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ASSOCIATIONS BETWEEN AMPHIPODS (CRUSTACEA: AMPHIPODA) AND SEA ANEMONES (ANTHOZOA, ACTINIARIA)

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SUMMARY

Published and unpublished records of amphipod–sea anemone associations are reviewed. They involve at least 22 amphipod species in 7 families, and 8 families of sea anemones. The associations are of 4 main types: protection only, ectocommensals, endocommensals and micropredators.

Morphological adaptations are not conspicuous, except for the specialised mouthparts of *Acidostoma* spp., but most obligate symbionts show inborn immunity against the toxic substances released by the host. Sex ratios are normal, sexual dimorphism small, and fecundity low compared to related free-living species.

The obligate commensal associates are usually host-specific, although able to survive in alternative hosts in the laboratory, while the micropredators and the facultative associates show low host specificity. The amphipod symbionts usually do not occupy the entire geographical and ecological range of their hosts' distribution.

Amphipod–sea anemone associations have evolved independently many times and do not seem to be of great evolutionary antiquity.

INTRODUCTION

The crustaceans of the order Amphipoda are according to most biology textbooks free-living animals, with some old and invariably cited exceptions such as the whale-lice on whales, *Hyperia* species on medusae and some Dexaminidae in sponges and tunicates. This view is certainly incorrect for the suborder Hyperiidea, most of which are obligate symbionts of gelatinous zooplankton (cf. Laval, 1980). Also among the Gammaridea and Caprellidea a large number of species live in association with a wide spectrum of invertebrates (e.g. Arndt, 1933; Vader, 1970b, 1971a–c, 1972, 1979, in prep.), fish (no review paper published) or even sea turtles (Barnard, 1967). These associations have in the past been largely overlooked or looked upon as incidental, in part because amphipods generally become easily dislodged from their host on capture, in part because most amphipod workers were museum taxonomists. With the advent of SCUBA-diving as a biological tool, large numbers of amphipod associations are now being discovered, although only few have been studied thoroughly.

Sea anemones are well-known as hosts of many symbionts: fishes (cf. Allen, 1972), shrimps, porcelain crabs, hermit crabs and spider crabs (Ross, 1967, 1971, 1974; Wolff, 1972; Suzuki & Hayashi, 1977), mysids (Clarke, 1955) and copepods (Bouligand, 1966; Gotto, 1979; Humes, 1982); such associations seem to be especially common in tropical waters. These associations occur in spite of the fact that most anemones are active predators and often feed on prey in the same size ranges as the associates, which they catch with the help of numerous batteries of toxic nematocysts and clinging spirocysts. Furthermore, digestion is largely extracellular and large amounts of proteolytic enzymes, also containing chitinases, are secreted into the gastrovascular cavity. The copious mucus production of sea anemones may also pose problems.

Once symbionts have been able to overcome these barriers, however, sea anemones offer many obvious advantages as hosts. They are long-lived animals and offer excellent protection, even to such large associates as hermit crabs (Ross, 1971; McLean & Mariscal, 1973). Sea anemones may collect more food than they can eat quickly, while the semi-digested and ejected food remains are also of high nutritive

Table 1 KNOWN SEA ANEMONE HOSTS AND THEIR AMPHIPOD PARTNERS. For further data see text.

ACTINIARIA	AMPHIPODA	
Tribe		
Subtribe		
Family		
Species	Family	Species
Athenaria		
Haloclavidae		
Peachia hastata Gosse	Lysianassidae	*Acidostoma obesum* (B & W)
Haliactiidae		
Haliactis arctica Carlgren	Stenothoidae	*Stenothoe* sp.
Thenaria		
Endomyaria		
Actiniidae		
Anemonia sulcata (Pennant)	Caprellidae	*Caprella acanthifera* Leach
	Melitidae	*Melita obtusata* (Montagu)
Anthopleura artemisia (Pickering in Dana)	Lysianassidae	*Orchomene recondita* (Stasek)*
A. elegantissima (Brandt)	Lysianassidae	*Orchomene recondita* (Stasek)
A. xanthogrammica (Brandt)	Pleustidae	Pleustidae indet.
Bolocera tuediae (Johnston)	Leucothoidae	*Leucothoe spinicarpa* (Abildgaard)
	Lysianassidae	*Aristias neglectus* Hansen
	Lysianassidae	*Onisimus normani* G.O. Sars*
Liponema multicornis (Verrill)	Lysianassidae	*Onisimus normani* G.O. Sars
Condylactis aurantiaca (Della Chiaje)	Lysianassidae	*Acidostoma obesum* (B & W)
Tealia coriacea (Cuvier)	Pleustidae	Pleustidae indet.
T. felina (Linnaeus)	Melitidae	*Melita obtusata* (Montagu)
Stoichactiidae		
Stoichactis haddoni Saville Kent	Leucothoidae	*Leucothoe* sp.
Mesomyaria		
Actinostolidae		
Actinostola callosa (Verrill)	Lysianassidae	*Acidostoma nodiferum* Stephensen
	Lysianassidae	*Onisimus normani* G.O. Sars
	Stenothoidae	*Stenothoe brevicornis* G.O. Sars
Acontiaria		
Hormathiidae		
Hormathia nodosa (Fabricius)	Lysianassidae	*Onisimus normani* G.O. Sars*
Calliactis armillatus Verrill	Melitidae	*Elasmopus calliactis* Edmondson
Calliactis sp.	Leucothoidae	*Leucothoe spinicarpa* (Abildgaard)
Metridiidae		
Metridium senile (Linnaeus)	Stenothoidae	*Metopa solsbergi* Schneider
Metridium sp.	Lysianassidae	"*Orchomene*" n.sp
Aiptasiidae		
Aiptasia couchii Cook)	Caprellidae	*Caprella acanthifera* Leach
Bartholomea annulata (Leseur)	Amphilochidae	*Amphilochus neapolitanus* Della Valle
	Stenothoidae	*Stenothoe* n. sp
host unknown	Lysianassidae	*Acidostoma laticorne* G.O. Sars
	Lysianassidae	*Onisimus turgidus* G.O. Sars
	Stenothoidae	*Stenothoe barrowensis* Shoemaker

* = probably rare alternative host.

value and in fact constitute the main food source for many associates. Finally, and this is important especially for smaller symbionts, the copious mucus secretions of the host are a high-quality source of food and are used as such by many copepods (Briggs, 1976, 1977; Gotto, 1979) and also by amphipods. A further step, feeding directly on host tissues, apparently has been taken by many copepods (e.g. Vader, 1970; Gotto, 1979; Lönning & Vader, in prep.), by the Pycnogonida, and by at least one genus of amphipods.

The present review of associations between amphipods and sea anemones is admittedly very incomplete. I know of the existence of a number of other such associations, usually involving Leucothoidea, which have been observed by divers in Caribbean waters and in the NE Pacific, but where the identity of the amphipod partners has not yet been established.

The known records of amphipod–sea anemone associations are listed below in alphabetical order of the families of the amphipod partners. Table 1 lists the known sea anemone hosts according to Carlgren's classification (Carlgren, 1949).

THE AMPHIPOD ASSOCIATES

Amphilochidae

Amphilochus neapolitanus Della Valle

This species was recently discovered to be quite common on *Bartholomea annulata* in southern Florida. "Each anemone has at least 1–2 specimens and some of the larger ones were host to as many as twelve specimens. The species also occurs on several other species of anemones and on the soft coral *Pterogorgia anceps*." (J. D. Thomas, pers. comm. 1980).

The biotope of *A. neapolitanus* is generally listed as among algae on rocks (Lincoln, 1979) and it has also been reported from sea urchins (cf. Vader, 1979).

Caprellidae

Caprella acanthifera Leach

This common and widespread caprellid has been found on sea anemones only in the western Mediterranean (Stroobants, 1969; R. Patzner, pers. comm. 1979); the hosts are *Anemonia sulcata* and *Aiptasia couchii*. Stroobants (1969) has described how the caprellids live among the tentacles and on the column of their host, where they apparently largely catch their own food, independent of the host.

Most caprellids are apparently free-living but a number of species are associated with starfish (cf. Vader, 1979; see also McCain, 1979); *C. ungulina* lives on a crab (Griffiths, 1977) and *G. gorgonia* is an obligate associate of soft corals (Laubitz & Lewbel, 1974).

Leucothoidae

Leucothoe spinicarpa (Abildgaard)

This well-known and apparently cosmopolitan species (or superspecies) shows a high tendency toward inquilinism, but with very low host specificity. It has twice been found on sea anemones: once on *Bolocera tuediae* in the northern North Sea (Vader, unpubl.), and once on *Calliactis* sp. in Cuban waters (Ortiz, 1975).

Leucothoe spinicarpa usually lives in sponges (cf. Connes, 1967) or tunicates, but it has also been found in molluscs (Ortiz, 1975; Vader & Beehler, in press) and brachiopods (cf. Vader, 1970d). The feeding biology of *Leucothoe* species is still unknown, but the closely related *Leucothoides*, likewise an inquiline of sponges and tunicates, has recently been shown to be a microphagous commensal (Thomas, 1979).

Leucothoe sp.

A single specimen of a *Leucothoe* species allied to *L. richiardii* Lessona has been collected from *Stoichactis haddoni* on the Great Barrier Reef by Dr S. Losey and sent to me.

Lysianassidae

Acidostoma Lilljeborg

The nomenclature of the European representatives of this genus has recently been revised by Lincoln (1979). He showed that *A. obesum* (Bate & Westwood) is a senior synonym of *A. neglectum* Dahl, and coined the name *A. sarsi* Lincoln for *A. obesum* auct., non Bate & Westwood. Lincoln also synonymised *A. nodiferum* Stephensen with *A. sarsi*, incorrectly under the latter name. To avoid further confusion, *A. nodiferum* is here provisionally kept apart.

Acidostoma laticorne G. O. Sars

Dahl (1964) found the proctodaeum of museum specimens filled with nematocysts, most probably of anthozoan origin.

Acidostoma nodiferum Stephensen

This species was found on the large sea anemone *Actinostola callosa* in deep water in western Norway (Vader, 1967). The faeces of the amphipods contained numerous nematocysts.

Acidostoma obesum (Bate & Westwood)   (= *A. neglectum* Dahl)

Della Valle (1893) collected this amphipod from the column of the sea anemone *Condylactis aurantiaca* in the Gulf of Naples, while Ansell (1969) found some specimens within the burrow of *Peachia hastata* in Scotland.

Dahl (1964) has studied the structure and function of the mouthparts of this and other species of *Acidostoma*. He concluded that the mouthparts are apparently adapted for sucking and that *Acidostoma* species live as ectoparasites on anthozoans.

Aristias neglectus Hansen

This is, like *Leucothoe spinicarpa*, a common inquilinous species with low host specificity. It is found sparsely but regularly in the gastrovascular cavity of the large mud-living sea anemone *Bolocera tuediae* in western Norway (Vader, 1970b). No egg-bearing females have been found inside the sea anemones.

A. neglectus usally lives in sponges and tunicates, but is has also been found in Brachiopoda (Vader, 1970d) and on echinoderms (cf. Vader, 1979).

Lysianopsis sp.

Dr E.L. Bousfield (pers. comm. 1980) has told me that he has several times collected an undescribed species of this genus on the Canadian Pacific coast from around the base of *Anthopleura xanthogrammica*, where gravel and sand had collected, but not in any other intertidal locations.

Onisimus Boeck (= *Boeckosimus* Barnard)

Barnard (1969) has pointed out that the name *Onisimus* Boeck is a senior synonym of *Pseudalibrotus* Della Valle, and he has coined the new name *Boeckosimus* for *Onisimus* auct. As pointed out by Just (1978, p. 10), this move disrupts the stability of an extensive literature and the problem should be referred to ICZN. In the meantime, I use the name *Onisimus* in the 'classic' sense.

Onisimus normani G. O. Sars

This N. Atlantic species appears to be an obligate inquiline of sea anemones. The normal host is *Bolocera tuediae*, but in northern Norway *O. normani* has also been found in *Actinostola callosa, Hormathia nodosa* and *Liponema multicornis* (Vader, unpubl.). The biology of the association has been studied by Vader (1967, 1970; Vader & Lönning, 1973). *Onisimus normani* live in the gastrovascular cavity among the mesenterial filaments and apparently feed mainly on the semi-digested prey of their host. They have a 2-year life cycle and exhibit seasonal reproduction. The amphipods enter the sea anemones as c. 3 mm young juveniles in spring and grow to fully adult size within the host in c. 18 months. They then leave their host and disappear; no ovigerous *O. normani* have ever been found within the host, and very few have been found elsewhere. Circumstantial evidence indicates that the species is single-brooded. Infection rates may be high: in a deep fjord in western Norway 70% of the *Bolocera* contained *Onisimus*, with a mean incidence of c. 3. The amphipods are strictly host-specific in western Norway, but much less so in northern Norway, although the same host species in about the same relative numbers occur in both areas.

Onisimus turgidus   G. O. Sars

This little-known arctic species was originally described as parasites on a large actinian in the Barents Sea (Sars, 1885, p. 147); the specific identity of the host remains unknown (Vader, 1967). Later records confirm the association, but add no further details.

Orchomene recondita (Stasek)

This species was originally described in the primarily Antarctic genus *Allogausia* Schellenberg (Stasek, 1958) but it is certainly not congeneric with its type, *A. paradoxa* Schellenberg (Vader, unpubl.). I therefore provisionally follow Barnard (1964, 1969b), who combined a number of genera into *Orchomene* s.l., although this enlarged genus is clearly not homogeneous (see e.g. Oleröd, 1975).

Orchomene recondita lives inside the gastrovascular cavity of the intertidal sea anemone *Anthopleura elegantissima* (a very few specimens have been found in *A. artemisia*). It has hitherto been found only at a few localities near San Francisco. The biology of the association has recently been studied by Vader & Lönning (in prep.). The amphipod spends its entire life cycle within its host. It feeds mainly on the half-digested prey of its host, probably augmented with mucus secretions and zooxanthellae, but usually not host tissues. *O. recondita* has seasonal reproduction and a 1-year life cycle. The females have several consecutive broods of 8–15 young in early spring and then die. Both young and adult amphipods spend long periods within a single host, although amphipods kept without a host are clearly night-active. The distribution of *O. recondita* is extremely patchy. Within patches, the infection rate may be as high as 80% with a mean incidence of up to 6 amphipods per sea anemone.

Orchomene (s.l.) n. sp.

A sample from Alaska in the National Museum of Natural Sciences, Ottawa, contained 1 ♂ and 1 ♀ of this undescribed species labelled as having been collected 'among tentacles of *Metridium*'. Further specimens of this taxon have been collected from an intertidal habitat in Washington (E.L. Bousfield, pers. comm.). Off the northern California coast white *Orchomene*-like lysianassids have been noted among the tentacles of *Metridium*, which had been dredged from deep water, but no material is extant (J. Chapman, pers. comm. 1980).

Melitidae

Elasmopus calliactis Edmondson

This little-known species was described by Edmondson (1951) as an obligate associate of a hermit crab–sea anemone symbiosis in Hawaii, but the role of the sea anemone partner, *Calliactis armillatus*, in the biology of the amphipod is not known.

Melita obtusata (Montagu)

This common European amphipod is best known as a regular associate of starfish, but it has also been found apparently free-living, as well as on other echinoderms and on hermit crabs (for ref. see Vader 1979), and on the sea anemones *Anemonia sulcata* (Brady & Robertson, 1869; Hartnoll, 1971) and *Tealia felina* (Reid, in Sanderson 1973). Hartnoll (1971) found the amphipods among the tentacles. He speculated that they perhaps feed upon the remains regurgitated by the anemone.

Pleustidae

Several as yet undescribed species of Pleustidae, among them at least one *Parapleustes* sp. (alluded to in Barnard, 1972, p. 17) and a *Pleusymtes* sp., have been observed by divers on subtidal Californian sea anemones, especially *Anthopleura xanthogrammica* and *Tealia coriacea* (D. Wobber, unpubl. rep. 1968; J. Ratliff, unpubl. rep. 1974; T. Chess, pers. comm. 1978). They appear to move away from the sea anemones frequently and to find most of their own food, but they flee to their host when danger threatens.

Stenothoidae

Metopa solsbergi Schneider

This is one of the many rarely collected *Metopa* species from the North Atlantic. Elmhirst (1925) found numbers of this amphipod to be present on *Metridium senile* on pier piling in western Scotland, the only known record from Great Britain (Lincoln, 1979). The amphipods crawled about on the oral

disc and the tentacles and also entered and left the stomodaeum unharmed. Elmhirst stated that the slime of the host, enriched with trapped food particles, constituted the natural food of the amphipods, but he did not say how he arrived at that conclusion.

The same association has recently also been found off the coast of Newfoundland, Canada (Fenwick & Steele, in prep.).

Stenothoe barrowensis Shoemaker

This species, known only from the two type specimens from off Point Barrow, Alaska (Shoemaker, 1955), is apparently closely related to *Stenothoe brevicornis* G. O. Sars and may likewise be an associate of sea anemones. The types were taken from a dredge haul which contained among other things 22 unidentified sea anemones (MacGinitie, 1955, p. 77).

Stenothoe brevicornis   G. O. Sars

This amphipod, widely distributed in the North Atlantic, in northern Norway is an obligate associate of the large sea anemone *Actinostola callosa*. The biology of the association is being studied by Vader (in prep.). *Stenothoe brevicornis* spends its entire life-cycle among the tentacles and on the oral disc of its host, where it crawls about unhampered. I have never seen the amphipods enter the stomodaeum. They apparently mainly feed on the mucus secretions of the sea anemones. Females with eggs are present among the tentacles at all seasons, but the number of broods is not yet known. Frequency of infection at the study-site in northern Norway is from 40–70%, with a mean of 1–4 amphipods per host. Many other populations of *Actinostola callosa* in the Norwegian fjords were examined, but most did not contain any *Stenothoe*.

Stenothoe n.sp.

An undescribed species of *Stenothoe* is apparently common on the sea anemone *Bartholomea annulata* in S. Florida waters (Vader, 1971c, in prep.; K. Cairns pers. comm. 1979; J.D. Thomas pers. comm. 1980). It lives among the tentacles of its host and may attain high frequencies: up to 70 specimens (including ovigerous ♀ ♀) have been collected from a single host. The association seems to be similar to that of *Stenothoe brevicornis* with *Actinostola callosa*.

Stenothoe sp.

A sample of 3 specimens collected off Point Barrow, Alaska in 1959 of an unidentified *Stenothoe* species in the collections of the National Museum of Natural History in Washington is labelled 'from coelenteron of *Haliactis arctica*'.

TYPES OF ASSOCIATIONS

The associations between amphipods and sea anemones as yet are little studied and any classification must therefore be regarded as preliminary. There seem, however, to be four categories.

I. *Protection only*

These amphipods find protection on their sea anemone host, but they collect all or most of their food independently; ejected food-remains may play a role in nutrition. The amphipods in this category are generally not very host specific and most are facultative symbionts. *Caprella acanthifera, Melita obtusata* and probably the as yet unstudied pleustid and *Lysianopsis* associations belong in this category.

This type of association is equivalent to that of clownfishes, porcelain crabs and spider crabs with sea anemones.

II. *Ectocommensals*

These amphipods live on the tentacles and oral disc of their host and feed primarily on host secretions, probably enriched with detritus and, in microphagous hosts, small prey animals. They usually do not penetrate into the gastrovascular cavity, although some apparently are able to do so with impunity. These amphipods spend their entire life cycle on their host.

To this category belong the amphilochid and stenothoid associates and probably also the leucothoids. Most stenothoids seem to be host-specific obligate symbionts, while the amphilochids and leucothoids have a low host specificity and are facultative.

This type of association is equivalent to that of many lichomolgid copepods on sea anemones (Briggs, 1976), to the stenothoids living among *Tubularia* polyps (Pirlot, 1932) and to the caprellids on starfish (cf. Vader, 1979).

III. *Endocommensals*

These amphipods live mainly in the gastrovascular cavity of their host and their main food is the semidigested prey of the sea anemone. In some cases the mucus secretions of the host mesenteria also may play a role in nutrition. The amphipods spend most or all of their lives inside their host, but in some cases the adults leave the host just prior to egglaying.

To this category belong the *Onisimus* species and *Orchomene recondita*, possibly also '*Orchomene*' sp. and *Aristias neglectus*, athough the latter seems to be mostly microphagous. *Aristias* has a very low host specificity, while the others are obligate, host specific symbionts.

This type of association is roughly equivalent to the mouth-living isopods in fishes and the food-stealing lysianassids in the stomachs of starfish (cf. Vader, 1979, p. 131), although the latter apparently do not consort permanently with their hosts.

IV. *Micropredators*

These amphipods live on the column or in the burrows of sea anemones and feed on host tissues; their mouthparts are strongly modified to this end. It is uncertain whether they live permanently on their hosts or leave them periodically.

To this group belong the lysianassid amphipods in the genus *Acidostoma*. They do not seem to be very host-specific, but information is as yet very scanty.

This type of association is equivalent to that of the sea spiders of the *Pycnogonum* type on sea anemones.

There are also endoparasitic crustaceans, chiefly copepods, in sea anemones (cf. Bouligand, 1966; Vader 1970c; Humes, 1982), but this type of association does not seem to have an equivalent among the Amphipoda. This reflects the general rule that associated amphipods usually are morphologically less altered in their adaptation toward symbiosis than are Copepoda, Cirripedia or Isopoda. The endoparasitic copepods in sea anemones are so apomorphic that it has not yet been possible to find their proper place in the copepod classification system (cf. Gotto, 1979).

Caprella acanthifera and *Melita obtusata* are here considered to belong to category I on the strength of the published descriptions of these associations (Stroobants, 1969; Hartnoll, 1971). It should be kept in mind, however, that *M. obtusata* and a number of *Caprella* species also occur on starfish (cf. Vader, 1979) where they have been shown to derive a large part of their nutrition from the skin secretions of their hosts. Further research may show that also in the sea anemone symbionts mucus secretions are more important than hitherto assumed.

Although leucothoid and stenothoid amphipods often are found inside sponges and tunicates, and some species even live within the mantle cavity of bivalve molluscs and brachiopods (Vader & Beehler, in press; Vader, in prep.), on sea anemones these groups are mostly restricted to the tentacles and oral disc of their hosts and generally do not penetrate into the gastrovascular cavity, with the possible exception of *Metopa solsbergi* and *Stenothoe* sp. Lysianassid amphipods, on the other hand, are most often endocommensals.

ADAPTATIONS

Morphological adaptations

Clearcut morphological adaptations are only found in the micropredators in the genus *Acidostoma* which have their mouthparts clearly specialised for piercing and sucking (Dahl, 1964). Similar mouthparts are found in a number of related lysianassid genera, but their biology is as yet unknown.

An obvious adaptation, but one that is found in most associates of soft-bodied invertebrates, is the generally weak development of the armament of the distal parts of the pereopods and, with the exception of chemosensory setae, of the antennae. This no doubt decreases the chance of becoming entangled in mucus, apparently a real danger. I have repeatedly found specimens especially of *Orchomene recondita* so covered with mucus that they were unable to extricate themselves. The lysianassids use their second gnathopod in trying to remove mucus from the body, but these appendages do not deviate in any obvious way in either form or armaments in the associates of sea anemones.

The obligate amphipod symbionts of sea anemones belong to the leucothoid-stenothoid group of amphipods (the Leucothoidea of Bousfield, 1978) or the lysianassids (the Lysianassoidea of Bousfield, 1978). The Leucothoidea as a group are adapted (or preadapted) towards associations with soft-bodied, mucus-producing invertebrates. They are smooth-bodied animals with large, shield-like coxal plates and sparsely spinose antennae and pereopods. They also have specialised mouthparts, often with reduced mandibular molars and palps, and small, more or less fused maxillipedal plates. They usually feed on fine flocculant detritus, host secretions or the food of microphagous hosts. The species on sea anemones do not show any obvious special adaptations to these particular hosts.

The Lysianassoidea as a group are adapted toward a scavenging way of life, although they are very diverse in their feeding ecology. This group, which is generally considered to be plesiomorphic (Bousfield, 1978), is characterised by smooth bodies, short and stout antennae with many chemosensory brush setae (especially in the males), mouthparts adapted for biting and chewing large pieces of food, and a highly specialised gnathopod 2, used for grooming.

The large genera *Onisimus* and *Orchomene* s. l. are both made up mainly of species which are generalised free-living scavengers. *Onisimus* species are most common in arctic and subarctic shallow seas. The mouthparts of *Onisimus normani* do not deviate in any obvious way from those of its scavenging congener, *O. edwardsi* Kröyer.

Orchomene s. l. is bipolar arctic/antarctic and cold-temperate, in both shallow and deep water, with a number of species in the deep sea. The fine structure and functional morphology of the mouthparts of *Orchomene* species have recently been studied by Oleröd (1975) and Dahl (1979). Briefly, *Orchomene* s. l. are quite generalised lysianassids in the structure of their mouthparts. The incisor of the mandible is quite narrow and the molar triturative, and as a whole the mouthparts are well able to shear off, chew and process large food items, but without the extreme adaptations of specialised necrophages like the deep sea genera *Hirondellea* (Hessler *et al.* 1978; Dahl, 1979) or *Paralicella* (Dahl, 1979; Thurston, 1979).

In *Orchomene recondita* the mouthparts are of the generalised *Orchomene*-type, although differing in several details from *Orchomene* s. s. (Oleröd, 1975). The mandibular molar is triturative, but lacks a border of setae, and the triturative elements are quite flat. The incisor is short, smooth, convex and not very sharp. There is no excessive development of the proctodaeum for food-storage in *O. recondita*, such as is found in some specialised necrophagous *Orchomene* species (Dahl, 1979).

Physiological adaptations

Sea anemones are predators and they often feed on prey of the same size-range as the associates. Some type of adaptation is therefore necessary. As shown by Mariscal (cf. 1970) and Schlichter (cf. 1976) the fish symbionts of sea anemones go through a long and gradual acclimatisation process, in which they gradually become covered with the mucus secretions of the tentacles of their host. When completely 'camouflaged' they are no longer recognised by the sea anemones as something extraneous and can move among the tentacles at will. It is the prudence and perseverance of the fishes, and not any special physiological or biochemical characteristics of their skin, that result in the association becoming established, and the adaptations are therefore primarily behavioural.

With the exception of the somewhat aberrant hermit crab associations little research has as yet been carried out on the many decapod symbionts of sea anemones, but the available evidence suggests that also in these cases a similar protective mucus covering is acquired. Apparent acclimatisation behaviour has been described for spider crabs by Schrieken (1966). *Inachus phalangium*, on the other hand, does not, as far as is known, show acclimatisation behaviour (Hartnoll, 1971). There are also some indications that spider crabs, dropped upon the oral disc of sea anemones, elicit less forceful reactions than do *Carcinus* species (cf. Davenport, 1962; Hartnoll, 1971). It is not quite clear, however, whether the spider crabs used in these experiments were thoroughly cleansed of their slime-cover. There is some old evidence that certain hermit crabs possess immunity against the nematocyst toxin of their host (Cantacuzène, 1925; Rey, 1940), but I know of no recent research on this subject.

For amphipod symbionts no acclimatisation behaviour has been described and all the available evidence suggests that the adaptations for these associates are not primarily behavioural, but physiological and/or biochemical. Stroobants (1969) and Hartnoll (1971) have shown that the facultative associates *Caprella acanthifera* and *Melita obtusa* elicit far lesser reactions from the tentacles of the host than do free-living amphipods from the same biotope, but the possible presence of a protective mucus covering was not excluded by the experimental design.

Our own work has mainly been with the endocommensals *Aristias neglectus, Onisimus normani* and *Orchomene recondita* (Vader & Lönning, 1973, in prep.). When e.g. *O. recondita* is dropped on the oral field of its host *Anthopleura elegantissima* there is some reaction by the tentacles. As the amphipod actively crawls down into the stomodaeum, the role of the tentacles is hard to determine; however, dead or narcotized *O. recondita* are swallowed. Tidepool amphipods of the genus *Hyale* are caught and swallowed quickly by *Anthopleura*, but the isopod *Exosphaeroma inornatum* Dow, which is often found among the debris surrounding the sea anemones, elicits less reaction and usually manages to escape. *Onisimus normani* is caught and swallowed by its host *Bolocera tuediae* in exactly the same way as prey animals.

The nematocysts of these sea anemones stun their prey animals, making it possible for the mesenterial filaments to adpress closely, but they usually do not kill them outright. If *Hyale* specimens are retrieved shortly after having been swallowed, they usually recover.

In order to separate the effect of the nematocyst toxin from that of the secretions of the mesenterial filaments, amphipods and isopods of different species were tied in cloth or nylon gauze bags and pushed directly into the gastrovascular cavity. After 6–9 hours, the free living amphipods and isopods were invariably dead, fragmented and often more or less digested, while there was no appreciable mortality among the symbionts. This 'immunity' is not confined to the proper host, but exists in all other sea anemones tested.

Extracts of the mesenterial filaments of *Bolocera tuediae* were tested in a series of bioassays, using *Aristias neglectus, Onisimus normani* and free-living Lysianassidae (Vader & Lönning, 1973). The results showed that under these circumstances, where behavioural responses were completely ruled out, *Aristias* and *Onisimus* survived quite high concentrations of the extracts, while the free-living lysianassids were invariably killed.

The secretions of the mesenterial filaments contain at least three substances: nematocyst toxin (but extracts of the tentacles were not toxic), mucus substances secreted by at least two different types of mucus cells, and proteolytic enzymes (Vader & Lönning, 1975). Further bioassays made it highly probable that the toxicity of the extracts was primarily caused by their proteolytic enzymes (Vader & Lönning, 1973).

The specimens of *Aristias neglectus* used in these experiments had been collected from sponges and had probably never been in contact with sea anemones. Nevertheless, tolerance of these amphipods to the extracts was very high. This tolerance thus appears to be genetically determined and is not acquired during the life of the individual.

The mechanism of this 'immunity' is, unfortunately, still unknown. Briggs (1978) has recently published a study of the fine structure of the integument of *Paranthessius anemoniae*, a copepod associate of sea anemones. He discovered subcutaneous glands opening through pores in the cuticle that appeared to secrete substances that he claimed may be responsible for the immunity of *Paranthessius* to the nematocysts of their host. Such cuticular pores also exist in *Orchomene recondita* and the fine structure of its cuticle is under further study.

Reproductive adaptations

Many endocommensal decapods have enlarged abdomens and thus higher fecundity than free-living relatives of the same size (cf. Patton, 1967). The same is true for parasitic and commensal copepods (Gotto, 1962, 1979).

The endocommensal amphipod *Orchomene recondita*, on the other hand, has a low fecundity compared to free-living amphipods of the same size (c. 5 mm): each female produces 2–3 broods of only 8–15 young each (Vader & Lönning, in prep.). *Onisimus normani* has a two-year life-cycle and probably only a single brood of eggs. The ectocommensal *Stenothoe brevicornis* has 7–15 eggs per brood (Vader, in prep.), less than the far smaller *S. monoculoides* (Montagu) (cf. Krapp-Schickel, 1976), but the number of broods is still unknown.

The low fecundity of the symbiotic amphipods is probably made possible by the protection afforded by the host. Moreover in *O. recondita* the reproductive season of the amphipod coincides with the period of maximum asexual reproduction of *Anthopleura elegantissima*.

The sex ratio in those investigated more closely, viz. *Onisimus normani, Orchomene recondita* and *Stenothoe brevicornis*, does not deviate significantly from 1:1, although males of *O. recondita* die slightly earlier than females. In the lysianassids the females are only a little larger than the male, while the difference is more clearcut in *Stenothoe*. In other *Orchomene* species, *O. gerulicornis* and *O. cavimanus*, the sex-ratio is clearly skewed in favour of the females and the females are markedly larger than the

males (Thurston, 1979). Thurston explained this as an expression of the greater energy involvement of the double-brooded *Orchomene* females (compared to single-brooded genera with normal sex ratio). However, *O. recondita* also produces several broods.

Bousfield (1978) has discussed plesiomorphic and apomorphic characters in the Amphipoda. Among the important primitive characters present in the Lysianassoidea he enumerated the presence of terminal pelagic males, calceoli, and coxal gills on pereopod 7. Many *Orchomene* species do have such calceolate terminal males, but *O. recondita* shows very little sexual dimorphism, is acalceolate and lacks a coxal gill on pereopod 7. It is possibly the most apomorphic species in *Orchomene* s.l. Sexual dimorphism is also very slight in *Onisimus normani* and much less obvious than usual for the genus in *Stenothoe brevicornis*.

RELATIONS BETWEEN AMPHIPOD AND HOST

Host specificity

Of the four groups used in the preliminary classification of amphipod associates of sea anemones (see p.146), the amphipods in categories I and IV do not appear to be strongly host specific. Among the commensal symbionts in categories II and III *Orchomene recondita* and *Stenothoe brevicornis* are strongly host-specific. *Onisimus normani* is almost exclusively found on *Bolocera tuediae* in western Norway (Vader, 1970b), but is much less host-specific in northern Norway, although the same sea anemone species occur in both areas. *Aristias neglectus* has been found on only one species of sea anemone, but this species also inhabits a wide spectrum of other invertebrates (cf. Vader, 1979). For most partnerships, the available data are not sufficient to allow any conclusions.

The strongly host-specific Lysianassidae are also able to survive for considerable periods in alternate hosts, if given no choice. *Metopa solsbergi*, on the other hand, was eaten 'without hesitation' when tested on an alternate host, *Tealia felina* (Elmhirst, 1925).

Preliminary experiments designed to test distant host location of *Anthopleura elegantissima* by *Orchomene recondita* have hitherto given inconclusive results. When visual and tactile clues are also available, *O. recondita* strongly prefers its own host in aquarium tests (Vader & Lönning, in prep.).

Variations in host infection

Many amphipod associates do not inhabit their sea anemone host throughout the latter's geographical and ecological range. Although *Anthopleura elegantissima* is a common sea anemone from southern Alaska to northern Mexico (Hand, 1955), *Orchomene recondita* has hitherto only been found at a few sites near San Francisco, in spite of several attempts to collect it further south (Barnard, 1969a; Vader & Lönning, unpubl.). In the San Francisco area *O. recondita* has a much more restricted ecological distribution than its host, being absent from exposed sites and from sand-embedded colonies of the host (Vader & Lönning, in prep.).

Onisimus normani occurs in western Norway in *Bolocera tuediae* at depths of 200–700 m, but not in shallower water, and in some fjords it seems to be absent altogether, in spite of the common occurrence of its host at appropriate depths (Vader, 1970b, in prep.).

There may also be large variations through time in infection rate. Mean incidence of infection of *Bolocera* with *Onisimus* in deep fjords in western Norway was, from 1967–1970, c. 3 amphipods per host. In 1970–1977 the mean incidence of infection was as low as 0.01 amphipods per host.

Effects on host

In no case do the amphipods seem to have any appreciable effect on the vitality or reproduction of the host. This is in spite of the fact that the total symbiont load may be appreciable. I have found *Aristias neglectus* and *Onisimus normani* within the same specimen of *Bolocera tuediae*, which also was heavily infested by the large endoparasitic copepod *Antheacheres duebeni* (Vader, 1970 b, c). In northern Norway *Actinostola callosa* may hold both *Onisimus normani* and *Stenothoe brevicornis*, and in California *Anthopleura elegantissima* is often host to both *Orchomene recondita* and the lichomolgid copepod *Metaxymolgus confinis* (Lönning & Vader, in prep.).

GENERAL CONCLUSIONS

Associations between amphipods and sea anemones are probably quite common, although as yet little known. They occur in arctic, temperate and tropical waters, and from the intertidal zone to depths of at least 1000 m.

When we compare the amphipod fauna of sea anemones with that of echinoderms (Vader, 1979) the most striking difference is the prominence of the Leucothoidea which are virtually unknown as echinoderm symbionts. The two faunas agree, however, in being very diverse, thus having evolved independently many times, and in not having developed dramatic morphological adaptations. Thus, although the sea anemones are among the oldest known multicellular groups and the amphipods may be of much greater antiquity then previously thought (cf. Dahl, 1977, 1979; Schram, 1979), symbiotic associations between the two groups show no evidence of great evolutionary age.

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