

# The mushroom coral as a habitat

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*The evolution of symbiotic relationships involving reef corals has had much impact on tropical marine biodiversity. Because of their endosymbiotic algae (zooxanthellae) corals can grow fast in tropical shallow seas where they form reefs that supply food, substrate and shelter for other organisms. Many coral symbionts are host-specific, depending on particular coral species for their existence. Some of these animals have become popular objects for underwater photographers and aquarists, whereas others are hardly noticed or considered pests. Loss of a single coral host species also leads to the disappearance of some of its associated fauna. In the present study we show which mushroom corals (Scleractinia: Fungiidae) are known to act as hosts for other organisms, such as acoel flatworms, copepods, barnacles, gall crabs, pontonine shrimps, mytilid bivalves, epi-toniid snails, coralliophilid snails, fish and certain types of zooxanthellae. Several of these associated organisms appear to be host-specific whereas other species are generalists and not even necessarily restricted to fungiid hosts. Heliofungia actiniformis is one of the most hospitable coral species known with a recorded associated fauna consisting of at least 23 species. The availability of a phylogeny reconstruction of the Fungiidae enables comparisons of closely related species of mushroom corals regarding their associated fauna. Application of a phylogenetic ecological analysis indicates that the presence or absence of associated organisms is evolutionarily derived or habitat-induced. Some associations appear to be restricted to certain evolutionary lineages within the Fungiidae, whereas the absence of associated species may be determined by ecomorphological traits of the host corals, such as coral dimensions (coral diameter and thickness) and polyp shape (tentacle size).*

**Keywords:** coral reefs, host-specificity, interspecific associations, marine biodiversity, phylogenetic ecology, stony corals

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## INTRODUCTION

Among marine ecosystems, coral reefs are particularly well known for their biodiversity, usually measured by numbers of coral and fish species (Bellwood & Hughes, 2001; Hughes *et al.*, 2002; Roberts *et al.*, 2002; Bellwood *et al.*, 2004; Hoeksema, 2007). These two prominent groups of organisms are important elements in two out of three major components of coral reef communities, i.e. suprabenthic reef fish and sessile epibenthic organisms that form the living cover and structure of reefs, such as corals, sponges and algae (Reaka-Kudla, 2007). The third component is formed by the cryptofauna, predominantly consisting of invertebrates dwelling in and on the (living) substrate, which forms the most species-rich group of coral reef communities (Austin *et al.*, 1980; Coles, 1980; Gotelli & Abele, 1983; Preston & Doherty, 1994; Reaka-Kudla, 2007; Plaisance *et al.*, 2009).

Although it is known that reef corals act as hosts for many endo- and episymbiotic organisms (Hutchings & Peurot-Clausade, 1988; Lewis & Snelgrove, 1990; Paulay, 1997; Oigman-Pszczol & Creed, 2006; Stella *et al.*, 2011), little information is available about how many species can be found on or in each coral host species (Nogueira, 2003; Plaisance *et al.*, 2009; Stella *et al.*, 2011). Furthermore, a coral may not only act as host when it is alive but it can also serve as substrate for some other species only when it is dead (Wilson, 1979; Kleemann, 1990; Morton, 1990; Hutchings *et al.*, 1992; Moreno-Forero *et al.*, 1998; Fonseca *et al.*, 2006; López *et al.*, 2008).

Many coral reef biodiversity studies concentrate on corals, especially in the Indo-Pacific centre of maximum marine biodiversity with boundaries based on coral species numbers, which therefore is called the Coral Triangle (Hoeksema, 2007). Hence it is relevant to know how many symbiont species depend on each host species, and especially how many of these are host-specific. This implies that with the local loss of a particular coral species (e.g. Hoeksema & Koh, 2009; Van der Meij *et al.*, 2010; Hoeksema *et al.*, 2011), a part of the associated assemblage is lost as well (Munday, 2004). In order to get more insight in this subject, mushroom corals belonging to the Fungiidae (Scleractinia), a family of Indo-Pacific reef corals (Hoeksema, 1989), are used as a model group to study their role as hosts for other kinds of organisms, such as zooxanthellae, shrimps, crabs, copepods, barnacles, snails, bivalves, worms and so on. We present an overview of mushroom coral species and their associates as known from the literature and as observed during our own surveys. With that we analyse whether these associated species are mostly generalists or host-specific. Since the number of associated organisms may vary per host species, we want to find out if there is a relation between host morphology and the number of associated species and if there is a phylogenetic component herein. By using mushroom corals as a model group we aim to obtain more insight in the ecology and evolution of the associated biodiversity of corals.

## MATERIALS AND METHODS

The identity of the host corals (Table 1) is based on the taxonomic revision of the Fungiidae by Hoeksema (1989) and subsequent studies in which new mushroom coral species were described (Veron, 1990, 2002; Hoeksema & Dai, 1991;

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**Table 1.** Mushroom coral host species (Fungiidae, N = 50) in the revised classification based on molecular analyses (Gittenberger *et al.*, 2011).

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<i>Cantharellus doederleini</i> (Von Marenzeller, 1907)
<i>Cantharellus jebbi</i> Hoeksema, 1993
<i>Cantharellus noumeae</i> Hoeksema & Best, 1984
<i>Ctenactis albitentaculata</i> Hoeksema, 1989
<i>Ctenactis crassa</i> (Dana, 1846)
<i>Ctenactis echinata</i> (Pallas, 1766)
<i>Cycloseris costulata</i> (Ortmann, 1889)
<i>Cycloseris curvata</i> (Hoeksema, 1989)
<i>Cycloseris cyclolites</i> (Lamarck, 1815)
<i>Cycloseris distorta</i> (Michelin, 1842)
<i>Cycloseris fragilis</i> (Alcock, 1893)
<i>Cycloseris hexagonalis</i> (Milne Edwards & Haime, 1848)
<i>Cycloseris mokai</i> (Hoeksema, 1989)
<i>Cycloseris sinensis</i> Milne Edwards & Haime, 1851
<i>Cycloseris somervillei</i> (Gardiner, 1909)
<i>Cycloseris tenuis</i> (Dana, 1846)
<i>Cycloseris vaughani</i> (Boschma, 1923)
<i>Cycloseris</i> sp.
<i>Danafungia horrida</i> (Dana, 1846)
<i>Danafungia scruposa</i> (Klunzinger, 1879)
<i>Fungia fungites</i> (Linnaeus, 1758)
<i>Halomitra clavator</i> Hoeksema, 1989
<i>Halomitra pileus</i> (Linnaeus, 1758)
<i>Heliofungia actiniformis</i> (Quoy & Gaimard, 1833)
<i>Heliofungia fralinae</i> (Nemenzo, 1955)
<i>Herpolitha limax</i> (Esper, 1797)
<i>Lithophyllon concinna</i> (Verrill, 1864)
<i>Lithophyllon ranjithi</i> Ditlev, 2003
<i>Lithophyllon repanda</i> (Dana, 1846)
<i>Lithophyllon scabra</i> (Döderlein, 1901)
<i>Lithophyllon spinifer</i> (Claereboudt & Hoeksema, 1987)
<i>Lithophyllon undulatum</i> Rehberg, 1892
<i>Lobactis scutaria</i> (Lamarck, 1801)
<i>Pleuractis granulosa</i> (Klunzinger, 1879)
<i>Pleuractis gravis</i> (Nemenzo, 1955)
<i>Pleuractis moluccensis</i> (Van der Horst, 1919)
<i>Pleuractis paumotensis</i> (Stutchbury, 1833)
<i>Pleuractis seychellensis</i> (Hoeksema, 1993)
<i>Pleuractis taiwanensis</i> Hoeksema & Dai, 1991
<i>Pleuractis</i> sp.
<i>Podabacia crustacea</i> (Pallas, 1766)
<i>Podabacia kunzmanii</i> Hoeksema, 2009
<i>Podabacia motuporensis</i> Veron, 1990
<i>Podabacia sinai</i> Veron, 2002
<i>Polyphyllia novaehiberniae</i> (Lesson, 1831)
<i>Polyphyllia talpina</i> (Lamarck, 1801)
<i>Sandalolitha dentata</i> Quelch, 1884
<i>Sandalolitha robusta</i> (Quelch, 1886)
<i>Sandalolitha</i> sp.
<i>Zoopilus echinatus</i> Dana 1846

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Hoeksema, 1993a, b, 2009; Ditlev, 2003). The classification has been adapted after a recent molecular phylogenetic study of the Fungiidae (Gittenberger *et al.*, 2011). The results of that study enable phylogenetic comparisons of symbiont–host associations. Coral species that may belong to the Fungiidae according to molecular studies, but which are still classified with the Siderastreidae (Benzoni *et al.*, 2007), i.e. *Psammocora explanulata* Van der Horst, 1922, and *Coscinaraea wellsii* Veron and Pichon, 1980, have not been included as hosts in the present study because formally they do not yet belong to the Fungiidae and because insufficient information on their associated fauna is available.

The associated organisms included in this study consist of zooxanthellae (*Symbiodinium* spp.), crustaceans (copepods, barnacles, gall crabs and shrimps), molluscs (mytilid bivalves, epitonid snails and coralliophilid snails) and fish. Data were obtained from the literature and from our own observations during fieldwork in the Coral Triangle countries Indonesia (South Sulawesi in 1994–1998, Ambon in 1996, Bali in 2001, East Kalimantan in 2003, Thousand Islands off Jakarta in 2005, Raja Ampat in 2007, Ternate in 2009), the Philippines (Cebu in 1999) and Malaysia (Semporna in 2010). Eventually, the numbers of the largest and most commonly represented associated taxa are plotted on a cladogram of the Fungiidae (Gittenberger *et al.*, 2011) in order to analyse the evolutionary and ecomorphological traits of coral hosts and their associated fauna.

## RESULTS

### Zooxanthellae (*Symbiodinium*)

Little specific information is available about zooxanthellae (symbiotic dinoflagellates (Dinophyceae) belonging to the genus *Symbiodinium* (Freudenthal, 1962)) that live in Fungiidae. They have been indicated as species, clades, or subclades (Pochon & Gates, 2010), although also preference is given over *Symbiodinium* types instead of clades (Cooper *et al.*, 2011). It is unclear how many species of *Symbiodinium* exist, although four species have been formally described based on morphological characters (Baker, 2003). Five types have been recognized to reside in scleractinian corals, types A, B, C, D and F (Baker, 2003; Knowlton & Rohwer, 2003). *Cycloseris vaughani* and *Lobactis scutaria* at Hawaii are known to host *Symbiodinium* type C (Weiss *et al.*, 2001; LaJeunesse *et al.*, 2004a). In a *L. scutaria* population introduced in Jamaica (Caribbean) also type C has been found (LaJeunesse *et al.*, 2005). Various Fungiidae from the Great Barrier Reef have also been reported with type C: *Ctenactis echinata*, *Danafungia horrida*, *Fungia fungites*, *Heliofungia actiniformis*, *Herpolitha limax* (recorded as *H. weberi*), *Lithophyllon undulatum*, *Pleuractis granulosa*, *P. paumotensis*, *Podabacia crustacea*, *Polyphyllia talpina* and *Sandalolitha robusta* (LaJeunesse *et al.*, 2004b). Compared to a locality in southern Japan two of these species, i.e. *Danafungia horrida* (listed as *Fungia danai*) and *Lobactis scutaria*, carry *Symbiodinium* type C, whereas *Sandalolitha robusta* has been found with types C and D (LaJeunesse *et al.*, 2004b), which is the only exception known so far. Type D in particular has been reported to be more resistant to elevated temperatures than the others (Stat & Gates, 2011). When coral bleaching is induced by heat, a different symbiont type may be found in the coral than before the bleaching occurred (Knowlton & Rohwer, 2003; Coffroth & Santos, 2005). This may explain why some species of mushroom corals are less sensitive to bleaching than others on a particular reef and also why bleaching susceptibility may vary geographically and among reef zones within fungiid species (Hoeksema, 1991a; Hoeksema & Matthews, 2011). Furthermore, partial bleaching in mushroom corals may also result from viruses that attack *Symbiodinium* in certain mushroom corals, although it is not yet clear how host-specific these viruses are (Cervino *et al.*, 2004, 2008).

### Acoel flatworms (Convolutidae)

Apparently, acoel flatworms (e.g. *Waminoa* spp.) that live in association with stony corals (Scleractinia) and soft corals (Alcyonacea) have just recently started to become studied (Ogunlana *et al.*, 2005; Haapkylä *et al.*, 2010; Matsushima *et al.*, 2010; Rawlinson *et al.*, 2011; Wijgerde *et al.*, 2011). These flatworms themselves are host to zooxanthellae, forming a three party symbiosis with the inclusion of the coral host (Barneah *et al.*, 2007a, b). Despite their striking appearance, virtually nothing is known about how many species exist and how host-specific they are. During recent fieldwork in Indonesia (Raja Ampat, West Papua; Ternate, northern Moluccas) and Malaysia (Semporna, eastern Malaysia) specimens of at least two *Waminoa* species were observed in association with *Cycloseris costulata* (Figure 1H), *C. sinensis*, *Heliofungia actiniformis*, *Lithophyllon scabra*, *Pleuractis gravis* and *P. moluccensis*.

### Copepods (Anchimolgidae)

Coral-associated copepods form an important component of the cryptofauna of coral reefs (Preston & Doherty, 1994). They have been reported from several fungiid host species in New Caledonia (Humes, 1973, 1996, 1997; Kim, 2003), the Moluccas (Humes, 1978, 1979, 1997; Humes & Dojiri, 1983; Kim, 2007) and Madagascar (Humes & Dojiri, 1983; Kim 2010). The following 26 fungiid-associated copepod species have been recorded: *Anchimoligus convexus* Humes, 1978; *A. gratus* Humes, 1996; *A. hastatus* Kim, 2007; *A. latens* Humes, 1978; *A. maximus* Kim, 2003; *A. notatus* Humes, 1978; *A. orectus* Humes, 1978; *A. pandus* Humes, 1978; *A. punctilis* Humes, 1978; *Asteropontius fungicola* Kim, 2007; *A. latioriger* Kim, 2010; *Mycoxynus fungianus* Humes, 1978; *M. longicauda* Humes, 1973; *M. villosus* Humes 1979; *Odontomoligus decens* Humes, 1978; *O. flammeus* Kim, 2007; *O. fultus* Humes, 1978; *O. scitulus* Humes, 1973; *Paramarda aculeata* Humes, 1978; *Schedomoligus dumbensis* Kim, 2003; *S. tener* (Humes, 1973); *Temanus halmaherensis* Humes, 1997; *Tondua tholincola* Humes, 1997; *Xarifia* sp.; and *Zazaranus fungicolus* Humes & Dojiri, 1983. *Anchimoligus* is with nine species the most species-rich genus in this list.

A list of 11 mushroom corals with their known associated copepod fauna suggests that many copepod species are host-specific (Table 2). There are two copepod species with four recognized hosts: *Anchimoligus pandus* and *Schedomoligus tener*. Four copepods have been recorded from two host species: *A. notatus*, *A. punctilis*, *Paramarda aculeata* and *Schedomoligus tener*. However, the list may not be complete because only a few localities have been investigated. Of these localities, the Moluccas is the only one inside the centre of maximum species richness for mushroom corals (Hoeksema, 2007), which implies that more species and more copepod–coral associations can be discovered. *Pleuractis paumotensis* has the richest copepod fauna, consisting of six species, succeeded by *Ctenactis echinata* and *Sandalolitha robusta*, each with five associated copepod species (Table 2; Figure 2).

### Coral barnacles (Pyrgomatidae)

Despite earlier overview studies on coral-inhabiting barnacles belonging to the Pyrgomatidae (Hiro, 1938; Ross & Newman,

1973, 2002; Foster, 1980; Soong & Chang, 1983; Anderson, 1992; Ogawa & Matzuki, 1992), only little and scattered information is available on cirripeds in mushroom corals. Altogether, 34 mushroom coral species have been recorded as host of a total of only eight barnacles (Table 3): *Armatobalanus allium* (Darwin, 1854); *Cantellius euspinulosus* (Broch, 1931); *C. pallidus* (Broch, 1931); *C. tredecimus* (Kolosváry, 1947); *Darwiniella conjugatum* (Darwin, 1854); *Galkinia indica* (Annandale, 1924); *Megatrema oulastreae* (Utinomi, 1962); and *Nobia halomitrae* (Kolosváry, 1948).

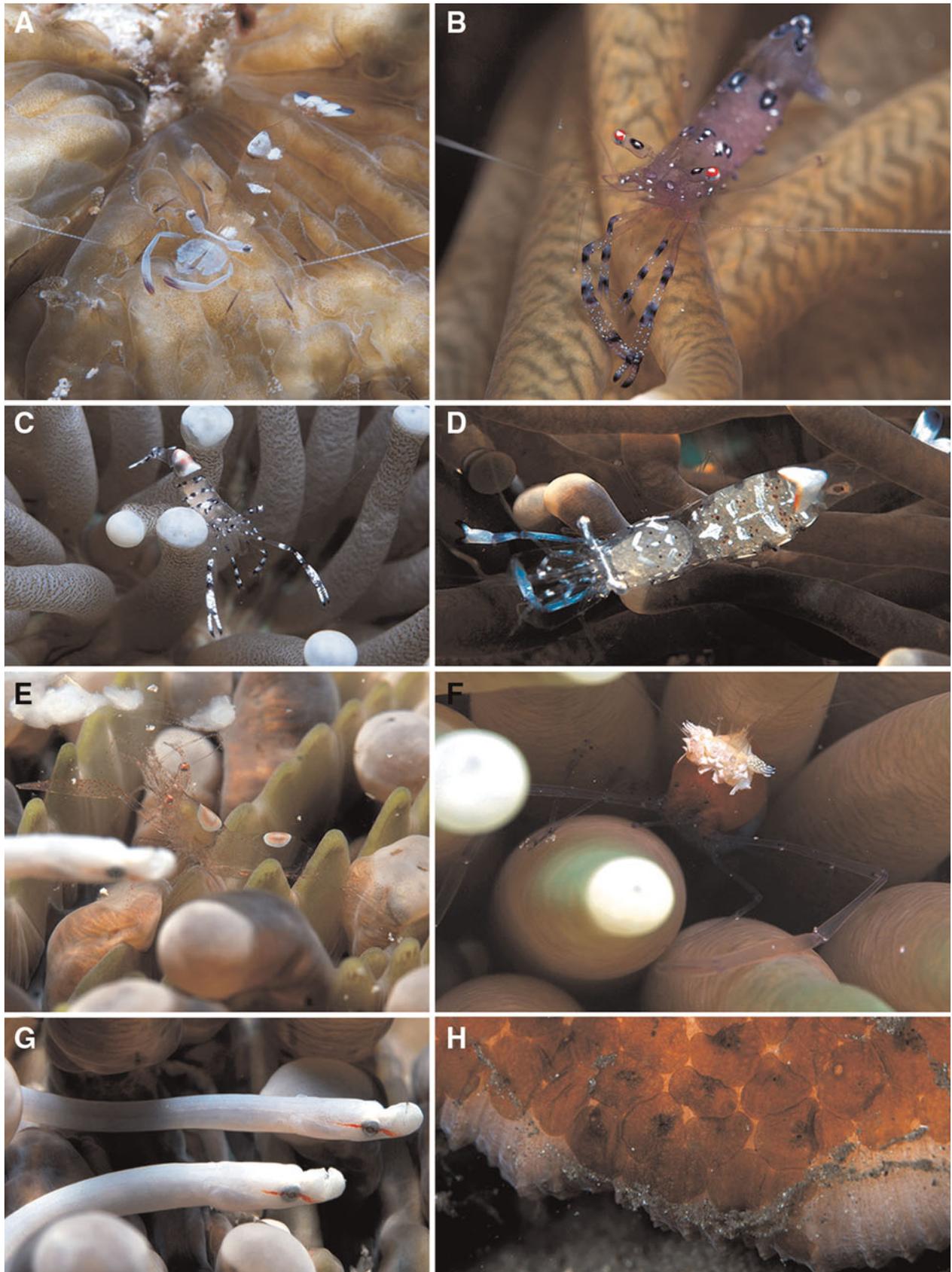
Annandale (1928) reported *Balanus arcuatus* (= *Armatobalanus allium*) from *Fungia fungites* (as *F. patella* Ellis & Solander, 1786), *Danafungia horrida* (as *F. danai* Milne Edwards & Haime, 1851) and *D. scruposa* (as *F. corona* Döderlein, 1901), whereas Hiro (1935) recorded *Cantellius pallidus* from the attached mushroom coral *Lithophyllon undulatum*. Furthermore, Kolosváry (1948) described *Darwiniella conjugatum* (= *Pyrgoma conjugatum*) forma *halomitrae* from a juvenile *Halomitra* sp., which is most likely the common species *H. pileus*. In a review, Ogawa & Matzuki (1992) refer to Fungiidae as hosts for barnacles: *Cantellius euspinulosus* in *Herpolitha* sp., *C. pallidus* in *Lithophyllon undulatum* (as *Podabacia lobata* Van der Horst, 1921), *Galkinia indica* (= *Creusia indica*) in *Lithophyllon undulatum* (as *L. lobata* (Van der Horst, 1921)) and *Podabacia crustacea*, and *Nobia halomitrae* in *Halomitra* sp., the latter referring to Kolosváry's *P. conjugatum* f. *halomitrae*, which is actually *Darwiniella conjugatum*.

A recent study on barnacles inhabiting mushroom corals from Indonesia (De Jong, 1995) concerned four cirriped species that revealed clear host preferences, including two new records of mushroom coral associates, i.e. *Cantellius tredecimus* and *Megatrema oulastreae*. Additional recent records were obtained by Poltarukha & Dautova (2007) in Vietnam, concerning *Cantellius euspinulosus* from *Fungia fungites* and *Galkinia indica* from Fungiidae. According to these authors, referring to the publication in Russian by Galkin (1986), *C. euspinulosus* has to be considered a senior synonym of *C. pallidus*. In general, the coral-inhabiting barnacles show little host-specificity (Table 3). *Fungia fungites* is recorded as host for six barnacle species, whereas other mushroom coral species are known to have at most four cirriped associates (Table 3; Figure 2).

### Coral gall crabs (Cryptochiridae)

Few coral gall crab studies are available in which the mushroom coral hosts are identified at species level, i.e. the reports by Fize & Serène (1956, 1957) and Takeda & Tamura (1979, 1981). Takeda & Tamura (1979) recorded three gall crabs species from the Fungiidae: *Fungicola fagei* (Fize & Serène, 1956), *F. utinomi* (Fize & Serène, 1956) and *Pseudocryptochirus ishigakiensis* Takeda & Tamura, 1979. The latter, which was associated with *Lithophyllon repanda*, became synonymized with *F. utinomi* by Kropp (1990) who only recognized two coral gall crab associates with Fungiidae, *F. fagei* and *F. utinomi*.

Many new associations are recorded and extensively discussed by Van der Meij *et al.* (unpublished results), who recognize at least one other species, *Dacryomaia* sp. Possibly more gall crab species are associated with mushroom corals, but for now we refer to the so far unidentified material as cryptochirid sp. In general, the three gall crab species found



**Fig. 1.** Associated organisms on mushroom corals at Raja Ampat Islands, West Papua, Indonesia (November 2007). (A–F) Pontonine shrimps: (A) *Ancylomenes magnificus* on *Cycloseris costulata*; (B) *A. sarasvati* on *Heliofungia actiniformis*; (C) *A. venustus* on *H. actiniformis*; (D) *A. holthuisi* on *H. actiniformis*; (E) *Hamopontonia corallicola* on *H. actiniformis*; (F) *Cuapates kororensis* on *H. actiniformis*; (G) pipefish *Stiokunichtys nigrolineatus* on *H. actiniformis*; (H) acael flatworm *Waminoa* sp. on *C. costulata*.

**Table 2.** Mushroom coral hosts and their associated copepods (based on references mentioned in the text).

Host species	Associated species
<i>Ctenactis echinata</i>	<i>Anchimoligus latens</i> <i>Anchimoligus pandus</i> <i>Mycoxynus fungianus</i> <i>Schedomoligus tener</i> <i>Xarifia</i> sp.
<i>Danafungia scruposa</i> , <i>Fungia fungites</i>	<i>Asteropontius latioriger</i> <i>Anchimoligus latens</i> <i>Anchimoligus punctilis</i> <i>Odontomoligus scitulus</i> <i>Schedomoligus dumbensis</i>
<i>Fungia</i> sp.	<i>Anchimoligus hastatus</i> <i>Anchimoligus orectus</i> <i>Asteropontius fungicola</i> <i>Odontomoligus flammeus</i> <i>Zazaranus fungicolus</i>
<i>Halomitra pileus</i>	<i>Odontomoligus fultus</i> <i>Paramarda aculeata</i>
<i>Heliofungia actiniformis</i>	<i>Anchimoligus notatus</i> <i>Anchimoligus pandus</i> <i>Odontomoligus decens</i>
<i>Herpolitha limax</i>	<i>Anchimoligus latens</i> <i>Mycoxynus villosus</i>
<i>Lithophyllon concinna</i>	<i>Anchimoligus maximus</i>
<i>Pleuractis paumotensis</i>	<i>Anchimoligus latens</i> <i>Anchimoligus notatus</i> <i>Anchimoligus orectus</i> <i>Anchimoligus pandus</i> <i>Anchimoligus punctilis</i> <i>Paramarda aculeata</i>
<i>Polyphyllia novaehiberniae</i>	<i>Anchimoligus gratus</i>
<i>Polyphyllia talpina</i>	<i>Anchimoligus pandus</i>
<i>Sandalolitha robusta</i>	<i>Anchimoligus convexus</i> <i>Mycoxynus longicauda</i> <i>Schedomoligus tener</i> <i>Temanus halmaherensis</i> <i>Tondua tholincola</i>

in 31 mushroom coral species are not very host-specific (Table 4). *Lithophyllon scabra* has a record with a maximum of three associated gall crab species (Table 4; Figure 2).

### Coral-dwelling shrimps (Hippolytidae and Palaemonidae)

Although mushroom corals are known to host shrimp species, information on shrimp species that live in association with fungiids is still scattered. In the present study, a total of 19 mushroom coral hosts and 18 associated shrimps species has been listed (Table 5; Figure 1A–F). These include one hippolytid shrimp, the circumtropical species *Thor amboinensis* (De Man, 1888), which has a wide range of anthozoan hosts (Fransen, 1989; Guo *et al.*, 1996), and the pontoniine shrimp species *Ancylomenes grandidens* (Bruce, 2005); *A. holthuisi* (Bruce, 1969); *A. kobayashii* (Okuno & Nomura, 2002); *A. luteomaculatus* Okuno & Bruce, 2010; *A. magnificus* (Bruce, 1979); *A. sarasvati* (Okuno, 2002); *A. venustus* (Bruce, 1989); *Cuapetes kororensis* (Bruce, 1969); *C. lacertae* (Bruce, 1992); *C. tenuipes* (Borradaile, 1898); *Hamopontonia corallicola* Bruce, 1970; *Metapontonia fungiacola* Bruce, 1967; *Periclimenes diversipes* Kemp, 1922; *P. goniopora* Bruce,

1989; *P. jugalis* Holthuis, 1952; *P. watamuae* Bruce, 1976; and *Periclimenes* sp.

Bruce (1985) and Yamashiro (1999) report on four mushroom coral hosts for *Metapontonia fungiacola*, whereas De Grave (1998) and Hoeksema & Fransen (2011) together report on seven shrimp species recorded from *Heliofungia actiniformis*, a mushroom coral with extremely long tentacles: *Ancylomenes sarasvati*, *A. venustus*, *Cuapetes kororensis*, *C. tenuipes*, *Hamopontonia corallicola*, *Periclimenes watamuae* and *Thor amboinensis*. In the present overview based on previous records and our own observations (Figure 1B–F) a total of 14 shrimp species is recorded from that host species (Table 5; Figure 2). Of the seven species presently recorded as new for the Fungiidae, *Ancylomenes kobayashii* was previously only recorded from *Polyphyllia novaehiberniae* (see Okuno & Nomura, 2002). *Ancylomenes holthuisi* has previously also been reported from *H. actiniformis* (see Fransen, 1989) but this record has been revised and concerns *A. venustus* (see De Grave, 1998; Okuno & Bruce, 2010; Figure 1C). Various additional records of shrimps that have been found in associations with mushroom corals have been reported by Fransen (1989, 2004, 2008, 2010).

### Mytilid bivalves (Mytilidae)

Boring mussels (Mytilidae: Lithophaginae) that live in mushroom corals belong to two genera, *Fungiacava* and *Leiosolenus* (Hoeksema & Achituv, 1993; Hoeksema & Kleemann, 2002; Kleemann & Hoeksema, 2002; Hoeksema & Gittenberger, 2008). *Leiosolenus* is considered a subgenus in *Lithophaga* in some studies (Wilson, 1979; Kleemann & Hoeksema, 2002) and a separate genus in others (e.g. Wilson, 1985; Owada, 2007; Owada & Hoeksema, 2011). There is only a single species of *Fungiacava*, i.e. *F. eilatensis* Goreau *et al.*, 1968, whereas there are at least seven *Leiosolenus* species living in mushroom corals: *Leiosolenus laevigatus* (Quoy & Gaimard, 1835); *L. lessepsianus* (Vaillant, 1865); *L. lima* (Jousseume in Lamy, 1919); *L. malaccanus* (Reeve, 1857); *L. mucronatus* (Philippi, 1846); *L. punctatus* (Kleemann & Hoeksema, 2002); and *L. cf. simplex* (Iredale, 1939). Together they have been found in 22 host species (Table 6).

Morphologically *Fungiacava* is very distinct from *Leiosolenus*, but phylogenetically not (Owada & Hoeksema, 2011). There appears to be little host-specificity among the mytilid species found, since some species also occur in corals belonging to other scleractinian families (Kleemann, 1980, 1990, 1994, 1995; Morton, 1990; Mokady *et al.*, 1994). Only two species are known to live exclusively in mushroom corals, *Fungiacava eilatensis* and *Leiosolenus punctatus* (Hoeksema & Kleemann, 2002; Kleemann & Hoeksema, 2002). Four mushroom coral species are host for a maximum of three mytilids: *Halomitra pileus*, *Lithophyllon scabra*, *Pleuractis moluccensis* and *Sandalolitha robusta* (Table 6; Figure 2).

### Wentletraps (Epitoniidae)

Wentletraps are epibiotic gastropods that are generally known as parasites of corals, sea anemones and other anthozoans (Gittenberger *et al.*, 2000; Gittenberger, 2003; Gittenberger & Gittenberger, 2005; Kokshoorn *et al.*, 2007; Hoeksema & Gittenberger, 2008). Seventeen species of wentletraps belonging to three genera have been recorded from 31 Fungiidae

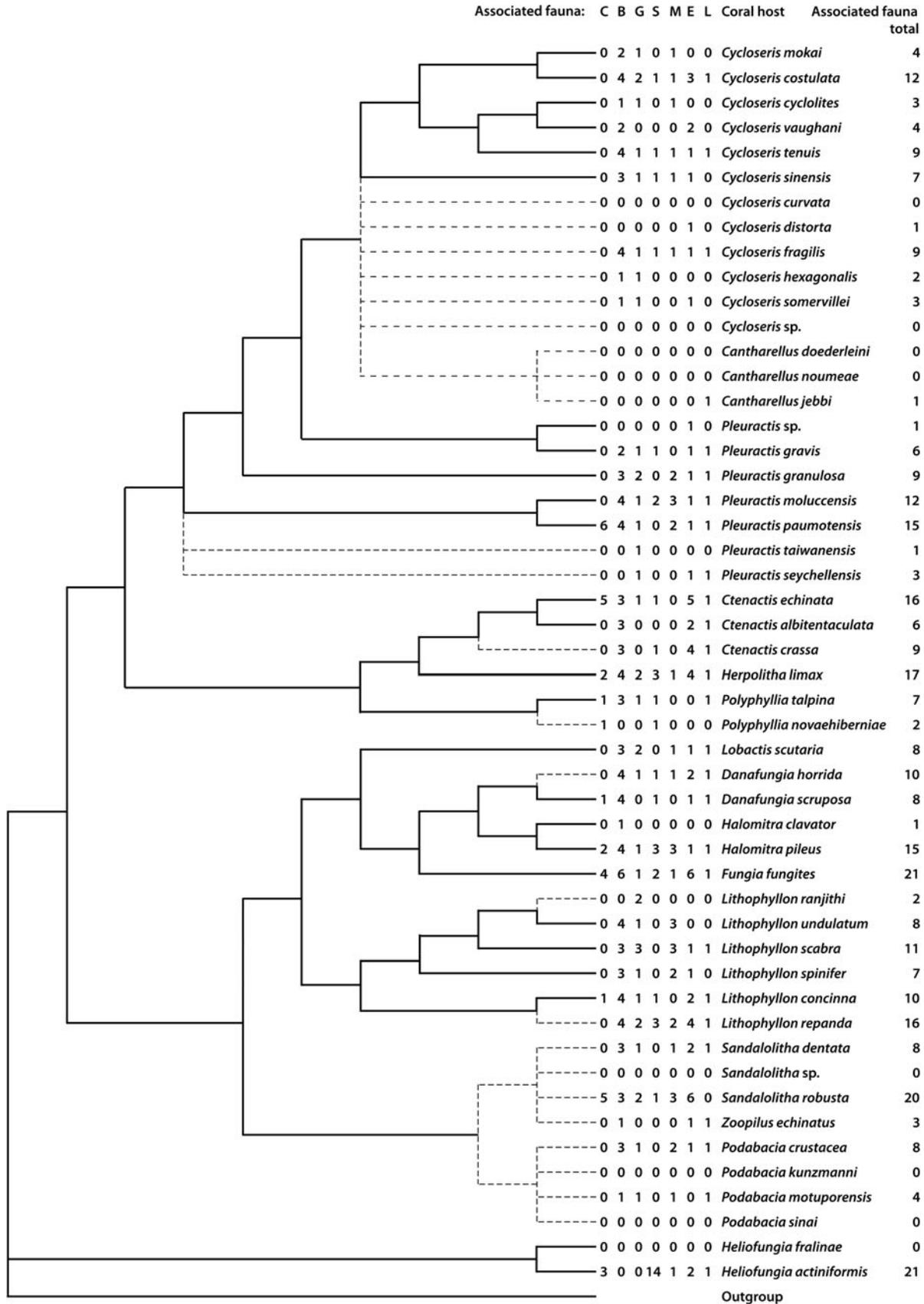


Fig. 2. Phylogeny reconstruction of the Fungiidae (after Gittenberger *et al.*, 2011), with an indication of numbers of associated fauna per mushroom coral species. Only well investigated taxa are included, while taxa with low or uncertain numbers of associated species are excluded. C, copepods; B, barnacles; G, gall crabs; S, shrimps; M, mytilid bivalves; E, epitoniid snails; L, *Leptoconchus* snails.

**Table 3.** Mushroom coral hosts and their associated barnacles (based on references mentioned in the text).

Host species	Associated species
<i>Ctenactis albitentaculata</i>	<i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Ctenactis crassa</i>	<i>Megatrema oulastreae</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Ctenactis echinata</i>	<i>Megatrema oulastreae</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Cycloseris costulata</i>	<i>Megatrema oulastreae</i> <i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Cycloseris cyclolites</i>	<i>Megatrema oulastreae</i>
<i>Cycloseris fragilis</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Cycloseris hexagonalis</i>	<i>Megatrema oulastreae</i>
<i>Cycloseris mokai</i>	<i>Cantellius tredecimus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Cycloseris sinensis</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Megatrema oulastreae</i>
<i>Cycloseris somervillei</i>	<i>Cantellius tredecimus</i>
<i>Cycloseris tenuis</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Cycloseris vaughani</i>	<i>Megatrema oulastreae</i> <i>Cantellius tredecimus</i> <i>Megatrema oulastreae</i>
<i>Danafungia horrida</i>	<i>Armatobalanus allium</i> <i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Danafungia scruposa</i>	<i>Armatobalanus allium</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Fungia fungites</i>	<i>Armatobalanus allium</i> <i>Cantellius euspinulosus</i> <i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Halomitra clavator</i>	<i>Galkinia indica</i>
<i>Halomitra pileus</i>	<i>Darwiniella conjugatum</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i> <i>Nobia halomitrae</i> <i>Herpolitha limax</i> <i>Cantellius euspinulosus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Lithophyllon concinna</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Lithophyllon repanda</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>

Continued

**Table 3.** Continued

Host species	Associated species
<i>Lithophyllon scabra</i>	<i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Lithophyllon spinifer</i>	<i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Lithophyllon undulatum</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Lobactis scutaria</i>	<i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Pleuractis granulosa</i>	<i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Pleuractis gravis</i>	<i>Cantellius tredecimus</i> <i>Megatrema oulastreae</i>
<i>Pleuractis moluccensis</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Pleuractis paumotensis</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Podabacia crustacea</i>	<i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Podacacia motuporensis</i>	<i>Cantellius tredecimus</i>
<i>Polyphyllia talpina</i>	<i>Cantellius pallidus</i> <i>Cantellius tredecimus</i> <i>Galkinia indica</i>
<i>Sandalolitha dentata.</i>	<i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Sandalolitha robusta</i>	<i>Cantellius tredecimus</i> <i>Galkinia indica</i> <i>Megatrema oulastreae</i>
<i>Zoopilus echinatus</i>	<i>Galkinia indica</i>

(Table 7): *Epifungium adgranulosa* Gittenberger & Gittenberger, 2005; *E. adgravis* Gittenberger & Gittenberger, 2005; *E. adscabra* Gittenberger & Gittenberger, 2005; *E. hoeksemai* (Gittenberger & Goud, 2000); *E. lochi* (Gittenberger & Goud, 2000); *E. marki* Gittenberger & Gittenberger, 2005; *E. nielsi* Gittenberger & Gittenberger, 2005; *E. pseudolochi* Gittenberger & Gittenberger, 2005; *E. pseudotwilae* Gittenberger & Gittenberger, 2005; *E. twilae* (Gittenberger & Goud, 2000); *E. ulu* (Pilsbry, 1921); *Epitonium crassicoatum* Gittenberger & Gittenberger, 2005; *E. graviarmatum* Gittenberger & Gittenberger, 2005; *Surrepifungium costulatum* (Kiener, 1838); *S. ingridae* (Gittenberger & Goud, 2000); *S. oliverioi* (Bonfitto & Sabelli, 2001); and *S. patamankanthini* Gittenberger & Gittenberger, 2005. No other coral family is known to have as many species of epitoniid associates. The Dendrophylliidae host four species and the Euphylliidae only one species (Gittenberger, 2003; Gittenberger & Gittenberger, 2005). Eleven species of the genus *Epifungium* are known to live as epibiont on the underside of mushroom corals, whereas four species of *Surrepifungium* live on the bottom surface or buried in the

**Table 4.** Mushroom coral hosts and their associated gall crabs (based on references mentioned in the text).

Host species	Associated species
<i>Ctenactis echinata</i>	<i>Fungicola utinomi</i>
<i>Cycloseris costulata</i>	<i>Dacryomaia</i> sp. <i>Fungicola fagei</i>
<i>Cycloseris cyclolites</i>	Cryptochirid sp.
<i>Cycloseris fragilis</i>	<i>Fungicola fagei</i>
<i>Cycloseris hexagonalis</i>	<i>Fungicola fagei</i>
<i>Cycloseris mokai</i>	Cryptochirid sp.
<i>Cycloseris sinensis</i>	Cryptochirid sp.
<i>Cycloseris somervillei</i>	<i>Fungicola fagei</i>
<i>Cycloseris tenuis</i>	<i>Fungicola fagei</i>
<i>Danafungia horrida</i>	<i>Fungicola utinomi</i>
<i>Fungia fungites</i>	<i>Fungicola utinomi</i>
<i>Halomitra pileus</i>	<i>Fungicola utinomi</i>
<i>Herpolitha limax</i>	<i>Fungicola fagei</i> <i>Fungicola utinomi</i>
<i>Lithophyllon concinna</i>	<i>Fungicola utinomi</i>
<i>Lithophyllon ranjithi</i>	<i>Fungicola fagei</i> Cryptochirid sp.
<i>Lithophyllon repanda</i>	<i>Fungicola fagei</i> <i>Fungicola utinomi</i>
<i>Lithophyllon scabra</i>	<i>Dacryomaia</i> sp. <i>Fungicola fagei</i> <i>Fungicola utinomi</i>
<i>Lithophyllon spinifer</i>	Cryptochirid sp.
<i>Lithophyllon undulatum</i>	<i>Dacryomaia</i> sp.
<i>Lobactis scutaria</i>	<i>Fungicola fagei</i> <i>Fungicola utinomi</i>
<i>Pleuractis granulosa</i>	<i>Dacryomaia</i> sp. <i>Fungicola fagei</i>
<i>Pleuractis gravis</i>	<i>Fungicola fagei</i>
<i>Pleuractis moluccensis</i>	<i>Fungicola fagei</i>
<i>Pleuractis paumotensis</i>	<i>Fungicola fagei</i>
<i>Pleuractis seychellensis</i>	<i>Fungicola fagei</i>
<i>Pleuractis taiwanensis</i>	<i>Fungicola fagei</i>
<i>Podabacia crustacea</i>	<i>Fungicola fagei</i>
<i>Podabacia motuporensis</i>	Cryptochirid sp.
<i>Polyphyllia talpina</i>	Cryptochirid sp.
<i>Sandalolitha dentata</i>	<i>Fungicola fagei</i>
<i>Sandalolitha robusta</i>	<i>Fungicola fagei</i> <i>Fungicola utinomi</i>

sediment underneath the corals. The species of the latter genus appear less host-specific than those of the first genus. Two *Epitonium* species have been found in association with Fungiidae, but both were only represented by an empty shell underneath the possible host coral (Gittenberger & Gittenberger, 2005). Previous records of *Epitonium* in association with mushroom coral hosts concern misidentifications (e.g. Yamashiro, 1990) prior to the revision by Gittenberger & Gittenberger (2005). Two fungiids are each hosting six wattletrap species, i.e. *Fungia fungites* and *Sandalolitha robusta*, whereas the other mushroom coral species have five or fewer associated species (Table 7; Figure 2).

### Coralliophilid snails (Coralliophilidae)

*Leptoconchus* snails (Coralliophilidae) are endosymbiotic gastropods dwelling inside scleractinian corals (Massin, 1988). Their taxonomy appears difficult because the species show very few distinctive morphological characters, with shells that are generally white and very thin. The most distinct

morphological characters concern the shape and position of the burrows and their openings inside the host coral (Massin, 1988; Massin & Dupont, 2003). Only with the help of molecular techniques it has become easier to distinguish species and their host-specificity (Gittenberger & Gittenberger, 2011). This implies that when the host species is known, the *Leptoconchus* species can usually also be identified. Therefore, the record of *L. striatus* Rüppell, 1835, from just *Fungia* cannot be confirmed (Bouillon *et al.*, 1983). The *Leptoconchus* specimens encountered in *Cantharellus jebbi* (see Hoeksema, 1993a), in *Cycloseris fragilis* (see Massin & Dupont, 2003), and in *Pleuractis seychellensis* (see Hoeksema, 1993b) could not be identified because no tissue was available for molecular analysis. Each mushroom coral host has only one associated *Leptoconchus* species (Table 8; Figure 2).

A total of 27 mushroom coral hosts has been found with 14 associated *Leptoconchus* species, eight of which are very host-specific and therefore named after their host (Table 8): *L. inactiniformis* Gittenberger & Gittenberger, 2011; *L. inalbechi* Gittenberger & Gittenberger, 2011; *L. incrassa* Gittenberger & Gittenberger, 2011; *L. incycloseris* Gittenberger & Gittenberger, 2011; *L. infungites* Gittenberger & Gittenberger, 2011; *L. ingrandifungi* Gittenberger & Gittenberger, 2011; *L. ingranulosa* Gittenberger & Gittenberger, 2011; *L. inlimax* Gittenberger & Gittenberger, 2011; *L. inpileus* Gittenberger & Gittenberger, 2011; *L. inpleuractis* Gittenberger & Gittenberger, 2011; *L. inscruposa* Gittenberger & Gittenberger, 2011; *L. inscutaria* Gittenberger & Gittenberger, 2011; *L. intalpina* Gittenberger & Gittenberger, 2011; and *L. massini* Gittenberger & Gittenberger, 2011.

### Fish (Syngnathidae)

The pipefish *Siokunichthys nigrolineatus* Dawson, 1983, appears to be strictly associated with one species of mushroom coral, *Heliofungia actiniformis*. All records are from the Coral Triangle, mainly Indonesia, the Philippines and Papua New Guinea, which is where most of the host coral's distribution-range is located. According to its original description the fish has a black diagonal stripe at each side of its head (hence its name) and that its type material has been collected from *Fungia echinata* (= *Ctenactis echinata*) and *Fungia* spp. (Dawson, 1983). However, all specimens photographed and collected by us have red lateral stripes and occurred in between the long tentacles of *H. actiniformis* corals (Figure 1G). A later publication confirmed that the fish occurs on *Fungia* sp. (perhaps *C. echinata*, but its photographs clearly indicate that the host concerns *H. actiniformis*; see Phillips & Pullin, 1987). However, no coral hosts were collected for further examination. Subsequent publications are also not specific about the host, indicating 'mushroom corals such as *Heliofungia actiniformis*' (Kuitert, 2000 p. 171, 2009 p. 269). A published picture of another pipefish, *Corythoichthys polynatus* Dawson, 1977, shows an individual situated on top of a mushroom coral, *Ctenactis echinata*, but other illustrated specimens of the same species appear on top of various other kinds of substrates, which indicates that there is no host-specificity (Kuitert, 2000 p. 119, 2009 p. 203). There are also records on pygmy seahorses that have been seen moving over fungiids (Lourie & Kuitert, 2008) but these observations are probably incidental and not based on associations (Reijnen *et al.*, 2011). Coral-dwelling

**Table 5.** Mushroom coral hosts and their associated shrimps as reported in previous works and present observations. B.W.H., B.W. Hoeksema (photographic record); RMNH, Rijksmuseum van Natuurlijke Historie (NCB Naturalis collection).

Host species	Associated species	Reference/registration number
<i>Ctenactis crassa</i>	<i>Periclimenes diversipes</i>	RMNH D 50723
<i>Ctenactis echinata</i>	<i>Periclimenes goniopora</i>	RMNH D 54528
<i>Cycloseris costulata</i>	<i>Ancylomenes magnificus</i>	B.W.H., personal observation
<i>Cycloseris fragilis</i>	<i>Ancylomenes magnificus</i>	B.W.H., personal observation
<i>Cycloseris sinensis</i>	<i>Ancylomenes magnificus</i>	B.W.H., personal observation
<i>Cycloseris tenuis</i>	<i>Ancylomenes magnificus</i>	B.W.H., personal observation, RMNH D 54532
<i>Danafungia horrida</i>	<i>Ancylomenes magnificus</i>	B.W.H., personal observation
<i>Danafungia scruposa</i>	<i>Hamopontonia corallicola</i>	RMNH D 54531
<i>Fungia fungites</i>	<i>Ancylomenes magnificus</i>	B.W.H., personal observation
	<i>Periclimenes goniopora</i>	RMNH D 54529
<i>Halomitra pileus</i>	<i>Periclimenes</i> sp.	RMNH D 48495
	<i>Metapontonia fungiacola</i>	Bruce, 1976
	<i>Periclimenes watamuae</i>	RMNH D 46471
<i>Heliofungia actiniformis</i>	<i>Ancylomenes grandidens</i>	RMNH D 50413
	<i>Ancylomenes holthuisi</i>	Bruce, 1978; De Grave, 1998; RMNH D 37390
	<i>Ancylomenes kobayashii</i>	RMNH D 54540
	<i>Ancylomenes luteomaculatus</i>	RMNH D 48478
	<i>Ancylomenes magnificus</i>	B.W.H., personal observation, RMNH D 54533
	<i>Ancylomenes sarasvati</i>	RMNH D 48478, 50413, 50414
	<i>Ancylomenes venustus</i>	De Grave, 1998; Bruce, 2005; Hoeksema & Franssen, 2011; RMNH D 47539, 48120
	<i>Cuapetes lacertae</i>	RMNH D 48449, 50398
	<i>Cuapetes kororensis</i>	Bruce, 1977, 1983; Bruce & Svoboda, 1984; Chace & Bruce, 1993; De Grave, 1998; RMNH D 47687, 48444
	<i>Cuapetes tenuipes</i>	De Grave, 1998; Hoeksema & Franssen, 2011; RMNH D 46347, 47514
	<i>Hamopontonia corallicola</i>	Bruce, 1978; 1981; De Grave, 1998; RMNH D 48373, 50170
	<i>Periclimenes jugalis</i>	RMNH D 54527
	<i>Periclimenes watamuae</i>	De Grave, 1998
	<i>Thor amboinensis</i>	De Grave, 1998; Hoeksema & Franssen, 2011
<i>Herpolitha limax</i>	<i>Ancylomenes magnificus</i>	B.W.H., personal observation
	<i>Metapontonia fungiacola</i>	Yamashiro, 1999
	<i>Periclimenes watamuae</i>	RMNH D 54537, 54538
<i>Lithophyllon concinna</i>	<i>Metapontonia fungiacola</i>	Yamashiro, 1999
<i>Lithophyllon repanda</i>	<i>Cuapetes tenuipes</i>	RMNH D 54539
	<i>Metapontonia fungiacola</i>	Yamashiro, 1999
	<i>Periclimenes goniopora</i>	RMNH D 54530
<i>Pleuractis gravis</i>	<i>Ancylomenes magnificus</i>	RMNH D 54534
<i>Pleuractis moluccensis</i>	<i>Ancylomenes holthuisi</i>	B.W.H., personal observation
	<i>Ancylomenes magnificus</i>	B.W.H., personal observation
<i>Polyphyllia novaehiberniae</i>	<i>Ancylomenes kobayashii</i>	RMNH D 54541
<i>Polyphyllia talpina</i>	<i>Periclimenes watamuae</i>	RMNH D 54535, 54536
<i>Sandalolitha robusta</i>	<i>Periclimenes goniopora</i>	RMNH D 48426

gobies are known to be host-specific, but so far no species have been recorded from Fungiidae (Munday *et al.*, 1997, 2004).

### Other taxa

There are various taxa with species that are usually associated with scleractinians (dead or alive) about which little or no information is available with regard to mushroom corals, such as endolithic cyanobacteria imbedded in the skeleton (Kühl *et al.*, 2008), polychaetes (Hutchings *et al.*, 1992; Martin & Britayev, 1998; Ten Hove & Kupriyanova, 2009; Samimi Namin *et al.*, 2010), sipunculans (Rice, 1984; Hoeksema & Best, 1991; Hutchings *et al.*, 1992), ophiuroids (Starmer, 2003), bryozoans (Zabla *et al.*, 1993) and boring sponges (Schönberg, 2000, 2001; Cruz-Barraza *et al.*, 2011).

### Phylogenetic ecology of associations

By plotting species numbers of associated taxa and their totals per mushroom coral host on a phylogenetic model of the Fungiidae (Gittenberger *et al.*, 2011), comparisons between host species can be made from an evolutionary perspective (Figure 2). There is much variation between the 50 mushroom coral species, some of which appear to have no record of associated fauna, whereas other corals host at least 23 species when only some taxa of associated fauna are considered.

Most *Cycloseris* and *Cantharellus* species show low numbers of associates. *Heliofungia actiniformis* has the highest record of associated fauna ( $N = 21$  in Figure 2 and two more), most of which consists of shrimp species, whereas its sister species, *H. fralinae*, has no recorded associates at all. This record does not include the pipefish that has

**Table 6.** Mushroom coral hosts and their associated mytilid bivalves (boring mussels) (based on references mentioned in the text).

Host species	Associated species
<i>Cycloseris costulata</i>	<i>Fungiacava eilatensis</i>
<i>Cycloseris fragilis</i>	<i>Fungiacava eilatensis</i>
<i>Cycloseris mokai</i>	<i>Leiosolenus punctatus</i>
<i>Cycloseris sinensis</i>	<i>Leiosolenus malaccanus</i>
<i>Cycloseris tenuis</i>	<i>Fungiacava eilatensis</i>
<i>Danafungia horrida</i>	<i>Leiosolenus lessepsianus</i>
<i>Fungia fungites</i>	<i>Fungiacava eilatensis</i>
<i>Halomitra pileus</i>	<i>Fungiacava eilatensis</i>
	<i>Leiosolenus lessepsianus</i>
	<i>Leiosolenus punctatus</i>
<i>Heliofungia actiniformis</i>	<i>Leiosolenus mucronatus</i>
<i>Herpolitha limax</i>	<i>Leiosolenus lessepsianus</i>
<i>Lithophyllon repanda</i>	<i>Fungiacava eilatensis</i>
	<i>Leiosolenus punctatus</i>
<i>Lithophyllon scabra</i>	<i>Leiosolenus laevigatus</i>
	<i>Leiosolenus mucronatus</i>
	<i>Leiosolenus lima</i>
<i>Lithophyllon spinifer</i>	<i>Leiosolenus laevigatus</i>
	<i>Leiosolenus punctatus</i>
<i>Lithophyllon undulatum</i>	<i>Leiosolenus malaccanus</i>
	<i>Leiosolenus lessepsianus</i>
	<i>Leiosolenus lima</i>
<i>Lobactis scutaria</i>	<i>Fungiacava eilatensis</i>
<i>Pleuractis granulosa</i>	<i>Fungiacava eilatensis</i>
	<i>Leiosolenus cf. simplex</i>
<i>Pleuractis moluccensis</i>	<i>Fungiacava eilatensis</i>
	<i>Leiosolenus mucronatus</i>
	<i>Leiosolenus lima</i>
<i>Pleuractis paumotensis</i>	<i>Fungiacava eilatensis</i>
	<i>Leiosolenus punctatus</i>
<i>Podabacia crustacea</i>	<i>Fungiacava eilatensis</i>
	<i>Leiosolenus malaccanus</i>
<i>Podabacia motuporensis</i>	<i>Fungiacava eilatensis</i>
<i>Sandalolitha dentata</i>	<i>Fungiacava eilatensis</i>
<i>Sandalolitha robusta</i>	<i>Fungiacava eilatensis</i>
	<i>Leiosolenus punctatus</i>
	<i>Leiosolenus cf. simplex</i>

not been found on any other mushroom coral. It also does not include any flatworm species on *H. actiniformis* because too little is known about the flatworm fauna on corals. Other species with relatively high records are *Fungia fungites* (N = 21), *Sandalolitha robusta* (N = 20), *Herpolitha limax* (N = 17), *Lithophyllon repanda* (N = 16), *Ctenactis echinata* (N = 16), *Pleuractis paumotensis* (N = 15), *Halomitra pileus* (N = 13), *Pleuractis moluccensis* (N = 12), and *Lithophyllon scabra* (N = 11). Other striking differences between sister species are shown by *Sandalolitha robusta* (N = 20), *S. dentata* (N = 8), and *Zoopilus echinatus* (N = 3); *Halomitra pileus* (N = 15) and *H. clavator* (N = 1); *Polyphyllia talpina* (N = 7) and *P. novaehiberniae* (N = 2). *Heliofungia actiniformis* is perhaps the only coral species with three recorded host-specific associates: the pipefish *Siokunichthys nigrolineatus*, the shrimp *Cuapetes kororensis* and the gastropod *Leptoconchus inactiniformis*.

## DISCUSSION

The present report presents the first review of organisms living in association with a monophyletic scleractinian coral family.

**Table 7.** Mushroom coral hosts and their associated epitoniid snails (wentletraps) (based on references mentioned in the text).

Host species	Associated species
<i>Ctenactis albitentaculata</i>	<i>Surrepifungium costulatum</i>
	<i>Surrepifungium ingridae</i>
<i>Ctenactis crassa</i>	<i>Epifungium twilae</i>
	<i>Surrepifungium costulatum</i>
	<i>Surrepifungium ingridae</i>
	<i>Surrepifungium patamakanthini</i>
<i>Ctenactis echinata</i>	<i>Epifungium twilae</i>
	<i>Epifungium ulu</i>
	<i>Surrepifungium costulatum</i>
	<i>Surrepifungium ingridae</i>
	<i>Surrepifungium patamakanthini</i>
<i>Cycloseris costulata</i>	<i>Epifungium lochi</i>
	<i>Epifungium pseudolochi</i>
	<i>Epitonium crassicostatum</i>
<i>Cycloseris distorta</i>	<i>Epifungium lochi</i>
<i>Cycloseris fragilis</i>	<i>Epifungium lochi</i>
<i>Cycloseris sinensis</i>	<i>Epifungium lochi</i>
<i>Cycloseris somervillei</i>	<i>Epifungium lochi</i>
<i>Cycloseris tenuis</i>	<i>Epifungium lochi</i>
<i>Cycloseris vaughani</i>	<i>Epifungium lochi</i>
	<i>Epitonium graviarmatum</i>
<i>Danafungia horrida</i>	<i>Epifungium ulu</i>
	<i>Surrepifungium patamakanthini</i>
<i>Danafungia scruposa</i>	<i>Epifungium ulu</i>
<i>Fungia fungites</i>	<i>Epifungium hoeksemai</i>
	<i>Epifungium ulu</i>
	<i>Surrepifungium costulatum</i>
	<i>Surrepifungium ingridae</i>
	<i>Surrepifungium oliverioi</i>
	<i>Surrepifungium patamakanthini</i>
<i>Halomitra pileus</i>	<i>Epifungium ulu</i>
<i>Heliofungia actiniformis</i>	<i>Epifungium hoeksemai</i>
	<i>Surrepifungium patamakanthini</i>
<i>Herpolitha limax</i>	<i>Epifungium twilae</i>
	<i>Epifungium ulu</i>
	<i>Surrepifungium costulatum</i>
	<i>Surrepifungium oliverioi</i>
<i>Lithophyllon concinna</i>	<i>Epifungium ulu</i>
	<i>Surrepifungium patamakanthini</i>
<i>Lithophyllon repanda</i>	<i>Epifungium ulu</i>
	<i>Surrepifungium ingridae</i>
	<i>Surrepifungium oliverioi</i>
	<i>Surrepifungium patamakanthini</i>
<i>Lithophyllon scabra</i>	<i>Epifungium adscabra</i>
<i>Lithophyllon spinifer</i>	<i>Epifungium ulu</i>
<i>Lobactis scutaria</i>	<i>Epifungium ulu</i>
<i>Pleuractis granulosa</i>	<i>Epifungium adgranulosa</i>
<i>Pleuractis gravis</i>	<i>Epifungium adgravis</i>
<i>Pleuractis moluccensis</i>	<i>Epifungium nielsi</i>
<i>Pleuractis paumotensis</i>	<i>Epifungium nielsi</i>
<i>Pleuractis seychellensis</i>	<i>Epifungium nielsi</i>
<i>Pleuractis sp.</i>	<i>Epifungium marki</i>
<i>Podabacia crustacea</i>	<i>Epifungium pseudotwilae</i>
<i>Sandalolitha dentata</i>	<i>Epifungium pseudotwilae</i>
	<i>Surrepifungium costulatum</i>
<i>Sandalolitha robusta</i>	<i>Epifungium pseudotwilae</i>
	<i>Epifungium ulu</i>
	<i>Surrepifungium costulatum</i>
	<i>Surrepifungium ingridae</i>
	<i>Surrepifungium oliverioi</i>
	<i>Surrepifungium patamakanthini</i>
<i>Zoopilus echinatus</i>	<i>Epifungium pseudotwilae</i>

**Table 8.** Mushroom coral hosts and their associated coralliophilid snails (based on references mentioned in the text).

Host species	Associated species
<i>Cantharellus jebbi</i>	<i>Leptoconchus</i> sp.
<i>Ctenactis albitentaculata</i>	<i>Leptoconchus inalbechi</i>
<i>Ctenactis crassa</i>	<i>Leptoconchus incrassa</i>
<i>Ctenactis echinata</i>	<i>Leptoconchus inalbechi</i>
<i>Cycloseris costulata</i>	<i>Leptoconchus incycloseris</i>
<i>Cycloseris fragilis</i>	<i>Leptoconchus</i> sp.
<i>Cycloseris tenuis</i>	<i>Leptoconchus incycloseris</i>
<i>Danafungia horrida</i>	<i>Leptoconchus massini</i>
<i>Danafungia scruposa</i>	<i>Leptoconchus inscruposa</i>
<i>Fungia fungites</i>	<i>Leptoconchus infungites</i>
<i>Halomitra pileus</i>	<i>Leptoconchus inpileus</i>
<i>Heliofungia actiniformis</i>	<i>Leptoconchus inactiniformis</i>
<i>Herpolitha limax</i>	<i>Leptoconchus inlimax</i>
<i>Lithophyllon concinna</i>	<i>Leptoconchus massini</i>
<i>Lithophyllon repanda</i>	<i>Leptoconchus massini</i>
<i>Lithophyllon scabra</i>	<i>Leptoconchus massini</i>
<i>Lobactis scutaria</i>	<i>Leptoconchus inscutaria</i>
<i>Pleuractis granulosa</i>	<i>Leptoconchus ingranulosa</i>
<i>Pleuractis gravis</i>	<i>Leptoconchus inpleuractis</i>
<i>Pleuractis moluccensis</i>	<i>Leptoconchus inpleuractis</i>
<i>Pleuractis paumotensis</i>	<i>Leptoconchus inpleuractis</i>
<i>Pleuractis seychellensis</i>	<i>Leptoconchus</i> sp.
<i>Podabacia crustacea</i>	<i>Leptoconchus ingrandifungi</i>
<i>Podabacia motuporensis</i>	<i>Leptoconchus ingrandifungi</i>
<i>Polyphyllia talpina</i>	<i>Leptoconchus intalpina</i>
<i>Sandalolitha dentata</i>	<i>Leptoconchus ingrandifungi</i>
<i>Zoopilus echinatus</i>	<i>Leptoconchus ingrandifungi</i>

Previous studies on coral-associated fauna concern massive corals of *Porites* and their macro-infaunal boring communities (Hutchings & Peyrot-Clausade, 1988; Sammarco & Risk, 1990; Hutchings *et al.*, 1992) or epifauna living in between the branches of *Pocillopora* (Austin *et al.*, 1980; Gotelli & Abele, 1983; Preston & Doherty, 1994). Octocorals also have been a topic of studies concerning selected taxa of their associated fauna (Reijnen *et al.*, 2010, 2011). Our study was initially inspired by an overview of associated organisms living with the European flat oyster, *Ostrea edulis* Linnaeus, 1758, which hosts many different animal species in its shell (Korringa, 1951; Hoeksema, 1983).

Altogether, 50 Fungiidae host at least 96 other animal species: two *Waminoa* spp., 26 copepods, seven barnacles, three (possibly four) gall crabs, 18 shrimps, eight mussels, 17 wentletraps, 14 *Leptoconchus* spp., and one pipefish. Some of them live inside the corals, others on top or below the corals, and some specifically inside the sediment underneath or in between the coral's tentacles.

Our results show that little information is available about certain taxa of coral-associated organisms, such as regarding the identity and host relations of acoel flatworms (*Waminoa* spp.). Species overviews concerning other taxa have become available just recently, such as coralliophiliid and epitoniid snails, or are just about to become published, such as those concerning cryptochirid crabs and pontonine shrimps. The host specificity in the associated fauna varies remarkably. Endosymbionts (such as *Leptoconchus* snails; Table 8) appear to be much more host-specific than epibionts, such as Epitoniidae (Table 7). Among the latter, species living in the substrate underneath the host are less host-specific than those that live attached to the coral's undersurface

(Gittenberger & Gittenberger, 2005). Snails that live attached to their host, or those living inside their host, may have a more specific diet than those that are able to move around in the proximity of their host, which is probably also the case in ovulid snails that eat the octocorals on which they live (Reijnen *et al.*, 2010). On the other hand, boring mussels appear to be little host-specific with regard to mushroom corals (Table 6) and other coral taxa (Kleemann, 1990, 1995). Some species (*Lithophaga* spp.) live in dead corals (Wilson, 1979; Kleemann, 1990; Owada, 2007), which indicates that they probably use the coral only for shelter. This may explain why some *Leiosolenus* species appear to show little selectivity regarding which specific mushroom coral host they select, unless the host itself has developed immunity against its intruder.

In general, coral-inhabiting barnacles are considered to be host-specific above species level (Brickner *et al.*, 2010), which agrees with the observation that coral barnacles in mushroom corals appear to be little host-specific at species level (Table 3). Coral barnacles live partly buried inside the host's skeleton while another part protrudes from the coral's surface in order to catch plankton, which is not necessarily a host-dependent activity. For the barnacle, the coral host may only function as substrate which is not able to prevent the settlement and penetration of the intruder. Likewise, copepods that live on corals also show little preference with regard to their host corals (Table 2).

The availability of a phylogeny reconstruction (Gittenberger *et al.*, 2011) has enabled comparisons of closely related species of mushroom corals regarding their hospitality towards other organisms. This approach is called phylogenetic ecology (Westoby, 2006) or historical ecology (Brooks & McLennan, 1994). We prefer to use the term phylogenetic ecology (or phylo-ecology) over historical ecology because the latter may also refer to studies concerning changes in biota over time (e.g. Van der Meij *et al.*, 2009, 2010). Thanks to this new phylogenetic approach we can see whether observed differences between closely related species can be attributed to scarcity of the host or to ecomorphological traits, such as coral dimensions (diameter or thickness), polyp shape (tentacle size), coral morphology (free-living versus attached) and substrate (sand versus rock).

Observed differences among some Fungiidae in the number of associated species (Figure 2) may indeed depend on how common and widespread the host species are. *Fungia fungites* (N = 21), *Sandalolitha robusta* (N = 20), *Herpolitha limax* (N = 17), *Ctenactis echinata* (N = 16), *Lithophyllon repanda* (N = 16) and *Pleuractis paumotensis* (N = 15) are moderately large, common and widespread species with relatively high numbers of associated fauna. Examples of little known host species with a poor associated fauna are *Pleuractis taiwanensis* (with one gall crab species), *Lithophyllon ranjithi* (with two gall crab species), and *Podabacia sinai* (no associates). These species have relatively large coralla that offer sufficient living space for other organisms. In contrast, *Podabacia kunzmanni* and species of the fungiid genera *Cycloseris* and *Cantharellus* remain relatively small (Hoeksema, 1991b; Gittenberger *et al.*, 2011), which may prevent the settlement of some associated organisms, especially if the corals are short-lived. Besides, as free-living species, many *Cycloseris* species live on sand, which may not be favourable to some associates by risking burial, especially if host corals are being moved by fish or other bottom

dwellers. If they produce asexually by autotomy, they may become even smaller (Yamashiro *et al.*, 1989; Yamashiro & Nishihira, 1998; Hoeksema & Waheed, 2011). Other species may grow very large (*Halomitra clavator*, *Polyphyllia novaehiberniae* and *Zoopilus echinatus*), but they show very few associates (Figure 2). Their coralla remain very thin and break easily (Hoeksema & Gittenberger, 2010) in comparison to those of their sister species and therefore they may be a less favourable habitat for other organisms. There is no clear difference regarding numbers of associated fauna between common fungiid species that are free-living (*Lithophyllon repanda* (N = 16), *L. concinna* (N = 10), *L. scabra* (N = 11), *L. spinifer* (N = 7) and those that remain attached in adult phase (*L. undulatum*, N = 8).

*Heliofungia actiniformis* is a remarkable coral host. Its rich associated fauna consists predominantly of 14 shrimp species (Figure 1B–F). One of these, *Cuapetes kororensis*, is host-specific, like the pipefish *Siokunichthys nigrolineatus*, which occurs in the same host (Figure 1G). The soft tissue of this species is thick while it also owns long tentacles, like those of sea anemones that extend during day time and may be an ideal habitat for other species (De Grave, 1998; Hoeksema & Fransen, 2011). This thick tissue may prevent the settlement of endosymbionts in *H. actiniformis*. Remarkably, its sister species, *H. fralinae*, has no known associated fauna at all, despite the fact that it may occur in large densities over large reef areas (Hoeksema, 2004). Its tentacles are also extended in daytime but are not as large as those of its congener and therefore this species may not offer a suitable habitat for other animals.

The 14 associated shrimp species of *H. actiniformis* do not only dwell in between its tentacles but also underneath and besides the corals (Hoeksema & Fransen, 2011). Another scleractinian coral species with a remarkable associated fauna is the euphyliid bubble coral *Physogyra lichtensteini* Milne Edwards & Haime, 1851, with the host-specific pontonine shrimps *Vir smiti* Fransen & Holthuis, 2007 and *V. longidactylus* Marin, 2008. These animals dwell in between the vesicles and tentacles of the host coral, which are usually extended in daytime (Fransen & Holthuis, 2007; Marin, 2008). Therefore, *H. actiniformis* is not unique among reef corals with regard to host-specific caridean associates. Considering the scattered information on coral-associated shrimp fauna and the many new shrimp species discovered (Fransen & De Grave, 2009; De Grave & Fransen, 2010, 2011) a review of coral-dwelling shrimps would be necessary to find out whether 14 associated shrimp species is a real record.

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## REFERENCES

- Anderson D.T. (1992) Structure, function and phylogeny of coral-inhabiting barnacles (Cirripedia, Balanoida). *Zoological Journal of the Linnean Society* 106, 277–339.
- Annandale N. (1928) Cirripedes associated with Indian corals of the families Astraeidae and Fungiidae. *Memoirs of the Indian Museum, Calcutta* 8, 61–68, pl. 7.
- Austin A.D., Austin S.A. and Sale P.F. (1980) Community structure of the fauna associated with the coral *Pocillopora damicornis* (L.) on the Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* 31, 163–174.
- Baker A.C. (2003) Flexibility and specificity in coral–algal symbiosis: diversity, ecology and biogeography of *Symbiodinium*. *Annual Review of Ecology, Evolution, and Systematics* 34, 661–689.
- Barneah O., Brickner I., Hooge M., Weis V.M., LaJeunesse T.C. and Benayahu Y. (2007a) Three party symbiosis: acoelomorph worms, corals and unicellular algal symbionts in Eilat (Red Sea). *Marine Biology* 151, 1215–1223.
- Barneah O., Brickner I., Hooge M., Weis V.M. and Benayahu Y. (2007b) First evidence of maternal transmission of algal endosymbionts at an oocyte stage in a triploblastic host, with observations on reproduction in *Waminoa brickneri* (Acoelomorpha). *Invertebrate Biology* 126, 113–119.
- Bellwood D.R. and Hughes T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292, 1532–1534.
- Bellwood D.R., Hughes T.P., Folke C. and Nyström M. (2004) Confronting the coral reef crisis. *Nature* 429, 827–833.
- Benzoni F., Stefani F., Stolarski J., Pichon M., Mitta G. and Galli P. (2007) Debating phylogenetic relationships of the scleractinian *Psammodora*: molecular and morphological evidences. *Contributions to Zoology* 76, 35–54.
- Bouillon J., Massin C. and Van Goethem J. (1983) *Fungiacava eilatensis* Soot-Ryen, 1969 (Bivalvia, Mytilidae) et *Leptoconchus striatus* Rüppell, 1835 (Gastropoda, Coralliophilidae), mollusques perforant des *Fungia* (Anthozoa, Fungiidae) récoltés en Papouasie Nouvelle-Guinée. *Bulletin des Séances Académie Royale des Sciences d'Outre-Mer* 4, 549–570.
- Brickner I., Simon-Blecher N. and Achituv A. (2010) Darwin's *Pyrgoma* (Cirripedia) revisited: revision of the *Savignium* group, molecular analysis and description of new species. *Journal of Crustacean Biology* 30, 266–291.
- Brooks D.R. and McLennan D.A. (1994) Historical ecology as a research programme: scope, limitations and the future. In Eggleton P. and Vane-Wright R.I. (eds) *Phylogenetics and ecology*. London: Academic Press, pp. 103–122.
- Bruce A.J. (1976) A synopsis of the pontonine shrimp fauna of Central East Africa. *Journal of the Marine Biological Association of India* 16 [for 1974], 462–490.
- Bruce A.J. (1977) *Periclimenes kororensis* n. sp., an unusual shrimp associate of the fungiid coral, *Heliofungia actiniformis*. *Micronesica* 13, 33–43.
- Bruce A.J. (1978) A report on a small collection of pontonine shrimps from Queensland, Australia. *Crustaceana* 33, 167–181.

- Bruce A.J.** (1981) Pontoniine shrimps of Heron Island. *Atoll Research Bulletin* 245, 1–33.
- Bruce A.J.** (1983) The pontoniine shrimp fauna of Australia. *Memoirs of the Australian Museum* 18, 195–218.
- Bruce A.J.** (1985) Some caridean associates of scleractinian corals in the Ryukyu Islands. *Galaxea*, 4, 1–21.
- Bruce A.J.** (2005) Pontoniine shrimps from Papua New Guinea, with designation of two new genera, *Cainonia* and *Colemonia* (Crustacea: Decapoda: Palaemonidae). *Memoirs of the Queensland Museum* 51, 333–383.
- Bruce A.J. and Svoboda A.** (1984) A report on a small collection of coelenterate-associated pontoniine shrimps from Cebu, Philippines Islands. *Asian Marine Biology* 1, 87–99.
- Cervino J.M., Hayes R., Goreau T.J. and Smith G.W.** (2004) Zooxanthellae regulation in yellow blotch/band and other coral diseases contrasted with temperature related bleaching: *in situ* destruction vs expulsion. *Symbiosis* 37, 63–85.
- Cervino J.M., Thompson F.L., Gomez-Gil B., Lorence E.A., Goreau T.J., Hayes R.L., Winiarski-Cervino K.B., Smith G.W., Hughen K. and Bartels E.** (2008) The *Vibrio* core group induces yellow band disease in Caribbean and Indo-Pacific reef-building corals. *Journal of Applied Microbiology* 105, 1658–1671.
- Chace F.A. and Bruce A.J.** (1993) The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition 1907–1910, Part 6: Superfamily Palaemonoidea. *Smithsonian Contributions to Zoology* 543, 1–152.
- Coffroth M.A. and Santos S.R.** (2005) Genetic diversity of symbiotic dinoflagellates in the genus *Symbiodinium*. *Protist* 156, 19–34.
- Coles S.L.** (1980) Species diversity of decapods associated with living and dead reef coral *Pocillopora meandrina*. *Marine Ecology Progress Series* 2, 281–291.
- Cooper T.F., Ulstrup K.E., Dandan S.S., Heyward A.J., Kuhl M., Muirhead A.N., O'leary R., Ziersen B. and Van Oppen M.J.H.** (2011) Niche specialization of reef-building corals in the mesophotic zone: metabolic trade-offs between divergent *Symbiodinium* types. *Proceedings of the Royal Society of London B, Biological Sciences* 278, 1840–1850.
- Cruz-Barraza J.A., Carballo J.L., Bautista-Guerrero E. and Nava H.** (2011) New species of excavating sponges (Porifera: Demospongiae) on coral reefs from the Mexican Pacific Ocean. *Journal of the Marine Biological Association of the United Kingdom* 91, 999–1013.
- Dawson C.E.** (1983) Synopsis of the Indo-Pacific pipefish genus *Siokunichthys* (Syngnathidae), with description of *S. nigrolineatus* n. sp. *Pacific Science* 37, 49–63.
- De Grave S.** (1998) Pontoniinae (Decapoda, Caridea) associated with *Heliofungia actiniformis* (Scleractinia) from Hansa Bay, Papua New Guinea. *Belgian Journal of Zoology* 128, 13–22.
- De Grave S. and Fransen C.H.J.M.** (2010) Contributions to shrimp taxonomy—Editorial. *Zootaxa* 2372, 5–6.
- De Grave S. and Fransen C.H.J.M.** (2011) Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). *Zoologische Mededelingen, Leiden* 85, 195–589.
- De Jong I.** (1995) *Mushroom coral-inhabiting barnacles of SW Sulawesi, Indonesia*. MSc thesis. Leiden University, Leiden, The Netherlands.
- Ditlev H.** (2003) New scleractinian corals (Cnidaria: Anthozoa) from Sabah, North Borneo. Description of one new genus and eight new species, with notes on their taxonomy and ecology. *Zoologische Mededelingen, Leiden* 77, 193–219.
- Fize A. and Serène R.** (1956) Note préliminaire sur huit espèces nouvelles, dont une d'un genre nouveau, d'*Hapalocarcinidae*. *Bulletin de la Société Zoologique de France* 80, 375–378.
- Fize A. and Serène R.** (1957) Les Hapalocarcinidés du Viet-Nam. *Mémoires de l'Institut Océanographique de Nha Trang* 10, 1–202.
- Fonseca A.C., Dean H.K. and Cortés J.** (2006) Non-colonial macroborers as indicators of coral reef status in the South Pacific of Costa Rica. *Revista de Biología Tropical* 54, 101–115.
- Foster B.A.** (1980) Shallow water barnacles from Hong Kong. In Morton B.S. and Tseng C.K. (eds) *Proceedings of the First International Marine Biological Workshop: the Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1980*. Hong Kong: Hong Kong University Press, pp. 207–232.
- Fransen C.H.J.M.** (1989) Notes on caridean shrimps collected during the Snellius-II Expedition. I. Associates of Anthozoa. *Netherlands Journal of Sea Research* 23, 131–147.
- Fransen C.H.J.M.** (2004) Pontoniine shrimps. In Hoeksema B.W. (ed.) *Marine biodiversity of the coastal area of the Berau region, East Kalimantan, Indonesia*. Leiden: Naturalis, pp. 19–21.
- Fransen C.H.J.M.** (2008) Pontoniine shrimps. In Hoeksema B.W. and Van der Meij S.E.T (eds) *Cryptic marine biota of the Raja Ampat Islands group*. Leiden: Naturalis, pp. 16–18.
- Fransen C.H.J.M.** (2010) Palaemonoid shrimps. In Hoeksema B.W. and Van der Meij S.E.T (eds) *Crossing marine lines at Ternate: capacity building of junior scientists in Indonesia for marine biodiversity assessments*. Leiden: NCB Naturalis, pp. 26–30.
- Fransen C.H.J.M. and De Grave S.** (2009) Evolution and radiation of shrimp-like decapods: an overview. In Martin J.W., Crandall K.A. and Felder D.L. (eds) *Decapod Crustacean phylogenetics. Crustacean Issues Volume 18*. Boca Raton, FL: CRC Press, pp. 245–259.
- Fransen C.H.J.M. and Holthuis L.B.** (2007) *Vir smiti* spec. nov., a new scleractinian associated pontoniine shrimp (Crustacea: Decapoda: Palaemonidae) from the Indo-West Pacific. *Zoologische Mededelingen, Leiden* 81, 101–114.
- Galkin S.V.** (1986) On the system of the genus *Cantellius* (Cirripedia, Pyrgomatidae). *Zoologicheskij Zhurnal* 65, 1267–1272. [In Russian.]
- Gittenberger A.** (2003) The wentletrap *Epitonium hartogi* spec. nov. (Gastropoda: Epitoniidae), associated with bubble coral species, *Plerogyra* spec. (Scleractinia: Euphyllidae), off Indonesia and Thailand. *Zoologische Verhandelingen, Leiden* 345, 139–150.
- Gittenberger A. and Gittenberger E.** (2005) A hitherto unnoticed adaptive radiation: epitoniid species (Gastropoda: Epitoniidae) associated with corals (Scleractinia). *Contributions to Zoology* 74, 125–204.
- Gittenberger A. and Gittenberger E.** (2011) Cryptic, adaptive radiation of parasitic snails: sibling species of *Leptoconchus* (Gastropoda: Coralliophilidae) in corals. *Organisms, Diversity and Evolution* 11, 21–41.
- Gittenberger A., Goud J. and Gittenberger E.** (2000) *Epitonium* (Gastropoda: Epitoniidae) associated with mushroom corals (Scleractinia: Fungiidae) from Sulawesi, Indonesia, with the description of four new species. *Nautilus* 114, 1–13.
- Gittenberger A., Reijnen B.T. and Hoeksema B.W.** (2011) A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. *Contributions to Zoology* 80, 107–132.
- Gotelli N.J. and Abele L.G.** (1983) Community patterns of coral-associated decapods. *Marine Ecology Progress Series* 13, 131–139.
- Guo C.C., Hwang J.S. and Fautin DG** (1996) Host selection by shrimps symbiotic with sea anemones: a field survey and experimental

- laboratory analysis. *Journal of Experimental Marine Biology and Ecology* 202, 165–176.
- Haapkylä J., Seymour A.S., Barneah O., Brickner I., Hennige S., Suggett D. and Smith D.** (2009) Association of *Waminoa* sp. (Acoela) with corals in the Wakatobi Marine Park, South-East Sulawesi, Indonesia. *Marine Biology* 156, 1021–1027.
- Hiro F.** (1935) A study of cirripeds associated with corals occurring in Tanabe Bay. *Records of Oceanographic Works in Japan* 7, 1–28.
- Hiro F.** (1938) Studies on the animals inhabiting reef corals II. Cirripeds of the genera *Creusia* and *Pyrgoma*. *Palao Tropical Biological Station Studies* 1, 391–416, pl. 1.
- Hoeksema B.W.** (1983) Excavation patterns and spiculae dimensions of the boring sponge *Cliona celata* from the SW Netherlands. *Senckenbergiana Maritima* 15, 55–85.
- Hoeksema B.W.** (1989) Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zoologische Verhandelingen, Leiden* 254, 1–295.
- Hoeksema B.W.** (1991a) Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. *Marine Ecology Progress Series* 74, 225–237.
- Hoeksema B.W.** (1991b) Evolution of body size in mushroom corals (Scleractinia: Fungiidae) and its ecomorphological consequences. *Netherlands Journal of Zoology* 41, 122–139.
- Hoeksema B.W.** (1993a) Mushroom corals (Scleractinia: Fungiidae) of Madang Lagoon, northern Papua New Guinea: an annotated checklist with the description of *Cantharellus jebbi* spec. nov. *Zoologische Mededelingen, Leiden* 67, 1–19.
- Hoeksema B.W.** (1993b) Historical biogeography of *Fungia* (*Pleuractis*) spp. (Scleractinia: Fungiidae), including a new species from the Seychelles. *Zoologische Mededelingen, Leiden* 67, 639–654.
- Hoeksema B.W.** (2004) Impact of budding on free-living corals at East Kalimantan, Indonesia. *Coral Reefs* 23, 492.
- Hoeksema B.W.** (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. In Renema W. (ed.) *Biogeography, time and place: distributions, barriers and islands*. Dordrecht: Springer, pp. 117–178.
- Hoeksema B.W.** (2009) Attached mushroom corals (Scleractinia: Fungiidae) in sediment-stressed reef conditions at Singapore, including a new species and a new record. *Raffles Bulletin of Zoology Supplement* 22, 81–90.
- Hoeksema B.W. and Achituv Y.** (1993) First Indonesian record of *Fungiacava eilatensis* Goreau et al., 1968 (Bivalvia: Mytilidae), endosymbiont of *Fungia* spp. (Scleractinia: Fungiidae). *Basteria* 57, 131–138.
- Hoeksema B.W. and Best M.B.** (1991) New observations on scleractinian corals from Indonesia: 2. Sipunculan-associated species belonging to the genera *Heterocyathus* and *Heteropsammia*. *Zoologische Mededelingen, Leiden* 65, 221–245.
- Hoeksema B.W. and Dai C.F.** (1991) Scleractinia of Taiwan. II Family Fungiidae (with the description of a new species). *Bulletin of the Institute of Zoology, Academia Sinica* 30, 201–226.
- Hoeksema B.W. and Franses C.H.J.M.** (2011) Space partitioning by symbiotic shrimp species cohabitating in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. *Coral Reefs* 30, 519.
- Hoeksema B.W. and Gittenberger A.** (2008) Records of some marine parasitic molluscs from Nha Trang, Vietnam. *Basteria* 72, 129–133.
- Hoeksema B.W. and Gittenberger A.** (2010) High densities of mushroom coral fragments at West Halmahera, Indonesia. *Coral Reefs* 29, 691.
- Hoeksema B.W. and Kleemann K.** (2002) New records of *Fungiacava eilatensis* Goreau et al., 1968 (Bivalvia: Mytilidae) boring in Indonesian mushroom corals (Scleractinia: Fungiidae). *Basteria* 66, 25–30.
- Hoeksema B.W. and Koh E.G.L.** (2009) Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s–2006) in changing reef conditions. *Raffles Bulletin of Zoology Supplement* 22, 91–101.
- Hoeksema B.W. and Matthews J.L.** (2011) Contrasting bleaching patterns in mushroom coral assemblages at Koh Tao, Gulf of Thailand. *Coral Reefs* 30, 95.
- Hoeksema B.W. and Waheed Z.** (2011) Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. *Coral Reefs*. DOI 10.1007/S00338-011-0807-6.
- Hoeksema B.W., Van der Land J., Van der Meij S.E.T., Van Ofwegen L.P., Reijnen B.T., Van Soest R.W.M. and De Voogd N.J.** (2011) Unforeseen importance of historical collections as baselines to determine biotic change of coral reefs: the Saba Bank case. *Marine Ecology* 32, 135–141.
- Hughes T.P., Bellwood D.R. and Connolly S.R.** (2002) Biodiversity hotspots, centres of endemism, and the conservation of coral reefs. *Ecology Letters* 5, 775–784.
- Humes A.G.** (1973) Cyclopoid copepods (Lichomolgidae) from fungiid corals in New Caledonia. *Zoologischer Anzeiger* 190, 312–333.
- Humes A.G.** (1978) Lichomolgid copepods (Cyclopoida) associated with fungiid corals (Scleractinia) in the Moluccas. *Smithsonian Contributions to Zoology* 253, 1–48.
- Humes A.G.** (1979) Coral-inhabiting copepods from the Moluccas, with a synopsis of cyclopoids associated with scleractinian corals. *Cahiers de Biologie Marine* 20, 77–107.
- Humes A.G.** (1996) *Anchimolgus gratus* n. sp. (Copepoda: Poecilostomatoida: Anchimolgidae), associated with the scleractinian coral *Lithactinia novaehiberniae* in New Caledonia. *Contributions to Zoology* 66, 193–200.
- Humes A.G.** (1997) Copepoda (Siphonostomatoida) associated with the fungiid coral *Parahalomitra* in the southwestern Pacific. *Journal of Natural History* 31, 57–68.
- Humes A.G. and Dojiri M.** (1983) Copepoda (Xarifiidae) parasitic in scleractinian corals from the Indo-Pacific. *Journal of Natural History* 17, 257–307.
- Hutchings P. and Peyrot-Clausade M.** (1988) Macro-infaunal boring communities of *Porites*: a biogeographical comparison. *Proceedings of the 6th International Coral Reef Symposium, Australia* 3, 263–267.
- Hutchings P.A., Kiene W.E., Cunningham R.B. and Donnelly C.** (1992) Spatial and temporal patterns of non-colonial boring organisms (polychaetes, sipunculans and bivalve molluscs) in *Porites* at Lizard Island, Great Barrier Reef. *Coral Reefs* 11, 23–31.
- Kim I.-H.** (2003) Copepods (Crustacea) associated with marine invertebrates from New Caledonia. *Korean Journal of Systematic Zoology Special Issue* 4, 1–167.
- Kim I.-H.** (2007) Copepods (Crustacea) associated with marine invertebrates from the Moluccas. *Korean Journal of Systematic Zoology Special Issue* 6, 1–126.
- Kim I.-H.** (2010) Siphonostomatoid Copepoda (Crustacea) associated with invertebrates from tropical waters. *Korean Journal of Systematic Zoology Special Issue* 8, 1–176.
- Kleemann K.** (1980) Boring bivalves and their host corals from the Great Barrier Reef. *Journal of Molluscan Studies* 46, 13–54.

- Kleemann K.** (1990) Evolution of chemically-boring Mytilidae (Bivalvia). In Morton B (ed.) *The Bivalvia. Proceedings of a Memorial Symposium in honour of Sir Charles Maurice Yonge (1899–1986)*, Edinburgh 1986. Hong Kong: Hong Kong University Press, pp. 111–124.
- Kleemann K.** (1994) Associations of coral and boring bivalves since the Late Cretaceous. *Facies* 31, 131–140.
- Kleemann K.** (1995) Associations of coral and boring bivalves: Lizard Island (Great Barrier Reef, Australia) versus Safaga (N Red Sea). *Beiträge zur Paläontologie* 20, 31–39.
- Kleemann K. and Hoeksema B.W.** (2002) *Lithophaga* (Bivalvia: Mytilidae), including a new species, boring in mushroom corals (Scleractinia: Fungiidae) at South Sulawesi, Indonesia. *Basteria* 66, 11–24.
- Knowlton N. and Rohwer F.** (2003) Multispecies microbial mutualisms on coral reefs: the host as a habitat. *American Naturalist* 162 Supplement, S51–S62.
- Kokshoorn B., Goud J., Gittenberger E. and Gittenberger A.** (2007) Epitoniid parasites (Gastropoda, Prosobranchia, Epitoniidae) and their host sea anemones (Cnidaria, Actinaria & Ceriantharia) in the Spermonde archipelago, Sulawesi, Indonesia. *Basteria* 71, 33–56.
- Kolosváry G.** (1948) New data of cirripeds associated with corals. *Annals and Magazine of Natural History Series* 11, 14, 358–368.
- Korringa P.** (1951) The shell of *Ostrea edulis* as a habitat. *Archives Néerlandaises de Zoologie* 10, 32–152.
- Kropp R.K.** (1990) Revision of the genera of gall crabs (Crustacea: Cryptochiridae) occurring in the Pacific Ocean. *Pacific Science* 44, 417–448.
- Kühl M., Holst G., Larkum A.W.D., and Ralph P.J.** (2008) Imaging of oxygen dynamics within the endolithic algal community of the massive coral *Porites lobata* (Dana). *Journal of Phycology* 44, 541–550.
- Kuiter R.H.** (2000) *Seahorses, pipefishes and their relatives*. Chorleywood, UK: TMC Publishing.
- Kuiter R.H.** (2009) *Seahorses and their relatives*. Seaford, Australia: Aquatic Photographics.
- LaJeunesse T.C., Bhagooli R., Hidaka M., DeVantier L., Done T., Schmidt G.W., Fitt W.K. and Hoegh-Guldberg O.** (2004a) Closely related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. *Marine Ecology Progress Series* 84, 147–161.
- LaJeunesse T.C., Thornhill D.J., Cox E.F., Stanton F.G., Fitt W.K. and Schmidt G.W.** (2004b) High diversity and host specificity observed among symbiotic dinoflagellates in reef coral communities from Hawaii. *Coral Reefs* 23, 596–603.
- LaJeunesse T.C., Lee S., Bush S. and Bruno J.F.** (2005) Persistence of non-Caribbean algal symbionts in Indo-Pacific mushroom corals released to Jamaica 35 years ago. *Coral Reefs* 24, 157–159.
- Lewis J.B. and Snelgrove P.V.R.** (1990) Corallum morphology and composition of crustacean cryptozoa of the hermatypic coral *Madracis mirabilis*. *Marine Biology* 106, 267–272.
- López K., Bone D., Rodríguez C. and Padilla F.** (2008) Biodiversity of cryptozoa associated with reefs of the Los Roques Archipelago National Park, Venezuela. *Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida* 2, 1359–1366.
- Lourie S.A. and Kuiter R.H.** (2008) Three new pygmy seahorse species from Indonesia (Teleostei: Syngnathidae: *Hippocampus*). *Zootaxa* 1963, 54–68.
- Marin I.N.** (2008) Description of two new species from the genera *Palaemonella* Dana, 1852 and *Vir* Holthuis, 1952 (Crustacea: Caridea: Palaemonidae: Pontoniinae). *Zoologische Mededelingen, Leiden* 82, 375–390.
- Martin D. and Britayev T.A.** (1998) Symbiotic polychaetes: review of known species. *Oceanography and Marine Biology: an Annual Review* 36, 217–340.
- Matsushima K., Fujiwara E. and Hatta M.** (2010) An unidentified species of acoel flatworm in the genus *Waminoa* associated with the coral *Acropora* from the field in Japan. *Galaxea, Journal of Coral Reef Studies* 12, 51.
- Massin C.** (1988) Boring Coralliophilidae (Mollusca, Gastropoda): coral host relationship. *Proceedings of the 6th International Coral Reef Symposium, Australia* 3, 177–184.
- Massin C. and Dupont S.** (2003) Study on *Leptoconchus* species (Gastropoda, Coralliophilidae) infesting Fungiidae (Anthozoa: Scleractinia). 1. Presence of nine Operational Taxonomic Units (OTUs) based on anatomical and ecological characters. *Belgian Journal of Zoology* 133, 121–126.
- Mokady O., Rozenblatt S., Graur D. and Loya Y.** (1994) Coral–host specificity of Red Sea *Lithophaga* bivalves: interspecific and intraspecific variation in 12S mitochondrial ribosomal RNA. *Molecular Marine Biology and Biotechnology* 3, 158–164.
- Moreno-Forero S., Navas G. and Solano O.** (1998) Cryptobiota associated to dead *Acropora palmata* (Scleractinia: Acroporidae) coral, Isla Grande, Colombian Caribbean. *Revista de Biología Tropical* 46, 229–236.
- Morton B.** (1990) Corals and their bivalve borers—the evolution of a symbiosis. In Morton B (ed.) *The Bivalvia, Proceedings of a Memorial Symposium in honour of Sir Charles Maurice Yonge (1899–1986)*, Edinburgh 1986. Hong Kong: Hong Kong University Press, pp. 11–46.
- Munday P.L.** (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology* 10, 1642–1647.
- Munday P.L., Jones G.P. and Caley M.J.** (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Marine Ecology Progress Series* 152, 227–239.
- Munday P.L., Van Herwerden L. and Dudgeon C.L.** (2004) Evidence for sympatric speciation by host shift in the sea. *Current Biology* 14, 1498–1504.
- Nogueira J.M.M.** (2003) Fauna living in colonies of *Mussismilia hispida* (Verrill) (Cnidaria: Scleractinia) in four south-eastern Brazil islands. *Brazilian Archives of Biology and Technology* 46, 421–432.
- Ogawa K. and Matsuzaki K.** (1992) An essay on host specificity, systematic taxonomy and evolution of the coral-barnacles. *Bulletin of the Biogeographical Society of Japan* 47, 87–101.
- Ogunlana M.V., Hooge M.D., Tekle Y.I., Benayahu Y., Barneah O. and Tyler S.** (2005) *Waminoa brickneri* n. sp. (Acoela: Acoelomorpha) associated with corals in the Red Sea. *Zootaxa* 100, 1–11.
- Oigman-Pszczol S.S. and Creed J.C.** (2006) Distribution and abundance of fauna on living tissues of two Brazilian hermatypic corals (*Mussismilia hispida* (Verrill, 1902) and *Siderastrea stellata* Verrill, 1868). *Hydrobiologia* 563, 143–154.
- Okuno J. and Bruce A.J.** (2010) Designation of *Ancylomenes* gen. nov., for the '*Periclimenes aesopius* species group' (Crustacea: Decapoda: Palaemonidae), with the description of a new species and a checklist of congeneric species. *Zootaxa* 2372, 85–105.
- Okuno J. and Nomura K.** (2002) A new species of '*Periclimenes aesopius* species group' (Decapoda: Palaemonidae: Pontoniinae) associated with sea anemone from Pacific coast of Honshu, Japan. *Natural History Research* 7, 83–94.
- Owada M.** (2007) Functional morphology and phylogeny of the rock-boring bivalves *Leiosolenus* and *Lithophaga* (Bivalvia: Mytilidae): a third functional clade. *Marine Biology* 150, 853–860.

- Owada M. and Hoeksema B.W. (2011) Molecular phylogeny and shell microstructure of *Fungiacava eilatensis* Goreau et al., 1968, boring into mushroom corals (Scleractinia: Fungiidae), in relation to other mussels (Bivalvia: Mytilidae). *Contributions to Zoology* 80, 169–178.
- Paulay G. (1997) Diversity and distribution of reef organisms. In Birkeland C. (ed.) *Life and death of coral reefs*. New York: Chapman and Hall, pp. 298–353.
- Phillips D.H.J. and Pullin R.S.V. (1987) *Siokunichthys nigrolineatus* (Syngnathidae) found on *Fungia* sp. *Copeia* 1987, 509–511.
- Plaisance L., Knowlton N., Paulay G. and Meyer C. (2009) Reef-associated crustacean fauna: biodiversity estimates using semi-quantitative sampling and DNA barcoding. *Coral Reefs* 28, 977–986.
- Pochon X. and Gates R.D. (2010) A new *Symbiodinium* clade (Dinophyceae) from soritid foraminifera in Hawai'i. *Molecular Phylogenetics and Evolution* 56, 492–497.
- Poltarukha O.P. and Dautova T.N. (2007) Barnacles (Cirripedia, Thoracica) of Nhatrang Bay. In Britayev T.A. and Pavlov D.S. (eds) *Benthic fauna of the Bay of Nhatrang, Southern Vietnam*. Moscow: KMK Scientific Press, pp. 89–123.
- Preston N.P. and Doherty P.J. (1994) Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. II. Cryptofauna. *Marine Ecology Progress Series* 104, 27–38.
- Rawlinson K.A., Gillis J.A., Billings R.E. and Borneman E.H. (2011) Taxonomy and life history of the *Acropora*-eating flatworm *Amakusaplana acroporae* nov. sp. (Polycladida: Prosthiostomidae). *Coral Reefs* 30, 693–705.
- Reaka-Kudla M.L. (1997) The global biodiversity of coral reefs: a comparison with rain forests. In Reaka-Kudla M.L., Wilson D.E. and Wilson E.O. (eds) *Biodiversity II. Understanding and protecting our biological resources*. Washington, DC: Joseph Henry Press, pp. 83–108.
- Reijnen B.T., Hoeksema B.W. and Gittenberger E. (2010) Host specificity and phylogenetic relationships among Atlantic Ovulidae (Mollusca: Gastropoda). *Contributions to Zoology* 79, 69–78.
- Reijnen B.T., Van der Meij, S.E.T. and Van Ofwegen L.P. (2011) Fish, fans and hydroids: review of the host species of pygmy seahorses. *ZooKeys* 103, 1–26.
- Rice M.E. (1974) Sipunculans associated with coral communities. *Micronesica* 12, 119–132.
- Roberts C.M., McClean C.J., Veron J.E.N., Hawkins J.P., Allen G.R., McAllister D.E., Mittermeier C.G., Schueler F.W., Spalding M., Wells F., Vynne C. and Werner T.B. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295, 1280–1284.
- Ross A. and Newman W.A. (1973) Revision of the coral inhabiting barnacles (Cirripedia: Balanidae). *Transactions of the San Diego Society of Natural History* 17, 137–174.
- Ross A. and Newman W.A. (2002) Coral barnacles: Cenozoic decline and extinction in the Atlantic/East Pacific versus diversification in the Indo-West Pacific. *Proceedings of the 9th International Coral Reef Symposium, Bali, Indonesia* 1, 179–184.
- Samini Namin K., Risk M.J., Hoeksema B.W., Zohari Z. and Rezai H. (2010) Coral mortality and serpulid infestations associated with red tide, in the Persian Gulf. *Coral Reefs* 29, 509.
- Sammarco P.W. and Risk M.J. (1990) Large-scale patterns in internal bioerosion of *Porites*: cross continental shelf trends on the Great Barrier Reef. *Marine Ecology Progress Series* 59, 145–156.
- Schönberg C.H.L. (2000) Bioeroding sponges common to the Central Australian Great Barrier Reef: description of three new species, two new records, and additions to two previously described species. *Senckenbergiana Maritima* 30, 161–221.
- Schönberg C.H.L. (2001) Small-scale distribution of Great Barrier Reef bioeroding sponges in shallow water. *Ophelia* 55, 39–54.
- Soong K.Y. and Chang K.H. (1983) The coral-inhabiting barnacles (Crustacea: Thoracica: Pyrgomatidae) from southern most coast of Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica* 22, 243–253.
- Starmer J.A. (2003) An annotated checklist of ophiuroids (Echinodermata) from Guam. *Micronesica* 35–36, 547–562.
- Stat M. and Gates R.D. (2011) Clade D *Symbiodinium* in scleractinian corals: a 'nugget' of hope, a selfish opportunist, an ominous sign, or all of the above? *Journal of Marine Biology* 2011, Article ID 730715, 1–9.
- Stella J.S., Jones G.P. and Pratchett M.S. (2010) Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* 29, 957–973.
- Takeda M. and Tamura Y. (1979) Coral-inhabiting crabs of the family Hapalocarcinidae from Japan. I. Three species obtained from mushroom coral, *Fungia*. *Bulletin of the National Science Museum Tokyo, Series A (Zoology)* 5, 183–194.
- Takeda M. and Tamura Y. (1981) Coral-inhabiting crabs of the family Hapalocarcinidae from Japan. VII. Genus *Faviacola*. *Researches on Crustaceans* 11, 41–50.
- Ten Hove H.A. and Kupriyanova E.K. (2009) Taxonomy of Serpulidae (Annelida, Polychaeta): the state of affairs. *Zootaxa* 2036, 1–126.
- Van der Meij S.E.T., Moolenbeek R.G. and Hoeksema B.W. (2009) Decline of the Jakarta Bay molluscan fauna linked to human impact. *Marine Pollution Bulletin* 59, 101–107.
- Van der Meij S.E.T., Suharsono and Hoeksema B.W. (2010) Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920–2005). *Marine Pollution Bulletin* 60, 1442–1454.
- Veron J.E.N. (1990) New Scleractinia from Japan and other Indo-Pacific countries. *Galaxea* 9, 95–173.
- Veron J.E.N. (2002) New species described in corals of the world. *Australian Institute of Marine Science Monograph Series* 11, 1–206.
- Weis V.M., Reynolds W.S., DeBoer M.D. and Krupp D.A. (2001) Host-symbiont specificity during onset of symbiosis between the dinoflagellates *Symbiodinium* spp. and planula larvae of the scleractinian coral *Fungia scutaria*. *Coral Reefs* 20, 301–308.
- Westoby M. (2006) Phylogenetic ecology at world scale, a new fusion between ecology and evolution. *Ecology* 87, S163–S165.
- Wijgerde T., Spijkers P., Verreth J. and Osinga R. (2011) Epizoic acelomorph flatworms compete with their coral host for zooplankton. *Coral Reefs* 30, 665.
- Wilson B.R. (1979) A revision of Queensland lithophagine mussels (Bivalvia, Mytilidae, Lithophaginae). *Records of the Australian Museum* 32, 435–489.
- Wilson B.R. (1985) Sibling species of *Leiosolenus* (Bivalvia, Mytilidae, Lithophaginae) boring in living corals in the Indo-West Pacific region. *Proceedings of the 5th International Coral Reef Congress, Tahiti* 5, 183–190.
- Yamashiro H. (1990) A wentletrap *Epitonium bullatum* associated with a coral *Sandalolitha robusta*. *Venus* 49, 299–305.
- Yamashiro H. (1999) Masking behaviour in a commensal shrimp, *Metapontonia fungiacola* Bruce, 1967 that uses the soft tissues of the

host coral (Decapoda, Palaemonidae, Pontoniinae). *Crustaceana* 72, 307–312.

**Yamashiro H. and Nishihira M.** (1998) Experimental study of growth and asexual reproduction in *Diaseris distorta* (Michelin, 1843), a free-living fungiid coral. *Journal of Experimental Marine Biology and Ecology* 225, 253–267.

**Yamashiro H.M., Hidaka M., Nishihira M. and Pong-in S.** (1989) Morphological studies on skeletons of *Diaseris fragilis*, a free-living coral which reproduces asexually by natural autotomy. *Galaxea* 8, 283–294.

and

**Zabala M., Maluquer P. and Harmelin J.G.** (1993) Epibiotic bryozoans on deep-water scleractinian corals from the Catalonia slope (western Mediterranean, Spain, France). *Scientia Marina* 57, 65–78.

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