Cnidarians and Their Polychaete Symbionts

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Abstract

Cnidarians, especially skeleton-bearing anthozoans and hydrocorals, are known to host abundant and diverse symbiotic fauna encompassing members of the majority of metazoan taxa, ranging from sponges and flat worms to fishes. Members of the class Polychaeta are between the most diverse and perhaps the least studied taxa of coral symbionts. The last revision (Martin and Britayev, Oceanogr Mar Biol 36:217–340, 1998) reckoned about 60 species of symbiotic polychaetes associated with more than 100 species of cnidarian hosts. However, this number is considerably underestimated. Some populations of scleractinians, sea fans and black corals show up to 100 % infestation by symbiotic polychaetes. Close association and inter-relation of highly host-specific symbionts and cnidarian hosts often lead to dramatic changes in the host morphology. At the moment, actual mechanisms of most of mutual relations between host and symbiont in such associations are generally unknown. The objective of the present paper is to summarize data on species composition and ecology of polychaetes associated with cnidarians. In our review, we report 281 species of cnidarian hosts involved in 324 relationships with symbiotic polychaetes. Most polychaete-hosting cnidarians belong to skeleton-bearing taxa, particularly Scleractinia (125 species or 44.48 % of the total cnidarian hosts), Alcyonaria (73 species or 25.97 %) and Hydrozoa (60 species or 21.35 %). About 120 species of symbiotic polychaetes of ten families are reported from cnidarian hosts. Polynoidae include the highest number of cnidarian-associated polychaetes (almost one half of the currently known species), followed by Syllidae and Serpulidae. Host symbiont interrelations, host specificity, location, infestation characteristics and adaptive modifications of symbionts, as well as host reaction on symbionts presence, have been considered. Our review highlights that (1) every group of cnidarians seems to have their own assemblage of symbiotic polychaetes, (2) some deep-sea alcyonaceans and black corals have never been reported without their often undetermined polynoid symbionts so that its presence has been considered as a species-specific, robust taxonomic character, and (3) we certainly expect the polychaete symbionts associated with deep-sea corals to be a hidden hot-spot of diversity, with many species still waiting to be described.

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25.1 Introduction. State of Knowledge

It is now well known and accepted that many marine organisms can harbor rich associated fauna. Cnidarians, and in particular skeleton-bearing corals, are between the most preferred hosts for such associations (see e.g. Buhl-Mortensen and Mortensen 2004; Stella et al. 2011; Watling et al. 2011). The complex three-dimensional network created by the massive skeleton or the characteristic branching pattern of alcyonaceans and black corals may provide food, substrate and shelter for various types of organisms. According to the comprehensive review on symbiotic polychaetes by Martin and Britayev (1998), cnidarians appeared to be the second dominant group harboring symbiotic polychaetes (20 % of the 569 by then known host species) yielding only to Echinodermata (36 % of host species). Buhl-Mortensen and Mortensen (2004) in the review of symbiosis in deep-sea water corals counted 311 and 112 species of obligate symbiotic invertebrates (all taxa) from shallow-water and deep-sea corals, respectively. Seven years later, the number of symbiotic invertebrates recorded in association with scleractinian corals only increased up to 869 species (Stella et al. 2011). Among them, only 29 species of polychaetes were recognized as facultative and obligatory coral symbionts. Little is still known about the biology of deep-sea symbionts, since many species are known only from the type localities, or based on limited number of historical dredge samples when hosts and symbionts were often separated during preliminary on-deck sorting. On the other hand, it is hard to distinguish the organisms inhabiting the coral framework and using it just for shelter from those living in close association with the host coral (i.e. real symbionts).

The purpose of the present paper is to revise the current data on host-symbiont relationships between cnidarians and their associated polychaetes. Also, we try to define main gaps in the present knowledge on the biology of the polychaete-cnidarian symbiosis.

25.2 Cnidarian Hosts Involved in Coral-Polychaete Associations

To date, 281 species of cnidarian hosts involved in 324 relationships with symbiotic polychaetes have been reported (Table 25.1). Most polychaete-hosting cnidarians belong to skeleton-bearing taxa (Fig. 25.1). Among the anthozoans, most belong to the Scleractinia (125 species or 44.48 % of the total cnidarian hosts), Alcyonacea (73 species or 25.97 %), Hydrozoa (60 species or 21.35 %), and Antipatharia (19 species or 6.76 %). The hosts lacking hard skeleton include only two species of Actiniaria: *Bolocera tuediae* associated with *Alentiana aurantiaca* and *Metridium senile* with *Arctonoe vittata*. One non-identified zoanthid hosted *Lumbrineris flabellicola* and several species of not obligate polychaetes are reported from ceriantid tubes. There are no polychaete symbionts reported in association with Corallimorpharia.

25.2.1 Ceriantharia

Species associated with tube anemones (Ceriantharia) generally inhabit the surface or are embedded into their thick felt-like tubes consisting of discharged ptychocyst threads incrusted with particles of mud and sand. About 30 species of polychaetes were reported from tubes of *Pachycerianthus multiplicatus* Carlgren, 1912 (Kilkerrin Bay, Ireland). However, most reported species were in fact associated with polychaetes and sipunculids inhabiting the ceriantid tube or use the ceriantid tube as elevated substrate for settlement. Apparently, *Myxicola infundibulum* is the only polychaete species that is not reported from the surrounding grounds but from ceriantid tubes (O'Connor et al. 1977) and thus this species is considered in the Table 25.1.

25.2.2 Scleractinia

Scleractinians are apparently the most attractive group of marine cnidarians for symbiotic organisms. Dead skeletons of reef-building scleractinians provide a substrate that is actively eroded and occupied by numerous excavating taxa, including many species of polychaetes (Hutchings 2008; Glynn and Enoch 2011). However, only 29 polychaetes (including borers and cryptic species) out of 869 invertebrates have been recently reported as scleractinian symbionts in coral reefs (Stella et al. 2011), while five and nine species have been reported as obligatory coral symbionts from shallow-water and deep-sea habitats, respectively (Buhl-Mortensen and Mortensen 2004).

Despite the relatively low number of symbiotic polychaete species, they are often reported in association with a wide range of scleractinian hosts from several families (Zibrowius et al. 1975; Martin and Britayev 1998). On coral reefs, symbiotic polychaetes more often inhabit massive, slow-growing species of Acroporidae, Poritidae, Faviidae etc. (Rowley 2008). In deep-sea habitats, polychates have been mostly reported during last decades in association with

Table 25.1 List of symbiotic polychaetes reported in associations with Cnidarian hosts

	Cnidarian host			
Polychaete	Taxon	Species	Type	Source
Chaetopteridae				
Spiochaetopterus sp.	SCL	*Montipora* spp.	1	Bergsma (2009)
Eunicidae				
Aciculomarphysa comes Hartmann-Schröder, 1998	ANT	Unid. antipatharian	1	Hartmann-Schröder and Zibrowius (1998), Molodtsova and Budaeva (2007)
Eunice antipathum (Pourtalès, 1867)	ANT	*Distichopathes filix* (Pourtalès, 1867)	1	Hartmann-Schröder and Zibrowius (1998), Molodtsova and Budaeva (2007)
	ANT	*Elatopathes abietina* (Pourtalès, 1874)	1	Hartmann-Schröder and Zibrowius (1998), Molodtsova and Budaeva (2007)
E. cf *dubiata* Fauchald, 1974	SCL	*Madrepora oculata* Linnaeus, 1758	1	Buhl-Mortensen and Mortensen (2004)
E. kristiani Hartmann-Schröder, 1998	ANT	cf. *Antipathes cylindrica* Brook, 1889	1	Hartmann-Schröder and Zibrowius (1998), Molodtsova and Budaeva (2007)
E. marianae Hartmann-Schröder, 1998	ANT	cf. *A cylindrica*	1	Hartmann-Schröder and Zibrowius (1998), Molodtsova and Budaeva (2007)
	ANT	*Cupressopathes* sp.2	1	Molodtsova and Budaeva (2007)
E. norvergica (Linnaeus, 1767)	SCL	*Lophelia pertusa* (Linnaeus, 1758)	1	Zibrowius (1980), Roberts (2005), Mueller et al. (2013)
	SCL	*M. oculata*	1	Zibrowius (1980), Roberts (2005)
	SCL	*Solenosmilia variabilis* Duncan, 1873	1	Zibrowius (1980), Roberts (2005)
	STY	*Errina atlantica* Hickson, 1912	1	Zibrowius and Cairns (1992)
Eunice pennata (OF Muller, 1776)	SCL	Unid. scleractinian	1	Fauvel (1923)
	SCL	*L. pertusa*	1	Fauchald (1992), Jensen and Frederksen (1992)
	SCL	*Primnoa resedaeformis* (Gunnerus, 1763)	1	Buhl-Mortensen and Mortensen (2005)
Eunice sp.	SCL	*M. oculata*	1	Cairns and Zibrowius (1997)
Eunice sp.	SCL	*M. arbuscula* (Moseley, 1881)	1	Cairns and Zibrowius (1997)
Eunice sp.	SCL	*M. minutiseptum* Cairns, Zibrowius, 1997	1	Cairns and Zibrowius (1997)
Eunice sp.	SCL	*M.* cf. *porcellana* (Moseley, 1881)	1	Cairns and Zibrowius (1997)
Eunice sp.	SCL	*Lobophyllia hemprichii* (Ehrenberg, 1834)	1	Chisholm and Kelley (2001)
Leodice antennata ? (Savigny, 1818)	SCL	Unid. coral	1	Gardiner (1976)
Unid. eunicid	STY	*Stylaster cocosensis* Cairns, 1991	1	Cairns (1991)
Unid. eunicid	STY	*S. marenzelleri* Cairns, 1986	1	Cairns (1986), Cairns (1991)
Unid. eunicid	STY	*S. spatula* Cairns, 1986	1	Cairns (1991)
Hesionidae				
Leocrates chinensis Kinberg, 1866		Corals	1	Pettibone (1970)
L. claparedii (Costa in Claparède, 1868)		Corals	1	Pettibone (1970)
Lumbrineridae				
Lumbrineris flabellicola Fage, 1936	SCL	*Balanophyllia cellulosa* Duncan, 1973	1	Zibrowius et al. (1975), Miura and Shirayama (1992)
	SCL	*Balanophyllia* sp.	1	Zibrowius et al. (1975), Cairns and Zibrowius (1997)
	SCL	*Caryophyllia quadrogenaria* Alcock, 1902	1	Miura and Shirayama (1992)
	SCL	*C. grayi* (Milne Edwards and Haime, 1848)	1	Cairns and Zibrowius (1997)
	SCL	*C. sarsiae* Zibrowius, 1974	1	Zibrowius et al. (1975)
	SCL	*C. smithii* Stokes and Broderip, 1828	1	Zibrowius et al. (1975)

(continued)

Table 25.1 (continued)

Polychaete	Cnidarian host		Type	Source
	Taxon	Species		
	SCL	*C. spinigera* (Saville-Kent, 1871)	1	Miura and Shirayama (1992), Cairns and Zibrowius (1997)
	SCL	*C. spinicarens* (Moseley, 1881)	1	Miura and Shirayama (1992), Cairns and Zibrowius (1997)
	SCL	*Caryophyllia* sp.	1	Zibrowius et al. (1975)
	SCL	*C. transversalis* Moseley, 1881	1	Cairns and Zibrowius (1997)
	SCL	*Ceratotrochus duodecimcostatus* (Goldfuss,1826) †	1	Zibrowius et al. (1975)
	SCL	*Conotrochus brunneus* (Moseley, 1881)	1	Cairns and Zibrowius (1997)
	SCL	*Dendrophyllia cornigera* (Lamarck, 1816)	1	Zibrowius et al. (1975)
	SCL	*Eguchipsammia cornucopia* (Pourtalès, 1871)	1	Zibrowius et al. (1975)
	SCL	Dendrophyllid coral	1	Cairns and Zibrowius (1997)
	SCL	*Desmophyllum dianthus* (Esper, 1794)	1	Zibrowius et al. (1975)
	SCL	*Flabellum avicula* Michelotti †	1	Zibrowius et al. (1975)
	SCL	*F. chunii* Marenzeller, 1904	1	Marenzeller (1904), Fage (1936), Bellan (1959), Zibrowius et al. (1975), Miura and Shirayama (1992)
	SCL	*F. fornasinii* Osasco, 1895†	1	Zibrowius et al. (1975)
	SCL	*Flabellum lamellulosum* Alcock, 1902	1	Cairns and Zibrowius (1997)
	SCL	*F. majus* Milne Edwards and Haime†	1	Zibrowius et al. (1975)
	SCL	*F. patens* Mozeley, 1881	1	Cairns and Zibrowius (1997)
	SCL	*F. pavoninum* Lesson, 1831	1	Zibrowius et al. (1975), Miura and Shirayama (1992)
	SCL	*F.* sp.	1	Zibrowius et al. (1975)
	SCL	*Rhizotrochus typus* Milne Edwards and Haime, 1848	1	Cairns and Zibrowius (1997)
	SCL	*Stephanocyathus moseleyanus* (Sclater, 1886)	1	Zibrowius et al. (1975)
	SCL	*Truncatoflabellum candeanum* (Milne Edwards and Haime, 1848)	1	Zibrowius et al. (1975)
	SCL	*T. inconstans* (Marenzeller, 1904)	1	Zibrowius et al. (1975)
	HYD	Unid. hydroids	1	Zibrowius et al. (1975)
	SCL	Unid. scleractinian	1	Miura and Shirayama (1992)
	SCL	*Stephanocyathus moseleyanus* (Sclater, 1886)	1	Zibrowius et al. (1975)
	ZOA	Unid. zoantharian	1	Zibrowius et al. (1975)
L. coccinea (Renier, 1804)	SCL	Unid. coral	1	Gardiner (1976)
Polynoidae				
Acanthicolepis zibrowii Barnich and Fiege, 2010	SCL	*Madrepora oculata*	1	Barnich and Fiege (2010), Núñez et al. (2011)
Alentiana aurantiaca (Verrill, 1885)	ACT	*Bolocera tuediae* (Johnston, 1832)	1	Pettibone (1963)
Antipathipolyeunoa nuttingi Pettibone, 1991	ANT	*Tanacetipathes tanacetum* (Pourtalès, 1880)	1	Pettibone (1991b), Wagner et al. (2012)
Arctonoe vittata (Grube, 1855)	ACT	*Metridium senile* (Linnaeus, 1761)	1	Britayev (1991)
Australaugeneria michelseni Pettibone, 1969	ALC	*Dendronephthya* sp.	1	Britayev and Antokhina (2012)
	ALC	Unid. alcyonacean	1	Pettibone (1969a)
	ALC	Unid. gorgonian	1	Pettibone (1969a)
Australaugeneria pottsi Pettibone, 1969	ALC	Unid. gorgonian	1	Pettibone (1969a, 1969b)

(continued)

Table 25.1 (continued)

Polychaete	Cnidarian host		Type	Source
	Taxon	Species		
A. rutilans (Grube, 1878)	ALC	*Xenia* sp.	1	Okuda (1950), Pettibone (1969a)
	ALC	*Dendronephthya* sp.	1	Britayev and Antokhina (2012)
Bayerpolynoe floridensis Pettibone, 1991	ANT	*Stylopathes litocrada* Opresko, 2006	1	Pettibone (1991b); Wagner et al. (2012), Britayev et al. (2014), present paper
Benhamipolynoe anthipaticola (Benham, 1927)	ANT	*Asteriopathes arachniformis* Opresko, 2004		Molodtsova and Budaeva (2007)
	ANT	*Cupressopathes cf. gracilis* (Thomson and Simpson, 1905)	1	Molodtsova and Budaeva (2007)
	ANT	*Cupressopathes* sp.	1	Molodtsova and Budaeva (2007)
	ANT	*S. tenuispina* (Silberfeld, 1909)	1	Pettibone (1970, 1989)
	ANT	*S. columnaris* (Duchassaing, 1870)	1	Pettibone (1970, 1989); Wagner et al. (2012)
B. cairnsi Pettibone 1989	STY	*Conopora adeta* Cairns, 1987	1	Pettibone (1989), Hanley and Burke (1991b)
Brychionoe karenae Hanley and Burke, 1991	ANT	*Leiopathes secunda* Opresko, 1998	1	Hanley and Burke (1991a), present paper
Eunoe purpurea Treadwell, 1936	ANT	*Bathypathes* cf. *alternata* Brook, 1889	1	Barnich et al. (2013)
	SCL	*Madrepora oculata*	1	Barnich et al. (2013)
E. spinulosa Verrill, 1879	ALC	*Acanella arbuscula* (Johnson, 1862)	1	Buhl-Mortensen and Mortensen (2004)
Gorgoniapolynoe bayeri Pettibone, 1991	ALC	*Narella clavata* (Versluys, 1906)	1	Pettibone (1991a)
G. caeciliae (Fauvel, 1913)	ALC	*Acanthogorgia aspera* Pourtalès, 1867	1	Pettibone (1991a)
	ALC	*A. armata* Verrill, 1878	1	Barnich et al. (2013)
	ALC	*Candidella imbricata* (Johnson, 1862)	1	Pettibone (1991a), Cairns and Bayer (2004), Eckelbarger et al. (2005), Barnich et al. (2013), Britayev et (2014)
	ALC	*Corallium bayeri* Simpson and Watling, 2011	1	Simpson and Watling (2011), Tu et al. (2015)
	ALC	*Corallium johnsoni* Gray, 1860	1	Fauvel (1913), Hartmann-Schröder (1985), Pettibone (1991a), Tu et al. (2015)
	ALC	*C. niobe* Bayer, 1964	1	Hartmann-Schröder (1985), Pettibone (1991a), Simpson and Watling (2011), Tu et al. (2015)
	ALC	*C. secundum* Dana, 1846	1	Stock (1986)
	ALC	*C. tricolor* (Johnson, 1899)	1	Hartmann-Schröder (1985), Tu et al. (2015)
G. cairnsi Pettibone 1991	STY	*Stylaster eguchii* (Boschma, 1966)	1	Pettibone (1991a)
G. corralophyla (Day, 1960)	STY	*S. bithalamus* Broch, 1936	1	Day (1967)
	STY	*Stylaster* sp.	1	Stock (1986)
	STY	*Conopora* sp.	1	Stock (1986)
	STY	*Crypthelia* sp.	1	Stock (1986)
G. galapagensis Pettibone, 1991	ALC	*Narella ambigua* (Studer, 1894)	1	Pettibone (1991a)
G. guadalupensis Pettibone, 1991	ALC	*Corallium imperiale* Bayer, 1955	1	Britayev (1981), Pettibone (1991a)
G. muzikae Pettibone, 1991	ALC	*Acanthogorgia bocki* Aurivillius, 1931	1	Pettibone (1991a)
	ALC	*Candidella helminthophora* (Nutting, 1908)	1	Pettibone (1991a)
	ALC	*Corallium* sp.	1	Pettibone (1991a)
G. uschacovi Britayev, 1981	STY	*Stylaster* sp. 1	1	Britayev (1981)
	ALC	*Callogorgia* sp.	1	Britayev (1981), Pettibone (1991a)
Gorgoniapolynoe sp.	ALC	*Narella vermifera* Cairns and Bayer 2008	1	Cairns and Bayer (2008)
Gorgoniapolynoe sp.	ALC	*N. macrocalyx* Cairns and Bayer 2008	1	Cairns and Bayer (2008)
Gorgoniapolynoe sp.	ALC	*Narella alata* Cairns and Bayer 2008	1	Cairns and Bayer (2008)
Gorgoniapolynoe sp.	ALC	*Candidella helminthophora* (Nutting, 1908)	1	Nutting (1908), Cairns (2009)

(continued)

Table 25.1 (continued)

Polychaete	Cnidarian host		Type	Source
	Taxon	Species		
Harmothoe dannyi Barnich et al. 2013	STY	*Stylaster erubescens* Pourtalès, 1868	1	Barnich et al. (2013)
H. gilchristi Day, 1960	SCL	*L. pertusa*	1	Miranda and Brasil (2014)
	SCL	*S. variabilis*		Miranda and Brasil (2014)
	SCL	*E. rostrata*		Miranda and Brasil (2014)
	SCL	*M. oculata*		Miranda and Brasil (2014)
	STY	*Errina sp*		Miranda and Brasil (2014)
H. oculinarum (Storm, 1879)	SCL	*L. pertusa*	1	Buhl-Mortensen and Mortensen (2004)
H. melanicornis Britayev, 1981	STY	*Stylaster* sp. 2	1	Britayev (1981)
H. ruthae Miranda and Brasil, 2014	SCL	*L. pertusa*	1	Miranda and Brasil (2014)
	SCL	*Solenismilia variabilis*		Miranda and Brasil (2014)
	SCL	*E. rostrata*		Miranda and Brasil (2014)
	SCL	*M. oculata*		Miranda and Brasil (2014)
	STY	*Errina sp*		Miranda and Brasil (2014)
H. vinogradovae Averincev, 1978	STY	Unid. hydrocoral	1	Britayev (1981)
Hemilepedia versluysi Horst, 1915	ALC	*Thouarella hilgendorfi* (Studer, 1879)	1	Horst (1915), Britayev (1981)
Hololepidella nigropunctata (Horst, 1915)	SCL	*Lobactis scutaria* (Lamarck, 1801)	1	Pettibone (1993)
Hololepidella sp.	SCL	*Galaxea astreata* (Lamarck, 1816)	2	Britayev and Antokhina (2012), Britayev et al. (2015)
Lagisca irritans Marenzeller, 1904	STY	*Errina macrogastra* Marenzeller, 1904	1	Marenzeller (1904), Zibrowius (1981), Cairns 1986
	STY	*Stenohelia concinna* Boschma, 1964	1	Marenzeller (1904), Zibrowius (1981), Cairns (1986)
L. zibrowii Hartmann-Schröder, 1992	HYD	*Pseudosolanderia* sp.	1	Hartmann-Schröder (1992)
Malmgreniella dicirra Hartman, 1967	STY	*Stylaster eguchii*	1	Pettibone (1993)
	STY	*S. densicaulis* (Studer, 1878)	1	Pettibone (1993)
	ALC	*Calyptopora reticulata* Boschma, 1968	1	Pettibone (1993)
	STY	*Conopora verrucosa* (Studer, 1878)	1	Pettibone (1993)
	STY	*Lepidopora* sp.	1	Pettibone (1993)
M. pettiti Pettibone, 1993	ALC	Unid. alcyonacean	1	Pettibone (1993)
Medioantenna variopinta Di Camillo, Martin and Britayev, 2011	HYD	*Solanderia secunda* (Inaba, 1892)	1	Nishi and Tachikawa (1999), Di Camillo et al. (2011)
Neohololepidella anthipathicola Hartmann-Schröder, 1998	ANT	*Elatopathes abietina*	1	Hartmann-Schröder and Zibrowius (1998), Molodtsova and Budaeva (2007)
	ANT	*Distichopathes filix*	1	Hartmann-Schröder and Zibrowius (1998), Molodtsova and Budaeva (2007)
Neopolynoe acanellae (Verrill, 1881)	ALC	*Acanella arbuscula*	1	Verrill (1881), Ditlevsen (1917)
	ALC	*Acanthogorgia armata*	1	Verrill (1881)
	ALC	*Pseudoanthomastus agaricus* (Studer, 1890)	1	Ditlevsen (1917), Molodtsova (2013)
	PEN	*Pennatula grandis* Ehrenberg, 1834	1	Pettibone (1963)
N. antarctica (Kinberg, 1858)	HYD	*Thuiaria* sp.	1	Hartmann-Schröder (1989), Barnich et al. (2012b)

(continued)

Table 25.1 (continued)

	Cnidarian host			
Polychaete	Taxon	Species	Type	Source
N. paradoxa (Anon, 1888)	SCL	*Lophelia pertusa*	1	Jensen and Frederiksen (1992)
Paradyte levis (Marenzeller, 1902)	ALC	*Dendronephthya* sp.	1	Okuda (1950), Imajima (1997), Britayev and Antokhina (2012)
P. tentaculata (Horst, 1915)	ALC	*Dendronephthya* sp.	1	Hanley and Morton (1992)
	ALC	*Nephthea* sp.	1	Pettibone (1969a), Hanley and Morton (1992)
Parahololepidella greeffi (Augener, 1918)	ANT	*Tanacetipathes* cf. *spinescens* (Gray, 1857)	1	Britayev et al. (2014)
Parapolyeunoa flynni (Benham, 1921)	STY	*Errina aspera* (Linnaeus, 1767)	1	Barnich et al. (2012b)
	STY	*Inferiolabiata labiata* (Moseley, 1879)	1	Barnich et al. (2012b)
	ALC	*Thouarella* sp.	1	Barnich et al. (2012b)
Polyeunoa laevis McIntosh, 1885	ALC	*Thouarella variabilis* Wright and Studer, 1889	1	Pettibone (1969c)
	ALC	*Thouarella* sp.	1	Hartmann-Schröder (1989), Barnich et al. (2012b)
	ALC	Acanthogorgiidae gen. sp.	1	Hartmann-Schröder (1989), Barnich et al. (2012b)
	ALC	*Primnosis* sp.	1	Stiller (1996), Barnich et al. (2012a, 2012b)
	ALC	*Dasystenella* sp.	1	Stiller (1996), Barnich et al. (2012a, 2012b)
Showascalisetosus shimizui Imajima, 1997	STY	*Stylaster* sp.	1	Imajima (1997)
Subadyte papillifera (Horst, 1915)	SCL	Unid. coral	1	Pettibone (1969a)
Tottonpolynoe symantipatharia Pettibone, 1991	ANT	*Parantipathes* sp.	1	Pettibone (1991b)
	ALC	*Sclerisis macquariana* Bayer and Stefani, 1987	1	Pettibone (1991b)
Uncopolynoe corallicola Hartmann-Schröder, 1960	ALC	Unid. alcyonacean	1	Hartmann-Schröder (1960), Wehe (2006), Britayev and Antokhina (2012)
Unid. polynoid	STY	*Conopora major* Hickson and England, 1905	1	Cairns and Zibrowius (2013)
Unid. polynoid	STY	*C. tenuiramus* Cairns and Zibrowius, 2013	1	Cairns and Zibrowius (2013)
Unid. polynoid	STY	*C. verrucosa*	1	Cairns and Zibrowius (2013)
Unid. polynoid	ALC	*Corallium sulcatum* Kishinouye, 1903		Tu et al. (2012)
Unid. polynoid	ALC	*Minuisis pseudoplanum* Alderslade, 1998	1	Alderslade (1998), Watling et al. (2011)
Unid. polynoid	ALC	*Minuisis granti* Alderslade, 1998	1	Alderslade (1998), Watling et al. (2011)
Unid. polynoid	ALC	*Narella hypsocalyx* Cairns, 2012	1	Cairns (2012)
Unid. polynoid	ALC	*N. vulgaris* Cairns, 2012	1	Cairns (2012)
Unid. polynoid	ALC	*N. mosaica* Cairns, 2012	1	Cairns (2012)
Unid. polynoid	ALC	*N. dampieri* Cairns, 2012	1	Cairns (2012)
Unid. polynoid	ANT	*Hexapathes hivaensis* Molodtsova, 2006	1	Molodtsova (2006)
Unid. polynoid	STY	*Stylaster amphiheloides* Kent, 1871	1	Cairns (1991), Cairns and Zibrowius (2013)
Unid. polynoid	STY	*S. bithalamus*	1	Cairns and Zibrowius (2013)
Unid. polynoid	ALC	*Thouarella affinis* Wright and Studer, 1889	1	Taylor et al. (2013)
Unid. polynoid	ALC	*T. bipinnata* Cairns, 2006	1	Cairns (2006)
Unid. polynoid	ALC	*T. laxa* Versluys 1906	1	Versluys (1906), Watling et al. (2011)
Unid. polynoid	ALC	*T. cristata* Cairns, 2011	1	Cairns (2011)

(continued)

Table 25.1 (continued)

Polychaete	Cnidarian host		Type	Source
	Taxon	Species		
Unid. polynoid	ALC	*Tokoprymno anais* Zapata-Guardiola and López-González, 2010	1	Zapata-Guardiola and López-González (2010)
Sabellidae				
Myxicola infundibulum (Linnaeus, 1767)	CER	*Pachycerianthus multiplicatus* Carlgren, 1912	1	O'Connor et al. (1977)
SERPULIDAE				
Floriprotis sabiuraensis Uchida, 1978	SCL	*Favites abdita* (Ellis and Solander, 1786)	1	Uchida (1978)
	SCL	*Dipsastraea speciosa* (Dana, 1846)	1	Bailey-Brock (1985)
	SCL	*Goniastrea pectinata* (Ehrenberg, 1834)	1	Bailey-Brock (1985)
	SCL	*Hydnophora* sp.	1	ten Hove (1989)
	SCL	*Platygyra* sp.	1	ten Hove (1989)
Propomatoceros sulcicarinata Ware, 1974†	SCL	*Glomerula lombricus* (Defrance, 1827)†	1	Garberoglio and Lazo (2011)
	SCL	*Mucroserpula mucroserpula* Regenhardt, 1961†	1	Garberoglio and Lazo (2011)
Pseudovermilia madracicola ten Hove, 1989	SCL	*Madracis pharensis* (Heller, 1868)	1	ten Hove (1989)
	SCL	*M. decactis* (Lyman, 1859)	1	ten Hove (1989)
Serpula sp.	SCL	*Echinopora gemmacea* (Lamarck, 1816)	1	ten Hove and Land (1994)
Spirobranchus corniculatus (Grube,1862)	SCL	*Acropora* sp.	1	ten Hove and Land (1994)
	SCL	*Acropora digitifera* (Dana, 1846)	1	Rowley (2008)
	SCL	*A. humilis* (Dana, 1846)	1	Rowley (2008)
	SCL	*A. hyacinthus* (Dana, 1846)	1	Rowley (2008)
	SCL	*A. loripes* Brook, 1892	1	Rowley (2008)
	SCL	*Astreopora cucullata* Lamberts, 1980	1	Rowley (2008)
	SCL	*Dipsastraea amicorum* (Milne Edwards and Haime, 1849)	1	Rowley (2008)
	SCL	*Coeloseris mayeri* Vaughan, 1918	1	Rowley (2008)
	SCL	*Cyphastrea chalcidicum* (Forskål, 1775)	1	Rowley (2008)
	SCL	*Cyphastrea microphthalma* (Lamarck, 1816)	1	Rowley (2008)
	SCL	*C. serailia* (Forskål, 1775)	1	Rowley (2008)
	SCL	*Dipsastraea favus* (Forskål, 1775)	3	Ben-Tzvi et al. (2006)
	SCL	*D. lax* (Klunzinger, 1879)	3	Ben-Tzvi et al. (2006)
	SCL	*D. pallida* (Dana, 1846)	1	Rowley (2008)
	SCL	*D. speciosa*	1	Rowley (2008)
	SCL	*Favites abdita*	1	Rowley (2008)
	SCL	*F. pentagona* (Esper, 1795)	1	Rowley (2008)
	SCL	*Galaxea astreata*	1	Rowley (2008)
	SCL	*Gardineroseris planulata*	1	ten Hove and Land (1994)
	SCL	*Hydnophora microconos* (Lamarck, 1816)	1	ten Hove and Land (1994)
	SCL	*Merulina ampliata* (Ellis and Solander, 1786)	1	Rowley (2008)
	MIL	*Millepora platyphylla* Hemprich and Ehrenberg, 1834	1	Rowley (2008)
	MIL	*M. tenera* Boschma, 1949	1	Rowley (2008)
	MIL	*Millepora* sp.	1	ten Hove and Land (1994)
	SCL	*Montipora aequituberculata* Bernard, 1897	1	Rowley (2008)
	SCL	*M. foliosa* (Pallas, 1766)	1	Rowley (2008)
	SCL	*M. foveolata* (Dana, 1846)	1	Rowley (2008)
	SCL	*M. grisea* Bernard, 1897	1	Rowley (2008)

(continued)

Table 25.1 (continued)

	Cnidarian host			
Polychaete	Taxon	Species	Type	Source
	SCL	*M. informis* Bernard, 1897	1	Rowley (2008)
	SCL	*M. spongodes* Bernard, 1897	1	Rowley (2008)
	SCL	*M. spumosa* (Lamarck, 1816)	1	Rowley (2008)
	SCL	*M. tuberculosa* (Lamarck, 1816)	1	Rowley (2008)
	SCL	*M. undata* Bernard, 1897	1	Rowley (2008)
	SCL	*M. venosa* (Ehrenberg, 1834)	1	Rowley (2008)
	SCL	*M. verrucosa* (Lamarck, 1816)	1	Rowley (2008)
	SCL	*Montipora* sp.	1	ten Hove and Land (1994)
	SCL	*Mycedium elephantotus* (Pallas, 1766)	1	Rowley (2008)
	SCL	*Pavona maldivensis* (Gardiner, 1905)	1	ten Hove and Land (1994)
	SCL	*Porites annae* Crossland, 1952	1	Rowley (2008)
	SCL	*P. lichen* Dana, 1846	1	Rowley (2008)
	SCL	*P. lobata* Dana, 1846	1	Rowley (2008)
	SCL	*P. lutea*	1	ten Hove and Land (1994), Rowley (2008)
	SCL	*P. nigrescens* Dana, 1848	1	Rowley (2008)
	SCL	*P. porites* (Pallas, 1766)	1	DeVantier et al. (1986)
	SCL	*P. rus* (Forskål, 1775)	1	Rowley (2008)
	SCL	*Porites* sp.	3	DeVantier et al. (1986)
	SCL	*Porites* sp.	1	Bailey-Brock (1985), Hunte et al. (1990)
	SCL	*Siderastrea siderea* (Ellis & Solander, 1768)	1	Hunte et al. (1990)
	SCL	*Seriatopora hystrix* Dana, 1946	1	Rowley (2008)
	SCL	*Stylocoeniella armata* (Ehrenberg, 1834)	1	Rowley (2008)
	SCL	*Stylophora pistillata* Esper, 1797	1	Rowley (2008)
	SCL	*Stylophora* sp.	1	ten Hove and Land (1994)
S. gardineri Pixell, 1913	SCL	*Gardineroseris planulata* (Dana, 1846)	1	ten Hove and Land (1994)
	SCL	*Porites lutea* Quoy and Gaimard, 1833	1	ten Hove and Land (1994)
	SCL	*Pavona varians* Verrill, 1864	1	ten Hove and Land (1994)
S. giganteus (Pallas, 1766)	SCL	*Agaricia* spp.	1	Hunte et al. (1990)
	SCL	*Diploria labyrinthiformes* (Linnaeus, 1758)	1	Hunte et al. (1990)
	SCL	*Pseudodiploria strigosa* (Dana, 1846)	1	Hunte et al. (1990)
	SCL	*Madracis* spp.	1	Hunte et al. (1990)
	MIL	*Millepora alcicornis* Linnaeus, 1758	1	Pallas (1766) in ten Hove (1989)
	MIL	*M. complanata* Lamarck, 1816	1	Hunte et al. (1990), Marsden (1992)
	SCL	*Orbicella annularis* (Ellis and Solander, 1786)	1	Hunte et al. (1990)
	SCL	*Montastraea cavernosa* (Linnaeus, 1767)	1	Hunte et al. (1990)
	SCL	*Porites astreoides* Lamarck, 1816	1	Hunte et al. (1990)
S. cf. nigranucha (Fischli, 1903)	SCL	*Porites* sp.	1	ten Hove (1989)
S. polycerus (Schmarda, 1861)	MIL	*Millepora complanata*	1	Marsden (1992)
	SCL	*Porites asteroides*	1	Marsden (1992)
S. richardsmithi Pillai, 1990	SCL	*Podabacia motuporensis* Veron, 1990	1	Hoeksema and ten Hove (2014)
S. tetraceros (Schmarda, 1861)	MIL	*Millepora exaesa* Forskål, 1775	1	ten Hove (1970), ten Hove and Land (1994)
	SCL	*Pavona maldivensis*	1	ten Hove (1970), ten Hove and Land (1994)
Sphaerodoridae				
Sphaerodoridium guilbaulti Rullier, 1974	ALC	*Paragorgia arborea* (Linnaeus, 1758)	1	Rullier (1974)
Spintheridae				
Spinther arcticus (M. Sars, 1851)	HYD	Unid. hydroids	1	George and Hartmann-Schröeder (1985)

(continued)

Table 25.1 (continued)

Polychaete	Cnidarian host		Type	Source
	Taxon	Species		
Spionidae				
Dipolydora armata (Langerhans, 1880)	SCL	*Leptastrea purpurea* (Dana, 1846)	3	Okuda (1937)
	MIL	*Millepora complanata*	2	Lewis (1998)
Polydora alloporis Light, 1970	STY	*Stylaster californicus* (Verrill, 1866)	2	Light (1970a), Lindner et al. (2004)
	STY	*Stylantheca papillosa* (Dall, 1884)	2	Cairns and Lindner (2011)
P. cf. alloporis Light, 1970	STY	*Distichopora robusta* Lindner, Cairns and Guzman, 2004	2	Lindner et al. (2004)
P. villosa Radashevsky and Hsieh, 2000	SCL	*Montipora angulata* (Lamarck, 1816)	2	Liu and Hsieh (2000)
	SCL	*Montipora hispida* Dana, 1846	2	Liu and Hsieh (2000)
	SCL	*M. informis* Bernard, 1897	2	Liu and Hsieh (2000)
	SCL	*Porites lichen*	2	Liu and Hsieh (2000)
	SCL	*P. lobata*	2	Liu and Hsieh (2000)
	SCL	*P. lutea*	2	Liu and Hsieh (2000)
	SCL	*Hydnophora exesa* (Pallas, 1766)	2	Radashevsky and Hsieh (2000)
	SCL	*Cyphastrea chalcidicum*	2	Radashevsky and Hsieh (2000)
P. wobberi Light, 1970	ALC	*Lophogorgia* sp.	3	Light (1970b)
Polydora sp.	STY	*Stylaster brochi* (Fisher, 1938)	2	Cairns and Lindner (2011)
Unid. spionid	STY	*S. parageus parageus* (Fisher, 1938)	2	Cairns and Lindner (2011)
Unid. spionid	STY	*S. repandus* Cairns and Lindner 2011	2	Cairns and Lindner (2011)
Unid. spionid	STY	*S. stejnegeri* (Fisher, 1938)	2	Cairns and Lindner (2011)
Unid. spionid	STY	*S. trachystomus* (Fisher, 1938)	2	Cairns and Lindner (2011)
Unid. spionid	STY	*S. venustus* (Verrill, 1870)	2	Cairns and Lindner (2011)
Unid. spionid	STY	*S. verrillii* (Dall, 1884)	2	Cairns and Lindner (2011)
Syllidae				
Alcyonosyllis aidae Álvarez-Campos, San Martín and Aguado, 2013	ALC	*Dendronephtya* sp.	1	Álvarez-Campos et al. (2013)
A. bisetosa (Hartmann-Schröder, 1960)	ALC	Unid. alcyonacean	1	Hartmann-Schröder (1960), Glasby and Aguado (2009)
A. exiliformis (Imajima, 2003)	ALC	*Verrucella* sp.	1	Imajima (2003)
A. glasbyi San Martín and Nishi. 2003	ALC	*Melithaea flabellifera* (Kükenthal, 1908)	1	San Martín and Nishi (2003), Kumagai and Aoki (2003)
A. gorgoniacolo (Sun and Yang, 2004)	ALC	Orange-red gorgonia	1	Sun and Yang (2004), Lattig and Martin (2009), Glasby and Aguado (2009)
A. hinterkircheri Glasby and Aguado, 2009	SCL	*Goniopora* cf. *stokesi* Milne Edwards and Haime, 1851	1	Glasby and Aguado (2009)
A. phili Glasby and Watson, 2001	ALC	*Dendronephthya* sp.	1	Glasby and Watson (2001)
	ALC	*Melithaea* sp.1	1	Glasby and Watson (2001)
	ALC	*Melithaea* sp.2	1	Glasby and Watson (2001)
	ALC	Nephthyidae gen. sp.	1	Britayev and Antokhina (2012)
	ALC	*Carijoa* sp.	1	Britayev and Antokhina (2012)
A. xeniacola (Hartmann-Schröder, 1993)	ALC	*Xenia viridis* Schenk, 1896	1	Hartmann-Schröder (1993), Glasby and Aguado (2009)
Bollandiella antipathicola (Glasby, 1994)	ANT	*Antipathes* sp.	1	Glasby (1994), Molodtsova and Budaeva (2007), Glasby and Krell (2009)

(continued)

Table 25.1 (continued)

Polychaete	Cnidarian host		Type	Source
	Taxon	Species		
Brania pusilla (Dujardin, 1851)	SCL	Unid. coral	1	Gardiner (1976)
Epigamia alexandri (Malmgren, 1867)	HYD	*Abietinaria turgida* (Clark, 1877)	2	Britayev and San Martín (2001)
	HYD	*Orthopyxis integra* (MacGillivray, 1842)	2	TA Britayev personal observations
Haplosyllides sp.	SCL	Unid. coral	1	Hartman (1954), Rullier and Amoureux (1979)
Haplosyllis anthogorgicola Utinomi, 1956	ALC	*Anthogorgia bocki* Aurivillius, 1931	1	Utinomi (1956), Imajima and Hartman (1964), Martin et al. (2002), Lattig and Martin (2009)
H. chamaeleon Laubier, 1960	ALC	*Paramuricea clavata* (Risso, 1826)	1	Laubier (1960), López et al. (1996), Martin et al. (2002)
	ALC	*P. grayi* (Johnson, 1861)	1	Lattig and Martin (2009)
H. villogorgicola Martin, Núñez, Riera and Gil, 2002	ALC	*Villogorgia bebrycoides* (Koch, 1887)	1	Martin et al. (2002)
Imajimea draculai (San Martín and López, 2002)	PEN	*Funiculina quadrangularis* (Pallas, 1766)	2	Nygren and Pleijel (2010)
Pachyprocerastea hydrozoicola (Hartmann-Schröder, 1992)	HYD	*Pseudosolanderia* sp.	2	Hartmann-Schröder (1992)
Proceraea cornuta Agassiz, 1862	HYD	Unid. hydroid	1	Pettibone (1963)
	SCL	Unid. coral	1	Gardiner (1976)
P. fasciata (Bosc, 1802)	HYD	*Eudendrium carneum* Clarke, 1882	2	Cruz-Rivera personal communication
Procerastea halleziana Malaquin, 1893	HYD	*Syncoryne eximia* (Allman, 1859)	2	Allen (1915,1921), Spooner et al. (1957), Alós (1989)
	HYD	*Tubularia indivisa* Linnaeus, 1758	2	Caullery (1925), Spooner et al. (1957)
	HYD	*Ectopleura crocea* (Agassiz, 1862)	2	Genzano and San Martín (2002)
P. simpliseta Hartmann-Schröder, 1990	HYD	*Pseudosolanderia* sp.	2	Hartmann-Schröder (1992)
Syllis gracilis Grube, 1840	ALC	*Elisella paraplexauroides* Stiasny, 1936	1	López et al. (1996)
	HYD	Unid. hydroid	1	López et al. (1996)
	ALC	*Paramuricea clavata*	1	Alós (1988), López et al. (1996)
Syllis onkylochaeta Hartmann-Schröder 1991	ALC	*Xenia* sp.	1	Hartmann-Schröder (1991)
Typosyllis sp.	SCL	*Cyphastrea microphthalma* (Lamarck, 1816)	1	Randall and Eldredge (1976)
	SCL	*Dipsastraea favus*	1	Randall and Eldredge (1976)
	SCL	*Dipsastraea speciosa* (Dana, 1846)	1	Randall and Eldredge (1976)
	SCL	*Favia* sp.	1	Randall and Eldredge (1976)
	SCL	*Favites pentagona*	1	Randall and Eldredge (1976)
	SCL	*Favites valenciennesi* (Milne Edwards and Haime, 1849)	1	Randall and Eldredge (1976)
	SCL	*Favites* sp.	1	Randall and Eldredge (1976)
	SCL	*Symphyllia recta* (Dana, 1846)	1	Randall and Eldredge (1976)
Unid. polychaete	ALC	*Sphaerasclera flammicerebra* (Williams, 2003)	1	Williams (2003)
Unid. polychaete	STY	*Inferiolabiata africana* Cairns and Zibrowius, 2013	1	Cairns and Zibrowius (2013)
Unid. polychaete	STY	*Errinopsis fenestrata* Cairns, 1983	1	Cairns and Zibrowius 2013

† – fossil record
In table: *ACT* Actiniaria, *ALC* Alcyonacea, *ANT* Antipatharia, *CER* Ceriantharia, *HYD* Hydrozoa without calcified skeleton, *MIL* Milleporidae, *PEN* Pennatulacea, *SCL* Scleractinia, *STY* Stylasteridae, *ZOA* Zoanthacea, association, 1 -commensalism, 2 – parasitism, 3 – mutualism

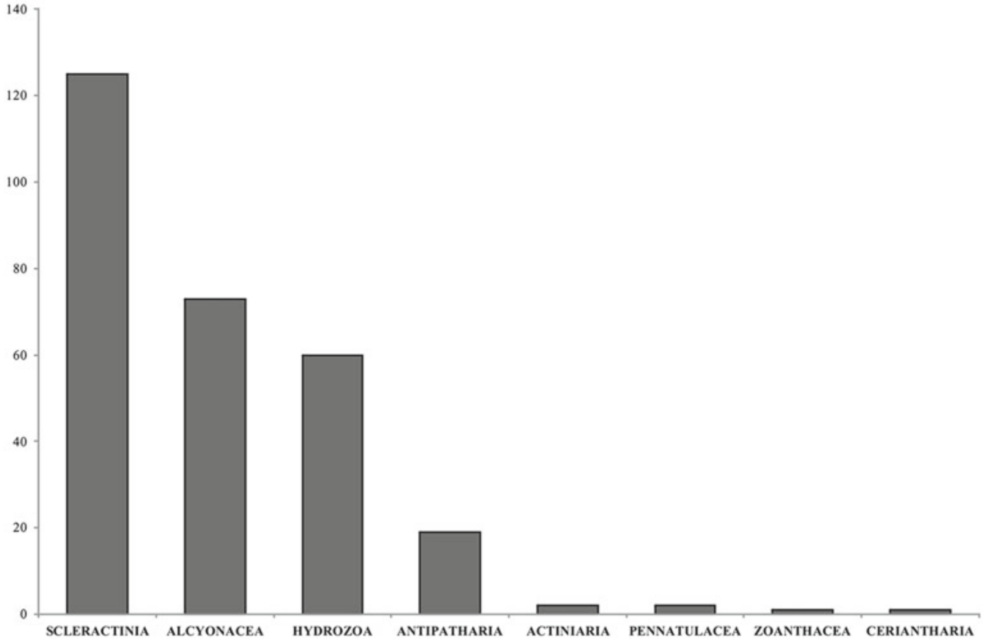

Fig. 25.1 Number of species in each cnidarian taxa hosting symbiotic polychaetes

intensively studied frame-building corals such as *Lophelia pertusa* (Fig. 25.2b), *Solenosmilia variabilis* and *Madrepora oculata* (Buhl-Mortensen and Mortensen 2004). However, solitary cup-corals (Fig. 25.2a) may be also involved in symbiotic associations (Zibrowius et al. 1975).

25.2.3 Antipatharia

Nineteen species of black corals hosting 14 species of symbiotic polychaetes are known to date (Martin and Britayev 1998; Opresko 2006; Molodtsova and Budaeva 2007; Wagner et al. 2012; Britayev et al. 2014), but the number of hosts is clearly underestimated. The genera of black corals infested by polychaetes (i.e., *Cupressopathes* Opresko, 2001, *Tanacetipathes* Opresko, 2001 (Fig. 25.3d), *Stylopathes* Opresko, 2006 (Fig. 25.3c), *Asteriopathes* Opresko, 2004, *Antipathella* Brook, 1889) often have bottle-brush colonies that seem to be more favorable for polychaete symbionts. However, the coral growth form may also be somehow influenced by the symbiont presence (Molodtsova and Budaeva 2007). Some species of black corals, like *Tanacetipathes spinescens* (Britayev et al. 2014), often host polychaete symbionts, while in all species of *Stylopathes* Opresko, 2006 (Stylopathidae) a symbiotic polynoid was always present living on the main stem of the monopodial colony.

25.2.4 Octocorallia

Among the 73 octocorals harboring symbiotic polychaetes, only two species of Pennatulacea (Pettibone 1963; Nygren and Pleijel 2010) and one Helioporacea (Martin et al. 2009) were reported. The remaining 70 hosts belong to the Alcyonacea. The shallow water octocorals hosting polychaetes (mainly Nephtheidae, Xeniidae and Melithaeidae) are relatively scarce and, when reported, they are rarely determined to species level. In turn, the alcyonaceans are the most important deep-sea cnidarians harboring polychaetes (Buhl-Mortensen and Mortensen 2004; Watling et al. 2011), particularly Primnoidae (24 species, mostly belonging to *Narella* Gray, 1870, *Candidella* Bayer, 1954 (Fig. 25.3a) and *Thouarella,* Gray 1870), Coralliidae (8 species), Nephthyidae (8 species), Isidiidae (6 species), Acanthogorgiidae (4 species) and Plexauriidae (3 species). Among the species of *Narella*, for instance, the presence of a symbiotic polychaete is considered as specific at the species level (Cairns 2012).

25.2.5 Hydrozoa

More than two thirds of the hydroids reported in association with polychaetes possess massive calcified skeleton and belong to the families Stylasteridae and Milleporidae.

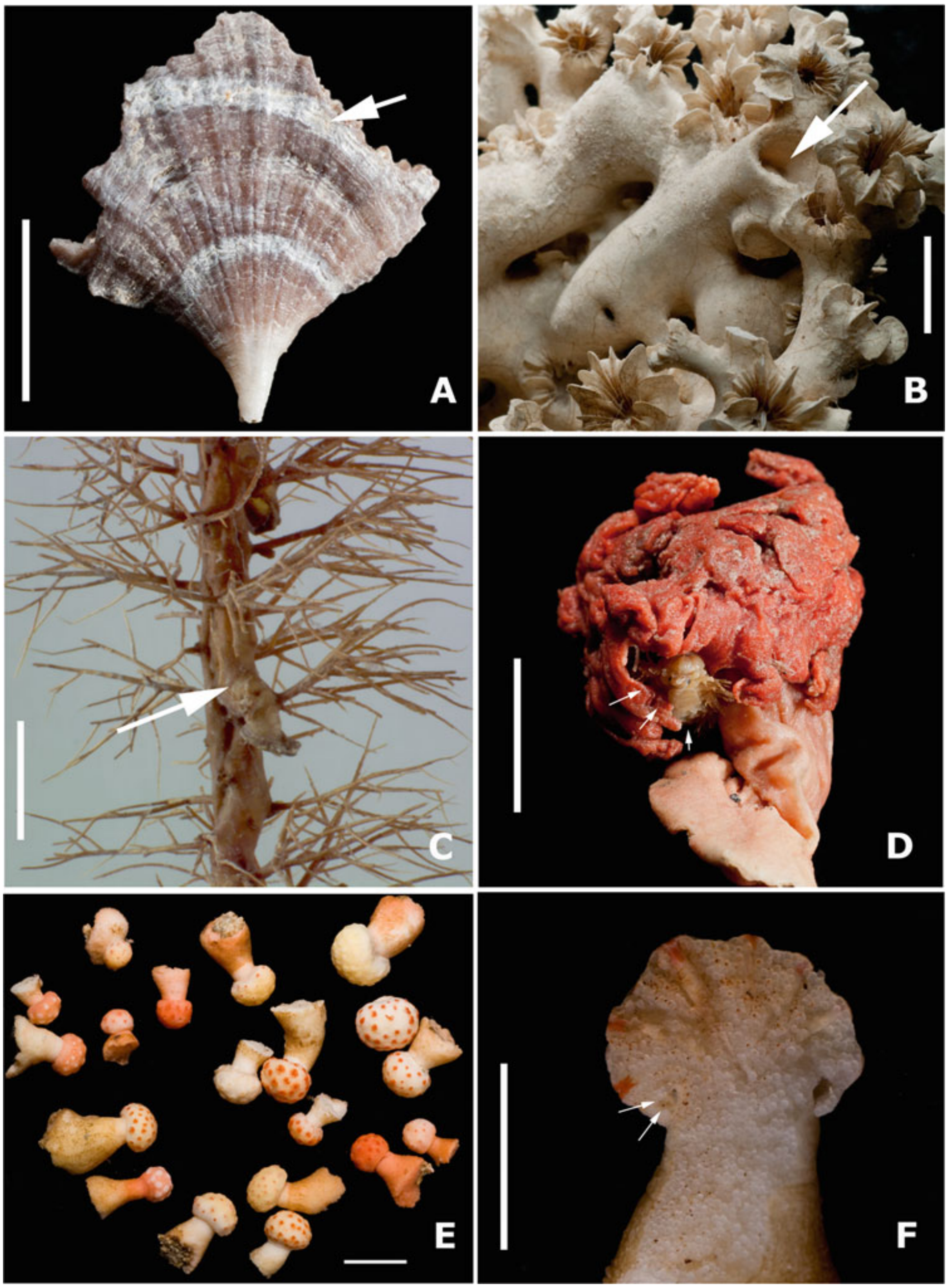

Fig. 25.2 Morphological modifications of cnidarian hosts. (**a**) *Flabellum chunii* with scars (*arrowhead*) from *Lumbriconeris flabellicola*; (**b**) tube of *Eunice* sp. (*arrowhead*) overgrown by *Lophelia pertusa*; (**c**) syntype of *Antipathes cylindrica* with eunicid tube (*arrowhead*) overgrown by coral tissue (Photo courtesy P. Lozouet); (d) *Pseudoanthomastus agaricus* hosting *Neopolynoe acanellae* (*small arrowheads*); (**e**) mushroom-like colonies of *Sphaerasclera flammicerebra*, (**d**) cross section of one specimen of *S. flammicerebra* showing a groove with symbiotic polychaete (*small arrowheads*). Scale: (**a**–**c**, **e**) 10 mm, (**d**, **f**) – 5 mm

Stylasterids or 'lace corals' (Anthoathecata: Filifera), are known from all oceans (i.e., from the Arctic circle to the Antarctica and from 0 to 2,789 m depth) but are more common from 200 to 400 m depth (Cairns 2011). Nearly 40 species of Stylasteridae have been reported to harbor polychaete symbionts (mainly the genera *Conopora* Moseley, 1879, *Errina* Gray, 1835 and *Stylaster* Gray, 1831). Particularly, *Conopora adeta* is known to live exclusively in association with the symbiotic polynoid *Benhamipolynoe cairnsi* (Cairns 1987).

The species of Milleporidae (Anthoathecata: Capitata) inhabit exclusively tropical shallow waters, being among the most conspicuous skeleton-forming coral reef organisms (Lewis 2006). The Milleporidae comprises only one genus, *Millepora* Linnaeus, 1758, with 15 valid species, 6 of them being reported as hosts of symbiotic polychaetes (Serpulidae and Spionidae).

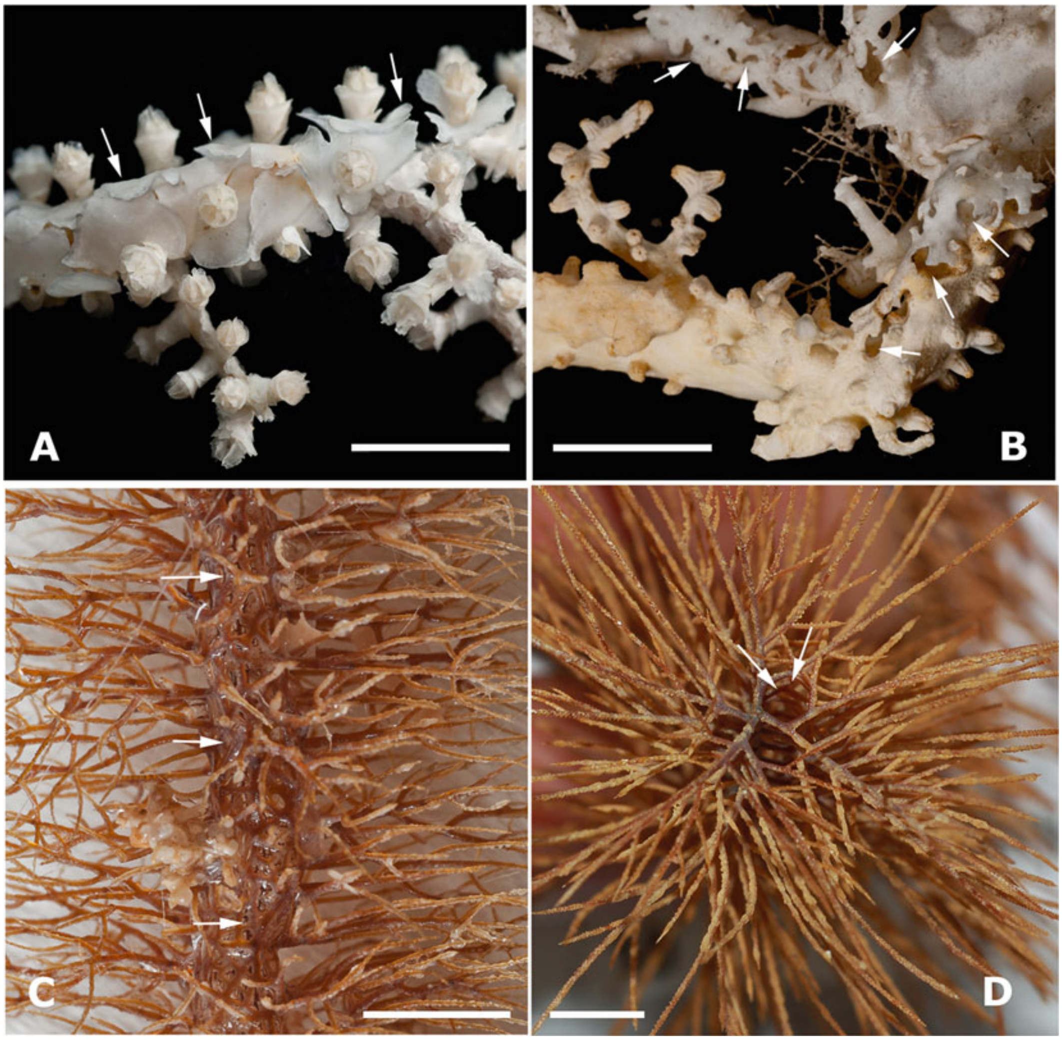

Fig. 25.3 Morphological modifications of cnidarian hosts. (**a**) *Candidella imbricata* with enlarged basal scales forming a tunnel (*arrowheads*) harboring *Gorgoniapolynoe caeciliae*; (**b**) tunnels (*arrowheads*) in branches of *Corallium* cf. *niobe* induced by *G. caeciliae*; (**c**) worm-run (*arrowheads*) in colony of *Stylopathes* sp. formed by densely anastomosed pinnules; (**d**) worm-run (*arrowheads*) along the stem of *Tanacetipathes* cf. *spinescens*. Scale: (**a**, **c**–**d**) – 5 mm, (**b**) – 10 mm

25.3 Polychaetes Involved in Associations with Cnidarians

About 120 species of symbiotic polychaetes of 10 families are reported from cnidarian hosts (Table 25.1, Fig. 25.4). It is hard to approximate the exact number of species as many host descriptions (e.g. Williams 2003; Cairns and Bayer 2004; Opresko 2006; Cairns 2012) report on symbionts that are not determined, even to the genus level. Apparently, the Polynoidae include the highest number of cnidarian-associated polychaetes: almost one half of the currently known species. They are followed by Syllidae, Serpulidae, Eunicidae and Spionidae. Spionids are generally considered as parasitic, however there are some indications that at least some cnidarian hosts can benefit from presence of these particular symbionts (see the next section). The families Hesionidae, Lumbrineridae, Spintheridae, Spherodoridae and Chaetopteridae comprise each only one or two species reported as symbiotic with cnidarians. The species of Sabellidae are known exclusively from cerianthid tubes (Table 25.1) and it is not clear if they can be considered as symbiotic.

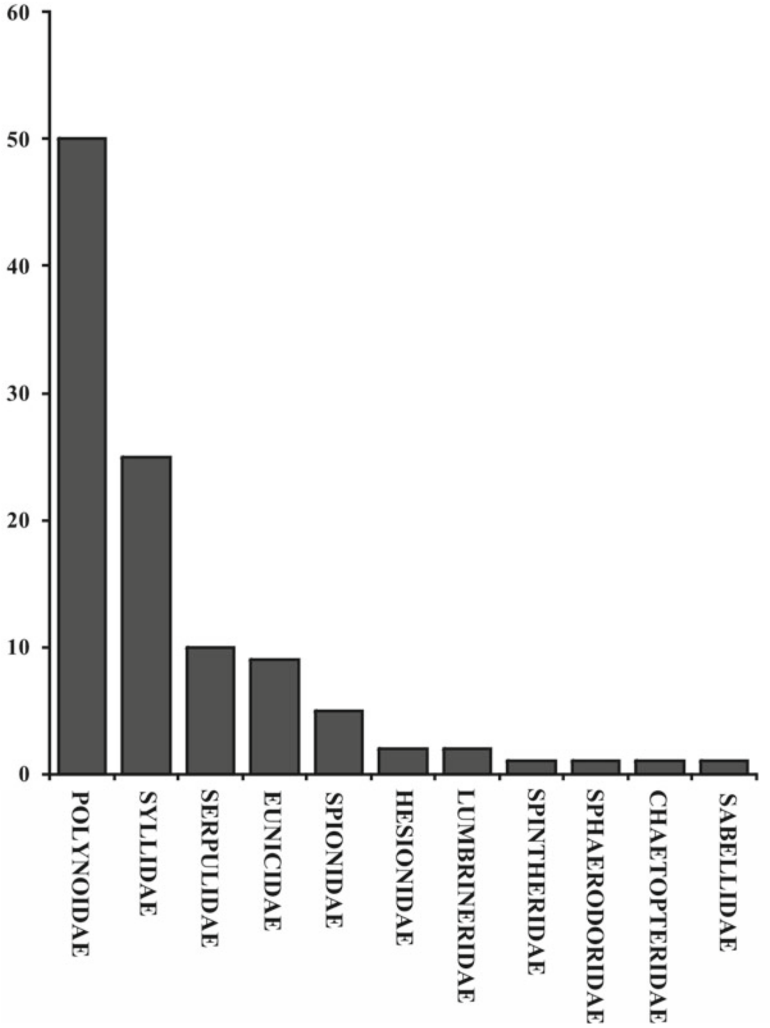

Fig. 25.4 Number of species in each polychaete family associated with cnidarian hosts

25.4 Host-Symbiont Interrelations

Symbiosis sensu De Bary (1879) is currently considered as a general term including close long-term associations between organisms of different species (Margolis et al. 1982), which are subsequently characterised according to the cost/benefit for partners (host:symbiont): commensalism (+:0), parasitism (+:−), and mutualism (+:+). More than 90 % of the relationships between coral hosts and symbiotic polychaetes are commensalisms (Table 25.1). However, the low level of knowledge and scattered available information on the biology of symbionts may artificially exaggerate their relevance (Martin and Britayev 1998). It is evident that coral colonies provide safety shelter for symbiotic polychaetes hidden among their three-dimensional network of branches, inside the skeleton, on the surface of coral branches beneath sclerites, or in tubular galls induced by the polychaetes themselves. So, if there are no clear evidences on negative (parasitism) or positive (mutualism) feedbacks for the host, the association is considered as commensalism.

The number of parasitic associates is significantly lower, while mutualists are virtually negligible (7.3 % and 1.8 % respectively). Among symbionts, some species from different families (i.e., spionids, syllids, polynoids) affect host growth (see section below). For instance, readdressing their energy resources to repair the damages induced by polychaetes instead to somatic growth and reproduction indicates a clear negative effect of the symbionts on their hosts. Moreover, there are indications on polychaetes feeding by stealing host food (Buhl-Mortensen 2001; Mueller et al. 2013) or by consuming coral mucus and tissues (Britayev and San Martín 2001; Britayev et al. 2014). At the same time symbionts may clean coral hosts from detritus, bacteria, fungi and algae, thus increasing their competitiveness, as well as protect them from predators attacks (e.g. Stewart et al. 2006; Bergsma 2009). However, the net outcome of these different processes on the metabolism and survivorship of corals is unknown. Accordingly, the status of some of these associations may need further re-evaluation depending on the appearing of new information on host symbionts relationships.

Nevertheless, there are some well studied associations between polychaetes and coral hosts, which are briefly summarized in the next sections.

25.4.1 Polynoidae

Polynoids are the most diverse group of polychaetes associated with gorgonian and antipatharian corals, but only one species has been well documented (Table 25.1). The unique species whose relationships with a host coral was studied is the scleractinian associate *Hololepidella* sp. (Britayev et al. 2015). Most studied specimens of *Hololepidella* sp. had up to one third of the gut length filled with mucus containing unicellular algae and cnidocysts, and a few of them also had copepod fragments. The algae were very similar in size, shape and color to the zooxantella living in host tissues, indicating that *Hololepidella* sp. was trophically related to the host coral and, thus, the species can be considered as parasite. In turn, the copepods closely resembled those obligatory associated with the scleractinian corals of the genus *Galaxea* Oken, 1815. The feeding of *Hololepidella* sp. on the parasitic siphonostomatoid copepod evidence that one symbiont may control the density of another one living in the same host. The high prevalence, specific location on the host, and feeding strategy clearly suggest that *Hololepidella* sp. is a specialized scleractinian symbiont, closer to a parasite. In turn, other scleractinians associates (i.e. crabs and shrimps) are known as mutualistic due to their cleaning or guarding activity (Stewart et al. 2006). However, like *Hololepidella* sp., they also feed on coral mucus and tissues. Therefore, further clarification of the ecological role (parasitism *vs.* mutualism) of *Hololepidella* sp. will require detailed studies including more field observation and experimental approaches.

25.4.2 Serpulidae

The single well-documented example of coral–polychaete relationship among serpulids is that of the filter-feeding species of *Spirobranchus*. In this case, the association is considered as mutualism, since the current created by the branchial crown of *Spirobranchus* spp. draws water up from the coral surface (Strathmann et al. 1984), enhancing the arrival rate of food particles to the coral polyps, improving the water circulation close to coral surface and, consequently, decreasing the susceptibility of the host corals to bleaching (Hunte et al. 1990; Nakamura et al. 2003). An additional advantage for the coral is that the worms may defense the host from the attaks of the carnivorous starfish *Acanthaster planci*. When contacted by the starfish, the worms hosted by *Porites* spp. immediately retract and reappear, pushing against the tube feet and arms of the starfish with the ornamented operculum and the branchial crown, forcing the predator to move away (DeVantier et al. 1986).

25.4.3 Spionidae

Data on the impact of spionids on their respective coral hosts are rare and controversial. In fact, polydorid worms may affect their hosts by weakening their branches and drawing energy to repair the skeletal tissue damaged by polychaete boring activity. For example, the burrow openings of *Dipolydora armata* on the surface of *Millepora complanata* develop distinctive, erect spines caused by the combined growth of worm tubes and host tissue. The zooids of *Millepora* were absent in the vicinity of tube openings and on spines and, thus, the potential feeding surface of the coral is reduced in heavily colonized branches. Burrows and openings were densest at the bases of the branches of *Millepora* where the skeleton weakening may easily occur (Lewis 1998).

In contrast, indirect evidences prove that the presence of spionids may enhance tissue growth/calcification rate in *Astreopora myriophthalma* (Wielgus and Levi 2006). In fact, the capture of particulate organic matter from the water column and the adjacent substrate and the production of nitrogen enriched metabolic waste products may affect primary production in coral reefs by influencing the physiology of the coral/zooxanthella association.

Another spionid, *Polydora villosa*, often inhabits the branched morph of *Montipora* spp., while is rare in encrusting or columnar morphs. Accordingly, this has been considered as an indirect evidence on the symbiont-mediated modification of *Montipora* spp. from an encrusting or columnar morph to a branched one (Liu and Hsieh 2000). Interestingly, similar morphological changes induced by a symbiotic amphipod apparently enhanced the resistence of *Montipora* spp. to predation by pincushion (*Culcita novaeguineae*) and crown-of-thorns (*Acanthaster planci*) sea stars. The fingers of the branched colonies of *Montipora* spp. were both less susceptible to be attacked and more likely able to survive to an attack than the colonies without fingers. Furthermore, the presence of fingers altered the preferences of *A. planci* prey, as the sea star preferred *Montipora* spp. without fingers over other common corals, but preferred these other corals when the specimens of *Montipora* spp. had fingers (Bergsma 2012).

25.4.4 Chaetopteridae

Finger-like skeletal modifications in the scleractinian coral *Montipora* spp. induced by the chaetopterid *Spiochaetopterus* sp. have been recently described by Bergsma (2009). Fingers inhabited by worms were similar in size and shape to those inhabited by amphipods in the same host, while their frequency (29.2 % of colonies and 9.3 % of fingers) and length (up to 122 mm) was lower. The fingers induced by chaetopterids are considerably longer than the 50 mm reported for the otherwise identical structures induced by spionids on *Montipora* spp. in Taiwan (Liu and Hsieh 2000). These fingers were frequently found detached from their parent colony, which evidences that symbionts may reduce the ability of *Montipora* spp. to withstand physical disturbances. However, detached coral fingers are able to survive and reattach to form new colonies, which can be helpful for coral dispersal. Morphological changes may also affect corals' ability to utilize resources and to compete for space. These observations indicate that symbiont-induced growth forms may enhance the reproductive potential and competitive ability of *Montipora* spp. in Moorea (French Polynesia).

25.4.5 Host Specificity

The host specificity of symbiotic polychaetes associated with corals is relatively high (Fig. 25.5): 69 out of 107 species determined to a species level (64.48 %) are known from a single cnidarian host, 17 from 2, 8 from 3, and 2 from 4. However, among the "monoxenous" species occurring in only one cnidarian host, some occur also in association with other non-cnidarian taxa, such as echinoderms or mollusks. For instance, *Arctonoe vittata*, a symbiont of *Metridium senile*, is also known from at least 30 more hosts including echinoids, asteroids, polychaetes and mollusks. *Hololepidella nigropunctata*, a symbiont of *Lobactis scutaria* in the Red sea, commonly occurs in association with at least 20 species, mostly asteroids and brittle-stars. Nevertheless, polyxenous cnidarian-symbiotic polychaetes are relatively scarce: Only 11 species are reported from more than 5 hosts, which usually belong to closely related taxa or inhabit the same ecological niche. For instance, *Spirobranchus corniculatus* (Serpulidae) occurs in association with 52 cnidarian hosts, all them belonging to the Scleractinia, except for three Milleporidae. *Lumbrineris flabellicola* (Lumbrineridae), reported in 31 associations, lives mostly with ahermatypic scleractinians (29 species), but also with one hydroid and one zoanthid (Zibrowius et al. 1975; Martin and Britayev 1998). Symbiotic polychaetes inhabiting black corals seem to be strict associates of antipatharians (Wagner et al. 2012), except *Tottonpolynoe symantipatharia*, which was also reported from *Sclerisis macquariana* (Alcyonacea: Isidiidae). Finally, some cnidarian taxa have no specific symbionts. For instance, all polychaetes reported from *Millepora* are also known from scleractinian hosts (Lewis 2006).

25.4.6 Location on the Host

Polychaetes are generally found on the surface of their cnidarian hosts (either on colonies or on individual polyps). Alternatively, tubes of symbiotic polychaetes can be embedded in the hard skeleton, with only part of the animal appearing at the surface, such as the precious Christmas tree worm *Spirobranchus* spp. (Serpulidae), whose calcareous tubes are deeply embedded inside the host (Scleractinia or Milleporidae) skeleton as they are overgrown by the coral skeleton while being formed.

Some polychaete symbionts live inside tunnels or galleries (formed by modifications of the coenenchyme or the sclerites) on branches of the host colony as, for example, *Gorgoniapolynoe* spp. on colonies of Primnoidae (Fig. 25.3a) and Corallidae (Fig. 25.3b) (Eckelbarger et al. 2005; Simpson and Watling 2011; Britayev et al. 2014). Alternatively, galleries may be formed (apparently excavated by the symbionts) inside the host coenenchyme, as in the case of *Haplosyllis anthogorgicola* (Syllidae) on *Anthogorgia bocki* (Martin et al. 2002).

Only few reports of life cycle stages of polychaete symbionts living inside cnidarian hosts are known to date. Among them, the larvae of the syllid *Epigamia alexandri* (reported as *Proceraea rzavskyi*) develop inside hydrothecae of *Abietinaria turgida*. At an early juvenile stage, they apparently begin to feed on the tissues of the hydranth, to the extent that they finally occupied the whole space inside of the zoothecae. When the juveniles reach about 1 mm, they leave the zootheca and start building a mucus tube attached to the main stem of the hydroid colony (Britayev and San Martín 2001). Early larval and juvenile stages of at least some symbiotic polychaetes are planktonic free-living (Eckelbarger et al. 2005; Rowley 2008), whereas in other species eggs are hatched inside the host (Britayev and San Martín 2001).

25.4.7 Prevalence of Infestations

The relationship between number of infested and total number of hosts, also known as "prevalence of infestation" (Martin and Britayev 1998), is not often discussed in literature. Such information for cnidarian hosts is even more rare and mostly available for easy to spot symbionts. As discussed by Martin and Britayev (1998), this value cannot be considered as characteristic at the species level. Each population of a given commensal species is usually characterized by a dif-

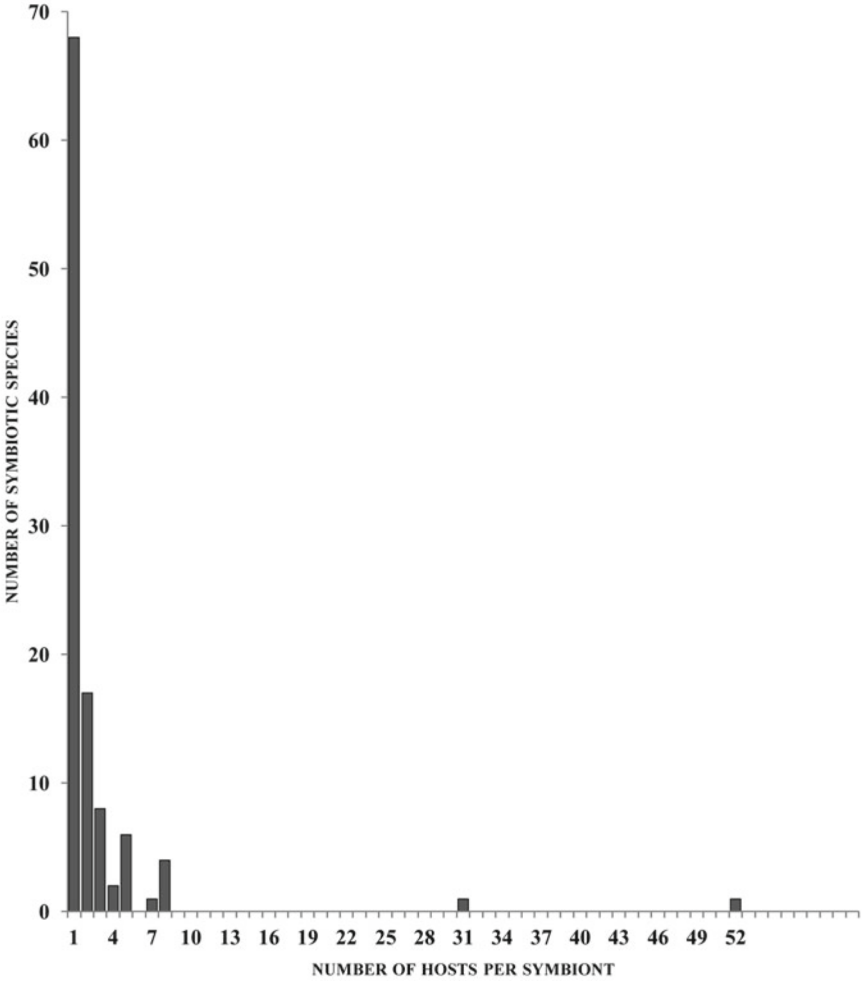

Fig. 25.5 Number of cnidarian hosts reported for symbiotic polychaetes

ferent prevalence. Prevalences may range from extremely low to considerable high percentages. For instance, the infestation by *Imajimaea draculai* reaches 10 % in the population of *Funiculina quadrangularis* (Pennatulacea) from the Bratten area (Skagerrak) (Nygren and Pleijel 2010). About 50 % of nephtheids from the Darwin region (Northern Australia) harbor *Alcyonosyllis phili*, while a 100 % of the colonies of some species of *Narella* (Primnoidae) are infested, to the extent that the presence of the symbiotic polynoid is considered a species level indicator (Cairns 2012). Also a 100 % of *Conopora adeta* (Stylasteridae) were reported to host the polynoid *Benhamipolynoe cairnsi* (Cairns 1987), and all hitherto known species of *Stylopathes* (Antipatharia) host polynoid polychaetes (Opresko 2006; Molodtsova and Budaeva 2007).

Factors that can be crucial for prevalence of infestation include bathymetry, spatial variability and hydrology (Martin and Britayev 1998). Another factor that can be important is the antropogenic disturbance. For instance, Wielgus et al. (2006) showed that the infestation of reef-building stony corals by spionids was significantly correlated with the total oxydized nytrogen in the water column in the vicinity of organic waste discharges.

If a symbiont occurs on different hosts, the prevalence may vary even within the same locality (Martin and Britayev 1998) depending on how suitable are the different hosts. For instance, *Spirobranchus polycerus* in Barbados occurs on several species of scleractinians and milleporids, but is most common on *Millepora complanata* and only occasionally occurs on scleractinian corals (Lewis 2006).

25.4.8 Intensity of Infestation

The number of symbionts per coral host is also highly variable. Martin and Britayev (1998) reported at least seven species of symbiotic polychaetes associated with cnidarian hosts with known intensities of one symbiont per host.

Apparently, the intensity is closely related to a territorial behavior, but no direct evidences have been reported for cnidarian symbionts. There are no references to isolated heterosexual pairs inhabiting the same coral host individual. On the other hand, some coral symbionts show very high intensities. For instance, 18 specimens of *Brychinoe karenae* were collected from a single relatively small colony of *Leiopathes secunda* (Hanley and Burke 1991a). About 120 specimens of *Gorgoniapolynoe caeciliae* were recovered from one-fourth of a single colony of *Candidella imbricata* (Eckelbarger et al. 2005), while intensities of about 0.2–0.4 of symbionts per 1 cm of the host were reported for the co-generic *G. uschacovi* (Britayev 1981) and *G. guadaloupensis* (Pettibone 1991). The intensity of the serpulid *Spirobranchus giganteus* range from 0.2–12 symbionts per 1 cm^2 of living coral surface (Martin and Britayev 1998).

Even closely related species can differ in their intensity. For instance, the maximum intensity reported for *H. chamaeleon* and *H. villogorgicola* are about ten symbionts per host colony, whereas *H. anthogorgicola* can reach up to 15 symbionts per 1 cm of colony (Martin et al. 2002).

25.5 Host Reactions to Symbiont Presence

The number of studies reporting changes in host morphology caused by the presence of symbiotic polychaetes is very limited. Quite often, these modifications are not attributed to the symbiont presence because the two partners are studied separately. In few cases, cnidarian host did not exhibit any morphological reactions to the presence of symbiotic polychaetes. *Haplosyllis chamaeleon* inhabiting the surface of the branchlets of *Paramuricea clavata* did not induce significant changes to the coral host morphology. However the symbiont usually occurred on parts of the colony with high number of living polyps (Martin et al. 2002). No changes in the host morphology were recorded for the *Alcyonosyllus phili* (Fig. 25.6b, d) (Glasby and Watson 2001; Britayev and Antokhina 2012) or in *Funiculina quadrangularis* hosting *Imajimaea draculai* (Nygren and Pleijel 2010).

Scars or grooves induced by *Lumbrineris flabellicola* were reported on the outer surface of the skeleton in several azooxanthelate scleractinians (Fig. 25.2a) (Zibrowius et al. 1975; Miura and Shirayama 1992; Cairns and Zibrowius 1997). This lumbrinerid polychaete inhabits soft membranous tubes attached to the external surface of the coral skeleton. However, the calcareous skeleton became partly dissolved beneath the tube, giving rise to a grove causing the tube to become partly embedded into the coral skeleton. In turn, the depth of the groove is highly dependent of the host species, being more pronounced in *Caryophyllia* spp. and *Flabellum chunii* (Zibrowius et al. 1975).

Frame-building scleractinian corals, such as *Lophelia pertusa*, *Madrepora oculata* or *Solenosmilia variabilis*, often overgrow the tubes of the symbiotic polychaete *Eunice* spp. (Fig. 25.3b) (Zibrowius 1980; Cairns and Zibrowius 1997). A similar effect was reported for *E. norvegica* on the stylasterid *Errina atlantica* (Zibrowius and Cairns 1992). Aquarium experiments with *E. norvegica* (Buhl-Mortensen 2001; Roberts 2005) showed that their tube-building stimulates the production of coral skeleton. The parchment-like tubes of *Eunice* spp. are used as cores for calcification and may serve as the main stem for the skeleton, supporting longer branchlets >25 cm long (Buhl-Mortensen 2001). In the presence of eunicid symbionts, calcification rates in *Lophelia pertusa* increase up to four times (Mueller et al. 2013). Molodtsova and Budaeva (2007) reported overgrowth of eunicid tubes by the chitinous skeleton of the black coral *Antipathes* cf. *cylindrica* Brook 1889 (Fig. 25.3c).

Overgrowth of symbiont tubes by host tissues and skeleton leading to changes in the cnidarian host morphology have also been reported from shallow-water reefs. Accordingly, the chaetopterid polychaetes *Spiochaetopterus* sp. inhabiting colonies of *Montipora* spp. induce the formation of finger-like branchlets in the host (Bergsma 2009). The spionid *Dipolydora* sp. from the Gulf of Eilat (Red Sea) was reported (Wielgus et al. 2002, 2006) to induce skeletal aberrations in 10 % of its host scleractinians, resulting in the formation of 5–25 mm high cones. *Dipolydora armata* can stimulate formation of distinctive, erect spines at the bases of branches in *Millepora complanata* on Barbados coral reefs (Lewis 1998).

Surprisingly, symbiotic polychaetes rarely induce gall formation. Apparently, the single case was reported for *Proceraea penetrans*, which builds calcified blister-like galls on the host *Stylaster californicus* (Wright and Woodwick 1977, Zibrowius 1981). On the other hand, the formation of tunnels and galleries is characteristic for practically all known taxa of cnidarian hosts harboring symbiotic polychaetes which, to some extent, may be considered as a particular case of gall formation. Symbiotic syllids and polynoids generally produce tunnels or galleries. In soft corals, such galleries can be distinguished by a grove at the edge of capitulum, as that in *Pseudoanthomastus* spp. induced by *Neopolynoe acanellae* (Molodtsova 2013), or by a rolled margin, as that in *Sphaerasclera flammicerebra* induced by an unidentified polychaete (Williams 2003) and giving a distinctive mushroom-shape look to the colony (Fig. 25.2d–f). In both cases, the groove is formed from overgrowths and processes of the soft tissue, and there are no indications in the literature on skeletal elements' affectation.

Galleries in primnoids are generally attributed to the presence of symbiotic polynoids of the genus *Gorgoniapolynoe* (Cairns and Bayer 2004; Eckelbarger et al. 2005; Cairns 2012; Britayev et al. 2014). In primnoids, the gallery is

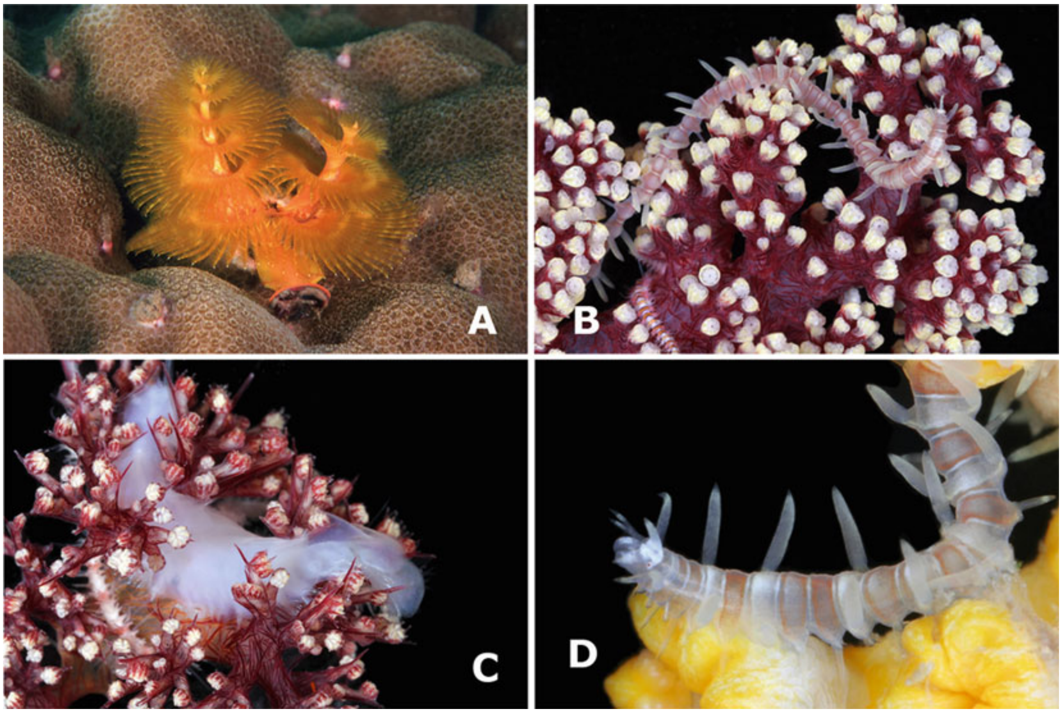

Fig. 25.6 Symbiotic polychaetes with their hosts (photos courtesy O. Savinkin). (**a**) *Spirobranchus corniculatus* on colony of *Porites* sp.; (**b**) *Alcyonosyllis phili* on undetermined nephtheid; (**c**) – *Paradyte levis* on *Dendronephthya* sp. (**d**) *A. phili* on *Carijoa* sp. (**a**) – in situ, (**b**–**d**) lab photos

formed by highly modified polyp scales: the basal ones of successive adjacent polyps became enormously enlarged and curved to meet together forming a tube that can attain up to 3 mm in diameter (Cairns and Bayer 2004, 2008; Cairns 2012) (Fig. 25.3a).

Galleries induced by symbiotic polynoids were reported on branches of several species of *Corallium* Cuvier, 1798 (Fig. 25.3b) and *Paracorallium* Bayer and Cairns, 2003 (Bayer 1964; Britayev 1981; Pettibone 1991a; Simpson and Watling 2011; Britayev et al. 2014). The gallery formation involves not only soft tissues but also the underlying calcareous axis. The mechanism of gallery formation in Corallidae is not really known. Obviously it does not result from any boring activity of the symbiont, but from a gradual formation as a response to its presence. Taking into account that the axial epithelium and free scleroblasts in *Corallium* have the same cellular origin (Grillo et al. 1993), we can speculate that the free scleroblasts of coenenchymal lobes involved in the gallery formation are induced somehow to form an additional layer of axial epithelium that begins to produce solid axis instead of loose sclerites.

Some symbiotic syllids also produce a kind of galleries in the coenenchyme of cnidarian hosts. For instance, *Alcyonosyllis glasbyi* is reported to form tubular nests or shelter-like structure on the surface of the host *Melithaea flabellifera* (San Martín and Nishi 2003). *Haplosyllis anthogorgicolla* forms galleries inside the coenchym of *Anthogorgia bocki*, opening near base of polyps as minute tube-like projections. The galleries are located between the surface of the host covered by spicules and inner axis, and appear as well-structured tubes, with tissue-built walls that can be easily distinguished from the remaining unaltered tissue (Martin et al. 2002). The species *H. villogorgicola* is assumed to induce fusion of two adjacent branchlets in the host *Villogorgia bebricoides* which forms a cavity inhabited by the symbiotic worm (Martin et al. 2002). The only case of gallery formation in scleractinians was reported for *Typosyllis* sp. forming so-called groove-and-tube structures in several species of reef-building scleractinian corals in Taiwan (Randall and Eldredge 1976).

Several species of symbiotic polynoids induce malformations in black corals, mainly of the genus *Stylopathes* (e.g. *Bayerpolynoe floridensis* inhabiting *S. litocrada*). These are the so-called "worm runs" (Totton 1923; Opresko 2006; Molodtsova and Budaeva 2007): tubular reticulated structures formed near the base of primary pinnules of numerous short highly anastomosing and fusing secondary and tertiary branchlets and pseudo-lateral pinnules that connect the stem with the worm run, but rarely extend beyond its surface (Fig.

25.3c). Feebly developed worm-runs with few or no anastomoses can be also found in species of the genus *Tanacetipathes* Opresko, 2001 (e.g. *Parahololepidiella greeffi* inhabiting *T. spinescens*) (Molodtsova and Budaeva 2007; Britayev et al. 2014) (Fig. 25.3d) and *Asteriopathes* Opresko, 2005 (Molodtsova and Budaeva 2007; Molodtsova unpublished data).

There are some other modifications that can affect the length of individual branchlets or the skeletal structures of individual zooids. For instance, the hydrothecae modification by the symbiotic syllid *Epigamia alexandri,* which caused the formation of an elongated tubular distal part in hydrothecae of *Abietinaria turgida* (Britayev and San Martín 2001). The spionid *Polydora wobberi* associated with *Lophogorgia* sp. apparently affect the length of branches. Worms inhabit narrow U-shaped burrows that open to the exterior at the tips of short stubby 20–30 cm long branches of the gorgonian, whose uninfested branches may reach up to 70 cm long. Molodtsova and Budaeva (2007) reported that presence of symbiotic polychaetes can alternate size and morphology of skeletal spines in black corals.

Changes of the host branching pattern induced by symbiotic polychaetes have also been reported. The presence of the spionid *Polydora villosa* may result in modifications of the growth form in hosts *Montipora* spp. from the encrusting or columnar morph to the branched one, but does not affect *Porites* spp. hosts (Liu and Hsieh 2000). Cairns (2011) described development of the third row of pinnules in a typically uniplanar colony of *Thouarella cristata* in the presence of undetermined commensal polynoid.

25.6 Adaptive Modification of Symbiotic Polychaetes

Symbiotic polychaetes have more or less defined morphological features allowing distinguishing them from their free-living relatives (Martin and Britayev 1998), which can be grouped in different categories: coloring, morphology, life cycle and behavioral. Also, these modifications can be adaptive or non-obviously adaptive. ‘Non-adaptive modifications’, either morphological or not, allow to differentiate the symbionts from their free-living relatives, but lack obvious adaptive significance. Cnidarian polychaete symbionts are not an exception. However, only two out of the nine families including cnidarian associates, Syllidae and Polynoidae, are sufficiently represented to evaluate trends in adaptive modifications. Moreover, as very little is currently known on life cycle and behavior adaptations, we have here considered only those affecting morphology and coloration.

25.6.1 Syllidae

Color adaptive modifications in Syllidae generally imply a correspondence with the host color. Worms inhabiting the surface of corals often have cryptic coloration, mimicking that of the host. Thus, the pale-yellowish *Haplosyllis villogorgicola* and orange *H. anthogorgicola* match exactly the color of their hosts; *H. chamaeleon* can demonstrate a range of colorations from yellow to dark red or violet, with dark violet dorsal marks, but generally matches exactly the color of their hosts *Paramuricea clavata* and *P. grayi*, which may exhibit all this color range in the same or in different colonies, respectively (Martin et al. 2002; Lattig and Martin 2009). An alternative color adaptation providing protection when living on the host surface is the disruptive coloration of *Alcyonosyllis phili* (Fig. 25.6b, d). This cream colored syllid with transverse brown bands can be hardly visible on brightly colored nephtheid or xeniid hosts (Glasby and Watson 2001; Britayev and Antokhina 2012).

The main morphological modifications reported in cnidarian associated Syllidae affect chaetal arrangement and shape (Fig. 25.7). For instance, the number of chaetae per

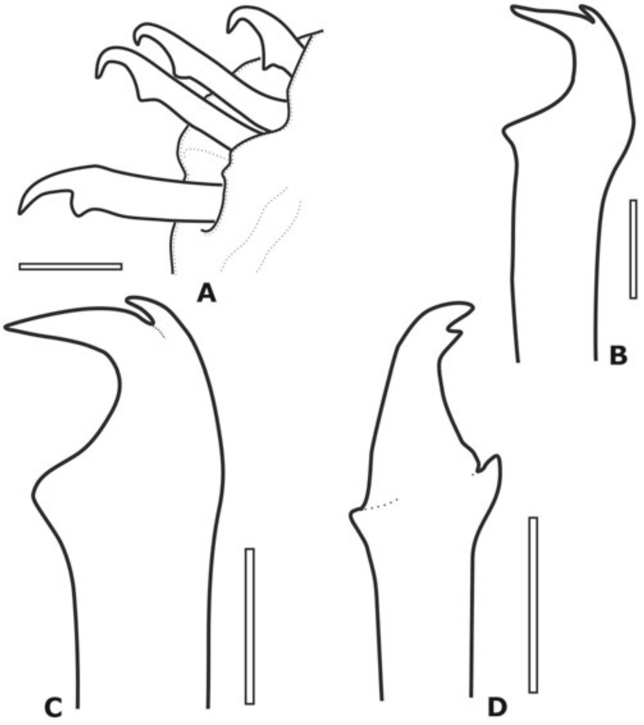

Fig. 25.7 Hooked chaeta in *Haplosyllis* spp (Syllidae) (After Martin et al. 2002). (**a**, **b**). *H. chamaeleon*: (**a**) Chaetae from the first chaetiger; (**b**) Tip of a chaeta from posterior-most chaetigers; (**c**) *H. villogorgicola*: Tip of ventral mid-body chaetae. (**d**) *H. anthogorgicola*: tip of pseudocompound chaeta of the first chaetiger. Scale: (**a**) – 15 mkm, (**b**) – 6 mkm, (**c**) – 4.3, (**d**) – 5 mkm

bundle tended to be reduced and their morphology tended to be simplified from the typically articulated type of most free-living forms to either pseudocompound chaeta (*H. anthogorgicola*), simplified, or hooked forms (*H. chamaeleon*, *Alcyonosyllis* spp., symbiotic Autolytinae) (Martin and Britayev 1998; Martin et al. 2002), which probably serve better to allow the worms to remain attached to the host surface.

25.6.2 Polynoidae

The adaptive modification in coloration of the Polynoidae strongly depends on the position of the symbiotic polychaete on the host. Polynoids inhabiting the host surface usually have cryptic colorations. For instance, *Australaugenira rutilans*, was described from *Xenia* sp. (Octocorallia Xeniidae) and reported as to be of 'exactly the same red color as host' (Wehe 2006) and mimic also the color of another host, *Dendronephthya* sp. (Britayev and Antokhina 2012). The special case of the almost transparent *Uncopolynoe corallicola* and *Paradyte laevis* (Fig. 28.8c) which are hardly visible on the bright surface of their nephtheid hosts *Dendronephthya* spp. (Britayev and Antokhina 2012), can also be considered as an example of cryptic coloration. Polynoids inhabiting galleries and tunnels formed by skeletal elements or tissues of cnidarian hosts are mostly whitish or fleshy in color as, for instance, the species of *Gorgoniapolynoe* inhabiting different species of Corallidae and Primnoidae (Eckelbarger et al. 2005; Simpson and Watling 2011; Britayev et al. 2014).

A true case of mimicry was described for *Medioantenna variopinta* associated with *Solanderia secunda* (Hydrozoa, Capitata). The orange body of this symbiotic worm mimics the large orange eumedusoids of the host colony, while the white pigmentation on the cephalic appendages and on dorsal cirri and the finger-like macropapillae of the elytra mimic the coloring of the host polyps (Di Camillo et al. 2011).

Developing hooked chaetae on anterior segments seems also to be a clear adaptive trend in symbiotic polynoids. *Uncopolynoe corallicola* has stout, strongly bent hooks on segments 2–4, while *Australaugeneria rutilans* has strongly hooked neurochaetae on the anteriormost segment (Wehe 2006).

While chaetal modifications seems to be an obvious adaption to the symbiotic mode of life, most of morphological modifications of elytra and parapodia in symbiotic polynoids cannot be easily considered as adaptive. The elytra of many commensal scale-worms are small, often leaving much of the dorsal surface uncovered, thin and smooth, and usually lack ornamentations (i.e. papillae and tubercules). *Parahololepidella greeffi* inhabiting colonies of *Tanacetipathes* cf. *spinescens* has soft transparent elytra lacking tubercules and papillae, which are large, covering mid-dorsum on the first 11–12 segments, and then become very small, leaving dorsum and parapodia uncovered (Fig. 25.8a–c) (Britayev et al. 2014). *Gorgoniapolynoe* spp. inhabiting mostly octocorals of the families Primnoidae, Corallidae and Acanthogorgidae also have relatively small transparent elytra without ornamentation, except on the first pair that is larger and completely cover the prostomium (Pettibone 1991; Britayev et al. 2014). However, these elytra shows an additional adaptive modification: just above the eyes, each elytron of the first pair has a crescent shaped, transparent, chitinized area with scattered microtubercules (Fig. 25.8d) that is apparently connected to the ability of the worm to distinguish between light and dark even from when lied inside the coral gallery. Taking into account the depth range of *Gorgoniapolynoe* spp. (300–2,000 m), it is hard to expect enough light at these depths. However, there is a number of reports about biolumenescence of corals and polynoids (see e.g. Nicol 1953; Herring 1991; Plyuscheva and Martin 2009; Johnsen et al. 2012) and apparently such adaptation may be connected with bioluminescence ability of host or symbiont. Parapodial modifications are most often reductions in size. Thus *P. greeffi* has small digitiform notopodia (Britayev et al. 2014) and *U. corallicola*, associated with undetermined alcyonaceans, completely lacks notopodia (Wehe 2006).

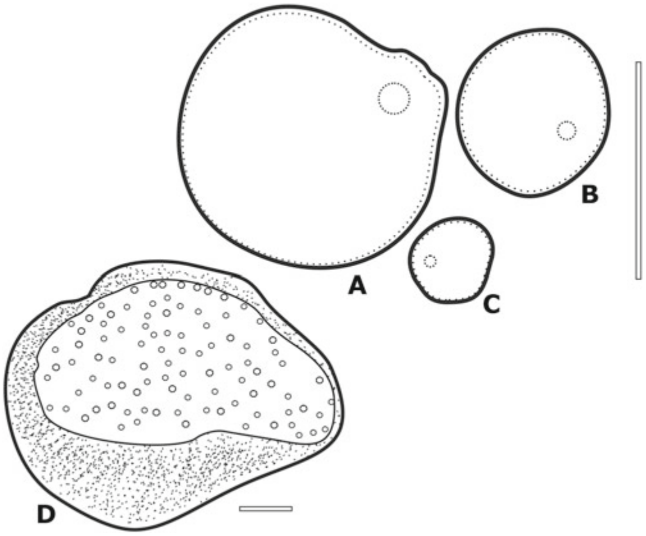

Fig. 25.8 Elytra modifications in Polynoidae (After Britayev et al. 2014). (**a–c**) *Paraholoepidella greeffi*: elitra of 9th (**a**), 32nd (**b**) and 87th (**c**) segments; (**d**) *Gorgoniapolynoe caeciliae*, elytron of the first pair. Scale (**a–c**) – 2 mm; (**d**) – 0.1 mm

25.7 Conclusions. Main Gaps in Our Present Knowledge in Biology of Polychaete-Coral Symbiosis

One of the most interesting results revealed by our review is that every group of cnidarians seems to have their own assemblage of symbiotic polychaetes. Accordingly, scleractinian corals more often harbor lumbrinerids, serpulids and spionids, which include a few symbiotic species inhabiting a wide range of hosts. On the other hand, the alcyonaceans and antipatharians are more often associated with polynoids and syllids, which include numerous symbiotic species. It is interesting to notice that the members of these families are among the symbionts inducing the most dramatic changes in host morphology. Also, the species of host genera such as *Narella* (Primnoidea) or *Corallium* (Corallidae), or even whole genera of deep-sea alcyonaceans or black corals such as *Stylopathes* (Antipatharia, Stylopathidae) have never been reported without their polynoid symbionts. Despite these hosts are so deeply involved in symbiotic associations that the presence of symbionts has been considered as a species-specific, robust taxonomic character, quite often little is known about their symbiotic partners, which usually remain undetermined even at the genus level. Taking this into account, as well as the high diversity in the host morphology, we certainly expect the fauna associated with deep-sea corals to be a hidden hot-spot of diversity, and many species of polychaete symbionts are waiting to be described in deep sea environments.

Symbiotic associations, particularly parasitic and mutualistic ones, are clearly bidirectional and, thus, a well-known source of co-evolution. This means that not only the symbionts may acquire modifications due to their mode of life, but also the hosts may tend to develop specific adaptations. However, very few studies have been addressed to understand the mechanisms leading the symbionts to influence on the host morphology, which quite often involve particular elements of the host skeleton (e.g., the extra-large sclerites of primnoids or the slow-growing processes of the central axis of corallids, the changes in spine morphology of antipatharians). Also, no studies have been addressed to assess how long it takes to produce the worm tubes or worm runs, neither on the mechanisms and chemical cues that influence skeletogenesis in cnidarian hosts. Implicitly, there are no studies on the extend of the associations or, in other words, whether the symbiont grows in parallel with the host or, if not, when the colonization occurs (i.e., larval settlement, juvenile or adult migration) and on the mechanisms leading the symbionts to recognize the presence of their hosts, and this is particularly true in deep-sea environments. Last, but not least, there are no studies focusing on how symbiotic worms affect the host fitness, as well as their metabolism, growth rate or reproductive potential.

Despite more than 15 years passed since Martin and Britayev (1998) published their review on the whole symbiotic polychaetes, one of their main conclusive statements still holds for the particular subset of coral associates: more than a closing analyses on a well-developed matter, our review still reveals many gaps in the study of polychaete-coral relationships, meaning that we highly encourage further work to be done on these highly interesting symbiotic associations.

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