (Mithraculus) cinctimanus* (Stimpson) with Jamaican sea anemones. *Crustaceana*, Supplement, **5**: 55–68.
- Patzner, R.A. 2004. Associations with sea anemones in the Mediterranean Sea. A review. *Ophelia*, **58**: 1–11.
- Ross, D.M. 1971. Protection of hermit crabs (*Dardanus* spp) from octopus by commensal sea anemones (*Calliactis* spp). *Nature*, **230**: 401–402.
- Ross, D.M. 1974. Evolutionary aspects of associations between crabs and sea anemones. In: *Symbiosis in the sea* (W.B. Vernberg, ed.), pp 111–125. University of South Carolina Press, Columbia, SC, USA.
- Ross, D.M. 1983. Symbiotic relations. In: *The biology of Crustacea. 7. Behavior and Ecology*. (F.J. Vernberg & W.B. Vernberg, eds.), pp. 163–212. Academic Press, New York.
- Sanderson, J.M. 1973. A catalogue of the Amphipoda (Crustacea) in the collection of the late D. M. Reid, now in the Royal Scottish Museum, Edinburgh. *Royal Scottish Museum, Information Series, Natural History*, **1**: 1–79.
- Sars, G.O. 1879. Crustacea et Pycnogonida nova in itinere 2do et 3tio expeditionis Norvegicae anno 1877 & 78 collecta. (Prodromus descriptionis). *Archiv for Mathematik og Naturvidenskab*, **4**: 427–476.
- Sars, G.O. 1883. Oversigt af Norges Crustaceer med foreløbige Bemærkninger over de nye eller mindre bekjente Arter. I. (Podophthalmata-Cumacea-Isopoda- Amphipoda). *Forhandlinger Videnskabs Selskab i Christiania*, **18**: 1–124.
- Sars, G.O. 1890–1895. *Amphipoda. An account of the Crustacea of Norway with short descriptions and figures of all the species* I. Alb. Cammermeyer, Christiania [Oslo], Norway.
- Schellenberg, A. 1926. Die Gammariden der Deutschen Sudpolar-Expedition 1901–1903. *Deutsche Sudpolar-Expedition 1901–1903*, **18**(10): 235–414.
- Schiecke, U. 1973. *Ein Beitrag zur Kenntnis der Systematik, Biologie und Autökologie mariner Peracarida (Amphipoda, Isopoda, Tanaidacea) des Golfes von Neapel*. Ph.D. thesis, Christian-Albrechts-Universität, Kiel, Germany.
- Schneider, J.S. 1884. Undersøgelser av dyrelivet i de arktiske fjorde. II. Crustacea og Pycnogonida innsamlede i Kvænangsfjorden 1881. *Tromsø Museum Årshefter*, **7**: 47–134.
- Schrieken, B. 1966. Spinkrabben en zeeanemonen. *De Levende Natuur*, **68**: 276–279.
- Shoemaker, C.S. 1955. Amphipods collected at the Arctic Laboratory, office of Naval Research, Point Barrow, Alaska, by G. E. Macginitie. *Smithsonian Miscellaneous Collections*, **128**: 1–78.
- Stasek, C.R. 1958. A new species of *Allogausia* (Amphipoda, Lysianassidae) found living within the gastrovascular cavity of the sea-anemone *Anthopleura elegantissima*. *Journal of the Washington Academy of Sciences*, **48**: 119–127.
- Stebbing, T.R.R. 1888. Report on the Amphipoda collected by H.M.S. *Challenger* during the years 1873–76. *Reports of the Voyage of the Challenger 1873–1876 (Zoology)*, **29**: 1–1737.
- Stevens, B.G. & Anderson, P.J. 2000. An association between the anemone, *Cribrinopsis fernaldi*, and shrimps of the families Hippolytidae and Pandalidae. *Journal of Northwest Atlantic Fisheries Science*, **27**: 77–82.
- Stoddart, H.E. & Lowry, J.K. 2012. Revision of the lysianassoid genera *Acidostoma* and *Shackletonia* (Crustacea: Amphipoda: Acidostomatidae fam. nov.). *Zootaxa*, **3307**: 1–34.
- Stroobants, G. 1969. Associations entre des anemones de mer (Anthozoaires) et un Crustacé Amphipode. *Les Naturalistes Belges*, **50**: 309–313.
- Suzuki, K. & Hayashi, K.I. 1977. Five caridean shrimps associated with sea anemones in central Japan. *Publications of the Seto Marine Biological Association*, **24**: 193–208.
- Tomikawa, K. O., Hendrycks, E. & Mawatari, S. F. 2004. A new species of the genus *Dactylopleustes* (Crustacea: Amphipoda: Pleustidae) from Japan, with a partial redescription of *D. Echinooides* Bousfield and Hendrycks, 1995. *Zootaxa*, **674**: 1–14.
- Vader, W. 1967. Notes on Norwegian amphipods 1–3. *Sarsia*, **29**: 283–294.
- Vader, W. 1970a. The amphipod, *Aristias neglectus* Hansen, found in association with Brachiopoda. *Sarsia*, **43**: 13–14.
- Vader, W. 1970b. Amphipods associated with the sea anemone, *Bolocera tuediae*, in western Norway. *Sarsia*, **43**: 87–98.
- Vader, W. 1970c. *Anthecheres duebeni* M. Sars, a copepod parasitic in the sea anemone, *Bolocera tuediae* (Johnston). *Sarsia*, **43**: 99–106.
- Vader, W. 1975. The sea anemone, *Bolocera tuediae*, and its copepod parasite, *Anthecheres duebeni*, in northern Norway. *Astarte*, **8**: 37–39.
- Vader, W. 1978. Associations between amphipods and echinoderms. *Astarte*, **11**: 123–134.
- Vader, W. 1983. Associations between amphipods (Crustacea: Amphipoda) and sea anemones (Anthozoa, Actiniaria). *Memoirs of the Australian Museum*, **18**: 141–153.
- Vader, W. 2020. *Orchomenella recondata* (Stasek, 1958), an amphipod living inside sea anemones. *Montenegrin Academy of Sciences and Arts Proceedings, Section of Natural Sciences*, **23**: 171–182.
- Vader, W. & Krapp-Schickel, T. 1996. Redescription and biology of *Stenothoe brevicornis* Sars (Amphipoda: Crustacea), an obligate associate of the sea anemone *Actinostola callosa* (Verrill). *Journal of Natural History*, **30**: 51–66.

- Vader, W. & Lønning, S. 1973. Physiological adaptations in associated amphipods. A comparative study of tolerance to sea anemones in four species of Lysianassidae. *Sarsia*, **53**: 29–40.
- Vader, W. & Tandberg, A.H.S. 2013. A survey of amphipods associated with molluscs. *Crustaceana*, **86**: 1038–1049.
- Vader, W. & Tandberg, A.H.S. 2015. Amphipods as associates of other Crustacea, a survey. *Journal of Crustacean Biology*, **35**: 522–532.
- Valdivia, N. & Stotz, W. 2006. Feeding behaviour of the porcellanid crab *Allopetrolisthes spinifrons* symbiont of the sea anemone *Phymactis papillosa*. *Journal of Crustacean Biology*, **26**: 308–315.
- Walker, A.O. 1906. Preliminary descriptions of new species of Amphipoda from the 'Discovery' Antarctic Expedition, 1902–1904. *Annals and Magazine of Natural History*, Series 7, **17**: 452–458a.
- Weinbauer, G., Nussbaumer, V. & Patzner, R.A. 1982. Studies on the relationship between *Inachus phalangium* Fabricius (Maididae) and *Anemonia sulcata* Pennant in their natural environment. *Marine Ecology*, **3**: 143–150.
- Wirtz, P. 1997. Crustacean symbionts of the sea anemone *Telmatactis cricoides* at Madeira and the Canary Islands. *Journal of Zoology*, **242**: 799–811.
- Wirtz, P. & Diesel, R. 1983. The social structure of *Inachus phalangium*, a spider crab associated with the sea anemone *Anemonia sulcata*. *Zeitschrift für Tierpsychologie*, **62**: 209–234.
- Wittmann, K.J. 2008. Two new species of Heteromysini (Mysida, Mysidae) from the island of Madeira (NE Atlantic), with notes on sea anemone and hermit crab commensalism in the genus *Heteromysis* S. I. Smith, 1873. *Crustaceana*, **81**: 351–374.
- Wittmann, K.J. 2013. Mysids associated with sea anemones from the tropical Atlantic: descriptions of *Ischiomysis* new genus, and two new species in this taxon (Mysida, Mysidae, Heteromysinae). *Crustaceana*, **86**: 487–506.