A preliminary review of zoanthid-hermit crab symbioses (Cnidaria; Zoantharia/Crustacea, Paguridea)

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Ates, R.M.L. A preliminary review of zoanthidhermit crab symbioses (Cnidaria; Zoantharia/Crustacea; Paguridea).
Zool. Verh. Leiden 345, 31.x.2003: 41-48, fig. 1.— ISSN 0024-1652/ISBN 90-73239-89-3.
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Key words: hermit crabs; Paguridea; colonial anemones; Zoantharia; symbiosis; review.
A preliminary review is presented of zoanthid-hermit crab symbioses reported in the literature. The records of Balss (1924) are included. Aspects of this type of symbiosis are discussed.

Introduction

Members of two anthozoan orders, Zoantharia and Actiniaria, may occur in close association with hermit crabs, either attached to the gastropod shell inhabited by the hermit crab (see fig. 1) or directly wrapped around its abdomen. More species of zoanthids than actinians were listed by Balss (1924) in his review of hermit crab symbioses. Because shallow-water actinians are so much easier to collect and to keep, they have generated vastly more interest than the deep sea zoanthids. Later review articles concerning symbionts of hermit crabs ignore or barely mention zoanthid partners (Hazlett, 1981; Ross, 1983).

The taxonomy of parapagurid hermit crabs has recently been cleared up to some extent (Lemaitre, 1989; 1990; 1994; 1996; 1997; 1999; etc.). Hopefully, the preliminary review of pagurid co-occurrence with zoanthids provided here, will eventually lead to the same for the latter.

Review of hermit crabs carrying zoanthids

As a stimulus for further study, a preliminary review of hermit crab/zoanthid co-occurrences recorded in the literature is presented (table 1). The records already provided by Balss (1924: 767/8), which see for (further) references and possible further hermit crab associates, are included and marked with *.

Table 1. Zoanthid-hermit crab symbioses

zoanthid	hermit crab	sources
Epizoanthus abyssorum Verrill, 1885	*Parapagurus pilosimanus* Smith, 1879	Verrill, 1885b Carlgren, 1913; Carlgren, 1923; Muirhead et al., 1986
**Epizoanthus arenaceus* (Delle Chiaje, 1823)	*Paguristes eremita* (Linnaeus, 1767); *Pagurus cuanensis* Bell, 1846	Milne Edwards & Bouvier, 1900; Pax, 1937; Stachowitsch, 1980

**Epizoanthus carcinophilus* Carlgren, 1923	*Parapagurus pilosimanus*; *P. bouvieri* Stebbing, 1910	Carlgren, 1938
**Epizoanthus chuni* Carlgren, 1923	*Parapagurus arcuatus monstrosus* Alcock, 1905 (= *Sympagurus brevipes* or *Oncopagurus monstrosus*; pers. comm. Lemaitre, 2002)	Carlgren, 1923
Epizoanthus egeriae Haddon & Duerden, 1896	hermit crabs	Haddon & Duerden, 1896 Lwowsky, 1913
Epizoanthus frenzeli Pax, 1937	*Paguristes eremita*	Pax, 1937
**Epizoanthus incrustatus* (Von Düben & Koren, 1847) (=*E. americanus* Verrill, 1864; *E. papillosus* Gray, 1867)	*Anapagurus laevis* (Thompson, 1844)	Crawshay, 1912; Carlgren, 1913; Bull, 1939; Manuel, 1981; Cranmer et al., 1983; Dyer et al., 1983; Muirhead et al., 1986
	Pagurus bernhardus (Linnaeus, 1758)	Ates, 1985; this paper, see caption to fig. 1
Epizoanthus indicus (Lwowsky, 1913)	*Parapagurus* spec.	Carlgren, 1934a
**Epizoanthus michael sarsi* Carlgren, 1923	?	Carlgren, 1923
Epizoanthus mortenseni Carlgren, 1934	probably hermit crabs	Carlgren, 1934a
Epizoanthus paguricola (Roule, 1900)	*Pagurus cuanensis*; *Anapagurus laevis*; *Anapagurus chiroacanthus* (Lilljeborg, 1856)	Roule, 1900a & 1900b; Herberts, 1972a & 1972b
Epizoanthus paguriphilus* Verrill, 1863 (=*E. hirondellei* Jourdan, 1891; =E. parasiticus* Hertwig, 1882)	*Parapagurus pilosimanus*	Verrill, 1882; Verrill, 1885a; Smith, 1886 Jourdan, 1891 & 1895; Milne Edwards & Bouvier, 1893 Carlgren, 1913; Lwowsky, 1913; Carlgren, 1923; Boone, 1930; Carlgren, 1934b; Muirhead et al., 1986
**Epizoanthus paguropsidis* Boas, 1926	*Paguropsis typica* Henderson, 1888	Boas, 1926
Epizoanthus parasiticus Verrill, 1861	*Pagurus pubescens* Kröyer, 1839	Verrill, 1866
Epizoanthus ramosus Carlgren, 1934	possibly *Paguristes* spec.	Carlgren, 1934a
**Epizoanthus sagaminensis* Pax, nomen nudum?	*Paguristes palythophilus* (Ortmann, ?)	Balss, 1924
Epizoanthus senegambiensis (Carter, 1882)	*Pagurus*? *Diogenes ovatus* Miers, 1879	Carter, 1882; Pax & Müller, 1956
Epizoanthus similis Carlgren, 1938	*Eupagurus* sp.?	Carlgren, 1938

Epizoanthus steueri Pax, 1937	*Paguristes eremita*	Pax, 1937
**Epizoanthus studeri* Carlgren, 1923 (= *Sidisia cancrisocia* Studer, 1879)	*Parapagurus dimorphus* = *Sympagurus dimorphus* (Studer, 1883)	Jourdan, 1895; Lwowsky, 1913; Carlgren, 1938
**Epizoanthus valdiviae* Carlgren, 1923	*Parapagurus armatus* var. *monstrosus* ?	Carlgren, 1923
Epizoanthus vatovai Pax & Lochter, 1935	*Paguristes eremita*	Pax & Lochter, 1935; Pax, 1937
**Epizoanthus* spec.	*Anapagurus pusillus* (Henderson, 1888)	Henderson, 1888
**Epizoanthus* spec.	*Nematopagurus muricatus* (Henderson, 1888)	Alcock, 1905
**Epizoanthus* spec.	*Oncopagurus minutus* (Henderson, 1888)	Alcock, 1905 Lemaitre, 2003
**Epizoanthus* spec.	*Paguristes balanophilus* (Alcock, 1905)	Alcock, 1905: 33
**Epizoanthus* spec.	*Paguristes puniceus* (Henderson, 1888)	Alcock, 1905: 39
**Epizoanthus* spec.	*Parapagurus bouvieri*	Stebbing, 1910: 357 Lemaitre, 1990; Lemaitre, 1999; Forest et al., 2000
Epizoanthus spec.	hermit crabs	Erdmann, 1886
Epizoanthus spec.	*Parapagurus abyssorum* (Filhol, 1885)	Lemaitre, 1989; Forest et al., 2000
Epizoanthus spec.	*Parapagurus andreui* MacPherson, 1984	Lemaitre, 1990; Lemaitre, 1999
Epizoanthus spec. (probably)	*Parapagurus latimanus* Henderson, 1888	Lemaitre & McLaughlin, 1992;
Epizoanthus spec. (e.g. *E. paguriphilus*, *E. incrustatus*)		Lemaitre, 1999; Forest et al., 2000
Epizoanthus spec.	*Parapagurus pilosimanus*	Lemaitre, 1989
Epizoanthus spec. (probably)	*Sympagurus dimorphus*	Lemaitre, 1996 Forest et al., 2000
Epizoanthus spec.	*Sympagurus papposus* Lemaitre, 1996 (= *S. burkenroadi* Lemaitre, 2003)	Lemaitre, 1996 Forest et al., 2000
Epizoanthus spec.	*Sympagurus villosus* Lemaitre, 1996	Lemaitre, 1996
Palythoa(?) *eupaguri* Marion, 1882 nomen nudum?	*Eupagurus jacobi* A. Milne Edwards, 1880	Marion, 1882
unknown zoanthid family		
colonial sea anemone (Order Zoanthidea)	*Iridopagurus globulus* García-Gómez, 1983	García-Gómez, 1983
? (anthozoan polyp)	*Oncopagurus indicus* (Alcock, 1905)	Lemaitre, 1996
?	*Oncopagurus orientalis* (De Saint Laurent, 1972)	Lemaitre, 1997
? (actinians or zoanthids)	*Oncopagurus bicristatus* (A. Milne Edwards, 1880)	Lemaitre, 1989
? (actinians or zoanthids)	*Parapagurus alaminos* Lemaitre, 1986	Lemaitre, 1989

? (actinians or zoanthids)	*Parapagurus nudus* (A. Milne Edwards, 1891)	Lemaitre, 1989
?	*Parapagurus furici* Lemaitre, 1999	Lemaitre, 1999
? (anthozoan polyp)	*Parapagurus richeri* Lemaitre, 1999	Forest et al., 2000; Lemaitre, 1999
?	*Parapagurus saintlaurentae* Lemaitre, 1999	Lemaitre, 1999
? (actinians or zoanthids)	*Sympagurus acinops* Lemaitre, 1989	Lemaitre, 1989
? (zoanthid)	*Sympagurus dofleini* (Balss, 1912)	Lemaitre, 1994
? (actinians or zoanthids)	*Oncopagurus gracilis* (Henderson, 1888)	Lemaitre, 1989 Lemaitre, 2003
? (actinians or zoanthids [*Epizoanthus*?])	*Sympagurus dimorphus*	Lemaitre, 1989

Discussion

Knowledge about zoanthid-hermit crab symbioses is limited compared to what is known about actinian-hermit crab symbioses and studies of live hermit crabs together with ditto zoanthids are altogether lacking. What is known about the zoanthid-hermit crab symbiosis will become apparent when comparing it with the actinian/hermit symbiosis.

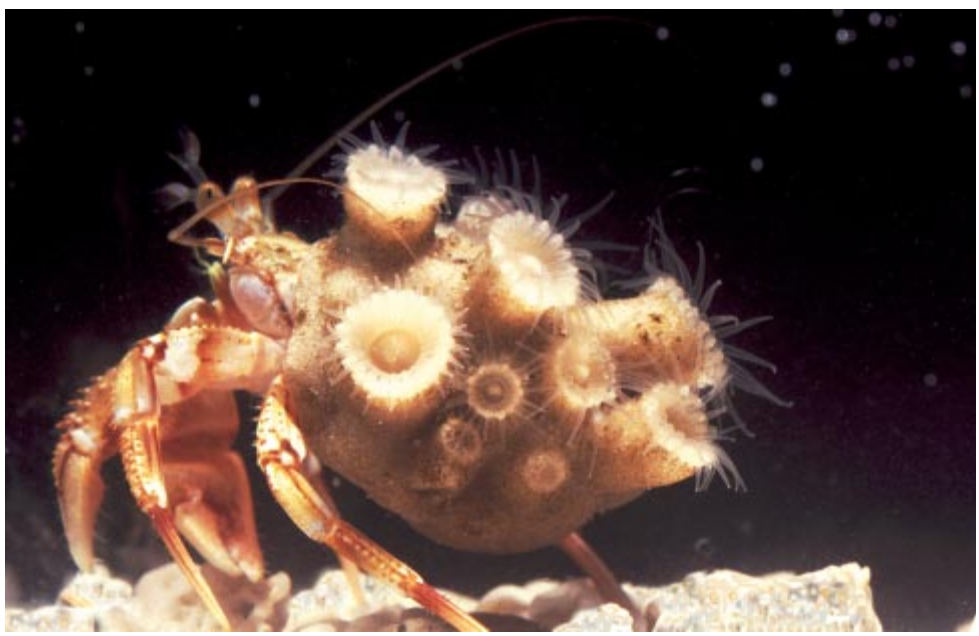

Fig. 1, Young colony of *Epizoanthus incrustatus* together with *Pagurus bernhardus*, its natural host; aquarium picture. The specimen was collected on 27-VIII-1996 at 54″12′00 N, 1″31′ O during a cruise of RV. 'Tridens', leg. Dr W. Dekker (RIVO, IJmuiden). This is the first published picture of live *E. incrustatus*.

Zoanthid morphology does not allow for replacement on shells used by hermit crabs which constitutes a major difference with actinians (cf. Brooks, 1989). Curiously some hermit crabs may occur with either zoanthid or actinian partners (e.g. *Parapagurus abyssorum*, see Lemaitre 1989: 34). It is unclear if and how zoanthids and actinians compete for hermit crabs and vice versa. It is also unknown whether during their lifetime hermit crabs may change from a zoanthid to an actinian partner or vice versa. This has been suggested for *Paguropsis typica* which in the glaucothoe stage has been found with an actinian (Schäfer et al., 1983), whereas as an adult it is only known to live with a zoanthid.

Hermit crabs derive protection from an associated actinian (e.g. Brooks, 1989). A similar protection has often been inferred to derive from zoanthids, but is unproven as yet. The enlargement of its gastropod shell by a carcinoecium building epizoanthid is, also for good reasons, inferred to be advantageous for a hermit crab, but it is likewise unproven. Zoanthids may prevent certain shell destructing epizoid organisms from colonizing the shell and shortening its lifespan as a hermit crab housing (Stachowitsch, 1980), but their role as such is unknown in the deep sea. Gastropod shells were said to be in short supply or absent (Balss, 1924: 776) in the deep sea. However, numerous species of hermit crabs in the deep sea inhabit gastropods shells, without zoanthid or actinian associates (e.g. Lemaitre, 1989: 23, 28, 51, 57, etc). One wonders about the source of these gastropod shells considering the idea (Correns, 1937) that calcium carbonate dissolves more rapidly in the deep sea than in shallow water.

Actinians derive protection from hermit crabs (Brooks & Gwaltney, 1993). Nothing is known about epizoanthids associated with hermit crabs in this respect. Among the possible advantages derived by zoanthids from living with a hermit crab, is the availability of a substrate offered by hermit crabs and their gastropod shells in muddy environments (Stachowitsch, 1980: 95). Currents produced by the hermit crab may benefit passive filter feeders (Stachowitsch, 1980: 94) like species of *Epizoanthus*.
As long as the exact conditions under which deep sea hermit crabs live are unknown, the importance of the (dis)advantages of living with epizoanthids, and vice versa, will be unknown.

For convenience of comparison, the diversity of zoanthid-hermit crab associations may be tentatively divided into three types:
a) zoanthid colonies occasionally occurring on gastropod shells occupied by a hermit crab, like *Epizoanthus arenaceus* (which covers 7% of the shells occupied by *Paguristes eremita* and *Pagurus cuanensis* in the Adriatic according to Stachowitsch, 1980: 87). Different species of more than one zoanthid genus may be involved, although at present only species of *Epizoanthus* seem to be known as hermit crab associates. The larvae of the zoanthids involved should at least not avoid calcium carbonate substrates for settlement.
b) species of *Epizoanthus* covering most part of a gastropod shell inhabited by a hermit crab and forming a carcinoecium like *Epizoanthus incrustatus*. The different species of *Epizoanthus* involved may have their polyps organized in different ways. Probably, hermit crabs in this category have adapted behaviourally, in relation with possessing a carcinoecium. Several species of hermit crabs in different genera are involved. Because of lack of information, it is in most cases impossible to relate a certain zoanthid-hermit crab pair to either category a) or b).

c) species of *Epizoanthus* held directly by the hermit crab, covering its abdomen and sometimes having a relatively large ventral polyp as in *Epizoanthus paguropsidis*. At least 13 hermit crab species listed in table 1 have been found to be involved in this type of symbiosis, namely *Paguropsis typica* (see Boas, 1926), *Parapagurus abyssorum* (see Lemaitre, 1989), *P. andreui*, *P. bouvieri*, *P. furici*, *P. latimanus*, *P. saintlaurentae* (see e.g. Lemaitre, 1999), *Sympagurus dimorphus* (see Forest et al., 2000), *S. dofleini* (see Lemaitre, 1994), *S. villosus*, *S. papposus* (see Lemaitre, 1996) and *Oncopagurus orientalis* (see Lemaitre, 1997). The hermit crabs in this category have adapted behaviourally and possibly also physically, like *P. typica* (see Boas, 1926: 17/18), in the possession of appendages able to hold the zoanthid colony like a sack.

All three types of zoanthid-hermit crab associations have an actinian-hermit crab analogue. Because of their equally non-obligate occurrence with hermit crabs, e.g. actinian species in the genus *Calliactis* form the counterpart of zoanthids in category a). The best known example of an actinian counterpart to the zoanthids in b) would be *Adamsia palliata* (O.F. Müller, 1776) with its large carcinoecium. In the same category are e.g. members of the genus *Stylobates* Dall, 1903, which make a near-perfect carcinoecium (originally described as a gastropod, see Dall, 1919). One of the actinian equivalents of the zoanthids in category c) is the undescribed partner of *Munidopagurus macrocheles* (A. Milne Edwards, 1880) which likewise is not known to use a gastropod shell (Provenzano, 1971).

Since the start of the revision of the Parapaguridae (Lemaitre, 1989), the taxonomic situation in respect of the hermit crabs has improved. Nevertheless, an attempt to arrange the contents of table 1 in the order of the hermit crab species remains fruitless as there are too many associations in which the identity of only one partner is known.

Taxonomical work on the genus *Epizoanthus* is wanting since the 1930s, and several species of *Epizoanthus* in table 1 have not been mentioned in the literature since their original description. The number of zoanthid species occurring with one hermit crab species will be unknown as long as their taxonomy remains in the present state.

Acknowledgments

Dr G.W.N.M. van Moorsel and Dr W. Dekker independently collected specimens of *Epizoanthus incrustatus* for me, in May 1986 and August 1996 respectively, while on board of Dutch research vessels. Thanks are also due to Dr. R. Lemaitre for checking the taxonomic status of the Parapaguridae in table 1.

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