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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-cating 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 crust-aceans, 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

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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 (Krapp-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-Garcia et al., 2014). Many species of Stegocephalidae appear to feed on Cnidaria. The pelagic Parandania boecki (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, Andaniexis abyssi (Boeck, 1871) and A. lupus Berge & Vader, 1997 being much more generalized feeders (Moore & Rainbow, 1992; Moore et al., 1994 (as Andaniexis sp.)). All these species occur bathypelagically or hyperbenthonically, and they are very rarely collected together with their prey. Another cnidarian feeder is the Antarctic iphimediid 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 *Amphilochus* 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 Allogaussia 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
Parametopella antholobae Krapp-Schickel & Vader, 2009	Antholoba achates (Drayton, 1849)	Chile	Krapp-Schickel & Vader, 2009
Stenothoe barrowensis Shoemaker, 1955	unknown	Point Barrow, Alaska	Shoemaker, 1955; Vader, 1983.
Stenothoe bartholomea Krapp-Schickel & Vader, 2015	Bartholomea annulata (Lesueur, 1817)	Florida Keys	Vader 1983 (as <i>Stenothoe</i> n. sp.), Krapp-Schickel & Vader, 2015
Stenothoe boloceropsis Krapp-Schickel et al., 2015	Boloceropsis platei McMurrich, 1904	Chiloe Island, Chile	Krapp-Schickel et al., 2015
Stenothoe brevicornis Sars, 1883	Actinostola callosa (Verrill, 1882)	Northern Norway Newfoundland, Canada	Vader & Krapp-Schickel, 1996 Fenwick & Steele, 1983
	Liponema multicornis (Verrill, 1880)	Stellwagen Bank, Canada	Auster et al., 2011
Stenula pugilla Krapp-Schickel & Vader, 2015	Haliactis arctica Carlgren, 1921	Chukchi Sea	Krapp-Schickel & Vader, 2015, (see Vader, 1983, as Stenothoe sp.)
Stenula solsbergi* (Schneider, 1884)	Metridium senile (Linnaeus, 1767)	Western Scotland Newfoundland, Canada	Elmhirst, 1925 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; Hartnoll, 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 Stenothoidae 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 Stenothoidae 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. boloceropsis (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 prev 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 'endocommensal' 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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