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A review of cnidarian epibionts on marine crustacea

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Abstract

An updated inventory of the cnidarian species living as epibionts on Crustacea was conducted. Cnidarian species that attach themselves to gastropod shells of hermit crabs were also considered. One hundred and forty-eight species of cnidaria were included, with similar numbers of hydrozoans and anthozoans. There were 163 basibiont species that were mostly decapod species. The presence of these epibionts on different crustacean species and their taxonomic positions were indicated. This review is intended to serve as a useful tool for future studies of this type of epibiosis.

INTRODUCTION

Epibiosis is the presence of life forms on the surface of other organisms (Wahl 1989). In many cases the form that colonises, i.e. the epibiont, can be an organism with a sessile phase of its life cycle. The organism on which the epibiont settles is referred to as a basibiont, which provides the attachment surface and is generally larger than the epibiont (Fernandez-Leborans, Cárdenas 2009). This phenomenon is very common in aquatic environments, where hard substrates available for sessile forms are limited (Wahl 1989, Gili et al. 1993). The existence of epibiosis implies ecological interactions between the partners. In aquatic environments, many crustacean groups, such as cladocerans, copepods, cirripedes, isopods, amphipods and decapods, serve as basibionts for protozoan micro-epibionts and invertebrate macro-epibionts (Ross 1983; Corliss 1979; Fernandez-Leborans, Tato-Porto 2000b). Epibiosis is the evolutionary effect of interactions between environmental factors and benthic life forms (Key et al. 1999). It is a dynamic process, and the benefits and disadvantages for the organisms involved vary depending on the environmental conditions (Bush et al. 2001).

Although, in principle, the epibiosis is not necessarily obligatory, and it does not meet all the requirements for the survival of each species, except for the attachment to a substrate, there may be several effects for both the epibiont and the basibiont. The symbiotic relationship could be either commensalism, mutualism, or parasitism. The epibiosis may produce extensive evolutionary changes in the partners; the effects can include advantages for the epibiont in terms of dispersal and geographical expansion (Gili et al. 1993, Threlkeld et al. 1993), an increase in the nutrient supply, and protection against predation or negative environmental conditions (Abelló et al. 1990). Epibiosis can also be disadvantageous to the epibiont by inducing ontogenetic or behavioural changes (Threlkeld et al. 1993). For example, epibiosis can be beneficial for the basibiont by providing both mimetic protection and cleaning (Ingle 1983; Maldonado, Uriz 1992). In contrast, epibiosis may be negative for the basibiont by restricting its mobility

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and affecting its growth, moulting and functioning of several organs (the eyes, gills, and appendages) (Overstreet 1983, 1987; Reaka 1978). Epibiosis may cause an increased risk of predation (Willey et al. 1990). Epibionts and basibionts may compete for nutrients (Fernandez-Leborans et al. 2006).

Cnidarians are one of the most frequent epibionts on crustaceans. Cnidarian species are frequent on copepods, cirripeds, isopods and decapods. Different aspects of the epibiotic relationships between cnidarians and crustaceans have been studied, i.a. the presence and spatial distribution of epibionts, interactions between the basibiont and the epibiont, patterns of colonisation, effects of abiotic parameters, and the influence on the life cycles and physiology of the organisms involved.

The comparison of presence/occurrence of cnidaria and other epibionts

Cnidaria have frequently been found with other epibionts of diverse crustacean species groups. Protozoan, molluscs, annelids, other crustacean, and bryozoa, etc. commonly share the hard substrates corresponding to the exoskeleton of crustacea (Fernandez-Leborans, Tato-Porto 2000). One of the most studied crustaceans, the hermit crab *Pagurus bernhardus,* may harbour 51 epibiont species belonging to 11 groups (foraminifers, cnidaria, platyhelminthes, nemertines, molluscs, polychaetes, crustacea, nematodes, foronids, bryozoa and tunicata) (Reiss et al. 2003).

Different species from different groups of organisms have been found as epibionts on the shell-crab complex of hermit crabs. The shells and crabs may present different epibionts. Cnidaria, especially hydrozoans, can in many cases dominate a large portion of the surfaces. Hydrozoans are frequently located on areas surrounding the aperture of the shell or define the edges of the apex of the shell's aperture. This location appears to be most effective for the epibiont to use the nutrient particles from crab's activities. Other epibionts, such as ciliate protozoans, cirripeds and polychaetes, are distributed on shell surfaces without hydrozoans. In many cases, the characteristics of the hydrozoan colonies determine an extensive colonisation of the basibiont surface, which is favored by the structure or the base of the colony and the development of zooids. This fact leads several epibiont species to follow an adaptation process for living as hyperepibionts on hydrozoan colonies. Bacteria, microalgae, foraminifera, and polychaetes have been observed on hydrozoans (Bavestrello et al. 2008) and also some ciliate protozoan species, such as the peritrich ciliate *Vorticella,* the suctorian *Ephelota*, the hypotrich ciliate *Kerona pediculus* (O.F. Müller, 1773)*,* and the licnophorid *Licnophora chattoni* Villeneuve-Brachon, 1939 (Bavestrello et al. 2008; Silva-Neto et al. 2012; Warren, Robson 1998). Some of the hydrozoan epibionts, such as *Hydractinia echinata* (Fleming, 1828), are obligate epibionts that account for the highest percentage of organisms on the basibiont surface (Reiss et al. 2003).

The coexistence between hydrozoans and other epibionts can be observed in other crustaceans, such as the lithoded decapod *Lithodes maja* (Linnaeus, 1758) *(as L. maia*). This decapod may have epibionts from diverse groups together with cnidarian epibionts. Two hydroid species of the genus *Obelia* have been found on this crab along with 4 polychaete species, 3 bivalves, 2 amphipods, 2 cirripeds, 3 bryozoans and 1 leech species. In this case, hydrozoan species were also the most abundant species. As in other cases of epibiosis on crustaceans, the structure of the carapace and the size of the basibiont affected the presence and the number of different epibionts (Dvoretsky, Dvoretsky 2008).

In the western areas of Scotland, the crab *Necora puber (*as *Liocarcinus puber)*, together with the epibiont hydrozoans *Clytia* sp. and *Leuckartiara* sp., has been shown to present the polychaetes *Pomatoceros triqueter* (Linnaeus, 1767) and *Hydroides norvegica* Gunnerus, 1768, the cirriped *Balanus crenatus* Bruguière, 1789, the entoproct *Barentsia matsushimana* Toriumi, 1951, the ciliate protozoans *Ephelota plana* Annandale, 1911, *Ephelota gemmipara* (Hertwig, 1875), *Chilodochona quennerstedti* Wallengren, 1895 and *Cothurnia longipes* Kahl, 1935 (Fernandez-Leborans, Gabilondo 2008). Furthermore, hydrozoans have been found on the carapace, chelipeds and anterior periopods of another related species of decapod crustaceans, i.e. *Liocarcinus depurator*. These hydrozoans coexist with the suctorian ciliate, which has been found on the same areas as the hydrozoan (Fernandez-Leborans, Gabilondo 2005).

The coexistence of the ellobiopsid *Thalassomyces* sp. and the hydroid *Earleria corachloeae* Widmer, Cailliet & Geller, 2010 on the shrimp *Pasiphaea pacifica* Rathbun, 1902 from Monterey Bay (California) was described (Widmer et al. 2010). *Thalassomyces* is a parasitic alveolate protozoan with a nutrient-absorbing "root" and has been documented to exist on diverse crustaceans, including a wide array of

pelagic marine malacostracan crustaceans (shrimp, euphausiids, mysids, amphipods, and copepods) (Silberman et al. 2004). The presence of the ellobiopsid and the hydroid on the shrimp carapace did not seem to affect the swimming behaviour of the shrimp when compared with an uninfected shrimp (Widmer et al. 2010).

The epibiont communities described on two species of the decapods *Cancer (C. gracilis* Dana, 1852, *C. productus* J. W. Randall, 1840 and *C. magister* Dana, 1852) included 29 epibiont species from ten phyla. The hydrozoan colonies have been observed on the ventral surfaces and limbs, with the cirripeds as the most abundant ones and the tube-dwelling polychaetes being less common. Other organisms, such as algae, bryozoa, mollusks, porifera and tunicates, have been found on these crabs sampled in Barkley Sound, Brisitsh Columbia (McGaw 2006).

The spatial distribution of species in these epibiotic communities, in which cnidaria may be present, can be considered in several ways:

1) on each basibiont, the colonisation can follow a selection of different habitats on the surface of the basibiont;
2) many species of epibionts show a particular pattern of distribution, which may correspond to, as appropriate, the concepts of aggregation, overlap, exclusion, and association (Hayashi, Tsuji 2007);
3) epibiont communities appear to behave as a whole, regardless of particular species, which can be verified by the colonisation process;
4) the epibiont species tend to occupy the available substrate within the particular requirements of each functional group but also tend to achieve the equilibrium among species and groups, compensating for diversity and density (Fernandez-Leborans et al. 2006);
5) as it was evidenced in the study of the epibiont communities of the shrimp *Caridina* from three lakes in Indonesia, the basibiont represents a dynamic environment in which species of the epibiont community develop a colonisation pattern.

The species were located on the host in a particular pattern, which is shown in the results: the species distribution patterns were associated with different lakes. Regardless of the species present, and in all cases, each species was found to follow the same general pattern of distribution (Fernandez-Leborans et al. 2006). The distribution of epibionts on the surface of basibionts is determined by the following factors:

1) biotic and abiotic microlocal parameters;
2) water currents generated by feeding and respiratory activities of the basibiont;
3) availability of nutrients (Threlkeld et al. 1993);
4) behaviour of the basibiont (e.g. burying in sediment, copulation, emersion, nocturnal activity, hiding under rocks);
5) the age, sex, body shape, and size of the host (Connell & Keough 1985; Key et al. 1999);
6) moult and intermoult periods;
7) the presence of particular chemical compounds;
8) the presence of protrusions and rugosities on the surface of the basibiont (Viljoen, Van As 1983) and other differences according to particular surfaces of the basibiont;
9) mucosity and sediment on the host surface preventing the adhesion of epibionts (Mulisch et al. 1986);
10) the presence of a bacterial community and the associated ciliate protozoan fauna on the basibiont surface (Fernández-Leborans, Herrero Córdoba 1997).

In the present revision, 159 crustacean species (including the genera) were recognized as basibionts for 189 species of cnidarian epibionts (Appendix 1), including decapods as the most frequently (92.02%) reported species, while hydrozoans and anthozoans had similar proportions (55.97% and 44.03%, respectively).

There were several reasons for conducting this review, including the following ones:

1) Although there are numerous academic contributions regarding the presence of cnidarian epibionts in crustaceans, there are no reviews of different species of cnidarian epibionts and the corresponding species of crustacean basibionts.
2) Cnidarians in many cases represent the largest fraction of the epibiont community in crustaceans, both in terms of biomass and the number of individuals.
3) Both the diversity of cnidarian epibionts and the crustacean basibiont species in which the former are found are remarkable.
4) The cnidarian-crustacean epibiosis has many singular aspects that are related to interactions

between both types of organisms (colonisation, behaviour, the choice of epibiont and basibiont, specificity, defence, predation, feeding, life cycles, synchronisation, physiology, mechanisms antifouling, etc.).

This review provides not only the idea of species diversity of cnidarians and crustaceans involved in the epibiosis but also the relative importance of different taxonomic groups of cnidarians and crustaceans as epibionts. The differences may be related to particular biological characteristics of each party in the community and the characteristics of the whole community in epibiosis and its environment.

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Appendix 1

List of cnidarian species found as epibiont on crustacea. (Classification according to Bouillon et al. 2006, Cairns et al. 2002)

Cnidaria	Crustacea	References	Geographical distribution
class Hydrozoa; subclass Hidroidolina; order Leptothecatae			
Egmundella valdiviae Stechow, 1921	*Parapylocheles scorpio* (Alcock, 1894)	Ruthensteiner et al. 2008	Western Sumatra; south-west of Pulo Nias
Aglaophenia kirchenpaueri (Heller, 1868), *Aglaophenia octadonta* (Heller, 1868) *Aglaophenia picardi* *Aglaophenia tubiformis* (Heller, 1868)	Barnacles *(Balanus perforatus)* (1)	Boero&Fresi 1986	Portofino, Italy
Clytia hemisphaerica (Linnaeus, 1767)	*Inachus dorsettensis* (Pennant, 1777); *Maja squinado* (Herbst, 1788); *Hymenosoma orbiculare* Desmarest, 1823; *Lernaeocera branchialis* (Linnaeus, 1767)	Marine Biological Association 1957; Ingle 1983; Millard 1975; Leloup 1931; Capart 1948	(Plymouth, UK); (Northern South West Africa to Mozambique)
Clytia hemisphaerica (as Campanularia johnstoni)	*Pagurus bernhardus*	Jensen&Bender 1973	Marine waters of Sweden
Campanularia hincksii Alder, 1856 *Campanularia integra* MacGillivray, 1842	Barnacles *(Balanus perforatus)* (1)	Boer&Fresi 1986	Portofino, Italy
Obelia geniculata (Linnaeus, 1758) (as *Laomedea geniculate*)	*Lernaeocera branchialis* (Linnaeus, 1767)	Leloup 1931, Capart 1948	
Obelia geniculata	*Macrocheira kaempferi* (Temminck, 1836); *Lithodes maja* (Linnaeus, 1758) (as *L. maia*); *Paralithodes camtschaticus* (Tilesius, 1815); *Anilocra physodes* (Linnaeus, 1758); *Pagurus bernhardus; Dardanus arrosor; Jasus lalandii* (H. Milne-Edwards, 1837); *Lernaeocera branchialis*	Dvoretsky&Dvoretsky 2008, Leloup 1931, Reiss et al. 2003, Ross&Zamponi 1982	Barents Sea, North Sea, Mediterranean Sea
Laomedea calceolifera (Hincks, 1871) (*Laomedea conferta*)	*Hyas araneus* (Linnaeus, 1758)	Hamond 1957; Ingle, 1983	(Monterey Bay, California, USA)
Earleria corachloeae Widmer, Cailliet & Geller, 2010	*Pasiphaea pacifica* Rathbun, 1902	Widmer et al. 2010; Hiro 1939	Tonda, Sakai, Wakayama-Ken, Japan
Obelia undotheca Stechow 1923	*Oregonia gracilis* Dana, 1851	Ruthensteiner et al. 2008	Bering Sea, Kamtschatka Peninsula, Awatsch
Obelia longissima (Pallas, 1766)	*Lithodes maia; Paralithodes camtschaticus* (Tilesius, 1815); *Syscenus infelix* Harger, 1880	Dvoretsky&Dvoretsky 2008, Vader et al. 1981	(Barents Sea)
Obelia commissuralis McCrady, 1859	*Balanus eburneus* Gould, 1841	Calder 1971	(Chesapeake Bay, USA)
Obelia dichotoma (Linnaeus, 1758)	*Dardanus arrosor, Lepas, Balanus eburneus, Mithraculus forceps* A. Milne-Edwards, 1875	Cuadras&Pereira 1977, Calder 1971	(Mediterranean Sea); (Chesapeake Bay, USA)
Obelia sp.	*Cancer productus* Randall, 1840	Mc Gaw 2006	(Barkley sound, British Columbia)
Orthopyxis integra (MacGillivray, 1842)	*Dehaanius dentatus* (H. Milne-Edwards, 1834)	Millard 1975	(Southern Africa)
Plumularia obliqua, *Plumularia setacea* (Linnaeus, 1758)	*Balanus perforatus*	Boero&Fresi 1986	Porotfino, Italy
Halecium crinis Stechow, 1913	*Macrocheira kaempferi*	Hiro 1939	(Tonda, Sakai, Wakayama-Ken, Japan)
Halecium beanii (Johnston, 1838), *Halecium mediterraneum*	Barnacles (*Balanus perforatus)* (1)	Boero&Fresi 1986	Portofino, Italy
Halecium labrosum Alder, 1859	*Hyas araneus* (Linnaeus, 1758), *Balanus perforatus* (1)	Hamond 1957; Boero&Fresi 1986	(Norfolk Coast, USA), Portofino, Italy
Sertularella gaudichaudi	*Balanus perforatus*	Boero&Fresi 1986	Portofino, Italy
Sertularella sinensis Jäderholm, 1896	*Macrocheira kaempferi*	Hiro 1939	(Tonda, Sakai, Wakayama-Ken, Japan)
Sertularella ellisii (Deshayes & Milne Edwards, 1836) *(as Sertularella polyzonias)*	*Maja squinado* (Herbst, 1788)	Ševčič 1966	
Sertularella turgida (Trask, 1857)	*Metacarcinus gracilis (*Dana, 1852*) (as Cancer gracilis); Metacarcinus magister (*Dana, 1852*) (as Cancer magister); Cancer productus* Randall, 1840	Mc Gaw 2006	(Barkley sound, British Columbia)
Sertularella	*Libinia spinosa* H. Milne-Edwards, 1834		
Sertularia argentea (Linnaeus, 1758) (as *Sertularia cupressina* var.*argentea*)	*Pisa armata* (Latreille, 1803)	Carrington&Lovett 1881	
Sertularia argentea LInnaeus, 1758	*Libinia, Amphibalanus improvisus* (Darwin, 1854) (as *Balanus improvisus)*	Calder, 1971	(Chesapeake Bay, USA)
Hydrallmania falcata (Linnaeus, 1758)	*Pisa armata, Pisa tetraodon* (Pennant, 1777)	Carrington&Lovett 1881	
Abietinaria elsaeoswaldae Stechow, 1923	*Oregonia gracilis* Dana, 1851	Ruthensteiner et al. 2008	(Pacific Grove, Monterey Bay, California, USA)
Abietinaria pacifica Stechow, 1923	*Oregonia gracilis*	Ruthensteiner et al. 2008	(Pacific Grove, Monterey Bay, California, USA)
Phialella sp.	*Pagurus bernhardus*	Fernandez-Leborans& Gabilondo 2006	Clyde and Argyll, Scotland)
Stegopoma plicatile (Sars, 1863)	*Bathynectes piperitus* Manning & Holthuis, 1981	Gili et al. 1993	(off southern Namibia, Africa)
	Neolithodes asperrimus Barnard, 1947	Gili et al. 1989	(Namibian coast)
Kirchenpaueria pinnata (Linnaeus, 1758)	*Hyas araneus*	Hamond 1957	(Norfolk coast, USA)
Ventromma halecioides (Alder, 1859) *Dynamena disticha* (Bosc, 1802)	Barnacles (*Balanus perforatus)* (1)	Boero&Fresi 1986	Portofino, Italy
Nemertesia antennina (Linnaeus, 1758)	*Hyas araneus*, *Hyas coarctatus* Leach, 1816	Hamond 1957	(Norfolk coast, USA)
*Halopteris tenella (*Verrill, 1874*) (as Schizotricha tenella)*	*Balanus eburneus* Gould, 1841, *Libinia*	Calder 1971	(Chesapeake Bay, USA)
order Anthoathecatae			
Stylaster californica (Verrill, 1866) (as *Allopora californica)*	*Armatobalanus nefrens* (Zullo, 1963) (as *Balanus nefrens)*	Little-Ostarello 1973	(Carmel river Beach, Bluefish Cove, Carmel, California, USA)
Leuckartiara octona (Fleming, 1823)	*Macrocheira kaempferi, Geryon longipes* (H. Milne-Edwards, 1882)	Hiro 1939, Di Camillo et al. 2008	(Tonda, Sakai, Wakayama-Ken, Japan); (Southern Adriatic Sea)
	Carcinus maenas (Linnaeus, 1758), *Hyas*, *Halicarcinus*, *Macrocheira kaempferi*	Marine Biological Association 1957; Ingle 1983	(Plymouth, UK)
Leuckartiara sp.	*Liocarcinus depurator, Pagurus bernhardus, Liocarcinus puber*	Fernandez-Leborans&Gabilondo 2005, 2006, 2008	(Isle of Cumbrae, Scotland)
Hydrichthys sp.	*Cardiodectes medusaeus* (Wilson C.B., 1908) (on the fish *Stenobrachius leucopsarus*) Eigenmann & Eigenmann, 1890	Moser&Taylor 1978	(Santa Barbara, San Diego, California, USA)
Hydrichthys (*Ichthyocodium*) *sarcotretis* (Jungersen, 1913)	*Sarcotretes scopeli* Jungersen, 1911 (on the fish *Benthosema glaciale* (Reinhardt, 1837) (as *Scopelus glacialis*)	Jungersen 1911, Templeman 1973	(SE coast Ireland); (NW Atlantic)
	Sphyrion lumpi (Krøyer, 1845) (on the fish *Sebastes mentella* Travin, 1951)	Jones 1966 Templeman 1973	(European Atlantic Ocean); (NW Atlantic)
Coryne muscoides (Linnaeus) *Coryne pusilla* Gaertner, 1774 *Cladocoryne floccosa* *Dicoryne conferta* (Alder, 1856)	Barnacles (*Balanus perforatus)* (1); *Hyas coarctatus* Leach,1815, *Anapagurus hendersoni* Barnard, 1947; *Anapagurus cf. hendersoni; Pagurus bernhardus*	Boero&Fresi 1986, Roper 1913, Millard 1975, Ingle 1983, Jensen&Bender 1973, Kramp 1935	(Porotofino, Italy); (Northumberland, UK); (Plymouth, UK); (False Bay to Mossel Bay, Southern Africa); (Roscoff, France)
Dicoryne valdiviae Stechow, 1923	*Parapylocheles scorpio* (Alcock, 1894)	Ruthensteiner et al. 2008	Western Sumatra
Eudendrium capillare Alder, 1856	*Hyas coarctatus, Balanus perforatus* (1)	Bruce et al. 1963; Ingle, 1983; Boero&Fresi 1986	(Isle of Man, UK); (Portofino, Italy)
Eudendrium racemosum	Barnacles (*Balanus perforatus)* (1)	Boero&Fresi 1986	Portofino, Italy
Eudendrium ramosum (Linnaeus, 1758)	Barnacles (Balanus perforatus) (1)	Boero&Fresi 1986	Portofino, Italy
Eudendrium album Nutting, 1898	*Balanus improvisus* Darwin, 1854	Calder 1971	(Chesapeake Bay, USA)
Peralella propagulata Bavestrello, 1987	Hermit crabs	Schuchert, 2007	
Hydractinia sp.	*Geryon longipes* A. Milne-Edwards, 1882	Di Camillo et al. 2008	(Southern Adriatic Sea)
Hydractinia echinata, (Fleming, 1828)	*Anapagurus chiroacanthus* (Liljeborg, 1856*); Cibanarius vittatus* (Bosc, 1802); *Dardanus arrosor; Paguristes hummi* Wass, 1955; *Pagurus acadianus* J. E. Benedict, 1901*; P. annulipes* (Stimpson, 1860); *P. bernhardus; P. carolinensis* McLaughlin, 1975; *P. cuanensis* Bell, 1845; *P. excavatus* (Herbst, 1791); *P. longicarpus* Say, 1817; *P. pollicaris* Say, 1817; *Petrochirus diogenes* (Linnaeus, 1758); *Balanus eburneus* Gould, 1841	Karlson&Cariolou 1982, Ingle&Christiansen 2004; Sandford 2003, Samuelsen, 1970; Mercando&Lytle 1980 (North American Coast Atlantic Ocean) Cuadras&Pereira 1977; Cunningham et al. 1991 Karlson&Shenk 1983 Puce et al. 2008 ; Reiss et al. 2003 (North Sea); Calder 1971	(Dog Island, St George Sound, Florida, USA); (Raunefjorden, Western Norway); (Mediterranean Sea); (North Atlantic areas and Gulf of Mexico); (Chesapeake Bay, USA)
	Pagurus sp.	Schijfsma 1935; Cazaux 1961; Bennet 1962; Rees 1967; Christensen 1967; Mills 1976 Mercando&Lytle 1980; Brooks&Mariscal 1986	(Knåhaken Reef in the Øresund, Denmark); (Gulf of Mexico); (North American Coast Atlantic Ocean), (northeastern Gulf of Mexico)
Hydractinia epiconcha Stechow, 1908	*Pagurus gracilipes* (Stimpson, 1858), *Dardanus arrosor* (Herbst, 1796) *(as Pagurus arrosor)*	Balss 1924; Mills 1976	Gulf of Mexico
Hydractinia sodalis Stimpson, 1859	*Pagurus constans* (Stimpson, 1858)	Goto 1910; Rees 1967	
Hydractinia symbiolongicarpus Buss & Yund, 1989	*Pagurus longicarpus* Say, 1817, *P. pollicaris*	Damiani 2003; Bach et al. 2006; Cunningham et al. 1991; Buss&Yund 1989	(Beaufort, NC, USA); (North Atlantic areas and Gulf of Mexico); (Long Island Sound, USA)
Hydractinia diogenes Millard, 1959	*Diogenes costatus* Henderson, 1893	Millard 1975	(Inhaca to Morrumbene, South Africa)
Hydractinia epiconcha Stechow, 1908	*Dardanus arrosor, Pagurus gracilipes*	Dales 1957	
Hydractinia polyclina L. Agassiz, 1862	*Pagurus acadianus* J. E. Benedict, 1901, *P. longicarpus,*	Cunningham et al. 1991; Folino&Yund 1998	(North Atlantic areas and Gulf of Mexico)
Hydractinia exigua (Haeckel, 1880)	*Diogenes pugilator* (Roux, 1829)	Puce et al. 2008	
Hydractinia pruvoti Motz-Kossowska, 1905	*Clibanarius erythropus* (Latreille, 1818)	Puce et al. 2008	
Hydractinia rubricata Schuchert, 1996 (Edwards, 1972) *(as Hydractinia selena)*	*Diacanthurus rubricatus* (Henderson, 1888) (as *Pagurus rubricatus)*	Schuchert, 1996	(Kaikoura Peninsula, New Zealand)
Hydractinia aculeata (Wagner, 1833) *Hydractinia fucicola* (Sars, 1857) *Hydractinia carica* Bergh, 1887	*Cestopagurus timidus* (Roux, 1830) *(as Catapaguroides timidus)* Hermit crabs Hermit crabs	Schuchert, 2008 Schuchert 2008 Schuchert 2008	Mediterranean. Type locality: Adriatic Sea, Trieste Western Meditarranean, Southern Brittany European coasts and Japan Sea
Hydrocorella africana Stechow, 1921	*Clibanarius* sp., *Dardanus arrosor, Diogenes brevirostris* Stimpson, 1858, *D. costatus, Pagurus cuanensis* Bell, 1845, *Pagurus placens* Stebbings, 1924	Millard 1975; Balss 1924	(Orange river mouth to Durban, South Africa)
Janaria mirabilis Stechow, 1921	*Manucomplanus cervicornis* (Benedict, 1892), *M. varians* (Benedict, 1892), *M. varians* Benedict, 1892) (as *Eupagurus varians)*	Cairns&Barnard 1984; Bouvier 1898 Ruthensteiner et al. 2008	(Eastern Pacific) (Gulf of California, USA)
Stylactis fucicola *Stylactis inermis* *Stylactis aculeata* *Stylactis carcinicola* Hiro, 1939	Barnacles (*Balanus perforatus)* (1) gastropod shell inhabited hermit crab *Macrocheira kaempferi*	Boero&Fresi 1986 Boero&Fresi 1986 Hiro 1939	Portofino, Italy Portofino, Italy (Tonda, Sakai, Wakayama-Ken, Japan)
Hydractinia pruvoti (Motz-Kossowska, 1905) (as *Stylactaria pruvoti)*	*Clibanarius erythropus* (Latreille, 1818)	Bavestrello et al. 2000	
Hydractinia spiralis (Hirihito, 1988) (as Stylactaria spiralis)	*Pagurus constans*	Bouillon et al. 1997	(western Mediterranean)
Stylactaria sp.	*Xanthias haswelli* Caiman, 1911	Bouillon 1994	
Podocoryne selena Mills, 1976	*Pagurus longicarpus, Pagurus pollicaris,*	Mills 1976; Brooks&Mariscal 1986	(Gulf of Mexico); (northeastern Gulf of Mexico)
	Clibanarius vittatus (Bosc, 1802), *P. longicarpus, P. pollicaris*	Brooks&Mariscal 1985; Mills 1976	(northeastern Gulf of Mexico); (Gulf of Mexico)
Podocoryne areolata (Alder, 1862)	*Hyas coarctatus,Anapagurus laevis, Pagurus bernhardus*	Evans 1978; Edwards 1972	(north east England, UK)

Podocoryne borealis (Mayer, 1900)	*Anapagurus laevis* (Bell, 1945), *Pagurus bernhardus*	Edwards 1972	(Clyde Sea Area, soth west Scotland)
Hydractinia carnea (M. Sars, 1846) *(as Podocoryne carnea)*	*Anapagurus laevis, Dardanus arrosor, Paguristes eremita, Pagurus bernhardus, P. longicarpus, P. pollicaris, P. cuanensis* Bell, 1845, *P. prideaux* Leach, 1815, *P. pubescens* Krøyer, 1838	Edwards 1972; Cuadras&Pereira 1977; Balss 1924; Stachowitsch 1980; Cunningham et al. 1991; McLean 1983	(Clyde Sea Area, soth west Scotland); (Mediterranean Sea); (North Adriatic Sea, Gulf of Trieste); (North Atlantic areas and Gulf of Mexico)
	Pagurus sp.	Schijfsma 1935; Cazaux 1961; Bennet 1962; Rees 1967; Christensen 1967; Mills 1976; Mercando&Lytle 1980	(Knåhaken Reef in the Øresund, Denmark); (Gulf of Mexico); (North American Coast Atlantic Ocean)
Podocoryne exigua (Haeckel, 1879)	*Diogenes pugilator (* Roux, 1829); *Paguristes eremita* (Linnaeus, 1767)	Cerrano et al. 1998; Bavestrello 1985	Ligurian Sea
Podocoryne sp.	*Pagurus bernhardus*	Matthews 1959	
Polyhydra spinifera Stechow, 1962	*Diogenes pugilator*	Ruthensteiner et al. 2008	(Côte d'Ivoire, Addah)
Leuckartiara octona (Fleming, 1823) *(as Perigonimus repens)*	*Pagurus bernhardus*	Kramp 1935 Jensen&Bender 1973	
Perigonimus sp.	*Paguristes eremita, Pagurus cuanensis*	Stachowitsch 1980	(North Adriatic Sea, Gulf of Trieste)
Bougainvillia ramosa (van Beneden, 1844) *Bougainvillia meinertiae* Jäderholm, 1923	Barnacles (*Balanus perforatus)* (1) *Ceratothoa imbricata* (Fabricius, 1775)	Boero&Fresi 1986 Millard 1975	(Portofino, Italy) (Cape Agulhas, Southern Africa)
Bougainvillia rugosa Clarke, 1882 *Bougainvillia superciliaris* (L. Agassiz, 1849)	*Libinia* various crustaceans	Calder 1971 Arai&Brinckmann-Voss 1980	(Chesapeake Bay, USA) (British Columbia and Puget Sound)
Bougainvillia sp.	*Paguristes eremita; Pagurus cuanensis*	Stachowitsch 1980	(North Adriatic Sea, Gulf of Trieste)
Turritopsis nutricola (McCrady, 1857) *Turritopsis nutricula* McCrady, 1857	Barnacles (*Balanus perforatus)* (1) *Balanus improvisus*	Boero&Fresi 1986 Calder 1971	Portofino, Italy (Chesapeake Bay, USA)
Tubularia larynx Ellis and Solander, 1786 *Tubularia mesembryanthenum* Allman, 1871	Barnacles (*Balanus perforatus)* (1) *Macrocheira kaempferi*	Boero&Fresi 1986 Hiro 1939	Portofino, Ligurian Sea, Italy (Tonda, Sakai, Wakayama-Ken, Japan)
Bouillonia denhartogi Svoboda, Stepanjants & Ljubenkov, 2006 *Ectopleura larynx* (Ellis and Solander, 1786)	*Paralomis formosa* Henderson, 1888 Barnacles (*Balanus perforatus)* (1)	Svoboda et al. 2006 Boero&Fresi 1986	Portofino, Ligurian Sea, Italy
Ectopleura dumortierii (Van Beneden, 1844)	*Balanus improvisus*	Calder 1971	(Chesapeake Bay, USA)
Clavactinia multitentaculata Millard, 1975	*Dardanus arrosor*	Millard 1975	(False Bay and Natal, Southern Africa)
Corymorpha (Euphysa) balssi Stechow, 1932	*Schizophrys dama* (Herbst 1804)	Ruthensteiner et al. 2008	(Heirisson Prong, Shark Bay, Western Australia)
Sarsia phiogaster *Sarsia tubulosa* M. Sars, 1835 *(as Sarsia sarsii)*	Barnacles (*Balanus perforatus)* (1) *Balanus*	Boero&Fresi 1986 Genzano&Rodriguez 1998	Portofino, Italy (Mar del Plata, Argentine)
Antennella africana Broch, 1914	*Macropodia falcifera* (Stimpson, 1857)	Millard 1975	(Lüderitz Bay to Natal, South Africa)
Gattya humilis Allman, 1885	*Dehaanius dentatus* (H. Milne Edwards, 1834)	Millard 1975	(Natal, Southern Africa)
Hydrichthys sarcotretis (Jungersen, 1913) *(as Icthyocodium sarcotretis)*	*Sarcotretes scopeli* Jungersen, 1911	Bouillon 1994	Northern Atlantic coasts
	Sphyrion lumpi (Krøyer, 1845)	Bouillon 1994	
Rosalinda incrustans (Kramp, 1947)	*Anamathia rissoana* (Roux, 1828)	Schuchert 2010	(Atlantic Ocean, west of Gibraltar; western Mediterranean: Costa Brava and Corsica)
class Anthozoa, subclass Octocorallia, order Alcyonacea			
Octocorallia			
Xeniidae			
Xenia	*Cryptodromiopsis unidentata* (Rüppell, 1830)	Lavaleye&Hartog 1995	(Indo-West-Pacific, Indonesia)
Alcyonium digitatum LInnaeus, 1758	*Cyclocoeloma tuberculata* Miers, 1880 *Pisa armata, Pisa tetraodon*	Hartog 1990 Carrington&Lovett 1881	
Nemanthus annamensis Carlgren, 1943	*Lauridromia intermedia* (Laurie, 1906)	Lavaleye&Hartog 1995	(Kenyan coast, Africa)
Anemonia sulcata (Pennant, 1777)	*Inachus phalangium* (Fabricius, 1775), *Macropodia rostrata* (Linnaeus, 1761), *Dromia marmorea* Forest, 1974, *Stenocionops furcata* (Olivier, 1791)	Hartnoll 1971 Lavaleye&Hartog 1995; Hartog 1990	(Canary Islands) (subtropical and temperate European waters)
Phymactis clematis (Drayton in Dana, 1846)	*Allopetrolisthes spinifrons* (H. Milne Edwards, 1837)	Baeza&Stotz 2003	(La Pampilla, Peninsula of Coquimbo, north-central Chile)
Sagartia expansa (Stimpson, 1856) *(as Cancrisocia expansa)*	*Doripppoides facchino* (Herbst, 1785)	Lavaleye&Hartog 1995	(SE Asia)
Phlyctenanthus australis Carlgren, 1949	*Libinia spinosa* H. Milne-Edwatds, 1834	Acuña et al. 2003	(Mar del Plata, Buenos Aires province, Argentine)
Isanthus homolophilus Chintiroglou & Doumenc, 1998	*Lamoha inflata* (Guinot & Richer de Forges, 1981) (as *Hypsophrys inflata)*	Chintiroglou&Doumenc 1998	(French Polynesia)
Diadumene cincta Stephenson, 1925	*Hyas araneus*	Ingle 1996	
Urticina felina (Linnaeus, 1761)	*Hyas araneus*	Ingle 1996	
Urticina consors Verril, 1882	*Parapagurus pilosimanus* S. I. Smith, 1879; *Sympagurus pictus* S. I. Smith, 1883	Balss 1924	
Aiptasia sp.	*Paguristes eremita, Pagurus cuanensis*	Stachowitsch 1980	(North Adriatic Sea, Gulf of Trieste)
Neoaiptasia commensali Parulekar, 1969	*Clibanarius padavensis* De Man, 1888, *Diogenes custos* (Fabricius, 1798)	Parulekar 1969	(Andaman and Nicobar Islands, western India)
Actinia equina (Linnaeus, 1758)	*Cancer pagurus*	Ingle 1983	(Plymouth, UK)
	Paguristes eremita	Balss 1924	
	Cancer pagurus	Holt 1890	
Triactis producta Klunzinger, 1877 *(as Actinia prehensa)*	*Lybia tesselata* (Latreille, in Milbert, 1812)	Karplus et al. 1998	(island of Oahu, Hawaii, USA)
Stylobates aeneus Dall, 1903	*Sympagurus dofleini (*Balss, 1912)	Dunn et al. 1980	(Hawaii, Guam, USA)
Stylobates cancrisocia (Carlgren, 1928)	*Sympagurus trispinosus* (Balss, 1911)	Dunn et al. 1980	(off east Africa)
Stylobates loisetteae Fautin, 1987	*Parapagurus* sp.	Fautin 1987	(western Australia)
Bunodactis chrysobathys Parry, 1951	*Leptomithrax longipes* (Thomson, 1902)	Hand 1975	(New Zealand)
Hormathia coronata (Gosse, 1858)	*Dardanus arrosor*	Balss 1924	
Calliactis polypus (Forskål, 1775)	*Dardanus pedunculatus* (Herbst, 1804), *D. arrosor, D. deformis* (H. Milne-Edwards, 1836), *D. impressus* (De Haan, 1849), *D. lagopodes* (Forskål, 1775), *D. tinctor* (Forskål, 1775), *D. sinistripes* (Stimpson, 1859), *D. gemmatus* (H. Milne-Edwards, 1848), *D. megistos* (Herbst, 1804), *Anapagurus polynesiensis* (Nobili, 1906), *Catapaguroides fragilis* (Melin, 1939), *Parapagurus pilosimanus, Cryptodromiopsis sarraburei* (M. J. Rathbun, 1910)	Imafuku et al. 2000; Carlgren 1949; England 1971; Dales 1957; Yusa et al. 2001; Lavaleye&Hartog 1995 ; Ross 1970 ; Paulay et al. 2003	(Shirahama, Wakayama Prefecture, Japan) (South Africa) (Mururoa Atoll Tuamotu, Polynesia) (western Japan) (Hawaii Islands) (Mariana Islands)
Calliactis parasitica (Couch, 1844) *(as Calliactis effoeta)*	*Pagurus bernhardus*	Balss 1924	
Calliactis japonica Carlgren, 1928	*Dardanus arrosor*	Carlgren 1949; Yusa et al. 2001	(Central Kuroshio Current, East and southern China, east sea Japan) (western Japan)
Calliactis algoaensis Carlgren, 1938	*Dardanus arrosor*	Dales 1957	
Calliactis conchiola Parry, 1952 *(as Calliactis conchicola)*	*Diacanthurus rubricatus* (Henderson, 1888), *Paguristes subpilosus* Henderson, 1888; *Leptomithrax longipes,*	Hand 1975	(New Zealand)
	Paguristes barbatus (Heller, 1862), *Areopaguristes pilosus* (H. Milne Edwards, 1836) (as *Paguristes pilosus), Diacanthurus spinulimanus* (Miers, 1876) (as *Pagurus spinulimanus)*	Schembri&McLay 1983	(Otago region, southeastern New Zealand)
Calliactis parasitica	*Pagurus bernhardus*	Reiss et al. 2003; Ingle&Christiansen 2004	(North Sea)
	Clibanarius erythropus, Dardanus arrosor, Paguristes eremita, Pagurus cuanensis, Pagurus alatus (Fabricius, 1775), *Pagurus excavatus, Pagurus cuanensis, Pagurus* sp.	Ross&Sutton 1961; Cuadras&Pereira 1977; Ross 1971; Christidis et al. 1997; Faurot 1932 Chintiroglou&Doumenc 1991	(Adriatic Sea, Aegean Sea, Celtic Seas, North Sea, South European Atlantic Shelf, South India and Sri Lanka) (Mediterranean Sea)
Calliactis tricolor	*Pagurus pollicaris* (shell), *Clibanarius vittatus* (Bosc, 1802), *Dardanus venosus, Pagurus impressus, Pagurus longicarpus, Petrochirus diogenes, P. granulatus* Olivier, 1811)	Brooks&Mariscal 1986; Cutress&Ross 1969 Brooks&Rittschof 1995; Sandford 2003; Frey 1987; Conover 1976 McLean 1983; Carlgren 1949	(northeasteern Gulf of Mexico); (Dog Island, Florida, USA); (Tampa Bay, Florida, USA); (Atlantic ocean: Eastern Atlantic, from all coasts of western Europe and Britain)
	Callinectes danae S. I. Smith, 1869, *Hepatus pudibundus* (J. F. W. Herbst, 1785), *Libinia ferreirae* Brito Capello, 1871, *L. spinosa, Stenocionops furcata* (Olivier, 1791), *Hepatus epheliticus*	Nogueira et al. 2006 ; Cutress et al. 1970	(South of Paraná and North of Santa Catarina coast) (Caribbean waters)
	Dardanus fucosus Biffar & Provenzano, 1972	López-Victoria et al. 2004	(Concha Bay,Tayrona Natural Park, Colombian Caribbean)
Calliactis sp.	*Paguristes eremita* (shell), *Dardanus* sp., *Loxopagurus loxochelis* (Moreira, 1901)	Caruso et al. 2003; Cowles 1920, Ayres-Peres&Mantelatto 2010	(Sicilian Channel, Italy) (northern coast of São Paulo, Brazil)
Paracalliactis lacazei Dechancé and Dufaure, 1959	*Anapagurus laevis* (Bell, 1945)	Dechancé&Dufaure 1959	
Paracalliactis mediterranea Ross & Zamponi, 1982	*Dardanus arrosor, Pagurus alatus, Pagurus variabilis* Milne-Edwards & Bouvier, 1892	Ross&Zamponi 1982	(Mediterranean Sea)
Paracalliactis japonica Carlgren, 1928	*Dardanus arrosor*	Carlgren 1928	
Paracalliactis rosea	*Diacanthurus rubricatus, Lophopagurus lacertosus* (Henderson, 1888), *Paguristes subpilosus, Parapagurus dimorphus* (Studer, 1883), *Pylopagurus crenatus* (Borradaile, 1916), *Leptomithrax longipes*	Hand 1975	(New Zealand)
Paracalliactis rosea Hand, 1975	*Paguristes barbatus, Parapagurus dimorphus, Lophopagurus,*	Schembri&McLay 1983	(Otago region, southeastern New Zealand)
Paracalliactis stephensoni Carlgren, 1928	*Parapagurus pilosimanus*	Carlgren 1928	
Paracalliactis valdiviae	*Oncopagurus bicristatus* A. Milne-Edwards, 1880); *Sympagurus andersoni* (Henderson, 1896)	Carlgren 1928	
Sagartiogeton undatus (Müller, 1778)	*Pagurus excavatus*	Chintiroglou et al. 1992	(French Polynesia)
Anthothoe	*Dardanus gemmatus, D. deformis, D. megistos*	Paulay et al. 2003	(Mariana Islands)
Verrilactis paguri (Verril, 1869)	*Diogenes edwardsii* (De Haan, 1849)	Goto et al. 2007	(Seto Inland Sea, Japan)
Sagartiomorphe carlgreni Kwietniewski, 1898 *(as Sagartiomorphe paguri)*	*Dardanus* sp., *Dardanus deformis,D. gemmatus, Diogenes edwardsii*	Cutress&Ross 1969; Haig&Ball 1988; Goto et al. 2007	(Australia and eastern Indonesian waters) (Seto Inland Sea, Japan)
Sagartiomorphe sp.	*Diogenes edwardsii*	Ross 1983	
Phymanthea pluvia (Drayton in Dana, 1846)	*Allopetrolisthes spinifrons* (H. Milne-Edwards, 1837)	Baeza&Stotz 2003	(La Pampilla, Peninsula of Coquimbo, north-central Chile)
Baloceroides	*Lilia*	Doumenc&Van Praët 1987	
Antholoba achates (Drayton in Dana, 1846)	*Libinia spinosa, Hepatus chilensis* H. Milne-Edwards, 1837	Acuña et al. 2003	(Mar del Plata, Buenos Aires province, Argentine)
Paranthus rapiformis (Le Sueur, 1817)	*Pontonia domestica* Gibbes, 1850	Strenth&Chace 1995	(south Texas Coast, USA)
subclass Hexacorallia; order Actiniaria			
Gonactinia prolifera (Sars, 1835)	*Anapagurus chiroacanthus, Pagurus bernhardus, P. cuanensis*	Samuelsen 1970 ; Jensen&Bender 1973	(Raunefjorden, Western Norway)
subclass Hexacorallia; order Zoanthidea			
Epizoanthus abyssorum Verril, 1885	*Parapagurus pilosimanus*	Ates 2003	(northern coast, USA)
Epizoanthus arenaceus Delle Chiaje, 1823	*Paguristes eremita, Pagurus cuanensis*	Ates 2003	(Adriatic Sea, Aegean Sea, Celtic Seas, Western Mediterranean)
Epizoanthus carcinophilus Carlgren, 1923	*Parapagurus bouvieri* Stebbing, 1910, *P. pilosimanus*	Carlgren 1938; Balss 1924; Ates 2003	(South Africa); (Agulhas Bank Natal, South Africa)
Epizoanthus chuni Carlgren, 1923	*Parapagurus arcuatus*	Balss 1924; Ates 2003	(East African Coral Coast)
Epizoanthus frenzeli Pax, 1932	*Paguristes eremita*	Ates 2003	(Adriatic Sea)
Epizoanthus incrustatus (Duben & Koren, 1847)	*Anapagurus laevis, Catapagurus sharreri* H. Milne-Edwards, 1880 *, Pagurus bernhardus, P. excavatus, P. politus* (S. I. Smith, 1882), *P. pubescens, Sympagurus pictus*	Muirhead et al. 1986; Balss 1924; Ates 2003	(north– east Atlantic); (Celtic Seas, North Sea, Scotian Shelf, South and West Iceland, Southern Norway, Virginian coast)
Epizoanthus indicus Lwowsky, 1913	*Parapagurus* sp.	Ates 2003	(Japan)

Epizoanthus paguricola (Roule, 1900)	*Anapagurus chiroacanthus, A. laevis, Pagurus cuanensis, Simpagurus dimorphus*	Roule 1900; Ates 2003 Schejter&Mantelatto 2009 (southwestern Atlantic Ocean)	(Mediterranean Sea) (Western Mediterranean, Western and Northern Madagascar)
Epizoanthus paguriphilus Verril, 1882	*Pagurus alatus, Parapagurus pilosimanus*	Urzelai et al. 1990 ; Muirhead et al. 1986; Balss 1924	(Cap Breton, Biscay Bay) (north– east Atlantic)
Epizoanthus paguropsidis Ates, 2003	*Paguropsis typica* Henderson, 1888	Boas 1926; Ates 2003	
Epizoanthus parasiticus Hertwig, 1882	*Pagurus pubescens*	Ates 2003	
Epizoanthus senegambiensis Pax & Muller, 1956	*Diogenes ovatus* Miers, 1879	Ates 2003	(sengambian coast)
Epizoanthus steueri Carlgren, 1923	*Paguristes eremita*	Ates 2003	(Adriatic Sea)
Epizoanthus studeri	*Parapagurus dimorphus*	Carlgren 1938 ; Ates 2003	
Epizoanthus vatovai Pax & Lochter, 1935	*Paguristes eremita*	Ates 2003	(Adriatic Sea)
Epizoanthus sp.	*Anapagurus pusillus* Henderson, 1888, *Nematopagurus muricatus* (Henderson, 1896), *Oncopagurus minutus* (Henderson, 1896), *Paguristes balanophilus* Alcock, 1905, *P. puniceus* Henderson, 1896, *Parapagurus abyssorum*, *P. andreui* Macpherson, 1984, *P. bouvieri*, *P. latimanus* Henderson, 1888, *P. pilosimanus*, *accepted as Sympagurus burkenroadi* Thompson, 1943(as *Sympagurus papposus)*, *S. villosus* Lemaitre, 1996	Balss 1924 ; Ates 2003; Lemaitre 1996	(Indian coasts, Indonesia, French Polynesia, South Africa) (Australia)
Palythoa nelliae Pax, 1935	*Cryptodromiopsis unidentata* (Rüppell, 1830)	Lavaleye&Hartog 1995	(South Africa)
Palythoa eupaguri Marion, 1882	*Parapagurus pilosimanus* Smith, 1879 (as *Eupagurus jacobi)*	Ates 2003	(Atlantic Ocean)
subclass Hexacorallia; order Corallimorpharia			
Discosoma	*Cyclocoeloma tuberculata* Miers, 1880	Lavaleye&Hartog 1995 (Indo-West-Pacific, Indonesia)	(Indo-West-Pacific, Indonesia)